Dear Dr. Tierney,

Thank you for the invitation to resubmit our paper, "Estimates of Chinook salmon consumption in Washington State waters by four marine mammal predators from 1970 – 2015". The reviews from the associate editor and 3 reviewers were very thorough. We have acknowledged the criticisms by the reviewers and have fully integrated their advice into our revised document.

The two largest concerns raised by reviewers were the need for additional sensitivity analyses and a better explanation of the methods. We have conducted three sets of sensitivity analyses that we think will clarify the relative importance of the bioenergetics parameters, and we have also included more detailed methods or explicitly referred the reader to details in the appendix.

There were a number of smaller concerns raised by the reviewers, which were either errors on our part, or small issues that needed additional clarity (including making all of the code public, and adding additional methods). These issues have been fixed, and we've incorporated all of these more minor suggestions into the manuscript. Our detailed response to each is included here - please let us know if any of these responses are unclear, or the reviewers request additional information.

Sincerely,

Brandon Chasco

Comments to the Author:  
All of the reviewers think this paper important and useful.  Two believe that major revisions and another cycle of review are necessary while the third would like to see minor revisions.  I agree with the majority and recommend that the authors address the new comments with the expectation of another review cycle.  
  
AE summary of major points:  
  
1) None of the reviewers are satisfied with the technical explanation of the modeling.  Reviewer 1 attributes this to a broken GitHub link or inadequate explanation in the text while the other reviewers see a need for more information in the text.  I am not comfortable with using GitHub to convey essential technical details and feel the paper should stand on it own.  Please enhance the level of technical details to a point that will satisfy the reviewers and without making the paper overly long (conflicting goals, unfortunately).

**We appreciate the opportunity to resubmit our manuscript (and acknowledgement of the conflicting goals between a paper that provides technical details but isn’t overly long). The Github issue was entirely our fault, not the reviewers (we’ve now changed the repository to be publicly accessible). We’ve also made significant changes (detailed below) that increase the detail in the modeling in the paper and we think address all of the reviewers’ concerns.**

2) Two of the reviewers feel that uncertainty in the results is not adequately described and I agree.  This was an issue in the previous review also.  The authors assert that the main sources of uncertainty have been addressed and believe that the main results are fairly certain.  However, this seems unlikely given the large number of assumed parameters, model simplifications and likely overconfidence in assumed functional relationships.  Please revise the paper to more completely list, describe and quantify uncertainties in the calculations and main results.  The extra explanation can be in the form of augmented calculations or more text in the Discussion section.  I think that acknowledging and describing the uncertainties is more important than arguing that they are minor.  In any case, it is easier to recommend publication for a paper with somewhat uncertain results than a paper that conveys a false sense of precision.  The paper will have to satisfy the reviewers in this regard.  I am likely to recommend rejection if these points are not addressed in the next and hopefully final revision.

**We thank the reviewers for the opportunity to improve the paper with additional sensitivity analyses. We have included three different methods for testing the sensitivity of the model and uncertainty in the model inputs: individual parameter perturbations (IPP), relative partial sums-of-squares (RPSS), and the 3x3 contingency plots from the previous analysis. The IPP and RPSS methods systematically test model sensitivity to 20 parameters or assumptions (two new figures added), identifying those that are most influential in driving model results; included in the tested parameters are diet fractions and energetic content of Chinook salmon based on O’Neill et al (2014). The contingency plots focus on uncertainty in the species-specific multipliers for the estimating predator energy demands from the Kleiber model, the weight and abundance of pinnipeds, the fraction of age-0 smolts in the pinniped diets, and the length of the smolts when they first reach the ocean.**  
Reviewer 3 suggests that more information about the salmon fishery would be helpful, particularly since the paper is driven by problems with rehabilitating it.  Please try to accommodate this suggestion.  
  
**We have included additional data on fisheries harvest in Figure 3 as per the reviewers request and made a point of these findings in the discussion.**  
  
Reviewer(s)' Comments to Author:  
\*\*If applicable, Reviewer File Attachments may be found in Manuscript Central in your Author Center. Click on "Manuscripts Awaiting Revisions". Click on View Decision Letter. Reviewer File Attachments are located at the bottom of the screen.\*\*  
  
Reviewer: 1  
  
Comments to the Author  
This is an important and timely paper that will be of interest to the readership of CJFAS.  It was a pleasure to review.  I have two fairly minor points about the analysis, but lack of clarity on those points make it difficult to assess whether the issues are minor or major.  First, the methods refer to code on GitHub, but the link is broken. Either the link should be fixed (so a reviewer can see the methods), or the methods require additional detail in the text. Either way, the methods should stand alone.  Secondly, the paper seems to make arbitrary decisions about sources of uncertainty (and potentially bias) that were included or excluded. Some parameters were given sensitivity tests.  Other sources of uncertainty (or even bias, see below) were dismissed with an unsupported statement that the model addressed the biggest source of uncertainty.  That may well be true, but I’ve outlined a few places where large sources of uncertainty may have been ignored, and where confident assertions at least need to be referenced.  Until seeing more detail on the model, it is difficult to know if the paper requires minor editorial revision or something more. I have provided a very long list of places where more clarity is needed. I suspect that the answers to many of these questions are in the code on GitHub, in which case a response could just refer to the code.  
  
