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Executive Summary

Understanding the essential fish habitats utilized by commercially important species has become a crucial component of Ecosystem-Based Fisheries Management (EBFM). Many larval and juvenile reef-associated and coastal pelagic fish populations are data-limited in the Hawaiian Islands. This study examines the spatial and temporal variability in larval distribution and abundance of ʻōpelu (*Decapterus macarellus*) and akule (*Selar crumenophthalmus*) in West Hawaiʻi Island from 1997 to 2018. In total, 55 ʻōpelu and 58 akule larvae were collected throughout the months of April, May, July, September, and November. The majority of recorded specimens (80/113) were collected in September 2016. The median length of ʻōpelu in this study was 4 ± 2.6 mm (SD), and the median length of akule was 3 ± 1.5 mm (SD). We conducted ecological assessments on these species, considering various factors such as the year and month of collection, distance from shore, habitat patterns (including vertical distribution), associations with surface slick convergence zones (i.e., areas of concentrated organic buildup on the surface caused mainly by internal waves), and sea surface temperature. These results identified a potential relationship of larval ʻōpelu occurrence with temperature and a concentrated akule spawning event in September 2016. The protracted spawning observed for ʻōpelu was likely related to temperature and other environmental drivers. Furthermore, these results reveal distinct depth habitat preferences during the early life stages of these co-occurring species where ʻōpelu mostly utilize the neustonic layer (<2 m) and akule are found more frequently in deeper water (0–10 m). Additional concentrated sampling effort is needed to better refine larval habitats and adult spawning conditions as well as provide insight into how environmental conditions may modulate recruitment.

Introduction

Understanding the habitat requirements of fishes throughout their lives provides insight into the environmental drivers that regulate their distribution and abundance. Identifying essential habitats used by larval and juvenile fishes has become a critical component of Ecosystem-Based Fisheries Management (EBFM), especially for commercially important fisheries species (Manson et al. 2005; Thrush and Dayton 2010). In the Hawaiian Islands, the overwhelming majority of reef-associated and coastal pelagic fish stocks have been designated data-poor (Nadon 2017; Friedlander 2004). For most taxa, there is a complete lack of stock-recruitment relationships and either no or inadequate data on early life history, which has restricted assessments to assuming constant recruitment. This is true for the coastal pelagic species 'ōpelu (mackerel scad, *Decapterus macarellus*) and akule (big-eye scad, *Selar crumenophthalmus*), which are among the most commercially important taxa in the region (Weng and Sibert 2000; McNaughton 2008). Despite their high commercial value, there is currently little to no published information on larval distribution, ecology, or recruitment for these local stocks (Weng and Sibert 2000). The lack of current studies on fish larval ecology renders it difficult to predict how environmental changes will impact larval survival, recruitment, and ultimately, replenishment of these important Hawaiian fisheries.

While we have a basic understanding of the adult life history of *D. macarellus* and *S. crumenophthalmus* (hereafter, 'ōpelu and akule, respectively), records of the distribution and abundance of these larvae in Hawai'i are limited and previous studies have provided conflicting information about spawning. The latest in-depth assessment of 'ōpelu biology in Hawai'i (McNaughton 2008) found that 75% of mature females were captured between April and August. Based on McNaughton's (2008) interviews, local fishers state that they observe juveniles in the summer months (June–August). Eighty percent of the local fishers interviewed suggested that an individual 'ōpelu might spawn twice throughout the season (McNaughton 2008); however, the frequency at which 'ōpelu spawn remains unmeasured. Analyses by Yamaguchi (1953), McNaughton (2008), and Sululu et al. (2022) described a unimodal distribution in oocyte size, which refers to a single batch of oocytes being released during the spawning season. Clarke and Privitera (1995) recorded a bimodal distribution from adults captured in Hawai'i, suggesting multiple spawning events or continuous oogenesis. Reports of 'ōpelu in Japan and Cabo Verde, Africa, provide evidence of iteroparity, or multiple spawning events, over the course of a lifetime (Shiraishi et al. 2010; Costa et al. 2020).

Adult 'ōpelu inhabit the neritic zone between 20 and 200 m and are occasionally observed at the surface near floating debris (Honebrink 2000; Weng and Sibert 2000; McNaughton 2008). 'Ōpelu are known to move offshore to spawn, with larvae recorded as far as 80 miles from the coast of O'ahu (Yamaguchi 1953). Recent work indicates that 'ōpelu larvae disperse into pelagic waters off West Hawai'i and are concentrated in surface slick convergence zones, which can provide enhanced prey availability and shelter in floating debris (Whitney et al. 2021).

Akule school offshore in waters as deep as 170 m and are known to move to shallow, sandy bottom areas before spawning (Smith-Vaniz 1986; Uchida and Uchiyama 1986). Akule are batch spawners with protracted spawning periods and the ability to carry eggs at different stages in their ovaries (Iwai et al. 1996). Postovulatory follicle assessment by Clarke and Privitera (1995) suggested akule can spawn approximately every three days during the spawning season, from April through November (Table 1). Clarke and Privitera (1995) noted that the mean relative fecundity of akule is approximately twice that of 'ōpelu. Akule larvae are also pelagic and will return to nearshore waters after flexion (Uchida and Uchiyama 1986, Weng and Sibert 2000). Larval akule have been found in plankton tows around the Hawaiian Archipelago and Johnston Atoll in waters as deep as 100 m (Boehlert et al. 1992; Boehlert and Mundy 1996).

'Ōpelu and akule make up the two most productive inshore fisheries by landings in the main Hawaiian Islands, (Honenbrink 2000; Akizuki 2021; WPRFMC 2022), yet little is known about their larval ecology in this region. The goal of our study is to examine the spatial and temporal variability in larval distribution and abundance of 'ōpelu and akule using a 20-year data set of ichthyoplankton collections off West Hawai'i. We specifically aim to address differences in seasonal occurrence, vertical distribution, habitat and temperature associations, and cross-shore distribution of larvae from both species. This study represents the most comprehensive assessment to date of the occurrence and environmental associations of 'ōpelu and akule larvae within the main Hawaiian Islands.

Table 1. Summary of the early life history of 'ōpelu (Decapterus macarellus) and akule (Selar crumenophthalmus).

