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Original Article

Seasonal ocean forecasts to improve predictions of Dungeness crab catch rates, co-developed with state and tribal fishery managers

Emily L. Norton [1,*], Isaac C. Kaplan[2], Samantha Siedlecki[3], Albert J. Hermann[1,4], Simone R. Alin[4], Jan Newton[5], Kelly Corbett[6], Daniel Ayres[7], Ervin Joe Schumacker[8], Nicholas A. Bond[1,4], Kate Richerson [9], and Michael A. Alexander[10]

[1]Cooperative Institute for Climate, Ocean, and Ecosystem Studies, University of Washington, Seattle, WA, USA
[2]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA
[3]Department of Marine Sciences, University of Connecticut, Storrs, CT, USA
[4]Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, WA, USA
[5]Applied Physics Laboratory, University of Washington, Seattle, WA, USA
[6]Oregon Department of Fish and Wildlife, Newport, OR, USA
[7]Washington Department of Fish and Wildlife, Montesano, WA, USA
[8]Quinault Department of Fisheries, Taholah, WA, USA
[9]Fisheries Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, OR, USA
[10]Physical Sciences Laboratory, National Ocean and Atmospheric Administration, Boulder, CO, USA

** Corresponding author: tel: +1(206)685-6341;* e-mail: emilyln@uw.edu.

The commercial Dungeness crab (*Metacarcinus magister*) fishery in Oregon and Washington (USA) is one of the most valuable fisheries in the region, but it experiences high interannual variability. These fluctuations have been attributed to environmental drivers on seasonal and annual timescales. In this study, researchers and state and tribal fisheries managers develop a statistical model for Dungeness crab catch per unit effort (CPUE) to help inform dynamic management decisions in Oregon and Washington. Fishing observations were matched to seasonally forecast and lagged ocean conditions from J-SCOPE, a regional forecast system (http://www.nanoos.org/products/j-scope/). Inclusion of dynamic and lagged ocean conditions improved model skill compared to simpler models, and the best model captured intraseasonal trends and interannual variability in catch rates, and spatial catch patterns. We also found that model skill relied on fishing behaviour, which varies interannually, highlighting the need for advanced fishing behaviour modelling to reduce uncertainty. The relationships between catch rates and ocean conditions may help elucidate environmental influences of catch variability. Forecast products were co-designed with managers to meet their needs for key decision points. Our results illustrate a seasonal forecasting approach for management of other highly productive, but also dynamic, invertebrates that increasingly contribute to global fisheries yield.

Keywords: decision support, ecological forecasting, ecosystem-based fisheries management, Metacarcinus magister, oceanography, regional ocean modeling system.

Introduction

In recent years, seasonal ocean forecasts have begun to inform decision making and proactive management of marine resources, including species-specific applications for tuna, hake, and lobster (Hobday *et al*., 2011; Eveson *et al*., 2015; Mills *et al*., 2017; Malick *et al*., 2020). On the US West Coast, the Dungeness crab (*Metacarcinus magister*) fishery is the most valuable, with landed values ranging from 77 to 216 million US dollars per year for the 2007/08 to 2019/20 crab seasons [Pacific Fisheries Information Network (PacFIN), pacfin.psmfc.org]. As described below, the ecology of the Dungeness crab and its management context lend themselves to seasonal forecasting for dynamic management. Conscious of the central importance of this fishery to West Coast fishing communities (Fuller *et al*., 2017), ethical considerations when providing forecasts (Hobday *et al*., 2019), and the need to co-produce forecasts with fishery managers and users, we present steps towards generating catch rate forecasts for state and tribal decision making.

Seasonal dynamic management for a particular fishery is of potential value when certain conditions are present (Hobday *et al*., 2016; Tommasi *et al*., 2017). First, short-term variability must dominate long-term trends. In the case of the crab fishery, landings vary substantially among years (Figure 1). Over the past 12 years, crab catch has ranged from 3.7 M–10.5 M kg per season for Oregon and from 3.4–7.6 M kg for the Washington state fishery (Oregon Department of Fish and Wildlife 2022 (ODFW); Washington Department of Fish and Wildlife 2022 (WDFW)), with swings in ex-vessel ("dockside") value of \$26–74 M for Oregon and \$26–64 M for Washington (PacFIN 2022). The degree to which ocean conditions contribute to this interannual variability of the Dungeness crab fishery is unknown, but earlier work suggests that environmentally-driven changes in larval settlement

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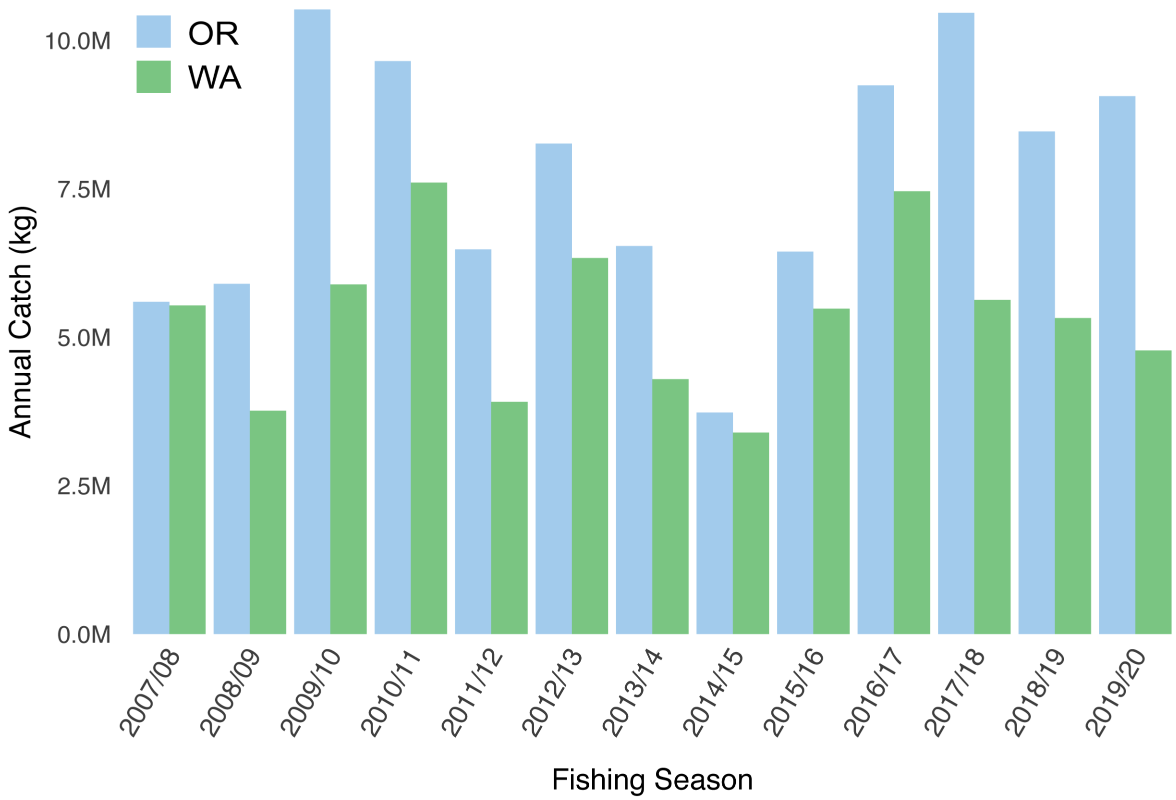

Figure 1. Dungeness crab landings per crab season for Oregon and Washington state fisheries. Fishing typically begins late in one calendar year and continues into the following year, so for example, the 2007–2008 fishery is labeled 2007/08.

could drive variability in the adult fishery (e.g. Armstrong *et al.*, 2010; Rasmuson, 2013; Shanks, 2013). Additionally, larval stages (e.g. Reed, 1969; Brown and Terwilliger, 1999; Miller *et al.*, 2016; Bednaršek *et al.*, 2020) and adult crabs (e.g. De Wachter and Wilkens, 1996; Bernatis *et al.*, 2007; McGaw, 2008) have been shown to be sensitive to ocean conditions.

