Mobility and flexibility enable resilience of human harvesters to environmental perturbation.

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Main text, including all main text figures

Supplemental tables and figures

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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, 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 adaptive, as it produced the greatest increase in profits. Our data-driven approach reveals behaviors that can be promoted to increase harvest sustainability and can inform management in other social-ecological systems in which human harvester dynamics are poorly understood.

climate change adaptation | environmental perturbation | marine heatwave | fisheries dynamics

Sustainability in social-ecological systems—the continued provision of human and ecological benefits from healthy ecosystems (1)—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 (2), human actors in a social-ecological system can exhibit diverse behaviors within the constraints imposed by the governance system (3). 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(4). 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 users is all the more important given the increasing prevalence of extreme climate events attributable to climate change (5–8), but empirical evidence making the link between climate extremes and contemporaneous human adaptation remains lacking.

Fisheries are a prominent example of a social-ecological system where complex links between resource user (harvester)behavior and natural resource dynamics drive sustainability(9). Fisheries represent the last large-scale wild harvest of food on Earth, but also one of the most traditional livelihoods in human history. Difficulties in achieving sustainability in fisheries have often been linked to an inadequate understanding of harvester dynamics(10, 11). Differences in fisher behaviors, both within and across fisheries, can affect the stability and sustainability of fish populations(12, 13) and of other species—for instance, endangered marine mammals or seabirds(14, 15).

Additionally, different behavioral segments of fishing fleets may respond in different ways to management measures, or may be differentially vulnerable to environmental perturbations (12). For example, (16) 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. These fisher responses, however, are difficult to study, despite the potential impact of differential behavioral responses on resource dynamics. Partly, this is 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 (17–19). 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 west coast of the United States often obtains in excess of $200 million in revenue from over 1,000 participating vessels each year(20, 21). It is a fishery that is central both ecologically (22) and economically (23) to the west coast social-ecological system, making it at once a safety valve within fishers' portfolios and a source of com-

Significance Statement

Large-scale environmental perturbations like heatwaves will likely become more common under climate change. Sustainability in social-ecological systems requires an understanding of behaviors that can promote resilience to these perturbations. We show how participants in a valuable fishery used spatial mobility and fishing portfolio diversification to buffer against negative effects of a record marine heatwave. Our data-driven approach combines satellite movement data with economic data to reveal adaptive behaviors, and can be used to inform the study of human harvesters dynamics in other social-ecological systems.

O.R.L., M.F., B.E.F., B.A., K.R., and J.F.S. designed research; O.R.L. and J.F.S. performed research and analyzed data; O.R.L., M.F., B.E.F., B.A., K.R., and J.F.S. wrote the paper.

The authors declare no conflict of interest.

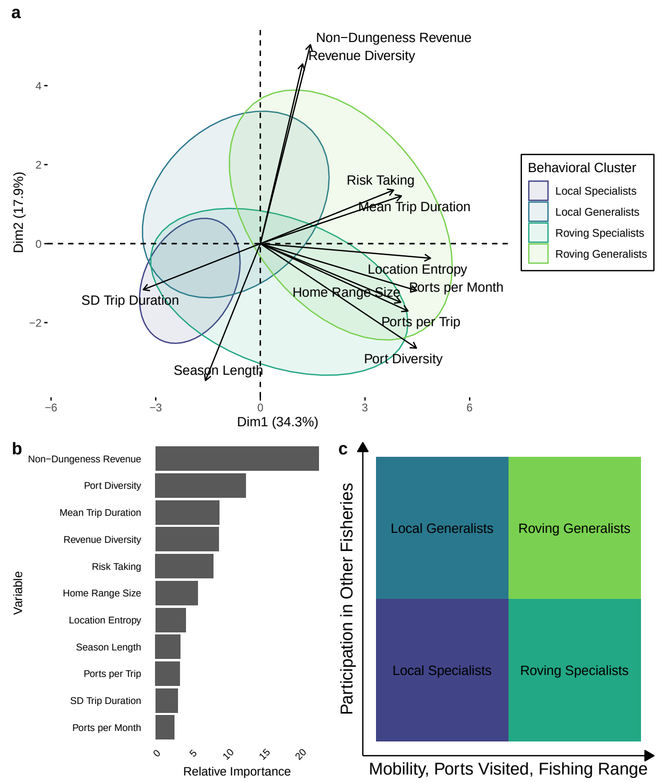

Fig. 1. Data-driven formation of fishing behavioral groups. (a) Principal component analysis of vessel-seasons. Clusters of vessel-seasons, which determine behavioral groups, are enclosed by ellipses. Arrows represent the association between metrics in the cluster analysis relative to the placement of 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.

plexity in fisheries governance(24, 25). The Dungeness crab fishery appears able to withstand immense fishing pressure, and although crab abundance can fluctuate markedly from year to year, long term abundance has been relatively stable for more than a half century (21).

However, recent environmental shocks have challenged the social sustainability of the Dungeness crab fishery. In 2014-2016, a record marine heatwave (MHW) led to a harmful algal bloom of unprecedented scale(26), causing toxin levels in Dungeness crabs to reach levels dangerous for human consumption and correspondingly lengthy delays in large regions of the coast in the 2015-16 and 2016-17 Dungeness fishing seasons. Concurrently, the MHW caused shoreward compression of the preferred feeding habitat of large whales, contributing to a rise in entanglements of whales in Dungeness crab fishing gear and increasing risk of fishery closure due to marine mammal interactions, effects that continued to directly affect fishery closures through the 2017-18 Dungeness crab season (22, 27). During this period, Dungeness crab fishers had to contend with significant ecological changes and with the management measures those changes precipitated. Like with climate extremes in other systems(28), the effects of this MHW were complex, reverberated through the social-ecological system, and persisted for years after the anomalous warming dissipated(29, 30). While much recent literature is dedicated to examination of biophysical and ecological impacts of the MHW (26, 32), to date far less attention has been given to exploring how social systems cope and change with these perturbations(33).

