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Abstract: Renewed interest in the estimation of spatial and temporal variation in fish traits, such as body size, is a result of computing advances and the development of spatially-explicit management frameworks. However, many attempts to quantify spatial structure or the distribution of traits utilize a priori approaches, which involve pre-designated geographic regions and thus cannot detect unanticipated spatial patterns. We developed a new, model-based method that uses the first derivative of the spatial smoothing term of a generalized additive model to identify spatial zones of variation in fish length-at-age. We use simulation testing to evaluate the method across a variety of synthetic, stratified age and length datasets, and then apply it to survey data for Northeast Pacific sablefish (Anoplopoma fimbria). Simulation testing illustrates the robustness of the method across a variety of scenarios related to spatially or temporally stratified length-at-age data, including strict boundaries, overlapping zones and changes at the extreme of the range. Results indicate that length-at-age for Northeast Pacific sablefish increases with latitude, which is consistent with previous work from the western United States. Model-detected spatial breakpoints corresponded to major oceanographic features, including the northern end of the Southern California Bight and the bifurcation of the North Pacific Current. This method has the potential to improve detection of large-scale patterns in fish growth, and aid in the development of spatiotemporally structured population dynamics models to inform ecosystem-based fisheries management.

To the Review Board:

Thank you for reviewing our manuscript. Below in boldface we have responded to the reviewer's comments, which we found fruitful and constructive. Where applicable, we have pasted in the changed text in blue both here and in the manuscript for the reviewer's convenience.

Reviewer #2's chief critiques regarded the parameter values used in the IBM simulation model, which they felt should be more sablefish-like. We have repeated this analysis using more sablefish-like parameters to demonstrate that the results (method performance) are indeed scale invariant. We also included a second analysis wherein the performance criteria were relaxed per R1's suggestion, which increased the method's accuracy to 100% for several scenarios.

Per R2's request regarding gear selectivity, we have modified the analysis of sablefish survey data to include a length-based selectivity penalty on the lognormal objective function for data collected from British Columbia, which uses externally-estimated length selectivity parameters in their age-based model. This change resulted in slight shifts to the estimated VBGF parameters and resultant length estimates, but not to the qualitative trends in sablefish growth throughout the region. Other changes included improving figure clarity and a rewrite of the discussion.

On behalf of my coauthors, I thank the reviewers for their careful consideration of our manuscript and useful feedback, which has improved the study.

Sincerely,

Maia Sosa Kapur

University of Washington

October 2019

Reviewers' comments:

Editor: I agree with the 2 reviews that the manuscript needs major revision to be publishable. Please address all comments by both reviewers in the revision.

Reviewer #1:

Review of Fish9315. Data-driven approach reveals…sablefish

This is a nice study that combines a simulation study of a new method, with a comparison to an existing method (STARS), and with an application to a real fishery data set (sablefish). Rather ambitious. The approach looks relevant and thoroughly done. My criticisms are mostly about presentation, recognizing that these can be addressed in a revision.

We appreciate your comments and have done our best to address your suggestions for improving the presentation of the approach and results.

A have a few of things to say about the science:

1. The exact match for identifying a true breakpoint (l. 220) was acceptable but the presentation of the results and discussion about this could be simplified. See minor comment about l 313.

Understood – see response below.

2. I did not understand why you accepted some change points in Figures 5 and 6 but not others. For example, in 5f, the smoother peaks twice, with confidence limits not overlapping with the zero line, but you only picked the larger one to place as a dashed line in 5g. Same thing with 5b,f, and 6b,d. Why only pick one and if so, which one? Please explain.

Our discussion has been updated to explain this L405: "Since the purpose of this analysis was diagnostic (the detection of where the spline is changing the most), we were able to avoid undue influence from this parameter by a) selecting only the value corresponding to the maximum first derivative and b) that had confidence intervals not containing zero, which are common in highly curved splines. We also chose to use only the maximum absolute value of the derivative to avoid splitting the spatio-temporal surface into many small zones, which may have led to problems of small sample size, or ultimately be unrealistic to implement in a population dynamics model of the fishery and stock."

3. I was wondering if you would point out that sablefish ages have some error associated with them. This started to come up in the discussion, l. 450-453, but more as an orphan sentence. Perhaps some statement that these ages across agencies should be comparable, based on age workshop results, is appropriate at the least.

A good point also raised by R2. We have added to the discussion L 422: "In addition, we did not simulate nor consider error or bias in the aging (i.e., otolith reading) process (Cope and Punt, 2007), which would potentially introduce uncertainty in breakpoint detection. Based on aging workshops conducted for sablefish, we consider aging results used in the case study to be roughly comparable between regions (Fenske et al., 2019)."

4. The introduction lays out the topic well but it overlook an application of GAMS with clustering analysis for defining spatial stock structure of a marine fish (Winton et al. 2014). I assume this is an oversight, and that it would be fruitful to comment on this method as something available, and if the authors have an opinion, then what do they think of this as an alternative.

Thank you for this reference, which strengthens the argument for a data-driven approach (it was indeed an oversight). We have included commentary on this approach in our discussion rewrite, L386: "Alternate GAM-based methods, such as the clustering approach applied in Winton et al. (2014), have also demonstrated that detecting spatial structure through a spatially explicit process can reveal distinct sub-areas in fish traits (e.g. mortality). That study also found that models did not necessarily require explicit ecosystem data (like temperature) to perform as well as models with only spatial information."

Presentation

1. The term 'region' becomes difficult to follow. It is used in both a general sense in some places (i.e., l. 26, 79) but also in more specific ways, such as 3 'regions' (AK, BC, CC) or 5 regions (Figure 7, or line 482-3 that identifies a specific 'region 3' in lowercase). By the discussion, I was confused enough that I could not follow some parts.

We have changed references to AK/BC/CC "regions" to "management area(s)" or "within political boundaries", and retained the term "region" for the growth zones detected via the GAM analyses.

2. In a related sense, the repeated use and disuse of acronyms for places was annoying (see bottom half of page 13, in particular).

We have replaced all acronyms with the full names for clarity.

3. The discussion seems bloated and came in and out of focus. For example, the paragraph beginning l. 447 did not seem to make a coherent point. Paragraph beginning l. 454 unnecessarily invokes ecosystem-based management, when the results of this paper clearly have relevance to single-species management (or I just did not understand what the authors intended here). By the time I got to Figure 7, I was pretty confused, likely resulting from a couple of factors: 1) no obvious outline structure to the discussion, 2) no background information on the ecosystem or management context (I am from the east coast), and 3) the confusing depiction of Figure 7 (see minor comments). I can see the point of mentioning counter-gradient growth variation, but the comparisons of sablefish to silversides is a stretch, considering that the latter is an annual species that spawns in the intertidal zone. I was less clear by discard rates were coming up on l 567. My recommendation for the discussion is to develop a clear outline that support the main thesis of this paper (see, for example. L 38) and revise to cut the discussion in half. Recommendation for major revision relates mostly to the discussion.

Helpful and fair. We have re-drafted the entire discussion beginning L362 to match the following outline, and the length has been reduced, principally by 1) removing repetition of study results 2) moving discussion of the model performance vs STARS to supplementary material.

Short outline of discussion:

1) **Implications of simulation results**
   a. **Performance of the method**
   b. **Caveats of the method**
   c. **Intended uses and future research of the GAM based method**
2) **Implication of sablefish results**
   a. **Contextualizing our findings with other work**
   b. **Conextualizing our findings within the ecosystem**
   c. **Future directions for sablefish research**

4. The conclusion section seems unnecessary.

We have deleted this section.

Minor **We have made the spelling-related corrections mentioned below.**

l. 1, it should be 'Data-driven' as this compound modifies approach

Another reviewer felt this nomenclature was redundant so it has been removed from the title, and replaced most occurrences with "model-based".

l. 151, please be more specific about how you rounded. For example was a value between 22.5 and 23.4 assigned as 23? Or was it 23.0-23.9 = 23? You have a strict threshold for accepting a simulated sample, so it seems worth being specific here.

Yes, we updated this sentence L137: "For each parameter, we identify at which predictor value (e.g., latitude) the maximum absolute value of the first derivative is obtained; this is rounded to the nearest integer (e.g. a value between 22.5 and 23.4 would be rounded to 23) and defined as the "breakpoint" if its 95% confidence interval (generated using the standard error estimates for the derivative) does not include zero."

l. 155, you define a degree in (standard, not nautical, if I understand that correctly) miles here but in km on l. 404; check journal format and pick one

L309 now defines a standard degree in km.

l. 205 start a new paragraph at 'Under each scenario'?

L195 A new paragraph now starts here.

l. 279 Waite and Mueter 2013 not in literature cited

This has been added.

l. 275, this begins a rather long paragraph that addresses more than one topic. Break up in to 2-3 paragraphs, emphasizing why you are estimating an asymptotic value for predicted length. I was a bit unsure of this, after the paper seems to say it would use a size at age data approach not estimated from models.

A good point; we have softened some of the introductory language to indicate that we are using a combination of a "data-driven" and information theoretic approach. This section starting L272 is now broken into several paragraphs and now clarifies how asymptotic length is treated with the following: "We employed a stepwise exploration of whether estimates of L_∞ were significantly different between detected regions using the method and generated from this ecosystem break using the entire, non-sub-sampled dataset. Asymptotic length was used to ease comparison between estimated values and those used in the current assessments."

l. 307-311, I consider it poor style to write sentences that do nothing but point to a figure. Generally editors want you to make a point in a sentence that ends with the corresponding figure or table in parentheses at the end of the sentence, if only to keep things short and concise.

A fair comment –the sentence pointing to Figure 4 L306 now states: "…displays the coverage probabilities for the 95% confidence intervals and proportion of simulations wherein the correct breakpoint was detected perfectly or with a "relaxed" criteria (within 2 degrees, roughly 220 km, or 2 years), demonstrating the success rate of the method across a variety of simulations."

l. 313+ some of this is rather tedious. It appears that section 3.1 is making two points: 1) the success of the method using 'exact match' and 2) the success if you loosen up the match criterion. I would rewrite strong topic sentences for these two paragraphs and revise accordingly. In association with that, why don't you add 3 panels to figure 4 that show the success rate with +/- 1 or 2 degrees latitude (rather than the exact match) which should simplify the text in this section 3.1.

This is a good suggestion; we have updated Figure 4 to have 3 additional panels which show the success rate when the criterion is relaxed to +/- 2 degrees. The text starting L312 has been shortened and now reads:

"For all scenarios, the method achieved the highest coverage probabilities for the length-at-age 0 (L_1) [48%-97% coverage for three scenarios and 27% in the scenario with overlap]. Coverage probabilities for length-at-age 15 (L_2) were slightly lower [43% - 74% for three scenarios and 16% in the scenario with overlap]. In terms of spatial breakpoint detection, there was not a qualitatively strong difference in the method's ability to correctly detect latitudinal vs. longitudinal breakpoints across scenarios. Our GAM-based method correctly detected the lack of a breakpoint in 86% of simulations without breaks; there was no discernable pattern to the spurious spatial breakpoints identified in the remaining

simulations. The method did less well at detecting the accurate breakpoints for scenario 4 (a "true" spatial break at 48°), assigning the break between 45° and 50° longitude in 100% of simulations; similarly, for the scenario with a single breakpoint at 25°, the GAM-based method was 100% accurate when the criteria were relaxed to include breaks from 24° to 26°. Relaxing the criteria in this manner increased the method's accuracy to over 90% for all scenarios except one…We computed the mean absolute error in both L_1 and L_2 estimates across scenarios and found the maximum error to be 1.84 cm for L_1 and 6.98 cm L_2, both obtained in scenario 1. Finally, we did not find the method's accuracy sensitive to either halving or reducing the sample size by 25%; see Supplementary Table A2."

l. 357 I was not sure what the antecedent of 'initial stratification' was so I had trouble following this.

This sentence has been clarified L348: "Parameter estimation at this temporal stratification generated 95% confidence intervals for L_∞ which overlapped for males within all regions and for females in region 5 (Supplementary Figure A12)."

l. 362 I was not sure what the antecedent of 'this set' was so I had trouble following this.

This sentence has been clarified L352: "Once re-aggregated and re-estimated, we did not find overlapping confidence intervals for L_∞ for any adjacent regions (Supplementary Figure A14), so this set of specifications (five spatial regions for both sexes, and a temporal break for females in regions 1 through 4) was retained as our final spatiotemporal stratification."

Figure 4. These colors did not work in my b/w hardcopy. Yellow, in particular, did not print well. Also, why is the order of scenarios different here than in Table 2? That seems like an unnecessary way to confuse the reader.

Thank you for noting this; we have changed the colors in all figures to be B/W friendly, and ensured the scenario order is consistent throughout tables/figures.

Figure 7. There is too much on this one figure and the legend explains too little. In the text, you talk about three regions in some places (AK, BC, CC. l. 111-113) but there are 5 regions here. I could figure out that dotted lines mark 10 degree latitudes or longitude lines (but maybe that should be in the legend), but I was not sure what demarked the 5 regions. There was some mention of a 4th and 5th region (l. 366-368) but I eventually realized I was not given enough information to understand the point of this figure or to follow much of the discussion.

