Mobility and flexibility enable resilience of human harvesters to environmental perturbation

Abstract

Sustainable management of ecosystem services requires knowledge of both natural and human systems, but the adaptive behaviors of human harvesters in response to management changes and environmental variability are poorly understood. Given the specter of accelerating climate change, it is especially critical to understand how human harvesters may respond to environmental perturbation. In this study, we identify characteristics that promoted resilience of one the most valuable fisheries on the west coast of the United States to a record marine heatwave. Using movement telemetry linked to fishery landings records from more than 500 fishing vessels, encompassing 2.2 million geolocations and more than USD two billion in revenue, we found that vessels employed two, non-mutually exclusive strategies to cope with the anomalous environmental and management conditions imposed by the heatwave: increasing spatial mobility and diversifying fishery participation. The combination of these strategies appeared to be the most adaptive, as it produced the greatest increase in profits. In contrast, participants that specialized in a single fishery and concentrated fishing effort in small spatial areas did not perform as well. Our data-driven approach reveals behaviors that can be promoted to improve the adaptive capacity of human harvesters in an era of unprecedented environmental perturbation.

Key words: climate change adaptation | environmental perturbation | marine heatwave | fisheries dynamics

1. Introduction

Sustainability in social-ecological systems—the continued provision of human and ecological benefits from healthy ecosystems (Leslie et al., 2015)—requires ecosystem and human resilience to environmental perturbations. Just as species with similar ecological niches may react differently to physical changes in their environments (Elmqvist et al., 2003), human and ecosystem responses to perturbations can be diverse. Resource users with diverse livelihood portfolios, available capital, or distinct spatial patterns of resource extraction behavior do not respond homogeneously to environmental or management changes (Young et al., 2019). The behavior of human actors is further confounded by the additional constraints associated with regulations and resource management (Mcginnis and Ostrom, 2014). More conservative users might rely on established knowledge and previously reliable spatial patterns of exploitation, while others might adopt riskier, more exploratory strategies that could lead to higher profits (Cohen et al., 2007). Understanding the adaptive behaviors of resource users is critical given the increasing frequency of extreme weather events fueled by climate change (Abatzoglou et al., 2019; Cook et al., 2018; Oliver et al., 2018; Townhill et al., 2018), but empirical evidence linking climate extremes with resource user adaptation is lacking.

Fisheries are a prominent example of a social-ecological system where sustainability is driven by complex links between resource user (harvester) behavior and natural resource dynamics (Branch et al., 2006). Fisheries represent the last large-scale wild harvest of food on Earth, but also one of the oldest livelihoods in human history. Difficulties in achieving sustainability in fisheries have often been linked to an inadequate understanding of harvester dynamics (Fulton et al., 2011; Hilborn, 1985). Differences in fisher behaviors, both within and across fisheries, can affect the stability and sustainability of fish populations (Fryxell et al., 2017; Salas and Gaertner, 2004), of other species—for instance, endangered marine mammals or seabirds—and of the fishery itself (Gladics et al., 2017; Hamilton and Baker, 2019).

Additionally, different behavioral segments of fishing fleets may respond in different ways to management measures, or may be differentially vulnerable to environmental perturbations (Salas and Gaertner, 2004). In an early study of fisher behavior, Allen and McGlade (1986) studied differences between the performance of "stochasts", or risk-taking fishers who explore new locations, and "cartesians" that follow high known catch rates, exploring the conditions under which each strategy is more successful. Recently, O'Farrell et al. (2019b) found that more exploratory fishing vessels—those that, on average, traveled further and more often traversed new fishing grounds—were better able to cope with an extended spatial closure. Heterogeneous behavioral response of fishers, however, are difficult to study, despite their potential impact on resource dynamics. This is partly due to a lack of detailed spatial and economic information on harvester behavior. However, recent years have seen a rise in availability of these types of fishery data, paired with methods to extract behavioral insights from them (Joo et al., 2015; Mendo et al., 2019; Watson and Haynie, 2016). In the following, we apply a range of data-driven methods to ask: how did human harvesters cope with and adapt to a major environmental perturbation in the most valuable fishery on the U.S. west coast?

The Dungeness crab fishery on the U.S. west coast often generates over USD 200 million in revenue from over 1,000 participating vessels each year (Rasmuson, 2013; Richerson et al., 2020). The fishery is both ecologically and economically central (Fuller et al., 2017) to the west coast social-ecological system, making it at once a cornerstone of fishers' portfolios and a source of complexity in fisheries governance (Holland et al., 2020, 2017). Dungeness crab populations appear able to withstand immense fishing pressure: although crab catch can fluctuate markedly from year to year, long term abundance has been relatively stable for more than a half century (Richerson et al., 2020). Harvester characteristics vary widely for an industrialized fishery—Dungeness crab vessels have a large range of sizes (in our data, 21 to 103 feet), and operate out of both large urban and small rural fishing ports across the U.S. west coast.

Many factors influence the livelihoods and decision making of Dungeness crab fishers, including crab stock abundance, market prices for crab, crab fishery regulations, and changes to productivity and management of other fisheries. It is thought that strong demand for crab and reduced availability of other species targeted by US west coast fishers has contributed to increasing participation in the crab fishery in recent decades (Hankin et al., 2005). More recently, environmental shocks have challenged the social and economic sustainability of the fishery. In 2015, the US west coast experienced a harmful algal bloom of unprecedented scale when the anomalously warm waters of a North Pacific marine heatwave were supplied nutrients via the spring upwelling. (McCabe et al., 2016). Algae-produced toxins in Dungeness crabs reached levels dangerous for human consumption, persisting even after the bloom subsided and causing lengthy delays to the 2015-16 and 2016-17 Dungeness fishing seasons. The MHW also compressed the preferred feeding habitat of large whales shoreward, leading to a rise in whale entanglements in Dungeness crab fishing gear and precipitating a series of fishery closures through the 2017-18 Dungeness crab season (Feist et al., 2021; Santora et al., 2020). During this period, Dungeness crab fishers had to contend with significant ecological changes and the management measures and market dynamics precipitated by those changes (Mao and Jardine, 2020). The effects of this MHW were complex, as is generally common with climate extremes (Van Loon et al., 2016), reverberating through the social-ecological system and persisting for years after the anomalous warming dissipated (Fisher et al., 2021; Smale et al., 2019; Suryan et al., 2021). While much recent literature is dedicated to examination of biophysical and ecological impacts of the MHW (Cavole et al., 2016; McCabe et al., 2016; von Biela et al., 2019), to date less attention has been given to exploring how social systems coped with these perturbations (Fisher et al., 2021; Jardine et al., 2020; Moore et al., 2020b).

In this study, we compare the adaptive responses of behavioral groups harvesting Dungeness crab to the multi-year MHW that directly affected Dungeness crab fishing seasons from 2015 to 2018. While previous work has investigated economic impacts (Holland et al., 2020; Jardine et al., 2020; Mao and Jardine, 2020) and changes in fishery participation due to the MHW-associated harmful algal bloom (Fisher et al., 2021), we focus on and quantify fishers' adaptive spatial behaviors in response to the MHW more broadly and across the full three-year period of the MHW. Using a 10-year time-series of more than 2 million satellite-derived fishing vessel location records, linked to fishery revenue and landings data, we derive quantitative behavioral metrics describing space use and mobility of Dungeness crab vessels, and then organize these behavioral metrics into characteristic behavioral groups. We explore the overlap of spatial behaviors with profitability, fishing season length, and revenue diversity. We track these behavioral groups over time, and identify key behavioral metrics that promoted adaptation during the MHW period. This analysis therefore offers insights into the types of adaptive behaviors that may promote sustainable outcomes in other commercial fisheries and perhaps in social-ecological systems more broadly.

