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**Variability in somatic growth over time and space determines optimal season-opening date in the Oregon ocean shrimp (*Pandalus jordani*) fishery**

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Highlights

3-5 bullet points, 85 characters, including spaces, per bullet point

* We developed a spatially, temporally and environmentally explicit size-at-age model
* Size-at-recruitment varied across time and space in the Oregon ocean shrimp fishery
* Optimal season opening dates depended on location, year, and fishing mortality rate
* No environmental drivers of size-at-recruitment were identified

Abstract

Will provide in next draft

Keywords

Somatic growth, revenue per recruit, shrimp, crustacean, environmental drivers

**1. Introduction**

In fisheries, there is an important trade-off between catching older, larger individuals with higher yield and catching younger, smaller individuals when catch rates are higher due to less cumulative exposure to natural mortality. This trade-off can be magnified if larger individuals also fetch higher prices. Failing to allow individuals to grow large enough to maximize yield is known as “growth overfishing” (Hilborn and Walters, 1992). In populations with weak stock-recruit relationships, as are common in large marine ecosystems, recruitment overfishing can only occur at extremely low spawning biomasses (Szuwalski et al., 2015; Sellinger et al., 2024). Growth overfishing is therefore a key consideration for management especially for opportunistic species with high natural mortality, fast growth, and variable recruitment, although ecosystem responses to low biomass likely occur well before recruitment overfishing (King and McFarlane, 2003; Caillouet et al., 2008; Cury et al., 2011).

Somatic growth in marine populations is highly variable, but often difficult to characterize. Variability in somatic growth has major implications for population dynamics and productivity, sometimes comparable to variability in early life history survival (Stawitz et al., 2015; Stawitz and Essington, 2019). This variability, in turn, influences optimal fishery management policies in important ways (Lorenzen, 2016). However, identifying environmental and density-dependent drivers of growth, as with many population processes, has proven difficult largely due to lack of data and the complexity of the marine environment (Stawitz et al., 2015). Growth frequently varies over both space and time, though because of the rich data and high model complexity needed to estimate spatial variation, methods to estimate how and where growth varies over space have been even slower to develop than strictly temporal methods (Kapur et al., 2020; Grüss et al., 2021; Indivero et al., 2023). In addition, most studies on growth variability in marine populations have focused on finfish due to their hard structures that can be reliably aged. In contrast, relatively few studies have quantified somatic growth variability in wild crustacean populations or attempted to identify drivers of that variability because of the difficulty in ageing. Lab studies have identified common factors such as temperature and food supply, as well as potentially important drivers in the future such as ocean pH (see Chang et al., 2012 for review). The more limited *in situ* research indicates that, as with finfish, somatic growth variability can be notable and have consequences for fishery production and management (Brylawski and Miller, 2006; McMahan et al., 2016).

Seasonal forecasting that provides actionable decision support can reduce uncertainty and manage business risks in wild capture fisheries and aquaculture (Hobday et al., 2016). However, reliable indicators that tie forecasts to population dynamics must be identified to take advantage of these gains. Unfortunately, several barriers exist in using operational forecasting in ecology and resource management. These can be categorized by data limitation, probabilistic limitations, model limitations, and social limitations (Dietze et al., 2018). The ability to move past these challenges and provide and assess the skill of seasonal-scale forecasts is key to adaptive management in the age of climate change (Walters and Hilborn, 1978; Brodie et al., 2023).

Ocean shrimp (sometimes referred to as “pink shrimp”, *Pandalus jordani*) are a relatively short-lived species (~3 years) and the target of the fifth-highest revenue fishery in the California Current (Free et al., 2023). The short lifespan leads to inherently variable population dynamics and productivity, and environmental drivers in the highly dynamic upwelling system magnify the intrinsic population fluctuations (Rouyer et al., 2012). For example, previous work has illustrated ties between ocean shrimp distribution and recruitment with the timing and magnitude of upwelling in the region (Hannah, 2011). As the California Current ecosystem experiences general warming and more frequent marine heat waves (Barkhordarian et al., 2022), it is increasingly valuable to improve pre-season forecasts for the ocean shrimp stock.

