Climate impacts and adaptation in the Dungeness crab fishery: a social-ecological systems perspective

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Abstract

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Dungeness crab (*Metacarcinus magister*, or *Cancer magister* Dana) is an iconic species on the U.S. West Coast, where it supports one of the largest and most valuable commercial fisheries, as well as culturally important recreational and subsistence harvests. Yet over the past decade, Dungeness crab fisheries have faced numerous closures from the effects of long-term ocean change and associated extreme events. My research examined climate change impacts and adaptation in the Dungeness crab fishery by exploring the changing inter-relationships within and between coupled human and ecological communities. I first considered trophic-mediated climate risk to juvenile Dungeness crab, demonstrating the value of molecular diet analysis ("dDNA") in understanding risk to, and potential adaptability of, marine species facing disrupted predator-prey relationships. I then examined Dungeness crab fishers' adaptation to an unprecedented, coastwide harmful algal bloom in 2015, which led to the most extensive closures

the California commercial fishery has ever seen. I quantified how fishers' use of certain coping and adaptative strategies varied by vessel size class and geographic region; I then asked how these strategies may have affected the distribution of climate impacts at the time of the closures, and fishing communities' vulnerability to secondary shocks. Finally, I collaboratively summarized Dungeness crab fishery dynamics in a social-ecological Qualitative Network Model. I then used this model to explore how planned climate adaptation can lead to unintended consequences for fishers' well-being, as it interacts with the effects of harmful algal blooms and fishery dynamics. I specifically considered climate adaptation strategies identified during regional, participatory scenario planning initiatives. Together, these inter- and multi-disciplinary research projects offer an integrated view of climate change in the Dungeness crab fishery, and illustrate the role of adaptation in how climate impacts manifest in marine fisheries.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

To the Dungeness crab –

and all who work to protect and preserve the waters in which they live.

INTRODUCTION

Marine food systems are being shaped by fundamental, long-term change in oceanic and terrestrial processes, as well as extreme events of increasing frequency and intensity (IPCC 2022). The year this dissertation was submitted, over 40% of the world's oceans experienced marine heatwaves (Koren 2023), defined by sea surface temperatures at least 10% warmer than the 1991-2020 average (Hobday et al. 2018). This included record high sea surface temperatures in the Gulf of Alaska, throughout the Caribbean Basin, and in the path of the Gulf Stream in the Northwest Atlantic (Gillespie 2023); off of the coasts of the United Kingdom and Ireland, in the Northeast Atlantic and North Sea (Berthou et al. 2023, McCarthy et al. 2023); and in much of the western basin of the Mediterranean Sea (Marullo et al. 2023). On the U.S. West Coast, the geographic focus of this dissertation, the 2023 commercial fishing season saw record low salmon returns that initiated multiple requests for federal disaster relief funding (Kotek, 2023; Kounalakis, 2023; Murphy and Dowd, 2023), and the loss of seasonal revenue for California Dungeness crab fishers, as elevated whale entanglement risk and poor crab condition delayed the start of the crabbing season (Bonham 2023a, 2023b). Such disruption to ecosystem services and socio-cultural relationships has severe and disproportionate consequences for fishers and their communities (USGCRP 2023).

The adverse consequences of climate change experienced by human and ecological communities are closely tied to those communities' capacity for adaptation, defined as: "the process of adjustment to … climate and its effects, in order to moderate harm or exploit beneficial opportunities" (IPCC 2022). In human systems, adaptation may be further delineated as 'adaptive maintenance,' in which adaptation maintains key processes and functions of a system, or ‘transformational adaptation,’ which creates a fundamentally new system (Barnes et al., 2017; Walker et al., 2004; Wilson et al., 2013). While adaptation is designed to help communities respond to climate change, it is increasingly recognized as itself a source of climate risk, in that it can also add to, or amplify, negative outcomes from climate change (Cinner et al. 2011, Schipper 2020, IPCC 2022).

My dissertation research considered climate change adaptation and impacts through the lens of social-ecological systems, which conceptualize coupled human-natural systems as nested, complex, and dynamic entities (Ostrom 2009, Levin et al. 2013). Social-ecological systems (SES) thinking marks a correction in Western scientific thought, which still carries the legacy of modernist perspectives of human and non-human systems as inherently separate (Latour 1993). My goal in taking a social-ecological systems approach is to acknowledge that the separation of coupled human-natural systems is arbitrary; to explicitly recognize the cross-scale linkages that affect the Dungeness crab fishery; and to emphasize feedbacks between individual behaviors and emergent, macroscopic properties of, or outcomes for, the fishery. However, while SES thinking greatly expands scientific capacity to understand coupled human-natural systems, many SES methodologies, including those that I employ, are still rooted in an entity- and stability-focused ontology which can undertheorize the evolving roles of power, agency, and other social processes (West et al. 2020, Mancilla García et al. 2020). In light of these limitations, it is particularly important to contextualize this body of research as only one of many perspectives that are needed to develop climate adaptation in marine food systems.

The Dungeness crab (*Metacarcinus magister*, or *Cancer magister* Dana), is an iconic species in U.S. West Coast food systems, supporting one of the largest and most valuable commercial fisheries. With over 25% of all West Coast commercial fishing vessels participating in the Dungeness crab fishery, annual landings have averaged 23,000mt for the past decade, worth approximately $155 million in annual ex-vessel revenue (Pacific Fisheries Information Network, pacfin.psmfc.org). The recreational and subsistence harvest of Dungeness crab is also culturally and socially important to coastal communities (Ritzman et al. 2018, Buckner et al. 2020), particularly tribal communities (Buckner et al. 2020, Nelson 2021, Kourantidou et al. 2022) which have harvested shellfish on what is now the U.S. West Coast since time immemorial.

Figure 0.1. Adult male Dungeness crab in a tank at Friday Harbor Seafood, WA

A number of entities and interactions, both within and beyond those directly involved in the commercial fishery, drive change in Dungeness crab populations and affect the well-being of the people who harvest them. Commercial Dungeness crab harvest is governed at the state and tribal level; the 1976 Magnuson-Stevens Fishery Conservation Act (16 U.S.C. et.seq.) granted management authority for Dungeness crab commercial and recreational fisheries to the States of Washington, Oregon, and California under the Pacific States Marine Fisheries Commission tri-state process. In 2017, after being extended three times, the States' management authority was made permanent by the West Coast Dungeness Crab Management Act (16 U.S.C. 1856). In Washington State, Dungeness crab fisheries are co-managed by the State and the Northwest Treaty Tribes, with 50% allocation to each, according to treaties signed in the 1850s and eventually enforced by the 1994 Rafeedie Decision (*United States of America v. State of Washington* 873 F. Supp. 1422, 1994). Other fisheries managed at the state or federal level are also part of the diverse portfolios of commercial Dungeness crab fishers (Fuller et al. 2017, Holland and Leonard 2020). In addition, while adult crab inhabit deeper marine benthos, the species' planktonic larvae, and benthic juvenile and sub-adult phases, inhabit pelagic, estuarine, and nearshore habitats, respectively (Gunderson et al. 1990, Armstrong et al. 2003), moving through a patchwork of governance structures and an array of environmental stressors.

My first chapter focuses on Dungeness crab themselves, considering the role of trophic interactions in mediating the impacts of long-term ocean change. This work was in response to research needs identified by members of the Pacific Northwest Crab Research Group, detailed in their 2020-2025 Research Guide (Buckner et al. 2020).

My second and third chapters are organized around an unprecedented, coastwide harmful algal bloom (McCabe et al. 2016) which closed commercial Dungeness crab fisheries in 2016 and 2017, disrupting important social-ecological relationships. Working with researchers at the Northwest Fisheries Science Center, and leaning on the rich context provided by interviews, surveys, and local news reporting (Callahan 2017, Ritzman et al. 2018, Moore et al. 2020), I used large fishery-dependent data sets to quantify how California crab fishers' adaptive responses to the fishery closures varied according to fishing vessel size and geographic region. In my second chapter, I also used fisheries participation networks (Fuller et al. 2017) and network theory to describe the implications of altered fishing activity patterns for community vulnerability to secondary shocks. In my third chapter, I explored how negative side-effects of spatial diversification may have contributed to unequal economic impacts to small vessel operators.

My fourth chapter looked further into how unintended consequences arise from climate adaptation. With members of the Ocean Modeling Forum's Climate and Communities Working Group, I used a qualitative modeling framework to explore how climate adaptation in response to a harmful algal bloom (HAB) may interact with Dungeness crab fishery dynamics to amplify the impacts of a HAB. Whereas the first three chapters of my proposal are fundamentally objectivist and focus on observable or physical dimensions of environmental change, my final chapter tends more toward a constructivist epistemology (Moon et al. 2021), drawing on expert knowledge and experience, and published socio-economic research.

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Chapter 1. CLIMATE RISK TO JUVENILE DUNGENESS CRAB FROM CHANGING ESTUARINE PREY COMMUNITIES

1.1 ABSTRACT

Changing prey quantity and quality associated with climate change can negatively affect the growth and survival of predator populations. Projecting such trophic-mediated risk from climate change relies on diet information of adequate breadth and taxonomic resolution. Yet obtaining consumption data through traditional methods like visual analysis of stomach contents can be challenging for certain species and life history stages. Juvenile Dungeness crab (*Cancer magister*) that have recently settled out of their larval stage into intertidal habitats (age 0+) rely on adequate food resources to maintain high rates of growth and molting, but there is little diet information in the published literature to consider trophic-mediated risk for this life history stage. We used DNA metabarcoding to identify a diverse range of taxa in the stomach contents of juvenile Dungeness crab at the early instar stages (5-15mm carapace width), overcoming challenges for visual analysis associated with the size and degree of mastication of crab prey. We identified 142 unique taxa in the stomach contents of 58 juvenile crab collected in three estuaries in the northern Puget Sound, WA. These included unicellular algae and protists, as well as taxa belonging to13 different phyla and two classes of multicellular organisms. Our results agreed with prior visual analysis for larger age 0+ Dungeness crab, which emphasized the consumption of crustaceans and molluscs. We further provided new direct evidence of a high degree of omnivory in juvenile crab diet, and documented the presence of a number of species composed of soft-tissue that have not been identified in prior work. Interpretation of our results underscored the limitations of DNA metabarcoding in distinguishing between predation - including

cannibalism - incidental ingestion, and secondary predation, but we suggest that juvenile crab ≤ 15mm carapace width are likely scavengers and detrivores. We then demonstrated the application of diet information produced by DNA metabarcoding to assessments of trophic-mediated climate risk, by calculating the risk from ocean acidification (OA) conferred by putative prey taxa. Arthropods and molluscs, particularly the gammarid amphipods *Monocorophium* spp. and the native shore crab *Hemigrapsus oregonensis*, conferred high risk to juvenile crab, while macroalgae, annelid worms, and unicellular taxa conferred medium to low risk from ocean acidification. While the taxonomic diversity in crab diet contained a number of existing prey items expected to experience little to no negative impacts from ocean acidification, field and laboratory experiments suggest that a wholesale shift in crab diet to only those taxa conferring low OA risk may have negative implications for juvenile crab growth and molting frequency due to lower prey energy densities.

1.2 INTRODUCTION

Rising ocean temperatures, ocean acidification, and oxygen depletion of coastal waters are drastically changing coastal environments, driving shifts in the growth, survival, and reproduction of marine species. Individual- and species-level responses to climate change have the potential to alter interspecies interactions, including predator-prey relationships. When prey decline in abundance or in energy content (Siddon et al. 2013, Von Biela et al. 2019, Piatt et al. 2020), or when spatial mismatches arise between predator and prey distributions (Selden et al. 2018, Moullec et al. 2019), predator populations can face severe negative consequences. Accounting only for the direct impacts of climate change, without considering effects from altered predator-prey interactions, may underestimate climate risk for a particular species.

Describing predator-prey interactions when predation cannot be directly observed largely depends on visual identification of stomach contents (Symondson 2002). However, this approach can be challenging for particular predator species and/or life history stages, including those which have specialized feeding apparatuses that thoroughly macerate prey (e.g., a gastric mill; McGaw & Curtis, 2013), those foraging on prey items or body parts composed of soft tissue, or those consuming micro or cryptic species (Symondson 2002, de Sousa et al. 2019). DNA metabarcoding for diet analysis ("dDNA") is an increasingly popular technique to simultaneously identify a portfolio of prey items from stomach contents, by amplifying a short, highly variable DNA sequence universal to life (de Sousa et al. 2019). dDNA may therefore be a powerful tool in advancing our understanding of climate risk mediated by predator-prey relationships.

As an economically and socio-culturally important species on the U.S. West Coast, Dungeness crab (*Cancer magister*) has been the subject of numerous laboratory experiments and field studies seeking to predict and measure the direct impact of individual and interacting climate stressors (most recently, Durant et al., 2023; McElhany et al., 2022; Schram et al., 2023; among other previous works cited in Berger et al. 2021). However, highly limited *in situ* diet information at earlier life stages has constrained evaluation of the climate risk to Dungeness crab from changing prey availability. Existing diet information for age 0+ juvenile Dungeness crab is derived primarily from studies which were completed in experimental enclosures (Jensen and Asplen, 1998; Palacios, 1994), which derived diet from indirect measures of putative prey abundance (Ruiz 1987), or which only evaluated stomach contents of crab above 30mm in size (Stevens et al. 1982). This is due in large part to the difficulty of visual stomach content identification for decapod crustaceans like crab, which shred their prey while eating and possess a gastric mill to further grind down ingested material (Stevens et al. 1982, McGaw and Curtis 2013, Thomas et al. 2020); visual analysis is further complicated at small early life history stages consuming even smaller prey (Stevens et al. 1982, Amundsen and Sánchez-Hernández 2019).

What diet information we do have suggests that Dungeness crab are generalist predators and scavengers, as is common in most crab species. Generalist or omnivorous diets can make predators resilient to changes in prey availability (Gutgesell et al. 2022, Goodenough et al. 2023); however, as was observed during the 2014-16 North Pacific marine heatwave, when novel prey assemblages have low energy densities, predator populations can suffer high mortality (von Biela et al. 2019, Piatt et al. 2020). The risk of decreased survival and growth associated with lower-energy prey may play a particularly outsized role in early instar stages for juvenile Dungeness crab, when crab have just settled out of the megalopa stage into intertidal habitats. During these early instar stages, juvenile crab grow quickly and molt frequently, benefiting from increased survival if they obtain a size refuge from predation at an earlier age (Fernández 1999). Both growing and molting are energy intensive processes; limited food resources during early juvenile stages has been found to significantly limit growth and to decrease molting frequency (McLean and Todgham 2015). Dungeness crab larval settlement into the juvenile stage occurs from mid-summer to early fall, and so higher water temperatures during this time also drive increased growth - and therefore greater energetic needs (Armstrong et al. 2011).

We first used DNA metabarcoding of the cytochrome oxidase I (COI) mitochondrial gene region to describe diet variability in early juvenile Dungeness crab (age 0+; J1-J4 instars) collected from three major estuaries in the Puget Sound, WA. Ours is the first analysis for this size class which resolves putative prey items to species. We then demonstrate how taxonomically-rich diet profiles from DNA metabarcoding can be applied to evaluations of climate risk associated with changing predator-prey relationships, by calculating the risk to juvenile Dungeness crab from the impacts of ocean acidification on prey survival.

1.3 METHODS

1.3.1 *Sample collection*

We collected juvenile Dungeness crab (age 0+) at seven sites around the northern Puget Sound, WA, in July and August 2021 (Table 1.1, Figure 1.1). Crab were collected opportunistically following the methods of the Swinomish Crab Abundance Monitoring Program (Grossman et al. 2021). In short, we excavated the top 3-5 cm of sediment and sieved the sediment through a 4mm mesh bag; the remaining contents were searched for juvenile crab on a sorting tray. Collected crab were euthanized immediately on dry ice; invertebrate research is not subject to review by the Institutional Animal Care and Use Committee, but we determined this to be the most humane method of collection available per the 2020 American Veterinary Medical Association guidelines and related literature (Morgan et al. 2001, Waterstrat and Pinkham 2005). Juvenile crab ranged in size from 5-15 mm carapace width (Figure 1.1), and fell within J1-J4 instar stages (pers. comm. Sarah Grossman and Claire Cook, Swinomish Indian Tribal Community Dept of Fisheries).

Table 1.1. Sampling sites in the northern Puget Sound, WA (South to North), and associated sample sizes. The number of crab with putative prey represents the number of crab sequenced which also had identifiable taxa in the stomach contents. Carapace width (measured to the nearest 0.5mm for each crab) is a standard measure of crab size. For each site, we also report the dominant vegetation and substrate (by percent cover), as well as the alpha (α) diversity of stomach contents across all crab collected from that site (calculated first from all identified taxa, and then excluding any unicellular organisms).

Estuary	**Site**	**Date(s)**	**Crab sequenced (with putative prey)**	**Mean carapace width (mm)**	**Dominant vegetation**	**Dominant substrate**	**Alpha diversity (multi-cellular taxa)**
Port Susan Bay	Kayak Point 1	7/23/2021 8/6/2021 8/19/2021	12 (12)	8.58 ± 1.68	*Zostera marina*	Sand	59 (41)
	Kayak Point 2	8/6/2021	11 (10)	8.55 ± 1.79	Algae (green blade)	Cobble	58 (42)
Padilla Bay	March Point	8/21/2021	12 (10)	10.60 ± 3 .25	*Z. marina* / Algae (green blade)	Sand	41 (29)
	National Estuarine Research Reserve (NERR)	8/7/2021 8/8/2021	2 (2)	11.25 ± 3.18	*Z. marina*	Sand	24 (16)
Samish Bay	Samish Island	8/22/2021	11 (11)	9.27 ± 2.77	Algae (green filament)	Sand	32 (24)
	Oyster Creek /Samish Bay	8/9/2021 8/10/2021	2 (2)	8.50 ± 2.12	*Z. marina*	Sand	16 (13)
	Larrabee	8/11/2021	11 (11)	8.86 ± 2.24	*Z. marina*	Sand	60 (49)

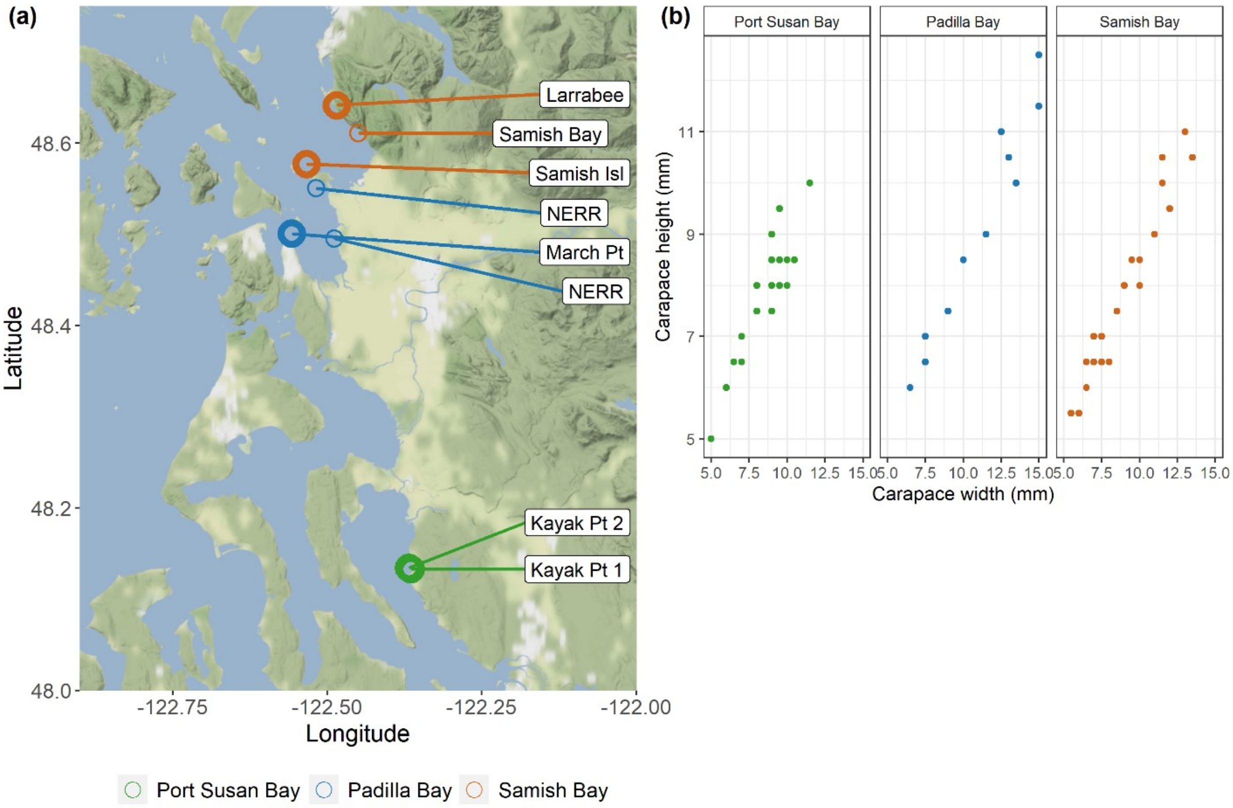

Figure 1.1. Sampling metadata, including **(a)** locations around the northern Puget Sound, colored by estuary (smaller points represent locations where only 1-2 crabs were sequenced), and **(b)** carapace width and height (mm) of each crab collected. The two NERR sampling locations labeled on the map (total n = 2 crabs) were aggregated for analysis.

We also evaluated habitat at each site by conducting a 30m transect survey using a $0.25m^2$ quadrat divided evenly into $0.5m^2$ squares (modified from Grossman et al. 2021). Every 7.5m, the following were recorded: (1) percent cover of algae and the eelgrass species *Zostera marina* and *Z. japonica,* as the number of $0.5m^2$ squares (out of 25) which had at least one rooted plant / alga; (2) density of the two eelgrass species, as the number of rooted plants in each of five diagonal $0.5m^2$ squares; and (3) substrate composition, as the percent total area in the $0.25m^2$ quadrat with one of seven size classes of substrate - cobble, coarse gravel, fine gravel, sand, mud, shell, and other (Wentworth 1922, Grossman et al. 2021). We used this information to identify the dominant vegetation and substrate for each site (Table 1.1).

1.3.2 *DNA extraction*

Crabs were stored at -80C until we dissected their stomachs, which were then stored in a -20C freezer. Stomach fullness was ranked at the time of dissection as 0 (empty / nearly empty), 1 (half full), or 2 (full). All dissection tools were sterilized between each individual with 20% NaClO, 100% etOH, and flame. To extract DNA from stomach contents, we either washed contents out of the stomach and discarded the stomach wall (fullness > 0) or extracted DNA from the intact stomach (fullness = 0) using the Qiagen DNEasy Blood & Tissue Kit (Qiagen Corp., Valencia, CA, USA), with some modifications.

1.3.3 *DNA metabarcoding*

We completed DNA metabarcoding using a two-step PCR protocol modified from Jacobs-Palmer et al. (2021). The first PCR step used a non-indexed, highly degenerate primer (mlCOIintF-XT/jgHCO2198; Leray et al., 2013; Wangensteen et al., 2018) to amplify a 313bp segment (“Leray fragment”) of the mitochondrial cytochrome oxidase subunit I (COI) marker. We chose this primer set because it amplifies a range of eukaryotic phyla (Leray et al. 2013, Jacobs-Palmer et al. 2021); has increased universality as a result of the higher number of degenerate bases and the addition of two inosine nucleotides (Wangensteen et al. 2018); and was tested in shallow marine benthos, which included small metazoan taxa (e.g., small arthropods) that have been observed in gut contents of Dungeness crab slightly larger than those analyzed here (Stevens et al. 1982). The PCR reaction contained 5X Platinum II Buffer + 1X Platinum II Taq (Invitrogen, Waltham, MA, USA), 8mM dNTPs, and 10uM each of the forward (mlCOIintF-XT) and reverse (jgHCO2198) primers. After an initial denaturation step (95C for 2 minutes), we ran the PCR for 35 cycles (95C, 45C, for 1 minute each), followed by a final extension at 72C for 5 minutes. We amplified all DNA samples in three separate reactions to produce three technical replicates per crab stomach. PCR product was visualized on a 1.5% agarose gel, cleaned to remove primer dimers using Mag-Bind Total Pure NGS beads (Omega Bio-Tek, Norcross, GA, USA), and quantified using Quant-iT dsDNA High Sensitivity Assay Kit (ThermoFisher Scientific, Waltham, MA, USA). We then diluted all samples with high enough concentrations of cleaned amplicon to 10ng DNA in 11.25uL by adding the appropriate amount of UltraPure DNase/RNAse-free water (Fisher Scientific, Pittsburgh, PA, USA).

The second PCR added identical index sequences (6-base pair nucleotide tags; IDT for Illumina DNA/RNA UD Indexes Set A) to the 3' and 5' ends of the amplicons using 1X HiFi HotStart Ready Mix (KAPA Biosystems, Wilmington, MA, USA) and 11.25uL of diluted (high concentration samples, >0.89 ng/uL) or pure (low concentration samples, ≤ 0.89 ng/uL) amplicon. We varied the number of PCR cycles for this second step between 5, 8, and 12 depending on amplicon concentration. Unique index sequences were used for each technical replicate. Indexed amplicons were visualized on a 1.5% agarose gel, cleaned, and quantified using the same procedures as the first PCR step. The same two-step PCR process was completed for a positive control (a DNA sample from kangaroo, genus *Macropus*), a PCR negative control, and a DNA extraction negative control. Positive and negative controls from across DNA extractions / PCR plates were pooled prior to indexing, so that each sequencing run contained one positive control sample and one negative control sample.

We pooled indexed amplicons and controls for 2x300 (paired end) sequencing on an Illumina MiSeq v3. The first sequencing run included n=31 crab (93 total samples) plus controls, and was completed by the University of California, Los Angeles' Technology Center for Genomics & Bioinformatics. The second run of sequencing included n=30 crab (90 technical replicates) plus controls; we prepared this sequencing run using the MiSeq Reagent Kit v3 600-cycle (Illumina, San Diego, CA, USA) , and conducted sequencing at the University of Washington's Center for Environmental Genomics Laboratory.

1.3.4 *Identification of stomach contents*

Demultiplexed sequencing data was processed in RStudio using custom R scripts calling third-party programs. Briefly, we used *cutadapt* (Martin 2010) to remove Nextera indices and PCR primers from DNA sequences, trimmed sequences according to base call quality, merged datasets across sequencing runs, and then used DADA2 (Callahan et al. 2016) to identify amplicon sequence variants (ASVs). DADA2 was run using default parameters (truncQ=2, maxEE=2); because we expected sequencing data to be dominated by Dungeness crab (predator) DNA, with the potential for prey sequence variants to be present at low frequencies, we used pseudo-pooling when running the core DADA2 sample inference algorithm. This allows information to be shared among samples, before samples are processed independently (Callahan et al. 2016). DADA2 output was then filtered to remove ASVs in controls, technical replicates with a low number of reads, and technical replicates with high Bray-Curtis dissimilarity from other replicates of the same crab. We filtered technical replicates by fitting each replicate to a normal distribution of reads / dissimilarities, and discarding those replicates outside of the 95% confidence interval (Gallego et al. 2020). Filtered ASVs were assigned to known taxa using NCBI's BLAST database, with *blastn* in the Ubuntu LTS app terminal. We ran *blastn* with a minimum percent identity of 85% and e-value of $1e^{-30}$, and a word size of 15.

From the taxonomy returned from the BLAST database, we conservatively removed (1) classifications annotated only to the level of class or phylum; (2) all ASVs identified as Dungeness crab (predator; Figure S1.1); and (3) ASVs assigned to non-target taxa (i.e., bacteria, fungi, amoeba, parasites). This produced a dataset of putative prey items. Taxa identified in two or more crab, and all insects, were then filtered manually for potential mis-identifications using the published literature alongside the World Register of Marine Species, Algae Base, Diatoms of North America, the Global Biodiversity Information Facility, and the Washington State Department of Health website (Washington State Department of Health 2022). We screened taxa that did not have Washington State / the Salish Sea as part of their known distribution. Manually screened taxa were nearly all present in only two crab, with the exception of the non-native brown algae *Hormosira banksia*; identifications for this species were changed to the respective order, *Fucales*, for which there are a number of known species in the Salish Sea.

1.3.5 *Exploring stomach content variability*

Prior to calculating diet-based risk from ocean acidification, we needed to investigate spatial and size-based variability in stomach contents. This informed our decision of whether to calculate the exposure component of risk for the entire dataset, or for subgroups of crab.

We first evaluated spatial variability in stomach contents by comparing the diversity of taxa within (alpha diversity) and between (beta diversity) the seven collection sites and three estuaries, according to taxa presence/absence information (R package *vegan*; Oksanen et al., 2022). We also evaluated zeta diversity decay among sites with the R package *zetadiv* (McGeoch et al. 2019). We then used a PERMANOVA to test for significant differences in stomach content composition, using both presence/absence data (Jaccard distance), and the eDNA index (Bray-Curtis distance; Guri et al., 2023). As an index of relative amplicon proportions, the eDNA index allows additional information from sequence read counts to be used in assessing differences between groups, without erroneously conflating amplicon abundance with true DNA abundance (Kelly et al. 2019). To calculate the eDNA index, we summed sequence reads for each taxon across technical replicates for a given crab, and divided by the number of technical replicates for that crab; this helped account for different technical replicates remaining per crab after filtering steps. Statistically significant PERMANOVA results were explored with a PERMDISP, to determine whether significance reflected true differences in group composition (as opposed to variation in sample dispersion between groups), and with post-hoc Tukey's HSD pairwise tests to explore which site or estuary differences were driving the PERMANOVA result. For the PERMANOVA, PERMDISP, and post-hoc testing, we removed rare taxa (those present in fewer than three crab stomachs, or ~5% of samples) prior to analysis; this left 57 putative prey taxa in the dataset (40 multicellular, 17 unicellular).

We explored two questions regarding changes in stomach contents associated with crab size. We first hypothesized that stomach contents would be more similar between crab that were of similar sizes; to test this, we used a beta regression with a logit link, for which the response variable was the Bray-Curtis distance between any two crab, calculated from eDNA index values (without rare taxa, as for the PERMANOVA). The regression was conducted using the *betareg* R package (Cribari-Neto and Zeileis 2010, Grün et al. 2012), using the maximum likelihood and bias correction / reduction estimators; when all three estimators provided similar results, we reported only the maximum likelihood output. We used Akaike's and Bayesian Information Criteria to identify the most informative of three nested models: one in which the predictor variable was the absolute value of the difference in carapace widths between the two crab, a second which added a binary predictor variable describing whether the two crab were collected from the same estuary, and a third which included an interaction term between these two predictors. We only included data for crab which had at least one putative prey taxon in common, such that the response variable ranged from [0, 1.0). Three crab had the same single taxon in their stomach contents, giving a Bray-Curtis distance of zero; to these distances we added a small fraction ($1x10^{-10}$) to run the beta regression.

We then sought to determine whether size-based variability in stomach contents was driven by the presence of any particular taxa. We conducted a constrained correspondence analysis (CCA) on the stomach content matrix with eDNA index values (which are relativized to the same scale), with carapace width as the explanatory variable. We used the resulting ordination to identify taxa with particularly high or low scores along the constrained component, and ran a permutation test for the CCA (10,000 permutations; Oksanen et al., 2022) under the reduced model to determine whether the constrained or canonical axis explained significantly more variability than would randomly occur (Legendre et al. 2011, Legendre and Legendre 2012, Oksanen et al. 2022). To gain a more detailed understanding of how each taxon's abundance functionally changed with carapace width, we also fit a zero-and one-inflated Dirichlet regression using a mixture model from the R package *zoid* (Jensen et al., 2022; Ward et al., 2022); this allowed us to estimate the mixture proportions of putative prey taxa, for each carapace width. Mixture proportions were estimated using Bayesian sampling with standard normal priors for the carapace width covariate (Jensen et al., 2022) from a stomach content matrix comprised of the proportion of sequence reads per taxon (columns), for each crab (rows). We ran the model with four chains with 5000 iterations. We then relativized mixture proportions within each taxon to the smallest carapace width in which that taxon was present, to visualize how each putative prey taxon's estimated mixture proportions changed with increasing carapace width. Relativization also prevents the comparison of absolute mixture proportions between taxa; we did not adjust for key species-specific biases in observed sequence read abundance that arise from PCR processes, and so such comparisons would be inappropriate (Kelly et al. 2019, Shelton et al. 2023).

For both the CCA and the mixture model, we used a more conservative threshold to exclude taxa from the analyses that were present in fewer than ten crab stomachs, leaving eight taxa (both unicellular and multicellular) in the dataset. This was necessary for the mixture model because the *zoid* algorithm for Markov Chain Monte Carlo sampling has difficulty identifying initialization values for sparse matrices. The higher threshold also helped account for the tendency of the chi-square distance measure used for the CCA to upweight rare species.

As discussed further in the results, we detected a number of unicellular organisms in crab stomachs, including those which commonly occur as small phytoplankton and zooplankton in marine and brackish waters. Field observations suggest juvenile Dungeness crab may forage for filamentous diatoms, and laboratory studies have shown it is possible for J1-3 instars to grow and molt on a diet of pure diatoms (Jensen and Asplen, 1998); however, there is some question about the energetic value of small phyto- and zooplankton to juvenile crab *in situ*. We therefore calculated diversity indices, and ran the PERAMANOVA and beta regression separately for all versus only multicellular taxa; to more clearly communicate which putative prey taxa we include for each analysis or figure, we specify whether the component data included “all,” “unicellular,” or “multicellular” taxa.

1.3.6 *Calculating risk from OA impacts to prey survival*

We define trophic-mediated ocean acidification (OA) risk to Dungeness crab as a combination of (1) crab exposure to estimated changes in putative prey availability driven by

OA, and (2) the potential sensitivity of crab growth to those changes. We quantified OA risk conferred by each of 57 taxa identified from the stomach contents of at least three crab (as for the PERMANOVA). We first calculated an index of crab exposure using the frequency of occurrence of each taxon detected in crab stomach contents, and the impact of OA on the given taxon; therefore, the index of exposure is essentially the OA impact on a given taxon, weighted by the frequency of that taxon in crab stomach contents. OA impact to putative prey taxa was drawn from the database prepared by Busch and McElhany (2016), who summarized OA impact for functional groups of marine taxa using "survival scalars." Busch and McElhany's raw survival scalar is a summary statistic which describes the direction and the degree to which survival of a functional group is affected by increased CO_2, while also accounting for similarity in responses among taxa within a functional group, and the overall amount of information available for the group (Busch and McElhany 2016). We re-scaled raw survival scalars by range, such that taxa with the greatest negative impact from OA received a score of "1," while those with the least negative (or positive) impact from OA received a score of "0." We then used energy density of each putative prey taxon as a proxy for crab sensitivity. We identified energy densities using the published peer-reviewed or gray literature; when energy densities were not reported in J/g AFDW (ash-free dry weight), we found and applied published conversion factors. Published energy densities could not be found for the rotifer *E. dilatata* (n=16 crab), the hydrozoa genus *Leptothecata* (n=8 crab), and the flatworm *Polycistidae* (n=3 crab).

1.4 RESULTS

We identified 142 unique taxa (hereafter, "putative prey") from the stomach contents of 58 juvenile Dungeness crab, out of the 61 crab prepared for sequencing (Table 1.1). 58% of the putative prey taxa were identified to the species level. On average, 95.8% of amplicon sequence variants (ASVs) from each laboratory sample were successfully matched to NCBI's Blast database; an average of 87.8% of these represented Dungeness crab DNA (Figure S1.1).

1.4.1 *High diversity and individual variability in stomach content composition*

Of the 142 taxa identified in crab stomachs, 34 were unicellular organisms representing four phyla and five classes (62% identified to species level), and 108 were multicellular organisms representing 13 phyla and two classes (56% identified to species level). Saturation curves for each estuary showed that our sampling achieved an apparent plateau in taxonomic richness only at Port Susan Bay, and only when excluding unicellular organisms; overall, novel taxa still appeared in the dataset with over 40 crab sampled (Figure S1.2). The Larrabee site in Samish Bay had the highest alpha diversity (α=60 all taxa; α=49 excluding unicellular taxa) for stomach contents, while the Oyster Creek site in Samish Bay had both the lowest alpha diversity (α=16 all taxa; α=13 excluding unicellular taxa) and sample size (n=2 crab; Table 1.1). Each individual crab had an average of eight unique taxa in its stomach contents including unicellular organisms, and an average of seven taxa excluding unicellular organisms (Figure S1.3).

Arthropods represented the majority of taxa identified in crab stomachs (~25%), and members of this group were among the most frequently occurring (Figure 1.2; Table S1.1): the gammarid amphipod *Monocorophium ascherusicum* (FO = 77%) and the barnacle *Balanus crenatus* (FO=39%) were the two most common taxa in crab stomach contents. Molluscs also had a relatively high median frequency of occurrence (FO=3.57%) among the prey groups summarized in Figure 1.2, and were also represented by a high diversity of unique taxa (n=15 taxa), as were brown algae within the class *Phaeophyceae* (Table S1.1). Altogether, *Chlorophyta*, which included only two unique taxonomic identifications, had the greatest median frequency of occurrence (FO= 8.04%); in contrast, annelid worms were represented by a large number of taxa (n=21), but had the lowest median frequency of occurrence (FO=1.79%). Among unicellular organisms, the unicellular algae *Raphidophyceae* had the highest median frequency of occurrence (FO=6.25%), followed by diatoms in *Bacillariophyta* (FO=5.36%), *Cryptophyceae* (FO=4.5%), and *Foraminifera* (FO=3.57%; Figure 1.2b). There were a number of taxa (n=87) that were identified in only one crab, with these rare taxa particularly represented within *Insecta* (seven out of eight taxa), *Rhodophyta* (three out of four taxa), and *Bryozoa / Nemertea / Chordata* (two out of every three taxa).

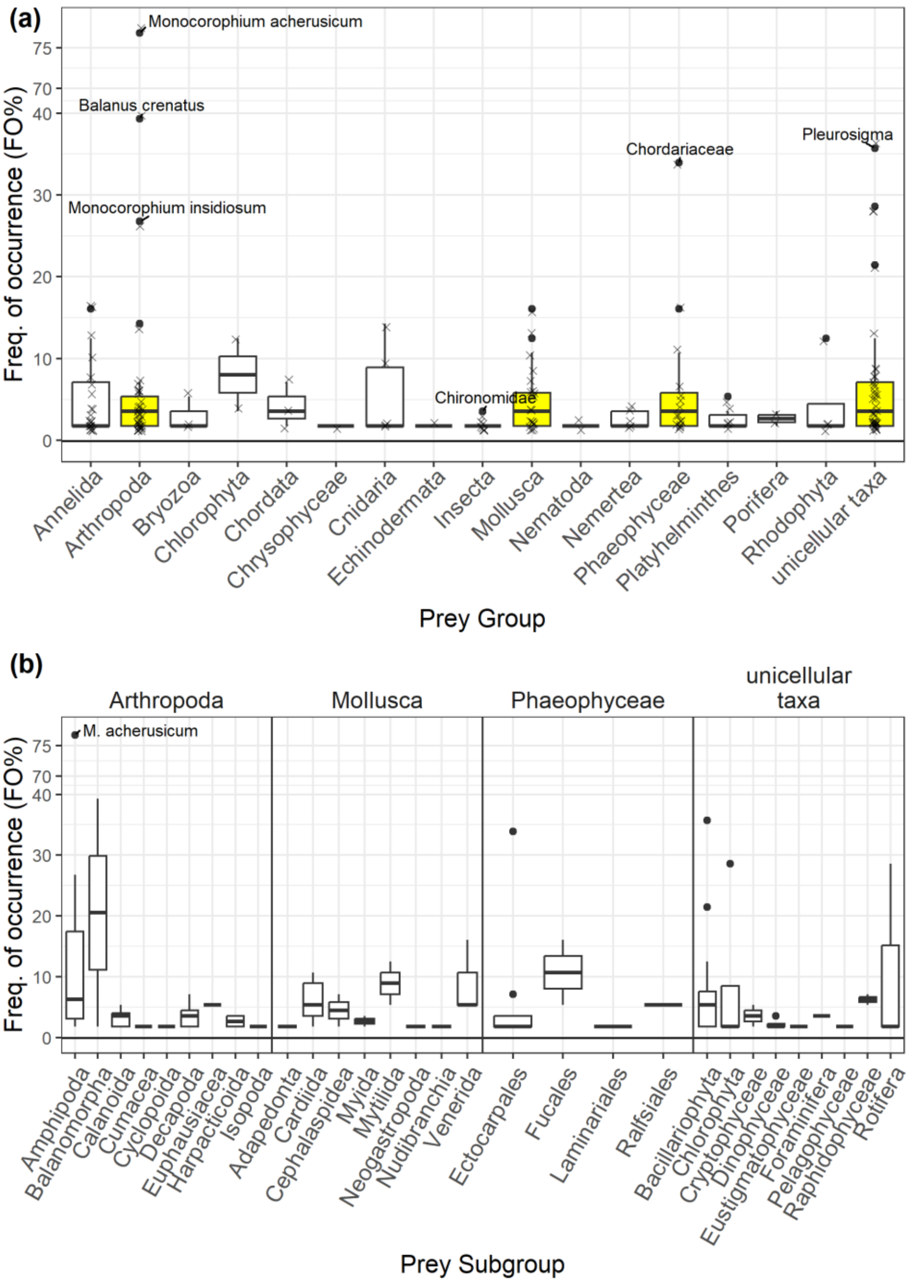

Figure 1.2. Frequency of occurrence (FO) as the percent of crab in which a given taxon was detected, summarized across **(a)** putative prey groups (phylum, or class when phylum was not available or spanned aquatic and terrestrial taxa); and **(b)** subgroups for four putative prey groups with among the highest median frequencies of occurrence highlighted in yellow in (a): Arthropoda (excluding terrestrial insects) and Mollusca, for which subgroups are orders, and Phaeophyceae and unicellular organisms, for which subgroups are classes. Specific taxa with high frequency of occurrence are labeled in (a); notably, the invasive amphipod *Monocorophium*

acherusicum is an outlier when frequencies of occurrence are summarized at both higher taxonomic levels, phylum (a - Arthropoda) and order (b - Amphipoda).

We considered both beta and zeta diversity to capture diet variability across space. Beta diversity was similar between all pairwise comparisons of the three estuaries (β = 0.208 - 0.234; Table 1.2). In Samish Bay and Padilla Bay, pairwise beta diversities between sites were similar for within- and between-estuary comparisons (Table S1.2). In contrast, the two Kayak Point sites within Port Susan Bay had the highest beta diversity observed among all estuary- and site-level comparisons (β = 0.396; Table S1.2). Pairwise beta diversity at both the site- and estuary-levels tended to be lower when unicellular organisms were removed from the dataset (i.e., diet composition was more similar between site and estuary pairs for multicellular than for unicellular taxa), but these changes were relatively small (Figure S1.4). Zeta diversity across all collection sites declined exponentially, with almost complete turnover in prey composition achieved between 4-5 collection sites (Figure S1.5, Figure S1.6).

Table 1.2. Beta diversity (β) between estuaries, based on presence/absence of prey taxa. The total number of crab with putative prey from each estuary is provided in parentheses. Estuaries are listed in geographic order, from most southern (Port Susan Bay) to most northern (Samish Bay).

	Port Susan Bay (n=22)	**Padilla Bay (n=12)**	**Samish Bay (n=24)**
Port Susan Bay	0	0.221	0.208
Padilla Bay		0	0.234
Samish Bay			0

1.4.2 *Stomach content variability across space and crab size*

Our PERMANOVAs to assess significant differences in stomach contents across sampling sites and estuaries were significant, both when using all taxa and only multicellular taxa (Table S1.3); however, a PERMDISP revealed significant differences in dispersion between sampling sites (Table S1.4), so we can only attribute significance from the PERMANOVA to true differences in stomach composition at the estuary scale. Despite this significance, estuary centroids were relatively close together in a Principal Coordinates Analysis (PCoA), with crab from the same estuary spread widely across the ordination space (Figure 1.3). PCoAs were similar when constructed using all taxa and only multicellular taxa, although Samish Bay crab appeared slightly more distinct from Port Susan and Padilla Bay when considering multicellular taxa alone (Figure 1.3b). The PCoA for sampling sites showed similarly high spread for individual crab compared to the spread between site centroids, with only Samish Island crab consistently separate in the ordination space from crab collected at other sites (Figure S1.7).

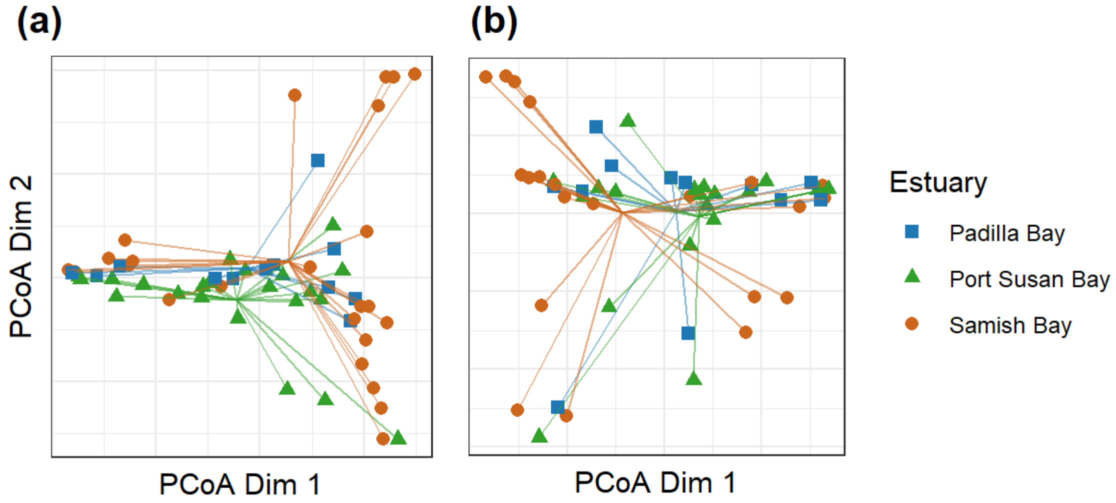

Figure 1.3. A Principal Coordinates Analysis (PCoA) using the eDNA Index to explore diet variability within- and between- estuaries, run with data from **(a)** all taxa, and **(b)** multicellular taxa only.

We also explored whether the similarity in stomach contents between any two crab was correlated with the difference in crab size (measured with carapace width; Figure S1.8, Figure S1.9). The most informative beta regression model when data from all taxa were used had the difference in crab size as the sole predictor variable (ΔAIC = -7.21 and ΔBIC = -1.41; Table S1.5; Figure S1.10); the regression showed a weak but significant ($p = 0.003$) positive correlation between the difference in crab size and the difference in crab diet composition (Table 1.3). In other words, as the size difference between two crab declined, their stomach contents are expected to become more similar. When data from only multicellular taxa were used, the most informative model included the second predictor variable, whether crab were from the same estuary, and an interaction term (ΔAIC = -36.3 and ΔBIC = -19.15; Table S1.5; Figure S1.11); in this model, the difference in crab size was not significantly correlated with the difference in crab stomach composition, whereas whether crab were from the same estuary, and the interaction between size and estuary, were both significant ($p < 0.01$ and $p < 0.05$, respectively; Table 1.3).

Table 1.3. Beta regression output, for the most informative model (Table S1.5) using **(a)** all taxa, and **(b)** only multicellular taxa in crab stomach contents. Size difference was measured as the absolute value of the difference in carapace widths (mm), and Estuary was coded as being the same source estuary for both crab (1) or different for each (0). The pseudo R-squared was **(a)** 0.004021, and **(b)** 0.01664.

(a) All Taxa

	Estimate	Std Error	z value	p value
Intercept	1.68	0.035	47.9	~0 **
Size difference	0.028	0.009	2.96	0.003 **
(phi)	4.51	0.134	33.6	~0 **

(b) Multicellular Taxa

	Estimate	Std Error	z value	p value
Intercept	1.14	0.050	22.9	~0 **
Size difference	0.020	0.013	1.53	0.1260
Estuary	-0.368	0.078	-4.70	~0 **
Size x Estuary	0.059	0.024	2.45	0.0142 *
(phi)	2.30	0.065	35.2	~0 **

When we looked into how the abundance of specific taxa changed with carapace width using a constrained correspondence analysis (CCA), we did not observe a wide spread of taxa across the constrained canonical axis in the ordination, particularly in comparison to the spread of crab (Figure 1.4a). In addition, the constrained canonical axis (representing diet variability attributable to carapace width) was not found to explain significantly more variability than random with a permutation test (Table S1.6). However, the ordination did show that the presence in the diet of the barnacle *Balanus crenatus,* and the diatom order *Naviculales* tended to be associated with larger crab (i.e., greater carapace widths), whereas the presence in the diet of the diatom genus *Pleurosigma* tended to be associated with smaller crab (Figure 1.4a).

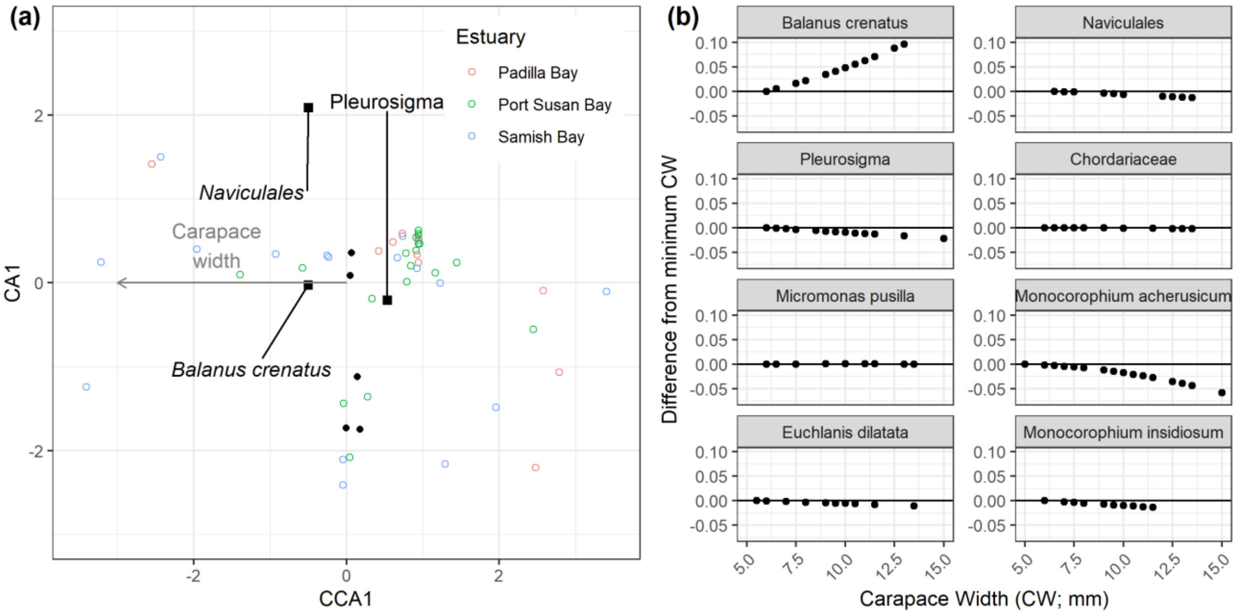

Figure 1.4. Variability in each taxon's proportional DNA abundance associated with crab carapace width (mm), according to **(a)** an ordination for the constrained correspondence analysis (CCA), in which the x axis (CCA1) shows variation associated with crab size; and **(b)** relativized posterior mean estimates of taxon DNA abundance from the *zoid* mixture model. In (a), the black solid points represent the 8 common taxa used for the analysis, with labels providing the names of putative prey taxa which had CCA1 scores outside of the 99% confidence interval of all CCA1 scores. The colored points represent individual crab. To better show the spread of putative prey taxa along CCA1, the full width of the x axis is not shown here and so some crab are excluded from the ordination. For (b), values above zero represent carapace widths at which the given species had a relatively greater proportional abundance than the smallest carapace width, and values below zero represent carapace widths at which the given species had a relatively smaller proportional abundance than the smallest carapace width.

The zero- and one-inflated Dirichlet regression implemented with *zoid* (Jensen et al., 2022; Ward et al., 2022) estimated increasing mixture proportions with increasing carapace width for the barnacle *B. crenatus*, whereas mixture proportions declined with increasing carapace width for the diatom genus *Pleurosigma* and order *Naviculales* (Figure 1.4b). In other words, we would expect *B. crenatus* to be more represented in the stomach contents of larger crab compared to smaller crab. Although not highlighted in the CCA, the gammarid amphipods *Monocorophium acherusicum* and *M. insidiosum* had higher mixture proportions at smaller carapace widths, as did the rotifer *E. dilatata* (Figure 1.4b). The magnitude of decline in the relative mixture proportions for *M. acherusicum* was noticeably greater than that for *Pleurosigma*, the taxon identified in the CCA as being the most strongly associated with smaller crab. However, when we considered the absolute rather than relativized (Figure 1.4b) mixture proportions, all of these taxa showed remarkably small changes in estimated mean proportions given the width of their respective 90% credible intervals (Figure S1.12). Even for *B. crenatus*, which showed the greatest relative change across carapace widths, the mean mixture proportion estimated for the smallest crab carapace width (6.5mm) was safely within the 90% credible interval associated with the largest crab carapace width (15mm; Figure S1.12).

1.4.3 *Risk to Dungeness crab from Ocean Acidification (OA) impacts on prey*

The 53 putative prey taxa identified in three or more crab, for which we identified energy densities, represented 20 functional groups from Busch & McElhany (2016). Benthic herbivorous grazers had the greatest projected negative impact to survival from OA, and gelatinous zooplankton were projected to experience positive outcomes for survival from OA (Table S1.7). Prey energy densities drawn from the literature ranged from ~13800 J/gAFDW (ash-free dry weight) for the cnidarian *Phacellophora camtschatica* and the algae family

Chordariaceae, to 30050 J/gAFDW for the amphipod *Monocorophium acherusicum* (Table S1.8).

Due to its high frequency of occurrence (contributing to high crab exposure; Figure 1.5) and high energy density (translating to high crab sensitivity), the gammarid amphipod *Monocorophium acherusicum* conferred the greatest OA risk to juvenile Dungeness crab (Figure 1.6); the conspecific *M. insidiosum,* while present in fewer crab than *M. acherusicum*, received a similar OA risk score due to the two species' equivalent assigned energy densities and impact from OA (Figure 1.6; Table S1.9). High OA risk to juvenile crab was also associated with three other arthropods, the native hairy shore crab *Hemigrapsus oregonensis* and the copepods *Paracalanus* spp.*,* each of which had low frequencies of occurrence in our dataset but were projected to be highly impacted by OA (contributing to high crab exposure) and had relatively high energy densities (contributing to high crab sensitivity; Figure 1.5, Figure 1.6). Generally, bivalve taxa also conferred higher OA risk due to their projected high negative impact from OA (Figure 1.5, Figure 1.6). In contrast, macroalgae and annelid worms conferred the least OA risk; although they occurred as frequently, if not more frequently, than many of the higher risk prey items, these taxa were estimated to be less impacted by OA as a whole than the arthropods, and had medium to medium-low energy densities (Figure 1.5, Figure 1.6).

