## Title

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# Fishers as foragers: Individual variation among small-scale fishing vessels as revealed by novel tracking technology

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ABSTRACT

Effective fisheries management requires an understanding of fisher behavior. Though vessel tracking systems are increasingly used to describe the movements and activities of industrial fishing fleets, their use has been limited within the small-scale fisheries employing the vast majority of the world's capture fishers. Here we combine novel vessel tracking technology with logbook data to conduct a high-resolution analysis of behavior and decision-making within a small-scale fishery. Our results indicate significant heterogeneity in fisher behavior, catch composition, and profits within a small-scale fleet operating in the central Gulf of California, even amongst fishing vessels using similar gear types. The weekly home ranges (75 % Kernel Utilization Distribution) occupied by fishers spanned 1.5–1121.8 km$^2$ across 13 vessels, while weekly profits ranged from -1810 to 26,160 pesos. Differences in the spatial interactions and catch profiles of observed vessels revealed the existence of behavioral associations linked with distinct fishing strategies. After identifying and describing the contextual factors driving such heterogeneity among vessels using hook and line fishing gear, we interpret emergent patterns and processes using insights from foraging theory and marine social science. In illustrating the applications and opportunities presented by recent advances in vessel tracking technology, we argue for the use of spatially explicit analytical approaches in assessing behavioral diversity within small-scale fisheries and in designing robust and equitable management strategies.

## 1. Introduction

Understanding the spatial ecology of fisheries and the foraging behavior of those individuals engaged in harvest is critical for estimating their impacts on marine species and evaluating different management scenarios (Watson et al., 2004; Anticamara et al., 2011). Knowledge of how people operate in a fishery system can provide insight into how that system works (Salas and Gaertner, 2004) and many researchers have argued that an incomplete or inaccurate understanding of fisher behavior has contributed to the collapse of many fisheries worldwide (Hilborn, 1985; Wilen et al., 2002; Branch et al., 2006). Substantial fisheries research has focused on long-term entry and investment decisions, such as which species to target and which fishing gear to use (Gordon, 1954; Costello et al., 2008). But after gear and target species have been selected, fishers must subsequently decide when and where to fish. These short-term choices impact the households and communities of which they are a part, and the marine ecosystems in which they are embedded (Eales and Wilen, 1986; Salas et al., 2004). High-resolution, georeferenced observations of fishing processes can provide useful information about fisher behavior and the spatiotemporal dynamics of the species they target (Defeo and Castilla, 1998; Bertrand et al., 2007), and aid in the development of targeted strategies designed to ensure their sustainability.

Small-scale fisheries (SSF) employ > 90 % of the world's capture fishers (Kolding et al., 2014) and provide livelihoods and food security for hundreds of millions of individuals around the world (FAO, 2018). In recent years, the sector has drawn increased attention from scholars, resource managers, and policy makers as its substantial contributions to

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global fishery landings, direct human consumption, and the international seafood trade have come to light (Chuenpagdee, 2011; Crona et al., 2015). Despite the critical role SSFs play in supporting coastal economies and human well-being, many nearshore coastal ecosystems are declining due to pollution, overfishing, and habitat loss (Jackson et al., 2001). In regions where management is weak and/or focused primarily on the industrial sector, SSF operations are often structured by local rules-in-use that may differ substantially from formal laws and regulations (Cinti et al., 2010). Effective management of such systems requires an understanding of fishers, their behaviors, and the diverse factors that influence their decisions (Naranjo-Madrigal et al., 2015). This need is especially acute across tropical and semi-tropical coastal regions where small-scale fisheries are often characterized by a diversity of gear types and target species, large spatial and temporal variation in landings, dispersed local landing sites, and uncertain resource access (Naranjo Madrigal and Salas Márquez, 2014). When fishing effort is applied to a multi-species resource, fishers make decisions regarding target species and fishing areas daily (Cabrera and Defeo, 2001). Yet, behavior and decision-making within such systems and their impacts on local livelihoods and resources remain poorly understood.

Fishing is an, "uncertain and competitive activity," (Salas and Gaertner, 2004) in which strategies and tactics are influenced by fishers' perceptions, preferences, abilities, and relationships. Short-term harvesting operations are influenced by variable environmental conditions (Salas et al., 2004) as well as changes in resource abundance, distribution (Shester, 2010), and market price (Defeo and Castilla, 1998). Within fisheries and fleet dynamics literatures, several bioeconomic (e.g., Random Utility Models; see Eales and Wilen, 1986; Holland and Sutinen, 1999) and ecological (e.g., the theory of Ideal Free Distribution; see Gillis et al., 1993; Gillis, 2003) frameworks have been used assess the relative importance of such drivers. Such approaches are based upon the assumptions that fishers have accurate knowledge concerning the distribution of target resources, can move between locations without constraint, and are driven by a desire to maximize profits. Debate continues concerning whether such models can explain decision making within small-scale fisheries where individual variability is thought to be more pronounced (Abernethy et al., 2007; Wallace et al., 2016). With small boat sizes and limited capital investment, small-scale fishers are often limited by weather conditions, the price of fuel, permits and equipment, and access to information (Cabrera and Defeo, 2001; Salas et al., 2004; Abernethy et al., 2007; Naranjo-Madrigal et al., 2015) in addition to social and cultural factors unique to specific local contexts (Béné and Tewfik, 2001; Frawley et al., 2019a). Indeed, recent research concerning both the small-scale (Wallace et al., 2016) and industrial (Girardin et al., 2017; Bourdaud et al., 2018) sectors has found that individual fishing habits and traditions may be more influential when selecting fishing grounds than economic opportunism.

In mixed fisheries, it is hypothesized that fishers attempt to maximize revenue, rather than catch volume (Girardin et al., 2017). While specialist fishers concentrate on a specific area, species, or fishing method, generalist fishers exploit multiple species using multiple gear types (Smith and McKelvey, 1986). Though generalists may sacrifice some degree of efficiency, particularly during resource booms, their flexibility is believed to mitigate the risk and income fluctuations associated with environmental and economic variability (Kasperski and Holland, 2013; Finkbeiner, 2015; Frawley et al., 2020). Likewise, it has been suggested that individual fishers differ in their willingness to accept risk and uncertainty. Decisions regarding the allocation of fishing effort are likely influenced by these risk profiles as certain species and habitats are more intrinsically variable than others (Girardin et al., 2017). Some fishers opt to explore new resources and unfamiliar fishing grounds; others prefer to exploit resources that have already been discovered, forgoing occasional high rewards for steady, but lower, economic returns (Allen and McGlade, 1986; Shester, 2010). Though agent-based modeling simulations capable of accommodating such variability are increasingly applied to small-scale fisheries and other natural resource systems, there is a recognized need to ground related theoretical insight with empirical data (Lindkvist et al., 2019).

