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

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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 long-term environmental 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

**Running head:** Tanner crab recruitment mechanisms

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**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 2020). This variability in stock size and fisheries outcomes underscores the need to better understand the factors regulating productivity in the stock. The need for increased understanding of stock productivity 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). 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 been implicated in the apparent collapse of EBS snow crab (*C. opilio*; 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 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).

Previous studies indicated a weak Ricker-style dome-shaped relationship between parental stock size and subsequent recruitment to the adult population at lags of 7-9 yr, though large year-classes resulted from both small and large breeding stocks (Zheng & Kruse 1998, 2003). Several issues hinder the ability to determine S-R relationships. First, the relatively long time lags between reproduction and recruitment increase the potential for confounding by secondary mechanisms. Second, the lack of age structures leads to uncertainty about the time from hatching to recruitment; absence of direct ageing necessitates inferences from modal analysis of size frequency distributions of a cohort observed repeatedly over time (e.g., Donaldson et al. 1981). Finally, owing to environmental and genetic variability in growth rates, members of multiple cohorts may recruit to the adult population within a given year and members of a given cohort recruit over multiple years (Rosenkranz 1998). The use of a smaller (younger) size class of crabs than used to date as an index of recruitment may be an important step in limiting the effects of such concerns, and identifying potential recruitment controls.

A number of biotic and abiotic environmental factors may influence juvenile crab survival. Snow crab, particularly mature females, co-occur with Tanner crab near the Pribilof Islands, and to a greater degree, to the northwest. Given larval advection patterns (Parada et al. 2010, Richar et al. 2014) and similar ecological niches, it is probable that juveniles of the two species compete where their settling regions overlap. Larval advection is itself largely driven by Ekman transport, due to generally sluggish tidal currents over the EBS shelf, and thus wind patterns may be an important determinant of juvenile survival (Rosenkranz et al. 1998, 2001).Predation by groundfish, in particular Pacific cod *(Gadus macrocephalus)*, and flathead sole *(Hippoglossoides elassodon)* may be a significant source of mortality for juvenile Tanner crabs, as these species consume immature crab in large quantities (Livingston 1989, Pacunski et al. 1998, Lang et al. 2003, 2005). Stomach contents suggest that Pacific cod alone may remove up to 95% of age-1 crab in some years, while also feeding on age 0 and 2 crab at lesser rates (Livingston 1989).

Ocean temperature may also be an important driver of juvenile survival (Paul et al. 1979, Incze 1983, Incze et al. 1982, Incze & Paul 1983, Paul & Paul 2001, Ciannelli & Bailey 2005, Spencer 2008). Surface temperatures may influence zoeal feeding environment, and developmental rate, and thus the period of vulnerability to direct predation while planktonic. Furthermore, environmental temperatures may lead to direct larval mortality when thermal tolerances are exceeded (Paul et al. 1979, Incze 1983, Incze et al. 1982, Incze & Paul 1983). Similarly, near bottom temperature (NBT) may influence post-settlement development rates, modulating vulnerability to predators, while also influencing predator access via thermal barriers, and driving mortality directly via crab thermal tolerances (Paul & Paul 2001, Ciannelli & Bailey 2005, Spencer 2008).

Large scale climatic indices, which may serve as proxies for multiple intertwined environmental variables have proven to be useful in understanding recruitment patterns of certain species (Menge et al. 2011, Tzeng et al. 2012, Harford et al. 2017, Litzow et al. 2018, Szuwalski et al. 2021). Two important indices in the EBS region are the Arctic Oscillation (AO), and the Pacific Decadal Oscillation (PDO). The AO, defined as the leading mode of Northern Hemisphere sea level pressure poleward of 20° N, indexes the north-south range of the jet stream, and may be used as an indicator of mid- and high-latitude temperatures, and storm activity (Thompson & Wallace 1998). The Pacific Decadal Oscillation, defined as the leading mode of North Pacific sea surface temperature (SST) anomalies and may also serve as an indicator for water temperatures, and again storm activity and related wind patterns and strength (Newman et al. 2016). Given the parameters these indices capture, either, or both may influence Tanner crab recruitment through regulation of sea surface and near-bottom temperatures, sea ice melt timing and water column stability and thus feeding environment, and larval advection patterns (Paul et al. 1979, Incze 1983, Incze et al. 1982, Incze & Paul 1983, Rosenkranz et al. 1998, Paul & Paul 2001, Rosenkranz et al. 2001, Ciannelli & Bailey 2005, Spencer 2008). Significantly, a recent study using assessment model recruitment estimates has linked the AO to recruitment variability in both snow crab and Bristol Bay red king crab, although not Tanner crab (Szuwalski et al. 2021).