In this study, we compare the adaptive responses of behavioral groups within the Dungeness crab fishery to the multi-year MHW that directly affected the 2015-16 through 2017-18 Dungeness crab seasons. The 2015-16 Dungeness crab season was the first season to be significantly delayed as a direct result of ecosystem changes, a trend that continued through the 2017-18 season. While previous work has investigated economic impacts(25, 33) and changes in fishery participation due to the MHW-associated harmful algal bloom(31), here we explicitly investigate and quantify fishers' adaptive spatial behaviors in response to the MHW more broadly and for the full three-year period over which the MHW impacts manifested. 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, then organize these behaviors 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 and after the MHW. This analysis therefore offers insights into the types of adaptive behaviors that may promote sustainable outcomes for human harvesters in social-ecological systems more broadly.

Results.

Describing Fisher Behavior. We characterized fisher behavior using variables derived from vessel telemetry and fisheries landings data. The combined dataset based on 596 different vessels spanned 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 S1). Our choice of behavioral variables to calculate was driven by previous evidence of the importance of each variable in describing fisher behavioral patterns(16, 23, 34, 35). 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.

Using a hierarchical clustering algorithm (see Methods), we found that the 3391 vessel-seasons in our data fell into four behavioral cluster groups (Fig. 1a). The most important discriminating variables driving the clustering 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

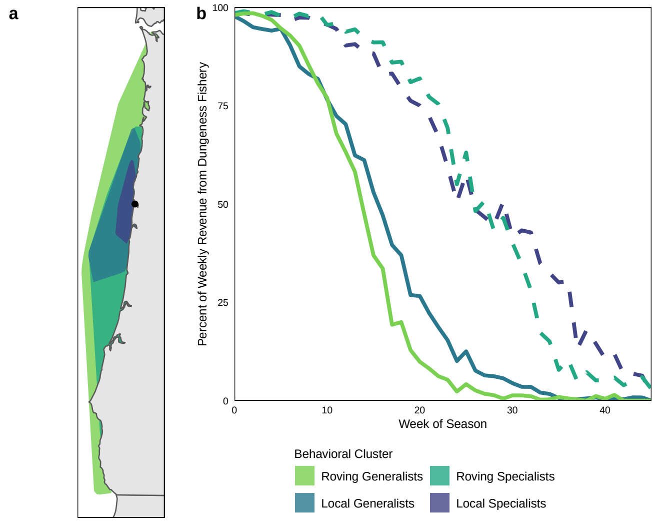

Fig. 2. Characteristic patterns in spatial mobility and fishery flexibility across behavioral groups in the west coast Dungeness crab fishery, exemplified by an Oregon port. (a) Fishing footprints of each behavioral group across all seasons for vessels originating from the Port of Newport, Oregon, USA. 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.

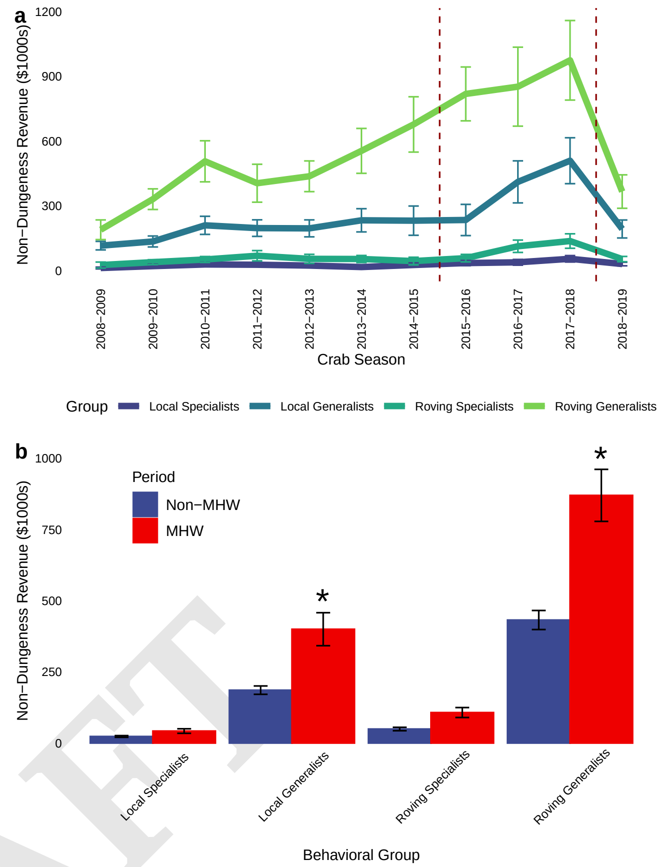

Fig. 3. Non-Dungeness revenue for vessels in the analysis. (a) Seasonal mean revenue (+/- 2SE) for vessels in each behavioral group coming from all non-Dungeness fisheries combined. Vertical lines delineate the period of the marine heatwave (MHW). (b) Barplot of mean revenue (+/- 2SE) for vessels in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

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).

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 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)(31, 37). 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.

