Abstract—To improve understanding between ontogeny and habitat use of early life history stages (ELHS; larvae and juveniles) of mesopelagic fish species, we analyzed a small set of discrete-depth samples collected by repeated 1-m^2 Multiple Opening/Closing Net Environmental Sensing System tows in one location over a 24-h period in the euphotic and upper mesopelagic zones (0–600 m) off central California in 1989. Species richness and abundance were significantly higher than in Bongo net samples from 0 to 200 m at nearby stations in both the shallow (0–100 m) and deep (400–600 m) strata both day and night. The overall abundance of ELHS mesopelagic fishes was largely influenced by depth, with a detectable diel influence in some strata. Early-stage larvae occurred primarily in the shallow strata and later stages in the deep strata. Myctophidae and Bathylagidae species had similar patterns of vertical distribution within life history stages for both daytime and nighttime samples. This study shows the importance of discrete depth sampling and fine-scale taxonomic resolution for understanding the ontogenetic patterns of habitat use in ELHS mesopelagic fish species. With the increasing interest in these fishes as potential commercial resources, it is critical to pursue this type of research to better define their role in the marine ecosystem.

Ontogenetic vertical distribution and abundance of early life history stages of mesopelagic fishes off central California

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Introduction

Mesopelagic fish species spawn at depth. The buoyant eggs of most hatch in the epipelagic zone where larvae reside before returning to deeper habitats during ontogeny (Kendall et al., 1984; Moser, 1996). Approximately half of mesopelagic fishes make daily vertical migrations from the mesopelagic during the day, where the relative darkness offers some protection from visual predators, up into the more productive epipelagic at night to feed (Salvanes and Kristoffersen, 2001; Sutton, 2013). Vertical distributions have been described for numerous juvenile and adult mesopelagic fish species that undertake these daily migrations (e.g., Lavenberg and Ebeling, 1967; Willis and Pearcy, 1982; Luo et al., 2000; Eduardo et al., 2021), but fewer studies have examined stage-specific vertical distributions of early life history stages (ELHS) (Loeb, 1979; Sassa et al., 2007; Olivar and Beckley, 2022). Given the need for fish to live where they can survive, feed, grow, and reproduce (Litchman et al., 2013), it is reasonable to assume that all life history stages partition themselves in the water column.

The relationship between ontogeny and depth of mesopelagic fish ELHS is not well studied because the majority of ichthyoplankton studies use integrated water column net tows rather than discrete-depth samplers (e.g., Wiebe et al., 1976; Smith and Richardson, 1977; Kelso and Rutherford, 1996). The Multiple Opening/Closing Net Environmental Sensing System (MOCNESS) (Wiebe et al., 1985) is a convenient, powerful tool for collecting discrete-depth biological samples with comparable sampling efficiency to other opening and closing sampling devices (Pakhomov and Yamamura, 2010).

An additional impediment to the study of depth distributions of mesopelagic fish ELHS is that the traditional visual identification method is difficult and time consuming, often resulting in resolution only to the level of family due to lack of taxonomic knowledge of species-specific ELHS (Hernandez et al., 2013).

Much of the knowledge of mesopelagic fish ELHS in California waters is from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (Moser and Watson, 2006; McClatchie, 2014), which began in 1949 and continues to the present. The original CalCOFI domain ranged from the California-Oregon border to the tip of Baja California Sur, Mexico, but after 1984 was largely limited to southern California until again expanding northward to central California during winter and spring in recent years. The primary ichthyoplankton time series produced by this program is based on integrated sampling in the upper 200 m of the water column. Although not useful for discrete-depth analyses, it provides an excellent context for such studies.

Here, we describe the vertical distribution of common mesopelagic fish ELHS based on samples collected with a 1-m^2 MOCNESS towed repeatedly over a 24-h period at a central California site within the CalCOFI domain during spring 1989. We analyze species richness (number of species) and larval abundance from the MOCNESS samples and compare them with values based on samples collected in CalCOFI oblique tows at nearby stations to aid in assessing potential habitat use by the mesopelagic ichthyoplankton.

Materials and methods

Field sampling

A CalCOFI cruise off southern and central California during 16 April–4 May 1989 aboard the R/V *David Starr Jordan* included MOCNESS sampling off central California. The MOCNESS was towed 3 times during the day and 3 times at night over a 24-h period (Table 1) at station 108 (34°45′18″N, 121°28′58.8″W), about 80 km northwest of Point Conception, California (Fig. 1). The MOCNESS had a 1-m^2 mouth opening with 10 individual 0.505-mm mesh nets, 9 of which collected discrete depth samples and one that collected an integrated water column sample. The MOCNESS was towed at 2.0–2.5 knots with the net frame angle maintained at 45° ± 8°, and discrete samples (nets) were collected through the 0–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–500, and 500–600 m strata. The net vertical velocity averaged 16 m/min for strata above 200 m and 10 m/min for the deeper strata. The water volume filtered per stratum ranged from 126–818 m^3 with a mean of 337 m^3. On board, the nets were rinsed and samples were preserved in 5% formalin buffered with sodium borate (Bowlin, 2016).

To provide a context for the fishes collected in the MOCNESS samples, we analyzed ichthyoplankton data from 4 nearby CalCOFI stations occupied during the same cruise (stations 76.7 55, 76.7 60, 80.0 55, and 80.0 60; Fig. 1). These samples were collected with a 0.71-m Bongo fitted with 0.505-mm mesh nets and towed obliquely through the upper 200 m at a ship speed of 1.5–2.0 knots with an angle of stray of 45° ± 8° and a vertical velocity of 20 m/min (Kramer et al., 1972; Smith and Richardson, 1977). The volume filtered per sample ranged from 411 to 437 m^3, with a mean of 423 m^3. Hydrographic data were collected by SBE 19 SeaCAT Profiler CTD (Sea-Bird Scientific, Bellevue, WA) vertical casts to 500 m depth or within 10 m of the bottom in shallow areas at the same 4 adjacent CalCOFI stations during the same cruise.

Laboratory work

All fishes were sorted, enumerated, identified to the lowest possible taxon following accepted nomenclature in the Integrated Taxonomic Information System (available from https://www.itis.gov/, accessed May 2023), and assigned to a life-history stage as defined by Kendall et al. (1984): yolk-sac stage (with a visible yolk sac), preflexion stage (after yolk absorption but before notochord flexion begins), flexion stage (from start to end of notochord flexion), postflexion (after flexed portion of notochord is in its final position, typically 45° from the notochord axis, to metamorphosis), transforming (loss of larval characters to start of juvenile stage), and juvenile (presence of juvenile or adult characters such as full complements of fin rays and pigment or photophore patterns). Too few yolk-sac stage larvae were collected to include in the analyses. For statistical analyses, preflexion and flexion stages were pooled as early stage, postflexion and transforming were pooled as late stage, and juvenile stage remained a separate category.

Statistical analysis

We investigated the patterns to answer the following questions: (i) Were there diel differences in mesopelagic fish ELHS species richness across depth strata? (ii) Were there diel differences in the abundance of the mesopelagic fish species across depth strata? (iii) Were there different patterns in depth distribution among species of mesopelagic ELHS? And if so, (iv) were those patterns related to ontogeny? To help answer these questions, a series of generalized linear models was fit using R, version 4.3.2 (R Core Team, 2023) as follows.