Species	Fishing Method	General Habitat	Spawning Period	Mean Fecundity	Size at Hatching (TL mm)	Size at Maturity	Max. Size Recorded (TL cm)	Incubation Time
Decapterus macarellus	Hoopnet, hook and line	Offshore waters	April-September [1]	136,000 eggs at unknown rate [3]	2.2 mm [4]	24-26 cm at 18 months old [6]	35 cm [7]	24 hours at 25- 26 ℃ [4]
Selar crumenophthalmus	Purse seine, gillnet, hook and line	Offshore waters & shallow, sandy bottoms	April-November [2]	92,000 eggs about every 3 days [3]	2.23 mm [5]	20 cm at 7 months old [3]	30 cm [7]	24 hours at 26 ℃ [2]

1. (McNaughton 2008), 2. (Iwai et al. 1996), 3. (Clarke and Privitera 1996), 4. (Baensch 2014), 5. (Welch et al. 2013), 6. (Weng and Sibert 2000), 7. (Honebrink 2000)

Methods

Sample Collection

This study is part of the broader West Hawaiʻi Ichthyoplankton Project which assembled data from 20 years (1997 to 2018) of neustonic ichthyoplankton collections to assess spatiotemporal variation in larval fish abundance and distribution. Beginning in 1997, the Pacific Islands Fisheries Science Center (PIFSC) conducted extensive neustonic ichthyoplankton surveys in West Hawaiʻi, focused on biosampling for targeted commercial species (e.g., billfish and tuna). Following a multi-year effort to compile existing data and process archived samples, data are now available and provide a valuable resource for examining patterns of larval distribution and abundance of commercially and ecologically important taxa, including ʻōpelu and akule.

Sampling targeted surface communities between 0.15 to 82 km from the western coast of the Island of Hawaiʻi (i.e., West Hawaiʻi), both inside surface slick convergence zones and outside of them (ambient surface water). A total of 660 neuston transects and 123 coupled vertical tows (352 vertical replicate tows) were conducted across all surveys (Figure 1). No surveys were conducted in 2007, 2008, 2010, and 2012–2015. Sampling times for all years varied between the spring and autumn seasons with no expeditions in the winter months (December–February; Table 2).

From 1997 to 2011, 512 neuston transects were conducted along West Hawaiʻi as part of the PIFSC Life History Program Surveys from the NOAA Ships *Townsend Cromwell* (1997–2002) and *Oscar Elton Sette* (2003–2011) using a 1.8 m (6 ft) Isaacs-Kidd (IK) trawl with a 505 μm mesh net. The IK net was mounted along the port side of the ship to sample the air-sea interface down to ~1.5 m depth. Because the IK is towed along the interface, the net mouth area below the surface is less than the total mouth area (3.44 m^2) and not constant due to vertical movement of surface waves and ship wake. We visually estimated that 20% of the net area typically sits above the surface while 80% of the net area is submerged; we used this estimation to set the net mouth area constant at 2.75 m^2. IK neuston tows were conducted for an average of ~60 minutes at an average speed of ~6 km/h (4.6–8.7 km/hr), resulting in a mean distance (±SD) of 5.66 ± 1.79 km per tow. The majority of those IK neuston tows were not equipped with a flowmeter. Therefore, to calculate distance sampled, we were limited to using the tow length determined from start and end coordinates. The total volume of water sampled (m^3) per tow was calculated using the product of the net area (2.75 m^2) and length of tow (m).

From 2016 to 2018, 148 surface transects were conducted off West Hawaiʻi as part of the Hawaiʻi Integrated Ecosystem Assessment (IEA). The Hawaiʻi IEA focused on characterizing ecological relationships of neustonic communities in slick convergence zones (Gove et al. 2019a; Whitney et al. 2021; Smith et al. 2021). Neuston tows and sample processing are detailed in Gove et al. (2019a) and Whitney et al. (2021). Most sampling occurred from small boats, with the exception of 16 transects in 2017 conducted from the *Oscar Elton Sette*. Each transect consisted of a single ~500 m neuston tow and three replicate vertical tows (surface to 10 m), performed both inside surface slicks and in adjacent ambient waters. Tows in ambient waters were typically run parallel with and in-between slicks, at a distance of 200 to 500 m. For surface tows, we used a 1-m diameter neuston net similar in design to the manta net (Brown and Cheng 1981), which is described in Gove et al. (2019a) and Whitney et al. (2021). Briefly, the net

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targets the air-sea interface to ~0.9 m; it was fitted with 300 μm mesh soft cod ends and a mechanical flowmeter (Sea-Gear Corp.). Neuston tows conducted from the small boat were hauled for an average of ~8 minutes at ~4 km/h. The mean tow length was 495 ± 157 m.

To assess the vertical distribution of larvae in the top 10 m, three replicate vertical tows per transect (at the origin, mid-point, and end of the neuston track) were conducted using a 1-m diameter drop net (335 μm mesh; Sea-Gear Corp.) with a 5 kg weight attached to the bridle. Drop nets were lowered over the side of a stationary boat from the surface to a depth of 10 m (sampling on the descent), and belly bands closed the net for the ascent. The net sank at a rate ~1 m s^{-1}. Plankton samples collected in soft cod ends were preserved immediately in a 5-gallon bucket of 95% undenatured ethanol and transferred to jars with fresh ethanol within 12 hours. Surface slicks were identified by visual inspection, specifically by locating smooth, meandering lines of water with clear, distinguishable edges at least 500 m in length and separated from adjacent ambient water by 5 to 200 m (Gove et al. 2019a; Whitney et al. 2021; Smith et al. 2021).

