

Mobility and flexibility enable resilience of human harvesters to environmental perturbation

Abstract

Characteristics of natural resources that enable sustainable management are often more fully understood than the adaptive behaviors of human harvesters in those same systems. Given increasing environmental variability due to 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 \$2 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 experienced the greatest losses driven by the heatwave. 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, and can inform management in other social-ecological systems in which human harvester dynamics are poorly understood.

1. Introduction

Sustainability in social-ecological systems—the continued provision of human and ecological benefits from healthy ecosystems (Leslie et al., 2015)—requires resilience to environmental perturbations. Often, though, people respond to environmental change in diverse and complex ways. Just as multiple species occupying similar ecological niches may react differently to physical changes in their environments (Elmqvist et al., 2003), human actors in a social-ecological system can exhibit diverse behaviors within the constraints imposed by the governance system (McGinnis and Ostrom, 2014). Groups of resource users with distinct livelihood portfolios, available capital, or spatial patterns of resource extraction will not respond the same way to environmental or management changes (Young et al., 2019). In response to change, some users might stick to established knowledge and reliable spatial patterns of exploitation, while others might employ more exploratory strategies that carry higher potential upsides but also higher risks and costs. Understanding the adaptive behaviors of resource

19 users is all the more important given the increasing prevalence of extreme climate
20 events attributable to climate change (Abatzoglou et al., 2019; Cook et al., 2018;
21 Oliver et al., 2018; Townhill et al., 2018), but empirical evidence making the
22 link between climate extremes and contemporaneous human adaptation remains
23 lacking.

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

34 Additionally, different behavioral segments of fishing fleets may respond in
35 different ways to management measures, or may be differentially vulnerable to
36 environmental perturbations (Salas and Gaertner, 2004). For example, O’Farrell,
37 Sanchirico, et al. (2019) found that more exploratory fishing vessels—those that,
38 on average, traveled further and more often traversed new fishing grounds—were
39 better able to cope with an extended spatial closure. These fisher responses,
40 however, are difficult to study, despite the potential impact of differential behav-
41 ioral responses on resource dynamics. Partly, this is due to a lack of detailed
42 spatial and economic information on harvester behavior. However, recent years
43 have seen a rise in availability of these types of fishery data, paired with methods
44 to extract behavioral insights from them (Joo et al., 2015; Mendo et al., 2019;
45 Watson and Haynie, 2016). In the following, we apply a range of data-driven
46 methods to ask: how did human harvesters cope with and adapt to a major
47 environmental perturbation in the most valuable fishery on the U.S. west coast?

48 The Dungeness crab fishery on the west coast of the United States often
49 obtains in excess of \$200 million in revenue from over 1,000 participating vessels
50 each year (Rasmuson, 2013; Richerson et al., 2020). It is a fishery that is central
51 both ecologically (Santora et al., 2020) and economically (Fuller et al., 2017) to
52 the west coast social-ecological system, making it at once a safety valve within
53 fishers’ portfolios and a source of complexity in fisheries governance (Holland and
54 Leonard, 2020; Holland et al., 2017). The Dungeness crab fishery appears able to
55 withstand immense fishing pressure, and although crab abundance can fluctuate
56 markedly from year to year, long term abundance has been relatively stable for
57 more than a half century (Richerson et al., 2020). The fishery represents aspects
58 of both industrial and small-scale fisheries: Dungeness crabs are commercially
59 harvested by vessels with a significant range of sizes (in our data, 21 to 103 feet),
60 operating out of both large and small fishing ports across the U.S. west coast.

61 Recent environmental shocks have challenged the social sustainability of the
62 Dungeness crab fishery. In 2014-2016, a record marine heatwave (MHW) led to a
63 harmful algal bloom of unprecedented scale (McCabe et al., 2016), causing toxin
64 levels in Dungeness crabs to reach levels dangerous for human consumption and