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. To address this question, we modeled costs of fishing for Dungeness crab based on vessel size and trip length (see Methods). Our fishing cost model provides an estimation of Dungeness crab profit (reported

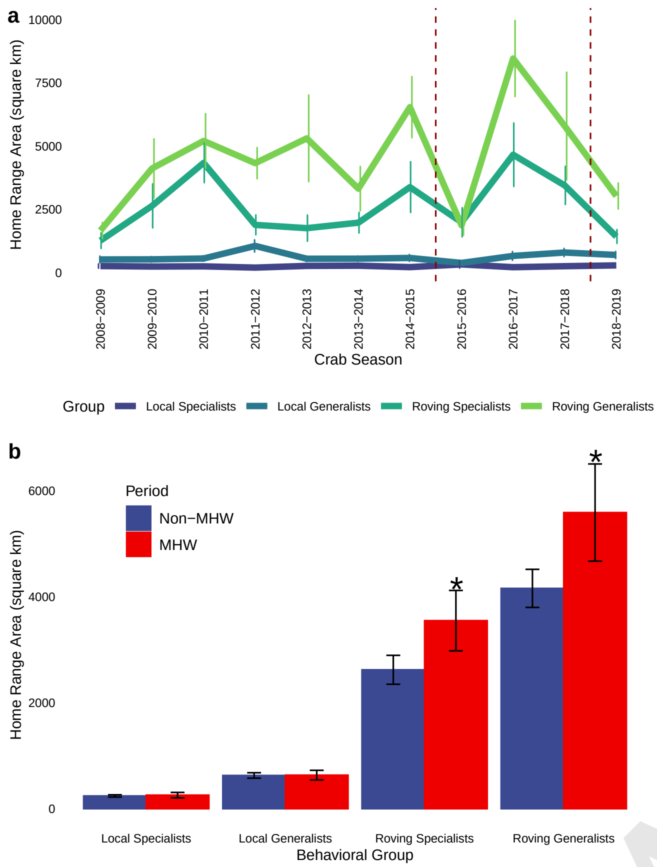

Fig. 4. Home range (fishing area) size for vessels in the analysis. (a) Seasonal mean home range area in square kilometers (+/- 2SE) for vessels in each behavioral group. Vertical lines delineate the period of the MHW. (b) Barplot of mean home range area (+/- 2SE) for vessels in each group during MHW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

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 S4). 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.

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 (38). 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 (37). 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.

The relative ability of specialists and generalists to cope with environmental change has been investigated in the economics (39), evolution (40), and ecology (41) literatures. The cross-disciplinary consensus is that generalists may adapt better to increasingly variable environments. Smith and McKelvey (1986)(39) 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(42). 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(41). While management dynamics, markets, stochastic resource abundance, and conditions in other fisheries are complicating factors (37), 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 and spatial restrictions on the Dungeness crab fishery may begin to favor a Generalist strategy. Within the US west coast context, existing fishery governance systems may constrain this type of generalist adaptation (43), but there are calls for "climate-ready" fisheries that include the flexibility for fishers to move between fisheries (44). 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 (45). Such an approach can also offer insights for the design of regulatory approaches that facilitate resilience to environmental perturbation in larger-scale fisheries and natural resource management contexts (12).

Diversification of fishery revenue was not the only axis of

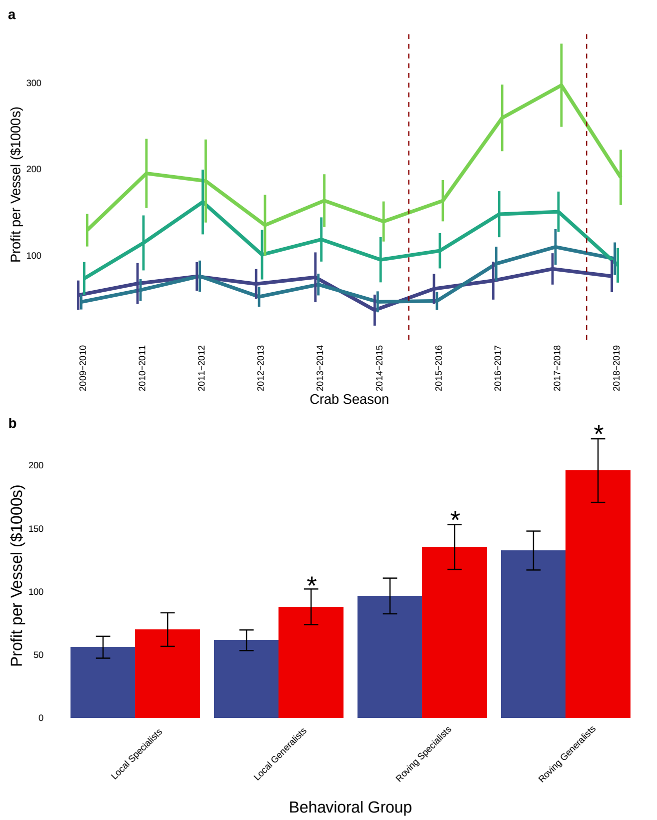

Fig. 5. Estimated profits by behavioral group. (a) Mean profit (+/- 2 SE) for vessels in each behavioral group over the full crab season. Vertical lines delineate the period of the marine heatwave. (b) Mean profit (+/- 2 SE) for each group in heatwave (MHW) versus non-MHW seasons. Stars indicate groups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

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 (46–48), 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 marine heatwave. 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 systems(16), 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 (49).

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. 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 (31). 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. 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 (50).

With climate change expected to increase the frequency of extreme environmental perturbations like MHWs (6), 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 solution 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 (16). Over time, management context, or failures of management to adapt, can drive changes in the makeup of fishing fleets as a whole (47). 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. More generally, these insights are congruent with an evolving understanding of adaptation in complex social-ecological systems (38). Because complex systems are an emergent product of the individual actions of human actors, 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.