'Ōpelu and akule larvae were identified morphologically to the lowest possible taxonomic unit using Miller et al. (1979) and Ozawa and Manabe (1986). Eggs and larvae < 2 mm could not be confidently identified as they usually lack key characteristics that denote species. Larvae were measured in total length (TL) to the nearest millimeter. All counts were standardized to the volume of water sampled and converted to densities per 1000 m^3. For vertical tows, counts were summed across replicate tows and divided by the total volume sampled (each replicate had a tow area of 7.9 m^2). Most transects with coupled neuston-vertical tows (107/123; 87%) had three replicate vertical tows, while the remainder had two (15/123) or one (1/123) replicate tows due to field constraints.
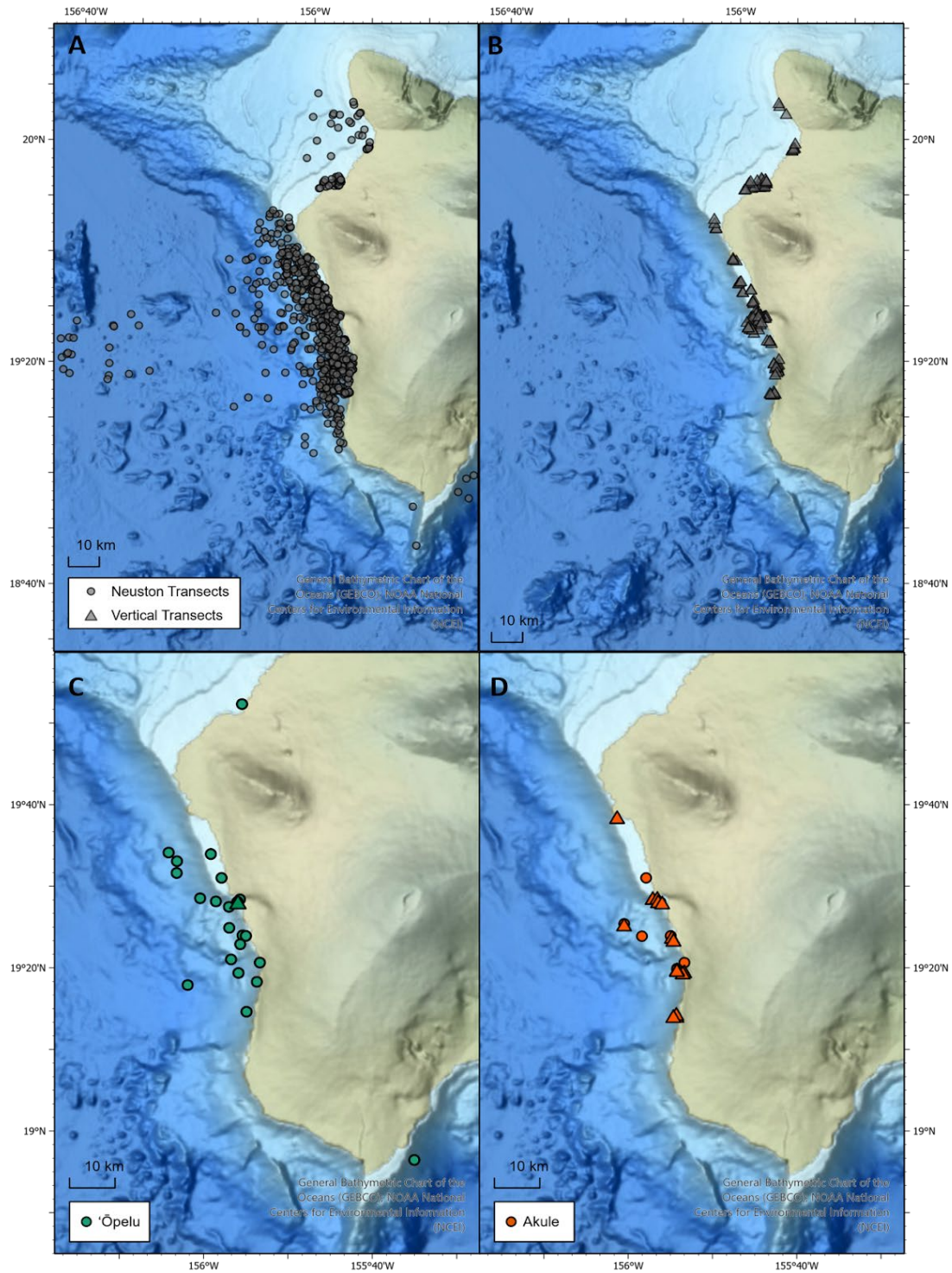
Figure 1. Maps of survey effort (A–B) and larval ʻōpelu and akule occurrences (C–D) along the west coast of Hawaiʻi Island from 1997–2018. Each point represents a single transect. Three vertical replicates were taken per transect, but only the first vertical replicates were taken per transect, but only the first vertical replicate is represented above. Circles represent neuston tows, and triangles represent vertical tows. A). Neuston transects from 1997 through 2018. B). Vertical tows were coupled with neuston transects from 2016 to 2018. C). Tows where ʻōpelu larvae were caught (green). D). Tows where akule larvae were caught (orange).

Table 2. Sampling effort and larval ʻōpelu and akule catches by month and year. Catches exclude eggs and larvae < 2 mm. Neuston tows were conducted from 1997–2018. Vertical tows were only conducted during surveys in 2016–2018.

Years	Month	Number of Neuston Transects	Number of Vertical Tows	Number of ʻŌpelu Caught	Number of Akule Caught
2005	March	30	0	0	0
1997, 1998, 2006, 2009, 2017	April	183	26	7	1
2000, 2002, 2003, 2005	May	94	0	6	0
2001	June	67	0	0	0
2000, 2004, 2018	July	100	45	7	0
2011	August	11	0	0	0
2016	September	145	52	34	57
1999	November	30	0	1	0
	TOTAL	660	123	55	58