Understood; the 5 regions are in fact those detected by the GAM analysis and are not strictly at 10-degree intervals. Line 355+ now states: "The stratification consists of three regions bounded on their western border by a break at 130˚W; from south to north, these regions (labeled 1, 2 and 3 on Figure 7) are defined by latitudes 36˚N and 50˚N. They correspond generally to Monterey, CA and the northern tip of Vancouver Island, BC. Region 4 is the area between 130˚W and the ecosystem break at 145˚W (roughly Cordova, AK). Datapoints collected to the west of the ecosystem break are assigned to region 5."

Table 1. reference to 1996-current in the foot note seems incomplete; what is the terminal year? **Good catch, 'current' has been replaced with '2018'**

Literature citations. Many are incompletely formatted.

We have double checked these and will work with the copy editor to ensure they meet journal specifications.

Cited.
Winton, M. V., Wuenschel, M. J., & McBride, R. S. (2014). Investigating spatial variation and temperature effects on maturity of female winter flounder (Pseudopleuronectes americanus) using generalized additive models. Canadian Journal of Fisheries and Aquatic Sciences, 71(9), 1279-1290. doi:10.1139/cjfas-2013-0617

Reviewer #2:

Data driven approach reveals oceanographic features delineate growth zones in northeast pacific sablefish.

General
This paper proposes to detect spatial and/or temporal breakpoints in fish size-at-age using estimated derivatives of spline-based smoothing functions of latitude, longitude, and time. The authors develop a individual-based model simulation to test the efficacy of the proposed method given hypothetical scenarios for regional differences (or lack of) in growth parameters. The method is then used to estimate spatio-temporal breakpoints in growth patterns of sablefish in the northeast Pacific.

Strengths: Overall, the paper presents a solid quantitative approach to a problem that is fairly common in fisheries oceanography. The simulation study is valuable in providing a way to "ground-truth" the method's reliability in absolute terms, as well as against other methods (although see below).

Weaknesses: The paper has a few weaknesses. First, the Introduction could be more concise and to the point about the actual method and its applicability. The stated justification of the method against "typical" approaches is not warranted and should be revised or removed.

Agreed; the introduction has been shortened.

Second, although the simulation study is warranted and presented reasonably well (but see below re IBM), I found the actual parameter and data scenarios unrealistic. For instance, the range of fish sizes in the simulations (from 6-8 cm at age-0 to 258 cm at age-15?) probably rules out any extant fish species. I don't know how the results would change, but I suspect that such as range provides an advantage to precision of growth parameter estimates (especially for a CV~10%), which are key to detecting regional differences in the simulations. Therefore, the simulations are impossible to judge and would need to be redone for a more realistic scenario.

Noted and revised; we repeated the IBM simulation using more sablefish-like parameters (see below).

Recommendation: Reconsider after major revision and review.

Introduction

L43-66. The first paragraph of the Introduction could be deleted without affecting the quality of the paper. In fact, it would probably help to clarify what the paper is actually about. The second paragraph (L67+) is more direct and clearly indicates the topic (which is not management boundaries as implied on L43).

This is a good suggestion. We deleted the first paragraph, and moved the ~3 descriptive sentences for the paper objective to the end of the Introduction. The paper now begins with L41 "There is no consensus on how to model region-specific growth patterns in assessment or population dynamics models. Fish somatic growth rates are …"

L52-66. This is not a particularly convincing argument for two reasons. First, the method presented here is just a variation of the "typical" approach described on L52 for linking biological observations to oceangraphic properties. Second, the "data-driven" approach was historically described as a "shotgun" search for correlations. One can always fit models to spatial data and then find oceanographic features to "explain" various observations. In the quest to separate correlation from causation, specifying a priori hypotheses that generate specific, falsifiable predictions is ALWAYS prefered over shotgun approaches. So, in this sense, the proposed data-driven approach sounds nice, but is the weaker form of scientific inference. One would have to ignore a lot of the philisophy of science to accept that a data-driven approach is more scientific than a priori hypotheses - exactly the opposite of the argument presented here.

This is a fair comment, and perhaps our explanation of our approach excessively denounced the *a priori* hypothesis approach, as in practice, we used a combination of the data-driven and information-theoretic methods by testing the ecosystem break at 145*. We have modified the language of this sentence L64+ to read: "An alternative tool is a model-based method that identifies break points in fish size-at-age, which can then be used to aggregate data and estimate parameters related to somatic growth. The significance of these breaks can be falsified by comparing overlap in growth parameter estimates and tested against or among pre-specified breaks of interest (i.e. an area with a known ecosystem regime). "

L102. I suggest that "our method", "the method", "the proposed method" be given a name.

We've updated these references to specify "the/our/the proposed GAM-based method".

L106. This should start a new paragraph. In any case, what is presented here could also be deleted since it is not really about detecting spatial patterns in fish growth parameters.

We have deleted this introductory paragraph as suggested above.

Why would spatial trends in size-at-age imply stock structure when (i) sablefish are highly mobile and (ii) there is already no genetic evidence of differentiation?

Agreed – we have replaced the mention of stock structure with 'spatial variation in stock traits' on L60 – as it should be considered in operating model development, but as you correctly point out doesn't mean that these are independent sup-populations.

Methods

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Why is the IBM so complicated for such a simple problem? Interactions between individual growth and selectivity seem more important than having a stock recruit relationship for a fish that is in unfished equilibrium.

The IBM was repurposed from more complex assessment studies by the first author for this work; the stock-recruit was simply an efficient way to generate new individuals in an accepted manner. We attempted to keep it simple by having the population remain unfished and without sampling bias. Below we describe how we've modified the analysis to account for selectivity in BC data during growth estimation.

L134. I would agree if I knew that that selectivity is a constant function of age across regions. So, what happens if selectivity is length-dependent (which it probably is) and there are spatial/regional differences in survey gear (which there are).

We understand this issue. Currently, selectivity is an independent function of length for both Alaska and the West Coast, and the revised operating model for BC also does not account for size-selectivity in sampling the population (which was the source of our confusion). We agree that there may in fact be spatial differences in gear selectivities leading to different ages sampled in the dataset, and we attempted to address this using the sub-sampling regime (to ensure even sampling across regions and ages when fitting the GAM) and only fitting the GAM to a single age and sex.

However, to address the fact that the BC model is still in development, we have modified the length estimation procedure to represent the length-based selectivity inherent in BC sampling practices and updated the text accordingly, which included removing the now-irrelevant speculation on selectivity from the discussion.

The methods section L279 describing this change now reads:

"To account for length-based selectivity, which is implemented only for the British Columbia data, we applied a penalty to the likelihood function as follows:

Equation 1 $L(D|\theta) = \prod_i S_{L_i} \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(L_i-\hat{L}_i)/(2[\sigma a_i]^2)} / \int_{-\infty}^{\infty} S_l \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(\hat{L}_i-l)/(2[\sigma a_i]^2)}\, dl$

Where L_i is the observed length at a given age a_i, $\hat{L}_i$ is the corresponding estimated based on VBGF parameters θ, S is a logistic selectivity function with parameter L_{50}, the length at which 50% of individuals (male or female) are fully selected, set to 52.976 cm (Samuel Johnson, SFU, pers. comm.)

Equation 2 $S_L = \frac{1}{1+\exp(L_{50}-L)}$

As length-based selectivity is assumed constant in both the California Current and Alaskan assessments, S_L is set to 1.0 when fitting data points from those regions."

Cited: Department of Fisheries and Oceans. (2016). A Revised Operating Model for Sablefish (Anoplopoma Fimbria) in British Columbia, Canada. ***Department of Fisheries and Oceans, Canada, 3190 Hammond Bay Road Nanaimo, BC V9T 6N7*****, (April). https://doi.org/http://www.dfo-mpo.gc.ca/csas-sccs/**

L142-143. The units of these variables are missing. **Thanks, we have updated L197.**

L146. "uncertainty" has many meanings. Specifically, you are computing the standard error of the estimated derivatives. **Thanks, clarified on L132: "The standard error of the derivative estimates are computed as…"**

L152: I don't understand the "95% confidence interval does not include zero". Aren't you estimating a latitudinal break-point? Maybe I am getting confused between estimation using actual data vs simulations. If so, then I suggest separating the two - i.e., don't even mention the simulation study until section 2.2. (note: reading the simulation section didn't clarify this question. L222 describes how breakpoints were detected?)

We see your confusion; the same approach for detecting breakpoints and estimating growth parameters (aside from the selectivity change described above) was used in both the simulation and sablefish application sections, which is why it's presented once here. Additionally, the simulation section uses the 95% CI of detected breakpoints as a performance metric (section 3.1), and we separately examine 95% CI of estimated Linf from the sablefish data to discard statistically insignificant breaks (see below).

To clarify, we updated the sentence on line 137 to read: "…defined as the "breakpoint" if its 95% confidence interval (generated using the standard error estimates for the derivative) does not include zero."

Later, when discussing the 95% CI for estimated growth parameters, we specify (L348): ". Parameter estimation at this temporal stratification generated 95% confidence intervals for L_∞ which overlapped for males within all regions and for females in region 5 (Supplementary Figure A12)."

L156. There is a lot to unpack in this one sentence. Within this sentence, is a general software package - TMB - really important to the point here? TMB mainly generates a gradient function.

We felt it useful to mention the software used, but have now simplified this sentence L146: "For each of these new aggregated data sets, the parameters of the VGBF; L_∞ - asymptotic length [cm], k - the rate at which asymptotic length is approached [cm/yr] and t_0 - the estimated age at length zero in years) are estimated using maximum likelihood assuming that

the error is normally distributed with zero mean and variance σ). This study performed estimation in Template Model Builder (Kristensen et al., 2016).”

L174: Eq 5 needs some editing of parentheses ()

Thanks, we added the missing parenthesis, L166.

L176. The "bias-corrected lognormal error" is unclear here.

Thanks, this was unnecessarily detailed; we have changed L168 to simply state “lognormal error”. The bias correction occurs when estimates are converted out of log space.

L180-182. Hopefully, there are typos in the L1 and L2 values here. Do you mean, e.g., 6.2 cm and 21.5 cm? There are no 258 cm (8.5 feet!) long sablefish. Also, do any of the actual datasets contain sablefish in the 6-8 cm size range? I don't see how bottom longline or trap surveys could ever catch individuals this size since sablefish are mostly pelagic during their first year and certainly wouldn't be able to mouth a large circle hook (or foolishly enter a trap full of adult sablefish). This range of L1 and L2 will be very optimistic about the estimability of the growth parameter k, since it is largely determine near the origin.

See next comment – these were not meant to be sablefish-like values, but we have since changed the analysis.

L208. Similar to above: L_inf = 150 cm is not realistic for sablefish.

We understand your confusion; the initial simulation study was not designed to imitate sablefish life history values specifically, and the study results are scale-invariant (i.e. the results would be identical with L1 and L2 were doubled). To demonstrate this, and per your comment below we decided to change the values used in the simulation study to more closely resemble sablefish (A1 @ 3 yrs, Linf ~ 70cm). The results (in terms of method performance) are unchanged.

L208. log(sigma) = 0.1 means sigma = 1.1 - is this on log(length) or length?

Sigma = 1.1 on length (this is only a start value for the estimation). For simplicity we changed the text to not state sigma in log space, L197.

L210. It is unrealistic to have age-0 fish in a length-at-age dataset, especially for sablefish. I would like to see how this method does with more realistic data, which would involve a1 ~ 3-5 yr and a L_inf ~ 70 cm. Lower L_inf would compress the growth pattern, while higher a1 would mask growth at young ages, making detecting differences in growth parameters more difficult and more sensitive to individual variation in growth - sigma - which is also high for sablefish.

This is fair – as noted above, we changed the simulation study to have values more similar to sablefish, and as expected the method performance is scale invariant.

L245. What "ecologists"? I expected a reference.

This sentence was removed with the discussion rewrite.

Results

I can't comment much on the simulation results because I don't think they are relevant.

Figure 1. Besides the values being unrealistic, it is hard to tell any differences in the bubble sizes in the figure. **We changed the values to be more sablefish-like (as described above) and have increased the scale of the contrast in bubble sizes in these figures to aid in interpretation. They are also now in greyscale.**

Figure 6. It is clear from Fig 6 that there could be multiple maxima/minima of spatial or temporal derivatives. Why chose the single largest one only?

This was also mentioned as a point of confusion by R1. Our discussion has been updated to explain this L405: "Since the purpose of this analysis was diagnostic (the detection of where the spline is changing the most), we were able to avoid undue influence from this parameter by a) selecting only the value corresponding to the maximum first derivative and b) that had confidence intervals not containing zero, which are common in highly curved splines. We also chose to use only the maximum absolute value of the derivative to avoid splitting the spatio-temporal surface into many small zones, which may have led to problems of small sample size, or ultimately be unrealistic to implement in a population dynamics model of the fishery and stock."

