**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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Abstract

Growth variability is a key contributor to the dynamic productivity of populations. Thus, better understanding and accounting for variation in growth can improve both tactical and strategic management. Using ocean shrimp (*Pandalus jordani*) from the U.S. West Coast as a case study, we demonstrate interactions between growth and optimal fishery opening dates. While the fishery opens on April 1, industry often delays fishing to minimize catches of small shrimp. Understanding drivers of size-at-recruitment can help managers optimize opening dates and shrimpers plan their participation in this and other fisheries. Using three decades of fishery-dependent sampling, we built a spatially-, temporally-, and environmentally-explicit Bayesian state-space model for shrimp size-at-age. Model outputs were then used to parameterize a revenue-per-recruit model and explore how variability in size-at-recruitment impacted optimal opening dates. Shrimp recruited at smaller sizes farther north. Delaying opening would likely benefit shrimpers in areas and years with smaller shrimp and higher fishing mortality. Broadly, choosing when to open the fishery is a complex decision requiring understanding of growth, but also recruitment, economic incentives, and life history.

Keywords

Growth, shrimp, crustaceans, environmental effects, fishery management

**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). Recruitment overfishing, where biomass is so low that spawners struggle to replenish the population, can only occur at extremely low spawning biomasses in populations with weak stock-recruit relationships, as is common in large marine ecosystems (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 (e.g., changes in predator-prey interactions) 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 and 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 space and time, although methods to estimate how and where growth varies over space have been even slower to develop than methods that focus solely on temporal changes in growth because of the rich data and high model complexity needed to estimate spatial variation (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 these animals. Laboratory 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).

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 fishery occurs across all three West Coast states (Washington, Oregon, California). The short lifespan leads to inherently variable population dynamics and productivity, and environmental drivers in this 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). In addition, several reports (e.g., Hannah 2011; Hannah and Jones 2014a, 2016; Groth and Hannah 2018; Groth 2022) have summarized the variability in growth, recruitment, and their relationship to density-dependent and -independent (i.e., environmental) factors. Further improving understanding of the dynamics of the ocean shrimp stock would be valuable, given that the California Current ecosystem is experiencing both long-term warming and more frequent marine heat waves (Barkhordarian et al. 2022).

For at least two decades, managers and participants in the ocean shrimp fishery in Oregon, where the fishery is centered, have been faced with the 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 to allow shrimp to grow to larger more profitable sizes, 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-2). Scientists also annually conduct a Virtual Population Analysis (VPA), allowing estimation of recruitment to following three years of repeat observations of a cohort (Hilborn and Walters 1992; Hannah and Jones 2014b). Despite these efforts, defining an optimal fishery opening date 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 abundant and small to avoid growth overfishing. 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*

The semi-pelagic trawl fishery for ocean shrimp is state-managed and 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 landed in Oregon ports (Pacific States Marine Fisheries Commission 2023). Fishery management actions are coordinated to be consistent among the states emphasizing: 1) reducing the chances of overfishing (i.e., size limit, season, number of vessels, harvest control rules based on population models) and 2) reducing bycatch (i.e., exclusion grates and light emitting diode fishing lights). Specific to limiting growth overfishing, the size limit employed (currently a maximum count per pound of 160 shrimp, equivalent to a minimum average weight of 0.1 ounces/shrimp) is intended to dissuade catch of small, fast growing age-one shrimp. Specific to limiting recruitment overfishing, scientists periodically compare the derived relative cohort strength from the VPA to likely covariates (e.g., sea level height) to determine primary drivers of recruitment (Hannah and Jones 2014a, 2016; Groth and Hannah 2018; Groth 2022). While the fishery legally operates from April 1 to October 31, fishing is often delayed if individual shrimp are expected to be small, and there are continuing conversations about whether to make this delay a permanent feature (S. Groth, pers. comm.). These conversations are focused on changing the opening date along the entire range of the fishery, but proposed opening dates would continue to be consistent among the three states.