For at least two decades, managers and participants in the ocean shrimp fishery in Oregon, where the fishery is centered, have been faced with a challenge to maximize revenue and yield each year and avoid growth overfishing given a highly dynamic population. Gallagher et al. (2004) found that to maximize revenue per recruit, season openings should be delayed under high fishing mortality rates, but not under low fishing mortality rates, even though the current early opening date maximized yield-per-recruit across all fishing mortality rates. Since 2004, the Oregon Department of Fish and Wildlife (ODFW), the agency responsible for providing scientific support for management decision making, has pursued several lines of research to better understand shrimp population dynamics as part of becoming the first Marine Stewardship Council (MSC) certified shrimp fishery, in 2007[[1]](#footnote-1). Managers conduct a Virtual Population Analysis (VPA) annually, allowing estimation of recruitment following a cohort’s third year being available to the fishery (Hilborn and Walters, 1992; Hannah and Jones, 2014a). In addition, several reports (e.g., Hannah, 2011; Hannah and Jones, 2014b, 2016; Groth and Hannah, 2018; Groth, 2022) have summarized the variability in growth, recruitment, and their relationship to density-dependent and density-independent (i.e., environmental) factors. Despite the new research, the question of when the fishery should open each year still remains a key question for managers, and the industry often elects to delay the start of the April – October fishing season for several weeks in years when age-one shrimp are expected to be small. Finally, because ocean shrimp are short-lived and fast-growing, length-frequency analysis is a reasonable approach to understand variability and drivers of somatic growth, unlike many other crustacean species (Chang et al., 2012).

In this study we 1) use multivariate autoregressive state space models to, for the first time, mechanistically quantify variation in shrimp size-at-age across time and space in the Oregon ocean shrimp fishery, 2) test whether environmental or density-dependent factors can improve predictions of shrimp length-at age, and 3) apply the growth model in a revenue-per-recruit analysis to explore how variation in shrimp growth across time and space impacts optimal management decisions on when to open the shrimp fishery. The novel framework propagates a spatiotemporally explicit model for size-at-age into a revenue-per-recruit model, providing information intended to help managers identify default dates on which to open the fishery across its spatial range, as well as to identify factors that may help adaptively manage the opening date as growth, abundance, and fishing effort vary across years.

**2 Materials and methods**

*2.1 Oregon ocean shrimp*

Ocean shrimp is a state-managed semi-pelagic trawl fishery that occurs across the three West Coast states (Washington, Oregon, California). While fishing vessels originate from each of the West Coast states, the fishery is centered around Oregon, with 67% of 9,140 mt US West Coast landings from 2003 to 2022 going into Oregon ports (Pacific States Marine Fisheries Commission, 2023). Fishery management methodology is coordinated to be consistent among the states emphasizing 1) reducing the chances of overfishing (i.e., size limit, season, number of vessels, HCRs based on population models) and 2) reducing bycatch (i.e., exclusion grates and LED fishing lights). Specific to limiting growth overfishing, the size limit employed (maximum count per pound of 160 shrimp) is intended to dissuade catch of small, quickly growing age-one shrimp. Specific to limiting recruitment overfishing, managers periodically compare the derived relative cohort strength from VPA to likely regressors to determine primary drivers of recruitment. These measures are implemented because fishery independent surveys are impractical to perform given the short lives and patchy spatial distribution of ocean shrimp. While the fishery legally operates from April 1 to October 31, fishing is often delayed if individuals are expected to be small, and there are continuing conversations about whether to make this delay a permanent feature (S. Groth, pers. comm.).