Discussion

Is growth zonation biologically significant? 95% intervals could be small bc of sample size. **That is a good point, and impacts on assessment results would have to be considered in the context of the fecundity relationships in given regions, which was outside the scope of this study. We've added a line L485: "We note, however, that the procedure used to eliminate 'overlapping' L_∞ estimates concerned only statistical differences in values (and are therefore sensitive to sample sizes). The biological significance of these values would need to be investigated in the context of fecundity and length-weight differences between regions."**

L443. What might one expect if ageing error were taken into account? How would the form of ageing error and growth parameters interact to affect the bias? For instance, if a fish reaches L_inf by age-25, then does an ageing error of +/- 5 years matter for fish length-at-age 35+? **This is a good point. We have included in our discussion a mention of aging error concerns for this region, L422: "In addition, we did not simulate nor consider error or bias in the aging (i.e., otolith reading) process (Cope and Punt, 2007), which would potentially introduce uncertainty in breakpoint detection. Based on aging workshops conducted for sablefish, we**

consider aging results used in the case study to be roughly comparable between regions (Fenske et al., 2019)."

L461. I remain sckeptical about these generalizations given that the simulation conditions favored highly precise growth parameter estimation. Try the simulations based on actual parameter estimates and size ranges representative of each region.

Per your comment above we decided to change the values used in the simulation study to more closely resemble sablefish (A1 @ 3 yrs, Linf ~ 70cm).

L480-481. Gear selectivity is not specific to fishery-dependent data. All sampling gear is size-/age-selective to some degree. **A good point, we have repeated the analysis of BC data to account for length-based selectivity (which is estimated externally for that region's assessment), see above.**

L481-487. I am curious as to why this is curious to the authors. The BC sablefish assessment clearly uses length-based selectivity in the assessment, so how could be it "unknown to" and "not reflected in" the current assessment? The growth parameter estimation doesn't account for size selectivity of trap gear (I don't think any of the other regions do either).

We recognize the confusion here. Please see comment regarding L134 above for how we now account for size selectivity of trap gear in the growth estimation. Per this change, we removed the entire section of the discussion which wrongly stated the absence of size selectivity in BC and discussed accounting for it as a future direction.

L543. I appreciate the theoretical discussion here and how it relates to the observed patterns for sablefish. Perhaps this could be expanded a bit to give a scenario that would explain sablefish observations.

Thanks. Another reviewer suggested a complete re-write and shortening of the discussion. We have retained some theoretical material, and included the following discussion of potential sablefish scenarios L504: "A plausible scenario which would generate our observed results could be that changes in fisher behavior or climate in the last ~10 years caused female sablefish to move northward in greater numbers, or simply experience size-based truncations in regions to the east of 145 due to fishing pressure. Each of these phenomenae would have an inverse effect on resultant size-at-age, with fish entering the northern ecosystem tending to grow larger and high, persistent fishing pressure in any region leading to truncations in terminal size. Because we only detected slight declines size-at-age between time periods for female sablefish, it is possible that either fishery-related effects simply have not lasted long enough to be strongly evident, or such effects are being counteracted by more fish entering ecosystems favorable to higher terminal sizes. A closer examination of sex-related movement would be useful towards this understanding."

L551. I don't see where this paragraph is going. The topic sentence doesn't seem related to the overall content.

The re-write of the discussion has updated this section (L482); this paragraph describes reasons why the temporal break could have been more pronounced for females than males.

L571. Are fishing mortality rates in the different regions actually large enough to substantially affect observed length-at-age? I doubt it, but you could test these hypotheses using the IBM.

To clarify, the IBM doesn't use *F*; it models an unfished population. You are correct that this could be explored with a re-configuration of the model to simulate different levels of fishing pressure, though the scope of this study was not to investigate if/how the method could detect changes in observed length-at-age due to F explicitly.

Table 1. There is not much discussion in this paper about how the survey methods could affect perception of regional differences in growth rates. For instance, it is likely that trawl surveys have dome-shaped selectivity for length, which would tend to generate smaller L_inf and higher k values (especially where trawls tend to be more selective for smaller fish compared to other gears).

As stated above, the trawl surveys used for Alaska and the West coast use asymptotic *age* based selectivity, with an independent selectivity function for length (all lengths = 1). See comments above regarding the updated analysis meant to address selectivity concerns for regions in which length-based selectivity is currently considered.

Oceanographic features delineate growth zonation in Northeast Pacific sablefish

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Keywords: growth, von Bertalanffy, ecosystem-based fisheries management, sablefish, spatiotemporal

Abstract

Renewed interest in the estimation of spatial and temporal variation in fish traits, such as body size, is a result of computing advances and the development of spatially-explicit management frameworks. However, many attempts to quantify spatial structure or the distribution of traits utilize *a priori* approaches, which involve pre-designated geographic regions and thus cannot detect unanticipated spatial patterns. We developed a new, model-based method that uses the first derivative of the spatial smoothing term of a generalized additive model to identify spatial zones of variation in fish length-at-age. We use simulation testing to evaluate the method across a variety of synthetic, stratified age and length datasets, and then apply it to survey data for Northeast Pacific sablefish (*Anoplopoma fimbria*). Simulation testing illustrates the robustness of the method across a variety of scenarios related to spatially or temporally stratified length-at-age data, including strict boundaries, overlapping zones and changes at the extreme of the range. Results indicate that length-at-age for Northeast Pacific sablefish increases with latitude, which is consistent with previous work from the western United States. Model-detected spatial breakpoints corresponded to major oceanographic features, including the northern end of the Southern California Bight and the bifurcation of the North Pacific Current. This method has the potential to improve detection of large-scale patterns in fish growth, and aid in the development of spatiotemporally structured population dynamics models to inform ecosystem-based fisheries management.

1 Introduction

There is no consensus on how to model region-specific growth patterns in assessment or population dynamics models. Fish somatic growth rates are typically modelled using the von Bertalanffy growth function (VBGF, von Bertalanffy, 1957) or an alternative functional form, with parameters estimated using model-fitting procedures. The spatial resolution of the resultant estimates is necessarily predicated on the aggregation of the data, which is often defined by survey stratification, political or management boundaries, and/or changes in sampling gear, not necessarily the ecology of the population (McGarvey and Fowler, 2002; Williams et al., 2012). For example, assessments of Alaskan sablefish stocks estimated separate VBGF parameters for two periods of survey data based on the *a priori* hypothesis that changes in survey gear type would affect estimates of fish growth from survey data (Echave et al., 2012; Hanselman et al., 2017; McDevitt, 1990), and imposed a time block between which estimates of the growth curve parameters were quite similar in the stock assessment (

Table 1). More sophisticated approaches that utilize hierarchical Bayesian methods to estimate latitudinal and regional effects on length- or weight-at-age require a design matrix of dimensions dictated by pre-supposed zones (e.g. Adams et al., 2018). Such approaches are useful within a management context with rigid spatial boundaries, but do not represent the underlying growth process explicitly, and preclude the discovery of spatially-structured trends in fish size that do not match current management boundaries.

Existing methods to quantify spatial variation in somatic growth pose a trade-off. On one hand, researchers may impose *a priori* beliefs about spatial variation in stock traits or generate purely descriptive models of trait 'gradients' across regions or time periods, without a clear way to identify significant break points within them (King et al., 2001). This presents a challenge when developing population dynamics models that accurately represent the structure of managed stocks. An alternative tool is a model-based method that identifies break points in fish size-at-age, which can then be used to aggregate data and estimate parameters related to somatic growth. The significance of these breaks can be evaluated by comparing overlap in growth parameter estimates and tested against or among pre-specified breaks of interest (i.e. an area with a known ecosystem regime). To meet this need we present a new method, which uses the first derivative of smooth functions (splines) from a generalized additive model (GAM) to detect change points in spatially- and temporally-structured fisheries growth data that minimizes the use of pre-supposed stratifications in a simple, rapid computational framework. The method does not require the specification of multiple error structures nor the construction of spatial meshes, which can be computationally expensive when large (Thorson, 2019). The analysis of first derivatives of regression splines in GAMs for change-point analysis has been recently used in terrestrial paleoecology (Simpson, 2018) and geophysics (Beck et al., 2018). The underlying assumption is that the rate of change (the first derivative) of a given predictor is an appropriate measure of the direction and magnitude of the predictor-response relationship. The spline itself may be highly non-linear, but predictor values at which the slope of the spline is largely positive or negative are taken to denote where the response variable is changing the most.

Our GAM-based method has the potential to improve detection of large-scale patterns in fish growth, and aid in the development of spatially-structured population dynamics models. We use simulation to test the robustness of the method using synthetic length-at-age data of varied complexity, and present a case study application to Northeast Pacific sablefish (*Anoplopoma fimbria*). Sablefish are a highly mobile, long-lived, and valuable groundfish that have high movement rates (10 – 88% annual movement probabilities across Alaska, with a mean great-circle distance of 191 km in a single year; Hanselman et al. 2015) and range from Southern California to the Bering Sea. Concurrent population declines across the entire range over the past few decades have increased concern about the status of sablefish, and interest in identifying the causes of the downward trend. Sablefish stock assessment and management occur independently within political boundaries, namely Alaska (AK), British Columbia (BC), and the US West Coast in the California Current (CC), assuming that these are closed stocks. However, recent work has shown that there is little genetic evidence for population differentiation in sablefish across the NE Pacific (Jasonowicz et al., 2017), although there is evidence for differences in growth rate and size-at-maturity throughout the range (McDevitt, 1990). This suggests that the current delineation of assessment and management areas may be incongruent with the stock's actual spatial structure and underscores the potential value of developing a population dynamics model that represents the heterogeneity of sablefish growth throughout their range.

We developed a data-model-based method that would simultaneously identify spatiotemporal zones between which fish length-at-age varies and illustrate correlations between growth and spatiotemporal covariates (such as an increase with latitude). A method to identify such patterns in important population traits can help researchers determine whether current management scales are appropriate given the dynamics present in the population. Because these dynamics are potentially environmentally linked, such a method can also uncover whether spatiotemporal patterns in investigated traits correspond to major environmental features (such as ocean currents) or forcings (such as climactic oscillations), which can help inform the implementation of ecosystem-based fisheries management.

2 Methods

2.1 Method summary

The method fits a GAM to the vector of observed lengths of fish of a single age as the response variable, predicted by separate smoothers at knots t for year, latitude, and longitude, using the mgcv package (Wood, 2011) in R (R Development Core Team, 2016), i.e.

Equation 1 $g(\boldsymbol{E}(\boldsymbol{X})) = \beta_0 + f(y_t) + f(s_t) + f(k_t) + \epsilon_t$

where ***E(X)*** represents the expected mean of fish length, g is an invertible, monotonic link function (in this case, the natural logarithm) that enables mapping from the response scale to the scale of the linear predictor, and the additive effects of latitude (s_t), longitude (k_t) and year (y_t), which are smoothed using a thin plate regression spline *f*. ϵ_t is a residual error term assumed to be normally distributed. The effects of latitude, longitude and year on expected length-at-age are estimated as separate smoothers. To simplify the analysis, we fit the GAM to data for a single age-class and sex at once (e.g., age six for the simulated datasets), thus precluding the need to control for age or sex. Using fish of only a single selected age from all regions also minimizes the concern of differing age-based survey selectivities between management areas.

The first derivatives of the linear predictor with respect to latitude, longitude and year are evaluated to identify areas or periods (breakpoints) between which there is evidence for changes in fish length-at-age. The equations below provide an example using latitude s_t, but the process is repeated for each smoother. The finite differences method (as in Simpson, 2018) approximates the first derivative of the trend from the fitted GAM. For instance, the vector of derivatives **G** for latitude is produced via the following:

Equation 2 $$\boldsymbol{G_t} = \frac{g(s_t+\alpha)-g(s_t)}{\alpha}$$

where $g(S_t)$ is a vector of predicted fish lengths at latitudes and α = 0.001 in this analysis, with other effects (year, longitude) held constant. Therefore, the numerators of the elements of **G** are predicted lengths at two adjacent latitudes, separated by interval α, which is necessarily small.

The standard error of the derivative estimates are computed as:

Equation 3 $$SE_t = \sqrt{\boldsymbol{G_t V}}$$

where **V** is the variance for the current spline; the square root provides the standard error for each derivative estimate of that predictor. These steps are repeated across the range of explored years and longitudes. All simulated datasets (Section 2.2.1) were fit using a link function g with smoothing functions f for both spatial covariates as well as for year. For each parameter, we identify at which predictor value (e.g., latitude) the maximum absolute value of the first derivative is obtained; this is rounded to the nearest integer (e.g. a value between 22.5 and 23.4 would be rounded to 23) and defined as the "breakpoint" if its 95% confidence interval (generated using the standard error estimates for the derivative) does not include zero (see Figure 1 and 2, which illustrate the raw data, smoothers and first derivatives thereof for two synthetic datasets). The rounding step was implemented to ease comparison in the simulation study; we did not wish to treat a breakpoint estimate as incorrect if it differed by less than half of one degree (approximately 55 kilometers) from the true breakpoint. The raw length and age data (including all ages of fish) are then re-aggregated based on the identified breakpoints. For each of these new aggregated data sets, the parameters of the VGBF (Equation 4; L_∞ - asymptotic length [cm], k - the rate at which asymptotic length is approached [cm/yr] and t_0 - the estimated age at length zero in years) are estimated using maximum likelihood, assuming that errors are normally distributed with zero mean and standard deviation σ). This study performed estimation using Template Model Builder (Kristensen et al., 2016).

