The Impacts of Sex-Specific Diets of a Marine Predator on Ecosystem Models

By

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ABSTRACT

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Ecosystem modeling is an increasingly popular method to understand how organisms within ecosystems interact, relying on robust data incorporating important inter- and intraspecies interactions to predict ecosystem changes. However, no study has included sex-specific intrapopulation variation in an ecosystem model. In the well-studied Salish Sea, harbor seals (*Phoca vitulina*) are an important marine mammal that have significant sex-specific diet variability, which I hypothesized would have indirect effects on other functional groups in the region. Male harbor seals consume a higher diet proportion of salmon, while female harbor seals consume a higher proportion of herring and small demersal fish. I created an ecosystem model of the Salish Sea using the Ecopath framework and calculated predictions of the overall mixed trophic impact that male and female harbor seals each exert on other functional groups. To assess the importance of the sex-specific diets on the indirect impacts, I varied the sex ratio of the harbor seals to simulate the range of sex ratios present spatiotemporally in the Salish Sea. Changing sex ratios also allows me to assess how mixed trophic impacts respond to changing predation pressure from each sex. Male harbor seals were predicted to have a strong negative impact on raptors and a strong positive impact on piscivorous seabirds, neither of which are part of the harbor seal diets, while female harbor seals had a very low impact on these groups. There was a negligible difference in impact on herring despite having the largest difference in diet contribution between male and female harbor seals. Male harbor seals consistently exerted a stronger negative impact on Pacific salmon than females, even when females were predicted to consume a greater proportion of Pacific salmon production. The results suggest that indirect

trophic cascades contribute to harbor seal sex-specific impacts on other groups, rather than predation alone. These sex-specific impacts may be lost in models that do not account for sex-specific diet variation within the harbor seal population in the Salish Sea.

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INTRODUCTION

Fish stocks, once thought to be undepletable by fishing (Mace, 1997), are now the focus of much research after many stocks declined from overharvesting in the 20th century (Mullon et al., 2005). Managing fish stocks became a priority for governments as fisheries suffered and the benefits of fishery management policies became clear (Hilborn et al., 2020; Worm et al., 2009; Zwolinski and Demer, 2012). Fishery policies initially focused on increasing one species or stock, but recent access to new methods and data have allowed fishery managers to begin focusing instead on how small changes to the ecosystem could impact seemingly unrelated fish stocks (Daniels and Walker, 1996; Slocombe, 1993). Ecosystem-based fishery management makes use of these new methods and is improving the understanding of how interspecific and intraspecific competition permeates marine food webs (Crowder and Norse, 2008). Ecosystem models have well defined interspecific interactions; however, many miss intraspecific interactions that have important impacts in the community, such as individual foraging specialization and intraspecific competition (Fogarty, 2014; Largaespada et al., 2012).

Ecosystem models are extremely powerful in their prediction abilities but are limited by their complexity and inherent assumptions in the modeling process (Christensen and Walters, 2004). It is impossible to create a comprehensive model that represents all components in an ecosystem, hence different models are created to address different types of questions with different assumptions, limitations, and biases (Christensen and Walters, 2004; Fogarty, 2014; Werner et al., 2007). One such model framework is Ecopath with Ecosim (EwE), an ecosystem-based model that takes a mass-balancing approach to show the relationship between predation, fishing, and population biomass (Christensen and Walters, 2004; Christensen et al., 2008). EwE focuses on defining interactions between functional groups (defined as species or groups of species occupying a similar niche). Defining these functional groups is sometimes complicated when accounting for known intraspecies variability. Intraspecies variability is usually captured through the use of age-structured functional groups, where changes in diet come from ontogenetic changes, and modeling ecotypes as different functional groups to capture differences between environmentally separated populations (Harvey et al., 2012; Koehn et al., 2016; Li et al., 2010). However, they rarely account for intrapopulation diet variation that occurs for other reasons, such as sex-based dietary differences caused by sexual dimorphism or individual specialization.

Sex-specific diet variation has been observed in many species and can be caused by differences in morphology, behavior, and habitat (Shine, 1989). Terrestrial species such as white-tailed deer (*Odocoileus virginianu*) and American bison (*Bison bison*) demonstrate sex-specific diets attributed to their sexual dimorphism (Beier, 1987; Berini and Badgley, 2017). In many marine mammal species, females are smaller than males, which can cause significant differences in diet between the sexes. In grey seals (*Halichoerus grypus*) there are significant differences in how males and females meet their respective caloric requirements (Beck et al., 2007). Additionally, the diets of juvenile grey seals closely resemble that of adult females, possibly because they hunt with their mothers while maturing (Beck et al., 2005). Southern elephant seals (*Mirounga leonina*), another sexually dimorphic species, also have sexual differences in diet as well as different levels of specialization within the sexes (Lewis et al., 2006).

Marine mammals are of special interest because of their unique interactions with other protected or declining species and competition with humans for marine resources (Chasco et al., 2017). The impact of marine mammals on economically important fishes has increased drastically since 1972, attributed to recovering populations caused by the Marine Mammal

Protection Act (Baum and Worm, 2009; Roman et al., 2013). One of the most successful marine mammal recoveries is that of the harbor seal (*Phoca vitulina*) in the Northeast Pacific Ocean, which is believed to have reached population carrying capacity in the late 1990s (Jeffries et al., 2003). However, it is unknown how the rapid increase in harbor seal population has impacted culturally important prey fishes (e.g. Pacific salmon (*Oncorhynchus* spp.)) and prey fishes in recovery (e.g. herring (*Clupea pallasii*)) and increased competition with other marine mammals still in recovery (e.g. Orcas (*Orcinus orca*)) (Marshall et al., 2016; Olesiuk, 2009).

While harbor seals are considered generalist predators, they have a diverse diet that is paired with significant spatial and temporal variation (Teilmann and Galatius, 2018). Harbor seals exhibit limited size dimorphism (Coltman et al., 1998), suggesting that there would be only small differences in prey consumption between the sexes. However, recent evidence from stable isotope analysis, scat analysis for hard parts and DNA, and fatty acid analysis suggests that harbor seals in the Salish Sea comprise a collection of specialists with significant differences in specialization between male and female harbor seals (Bjorkland et al., 2015; Bromaghin et al., 2013; Lance et al., 2012; Schwarz et al., 2018; Voelker et al., 2020). The level of specialization is variable between male and female harbor seals, with female harbor seals tending to be more generalist than their male counterparts. Male harbor seals have a larger part of their diet composed of Pacific salmon, while females tend to consume more herring and demersal fish (Schwarz et al. 2018, Figure 1). The specific diet composition for each sex varies spatially and temporally (Schwarz et al., 2018), suggesting that harbor seal sex ratio, location, and season could all modify the ecological impact that each sex and thus the species as a whole has on other functional groups.

If the harbor seal sex ratio was consistent across the model domain, it could be reasonable to assume an average harbor seal diet. Previous models of the Salish Sea employed this average diet from all prey sources across the regional harbor seal populations (Harvey et al., 2012; Li et al., 2010; Preikshot et al., 2013). However, the significant spatial and temporal variation in harbor seal sex ratio, which can vary from 12% female to 90% female within the Salish Sea (Allegue et al., 2020; Schwarz et al., 2018), shows that this assumption may not be practicable. Because of the significantly different diets exhibited by male and female harbor seals, one would expect the sexes to have very different ecological impacts on groups that they consume at different proportions. Seasonally variable or consistently skewed sex ratios in localized regions or for long time periods within the domain could lead to alternative ecological impacts that may be underrepresented by an ecosystem model that does not take sex-variable diets or changing sex ratios into account.

The aim of my study is to examine how intraspecific, sex-based variability in the diets of a marine predator affects ecosystem model predictions of impacts on prey populations and how those impacts change with variable sex ratios. To my knowledge, this is the first time that Ecopath will be used to model sex-specific trophic interactions. To illustrate this concept, I will use the sex-based intraspecific variability of harbor seal diet in the southern Salish Sea to produce an ecosystem model that describes how changes in diet between otherwise equal groups impact consumption rates and prey populations. The Ecopath model I built focuses on the southern Salish Sea because the results can be compared to pre-existing Ecopath models of the same area that did not include intraspecific diet variation.

METHODS

The study system for this model was the central and southern Salish Sea, which includes the inland waters of Washington State, US, and southern British Columbia, Canada, specifically the Strait of Juan de Fuca, the San Juan Islands, and the Puget Sound (Figure 2). I selected this region based on the spatial distribution of the existing sex-specific harbor seal diet data and because many ecosystem models have previously been developed for this area. Consequently, other model parameters were easily accessible, ensuring that the model I produce with the inclusion of intraspecific variation is comparable to previously published studies. I chose 2011 as the study year because data are readily available for that year and would allow for ease of data gathering and comparison with contemporary models. Across the whole model domain (the southern Salish Sea), harbor seals maintain a roughly even sex ratio (Jeffries et al., 2003); however, within the model domain, the sex ratio varies between 12-90% females by season and haul out site (Allegue, 2017; Schwarz et al., 2018).

To explore the role of sex-specific harbor seal diet differences and their impacts on Pacific salmon and their population levels, I used the Ecopath model framework (Christensen and Walters, 2004; Christensen et al., 2008). This model represents a mass-balanced, instantaneous snapshot of the ecosystem. The model is comprised of functional groups that serve as representations for individual species or groupings of closely related species. All the energy inputs for a functional group (through consumption) are equal to all the energy output of that group, through production, predation, respiration, or excretion. Ecopath relies on two principal, master equations. The first equation describes how the production of each functional group and is calculated as:

$$P_i = B_i + M2 + C_i + E_i + BA_i + \mathrm{M0}$$

Where P_i is the production of group *i*; B_i, the biomass; M2, the mortality from predation; C_i, the fishery take; E_i, the emigration; BA_i, the biomass accumulation (accounts for any increase or decrease in standing biomass during the modeling period); and M0, other mortality. The second equation describes the mass-balanced portion of the framework:

$$B_i \times PB_i \times EE_i = C_i + \sum_{j=1}^{n} B_j \times QB_j \times DC_{ji}$$

Where B_i refers to the biomass of the consumed group; PB_i, the production to biomass ratio; EE_i, the ecotrophic efficiency (i.e. the proportion of the total production consumed by predators or caught by fisheries); C_i, the fishery take; *n*, the number of functional groups in the model; B_j, the biomass of the consuming group; QB_j, the consumption to biomass ratio of the consuming group; and DC_{ij}, which represents a diet matrix that includes the proportional diet content of prey *i* in the diet of predator *j*. This model framework requires that three of four main parameters (B, PB, QB, and EE) be defined for each functional group. The model then solves *n* number of linear equations to solve for the missing parameter of each functional group, which is most commonly the ecotrophic efficiency because no field method exists for its estimation.

Since there are many modeling efforts focused on the Salish Sea (Harvey et al., 2012; Howard et al., 2013; Li et al., 2010; Preikshot et al., 2013), collaboration with other modelers and sharing of data were necessary for results to be comparable between models and to previous work. As such, many of the parameters for my model were sourced from personal communication with modelers or from their published research (Tables 1 - 3).

Isaac Kaplan and Hem Morzaria-Luna at the National Oceanic and Atmospheric Administration (NOAA) graciously provided functional groupings, biomass, and diet data from a more complex model framework (Atlantis; (Fulton et al., 2004) than the one that I am parameterizing (Table 1, Table 3). Hence, I simplified some functional groups (e.g., combining stocks of Pacific salmon and herring groups into species level groups because of limitations in the sex-differentiated harbor seal diet information). I also made other groups more complex (e.g., the gadoid group was split into cod (*Gadus macrocephalus*), Walleye pollock (*Gadus chalcogrammus*), and hake (*Merluccius productus*) because there is a large variation between male and female harbor seal consumption of hake). Separating functional groups allowed a finer scale assessment of the impact of sex-based diet differences. The final model structure contained 48 functional groups ranging from phytoplankton to humpback whales (*Megaptera novaeangliae*) with male and female harbor seals modelled as separate functional groups (Table 1). Fishery data for 30 different fleet types were also sourced from the PacFin database for 2011 (the target year for the model), courtesy of Hem Morzaria-Luna. The Ecopath specific parameters PB, QB, and some EE values were taken from a published Ecopath model (Harvey et al., 2012) (Table 1 and Table 2). Given that their functional groups were not the same as in my model, I calculated means of P/B and Q/B weighted by each group's biomass for any groups that were collapsed into a single group.

The sex-specific diet data for harbor seals comes from molecular analysis of scat (Schwarz et al., 2018) (Table 3). These data were collected in the central and northern Salish Sea but are similar to diets used for harbor seals in other models in the region (Fulton et al., 2004; Harvey et al., 2012; Li et al., 2010). Thus, it is reasonable to extrapolate the sex diets across the domain range. The diet data reported was averaged across season and site to provide a more generalizable diet composition for male and female harbor seals. The study by Schwarz et al. (2018) also provided the range of haul-out site sex ratios, which sets the bounds of the sex ratio testing for this model. The sex ratios reported ranged from 12% to 79% females, which were extended to 10% to 90%. While the extreme sex ratios reported by Allegue et al. (2017) and Schwarz et al. (2008) would be unrealistic for the whole model domain, there could be small localities with such skewed sex ratios. Therefore, by including such extreme values in my model, one can gain insight into localized community effects of female and male harbor seals.

The final parameters needed for the model were for the marine mammal groups, which I obtained from a published Ecopath model of the region (Li et al., 2010). These parameters are important because harbor seals, California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), and orcas all consume Chinook salmon (*Oncorhynchus tshawytscha*) (Table 1 and Table 2). Because the model domain of Li et al. (2010) partially overlaps with my model domain, I assumed their values were also representative of the southern Salish Sea.

All model parameters were input into the EwE software. Balancing of the model followed both the accepted guidelines for model balancing (Christensen et al., 2008; Heymans et al., 2016) and pre-balance diagnostics for increasing the rigor of ecological modeling (Link, 2010) (See Supplementary Material). This model, hereafter referred to as the base model, uses the parameters described in Tables 1 - 3.

The EwE software package provides a Monte Carlo sampling method to generate various balanced models by sampling input parameters from a normal distribution with the base model parameter as the mean and a coefficient of variation of 10%. I used this tool to randomly sample the main 4 inputs, B, P/B, Q/B, and EE, for each functional group and produced 100 viable Ecopath models using the base model as the mean parameter values. If any generated model was not balanced, it was discarded, and a new model was generated. These models describe a range of viable ecosystem states to provide some variation given that Ecopath is a deterministic model. The diet proportions of male and female harbor seals in the model were not varied because those are key parameters of interest. Variability in the diet proportion would decrease the ability to attribute differences in impact to sex ratio and not to random variation in diet proportions. The fishery take was also not varied as it is more reliable than any of the parameter estimates included in the model.

The 100 generated Ecopath models were imported into R (R Development Core Team, 2019) using the Rpath package (Aydin, 2016) to generate models with variable sex ratios. This package is the R implementation of the Ecopath algorithm. An R script took each of the 100 models and generated 17 new models with the harbor seal sex ratio varied from 10% female to 90% female in 5% increments. The total biomass of the combined sexes within each model did not change, only the allocation between sexes. Given that there are no data on differential predation on male and female harbor seals, the proportion of male and female harbor seals in the diets of their predators (six-gill sharks (*Hexanchidae griseus*) and transient orcas) was adjusted to be relative to the sex ratio of harbor seals in each model. A total of 1,700 models were generated with all these specifications.

The impact of each harbor seal sex was assessed using a tool built into the EwE software package and included in the Rpath package: Mixed Trophic Impact (MTI). MTI is the measure of the direct and indirect effects that a group has on all other groups in the model (Ulanowicz and Puccia, 1990). MTI is calculated using a matrix of interactions of size *n* x *n*, where each element is the interaction of the impacted group (*j*) and the impacting group (*i*):

$$MTI_{i,j} = \left(1 - \left(DC_{i,j} - FC_{i,j}\right)\right)^{-1} - 1$$

where $DC_{i,j}$ is a matrix of the proportional contribution of prey *i* to the diet of predator *j* and $FC_{i,j}$ is a matrix of the proportion of predation on prey *i* that is attributed to predator *j* (Ulanowicz and Puccia, 1990). MTI is bounded by -1, being an extreme negative impact, and 1, being an extreme positive impact. Impact in this context means that a small increase in the biomass term of the impacting group can have a positive or negative impact on the biomass of the impacted group (Christensen et al., 2008). Thus, the MTI value quantifies direct effects and indirect effects caused by trophic cascades in a system with many complex interactions, though this makes no attempt to determine what pathway creates those impacts.

