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# Cross-sectional scat sampling reveals intrapopulation feeding diversity in a marine predator

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**Cross-sectional scat sampling reveals intrapopulation feeding diversity in a marine predator**

By

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Accepted in Partial Completion
of the Requirements for the Degree
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**Master's Thesis**

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Madelyn Voelker

8/6/2018

# Cross-sectional scat sampling reveals intrapopulation feeding diversity in a marine predator

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Madelyn Voelker
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## Abstract

Harbor seals (*Phoca vitulina*) have substantial impacts on species of concern. To understand and predict the impact that harbor seals have in their communities, we need to describe their level of individual specialization because it can affect food web dynamics, responses to changes in prey availability, and the accuracy of predictive models. I estimated intrapopulation feeding diversity, a proxy for individual specialization, of *P. vitulina* in the Salish Sea relative to sex, time, and location using repeated cross-sectional sampling of scat. Based on 1,083 scat samples collected from five haul-out sites over the course of four, non-sequential years, diet was quantified using traditional and metabarcoding techniques, and sex was determined using a molecular assay. Though variable spatially and temporally, high levels of specialization at a short-time scale (24 - 48 hours) ($PS_i$ = 0.392, 95% CI = 0.013, R = 100,000), combined with previous knowledge of *P. vitulina* feeding strategies, suggested that specialization was pervasive in Salish Sea populations. Males showed less specialization than females, particularly in the summer and fall, and demersal and benthic prey species were correlated with higher levels of diversity. These results suggest that although females consumed a wider range of prey species than males, they had a higher degree of specialization, likely driven by consumption of benthic species. Further, this finding also suggests benthic species likely require more specialized foraging strategies and that there are trade-offs between a pelagic and benthic foraging style for *P. vitulina*. Differential specialization on prey species as well as between sexes of *P. vitulina* indicate that predator-prey interactions are not well understood. Therefore, the likelihood of specialist versus generalist interactions with a prey species should be considered when management decides how to address *P. vitulina* influence on prey of conservation concern.

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## Introduction

Predator-prey relations are an integral force in many ecosystems and are often key to understanding how those ecosystems function. One phenomenon that can complicate understanding predator-prey interactions is individual specialization (Bolnick et al. 2003). The concept of individual specialization was first described in terms of niche width variation. Individuals using a smaller subset of resources than the population as a whole are defined as individual specialists (Van Valen 1965). Previous work has shown that ignoring individual specialization can be an oversimplification of the ecological interactions in the community (Bolnick 2003, 2011, Araújo 2011, Dall et al. 2012). The level of specialization can affect food web dynamics, responses to changes in prey availability, and the accuracy of predictive models (Bolnick et al. 2003). For example, high levels of individual specialization can produce a delayed response to changes in prey availability (Bolnick et al. 2003). This delay was demonstrated in a population of blue gill sunfish *Lepomis macrochirus* where prior experience foraging on a single prey type increased the likelihood of an individual using that resource, even when another resource became more profitable (Werner et al.1981). A different example of how predator-prey relations can affect specialization at the individual level is through variations in prey biomass. For instance, in the isopod *Saduria entomon* the level of individual diet specialization was mainly determined by the density of preferred prey *Monoporeia affinis*, not the density of the prey population itself (Svanbäck et al. 2011). This finding implies that shifts in prey size or type can alter the level of specialization observed in predators and subsequent likelihood of predation for the prey. The effects of specialization can be seen at the population level as well. As a population, southern resident *Orcinus orca* are highly specialized on *O. tshawytscha* (Ford et al. 2010, Hanson et al. 2010,). Unfortunately, *O. tshawytscha* populations have been declining since

1997 and remain well below historic levels (Ford 2011). Low abundance of *O. tshawytscha* is likely causing problems for southern resident *O. orca* as no new alternate main food source has been documented (Ford et al. 2010), even though you might expect organisms to switch to a more available food source if the current one is dwindling. While this example is based at the population level it demonstrates how specialization can cause different effects than expected. In summary, including individual specialization metrics in ecosystem studies provides a more clear and accurate description of the system (Bolnick et al. 2003, Araújo et al. 2011).

The expected level of individual specialization within a population can be affected by many mechanisms such as inter- and intra-specific competition and predicted by characteristics of the organism in question, such as trophic level and sex. Competition theory suggests that total niche width is wider when interspecific competition is low because less competition allows for more overlap of individual niche width and less need for specialization (Van Valen 1965). However, recent studies have documented species-rich communities, which can be treated as a proxy for high levels of interspecific competition, to be linked with low levels of individual specialization (Costa et al. 2008, Araújo et al. 2011). Yet, many other studies have suggested that the effects of interspecific competition are multidirectional and dependent on multiple factors, such as trophic position or predator morphology (Bolnick et al. 2010, Kernaléguen et al. 2015, Snowberg et al. 2015, Svanbäck et al. 2015). Increased levels of intraspecific competition consistently produce higher levels of individual specialization in both correlative (Svanbäck et al. 2008, Svanbäck and Persson 2004, 2009, Frederick et al. 2010) and experimental studies (Svanbäck and Bolnick 2007, Huss et al. 2008). Theoretically, if more individuals are competing for the same resource, then some individuals will have to either diversify to new resources or specialize on fewer resources so that they are more successful at exploiting those resources than

their conspecifics (Araújo et al. 2011). Thus, a high level of intraspecific competition is a consistent predictor for individual specialization. A second seemingly consistent predictor of individual specialization is trophic level. A review by Araújo et al. (2011) found individual specialization to be disproportionality represented in upper trophic levels. Further, a field study of threespine sticklebacks *Gasterosteus aculeatus* documented a positive correlation between trophic position and individual specialization (Matthews et al. 2010). Unsurprisingly, marine mammals, which are largely top predators, have repeatedly been documented as individual specialists (Tinker et al. 2008, Kernaléguen et al. 2015, Rossman et al. 2015, Rita et al. 2017). Lastly, in some species, such as sea otters *Enhydrus lutris* and various seabird species, the sex of an individual is also a predictor of that individual's level of specialization (Fujii et al. 2017, Phillips et al. 2017). Knowing the common predictors of specialization is a good starting point. However, to predict the effect of specialization in a predator species on a prey species, we require specific information about the level of, and factors influencing, specialization for that species. One important species for which we do not have specialization information is the harbor seal *Phoca vitulina*.

*P. vitulina* have the largest distribution of any pinniped in coastal areas (Teilmann & Galatius 2018) and are an abundant marine predator in the Salish Sea (Jeffries et al. 2003, Olesiuk 2009). During the twentieth century, *P. vitulina* were hunted by humans to very low population levels; however, after they were given protection under the Marine Mammal Protection Act in 1972 their numbers rebounded. *P. vitulina* appeared to reach carrying capacity in the region in the late 1990s or early 2000s (Jeffries et al. 2003, Olesiuk 2009). Because *P. vitulina* are abundant in the ecosystem and feed on a huge range of species, they have significant impacts on prey populations in the Salish Sea (Olesiuk 1990, Lance et al. 2012, Howard et al.

2013). Some of their prey species are of conservation concern, such as Pacific salmon *Oncorhynchus* spp., rockfish *Sebastes* spp., and Pacific herring *Clupea pallasii pallasii* (Lance et al. 2012, Bromaghin et al. 2013, Bjorland et al. 2015). There is special interest surrounding their impact on *O. tshawytscha* as their consumption of this species is thought to have increased over the last few decades (Adams et al. 2016, Chasco et al. 2017). *O. tshawytscha* are of special concern given their cultural and economic importance in the Pacific Northwest and their role as prey for species of concern, such as *O. orca* (Ford et al. 2010, Hanson et al. 2010,). Further, *O. tshawytscha* runs have been in steady decline for a number of years (Ford 2011). As a result, many government, academic, and conservation organizations have prioritized establishing the reasons for the declines. *P. vitulina*'s effect on *Oncorhynchus* spp. is of special interest because they eat both juvenile and adult individuals (Thomas et al. 2017). Eating juveniles can have an increased impact on *Oncorhynchus* spp populations as typically more juveniles are consumed than adults (Thomas et al. 2017).

Due to the large range of prey that *P. vitulina* populations eat, the species has historically been considered a generalist predator (Teilmann & Galatius 2018). However, *P. vitulina* have various life-history traits that suggest the species may actually be comprised of individual specialists (Bjorland et al. 2015, Schwarz et al. accepted). They are thought to be central place foragers (favor one central primary feeding ground) due to high haul-out site fidelity (Suryan and Harvey 1988, Peterson et al. 2012). Haul-out sites consist of rocks or beaches exposed at low tide and log booms or other floating structures on which *P. vitulina* rest between foraging bouts (Teilmann & Galatius 2018). Central place foraging, in combination with their high abundance in the region, make high intraspecific competition likely, which in turn increases the likelihood of individual specialization. Further, their place as a top predator is also indicative of a high

likelihood for specialization. Because *P. vitulina* impact prey populations of conservation concern (such as *O. tshawytscha*)., and their life history traits are in line with what we expect to see in specialists, it is important to test for the prevalence of specialization to get a clear understanding of their impact on prey species.

It is important to have a clear understanding of how harbor seals impact prey populations from a management standpoint. As discussed, *P. vitulina* are abundant and eat many species of concern, thus, management strategies need to take into account where and how many prey *P. vitulina* consume. However, if individual specialization levels are high this can be difficult as specialization can alter predator-prey relations from expected patterns (Bolnick et al. 2003). A theoretical example in this system could involve an individual *P. vitulina* that specializes on *Sebastes* spp. and one that specializes on *Sebastes* spp. predators. From the perspective of the prey species, these two *P. vitulina* individuals have very different effects. Thus, managing *Sebastes* spp. with the assumption that all *P. vitulina* are the same is incorrect. Management could potentially take this into account by identifying and removing seals that are doing damage to the fish species we are interested in, while leaving the majority of the population intact. Unfortunately, identifying and following individuals has many logistical challenges and is not yet a viable option. However, there are currently efforts to track individuals through their scat which may prove useful. Further, if there are spatial and temporal differences in the level of specialization, then there is the potential for differential effects throughout the region and throughout time. Essentially, if specialization is present and/or variable, you should not manage all areas or seasons the same. For example, management could adjust recreational and commercial fishing areas (spatially and temporally) to not overlap with areas where we know there are high levels of specialization on prey species of concern. There is already a Marine

Protected Area system in place (Van Cleve et al. 2009), as well as extensive fishing regulations, so both systems could be expanded using the information about specialization. However, before these management actions can potentially take place to mitigate specialization, we should determine if they are necessary. A first step to knowing if changes to management are needed, and the best way to implement them, is to determine the level of specialization and factors influencing it.

Prey consumption and specialization are linked, thus, factors affecting prey consumption in *P. vitulina* are likely influencing specialization levels as well. Therefore, factors affecting prey consumption should be considered when examining specialization. Prey consumption and foraging dive behavior of *P. vitulina* in the Salish Sea vary throughout the year (Olesiuk et al. 1990, Lance et al. 2012, Wilson et al. 2014). Additionally, *P. vitulina* eat different types of prey depending on the type of environment in which they forage. Scat samples from haul-outs located in estuaries have higher prey diversity than those coming from outside estuaries (Lance et al. 2012, Luxa & Acevedo-Gutiérrez 2013). Further, males and females consume different prey (Bjorland et al. 2015, Schwarz et al. accepted) and have different foraging dive patterns (Wilson et al. 2014). Specifically, females frequently perform longer and deeper foraging dives than males, and more commonly consume benthic species (Wilson et al. 2014, Schwarz et al. accepted). Unfortunately, these patterns in prey consumption are not yet linked to levels of individual specialization, which leaves a blind spot for management strategies as consumption estimates and patterns can be shifted where high specialization is present. Therefore, methods to quantify individual specialization in this system should be discussed.

*Quantifying individual specialization*

Traditionally, individual specialization has been quantified using a niche-partitioning framework developed by Roughgarden (1972, 1974). This framework partitions niche use variance into two main components: within individual component (WIC) and total niche width (TNW). WIC is the average niche width of individuals within a population whereas TNW is the total niche width of the entire population. By dividing WIC by TNW, one obtains a measure of how much smaller an average individual's niche is compared to the population as a whole (Roughgarden 1972, 1974). Within this metric, a value of one indicates that the entire population is composed of generalists. However, I did not use this metric because it was designed to work with continuous data and my data was discrete. An excellent alternative, that follows a similar theoretical framework but allows for the use of discrete data, is the proportional similarity index ($PS_i$). $PS_i$ takes into account all of the resources being used by the population and determines the similarity, or overlap, with the resources used by an individual (Bolnick et al. 2002).

Regardless of the specialization metric, the ideal way to measure individual specialization is through longitudinal samples (Bolnick et al. 2002, 2003). However, this approach requires following individuals over a period of time or taking samples from which multiple time points can be measured, such as hair or nails. Unfortunately, both following individuals through time and taking samples such as hair or nails is logistically complicated, expensive, and invasive when studying wild animals, particularly marine mammals. For these reasons, it tends to limit the spatial and temporal scales of individual specialization studies of marine mammals to single years and relatively few collection sites (≤3) and samples (≤100) (e.g., Kernaléguen et al. 2015, Rossman et al. 2015, Rita et al. 2017). Cross-sectional sampling is an alternative approach that circumvents these issues because it only requires measurements from a single timepoint. Studies

of northern pike *Esox lucius* and blue tilapia *Oreochromis aureus* showed a correlation between specialization levels calculated from longitudinal and cross-sectional data (Gu et al. 1997, Beaudoin et al. 1999), indicating that the latter can be a good estimate of long-term individual specialization.

Cross-sectional diet studies assume that each sample consists of multiple prey items and that each item represents an independent capture decision (Araújo et al. 2011). It is also assumed that the sampled diet is representative of the complete diet of the individual (Araújo et al. 2011). As such, this metric is an estimate of true individual specialization. In this study, I used cross-sectional diet data to describe intrapopulation feeding diversity and estimate individual specialization of *P. vitulina* at relatively large spatial and temporal scales in the Salish Sea. To avoid confusion with true individual specialization, throughout this thesis I will simply use the term specialization to refer to my results.

*Fecal collection and analysis*

Obtaining diet data necessary to measure specialization from large, mobile, and difficult to catch organisms, such as marine mammals is often carried out by taking a biological sample within which stable isotopes are laid down over time, such as blubber, whiskers, nails, or teeth. The ratios of stable isotopes of carbon and nitrogen provide a metric of the trophic level at which individuals are feeding, and in what environment they are feeding (Kernaleguen et al. 2015, Rossman et al. 2015). While this method can successfully document individual specialization, there are several drawbacks. First, it only provides coarse taxonomic resolution of an individual's prey because it cannot identify specific prey items. Second, the live capture process

is dangerous to the researchers and the animals that they are attempting to study. Third, live capture of marine mammals is costly and time consuming.