Second, seasonal dynamic management requires that skillful forecasts be available with enough lead time for managers and fishermen to make and implement informed decisions (Marshall *et al.*, 2011; Hobday *et al.*, 2016). For Washington and Oregon, ocean forecasts are available through the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) Seasonal Coastal Ocean Prediction of the Ecosystem (J-SCOPE; Siedlecki *et al.*, 2016; http://www.nanoos.org/products/j-scope/). J-SCOPE is a high-resolution (grid spacing ∼1.5 km, 40 vertical levels), Regional Ocean Modeling System (ROMS) model that uses initial and boundary conditions from NOAA's Climate Forecast System (CFS) global coupled climate model. J-SCOPE produces oceanographic predictions (i.e. forecasts) initialized in January and April that span 9 months, as well as 12 month historical simulations (i.e. hindcasts). Biogeochemical variables from J-SCOPE, including oxygen, carbon variables [e.g. saturation state (Ω) and pH], and physical ocean conditions (e.g. temperature and salinity) have been extensively validated (e.g. Siedlecki *et al.*, 2016; Norton *et al.*, 2020), and these ocean conditions have been used to develop statistical models to predict spatiotemporal variations in suitable habitat for sardine (*Sardinops sagax*; Kaplan *et al.*, 2016), Pacific hake (*Merluccius productus*; Malick *et al.*, 2020), and larval Dungeness crab (Norton *et al.*, 2020).

Finally, seasonal dynamic management requires that decision makers have proactive options available (Sarachik, 2000) that will allow the fishery to minimize losses in "bad" years and maximize opportunity in "good" years (Marshall *et al.*, 2011; Hobday *et al.*, 2016). These options may include the ability to change catch rules or modify season opening and/or closing dates (Melnychuk *et al.*, 2014). Dungeness crab is a culturally important species, and under the Stevens Treaties, the tribes in Washington are guaranteed the right to harvest 50% of the shellfish in their traditional fishing grounds (United States vs. State of Washington, 1995). Thus, Dungeness crab are co-managed between the states and tribes on the outer coast of Washington within the "3S" framework (i.e. "season," "size," and "sex"), where the season opening dates as well as the opening location (i.e. Washington state vs. tribal areas) is adjustable by the managers; a minimum size is also in place, and catch is restricted to males only (Rasmuson, 2013). By the Stevents Treaties, the timing of opening dates in co-managed areas must strive towards equal sharing of the crab catch among the state and tribal fishermen (Figure 2). Due to disparate fleet sizes, the tribal fishery opens first in the co-managed areas, typically in November or December, to allow tribal fishermen the opportunity to harvest half of the legal crab (Supplementary Table 1). Then the state fishery is usually opened in December or January. Due to the nature of this derby-style fishery, which is characterized by high catch rates initially that taper over time (Dewees *et al.*, 2004), if managers open the state fishery too early or too late, equal sharing will not be attained. The decision of when to open the state fishery is currently based on the initial incoming crab tonnage for the tribal fishery, but this information is not always sufficient

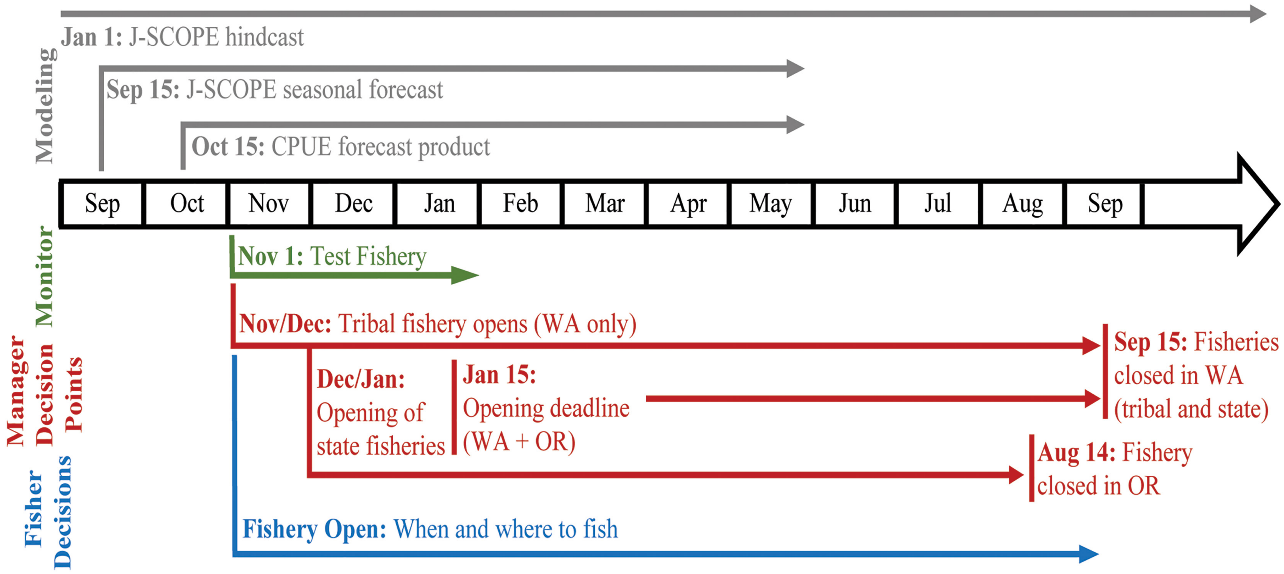

Figure 2. Schematic of the Oregon and Washington annual management of the Dungeness crab fishery and corresponding timeline of J-SCOPE model products, which can support decision-making.

to estimate the total catch for the season (J.S. and D.A., pers. obs.), and state opening dates are often debated, suggesting the need for improved forecasting tools.

In our study, a team of oceanographers, fish biologists, and state and tribal fisheries managers developed forecast products to support decision-making for the Dungeness crab fisheries in Oregon and Washington. We used seasonal ocean forecasts from J-SCOPE to develop statistical catch rate models for Dungeness crab. We also investigated the relative importance of ocean conditions, including the effect of static, dynamic, and historical (i.e. lagged) conditions, on adult crab catch rates. We then tested the model's skill, which is critically important before operationalizing forecasts for dynamic management applications.

Ecological context

Like many marine invertebrates, Dungeness crabs exhibit a biphasic life history, living both in the water column and on the seafloor over the course of their development. In the fall, bottom-dwelling adult females release fertilized eggs that hatch into planktonic larvae called zoeae. Zoeae grow and molt through five stages before molting into their final pelagic stage, known as the megalopae stage (Poole, 1966; Reed, 1969; Reilly, 1983). Megalopae are powerful swimmers compared to zoeae (e.g. Fernandez *et al.*, 1994), but their movement is still affected by oceanographic currents (Hobbs *et al.*, 1992; Morgan and Fisher, 2010). After developing in the water column for about 4–6 months total, megalopae metamorphose into juvenile crabs and settle back to the benthic environment (Poole, 1966; Reilly, 1983). Crabs continue to grow rapidly, reaching sexual maturity (100 mm carapace width) at approximately two or three years of age and legal size (146-159 mm carapace width) at age four or five (Tasto, 1983; Botsford, 1984).