In this study we examined the factors regulating juvenile Tanner crab abundance as measured by a bottom trawl survey over the period of 1978-2019. Specifically, we evaluated the effects of spawning stock size, competition (as indexed by female opilio abundance), predation (as indexed by the abundance of two groundfish predators, Pacific cod and flathead sole and a suite of physical variables (wind patterns, the PDO, AO, NBT, SST).

**Methods**

Tanner Crab Abundance Estimates

Tanner crabdata from an annual bottom trawl survey of the EBS continental shelf (Fig. 1a) conducted by the National Marine Fisheries Service (NMFS) over 1978-2019 were provided by the NMFS Alaska Fisheries Science Center (AFSC). During the first decade, 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 annually 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 an eastern otter trawl using an 83 ft (25.m) head rope and a 112 ft (34.1 m) footrope (Rugolo & Turnock 2011, 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 yr 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).

Mature female Tanner crabs were defined as females of shell condition 3 (SC3, 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 likely to be primiparous crabs. These have 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. Exploratory models showed that S-R results were not appreciably different whenshell condition 4 (SC4) females were excluded, consequently this class was excluded from analysis, as they may have lower fecundity. 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) for size/SC class *k* in year *i* for strata *s* () was calculated as:

, (eq. 1)

where = the estimated sampling factor for crabs in size/SC class *k* at station *j*, used to account for subsampling based on sex, size and SC in the case of large hauls, = the estimated area swept at station *j* in year *i*, in terms of km2 and *nsi*= the number of stations sampled in strata

Annual area swept abundance estimates for a given class *k* in year *i* () were then calculated as:

(eq. 2)

where is the area swept abundance estimate for class k year *i*, is the mean station CPUE for strata *s* in year *i*, and is the area of strata *s* in year *i*.

Juvenile Tanner crab recruitment was 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 (Figure 1b). An extreme abundance estimate for females was observed in 1983 (Figure 1b). Given that this estimate far exceeded all other estimates, and was not reflected in the estimates for following years, it was concluded that it likely resulted from a sampling design issue. Consequently, this and the matching juvenile estimate were removed prior to conducting further analyses.

Environmental covariates

Data for hypothesized environmental covariates (Table 1) were obtained from multiple sources. As with the Tanner indices, data for ovigerous female snowcrab were obtained from the AFSC survey database, and estimates were calculated using eqs (1, 2). Near bottom temperature (NBT) measurements were also obtained from the survey database, and annual averages were calculated across all hauls. 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 *y*, *y*-1 and *y*-2, the rolling average estimate was credited to year *y*.

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, northeastern 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/>, and averaged by year.

For groundfish, population estimates were taken from recent stock assessment model results for Pacific cod (Thompson and Thorson, 2019), and flathead sole (McGilliard et al. 2019). For Pacific cod, we used abundance estimates for ages 3-7 only, because cod of size 30-59 cm, generally corresponding to these ages, feed more heavily on juvenile Tanner crab than those ≥ 60 cm (Livingston 1989). Three-year rolling averages were then calculated as per procedures used for previous covariates. For flathead sole, we considered the minimum age likely capable of feeding on juvenile Tanner crab based on mean fish length-at-age (McGilliard et al. 2019), estimated maximum gape size based on visual comparison of mouth and body sizes, and mean crab size-at-age (Rugolo & Turnock 2011). Based on these considerations, we used estimated total biomass for age 3+ flathead sole (FHS TBM) to represent the age groups capable of consuming juvenile Tanner crab. To assess potential for multicollinearity/confounding, correlation analyses were run between all covariates employed (Table 2).