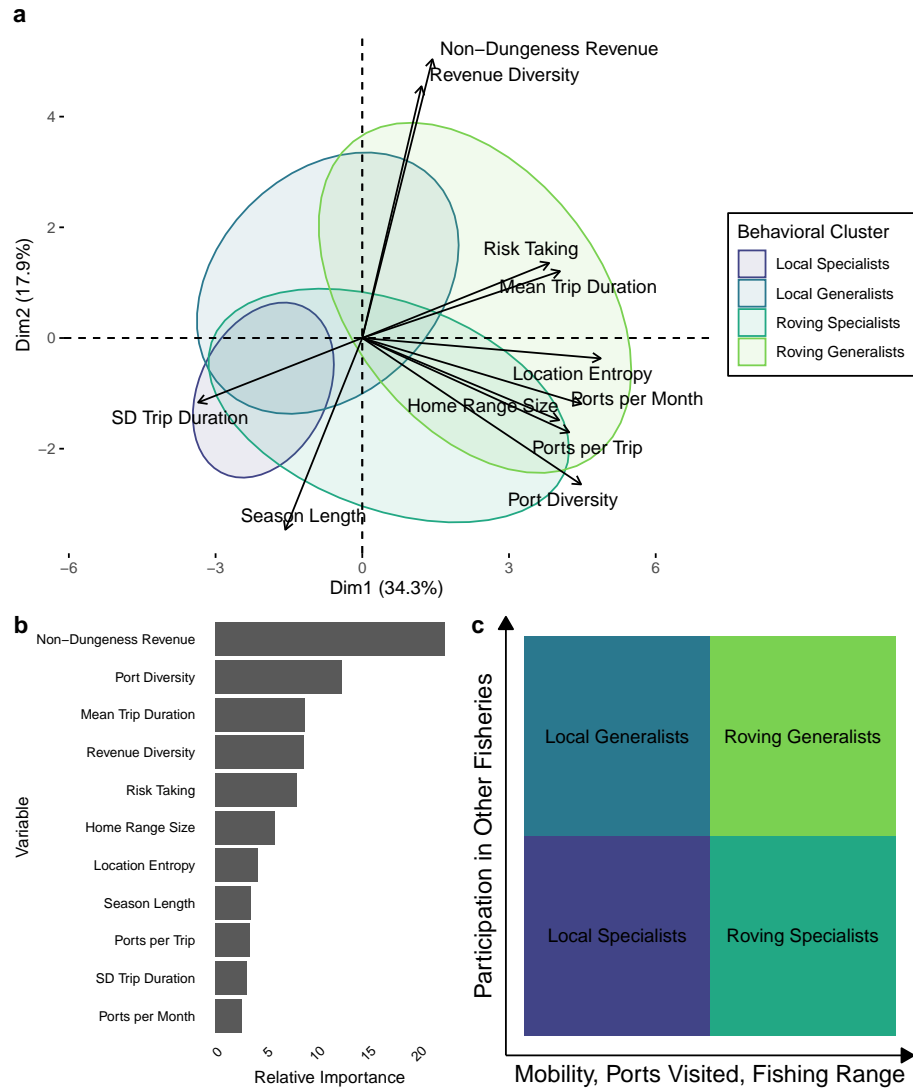


Figure 1: Data-driven formation of fishing behavioral groups. (a) Principal component analysis of vessel-seasons. Clusters of vessel-seasons, which determine behavioral groups, are enclosed by ellipses. Arrows represent the association between metrics in the cluster analysis relative to the placement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

65 correspondingly lengthy delays in large regions of the coast in the 2015-16 and
66 2016-17 Dungeness fishing seasons. Concurrently, the MHW caused shoreward
67 compression of the preferred feeding habitat of large whales, contributing to a
68 rise in entanglements of whales in Dungeness crab fishing gear and increasing risk
69 of fishery closure due to marine mammal interactions, effects that continued to
70 directly affect fishery closures through the 2017-18 Dungeness crab season (Feist
71 et al., 2021; Santora et al., 2020). During this period, Dungeness crab fishers had
72 to contend with significant ecological changes and with the management measures
73 those changes precipitated. Like with climate extremes in other systems(Loon
74 et al., 2016), the effects of this MHW were complex, reverberated through the
75 social-ecological system, and persisted for years after the anomalous warming
76 dissipated(Fisher et al., 2021; Smale et al., 2019; Suryan et al., 2021). While
77 much recent literature is dedicated to examination of biophysical and ecological
78 impacts of the MHW (Biela et al., 2019; McCabe et al., 2016), to date far less
79 attention has been given to exploring how social systems cope and change with
80 these perturbations(Fisher et al., 2021; Jardine et al., 2020).

81 In this study, we compare the adaptive responses of behavioral groups within
82 the Dungeness crab fishery to the multi-year MHW that directly affected the 2015-
83 16 through 2017-18 Dungeness crab seasons. The 2015-16 Dungeness crab season
84 was the first season to be significantly delayed as a direct result of ecosystem
85 changes, a trend that continued through the 2017-18 season. While previous work
86 has investigated economic impacts(Holland and Leonard, 2020; Jardine et al.,
87 2020) and changes in fishery participation due to the MHW-associated harmful
88 algal bloom(Fisher et al., 2021), here we explicitly investigate and quantify
89 fishers' adaptive spatial behaviors in response to the MHW more broadly and
90 for the full three-year period over which the MHW impacts manifested. Using a
91 10-year time-series of more than 2 million satellite-derived fishing vessel location
92 records, linked to fishery revenue and landings data, we derive quantitative
93 behavioral metrics describing space use and mobility of Dungeness crab vessels,
94 then organize these behaviors into characteristic behavioral groups. We explore
95 the overlap of spatial behaviors with profitability, fishing season length, and
96 revenue diversity. We track these behavioral groups over time, and identify key
97 behavioral metrics that promoted adaptation during and after the MHW. This
98 analysis therefore offers insights into the types of adaptive behaviors that may
99 promote sustainable outcomes for human harvesters in social-ecological systems
100 more broadly.

