Cooperative conservation and long-term management of false killer whales in Hawai‘i: geospatial analyses of fisheries and satellite tag data to understand fishery interactions

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Prepared by

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Introduction

False killer whales (*Pseudorca crassidens*) are long-lived upper trophic level odontocetes that are found throughout the tropics and sub-tropics. Until recently relatively little was known about this species anywhere in its range. Studies of this species originally begun around the main Hawaiian Islands in 1999 have provided the most detailed information on false killer whales anywhere in the world (Baird 2018a, 2018b). Three populations of false killer whales have been recognized in Hawaiian waters: an offshore (pelagic) population that ranges widely in the central tropical Pacific, and two insular populations, one around the northwestern Hawaiian Islands and one around the main Hawaiian Islands (MHI), with overlap of all three populations around Kaua'i and Ni'ihau (Baird et al. 2013; Bradford et al. 2015; Baird 2016). False killer whales from the main Hawaiian Islands insular population are known to eat a variety of pelagic and reef-associated game fish as well as squid (Baird 2016; Table 1), most of which are the target of commercial and recreational fisheries around the islands. False killer whale depredation of catch from fisheries around the islands has been documented for over 50 years. Pryor (1975) reported false killer whales taking catch off longlines off the Kona coast in 1963, and Shallenberger (1981) noted that depredation behavior "is very common in Hawaii where Pseudorca frequently steal tuna of up to 70 lbs., and sometimes take much larger fish." Zimmerman (1983) described a group of false killer whales consuming most of an estimated 250 kilogram hooked Pacific blue marlin (*Makaira mazara*) off Kona in 1983.

Evidence that the MHI insular population was facing a variety of threats and appeared to have undergone a large-scale decline became apparent in the mid- to late-2000s (Baird and Gorgone 2005; Baird 2009; Reeves et al. 2009; Ylitalo et al. 2009). In response to a 2009 petition from the Natural Resources Defense Council to list this population under the Endangered Species Act (ESA), NOAA Fisheries convened a Biological Review Team in early 2010 to review the status of the population. That effort recognized that Hawaiian insular false killer whales should be considered a "Distinct Population Segment" (DPS) under the ESA and that this DPS was under threat of extinction (Oleson et al. 2010). Based on that review, NOAA Fisheries listed the DPS as endangered under the ESA in 2012. In 2014, NOAA Fisheries and the State of Hawai'i amended a cooperative agreement under section 6 of the ESA to include false killer whales, allowing the State and the federal government to work cooperatively toward conservation of this population. Under that cooperative agreement, in 2015 the State of Hawai'i received a Species Recovery Grant from NOAA Fisheries focusing on false killer whales, in order to fill data gaps and begin outreach efforts in local communities.

Cascadia Research Collective (CRC) has been undertaking research on false killer whales in Hawai'i since the early 2000s (Baird et al. 2005; Baird and Gorgone 2005). These studies, along with collaborating researchers from NOAA Fisheries and other organizations, have included estimation of abundance (Bradford et al. 2018), examination of social organization and stock structure (Chivers et al. 2007; Baird et al. 2012; Martien et al 2014, in press), assessment of evidence for fishery interactions (Baird et al. 2015, 2017), and examination of spatial use (Baird et al. 2010, 2012; Bradford et al. 2015), among other topics. Evidence for fishery interactions has primarily been indirect: individuals from this population have high levels of line injuries on the dorsal fin (Baird et al. 2015) and mouthline (Baird et al. 2017) that are consistent with being hooked in fishing gear. One of the other findings from these studies was the existence of discrete social clusters within the MHI insular population, representing long-term social units of highly-related individuals (Baird et al. 2012; Martien et al. 2014, in press), analogous to the highly-stable killer whale (*Orcinus orca*) "pods" documented along the west coast of North America (Baird 2000). The initial analysis recognizing these discrete social clusters identified several peripheral clusters that were pooled with the three main clusters (Baird et al. 2012), although it was unclear at the time of the analysis whether some or all of these peripheral clusters were sampling artifacts or represented real social entities. As the sample size of photographic identifications increased subsequent to those analyses, one of the three clusters was initially considered to be composed of two sub-clusters (Baird 2016), and later split with recognition of a fourth cluster (Mahaffy et al. 2017).

Collection of samples and photographic data for these studies has often been undertaken opportunistically, piggybacking work with false killer whales on field studies funded to work with other species (see Baird 2016) and benefiting from community-based science contributions (Bradford et al. 2018). Given their small population size (estimated at ~167 individuals in 2015, see Bradford et al. 2018) and a range that extends throughout the main Hawaiian Islands and as far as about 120 km from shore, sample sizes for analyses have been limited and subject to a variety of seasonal and geographic biases (see e.g., Baird et al. 2012; Bradford et al. 2018). Addressing these biases and limitations have been the focus of most of the directed research efforts with this population supported under the Species Recovery Grant obtained by the State of Hawai'i in 2015. Contracts from the State to CRC supported dedicated field efforts in areas with relatively limited sample sizes and at times of the year when information was lacking, as well as analyses of data obtained during those efforts, which were combined with existing CRC photographic and satellite tag data sets. This report summarizes field efforts and the results of these analyses.

Developing solutions to marine mammal bycatch in fisheries is challenging at the best of times. In the U.S., when bycatch is known to exceed a population's Potential Biological Removal (PBR) level (Wade 1998), Take Reduction Teams can be formed to bring fishermen, scientists, conservationists and managers together to develop ways to reduce bycatch (Young 2001). Determining whether bycatch exceeds the PBR level requires information both on population abundance and on bycatch rates, the latter usually obtained through fishery observer programs. When there are no observer programs to determine bycatch rates, as is the case for nearshore fisheries in Hawai'i, managing fishery bycatch is much more complicated, in part because fishermen are often unwilling to recognize that a bycatch problem exists in the first place.

In the case of the endangered MHI insular population of false killer whales, getting fishermen to recognize that there may be a bycatch issue has been a slow process for a number of reasons. Most importantly, there are a large number of commercial and recreational fishermen around the main Hawaiian Islands (Pooley 1993; McCoy et al. 2018), while the false killer whale population is small (Bradford et al. 2018), so any one fisherman may only infrequently encounter false killer whales. Compounding this problem are three other similar looking species of "blackfish" around the islands that are both more abundant than and often confused with false killer whales (Carretta et al. 2019; Yahn et al. 2019), leading to a common distrust of the false killer whale abundance estimates.

Discussions with fishermen regarding false killer whale bycatch in nearshore fisheries in Hawai'i have been occurring in a variety of venues since information emerged that individuals from the main Hawaiian Islands population have relatively high levels of fishery-related injuries (Baird and Gorgone 2005; Baird et al. 2015, 2017). These discussions have included annual meetings of the Pacific Scientific Review Group[1] — an advisory body to NOAA Fisheries; various meetings of the Western Pacific Regional Fishery Management Council and its advisory bodies; a recovery-planning workshop held by NOAA Fisheries in Honolulu in October 2016; and the annual meeting of the Marine Mammal Commission in Kona in May 2019. Fishermen at these meetings have often commented that they've never had interactions with false killer whales and expressed their belief that depredation by or bycatch of false killer whales in nearshore fisheries in Hawai'i rarely, if ever, occurs.

The ultimate goals of this effort are to understand what factors influence spatial use and movement patterns of false killer whales, and how they overlap and potentially interact with nearshore fisheries around the main Hawaiian Islands. Since spatial use varies by social cluster (Baird et al. 2012), which may also influence the probability of interacting with fisheries (Baird et al. 2015), we first use the updated full CRC photo-identification catalog to re-assess social clusters within the main Hawaiian Islands insular population. To examine overlap and potential interactions with fisheries, we characterize both false killer whale satellite tag data (Baird et al. 2012) and the spatial and temporal trends in nearshore commercial fisheries using data from the state's Commercial Marine Licensing (CML) reporting system. Fishermen who sell their catch in Hawai'i are required to have a CML and have mandatory reporting requirements for catch and effort in commercial fisheries statistical areas. We use data from these fishing reports for 2007 through 2017, a period that overlaps with almost all of the satellite tag data available for the main Hawaiian Islands insular population of false killer whales (2007-2018). We then combine these two data streams (false killer whale satellite tag data and information on fishing effort) to identify areas where individual fishermen are most likely to interact with false killer whales. In particular, we develop fishery overlap indices to assess the relative probability of an individual fisherman having false killer whales in their area when fishing. Such indices should allow for identifying which fishermen likely have the highest interaction rates, and thus may be the most qualified for assisting in the development of solutions to the depredation and bycatch issue. Finally, we explore movement patterns of false killer whales in relation to environmental variables to attempt to assess what factors play the greatest role in describing and understanding their spatial use. Combined these efforts are meant to contribute to ongoing efforts to create a recovery plan and implement recovery actions for this endangered population.

Methods

Analyses of both false killer whale tag data and fisheries effort data undertaken in relation to season were based on Hawai'i oceanographic seasons (based on average surface water temperatures; Flament 1996): winter – February-April; spring – May-July; summer – August-October; fall – November-January. CML commercial fisheries statistical areas include narrow strips extending approximately 3-4 km offshore along each of the main Hawaiian Islands, contiguous blocks that extend the nearshore strips offshore approximately 30-35 km, and a grid

[1] https://www.fisheries.noaa.gov/national/marine-mammal-protection/scientific-review-groups

system of blocks approximately 35-38 km per side in pelagic areas around the islands (Figure 1). We used these fisheries reporting areas for comparisons of satellite tag and fisheries effort data. All analyses of satellite tag and fisheries data were completed using the program R 3.6.0 (R Core Team 2019).

Field data collection

Photographs were obtained both from directed field efforts and from community-based science contributions. Field efforts were primarily targeted to areas where previous tag data suggested high probabilities of encountering different social groups, including western Oʻahu (in 2016 and 2017), Lānaʻi (in 2017 and 2018), and based out of Kawaihae Harbor on Hawaiʻi (in 2017). In addition, field days were added to a planned field project off Kauaʻi (in 2017). Field efforts were undertaken with a 7.3 m rigid-hulled Zodiac, with five to seven observers scanning 360 degrees around the vessel as it transited typically at speeds of 15-25 km/h. Prior to each field project, outreach efforts were directed to tour operators, fishermen, and any other researchers working in the area requesting calls regarding false killer whale sightings. Prior to one of the CRC field efforts (October 2017), the Pacific Islands Fisheries Science Center satellite tagged a false killer whale from the main Hawaiian Islands population, and information on the location of that tagged individual was used to locate the group during the CRC field effort. In the absence of any current reports (from sightings or a tagged individual), search effort was spread as widely as possible in areas of known high density based on previous tag data. We also coordinated with other researchers and tour vessels that would report sightings, in order to minimize an overlap of coverage. Distribution of search effort was influenced by sea conditions, with the research vessel searching in areas of Beaufort 3 or less when possible.

During each encounter, information was recorded on the start and end location of the group (recorded with a GPS), initial and end behavior and direction of travel, group size (minimum, best and maximum), the spatial spread of the group, and any observations of predation. Photographs were taken by two to four photographers throughout each encounter of all individuals with attempts to obtain series of both head and body/dorsal fin photos perpendicular to the body. When sea conditions and individual behavior were conducive to satellite tagging, we attempted to deploy one or more LIMPET satellite tags on individuals within the group, unless there were already two or more tags deployed on individuals within the group. Tags used were primarily location-only SPOT 6 tags (Wildlife Computers, Redmond, WA), although one SPLASH10-F tag was also deployed. Tags were deployed with a pneumatic projector and attached with two 6.7 cm titanium darts. When a second tag deployment was attempted, we would target individuals away from the first tagged animal to minimize the likelihood that tagged individuals would act in concert. Larger, slow-moving adults were chosen for tagging.

After tagging or if no suitable individuals were available for tagging, biopsy sampling was attempted. Biopsy samples were collected with a crossbow using a stainless steel biopsy tip 8 mm in diameter that penetrated approximately 15 mm. Biopsy samples were stored on ice immediately after collection until processing. Skin samples were subdivided with 1/3 of the skin frozen to be sent to the Southwest Fisheries Science Center for sex determination and population genetics (Martien et al. 2014) and for contribution to a study on epigenetic aging, and 2/3 of the skin and attached blubber stored at the University of Hawaiʻi in a -80°C freezer for later analyses. Tagging and biopsy sampling were undertaken under NMFS Scientific Research Permits No. 15330 and 20605 and was conducted pursuant to animal care and use protocols approved by the CRC Institutional Animal Care and Use Committee.

Photographic matching and association analyses

Photographs obtained from community-based science contributions, other researchers, and directed CRC field projects were first sorted within encounters by individual and then matched to a long-term photo-identification catalog (Baird et al. 2008). Each individual was given a distinctiveness rating from 1-4: 1=not distinctive; 2=slightly distinctive; 3=distinctive; 4=very distinctive. The best photo quality for each individual was rated based on the focus, contrast, size and angle of the fin relative to the photographic frame, categorized from 1-4: 1=poor; 2=fair; 3=good; 4=excellent.

Association analyses to determine social cluster (see Baird et al. 2012; Mahaffy et al. 2017) were undertaken using the individual sighting histories from the updated full CRC photo-identification catalog, using photos obtained from 2000 through April 2019. Analyses were conducted in Socprog 2.9 (Whitehead 2009) and illustrated in Netdraw 2.158 (Borgatti 2002). Previously recognized social clusters constructed using eigenvector-based modularity (Newman 2004, 2006) were re-evaluated in the expanded data set using the same methodology to determine whether any changes in cluster membership occurred and to resolve associations for socially ambiguous individuals. Division of the population into social clusters was considered meaningful when network modularity (Q) was ≥0.3 (Newman 2004, 2006). Social clusters were then visualized as a social network using a spring embedding layout (Croft et al. 2008), and association strength (calculated using a half-weight association index) was used to evaluate whether associations within and among all clusters were weak or robust. Durrell et al. (2004) noted that preferential associations among dyads are those with association indices more than twice that of the study population. In our case, the mean association index (restricted to individuals that were considered distinct or very distinct, with good or excellent quality photos and seen five or more times) was 0.12 (SD = 0.05, unpublished data). We used dyadic association strengths ≥0.3 in assessing clusters (Mahaffy et al. 2017), and considered groupings persisting above this threshold as socially meaningful clusters of individuals. Analyses were run both on the complete data set (i.e., no restrictions by photo quality, distinctiveness, or the number of times seen) as well as on restricted versions (e.g., with photo quality 2+ and distinctiveness 2+, and photo quality 3+ and distinctiveness 3+, as well as those seen 3+ times), and differences in cluster assignments were compared among them. Social cluster assignment of tagged individuals was used in analyses of tag data.

Tag data analyses

Methods related to the false killer whale satellite tagging data set have been published in detail (Baird et al. 2010, 2012) and so are only briefly summarized here. Analyses included tag data obtained during field efforts under this contract combined with tag data obtained during previous CRC field efforts. In addition, data from one tag deployed on an individual from the main Hawaiian Islands insular population by the Pacific Islands Fisheries Science Center were used in these analyses. This combined data set included Wildlife Computers SPOT5 (through early 2016) and SPOT6 (in 2016-2018) location-only tags as well as a small number of SPLASH10 location-dive tags (in 2010). Location data were first processed by Argos using a least-squares method, and subsequently filtered with a Douglas Argos-filter using a distance-angle-rate filter (Douglas et al. 2012), with user defined parameters as noted in Baird et al. (2012). We used the default rate coefficient for marine mammals (Ratecoef=25), retained locations with location class 2 and 3, and used a maximum rate of movement of 20 km/h. For cases where there was more than one satellite tag transmitting at a time, we assessed potential coordination of individuals by measuring the straight-line distances between all pairs of individuals when locations were received during the same satellite overpass. To avoid pseudoreplication, when mean distances between a pair were less than 5 km and maximum distances were less than 25 km, we used only one of each pair (the longest duration track) in analyses.

We first compared several metrics to determine false killer whale use of different commercial fisheries statistical areas, following the approach of Baird et al. (2012). We assessed density of whale use based on: 1) number of filtered Argos locations in each area, 2) the total amount of time (i.e., total visit duration) in each area; and 3) the number of unique tags. While the Baird et al. (2012) analysis used a 5 km x 5 km grid overlaid on the false killer whale satellite tag tracks, the fisheries statistical areas vary in size from 56 to 2,449 km^2 (median=1,007 km^2). Because the interpretation of whale use measures may vary by area size (e.g., a 100 km^2 with 10 unique tags should be ranked higher than a 1,000 km^2 area with 10 unique tags), we calculated density by dividing each measure by the size of each fisheries statistical area. To provide a common basis for visualization of different measures, we plotted each measure of whale density for fisheries areas as standard deviations above or below the mean value. We interpret values from 1 to 2 SDs above the mean as high density areas, and values of >2 SDs above the mean as very high-density areas.