Morphological identification and measurement of larvae

ʻŌpelu and akule are morphologically similar during their larval stages (Miller et al. 1979). These species have notable commonalities, such as pigmentation outlining the gut and lateral midline, as well as typical carangid characteristics (e.g., supraoccipital crests, preopercular spines, and a generally deep body shape). For larvae, the difference in internal pigment outlining the hypaxial myosepta (sheets of connective tissue that separate myomeres) was used to differentiate these species (Figure 2). In akule larvae, these melanophores also tend to be more elongate in shape than those in ʻōpelu, which tend to be circular or stellate and can overlay but not outline the myosepta. Larvae were manually measured in total length to the nearest millimeter.
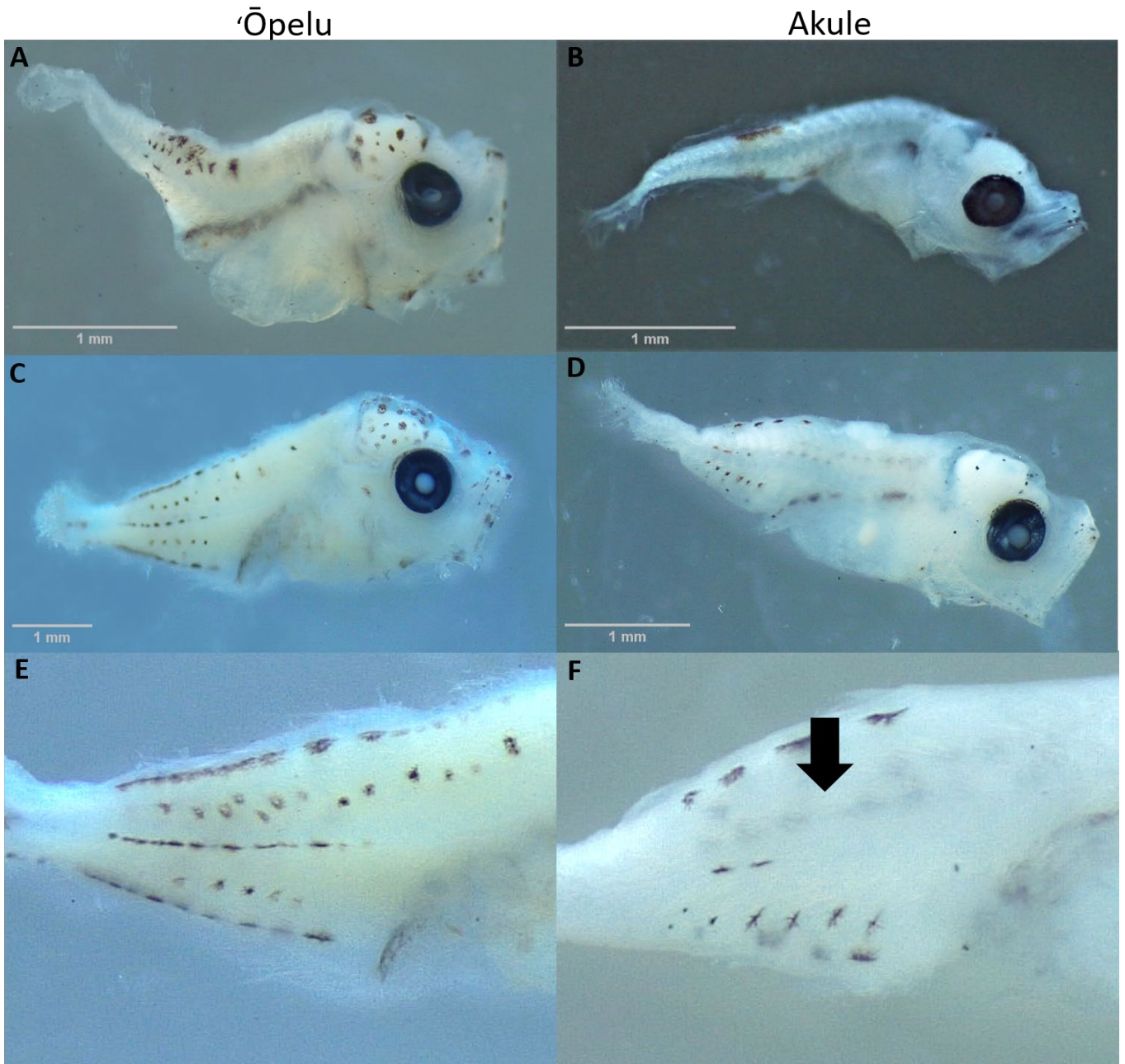
Figure 2. Morphological characteristics of early larval stages of 'ōpelu and akule. (A-B) Preflexion larvae: A) 'Ōpelu larvae at 3 mm TL display dark pigmentation on the hindbrain region, outlining the gut, lower mandible, on the dorso- and ventro-lateral edges towards the center of the body. B) Akule larvae at 3 mm display light pigmentation at the tip of the mouth, a cluster of melanophores on the dorsal and ventral edges between the gut and caudal region, as well as outlining the gut. (C-D) Flexion larvae: C) At 6 mm, pigmentation on 'ōpelu larvae stays in the same general regions as in preflexion larvae. D) At 4 mm, akule larvae display pigmentation along the lateral midline and the dorsal and ventral edges of the body, on the hypaxial myosepta posterior to the gut, internally outlining the dorsal aorta, notochord, and gut, as well as light pigment along the tip of the mouth and between the eyes. (E-F) Highlighting one of the key differences between the two species: E) 'Ōpelu melanophores on the lower half of the tail are circular and haphazardly distributed at 6 mm TL. F) Akule melanophores on the lower half of the tail are elongated and outline the hypaxial myosepta at 4 mm TL.

Environmental associations with ʻōpelu and akule occurrence

We aimed to elucidate environmental associations of ʻōpelu and akule occurrence throughout the collections, specifically focused on effect of year, month of collection, association with surface slick habitats, distance from shore, and sea surface temperature. Analyses focused on presence/absence data rather than abundance or density due to the low frequency of occurrence of both species in collections.

Sea surface temperature estimates originated from the NOAA Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring sea surface temperature data set, which is a level 4 night-only blended spatially-gap free product (NOAA Coral Reef Watch 2019). In the case of unavailable SST values for a given location and day, the SST for the nearest day was used, not to exceed 2 days. Surface slicks were used as a binary predictor (inside slick or ambient water) and included in the models and classified based on the observed effects of surface slicks on concentrating larvae in West Hawaiʻi. They were identified following the methods within Whitney et al. (2021). Distance to shore for each tow was calculated as the shortest distance from the shoreline to the centroid of the GPS track or midpoint of start/end coordinates using Near Analysis tools in ArcGIS Desktop 10.6 software (http://desktop.arcgis.com) as in Gove et al. (2019a).

We assessed environmental associations in relation to occurrence of both species through generalized additive models (GAM hereafter; Wood 2006). GAM represent a non-linear extension of generalized linear models, where the relationships between predictors and response variables are estimated through smoothing splines (Wood 2006). We specifically used GAM rather than linear models for these assessments due to the use of both temperature and distance to shore as predictors. In the case of temperature, we expect there to be a non-linear thermal niche that does not represent a symmetric quadratic response. For distance to shore, we expect the response to also be non-linear as the additive effect of distance to shore may level off at greater distances.