Equation 4 $$\overline{L_a} = L_\infty \times (1 - \exp(-k(a - t_0)) + \varepsilon\,; \qquad \varepsilon \sim N(0, \sigma^2)$$

2.2 Simulation testing

2.2.1 Outline and design

We conducted a simulation study to evaluate the performance of the proposed GAM-based method, based on datasets generated using an individual-based model (IBM, see Supplementary Material for full details). The IBM is capable of simulating individual characteristics by following the life history processes (survival and growth) of individual fish, with reproduction governed by a generalized stock-recruitment relationship to produce new individuals. An IBM was used to capture these key processes to simulate data similar in form to what would be included in a fishery stock assessment, which is difficult to do analytically or using age/size aggregated models. We simulate spatial variation by generating length-at-age datasets under different growth 'Regimes' (defined as distinct L_1 and/or L_2 values, leading to varied L_∞) and assign latitudes and longitudes to fish grown under each regime. The IBM implements the VBGF using Schnute's (1981) formulation, which requires k, L_1, and L_2, with L_∞ computed as:

Equation 5 $L_\infty = L_1 + \frac{L_2 - L_1}{1 - \exp(-k \times (a_2 - a_1))}$

where L_1, L_2 represent the expected lengths of fish at ages a_1, a_2, (3 and 30 years, respectively) and k is the growth coefficient. Each annual increment for every individual fish is subject to lognormal error. We considered five growth scenarios consisting of two growth "Regimes" with either completely distinct spatial or temporal ranges, or spatial ranges with some overlap. We designed our growth regimes to mimic the level of variation in L_1 and L_2 present in the sablefish dataset, which was as high as 26%. In our synthetic population for regime 1 L_1 = 10 cm, L_2 = 70 cm and $k = 0.30$ yr^{-1}; regime 2 was designed using L_1 and L_2 parameters 20% higher than regime 1 (L_1 = 12 cm, and L_2 = 84 cm, $k = 0.30$ yr^{-1}). Expected growth curves for the simulated Regimes are present in Supplementary Figure A2.

The simulated spatial extent ranges from 0° to 50° in latitude and longitude. The five simulation scenarios (Table 2) were designed to represent a variety of possibilities for spatial growth variation, with one scenario including a temporal regime change in growth. To simulate spatial zones, locations of fish grown under a certain regime were sampled from a uniform distribution with boundaries defined by the spatio-temporal scenario at hand (Figure 3). All fish in scenario 1 (no spatial or temporal variation) were grown under regime 1 and sampled (uniformly) over latitude and longitude between 0° to 50°. In scenario 2, fish were grown in two regimes, and fish grown under regime 1 were between 0° and 25° (latitude and longitude) while fish grown under regime 2 had coordinates sampled between 25° to 50°. The same approach was applied for scenario 3, except that fish grown under regime 2 were sampled from 20° to 50°, thus creating an overlap zone between 20° and 25°. All simulated fish in scenario 4, had latitudes sampled from 0° to 50°. Fish simulated under regime 1 were assigned longitudes sampled randomly from 0° to 48° and fish simulated under regime 2 have longitudes sampled randomly from 48° to 50°, forming a vertical "band" of larger fish in higher longitudes.

The final simulation scenario (5) involved temporal changes in growth, with a change from growth regime 1 to regime 2 in year 50. This meant that the growth increment generally increased for individuals whose lifespan covers this breakpoint, though note that the GAM is fit to fish of a fixed age. Fish locations for the temporal break scenario are sampled identically to the scenario without spatial variation.

Under each scenario, 100 replicate datasets were generated, which averaged 530 age-six fish per dataset (a sensitivity analysis was performed reducing the sample size by 25% or 50%). For all runs, the initial values for the parameters were t_0 = 0.1 yrs, $\sigma = 1.1$, with L_∞ = 150cm and k = 0.1. The estimation procedure also calculated the predicted length at the endpoints of the estimated growth curve (Equation 5; the length at pre-specified minimum (L_1) and maximum (L_2) ages, which were 3 and 30 years in the simulation studies). These values and their standard errors were used in the evaluation of the method (see Section 2.2.2 Performance metrics), as L_∞ and k are typically negatively correlated.

2.2.2 Performance metrics

We considered two performance metrics: 1) the proportion of simulations in which the correct spatial and/or temporal breakpoints were detected - we tabulated the number of times a breakpoint found using a GAM fit to a dataset matched the true latitude, longitude, and year; and 2) the coverage probabilities (determined by the 95% confidence intervals) for L_1 and L_2. For all but the scenario with overlapping ranges (scenario 3), we only considered the GAM analysis to have correctly identified the true breakpoint only if it was an exact match. The 'true' dataset for scenario 3 contained fish grown under regimes 1 and 2 in a shared region between 20° and 25° latitude and longitude, so the detected breakpoint was counted as an accurate match if it fell within this range.

For each scenario, after aggregating each of the 100 simulated datasets into the GAM-designated spatiotemporal strata and estimating the growth curve, we determined whether the 95% confidence intervals of the estimated fish lengths at ages zero and fifteen (our a_1 and a_2) contained the true L_1 and L_2 values. For example, fish generated under regime 1 and occupying latitudes and longitudes between 0° and 25° may have been re-aggregated via the GAM analysis into a *de facto* 'region' ranging from 0° to 24° degrees for an "early" period of years 1 through 37; the parameters of the VBGF were estimated on this per-strata basis, and the terminal lengths of the estimated curve compared to those from which they were generated, in this case, regime 1. Fits from the complementary *de facto* 'region' ranging from 24° to 50°, and/or a "late" period, would be compared to whichever regime generated the majority of fish therein. An estimated endpoint from a GAM-defined region was considered a match if the 95% confidence interval for it contained the true value of L_1 or L_2.

To facilitate comparison between the proposed GAM-based method and an extant approach, we applied the sequential t-test analysis of regime shifts (STARS, Rodionov, 2004) using length-at-age for age 6 to our simulated datasets for both spatial and temporal changes. The STARS method was originally developed to detect climate regime shifts in time-series data, and was noted for its sensitivity to changes towards the end of a series. The method examines the sequential differences in the value of a t-distributed variable, and determines whether subsequent measurements (at the next year or latitude, for example) exceed the expected range. We used a minimum regime 'length' of five, meaning detected shifts between latitudes, longitudes or years must persist for at least five consecutive units, and the default p-value cutoff of 0.05. We believe this captures the timescale of regime shifts of interest to ecologists, and a significance cutoff frequently used in such analyses. From the STARS analysis of each dataset, we selected the breakpoint(s) with the largest positive "regime shift index", which represents a cumulative sum of the normalized anomalies. This is qualitatively similar to the "largest first derivative" metric used in the proposed GAM-based method and, as in that case, was applied regardless of where the breakpoint was detected. We implemented the same steps, whereby the detected spatial and/or temporal breakpoint(s) were used to re-aggregate and estimate growth parameters, and the proportion of accuracy and coverage probabilities for L_1, and L_2 tabulated.

2.4 Application to Northeast Pacific Sablefish

We obtained fishery-independent length and age data from the Bering Sea, Aleutian Islands, and Gulf of Alaska Sablefish Longline Survey (Rutecki et al., 2016) and the U.S. West Coast Groundfish Bottom Trawl Survey (Northwest Fisheries Science Center, 2019) conducted annually by the Alaska Fisheries Science Center and the Northwest Fisheries Science Center, respectively. We also obtained length and age records from the Canadian Department of Fisheries and Oceans (Wyeth et al., 2005); see

Table 1 for a summary of survey data used in the application. Data from each management area included measured length, sex, age, and the starting latitude and longitude, which determined the survey station. Due to computational constraints, and to avoid disproportionate influence of more heavily-sampled areas on breakpoint estimates, we randomly subsampled 15,000 total records from each of the three management areas. The subsampling was random with respect to latitude, longitude, age and sex, using the sample_n function from the package *dplyr* (Wickham et al., 2019).

We applied the method to identify spatial and temporal breakpoints for each sex separately at several key ages: age 4 (before length-at-50%-maturity for both males and females in all management areas), age 6 (after length-at-50%-maturity for both males and females in all management areas) and age 30, roughly the length at which sablefish are expected to obtain their maximum length (Johnson et al., 2015). Our sampling method produced a data set with an average of 1,315 age 4, 1,283 age 6, and 65 age 30 sablefish of each sex from each management area. Growth model fitting was performed using all available data from each of the three management areas (see Supplementary Table A3 for sample sizes). In constructing the GAM, we investigated the use of an AR1 temporal structure for the residual ϵ_t with lags of 1 to 3 years, but these models did not improve AICc over the initial model (without autoregressive structure).

We re-aggregated all data to match the breakpoints that appeared in the GAM analysis for key ages, as well as an ecosystem-based breakpoint at 145°W. We selected this breakpoint based on work by Waite and Mueter (2013) who used cluster analysis to delineate unique zones of chlorophyll-*a* variability, which has been shown to be influential in the sablefish recruitment process (Shotwell et al., 2014) but by definition such an effect is not detectable in our analysis that only examines fish larger and/or older than recruits. The North Pacific Fishery Management Council uses 145°W, which includes a cluster of several seamounts in the Gulf of Alaksa, to delineate a groundfish slope habitat conservation area (Siddon and Zador, 2018). We employed a stepwise exploration of whether estimates of L_∞ were significantly different between detected regions using the method and generated from this ecosystem break using the entire, non-sub-sampled dataset. Asymptotic length was used to ease comparison between estimated values and those used in the current assessments. This involved first aggregating and estimating the VBGF for ten unique spatiotemporal strata for each sex, defined by the one temporal and three spatial breakpoints found among the key ages selected for analysis using the GAM in addition to the break at the aforementioned ecosystem feature. To account for length-based selectivity, which is implemented only for the British Columbia data, we applied a penalty to the likelihood function as follows:

Equation 6 $$L(D|\theta) = \prod_i S_{L_i} \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(L_i-\hat{L}_i)/(2[\sigma a_i]^2)} \Big/ \int_{-\infty}^{\infty} S_l \frac{1}{\sqrt{2\pi}\sigma a_i} e^{-(\hat{L}_i-l)/(2[\sigma a_i]^2)}\, dl$$

where L_i is the observed length at a given age a_i, $\hat{L}_i$ is the corresponding estimate based on VBGF parameters θ, S is a logistic selectivity function with parameter L_{50}, the length at which 50% of individuals (male or female) are fully selected, set to 52.976 cm (Samuel Johnson, SFU, pers. comm.)

Equation 7 $$S_L = \frac{1}{1+\exp(L_{50}-L)}$$

As length-based selectivity is assumed constant in both the California Current and Alaskan assessments, S_L is set to 1.0 when fitting data points from those regions.

We then examined whether the 95% confidence intervals for L_∞ overlapped for any temporally-split datasets from the same region (e.g., region 1 female sablefish data before and during 2010 and after 2010). If they did, we pooled the data for that region and sex for all years. In the second step, we examined if spatially-adjacent regions (from any time period) for the same sex had 95% confidence intervals for L_∞ that overlapped, and combined regions for which this was the case on a by-sex basis. This stepwise approach reduces unnecessary partitioning of the data into spatiotemporal strata that do not ultimately result in different estimates of L_∞, and allowed us to examine whether any of our detected breakpoints or the *post hoc* ecosystem split was informative regarding growth estimates. Once the most parsimonious structure was identified through this method, we generated predicted lengths-at-age for the entire dataset.

3 Results

3.1 Simulation Study

The simulation study demonstrated that the first-derivative GAM-based method is able to detect both spatial and temporal breakpoints correctly in the majority of scenarios, with the exception a scenario where the spatial break occurred near the edge of the simulated spatial extent at 48° longitude, where it only detected the break location correctly in 15% of simulations. Figure 4 displays the coverage probabilities for the 95% confidence intervals and proportion of simulations wherein the correct breakpoint was detected perfectly or with a "relaxed" criteria (within 2 degrees, roughly 220 km, or 2 years), demonstrating the success rate of the method across a variety of simulations. Supplementary Figure A3 and A4 presents a histogram of detected breaks for each scenario.

For all scenarios, the method achieved the highest coverage probabilities for the length-at-age 0 (L_1) [48%-97% coverage for three scenarios and 27% in the scenario with overlap]. Coverage probabilities for length-at-age 15 (L_2) were slightly lower [43% - 74% for three scenarios and 16% in the scenario with overlap]. In terms of spatial breakpoint detection, there was not a qualitatively strong difference in the method's ability to correctly detect latitudinal vs. longitudinal breakpoints across scenarios. Our GAM-based method correctly detected the lack of a breakpoint in 86% of simulations without breaks; there was no discernable pattern to the spurious spatial breakpoints identified in the remaining simulations. The method did less well at detecting the accurate breakpoints for scenario 4 (a "true" spatial break at 48°), assigning the break between 45° and 50° longitude in 100% of simulations; similarly, for the scenario with a single breakpoint at 25°, the GAM-based method was 100% accurate when the criteria were relaxed to include breaks from 24° to 26°. Relaxing the criteria in this manner increased the method's accuracy to over 90% for all scenarios except one (Figure 4c). We computed the mean absolute error in both L_1 and L_2 estimates across scenarios and found the maximum error to be 1.84 cm for L_1 and 6.98 cm L_2, both obtained in scenario 1. Finally, we did not find the method's accuracy sensitive to either halving or reducing the sample size by 25%; see Supplementary Table A2.