Currently, few tools exist within SSFs to identify, monitor, and manage behavioral heterogeneity. Spatially explicit, high resolution time series provided by electronic vessel tracking systems are increasingly used to assess the dynamic footprint of large-scale and/or industrial fisheries worldwide (Amoroso et al., 2018; Kroodsma et al., 2018; McCauley et al., 2018). In recent years, vessel tracking technology has been used to estimate the environmental and economic drivers of global fisheries (Kroodsma et al., 2018), to quantify the proportion of fished habitat (Amoroso et al., 2018), to assess the effectiveness of marine protected areas (McCauley et al., 2016; White et al., 2020), and to predict hotspots of bycatch for threatened species (Queiroz et al., 2016; White et al., 2019). However, these emerging tools have not yet been applied to small-scale fisheries. Here we present an application of novel tracking technology, the Pelagic Data Systems (PDS) vessel tracking system (VTS), to examine the behavior of individual small-scale fishing vessels within a dynamic marine environment. We describe heterogeneity among vessels within a small-scale fishing fleet and attempt to identify local factors and conditions driving individual variation in spatial allocation of effort, movement ecology, catch composition and profit. When combined with traditional fisheries data sources, PDS technology provides the opportunity to apply insights from foraging theory and marine social science to improve our understanding of fishing behavior and local resource dynamics within data-poor SSF systems. By integrating a novel technology with environmental and catch data, we illustrate how knowledge of fisher behavior can improve scientific understanding of SSF as dynamic marine social-ecological systems and aid in the development of management strategies designed to ensure their sustainability.

## 2. Study system

Depending on the season, anywhere between 10,000 and 24,000 small-scale fishing boats operate in the Gulf of California, directly employing more than 56,000 people (Carvajal et al., 2004; Azuz-Adeath and Cortés-Ruiz, 2017). Though the Gulf represents Mexico's chief source of fishery resources for national and international markets, inefficiency within the fisheries sector and the government at-large have led to a marked decline in many marine resources (Espinoza-Tenorio et al., 2011). Following recent anomalous oceanographic conditions (Robinson et al., 2016; Myers et al., 2018; Frawley et al., 2019b) and decades of intensive and unsustainable marine resource exploitation (Cisneros-Mata, 2010), today many marine resource-dependent livelihoods are being pushed beyond the point of viability (Vásquez-León, 2012; Giron-Nava et al., 2018).

Santa Rosalía (population = 14,160 inhabitants) is located on the western coast of the Gulf in the northeast portion of the state of Baja California Sur, Mexico (INEGI 2015). Fishing and mining comprise the principal economic activities of the region, with multi-species and multi-gear fishers using 5.5–7.5 m open-hulled fiberglass boats equipped with outboard motors (referred to regionally as 'pangas') to target jumbo squid (*Dosidicus gigas*), groupers (*Serranidae* spp.), snappers (*Lutjanidae* spp.), sharks (*Carcharinidae* spp.), octopus (*Octopodidae* spp.), and other commercial groups (Arce-Acosta et al., 2018). Available fishery data are scarce and are largely limited to monthly landings totals and official "trip-ticket" records which report information on economic units (i.e. permits), typically encompassing 3–10 individual fishing vessels (Arce-Acosta et al., 2018; Gonzalez-Mon et al., 2021). As recently as 2008, jumbo squid landings (~36,000 metric tons) represented 89.9 % of the weight and 51.2 % of the value of total fishery landings in the region (Frawley et al., 2019b). Though jumbo squid has long been considered an important regional source of employment and income (de la Cruz-González et al., 2007), the fishery collapsed in 2015 and has yet to recover (Frawley et al., 2019b). A large number of individuals have left the small-scale fishing sector and those who remain increasingly rely upon novel fishing grounds, technologies, and species assemblages (Frawley et al., 2019a).

## 3. Materials and methods

### 3.1. Collaborative fisheries research program (logbooks and vessel tracking devices)

We conducted fieldwork in Santa Rosalía between April and June of 2016. After initial scoping, we recruited thirteen small-scale fishing vessels to participate in the study. Efforts were made to choose vessels that were broadly representative of local SSF operations (in terms of vessel size, engine power, gear type etc.) but our sample was ultimately limited to those full-time fishers willing to engage in the research process and provide data documenting legal fishing operations. The total size of the active fishing fleet was ~30 fishing boats, though we observed a steady attrition in fishing effort as the study period progressed. In order to document the behavior of individual small-scale fishing vessels, we issued logbooks and deployed solar-powered, ultra-light VTS devices (designed and manufactured by Pelagic Data Systems). VTS devices recorded the position, heading, and speed of each vessel at 10-second intervals and uploaded this information to cloud-based data storage platform via the local cellular networks. We asked vessel captains and/or designated crew members to provide details concerning each fishing trip in logbook entries, documenting time and date of departure, time and date of return, type of fishing gear(s) used, costs (food, gas, oil, etc.), and the weight (kg) and value (pesos/kg) of each species landed. Profit was calculated post hoc by subtracting self-reported costs from gross revenue. We aggregated VTS and logbook data on a weekly (Monday-Sunday) basis rather than a per trip basis for those analyses designed to integrate the two data sources and/or facilitate their comparison over discrete time intervals. This allowed us to standardize differences in logbook reporting frequency amongst participating vessels (e.g. several individuals choose to aggregate information derived from multiple fishing trips within single logbook entries).

### 3.2. Spatial data processing and derived metrics

Kernel utilization distributions (KUDs) (Worton, 1989), a technique originally developed in order to estimate the home range distribution of animals, are increasingly used to quantify and evaluate vessel behavior (Tolotti et al., 2015; Natale et al., 2015). A KUD is a model where the use of space (e.g. spatially explicit fishing effort) is evaluated by a bivariate probability density function (Worton, 1989; Natale et al., 2015). To measure differences in the spatial allocation of effort among vessels, we used VTS data to calculate KUDs for each vessel each week. In order to remove redundant data points and linearly interpolate missing information, we applied a filter to VTS data to obtain one location every five minutes using the zoo package (Zeileis and Grothendieck, 2005) in the R programming language (R Core Team, 2016). We estimated the smoothing parameter (*h*) for KUD analysis using the “href” or reference bandwidth and assuming a bivariate normal distribution (Calenge, 2006). We calculated a 75 % KUD for the subsequent analyses after home range size versus home range level comparisons reached an asymptote for all vessels around the 75 % distribution level (Calenge, 2006). Observation points were not distinguished by “fishing” or “non-fishing” activity prior to KUD analysis, as is common in studies on industrial-scale vessel behavior (Kroodsma et al., 2018; de Souza et al., 2016; Hu et al., 2016). Unlike many industrial vessels, SSF vessels employ a diversity of fishing strategies and tactics within any single trip making it difficult to classify any individual point as “non-fishing”. After calculating the KUD area to characterize each boat’s weekly home range, we measured distance from port within ArcGIS (ESRI, 2018) as the straight-line distance from the centroid of each KUD to the entrance of the port of departure in Santa Rosalía.