Ocean shrimp mate in fall. Females carry externally fertilized eggs from around October to March, and release larvae in March and April after which the fishery opens (Butler, 1980). Larvae inhabit the water column during the spring and summer, and then settle to the seafloor where they begin occasionally showing up in trawl catches as age-0s in September and October. Fishery recruitment is generally measured as the cohort strength of age-1 shrimp the following spring, one year after they were released as larvae. The first reproductive season is the winter between their first and second years (Butler, 1980). Ocean shrimp are also protandrous hermaphrodites with sexually dimorphic growth (females are larger), and year class-strength impacts the observed sex ratios (Charnov and Hannah, 2002; Charnov and Groth, 2019). Natural mortality must be relatively high to support their short lifespans, but the rate is highly uncertain. In addition, natural mortality may be higher during the summer months due to increased predation from migratory Pacific hake (*Merluccius productus*), which have highest spatial overlap with shrimp during the summer (Hannah, 1995).

ODFW biologists perform sampling and processing to understand population cohort ratios, sex ratios, growth, etc. As available, samples from fishery landings are obtained monthly from April to October in each of 12 distinct areas along the U.S. West Coast (Fig. 1). Staff measure the carapace length (posterior dorsal point of the carapace to the posterior point of the orbit) of 400-600 individual shrimp each sampled month from each area. Ageing is developed by visualizing data stratified to month and area, identifying nadirs (i.e., low points between cohorts indicating an age break), then assigning ages 1, 2, or 3 depending on individual size of shrimp (Zirges et al., 1981). Because the three age classes are clearly defined in the length-frequency plots, this is considered a sufficiently reliable method (Chang et al., 2012)

*2.2 Drivers of population dynamics*

Shrimp productivity has previously been found to be correlated with sea level height and the Bakun upwelling index (Hannah, 2011; Rothlisberg and Miller, 1983). The strength and timing of upwelling of cold deep nutrient-rich waters impacts the temperature shrimp experience, ocean transport during the larval stage to adult habitat, and quantity and quality of food resources. For this analysis, we used the coastal upwelling transport index (CUTI) and biologically effective upwelling transport index (BEUTI) calculated monthly and averaged across 42, 45, and 47°N, the approximate latitudinal range of the data, and from March through June, the key spring upwelling period (Jacox et al., 2018). These upwelling indices are improved measures of upwelling strength relative to the Bakun index and are more relevant for marine organisms (Jacox et al., 2018). Growth of young ocean shrimp growth has also been found to be directly influenced by temperature (Rothlisberg, 1979). We took monthly sea surface temperature (SST) data smoothed into two-degree bins (Huang et al., 2017) and averaged it from 40-48°N, 124-126°W, and March-August, which covers the pelagic larval period and the general spatial extent of the population. Bottom layer temperature would be an appropriate temperature metric for settled juveniles during the fall and winter months, but no continuous bottom layer temperature time series exists for the California Current that covers the full temporal extent of the length data. Finally, we also included log-recruitment as a density-dependent variable because shrimp from large year classes may grow more slowly due to competition with conspecifics (Groth and Hannah, 2018).

*2.3 Growth model*

Variability in size-at-age over time and space was estimated using a multivariate autoregressive state-space model (e.g., De Valpine, 2003; Stawitz et al., 2015; Table 1). Let *La,c,r* be length in millimeters of age *a* (in months) shrimp from the cohort *c* in state area (region) *r*. Then:

(1a)

(1b)

