

Drivers of bitter crab disease occurrence in eastern Bering Sea snow crab (*Chionoecetes opilio*)

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Abstract

A recent population collapse of eastern Bering Sea (EBS) snow crab (*Chionoecetes opilio*) led to the first-ever closure of the snow crab fishery in 2022. The population collapse, caused, in part, by unprecedented warming, was preceded by peaks in juvenile snow crab density (2018) and bitter crab disease (BCD, *Hematodinium* sp.; 2016), a fatal crustacean disease. Annual bottom trawl surveys in the EBS show high year-to-year spatiotemporal variation in BCD-infected crab, yet it remains unclear what ecological drivers might explain the variation. We used statistical models of BCD presence/absence to examine the relative importance of intrinsic and extrinsic factors as drivers of BCD. We found a dome-shaped relationship between temperature and BCD presence, and results suggest that 2–4°C bottom temperatures are more likely to support BCD. Matching with past work across the globe, we find that stations with high population density of small, new shell crab are most likely to be BCD-positive. While our work highlights the challenges of disease monitoring in the EBS, our results indicate that indirect management measures related to snow crab rebuilding and recruitment may be more appropriate than directed fisheries management in mitigating BCD impacts.

Keywords: borealization; marine disease management; snow crab; bitter crab disease; *Hematodinium*; disease triangle; fishing out

Introduction

Parasites represent potential ecological and economic concerns to commercially important fisheries worldwide. Ecologically, parasites can play key roles in controlling population dynamics (Anderson and May 1978, Marcogliese 2004, Lafferty et al. 2006). Economically, these changes in population dynamics can lead to decreases in fishery profits; moreover, catch with high parasite burdens can decrease value (Lafferty et al. 2015). Yet predicting and managing marine disease remains challenging because of spatiotemporal heterogeneity in disease patterns (Groner et al. 2016, Glidden et al. 2022). Identifying both intrinsic and extrinsic drivers of marine disease can help guide fisheries management strategies to avoid negative impacts of disease.

Bitter crab disease (BCD; *Hematodinium* sp.) in eastern Bering Sea (EBS) snow crab (*Chionoecetes opilio*) is an emerging management concern following a BCD prevalence peak in 2016 and the 2018–2022 snow crab population collapse (Fedewa et al. 2022, Szuwalski et al. 2023) and subsequent fishery closure. Infected snow crabs have a bitter taste and are unmarketable; moreover, infections are fatal, creating potential ecological consequences for fisheries (Meyers et al. 1987, Shields et al. 2005, Hoenig et al. 2017). In the EBS, annual BCD prevalence is considered relatively low (average annual prevalence of ~0.4%; Fig. 1a) using visual diagnosis methods; however, annual station-level prevalence (i.e. percent of stations with at least one BCD-positive crab) can exceed 20% (Fig. 1b) with great variation within and among sta-

tions across time (Fig. 2, left). Little is known about the parasitic dinoflagellate's basic biology, transmission strategies, and distribution in the EBS, making mitigation of BCD impacts via management action difficult (Meyers et al. 1996, Shields et al. 2005, Stentiford and Shields 2005, Morado et al. 2010). Identifying intrinsic and extrinsic drivers of BCD spatiotemporal patterns can provide insight into the disease ecology of BCD, informing potential management actions (Escobar and Craft 2016, Glidden et al. 2022).

Snow crab population structure and dynamics could act as an intrinsic factor driving BCD spatiotemporal patterns. Across the globe, BCD tends to infect small, new shell crab (Shields et al. 2005, Stentiford and Shields 2005, Mullowney et al. 2011, Behringer 2012, Lycett et al. 2018). This suggests transmission is potentially related to the molting process, and crab that experience more frequent molting (i.e. small, juvenile crab) are more vulnerable to infection (Eaton et al. 1991). Moreover, in a Newfoundland study, Mullowney et al. (2011) demonstrated that more dense populations of small snow crab tend to have higher BCD occurrences; this suggests a potential density-dependent transmission of BCD. For the EBS snow crab population, dense populations of small, juvenile crab tend to be concentrated in the northern EBS. Older and larger crabs, often targeted by the fishery, have reached their terminal molt and are often geographically separated from smaller, younger crab as a result of ontogenetic migration into deeper, warmer waters (Ernst et al. 2005, Parada et al. 2010).

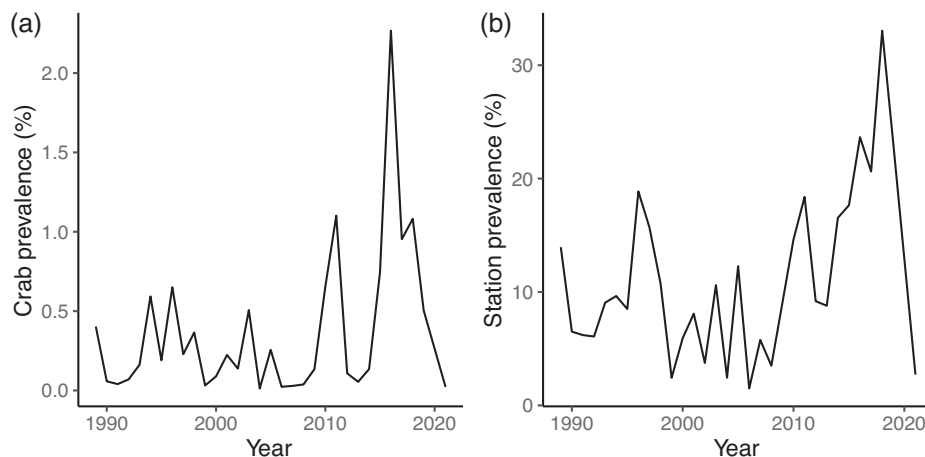


Figure 1. Data overview. (a) The prevalence of BCD varies through time in the eastern Bering Sea (EBS), with a maximum annual crab prevalence, i.e. the percent of all crabs within a year that are BCD-positive, of ~2%. (b) BCD can be widespread in the EBS, with station prevalence, i.e. the percent of sampled stations with at least one BCD-positive crab, reaching up to 33%.