### 3.3. Environmental data

3-day composite environmental data products for sea surface temperature (SST) and chlorophyll *a* (Chl *a*), selected to mitigate gaps in regional cloud cover associated with Chl *a* data, were downloaded across the spatial extent of the study area from the NOAA Coast Watch server (Multi-scale Ultra-high Resolution Sea Surface Temperature Analysis, 0.01°; Aqua MODIS Chlorophyll *a*, 0.0125°) and aggregated on a weekly basis. To identify the environmental conditions encountered by individual fishing vessels, we selected the spatial subset (i.e. ‘clip’) of weekly environmental data encompassed by the individual KUDs described above. We calculated SST and Chl *a* means and variances (i.e. standard deviations) from each of these weekly spatial subsets using the R package ‘raster’ (Hijmans, 2015).

### 3.4. Catch composition

To assess variation in catch composition within and among boats, we used catch data recorded in logbook entries to calculate two distinct catch composition metrics: catch diversity (as inferred by Shannon’s Diversity Index) and individual specialization (as inferred by the Proportional Similarity Index). The Shannon’s Diversity Index (*H*), calculated here using the R package ‘vegan’ (Oksanen et al., 2013), is an index commonly used to characterize species diversity in a community which accounts for both the abundance and evenness of the species present:

$$H = -\sum_{i=1}^{R} p_i \ln p_i$$

where ($p_i$) is the proportion of species *i* relative to the total number of species. We used the Proportional Similarity Index ($PS_i$) to describe the overlap between a vessel *v*’s catch and the catch of the observed fleet as a whole:

$$PS_i = 1 - 0.5\sum_i |\rho_{vi} - q_i|$$

where $p_{vi}$ is the frequency of species *i* in the vessel *v*’s catch and $q_i$ is the frequency of species *i* in the fleet as a whole. For individuals landing fishing in direct proportion to the fleet as a whole, $PS_i$ will be 1 and it will decrease as individual specialization increases.

In order to assess intraspecific catch overlap among individual fishing boats, we used the individual specialization index (*IS*). The *IS* index, which is an average of individual $PS_i$ values, is a general measure of individual specialization at the population level. Statistical significance for this index was calculated by generating 999 simulated populations through Monte Carlo resampling, recalculating IS for each resampled dataset and determining a non-parametric p-value on the basis of the proportion of resampled populations which had lower index values than the observed population (Bolnick et al., 2002; Costa et al., 2015). We used the R package ‘RInSp’ (Zaccarelli et al., 2013) to calculate $PS_i$, and *IS* values. To graphically examine similarity in catch composition among boats across the entire study period, we used hierarchical clustering with the Jaccard distance method in the R package ‘vegan’, summarizing the overlap in catch between two boats by summing the number of landed species shared between them and dividing by the total number of landed species of both boats.

### 3.5. Fidelity in foraging behavior

To determine the degree of fidelity in foraging behavior, we correlated KUD, distance from port, time at sea, proportional similarity, and catch diversity calculated for each boat during a given sampling interval (i.e. $Week_i$) with values observed during the following sampling interval (i.e. $Week_{i+1}$). Analysis conducted using Pearson’s product-moment correlations (reported) and univariate mixed models (with boat ID included as a random effect) were consistent and reinforcing.

### 3.6. Drivers of variation in catch composition among hook and line vessels

To examine the spatial (KUD, distance from port) and environmental (mean SST, SD SST, mean log(Chl a)) drivers of variation in catch composition, we used constrained ordination based on Euclidean distance (i.e. redundancy analysis). For this analysis, we choose to focus on vessels exclusively reliant on hook and line fishing gear because this gear type had the largest sample size and is the most common gear type used in the region. Though the use of different fishing gears is likely a major driver of variation within our study system, our statistical power to evaluate such dynamics was constrained by sparse representation of vessels using alternative gear types in our sample population. We used pairwise comparisons and variance inflation factors (VIF) to evaluate collinearity and deemed explanatory variables with VIF scores above 5 (i.e. mean SST) to be problematic, dropping them from the analysis. Boat ID was included as a categorical sampling unit and species composition data was transformed using a logarithmic scale in order to accommodate the large number of zero values (Legendre and Legendre, 2012). Following stepwise model selection based on AIC criteria, we used an ANOVA to determine the significance and effect size of spatial and environmental explanatory variables (Oksanen et al., 2013). All constrained ordination analyses were conducted using the R package 'vegan'.

### 3.7. Dynamic interactions between fishing vessels

Dynamic interaction refers to the degree which the movements of two individuals are related (Macdonald et al., 1980) or interdependency in the movement of two individuals (Doncaster, 1990). To measure dynamic interactions between fishing vessels we calculated the movement correlation coefficient (*Cr*) characterizing the similarity between each pair of vessel tracks observed each day. This index, which is useful for detecting the tendency of individuals to move in a coordinated fashion (Shirabe, 2006), takes the form of a Pearson product-moment correlation statistic formulated for the use of movement data (represented as paths rather than points) and is sensitive to both movement direction and displacement (Long et al., 2014). To calculate this index we used the 'wildlifeDI' package in R (Long, 2014), generating a unique value for each pair of vessel tracks recorded on the same day of sampling ($n = 1034$).

Daily *Cr* values were averaged for each vessel pair and resulting values > 0 (indicating some degree of relatedness of movement) were used to derive a social network characterizing differences in the strength of observed interactions amongst vessels. Behavioral associations were subsequently parsed using the 'fast greedy' community detection algorithm (Clauset et al., 2004), a method previously employed in vessel tracking (Iacarella et al., 2020) and animal movement studies (Finn et al., 2014; Casselberry et al., 2020) which relies upon the the 'igraph' R package for network analysis (Csardi and Nepusz, 2006). Following the identification of distinct behavioral groups, differences in movement relatedness amongst groups was quantified by assessing the means of daily *Cr* values associated with vessel pairs that were part of the same group as compared with those associated with vessel pairs from distinct groups.

## 4. Results

We deployed tracking devices on 13 small-scale fishing boats operating out of the port of Santa Rosalía and monitored 435 fishing trips which took place over a 10-week study period (Table 1). Spatial data for Boat_L and logbook data for Boat_M were not included in the final analysis due to tracking device failure and incomplete reporting. Overall, the weekly home ranges (75 % KUD) occupied by observed vessels ranged from 1.5 to 1121.8 $km^2$, while weekly profits varied from -1810 to +26,160 pesos. Of the boats comprising our sample population, nine primarily used hook and line fishing gear, two primarily used gillnets, and two primarily used other gear types (i.e. diving equipment and fish traps).