Each model followed the format:

$$PA_i = binomial(n_i, p_i)$$

$$(PA_i) = \alpha + Par.Pred._i + offset(Vol.Filtered_i) + f_1\left(Env.Pred._{1_i}\right) + f_2\left(Env.Pred._{2_i}\right) \dots + f_n\left(Env.Pred._{n_i}\right) + \varepsilon$$

where *PA* (presence-absence) of ʻōpelu or akule within tow *i* is treated as a binomially distributed variable with a number of trials (hauls) *n*, and number of successes (presence) *p*. *Par. Pred._i* indicates a parametric fixed effect (e.g., year, gear, surface slick). f_n represents a thin plate regression spline for environmental predictor *n*. Volume filtered by tow is treated as an offset variable to account for inter-tow variability in sampling effort. In the case of collinear predictors, separate candidate models were made for each combination of non-collinear predictor variables (Table 3).The larvae of each species were found to have different patterns in depth distribution and seasonality of occurrence. This resulted in the creation of two different model frameworks: ʻōpelu models which focused on all neuston collections, and akule models which focused on the

month with the highest collection across gears ([Table 3](#)). For both species, best fit of these candidate models was determined through percent deviance explained.

Table 3. Collections used for candidate generalized additive models to describe environmental associations between larval ‘ōpelu and akule occurrence and deviance explained by each candidate model. A single year is used for akule given the majority of collections of this species occurred in September 2016.

Species	Gear	Months	Years	Model Format	Deviance Exp.
‘Ōpelu	Neuston: 1-m ring net, 6' IK trawl	3–9, 11	1997-2006, 2009, 2011, 2016-2018	Pr(1)~offset (Vol. filtered)+ Year+Gear+s (log10(Dist. Shore))+s(SST)	44.7%
‘Ōpelu	Neuston: 1-m ring net, 6' IK trawl	3–9, 11	1997-2006, 2009, 2011, 2016-2018	Pr(1)~offset (Vol. filtered)+ Year+Gear+s (log10(Dist. Shore))+ s(Month, bs="cc")	43.6%
Akule	Vertical Tow: 1-m ring net	9	2016	Pr(1)~offset (Vol. filtered)+ s(log10(Dist. Shore)+s(SST)	39.8%

Results

A total of 55 ‘ōpelu and 58 akule larvae were collected from West Hawai‘i between 1997 and 2018. Ninety-six percent of akule individuals and 44% of ‘ōpelu were caught in September 2016. There were no records of larval specimens collected in surveys conducted in 1997, 2001, 2002, 2003, or 2018. Two ‘ōpelu specimens that were collected in 1998–1999 were identified previously but were unable to be located in the lab and no information on size was noted. However, other metadata including coordinates, tow type, species, depth, and identification of specimens were recorded and also included in the presence/absence analysis. The median length of ‘ōpelu was 4 ± 2.6 mm (SD), and the median length of akule was 3 ± 1.5 mm (SD:

Figure 3). The largest recorded individuals in this data set were 10 mm ('ōpelu) and 12 mm (akule), which is around the size of transformation to the pelagic juvenile stage for both species (Laroche et al. 2005).

Larval 'ōpelu were caught almost exclusively in neuston tows (i.e., < 2 m from surface). 'Ōpelu were caught in 23 out of 660 neuston tows (n=54 individuals) and one out of 123 vertical tows (n=1 individual). Larval akule were caught in eight out of 660 neuston tows (n=27 individuals) and 15 out of 123 vertical tows (n=31 individuals). Nearly 65% (35/55) of 'ōpelu larvae and 53% (31/58) of akule larvae were collected inside slicks.

Due to the low catchability, median densities were calculated from tows where at least one individual was caught per transect. The median densities for 'ōpelu and akule in neuston tows from 1998 to 2016 were $0.10/1000$ m^3 (Interquartile Range, IQR= 0.059-$0.28/1000$ m^3) and $0.061/1000$ m^3 (IQR=0.050-$0.073/1000$ m^3), respectively. Assessing 2016–2018 data for which both methods of collection (e.g., neuston and vertical tows) were used, the median density of 'ōpelu and akule in positive neuston transects was $3.6/1000$ m^3 (IQR= 2.4-$8.4/1000$ m^3) and $7.4/1000$ m^3 (IQR= 2.8-$30/1000$ m^3). The median density of 'ōpelu and akule in vertical tows was $42/1000$ m^3 and $63/1000$ m^3 (IQR= 42-$130/1000$ m^3), respectively.

Larvae of either species were caught in April, May, July, September, and November. There were no specimens collected in surveys conducted in March (2005), June (1998, 2001) or August (2011). Larval 'ōpelu were caught in April, May, July, September, and November, while larval akule were caught in April (n=1) and September (n=57) (Table 2). Both 'ōpelu and akule were collected in the highest relative abundance in September of 2016 (Figure 4).

For 'ōpelu larvae collections in the neuston, the GAM fit with temperature as a covariate weakly outperformed the model fit with month (Δ Dev. Expl: 1.1%). No environmental predictors were significantly related to occurrence at α=0.05 level, though temperature and distance to shore were significantly related to probability of 'ōpelu larvae occurrence at α = 0.10 (p=0.057; p=0.063, respectively). Response curves for these predictors indicate the probability of 'ōpelu larvae occurrence within the neuston is higher with increased surface temperatures and tows that occur close to shore, though both relationships have high uncertainty (Figure 5). Surface slick habitat, year, and gear effects were not significant at α = 0.10 (Table 4).