An alternative to describing individual specialization using live capture of animals and subsequent stable isotope analysis is scat collection and analysis. Analysis of prey contents in scat is cheaper, safer, and less time consuming than live capture of animals and allows for larger sample sizes. Additionally, prey content analysis gives specific diet data at a high level of taxonomic resolution, that is, to species level. The level of resolution used to measure resource use effects the accuracy of individual specialization estimates (Bolnick et al. 2002). Therefore, diet data are a more direct and accurate measure of niche width and individual specialization than stable isotope data (Araújo et al. 2011).

Analysis of diet via scat can be completed using a variety of techniques, each with their own benefits and drawbacks. While molecular techniques are more expensive than traditional diet analyses (which are based on morphological identification of prey hard parts in scat), there are many reasons to use molecular tools (Deagle et al. 2018). For instance, DNA-based methods are useful to determine the diet of animals that consume a wide variety of food because it decreases the likelihood of misidentification or missed identification of prey species (Deagle et al. 2005). Additionally, it is often difficult to identify prey to species level using only hard parts, especially in the case of salmonids (Tollit et al. 2009). Further, soft-bodied prey — or prey of which predators only eat soft parts, as sometimes happens with *Oncorhynchus* spp. — are not represented in hard part analysis (Olesiuk et al. 1990). However, traditional hard part analysis is still valuable in gaining information about the size and age of prey being consumed as molecular techniques cannot provide this information. Another drawback to molecular methods is that estimates of prey quantity in scat collected from the field are only relative because the level of

degradation that occurred via digestion or after defecation due to environmental factors is unknown (Bowen & Iverson 2012). Further, a single scat only represents the last few feeding bouts (Bowen & Iverson 2012). Therefore, conclusions about individual specialization based on scat are limited in their temporal scope. However, valuable information about the level of specialization can still be gained from cross-sectional sampling of scat because one can learn about the level of variation in the population in many snap shots. As such, this method is a viable option to gain information about individual specialization in *P. vitulina*. This is important because management strategies do not currently address the potential for individual specialization in *P. vitulina*.

This study addresses the potential for individual specialization in *P. vitulina* by answering the following questions: 1. What is the level of individual specialization in Salish Sea *P. vitulina*? 2. How do the factors Sex, Time of year, Location, and Year affect individual specialization? 3. What prey items correlate with high levels of individual specialization? To answer these questions, I collected and analyzed scat from wild *P. vitulina* in the Salish Sea. Diet of *P. vitulina* was determined from the scat using both molecular and traditional techniques. Sex of the depositor was also determined using molecular techniques. Using a proportional similarity index (Bolnick et al. 2002), diet data were used to calculate cross-sectional specialization as an estimate of the level of true individual specialization in *P. vitulina*.

## Methods

### *Collection and processing of scat samples*

Scat collections were conducted by multiple researcher groups at five known seal haul-outs in the Salish Sea over a period of four non-sequential years (Figure 1). Haul-outs varied in seal population size as well as by habitat type (Table 1). Not all sites were visited every year and the

months during which each site was visited varied between years (Table 1). Collections at Belle Chain, Cowichan, Comox, and Fraser River were conducted by teams from University of British Columbia under Fisheries and Oceans Canada Marine Mammal Research License (MML 2011-10) and a University of British Columbia Animal Care Permit (A11-0072) awarded to University of British Columbia Marine Mammal Research Unit. Collections at Baby Island were conducted by a team from Western Washington University under Federal Permit 18002 from the United States Office of Protected Resources, National Marine Fisheries Service, awarded to Alejandro Acevedo-Gutiérrez.

Collection of scat followed the general procedure described in Thomas et al. (2016). Briefly, upon arrival at a haul-out we searched the entire area for scat. Once a scat was found, the entire scat was collected into a 126 $\mu l$ nylon strainer inside of a 500 ml sealable container using a wooden tongue dispenser and plastic spoon. The container was then stored in a cooler with ice until transfer to a -20℃ freezer later that day. At Baby Island and Cowichan Bay in 2014 the entire outside of the scat was swabbed before collection. Swabbing focused on any mucus material, as it likely contains higher proportions of seal DNA (Rothstein 2015). The swab was then placed in a vial of ethanol and stored in a cooler with ice until transfer to a -20℃ freezer later that day.

A DNA slurry of homogenized scat in ethanol was prepared for each sample to obtain a representative set of DNA content following the procedure described in Thomas et al. (2016). Briefly, the entire scat was thawed in ethanol and homogenized within the mesh bag. After homogenization, a representative sample of DNA slurry was allowed to pass through the bag. The mesh bag was then removed, zip-tied, and stored at -20℃ for later use in prey hard part analysis. I then let the DNA slurry settle in the containers on the bench top overnight. The next

day I pipetted the settled slurry into 20 mL scintillation vials that were subsequently stored at -20℃ until further analysis.

*Sex determination of harbor seals via scat*

To obtain DNA for sex determination DNA was extracted from the scat matrix-ethanol slurry for all locations, except Cowichan 2014 and Baby Island. For these last two sites, DNA was extracted from the swabs. To extract DNA from swabs, the excess ethanol from the vial was poured off and the swab was dried in a vacuum centrifuge at 39°C until all ethanol had evaporated, approximately one hour. I then used QIAGEN DNeasy Blood and Tissue Kit to extract DNA from the dried swabs. DNA was extracted from slurry matrixes using QIAGEN QIAamp DNA Stool Mini Kit. Extracted DNA, from either the ethanol slurry or swab, was used in Taqman quantitative polymerase chain reactions (qPCR) to determine the presence and absence of X and Y chromosomes. The procedure was modified from Matejusová et al. (2013) and is described in depth in Rothstein (2015). The two probes that I used targeted the paralogous zinc finger X (ZFX) and zinc finger Y (ZFY) genes. Both probes are described in Matejusavá et al. (2013). Two reactions were run for each sample with each probe (four reactions total per sample). Each reaction consisted of: 4.5$\mu l$ of ABI Taqman gene expression master mix, 0.5$\mu l$ of either the ZFX or ZFY probe, and 5$\mu l$ of DNA template or PCR grade water. Reactions were run on a quantitative thermocycler with the following protocol: one holding cycle (50°C for 2 min, 95°C for 10 min) followed by 60 cycles of denaturation and annealing/extension (95°C for 15 sec, 60°C for 1 min). Four positive (two reactions for each sex, one ZFX and one ZFY probe each) and four negative controls (two reactions for each ZFX and ZFY probe) were run with each set of reactions. Positive controls came from captive harbor seals of known sex at the

Vancouver Aquarium in Vancouver, BC and Point Defiance Zoo & Aquarium in Tacoma, WA. Negative controls consisted of PCR grade water in place of a DNA template.

If no amplification occurred in either ZFX reactions, the sample was excluded from further analysis. If no amplification occurred in either ZFY reaction, but amplification did occur in either or both reactions with the ZFX probe, the sample was assumed to be deposited by a female. If amplification was observed in either or both ZFY reactions, as well as in either or both ZFX reactions, the sample was assumed to be deposited by a male. The false negative rate for two failed ZFY reactions (and thereby incorrectly classifying a male as a female) was 1.35%. This value was calculated from the occurrence of only one of the two ZFY reactions having positive amplification within a sample that was classified as male.

*Prey determination in harbor seal scat*

The diet of *P. vitulina* was determined by combining DNA and hard-part data. The DNA prey identification and quantification were completed following the procedure outlined in Thomas et al. (2016). Briefly, for all locations the scat matrix DNA (obtained from extracting DNA out of the DNA slurry using QIAGEN QIAamp DNA Stool Mini Kit) for each sample underwent a multiplex PCR using primers for a 16s mtDNA barcoding fragment (~260 bp) described by Deagle et al. (2009). Amplicons were labelled using a combination of unique F and R primer tags, in addition to indexed, post-PCR ligated Illumina TruSeq™ adapter sequences (see Thomas et al., 2016 for details). An Illumina MiSeq was then used to sequence the amplified DNA fragments. Lastly, a custom BLAST database comprised of publicly available reference sequences specific for known prey species was used to produce identifications to the lowest taxonomic level possible for each amplified sequence.

Extraction and preparation of prey hard parts were completed by Thomas et al. (2017) for Belle Chain, Comox, Cowichan Bay, and Fraser River samples, and by myself for Baby Island samples. Each scat was placed in a set of nested sieves, and then rinsed and stirred until all that was left in the sieves were prey hard parts. All hard parts, except cephalopod beaks, were transferred to 20 ml scintillation vials with 70% ethanol. They were allowed to sit for a minimum of two weeks before the liquid was poured off and the hard parts were allowed to dry. The cephalopod beaks were transferred to separate 20 ml scintillation vials with ethanol. All diagnostic prey hard parts were identified to the lowest taxonomic level possible using reference sets of prey bones from Washington and British Columbia by Thomas et al. (2017) for Belle Chain, Comox, Cowichan Bay, and Fraser River, and by collaborators at Long Live The Kings for Baby Island samples. Published keys for both fish bones and cephalopod beaks were used as described in Thomas et al. (2017). Notably, this analysis allowed differentiation between the proportion of adult and juvenile *Oncorhynchus* spp. consumed. The percentage of juvenile versus adult salmon was determined using the method by Thomas et al. (2017).

*Quantification of diet specialization*

As described earlier, longitudinal data are the ideal approach to measure individual specialization. However, cross-sectional sampling, which only requires data from a single timepoint, is a viable alternative, particularly when attempting to determine individual specialization at large spatial and temporal scales. For pinnipeds, a single time point can be examined via scat collection and analysis, as previously described. In the case of *P. vitulina*, scat represents the last one or two feeding bouts (Bowne & Iverson 2012), and thus a reasonable single timepoint.

I quantified the level of specialization represented by each sample using the proportional similarity index ($PS_i$) function in the R package RInSp (Zaccarelli et al. 2015). $PS_i$ calculates the overlap between what an individual is eating and what the population is eating using the following formula:

$$\mathrm{PS}_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

Where $p_{ij}$ represents the proportion of resource $j$ used by the individual $i$ and $q_j$ represents the proportion of resource $j$ used by the population. It is bounded by a theoretical minimum, which is population dependent as described below, and one. The variable population dependent minimum indicates a complete specialist and a $PS_i$ of one indicates a generalist (Bolnick et al. 2002). Because it is bounded, the average $PS_i$ value is reported with 95% confidence intervals calculated using Monte-Carlo resampling in the R 3.3.1 with the package "resample". Specialization values for each sample are important because they allow replicates within the groups that one defines for analysis.

To define my groups for analysis, samples were initially separated by the factor of Location. Samples were then further subdivided by the factors of Sex, Year, and Month of collection, yielding a total of 89 groups (Table 1). $PS_i$ values for each sample were then calculated for each one of these groups. Within each group, each sample was treated as coming from a different individual due to the low probability of resampling the same individual (Rothstein et al. 2017).

Because different groups for analysis can have different theoretical minima, there is potential bias when comparing specialization values across groups. Differences in theoretical minima occur due to differences in sample size (the number of scat in each group) and/or differences in minimum prey densities (the smallest occurring proportion of a prey species in a

group's diet). Due to very low minimum prey densities in our data set, the theoretical minima are determined by sample size (Table 1). I examined this potential bias in multiple ways. First, I excluded from analysis the smallest groups (those with < 5 samples) as they have the highest theoretical minimum and thus the most potential for bias. I also used Spearman's rank correlation to estimate how much variance was explained by differences in sample size. This correlation was accomplished by comparing sample size to the average $PS_i$ for each group I kept. I also calculated the theoretical minima for each group by dividing one by the number of samples in the group and then examined the range, average, and median of those minima. Additionally, sample sizes of each group were included in modeling of the data, which is described below. Lastly, the seasonal changes in sample size were visually compared with the seasonal patterns in $PS_i$ values.

*Comparison of factors influencing individual specialization*

I analyzed the relative influence of the factors Sex, Month, Location, Year, and Sample Size on the level of specialization using generalized linear mixed models (GLMMs). I chose mixed models because they allowed me to include Sample Size, Location, and Year as random variables. Restricted maximum likelihood estimation was used because it considers the loss of degrees of freedom when estimating fixed effects and thus offers a more unbiased estimate than maximum likelihood methods (West et al. 2015). Before modeling the data, I performed a logit transformation ($\log(\frac{PS_i}{1-PS_i})$) on the $PS_i$ values to normalize them. This was necessary because $PS_i$ is bounded by a theoretical minimum and one, which affects the variance distribution (Bolnick et al. 2002, Sokal & Rohlf 2012). When numbers are bounded, the variance distribution is shifted towards the mean (Sokal & Rohlf 2012). A logit transformation is an excellent choice for

addressing this shift because it extends the tails of the distribution more than other alternatives (Warton & Hui 2011).

All models were tested in R 3.3.1 package lme4 (Bates et al. 2015). This package provides basic measurements of goodness including AIC and coefficients. R package MuMIn was used to determine the $r^2$ values for mixed models. Subsequent calculations of $\Delta AIC$, and $w_i$ (positive Akaike weights or likelihood of being the best model (Anderson 2008)) were completed using excel. $\Delta AIC$ was calculated as the difference between two AIC scores. $w_i$ was calculated following Burnham and Anderson (2010). The equation used was:

$$w_i = \frac{exp(-\frac{1}{2} * \Delta AIC)}{\sum exp(-\frac{1}{2} * \ \Delta AIC)}$$

To more clearly understand the relationship between sex ratio of the population and specialization, sex ratios were produced for every paired group (groups of males and females from the same location, month, and year) by calculating the percent of scat identified as female. The average $PS_i$ for each paired group was then compared with this female percentage using a Spearman's rank correlation. The Spearman's rank correlation was used to account for the heteroscedasticity of the dataset. This correlation was completed using R 3.3.1. Additionally, the average proportion of female scat for each month and location are visualized in the supplemental material (Figure S1).

To describe differences in prey resource use distribution between female and male *P. vitulina*, I quantified the Shannon-Weaver index for each of the 89 groups. Prey proportions within each scat were averaged within each group. The averaged proportions were then used to calculated the Shannon-Weaver index using the Vegan package in R 3.3.1 (Oksanen et al. 2018).

The Shannon-Weaver index was used to give an idea of the breadth of prey consumed within each group to allow comparisons of the overall niche width between groups.

*Correlations between prey items and specialization*

For each scat, prey items were lumped into orders and summed. I then performed correlations between the proportion of the diet that each order comprised in each sample and the $PS_i$ for that sample. After eliminating prey items that occurred < 3 times in the whole dataset, I also ran correlations between each prey species and the $PS_i$ for each scat. Correlations of orders and species were calculated for the dataset as a whole, as well as for females and males separately. Due to the heteroscedasticity of the data set, I used Spearman's rank correlation (Sokal & Rohlf 2012). All correlation analysis was conducted in R 3.3.1. Because smaller $PS_i$ values indicate higher levels of specialization, a negative correlation value suggests a positive relationship with specialization.