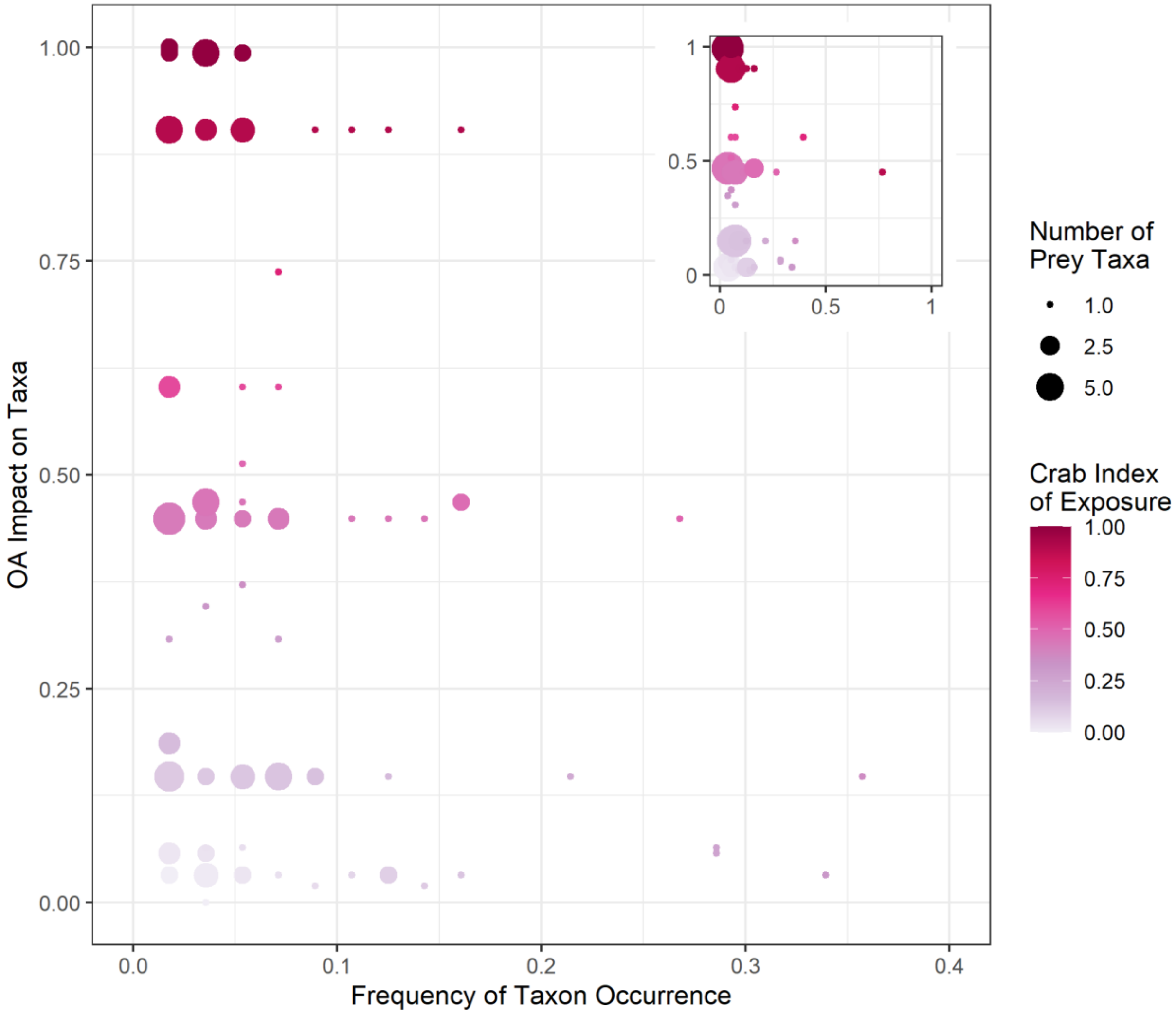

Figure 1.5. The two components used to calculate the Dungeness crab index of exposure to ocean acidification (re-scaled by range for color scale): the frequency of the given prey item's occurrence (x axis), and the impact of ocean acidification on prey survival (y axis), which is based on the prey survival scalars from Busch & McElhany (2016). The prey survival scalars on the y axis have been re-scaled to range from 0 and 1. The inset shows the main graph inclusive of one additional prey item, *M. ascherusicum* (FO = 0.77%), which was removed for clearer visualization of all other prey. Because the prey survival scalars and frequencies of occurrence can be identical between two or more prey items, the point size is scaled to the number of prey taxa represented by each point.

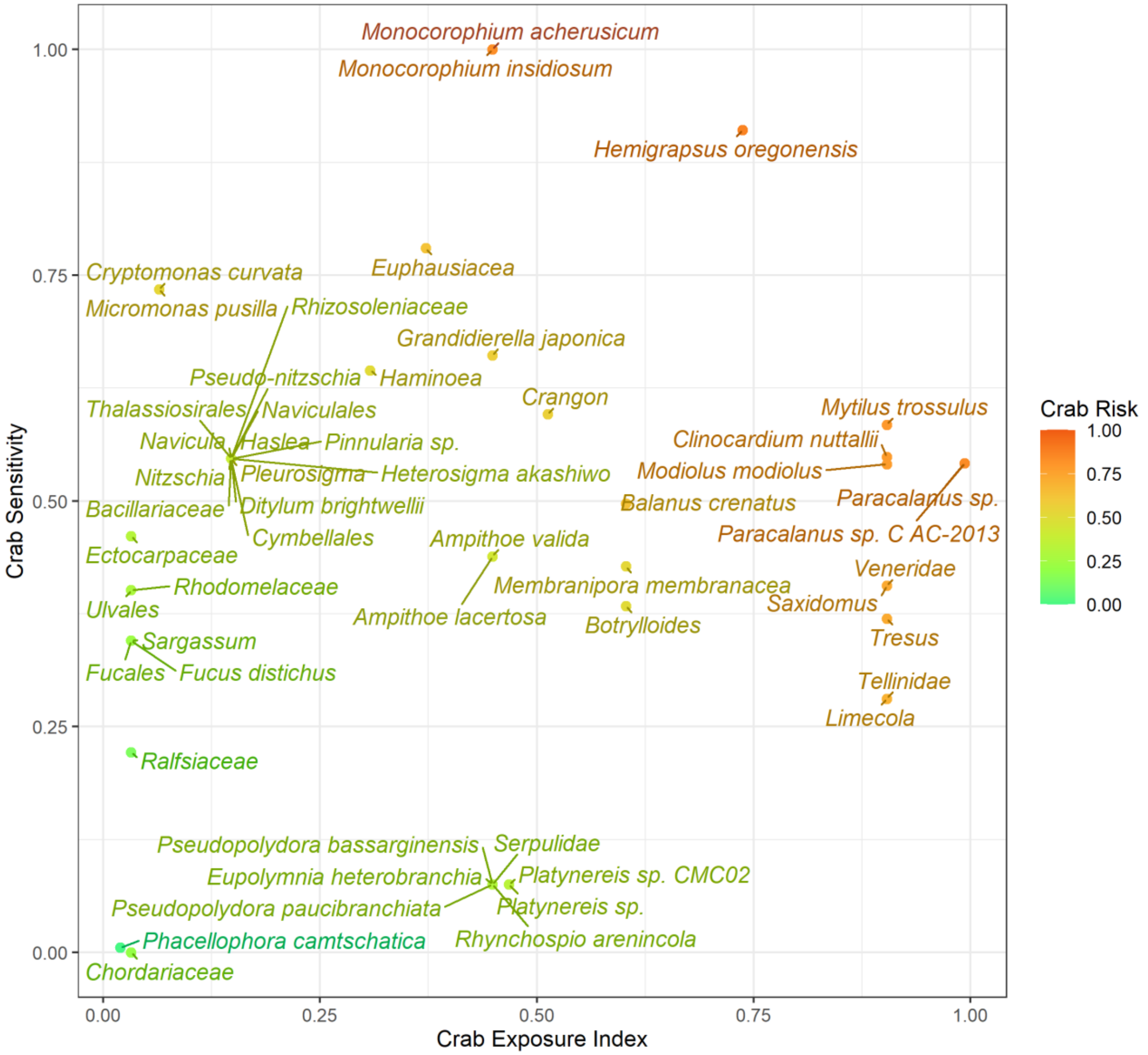

Figure 1.6. Ocean acidification risk to Dungeness crab from changing prey availability (color scale), calculated from the re-scaled index of crab OA exposure (Figure 1.5) and crab sensitivity to loss of the given prey item, which we represent by the prey item's energy density re-scaled by range.

Crab from Samish Bay had fewer high-risk taxa than crab from Port Susan or Padilla Bay, as their stomach contents were notably missing the *Paracalanus* copepods and several different bivalve molluscs (Figure S1.13, Figure S1.14). However, the overall distribution of crab risk from putative prey items was similar between estuaries. This is likely due in part to only one aspect of the risk score varying between the three estuaries (frequency of occurrence), while the impact from OA (one half of the crab exposure index) and energy densities (crab sensitivity) remained the same.

1.5 DISCUSSION

We provided the first description of the stomach contents of wild juvenile Dungeness crab ≤15mm carapace width, by conducting DNA metabarcoding for 58 crab from three Puget Sound, WA, estuaries. We identified 142 unique taxa in crab stomach contents, which were dominated by arthropods but spanned 17 phyla and 7 classes of multi- and unicellular organisms. Our research confirms that juvenile Dungeness crab at early instar stages can be highly omnivorous and, similar to other life stages of this species, are likely generalists and scavengers. While we cannot directly speak to prey selectivity without environmental samples, patterns of beta diversity and zeta diversity decay suggest that the global prey assemblage for juvenile Dungeness crab varies widely and over small spatial scales. We did observe significant differences in stomach content composition between estuaries; however, the significance of the relationship between stomach content composition and crab size (carapace width) varied depending on whether we consider all or only multicellular taxa, potentially due to the high variability in stomach content composition between individuals and the related lack of saturation in taxa accumulation curves.

The highly specific stomach content data provided a more extensive profile of trophic-mediated risk from ocean acidification (OA) than would have been achieved using previously published diet information. The highest OA risk to Dungeness crab was primarily associated with four taxa, the amphipods *Monocorophium acherusicum* and *M. insidiosum*, the native hairy shore crab *Hemigrapsus oregonensis*, and the copepod genus *Paracalanus*. Most putative prey taxa tended to confer either medium-high risk (bivalves), or medium-low risk (microalgae, macroalgae, annelid worms), with differences in risk scores primarily driven by prey energy density and OA impact to prey survival.

1.5.1 *Comparison to previous diet analyses*

Although existing descriptions of wild Dungeness crab diet are lacking for the size class observed in our study, our results mostly align with, and build upon, the scientific literature for larger age 0+ juvenile Dungeness crab. From their visual stomach content analysis using both frequency of occurrence and gravimetric measurements, Stevens et al. (1982) concluded that small bivalves or crustaceans comprise the majority of prey for age 0+ juvenile crab > 15mm carapace width; our frequency of occurrence data generally support this claim for juvenile crab ≤ 15mm carapace width, although we also identified a highly diverse collection of other taxa in crab stomach contents, including many marine micro- and macro-algae, which supports subsequent work on omnivory in juvenile crab diet (Jensen and Asplen 1998).

The smallest size class in visual stomach content analysis conducted by Stevens et al. (1982) (15-40mm and 15-47.4mm carapace width for inner and outer Grays Harbor, WA) were reported to have consumed primarily small bivalves (approx. 30- 60% FO) and crustaceans (approx. 25-65% FO), which were mostly unidentified but did include *Crangon spp.* and the order *Balanomorpha*. In our data set, crustaceans occurred in 89% of crab collected, including *Crangon spp.* (n=3 crab) and the acorn barnacle *Balanus crenatus* (n=22 crab). We found *B. crenatus* to be proportionally more abundant in sequencing data from larger crabs (up to 15mm carapace width), which agrees with the high relative importance of this prey item in the Stevens et al. (1982) data set of age 0+ crab > 15mm carapace width. We were also able to greatly expand upon the taxonomic diversity of other crustaceans that may have gone unspecified in the Stevens et al. (1982) visual analysis, identifying a total of 14 species with an additional 14 genus- and family-level identifications. Bivalves were also common in our data set, although at a lower frequency of occurrence than crustaceans (~43% FO); this included the family *Tellinidae,* corresponding to the genus *Tellina* in the Stevens et al. (1982) analysis, but did not include the other two species that Stevens et al. (1982) cited as important for age 0+ crab in Grays Harbor, WA (*Macoma* sp., *Cryptomya californica*). Other field research has suggested that *Macoma sp.* may occur at depths in the sediment which limit their consumption by recently settled juvenile Dungeness crab (Ruiz 1987). We did observe consumption of *Mya arenaria* (n=3 crab), which was not reported by Stevens et al. (1982); however, in laboratory experiments, juvenile Dungeness crab within the size range of our research (12 – 27.9mm carapace width) consumed this species at relatively high rates (Palacios, 1994).

Our DNA metabarcoding also revealed diverse taxa of brown, red, and green macroalgae as well as various microalgae that have not been previously identified in visual stomach content analysis, which is known to under-emphasize food items like plant and algae material (Amundsen and Sánchez-Hernández 2019). However, Stevens et al. (1982) did note that some crab 15-30mm carapace width had stomachs that appeared to only contain sand and unidentified organic material. Such otherwise 'empty' stomachs likely contained some mixture of macro- and micro-algae. Juvenile crab have been raised through early instar stages in the laboratory using a diet composed exclusively of diatoms (Jensen and Asplen, 1998), and recent fatty acid analysis of age 0+ Dungeness crab (20-30mm carapace width) found that wild-caught individuals had fatty acid profiles most similar to laboratory-raised crab fed algae and urchin feces (Thomas et al. 2020).

Some microalgae, including diatoms of the order *Naviculales*, as well as microfauna, like the rotifer *Euchlanis dilatata*, had among the greatest frequencies of occurrence of all taxa in our data set. We also did not observe declines in the presence of most of these unicellular organisms with increasing crab size. The prevalence of unicellular organisms in crab stomachs across the size range we studied raises the question of whether their consumption by juvenile crab is intentional, incidental - in that consumption occurs as crab target other prey, either because the organism is located on the prey item or in the surrounding environment - or represents secondary predation by crab prey items. The answer likely varies by taxon, although there is anecdotal evidence that certain filamentous diatoms, for example, may be intentionally grazed upon by J1-2 Dungeness crab instars (Jensen and Asplen, 1998). It should also be noted in the context of these results that high frequency of occurrence does not necessarily translate to importance in the diet; one of the weaknesses of presence/absence data for diet analysis is that it overestimates the importance of prey types that are commonly occurring but consumed in low abundance.

The unanswered question of how certain DNA were consumed by juvenile crab is relevant beyond the presence of unicellular taxa in our data set. We frequently identified a remarkably high diversity of taxa in a single crab stomach - 16 crab collected across the three estuaries were found to have ten or more unique multicellular taxa in their stomach contents. We also identified genetic material from organisms that are larger in size than juvenile crab themselves, at some or all life stages. For example, two crab stomachs contained DNA from the shiner perch *Cymatogaster aggregata*, and five contained DNA from the jellyfish *Phacellophora camtschatica*. Several crab stomachs contained DNA from larger terrestrial insects (e.g., the wasp *Vespula germanica*). This may be a signal of the ingestion of detritus, which contains shed scales and other organic material from an array of organisms, which could then be detected with DNA metabarcoding.

The presence of certain larger taxa in the stomach contents may also be the product of scavenging, or predation on early life stages; *C. aggregata*, for example, are present as embryos and larvae in shallow West Coast estuaries during the summer months (Odenweller 1975). Similarly, other crab species including *Hemigrapsus* spp. were present in the intertidal as megalopae and/or recently-settled juveniles during collection of juvenile Dungeness crab for this study.

A trade-off to the ability of DNA metabarcoding to identify such a diverse range of taxa, is that it is unable to differentiate at the sub-species level between predator DNA and DNA from cannibalized conspecifics. Visual diet analysis, and laboratory and field experiments, have emphasized the importance of cannibalism in the diet of juvenile Dungeness crab (Gotshall 1977, Stevens et al. 1982, Fernández et al. 1993, Fernández 1999). It is estimated that conspecifics may comprise approx. 25% of stomach contents in crab at the upper end of the size range in our study (15-60mm carapace width; Stevens et al. 1982). While we cannot speak to rates of cannibalism from our data, other molecular techniques like the genotyping of microsatellite loci have been used to study cannibalism in other marine organisms (Dahl et al. 2018). Alternative molecular methods of diet analysis may be particularly important to assessing rates of cannibalism among juvenile crab; prior experimental research suggests that juvenile Dungeness crab < 29mm carapace width often do not consume the carapaces of conspecifics, and so relying on the presence of hard parts for visual analyses could underestimate cannibalism in early juvenile instar stages (Fernández 1999).

1.5.2 *Risk to Dungeness crab from OA impacts to prey*

As discussed above, prior analysis of juvenile Dungeness crab stomach contents emphasized the role of small crustaceans and bivalves in crab diets (Stevens et al. 1982), while field observations and fatty acid analysis suggested the likely consumption of diatoms and macro-algae (Jensen and Asplen, 1998; Thomas et al., 2020). In our analysis, crustaceans and bivalves conveyed the highest risk to crab from ocean acidification, primarily due to higher energy densities and greater impacts of OA on the survival of shell-forming organisms. While we were unable to speak to the frequency of cannibalism in our study, we can use published rates of cannibalism for slightly larger juvenile crab (approx. 25%, crab 15-60mm carapace width; Stevens et al. 1982), and published energy densities for subadult crab (19380 J/gAFDW; Holsman et al., 2003) to estimate a medium-high OA risk value for cannibalized conspecifics. Confirming the widespread presence of a diversity of micro- and macro-algae in crab stomach contents, as well as identifying taxa that had not been previously identified as putative prey items (e.g., annelid worms, the cnidarian *Phacellophora camtschatica*, among others), added a number of taxa which had lower risk scores than crustaceans and bivalves. This represents a significant addition to the overall profile of crab risk from OA impacts on prey assemblages.

When calculating crab risk, taxa tended to cluster by functional group; this was driven by the use of functional group to assign OA impact scores from the literature (Busch and McElhany 2016), and by the low specificity of energy densities drawn from the literature for certain taxonomic groups (e.g., all polychaete worms were assigned the same energy density; Table S1.8). However, there was some variability in crab risk scores within functional groups of putative prey taxa, and so previously unidentified within-group diversity achieved with DNA metabarcoding was important to a more accurate depiction of the spread of trophic-mediated OA risk. For example, the crustaceans *Monocorophium* spp. and *Ampithoe valida* received similar OA impact scores as part of the “Deposit feeders” functional group (Busch and McElhany 2016), but conferred drastically different relative risk to juvenile crab due to their different frequencies of occurrence and estimated energy densities. The spread of crab risk from other taxonomic groups, such as the annelid worms, may be better revealed if future work used more taxonomically-specific energy densities.

Assuming that juvenile crab are similar to other generalist predators and scavengers, which are capable of displaying high plasticity in consumption patterns (Gutgesell et al. 2022, Goodenough et al. 2023), we may consider the hypothetical scenario of how crab growth and survival would be impacted by a whole-sale shift in prey availability to only putative prey taxa which are expected to experience positive impacts to survival from OA (Busch and McElhany 2016). In our dataset, these include gelatinous zooplankton (energy densities in lower 10% of taxa included in crab risk analysis), macroalgae (energy densities in lower 50%), microzooplankton (energy densities between 50-75%), and small phytoplankton (energy densities between 50-75%). Based on prior research, and the energy densities we drew from the literature, diets comprised of these functional groups alone may delay crab molting and slow crab growth. Although the energy density used in our study for *Mytilis trossulus* was only slightly higher than those for diatoms in the phylum *Bacillariophyta*, feeding experiments by Jensen and Asplen (1998) found that a diet of exclusively diatoms increased intermolt periods 20-25% (i.e., delayed molting) compared to a diet composed solely of mussel (*Mytilis* sp.) tissue. Similarly, Thomas et al. (2020) observed that juvenile crab fed a diet of macroalgae (*Ulva* sp.) grew and molted less over the course of six weeks in the laboratory, compared to those fed bivalve meat, fish meat, or conspecific megalopae. While annelid worms have not been used as food in laboratory studies, their collective energy density drawn from the literature for our work suggests that they may also provide a lower quality alternative to high risk prey.

1.5.3 *Limitations and next steps in understanding OA risk to juvenile crab*

We used energy densities of putative prey taxa, which ranged from 13.8 (*Chordariaceae; P. camtschatica*) to 30.05 (*Monocorophium* spp.) kJ/gAFDW, as a proxy for Dungeness crab sensitivity to the loss of any given taxon. This relies on several assumptions, including that the range of energy densities in our study translates to an ecologically significant change in Dungeness crab growth rate, and that this change in growth rate occurs linearly with changing prey energy density. Estimating crab growth rates associated with the consumption of each putative prey taxa would be a more precise metric for sensitivity, and could be achieved through bioenergetic modeling. Bioenergetic models are a robust and widely used tool to estimate growth and consumption (Madenjian 2011), and Holsman et al. (2003) describe a bioenergetic modeling framework for subadult (age 1+) Dungeness crab which could be re-parameterized for age 0+ juvenile Dungeness crab. The sensitivity component of Dungeness crab OA risk could then be based on modeled average daily growth rate.

Investment in bioenergetic modeling may also call for species-, season-, and location-specific energy density estimates, whereas we relied upon energy density values from the existing literature. Percent ash-free dry weight has been found to be a robust predictor of energy density (Weil et al. 2019), and may be a less resource-intensive approach than bomb calorimetry to obtain energy densities for the broad range of taxa identified in juvenile crab stomachs. However, obtaining energy densities from newly collected organisms still leaves the challenge of deciding which life stage of a given taxon to measure. Energy densities may vary widely depending on whether the presence of certain taxa in juvenile crab stomach contents represented scavenging of adults or adult-derived organic matter, versus predation on earlier (smaller) life history stages; crab themselves vary in energy content even between different larval stages (Connelly et al. 2018).

The development of a bioenergetic model for juvenile Dungeness crab could also be used to compare the relative impact of trophic-mediated OA risk, discussed here, to direct effects of OA on crab growth and survival. Dynamic energy budget modeling has been used to project the direct effects of ocean acidification in other shell-forming marine species (Muller and Nisbet 2014, Pousse et al. 2022). Juvenile Dungeness crab are believed to have a relatively low sensitivity to the direct effects of ocean acidification in comparison to temperature or dissolved oxygen (Berger et al. 2021), and a multi-stressor experiment found that nutritional condition of juvenile crab was more negatively impacted by reduced food availability than reduced seawater pH (Schram et al. 2023). However, recent research suggests that near-future CO_2 levels could result in smaller juveniles with higher resting metabolic rates, which are associated with increased natural mortality and energy requirements (McElhany et al. 2022), while negatively impacting the species' ability to detect food (Durant et al., 2023).

1.5.4 *Other considerations for climate change impacts based on DNA metabarcoding*

While not a possible prey item, we also detected DNA from the dinoflagellate parasite *Hematodinium* in five crab collected at the Kayak Point (Port Susan Bay) and Larrabee (Samish Bay) sites. *Hematodinium* spp., which is the cause of bitter crab syndrome, infects over 40 species of crustaceans worldwide and is commonly associated with the Alaska king crab (*Paralithodes camtschaticus*) and Tanner crabs (*Chionoecetes bairdi* and *C. opilio*) in the Northeastern Pacific (Morado et al., 2012). *Hematodinium* spp. has been shown to infiltrate midgut tissues (Field and Appleton 1996), which would explain its presence in our DNA metabarcoding data. To the authors' best knowledge, the only other recorded case of dinoflagellate parasitism in Dungeness crab from the Northwestern Pacific was from a single subadult crab collected near Kodiak Island, Alaska (Meyers and Burton 2009). The upper temperature range of *Hematodinium* spp. occurring in Northeastern Pacific crab hosts is not well known, but warmer sea temperatures have been associated with outbreaks of bitter crab disease, potentially associated an increase in molting frequency (Shields 2019).

1.6 CONCLUSIONS

Our DNA metabarcoding of stomach contents expanded scientific knowledge of the role of recently-settled juvenile Dungeness crab in estuarine food webs. We described omnivorous and highly diverse stomach contents, which suggested a generalist feeding strategy with a role for scavenging and the consumption of detritus. However, interpretation of certain results – such as the high average count of unique taxa identified in each crab, and the high frequency of occurrence of unicellular taxa – stressed key limitations of DNA metabarcoding, particularly the inability to distinguish between predation, scavenging, incidental ingestion, and secondary predation. Taxa that conferred low crab risk from OA (e.g., macro- and microalgae, diatoms) were assigned similar sensitivity scores to taxa that conferred high crab exposure to OA (e.g., bivalves); this, combined with the tendency for generalist predators to display diet plasticity in changing environments, suggests that OA impacts on prey communities may be of lesser concern than other direct or indirect impacts to juvenile crab from climate change. However, previous work has demonstrated that early stage juvenile crab may experience delayed molting and slower growth when feeding on lower-risk crab prey items, and so we cannot definitively say that the spread of crab risk calculated from our consumption data means low overall trophic-mediated OA risk. Future research which more directly assesses energy density of putative prey items, and uses bioenergetic modeling to translate energy densities to crab growth, could provide key additional insights. Finally, although we specifically considered risk from OA-associated changes to prey assemblages, the diet information presented in this study could be used to consider other forms of climate risk that may be perpetuated through altered predator-prey or host-parasite relationships.

Return to Table of Contents.

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1.8 APPENDIX

1.8.1 *Supplemental Tables*

Table S1.1. For each prey group (phylum, or class where phylum was not available), the median frequency of occurrence (as in Figure 1.2), the number of unique taxa, and the percent of total taxa (n=136) that this count represents.

Prey group	**Number of unique taxa**	**Percent of all taxa**	**Median FO %**
Arthropoda	35	0.246	3.57
Annelida	20	0.141	1.79
Bacillariophyta	15	0.106	5.36
Mollusca	15	0.106	3.57
Phaeophyceae	11	0.077	3.57
Chlorophyta	5	0.035	8.04
Nemertea	5	0.035	1.79
Cnidaria	4	0.028	1.79
Dinophyceae	4	0.028	1.79
Platyhelminthes	4	0.028	1.79
Cryptophyceae	3	0.021	3.57
Rhodophyta	3	0.021	1.79
Rotifera	3	0.021	1.79
Bryozoa	2	0.014	1.79

Chordata	2	0.014	3.57
Nematoda	2	0.014	1.79
Porifera	2	0.014	2.68
Raphidophyceae	2	0.014	6.25
Chrysophyceae	1	0.007	1.79
Echinodermata	1	0.007	1.79
Eustigmatophyceae	1	0.007	1.79
Foraminifera	1	0.007	3.57
Pelagophyceae	1	0.007	1.79

Table S1.2. Beta (β) diversity between the seven sites, according to prey presence / absence. Sites are grouped by the estuary in which they are located.

	Kayak Pt 1	Kayak Pt 2	March Pt	NERR	Samish Island	Samish Bay	Larrabee
Kayak Pt 1		0.396	0.146	0.139	0.179	0.065	0.129
Kayak Pt 2			0.202	0.115	0.157	0.068	0.174
March Pt				0.207	0.215	0.107	0.181
NERR					0.255	0.273	0.123
Samish Island						0.133	0.124
Samish Bay							0.153
Larrabee							

Table S1.3. Results of the PERMANOVA for variability between estuaries and sites, using (a) all taxa, and (b) multicellular taxa only.

(a)

	Degrees of freedom	**Sum of squares**	$\mathbf{R^2}$	**F**	**p-value**
Estuary	2	1.4931	0.06416	1.8853	0.002**
Residual	55	21.7789	0.93584		
Total	57	23.272	1		
Site	6	3.9621	0.17025	1.7441	0.001**
Residual	51	19.3099	0.82975		
Total	57	23.272	1		

(b)

Estuary	2	1.6345	0.07846	2.2563	0.002**
Residual	53	19.1972	0.92154		
Total	55	20.8317	1		
Site	6	3.9236	0.18835	1.8951	0.001**
Residual	49	16.9081	0.81165		
Total	55	20.8317	1		

Table S1.4. Results of the PERMDISP for variability in stomach contents between estuaries and sites, using (a) all taxa, and (b) multicellular taxa only.

(a)

	Degrees of freedom	**Sum of squares**	**Mean Sq**	**F**	**p-value**
Groups (Estuary)	2	0.02083	0.010417	1.2487	0.295
Residuals	55	0.45885	0.008343		
Groups (Site)	6	0.24856	0.041426	3.1564	0.010*
Residuals	51	0.66934	0.013124		

(b)

Groups (Estuary)	2	0.06025	0.030126	1.7858	0.178
Residuals	53	0.8941	0.01687		
Groups (Site)	6	0.51251	0.085418	3.0784	0.0123*
Residuals	49	1.35964	0.027748		

Table S1.5. Aikake and Bayesian Information Critera for the nested models investigating the assocation between stomach content composition and crab size, constructed using (a) all taxa, and (b) only multicellular taxa. Size difference (ΔSize) was measured as the absolute value of the difference in carapace widths (mm), and Estuary (ΔEstuary) was coded as the same source estuary for both crab (1) or different for each (0).

Model	**ΔAIC**	**ΔBIC**
(a) All Taxa		
B-C Distance ~ 1	0.00	0.00
B-C Distance ~ ΔSize	-7.21	-1.41
B-C Distance ~ ΔSize + ΔEstuary	-12.32	-0.71
B-C Distance ~ ΔSize + ΔEstuary + ΔSize*ΔEstuary	-13.87	3.55
(b) Multicellular Taxa		
B-C Distance ~ 1	0.00	0.0
B-C Distance ~ ΔSize	-13.90	-8.2
B-C Distance ~ ΔSize + ΔEstuary	-31.80	-20.4
B-C Distance ~ ΔSize + ΔEstuary + ΔSize*ΔEstuary	-36.27	-19.2

Table S1.6. Permutation test for the constrained correspondence analysis in which carapace width was the explanatory variable (X) for a diet composition matrix of eDNA index values (Y).

	Degrees of freedom	**Chi-squared**	**F**	**p-value**
Model	1	0.01249	1.47505	0.1634
Residual	54	0.46490		

Table S1.7. For each functional group represented by at least one prey taxon in the DNA metabarcoding data set, the projected impact of ocean acidification on that prey taxon, re-scaled from 0 (most positive impact) to 1 (most negative impact). The projected OA impact values are derived from the Busch & McElhany (2016) raw survival scalars.

Functional Group	**Raw Survival Scalar**	**Re-scaled Survival Scalar**
Benthic herbivorous grazers	-1.37	1.00
Mesozooplankton	-1.36	0.99
Bivalves	-1.22	0.90
Crabs	-0.96	0.74
Shallow benthic filter feeders	-0.75	0.60
Crangon shrimp	-0.61	0.51
Carnivorous infauna	-0.54	0.47
Deposit feeders	-0.51	0.45
Large zooplankton	-0.39	0.37
Fish	-0.35	0.35
Sea stars moonsnail whelk	-0.29	0.31
Meiobenthos	-0.10	0.19
Large phytoplankton	-0.04	0.15
Small phytoplankton	0.09	0.06
Microzooplankton	0.10	0.06
Macroalgae	0.14	0.03
Gelatinous zooplankton	0.16	0.02
Deep benthic filter feeders	0.19	0.00

Table S1.8. Energy densities for each of the putative prey taxa used in the modeled diets, rounded to the nearest five J/g AFDW, and the source of the value. Taxa are listed alphabetically, first by phylum and then by taxon name within each phylum. Since energy densities were not available for all prey items, we also specify which taxon/taxa the energy density is extrapolated from ("Published Taxon") with the lowest common ancestor for the prey item and the energy density source taxon in parentheses. When multiple published values are listed, we took the average of the listed values. Where necessary, we also report the conversion factor its source used to convert published energy densities (which are reported here in original units) to J/g AFDW from J/g wet weight (WW) or dry weight (DW).

Prey Taxon	**Energy Density J/g AFDW**	**Published Energy Density**	**Published Taxon**	**Conversion Factor, Taxon**	**Source (Energy Density)**	**Source (Conversion Factor)**
All *Annelida*	15030	1.981 kJ/g WW	Nereididae (Phylum, Family)	0.1318, *Polychaeta*	Gray (2005)	Gogina et al. (2022)
Amphithoe valida	20930	4.358, 5.647 kcal/g AFDW	*Amphithoe lacertosa* (Genus)	NA	Thayer et al. (1973)	
Balanus crenatus	21655	5.22 kcal/g AFDW	*B. balanoides* (Genus)	NA	Thayer et al. (1973)	
Crangon sp.	28275	4.1 kJ/g WW	*C. Crangon* (Genus)	0.145, *C. crangon*	Andersen (1999)	Gogina et al. (2022)
Euphausiacea	26475	3150 J/g WW	*Euphausia lucens* (Order)	WW to DW: 0.138, *E. lucens* DW to AFDW: 0.862, *E. superba, E. triacantha, T. macura*	Ciancio et al. (2007) as reported in James et al. (2012)	Ciancio et al. (2007) (WW to DW) Torres et al. (1994) (DW to AFDW)
Grandidierella japonica	24545	2970 J/g wet mass	*G. japonica* (Species)	0.121, *G. japonica*	David et al. (2014)	Gogina et al. (2022)
Hemigrapsus oregonensis	28605	4225 J/g WW	*H. oregonensis* megalope (Species)	0.1447, *H. takanoi*	Connelly et al. (2018)	Gogina et al. (2022)
Monocorophium ascherusicum	30050	3065 J/g WW	*Corophiidae* (family)	0.102, *M. insidiosum*	David et al. (2014)	Gogina et al. (2022)
Monocorophium insidiosum	30050	3065 J/g WW	*Corophiidae* (family)	0.102, *M. insidiosum*	David et al. (2014)	Gogina et al. (2022)
Paracalanus	21880	[1]22610 J/g AFDW [2]21.3 kJ/g DW [3]17.6 kJ/g DW	[1]*Calanus helgolandicus* [2]*Calanus propinquus* [3]*Calanoides acutus* (order)	0.904, *C. propinquus* *C. acutus*	[1]Slobodkin and Richman (1961), reported in Cauffopé and Heymans (2005) [2]Donnelly et al. (1994) [3]Donnelly et al. (1994)	Cauffopé and Heymans (2005)

Prey Taxon	**Energy Density J/g AFDW**	**Published Energy Density**	**Published Taxon**	**Conversion Factor, Taxon**	**Source (Energy Density)**	**Source (Conversion Factor)**
All *Bacillariophyta*	22690	5.47 kcal/g AFDW	*Nitzschia paradoxa* (Genus, Family, Phylum)	NA	Paine and Vadas (1969)	
Membranipora membranacea	20750	4.96 cal/mg AFDW	Bryozoa and Brachiopoda (Phylum)		Norrbin and Båmstedt (1984) reported in Beukema (1997)	
Ulvales	20325	[1]4.94, [2]4.75, [3]4.94, [4]4.8 kcal/g AFDW	[1]*Ulva fenestrata* [2]*Ulva lactuca* [3]*Ulva sp.* [4]*Ulva rigida* (Order)	NA	Paine and Vadas (1969)	
Botrylloides	12761	3050 cal/g AFDW	*B. violaceus* (Genus)	NA	Kincaid and de Rivera (2021)	
Phacellophora camtschatica	18960	6.2 kJ/g dry mass	*P. camtschatica* (Species)	0.327 *P. camtschatica*	Lüskow et al. (2021)	Lüskow et al. (2021)
Cryptophyceae (incl. *Cryptomonas curvata* and *Micromonas pusilla*)	25735	2.76 cal/mg DW	April phytoplankton bloom in Nova Scotia (family)	0.448	Platt and Irwin (1973)	Platt and Irwin (1973)
Chordariaceae	13805	5.14 kcal/g AFDW	*Chordariaceae* (family)	NA	Paine and Vadas (1969)	
Ectocarpaceae (incl. *Ectocarpus spp.*)	21295	5.09 kcal/g AFDW	*Ectocarpus dimorphus* (Genus, Family)	NA	Paine and Vadas (1969)	
Fucus distichus *Sargassum sp.*	19415	4.64 kcal/g AFDW	*F. distichus* (Species)	NA	Paine and Vadas (1969)	
Ralfsiaceae	17405	4.16 kcal/g AFDW	*Ralfsia sp.* (Family)	NA	Paine and Vadas (1969)	
Rhodomelaceae (incl. *Polysiphonia sp.*)	20325	5, 4.88 kcal/g AFDW	*Polysiphonia hrodiae* *Polysiphonia sp.* (Genus, Family)	NA	Paine and Vadas (1969)	
Clinocardium nuttallii	22720	5.43 cal/mg AFDW	*C. ciliatum* (Genus)	NA	Wacasey and Atkinson (1987), reported in Beukema (1997)	
Haminoea	24280	1.843 kJ/g WW	*Buccinanops cochlidium* (Class)	0.075903, *Haminoea solitaria*	Averbuj et al. (2017)	Gogina et al. (2022)
Modiolus modiolus	22595	5.4 cal/mg AFDW	*M. modiolus* (Species)	NA	Steimle and Terranova (1985), reported in Beukema (1997)	
Mytilus trossulus	23300	5.55 cal/mg AFDW 23.3, 24, 22.6 kJ/g AFDW	*M. edulis* (Genus)	NA	Zwarts and Wanink (1993)	
Tellinidae (incl. *Limecola sp.)*	18370	4.391 kcal/g AFDW	*Macoma balthica* (Family)	NA	Thayer et al. (1973)	

Prey Taxon	Energy Density J/g AFDW	Published Energy Density	Published Taxon	Conversion Factor, Taxon	Source (Energy Density)	Source (Conversion Factor)
Tresus	18370	4.64, 4.83 cal/mg AFDW	*Spisula elliptica,* *Spisula solidissima* (Family)	NA	Dauvin and Joncourt (1989), Steimle and Terranova (1985), reported in Beukema (1997)	
Veneridae (incl. *Saxidomus*)	19810	^{1}4.73, ^{2}4.73, ^{3}5.17 cal/mg AFDW	^{1}*Venus casina,* ^{2}*Venus fasciata,* ^{3}*Venus ovata* (Family)	NA	Dauvin and Joncourt (1989), reported in Beukema (1997)	

Table S1.9. For each prey taxon in the DNA metabarcoding data set that occurred in two or more crab stomachs, the frequency of occurrence over all sites, and the crab index of exposure / sensitivity / OA risk. Crab exposure / sensitivity / risk have each been re-scaled from 0 (lowest exposure / risk and least sensitivity) to 1 (highest exposure / risk and greatest sensitivity).

Taxon	FO %	Exposure Index	Sensitivity	Crab Risk
Monocorophium acherusicum	0.768	0.885	1.000	1.000
Hemigrapsus oregonensis	0.071	0.731	0.911	0.869
Paracalanus sp.	0.054	0.995	0.542	0.841
Paracalanus sp. C AC-2013	0.054	0.995	0.542	0.841
Monocorophium insidiosum	0.268	0.505	1.000	0.832
Mytilus trossulus	0.054	0.902	0.584	0.796
Clinocardium nuttallii	0.107	0.907	0.549	0.784
Modiolus modiolus	0.125	0.909	0.541	0.783
Saxidomus	0.054	0.902	0.406	0.729
Veneridae	0.054	0.902	0.406	0.729
Tresus	0.161	0.915	0.370	0.727
Tellinidae	0.089	0.905	0.281	0.696
Limecola	0.054	0.902	0.281	0.694
Balanus crenatus	0.393	0.709	0.497	0.632
Euphausiacea	0.054	0.352	0.780	0.625
Grandidierella japonica	0.071	0.434	0.661	0.574
Micromonas pusilla	0.286	0.267	0.734	0.566
Crangon	0.054	0.498	0.596	0.563
Cryptomonas curvata	0.054	0.050	0.734	0.531
Membranipora membranacea	0.054	0.590	0.428	0.525
Haminoea	0.071	0.290	0.645	0.508
Botrylloides	0.071	0.592	0.384	0.507

Pleurosigma	0.357	0.364	0.547	0.469
Ampithoe valida	0.143	0.451	0.439	0.447
Ampithoe lacertosa	0.054	0.432	0.439	0.436
Naviculales	0.214	0.233	0.547	0.420
Nitzschia	0.125	0.163	0.547	0.401
Cymbellales	0.089	0.142	0.547	0.397
Rhizosoleniaceae	0.089	0.142	0.547	0.397
Ditylum brightwellii	0.071	0.133	0.547	0.395
Haslea	0.071	0.133	0.547	0.395
Navicula	0.071	0.133	0.547	0.395
Pseudo-nitzschia	0.071	0.133	0.547	0.395
Bacillariaceae	0.054	0.126	0.547	0.394
Heterosigma akashiwo	0.054	0.126	0.547	0.394
Pinnularia sp.	0.054	0.126	0.547	0.394
Thalassiosirales	0.054	0.126	0.547	0.394
Platynereis sp.	0.161	0.476	0.075	0.332
Platynereis sp. CMC02	0.161	0.476	0.075	0.332
Ectocarpaceae	0.071	0.044	0.461	0.317
Pseudopolydora paucibranchiata	0.125	0.446	0.075	0.309
Pseudopolydora bassarginensis	0.107	0.441	0.075	0.305
Eupolymnia heterobranchia	0.071	0.434	0.075	0.300
Serpulidae	0.071	0.434	0.075	0.300
Rhynchospio arenincola	0.054	0.432	0.075	0.298
Ulvales	0.125	0.097	0.401	0.278
Rhodomelaceae	0.125	0.097	0.401	0.278
Fucales	0.161	0.133	0.345	0.244
Fucus distichus	0.107	0.079	0.345	0.232
Sargassum	0.054	0.028	0.345	0.226
Chordariaceae	0.339	0.316	0.000	0.202
Ralfsiaceae	0.054	0.028	0.222	0.129
Phacellophora camtschatica	0.089	0.058	0.005	0.000

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1.8.2 *Supplemental Figures*

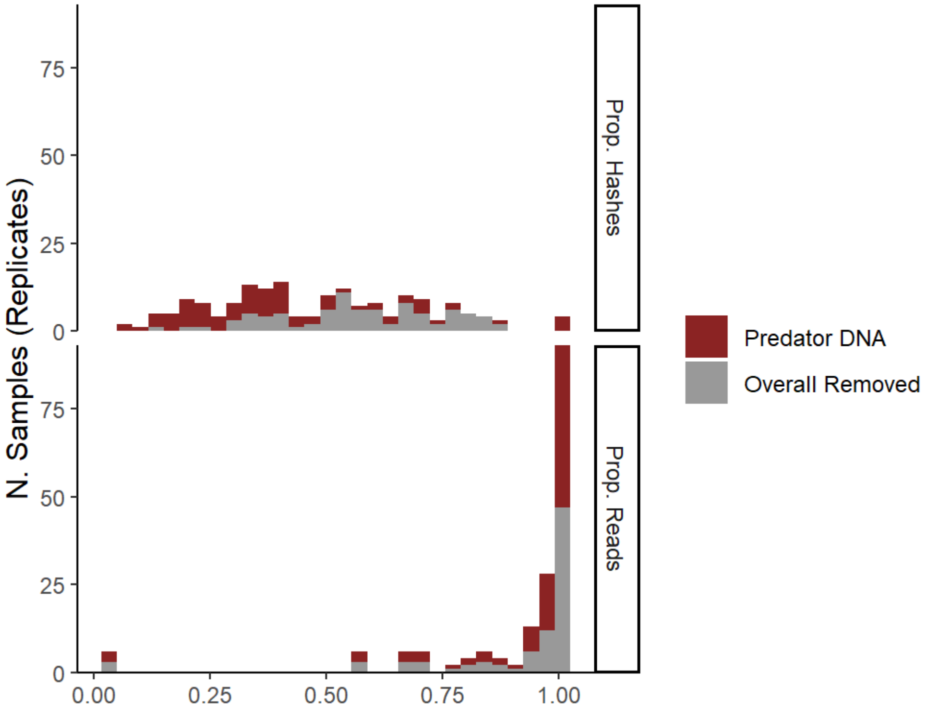

Figure S1.1. The proportion of unique ASVs (“Hashes”) and proportion of sequencing reads (“Reads”) that were removed per sample during the filtering process, overall (gray) and specifically for predator DNA (red). A sample is defined as each technical replicate (up to three) derived from each crab stomach.

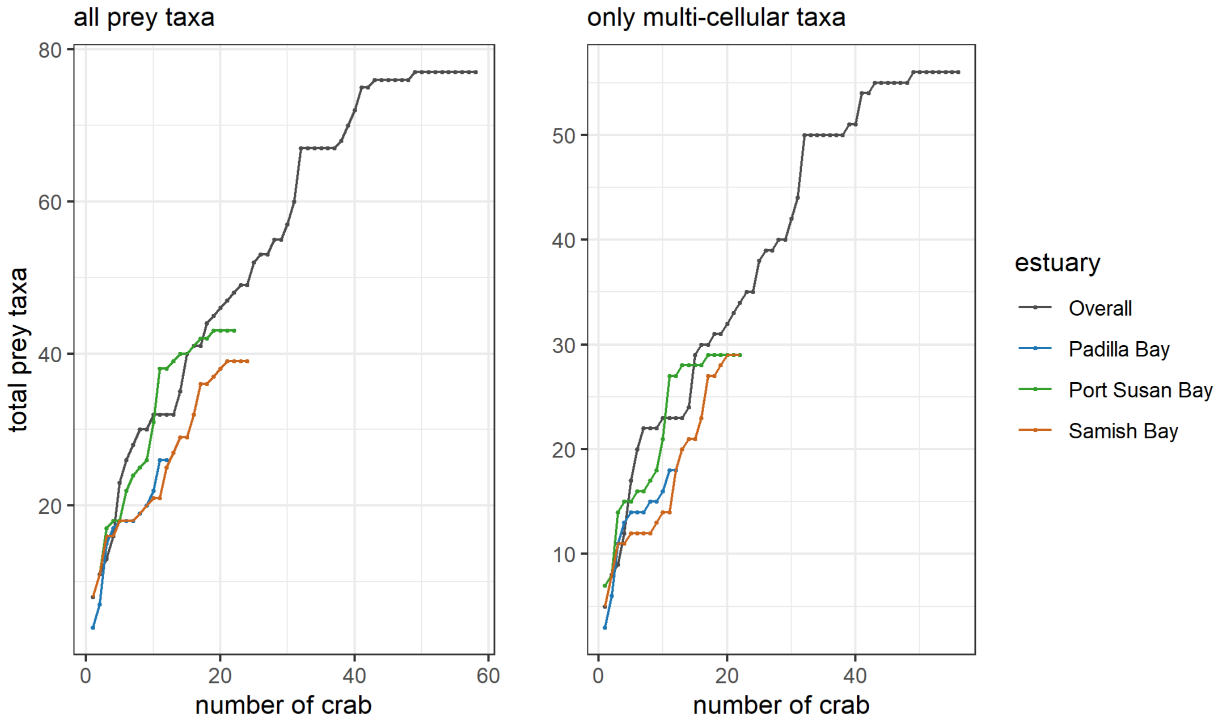

Figure S1.2. Saturation curves showing the number of unique taxa added per additional crab sampled, for each estuary.

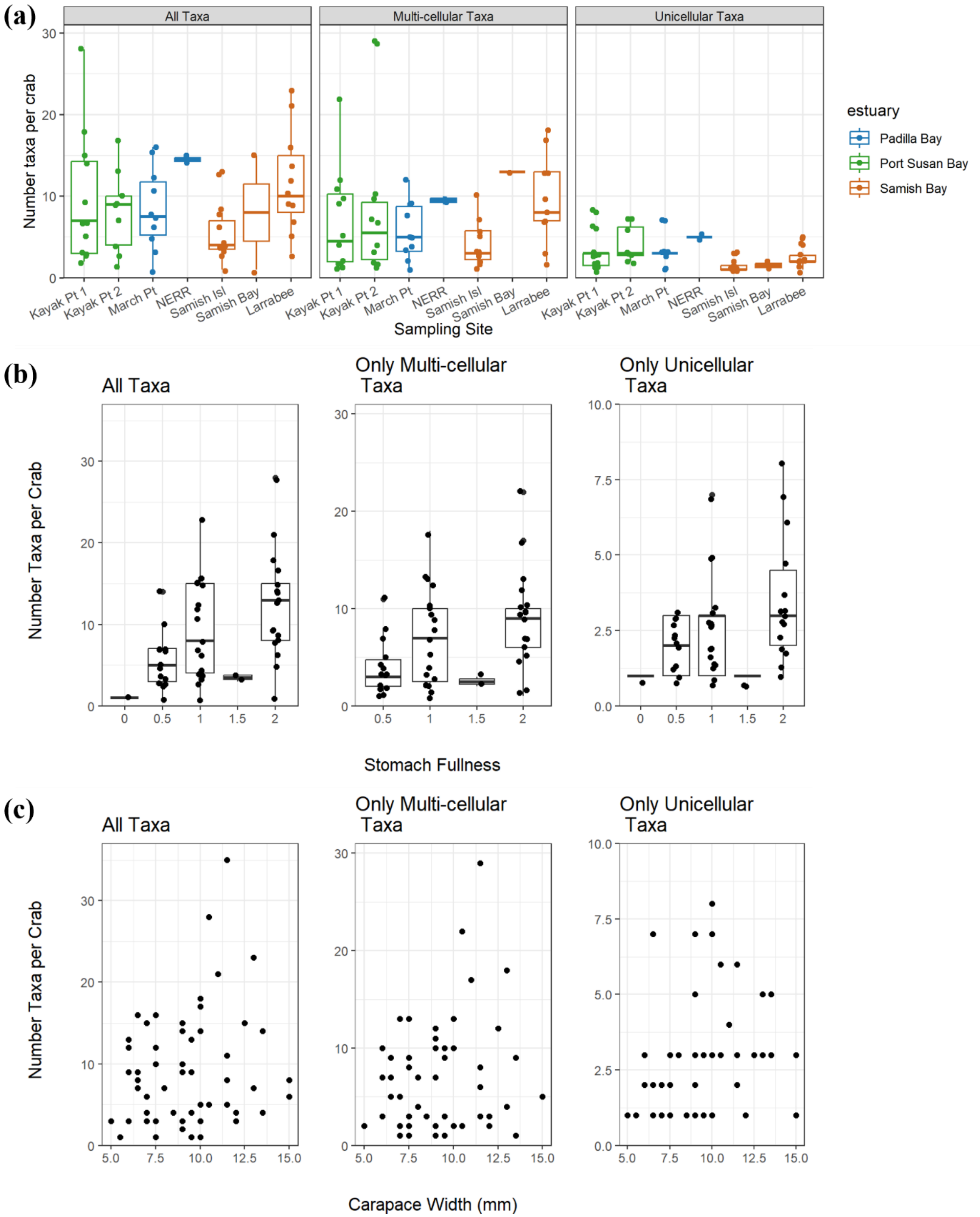

Figure S1.3. Distributions of the alpha diversity of prey items in each crab stomach, broken down by **(a)** collection site, **(b)** stomach fullness, and **(c)** carapace width (mm). Diversity is shown for all taxa (left), excluding unicellular organisms (middle) and only for unicellular organisms (right).

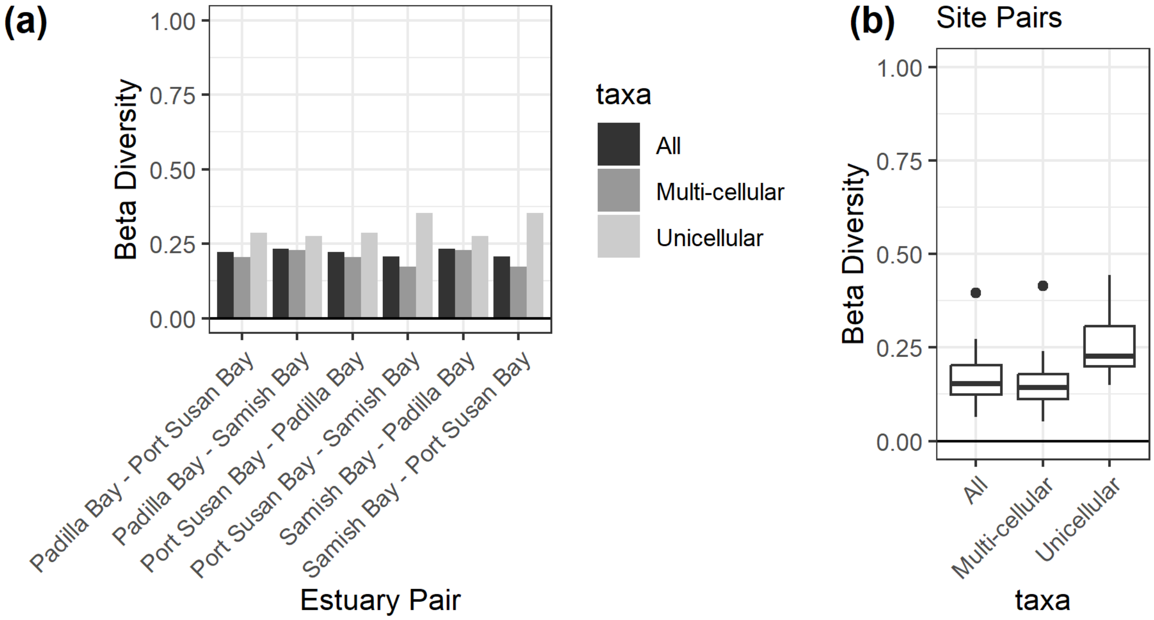

Figure S1.4. Beta diversity (Jaccard similarity, presence/absence data) calculated using all taxa in the data set (“All”), only unicellular organisms (“Unicellular”) and only multicellular taxa (“Multi-cellular”) for each pair of **(a)** estuaries, and **(b)** sites (summarized by taxa).

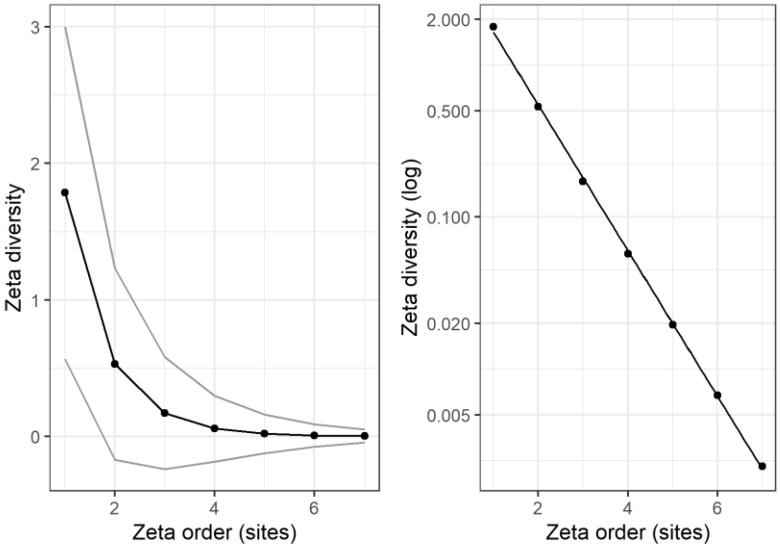

Figure S1.5. Zeta diversity decay across seven sampling sites. The best fit model (right panel) was exponential decay ($y=1.0033 – 0.3169^x$; AIC = -28.63 compared to AIC = 5.84 for the power law model).