Analysis

For analysis, the recruitment time series was recast as log recruitment-per-spawner (ln(R/S)), as is traditionally done in linearized Ricker stock-recruit models. To further explore autocorrelation in the data, and inform model design, the sample autocorrelation function (ACF) was calculated for each ln(R/S) series. Significant positive autocorrelations were indicated at lag 1 yr; therefore, a first‑order auto-regressive process was employed in generalized additive mixed effect (GAMM) modeling of the stock-recruit (S-R) relationship, using the *R* package *mgcv*, and with the structure:

ε*t* = φ ε*t*-1 + ν*t* , (eq. 3)

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*} = .

The stock-recruit relationship was modeled using the log-transformed, linearized Ricker model:

, (eq. 4)

Where R is estimated recruitment, S is the corresponding properly lagged spawner estimate, α and β are model estimated parameters and *εt* is as previously described. The resulting estimated value, ln(R/S) is referred to as log recruits per spawner. To assess significance while allowing autocorrelation, and to test robustness of the S-R relationship across multiple lags, exploratory S-R models using this structure were run using GLS procedures at lags of 2, 3 and 4 yrs between the female abundance index, and the juvenile recruitment index.

Analyses were conducted using Generalized Additive Mixed-Effect Modeling (GAMM) procedures native to the *R* package *mgcv* to model the S-R relationship in the presence of one or more environmental covariates while allowing for autocorrelation:

(eq. 5)

Where α is the intercept/productivity term, ƒ is a smooth function with a user-specified number of effective degrees of freedom (*k* = 4), *R* and *S* are as before, the *Xi* are environmental covariates and εt is the autocorrelated error term as per eq. 3.

Results for exploratory lag-2 yr and lag 4-yr stock-recruit models were similar to those for the primary lag-3 yr models, although the lag-3 model enjoyed the best AICc value, supporting our use of lag-3 yr for further analysis (Table 5). For followup analyses, a baseline model with only a stock-recruit effect was specified, then iterated on via forward model selection, whereby variable are progressively added with each iteration. Environmental covariates were lagged relative to recruitment to the juvenile index based on their hypothesized mechanism (Table 1). Where multiple covariates were included in one model, care was taken to reduce multicollinearity, although moderate levels were tolerated for exploratory purposes (Table 2). 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**

A density-dependent S-R relationship is suggested by a curvilinear log recruits per spawner relationship (Figure 4). This is reinforced by a statistically significant Ricker-style stock-recruit relationship observed in the corresponding GAMM model (Table 3), although autocorrelation was also notable (Table 3).

Fitting of GAMMs combining an S-R effect and one or more environmental covariates demonstrated the continuing importance of the S-R effect in all models investigated (Figure 5, Tables 4). Examination of graphical output suggested most environmental factors could be incorporated with a linear response, rather than non-linear (e.g. Figure 3); consequently models were re-fit using linear terms, resulting in a larger selection of models providing improved AICc values relative to the baseline S-R model, and the “best” model providing a much greater difference in its AICc score (*Δ*AICc = -11.55, Table 5).

Based on AICc values, the best model incorporated the S-R effect, FHS TBM, and 2-yr rolling averages of the AO and the winter PDO, although autocorrelation remains significant (Figure 3, Table 5). Of the covariates investigated, FHS TBM provided the single greatest improvement in model AICc scores (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. Further, while inclusion of the PDO and AO covariates 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). These covariates performed markedly worse when considered as the only covariate, and when considered singly in concert with FHS TBM (Table 5).

**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 AO, and 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 relationships between the AO and PDO. An alternative, for at least the summer PDO, is that as it 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.