**We agree with the editors and reviews’ comments that the paper should stand alone. All of the material on Github is meant to make all of the methods, the compilation of considerable amounts of data and previous results, as well as calculations done for the paper entirely transparent, and allow other researchers to use this code for similar exercises (either in the NE Pacific) or focused on other species in other ecosystems. The broken link to Github was entirely an oversight on our part – the repository was set to private, and we’ve since made it public (this was our original intent). The paper also now refers to the buildModel.r for the base case scenario for this paper.**

**To address major sources of uncertainty and model sensitivity, we have now added new systematic sensitivity tests (two new figures), applying an individual parameter perturbation method, and a residual partial sums of squares method. These complement the 3x3 contingency plots (which test effects of large uncertainties in key inputs) and illustrate the importance of parameters such as smolt length, Chinook salmon energy consumption, and most parameters related to harbor seals.**

**We have added some additional detail in the methods, as noted below.**   
  
Title:  Is the area broader than Puget Sound? As written, it sounds as though it covers the Salish Sea. If not, perhaps “Puget Sound and adjacent waters” or “Washington state inshore waters”

**Thanks – we have now changed the title and text throughout to reflect that this is meant to be state-wide, not just Puget Sound**

Scope:  
There seems to be some overlap in themes and authorship between this paper and a recent one by Adams (<https://www.researchgate.net/profile/Jesse_Adams7/publication/301779569_A_century_of_Chinook_salmon_consumption_by_marine_mammal_predators_in_the_Northeast_Pacific_Ocean/links/57335b1208ae9f741b2611ff.pdf>), which is not cited. As I read it, this paper picks up where Adams et al. (2016) left off, and implements a recommendation made by that paper to develop energetic models for important predators of Chinook salmon.  That context should be noted, because the paper by Adams helpfully makes the raw diet data available in the supporting information file.  Perhaps the authors could make some comment about the ability to modify their code for use in other systems? The discussion could use some additional commentary on the generalizability of the issue, and the model/approach as a way to explore it.

**We agree that referencing the Adams et al. paper is useful, since that paper was largely a review / synthesis of US West Coast marine mammal diet studies (all available on Github) that is particularly relevant as we consider scaling the present work to cover a broader geographic range.**

**Text added:**

**“…In reality the Chinook salmon in inland waters are a mixture of U.S. and Canadian stocks, and the marine mammals predators on the outer coast (from California to Alaska) and their consumption of Chinook salmon (Adams et al. 2016) may also be impacting these U.S. stocks….”**

**The repository is now public. I have included a buildModel.r that runs the model and produces the output for the base case scenario. All of the figure outputs are listed as scripts as well.**

L 85/86.  Are there predators other than avian and marine mammal predators worth mentioning? Is it worth noting that fish (including sharks) may also be important predators of Chinook salmon, either at the juvenile or adult stage? This perspective is important, because many countries use incomplete information to justify culling marine top predators:

**We agree that it is not appropriate to place so much of the emphasis of declining salmon stocks on a single predator. We thank the reviewer for raising this point.**

**Text added:**

**“ In addition to marine mammals, other non-marine mammal predators may be also limiting Chinook salmon recovery: aggregations of avian predators along the Columbia River are thought to consume 5-12 million Chinook salmon juveniles annually (Roby et al. 2003), and spiny dogfish that congregate near hatcheries in British Columbia are thought to consume between 0.5 - 7 million juvenile salmon annually (Beamish et al. 1992). Additional Chinook salmon predators include herring (Ito and Parker 1971) and salmon sharks (Nagasawa 1998). Quantifying the magnitude of marine mammal predation and putting this in the context of other factors impacting Chinook salmon is therefore becoming increasingly important.”**

**In the conclusion we also emphasize additional predators:**

**“Further, there are other potential predators (harbor porpoise (*Phocoena phocoena*), cormorants (*Phalacrocorax* spp.)) that are not included in our modeling efforts”**

L 148.  Thanks for including the link to the code on GitHub, but the link is broken. I have done my best to review the paper without seeing the detailed methods, but I suspect the answers to many of my questions are included in that code.

**Thank you, we have now made the link public.**

L192-194:  “we focused our modeling work on the largest source of uncertainty (fraction of Chinook salmon in the diet of each predator) rather than uncertainty in bioenergetics parameters.”

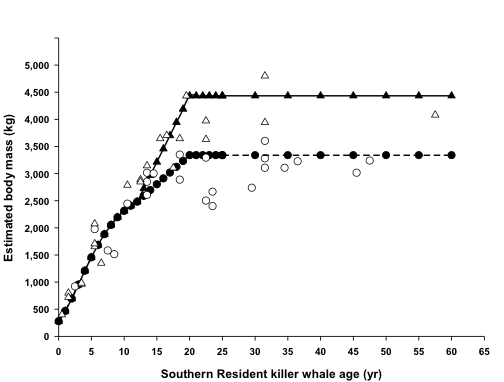
Is there a reference for this claim?

**This statement has been removed, and we now systematically test model sensitivity to 20 different input, using two methods (RPSS and IPP), considering parameter or input CVs of 2%, 10%, and 20%. For several key parameter we also test the effects of very large (50%) uncertainties in data or model inputs (3x3 plots). These methods illustrate that the model is indeed sensitive to fraction of Chinook salmon in the diets of harbor seals; however we also consider impacts of uncertainty in bioenergetics parameters (e.g. activity multipliers).**

For southern resident killer whales, there is evidence that uncertainty in body size may be almost as important in estimating prey requirements than uncertainty in winter diet (Williams et al. 2011). Has this been resolved with new field measurements of body size and a consensus view of the best model to use when predicting mass from length? If not, the statement in the methods should be reworded to be less conclusive, and it should be noted in the discussion as a caveat.  To clarify, the fact that North Pacific killer whales are much larger than the captive Icelandic killer whales used in previous bioenergetics studies means that this may be a source of bias, not uncertainty. That would call into question the statement on L195-196, “this uncertainty would not alter the average consumption estimates…”  No doubt the authors have thought of this, but the statement needs support.