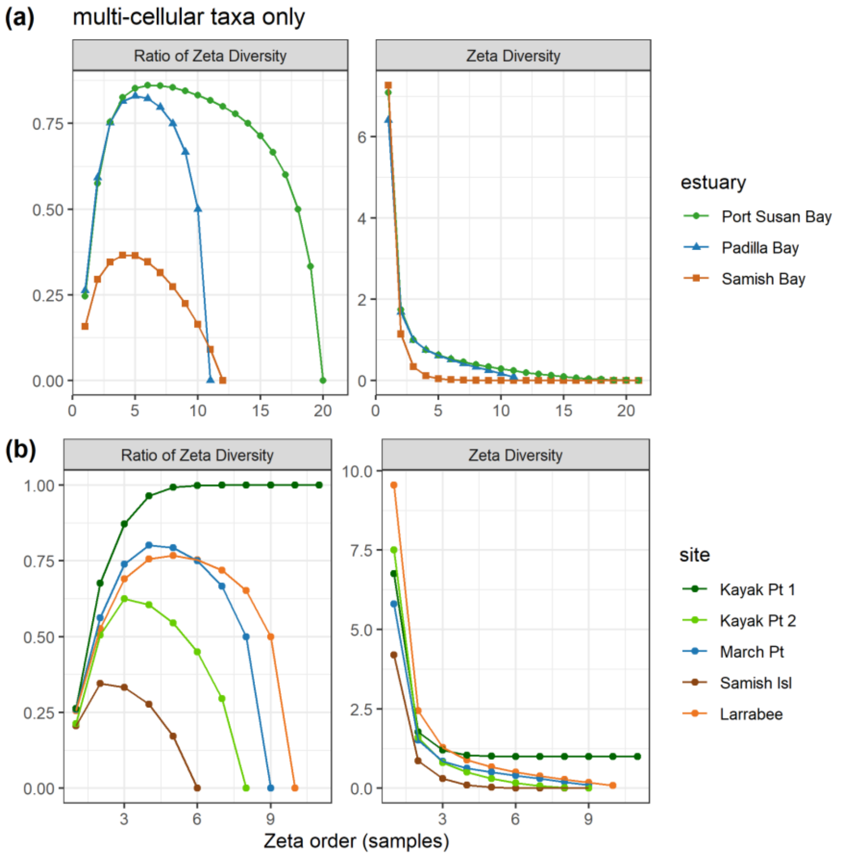

Figure S1.6. Zeta diversity decay for **(a)** estuaries, and **(b)** sites, with zeta orders representing individual crab.

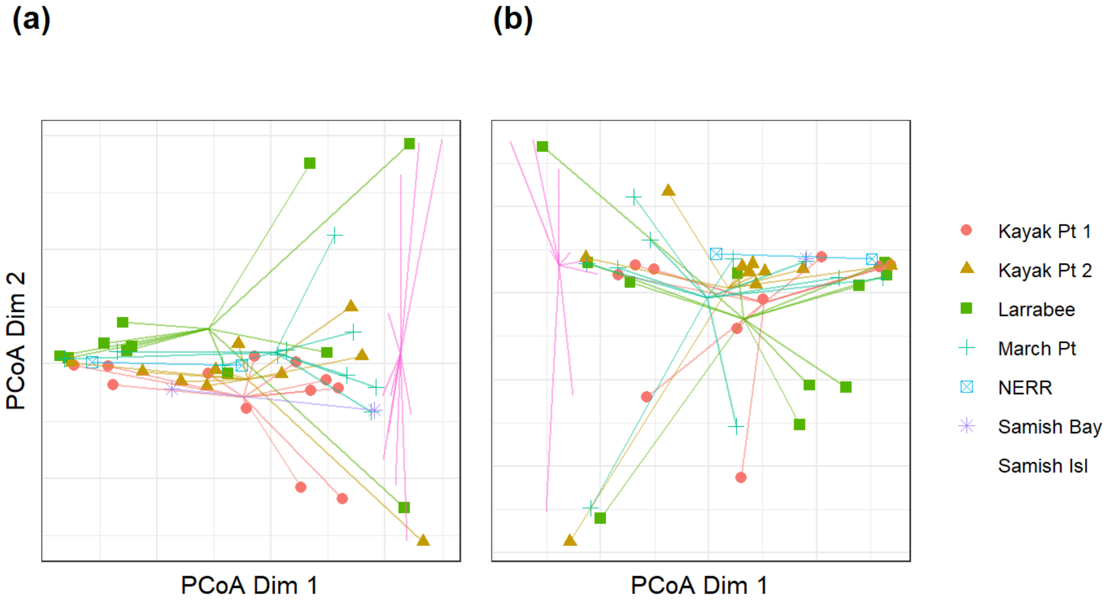

Figure S1.7. PCoA for sites, from a PERMDISP with **(a)** all taxa, and **(b)** multicellular taxa.

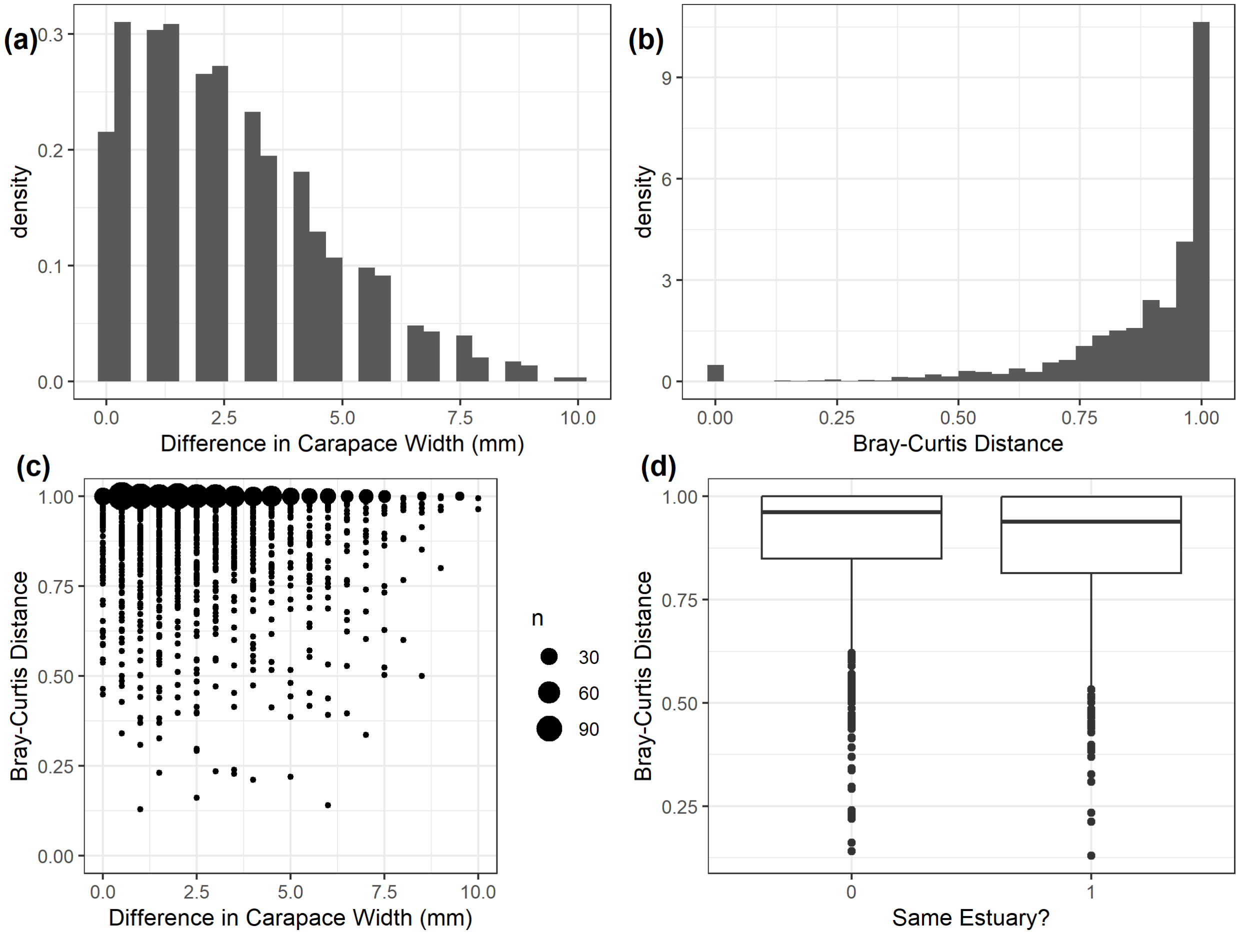

Figure S1.8. Input data for the nested beta regression using all taxa in the data set. Distribution of the **(a)** differences in carapace width (mm; x axis) and **(b)** Bray-Curtis distance between stomach contents (y axis) for all pairs of crabs. The two variables are then plotted against each other in **(c)**, on their respective axes, and Bray-Curtis distance is also graphed **(d)** according to whether the given pair of crab are from the same (1) or different (2) estuaries (x axis).

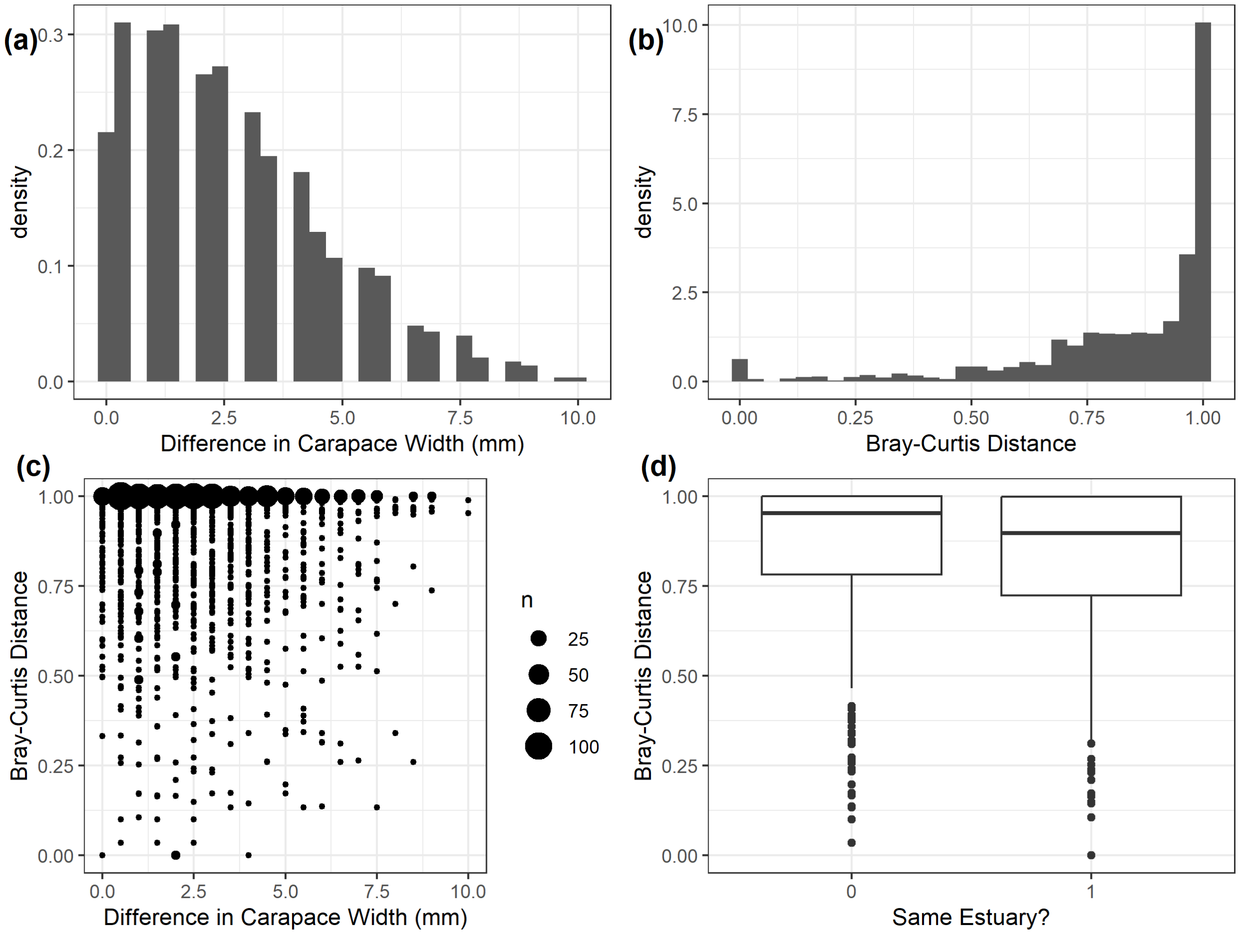

Figure S1.9. Input data for the nested beta regression using only the multicellular taxa. Distribution of the **(a)** differences in carapace width (mm; x axis) and **(b)** Bray-Curtis distance between stomach contents (y axis) for all pairs of crabs. The two variables are then plotted against each other in **(c)**, on their respective axes, and Bray-Curtis distance is also graphed **(d)** according to whether the given pair of crab are from the same (1) or different (2) estuaries (x axis).

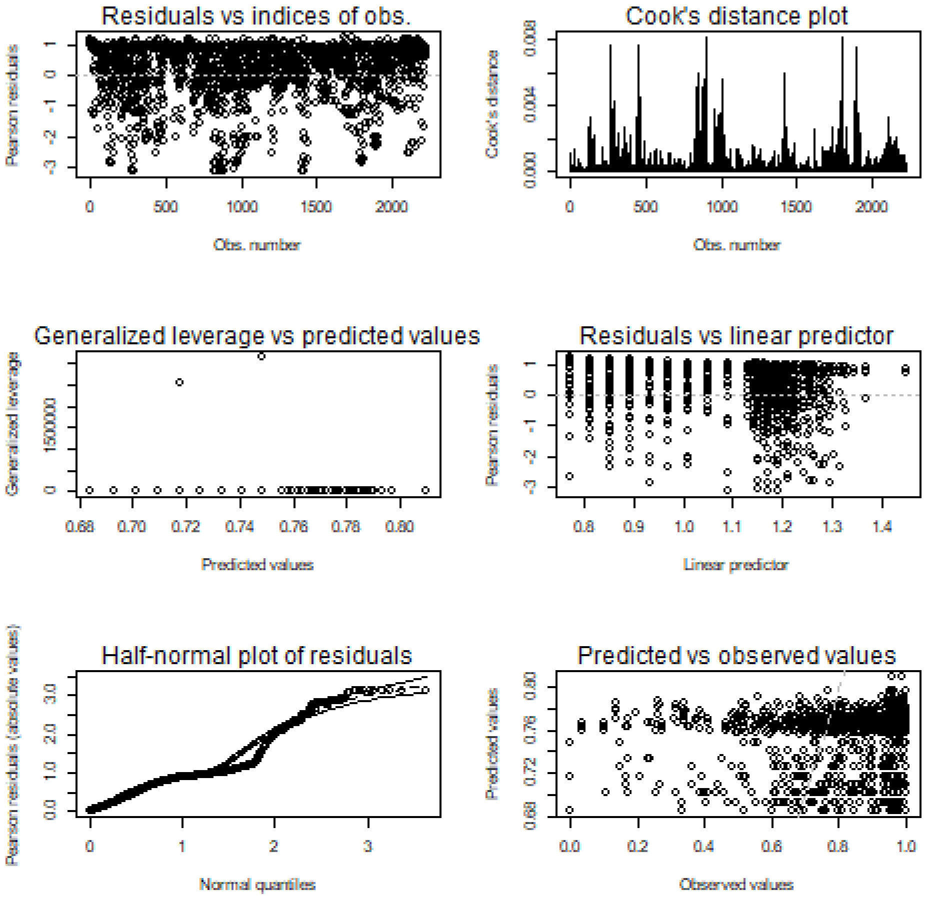

Figure S1.10. Diagnostics plots of the most informative beta regression model for size-based differences in stomach contents, using all taxa in the data set. (Bray-Curtis Distance ~ ΔSize)

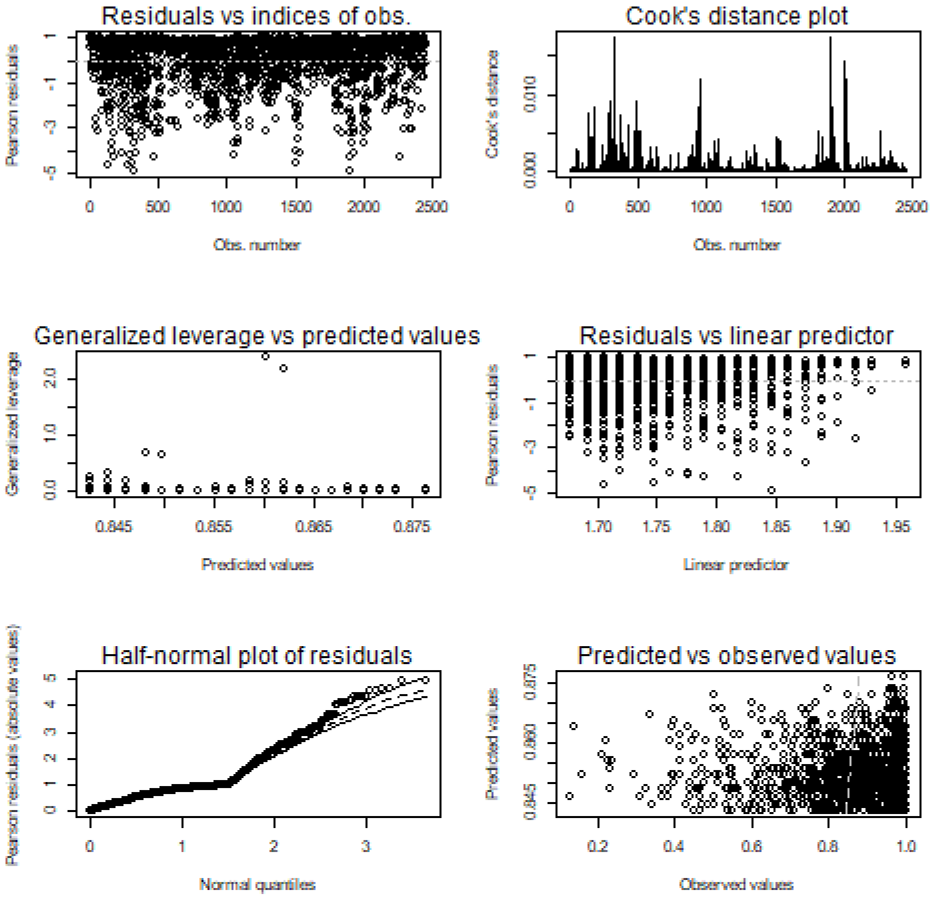

Figure S1.11. Diagnostics plots of the most informative beta regression model for size-based differences in stomach contents, using only multicellular taxa. (Bray-Curtis Distance ~ ΔSize + ΔEstuary + ΔSize*ΔEstuary)

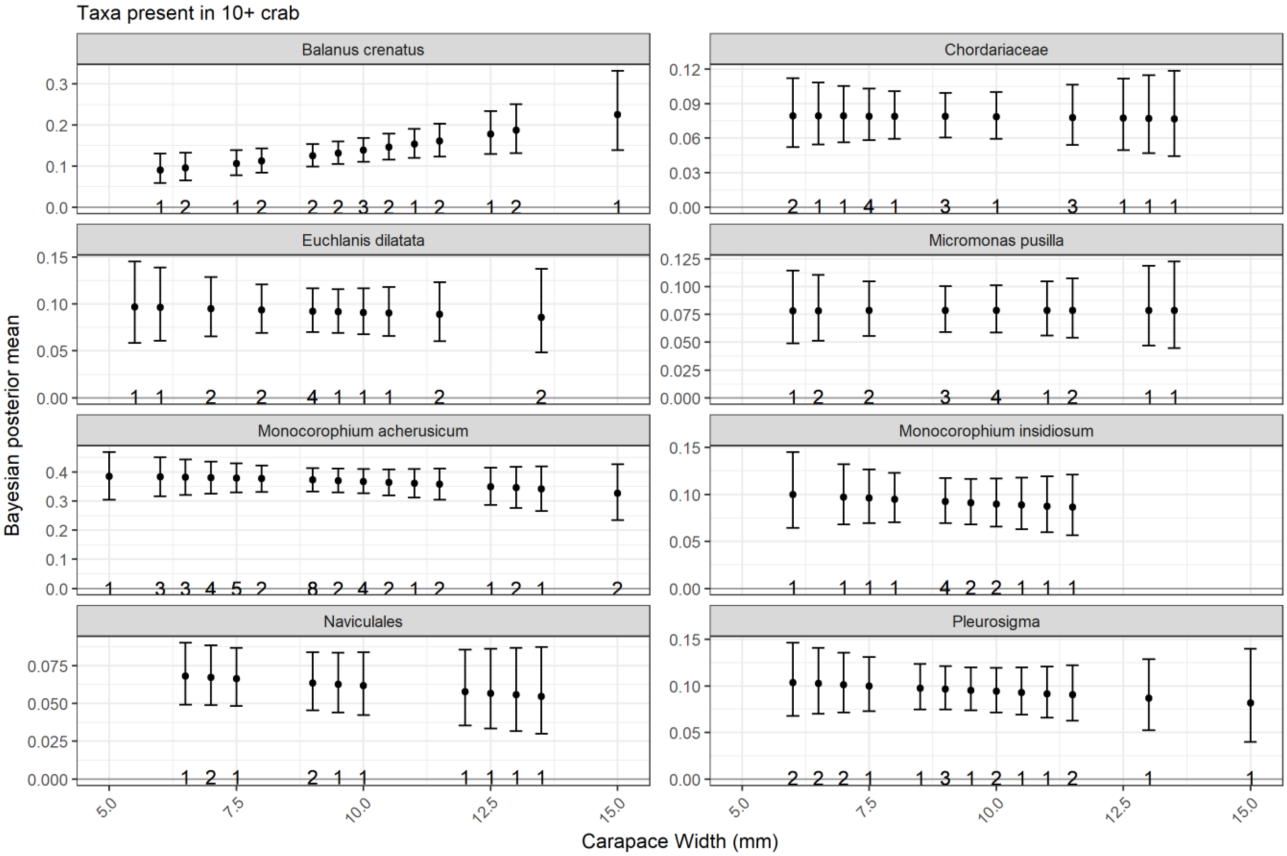

Figure S1.12. Posterior means and 90% credible intervals from the *zoid* mixture model fit. These values are not relativized to the lowest carapace width, as in Figure 1.4b. The numbers along the x axis provide the number of crab at the given carapace width in which that species was found, and therefore the sample size for the model estimate.

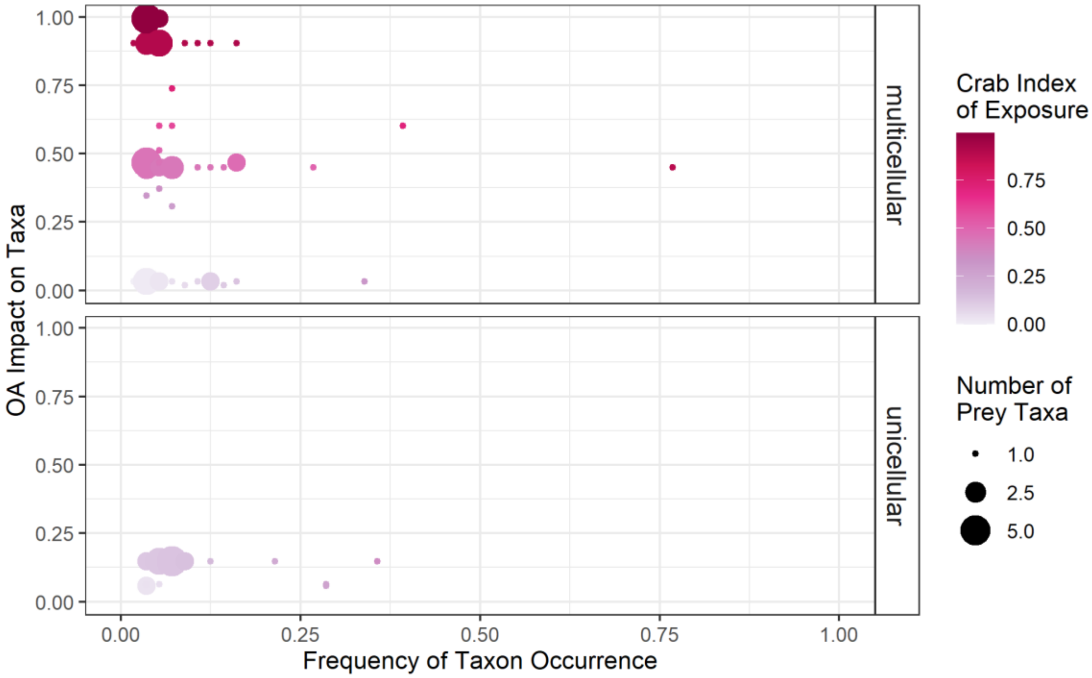

Figure S1.13. For unicellular v. multicellular taxa the two components use to calculate the Dungeness crab index of exposure to ocean acidification (re-scaled by range for color scale): the frequency of the given prey item's occurrence in crab stomach contents from that estuary (x axis), and the impact of ocean acidification on prey survival (y axis; prey survival scalars from Busch and McElhany 2016). The prey survival scalars on the y axis have been re-scaled by range using all prey taxa at all estuaries (as for Figure 1.6). Because the prey survival scalars and frequencies of occurrence can be identical between two or more prey items, the point size is scaled to the number of prey taxa represented by each point.

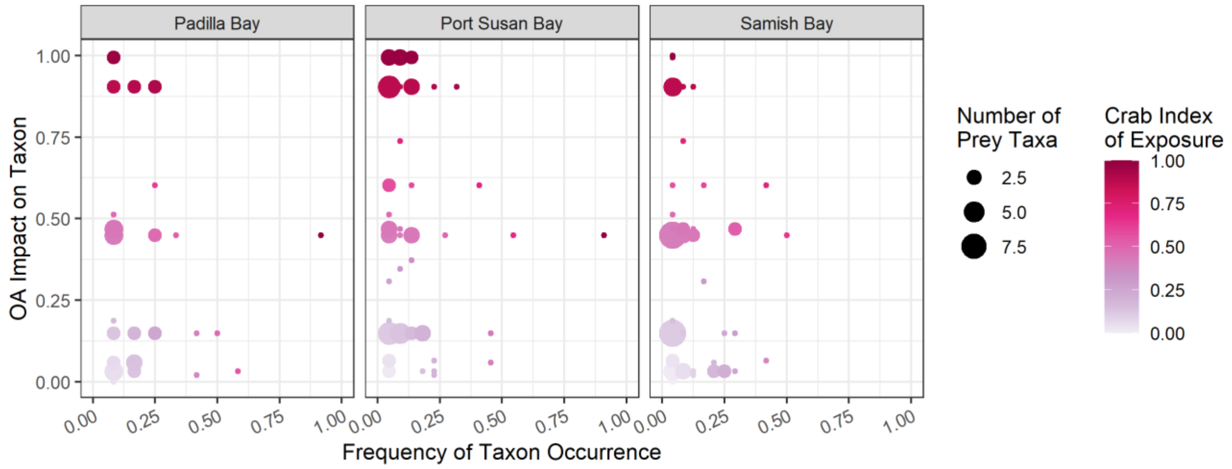

Figure S1.14. For all taxa in each estuary, the two components use to calculate the Dungeness crab index of exposure to ocean acidification (re-scaled by range for color scale): the frequency of the given prey item's occurrence in crab stomach contents from that estuary (x axis), and the impact of ocean acidification on prey survival (y axis; prey survival scalars from Busch and McElhany 2016). The prey survival scalars on the y axis have been re-scaled by range using all prey taxa at all estuaries (as for Figure 1.6). Because the prey survival scalars and frequencies of occurrence can be identical between two or more prey items, the point size is scaled to the number of prey taxa represented by each point.

Chapter 2. CLIMATE SHOCK EFFECTS AND MEDIATION IN FISHERIES

2.1 ABSTRACT

Climate shocks can reorganize the social–ecological linkages in food-producing communities, leading to a sudden loss of key products in food systems. The extent and persistence of this reorganization are difficult to observe and summarize, but are critical aspects of predicting and rapidly assessing community vulnerability to extreme events. We apply network analysis to evaluate the impact of a climate shock - an unprecedented marine heatwave - on patterns of resource use in California fishing communities, which were severely affected through closures of the Dungeness crab fishery. The climate shock significantly modified flows of users between fishery resources during the closures. These modifications were predicted by pre-shock patterns of resource use and were associated with three strategies used by fishing community member vessels to respond to the closures: temporary exit from the food system, spillover of effort from the Dungeness crab fishery into other fisheries, and spatial shifts in where crab were landed. Regional differences in resource use patterns and vessel level responses highlighted the Dungeness crab fishery as a seasonal "gilded trap" for northern California fishing communities. We also detected disparities in climate shock response based on vessel size, with larger vessels more likely to display spatial mobility. Our study demonstrates the importance of highly connected and decentralized networks of resource use in reducing the vulnerability of human communities to climate shocks. This work has been published as: Fisher, M.C. et al. 2021. *Proceedings of the National Academy of Sciences* 118(2): e2014379117 (DOI: 10.1073/pnas.2014379117).

2.2 INTRODUCTION

Climate shocks threaten food systems around the world and are expected to increase in frequency and intensity under climate change (Bender et al. 2010, Fischer and Schär 2010, Banholzer et al. 2014, Stott 2016, Cottrell et al. 2019). Distinct from climate change (e.g., long-term warming), climate shocks rapidly outstrip the capacity of a system to cope by inflicting unexpected and highly concentrated damage (de la Fuente 2007). Vulnerability of communities to climate shocks varies within and across food systems, depending on the severity of the shock and the sensitivity and adaptive capacity of community members (Adger 2006). Communities that form the harvesting and processing base of food systems - especially agrarian and fishing communities - are often among the most vulnerable to climate shocks (Porter et al. 2014), as their resource-based economies operate at the interface of environment and society. Marine heatwaves represent one such climate shock of growing importance, as they impact fishing communities by compromising seafood safety, shifting species distributions, and lowering recruitment and survival of fished species (Bond et al. 2015, Basilio et al. 2017, Frölicher and Laufkötter 2018, Smale et al. 2019).

Diversifying harvest portfolios is one strategy used by fishers to manage risk (Kasperski and Holland 2013, Cline et al. 2017, Anderson et al. 2017). If marine heatwaves disproportionately affect a subset of species, fishers may respond by shifting participation into less affected fisheries. This response, referred to as “leakage” or “spillover” (Cunningham et al. 2016, Fuller et al. 2017, Yletyinen et al. 2018, Addicott et al. 2019, Kroetz et al. 2019), restructures the networks that form as fishers participate in multiple fisheries (Yletyinen et al. 2018, Addicott et al. 2019, Kroetz et al. 2019). The topology of these fisheries participation networks can reveal the extent to which climate shocks lead to indirect or lasting changes in patterns of resource use within fishing communities and, by drawing on network theory, indicate the sensitivity of these communities to perturbations (Fuller et al. 2017).

The 2014-2016 North Pacific marine heatwave (Bond et al. 2015, Di Lorenzo and Mantua 2016) was a climate shock that led to a massive harmful algal bloom (HAB), contaminating Dungeness crab with biotoxins and compelling state managers to coordinate fishery closures along the entire U.S. West Coast (McCabe et al. 2016). In California, where the Dungeness crab fishery represents ~26% of all annual fishery revenue (California Department of Fish and Wildlife; wildlife.ca.gov) and supports >25% of all commercial fishing vessels (Pacific Fisheries Information Network; pacfin.psmfc.org), the HAB significantly delayed the 2015-16 commercial Dungeness crab fishing season (Moore et al. 2019). California Dungeness crab landings for the 2015-16 season reached only 52% of the average catch from the previous five years, spurring Congress to appropriate >$25 million in federal disaster relief funding (Holland and Leonard 2020). Dungeness crab fishers reported shifting participation to alternative fisheries during the 2015-16 season to offset socioeconomic impacts (Moore et al. 2020a, Jardine et al. 2020); however, to date there has been no quantitative demonstration of spillover from the Dungeness crab fishery, or analysis of how the resulting changes in fisheries participation networks may have varied geographically or persisted after the closures were lifted.

Our study examined the impact of the 2015-16 Dungeness crab fishery closures (hereafter 2016 closures) on patterns of resource use in California fishing communities. We considered seven fishing communities representing a total of 2,516 individual fishing vessels (Table 2.1). We found significant changes in fisheries participation network topology during the 2016 closures, which corresponded with a severe reduction in fishing activity, spillover of fishing effort from the Dungeness crab fishery, and spatial variation in pre-shock network topology. Our analysis captured changing patterns of resource use during a severe climate shock, and demonstrated how this emergent social outcome in fishing communities can be predicted by pre-shock network metrics and related to the adaptive strategies of community member vessels. We discuss the implications of fishery management measures for adaptive decision making and network structure, and provide recommendations for sustainable fishery management during climate shocks.

Table 2.1. Ports of landing and vessel counts for the seven California fishing communities included in this study. The number and proportion of commercial Dungeness crab fishing vessels in the given community is reported for the 2015 crab year, with large v. small vessel counts in parentheses. "Total annual vessels" reports the mean annual number of active commercial vessels in the given fishing community, with standard deviation, for crab years 2008 to 2017.

Region	Fishing community	Ports of landing	Total annual vessels, 2008-17	Dungeness crab vessels (large/small) 2015	Dungeness crab vessel proportions 2015
North	Crescent City	Crescent City, Other Del Norte County	109 ± 16	68 (40/28)	0.75
	Eureka	Eureka, Fields Landing, Trinidad, Other Humboldt County	150 ± 24	77 (34/43)	0.51
	Fort Bragg	Albion, Point Arena, Fort Bragg, Other Mendocino County	237 ± 96	41 (22/19)	0.12
	Bodega Bay	Bodega Bay, Bolinas, Point Reyes, Tomales Bay, Other Sonoma/Marin County	208 ± 77	105 (56/49)	0.44
	Total		*753 ± 149*	*291 (152/139)*	
Central	San Francisco	Alameda, Berkeley, Oakland, Princeton/Half Moon Bay, Richmond, San Francisco Sausalito, Other San Francisco Bay/San Mateo County	388 ± 97	221 (121/100)	0.49
	Monterey Bay	Santa Cruz, Monterey, Moss Landing, Other Santa Cruz/Monterey County	286 ± 83	47 (15/32)	0.14
	Morro Bay	Avila, Morro Bay, Other San Luis Obispo County	187 ± 26	30 (17/13)	0.14
	Total		*567 ± 98*	*298 (153/145)*	

2.3 EVALUATING CHANGE IN FISHERIES PARTICIPATION NETWORKS

Our analysis used historical landings data and network methodology to quantify the sensitivity of fishing communities to perturbations in the Dungeness crab fishery. We then related expected sensitivity to changes in network topology during and after the 2016 closures, and qualitatively linked those changes to adaptive responses by Dungeness crab vessels. We used a shore-based definition of fishing communities as port groups (Fuller et al. 2017, Richerson et al. 2018), with vessels landing catch in a given port group as proxies for fishers. We defined fishing community sensitivity as the magnitude of change in fisheries participation network topology caused by a perturbation.

2.3.1 *Participation network framework*

We used two types of participation networks to 1) quantify patterns of resource use in fishing communities, and 2) deconstruct Dungeness crab vessel activity. In both networks, nodes are fisheries, with edges connecting pairs of fisheries based on shared vessel participation. Undirected fisheries participation networks show participation by all vessels in a fishing community, with nondirectional edge weights defined by the number of vessels participating in, and the evenness of revenue generation from, pairs of connected fisheries (Fuller et al. 2017). Directed networks capture spillover from the Dungeness crab fishery during and immediately after the 2016 closures; edges, weighted by the number of vessels, indicate Dungeness crab vessel movement out of fisheries in which they participated during the previous season and into alternative fisheries, to a different fishing community, or out of the California commercial fishing industry for the 2015-16 fishing season.

Drawing on >286,000 landing records, we constructed directed and undirected networks for each Dungeness crab season. We refer to each season using “crab years,” from November through October of the following year; the 2016 crab year corresponds to the 2015-16 fishing season (i.e., November 2015 to October 2016). To observe behavioral responses during and immediately after the 2016 closures, we further subdivided each crab year into an early season and a late season, delineated by the dates of the 2016 closures (Table S2.1). The early season spanned from the typical Dungeness crab fishing season start date (November 15 or December 1) to when the 2016 closures were lifted, and the late season encompassed the remainder of the crab year (Table S2.1). Spatial variation was observed at a regional level, with fishing communities clustered into northern and central regions (Table 2.1).

2.3.2 *Quantifying patterns of cross-fishery participation*

We examined three aspects of participation network topology that network theory relates to the ability of individuals and communities to respond to a perturbation (Table S2.2). The first is overall connectedness, or fisheries connectivity, measured using edge density. In a fisheries context, greater connectivity suggests more flexibility in fishers' participation (Fuller et al. 2017, Stoll et al. 2017) and thus a greater capacity to adapt to a perturbation without leaving the fishing industry. The second is the degree to which the network is divided into subgroups, quantified by modularity. Modularity is inversely related to sensitivity, because more modular networks tend to limit perturbations to the subgroup in which they occur (Levin and Lubchenco 2008, Fuller et al. 2017). The third is the degree to which the network is concentrated around a central fishery, represented by network centralization (Cinner and Bodin 2010). Networks with high centralization display little sensitivity to a perturbation unless the perturbation impacts the central node. Modularity and centralization were calculated using network edge weights (Table S2.2); we also calculated unweighted modularity and centralization, as well as mean degree for a size-scalable alternative to edge density, and report these results in the Appendix.

Participation networks are highly dynamic over time in both size and structure (Figure S2.2, Figure S2.3, Figure S2.4), and can be influenced by a number of social and ecological factors. We used generalized linear models to attribute topological changes during the 2016 crab year to the 2016 Dungeness crab fishery closures, with network metrics as the response variables. Since the Dungeness crab fishery experienced shortened seasons prior to the 2016 crab year (Table S2.3), we captured the effect of the 2016 closures using a closure duration (D) categorical predictor variable. The 2016 closures represented the highest level of closure duration. We also included network size, crab year, community, and region as predictor variables in our nested models (Table S2.4, Table S2.5).

2.4 RESULTS

2.4.1 *Network-based expectations of community vulnerability*

Prior to the 2016 closures, patterns of fishery participation in California varied substantially between regions (Figure 2.1; Figure S2.3). Networks for the northern region fishing communities of Crescent City, Eureka, Fort Bragg, and Bodega Bay were composed of fewer fisheries; more highly centralized around Dungeness crab; had lower size-scaled fisheries connectivity (mean degree); and exhibited less modularity than the central region fishing communities of San Francisco, Monterey, and Morro Bay. These regional differences were particularly pronounced during the early season, when the majority of Dungeness crab landings occur (Dewees et al. 2004, Richerson et al. 2018). In the late season, northern region networks were more com-plex and less centralized, lessening most topological differences between regions (Figure S2.3). Network theory predicts that fishing communities in the northern region would be more vulnerable to a perturbation in the Dungeness crab fishery due to higher sensitivity (centralization, modularity) and lower adaptive capacity (fisheries connectivity, network size), particularly during the winter months of the early season.

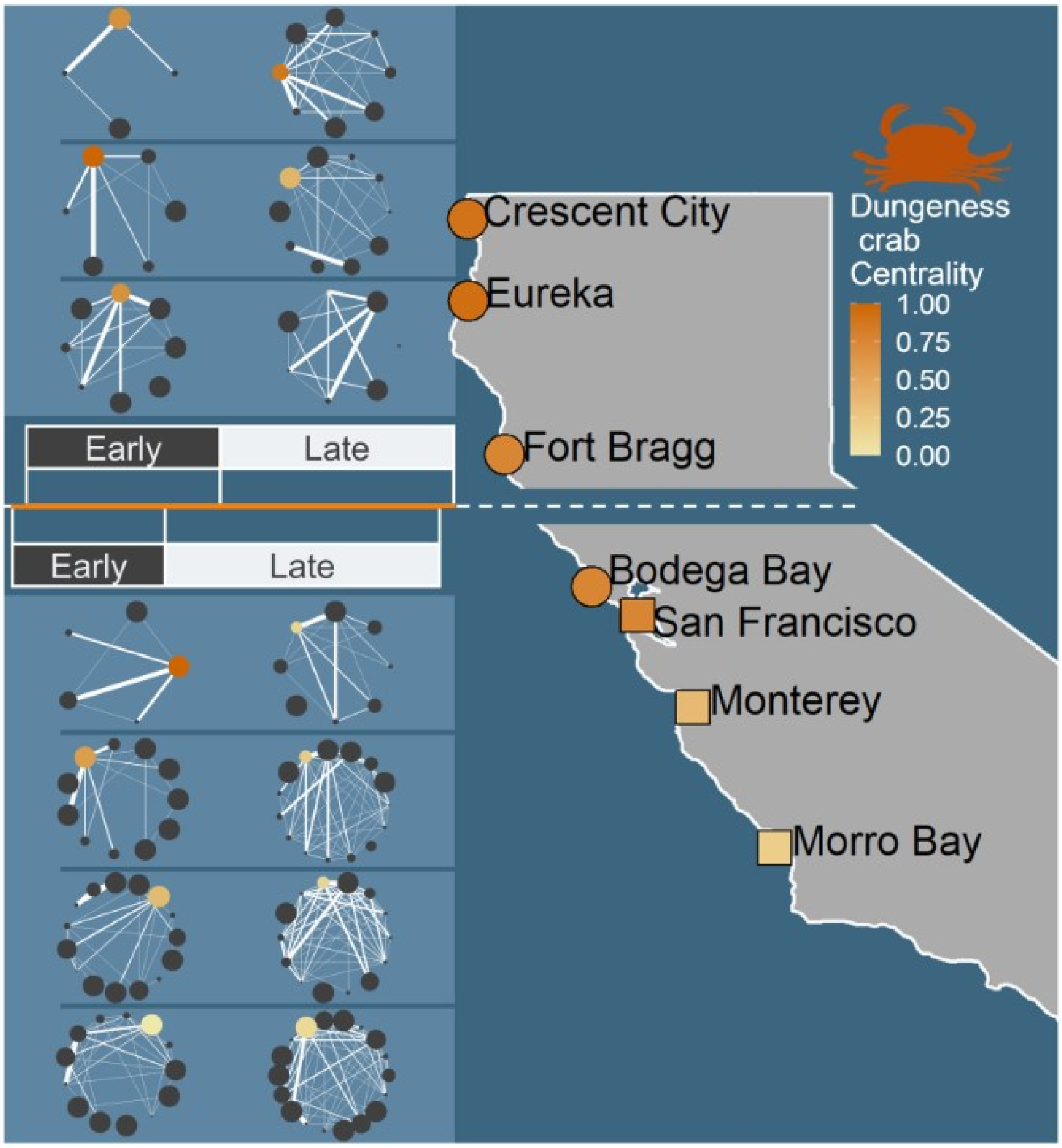

Figure 2.1. The seven California fishing communities included in this study, and their pre-shock fisheries participation networks. Pre-shock early (left) and late (right) networks represent a three-year average (crab years 2013-2015) of participation prior to the 2016 fishery closures. The Dungeness crab fishery node is shaded orange in each network according to its betweenness centrality, a measure of importance (note that nodes are not consistently positioned across networks). The timeline shows the relative duration of the early and late seasons for fishing communities in the two California management districts (above/below timeline). Point color on the map indicates average Dungeness crab betweenness centrality across the early and late

season, and point shape indicates whether the fishing community was considered part of the northern (circle) or central (square) region for this study.

2.4.2 *Northern region impacts during the shock*

Patterns of fishery participation during the early season were significantly more affected by the 2016 closures in the northern region than in the central region. Networks of fishing communities in the northern region saw significant declines in fisheries connectivity (edge density; -58%) and reduced concentration of participation around a single fishery (centralization; -31%) (Figure 2.2a; Table S2.6).

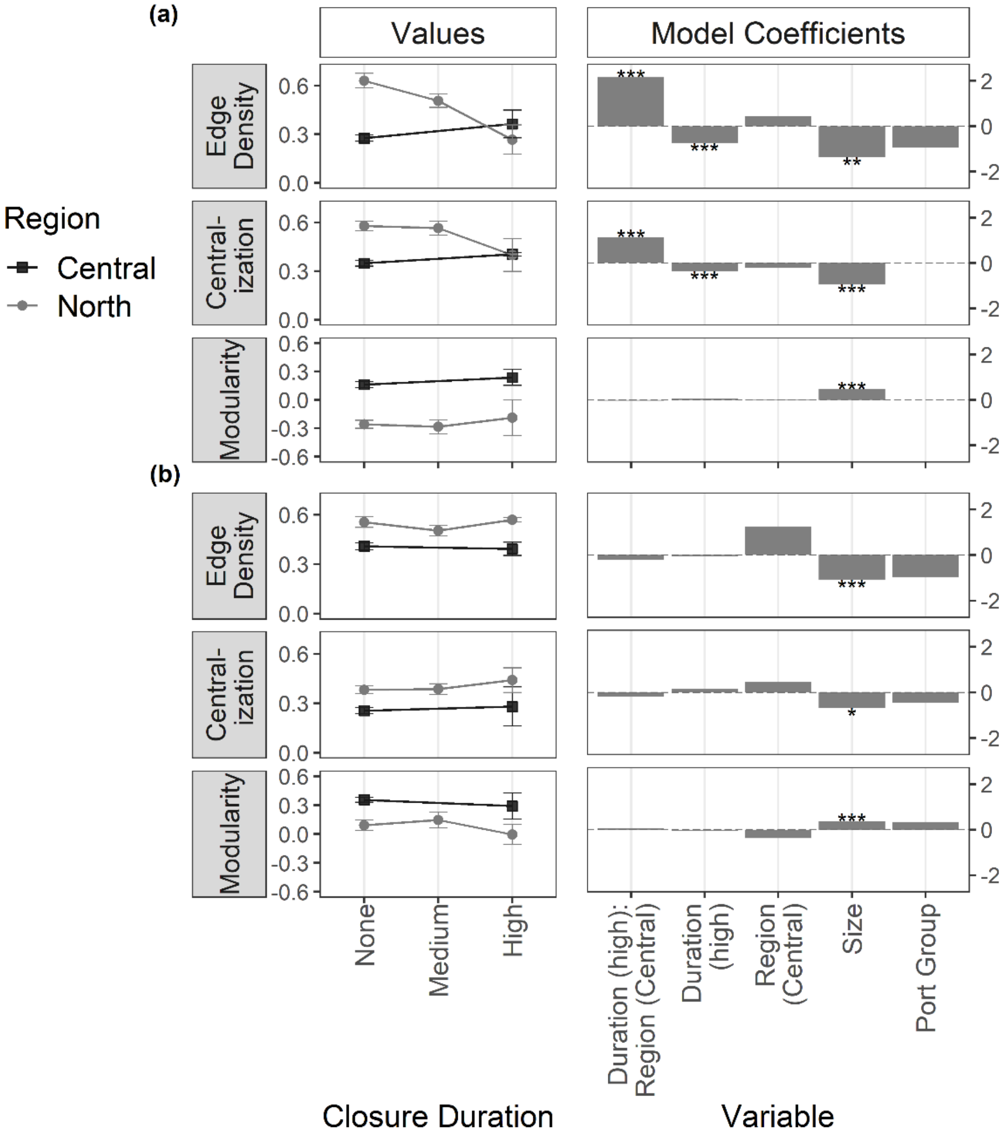

Figure 2.2. For each network metric in the **(a)** early and **(b)** late season, the mean value and standard error at every closure duration level (left), and the coefficients from the generalized linear models (right). Coefficients for edge density and centralization are on the logit scale. The Duration (high) x Region (central) term describes the change to the coefficient of the Duration (high) term when observing central, compared to northern, region networks. For example, the coefficient for Duration (high) x Region (central) in the model for early season edge density (a-top), is positive; this indicates that observing a network from the central region, compared to the northern region, makes the negative association of the 2016 closures with edge density more positive. Significance is indicated above each column (*p<0.05; **p<0.01; ***p<0.001).

These network changes represent three strategies undertaken by northern region Dungeness crab vessels to cope with, or adapt to, the 2016 closures: vessel dropout, spatial mobility, and spill-over into alternative fisheries. The majority of Dungeness crab fishing vessels in the northern region (56.4 ± 16.7%) discontinued all fishing in California during the 2016 closures. Early season vessel dropout was relatively consistent between large (≥40 ft) and small (<40 ft) vessels. Landing catch in a different community, representative of spatial mobility, was mostly undertaken by large vessels, particularly those that spent the previous crab year fishing in Eureka and Crescent City (Figure 2.3). Dropout and spatial mobility could have decreased fisheries connectivity if vessels that stopped fishing entirely or moved to a different fishing community would normally have participated in multiple fisheries during the early season.

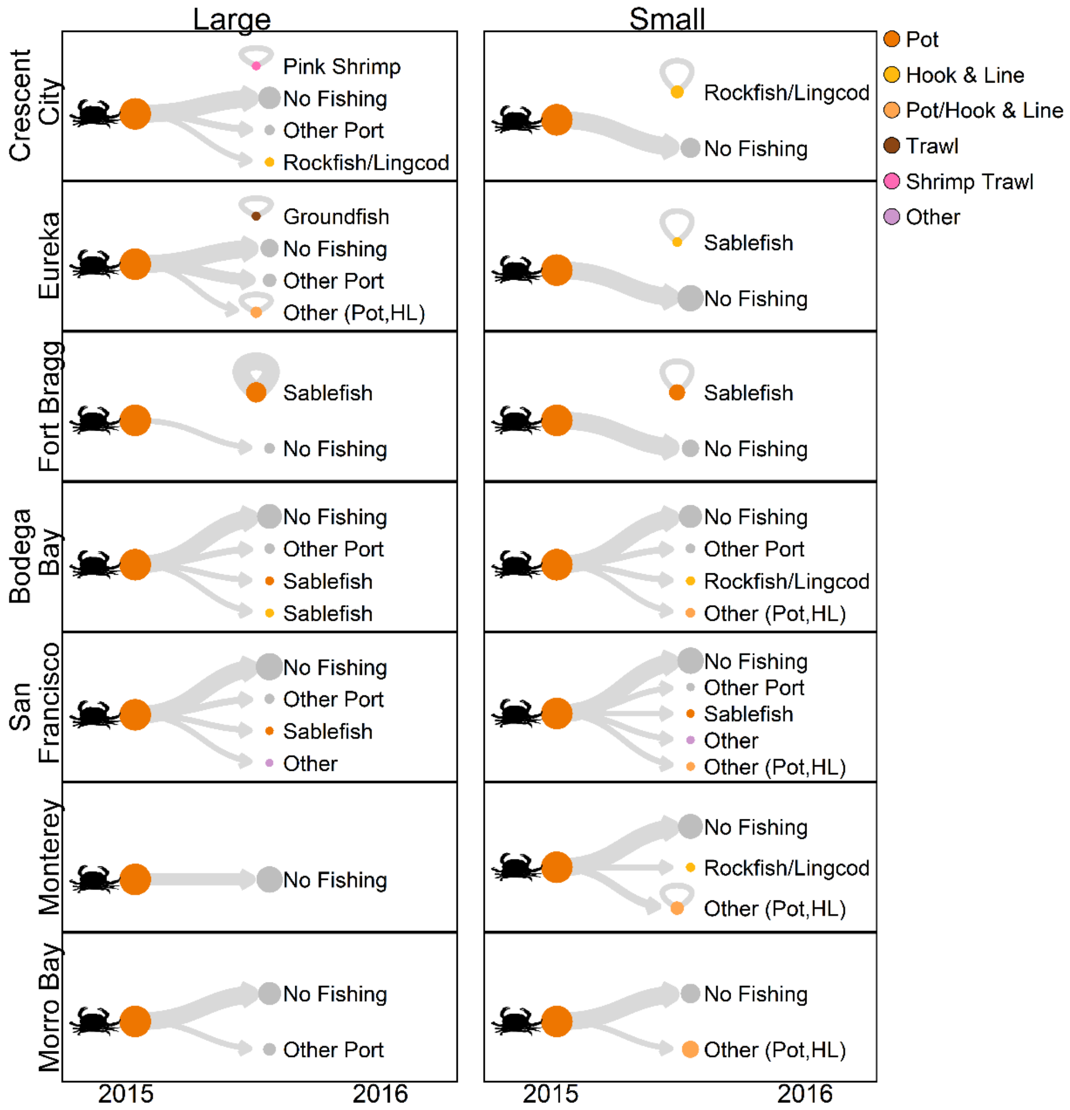

Figure 2.3. Change in early season fishery participation by large (left), and small (right) Dungeness crab vessels from the 2015 to the 2016 crab year. Edges show the flow of vessels out of the 2015 Dungeness crab fishery (left of each network graph, labeled with crab icon) into 2016 alternatives (right of each network graph). Self-loops were included if Dungeness crab vessels participated in a non-Dungeness fishery during both crab years; otherwise, the directed edge represents new early season participation in the 2016 alternative. Edge-weight is proportional to the number of Dungeness crab vessels which undertook the indicated shift in participation. Node size is proportional to the number of Dungeness crab vessels participating in each fishery during the associated crab year (x axis). When multiple fisheries using pot or hook-

and-line gear had fewer than three participating vessels, we collapsed the fisheries into a single "Other (Pot, HL)" node; the "Other" node is a similar aggregate, but with fisheries using any gear type. We added two non-fishery nodes to indicate whether a vessel stopped fishing altogether during the 2016 Dungeness crab closures ("No Fishing"), or whether the vessel stopped fishing at the given fishing community but was recorded landing catch at another California port ("Other Port").

The observed declines in fisheries connectivity were also tied to vessels that remained active within the same fishing community. Approximately 87% and 84% of active small and large vessels, respectively, concentrated participation in a single alternative fishery and thus did not contribute to fisheries connectivity during the early season of the 2016 crab year. During the early season of the previous crab year, 61% of these vessels spread participation across multiple fisheries (Dungeness crab and others). Spillover resulting from the 2016 closures was concentrated primarily in the sablefish and mixed rockfish/ling-cod fisheries (Figure 2.3), although northern region Dungeness crab vessels participated in a total of 16 alternative fisheries. Because vessels that normally would have concentrated participation in the Dungeness crab fishery dispersed into different alternatives, network centralization declined.

2.4.3 *Central region impacts during the shock*

Fisheries connectivity and centralization in the central region increased by 32% and 16%, respectively, during the early season of the 2016 crab year (Figure 2.2a). These changes were significantly different from the declines that occurred in the northern region during the closures (Figure 2.2a; Table S2.6).

Smaller changes in fisheries connectivity and centralization in the central region are consistent with network theory: lower reliance on the Dungeness crab fishery, represented by lower pre-shock Dungeness crab centrality (Figure 2.1), translated to less sensitivity to the loss of access to Dungeness crab. Increases in fisheries connectivity within central region fishing communities coincided with an increase in the diversity of fishery participation by Dungeness crab vessels, particularly in Monterey (n=18 active vessels). While northern region Dungeness crab vessels exhibited more single-fishery participation during the early sea-son of the 2016 crab year compared with the previous year, the proportion of active Dungeness crab vessels participating in two or more fisheries in the central region more than doubled be-tween the 2015 and 2016 early season (from 9% to 20%).