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 |
| Ovigerous 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 |
| NBT - 3 yr rolling average | 1 yr | Megalopae - age 2 juvenile | (+) | Growth/thermal tolerances |
| SST-May to July average | 3 yr | Zoeae | (+) | Feeding/growth |
| PDO – 2, 3 yr rolling averages | 1 yr | Zoeae-age 2juvenile | (+) | Feeding/growth/thermal tolerances |
| SE wind | 3 yr | Zoeae | (+) | Larval retention |
| NE wind | 3 yr | Zoeae | (-) | Reduced larval retention |

Table 1. Environmental covariates used in GAM modeling, lag applied to value, crab life stage affected, hypothesized relationship, and proposed mechanism. For rolling averages, note that average is applied to final year of set used to calculate a given value.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Bairdi females | Pacific cod | FHS TBM RA2 | FHS TBM | Opilio females | PDO RA3 | PDO RA2 | SST MJ | AO RA3 | AO RA2 | NBT RA3 | SE wind | NE wind |
| Bairdi females | 1.00 | -0.06 | 0.02 | 0.02 | 0.35 | -0.18 | -0.09 | 0.01 | 0.56 | 0.34 | -0.07 | 0.01 | -0.37 |
| Pacific cod | -0.06 | 1.00 | -0.45 | -0.45 | -0.07 | -0.28 | -0.10 | -0.54 | -0.27 | -0.28 | -0.17 | -0.07 | 0.00 |
| FHS TBM RA2 | 0.02 | -0.45 | 1.00 | 0.90 | 0.36 | -0.18 | -0.16 | 0.34 | 0.37 | 0.31 | -0.02 | 0.09 | 0.06 |
| FHS TBM | 0.02 | -0.45 | 0.90 | 1.00 | 0.35 | -0.14 | -0.08 | 0.38 | 0.34 | 0.21 | 0.11 | 0.02 | 0.04 |
| Opilio females | 0.35 | -0.07 | 0.36 | 0.35 | 1.00 | -0.30 | -0.33 | -0.15 | 0.51 | 0.52 | -0.09 | -0.13 | -0.17 |
| PDO RA3 | -0.18 | -0.28 | -0.18 | -0.14 | -0.30 | 1.00 | 0.90 | 0.38 | -0.22 | -0.13 | 0.43 | -0.17 | -0.02 |
| PDO RA2 | -0.09 | -0.10 | -0.16 | -0.08 | -0.33 | 0.90 | 1.00 | 0.43 | -0.23 | -0.20 | 0.54 | -0.12 | -0.02 |
| SST MJ | 0.01 | -0.54 | 0.34 | 0.38 | -0.15 | 0.38 | 0.43 | 1.00 | 0.09 | -0.04 | 0.50 | -0.07 | -0.23 |
| AO RA3 | 0.56 | -0.27 | 0.37 | 0.34 | 0.51 | -0.22 | -0.23 | 0.09 | 1.00 | 0.83 | 0.08 | 0.03 | -0.01 |
| AO RA2 | 0.34 | -0.28 | 0.31 | 0.21 | 0.52 | -0.13 | -0.20 | -0.04 | 0.83 | 1.00 | 0.05 | -0.01 | 0.03 |
| NBT RA3 | -0.07 | -0.17 | -0.02 | 0.11 | -0.09 | 0.43 | 0.54 | 0.50 | 0.08 | 0.05 | 1.00 | 0.04 | 0.20 |
| SE wind | 0.01 | -0.07 | 0.09 | 0.02 | -0.13 | -0.17 | -0.12 | -0.07 | 0.03 | -0.01 | 0.04 | 1.00 | 0.35 |
| NE wind | -0.37 | 0.00 | 0.06 | 0.04 | -0.17 | -0.02 | -0.02 | -0.23 | -0.01 | 0.03 | 0.20 | 0.35 | 1.00 |

Table 2. Correlations among investigated biophysical variables for full time series.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Lag 2 | Lag 3 | Lag 4 |
| Intercept | 1.8 (3.13e-09) | 1.36 (3.7e-10) | 1.37(1.39e-09) |
| S (edf) | 3.448(<2e-16) | 3.53 (<2e-16) | 3.092 (<2e-16) |
| phi | 0.38 | 0.4 | 0.36 |
| AICc | 90.73 | 86.42 | 91.57 |