For the total visit duration analyses, a spatial join was used to associate locations for each area. Tracks were developed by connecting the locations in temporal sequence and intersecting tracks within each fisheries statistical area, allowing for an assessment of the time spent by each tagged whale in each area. For each of these metrics, we generated maps both with and without a "late start," i.e., excluding an initial period of time post-tagging for each individual to reduce any potential bias related to the island off which the animal was tagged. To do this we calculated the time needed to travel to the farthest point of the known range of the population, and removed that period of time. This calculation was based on where the animal was tagged and the average travel speed for that individual. For example, for an individual tagged off Hawai'i, the farthest point of the range is west of Ni'ihau, a distance spanning almost the entire range of the population. Calculated periods of time excluded ranged from 2.54 to 9.66 days (median=4.72 days), representing from 3.6% to 53.4% (median=9.6%) of each tag record. Following Baird et al. (2012), for subsequent comparisons of spatial use by social cluster and season we used the total visit duration with a late start.

Fisheries data analyses

Commercial marine license data were obtained from the Hawai'i Department of Land and

Natural Resources Division of Aquatic Resources (DAR). To address confidentiality concerns, data were summarized for all presentations such that there were no less than three licensees reporting landings in any data strata, or the number of licenses were intentionally obscured by presenting summarized data products as standard deviations above or below the mean. We restricted analyses of DAR data to years that overlapped with the main Hawaiian Islands insular false killer whale satellite tag data (2007 through 2017). Although there were satellite tag data available for February and March 2018, DAR data was not available for the entire year at the time of these analyses, thus partial data for 2018 were excluded. Catch data for each fishery were examined to assess which species of fish with the highest levels of catch (i.e., the species responsible for the greatest weight of catch) were known to be part of the diet of the MHI insular false killer whale population (Table 1). Utilized gear types (as defined in the DAR reporting database) include aku boat, deep-sea handline, float line, hybrid (troll/handline/other), ika-shibi, kaka line, palu-ahi, rod & reel/cast/jib, short line, troll, troll bait, troll lure, troll stick, vertical longline, and "other". A number of other gear types (e.g., inshore handline) did catch species that are false killer whale prey (e.g., ahi), but catch of those species was lower than for other species, and thus these fisheries were excluded from analyses. Analyses were also undertaken restricted to the troll fishery, as preliminary analysis revealed the troll fishery as the dominant fishery throughout the whales' range. Gear types included for the troll fishery analysis included troll, troll bait, troll lure, troll stick, and hybrid (troll/handline/other).

Annual, seasonal, monthly, and overall (i.e., entire study period) fishing effort metrics were computed. Fishing effort metrics were also summarized for the time period when the greatest number of false killer whale tags were transmitting: October 2009 through March 2010. This was undertaken to assess whether patterns over short periods are similar to the overall trends seen in the larger data set. Fishing effort was assessed using several metrics, including total number of vessels, total number of days of fishing effort, and total catch, both within each fisheries statistical area and over the entire study area (i.e., all fisheries statistical areas within the insular false killer whale range). The total number of vessels was computed as the sum of unique fishing licenses reporting catch in any fisheries statistical area over the 11-year period of interest (2007 through 2017). Total number of days of fishing effort was calculated as the sum of days fished by each unique license. Total catch was calculated as the sum of kilograms of fish caught over the entire period of interest. As per the false killer whale density maps, fishing effort metrics were adjusted for the size of each fishing area by dividing the effort metric by the fishing area size. To provide a common basis for visualization of different fishing effort density measures, we plotted each measure as standard deviations above or below the mean value. Following the analyses for whale density, we interpret values from 1 to 2 SDs above the mean as high density areas, and values of >2 SDs above the mean as very high-density areas.

Fisheries overlap indices

The primary goal of the indices is to represent the perspective of the fishermen in a way that reflects the probability of interactions with false killer whales such as depredation of catch. For example, if there is a single vessel fishing in an area with a large number of false killer whales, the probability of having a false killer whale overlapping in space and time when the vessel hooks a fish would be relatively high. By comparison, if there were a single false killer whale in an area with multiple fishing vessels all catching fish, any individual fisherman's probability of having that false killer whale overlap in space and time when a fish is caught is relatively low. These indices presuppose that there is some probability that false killer whales will actively approach fishing vessels or attempt to depredate catch if they are nearby when a fish is hooked.

Fishery effort was restricted to the same hook-and-line fisheries included in the fishery effort analyses above, restricted to 2007 through 2017, and excluding areas where there were fewer than three licenses, as well as areas with less than the equivalent of one day of fishing effort per month over the 11-year period. We also examined a subset of fisheries effort data corresponding to the period with the largest number of false killer whale satellite tag deployments (i.e., October 2009 through March 2010). As with the computations for fishing effort metrics, the purpose of this restricted period was to assess whether the broader trends in overlap between false killer whales and fisheries also applied to the period where we had the most comprehensive false killer whale location data set.

Satellite tag data were restricted to the same data set as used in the false killer whale analyses above (i.e., controlled for pseudoreplication), using total visit duration with a late start to minimize any bias associated with where the individuals were tagged. Data from individuals from all social clusters (Baird et al. 2012; Mahaffy et al. 2017) were pooled. For any given amount of time spent in an area, the probability of overlap between a false killer whale and a fishing vessel in that area will vary according to the size of the area. Thus, we calculated the time spent per unit area:

$$\text{Time spent per unit area} = \frac{False\ killer\ whale\ cumulative\ time\ in\ fisheries\ area}{size\ of\ fisheries\ area}$$

False killer whale time spent per unit area was calculated both for the entire period (2007 through March 2018) and for the restricted time period (October 2009 through March 2010) matching the restricted fishery effort data.

Three measures of fishing effort were used in fishery overlap index (FOI) calculations: 1) total catch in each area; 2) number of days fished in each area; and 3) number of unique licenses in each area. To provide a basis for comparison among areas with a reference value that could be broadly relevant to fishing communities in Hawai'i, we scaled the FOIs in reference to values for Kona (area 121). This area had the largest catch (17.7% of all fish caught by weight), number of licenses (a combined 1,228 over the 11-year period), and days fished (a combined 59,442 over the 11-year period) of any of the fisheries statistical areas. This area also receives a lot of attention throughout Hawai'i as the premiere location for fishing tournaments, and thus fishermen throughout the state may be able to relate to this area when making comparisons with other areas where only a smaller number of fishermen have experience. Three separate Kona FOIs were calculated (each using a different measure of effort, see above) as:

$$\text{Kona FOI} = \frac{Time\ spent\ per\ unit\ area\ in\ area\ 121}{measure\ of\ effort\ (catch, days\ fished, licenses)\ in\ area\ 121}$$

The scaled FOIs for each area (using each of the three measures of effort) were thus calculated as:

$$\text{FOI} = \frac{\textit{Time spent per unit area}}{\textit{measure of effort (catch,days fished,licenses) in area}} * \frac{1}{\textit{Kona FOI}}$$

Thus the scaled FOI values for Kona (area 121) were all 1, and all other areas were calculated relative to this. For visual comparisons index values were graphically represented relative to Kona in bins (e.g., < 5 times, 5 – 10 times, 10 – 50 times, 50 – 200 times, etc).

False killer whale spatial use in relation to environmental variables

The influence of environmental factors (e.g., chlorophyll-a concentration, moon illuminated fraction, sea surface temperature) on false killer whale spatial use was analyzed as this could indicate conditions that may increase the likelihood of individuals being in closer proximity to fishing efforts, and therefore increased susceptibility to bycatch. Of particular interest were environmental conditions associated with nearshore or offshore false killer whale locations (i.e., distance from shore). For these analyses, filtered tag data were processed with R package *bsam* v. 1.1.2[2], a Bayesian switching state-space model (Jonsen et al. 2005), that produces equally spaced time-steps (i.e., locations). Locations were generated for every four hours. This reduces bias associated with locations due to tag programming and variable satellite overpasses in low latitude areas. Tag locations derived from the switching state-space model (SSSM) were annotated with distance (kilometers) to shore, defined as the nearest projection from the water, including islands, atolls, reefs, and rocks.

Linear mixed effects models were used to model distance to shore in response to a number of environmental factors (Table 2) through the R package *nlme*[3] (Pinheiro et al. 2019). Individual/tag ID was included as a random effect to account for pseudoreplication inherent among serial observations within each tagged animal. Prior to modelling, data exploration was carried out following the protocol described in Zuur et al. (2010). Briefly, univariate analyses of each covariate (i.e., environmental variable) with respect to the response variable (distance to shore) was undertaken to examine potential relationships that may arise in multivariate analysis and to determine if any variable transformations may be warranted. Correlation analysis was carried out to identify multicollinearity among continuous variables. Where two variables were collinear, the variable more strongly correlated with the response variable was retained.

Following data processing, the remaining variables were fit to a mixed effects model. All continuous variables were standardized to account for differing measurement scales and to avoid imprecision in parameter estimates (Kinney et al. 2017). A backwards stepwise selection process was used to eliminate negligible variables through the package *MASS*[4] (Venables and Ripley, 2002). Variables retained from this process were used in several combination models and tested for best model fit. All models were assessed for presence of temporal autocorrelation and correlation structures were added to models as needed. Model fit was based on corrected Akaike's Information Criterion (AICc) and associated weights, and marginal and conditional r-squared values (Nakagawa and Schielzeth, 2012). The relative importance (RI) of predictor

[2] https://cran.r-project.org/web/packages/bsam/index.html
[3] https://cran.r-project.org/web/packages/nlme/nlme.pdf
[4] https://cran.r-project.org/web/packages/MASS/MASS.pdf
[5] https://cran.r-project.org/web/packages/relaimpo/relaimpo.pdf

variables was calculated using the *relaimpo*[5] package, although this function does not account for random effects and therefore these values were not given significant weight in interpretation, but rather provided indication of relative importance (Grömping 2006). The model with the best ensemble of these criteria was selected as the best fit model in accordance with model assumptions.

Results

Sightings and individual photo-identification

Field efforts undertaken in 2016, 2017, and 2018 had a combined 10,022 km of search effort resulting in 22 false killer whale sightings in three of the four areas studied (Figure 2, Table 3). During those sightings 14 LIMPET satellite tags were deployed (Table 4) and 24 biopsy samples were collected.

From the encounters 214 identifications were obtained, and of those 171 were good or excellent photo quality, representing 114 individuals. Identifications are being provided to collaborating researchers with the Pacific Islands Fisheries Science Center for mark-recapture abundance estimation. All encounters were with individuals from the main Hawaiian Islands population. For association analyses to determine social cluster of individuals present, identifications were combined with recent (2016-2018) community-based science and other researcher contributions from the main Hawaiian Islands population (139 identifications with good or excellent quality photos) as well as good/excellent quality photos from this population in the CRC photo-ID catalog from 2000 through 2015 and encounters from mid-2018 (after the end of the field effort supported by this grant) through April 2019 (1,244 identifications).

Association analyses for the combined data set without restrictions revealed nine social clusters (modularity Q=0.66). Four of these nine were the clusters previously recognized (i.e., Clusters 1, 2, 3, and 4; see Mahaffy et al. 2017). Four of the remaining five clusters were small clusters peripheral to either Cluster 1 (one cluster) or Cluster 2 (three clusters), mostly composed of younger individuals seen 1-2 times (Figure 3). For example, one of these peripheral clusters was composed of two calves of Cluster 1 individuals that have only been seen with Cluster 1 individuals. Thus, these four clusters were considered artifacts of sample size and were lumped with either Cluster 1 or 2, following the approach of Baird et al. (2012). The remaining cluster identified by modularity was intermediate between Clusters 1 and 3 and included many individuals seen over longer time spans (i.e., > 8 years), and was designated as Cluster 5. Prior association analyses had identified this as a possible cluster, but a number of sightings of this group during field efforts in 2016, 2017, and 2018 provided a large enough sample size to clarify cluster identity. When visualized as a social network without restrictions, all five clusters are inter-connected. However, restricting analyses to individuals seen on three or more occasions and removing associations among dyads with association index values of <0.3 fractures the social network in several locations: Cluster 4 is no longer associated with the main network, and Clusters 1, 2, and 3 are only indirectly connected through Cluster 5 (Figure 3). Restrictions placed on the social network demonstrate that although associations among clusters are extensive, they are also weak and likely represent casual associations.

We tested the sensitivity of cluster assignments to various levels of restrictions for photo quality and distinctiveness as well as number of times seen. In all cases modularity values were high (0.651 to 0.688), with from five to seven clusters identified. In cases of 7 (distinctiveness 2+, photo quality 2+) or 6 (distinctiveness 3+, photo quality 3+) clusters, small peripheral clusters were lumped with one of the five main clusters (Table 5). Overall, few changes (i.e., two percent of individuals or less) were assigned to a different cluster than those they were assigned to in the analysis without restrictions (Table 5). One of the individuals that was assigned to a different cluster was one of the tagged individuals (PcTag031), who was assigned to Cluster 5 (with no restrictions) or Cluster 1 (with restrictions). For the purposes of mapping spatial use of fisheries statistical areas by cluster (see below) we did two iterations, one with PcTag031 in the Cluster 1 sample, and one with PcTag031 in the Cluster 5 sample.

False killer whale spatial use in relation to commercial fisheries statistical areas

After restrictions for pseudoreplication, data from 38 satellite tag deployments from 2007 through 2018 were used in false killer whale density analyses. After late start analyses (i.e., removing the initial period of each deployment), individual tracking data used ranged from periods of 6.1 to 189.0 days (median=45.0 days), for a cumulative total of 2,205.7 days. Location data were obtained from all years over the 12-year span, although with substantial gaps throughout that period (Figure 4). Tags used in analyses were deployed off Kaua'i (n=1), O'ahu (n=13), Lāna'i (n=2), Maui (n=2), and Hawai'i (n=20), and were deployed on individuals from all five social clusters (Cluster 1, n=22; Cluster 2, n=3; Cluster 3, n=5; Cluster 4, n=3; Cluster 5, n=5)[3]. For Cluster 1, the 22 deployments involved 20 individuals, with two individuals each tagged twice (one individual tagged in 2008 off Hawai'i and 2009 off O'ahu (see Figure 3A & 3B in Baird et al. 2012), and one tagged in 2008 off Hawai'i and in 2016 off O'ahu). A comparison of movement patterns for each pair of deployments (not shown) indicated the individuals had very different spatial use patterns for each of their two deployments, and thus both deployments for each pair were used in analyses. While there were tag location data from throughout the year, there were strong seasonal biases by cluster (Figure 4).

Plots of density of number of individuals (i.e., number of unique tags) documented in fisheries statistical areas indicated that the only areas with high or very high density were nearshore areas around O'ahu and Maui Nui, with or without a late start (Figure 5). The other two metrics of false killer whale spatial use (i.e., number of locations, total visit duration) revealed high or very high use primarily in offshore areas, with and without a late start (Figure 5). In all six metrics, low density areas (from -1 to 1 SDs around the mean value) were found off Kaua'i, Ni'ihau, and the southern half of Hawai'i. Differences in spatial use with and without a late start, to reduce bias associated with tagging site location, were apparent for all three metrics. Using a late start only resulted in changes in areas that were considered high density in the case of total visit duration, with nearshore areas off Wai'anae (areas 402 and 403) and Kohala (area 103) no longer being considered high density in the late start analyses (Figure 5). Each metric provides a slightly different perspective on area use. The number of unique individuals emphasizes areas that are travel corridors, over those where individuals spend extensive periods of time. The number of locations and total visit duration were similar, but the former may be more subject to biases associated with satellite tag programming regimes (e.g., temporal

[3]When PcTag031 is assigned to Cluster 5.

clustering of locations in certain hours of the day). Of the various metrics used (number of individuals, number of locations, total visit duration), we used total visit duration with a late start for subsequent comparisons of spatial use by cluster and by season, as this approach should minimize biases associated both with tagging site location and with satellite tag programming regimes.

