Title
Ontogenetic changes in the distribution and abundance of early life history stages of mesopelagic fishes off California

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Ontogenetic changes in the distribution and abundance of early life history stages of mesopelagic fishes off California

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Oceanography

by

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The Dissertation of Noelle Maria Bowlin is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

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DEDICATION

In memory of my good friend and colleague, Robert Emmett, for encouraging me to find my niche in fisheries science.

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Chapters 2, 3, and 4, in part, are currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of the material in all chapters of this dissertation.

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ABSTRACT OF THE DISSERTATION

Ontogenetic changes in the distribution and abundance of early life history stages of mesopelagic fishes off California

by

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Doctor of Philosophy in Oceanography

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Professor Philip Hastings, Chair

It is widely accepted that mesopelagic fishes are very abundant and maintain a high global biomass, but there exists a high degree of uncertainty in these biomass estimates. These fishes carry out all of their life stages in the water column and many undergo daily vertical migrations from the depths of the mesopelagic to the surface waters at night, returning to depth at dawn. This migratory behavior is one of the ecological factors that complicates our abilities to confidently evaluate the biomass of this group of fishes. Assessing the habitat use throughout ontogeny of mesopelagic fishes is a critical first step in understanding their role in the ecosystem. Additionally, the onset of diel vertical migration is relatively known for these fishes. Furthermore, larval fish identification is difficult and time consuming, and is often resolved only to the family level due to lack of taxonomic knowledge of species-specific ELH stages. Larval fishes

undergo profound changes during the early life history stages, therefore it is plausible that the earliest stages respond to environmental perturbations very differently than the later stages.

This dissertation is an examination of the importance of ontogenetic stage-specific investigation of larvae relative to habitat use. I describe the vertical distribution of ELH stages of the common mesopelagic fish species off central California by analysis of repeated tows of a discrete depth sampler, collected with a 1m^2 MOCNESS from the same station during both day and night. I determined that common species of mesopelagic fish larvae off central and southern California exhibit differences in their diel distributions and that there are substantially more species of mesopelagic fish larvae below the epipelagic zone. Investigation using a larger sample set of MOCNESS data collected in central and southern California confirmed that mesopelagic fish larvae are more deeply distributed than previously realized. The patterns suggested that DVM begins in the larval stages for some species, which is much earlier in development than previously described for species in this geographic region. I then describe the ontogenetic changes in abundance and horizontal distribution of common species of mesopelagic fish larvae affected by the extreme El Nino event in 1997-1998 followed by the La Nina in the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The results indicated that within the CalCOFI sampling area, mesopelagic fish species with an affinity for warm water conditions had a higher larval abundance and were closer to shore during the El Niño, and were less abundant and farther offshore during the La Niña. The opposite pattern was generally observed for mesopelagic fishes with an affinity for cold water conditions. Additionally, I discovered that the mesopelagic fish larval abundance in the CalCOFI region is dominated by the earliest stages of the larval period.

Finally, I discuss the conclusions of this dissertation that highlight the importance of ontogenetic habitat use patterns of mesopelagic fishes. Given their high global abundance, importance in the oceanic food web, and the potential for fisheries exploitation, this is an essential first step towards a reliable biomass assessments of mesopelagic fishes.

CHAPTER 1:

Introduction

Ontogenetic changes are especially profound for many marine fishes that begin life as pelagic eggs, develop through multiple larval stages, transform into juveniles, and ultimately grow into adults. Their life histories involve increases in swimming and foraging abilities, as well increases in body size by several orders of magnitude (Hunter 1975, Margulies 1989). While often considered as passive planktonic organisms (Hannan 1984), recent studies have shown that the larvae of reef fishes are much more capable and often have the ability to actively swim against currents, avoid predators, and select specific habitats (Leis 2006).

Details of habitat shifts throughout the transitions from eggs to larvae to juveniles and adults are well documented for some fishes such as the Atlantic cod (Tupper and Boutilier 1995), and California halibut (Moser and Watson 1990). However, habitat requirements for early life history stages as well as ontogenetic changes throughout early development are poorly known for most fishes, and virtually unknown for mesopelagic species.

Mesopelagic fishes, by definition (Weitzman 1997), occupy offshore areas above 1000 meters below the surface of the ocean where penetrable light fades to non-detectable levels. While mesopelagic fishes are found worldwide from the Arctic to the Antarctic, the highest annual production occurs in the tropics and subtropics (Gjøsaeter and Kawaguchi 1980). Mesopelagic fishes are generally not yet commercially exploited because of their sparse dispersion in the expansive mesopelagic zone (about 1 g/m^3), and possibly because of their high lipid content, but they are an important prey source for many commercial fishery species as well as marine mammals and birds (Lam and Pauly 2005). The global biomass of mesopelagic fishes was estimated at 945 million tons (g/m^2) in 1980 (Gjøsaeter and Kawaguchi) and later recomputed at 999 million tons (Lam and Pauly 2005). Recent studies that incorporate acoustic data (Irigoien et al. 2014) and net avoidance (Kaartvedt et al. 2012) conclude that current estimates are low by at least an order of magnitude.

Most mesopelagic fishes are small bodied (2-40 cm as adults), short-lived (one to several years), and exhibit low fecundity. They are broadcast spawners, producing hundreds to several thousand eggs that are found in the epipelagic. Newly hatched larvae inhabit the productive epipelagic zone and at some point, generally assumed to be as juveniles, move into deeper habitats in the mesopelagic (Moser 1996). Most mesopelagic fishes are zooplanktivores, but food availability in the mesopelagic zone is limited, thus, many species migrate vertically to the surface at night to the nutrient rich epipelagic where they feed primarily on copepods, and return to the mesopelagic at dawn. These daily vertical migrations are well-known for juveniles and adults of many species, but details of the development of this behavior are unknown. Recognition of the increased swimming abilities of larval fishes presents the intriguing possibility that these migratory behaviors and active habitat selection develop in the larval stage for some mesopelagic fish species.