GAM for the probability of akule larvae presence in September 2016 indicated that larval akule presence was significantly higher in vertical tows compared to neuston tows (Table 4). However, there were no discernible effects of sea surface temperature, surface slick habitat, or distance from shore on the occurrence of akule larvae, with p-values all exceeding 0.13 (Table 4).
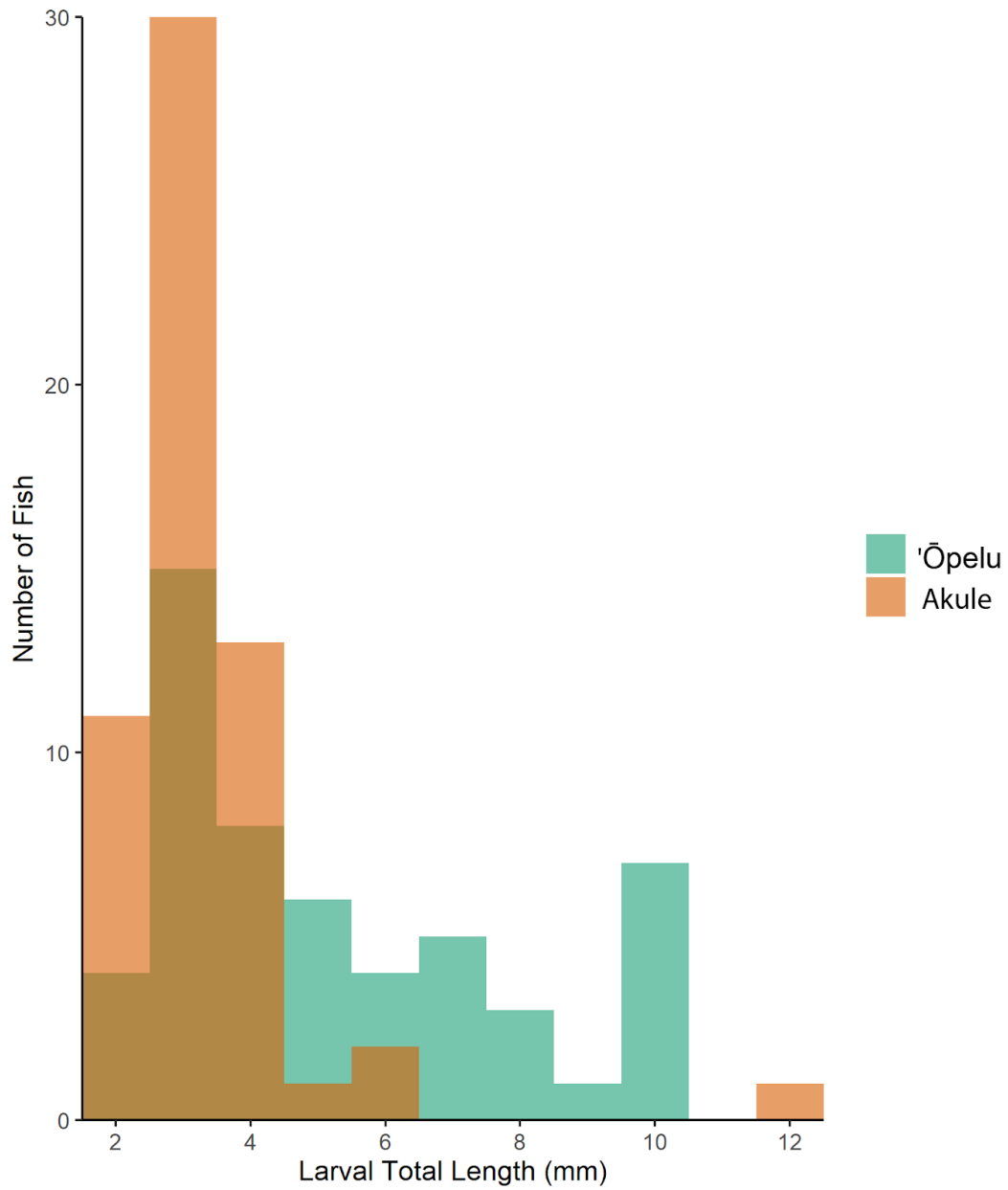
Figure 3. Histogram comparing individual sizes (total length, mm) between 'ōpelu and akule larvae. Peaks for both species occur in the 3-4mm size range. There were no observations of larval akule in the 7-11mm size class.
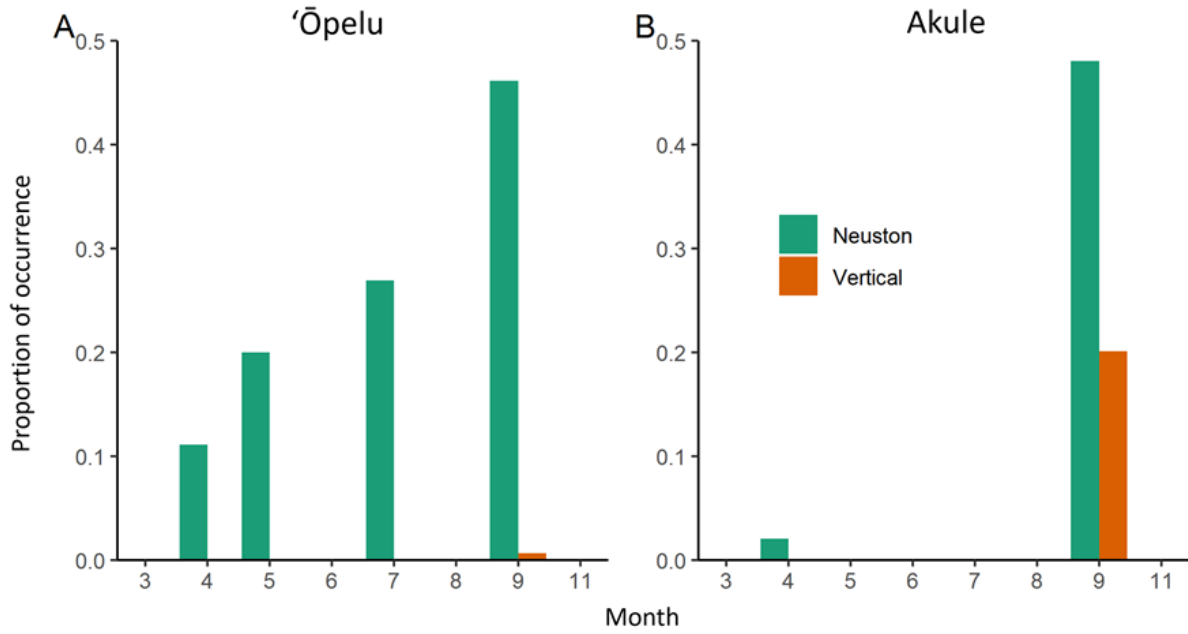
Figure 4. Proportion of occurrence for (A) larval 'ōpelu and (B) larval akule by month and tow type. The proportion of occurrence represents the number of positive tows per month with respect to the total amount of tows per month. Sampling did not occur in January, February, October, or December. Vertical tows were conducted in April, July, and September.
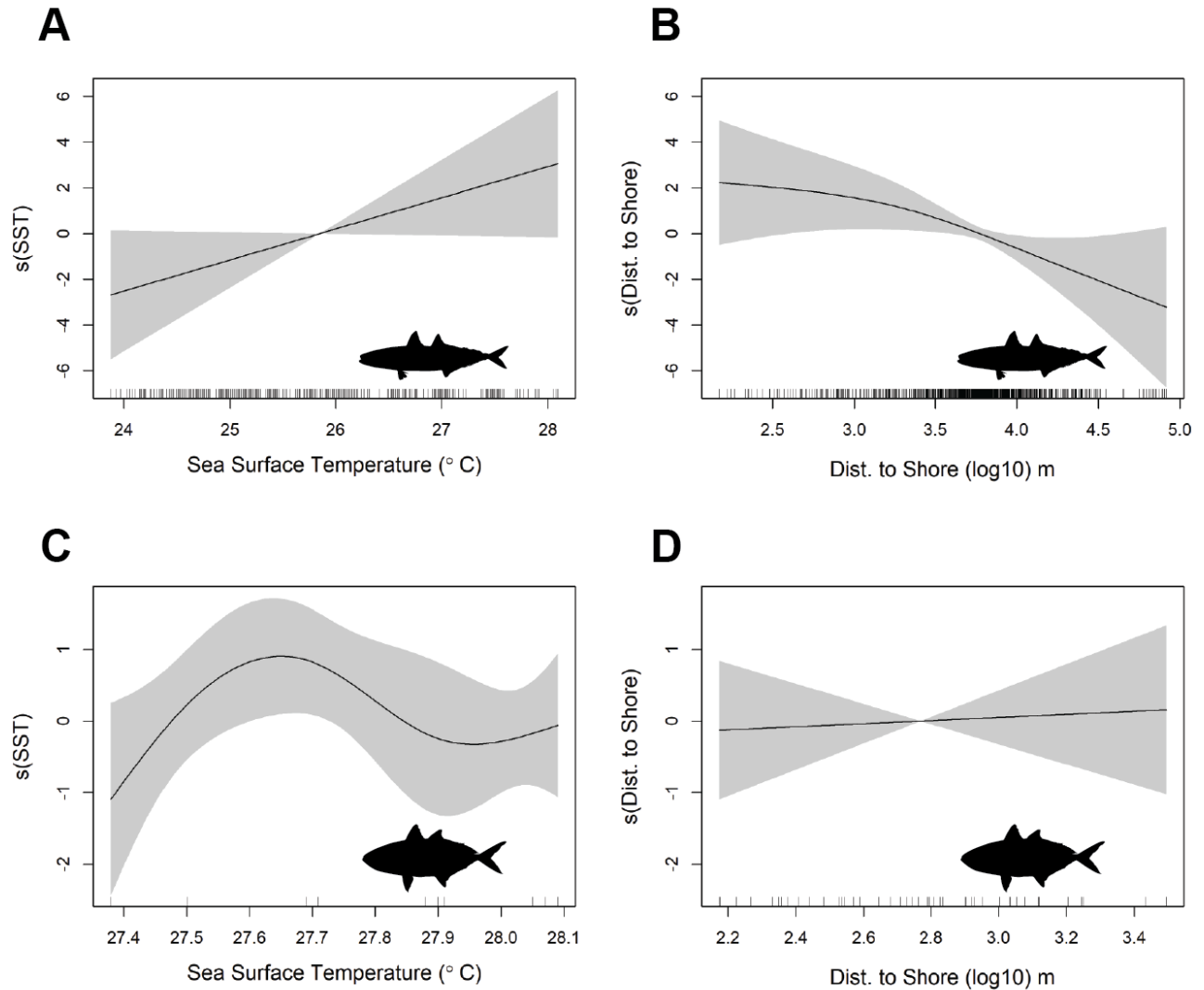
Figure 5. Response curves for GAM describing the occurrence of larval 'ōpelu (A, B) and akule (C, D) in relation to sea surface temperature (A, C) and distance to shore (log10 scale; B, D) off West Hawai'i. Vertical axes represent additive effect of each predictor on the occurrence of each species. 'Ōpelu models were formed using all neuston tows throughout sampling. Akule models were restricted to collections in September 2016. Note the difference in scales between species, particularly regarding temperature. Tick marks on x-axes represent observations of the given predictor. The low number of tick marks in panel C are a result of the coarse spatial resolution and limited spatial variability in temperature relative to sample spacing.