The direct impacts of male and female harbor seals were measured by the percent production of a prey group that can be attributed to consumption by the male or female harbor seal group. The direct impact is calculated as follows:

$$\text{Direct Impact}_{i,j} = ((QB_j \times B_j) \times DC_{i,j}) \div (PB_i \times B_i)$$

where QB_j describes the consumption to biomass ratio of the consuming group; B_j, the biomass of the consuming group; $DC_{i,j,k}$, represents a diet matrix that includes the proportion of prey *i* that is in the predator j's diet; PB_i, the production to biomass ratio of the consumed group; B_j, the biomass of the consumed group.

By comparing the direct impact (% production consumed) and cumulative direct and indirect impact (MTI), I can infer the level of indirect control male and female harbor seals were exerting on a specific prey group. The level of indirect control allowed me to assess the importance of trophic cascades to the impact on a specific prey group. Sex-based impact variability is best compared at the sex ratio where male harbor seals and female harbor seals both consume similar proportions of the prey group production, because then both harbor seal groups would be assumed to have comparable direct impacts on the prey group. Therefore, the differences in male and female harbor seal MTI on that group may be attributed to indirect impacts.

I selected some groups for detailed analysis based on the largest differences in diet between male and female harbor seals (Pacific salmon, hake, and small demersal fish), as well as groups which composed a significant proportion of either sex's diet (herring). These groups were selected to best show the impacts of sex-specific diet and are also groups of significant ecological and economic concern.

RESULTS

The final balanced base model had 50 functional groups, which ranged in biomass from 0.001 tons/km^2 to 600.94 tons/km^2 (Figure 3). Male harbor seals had a calculated trophic level of 4.664, and female harbor seals had a calculated trophic level of 4.536. Figure 3 demonstrates the complexity of the modeled food web in the Salish Sea. Overall MTI for each group on all other functional groups was calculated from the first sampled model at the 50/50 sex ratio (Figure 4), and the overall average MTI of each impacting group was not unusual for their trophic level (Figure 5).

Male and female harbor seals impacted functional groups differently at the assumed 50/50 sex ratio (Table 4) and their impacts also varied differently in relation to biomass, and thus sex ratio. Male harbor seal impact on other groups ranged from -0.280 (raptors, consisting solely of the bald eagle, *Haliaeetus leucocephalus*) to 0.145 (transient orcas), and female harbor seal impact ranged from -0.147 (female harbor seals) to 0.141 (transient orcas). Eleven functional groups had differences in impact by male and female harbor seals greater than 0.01. The largest difference in MTI between male and female harbor seals was on the Raptor group (difference in impact of 0.3185; Table 4) with male harbor seals having a moderate negative impact and females having a weak positive impact though neither sex directly consumes raptors. The SkateRay group (*Raja rhina* and *Beringraja binoculata*) had the largest difference in MTI (difference in impact of 0.0778; Table 4) between male and female harbor seals when the impacted group was consumed by both sexes; males had a weak positive MTI and females had a strong positive MTI.

Male and female harbor seals each had an average MTI within expected limits for other functional groups of their trophic level (Figure 5). As expected, female harbor seals had their largest average MTI at a 90% sex ratio, and male harbor seals experienced their largest average MTI at a 10% sex ratio. Male harbor seals showed a slightly larger range in average MTI at the varying sex ratios, suggesting that sex ratio impacted male MTI more than it did female MTI (Figure 5).

Harbor seals, regardless of sex, had one of the highest impacts on Pink salmon (*Oncorhynchus gorbuscha*) out of any other salmon group. Combined, harbor seals were estimated to consume 35% to 43% of the total Pink salmon production (Figure 6B). Male harbor seals consumed more Pink salmon and thus impacted the species more than female harbor seals (Figure 6A-B). Both sexes had some of the strongest negative impacts on Pink salmon of any human or predator group in the model (Figure 6C).

Male and female harbor seals had different impacts on Coho salmon (*Oncorhynchus kisutch*) at all sex ratios (Figure 7A). When female harbor seals consumed similar proportions of Coho production as males (at a 60% - 70% female population), females had a much less negative impact or small positive impact on Coho salmon (Figure 7A-B). Male harbor seals had a more variable impact depending on sex ratio compared to female harbor seals, but the impact was consistently more negative than the impact of female harbor seals and many other groups in the model (Figure 7C).

Harbor seals had a very small impact on Chum salmon (*Oncorhynchus keta*) and Chinook salmon even though they both made up 5-8% of the harbor seal diet. Chum salmon consistently experienced a stronger negative impact from male harbor seals, even at sex ratios where female harbor seals consumed a larger proportion of Chum salmon production (Figure 8 A-B). However, the difference in male and female harbor seal MTI at all sex ratios was considered negligible (<0.01), and the MTI for both sexes was most similar at a 90% female sex ratio

(Figure 8A). Male harbor seals consumed the largest proportion of Chum salmon production at a sex ratio of 10%, but had a MTI at this sex ratio of only -0.002 (Figure 8A). Male and female harbor seals had a similar impact on Chinook salmon. Male harbor seals consumed the largest proportion of Chinook salmon production at a sex ratio of 10%, but had a MTI at this sex ratio of only 0.006 (Figure 9A-B). Male and female harbor seals also had a negligible difference in MTI (<0.01) on Chinook salmon at all sex ratios (Figure 9A). While females consumed less Chinook salmon than males, their impact appeared to be similar (Figure 9A-B). At a 55% - 60% female sex ratio, the sexes consumed similar proportions of Chinook production, but female harbor seals had a more negative impact than male harbor seals, indicating a small amount of indirect control through trophic cascades. Neither harbor seal sex had a large impact on Chinook salmon compared to other groups in the model (Figure 9C).

Male harbor seals had a more negative impact on hake than female harbor seals for most sex ratios (Figure 10A) but this is proportional to the difference in production consumed between male and female harbor seals (Figure 10B). Hake make up the third largest proportion of the female diet and the second largest proportion of the male harbor seal diet (Table 3), yet both sexes have a relatively small impact on hake (Figure 10A). While male harbor seals had a more negative impact on hake than other groups in the model, several other groups exerted an even stronger impact (Figure 10C).

Herring makes up the largest proportion of both male and female harbor seal diets (Table 3). The proportion of herring production consumed by both harbor seals combined remained fairly stable (between 0.8% – 0.9%) at all sex ratios (Figure 11B), but as the sex ratio shifted to female dominated the male harbor seal impact became more strongly negative (Figure 11A). Both male and female harbor seals had very small impacts on herring compared to other groups in the model (Figure 11C). A similar trend is seen in harbor seal impacts on small demersal fishes (Figure 12). As the sex ratio shifted to female dominated the male harbor seal impact changed from slightly positive to more strongly negative (Figure 12A). Both harbor seal groups had small impacts on small demersal fishes compared to other groups in the model (Figure 12C).

DISCUSSION

This study demonstrates that male and female harbor seals can have different predicted impacts on their ecosystem when accounting for their sexually-differentiated diets. The diet differences impacted the types and magnitude of each sex's trophic interactions which can lead to unintuitive impacts on economically and culturally important species. All salmon functional groups had similar patterns, with female harbor seals having a smaller impact than males despite consuming similar percentages of the prey group's production. The group that made up the largest proportion of the harbor seal diet (males, 31.2%; females, 34.8%; Table 3), Pacific herring, had only a small impact caused by harbor seals (Table 4). Male harbor seals' impact on herring grew increasingly negative as the sex ratio skewed to female-dominated which reduced the production consumed by male harbor seals (Figure 11A-B). Harbor seals had a similar average impact on the groups in the model as other groups at a similar trophic level (Figure 5). However, they had some of the weakest impacts on Chinook, Chum, Coho salmon, and Pacific herring of any functional group (Figure 7C, Figure 8C, Figure 9C, and Figure 11C).

Male and female harbor seals had large differences in impact for many groups in the model (Table 4). Raptors and piscivorous seabirds were the most differently impacted by male and female harbor seals, even though neither sex directly consumed nor is known to prey on raptors or piscivorous seabirds. Thus, any impact and differences in impact between the harbor seal sexes on these groups were solely through indirect trophic cascades or through competition for similar resources. The impact on piscivorous seabirds appears to be a cascading impact from harbor seals' impact on raptors, considering that raptors are predicted to negatively impact piscivorous seabirds (Figure 4), presumably through direct predation and competition for similar prey species. The negative impact that male harbor seals are having on raptors would then cascade into a positive impact on piscivorous seabirds, and the opposite for female harbor seals, though with a much lower magnitude. The main driver for the impact of harbor seals on raptors is most likely through transient orcas. Transient orcas consume harbor seals and piscivorous seabirds, but not raptors (Table 3). Thus, transient orcas would be benefiting raptors by reducing their competitors. This pathway could explain the positive impact that female harbor seals have on raptors, because orcas consume harbor seals and thus reduce competition for raptors; however, this pathway does not explain the negative impact that male harbor seals have on raptors. Male harbor seals likely compete heavily with raptors for prey, most likely Pacific salmon and small demersal fish, which outweighs their positive impact through transient orcas. Though the impacts on the prey fishes from male harbor seals are relatively small, the cumulative impact of small negative impacts on many of the raptors' prey could have a stronger negative impact on the raptor group.

Disparity in male and female harbor seal MTI on the functional groups was expected at the assumed 50/50 sex ratio because of known differences in diet composition between the sexes. As described in the methods section, comparing the MTI at the sex ratio where male and female harbor seals consumed a similar percent of production shows most clearly the magnitude of possible indirect impacts. Harbor seals demonstrated similar patterns of impact on some functional groups that occupy similar niches; specifically, the Pacific salmon groups (Figure 6 - Figure 9). Each Pacific salmon group experienced a stronger negative impact from male harbor seals than females, even when male and female harbor seals consumed similar proportions of their production. The Pink salmon group was the most impacted and most differently impacted Pacific salmon group (Table 4). Coho salmon were weakly impacted, and while Chinook and

Chum salmon experienced negligible impacts, all four Pacific salmon groups shared the same pattern of impact in which male harbor seals consistently had a stronger negative MTI.

The pattern of dissimilarity between male and female impact on Pacific salmon potentially indicates that the same indirect pathway could impact all the Pacific salmon, though to different magnitudes depending on their own differences in diet and changing predation pressure from other predators. The variation in diet and predation pressure among the Pacific salmon groups may account for the variability in strength of harbor seal impact on each Pacific salmon group. There are many potential pathways that could account for the different harbor seal sex impacts on salmon; any effect is cumulative and can be influenced by multiple pathways and mechanisms. However, some hypotheses can be generated from the results of this study. For example, one potential pathway could be caused by the negative impact that harbor seals have on the hake and pollock functional groups, which then reduce competition for prey consumed by Pacific salmon. Male harbor seals more negatively impacted hake (MTI = -0.015; Table 4) than females (MTI = -0.004; Table 4), which could be attributed in part to the fact that hake make up 20.8% of the male harbor seal diet and only 10.0% of the female diet (Table 3). In contrast, female harbor seals more negatively impacted pollock (MTI = -0.013) than male harbor seals (MTI = -0.005) (Table 4), although pollock make up similar proportions of each harbor seal diet (male 6.9%, female 7.1%; Table 3). Male harbor seals may have a less negative impact on pollock because of the strong negative impact that male harbor seals have on hake, which in turn are predicted to very negatively impact pollock (Figure 4). Therefore, any negative direct impact that male harbor seals exert on pollock due to consumption could be countered by a positive indirect impact caused by removing hake, a primary competitor of pollock. This effect would not be prevalent for female harbor seals since they had a greater impact on pollock than on hake, and pollock were not predicted to negatively impact hake (Figure 4). This relationship could mean that female harbor seals more effectively reduce competition for prey consumed by hake, pollock, and Pacific salmon by directly reducing both pollock and hake populations. Reducing competition for prey consumed by Pacific salmon could act as a positive indirect impact that counters the direct impact that female harbor seals exert through consumption. In contrast, male harbor seals preferentially consume hake over pollock, which may not reduce the competition for Pacific salmon prey as much as the female harbor seal diet. This potential pathway could explain why female harbor seals are predicted to have a smaller impact on Pacific salmon compared to male harbor seals, but it is important to note that the MTI is the result of all potential pathways in which one group may affect another.

Harbor seal impacts on salmon in the Salish Sea are of special interest because of the reliance of Southern Resident Killer Whales on Chinook salmon and the cultural value of salmon in this region (Hilborn et al., 2012). Southern Resident Killer Whales are declining in population size, which has been attributed to the matched decline in prey populations and anthropogenic environmental changes (Alava et al., 2012; Hilborn et al., 2012; Ward et al., 2009). Harbor seals are predicted to consume about 7x as many salmon individuals as fisheries catch, based on a bioenergetics model (Chasco et al., 2017). In contrast, my model predicted harbor seals to consume less biomass than fisheries and to have a smaller MTI on Pacific salmon than other predator groups and fisheries. It is possible that the conflicting predictions of bioenergetics-based models (i.e., Chasco et al. 2017) versus biomass-based models (this study) could be attributed to the complex life cycle of salmon species. For example, the ecological value of one high-biomass reproductive adult salmon may differ from the value of ten low-biomass smolts; therefore, the number of individuals consumed from each life stage could determine the overall trophic impact.

While my model predicted harbor seals to have a much smaller impact on salmon than previous individual-based models, more research is necessary to determine the true impact of harbor seals on Pacific salmon populations.

Herring are of interest because they are the largest contributors to the diet of both harbor seal sexes and they are an important prey fish for the other large fishes and marine mammals in the model. Harbor seals had a very small MTI overall on herring, but the relationship between sex ratio and MTI did not follow the usual pattern. As the sex ratio shifted to female-dominated, the male MTI became more negative even though they were consuming a smaller proportion of the herring production (Figure 11B). This pattern was also observed in the small demersal fish impacts (Figure 12B), which suggests a similar pathway is impacting both of these prey groups. This relationship indicates that male harbor seals may be having a positive indirect impact through trophic cascades on herring relative to female harbor seals. These indirect controls have been described before; using the EwE framework, Li et al. (2010) predicted a decline in herring populations with a reduction in the harbor seal population due to harbor seal's control of Pacific hake populations in the Strait of Georgia. My results show that male harbor seals had a more negative impact on Hake than female harbor seals (Figure 10A) but the impact on herring from harbor seals was very small. The predicted impacts of harbor seals in my model suggest that male harbor seals could have a larger impact on the pathway described in Li et al. (2010) than female harbor seals (Figure 11A).

Sex ratio seems to be an important parameter in predicting impact on the ecosystem as a whole and how the sexes compete for resources. Harbor seals consumed 20 of the 51 (39%) non-fishery groups in the model. Both sexes consumed the same number of groups, but the average female harbor seal diet was spread more evenly across their prey species while the male diet was more heavily focused on salmon groups (Schwarz et al., 2018). Because female harbor seals consume their prey groups more evenly, they could be more influential in indirect trophic cascades, which could then counter their direct negative impact on their prey. This is important because the true sex ratio of harbor seals in this region is not well described and varies spatiotemporally (Allegue et al., 2020; Schwarz et al., 2018). Changing sex ratios within the model domain would also change the level of intrapopulation competition between male and female harbor seals, which can be modeled as the impact males and females have on each other and themselves. Female harbor seals seem to be more resistant to intrapopulation competition, as they have a less negative impact on themselves than male harbor seals have on themselves (Table 4). Hence, harbor seal management policies could have different impacts depending on the actual or modeled sex ratio at specific haul outs.

There are some limitations in my model and analysis that would benefit from continued research. I was unable to assess the impact of harbor seal diet through time because of the limitations when splitting harbor seals into two functional groups within the Ecopath framework. In the present model, the production between the sexes is unlinked, meaning if this ecosystem was modeled through time, the male harbor seals population could theoretically be reduced to 0 while the female harbor seals population remained stable (or vice versa). The time dynamic modeling would require either new functionality to be added to the model framework, or the use of a different model framework. Sex-specific diet information from samples throughout the study area would provide more robust diet data for this model and would increase the applicability of the results. Inclusion of the spatiotemporal variability in diet would be key due to the highly seasonal and spatial abundance of Pacific salmon in the study area. Further studies into intrapopulation variation would increase predictive power of models but also their complexity.

Additionally, my model predicts total impact of each functional group on every other group but is unable to differentiate how much of the MTI is due to direct impacts through consumption versus indirect impacts through trophic cascades. Further research is necessary to determine not only the magnitude and direction of indirect impacts, but also an appropriate conversion for comparison to direct impacts. This characteristic of the model allows for impartial analysis of overall impact of one functional group on another regardless of direct consumption.