Depth occurrences of many species of mesopelagic fishes have been described based on net sampling of juveniles and adults (Pearcy and Laurs 1966, Lavenberg and Ebeling 1967, Paxton 1967, Badcock and Merrett 1976, Frost and Mccrone 1979, Kinzer and Schulz 1985, Miya and Nemoto 1987, Beamish et al. 1999, Luo et al. 2000), but very few studies have investigated the depth distributions of the early life history (ELH) stages of these fishes (Loeb 1979, Sassa et al. 2007, Moteki et al. 2009, Sutton 2013). This type of detailed assessment requires discrete depth samples but the majority of ichthyoplankton studies have used integrated water column net tow samples. The development of the MOCNESS sampling device over-comes the inherent loss of depth of occurrence information that result from integrated tows (Wiebe 1976). Additionally, larval fish identification is difficult and time consuming, and is often only resolved to the family level due to lack of taxonomic knowledge of species-specific ELH stages (Hernandez et al. 2013). Thus early life history information for individual species is generally lacking.

In chapter 2, I describe the vertical distribution of ELH stages of the common mesopelagic fish species off central California by analysis of repeated tows collected with a 1m^2 MOCNESS from the same station during both day and night.

The occurrence of a significant abundance of mesopelagic fish larvae below the epipelagic zone led to a larger investigation of the relationship between ontogeny and habitat selection of the ELH stages of mesopelagic fishes. In Chapter 3, I employed a much larger set of MOCNESS samples collected in Central and Southern California.

Finally in Chapter 4 I examined the potential changes in ontogenetic distribution and abundance of mesopelagic fish larvae in the southern California Bight during a period of extreme environmental change. I analyzed the larval abundance time series data collected during the quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises during 1997, 1998, and 1999. During this time period, one of the strongest recorded El Niño events occurred between 1997-1998 (Bograd et al. 2000), followed by a La Niña event (1999-2002; Venrick et al. 2003).

The results of this dissertation contribute to our broader understanding of the complexity of the ELH stages of mesopelagic fishes in the California Current system and highlight the need to incorporate analyses of discrete stages of larval fishes rather than treating them as one demographic unit. A more complete understanding of the ELH stages of mesopelagic fishes is key as these species provide significant forage for a wide variety of oceanic species (e.g., Pitman and Ballance 1990, Ohizumi et al. 2003, Field et al. 2007, Potier et al. 2007, Robinson et al. 2012) and have increasingly been considered targets for increased fisheries exploitation (Smith et al. 2011).

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CHAPTER 2:

Mesopelagic fish ontogenetic distribution and abundance off central California

INTRODUCTION

Mesopelagic fishes carry out all of their life stages in the water column. Typical of broadcast spawners, they generally have buoyant eggs that hatch into larvae which inhabit the productive epipelagic zone, but move into deeper habitats as they mature (Moser 1996). While a variety of studies have described the vertical distributions of juvenile and adult mesopelagic fishes (e.g., Pearcy and Laurs 1966, Lavenberg and Ebeling 1967, Paxton 1967, Badcock and Merrett 1976, Frost and Mccrone 1979, Kinzer and Schulz 1985, Miya and Nemoto 1987, Beamish et al. 1999, Luo et al. 2000), relatively few have focused on stage-specific vertical distribution of early life history stages (Loeb 1979, Sassa et al. 2007, Moteki et al. 2009, Sutton 2013). Given the need to choose a habitat that optimizes the balance between foraging and predation, it is plausible that larval fishes, not just juveniles and adults, partition themselves in the water column.

The relationship between ontogeny and depth occurrences of mesopelagic fishes is poorly studied in part because commonly used sampling methods do not generally permit detailed assessment of vertical distributions of early life history (ELH) stages. This requires the use of discrete depth samples, but the majority of ichthyoplankton studies have employed integrated water column net tow samples (e.g., Wiebe 1976, Smith and Richardson 1977, Ohman and Smith 1995). Development of the Multiple Opening/Closing Net Environmental Sensing System or MOCNESS (Wiebe 1976) provides a convenient and powerful tool for taking biological samples from discrete depths. However, little is known regarding potential biases in MOCNESS sampling of mesopelagic ichthyoplankton.

The depth distributions of ELH stages of species of mesopelagic fishes are poorly known also because larval fish identification is difficult and time consuming, and is often resolved only to the family level due to lack of taxonomic knowledge of species-specific ELH stages (Hernandez et al. 2013). Moreover, species within the same family or genus are often assumed to behave similarly (Moser 1996, Sassa et al. 2007) but this assumption has not been widely tested.

Here, we aim to describe the vertical distribution of ELH stages of the common mesopelagic fish species off central California by analysis of repeated tows collected with a 1m^2 MOCNESS from the same station during both day and night.