### 4.1. Spatial distribution of fishing effort

Vessel tracks (Fig. 1A) were distributed across the nearshore environment in the waters north (max. range = 84.85 km) and south (max. range = 29. 69 km) of Santa Rosalía and in the waters surrounding Isla Tortuga and Isla San Marcos. A KUD analysis of all vessels over the entire study period (Fig. 1B) indicates that while the largest amount of activity was concentrated in waters located less than 10 km southeast of the port of departure (a region known locally as Los Frailes), substantial activity was also recorded in discrete fishing zones (e.g., Estero San Carlos, Punta Prieta, Isla Tortuga, and Isla San Marcos) further distances from port. Examination of the weekly KUDs of individual fishing boats reveals heterogeneity in foraging behaviors by boat (Fig. 2). Some boats (e.g., Boat_J & Boat_G) with comparatively small KUDs displayed a high degree of site fidelity with respect to specific fishing grounds. Other boats with comparatively large KUDs (e.g., Boat_B), targeted a number of different fishing grounds. Results of Kruskal-Wallis test indicate significant differences in mean values of distance from port ($p < .001$) and KUD ($p < .001$) observed by boat, while the results of Levene's test indicate that variance in distance from port ($F = 2.099$, $p = .027$), and KUD ($F = 2.232$, $p = .019$) was statistically different among boats (Fig. 3). However, within individuals, KUD ($r = .418$, $p < .001$) and distance from port ($r = .759$, $p < .001$) were significantly correlated from one week to the next, suggesting that individual boats displayed consistent foraging strategies.

### 4.2. Variation in catch composition

Results of Kruskal-Wallis test indicate significant differences in mean weekly values of catch diversity ($p < .001$) and proportional similarity ($p < .05$) calculated by boat. The IS index value of the observed fleet was

**Table 1**
Summary of mean weekly ($n = 10$) spatial allocation of effort, catch composition, and profit metrics assessed by boat. Standard deviations are presented in parentheses.

| Boat ID | Dominant Gear | Time at Sea (hrs) | Mean Distance from Port (Km) | Mean KUD ($Km^2$) | Mean Proportion Similarity ($Ps_i$) | Mean Profit (Pesos) |
|---|---|---|---|---|---|---|
| Boat_A | Hook & Line | 381 | 32.7 (+/- 14.7) | 181.1 (+/- 118.9) | 0.32 (+/- 0.16) | 5661.0 (+/- 4687.0) |
| Boat_B | Hook & Line | 516 | 14.5 (+/- 5.6) | 517.6 (+/- 282.8) | 0.42 (+/- 0.16) | 5513.5 (+/- 3875.9) |
| Boat_C | Other | 149 | 42.2 (+/- 23.3) | 179.1 (+/- 182.2) | 0.28 (+/- 0.12) | 1338.3 (+/-1599.4) |
| Boat_D | Hook & Line | 148 | 28.2 (+/- 10.3) | 282.1 (+/- 272.9) | 0.18 (+/- 0.17) | 1605.1 (+/- 4885.8) |
| Boat_E | Hook & Line | 535 | 10.5 (+/- 6.7) | 123.7 (+/- 144.8) | 0.42 (+/- 0.18) | 3971.5 (+/- 3612.7) |
| Boat_F | Hook & Line | 609 | 22.4 (+/- 13.2) | 309.7 (+/- 196.4) | 0.39 (+/- 0.15) | 3448.2 (+/- 2018.2) |
| Boat_G | Hook & Line | 287 | 4.8 (+/- 2.1) | 16.8 (+/- 9.4) | 0.28 (+/- 0.11) | 726.9 (+/- 408.3) |
| Boat_H | Hook & Line | 432 | 18.7 (+/- 18.7) | 232.4 (+/- 260.8) | 0.42 (+/- 0.14) | 3772.0 (+/- 1804.8) |
| Boat_I | Gillnet | 225 | 7.7 (+/- 6.2) | 60.4 (+/- 39.6) | 0.42 (+/- 0.20) | 9317.0 (+/- 11941.2) |
| Boat_J | Gillnet | 261 | 60.5 (+/- 6.7) | 144.8 (+/- 96.9) | 0.39 (+/- 0.05) | 9426.8 (+/-6216.4) |
| Boat_K | Hook & Line | 375 | 23.9 (+/- 10.6) | 131.9 (+/- 94.3) | 0.39 (+/-0.13) | 3150.3 (+/- 2142.5) |
| Boat_L | Hook & Line | NA | NA | NA | 0.47 (+/- 0.12) | 6129.8 (+/- 3282.9) |
| Boat_M | Other | 217 | 19.8 (+/- 5.3) | 293.7 (+/- 259.9) | NA | NA |