3.2 Comparison to STARS Method

The STARS method (Supplementary Figure A1) was inferior to the proposed GAM-based method at detecting spatial or temporal break points for all simulated scenarios, with a slight exception for the break at edge case (scenario 4). For all other scenarios, the STARS method performed up to 90% worse than the proposed GAM-based method at detecting latitude and longitude breaks, and 20% worse at detecting year breaks. It also performed worse in terms of the coverage probability of L_1 (63% vs 67% for the GAM-based method) and L_2 (18% vs 52%), and did slightly better than the proposed method in detecting the break-at-edge, though only at 31% (vs 11%).

3.3 Application to NE Pacific Sablefish

The latitude smoother suggested a generally increasing cline in length-at-age with latitude, with a significant breakpoint around 50˚N (approximately the northern end of Vancouver Island, Canada) detected when the GAM was fit for age four and six sablefish (Figure 5c, 6c; Supplementary Figures A4, A7, A9). North of this breakpoint, female L_2 estimates were consistently larger than 70 cm, where they averaged 65 cm south of it. Both age six and age 30 female sablefish identified a breakpoint at 36˚N (approximately Monterey, CA, USA). Both males and females obtained the lowest estimated L_2 south of this breakpoint, at 55 cm for males and 60 cm for females. In all GAM-detected regions, L_∞ was higher for female sablefish than males, and the resultant L_2 differed between regions within sexes by up to 26%. The temporal smoother did not exhibit a strong one-way trend, and was flat for age-30 fish of both sexes, though it did detect a break in 2009-2010 for both sexes of age 4 and 6 sablefish. Parameter estimation at this temporal stratification generated 95% confidence intervals for L_∞ which overlapped for males within all regions and for females in region 5 (Supplementary Figure A14). The number of spatiotemporal strata was reduced to 14 after combining years of data for region-sex combinations where overlap was found in the second phase. Once re-aggregated and re-estimated, we did not find overlapping confidence intervals for L_∞ for any adjacent regions, so this set of specifications (five spatial regions for both sexes, and a temporal break for females in regions 1 through 4) was retained as our final spatiotemporal stratification. The stratification consists of three regions bounded on their western border by a break at 130˚W; from south to north, these regions (labeled 1, 2 and 3 on Figure 7) are defined by latitudes 36˚N and 50˚N. They correspond generally to Monterey, CA and the northern tip of Vancouver Island, BC. Region 4 is the area between 130˚W and the ecosystem break at 145˚W (roughly Cordova, AK). Datapoints collected to the west of the ecosystem break are assigned to region 5.

4 Discussion

Empirical work has suggested that somatic growth in fishes follows ecosystem gradients rather than management boundaries (Pörtner and Knust, 2007; Taylor et al., 2018). The ongoing emphasis on ecosystem-based fisheries management calls for the analysis of fish stocks (ideally in a multi-species context, but also as single species) at meaningful spatial scales, across which changes can be detected. Our goal was to investigate the performance a method to improve detection of large-scale patterns in fish growth and apply it to length-at-age data from the Northeast Pacific sablefish. Our method determined that the current management scale (three political breaks at national boundaries) is incongruent with the underlying pattern of variation in sablefish growth. We discerned that the spatial variation in sablefish growth corresponds well with major oceanographic features, principally the splitting of two major ocean features and the edge of a highly productive zone. Below, we discuss the results of the simulation study and provide further guidance on how researchers could apply our proposed method to new datasets. We then discuss the results found during the application to northeast Pacific sablefish, with respect to ecosystem concerns.

4.1 Implications of Simulation Results

Our GAM-based method indicated tradeoffs between the accuracy of breakpoint detection and resultant coverage probabilities in the estimated growth curve, as well as large differences in the coverage probabilities of fish length at younger versus older ages. We find it encouraging that the approach could correctly detect breakpoints for the scenario with overlapping ranges, which is likely more like real-world fish populations than the singular, immediate breakpoints simulated in other scenarios. However, the assigned 'zonation' of these populations necessarily combined fish with contrasting growth curves into a single dataset for estimation and resulted in a loss in accuracy (coverage probability) for the endpoints of the growth curve. Alternate GAM-based methods, such as the clustering approach applied in Winton et al. (2014), have also demonstrated that detecting spatial structure through a spatially explicit process can reveal distinct sub-areas in fish traits (e.g.

mortality). That study also found that models did not necessarily require explicit ecosystem data (like temperature) to perform as well as models with only spatial information.

We suggest that our method be used as a tool to guide the identification of general zones between which growth could vary, and not take detected breakpoints as the absolute truth. Importantly, suggestions of spatial breakpoints produced by the method should necessarily be considered in the context of the ecosystem, and prior knowledge of how the fishery at hand responds to features (e.g., temperature, depth) which vary with latitude and/or longitude. Absent an ecosystem-wide analysis, strong directional trends in any generalized additive term (such as the positive trend with latitude observed here) or a breakpoint at the edge of the study area can be indicative of a change somewhere in the margins and extend the reach of future survey designs.

The method performed best for both performance metrics for the scenario in which growth regimes 1 and 2 overlapped in space (which had the advantage of being 'matched' whenever the detected breakpoint fell within the range of overlap, 20° to 25°). The most commonly detected breakpoint in latitude and longitude for that scenario, before rounding, was the midpoint of this range (22.5°), likely an artifact of the penalization function within the GAM, which seeks to minimize curvature on either side of a given knot (i.e., the breakpoint). This penalization function controls the degree of smoothness on the spline and can lead to fitting overly-complex models when unchecked (Wood, 2003). Since the purpose of this analysis was diagnostic (the detection of where the spline is changing the most), we were able to avoid undue influence from this parameter by a) selecting only the value corresponding to the maximum first derivative and b) that had confidence intervals not containing zero, which are common in highly curved splines. We also chose to use only the maximum absolute value of the derivative to avoid splitting the spatio-temporal surface into many small zones, which may have led to problems of small sample size, or ultimately be unrealistic to implement in a population dynamics model of the fishery and stock.

We detected spurious spatial or temporal breaks in ~10% of simulations for which no breakpoints were present. However, some erroneous detection can be expected considering the inherent noise in our datasets, and that there is no minimum threshold for breakpoint detection; a single, small derivative among many zeros that did not have a confidence interval containing zero could be 'picked'. This observation partially motivated the two-phase procedure employed for the sablefish application, so it is likely that such erroneous detection would be reduced if overlapping growth estimates were disregarded (our simulation analysis investigated the accuracy of the first stage). We evaluated if an autoregressive structure improved our simulation models as length-at-age can be time-dependent, but it did not; this may not be the case for other fisheries.

In addition, we did not simulate nor consider error or bias in the aging (i.e., otolith reading) process (Cope and Punt, 2007), which would potentially introduce uncertainty in breakpoint detection. Based on aging workshops conducted for sablefish, we consider aging results used in the case study to be roughly comparable between regions (Fenske et al., 2019). With these caveats in mind, we envision (and demonstrate) using the method as a tool to identify general regions and periods of change in fish length-at-age, which will necessarily be evaluated against pre-existing knowledge of the fish population and its ecosystem.

Neither the GAM-based nor the STARS approach is appropriate for extrapolation (prediction beyond the range of covariates, or outside of the ecosystem, used in model fitting), particularly because they use indirect variables such as latitude which may have nonlinear or inverted relationships with fish physiology in other ecosystems (Austin, 2002). It is likely there are thresholds in, or types of, spatiotemporal growth variation that will be poorly detected by most methods, which we see as a promising area for future research.

4.2 Implications of detected breakpoints for Northeast Pacific Sablefish

Our evaluation of size-at-age for NE Pacific sablefish was directly motivated by the notion that sablefish growth may vary at a scale that differs from present management boundaries. For NE Pacific sablefish, we applied the method to each sex separately at a set of key biological ages and determined that sablefish length-at-age differs most significantly across five regions, whose boundaries can be defined by major oceanographic features (the Southern California Bight, and the bifurcation of the North Pacific Current) as well as a known ecosystem boundary in the Gulf of Alaska. It is evident from this and previous work (Echave et al., 2012; Gertseva et al., 2017; McDevitt, 1990) that there is some level of variation in sablefish growth, whether in the growth rates themselves or the spatiotemporal scale at which variation in growth occurs. Previous work with sablefish data has utilized an *a priori* method, wherein length and age data were aggregated into pre-hypothesized spatial zones and fitted VBGF curves were compared using Akaike's Information Criterion. This 'information-theoretic' (Guthery et al., 2003) method is fairly straightforward computationally, and has been implemented separately for the California Current (Gertseva et al., 2017) and Alaska federal sablefish fisheries (Echave et al., 2012; McDevitt, 1990). The California Current analysis identified a statistically significant break in VBGF parameters for sablefish at approximately 36° N, between Point Conception and Monterey, CA, with additional evidence for an increasing cline in L_∞ with increasing latitude and a general increase in estimated L_∞ and L_2 for more northerly regions. These results mirror the trend in our latitudinal smoother (Figure 5 and 6) and our detected breakpoint at 36˚N (Figure 7), which is incidentally a management sub-boundary used by the US Pacific Fishery Management Council. That work also found an increase in k estimates for areas sampled south of the Vancouver area (ca. 49˚N), which was posited to be the result of samples coming from the "southern end of a faster-growing northern stock", a suggestion supported by our findings of another breakpoint at 50˚N. Preliminary analyses of sablefish tagged in Alaska suggest that the British Columbia management area exports fish into the California Current and Gulf of Alaska, a diffusion pattern that could potentially taper off with decreasing latitude; the distance between Vancouver, B.C. and Monterey, C.A. is approximately three times the mean great-circle movement distance for sablefish determined by Hanselman et al. (2015), which is a measure of the shortest possible distance traveled between tagged and recovered animals. Gertseva et al. (2017) described how sablefish have been shown to be highly mobile, with ontogenetic movements off the coastal shelf; such combined, complex life patterns could yield higher growth rates in northern latitudes that interact with a more generalized shelf-slope pattern of ontogenetic movement observed in groundfish overall.

There are several noteworthy trends in the stratified growth estimates (Figure 8) that warrant future research. Firstly, the *post hoc* incorporation of a spatial break at 145°W based on ecosystem data was not ruled out during the significance testing of L_∞. This supports the notion that environmental features may result in variations in growth, and that the proposed GAM-based method is amenable to improvements based on the incorporation of climate or ecosystem knowledge. Additionally, both latitudinal breakpoints are loosely associated with significant oceanographic features, namely start of the southern California Bight at Point Conception (~34°N) and the bifurcation of the North Pacific Current, which splits into the Alaska and California currents as it approaches the west coast of North America. The breakpoint at 36°N is slightly north of the beginning of the bight, but also characterized by dynamic, mostly southward floor in the nearshore environment. The formal location of the North Pacific bifurcation varies, but is generally centered off the coast of British Columbia (Cummins and Freeland, 2007; Figure 7). In common with the ecosystem split identified in the Gulf of Alaska, these oceanographic features lead to distinct zones of productivity (Kim et al., 2009; Mackas et al., 2011) that could influence resource availability and subsequent growth.

The temporal break in year 2010 was conserved (supported by significantly different L_∞ estimates) only for female fish, and more so in the southerly latitudes (such as regions 1 through 4, which are mostly comprised of California Current data), and exist along a steeper north-south cline. We note, however, that the procedure used to eliminate 'overlapping' L_∞ estimates concerned only statistical differences in values (and are therefore sensitive to sample sizes). The biological significance of these values should need to be investigated in the context of fecundity and length-weight differences between regions.

Preliminary analyses of sablefish movement rates from tagging data from Alaska (as analyzed in Hanselman et al., 2015) indicate that male sablefish seem to move more frequently to and from sea mounts, which are situated within the GAM-defined regions identified here. There are several possibilities for why female sablefish seem to exhibit finer spatiotemporal structure in growth. Empirical work in Canada (Mason et al., 1983) that examined early life history of fishery-caught coastal sablefish observed a slight cline in mean fork length with increasing latitude, although the sex ratio within the study was biased towards females. That study suggested that selectivity for female sablefish may be higher due to higher congregating or feeding activity, in addition to the fact that females grow larger and are likely preferentially targeted in the commercial fishery in BC, which is also true for the fixed-gear fisheries in the California Current (Johnson et al., 2015). This could render females more sensitive to changes in fisher behavior, such as the implementation of catch shares off the US west coast in 2011. Expanding the method to allow for detection of multiple spatial and/or temporal breaks at once may enable further investigation of this phenomenon, although it may lead to the creation of spurious regions with insignificant difference in growth parameters, as observed in the first phase of the case study.

A plausible scenario that would generate our observed results could be that changes in fisher behavior or climate in the last ~10 years caused female sablefish to move northward in greater numbers, or simply experience size-based truncations in regions to the east of 145 due to fishing pressure. Each of these phenomena would have an inverse effect on resultant size-at-age, with fish entering the northern ecosystem tending to grow larger and high, persistent fishing pressure in any region leading to truncations in terminal size. Because we only detected slight declines size-at-age between time periods for female sablefish, it is possible that either fishery-related effects simply have not lasted long enough to be strongly evident, or such effects are being counteracted by more fish entering ecosystems favorable to higher terminal sizes. A closer examination of sex-related movement would be useful towards this understanding.