Crab abundance, often estimated by catch rate (Methot and Botsford, 1982; Richerson *et al.*, 2020), is influenced by population-level drivers as well as local ocean conditions that affect movement and response of adult crabs at the time of capture. At the population level, Shanks (2013) reported a significant, parabolic relationship between the abundance of Dungeness crab megalopae in coastal habitats and recruitment into the adult fishery 4–years later. In combination with studies that have demonstrated sensitivity of crab larvae to variable ocean conditions (e.g. Reed, 1969; Sulkin *et al.*, 1996; Brown and Terwilliger, 1999; Miller *et al.*, 2016; Bednarsek *et al.*, 2020), these exposures by larvae may drive future abundance of adults. Adult crabs have also been shown to prefer certain environmental conditions. For example, there is strong *in situ* evidence that adult crabs are unable to withstand exposure to severe hypoxic events (Grantham *et al.*, 2004; Bernatis *et al.*, 2007; Froehlich *et al.*, 2014), and in Puget Sound, hypoxia can compress habitat for adult populations (Bernatis *et al.*, 2007; Froehlich *et al.*, 2014). While these dynamic ocean conditions have the potential to impact the distribution or abundance of adult crabs, their influence on population size or catch rates has yet to be shown.

Methods

Hypotheses and selection of predictor variables

Following the approaches of Tolimieri *et al.* (2018) and Haltuch *et al.* (2020), we considered distinct crab life stages and their habitat use to identify ecological and oceanographic drivers demonstrated by other studies to affect Dungeness crab (Supplementary Table 2). These drivers were categorized as either static variables, or variables related to dynamic or lagged oceanography. We also included "fishing behaviour" variables that may affect catch rates, specifically fishing location, date, and soak time for pots.

Crab logbook data and fishing behaviour variables

Oregon and Washington state logbook data spanned crab seasons 2007/08–2017/18 and 2009/10–2018/19, respectively, and state fishery opening dates ranged from December 1–February 7 during our study period (Supplementary Table 1). Prior to data screening (see Supplementary Materials), our model training set, which included crab seasons 2007/08–

2015/16, consisted of 137,845 strings (i.e. a series of crab pots attached along one line) from Oregon logbooks and 139,594 strings from Washington logbooks. We reserved data from crab seasons 2016/17–2018/19 as a model testing set that consisted of 17,706 and 66,849 strings from Oregon and Washington logbooks, respectively. As in Malick *et al.* (2020), this test set is used to evaluate the out-of-sample forecast skill, as measured against data not originally included in the fitting procedure.

We modeled catch rates as kilograms per pot. This was calculated from logbook records of crab catches per string, in either weight (pounds) or counts, and number of pots per string (see Supplementary Materials for conversion details). Logbook data for both states also provided fishing location, date, and soak time. The fishing location was reported as the beginning latitude and longitude where strings of pots were deployed. Since the fishery opening dates vary by year and area (Supplementary Table 1), we calculated a relative "day in season" on which fishing occurred. We also estimated a year-effect term, which was treated as a smoothed continuous variable, to account for unexplained interannual variability. Finally, soak time is a measure of the duration (days) that each string of pots was fished. We estimated the relationship between soak time and catch rates per pot, expecting a positive relationship, but allowing for the potential of trap saturation or bait degradation over time.

Static variables

We use the term "static" to refer to variables that were gleaned from the fishery logbooks (i.e. latitude, longitude, soak time, day in season, and year), as well as two additional variables (bottom depth, sediment grain size) that remain relatively constant over time. These variables are expected to help explain spatial variability in catch rates (H1-6 in Supplementary Table 2).

Dynamic and lagged ocean conditions from J-SCOPE

Due to the timing of decisions made in the Dungeness crab fishery (Figure 2), we generated a suite of 9 month forecasts of physical, biogeochemical, and biological dynamics in J-SCOPE that would allow enough lead time to inform decision-making while spanning most of the crab season. The J-SCOPE forecasts were generated following the methodology in Siedlecki *et al.* (2016) but were initialized using September conditions from CFSv2. The season typically opens sometime between December and February, and although fishing can continue into summer months, ~80–90% of logged catches occur by the end of May. Because J-SCOPE forecasts on a seasonal timescale, we used monthly-averaged ocean conditions in the catch rate model. We developed hypotheses (H7-12 in Supplementary Table 2) to explain the inclusion of seven dynamic predictor variables (i.e. sea surface height, 2-m integrated chlorophyll a, bottom salinity, bottom temperature, bottom oxygen, bottom aragonite saturation state, bottom pH) that may affect spatial and temporal catch rates of bottom-dwelling adult crabs. pH and aragonite saturation state were calculated based on an empirical relationship (Norton *et al.*, 2020).

To investigate the influence of environmental conditions on early life stages (H13-16 in Supplementary Table 2), ocean conditions were considered at lags accounting for the time between early life stages and harvested adults (i.e. 3 and 4 yr lagged bottom temperature, bottom oxygen, and 2-m integrated chlorophyll a, and 4 yr lagged PDO). Annual average conditions were generated from J-SCOPE historical ocean simulations (hindcasts). To simplify the analysis, we applied the most basic assumption that earlier life stages occupy the same location as where their adult counterparts were caught. This assumption was based on the concept of self-recruitment, which has been demonstrated in Dungeness crab populations in prior modelling work (Rasmuson *et al.*, 2022), and tagging studies that indicate minimal distance travelled by adults (Hildenbrand *et al.*, 2011).

For each fishing observation from the logbooks, we identified the nearest point on the J-SCOPE grid and assigned the predicted ocean conditions from that grid point for the corresponding calendar month in the same year or at the appropriate lag. J-SCOPE model validation methods are available in the "Methods" section of the Supplementary Materials.

Statistical methods for generalized additive model (GAM)

We used GAMs to predict crab catch rates as a function of "static," "dynamic," and "lagged" ocean conditions. These models were trained with a subset of available logbook data pooled for Oregon and Washington (2007/08–2015/16 for OR; 2009/10–2015/16 for WA); more recent crab seasons were retained for model validation (2016/17–2017/18 for OR; 2016/17–2018/19 for WA). Predictors were considered individually (univariate GAMs, see Supplementary Materials and Supplementary Table 3) and in combination to investigate the importance of individual variables on crab catch rates as well as to develop a best-fit model for operational forecasting. As is common in oceanographic studies, preliminary investigation suggested a correlation between depth and other covariates, and between the same covariate but at different lags (e.g. bottom oxygen at 3 vs. 4 year lag; Supplementary Table 4). We use Akaike Information Criterion (AIC) model selection to test whether these covariates add explanatory power even when penalized for the increased model complexity.

We used a Gaussian error distribution and an identity link function (*mgcv* package in *R*; Wood, 2004). To improve normality, we log transformed the response variable after adding 0.01 to account for any catch records of zero kilograms ($N = 196$; ~0.1% of total records). All but three explanatory variables were smoothed with a spline function and allowed three knots (k), which captures a unimodal niche response to environmental conditions (e.g. Chust *et al.*, 2014). The exceptions were that the year effect term was allowed to vary each crab season (i.e. $k = 9$) to account for unexplained interannual variability, and the latitude and longitude terms were treated as an interactive tensor term to account for spatial autocorrelation. Additionally, spatial autocorrelation was evaluated with variograms and Moran's "I" statistic (Moran, 1948; see Supplementary Materials).

Model fit was estimated with % deviance explained and an AIC score (Akaike, 1974). AIC is a metric used for model selection that optimizes model complexity by taking into account model fit while penalizing for additional terms (Akaike, 1974; Burnham and Anderson, 2002). The GAM with the lowest AIC score was selected as the best model and was used to develop forecast products.

Table 1. GAMs fit to predict Dungeness crab catch rates (ln(kg/pot)]. Deviance explained (%) and ΔAIC (relative to the best model, GAM_SDL, for which ΔAIC = 0) estimate model fit. s indicates smoothed terms; t indicates a tensor interaction term. DS = day in season, DH = depth; ST = soak time; YR = year, LL = latitude x longitude, SSH = sea surface height, BA = bottom aragonite, BpH = bottom pH, BS = bottom salinity, BT = bottom temperature, BO = bottom oxygen, CH = 2 m integrated chlorophyll, PDO = Pacific Decadal Oscillation, l4 = variable that was lagged four years, l3 = variable that was lagged 3 years. GAM models included D = "dynamic," L = "lagged," and S = "static" groups of predictor variables.