To address question (i) we set a model to summarize species richness by stratum and time of day. In a generalized linear model framework, the model was fit as

$$\log(\mu_{i,d}) = \mathit{offset}(\log(\mathit{volume})) + \mathit{stratum}_i \times \mathit{day}_d, \quad yi \sim P(\lambda_{i,d}) \qquad (1)$$

where $\log(\mu_{i,d})$=logarithm of the expected number of mesopelagic fish species in depth stratum i and daytime d;

Table 1

Counts of individual mesopelagic fish species collected in each depth stratum from each of the 3 replicate daytime (108c, 108d, 108e) and nighttime (108a, 108b, 108f) Multiple Opening/Closing Net Environmental Sensing System tows off the coast of central California during 16 April–4 May 1989. Day and night conditions were categorized based on the local sunrise in the Pacific Standard Time Zone (0512) and sunset (1854).

	Day			Night		
Station	108c	108d	108e	108a	108b	108f
Time	0731	0944	1226	0123	0445	1841
Depth (m)						
0–50	66	68	10	84	26	8
50–100	6	21	25	9	8	8
100–150	0	3	1	2	5	6
150–200	3	1	5	0	0	1
200–300	0	1	4	2	2	5
300–400	24	16	31	11	31	17
400–500	28	17	39	18	14	30
500–600	6	20	23	6	10	5
Total	133	147	138	132	96	80

offset(log(*volume*))=the sample volume set in the model with a coefficient of one and standardizes the species counts;

stratum and *day*=factors with 8 and 2 levels, respectively; and

$P(\lambda_{i,d})$,=Poisson distribution with parameter $\lambda_{i,d}$, where i and d represent a generic stratum and time of day.

This model is analogous to a 2-way analysis of variance but with the generalizations that the distribution of the mean value of species richness is assumed to follow a Poisson distribution (Kabacoff, 2011) and the logarithm of the mean value is related to the linear predictor. The model assumptions of independence and homogeneity of residuals were verified by diagnostic plots (McCullagh and Nelder, 1989) and the significance level was set at 0.05.

For question (ii), we fit a model similar to Equation 1, but used the abundance of all mesopelagic species combined as a response variable. To help us answer question (iii) we fit: 1) a model similar to that used for question (ii) but separately for the 6 most abundant species, and 2) the same model for all species but with northern lampfish (*Stenobrachius leucopsarus*) and showy bristlemouth (*Cyclothone signata*) removed. Northern lampfish and showy bristlemouth were an order of magnitude more abundant than the other species in this study (Table 2) and were thus removed in case they were obscuring any discernible patterns among the remaining species. Finally, to understand ontogenetic and phylogenetic patterns of vertical distribution (question [iv]), we performed a descriptive analysis of species abundance by larval stage and by depth using the same clustering of the data as in the models above: 1) all mesopelagic species combined, 2) the 6 most abundant species analyzed separately, 3) all species except northern lampfish and showy bristlemouth, and 4) fishes grouped by family.

Although the 1-m^2 MOCNESS has been shown to catch 3–5 times more fish larvae than the Bongo net with differences among taxa (Johnson and Fogarty, 2013), we compared the samples from each gear type. Juvenile specimens from the MOCNESS samples were excluded from this comparison because the CalCOFI Bongo data only include larval specimens. At the 4 selected Bongo stations (Fig. 1), ichthyoplankton data were used to calculate mean species richness and mean larval abundance and compared to the mean richness and mean larval abundance of mesopelagic fish species collected in the 6 MOCNESS tows in 2 depth categories: the upper 200 m, sampled by the Bongo, and the upper 600 m, sampled by the MOCNESS. The deep category (0–600 m) provides a snapshot comparison of larval mesopelagic fish distribution in the epipelagic versus the combined epi- and upper mesopelagic zones. We performed Kruskal–Wallis tests with a significance level of 0.05 to determine if the mean abundances and richness differed between MOCNESS and Bongo samples.

The environmental data were not recoverable from the MOCNESS tows; thus conductivity, temperature, and depth data from the 4 spring CalCOFI stations, for each cast to a depth of 500 m, were analyzed for each of 5 physical variables: temperature (in degrees Celsius), salinity, potential density (in kilograms per cubic meter),

Table 2

Counts and ontogenetic stages of individual mesopelagic collected off the coast of central California during 16 April–4 May 1989. The ontogenetic stages include preflexion (PREF), flexion (FLEX), postflexion (POST), transforming (TRNS), and juvenile (JUVE). The distribution of the 6 most abundant species collected in the Multiple Opening/Closing Net Environmental Sensing System samples (those above the dashed line) were analyzed separately to determine if there were different patterns in depth distribution.

Species	PREF	FLEX	POST	TRNS	JUVE	Total
Stenobrachius leucopsarus	128	98	50	17	9	302
Cyclothone signata	0	0	4	1	238	243
Leuroglossus stilbius	5	3	19	13	0	40
Tarletonbeania crenularis	8	12	10	0	1	31
Lipolagus ochotensis	5	4	9	5	0	23
Protomyctophum crockeri	6	1	10	5	1	23
Cyclothone acclinidens	0	0	0	0	9	9
Myctophidae	2	4	1	0	0	7
Bathylagus pacificus	0	2	2	1	0	5
Chauliodus macouni	1	0	3	0	1	5
Danaphos oculatus	0	0	3	2	0	5
Diogenichthys atlanticus	0	0	3	1	0	4
Melamphaes lugubris	0	0	4	0	0	4
Nannobrachium ritteri	0	0	0	0	4	4
Argyropelecus sladeni	0	0	0	3	0	3
Bathylagoides wesethi	0	0	1	0	2	3
Argyropelecus affinis	0	0	0	1	1	2
Argyropelecus hemigymnus	0	0	1	0	1	2
Cyclothone pseudopallida	0	0	0	0	2	2
Nannobrachium regale	2	0	0	0	0	2
Sagamichthys abei	0	1	1	0	0	2
Argyropelecus lychnus	0	0	0	1	0	1
Diaphus theta	0	0	0	0	1	1
Holtbyrnia latifrons	0	1	0	0	0	1
Microstoma sp.	1	0	0	0	0	1
Scopelarchus analis	1	0	0	0	0	1

chlorophyll-*a* concentration (in micrograms per liter), and oxygen concentration (in milliliters per liter) (Fig. 2). The potential density data were analyzed to calculate the mixed layer depths (Weber and McClatchie, 2009), and temperature data were analyzed to calculate the thermocline depths (Winslow et al., 2022) at the 4 stations (Fig. 3). These analyses were used to explore potential environmental influences on the mesopelagic fish distribution patterns revealed from the MOCNESS data.