For fishers and other human harvesters, future work using mixed methods from the social sciences like participatory mapping and semi-structured interviews (50, 51) will provide complementary insights into the motivations and social drivers behind adaptive decisions. Furthermore, as integrated biophysical and socioeconomic data streams become increasingly available for environmental management (53), data-driven, interdisciplinary studies of resilience and adaptation will enable dynamic management of natural resources (54, 55). 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 leading to a more predictive and adaptable landscape and fire management plans (56, 57).

This study revealed the elements of behavioral diversity among human harvesters in a lucrative keystone fishery, and described how those elements enabled adaptation during an extreme environmental event attributable to climate change (58). Just as biological response diversity can lead to enhanced ecosystem resilience to environmental change (2), behavioral diversity among natural resource users may promote resilience of social-ecological systems. Given the impending increase in extreme climatic events such as marine heatwaves (29, 59), recognition of social and ecological traits that enable resilience now can help to build toward a more prepared future. Behavioral analyses like ours can be used in the design of adaptive management measures, to bolster policy analyses, and to inform decision-making under environmental uncertainty.

Materials and Methods.

Data sources. We used satellite-based Vessel Monitoring System (VMS) data and port level fishery landings data to define most of the behavioral variables. 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 (17, 18, 27, 34). 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/cgi-bin/iso?id=gov.noaa.nodc:AVHRR_Pathfinder-NCEI-L3C-v5.3#, 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.

Construction of Fishing Behavioral Metrics. Fishing behavioral metrics were calculated from fish ticket, VMS, and wind speed data. The unit of analysis used for clustering was vessel-season. Therefore, 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 Supplementary Information 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. S5). 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 (36).

Exploration and mobility were measured with home range and location choice entropy, adopting the definitions in O'Farrell et al. (2019)(16). 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 (16). 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 Supplementary Information.

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, 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 (60). 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.

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 (61) 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:

$$C_t = C_f + C_c$$

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

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

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

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

The above cost relationships were parameterized using data from Dewees et al. (2004) (61), who administered a survey to 243 Dungeness crab fishers and compiled estimates of fishing costs by vessel size. The survey estimated costs associated with bait, fuel, and labor (crew) for small (less than 9.1m), medium (9.1-15.2 m) and large (greater than 15.2 m) fishing vessels. Using the means and standard deviations of these costs reported in Dewees et al. (2004) (61), we simulated 10,000 trip costs for vessels ranging in length from 6.4 to 31.4 m, which is the range of vessel sizes in our data. Then, linear relationships between vessel size and both types of costs were estimated with simple linear regression. The resulting relationships,

$$C_f = d(150 + 3.5L) * 1.02^{y-2004}$$
$$C_c = R(0.17 + 0.0018L)$$

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

Using the fish ticket revenue data, 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).

Adaptation to 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 late 2014 (26), the 2015-16 Dungeness crab season was the first to be significantly delayed as a direct result of ecosystem changes (33), 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(62). All code and reproducible analyses are included in the Supplementary Information.

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Supplemental Information

Supplementary Table 1. Fisher behavioral and demographic variables 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.

Category	Variable	Definition
Port Use	Ports per Trip	Average ports visited per trip
	Ports per Month	Number of ports visited per month
	Port Diversity	Shannon 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	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

7

Supplementary Table 2. Tukey's honest significant difference analysis on seasonal non-Dungeness crab revenue per vessel, corresponding to Figure 3b in the main text. MHW: marine heatwave period; Non-MHW: non-marine heatwave period. Bolded rows are within-behavioral-group, between-period comparisons. Of these within-group comparisons, differences with a p-value<0.05 are indicated with stars in Fig. 3b.

Group 1	**Group 2**	**Difference**	**Lower**	**Upper**	**Adjusted p-value**
MHW:Local Specialists	**Non-MHW:Local Specialists**	**19014**	**-51710**	**89738**	**0.992**
Non-MHW:Local Generalists	Non-MHW:Local Specialists	162616	114336	210897	0.000
MHW:Local Generalists	Non-MHW:Local Specialists	376497	311019	441974	0.000
Non-MHW:Roving Specialists	Non-MHW:Local Specialists	26136	-27947	80219	0.826
MHW:Roving Specialists	Non-MHW:Local Specialists	83978	21786	146169	0.001
Non-MHW:Roving Generalists	Non-MHW:Local Specialists	408766	352788	464743	0.000
MHW:Roving Generalists	Non-MHW:Local Specialists	846315	773088	919542	0.000
Non-MHW:Local Generalists	MHW:Local Specialists	143602	80018	207187	0.000
MHW:Local Generalists	MHW:Local Specialists	357483	280027	434938	0.000
Non-MHW:Roving Specialists	MHW:Local Specialists	7122	-60974	75217	1.000
MHW:Roving Specialists	MHW:Local Specialists	64964	-9734	139662	0.143
Non-MHW:Roving Generalists	MHW:Local Specialists	389751	320141	459361	0.000
MHW:Roving Generalists	MHW:Local Specialists	827301	743193	911410	0.000
MHW:Local Generalists	**Non-MHW:Local Generalists**	**213880**	**156187**	**271574**	**0.000**
Non-MHW:Roving Specialists	Non-MHW:Local Generalists	-136481	-180822	-92139	0.000
MHW:Roving Specialists	Non-MHW:Local Generalists	-78639	-132573	-24704	0.000
Non-MHW:Roving Generalists	Non-MHW:Local Generalists	246149	199515	292783	0.000
MHW:Roving Generalists	Non-MHW:Local Generalists	683699	617341	750057	0.000
Non-MHW:Roving Specialists	MHW:Local Generalists	-350361	-412991	-287731	0.000