Assuming homogeneity within species could be leading researchers into missing ecologically important interactions that can have extensive consequences. Intraspecific variability could potentially be as important in ecosystem modeling as interspecific variability. Models already include some intraspecific variability like ecotypes and age classes (Harvey et al., 2012; Koehn et al., 2016; Li et al., 2010). In the Prince William Sound, intraspecific diet variability among different size classes of longnose skates has been shown to change the calculated trophic level of the skate, changing their trophic ecology (Kemper et al., 2017). This study showed that sex differentiated diet can influence trophic position and the magnitude of effects on the broader ecosystem, with differential impacts on commercially important prey groups. Using intraspecific modeling techniques, we can assess the impacts of intraspecific variability which creates more robust models for informing resource management policies.

LITERATURE CITED

Alava, J.J., Ross, P.S., Lachmuth, C., Ford, J.K., Hickie, B.E., Gobas, F.A., 2012. Habitat-based PCB environmental quality criteria for the protection of endangered killer whales (Orcinus orca). Environmental Science & Technology 46, 12655-12663.

Allegue, H., 2017. Variability of harbour seal (Phoca vitulina) foraging behaviour during out-migrations of salmon smolts.

Allegue, H., Thomas, A.C., Liu, Y., Trites, A.W., 2020. Harbour seals responded differently to pulses of out-migrating coho and Chinook smolts. Marine Ecology Progress Series 647, 211-227.

Baum, J.K., Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78, 699-714.

Beck, C.A., Iverson, S.J., Bowen, W.D., 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. Canadian Journal of Zoology 83, 377-388.

Beck, C.A., Iverson, S.J., Bowen, W.D., Blanchard, W., 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. Journal of Animal Ecology 76, 490-502.

Beier, P., 1987. Sex differences in quality of white-tailed deer diets. Journal of Mammalogy 68, 323-329.

Berini, J.L., Badgley, C., 2017. Diet segregation in American bison (Bison bison) of Yellowstone National Park (Wyoming, USA). BMC Ecology 17, 27.

Bjorkland, R.H., Pearson, S.F., Jeffries, S.J., Lance, M.M., Acevedo-Gutiérrez, A., Ward, E.J., 2015. Stable isotope mixing models elucidate sex and size effects on the diet of a generalist marine predator. Marine Ecology Progress Series 526, 213-225.

Bromaghin, J.F., Lance, M.M., Elliott, E.W., Jeffries, S.J., Acevedo-Gutiérrez, A., Kennish, J.M., 2013. New insights into the diets of harbor seals (Phoca vitulina) in the Salish Sea revealed by analysis of fatty acid signatures. Fishery Bulletin 111, 13.

Chasco, B., Kaplan, I.C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M.J., Hanson, M.B., Scordino, J., Jeffries, S., Pearson, S., 2017. Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. Canadian Journal of Fisheries and Aquatic Sciences 74, 1173-1194.

Christensen, V., Walters, C., 2004. Ecopath With Ecosim: Methods, Capabilities and Limitations 109-139 pp.

Christensen, V., Walters, C., Pauly, D., 2008. Ecopath with Ecosim: A User's Guide.

Coltman, D., Bowen, W., Wright, J.M., 1998. Male mating success in an aquatically mating pinniped, the harbour seal (Phoca vitulina), assessed by microsatellite DNA markers. Molecular Ecology 7, 627-638.

Crowder, L., Norse, E., 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy 32, 772-778.

Daniels, S.E., Walker, G.B., 1996. Collaborative learning: improving public deliberation in ecosystem-based management. Environmental Impact Assessment Review 16, 71-102.

Fogarty, M.J., 2014. The art of ecosystem-based fishery management. Canadian Journal of Fisheries and Aquatic Sciences 71, 479-490.

Fulton, E.A., Smith, A.D., Johnson, C.R., 2004. Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. Ecological Modelling 174, 267-307.

Harvey, C.J., Williams, G.D., Levin, P.S., 2012. Food web structure and trophic control in central Puget Sound. Estuaries and Coasts 35, 821-838.

Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecological Modelling 331, 173-184.

Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., 2020. Effective fisheries management instrumental in improving fish stock status. Proceedings of the National Academy of Sciences of the United States of America 117, 2218.

Hilborn, R., Cox, S., Gulland, F., Hankin, D., Hobbs, N., Schindler, D., Trites, A., 2012. The effects of salmon fisheries on Southern Resident killer whales: Final report of the independent science panel. Prepared with the assistance of DR Marmorek and AW Hall, ESSA Technologies Ltd., Vancouver, BC for National Marine Fisheries Service (Seattle. WA) and Fisheries and Oceans Canada (Vancouver. BC). xv.

Howard, S., Lance, M.M., Jeffries, S.J., Acevedo-Gutiérrez, A., 2013. Fish consumption by harbor seals (Phoca vitulina) in the San Juan Islands, Washington. Fishery Bulletin 111, 27.

Jeffries, S., Huber, H., Calambokidis, J., Laake, J., 2003. Trends and status of harbor seals in Washington State: 1978-1999. The Journal of Wildlife Management, 207-218.

Kemper, J.M., Bizzarro, J.J., Ebert, D.A., 2017. Dietary variability in two common Alaskan skates (Bathyraja interrupta and Raja rhina). Marine Biology 164, 52.

Koehn, L.E., Essington, T.E., Marshall, K.N., Kaplan, I.C., Sydeman, W.J., Szoboszlai, A.I., Thayer, J.A., 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. Ecological Modelling 335, 87-100.

Lance, M.M., Chang, W.-Y., Jeffries, S.J., Pearson, S.F., Acevedo-Gutiérrez, A., 2012. Harbor seal diet in northern Puget Sound: implications for the recovery of depressed fish stocks. Marine Ecology Progress Series 464, 257-271.

Largaespada, C., Guichard, F., Archambault, P., 2012. Meta-ecosystem engineering: nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. Ecology 93, 324-333.

Lewis, R., O'Connell, T.C., Lewis, M., Campagna, C., Hoelzel, A.R., 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (Mirounga leonina). Proceedings of the Royal Society B: Biological Sciences 273, 2901-2907.

Li, L., Ainsworth, C., Pitcher, T., 2010. Presence of harbour seals (Phoca vitulina) may increase exploitable fish biomass in the Strait of Georgia. Progress in Oceanography 87, 235-241.

Link, J.S., 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. Ecological Modelling 221, 1580-1591.

Mace, P.M., 1997. Developing and sustaining world fisheries resources: the state of the science and management, Proceedings of the 2nd World Fisheries Congress: Developing and Sustaining World Fisheries Resources—The State of Science and Management. CSIRO Publishing, Collingwood (Australia), pp. 1-20.

Marshall, K.N., Stier, A.C., Samhouri, J.F., Kelly, R.P., Ward, E.J., 2016. Conservation challenges of predator recovery. Conservation Letters 9, 70-78.

Mullon, C., Fréon, P., Cury, P., 2005. The dynamics of collapse in world fisheries. Fish and Fisheries 6, 111-120.

Olesiuk, P., 2009. An assessment of population trends and abundance of harbour seals (Phoca vitulina) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc 105.

Preikshot, D., Beamish, R.J., Neville, C.M., 2013. A dynamic model describing ecosystem-level changes in the Strait of Georgia from 1960 to 2010. Progress in Oceanography 115, 28-40.

R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Roman, J., Altman, I., Dunphy-Daly, M.M., Campbell, C., Jasny, M., Read, A.J., 2013. The Marine Mammal Protection Act at 40: status, recovery, and future of US marine mammals. Annals of the New York Academy of Sciences 1286, 29-49.

Schwarz, D., Spitzer, S.M., Thomas, A.C., Kohnert, C.M., Keates, T.R., Acevedo-Gutiérrez, A., 2018. Large-scale molecular diet analysis in a generalist marine mammal reveals male preference for prey of conservation concern. Ecology and Evolution 8, 9889-9905.

Shine, R., 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64, 419-461.

Slocombe, D.S., 1993. Implementing ecosystem-based management. BioScience 43, 612-622.

Teilmann, J., Galatius, A., 2018. Harbor Seal: Phoca vitulina, in: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (eds.), Encyclopedia of Marine Mammals (Third Edition). Academic Press, pp. 451-455.

Ulanowicz, R., Puccia, C., 1990. Mixed trophic impacts in ecosystems. Coenoses, 7-16.

Voelker, M.R., Schwarz, D., Thomas, A., Nelson, B.W., Acevedo-Gutiérrez, A., 2020. Large-scale molecular barcoding of prey DNA reveals predictors of intrapopulation feeding diversity in a marine predator. Ecology and Evolution 10, 9867-9885.

Ward, E.J., Holmes, E.E., Balcomb, K.C., 2009. Quantifying the effects of prey abundance on killer whale reproduction. Journal of Applied Ecology 46, 632-640.

Werner, F.E., Ito, S.-I., Megrey, B.A., Kishi, M.J., 2007. Synthesis of the NEMURO model studies and future directions of marine ecosystem modeling. Ecological Modelling 202, 211-223.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., 2009. Rebuilding global fisheries. Science 325, 578-585.

Zwolinski, J.P., Demer, D.A., 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. Proceedings of the National Academy of Sciences 109, 4175-4180.

TABLES

Table 1: Southern Salish Sea basic input parameters for the base Ecopath model. Trophic level (estimated from the diet matrix (Table 3)), biomass, and ecotrophic efficiency for all groups. Parameters estimated by Ecopath are bolded.

	Group	Trophic Level	Biomass (t/km^2)	Source	Ecotrophic Efficiency	Source
1	Hump_Whale	4.09	0.017	Atlantis		
2	Trans_Orca	5.33	0.014	Atlantis		
3	Res_Orca	4.95	0.033	Atlantis		
4	Porpoise	4.54	0.077	Atlantis		
5	Sea_Lions	4.68	0.061	Atlantis		
6	F_Harbor_Seals	4.54	0.039	Atlantis		
7	M_Harbor_Seals	4.66	0.039	Atlantis		
8	Raptors	4.02	0.003	Atlantis		
9	NonPisc_Seabird	3.70	0.020	Atlantis		
10	Pisc_Seabird	4.36	0.028	Atlantis		
11	RatFish	3.22	8.934	Atlantis		
12	SkateRay	3.62	1.430	Atlantis		
13	Sixgill_Shark	4.82	0.001	Atlantis		
14	Spinydog_Fish	4.05	1.270	Atlantis		
15	PiscFlat_Fish	4.05	1.155	Atlantis		
16	SmFlat_Fish	3.24	7.962	Atlantis		
17	SmDem_Fish	3.37			0.90	Harvey
18	DemRock_Fish	3.62			0.90	Harvey
19	LgDem_Fish	4.17			0.80	Harvey
20	Pollock	3.81			0.90	Harvey
21	Pacific Cod	4.10			0.52	Harvey
22	Hake	3.92			0.90	Harvey
23	Chum_Sal	3.95	3.420	Atlantis		
24	Coho_Sal	3.82	0.959	Atlantis		
25	Pink_Sal	3.67	6.245	Atlantis		
26	Chin_Sal	3.97	1.834	Atlantis		
27	Perch	3.09			0.80	Harvey
28	Sm_Plank_fish	3.17			0.80	Harvey
29	Herring	3.39			0.88	Harvey
30	Carn_Infauna	2.00	21.864	Atlantis		
31	Geoduck	2.00	29.149	Atlantis		
32	Bivalve	2.00			0.80	Harvey
33	Filter_Other	2.30			0.90	Harvey
34	Shrimp	2.56			0.90	Harvey
35	Crab	2.75	38.0	Atlantis		
36	Dungeness	3.75	3.097	Atlantis		

Table 1 (continued)

	Group	Trophic Level	Biomass (t/km^2)	Source	Ecotrophic Efficiency	Source
37	Octopi	3.34			0.90	Harvey
38	Benthic_Grazer	2.03			0.75	Harvey
39	Deposit_Feeder	2.24			0.80	Harvey
40	Macrobenth_deep	3.24	9.799	Atlantis		
41	Squid	4.02	0.549	Atlantis		
42	Gel_Zoo	3.11			0.80	Harvey
43	Lrg_Zoo	3.11			0.80	Harvey
44	Meso_zoo	2.20			0.80	Harvey
45	Micro_Zoo	2.00			0.80	Harvey
46	Seagrass	1.00	16.705	Atlantis		
47	Macroalgae	1.00	220.736	Atlantis		
48	Phytoplankton	1.00			0.30	Harvey
49	Bacteria	1.00	693.955	Atlantis		
50	Detritus	1.00	0.928	Atlantis		

Table 2: Southern Salish Sea basic input parameters for the base Ecopath model. P/B. Q/B, and P/Q for all functional groups. Parameters estimated by Ecopath are bolded.

	Group	P/B ($year^{-1}$)	Source	Q/B ($year^{-1}$)	Source	P/Q	Source
1	Hump_Whale	0.02	Li	9.10	Li		
2	Trans_Orca	0.04	Li	7.40	Li		
3	Res_Orca	0.04	Li	13.00	Li		
4	Porpoise	0.09	Osmek	25.55	Kastelein		
5	Sea_Lions	0.08	Harvey (combined multi)	24.35	Harvey		
6	F_Harbor_Seals	0.31	Harvey	24.59	Harvey		
7	M_Harbor_Seals	0.31	Harvey	24.59	Harvey		
8	Raptors	0.31	Harvey	39.74	Harvey		
9	NonPisc_Seabird	0.43	Harvey	329.08			
10	Pisc_Seabird	0.29	Harvey	160.00			
11	RatFish	0.31	Harvey	1.65	Harvey		
12	SkateRay			3.20		0.30	Li
13	Sixgill_Shark	0.10	Li	1.00	Li		
14	Spinydog_Fish	0.54	Harvey	2.69	Harvey		
15	PiscFlat_Fish	0.47	Harvey	6.01	Harvey		
16	SmFlat_Fish	2.42	Harvey	5.51	Harvey		
17	SmDem_Fish	1.20	Harvey	6.00	Harvey		
18	DemRock_Fish	0.28	Harvey (combined multi)	1.99	Harvey		
19	LgDem_Fish	0.35	Harvey	2.62	Harvey		
20	Pollock	0.80	Li	4.00	li		
21	Pacific Cod	0.26	Harvey	3.78	Harvey		
22	Hake	0.41	Harvey	2.60	Harvey		
23	Chum_Sal	5.69	Harvey			0.30	Harvey
24	Coho_Sal	3.02	Harvey			0.20	Harvey
25	Pink_Sal	0.26	Harvey			0.15	Harvey
26	Chin_Sal	5.63	Harvey			0.17	Harvey
27	Perch	1.30	Harvey	6.00	Harvey		
28	Sm_Plank_fish	1.70	Harvey	7.00	Harvey		
29	Herring	2.30	Harvey (combined multi)	12.96	Harvey		
30	Carn_Infauna	4.40	Harvey	22.00	Harvey		
31	Geoduck	0.04	Harvey	2.00	Harvey		
32	Bivalve	2.00	Harvey (avg)	6.67	Harvey		
33	Filter_Other	1.30	Harvey (avg)	6.48	Harvey		
34	Shrimp	2.25	Harvey	12.00	Harvey		
35	Crab	6.82	Harvey	25.00	Harvey		
36	Dungeness	1.50	Harvey	3.08	Harvey		
37	Octopi	0.86	Harvey	2.50	Harvey		
38	Benthic_Grazer	0.74	Harvey	8.93	Harvey		
39	Deposit_Feeder	1.42	Harvey	25.00	Harvey		

Table 2 (continued)

	Group	P/B ($year^{-1}$)	Source	Q/B ($year^{-1}$)	Source	P/Q	Source
40	Macrobenth_deep	0.88	Harvey	5.66	Harvey		
41	Squid	3.00	Harvey	15.00	Harvey		
42	Gel_Zoo	9.00	Harvey	30.00	Harvey		
43	Lrg_Zoo	7.00	Harvey	35.00	Harvey		
44	Meso_zoo	15.00	Harvey	75.00	Harvey		
45	Micro_Zoo	100.00	Harvey	285.71	Harvey		
46	Seagrass	24.54	Harvey		Harvey		
47	Macroalgae	15.62	Harvey		Harvey		
48	Phytoplankton	226.30	Harvey (combined multi)		Harvey		
49	Bacteria	150.00	Harvey (combined multi)		Harvey		

Table 3: Diet matrix for the base Ecopath model. All data are from Isaac Kaplan and Hem Morzaria-Luna (pers. comm.)