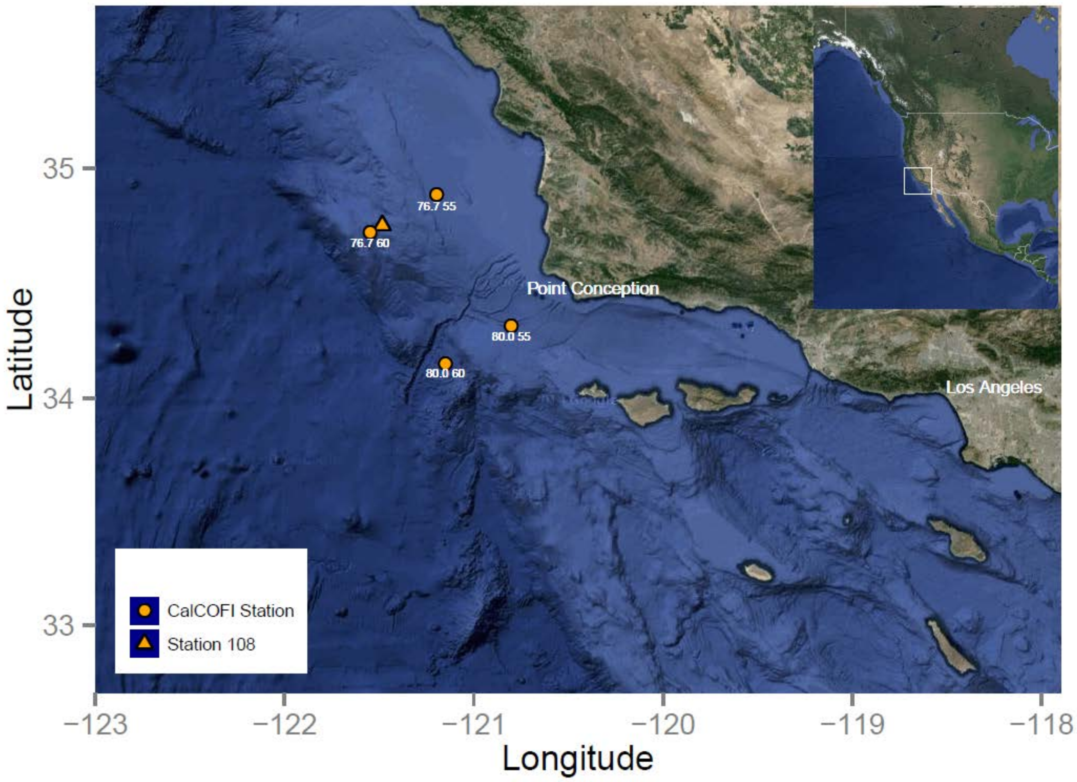

Figure 1:
Map of survey area. The MOCNESS samples were collected from Station 108 (34.755° N, 121.483° W); filled orange triangle. Ichthyoplankton time series data were analyzed from CalCOFI stations 76.7 55, 76.7 60, 80.0 55, and 80.0 60 (34.887° N, 121.197° W; 34.722° N, 121.548° W; 34.317° N, 120.802° W; 34.152° N, 121.15° W, respectively); filled orange circles.

METHODS

Field Sampling

A California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey (McClatchie 2013) was conducted 16 April – 4 May 1989 aboard the *R/V David Starr Jordan* near the coast of central and southern California. A MOCNESS was towed six times over station 108 (34.755° N, 121.483° W), about 80 kilometers northwest of Point Conception, California (Figure 1). The six replicate tows were conducted during a 24 hour period on 4 May 1989; three during the day and three at night. The MOCNESS had a 1 m^2 mouth opening with ten individual 0.505mm mesh nets, nine of which collected discrete depth samples and one that collected an integrated water column sample. The MOCNESS nets were consistently towed at a speed of 2-2.5 knots and discrete samples (nets) were collected from eight depth strata: 0-50, 50-100, 100-150, 150-200, 200-300, 300-400, 400-500, and 500-600 meters. The MOCNESS was towed such that the net frame angle was 45°±8°. The net vertical velocity averaged 16m min^{-1} for the shallow strata (0-200m) and 10m min^{-1} for the deeper strata (200-600m). Volume of filtered seawater, and depth data were also collected by the MOCNESS. Once onboard, the nets were washed and samples were preserved in 5% formalin buffered with sodium borate.

To provide a contextual guide for the fishes collected in the MOCNESS samples, we analyzed ichthyoplankton time series data from four stations occupied by the spring CalCOFI surveys for a period of ten years, including the 1989 survey when the MOCNESS samples were collected. The ichthyoplankton time series samples were collected using a Bongo net with a 0.505mm mesh net, lowered to approximately 200 meters depth, towed at a speed of 1.5-2 knots with an angle of stray of 45°±8° and a vertical velocity of 20m min^{-1} as described in by Kramer (1972) and Smith and Richardson (1977). The geographic locations of the CalCOFI samples used for comparison were chosen by determining the stations in the area that most resembled the environment where the MOCNESS samples were collected. Analysis of hydrographic time series data from the same ten year period, collected by CTD Seabird SBE-19 vertical casts to 500 meters or within 10 meters of the bottom in shallow areas in the

CalCOFI survey area resulted in the four stations we used for analysis (76.7 55, 76.7 60, 80.0 55, and 80.0 60; Figure 1).

Laboratory Work

All fish larvae were sorted, enumerated, identified to the lowest possible taxon, and assigned to a life-history stage as defined by Kendall (1984). This includes yolk-sac stage (with a visible yolk sac), preflexion stage (after the yolk is fully absorbed 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, approximately 45 degrees from the notochord axis, to metamorphosis), transformation (loss of larval characters to start of juvenile stage), and juvenile (development of juvenile/adult characters such as full complements of fin rays and pigment or photophore patterns). In this study yolk-sac larvae were not included in the analysis due to the paucity of specimens. Preflexion (PREF), flexion (FLEX), postflexion (POST), transforming (TRNS), and juvenile (JUVE) stages were all included in the analysis.

Data Analysis

CTD data from the spring CalOFI surveys were integrated over the water column for each cast, for each of five physical variables: temperature (°C), salinity (psu), potential density (kg m^{-3}), chlorophyll-a concentration (µg/L), and oxygen concentration (ml L^{-1}), for the ten year period 1984-1994 (Figure 2). The potential density data were further analyzed to calculate time series of the mixed layer depths at these four stations (Figure 3). Stations nearest to MOCNESS station 108 were selected for the ichthyoplankton analysis. At the four selected stations (Figure 1) ichthyoplankton time series data from the spring CalCOFI surveys were used to analyze the number of species and larval abundance of mesopelagic species. These data were compared to the mesopelagic fish larvae collected in the six MOCNESS tows at station 108 in two depth categories: the upper 200 meters of the water column, and the entire depth distribution sampled by MOCNESS (0-600m). The shallow category was chosen because the CalCOFI data are from the same depth stratum (0-200m), thus providing a direct comparison of the mean number of larval mesopelagic fish species and mean abundance collected by the MOCNESS. The deep category (0-600m) provides a snapshot comparison of larval mesopelagic fish distribution in the epipelagic vs epi- and upper mesopelagic zones.

For the analysis of the MOCNESS data, a sampling unit was defined as the mesopelagic fishes collected in each net, per depth stratum, per station.

Generalized linear models were built to test the following hypotheses: (i) there are day and night differences in the mean number of mesopelagic fish species between the depth strata, (ii) there are day and night differences in the overall abundance of mesopelagic fishes between the depth strata and these differences are driven by the most abundant species, (iii) the most abundant species exhibit ontogenetic depth stratification, (iv) species within the same family have a common pattern.