MHW:Roving Specialists	MHW:Local Generalists	-292519	-362271	-222768	0.000
Non-MHW:Roving Generalists	MHW:Local Generalists	32269	-32004	96542	0.795
MHW:Roving Generalists	MHW:Local Generalists	469819	390071	549566	0.000
MHW:Roving Specialists	**Non-MHW:Roving Specialists**	**57842**	**-1344**	**117027**	**0.061**
Non-MHW:Roving Generalists	Non-MHW:Roving Specialists	382630	330012	435248	0.000
MHW:Roving Generalists	Non-MHW:Roving Specialists	820180	749488	890872	0.000
Non-MHW:Roving Generalists	MHW:Roving Specialists	324788	263866	385709	0.000
MHW:Roving Generalists	MHW:Roving Specialists	762338	685266	839410	0.000
MHW:Roving Generalists	**Non-MHW:Roving Generalists**	**437550**	**365398**	**509702**	**0.000**

Supplementary Table 3. Tukey's honest significant difference analysis on seasonal home range size (in square km) per vessel, corresponding to Figure 4b in the main text. MHW: marine heatwave period; Non-MHW: non-marine heatwave period. Bolded rows are within-behavioral-group, between-period comparisons. Of these within-group comparisons, differences with a p-value<0.05 are indicated with stars in Fig. 4b.

Group 1	Group 2	Difference	Lower	Upper	Adjusted p-value
MHW:Local Specialists	**Non-MHW:Local Specialists**	**14.9**	**-924.2**	**954.1**	**1.000**
Non-MHW:Local Generalists	Non-MHW:Local Specialists	386.0	-231.0	1003.0	0.553
MHW:Local Generalists	Non-MHW:Local Specialists	391.9	-489.3	1273.1	0.880
Non-MHW:Roving Specialists	Non-MHW:Local Specialists	2378.2	1734.2	3022.3	0.000
MHW:Roving Specialists	Non-MHW:Local Specialists	3305.1	2545.8	4064.3	0.000
Non-MHW:Roving Generalists	Non-MHW:Local Specialists	3913.4	3248.4	4578.4	0.000
MHW:Roving Generalists	Non-MHW:Local Specialists	5342.7	4494.1	6191.3	0.000
Non-MHW:Local Generalists	MHW:Local Specialists	371.1	-492.1	1234.2	0.898
MHW:Local Generalists	MHW:Local Specialists	376.9	-691.1	1445.0	0.963
Non-MHW:Roving Specialists	MHW:Local Specialists	2363.3	1480.6	3246.0	0.000
MHW:Roving Specialists	MHW:Local Specialists	3290.1	2320.2	4260.1	0.000
Non-MHW:Roving Generalists	MHW:Local Specialists	3898.5	3000.4	4796.6	0.000
MHW:Roving Generalists	MHW:Local Specialists	5327.8	4286.4	6369.2	0.000
MHW:Local Generalists	**Non-MHW:Local Generalists**	**5.9**	**-793.8**	**805.6**	**1.000**
Non-MHW:Roving Specialists	Non-MHW:Local Generalists	1992.3	1465.2	2519.3	0.000
MHW:Roving Specialists	Non-MHW:Local Generalists	2919.1	2256.1	3582.0	0.000
Non-MHW:Roving Generalists	Non-MHW:Local Generalists	3527.4	2974.9	4079.9	0.000
MHW:Roving	Non-MHW:Local	4956.7	4193.0	5720.4	0.000

Generalists	Generalists				
Non-MHW:Roving Specialists	MHW:Local Generalists	1986.4	1165.6	2807.1	0.000
MHW:Roving Specialists	MHW:Local Generalists	2913.2	1999.3	3827.1	0.000
Non-MHW:Roving Generalists	MHW:Local Generalists	3521.6	2684.3	4358.8	0.000
MHW:Roving Generalists	MHW:Local Generalists	4950.8	3961.4	5940.3	0.000
MHW:Roving Specialists	**Non-MHW:Roving Specialists**	**926.8**	**238.6**	**1615.0**	**0.001**
Non-MHW:Roving Generalists	Non-MHW:Roving Specialists	1535.2	952.6	2117.7	0.000
MHW:Roving Generalists	Non-MHW:Roving Specialists	2964.5	2178.8	3750.2	0.000
Non-MHW:Roving Generalists	MHW:Roving Specialists	608.4	-99.4	1316.2	0.154
MHW:Roving Generalists	MHW:Roving Specialists	2037.7	1155.1	2920.2	0.000
MHW:Roving Generalists	**Non-MHW:Roving Generalists**	**1429.3**	**626.3**	**2232.2**	**0.000**