Very high-density areas (defined as >2 SD above the mean) varied by cluster (Figure 6). Cluster 3 and Cluster 5 had the greatest overlap in very high-density areas, sharing E Oʻahu (offshore) and NW Molokaʻi (offshore), with Cluster 3 also having a very high-density area off Kāneʻohe (offshore), and Cluster 5 off NE Molokaʻi (offshore). Cluster 2 (SE Maui (nearshore), N Kona (offshore), and N end Hawaiʻi (nearshore and offshore)) and Cluster 4 (SE Oʻahu (offshore), NW Molokaʻi (offshore), Penguin Bank (nearshore and offshore), and W and S of Lānaʻi (offshore)) had no overlap in very high-density areas. Cluster 1 had overlap in high-density areas with Cluster 2 (N end Hawaiʻi (nearshore and offshore)) and Cluster 4 (Penguin Bank (offshore), and SE Oʻahu (offshore)), but also had very high-density areas not shared by any other social cluster (northern Waiʻanae (nearshore), SE Oʻahu (nearshore), NE Molokaʻi (nearshore), and N Maui (offshore)). Comparisons of spatial use patterns by cluster were largely unaffected for Cluster 1 when PcTag031 was considered part of Cluster 1, although there were some small changes for Cluster 5 (Figure 7).

Very high-density areas also varied seasonally (Figure 8), with fall (November – January) and winter (February – April) having highest density areas off eastern Oʻahu and Molokaʻi, a broadening of high density areas in spring (May – July) from eastern Oʻahu to northern Hawaiʻi, and with highest density areas concentrated off northern Hawaiʻi in summer (August – October). Because of the potential interaction between social cluster and season (Figure 4), we also examined seasonality using information only from Cluster 1, the group with the largest number of tag deployments (n=22; Figure 9). Seasonal patterns for Cluster 1 were broadly similar to the overall pattern (e.g., a shift from Hawaiʻi to Molokaʻi from summer to fall; Figure 9), but also showed some patterns that were obscured when examining the larger data set (e.g., high-density areas off nearshore Kona and Hāmākua in spring).

Variability in fisheries effort

Data from 14 fisheries as noted in the CML database were included in analyses of fishing effort (Table 6) based on overlap of primary catch species with false killer whale diet (Table 1). Of the 125 commercial fisheries statistical areas with overlap by false killer whale satellite track lines, 117 had fishing effort during the 2007-2017 period. Three of the 117 were excluded with fewer than three licenses, and 24 additional areas were excluded as they had less than an average of one day per month of fishing effort, resulting in calculation of fishery effort statistics for 90 areas. With the exception of area 307, an area along the north side of Kahoʻolawe where fishing is generally restricted, and area 312, along the NW coast of Molokaʻi, all excluded areas were in offshore areas.

The troll lure fishery was by far the largest fishery based on number of licenses, total days fished, and weight of primary catch species caught (Table 6). All three measures of fishing effort (i.e., catch, number of days fished, number of licenses) were highly correlated (correlation coefficients 0.84 to 0.95). Regardless of the measure of fishing effort used (Table 7), or density of those measures (i.e., effort divided by area size; Figure 10), there was broad similarity among the islands in terms of relative fishing effort. Based on density (effort per unit area), a number of areas had high or very high levels of fishing effort with one or more metrics (Figure 10): eastern Kaua'i (nearshore), Wai'anae and the south and northeast shore of O'ahu (nearshore and offshore), Kona (nearshore and offshore), south Kohala (nearshore), South Point (nearshore), Puna (nearshore), and Hilo (nearshore and offshore). Fishing effort did vary slightly over the 11-year period, with a gradual increase in the number of licenses and number of days fished up until 2012, and a slow decrease from 2013 through 2017 (Figure 11). Fishing effort peaked in May through July (Figure 11). Patterns for troll fisheries (including troll lure, troll stick, troll bait, and troll) were similar (Figure 12), but with a stronger seasonal decline, with lowest fishing efforts in November through January. Spatial distribution of fishing effort also varied seasonally (Figure 13).

Fishery overlap indices

Fishery overlap indices were calculated for 90 areas. These 90 areas accounted for 95.4% of all of the false killer whale time from satellite tag data analyses. In the excluded areas (i.e., those with fewer than three licenses or an average of one day of fishing effort per month), the percentage of time spent by false killer whales ranged from 0.001% to 0.748% (median=0.036%). For the 90 areas, the percentage of time spent by tagged false killer whales ranged from 0.007% to 14.89% (median=0.17%). There were 62 areas where false killer whales spent less than half of one percent of their time, and five areas where they spent more than five percent of their time (a combined 44.8% of their time). None of these five areas were in the top 10 areas for kilograms of fish caught, although one of them (area 122, N Kona offshore, see Figure 1) ranked fifth for number of days fished and fourth for number of licenses (Table 7).

Of the 90 areas for which FOIs were calculated, FOI values for Kona (area 121) were ranked the 7th lowest using catch, 4th lowest using days fished, and 8th lowest using number of licenses. FOIs were highly correlated for the three effort measures used (correlation coefficients 0.79-0.90). Regardless of the effort measure used, there were relatively low FOI values offshore around Kaua'i and off the southern half of Hawai'i (nearshore and offshore), intermediate to high FOI values off parts of O'ahu, Maui and Lāna'i, and very high FOI values off Moloka'i, southern Wai'anae (nearshore) and the east side of O'ahu, in some nearshore areas off Maui and Lāna'i, and off the north end of Hawai'i (Figure 14; Table 8, 9).

For the restricted period (October 2009 through March 2010), we used data from eight tagged false killer whales (four tagged in October 2009 off O'ahu and four tagged in December 2009 off Hawai'i), representing individuals from three of the five social clusters (clusters 1, 4, and 5). Tag data used in analyses covered periods ranging from 11.0 to 97.2 days, for a combined 485 days of false killer whale movements. Thus, over the entire six-month period we had tracks from the equivalent of 2.67 individual false killer whales each day. All three measures of fishing effort and the amount of time false killer whales spent per unit area were highly correlated in comparisons between the complete data set and the restricted data set (correlation coefficients ranging from 0.92 to 0.98). It should be noted however that the restricted data set is a subset of the complete data set, although only covering ~5% of the time span of the complete data set. There were some differences among the complete and restricted data sets. Of the 125 areas where false killer whales spent time in the complete data set, there were 18 with no false killer whale usage in the restricted time period. In the complete data set these 18 areas accounted for only a combined 0.3% of all false killer whale time. Of these, 12 were excluded in the complete analysis as they had fewer than three licenses or less than one month per day of fishing effort on average. The remaining six areas were either in pelagic waters or around Kauaʻi or Niʻihau. For comparisons restricted to the 90 areas for which FOIs were calculated for the complete data set, false killer whales were recorded in 84 areas, and fishing effort was documented in 89 areas in the restricted data set. For the areas with no false killer whales documented in the restricted data set, the FOI based on catch in the complete data set were relatively low for all of them (<100 times the Kona FOI). FOI values between the two data sets were strongly correlated (catch = 0.59, days fished = 0.81, licenses = 0.70) and geographic patterns were similar (Figure 15), although again the restricted data set is a subset of the complete data set so some level of correlation is expected. Regardless, these results suggest that the fishery effort and false killer whale spatial use patterns seen in the complete data set are relatively robust over shorter time periods.

False killer whale spatial use in relation to environmental variables

A total of 21 environmental variables and 3 demographic variables were considered for analyses (Table 2). Individual ID and sex were not included as model covariates, as the former would cater to inter-individual variation not of interest for our objectives and the latter was incomplete for several tagged individuals (i.e., sex unknown). Depth is inherently strongly correlated with distance from shore and would likely dominate the predictive power of the model, muting detections of influences from other covariates, and therefore was excluded. Distance to eddy edge was considered to be related to other variables included in the model (e.g., current velocity), so was excluded as a covariate to simplify the model. Categorical variables windward/leeward, year, island where tagged, and nearest island were also excluded as they would add a level of complexity that would lessen the statistical interpretability of the model, but could be considered in additional analyses. Tag locations with incomplete environmental data (missing variables) were removed prior to analysis. The final analytical data set contained 9,641 SSSM observations, constituting 83% of the original data set (11,488 SSSM observations).

The response variable, distance to shore (km), was log-transformed to meet model assumptions of normality. Univariate analyses revealed that most continuous environmental variables did not have a linear relationship with the response variable and were log-transformed. These variables included terrain roughness index, sea surface temperature, surface chlorophyll-a concentration, current velocity, and total significant wave height. Following correlation analysis, the final set of variables included season, cluster, day/night, terrain roughness index, sea surface temperature, surface chlorophyll-a, moon illuminated fraction, PDO index, wind speed, sea surface salinity, current velocity, and total significant wave height.

The backwards stepwise selection process removed sea surface salinity, and remaining variables were fit to a linear mixed effects model. A continuous first-order autoregressive correlation structure was included in models to account for temporal autocorrelation. Because there is unequal sample representation among all five social clusters (Cluster 1, n = 22; Cluster 2, n = 3; Cluster 3, n = 5; Cluster 4, n = 3; Cluster 5, n = 5), any significant findings related to social cluster would be biased and driven by relatively limited observations (for clusters 2-5). Therefore, a variance covariance structure, *varIdent* weight, was added to the model and covariate for cluster was excluded. This structure allowed us to model different residual variances per social cluster and broadly describe environmental drivers of spatial use among false killer whales from our study population.

The best candidate model explained approximately 40% of the variance (conditional R^2 = 0.396) in distance from shore locations (Table 10). Covariates included, in decreasing importance, were current velocity, surface chlorophyll-a, total significant wave height, sea surface temperature, wind velocity, day/night, Pacific decadal oscillation (PDO) index, roughness, and moon illuminated fraction (Table 11). Quantile-quantile and standardized versus fitted residual plots revealed a slightly skewed trend towards lower values (not shown), albeit not tremendously. This may reflect further complexity in relationships among predictor variables or factors influencing movements closer to shore.

All covariates included in the top model were significant predictors yet differed in their relative contribution to the model (Table 11). Strong positive relationships with distance from shore (i.e., increase in distance from shore with increase of predictor variable) were seen for current velocity (RI = 38%), total significant wave height (RI = 12%), and sea surface temperature (RI = 6.3%). Wind velocity and moon illuminated fraction showed the same positive trend with increased distance from shore, yet were relatively unimportant compared to other model covariates (RI = 4.2%, 0.76%, respectively). Results showed a strong negative relationship between distance to shore and surface chlorophyll-a levels (RI = 32%), indicating nearshore locations are associated with increased chlorophyll-a levels. Covariates day/night (nighttime compared to daytime), PDO, and roughness exhibited the same trend, however were relatively unimportant compared to other variables driving the model (RI = 4%, 3.6%, and 1.2%, respectively).

Discussion

Overall, the field efforts supported under the Species Recovery Program grant were extremely successful in terms of the number of false killer whale encounters, photos and biopsy samples obtained, and satellite tags deployed (Figure 2; Tables 3, 4), helping address some of the biases in data available for this population and providing a much stronger basis for understanding and managing it. Unlike the majority of prior CRC field efforts that have been funded primarily for working with a broad range of species, the success of these field efforts was largely due to the ability to target times and locations where encounter rates with false killer whales were expected to be relatively high. False killer whales were encountered in all five of the field efforts that were targeted to areas with expected high encounter rates; the only field effort where false killer whales were not encountered was off Kaua'i, an area that is not a high density area for this population (Figure 5). Photographs obtained, particularly of social groups for which sample sizes were relatively small, have been critical in the assessment of previously unrecognized social structure within this population. When social organization was first assessed, it was thought that there were three social clusters (Baird et al. 2012), and as sample sizes increased it became apparent that there were probably four or five social clusters (Baird 2016; Mahaffy et al. 2017).

Analyses of the larger data set available, including photos both from our encounters and from encounters by other researchers and community-based science contributions, now reveals five distinct social clusters within this population (Figure 3). Importantly, obtaining photos of individuals from all five social clusters in this effort will reduce uncertainty in mark-recapture abundance estimation (see Bradford et al. 2018).

We undertook sensitivity analyses to assess how restrictions on the data set by photo quality, individual distinctiveness, or the number of times seen influence cluster assignments (Table 5). Both photo quality and distinctiveness play a role in terms of the likelihood of missed matches or mismatches (Baird et al. 2008), and cluster assignments are dependent on association values. Thus, confidence in association patterns increases with restrictions on both photo quality and distinctiveness, and the sample size of the number of times individuals are seen. These analyses indicated that there is some uncertainty regarding cluster membership of a small proportion of the individuals in the population (≤2%), and an increased sample size of photos, particularly of Cluster 5, are needed to help clarify the association patterns and cluster affiliations of those individuals.

In terms of satellite tagging, tags were deployed widely throughout the islands, including deployments off Oʻahu (in 2016 and 2017), and Hawaiʻi (in 2017), as well as the first deployments of tags on false killer whales off either Lānaʻi or Maui (in both 2017 and 2018), helping reduce the bias associated with the majority of tags previously deployed on individuals in this population off Hawaiʻi (Baird et al. 2012). Although there are still strong seasonal biases and small sample sizes for four of the five social clusters (Figure 4), analyses of spatial use reveal considerable variability in spatial use by cluster (Figure 6). Based on data available to date, three of the five social clusters have relatively restricted high density (1 to 2 SD above the mean) and very high density (>2 SD above the mean) areas. For Cluster 2 these areas are off Hawaiʻi and SE Maui, for Cluster 4 they are off eastern Oʻahu, Molokaʻi, Lānaʻi, Kahoʻolawe, and W Maui, and for Cluster 5 they are off Oʻahu, Molokaʻi, and NW Maui (Figure 6). By comparison, both Cluster 1 and Cluster 3 have high density areas that range from Oʻahu to Hawaiʻi. Given the seasonal patterns documented for Cluster 1, the group with the largest number of tag deployments (Figure 9), it will be important to assess whether seasonal patterns in high density areas also exist for social clusters with smaller sample sizes. Regardless, such cluster-specific and seasonal variations in spatial use have implications for overlap with nearshore fisheries in Hawaiʻi.

Our development of fishery overlap indices to reflect the relative probability of overlap between false killer whales and individual commercial fishermen showed that the area off Kona (area 121) is one of the areas in the main Hawaiian Islands where a fisherman may be least likely to experience false killer whale depredation of his catch. Regardless of which measure of fishing effort was used (total catch, days fished, or the number of licenses), Kona was in the bottom 10% of the 90 areas for which FOIs were calculated. This finding has important implications for discussions going forward with fishermen on how to address both depredation by and potential bycatch of false killer whales in nearshore fisheries. Despite the fact that Kona is responsible for the greatest levels of catch, licenses, and days fished (Table 7), fishermen off Kona likely have little experience with depredation or false killer whale bycatch, particularly in comparison to areas with high FOIs. From the perspective of identifying fishermen that may have the most frequent interactions with false killer whales, those that fish off the north and east side of Oʻahu, Molokaʻi, the north side of Maui, and the north end of Hawaiʻi are all likely to have interaction rates many times higher than those that fish in areas off the southern half of Hawaiʻi or off Kauaʻi (Figure 14). Depending on the fishery effort measure used, the highest FOI values are up to several hundred (based on licenses) or several thousand (based on catch or days fished) times higher than that off Kona (Table 9). For the restricted data set, including tag data from eight deployments and fishery data over a 6-month period, there were broad similarities in FOIs in the area ranging from northwest Molokaʻi east to Hawaiʻi (Figure 15). There were a number of areas in the complete data set with high FOI values (i.e., >100 x Kona) that had low values in the restricted data set (i.e., <15 x Kona), primarily around Oʻahu. Most of these were relatively small nearshore areas (e.g., areas 400 through 409). These differences could reflect seasonal variation in fishing effort, the limited number of social clusters tagged during the restricted time period analysis, or seasonal or inter-annual variability in false killer whale spatial use.

Our findings have important implications for how to address depredation and bycatch of false killer whales in nearshore fisheries in Hawaiʻi. A study by Madge (2016) involving interviews of fishermen in Hawaiʻi found that many had difficulty discriminating among species of "blackfish." Fishermen that regularly fish in areas with high FOI values could be the focus for targeted outreach efforts to aid in improving identification skills and generally raising awareness of the behavior of different species, particularly as it relates to the likelihood of depredation of catch. For example, melon-headed whales (*Peponocephala electra*) and short-finned pilot whales (*Globicephala macrorhynchus*), two other similar looking species, feed primarily at night and deep in the water column on squid or small fish (West et al. 2018; Owen et al. in press) that are unlikely to overlap with the catch of most nearshore fisheries.