For the first hypothesis (i) we set the following model,

$$E(count_{\#spp}) = depth\ stratum + time\ of\ day + depth\ stratum * time\ of\ day, \qquad (1)$$

where $count_{\#spp}$ is the number of mesopelagic fish species found in each sample, $depth\ stratum$ is a factor depicting the sample depth as explained in the Field Sampling section, and $time\ of\ day$ is a binary variable indicating if the samples were collected at night or during the day. The operator $*$ indicates that the two predictor variables were fit with interactions as in a two-way ANOVA model. The model was fit using a Gaussian error distribution for the response variable.

For hypothesis (ii) we set the following model,

$$E(count_{all\ spp}) = g^{-1}(offset(\log(water\ volume)) + depth\ stratum + time\ of\ day + depth\ stratum * time\ of\ day), \tag{2}$$

where $count_{allspp}$ is the abundance of all mesopelagic larvae and mesopelagic juveniles found in each sample, $offset(\log(water\ volume))$ is the logarithm of the volume of the water filtered in each sample fitted in the model with a coefficient of 1, $depth\ stratum$ and $time\ of\ day$ as defined in equation (1). The model was fit in a generalized linear model framework, using a Poisson error distribution for the counts, and the logarithmic link function $g()$.

Having found significant differences between day and night in the above model, we pursued subsequent analyses separately for each period. The following model was applied to the six most abundant species for hypothesis (iii).

$$E(count_{sp}) = g^{-1}(offset(\log(water\ volume)) + depth\ stratum + stage + depth\ stratum * stage), \tag{3}$$

where $count_{sp}$ is the number of specimens for each of the six most abundant species, $stage$ is the respective life history stage, and the other parameters are the same as described for equation (2). The fitting of this model attempted to infer if fish of different stages occupy different strata in day and night samples.

Counts of all species except for the two most abundant were combined by family for hypothesis (iv) and the following model was fit for the day and night samples and used to infer if there is a common pattern within the three most abundant families in the vertical stratification of stages.

$$E(count_{family}) = g^{-1}(offset(\log(water\ volume)) + depth\ stratum + stage + depth\ stratum * stage), \tag{4}$$

The Poisson distribution was used for all models in which the response variable was counts, as recommended for biological census data (Kabacoff 2011). The Guassian distribution was used for the model of the number of species. The model assumptions of independence and homogeneity of residuals were verified by diagnostic plots (McCullagh and Nelder 1989) and the p-value for significance was set at 0.05.

RESULTS

Laboratory Work

A total of 774 fishes was collected in the six replicate MOCNESS tows. Demersal species accounted for 6% of the specimens (48 individuals) from four families: Gobiidae, Paralichthyidae, Pleuronectidae, and Scorpaenidae. The remaining 94% or 726 specimens were mesopelagic species, of which seven individuals could only be identified to the family level (Myctophidae) and the remaining 719 to species. For the rest of the paper, only mesopelagic species are considered. The mesopelagic specimens were representatives from nine families: Bathylagidae, Gonostomatidae, Melamphaidae, Microstomatidae, Myctophidae, Platytroctidae, Scopelarchidae, Sternoptychidae, and Stomiidae. The six most abundant mesopelagic species constituted 91% of the specimens and represent three families (Table 1). The two most abundant species *Stenobrachius leucopsarus* (Myctophidae) and *Cyclothone signata* (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 four most abundant species, *Leuroglossus stilbius* (Bathylagidae), *Tarletonbeania crenularis* (Myctophidae), *Lipolagus ochotensis* (Bathylagidae), and *Protomyctophum crockeri* (Myctophidae), together accounted for 16% of the mesopelagic specimens. The remaining 9% included 19 species from all nine families.

Juvenile stage fishes were the most abundant (37%), followed by preflexion (22%), flexion (17%), postflexion (17%), and transformation (7%). The majority of the juvenile stage fishes (238/270 or 88%) were *Cyclothone signata*, the second most abundant species, and the majority of the preflexion stage fishes (128/159 or 81%) were *Stenobrachius leucopsarus*, the most abundant species.

Daytime tows yielded a higher abundance of mesopelagic fishes than the nighttime tows (Table 2). The three daytime tows each had a total of 133, 147, and 138 specimens, respectively. The nighttime tows had smaller totals of 132, 96, and 80 specimens, respectively. All six tows had the majority of the specimens in the shallow and deep strata, with very few specimens in the middle strata.

Table 1:
Counts of individual mesopelagic fish species collected per ontogenetic stage. The distribution of the six most abundant species collected in the MOCNESS samples (those above the dashed line) were analyzed separately.

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

Table 2:
Counts of individual mesopelagic fishes collected in each depth stratum from each of the 3 replicate daytime (108c, 108d, 108e) and nighttime (108a, 108b, 108f) MOCNESS tows.

	DAY			**NIGHT**		
Depth (m)	108c	108d	108e	108a	108b	108f
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

Data Analysis

The mean number of species of mesopelagic fish larvae collected at MOCNESS station 108 in the upper 200 meters (7 species) was the same as the number of species in the CalCOFI bongo tow collected on the same 1989 cruise at the nearest station, 76.7 60 (7 species) and was generally comparable to the time series of the number of species for all four stations (Figure 4). Larval abundance for both depth categories (0-200m and 0-600m) of the MOCNESS were slightly below the abundance collected at the nearest CalCOFI station (76.7 60) and slightly below (0-200m) and above (0-600m) the abundance at the next nearest station (76.7 55). Although the larval abundance time series was highly variable, the MOCNESS mean abundances for both categories were generally comparable (Figure 5).

Comparison of the three day and three night MOCNESS samples revealed no significant differences in number of mesopelagic species collected (hypothesis (i), equation 1). The time of day did not make a difference in the number of species within each stratum, but the actual strata did (Appendix A, Table 1). The number of species was highest in the shallow (0-100m) and deep (400-600m) strata, and lowest in the middle strata (Figure 6).