101 2. Materials and Methods

102 2.1. Data sources

103 We used satellite-based Vessel Monitoring System (VMS) data and port
104 level fishery landings data to define most of the behavioral variables used in
105 the study. The VMS database is maintained by the National Marine Fisheries
106 Service's Office of Law Enforcement, and records the positions of vessels at
107 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, Chollett, et al., 2019; 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 state (California, Oregon, or Washington). Oregon has the highest relative VMS representation, followed by California, then Washington.

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 on the individual fish ticket were at least 10 percent greater than the landed weight of the next greatest species.

We joined the fish ticket data to the VMS data through unique vessel identification numbers and timestamps. 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 trips in which the final VMS data point for a trip was greater than 50km from the port of landing recorded on the ticket. 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.

Dungeness crab fishing seasons on the west coast typically begin in the middle of November (for Central California) or beginning of December (for Northern California, Oregon, and Washington), but can be variable in their starting dates, depending on state (California, Oregon, or Washington), harmful algal bloom closures, price and market conditions, crab condition and meat quality, and potential interactions with protected species like humpback whales. Therefore, we used a data-driven approach to define the start date for each crab season in each of the 20 fishing port groups on the west coast. Port groups are defined by PacFIN and include clusters of small, neighboring fishing ports. For each port group in each season, we found the date after October 31 of each season that the total Dungeness crab landings into that port reached 1 percent of the eventual, season-long landings. This approach identifies the realized start date of the crab fishery in each portion of the coast in each year.

The maximum length of a Dungeness fishing trip was defined as seven days (S. Jardine, pers. comm.). That is, if there was a gap of greater than seven days between consecutive tickets, the VMS geolocations greater than seven days prior to the landed ticket were discarded. The final dataset comprises a clean record of geolocations associated with each Dungeness crab fishing trip.

The only other data source used in the calculation of behavioral metrics is a

measure of average daily wind speeds, from AVHRR Pathfinder satellite-derived measurements (<https://data.nodc.noaa.gov>; <https://doi.org/10.7289/v52j68xx>). The data are modelled daily on a 0.04 degree grid (approximately 5 km at the equator) and are available from 1981-present.

2.2. Construction of Fishing Behavioral Metrics

Fishing behavioral metrics were calculated from fish ticket, VMS, and wind speed data. Our choice of behavioral variables 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, Chollett, et al., 2019; O’Farrell, Sanchirico, et al., 2019; Pfeiffer and Gratz, 2016). Each of the fisher behavioral variables described one characteristic of a vessel’s apparent behavior over the course of a fishing season—a vessel-season. Vessel-season was unit of analysis used for clustering, and individual vessels could be clustered into different behavioral groups in different seasons. To determine whether a vessel would be included in the analysis, we calculated the total Dungeness crab revenue for each vessel in each season from 2008-09 to 2018-19. The 5th percentile for annual Dungeness revenue per vessel was \$5828. We retained all vessel-seasons with greater than \$5828 in revenue in any season (i.e., we retain the top 95 percent of all vessel-seasons as measured by revenue).

Our behavioral metrics fall into five general categories: port use, fishing trip characteristics, participation in other fisheries, risk-taking behavior, and exploration and mobility (see Table A.1 for full technical definitions of metrics). 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 (in km) and duration (in days).

Fishery participation metrics include season length, proportion of revenue and fish tickets from other (non-Dungeness) fisheries, and revenue diversity. The Dungeness fishery operates as a derby, where the majority of the landings and profits are obtained in the first few months of each season (Fig. A.4). Our season length metric captures this phenomenon and indicates the day of the crab season that each vessel reaches 90 percent of its cumulative landings for that season. To calculate the proportion of revenue and tickets from other fisheries, and revenue diversity, we use a version of the fish ticket data that includes all fishery targets (not just Dungeness crab). Using these tickets, the proportion of non-Dungeness revenue is calculated, as well as the proportion of fish tickets submitted by that vessel with a target other than Dungeness crab. Revenue diversity for each vessel-season is an inverse Simpson index calculated on the proportion of revenue obtained from each species in a vessel’s fishing portfolio.

Risk-taking behavior is modelled after the definition in Pfeiffer and Gratz (2016), who also studied west-coast fisheries, as propensity to fish in high-wind conditions. 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 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, and is calculated cumulatively across each vessel’s fishing season (O’Farrell, Sanchirico, et al., 2019). 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 repeatedly. The season-long metric for exploration for each vessel is defined as the 90th percentile of maximum location choice entropy in that season.

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

2.3. Cluster Analysis

All 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. Clustering was performed using Euclidean distances and Ward aggregation that minimizes total within-cluster variance. The number of clusters was determined using the Nbclust package in R (Charrad et al., 2014), which calculates 22 clustering 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 clusters 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 clusters from the previous step. Then, these random forests were used to predict withheld data. Variable importance was defined as the increase in the rate of mis-classification of vessel-seasons into clusters when the particular variable was randomly permuted.