2. Materials and Methods

2.1. Data sources and processing

We used satellite-based Vessel Monitoring System (VMS) data and port level fishery landings data (hereafter, fish tickets) to define most of the behavioral metrics used in the study. The VMS database is maintained by the National Marine Fisheries Service's Office of Law Enforcement, and records the positions of vessels at approximately one hour intervals. Similar VMS data has been used in other studies of fishery spatial dynamics (Feist et al., 2021; Joo et al., 2015; O'Farrell et al., 2019a; Watson and Haynie, 2016). A subset of the vessels that participate in the Dungeness crab fishery are equipped with VMS transponders (primarily vessels that also participate in the west coast groundfish fishery, where VMS transponders are mandatory). This subset varies between 19 and 26 percent of all vessels recording landings for Dungeness crab between the 2008-2009 and 2018-2019 seasons, representing between 10 and 57 percent of all Dungeness crab landings by weight, and between 15 and 42 percent of Dungeness revenue, depending on the year and month. At the state level, Oregon has the highest relative VMS representation (22-62 percent of revenue), followed by California (14-42 percent), then Washington (4-44 percent) (Figure A.9 and A.10).

Fish ticket information was obtained through the Pacific Fisheries Information Network (PacFIN). These data represent 1949 vessels targeting Dungeness crab in California, across more than 300,000 fish tickets (i.e., fishing trips). Fishing trips were defined as targeting Dungeness crab if the total landings of Dungeness crab on the individual fish ticket were at least 10 percent greater than the landed weight of the next highest species.

We characterized the movement patterns of fishing vessels targeting Dungeness crab by joining the fish ticket data to the VMS telemetry data using unique vessel identification numbers and timestamps, building on the work of others (Watson et al., 2018). VMS geolocations comprising a fishing trip were defined as all of the geolocations between a landed fish ticket and the one immediately preceding it (i.e., the previous ticket landed by the same vessel). After joining the VMS and fish ticket data, we removed the small number of trips in which the final VMS data point for a trip was greater than 50km from the port of landing recorded on the ticket, reasoning that these are unreliable records. Finally, we removed VMS records from vessels sitting idle in port. To do so, we truncated all but the first and last VMS records for each trip that fell within a small buffer zone (1.5 to 3 km) around each port of landing and with an average calculated speed of less than 0.75 m/s. The maximum lookback window over which VMS geolocations were associated with any given fish ticket was seven days prior to the landing data. If there was another Dungeness crab fish ticket reported less than seven days previous, the fishing trip was shortened to the corresponding time interval. This choice of a seven day cutoff was made after conversations with state Dungeness crab fishery managers regarding the maximum reasonable length for a crab fishing trip (Oregon Department of Fish and Wildlife, pers. comm.). The seven day cutoff did not affect the majority of crab trips (especially during the early, busiest part of the season, Fig. A.11). The final dataset comprises a clean record of VMS-derived geolocations associated with each Dungeness crab fishing trip.

The timing of Dungeness crab fishing seasons on the west coast can be complex and inconsistent over space and time. Under ideal or "normal" circumstances, most seasons begin in the middle of November (for Central California) or beginning of December (for Northern California, Oregon, and Washington). However, the exact start date in any given season in each region is determined by harmful algal bloom status, price and market conditions, crab condition and meat quality, and potential interactions with protected species like humpback whales. Further, since start dates listed in official state fishery records do not necessarily reflect when crab were first landed at each of the dozens of ports on the west coast, we used a data-driven approach to define the start date for each crab season in each of the 20 fishing port groups. Port groups are defined by PacFIN and include clusters of small, neighboring fishing ports. For each port group in each season, we defined the season start as the date after October 31 that the cumulative Dungeness crab landings into that port reached 1 percent of the eventual total landings for the entire season. This approach identifies the realized start date of the crab fishery in each portion of the coast in each year.

The last data source used in the calculation of behavioral metrics was mean daily wind speed (AVHRR Pathfinder satellite-derived measurements https://data.nodc.noaa.gov; https://doi.org/10.7289/v52j68xx),aggregated on a 0.04 degree grid. These wind speed data were used in the construction of one of the behavioral metrics, described in the next section. All analyses in the study were performed in R (R Core Team, 2021).

2.2. Construction of Fishing Behavioral Metrics

We calculated fishing behavioral metrics using a combination of the fish ticket, VMS, and wind speed data. While VMS and wind speed data provide information on vessel movements and environmental context of fishing trips, the fish ticket data allow us to derive important variables like revenue, season length, fishing port use, and vessel size, then link those variables directly to vessel movements. Each of the fisher behavioral metrics described one characteristic of a vessel's behavior over the course of a fishing season—a vessel-season (Table 1).

To determine whether a vessel would be included in the analysis, we first calculated the total Dungeness crab revenue for each vessel-season from 2008-09 to 2018-19 using the fish ticket data. All revenue values were converted to 2010 USD using a consumer price index (https://www.minneapolisfed.org/about-us/monetary-policy/inflation-calculator/consumer-price-index-1913-). The 5th percentile for season-long Dungeness revenue per vessel was $USD 5227 (in 2010-adjusted dollars). We retained all vessel-seasons with greater than USD $5227 in revenue in any season (i.e., we retained the top 95 percent of all vessel-seasons in terms of revenue).

Our choice of behavioral metrics to calculate was driven by previous evidence of the importance of each variable in describing fisher behavioral patterns (Fuller et al., 2017; Kasperski and Holland, 2013; O'Farrell et al., 2019a, 2019b; Pfeiffer and Gratz, 2016). The metrics fall into five general categories: port use, fishing trip characteristics, participation in other fisheries, risk-taking behavior, and exploration and mobility (Table 1). Port use metrics include the number of ports visited per fishing trip, ports visited per month, diversity of port use (calculated as a Shannon diversity index on the proportions of trips landed in each port), and the total number of ports visited across the entire season. The trip metrics are the mean and standard deviation of trip distance (kilometers) and duration (days). We also included vessel size as a metric, as it has been used as a proxy for fleet segments in other studies (Jardine et al., 2020). As a point of comparison to these other studies, we also correlated vessel size with the other behavioral metrics in the analysis (Fig. A.6).

Fishery participation metrics include season length, revenue diversity, and proportion of revenue from non-Dungeness fisheries. The Dungeness fishery is considered "derby-style", where the vast majority of fishing activity and associated landings and profits occur within the first few months of each season (Fig. A.4). Our season length metric captures this temporal compression by identifying the day of the season when each vessel reached 90 percent of its eventual total landings. To assess revenue diversity from non-Dungeness crab fishing, we used the fish tickets to calculate the inverse Simpson index for each vessel-season, based on the proportion of revenue obtained from each managed species group in a vessel's fishing portfolio. We used the species management groups defined by the Pacific Fisheries Management Council (https://pacfin.psmfc.org/pacfin_pub/codes.php) to group species for the revenue diversity calculation (Fig. A.14). We chose the inverse Simpson index for revenue diversity because of its sensitivity to dominance relative to other diversity metrics (DeJong 1975); in this case, we were interested in the dominance of the Dungeness crab fishery relative to other fisheries in a vessel's portfolio. In contrast, we used a Shannon index to measure port use diversity because of its relative sensitivity to the total number of ports rather than the dominance of any one port.

