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**Evidence for a stock-recruit relationship in Bering Sea Tanner crab survey data**

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**Abstract** We investigated hypotheses concerning the effects of spawning female abundance and a suite of environmental covariates on recruitment of juvenile Tanner crabs, *Chionoecetes bairdi*, in the eastern Bering Sea (EBS). Hypotheses about causal relationships were tested using generalized least squares and generalized additive modeling procedures. We found robust statistically significant (p < 0.05) negative relationships between juvenile crab recruitment and spawning female crab abundance using a linearized Ricker stock-recruit model. Generalized additive modeling suggested an additional negative effect by flathead sole biomass, and a positive relationship with both the Pacific Decadal Oscillation and Arctic Oscillation. Our findings suggest that parental stock size, groundfish predation and climatic conditions may influence year-class strength for the EBS Tanner crab stock.

**Key words:** Climate, *Chionoecetes bairdi*, eastern Bering Sea, recruitment, stock-recruit relationship, Tanner crab

**Introduction**

The brachyuran Tanner crab, *Chionoecetes bairdi*, has supported a lucrative commercial fishery in the eastern Bering Sea (EBS) since the 1960s. However, this stock has also experienced strong variability in recruitment and adult biomass. This has led to a “boom and bust” fishery, with peak landings of 30,209 t in 1977 and 18,189 t in 1990, followed by crashes leading to multiple fishery closures over the intervening decades (Rugolo & Turnock 2011, Stockhausen 2023). This variability in stock size and fisheries outcomes underscores the need to better understand the factors regulating productivity in the stock. This need has been accentuated given that the EBS has experienced a series of extreme marine heatwaves which have been formally attributed to anthropogenic causes (Walsh et al. 2018, Laufkötter et al. 2020, Litzow et al. 2024). Climate change results in the borealization of Arctic communities, in particular through the introduction of generalist groundfish predators (Kortsch et al. 2015, Frainer et al. 2017), and predation on juvenile snow crab by boreal groundfish has long been hypothesized to be a major source of year class mortality (Livingston 1989, Marcello et al. 2012, Burgos et al. 2013,Szuwalski et al. 2020). The effects of predation and climate change on EBS crab recruitment are long-standing research topics (e.g., Zheng & Kruse 2006, Thorson et al. 2021), and the ongoing borealization of the EBS underscores the need for better understanding of these effects.

Mechanisms affecting the survival of Tanner crabsfrom age 0 to age 3 are likely to exert the most significant effects on recruitment to the adult stock (Tyler & Kruse 1997). Accordingly, early life history stages have been a focus of previous studies attempting to unravel the causes of fluctuations in crab abundance (Livingston 1989, Rosenkranz et al. 1998, 2001). A putative 13-14 year cycle in both legal-sized male recruitment to the fishery and total adult population size has been interpreted to indicate that long-term cyclicity in the biophysical environment may mediate recruitment strength (Zheng & Kruse 1998, 2003). This putative cycle is also approximately double the mean age of maturity of female Tanner crabs in this region, suggesting the possibility of an endogenous rhythm associated in some way with a stock-recruit (S-R) relationship (Zheng & Kruse 1998).

Current management for EBS Tanner crab operates under the assumption that a spawner-recruit (S-R) relationship goes not exist (i.e., the number of recruits to the stock is independent of mature biomass at spawning; Stockhausen 2023). As a result, reference points for managing the fishery, such as biomass at maximum sustained yield (*B*MSY), are estimated with proxies rather than being estimated directly from population dynamics (e.g., 35% of estimated unfished biomass is used as a proxy for *B*MSY; Stockhausen 2023). An empirical demonstration of a S-R relationship, if it did exist for this stock, would provide better scientific support for management through the ability to estimate management quantities directly from population dynamics (cite). Previous studies have found only weak evidence for a Ricker-style, dome-shaped relationship between spawning stock size and subsequent recruitment to the adult population at lags of 7-9 years, with large year-classes resulting from both high and low spawning abundance (Zheng & Kruse 1998, 2003). Several issues may hinder the ability to detect S-R relationships for this stock. First, the relatively long time lags between reproduction and recruitment increase the potential for confounding S-R relationships by exogenous mechanisms such as predation or competition. Second, the inability to age crab (since no hard parts are retained through molts) necessitates inferring pseudo-cohorts from modal analysis of size frequency distributions observed over time (e.g., Donaldson et al. 1981), leading to uncertainty about the time between hatching and recruitment to the adult population.