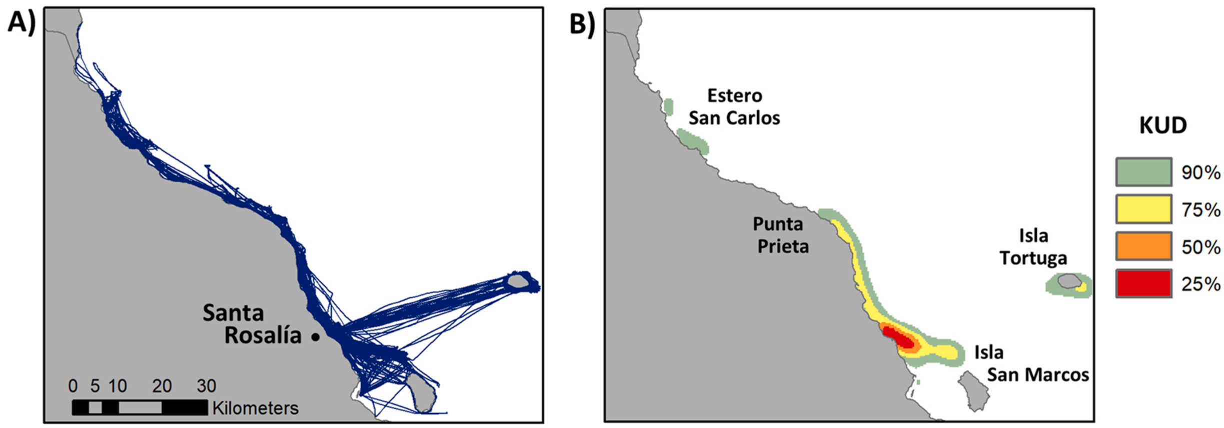


**Fig. 1.** Distribution (**A**) and density (**B**) of all boats tracks observed over the duration of the study period.

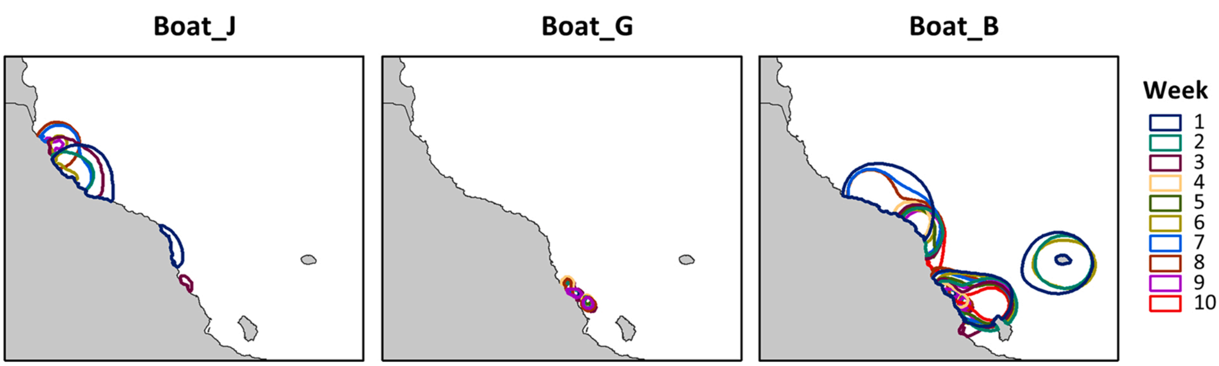


**Fig. 2.** Heterogeneous spatial distribution of fishing effort as revealed by Kernel Utilization Distributions of individual fishing boats across sampling weeks. Boat_J is a gillnet vessel while Boat_G and Boat_B use hook and line.

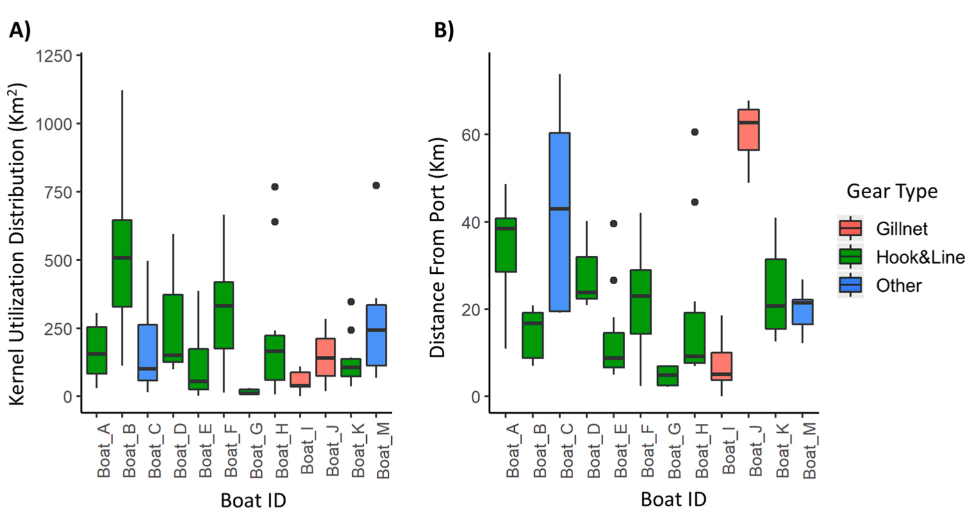


**Fig. 3.** Boxplots displaying the distribution of data points and median weekly values of **A**) kernel utilization distributions (km$^2$) and **B**) distance from port (km) observed by each tracked boat.

0.46 with Monte Carlo resampling confirming that significant specialization ($p < .001$) occurred amongst the boats in our study sample. Indeed, fishers landed heterogeneous species assemblages (Fig. 4A) with Jurel being the dominant species (36.3 % of landings by weight), followed by Chano (16.4 %) and Cazon (8.6 %). While some boats landed a diversity of species (i.e. Boat K; $H = 1.90$, $PS_i = 0.56$) over the duration of the study period, others relied principally on one (i.e. Boat E, $H = 0.64$, $PS_i = 0.49$), or two (Boat_G; $H = 1.09$, $PS_i = 0.30$) targets. Within individuals, proportional similarity ($r = .35$, $p < .001$) and catch diversity ($r = .429$, $p < .001$) were significantly correlated from one week to the next indicating consistency in target species selection within boats. In aggregate, catch weight progressively declined throughout the study period (Fig. 4B) as sea surface temperatures across targeted fishing grounds warmed from 19.48 °C (± .58) in Week 15 to–27.78 °C (± 0.75) in Week 24. Results of hierarchical cluster analysis (Fig. 5) indicate that similarities in catch composition among boats can be classified by

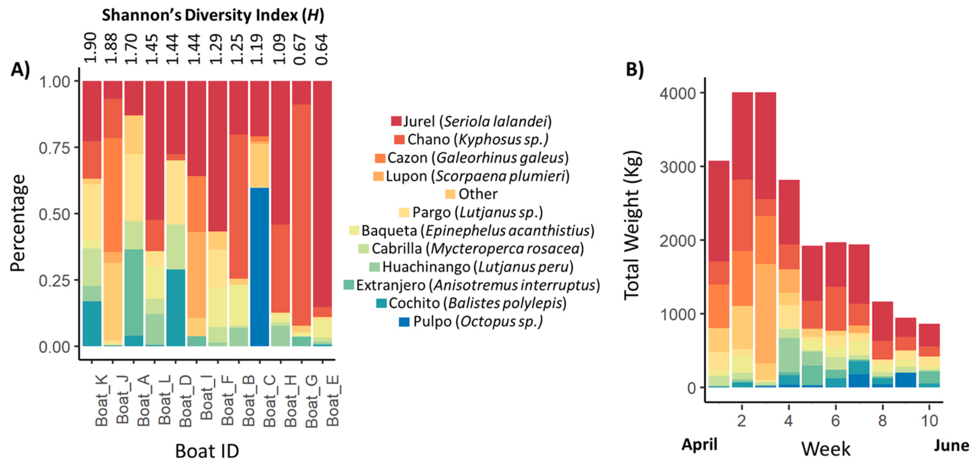


**Fig. 4.** Catch composition displayed by Boat ID (A) and Sampling Week (B). Species are ordered in the legend according to their relative contribution to total landings.