In this application, we specifically define safety at sea and risk-taking behavior based on propensity to fish in high-wind conditions (following Pfeiffer and Gratz (2016), who also studied west-coast fisheries). We acknowledge that risk within fisheries is a subjective perception based on fisher age, fishing equipment, fisher and crew experience, and psychocultural profiles which have economic (i.e., potential loss of revenue) and human dimensions (i.e., safety concerns) (Pollnac and Poggie, 2008; Pollnac et al., 1998). However, at the scale of the full US west coast over the 12 year study period, we only had access to quantitative data for the physical safety component of the fishery. Using the Pathfinder winds data, we extracted the wind speed at each VMS location, then calculated the 95th percentile of wind speed experienced by each vessel on each trip. Finally, the risk-taking metric was defined as the proportion of trips in a vessel-season where the 95th percentile of experienced wind speed was greater than 7.5 m/s (Pfeiffer and Gratz, 2016).

Exploration and mobility were measured with home range and location choice entropy, adopting the definitions in O'Farrell et al. (2019). Home range was calculated as the area of the minimum convex polygon encompassing all VMS locations in a vessel-season, after removing the five percent of locations that were the furthest from other points (i.e., spatial outliers). Location choice entropy measures the propensity of vessels to explore new locations versus returning to the same locations(O'Farrell et al., 2019b). Spatial locations were defined as individual cells on a 5x5km grid. As a season progresses, entropy increases as vessels explore novel locations and decreases as the same locations are revisited. At a given point in a season, the choice entropy E_{im} of vessel i at time point m is defined as,

$$E_{im} = -\sum_{j=1}^{N_{im}} f_i(j) log_2 f_i(j) \tag{1}$$

where N_{im} is the number of cumulative, unique fishing locations visited by vessel i from the beginning of the season until time m, and $f_i(j)$ is the frequency at which the vessel visited location j. An example choice entropy time series is provided in Figure A.15.

Definitions of all metrics used in the clustering analysis are provided in Table 1.

2.3. Cluster Analysis

We used cluster analysis on the metrics described above in order to group vessel-seasons into behavioral groups. First, all behavioral metrics were checked for collinearity, and thinned such that no two metrics had a Pearson correlation greater than 0.7. This thinning removed mean and standard deviation of trip distance, total number of visited ports, and proportion of non-Dungeness tickets from the analysis. The remaining 11 metrics were scaled to range from zero to one by dividing each metric by its maximum value (across all seasons). Clustering was performed using Euclidean distances and a k-means algorithm. In k-means, an algorithm guesses an initial placement of cluster centers, and places each observation in the cluster to which it is closest. The cluster centers are then recalculated, and the entire process is repeated until the cluster centers reach a stable position (Hartigan and Wong, 1979). The algorithm is repeated with multiple initial clusters. The best number of clusters (i.e., behavioral groups) was then determined using the Nbclust package in R (Charrad et al., 2014), which calculates 22 indices before recommending an optimal number of clusters via majority vote amongst indices. Adopting the optimal clusters defined by NbClust, we visualized results graphically using principal component analysis. After vessel-seasons were assigned to groups, we tested for differences between groups along specific behavioral metrics using Tukey's HSD.

The importance of individual metrics in discriminating between behavioral groups was calculated using random forest analysis, utilizing the randomForest package in R (Liaw and Wiener, 2002). Random forests were grown on subsamples of the data to classify vessel-seasons according to their defined groups from the previous step. These random forests were used to predict withheld data. A given metric's importance was defined as the increase in the rate of mis-classification of vessel-seasons into clusters when the metric was randomly permuted.

Category	Metric	Definition
Port Use	Ports per Trip	Average ports visited per trip
	Ports per Month	Number of ports visited per month
	Port Diversity	Inverse Simpson diversity index of port use across the entire season
	Total Ports*	Total number of ports visited across the entire season
Trip Length	Mean Trip Distance*	Mean distance per fishing trip
	Mean Trip Duration	Mean number of days per fishing trip
	SD Trip Distance*	Standard deviation of distance traveled per trip
	SD Trip Duration	Standard deviation of days per fishing trip
Participation in Other Fisheries	Season Length	Day-of-season on which fisher reached 90% of eventual, cumulative catch
	Proportion Non-Dungeness Revenue	Proportion of revenue from non-Dungeness crab fisheries
	Proportion Non-Dungeness Tickets*	Proportion of all fish tickets from non-Dungeness crab fisheries
	Revenue Diversity	Inverse Simpson diversity index of revenue by fished species
Risk-Taking	Risk Taking/Safety at Sea	Propensity to fish in high winds. Proportion of trip pursued where the 95% quantile of wind speed was greater than 7.5 m/s
Exploration & Mobility	Location Entropy	Cumulative choice entropy, measuring how likely a vessel is to fish in new versus past locations. The metric used is the 90th percentile of maximum choice entropy per vessel per season
	Home Range Size	Home range defined as the area of the convex hull surrounding all of a vessel's VMS pings during the season, excluding the top 5% spatial outliers
Vessel Size	Vessel Length in Feet	Registered length of the fishing vessel

Table 1: Fisher behavioral and demographic metrics derived and used in the clustering and random forest analyses. Variables with asterisks were removed from the final clustering analysis due to high collinearity with other variables.

2.4. Dungeness Fishing Profitability

Fishing trips incur daily costs C_d that are associated with fuel C_f, bait C_b, and other variable costs C_v like the fixing of traps. Additionally, there are costs associated with the entire fishing trip, most notably the share of trip revenue R_i that goes to crew members, C_c. Revenue share to crew increases with vessel size, since larger vessels require more crew. We simulated the following relationships to estimate the cost Ci of fishing trip i lasting d_i days:

$$C_i = d_i C_d + R_i C_c \tag{2}$$

$$C_d = C_b + C_f + C_v \tag{3}$$

To simulate these costs, we adopted data from Dewees et al. (2004), who conducted a survey of small (<30 feet in length), medium (30 to 50 feet), and large (more than 50 feet) size-class vessels. We used their estimates of C_b, C_f, C_v and C_c to simulate 10,000 draws from the distributions below for all combinations of year y (2008-2019) and state s (California, Oregon, and Washington). We accounted for fuel price differences between states using a relative marine fuel price index $r_{s,y}$ from the Pacific States Marine Fisheries Commission (Fig. A.16). All dollar values were normalized to 2010 USD.

$$C_b = \begin{cases} \sim N(66,73) & 0 < \text{length} < 30 \\ \sim N(178,269) & 30 <= \text{length} <= 50 \\ \sim N(261,188) & \text{otherwise} \end{cases} \tag{4}$$

$$C_f = \begin{cases} \sim N(47,51) * r_{s,y} & 0 < \text{length} < 30 \\ \sim N(78.5,158) * r_{s,y} & 30 <= \text{length} <= 50 \\ \sim N(173,96) * r_{s,y} & \text{otherwise} \end{cases} \tag{5}$$

$$C_v = \begin{cases} \sim N(46,62) & 0 < \text{length} < 30 \\ \sim N(47,62) & 30 <= \text{length} <= 50 \\ \sim N(72,33) & \text{otherwise} \end{cases} \tag{6}$$

$$C_c = \begin{cases} \sim N(0.15,0.1) & 0 < \text{length} < 30 \\ \sim N(0.24,0.11) & 30 <= \text{length} <= 50 \\ \sim N(0.31,0.1) & \text{otherwise} \end{cases} \tag{7}$$

This fishing costs simulation allowed us to extract estimates of C_d and C_c for every trip in the data based on the vessel's length and the trip's year, month, and state of landing (Figs. A.17, A.18). When combined with individual trip revenue R_i and duration d_i, we were able to estimate the total cost of each fishing trip, which in turn allowed us to measure profits as revenue minus cost.