## Results

*Quantification of individual specialization*

Over the course of four non-sequential years, at five different locations, I quantified the diet of 1,520 scat samples. I successfully determined the sex of the depositor for 1,145 of those scats (75% success rate). The number of scat with successful sex determination varied by location and month (Table 2). Samples with successful sex determination were then binned into groups split by the factors Sex, Location, Time of Year (Month), and Year to form unique groups for analysis (Table 1). After eliminating samples without sex determination and with small sample sizes (< 5 samples), I was left with 1,083 samples in 89 groups. Only these 1,083 samples were used in all further analyses. The average $PS_i$ of these samples was 0.399 (95% CI = 0.026, R = 100,000).

The $PS_i$ values of the 1,083 samples were not normally distributed (kurtosis = 2.66, skewness = 0.65, Figure 2). Therefore, a logit transformation was used to adjust the variance distribution (kurtosis = 5.21, skewness = 1.01, Figure 2). These transformed $PS_i$ values were used to run the GLMMs. Additionally, the range of theoretical minima across the 89 groups was 0.027 – 0.2 (average = 0.103, median = .091); there was also a slight correlation between average $PS_i$ and theoretical minimum $PS_i$ (rho = -.231, p = .03). This potential bias is addressed in the discussion.

*Comparison of factors influencing individual specialization*

Based on AIC values, $r^2$ results, and model likelihood, the best fit GLMM was Month*Sex + (1|Sample Size) + (1|Location) + (1|Year) (Table 2). The $r^2$ value as well as residual plots indicate that this model fit the data well (Table 3, Figure 3). The random factors of Sample Size, Location, and Year explained 0.39, 0.36, and 0.002 of the variance (SD = 0.62, 0.597, 0.05), respectively. The $r^2$ value calculated with fixed and random effects was over four times that of the $r^2$ value calculated using just fixed effects. Removing Month from the model caused a larger decrease in goodness measurements than removing Sex (Table 3). Removal of the interaction term also caused a decrease in goodness measurements (Table 3). Further, the interaction terms for Sex and the Months of August and October were significant (t = 2.86, 2.68, p = 0.004, 0.007 respectively). However, correlation analysis between the percent female scat collected for each paired group (which acted as a proxy for the effect of sex ratio in the population) and the average $PS_i$ for that pairing revealed no significant trend (rho = -0.071, p = 0.655).

To further examine the interaction between Sex and Month, the factor of Month was split into three levels: spring (April and May), summer (June, July, August), and fall (September, October, and November). The data showed a distinct shift in specialization throughout the year

in males but not females (Figure 4). In summer and fall, females had higher levels of specialization than males (Figure 4). To address the potential bias introduced by sample size for this mode of data analysis, I plotted the sample size for each group by season. The pattern observed in $PS_i$ values was not reflected in sample size (Figure 5).

Visual inspection of the data by month suggested males had a decrease in specialization in July through October (Figure 6). Based on 95% confidence intervals of logit transformed $PS_i$ values, $PS_i$ during these months only overlapped with April (Figure 6). The same pattern was not apparent in females because the 95% confidence interval for logit transformed $PS_i$ of female groups overlapped for all months (Figure 6). This trend varied in intensity by location (Figure 7). The described pattern was reflected most strongly in Belle Chain, Comox, and Fraser River (Figure 7). However, because scat were not collected at Baby Island after July, no comparison could be made with that location (Figure 7, Table 1).

Lastly, to help describe any differences in prey resource use distribution of female versus male *P. vitulina*, I quantified the Shannon-Weaver index as a measure of diet diversity within each group. While the confidence intervals overlapped, this measurement revealed consistently larger average diet diversity in females than males throughout all seasons (Figure 8).

*Correlations between prey items and individual specialization*

Correlation analysis between diet proportions of prey orders and $PS_i$ revealed that nine orders out of twelve showed significant correlations ($p < 0.05$, Table 4). Adult Salmoniformes, a largely pelagic group, were correlated with a generalist diet (rho = 0.27, $p < 0.001$) while juvenile Salmoniformes showed no significant correlation. Clupeiformes, another largely pelagic group, correlated with a generalist diet as well (rho = .24, $p < 0.001$). Conversely, Pleuronectiformes, a

demersal and benthic group, correlated with a specialist diet (rho = -0.38, $p < 0.001$). Further, Gadiformes, which has both pelagic and demersal representatives, showed no correlation (rho = -0.04, $p = 0.38$).

Correlation analysis between diet proportions of prey species and $PS_i$ revealed a total of 24 prey species with significant correlations ($p < 0.05$, Table 5). Seventeen out of the 18 species correlated with a specialized diet reside low in the water column (i.e. demersal, benthic, benthopelagic, bathypelagic, bathydemersal) (Table 5). Conversely, only three out of the seven species correlated with a generalist diet reside low in the water column (Table 5). Further, two of the eight adult Salmoniformes species observed in scat were correlated with generalist diets (adult pink *Oncorhynchus gorbuscha*, rho = 0.38, $p < 0.001$; adult sockeye *Oncorhynchus nerka*, rho = 0.36, $p < 0.001$) while the others showed no correlation. Lastly, only one of the eight juvenile salmon species was correlated with a generalist diet (juvenile *O. nerka*, rho = 0.22, $p = 0.004$), the other juvenile salmon species showed no significant correlation.

Correlations preformed with just data from female scat showed similar patterns. All orders of prey showed the same relationship with $PS_i$, or were no longer significant, such as Salmoniformes (Table 6). The only new order to show significance was Batrachoidiformes. Prey species also showed similar patterns, with all except one species correlated with specialization residing low in the water column (Table 7). Of the four species correlated with a generalist diet, only two were deep water species (Table 7). However, the relationship with adult *O. nerka* was different as they showed correlation with specialization as did one new juvenile salmon species, Coho salmon *Oncorhynchus kisutch* (Table 7).

Correlations performed with only male scat once again showed similar patterns. New orders to show significance were Chimaeriformes and Rajiformes (with a specialist diet) and

adult Salmoniformes (with a generalist diet) (Table 8). All species associated with a specialist diet were deep-water species (Table 9). Two of the seven species associated with a generalist diet were deep-water species (Table 9).

## Discussion

I successfully assigned specialization values to 1,083 scat collected from five different locations over the course of four non-sequential years (Table 1, Figure 1). As measured by repeated cross-sectional sampling, the overall level of intra-population feeding diversity in the region was high ($PS_i$= 0.399, 95% CI = 0.026, R = 100,000), which suggests that individual specialization was prevalent on the time-scale represented by scat (24 – 48 hours). Further, Time of year, Sex, and Location were all important factors influencing specialization. Interestingly, Time of Year and Sex had a significant interaction. Specialization also seems to have been driven by the habitat of an individual's primary prey (deep water species showed more correlations with specialist diets).

### *Estimated level of specialization*

I used cross-sectional sampling to estimate long-term individual specialization in Salish Sea harbor seals *P. vitulina* because I was unable to follow individuals through time. My data confirmed intra-population feeding diversity across the spatial (hundreds of km) and temporal (years) scales that the scat samples represented. Because I detected such patterns at large spatial and temporal scales (average $PS_i$ = 0.399, 95% CI = 0.026, R = 100,000), it is possible that the intrapopulation feeding diversity I described reflected long-term individual specialization in the region. However, these data leaves room for two alternative hypotheses: the occurrence of congruent long-term generalists and short-term specialists, or the occurrence of long-term specialists. These opposing hypotheses will be addressed throughout this discussion.

Given that a value of one indicates a complete generalist (Bolnick et al. 2002), the overall average $PS_i$ suggests that individual specialization occurred in Salish Sea *P. vitulina*. However, as previously stated, my data cannot confirm long-term specialization as scat samples only represent the last 24-48 hours of foraging. Though not directly comparable due to the variety of different methods, other studies have found a range of specialization that encompasses the average displayed in my data. A review by Araújo et al. (2011) listed the average $PS_i$ reported from 142 different species as 0.47 (±0.197). This review included values reported for various fish, bird, and mammal species. Individual specialization information on closely-related species may give a more context-appropriate range. Two populations of California sea otters *Enhydra lutris nereis* had average $PS_i$ values of 0.547 and 0.819 (Tinker et al. 2008). Average WIC/TNW (calculated differently than but on the same scale as $PS_i$) for Antarctic fur seals *Arctocephalus gazella* and subantarctic fur seals *Arctocephalus tropicalis* based on stable isotopes were 0.71 and 0.6 respectively (Kernaléguen et al. 2015). The individual specialization metric for southern elephant seals *Mirounga leonina* (calculated in the same way as that described for *A. gazella and A. tropicalis*) was 0.21 (Rita et al. 2017). Further, both Rita et al. (2017) and Hückstädt et al. (2012), who also worked with *M. leonina*, classified values <0.5 as specialists and values <0.2 as extreme specialists. Therefore, if my data is reflective of long-term specialization, *P. vitulina* in the Salish Sea have a high degree of specialization and should not be regarded as generalists. The likelihood of my data reflecting a longer time-scale will be addressed further later in the discussion. At the very least, my data confirms high levels of specialization on 24 - 48 hour periods.

*Relative importance of Time of year, Sex, Location, and Year on specialization*

Time of year was an important predictor of the level of specialization because removing Month from the model caused a big drop in goodness of fit measurements (Table 2). This pattern, described fully below, makes intuitive sense as the type of prey eaten by *P. vitulina* (Olesiuk et al. 1990, Lance et al. 2012) as well as their dive foraging behavior (Wilson et al. 2014) vary throughout the year. Therefore, changes in foraging behavior (both prey choice and dive type) are likely mechanisms behind the observed change in specialization throughout the year. However, there are likely other factors influencing specialization in addition to the time of year.

Sex also had an impact, yet less than that of Month (Table 2). Differences in the level of specialization between female and male *P. vitulina* were likely due to the fact that females and males in the region eat different prey items and have different foraging strategies (Wilson et al. 2014, Bjorland et al. 2015, Schwarz et al. accepted). For instance, females more often perform deeper foraging dives, eat benthic prey more commonly, and have smaller home ranges than males (Peterson et al. 2012, Wilson et al. 2014, Schwarz et al. accepted). My results also showed that females consistently consumed a larger average diversity of prey than males (Figure 8). Therefore, I propose the following theoretical resource distribution: as a group, males have smaller niche width, with more overlap between individuals while the female niche width is larger, with less overlap between individuals, with variation driven in this pattern associated with prey type (which will be addressed in the following section) (Figure 9). A similar resource distribution occurs in American bison *Bison bison*. Female *B. bison* have more selective and consistent diets than males, which suggests higher individual specialization in response to nutritional needs (Berini and Badgley 2017). However, contrary to what we presume is occurring in *P. vitulina*, male *B. bison* as a group showed a larger diet distribution than females (Berini and

Badgley 2017). Additionally, a closely related species to *P. vitulina*, *E. lutris*, displays an even more similar resource distribution. Female *E. lutris* have a larger total niche width as a group (broader overall resource use) but smaller within individual variation (more individual specialists) compared to males (Smith et al. 2015).

Including an interaction term between Month and Sex increased the fit of the model (Table 3). This result indicates that differences between male and female seals likely varied throughout the year. Specifically, there were clear decreases in specialization in male *P. vitulina* during the summer and fall months that were not reflected in females (Figure 4), indicating that the behavior of both sexes was similar in the spring but diverged in the summer and fall. This behavior is likely due to changes in feeding patterns of females and males throughout the year that occur in the region (Lance et al. 2012, Wilson et al. 2014). A possible reason for the different feeding patterns in the summer months is pupping. In this region, during the months of July and August, females are pupping and subsequently weaning those pups (Tempte et al. 1991). While nursing, females spend most of their time on the haul-out and make short foraging trips (Boness et al. 1994, D'agnese 2015). Males do not have the same constraints and could theoretically range more widely during this time. A large foraging range could result in less intraspecific competition, reducing the need for specialization. A similar difference was seen between sexes during the fall; however, both sexes were less specialized during the fall than at any other time of the year. During the fall, there is a large influx of adult Salmoniformes as they return from the open ocean (Quinn 2005). This is a resource that both female and male *P. vitulina* use, particularly in November (Schwarz et al. accepted). In the Salish Sea, Salmoniformes can compose >50% of the population diet in the summer and fall (Lance et al. 2012). This resource could be rich enough that it is beneficial for a large majority of seals to use,

both males and females, again, resulting in less need for specialization. This explanation is further supported by the fact that adult Salmonifomes were correlated with a generalist diet (Table 4), indicating it was a widely used resource in the region.

My data also suggest that location was a large driving factor for specialization. The random factors of Year and Location increased the $r^2$ by more than four times, indicating they had a large influence. However, because Sample Size, Location, and Year explained 0.39, 0.36, and 0.002 of the variance (SD = 0.62, 0.597, 0.05), respectively, one can assume that Sample Size and Location were the random factors responsible for the increase in goodness of fit of the model, not Year. This result indicates that where the seals were foraging impacted the level of specialization in the population, without noticeable changes from year to year. My results also indicate that there was likely some bias introduced by the number of samples in a group. However, the large spatial and temporal range of this dataset, the lack of effect of year, as well as the lack of pattern between sample size and $PS_i$ (Figure 4, 5), all indicate this bias was likely minimal.

The importance of location as a factor in specialization could be due to varied levels of prey diversity in different environments, given that prey availability affects the level of specialization (Araújo et al. 2011). For example, scat of *P. vitulina* from haul-outs in estuaries have higher diversity in prey use than haul-outs outside estuaries (Lance et al. 2012, Luxa & Acevedo-Gutiérrez 2013). Cowichan, Comox, and Fraser River are all situated within estuaries while Baby Island is located near (but not within) multiple estuaries; Belle Chain is considered a rocky reef environment. More specific examples in the Salish Sea are regional differences in the occurrence of sand lance *Ammodytes hexapterus* and rockfish *Sebastes* spp. in *P. vitulina* scat (Lance et al. 2012) and spatial differences in diet in *P. vitulina* fatty acid signatures (Bromaghin

et al. 2013). Therefore, it is likely that variation in habitat types caused differences in prey availability. Differences in prey availability offer more or less choice to *P. vitulina* in the area, which could subsequently affect the level of competition and ultimately specialization.

Due to the likely variation in specialization throughout the entire region both temporally and spatially, blanket assumptions should not be used to inform management strategies. There are probably spatial and temporal hot-spots of high levels of specialization that should receive more focus when incorporating information about specialization into management strategies. Understanding where these hotspots are will help make future studies as well as management strategies more efficient.