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. Recruitment to the fishery 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 sequential protandrous hermaphrodites (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 (~3 years), 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 relative cohort strength, 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. S1). ODFW biologists 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 (Fig. S5; Zirges et al. 1981). This is considered a sufficiently reliable method because the three age classes are clearly defined in the length-frequency plots (Chang et al. 2012). For more details on ageing, see supplementary materials.

*2.2 Drivers of population dynamics*

Shrimp productivity has previously been found to be correlated with sea level height and the Bakun upwelling index (Rothlisberg and Miller 1983; Hannah 2011). The strength and timing of upwelling of cold deep nutrient-rich waters impacts the temperature young shrimp experience, ocean transport during the larval stage to adult habitat, and the quantity and quality of food resources. 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 has been found to be directly influenced by temperature (Rothlisberg 1979). We took monthly sea surface temperature (SST) data from the NOAA Extended Reconstructed Sea Surface Temperature dataset 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 in our analysis 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 (defined here forward as carapace 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 aged *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.* 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 using Markov chain Monte Carlo (MCMC) conducted by Stan (Stan Development Team 2022) and implemented with the Rstan package (Stan Development Team 2023) in R version 4.3.2 (R Core Team 2023). 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 , using the accepted threshold of 1.01, and by ensuring effective sample sizes of at least 400 (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 the size-at-recruitment for 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 the density-dependent term, 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 package in R (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 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, S1). 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 using 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 to be 1. The approach allows us to compare the gain achieved from the higher price of bigger shrimp caught after delaying harvest against the loss associated with the natural mortality that occurs in the period that harvest is delayed. There may be other economic implications of delaying the season, but quantifying them is beyond the scope of this analysis, and there is insufficient data on fishing costs and how they are impacted by shrimp biomass or size to undertake such an analysis. 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, assuming uniform age and size selectivity, similar to the VPA. Catch-in-numbers during each bimonthly period follows the Baranov catch equation:

(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). There is no straightforward analytical solution for the plus group because of the seasonal nature of both fishing and natural mortality. Few shrimp survive past their third summer, so expected revenue was assumed to be zero at this point. The VPA used to manage the fishery also assumes that all shrimp die after their third summer (Hannah and Jones 2014b).

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 S1, Fig. S2). Total yield-per-recruit was calculated as yield summed across all bimonthly (i.e., April 1-14, April 15-30, May 1-14, etc.) 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 2017-2020 matched with biological port sampling data on count-per-pound available from ODFW. As expected, count-per-pound had a negative effect on price (Tables S1, S2, Fig. S6). For more details on the price model, see supplementary materials.

**3. Results**

*3.1 Modelling length-at-age*

Shrimp size-at-age varied across time and space (Fig. 1). 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 during the winter months, as evidenced by the slight stairstep pattern. 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 (Fig. S1). Across years and regions, average size-at-recruitment varied by approximately 2-3 mm.

The model generally fit the data well, and convergence diagnostics indicated that the model successfully converged and produced an adequate effective sample size for all key parameters; MCMC mixing was worst for the average size-at-recruitment (*µL*1) as evidenced by its higher and lower effective sample size (Fig. S3, Table 2). 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. S3, S4). Various approaches were attempted 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 2). The smallest variance estimate was for process error (*σp*), which is the monthly variation in the growth increment and is shared across all areas. The observation variance (*σo*), which includes both 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, sea surface temperature, 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 3). The model with log-recruitment had the highest (best-fitting) ELPD. The model with a single linear term for sea surface temperature also had a marginally higher ELPD than the base model with no covariates. However, the difference across all models was only 1.03 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 log-recruitment effect indicated a 0.078 mm increase in length-at-recruitment for every 1 unit increase in standardized log-recruitment. This result suggests faster early growth when year classes are larger, counter to the principle of density-dependence. However, the 95% credible interval was (-0.145, 0.305), indicating the effect was ambiguous. Subsequent results are from the base model with no covariates because no variables substantially improved the model.