Using trip-level profits, we calculated season-long profits and mean profits per week for vessels in each behavioral group. Finally, we also calculated total revenue from all non-Dungeness fisheries for each vessel-season in the analysis.

We constrained the calculation of non-Dungeness revenue to only those fishing trips that occurred within each vessel's apparent Dungeness season (that is, within the time period where the vessel was also landing Dungeness crab).

2.5. Adaptation During the Marine Heatwave

Using the results of cluster analyses, we compared key characteristics of behavioral groups in MHW versus non-MHW crab seasons. We defined the MHW as encompassing the crab fishing seasons from 2015-16 to 2017-18. Although there is evidence that the MHW began affecting west coast ecosystems as early as the fall of 2014 (Cavole et al., 2016; McCabe et al., 2016), the 2015-16 Dungeness crab season was the first to be significantly delayed as a direct result of ecosystem changes (Jardine et al., 2020). The 2015 harmful algal bloom caused toxin levels in Dungeness crabs to become dangerous for human consumption, an effect that persisted even after the bloom subsided and resulted in lengthy delays of the 2015-16 and 2016-17 Dungeness fishing seasons. Even the 2017-18 season may have been affected by the MWH, via its effects on meat quality of crabs, which also led to delayed season openings. Adopting this definition of the MHW period (2015-2018), we compared mean Dungeness profit, non-Dungeness revenue (i.e., external fishery revenue), and home range size over time among behavioral groups to explore potential spatial and economic behavioral adaptation. For each of these three comparisons, we performed a two-way ANOVA to test for significant differences in mean profits, revenue, and home range by behavioral group and period (non-MHW or MHW).

3. Results

3.1. Describing Fisher Behavior

The combined vessel telemetry and fisheries landings dataset captured the behaviors of 596 different vessels spanning 11 fishing seasons (2008-2019), with approximately 2.2 million satellite-derived VMS geolocations, and 315,000 fishery landing records. Using these combined data, we identified and analyzed 11 behavioral metrics in five general behavioral categories: fishing port use, fishing trip characteristics, participation in other fisheries, risk-taking behavior, and exploration and mobility (definitions of all metrics are provided in Table 1).

The 3391 vessel-seasons (characteristics of a vessel's apparent behavior over the course of a fishing season) in our data clustered into four behavioral groups (Figs. 1a, A.1). The most important discriminating variables driving the clustering according to random forest analysis were proportion of revenue from non-Dungeness crab fisheries, followed by revenue diversity, risk taking, and vessel size (Fig. 1b). These analyses suggest that the behavior of the four groups can be conceptualized as varying along two major axes (Fig. 1c): (1) spatial mobility (principal component 1 in Fig. 1a) and (2) propensity to fish in non-Dungeness crab fisheries (fishery flexibility, principal component 2 in Fig. 1a).

Vessels with higher spatial mobility, which we term Roving groups, move between ports throughout a fishing season and have large fishing ranges, while those with lower mobility—Local groups—show greater fidelity to a single port. Vessels with greater fishery flexibility, deemed Generalist groups, have high revenue diversity and derive a relatively greater portion of their total fishery revenue from fisheries other than Dungeness crab. Vessels exhibiting less flexibility—Specialists—concentrate fishing effort within the Dungeness crab fishery. Therefore, a vessel-season is classified as either Roving or Local, and either Specialist or Generalist. As an example, for crab vessels fishing out of Newport, Oregon, Local Specialists have the smallest fishing grounds, followed by Local Generalists, Roving Specialists, and Roving Generalists (Fig 2a). Across all vessel-seasons, Generalist vessels have shorter crab fishing seasons, exiting the Dungeness crab fishery earlier to pursue other fishing opportunities, while Specialists continue to garner a large percentage of their weekly landed revenue from Dungeness crab over the course of the season (Fig. 2b).

3.2. Behavioral Changes During the Marine Heatwave

The four fishing behavioral groups defined by our cluster analysis responded to the social-ecological disruption of the MHW period by increasing their dependence on other, non-Dungeness fisheries and expanding their fishing ranges. There were fluctuations in the number of vessel-seasons in each behavioral group over time, but no clear directional pattern in group membership or flows between groups over time (Figs. A.3, A.12, A.13). All groups had higher non-Dungeness fishery revenue during the MHW period than during other seasons, indicating a potential fallback to other fisheries during a period of delays and management disruptions in the crab fishery (Fig. 3, Fisher et al. (2021); Holland et al. (2020)). The 2016-17 and 2017-18 seasons had the highest non-Dungeness crab revenue in the time series (Fig. 3a). The Generalist groups in particular more than doubled their revenues from non-Dungeness fisheries (ANOVA $p < 0.01$; Fig. 3b). The Specialist groups also had greater non-Dungeness revenues during the MHW period, but the differences were only marginally significant for Roving Specialists (ANOVA $p = 0.06$) and non-significant for Local Specialists (ANOVA $p=0.99$, Table A.2).

Some Dungeness fishers also expanded their Dungeness crab fishing grounds during the MHW, particularly the two Roving groups (Fig. 4). Prior to the MHW (2008-15), Roving Generalists had the largest mean home range size at more than 4000 square kilometers (Fig. 4a). Roving Specialists had the second-largest ranges on average (around 2500 square kilometers), while the Local groups had much smaller ranges (less than 1000 square kilometers). In the MHW period from 2015-18, the Roving groups fished significantly larger areas, with the Roving Generalist and Roving Specialist groups averaging more than 5500 and 3500 square kilometers fished, respectively ($p=0.001$ and $p<0.001$ for Roving Specialists and Roving Generalists). In contrast, the areas fished for the Local groups did not change significantly (Fig. 4b and Table A.2, $p>0.99$ for both Local groups). For all four groups, within the MHW period, the most pronounced change in mobility occurred during the 2016-17 fishing season.

3.3. Profitability of Behavioral Groups during the Marine Heatwave

An open question is whether the adaptive responses we detected and quantified—greater spatial mobility and more flexible fishing—allowed fishers to maintain profits in the face of this major environmental perturbation. Our fishing cost model provides an estimation of Dungeness crab profit (reported revenue minus estimated cost) for every fishing trip in the data, and allowed us to describe how profits within each behavioral group varied over time (Fig. 5).