In this study we examine the evidence for a S-R relationship for the EBS Tanner crab stock and the role that physical and biological covariates may play in driving variability in a S-R relationship, using data from a fisheries-independent bottom trawl survey for the years 1978-2019. Our specific goals are to 1) test for a S-R relationship by examining the relationship between spawning stock biomass and the biomass of juvenile crab at a 2-4 year lag; 2) evaluate the effects of competition, predation, and physical covariates on the strength of the observed S-R relationship.

**Methods**

Data

Tanner crab abundancedata come from a bottom trawl survey of the EBS continental shelf conducted annually since 1978 (Fig. 1a). No survey was conducted during 2020 because of the COVID-19 pandemic, and we use data from 1978-2019 to avoid complications involved with the missing year. During the first decade of the time series there was a gradual expansion of the survey area leading to variability in the number of stations sampled. The survey extent was standardized in 1988, and 376 stations have been consistently sampled since. A 0.5-hr tow is made near the center of each 20 x 20 nmi2 (37 x 37 km2) square on a sampling grid. Since 1982, the standardized sampling gear has been the 83-112 eastern otter trawl (Zacher et al. 2021).

For purposes of our analysis, we defined juvenile crab as those of both sexes with a carapace width (CW) of 30-50 mm. Crabs in this size range are likely predominately 3 years old, based on size-at-age relationships estimated for Tanner crabs in the Gulf of Alaska (Donaldson et al. 1981) corrected for the greater intermolt period in the colder temperatures of the EBS (Paul & Paul 2001). To account for possible error in age estimates we also considered the possibility that 30-50 mm CW crabs were predominantly 2 or 4 years old, for sensitivity analysis in our initial S-R models. ~~Use of design-based estimates for this size range and at this lag is an important distinction relative to Szuwalski et al. (2021), who used model recruitment estimates at a lag of 5 yrs in their work, increasing the potential for variables external to the model system to affect recruitment, confounding any effects by the investigated variable(s). In addition, comparative environmental effect models were run assuming recruitment to this size bin at age 4, and using an alternative age 3-yr recruitment size range of 30-40 mm. Estimates for this alternative size bin were highly correlated with those for the primary size bin (r = 0.906)~~

Mature, multiparous (repeat spawning) female Tanner crabs were defined as females of shell condition 3 (SC3, old shell) and shell condition 4 (SC4, very old shell). Tanner crab experience a terminal molt upon reaching sexual maturity. Shell-age classification approximates the time since the last molt using criteria described by Jadamec et al. (1999). Shell condition 2 female crabs were ignored in our study as these are primiparous crabs and have both a reduced fecundity (Webb XXXX) and an extended brooding period, mating in late winter immediately following the terminal molt and carrying the resultant embryos until the following year (Swiney 2008). Consequently, primiparous females sampled in year *t* will hatch their eggs in year *t+1* andwill not contribute to the hypothesized age 3 juvenile pseudocohort in year *t+3* used as the response variable in our S-R analyses. This lag differential complicates use of SC2 females in SR modeling, as the extended lag increases the possibility of confounding of effect, for example through female mortality events, when these crab are considered in isolation. If considered in combination with older shell crab, this lag would result in many female crab being included twice using our methods: once as an SC2 crab, and again as an SC3. While this might be resolved by lagging for release the year after sampling (*t+1*) for all females, this would again increase the potential for effect confounding.. Finally, SC5 crabs (very, very old shell) were ignored due to comparatively high rates of barrenness, lower fecundity and low abundance.