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

Using the growth model to inform the revenue-per-recruit model indicated that an opening date of April 1 maximized expected revenue-per-recruit up until a fishing mortality rate of approximately 0.15 mo-1, under average size-at-recruitment in both space and time (i.e., *γ* = *ε*1 = 0) (Fig. 2, center panel). Later opening dates were more beneficial under high fishing pressure (*F* > 0.15 mo-1). 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 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. 2). 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 2014b).

Across space, a wider range of fishing intensities supported later opening dates in state areas farther north (e.g., >0.11 mo-1 for area 32 versus >0.18 mo-1 for area 18), assuming average recruitment over time (i.e., *ε*1 = 0; Fig. 3). These northern areas, where shrimp tended to be smaller (Fig. 1), 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 serves 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. 1, 4). For years when shrimp recruited at larger sizes, such as 2020, an early opening was optimal regardless of fishing mortality rate. For years when shrimp recruited at smaller sizes, such as 2012, 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 (i.e., all opening dates are similarly optimal, points overlap) around the long-term average fishing mortality rate of 0.1 mo-1. Thus, an early opening date is best if fishing mortality is average or 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). 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. 5). In years where shrimp recruited at small sizes (e.g., 2012), it was generally beneficial to postpone opening in the 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., 2020), 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 that employed here, directly modeling the data as they were collected (Hannah and Jones 2014a, 2016; Groth and Hannah 2018; Groth 2022). Second, previous work studying when to open the fishery examined 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 could use to adaptively manage the fishery.

*4.1 Growth modeling approach*

Our multivariate state-space model for size-at-age was a powerful tool for quantifying variability in, and drivers of, shrimp size-at-age and propagating that forward into population dynamics models relevant to management. Our approach required more complex models with extra parameters compared to the simpler regression approach previously used to study growth (e.g., Hannah and Jones 1991; Groth and Hannah 2018), which derived annual indicators of growth across all age classes and months of the year. 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 was born out in the results (ambiguous temperature effect). Future work could explore a wider range of drivers or the possibility of multiple drivers acting concurrently. 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 from temporal variation while using a flexible approach that allows for the straightforward incorporation of covariates and estimation of trends. Finally, the use of MCMC to perform Bayesian inference allowed us to easily propagate uncertainty in the growth process into uncertainty in the revenue-per-recruit model (e.g., Fig. 2). MCMC eases the propagation of uncertainty from estimation models into other mathematical process models.

*4.2 Optimal opening dates*

Our analysis and modeling may 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 and a proxy for how high they expect fishing mortality to be relative to past years. Both quantities, and especially fishing mortality, are admittedly difficult to obtain prior to opening the fishery. A small test fishery may provide sufficient information on size of new recruits, or future work successfully identifying environmental covariates could prove useful. Fishing mortality is likely to be higher in years with lower abundance given the strong patterns of depletion over the short lifespan, so robust recruitment drivers or catch-per-unit-effort from a test fishery may provide some early indications of expected fishing mortality rates, but it would be a prediction as fishing mortality cannot occur prior to the season opening. In years with small shrimp, managers can optimize revenue-per-recruit by delaying opening until June in northern areas and 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. There is a clear benefit to delaying the opening to June in the most northerly areas 30 and 32, if fishing mortality is expected to be high. In contrast, there may be a slight benefit to opening in April if fishing mortality is expected to be low or average, 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.