**The reviewer is correct that there are length (and subsequently body mass) differences between Icelandic killer whales and killer whales in the NE Pacific. To clarify, body masses of Icelandic whales were not used in the Noren (2011) paper. Noren used the body mass growth curve for captive whales from Clark et al. 2000 (this curve was comprised of Icelandic and NE Pacific resident whales) for southern resident killer whales up to 12 yrs of age and then constructed the growth curve for animals aged 13 yrs and older based on the shape of growth curves from wild Icelandic whales but calibrated with larger masses of resident killer whales in the NE Pacific.**

**The estimated mass at age in Noren 2011 are verified from length measurements of free-ranging, known-aged individual southern resident killer whales. The weight-at-age estimates in the Noren (2011) paper are equivalent to weights calculated from lengths** **of known-aged individuals measured by Fearnbach et al. (2011). Weights are calculated from body length using the equation from Bigg & Wolman (1975) that was derived from actual measurements taken from captured north east Pacific killer whales, which mainly consisted of residents. The masses for female and male killer whales aged 1-65 years old reported in Noren (2011, solid shapes) and the masses calculated from body lengths of known-aged individuals measured in the field by Fearnbach et al. (2011,open shapes) are shown in the figure below. The comparison shows consistency between the two for both males (tirangles) and females (circles).**



**Reference: Bigg, M. A., and A. A.Wolman. 1975. Live-capture killer whale (Orcinus orca) fishery, British**

**Columbia and Washington waters, 1962–1973. Journal of Fisheries Research Board Canada 32:1213–1221.**  
  
L207-208.  It seems odd to refer to Center for Whale Research data as “mark-recapture surveys” and the phrase “since 1976 there has been a complete census of the population” implies that there is only one census. Perhaps reword to remove the mark-recapture comment and note that there have been complete censuses conducted annually since 1976?

**We have updated to include the comment about perfect detection probability.**

**The CWR data of adults can be considered a mark-recapture survey with perfect detection probability. While the adults have been censused since 1976, it’s important to keep in mind that these data are opportunistic, and imperfect. To get into the weeds, the CWR data include approximate birth dates for animals that have been born and lived, but don’t include a complete census of all births (neonate animals that were born but didn’t survive). All other killer whale datasets used to generate population counts in the NE Pacific are based on mark-recapture, so for consistency, we left the language as is.**

L265:  Are killer whales absent during the winter months? I thought Hauser only looked at summer months, but that the whales do use this area to some extent in winter (Fig 6; <http://www.nmfs.noaa.gov/pr/pdfs/recovery/whale_killer.pdf>).  You say “nearly absent” on line 426. Should this statement be qualified? Does it affect the result?

**The text has been updated to reflect SRKW are present infrequently and in very low numbers.**

**Killer whales are largely not present in inland waters from ~ November or December through April. The historical distribution is largely unknown, but since the recovery plan for SRKW was written, NOAA has conducted a number of years of satellite tagging.** [**https://www.nwfsc.noaa.gov/research/divisions/cb/ecosystem/marinemammal/satellite\_tagging/**](https://www.nwfsc.noaa.gov/research/divisions/cb/ecosystem/marinemammal/satellite_tagging/)

**We’ve largely learned that J pod tends to spend the majority of its time in the Salish Sea or mouth of the Strait of Juan de Fuca, with occasional trips to the outer Washington coast. The other pods are largely coastal during this period (they’ve made several very short trips at the end of December to Puget Sound in recent years – possibly targeting chum salmon) – but these visits are short, and don’t include the entire pod and / or population.**

L464-465; 534 etc.  The term, “loss” implies a value judgment here, because consumption by pinnipeds is called a loss but consumption by killer whales is not. Suggest you stick with “consumption” as used elsewhere in the paper, or “mortality” as used in Figure 4.

**Agreed, and changed to mortality.**   
  
L539-540:  “Though our model is sensitive to assumptions regarding both marine mammals and Chinook salmon, the main results are robust to these uncertainties” — This reads like an overconfident statement begging to be challenged. The methods (and points raised above) include a long list of parameters in which uncertainty was ignored or underestimated. Perhaps this could be toned down, or identified as an action item to follow up with additional research? I don’t think it detracts from the paper’s main conceptual points to note that it is difficult to assess model robustness until you’ve included (or simulated) the main sources of uncertainty.

**In terms of tone, we now state that “Though our model is sensitive to assumptions regarding both marine mammals and Chinook salmon, the main results consistently suggest that across a broad range of parameter values, harbor seals and fish-eating ‘resident’ killer whales account for the large majority of consumption of Chinook salmon biomass…”**

**In terms of analyses to address uncertainty and sensitivity, we have added the two sensitivy tests (RPSS and IPP), in addition to the 3x3 contingency plot testing effects of large variations (+/- 50%) of some model inputs. The methodology identifies that our results are consistent across tested parameterizations, though certainly more elaborate uncertainty tests could be performed (for instance related to bias).**

L575.  The California sea lion range does go slightly north of Puget Sound, but I doubt it affects your inference.  I understand that the last estimate was ~3000 in southern BC. Olesiuk’s estimate is large, relative to N reported in Figure A-2. Olesiuk may have included Washington inland waters, or it may be out of date, but it’s worth revisiting the statement that this species is at low abundance north of Puget Sound.  
  
Olesiuk, P.F. and M.A. Bigg. 1988. Seals and sea lions on the British Columbia Coast. DFO Special Publication, Pacific Biological Station, Nanaimo, B.C.

**Thanks, we’ve included this additional citation. We’d wrestled at length with the best population size estimate for the region, and ultimately deferred to expertise of Bob DeLong and other researchers at the Alaska Fisheries Science Center who have been involved in these surveys. Unfortunately, many of the federal (NOAA, DFO) and state surveys are out of date, or difficult to interpret (e.g. some only surveyed only a portion of the range). Those that do exist lack the temporal and spatial overlap needed to provide a good estimate of abundance. The other important point to make is that peak counts in inland waters are thought to have declined since the mid-late 1990s, and there are no females present.**

References:  Check reference software, because several citations are duplicates (e.g., Ford et al. 1998; Winship et al. 2002). Some are incomplete and would be difficult to track down without URLs or some other information (e.g., the NMFS Stock Assessment Reports).

**Thank you, references are corrected now. We have included URL for all technical memos.**

Table 1.  
The predicted weight at age of North Pacific resident killer whales relies heavily on length-weight relationships derived from Icelandic killer whales applied to lengths of Pacific resident at known age and guessed weights (Bigg & Wolman 1975). That is to say, Pacific resident killer whale carcasses have not been weighed. Predictions from various length-weight curves differed substantially, which would affect predictions of prey requirements (Williams et al. 2011).  Is this model robust to that source of uncertainty (or potentially bias)? The energetic demand reported in Williams et al. (2011) includes uncertainty in body size, winter diet and caloric content of Chinook salmon. Does Noren (2011) include those sources of uncertainty, or resolve them somehow?  Noren (2011) is not in the reference list.