Consideration of temporal variation in sablefish growth is further complicated by the exploitation history of the fishery, which has steadily moved north- and west-ward in the California Current and Alaska over the last several decades, encountering 'larger' fish with subsequent expansion (Pacific Fisheries Management Council (PFMC), 2013) This suggests that differences in mean length across the region could be attributable to different degrees, durations, or patterns of fishing pressure (Hilborn and Minte-Vera, 2008), interacting with inherent growth variation to produce such spatiotemporal patterns. A principal conclusion of Stawitz et al. (2015) was that the form of sablefish growth variation differed among ecosystems, wherein the California Current is a more climactically variable ecosystem. Such ecosystem-driven trends may be diluted when analyzing the data as a composite, as in our study. Notably, our temporal smoother did not produce a distinct annual or cyclic trend. Methods that consider the space and time components co-dependently (as in vectorized auto-regressive spatiotemporal models, Thorson, 2019a) may strengthen the ability to disentangle such trends, and also to consider covarying spatial effects (e.g. near- and offshore).

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Figures

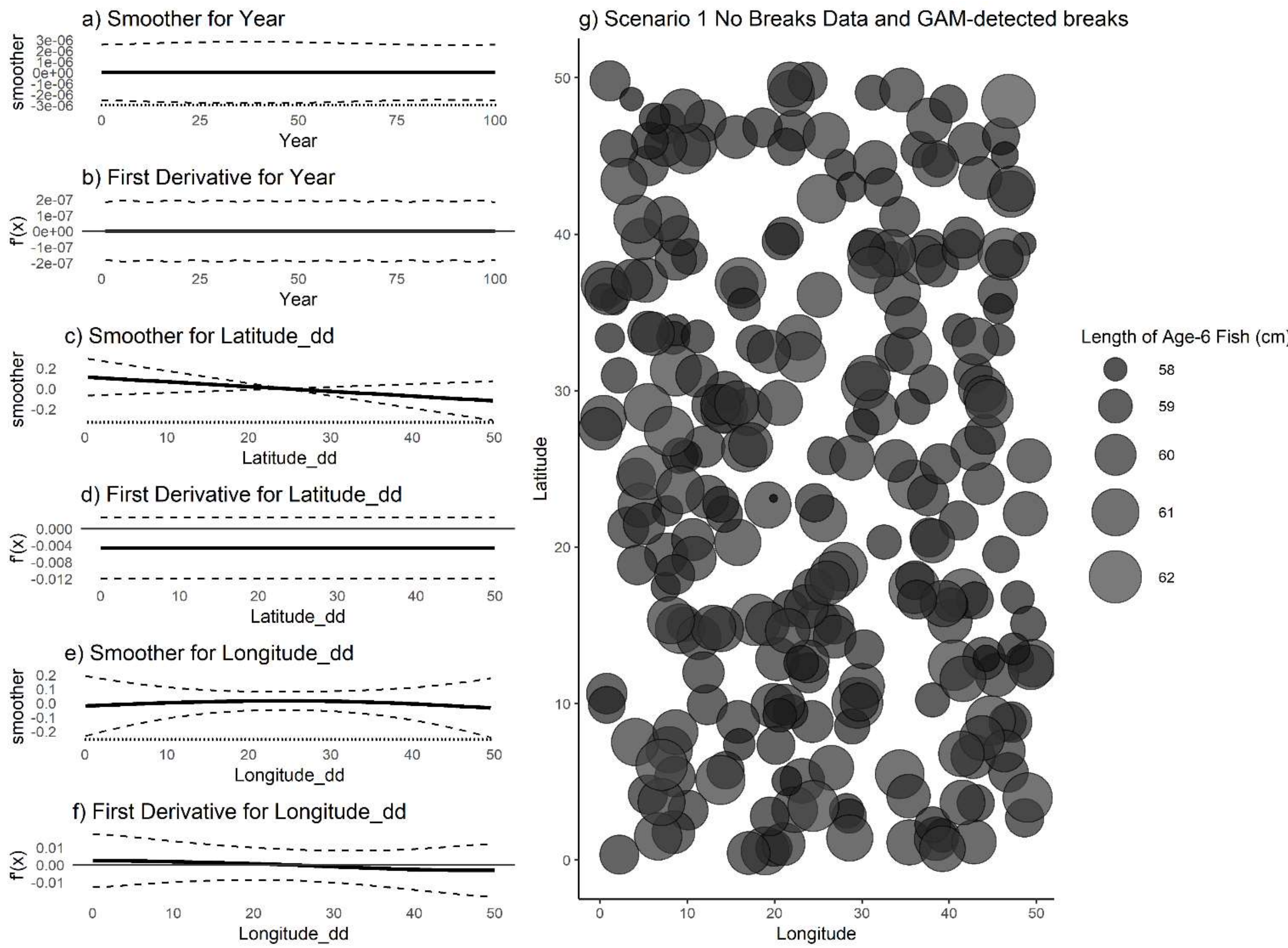

Figure 1. (a,c,e) raw value of GAM smoothers for Year, Latitude and Longitude; (b,d,f) mean (black line) and 95% CI (black dashed lines) of first derivative of the smoothers; (g) map of age-6 fish for a single simulated dataset with no designated spatial or temporal breaks. No break points were detected by the GAM.

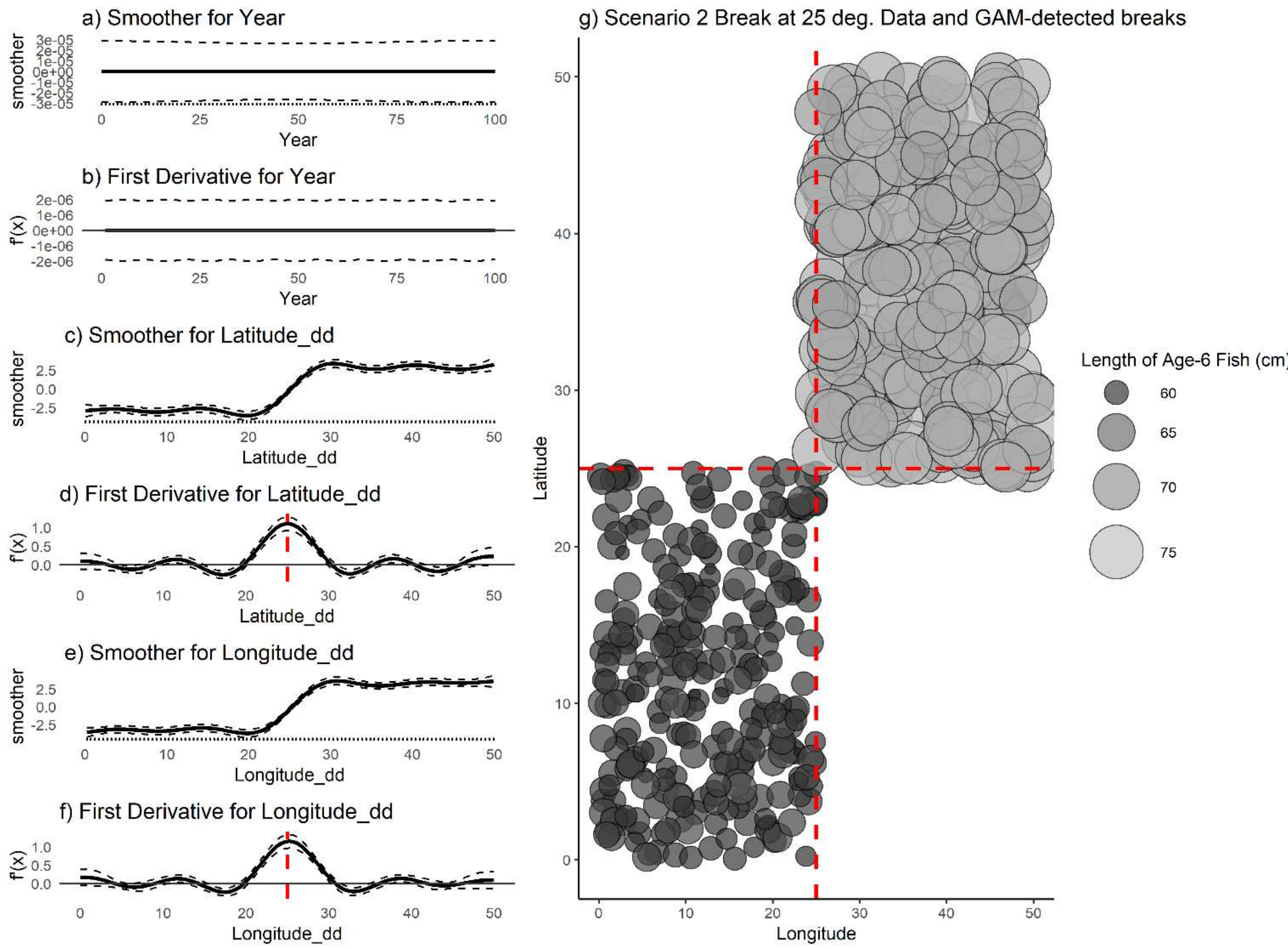

Figure 2. (a,c,e) raw value of smoothers (fitted regression splines) for year, latitude, and longitude; (b,d,f) mean (black line) and 95% CI (black dashed lines) of the first derivatives of the smoothers; (g) map of age-6 fish for a single simulated dataset with a single, symmetrical break at 25° latitude and longitude. Dashed red lines indicate detected break points, which are the maximum value obtained for this data set and do not have a confidence interval that contains zero.

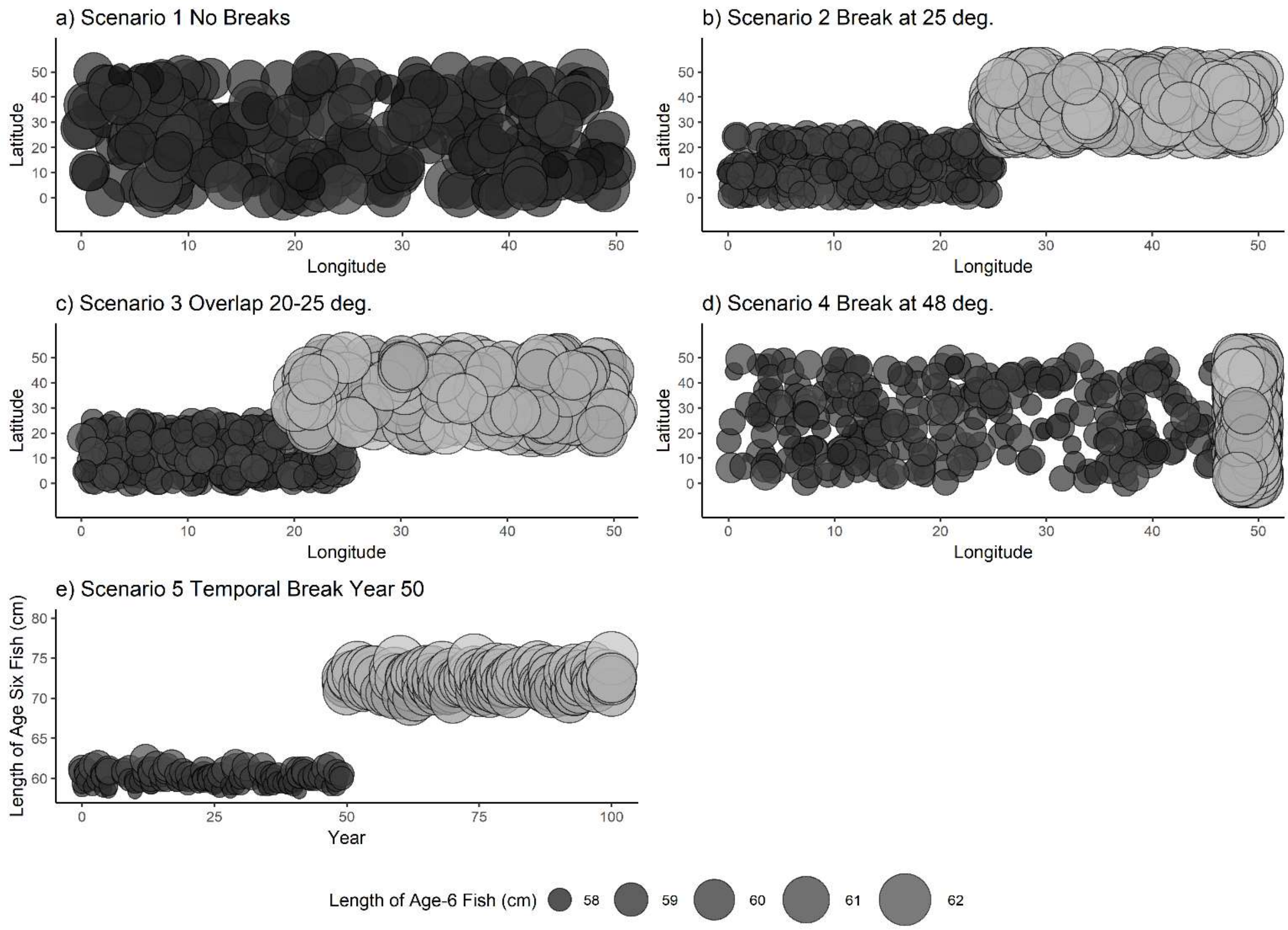

Figure 3. Example dataset for each of the scenarios in Table 2. For each of the five scenarios, points represent the length and location of a single simulated fish at age six. Fish locations (latitudes and longitudes) were sampled from a uniform distribution of the boundaries indicated in Table 2.