Table 4. Parameter estimates and p-values for terms included in final GAM for larval ʻōpelu and akule (slope estimates only included for parametric fixed effects). Plot of thin-plate regression splines for other predictors are displayed in Figure 5. IK= Isaacs-Kidd trawl, SST= sea surface temperature.

Species	Predictor	Param. Est.	*p*-value
ʻŌpelu	Year	Varies	1
	Gear-IK	0.112	0.936
	Slick	0.747	0.162
	SST		0.057
	Dist. to Shore		0.065
Akule	Tow-vertical	3.845	<0.001
	Slick	-0.197	0.741
	SST		0.135
	Dist. to Shore		0.79

Discussion

This study provides new insights on the larval ecology and distribution of ʻōpelu and akule, both commercially and culturally important species in the main Hawaiian Islands. ʻŌpelu larvae were found primarily in neuston tows, suggesting that this species utilizes the upper two meters of the water column, whereas akule were collected in a higher relative density from 1 to 10 m depth vertical tows. ʻŌpelu were also associated with warmer temperatures and shorter distance from shore at the time of collection. Based on larval abundance, a peak in the spawning period occurred in September for both species, with a near absence of akule larvae in any other month.

Previous sampling around West Hawaiʻi by Whitney et al. (2021) discovered a 15.5× higher density (individuals per 1000 m^3) of larval ʻōpelu in surface slicks than in ambient water (water outside of slicks). Larval akule, however, were not necessarily slick-associated as they occurred almost as frequently inside slicks (n=3 tows) and in ambient water out of slicks (n=2 tows). Our data show that nearly 65% (35/55) of ʻōpelu larvae and 53% (31/58) of akule larvae were collected inside slicks. These findings indicate that larval ʻōpelu mostly inhabit surface (< 2 m) slicks in pelagic waters, whereas larval akule occupy a broader niche in the vertical water column. This observed pattern is consistent with ichthyoplankton studies around Johnston Atoll, which found that larval akule inhabit waters as deep as the 50 to 100 m strata (Boehlert et al. 1992). Larval ʻōpelu were absent from these studies around Johnston Atoll; however, this taxon has been recorded around the island of Oʻahu, most abundantly in the 0 to 40 m strata (Boehlert and Mundy 1996). Therefore, the larvae of these two species demonstrate differences in vertical habitat use at these early life stages.