For both juveniles and mature female crabs, average catch per unit effort (CPUE, number of crab km-2) for size/SC class and the population level abundance estimate derived by expanding the mean CPUE to the survey grid area were calculated using the procedures outlined in Zacher et al.(2023)*.*

Juvenile Tanner crab recruitment is characterized by large interannual variability, with periodic peaks and troughs occurring on a roughly decadal scale (Figure 1a).Female abundance showed peaks in the 1980s and 1990s, with an extremely high abundance estimate in 1983 (Figure 1b).

Data for candidate environmental and biological covariates were selected based on a literature review of proposed mechanisms controlling Tanner crab recruitment (Table 1). Annual point estimates and 2 and/or 3-yr rolling averages were used for covariates. Rolling averages were used in cases where the covariate may affect the crab at multiple ages, and because the juvenile recruitment index may include crab of multiple ages, and offer the additional benefit of leveling extreme observations. These were calculated on the final year of the given rolling average i.e. for an average of temperatures in years *t*, *t*-1 and *t*-2, the rolling average estimate was applied to year *t*.

Annual values for mature female snowcrab abundance and mean near bottom temperature (NBT) came from the Bering Sea bottom trawl survey. Three-year rolling averages were then calculated on the final year used for the given rolling average i.e. for an average of temperatures in years *t*, *t*-1 and *t*-2, the rolling average estimate was applied to year *t*.

Data for the Arctic Oscillation (AO, Thompson and Wallace 1998) and Pacific Decadal Oscillation (PDO, Hare 1996) were obtained from <https://www.ncdc.noaa.gov/teleconnections/>. We used winter data for the PDO (December- February mean for the year corresponding to January). Winter values of the AO were calculated as January- March means. Two and three-year rolling averages were then calculated for each index using the same procedures as applied for NBT. May – June Sea surface temperature (SST MJ), estimates were obtained from the Extended Reconstructed Sea Surface Temperature (ERSST) v5 dataset (Huang et al. 2017), available from <https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v5>. Estimates for the months of May, June and July, and corresponding to the EBS region were extracted, and averaged annually. Finally, northwestern and southeastern wind vector components during the summer (May-September) were resolved via analysis of v- and u-components from the NCAR-NCEP database, obtained from <http://apdrc.soest.hawaii.edu/erddap/griddap/>. Monthly proportions of days with wind from the specified direction were calculated, then averaged by year.

Analysis

We used the linearized version of the Ricker model in order to analyze the influence of density dependence and external covariates on Tanner crab productivity (log recruits per spawner; cite). Exploratory analysis indicated significant lag-1 autocorrelation in productivity time series, and we were also interested in accounting for possible non-linear effects of density on productivity, so we implemented the Ricker model in a Generalized Additive Mixed Model (GAMM) framework, using the R package *mgcv* (cite):

Where *R* is the abundance of juvenile crab in year *t*, *S* is the abundance of mature female crab in year *t*-3, *α* is the intercept/productivity term, ƒ is a semi-parametric smooth function, are linear slopes, *Xi* are external covariates and ε*t* is the residual error term at time *t*. To account for autocorrelation, we modeled residuals with first-order autocorrelation:

ε*t* = φ ε*t*-1 + ν*t* ,

where ν*t* is assumed to be Gaussian white noise at time *t*, NID(0, σ2ν), and φ is the autocorrelation parameter such that at lag *t*-1, -1 < < 1, and σ2{ε*t*} = .

Exploratory analysis showed that fully semi-parametric models that fit smooth functions to all covariates were consistently out-performed in AICc comparison by models fitting a smooth to spawner density and a linear effect for other covariates, so we did not consider the fully semi-parametric models further. To avoid over-fitting the data, we limited the smooth functions to three effective degrees of freedom (i.e., *k* = 4 in the model syntax; cite Woods mgcv reference). Where multiple covariates were included in one model, care was taken to reduce multicollinearity, although moderate levels (r ~0.50) were tolerated for purposes of exploring a combined climate (Arctic Oscillation) and competition (mature female opilio) effect. (Model performances were assessed using small sample-size Akaike Information Criterion (AICc) calculated with the R package MuMIn (Barton 2020). All analyses were conducted using R version 4.0.3 (R Core Team 2020).