2.4. Dungeness Fishing Profitability

We used fish ticket data to assess the per-trip, per-week, and per-season landings and revenue of vessels in each fisher behavioral group over time. Additionally, we modeled fishing costs following the approach of (Deweese et al., 2004) to assign an estimated profit to each fishing trip. The cost of a fishing trip C_t is assumed to be a function of fuel C_f and bait costs, and the costs of labor (i.e., crew) C_c :

$$C_t = C_f + C_c$$

243 Fuel and bait cost is a function of vessel size L and number of days fished d , as
 244 well as trip year y to adjust for an assumed 2 percent inflation rate.

$$C_f = f(L, d, y)$$

245 Crew cost is a function of vessel size (because larger vessels require more crew
 246 members) and total trip revenue R (since crew members receive a proportion of
 247 revenue).

$$C_c = f(L, R)$$

248 The above cost relationships were parameterized using data from Dewees
 249 et al. (2004), who administered a survey to 243 Dungeness crab fishers and
 250 compiled estimates of fishing costs by vessel size. The survey estimated costs
 251 associated with bait, fuel, and labor (crew) for small (less than 9.1m), medium
 252 (9.1-15.2 m) and large (greater than 15.2 m) fishing vessels. Using the means
 253 and standard deviations of these costs reported in Dewees et al. (2004), we
 254 simulated 10,000 trip costs for vessels ranging in length from 6.4 to 31.4 m,
 255 which is the range of vessel sizes in our data. Then, linear relationships between
 256 vessel size and both types of costs were estimated with simple linear regression.
 257 The resulting relationships,

$$C_f = d(150 + 3.5L) * 1.02^{y-2004}$$

$$C_c = R(0.17 + 0.0018L)$$

258 were used to deterministically assign a cost to each Dungeness fishing trip in
 259 our data. From there, a profit for each trip could be estimated by subtracting
 260 costs from revenue. Using trip-level profits, we calculated mean profits per week—
 261 across seasons—for vessels in each behavioral group, as well as season-long
 262 profits.

263 Using the fish ticket revenue data, we also calculated total revenue from all
 264 non-Dungeness fisheries for each vessel-season in the analysis. We constrained
 265 the calculation of non-Dungeness revenue to only those fishing trips that occurred
 266 within each vessel's apparent Dungeness season (that is, within the time period
 267 where the vessel was also landing Dungeness crab).

268 *2.5. Adaptation to the Marine Heatwave*

269 Using the results of cluster analyses, we compared key characteristics of
 270 behavioral groups in MHW versus non-MHW crab seasons. We defined the MHW
 271 as encompassing the crab fishing seasons from 2015-16 to 2017-18. Although
 272 there is evidence that the MHW began affecting west coast ecosystems as early
 273 as late 2014 (McCabe et al., 2016), the 2015-16 Dungeness crab season was the
 274 first to be significantly delayed as a direct result of ecosystem changes (Jardine
 275 et al., 2020), a trend that continued through the 2017-18 season.

Adopting this definition of the MHW period, we compared mean Dungeness profit, non-Dungeness revenue (i.e., external fishery revenue), and home range size over time among behavioral groups to assess potential adaptive strategies. For each of these three comparisons, we performed a two-way ANOVA to test for significant differences in means by behavioral group and period (non-MHW or MHW).

All analyses in the study were performed in R (R Core Team, 2021).

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 ~2.2 million satellite-derived Vessel Monitoring System (VMS) geolocations, and 315,000 fishery landing records. Using these combined data, we analyzed 11 behavioral variables 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 A.1).

The 3391 vessel-seasons in our data fell into four behavioral cluster 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 diversity of port use, revenue diversity, and mean trip duration (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. A vessel-season is therefore defined 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 marine heatwave (MHW) by increasing