**Please see comments above regarding killer whale weight-at-age. Additionally, we have included the weight-at-age of predators, including killer whales, in our two sensitivity analyses (labeled as “mass” in the figures). As noted in the main text, parameters for killer whales (including weight-at-age) have minimal effects on predicted numbers of Chinook salmon consumed, but do strongly influence the predicted biomass of Chinook salmon consumed in the cases where we allowed very large CVs (20%) around parameters. Also note that these sensitivity tests now include caloric content of salmon and diet fractions (labeled as “salmon condition” and “chinook diet fraction” in the figures).**

**Text added:**

***Model predictions were more sensitive to parameterization of harbor seals than they were to parameterization of other marine mammal predators. However, total biomass consumed responded substantially when parameters for killer whales had a high CV of 20% (grey bars in Figures 5 and 6) .***

**Noren (2011) has been added to the reference list.**

The predicted weight at age for pinnipeds relies on data from the Gulf of Alaska. How do these estimates differ from the predictions of Trites & Pauly (<http://www.nrcresearchpress.com/doi/abs/10.1139/z97-252#.V3L575NViko>)?

**We believe the estimates of weight-at-age from actual observations of dead Steller sea lions used in the Winship et al. (2001) are likely to be more appropriate than mean weight estimates using a meta-analysis in Trites and Pauly (1998) paper. In the context of the broader goals of the paper, we demonstrate via the sensitivity tests (RPSS and IPP methods) that estimates of total consumption of Chinook salmon are not strongly influenced by assumptions regarding California or Steller sea lion size-at-age; harbor seal size at age is more important.**

Table 6.  Is this in units of 5-year-old Chinook of the size listed on line 315?  Suggest repeating this year, because Tables 4 and 5 do not include a 5-year-old Chinook. Or maybe it does, depending on local syntax to account for the time Chinook spend in freshwater. Suggest clarifying, either here or in the methods, what is meant by a generic adult Chinook in these among-species comparisons.

**This has now been clarified in the text and table to reflect that a 5 year old Chinook is ocean age 4. Additionally, the number of adults in table 6 refers to the number of adults integrated across all adult ages.**  
  
Reviewer: 2  
  
Comments to the Author  
Overall this manuscript adds important information to the broader context of consumption by marine mammals, and specifically to the application of Chinook salmon population impacts. With a few clarifications and additional discussion, I would recommend this manuscript for publication at CJFAS.  
  
The “Modeling energetic demands of predators” section of the methods need some clarification. Wording is ambiguous for describing the energetic equations with phrases like “often disaggregated” or “can be extended”, and clarification needs to be made as to what equations were actually used in the model. It would help to have a total bioenergetics equation included with all parameters that were used to see where things like the generic stage-specific parameter fits in. Table 3 should include the parameter values that are referred to in the methods text.

**We thank the reviewer for pushing for clarity on the presentation of the bioenergetics. We now emphasize this (text added below)**

***… The body mass for the predators was taken from life history tables or estimated based on growth models in the published literature (see Table 1 for references). Overall, the core energetic equations are Equation 2 for total energetic demand, combined with detailed representation of activity costs (Equation 3).***

**Table 3 lists the \*processes\* that are explicitly included in each model: reproduction (P), Growth (GC), efficiency (Ef), and Activity Costs (AC). To keep the table readable the functional forms and related parameters for these processes are detailed in Tables A1, A3, and A4, taken from the published bioenergetics studies. To clarify this, Table 3 legend now reads:**

**Table 3. Processes of the bioenergetics models by species where “X” denotes the processes explicitly included in the energetic models: P = reproductive costs; GC = growth costs; Ef = metabolic efficiency; AC = activity costs. Parameter values and functional forms are detailed in Tables A1, A3, and A4.**

**The phrase “any generic stage-specific parameter” may have been misleading; we simply intended to illustrate that we had a consistent methodology for applying juvenile and adult parameterization to each age class of marine mammal. We have now deleted “generic” to avoid this confusion.**

More information needs to be included in the methods section on diet compositions including sources used in this study, perhaps in a table. The discussion section needs to include a discussion of potential biases of the diet data used. If only scat analyses are used, the potential for pinnipeds feeding by belly biting larger salmon needs to be discussed, as otoliths would be missed in scat analyses. Also, scat may greatly overestimate consumption of salmon if they are biased towards very inshore samples.

**Thank you for the suggestion. We feel we have improved our description of how we estimated the pinniped diet fractions in our paper. Please see lines 301 – 326. Given the number of tables and figures currently in the paper, we chose to keep our description confined to the text only. However, I believe this new text illustrates specifically how the fractions were calculated, as well as the two sources from which the information was collected.**

**It is true that there are undoubtedly many biases in the diet data, and local scientists are working hard to resolve how these biases may arise from spatial and temporal differences in pinniped behavior and prey availability. However, even for a well-studied system such as Puget Sound the level of bias in the diet data is only just not beginning to be understood. We have chosen to focus our discussion on the sensitivity of the model to estimates of juvenile and adult diet composition, and recognize that more accurate and precise estimates of diet composition will always be needed.**

Figures 1-3 seem to be low resolution.

**We have updated the figures with tiff instead of png files, to improve resolution. However, the some of the low resolution pixelation is actually just the low abundance or biomass.**

Figure 2: Explain what Ocean0-Ocean4 represent.

**We have now clarified this in response to comments from Reviewers 1 and 2. We use Ocean age throughout the text to refer to the number of years a salmon has spent in the ocean.**  
  
Reviewer: 3  
  
Comments to the Author  
Please see attached file**Review of CJFAS-2016-0203.R1 (Chasco et al.)**

Manuscript title: Estimates of Chinook salmon consumption in Puget Sound area waters by four marine mammal predators from 1970-2015.