The model results of the comparison of the overall abundance of all mesopelagic fishes (hypothesis (ii), equation 2) indicate that abundance in each stratum differed significantly from that in one or more other strata, with significant interactions between some strata and time of day (Appendix A, Table 2). The interaction terms negate the ability to effectively describe the main effects of each of the parameters (Kabacoff 2011), but the results suggest that depth in the water column had the largest influence on abundance with the influence of time of day detectable in some strata. Similar to the number of species results, the pattern of overall abundance revealed a bimodal distribution with the greatest abundances in the shallow strata and a smaller increase in the deep strata (Figure 7). A further look at these two modes reveals a pattern with the early stages in the shallow strata and the later stages in the deep strata (Figure 7).

Further investigation of species-specific patterns of ontogenetic stratification (hypothesis (iii), equation 3) led to significant results for the most abundant species, *S. leucopsarus*, for both depth and stage parameters, as well as a significant interaction term (Appendix A, Tables 3 and 4). The interaction terms compromise our ability to tease apart the main effects of the model parameters but the distribution of early stage *S. leucopsarus* larvae are clearly contained within the two shallowest strata (0-50 and 50-100m) with the relatively few later stage individuals in the lowest three strata (300-600m) for both day and night samples (Figure 8). Analysis of the second most abundant species

(*C. signata*) did not produce any significant results (Appendix A, Tables 5 and 6). Early stages of *C. signata* were not present in these samples, but later stage individuals were, primarily in the lowest three strata (300-600m) (Figure 8). Model analysis of the next four most abundant species (*L. stilbius*, *T.crenularis, L. ochotensis*, and *P. crockeri*) did not reveal any significant results in time of day or depth stratum (Appendix A, Tables 7-14). Although not statistically significant, each species had a qualitatively different pattern of vertical distribution.

Leuroglossus stilbius early stage larvae were in the two shallowest strata during the day (0-50 and 50-100m) and a little deeper at night (50-150m) (Figure 8). The postflexion larvae inhabited the deeper strata (150-600m) during the day, but were only found in shallow strata at night (50-150m). With the exception of a few specimens near the surface (0-50m) during the day, the transforming larvae were deep in the water column both day and night (400-600m).

The fourth most abundant species, *Tarletonbeania crenularis*, remained almost entirely in the upper water column (0-150m) both day and night (Figure 9). Preflexion and flexion larvae were in the 0-100m range and postflexion larvae were a little deeper in the 50-150m range. While preflexion and flexion larvae were concentrated in the shallowest strata, postflexion larvae appear to concentrate in the shallowest strata (0-50 and 50-100m) during the day, then shift downward, or spread out at night.

Both *L. ochotensis* and *P. crockeri* were fifth in species abundance. The distribution patterns for these two species are not as clear as they are for the four most abundant species, probably due to their relatively low counts (Figures 9). Preflexion and flexion stage *L. ochotensis* larvae were found in the three shallowest strata (0-150m), postflexion stage larvae in the deep strata (300-600m), and a few transforming specimens deep during the day (500-600m) and mostly shallower at night (100-200m). *Protomyctophum crockeri* preflexion and flexion stage larvae were in the two shallowest strata (0-100m), postflexion stage larvae had a broad range (50-600m), and transforming larvae were found in the deepest two strata (400-600m).

To explore whether the two most abundant species were driving the observed patterns (hypothesis (iii)), we removed both species from the analysis (equation 2). This provided significant results similar to the analysis that included *S. leucopsarus* and *C. signata*: there was a significant stratum effect on abundance, with a significant interaction between the stratum and time of day (Appendix A, Table 15). The general pattern still held, with the majority of early stage individuals in the shallow strata and later stage individuals in the deep strata, but the daytime distribution has a secondary peak of postflexion stage larvae in middle stratum at 150-200m (Figure 10).

The model analysis of the three most abundant families (Myctophidae, Gonostomatidae, and Bathylagidae) without the two most abundant species (*S. leucopsarus* and *C. signata*) did not reveal any significant differences between depth strata or life-history stages for the day or night samples (equation 4; Appendix A, Tables 16-21). The significant results from the models that included the two most abundant species were most likely due to the overwhelming abundance of those fishes.

Although not statistically significant, the distributions of myctophids (other than *S. leucopsarus*) appear to differ between day and night and were thus similar to the most abundant myctophid (hypothesis (iv); equation 4; Figure 11). During the day the preflexion, almost all flexion, and most of the postflexion larvae are in the two shallowest strata (0-50 and 50-100m), with the remaining postflexion larvae deeper in the water column. At night it appears as though many individuals of those stages move up to shallower strata.

Preflexion and flexion stage gonostomatids were not collected in these MOCNESS samples (Figure 11). All (excluding *C.* signata) were collected below 150m, regardless of day or night. Postflexion stage had the shallowest distribution (150-200m) of this group and was collected only during the day. The few transformation specimens were in the next deepest stratum (200-300m) and only collected at night, while all juveniles were found below 300m day and night.

Distributions of all stages of bathylagids appear to be centered somewhat deeper during the day, moving closer to the surface at night (Figure 11). During the day postflexion larvae are present in all strata below 150m and absent from the waters above. At night some postflexion larvae are in shallower water (50-150m), absent in the middle strata, and again present in deeper water (300-600m).

Although the MOCNESS fishes were collected down to 600m, the CTD Seabird SBE-19 vertical cast hydrographic data were collected from 0-500m depth. The oxygen profile shows the presence of an oxygen minimum zone near 500m. We do not have hydrographic data deeper than 500m, but from the appearance of the trend, it is likely that the oxygen minimum zone extended below 500m into the deepest stratum sampled by the MOCNESS.

DISCUSSION

This study revealed a reoccurring pattern of highest concentrations of ELH stages of 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 the number of species and ontogenetic stage abundance.

The number of species and the overall abundance of mesopelagic fish larvae collected in the upper 200m of the water column by the 1m^2 MOCNESS were comparable to the CalCOFI ichthyoplankton time series values (Figures 4 and 5). Comparison of the entire water column sampled by the MOCNESS suggests that there are ELH stages of more species below the epipelagic zone that are potentially not captured by standard CalCOFI-type ichthyoplankton sampling.

