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Abstract—Opah (*Lampris* spp.) are commercially valuable, non-target fish that are regularly landed in pelagic longline fisheries in the central and eastern North Pacific Ocean. Genetic studies have confirmed 2 species in the region: bigeye Pacific opah (*L. megalopsis*) and small-eye Pacific opah (*L. incognitus*). Spatial distributions of each species are not well-defined, and little is known about species-specific catch distributions because the 2 species are difficult to distinguish visually. The objectives of this study were to characterize spatiotemporal patterns of opah landings by using catch per unit of effort (CPUE) from logbook and observer data, for the period 1995–2018, and genetics-based species identifications. Results from generalized additive models indicate that bigeye Pacific opah dominate west of 140°W and that small-eye Pacific opah dominate waters east of 130°W (dominance is defined as a proportion of catch ≥ 0.7). The deep-set pelagic longline fishery had higher opah CPUE than the shallow-set fishery across the geographic range of these fisheries. Opah CPUE increased from west to east on both longline gears, indicating higher overall opah CPUE in the eastern regions of both fisheries, primarily dominated by small-eye Pacific opah. Opah CPUE also increased over time as the Hawaii-based longline fisheries expanded eastward. The results of this study highlight the need for species-specific catch data and will inform management of opah species.

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Spatiotemporal catch patterns and population distributions of bigeye Pacific opah (*Lampris megalopsis*) and small-eye Pacific opah (*L. incognitus*) in the eastern North Pacific Ocean

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Opah (*Lampris* spp.), also known as moonfish, are large, laterally compressed teleosts that can reach upwards of 90 kg and 2 m fork length (Hawn and Collette, 2012). Opah occur across a broad latitudinal range in tropical, temperate, and subpolar marine regions (Hyde et al., 2014). Previous studies have found that opah have unique adaptations to retain heat created by their pectoral-fin swimming mode and distribute it throughout their entire body (Wegner et al., 2015). This full-body endothermy enhances capture of prey because opah can maintain a higher activity level and forage in cold deep water for long periods before returning to warmer surface waters (Wegner et al., 2015). Despite these intriguing discoveries, much is still unknown about the life history, distributions, and populations of opah, especially at the species level.

As recently as 2010, only 1 species of opah had been reported to reside in the North Pacific Ocean. Genetic studies, however, have confirmed the presence

of 2 distinct species: the bigeye Pacific opah (*L. megalopsis*) and the small-eye Pacific opah (*L. incognitus*) (Hyde et al., 2014; Underkoffler et al., 2018). Although most biological data and studies in the North Pacific Ocean do not distinguish between the 2 species, some species-specific information is available. Results from gut content studies indicate that bigeye Pacific opah forage deeper in the water column than small-eye Pacific opah because their diet was almost entirely composed of mesopelagic species and the diet of small-eye Pacific opah included both epipelagic and mesopelagic species (Choy et al., 2013). This finding is consistent with relationships between eye size and foraging depth seen in other species (e.g., Kröger et al., 2009). In a study by Hyde et al. (2014), the spatial distribution of the 2 species were examined by using genetic analyses, and although results indicate that most small-eye Pacific opah were caught near the West Coast of the United States and that most

bigeye Pacific opah were caught near the main Hawaiian Islands (Hyde et al., 2014), there was a gap in sampling between ~140°W and 125°W. Consequently, the species distributions in the eastern North Pacific Ocean could not be determined.

Both species of opah are a relatively common incidental catch in the drift gill-net fishery targeting swordfish (*Xiphias gladius*) in the California Current system, a productive eastern boundary current system that is an important foraging ground for many highly migratory species (Block et al., 2011), and in pelagic longline fisheries targeting swordfish and bigeye tuna (*Thunnus obesus*) in the North Pacific Ocean. Although opah have not been a primary target of commercial fisheries, seafood marketing efforts and new culinary uses for previously discarded cuts of these fish have recently increased the popularity of opah, and they are an increasingly valuable secondary target. Reported landings of opah in Hawaii increased from approximately 400 metric tons (t) per year in the early 2000s to more than 800 t by 2017 (National Marine Fisheries Service, Office of Science and Technology, commercial fisheries landings, available from [website](#), accessed May 2020). Additionally, in the California large-mesh drift gill-net fisheries, nominal catch per unit of effort (CPUE) of opah increased roughly 4-fold from 1982 to 2017 (Walker and Teo¹).

The regions where opah are landed by U.S. fleets fall under the jurisdiction of 2 management councils: the Western Pacific Regional Fishery Management Council and the Pacific Fishery Management Council. In the Western Pacific Regional Fishery Management Council, opah are listed as a “pelagic management unit” in the fishery ecosystem plan. In contrast, they are not listed in the fishery management plan of the Pacific Fishery Management Council. There is currently no stock assessment for opah in the Pacific Ocean, nor are there any management measures in place for these species (WPRFMC, 2021).

Stock assessments are a key component of fisheries management, and any effort to assess or manage opah in the North Pacific Ocean will require species-specific information on population distributions and fisheries data such as CPUE. However, past difficulties with visual identification have led to both bigeye Pacific opah and small-eye Pacific opah being simply recorded as *opah* in fisheries records and most scientific studies. Information on the spatial distributions of bigeye and small-eye Pacific opah is limited (Hyde et al., 2014), and the species-specific CPUE is unknown. Fisheries observers are now able to more effectively identify opah in landings to species level using new visual identification keys that illustrate the differences between species in spot patterns and the trailing margin of the caudal fin. Differentiating between morphologically similar species is essential to effectively characterize the fishing mortality of each species and contribute to accurate stock assessments (Beerkircher et al., 2009).

The primary objectives of this study were to examine spatial and temporal patterns of catch rates of opah on pelagic longline fishing gear and to estimate the species-specific distributions and CPUE within the central and eastern North Pacific Ocean. First, we characterized the spatial and temporal patterns of fisheries effort and non-species-specific opah CPUE of the U.S. pelagic shallow- and deep-set longline fleets. We then combined the use of genetic analyses and generalized additive models (GAMs) to estimate the proportions of bigeye Pacific opah and small-eye Pacific opah caught in different areas and to estimate CPUE in regions dominated by the 2 species. Finally, patterns in species distributions and CPUE were linked to oceanography to gain insight into preferred habitat.

Materials and methods

Fisheries data

Fisheries data were obtained from pelagic longline vessels based in California and Hawaii. Since 1990, captains of vessels in the U.S. pelagic longline fleet have been required to fill out logbooks with details describing fishery-specific gear and effort, latitude and longitude, and catch information for each set (Walsh and Brodziak, 2016). In the logbook data, the species of opah that was caught on each set is not specified; instead, catch taxa are listed as *opah* or *moonfish*.