Results

Taxonomic composition

In total, 774 ELHS fishes were collected in the MOCNESS tows. Demersal species from 4 families—Gobiidae, Paralichthyidae, Pleuronectidae, and Scorpaenidae—accounted for 6% of the specimens (48 individuals). The remaining 94% (726 specimens) were mesopelagic species, of which 7 individuals were identifiable only to family (Myctophidae), with the remaining 719 specimens identified to species. Hereafter, only mesopelagic species are considered. These belonged to 9 families: Bathylagidae, Gonostomatidae, Melamphaidae, Microstomatidae, Myctophidae, Platytroctidae, Scopelarchidae, Sternoptychidae, and Stomiidae. The 6 most abundant mesopelagic species constituted 91% of the specimens and represented 3 families (Table 2). The 2 most abundant species, northern lampfish (Myctophidae) and showy bristlemouth (Gonostomatidae), exceeded the abundance of all other species by an order of magnitude and together accounted for 75% of the total mesopelagic specimens. The next 4 most abundant species—California smoothtongue (*Leuroglossus stilbius*) (Bathylagidae), blue lanternfish (*Tarletonbeania crenularis*) (Myctophidae), popeye blacksmelt (*Lipolagus ochotensis*) (Bathylagidae), and California flashlightfish (*Protomyctophum crockeri*) (Myctophidae)—together accounted for 16% of the

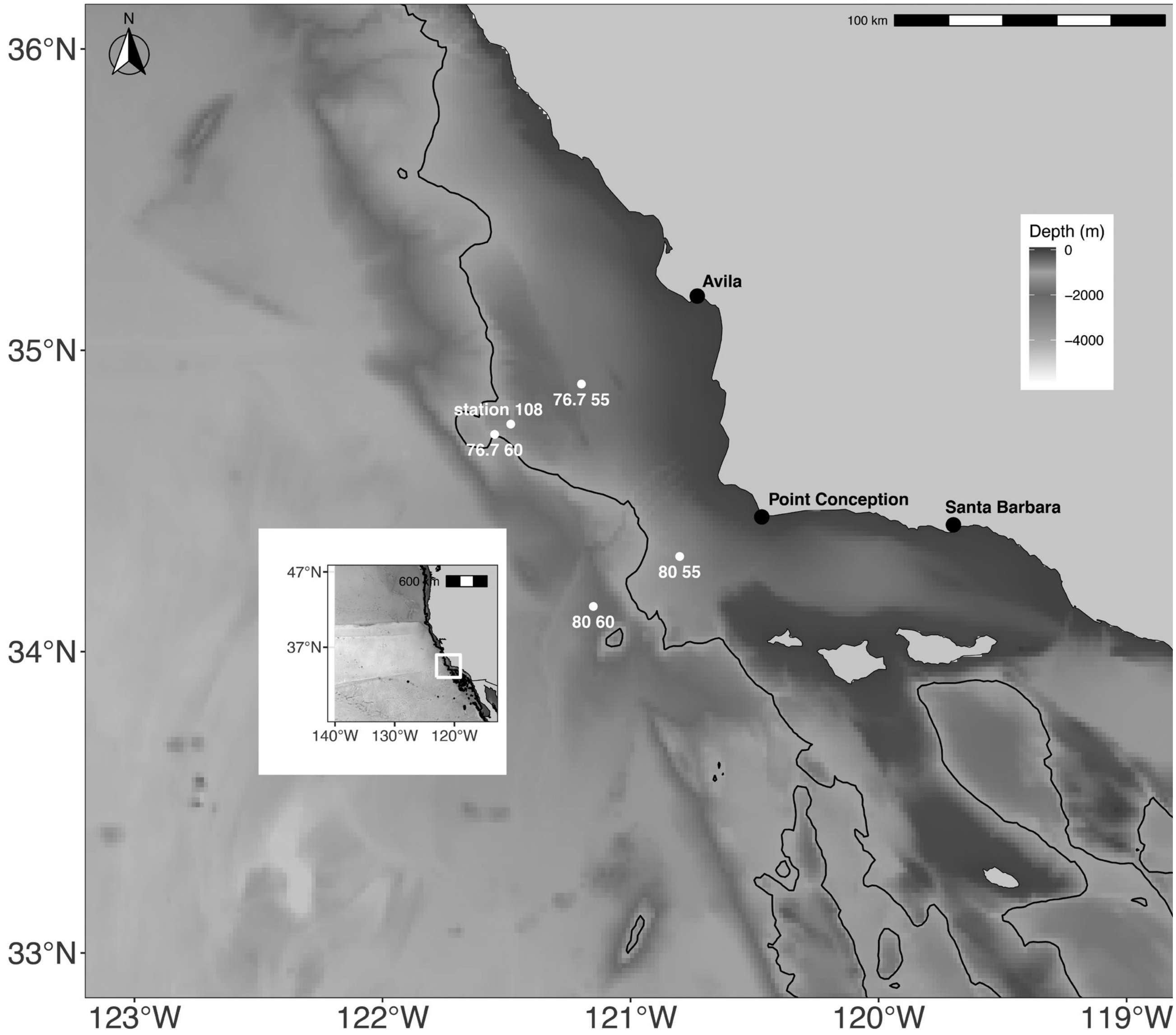

Figure 1

Map of central and southern California where mesopelagic fishes were collected on a California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise during 16 April–4 May 1989. A Multiple Opening/Closing Net Environmental Sensing System was towed 6 times at station 108 (34°45′18″N, 121°28′58.8″W). Ichthyoplankton time series data were analyzed from CalCOFI stations 76.7 55, 76.7 60, 80.0 55, and 80.0 60 (34°53′13.2″N, 121°11′49.2″W; 34°43′19.2″N, 121°32′52.8″W; 34°16′1.2″N, 120°48′7.2″W; 34°9′7.2″N, 121°9′0″W, respectively). The inset map shows the location of the study area (square) in relation to the West Coast.

mesopelagic specimens. The remaining 9% included 19 species from all 9 families.

Juvenile fish species were the most abundant ELHS (37%), followed by preflexion (22%), flexion (17%), postflexion (17%), and transforming (7%) stages. The majority of the juvenile fishes (238/270 or 88%) were showy bristlemouth, the second most abundant species, and the majority of the preflexion stage fish species (128/159 or 81%) were northern lampfish, the most abundant species.

Daytime abundance of mesopelagic fish species was higher than nighttime abundance (Table 1). On average, daytime samples contained about 36% more fish than nighttime samples. For all 6 tows the majority of the