Our results also provide evidence of the repeatability of samples using the 1m^2 MOCNESS for the number of species of mesopelagic fishes. The number of species within the defined depth strata was comparable in both day and night samples across all tows (Figure 6). The abundance of all mesopelagic species differed significantly between day and night samples (Figure 7). This could be the result of net avoidance (Margulies 1989), patchiness, diel movements, or a combination of these potential factors. Many mesopelagic fishes are known to exhibit diel vertical migration during the juvenile stage (Clarke 1973, Nafpaktitis et al. 1977, Giske and Aksnes 1992, Moser 1996, Salvanes and Kristoffersen 2001, Sassa et al. 2002). It is also possible that juveniles have the sensory and physical abilities to avoid plankton nets (Margulies 1989, Moser and Watson 2006, Kaartvedt et al. 2012). Juvenile fishes are about one-third of the mesopelagic specimens in this study. Therefore, the remaining two-thirds are larvae and it is likely that their behavior is an important contributor to the observed patterns. It is unlikely that patchiness is the only contributor to the larval abundance and distribution patterns. Patchiness is a likely contributor to the differences in abundance among the replicate tows, but this is not to be confused with behavior (Wiebe et al. 1982). It is possible that the larvae exhibit both diel migration and avoidance behaviors, as many larval fishes have been described as nektonic with directional swimming capabilities in the later ELH stages (Leis 2006).

Five of the six most abundant species (*S. leucopsarus, L. stilbius, T. crenularis, L. ochotensis,* and *P. crockeri*) have been described as diel vertical migrators in their juvenile and adult stages (e.g., Pearcy and Laurs 1966, Paxton 1967, Cailliet and Ebeling 1990, Neighbors and Wilson 2006). Although the only significant species-specific model result was for *S. leucopsarus*, the distribution patterns of three of the other abundant diel vertical migrators suggest that this adult behavior may begin in earlier life-history stages. *Leuroglossus stilbius* postflexion larvae were found in the deeper strata (150-600m) during the day in contrast to the shallow strata at night (50-150m) (Figure 8). Although fewer in number, *Lipolagus ochotensis* transforming stage larvae likewise were only found in the deepest stratum (500-600m) during the day and shallower at night (100-200 and 400-500m) (Figure 9). *Protomyctophum crockeri* postflexion larvae were more abundant in the shallow water (above 150m) at night than during the day (Figure 9). *Tarletonbeania crenularis* larvae did not have distribution patterns suggesting earlier life-history stage diel vertical migration. However, only preflexion and flexion stage larvae were found in the shallowest stratum (0-50m), while all later stage specimens were found below 50 meters (Figure 9). This is consistent with the idea that as larvae of these species progress through ontogeny, they begin to transition to their adult habitats (Miller and Kendall 2009).

The sample size for most species collected in this study is low and therefore yields low statistical power. This is probably the reason that there were only a few significant model results which included the tests of overall mesopelagic fish abundance with and without the two most abundant species between depth strata in the day and night samples (equation 2; Figures 4, 5, 12, and 13). In addition the only significant species-specific model testing for ontogenetic differences in habitat was for *S. leucopsarus* (the most abundant species) in day and night samples (equation3; Figure 8).

This study provides information regarding the relationship between ontogeny and the diel vertical movements of larvae that inhabit the epipelagic zone. Regardless of day or night, the overall abundance of larval mesopelagic fishes was bimodal, concentrated in either the shallow or deep strata. A potential underlying cause of this pattern is elucidated when we analyze abundances per stratum by ELH stages (Figures 7 and 10). As expected, the majority of the early stage larvae were in the productive near-surface epipelagic waters, a pattern that has been well studied and described for marine teleosts (e.g., Ahlstrom 1959, Moser and Ahlstrom 1974, Kendall et al. 1984, Miller and Kendall 2009). Transforming and juveniles were more abundant in the deeper strata, consistent with an ontogenetic shift to deeper waters with growth.

The overall patterns of larval abundance and distribution in this data set were driven by the presence of *S. leucopsarus,* which is commonly the most abundant mesopelagic larval fish collected in the central and southern California Current System (Moser 2001). *Stenobrachius leucopsarus* larval abundance was an order of magnitude higher than that of all other species in the MOCNESS samples. This relatively high abundance clearly contributed to the significant species-specific model results for *S. leucopsarus*.

The 1m^2 MOCNESS is designed to collect plankton (Wiebe 1976, Wiebe et al. 1985) but the samples in this study contained a large proportion of juvenile fishes mostly represented by *C. signata* (Figure 8). Few larval *C. signata* were present in the samples, all of which were late stages, most likely because this species generally spawns farther offshore and not in the spring when these samples were taken (Moser 1996, Moser 2001). However, given the ability of juveniles to avoid the MOCNESS and other plankton nets (Kaartvedt et al. 2012), the collection of a relatively high number of *C. signata* with a plankton net suggests that there were many more juvenile *C. signata* in the study area, which is consistent with other observations that members of this genus are among the highest in abundance and biomass of marine fishes in the world (Gjøsaeter and Kawaguchi 1980, Lam and Pauly 2005).

Cyclothone signata juveniles remained in the deeper strata both day and night, which is consistent with other studies that describe this species as a non-vertical migrator (Kobayashi 1981, Miya and Nemoto 1991). Juveniles occurred primarily at depths with oxygen concentrations below 2 ml/L, near the threshold for hypoxia (e.g., Vaquer-Sunyer and Duarte 2008) and into the deepest strata sampled which corresponded with an oxygen minimum zone. These fish are thought to inhabit depths with lower oxygen as a refuge from predators that cannot exist in such extreme environments (Robison 1972, Douglas et al. 1976, Lampert 1989).

Two studies utilizing similar sampling schemes in the north Pacific found that the majority of fish larvae occur in one of two broad depth zones defined by physical features rather than precise depths: (1) within the thermocline and upper mixed layer, or (2) below the thermocline (Ahlstrom 1959, Loeb 1979). In both of those studies, the thermocline and upper mixed layer were within 100m of the surface. In the present study the majority of the fish larvae occurred in the upper 100 meters of the water column while the mixed layer at the two nearest stations was near 20 meters depth (Figure 3). Although the time series of mixed layer depth occurrence at the four CalCOFI stations is also in the upper 100 meters of the water column, not much can be inferred from these data. The MOCNESS depth strata might be too course to glean any useful mechanistic information from the mixed layer depth occurrence.