Predator	Prey	Diet
Hump_Whale	Lrg_Zoo	0.983
	Meso_zoo	0.017
Trans_Orca	Porpoise	0.019
	Sea_Lions	0.022
	F_Harbor_Seals	0.110
	M_Harbor_Seals	0.110
	NonPisc_Seabird	0.050
	Pisc_Seabird	0.017
	PiscFlat_Fish	0.095
	Squid	0.049
Res_Orca	PiscFlat_Fish	0.075
	SmFlat_Fish	0.012
	SmDem_Fish	0.004
	DemRock_Fish	0.002
	LgDem_Fish	0.007
	Chum_Sal	0.093
	Coho_Sal	0.035
	Pink_Sal	0.036
	Chin_Sal	0.665
	Herring	0.001
	Squid	0.070
Porpoise	SmFlat_Fish	0.002
	SmDem_Fish	0.340
	DemRock_Fish	0.0002
	Hake	0.003
	Perch	0.001
	Sm_Plank_fish	0.001
	Herring	0.010
	Shrimp	0.0002
	Crab	0.0002
	Octopi	0.346
	Benthic_Grazer	0.006
	Squid	0.290
Sea_Lions	SkateRay	0.027
	Spinydog_Fish	0.075
	PiscFlat_Fish	0.011
	SmFlat_Fish	0.020
	SmDem_Fish	0.017
	DemRock_Fish	0.055

Predator	Prey	Diet
	LgDem_Fish	0.002
	Pollock	0.027
	Hake	0.090
	Chum_Sal	0.192
	Coho_Sal	0.030
	Pink_Sal	0.034
	Chin_Sal	0.102
	Sm_Plank_fish	0.182
	Herring	0.098
	Octopi	0.028
	Squid	0.011
F_Harbor_Seals	SkateRay	0.001
	PiscFlat_Fish	0.0004
	SmFlat_Fish	0.056
	SmDem_Fish	0.144
	DemRock_Fish	0.006
	LgDem_Fish	0.022
	Pollock	0.071
	Pacific Cod	0.002
	Hake	0.100
	Chum_Sal	0.036
	Coho_Sal	0.026
	Pink_Sal	0.049
	Chin_Sal	0.051
	Perch	0.065
	Sm_Plank_fish	0.017
	Herring	0.348
	Octopi	0.002
	Squid	0.005
M_Harbor_Seals	RatFish	0.004
	SkateRay	0.005
	SmFlat_Fish	0.007
	SmDem_Fish	0.055
	DemRock_Fish	0.001
	LgDem_Fish	0.012
	Pollock	0.069
	Pacific Cod	0.003
	Hake	0.208
	Chum_Sal	0.080

Predator	Prey	Diet
	Coho_Sal	0.049
	Pink_Sal	0.081
	Chin_Sal	0.069
	Perch	0.020
	Sm_Plank_fish	0.013
	Herring	0.312
	Dungeness	0.0002
	Octopi	0.005
	Squid	0.007
Raptors	NonPisc_Seabird	0.019
	Pisc_Seabird	0.045
	Spinydog_Fish	0.010
	SmFlat_Fish	0.230
	SmDem_Fish	0.180
	DemRock_Fish	0.010
	LgDem_Fish	0.010
	Chum_Sal	0.038
	Coho_Sal	0.019
	Pink_Sal	0.055
	Chin_Sal	0.038
	Bivalve	0.024
	Deposit_Feeder	0.005
	Detritus	0.150
NonPisc_Seabird	SmDem_Fish	0.345
	Perch	0.124
	Sm_Plank_fish	0.029
	Herring	0.019
	Carn_Infauna	0.059
	Bivalve	0.222
	Filter_Other	0.001
	Shrimp	0.003
	Crab	0.075
	Benthic_Grazer	0.054
	Deposit_Feeder	0.010
	Macrobenth_deep	0.013
	Seagrass	0.047
Pisc_Seabird	SmFlat_Fish	0.025
	SmDem_Fish	0.213
	Chum_Sal	0.019
	Coho_Sal	0.014
	Pink_Sal	0.003
	Chin_Sal	0.004

Predator	Prey	Diet
	Perch	0.031
	Sm_Plank_fish	0.226
	Herring	0.428
	Bivalve	0.001
	Crab	0.004
	Macrobenth_deep	0.001
	Squid	0.031
RatFish	Carn_Infauna	0.152
	Bivalve	0.348
	Shrimp	0.049
	Crab	0.186
	Benthic_Grazer	0.054
	Deposit_Feeder	0.173
	Lrg_Zoo	0.006
	Meso_zoo	0.029
	Macroalgae	0.003
SkateRay	SmFlat_Fish	0.019
	SmDem_Fish	0.023
	Pollock	0.001
	Sm_Plank_fish	0.001
	Herring	0.009
	Shrimp	0.861
	Crab	0.079
	Deposit_Feeder	0.001
	Lrg_Zoo	0.006
Sixgill_Shark	Hump_Whale	0.072
	F_Harbor_Seals	0.0004
	M_Harbor_Seals	0.0004
	SkateRay	0.210
	Spinydog_Fish	0.418
	SmFlat_Fish	0.014
	SmDem_Fish	0.006
	DemRock_Fish	0.010
	LgDem_Fish	0.006
	Pollock	0.156
	Herring	0.001
	Shrimp	0.022
	Dungeness	0.022
	Octopi	0.064
	Squid	0.001
Spinydog_Fish	RatFish	0.011

Predator	Prey	Diet
	SmFlat_Fish	0.021
	SmDem_Fish	0.004
	DemRock_Fish	0.001
	LgDem_Fish	0.007
	Pollock	0.180
	Hake	0.019
	Perch	0.002
	Sm_Plank_fish	0.054
	Herring	0.096
	Carn_Infauna	0.011
	Shrimp	0.031
	Crab	0.019
	Octopi	0.019
	Benthic_Grazer	0.0004
	Deposit_Feeder	0.017
	Squid	0.052
	Gel_Zoo	0.044
	Lrg_Zoo	0.216
	Micro_Zoo	0.170
	Phytoplankton	0.027
PiscFlat_Fish	Pollock	0.161
	Pacific Cod	0.161
	Hake	0.162
	Shrimp	0.016
	Meso_zoo	0.500
SmFlat_Fish	Carn_Infauna	0.319
	Bivalve	0.193
	Filter_Other	0.015
	Shrimp	0.057
	Crab	0.122
	Deposit_Feeder	0.224
	Lrg_Zoo	0.045
	Meso_zoo	0.024
	Macroalgae	0.001
SmDem_Fish	Herring	0.0002
	Carn_Infauna	0.018
	Bivalve	0.003
	Filter_Other	0.032
	Shrimp	0.084
	Crab	0.116
	Deposit_Feeder	0.216
	Lrg_Zoo	0.075

Predator	Prey	Diet
	Meso_zoo	0.454
	Macroalgae	0.002
DemRock_Fish	SmFlat_Fish	0.001
	SmDem_Fish	0.001
	Perch	0.001
	Sm_Plank_fish	0.004
	Herring	0.181
	Carn_Infauna	0.002
	Shrimp	0.224
	Crab	0.198
	Deposit_Feeder	0.012
	Gel_Zoo	0.001
	Lrg_Zoo	0.009
	Meso_zoo	0.368
LgDem_Fish	SmFlat_Fish	0.016
	SmDem_Fish	0.224
	DemRock_Fish	0.177
	Pollock	0.040
	Hake	0.018
	Sm_Plank_fish	0.095
	Herring	0.160
	Shrimp	0.176
	Crab	0.002
	Meso_zoo	0.094
Pollock	SmDem_Fish	0.009
	Pacific Cod	0.030
	Carn_Infauna	0.001
	Bivalve	0.001
	Shrimp	0.134
	Crab	0.378
	Lrg_Zoo	0.318
	Meso_zoo	0.099
	Micro_Zoo	0.030
Pacific Cod	SmFlat_Fish	0.025
	SmDem_Fish	0.275
	Pollock	0.050
	Sm_Plank_fish	0.050
	Herring	0.225
	Bivalve	0.020
	Shrimp	0.050
	Crab	0.150

Predator	Prey	Diet
	Dungeness	0.025
	Benthic_Grazer	0.050
	Squid	0.005
	Lrg_Zoo	0.025
	Meso_zoo	0.025
	Micro_Zoo	0.025
Hake	Pollock	0.023
	Hake	0.023
	Sm_Plank_fish	0.059
	Herring	0.060
	Carn_Infauna	0.012
	Shrimp	0.150
	Crab	0.021
	Deposit_Feeder	0.002
	Lrg_Zoo	0.504
	Meso_zoo	0.147
Chum_Sal	Sm_Plank_fish	0.093
	Herring	0.331
	Carn_Infauna	0.005
	Shrimp	0.020
	Crab	0.233
	Deposit_Feeder	0.181
	Lrg_Zoo	0.132
	Meso_zoo	0.005
Coho_Sal	Sm_Plank_fish	0.018
	Herring	0.157
	Crab	0.576
	Deposit_Feeder	0.148
	Lrg_Zoo	0.102
Pink_Sal	DemRock_Fish	0.003
	Herring	0.022
	Filter_Other	0.049
	Shrimp	0.018
	Crab	0.443
	Deposit_Feeder	0.155
	Lrg_Zoo	0.199
	Meso_zoo	0.112
Chin_Sal	Sm_Plank_fish	0.105
	Herring	0.355
	Carn_Infauna	0.004
	Shrimp	0.021

Predator	Prey	Diet
	Crab	0.236
	Deposit_Feeder	0.164
	Lrg_Zoo	0.108
	Meso_zoo	0.006
Perch	Carn_Infauna	0.017
	Bivalve	0.170
	Filter_Other	0.044
	Shrimp	0.024
	Crab	0.007
	Deposit_Feeder	0.126
	Lrg_Zoo	0.094
	Meso_zoo	0.269
	Micro_Zoo	0.123
	Macroalgae	0.129
Sm_Plank_fish	Carn_Infauna	0.004
	Filter_Other	0.040
	Shrimp	0.042
	Crab	0.028
	Deposit_Feeder	0.147
	Lrg_Zoo	0.006
	Meso_zoo	0.669
	Phytoplankton	0.052
	Detritus	0.013
Herring	Sm_Plank_fish	0.006
	Bivalve	0.025
	Filter_Other	0.033
	Shrimp	0.007
	Crab	0.131
	Deposit_Feeder	0.107
	Lrg_Zoo	0.121
	Meso_zoo	0.569
	Phytoplankton	0.001
Carn_Infauna	Macroalgae	0.100
	Bacteria	0.100
	Detritus	0.800
Geoduck	Macroalgae	0.750
	Bacteria	0.025
	Detritus	0.225
Bivalve	Micro_Zoo	0.003
	Phytoplankton	0.190
	Bacteria	0.027

Predator	Prey	Diet
	Detritus	0.780
Filter_Other	Carn_Infauna	0.022
	Bivalve	0.087
	Meso_zoo	0.087
	Micro_Zoo	0.087
	Macroalgae	0.087
	Phytoplankton	0.385
	Detritus	0.247
Shrimp	Carn_Infauna	0.075
	Bivalve	0.183
	Filter_Other	0.006
	Shrimp	0.029
	Crab	0.055
	Deposit_Feeder	0.029
	Lrg_Zoo	0.047
	Meso_zoo	0.012
	Micro_Zoo	0.001
	Seagrass	0.006
	Macroalgae	0.023
	Phytoplankton	0.045
	Bacteria	0.025
	Detritus	0.465
Crab	SmDem_Fish	0.009
	Perch	0.003
	Sm_Plank_fish	0.003
	Carn_Infauna	0.006
	Bivalve	0.466
	Filter_Other	0.016
	Shrimp	0.016
	Crab	0.022
	Deposit_Feeder	0.132
	Seagrass	0.002
	Macroalgae	0.113
	Phytoplankton	0.151
	Detritus	0.061
Dungeness	SmFlat_Fish	0.078
	SmDem_Fish	0.070
	Chin_Sal	0.050
	Perch	0.152
	Sm_Plank_fish	0.002
	Herring	0.021

Predator	Prey	Diet
	Carn_Infauna	0.034
	Bivalve	0.203
	Filter_Other	0.032
	Shrimp	0.171
	Crab	0.070
	Dungeness	0.054
	Benthic_Grazer	0.001
	Deposit_Feeder	0.045
	Macrobenth_deep	0.007
	Seagrass	0.003
	Macroalgae	0.009
Octopi	Carn_Infauna	0.377
	Bivalve	0.138
	Filter_Other	0.078
	Crab	0.302
	Dungeness	0.008
	Benthic_Grazer	0.033
	Macrobenth_deep	0.064
Benthic_Grazer	Carn_Infauna	0.004
	Filter_Other	0.011
	Crab	0.009
	Macroalgae	0.680
	Phytoplankton	0.296
Deposit_Feeder	Meso_zoo	0.200
	Detritus	0.800
Macrobenth_deep	Carn_Infauna	0.006
	Bivalve	0.199
	Filter_Other	0.391
	Crab	0.018
	Benthic_Grazer	0.123
	Deposit_Feeder	0.116
	Macrobenth_deep	0.099
	Micro_Zoo	0.001
	Macroalgae	0.007
	Phytoplankton	0.004
	Bacteria	0.001
	Detritus	0.033
Squid	SmDem_Fish	0.078
	DemRock_Fish	0.001
	Perch	0.052
	Sm_Plank_fish	0.002

Predator	Prey	Diet
	Herring	0.026
	Carn_Infauna	0.010
	Shrimp	0.003
	Crab	0.259
	Octopi	0.002
	Deposit_Feeder	0.004
	Squid	0.001
	Gel_Zoo	0.060
	Lrg_Zoo	0.495
	Meso_zoo	0.007
Gel_Zoo	Bivalve	0.084

Predator	Prey	Diet
	Filter_Other	0.186
	Meso_zoo	0.247
	Micro_Zoo	0.483
Lrg_Zoo	Filter_Other	0.021
	Meso_zoo	0.496
	Micro_Zoo	0.484
Meso_zoo	Micro_Zoo	0.200
	Phytoplankton	0.800
Micro_Zoo	Phytoplankton	0.900
	Bacteria	0.050
	Detritus	0.050

Table 4: Male and female harbor seal Mixed Trophic Impact on all functional groups in the model. Impacts shown are the average impact at the 50/50 sex ratio for 100 randomly sampled models. The Mixed Trophic Impacts are sorted by the absolute difference in impact between male and female harbor seals. ♀ indicates the group is consumed by female harbor seals; ♂ indicates the group is consumed by male harbor seals.