We did not identify any density-dependent or density-independent covariates of size-at-recruitment that improved model predictions, as is common in fisheries generally, and in similar shrimp fisheries specifically (Myers 1998; Plagányi et al. 2021). 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 such as the one we fit (Ward et al. 2024). Second, we may not have selected the correct drivers to test. Identifying oceanographic drivers of marine population dynamics and quantifying them at the appropriate spatiotemporal scale is notoriously difficult (Myers 1998; Brooks and Deroba 2015; Haltuch et al. 2019). For example, we attempted to develop an upwelling index relevant to the biology of ocean shrimp. The metrics we used are generally considered advances over previous metrics (e.g., Bakun index, sea surface height), and we averaged them over relevant latitudes and times of year. However, different metrics or the same metrics summarized across different latitudes or times of year may have yielded more predictive results. In addition, limitations in existing ocean models prevented us from testing bottom layer temperature. Finally, growth could be a truly stochastic and unpredictable process.

Seasonal forecasting of population dynamics that provides actionable decision support can reduce uncertainty and manage business risks in wild capture fisheries and aquaculture (Hobday et al. 2016). Unfortunately, several barriers exist in producing and using operational forecasting in ecology and resource management. These barriers include having sufficient and rapidly available data, robust theory and methods, and a cultural emphasis on forecasting in ecological training and institutions (Dietze et al. 2018). The ability to move past these challenges and provide and assess the skill of seasonal-scale forecasts of population dynamics is key to adaptive management in the age of climate change (Walters and Hilborn 1978; Brodie et al. 2023). However, even modern methods for conducting and assessing forecasts can struggle to identify reliable predictors of population dynamics (Ward et al. 2024). We were not able to identify covariates that improved forecasts of shrimp size-at-recruitment, although the general pattern of smaller shrimp farther north tended to be conserved across years. The second major factor we examined in driving optimal season opening dates, fishing mortality, is even more difficult to forecast, as it depends on being able to predict both recruitment and fishing effort prior to the season opening.

*4.3 Caveats and future work*

Field 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 the impacts of density-dependent and density-independent factors on growth in controlled laboratory settings instead (see Chang et al. 2012 for a 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 length-frequency-derived ages the most viable application. We were able to use these ages to quantify variability of growth over time and space, and to develop models that suggest when it 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, the results of our revenue-per-recruit model depend on the fishing mortality rate which is often difficult to control for short lived species, such as shrimp, because the population biomass generally changes more quickly than it can be assessed. In some cases, 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 often capitalize on this by targeting larger age-2 and age-3 year classes early during the season and the 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 among 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. Third, we modeled revenue-per-recruit, but shrimpers ultimately make decisions to fish based on profits (i.e., revenue *and* costs) in both the shrimp fishery, and other fisheries in which they participate. Finally, shrimp are protandrous hermaphrodites and sexually dimorphic, which we did not account for. Furthermore, more primary females are observed when the age-2 and age-3 year classes are weak, resulting in a larger average size-at-recruitment because females are larger (Charnov and Hannah 2002; Charnov and Groth 2019). Accounting for variation in the sex ratio could make the average size-at-recruitment more predictable.

*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 those for 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). 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 the year, is also an important 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, although there are no current efforts to initiate different opening dates along the fishery’s range (S. Groth, pers. comm.). Our results here do not suggest large revenue benefits associated with changing the season dates that would be likely to outweigh other considerations that season opening is based on (e.g., availability of alternative fishing opportunities, fishing costs, shrimp reproductive biology). 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).

**6. Acknowledgements**

The authors are grateful to ODFW biologists over the past four decades who collected the data used in this study, and the fishery managers’ long-term investment in monitoring. Mary Hunsicker, three anonymous reviewers, and the associate editor provided valuable comments on previous versions of this manuscript.

**7. Data availability**

All code and most data are available at <https://github.com/okenk/shrimp> (DOI: 10.5281/zenodo.13362802). Price data used to parameterize the revenue-per-recruit model are confidential.

**8. Competing interests**

The authors declare there are no competing interests.

**9. Funding**

KLO was partially supported by National Science Foundation grant no. 1616821.

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1. <https://fisheries.msc.org/en/fisheries/us-west-coast-pink-shrimp-pandalus-jordani-trawl-fishery/> [↑](#footnote-ref-2)