General Comments:

This manuscript uses a bioenergetics modeling approach to estimate consumption of Chinook salmon in the Puget Sound region of Washington by three species of pinnipeds that have been increasing in the region since the passage of the Marine Mammal Protection Act of 1972. The impetus for this study is to test the hypothesis that consumption of salmonids by these recovering pinnipeds is limiting recovery of the ESA-listed Puget Sound population of Chinook salmon through predation, and limiting the recovery of the ESA-listed population of killer whales through competition. I agree with the authors that “this research is a valuable step toward [understanding] the mechanisms that lead toward trends in marine survival [of] threatened Chinook salmon, and provides a framework for coast-wide understanding of [pinniped] predation impacts on Chinook salmon and dependent predators such as Southern Resident killer whales.” The study’s conclusion is that, of the three species of pinniped investigated, harbor seals are the most likely to be competing with commercial/sport fisheries and killer whale dietary requirements in the Puget Sound area, and that the two sea lion species are unlikely to be having a significant impact on Chinook salmon recovery.

Despite the value of this research and the importance of its findings, there are parts of the manuscript where this reader became uncomfortable with the strength of inferences drawn from model outputs based on the limited available data for the input parameters. One crucial assumption inherent in the analysis, namely that all mortality of Chinook salmon smolts due to pinniped predation is 100% additive, was not apparently acknowledged by the authors. It seems very unlikely to this reader that there is no compensatory mortality associated with consumption of juvenile salmonids by pinniped predators, especially harbor seals. In other words, it seems very likely that at least a fraction of the smolts consumed by pinnipeds where more likely to have died from other causes than the run at large, and this would necessarily reduce the adult equivalents of smolt consumption by pinnipeds. Of course, measuring the degree of compensation in smolt mortality associated with pinniped predation would be extraordinarily difficult, but acknowledging that it is almost certainly greater than 0% seems obligatory.

**Response: this is a good point. You’re right that it’s exceedingly difficult to measure well, but we agree that it’s something worth acknowledging and have altered the text to reflect this.**

***Text added: paragraph “One of the strong assumptions made by our model is that Chinook mortality is additive (rather than compensatory….”***

**As background, motivation for this project and future development of our coastwide model was largely driven by feedback and peer-review of salmon management and evaluating relative effects of cetaceans (killer whales) and fisheries on Chinook salmon (Hilborn et al. 2012, see** [**http://www.westcoast.fisheries.noaa.gov/publications/protected\_species/marine\_mammals/killer\_whales/recovery/kw-effects\_of\_salmon\_fisheries\_on\_srkw-final-rpt.pdf**](http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/killer_whales/recovery/kw-effects_of_salmon_fisheries_on_srkw-final-rpt.pdf) **)**

**One of the largest areas of criticism of the bilateral panel was assumptions about Chinook natural mortality; issues include (1) the management models assume M is static across years, (2) mortality from predators should be density dependent, etc. These concerns and others were outlined in Appendix B of the above report, titled “Competing Risks of Death Modeling”. The panel’s suggestion was to construct a model similar to what we’ve done here, partitioning total mortality into natural mortality, mortality from various predators, and mortality from fishing. Our model is more complex than that proposed in the CRD framework, and although mortality is still additive, our opinion is that this represents a step forward to better understanding the potential roles of predation and species interactions on salmon.**

**The compensatory mortality hypothesis has been described in various ways. One interpretation is that prey consumed by predators would “otherwise be lost to natural mortality” (see Bowen & Lidgard 2013, Mammal Review). In this description, natural mortality may be a catch-all for all non-fisheries mortality, but if it is interpreted only as representing non-predation or fisheries mortality, we don’t know that this would be the case with Chinook (though we agree, from our adult equivalents calculations, that the majority of juvenile Chinook that would escape predation would otherwise die). As we’re interpreting it, compensatory mortality arises when one force of mortality increases in response to another being reduced (e.g. predation from one predator is replaced with another). Support for compensatory mortality on salmon has been suggested in the region (Steve Haeseker’s work on cormorant predation of steelhead in the Columbia River) and in other ecosystems around the world that include avian or marine mammal predation on fishes.**

**Part of the challenge in thinking about compensatory mortality for this system is attempting to identify which other sources of mortality might replace pinniped predation (if for example, there was a reduction in pinniped numbers). During their adult life stages, the total number of Chinook consumed by fisheries and killer whales is thought to be essentially constant (see a longer discussion of this in Hilborn et al. 2012, link above). So juveniles that escaped predation wouldn’t experience lower survival as adults. Much of the salmon mortality is also thought to occur early in the life stage, perhaps as smolts are reaching the ocean (seals may capitalize on larger aggregations near river mouths), so increased mortality during this life stage may make the most sense. For mortality to exactly be compensated for, however, there would likely have to be an increase in other predator populations (and many species in the region are thought to be declining – see for example Vilchis et al. 2014).**

**One of the other changes in the region has been increases in populations of mammal-eating transient killer whales. While these transient whales are present for much of the year (consuming pinnipeds), there have been several recent years when transients have made extended visits to Hood Canal. Under the compensatory mortality hypothesis, salmon or steelhead survival would not be sensitive to the abundance of seals. However, recent estimates of fish survival has shown that survival is extremely high when transient killer whales are present (and seal abundance is locally depleted) (B. Berejekian, pers. comm).**

Specific comments:

Page 2; line 31: Include scientific names for Chinook salmon and killer whales.

**Added**

Page 2; line 34: “juveniles” should be singular.

**Emended**

Page 2; line 36: “consume” should be past tense.

**Emended**

Page 2; lines 34-36: Need to add that this finding assumes that mortality of smolts due to pinniped predation is 100% additive.

**The assumption of additive mortality is now handled in the Discussion:**

**Paragraph beginning:**

**“*One of the strong assumptions made by our model is that Chinook mortality is additive (rather than compensatory)…”***

Page 2; lines 36-38: While this reader agrees with this assertion of the importance of ecosystem perspectives, the manuscript doesn’t really address the question of whether pinniped predation and killer whale predation, in conjunction with commercial/recreational fisheries, is limiting the recovery of Puget Sound Chinook salmon. It seems that smolt:adult returns (SARs) have declined for Puget Sound Chinook, and that there is some evidence that much of this mortality occurs soon after leaving freshwater. This ambiguity could be at least partly resolved by expressing numbers of Chinook salmon consumed as a predation rate (estimated number of adult equivalents consumed/estimated number of adult equivalents available). I also think that human harvest should at least be mentioned in the abstract, since it is roughly equivalent to killer whale take and pinniped take, taken separately.