The ocean depth at station 108 was 732 meters, 132 meters deeper than the lowest stratum sampled by the MOCNESS. Because we did not sample the entire depth distribution available to the mesopelagic fishes at this location we may have missed the lowest part of their depth distribution. However, the deepest sampled stratum (500-600m) corresponded with an oxygen minimum zone which is seemingly a refuge for later stage fishes, such as *C. signata*, but is likely uninhabitable for early stage larvae because they are not physiologically equipped to thrive in low oxygen (O'Connell 1981). Additionally, larval fishes are primarily visual feeders, and with little to no light that deep, it would be difficult to avoid starvation. Therefore, even though we did not sample the entire water column at station 108, we probably did not miss a critical component of the distribution and abundance of larval mesopelagic fishes at this site.

Generally we found that families showed a downward shift in distribution of the center of concentration of individuals during ontogeny which is consistent with other studies of mesopelagic fishes (Ahlstrom 1959, Loeb 1979, Sassa et al. 2007, Moteki et al. 2009). Ontogenetic shifts in distribution may be linked to the most common explanation for diel vertical migratory behavior in which organisms stay hidden at depth from visually orienting predators and go up to shallower water at night to feed (Lampert 1989). As larvae grow larger and develop more pigment, the depths at which they remain “hidden” from predators naturally increase with the decrease of light penetration (Job and Bellwood 2000). There is a tradeoff between inhabiting shallow, productive waters, with higher food density, where light levels are highest, and deeper waters, where food and predators are less common (Fortier and Harris 1989).

The use of larval fishes as a proxy for understanding the dynamics of adult populations is not a new concept, but the vast majority of those practices utilize larval fish data from integrated water column net tows that sample the upper 200 meters. These studies have provided valuable information about the marine ecosystem in areas such as spawning biomass and stock assessment estimates (e.g., Hewitt 1985, Lasker 1985, Hewitt 1988, Hunter and Lo 1993, Lo et al. 2010), physical features (e.g., Moser and Smith 1993, Koslow et al. 2011, Asch and Checkley Jr 2013), and climate and environmental trends and changes (e.g., Moser et al. 1987, Smith and Moser 2003, Hsieh et al. 2005, Brodeur et al. 2008, Hsieh et al. 2009). However, relatively few studies differentiated larval fishes by their life-history stages and instead viewed them as one demographic category (e.g., Moser and Ahlstrom 1974, Margulies 1989, Leis et al. 2006, Irisson et al. 2010).

Given the global high abundance and biomass of mesopelagic fishes and their importance in the food web (e.g., Pitman and Ballance 1990, Ohizumi et al. 2003, Field et al. 2007, Potier et al. 2007, Cherel et al. 2008), additional research is needed to explain their role in the ecosystem.

This study shows the importance of discrete depth sampling and fine scale taxonomic identifications for understanding the ontogenetic patterns of habitat use in ELH stages of mesopelagic fishes.

We utilized a relatively small set of MOCNESS samples to investigate patterns of ontogeny and habitat use in some of the common species of mesopelagic fishes in the northeast Pacific. Additional discrete depth samples are needed with greater abundances, greater geographic coverage, more seasons, more years, and more corresponding physical data to achieve a better understanding of mesopelagic fishes in the marine ecosystem.

Chapters 2, 3, and 4, in part, are currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of the material in all chapters of this dissertation.

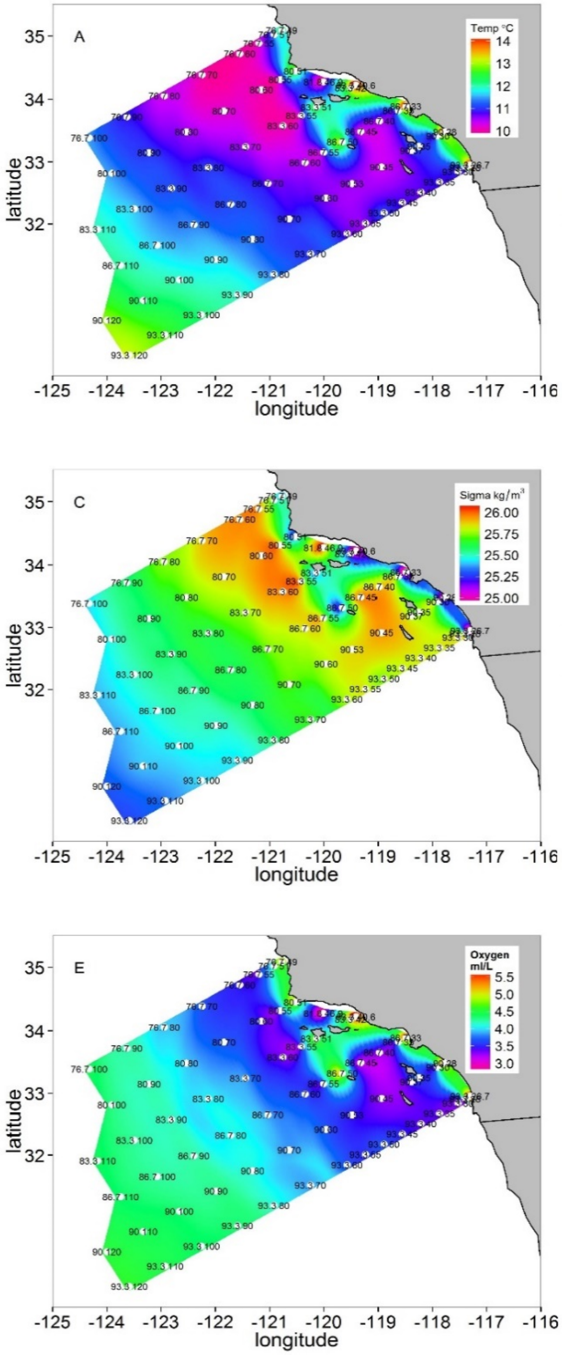

Figure 2:
CTD casts from the spring CalOFI surveys integrated over the water column for each cast, for each of five physical variables: temperature (A), salinity (B), potential density (C), chlorophyll-a concentration (D), and oxygen concentration (E), averaged over the ten year period 1984-1994.