Larvae of both species ranged between 2 to 12 mm in total length and therefore our results characterize their early life stages (hatching to post-flexion). Combining both species, the most frequent size class (3–4 mm) represents larvae that are roughly 2 to 3 days post-hatching and 3 to 5 days post-spawning at 25 to 26 °C (Welch 2013; Baensch 2014). The majority (71%) of specimens (80/113) were collected from September 12 to 23, 2016, suggesting spawning for both species may have occurred in early September in that year. Due to this anomalous spike in positive catches, we look to an environmental shift that may have led to this effect. For example, Weng and Sibert (2000) estimated that the precipitation at Mauna Loa (the adjacent volcano on Hawaiʻi Island) could be related to an increase in akule biomass given a two-year time lag. The proposed mechanism was that nutrient-dense runoff entering the ocean from large precipitation events in Hawaiʻi influenced larval growth and recruitment success or adult condition (i.e., income breeding where resource availability for adults during spawning can be translated into higher reproductive output). The effect of these nutrients was then reflected in the adult population two years later. West Hawaiʻi experienced the highest rainfall event of the last 42 years as well as the hottest month recorded in the last century in September 2015 (Gove et al. 2019b). Though there was no sampling conducted in the present study from 2012 through 2015, we cannot rule out the effect that higher-than-normal runoff and sea surface temperatures (SST) might have on ʻōpelu and akule populations and spawning.

While our results did not elucidate any strong environmental relationships with the occurrence of ʻōpelu or akule larvae, they did provide indications that ʻōpelu larvae occur more frequently in warmer surface temperatures. Hurt et al. (2020) examined a possible positive effect of temperature and salinity on ʻōpelu spawning and behavior in West Hawaiʻi but were unable to

find a strong correlation. Hales (1987) found that temperature was a main factor in driving the seasonal distribution of the round scad (*Decapterus punctatus*) in the South Atlantic Bight, where relative abundance was consistently high during the summer and autumn seasons in shallow water (< 55 m) compared to winter months and deeper water. In the current study, occurrence of ʻōpelu larvae off West Hawaiʻi exhibited a positive relationship with warmer water surface temperature at the time of capture, indicating that waters greater than 26 °C may be important for either the spawning or larval habitat of ʻōpelu, as observed for the congener *D. punctatus* (Hales 1987). Further exploration of temperature dependent spawning is warranted given the model incorporating sea surface temperature slightly outperformed the model using month as a predictor. This result may indicate that larval occurrence (and thus spawning) is linked to environmental conditions rather than a fixed phenological cycle. Previous work on ʻōpelu spawning indicated that the gonadosomatic index value for adult female ʻōpelu in West Hawaiʻi peaked from April through August (Hurt et al. 2020). Oocyte analysis found that spawning may occur multiple times and outside of predicted spawning dates, as a number of females (n=8) contained healthy primary oocytes in October through December. This further indicates an environmental link rather than a fixed seasonal spawning progression (Hurt et al. 2020). Indeed, fishers in West Hawaiʻi have initiated a long-standing and self-regulated ban from fishing ʻōpelu from January to July to maintain healthy local stocks, likely corresponding to a variable and protracted spawning period (McNaughton 2008; Hurt et al. 2020).

The low number of collected akule larvae and constrained sampling effort through time (i.e., most samples were from September 216) limited our ability to assess the effects of temperature on larval occurrence. Akule in captivity begin to spawn throughout spring-autumn, and field observations of the spawning season for akule can begin as early as April and last through December based on oocyte analysis (Welch 2013). Thus, our collection times represent the primary spring-autumn spawning periods observed for both ʻōpelu and akule. In the main Hawaiian Islands, there is a seasonal no-catch period for juvenile akule from July through October, creating opportunity for improved spawning and recruitment (Wiley et al. 2021). Our limited sampling with vertical nets (2016–2018) likely contributed to our relatively poor frequency of observation of akule larvae across the study period. However, we still did not capture many akule larvae in 2017 or 2018 when vertical nets were deployed, further indicating that akule spawning may be highly patchy and localized or that akule larvae occur deeper in the water column. Additional concentrated and targeted sampling effort is needed to better refine larval akule habitat and adult akule spawning conditions, particularly in the summer months when spawning likely occurs.

It is important to note that a limitation of this study is that vertical tows were not conducted in West Hawaiʻi before 2016, leaving a gap in the tracking of the vertical distribution of these larvae throughout the years. Research efforts with consistent gear types throughout time would help establish a clearer description about the ecology of larval ʻōpelu and akule, namely confirming vertical separation in larval habitat between species and better defining larval akule habitat. A time series study with consistent neuston and vertical sampling, and depth-stratified sampling or oblique tows down to 100 m, could better describe both the occurrence and density of ʻōpelu and akule larvae around Hawaiʻi.

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Conclusion

We provide the first in-depth assessment on the ecology of larval ʻōpelu and akule in Hawaiʻi. We observe two distinct depth habitat preferences for the early life stages of these two co-occurring species; ʻōpelu mostly utilize the neustonic layer and akule are found slightly deeper in the water column (0–10 m). We also identified a potential thermal relationship with larval ʻōpelu occurrence associated with warmer temperatures. All individuals collected in these habitats from 1997 to 2018 were between 2 and 12 mm in length, suggesting an ontogenetic shift in habitat use in larger larvae, most likely into deeper water. Both species had a peak in spawning period in September, and the concentration of akule larvae indicate a distinct spawning event in September 2016. Further research is needed to better understand potential environmental drivers of ʻōpelu and akule spawning and further refine our knowledge of larval habitat use. Studies on the behavior of larvae and their response to oceanographic conditions could provide insight into how the environment may modulate recruitment and how to better predict larval distributions in the future.

Acknowledgements

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