Lower reliance on the Dungeness crab fishery also makes it possible for dynamics external to the Dungeness crab fishery to have an equal or greater effect on patterns of resource use in central region fishing communities. Dungeness crab vessels represented only 14% of all commercial fishing vessels in Monterey and Morro Bay (Table 2.1), and the majority of central region. Dungeness crab vessels stopped fishing entirely during the early season (72.5 ± 0.1%). Therefore, even as concentrated participation in the Dungeness crab fishery was replaced with a number of alternative fisheries, decentralizing participation among Dungeness crab vessels, at a community scale these effects were relatively weak.

2.4.4 *California impacts immediately after the shock*

We observed minimal, nonsignificant effects of the 2016 closures on late season patterns of fishery participation (Figure 2.2b). None of the network metrics for either region exhibited significant change during the late season, although increases in centralization in the northern and central regions were significant when not weighted by revenue (Table S2.7). Increased centralization was likely from the concentration of participation in the high-revenue Dungeness crab fishery after the closures were lifted, at a time when fishers would normally have been prioritizing a variety of other fisheries, such as Chinook salmon (Figure S2.5).

2.5 DISCUSSION

As climate shocks become more frequent and intense under climate change, it is increasingly critical to predict, rapidly assess, and reduce the vulnerability of natural resource-based communities. For fishing communities, vulnerability to resource loss can be closely tied to access to alternative fisheries, an important source of adaptive capacity (Kasperski and Holland 2013, Cline et al. 2017). In this study, we found significant changes in patterns of fishery participation in response to fishery closures, forced by a heatwave-associated HAB. Greater changes in northern California fishing communities corresponded with greater sensitivity (increased specialization or network centralization), less adaptive capacity (lower fisheries connectivity and smaller network size), and heightened exposure (longer duration fishery closures). Patterns of fishery participation mostly returned to their pre-disturbance state following the opening of the Dungeness crab fishery, indicating community-level resilience to this singular perturbation. This study quantified the impact of a climate shock and subsequent management measures on natural resource use in fishing communities, and revealed the underlying behavior of fishing vessels.

A challenge in predicting community response to anthropogenic and environmental perturbations lies in quantifying community sensitivity and adaptive capacity (Adger 2006). Network metrics help us do this, serving as indicators of system sensitivity (centralization, modularity) and adaptive capacity (network size, connectivity) in the face of perturbations (Barnes et al. 2017, Fuller et al. 2017, Meng et al. 2018). We can therefore interpret our results through the lens of network theory and the vulnerability framework (Adger 2006) to provide a forward-looking glimpse into an alternative state under climate change, in which more frequent marine heatwaves and HABs (Moore et al. 2008, Lewitus et al. 2012) cause the loss of key resources for California fishing communities. On the one hand, minimal spillover and topological changes to fisheries participation networks following the 2016 closures suggest that patterns of fishery participation in California were resilient to this climate shock. However, if Dungeness crab vessel owners and operators were to permanently adopt the alternative fishing strategies observed during the 2016 closures, then our results imply that the northern fishing communities could become more vulnerable to secondary social and ecological perturbations. Even as participation becomes more evenly spread across existing fisheries, the sharp decline of fisheries connectivity (captured here with edge density) predicts a lower capacity for individuals to switch between fisheries. For the central region fishing communities, a more diverse portfolio of early season fishery participation could buffer the impacts of future perturbations if diversification were adopted as a long-term adaptive strategy (as was done by Pacífico Norte fishers; McCay et al. 2011); however, it is important to note that the lower reliance on Dungeness crab in the central region is also a key factor in maintaining low community vulnerability to secondary perturbations. The ability to reallocate fishing effort conferred by diverse harvest portfolios reduces variation in annual fishing revenue (Cline et al. 2017) and is critical for individual adaptation not only to climate shocks, but also to fishery management changes (e.g., catch share programs; Addicott et al. 2019, Kroetz et al. 2019). More generally, diversification is a fundamental tenet of resilience theory for social-ecological systems, which emphasize strategies that integrate over variability, shocks, and reorganization to sustain species, economies, and livelihoods (Folke et al. 2010).

There can be many counterincentives to diversification, however, especially when common species are highly valuable (Steneck et al. 2011) or when there are high barriers to access for certain resources (e.g., permitting structures, capital, knowledge; Anderson et al. 2017). In fisheries, concentration of effort into a single, highly lucrative fishery can result in a "gilded trap" (McCay 1978, Steneck et al. 2011). Most notably observed in the Maine American lobster industry, this type of social trap is formed as social drivers increase the value of the resource, even as the resource itself moves closer to an ecological tipping point (Steneck et al. 2011). Our research and community interviews (Ritzman et al. 2018) suggest that Dungeness crab might be considered a gilded trap for northern California fishing communities and associated coastal communities. While economically lucrative for fishers and fishing- related industries in the short term, a focus of effort on Dungeness crab increases vulnerability to climate shocks during the winter months when there is little existing activity in other fisheries. The Dungeness crab fishery is presently at risk not only from seafood safety concerns, but also from the bycatch of protected species (Santora et al. 2020) and the effects of ocean acidification on early life history stages (Bednaršek et al. 2020). Escape from social traps in re-source-based economies requires incentives and policies that address the underlying socioeconomic conditions and behavior reinforcing the trap. This can be a complex undertaking that requires careful investment in institutional capacity at multiple scales (Platt 1973, Cinner 2011).

These community patterns summarized in fisheries participation networks emerge from decisions made by individuals, which in turn are influenced by community-scale properties. The vessel activity that we describe highlights how the impacts of climate shocks are likely to be felt unequally within fishing communities, in California and beyond (Mearns and Norton 2009, Jardine et al. 2020). Differences in adaptive capacity during the 2016 closures were related to vessel size, with larger vessels conferring a greater ability to move out of closed areas to fish; we observed a greater proportion of large vessels than small vessels moving between fishing communities, particularly during the longer closures in the northern region. Our findings agree with those of Jardine et al. (2020), who used a three year baseline of Dungeness crab landings at the same California fishing communities to show that large Dungeness crab vessels were more mobile than small vessels in the 2016 crab year. Fishers with smaller vessels instead relied on alternative fisheries to remain active in-place. This discrepancy arose despite state management measures that seek to restrict mobility during fishery closures, requiring vessels landing Dungeness crab outside a delayed district to wait 30 days before fishing within the delayed district (1997, Cal. Fish and Game Code §8279.1). Recent amendments (Jardine et al. 2020), motivated in part by vessel movement during the 2016 crab year, may limit the feasibility of spatial redistribution as a strategy to cope with future climate shocks.

Yet, moving to a location where social and ecological conditions are more favorable may be more effective than reliance on strategies to remain active in-place, such as shifting effort to alternative fisheries. Keeping pace with shifting species ranges and abundance under climate change often requires resource users to modify the spatial distribution and intensity of their efforts (Wang et al. 2013, Young et al. 2019). In addition, the adoption of limited entry and catch share programs may make it increasingly difficult to remain active in-place by accessing alternative fisheries. For example, on the U.S. West Coast, the 2012 Pacific groundfish trawl rationalization and 2002 Pacific sablefish permit stacking programs restricted access to certain groundfish and sablefish fisheries. This led to historically active vessels exiting the affected fisheries (Holland et al. 2017) and higher costs to new participants (Russell et al. 2018). A comprehensive comparison of climate adaptation through in-place strategies as opposed to movement must also account for access to diverse employment opportunities beyond fishing (often captured by education and economy size; Adger 1999, Colburn et al. 2016). Extending participation networks to include non-fisheries job participation (i.e., “livelihood landscapes;” (Cinner and Bodin 2010) provides this more holistic view of in-place adaptive capacity and may capture co-occurring effects of climate shocks across food systems (Cottrell et al. 2019). Livelihood landscapes also focus on individuals or households and so can speak to the heterogeneity in capacity and agency among fishers, something not captured with vessel-level data.

While some individuals move or modify behavior in response to climate shocks, others are unable to access viable alternatives and must simply absorb the impact and rebuild. This “duck-and-cover” strategy is particularly common in fishing and agrarian communities following major storms (Campbell and Beckford 2009, Valdez et al. 2019). In the California Dungeness crab fishery, a surprisingly high proportion of large and small Dungeness crab vessels adopted this duck-and-cover strategy and ceased all fishing activity during the 2016 closures. Most vessels waited out the closures in port (Ritzman et al. 2018, Moore et al. 2020a), despite later evidence that alternative fishing activities contributed significantly to fishers’ income loss recovery (Moore et al. 2020b).The prevalence of this strategy, and adaptive actions more broadly, may be best understood as the outcome of nested decision making processes at both individual and institutional levels (Adger and Vincent 2005). On the U.S. West Coast, HAB monitoring and associated fishery closures are implemented by state and tribal governments; as a result, the structure and effectiveness of early warning systems and communication with stakeholders varies by region (Ekstrom et al. 2020). California fishers have requested more reliable and clear communication by scientific and regulating institutions during future HAB events to facilitate more effective decision-making (Ritzman et al. 2018). Communication and prediction are both important for climate shock preparedness and, more generally, in “climate-ready” fisheries management (Wilson et al. 2018).

Another key consideration for developing climate-ready fisheries management is how to facilitate fishing effort spillover in such a way as to increase adaptive capacity and achieve a net decline in vulnerability. Fishers are creative problem solvers with a long history of adapting to challenging conditions (Stoll et al. 2017), but they must also be supported by governance systems. This will require coordination and partnership between governing institutions; in our study system, the Dungeness crab fishery is managed at the state level, but alternatives during the 2016 closures consisted of both state- and federally-managed fisheries. Also needed is careful consideration of unintended outcomes that may arise from improving mobility between fisheries, such as increased or novel interactions with protected species (Santora et al. 2020) and other ocean use sectors, the potential for overcapitalization of remaining open access fisheries, and incentivization of a “roving bandit” strategy of sequential overharvesting across a participation network (Berkes et al. 2006). When designing governance measures to temporarily facilitate spillover during a climate shock, combining networks of economic and ecological connectivity among fisheries, and considering networks that represent different types of fishery participants, could help to assess direct and indirect social and ecological impacts (Yletyinen et al. 2018).

Our findings suggest that management approaches that account for connectivity and spillover between fisheries during a climate shock are more likely to anticipate, and potentially mediate, impacts on fishing communities. The impacts of climate shocks are a materialization of underlying risk and vulnerability (Birkmann et al. 2013) in fisheries and other components of food systems. Quantifying connectivity between alternative resources can capture these impacts and uncover sources of sensitivity and adaptive capacity in highly dynamic, resource-based communities - a critical step toward achieving sustainability in the face of climate shocks and long-term change.

2.6 MATERIALS & METHODS

2.6.1 *Harmful algal bloom monitoring and management in California*

On the U.S. West Coast, state and tribal governments implement public safety thresholds of harmful algal bloom (HAB) toxin concentrations set at the federal level by the U.S. Food and Drug Administration (Ekstrom et al. 2020). The California Department of Public Health, in collaboration with fishers, monitors seawater and shellfish for HAB toxins as part of the Biotoxin Monitoring Program (Ekstrom et al. 2020). Forecast models developed and operated by academic and government scientists improve the state's ability to anticipate the occurrence and toxicity of HABs (Anderson et al. 2016). Forecast products were provided routinely beginning February 2014 (via the Central and Northern California Ocean Observing System), but were not made operational until June 2018 (NOAA CoastWatch, https://coastwatch.noaa.gov). By recommendation from the California Department of Public Health, the California Department of Fish and Wildlife implements state-level commercial and recreational fishery closures and coordinates with state officials in Oregon and Washington per the Tri-State Dungeness crab Agreement to prevent out-of-state harvest during season delays (Ekstrom et al. 2020, Jardine et al. 2020). The Tri-State Dungeness crab Agreement formalizes procedures for interstate cooperation between California, Oregon, and Washington in managing the Dungeness crab fishery (S.Rpt.114-260, 2016). The California Department of Fish and Wildlife also communicates fishery closures through publicly posted advisories, although a survey of fishing industry members after the 2015 HAB event suggests that these advisories are secondary to local television news programs as a source of HAB information (Ekstrom et al. 2020). Federal disaster relief funds are provided through the National Oceanic and Atmospheric Administration, after approval by Congress (Ekstrom et al. 2020, Brown 2016).

2.6.2 *Data*

Fisheries landings and vessel registration data for the 2008-2017 crab years were retrieved from the Pacific Fisheries Information Network (PacFIN, pacfin.psmfc.org) database. Landings data was filtered to include commercial landings from 30 California ports of landing, or seven port groups, where Dungeness crab is an important source of revenue (Figure 2.1; Table 2.1). Since we expected length-based differences in adaptive capacity (Jardine et al. 2020), we used registration data to calculate vessel length in feet (see below) and distinguished between vessels ≥ 40 and < 40 feet in length as large and small vessels, respectively (Kasperski and Holland 2013, Jardine et al. 2020).

2.6.3 *Calculating vessel lengths*

The vessel length information included in the California Department of Fish and Wildlife vessel registration data is self-reported, and so is subject to human error. To account for this, we calculated vessel length as the median of the two most recent lengths recorded, searching the registration data up to three years prior to the given calendar year. If fewer than two years of vessel length data was available, or if the maximum vessel length recorded was more than 10 feet longer than the minimum vessel length, the search space was expanded to up to five years. Vessel length was considered unavailable if there were still fewer than two years of length data recorded, or if there were exactly two years of length data recorded where the maximum length was more than 10 feet larger than the minimum length.

Since vessel registration is recorded by calendar year and the California Dungeness crab season spans two calendar years, approximately 0.9% of vessels were reported as both large and small vessels in a single crab season. These vessels were assigned a length category according to the calendar year in which they recorded the greatest landed pounds of Dungeness crab.

2.6.4 *Defining fisheries and fishing communities*

We defined fisheries by grouping PacFIN fish tickets based on gear type, species composition of catch, and ex-vessel revenue using a métier analysis (Deporte et al. 2012) modified from Fuller et al. (2017). In short, we ran the *infoMap* community detection algorithm (Rosvall and Bergstrom 2008) implemented in the R package *igraph* (Csardi and Nepusz 2006) on data from fish tickets collected during the 2011 and 2012 crab years (chosen because they occurred in the middle of our pre-shock study period). The remaining fish ticket data were matched to the *infoMap*-processed fish tickets using a k-nearest neighbor (KNN) approach. Fish tickets that failed to be assigned métiers with KNN (i.e. those that recorded unique species / gear combinations), were compiled across crab years and re-run through the *infoMap* algorithm. Fish tickets are linked to vessels, which form the foundation of our participation analyses. Thus our definition of a fishing community is a set of vessels which land their catch at a given shore-based port group. We use vessels as proxies for fishers due to the limitations of available data (Fuller et al. 2017, Holland et al. 2017), not the notion that a collection of vessels is a better way to characterize a community than a group of people. While this is an imperfect approximation, it does allow us to track changes in harvesting practices through time, across vessel sizes and geographic regions.

2.6.5 *Constructing networks*

Participation networks summarized cross-fishery participation for all vessels in a fishing community. If a single fishing vessel recorded catch in multiple fishing communities within a single crab year, it was considered to be a member of each fishing community. We used the Fuller et al. (2017) network framework, in which the weight of a non-directional edge between fisheries *i* and *j* represents a measure of fisheries connectivity which is proportional to the number of vessels participating in both fisheries, and the evenness with which each vessel generates revenue from fishery *i* versus fishery *j*. We constructed directed networks to observe changes in fishery participation by Dungeness crab vessels in each fishing community. "Dungeness crab vessels" were defined as any fishing vessel which recorded at least one commercial Dungeness crab landing in California in the 2015 crab year (N=477 unique vessels).

2.6.6 *Generalized linear models*

We evaluated a series of nested models (Table S2.4) and chose the most informative model using an F-test. Participation network size varies through time and across fishing communities, and certain network metrics like edge density and centralization are known to be dependent on network size. In order to distinguish between a meaningful signal of change and variability related to network size, we conservatively included network size (N) as a predictor variable based on results from a Spearman's Rank Correlation test (Spearman 1904) between each metric and the number of nodes in the network (Table S2.5). Standardized residuals and Q-Q plots were used to assess normality, linearity and homoscedasticity assumptions, and the model was tested for sensitivity to outliers detected with Cook's distance.

2.6.7 *Data availability*

Confidential vessel-level landings and registration data may be acquired by direct request from the California Department of Fish and Wildlife, subject to a non-disclosure agreement. Aggregated, non-confidential data to construct network graphs, network metrics data used as input for the GLMs, and R code are available on Github (DOI: 10.5281/zenodo.4177949).

Return to Table of Contents.

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2.8 APPENDIX

2.8.1 *Supplemental Tables*

Table S2.1. 2016 California Dungeness crab commercial fishing closures by fishing community, used to determine whether landings data was considered part of the early or late season. Region is based on NMDS analysis (Figure S2.1). (*) indicates this date was used to delineate early season for all fishing communities in the given region. Source: California Department of Fish and Wildlife.

Date Opened	**Ports Available to Land**	**Region**	**Fishing Communities**
March 26, 2016*	Bodega Bay and south	Central	Bodega Bay, San Francisco, Monterey, Morro Bay
May 12, 2016*	Crescent City, Eureka, Fields Landing, Shelter Cove, Fort Bragg, Point Arena	North	Crescent City, Eureka, Fort Bragg
May 26, 2016	Trinidad	North	Eureka

Table S2.2. Equations for network metrics.

	Unweighted	Weighted	Variables
Edge Density	$\frac{m}{\frac{n*(n-1)}{2}}$		m: number of edges n: number of nodes
Mean Degree	$2*\frac{m}{n}$		m: number of edges n: number of nodes
Modularity (Q)	$\frac{1}{2m}\sum_{ij}\left[A_{ij} - \frac{k_ik_j}{2m}\right]\delta(c_ic_j)$	$\frac{1}{2m}\sum_{ij}\left[A_{ij} - \frac{k_ik_j}{2m}\right]\delta(c_ic_j)$	m: number of edges A_{ij}: element in row i, column j of adjacency matrix k: degree (unweighted) or sum of weights of adjacent edges (weighted) of nodes i, j c: component of i, j
Network centralization (C_d)	$\frac{\sum_{i=1}^{n}[d^* - d_i]}{[(n-2)(n-1)]}$	$\frac{\sum_{i=1}^{n}[s^* - s_i]}{[(n-2)(n-1)] * \bar{w}}$	d^*: maximum degree centrality d_i: degree of node i s^*: maximum node strength s_i: strength of node i n: number of nodes $\bar{w}$: average edge weight

Table S2.3. Duration (D) of Dungeness crab closures for crab years 2008-2017. When there was variation in delay duration within a fishing community, the longest delay period was selected to represent the community. Source: California Department of Fish and Wildlife.

Crab Year	**Communities**	**Days of Closure**	**Closure Duration**	**Cause of Closure**
2012	Crescent City, Eureka, Fort Bragg	45	Medium	Soft shell or poor quality crab
2013	Crescent City, Eureka, Fort Bragg	45	Medium	Soft shell or poor quality crab
2016	All	88 - 177	High	Domoic acid
2017	Eureka, Fort Bragg, Bodega Bay	18 - 28	Medium	Domoic acid

Table S2.4. Summary of models tested for each network metric (response). Predictor variables consist of Closure Duration (D), Region (R), Network Size (N), Crab Year (Y), and Fishing Community (P). The most informative model used for final analysis is indicated by bolded text. If no text is bolded, the base model was used. Significant indicated as: (.) p<0.10, (*) p<0.05, (**) p<0.01, (***) p<0.001

			Early Season		*Late Season*	
Network Metric	***Distribution, Link***	***Model***	***F statistic***	***p-value***	***F statistic***	***p-value***
Edge Density	Quasi-binomial, logit	D:R + N + D + R				
		D:R + N + D + R + Y	1.13	0.292	1.16	0.286
		D:R + N + D + R + P	**4.42**	**0.004****	**6.96**	**0.000*****
		D:R + N + D + R + Y + P	1.17	0.285	0.757	0.388
		D:R + N + Y:R + D + R + Y + P	1.71	0.197	0.011	0.918
Centralization (Weighted)	Quasi-binomial, logit	D:R + N + D + R				
		D:R+ N + D + R + Y	0.007	0.934	1.24	0.270
		D:R+ N + D + R + P	1.84	0.137	**6.15**	**0.000*****
		D:R + N + D + R + Y + P	0.051	0.822	1.50	0.227
		D:R+ N + Y:R + D + R + Y + P	0.175	0.677	1.77	0.189
Modularity (Weighted)	Gaussian, identity	D:R + N + D + R				
		D:R + N + D + R + Y	1.50	0.226	0.037	0.848
		D:R + N + D + R + P	2.12	0.092 **.**	**5.91**	**0.001*****
		D:R + N + D + R + Y + P	0.962	0.331	0.121	0.729
		D:R + N + Y:R + D + R + Y + P	0.046	0.831	2.50	0.120
Mean Degree	Gamma, inverse	D:R + N + D + R				
		D:R + N + D + R + Y	0.088	0.768	1.09	0.301
		D:R + N + D + R + P	**6.50**	**0.000*****	**2.95**	**0.029***
		D:R + N + D + R + Y + P	0.010	0.923	0.896	0.348
		D:R + N + Y:R + D + R + Y + P	0.004	0.952	0.741	0.393
Centralization	Quasi-binomial, logit	D:R + D + R				
		D:R + D + R + Y	0.592	0.445	0.368	0.547
		D:R + D + R + P	2.10	0.096	1.64	0.179
		D:R + D + R + Y + P	0.330	0.568	0.347	0.558
		D:R + Y:R + D + R + Y + P	1.62	0.210	0.020	0.887
Modularity	Gaussian, identity	D:R + N + D + R				
		D:R + N + D + R + Y	0.703	0.405	1.60	0.211
		D:R + N + D + R + P	**4.43**	**0.004****	**2.92**	**0.030***
		D:R + N + D + R + Y + P	0.278	0.600	1.30	0.259
		D:R + N + Y:R + D + R + Y + P	2.04	0.159	0.786	0.379

Table S2.5. Spearman's rank correlation tests between network metrics and node count. Final column indicates whether the nested generalized linear models for the given metric included network size, quantified by node count (see Table S2.4). Significance indicated as: (.) p<0.10, (*) p<0.05, (**) p<0.01

Network Metric	**Period**	**Spearman's ρ (North)**	**Spearman's ρ (Central)**	**GLM contains N**
Edge Density	Early	-0.414**	-0.106	Yes
	Late	-0.630**	-0.488**	
Centralization (W)	Early	-0.570**	-0.064	Yes
	Late	-0.413**	-0.164	
Modularity (W)	Early	0.725**	0.458*	Yes
	Late	0.653**	0.279	
Mean Degree	Early	0.846**	0.271	Yes
	Late	0.325*	0.154	
Centralization	Early	-0.143	0.270	No
	Late	0.044	-0.036	
Modularity	Early	0.706**	0.307 .	Yes
	Late	0.674**	0.212	

Table S2.6. Unscaled coefficient estimates and standard errors in the most informative generalized linear models for each network metric, for early season networks. Coefficients are in rows, with network metrics listed by column. The final model used for analysis is listed beneath the metric name (also see Table S2.4). The “high” category of the duration predictor variable represents the 2016 closures. The Duration (high) x Region (central) interaction term indicates that the association between the 2016 closures and the network metrics was more positive (edge density, centralization) or more negative (modularity, mean degree) when observing central region networks, as opposed to northern region networks.

	Edge Density	Centralization	Modularity	Mean Degree	Centralization (UnW)	Modularity (UnW)
	D*R+P+N	D*R+N	D*R+N	D*R+P+N	D*R	D*R+P+N
Duration (high)	-1.66***	-0.85***	0.09	0.58	-1.02	-0.04
	(0.39)	(0.25)	(0.12)	(0.45)	(0.56)	(0.07)
Duration (med.)	-0.42	-0.09	-0.05	0.04	0.17	-0.07
	(0.28)	(0.17)	(0.07)	(0.04)	(0.48)	(0.05)
Duration (high) : Region (C)	2.14***	1.14***	-0.04	-0.68	1.03	-0.02
	(0.41)	(0.29)	(0.15)	(0.45)	(0.58)	(0.08)
Region (Central)	-1.14	-0.21	0.003	0.10	-1.02***	0.44**
	(0.62)	(0.25)	(0.09)	(0.14)	(0.30)	(0.16)
Node Count	-0.22**	-0.15***	0.08***	-0.05***		0.02
	(0.07)	(0.04)	(0.01)	(0.01)		(0.02)
Port Group (Crescent City)	-0.37			0.05		0.08
	(0.46)			(0.15)		(0.07)
Port Group (Eureka)	-0.71			-0.15		0.22**
	(0.48)			(0.11)		(0.08)
Port Group (Fort Bragg)	-0.10			-0.30*		0.29**
	(0.52)			(0.12)		(0.10)
Port Group (Monterey)	0.44*			-0.12		-0.01
	(0.18)			(0.06)		(0.04)
Port Group (Morro Bay)	0.87***			-0.26***		-0.17***
	(0.17)			(0.06)		(0.05)
Intercept	1.78***	1.04***	-0.58***	0.94***	0.61*	-0.46***
	(0.47)	(0.23)	(0.08)	(0.10)	(0.28)	(0.06)
Observations	69	64	70	70	65	70

Note: $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

Table S2.7. Unscaled coefficient estimates and standard errors in the most informative generalized linear models for each network metric, for late season networks. Coefficients are in rows, with network metrics listed by column. The final model used for analysis is listed beneath the metric name (also see Table S2.4). The "high" category of the duration predictor variable represents the 2016 closures. The Duration (high) x Region (central) interaction term indicates that the association between the 2016 closures and the network metrics was more positive (modularity, mean degree) or more negative (edge density, centralization) when observing central region networks, as opposed to northern region networks.

	Edge Density D*R+P+N	Centralization D*R+P+N	Modularity D*R+P+N	Mean Degree D*R+P+N	Centralization (UnW) D*R	Modularity (UnW) D*R+P+N
Duration (high)	0.05	0.25	-0.10	-0.01	0.75^{**}	-0.01
	(0.19)	(0.21)	(0.10)	(0.03)	(0.25)	(0.05)
Duration (med.)	0.05	0.19	-0.04	-0.02	0.38^{**}	0.001
	(0.12)	(0.14)	(0.07)	(0.02)	(0.15)	(0.04)
Duration (high) : Region (C)	-0.22	-0.21	0.06	0.03	-0.68	-0.03
	(0.23)	(0.56)	(0.14)	(0.03)	(0.39)	(0.06)
Region (Central)	-0.36	-0.37	0.12	0.02	0.32^{*}	-0.07
	(0.25)	(0.34)	(0.11)	(0.03)	(0.13)	(0.06)
Node Count	-0.15^{***}	-0.10^{*}	0.05^{***}	-0.01^{**}		0.03^{***}
	(0.03)	(0.04)	(0.01)	(0.004)		(0.01)
Port Group (Crescent City)	-0.60^{***}	-0.52^{***}	0.25^{**}	0.04^{*}		0.05
	(0.16)	(0.15)	(0.08)	(0.02)		(0.04)
Port Group (Eureka)	-0.94^{***}	-0.34^{*}	0.36^{***}	0.08^{**}		0.13^{***}
	(0.18)	(0.16)	(0.07)	(0.03)		(0.04)
Port Group (Fort Bragg)	-0.52^{**}	-0.63^{**}	0.16	0.02		0.03
	(0.19)	(0.21)	(0.09)	(0.02)		(0.04)
Port Group (Monterey)	0.33^{*}	0.36	-0.01	-0.04^{*}		0.03
	(0.15)	(0.21)	(0.06)	(0.02)		(0.03)
Port Group (Morro Bay)	0.23	-0.39	0.01	-0.03^{*}		0.01
	(0.12)	(0.21)	(0.06)	(0.01)		(0.03)
Intercept	1.82^{***}	0.55	-0.47^{***}	0.35^{***}	-0.48^{***}	-0.27^{***}
	(0.32)	(0.29)	(0.10)	(0.03)	(0.10)	(0.06)
Observations	70	70	70	70	70	70

Note: $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

2.8.2 *Supplemental Figures*

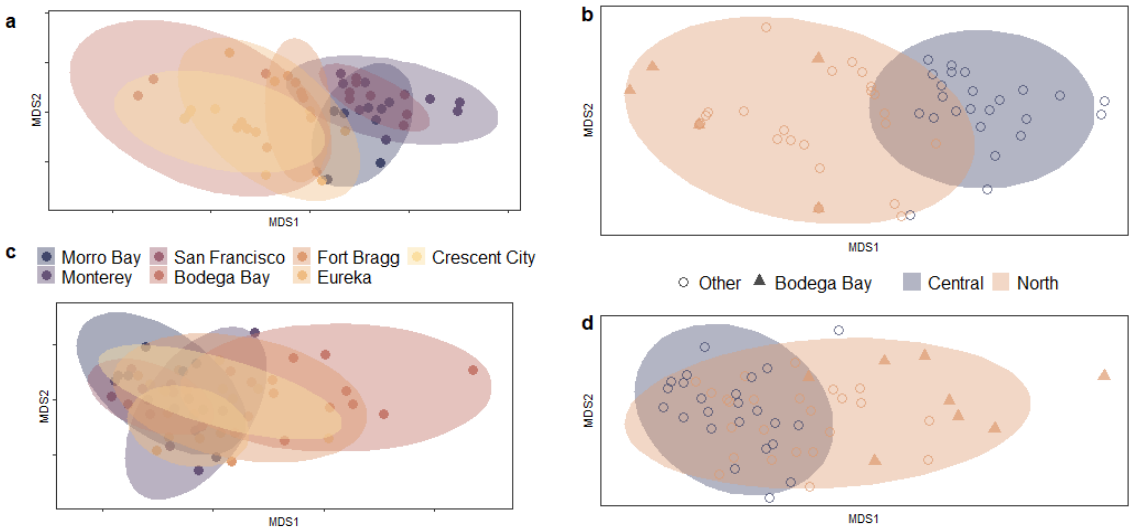

Figure S2.1. Nonmetric Multidimensional Scaling (NMDS) Analysis of seven California fishing communities, during the **(a, b)** early (stress: 0.068) and **(c, d)** late season (stress: 0.067). Groups are shown as individual fishing communities (a, c) and as regions defined for generalized linear models (b, d). NMDS was conducted with the network metrics (edge density, network centralization, modularity) from each crab year used in the generalized linear models, 2008-2017. Ellipses represent 90% confidence intervals around yearly observations for each fishing community or region. We placed the fishing community of Bodega Bay in the northern region for our analysis, despite its geographic location in the central California management district, to reflect its network structure (b, d).

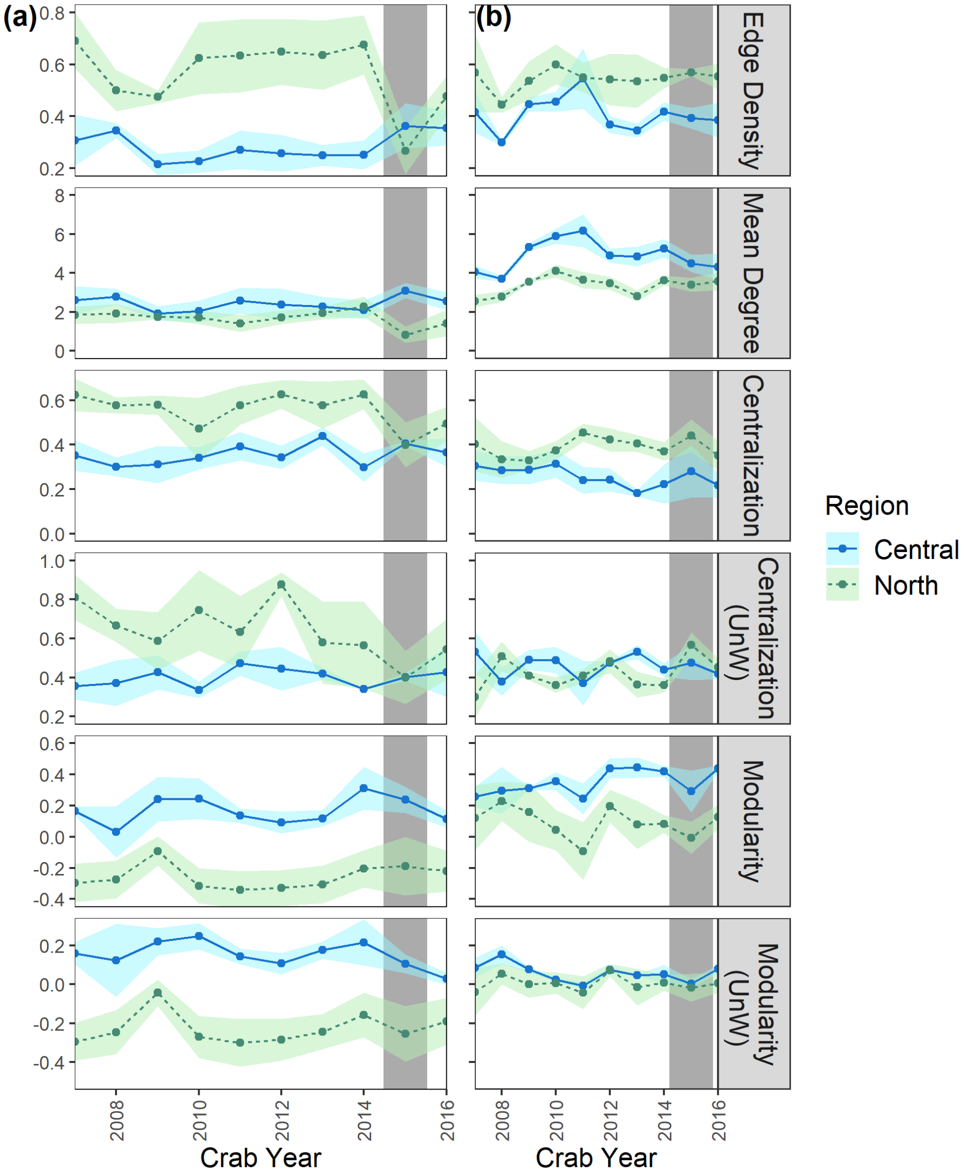

Figure S2.2. Mean value of network metrics by crab year, for the **(a)** early season, and **(b)** late season. Shaded area around mean line shows standard error across fishing communities within each region. Grey shading highlights the 2016 crab year. “UnW” indicates that the metric was not calculated using edge weights; mean degree is a size-scaled measure of connectivity, presented as an alternative to edge density.

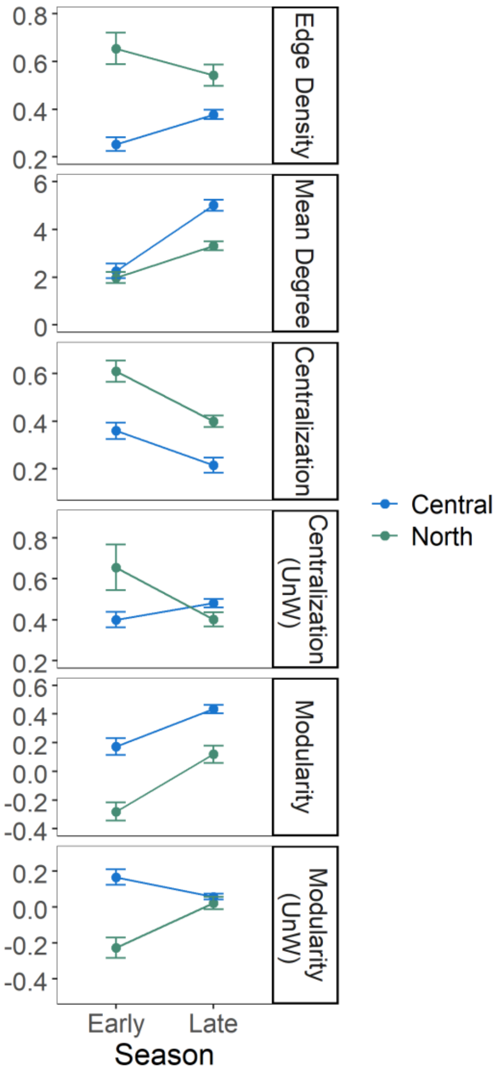

Figure S2.3. Mean value of network metrics during the three-year pre-shock period (2013-2015 crab years; see Figure 2.1) for the early and late seasons. Error bars show standard error across fishing communities within each region and season. “UnW” indicates that the metric was not calculated using edge weights; mean degree is a size-scaled measure of connectivity, presented as an alternative to edge density.

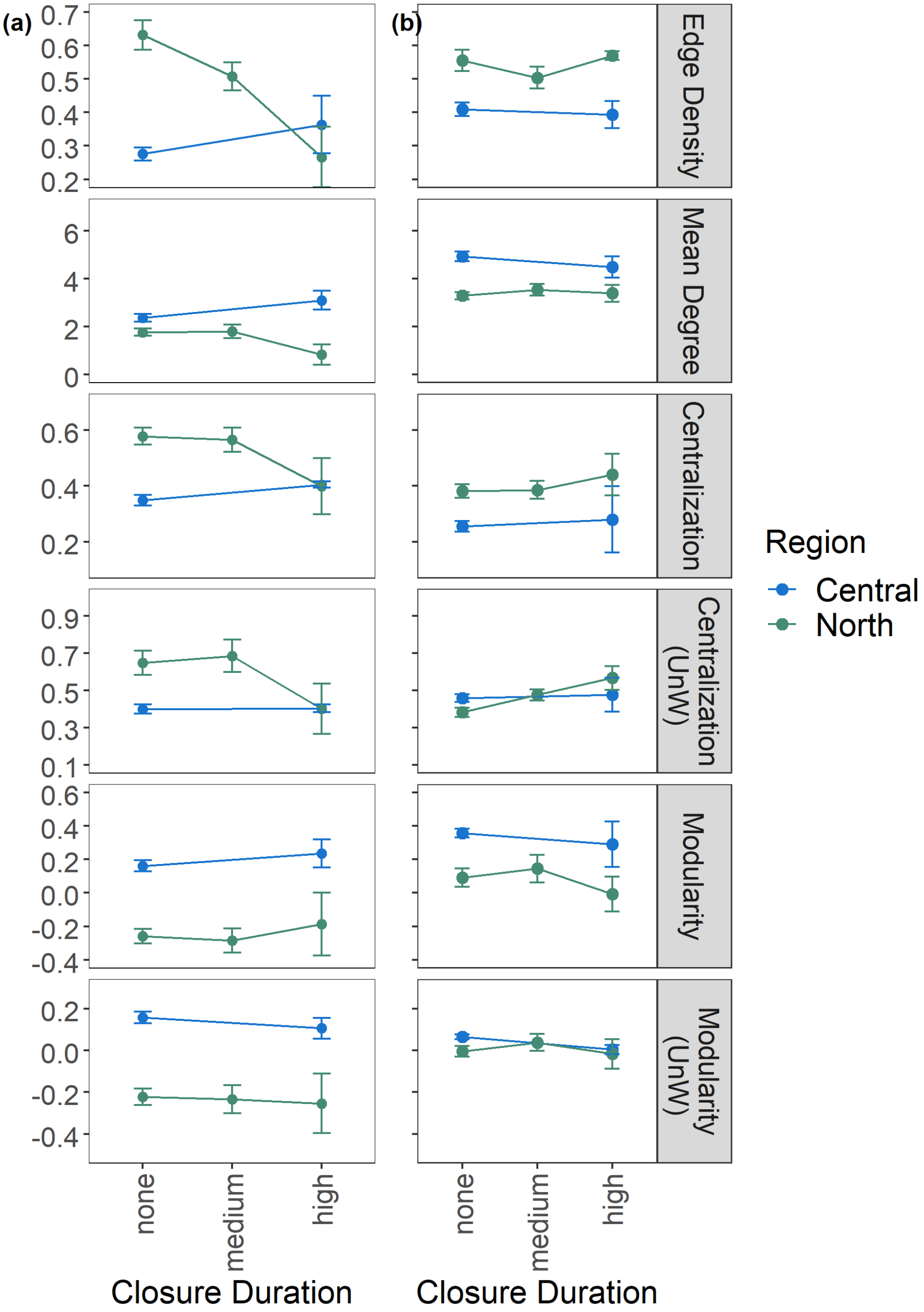

Figure S2.4. Mean value of network metrics by level of closure duration, for the **(a)** early season, and **(b)** late season. Error bars show standard error across fishing communities and crab years. "UnW" indicates that the metric was not calculated using edge weights; mean degree is a size-scaled measure of connectivity, presented as an alternative to edge density.

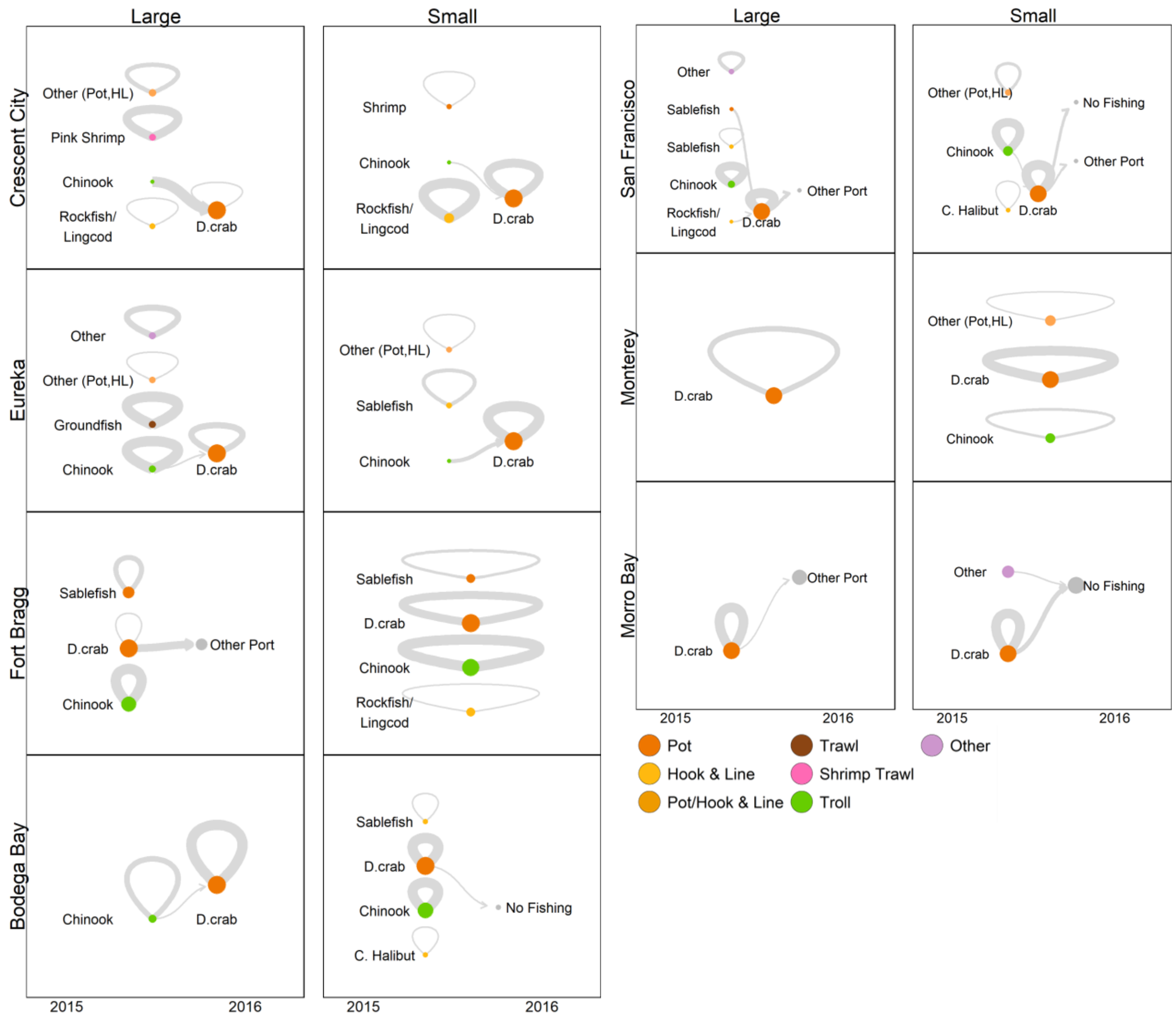

Figure S2.5. Late season change in fishery participation by large (left), and small (right) Dungeness crab vessels from the 2015 to the 2016 crab year. Edges show the flow of vessels out of the 2015 fisheries (left of each network graph) into the 2016 alternatives (right of each network graph). If the Dungeness crab fishery ("D. crab") had participants both enter and exit during the late season of the 2016 crab year, it is placed in the center of the network graph. Self-loops were included if Dungeness crab vessels participated in a fishery during both crab years; otherwise, the directed edge represents new late season participation in the 2016 alternative. Edge-weight is proportional to the number of Dungeness crab vessels which undertook the indicated shift in participation. Node sizes are proportional to the number of Dungeness crab vessels that participated in the given alternative in the 2016 crab year. When multiple pot-based or hook and line-based fisheries had fewer than three vessels participating, we collapsed the fisheries into a single “Other (Pot, HL)” node. “Other” is a similar compilation of fisheries with fewer than three vessels participating, of any gear type. We added two non-fishery nodes to indicate whether a previously active vessel stopped fishing in California during the 2016 late season (“No Fishing”), or whether the vessel stopped recording catch at the given fishing community, but was recorded at another California fishing community (“Other Port”).

A number of Dungeness crab vessels in Crescent City, Eureka, San Francisco, and Monterey, participated in the late season Dungeness crab fishery when they would not otherwise have been landing any catch in the given fishing community. This participation is incorporated into the node size of the Dungeness crab fishery in the network graphs, although we do not include a network edge to describe this pattern.

Chapter 3. SPATIAL DIVERSIFICATION IN THE DUNGENESS CRAB FISHERY, AND IMPLICATIONS FOR SMALL VESSEL OPERATORS

3.1 ABSTRACT

Spatial diversification of fishing grounds confers resilience for fishers facing area closures and shifting species distributions under climate change. Yet it can also have unintended consequences for ecosystems and fisheries. We explored differential capacity for spatial diversification in one of the most valuable fisheries on the U.S. West Coast before, during, and after unprecedented area closures due to harmful algal blooms (HABs). To do so, we used over 287,000 vessel geolocations for the California Dungeness crab fishery to quantify and map inter-annual changes in Dungeness crab fishing grounds between the 2013 and 2018 fishing seasons. We then asked whether spatial diversification was associated with changes in fishing ground overlap between groups of fishing vessels, thereby affecting crowding and competition. We considered six vessel groups, classified by 'home' fishery management area and vessel size class (large, ≥40ft; and small, <40ft). Based on fishers' experiences and previous research, we hypothesized that spatial diversification by large crab fishing vessels in HAB-impacted fishing seasons would temporarily increase spatial overlap in fishing grounds between vessel groups that were otherwise spatially separated. Our analyses showed that large fishing vessels did change their fishing grounds significantly more than small vessels; however, this was true across all fishing seasons, and not just the two seasons impacted by HABs. Spatial diversification by certain large vessels in HAB-impacted fishing seasons was associated with two notable increases in fishing ground overlap with small vessels: a 30% increase in overlap for central California

small vessels (2016 fishing season) and a 73% increase in overlap for northern California small vessels (2017 fishing season). Otherwise, changes in fishing ground overlap varied according to vessel group and area closure location. Our work demonstrates that extensive area closures from HABs can create the conditions for smaller fishing vessels to experience increased competition for resources, including an intensified "race-to-fish." However, our results also suggest that the erosion of spatial niche partitioning in the California Dungeness crab fishery has been associated with other environmental drivers, such as pre-season crab distribution, and the implications of this erosion for vessel overlap are context-dependent.

3.2 INTRODUCTION

Flexibility can increase the capacity of individuals and communities to adapt to environmental and socio-economic change (Cinner et al. 2018, Cinner and Barnes 2019). In fisheries, individual flexibility can be pursued through a variety of means, including the diversification of gear or permits, allowing for flexibility in target species (Sethi 2010, Kasperski and Holland 2013, Finkbeiner 2015, Cline et al. 2017); diversification of livelihood activities, allowing for temporary or permanent flexibility in income-generation beyond fisheries (Brugère et al. 2008, Barnes et al. 2020); diversification of markets, which can increase flexibility in the face of supply chain disruptions or shifting consumer demand (Smith et al. 2022, Drakopulos and Poe 2023); and spatial diversification, or the flexibility to use alternative fishing grounds.

Spatial diversification may involve seasonal mobility over large spatial scales, spatial displacement beyond local fishing areas or communities, and internal migration (Gonzalez-Mon et al. 2021), and has been documented in both industrial (Hsueh and Kasperski 2018, Young et al. 2019, O'Farrell et al. 2019b, Cole et al. 2021) and small-scale (Nunan 2010, Stevenson et al. 2013, Costa et al. 2013, Sievanen 2014, Gonzalez-Mon et al. 2021) fisheries. Spatial diversification is differentiated from spillover of fishing effort in that it involves exploitation of new fishing grounds, or fishing activity over contextually large spatial scales (including across major political or geographic boundaries). Because spatial diversification can help fishers cope with area closures (Stevenson et al. 2013, O'Farrell et al. 2019b, Cole et al. 2021) or adapt to long-term shifts in resource distributions (Young et al. 2019) without having to exit the fishery, it can be an important strategy for fishers adapting to climate change (Islam and Herbeck 2013, Gonzalez-Mon et al. 2021).

As with other forms of diversification in fisheries, the capacity and willingness to spatially diversify varies across fisheries and among individuals. Spatial diversification in United States commercial fisheries is more commonly associated with larger vessels (Young et al. 2019, Jardine et al. 2020), which can often travel farther distances, and have access to greater capital. Use of alternative fishing grounds is also dependent on regulatory structures (Dubik et al. 2019), can require the acquisition of new place-specific knowledge (Powell et al. 2022), and may be influenced by individual fishing habits and personalities, including fishers' level of risk aversion (Holland and Sutinen 2000, Holland 2008, Dubik et al. 2019, O'Farrell et al. 2019a).

While spatial diversification is an individual-level adaptive strategy, it can have broader ecological and socioeconomic consequences. Spatial displacement during area closures can lead to overexploitation (McClanahan and Mangi 2000, Kellner et al. 2007, van der Lee et al. 2013) or increased risk to protected species (Samhouri et al. 2021, Cole et al. 2021). Shifts to alternative fishing grounds may also incite conflicts between fishery actors, exacerbated by capacity differences among vessels. This can include gear conflicts (Hattam et al. 2014) or more general tension around overcrowding of fishing grounds (van de Geer et al. 2013). Exploitation or interference competition as a result of crowded fishing grounds can both reduce the catch available to any one fisher, and therefore the possible revenue from a fishing trip (Sys et al. 2016). On larger geographic and institutional scales, conflict can arise from efforts to follow shifting species distributions across management boundaries (McMahan 2017, Dubik et al. 2019, Swetz 2022) or national jurisdictions (Cheung et al. 2012, 2012, Miller et al. 2013, Oremus et al. 2020, Mendenhall et al. 2020).

The commercial Dungeness crab fishery is one of the most economically important fisheries on the U.S. West Coast, drawing high participation from a variety of fishing operations (Rasmuson 2013, Richerson et al. 2020, Liu et al. 2023). During the 2016 and 2017 crab fishing seasons, the California Dungeness crab fishery faced a complex series of area closures as a management response to a sustained harmful algal bloom (HAB; McCabe et al. 2016, Jardine et al. 2020, Trainer et al. 2020). The HAB-associated area closures were implemented as staggered season delays in subdivided fishing districts, designed to maximize fishing opportunity across the coast (Ekstrom et al. 2020).

Local news coverage of the HAB-associated closures highlighted crabbers' frustration with overcrowding on local fishing grounds after re-opening, and the disproportionate advantage possessed by large vessels, which reportedly moved along the coast following the staggered area openings (Callahan 2016, 2017)[1,2]. This reporting is paralleled by analyses of Dungeness crab

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[1] "'Everybody's moving their gear and fishing on top of each other, and that makes it miserable…' 'At least 10 of the biggest slammers on this whole coast - the biggest boats on this whole coast - are moving north of Point Reyes today … They're getting the worst of it, Bodega Bay. There's definitely going to be a lot of the smaller operators here that won't have much of a season because it's all going to get mopped up really quickly because of this scenario.'" (Callahan 2016)

[2] "'The staggered openings meant big boats cleaned up and the small boats were left behind. 'Good numbers mask the fact that many fishermen had an abysmal season,' said Noah Oppenheim, executive director of the Pacific Coast Federation of Fishermen's Associations. 'There were opportunities for fishermen who are more mobile to access a number of different

fishery landings and vessel-level fishing locations, which have emphasized mobility as one key mechanism that some crabbers used to weather this period. (Jardine et al. 2020, Fisher et al. 2021, Liu et al. 2023). Vessel geolocations show that certain larger vessels significantly increased their crab fishing footprint (in km^2) between the 2016, 2017, and 2018 fishing seasons (Liu et al. 2023), while shoreside fishery landings data show that larger vessels also shifted or diversified their ports of landing in 2016 and 2017 compared to prior years (Jardine et al. 2020, Fisher et al. 2021). Fishery landings records have also revealed that a significantly greater share of Dungeness crab landings and revenue went to larger, over smaller, vessels during the two HAB-impacted seasons (Jardine et al. 2020). It has therefore been hypothesized that the distributional economic effects of the 2016 and 2017 HAB-associated closures were associated with novel spatial diversification by larger vessels. However, this hypothesis has not been empirically evaluated. Doing so requires connecting observations of vessel mobility with context-specific analyses of how the distribution of crab fishing activity changed this period, and the consequences for overlap or crowding of crab fishing grounds.

In this paper, we tie quantitative metrics of fishing ground change to observations of crab fishing location, to better describe the frequency and forms of spatial diversification adopted by commercial Dungeness crab vessels within a six-year period around the HAB-associated area closures. Informed by the experiences of crabbers and prior research, our hypothesis is that larger fishing vessels undertook novel spatial diversification during the 2016 and 2017 HAB-impacted crab seasons, in order to fish in newly opened management areas outside of their established fishing grounds. We then ask whether spatial diversification in these two seasons increased the

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openers and have a hell of a season, where there were small-boat fishermen that were really limited in their ability to access the resource and have a good season.'" (Callahan 2017) overlap in crab fishing grounds between vessels that would otherwise have been spatially separated. We do so by drawing on the unique, multi-source data set developed in Liu et al. (2023) and Samhouri et al. (2021), in which Dungeness crab fishery landings information is matched to vessel registration and geolocation data. With the rising frequency and intensity of harmful algal blooms and other extreme events like marine heatwaves, which can also precipitate area closures (Samhouri et al. 2021), interrogating the conditions produced by previous events may help prevent unintended consequences from management response to future ones.

3.3 METHODS

3.3.1 *The Dungeness crab fishery*

The U.S. West Coast Dungeness crab fishery is managed at the state and tribal level; in California, commercial crab fishing grounds for the state fishery are divided into two large management areas that we will refer to as the northern and central districts (Jardine et al. 2020), delineated by the Mendocino-Sonoma County line (38°46.125’ N). The codified opening date is December 1st in the northern California management district (hereafter “northern California” or “northern district”), and November 15th in the central California district (hereafter “central California” or “central district”). The fishery can run until June 30th (northern California) or July 15th (central California). Because each crab fishing season spans two calendar years, crab seasons are hereafter referred to according to the second corresponding calendar year (Richerson et al. 2020); for example, the 2016 crab season runs from Nov. 2015 - Oct. 2016, and corresponds to the 2015-16 fishing season. Our analysis covers the 2013 through 2018 crab seasons, which include two crab seasons with staggered area closures associated with HABs

(2016, 2017), two years with less extensive area closures not associated with HABs (2013, 2018), and two years without area closures (2014, 2015; Table 3.1).