Climate change and resulting borealization of the EBS could act as an extrinsic factor that drives BCD spatiotemporal patterns. Abiotic conditions, like temperature, influence parasite reproduction, transmission, and disease progression, all of which can shape spatiotemporal disease patterns (Lafferty 2009, Gehman et al. 2018, Shields 2019, Rohr and Cohen 2020). Past work suggests a variety of relationships between BCD occurrence and temperature (Shields et al. 2007, Gandy et al. 2015, Huchin-Mian et al. 2018); in EBS snow crab, Morado et al. (2010) noted qualitative patterns between increasing temperature, decreasing depth, and higher BCD prevalence. Beyond direct modifications to the abiotic environment, climate change shifts the broader ecological community (i.e. borealization; Mueter et al. 2021), which can also shape spatiotemporal disease patterns (Johnson et al. 2015, Escobar and Craft 2016). Cross-contact between parasite hosts of different species, such as Tanner crab (*C. bairdi*) and snow crab, could allow for cross-transmission and increased spread of BCD (Meyers et al. 1987, 1996). In contrast, predation by generalist predators, such as Pacific cod (*Gadus macrocephalus*), could decrease host population density and remove infected individuals from the population, decreasing spread of BCD (Packer et al. 2003, Lopez and Duffy 2021, Richards et al. 2022). Understanding the current abiotic and community drivers of BCD can aid managers in predicting future BCD impacts.

To understand patterns of BCD in the EBS, we leverage long-term, large-footprint survey data to identify environments that support *Hematodinium*, i.e. the BCD niche in the EBS snow crab. Survey data includes potential drivers of disease, as well as disease patterns (presence/absence) on fine scales (station-level), allowing us to identify environments that support BCD (Groner et al. 2016). Managers can use this information to understand how disease-management interventions and future conditions might change BCD patterns. We model *Hematodinium* niche (i.e. BCD occurrence) using a mix of intrinsic (e.g. population structure) and extrinsic (e.g. abiotic and community-level dynamics) covariates (Scholthof 2007, Morado et al. 2012, Escobar and Craft 2016, Glidden

et al. 2022). Considering not only intrinsic population factors, but also extrinsic community and abiotic factors that moderate BCD occurrence can help guide fisheries managers as they navigate the challenges associated with a changing EBS ecosystem.

Methods

Data collection

We used data within the National Oceanic and Atmospheric's (NOAA) standard summer grid (375 fixed stations) collected during NOAA's annual EBS trawl survey from 1989–2019 to 2021. Generally, the survey begins in the southeastern EBS in May and moves northwest, ending in August (Zacher et al. 2023). Among the 375 stations, at least 1 snow crab was identified at 340 stations; the 35 stations that had no snow crab data across the entire time series were excluded from analysis. The survey collects station-level information on snow crab density and biometrics, BCD presence/absence, and abundance of other commercially important and ecologically relevant species. We converted raw count data for snow crab into catch per unit effort (CPUE, number per km²) at each station using area-swept estimates (Weinberg and Kotwicki 2008). Catch data include sex, carapace width, and shell condition for each crab collected. Shell condition is a qualitative, Likert-scale measurement, ranging on a scale from 0 (soft) to 5 (very, very old shell). For each station, we calculated demographic features such as average carapace width and average shell condition by taking a CPUE-weighted station average. Environmental information, such as station depth (m) and bottom temperature (°C), was directly obtained from survey data. We converted raw count data of Tanner crab (alternative hosts) and Pacific cod (predator) into presence/absence information for each station. We removed any station-year combinations that did not contain snow crab demographic data (e.g. no snow crab carapace width measurements) and/or station-year combinations that did not contain temperature data.