For all groups, average revenues and estimated costs both increased during the MHW period, but revenue increases outweighed the increases in estimated cost (Figs. A.7, A.8). As a result, Dungeness crab profits for all behavioral groups increased during the MHW, significantly so for Roving Generalists ($p \ll .0001$) and Roving Specialists ($p=0.001$, Table A.3). The Roving Generalist group saw the largest increase in mean estimated profits (more than a USD 40,000 increase per vessel, a 35 percent increase, on average), while Local Generalists generated the highest percent increase (more than 60 percent, although this increase was not statistically significant). Local Specialists experienced the smallest increase in profits of all groups (USD 13,000, 25 percent) during the MHW period. In the season after the dissipation of the MHW, estimated profits declined, particularly for the Roving groups.

4. Discussion

The pace and magnitude of environmental change in the Anthropocene demand assessment of how social-ecological systems will respond. Ideally, management approaches can be designed to help humanity adapt by meeting the basic needs of people without compromising ecosystems for future generations (Lubchenco et al., 2016). As one of the last remaining ways that humans capture wild foods at large scales, commercial fisheries offer an important lens through which to understand human adaptations to novel and extreme conditions. The 2014-2016 marine heatwave on the U.S. west coast stressed the adaptive ability of participants in the highly lucrative Dungeness crab fishery, because an environmental perturbation—the MHW and associated harmful algal bloom and shoreward compression of large whale habitat—led to cascading regulatory actions and market effects (Holland et al., 2020). Our analysis revealed that Dungeness crab fishers that remained in the fishery responded to unprecedented environmental and management changes in multiple ways. Behavioral groups characterized by spatial mobility used expanded fishing grounds in the 2016-17 and 2017-18 seasons to maintain or increase revenues. Similarly, fishers with strategies based around diversified fishing portfolios (Generalists) were able to increase their revenue from other fisheries to bolster their total fishing income. We found that vessels combining greater spatial mobility with higher participation rates in other fisheries were the most profitable, and that these financial benefits were maintained or magnified during the MHW. The behavioral strategies observed in the Dungeness crab fishery suggest that both portfolio and spatial diversification pathways can improve adaptive capacity for human harvesters during an era in which the magnitude, frequency, and intensity of environmental perturbations are increasing.

Our work builds on research from the economics (Gordon, 1954; Smith and McKelvey, 1986), evolution (Gallagher et al., 2015), and ecology (Beever et al., 2017) literatures investigating the relative ability of specialists and generalists to cope with environmental change. The cross-disciplinary consensus is that generalists may adapt better to increasingly variable environments. Smith and McKelvey (1986) suggested that specialists and generalists in fisheries use different strategies to cope with variability and uncertainty in income—specialists are efficient and may minimize income risk or maximize returns through fishery-specific acumen or leveraging economies of scale, while generalists hedge against risk by building diverse portfolios (Finkbeiner, 2015; Kasperski and Holland, 2013; Oken et al., 2021). In a direct ecological analogy, generalist consumers in an ecosystem experiencing novel environmental conditions may be able to gain a competitive advantage over specialists by efficiently switching to alternative prey sources (Beever et al., 2017).

While management dynamics, markets, stochastic resource abundance, and conditions in other fisheries are complicating and influential factors (Holland et al., 2020), the relative performance of specialist versus generalist strategies in the Dungeness crab fishery largely adhere to these existing economic and ecological models. Although both Specialists and Generalists persisted through the MHW period, repeated environmental disruptions in the future that cause further seasonal and spatial restrictions on the Dungeness crab fishery may begin to favor a Generalist, diversified strategy. Within the US west coast context, existing fishery governance systems may constrain this type of generalist adaptation (Kasperski and Holland, 2013; Russell et al., 2018), but there are calls for "climate-ready" fisheries that include the flexibility for fishers to move between fisheries (Wilson et al., 2018). A better understanding of the social, economic, and cultural drivers of fishers' decisions to be specialists or generalists is a core component of a sustainable livelihoods approach to small-scale fisheries management (Allison and Ellis, 2001; Finkbeiner, 2015). Such an approach can also offer insights for the design of regulatory approaches that facilitate resilience to environmental perturbation in larger-scale fisheries and other natural resource management contexts (Salas and Gaertner, 2004).

Diversification of fishery revenue was not the only axis of variation associated with persistence in the face of the MHW. Spatial mobility was also a key component of the fishing strategies we observed. Following others who have used recently emerging technologies to understand the sustainability of human harvester strategies (Brodie and Fragoso, 2020; Frawley et al., 2020; Renner and Kuletz, 2015), we used satellite data to characterize the spatial behavior of vessels. Roving groups, whether Specialists or Generalists, were more profitable than their Local counterparts under all conditions. The benefits of this spatial mobility were clear during the MHW. We hypothesize that Roving vessels were the most capable of responding to management actions, market forces, and ecological factors (e.g., product quantity and quality) that shifted spatially during the heatwave. The ability of more exploratory fishers to cope during an environmental disturbance has recently been demonstrated in other commercial fisheries systems (O'Farrell et al., 2019b), and our findings confirm that more mobile vessels performed better during the environmental perturbation. Similar patterns have been shown among foraging marine mammals, where individual animals that are more exploratory have greater foraging success during anomalous climate conditions than more site-faithful conspecifics (Abrahms et al., 2018).

Importantly, the nature of the data used in this study means that we studied the behavior of the 'survivors'—that is, the fishers who decided or were able to remain in the Dungeness crab fishery during the MHW period. The MHW acted as a selective force on Dungeness crab fishery participation, and occurred amidst a variety of other influential factors acting within and external to the crab fishery. For example, the Dungeness crab population abundance was lower in the 2015-16 season than the average for the previous five seasons (Richerson et al., 2020), likely due to population cycles somewhat independent of the MHW, and, along with variation in meat quality, may have affected the expected profits of crab fishers. Furthermore, ex-vessel prices for crab dropped by about 10 percent in 2015-16, perhaps due to perceptions around seafood safety and consumer demand (Mao and Jardine, 2020). Current concern around whale entanglements (Feist et al., 2021; Samhouri et al., 2021; Santora et al., 2020) and whether the Dungeness crab fishery is 'whale-safe' may have influenced crab prices as well. Many Dungeness crab fishers during the 2016 and 2017 fishery closures chose or were forced by circumstance to not participate in the fishery at all, instead opting to exit fishing entirely or to re-concentrate all effort in alternative fisheries (Fig. A.13). In California, these alternatives included groundfish fixed-gear, groundfish trawl, and pink shrimp fisheries (Fisher et al. 2021). Some of the relative success of the Dungeness crab fishers during the MHW observed in this study, therefore, may be due to reduced competition, as well as periods of supply shortages and high prices. Indeed, the Dungeness crab fishery is by far the largest revenue generating fishery of the alternatives available to Dungeness crab vessels, making it a difficult opportunity to look past. Although outside the scope of the current analysis, an important area for further research is to determine how and why, when faced with an environmental perturbation, fishers choose to remain or exit a fishery (Moore et al., 2020a). The answer almost certainly lies in the complex interactions between social and environmental influences on fisher livelihoods and decision making (Barnes et al., 2020).