**Results**

The strongest evidence for a S-R relationship was found when juvenile and spawner abundance were compared at a lag of 2 years, with weaker support for a relationship at lag 3 (Δ-AICc = 2.26) and lag 4 (Δ-AICc = 0.11). Based on probable size-at-age, lag 2 was dismissed, while a combination of this consideration, and high similarity between models using lags to recruitment of 3 and 4 years versus the full suite of environmental covariates lead to the selection of lag-3 yr for the results presented here. Models using recruitment to the 30-40 mm bin at a lag of 3 yrs also gave fairly similar results, in particular regarding the most significant variables affecting recruitment, providing further support for the use of recruitment to the 30-50 mm bin at a lag of 3 yrs.

The lag-3 relationship provided strong evidence for a S-R relationship, with productivity (log recruits per spawner relationship) showing a non-linear decrease with mature female abundance (p < 0.0001; Figure 2a). The best model incorporating additional covariates showed a marked improvement over the basic S-R model (Δ-AICc = 14.78; Table 2). This model explained \_\_ % of deviance in the data and showed evidence for negative relationships with lag 2 flathead sole abundance (p <0.001; Fig. 2b) and a positive relationships with both two-year rolling mean PDO values (p = 0.024; Fig. 2c)). Although a second model incorporating the AO did not differ significantly from this model (Δ-AICc= 1.80), the AO term was statistically insignificant (p = 0.235).

Of the covariates investigated, FHS TBM provided the single greatest improvement in model AICc scores, both as a point-estimate, and a rolling average (Table 5), no other single variable models provided a significant improvement over the baseline model, while all multiple-variable models that gave an improvement incorporated FHS TBM, suggesting that this variable was responsible for much of the given model’s improved explanatory power. This was also observed in all sensitivity analyses. Althoughinclusion of the PDO singly, and in combination with the AO improved AICc values when considered together with FHS, and included with a linear effect, improvements were limited in comparison to a model with only the S-R effect and FHS (Table 5). Both the PDO and AO performed markedly worse when considered as the only covariate, and AO when considered singly in concert with FHS TBM (Table 5), with this term also not being statistically significant (p<0.05) in any model.

**Discussion**

Our results suggest the presence of a density-dependent S-R relationship for the Tanner crab population in the EBS. Furthermore, we found evidence of a predator-prey relationship with flathead sole biomass, and potential environmentally mediated survival related to the AOand PDO.

Over-compensatory density-dependent effects, as are observed in our S-R results may arise through several processes (Botsford et al. 2014). Intercohort/intrqacohort competition and cannibalism have been proposed as drivers of recruitment in the congener snow crab (Caddy et al. 2005, Émond et al. 2015). Synchronized release of larvae by dense aggregations of female crab may create dense patches of first-feeding zoeae that compete for prey (Stevens et al. 1994). Although there are no direct observations of this behavior in the EBS, as there are for the Gulf of Alaska (Stevens et al. 1994), high-density stations encountered during bottom trawl surveys are consistent with this behavior. It is thus reasonable to expect that in the relatively sluggish currents over the EBS continental shelf, larvae may maintain dense aggregations (Stabeno et al. 2001). To successfully feed, larval Tanner crab require high densities of copepods, potentially exceeding the mean concentration typically experienced in much of the natural environment (Paul et al. 1979, Incze & Paul 1983). In years of high reproductive output, we can speculate that zoeae in dense aggregations may thus experience increased mortality rates due to starvation as they deplete the local copepod population through feeding (Paul et al. 1979). The positive relationships observed in environmental indices that are likely to impact copepod productivity, particularly the PDO are consistent with this hypothesis, as these mechanisms are expected to improve copepod production as their values increase (Hunt et al. 2002, Hunt & Stabeno 2002, Hunt et al. 2022). Contrary to this, we found early summer SST to not be an important explanatory variable, suggesting that any temperature-effect may be more nuanced than expected.