**This is true we do not calculate predation rate directly. There is a lot of evidence from Puget Sound (Quinn et al. 2005) and Canada that producing more smolts has led to lower survival rates (Noakes et al. 2000), and Beamish has co-authored numerous papers showing that much of the mortality is occurring in the early marine phase. While we definitely agree that a full life cycle model is a worthy task, this paper is more focused on the bioenergetics demands of the predators and the relative consumption of those predators. We also now add panels to Figure 3 to include information on the scale of commercial and recreational harvest.**

Human harvest is now mentioned in the Abstract as well as the Discussion, and Figure 3:

Abstract:

**, and roughly five time greater than the combined recreational and commercial harvest**

Discussion:

**As a comparison, potential mortality from pinnipeds based on adult equivalents are comparable to commercial catches of Chinook salmon from Washington State inland waters, which have declined from approximately 250,000 adult salmon in 1980 to 100,000 in 2007, and recreational catches within Puget Sound have declined from approximately 150,000 to 50,000 (Comprehensive Management Plan for Puget Sound Chinook salmon: Harvest Management Component 2010)**

Page 3; lines 58-68: At least two of the examples of marine mammal-fisheries conflicts cited here are confounded by known overharvest by the fishery. The scientific name for the genus of Pacific salmonids should be included on line 67.

**We changed ‘impacts’ to ‘interactions’ to soften the inference.**

Page 4; line 70: (*O. tshawytscha*)

**Changed**

Page 4; line 71: “northeastern”

**Changed**

Page 4; lines 78-79: Should specify that the ESA applies to only the U.S.

**Updated to refer US stocks only.**

Page 5; lines 87-89: I agree that it is important to quantify the magnitude of marine mammal predation on Chinook salmon in the Puget Sound area and put it in the context of other factors affecting population growth. I think that quantifying magnitude depends on expressing losses as a predation rate (consumed/available), and putting this predation in context necessitates comparison with fisheries harvest. This is briefly discussed in the Discussion section, but I think it deserves more attention.

**Our discussion section assumes that all fish in Puget Sound are hatchery and calculates the predation rate. As we mention above, a full salmon life cycle model that would include calculating predation rates is a worthy task, but the scope of this paper is more focused on the bioenergetics demands of the predators.**

Page 5; line 94: Change “endangered resident killer whales” to “resident killer whales, which are listed as Endangered in the U.S. (the Southern Resident population)”.

**Done**

Page 5; line 104: Change “season and spatial location of feeding.” to “spatial and temporal distribution of foraging on salmon.”

**Done**

Page 6; line 117: Replace “was” with “were” and add “U.S.” before “Endangered Species Act”.

**Done**

Page 7; lines 155-160: I don’t see where the model for energetic demands of the predators incorporates thermoregulatory costs. Was the assumption that these pinnipeds were always in their thermoneutral zone, or that the heat increment of feeding always was adequate to meeting thermoregulatory costs? How the model incorporates thermoregulatory costs in estimating energy demands needs to be stated explicitly in the Methods.

**Our approaches synthesizes the published bioenergetics models from Howard et al. (2013), Winship et al. (2002), Weise and Harvey (2008), and Noren (2011); thermoregulatory costs are not explicitly included in those models. The assumption is that thermoregulatory costs are included implicitly, primarily in the activity costs. We now state this in the methods (with bold text added):**

***…California sea lions and killer whales are sufficiently small and that the majority of the energetics costs are accounted for by the activity costs (i.e., the reproductive and growth costs implicitly included in activity costs). Consistent with the published bioenergetics literature (Table 1), we assume thermoregulatory costs are also implicitly included in activity costs.***

Also, is the “fraction of total energy not lost to heat or excretion” equivalent to metabolizable energy coefficient (MEC)? If so, I suggest using this terminology.

**Efficiency in our model () is efficiency after accounting for digestive heat and excretion (see Table A-4). This is now clarified in the main text (bold text changed) as:**

***… and is the fraction of total energy not lost to digestive heat or excretion (Appendices Tables A1-A3, Figure A-1, Figure A-2).***

**And is also now clarified in the Appendix, subsection *Efficiency:***

***Efficiency measures the energy that is lost through excretion and digestive heat before…***

**We are reluctant to use the phrase “metabolizable energy coefficient” because at least in some instances this does not include digestive heat (Beaupre et al. 1993, *Functional Ecology***

**Vol. 7, No. 3 )**

Page 13; line 261: Here and throughout the manuscript, insert “,” after e.g.

**Corrected, thank you.**

Page 13; line 277: “Chinook salmon” instead of “Chinook” here and throughout the manuscript.

**Corrected, thank you.**

Page 13; line 280: Change “predator’s energy” to “a predator’s energy demand.”

**Corrected, thank you.**

Page 14; lines 292-294: The estimate of the fraction of Chinook salmon in harbor seal diets (0.068) is a crucial input parameter for the bioenergetics model and the main conclusion from this study, yet no estimate of variation or error in this estimate is provided, and the paper that is cited for this point estimate (Thomas et al. 2016) is not in the Literature Cited section. This same paper is cited subsequently a number of time for key input data to the bioenergetics model. Because the Chinook salmon fraction is so small (< 10% of the diet), any error in this estimate could result in large changes to the take-home message of this study, so bolstering its reliability seems important. The fraction of Chinook salmon in the diets of Steller and California sea lions are nearly the same as for harbor seals, presumably because of the similar approaches to estimating diet composition? This makes the 0.068 value for harbor seals even more important to justify.

**We now properly cite the recent Thomas et al. paper.**

**Two new sensitivity analyses now include consideration of diet fraction, and identify that model estimates of total Chinook salmon consumption is more influenced by harbor seal parameters (including fraction of the diet that is Chinook salmon) than by parameters for other pinnipeds.**

Page 15; line 312: Shouldn’t the SI unit for heat/work (kJ) be used throughout instead of kcal?