With climate change expected to increase the frequency of extreme environmental perturbations like MHWs (Oliver et al., 2018) against a background of more gradual directional change, established patterns of natural resource management and human harvester behavior will be challenged. In our study, following multiple adaptive pathways by both diversifying and mobilizing appears to be one response to an extreme environmental event and rapid management changes in the Dungeness crab fishery. Management measures that restrict the fishery temporally or spatially—such as spatially-explicit biotoxin-related closures or early termination of the fishing season due to risk of interactions with protected or bycatch species—will differentially affect distinct groups of fishers. Single-fishery specialists may thrive when the harvested resource is stable and productive, but these fishers may struggle to adapt if management measures restrict fishing season lengths. Likewise, localized fishers can thrive through intimate knowledge of fishing grounds, but if large-scale environmental perturbations have spatially-explicit negative effects, fishers with knowledge of a wider array of fishing grounds and greater mobility will naturally gain an advantage (O'Farrell et al., 2019b). Over time, management context, or failures of management to adapt, can drive changes in the makeup of fishing fleets as a whole (Frawley et al., 2020). These changes are not inherently negative, but in order to maintain the social, economic, and cultural benefits provided by a fishery, managers should endeavour to anticipate behavioral changes within fleets. Simultaneously, managers should consider policies that enhance the capacity of resource users to adapt to environmental change. For example, policies in the Dungeness crab fishery could increase access to diversified fishing permit portfolios (Oken et al., 2021) or provide opportunities for marketing crab products following evisceration of toxic crab tissues during harmful algal blooms.

Managers will also have to consider both short- and long-term changes in productivity and profitability across fisheries. For example, in the Dungeness crab fishery, the impacts of the MHW occurred during a longer period of steadily increasing prices attributable to a booming export market, as well as regulatory, economic, and biological changes in fisheries linked by cross-participation (e.g. groundfish). Though we focus on season-level performance, both long-term mean and variation in revenue will impact fishers' ability to adapt and persist. More generally, these insights are congruent with an evolving understanding of adaptation in complex social-ecological systems (Lubchenco et al., 2016). Because complex systems are in part an emergent product of the individual actions of human actors, which are mediated by local, regional, and global governance structures (Mancilla Garcia et al., 2020; Scholes et al., 2013), informed adaptive management requires an understanding of the drivers of behaviors like those identified in this study along with well-calibrated and nimble responses within governance systems that work across local and regional scales.

For fishers and other human harvesters, future work using mixed methods from the social sciences like participatory mapping and semi-structured interviews (Frawley et al., 2020; Moore et al., 2020a; Pellowe and Leslie, 2019; Ritzman et al., 2018) will provide complementary insights into the motivations and social drivers behind adaptive decisions, and could help identify system-specific metrics of success or performance beyond profitability. Furthermore, as integrated biophysical and socioeconomic data streams become increasingly available for environmental management (Bradley et al., 2019), data-driven, interdisciplinary studies of resilience and adaptation will enable dynamic management of natural resources (Hazen et al., 2018; Maxwell et al., 2015). This push for the incorporation of multiple data streams in environmental management extends beyond marine fisheries. For example, in wildland fire management in the United States, integrated data platforms that combine geospatial data with risk models and fuel treatment scenarios are empowering adaptive fire management plans (Ager et al., 2011; Krofcheck et al., 2018).

This study revealed the elements of behavioral diversity among human harvesters in a lucrative, keystone commercial fishery, and described how those elements enabled adaptation during an extreme environmental event attributable to climate change (Hinder et al., 2012). Just as biological response diversity can lead to enhanced ecosystem resilience to environmental change (Elmqvist et al., 2003), behavioral diversity among natural resource users may promote resilience of social-ecological systems. Given the impending increase in extreme climatic events such as MHWs (Burge et al., 2014; Smale et al., 2019), recognition of social and ecological traits that enable resilience now can help to build toward a more prepared future. As quantitative data become increasingly available in the United States and far beyond, behavioral analyses like ours can be used in the design of adaptive management measures, to bolster policy analyses (Cabral et al., 2018), and to inform decision making under environmental uncertainty.

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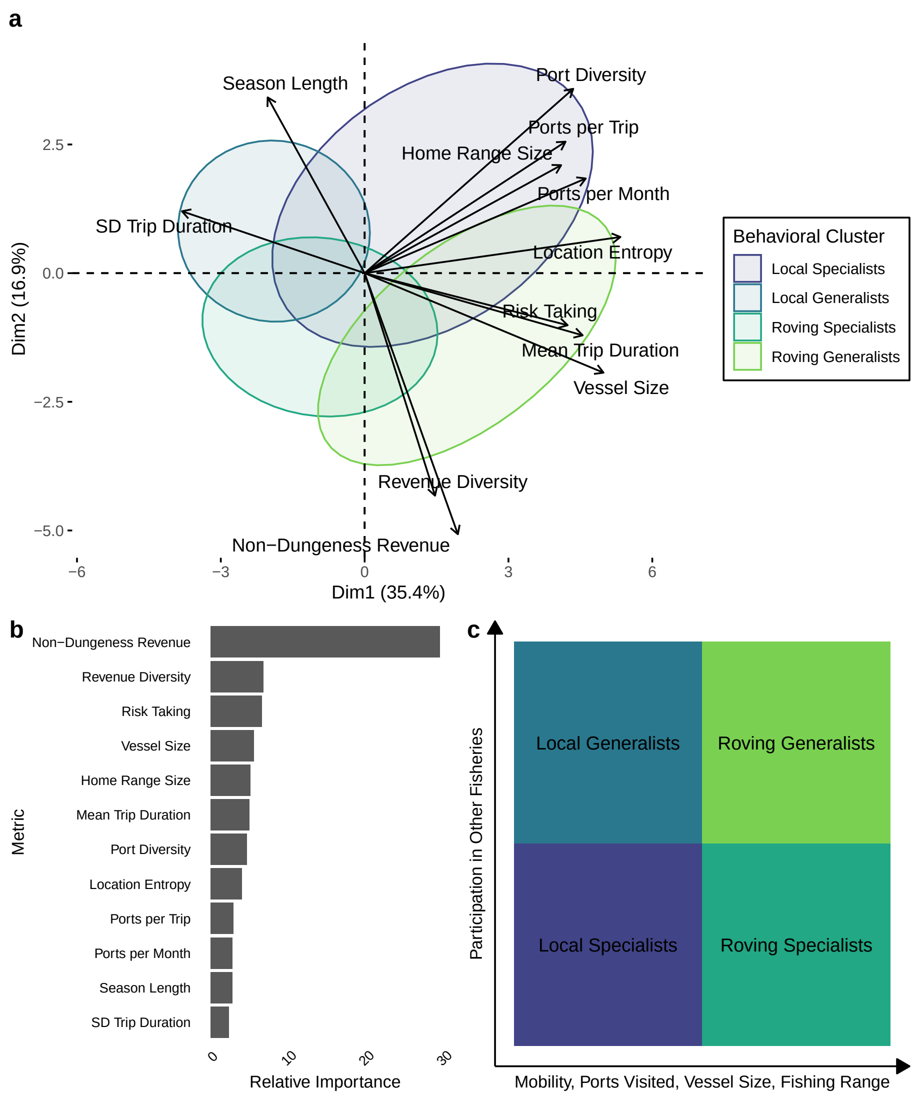

Figure 1: Data-driven formation of fishing behavioral groups. (a) Principal component analysis of vessel-seasons. Clusters of vessel-seasons, which determine behavioral groups, are enclosed by ellipses. Arrows represent the association between metrics in the cluster analysis relative to the placement of vessel-seasons. (b) Ranked importance of metrics used to classify vessel-seasons into behavioral groups, as determined by random forest analysis.(c) Conceptual visualization of the major axes defining behavioral groups.