Cannibalism, particularly between cohorts may also play an important role generating a density-dependent relationship, and has been proposed or observed to be a significant recruitment mechanism in many crab species, including the congener snow crab, where younger (age 0-4) juvenile crab are the most fed-upon (Dutil et al. 1997, Lovrich & Sainte-Marie 1997, Moksnes et al. 1997, 1998, Caddy et al. 2005). Unfortunately, only very limited work has been done examining cannibalism in Tanner crab, though the work that has been done suggests that it may be significant, with conspecifics being found to comprises ~11% of stomach contents by weight in crab sampled near Kodiak Island (Jewett & Feder 1983).

Finally, our density-dependent effect findings may also be explained by the observation that high population densities may also lead to significantly increased disease prevalence, increasing natural mortality rates, particularly in the high-density aggregations often observed in juvenile crabs. In the EBS region, the dinoflagellate *Hematodinium*, also known as bitter crab disease (BCD) infects *Chionoecetes* *spp*. crabs, leading to mortality rates of up to 100% (Meyers et al. 1996). Although all life stages may be infected, current evidence suggests that juvenile crab are the most susceptible to infection, likely due, at least in part, to increased molting frequencies, particularly for juveniles (Pestal et al. 2003, Shields et al. 2005).

Our work provides support for the hypothesis of a predation effect in the case of flathead sole, with a negative relationship observed between juvenile recruitment and flathead sole biomass. This is consistent with observations that flathead sole are second only to Pacific cod in terms of Tanner crab predation; and are occasionally the top predator of Tanner crab, based on stomach contents (Lang et al. 2005). Conversely, our results do not support the hypothesis of a significant predator effect for Pacific cod. These findings appear contrary to previous work, in particular an analysis of cod stomachs which indicated intense predation by young cod on Tanner crab, particularly for crab of age 1 yr (Livingston 1989), which has been corroborated by more recent analyses (Livingston et al. 1993, Lang et al. 2005). Of note, in unpublished work exploring cod densities at model-simulated larval settling locations, it was found that cod densities were much higher at these locations in the early-mid 1980s, coincident with the seminal work by Livingston (1989), than they have been for much of the time since (pers obs). Elucidation of potential relationships between cod and Tanner crab may depend on spatial considerations. For instance, in a recent analysis, cod was the strongest predictor of changes in the longitude of Tanner crab centroids of abundance; that is, when cod biomass is high, Tanner crab tend to be distributed farther offshore (Szuwalski et al., 2020).

Complexities present in predator-prey relationships may confound the ability to detect significant relationships in retrospective analyses such as ours. The degree of overlap between predator and prey may vary interannually, as both populations respond to interactions between dynamic environmental conditions and their respective environmental tolerances, with this reflected in predatory pressure experienced by the prey species (Ciannelli & Bailey 2005, Spencer 2008). If non-specialist predators experience a glut of prey items of various species, feeding pressure on a particular species might be reduced due to prey switching as predators optimize their foraging success (Krivan 1996). In addition, predator-prey relationships can be mediated through indirect effects by the presence of another predator (Siddon & Witman 2004), thus altering the observed functional response. Consequently, absence of an apparent predatory effect here should not be considered as conclusive evidence of a lack of a groundfish predation effect on recruitment strength of juvenile Tanner crab.

Contrary to previous studies (Rosenkranz et al. 2001), the results from this project do not offer strong support for the hypothesis of an effect by mean-bottom temperature on juvenile survival and recruitment. Conversely, our findings for sea surface temperature were generally in accordance with prior studies, which were at best inconclusive once temporal autocorrelation was accounted for (Rosenkranz 1998). If these results for SST are valid, then they suggest that any link between SST and crab recruitment is weak, or nuanced and confounded by other variables. As an example, it may be that while increased temperatures improve feeding conditions and growth for larval crab, they may offset this by also improving growth and feeding conditions for planktonic predators (e.g. Conway & Williams 1986). As a consequence of these poor results, temperature-related effects may not be the best explanation for the observed relationship with the PDO. Alternatively, because the PDO, is associated with the Aleutian Low, it is indicative of atmospheric circulation patterns which may themselves influence surface currents, and thus potentially, larval advection patterns (Bond & Harrison 2000). Thus, an additional explanation for the results of this study is that wind patterns associated with the positive phase of the summer PDO influence larval transport and retention in a manner that we did not detect with the wind-based variables we employed.