Group	Male Harbor Seals	Female Harbor Seals	Absolute Value of Difference in Impact
Raptors	-0.28047	0.03807	0.3185
Pisc_Seabird	0.13348	-0.07230	0.2058
RatFish (♂)	-0.19849	-0.09946	0.0990
SkateRay (♂♀)	0.03198	0.10983	0.0778
Pink_Sal (♂♀)	-0.13635	-0.06100	0.0754
NonPisc_Seabird	-0.05457	-0.11706	0.0625
Coho_Sal (♂♀)	-0.03440	-0.00103	0.0334
LgDem_Fish (♂♀)	-0.02259	-0.05153	0.0289
M_Harbor_Seals	-0.16647	-0.14436	0.0221
Squid (♂♀)	0.01943	0.03715	0.0177
SmFlat_Fish (♂♀)	-0.00368	-0.01988	0.0162
Spinydog_Fish	0.13927	0.12451	0.0148
Hake (♂♀)	-0.01508	-0.00416	0.0109
Hump_Whale	-0.05502	-0.06512	0.0101
Sea_Lions	-0.14111	-0.13104	0.0101
Porpoise	-0.12896	-0.11922	9.74E-03
Gel_Zoo	-0.04763	-0.05722	9.60E-03
F_Harbor_Seals	-0.15651	-0.14771	8.80E-03
Pollock (♂♀)	-0.00544	-0.01303	7.59E-03
Seagrass	-0.00085	0.00585	6.70E-03
Sixgill_Shark	0.06099	0.06732	6.34E-03
Perch (♂♀)	0.00081	0.00660	5.79E-03
Res_Orca	-0.00750	-0.00200	5.50E-03
Benthic_Grazer	0.01090	0.00552	5.38E-03
Shrimp	0.00298	-0.00169	4.67E-03
Pacific Cod (♂♀)	0.00465	0.00905	4.40E-03
Trans_Orca	0.14564	0.14154	4.10E-03
Lrg_Zoo	0.00609	0.00225	3.85E-03
Dungeness (♂)	-0.00325	-0.00650	3.25E-03
Sm_Plank_fish (♂♀)	0.00044	0.00350	3.06E-03
DemRock_Fish (♂♀)	0.00392	0.00127	2.64E-03
Carn_Infauna	0.00326	0.00585	2.59E-03
SmDem_Fish (♂♀)	-0.00087	0.00158	2.45E-03
Crab	0.00522	0.00303	2.19E-03
Macroalgae	-0.00477	-0.00295	1.82E-03
Bivalve	-0.00217	-0.00052	1.65E-03

Table 4 (continued)

Group	Male Harbor Seals	Female Harbor Seals	Absolute Value of Difference in Impact
Geoduck	-0.00362	-0.00227	1.35E-03
Chum_Sal (♂♀)	-0.00150	-0.00037	1.13E-03
Chin_Sal (♂♀)	-0.00318	-0.00207	1.11E-03
Filter_Other	-0.00200	-0.00091	1.09E-03
Octopi (♂♀)	0.03280	0.03188	9.19E-04
PiscFlat_Fish (♀)	-0.00443	-0.00522	7.82E-04
Macrobenth_deep	0.00002	0.00067	6.56E-04
Meso_zoo	-0.00110	-0.00046	6.41E-04
Deposit_Feeder	0.00069	0.00019	4.95E-04
Herring (♂♀)	-0.00198	-0.00155	4.31E-04
Phytoplankton	0.00042	0.00016	2.60E-04
Micro_Zoo	0.00025	0.00012	1.31E-04
Bacteria	-0.00026	-0.00036	9.21E-05
Detritus	-0.00017	-0.00021	3.39E-05

FIGURES

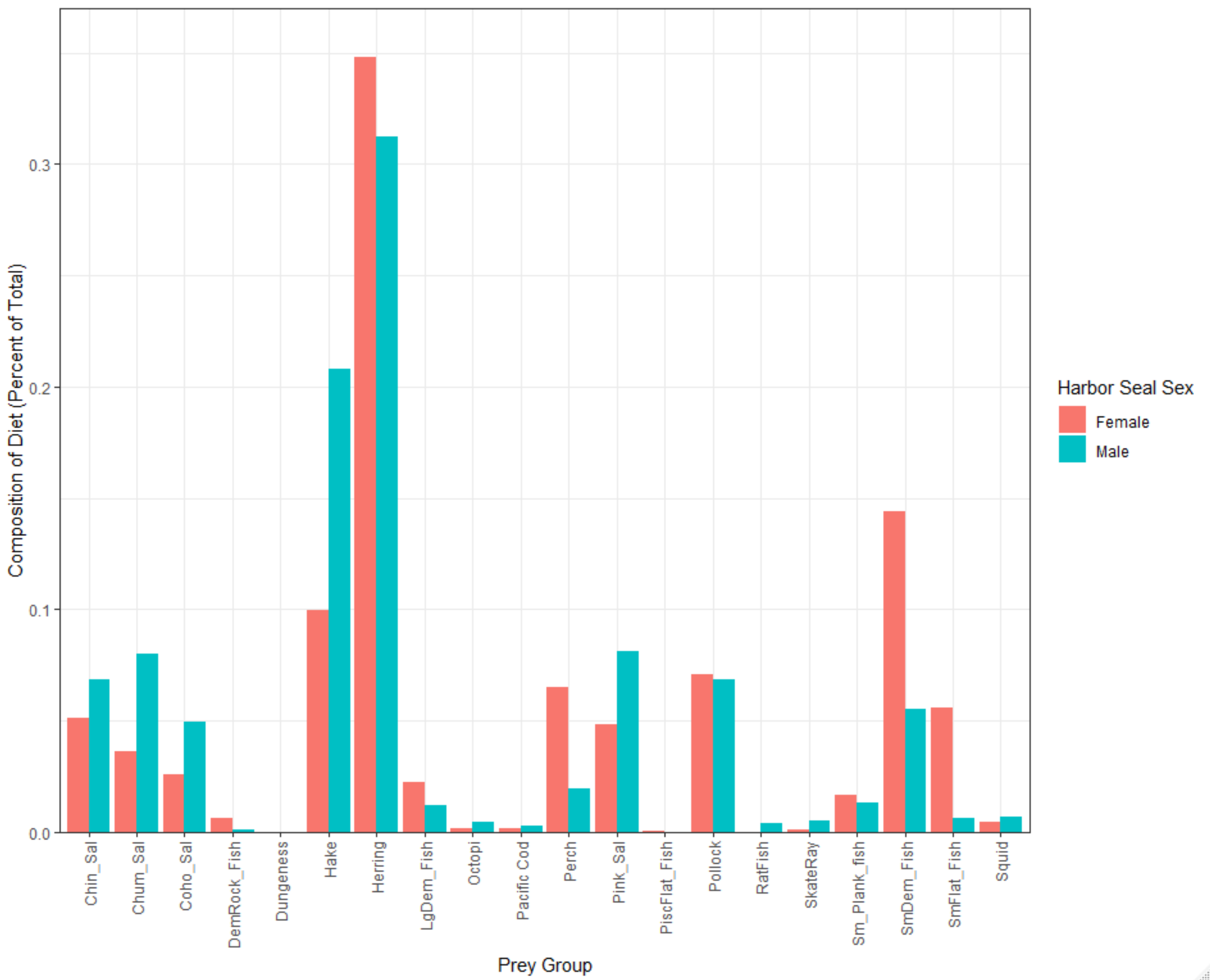

Figure 1: Diet differences between male and female harbor seals as reported by (Schwarz et al., 2018)

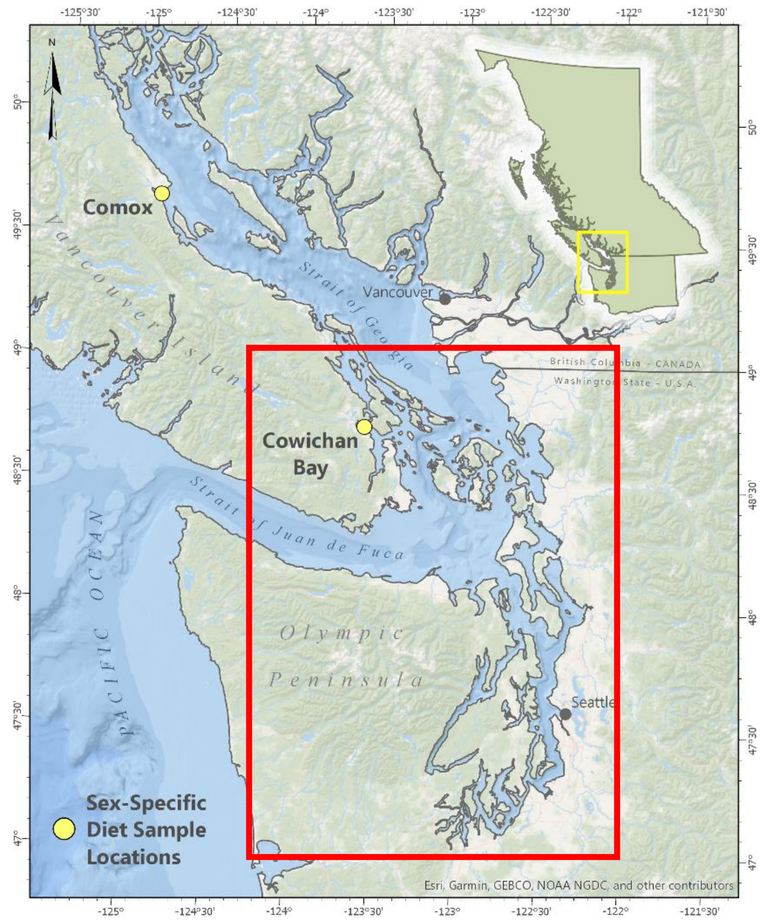

Figure 2: Map depicting the Salish Sea model domain (red rectangle) with the sampling locations for the harbor seal sex-specific diet (yellow).

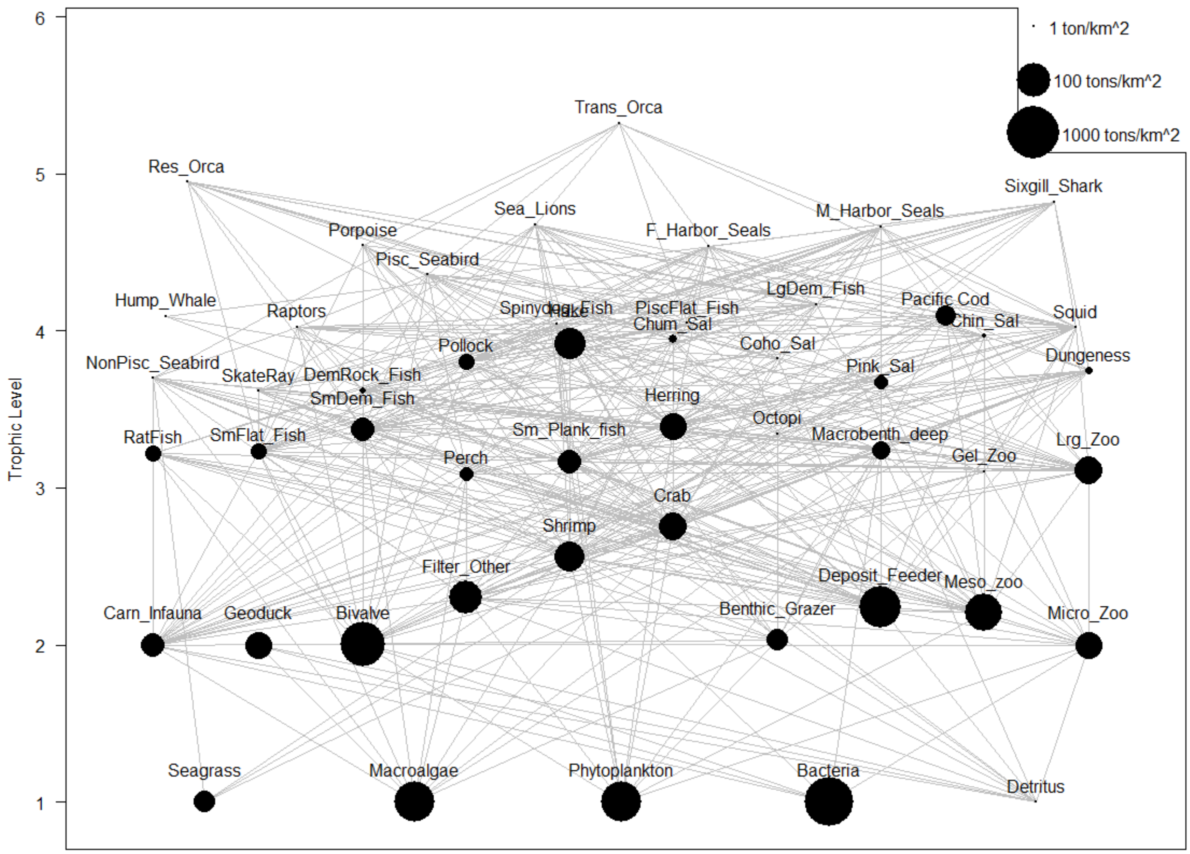

Figure 3: Food web generated for the base Ecopath model. Groups are arranged by trophic level, connections are based on the diet matrix, and point size is proportional to the log of the biomass.

Figure 4: Mixed Trophic Impacts for all impacting groups on all impacted groups. Blue is more positively impacted; red is more negatively impacted.

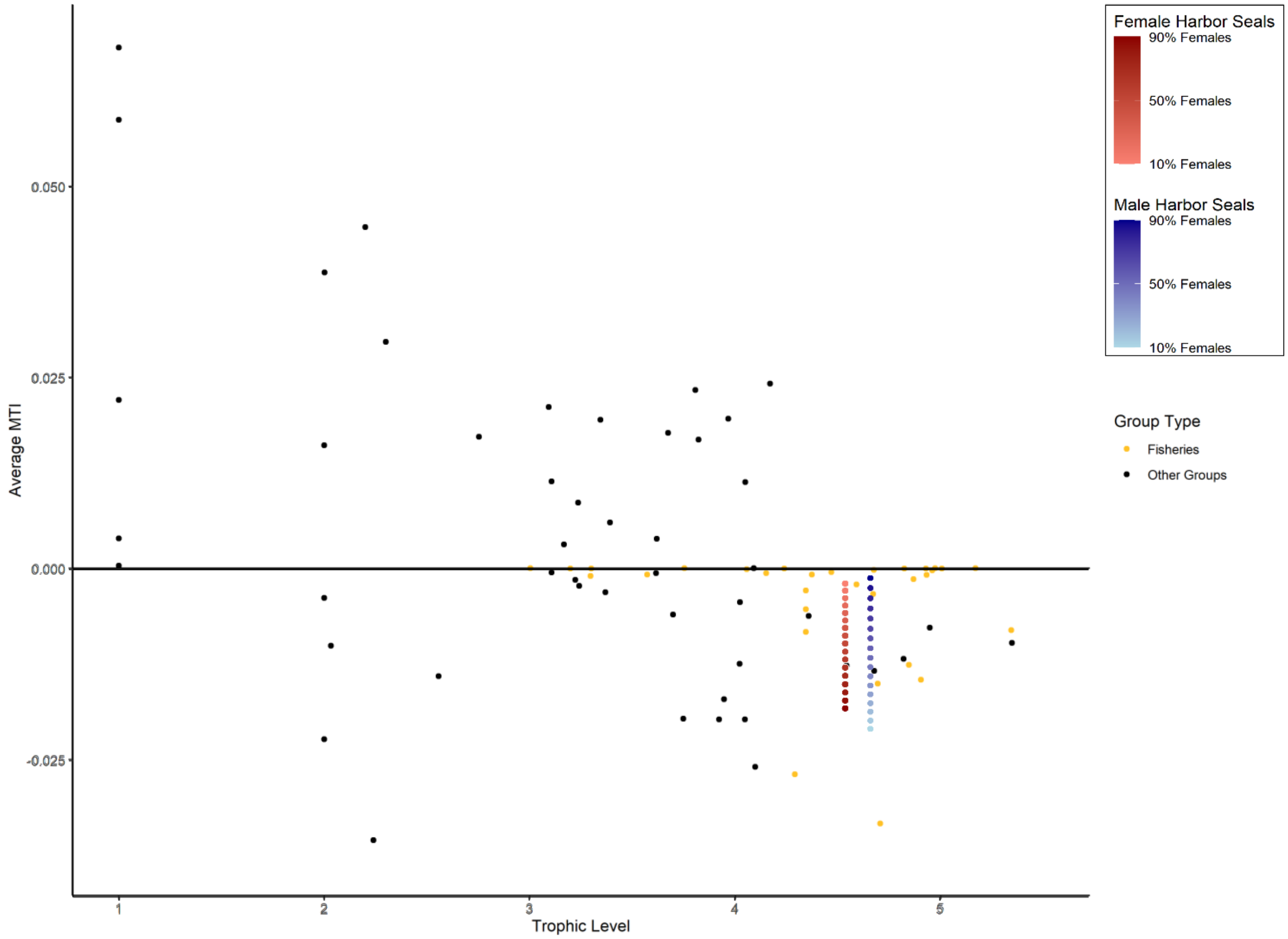

Figure 5: Scatterplot of the impacting group's average MTI on the other functional groups in the model by trophic level. For non-seal groups, each point is the average impact a group has on every other group in the model for the 1700 models. Male (blue) and female (red) seals are colored in gradient by sex ratio, with darker shading indicating a higher female sex ratio. Each of these colored points is the average impact on every other group for 100 models, with an average for each of the 17 sex ratio.