(1c)

where *c* denotes annual cohort, *r* denotes region, *µL1* is the average length of age 1 shrimp in April, *α0* and *α1* describe the average monthly growth increment, *αs* is the magnitude of the seasonality component, and*ma* is the month of the year for shrimp of age *a* months (growth increases into early summer, declines into the winter and increases to the next spring). To align *m* with the seasonal cycle of growth, *m* = 1 corresponds with March. The seasonality component was included due to a cyclical pattern initially observed in the process errors and because crustaceans commonly experience temperature-driven seasonal growth variation (Chang et al., 2012). is the observed average length of a shrimp of age *a* (in months) from cohort *c* caught in region *r* as measured by port samplers*.* We furthermore assume that process errors (*ε*), observation errors (*δ*), and spatial variation (*γ*) are all normally distributed with mean zero and standard deviations *σL1* (*ε1*, variability of size-at-recruitment in April), *σp* (*εa*, *a* ≠ 1, variability of process errors after recruitment), *σo* (*δ,* variability of observation error), and *σr* (*γ*, regional variability in size-at-recruitment). Note that this model is akin to a discretized version of the differential equation for the Von Bertalanffy growth model:

(2)

where *α0* is analogous to *kL*∞ and *α*1 is analogous to 1-*k*.

We fit equation 1 in a Bayesian framework via Markov chain Monte Carlo (MCMC) conducted by Stan (Stan Development Team, 2022) and implemented with the Rstan package (Stan Development Team, 2020) in R (R Core Team, 2021). We subtracted the mean observed length from the data before fitting to improve numerical stability. We ran four chains for 4,000 iterations each, retaining the final 2,000 draws. Convergence was determined based on R-hat, using the accepted threshold of 1.05, and by ensuring effective sample sizes of at least 100 (Vehtari et al., 2021).

The fit to equations 1a-1c indicated high variability in size-at-recruitment across space and time (i.e., high estimates of *σL1* and *σr* relative to the other variance estimates). Thus, environmental covariates were included in a way that modified size-at-recruitment:

(3)

where ***x****c* is a vector of environmental covariates during the period that impacts size-at-recruitment of cohort *c*, ***β*** is a vector of estimated parameters quantifying the impact of the covariates on size-at-recruitment, and the *T* superscript indicates the vector transpose. For simplicity and due to the computational limitations of the Bayesian model, ***x****c* was either a scalar representing a single covariate, or a vector of length two, representing a single covariate and its quadratic term. CUTI and BEUTI were lagged by one year (i.e., upwelling impacts larval age-0 growth, which is observed when shrimp recruit to the fishery the next year). The covariates were standardized by subtracting their means and dividing by their standard deviations. We did not include a quadratic term for log-recruitment because there was no clear mechanism for an intermediate optimum.

Model selection was conducted using Pareto smoothed importance sampling leave one out cross validation (PSIS-LOO CV), which efficiently approximates leave one out cross validation from MCMC samples (Vehtari et al., 2017, 2022b), and implemented in the loo R package (Vehtari et al., 2022a). While the PSIS-LOO CV does not explicitly account for the autoregressive nature of the data, there are limited methods available for reliable and computationally tractable Bayesian model selection. We summarized results of PSIS-LOO CV using the expected log-predictive density (Sivula et al., 2023).

*2.4 Bioeconomic model*

The estimated growth model was then used as an input into a revenue-per-recruit model to assess the impact of growth and different season opening dates on expected revenue (Tables 1, 2). Specifically, we analyzed the revenue-per-recruit curves for opening dates between April 1 and June 1 in bimonthly increments (i.e., April 1, April 15, May 1, etc.).

A revenue-per-recruit model begins with a population with a single recruit, projects that recruit through a population model, and then sums expected revenue over its lifetime. Thus, the number of shrimp-per-recruit at age *a* = 0 months, *N0,* is assumed 1. The model was implemented in bimonthly increments because of the set of opening dates tested, but all time units are in months. Thus, the number of shrimp-per-recruit at age *a* + 0.5 months is:

(4)

where *Ms* is the monthly natural mortality rate during season *s*, *I*open is an indicator variable that is equal to 1 if the fishery is open and 0 otherwise, and *F* is the presumed monthly fishing mortality rate. Catch-in-numbers during each bimonthly period follows the Baranov catch equations and is

(5)

Season *s* is either summer (April-October), when natural mortality is higher or winter (November-March), when natural mortality is lower (Gallagher et al., 2004). Because of the seasonal nature of both fishing and natural mortality, there is no straightforward analytical solution for the plus group. Few shrimp survive past their third summer, so expected revenue was assumed to be zero at this point. The virtual population analysis used to manage the fishery makes the same assumption (Hannah and Jones, 2014a).