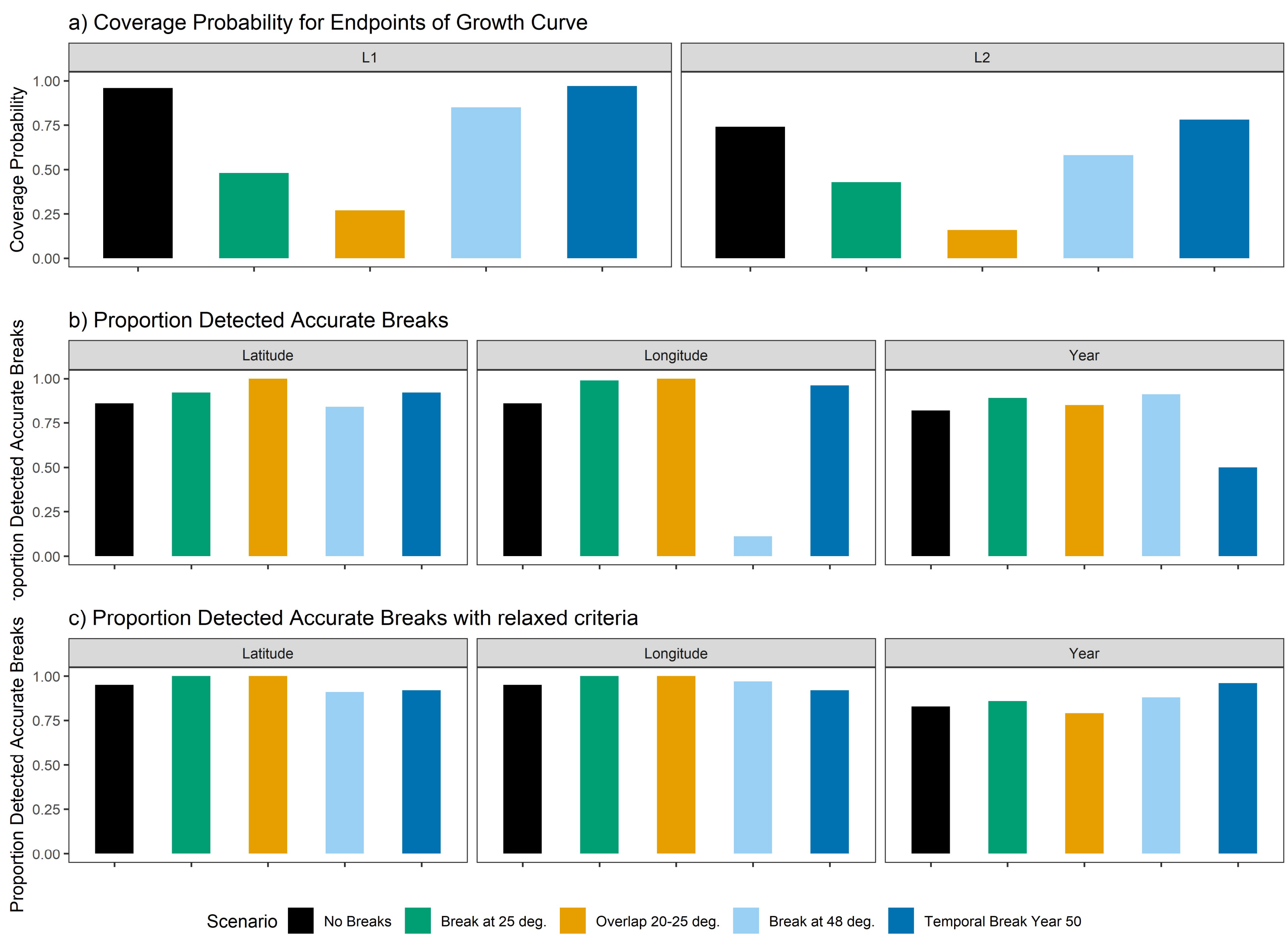

Figure 4. a) coverage probabilities for the endpoints of the growth curve, L_1 (left) and L_2 (right);b) proportion of 100 simulations for each spatial scenario wherein the correct latitudinal breaks (left), or longitudinal breaks (center) or temporal break (right) were detected, c) the same as b) but with the criteria for a 'match' relaxed to include breakpoints within two degrees or years of the truth.

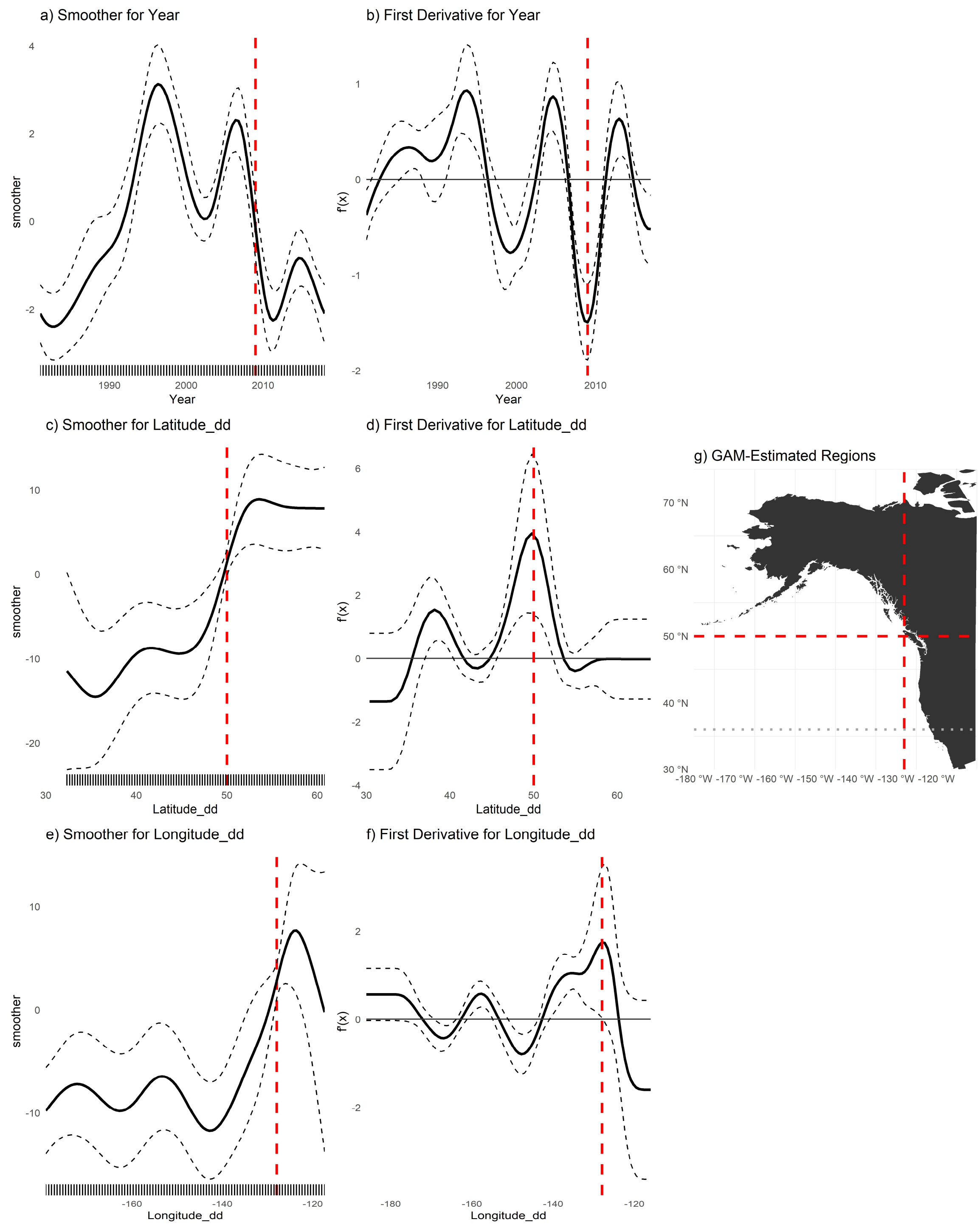

Figure 5. (a,c,e) Plots of smoothers (fitted regression splines) for year, latitude, and longitude, and first derivatives thereof for female age four sablefish (b,d,f). On a-f, vertical dashed lines indicate latitudes, longitudes or years that correspond to the highest first derivative and had a confidence interval that did not include zero. g) map with model-detected breakpoints (red dashed lines) and breakpoints detected for other ages (grey dotted line).

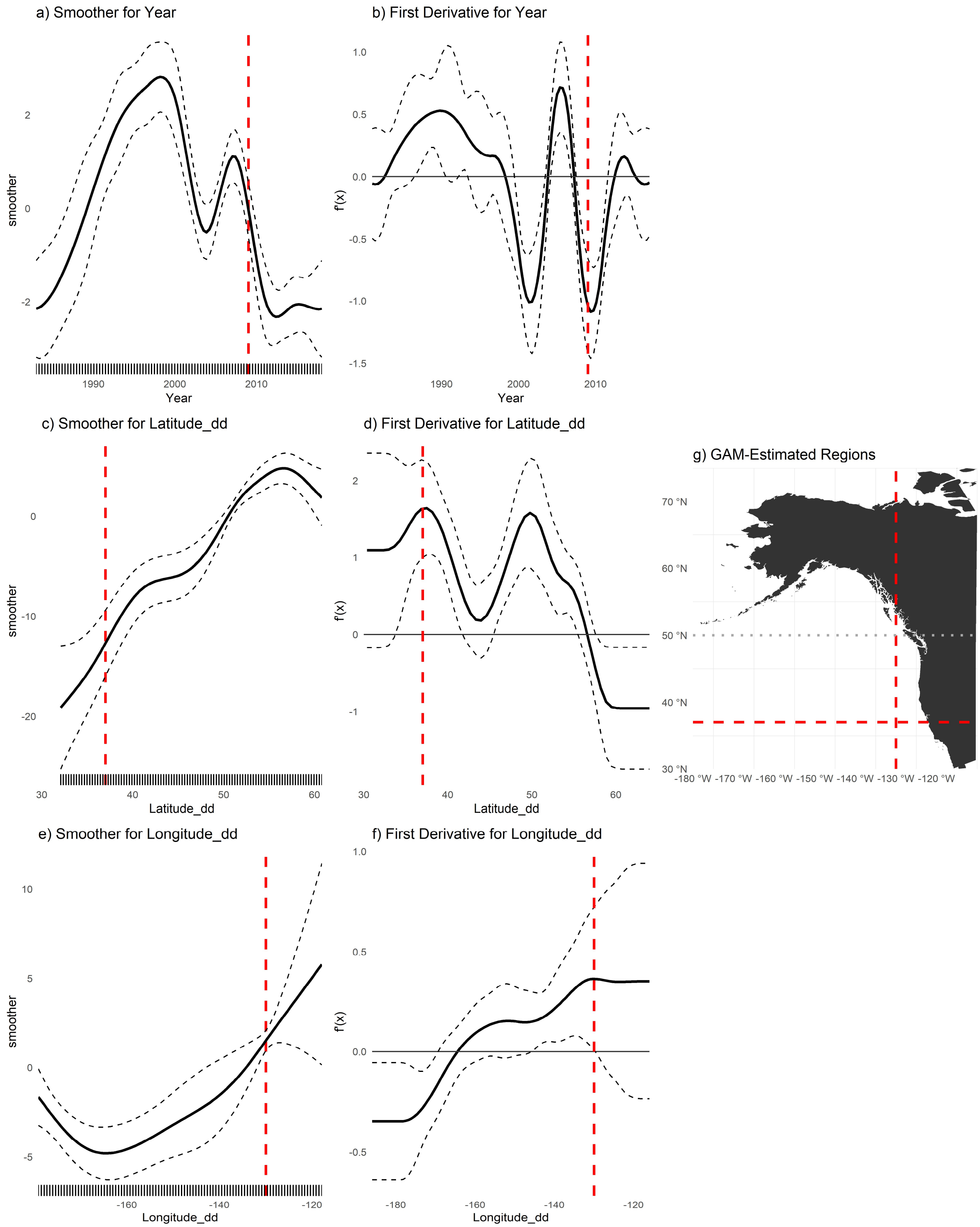

Figure 6. (a,c,e) Plots of smoothers (fitted regression splines) for Year, Latitude, and Longitude, and first derivatives thereof for female age six sablefish (b,d,f). On a-f, vertical dashed lines indicate latitudes, longitudes or years that corresponded to the highest first derivative and had a confidence interval that did not include zero. g) map with model-detected breakpoints (red dashed lines) and breakpoints detected for other ages (grey dotted line).