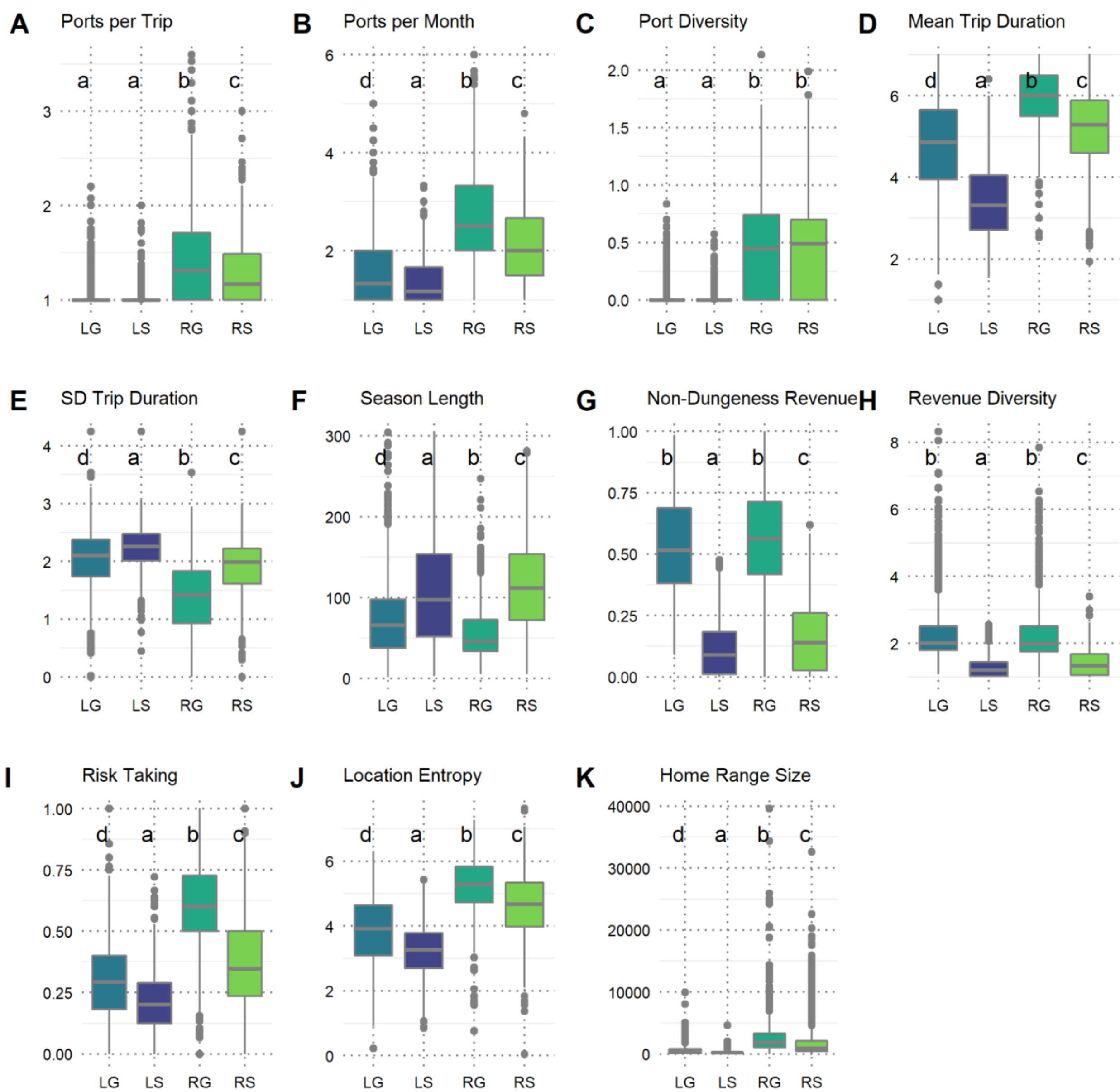
Supplementary Table 4. Tukey's honest significant difference analysis on seasonal profit per vessel, corresponding to Figure 5b in the main text. MHW: marine heatwave period; Non-MHW: non-marine heatwave period. Bolded rows are within-behavioral-group, between-period comparisons. Of these within-group comparisons, differences with a p-value<0.05 are indicated with stars in Fig. 5b.

Group 1	Group 2	Difference	Lower	Upper	Adjusted p-value
MHW:Local Specialists	**Non-MHW:Local Specialists**	**6532**	**-20938**	**34003**	**0.996**
Non-MHW:Local Generalists	Non-MHW:Local Specialists	-2143	-21592	17305	1.000
MHW:Local Generalists	Non-MHW:Local Specialists	20129	-5354	45613	0.244
Non-MHW:Roving Specialists	Non-MHW:Local Specialists	41291	19782	62800	0.000
MHW:Roving Specialists	Non-MHW:Local Specialists	71946	47704	96187	0.000
Non-MHW:Roving Generalists	Non-MHW:Local Specialists	96469	73885	119054	0.000
MHW:Roving Generalists	Non-MHW:Local Specialists	161547	133127	189966	0.000
Non-MHW:Local Generalists	MHW:Local Specialists	-8676	-33416	16064	0.964
MHW:Local Generalists	MHW:Local Specialists	13597	-16123	43317	0.863
Non-MHW:Roving Specialists	MHW:Local Specialists	34759	8368	61149	0.002
MHW:Roving Specialists	MHW:Local Specialists	65413	36752	94075	0.000
Non-MHW:Roving Generalists	MHW:Local Specialists	89937	62663	117211	0.000
MHW:Roving Generalists	MHW:Local Specialists	155014	122742	187287	0.000
MHW:Local Generalists	**Non-MHW:Local Generalists**	**22273**	**-241**	**44787**	**0.055**
Non-MHW:Roving Specialists	Non-MHW:Local Generalists	43434	25544	61325	0.000
MHW:Roving Specialists	Non-MHW:Local Generalists	74089	52992	95186	0.000
Non-MHW:Roving Generalists	Non-MHW:Local Generalists	98613	79442	117783	0.000
MHW:Roving Generalists	Non-MHW:Local Generalists	163690	137900	189480	0.000
Non-MHW:Roving	MHW:Local Generalists	21161	-3154	45477	0.142