*Patterns between specialization and prey consumption*

Many prey species and orders had significant correlations with both a specialist and generalist diet. There were many demersal and benthic species, such as Pleuronectiformes, that where associated with a specialist diet. Conversely, open water species, especially forage fish such as Clupeiformes, where associated with a generalist diet. This pattern of the ecology of fishes being linked with the level of specialization was even present within orders. For example, the order Gadiformes includes pacific hake *Merluccius productus*, and walleye polluck *Gadus chalcogrammus*. The order did not show significant correlation with either specialist or generalist diets. However, when broken down into species, *M. productus*, which is a pelagic species, was correlated with a generalist diet. Conversely, *G. chalcogrammus*, a more demersal species, was correlated with a specialist diet. Specifically, *M. productus* are pelagic and more commonly eaten by males while *G. chalcogrammus* is benthic and eaten more commonly by females (Schwarz et al. in rev). This information ties to our knowledge of the foraging patterns

of male versus female *P. vitulina* in the region. Females more often perform deeper foraging dives (Wilson et al. 2014) and eat more benthic species than males, who eat more pelagic species (Schwarz et al. accepted). Peterson et al. (2012) offered some evidence that males also travel farther than females to forage, however they were only able to track four females in comparison to 16 males, thus, they were not able to fully examine the effect of sex on movement patterns. However, in Scotland *P. vitulina* scat samples represented either a largely pelagic foraging strategy or largely benthic foraging strategy (Tollit et al. 1997), and males had larger range and duration in foraging trips (Thompson et al. 1998), which may indicate this separation between the two foraging strategies is not only a regional phenomenon.

The described patterns of prey species correlation with specialization were observed in both the full dataset as well as when only female and only male data were considered (Table 3-9). This result indicates that specialization patterns linked to prey species were reflective of foraging strategies specific to the ecology of prey species, and not just indicative of differences of diet preferences between males and females. I hypothesize that this pattern between prey species and specialization was ultimately caused by higher variability in benthic environments. Benthic environments are more variable than open water, which allows for more different species to occur to fill the many niches (Lalli & Parsons 1997). Thus, if prey have more variable life strategies, a single foraging strategy will not work to catch them all. Because an organism is likely limited in the number of foraging strategies it can be effective at, an individual could be limited in the number of variable prey species it consumes. This concept is best explained through optimal foraging theory and tradeoffs.

A useful theoretical framework to explain how ecological interactions affect specialization is optimal foraging theory (Bolnick et al. 2003, Araújo et al. 2011). Optimal

foraging theory states that individuals will always strive to maximize foraging efficiency and feed on the most profitable resources (Schoener 1971). By specializing on a subset of resources, and becoming efficient at exploiting those resources (i.e. able to minimize energy used while maximizing energy gained per unit time), an individual will have resources that are most profitable to it that differ from the resources that are most profitable to others in their population, resulting in higher fitness for that individual (Bolnick et al. 2003). Such differences in profitability arise because there are limits to exploiting multiple resources with the same efficiency (Bolnick et al. 2003). There are many physiological trade-offs related to foraging success that limit the number of prey species on which individuals can effectively specialize (Bolnick et al. 2003). These tradeoffs are best understood through examples such as the inverse relationships between jaw closing strength versus speed (Wainwright & Richard 1995) and foraging speed versus maneuverability in various fish species (Ehlinger 1990, Svanback & Eklov 2002). Thus, theoretically a fish might either specialize on small agile prey or large fast prey. Additionally, in blue jays *Cyanocitta cristata*, neural capacity limits the number of foraging behaviors and search images that individuals can maintain (Pierewicz & Kamil 1979). Models of sea otter *Enhydrus lutris* behavior a known specialist (Tinker et al. 2008), also indicate that there are top limits to the number complex foraging skills that can be retained (Tinker et al. 2009). Further, both free ranging *A. gazella* (Arthur et al. 2016) and northern fur seals *Callorhinus ursinus* (Jeanniard-du-Dot et al. 2017) use one of two distinct foraging strategies suggesting that pinnipeds must choose between opposing foraging strategies. Something similar may be occurring with *P. vitulina* as there are distinct foraging patterns associated with male (long range and shallow) and female seals (small range and deep) (Peterson et al. 2012, Wilson et al. 2014).

Together, all of these findings suggest that it may be more effective for *P. vitulina* to conduct either deep or shallow foraging strategies, which also means they will be consuming the prey in each of those environments. Benthic environments are more variable than pelagic environments which is in part responsible for the higher number of benthic species of animals residing there (Lalli & Parsons 1997). Further, rocky bottoms provide crevices and depressions for prey to hide in and sandy or muddy bottoms provide cover for burrowing species (Lalli & Parsons 1997). Thus, the higher number of different prey species, and the potential for more avoidance strategies in the variable sea floor, could lead to the need for specialized foraging strategies associated with benthic species. Conversely, in open water environments one foraging strategy/search image may work for many prey species as open water is a less variable environment (Lalli & Parsons 1997). Unfortunately, my data prevent me from confirming how often *P. vitulina* switch between these two strategies or what the limit is for the number of foraging skills *P. vitulina* can maintain and how that might impact its foraging behavior. However, current knowledge of the system suggests that *P. vitulina* consistently persist in either the benthic or pelagic environments. For example, both dive recordings (Wilson et al. 2014) and fatty acid signatures (Bromaghin et al. 2013) indicate consistent foraging patterns on a longer scale than scat represent. Further, GPS tracking of *P. vitulina* in the Georgia Strait, Canada, over a month-long period confirmed that seals would consistently forage in one of four spatially distinct areas (Allegue 2017). *P. vitulina* in the southern end of the Strait of Georgia, as well as in and near the San Juan Islands, also showed preferential use of, and purposeful movement to, foraging areas that differed between individuals (Peterson et al. 2012), again suggesting individual choice in foraging strategy. The consistency in foraging patterns observed using these

methods suggest foraging patterns are retained on longer time-scales than scat represent, which supports the hypothesis of long-term specialization.

There is the possibility that the sex of the individual determines the level of specialization regardless of the prey consumed. However, I argue that sex determines the feeding strategy taken up and the species within each feeding strategy determine the level of specialization. The repetition of benthic prey being associated with a specialist diet, and pelagic prey being associated with a generalist diet, in both the complete, only female, and only male data set suggests that prey species ecology is driving the pattern more than sex of the seal. Additionally, within only males, different behaviors were used when foraging for non-conspicuous (benthic) versus conspicuous (pelagic) prey (Bowen et al. 2002). Further, larger seals are more likely to forage in pelagic environments regardless of sex (Bjorkland et al. 2015). Because *P. vitulina* display slight sexual dimorphism (Teilmann & Galatius 2018) there is the potential for trade-offs between speed and maneuverability within the population. If that is the case, then females, being slightly smaller on average, would have slightly less speed and more maneuverability. I hypothesize that this combination would be more successful in a benthic environment to deal with variations in the seafloor that benthic prey relies on to escape. If this is correct, it suggests the environment and prey species in that environment drive the type of foraging that will be most successful, and that sex (or size) of *P. vitulina* predisposes an individual to be better at one type than the other.

If prey species ecology is driving specialization levels, then it is especially interesting to consider *P. vitulina* consumption of juvenile Salmoniformes. As a group, juvenile Salmoniformes did not correlate with a generalist diet. However, when split into species, juvenile sockeye *O. nerka* did correlate with a generalist diet (rho = 0.22, p = 0.004). This could indicate

that seals were not seeking out juvenile Salmoniformes specifically but rather eating them as a byproduct of focusing on fish that match the image of forage fish (e.g. small and silver) while conducting a pelagic foraging strategy. This is just one example of how understanding specialization could deepen our scope of knowledge regarding *P. vitulina* impacts on prey species of concern.

*Management implications*

Current ecosystem models are ecologically meaningful and useful in some cases. However, estimates of specialization could be incorporated into these models to test the theoretical effects of specialization on predator-prey interactions in this system. My data indicates a moderate level of individual specialization occurs on a short time-scale (24-48 hours), which likely reflects a longer time-scale. The data also indicates that the level of specialization varies temporally and spatially. Because specialization can change predator-prey relations from expected patterns (Bolnick et al. 2003), including information about specialization in the region would likely help models more accurately inform where the largest impacts on species of concern are. With this knowledge, management could then direct human fishing efforts elsewhere. Specifically, management could use this information to determine the most effective places to expand marine protected areas (MPAs). MPAs are areas of restricted access and/or fishing that protect critical habitat for species of concern and have proven effective in species conservation (Lubchenco et al. 2013).

Additionally, as previously discussed, *P. vitulina* appear to specialize upon some prey species, such as benthic fish, more commonly than others. Because specialization effects the accuracy of predictive models these species should be of special concern when estimating

consumption and the subsequent need for management. For example, rockfish *Sebastes* spp. are a benthic species of conservation concern. While they were not common in my dataset (the highest occurring *Sebastes* spp. was the China rockfish *S. nebulosus*, which occurred nine times) they are a food source of *P. vitulina* in this region (Lance et al. 2012, Bromaghin et al. 2013, Bjorland et al 2015). Because of the low abundance of *Sebastes* spp. in this dataset we cannot confidently say whether *P. vitulina* specialize on them. However, given that *P. vitulina* specialize on benthic species more commonly than on other type of species, it seems plausible that *Sebastes* spp. are specialized on. Given the effect specialization can have on the accuracy of predictive models, specialization on *Sebastes* spp. opens up the possibility that there is a difference between expected and actual impact of *P. vitulina*. Management could address this by identifying individuals who eat *Sebastes* spp. and removing only those individuals. This would have a larger positive impact on the prey species of concern than removing *P. vitulina* individuals at random. Unfortunately, there is not currently the technology to identify and following individuals efficiently. However, this is an issue being addressed and will hopefully be more viable in the near future.

*Study limitations*

There are a few notable limitations to this study. First, I was unable to follow individuals through time. Therefore, my data are cross-sectional in nature which can confirm specialization only over the time scale for which the samples represent (Araújo et al. 2011). However, other studies on *P. vitulina* suggests foraging patterns are retained over longer time periods, which indicates long-term specialization occurs. Second, there was the potential for variation in sample size to introduce bias. However, there were no discernable patterns between sample size and average

specialization by season (Figure 4, 5). I also included sample size as a random factor in the model to account for any bias introduced there. Hence, any bias introduced by sample size was likely minimal. Third, because scat were collected from the same haul-out multiple times there is a chance that some scat collected came from the same individual. However, the likelihood of this is low. Rothstein et al. (2017) estimated the sampling scheme to track five individuals at Cowichan Bay as 440 samples over 22 sampling bouts. Compared to the 1,083 samples used in this analysis from five different haul-outs, it seems unlikely there was a high rate of resampling the same individuals. Fourth, there are biases in the metabarcoding PCR process for determining diet (Thomas et al. 2014). The prey proportions recorded for each sample are not directly proportional to the amount of prey that was ingested (Bowne & Iverson 2012, Thomas et al. 2014). However, this approach is accepted to be semi-quantitative, biases are assumed to be consistent between samples (Thomas et al. 2014) and have been used as such in other studies (Deagle et al. 2009, Pompanon et al. 2012, Thomas et al. 2014, Thomas et al. 2017, Schwarz et al. accepted). Furthermore, this method has been shown to be superior to the alternative occurrence-based methods for generating diet proportions (Deagle et al. 2018). On a related note, these molecular methods do not provide data that directly equates to counts of prey consumed. Traditionally, prey counts have been used for calculating specialization, not proportions, as each count is assumed to represent an independent prey capture decision (Bolnick et al. 2002, Araújo et al. 2011). Therefore, my assumption is that diet proportions represent the same relative relationship of prey capture decisions as counts of individual prey items would. Thus, using proportions to estimate specialization potentially introduces bias but it is currently unclear what the effect of using proportion data might be. However, there are many benefits to using this type of data. Coupled with scat collection, it allows for large samples sizes, is non-invasive, and gives

high taxonomic resolution. Further investigation into potential biases introduced by using proportion type data would be useful as this methodology has many benefits and is a valuable tool that should be used in the future.

*Future directions*

My results indicate that specialization could be examined on a broader spatial and temporal scale using additional existing diet data to gain a clearer understanding of the phenomenon in the region; for example, from Puget Sound, at the southern end of the Salish Sea, and the San Juan Islands. Additionally, because location seemed to have such a large impact on specialization, it would be beneficial to determine which types of environments effect the level of specialization the most. This information would allow for easier identification of hot-spots of specialization. Further, scientists should incorporate specialization metrics into models that predict impacts on prey populations. This could determine if changes in the level of specialization, based on what is reasonable for this region (as estimated in this study), make a sizeable difference on the expected impact of *P. vitulina* on prey populations. This would confirm if the level of specialization in the region is large enough to warrant management action.

*Conclusion*

This study has shown that specialization occurs in Salish Sea *P. vitulina* at short time-scales. However, other studies have shown that *P. vitulina* maintain foraging strategies at longer time-scales. Thus, it seems likely that long-term individual specialization occurs in the population. I also demonstrated that there is likely temporal and spatial variability in the level of specialization. At a finer scale, the sex of *P. vitulina* also impacted the level of specialization,

with females displaying higher levels of specialization. However, in both male and female *P. vitulina* benthic prey were more commonly specialized on, suggesting the prey's ecology had a larger role in driving the level of specialization. All of these results imply that specialization impacts how *P. vitulina* are interacting with their environment, which is likely different than current models are predicting. These different impacts of male versus female on benthic versus pelagic prey should be considered when management address *P. vitulina* interactions with species of concern. In summary, specialization should be studied further and incorporated into knowledge of *P. vitulina* predator-prey interactions.