Table 3. Generalized additive mixed effect model (GAMM) stock-recruit model output. Parameter estimates and associated p-values for linearized Ricker stock-recruit models by lag. Phi values denote strength of autocorrelation, which is then accounted for in GAMM procedures.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | AICc | *Δ*AICc | Phi | Model variables |
| 6 | 66.71 | -5.90 | 0.49 | Female Bairdi, FHS lag 2 |
| 29 | 68.86 | -3.74 | 0.52 | Female Bairdi, FHS lag 2, PDO RA2 |
| 27 | 71.12 | -1.48 | 0.44 | Female Bairdi, FHS lag 2, PDO RA3 |
| 19 | 72.54 | -0.06 | 0.42 | Female Bairdi, FHS lag 2, ovigerous female opilio |
| 1 | 72.60 | 0.00 | 0.41 | Female Bairdi |
| 30 | 72.70 | 0.10 | 0.49 | Female Bairdi, FHS lag 2, AO RA2 |
| 28 | 72.81 | 0.21 | 0.47 | Female Bairdi, FHS lag 2, AO RA3 |
| 34 | 73.29 | 0.69 | 0.55 | Female Bairdi, FHS lag 2, PDO RA2, AO RA2 |
| 8 | 73.49 | 0.89 | 0.47 | Female Bairdi, Pacific cod lag 1, FHS lag 2 |
| 31 | 73.69 | 1.08 | 0.48 | Female Bairdi, FHS lag 2, May-July SST |
| 2 | 74.06 | 1.45 | 0.26 | Female Bairdi, ovigerous female opilio |
| 7 | 74.69 | 2.09 | 0.35 | Female Bairdi, FHS RA2 |
| 32 | 74.73 | 2.13 | 0.52 | Female Bairdi, FHS lag 2, SE wind |
| 15 | 75.57 | 2.97 | 0.33 | Female Bairdi, PDO RA3 |
| 14 | 76.00 | 3.40 | 0.32 | Female Bairdi, PDO RA2 |
| 5 | 76.21 | 3.60 | 0.44 | Female Bairdi, Pacific cod RA3 |
| 11 | 76.66 | 4.06 | 0.39 | Female Bairdi, NBT 3 yr minimum |
| 22 | 77.02 | 4.42 | 0.53 | Female Bairdi, FHS lag 2, ovigerous female opilio, PDO RA2 |
| 23 | 77.43 | 4.83 | 0.29 | Female Bairdi, FHS lag 2, ovigerous female opilio, AO RA2 |
| 33 | 77.62 | 5.01 | 0.42 | Female Bairdi, FHS lag 2, PDO RA3, AO RA3 |
| 4 | 77.78 | 5.18 | 0.44 | Female Bairdi, Pacific cod RA2 |
| 10 | 77.92 | 5.31 | 0.37 | Female Bairdi, NBT RA3 |
| 16 | 77.93 | 5.33 | 0.45 | Female Bairdi, May-July SST |
| 12 | 78.18 | 5.57 | 0.45 | Female Bairdi, AO RA2 |
| 17 | 78.42 | 5.82 | 0.40 | Female Bairdi, SE wind |
| 21 | 78.64 | 6.03 | 0.29 | Female Bairdi, FHS lag 2, ovigerous female opilio, AO RA3 |
| 18 | 78.67 | 6.07 | 0.40 | Female Bairdi, NE wind |
| 3 | 78.76 | 6.16 | 0.41 | Female Bairdi, Pacific cod lag 1 |
| 13 | 78.76 | 6.16 | 0.41 | Female Bairdi, AO RA3 |
| 20 | 80.02 | 7.41 | 0.30 | Female Bairdi, FHS lag 2, ovigerous female opilio, PDO RA3 |
| 26 | 80.74 | 8.14 | 0.40 | Female Bairdi, FHS lag 2, ovigerous female opilio, NE wind |
| 24 | 80.91 | 8.31 | 0.41 | Female Bairdi, FHS lag 2, ovigerous female opilio, May-July SST |
| 9 | 81.87 | 9.27 | 0.36 | Female Bairdi, Pacific cod RA2, FHS RA2 |
| 25 | 81.97 | 9.37 | 0.45 | Female Bairdi, FHS lag 2, ovigerous female opilio, SE wind |