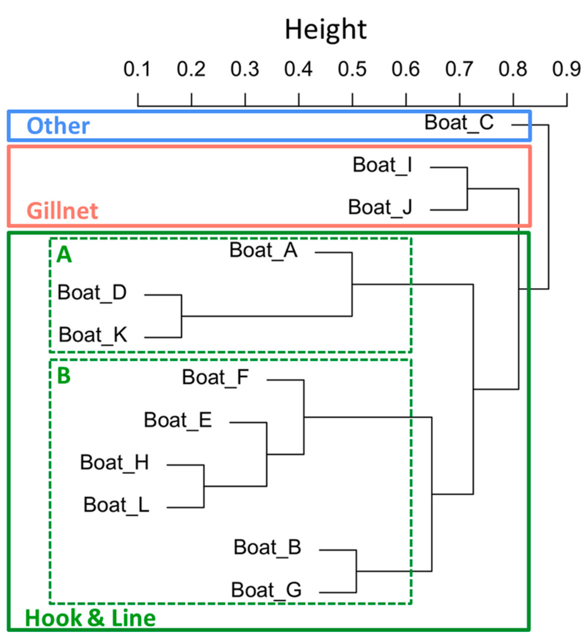


**Fig. 5.** Hierarchical clustering of individual catch composition as classified by the dominant gear type across the first 3 levels of organization. Four levels of organization are needed to differentiate catch composition amongst vessels using similar gear types (i.e. hook and line fishing gear).

differences in dominant gear types across the first three levels of hierarchical organization. Fishers using gillnets reported weekly landings that were on average more diverse ($H = 0.88 \pm 0.54$) and less specialized ($IS = 0.41 \pm 0.16$) than fishers using hook and line ($H = 0.70 \pm 0.46$; $IS = 0.37 \pm 0.16$). Only at four levels of organization did differences in catch composition among vessels using similar gear types (i.e. hook and line) become evident.

### 4.3. Spatial and environmental drivers of variation in hook and line catch

Stepwise selection determined that the constrained ordination model explaining the largest amount of variance in catch composition ($R^2 = 0.44$) among boats using hook and line fishing gear included boat ID as well as KUD and distance from port as spatial explanatory variables, and log(Chl a) and SD SST as environmental explanatory variables. The results of ANOVA indicate that the effects of boat ID ($p < .001$), distance from port ($p < .001$), log(Chl a) ($p < .01$), and KUD ($p < .05$), and were statistically significant and that boat ID and distance from port were associated with the highest explanatory variable scores (2.81 and 1.24, respectively). Analysis of the corresponding triplot (Fig. 6), suggests that reef affiliated species like Pargo (*Lutjanus* spp.) and Cabrilla (*Mycteroperca roseacea*) were most commonly associated with those distant fishing grounds targeted by Boat_A, Boat_D, and Boat_K while migratory species like Jurel (*Seriola lalandei*) and Huachinango (*Lutjanus Peru*) were more commonly associated with ephemeral oceanographic features (i.e. fronts and primary productivity blooms) targeted by Boat_F, Boat_E, and Boat_H.

### 4.4. Movement relatedness and behavioral associations

Analysis of dynamic interactions used to assess and compare relatedness of movement between vessels during individual fishing trips revealed the existence of discrete behavioral associations. Qualitative inspection of a social network where the existence and strength of linkages between vessels were derived from average, daily movement correlation (*Cr*) values suggested that the movement of some vessel pairs was more similar than others; subsequent application of a community detection algorithm used to parse the networks highlighted the existence of 3 distinct behavioral clusters (Fig. 7). For both Group C (a pair of vessels that frequently worked as a team when conducting diving

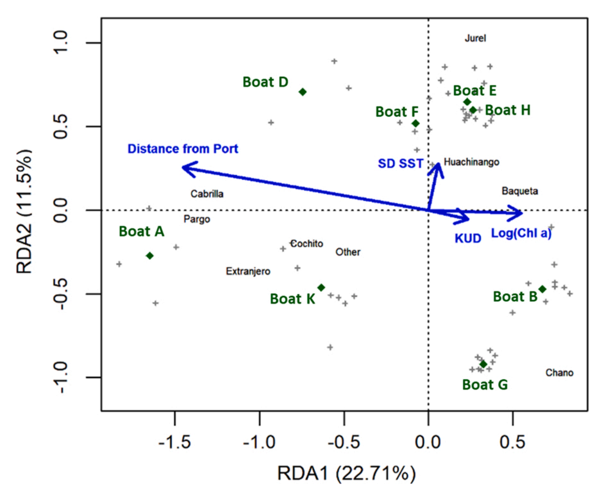


**Fig. 6.** Redundancy Analysis depicting the relative contribution of explanatory variables to variance in catch composition. Continuous explanatory variables are represented by blue lines while nominal explanatory variables are represented by green points. (+) is used to denote individual boat-sampling weeks.

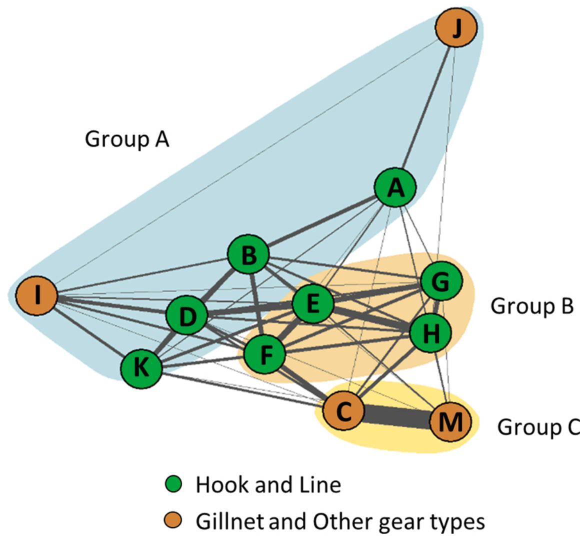


**Fig. 7.** Social network characterizing relatedness in movement amongst observed vessels. The strength of connections (i.e. edge-weights) between vessels (i.e. nodes) was determined by the average of movement correlation coefficients (*Cr*) assessing relatedness of individual fishing trips; group membership was assigned via a community detection algorithm designed to optimize network modularity.

operations) and Group B (a group of 4 hook and line vessels), movements of vessel pairs within the same group were significantly more correlated than movements between a group member and a non-group member (Student's T-test; $p < 0.01$ and $p < 0.001$, respectively). For Group A, there was no significant difference in the relatedness of movement between two group members as compared to between group members and non-group members ($p = 0.22$). Overall, vessel pairs within Group C had the highest average movement correlation ($Cr = 0.61 \pm 0.14$) while vessel pairs within Group A had the lowest ($Cr = 0.06 \pm 0.01$). With the exception of Boat_B, behavioral associations among vessels using hook and line fishing gear were partitioned in a manner consistent with the distinctions made by the fourth level of organization in hierarchical catch clustering (Fig. 5).