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## Tables

Table 1. Groups for analysis of specialization in *Phoca vitulina* in the Salish Sea. Location denotes where the group of scat was collected. BC = Belle Chain, BI = Baby Island, CB = Cowichan Bay, CM = Comox, FR = Fraser River. Month, Year, and Season show when the group of scat was collected. The minimum prey density column indicates the lowest occurring prey proportion within a single scat within the group. The theoretical minimum column indicates the theoretical minimum that was assigned to each group. The theoretical minimum was calculated by dividing one by the total sample size of each group. N indicates the total number of samples within each group. SI indicates the average $PS_i$ within each group. The Use column indicates whether or not the group was used in downstream analysis based off of sample size (groups with <5 samples were excluded). The Shannon-Weaver column indicates the Shannon-Weaver index assigned to each group. This index was calculated by averaging prey proportions from each scat within each group and subsequent use of the diversity function in VEGAN package in R 3.3.1.

| Location | Month | Year | Season | Sex | Minimum prey density | Theoretical minimum | N | SI | Use | Shannon-Weaver |
|---|---|---|---|---|---|---|---|---|---|---|
| BC | June | 2012 | Summer | Male | 0.0110 | 0.2000 | 5 | 0.549 | Yes | 0.928 |
| BC | June | 2012 | Summer | Female | 0.0160 | 0.5000 | 2 | 0.680 | No | 1.236 |
| BC | July | 2012 | Summer | Male | 0.0002 | 0.1111 | 9 | 0.380 | Yes | 1.935 |
| BC | July | 2012 | Summer | Female | 0.2968 | 1.0000 | 1 | 0.000 | No | 0.608 |
| BC | Aug | 2012 | Summer | Female | 0.0001 | 0.0556 | 18 | 0.421 | Yes | 1.567 |
| BC | Aug | 2012 | Summer | Male | 0.0002 | 0.0588 | 17 | 0.390 | Yes | 1.618 |
| BC | Sept | 2012 | Fall | Female | 0.0124 | 0.0526 | 19 | 0.572 | Yes | 0.987 |
| BC | Sept | 2012 | Fall | Male | 0.0076 | 0.0833 | 12 | 0.427 | Yes | 1.600 |
| BC | Aug | 2013 | Summer | Female | 0.0139 | 0.2000 | 5 | 0.314 | Yes | 2.121 |
| BC | Aug | 2013 | Summer | Male | 0.0114 | 0.2000 | 5 | 0.478 | Yes | 1.145 |
| BC | Sept | 2013 | Fall | Female | 0.0103 | 0.0714 | 14 | 0.527 | Yes | 1.514 |
| BC | Sept | 2013 | Fall | Male | 0.0105 | 0.0769 | 13 | 0.487 | Yes | 1.403 |
| BC | Oct | 2013 | Fall | Male | 0.0107 | 0.0833 | 12 | 0.588 | Yes | 1.144 |
| BC | Oct | 2013 | Fall | Female | 0.0104 | 0.3333 | 3 | 0.614 | No | 0.884 |
| BI | Apr | 2016 | Spring | Female | 0.0120 | 0.1429 | 7 | 0.426 | Yes | 1.754 |
| BI | Apr | 2016 | Spring | Male | 0.0297 | 0.1429 | 7 | 0.387 | Yes | 1.169 |
| BI | May | 2016 | Spring | Male | 0.0094 | 0.0278 | 36 | 0.387 | Yes | 1.587 |
| BI | May | 2016 | Spring | Female | 0.0118 | 0.0370 | 27 | 0.305 | Yes | 1.751 |
| BI | June | 2016 | Summer | Male | 0.0122 | 0.0833 | 12 | 0.246 | Yes | 2.123 |
| BI | June | 2016 | Summer | Female | 0.0251 | 0.1250 | 8 | 0.214 | Yes | 1.942 |
| BI | July | 2016 | Summer | Female | 0.0477 | 0.1250 | 8 | 0.341 | Yes | 1.193 |
| BI | July | 2016 | Summer | Male | 0.2368 | 0.3333 | 3 | 0.529 | No | 0.879 |
| CB | June | 2012 | Summer | Female | 0.0006 | 0.1111 | 9 | 0.474 | Yes | 1.634 |
| CB | June | 2012 | Summer | Male | 0.0002 | 0.1429 | 7 | 0.344 | Yes | 1.717 |
| CB | July | 2012 | Summer | Male | 0.0003 | 0.0500 | 20 | 0.447 | Yes | 1.557 |
| CB | July | 2012 | Summer | Female | 0.0034 | 0.0625 | 16 | 0.395 | Yes | 2.115 |

Table 1. continued

| Location | Month | Year | Season | Sex | Minimum prey density | Theoretical minimum | N | SI | Use | Shannon-Weaver |
|---|---|---|---|---|---|---|---|---|---|---|
| CB | Aug | 2012 | Summer | Female | 0.0002 | 0.1429 | 7 | 0.316 | Yes | 1.556 |
| CB | Sept | 2012 | Fall | Female | 0.0007 | 0.0526 | 19 | 0.313 | Yes | 1.846 |
| CB | Sept | 2012 | Fall | Male | 0.0029 | 0.1429 | 7 | 0.330 | Yes | 1.580 |
| CB | Oct | 2012 | Fall | Male | 0.0002 | 0.0625 | 16 | 0.263 | Yes | 2.059 |
| CB | Oct | 2012 | Fall | Female | 0.0004 | 0.0769 | 13 | 0.320 | Yes | 1.745 |
| CB | Nov | 2012 | Fall | Male | 0.0137 | 0.2500 | 4 | 0.988 | No | 0.063 |
| CB | Nov | 2012 | Fall | Female | 0.0110 | 0.5000 | 2 | 0.995 | No | 0.034 |
| CB | Apr | 2013 | Spring | Female | 0.0278 | 0.1000 | 10 | 0.352 | Yes | 1.705 |
| CB | Apr | 2013 | Spring | Male | 0.1160 | 1.0000 | 1 | 0.000 | No | 0.359 |
| CB | May | 2013 | Spring | Female | 0.0112 | 0.0909 | 11 | 0.313 | Yes | 1.979 |
| CB | May | 2013 | Spring | Male | 0.0123 | 0.2500 | 4 | 0.374 | No | 1.059 |
| CB | June | 2013 | Summer | Female | 0.0167 | 0.1111 | 9 | 0.489 | Yes | 1.337 |
| CB | June | 2013 | Summer | Male | 0.0154 | 0.3333 | 3 | 0.337 | No | 1.328 |
| CB | July | 2013 | Summer | Female | 0.0114 | 0.1250 | 8 | 0.400 | Yes | 1.610 |
| CB | July | 2013 | Summer | Male | 0.0116 | 0.1429 | 7 | 0.384 | Yes | 1.728 |
| CB | Aug | 2013 | Summer | Female | 0.0103 | 0.0667 | 15 | 0.228 | Yes | 2.147 |
| CB | Aug | 2013 | Summer | Male | 0.0143 | 0.2500 | 4 | 0.393 | No | 1.256 |
| CB | Sept | 2013 | Fall | Female | 0.0187 | 0.0833 | 12 | 0.327 | Yes | 1.687 |
| CB | Sept | 2013 | Fall | Male | 0.0108 | 0.1000 | 10 | 0.354 | Yes | 1.959 |
| CB | Oct | 2013 | Fall | Female | 0.0122 | 0.0833 | 12 | 0.546 | Yes | 1.313 |
| CB | Oct | 2013 | Fall | Male | 0.0103 | 0.1111 | 9 | 0.463 | Yes | 1.362 |
| CB | Nov | 2013 | Fall | Male | 0.0116 | 0.1250 | 8 | 0.531 | Yes | 0.932 |
| CB | Nov | 2013 | Fall | Female | 0.0110 | 0.1429 | 7 | 0.486 | Yes | 1.317 |
| CB | May | 2014 | Spring | Male | 0.0047 | 0.1000 | 10 | 0.222 | Yes | 1.911 |
| CB | May | 2014 | Spring | Female | 0.0126 | 0.1667 | 6 | 0.412 | Yes | 1.495 |
| CB | June | 2014 | Summer | Male | 0.0113 | 0.1250 | 8 | 0.365 | Yes | 1.509 |
| CB | June | 2014 | Summer | Female | 0.0105 | 0.1667 | 6 | 0.349 | Yes | 1.542 |
| CB | July | 2014 | Summer | Male | 1.0000 | 1.0000 | 1 | 0.000 | No | 0.000 |
| CB | Aug | 2014 | Summer | Male | 0.0008 | 0.3333 | 3 | 0.341 | No | 1.572 |
| CB | Aug | 2014 | Summer | Female | 0.0200 | 0.5000 | 2 | 0.600 | No | 1.292 |
| CB | Sept | 2014 | Fall | Male | 0.0139 | 0.1111 | 9 | 0.256 | Yes | 1.729 |
| CB | Sept | 2014 | Fall | Female | 0.0007 | 0.1250 | 8 | 0.601 | Yes | 1.127 |
| CB | Oct | 2014 | Fall | Male | 0.0024 | 0.0270 | 37 | 0.265 | Yes | 2.048 |
| CB | Oct | 2014 | Fall | Female | 0.0104 | 0.0417 | 24 | 0.225 | Yes | 2.230 |
| CB | Nov | 2014 | Fall | Male | 0.0003 | 0.0435 | 23 | 0.249 | Yes | 1.820 |
| CB | Nov | 2014 | Fall | Female | 1.0000 | 1.0000 | 1 | 0.000 | No | 0.000 |
| CM | May | 2012 | Spring | Male | 0.0001 | 0.0667 | 15 | 0.570 | Yes | 1.568 |
| CM | May | 2012 | Spring | Female | 0.0144 | 0.2500 | 4 | 0.586 | No | 0.993 |
| CM | June | 2012 | Summer | Male | 0.0017 | 0.0556 | 18 | 0.295 | Yes | 2.150 |

Table 1 continued

| Location | Month | Year | Season | Sex | Minimum prey density | Theoretical minimum | N | SI | Use | Shannon-Weaver |
|---|---|---|---|---|---|---|---|---|---|---|
| CM | June | 2012 | Summer | Female | 0.0007 | 0.0909 | 11 | 0.338 | Yes | 2.362 |
| CM | July | 2012 | Summer | Male | 0.0004 | 0.0455 | 22 | 0.269 | Yes | 2.357 |
| CM | Aug | 2012 | Summer | Male | 0.0012 | 0.0909 | 11 | 0.272 | Yes | 1.945 |
| CM | Aug | 2012 | Summer | Female | 0.0008 | 0.1111 | 9 | 0.232 | Yes | 2.216 |
| CM | Sept | 2012 | Fall | Female | 0.0105 | 0.0500 | 20 | 0.240 | Yes | 2.200 |
| CM | Sept | 2012 | Fall | Male | 0.0019 | 0.1000 | 10 | 0.268 | Yes | 1.986 |
| CM | Oct | 2012 | Fall | Female | 0.0000 | 0.0625 | 16 | 0.251 | Yes | 1.814 |
| CM | Oct | 2012 | Fall | Male | 0.0000 | 0.1250 | 8 | 0.575 | Yes | 0.691 |
| CM | Apr | 2013 | Spring | Male | 0.0015 | 0.0769 | 13 | 0.317 | Yes | 1.560 |
| CM | Apr | 2013 | Spring | Female | 0.0120 | 0.2500 | 4 | 0.304 | No | 1.761 |
| CM | May | 2013 | Spring | Female | 0.0116 | 0.0833 | 12 | 0.213 | Yes | 2.219 |
| CM | May | 2013 | Spring | Male | 0.0144 | 0.2000 | 5 | 0.292 | Yes | 1.334 |
| CM | June | 2013 | Summer | Male | 0.0105 | 0.1250 | 8 | 0.206 | Yes | 1.901 |
| CM | June | 2013 | Summer | Female | 0.0179 | 0.2000 | 5 | 0.361 | Yes | 1.455 |
| CM | July | 2013 | Summer | Male | 0.0135 | 0.0909 | 11 | 0.600 | Yes | 1.203 |
| CM | July | 2013 | Summer | Female | 0.0220 | 0.1429 | 7 | 0.540 | Yes | 0.985 |
| CM | Aug | 2013 | Summer | Female | 0.0135 | 0.1000 | 10 | 0.275 | Yes | 2.141 |
| CM | Aug | 2013 | Summer | Male | 0.0125 | 0.1000 | 10 | 0.423 | Yes | 1.615 |
| CM | Sept | 2013 | Fall | Female | 0.0112 | 0.0625 | 16 | 0.256 | Yes | 1.995 |
| CM | Sept | 2013 | Fall | Male | 0.0133 | 0.1111 | 9 | 0.506 | Yes | 1.296 |
| CM | Oct | 2013 | Fall | Female | 0.0120 | 0.0909 | 11 | 0.328 | Yes | 1.778 |
| CM | Oct | 2013 | Fall | Male | 0.0111 | 0.1429 | 7 | 0.463 | Yes | 1.333 |
| FR | May | 2012 | Spring | Male | 0.0025 | 0.0769 | 13 | 0.302 | Yes | 2.388 |
| FR | June | 2012 | Summer | Male | 0.0055 | 0.0588 | 17 | 0.372 | Yes | 2.479 |
| FR | June | 2012 | Summer | Female | 0.0005 | 0.3333 | 3 | 0.574 | No | 1.865 |
| FR | July | 2012 | Summer | Male | 0.0101 | 0.0476 | 21 | 0.771 | Yes | 0.728 |
| FR | July | 2012 | Summer | Female | 0.0118 | 0.5000 | 2 | 0.585 | No | 1.341 |
| FR | Aug | 2012 | Summer | Male | 0.0105 | 0.1667 | 6 | 0.974 | Yes | 0.127 |
| FR | Aug | 2012 | Summer | Female | 0.0130 | 0.5000 | 2 | 0.976 | No | 0.140 |
| FR | Sept | 2012 | Fall | Male | 0.0102 | 0.0345 | 29 | 0.388 | Yes | 1.310 |
| FR | Sept | 2012 | Fall | Female | 0.0016 | 0.0769 | 13 | 0.206 | Yes | 2.020 |
| FR | Oct | 2012 | Fall | Male | 0.0110 | 0.0769 | 13 | 0.976 | Yes | 0.092 |
| FR | Oct | 2012 | Fall | Female | 0.0124 | 0.2000 | 5 | 0.648 | Yes | 0.701 |
| FR | Apr | 2013 | Spring | Male | 0.0110 | 0.1111 | 9 | 0.523 | Yes | 0.955 |
| FR | Apr | 2013 | Spring | Female | 0.0108 | 0.2000 | 5 | 0.463 | Yes | 1.190 |
| FR | May | 2013 | Spring | Male | 0.0152 | 0.0667 | 15 | 0.246 | Yes | 2.325 |
| FR | May | 2013 | Spring | Female | 0.0123 | 0.2500 | 4 | 0.373 | No | 1.413 |
| FR | June | 2013 | Summer | Male | 0.0135 | 0.3333 | 3 | 0.361 | No | 1.623 |
| FR | June | 2013 | Summer | Female | 0.0107 | 1.0000 | 1 | 0.000 | No | 0.059 |

Table 1 continued

| Location | Month | Year | Season | Sex | Minimum prey density | Theoretical minimum | N | SI | Use | Shannon-Weaver |
|---|---|---|---|---|---|---|---|---|---|---|
| FR | Aug | 2013 | Summer | Male | 1.0000 | 0.5000 | 2 | 1.000 | No | 0.000 |
| FR | July | 2013 | Summer | Male | 0.0118 | 0.2000 | 5 | 0.269 | Yes | 1.808 |
| FR | July | 2013 | Summer | Female | 0.0455 | 1.0000 | 1 | 0.000 | No | 1.679 |
| FR | Aug | 2013 | Summer | Female | 0.0119 | 0.3333 | 3 | 0.420 | No | 1.483 |
| FR | Sept | 2013 | Fall | Female | 0.0112 | 0.1429 | 7 | 0.811 | Yes | 0.626 |
| FR | Oct | 2013 | Fall | Male | 0.0105 | 0.0833 | 12 | 0.772 | Yes | 0.731 |
| FR | Oct | 2013 | Fall | Female | 0.0047 | 0.2000 | 5 | 0.562 | Yes | 1.316 |