Model Name	*Description*	*% Dev. Explained*	*Delta AIC*
Day in Season (DS)	s(DS)	35.6	66 714
DS + static (GAM_S)	s(DS) + s(DH) + s(ST) + s(YR) + t(LL)	54.6	5 941
DS + dynamic (GAM_D)	s(DS) + s(SSH) + s(BA) + s(BpH) + s(BS) + s(BT) + s(BO) + s(CH)	47.3	31 858
DS + lagged (GAM_L)	s(DS) + s(BTl4) + s(BOl4) +s(CHl4) + s(PDOl4) + s(BTl3) + s(BOl3) + s(CHl3)	50.5	20 928
DS + dynamic + lagged (GAM_DL)	s(DS) + s(SSH) + s(BA) + s(BpH) + s(BS) + s(BT) + s(BO) + s(CH) + s(BTl4) + s(BOl4) +s(CHl4) + s(PDOl4) + s(BTl3) + s(BOl3) + s(CHl3)	51.7	16 626
DS + static + dynamic + lagged (GAM_SDL)	s(DS) + s(DH) + s(ST) + s(YR) + t(LL) + s(BA) + s(BS) + s(BT) + s(BO) + s(CH) + s(BTl4) + s(BOl4) +s(CHl4) + s(BTl3) + s(BOl3)	56.2	0

GAM performance testing

Over the model training period (2007/08–2015/16), we evaluated the spatially explicit skill of the GAM in two ways. The first strategy was to compare the raw values of the observed and reforecast CPUEs. We generated a CPUE reforecast for each year using known fishing behaviours from the logbooks (i.e. fishing location, date, and soak time for pots) and dynamic and lagged ocean conditions from J-SCOPE as input for the catch rate model. These raw CPUE values were averaged within each 0.1° latitude x 0.1° longitude grid cell, and a correlation coefficient was calculated between the raw observed and reforecast CPUE values to quantify model performance. The second strategy relied on anomaly values, which are used to understand how different a particular year is from climatological, or average, values. Observed and reforecast climatologies were generated by averaging the CPUE values within each grid cell across all model training years. By subtracting the raw CPUE value (either observed or forecast) for each year from the climatology, we compared the observed and reforecast anomalies by calculating an anomaly correlation coefficient (ACC). We also estimated the spatial bias of the model by subtracting the observed CPUE climatology from the reforecast CPUE climatology.

Finally, we investigated changes in model performance over time. Given the decision context of this derby-style fishery, we calculated the correlation coefficient (r) over the first 10, 20, 30, 50, 75, 100, 125, 150, and 180 days into the crab season. We also generated spatial CPUE maps integrated from the start of the season to these same time points to understand how fishing effort and model skill change spatially.

Model predictions

We predicted spatial distribution of catch rates averaged over the entire forecast season using various fishing behaviours. These catch rate maps allow a general understanding of shifts in crab density and persistence of low-catch areas over time. For reforecasts, these gridded maps (0.1° latitude x longitude) were based on dynamic J-SCOPE ocean conditions and fishing behaviour as reported in the logbooks; these were generated to calculate a baseline estimate of model skill on crab seasons for which the GAM had not been trained, assuming we could forecast fishing effort perfectly. For true forecasts, for which the fishing effort would be unknown, we estimated fishing behaviour based on two hypotheses: (1) fishing behaviour for a given season should be most similar to the prior season, so we used fishing behaviour from logbooks from one crab season prior; or (2) assuming the absence of any trends in fishing effort, long-term average fishing behaviour should approximate fishing effort for the forecast, so we used fishing behaviours from all previous crab seasons for which logbooks were available for both Washington and Oregon (i.e. 2009/10 to the prior crab season). These forecasts are of interest to managers concerned about zones of poor ocean conditions (such as hypoxic areas) or unproductive local fisheries; we do not intend these maps to guide crab fishers to "hotspots." At a 0.1° resolution, we expect fishers to be more skilled than any model (and see Hobday *et al.* (2019) regarding pitfalls of mis-applying forecasts).

Results

GAM selection

Several combinations of predictor variables were fit as GAMs to predict Dungeness crab catch rates (ln(kg/pot); Table 1), and the model with the lowest AIC score was identified as the best fit model (Akaike, 1974; Burnham and Anderson, 2002). The most basic GAM contained only "day in season," which was shown to explain the most variance of any single predictor variable (~36%; Supplementary Table 3). Adding static variables to the "day in season" GAM led to a substantial increase in deviance explained (54.6%), and improvement in ΔAIC. Adding only dynamic (GAM_D) or only lagged (GAM_L) oceanographic variables to the "day in season" GAM also led to increases in deviance explained (to 47.3 and 50.5%, respectively) and improvements in ΔAIC. When both dynamic and lagged variables were added (GAM_DL) to the "day in season" GAM, the model fit improved slightly (deviance explained = 51.7%). Finally, when static, dynamic and lagged variables were included (GAM_SDL), and non-significant terms were removed, the model had the highest deviance explained (56.2%) and the best (i.e. lowest) AIC score (Table 1). In terms of AIC, this optimal model is 5941 units better than the "next-best" model (the GAM with day in season and static variables), with 1.6% higher deviance explained.