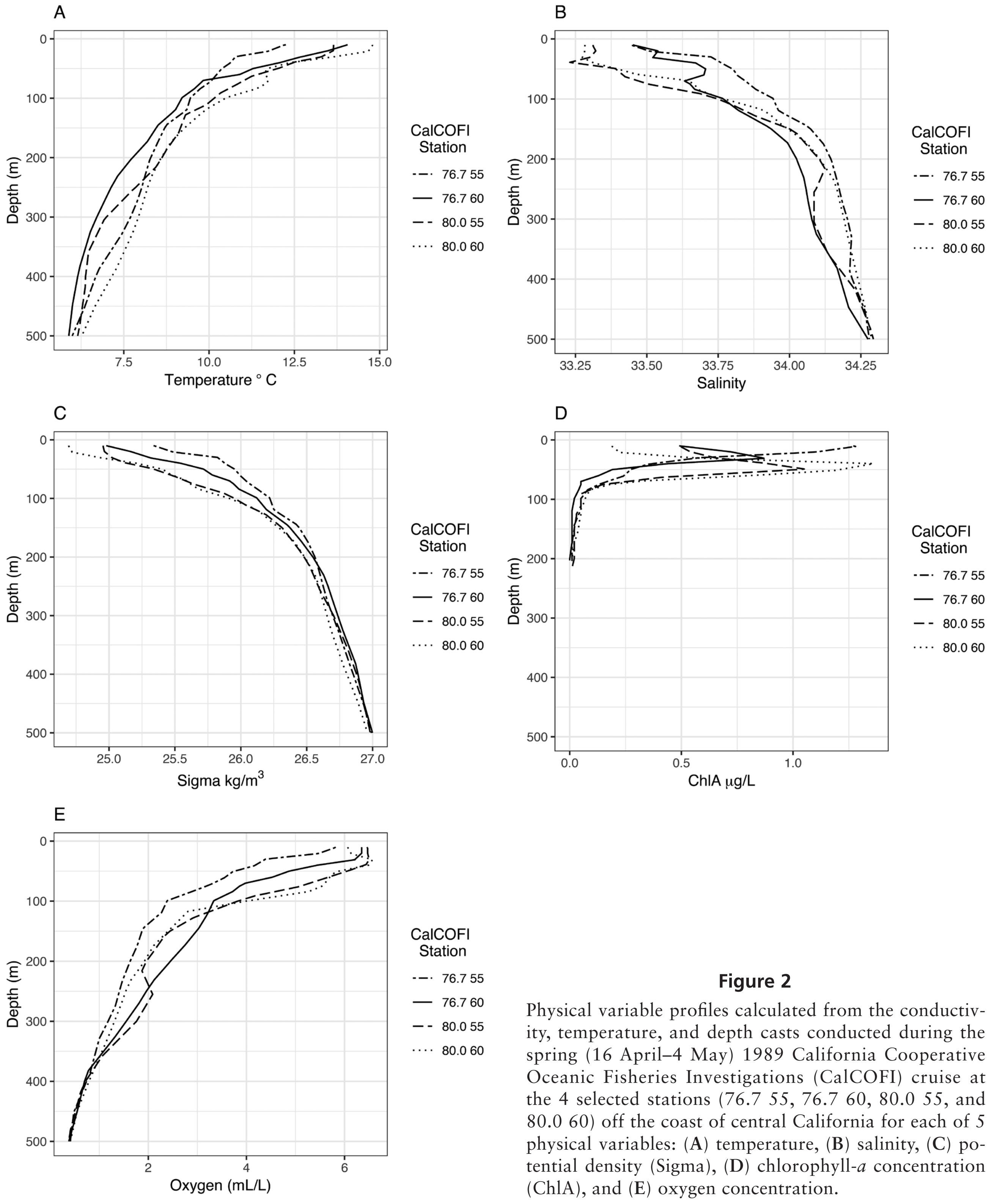

Figure 2

Physical variable profiles calculated from the conductivity, temperature, and depth casts conducted during the spring (16 April–4 May) 1989 California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise at the 4 selected stations (76.7 55, 76.7 60, 80.0 55, and 80.0 60) off the coast of central California for each of 5 physical variables: (**A**) temperature, (**B**) salinity, (**C**) potential density (Sigma), (**D**) chlorophyll-*a* concentration (ChlA), and (**E**) oxygen concentration.

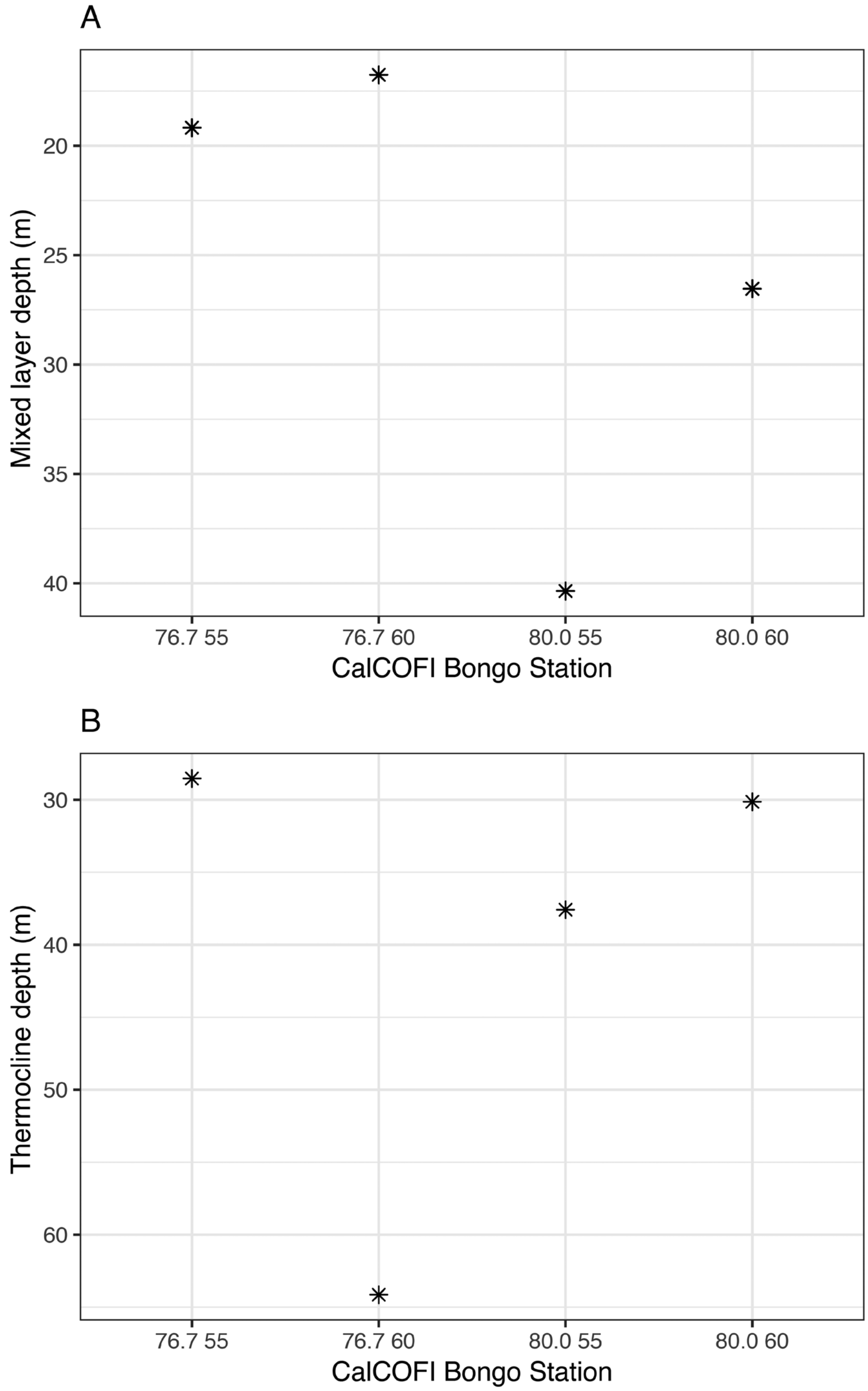

Figure 3

(**A**) Mixed layer and (**B**) thermocline depths calculated from the SBE 19 SeaCAT Profiler CTD potential density and temperature data, respectively, collected from the 4 selected California Cooperative Oceanic Fisheries Investigations (CalCOFI) stations (stars) during the spring (16 April–4 May) 1989 cruise off the coast of central California.