Table 3.1. The opening dates of the California Dungeness crab commercial fishery for each crab season, by management district. When opening dates differed among ports of landing or fishing areas within a district, the earliest ("first") and latest ("last") opening dates across the district are reported. The coded opening date is November 15th for the central district, and December 1st for the northern district; a delay is noted with a (*), and the stated cause of the delay reported in the final column.

Crab season	***Central District*** **First**	**Last**	***Northern District*** **First**	**Last**	**Cause of Delay**
2013	Nov. 15, 2012		Jan. 15, 2013*		Meat Condition
2014	Nov. 15, 2013		Dec. 1, 2013		
2015	Nov. 15, 2014		Dec. 1, 2014		
2016	Mar. 26, 2016*		May 12, 2016*	May 26, 2016*	HAB
2017	Nov. 15, 2016	Dec. 24, 2016*	Dec. 1, 2016	Jan. 16, 2016*	HAB
2018	Nov. 15, 2017		Jan. 15, 2018*		Meat Condition

The management structure of the Dungeness crab fishery makes it one of the few remaining derby-style fisheries on the U.S. West Coast. As a result, most revenue in the Dungeness crab fishery is made in the first six weeks, and vessel participation can drop off sharply after this period (Figure 3.1; Richerson et al. 2020). To reflect this dynamic, we quantified overlap in fishing grounds for the full crab season, as well as for the first six weeks after the first port of landing opened to crab fishing in the central / northern districts, which we refer to as the central / northern "primary" season.

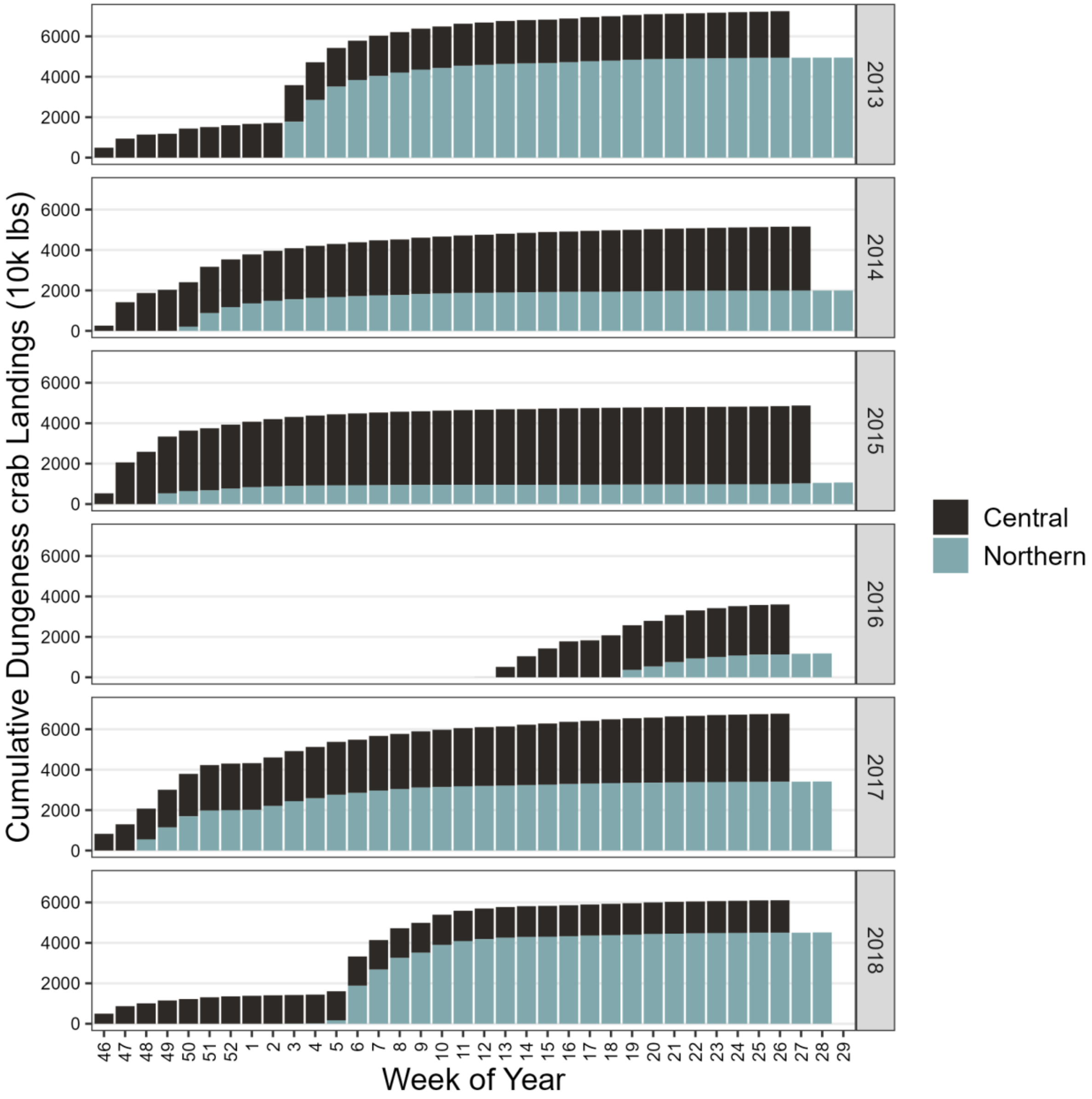

Figure 3.1. Cumulative Dungeness crab landings for each calendar week, for each of the six crab seasons included in our study. Each row indicates a separate crab season; the column fill color shows whether landings were made in the northern or central district.

Commercial crabbers have had to adapt to variability in Dungeness crab abundance and distribution for decades, with oscillations in catch first recorded in Oregon in 1948 (Demory

1990, Rasmuson 2013). Until 1980, northern California landings (as well as those in Washington and Oregon) appeared to follow approximately 10-year cycles of abundance, while central California landings displayed weak periodicity (Botsford and Lawrence 2002, Richerson et al. 2020). In recent years, these consistent cycles in catch have disappeared, potentially due in part to intensified fishing effort (Shanks and Roegner 2007, Richerson et al. 2020). Models also show spatial variability in crab distribution, such that the highest abundance of legal-sized male crab can alternate between the northern and central districts (Figure S3.1; Richerson et al. 2020). The need to work through boom-and-bust cycles of crab populations was recently highlighted by Oregon crabbers in interviews conducted by Strawn (2015), and crabbers have been reported changing fishing grounds to follow changes in pre-season abundance even in years without mandated closures (Spencer 2014)[3].

In California, such vessel mobility is somewhat limited during crab season delays by the Fair Start Provisions (1997, Cal. Fish and Game Code §8279.1). Under the Provisions, any persons (amended to any *vessel* in 2017) landing Dungeness crab outside of a closed district experiencing a season delay, cannot fish inside the delayed district until 30 days after it opens. The opening date of the given district was set as the first date on which any area within that district opened to crab fishing. The law was amended in 2018, in part as a response to events in the 2016 and 2017 crab seasons, so that the Fair Start Provisions applied at the spatial scale of delayed fishing areas, rather than fishing districts; this activates the Fair Start Provisions to

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[3] "Most of the Crescent City commercial crab fleet set out this week on the 36-hour ride to California's Central Coast, where the commercial Dungeness season opens Friday and early sport reports indicate a much higher volume of Dungeness crab than on the North Coast… Additionally, last season on the Central Coast there were a significant amount of 'measuring crabs' - Dungeness below the 6.25-inch limit on what can be kept - that were thrown back to the sea." (Spencer 2014)

temporarily limit mobility during finer-scale closures (Jardine et al. 2020). The Fair Start Provisions are essentially designed to encourage a certain level of spatial niche partitioning (Schoener 1974): vessels that overlap in target catch ("diet") are separated by geographic range, limiting competition and crowding on the water. Discouraging movement between fishing areas during and immediately after area closures should, in theory, prevent the breakdown of this partitioning from non-local vessels moving into one or more open fishing areas.

3.3.2 *Data*

We used a combined dataset of California fishery landings, vessel registrations, and fishing vessel geolocations for our analyses. Fishery landings data are reported on fish tickets when fish are landed at authorized dealers on the U.S. West Coast. We obtained California fish tickets from the 2012-2018 calendar years (2013-2018 crab seasons) from the Pacific Fisheries Information Network (PacFIN). Vessel registration data, which included self-reported vessel lengths, were used to categorize fishing vessels by size. Only fishing vessels which had self-reported vessel lengths were represented in our analyses.

We also obtained fishing vessel geolocations from the National Marine Fisheries Service Office of Law Enforcement, for the subset of California fishing vessels which are required to carry a satellite-based vessel monitoring system (VMS) transponder (i.e., those which also participate in the limited entry groundfish fishery). Vessel geolocation data represented annually between 18-24% of California Dungeness crab fishing vessels, taking 12-22% of California commercial Dungeness crab fishing trips, during the period of this study. We used the methods described by Liu et al. (2023) to match fishery landings information to vessel geolocations, for all Dungeness crab fishing trips in California. Briefly, vessel identification numbers and geolocation time stamps were used to match vessel geolocations to fishery landings data, resulting in a geolocation data set grouped by fishing trips for individual vessels (Liu et al. 2023). This trip-based geolocation data set was then filtered to remove (1) fishing trips where the last geolocation was greater than 50km from the port of landing reported in the fishery landings information, (2) geolocations which reported improbable vessel speeds (> 20m/s; Cimino et al., 2019), (3) in-port geolocations, identified as reporting an average speed of <0.75m/s within 1.5-3km of the port (adapted from Watson & Haynie, 2016), (4) trips with > 4hr time gaps between successive geolocations. Vessel geolocations for the remaining fishing trips were then linearly interpolated using the *move* R package (Kranstauber et al. 2020) to produce vessel locations that were consistently 60 minutes apart. A fishing trip with associated geolocations was considered representative of a Dungeness crab fishing trip if ex-vessel revenue for Dungeness crab was > $0, and if the ex-vessel revenue derived from Dungeness crab was at least 10% greater than the next highest-revenue species (Liu et al. 2023). The average Dungeness crab ex-vessel revenue across all VMS-covered Dungeness crab fishing trips in our study period was $16,230 (SD $23,104).

We further filtered the regularized crab fishing trip data set so that geolocations represented likely crab fishing activity. For certain fisheries, distinguishing fishing and non-fishing activity from vessel location data can be done reliably using speed and directional parameters (Mills et al. 2007, Fock 2008) or by probabilistically classifying patterns in geolocations (e.g., with Hidden Markov Models; Charles et al., 2014, Peel et al., 2011). However, it is much more difficult to distinguish fishing and non-fishing activity in fixed gear fisheries, like Dungeness crab, where gear setting is completed at higher speeds (Charles et al. 2014); or when vessel geolocation frequencies yield sparse patterns of vessel movement (Cimino et al. 2019). Following Charles et al. (2014) and Feist et al. (2021), we conservatively identified crab fishing activity as including geolocations with an average speed less than 4.2m/s, under the assumption that higher speeds represented transiting activity between fishing grounds and/or ports; and geolocations recorded at depths < 150m, since California Dungeness crab fishing grounds are predominantly shallower than that limit (Feist et al. 2021).

3.3.3 *Grouping vessels*

In order to track directional changes in fishing grounds, we clustered individual vessels into groups according to (1) the proportion of a vessel's 2014 geolocations which fall within the central or northern district, as a proxy for the time spent fishing Dungeness crab in each area; and (2) vessel size class, with small vessels as < 40ft in length and large vessels as ≥ 40ft in length following Jardine et al. (2020) and Liu et al. (2023). Liu et al. (2023) include a distribution of vessel lengths for the dataset used in our study. We first used k-means clustering with Ward's distance on the proportion of 2014 geolocations within each district, and then split the resulting geolocation-based clusters by vessel size class. We chose the 2014 crab season because the fishery followed coded season openings (i.e., no area closures). Our vessel groups approach "communities-at-sea," which are fishing communities that have shared fishing practices, history, and knowledge as a result of using shared spaces at sea and possessing other key similarities such as gear type and vessel size (St. Martin and Hall-Arber 2008, St. Martin and Olson 2017). However, identifying communities-at-sea requires a mixed method approach that includes community-based interviews and workshops (St. Martin and Hall-Arber 2008), which we did not conduct for this study. We mapped fishing activity for each vessel group as the density of vessel geolocations within a $10km^2$ area. For confidentiality, any $10km^2$ area with fewer than three fishing vessels was not included; in certain cases, this contributed to inconsistencies between the fishing activity represented on our maps and the quantitative measure of fishing ground overlap (BA index) described below.

3.3.4 *Fishing ground identification and year-over-year change*

If a vessel recorded at least five different geolocations during a given crab season, vessel geolocations were used to construct a 90% utilization distribution for that season. A utilization distribution is a probability distribution that defines an individual's use of space, and is widely used in wildlife ecology studies to examine site fidelity and space-use sharing (Fieberg and Kochanny 2005). While the 95% utilization distribution is most commonly recognized as an individual's "home range" (White and Garrott 1990), we used a more conservative 90% utilization distribution to provide a wider margin of error for the assumptions we made during our filtering steps. We also constructed 90% utilization distributions for each vessel group, using all fishing activity geolocations across all vessels in the group; for confidentiality, utilization distributions for vessel groups were only calculated when the group was represented by three or more vessels. Separate utilization distributions were also constructed from geolocations within the first six weeks after central California opened to Dungeness crab fishing (central primary season), and the first six weeks after northern California opened to Dungeness crab fishing (northern primary season). Fishing grounds visited in the central / northern primary seasons capture the derby-style period in the crab fishery, and were not constrained to fishing geolocations within the given management district (i.e., could occur in either northern or central California, if both areas were open to fishing in that period).

With the 90% utilization distributions, we quantified year-over-year change in fishing grounds using the Earth Mover's Distance (EMD), implemented in the R package *move* (Figure S3.2; Kranstauber et al. 2020). Each EMD value therefore captures the change in fishing ground location for a given vessel (or vessel group) between the first crab season and the second crab season; for example, the EMD value for 2015-2016 quantifies how fishing grounds changed from the 2015 to the 2016 crab season. The EMD calculates the minimal work to shape one utilization distribution into another, and thereby captures not only the overlap between two utilization distributions, but also the distance between utilization distributions in projected space. As a result, EMD will increase with decreasing overlap and increasing spatial distance (Kranstauber et al. 2017). We used an unpaired, two-sample Wilcoxon rank sum test from the *stats* R package (R Core Team 2020) to determine whether EMD for each year-over-year comparison differed significantly, on average, when vessels were split according to size class (large / small) only, and between large and small vessel groups fishing in the same district (with a Bonferroni correction to the p value to account for multiple comparisons; Dunn, 1961). We also conducted a one-way analysis of variance (ANOVA) to test the hypothesis that mean EMD varied between year-over-year comparisons (e.g., is there significant variability in year-over-year EMD across the full study period for the small Local Northern vessel group?); and whether overall mean EMD differed significantly between the different vessel groups. A post-hoc Tukey's Honestly Significant Difference (HSD) test was conducted on ANOVAs that showed significant differences across all year-over-year comparisons. ANOVAs and Tukey's HSD tests were conducted with the *stats* R package (R Core Team 2020).

3.3.5 *Overlap between fishing grounds*

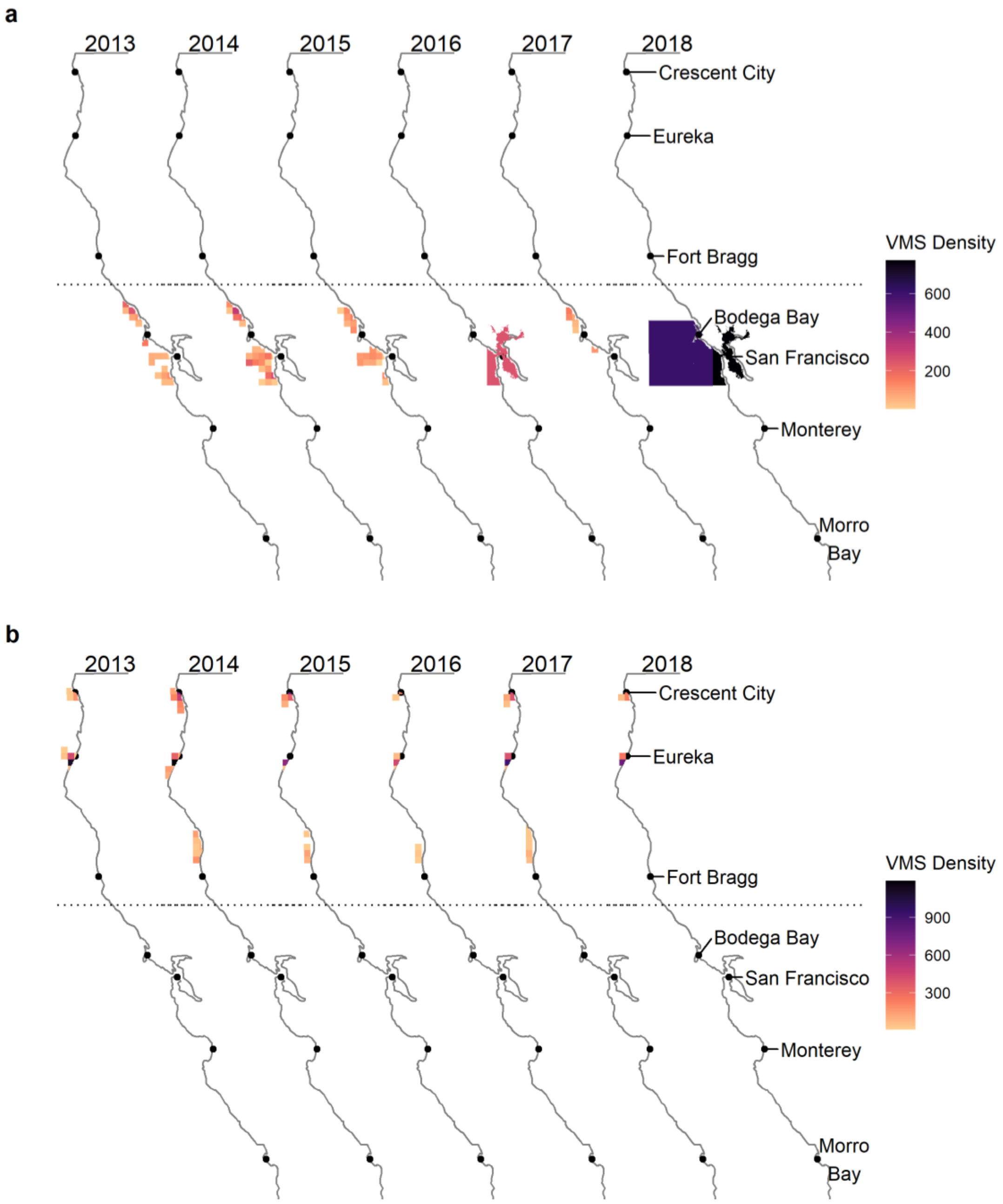
To quantify the overlap between fishing grounds of different vessel groups, we calculated the Bhattacharyya's affinity (BA) index in the *adehabitatHR* R package (Calenge 2006) from each vessel group's 90% utilization distribution for each crab season. Unlike Earth Mover's Distance, the BA index does not account for distance in projected space between two utilization distributions, and is bound between 0 (no overlap) and 1 (complete overlap; Fieberg and Kochanny 2005). Since the combined fishing grounds of each vessel group are represented by a single utilization distribution, we constructed standard deviations and errors through bootstrap re-sampling using the *rsample* R package (Frick et al. 2022) by: resampling 60% of the fishing geolocations records with the *bootstraps* function, re-constructing 90% utilization distributions, and recalculating the BA index (n=1000). We completed this process for fishing grounds used across the entire crab season ("annual" or "full season" fishing grounds), fishing grounds used within the first six weeks after central California opened to commercial crab fishing (central primary season), and fishing grounds used within the first six weeks after northern California opened to commercial crab fishing (northern primary season).

3.4 RESULTS

We identified six vessel groups from the cluster analysis of 2014 Dungeness crab fishing geolocations (Table 3.2; Figure 3.2): two "Local" groups of each size class, which fished almost entirely in a single district (Local Northern small and large vessels; Local Central small and large vessels), and two groups of large vessels which fished across the north/central California management boundary. One group of large vessels fished consistently across both districts ("Coastwide" vessels), while the second primarily fished the northern district, with occasional forays into central California ("Mobile Northern" vessels). The majority of VMS-covered vessels belonged to one of the four Local vessel groups in the 2014 crab season, only fishing for Dungeness crab in either the northern or central district; only 7 vessels fished in both districts (Coastwide, Mobile Northern groups combined). For confidentiality purposes, and to obtain more robust sample sizes, we present the two Coastwide and Mobile Northern large vessel groups pooled together as the "cross-district group" for all statistical analyses. We did not find evidence of significant differences in year-over-year fishing ground change (indicated by Earth Movers Distance) between the Coastwide and Mobile Northern groups (Table S3.1).

Table 3.2. Vessel groups derived from the k-means cluster analyses, the management districts in which group member vessels fished, and the mean vessel length and number of vessels for each size class in the group. Samples sizes (as the number of member vessels, and the total number of commercial Dungeness crab fishing trips covered by VMS) are also provided for each group.

Cluster ID: Name	District(s)	Vessel Size Class	Mean Vessel Length (ft)	No. Vessels	No. Crab Fishing Trips
1: Local central	Central	Large	47.9 ± 7.11	22	285
		Small	35.4 ± 3.90	19	374
2: Local northern	North	Large	52.1 ± 9.98	28	225
		Small	33.4 ± 5.45	17	364
3: Coastwide	Central & North	Large	55.3 ± 7.01	4	25
4: Mobile Northern	Central & North	Large	53.0 ± 5.57	3	38
(pooled cross-district group)	Central & North	Large	55.2 ± 6.65	7	63


a
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Eureka
Fort Bragg
Bodega Bay
San Francisco
Monterey
Morro Bay
VMS Density
600
400
200
b
2013
2014
2015
2016
2017
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Crescent City
Eureka
Fort Bragg
Bodega Bay
San Francisco
Monterey
Morro Bay
VMS Density
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600
300

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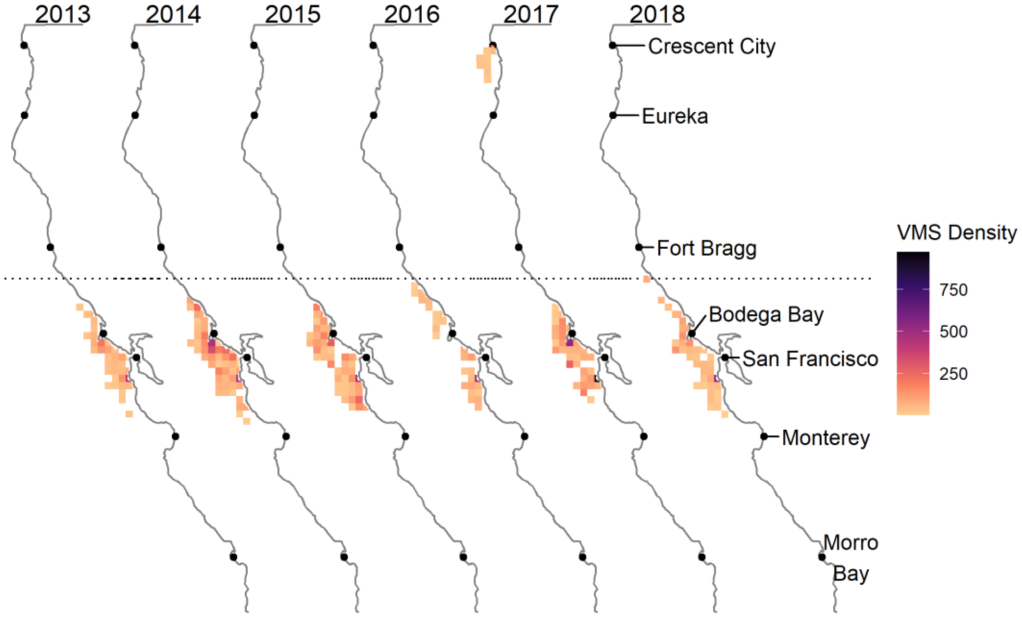
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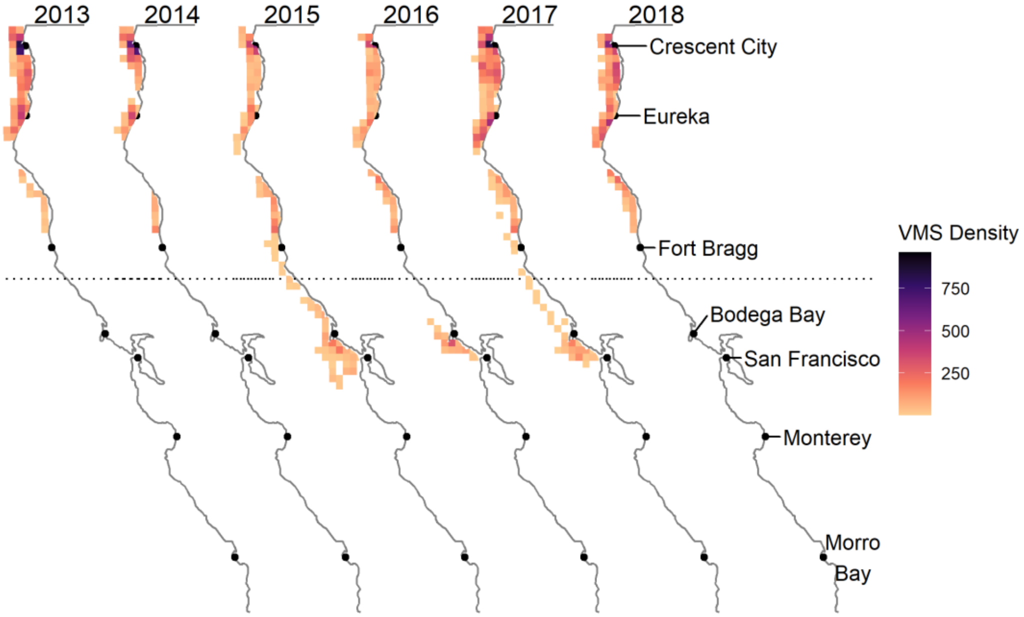
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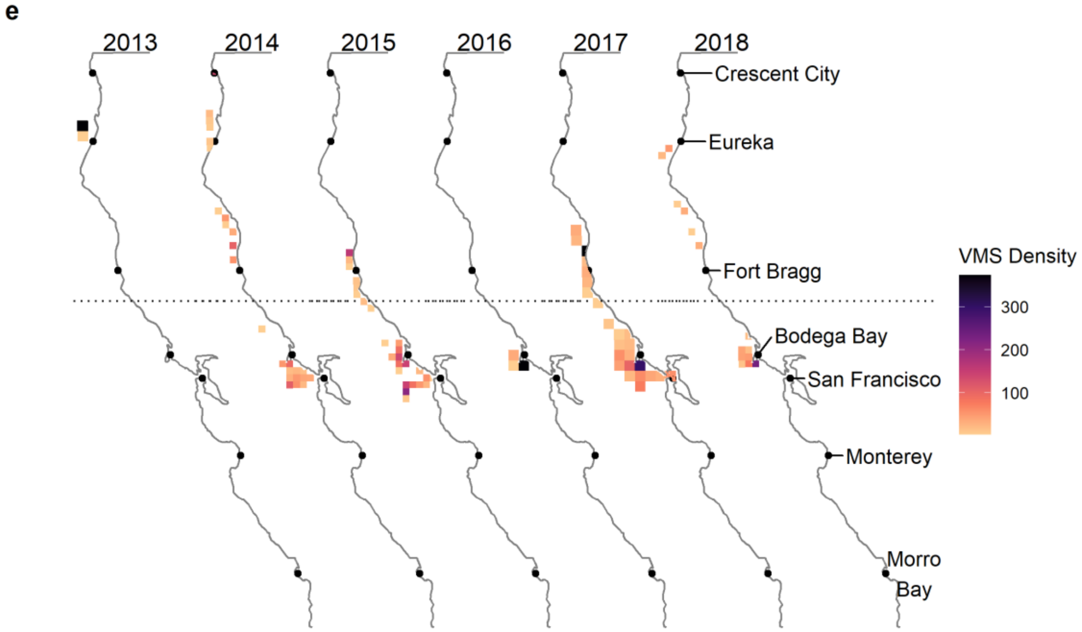

Figure 3.2. Annual Dungeness crab fishing grounds of the Local small vessel **(a)** Central and **(b)** Northern vessel groups, Local large vessel **(c)** Central and **(d)** Northern vessel groups, and the **(e)** large vessel cross-district group. Vessel activity on fishing grounds is shown according to the number of vessel geolocations (VMS) in 10km^2 grid cells for the given crab season. Only grid cells in which three or more vessels were present are mapped, for confidentiality. For certain maps, grid cell size was expanded to account for confidentiality: for the large cross-district vessel group, grid cells are 15km^2 in the 2013, 2014 and 2017 maps; and for the small Local Central group, grid cells are 100km^2 for the 2016 and 2018 maps. The dotted line marks the boundary between the northern and central districts (Sonoma-Mendocino County line). Ports of landing in the fishery landings data set are grouped into the six port groups labeled on the map.

3.4.1 *Year-over-year fishing ground change by size class*

Large vessel Earth Mover's Distance (EMD) was, on average, 2.4x greater than small vessel EMD ("Overall" Figure 3.3a; n=157 vessels total). The greatest difference in mean EMD between the two size classes occurred from fishing ground change between the 2015 - 2016 seasons, which resulted in a large vessel EMD that was 5.3x greater on average than the small vessel EMD. There was only one year-over-year comparison in which the means for the two size classes were within one standard error of each other (2013 - 2014 seasons; Figure 3.3a). Differences in mean EMD were significant for every year-over-year comparison, and when EMD was aggregated across the study period (p<0.05; Table S3.2). Within-class variation in EMD across the study period was non-significant for both large and small vessels (Table S3.3).

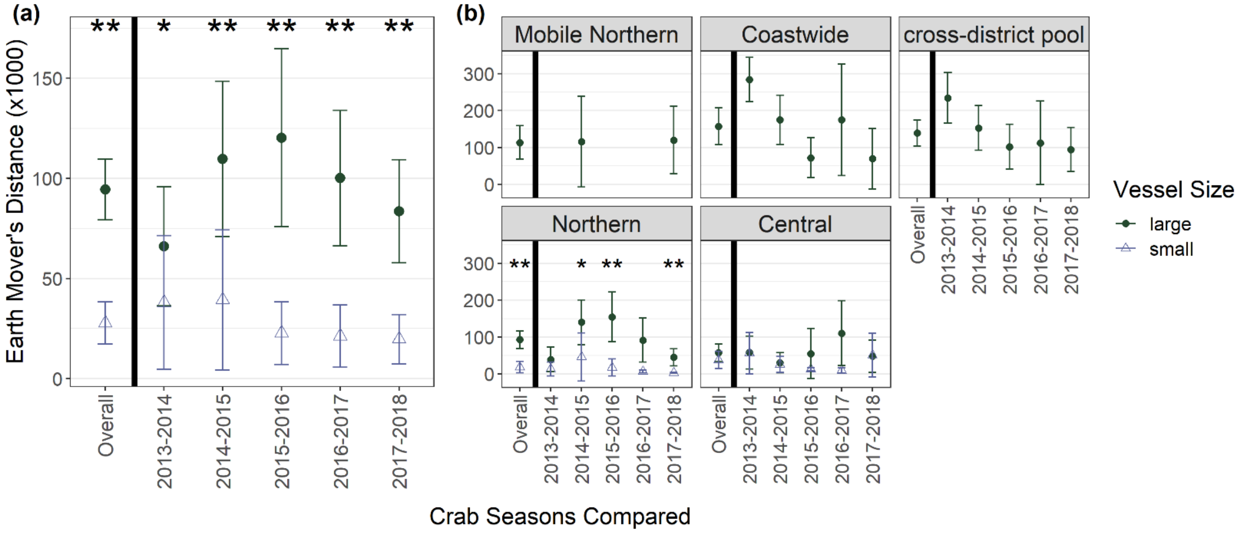

Figure 3.3. Change in fishing grounds (measured with Earth Mover's Distance; EMD) between consecutive crab seasons, and averaged across all comparisons ("Overall"). For example, the "2013-2014" comparison describes the change in fishing ground location between the 2013 crab season (Nov 2012 – Oct 2013) and the 2014 crab season (Nov 2013 – Oct 2014). Larger EMD values indicate greater change in fishing grounds between the given crab seasons. We show the mean EMD for all vessels by size class **(a)**, and for each vessel group **(b)**. In **(b)**, the two Local vessel groups are shown by size class, indicated by the color. The "cross-district group" shows mean EMD when Mobile Northern and Coastwide vessel groups were pooled. Error bars provide 2x standard error around the mean. (* / **) indicates significant differences (p<0.05 / p<0.01; Bonferroni correction applied) in EMD between large and small vessels for the given seasons and vessel groups. Some data points may be missing for confidentiality.

3.4.2 *Year-over-year fishing ground change by group: Local vessels*

We compared year-over-year change in fishing grounds between large and small Local vessels that fished primarily in the same district (n=93 vessels total). Both Local groups of small vessels showed less change in fishing grounds on average than their large Local counterparts (Figure 3.3b, “Overall”), but this difference was only statistically significant between the two Local Northern vessel groups ($p<0.05$; Table S3.4). Large Local Northern vessels were the only Local group that showed significant variation in mean EMD across the study period (Table S3.5, Table S3.6).

The significant difference in overall EMD between large and small Local Northern vessels appears driven by fishing ground change between the 2014-2015, 2015-2016, and 2017-2018 crab seasons, when large vessels showed significantly higher mean EMD than small vessels (Figure 3.3b; $p<0.05$). Two year-over-year comparisons, 2014-2015 and 2015-2016, were also distinguished by significantly higher mean EMD of the Local Northern vessels compared to the mean EMD between the 2013-2014 crab seasons ($p<0.05$; Table S3.4, Table S3.5).

We can better understand the directional change underlying these statistics using the mapped fishing activity of the two Local Northern vessel groups through time (Figure 3.2b,d). Large Local Northern vessels showed a southward expansion of their fishing grounds between 2014 and 2015, with increased fishing activity in the central district around Bodega Bay and San Francisco; this corresponds with high mean EMD between 2014-2015, and falls under the definition of spatial diversification as spatial displacement beyond local fishing areas. While there is some continued fishing activity in the central district in 2016 by these large vessels, the footprint of fishing activity is smaller than it was in 2015. This likely explains the high mean EMD for large Local Northern vessels between 2015-2016. The large Local Northern vessel group returned to fishing only in the northern district in 2018, maintaining similar fishing activity north of Fort Bragg as in 2017 (Figure 3.2b).

While small Local Northern vessels did not show significant variability in mean EMD across the study period (Table S3.5), there were some differences in fishing ground use through time (Figure 3.3b). The fishing activity maps (Figure 3.2b) show a contraction of activity for small northern vessels in 2013 and 2018 crab seasons, when no 10km^2 grid cells in the Fort Bragg area were fished by three or more vessels.

Among Local vessels in the Central district, there were no significant differences in year-over-year EMD between large and small vessels (Figure 3.3b; Table S3.4), and the mean EMD of these groups did not vary significantly between year-over-year comparisons (Table S3.5). Although not statistically significant, the 2017 crab season appears to differ from other seasons in that the large Local Central vessel group did show spatial diversification into the northern district, off the coast from Crescent City area ports (Figure 3.2c). Overall mean EMD did not significantly differ between the large Local Central / Northern vessel groups, nor between the small Local Central / Northern vessel groups (Table S3.4).

3.4.3 *Year-over-year fishing ground change by group: cross-district vessels*

We identified two vessel groups that fished across both the northern and central districts, the Mobile Northern and Coastwide vessels. Both groups had higher overall mean EMD than any of the four Local vessel groups (Figure 3.3b). Between the two, Coastwide vessels had the highest overall mean EMD (157 x 10^3, compared to 113 x 10^3). Both groups also had, on average, greater variation in EMD across most year-over-year comparisons, indicating greater variability in fishing ground use among member vessels. While this is likely due in part to smaller sample sizes, we did observe similar standard errors for certain year-over-year comparisons among the Local vessel groups, which had a greater number of member vessels (Figure S3.3).

For all statistical analyses and the fishing ground maps, we pooled these two groups of large vessels together as the “cross-district group.” The cross-district group had significantly greater mean EMD across all year-over-year comparisons than the small Local Northern, and the small and large Local Central, vessel groups ($p<0.05$; Table S3.7, Table S3.8). The large Local Northern vessel group did not have a significantly different mean EMD than the cross-district group (Table S3.8) and even displayed greater mean EMD than the cross-district group between 2015-2016 ($155 \times 10^3 \pm 34 \times 10^3$ compared to $102 \times 10^3 \pm 30 \times 10^3$; Figure 3.3b).

The cross-district group did not display significant variability in mean EMD across the full study period ($p=0.09$), but our fishing ground map shows expansion and contraction of group fishing grounds through time. The 2016 crab season was the only season in which there was no fishing activity (by three or more member vessels in a single grid cell) in the northern district, whereas in 2013, northern fishing grounds off of Eureka were the only location where three or more of these large vessels were concentrated (Figure 3.2e). The scarcity of grid cells on the large cross-district group map is reflective of the lower group size, and the greater variability in fishing ground location across member vessels (and therefore, the confidentiality of the fishing footprint).

3.4.4 *Overlap in fishing grounds: Locals*

We considered spatial overlap in “annual” or “full season” fishing grounds that captured fishing locations for the entire crab season, and fishing grounds used in the primary seasons (first six weeks) of the central and northern districts. We hypothesized that large vessel mobility would be associated with a temporary breakdown in spatial partitioning between Local vessel groups in the 2016 and 2017 crab seasons, resulting in greater overlap in fishing grounds between large v. large or large v. small Local vessels from different districts (Figure S3.4).

During the 2016 primary season for central California, fishing ground overlap between the large Local Northern and small Local Central vessel groups was the highest across the entire study period (mean BA index = 0.640 ± 0.011 standard deviation; Figure 3.4a). We did not observe similarly high overlap in the 2017 central primary season; instead, the overlap in fishing grounds during this period was the second lowest (out of four non-confidential values) across the study period. When considering annual fishing grounds, or fishing grounds used within the northern primary season, we observed greater fishing ground overlap in 2015 (mean BA index = 0.408 ± 0.005 and 0.449 ± 0.005 for the full season and northern primary season, respectively), 2013 (mean BA index = 0.386 ± 0.006 and 0.445 ± 0.006) and 2018 (mean BA index = 0.452 ± 0.006 and 0.393 ± 0.01) than in either 2016 or 2017 (Figure 3.4a). High fishing ground overlap between these two groups in 2015 and 2016 corresponded to movement by large Local Northern vessels into central district fishing grounds off of Bodega Bay and San Francisco (Figure 3.2d). Overall, this group pair displayed the greatest variation in fishing ground overlap across the study period, with the mean BA index ranging between 0.640 ± 0.011 (2016, noted above) and 0.007 ± 0.001 (2014, the crab season used for clustering; Figure 3.4a).

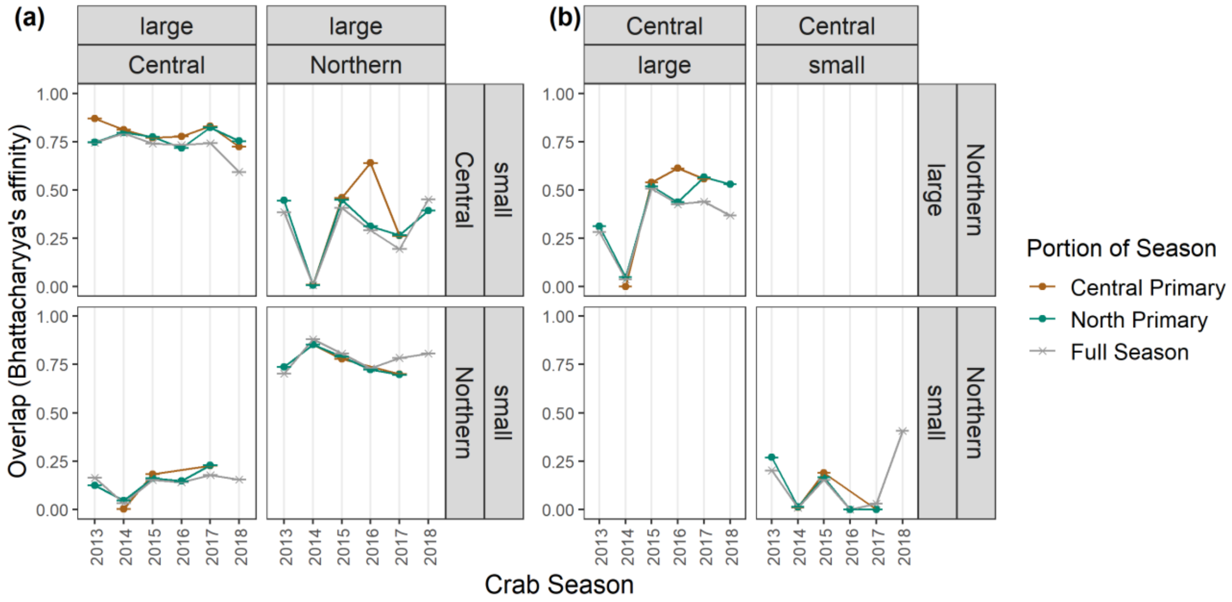

Figure 3.4. Overlap in fishing grounds (measured with Bhattacharyya's affinity, or BA index) between Local Northern / Central vessel groups, between **(a)** and within **(b)** size classes. Overlap is shown for fishing grounds used across the entire crab season ("Full Season"), and for northern and central primary seasons. Error bars indicate 2x standard error calculated from bootstrap re-sampling; points are means.

The 2016 central primary season was also the period of greatest overlap between large Local Central and large Local Northern vessels (mean BA index = 0.612 ± 0.009); the 2017 northern and central primary seasons saw the second and third highest overlap between these two groups (mean BA index = 0.566 ± 0.006 and 0.558 ± 0.006, respectively; Figure 3.4a). However, fishing ground overlap between large Local Central and large Local Northern vessels was similarly high in the 2015 and 2018 northern / central primary seasons. For example, mean BA index increased only 14% from the 2015 to 2016 central primary season for these two groups (compared to a 39% increase for small Local Central and large Local Northern vessels). High fishing ground overlap between the two large Local groups in 2015 and 2016 is attributable to large Local Northern vessel activity in central California, whereas high overlap in 2017 reflects spatial diversification by three or more member vessels from both large Local vessel groups into the opposite district (Figure 3.2c,d).

The expansion of the large Local Central vessel group into northern district fishing grounds in 2017 also elevated fishing ground overlap between this group and small Local Northern vessels in the northern / central primary seasons (mean BA index of 0.229 ± 0.006 and 0.227 ± 0.006 respectively), during which the two groups had 56% and 24% greater overlap, on average, compared to the prior graphed years (Figure 3.4a). Fishing ground overlap in 2016 was lower than that of 2017, as well as 2015 (Figure 3.4a).

The two small Local vessel groups showed strong spatial partitioning in fishing grounds between the northern and central districts, with zero overlap in the 2016 full crab season and the 2017 central / northern primary seasons (Figure 3.4b). Some of the greatest overlap in fishing grounds between these groups occurred over the full season in 2018 (mean BA index = 0.406 ± 0.007) and for the full and central primary seasons in 2013 (mean BA index = 0.202 ± 0.007 and 0.269 ± 0.008, respectively); although, this appeared to be driven by fewer than three member vessels or by highly diffuse fishing activity, and so cannot be explained by our fishing ground maps (Figure 3.2a,b). As might be expected, fishing ground overlap was consistently high between large and small vessels with “home” fishing grounds in the same district (Figure 3.4a).

3.4.5 *Overlap in fishing grounds: Cross-district*

The highest overlap in fishing grounds between the cross-district vessels and any other group occurred in the 2016 central primary season, when the mean BA index between cross-district vessels and large Local Northern vessels was 0.883 ± 0.009 (standard deviation; Figure 3.5). This can be explained by similar fishing ground use in the central district by both vessel groups during that season (Figure 3.2d,e). The 2017 BA index for the central primary season was the second-highest across the study period for these two groups (0.739 ± 0.006), and the 2017 BA indices for the full and northern primary seasons were the highest for those portions of the season (0.727 ± 0.005 and 0.741 ± 0.006 respectively). However, the difference in BA index values between 2017 and other crab seasons represented a far weaker increase than seen in the 2016 central primary season. The mapped fishing grounds of cross-district vessels (Figure 3.2e) were generally concentrated within the large Local Northern vessel footprint (Figure 3.2d) across most crab seasons; both vessel groups used similar fishing grounds around Fort Bragg in the 2014, 2015, 2017, and 2018 crab seasons, and both had a relatively high density of vessel location data points around Bodega Bay and San Francisco from 2015-2017.

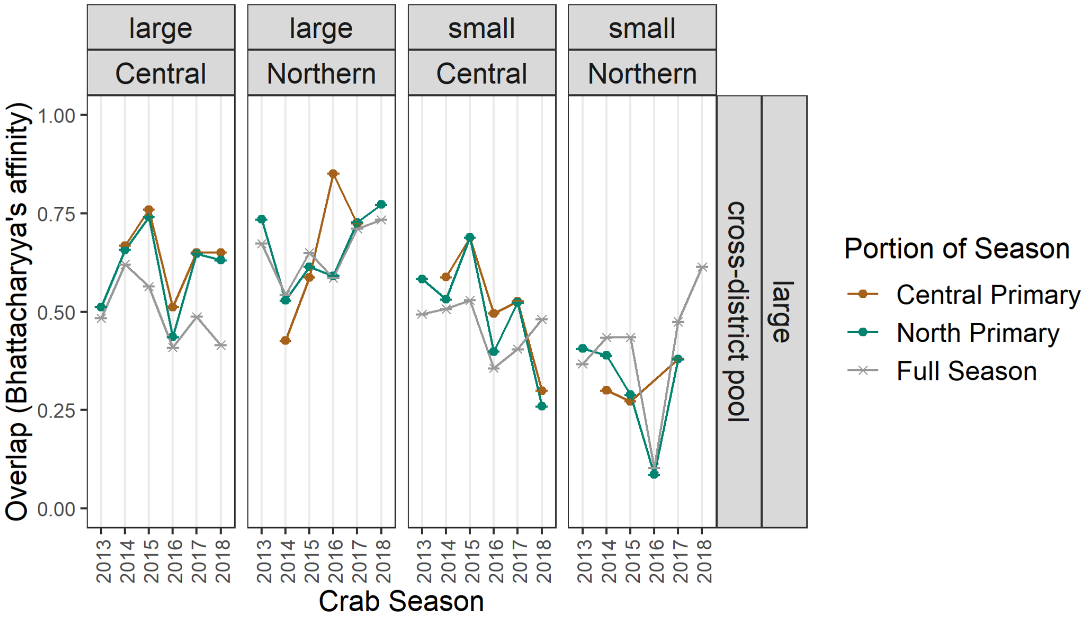

Figure 3.5. Overlap in fishing grounds between all four Local vessel groups and the pooled cross-district vessel group. Overlap is shown for fishing grounds used across the entire crab season, for the first six weeks after the northern district opened to commercial crab fishing, and

for the first six weeks after the central district opened to commercial crab fishing. Error bars indicate 2x standard error calculated from bootstrap re-sampling; points are means.

In contrast, 2016 saw the lowest overlap in fishing grounds between the cross-district group and large Local Central / small Local Northern vessels (Figure 3.5). Although both large Local Central vessels and the cross-district group fished in the central district in 2016, non-confidential fishing activity for the large cross-district group was concentrated in three grid cells around Bodega Bay, where there appears to have been few to no large Local Central vessels (Figure 3.2c,e). While fishing ground overlap between cross-district vessels and large Local Central / small Local Northern vessels was higher in 2017 than in 2016, the 2017 BA index values were similar to, or less than, BA indices from other crab seasons without HAB-associated area closures (Figure 3.5).

Although not specific to the 2016 and 2017 crab seasons, we observed an interesting de-coupling of BA indices between the three different time periods for which we considered fishing ground overlap. For example, the mean BA index between the large cross-district vessels and large Local Central vessels was notably higher in the 2015 and 2018 northern/central primary seasons than for the full year. Similarly, the mean BA index between the large cross-district vessels and the small Local Central vessels was notably lower for the 2018 northern/central primary seasons than for the full year (Figure 3.5).

3.5 DISCUSSION

The capacity to change fishing grounds is one aspect of diversification that keeps fishers on the water despite climate impacts like extreme events. However, this capacity is not evenly distributed among fishers, nor are the socioeconomic impacts that can result from individual mobility. Here, we explored spatial diversification and fishing ground overlap in the California Dungeness crab commercial fishery before, during, and after an extensive harmful algal bloom (HAB) caused unprecedented fishing area closures in the 2016 and 2017 crab seasons. We were specifically interested in testing the hypothesis that HAB-induced area closures precipitated novel spatial diversification by larger vessels; and that this, in turn, increased the overlap in fishing grounds between vessel groups that were otherwise spatially partitioning fishing effort. We found that large vessels undertook significantly greater year-over-year change in fishing grounds than small vessels, for all of the crab seasons we studied (2013 – 2018). Combining quantitative metrics with maps of fishing ground location revealed that spatial diversification by large vessels took the form of (1) inter-annual mobility across large spatial scales (i.e., across intrastate management boundaries; cross-district vessel group), and (2) spatial displacement to fishing grounds outside of a vessel's local district. Although both forms of spatial diversification did occur in the 2016 and 2017 crab seasons, they were not exclusive to these two HAB-impacted seasons.

Spatial diversification by certain larger fishing vessels did lead to notably greater fishing ground overlap with small Local Central vessels during the "derby-style" 2016 central primary season. This demonstrates how differential capacity for mobility within a fleet can cause some vessels to experience different or novel fishing conditions even though they themselves did not spatially diversify. Otherwise, contrary to our expectations, fishing ground overlap during the two seasons with HAB-associated area closures rarely stood out from that of other crab seasons in our study period. These results reflect the complex factors that go into the decision of where to fish, and that spatial redistribution of crab fishing effort across management boundaries has been - and may continue to be - precipitated by other drivers. This speaks to both the adaptability required of Dungeness crab fishers, and the potential for certain side effects of spatial diversification (e.g., the "race-to-fish" and competition for space) to occur even without extensive area closures.

3.5.1 *How did year-over-year fishing ground change differ between vessels?*

The significant differences in year-over-year fishing ground change that we observed between the two vessel size classes are in line with Jardine et al. (2020), who found that during the 2016 and 2017 crab seasons, larger vessels (>40ft in length) undertook greater shifts in shoreside fishery landing locations. Similarly, Liu et al. (2023) found that greater vessel length was associated with "roving" intra-seasonal behavioral strategies, which included larger within-season fishing ranges, longer fishing trips, and use of a greater number of ports of landing in a single season. Fishers on larger vessels have also been shown to display lower fidelity to historical fishing grounds in the Northeast U.S. groundfish trawl fishery (Papaioannou et al. 2021). Safety concerns for smaller vessels were linked to high fishing ground fidelity in the Northeast groundfish trawl fleet, along with socio-cultural expectations, fuel costs, local environmental knowledge, and geographic limits (Papaioannou et al. 2021). In other California fisheries, smaller vessel size has been significantly associated with fishers citing constraints on spatial diversification, related to the ability to travel long distances and knowledge of other locations (Powell et al. 2022).

Contrary to our preliminary hypotheses, spatial diversification was not exclusive to crab seasons with HAB-associated area closures (2016, 2017). We did observe spatial diversification by the large Local Northern / Central vessel groups into the opposite management district in 2016, and by the large Local Northern group in 2017. Yet we mapped similar spatial diversification by large Local Northern vessels in 2015, a season without area closures. We also identified a group of "cross-district" large vessels (combined post-hoc from two vessel clusters), which did not significantly change their year-over-year mobility around the HAB-associated area closures, but rather showed consistently strong mobility across large-scale management boundaries for the entire study period, fishing across the two management districts in 2014, 2015, 2017, and 2018.

The patterns we observed for large Local Northern vessels around the 2015 crab season are likely associated with the distribution of crab populations along the California coast. At the start of our study period in 2013, there was a higher pre-season abundance of legal-sized male crab in Northern California; by 2015, pre-season abundance was highest in central California, with a discrepancy of over 4,000 MTs between the two districts (Richerson et al., 2020; Figure S3.1). Local news from the start of the 2015 crab season reported that many crabbers who operated out of Crescent City in northern California were preparing to travel to the central district following sport fishing reports of greater pre-season abundance in the San Francisco Bay area (Spencer 2014). Liu et al. (2023) also found that the 2015 crab season was associated with greater Dungeness crab fishing ranges (in total sq km) for certain fishing behavioral groups. From our data, it appears that responsiveness to fluctuations in pre-season abundance can indicate the ability to respond to other drivers (such as area closures) with similar spatial diversification.

3.5.2 *Did fishing ground overlap differ in seasons impacted by HABs?*

We did observe notable changes in fishing ground overlap during the HAB-impacted 2016 crab season, associated with two spatially diversified vessel groups. Spatial diversification by large Local Northern vessels in the 2016 crab season contributed to the highest observed fishing ground overlap between that group and (1) small Local Central vessels, and (2) the cross-district group (which were also spatially diversified large vessels). These two peaks in overlap were specific to the derby-style "race-to-fish" primary season in central California, and related to an influx of fishing activity by large Local Northern vessels and the large cross-district group into the central district immediately post-closure. These results align with local reporting on the 2016 area closures, which emphasized the movement of larger vessels into newly open fishing areas - particularly around Bodega Bay - as leading to crowded fishing grounds (Callahan 2016). In addition, Jardine et al. (2020) identified significant reductions in the proportion of revenue and participation to small vessels (<40ft in length) landing crab in Bodega Bay-area ports, as well as more southern ports in the Monterey area, in the 2016 crab season.

In the HAB-impacted 2017 crab season, we observed an increase in fishing ground overlap between large Local Central vessels and small Local Northern vessels - albeit to a far lower magnitude than the 2016 increases above. This increase appeared driven by spatial diversification of large Local Central vessels into northern district fishing grounds around Crescent City. Jardine et al. (2020) also showed significant reductions in the proportion of revenue and participation captured by small vessels landing catch at Crescent City and Eureka ports that season (Jardine et al. 2020).

Taken together, this is evidence that spatial diversification by larger vessels may have increased interference competition in the first six weeks of the 2016 (central California) and

2017 (northern California) crab seasons, or facilitated faster local depletion in each area, with negative economic consequences for small Local vessels. While there are a number of other likely factors that could have influenced patterns of revenue capture in these seasons, which cannot be ruled out with the information at hand (e.g., the ability to land catch from multiple open fishing areas; Jardine et al., 2020; Liu et al., 2023), we argue that competition could be one contributing mechanism and is worthy of further study. Exploring links between spatial diversification and competition beyond the 2018 crab season may also reveal important patterns associated with recently implemented management alternatives to area closures, such as pot limits. Doing so by directly relating an increase in vessel density concurrent with a decrease in catch rate (Sys et al. 2017; Gillis et al. 1993), or revenue per unit effort (Poos and Rijnsdorp 2007), may not be appropriate for the California Dungeness crab fishery (because changes in the spatial distribution of crab catch are likely linked to environmental drivers; Richerson et al., 2020), but more tractable methods might include IFD-based isodars (Gillis et al. 2012) and discrete choice distributions (Tidd et al. 2012, O'Farrell et al. 2019a).