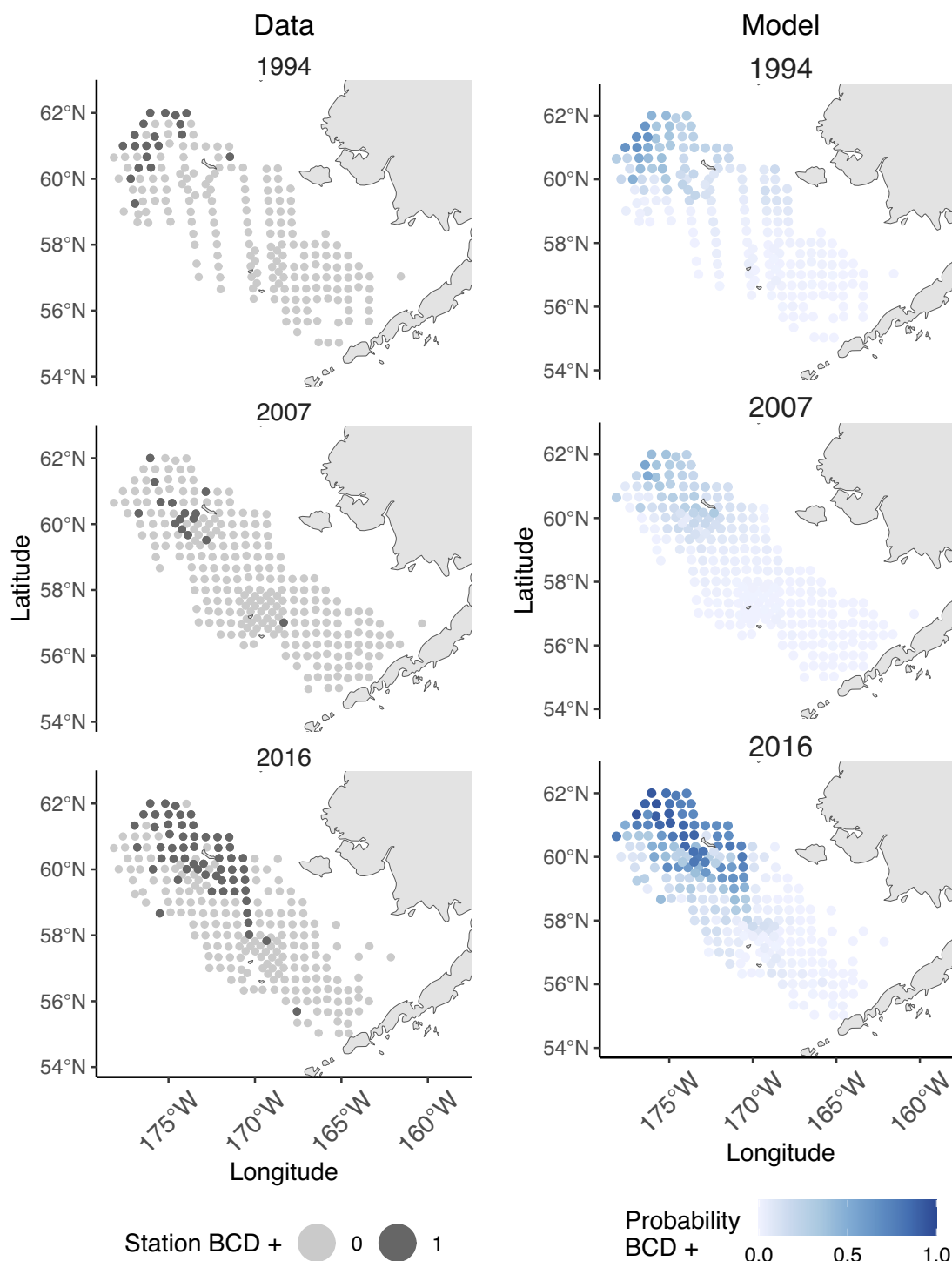


Figure 2. Comparison of data and model predictions of BCD presence in the EBS for subset of years. Survey data of BCD presence on the left: dark gray circles indicate the station is BCD-positive (1), and light gray circles indicate the station is BCD-negative (0). Model predictions from best-fit model on right, darker blues indicate a higher probability of encountering BCD at the station. Years here represent a low coverage year (1994), a low occurrence year (2007), and a high occurrence year (2016).

Starting in 1989, after initial identification of BCD, the survey used visual diagnosis to identify BCD-positive crab (Meyers et al. 1987). Visual diagnosis evaluates crab abdomen and membrane coloration: crab with a more creamy coloration on the ventral side of the carapace are diagnosed as BCD-positive, while crab with more translucent

coloration are diagnosed as BCD-negative. Visual diagnosis of BCD is not a sensitive method of identifying BCD-positive crab as only the most heavily infected crab are identified as BCD-positive; thus, visual BCD infection rates are likely an underestimation of the true infection rate (Pestal et al. 2003). Nevertheless, tracking the presence of visual

BCD-positive crab at a station can provide insights into the types of station-level environments that support diseased hosts.

Spatiotemporal station-level modeling

For our model, any station where at least one BCD-positive crab was encountered is considered a BCD present station (the station conditions are within infected host's niche; Groner *et al.* 2016); stations where no BCD-positive crab were encountered are considered BCD-negative stations. Note that here, we use BCD-positive stations as our metric for BCD infection, rather than station-level BCD prevalence. By focusing on stations, which are BCD-positive, rather than the proportion of individual crab, which are BCD-positive, we ask, "What fine-scale factors help explain BCD presence within the EBS snow crab population?"

We tested hypothesis-driven combinations of intrinsic and extrinsic covariates (Table 1) to understand the potential drivers of BCD spatiotemporal patterns in EBS snow crab. We generated hypotheses using the disease triangle framework (Scholthof 2007, Morado *et al.* 2012, Escobar and Craft 2016, Glidden *et al.* 2022). The disease triangle framework considers the roles of biotic and abiotic factors, which define the parasite's niche and shape parasite distribution: disease occurs when (i) susceptible hosts encounter (ii) parasites in (iii) suitable environments. We include both intrinsic (snow crab demographics) and extrinsic (e.g. community interactions) biotic factors, which might shape spatiotemporal disease patterns. We include extrinsic abiotic factors, which might limit the parasite's ability to reproduce, disperse, and survive between and within a host, as well as a host's ability to clear pathogens, e.g. temperature (Morado 2011, Coates and Söderhäll 2021). Note abiotic factors will also influence host distribution, which similarly shapes parasite distribution over space and time. Focusing on the host qualities and environment most supportive of disease helps identify long-term trends and possible interventions to mitigate the impacts of disease (Groner *et al.* 2016, Glidden *et al.* 2022).