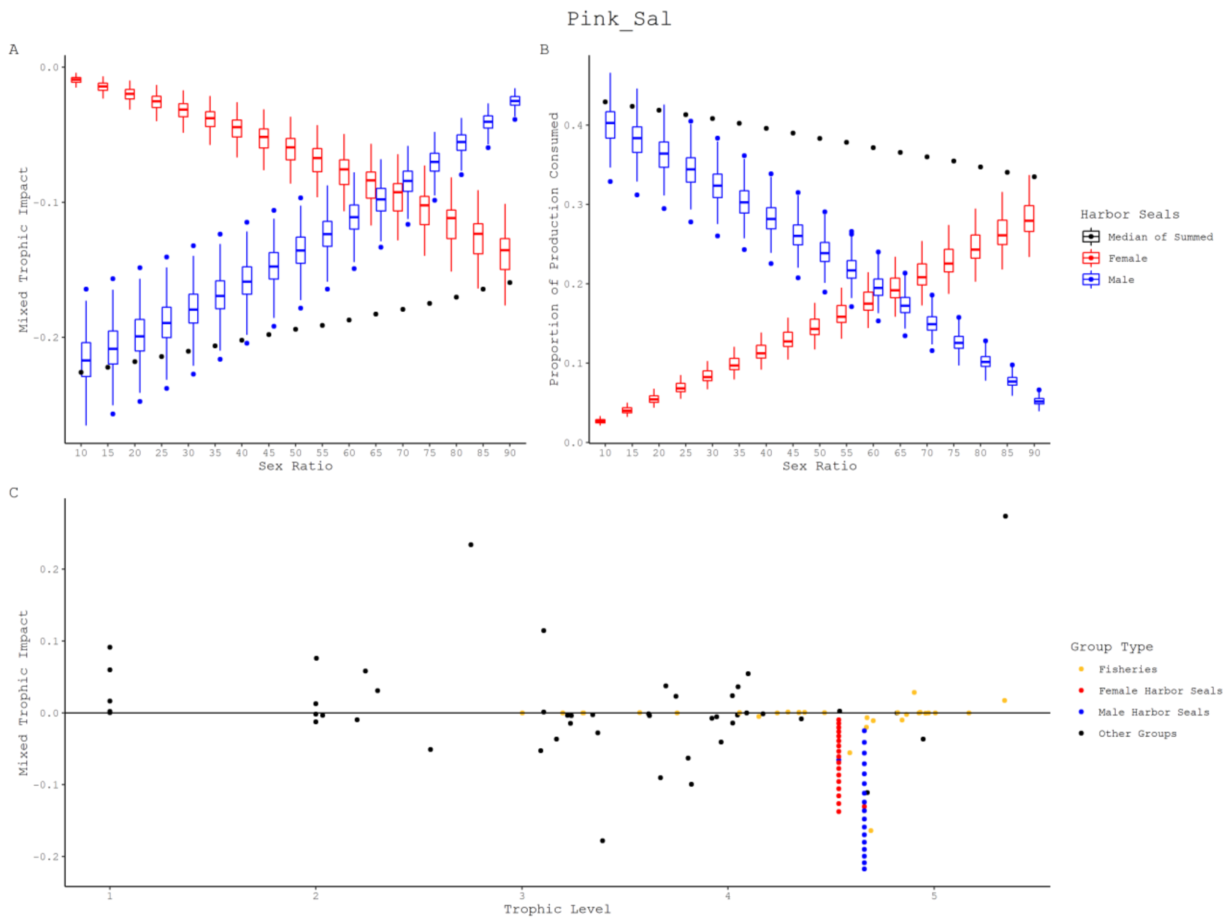

Figure 6: Summary plots for harbor seal impact on Pink salmon. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Pink salmon. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Pink salmon consumed by male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed production consumed to show how sex ratio impacts the overall production consumed. (c) Scatterplot of each group's average MTI on Pink salmon and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Pink salmon. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

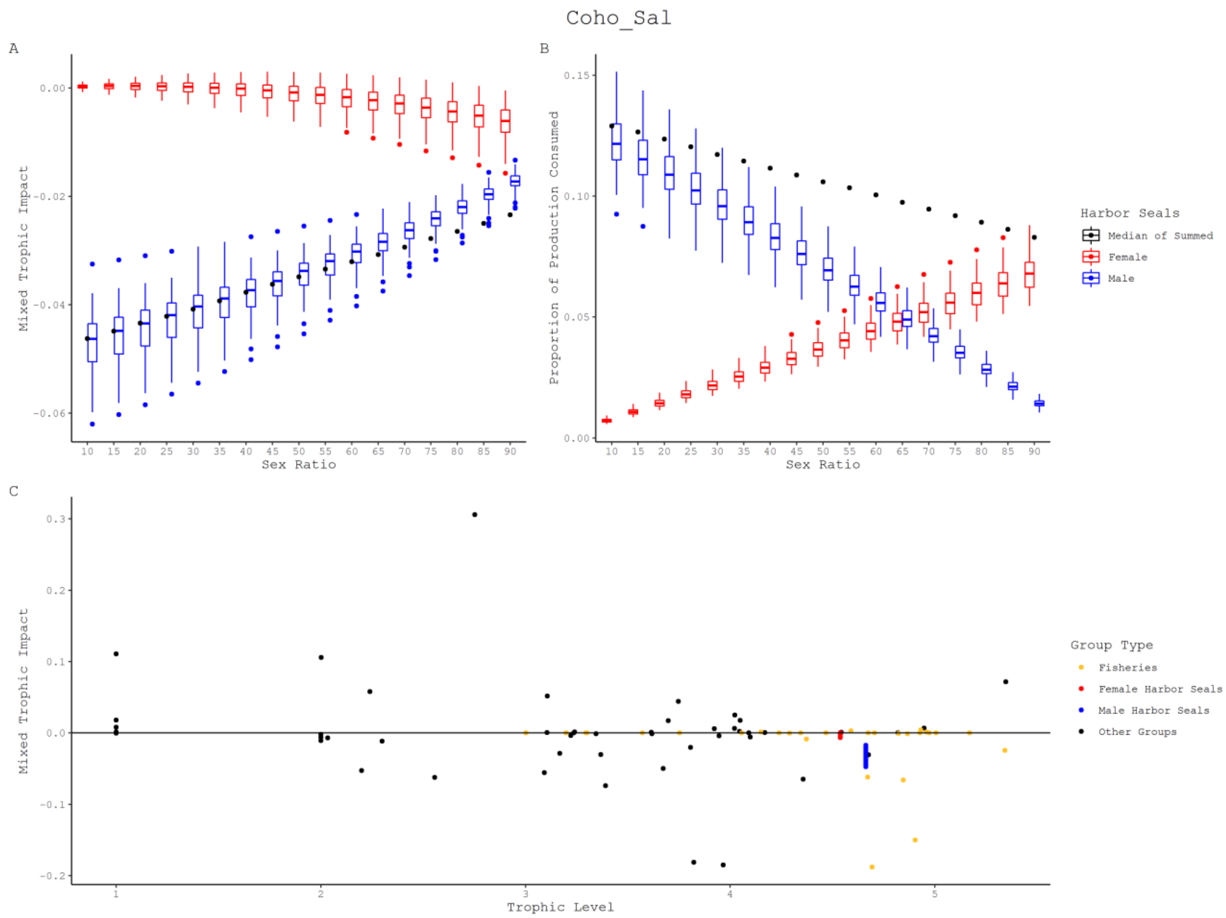

Figure 7: Summary plots for harbor seal impact on Coho salmon. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Coho salmon. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Coho salmon consumed by male (blue) and female (red) harbor seals at different sex ratio on Coho salmon. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on Coho salmon and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Coho salmon. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

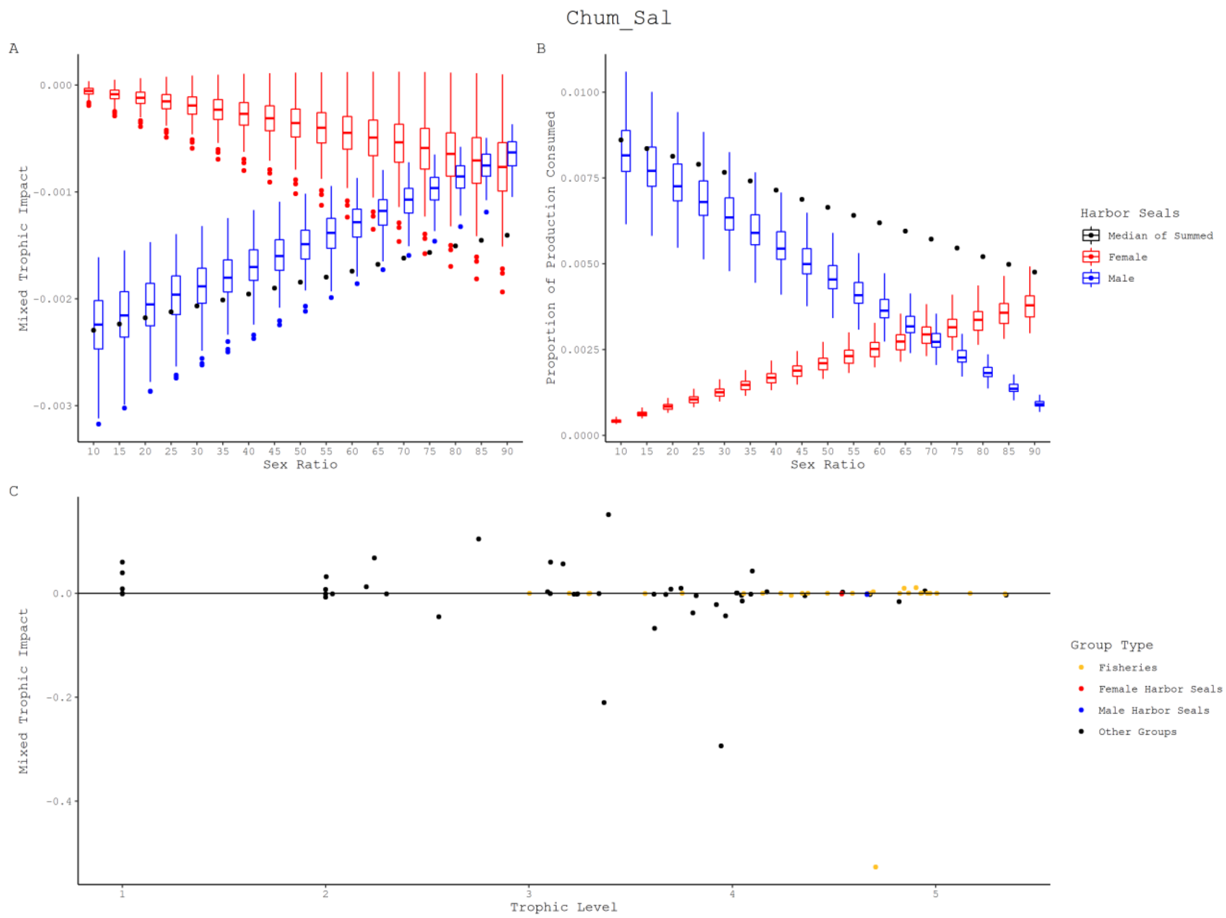

Figure 8: Summary plots for harbor seal impact on Chum salmon. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Chum salmon. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Chum salmon consumed by male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on Chum salmon and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Chum salmon. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

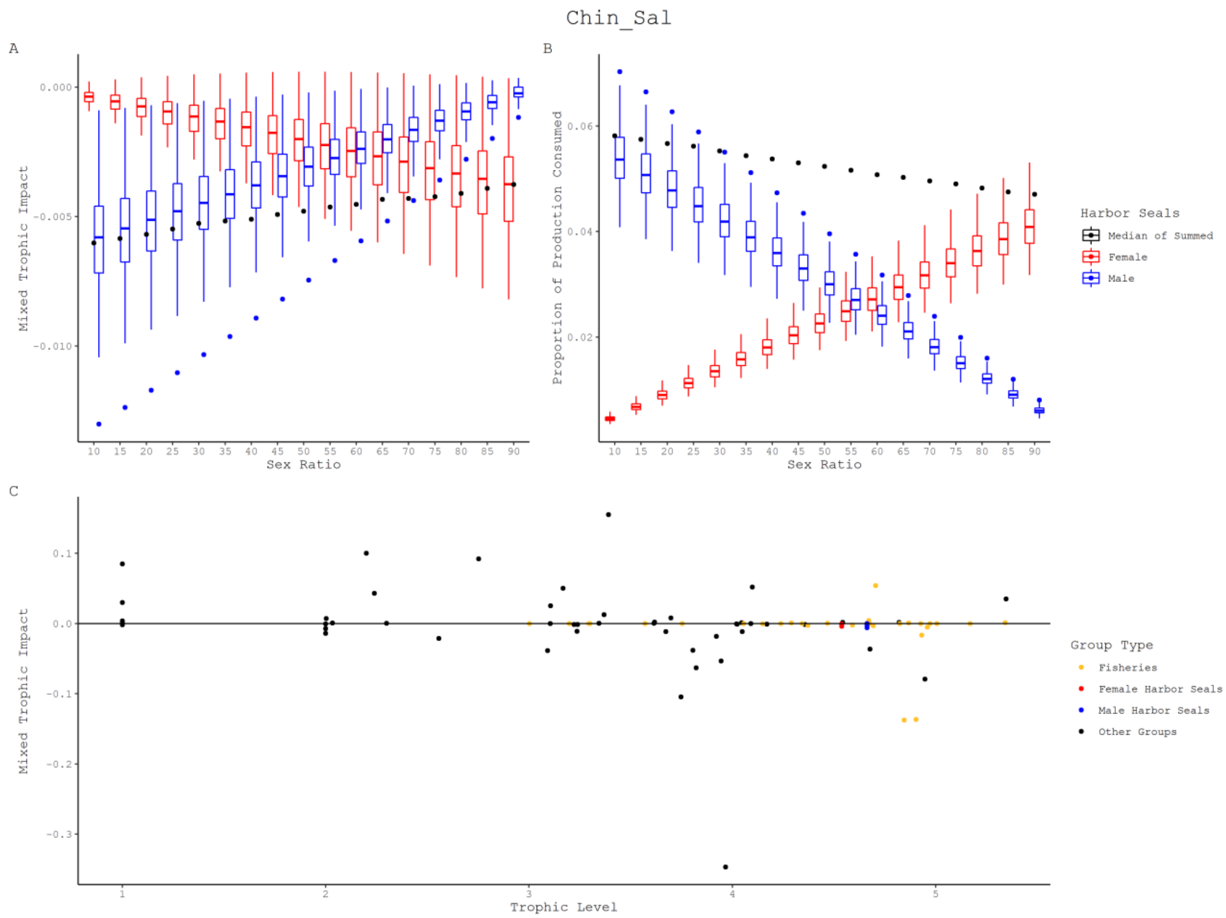

Figure 9: Summary plots for harbor seal impact on Chinook salmon. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Chinook salmon. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Chinook salmon consumed by male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on Chinook salmon and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Chinook salmon. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

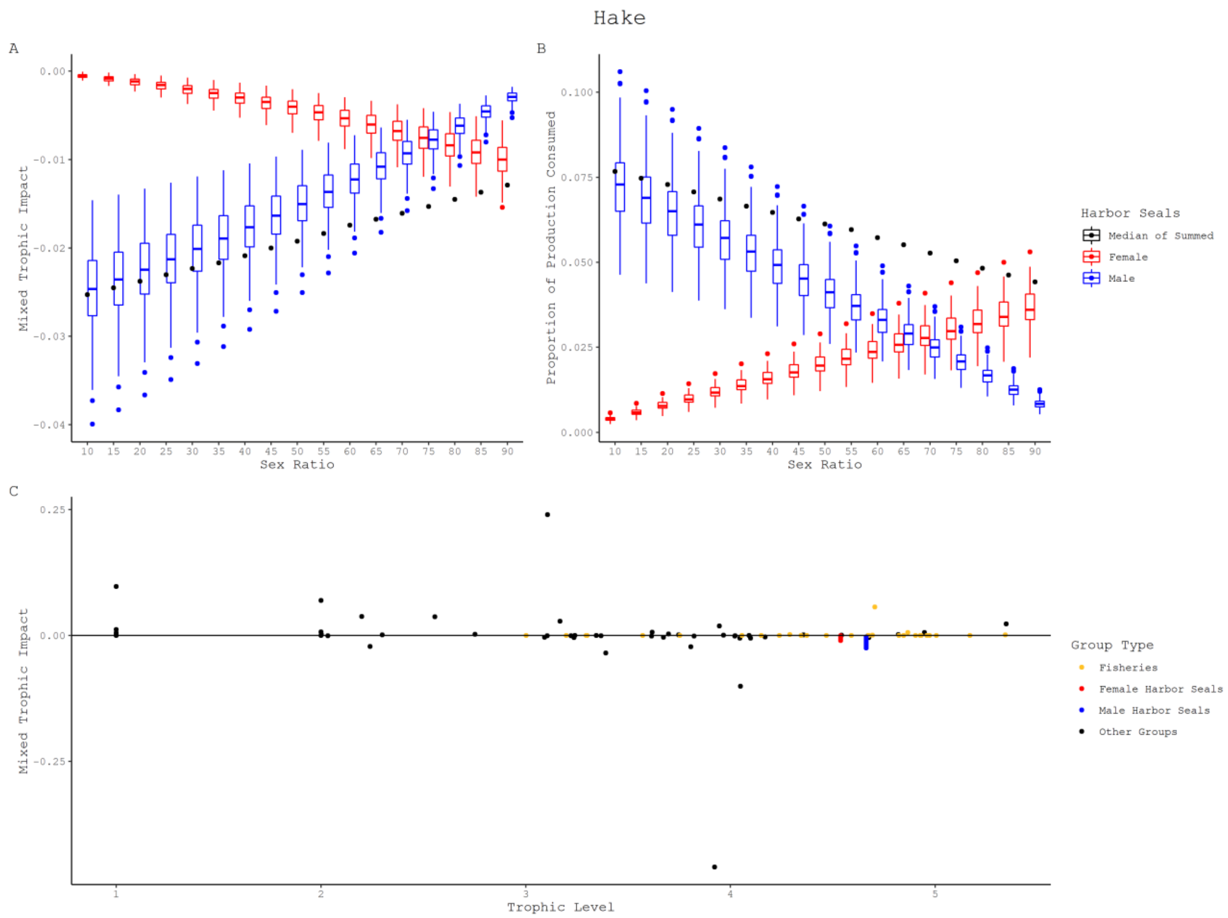

Figure 10: Summary plots for harbor seal impact on Hake. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Hake. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Hake consumed by male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on Hake and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Hake. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