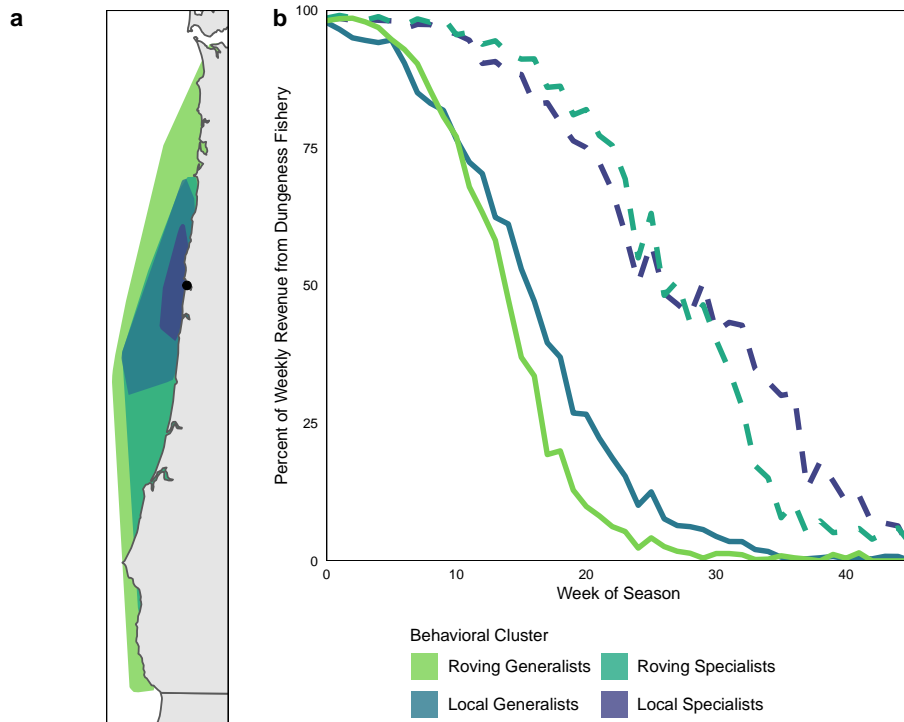


Figure 2: Characteristic patterns in spatial mobility and fishery flexibility across behavioral groups in the west coast Dungeness crab fishery, exemplified by an Oregon port. (a) Fishing footprints of each behavioral group across all seasons for vessels originating from the Port of Newport, Oregon,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

their dependence on other, non-Dungeness fisheries and expanding their fishing ranges. 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 not as substantial as for the Generalist groups (Table S2, ANOVA $p = 0.06$ for Roving Specialists, $p=0.99$ for Local Specialists).

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 S3, $p>0.99$ 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 (i.e., for those vessels that continued to fish), 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 cost, resulting in increased profits. Dungeness crab profits for all behavioral groups increased during the MHW, significantly so for Local Generalists ($p=0.05$), Roving Generalists ($p<.0001$) and Roving Specialists ($p=0.001$, Table A.4). The Roving Generalist group saw the largest increase in estimated profits in both raw and percent increase in profits (more than a \$63,000 increase per vessel, a 48 percent increase, on average). Local Specialists experienced the smallest increase in profits of all groups (25 percent) during the MHW, while Roving Specialists and Local Generalists experienced a greater than 40 percent increase. In the season after the dissipation of the MHW, estimated profits declined, particularly for the Roving groups.