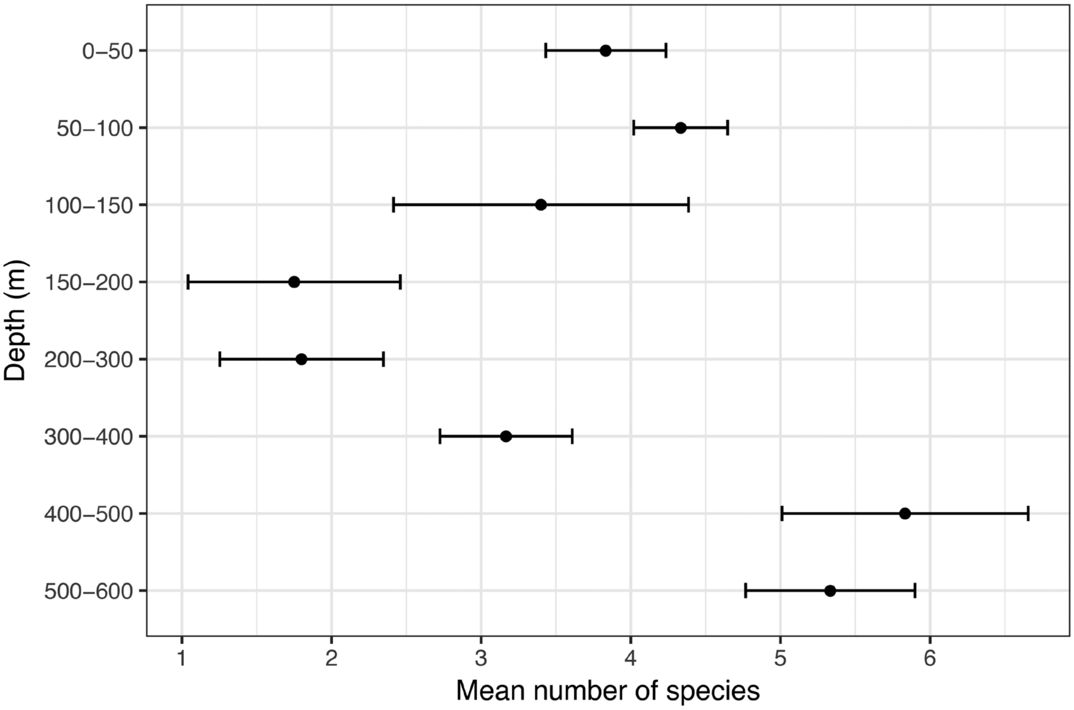

Figure 4

Mean species richness (mean number of species) of early life history stages of mesopelagic fish species (dots) collected in each of the 8 depth strata for 6 Multiple Opening/Closing Net Environmental Sensing System tows at station 108 with 95% confidence intervals (error bars) during the spring (16 April–4 May) 1989 California Cooperative Oceanic Fisheries Investigations cruise off the coast of central California. Day and night samples are combined because depth stratum was the only significant predictor for the number of species in the water column; time of day was insignificant.

specimens occurred in the shallow and deep strata, with very few specimens in the middle strata.

The context provided by the CalCOFI Bongo time series indicates that the species richness and abundances from the spring 1989 cruise for both the Bongo and MOCNESS samples are within the range of expected values (Suppl. Fig. 1).

Statistical analysis

Comparison of the 3 day and 3 night MOCNESS samples revealed no significant diel difference in richness (Suppl. Table 1), but it revealed a significant vertical distribution pattern. Richness was highest below 400 m, decreased considerably between 400 and 150 m, and then increased again in the upper 100 m (Fig. 4).

The model results comparing vertical distributions of mesopelagic fishes (question [ii]) indicate that abundances differed significantly among strata, with some significant interactions between stratum and time of day (Suppl. Table 2). Although these interactions limit our ability to describe main effects (Kabacoff, 2011), the results suggest that stratum (depth) had the largest influence on abundance, with time of day influencing abundance in some strata (100–150 m and 500–600 m). Similar to the results for richness, overall abundance was bimodally distributed with the highest abundances in the 2 shallowest strata and a smaller increase in deep strata (300–500 m; Fig. 5). Most fish in the shallow strata were in early stages, while late stages dominated the deep strata (Fig. 5).

Further investigation of species-specific patterns (question [iii]) revealed significant depth differences for the abundance of northern lampfish, with a slight interaction with time of day (Suppl. Table 3). Visually, the early-stage larvae were clearly in the 2 shallowest strata (0–50 m and 50–100 m), and the relatively few transforming and juvenile individuals were mostly in the deepest 3 strata (300–600 m), both day and night (Suppl. Fig. 2). The second most abundant species (showy bristlemouth) had a significant vertical stratification pattern of abundance but no clear diel differences (Suppl. Table 4). Early stages of showy bristlemouth were

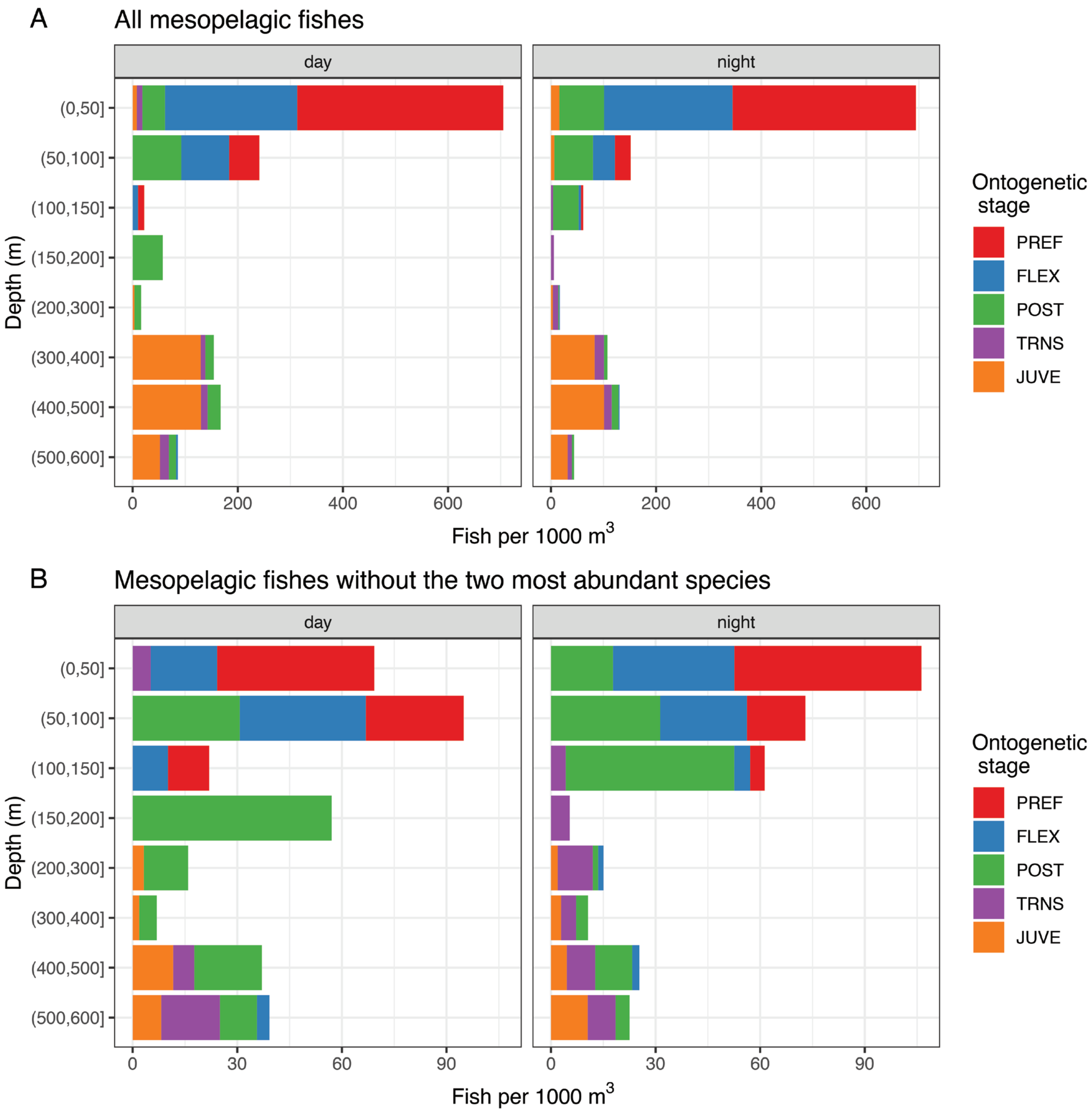

Figure 5

Ontogenetic stage-specific distribution and standardized abundance of (**A**) all early life history stages of mesopelagic fish species and (**B**) all except for the 2 most abundant mesopelagic fish species collected from day and night Multiple Opening/Closing Net Environmental Sensing System samples at station 108 during the spring (16 April–4 May) 1989 California Cooperative Oceanic Fisheries Investigations cruise off the coast of central California. The ontogenetic stages include preflexion (PREF), flexion (FLEX), postflexion (POST), transforming (TRNS), and juvenile (JUVE).