Table 4. Model output for full time series GAMM models. 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. Delta AICc for each model is determined relative to the baseline model (Model 1).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | AICc | *Δ*AICc | Phi | Model variables |
| 34 | 61.05 | -11.55 | 0.55 | Female Bairdi, FHS lag 2, PDO RA2, AO RA2 |
| 29 | 61.67 | -10.94 | 0.52 | Female Bairdi, FHS lag 2, PDO RA2 |
| 6 | 63.51 | -9.09 | 0.49 | Female Bairdi, FHS lag 2 |
| 27 | 63.93 | -8.67 | 0.44 | Female Bairdi, FHS lag 2, PDO RA3 |
| 22 | 64.87 | -7.73 | 0.47 | Female Bairdi, FHS lag 2, ovigerous female opilio, PDO RA2 |
| 23 | 65.19 | -7.41 | 0.29 | Female Bairdi, FHS lag 2, ovigerous female opilio, AO RA2 |
| 19 | 65.35 | -7.26 | 0.42 | Female Bairdi, FHS lag 2, ovigerous female opilio |
| 33 | 65.38 | -7.23 | 0.42 | Female Bairdi, FHS lag 2, PDO RA3, AO RA3 |
| 30 | 65.51 | -7.09 | 0.49 | Female Bairdi, FHS lag 2, AO RA2 |
| 28 | 65.62 | -6.98 | 0.47 | Female Bairdi, FHS lag 2, AO RA3 |
| 8 | 66.30 | -6.30 | 0.47 | Female Bairdi, Pacific cod lag 1, FHS lag 2 |
| 20 | 66.32 | -6.28 | 0.37 | Female Bairdi, FHS lag 2, ovigerous female opilio, PDO RA3 |
| 21 | 66.40 | -6.21 | 0.29 | Female Bairdi, FHS lag 2, ovigerous female opilio, AO RA3 |
| 31 | 66.49 | -6.11 | 0.48 | Female Bairdi, FHS lag 2, May-July SST |
| 32 | 66.63 | -5.97 | 0.48 | Female Bairdi, FHS lag 2, SE wind |
| 26 | 68.50 | -4.10 | 0.40 | Female Bairdi, FHS lag 2, ovigerous female opilio, NE wind |
| 24 | 68.67 | -3.93 | 0.41 | Female Bairdi, FHS lag 2, ovigerous female opilio, May-July SST |
| 25 | 68.73 | -3.88 | 0.41 | Female Bairdi, FHS lag 2, ovigerous female opilio, SE wind |
| 2 | 70.91 | -1.70 | 0.24 | Female Bairdi, ovigerous female opilio |
| 7 | 71.49 | -1.11 | 0.35 | Female Bairdi, FHS RA2 |
| 15 | 72.37 | -0.23 | 0.33 | Female Bairdi, PDO\_RA3 |
| 1 | 72.60 | 0.00 | 0.41 | Female Bairdi |
| 14 | 72.81 | 0.20 | 0.32 | Female Bairdi, PDO RA2 |
| 11 | 73.46 | 0.86 | 0.39 | Female Bairdi, NBT 3 yr minimum |
| 4 | 74.59 | 1.99 | 0.44 | Female Bairdi, Pacific cod RA2 |
| 9 | 74.68 | 2.07 | 0.36 | Female Bairdi, Pacific cod RA2, FHS RA2 |
| 10 | 74.72 | 2.12 | 0.37 | Female Bairdi, NBT RA3 |
| 16 | 74.73 | 2.13 | 0.45 | Female Bairdi, May-July SST |
| 12 | 74.98 | 2.38 | 0.45 | Female Bairdi, AO RA2 |
| 17 | 75.23 | 2.63 | 0.40 | Female Bairdi, SE wind |
| 5 | 75.27 | 2.67 | 0.43 | Female Bairdi, Pacific cod RA3 |
| 18 | 75.47 | 2.87 | 0.40 | Female Bairdi, NE wind |
| 3 | 75.56 | 2.96 | 0.41 | Female Bairdi, Pacific cod lag 1 |
| 13 | 75.57 | 2.96 | 0.41 | Female Bairdi, AO RA3 |