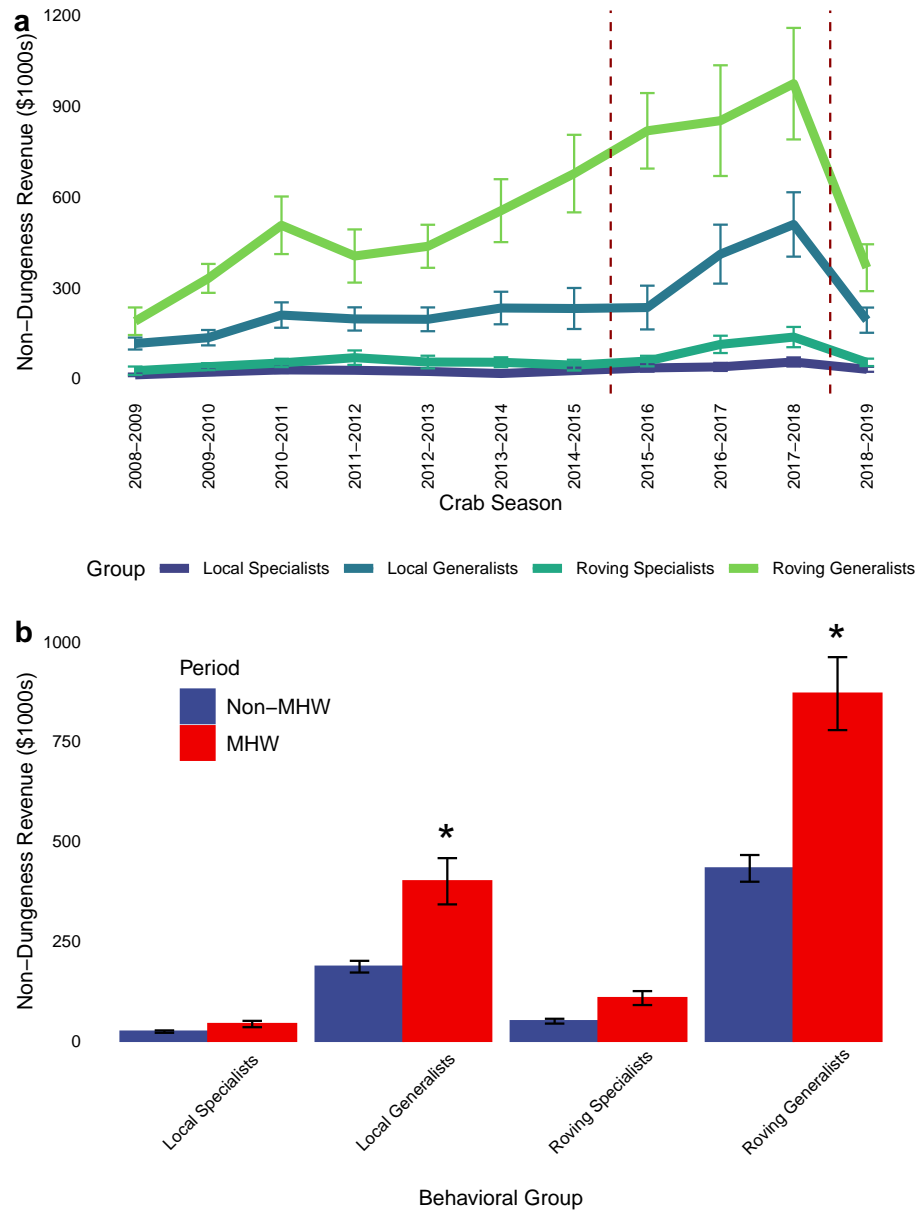


Figure 3: Non-Dungeness revenue for vessels in the analysis. (a) Seasonal mean revenue (\pm 2SE) for vessels in each behavioral group coming from all non-Dungeness fisheries combined. Vertical lines delineate the period of the marine heatwave (MHW). (b) Barplot of mean revenue (\pm 2SE) for vessels in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

4. Discussion

The pace and magnitude of environmental change 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 hunter-gatherer activities occurring at scale, commercial fisheries offer an important lens through which to understand human adaptations to novel and extreme conditions, with potential lessons for other natural resource harvesting contexts. The 2014-2016 MHW 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 may suggest pathways to improve adaptive capacity for human harvesters more broadly during an era in which the magnitude, frequency, and intensity of environmental perturbations are increasing.

Our work builds on research from the economics (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 minimize income risk through fishery-specific acumen, while generalists hedge against risk by building diverse portfolios (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 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 some Specialists and Generalists persisted through the MHW period, repeated environmental disruptions in the future that cause further seasonal