We fit general additive models (GAMs; Wood 2011) to BCD presence/absence at the station-level (B_i , where i references the station-year pair), given various intrinsic and extrinsic covariates (Table 1). This allows us to identify possible patterns in disease seasonality and spatial distribution, while also accounting for collinearities between time, space, and disease progression. Moreover, we can identify potential non-linearities in trends, which can inform possibilities and limitations of management actions. To account for covariance between survey collection time and disease progression, our null model includes fixed year intercepts (Y_i) and a fixed, smooth effect for collection time (D_i), as well as tensor interaction of northings (X_i , km) and eastings (E_i , km) using the $t2()$ function in *mgcv* (Pedersen *et al.* 2019). Both collection day and space are used in all our models, despite relatively high correlation between the two (Appendix A), as we expected they contribute to disease occurrence differently. Collection day is likely correlated with disease progression and increased probability of visual diagnosis; note collection day is a fixed effect since we use collection day to describe how infected crabs at later stages are more likely to be heavily infected and able to be identified as BCD-positive using visual diagnosis. Our model's spatial plane captures latent covariation between survey sites our models do not explicitly include, e.g. salinity, which could

contribute to disease occurrence (Eaton *et al.* 1991). Our null model is then given by

$$B_i \sim \text{Bernoulli}(p_i) \\ \text{logit}(p_i) = Y_i + f_1(D_i) + f_2(X_i, E_i). \quad (1)$$

Several of the factors are correlated with space (GGally; Schloerke *et al.* 2021), which is expected given the strong climatic and temporal gradient of the survey (see "Model limitations" section and Appendix A in the supplementary materials); we only excluded non-spatial factors from the model if they strongly covaried with other non-spatial factors ($r > 0.6$). CPUE data for snow crab were log-transformed to address skewness. Our full model describes the probability a station-year combination (i) has at least one BCD-positive crab (B_i) as the additive effect of the overall year intercept (Y_i), collection date (D_i), station-level presence of cod [$C_i \in c(0, 1)$], station-level presence of Tanner crab [$T_i \in c(0, 1)$], and spline functions for the station-level snow crab CPUE (log-corrected; S_i), station-level average carapace width (W_i), station-level average shell condition (SC_i), station-level bottom temperature (BT_i), and station-level depth (BD_i). Our full model structure, accounting for space, time, environmental, demographic, and community covariance, is then

$$B_i \sim \text{Bernoulli}(p_i) \\ \text{logit}(p_i) = Y_i + f_1(D_i) + f_2(X_i, E_i) + C_i + T_i \\ + f_3(\log(S_i + 1)) + f_4(W_i) + f_5(SC_i) \\ + f_6(BT_i) + f_7(BD_i). \quad (2)$$

All models (Table 1) were initially fitted with penalized smoothers ("select = TRUE" option for shrinkage penalization in *mgcv*; Marra and Wood 2011) to avoid overfitting, using maximum likelihood in the package *mgcv*. Models were compared using AIC values. Our most parsimonious model was then refitted using restricted maximum likelihood to calculate covariate significance (Zuur *et al.* 2009). Our final model's residuals were simulated using the *DHARMA* package (Hartig 2022); we checked our model for residual normality and independence. For our most parsimonious model, we calculated conditional values using *ggeffects* (Lüdtke 2018) for each individual model variable, while all other model variables were held at their mean values for all station-year pairs; year-intercept was fixed to 2010, a year with moderately high BCD prevalence. The calculation of conditional effects reveals individual patterns across each variable of interest, since each variable has an additive, non-interacting effect to the probability of BCD at a station. All analyses were completed using R 4.2.1 (R Core Team 2022).

Results

The spatiotemporal station-level model including both demographic and environmental information, but not community-level information, was the most parsimonious and had the lowest AIC values (Tables 2 and 3, Fig. 2). The full model, which included demographic, environmental, and community information, performed similarly ($\Delta \text{AIC} < 1$), but the addition of community-level information (cod and Tanner crab station-level presence) did not greatly improve model fit or performance (Table 2). Table 3 gives covariate significance for our most parsimonious model. Re-fitting without

Table 1. Model formulas.

Predictor	Null Model	Demo.	Demo. Environment	Demo. Community	Full Model	Covariate Type
Space (N/E)	×	×	×	×	×	
Year intercept	×	×	×	×	×	
Collection date	×	×	×	×	×	
Snow crab CPUE		×	×	×	×	Intrinsic
Mean carapace width		×	×	×	×	Intrinsic
Mean shell condition		×	×	×	×	Intrinsic
Bottom temperature			×		×	Extrinsic
Bottom depth			×		×	Extrinsic
Tanner crab pres				×	×	Extrinsic
Cod pres				×	×	Extrinsic

All models control for time (year intercept and collection date) and include a spatial component, modeled as a tensor plane of Northings and Eastings. Demographic factors (intrinsic) include station-level snow crab CPUE, station-level snow crab average carapace width, and station-level snow crab average shell condition. Environmental factors (extrinsic) include station-level bottom temperature and station-level depth. Community factors (extrinsic) are modeled as the station presence or absence of Tanner crab and Pacific cod.

Table 2. Spatiotemporal station-level model selection characteristics.

Model	Est Deg Freedom	AIC	Adj R^2	Deviance Explained
Demo. environment	56.76	3332.67	0.4	43.55
Full model	59.3	3333.1	0.4	43.63
Demo. community	57.56	3364.34	0.39	43.02
Demo.	55.78	3368.81	0.39	42.88
Null model	43.28	3626.25	0.33	37.93

Models fit with maximum likelihood estimation and penalized smoother terms. Note all models had similar deviance explained metrics and both the demographic–environmental and full models had similar AIC values (Δ AIC < 1).

Table 3. Demographic–environmental model parameters and significance estimates.

Intercept Terms	Value	Standard Error	Deg. Freedom	P value
Grand intercept	−4.3	0.28		
Year	Range: −1.98 to +2.12		31	<2E-16*
Smoother Terms	Eff. Deg. Freedom	Ref. Deg. Freedom	Chi Sq	P value
Collection date	1.89	9	4.7	.0501
Space	7.53	22	67110.32	.015*
Bottom temperature	3	9	43.22	<2E-16*
Depth	1.33E-04	9	7.23E-05	.521
Population density	4.54	9	168.42	<2E-16*
Avg carapace width	2.37	9	15.35	<.001*
Avg shell condition	0.95	9	19.3	<.001*

Model fit with restricted maximum likelihood and penalized smoother terms. Parameters that are significant ($P < .05$) are asterisked (*).

penalized smoothers led to little difference in model outcomes (Appendix B).