The pelagic longline vessels that operate in California and Hawaii are also required to use trained observers to document catch and bycatch, ensure regulatory compliance, and record exact catch locations. On Hawaii-based vessels, observers are present on 20% of deep-set longline trips and on 100% of shallow-set longline trips (Sippel et al.²). California-based vessels participate only in the deep-set fishery and have been required to have 20% observer coverage since 2016 (NMFS, 2016). Logbook and observer data for vessels based in both Hawaii and California were provided by the NOAA Pacific Islands Fisheries Science Center (Sippel et al.²; PIFSC³).

Both the logbook and observer data contained substantial fishing information. To standardize the data for analyses, the fields selected were number of opah, date of the set, effort (number of hooks), number of hooks per float (which affects fishing depth), set and haul times, and the longitude and latitude of the set.

Opah are caught on both deep- and shallow-set longline gear configurations. Both fleets operate in the eastern and central Pacific Ocean but do so with different spatial extents, reflecting the habitat of their respective target species (Figs. 1 and 2). Deep-set gear is used primarily to

¹ Walker, J. M., and S. L. H. Teo. In review. Distribution and relative abundance trends of opah in California waters.

² Sippel, T., N. Nasby-Lucas, and S. Kohin. 2014. Description of the Hawaii longline observer program. Int. Sci. Comm. Shark Work. Group ISC/14/SHARKWG-1/05, 6 p. [Available from [website](#).]

³ PIFSC (Pacific Island Fisheries Science Center). 2019. Hawaii longline logbook. [Available from [website](#), accessed March 2019.]

target bigeye tuna at depths between 100 and 400 m, with a median depth of 250 m (Bigelow et al., 2006; Woodworth-Jefcoats et al., 2018). This gear has a mainline that spans an average of 65 km, with an average total number of hooks of 1700 and with 27 hooks per float (Bigelow et al., 2006). The hooks are baited with either Pacific saury (*Cololabis saira*) or Pacific sardine (*Sardinops sagax*) and generally are set in the morning and hauled in the afternoon or evening (Bigelow et al., 2006). Shallow-set gear is used primarily to target swordfish at depths between 30 and 90 m. The mainlines of this gear span 75 km, with a total of 700–1000 hooks and roughly 5 hooks per float. The hooks are baited with Pacific chub mackerel (*Scomber japonicus*) and generally are set at night when swordfish are closer to the surface (Dewar et al., 2011). In 2019, there were an estimated 22 vessels using shallow-set gear and an estimated 143 vessels using deep-set gear in the North Pacific Ocean (PIFSC³).

Prior to analyses, the data were filtered and separated into deep and shallow sets by using the methods of Bigelow et al. (2006), with deep-set data containing sets with 15 or more hooks per float and shallow-set data containing sets with less than 15 hooks per float. However, >95% of deep sets had 19–32 hooks per float and 500–3500 hooks per set, and >95% of shallow sets had 4–8 hooks per float and 500–1500 hooks per set. We therefore excluded sets outside these ranges, to focus our analyses on typical deep-set and shallow-set gear configurations. Data were removed from analyses if soak times (the duration over which the fishing gear is completely submerged) were outside of reasonable bounds based on knowledge of fishery operations: 2–8 h for deep sets and 2–10 h for shallow sets. Records were also removed if they were outside the general geographic range of each fishery (deep sets: 180–125°W, 0–45°N; shallow sets: 180–125°W, 15–45°N). All data from 1995 did not meet the filtration criteria and were removed, effectively