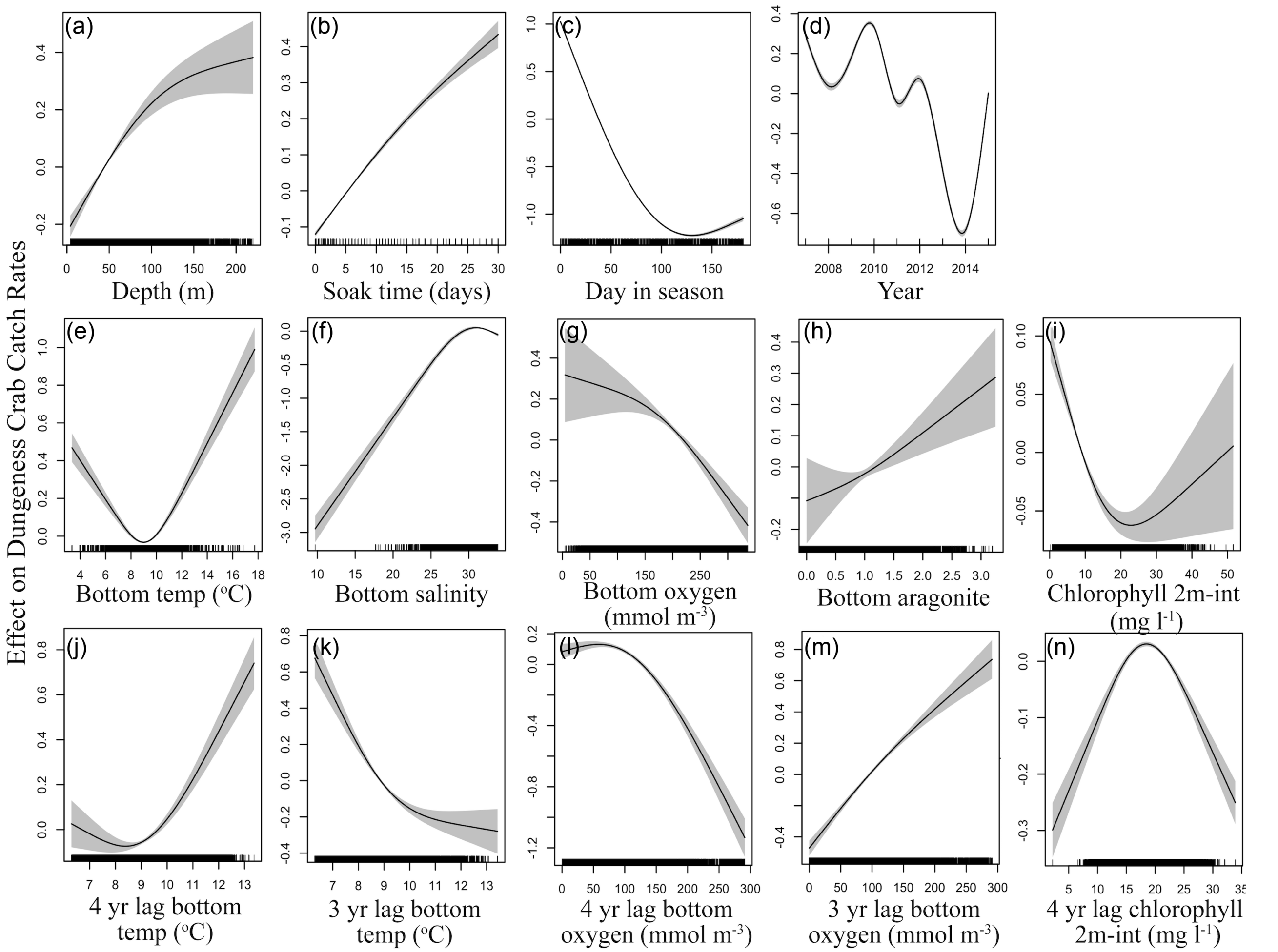

Figure 3. The effect of predictor variables on Dungeness crab catch rates. The response scale reflects natural log-transformation. Smooth functions represent additive effects of each predictor in the GAM while the other predictors are held at their average value; shading indicates ± 2 SE, and the "rug plot" along the *x*-axis represents occurrence of observations. The range of the *y-axis* indicates the relative importance of the covariate. All variables were limited to a maximum of three inflection points (i.e. "knots" ≤ 3) except "year," which was allowed nine knots. Static variables (top row): (A) depth, (B) soak time, (C) day in season, and (D) year effect; dynamic variables (second row): (E) bottom temperature, (F) bottom salinity, (G) bottom oxygen, (H) bottom aragonite saturation state, and (I) 2 m integrated chlorophyll a; and lagged variables (bottom row): (J) 4 yr-lagged bottom temperature, (K) 3 yr-lagged bottom temperature, (L) 4 yr-lagged bottom oxygen, (M) 3 yr-lagged bottom oxygen, and (N) 4 yr-lagged 2 m integrated chlorophyll a.

To better understand the relationships between individual predictors and crab catch rates within the best-fit GAM, diagnostic plots were generated in which one variable was plotted over its entire range (*x*-axis) while all other variables were held at their average value (Figure 3; Supplementary Fig. 1). The range on the *y*-axis indicates the relative importance of a covariate, with day in season being the strongest predictor of catch rate, as identified previously in the univariate GAMs.

Evaluation of GAM performance

The correlation coefficients (r) and ACCs calculated for spatial forecasts showed that the GAM demonstrated moderate forecast skill for the model training period (r = 0.60 +/− 0.09; ACC = 0.50 +/− 0.09; Supplementary Fig. 2; Supplementary Table 5).

Spatially explicit forecasts of catch rates revealed the model's tendency to underpredict catch rates over much of the domain [Figure 4; -21 ± 20% (mean ± *SD*)]. However, the highest rates of underprediction (~50–80% lower) and overprediction (~50–70% higher) of the model tended to occur in isolated areas along the coast and at the shelf break.

We also investigated temporal changes in the fishery. As expected in this derby-style fishery, predicted CPUE averaged over the model domain decreased rapidly over the first ~100 days of the crab season (Figure 5). Then the change in CPUE flattened out (~100–120 days after the season opening) and eventually began to increase slightly (>120 days after the season opening). Critically, the GAM was able to qualitatively capture observed differences between years, including peak CPUE as well as the rate of decline over the crab season.

Finally, when we considered model skill over time and space (Supplementary Fig. 3), we found that model skill for almost all locations improved when integrated over longer time periods (average r = 0.47 at day 10; average r = 0.65 at day 180). By the end of the forecast period, the model is skillful in most locations (r > 0.5), with the exception of low skill (r < 0.25) for isolated areas along the shelf break and in the farthest northern extent of fishing in Washington.

Forecast products for 2016/17–2018/19 crab seasons

Spatiotemporal forecasts of crab CPUE displayed moderate skill when fishing behaviour—i.e. fishing location, date, and