BCD presence was generally concentrated in the northwestern section of the trawl survey's footprint (Fig. 3a; $P = .015$), and was more common in later survey years (Fig. 3c; $P < .001$). There was a non-significant effect of collection date (Fig. 3b; $P = .0501$). Disease tended to increase later in the survey as the survey moved north and occurred later within the year.

Our most parsimonious model showed that BCD was most likely to be encountered at stations with dense populations of small, new shell crab (Fig. 4a–c). Stations with higher average shell condition were related to a decrease in the probability of encountering BCD at a station (Fig. 4c; $P < .001$). Generally, small average carapace widths were associated with increases in the probability of encountering BCD at a station, though for the smallest crab, this was not true (Fig. 4b; $P < .001$). Population size showed a non-linear relationship

with BCD presence (Fig. 4a; $P < .001$). At stations with low densities of crab, the probability of encountering BCD was low; as station-level population density reached moderate levels, the probability of encountering BCD-positive crab increased. However, further increases in station-level density were not related to further increases in the probability of encountering BCD-positive crab, indicating a potential critical snow crab density threshold needed for BCD to be established (Anderson and May 1978, Krkošek 2010, Dallas et al. 2018).

Temperature showed a non-linear relationship with BCD presence (Fig. 4d; $P < .001$). When temperatures were low, initial increases in temperature were related to an increasing probability of BCD, though after station temperature exceeded $\sim 4^\circ\text{C}$, the probability of station-level BCD presence decreased on average (Fig. 4d). Broadly, results suggest that BCD is more successful when temperatures are moderately warm (e.g. thermal mismatch hypothesis described by

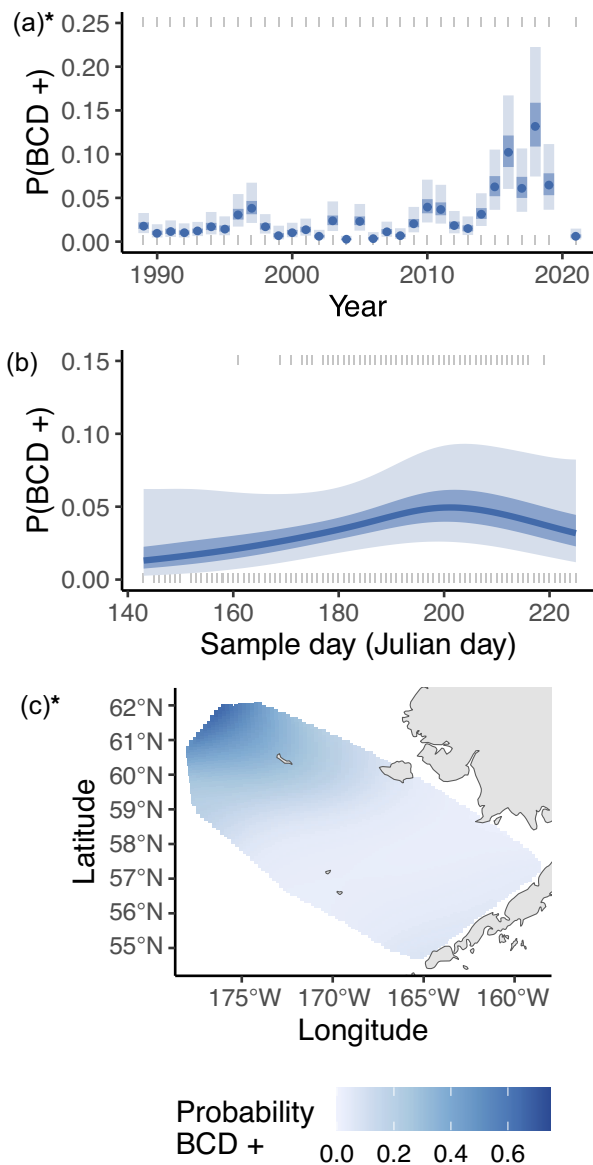


Figure 3. Conditional spatiotemporal predictions for station-level BCD. Conditional predictions for probability of station-level BCD across each spatiotemporal factor (a) year, (b) within-year collection date, and (c) collection site, when all other factors are held at their averages across all station-year pairs. For panels (b) and (c), the year-intercept is fixed to be 2010. For panels (a) and (b), dark shading gives 50% confidence interval and light shading gives 95% CI; gray dashes give data, i.e. if a station sampled in that year (panel (a)) or sampled on the day of year within a survey period (panel (b)) is BCD-positive (dash at top of panel, at least one crab at the station had BCD) or BCD-negative (BCD+ = 0). Panel (c) shows the expected spatial effect generated from a tensor plane. Asterisks give significance $P < .05$.

Cohen *et al.* 2017). However, there is a high amount of uncertainty for the highest station-level temperatures, likely because there are not many stations occupied by snow crab which exceed 4°C; this indicates that caution should be taken when predicting station-level BCD presence for the most extreme temperatures. Depth showed a non-significant pattern; model penalization removed the depth covariate from the model (i.e. $f_7(BD_i) = k$, where k is constant, Fig. 4e; $P = .521$).