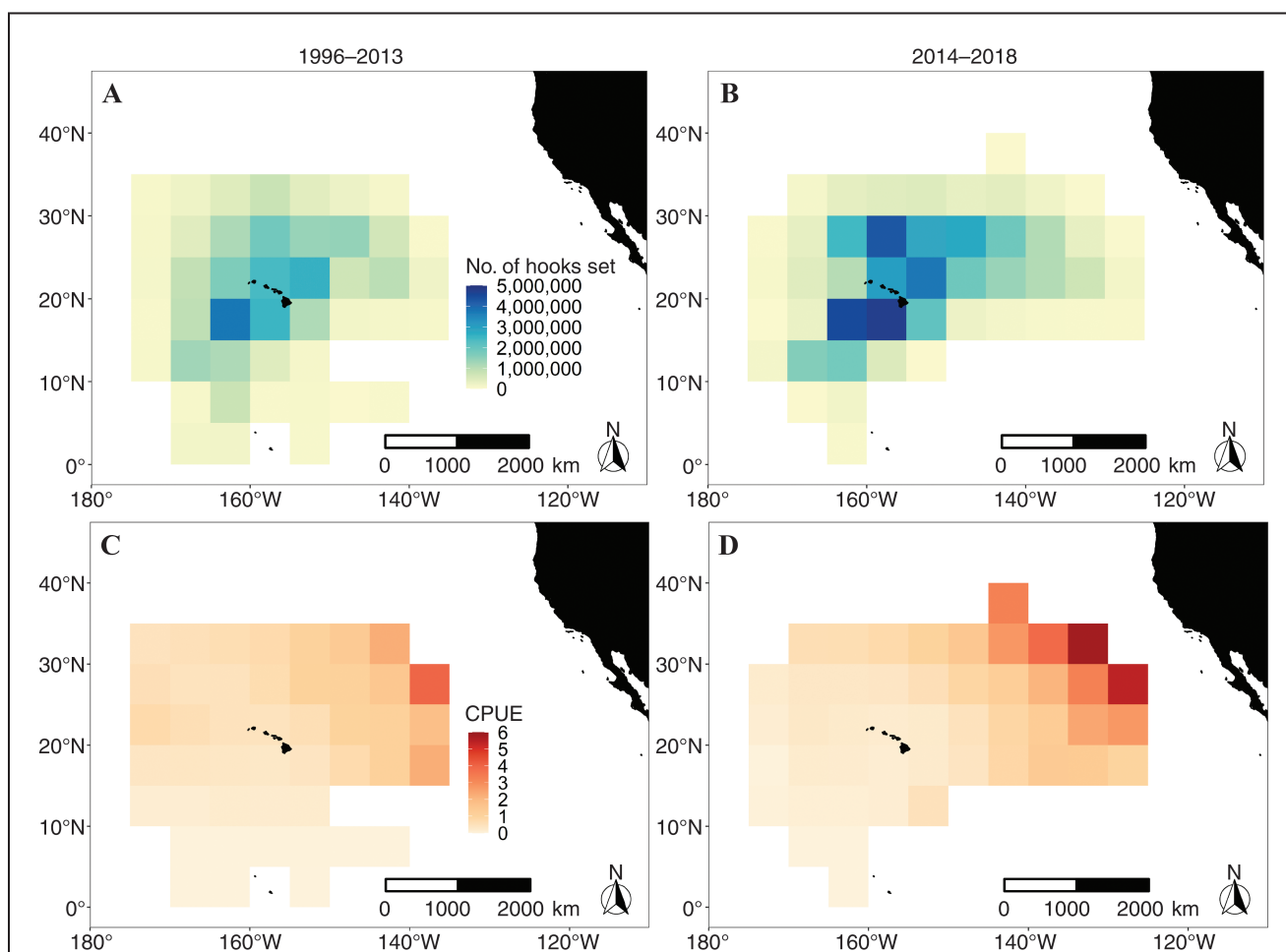


Figure 1

Map of the (A and B) average annual effort, measured as number of hooks, and (C and D) aggregate nominal catch per unit of effort (CPUE), measured as number of individuals per 1000 hooks, for opah (*Lampris* spp.) caught by the U.S. deep-set longline fishery during 1996–2013 and 2014–2018 in the central and eastern North Pacific Ocean. Logbook data are binned into 5°-by-5° blocks, and blocks with data from less than 3 vessels are not shown to maintain confidentiality.

changing the beginning of the fisheries data time series to 1996. The use of these criteria resulted in a final data set of 330,599 deep-set gear sets and 43,326 shallow-set gear sets spanning from 1996 through 2018, with 89% and 54% of data remaining from the original unfiltered data sets, respectively. Almost 40% of the shallow-set data were filtered out simply because of missing critical fields in the data set (hooks per float, hooks per set, soak time, or geographic coordinates).

The areas fished by both fleets have changed since the beginning of the longline fisheries. During the 1990s, the deep-set fishery was primarily confined to the waters around the main Hawaiian Islands, but effort began to expand eastward in the 2000s (Woodworth-Jefcoats et al., 2018). This expansion accelerated after 2013. From 1996 through 2013, only 9% of the longline sets in the deep-set fishery occurred in waters east of 150°W, and that percentage increased to 26% during 2014–2018.

The percentage of sets in the shallow-set fishery that occurred east of 150°W increased from 25% to 53% over those same time frames.

Consequently, 2 periods were considered for analyses: 1996–2013 and 2014–2018. Filtered logbook data were binned into 5°-by-5° blocks to visualize effort (number of hooks set) and CPUE (number of individual opah landed per 1000 hooks). For confidentiality purposes, visualizations of effort and CPUE do not display blocks containing less than 3 unique vessels within each figure's specified period, although the data were still included in the overall calculations and analyses of fishery trends. Blocks containing less than 20 total sets of deep-set longlines or less than 10 total sets of shallow-set longlines were also removed from their respective analyses to ensure sufficient sample sizes. The shallow-set fishery had overall lower amounts of data and effort; therefore, a lower threshold was established to maximize spatial data.

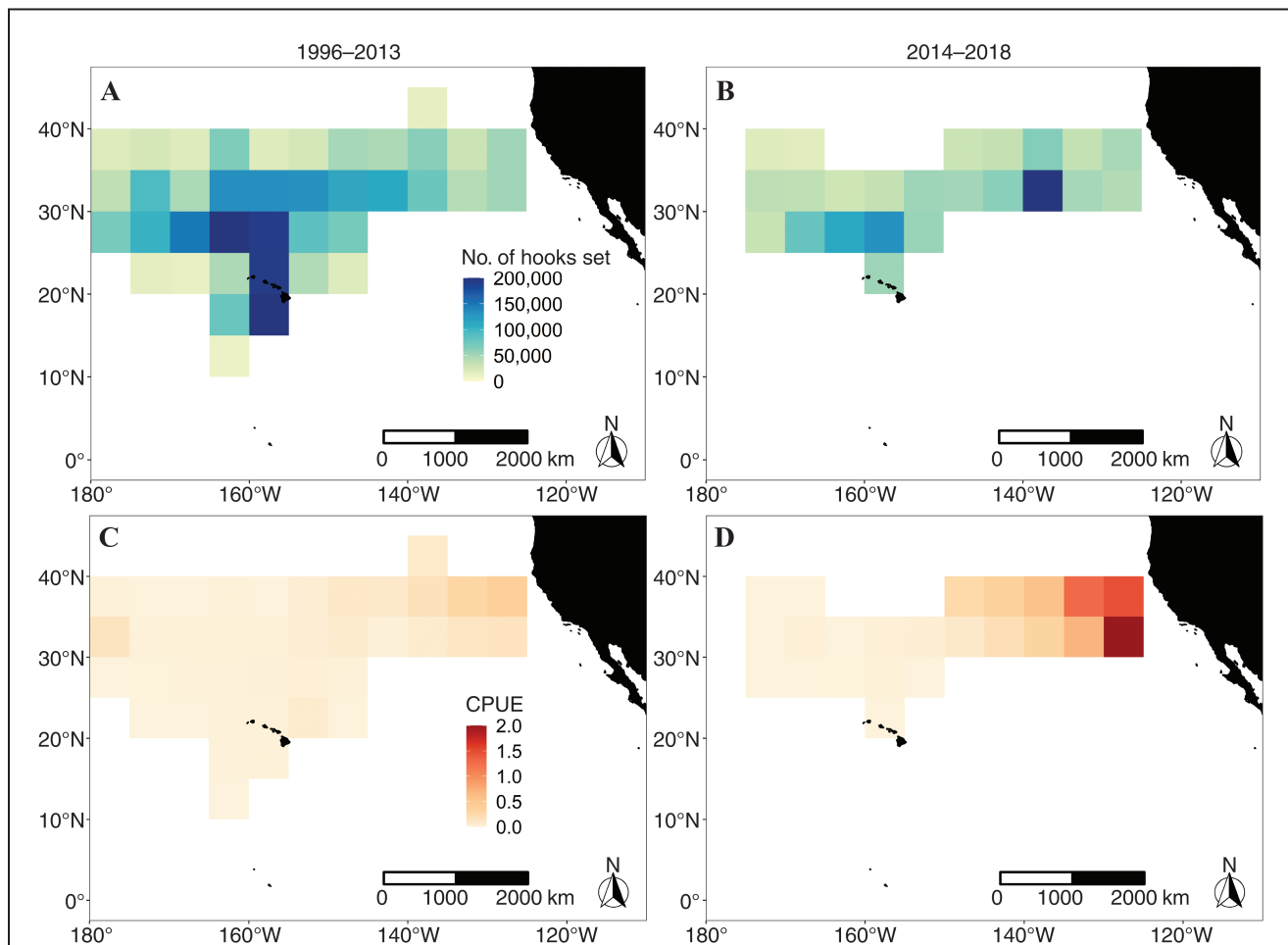


Figure 2

Map of the (A and B) average annual effort, measured as number of hooks, and (C and D) aggregate nominal catch per unit of effort (CPUE), measured as number of individuals per 1000 hooks, for opah (*Lampris* spp.) caught by the U.S. shallow-set longline fishery during 1996–2013 and 2014–2018 in the central and eastern North Pacific Ocean. Logbook data are binned into 5°-by-5° blocks, and blocks with data from less than 3 vessels are not shown to maintain confidentiality.