Our research faced several complications related to our juvenile crab data. First, there is uncertainty in determining age of the crabs, as all hard structures that might be used for age determination are lost during molting. Due to variability in growth, it is also not possible to accurately infer individual ages based on carapace width. We judged that a majority of crab in the 30-50 mm CW size range would be age 3 yr based on size-at-age data for the Kodiak area in the northern Gulf of Alaska (Donaldson et al. 1981), coupled to recognition that colder temperatures are likely to be less favorable for growth in the EBS compared to the Gulf of Alaska. Finally, the survey sampling gear is size-selective for adult and subadult crab; younger, smaller crabs are not fully represented in the catch (Somerton & Otto 1999). Differences between the magnitudes of our juvenile and subsequent adult estimates were however consistent with current estimates of natural mortality (*M* = 0.23), while juvenile crab abundance exhibited trends similar to those experienced by the adult population 2-4 yr. later. Therefore, we feel that our juvenile abundance estimates are reasonable.

We anticipate that the greatest promise for future research into environmental recruitment factors lies in recruitment investigations that consider the spatial scales at which the regulating processes operate. Detailed comparisons of spatial distributions of juvenile Tanner crab, together with those of key limiting ecological factors, may be essential to more completely understand recruitment mechanisms that likely operate on finer-than-regional spatial scales and which likely vary interannually with changing oceanographic conditions. This approach may also resolve discrepancies in predation studies between stomach content analyses and statistical analyses, such as reported here.

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|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Covariate | Lag prior to recruitment | Crab life stage | Relationship | Mechanism |
| Mature female opilio | 3 yr | Zoeae-juvenile | (-) | Interspecific competition |
| Pacific cod - 3 yr rolling average | 1 yr | Megalopae-age 2 yr juvenile | (-) | Predation |
| Flathead sole | 2 yr | 1st year juvenile | (-) | Predation |
| Flathead sole - 2 yr rolling average | 1 yr | 1st and 2nd yr juveniles | (-) | Predation |
| Arctic oscillation - 2, 3-yr rolling averages | 1 yr | Zoeae-age 2 yr juvenile | (+) | Feeding and growth |
| PDO - 2, 3 yr rolling averages | 1 yr | Zoeae-age 2 yr juvenile | (+) | Feeding/growth/thermal tolerances |
| NBT - 3 yr rolling average | 1 yr | Megalopae - age 2 juvenile | (+) | Growth/thermal tolerances |
| SST-May to July average | 3 yr | Zoeae | (+) | Feeding/growth |
| SE wind | 3 yr | Zoeae | (+) | Larval retention |
| NE wind | 3 yr | Zoeae | (-) | Reduced larval retention |