Obtaining yield-in-weight from catch in numbers required a length-age relationship, fit above, and a length-weight relationship. Shrimp in the middle of the month were assigned length based on their age at the start of the month. A time-invariant weight-length power relationship was fit to available ODFW data from 2014-2021 as a linear model on a log-log scale using ordinary least squares regression and then bias corrected (Table 2, Fig. S1). Total yield-per-recruit was calculated as yield summed across all bimonthly age increments.

Processors generally pay higher prices per pound for shrimp when the count per pound is lower (i.e., when individual shrimp are larger). We accounted for this in our revenue-per-recruit model by fitting a linear model of ex-vessel price as a function of count-per-pound, including each year-month combination as a fixed effect to account for market effects on price. The model was fit to data from shrimp tickets in PacFIN (Pacific Fishery Information Network; https://pacfin.psmfc.org/) between 2016-2020 matched with biological port sampling data on count-per-pound available from ODFW. As expected, count-per-pound had a negative effect on price. For more details on the price model, see supplemental materials.

**3. Results**

*3.1 Modelling length-at-age*

Shrimp size-at-age varied across time and space (Fig. 2). Across years, the largest shrimp age 2 and older tended to be observed in cohorts that recruited prior to 2000. This trend over time was not as apparent for age 1 shrimp. Growth slowed somewhat during the winter months. Across space, there is a clear pattern of smaller shrimp at age in more northerly areas, particularly areas 30 and 32, which cover most of the Washington state coastline. Across years and regions, average size-at-recruitment varied by approximately 2-3 mm

The model generally fitted the data well, and convergence diagnostics indicated that the model successfully converged and produced an adequate effective sample size for all key parameters; mixing was worst for the average size-at-recruitment and the process variance (Fig. S2, Table 3). The model does not estimate slowing down of growth at older ages, as indicated by the estimate of *α1* close to 1, although the model does tend to estimate decreasing process errors as age increases (Figs. S2, S3). Various approaches were tried to make process errors centered around zero for all ages (e.g., informative priors on *α1*), but this slowed mixing, and the model consistently estimated *α1* close to 1. The two largest variance estimates described variability in size-at-recruitment across time, *σL1*, and across space, *σr* (Table 3). The smallest variance estimate was for process error, which is the monthly variation in the growth increment and is shared across all areas. The observation variance, which includes both actual sampling error and true differences in size-at-age across state areas unexplained by size-at-recruitment, was larger than the process variance.

*3.2 Environmental drivers of size-at-recruitment*

None of the variables tested to influence size-at-recruitment (CUTI, BEUTI, log-recruitment) markedly improved the expected log-predictive density (ELPD) compared to a base model that relied on random variation about a mean size-at-recruitment (Table 4). The model with a single linear term for CUTI had the highest (best-fitting) ELPD, and the base model with no covariates had the lowest ELPD. However, the difference between these two models was 3.6 log-density units. In general, differences in the ELPD of less than four units are considered small, and differences greater than four should be compared to the standard error of the difference (Sivula et al., 2023). The mean of the posterior distribution of the CUTI effect indicated a 0.112 mm decrease in length at recruitment for every 1 unit increase in standardized CUTI during the spring of larval release. This result suggests slower growth under stronger upwelling of cool nutrient-rich waters. However, the 95% credible interval was (-0.345, 0.125), indicating the effect was ambiguous. Therefore, because no variables substantially improved the model, subsequent results are from the base model with no covariates.