Our results also suggest that measures to gather additional information on interactions between fishermen and false killer whales, such as observer efforts or electronic monitoring, should be focused on fishing that occurs within these high FOI areas. Given the large number of fishermen with CMLs in Hawaiʻi and the small number of false killer whales in the population, any sort of observer program or electronic monitoring would require a substantial investment if applied uniformly across the fishing fleet. As noted however, fishermen in some areas (e.g., offshore of Kauaʻi or the southern half of Hawaiʻi) likely have very low interaction rates in comparison to those fishing in areas such as off Molokaʻi, eastern Oʻahu or Kohala. Selectively targeting such areas for monitoring would reduce costs and increase the likelihood of obtaining a useful sample size of interactions.

There are a number of limitations or potential biases with our fishery overlap indices. These include: fishing methods that were excluded from our analyses; potential heterogenous false killer whale (or fishery) spatial use of the larger offshore fishing statistical areas; bias associated with islands where individuals were tagged; and the restriction of our analyses to commercial fishing effort. False killer whales in Hawaiʻi have a diverse diet that includes both pelagic and reef-associated game fish (Table 1), and fishing methods included in the analyses were those that had pelagic game fish as the primary catch species. Many other fishing methods in Hawaiʻi catch both pelagic and reef-associated game fish that are known to be part of the diet of this population of false killer whales, but these species were not the primary species caught. In addition, recreational fishing effort in Hawaiʻi is likely responsible for a much greater total catch than commercial fisheries, particularly of reef-associated fish (McCoy et al. 2018), but the lack of comprehensive recreational fishing statistics (i.e., effort metrics by area) limits the ability to assess how recreational fishing effort might influence such indices. We attempted to address tagging site (i.e., island) bias by removing the initial portion of each tag deployment period equivalent to the amount of time needed for that tagged individual to travel to the periphery of the population range. That said, there is a possibility the low FOI values off Kaua'i reflect in part the small number of tags (n=1) deployed off that island. Ironically, for the one individual tagged off Kaua'i, the animal had moved away from Kaua'i during that initial period of time where data were excluded, reducing the amount of time false killer whales spent around Kaua'i in the analyses. Regardless, additional tag deployments in the central (O'ahu) and western (Kaua'i) part of the range of this population would be of value for addressing this potential bias. Lastly, while the nearshore fisheries statistical areas were relatively small (~100-250 km^2), the contiguous offshore areas are much larger (~500-2,500 km^2). Both large and small areas were ranked high in terms of FOIs (Table 9, Figure 14). However, our indices implicitly assume that false killer whales use these areas randomly or uniformly, when in fact satellite tag data examined on a small spatial scale show higher densities in some areas (Baird et al. 2012), and spatial patterns may vary due to a wide range of environmental factors (Table 10, 11). Given the spatial resolution of the fishery effort data we are unable to address this potential bias, but it could have some influence on the probabilities of overlap between false killer whales and individual fishermen.

We also attempted to assess what environmental or other factors may be influencing false killer whale spatial use, to try to get a better idea of whether certain environmental conditions might be more likely to influence spatial use in a way that affects the probability of fishery interactions. Mixed effects models revealed that locations relative to distance from shore are strongly influenced by current velocity, surface chlorophyll-a concentrations, total significant wave height, and sea surface temperature. Other variables found to influence distance from shore locations included wind velocity, moon illuminated fraction, time of day, PDO index, and roughness, although their contribution to the model did not match those of the more influential predictors based on t-values, coefficient estimates and confidence intervals, and relative importance (Table 11). Results indicated that nearshore locations were associated with higher surface chlorophyll-a concentrations, suggesting a shift in animal space use to nearshore areas is associated with increased chlorophyll-a levels. Conversely, locations farther offshore were strongly correlated with increased current velocity, sea surface temperature, and total significant wave height. These variables are associated with rougher sea conditions (e.g., storms), where turbulence and nutrient mixing may occur (Rumyantseva et al. 2015). Both negative and positive relationships were associated with conditions indicative of increased productivity potentially associated with upwelling and mixing processes. Thus, the remaining variables may provide underlying context as to when individuals are located in productive offshore or inshore locations. For instance, greater fractions of illumination of the moon were correlated with increased distance from shore, suggesting that during full and waxing/waning gibbous moon phases individuals may tend to be farther offshore. This could be related to changes in prey behavior, as has been suggested by Owen et al. (in press) for short-finned pilot whales in Hawai'i. Further, locations during the night were negatively correlated with distance from shore. This indicates that insular false killer whales may tend to move closer to shore during the nighttime, which could also be associated with prey behavior, if false killer whale prey were following the inshore movements of organisms associated with the mesopelagic boundary community (Reid et al. 1991). Similarly, higher PDO indices were correlated with locations closer to shore. A positive PDO index describes conditions where sea surface temperatures are anomalously cool in the interior North Pacific and warmer around the Pacific coasts, as well as when sea level pressures are below average over the North Pacific (Mantua and Hare 2002). These conditions have been linked to shallow upwelling processes, which may help explain why individuals may tend closer to shore during periods with higher PDO indices (Chhak and DiLorenzo 2007). However, metrics such as the PDO index explain changing conditions over long time scales, and therefore may not be as informative in predicting fine scale movements as more frequently occurring environmental processes, such as lunar phase and time of day.

Although our models incorporated a weight to allow residuals to vary among social clusters, investigating differences in what environmental conditions drive differences among distance to shore or high use areas by social cluster would be valuable. Because these social groups differ in their high-use domains which are often characterized by different static environmental features (e.g., bathymetry, depth, slope, roughness, etc.), we might expect these groups to respond to varying dynamic environmental conditions differently. For example, spatial use of Cluster 1 appears to vary seasonally among the main Hawaiian Islands (Figure 8), suggesting the need for subsequent analyses investigating seasonal drivers of spatial use. Recently applied methods in dynamic habitat suitability modeling, such as random forest analysis (Kinney et al. 2017), generalized additive models, and boosted regression trees (Abrahms et al. 2019) could potentially be useful for such analyses. With a more comprehensive tag data set for all clusters, future statistical analyses could be undertaken to decipher confounding factors driving spatial use in this population (e.g., social cluster and season) and how those relate to nearshore fishing effort. Increased sample sizes of tag deployments of some of the less frequently tagged groups could be obtained by additional targeted research efforts in areas and at times of the year where these social clusters are known to concentrate.

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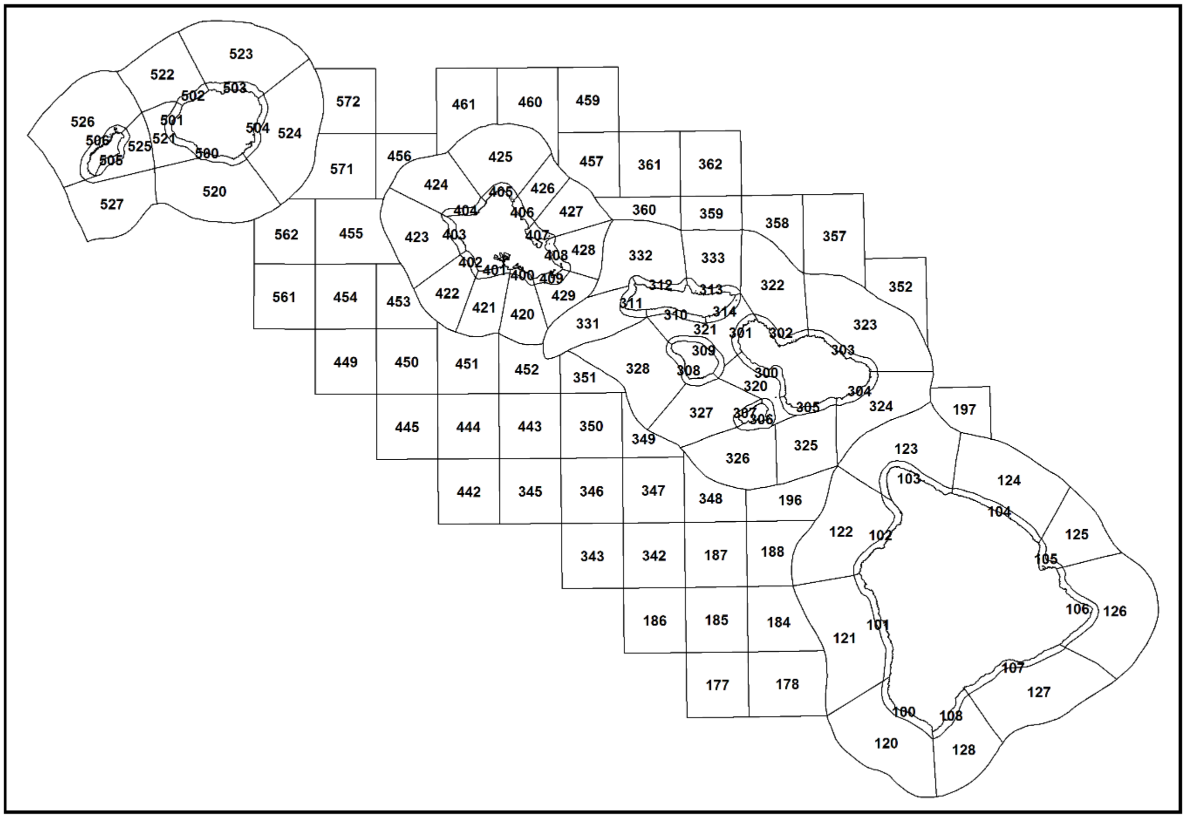


Figure 1. Commercial fisheries statistical areas used for the Hawai'i Commercial Marine License reporting system. Only those areas where satellite tagged individuals from the main Hawaiian Islands insular false killer whale population have been recorded or have passed over on interpolated tracks from satellite tag locations are shown.

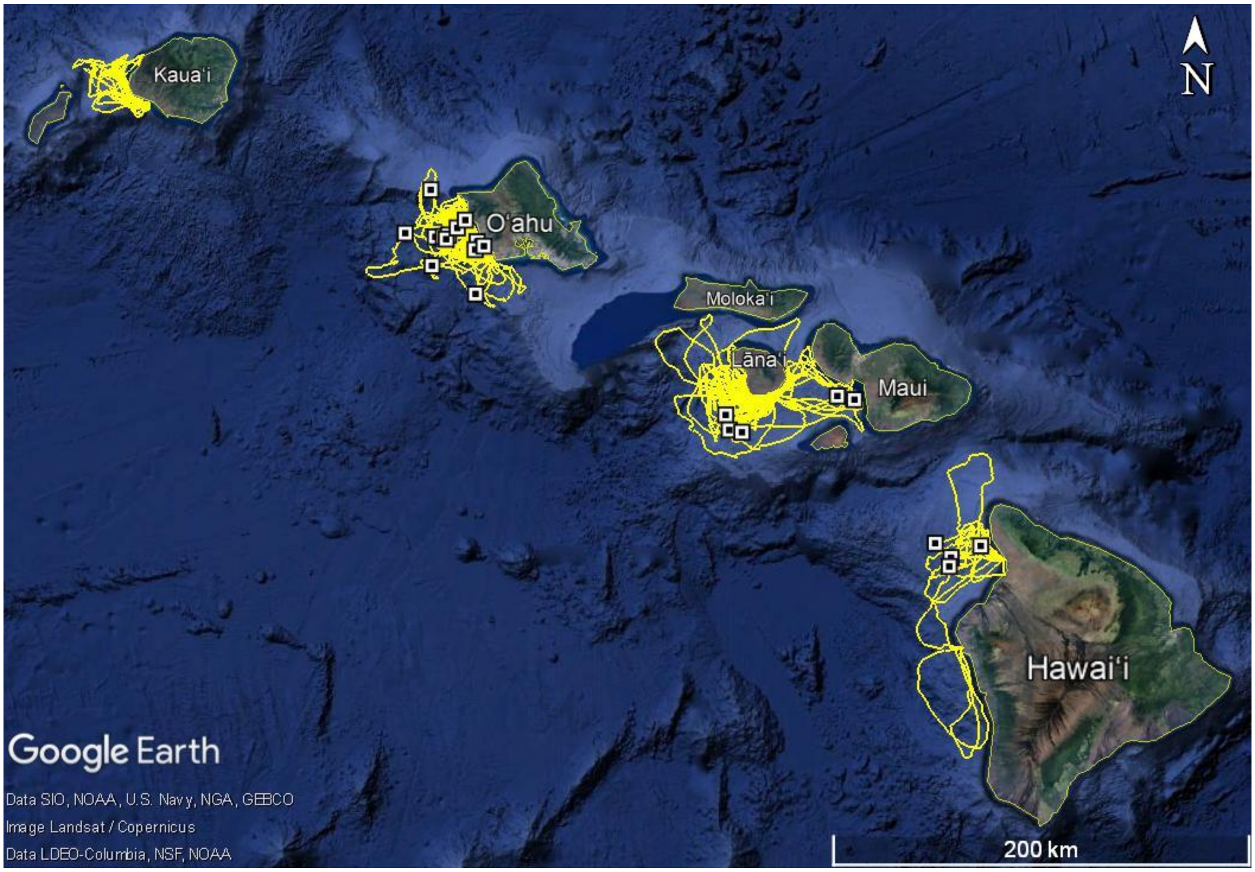


Figure 2. Survey effort and false killer whale sightings during fieldwork supported under the Species Recovery Grant in 2016, 2017, and 2018. See Table 3 for details of field efforts.

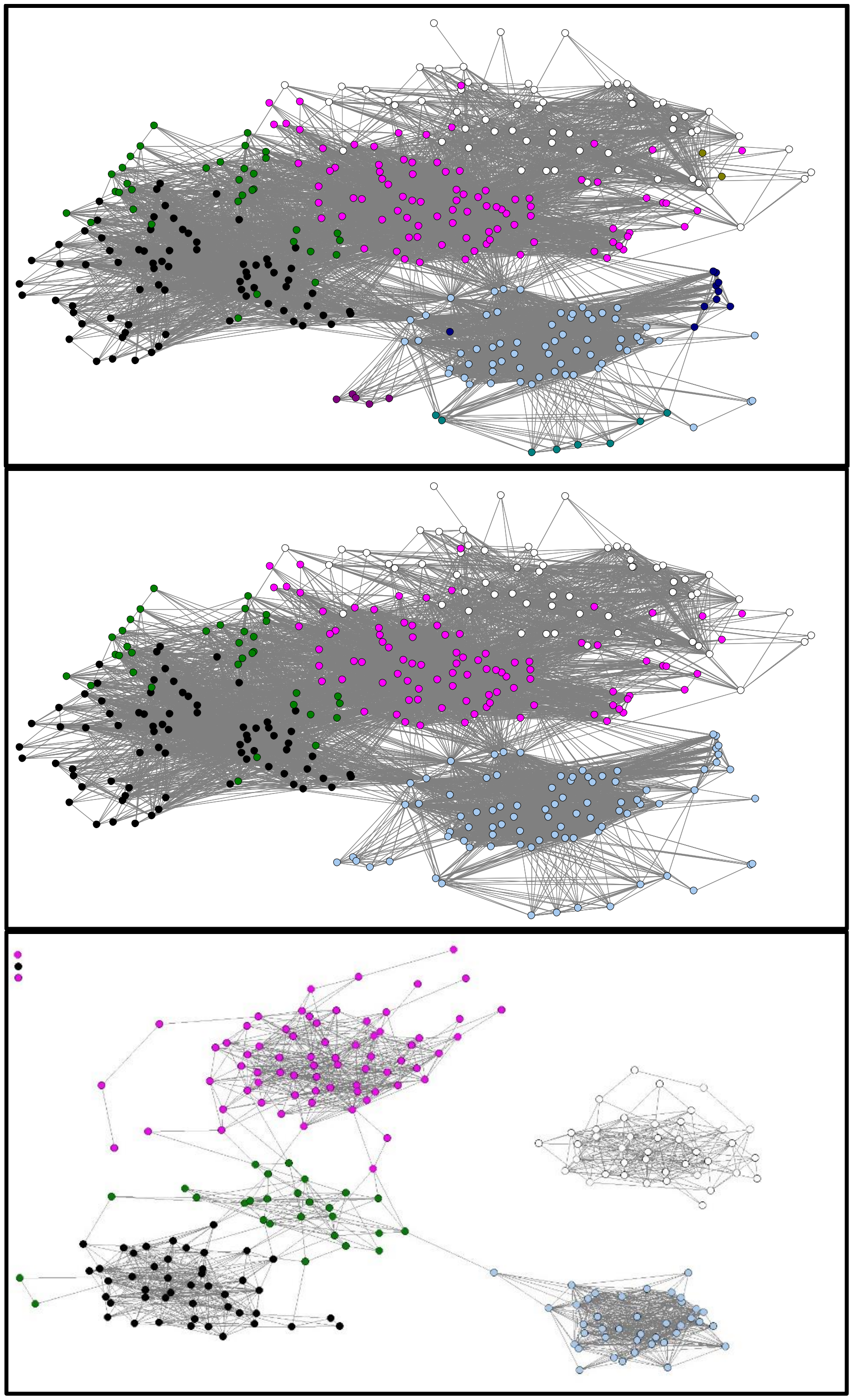
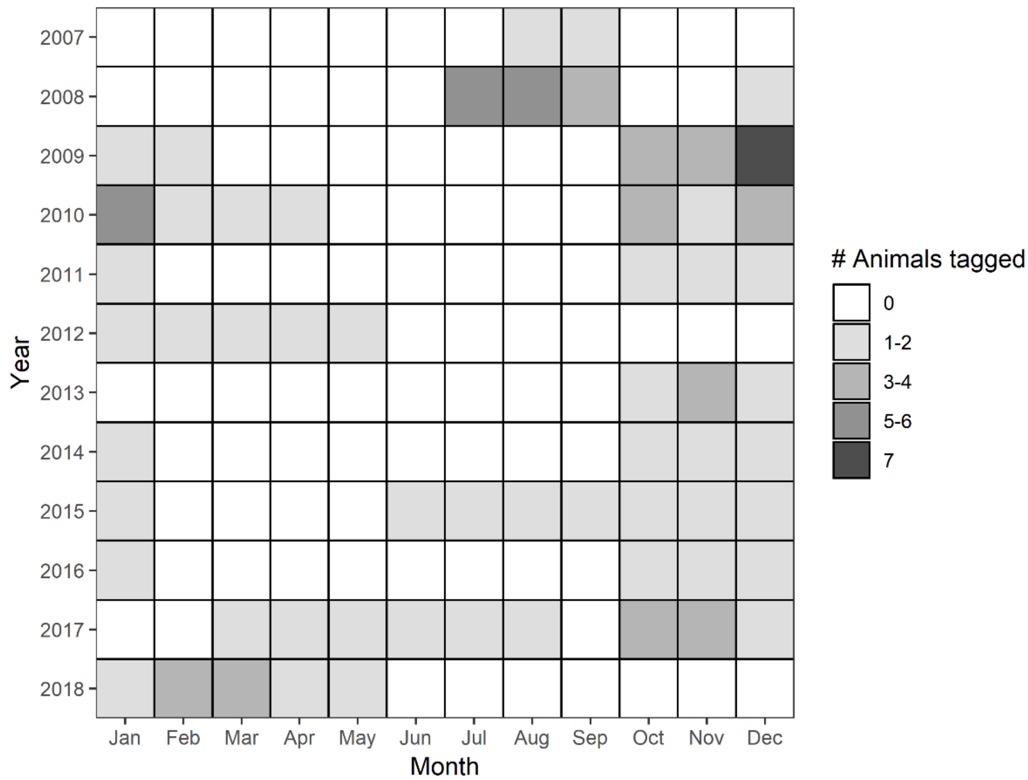