Table 5. Model output for full time series GAMM models with 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).

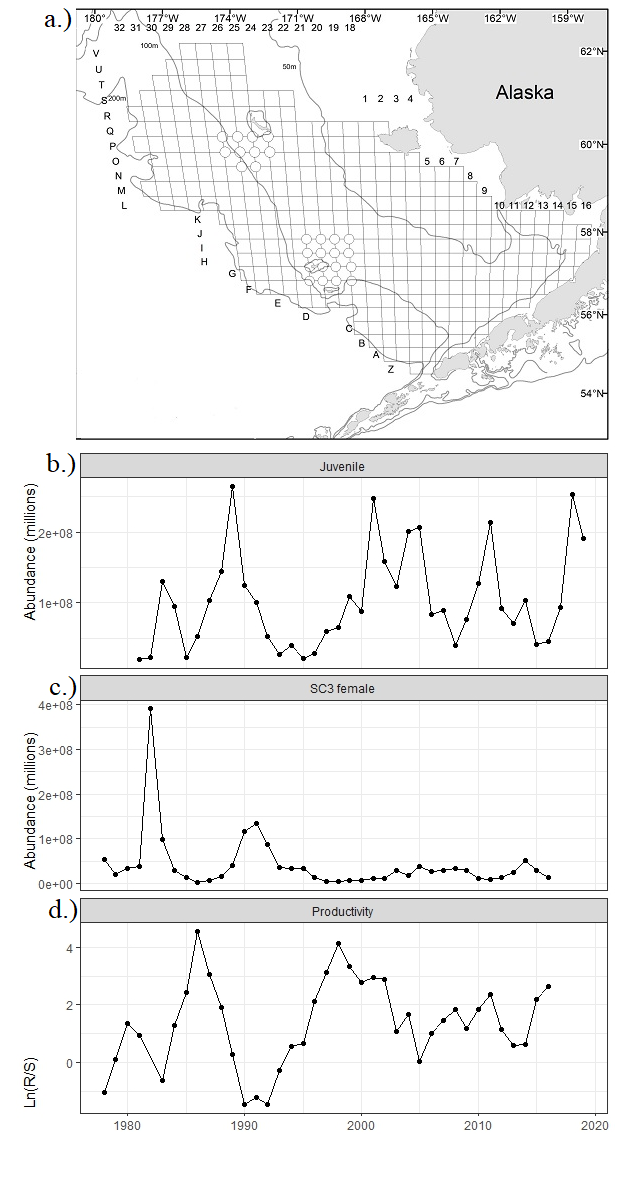


Figure 1. Study system. a.) Map of eastern Bering Sea study region with EBS survey grid; b.) Juvenile abundance time series, c.) Old shell female abundance time series lagged appropriately versus the juvenile series and d.) Productivity time series derived from juvenile and old shell female time series.