absent, but later stages were primarily in the deepest 3 strata (300–600 m) (Suppl. Fig. 2). Abundances of the next 4 most abundant species (California smoothtongue, blue lanternfish, popeye blacksmelt, and California flashlightfish) had a mixture of depth and diel patterns, but their relatively low abundances precluded confident descriptions of distributions. Visually, each species had a different vertical distribution pattern (Suppl. Figs. 2 and 3).

Analysis without northern lampfish and showy bristlemouth abundances showed significant stratum effects, with significant interactions between stratum and time of day (Suppl. Table 5). The general pattern still held, with the majority of early-stage individuals in the shallow strata and late-stage individuals in the deep strata, but the daytime distribution had a secondary peak of postflexion stage larvae in a middle stratum at 150–200 m (Fig. 5).

The descriptive analysis of the 3 most abundant families (Myctophidae, Gonostomatidae, and Bathylagidae) without the 2 most abundant species did not reveal clear differences in abundance between depth strata during the day or at night. However, there is a prominent pattern suggesting vertical migration for Myctophidae and Bathylagidae (Fig. 6). The distributions of myctophids (other than northern lampfish) appeared to differ between day and night and resembled the distribution of northern lampfish (Fig. 6, Suppl. Fig. 2). During the day the preflexion, almost all flexion, and most of the postflexion larvae were in the upper 100 m, with the remaining postflexion larvae deeper in the water column. At night it appeared that many of those larvae had moved up to shallower strata.

Early stage gonostomatids were not collected in the MOCNESS samples (Fig. 6, Suppl. Fig. 2). All later stages (excluding showy bristlemouth) were collected below 150 m, regardless of collection time. Postflexion stage larvae had the shallowest distribution (150–200 m) and were collected only during the day. The few transforming specimens were in the 200–300 m stratum and only collected at night, while all juveniles were found below 300 m both day and night.

Distributions of bathylagid stages (except juveniles) appeared to be centered somewhat deeper during the day, moving closer to the surface at night (Fig. 6). During the day, postflexion larvae were present only below 150 m depth. At night, some postflexion larvae were present in the 50–150 m strata and below 300 m but none were present in the strata between.

Mesopelagic larval fish species richness in the upper 200 m in MOCNESS samples was only slightly higher than richness in the Bongo samples (Kruskal–Wallis, $P>0.05$; Fig. 7) and was generally comparable to species richness for all 4 CalCOFI stations in the historic time series data (Suppl. Fig. 1). However, species richness from 0 to 600 m in the MOCNESS was higher than that in both the 1989 Bongo tows (Kruskal–Wallis, $P<0.05$; Fig. 7) and the additional years of CalCOFI larval fish data at those stations (Suppl. Fig. 1). The MOCNESS larval abundances for both the shallow and deep categories were higher than the larval abundance in the CalCOFI Bongo tows (Kruskal–Wallis, $P<0.05$; Fig. 7). However, larval abundances were generally similar for the shallow and deep MOCNESS depth categories (Kruskal–Wallis, $P>0.05$; Fig. 7).

The mixed layer and thermocline depths were at 50 m and 65 m depth, respectively, at all 4 CalCOFI stations (Fig. 3) and thus were within the 2 shallowest strata (0–100 m), corresponding with the highest concentrations of the earliest stage larvae. An oxygen minimum zone was present near 200 m (Fig. 2). We have no hydrographic data below 500 m depth, but based on the trend it appears that the oxygen minimum zone extended into the deepest stratum (to 600 m) sampled by the MOCNESS.

Discussion

Larval fishes undergo many profound changes during ontogeny that affect their behaviors, such as where they reside in the water column, their prey choices, and predator avoidance. Although we analyzed a relatively small dataset, yielding low statistical power, and samples were not collected during crepuscular periods when diel migratory behavior occurs, evidence of some of the complexities of ontogeny are evident in this study. A reoccurring pattern was revealed, with highest concentrations of ELHS mesopelagic fishes in the shallow and deep strata and lowest concentrations in the middle strata. This was generally true for species-specific and family-level abundances, as well as for species richness and ontogenetic stage abundances. This pattern suggests that the shallow strata (0–150 m) are where the earliest larvae reside, the middle strata (150–300 m) are a transition zone for some species that are settling into deeper strata where they will remain, while other species will begin their diel vertical migratory behavior as they pass through the transformation stage of development (Figs. 5 and 6, Suppl. Figs. 2 and 3).

Species richness within the depth strata was comparable in both day and night samples (Fig. 4), but the pooled abundance of all mesopelagic species differed significantly between day and night samples (Fig. 5). The lower daytime abundance could be the result of net avoidance (Margulies, 1989), patchiness, diel movements, or a combination of these factors. About one-third of the mesopelagic specimens in this study were juveniles. Many mesopelagic fish are known to undertake diel vertical migrations during the juvenile stage (e.g., Clarke, 1973; Giske