Figure 3. Social networks of false killer whales from the main Hawaiian Islands insular population using data from 2000 through April 2019, color coded by cluster: 1) pink; 2) light blue; 3) black; 4) white; 5) green. Top: Network with no restrictions with nine clusters identified through modularity (note the five peripheral clusters are olive green, plum, teal and dark blue). Middle: Network after collapsing individuals from four peripheral clusters into adjacent primary clusters. Bottom: Network restricted to individuals seen on three or more occasions with dyadic association indices (lines) shown of 0.3 or greater.



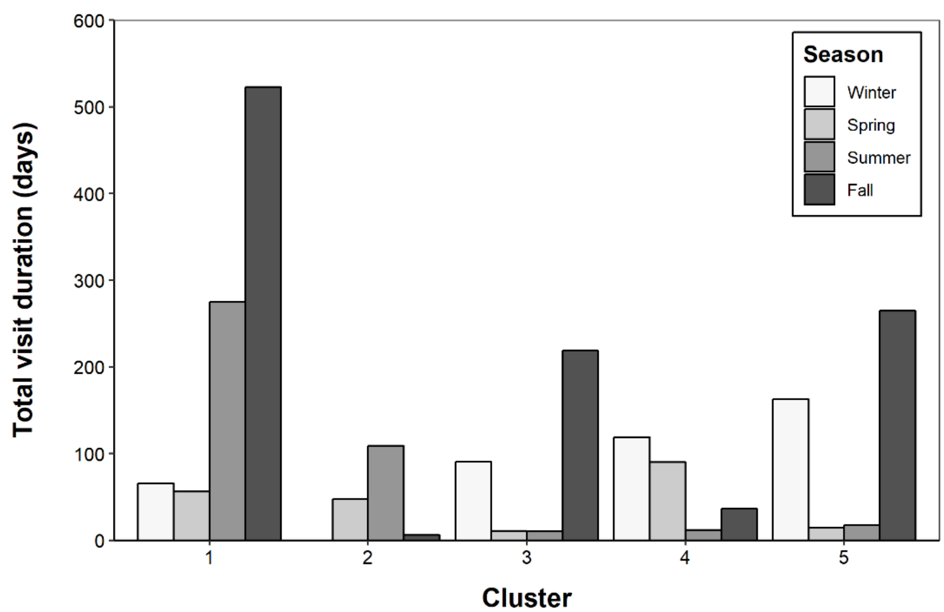


Figure 4. Top: A heatmap showing the number of tagged false killer whales from the main Hawaiian Islands insular population used in analyses, after controlling for pseudoreplication. Bottom: Total visit duration by social cluster broken down by oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan. Note: PcTag031 is included in this graph as a member of Cluster 5.

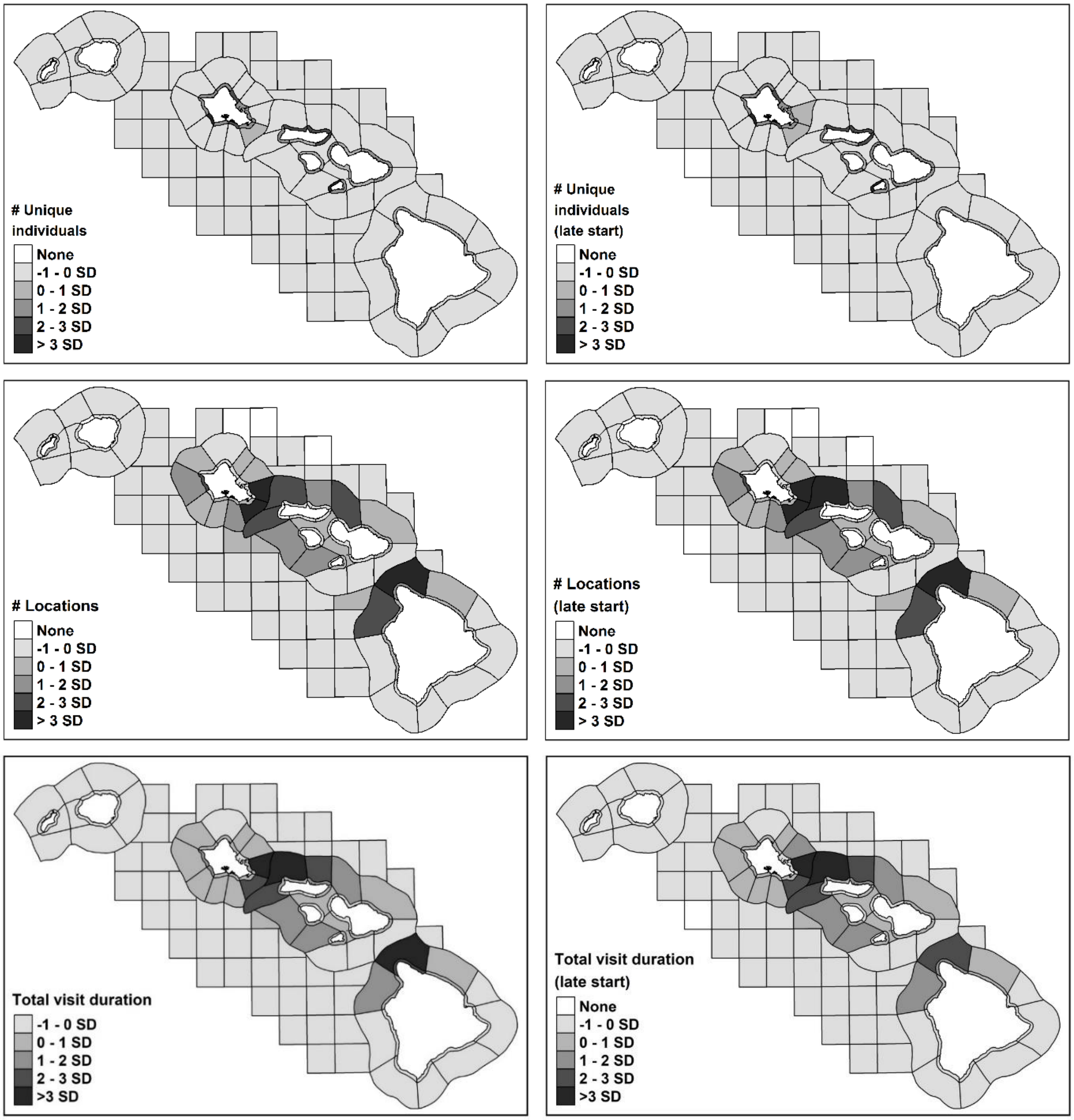


Figure 5. Comparison of false killer whale metrics (all clusters combined) used to assess spatial use of the Hawai'i commercial fisheries statistical areas, adjusted for the size of each area. Top: number of unique individuals. Middle: number of locations. Bottom: total visit duration. Plots in the right column all show results with a "late start."

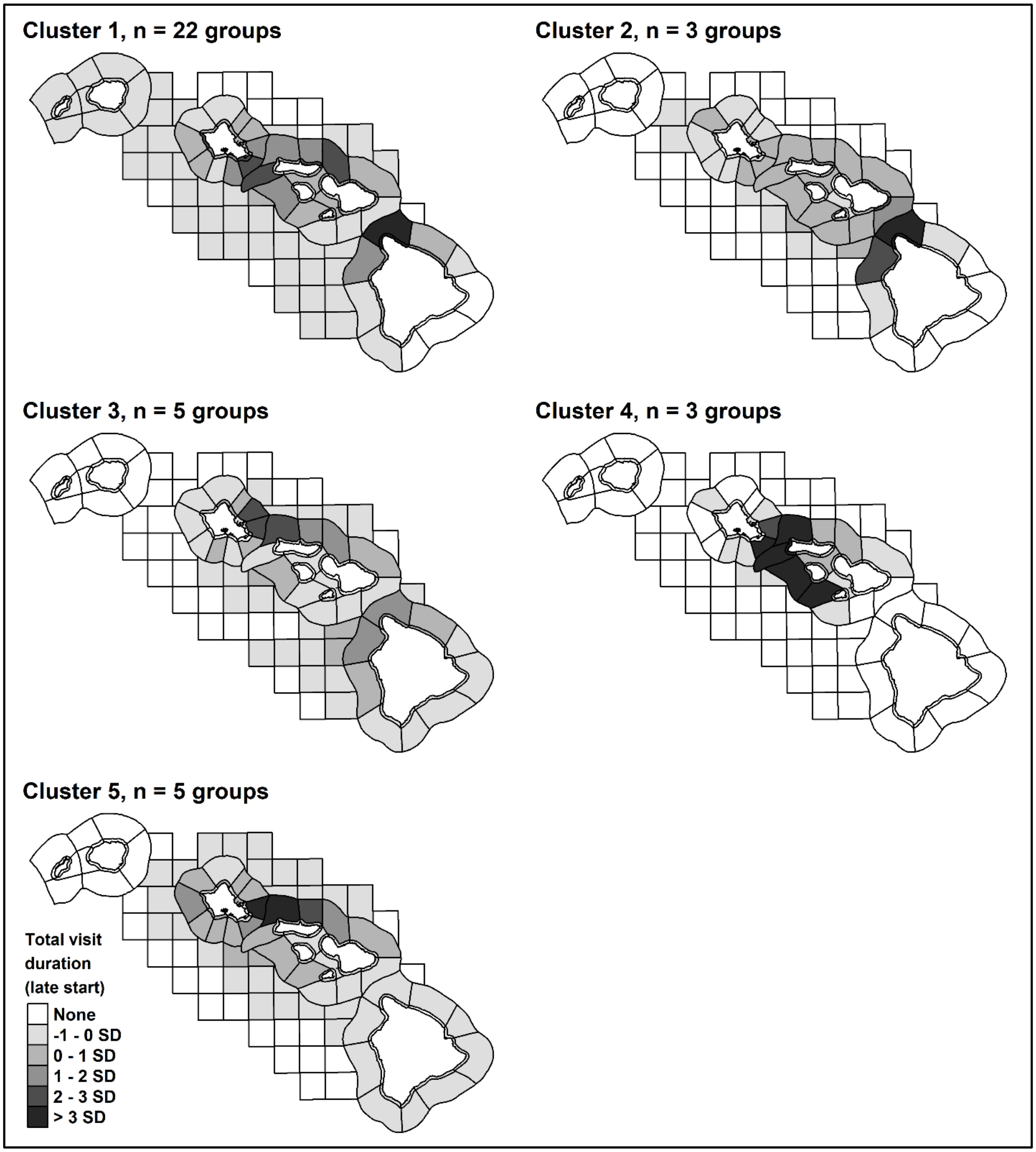


Figure 6. False killer whale use of Hawai'i commercial fisheries statistical areas by social cluster, using the total visit duration with a late start adjusted for the size of each area. For this analysis, PcTag031 was included with Cluster 5.

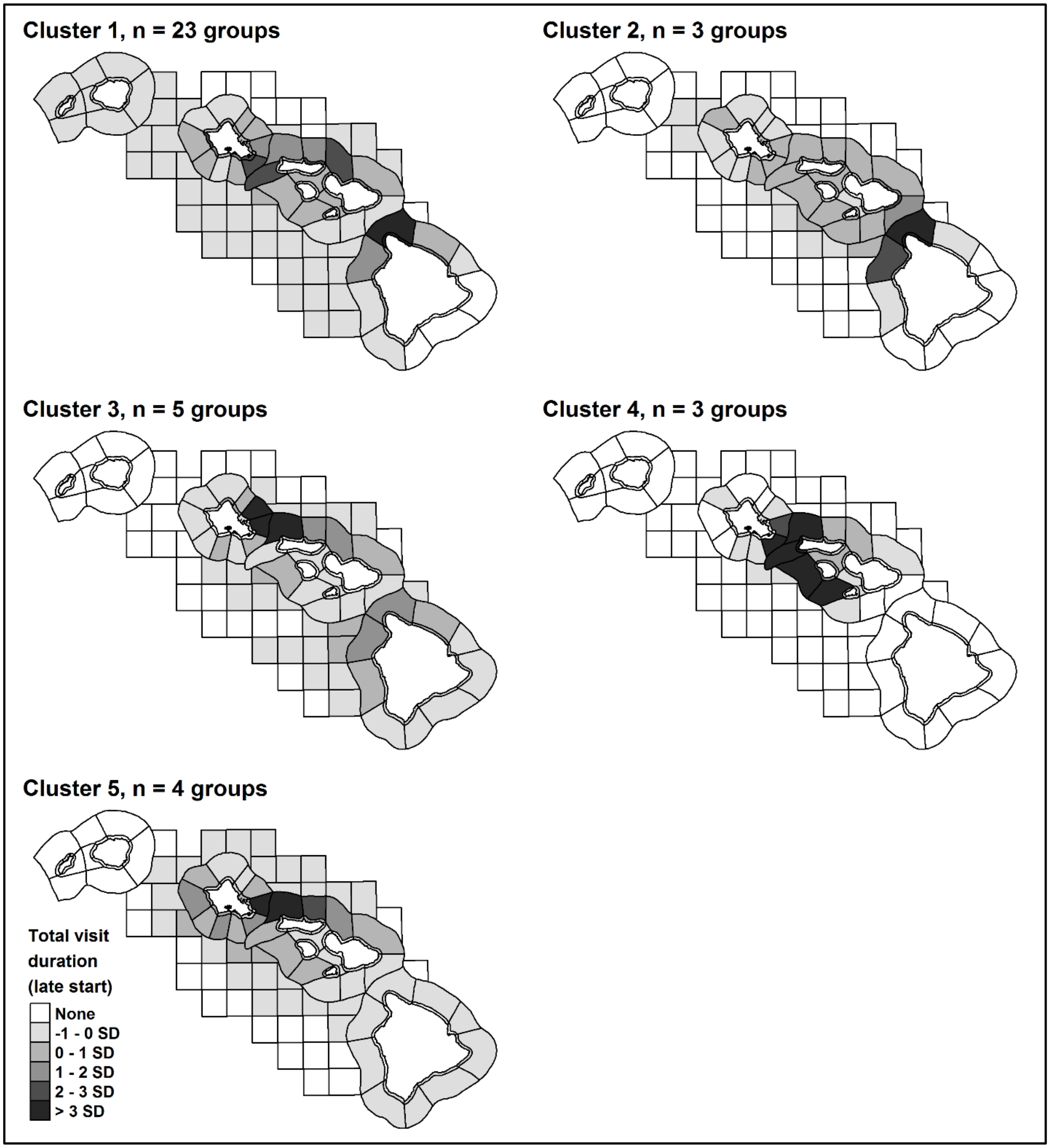


Figure 7. False killer whale use of Hawai'i commercial fisheries statistical areas by social cluster, using the total visit duration with a late start adjusted for the size of each area. For this analysis, PcTag031 was included with Cluster 1.