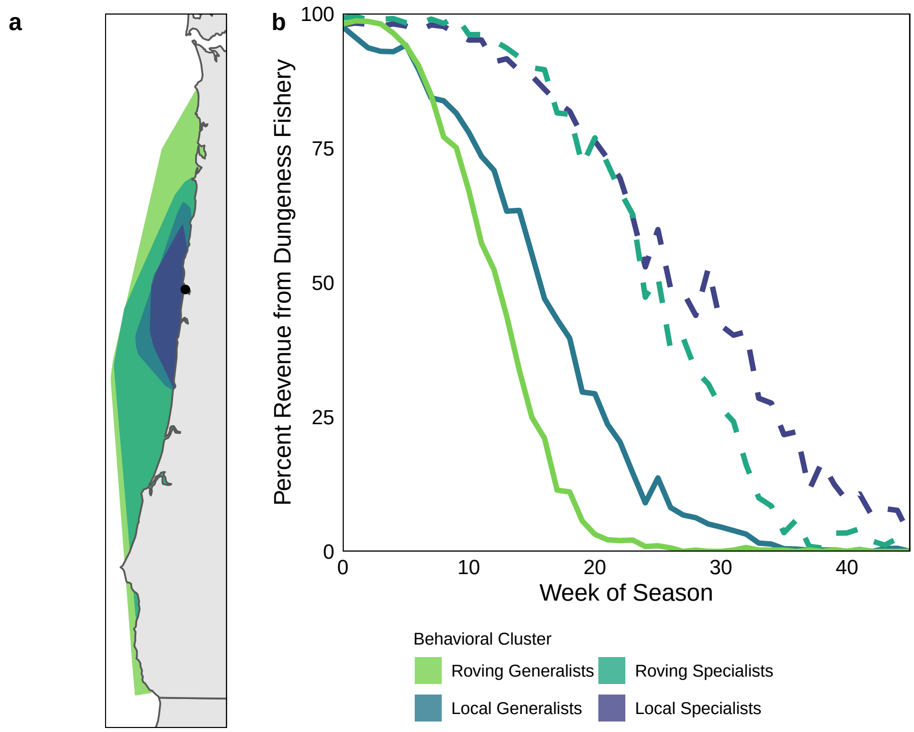

Figure 2: Characteristic patterns in spatial mobility and fishery flexibility across behavioral groups in the west coast Dungeness crab fishery, exemplified by an Oregon port. (a) Fishing footprints of each behavioral group across all seasons for vessels originating from the Port of Newport, Oregon, USA. Shaded polygons are 95 percent convex hulls of all VMS locations for each group. (b) Fishery flexibility, displayed as the percent of Dungeness crab revenue relative to total weekly revenue (across all fisheries) for vessels in each behavioral group. Weekly revenues are averaged across crab seasons and across all vessels in each group. Generalist groups are represented with solid lines, while Specialist groups are represented with dashed lines.

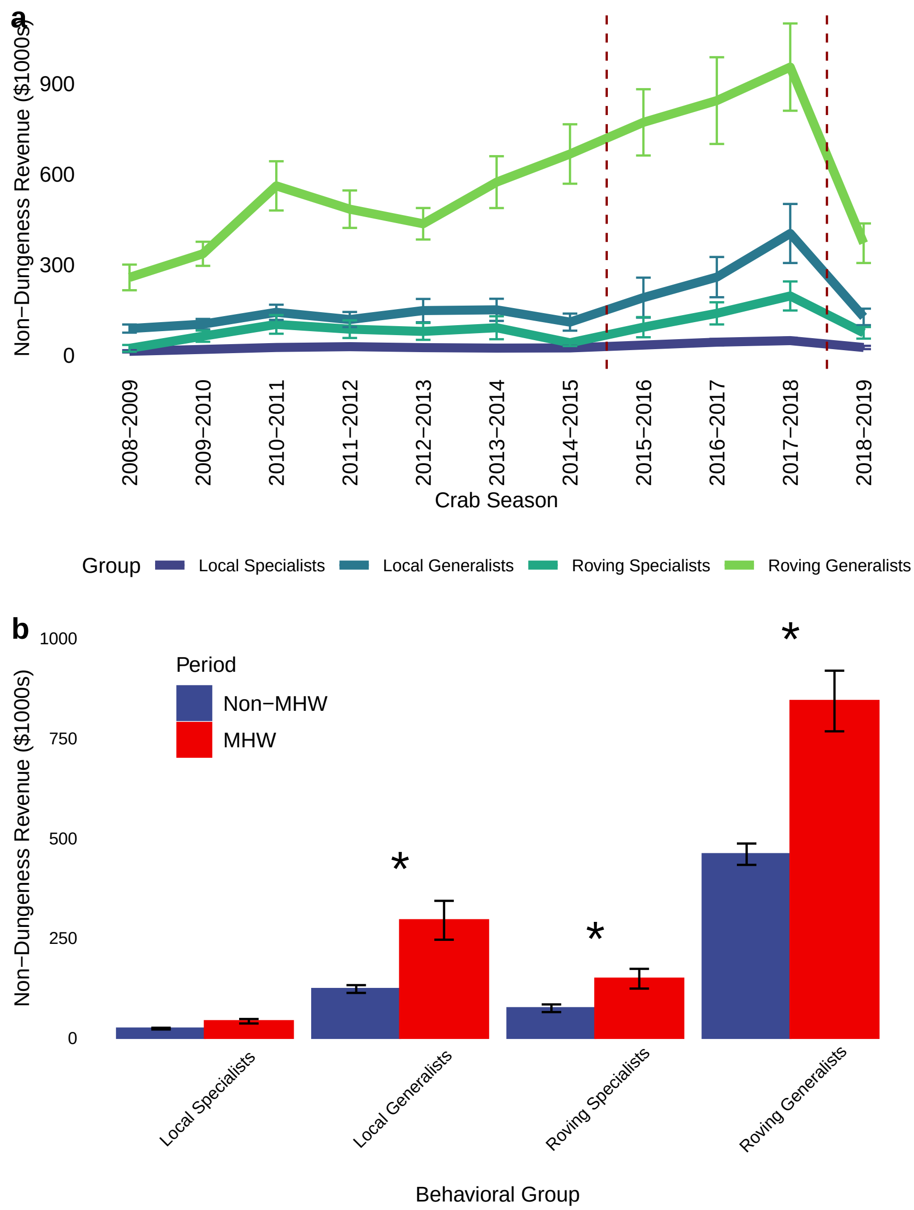

Figure 3: Non-Dungeness revenue for vessels in the analysis. (a) Seasonal mean revenue (+/- 2SE) for vessels in each behavioral group coming from all non-Dungeness fisheries combined. Vertical lines delineate the period of the marine heatwave (MHW). (b) Barplot of mean revenue (+/- 2SE) for vessels in each group during MHW and non-MHW seasons. Stars indicate groups with significantly different non-Dungeness revenue in MHW seasons.