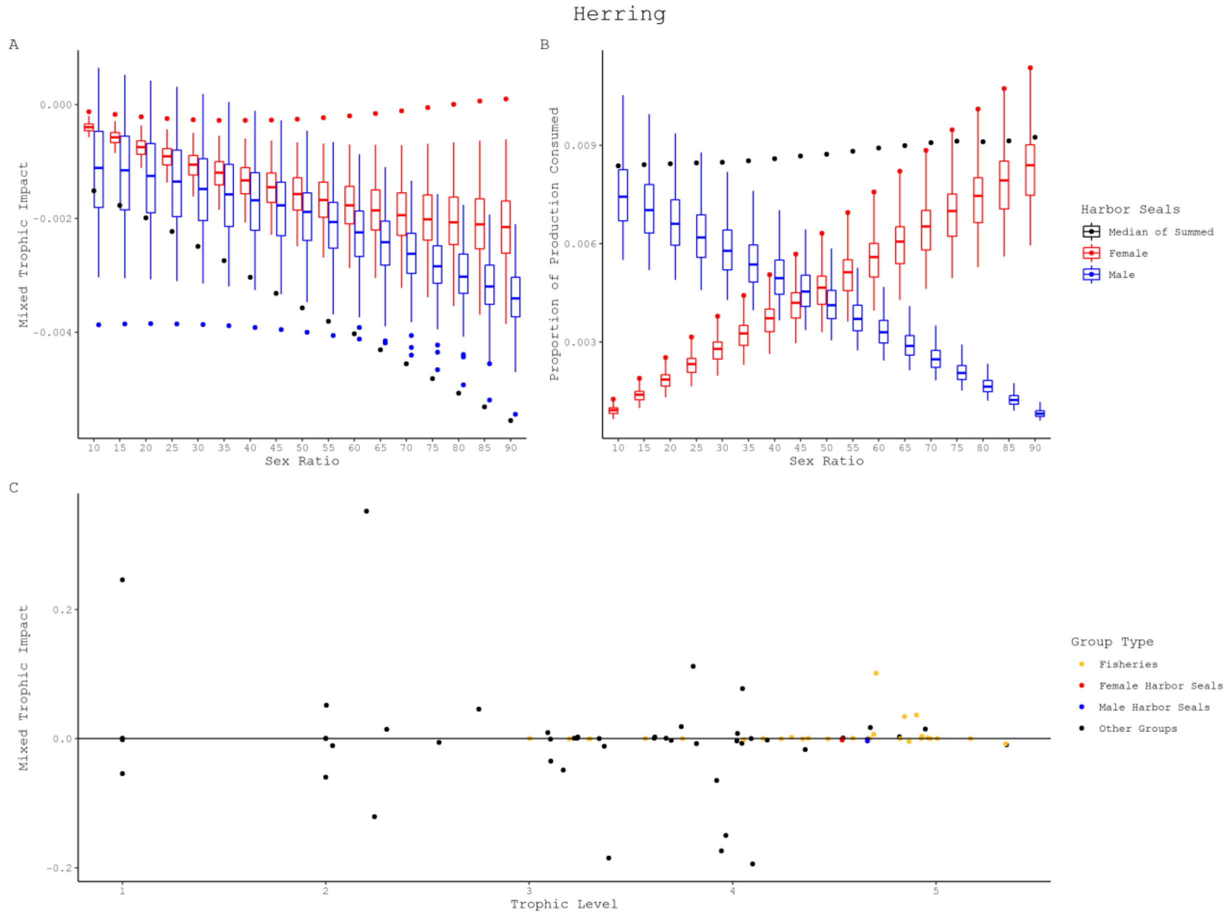

Figure 11: Summary plots for harbor seal impact on Herring. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on Herring. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of Herring consumed for male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on Herring and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on Herring. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

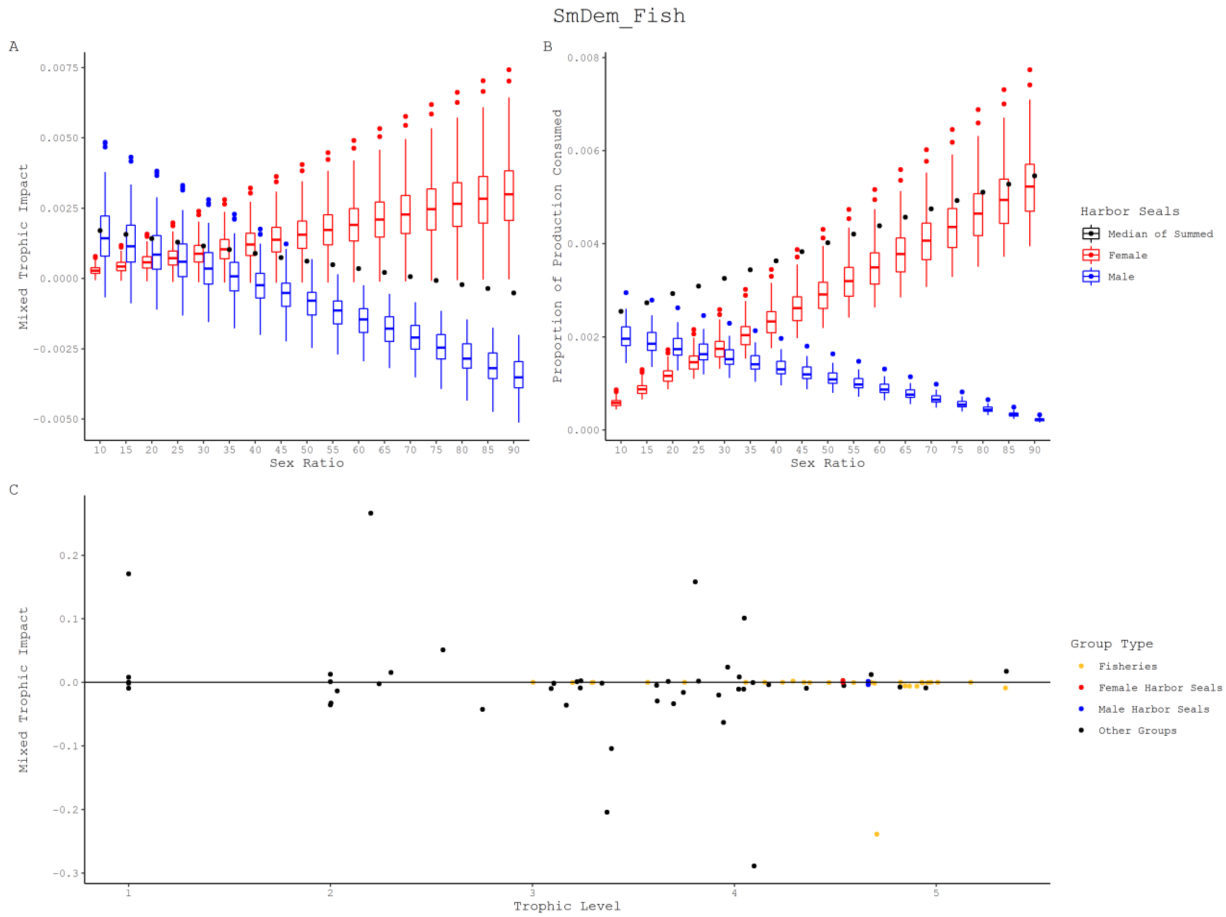

Figure 12: Summary plots for harbor seal impact on small demersal fish. (a) Boxplot of MTI for male (blue) and female (red) harbor seals at different percent female sex ratios on small demersal fish. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (b) Boxplot of percent production of small demersal fish consumed for male (blue) and female (red) harbor seals at different sex ratios. Black dots represent the median of the summed MTI to show how sex ratio impacts the overall species impact. (c) Scatterplot of each group's average MTI on small demersal fish and trophic level. Fisheries (yellow) and other groups (black) points are the average of 1700 impacts on small demersal fish. Male (blue) and female (red) are plotted as 17 averages of 100 models each, one point for each sex ratio.

SUPPLEMENTARY MATERIAL

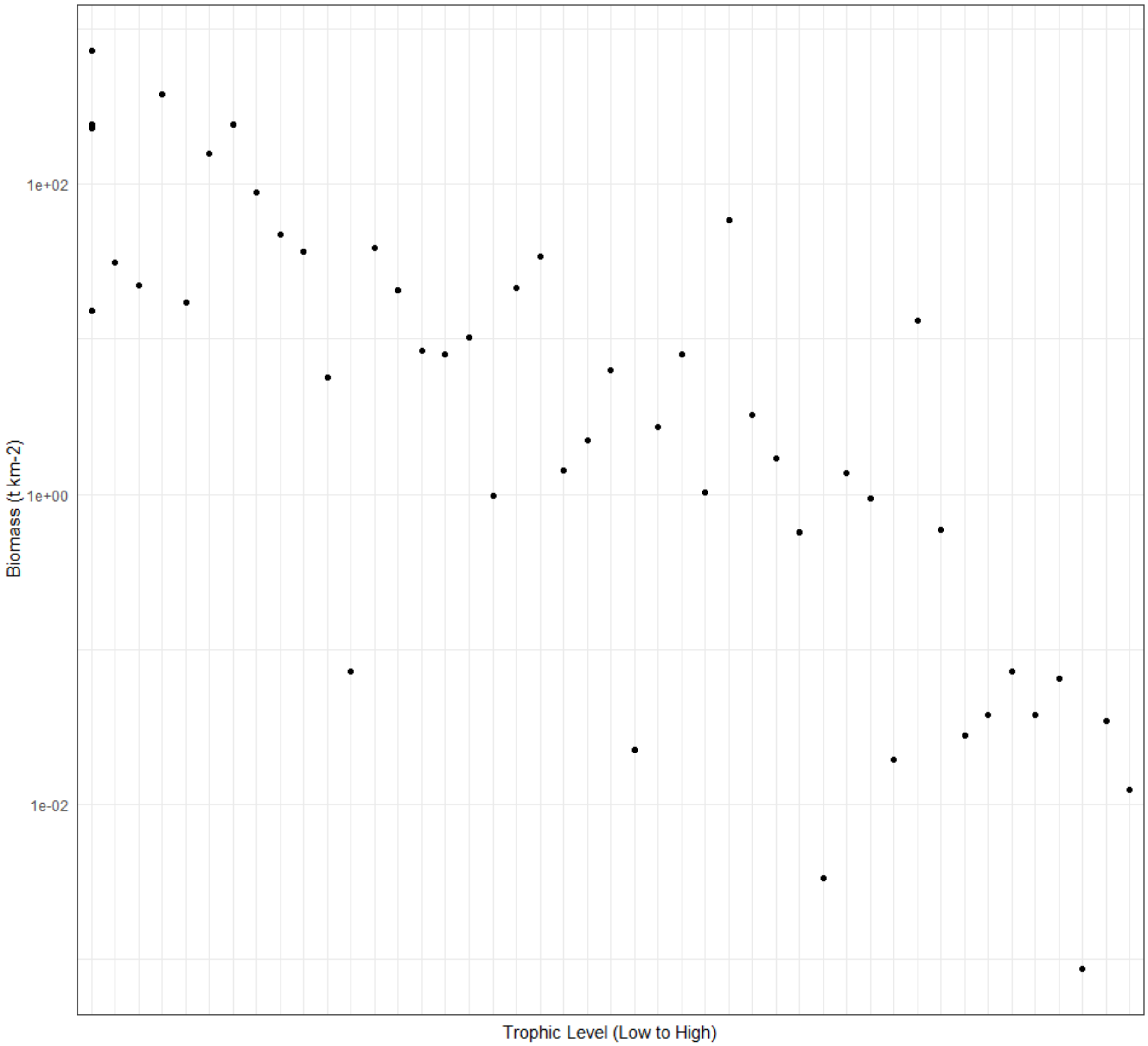

Figure S1: Scatter plot of biomass and trophic level as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.

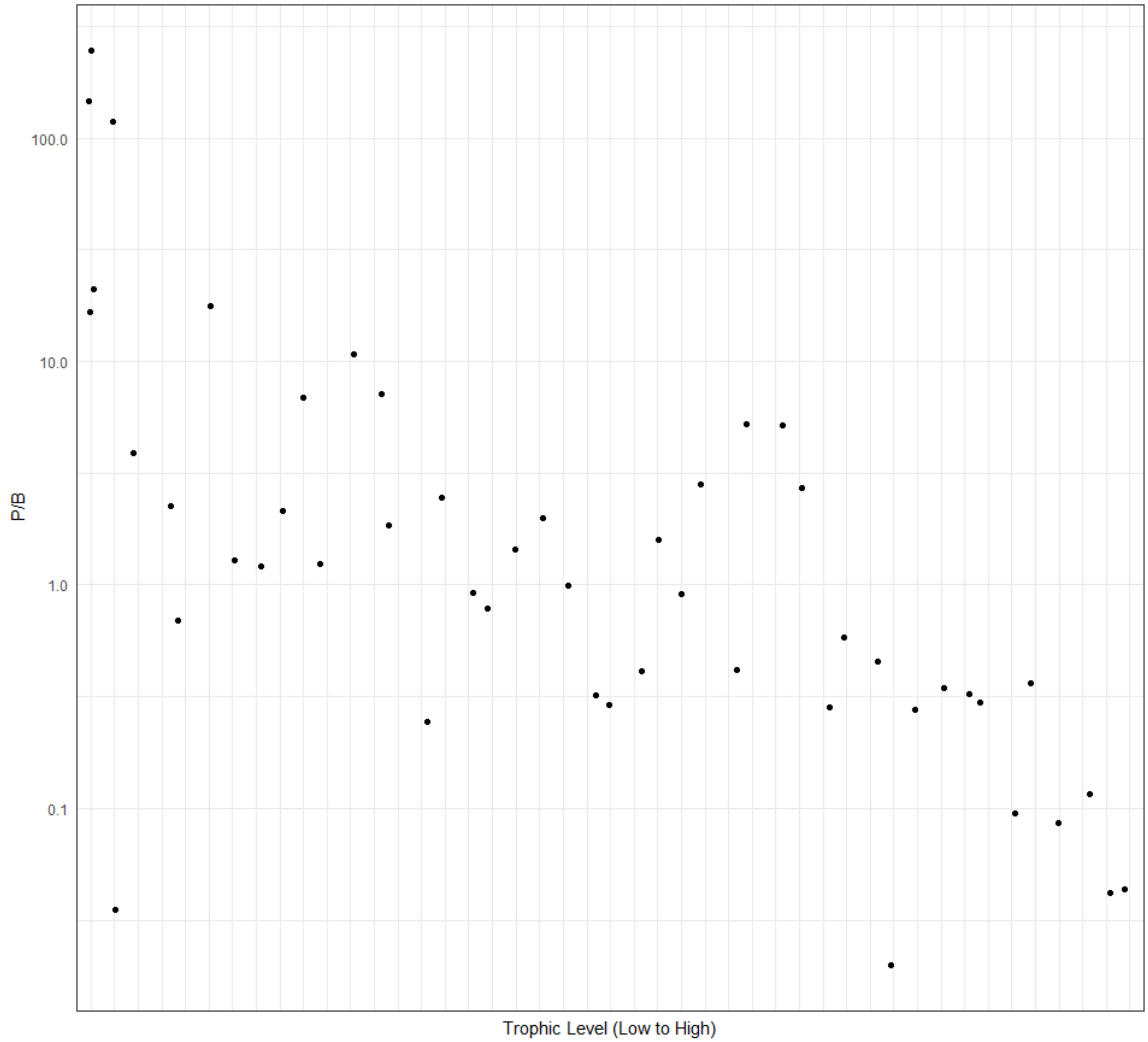

Figure S2: Scatter plot of production per biomass and trophic level as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.