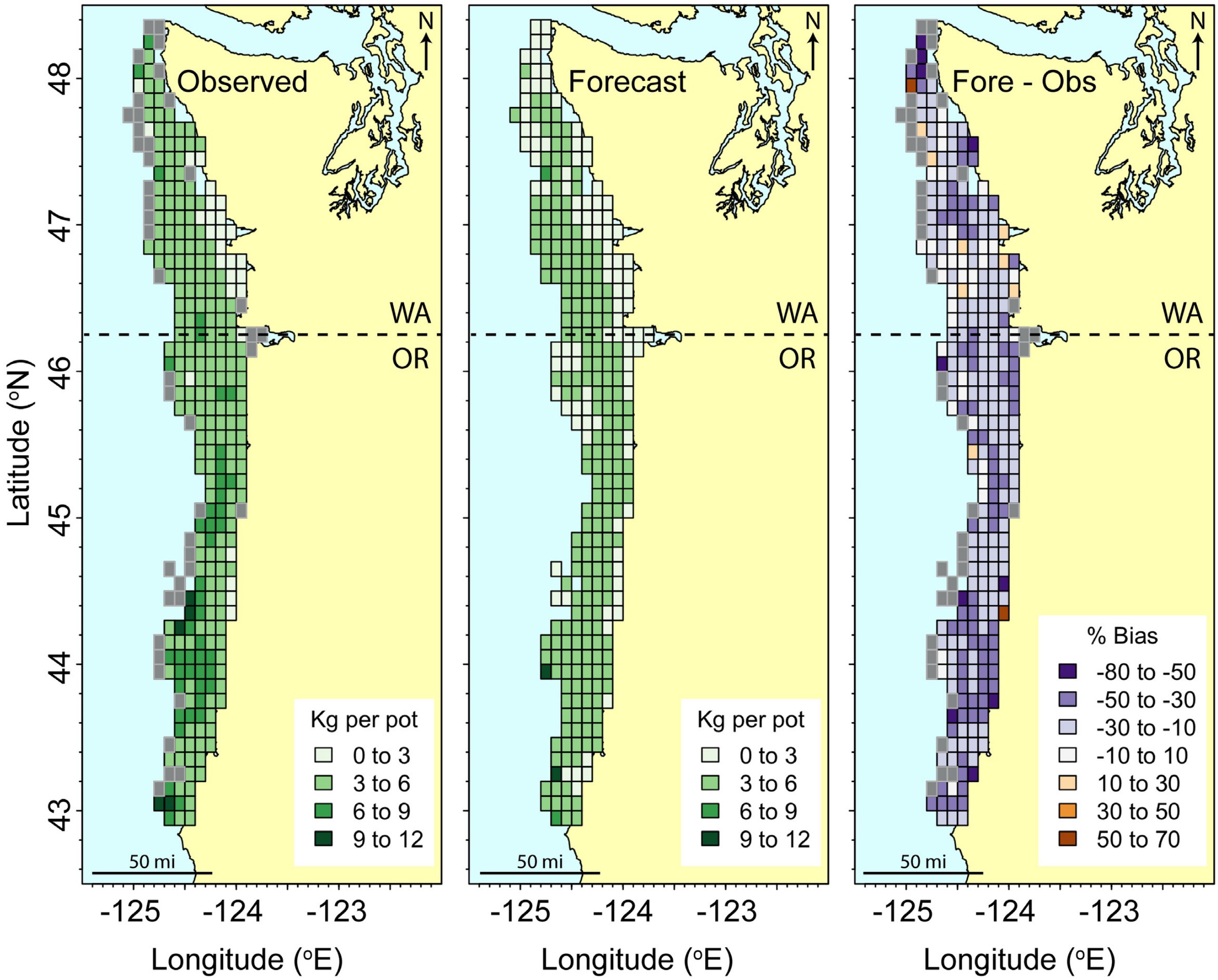

Figure 4. Observed (A) and forecast (B) CPUE climatologies for 2007/08–2015/16 crab seasons. Deeper green colors indicate higher CPUE yields. Percent model bias (C) was calculated by subtracting the observed from the forecast climatology and then normalizing by the observed catch. Orange indicates that the forecast is biased high (overprediction), while purple indicates that the forecast is biased low (underprediction); white indicates little or no model bias. Gray cells have small sample sizes (strings) so those cells have been obscured in the observations and bias figures.

soak time—was known, but skill declined sharply in true forecast mode, without knowledge of actual fishing behaviour. Spatial CPUE forecasts were produced for the crab logbooks that had been excluded from the GAM model training (i.e. crab seasons 2016/17–2018/19 for Washington and 2016/17–2017/18 for Oregon; e.g. Figure 6). Forecasts performed on par with prior crab seasons (Supplementary Table 5) when they were generated using known fishing behaviour (Figure 6A; first two columns of Table 2). True forecasts, however, require assumptions about fishing behaviour, which is difficult because of its wide spatial and temporal variability in the past (Supplementary Fig. 4). When fishing behaviour was approximated using fishing effort from the prior crab season (Figure 6B; columns 3 and 4 of Table 2) or an average from all years prior (Figure 6C; columns 5 and 6 of Table 2), GAM model skill (r and ACC values) was lower than when known fishing behaviour was used, though using fishing behaviour from all previous crab seasons performed better (for forecasts for 2016/17–2018/19, average $r = 0.43$ and average ACC = 0.17).

Discussion

Globally, marine invertebrate fisheries are rapidly expanding and filling increasingly important roles as target species (Anderson *et al.*, 2011; Harvey *et al.*, 2021). Dungeness crab in particular plays a central role for US West Coast fishing communities (Fuller *et al.*, 2017; Fisher *et al.*, 2021), yet its management differs starkly from that of high-value finfish. Dungeness crab are managed within the "3S" framework (i.e. "season," "size," and "sex"), by which managers adjust the season opening dates, set minimum size limits, and restrict the retained catch to males (Rasmuson, 2013). This relatively simple management system has been successful in coping with strong interannual fluctuations in landings of this short-lived species. In our research, we ask to what extent foresight about the potential drivers of those fluctuations could supplement the management system. We see this as an extension of dynamic ocean management approaches (e.g. Lewison *et al.*, 2015; Maxwell *et al.*, 2015), by leveraging advances in seasonal ocean forecasting (Siedlecki *et al.*, 2016) rather than solely relying on real-time observations. Overall our work (1) establishes the

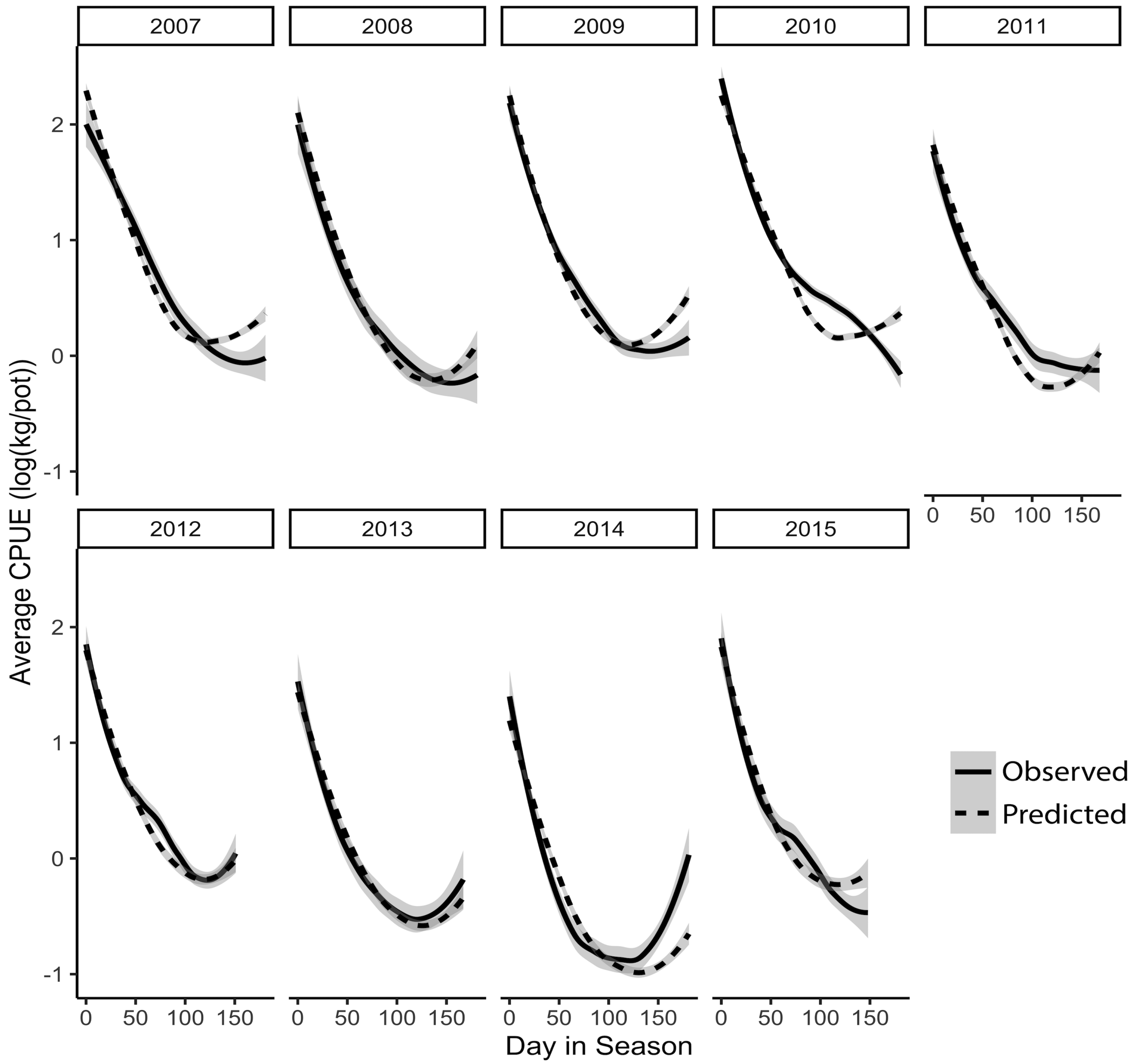

Figure 5. Smoothed lines show each year's observed (solid) and forecast (dashed) CPUE (log(kg/pot)) by day in season for this derby-style fishery. Shading indicates the 0.95 confidence interval.

importance of ocean conditions as drivers of Dungeness crab catch rates, (2) illustrates that ocean forecasts are one of several necessary components to build a forecast system predicting spatial catch rates, and (3) suggests that a skillful forecast of fishing behaviour would be needed for true forecasts to inform managers of how future catch rates will deviate from average catches. Alternatively, consistent, spatially explicit observations of crab abundance, independent of the fishery data, co-located with *in situ* ocean conditions would also enable this kind of forecasting, as has been successfully demonstrated in other J-SCOPE forecasting work (Kaplan *et al.*, 2016; Malick *et al.*, 2020; Norton *et al.*, 2020). Our results are relevant for other highly productive, but also highly dynamic, global invertebrate fisheries.