At the same time, the HAB-associated area closures did not uniformly escalate fishing ground overlap between large vessels and smaller-scale fishing operations; nor did our results universally align with the economic analyses of Jardine et al. (2020). For example, the 2016 crab season saw a steep decline in the overlap of fishing grounds between the large cross-district vessels and small Local Northern vessels in the northern district's primary season, as the large cross-district vessels concentrated in the central district. Yet Jardine et al. (2020) found significant reductions in the proportion of revenue and participation captured by small vessels landing catch at Crescent City and Eureka area ports in 2016. In the 2017 crab season, we did not observe notable increases in fishing ground overlap between the small Local Central vessel group and large vessel groups. However, small vessels claimed a significantly lower proportion of Dungeness crab revenue and fishery participation at Bodega Bay, San Francisco, and Monterey ports that season (Jardine et al. 2020). One reason for these mismatches may be that, in contrast to Jardine et al. (2020), our spatial clustering analysis was not fine-scale enough to capture heterogeneous changes in fishing ground overlap between vessels within a single management district; in 2016, even as revenue share to small vessels declined in the northern district ports around Crescent City, it significantly increased at other northern district ports around Fort Bragg (Jardine et al. 2020). It is also possible that other factors, beyond competition on fishing grounds, led to the disproportionate economic impacts for small vessels observed in 2017. For example, since small vessels tend to fish farther into the season than large vessels (Liu et al. 2023), the simple matter of this area enduring the longest area closures may have caused the observed changes in revenue share (Jardine et al. 2020).

It is also important to reiterate, in the context of these conclusions, that our analyses only represent the subset of the Dungeness crab fishing fleet that are equipped with vessel monitoring systems (VMS). Liu et al. (2023) suggest that many of the non-VMS fishing vessels participating in the Dungeness crab fishery likely employ a “Local Specialist” strategy. Liu et al.’s “Local Specialist” strategy most closely aligns with our small Local Northern and large/small Local Central vessel groups. As a result, more small fishing vessels, and/or more Local Central vessels, could have been impacted by fishing ground encroachment than is shown by our study. However, with our conclusion that changes in fishing ground overlap were dependent on both home fishing grounds and area closure location, further work showing where non-VMS covered vessels were fishing in 2016 and 2017 would be needed to understand how the trends observed in our study translate to fleet-wide impacts.

Another related constraint on our analysis was the small sample size for some of the large vessel groups, which contributed to inconsistencies between fishing ground maps and quantified overlap to maintain confidentiality. For example, the large vessels in the cross-district group and the small Local Northern vessels shared the highest BA index in the 2018 crab season, but the mapped fishing grounds show no overlap between these two groups. In cases like this, we are quantifying overlap in fishing grounds that may be created by more diffuse fishing activity of two or fewer vessels. While, as a result, it is sometimes difficult to describe the spatial diversification (or lack thereof) driving changes in fishing ground overlap, this does highlight the importance of using quantitative summary statistics when working with confidential fishery datasets to understand patterns across finer-scale subdivisions of a fishing fleet.

3.5.3 *Implications for shifting vulnerability and management priorities in the Dungeness crab fishery*

Our results specific to small Local Central vessels in the 2016 crab season, and small Local Northern vessels in the 2017 crab season, raise concerns around competition as a mechanism of shifting vulnerability from larger-scale to smaller-scale fishery participants. Crowding and interference competition during area closures may cause catch rates to decline on remaining open fishing grounds (Poos and Rijnsdorp 2007), while the “race-to-fish” a newly opened area can quickly lead to local depletion (exploitation competition; Sys et al. 2017). Smaller Local vessels may be disproportionately impacted by local depletion in particular, as these vessels tend to fish for Dungeness crab later into the season, whereas large vessels may switch fisheries after the first few weeks of the season when catch rates start to decline (Liu et al. 2023).

Other responses by crabbers to the HAB-associated area closures - which ranged from staying on the water by fishing other species, to seeking employment outside of the fishing sector, to borrowing from friends and family - played an important role in helping crabbers and coastal communities weather the 2016 crab season (Moore et al. 2020a). These other strategies may even have lessened how individuals on smaller vessels experienced the shifting vulnerability we describe based on spatial diversification and fishery revenue alone. Analyzing the role of spatial diversification and competition within this broader economic and adaptive landscape is beyond the scope of this study, but has been approached by previous research (Moore et al. 2020a, 2020b, Holland and Leonard 2020, Fisher et al. 2021, Liu et al. 2023).

Regulatory barriers to mobility may also be leveraged to limit shifting vulnerability during future events. As described in the Methods, the California Dungeness crab fishery's Fair Start Rules are designed to limit spatial diversification in seasons with district closures, such that any individual fishing outside of the northern (or central) district cannot move into the opposite district until 30 days after it opens. In 2018, the California Department of Fish & Wildlife amended the Fair Start Rules to apply to smaller area closures associated with HABs. However, even with this further disincentive to fish in non-"local" areas, spatial diversification may still be a desirable adaptive strategy. During the 2023 protected species delay in central California, years after the 2018 adjustment of the Fair Start Rules, at least one crabber reported investing in a larger vessel to travel to an open area north of their usual fishing grounds (Belli 2022). Crabbers have also been reported investing in larger vessels to adapt to area-specific pot limits, an alternative to full area closures (Belli 2022). Beyond revenue considerations, the ability to continue fishing despite area closures may have mental and emotional health benefits; surveys of crabbers about the 2016 HAB-associated area closures found that the flexibility to continue fishing during closures, albeit by harvesting other species, caused less stress than other response strategies (Moore et al. 2020a).

Yet spatial diversification is not an unconditionally positive solution for larger vessels. Crabbers who have the capacity to spatially diversify also face the risk of increasing their own vulnerability to climate change in the long-term (rebounding vulnerability), and introducing new problems (negative externalities; Schipper, 2020). In their work with the Alaska sablefish fishery, Szymkowiak & Rhodes-Reese (2020) noted that spending more time on the water, and fishing new waters, could be associated with negative impacts to family connections and physical safety. Compounding stressors faced by crabbers, including the loss of skilled labor and more severe winter weather, may amplify physical safety risks associated with traveling to fishing grounds farther from port (Drakopulos and Poe 2023). In cases where vessel owners are not operating their own vessels, these risks and negative impacts to well-being may only be born by crew members rather than all profit-sharing parties. Finally, some smaller vessel owners may choose to increase their capacity for spatial diversification, investing additional assets into a fishery that could continue to suffer in other ways under climate change. While it is important to maintain space for autonomous adaptation like spatial diversification, lauding highly mobile fishers as particularly resilient can also divert responsibility for climate adaptation, and any unforeseen consequences, onto individuals (Kaika 2017, Woods 2017).

Our work also has important implications for other current management priorities in the West Coast Dungeness crab fishery, including efforts to mitigate entanglement risk. A trade-off analysis by Samhouri et al. (2021) found that spatial redistribution of Dungeness crab fishing effort played a key role in whether a management strategy successfully reduced the risk of blue and humpback whale entanglement in crab fishing gear; for example, depth restrictions without fishing effort reductions actually increased entanglement risk because fishing effort became more highly concentrated in certain areas (Samhouri et al. 2021). Our findings validate the decision by Samhouri et al. (2021) to include effort redistribution in their analyses, while also suggesting that other sources of variability which incentivize spatial redistribution of effort, including the distribution of pre-season crab abundance (e.g., in 2015), may influence entanglement risk reduction strategies. Highly variable patterns of fishing behavior between years, which we have documented here, can also make it challenging to develop accurate, short-term forecasts of abundance (Norton et al. 2023). Since the Dungeness crab fishery does not have a formal stock assessment, recent efforts have focused instead on developing short-term forecasts to estimate abundance and meat quality at the start of the fishing season (Norton et al. 2023). These forecasts rely on fishery-dependent landings and geolocation data. With the high year-over-year change in fishing grounds we observed, we might expect future short-term forecasts to struggle with accuracy, particularly between years with different area closures or highly variable crab population distributions.

3.6 CONCLUSIONS

Understanding the effects of ecological disturbance and associated management responses on fishing fleet dynamics is important for anticipating the impacts of ongoing climate change and extreme events on fishing communities. We build on existing literature (e.g., Fisher et al., 2021; Jardine et al., 2020; Liu et al., 2023) to describe differential capacity for spatial diversification between large and small vessels in the California commercial Dungeness crab fishery, and to explore how year-over-year changes in fishing location affected the degree of overlap in crab fishing grounds between vessel groups. While much previous work on vessel mobility has focused on the HAB-associated area closures in the 2016 and 2017 crab seasons

(Holland and Leonard 2020, Jardine et al. 2020, Fisher et al. 2021), or more broadly the North Pacific marine heatwave that impacted the 2016 through 2018 crab seasons (Feist et al. 2021, Liu et al. 2023), our results show that the capacity to change fishing grounds has been used by certain large vessel operators in other fishing seasons with shorter area closures (in 2018) and shifts in pre-season crab distribution (in 2015). While we documented strong increases in fishing ground overlap between two small / large vessel group pairs during the HAB-impacted season, certain small and large vessel groups remained spatially separated in seasons with area closures, while others experienced fluctuating overlap in fishing grounds throughout the full study period. These results highlight the importance of fine-scale, context-specific analyses in understanding fishery response to management decisions and changing environmental conditions, particularly in fisheries like those for Dungeness crab which support diverse fishing operations and are defined by complex intra-seasonal dynamics.

We observed spatial diversification as an autonomous adaptation strategy, an organic response to fishing area closures driven by crabbers themselves (Schipper 2020). The difficulty of autonomous adaptation lies in the uncertainty of consequences under ever-changing human and natural systems, which are not easily identified and accounted for under the pressure of addressing immediate negative impacts. We argue that differential use of spatial diversification in the Dungeness crab fishery is contributing to the manifestation of some of these risks, and that it is important for future work to evaluate the role of specific mechanisms like exploitation or interference competition. To minimize the amplification or redistribution of climate vulnerability from adaptative strategies like spatial diversification, it will be important for fishery management to adjust policies in response to feedback from fishery participants and other stakeholders - such as the California Department of Fish and Wildlife's 2018 adjustment of the Fair Start Rules - and to see through planned adaptation measures at higher institutional levels.

Return to Table of Contents.

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3.8 APPENDIX

3.8.1 *Supplemental Tables*

Table S3.1. Results from the unpaired two-sample Wilcoxon rank sum tests to evaluate significant differences in Earth Mover's Distance between the Mobile Northern and Coastwide vessel groups. Crab season comparisons are provided only for those sequential years in which both vessel groups had n=3 or more member vessels. The p-value is provided before and after applying a Bonferroni correction for multiple testing.

Crab season comparison	**W**	**p-value**	**Adj. p-value**
2014-2015	10	0.5714	1.143
2017-2018	2	0.400	0.800
Overall	61	0.5162	

Table S3.2. Results from the unpaired two-sample Wilcoxon rank sum tests to evaluate significant differences in Earth Mover's Distance between size classes (all large vessels, all small vessels). Significance values provided before and after applying a Bonferroni correction for multiple testing. (*) indicates significant result at α=0.05.

Crab season comparison	**W**	**p-value**	**Adj. p-value**
2013-2014	1094	0.008	0.041*
2014-2015	1006	0.001	0.009*
2015-2016	783	0.000	0.002*
2016-2017	1451	0.000	0.000*

2017-2018	1856	0.000	0.000*
Overall	63607	0.000	0.000*

Table S3.3. Results from ANOVAs, to evaluate significant differences in Earth Mover's Distance across the study period for all large / all small vessels.

Vessels		Degrees of freedom	Sum of squares	Mean square error	F statistic	p-value
Small (all)	Crab seasons	4	1.10E+10	2.76E+09	0.66	0.62
	Residuals	144	6.01E+11	4.17E+09		
Large (all)	Crab seasons	4	9.57E+10	2.39E+10	1.515	0.198
	Residuals	272	4.30E+12	1.58E+10		

Table S3.4. Results from the unpaired two-sample Wilcoxon rank sum tests to evaluate significant differences in Earth Mover's Distance between size classes (large, small) for the Local Northern / Central vessel groups. Significance values provided before and after applying a Bonferroni correction for multiple testing. (*) indicates significant result at $\alpha=0.05$.

Vessel Group	Crab season comparison	W	p-value	Adj. p-value
Local Northern	2013-2014	310.5	0.012	0.059
Local Northern	2014-2015	308.5	0.006	0.033*
Local Northern	2015-2016	231.5	0.001	0.006*
Local Northern	2016-2017	184.5	0.030	0.150
Local Northern	2017-2018	238.5	0.002	0.008*
Local Northern	Overall	6279.5	0	0*
Local Central	2013-2014	219.5	0.234	1.17
Local Central	2014-2015	122	0.859	4.30
Local Central	2015-2016	20	0.851	4.26
Local Central	2016-2017	48	0.064	0.318
Local Central	2017-2018	38	0.892	4.46
Local Central	Overall	1974.5	0.090	0.090

Table S3.5. Results from ANOVAs to evaluate whether there were significant differences in Earth Mover's Distance across the study period for each vessel group.

Vessel Group		Degrees of freedom	Sum of squares	Mean square error	F statistic	P-value
Small Local Northern	Crab seasons	4	1.54E+10	3.84E+09	0.999	0.415

	Residuals	59	2.27E+11	3.84E+09		
Large Local Northern	Crab seasons	4	2.93E+11	7.32E+10	4.43	0.00223
	Residuals	122	2.02E+12	1.65E+10		
Small Local Central	Crab seasons	4	1.53E+10	3.83E+09	0.592	0.67
	Residuals	40	2.58E+11	6.46E+09		
Large Local Central	Crab seasons	4	5.28E+10	1.32E+10	1.353	0.259
	Residuals	73	7.13E+11	9.76E+09		
Large pooled cross-district	Crab seasons	4	6.94E+10	1.73E+10	2.259	0.0926
	Residuals	24	1.84E+11	7.68E+09		

Table S3.6. Results from Tukey's HSD test on significant ANOVAs in Table S5 (large Local Northern vessels).

Vessel Group	**Crab seasons 1**	**Crab seasons 2**	**Difference**	**Lower**	**Upper**	**Adj. p-value**
Large Local Northern	2013-2014	2014-2015	100561.34	17237.82	183884.85	0.026
	2013-2014	2015-2016	115344.90	26667.16	204022.63	0.013
	2017-2018	2014-2015	-94873.47	-183168.15	-6578.79	0.064
	2017-2018	2015-2016	-109657.03	-203021.28	-16292.78	0.033

Table S3.7. Results from ANOVA to evaluate whether there were significant differences in overall Earth Mover's Distance across all vessel groups.

	Degrees of freedom	**Sum of squares**	**Mean square error**	**F statistic**	**p-value**
Vessel Group	4	4.32E+11	1.08E+11	9.406	3.25E-07
Residuals	334	3.84E+12	1.15E+10		

Table S3.8. Results from Tukey's HSD test on ANOVA in Table S3.7, which found significant differences in overall Earth Mover's Distance across vessel groups.

Group 1	**Group 2**	**Difference**	**Lower**	**Upper**	**Adj. p-value**
Small Local Central	Large Local Central	-20115	-75676	35446	0.858
Large Local Northern	Large Local Central	34956	-8027	77939	0.171
Small Local Northern	Large Local Central	-39584	-89755	10587	0.196
Large cross-district group	Large Local Central	81293	16903	145684	0.005**
Large Local Northern	Small Local Central	55071	4082	106060	0.027*
Small Local Northern	Small Local Central	-19469	-76647	37710	0.884
Large cross-district group	Small Local Central	101409	31420	171398	0.001**
Small Local Northern	Large Local Northern	-74539	-119594	-29484	0.000**
Large cross-district group	Large Local Northern	46338	-14152	106827	0.222
Large cross-district group	Small Local Northern	120877	55085	186669	0.000**
Small Local Central	Large Local Central	-20115	-75676	35446	0.858

3.8.2 *Supplemental Figures*

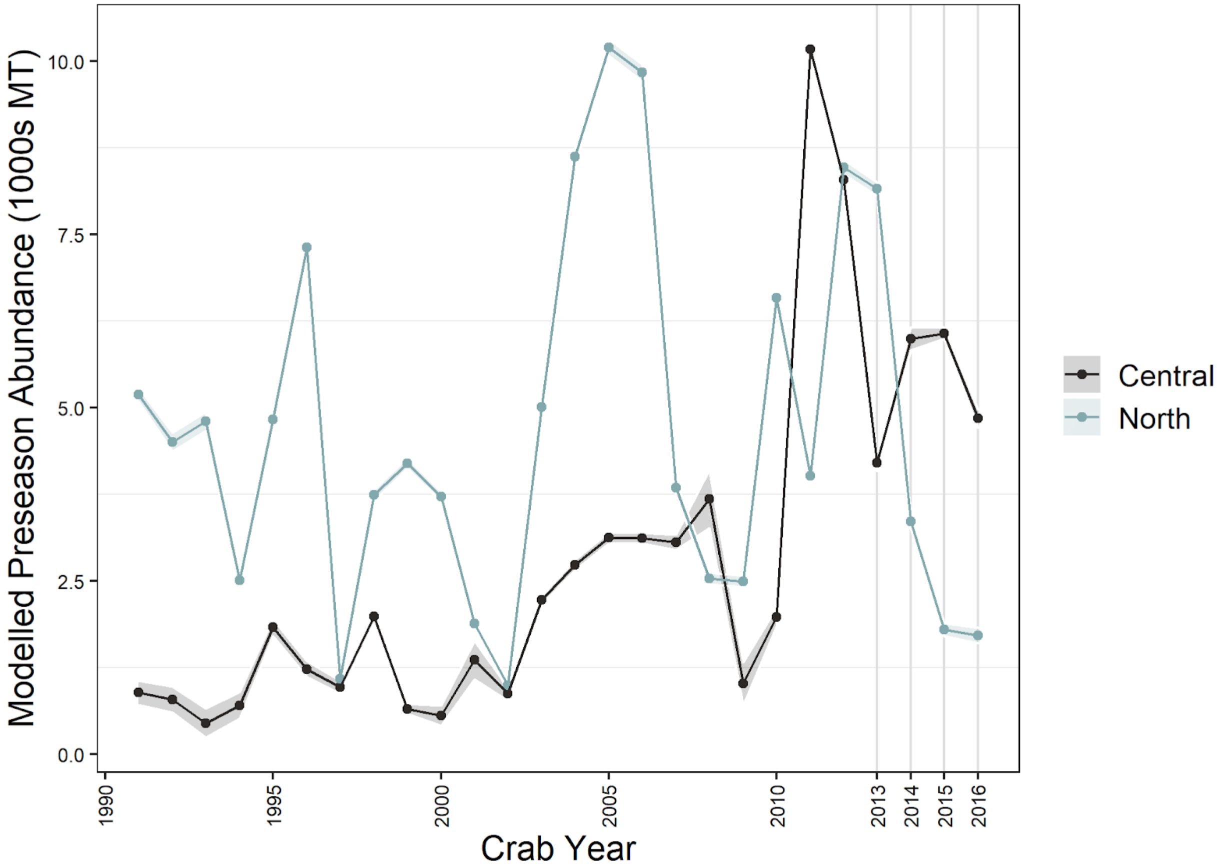


Figure S3.1. Modelled Dungeness crab pre-season abundance from Richerson et al. (2020), within the northern (light blue) and central (dark grey) districts. Estimates for crab seasons used in this study are marked on vertical gray lines.

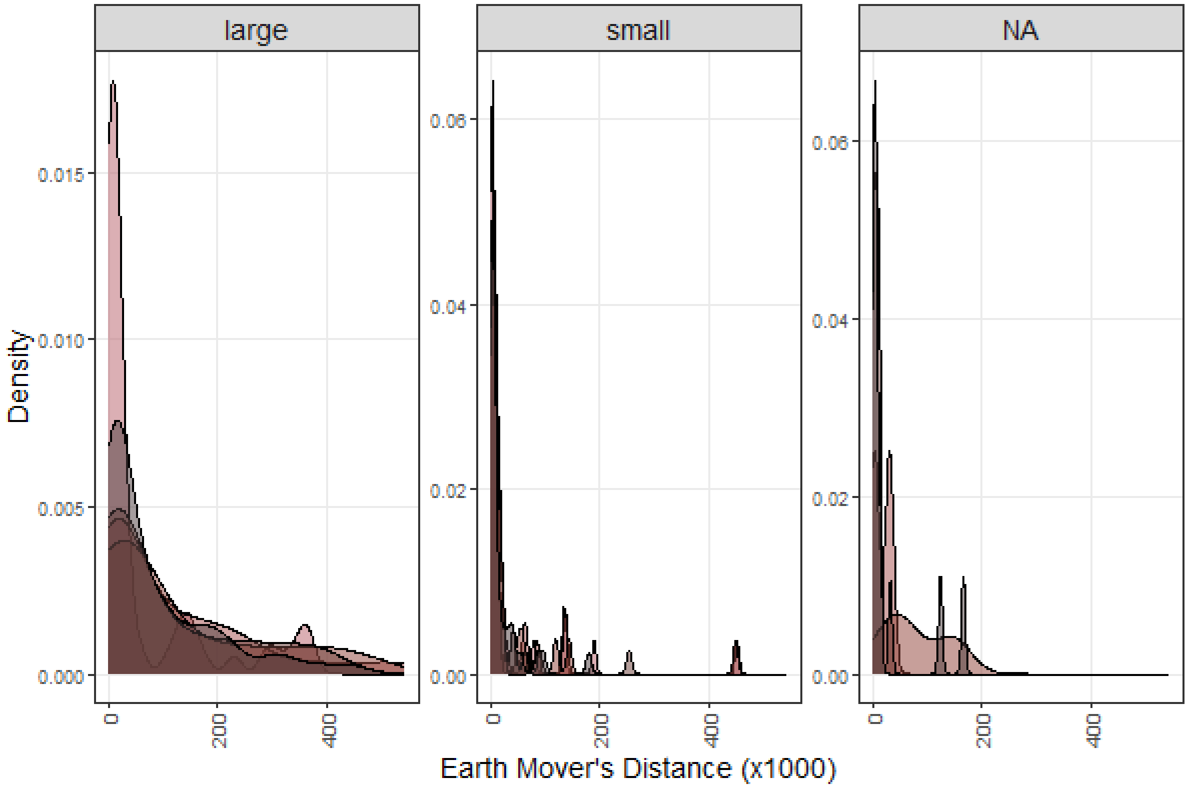


Figure S3.2. Distributions of Earth Mover's Distance (EMD) by vessel size class (large / small), including those vessels which could not be assigned a size class due to missing or filtered self-reported length in vessel registration data ("NA").

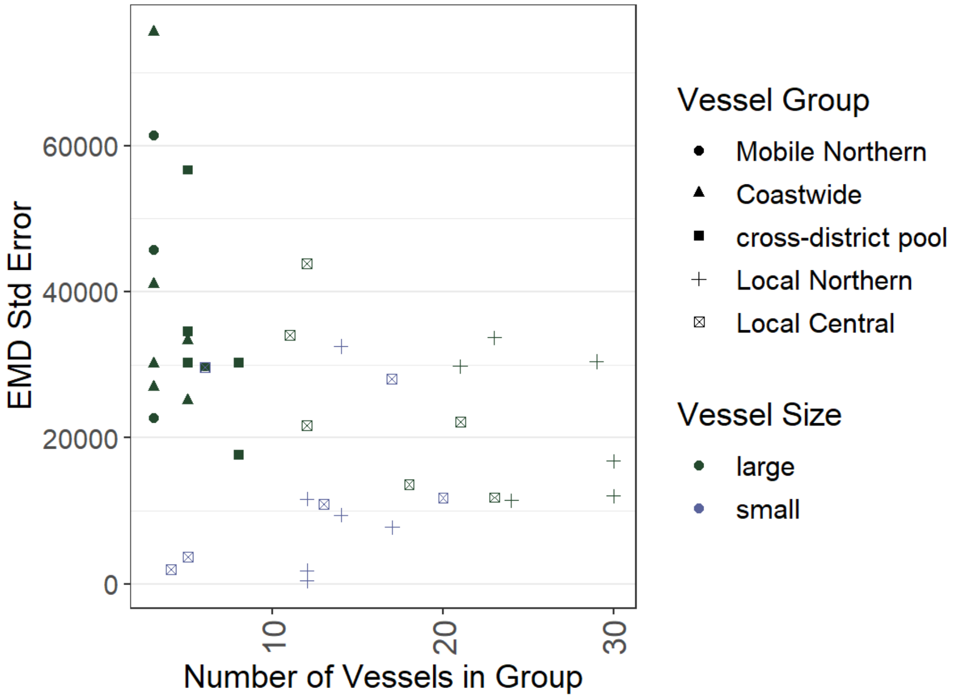


Figure S3.3. Within-group variation in Earth Mover's Distance (EMD), represented by standard error, against the number of active member vessels (i.e., sample size). Corresponds to Figure 3.3 in the main text.

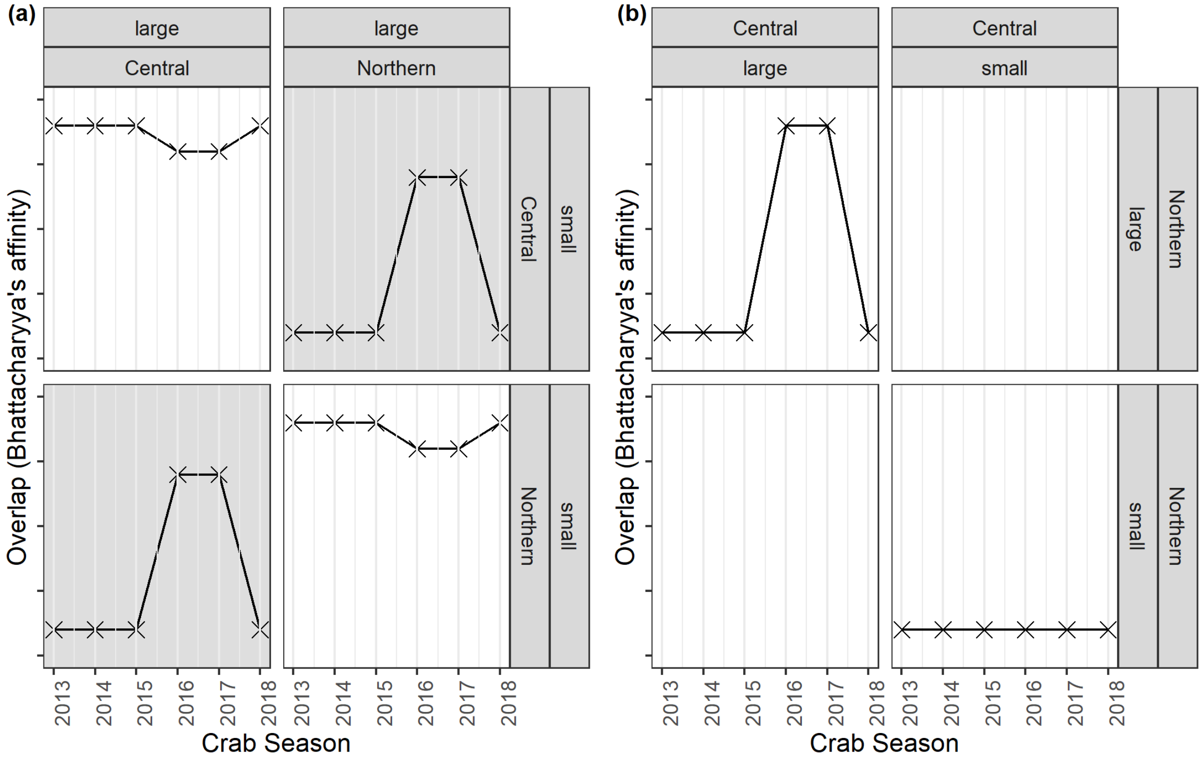


Figure S3.4. Graphical approximation of our hypothesis for overlap in fishing grounds (measured with Bhattacharyya's affinity) between Local vessel groups. Figure layout is the same as Figure 3.4 in the main text for comparison, with **(a)** showing overlap between size class (both within and between districts), and **(b)** showing overlap within size classes (between districts). Since we expected large vessel mobility to drive changes in fishing ground overlap, a highly simplified prediction of dynamics would be that the BA index between large Local vessel groups would increase from negligible to near 1.0 in 2016 and 2017 (b-top left); the BA index between small Local vessel groups would remain negligible (b-bottom right); the BA index between small v. large Local vessel groups from different districts would increase from negligible, as large vessels moved into the opposite district (a-gray panels); and the BA index between small v. large Local vessel groups from the same district may decline slightly as large vessels moved into the opposite district for a certain period of time (a-white panels).

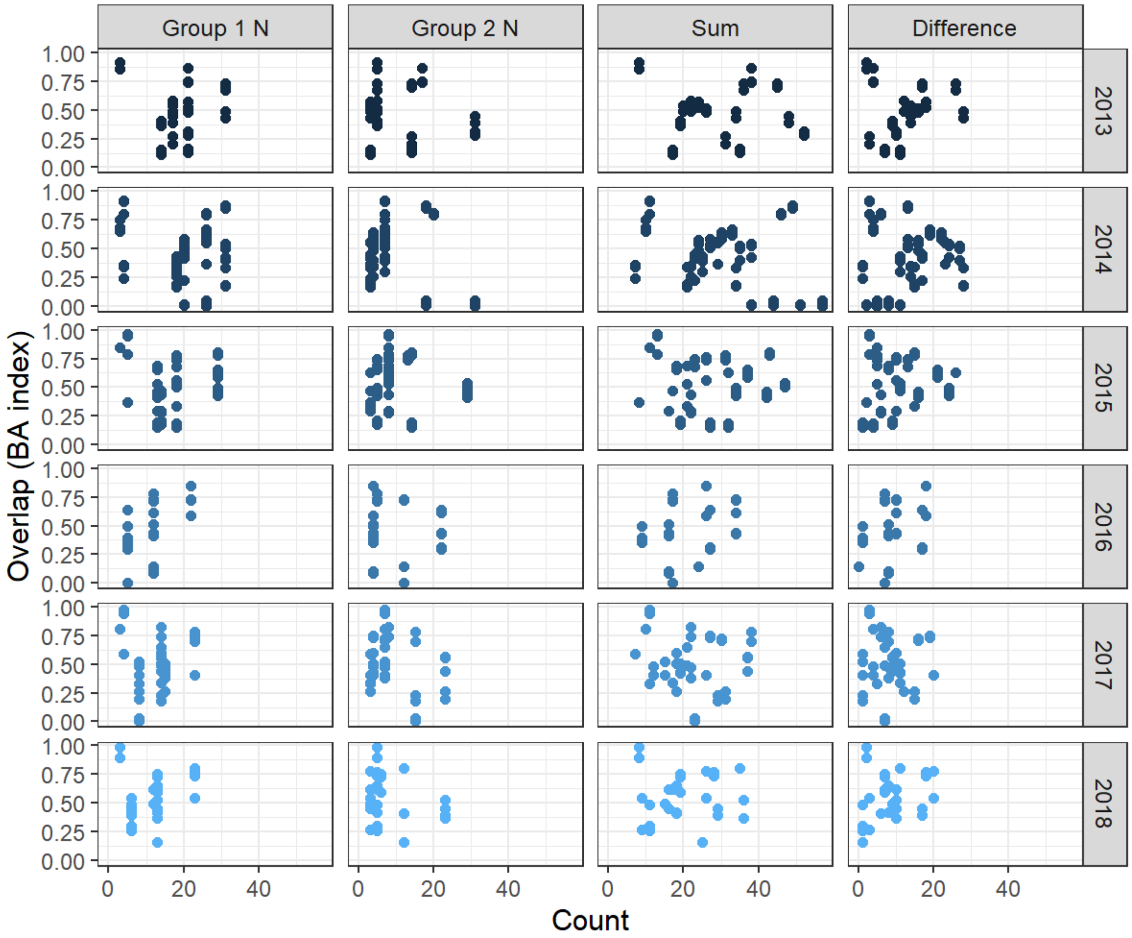


Figure S3.5. Overlap in fishing grounds between two vessel groups measured using Bhattacharyya's affinity (y axis), against sample size (x axis) – provided as the number of vessels in vessel group 1 ("Group1 N"), the number of vessels in group 2 ("Group 2 N"), the combined number of vessels across both groups ("Sum") and the difference in the number of vessels between the two groups ("Difference").

3.8.3 *Checking the influence of seasonality on primary season overlap*

The particularly strong increase in fishing ground overlap from the 2015 to the 2016 primary season that we observed between large Northern and small Central vessels (Figure 3.4a) may reflect a transition from winter (2015 central primary season: Nov 15 - Dec 27) to spring (2016 central primary season: Mar 26 - May 7) fishing grounds, rather than unique fishing activity associated with the HAB closures. To examine the influence of seasonality on this particular pattern of overlap, we recalculated overlap values to compare fishing grounds used between the dates (month-day) for each central primary season, rather than allowing those dates to vary. To determine if fishing ground overlap during the 2016 central primary season was similar to overlap in spring fishing grounds in other crab seasons, this meant calculating fishing ground overlap using vessel geolocations from Mar 26 – May 7 in each preceding / subsequent crab season. If the observed 2016 jump in overlap (Figure 3.4a) were driven by seasonality, we would expect *not* to see a similar jump in fishing ground overlap in 2016 in Figure S3.6, for the 2016 data group (light orange line/points; see color scale). However, this is not the case; in Figure S3.6, fishing ground overlap in the 2016 crab season is much greater than any other crab season for the period Mar 26-May 7.

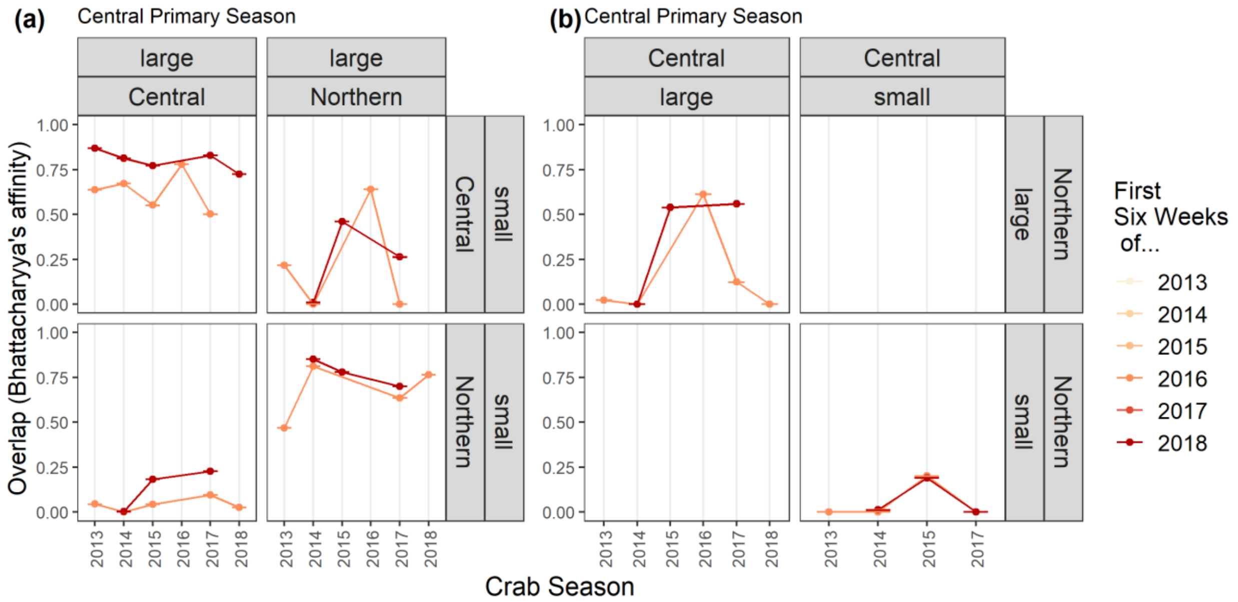


Figure S3.6. Overlap in fishing grounds per crab season, measured with Bhattacharyya's affinity, between Local Northern / Central vessel groups within the date (month-day) range of the given crab seasons' central district primary season (color scale). For example, the 2018 central primary season spanned from November 15, 2017 to December 27, 2017; the darkest orange line / points in the graph above (corresponding to the "2018" data group in the color scale) represent fishing ground overlap between Nov 15 – Dec 27 for each of the crab seasons on the x axis. This means that (1) the 2018 overlap value in the 2018 data group will be equivalent to the 2018 overlap value in Figure 3.4; and (2) the overlap value for any other crab season in the 2018 data group may be different to that crab season's overlap value in Figure 3.4. Any crab seasons in which the central primary season started later than Dec 27 (i.e., the 2016 crab season) cannot be represented in the 2018 data group. Note that some lines within the given color scale are obscured by the 2018 trend line; since the central primary season started at or around the same date (month-day) in each of those crab seasons, the calculated overlap is equivalent or nearly so. Overlap is shown between size classes (**a**) and within size classes (**b**). Error bars indicate 2x standard error calculated from bootstrap re-sampling, and points are means.

We similarly checked for the influence of seasonality on the increase in fishing ground overlap between large Central and small Northern vessels, from the 2015 to the 2017 northern primary seasons (Figure 3.4a). Overlap in fishing grounds in 2017 was still higher than in 2015 (Figure S3.7). We expected less influence of seasonality in this particular comparison because the 2017 crab fishing season, while delayed, still opened in the winter months in the northern district.

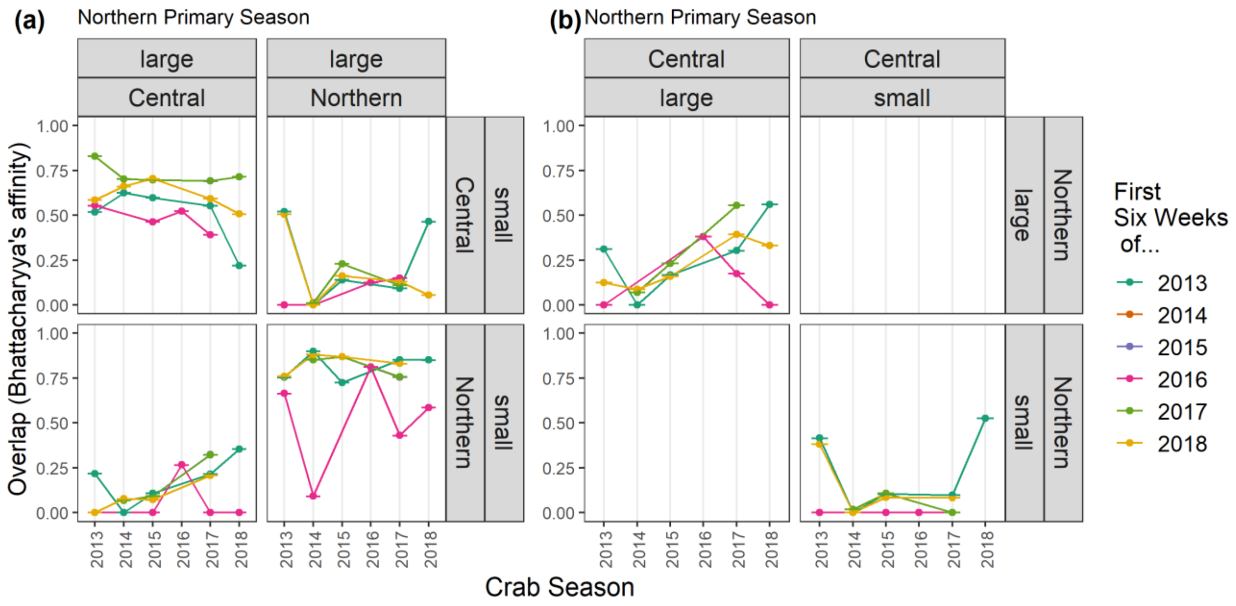


Figure S3.7. Overlap in fishing grounds per crab season, measured with Bhattacharyya's affinity, between Local Northern / Central vessel groups within the date (month-day) range of the given crab seasons' northern district primary season (color scale). Overlap is shown between **(a)** and within **(b)** size classes. Error bars indicate 2x standard error calculated from bootstrap re-sampling, and points are means.

Chapter 4. UNEXPECTED OUTCOMES AND TRADE-OFFS OF CLIMATE ADAPTATION IN FISHERIES, EXPLORED USING SOCIAL-ECOLOGICAL QUALITATIVE NETWORK MODELS

4.1 ABSTRACT

Adaptation to climate change can have trade-offs and unintended consequences that may add to, or amplify, climate impacts. Identifying how these unintended consequences arise in local contexts is an important step in climate adaptation planning, but the tools for doing so are still evolving. We used social-ecological Qualitative Network Models (QNMs) to explore the potential unintended consequences of climate adaptation in a representative U.S. West Coast commercial fishing community. We compared modeled outcomes for commercial fishers' material and non-material well-being from a harmful algal bloom (HAB) perturbation, with and without the implementation of eight climate adaptation strategies. Climate adaptations ranged from coping mechanisms to transformational adaptation, and were based on actions identified in regional, participatory scenario planning initiatives. We first used the QNMs to identify common weaknesses or trade-offs across adaptation strategies, specifically highlighting persistent negative outcomes for cultural practices and community relationships. We then explored alternative configurations of influential dynamics and feedback loops, which represented important assumptions made when conceptualizing the social-ecological system. We found that in-season flexibility and effort allocation - specifically, fishers' capacity to immediately increase effort in alternative fisheries not affected by a HAB - greatly influenced outcomes from climate adaptation. When we effectively limited this capacity in the QNM, negative consequences from the HAB were newly amplified by certain climate adaptation strategies. While not intended to

predict outcomes for a specific community, these results point to the potential for inequitable outcomes from climate adaptation based on individuals' capacity for in-season flexibility, which could justify more tailored adaptive action and fine-scale monitoring post-implementation. Based on this exercise, we propose that QNMs are a useful tool for climate adaptation planning because they can be used to explore common or disparate assumptions about a local social-ecological system; identify influential dynamics and common trade-offs across adaptation options; and direct future research and monitoring priorities to help prevent unintended consequences.

4.2 INTRODUCTION

Changes in global temperature and patterns of precipitation have increased the frequency and intensity of extreme environmental events, disrupting coastal food systems and deeply affecting fishers and their communities (FAO 2015, Cottrell et al. 2019). In response, fishing communities have leveraged a long history of adapting to novel and challenging conditions. In recognition that such autonomous adaptation must be supported and complemented by institutions across multiple levels of governance (Brondizio et al. 2009, FAO 2015), government actors from the local to the international stage have been conducting climate scenario planning (Pacific Fishery Management Council 2020), developing climate action plans (FAO 2023), and directing funds toward climate resilience (Joseph R Biden Jr. E.O. 14008 12/27/2021).

As climate adaptation planning progresses globally, there has been increasing concern around the risk of ineffective adaptation. Ineffective climate adaptation often arises from the failure to account for unintended negative consequences (Singh et al. 2022), which may not only hinder adaptation goals, but may also leave the intended beneficiaries of adaptive action worse off than they would have been if no action were taken. Adverse impacts of adaptation include the intensification of negative environmental or societal effects from an extreme event; for example, a sudden local decline in fish abundance that reduces fishing opportunity can negatively affect the connection of fishing communities to local ecosystems, which may then promote industry consolidation, further limiting fishing opportunities for existing and next-generation fishers (Szymkowiak and Rhodes-Reese 2020). Adverse impacts can also increase community vulnerability to climate change; such *rebounding vulnerability* (Schipper 2020) may occur through an increase in exposure or sensitivity to future climate change (e.g., through amplifying feedbacks that accelerate negative trends in ecosystem services; Cinner et al., 2011), or through a reduction in the community's capacity for future adaptation.

It is therefore crucial for adaptation planning to identify strategies that risk intensifying the impacts of extreme events, or lead to rebounding vulnerability (Magnan et al., 2016; Schipper, 2022). Prior research has developed general principles to guide adaptation planning in doing so. These principles include, among others, addressing the main drivers of system vulnerability, instead of just climate-related stressors (Magnan et al. 2016, Schipper 2022); avoiding technological or engineering solutions that lock in potentially undesirable pathways (Magnan et al., 2016; Bertana et al. 2022); avoiding additional depletion of the local environment (Cinner et al. 2011); and ensuring those involved in planning have strong knowledge of local social and ecological processes (Schipper 2020). Yet there may also be system-specific, local contexts that increase the risk of unintended negative consequences from certain adaptive actions. Early identification and exploration of system dynamics that contribute to such risk could provide a tangible starting point for planning processes to prioritize aspects of strategy development, implementation, and assessment that pre-emptively identify, avoid, and detect unintended negative consequences.

Qualitative network models (QNMs; Levins 1974, Puccia and Levins 1985) have several properties that make them particularly conducive to exploring adaptation in social-ecological systems: they allow the inclusion of variables that are not readily measurable (such as aspects of human well-being and adaptive capacity), they allow variables to differ in their form and measurement, and they don't require prior knowledge of the absolute magnitude or function of relationships between variables (Levins 1998). One of the primary uses of QNMs is to qualitatively capture feedback effects in complex systems (Melbourne-Thomas et al. 2012, Harvey et al. 2016). Because of their relatively intuitive structure as signed directed graphs, QNMs can also be useful in generating or clarifying a shared understanding of the local social-ecological system among those involved in climate adaptation planning.

In this paper, we demonstrate the utility of Qualitative Network Models in examining climate adaptation strategies in fisheries social-ecological systems. We first summarize expert knowledge and the existing literature into a social-ecological QNM for a case study on U.S. West Coast fisheries. We then consider how a simulated climate extreme (harmful algal bloom, or HAB) may affect aspects of human well-being with and without the use of eight adaptive strategies. Specifically, we develop three sets of simulations to demonstrate how QNMs can identify important system dynamics that may contribute to unintended consequences from climate adaptation, and subsequently generate research and monitoring priorities to help prevent those consequences. The first set of simulations evaluates patterns in the intensification of HAB impacts across different climate adaptation strategies. The second and third sets explore how assumptions made when conceptualizing the social-ecological system can affect model outcomes, by comparing alternative configurations of influential model dynamics (second set of simulations), and adding socio-economic feedback relationships (third set of simulations).

4.3 METHODS

4.3.1 *Case study: U.S. West Coast fisheries*

Fisheries on the U.S. West Coast are a timely case study to demonstrate the utility of QNMs for climate adaptation planning in fisheries social-ecological systems. U.S. West Coast fisheries operate within the highly productive California Current marine ecosystem, which is defined by a powerful eastern boundary current and dynamic coastal upwelling. In 2020, these fisheries brought in over $582 million in revenue and supported an estimated 20.1 million jobs (National Marine Fisheries Service 2023). Many fisheries are also socially and culturally significant for coastal communities, and provide an important source of subsistence (Poe et al. 2015). The highest value single-species fishery on the U.S. West Coast, Dungeness crab (National Marine Fisheries Service 2023), has been affected in recent years by numerous fishery closures associated with marine heatwaves, which have seeded recurring harmful algal blooms (Trainer et al. 2020) and heightened the risk of marine mammal entanglement in fishing gear (Santora et al. 2020, Feist et al. 2021). A large body of cross-disciplinary work has investigated the impacts of these closures on the economic and non-material well-being of Dungeness crab fishers, and coastal and Indigenous communities (Ritzman et al. 2018, Moore et al. 2020b, Holland and Leonard 2020, Jardine et al. 2020, Kourantidou et al. 2022), as well as the actions taken by crabbers to autonomously adapt to fishery closures.

Participants in the Dungeness crab fishery range from small-scale owner/operators in rural ports to large vessels that traverse the coast to fish for crab across management boundaries. The fishery operates mid-fall through late summer, and is characterized by highly seasonal, derby-style participation; the majority of the catch is brought in within the first six weeks of the season (hereafter “early” season), and this period generates most annual revenue for many small-scale operations. However, crab fishing vessels are frequently diversified into other fisheries targeting salmon, a wide variety of groundfish, and pink shrimp, among other species (Holland and Leonard 2020, Fisher et al. 2021). In the words of one northern California-based crabber interviewed by Ritzman et al. (2018): "…a lot of these boats do more than just crab, but without crab, a lot of boat owners would probably lose their boats."

The regional fisheries management body for the U.S. West Coast recently conducted a climate change scenario planning process, which included developing a set of stakeholder-identified adaptive actions for harvesters, communities, fishery managers, and scientists (Pacific Fishery Management Council 2022). These action items reflect a combination of prior or ongoing adaptations (e.g., fisheries portfolio diversification), as well as proposed novel actions that require institutional or collective action to implement (e.g., development of an insurance program). The Pacific Fishery Management Council is considering what activities may be incorporated into ongoing activities and initiatives (Pacific Fishery Management Council 2022). This stage of the climate change scenario planning process provides an opportunity to explore the potential unintended consequences of proposed actions prior to further investment in their implementation.

4.3.2 *Qualitative Network Modeling approach*

We developed a Qualitative Network Model (QNM) to capture key dynamics in a Dungeness crab fishing community (Figure 4.1). We refer to this QNM throughout the paper as the Status Quo model. QNMs are signed, directed graphs (digraphs) in which variables (nodes) are connected by links (edges). A QNM can also be represented as a community matrix in which positive links are denoted as a *+1*, and negative links as a *-1*. The variables in our QNM represented: livelihood activities, focused on commercial fishing in the Status Quo;

socioeconomic drivers and outcomes of fishing activity and harvest; and aspects of human well-being derived from livelihood activities. Well-being was organized according to the Breslow et al. (2016) 4Cs framework, with various attributes (e.g., *Identity, Subsistence*) contributing to domains (e.g., *Social relationships*). In certain cases, informed by expert knowledge, we adjusted well-being attributes to be inclusive of a certain facet of adaptive capacity (such as *Shoreside infrastructure & support services*; Cinner & Barnes, 2019). All QNMs were constructed using Dia software (Breit et al. 2009).

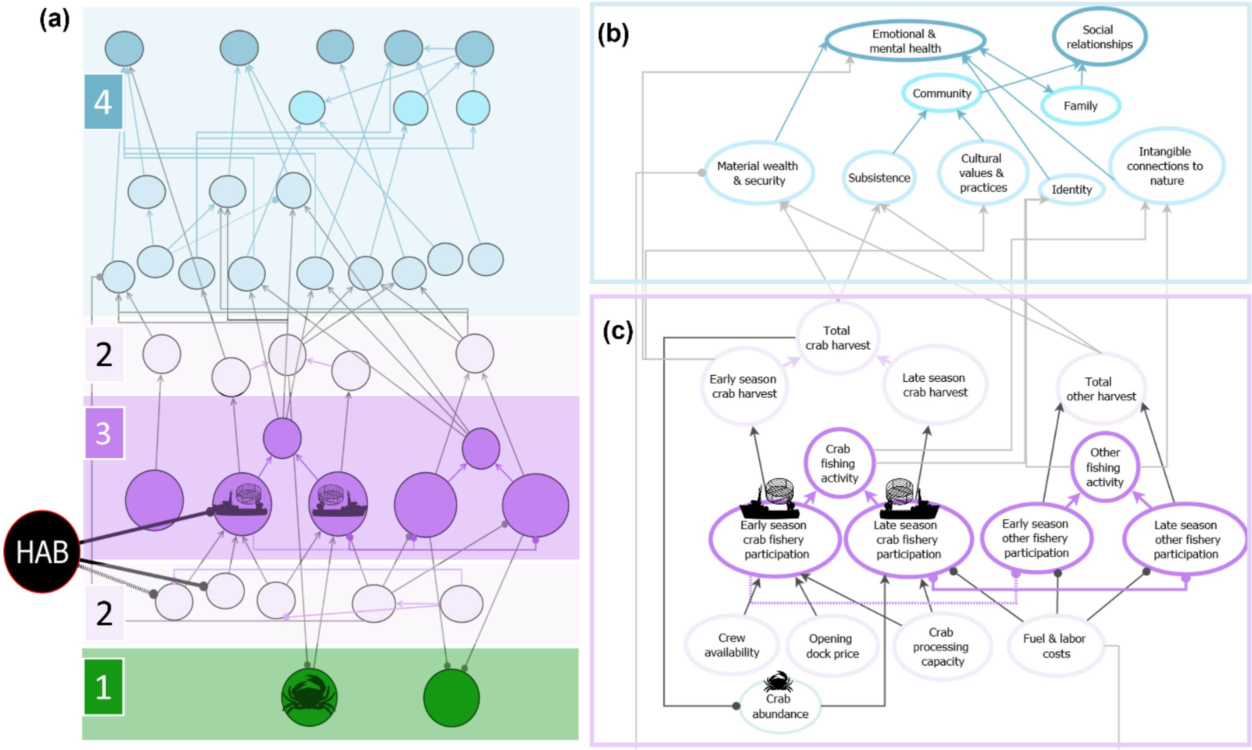


Figure 4.1. The Status Quo qualitative network model's **(a)** full hierarchical structure, with a simulated harmful algal bloom (HAB), in which variables represent (1) ecosystem components, including Dungeness crab populations (crab icon), (2) socioeconomic drivers and outcomes from livelihood activities, (3) livelihood activities, including commercial fishing for crab (vessel icons) and alternative species, and (4) interacting aspects of human well-being. We also provide labeled variables and associated relationships for **(b)** a subset of well-being variables, and **(c)** all

variables representing fishing activity and socioeconomic drivers and outcomes; for a detailed image of the full Status Quo QNM, see Figure S4.1. Well-being variables are broken down into those directly influenced by fishing and other livelihood activities (light blue fill or outline); those with only incoming relationships from other well-being variables (bright blue fill or outline); and higher-order, well-being "domains" (Breslow et al. 2016; dark blue fill or outline). We consider all well-being attributes to be equally important; tiered well-being therefore speaks to the increasing uncertainty that results from the subjective importance of different well-being attributes contributing to a single higher-order variable, or domain. See Table S4.1 for variable definitions, and Table S4.2 for the rationale behind key relationships.

The QNM was developed through an iterative process drawing on expert knowledge, published literature, and test simulations. The first draft of the model was developed collaboratively by co-authors with case study and disciplinary expertise, through the Ocean Modeling Forum's Climate & Communities Working Group. Crucial dynamics were refined according to consultations with external experts who hold system-specific knowledge and experience, with representation from academic and non-profit institutions, and fishery stakeholders.

Our modeled fishing community was representative of more rural, medium-small U.S. West Coast communities that are highly engaged and reliant on commercial fishing ("Coastal Fishing Town" typology; Nelson et al in prep). Our QNM assumed that community members had some decision-making power based on the dock prices set for crab, crew availability, and variable costs, reflective of vessel owner/operators. Because of the knowledge possessed by co-authors, the focus of the QNM (and this paper) was non-tribal commercial Dungeness crab fisheries.

4.3.3 *Describing and implementing adaptive strategies*

We focused on eight strategies for climate adaptation that range from coping mechanisms to transformative adaptation (Table 4.1). We considered a coping strategy a short-term response that is reactive rather than anticipatory (Ojea et al. 2020; Bennett et al. 2014, Green et al. 2021), drawing on some form of capital (Moore et al. 2020) in order to survive a sudden shock or change. Strategies that represented adaptive maintenance were those which combined experience and knowledge to adjust to external drivers, while continuing to maintain the current system state (i.e., a community organized around commercial fishing activity; Berkes et al. 2003, Barnes et al. 2017). Livelihood diversification with fishery exit is transformative, as it involves a deeper change that creates a fundamentally new system, with a different structure, feedback processes, and functions (Walker et al. 2004); the two transformative strategies we considered (Imposed New Livelihoods, Invested New Livelihoods) differed in the type of transformations that occurred within the adaptation space (Table 4.1; Pelling et al., 2015).