Table 2. Number of *Phoca vitulina* scat from the Salish Sea with successful sex determination from all locations, months, and years. Within each monthly column the numbers are as follows: female scat, male scat. If multiple collection bouts occurred at a single haul-out within one month the total number of scat for that month is listed. An "na" indicates no scat were collected at that site during that month. Population estimates for Belle Chaine, Cowichan Bay, Comox, and Fraser River where calculated from Olesiuk et al. 2009. The population estimate for Baby Island was taken from Jefferies et al. 2003.

| Location | Environment | Population | Year | Apr | May | June | July | Aug | Sept | Oct | Nov | Total (by location) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Belle Chaine | Rocky reef | 834 | 2012 | na | na | 2,5 | 1,9 | 18,17 | 19,12 | na | na | 83 |
| Belle Chaine | Rocky reef | | 2013 | na | na | na | na | 5,5 | 14,13 | 3,12 | na | 52 |
| Baby Island | Near estuary | <100 | 2016 | 7,7 | 27,36 | 8,12 | 8,3 | na | na | na | na | 108 |
| Cowichan Bay | Estuary | 167 | 2012 | na | na | 9,7 | 16,20 | 7,13 | 19,7 | 13,16 | 2,4 | 133 |
| Cowichan Bay | Estuary | | 2013 | 10,1 | 11,4 | 9,3 | 8,7 | 15,4 | 12,10 | 12,9 | 7,8 | 130 |
| Cowichan Bay | Estuary | | 2014 | na | 6,10 | 6,8 | 0,1 | 2,3 | 8,9 | 24,37 | 1,23 | 138 |
| Comox | Estuary | 121 | 2012 | na | 4,15 | 11,18 | 13,22 | 9,11 | 20,10 | 16,8 | na | 157 |
| Comox | Estuary | | 2013 | 4,13 | 12,5 | 5,8 | 7,11 | 10,10 | 16,9 | 11,7 | na | 128 |
| Fraser River | Estuary | 76 | 2012 | na | 0,13 | 3,17 | 2,21 | 2,6 | 13,29 | 5,13 | na | 124 |
| Fraser River | Estuary | | 2013 | 5,9 | 4,15 | 1,3 | 1,5 | 3,2 | 7,20 | 5,12 | na | 92 |
| Total (by month) | na | na | na | 56 | 162 | 135 | 155 | 142 | 247 | 203 | 45 | 1145 |

Table 3. GLMM models of prey specialization in Salish Sea *Phoca vitulina*. The fixed $r^2$ column indicates how much variance was explained by only the fixed effects. The $r^2$ column indicates how much variance was explained by both fixed and random effects. The AIC column indicates the fit of each model, lower values indicate a better model. The $w_i$ column indicates the relative likelihood of each model being the best model of those tested. Analysis represents 1,083 samples from groups with >5 samples.

| Predictors | $r^2$ fixed | $r^2$ | AIC | $w_i$ |
|---|---|---|---|---|
| Sex*Month + (1\|Sample size) + (1\|Location) + (1\|Year) | 0.105 | 0.502 | 3141.78 | .99 |
| Sex + Month + (1\|Sample size) + (1\|Location) + (1\|Year) | 0.076 | 0.462 | 3157.91 | 0.03 |
| Month + (1\|Sample size) + (1\|Location) + (1\|Year) | 0.061 | 0.459 | 3172.53 | 2.10E-07 |
| Sex + (1\|Sample size) + (1\|Location) + (1\|Year) | 0.017 | 0.406 | 3191.43 | 1.65E-11 |

Table 4. Correlations of prey proportions by taxonomic order to $PS_i$ values of Salish Sea *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 1,083 samples from groups with >5 samples. Data are organized by correlation value.

| Order | rho | p | Number of occurrences |
|---|---|---|---|
| Chimaeriformes | -0.62 | < 0.001 | 28 |
| Rajiformes | -0.52 | 0.002 | 32 |
| Scorpaeniformes | -0.50 | < 0.001 | 132 |
| Perciformes | -0.48 | < 0.001 | 194 |
| Batrachoidiformes | -0.40 | < 0.001 | 82 |
| Pleuronectiformes | -0.38 | < 0.001 | 154 |
| Adult Salmoniformes | 0.27 | < 0.001 | 595 |
| Clupeiformes | 0.24 | < 0.001 | 538 |
| Cephalopoda | 0.39 | < 0.001 | 163 |

Table 5. Correlations of prey proportions by species to $PS_i$ values of Salish Sea *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 1,083 samples from groups with >5 samples. Prey species with <3 total occurrences were discarded before analysis. Data are organized by correlation value.

| Species | Scientific name | Habitat | rho | p | Number of occurrences |
|---|---|---|---|---|---|
| Prickly Sculpin | Cottus asper | Demersal | -0.81 | 0.022 | 7 |
| Wolf-eel | Anarrhichthys ocellatus | Demersal | -0.73 | 0.015 | 10 |
| Snake Prickleback | Lumpenus sagitta | Benthopelagic | -0.72 | < 0.001 | 24 |
| Dover Sole | Microstomus pacificus | Demersal | -0.69 | 0.016 | 11 |
| Pacific Sand Lance | Ammodytes hexapterus | Benthopelagic | -0.66 | 0.004 | 17 |
| Spotted Ratfish | Hydrolagus colliei | Demersal | -0.62 | < 0.001 | 28 |
| Longfin Smelt | Spirinchus thaleichthys | Benthopelagic | -0.62 | 0.008 | 17 |
| English Sole | Parophrys vetulus | Demersal | -0.53 | < 0.001 | 39 |
| Pacific Staghorn Sculpin | Leptocottus armatus | Demersal | -0.48 | < 0.001 | 76 |
| Starry Flounder | Platichthys stellatus | Demersal | -0.47 | 0.002 | 38 |
| Northern Anchovy | Engraulis mordax | Pelagic-neritic | -0.45 | 0.006 | 35 |
| Lingcod | Ophiodon elongatus | Demersal | -0.45 | 0.030 | 23 |
| Shiner Surfperch | Cymatogaster aggregata | Demersal | -0.45 | < 0.001 | 112 |
| Surf Smelt | Hypomesus pretiosus | Benthopelagic | -0.44 | 0.025 | 25 |
| Big Skate | Beringraja binoculata | Demersal | -0.41 | 0.030 | 27 |
| Plainfin Midshipman | Porichthys notatus | Demersal | -0.40 | < 0.001 | 82 |
| Northern Smoothtongue | Leuroglossus schmidti | Bathypelagic | -0.40 | 0.042 | 25 |
| Walleye Pollock | Gadus chalcogrammus | Benthopelagic | -0.26 | < 0.001 | 228 |
| Pacific Hake | Merluccius productus | Pelagic-neritic | 0.12 | 0.048 | 280 |
| Juvenile sockeye salmon | Oncorhynchus nerka | Pelagic-oceanic | 0.22 | < 0.001 | 170 |
| Pacific Herring | Clupea pallasii pallasii | Pelagic-neritic | 0.29 | < 0.001 | 498 |
| Speckled Sanddab | Citharichthys stigmaeus | Demersal | 0.34 | 0.02 | 48 |
| Adult sockeye salmon | Oncorhynchus nerka | Pelagic-oceanic | 0.36 | < 0.001 | 179 |
| Adult pink salmon | Oncorhynchus gorbuscha | Demersal | 0.38 | < 0.001 | 218 |
| Pacific Red Octopus | Octopus rubescens | Benthic | 0.53 | < 0.001 | 128 |
| Eulachon | Thaleichthys pacificus | Pelagic-neritic | 0.61 | < 0.001 | 23 |

Table 6. Correlations of prey proportions by taxonomic order to $PS_i$ values of Salish Sea female *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 498 samples from groups with >5 samples. Data are organized by correlation value.

| Species | rho | p | Number of occurrences |
|---|---|---|---|
| Scorpaeniformes | -0.55 | < 0.001 | 76 |
| Perciformes | -0.45 | < 0.001 | 121 |
| Pleuronectiformes | -0.44 | < 0.001 | 70 |
| Batrachoidiformes | -0.41 | 0.013 | 35 |
| Clupeiformes | 0.39 | < 0.001 | 232 |
| Cephalopoda | 0.40 | 0.001 | 63 |

Table 7. Correlations of prey proportions by species to $PS_i$ values of Salish Sea female *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 498 samples from groups with >5 samples. Prey species with <3 total occurrences were discarded before analysis. Data are organized by correlation value.

| Species | Scientific name | Habitat | rho | p | Number of occurrences |
|---|---|---|---|---|---|
| Blackbelly Eelpout | Thaleichthys pacificus | Bathydemersal | -0.89 | 0.012 | 6 |
| Pacific Sand Lance | Ammodytes hexapterus | Benthopelagic | -0.78 | 0.017 | 8 |
| Longfin Smelt | Spirinchus thaleichthys | Benthopelagic | -0.78 | 0.007 | 10 |
| Pacific Sandfish | Trichodon trichodon | Demersal | -0.77 | 0.021 | 8 |
| Lingcod | Ophiodon elongatus | Demersal | -0.74 | 0.008 | 11 |
| Snake Prickleback | Lumpenus sagitta | Benthopelagic | -0.61 | 0.030 | 12 |
| Pacific Staghorn Sculpin | Leptocottus armatus | Demersal | -0.55 | < 0.001 | 46 |
| Plainfin Midshipman | Porichthys notatus | Demersal | -0.41 | 0.013 | 35 |
| Shiner Surfperch | Cymatogaster aggregata | Demersal | -0.35 | 0.002 | 74 |
| Juvenile coho salmon | Oncorhynchus kisutch | Demersal | -0.33 | 0.017 | 50 |
| Walleye Pollock | Gadus chalcogrammus | Benthopelagic | -0.32 | 0.002 | 91 |
| Adult sockeye salmon | Oncorhynchus nerka | Pelagic-oceanic | -0.27 | 0.037 | 61 |
| Adult pink salmon | Oncorhynchus gorbuscha | Demersal | 0.30 | 0.004 | 88 |
| Pacific Herring | Clupea pallasii pallasii | Pelagic-neritic | 0.40 | < 0.001 | 214 |
| Pacific Red Octopus | Octopus rubescens | Benthic | 0.55 | < 0.001 | 52 |
| Eulachon | Thaleichthys pacificus | Pelagic-neritic | 0.68 | 0.035 | 9 |

Table 8. Correlations of prey proportions by taxonomic order to $PS_i$ values of Salish Sea male *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 647 samples from groups with >5 samples. Data are organized by correlation value.

| Order | rho | p | Number of occurrences |
|---|---|---|---|
| Chimaeriformes | -0.70 | < 0.001 | 21 |
| Rajiformes | -0.53 | 0.005 | 26 |
| Perciformes | -0.52 | < 0.001 | 72 |
| Batrachoidiformes | -0.41 | 0.004 | 46 |
| Scorpaeniformes | -0.40 | 0.002 | 55 |
| Petromyzontiformes | -0.34 | 0.088 | 25 |
| Pleuronectiformes | -0.30 | 0.005 | 83 |
| Clupeiformes | 0.12 | 0.044 | 305 |
| Adult Salmoniformes | 0.33 | < 0.001 | 316 |
| Cephalopoda | 0.43 | < 0.001 | 99 |

Table 9. Correlations of prey proportions by species to $PS_i$ values of Salish Sea male *Phoca vitulina*. Only correlations with $p < 0.05$ are shown. A negative rho value indicates a positive correlation with specialization. Analysis represents 647 samples from groups with >5 samples. Prey species with <3 total occurrences were discarded before analysis. Data are organized by correlation value.

| Species | Scientific name | Habitat | rho | p | Number of occurrences |
|---|---|---|---|---|---|
| Snake Prickleback | *Lumpenus sagitta* | Benthopelagic | -0.73 | 0.009 | 11 |
| English Sole | *Parophrys vetulus* | Demersal | -0.70 | 0.002 | 16 |
| Spotted Ratfish | *Hydrolagus colliei* | Demersal | -0.70 | < 0.001 | 21 |
| Shiner Surfperch | *Cymatogaster aggregata* | Demersal | -0.64 | < 0.001 | 37 |
| Surf Smelt | *Hypomesus pretiosus* | Benthopelagic | -0.62 | 0.020 | 13 |
| Northern Smoothtongue | *Leuroglossus schmidti* | Bathypelagic | -0.58 | 0.007 | 19 |
| Plainfin Midshipman | *Porichthys notatus* | Demersal | -0.41 | 0.004 | 46 |
| Pacific Staghorn Sculpin | *Leptocottus armatus* | Demersal | -0.38 | 0.040 | 29 |
| Walleye Pollock | *Gadus chalcogrammus* | Benthopelagic | -0.23 | 0.007 | 136 |
| Pacific Hake | *Merluccius productus* | Pelagic-neritic | 0.17 | 0.022 | 171 |
| Pacific Herring | *Clupea pallasii pallasii* | Pelagic-neritic | 0.20 | 0.001 | 283 |
| Juvenile sockeye salmon | *Oncorhynchus nerka* | Pelagic-oceanic | 0.29 | 0.005 | 92 |
| Adult pink salmon | *Oncorhynchus gorbuscha* | Demersal | 0.39 | < 0.001 | 129 |
| Adult sockeye salmon | *Oncorhynchus nerka* | Pelagic-oceanic | 0.53 | < 0.001 | 117 |
| Pacific Red Octopus | *Octopus rubescens* | Benthic | 0.56 | < 0.001 | 75 |
| Eulachon | *Thaleichthys pacificus* | Pelagic-neritic | 0.70 | 0.007 | 13 |