Ocean conditions affect crab catch rates

To our knowledge, this is the first time continuous relationships between static, dynamic, and lagged environmental variables and Dungeness crab catch rates have been reported. We found that both dynamic and lagged oceanography were important for predicting crab catch rates as indicated by the results of the best-fitting GAM. Although "day in season" alone explained about one third of the variability in crab catch rates (35.6% of deviance explained), when we added predictor variables both concurrent with the fishing period ("dynamic" conditions) and historical ("lagged" conditions) to account for egg and/or larval environmental exposure, our model fit improved. Finally, by adding a few more "static" conditions associated with fishing location, our best fit model (GAM_SDL) explained the majority of deviance in catch rates (56.2%) and was able to forecast catch rates with moderate skill (ACC = 0.45 and $r = 0.54$ in predict mode, using known fishing behaviour). These results build on prior studies focused on generating statistical habitat models for other species that have reported increased model fit and skill when dynamic oceanographic variables were included in addition to static variables (e.g. Brodie *et al.*, 2018; Abrahms *et al.*, 2019).

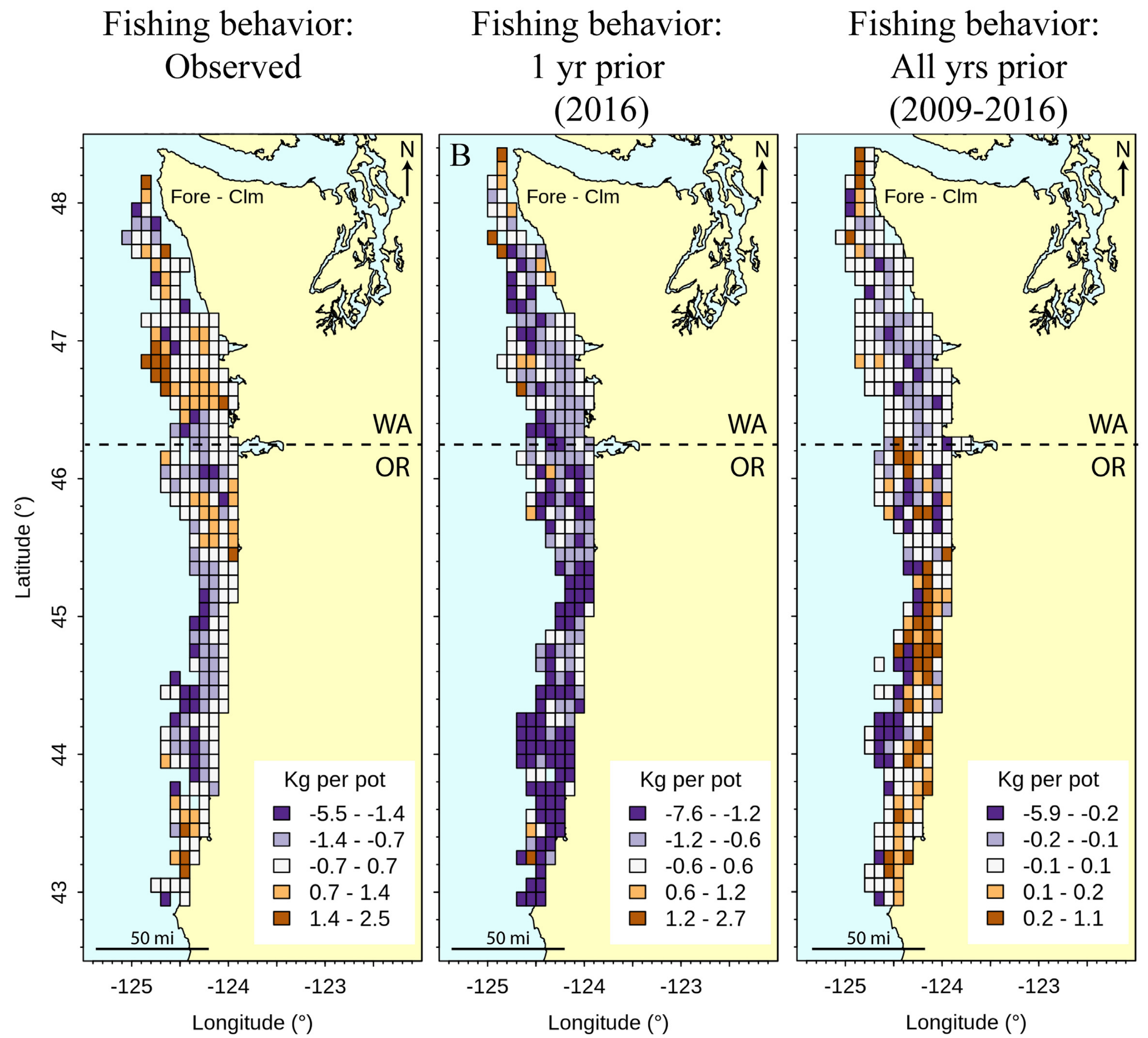

Figure 6. Case study of 2017/18 forecast showing how fishing behaviour affects predicted CPUE anomaly from forecasts using (A) observed fishing behaviour, (B) fishing behaviour from one crab season prior (2016/17), and (C) fishing behaviour from all prior crab seasons for which both Oregon and Washington logbooks were available (2009/10–2016/17).

Table 2. Forecast skill of the GAM_SDL model depended on which fishing behaviours were used. Correlation coefficient (r) and ACC were calculated for the observed versus forecast crab catch rates for each year in the testing subset (2016/17–2018/19) when the following fishing behaviours were used: (A) true (observed) fishing behaviour, (B) fishing behaviour from one year prior, or (C) fishing behaviour from all previous years for which data from Washington and Oregon were available (2009/10–prior yr). Only Washington logbooks were available for the 2018/19 crab season, so fishing behaviours from Oregon logbooks were omitted for these forecasts.

	Re-forecast: Observed fishing behaviour		*Forecast: Fishing behaviour from one year prior*		*Forecast: Fishing behaviour from all years prior*	
Crab Year	r	ACC	r	ACC	*r*	*ACC*
2016/17	0.48	0.44	0.27	-0.08	0.38	0.14
2017/18	0.41	0.32	0.31	0.21	0.41	0.05
2018/19	0.72	0.59	0.41	0.22	0.48	0.31
Avg	0.54	0.45	0.33	0.12	0.43	0.17
Std	0.17	0.13	0.07	0.17	0.05	0.13

The variables selected by the model and their relationships with catch provide insights into the controls over observed interannual fishery variability. For example, although we had hypothesized that chlorophyll concentration would be positively correlated with catch rates, our best fit model predicts that catch rates are high at both high and low chlorophyll levels (Figure 3I). One possible explanation of this correlation is that high chlorophyll levels correspond to high food availability and the crab population may increase commensurately. Conversely, low chlorophyll concentrations may correspond to low local prey productivity, and crabs may seek food wherever they can find it, including bait in a crab pot, elevating their catchability. Curtis and McGaw (2012) showed that adult crabs in the laboratory exposed themselves to deleterious conditions to obtain food. Stevens *et al.* (1984) also reported that food-limited adult crabs would enter lower quality habitat to pursue prey. Further work is needed to mechanistically determine the causality of the relationships between chlorophyll concentrations and crab catch rates.