Discussion

Understanding drivers of BCD spatiotemporal heterogeneity at the station-scale can provide insights into the disease ecology, management strategies, and potential future incidence (Groner *et al.* 2016). Our results showed a dome-shaped response of BCD to bottom temperature, though our model showed substantial uncertainty at the highest temperatures (>4°C). Stations with dense populations of small, new shell crab tended to have higher BCD incidence, indicating BCD is more likely to infect juvenile snow crab hosts over adult hosts. While there are several limitations to our model (see “Model limitations” section), these results suggest that future warming could decrease BCD incidence in EBS snow crab, both through direct influence of temperature and temperature-related decreases in availability of optimal hosts (Szuwalski *et al.* 2023). Since fisheries tend to target larger, mature crabs, managers might have limited ability to mitigate BCD presence via directed fisheries management; instead, considering the effects of BCD on rebuilding or recruitment into the fishery might be more appropriate management actions. Future work prioritizing more sensitive testing metrics, lab studies, and theoretical approaches could help elucidate further management concerns and insights related to BCD.

Our work largely supports past findings around the globe. Meyers *et al.* (1996) and Morado *et al.* (2010) similarly identified a positive latitude gradient in the EBS snow crab-BCD system, and Eaton *et al.* (1991) suggested a molt-related seasonality to BCD for Tanner crab in southeastern Alaska, USA. Multiple studies have demonstrated a relationship between small, dense populations of crustaceans and BCD, indicating a global life stage preference for juvenile crab (Shields *et al.* 2005, 2007, Mullowney *et al.* 2011, Behringer 2012, Lycett *et al.* 2018). Our model showed non-linear relationships between BCD presence and temperature, which differs slightly from the linear relationships between BCD and temperature previously reported (Shields *et al.* 2007, Mullowney *et al.* 2011).

Fisheries management actions might have limited success in mitigating BCD impacts

Fisheries ecology has historically emphasized population thinning and culling as a primary strategy for managing fisheries diseases, despite limited success of culling in marine systems (Dobson and May 1987, McCallum *et al.* 2004, Wood and Lafferty 2015, Prentice *et al.* 2019). In particular, parasite life history, host specificity, and population mixing all moderate the success of population thinning (Dobson and May 1987, Wood *et al.* 2014, Wood and Lafferty 2015). While our model identified that intrinsic factors, like population density, are related to BCD occurrence, our model also identified several biological limitations to reducing negative effects of BCD via population thinning.

First, there is a mismatch between fishery targeted sizes and BCD preferred host life stage, which would make population thinning ineffective. Fishery-preferred crabs are males with a carapace >101 mm; as a result, commercial crab pots selectively exclude small crabs. Moreover, fishermen actively avoid stations with high densities of juvenile crab to avoid sorting crab too small for market. BCD-preferred hosts tend to be smaller: the average size of a BCD-positive crab in our data was 56.6 mm, and 99% of BCD-positive crab identified in the survey were <101 mm. This suggests the fishery would not