### 4.5. Heterogenous fishing strategies and tactics

Results of Levene's tests indicate that the variance in fishing profit was statistically different among boats, irrespective of whether the logbook entries were examined individually ($p < 0.001$) or aggregated on a weekly basis ($p < 0.01$). Though efforts to evaluate variation in efficiency and productivity associated with the use of different fishing gears were constrained by our small and unevenly distributed sample, a holistic review of aggregated logbook data suggests several key distinctions. Gillnet boats reported larger, though substantially more variable average weekly profits as compared to hook and line vessels (9233 ± 10,155 pesos vs 3712 ± 3411 pesos) while landing larger quantities (604.66 ± 606.53 kg vs 234.98 kg ± 275. 91 kg) of lower value (18.8 ± 4.26 pesos/kg vs 28.26 ± 9.84 pesos/kg) catch.

Among vessels using hook and line fishing gear, a comparison of the characteristics of individual fishing trips illuminates operational distinctions associated with the differences in catch and movement described above. Inferences are consistent whether using movement correlation associations (Fig. 8) or catch clustering (Supplemental Fig. 1) as the basis for distinction. Fishing trips undertaken by hook and line members of Group A were of longer duration than those undertaken by Group B (Fig. 8A), frequently spanning multiple days and targeting fishing grounds located a much farther distance from port (Fig. 8B). While spending more time on distant fishing grounds Group A members reported larger costs, but also landed catch of higher gross value and secured larger net profits as compared to the members of Group B (Fig. 8C). Though Groups A's profits were larger, they were also significantly more variable (Levene's Test; $p < 0.001$) and during fishing trips were vessels reported operating at a loss, those losses were significantly greater ($p < 0.01$).

## 5. Discussion

Fishers are increasingly recognized as top predators within marine ecosystems (Bertrand et al., 2007; Watson et al., 2018), yet scientific understanding of the behaviors and decision-making processes influencing selection of fishing grounds and target species remains limited. This is particularly true within the context of data-poor SSF where the strategies and tactics individuals employ are likely informed by the diverse environments in which they operate, the constraints they may encounter, and their intended objectives given unique social and economic contexts (Béné, 1996; Gonzalez-Mon et al., 2021). In order to

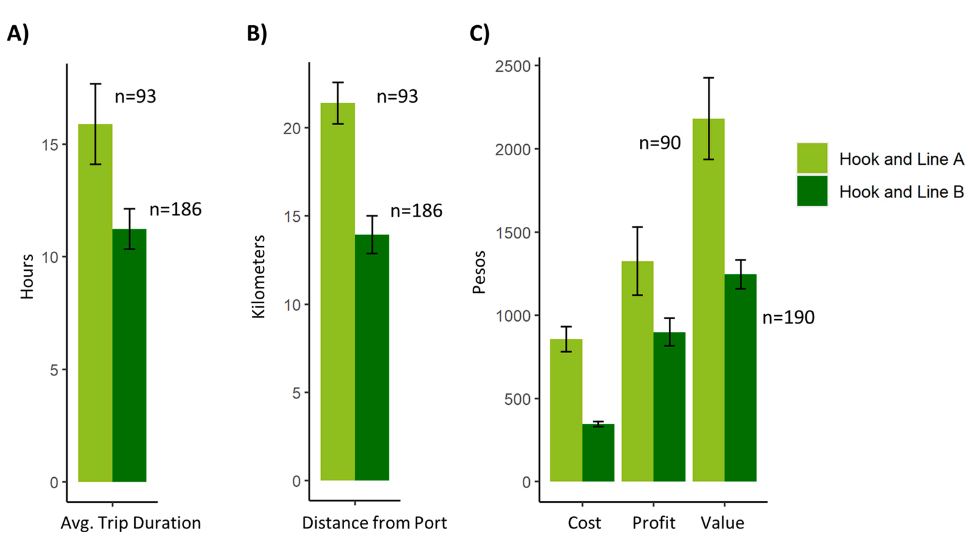


**Fig. 8.** Comparison of average Trip Duration (A); Distance from Port (B); and self-reported Cost, Profit, and Value (C) between hook and line fishing vessels with distinct behavioral associations. Data sourced from individual fishing trips (A & B) and logbook entries (C). Comparisons are consistent whether using movement similarity (shown) or catch composition (**Supplemental** Fig. 1) as the basis for distinction.

develop robust and effective natural resource management policies, knowledge concerning how fishers allocate effort in time and space is critically important (Hazen et al., 2018). With recent advances in tracking technology, SSF scholars and practitioners can leverage the methodology and insight generated by animal telemetry and movement ecology studies (Long and Nelson, 2013; Miller et al., 2019) and begin to conduct the kind of spatially explicit analyses previously limited to the examination of industrial fisheries (Amoroso et al., 2018; Kroodsma et al., 2018; McCauley et al., 2018). Here we provide proof of concept for this novel technology in order to guide future studies, generate useful hypotheses, and identify sources of variability and appropriate scales of analysis. Our results make clear that even in a remote location, where individuals have access to similar technologies and markets, there is no such thing as an average fishing vessel. Fishers are heterogeneous in terms of the gear they use, the fishing grounds they select, the species they target, and the income they generate.

### 5.1. Emergent patterns and processes

Despite differences in gear choice, spatial distribution, and target species selection, fishing vessels tended to be habitual and employed similar tactics and strategies from week-to-week. For individual vessels KUD, distance from port, proportional similarity and catch diversity were all significantly correlated from one sampling interval to the next. Such findings are consistent with previous literature suggesting low temporal variation in fishing behavior as fishers with incomplete information rely on previous experience to make decisions (Marchal et al., 2009; Davies et al., 2014). Overall, whether comparing multiple gear types or vessels within a single gear type, we found that fishing strategies yielding larger profits were associated with increasing revenue variability. Within the context of our study system, such findings suggest that many lucrative marine resources may be unevenly distributed and/or difficult to access. Indeed, others have shown that knowledge of and response to patchy resource dynamics are critical factors in meditating the success of fishers (Sanchirico and Wilen, 1999) and other foraging animals (Ford, 1983).

Even amongst vessels using the same gear type (i.e. hook and line fishing gear), substantial heterogeneity in foraging behaviors was evident. Foraging behavior is a key driver of spatial-temporal distribution in many taxa (Kowalczyk et al., 2015; Barry et al., 2016) with foragers often expanding their home ranges in response to shifting prey availability (Bertrand et al., 2012). Some individuals may forage over a wider area in order to overcome local resource depletion, while others display higher site fidelity, targeting specific patches to pursue fewer high-value (or low-cost) prey species (Zhang and Sanderson, 1997). Within our study, the apparent relationship between distance from port and profit suggests increased foraging success amongst those vessels willing and able to access remote fishing grounds. Overnight and/or multi-day fishing trips were common amongst the members of our study population who most frequently targeted distant waters (Frawley, *personal observation*). This strategy appeared designed to maximize economic returns while mitigating the fuel expenditures required to reach distant fishing grounds were fishing pressure was reduced and many high-value, reef affiliated species (i.e. Cabrilla and Pargo) were less intensively exploited and comparatively more abundant.