The relationship between oxygen concentration and crab catch rates was also unexpected; we found a negative correlation where we had expected a positive correlation. Anecdotally, it is reported that crabs are usually highly mobile under normoxic conditions and are still active even in hypoxic conditions (~2 mg O_2 l^{-1}; ~60 μmol/kg); however, crabs may experience strong low oxygen effects at oxygen concentrations <1 mg l^{-1} (~22 μmol/kg; Jack Barth, pers. comms.), making them more docile and lethargic (J.S., pers. obs.), and perhaps easier to catch. Another possible explanation is that low oxygen concentrations drive habitat compression, elevating catch rates in surrounding areas (Froehlich *et al.*, 2014). Alternatively, the relationship between oxygen concentration and catch rates may be influenced by other processes, such as La Niña conditions, which may raise the thermocline, potentially spurring increased primary production while decreasing bottom oxygen simultaneously (Turi *et al.*, 2018). We also observe a high degree of model uncertainty at low oxygen concentrations (Figure 3), which may result from fewer observations in this range or may indicate variable relationships over space or time.

Interestingly, individual predictor variables (e.g. temperature, oxygen, or chlorophyll concentration) often exhibited a distinct relationship with crab catch rates when considered "dynamically" versus lagged by 3 or 4 yrs. These results may arise because eggs, larvae/juvenile, and adult crabs have different habitat needs and tolerances (Sulkin *et al.*, 1996; Brown and Terwilliger, 1999; Berger *et al.*, 2021). Alternatively, since their early life stages are planktonic (~70–180 days; Moloney *et al.*, 1994) and they undergo ontogenetic migrations (Shanks, 1986; Rasmuson, 2013), our assumption that eggs, larvae, and juvenile crabs experience the environmental conditions at the locations where they are ultimately caught as adults may be an oversimplification. Future studies might benefit from incorporating larval dispersal modelling (Norton *et al.*, 2020; Berger *et al.*, 2021) or estimates of crab movement to further examine relationships between lagged conditions and crab catch. Additionally, given the low-frequency variability of some of the lagged predictors, such as the PDO (Mantua *et al.*, 1997), the relationships between potential predictor variables and crab catch rates should be re-evaluated when we have a longer observational record available.

Catch forecasts: skill assessment and gaps identified

A key part of CPUE forecast development is rigorous performance testing and identification of bias. Our forecasts predict crab catch rates for Oregon and Washington, spanning crab years 2007/2008–2018/2019, with some notable challenges. Our CPUE model is capable of forecasting seasonal trends and interannual variability in catch rates (Figure 5) with minimal bias over the majority of the domain (<30% bias; Figure 4), although some isolated areas along the shelf break (~200 m depth) or nearshore exhibit poorer skill and/or higher bias. Limited fishing observations in these regions (Figures 4C; Supplementary Figures 3 and 4) as well as late-season fishing in the north likely make these regions less predictable (Supplementary Figure 3).

Seasonal forecasts of ocean conditions typically experience skill that decays the further they are from their initialized state. However our CPUE forecasts showed the highest correlation between observed and predicted CPUE when calculated over a full 180 fishing days. This implies that the September-initialized ocean forecasts add skill as far as late May. One possibility is that this is driven by inherently more predictable ocean dynamics after the spring transition, reported for NOAA's CFS model (CFSv2) which forces J-SCOPE (Jacox *et al.*, 2019). Additionally, since day in the crab season is a strong predictor of catch rate, the model's ability to predict the sharp decline in CPUE over the course of the crab season contributes to its strong skill.

The importance of fishing behaviour in driving economic and ecosystem outcomes in marine systems is well documented (Fulton *et al.*, 2011), and we found that fishing behaviour impacted our CPUE forecast skill as well. When fishing patterns were known, we skillfully predicted crab catch rates (>50% variance explained in the historical training set; average $r = 0.6$; average ACC = 0.5; Supplementary Table 4). However, fishing behaviour varied widely among years (Supplementary Figure 4), making it challenging to select accurate fishing behaviour in true forecast cases. Payne *et al.* (2017) emphasize that fisherman behaviour responds not only to changes in species abundance, but also to markets, management, and social dynamics. Recent studies of US West Coast fishery participation indicate that Dungeness crabbing involves a wide variety of vessel types, fishing strategies, and diverse alternative target species, which may affect fishing behaviour in complex ways (Fuller *et al.*, 2017; Fisher *et al.*, 2021). Furthermore, recent years have tended to have later season opening dates (Supplementary Table 1), potentially changing fishing behaviour. In part, these later opening dates have been managers' responses to harmful algal blooms, with subsequent adjustments by fishermen (Moore *et al.*, 2020). In our true forecasting cases (Figure 6; Table 2), when fishing behaviour was approximated rather than known, the forecasts had decent correlation with observed catches, but anomaly correlations degraded. This means that the model replicates the typical seasonal and spatial trends in catch rate, but not year-to-year variation in catch rates. Overall, the challenge of predicting anomalous commercial fishery catch rates illustrates the importance of fishing behaviour in forecasts for coupled systems.

The forecast's reliance on accurate fishing behaviour may be entrenched in this method since we not only use fishing behaviour covariates directly in the GAM (e.g. day in season, location, and soak time), but we also match the catch data to the spatially-explicit dynamic and lagged oceanographic conditions based on fishing location. Simulation approaches such as agent-based modelling (Bailey *et al.*, 2019; Dolder *et al.*, 2020) offer great promise to understand fishing fleet dynamics and choices of fishing location and timing. Alternatively, fishery-independent standardized surveys, often conducted for finfish and integrated into dynamic habitat modelling and management strategies (e.g. Kaplan *et al.*, 2016; Clavel-Henry *et al.*, 2020; Malick *et al.*, 2020), would help eliminate this source of uncertainty in our forecasts. This would require additional resources, and given the apparent sustainability of the "3S" management scheme (Richerson *et al.*, 2020), state and tribal fishery managers (authors K.C., D.A., and J.S.) do not consider increased investment in systematic surveys to be feasible or necessary for effective management currently. Finally, our method assumes that the majority of legal-sized male crabs are caught annually, but in practice the proportion of crabs caught may vary significantly between years (Methot and Botsford, 1982). Estimates from Richerson *et al.* (2020) suggest that ∼65–95% of legal-sized male crabs were caught each year in Washington and Oregon during our study period (2007–2016). This variability may be due in part to crab density effects and variable fishing effort.

Co-production of forecast products

To support management decisions with ocean forecasts, engagement with managers, from the grant proposal through to this paper, was critical. Managers were able to indicate highest priority needs for forecast products and contributed on-the-ground knowledge throughout the process, e.g. by identifying key drivers to consider as predictors in the GAM. Advances for both state and tribal applications require a cycle of feedback and revision to tailor, update, and improve forecasts for specific use. In the future, additional forecast products for Washington could help inform co-management by the state and coastal tribes, which is a unique situation guaranteed by treaty but also particularly vulnerable to shifting ocean conditions.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

Author contributions

S.S., I.K., D.A., and J.N. conceived the project idea, and all authors helped develop the methodology. K.C., D.A., J.S., E.N., I.K., S.S., J.N., and S.A. curated the data. E.N. and I.K. conducted the analyses and generated visualizations. S.S. obtained funding with help from I.K., J.N., S.A., and M.A. S.S. and N.B. administered the project. E.N., I.K., and S.S. drafted the manuscript, and all authors contributed revisions. This manuscript is submitted with the approval of all authors.

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Data availability

The oceanographic data underlying this article are available in Zenodo, at DOI: 10.5281/zenodo.7576958. Code for the generalized additive models of crab catch per unit effort is publicly available on GitHub https://github.com/mlenorton/dungeness-catch-model. The fishing location and catch data underlying this article cannot be shared publicly due to requirements regarding fisherman privacy and business confidentiality. These fishing locations and catch data can be requested from co-authors, D. Ayres (Washington Department of Fish and Wildlife) and K. Corbett (Oregon Department of Fish and Wildlife).

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