Genetic analyses

Genetic identification of opah was completed as described in Hyde et al. (2014). Briefly, Hyde et al. (2014) used samples of fin tissue collected either by fishery observers at sea during research cruises or by researchers after whole fish were landed in port (in either Hawaii or California) and preserved in 95% ethanol until processed. From each sample, DNA was extracted by using a boiling protocol with Chelex 100⁴ resin (Bio-Rad Laboratories Inc., Hercules, CA), and a portion of the mitochondrial cytochrome *c* oxidase gene was amplified, sequenced, and compared to reference sequences for bigeye Pacific opah (accession no. JF931871, GenBank, available from [website](#)) and small-eye Pacific opah (accession no. JF931880, GenBank, available from [website](#)) to identify species.

This study incorporated samples collected by researchers and observers and used in the Hyde et al. (2014) study and samples collected by commercial fishermen since that paper was published. For samples collected by observers, sampling locations were identified to specific sets, whereas the more recent samples collected by fishermen were associated only with specific trips, not with individual sets. To standardize the spatial resolution of sampling of tissue for genetic analysis, location data for all samples were aggregated to trip level by taking the average latitude and longitude of all sets within the trip in which opah were landed (an average of 13 sets per trip), on the basis of logbook data from the same sampled trip. There were 141 deep-set and 2 shallow-set longline trips associated with genetic samples of opah. Given the lack of genetic samples from shallow-set trips, only the genetic samples from deep-set trips were retained for further analysis. In addition, 2 deep-set trips had a difference of more than 5° between the maximum and minimum latitude or longitude of a trip, and they were excluded, yielding a total of 139 deep-set longline trips that were used for estimating distribution of opah species.

Spatial distributions of species

Based on the genetic analyses described above, the proportion of bigeye Pacific opah versus small-eye Pacific opah within 5°-by-5° grid cells were calculated. A series of GAMs were then developed by using the *mcgv* package (vers. 1.8-33; Wood, 2017) in R, vers. 3.6.1 (R Core Team, 2019), to explain the differences in the proportions of bigeye Pacific opah. Latitude (*lat*) and longitude (*lon*) were used to predict the proportion of bigeye Pacific opah (*propnBigeye*) through beta regression, weighted by the total number of opah caught (sample size) within each grid cell:

$$\text{propnBigeye} \sim s(\text{lon}, \text{lat}),$$

where *s* = a thin-plate regression spline (Wood, 2017).

We tested the inclusion of season (quarter of the year) as an additional predictor in the GAMs, to assess whether spatial patterns in species distributions varied throughout the year. However, the GAMs that include season were not superior to those without that variable, with <1% difference in variance explained and higher Akaike information criteria. As such, for further analysis, we proceeded with GAMs that include just latitude and longitude as predictors.

Three GAMs were built by using identical predictor and response variables but different knot (*k*) values for the isotropic thin-plate regression spline: 4 (low), 6 (medium), and 8 (high). We chose to vary *k* to capture some of the uncertainty in the spatial prediction surface because the locations of genetically identified opah did not cover the full geographic range of the pelagic longline fleet. Values of 4, 6, and 8 allowed different patterns of spatial extrapolation outside the sampled area, without obvious overfitting.

The fitted GAMs were then used to generate maps with the expected proportions of bigeye Pacific opah over the study area and were used to identify areas dominated by either bigeye Pacific opah or small-eye Pacific opah, by using an arbitrary threshold of 0.7. Areas with expected proportions of bigeye Pacific opah ≥0.7 and ≤0.3 were classified as dominated by bigeye Pacific opah and small-eye Pacific opah, respectively. Areas with expected proportions between 0.3 and 0.7 were considered *mixed areas* without dominance of a single species of opah. The logbook data from the deep-set longline fishery were divided into 3 subsets—data for areas dominated by bigeye Pacific opah, data for areas dominated by small-eye Pacific opah, and data for mixed areas—and were used to calculate the number of sets and average CPUE in each type of area.

To estimate the uncertainty of the GAM predictions, an iterative jackknife procedure was performed. Jackknifing resamples data with a leave-one-out method; the medium (*k*=6) GAM with 139 trip-level data points was rerun 139 times, each time with a single trip removed (with replacement) to predict species proportion for each 1°-by-1° block in a grid spanning the study area. To visualize the uncertainty of the GAM predictions, the mean, standard deviation, and coefficient of variability were estimated for each block, with the coefficient of variability calculated as (standard deviation/mean)100.

Results

Spatial and temporal patterns: fishing effort and catch per unit of effort

A compilation of all data across the time series reveals differences in the deep- and shallow-set longline fisheries. Effort in the deep-set fishery increased from roughly 375 sets in 1996 to 18,700 sets in 2018. In contrast, effort in the shallow-set fishery peaked in 1998 at roughly 4700 sets. The shallow-set fishery was temporarily closed from 2001 through 2004 (Federal Register, 2004), and annual effort remained below 2000 sets per year from 2005 through 2018.

⁴ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

The spatial range of the deep-set fishery also changed over time. In 2014–2018, the fishery expanded eastward to 125°W (compared with a limit of 135°W in 1996–2013), and less area was fished south of 10°N (Fig. 1). Even after the eastward expansion in 2014, the majority of deep-set fishery operations were still centered around the main Hawaiian Islands, with 74% of the fishery operating west of 150°W during 2014–2018 in comparison with 91% during 1996–2013.

As with effort, the spatial range of the shallow-set fishery also decreased in 2014–2018 compared with the range in 1996–2013 (Fig. 2). As with the deep-set fishery, effort for the shallow-set fishery was centralized around the Hawaiian Islands in 1996–2013 but transitioned to more of a bimodal distribution, with one peak around the Hawaiian Islands and another around 140°W, 30°N in 2014–2018.