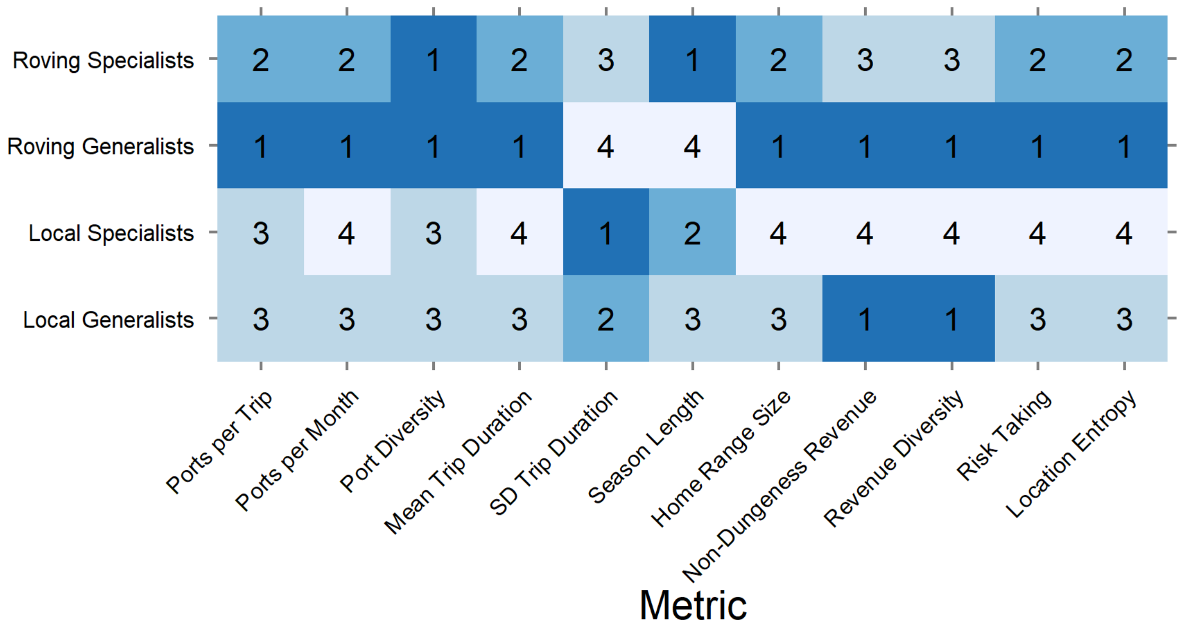
Specialists					
MHW:Roving Specialists	MHW:Local Generalists	51816	25053	78580	0.000
Non-MHW:Roving Generalists	MHW:Local Generalists	76340	51068	101612	0.000
MHW:Roving Generalists	MHW:Local Generalists	141417	110818	172016	0.000
MHW:Roving Specialists	**Non-MHW:Roving Specialists**	**30655**	**7644**	**53665**	**0.001**
Non-MHW:Roving Generalists	Non-MHW:Roving Specialists	55178	33921	76436	0.000
MHW:Roving Generalists	Non-MHW:Roving Specialists	120256	92879	147633	0.000
Non-MHW:Roving Generalists	MHW:Roving Specialists	24524	505	48543	0.041
MHW:Roving Generalists	MHW:Roving Specialists	89601	60029	119174	0.000
MHW:Roving Generalists	**Non-MHW:Roving Generalists**	**65077**	**36847**	**93308**	**0.000**

Supplementary Figures

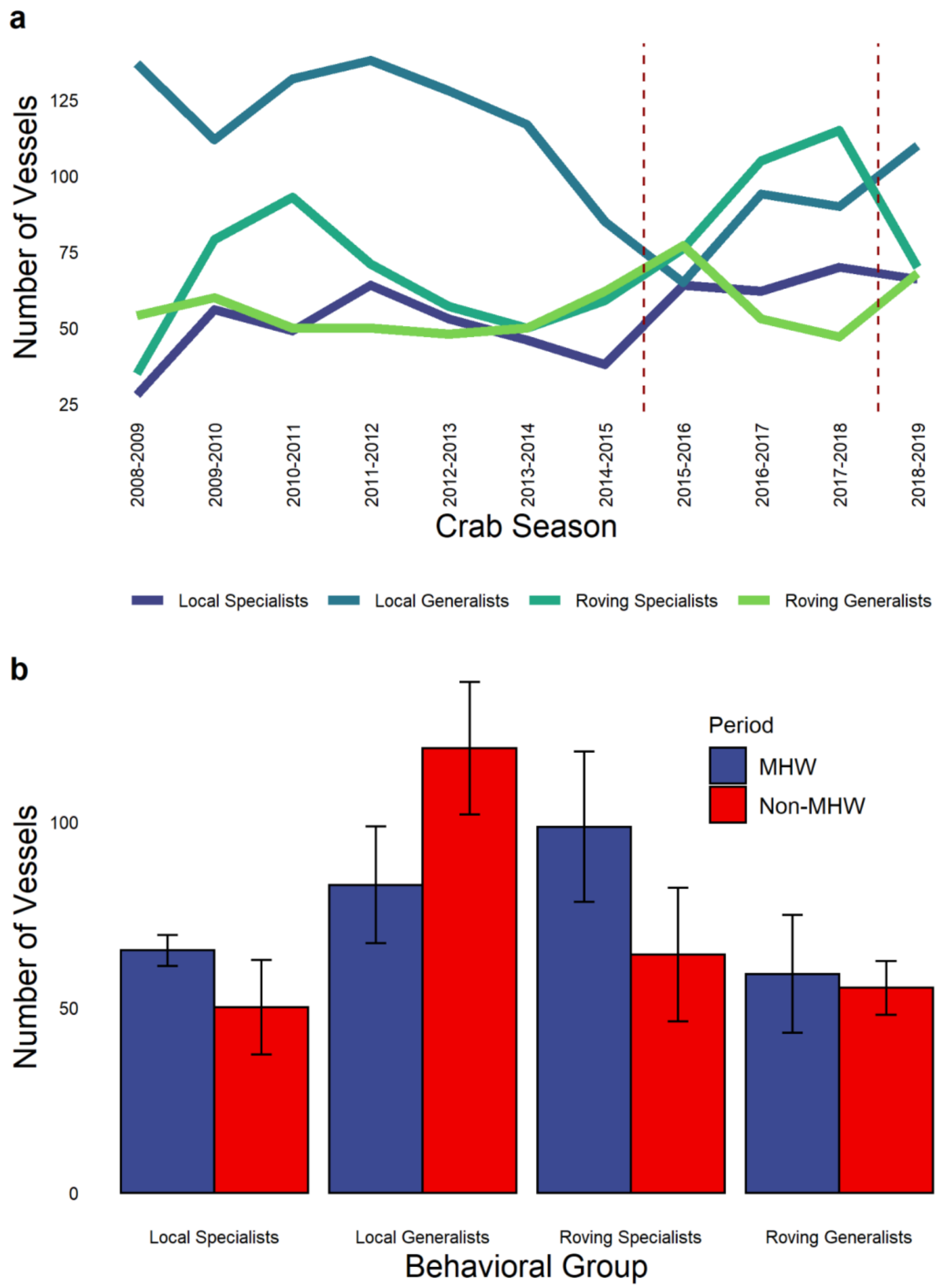
Supplementary Figure 1. Distribution of behavioral variables by behavioral groups (LG: Local Generalists; LS: Local Specialists; RG: Roving Generalists; RS: Roving Specialists). Letters represent significant group differences based on Tukey's HSD.