## Figures

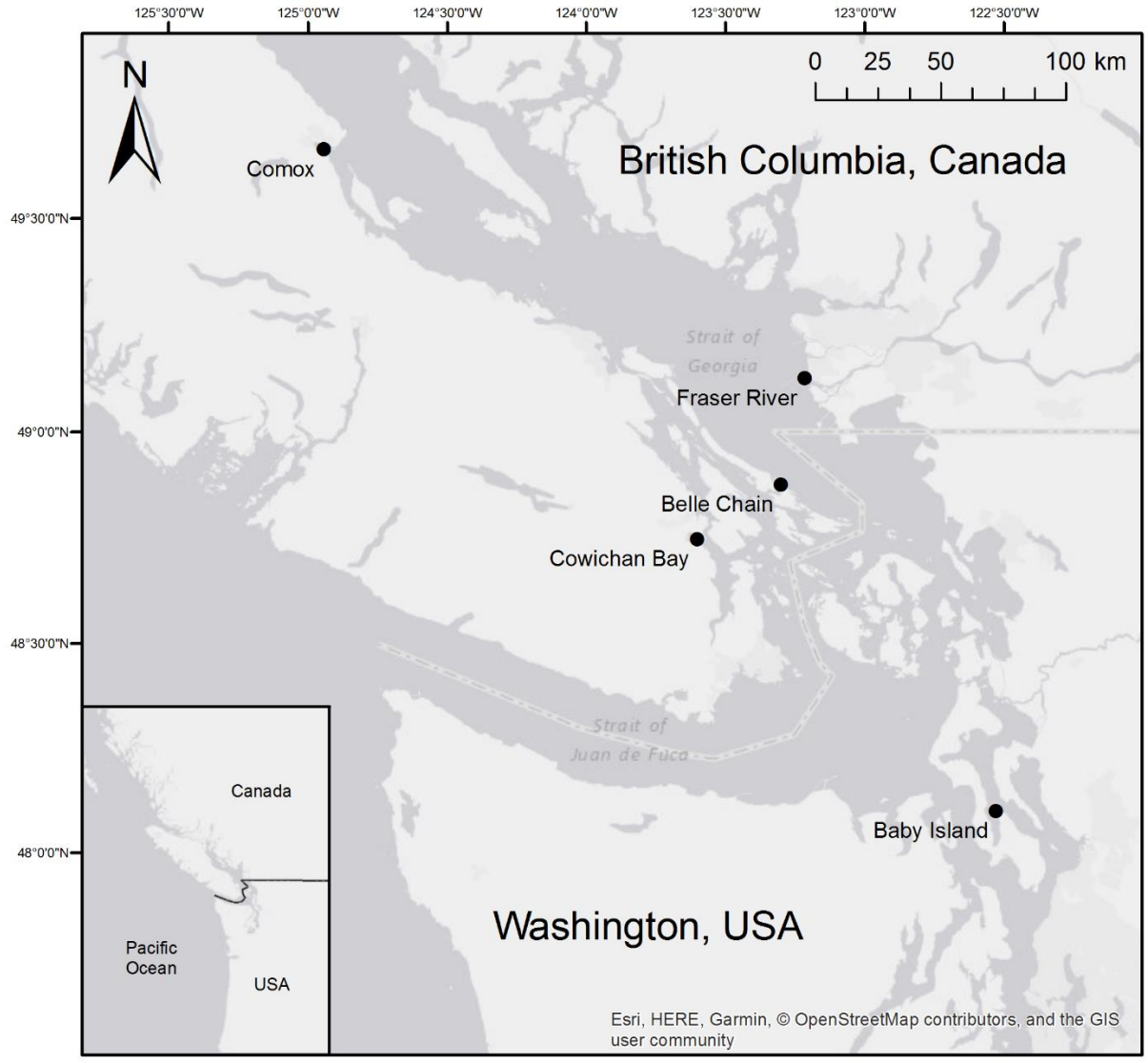



Figure 1. Haul-out sites from where *Phoca vitulina* scat was collected in the Salish Sea. Collection locations are indicated by black dots and labeled with the name used throughout this paper.

A) B)

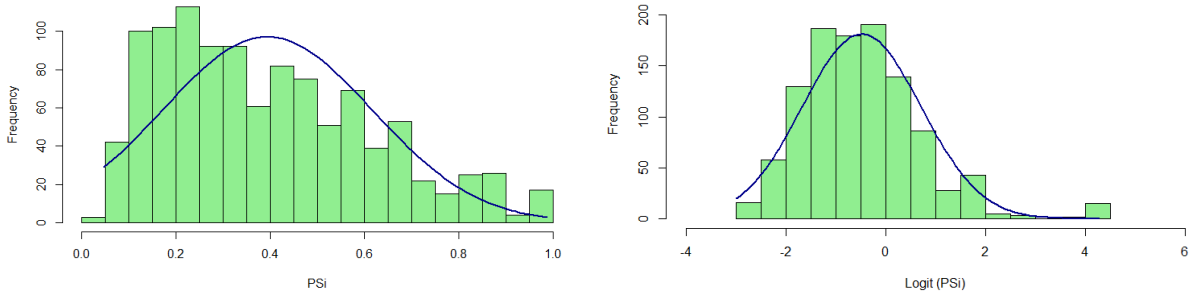



Figure 2. Histogram of $PS_i$ values derived from *Phoca vitulina* scat with kurtosis curve and normal QQ plot for all samples with successful sex determination (n = 1,145 scat samples) (A) untransformed $PS_i$ and B) logit transformed $PS_i$.

A) B)

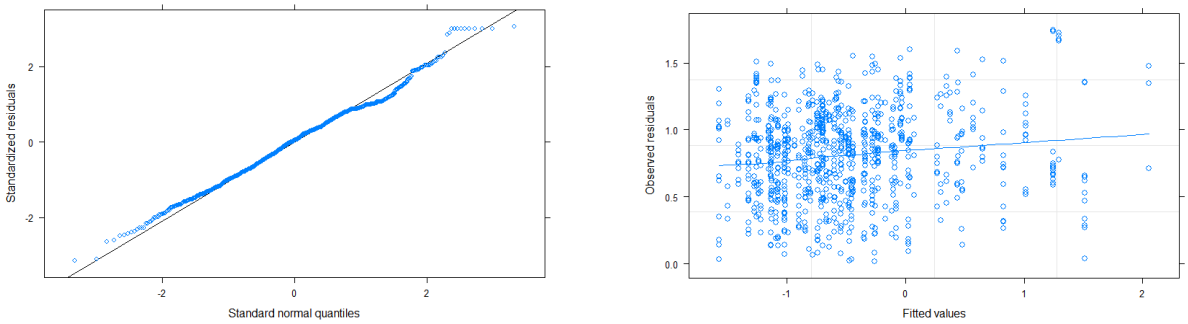



Figure 3. Analysis of fit of the model Sex*Month + (1|Sample Size) + (1|Location) + (1|Year) for *Phoca vitulina* groups for analysis with >5 samples (n = 1,083 scat samples). A) Standard normal quantiles versus standardized residuals. B) Fitted values versus observed residuals.

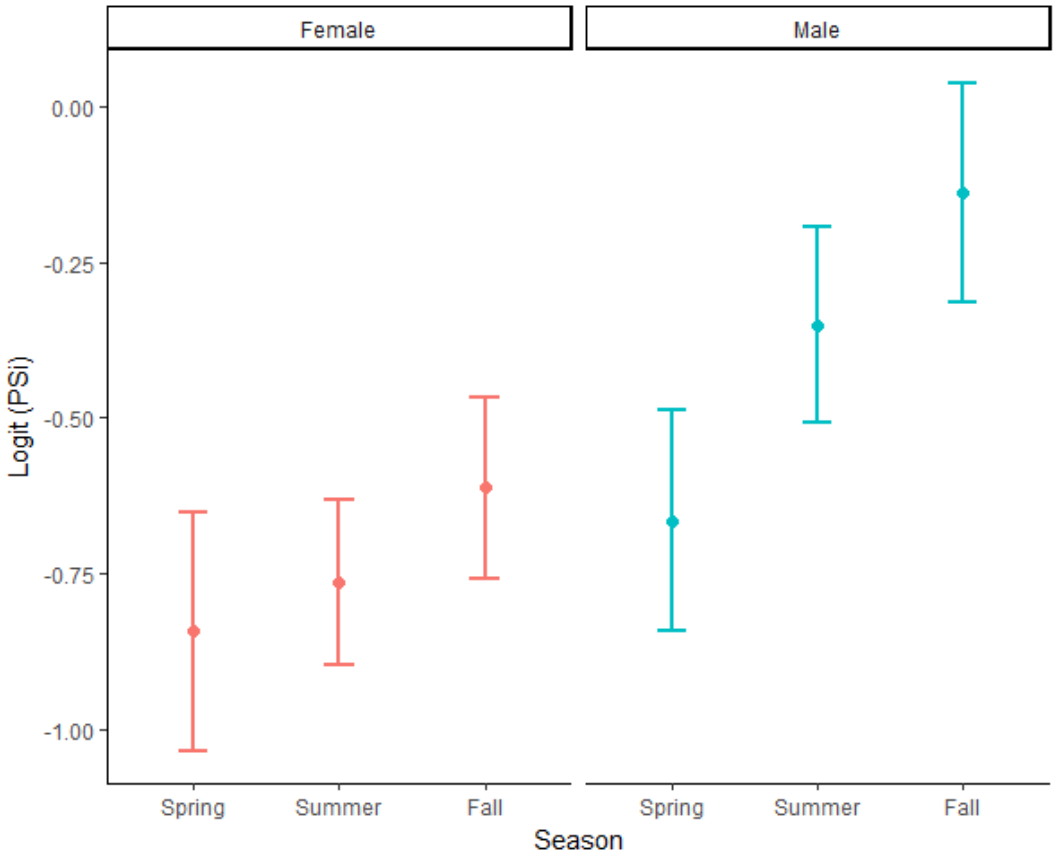



Figure 4. Logit transformed average $PS_i$ values with 95% confidence intervals of all *Phoca vitulina* scat from groups with >5 samples (n = 1,083 scat samples). Average $PS_i$ was calculated for each group. Groups were then split be sex and lumped by season. Spring = April, May; Summer = June, July, August; Fall = September, October, November. A lower value indicates more specialization.

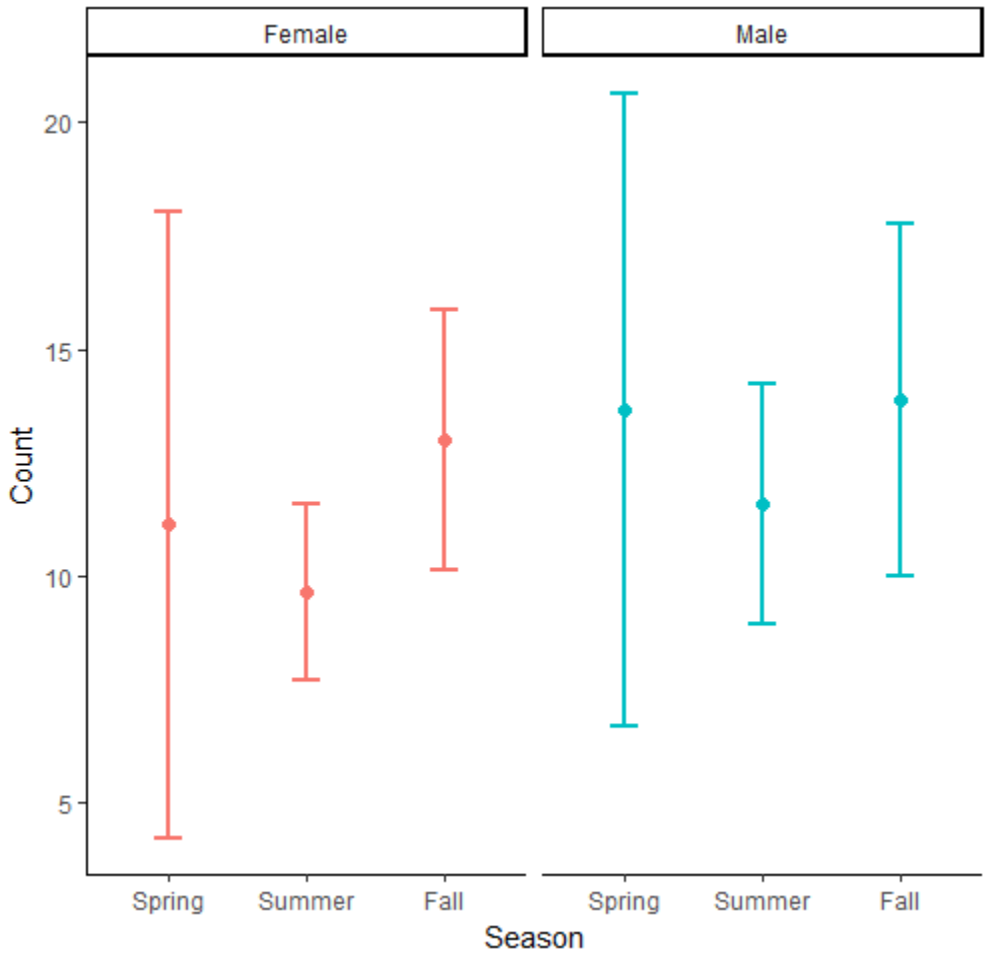



Figure 5. Average sample size of *Phoca vitulina* groups for analysis with >5 samples (n = 1,083 scat samples). Groups were then split be sex and lumped by season. Spring = April, May; Summer = June, July, August; Fall = September, October, November.

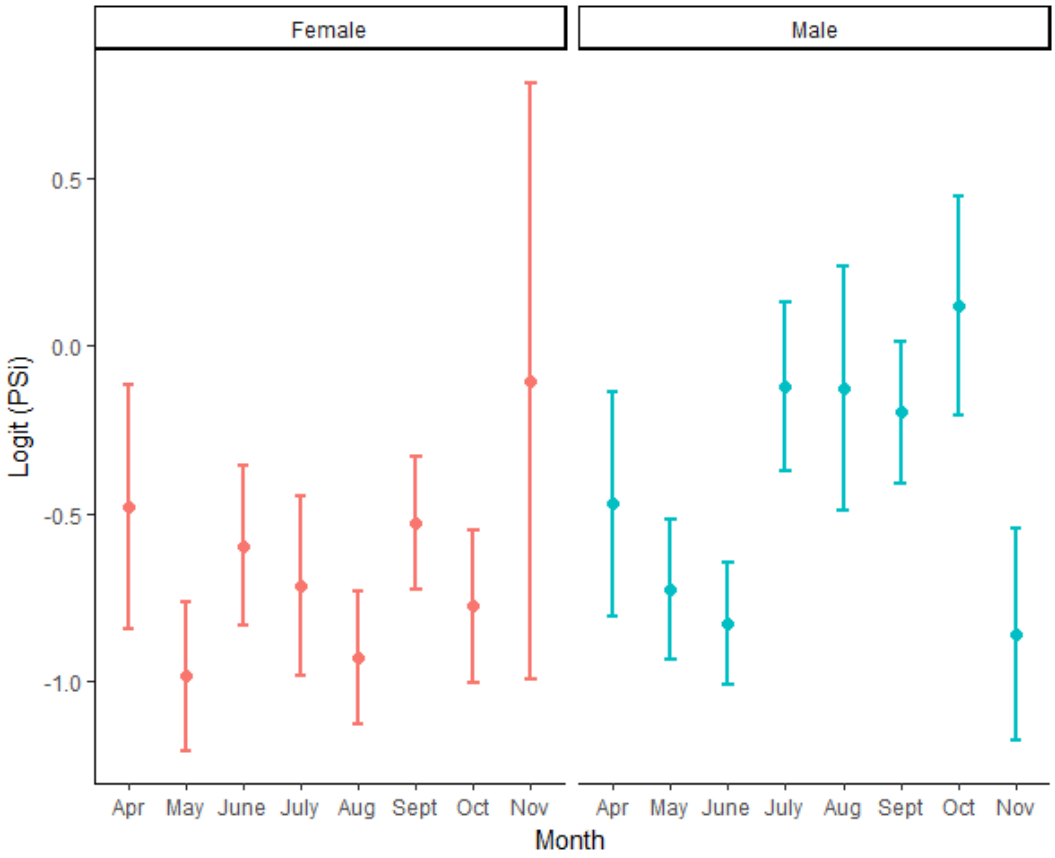



Figure 6. Logit transformed average $PS_i$ values with 95% confidence intervals of all *Phoca vitulina* scat from groups with >5 samples (n = 1,083 scat samples). Average $PS_i$ was calculated for each group. Groups were then split be sex and lumped by Month. The left graph shows females, the right graph shows males. A lower value indicates more specialization.