*3.3 Revenue-per-recruit model and opening dates*

Using the growth model to inform the revenue-per-recruit model indicated that, under average size-at-recruitment in both space and time (i.e., *γ* = *ε*1 = 0), an opening date of April 1 maximized expected revenue-per-recruit up until a fishing mortality rate of around 0.15 mo-1 (Fig. 3b). Later opening dates were more beneficial under high fishing pressure (F > 0.15). However, when propagating growth model uncertainty, the 95% credible interval based on the April 1 opening date contains the median revenue-per-recruit curve for all five opening dates; thus, growth uncertainty overwhelms the revenue differences among different opening dates. Across all fishing mortality rates, intermediate opening dates were never beneficial; the date that maximized revenue-per-recruit was always the earliest (April 1) or latest (June 1). Changing the natural mortality rate, a highly uncertain parameter, shifted this inflection point. Higher natural mortality rates pushed the inflection point to higher fishing mortality and lower revenue while lower natural mortality rates pushed the inflection point to lower fishing mortality and higher revenue (Fig. 3). Estimates of actual monthly fishing mortality in the fishery averaged around 0.1 mo-1 during the fishing season from 1980-2011, ranging from approximately 0.03 to 0.2 mo-1 (Hannah and Jones, 2014a).

Across space, a wider range of fishing intensities (range) supported later opening dates in state areas farther north, particularly areas 30 and 32, assuming average recruitment over time (i.e., *ε*1 = 0; Fig. 4). These northern areas, where shrimp tended to be smaller (Fig. 2), led to lower revenue-per-recruit overall, although total revenue and profits depend on a variety of additional factors such as catch rates and market forces. On the other hand, the early April 1 opening was optimal across the entire range of observed fishing mortality rates for southern fishing areas that served as habitat for the largest size shrimp.

Size-at-recruitment has varied substantially across time, and this has also had economic implications for the fishery (Figs. 2, 5). For years when shrimp recruited at larger sizes, such as 1991, an early opening was optimal regardless of fishing mortality rate. For years when shrimp recruited at smaller sizes, such as 2011, the best opening date was ambiguous and depended on the fishing mortality rate. An early opening was optimal at lower fishing mortality rates, but a delayed opening was better at higher fishing mortality rates, with an inflection point right (i.e., all opening dates are similarly optimal), around the long-term average fishing mortality rate of 0.1 mo-1. Thus, if fishing mortality is low (e.g., shrimpers are not incentivized to fish due to low prices, high costs, or other opportunities, a large year class overwhelms fishing capacity) or average, an early opening date is best. If fishing mortality is high, however, the optimal decision on opening depends on the size of the shrimp.

Accounting for spatial *and* temporal variation illustrated that both factors operated jointly in determining optimal opening dates (Fig. 6). In years where shrimp recruited at small sizes (e.g., 2011), it was generally beneficial to postpone opening in northern areas (e.g., area 32), whereas the optimal opening date in southern areas with larger shrimp (e.g., area 19) depended on the fishing mortality rate. In years where shrimp recruited at large sizes (e.g., 1991), the early opening date was optimal in areas with large shrimp within the observed fishing mortality range, but the optimal opening date depended on the fishing mortality rate in the areas with small shrimp.

**4. Discussion**

This study contributes to an existing body of work on the ecology and management of Oregon ocean shrimp in two key ways. First, while annual growth indices summarized across cohorts and months have been derived to explore the influence of density-dependent and density-independent factors on growth, no work to date has explored growth variability in a mechanistic fashion such as the one employed here, more directly modeling the data as they were collected (Hannah and Jones, 2014b, 2016; Groth and Hannah, 2018; Groth, 2022). Second, previous work studying when to open the fishery looked at the joint impact of natural mortality, fishing mortality, and the response metric- revenue versus yield-per-recruit (Gallagher et al., 2004). We chose to use the metric more relevant to the fishing fleet (revenue-per-recruit), and added a new dimension to the analysis in its place: size-at-recruitment. This allowed us to provide more dynamic advice over both time and space, giving managers information they can use to adaptively manage the fishery.