The CPUE for opah was highest in the northeast region of both the deep-set and shallow-set fishery, roughly east of 140°W and north of 25°N, with a noticeable gradient increasing from west to east (Figs. 1 and 2). The results of comparing data between the gear types indicate that CPUE was highest in the deep-set fishery. From 2014 through 2018, CPUE of deep-set longlines in 5°-by-5° blocks ranged from 3.0 to 6.0 opah/1000 hooks in the northeast extent of the fishery and from 0.5 to 2.0 opah/1000 hooks west of 140°W. The CPUE of shallow-set longlines peaked at about 2 opah/1000 hooks in the northeast area and was generally <1 opah/1000 hooks throughout the rest of the fishery range.

Spatial distributions of species

For species identification in this study, an additional 679 samples from 37 trips were added to the 415 samples from 102 trips used in the study conducted by Hyde et al. (2014), to examine distribution in the region that overlaps with the pelagic longline fisheries. The region and time frame over which the samples were collected differed for the 2 programs (Table 1). The samples from Hyde et al. (2014) came from west of 139°42'W, whereas the more recent samples came from east of 139°6'W. Both programs sampled across months, although no samples from November were available to Hyde et al. (2014). Bigeye Pacific opah were identified in all 5°-by-5° blocks, although percent occurrence varied spatially. In the region around Hawaii and to the south, only bigeye Pacific opah were identified in the blocks. North of the Hawaiian Islands (>25°N), smallmouth Pacific opah were identified in all blocks with the proportions ranging from 0.1 through 0.8 and with the highest proportional abundance in the blocks closest to the U.S. West Coast. (Fig. 3).

The Akaike information criteria for GAMs with k of 4, 6, and 8 were -2669.9, -2726.1, and -2742.0, respectively. The effective degrees of freedom for these GAMs were 2.98, 4.88, and 6.75, respectively. The effective degrees of freedom of 2.98 for the GAM with a k of 4 is very close to 3, which is 1 less than k , indicating that this GAM may be over-smoothed. The 3 GAMs explained 56.2%, 59.1%, and 60.0% of the deviance in the genetic sampling data, respectively.

Table 1

Overview of sampling of bigeye Pacific opah (*Lampris megalopsis*) and smallmouth Pacific opah (*L. incognitus*) from which genetic data used in this study were obtained. Data were compiled from Hyde et al. (2014) and from genetic analyses conducted since 2014 of samples from the eastern North Pacific Ocean.

Data type	Period	
	2009–2010 (from Hyde et al.)	2017–2018
Effort (no. of trips)	102	37
Sample size	415	679
Latitude mode	30.00°N	22.45°N
Latitude range	10.68–31.72°N	19.83–33.39°N
Longitude mode	217.56°E	227.53°E
Longitude range	190.52–220.27°E	220.93–232.89°E

Model fits appeared adequate, and residuals were approximately normally distributed in each case.

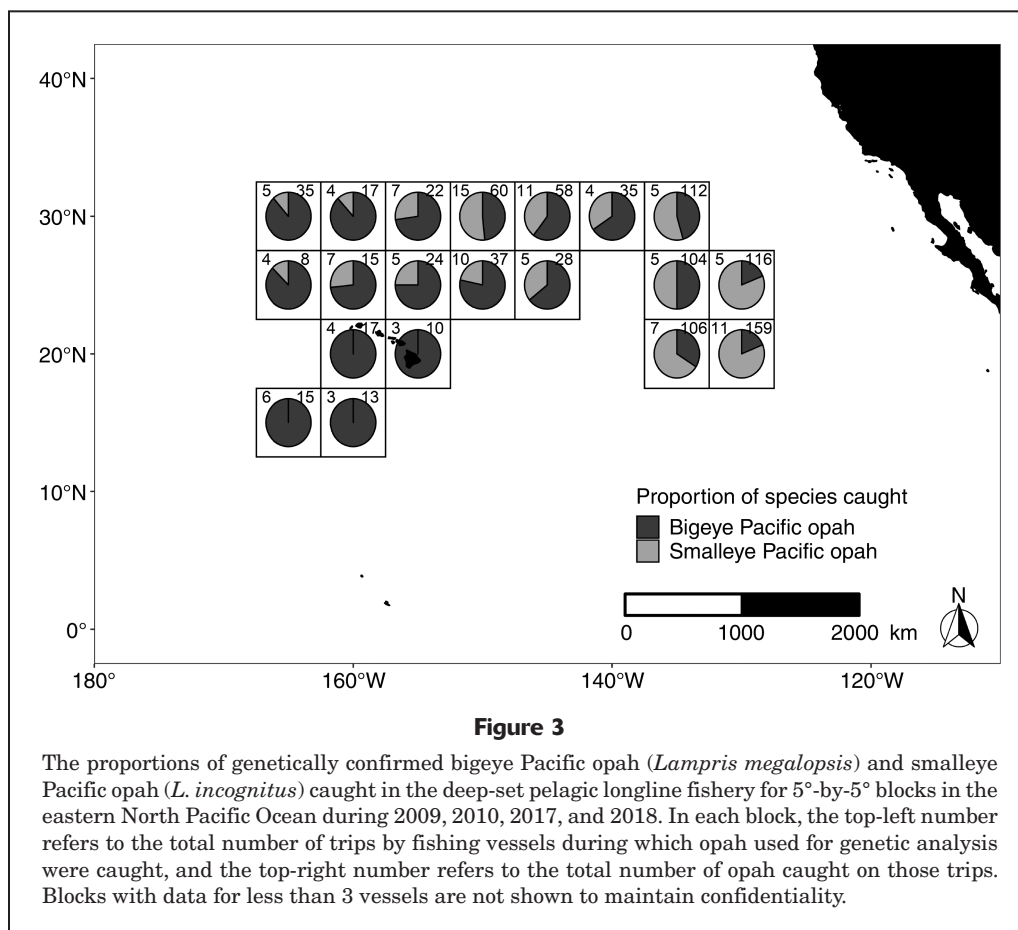
All 3 GAMs predicted that bigeye Pacific opah would dominate (with proportions of bigeye Pacific opah ≥ 0.7) in waters west of 140°W, particularly in the southwest extent of the study area, and that smallmouth Pacific opah would dominate (with proportions of bigeye Pacific opah ≤ 0.3) in waters east of 130°W (Fig. 4). The 2 species were predicted to co-occur in roughly equal proportions between 140°W and 130°W. Predictions from the 3 GAMs varied spatially, particularly in the area north of 25°N and east of 150°W, where fishing effort was generally lower. However, estimates from all models indicate a strong west-to-east gradient of high-to-low probability of occurrence of bigeye Pacific opah.

The results from jackknifing indicate low levels of variance over the study area, with a maximum coefficient of variability of ~4% (Fig. 5). The area with the highest coefficient of variability (155–140°W, 30–35°N) was the area with the least data, and it encompasses waters predicted to have areas dominated by bigeye Pacific opah and mixed areas. Generally, waters predicted to be dominated by one species or the other had lower variability.

Catch per unit of effort by species dominance

The results from the GAMs and the maps of CPUE were combined to examine CPUE in the 3 types of areas classified by species dominance: dominated by bigeye Pacific opah, dominated by smallmouth Pacific opah, and mixed areas. The lowest CPUE was in areas predicted to be dominated by bigeye Pacific opah (west of 140°W), and the highest CPUE was in the eastern portion of the mixed area and the area predicted to be dominated by smallmouth Pacific opah (east of 130°W) (Table 2, Figs. 1 and 2).

The results from comparing data for the 2 periods indicate that CPUE declined slightly in areas dominated by



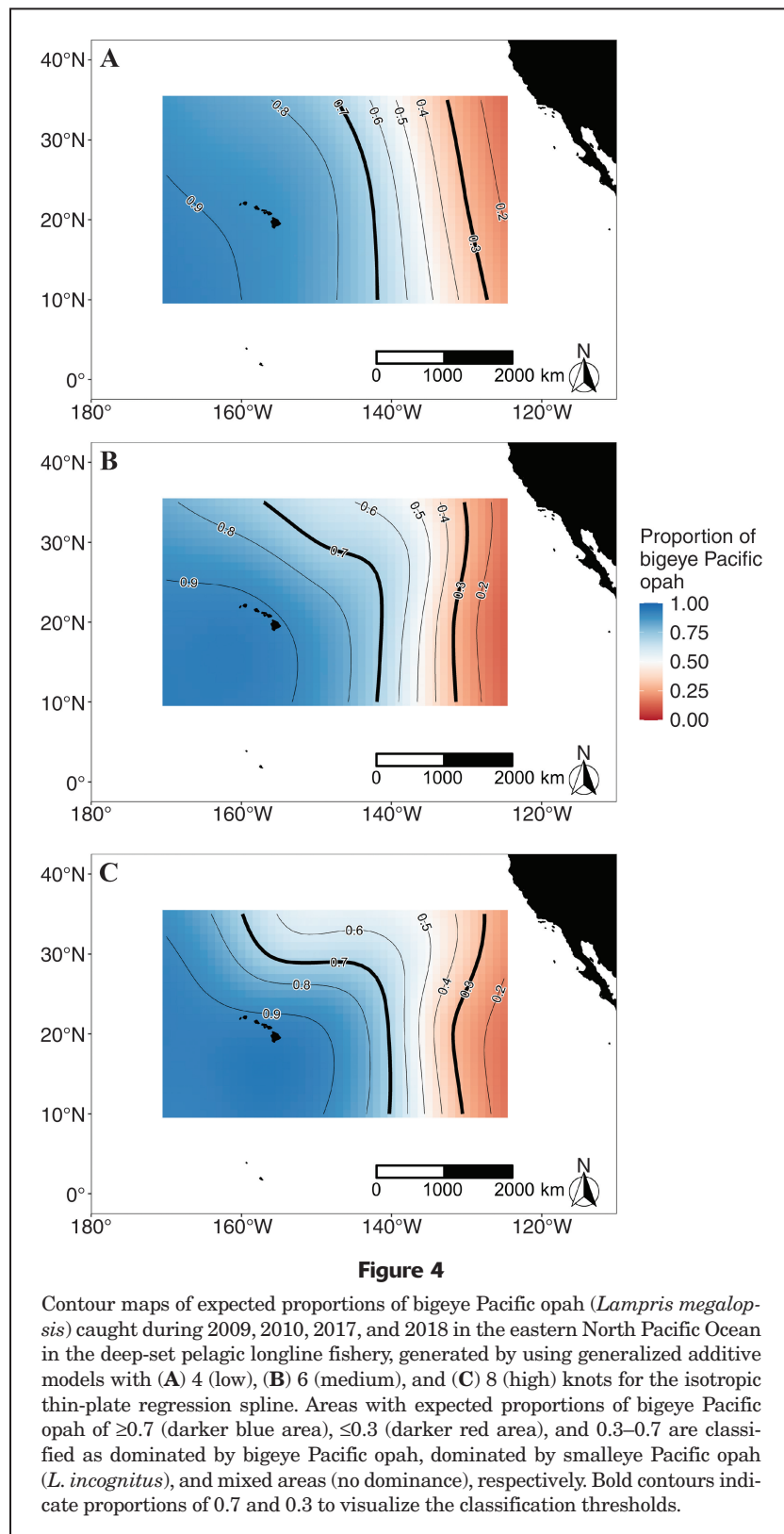
bigeye Pacific opah in 2014–2018 but remained fairly consistent in mixed areas. Because of the low effort in the eastern region during 1996–2013, it was not possible to compare CPUE across periods. It is apparent, however, that the CPUE in the region dominated by smalleye Pacific opah during 2014–2018 was consistently higher than in the regions dominated by bigeye Pacific opah and in the mixed area across both periods. Table 2 also highlights that the majority of fishing activity in this region has occurred since 2014.

Discussion

The results of this study, linking fisheries data with more detailed information on the distribution of bigeye Pacific opah and smalleye Pacific opah, advance our understanding in important ways. First, our analyses allowed examination of shifts in fisheries interactions in the context of opah distribution. Second, the results of this work provide a more complete picture of the range of the 2 species and insight into temporal and spatial patterns in catch in a species-specific context. This study represents an important step toward understanding the basic biology and fisheries interactions of the 2 opah species in the eastern North Pacific Ocean.

Fisheries distribution and catch per unit of effort

The effort and spatial distribution of both the U.S. pelagic longline fleets targeting bigeye tuna and swordfish in the Pacific Ocean have changed from 1996 to 2018. In the shallow-set fishery, the range and effort decreased. In contrast, the deep-set fishery increased in both effort and range, with substantially more effort east of 140°W. Although observations of these shifts in fisheries are not new (Woodworth-Jefcoats et al., 2018), it is important to understand the dynamics of the fishery in the context of interactions with opah. Total effort has increased in the region where the overall CPUE and proportion of smalleye Pacific opah are higher. In addition, effort has shifted from shallow-set gear to deep-set gear, and CPUE of opah is also higher in the deep-set fishery than in the shallow-set fishery. These findings are consistent with the increase in landings of opah in the deep-set longline fishery (National Marine Fisheries Service, Office of Science and Technology, commercial fisheries landings, available from [website](#), accessed May 2020). However, variable fishing footprints, the limit of evaluation to only 2 periods, and multiple regulatory shifts make direct temporal comparisons of CPUE and effort challenging. The relative contribution of the 2 species to this increase in landings



cannot be calculated because of the lack of species-specific landings data, and estimation of the relative contributions is beyond the scope of this paper.

Spatial distributions of species

Paired with data from Hyde et al. (2014), the results of the additional genetic analyses in this study have filled the gap east of 140°W, outside of the U.S. exclusive economic zone, providing a more spatially complete picture of the distributions of bigeye and smalleye Pacific opah. Results of our evaluation of species distribution indicate that, during 2009–2019, bigeye Pacific opah occurred throughout the region and smalleye Pacific opah occurred predominantly in the eastern and northern boundaries of the range of longline fisheries, with proportional abundance decreasing toward the west. There was no defined boundary between the distributions of the 2 species within the geographic scope of this study. South of 25°N, the approximate location of the North Pacific Transition Zone (Roden, 1991; Polovina et al., 2001), the transition from blocks dominated by smalleye Pacific opah to blocks dominated by bigeye Pacific opah occurred approximately between 140°W and 130°W. With the addition of new genetic samples collected for our study, the delineation of the species between 140°W and 130°W is less defined than the distributions indicated by results from Hyde et al. (2014), who reported that a number of the eastern blocks were all dominated by smalleye Pacific opah. In the North Pacific Transition Zone, the transition was even less well-defined, and smalleye Pacific opah occurred across our entire study area. Additional genetic samples from this region would allow expansion of the model into the North Pacific Transition Zone in future studies. The considerable overlap between the distributions of the 2 opah species could complicate retroactive examination of species-specific trends.

Although this study was confined to the approximate spatial extent of the U.S. pelagic longline fisheries in the North Pacific Ocean, data are available for regions outside this area and provide additional insight into the broader range of the 2 opah species in the Pacific Ocean. Results from genetic analyses of samples from the western Pacific Ocean near Japan and the southcentral Pacific Ocean

near America Samoa indicate that 100% of samples are bigeye Pacific opah (Hyde et al., 2014), indicating that the dominance of bigeye Pacific opah continues both west and south

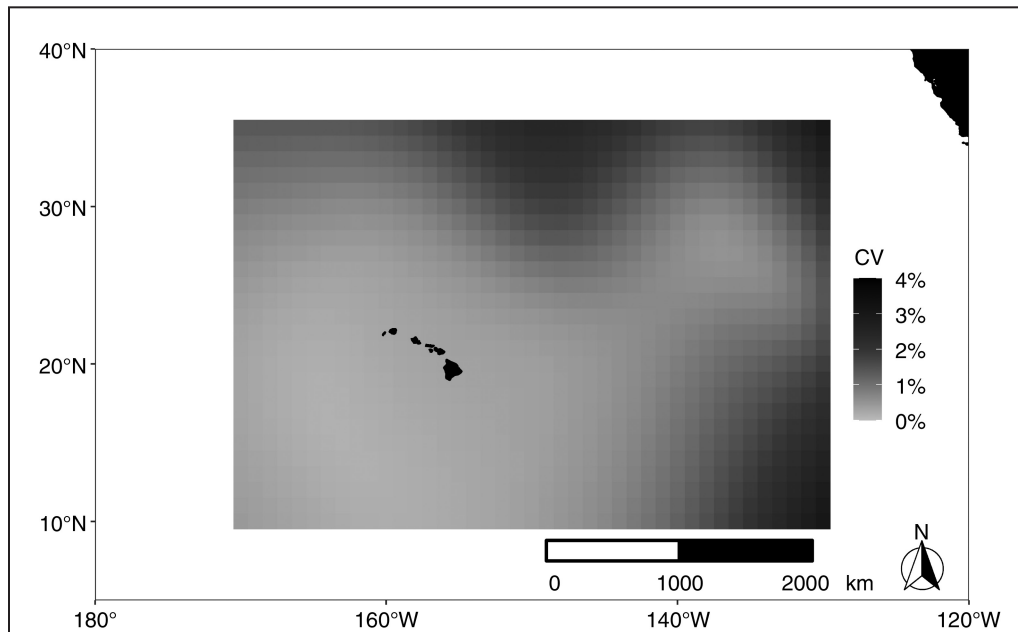


Figure 5

Coefficient of variability (CV) estimated by using a jackknife procedure and the generalized additive model with 6 knots for the thin-plate regression spline, for each 1°-by-1° block over the study area in the eastern North Pacific Ocean where opah (*Lampris* spp.) were caught with deep-set pelagic longlines during 2009, 2010, 2017, and 2018. Darker areas of the map show higher levels of variability in the data. The CVs were calculated as (standard deviation/mean)100.

Table 2

Number of sets and catch per unit of effort (CPUE), measured as number of individual opah per 1000 hooks, for the deep-set pelagic longline fishery operating in areas in the eastern North Pacific Ocean dominated by bigeye Pacific opah (*Lampris megalopsis*), small-eye Pacific opah (*L. incognitus*), or mixed species. Values are given by the number of knots (*k*) for the isotropic thin-plate regression spline in each generalized additive model: 4 (low), 6 (medium), and 8 (high). Some cells are blank because values are included only when data for more than 20 sets were available.

<i>k</i>	Bigeye		Smalleye		Mixed species	
	No. of sets	CPUE	No. of sets	CPUE	No. of sets	CPUE
Sampling period: 1996–2013						
4	236,152	0.43			3042	1.89
6	233,340	0.42			5848	1.64
8	227,167	0.40			12,028	1.22
Sampling period: 2014–2018						
4	80,382	0.34	364	4.28	10,645	1.76
6	79,114	0.32	616	2.93	11,661	1.72
8	77,311	0.31	584	2.62	13,496	1.60

of the main Hawaiian Islands and that the range of small-eye Pacific opah does not extend across the Pacific Ocean. Although pelagic longline fisheries cannot operate within 200 nautical miles of the U.S. West Coast, data are available for this region from other fisheries and research cruises. Catch composition in the California Current from the state of Washington to Mexico is nearly 100% small-eye Pacific opah (Hyde et al., 2014). It should be noted that most opah sampled were relatively large (>80 cm fork length) and presumed to be adults, and even less information is available on the geographic range of larvae and juveniles. Additional species-specific information across size classes is needed to determine the full distribution of each species.

The movement patterns of highly migratory species and the dynamic nature of their habitat make it difficult, if not impossible, to establish static boundaries of species ranges (Maxwell et al., 2015; Dunn et al., 2016). Although this study classified fixed areas for each species within the range sampled, the distribution of species can shift over time with variations in abundance, natural climate variability on interannual (e.g., El Niño–Southern Oscillation) and decadal (e.g., Pacific Decadal Oscillation) timescales, as well as with longer-term climate change.

A number of factors indicate the potential for shifts in the distribution of opah. First, the distributions of bigeye tuna and swordfish, which have habitats and diets that overlap with those of opah, have shifted with climate

variability (Bigelow et al., 1999; Howell and Kobayashi, 2006; Choy et al., 2013; Sculley and Brodziak, 2020). Second, evidence indicates that the abundance of some large pelagic predators, including opah, has decreased on the high seas. Results from both our study and that of Polovina and Woodworth-Jefcoats (2013) indicate a decline in CPUE in areas where bigeye Pacific opah are expected to dominate landings. Polovina and Woodworth-Jefcoats (2013) used longline data collected through 2011, prior to the eastward expansion of the deep-set fishery. Conversely, CPUE of opah has increased in coastal waters off California (Walker and Teo¹). The likely influences of natural climate variability, long-term climate change, and apparent changes in abundance highlight the potential for shifts in distribution of opah and the importance of long-term monitoring of species ranges.

Opah and oceanography

Although the ecological drivers for the spatial distributions of both opah species are unknown, insights were gained by examining patterns in CPUE. Caution should be used when interpreting patterns in CPUE, but standardized CPUE trends are commonly used as indices of relative abundance for both target and non-target species (Bigelow et al., 2002; Woodworth-Jefcoats et al., 2018; Ducharme-Barth and Vincent⁵). For both pelagic longline fisheries, the highest CPUE of opah was recorded in the northeastern extent of the fishery ranges, starting at approximately 140°W.

Quantification of the relative contribution of the 2 species to the overall opah CPUE is beyond the scope of this paper; however, a number of factors may contribute to this pattern, with insights coming from the relatively high CPUE of bigeye tuna in the same region (Hanamoto, 1987; Woodworth-Jefcoats et al., 2018; Ducharme-Barth and Vincent⁵). East of ~130°W, dissolved oxygen at depth declines rapidly because of the presence of the eastern Pacific oxygen minimum zone (Karstensen et al., 2008). It has been hypothesized that, where low-oxygen waters encompass the deep scattering layer, bigeye tuna are less able to access mesopelagic prey (Hanamoto, 1987). Given that the diets and vertical habitats of bigeye tuna and opah overlap (Nakano et al., 1997; Polovina et al., 2008; Choy et al., 2013), the same forces may influence abundance of opah. East of this region, productivity is enhanced by the California Current (Ryckaczewski and Checkley, 2008). Although additional research on species-specific essential habitat and gear vulnerability is needed, the apparent increase in abundance of opah in the eastern Pacific Ocean is likely linked to regional oceanography, productivity, and prey availability, as has been observed for other highly migratory species. This study did not incorporate

seasonality as a predictor in the GAMs, but seasonal shifts in oceanographic conditions, and therefore potentially in distributions of opah species, could be occurring and could be revealed with additional sampling.

Insights into species-specific habitats are gained by comparing the distribution of the 2 species, particularly in regions that are dominated by a single species. Although examining the broad range of factors that influence distributions is beyond the scope of this paper, insights can come from examining distributions in the context of oceanographic conditions and prey availability.

Off the coast of California, where smalleye Pacific opah are dominant, both dissolved oxygen and temperature decline rapidly with depth, and these decreases may limit access for smalleye Pacific opah to favorable thermal habitat and mesopelagic prey species (Karstensen et al., 2008; Choy et al., 2013; Aksnes et al., 2017). At the same time, the shallow oxygen minimum zone may compress the habitat of the epipelagic species that are important prey of the smalleye Pacific opah (Prince and Goodyear, 2006; Choy et al., 2013). In contrast, in oligotrophic gyre waters south of Hawaii, where bigeye Pacific opah dominate, productivity in surface waters and epipelagic prey biomass are low (Signorini et al., 2015) and the deep scattering layer is deeper. For example, Tont (1976) listed a difference of ~100 m in the depth of the top of the deep scattering layer between the California Current and the central Pacific Ocean (an average of 282 m versus 394 m). In addition, sea-surface temperatures are warmer in the central Pacific Ocean compared with those in comparable latitudes in the California Current, and winter mixed layer depths are deeper (de Boyer Montégut et al., 2004; Deser et al., 2010). Bigeye Pacific opah tagged with pop-up archival tags north of the main Hawaiian Islands frequently occupied depths as deep as 400 m during the day, potentially reflecting targeting of mesopelagic prey (Polovina et al., 2008). Similar information on the physiological capabilities and habitat use of bigeye and smalleye Pacific opah, and their prey, will help resolve niche separation and essential habitat.

Implications of sympatric or cryptic species for fisheries management

The presence of morphologically similar species in landings can cause issues with fisheries management. For example, the population status of white marlin (*Kajikia albida*) had to be reevaluated when it was discovered that pelagic longline fisheries in the North Atlantic Ocean were unknowingly landing significant amounts of the similar-looking roundscale spearfish (*Tetrapturus georgii*) without separating them in the catch records (Beerkircher et al., 2009). Although we have studied the spatial distributions of both opah species, they are still listed as a single species in logbooks and landings data. It will, therefore, be important to collect fisheries data and conduct scientific studies for specific species. Establishing distinct, species-specific management strategies and techniques is important because changes to the fishery range, gear, or landing

⁵ Ducharme-Barth, N., and M. Vincent. 2020. Analysis of Pacific-wide operational longline dataset for bigeye and yellowfin tuna catch-per-unit-effort (CPUE). Sci. Comm. sixteenth regular session; online, 11–20 August. West. Cent. Pac. Fish. Comm., Inf. Pap. WCPFC-SC16-2020/SA-IP-07, 55 p. [Available from [website](#).]

rates may disproportionately affect 1 species and unknowingly lead to unsustainable harvest rates.

Conclusions

In this study, species-specific spatial distributions were estimated for bigeye Pacific opah and smalleye Pacific opah in U.S. longline fisheries in the North Pacific Ocean, information that has filled important knowledge gaps. Future work incorporating genetic and fisheries data—including latitude, longitude, and depth of capture—for samples collected in a broader spatial range—would help reduce uncertainty regarding the spatial distributions of and overlap between the 2 species. In addition, it would be important to determine differences and similarities between the essential habitats of each opah species, including foraging ecology, to better quantify the vulnerability of each species to different gear configurations. Better understanding of the species ranges and associations with different pelagic environments will improve efforts for management of bigeye and smalleye Pacific opah.

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