Table 1. Environmental covariates used in analysis, including lag applied to each covariate, the crab life stage affected, hypothesized relationship, and proposed mechanism.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | df | AICc | Delta | Model variables |
| 29 | 7 | 64.61 | 0.00 | Female Bairdi, FHS lag 2, PDO RA2 |
| 34 | 8 | 66.41 | 1.80 | Female Bairdi, FHS lag 2, PDO RA2, AO RA2 |
| 27 | 7 | 67.02 | 2.41 | Female Bairdi, FHS lag 2, PDO RA3 |
| 6 | 6 | 67.08 | 2.46 | Female Bairdi, FHS lag 2 |
| 22 | 8 | 67.59 | 2.98 | Female Bairdi, FHS lag 2, mature female opilio, PDO RA2 |
| 8 | 7 | 67.61 | 3.00 | Female Bairdi, Pacific cod lag 1, FHS lag 2 |
| 19 | 7 | 68.34 | 3.72 | Female Bairdi, FHS lag 2, mature female opilio |
| 33 | 8 | 68.75 | 4.14 | Female Bairdi, FHS lag 2, PDO RA3, AO RA3 |
| 20 | 8 | 68.92 | 4.31 | Female Bairdi, FHS lag 2, mature female opilio, PDO RA3 |
| 32 | 7 | 69.14 | 4.52 | Female Bairdi, FHS lag 2, SE wind |
| 28 | 7 | 69.58 | 4.96 | Female Bairdi, FHS lag 2, AO RA3 |
| 31 | 7 | 69.80 | 5.18 | Female Bairdi, FHS lag 2, May-July SST |
| 21 | 8 | 69.97 | 5.35 | Female Bairdi, FHS lag 2, mature female opilio, AO RA3 |
| 30 | 7 | 70.00 | 5.38 | Female Bairdi, FHS lag 2, AO RA2 |
| 23 | 8 | 70.14 | 5.52 | Female Bairdi, FHS lag 2, mature female opilio, AO RA2 |
| 25 | 8 | 70.59 | 5.97 | Female Bairdi, FHS lag 2, mature female opilio, SE wind |
| 24 | 8 | 71.43 | 6.82 | Female Bairdi, FHS lag 2, mature female opilio, May-July SST |
| 26 | 8 | 71.69 | 7.08 | Female Bairdi, FHS lag 2, mature female opilio, NW wind |
| 2 | 6 | 76.65 | 12.03 | Female Bairdi, mature female opilio |
| 7 | 6 | 76.97 | 12.36 | Female Bairdi, FHS RA2 |
| 15 | 6 | 78.91 | 14.30 | Female Bairdi, PDO\_RA3 |
| 1 | 5 | 79.40 | 14.78 | Female Bairdi |
| 14 | 6 | 80.02 | 15.40 | Female Bairdi, PDO RA2 |
| 9 | 7 | 80.11 | 15.50 | Female Bairdi, Pacific cod RA2, FHS RA2 |
| 11 | 6 | 80.89 | 16.28 | Female Bairdi, NBT 3 yr minimum |
| 4 | 6 | 81.13 | 16.52 | Female Bairdi, Pacific cod RA2 |
| 17 | 6 | 81.27 | 16.66 | Female Bairdi, SE wind |
| 16 | 6 | 81.43 | 16.82 | Female Bairdi, May-July SST |
| 10 | 6 | 81.68 | 17.07 | Female Bairdi, NBT RA3 |
| 5 | 6 | 81.78 | 17.17 | Female Bairdi, Pacific cod RA3 |
| 3 | 6 | 82.09 | 17.47 | Female Bairdi, Pacific cod lag 1 |
| 12 | 6 | 82.22 | 17.61 | Female Bairdi, AO RA2 |
| 13 | 6 | 82.25 | 17.64 | Female Bairdi, AO RA3 |
| 18 | 6 | 82.32 | 17.71 | Female Bairdi, NW wind |

Table 2. Model comparison results for GAMMs invoking linear effects for non stock-recruit terms. AO = Arctic oscillation, PDO = Pacific Decadal Oscillation, FHS = flathead sole, TBM = total biomass, NBT = near bottom temperature, SST = sea surface temperature, RA2 = 2 yr rolling average, RA3 = 3 yr rolling average. *Δ*AICc for each model is determined relative to the baseline model (Model 1).