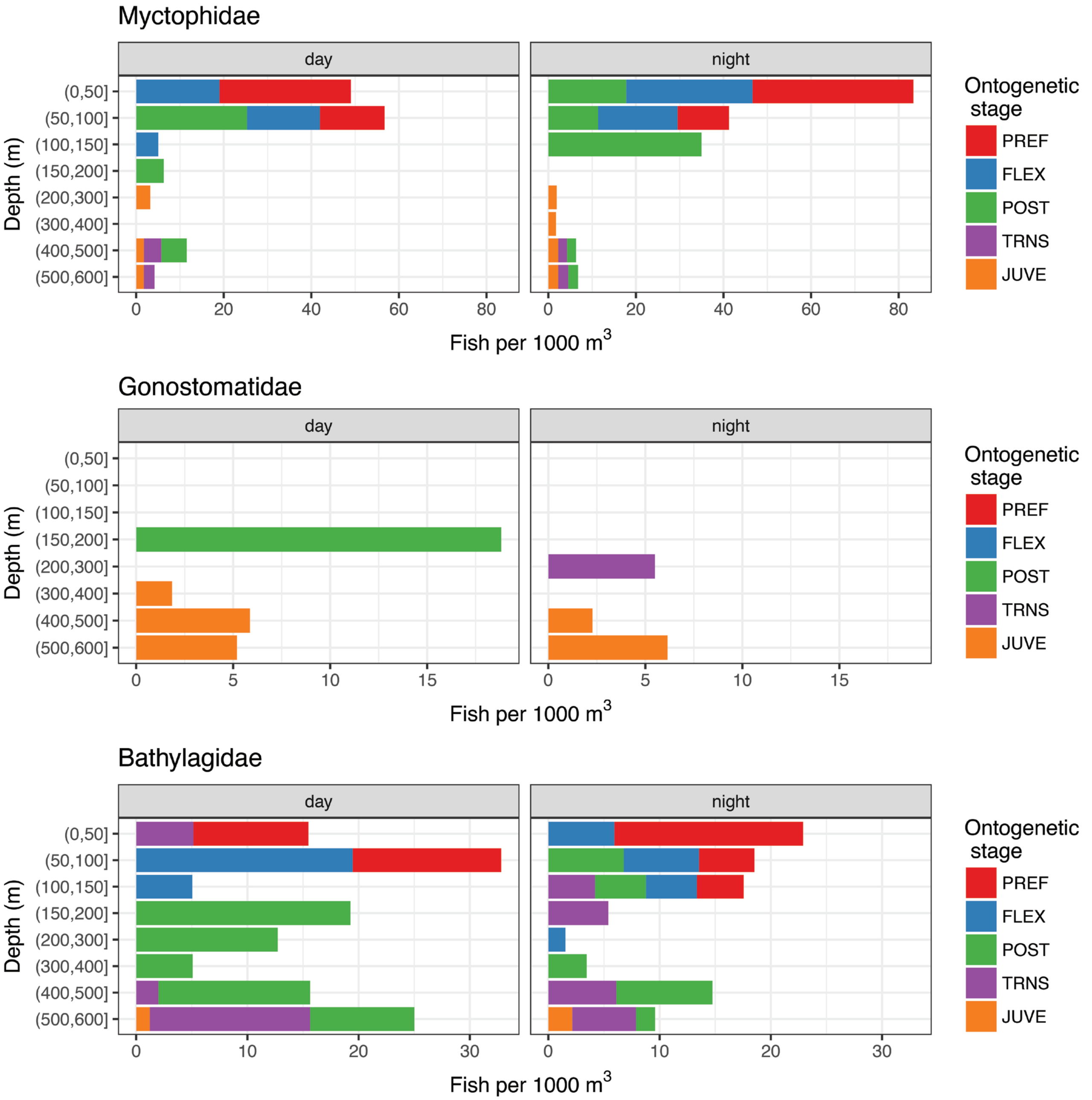

Figure 6

Ontogenetic stage-specific distribution of families Myctophidae (except northern lampfish [*Stenobrachius leucopsarus*]), Gonostomatidae (except showy bristlemouth [*Cyclothone signata*]), and Bathylagidae collected from the day and night Multiple Opening/Closing Net Environmental Sensing System samples at station 108 during the spring (16 April–4 May) 1989 California Cooperative Oceanic Fisheries Investigations cruise off the coast of central California. The ontogenetic stages include preflexion (PREF), flexion (FLEX), postflexion (POST), transforming (TRNS), and juvenile (JUVE).

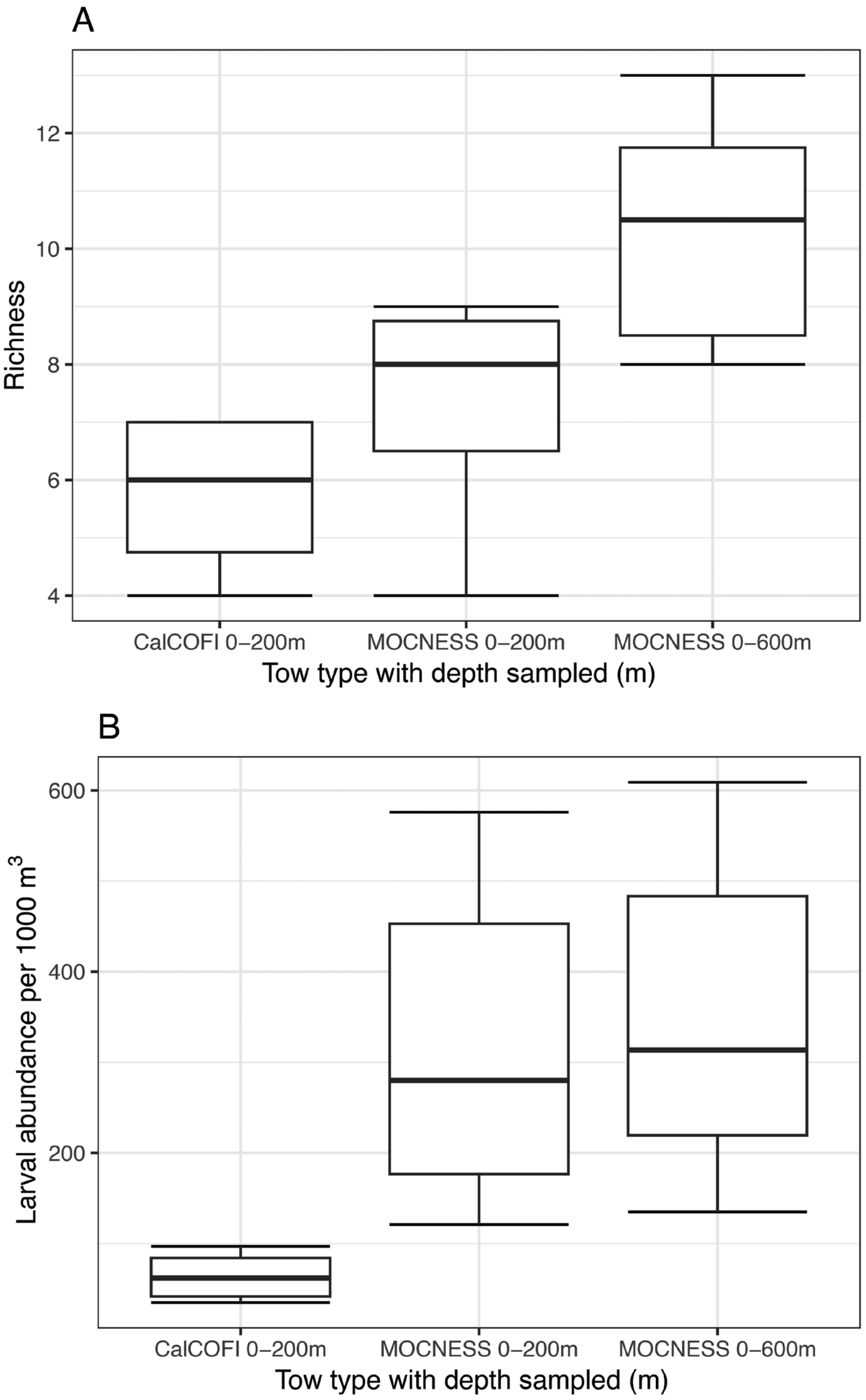

Figure 7

Box plots comparing (**A**) mean species richness and (**B**) mean larval standardized abundance by tow type and depth sampled for mesopelagic fish collected during the spring (16 April–4 May) 1984 California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise off the coast of central California. Samples were collected from Bongo tows (0–200 m) at the 4 selected stations and from the 6 Multiple Opening/Closing Net Environmental Sensing System (MOCNESS) tows in the epipelagic strata (0–200 m) and the epi- and mesopelagic strata (0–600 m). In each box plot, the black line in the middle is the median. The upper and lower parts of each box represent the first and third quartiles (25th and 75th percentiles). The whiskers extend above and below each box no more than 1.5 times the interquartile range.

and Aksnes, 1992; Contreras et al., 2020), and it is likely that juveniles have the sensory and physical abilities to avoid plankton nets (Kaartvedt et al., 2012). The remaining two-thirds are larvae and it is likely that their behavior, rather than solely patchiness, is an important contributor to the observed patterns. Our data are consistent with the hypothesis that the larvae exhibit both diel migration and avoidance behaviors, as many larval fishes are nektonic with directional swimming capabilities in the later ELHS (Leis, 2006).