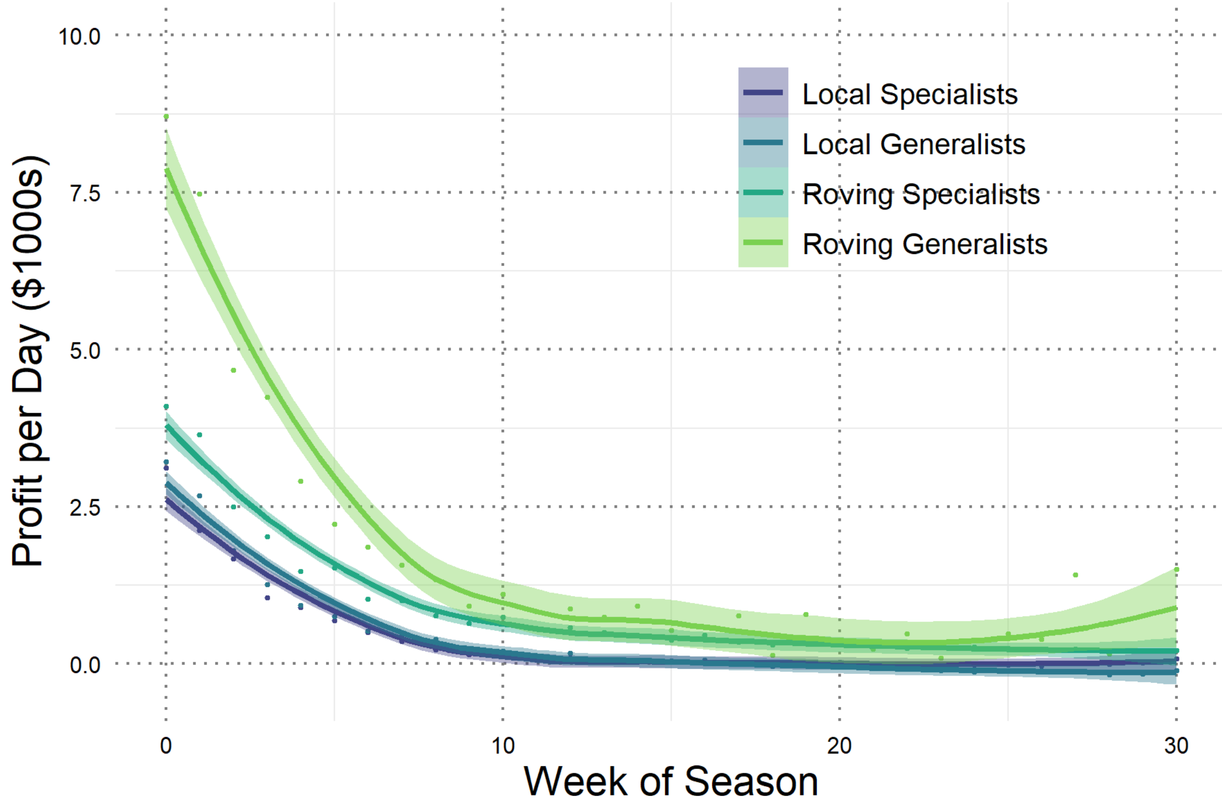
Supplementary Figure 2. Rankings of each behavioral group relative to each variable included in the cluster analysis. Groups with non-significant differences (according to Tukey's HSD, Supplementary Figure 1) are assigned the same rank.



Supplementary Figure 3. Number of vessels in each clustered behavioral group across crab seasons. (a) Number of vessels in each behavioral group in each crab season. Vertical lines delineate the period of the marine heatwave. (b) Mean number of vessels (+/- 1 SD) in each group in heatwave (MHW) versus non-MHW seasons.



Supplementary Figure 4. Mean profit per day fished for each behavioral group in each week of the crab season, averaged across all seasons. Lines show a loess smooth across weeks for each group.



Supplementary Figure 5. Smoothed kernel density distributions of vessel length by behavioral group and crab season. We used vessel registration data from PacFIN to obtain vessel lengths in feet. Vessel lengths were checked for reporting errors, and only the most recent length value was used if a vessel reported multiple different lengths.