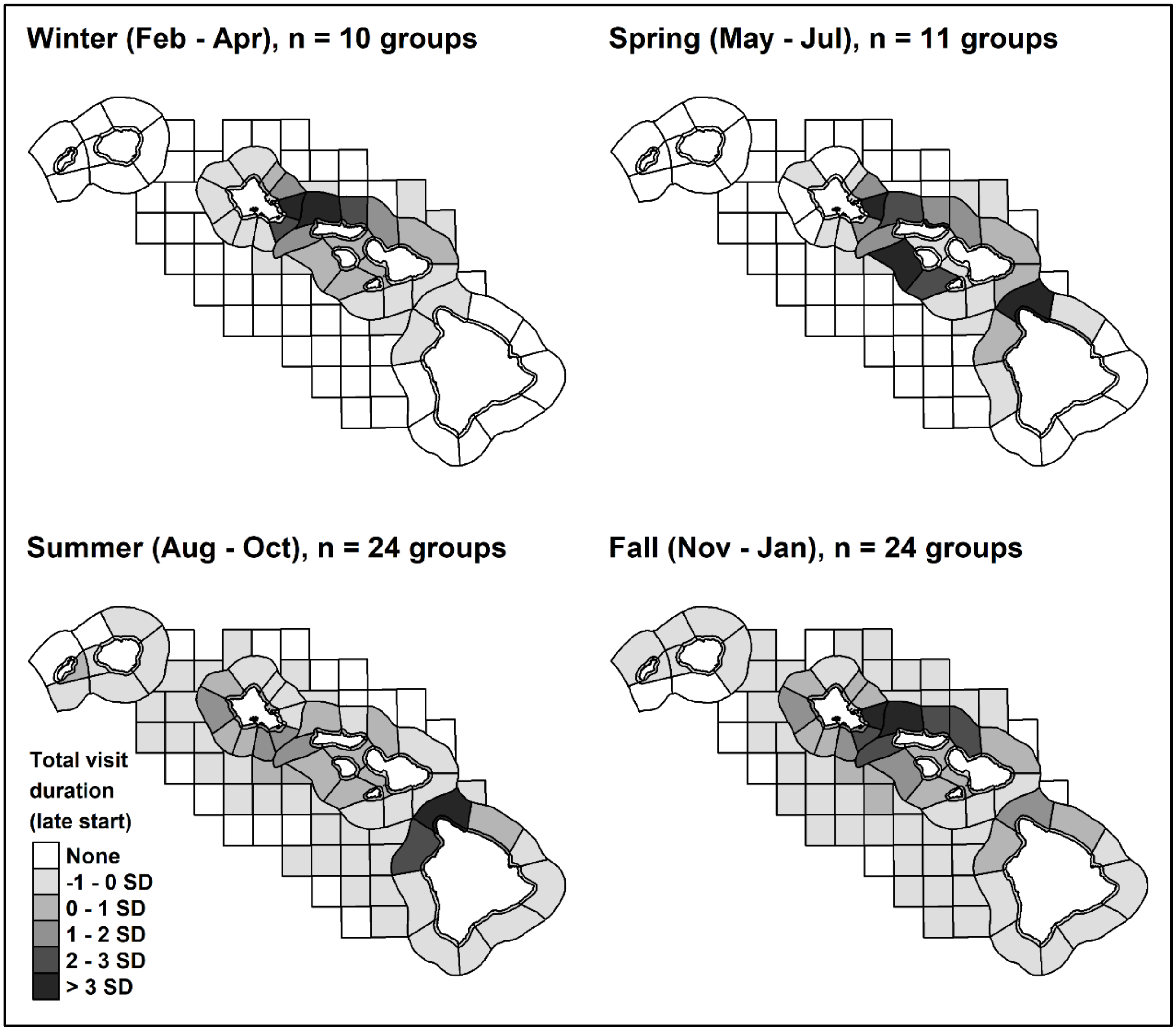


Figure 8. False killer whale use of Hawai'i commercial fisheries statistical areas by season, using the total visit duration with a late start adjusted for the size of each area. Seasons were defined as oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan.

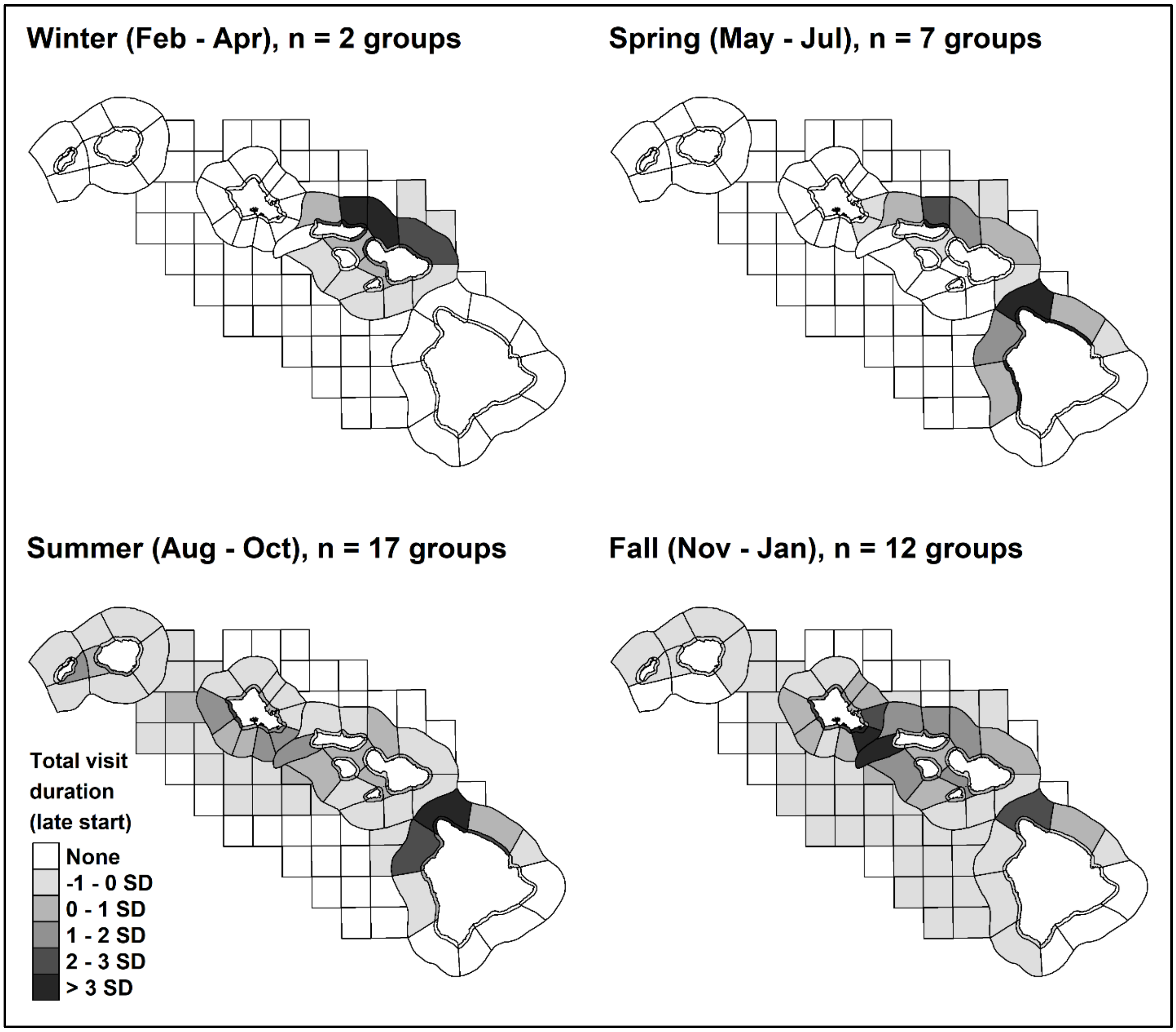


Figure 9. False killer whale use of Hawai'i commercial fisheries statistical areas by season restricted to individuals from Cluster 1 (not including PcTag031), to remove the potential influence of social cluster. Analyses shown use the total visit duration with a late start, adjusted for the size of each area. Seasons were defined as oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan.

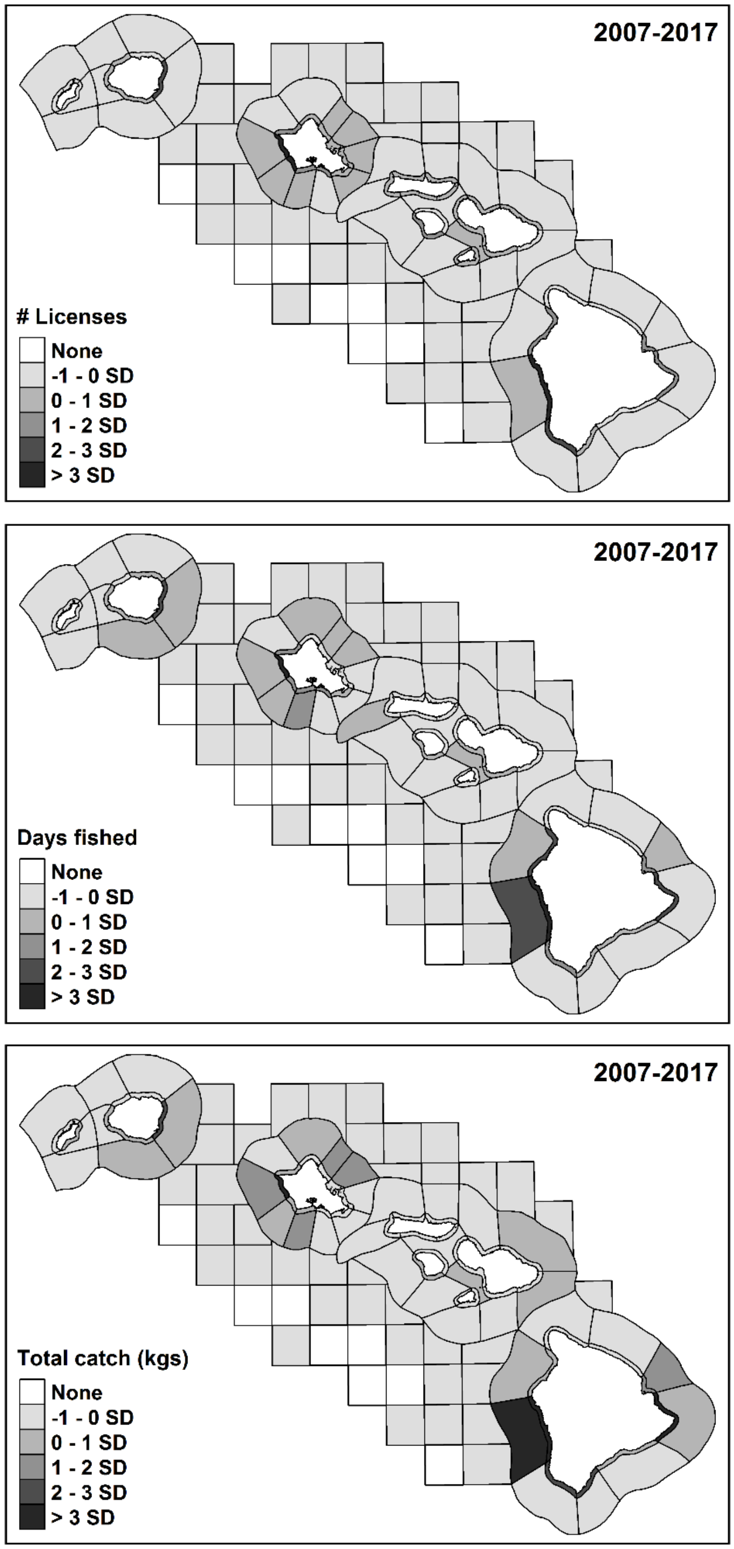


Figure 10. Spatial distribution of fishing effort density (i.e., effort corrected for area size) across Hawai'i commercial fisheries statistical areas. Fisheries were restricted to those listed in Table 6, for the time period (2007-2017). Top: Number of ommercial marine licenses. Middle: Number of days fished. Bottom: Total catch.

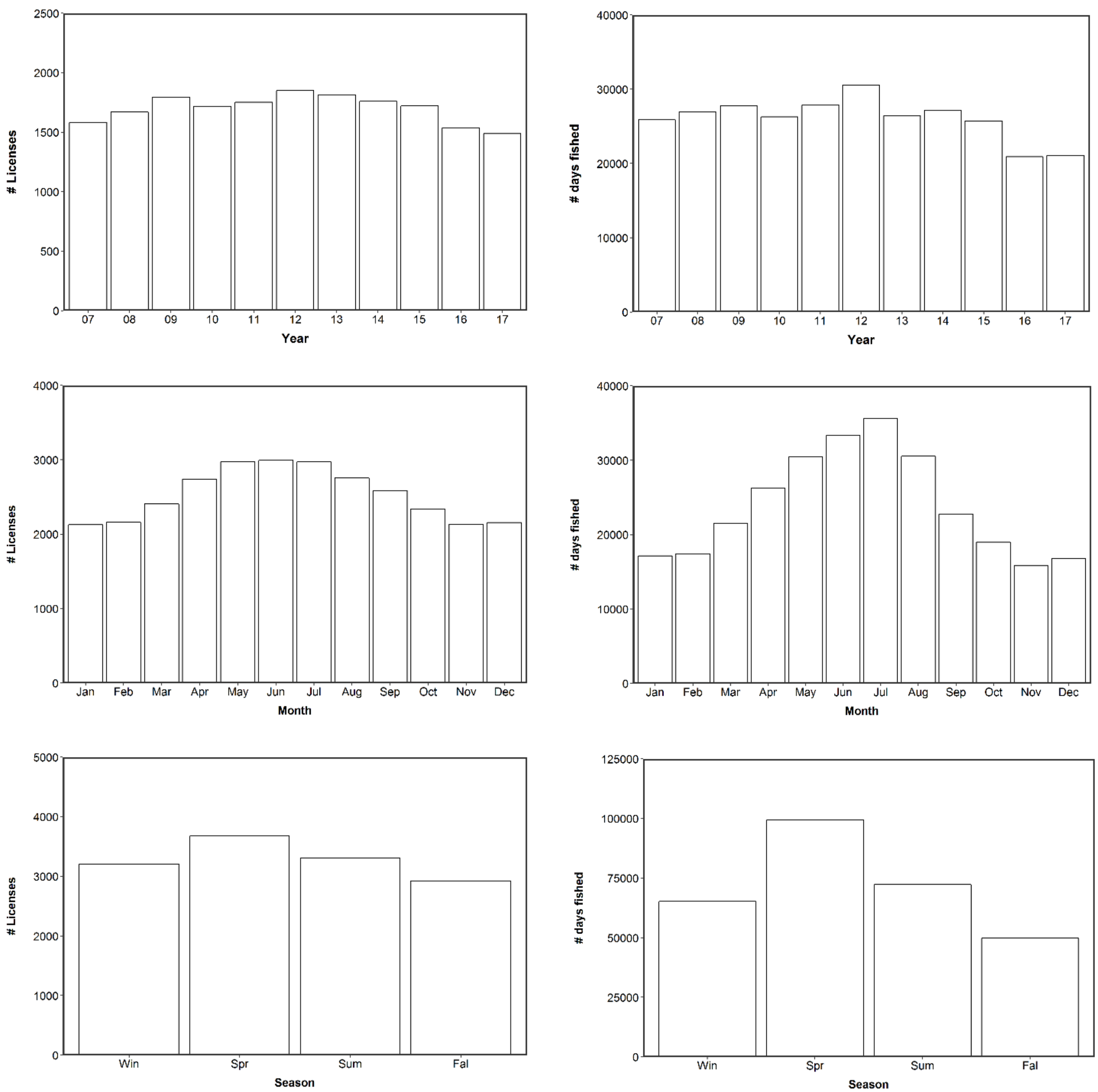


Figure 11. Inter-annual and seasonal measures of fishing effort for the period 2007-2017, restricted to fisheries noted in Table 6. Left: Number of licenses by year (top), month (middle), and season (bottom). Right: Days fished by year (top), month (middle), and season (bottom). Seasons were defined as oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan.