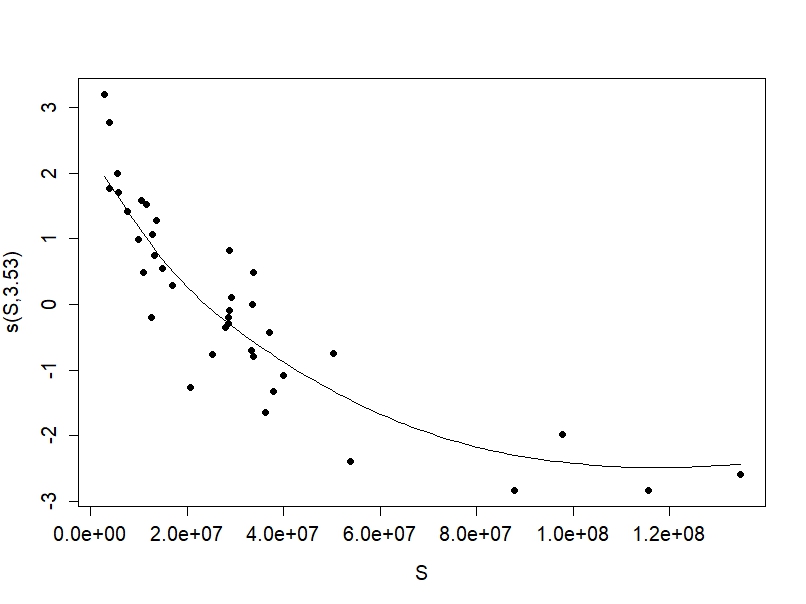


Figure 2. Lag-3 yr stock-recruit results for GAMM stock-recruit effect-only model.

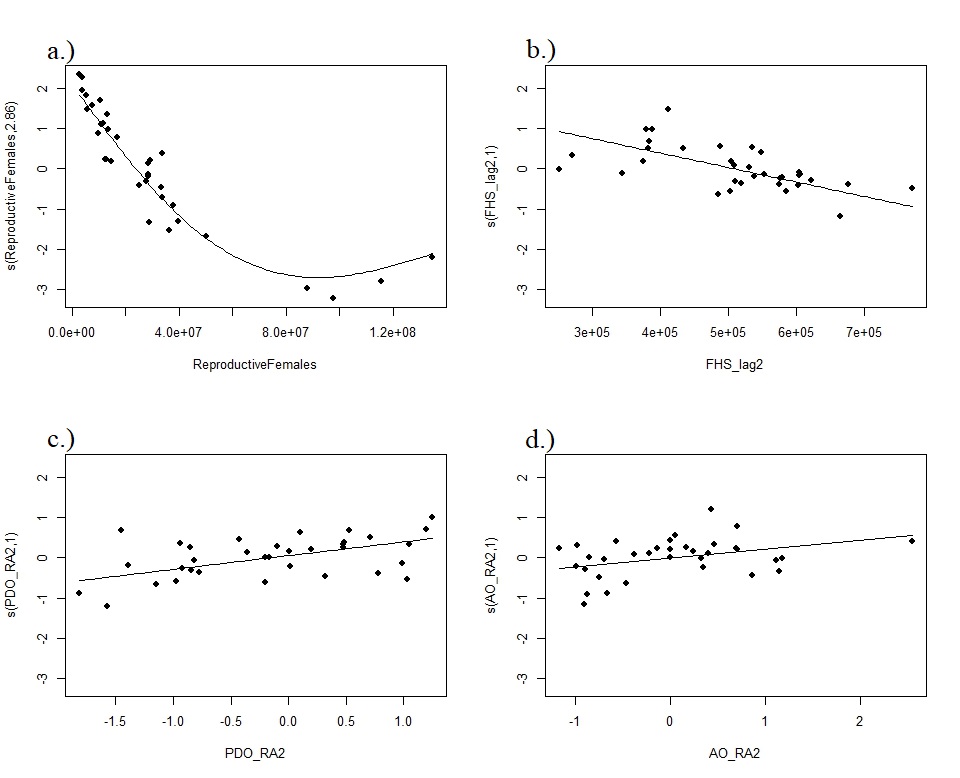


Figure 3. Graphical output for generalized additive model (GAM) combining a.) stock-recruit (S-R) relation with b.) flathead sole (FHS) and 2 yr rolling average (RA2) of the winter Pacific Decadal Oscillation (PDO, c.) and the Arctic Oscillation (AO, d.) as the environmental covariates. Note linear relationships for non S-R variables.