*4.1 Section on methods – benefits thereof*

Add what you think the benefits are. Our approach did require more complex models with extra parameters compared to the simpler regression approach used to model the derived growth index. Although we were less likely to identify spurious drivers using our approach, and the results can provide more actionable management guidance, we also had less statistical power to identify true drivers, which bore out in the results (ambiguous CUTI effect). Our multivariate state-space approach is similar to that used by Buckner et al. (2023) to study drivers of declines in salmon size over time, and an advance over other linear autoregressive modeling approaches for size-at-age (e.g., Stawitz et al., 2015; Indivero et al., 2023) in that it explicitly models the growth process in a way that can be connected to common mechanistic models of somatic growth; the size at one time and age directly depends on the size of the cohort at the previous time step plus some growth increment. Another benefit of the approach is that it allows us to disentangle spatial variation and temporal variation while using a flexible approach that allows for the straightforward incorporation of covariates and estimation of trends.

*4.2 Optimal opening dates*

Our analysis and modeling can help provide advice to managers on when to optimally open the fishery for ocean shrimp, accounting for variability in growth across years and across the population’s spatial range. Decision-makers are best prepared to account for this heterogeneity if they have information on the size of the shrimp recruiting to the fishery in a given year (e.g., from a test fishery), and a proxy for how high they expect fishing mortality to be relative to past years (based on factors such as shrimp prices, fuel costs, fishery CPUE, etc.). In years with small shrimp, managers can optimize revenue-per-recruit by delaying opening until June in northern areas and delaying in southern areas if proxies indicate fishing mortality will be average to high. If fishing mortality is expected to be low, revenue-per-recruit in southern areas is slightly higher if the fishery is opened in April, but the benefits are small and may not warrant the additional administrative complexity. In years with average size shrimp, the April 1 opening produced either optimal revenue-per-recruit or similar revenue-per-recruit to other opening dates for state areas 12-29 across all fishing mortality rates. In the most northerly areas 30 and 32, if fishing mortality is expected to be high, there is a clear benefit to delaying the opening to June. If fishing mortality is expected to be low or average, there may be a slight benefit to opening in April, but the differences in revenue-per-recruit are small across opening dates. Finally, in years with large shrimp, the early April 1 opening date is generally a good option across all state areas. Notably, we did not find support for intermediate opening dates between April 1 and June 1.

There would be benefit to being able to predict whether size-at-recruitment is likely to large, average or small. However, we did not identify any density-dependent or density-independent covariates of size-at-recruitment that improved model predictions and could promote seasonal forecasting and assist with management decisions on when to open the fishery. There are several possible explanations for this result, and they are not mutually exclusive. First, growth could respond non-linearly to drivers, or the effects of drivers may only arise when accounting for interactions among them. Machine learning methods such as boosted regression trees (De’ath, 2007; Elith et al., 2008) would be better-suited to infer these types of effects, but require larger datasets than were available and are not well-suited to mechanistic models like the one we fit (Ward et al., In review). Second, we may not have selected the correct divers to test. Identifying appropriate oceanographic drivers of marine population dynamics is notoriously difficult (Myers, 1998; Brooks and Deroba, 2015; Haltuch et al., 2019). Finally, growth could be a truly stochastic and unpredictable process.