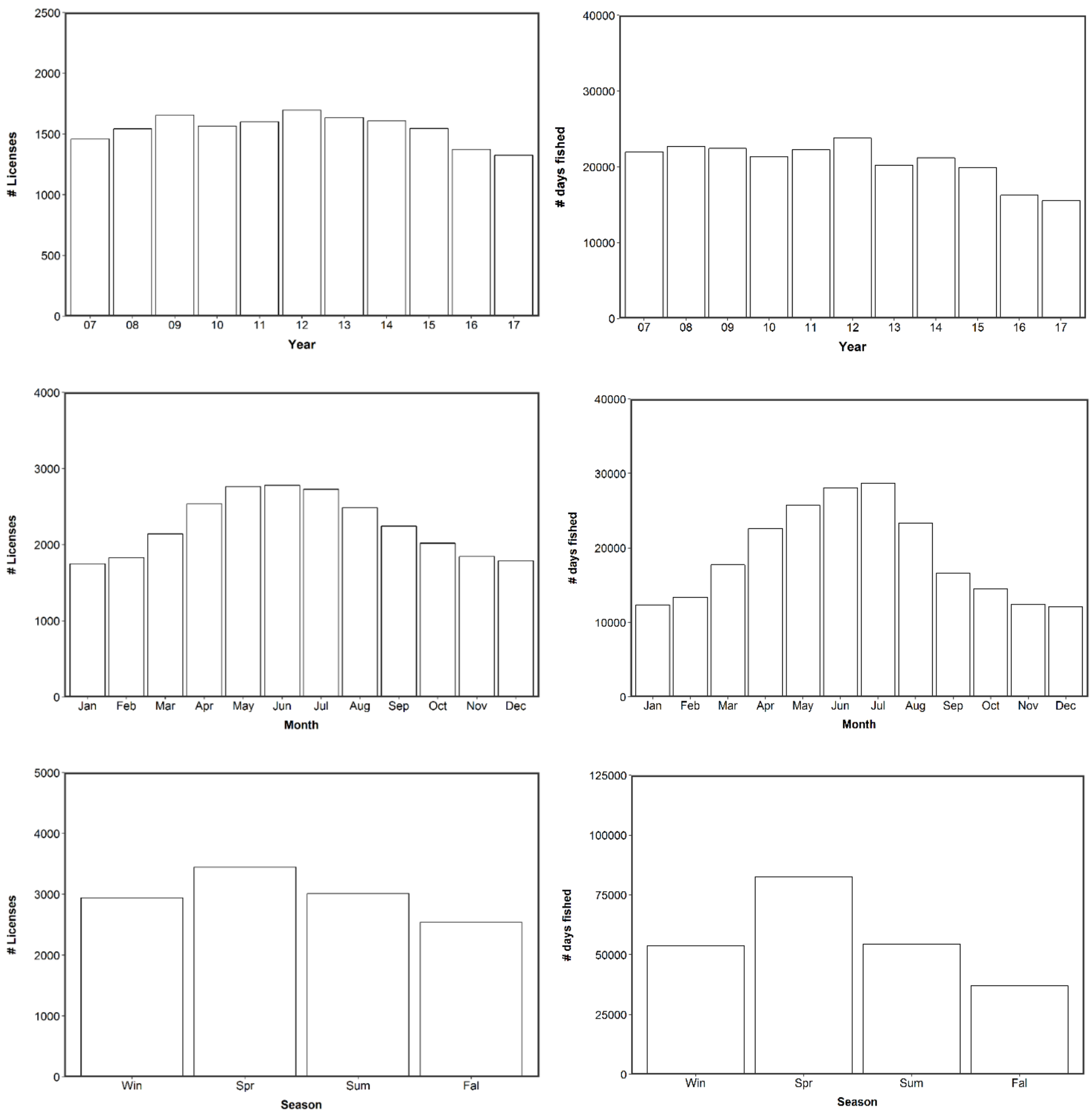


Figure 12. Inter-annual and seasonal measures of troll fishing effort for the period 2007-2017. Left: Number of licenses by year (top), month (middle), and season (bottom). Right: Days fished by year (top), month (middle), and season (bottom). Seasons were defined as oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan.

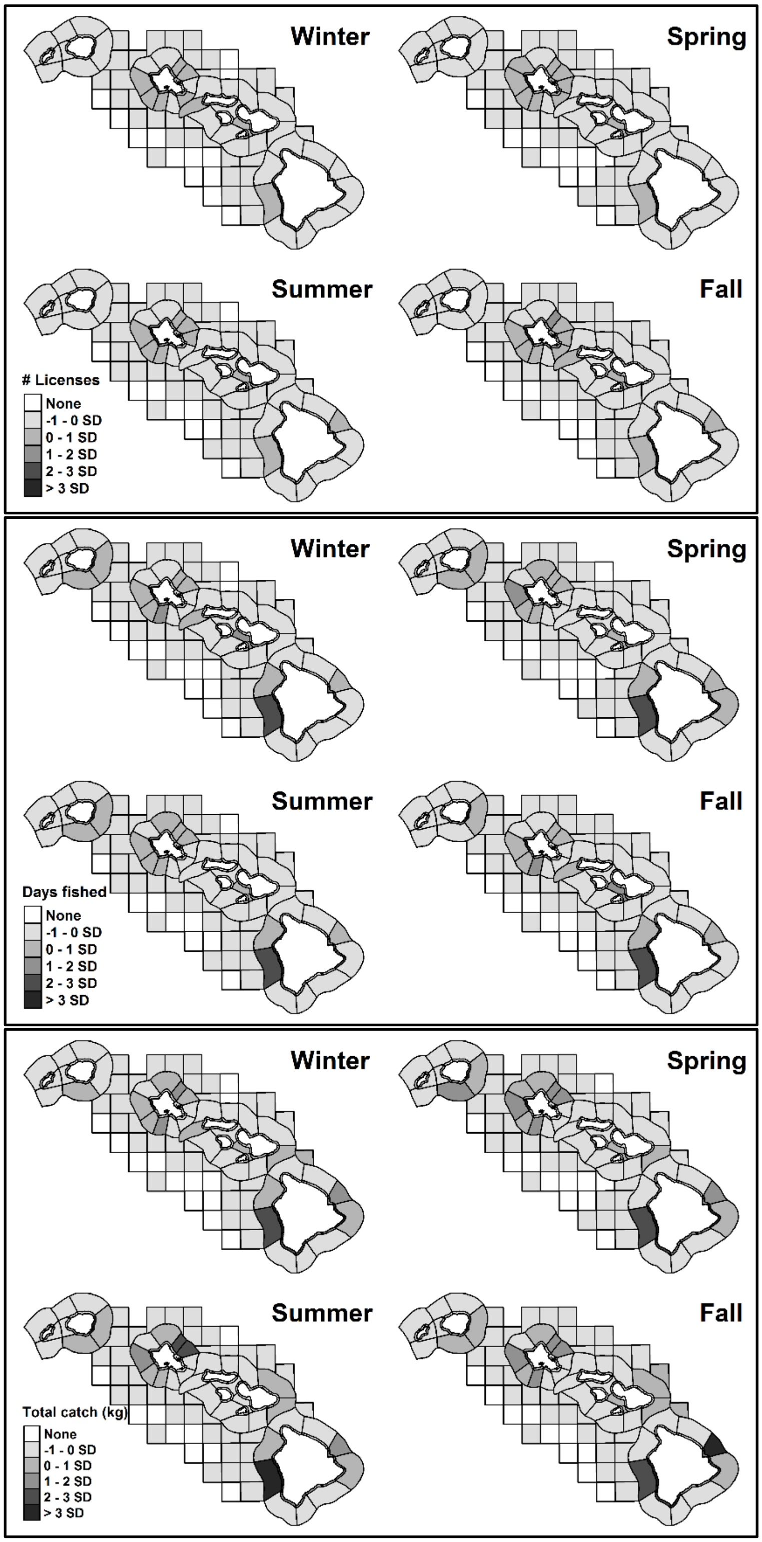


Figure 13. Seasonal variation in fishing effort for the period 2007-2017 by Hawai'i fisheries statistical areas, based on licenses (top), days fished (middle), and catch (bottom), corrected for the size of areas. Seasons were defined as oceanographic season (after Flament 1996): winter – Feb-Apr; spring – May-Jul; summer – Aug-Oct; fall – Nov-Jan.

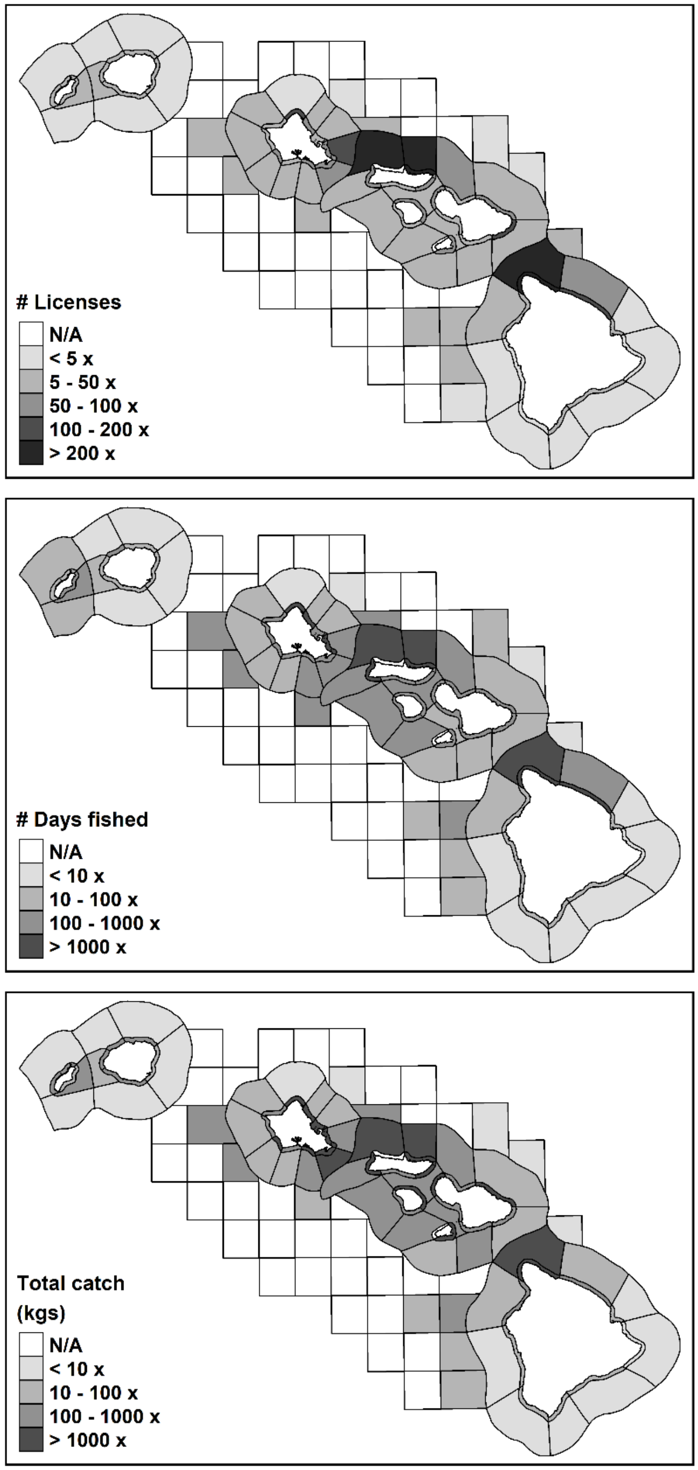


Figure 14. Fishery overlap indices using the Hawai'i commercial fisheries statistical areas, with values shown relative to Kona offshore (area 121). Three indices are shown, based on number of licenses (top), number of days fished (middle), and total catch (bottom). Areas with fewer than three licenses or with less an average of one day of fishing effort per month area are shown as N/A. Fishery areas shown are all those with overlap from satellite tagged false killer whales from the main Hawaiian Islands population.

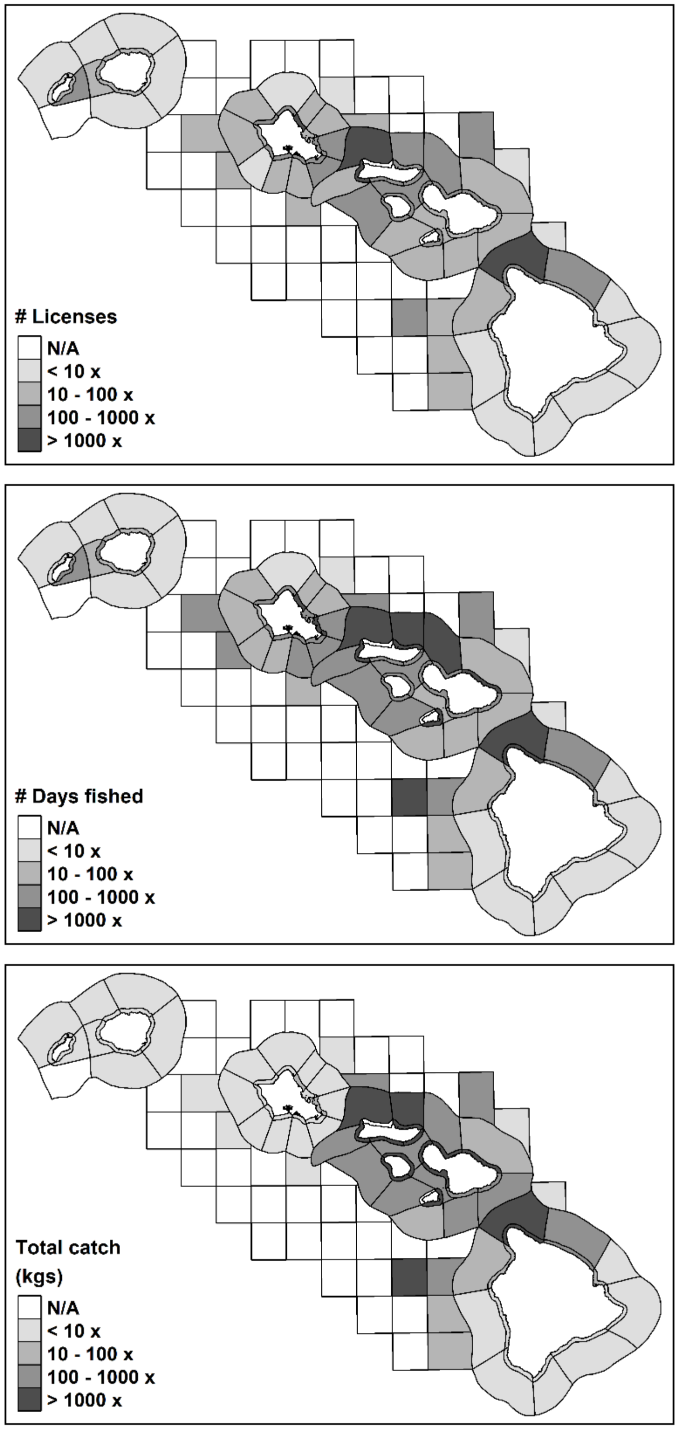


Figure 15. Fishery overlap indices using the Hawai'i commercial fisheries statistical areas for the time period October 2009 through March 2010, with values shown relative to Kona offshore (area 121). Three indices are shown, based on number of licenses (top), number of days fished (middle), and total catch (bottom). Areas with fewer than three licenses or with less an average of one day of fishing effort per month area are shown as N/A. Fishery areas shown are all those with overlap from satellite tagged false killer whales from the main Hawaiian Islands population.

Table 1. Prey species documented in the diet of main Hawaiian Islands insular false killer whales. Data from stomach contents from K. West et al. unpublished, U. Hawaiʻi. Photographic data from Baird et al. (2008), Baird (2016), and unpublished data.