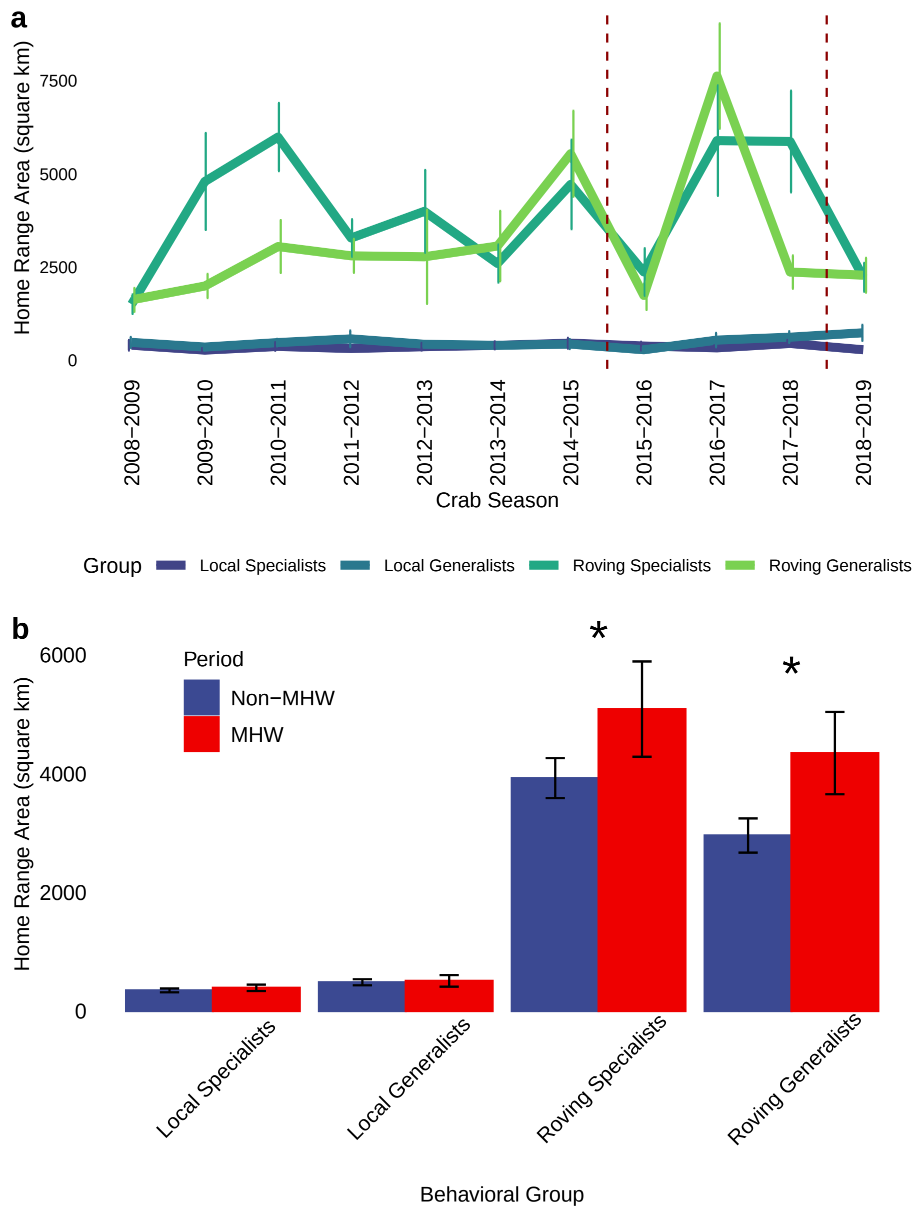

Figure 4: Home range (fishing area) size for vessels in the analysis. (a) Seasonal mean home range area in square kilometers (+/- 2SE) for vessels in each behavioral group. Vertical lines delineate the period of the MHW. (b) Barplot of mean home range area (+/- 2SE) for vessels in each group during MHW and non-MHW seasons. Stars indicate groups with significantly different home range size during MHW seasons.

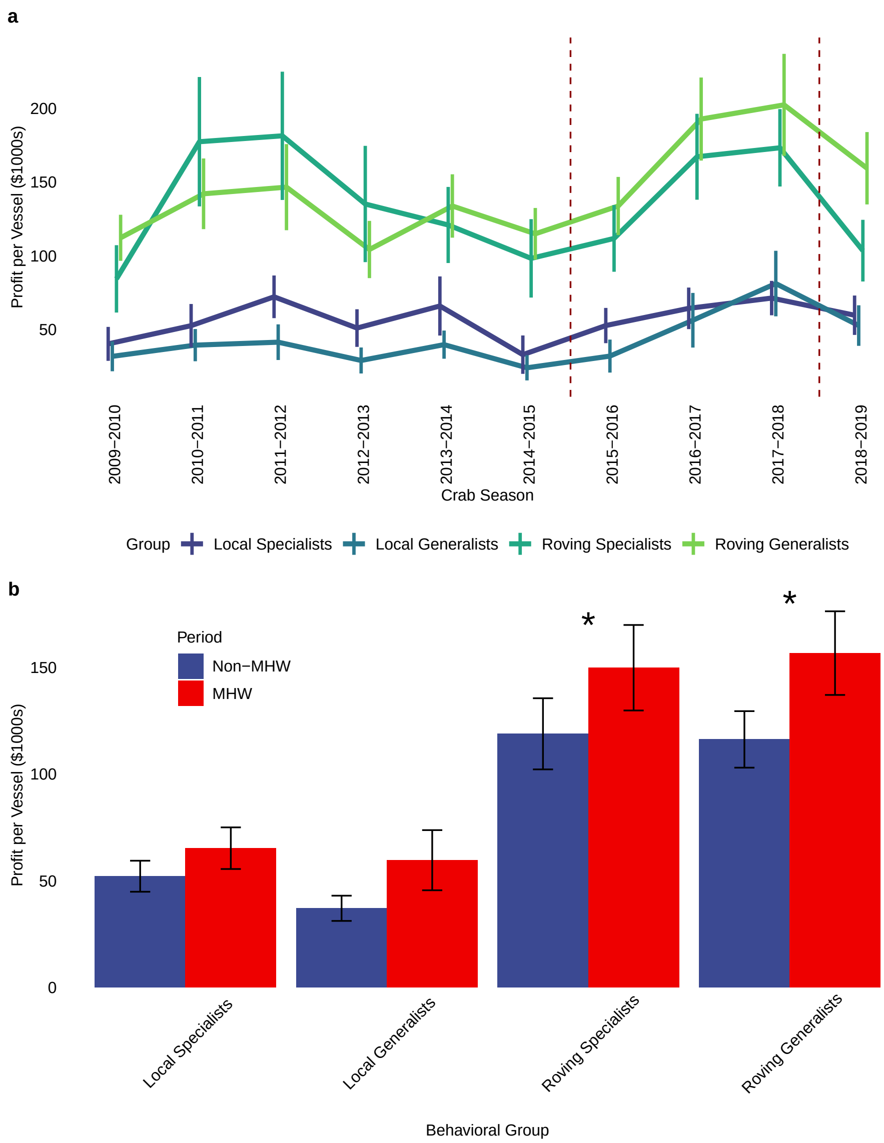

Figure 5: Estimated profits by behavioral group. (a) Mean profit (+/- 2 SE) for vessels in each behavioral group over the full crab season. Vertical lines delineate the period of the marine heatwave. (b) Mean profit (+/- 2 SE) for each group in heatwave (MHW) versus non-MHW seasons. Stars indicate groups with significantly different estimated profits during MHW seasons.

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