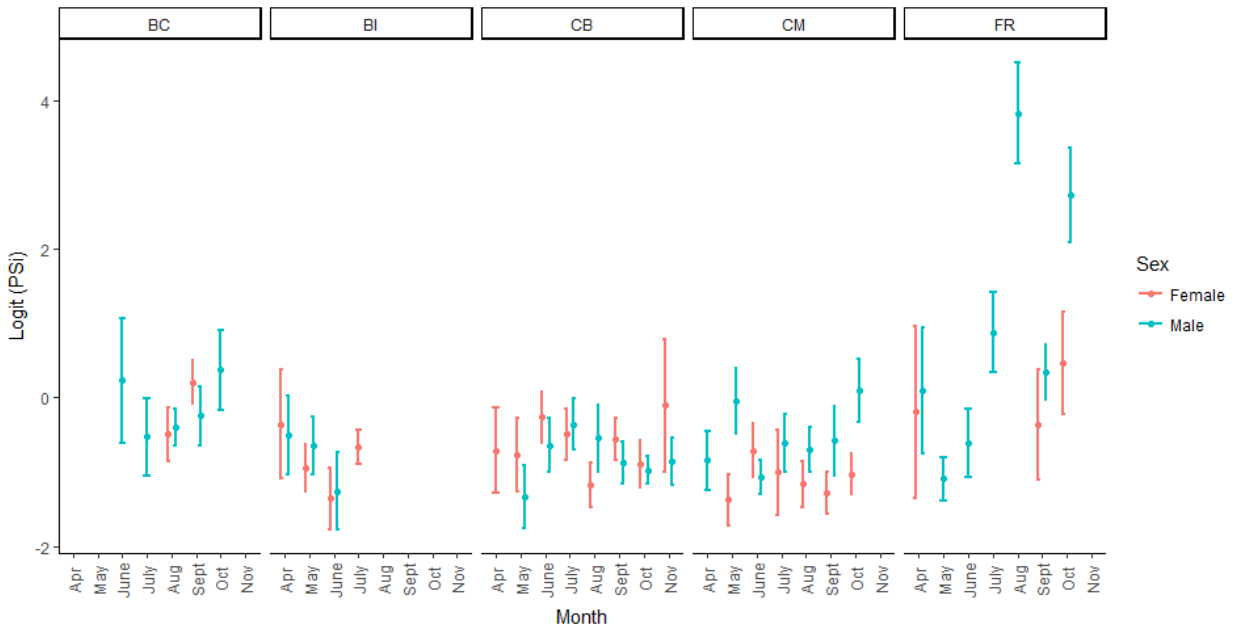



Figure 7. Logit transformed average $PS_i$ values and 95% confidence intervals for all *Phoca vitulina* scat from groups with >5 samples (n = 1,083 scat samples). Average $PS_i$ was calculated for each group. Groups were then split by sex and location and then lumped by month. A lower value indicates more specialization. BC = Belle Chain, BI = Baby Island, CB = Cowichan Bay, CM = Comox, FR = Fraser River.

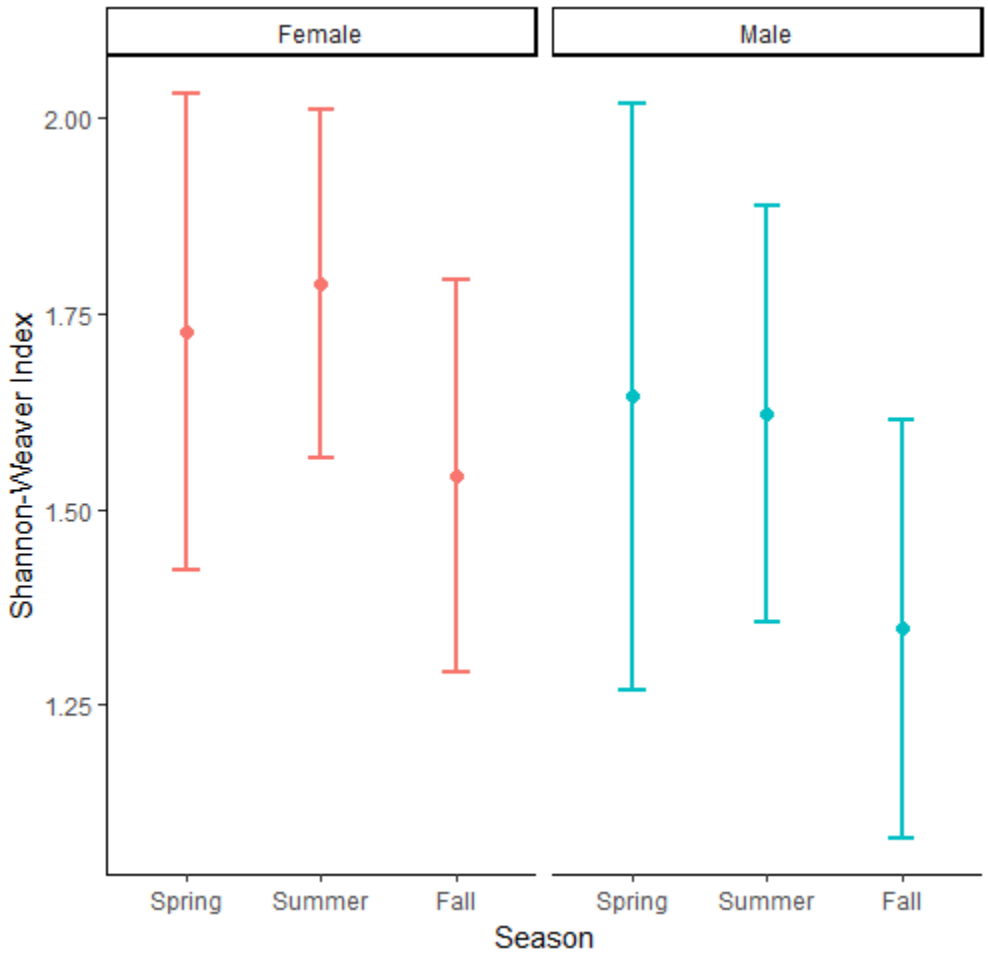
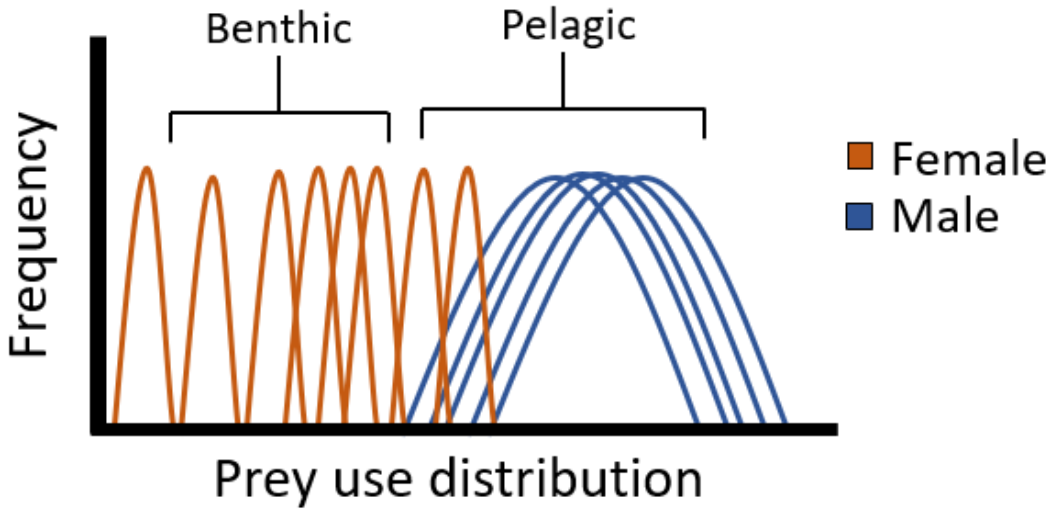



Figure 8. Shannon-Weaver index for each *Phoca vitulina* group for analysis with >5 samples (n = 1,083 scat samples). Prey proportions from each scat were averaged within each group. The Shannon-Weaver index was then calculated for each group using the average proportions. Groups were then split by sex and then lumped by season. Spring = April, May; Summer = June, July, August; Fall = September, October, November.

A)




B)

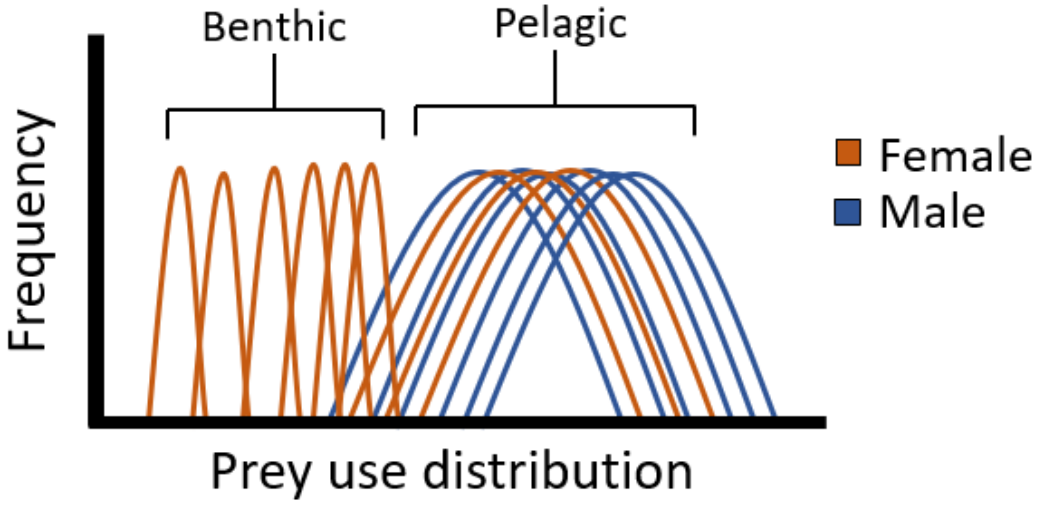



Figure 9. Model of resource distribution of *Phoca vitulina* in the Salish Sea based on my results. This theoretical schematic demonstrates the smaller within-individual but broader within-group resource use of female *P. vitulina* with regards to benthic prey in the Salish Sea. A) The relationship in the spring (more specialist behavior). B) The relationship in the summer and fall (less specialist behavior).

**Supplementary Material**

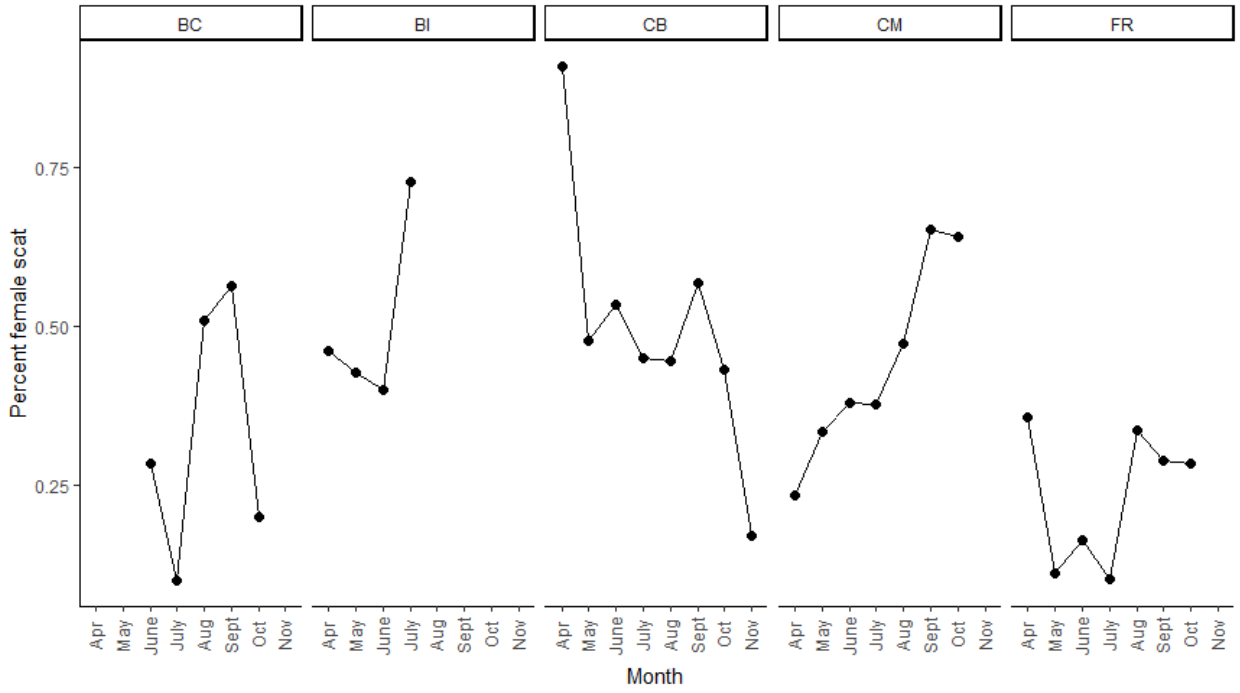



Figure S1. Proportion of female *Phoca vitulina* scat identified during each month at each site. If no dot is present, no scat were collected at the site in that month. Proportions were calculated by pairing male and female groups for analysis from the same month, location, and year. The number of samples in the female group was divided by the total number of samples in both the female and male group.