Five of the 6 most abundant species (northern lampfish, California smoothtongue, blue lanternfish, popeye blacksmelt, and California flashlightfish) are considered diel vertical migrators in their juvenile and adult stages (e.g., Paxton, 1967; Cailliet and Ebeling, 1990; Neighbors and Wilson, 2006). Although the only significant species-specific model result supporting diel vertical migration was for northern lampfish, the distribution patterns of 3 other abundant diel vertical migrators suggest that this behavior may begin before the transition to juvenile stage. This is consistent with the idea that during ontogeny the larvae of these species begin to transition from larval to adult habitats and behaviors (Miller and Kendall, 2009).

Regardless of the time of day, the overall vertical abundance pattern of larval mesopelagic fishes was bimodal, with concentrations in either the shallow or deep strata, or both. A potential underlying cause of this pattern was revealed when we analyzed abundances per stratum by ELHS (Figs. 5 and 6, Suppl. Figs. 2 and 3). As expected, the majority of the early-stage larvae were in the productive upper epipelagic waters, a pattern that is well known for marine teleosts (e.g., Ahlstrom, 1959; Moser and Pommeranz, 1999; Miller and Kendall, 2009). Transforming larvae and juveniles were more abundant in the deeper strata, consistent with an ontogenetic shift to deeper waters.

The overall patterns of larval abundance and distribution in this data set were driven by northern lampfish, often the most abundant mesopelagic larval fish collected in the central and southern California Current System, especially during spring (Moser et al., 2001). Northern lampfish larval abundance was an order of magnitude higher than that of any other species in the MOCNESS samples.

Two studies utilizing similar sampling methods in the North Pacific found that the majority of fish larvae occur in one of 2 broad depth zones defined by physical features rather than at precise depths: (1) within the thermocline and upper mixed layer, or (2) below the thermocline (Ahlstrom, 1959; Loeb, 1979). In our study, the majority of the fish larvae occurred in the upper 50 m and the mixed layer was within 50 m of the surface during MOCNESS sampling (Fig. 3). Both the mixed layer and thermocline depths at the 4 CalCOFI stations were also in the upper 100 m (Fig. 3), which is consistent with the co-location of mesopelagic larvae and these physical features, both in the aforementioned studies and in descriptions of pelagic larvae in the same region (Moser and Watson, 2006).

The ocean depth at station 108 was 732 m, 132 m deeper than the lowest stratum sampled by the MOCNESS. Because we did not sample the entire water column, we have no data on the occurrence and abundance of mesopelagic ELHS in the deepest part of their potential habitat at this location. However, since larval fishes are primarily visual feeders (Hunter, 1980), the declining light levels at those depths likely make it difficult for them to avoid starvation. Therefore, it is unlikely that we missed a critical part of the distribution of larval mesopelagic fishes at this site.

Generally, we found that families showed a downward shift in the center of concentration of individuals during ontogeny, as has been shown in other studies of mesopelagic fishes (e.g., Ahlstrom, 1959; Loeb, 1979; Sassa et al., 2007; Moteki et al., 2009). Ontogenetic shifts in distribution may be linked to diel vertical migratory behavior in which organisms stay hidden at depth from visually orienting predators during the day and move up to more productive, shallower water at night to feed (Lampert, 1989). This diurnal movement of mesopelagic fishes and invertebrates is common in marine systems worldwide (Robison, 2003). As larvae grow and become more pigmented, the depth at which they remain hidden from visual predators naturally increases with decreasing light penetration (Job and Bellwood, 2000). There is a tradeoff between inhabiting shallow, productive waters, with higher food density, where light levels and predator pressure are highest, and deeper waters, where food and predators are less common (Fortier and Harris, 1989).

The 1-m^2 MOCNESS has a larger net opening than the Bongo (1 m^2 versus 0.4 m^2), and the range of volume filtered by the MOCNESS was broad (126–818 m^3), with the mean volume filtered comparable to that of the Bongo (337 m^3 versus 423 m^3), due to shorter towing time of the MOCNESS. The significant size difference in nets likely contributes to the higher abundance and richness captured by the MOCNESS, which is consistent with other findings comparing these gear types (Johnson and Fogarty, 2013).

Comparison of the deeper water column sampled by the MOCNESS suggests that there are ELHS of more species and higher larval abundance of mesopelagic fish below the epipelagic zone that may not be captured by standard CalCOFI-type ichthyoplankton sampling. Although CalCOFI was designed to sample larvae of coastal pelagic species, whose distributions are largely limited to the upper 200 m, rather than mesopelagic species, this implies that the overall diversity and abundance of larval mesopelagic species is under-sampled by the CalCOFI ichthyoplankton time series.

The use of larval fishes as a proxy for understanding some of the dynamics of adults is not new, but the vast majority of those practices utilize larval fish data from integrated water column net tows that sample within the upper 200 m. These studies can provide valuable information about marine ecosystems, such as spawning biomass estimates for use in stock assessments (e.g., Lasker, 1985; Hunter and Lo, 1993; Lo et al., 2010), importance of physical features (e.g., Moser and Smith, 1993; Asch and Checkley, 2013), and climate and environmental trends and changes (e.g., Moser et al., 1987; Brodeur et al., 2008; Hsieh et al., 2009). However, collecting larval fishes from integrated water column samples eliminates the ability to discern ecological differences related to depth and the dynamic habitats within the water column. Additionally, relatively few of these studies categorize larval fish species into their life-history stages (e.g., Moser and Ahlstrom, 1974; Leis et al., 2006; Irisson et al., 2010) and instead view them as one demographic category. The complexities of ontogeny for larval fish species include tremendous behavioral changes such as where they live in the water column, prey selection and capture, and predation avoidance. Many of these studies do not distinguish between day and night samples (e.g., Ahlstrom, 1969; Koslow et al., 2011), failing to account for the vertical migratory behavior of some mesopelagic fish larvae.

Given the global high abundance and biomass of mesopelagic fish species (Irigoien et al., 2014) and their importance in marine food webs (e.g., Ohizumi et al., 2003; Potier et al., 2007; Cherel et al., 2008), additional research is needed to more fully understand their role in the ecosystem. A critical component of this understanding is improved knowledge of these early life history dynamics.

Conclusions

We utilized a relatively small set of discrete depth (MOCNESS) samples to investigate patterns of ontogeny and habitat use in some of the most common and abundant species of mesopelagic fish species in the Northeast Pacific, with additional informative context from the CalCOFI ichthyoplankton and hydrographic data. A general pattern emerged for the mesopelagic species that are known migrators. The earliest stage larvae were in the upper epipelagic within or near the mixed layer and thermocline depths. Later stages were upper and middle mesopelagic with some qualitative evidence of diel migratory behavior beginning as early as the mid-larval stage. The presence of larval mesopelagic species in the mesopelagic zone suggests that sampling only the upper 200 m for larvae (e.g., using the standard CalCOFI sampling protocol) potentially misses a significant number of primarily later-stage larvae and additional species of larvae found at greater depths. Ichthyoplankton studies and key aspects of fisheries research primarily focus on the upper 200 m of the water column. This study shows that there is more to learn about the population dynamics by looking beyond the upper 200 m.

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