More distant fishing grounds can produce higher yields and economic rents (Cabrera and Defeo, 2001), but some fishers may display risk-averse attitudes when evaluating the spatial allocation of effort (Salas et al., 2004). In our study, the movements of vessels targeting distant fishing grounds were substantially less correlated with one another as compared to those targeting frequently visited fishing grounds located close to the port of operation. Though vessels displaying increased autonomy while targeting distant waters were more profitable, their expenses were higher and more variable. Previous research has described the existence of such "high risk, high reward" fishing strategies (Allen and McGlade, 1986) and argued that the choice of where to allocate fishing effort ultimately depends on subjective evaluations of the profits and risks of fishing different areas (Abernethy et al., 2007; Wallace et al., 2016). When faced with uncertain environmental and economic conditions, as is common within SSF (Naranjo Madrigal and Salas Márquez, 2014), many individuals may be primarily driven by subsistence goals and/or the desire to obtain sufficient revenue to cover trip costs (Chaboud, 1995). Fishers are likely to allocate more effort than is optimal to familiar grounds located closer to port due to safety concerns (e.g. mechanical failure and adverse weather conditions) and a desire to minimize expenditures (Swain and Wade, 2003) despite their limited productivity. Indeed, exploratory fishing is inherently uncertain and those most willing to take risks may be wealthier fishermen with financial reserves (Oostenbrugge et al., 2001).

The results of our multivariate analyses suggest that ephemeral oceanographic conditions (i.e. primary production as represented by log (Chl *a*) and/or sea surface temperature gradients as represented by SD SST) likely impact catch quantity and composition. Oceanographic fronts and transition zones have been identified as critical foraging habitat for many marine predators (Bakun, 2006; Etnoyer et al., 2006; Belkin et al., 2014) and are increasingly recognized for their impact on fisheries (Woodson and Litvin, 2015). Previous research has demonstrated a significant positive correspondence between the spatial distribution of fine-scale physical oceanographic features and fisher's income (Watson et al., 2018). Though the temporal resolution of our multivariate analysis (i.e. weekly rather than daily) may obscure such processes, others have argued that transition zone dynamics mediate fishery production across the central Gulf of California (Lluch-Belda et al., 2003; Bakun et al., 2010; Frawley et al., 2019b). Indeed, we hypothesize that declines in aggregate landings observed over the course of the study period can be attributed, in part, to a seasonal influx of warm water which pushed the transitional area between regional temperate and tropical water masses (Lluch-Belda et al., 2003) further north. This hypothesis is supported by fisher's logbook entries, several of which noted the increasing strength and duration of southeasterly winds typically associated with such phenological changes (Sievanen, 2014), over the course of the study period and previous studies which show local landings peaking in May before progressively diminishing throughout the summer months (Arce-Acosta et al., 2018). Such seasonal dynamics can help explain the attrition of effort observed over the course of the study; many part-time fishers typically only remain active during the year's most productive fishing periods.

### 5.2. Study limitations

Despite recent advances in the study of fleet dynamics and fisher behavior (Marchal et al., 2013; Girardin et al., 2017), uncertainty persists regarding why some fishers catch more fish and make more money than others (Hilborn, 1985; Fulton et al., 2011). We acknowledge that our statistical power to address these questions is limited by the scope of our field research program (e.g., relatively small sample size and study duration). However, as others have done with reference to animal telemetry (Sequeira et al., 2019), we would argue that productive insight can be derived from tracking studies with small sample sizes, especially if they primarily concern themselves with describing individual variability and/or unknown phenomenon in understudied systems (i.e. the behavior of small-scale fishermen in the Gulf of California).

Beyond the limitations posed by our sample size and study duration, we would argue that fishing is mercurial by nature and that research seeking to quantify and evaluate fishermen behavior would be well-served to move beyond analysis of discrete environmental and economic parameters. The ethnographic record has repeatedly contradicted fisheries economists' characterization of fishers as self-interested rational actors driven by the desire to maximize profit (McCay and Acheson, 1990; Durrenberger, 1997; Pollnac and Poggie, 2008). Subjective factors as related to skill, information availability, risk profiles, comfort, peer pressure, cooperation, and job satisfaction all influence fisher behavior and decision-making (Béné and Tewfik, 2001; Salas and Gaertner, 2004; Naranjo Madrigal and Salas Márquez, 2014) and concurrent investigations conducted in the Gulf of California confirm that many small-scale fisheries processes and operations are unique to local context (Frawley et al., 2019a). Beyond quantitative analysis, future research should consider how qualitative data could be used to document local perceptions and beliefs, and improve understanding of the social, economic and cultural dimensions of small-scale fishing communities. Just as biological and physical parameters have been examined in the past, social system components need to be documented and empirically assessed (Salas and Gaertner, 2004).

## 6. Conclusion

Fisheries are complex and adaptive socio-ecological systems where the exploitation of marine resources is driven by individuals' interactions with dynamic environmental and socioeconomic conditions. Yet, uncertainty surrounding how and why fishermen behave the way they do remains a major challenge in the design and implementation of sustainable fisheries management (Fulton et al., 2011; Hobday et al., 2011; Watson et al., 2018). Even where formal governance and management capacity exists, fishers are often treated as uniform elements, with no consideration of the attributes associated with individual histories, goals and scales of operation (Begossi, 1998; Salas and Gaertner, 2004). Given the importance of intra-population variation in foraging behavior for population responses to external drivers of change (Bolnick et al., 2003; Woo et al., 2008; Votier et al., 2010), a better understanding of those factors driving individual variation is of great value. Recent advances in vessel tracking technology provide the opportunity to address such knowledge gaps within small-scale fisheries, enabling researchers to conduct investigations at novel scales of analysis. When combined with environmental and/or catch data, high-resolution information concerning the spatial allocation of fishing effort can improve our understanding of behavioral heterogeneity within such systems. Given the diversity of user groups that comprise SSF and their importance to global economies, livelihoods, and human well-being, we suggest that as vessel tracking technology continues to develop, its applications within the sector are particularly salient.

## CRediT authorship contribution statement

**Timothy H. Frawley:** Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Writing - review & editing. **Hannah E. Blondin:** Methodology, Formal analysis, Visualization, Writing - review & editing. **Timothy D. White:** Methodology, Writing - review & editing. **Rachel R. Carlson:** Formal analysis, Visualization, Writing - review & editing. **Brianna Villalon:** Data curation, Visualization, Writing - review & editing. **Larry B. Crowder:** Conceptualization, Supervision, Methodology, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2021.105896.

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