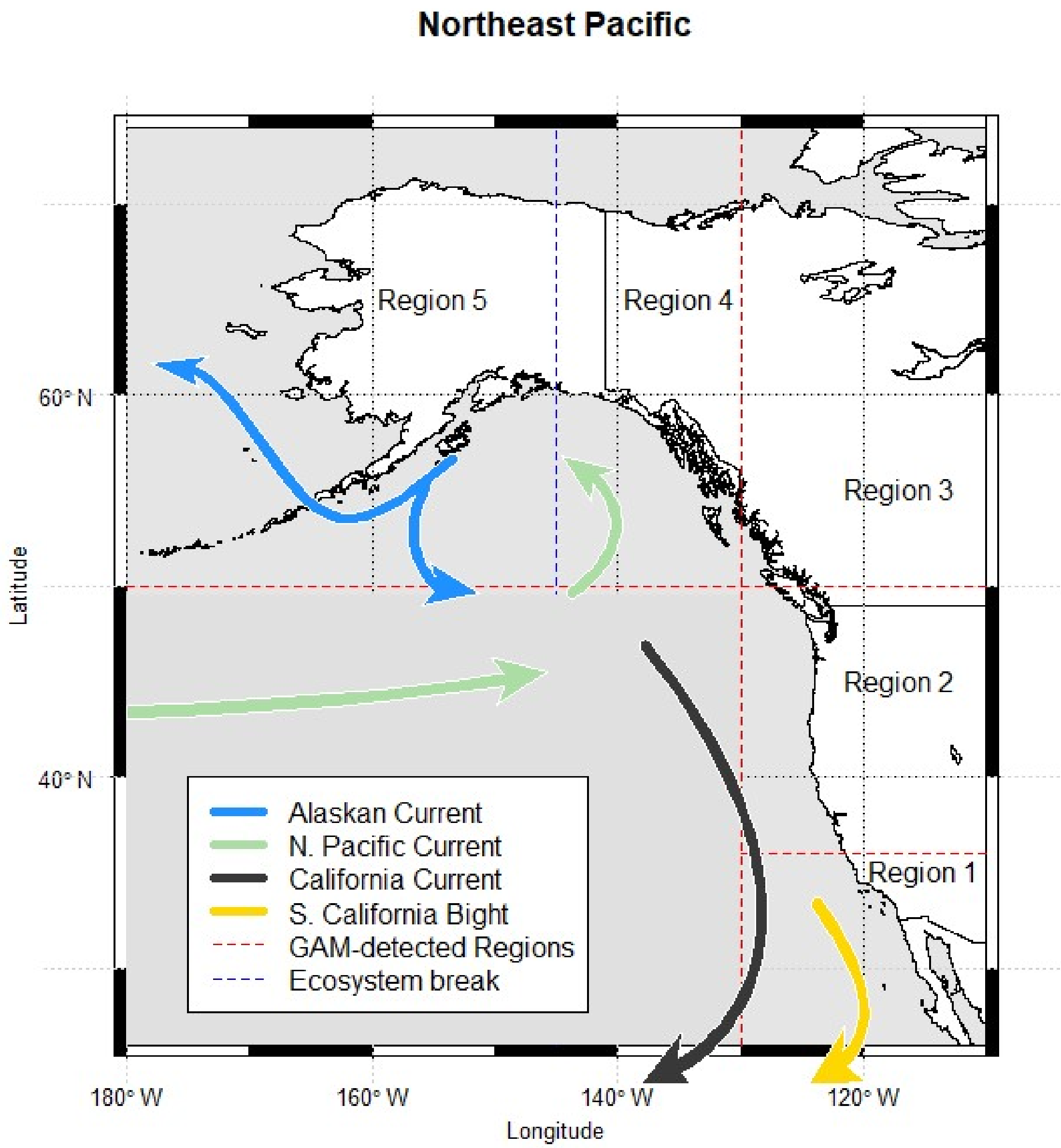

Figure 7. Method-detected breakpoints (red dashed lines) and ecosystem-based break (blue dashed lines) used to delineate growth regions for sablefish. Map made in R using current data from: https://data.amerigeoss.org/en_AU/dataset/major-ocean-currents-arrowpolys-30m-85

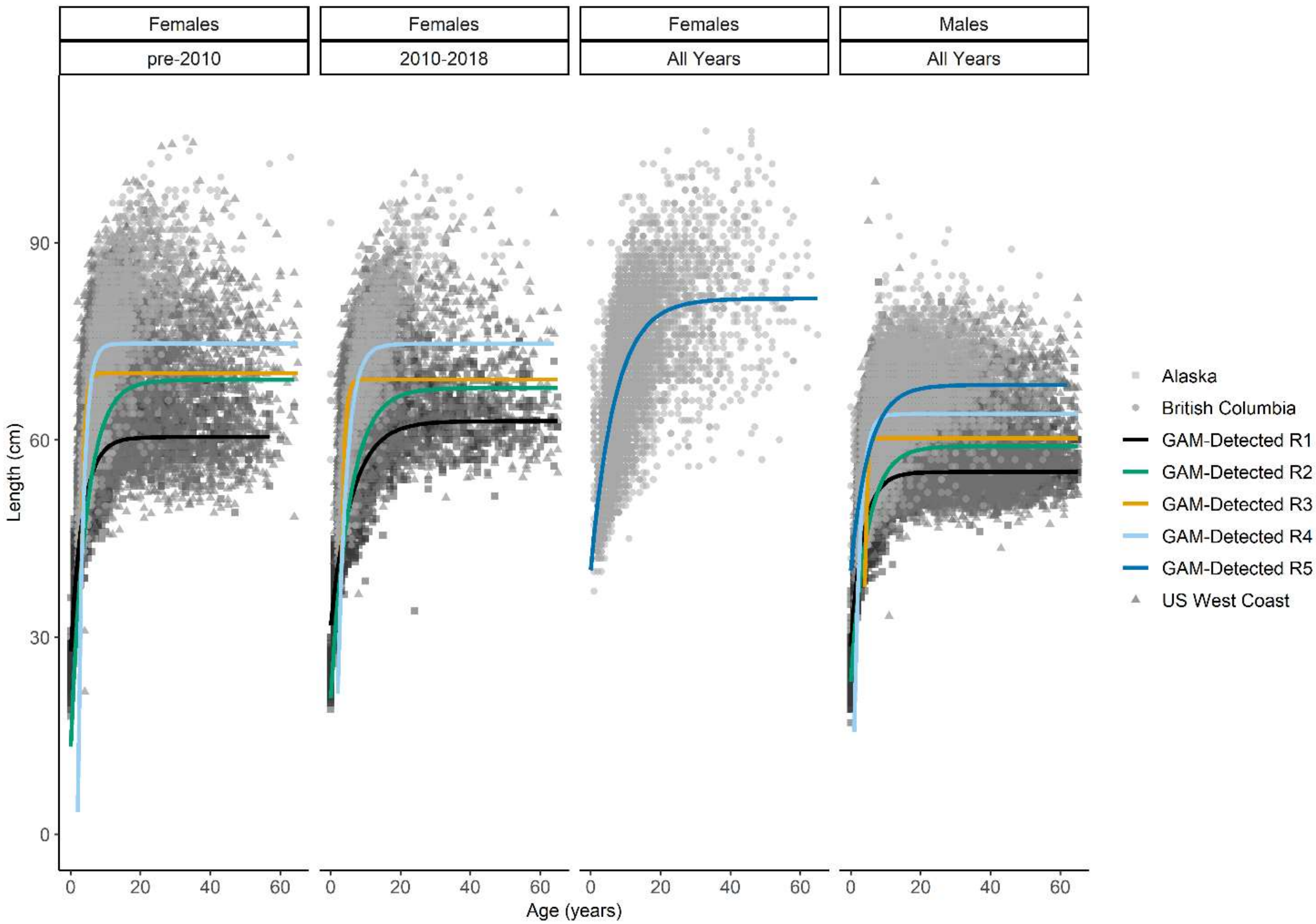

Figure 8. Fits of von Bertalanffy growth function (colored lines) to data at the final spatiotemporal aggregation (panels). Points are raw survey data with color and shape corresponding to their source.

Tables

Region	Survey Method	Sample size used in this analysis to fit GAM		VBGF parameters from recent stock assessments					
		M	F	L_∞ (cm)		k (years $^{-1}$)		t_0 (years)	
				M	F	M	F	M	F
West Coast of US (Johnson et al., 2015)	Trawl on chartered commercial fishing vessels	7,778	7,222	57	64	0.41	0.32	0 (fixed)	0 (fixed)
British Columbia	Stratified trap survey	6,912	8,088	68.99	72.00	0.29	0.25	^	^
Alaska Federal (Hanselman et al., 2017)	Longline on chartered commercial fishing vessels	6,818	8,182	*67.8 ⁑65.3	*80.2 ⁑75.6	*0.29 ⁑0.28	*0.22 ⁑0.21	*⁑2.27	*⁑1.95

Table 1. Overview of survey methods, data available and most recent VBGF parameters used for sablefish in stock assessments.
*Time-blocked VBGF parameters for Alaska Federal assessment 1996-2018
⁑Time-blocked VBGF parameters for Alaska Federal assessment from 1960-1995 (Hanselman et al., 2017)
^The BC assessment fixes length at age-1 to 32.5cm.

Scenario Number	Scenario Description	Stratification
1	No spatial breaks	Latitude and Longitude ~ U[0,50], all fish under regime 1
2	Single, spatial break in middle of range, with no overlap	Latitude and Longitude ~ U[0,25] under regime 1; Latitude and Longitude ~ U[25,50] under regime 2
3	Some overlap between regions	Latitude and Longitude ~ U[0,25] under regime 1; Latitude and Longitude ~ U[20,50] under regime 2
4	Single spatial break at edge of range with no overlap	Latitude ~ U[0,50] for regimes 1 and 2; Longitude ~ U[0,48] for regime 1 Longitude ~ U[48,50] for regime 2
5	Single temporal break at year 50 (of 100); no spatial variability	Latitude and Longitude ~ U[0,50], all fish under regime 1 from years 0 to 49 and regime 2 thereafter

Table 2. Summary of simulation scenarios used to test the proposed GAM-based method given various extents of spatial growth variation, and a single temporal scenario.

Region	Sex	Period	Sample size used to fit GAM	Estimated VGBF Parameters			Corresponding estimated endpoints of growth curve	
				L_∞ (cm)	k (years $^{-1}$)	t_0 (years)	L_1 (cm)	L_2 (cm)
R1	Female	Early	985	60.44	0.29	-2.15	32.21	60.43
R1	Female	Late	1,101	62.86	0.16	-4.31	34.22	62.63
R1	Male	All Years	2,048	55.11	0.28	-2.59	32.08	55.11
R2	Female	Early	8,412	69.14	0.22	-0.96	19.22	69.08
R2	Female	Late	5,557	67.91	0.19	-1.96	24.84	67.73
R2	Male	All Years	14,990	59.04	0.21	-2.34	26.83	58.98
R3	Female	Early	2,517	70.15	1.29	2.41	61.09*	70.15
R3	Female	Late	852	69.21	1.18	2.32	59.72*	69.21
R3	Male	All Years	2,698	60.26	2.12	3.54	37.56*	60.26
R4	Female	Early	9,411	74.66	0.66	1.93	55.49*	74.66
R4	Female	Late	4,155	74.62	0.39	1.14	50.37*	74.62
R4	Male	All Years	11,640	63.94	0.58	0.52	55.4*	63.94
R5	Female	All Years	13,212	81.5	0.14	-4.74	43.03	80.94
R5	Male	All Years	10,411	68.36	0.2	-4.51	42.82	68.28

Table 3. Description of final spatiotemporal regions, and the sex-specific growth parameters estimated in the analysis. The Region column corresponds to regions depicted in Figure 7, with "early" period being observations before or during 2010, where applicable. Parameter estimates are those used to plot fitted curves in

Figure 8. *Age 0.5 yrs was used to report L_1 estimates, except for values from Regions 3 and 4 for which $\boldsymbol{L_1}$ corresponds to lengths at age 4.

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Oceanographic features delineate growth zonation in Northeast Pacific sablefish

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Abstract

Renewed interest in the estimation of spatial and temporal variation in fish traits, such as body size, is a result of computing advances and the development of spatially-explicit management frameworks. However, many attempts to quantify spatial structure or the distribution of traits utilize *a priori* approaches, which involve pre-designated geographic regions and thus cannot detect unanticipated spatial patterns. We developed a new, model-based method that uses the first derivative of the spatial smoothing term of a generalized additive model to identify spatial zones of variation in fish length-at-age. We use simulation testing to evaluate the method across a variety of synthetic, stratified age and length datasets, and then apply it to survey data for Northeast Pacific sablefish (*Anoplopoma fimbria*). Simulation testing illustrates the robustness of the method across a variety of scenarios related to spatially or temporally stratified length-at-age data, including strict boundaries, overlapping zones and changes at the extreme of the range. Results indicate that length-at-age for Northeast Pacific sablefish increases with latitude, which is consistent with previous work from the western United States. Model-detected spatial breakpoints corresponded to major oceanographic features, including the northern end of the Southern California Bight and the bifurcation of the North Pacific Current. This method has the potential to improve detection of large-scale patterns in fish growth, and aid in the development of spatiotemporally structured population dynamics models to inform ecosystem-based fisheries management.

*Declaration of Interest Statement

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: