



# Spatiotemporal segregation of ocean sunfish species (Molidae) in the eastern North Pacific

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**ABSTRACT:** Ocean sunfishes or molas (Molidae) are difficult to study as a result of their extensive movements and low densities in remote waters. In particular, little is known of the environmental niche separation and differences in the reproductive or movement ecology of molids in sympatry. We investigated spatiotemporal dynamics in the distribution of the common mola *Mola mola*, sharptail mola *Masturus lanceolatus*, and slender mola *Ranzania laevis* in the eastern North Pacific. We used observer data from a commercial fishery consisting of 85 000+ longline sets spanning 24 yr, >50° in longitude, and >45° in latitude. Satellite altimetry analysis, species distribution modeling, and multivariate ordination revealed thermal niche separation, spatiotemporal segregation, and distinct community associations of the 3 molid species. Our quantitative findings suggest that the common mola is a more temperate species, while slender and sharptail mola are more (sub)-tropical species, and that slender (and possibly also sharptail) mola undergo spawning migrations to the region around the Hawaiian Islands. In addition, we identified potential effects of fishing gear type on molid catch probability, an increasing trend in catch probability of a vulnerable species perhaps related to a shift in the distribution of fishing effort, and the possible presence in the fishery of a fourth molid species being misidentified as a congener, all of which are important conservation considerations for these enigmatic fishes.

**KEY WORDS:** *Mola mola* · *Masturus lanceolatus* · *Ranzania laevis* · Bycatch · Species distribution modeling · Longline

## 1. INTRODUCTION

Fishes in the family Molidae (molids, commonly known as ocean sunfishes or molas) are enigmatic, and scientific perceptions of these species have changed dramatically in recent years as they have received increased research attention (e.g. Pope et al. 2010, Phillips et al. 2015, Nyegaard et al. 2018b). Easily recognized by their lack of a caudal fin (Johnson & Britz 2005), molids constitute an evolutionary exception within the order Tetraodontiformes be-

cause their family is the only one that primarily diversified into the open ocean rather than fresh/brackish, coastal, or deep shelf waters (Yamanoue et al. 2008). The family consists of 3 genera (*Mola*, 3 species; *Masturus*, 1 species; and *Ranzania*, 1 species) (Froese & Pauly 2019) and is circumglobally distributed in neritic and oceanic waters from tropical to temperate latitudes (Nyegaard et al. 2018a, Sawai et al. 2018).

There is notable diversity among molids, as a closer evolutionary relationship between *Mola* and *Masturus* than of either of these to *Ranzania* is supported

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by phylogenetic (Yamanoue et al. 2004, Bass et al. 2005) and morphological studies (Santini & Tyler 2002, Katayama & Matsuura 2016). The species of *Mola* and *Masturus* achieve maximum sizes of 3+ m in length (Hutchins 2001), whereas *Ranzania* only reaches <1 m in length (Smith et al. 2010). There are also marked differences in the dietary specialization (Bakenhaster & Knight-Gray 2016, Nyegaard et al. 2017) and early development (Lyczkowski-Shultz 2003) of *Mola* and *Masturus* versus *Ranzania*, which suggests ecological divergence among these species.

While knowledge of individual molid species has increased in recent years, little is known of the environmental niche separation and differences in the reproductive or movement ecology of molids in sympatry. Limited evidence suggests that molid species exhibit distinct distributions in relation to sea surface temperature (SST) and latitude in the western South Pacific (Nyegaard et al. 2018b), segregated spawning activity in the western North Atlantic (Hellenbrecht et al. 2019), and different patterns in seasonal abundance in the Mediterranean Sea (Dulčić et al. 2007). Comparisons of molids in allopatry have noted potential differences in their environmental preferences or behavior but were confounded by the disparate regions or oceans in which the underlying studies were conducted (e.g. Dewar et al. 2010). Thus, there is a need for further research into the habitat use and ecological separation of molids in sympatry; however, such data are difficult to procure given the lengthy migrations (Potter et al. 2011), deep vertical descents (Phillips et al. 2015, Thys et al. 2017), low densities (Houghton et al. 2006), and rarely encountered aggregations of these fishes in remote waters (Castro & Ramos 2002, Horn et al. 2016).

Interaction with commercial fisheries is a primary conservation concern for molids, yet at the same time represents a source of valuable information on their distribution, behavior, and life history (e.g. Castro & Ramos 2002, Liu et al. 2009, Nakamura & Sato 2014). Molids are primarily taken as bycatch in pelagic driftnet (Silvani et al. 1999, Horn et al. 2016, Hahlbeck et al. 2017) and longline fisheries across the globe (Coelho et al. 2012, Domingo et al. 2012, Nyegaard et al. 2018a) and are only rarely targeted for commercial harvest (Sagara & Ozawa 2002, Liu et al. 2009). In the eastern North Pacific, at least 3 molid species are exposed to fishery interactions: common mola *Mola mola*, the most studied species in the family (Pope et al. 2010), as well as sharptail mola *Masturus lanceolatus* and slender mola *Ranzania laevis*, for which comparatively little information is available. In particular, these species are captured as bycatch in

the ~150 vessel fleet of the Hawaiian longline fishery, which is the largest fishery managed under the US Western Pacific Regional Fishery Management Council. The Hawaiian longline fishery conducts >1000 trips yr<sup>-1</sup> (Pan & Walden 2015) over an area spanning more than 50° in longitude and 45° in latitude, enabling sampling of rare and highly migratory species. Long-term data from federal observers of this fishery, established for the quantification of protected species bycatch (e.g. sea turtles), have been used to document distributions (Walsh et al. 2009, Gilman et al. 2012), environmental associations (Walsh & Kleiber 2001) and temporal population trends of pelagic species (Brodziak & Walsh 2013, Walsh & Brodziak 2015), as well as ecosystem changes (Polovina et al. 2009, Polovina & Woodworth-Jefcoats 2013).

The purpose of this study was to investigate spatiotemporal dynamics in the distribution of common, sharptail, and slender mola in the eastern North Pacific. There have been qualitative, global comparisons of these 3 species (e.g. Gudger 1937) but no quantitative, regional assessments critically analyzing their distributional differences and the underlying drivers. We hypothesized species-specific, latitudinal distributions varying with seasonal thermal cycles and temporally distinct migrations, among species, to areas previously identified as spawning hotspots. We used 24 yr of observer data from the Hawaiian longline fishery to determine thermal associations, model distributions, identify migrations, and characterize associated fish communities for each species. Our quantitative findings included spatiotemporal segregation, environmental niche separation, distinct community associations, and potential spawning migrations. In addition, we identified potential effects of fishing gear type on molid catch probability, an increasing trend in catch probability for a vulnerable species, and the possible presence in the fishery of a fourth molid species being misidentified as a congener.

## 2. METHODS

### 2.1. Fishery observer data

The Hawaiian longline fishery is divided into 2 sectors (deep-set and shallow-set) with disparate fishing methodologies and spatial distributions. The deep- and shallow-set sectors are legally defined by the number of hooks used between floats on the longline (deep-set ≥ 15; shallow-set < 15), as using more hooks per float results in a deeper fishing depth (Depart-

ment of Commerce 2004). The deep-set sector primarily fishes at 100–400 m depth during the daytime in (sub)tropical waters from 5°–35° N to target tunas (*Thunnus* spp. and skipjack tuna *Katsuwonus pelamis*), whereas the shallow-set sector primarily fishes at <60 m depth during the nighttime in temperate waters from 28°–32° N to target swordfish *Xiphias gladius* (Bigelow et al. 2006, Brodziak & Walsh 2013, Woodworth-Jefcoats et al. 2018). The catchability of various pelagic fishes changes with depth and diel period due to their distinct diurnal and nocturnal movement patterns, with certain species being more vulnerable to daytime, deep-set operations than nighttime, shallow-set operations (and vice versa) depending on the degree of overlap between fishing gear and species' vertical distributions (He et al. 1997, Ward & Myers 2005). Observer coverage of deep-set sector effort was ~4% from 1995–2000 but increased to ~20% in 2001 and has remained at that required level since (NMFS 2010, Woodworth-Jefcoats et al. 2018), whereas coverage of shallow-set sector effort ranged from ~5–25% in the years prior to a 2001–2004 emergency fishery closure but has been 100% since (Walsh et al. 2005, Gilman et al. 2007, Howell et al. 2008). Observers record the date, time, and location of all effort, the number of hooks set, number of hooks per float, bait type, and hook type for each longline set, as well as the visually determined species identification and number of all fish captured. In addition, observers measure every third fish caught (since February 2006), providing an actual fork length measurement when the fish can safely be brought on board or an estimated fork length when it cannot. Catch rates of species recorded in both the observer dataset and commercial vessel logbooks are highly correlated (Polovina et al. 2009), indicating that the observed portion of the fishery adequately represents the fishery at large. We used observer data from the eastern North Pacific (east of 180° W, north of the equator) as the Hawaiian longline fishery occurs almost exclusively within this region (only 0.1% of longline sets occurred elsewhere during the 24 yr study period).

It is important to note that, while the 3 genera of molids (*Mola*, *Masturus*, and *Ranzania*) are easily distinguished by their external morphology, the currently valid taxonomy of the genus *Mola* was not established until the last year of the study period (Nyegaard et al. 2018b, Sawai et al. 2018). Of the 3 species now recognized in the genus *Mola*, *M. tecta* is thought to occur almost exclusively in temperate waters of the southern hemisphere (Nyegaard et al. 2018a,b) but a few individuals have been recorded

along the coast of California, USA, in the eastern North Pacific (e.g. Walker et al. 2020). In contrast, both *M. mola* and *M. alexandrini* are thought to regularly occur in both hemispheres in the Pacific Ocean (Yoshita et al. 2009, Sawai et al. 2018). While documented extensively in the western North Pacific, the only genetically verified *M. alexandrini* recorded in the eastern North Pacific were sampled in the Galápagos Islands (Thys et al. 2013, Sawai et al. 2018). Thus, we know little about this species in the study region, and it is possible that some of the fish identified as *M. mola* by Hawaiian longline observers prior to the taxonomic revision of the genus were in fact *M. alexandrini*. Limited data on these 2 species in sympatry suggest that *M. mola* may occupy a cooler thermal niche than *M. alexandrini* (Sawai et al. 2011, Nyegaard et al. 2018a, Chang et al. 2020). Also, while the federal observer program has counted sharptail mola separately from the other molid species since 2004 when positive photographic identification of the species was first provided by an observer, this species was likely aggregated with the more frequently encountered common mola prior to 2004 (S. Arceneaux pers. comm.).

## 2.2. Oceanographic data

SST at the date and location of each longline set was extracted from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation 1/4 Degree Daily SST (OISST) Analysis, Version 2 (Reynolds et al. 2008) for assessment of molid thermal associations. Temperature at depths approximating the medians of the vertical distributions of the shallow-set (45 m) and deep-set (262 m) sectors was similarly extracted from the National Centers for Environmental Prediction (NCEP) Global Ocean Data Assimilation System (GODAS) (Behringer & Xue 2004), to investigate thermal patterns at the points in the water column where molas are captured in the fishery. To explore the influence of temperature on the spatial and intra-annual distribution of molids, both overall and monthly climatologies of SST and temperatures at 45 and 262 m were constructed in the study region for the period 1 January 1995 to 31 December 2018.

## 2.3. Species distribution modeling

We constructed species distribution models from longline presence/absence data to investigate spatio-

temporal segregation of common, sharptail, and slender mola. Catches of each mola species per longline set were converted to binary values to inform generalized additive models using a binomial distribution and logit link. Two models were constructed for common mola, one using only deep-set data and a second using only shallow-set data, due to the disparate spatial distribution of effort as well as time and depth of gear deployment in these sectors (Table 1). Models for sharptail and slender mola solely used deep-set data due to their nearly exclusive occurrence in this sector (Table 1).

To explore the primary hypotheses regarding the distribution of the mola species, we tested a model term for spatiotemporal variation (bivariate tensor product of month and latitude) that quantifies intra-annual shifts in distribution along a north–south axis. A potential gear effect was tested for fishing depth (proxied by a univariate smooth of hooks per float). An interannual effect was tested (factor for year) from 1995–2018 for deep-set common mola and slender mola, 1995–2000 and 2005–2018 for shallow-set common mola, and 2004–2018 for sharptail mola (Table 1). The gap in years tested in the model of shallow-set common mola is due to the emergency closure of that fishery sector from March 2001–April 2004. The shorter year-span for sharptail mola is due to the observer program not beginning to tally that species until 2004. Hook type and bait type could not be included in any models due to high collinearity with year in both the deep- and shallow-set sectors (Pearson correlation coefficients >|0.4|). These collinearities are the result of regulatory changes during the study period requiring the use of circle hooks in both fishery sectors and banning the use of squid bait in the shallow-set sector (which led fishers to willingly cease using squid bait in the deep-set sector). Furthermore, latitude and SST exhibited high collinearity over the broad spatial domain of the study region (Pearson correlation coefficients >|0.5|), precluding inclusion of both variables in the models. Thus, we could either include latitude in the model and explain the underlying temperatures or include

temperature in the model and explain its latitudinal distribution; we chose the former to directly assess potential spatial overlap or segregation of molid species and facilitate identification of migrations in the study region. All models included an offset of the log-transformed number of hooks to account for variation in the number of hooks per longline set—this term was always retained and not subjected to model selection. Smooth terms for latitude and hooks per float used a thin-plate regression spline while that for month used a cyclic cubic regression spline (ensuring continuity from December to January). Models were constructed via forward selection with Akaike's information criterion (AIC), which identifies better models with lower scores (Akaike 1974), as well as AIC weight, which measures the probability of a model being the best among those tested (Wagenmakers & Farrell 2004). Model performance was assessed using the area under the receiver operating curve (AUC), which is a measure, ranging from 0–1, of how well a model predicts the outcome, with scores >0.5 indicating that a model provides better than random predictions (Hanley & McNeil 1982). Models with AUC scores of 0.7–0.9 are considered useful, and those with scores >0.9 are considered highly accurate (Swets 1988). Models were built in R version 3.6.1 (R Core Team 2019) using the 'mgcv' package (Wood 2019).

## 2.4. Community ecology

To assess ecological segregation among the mola species, we conducted a principal component analysis (PCA) on the catch composition of the 85 000+ longline sets observed in the fishery. We used counts of the 15 most abundant species captured across the deep- and shallow-set sectors as descriptors. These 15 non-mola species represented variation along the tropical–temperate and epipelagic–mesopelagic axes, and included—in decreasing order of abundance—longnose lancetfish *Alepisaurus ferox*, bigeye tuna *Thunnus obesus*, blue shark *Prionace glauca*, common dolphin *Coryphaena hippurus*, swordfish, snake mackerel *Gempylus serpens*, sickle pomfret *Taractichthys steindachneri*, escolar *Lepidocybium flavobrunneum*, yellowfin tuna *Thunnus albacares*, skipjack tuna, albacore *Thunnus alalunga*, opah (*Lampris* spp.), wahoo *Acanthocybium solandri*, striped marlin *Kajikia audax*, and shortbill spearfish *Tetrapturus angustirostris*. We

Table 1. Summary of input data for mola species distribution models. Presences represent the number of longline sets with positive catch, and absences represent the number of longline sets with zero catch

Species	Sector	Years	Presences	Absences
Common mola	Deep-set	1995–2018	441	65045
Common mola	Shallow-set	1995–2000, 2005–2018	574	18872
Sharptail mola	Deep-set	2004–2018	230	53843
Slender mola	Deep-set	1995–2018	3221	62265

used a Hellinger transformation on the catch data, as recommended for ordination of abundance data containing many zeros (Legendre & Gallagher 2001), and conducted the PCA on the variance–covariance matrix because units were shared and scales were similar among all descriptors. We assessed the significance of the eigenvalues of the first 2 principal components (PCs) with a Monte Carlo randomization test. PCA was conducted with the ‘stats’ package (R Core Team 2019) and the ‘biostats’ R collection (McGarigal 2016).

### 3. RESULTS

#### 3.1. Catch metrics

Molas are rare catches in the Hawaiian longline fishery; they constitute only 0.2% of the catches of all species (by number) when summed across the observed deep- and shallow-set sectors. Likewise, only 5.3% of the 85 000+ longline sets observed across the sectors from 1995–2018 resulted in a catch of at least 1 mola species. Catch of common mola was nearly equally distributed among the observed deep- and shallow-set sectors, although the catch per set, nominal CPUE, and percentage of sets with positive catches were higher in the shallow-set sector (Table 2). The length of common mola captured in deep- and shallow-sets, on average ( $\pm$  SD), was estimated to be  $1.5 \pm 0.3$  m (range: 0.6–2.9 m,  $n = 72$ ) and  $1.5 \pm 0.4$  m (range: 0.9–2.4 m,  $n = 122$ ), respectively.

In contrast, the deep-set sector yielded nearly all the catch, as well as higher catch per set, nominal CPUE, and percentage of sets with positive catches than the shallow-set sector for both sharptail and slender mola (Table 2). The length of sharptail mola captured in deep-sets, on average, was estimated to be  $1.4 \pm 0.4$  m (range: 0.9–2.1 m,  $n = 48$ ) and the length of slender mola captured in deep-sets, on average, was measured to be  $0.51 \pm 0.06$  m (range: 0.25–0.96 m,  $n = 1075$ ). The actual measurement (not an estimate) of a 0.96 m slender mola by a fishery observer represents the largest individual of the species ever recorded. Among sets with positive catches, sharptail and common mola catches rarely consisted of multiple individuals (0.4 and 5.6%, respectively), whereas slender mola catches frequently consisted of multiple individuals (39.8%), as many as 22 molas per set. Furthermore, only 0.06% of sets with positive mola catches yielded 2 mola species, and none yielded all 3; these limited instances of overlapping mola species in the catch exclusively occurred in the deep-set sector.

The 3 mola species exhibited distinct spatial distributions of catch across the eastern North Pacific (Fig. 1). Common mola were caught from  $4.3^\circ$ – $41.8^\circ$  N and  $176.5^\circ$ – $125.2^\circ$  W, but were primarily encountered in the area around the Hawaiian Islands and offshore of the southwestern continental USA; the latter area exhibited particularly high catch relative to the local effort. Sharptail mola were captured from  $4.7^\circ$ – $37.1^\circ$  N and  $177.5^\circ$ – $134.3^\circ$  W, with their catch distribution largely reflecting the distri-

Table 2. Summary metrics of the 3 mola species observed across fishery sectors and separately in the deep- and shallow-set sectors from 1995–2018. Catch per set and nominal catch per unit effort (CPUE, per 1000 hooks) are provided as averages (with SD in parentheses)

Fishery metric	Sector	Common mola	Sharptail mola	Slender mola
Catch (n)	Both	1099	249	6165
	Deep-set	469	231	6141
	Shallow-set	630	18	24
Catch per set	Both	0.013 (0.123)	0.003 (0.059)	0.072 (0.500)
	Deep-set	0.007 (0.091)	0.004 (0.066)	0.094 (0.569)
	Shallow-set	0.032 (0.193)	0.001 (0.032)	0.001 (0.044)
Nominal CPUE	Both	0.010 (0.106)	0.002 (0.029)	0.033 (0.225)
	Deep-set	0.003 (0.042)	0.003 (0.029)	0.043 (0.255)
	Shallow-set	0.033 (0.205)	0.001 (0.030)	0.001 (0.052)
Sets with zero catches (%)	Both	98.8	99.7	96.2
	Deep-set	99.3	99.6	95.1
	Shallow-set	97.1	99.9	99.9
Sets with positive catches (%)	Both	1.2	0.3	3.8
	Deep-set	0.7	0.4	4.9
	Shallow-set	2.9	0.1	0.1

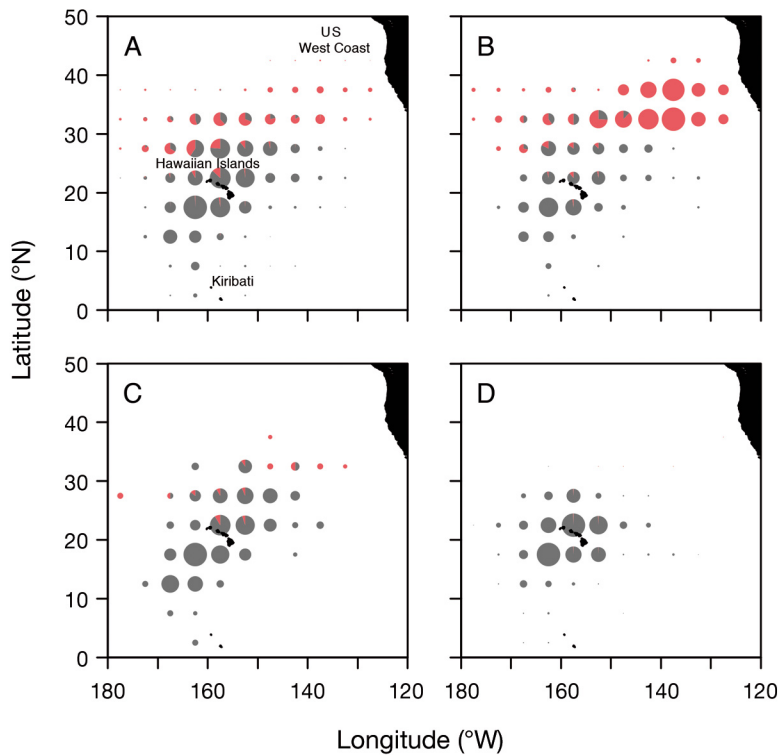


Fig. 1. Distribution of (A) observed effort, and catches of (B) common mola, (C) sharptail mola, and (D) slender mola in the Hawaiian longline fishery from 1995–2018 at 5° resolution. Effort is the number of longline sets and catch is the number of individuals. Sector contributions are color coded (grey: deep-set; red: shallow-set). Point sizes are scaled relative to the maximum value of each respective panel. Note that any 5° × 5° area within which <3 unique vessels operated is excluded from these plots for the purpose of location data confidentiality

bution of effort except at high latitudes where they were less present. Slender mola were captured from 2.0°–35.5° N and 175.1°–127.5° W, predominantly in the close vicinity of the Hawaiian Islands. In the region from 30°–40° N and 155°–125° W, where the majority of common mola but few sharptail and slender mola were captured, the average temperatures at 0 (sea surface), 45 (median shallow-set depth), and 262 m (median deep-set depth) were 13–22, 11–20, and 8–13°C, respectively (Fig. 2A,C,E). In the region from 10°–30° N and 170°–150° W, where a plurality of common mola and the majority of sharptail and slender mola were captured, the average temperatures at 0, 45, and 262 m were 22–28, 20–27, and 10–13°C, respectively (Fig. 2A,C,E). SST ranges recorded for the 3 species were similar (common mola: 15.3–29.5°C; sharptail mola: 15.6–29.0°C; slender mola 17.1–28.9°C), but their ranges of increased association (where the density of catches exceeded that of fishing effort) were distinct (Fig. 3). Relative to the density of effort, common mola catches were highest at SSTs from approximately

15–19°C, sharptail mola catches were highest from 24–28°C, and slender mola catches were highest from 22–26°C. In comparison, common mola exhibited a broadly temperate to tropical catch distribution, whereas sharptail and slender mola exhibited more (sub)tropical catch distributions.

### 3.2. Species distribution modeling

The best-fit model for each mola species suggested spatiotemporal patterns in their eastern North Pacific distribution, as well as interannual (and, in some instances, gear-related) effects. For common mola in the deep-set sector, the top model included the tensor product of latitude and month, the factor for year, plus the smooth of hooks per float (Table 3), and exhibited an explained deviance of 5.5% and an AUC score of 0.71. The spatiotemporal pattern suggested that common mola catch probability was highest north of 25° N from October–February, shifted north of 35° N from March–June, and then returned southward from July–September (Fig. 4A). Additionally, there was a secondary area of high (but comparatively lower) catch probability from ~10°–20° N that was variable throughout the year. Catch probability was consistently lowest south of 10° N. Among deep-sets, the shallowest deployments (i.e. with fewer hooks per float) yielded higher catch probability than those of intermediate depth (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m654p109\\_supp.pdf](http://www.int-res.com/articles/suppl/m654p109_supp.pdf)). No linear interannual trend in catch probability was present in a regression of the back-transformed, year-specific intercepts from the species distribution model ( $p = 0.11$ ).

For common mola in the shallow-set sector, the top model included the tensor product of latitude and month, the factor for year, and the smooth of hooks per float (Table 3), and exhibited an explained deviance of 17.5% and an AUC score of 0.84. The spatiotemporal pattern suggested that common mola catch probability was highest north of 28° N from October–February, shifted north of 35° N from March–May, and then returned southward from June–September (Fig. 4B). Catch probability was consistently lowest south of 28° N throughout the year (Fig. 4B). The term

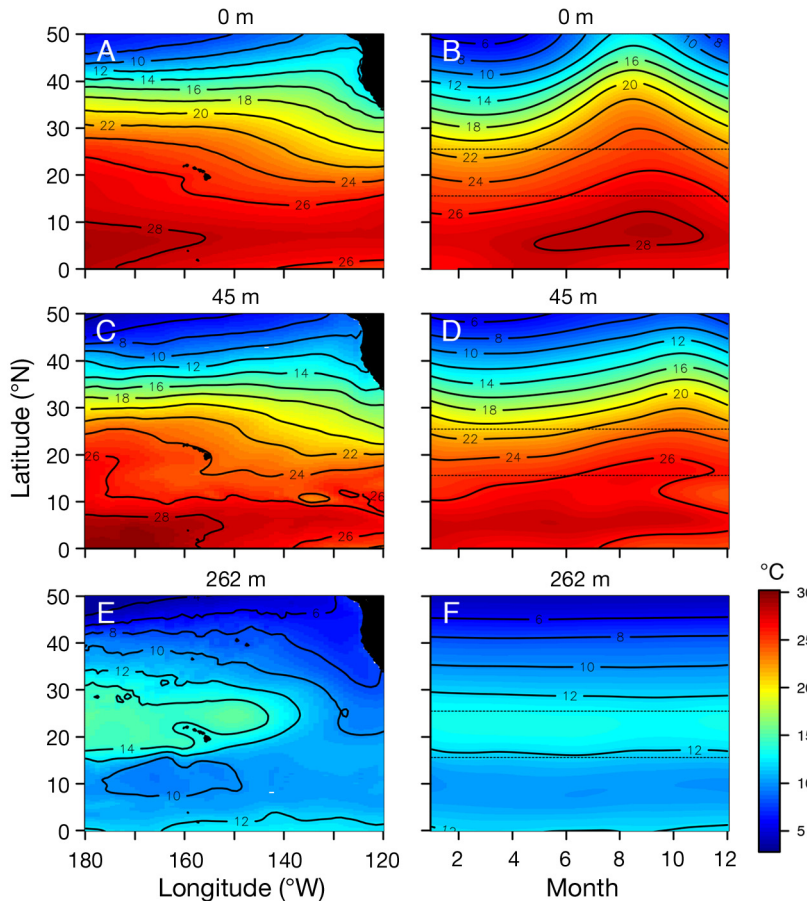


Fig. 2. Climatological average temperature by longitude and latitude (year-round) and month and latitude at (A,B) 0, (C,D) 45, and (E,F) 262 m depth in the eastern North Pacific from 1995–2018. In panels B, D, and F, the dashed horizontal lines indicate the latitudinal bounds of the US exclusive economic zone surrounding the 8 main Hawaiian Islands. The 0 m (sea surface) temperature data come from the NOAA 1/4 degree daily OISST analysis and the 45 m (median shallow-set sector depth) and 262 m (median deep-set sector depth) temperature data come from the NCEP GODAS analysis

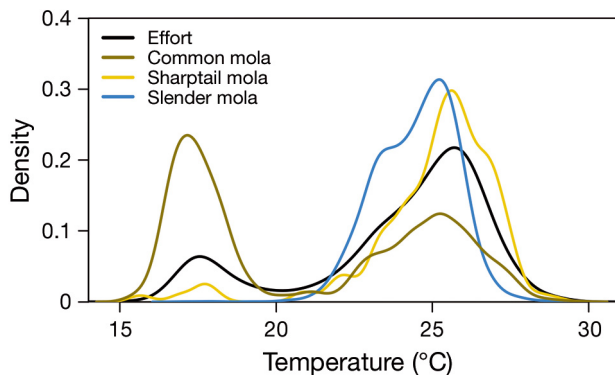


Fig. 3. Sea surface temperature (SST) distribution of mola catches relative to effort. Increased associations are indicated where catch density of a given species is greater than effort density. Decreased associations are indicated where catch density of a given species is less than effort density. Density estimates were calculated with a Gaussian smoothing kernel using a 0.35 bandwidth

for hooks per float improved model fit but did not have a significant effect on catch probability. The mean estimated catch probability was >4 times higher in the 6 yr prior to the fishery closure than in the 14 yr after the fishery closure, coinciding with bait and hook type regulation changes (Fig. 5). Linear regression revealed a significant increase in catch probability over time in the years after the fishery closure when no further bait or hook type regulations were enacted ( $F = 27.2$ ,  $p = 0.0002$ ,  $R^2 = 0.67$ ). However, there was a concurrent eastward shift in longitude at which the sector was operating (i.e. an average of  $1.1^\circ$  to the east per year:  $F = 2239$ ,  $p < 0.0001$ ,  $R^2 = 0.11$ ; Fig. S2).

For sharptail mola in the deep-set sector, there were 2 competing models of similar relative probability according to AIC weight and similar predictive performance according to the AUC (Table 3). Among these, the most parsimonious model with the lowest number of terms included the tensor product of latitude and month, as well as the factor for year (Table 3), and exhibited an explained deviance of 2.7% and an AUC score of 0.67. The spatiotemporal pattern suggested that sharptail mola catch probability was highest south of  $16^\circ\text{N}$  from December–March, expanded

northward to south of  $28^\circ\text{N}$  from April–September, and then retracted southward from October–November (Fig. 4C). No linear interannual trend in catch probability was present in a regression of the back-transformed, year-specific intercepts from the species distribution model ( $p = 0.06$ ).

For slender mola in the deep-set sector, there were 2 competing models of similar relative probability according to AIC weight and equivalent predictive performance according to the AUC (Table 3). Among these, the most parsimonious model with the lowest number of terms included the tensor product of latitude and month, as well as the factor for year (Table 3), and exhibited an explained deviance of 35.1% and an AUC score of 0.91. The spatiotemporal pattern suggested that slender mola catch probability was highest in the fishery between  $\sim 10^\circ$  and  $30^\circ\text{N}$  from December–March, shifted southward to the equator

Table 3. Species distribution model forward selection results, including the difference in Akaike’s information criterion (AIC) relative to the model with the lowest score ( $\Delta$ AIC), AIC weight (AICw), and area under the receiver operating curve (AUC). Model terms are represented as follows: o(): offset; s(): univariate smooth; te(): bivariate tensor product; f: factor

Species	Sector	Model	$\Delta$ AIC	AICw	AUC
Common mola	Deep-set	o(Hooks) + te(Month, Latitude) + fYear + s(Hooks Per Float)	0	0.98	0.71
		o(Hooks) + te(Month, Latitude) + fYear	7.7	0.02	0.70
		o(Hooks) + te(Month, Latitude) + s(Hooks Per Float)	73.0	0	0.65
		o(Hooks) + te(Month, Latitude)	99.2	0	0.64
		o(Hooks) + fYear	106.5	0	0.64
		o(Hooks) + s(Hooks Per Float)	166.8	0	0.55
		o(Hooks)	191.9	0	0.48
Common mola	Shallow-set	o(Hooks) + te(Month, Latitude) + fYear + s(Hooks Per Float)	0	0.75	0.84
		o(Hooks) + te(Month, Latitude) + fYear	2.2	0.25	0.84
		o(Hooks) + te(Month, Latitude) + s(Hooks Per Float)	139.4	0	0.81
		o(Hooks) + te(Month, Latitude)	150.1	0	0.81
		o(Hooks) + fYear	668.4	0	0.67
		o(Hooks) + s(Hooks Per Float)	806.5	0	0.60
		o(Hooks)	833.1	0	0.57
Sharptail mola	Deep-set	o(Hooks) + te(Month, Latitude) + fYear	0	0.51	0.67
		o(Hooks) + te(Month, Latitude) + fYear + s(Hooks Per Float)	0.2	0.45	0.68
		o(Hooks) + te(Month, Latitude) + s(Hooks Per Float)	5.3	0.04	0.64
		o(Hooks) + te(Month, Latitude)	8.8	0.01	0.63
		o(Hooks) + fYear	23.9	0	0.62
		o(Hooks) + s(Hooks Per Float)	26.1	0	0.56
		o(Hooks)	28.5	0	0.54
Slender mola	Deep-set	o(Hooks) + te(Month, Latitude) + fYear + s(Hooks Per Float)	0	0.61	0.91
		o(Hooks) + te(Month, Latitude) + fYear	0.9	0.39	0.91
		o(Hooks) + te(Month, Latitude) + s(Hooks Per Float)	457.6	0	0.90
		o(Hooks) + te(Month, Latitude)	487.5	0	0.90
		o(Hooks) + fYear	8348.8	0	0.61
		o(Hooks) + s(Hooks Per Float)	8820.0	0	0.53
		o(Hooks)	8949.0	0	0.52

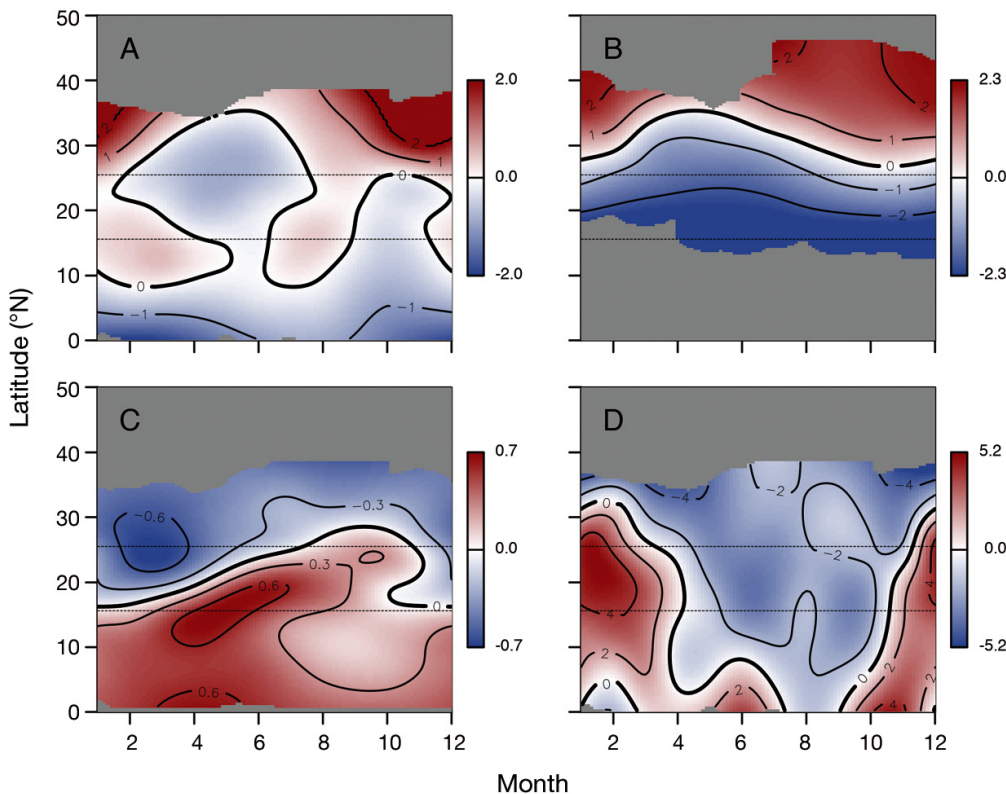


Fig. 4. Spatiotemporal partial effects on the catch probability of (A) common mola in the deep-set sector, (B) common mola in the shallow-set sector, (C) sharptail mola in the deep-set sector, and (D) slender mola in the deep-set sector. These bivariate tensor products of month and latitude are presented at the scale of the linear predictor. Red denotes month/latitude combinations of relatively increased catch probability, blue denotes month/latitude combinations of relatively decreased catch probability, and grey denotes when/where no proximal data were available. Note the different effect ranges among models: larger effect ranges indicate greater relative differences in catch probability. In this plot, effect ranges are truncated at the extremes to ensure equal color gradient discernment above and below the zero centers. The dashed horizontal lines indicate the latitudinal bounds of the US exclusive economic zone surrounding the 8 main Hawaiian Islands



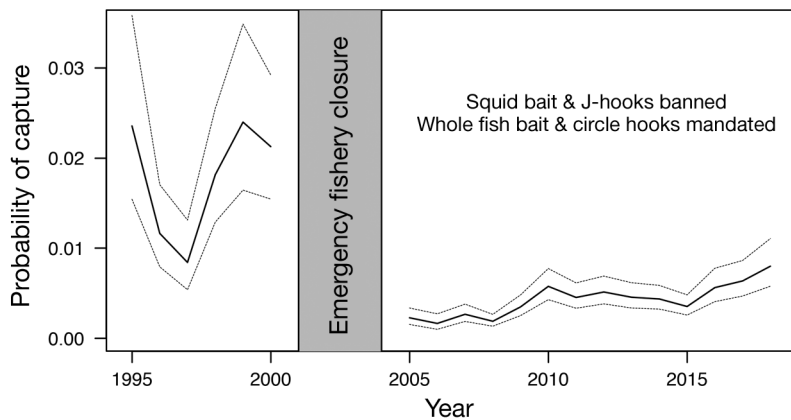


Fig. 5. Model-predicted probability of common mola capture by a shallow-set longline from 1995–2000 and 2005–2018. The solid line is the mean estimated probability and the dashed lines represent  $\pm 1$  SE. Predictions were made using the median latitude, month, total number of hooks, and hooks per float in the sector across the full study period. No bait or hook type regulations were in place prior to the fishery closure, but squid bait and J-hooks were banned and whole fish bait and circle hooks were mandated in the sector once it reopened. Greater uncertainty of the year-specific estimates from 1995–2000 than those from 2005–2018 is due to the relatively lower fishing effort and observer coverage in the sector in the years prior to the closure

from April–June, became particularly low across the entire region from July–September, and then increased northward from the equator from October–November (Fig. 4D). Also, the catch probability was always low north of  $32^{\circ}$  N. No linear interannual trend in catch probability was present in a regression of the back-transformed, year-specific intercepts from the species distribution model ( $p = 0.39$ ).

### 3.3. Community ecology

PC1 explained 28.4% of the variance in the community dataset (eigenvalue randomization test:  $p < 0.001$ ), while PC2 explained 13.0% (eigenvalue randomization test:  $p < 0.001$ ) (Fig. 6). The variation in catch composition along PC1 primarily reflected a tropical (deep-set)–temperate (shallow-set)

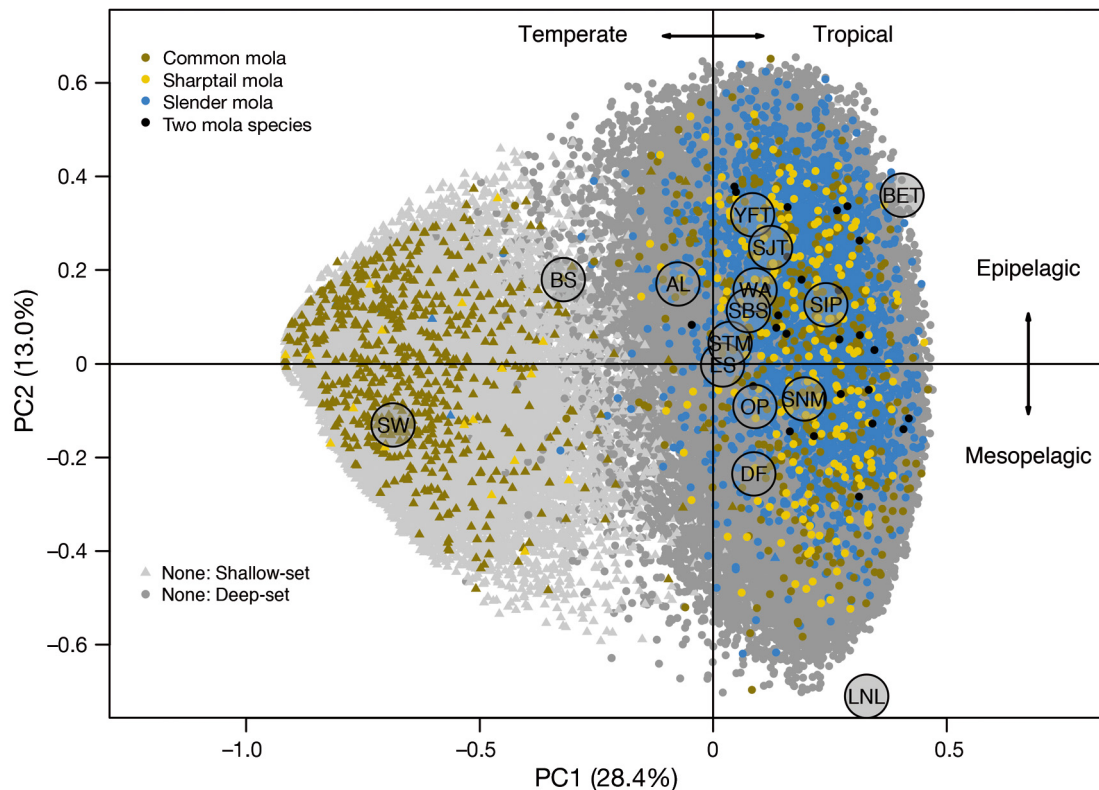


Fig. 6. PCA of the community composition of non-mola fish species captured on longline sets. Points are color coded by the mola species for which there was positive catch on that particular set, or by sector if no molas were caught. Shaded circles with inset abbreviations indicate eigenvectors of the corresponding species along PC1 and PC2. See Table 4 for full species names. Labeled arrows indicate primary axes of differentiation

Table 4. Pearson correlations of each non-mola species with the longline-set scores along principal component (PC) 1 and 2; relationships may be positive or negative, and greater absolute values indicate stronger relationships. Species are listed in decreasing order of abundance when summed across the observed deep- and shallow-set sectors

Species	Abbreviation	PC1	PC2
Longnose lancetfish	LNL	0.51	-0.74
Bigeye tuna	BET	0.67	0.40
Blue shark	BS	-0.60	0.23
Common dolphinfish	DF	0.16	-0.28
Swordfish	SW	-0.93	-0.12
Snake mackerel	SNM	0.40	-0.10
Sickle pomfret	SIP	0.48	0.17
Escolar	ES	0.05	-0.00
Yellowfin tuna	YFT	0.19	0.49
Skipjack tuna	SJT	0.30	0.41
Albacore	AL	-0.19	0.28
Opah	OP	0.28	-0.19
Wahoo	WA	0.28	0.33
Striped marlin	STM	0.11	0.09
Shortbill spearfish	SBS	0.25	0.25

axis as PC1 scores were positively correlated with more tropical species, such as skipjack tuna and common dolphinfish, but negatively correlated with more temperate species, such as swordfish and blue shark (Table 4). In contrast, variation in catch composition along PC2 primarily reflected an epipelagic-mesopelagic axis as PC2 scores were positively correlated with epipelagic species, such as yellowfin tuna and wahoo, but negatively correlated with mesopelagic species, such as longnose lancetfish and snake mackerel (Table 4). Longline sets yielding slender or sharptail mola almost exclusively exhibited high PC1 values and a wide range of PC2 values, indicative of a generally tropical assemblage of variably epipelagic and mesopelagic composition. In contrast, longline sets yielding common mola exhibited high or low PC1 values in concert with a wide range of PC2 values, indicating a tropical (deep-set) or temperate (shallow-set) assemblage of variably epipelagic and mesopelagic composition. The few longline sets yielding 2 mola species (slender/common, slender/sharptail, or sharptail/common) exhibited high PC1 values and a wide range of PC2 values, indicative of a tropical assemblage of epi- and mesopelagic species.

#### 4. DISCUSSION

Common, slender, and sharptail mola exhibit spatiotemporal segregation within the eastern North Pacific in accordance with distinct thermal niches

and seasonal movement patterns. Species distribution modeling and analysis of community composition informed by catches from the Hawaiian longline fishery revealed that, comparatively, the common mola is a more temperate species while slender and sharptail mola are more (sub)tropical species, consistent with previous studies on this family of enigmatic fishes (e.g. Gudger 1937, Pope et al. 2010, Horn et al. 2016, Nyegaard et al. 2018a). Fishery observer data also provided evidence of temporally segregated migrations of adult slender and sharptail mola to the region around the Hawaiian Islands that, in the context of previous studies on their eggs and/or larvae (Fitch 1950, Sherman 1961, Leis 1977), suggest these may constitute spawning migrations. Furthermore, catch probability of molid species seemingly changed with fishing gear type and across the 24 yr of the study period, highlighting the effects of dynamic management and fisher behavior on bycatch in a pelagic longline fishery.

The spatiotemporal distribution of common mola in the eastern North Pacific reflects the broad range and cool thermal association of the species, and seasonal temperature cycles of the region. The presence of common mola from tropical to temperate waters of the open ocean matches global model predictions of suitable habitat for the genus occurring over a wide latitudinal range (Phillips et al. 2017). The common mola, which often spends the majority of its time in near-surface waters (Cartamil & Lowe 2004, Dewar et al. 2010), exhibited an increased association with SSTs of 15–19°C (Fig. 3), matching results from other fisheries-dependent studies (Nakamura & Sato 2014, Hahlbeck et al. 2017) as well as telemetry studies (e.g. Sims et al. 2009b, Potter et al. 2011, Sousa et al. 2016). The spatiotemporal pattern seen in both the deep- and shallow-set common mola models, i.e. of a more temperate distribution in the warming spring/summer and more subtropical distribution during the cooling fall/winter (Figs. 2B,D & 4A,B), is corroborated by similar findings from visual surveys in the northeast Atlantic (Sims & Southall 2002, Houghton et al. 2006, Breen et al. 2017), satellite archival tagging from both sides of the North Atlantic (Sims et al. 2009b, Potter et al. 2011, Sousa et al. 2016) and North Pacific (Dewar et al. 2010, Thys et al. 2015), and global distribution modeling of the genus *Mola* (Phillips et al. 2017). Thus, seasonal shifts in latitudinal distribution during periods of regional warming or cooling enable common mola to occupy their specific thermal niche throughout most of the year (Sims et al. 2009b, Potter et al. 2011, Sousa et al. 2016). Furthermore, such seasonal north-south migrations, as

are documented for common mola and myriad pelagic predators inhabiting the eastern North Pacific, may be initiated in response to changing temperature but are likely also driven in part by related changes in productivity and the availability of prey (Block et al. 2011).

The pattern of higher nominal CPUE and higher probability of capturing common mola in the shallow than in the deep-set sector is likely at least partially attributable not only to temperature differences at the sea surface but also at depth, as it is consistent with diel and regional differences in the vertical movement patterns of the species as well as fishery operations in the different sectors. At nighttime, common mola remain in near-surface waters, whereas in the daytime, they typically undergo repeated movements from the surface to below the thermocline and back (e.g. Cartamil & Lowe 2004, Sims et al. 2009b, Thys et al. 2015). Furthermore, common mola exhibit a comparatively shallower and narrower depth distribution in cooler, more temperate regions than in warmer, more tropical regions, likely as a result of behavioral thermoregulation (Dewar et al. 2010, Potter & Howell 2011). The shallow-set sector operates during the nighttime (when common mola exhibit a narrower depth distribution) and at more northerly latitudes (where cooler temperatures at depth should promote a narrower depth distribution; Fig. 2C,D), thereby encountering common mola concentrated in a restricted depth range that enhances catchability. In contrast, the deep-set sector operates during the daytime (when common mola exhibit a wider depth distribution) and at more southerly latitudes (where warmer temperatures at depth should promote a wider depth distribution; Fig. 2E,F), thereby encountering common mola dispersed over a broad depth range that reduces catchability. This mirrors diel changes in the depth distribution of catchability for other species captured in Pacific longline fisheries (Ward & Myers 2005) that exhibit distinct diel movement patterns (e.g. Abecassis et al. 2012, Arostegui et al. 2019b), as well as the more restricted descents and increased CPUE of pelagic fishes in regions where they experience vertical habitat compression (Prince & Goodyear 2006, Stramma et al. 2012, Carlisle et al. 2017, Arostegui et al. 2019a). While past telemetry of common mola suggested that they may track vertically migrating prey and feed during the day and night (Sims et al. 2009a), more recent animal-borne data from the species revealed they only rarely feed at night (Nakamura et al. 2015). Thus, common mola catches in the shallow-set sector, which typically deploys fishing gear around dusk and retrieves it

around dawn, may predominantly occur when these fish are active during crepuscular periods rather than in the middle of the night when they are less active, but the specific timing of capture is not resolved in these fishery data.

In direct contrast to the seasonal migration pattern of common mola in the eastern North Pacific, species distribution modeling revealed a potential spawning migration of slender mola northward across the equator in boreal fall/early winter and southward across the equator in boreal spring/early summer (Fig. 4D). The aggregation of slender mola around the Hawaiian Islands in late winter and early spring is consistent with previous studies in the area that found peak abundances of slender mola larvae at this time of year and identified it as the species' spawning season (Sherman 1961, Leis 1977). Furthermore, the average length of slender mola captured in the Hawaiian longline fishery matches that of adults of this species (Smith et al. 2010), and occasional catches of large numbers of slender mola on a single longline set are in accordance with previous findings of schooling behavior (Castro & Ramos 2002, Smith et al. 2010, Horn et al. 2016). The boreal winter/spring timing of this potential spawning aggregation around the Hawaiian Islands is paralleled by that of the Adriatic Sea, where peak abundance of adult slender mola and the presence of a sexually mature, pre-spawning individual have been documented in boreal winter, while post-spawning individuals have been documented in boreal spring (Jardas & Knežević 1983, Dulčić et al. 2007). The wintertime northern limit of slender mola aggregation at  $\sim 32^\circ\text{N}$  in the eastern North Pacific (Fig. 4D) closely corresponds to the long-term average latitude ( $30^\circ\text{--}32^\circ\text{N}$ ) of the subtropical convergence zone north of Hawai'i (Roden 1980, Dinniman & Rienecker 1999). This is consistent with the distribution of slender mola larvae inside or south of a thermal front within the Sargasso Sea subtropical convergence zone at nearly the same latitude in the North Atlantic (Hellenbrecht et al. 2019). Furthermore, the region from  $\sim 15^\circ\text{--}28^\circ\text{N}$  and to the west of  $150^\circ\text{W}$ , where slender mola catch is concentrated (Fig. 1D), consistently exhibits high eddy kinetic energy (Fig. S3) as the result of eddy generation in the lee of the islands and nearby seamounts (Royer 1978, Qiu & Chen 2010, Liu et al. 2012). These mesoscale oceanographic features around Hawai'i, which experience a springtime peak in genesis (Lindo-Atichati et al. 2020) that matches the timing of the potential spawning aggregation, may entrain slender mola eggs and aid in the development and transport of the larvae (sensu Govoni et al. 2010,

Mullaney & Suthers 2013). The eddy dynamics of this region are also thought to yield a spawning hotspot for other pelagic fishes (Hyde et al. 2005) including the blue marlin *Makaira nigricans*, a tropical billfish that similarly associates with warm SSTs and undergoes trans-equatorial migrations to and from the Hawaiian Islands (albeit at opposite times of year as the slender mola; Carlisle et al. 2017). Although the slender mola achieves its northernmost distribution in the eastern North Pacific in boreal winter when temperatures above the thermocline are lowest (Fig. 2B,D), it is predominantly found in tropical and subtropical waters, consistent with the more tropical fish assemblage with which it is encountered (Shimose et al. 2010, 2013, this study; Fig. 6) as well as rare sightings of this species in temperate waters (e.g. Wheeler 1969, Eschmeyer et al. 1983).

Sharptail mola exhibited a (sub)tropical distribution more similar to that of slender mola but a temporally distinct range extension to the Hawaiian Islands more similar in its seasonal dynamics to the pattern found for common mola. The northward movement of sharptail mola in mid-spring to late summer (Fig. 4C) coincides with seasonal warming of the eastern North Pacific (Fig. 2B,D) and potentially also represents a spawning migration. The model prediction for sharptail mola to be found at more tropical latitudes during the boreal fall and winter, when seasonal cooling occurs in the study region, is consistent with the increased association of this species with warm waters (Seitz et al. 2002, this study; Fig. 3), co-occurrence with other tropical species (Gudger 1939, Fitch 1950, King 1951, Prakash et al. 2016, this study; Fig. 6), and rarity at temperate latitudes of both hemispheres (Houghton et al. 2006, Nyegaard et al. 2018a). Given the documented thermal segregation of sharptail mola from more temperate species of the genus *Mola* (Nyegaard et al. 2018a, this study), the northward range extension of sharptail mola in spring and summer during seasonal warming of the eastern North Pacific parallels seasonal migrations of common mola that enable them to track sea surface isotherms (Sims et al. 2009b, Potter et al. 2011, Sousa et al. 2016) and possibly respond to related spatio-temporal changes in foraging opportunity (sensu Block et al. 2011). The potential for this northward range extension to also represent a spawning migration is suggested by research cruises in Hawaiian waters in August and September of 1948 that found nearly 100 early life-stage *Masturus lanceolatus* in the stomachs of numerous yellowfin tuna (Fitch 1950). These <1 yr old fish (according to growth models by Liu et al. 2009) would have been hatched ear-

lier in the season, possibly coinciding with the model-predicted summertime peak of adult sharptail mola in the area. Furthermore, there is evidence of segregated spawning activity by sharptail and slender mola in the Sargasso Sea (Hellenbrecht et al. 2019). Thus, the temporally disjoint presence of adult sharptail and slender mola near the Hawaiian Islands (this study, Fig. 4C,D), and of early developmental stages of the 2 species (Fitch 1950, Sherman 1961, Leis 1977), is suggestive of distinct spawning seasons, although research into adult reproductive status in the region is needed to confirm this possibility.

Fishing gear type affects molid catch probability in longline fisheries and represents an important consideration for conservation of these bycatch species. The notable decrease in catch probability of common mola in the shallow-set sector before versus after the emergency fishing closure in the early 2000s is possibly due to gear type regulatory changes aimed at protecting endangered sea turtles. Interactions with sea turtles by shallow-set longliners resulted in the emergency closure of the sector from 2001–2004 before it was reopened with new regulations banning the use of both squid bait and J-hooks, and mandating the use of whole fish bait and circle hooks; these combined gear type regulatory changes were demonstrated to reduce sea turtle catch rates by 89% (Gilman et al. 2007). The effect of bait type on common mola catches is inconsistent among longline studies, as one documented a significantly higher catch rate with squid than mackerel bait (Coelho et al. 2012) while another found no significant difference in catch rate among those bait types (Fernandez-Carvalho et al. 2015). Similarly, studies from pelagic longline fisheries have documented either a significantly higher catch rate of common mola when using J- versus circle hooks (Fernandez-Carvalho et al. 2015) or no significant difference in catch rate among those hook types (Coelho et al. 2012, Domingo et al. 2012). Thus, while we could not isolate the effect of bait or hook type from year in any of our models due to collinearity, it seems probable that the combined regulatory changes, from squid to whole fish bait and J- to circle hooks, reduced the probability of common mola bycatch in the shallow-set sector from before to after the emergency closure (Fig. 5). Furthermore, a ~27:1 catch ratio of common to sharptail mola in the shallow-set sector since its reopening suggests that any sharptail mola accidentally counted as common mola prior to the emergency closure (when they were potentially aggregated by observers) would have had negligible influence on the modeled, year-specific catch probabilities. In contrast, the trend of in-

creasing catch probability of common mola in the shallow-set sector in the years since the emergency closure is possibly due to the observed eastward shift in effort along temperate latitudes into a region of persistently high habitat suitability (Fig. 2A,C; Phillips et al. 2017) that is closer to the California Current large marine ecosystem, a well-documented common mola hotspot (Thys et al. 2015, Hahlbeck et al. 2017). Although the deep-set sector shifted effort northeast during part of this same time period (Woodworth-Jefcoats et al. 2018), its effort distribution remained predominantly at tropical and subtropical latitudes where common mola catch likelihood is comparatively lower; this is consistent with our finding of no interannual trend in catch probability in the deep-set sector. The common mola is listed as Vulnerable with a decreasing population trend by the International Union for the Conservation of Nature (IUCN; Liu et al. 2015), which is of potential concern for the species in the eastern North Pacific due to its increasing number of interactions in the shallow-set sector of the Hawaiian longline fishery as well as its more than an order of magnitude higher bycatch rate in the California large-mesh drift gillnet fishery (Hahlbeck et al. 2017).

The primary limitation of this study is the uncertainty of our distribution models for the more rarely encountered species among those analyzed. Slender mola in the deep-set sector and common mola in the shallow-set sector were caught on 4.9 and 2.9% of longline sets, respectively, and their models exhibited greater explained deviance and AUC scores indicative of notable accuracy. In contrast, sharptail and common mola in the deep-set sector were caught on only 0.4 and 0.7% of longline sets, respectively, and their models exhibited lower explained deviance and AUC indicative of moderate accuracy with some unaccounted randomness in the species' distributions. The randomness in those models may be due to the sheer rarity of sharptail mola across the region and common mola outside of their preferred temperature range (only 0.1% of deep-set longlines occurred at SSTs <19°C). Alternatively or in addition, deep-set longline gear may be inefficient at sampling those species, which is likely given the dietary preferences of adult sharptail and common mola for gelatinous prey over the fish bait types used in the sector (Nakamura & Sato 2014, Nakamura et al. 2015, Bakenhaster & Knight-Gray 2016). Fisheries-dependent studies of other rarely encountered species have faced parallel issues and similarly yielded distribution models with low explained deviance but moderate predictive performance that provided valuable

insight (e.g. Rooper et al. 2014, Barnett et al. 2017, Hazen et al. 2018). Even with its uncertainty, the deep-set common mola model yielded spatiotemporal patterns that were largely consistent with those of the higher quality shallow-set model for the same species; both identified higher catch likelihood in temperate waters and exhibited parallel seasonal shifts in the latitudinal threshold of that likelihood that were consistent with the species' documented behavior. The only difference among these *Mola mola* models was the presence of a secondary, tropical area of high (but comparatively lower) catch probability in the deep-set model that was not seen in the shallow-set model. This may be due to some molid species occupying a warmer niche being counted as *M. mola* in the tropical deep-set sector, namely *Masturus lanceolatus* prior to 2004 (when observers started enumerating the species separately) and *Mola alexandrini* potentially throughout the study period (since it was recently redescribed taxonomically). Rebuilding the deep-set common mola model only with data from 2004–2018 (when sharptail mola were no longer potentially included) yielded similar spatiotemporal results (Fig. S4), suggesting the possibility that *M. alexandrini* is present in the region and driving the modeled pattern of elevated, tropical catch probability. Ultimately, our models for all species were highly consistent with the existing literature on their spatial segregation (e.g. Gudger 1937, Houghton et al. 2006, Nyegaard et al. 2018a), thermal associations (e.g. Seitz et al. 2002, Nakamura & Sato 2014), spatiotemporal dynamics (e.g. Pope et al. 2010, Phillips et al. 2017), spawning seasons (e.g. Fitch 1950, Leis 1977), associated fish communities (e.g. King 1951, Shimose et al. 2010), and susceptibility to fishing gear (e.g. Coelho et al. 2012).

## 5. CONCLUSION

Our results demonstrated the spatiotemporal segregation of 3 molid species in the eastern North Pacific and identified potential underlying drivers of their separation. Paralleling their evolutionary relationships, there was greater similarity among the seasonal movement dynamics of common and sharptail mola (in sync with thermal cycles) than among either of these species and those of the slender mola (in sync with eddy genesis cycles). In addition, we discovered temporally segregated, potential spawning migrations of slender mola (from boreal fall to early winter) and sharptail mola (from mid-spring to late summer) to the region around the Hawaiian Islands. Fishery gear

type and a shifting distribution of effort were found to have potential effects on molid catch probability; in particular, the increasing catch probability of common mola in the shallow-set sector is of potential concern given that this species is currently listed by the IUCN as Vulnerable, with a decreasing population trend (Liu et al. 2015). Additionally, comparison of our distribution models for common mola highlighted the possibility that the recently redescribed *Mola alexandrini* is being encountered and misidentified as its congener *M. mola* in the Hawaiian longline fishery. This study highlights the value of fishery observer programs, as the data they provide yield insight into the behavior and ecology of rare, understudied, and underappreciated species. Future work on molids should focus on identifying stock structure and additional aggregation sites of the various species, as well as clarifying the differences in distribution, behavior, and fishery interactions of *M. mola* and *M. alexandrini* in the North Pacific.

**Data availability.** The confidential fishery observer data used in this study are subject to NOAA order NAO 216-100: Protection of Confidential Fisheries Statistics and can only be disclosed under the conditions listed therein. The oceanographic data used in this study are publicly available from the EU Copernicus Marine Environment Monitoring Service (CMEMS, <https://marine.copernicus.eu/>) NOAA OISST (<https://www.ncdc.noaa.gov/oisst/>), and NCEP GODAS (NOAA/OAR/ESRL PSL, Boulder, Colorado, <https://psl.noaa.gov/>) online databases.

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