Table 4.1. Strategies for coping, adaptive maintenance, and transformative adaptation implemented in the QNM in response to a high-intensity HAB. The sources listed for each strategy include the scenario planning documents in which the adaptation was identified, and other literature used to develop strategy narratives. We specify when we used a strategy in the second ("Influential dynamic") or third ("Feedback") set of simulations. Associated changes to QNM structure are detailed in Table S4.3-Table S4.6 (#1-6), and Figure S4.2-Figure S4.3 (#7,8).

[1] *Parametric or index-based insurance uses an objective measure (index) of the causal event, rather than an assessment of damages.* [2] *A commercial fishery failure is a federal determination from the Secretary of Commerce, based primarily on revenue loss; losses < 80% compared to the most recent 5-yr average require further evaluation (NMFS Policy 01-122, 2007).*

Strategy	Description	Set	Sources
(1) Parametric Insurance (Coping)	A parametric insurance payout for crab fishing vessel owner / operators is initiated by some direct measure of the HAB[1]. Insurance is not required for participation in the crab fishery, so it does not create a new financial barrier to access, but our model assumes that there is majority buy-in from the community.	Influential dynamic	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020:* Washington region, Southern California. *Planning for the Future of Oregon's Dungeness crab Fisheries* (Kirchner and Star 2021) (Kousky et al. 2021, Szymkowiak and Rhodes-Reese 2022)
(2) Direct Assistance Disaster Relief (Coping)	Federal funds are disbursed as direct assistance to the community (e.g., the existing response to a commercial fishery failure[2]). An improved federal fishery disaster process includes a shorter delay in disbursing direct assistance, so that the assistance better offsets loss of fishery revenue and associated stresses.	Influential dynamic Feedback	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region. (Bonham et al. 2018, Ritzman et al. 2018, Marshak 2020, California Department of Fish and Wildlife 2020, Cha 2023)
(3) Multi-Objective Disaster Relief (Adaptive maintenance)	Similar to Direct Assistance Disaster Relief, except that federal funds are also used to invest in research and monitoring capacities that help to prepare for and prevent a similar fishery failure in the future.	Influential dynamic Feedback	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region, Northern California, Southern California. *Planning for the Future of Oregon's Dungeness crab*

			Fisheries (Kirchner and Star 2021) (Smith and Gilden 2000, Bonham et al. 2018, Ritzman et al. 2018, Marshak 2020, Moore et al. 2020b, California Department of Fish and Wildlife 2020, Free et al. 2022, Cha 2023)
(4) Existing Fisheries Diversification (Adaptive maintenance)	Institutional and individual action makes 'early season' fishery participation flexible between crab and equally lucrative alternative fisheries that are unaffected by the HAB. These are species (or species assemblages) that have been fished by the community in the past, but at low levels or by only a few individuals. The barrier to entry is low, and any start-up costs have a transitory effect.	Influential dynamic (Appendix)	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region, Oregon region, Northern California, Southern California. *Planning for the Future of Oregon's Dungeness crab Fisheries* (Kirchner and Star 2021) (Moore et al. 2020a, Fisher et al. 2021)
(5) New Fisheries Diversification (Adaptive maintenance)	Institutional and individual action makes 'early season' fishery participation flexible between crab and an equally lucrative alternative fishery that is unaffected by the HAB. This is a species (or species assemblage) that has **not** been harvested by the community in the past, but for which markets do exist. Accessing the new fishery involves additional financial investment.	Influential dynamic (Appendix)	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region, Oregon region. (Moore et al. 2020a, Drakopulos & Poe 2023)
(6) Supplementary Diversification (Adaptive maintenance)	Alternative livelihoods outside of fishing widely supplement, but do not fully replace, commercial fishing activity. These alternative livelihoods are insulated from HABs, but do not support the same non-material aspects of well-being as commercial fishing activity.	Influential dynamic Feedback	*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region, Southern California. *Planning for the Future of Oregon's Dungeness crab Fisheries* (Kirchner and Star 2021)

			(Moore et al. 2020a, Holland et al. 2020, Treakle et al. 2023, Nelson et al. 2023)
(7) New Livelihoods (Transformative)	The community exits commercial fishing for new livelihood activities, which are still associated with the blue economy (e.g., aquaculture, tourism, etc.). This exit was imposed through top-down policies, with limited engagement or institutional assistance for occupational re-training. Community members shift participation to recreational crab fisheries for subsistence use. Transformation is focused on production and labor processes in the adaptation activity space (Pelling et al. 2015), such that non-fishing livelihoods do not contribute to non-material aspects of well-being, which are instead tied to recreational fishing activity.		*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region. (Brugère et al. 2008, Ritzman et al. 2018, Stoll et al. 2019, Holland et al. 2020, Ojea et al. 2020, Nelson et al. 2023)
(8) Invested New Livelihoods (Transformative)	As for (7) above, the community exits commercial fishing for new livelihood activities, and participates in recreational crab fisheries. However, the commercial fishery exit was conducted through community-led processes, and with strong institutional support for occupational transitions. Transformation occurs across livelihoods, institutions, individuals, and behavior (Pelling et al. 2015), such that non-fishing livelihoods contribute to certain non-material aspects of well-being.		*Completed worksheets for Climate Change Scenario Planning online workshops, 2020*: Washington region. (Brugère et al. 2008, Ritzman et al. 2018, Stoll et al. 2019, Holland et al. 2020, Ojea et al. 2020, Nelson et al. 2023)

These eight response strategies were developed from a larger set of action items identified during two scenario planning initiatives - one directed by the Pacific Fishery Management Council for U.S. West Coast fisheries more broadly, and one hosted by The Nature

Conservancy specific to the Oregon Dungeness crab fishery - which were then coded and summarized by Nelson et al. (in prep). We identified which Nelson et al. (in prep) strategies were feasible to implement in our QNM representation of a fishing community, then drew on workshop documents, co-author expertise, and the existing literature to develop narratives describing each strategy and relevant structural changes to our Status Quo QNM (Figure S4.2 - Figure S4.3; Table S4.3-Table S4.6). The result of this process was a separate QNM for each adaptation strategy (hereafter "strategy QNMs").

4.3.4 *Simulating a climate perturbation*

We simulated a harmful algal bloom (HAB) in each QNM. Drawing on past events, we assumed that a harmful algal bloom had three major impacts on the modeled community: (1) area closures in the commercial fishery reduced winter fishing activity (Ekstrom et al. 2020); (2) labor availability was lower when the fishery re-opened (uncertain); and (3) the opening dock price for crab was lower when the fishery re-opened (Mao and Jardine 2020). When the community had undertaken livelihood diversification with fishery exit, we instead assumed that a HAB had a negative impact on recreational fishing activity, by restricting recreational harvest for Dungeness crab.

Each HAB simulation was conducted using the *QPress* package in R (Melbourne-Thomas et al. 2012), and visualized with custom R scripts. The *QPress* package simulates one or more press perturbations to a given QNM, and predicts the direction of change (positive, negative, none) for each response variable. To run the simulation, random magnitudes are assigned to non-zero values of the community matrix, ranging [-1, 0) for negative links and (0,1] for positive links; if the matrix is determined to be stable, then all direct and indirect effects from the perturbed variable to each response variable are summed, and the direction of the response reported (Dambacher et al. 2003, Melbourne-Thomas et al. 2012). We used the assumptions detailed above to identify appropriate press perturbations to simulate a HAB, and ran all simulations until 10,000 stable model structures were achieved (Melbourne-Thomas et al. 2012, Harvey et al. 2016, Magel and Francis 2022). We reported model outcomes for each variable on a semi-qualitative scale from "Weak Negative" to "Strong Positive." If a given variable showed a positive/negative response to the harmful algal bloom perturbation in 60% or more (>6,000) of the stable model structures, we reported the model output for that variable as positive/negative. The positive/negative response was then categorized as "Weak" if it occurred in 60-80% of the stable model structures, or "Strong" if it occurred in >80% of the stable model structures (Magel and Francis 2022).

For our first set of simulations, we simulated a HAB in the Status Quo model, with no response strategies applied, as well as in each of the eight strategy QNMs. For the second set of simulations, we identified influential dynamics using model sensitivity analysis (following Magel & Francis, 2022; Melbourne-Thomas et al., 2012; see 4.8.1), and according to important uncertainties identified during the model-building process. We then adjusted the associated relationship(s) in the Status Quo and strategy QNMs and simulated a HAB. For the third set of simulations, we identified a self-reinforcing socio-economic feedback loop drawing on expert knowledge and gray literature. We then simulated a HAB, and compared the output between QNMs with and without the feedback.

4.4 RESULTS

4.4.1 *What HAB impacts are intensified / reduced across adaptation strategies?*

4.4.1.1 Strategies for coping, adaptive maintenance

The Supplementary Diversification strategy performed the worst overall, whereas the two fisheries diversification strategies (Existing Fisheries Diversification, New Fisheries) performed the best overall, based only on the number of well-being variables which still had negative outcomes from the HAB simulation (Figure 4.2a). The two fisheries diversification strategies facilitated a shift of fishing activity from the HAB-impacted fishery (Dungeness crab) into unaffected fisheries, and so maintained levels of fishing activity and harvest necessary for supporting non-material well-being. Insurance and the two Disaster Relief strategies fell out between Supplementary Diversification and fisheries diversification.

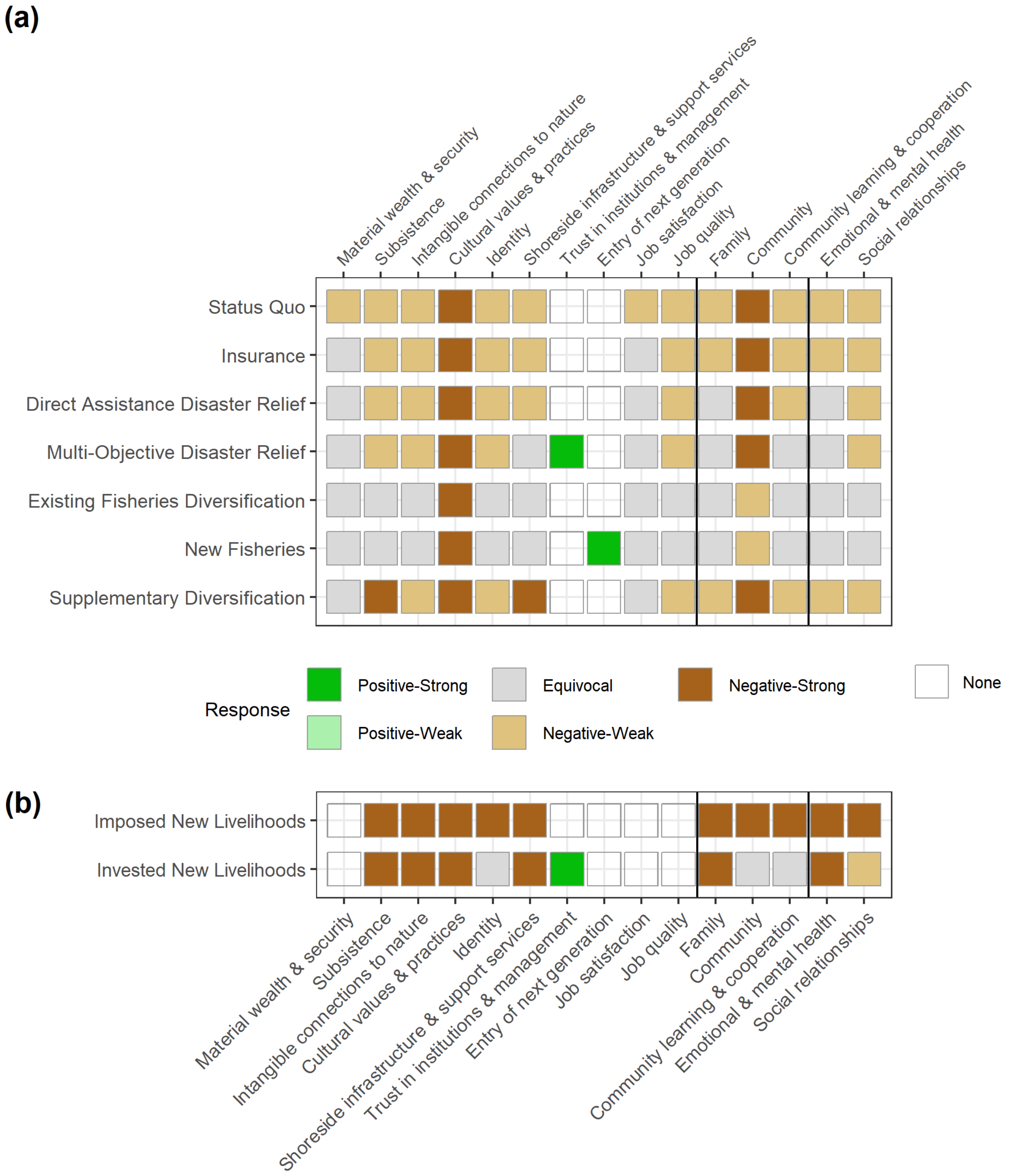


Figure 4.2. Well-being outcomes from a HAB simulation, across climate adaptation strategies. We show responses for a subset of variables representing aspects of well-being (columns) under **(a)** the Status Quo (first row) versus when six of the non-transformative strategies were implemented, and **(b)** when transformative strategies were implemented. Well-being variables are tiered by vertical black lines following Figure 4.1a.

We observed several common outcomes across the six non-transformative response strategies (#1-6 in Table 4.1; Figure 4.2a). All strategies fully offset HAB impacts on *Material wealth & security* as well as *Job satisfaction*, which we associated with predictability of earnings (Holland et al., 2020; Table S4.1). None of these six strategies affected the strong negative impact of the HAB on *Cultural values & practices*. *Community* was also negatively impacted across all strategies, although the two strategies involving fisheries diversification (Existing Fisheries Diversification, New Fisheries) did lead to a weaker negative outcome for that variable.

The only strategy which intensified HAB impacts was Supplementary Diversification (*Subsistence* and *Shoreside infrastructure & support services*; Figure 4.2a). The Supplementary Diversification strategy spread the spillover from lost fishing opportunity between non-fishing employment and unaffected fisheries, and non-fishing employment activities did not contribute to non-material aspects of well-being like *Subsistence*. In further drawing economic activity away from fishing-associated businesses, Supplementary Diversification also intensified HAB-associated losses to commercial fishing infrastructure and shoreside support services.

In contrast, HAB impacts to *Shoreside infrastructure & support services* were reduced by three out of the five other non-transformative strategies - both fisheries diversification strategies, and Multi-Objective Disaster Relief - and the two fisheries diversification strategies reduced HAB impacts to *Subsistence*. Broadly, this is because both forms of fisheries diversification boosted certain existing system dynamics that compensate for HAB impacts, whereas Multi-Objective Disaster Relief acted through several different interventions that target specific aspects of well-being. The fisheries diversification strategies compensated for the HAB-driven loss in early season crab harvest with an increase in harvest from unaffected fisheries, and the late season crab fishery; harvest contributes to both *Subsistence* and *Shoreside infrastructure &*

support services. Multi-Objective Disaster Relief included a direct infusion of assistance to *Shoreside infrastructure & support services*, but did not compensate for losses to harvest – and so negative HAB impacts to *Subsistence* remain. We also assumed that Multi-Objective Disaster Relief includes funding for biological monitoring and forecasting of HABs, which improved outcomes for *Emotional & mental health* by reducing stress related to the uncertainty of HAB duration and building trust in management (Ekstrom et al., 2020; Free et al., 2022).

Direct Assistance Disaster Relief, in contrast, assumed all disaster relief went toward direct assistance for impacted fishers. This and the Parametric Insurance strategy are implemented almost identically in the QNMs, but only Direct Assistance Disaster Relief reduced the negative HAB impact to *Emotional & mental health.* The contrasting outcome for *Emotional & mental health* between these two strategies resulted from the cumulative effects of minor differences in other aspects of well-being that are not strong enough alone to be reflected in the qualitative output table; namely, the use of Insurance resulted in a slightly greater proportion of simulations in which *Identity* and *Intangible connections to nature* decrease, which has a cumulative negative effect on *Emotional & mental health.*

4.4.1.2 Strategies for transformation

We evaluated two transformative forms of livelihood diversification with fishery exit – Imposed and Invested New Livelihoods (#7-8, Table 4.1). In both strategies, the HAB simulation had no effect on *Material wealth & security* or *Job satisfaction/quality* (Figure 4.2b), because livelihood activities were not tied to Dungeness crab fishing under these scenarios. However, the Imposed New Livelihoods QNM showed new or intensified outcomes for non-material aspects of well-being compared to the Invested New Livelihoods QNM (Figure 4.2b). While we expected to see few impacts to well-being variables from exiting the commercial fishery, the switch out of commercial fisheries also eliminated built-in compensating mechanisms (i.e., alternative commercial fishing opportunities) for community members to adjust to non-material HAB impacts. Instead, most non-material aspects of well-being are supported by recreational crab fishing activity alone (Table 4.1). However, we did model a sociocultural transition away from fishing for the Invested New Livelihoods strategy, which limited HAB impacts to *Identity*, *Community*, *Community cooperation & learning*, and, to a lesser degree, *Social relationships*; although there were still negative outcomes for variables such as *Cultural values & practices* and *Emotional & mental health* as recreational fishing still had some role in well-being.

It is crucial to note that outcomes for well-being variables are not directly comparable between these transformative strategy QNMs and the Status Quo / non-transformative QNMs; negative outcomes that were coded as qualitatively equivalent between the two (Figure 4.2) would have affected community members differently. This is because the HAB had a different maximum negative effect on overall well-being for the New Livelihoods QNMs (in which most non-material well-being was derived from recreation) compared to the QNMs for the Status Quo or non-transformative strategies (in which modeled non-material well-being focused on commercial activities). In other words, we were modeling different facets or degrees of each well-being variable between the two groups (Figure 4.3).

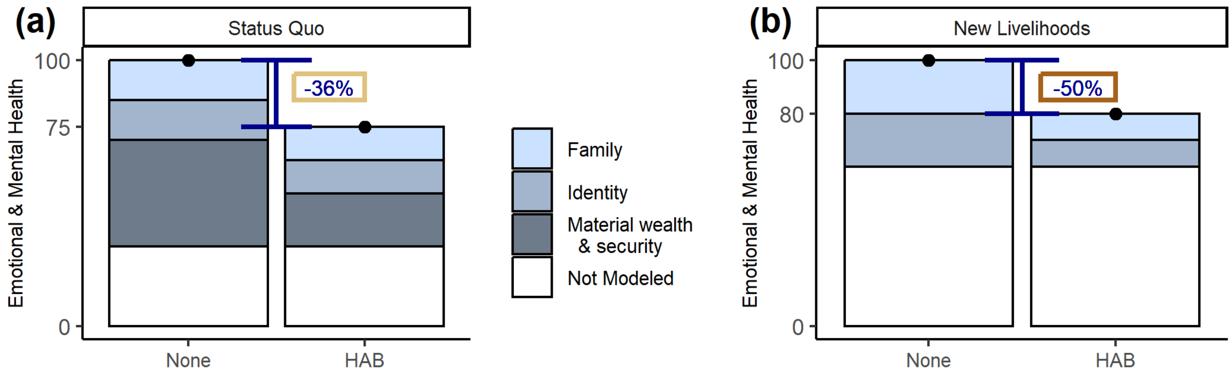


Figure 4.3. A demonstration of the difference in modeled well-being (blue shades) between the Status Quo / non-transformative strategy QNMs **(a,** "Status Quo"**)** and transformative strategy QNMs **(b,** "New Livelihoods"**)**. The graphs show how a relatively smaller reduction in <u>overall</u> *Emotional & mental health* in a transformative strategy QNM may be represented as a relatively greater reduction in <u>modeled</u> *Emotional & mental health* - and therefore, a stronger negative outcome in the simulation output tables (e.g., Figure 4.2). In this example, a 20% decline in overall *Emotional & mental health* (y axis) for the transformative New Livelihoods QNM corresponded to a 50% decline in modeled well-being (blue text); whereas for the Status Quo QNM, a 25% decline in overall *Emotional & mental health* (y axis) corresponded to a 35% decline in modeled wellbeing (blue text). As a result, the QNM simulation output (e.g., Figure 4.2), which describes changes to modeled well-being, would show a weaker negative decline in *Emotional & mental health* for the Status Quo QNM than for the New Livelihoods QNM (35%, compared to 50%), despite a greater overall decline in *Emotional & mental health* under the Status Quo (25%, compared to 20%). Percentage values are given as examples only, and do not directly correspond to the data underlying responses reported in Figure 4.2.

4.4.2 *How do model assumptions alter the intensifying / reductive role of adaptation strategies?*

Building social-ecological QNMs puts the modeler in the position of the "filter and [the] lens" through which a highly complex system is abstracted to a simplified structure (Williams et al. 2022). For our application of QNMs, this meant that the positionalities of the authors could limit the identification and prioritization of unintended consequences from climate adaptation, according to the model structure that was ultimately decided on. Here, we demonstrated several ways in which changing QNM structure affects the modeled outcomes for human well-being and, ultimately, conclusions for climate adaptation planning. We first explored alternative configurations of an existing model dynamic which was identified as particularly influential by sensitivity analyses. We then introduced a feedback loop from well-being variables to socioeconomic drivers; feedbacks are a crucial aspect of complexity in social-ecological systems, and were not otherwise present between these two variable groups in our QNMs.

4.4.2.1 Alternative configurations of an influential dynamic

The most influential model dynamic was the trade-off in fishing activity during the early season (Table S4.7; Figure S4.4), when Dungeness crab was favored over alternative fisheries and when the crab fishery was negatively impacted by the HAB. We assumed that early season participation in Dungeness crab, the more lucrative or preferred fishery, may have reduced participation in other concurrent fisheries (rationale in Table S4.2). Therefore, when we simulated a HAB that "closed" the Dungeness crab fishery, alternative fishery participation increased over 50% of the time as community members reallocated their effort. However, it was also plausible that (a) fishing crab enabled participation in an alternative fishery ("crab facilitates"), such that a HAB decreased alternative fishery participation; (b) crab fishing activity did not influence participation in an alternative fishery ("crab has no effect"); or (c) fishing crab prevented participation in an alternative fishery ("crab limits"), such that a HAB led to an increase in alternative fishery participation over 80% of the time. We constructed alternative model configurations, and re-ran the HAB simulation, to represent these three additional scenarios.

More adaptive strategies intensified HAB impacts on non-material aspects of well-being under the “crab facilitates” and “crab has no effect” configurations (Figure 4.4a,b) than we observed in the first set of simulations (Figure 4.2). Insurance, Multi-Objective Disaster Relief, and Supplementary Diversification intensified HAB impacts on *Intangible connections to nature*, such that the variable response went from weakly negative in the Status Quo to strongly negative for all three strategies; Insurance and Supplementary Diversification also intensified the negative HAB impact on *Identity*, from weakly to strongly negative (Figure 4.4a,b). We also found that strategies were less effective at reducing HAB impacts under the “crab facilitates” and “crab has no effect” configurations. For example, with the “crab facilitates” configuration, Insurance was ineffective at reducing negative HAB impacts to *Material wealth & security*; while Insurance partially reduced this negative impact when “crab has no effect,” the “crab has no effect” community with Insurance saw the same weak negative impact to *Material wealth & security* as the Status Quo (no adaptive response) under our default configuration (Figure 4.4a,b).

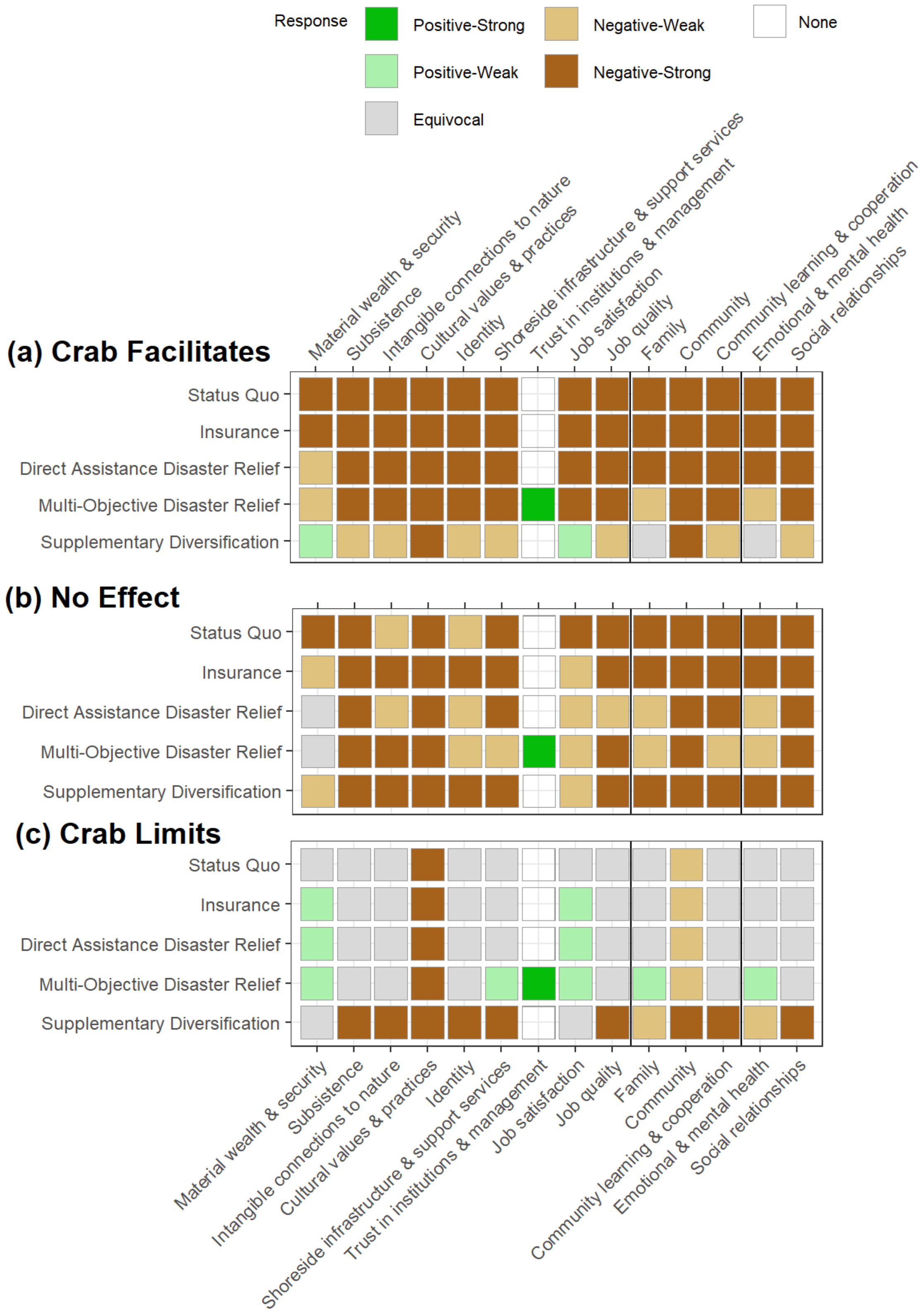


Figure 4.4. Demonstration of how model structure, through influential dynamics, can alter well-being outcomes from HAB response strategies. The effects of different winter fishing

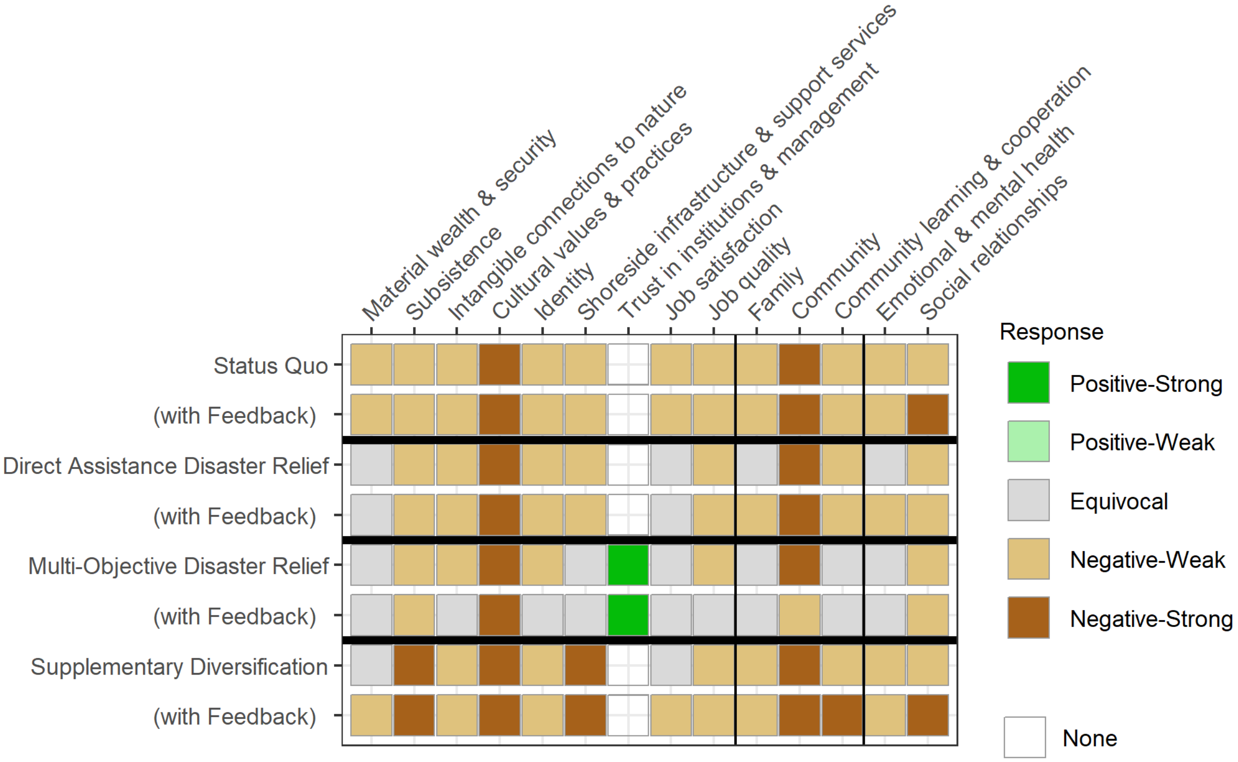
opportunities (**a**-Crab Facilitates, **b**-Crab Has No Effect, **c**-Crab Limits) are summarized for the Status Quo and three non-transformative strategies. The first table (left) shows the response of each well-being variable to the HAB simulation, as in Figure 4.2.

The "crab limits" configuration was the only instance in which we observed multiple positive responses to a HAB across different strategies (Figure 4.4c). For example, *Material wealth & security* actually improved from a simulated HAB, as the modeled community received insurance pay-outs or disaster assistance even as it autonomously made up for lost crab revenue by increasing effort in other fisheries. This was in stark contrast to the material and non-material outcomes we observed with all other configurations, particularly "crab facilitates."

4.4.2.2 Adding a feedback loop

We added a negative feedback between *Shoreside infrastructure & support services* and variable operating costs (represented by *Fuel & labor costs*; Table S4.1b), drawing on results from the first set of simulations (Figure 4.2) and the rationale for prior fishery disaster relief spending (Bonham et al. 2018). This could be a self-reinforcing feedback because our HAB simulation negatively impacted *Shoreside infrastructure & support services* in the Status Quo QNM, which raised operating costs through the feedback, which in turn lowered fishing activity and its positive contribution to *Shoreside infrastructure & support services*. We also simulated a negative feedback loop between *Social relationships* and *Non-fishing employment activity*, and reported those results in the Appendix (section 4.8.4.2).

Whether the feedback from *Shoreside infrastructure & support services* interacted with an adaptation strategy to intensify or further reduce HAB impacts varied by adaptation (Figure 4.5; Figure S4.5). For Multi-Objective Disaster Relief, there were fewer negative outcomes for well-being with the feedback than without (Figure 4.5). This included the reduction of negative HAB impacts on *Intangible connections to nature*, *Identity*, and *Job quality* - which all had equivalent outcomes with the feedback - and a reduction of the negative impact to *Community* from “strong” to “weak.” The feedback facilitated these outcomes because investment in port infrastructure and fishery support services for the Multi-Objective Disaster Relief strategy reduced operating costs through the feedback loop, and facilitated fishing activity outside of the HAB-impacted crab fishery; this in turn helped offset HAB impacts to non-material well-being (Figure S4.6).



	Material wealth & security	Subsistence	Intangible connections to nature	Cultural values & practices	Identity	Shoreside infrastructure & support services	Trust in institutions & management	Job satisfaction	Job quality	Family	Community	Community learning & cooperation	Emotional & mental health	Social relationships
Status Quo	🟨	🟨	🟨	🟫	🟨	🟨	☐	🟨	🟨	🟨	🟫	🟨	🟨	🟨
(with Feedback)	🟨	🟨	🟨	🟫	🟨	🟨	☐	🟨	🟨	🟨	🟫	🟨	🟨	🟫
Direct Assistance Disaster Relief	▒	🟨	🟨	🟫	🟨	🟨	☐	▒	🟨	▒	🟫	🟨	▒	🟨
(with Feedback)	▒	🟨	🟨	🟫	🟨	🟨	☐	▒	🟨	🟨	🟫	🟨	🟨	🟨
Multi-Objective Disaster Relief	▒	🟨	🟨	🟫	🟨	▒	🟩	▒	🟨	▒	🟫	▒	▒	🟨
(with Feedback)	▒	🟨	▒	🟫	▒	▒	🟩	▒	▒	▒	🟨	▒	▒	🟨
Supplementary Diversification	▒	🟫	🟨	🟫	🟨	🟫	☐	▒	🟨	🟨	🟫	🟨	🟨	🟨
(with Feedback)	🟨	🟫	🟨	🟫	🟨	🟫	☐	🟨	🟨	🟨	🟫	🟫	🟨	🟫

Response
🟩 Positive-Strong
▩ Positive-Weak
▒ Equivocal
🟨 Negative-Weak
🟫 Negative-Strong
☐ None

Figure 4.5. Demonstration of how model structure, through a feedback loop between *Shoreside infrastructure & support services* and variable operating costs, can alter well-being outcomes from select HAB response strategies.

In contrast, Direct Assistance Disaster Relief was less effective at reducing HAB impacts with the feedback – namely, for *Family* and *Emotional & mental health* (Figure 4.5). Unlike Multi-Objective Disaster Relief, the Direct Assistance strategy did not include investments in *Shoreside infrastructure & support services*, and so the negative HAB impacts to *Shoreside infrastructure & support services* increased variable costs and limited participation in unaffected, alternative fisheries; while Direct Assistance Disaster Relief was still able to maintain material well-being, certain aspects of non-material well-being suffered from the loss of fishing activity caused by the feedback loop (Figure S4.6). Through a similar process, the feedback caused Supplementary Diversification to intensify HAB impacts to *Community learning & cooperation* compared to the Status Quo, and prevented a reduction of HAB impacts to *Material wealth & security* and associated *Job satisfaction* (Figure 4.5). The remaining non-transformative strategies were unaffected by the addition of the feedback loop (Insurance, Existing Fisheries Diversification, New Fisheries; Figure S4.5).

4.5 DISCUSSION

We used Qualitative Network Models (QNMs) to simulate an extreme environmental event in a fishing community's social-ecological system. Without climate adaptation, the simulated harmful algal bloom (HAB) resulted in negative outcomes for all modeled aspects of human well-being, although with different strengths across well-being variables. Only one climate adaptation strategy caused the unintentional intensification of HAB impacts, although the remaining seven adaptation strategies frequently failed to reduce HAB impacts to non-material well-being. When we explored the influence of model structure on outcomes for human well-being, we found that adaptation strategies were highly sensitive to adjustments to the system dynamic representing in-season fishing flexibility, which created contrasting intensification or reduction of HAB impacts across alternative configurations of the dynamic. Addition of a feedback loop also affected well-being outcomes for a subset of adaptation strategies, although the direction of change in outcomes was more strategy-specific. QNMs are not designed to act prescriptively or provide exact predictions, but we can use our results to identify key structural uncertainties and aspects of strategy implementation that are likely to contribute to unintended negative consequences from climate adaptation.

4.5.1 *Common negative outcomes for community, culture*

The *Community* and *Cultural values & practices* variables showed consistent negative responses to a HAB simulation even with the implementation of our six non-transformative strategies (#1-6, Table 4.1). While this does not represent an unintentional intensification of HAB impacts, it does demonstrate that a focus on material well-being alone may result in climate adaptation that fails to address key climate impacts, especially when a fishery is deeply important to a community's social fabric (as is Dungeness crab for our study system; Poe et al., 2015; Ritzman et al., 2018; Strawn, 2019). Even combining the seemingly disparate strategies modeled here could fail to holistically address sociocultural impacts from climate change. On longer time-scales, reduced community connections can become a pathway for rebounding vulnerability by limiting capacity for social organization, which is key to community resilience. In U.S. West Coast fisheries, local fundraisers and other community organizing have played an important role in helping fishing communities through HAB events (Ritzman et al. 2018), and "women-in-fisheries" groups like the Newport Fishermen's Wives facilitate knowledge exchange, act as advocacy groups, and raise financial support for community members when needed (Calhoun et al. 2016). As a result, when implementing asset-focused adaptive maintenance for systems similar to our modeled community, it will be important to closely monitor aspects of adaptive capacity that are particularly affected by sociocultural values and community relationships.

These conclusions are based on our conservative assumption that all of the non-transformative strategies maintain the strong Status Quo relationship between early season crab harvest and *Cultural values & practices*. However, altered nature-society relationships from adaptive maintenance - such as the two fisheries diversification strategies modeled here, which de-emphasize economic reliance on Dungeness crab - could shift community-building activities to focus on other fisheries that are less vulnerable to HABs, or to climate change more broadly. Cultural transitions like these may be more likely to occur within certain subgroups of the community, leaving other community members more sensitive to the weaknesses of asset-focused adaptive maintenance.

Although not directly comparable in magnitude, we also observed the persistence of negative HAB impacts to non-material well-being with our transformative New Livelihood strategies. Our HAB simulations had a strong negative effect on *Cultural values & practices* for both New Livelihoods strategies; however, this only resulted in a negative impact to *Community* with the Imposed New Livelihoods strategy, which modeled transformation for livelihood activities but not for associated sociocultural behavior. Imposed New Livelihoods therefore parallels our non-transformative strategies, but with the maintenance of crab-focused *Cultural values & practices* reliant on recreational, instead of commercial, harvest. That the Imposed New Livelihoods strategy had more, and stronger, negative outcomes from the HAB simulation than the Invested New Livelihoods strategy demonstrates how communities or individuals who go beyond adaptation to transform livelihood activities, but shift culture and values to similar recreational activities, may remain highly sensitive to climate change impacts. Previous HABs on the U.S. West Coast have proven that recreational fishery closures can deeply affect coastal communities' well-being when recreational activity is central to community identity, culture, and social relationships (Ritzman et al. 2018). As a result, planned transformative change to climate-resilient livelihoods may need to occur alongside more holistic, community-driven efforts to ensure that existing and new sources of non-material well-being outside of livelihood activities, such as forms of *Community* and sources of *Identity*, are similarly resilient or flexible to climate change.

In practice, the realized or perceived effectiveness of climate adaptation in supporting non-material well-being will depend on how individuals rank the importance of certain aspects of well-being. Our model assumes that income and material wealth have some influence on non-material well-being (*Emotional & mental health*, *Family relationships*), but we underemphasize the contribution of material wealth to most other well-being variables, including *Community*. In applications for other systems, and for specific U.S. West Coast communities, it will be important to establish what aspects of well-being are a priority for local beneficiaries of climate adaptation, before investing resources in preventing negative outcomes for specific well-being domains. If our assumptions around non-material well-being are representative of a given community, our results highlight the importance of considering climate adaptation strategies that support and facilitate alternative sources of non-material well-being, or (potentially transformative) sociocultural change.

4.5.2 *Intensification of HAB impacts: the importance of seasonal fishing opportunity and in-season flexibility*

The fishing portfolio diversification that we built into the Status Quo appears to have been a powerful mitigating force, limiting direct impacts from the simulated HAB and unintentional negative consequences from climate adaptation. In our first set of simulations, only the Supplementary Diversification strategy (i.e., diversifying livelihoods without fishery exit) resulted in the amplification of HAB impacts compared to the Status Quo. Whereas Supplementary Diversification directed livelihood activity away from fishing, all other non-transformative strategies assumed that fishers still have the option to participate in unaffected fisheries while also benefiting from climate adaptation. Even when strategy implementation included direct negative impacts to variables such as *Community*, *Family*, and *Job satisfaction* (as for the New Fisheries strategy), we did not see intensification of HAB impacts. Without access to alternative, unaffected fisheries, and the ability to shift crab fishing effort later in the season, we might expect more unintended negative consequences to well-being from climate adaptation.

Trade-offs in fishing activity in the HAB-affected early season was the most influential dynamic governing nearly all well-being outcomes. When we explored alternative configurations of this dynamic, we observed notable changes in well-being outcomes for all non-transformative adaptation strategies - including more widespread intensification of HAB impacts from climate adaptation when we limited the capacity to adjust fishing participation in alternative fisheries. This included unintended negative consequences from the Insurance and Multi-Objective Disaster Relief strategies, in addition to Supplementary Diversification. These results suggest that even when pursuing other forms of climate adaptation, it may still be important to maintain or improve diverse fishing opportunities. Diversification into multiple fisheries has long been recognized as important to hedging risk and building adaptive capacity in fisheries (McCay 1978, Sethi 2010, Kasperski and Holland 2013, Cline et al. 2017), but our analysis shows how the outcomes of other adaptive strategies may be mediated by finer-scale, in-season flexibility and effort allocation among those who have diversified. Fishery managers who are focused on other adaptive actions - particularly those which primarily address material needs, like insurance and disaster relief - may therefore also want to facilitate in-season flexibility in response to extreme events.

The issue of flexibility in control rules and spatial management is well-represented in U.S. West Coast case studies (Chavez et al. 2017, Hazen et al. 2018) and the broader adaptive management literature (Grafton et al. 2007, Hobday et al. 2014, Hilborn et al. 2022), and developing a framework that allows fishery managers to respond to changing in-season conditions (e.g., with short-term adjustments to allowable catch) was proposed multiple times during the Pacific Fishery Management Council's scenario planning (Nelson et al. in prep). In practice, responsive in-season management is rare, with barriers for both fishery managers and fishers (Hobday et al. 2014, Ritzman et al. 2018, Drakopulos and Poe 2023). Yet overcoming these legal, communication, and operational challenges could be essential in fisheries with highly seasonal dynamics, like Dungeness crab.

Our exploration of influential dynamics also demonstrated how climate adaptation designed under certain assumptions can have drastically different, and potentially inequitable, effects for different fishing communities or individual fishers – in this case, dependent on in-season flexibility and access to alternative fisheries. For example, when our modeled community had less in-season flexibility than we first assumed, non-material well-being suffered more from the implementation of certain adaptation strategies (e.g., improved Multi-Objective Disaster Relief) than with no action at all; whereas when that same adaptation strategy was implemented under high in-season flexibility ("crab limits" configuration), the community saw an increase in material well-being from the HAB. These disparate outcomes also carry implications for monitoring the effectiveness of adaptive strategies; assessment efforts may need to differentiate outcomes according to contrasting experiences of influential system dynamics - in our model community, an individual's in-season flexibility and realized fishing opportunity - to capture potentially unequal outcomes. If differential experiences trend with certain socioeconomic factors, planned adaptation for climate events like HABs may provide an opportunity to address underlying drivers of social vulnerability.

4.5.3 *Considerations for adaptive capacity & rebounding vulnerability*

When aspects of human well-being are closely tied to a community's or individual's adaptive capacity, climate adaptation can cause rebounding vulnerability over longer time-scales. For example, in our first set of simulations, the Supplementary Diversification strategy intensified negative HAB impacts to two well-being variables: *Subsistence* and *Shoreside infrastructure & support services*. We defined *Shoreside infrastructure & support services* as encompassing physical port infrastructure as well as the local industry and commerce that supports commercial fishing activity (e.g., gear producers, mechanics, seafood distributors, etc.). There are several ways that intensified negative impacts to *Shoreside infrastructure & support services* could reduce a fishing community's long-term adaptive capacity. Loss of suppliers can increase costs, reducing the material assets that fishers may need to adapt to climate change. Shuttering of local support services may end long-time working relationships and bridging social ties that can enable social learning (Barnes et al. 2017, Salgueiro-Otero et al. 2022). Consolidation of fish buyers and processors, which creates unequal power relationships, is already recognized as a barrier for U.S. West Coast fishers attempting to diversify into new markets, a strategy to weather both environmental and socioeconomic shocks to food chains (Drakopulos and Poe 2023). In applying these results to preventative planning, it would first be important to establish the scenarios in which a decline in fishing activity is large enough to affect the diversity and viability of fishery support services; and pre-emptively establish baseline measurements that speak to economic diversity and socio-economic networks. Climate adaptation planning with the goal of maintaining fishing economies might then identify how to pair strategies designed to benefit fishers with those that can help support services adapt to changing fishing activity.

In exploring alternative configurations of model structure, we found that three different adaptation strategies (Insurance, Multi-Objective Disaster Relief, Supplementary Diversification) intensified negative impacts to *Intangible connections to nature* in configurations with reduced in-season flexibility. Direct observation of nature, including first-hand experience with extreme environmental events, builds local knowledge and memory, which increases the capacity of individuals and communities to recognize and learn from change (Berkes et al. 2003, Cinner et al. 2018). This knowledge and learning also contributes to risk or vulnerability perception, which drives action (Spence et al. 2011, Akerlof et al. 2013, Myers et al. 2013). While recent work on climate risk perception among U.S. West Coast fishers did not find that fishing experience had an effect on perceived vulnerability, the authors did note that fishers commonly linked observations of changing ocean conditions (specifically, warming water temperatures) with declines in abundance of certain harvested species (Nelson et al. 2022). Climate adaptation planning concerned with rebounding vulnerability from impacted connections to nature might prioritize investigating whether (and how) in-season flexibility can mediate impacts to non-material well-being during sustained or repeated extreme environmental events.

4.6 CONCLUSIONS

We used Qualitative Network Models (QNMs) to explore social-ecological dynamics linked to unintended negative consequences from climate adaptation. We specifically evaluated the potential intensification of harmful algal bloom (HAB) impacts from stakeholder-identified climate adaptation strategies for U.S. West Coast fisheries. Contrasting outcomes between different adaptation strategies, and exploring assumptions underlying the model structure, identified influential system relationships that could lead climate adaptation to intensify negative HAB impacts. Identifying common outcomes across adaptive strategies highlighted shared shortcomings which could reproduce pathways for rebounding vulnerability. Finally, by representing the complex interrelationships between different aspects and domains of well-being (Breslow et al. 2016), our QNMs captured significant negative outcomes of cumulative, low-level effects that otherwise would not have been represented in qualitatively coded responses. Our results demonstrate the value of using QNMs to inform development, prioritization, and monitoring of climate adaptation strategies.

We can also use our case study to reflect on crucial limitations to the QNM approach, which are important to compensate for in other areas of climate adaptation planning. The linear relationships in a QNM limited our ability to explore important system-specific dynamics and feedback effects, which led us to exclude those relationships from the model. For example, a certain level of physical risk contributes to job satisfaction and identity for some Dungeness crab fishers (Holland et al. 2020), but that risk can reach a threshold where safety becomes an issue of life or death (Kaplan and Kite-Powell 2000, Oregon Institute of Occupational Health Sciences 2020a, 2020b) at great detriment to community well-being. Additionally, although the qualitative nature of QNMs is a strength of the method, it can also make it difficult to detect compounding negative effects; if a variable is already strongly negatively perturbed, negative impacts from other system dynamics, including those that result from strategy implementation or a feedback loop, cannot change model outcomes. We believe that this played a role in the similarity of outcomes from the Existing Fisheries Diversification and New Fisheries strategies, despite the additional operational costs we included in the New Fisheries QNM. This particular limitation has implications for expanded applications of QNMs, including simulating multiple extreme events that affect the same part of the model, or exploring the interaction between climate change and compounding socioeconomic pressures that act on similar sources of underlying vulnerability. However, the goal of applying QNMs to climate adaptation planning is not to remove the need for all other steps; we seek to show that this approach has a role in early planning processes alongside other methods with complementary strengths (e.g., frameworks designed to prevent rebounding vulnerability without modeling; Magnan et al., 2016).

In considering the role of QNMs within climate adaptation planning, it is also important to recognize that QNMs, as with many social-ecological systems approaches, emphasize the worldview of a bounded system composed of interacting entities (in contrast with process-relational ontologies; Mancilla García et al. 2020). This makes QNMs easiest to apply to normative and goal-oriented agendas for operationalizing climate adaptation (e.g., avoiding maladaptation or improving human well-being) over process-based approaches (Singh et al. 2022); and makes it challenging to use QNMs to investigate certain types of climate adaptation strategies (e.g., more collaborative and inclusive ocean use planning processes; *Completed Worksheets for Climate Change Scenario Planning Online Workshops, Northern California*, 2021). Process-based approaches, which are pluralistic, contextual, and make space for self-determination, are central to advancing climate equity and justice in adaptive transformation

(Táíwò 2022), and therefore important in avoiding rebounding vulnerability to those most affected by climate change. Because normative and process-based frames privilege different types of outcomes, a combination of frames should be used to identify and assess climate adaptation pathways (Singh et al. 2022). This again emphasizes the role of QNMs as part of, and not exclusively comprising, a process to identify "effective" adaptive actions.

We see strong potential in future applications of the QNM approach that make use of participatory modeling, eliciting mental models from diverse actors to create a collective representation of the system as a QNM. This process can help build a shared understanding of the social-ecological system and support social learning processes, which can be particularly important in building consensus on how to address difficult problems in complex systems (Sandker et al. 2010, Jones et al. 2011). Careful articulation of local social-ecological context can also help to disentangle structural artifacts when translating simulation outcomes; this case study greatly benefited from the extensive body of work on harmful algal bloom impacts to U.S. West Coast fishing and coastal communities, which supported ground-truthing efforts during the iterative model-building process. Participatory modeling processes can also include stakeholder identification of preferred system states and outcomes specific to model variables and structure (Gray et al. 2015), informing which well-being outcomes to prioritize. One aspect of participatory modeling that will be particularly crucial in the context of climate adaptation planning is to ensure that a diversity of community members and intended beneficiaries are carefully, effectively engaged in the modeling process, including those that may not otherwise hold positions of power in management structures. This can help ensure that planning for unintended consequences and rebounding vulnerability addresses pathways and dynamics that affect those most vulnerable to climate change, and may help model a greater breadth of transformative adaptations (Barnes et al. 2017), which are arguably necessary to address the underlying vulnerabilities that drive climate change impacts (Berrang-Ford et al. 2015).

Return to Table of Contents.

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4.8 APPENDIX

4.8.1 *Model Sensitivity Analysis*

We evaluated model sensitivity using boosted regression trees, according to the procedures outlined in Melbourne-Thomas et al. (2012), and using mean interaction strengths, following Magel & Francis (2022). Boosted regression trees were used to identify links with strong relative influence on well-being variables; with the R package *dismo* (Hijmans et al. 2023), we fitted boosted regression trees with an individual tree complexity of five, a learning rate of 0.5, and by using 50% of observations in selecting variables (*bag.fraction*=0.5; Harvey et al. 2016, Melbourne-Thomas et al. 2012). Results for the Status Quo QNM are in Table S4.7. We then identified links with strong mean interaction strengths (> 0.05 or < - 0.5) calculated with custom R code from the stable community matrices generated by the *QPress* function *system.simulate* (Melbourne-Thomas et al. 2012). Results for the Status Quo QNM and non-transformative strategy QNMs are summarized in Figure S4.4.

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4.8.2 *Supplemental Tables*

Table S4.1. Definitions of **(a)** well-being variables in the Status Quo QNM; (**b)** all other variables in the Status Quo QNM, referenced by group from Figure 4.1; and **(c)** additional variables in adaptation QNMs. Well-being variables in (a) are primarily based on "domains" and lower-order "attributes" from the Breslow et al. (2016) 4C's framework; we chose to work at these two levels of the framework because our models are designed as a generalized case study, not representative of a specific community. We provide definitions for any QNM variable that represents a Breslow et al. (2016) "attribute," or a "domain" without additional QNM variables for lower-order "attributes;" our variable definitions are based on the Breslow et al. (2016) attribute definitions and indicator topics, or, when appropriate, custom definitions informed by experts and other literature. We chose to work with the Breslow et al. (2016) well-being framework because it was designed to "focus attention on aspects of human wellbeing for which managers and decision-makers may be held accountable… for the U.S. West Coast" (Breslow et al. 2016); since our work considers climate adaptation planning in the context of West Coast fisheries, this functionality / operationalization seemed particularly relevant.

(a) Well-being variables

Domain	**Attribute**	**QNM Variable**	**Definition**
Tangible Connections to Nature	--	Tangible connections to nature	Direct avenues of access to natural resources, nature, and natural places; active sustainability practices
Intangible Connections to Nature	--	Intangible connections to nature	Activities on the landscape (level of satisfaction derived from or associated with participation in fisheries*)
Social Relationships	--	Social relationships	--
	Family	Family	Family / joint family endeavors, marriage & divorce
	Community	Community	Sense of community, trust in neighbors
		Community learning & cooperation	Community support. This customized variable was added to cover multiple aspects of well-being that also contribute to the 'learning' and 'social organization' domains of

			adaptive capacity (Cinner & Barnes 2019).
	Civil Society	Community learning & cooperation	Private and non-profit organizations (e.g. social service groups); volunteering
Culture & Identity	--	Culture & identity	--
	Identity	Identity	Sense of self or community
	Cultural values & practices	Cultural values & practices	Cultural practices (winter holiday traditions with Dungeness crab*)
	Heritage	Entry of next generation	Multi-generational interaction with resources. This customized variable was added because of the prevalence of existing barriers to entry for the younger generation to become an owner/operator in a West Coast fishery (Strawn 2019, Drakopulos & Poe 2020, Nelson et al. 2023).
Livelihood & Activities	--	Livelihood & activities	--
	Subsistence	Subsistence	Harvest of food for self, family, community
	Job quality	Job satisfaction	Living wage, job duration, benefits (Holland et al. 2020)
	Job quality	Job quality	Job satisfaction; time on water (Holland et al. 2020)
Freedom & Voice	Trust in institutions & management	Trust in institutions & management	Perceptions of management, which are assumed to reflect the receptivity, trust, and attitude of stakeholders (Ekstrom et al. 2020)
	Political Participation	Community learning & cooperation	Participation in decision-making processes and leadership
Knowledge & Technology	Education & Information	Community learning & cooperation	Possession & transmission of knowledge, information & skills
Health	Emotional & Mental Health	Emotional & mental health (*treated as domain in place of Health*)	Happiness, stress, subjective well-being
	Physical Health	Physical health	Health conditions
Safety	Physical safety	Physical safety	Safety at work; occupational risks and injuries

Economy	Material wealth & security	Material wealth & security	Material assets & consumption
	Local & Informal Economies	Subsistence	Exchange of goods and services locally and/or outside of money economy; gifting, trading, reciprocal, and in-kind “transactions”
Environment	Infrastructure	Shoreside infrastructure & support services	Physical shoreside infrastructure required for fishing activities, along with the presence of local marine support services that contribute to a working waterfront. This customized variable reflects the importance of quality physical infrastructure and local marine support services, expressed in scenario planning documents, and emphasized by co-author expert knowledge.