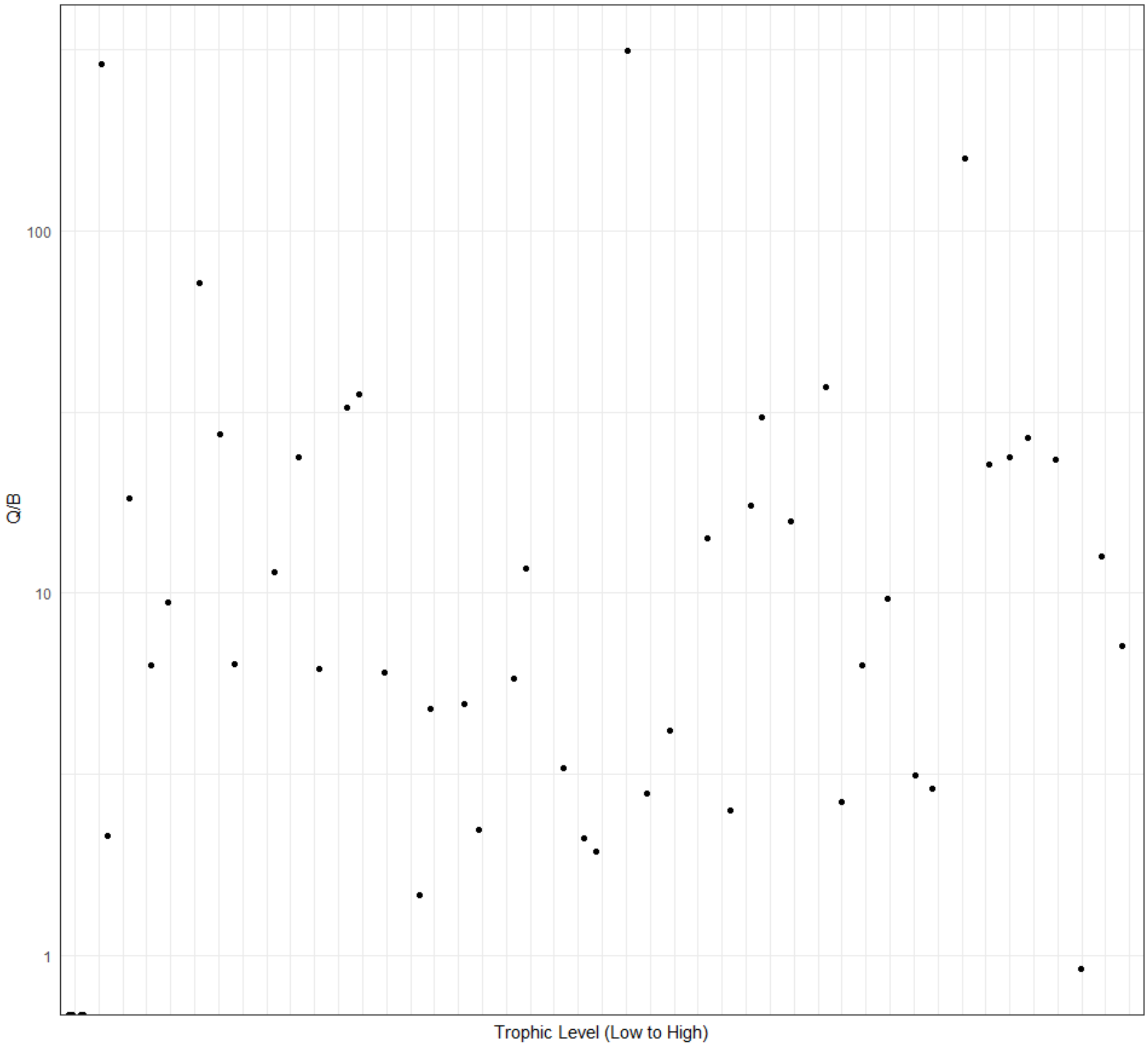

Figure S3: Scatter plot of consumption per ton of biomass and trophic level as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.

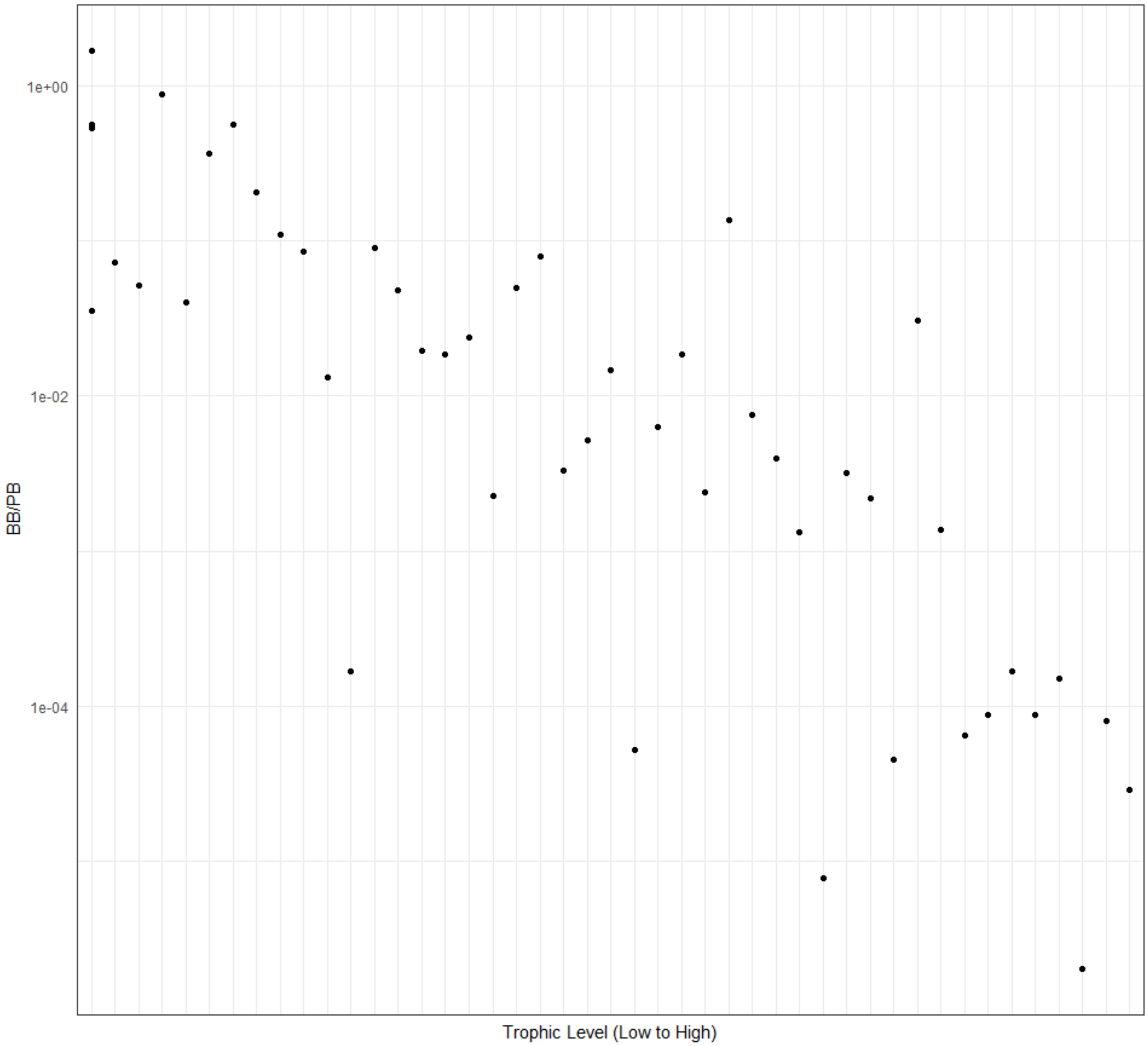

Figure S4: Scatterplot of biomass divided by production per biomass plotted by trophic level as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.

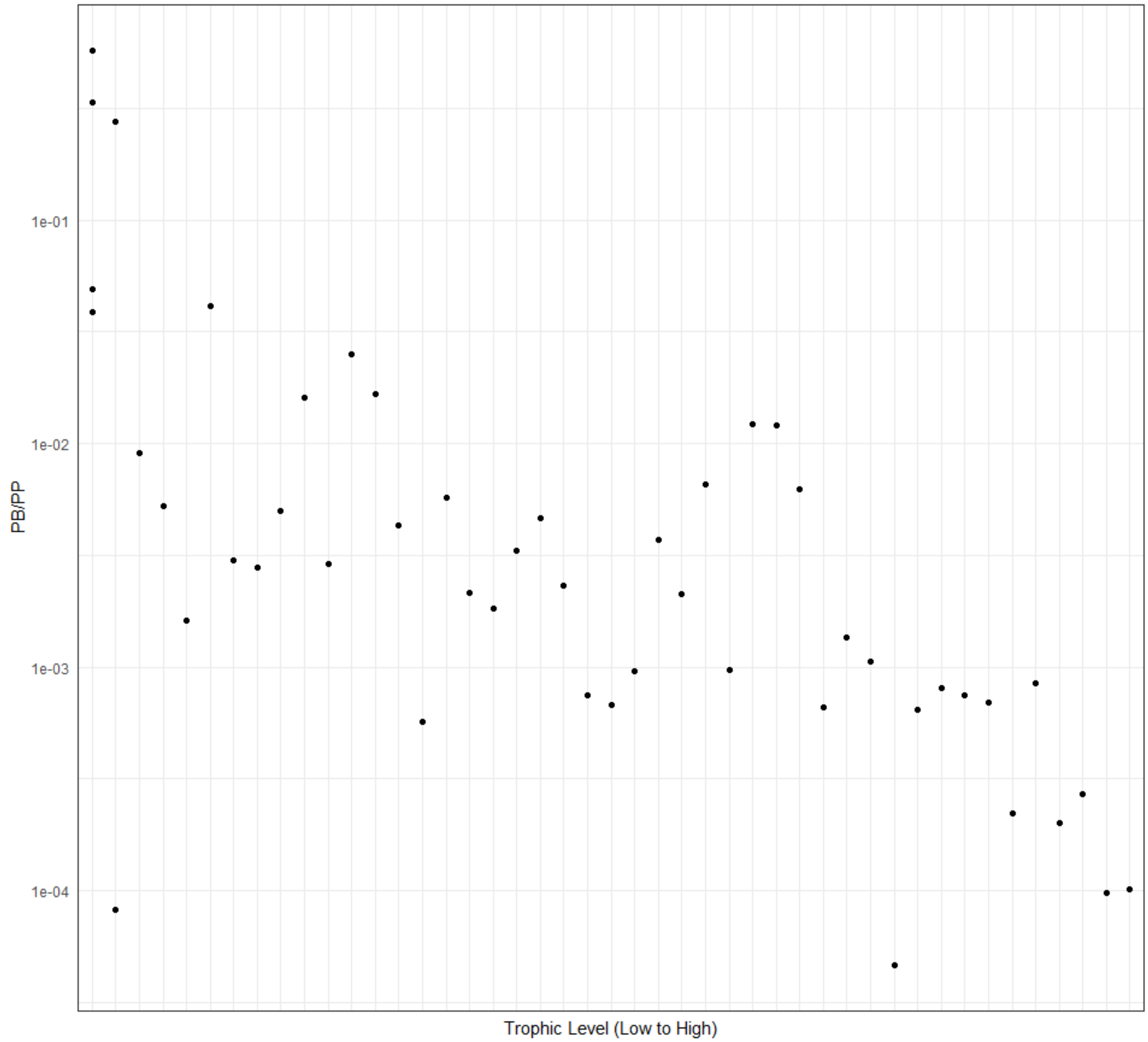

Figure S5: Scatterplot of proportion of total primary production that each group makes up production per ton of biomass as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.

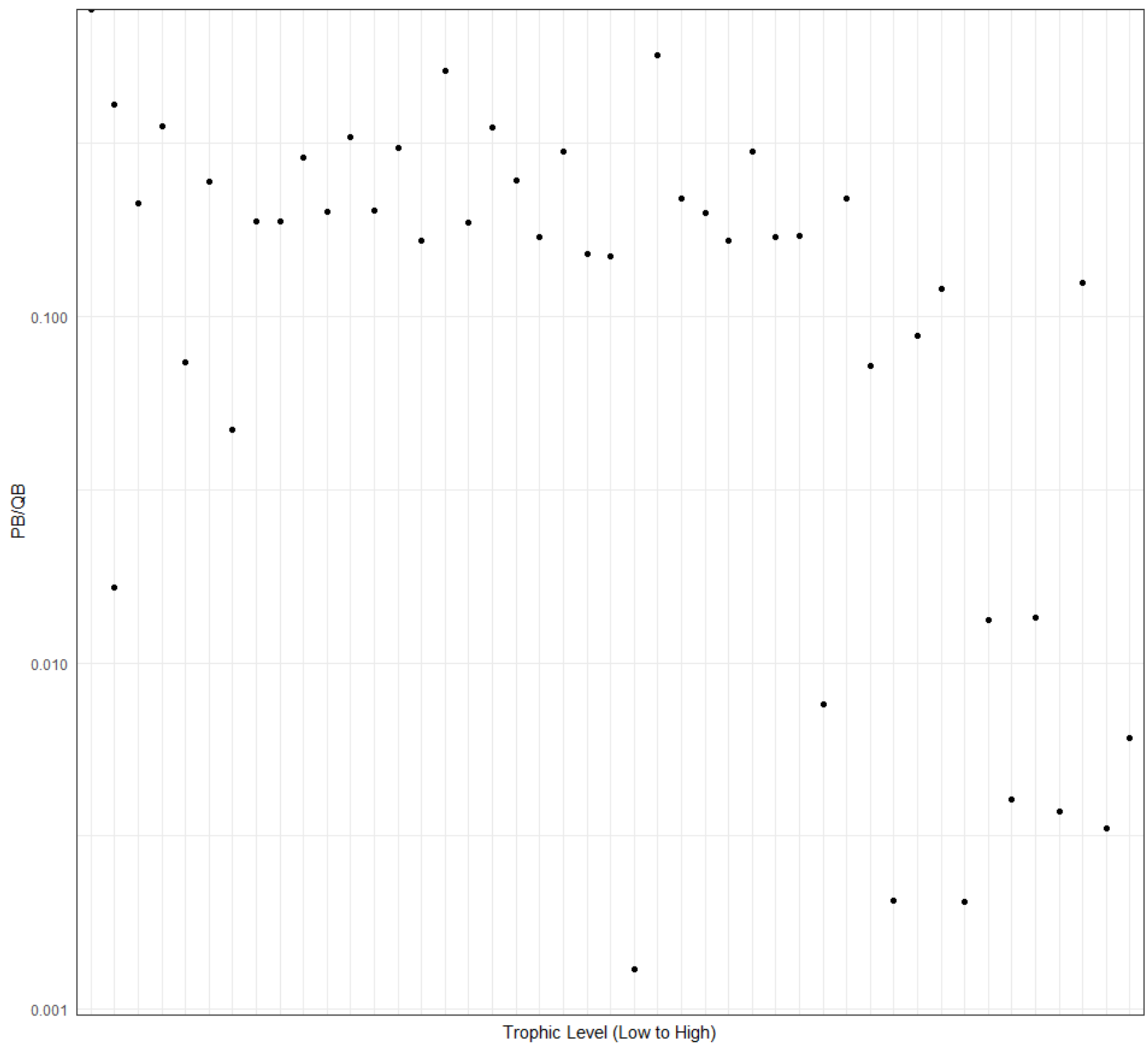

Figure S6: Scatter plot of production per consumption by trophic level as part of the pre-bal diagnostics (Link et al. 2010) as part of the pre-bal diagnostics (Link et al. 2010). Trophic level increases from left to right.