**We have updated the table to include kcal = 4.184 kJ**

Page 18; lines 374-379: These survival rates suggest that smolt mortality due to pinniped predation is 100% additive, and this assumption should be stated explicitly, since it is almost certainly inaccurate.

**We thank the reviewer for their suggestion and have included it within the text.**

**As background, motivation for this project and future development of our coastwide model was largely driven by feedback and peer-review of salmon management and evaluating relative effects of cetaceans (killer whales) and fisheries on Chinook salmon (Hilborn et al. 2012, see** [**http://www.westcoast.fisheries.noaa.gov/publications/protected\_species/marine\_mammals/killer\_whales/recovery/kw-effects\_of\_salmon\_fisheries\_on\_srkw-final-rpt.pdf**](http://www.westcoast.fisheries.noaa.gov/publications/protected_species/marine_mammals/killer_whales/recovery/kw-effects_of_salmon_fisheries_on_srkw-final-rpt.pdf) **)**

**One of the largest areas of criticism of the bilateral panel was assumptions about Chinook natural mortality; issues include (1) the management models assume M is static across years, (2) mortality from predators should be density dependent, etc. These concerns and others were outlined in Appendix B of the above report, titled “Competing Risks of Death Modeling”. The panel’s suggestion was to construct a model similar to what we’ve done here, partitioning total mortality into natural mortality, mortality from various predators, and mortality from fishing. Our model is more complex than that proposed in the CRD framework, and although mortality is still additive, our opinion is that this represents a step forward to better understanding the potential roles of predation and species interactions on salmon.**

**The compensatory mortality hypothesis has been described in various ways. One interpretation is that prey consumed by predators would “otherwise be lost to natural mortality” (see Bowen & Lidgard 2013, Mammal Review). In this description, natural mortality may be a catch-all for all non-fisheries mortality, but if it is interpreted only as representing non-predation or fisheries mortality, we don’t know that this would be the case with Chinook (though we agree, from our adult equivalents calculations, that the majority of juvenile Chinook that would escape predation would otherwise die). As we’re interpreting it, compensatory mortality arises when one force of mortality increases in response to another being reduced (e.g. predation from one predator is replaced with another). Support for compensatory mortality on salmon has been suggested in the region (Steve Haeseker’s work on cormorant predation of steelhead in the Columbia River) and in other ecosystems around the world that include avian or marine mammal predation on fishes.**

**Part of the challenge in thinking about compensatory mortality for this system is attempting to identify which other sources of mortality might replace pinniped predation (if for example, there was a reduction in pinniped numbers). During their adult life stages, the total number of Chinook consumed by fisheries and killer whales is thought to be essentially constant (see a longer discussion of this in Hilborn et al. 2012, link above). So juveniles that escaped predation wouldn’t experience lower survival as adults. Much of the salmon mortality is also thought to occur early in the life stage, perhaps as smolts are reaching the ocean (seals may capitalize on larger aggregations near river mouths), so increased mortality during this life stage may make the most sense. For mortality to exactly be compensated for, however, there would likely have to be an increase in other predator populations (and many species in the region are thought to be declining – see for example Vilchis et al. 2014).**

**One of the other changes in the region has been increases in populations of mammal-eating transient killer whales. While these transient whales are present for much of the year (consuming pinnipeds), there have been several recent years when transients have made extended visits to Hood Canal. Under the compensatory mortality hypothesis, salmon or steelhead survival would not be sensitive to the abundance of seals. However, recent estimates of fish survival has shown that survival is extremely high when transient killer whales are present (and seal abundance is locally depleted) (B. Berejekian, pers. comm).**

Page 18; lines 381-390: Why wasn’t the sensitivity of model outputs to the estimated fraction of Chinook salmon in predator diets (0.068, 0.064, 0.061) also explored? It seems likely that model outputs are highly sensitive to variation in the value of this key input variable, one for which no estimate of potential error is provided.

**We thank the reviewer for the opportunity to improve the paper with additional sensitivity analyses. We have now included two different methods for testing the sensitivity of the model to input parameters: individual parameter perturbations (IPP) and relative partial sums-of-squares (RPSS). The IPP and RPSS methods systematically test model sensitivity to 20 parameters or assumptions (two new figures added), identifying those that are most influential in driving model results; included in the tested parameters are diet fractions.**

Page 18; line 393: It is not clear to this reader why the values for daily energy demand of predators are considered “maximum”. Why weren’t average values or “best estimates” provided instead of maximums?

**The word ‘maximum’ was confusing and has been removed from the sentence. There are seasonal differences in the harbor seal energetic demands and the word maximum was intended to imply that the number reported was the within-year maximum energetic value.**

Page 19; lines 397-398: The range in numbers of juvenile salmonids consumed by pinnipeds presented here varies over an order of magnitude, yet it is not clear to this reader why harbor seal smolt consumption on a per capita basis is so much higher than for sea lions, especially when sea lion energy demands are an order of magnitude greater than for harbor seals.

**This is a good point and one that we have clarified in the text clarified. The peak abundance of sea lions occurs from late fall through winter and when smolts have grown considerably larger. Although sea lions are five to ten times larger than harbor seals, the smolts that are being consumed during winter are much larger and thus fewer numbers of them are needed to meet their energy demands (with additions in bold).**

**The peak period of occupancy within inland waters varies among predators (Figure A-3), thus estimates of the average number of juvenile Chinook salmon consumed daily by pinnipeds is affected by the growth of Chinook salmon throughout the year. B**ased on their period of peak occupancy within inland waters, numbers of Chinook salmon consumed ranged from 0.24 individual fish (**average smolt length of 300mm**) for male California sea lions during the winter months, to 5.4 smolts (**average smolt length of 95 mm**) per day for male and female harbor seals during the spring and summer months (Table 6).

Page 19; lines 398-400: Does this consumption of adult salmon include adult equivalents of juvenile salmon consumed?

**Clarified. Now states “not including adult equivalents...**

Page 19; line 401: Replace “their size” with “sexual dimorphism.”