*4.3 Caveats and future work*

Lab studies to understand growth variability in wild crustacean populations have often been limited by the difficulty in determining reliable ages of wild-caught individuals. Many studies have explored impacts of density-dependent and density-independent factors on growth in controlled laboratory settings (see Chang et al., 2012 for review). Intensive tagging studies have shed light on growth variability in real-world conditions, but these are generally limited to data-rich populations with long-term fishery-independent monitoring programs (e.g., McMahan et al., 2016). Using ages determined from length-frequency distributions is not a gold standard and can result in biased estimates of biological reference points, particularly when confounded with estimation of mortality rates in stock assessments (Fournier et al., 1991). However, such ages can still be a valuable and sufficient source of information on somatic growth in management-relevant contexts for appropriate species. Ocean shrimp in Oregon are short-lived and fast-growing with good long-term fishery-dependent data, but limited fishery-independent monitoring, making them an excellent candidate for the application of length-frequency-derived ages. We were able to use these ages to quantify variability of growth over time and space, and to develop models that suggest when is optimal to open the fishery in different locations and years.

The models used in this study made several assumptions that may have influenced our conclusions. First, results of our revenue-per-recruit model are dependent on the fishing mortality rate that the fishery prosecutes. However, the fishing mortality rate is extremely difficult to control in a short-lived population such as shrimp because the population biomass generally changes much more rapidly than it can be assessed. Proxies for the fishing mortality rate may be able to be approximated using early season catch rates to identify relative year-class strength, and in-season data on fishing effort. Second, the shrimp population distribution generally stratifies by age, and shrimpers capitalize on this by fishing larger age-2 and age-3 year classes early in the season and smaller age-1 year classes later in the season. Our revenue-per-recruit model assumes constant monthly fishing mortality on each year class within and across seasons. This means that the fishery may effectively be delayed in most years for newly recruited shrimp, in particular, and monthly fishing mortality rates when the year-classes are being targeted may be higher than the range reported. Finally, shrimp are protandrous hermaphrodites and sexually dimorphic, but we did not account for either of these factors. Furthermore, more primary females are observed when the age-2 and age-3 year classes are weak (Charnov and Hannah, 2002), and these primary females tend to be larger than primary males. Accounting for variation in the sex ratio could make the average size-at-recruitment more predictable. For example, if the age-2 and age-3 year classes are known to be weak, the age-1 year class may have an above-average proportion of primary females, leading to a larger size-at-recruitment. In addition, the relative number of primary females could influence the process error estimates across the cohort’s lifespan (e.g., more primary females means shrimp have already reaped the “female size bump” and there is less growth during older life stages). Other caveats I could include: condition factor (Scott, is there anything to cite on this?), ageing methods, other? But am also trying not to have this paragraph be half of the discussion so if you suggest adding something consider also suggesting taking something out…

*4.4 Implications for management*

Ocean shrimp was the fifth most important fishery species on the U.S. West Coast over the last decade in terms of revenue, and it can be a key source of income for fishery participants in some years (Free et al., 2023). For example, during the 2014-2016 marine heatwave when key fisheries such as salmon experienced precipitous declines, strong recruitment prior to the heatwave coupled with high prices set by global markets allowed for record revenue from the ocean shrimp fishery. Therefore, sustainable fishery management that prioritizes population and ecosystem health while also seeking to maximize fishing revenue can help sustain and stabilize local coastal economies by allowing them to rely on a diversity of fisheries (Kasperski and Holland, 2013; Sethi et al., 2014; Oken et al., 2021). The work in this study can inform when the fishery should open each year in different management areas along the coast, giving targeted advice on when and where it should be delayed, thus helping to maximize fishing revenue each year. However, temporal diversification, that is, spreading fishing activities evenly across year, is also a key way that fishery participants reduce risk and make full use of their fishing capital (Oken et al., 2021; Abbott et al., 2023). Changing the time of year that the shrimp fishery operates may impact the temporal diversity that it provides. Shrimpers themselves have initiated discussions on delaying the opening of the shrimp fishery. However, as with many fishery management decisions, the fishing community should have an opportunity to respond to any significant changes to the timing of the fishery to ensure their goals and priorities are being considered (Wiber et al., 2004).

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1. <https://fisheries.msc.org/en/fisheries/us-west-coast-pink-shrimp-pandalus-jordani-trawl-fishery/> [↑](#footnote-ref-1)