English name	**Hawaiian name**	**Scientific name**	**Type of evidence**
Yellowfin tuna	Ahi	*Thunnus albacares*	Photos, stomach
Bigeye tuna	ʻAhi poʻonui	*Thunnus obesus*	Photos
Albacore tuna	ʻAhi palaha	*Thunnus alalunga*	Photos
Skipjack tuna	Aku	*Katsuwonus pelamis*	Photos
Scrawled file fish	Loulu or Oilepa	*Aluterus scriptus*	Photos
Broadbill swordfish	Aʻu ku	*Xiphias gladius*	Photos, stomach
Dolphin fish	Mahimahi	*Coryphaena hippurus*	Photos, stomach
Wahoo	Ono	*Acanthocybium solandri*	Photos
Lustrous pomfret	Monchong	*Eumegistus illustrus*	Photos
Opah		*Lampris guttatus*	Photos, stomach
Threadfin jack	Kagami ulua	*Carangoides otrynter*	Photos
Amberjack	Kāhala	*Seriola quinqueradiata*	Photos
Giant trevally	Ulua aukea	*Caranx ignobilis*	Photos
Unidentified jack		*Caranx sp.*	Stomach
Shortbill spearfish	Aʻu	*Tetrapterus angustirostris*	Stomach
Bonefish	Oio	*Albula spp.*	Photos, stomach
Diamondback squid		*Thysanoteuthis rhombus*	Stomach
Purpleback flying squid		*Sthenoteuthis oualaniensis*	Stomach

Table 2. Description of variables used in environmental modelling.

Variable	**Abbreviation**	**Units**
Distance from shore	DTS	km
Sea surface salinity	Sal	psu
Sea surface temperature	SST	˚C
Current velocity	CV	m/s
Moon illuminated fraction	MIF	%
Wind speed	WindV	m/s
Total significant wave height	TSWH	m/s
Sea surface chlorophyll-a	Chl-a	mg/m^3
Photosynthetically available radiation	PAR	Einstein m^{-2} d^{-1}
Terrain Roughness Index	Rough	m
Pacific decadal oscillation index	PDO	-
El Nino/Southern Oscillation index	ENSO	-
Number of daylight hours	DayHours	-
Time of day	DayNight	-
Season	Season	-
Social cluster	Cluster	-
Individual	ID	-
Sex	Sex	-
Year	Year	-
Island where tagged	TagIsland	-
Nearest island	Island	-
Windward/leeward	WL	-
Depth	Depth	m
Distance to eddy edge	EdDist	m

Table 3. Field efforts supported in whole or in part under the Species Recovery Grant. FKW=false killer whale.

Dates	**Island(s)**	**# km effort**	**# FKW sightings**	**Clusters photographed***	**# FKW LIMPET tags**	**# FKW biopsies**
5-23 Oct 16	O‘ahu	1,741	7	1, 3, 5	2	7
28 Feb-21 Mar 17	Lāna‘i/Maui	2,557	2	1, 4	4	5
4-14 Aug 17	Kaua‘i	1,116	0	n/a	0	0
7-16 Oct 17	Hawai‘i	1,292	4	2	3	6
2-21 Nov 17	O‘ahu	1,902	6	1, 3, 5	2	5
20 Feb-6 Mar 18	Lāna‘i/Maui	1,414	3	1, 4	3	1
Total		10,022	22		14	24

*Cluster identities determined after association analyses using the complete data set

Table 4. False killer whale tags deployed during field efforts supported under the Species Recovery Grant. The 14 tags deployed represent eight different groups.

Tag ID	**Individual ID**	**Social cluster**	**Date tagged**	**Tag duration (days)**	**Island tagged**
PcTag051	HIPc217	Cluster 1	8 Oct 2016	39.4	Oʻahu
PcTag052	HIPc205	Cluster 1	10 Oct 2016	60.9	Oʻahu
PcTag053	HIPc353	Cluster 4	9 Mar 2017	157.9	Lānaʻi
PcTag054	HIPc702	Cluster 4	9 Mar 2017	89.0	Lānaʻi
PcTag055	HIPc262	Cluster 4	9 Mar 2017	8.7	Lānaʻi
PcTag056	HIPc363	Cluster 1	10 Mar 2017	75.9	Maui
PcTag057	HIPc231	Cluster 2	12 Oct 2017	13.8	Hawaiʻi
PcTag058	HIPc498	Cluster 2	12 Oct 2017	12.7	Hawaiʻi
PcTag059	HIPc271	Cluster 2	12 Oct 2017	21.8	Hawaiʻi
PcTag060	HIPc648	Cluster 5	4 Nov 2017	193.9	Oʻahu
PcTag061	HIPc218	Cluster 5	18 Nov 2017	81.9	Oʻahu
PcTag062	HIPc114	Cluster 1	25 Feb 2018	29.8	Maui
PcTag063	HIPc106	Cluster 1	25 Feb 2018	17.7	Maui
PcTag064	HIPc373	Cluster 4	3 Mar 2018	25.9	Lānaʻi

Table 5. Restrictions on association analyses to test sensitivity of cluster assignments, using individual identifications available for the period 2000 through April 2019.

Restrictions[±]	**No. IDs included**	**No. clusters***	**No. (%) individuals moving cluster from no restrictions**	**Comments**
All Dist all PQ	351	9 (5)	-	peripheral clusters lumped with C1 or C2
All Dist all PQ seen 3+	224	5	2 (0.9)	moves from C5 to C1
Dist2+ PQ2+	286	7 (5)	2 (0.7)	peripheral clusters lumped with C2 or C4, moves from C5 to C1
Dist3+ PQ3+	199	6 (5)	4 (2.0)	peripheral cluster lumped with C4, moves from C5 to C1 or C2
Dist3+ PQ3+ seen 3+	137	5	1 (0.7)	move from C5 to C1

[±]Dist=Distinctiveness; PQ=Photo Quality. *Number of clusters in parentheses after lumping of peripheral clusters

Table 6. Fisheries considered in analyses of fishery effort based on primary fish species caught. Measurements of effort span 2007 – 2017. List ranked based on catch of primary species in decreasing order.

Fishery	**# licenses**	**Total days fished**	**% of days fished**	**Total kilograms primary catch species**	**Primary catch species[1] (>10% by weight) in decreasing order**
troll lure	3,945	207,831	73.0	9,830,102	ahi, mahimahi, ono, a'u
palu ahi	963	25,638	9.0	2,567,336	ahi, 'ahi po'onui
ika-shibi	725	15,362	5.4	2,439,400	ahi, tombo ahi, 'ahi po'onui
hybrid	28	2,308	0.8	1,866,108	'ahi po'onui, ahi
troll bait	1,522	2,705	1.0	1,836,192	mahimahi, ahi
aku boat	8	718	0.3	1,157,469	aku
short line	46	2,383	0.8	754,074	'ahi po'onui, ahi
troll stick	181	1,894	0.7	336,417	ahi, 'ahi po'onui
deep-sea handline	1,030	13,297	4.7	265,946	monchong, ahi, kāhala
rod & reel/cast/jig	938	11,646	4.1	136,580	ahi, mahimahi
vertical longline	43	200	0.1	27,387	'ahi po'onui, monchong, ahi
troll	72	254	0.1	22,371	ahi, mahimahi, ono
other	64	117	0.0	7,486	'ahi po'onui, ahi
kaka line	51	197	0.1	7,458	monchong

[1]See Table 1 for English and scientific names of fish species

Table 7. Three measures of fishing effort data for the Hawai'i commercial fisheries statistical areas from 2007-2017, restricted to fisheries whose primary catch are pelagic fish known to be false killer whale prey (see Table 6). The top 30 areas (based on number of licenses in decreasing order) are shown, representing 84.2% of the total catch during this period. See Figure 1 for boundaries of areas.

Area #	**Description**	**Area size km^2**	**FKW % of time in cell**	**Fishery effort data**		
				% of overall catch	**# licenses**	**# days fished**
121	Kona offshore	2,376	0.72	17.7	1,228	59,442
423	Wai'anae N offshore	1,453	3.25	5.7	838	16,017
101	Kona nearshore	248	0.22	3.0	708	12,099
122	Kona N offshore	2,171	6.14	2.8	600	12,166
421	Pearl Harbor offshore	727	0.93	2.7	543	9,679
422	Wai'anae S offshore	856	1.06	2.4	501	6,013
427	Kāne'ohe offshore	786	1.84	3.6	431	6,151
425	O'ahu N offshore	1,584	0.48	4.4	424	7,711
424	O'ahu NW offshore	1,099	1.21	1.2	405	3,701
126	Puna offshore	2,449	0.23	6.4	380	10,337
426	Kāne'ohe N offshore	518	0.64	2.5	378	3,835
520	Kaua'i S offshore	1,926	0.07	5.3	374	12,344
331	Penguin Bank offshore	1,107	4.34	0.9	371	6,033
125	Hilo offshore	1,132	0.21	5.8	369	8,617
328	Lana'i W offshore	1,909	6.89	1.5	318	6,192
403	Wai'anae nearshore	92	0.23	0.8	314	4,275
320	'Au'au Channel S	538	0.70	0.7	308	6,634
120	S Point W offshore	2,118	0.03	1.4	294	3,914
100	S Point W nearshore	187	0.05	1.1	290	3,760
524	Kaua'i E offshore	2,131	0.16	3.7	286	12,210
429	O'ahu SE offshore	563	2.68	0.2	281	1,561
323	Maui NE offshore	2,431	3.90	3.1	278	6,653
428	O'ahu E offshore	644	4.67	0.5	274	1,489
420	Honolulu offshore	773	1.51	0.4	234	2,121
102	Kohala S nearshore	204	0.25	0.7	220	4,710
106	Puna nearshore	220	0.04	1.7	213	5,569
327	Lana'i S offshore	1,356	3.41	0.6	213	4,112
452	Penguin Bank west tip	934	0.80	0.7	213	1,202
324	Maui SE offshore	1,338	0.67	2.1	209	3,516
504	Kaua'i E nearshore	140	0.04	0.9	208	3,485

Table 8. Fishery overlap indices (FOI) for the 30 commercial fisheries statistical areas with the highest levels of fishing effort (shown in Table 6) scaled to the value off Kona (area 121).

Area #	**Description**	**Fishery overlap indices**		
		catch	**days fished**	**licenses**
121	Kona offshore	1.0	1.0	1.0
423	Wai‘anae N offshore	22.6	28.4	10.8
101	Kona nearshore	16.7	14.7	5.0
122	Kona N offshore	58.3	47.3	19.1
421	Pearl Harbor offshore	27.3	26.8	9.5
422	Wai‘anae S offshore	30.2	42.0	10.1
427	Kāne‘ohe offshore	37.4	77.6	22.1
425	O‘ahu N offshore	4.0	7.9	2.9
424	O‘ahu NW offshore	52.4	60.4	11.0
126	Puna offshore	0.9	1.9	1.0
426	Kāne‘ohe N offshore	28.4	65.4	13.2
520	Kaua‘i S offshore	0.4	0.6	0.4
331	Penguin Bank offshore	267.4	132.3	42.9
125	Hilo offshore	1.9	4.5	2.1
328	Lana‘i W offshore	137.8	118.6	46.1
403	Wai‘anae nearshore	185.8	121.6	33.0
320	‘Au‘au Channel S	109.4	40.0	17.2
120	S Point W offshore	0.6	0.7	0.2
100	S Point W nearshore	14.9	15.5	4.0
524	Kaua‘i E offshore	1.2	1.2	1.0
429	O‘ahu SE offshore	1287.7	619.1	68.6
323	Maui NE offshore	30.2	49.1	23.4
428	O‘ahu E offshore	847.7	991.7	107.5
420	Honolulu offshore	297.9	187.8	34.0
102	Kohala S nearshore	109.6	53.3	22.8
106	Puna nearshore	6.8	7.0	3.7
327	Lana‘i S offshore	261.2	124.6	48.0
452	Penguin Bank west tip	73.8	145.7	16.4
324	Maui SE offshore	13.9	28.8	9.7
504	Kaua‘i E nearshore	19.4	18.1	6.0

Table 9. Fishery overlap indices (FOI) for the 30 commercial fisheries statistical areas with the highest FOI values (sorted by catch in decreasing order), scaled to the value off Kona (area 121).

Area #	Description	Area size km^2	FKW % of time in cell	Fishery overlap indices		
				catch	days fished	licenses
408	O'ahu E nearshore	95	0.10	6463.3	1213.7	89.0
123	Kohala offshore	1,926	11.15	5334.2	3789.9	255.6
332	Moloka'i NW offshore	1,615	14.98	4026.8	4302.4	238.4
311	Penguin Bank nearshore	125	0.21	3980.5	1425.8	92.0
406	O'ahu NE nearshore	76	0.11	3813.0	2060.5	106.9
103	Kohala nearshore	212	0.90	3496.5	1584.5	219.3
333	Moloka'i NE offshore	1,013	4.18	3222.3	3503.6	204.6
313	Moloka'i NE nearshore	127	0.41	2891.6	2373.2	218.6
409	O'ahu SE nearshore	98	0.21	2796.7	694.7	101.6
405	O'ahu N nearshore	95	0.16	2486.2	1197.4	140.8
314	Moloka'i SE nearshore	97	0.12	2469.5	815.3	84.4
301	Maui W nearshore	96	0.08	2217.5	572.9	75.0
309	Lana'i E nearshore	155	0.12	2208.2	588.7	98.1
400	Honolulu nearshore	60	0.10	1524.0	373.6	85.0
407	Kāne'ohe nearshore	104	0.09	1481.5	374.9	38.3
303	Maui NE nearshore	174	0.28	1314.1	567.1	81.9
429	O'ahu SE offshore	563	2.68	1287.7	619.1	68.6
402	Wai'anae S nearshore	56	0.15	1218.2	562.1	79.2
306	Kaho'olawe S nearshore	134	0.15	1126.2	679.0	61.4
428	O'ahu E offshore	644	4.67	847.7	991.7	107.5
104	Hāmākua nearshore	215	0.44	766.1	1179.1	191.5
401	Pearl Harbor nearshore	99	0.16	723.2	254.2	60.7
302	Maui NW nearshore	142	0.09	711.8	300.2	29.7
310	Moloka'i S nearshore	127	0.06	711.3	184.0	33.1
404	O'ahu NW nearshore	102	0.14	609.4	190.8	52.0
304	Maui SE nearshore	122	0.16	551.5	664.7	137.6
305	Maui S nearshore	143	0.17	514.7	204.7	52.8
321	Maui Nui basin N	711	0.79	344.8	136.0	36.0
300	Mā'alaea nearshore	153	0.07	338.7	123.1	18.8
308	Lana'i SW nearshore	151	0.24	338.6	190.1	43.6

Table 10. Top models chosen in analyses of false killer whale distance from shore in relation to environmental variables. See Table 2 for description of variables.

Model	**AICc**	**ΔAICc**	w_i	**marginal R^2**	**conditional R^2**
Day/night + PDO + Rough + SST + Chl-a + MIF + CV + TSWH + WindV	-2235.0	0	0.947	0.203	0.396
Day/night + PDO + Rough + SST + Chl-a + MIF + CV + TSWH	-2229.3	5.7	0.053	0.204	0.397
Day/night + PDO + Rough + SST + Chl-a + CV + TSWH + WindV	-2217.3	17.7	0.000	0.199	0.389
Day/night + PDO + Rough + Chl-a + MIF + CV + TSWH	-2190.9	44.1	0.000	0.198	0.404
Day/night + PDO + SST + Chl-a + MIF + CV + TSWH + WindV	-2179.9	55.1	0.000	0.200	0.389

Table 11. Output from top model (from Table 9). Degrees of freedom = 9,596.

Variable	**Estimate**	**95% CI**		**SE**	**t-value**	**p-value**	**% Relative importance**
		Lower	**Upper**				
Intercept	-1.029	-2.160	0.103	0.578	-1.781	0.075	-
Day/night	-0.033	-0.041	-0.025	0.004	-7.958	<0.001	3.66
PDO	-0.050	-0.078	-0.021	0.014	-3.438	0.001	3.27
Rough	-0.030	-0.038	-0.023	0.004	-7.643	<0.001	1.01
SST	2.592	1.781	3.403	0.414	6.262	<0.001	6.32
Chl-a	-1.506	-1.582	-1.430	0.039	-38.840	<0.001	31.60
MIF	0.020	0.011	0.029	0.005	4.453	<0.001	0.76
CV	0.130	0.114	0.146	0.008	15.744	<0.001	37.64
TSWH	0.362	0.327	0.397	0.018	20.107	<0.001	11.57
WindV	-0.009	-0.016	-0.003	0.003	-2.810	0.005	4.17