**Done**

Page 19; line 402: Replace “was” with “were.”

**Done**

Page 19; line 405: Replace “predator” with “predators.”

**Done**

Page 19; lines 415-417: Replace this sentence with “In 2015, estimated consumption of individual Chinook salmon by Steller and California sea lions was closer to that of killer whales, …”

**Done**

Page 20; line 419: Add the word “estimated” to the end of the line.

**Done**

Page 20; line 429: Remove the word “thousand.”

**Done**

Page 21; line 459: Insert “compensatory mortality from” before “other sources of predation.”

**Done**

Page 21; lines 461-463: This sentence presents a key finding of the study, namely that there is likely a two order of magnitude difference in the impact of harbor seal predation compared to sea lion predation. This important result is largely obscured by the major differences in the scale of the y-axes in Figure 3 a-d. I suggest that the scale of the y-axes be the same, or at least make it clear in the Figure caption that there are major differences in the scale of the y-axes. These comments also apply to Figure 2; either make the scale of the y-axes the same or point out that they are different. Figure 3 would also be a good place to add Figure 3e, depicting the commercial and sport fishery harvest of Puget Sound Chinook salmon as a function of year.

**We also now add panels to Figure 3 to include information on the scale of commercial and recreational harvest and scaled all of the axes to the same range. As a result, the impacts of sea lions are almost undetectable relative to the other predators.**

**The comparison to commercial and sport harvest is also made in the text of the Discussion**

**“As a comparison, potential mortality from pinnipeds based on adult equivalents are comparable to commercial catches of Chinook salmon from Washington State inland waters, which have declined from approximately 250,000 adult salmon in 1980 to 100,000 in 2007, and recreational catches within Puget Sound have declined from approximately 150,000 to 50,000 (Comprehensive Management Plan for Puget Sound Chinook salmon: Harvest Management Component 2010)”.**

Page 21; line 464: Add the phrase “expressed as adult equivalents” after “potential losses.”

**Done.**

Page 22; lines 474-477: This is where the proportion of smolt losses to pinniped predation that is compensatory could have a large impact on the population level effects for Chinook salmon. Predicted impacts described here appear to be based on the assumption that smolt mortality due to pinniped predation is 100% additive, an assumption that is almost certainly not met.

**Please see above response regarding compensatory mortality, and the added paragraph “One of the strong assumptions made by our model is that Chinook mortality is additive (rather than compensatory….”**

Page 23; line 493: “Thomas et al. In review” is not cited in the Literature Cited section.

**We now properly cite the recent Thomas et al. publication.**

Page 23; line 503: Where does the estimate of 40 million smolts come from? Is there a source that can be cited? Does the 40 million include wild and hatchery released smolts, or just hatchery released? Is this number reliable enough to use in estimating predation rates (proportion of available smolts consumed by pinniped predators)?

**A reference has been added: Puget Sound Chinook Salmon Hatcheries. 2004. Washington Department of Fish and Wildlife & Puget Sound Treaty Tribes.**

Page 23; line 507: Insert “, respectively” after “1990s.”

**Added.**

Page 24; line 518: These are important estimates of harbor seal predation rates on smolts, but it is not clear from the information provided whether these estimates are major overestimates or whether these estimates are likely overestimates by trivial amounts.

**As mentioned above, a full salmon life cycle model that would include more careful calculation of predation rates on smolts is a worthy task, but the scope of this paper is more focused on the bioenergetics demands of the predators. At present we can only provide the rough estimates of predation rates for context (in the Discussion), with the caveat that they are certainly overestimates.**

Page 25; lines 533-536: This is a very important comparison and, in this reader’s opinion, should receive more emphasis, including adding as Figure 3e.

**To highlight this comparison, we have now added panels to Figure 3 to include information on the scale of commercial and recreational harvest.**

Page 25; lines 541-542: Does this statement apply to just consumption of Chinook salmon biomass by marine mammals, or by all predators, including humans? Need to clarify this statement.

**We highlighted that it is relative to the predators in our study:**

**Text edited:**

**… across a broad range of parameter values for predators in our study**

Page 25; lines 548-552: This sentence sums up a crucial caveat of this study: the uncertainty around estimates of diet composition of the pinniped predators. Until better, more reliable diet composition data are available for harbor seals and sea lions in the Puget Sound area, uncertainty will remain over the reliability of these estimates of Chinook salmon consumption.

**We agree, and to begin to address this we present sensitivity analyses that include pinniped diet composition These two systematic sensitivity analyses and the uncertainty analysis (which varied key parameters by +/- 50%) point to the importance of parameters related to harbor seals (including diet composition) and the proportion of chinook consumed which are smolts.**

Pages 26-27; lines 561-582: It is not apparent to this reader the purpose of this long paragraph on future research. There are enough uncertainties regarding the estimates of impacts of Puget Sound predators that it seems that future research should address those uncertainties before expanding the modeling effort to the entire northeastern Pacific. I recommend removing this section, as it adds very little to the scientific findings of the study.

**We agree and have removed this paragraph on future research, and have bolstered the handling of sensitivity and uncertainty with two new figures.**

Page 27; line 590: I don’t see the modeling results that support the assertion that harbor seal impacts are “larger” than fisheries or killer whale consumption, especially since fisheries and killer whales take almost exclusively adult salmon, and harbor seals take primarily smolts, mortality that is likely to be at least partly compensatory.

**This statement refers specifically to Figure 3, and we have now incorporated Reviewer 3’s suggestion that we add panels E and F to include time series of commercial and recreational catches.**

Page 27; lines 598-599: (e.g., harbor porpoise [*Phocoena phocoena*], cormorants [*Phalacrocorax* spp.])

**Added**

Page 42; Table 1: Replace “Bob de Long” with “R. DeLong.” Also, no citation for “Thomas et al. (In review).

**Thomas citation added and name of R. DeLong corrected.**

Page 43; line 924: Replace “papers” with “parameters.”

**Corrected.**

Page 45; Table 4: Use SI units (kJ) instead of kcal.

**Change kcal to kJ.**