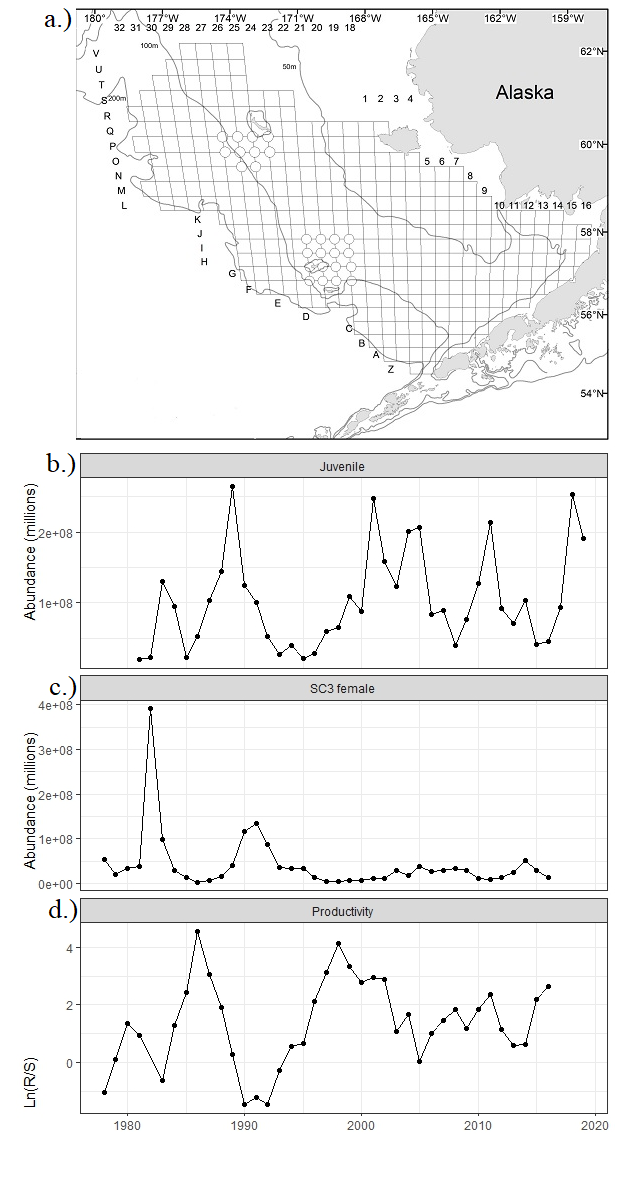


Figure 1. Study system. a.) Map of eastern Bering Sea study region with EBS survey grid; b.) Juvenile abundance time series, c.) Old shell female abundance time series lagged appropriately versus the juvenile series and d.) Productivity time series derived from juvenile and old shell female time series.

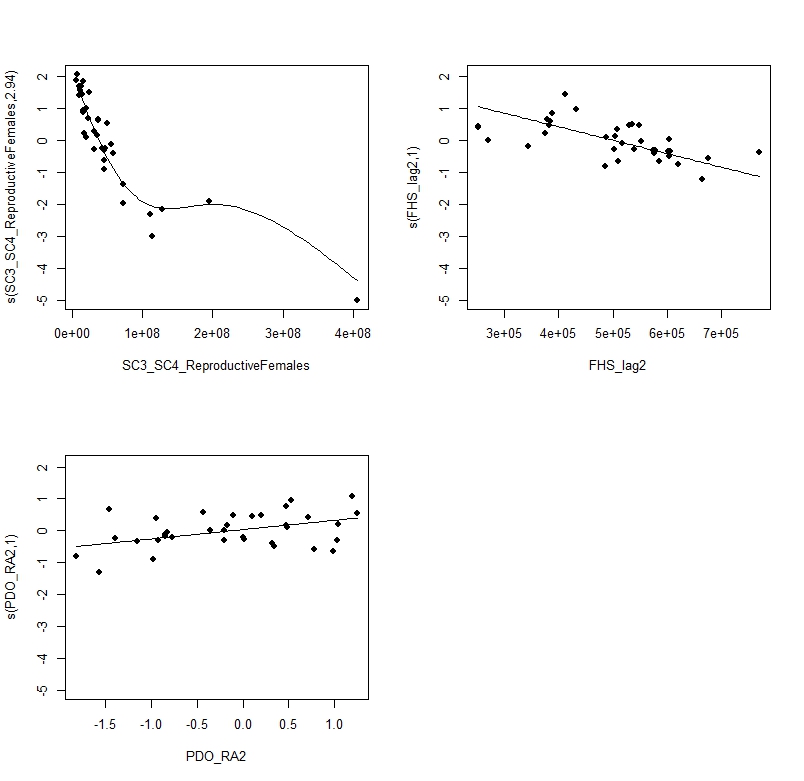


Figure 2. Graphical output for generalized additive model (GAM) combining a.) stock-recruit (S-R) relation with b.) flathead sole (FHS) and 2 yr rolling average (RA2) of the winter Pacific Decadal Oscillation (PDO, c.) as the environmental covariates. Note linear relationships for non S-R variables.