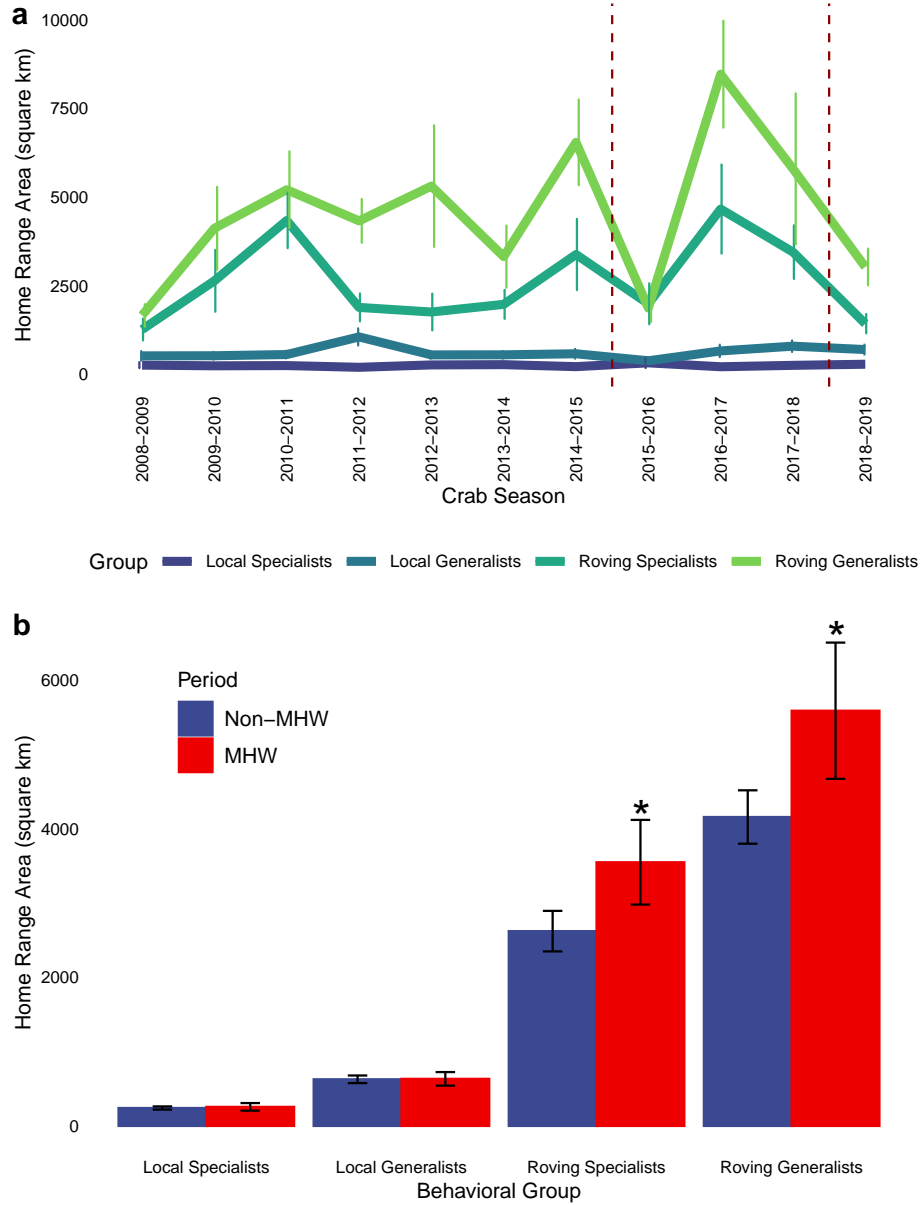


Figure 4: Home range (fishing area) size for vessels in the analysis. (a) Seasonal mean home range area in square kilometers (± 2 SE) for vessels in each behavioral group. Vertical lines delineate the period of the MHW. (b) Barplot of mean home range area (± 2 SE) for vessels in each group during MHW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

408 and spatial restrictions on the Dungeness crab fishery may begin to favor a
409 Generalist, diversified strategy. Within the US west coast context, existing fishery
410 governance systems may constrain this type of generalist adaptation (Kasperski
411 and Holland, 2013; Russell et al., 2018), but there are calls for “climate-ready”
412 fisheries that include the flexibility for fishers to move between fisheries (Wilson
413 et al., 2018). A better understanding of the social, economic, and cultural drivers
414 of fishers’ decisions to be specialists or generalists is a core component of a
415 sustainable livelihoods approach to small-scale fisheries management (Allison
416 and Ellis, 2001; Finkbeiner, 2015). Such an approach can also offer insights for
417 the design of regulatory approaches that facilitate resilience to environmental
418 perturbation in larger-scale fisheries and natural resource management contexts
419 (Salas and Gaertner, 2004).

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

438 Importantly, the nature of the data used in this study means that we studied
439 the behavior of the ‘survivors’—that is, the fishers who decided or were able to
440 remain in the Dungeness crab fishery during the MHW period. The MHW acted
441 as a selective force on Dungeness crab fishery participation. Many Dungeness
442 crab fishers during the 2016 and 2017 fishery closures chose (or were forced
443 by circumstance) to not participate in the fishery at all, instead opting to exit
444 fishing entirely or to re-concentrate all effort in alternative fisheries (Fisher et
445 al., 2021). Some of the relative success of the Dungeness crab fishers during the
446 MHW observed in this study, therefore, may be due to reduced competition, as
447 well as periods of supply shortages and high prices. Although outside the scope
448 of the current analysis, an important area for further research is to determine
449 how and why, when faced with an environmental perturbation, fishers choose to
450 remain or exit a fishery (Moore et al., 2020).

451 With climate change expected to increase the frequency of extreme environ-
452 mental perturbations like MHWs (Oliver et al., 2018), established patterns of
453 natural resource management and human harvester behavior will be challenged.

454 In our study, following multiple adaptive pathways by both diversifying and
 455 mobilizing appears to be one solution to an extreme environmental event and
 456 rapid management changes in the Dungeness crab fishery. Management mea-
 457 sures that restrict the fishery temporally or spatially—such as spatially-explicit
 458 biotoxin-related closures or early termination of the fishing season due to risk
 459 of interactions with protected or bycatch species—will differentially affect dis-
 460 tinct groups of fishers. Single-fishery specialists may thrive when the harvested
 461 resource is stable and productive, but these fishers may struggle to adapt if
 462 management measures restrict fishing season lengths. Likewise, localized fishers
 463 can thrive through intimate knowledge of fishing grounds, but if large-scale
 464 environmental perturbations have spatially-explicit negative effects, fishers with
 465 knowledge of a wider array of fishing grounds and greater mobility will naturally
 466 gain an advantage (O’Farrell, Sanchirico, et al., 2019). Over time, management
 467 context, or failures of management to adapt, can drive changes in the makeup
 468 of fishing fleets as a whole (Frawley et al., 2020). These changes are not in-
 469 herently negative, but in order to maintain the social, economic, and cultural
 470 benefits provided by a fishery, managers should endeavour to anticipate behav-
 471 ioral changes within fleets. More generally, these insights are congruent with
 472 an evolving understanding of adaptation in complex social-ecological systems
 473 (Lubchenco et al., 2016). Because complex systems are an emergent product of
 474 the individual actions of human actors, informed adaptive management requires
 475 an understanding of the drivers of behaviors like those identified in this study
 476 along with well-calibrated and nimble responses within governance systems.