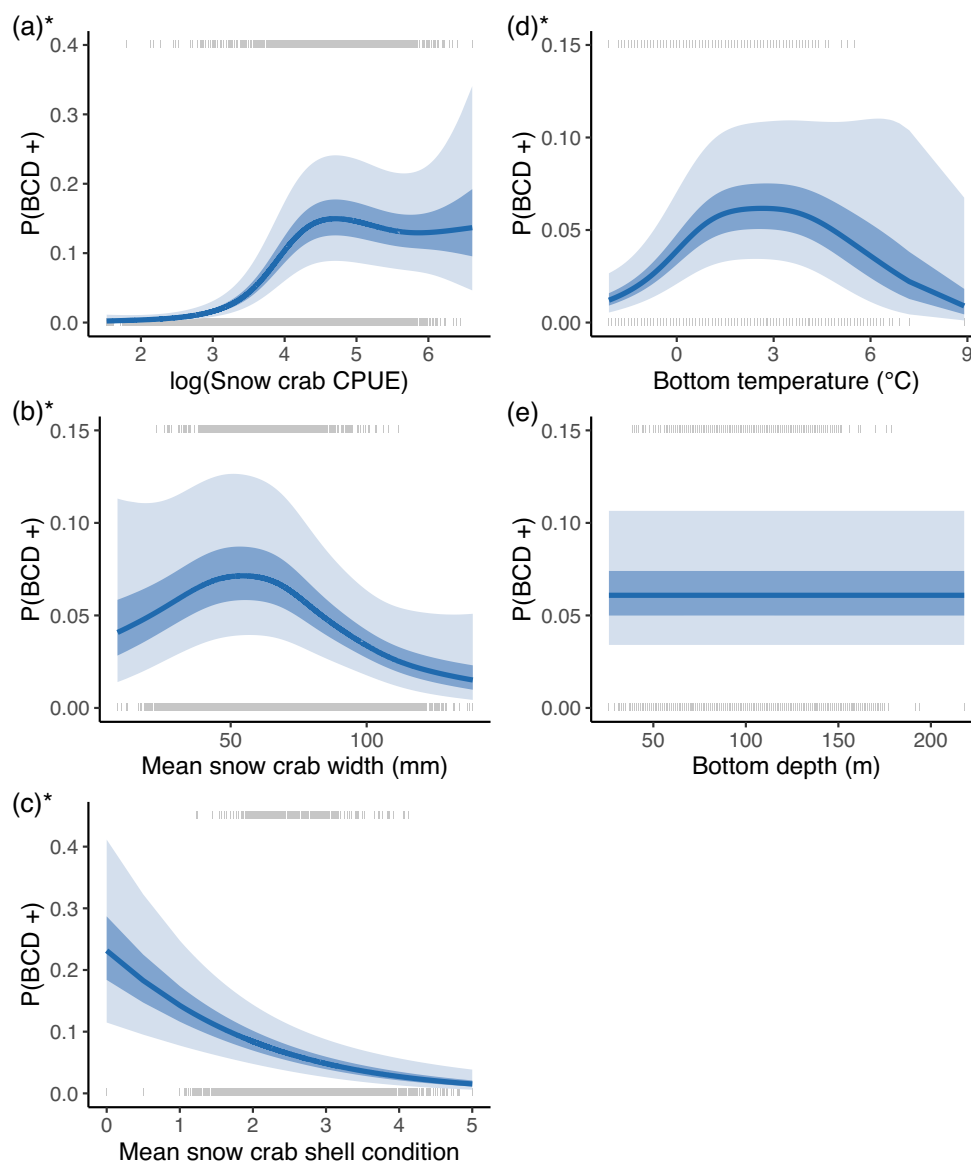


Figure 4. Conditional demographic and environmental factors predictions for station-level BCD. Conditional predictions for BCD across each factor (a) crab density, (b) station-level mean carapace width, (c) station-level mean shell condition, (d) station bottom temperature, and (e) station bottom depth, when all other factors are held at their averages across all station-year pairs and year-intercept fixed at 2010. For all panels, dark shading gives 50% *CI* and light shading gives 95% *CI*; gray dashes give data, i.e. if a station sampled at that condition is BCD-positive (dash at top of panel, at least one crab at the station had BCD) or BCD-negative (BCD+ = 0). Asterisks give significance $P < .05$.

adequately thin crab most susceptible to BCD, allowing disease to persist (Kuris and Lafferty 1992). Additionally, catching BCD-positive crab is undesirable because they are unmarketable; as a result, active culling of BCD-positive crab is not economically feasible.

Second, our model identifies a critical density threshold that exists on the station level. Without accounting for population structure, at the station level, there is a density threshold for BCD to establish; lowering below this station-level density threshold at individual stations could help reduce disease. However, most fisheries management operates at a regional level; it is not clear that the station-level density threshold identified here would scale up to some regional-level density threshold. This indicates that, even in the absence of fishery preferences and current fishery closures, population thinning would depend on station-level (local) fishing effort, a scale

smaller than current management action. Fishers would need to increase fishing by targeting stations with dense populations of juvenile crab (i.e. stations more likely to be BCD-positive) or BCD-positive crab to lower BCD presence, rather than generally increase regional-level fishing effort.

Life stage preference suggests BCD might moderate crab rebuilding and recruitment into the fishery

Our model highlights that indirect management approaches, such as using BCD statistics to help set context for management choices, might be more appropriate than direct management action (e.g. increases in fishing effort). Given that BCD preferentially infects smaller, new shell crab and is fatal, managers might expect disease to have impacts to juvenile mortality and rebuilding efforts (Mullowney et al. 2011). Years with

high BCD could have higher than expected juvenile mortality; this can be reflected through use of time-varying natural mortality and slight increases to natural mortality priors in stock assessment models to account for increased BCD-related mortality. For years with extreme BCD events, BCD mortality could be considered as an addition to natural mortality (e.g. Sagarese *et al.* 2021). Managers can also consider being more cautious (e.g. lowering total allowable catch) in years with high BCD to reflect concerns and uncertainty in juvenile survival.

Intuitively, the effects of BCD on juvenile mortality could translate into BCD altering rebuilding timelines. At the start of rebuilding, we might see low BCD prevalence because population density is low. As the population begins to increase, we would expect the snow crab population to be skewed towards small, juvenile crab, potentially leading to stronger effects of BCD mortality and potentially slowing rebuilding. For example, Siddeek *et al.* (2010) simulated BCD-positive populations and found that stocks that are heavily infected (such as Stephan's Passage and Alaska Tanner crab populations) would take longer than expected to rebuild. In contrast, EBS snow crab tend to have low annual visual BCD prevalence, which could result in little to no increase in expected rebuilding time (Siddeek *et al.* 2010); however, the existence of a density-dependent invasion threshold and more sensitive disease testing (Pestal *et al.* 2003) could moderate this expectation.

More information is needed to understand the relationship between temperature and BCD

Past work has largely suggested or assumed that increasing temperature drives higher BCD prevalence across the region (Morado *et al.* 2012, Shields 2019, Coates and Söderhäll 2021). Our model adds nuance to this by focusing on BCD niche at the local, station-level (i.e. BCD presence), rather than BCD prevalence. In our model, stations with intermediate temperatures and high snow crab density were most likely to support BCD. As station-level temperature continues increasing, we might expect declines in snow crab populations (Mullowney *et al.* 2011, Fedewa *et al.* 2020, Szuwalski *et al.* 2023), which could lead to a decreased incidence of BCD in EBS snow crab (Groner *et al.* 2016, Nova *et al.* 2022). Moreover, temperature affects snow crab phenology, especially molt timing and frequency (Shields *et al.* 2007, Dawe *et al.* 2012, Shields 2019). Past work has proposed that BCD might transmit via the crab molting process (Eaton *et al.* 1991); thus, molt timing would drive disease seasonality progression. As a result, changes to molt timing could shift BCD seasonality (Groner *et al.* 2018, Shields 2019).

Our model suggests a dome-shaped relationship between temperature and BCD; accurately describing this non-linearity could be particularly important for creating future disease projections (Maynard *et al.* 2016). The survey data period used in this study (1989–2021) lacks information about snow crab and BCD in the warmest conditions ($>4^{\circ}\text{C}$). In our station-level model, this results in substantial uncertainty about how BCD might respond to warming conditions. On average, our model predicts that temperatures $>4^{\circ}\text{C}$ are associated with decreased BCD presence. This aligns with disease ecology literature, which posits that disease dynamics show strong non-linearities in response to temperature changes, either due to intrinsic parasite limitations or altered host

availability at extreme temperatures (Lafferty 2009, Nova *et al.* 2022). Additional laboratory studies that specifically explore the relationship between extreme temperatures and BCD could supplement our model by providing mechanistic understandings of non-linearities between temperature and BCD.