(b) All Other Variables

Variable group	**Variable name**	**Description**
3	Dungeness crab fishery participation: early or late season	Extent of participation in the Dungeness crab fishery; results in the harvest of Dungeness crab. In fleet-stock models, fishery participation can be more explicitly modeled as fishing effort. In a QNM, the fishery participation variables don’t have to strictly represent effort. We split participation to reflect the highly seasonal dynamics of the fishery.
3	Dungeness crab harvest: early or late season	The seasonal Dungeness crab fishery landings resulting from fishery participation. This provides some additional flexibility in the model to build out relevant economic variables, well-being variables, and/or as an entry point for certain perturbations (following Szymkowiak & Reese, 2020). Harvest is split by season to reflect the dynamics we’ve included in the fishery participation variables. There are also important seasonal relationships between harvest and certain well-being variables.
3	Total crab harvest	Positively influenced by the two seasonal Dungeness crab harvest variables. This is primarily a structural variable, so that certain aspects of well-being can be tied to overall crab harvest (e.g., subsistence).

3	Crab fishing activity	Positively influenced by the two seasonal Dungeness crab participation variables. This is primarily a structural variable, so that certain aspects of well-being can be tied to overall participation (e.g., connection to nature, derived from time spent on the water).
3	Other fishery participation: early or late season	Same as *Dungeness crab fishery participation*, but for all other fisheries. For this case study, other fisheries could include, for example, salmon fisheries, the fixed-gear groundfish fishery, the groundfish trawl fishery, the albacore fishery, or the pink shrimp fishery (Fisher et al. 2021; Frawley et al. 2020)
3	Total other harvest	The fishery landings resulting from fishery participation in all fisheries other than Dungeness crab. This provides some additional flexibility in the model to build out relevant economic variables, well-being variables, and/or as an entry point for certain perturbations. We did not model seasonal relationships for other fisheries harvest.
3	Other fishing activity	Positively influenced by the two seasonal participation variables for other fisheries. This is primarily a structural variable, so that certain aspects of well-being can be tied to overall participation (e.g., connection to nature, derived from time spent on the water).
3	Non-fishing employment activity	Income-generating activity outside of commercial fishing activity. This variable is present in the Status Quo QNM, but assumed to be a constant (unaffected by changes in commercial fishing activity or the HAB). Research indicates that most of the Dungeness crab harvest goes to crabbers that do not have income from non-fishing employment (Treakle et al. 2023). Occupations of part-time crabbers include those in the construction, transportation, and fishing/farming/forestry industries; and management (rental income, business owners; Treakle et al. 2023).
3	Non-fishing income	Income from Non-fishing employment activity. This is primarily a structural variable, so that certain aspects of well-being can be tied to income versus the activity itself.
2	Crab processing capacity	The capacity to process landed Dungeness crab into various products for retail sale. Processing capacity is associated with the labor force (tied into human capital, housing availability, population) and can contribute to adaptive capacity
2	Crab opening dock price	The ex-vessel price for Dungeness crab, set in pre-season negotiations between harvesters and processors. More on how the Dungeness crab ex-vessel prices are set, and associated harvester strikes, can be found in Mao & Jardine (2020).
2	Crew availability	The availability of trained or experienced crew members in the Dungeness crab fishery. This has been impacted by past fishery delays; crew are asked to "stand-by to stand-by,"

		they might pursue an opportunity to fish something, or somewhere, else instead.
2	Fuel & labor costs	Variable costs of fuel and labor for a fishing vessel, assumed to have a negative relationship with fishery participation. Fuel and labor costs will influence other variable costs, and vary by fishery and vessel size. Dewees et al. (2004) report on annual / daily costs and crew share for California crabbers.
2	Housing disruption	This is a capacity variable, which reflects that in areas where crew housing and cost of living is more expensive, crew have less capacity to wait around for a paycheck during a delay. Housing disruption is measured by the NOAA Social Vulnerability Index, to represent fluctuating housing markets and homeowner costs compared to income (Colburn and Jepson 2012), and tends to be higher in mid-sized, more rural coastal towns.
1	Crab abundance	Abundance of legal-sized male Dungeness crab, which will decline with fishing activity and, in turn, influences continued fishery participation in the late season.
1	Target species abundance	Abundance of all other species targeted by fisheries in which crabbers participate. Declines with fishing activity.

(c) Variables added to strategy QNMs

Strategy QNM	**Variable name**	**Description**
Multi-Objective Disaster Relief	Biological Monitoring	This is a custom variable that represents scientific infrastructure to conduct biological monitoring and forecasting (requiring both physical infrastructure and human capital), as well as the dispersal of that information to the public and management agencies. We assume that monitoring efforts and data are trusted by fishers. This variable contributes to the ‘learning’ and ‘assets’ domains of adaptive capacity (Barnes & Cinner 2019).

Table S4.2. Rationale, including quotes from the literature or expert knowledge, for certain links (edges) identified as particularly influential from model sensitivity analysis (Table S3; Fig. S4), and those altered for strategy QNMs. The type of relationship represented by each link is provided using the following shorthand: "*" indicates a negative relationship; ">" indicates a positive relationship; "--*" and "-->", represent a unidirectional relationship of Variable 1 on Variable 2, whereas "*--" and "<--" represent a unidirectional relationships of Variable 2 on Variable 1; and "*--*", "*-->", "<-->", etc. represent two-way relationships. [U] indicates there is less certainty in this relationship, so the link is modeled as an uncertain link in *QPress*.

Variable 1		**Variable 2**	**Supporting evidence**
Early season crab fishery participation	--* [U]	Early season alternative fishery participation	Co-authors familiar with fishery landings data have observed a trade-off in the number of trips taken for Dungeness crab with the number of trips taken for other species. This follows from the logic that effort and time spent in one fishery, is effort and time not spent in another. However, fishery landings data and analyses from the HAB-related delays in the 2015-16 Dungeness crab fishing season made the co-authors uncertain about the consistency of this relationship. In some cases, if a vessel was not active in the Dungeness crab fishery, then it stopped participating in other fisheries as well. From Holland & Leonard (2020), emphasis our own: "Thus, over half of the estimated loss in total revenues for the California Dungeness crab fleet is attributable to reduced revenues in other fisheries – from vessels that either dropped out of fishing in 2016 all together or reduced their fishing in other fisheries in order to participate in the delayed crab fishery."
Early season crab fishery participation	→	Cultural values & practices	Ritzman et al. (2020): "In Crescent City… the stories shared by many interviewees indicated deep cultural ties to the Dungeness crab fishery... For instance, interviewees recounted that, once the crab season begins, 'you'll find a bucket of crabs sitting on your front porch,' along with other stories of how sharing shellfish is interwoven with community traditions... shellfish resources play a meaningful role in social activities and traditions focused around consumption. For example, in Crescent City, an interviewee recalled that they 'almost always had crab on Thanksgiving and Christmas' and that 'crab is always the star of the show on holidays.'" From Strawn (2019) interviews with Oregon crabbers: "Family level impacts showed a dependence on the [Dungeness crab] fishery for anything extra, especially around the winter holiday season. 'Whether or not to have

			Christmas is dependent on the season, which can be really stressful for a lot of families.'"
Intangible connections to nature	→	Emotional & mental health	From interviews in Novia Scotia, Brown (2015) noted that fishery participants and youth community members expressed a "sense of peace", "calmness", and "emotional security" associated with fishing activity, and certain sentimental / scenic shoreside locations.
Early season crab harvest	→	Emotional & mental health	The Dungeness crab fishery is a derby-style fishery, in which most of the annual harvest is landed within the first six weeks of the season (early season); additionally, Dungeness crab represents an important source of fishery revenue for many crabbers. Therefore, a good crab harvest during this period contributes to peace of mind.
Total crab harvest	→	Subsistence	Poe, Levin, & Norman (2015) summarized the top ten species kept for personal use from commercial fishing vessels in Washington and California. Dungeness crab was 4th overall by landed pounds for California and non-tribal Washington fishermen.
Total crab harvest	→	Shoreside infrastructure & support services	Revenue from the crab harvest covers fishers' expenses, distributing it among marine support services. The updated 2018 Spend Plan for the federal disaster relief provided after the 2016 California Dungeness crab season reasoned that "reinvesting funds back into local fishing communities will not only benefit the Dungeness crab fishery, but the ports… This will strengthen infrastructure" (Bonham et al. 2018). Other research has highlighted how vessel maintenance and upgrades provides business for marine support services (Szymkowiak and Himes-Cornell 2015).

Table S4.3. Summary of how the Status Quo QNM was adjusted for each of the non-transformative strategy QNMs. Strategy QNMs could include a new variable (Table S4.1c), an indirect perturbation to a variable (Table S4.4), a new or changed link (Table S4.5), and/or a new or changed link constraint (Table S4.6).

	Structural change		**Non-structural change**	
	New variable(s)	Changed or new link(s)	Changed or new link constraint(s)	Indirect perturbation of variable(s)
(1) Parametric Insurance			(√)	(√)
(2) Direct Assistance Disaster Relief			(√)	(√)
(3) Multi-Objective Disaster Relief	(√)	(√)	(√)	(√)
(4) Existing Fisheries Diversification		(√)	(√)	
(5) New Fisheries Diversification		(√)	(√)	
(6) Supplementary Diversification		(√)		(√)

Table S4.4. Summary of the indirect perturbations to variables used in each of the non-transformative strategy QNMs. The direction of the perturbation is indicated as positive (dark green) or negative (light orange). Variable perturbations are indirect because they were enacted by positively perturbing a single variable meant to represent implementation of the given strategy, which then had the specified positive or negative effects on QNM variables. For example, the Parametric Insurance QNM had a variable "Insurance" which, when perturbed, had a positive effect on two QNM variables and a negative effect on one QNM variable. This structure allowed us to specify uncertainty in the effect of strategy implementation, marked in this table with a "[U]."

	Material wealth & security	Job satisfaction	Early season other fishery participation	Shoreside infrastructure & support services	Biological monitoring	Community	Family	Crab processing capacity	Crew availability	Entry of next generation
(1) Parametric Insurance	🟩	🟩	🟧 [U]							
(2) Direct Assistance Disaster Relief	🟩	🟩								
(3) Multi-Objective Disaster Relief	🟩	🟩		🟩	🟩					
(4) Existing Fisheries Diversification										
(5) New Fisheries Diversification	🟧	🟧	🟩			🟧 [U]	🟧 [U]	🟧 [U]	🟧 [U]	🟩
(6) Supplementary Diversification										

Table S4.5. Summary of the new or changed links used in each of the non-transformative strategy QNMs (first column). The type of relationship represented by each link is provided using the following shorthand: “*” indicates a negative relationship; “>” indicates a positive relationship; “--*” and ”-->”, represent a unidirectional relationship of Variable 1 on Variable 2, whereas “*--” and “<--” represent a unidirectional relationship of Variable 2 on Variable 1; and “*--*”, “*-->”, “<-->”, etc. represent two-way relationships. Uncertain links have a “[U]” notation, and deleted links are marked with “[X]”.

	Variable 1		**Variable 2**	**Rationale**
(1) Parametric Insurance	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. With insurance available, *Emotional & mental health* associated with financial security is not as dependent on a good early season crab harvest.
(2) Direct Assistance Disaster Relief	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. With timely direct assistance available, *Emotional & mental health* associated with financial security is not as dependent on a good early season crab harvest.
(3) Multi-Objective Disaster Relief	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. With timely direct assistance available, *Emotional & mental health* associated with financial security is not as dependent on a good early season crab harvest.
	Biological monitoring	→	Community learning & cooperation	Carefully planned, collaborative monitoring and research programs that engage fishing and coastal communities early and often can promote cooperation between community members, and promote community learning and two-way flows of information (Conway and Pomeroy 2006).
	Biological monitoring	→	Trust in institutions & management	Community members expressed mistrust of the HAB-associated Dungeness crab fishery closures in 2015-16, particularly skepticism about the severity of the stated health risk (Ekstrom et al. 2020, Free et al. 2022). Collaborative research and monitoring has a role in building

				trust and partnerships between fishermen and scientists / managers (Kaplan and McCay 2004); this role was cited in scenario planning documents in reference to collaborative research as an action item (Completed worksheets for Climate Change Scenario Planning online workshops, Washington region 2021).
	Biological monitoring	→ [U]	Emotional & mental health	Better monitoring and forecasting could reduce stress associated with making operational decisions without knowledge of how long HAB-associated fishery closures may last. Uncertainty around duration or extent of closures can contribute to stress around financial security, which was observed during the Dungeness crab fishery closures in 2015-16 (Ritzman et al. 2018).
(4) Existing Fisheries Diversification	Early season other fishery participation	*–*	Early season crab fishery participation	This strategy represents a shift in fishing priorities with diversification, such that fishers are not more likely to fish crab in the crab fishery's early season, as opposed to anything else. This edited relationship mirrors the relationship between crab and other fishery participation in the late season.
	Fuel & labor costs	–*	Early season crab fishery participation	With a de-emphasis on crab fishing, the decision to participate in the early crab season is influenced by fuel and labor costs just like other fisheries, rather than being relatively inflexible.
	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. With a shift of participation into, and revenue from, other early season fisheries, *Emotional & mental health* associated with financial security is not as dependent on a good early season crab harvest.
(5) New Fisheries Diversification	Early season other fishery participation	*–*	Early season crab fishery participation	This strategy represents a true shift in priorities for crabbers, such that there is more flexibility around the decision to fish crab or

				something else in the crab fishery's early season. This edited relationship mirrors the relationship between crab and other fishery participation in the late season.
	Fuel & labor costs	–*	Early season crab fishery participation	With a de-emphasis on crab fishing, the decision to participate in the early crab season is influenced by fuel and labor costs just like other fisheries, rather than being relatively inflexible.
	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. With a shift of participation into, and revenue from, other early season fisheries, *Emotional & mental health* associated with financial security is not as dependent on a good early season crab harvest.
(6) Supplementary Diversification	Non-fishing employment activity	*--	Early season crab fishery participation	While supplementary income from activities outside of fishing plays a greater role, participation in the early season crab fishery is still preferred.
	Non-fishing employment activity	*--*	Early season other fishery participation	A two-way dampening relationship represents diversification and flexibility in income-generating activities between fishing for species other than crab, and employment outside of fishing.
	Material wealth & security	→	Job satisfaction	Diversification in income-generating activities means that J*ob satisfaction*, which is associated with predictability of earnings (Holland et al. 2020), is tied to overall *Material wealth & security*, rather than just wealth and security derived from fishing activity.
	Material wealth & security	→	Emotional & mental health	Diversification in income-generating activities means that overall material security contributes to greater *Emotional & mental health*, rather than *Emotional & mental health* associated with financial security being heavily dependent on a good early season crab harvest.

	Non-fishing employment activity	–*	Emotional & mental health	Seeking alternate jobs outside of the fishing industry during the 2015-16 HAB-associated fishery closures made it more likely that an individual experienced stress (Moore et al. 2020).
	Early season crab harvest	→ [X]	Emotional & mental health	Link removed. *Emotional & mental health* associated with financial security instead tied to overall material security.
	Total crab harvest	→ [X]	Job satisfaction	Link removed. *Job satisfaction* is instead tied to overall material wealth.

Table S4.6. Summary of the new or changed link constraints used in each of the non-transformative strategy QNMs (first column), along with the rationale for the addition / change.

	Link 1		**Link 2**	**Constraint Rationale**
(1) Parametric Insurance	Insurance → Material wealth & security	>	Early season crab harvest → Total crab harvest	This constraint ensures that the insurance payout makes up for the reduction to *Material wealth & security* from HAB-associated losses to early season crab harvest.
(2) Direct Assistance Disaster Relief And (3) Multi-Objective Disaster Relief	Direct assistance → Material wealth & security	>	Total crab harvest → Material wealth & security	This constraint ensures that direct assistance makes up for the reduction to *Material wealth & security* from HAB-associated losses to early season crab harvest.
	Direct assistance → Material wealth & security	>	Total other harvest → Material wealth & security	Since the contribution of Dungeness crab harvest to *Material wealth & security* is constrained to be greater than harvest from other fisheries, direct assistance from disaster relief should be the same.
(4) Existing Fisheries Diversification And (5) New Fisheries Diversification	Total other harvest → Material wealth & security	>=<	Total crab harvest → Material wealth & security	Replaces constraint from Status Quo model (Figure S4.1), which assumed that the crab harvest contributes more to *Material wealth and security* than other harvest.
	Total other harvest → Identity	>=<	Total crab harvest → Identity	Replaces constraint from Status Quo model (Figure S4.1), which assumed that the crab harvest contributes more to *Identity* than other harvest.
	Crab abundance → Late season crab fishery participation	<	Early season crab fishery participation --* Early season other fishery participation	The feedback from crab abundance to late season crab fishery participation allowed us to model crab fishing activity as the priority or preferred fishery, such that there is: (1) more crab fishing in the late season if crab abundance stays high, and (2) a shift in crab fishing effort to the late season if crabbers need to make up for lost early season crab fishing opportunity. By weakening this feedback here, we are de-prioritizing crab fishing.

Table S4.7. The Status Quo QNM links with the greatest relative influence on outcomes for select human well-being variables, and their rank orders. Only the five most influential relationships for each variable are shown here.

Variable 1		**Variable 2**	Emotional & mental health	Shoreside infrastructure & support services	Subsistence	Intangible connections to nature	Identity	Family	Community learning & cooperation	Social relationships
Early season crab fishery participation	--* [U]	Early season other fishery participation	**1**	**1**	**1**	**2**	**2**	**1**	**1**	**1**
Early season crab fishery participation	→	Crab fishing activity	**3**	**5**	**5**	**1**	**1**	**3**	**3**	**3**
Early season crab harvest	→	Emotional & mental health	**2**	11	9	**3**	**4**	**2**	**2**	**2**
Early season crab fishery participation	→	Early season crab harvest	**5**	6	6	16	18	**5**	**5**	**5**
Early season other fishery participation	→	Total other fishing activity	**4**	51	37	**4**	**3**	**4**	**4**	6
Early season crab harvest	→	Total crab harvest	14	**4**	**4**	20	27	14	20	11
Early season other fishery participation	→	Total other harvest	6	**3**	**3**	42	49	6	6	**4**
Late season other fishery participation	→	Total other fishing activity	20	37	50	**5**	**5**	20	18	33
Total crab harvest	→	Subsistence	31	21	**2**	35	52	35	8	7
Total crab harvest	→	Shoreside infrastructure & support services	28	**2**	17	54	50	27	37	23

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4.8.3 *Supplemental Figures*

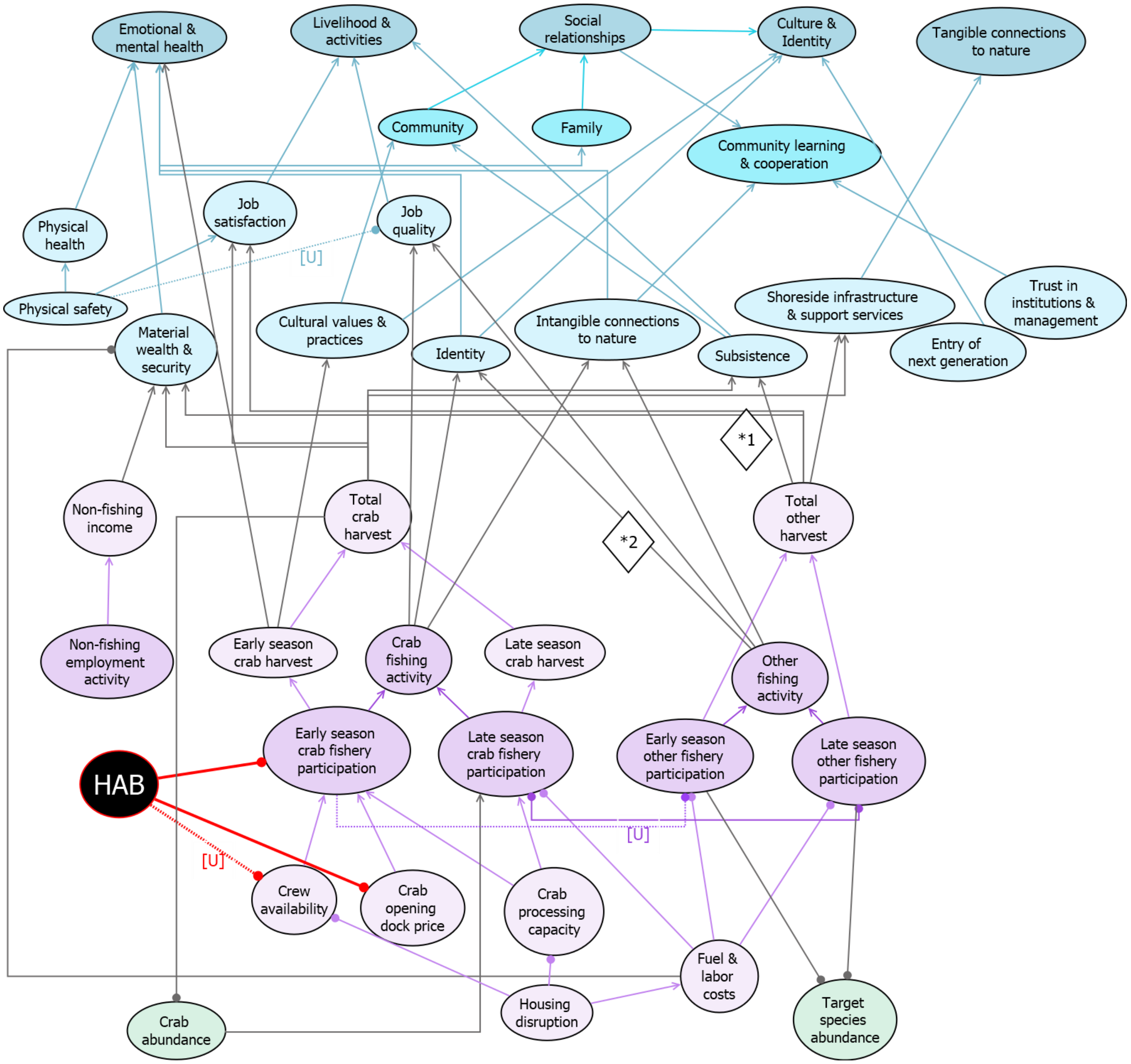

Figure S4.1. The Status Quo Qualitative Network Model (QNM), with all variables labeled. Links annotated with a diamond were constrained: (*1) Contribution of "*Total other harvest*" to "*Material wealth & security*" must be less than the contribution of "*Total crab harvest*" to "*Material wealth & security*;" (*2) Contribution of "*Other fishing activity*" to "*Identity*" must be less than the contribution of "*Crab fishing activity*" to "*Identity*." Links that are dashed and marked with a "[U]" were uncertain.

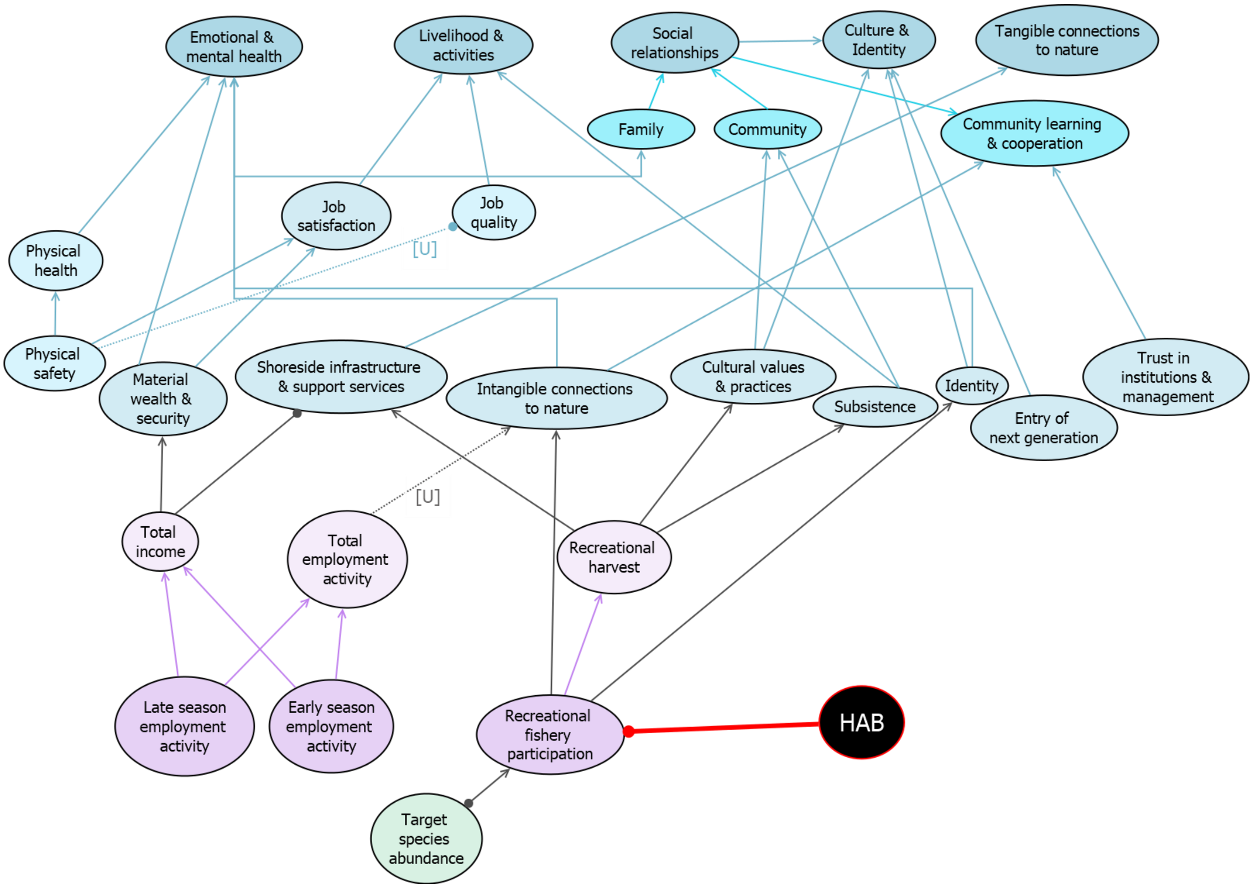

Figure S4.2. The transformative QNM for Imposed New Livelihoods, with all variables labeled. There were no link constraints. Links that are dashed and marked with a "[U]" were modeled as uncertain. Even though there is no longer commercial Dungeness crab fishing activity, we retained the "early season" / "late season" terminology to (1) maximize cross-talk between the transformative and other QNMs, and (2) represent that there may still be some seasonal dynamics in employment, which is tied to the "blue economy."

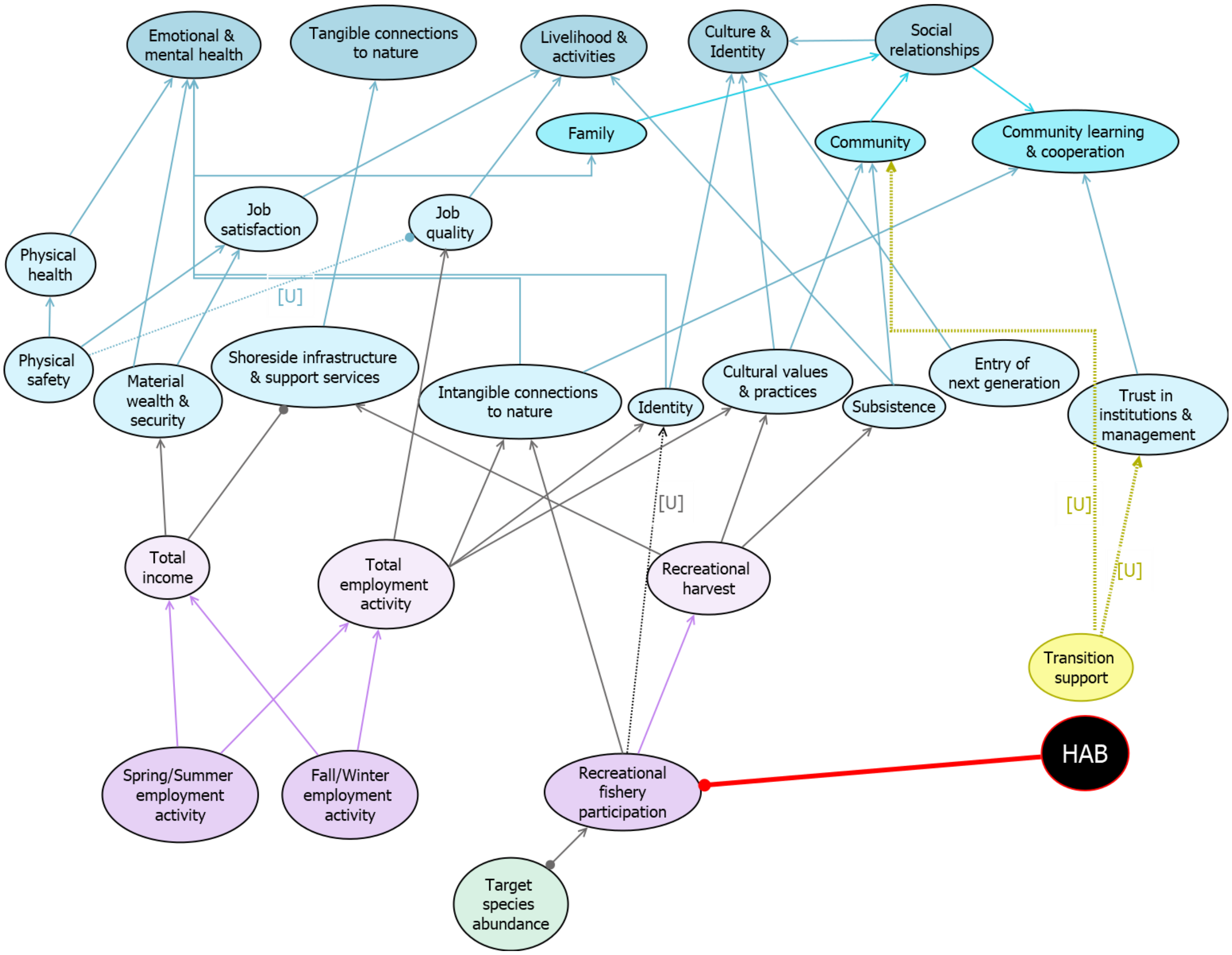

Figure S4.3. The transformative QNM for Invested New Livelihoods, with all variables labeled. There were no link constraints. Links that are dashed and marked with "[U]" were modeled as uncertain. Even though there is no longer commercial Dungeness crab fishing activity, we retained the "early season" / "late season" terminology to (1) maximize cross-talk between the transformative and other QNMs, and (2) represent that there may still be some seasonal dynamics in employment, which is tied to the "blue economy."

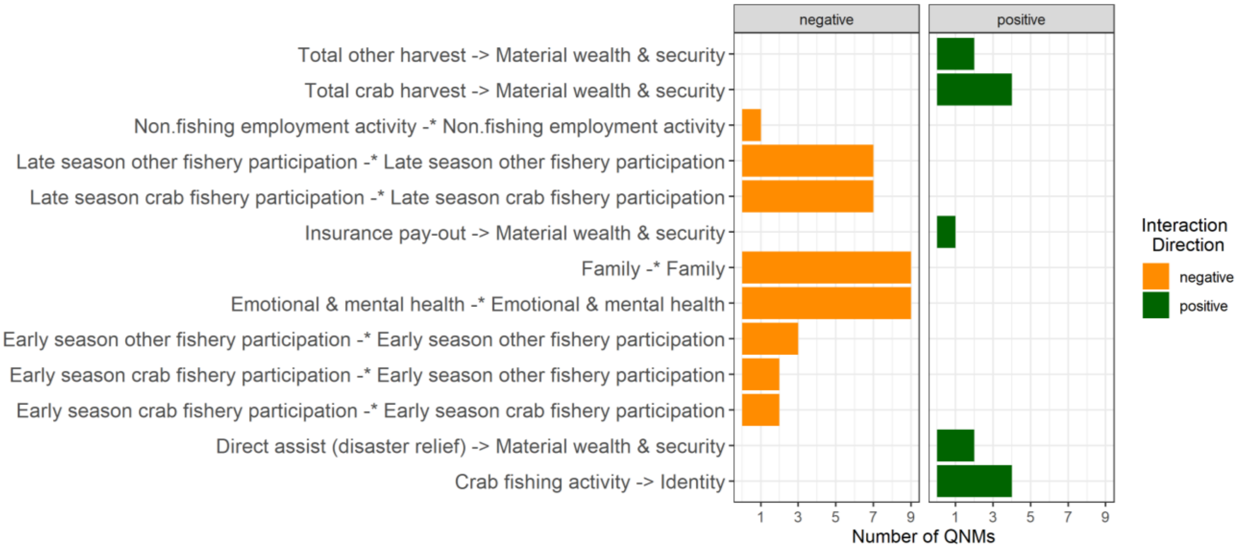

Figure S4.4. Strong links (vertical axis) across the Status Quo and all eight strategy QNMs (horizontal axis). We defined a strong link as one with an average weight across stable matrices of > 0.5 (positive interaction direction) or < -0.5 (negative interaction direction; see Section 4.8.1).

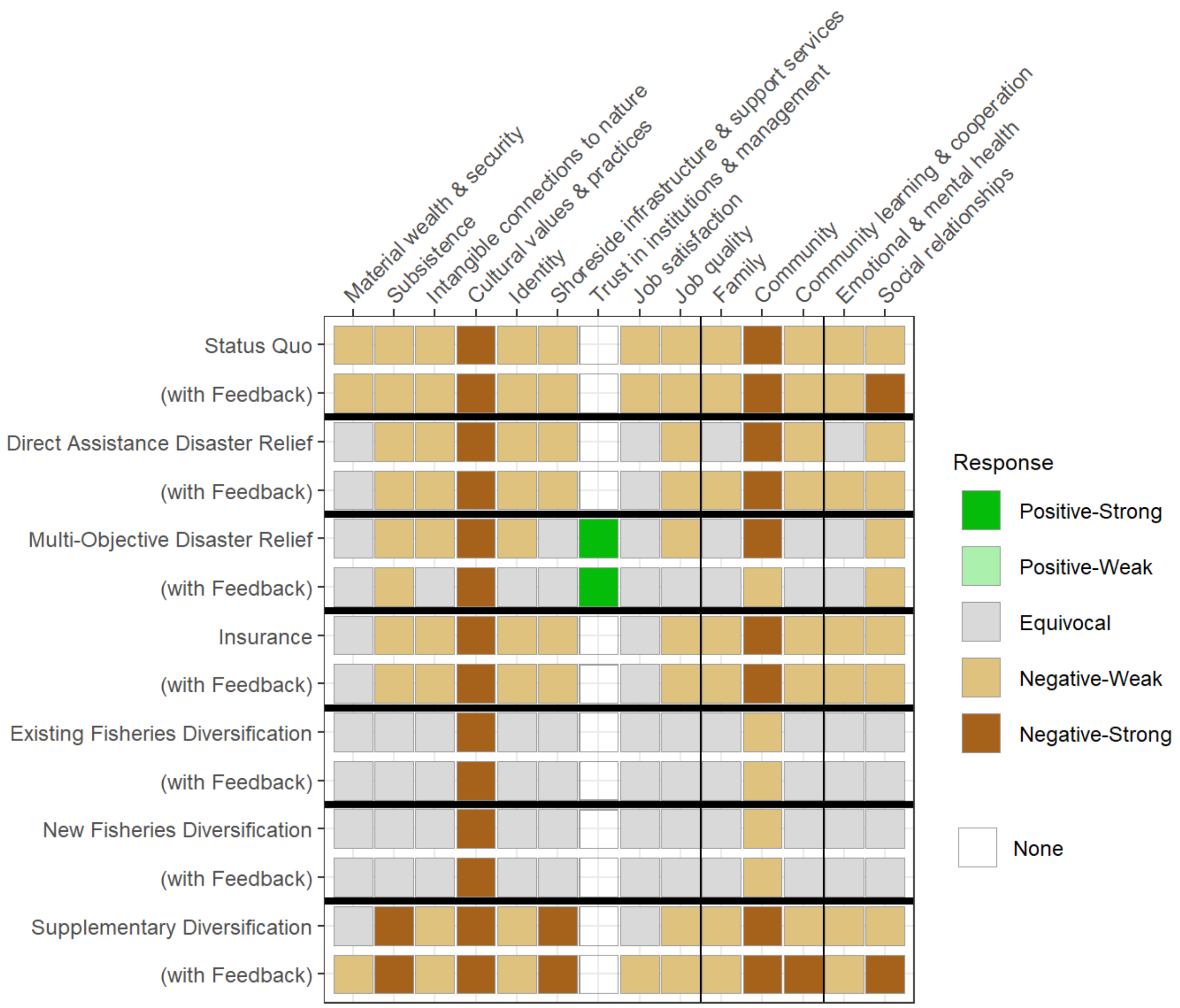

Figure S4.5. Demonstration of how model structure, through a feedback between *Shoreside infrastructure & support services* and variable operating costs (*Fuel & labor costs*)**,** can alter the well-being outcomes associated with HAB response strategies. Outcomes for all non-transformative strategies are shown here, including those not in the main text. For outcomes for other QNM variables (i.e., not well-being variables), see Figure S4.6.

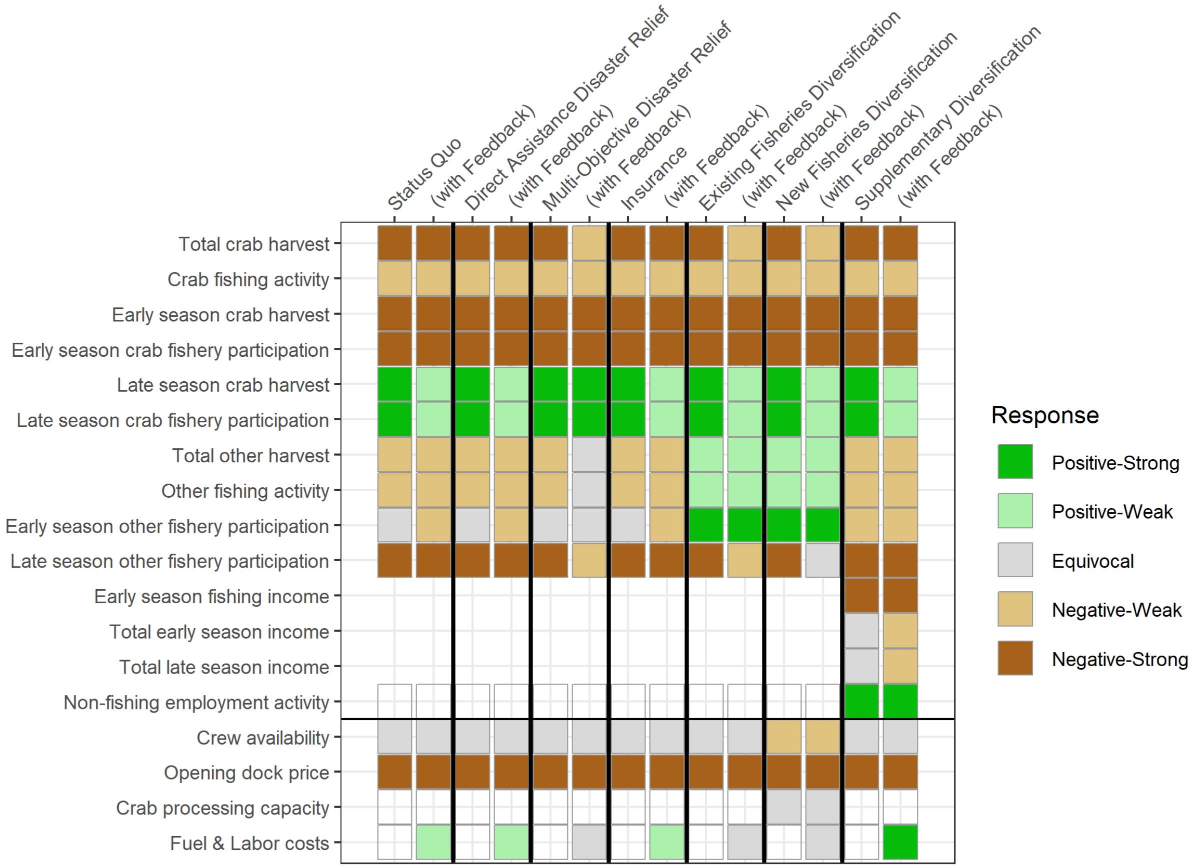

Figure S4.6. Demonstration of how model structure, through a feedback loop between *Shoreside infrastructure & support services* and variable operating costs**,** can alter the outcomes associated with HAB response strategies. Note that for this figure alone, models are on the horizontal axis, and variables are on the vertical axis. Outcomes for QNM variables that are not shown in Figure S4.5 are shown here. Some variables were specific to singular QNMs.

4.8.4 *Section 4.4.2. Extensions*

4.8.4.1 Alternative configurations based on assumptions that are not influential dynamics

As discussed in Section 4.4.2, while developing our QNMs, we made assumptions about social-ecological relationships that were variable within and across communities. Not all of these assumptions were also identified as influential dynamics (Table S4.7; Figure S4.4). Here, we compare alternative QNM configurations designed to explore three key assumptions that were not influential dynamics: (1) whether costs associated with Existing Fisheries Diversification are transient (and therefore not included in the QNM; used for main text) or permanent; (2) whether costs associated with New Fisheries were transient or permanent (used for main text); and (3) whether direct assistance from disaster relief has a positive (used for main text) or negative impact on *Trust in institutions & management*. Overall, we found that when key assumptions are not also influential dynamics, modeling alternative configurations resulted in few notably different qualitative outcomes.

Diversification can require investment of material assets (Cinner et al. 2018, Cinner and Barnes 2019), and can come at certain operational costs. For the main text, we assumed that Existing Fisheries Diversification had transitory material costs, and therefore did not include negative impacts to *Material wealth & security* in the Existing Fisheries Diversification QNM. To test the impact of this assumption, we created an alternative configuration of the Existing Fisheries Diversification QNM with a negative (indirect) perturbation to *Material wealth & security*. This addition of material costs affected a small number of outcomes from Existing Fisheries Diversification (Figure S4.7, “With Costs”) in a HAB simulation. We observed a weak negative response for *Material wealth & security*, as the cost of diversification outweighed any benefits that may have helped to offset HAB impacts. Perhaps more interestingly, adding material costs to Existing Fisheries Diversification meant that the implementation of the strategy did not mitigate the weak negative response of *Social relationships* to a simulated HAB. Even though the two aspects of well-being that contribute to *Social relationships* (*Family* and *Emotional & mental health*), show equivocal responses both with and without material costs of diversification, when material costs are included in the QNM, there is a marginally higher proportion of stable model structures (out of 10,000) that show a decrease in those two variables. This does not change the qualitative output for *Family* or for *Emotional & mental health*, but does tip the downstream variable *Social relationships* over our imposed threshold (60% of stable model structures) from equivocal to weakly negative.

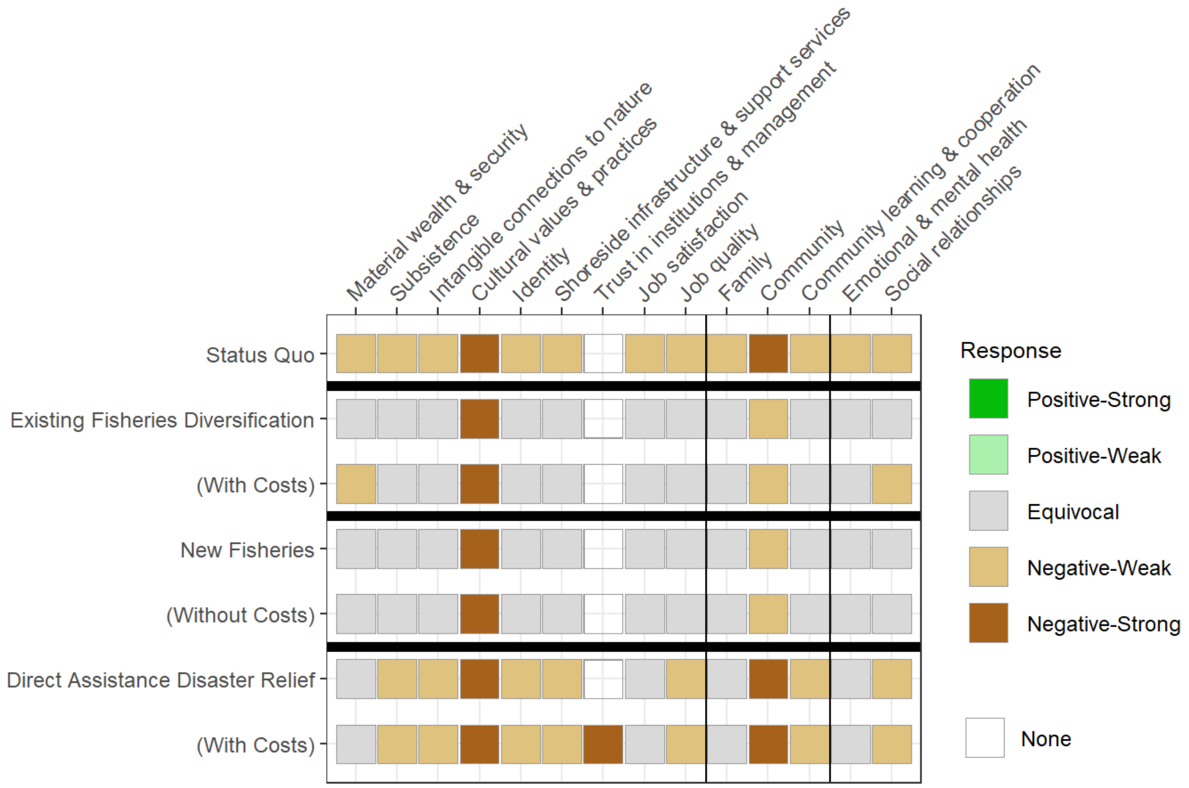

Figure S4.7. Demonstration of how model assumptions that are not influential dynamics can alter well-being outcomes. Variable responses from the default Status Quo, Existing Fisheries Diversification, New Fisheries, and Direct Assistance Disaster Relief QNMs, are compared against well-being outcomes when costs are added to (Existing Fisheries Diversification, Direct Assistance Disaster Relief), or removed from (New Fisheries), each respective QNM.

We made the opposite assumption about costs of diversification for the New Fisheries QNM; for the main text, we assumed that New Fisheries had negative impacts to *Material wealth*

& security / *Job satisfaction* from significant or persistent start-up costs; and that the introduction of new fisheries could potentially negatively impact Dungeness crab processing capacity and crew availability (Table S4.4). Here, we constructed an alternative configuration of the New Fisheries QNM in which all of these negative effects were absent. We found that the dampening effect of New Fisheries on HAB impacts is robust to the inclusion / exclusion of material and operational costs. Prior research and knowledge of our case study system suggests that this particular result is not realistic for fishing communities. West Coast fishers interviewed by Drakopulos & Poe (2023) identified start-up capital and financial backing, a crew labor hub website, and diversification of the processor / buyer sector as adaptation pathways to address key barriers to fisheries diversification. The fact that these actions were identified as crucial to fisheries diversification by fishers themselves emphasizes the fact that material and operational costs are limiting and can create stress or affect material wealth, especially when compounded with HABs. We believe that we failed to capture this dynamic in our HAB simulation because of the qualitative nature of QNMs. The operational costs included in the New Fisheries QNM were modeled as negative impacts to Dungeness crab processing capacity and Dungeness crab labor availability, as labor / processing capacity is assumed to be somewhat finite, and we assume the new fishery may be preferred over crab. However, there is already such a negative impact to early season Dungeness crab fishery participation from the simulated HAB (100% simulations show a negative response), that these additional negative impacts don't appear in the raw or qualitative simulation output.

Lastly, we constructed an alternative configuration of the Direct Assistance Disaster Relief QNM, in which *Trust in institutions & management* and *Community* were (indirectly) negatively perturbed to simulate declines in relationships from the perceived inequitable distribution of direct assistance (Smith & Gilden 2000). When we simulated a HAB with the addition of these social impacts, the outcome for *Trust in institutions & management* changed to strongly negative from no response (because it had no incoming relationships in the main text Status Quo and Direct Assistance Disaster Relief QNMs); however, there were no other differences in well-being outcomes with and without social costs (Figure S4.7).

4.8.4.2 Adding feedback loops that introduce too much uncertainty

We added a negative feedback loop between *Social relationships* and *Non-fishing employment activity* in the Supplementary Diversification QNM. In U.S. West Coast fisheries and elsewhere, strong fishing identity and social capital has been associated with a reluctance to switch occupations, even to those which may provide higher income and less physical risk (Pollnac et al. 2001, Holland et al. 2020, Treakle et al. 2023). Although causation in this relationship has not been empirically proven, the predominant hypothesis is that weaker social attachment to fisheries and a weaker fishing identity causes a greater willingness to participate in non-fishing occupations (Treakle et al. 2023).

In the Supplementary Diversification QNM, the feedback between *Social relationships* and *Non-fishing employment activity* can be self-reinforcing; as the simulated HAB negatively impacts *Social relationships*, the resulting increase in *Non-fishing employment activity* is expected to come at the cost of commercial fishing activity, which would then cause declines in multiple well-being attributes that contribute to *Social relationships*.

We did indeed see a stronger negative response for *Social relationships* when the feedback was in place for a HAB simulation (Figure S4.8). Otherwise, Supplementary Diversification intensified the same HAB impacts with and without the feedback. Interestingly, we also observed a positive response from the HAB simulation to *Material wealth & security* and related *Job satisfaction* with the feedback - although, we did not see any clear changes in livelihood activity variables that could explain this increase (Figure S4.8).

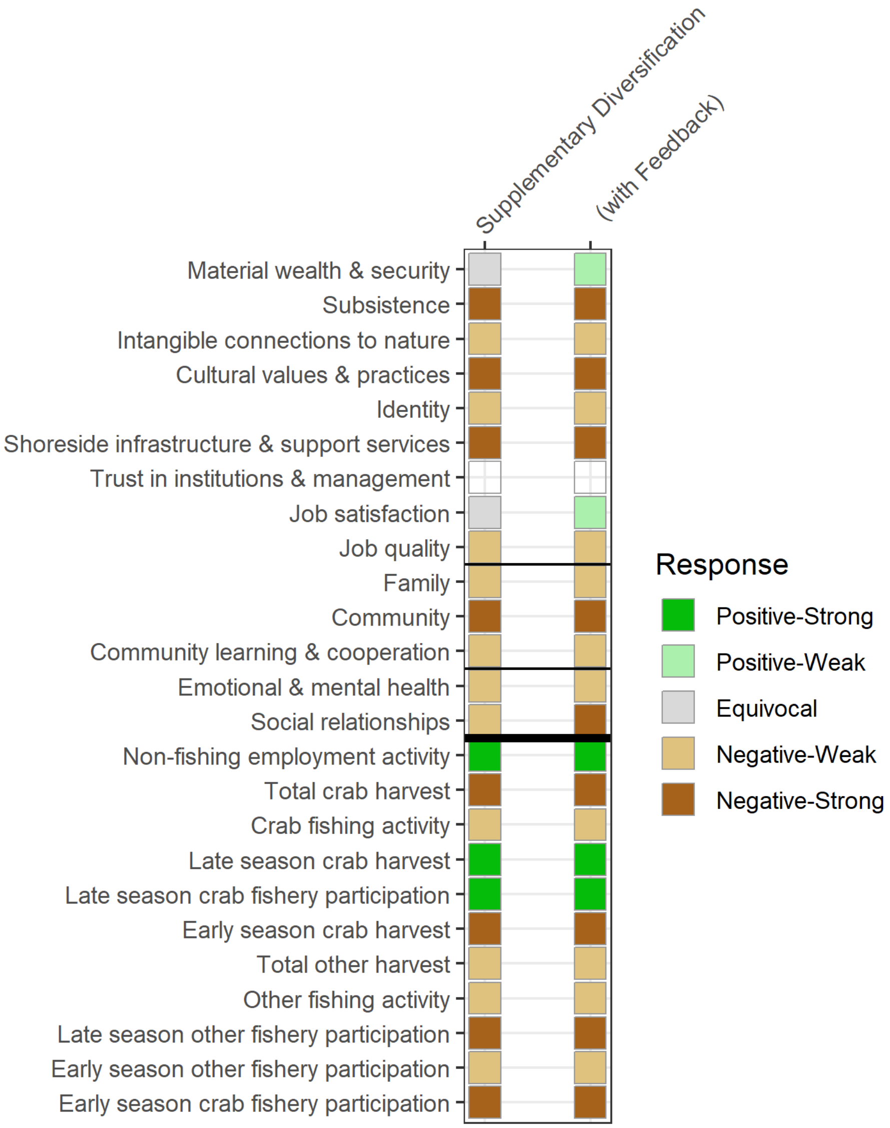

Figure S4.8. Demonstration of how feedback loops can alter well-being outcomes. This figure shows QNM configurations with and without the negative feedback between *Social relationships* (“Relationships”) and *Non-fishing employment activity*. The thick vertical black line separates well-being variables (above) from other variables (below); and the thin vertical black lines separates the higher-order well-being domains (Breslow et al. 2016) from other well-being variables.

The limited impact of this feedback on well-being outcomes and livelihood activity variables may result from an inherent limitation of QNMs. To represent trade-offs in effort allocated to different livelihood activities in our Supplementary Diversification QNM, we have a set of negative relationships linking the different fishing and non-fishing activity variables. Together, these create complex indirect interactions, which may have counteracted the effect of the feedback loop on certain QNM variables. One of the weaknesses of QNMs for applications to social-ecological systems is that increasingly complex direct and indirect interactions between variables introduce greater uncertainty in the model, producing more equivocal outcomes (Zador et al. 2017, Magel and Francis 2022). As a result, where feedbacks interact directly with complex and potentially nonlinear relationships between exclusive livelihood activities, other tools are needed to understand the role of those feedback loops in creating unintended negative consequences from climate adaptation. Feedback effects in complex systems are generally understood to be abundantly nonlinear, which is why adopting preventative frameworks and adaptive management (and not relying solely on models) is crucial to guiding complex social-ecological systems through climate change (Preiser et al. 2018).

4.8.4.3 References

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VITA

Mary Fisher was born and raised in New Jersey; she developed a love for the water at an early age, by swimming in local lakes and visiting her extended family in coastal towns across the U.S. While completing her undergraduate degree at Cornell University, she spent three summers at the Shoals Marine Lab which inspired her to pursue graduate research in marine science. After graduating with a Bachelor of Science in Natural Resources, she spent a humid but rewarding summer conducting field research on the Chesapeake Bay. She then moved to Seattle WA to enter the Master's program in the University of Washington's School of Aquatic and Fishery Sciences. On attaining her Master of Science, she relocated across campus to the School of Environmental and Forest Sciences to complete her Ph.D. She feels immensely lucky to have spent the last eight years living and working (and crabbing) in the Pacific Northwest, especially the time she spent on and in the Salish Sea.