477 For fishers and other human harvesters, future work using mixed methods
 478 from the social sciences like participatory mapping and semi-structured interviews
 479 (Frawley et al., 2020; Moore et al., 2020; Pellowe and Leslie, 2019; Ritzman et
 480 al., 2018) will provide complementary insights into the motivations and social
 481 drivers behind adaptive decisions. Furthermore, as integrated biophysical and
 482 socioeconomic data streams become increasingly available for environmental
 483 management (Bradley et al., 2019), data-driven, interdisciplinary studies of
 484 resilience and adaptation will enable dynamic management of natural resources
 485 (Hazen et al., 2018; Maxwell et al., 2015). This push for the incorporation of
 486 multiple data streams in environmental management extends beyond marine
 487 fisheries. For example, in wildland fire management in the United States,
 488 integrated data platforms that combine geospatial data with risk models and fuel
 489 treatment scenarios are leading to a more predictive and adaptable landscape
 490 and fire management plans (Ager et al., 2011; Krofcheck et al., 2018).

491 This study revealed the elements of behavioral diversity among human
 492 harvesters in a lucrative keystone fishery, and described how those elements
 493 enabled adaptation during an extreme environmental event attributable to
 494 climate change (Hinder et al., 2012). Just as biological response diversity can
 495 lead to enhanced ecosystem resilience to environmental change (Elmqvist et
 496 al., 2003), behavioral diversity among natural resource users may promote
 497 resilience of social-ecological systems. Given the impending increase in extreme
 498 climatic events such as marine heatwaves (Burge et al., 2014; Smale et al., 2019),
 499 recognition of social and ecological traits that enable resilience now can help to

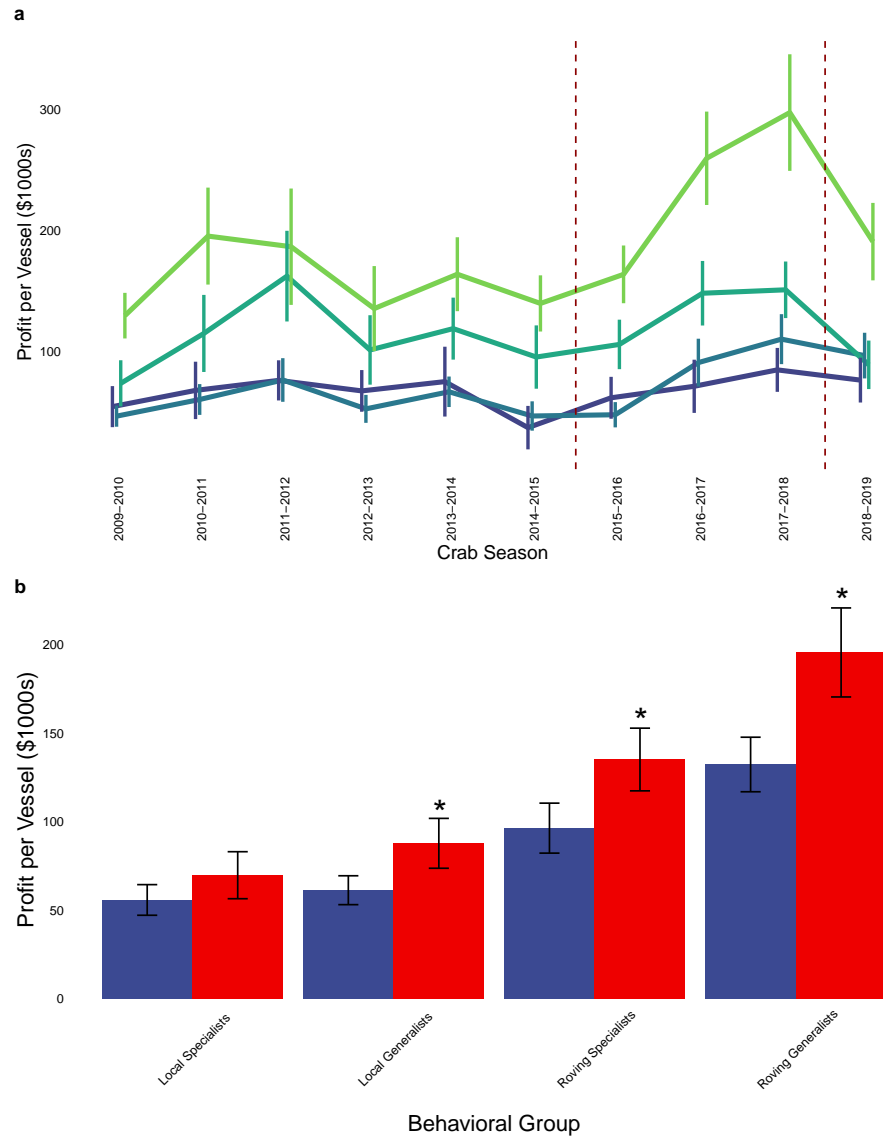


Figure 5: Estimated profits by behavioral group. (a) Mean profit (\pm 2 SE) for vessels in each behavioral group over the full crab season. Vertical lines delineate the period of the marine heatwave. (b) Mean profit (\pm 2 SE) for each group in heatwave (MHW) versus non-MHW seasons. Stars indicate groups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

500 build toward a more prepared future. Behavioral analyses like ours can be used
501 in the design of adaptive management measures, to bolster policy analyses, and
502 to inform decision-making under environmental uncertainty.

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