Model limitations

While our model captures coarse spatiotemporal BCD patterns in the EBS, the data and model provide only a brief snapshot into BCD presence each year. The EBS trawl occurs only once a year, at a time that might not capture major transmission or mortality events related to BCD. For example, given past work suggesting transmission occurs during molting (Eaton *et al.* 1991), the summer trawl survey might miss key transmission periods during the spring molting season. Our model's reliance on visual infection underrepresents the incidence of BCD (Pestal *et al.* 2003); this is especially true in early stages of the survey, when there might not have been sufficient time for infection progression to reach the high burdens needed for visual diagnosis. Our model highlights this uncertainty in disease status for stations visited at the start of the survey within each year (Fig. 3b). Teasing apart the effects of survey design and survey movement from the ecological patterns that explain spatiotemporal BCD patterns remains a challenge. More sensitive test metrics, or repeated sampling across seasons could help identify key patterns related to transmission and mortality which managers can exploit to mitigate possible negative impacts of BCD.

Several of the metrics used as covariates might be limited in their scope. For example, station-level bottom temperature at the survey time likely reflects disease progression, rather than identifying how temperature directly affects BCD transmission or mortality (Maynard *et al.* 2016). As a result, there might be additional non-linearities between temperature and BCD spatiotemporal patterns that could be identified by understanding how temperature affects the full life cycle of *Hematodinium* (transmission, progression, and mortality). Gaining this understanding would help managers better predict future BCD patterns in the warming EBS (Lafferty 2009, Nova *et al.* 2022). Similarly, community metrics like Tanner crab and cod presence might reflect parallel responses to borealization among Tanner crab, cod, and *Hematodinium* (McLean *et al.* 2021, Mueter *et al.* 2021), in addition to possible cross-species transmission or predation-based culling. Understanding species interactions with infected crab is complex (Packer *et al.* 2003, Lopez and Duffy 2021) and likely better done by experimental approaches (e.g. Stentiford *et al.* 2001, Butler *et al.* 2014) than through spatiotemporal modeling.

In our models, we mapped station-level BCD presence, rather than the BCD-associated mortality rate. Our choice to use station-level BCD presence helps identify environments that support BCD-positive crab; this provides information about BCD disease ecology that managers can use to identify appropriate management actions to mitigate possible negative impacts of BCD. However, our model does not identify how BCD mortality interacts with or influences broader snow crab population dynamics. Accurately extrapolating between visual BCD presence during the summer and BCD-associated mortality rate is non-trivial; laboratory and field studies, which quantify BCD mortality rates across multiple temperatures would be more helpful to understand the

possible impact of BCD on population dynamics (e.g. Shields et al. 2005, Hoenig et al. 2017).

Future directions

Our model highlights that management strategies that use increased fishing effort to minimize the impacts of BCD might be unsuccessful; however, future research should consider non-fishing-effort-related strategies that might help moderate BCD. For example, ensuring fisheries are properly retaining and disposing of infected crab, when caught, is a key way to minimize spreading disease, especially for areas which have high BCD prevalence (Meyers et al. 1987, Stentiford and Shields 2005, Stentiford et al. 2012, Rebert et al. 2021). Additionally, crustacean disease research has highlighted that stress and shell damage can increase disease (Wootton et al. 2012, Davies et al. 2015, Coates and Söderhäll 2021). Considering how bycatch and fishing practices might increase stress to crabs and alter spatiotemporal BCD patterns, could allow for additional management options to mitigate possible negative impacts of BCD.

Climate change, including borealization, is expected to interact with disease in complex ways: increasing temperature shifts host distribution and host susceptibility, and non-linearly alters disease transmission, progression, and mortality rates (Lafferty 2009, Gehman et al. 2018, Shields 2019, Rohr and Cohen 2020, Nova et al. 2022). Accurately predicting future BCD incidence requires careful understanding of all these components. In particular, a better understanding of how temperature influences BCD transmission, progression, and mortality might reveal additional non-linearities that help predict future BCD occurrences. More careful understanding of temperature's influence on BCD could also help identify if BCD significantly contributes to snow crab mortality in some years; the only partitioning of snow crab mortality to specific causes, to date, did not find statistical patterns between visual BCD and snow crab mortality rates (Szuwalski et al. 2023). It is unclear the degree to which visual BCD prevalence underestimates the true BCD prevalence, and it is uncertain how quickly infected crab die in the EBS context. Using more sensitive disease tests and better estimating mortality rates of BCD could help identify the degree to which BCD interacts with or influences broader snow crab population dynamics.

Our modeling approach showed considerable uncertainty in the patterns identified (Figs 3 and 4), indicating the need for additional, higher-quality data (e.g. higher-sensitivity diagnosis, year-round data collection) or non-statistical approaches to understanding BCD. Future studies should consider theoretical, simulation, and laboratory-based methods to better understand factors that might be related to BCD. These methods can take advantage of high-quality sampling techniques (e.g. PCR testing, controlled covariates) and ecological theory to better identify which (if any) ecological and environmental covariates influence BCD, while also providing quantitative insights into BCD disease ecology, management strategy effectiveness, and snow crab population dynamics.

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Author contributions

Study conception by C.S.S. Formal analysis conducted by L.J.B. with input from all authors. Original draft of manuscript prepared by L.J.B. with revisions and edits provided by all authors.

Supplementary data

Supplementary data, including Appendix A and B, is available at the ICES Journal of Marine Science online version of the manuscript.

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Data availability

The data underlying this article are available via GitHub at https://github.com/lauriebalstad/ebs_vis_bcd, and can be accessed via the repository identified as [lauriebalstad/ebs_vis_bcd](https://github.com/lauriebalstad/ebs_vis_bcd).

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