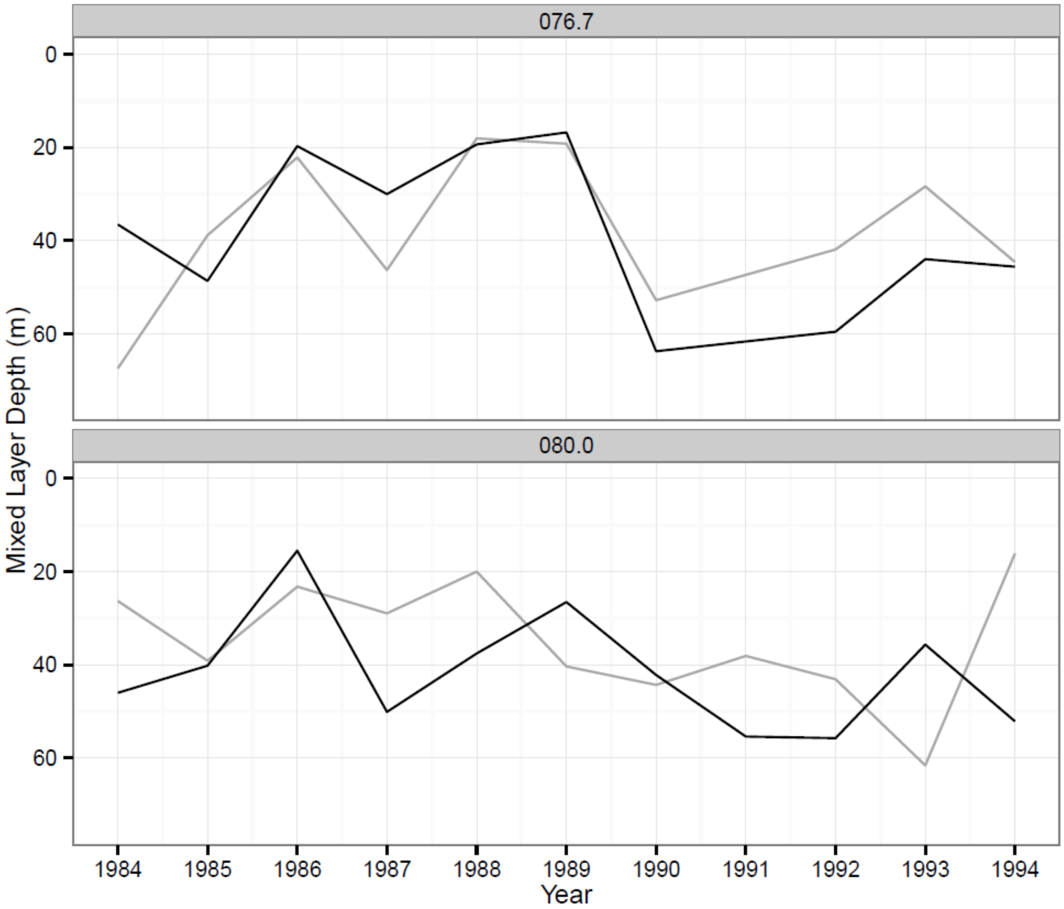

Figure 3:
CalCOFI time series of mixed layer depth at four selected stations from 1984-1994. Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey line, bottom panel; 80.0 60 = black line, bottom panel.

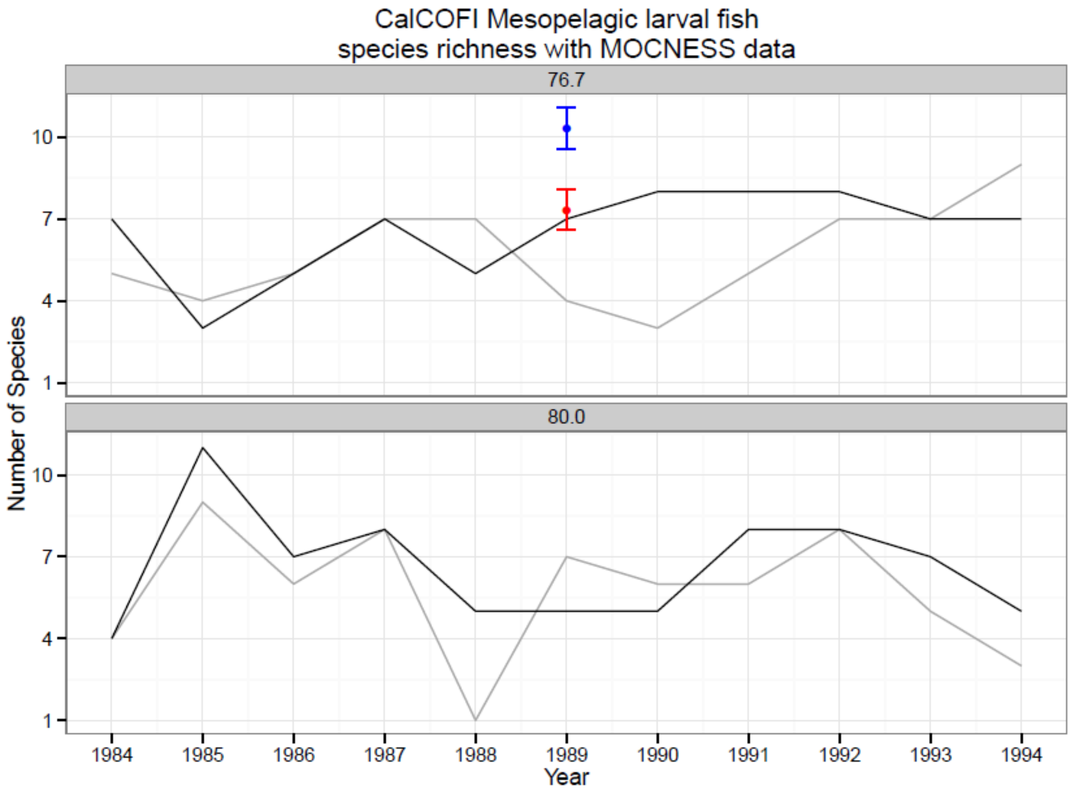

Figure 4:
CalCOFI time series of the number of mesopelagic fish larvae species at four stations from 1984-1994. Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey line, bottom panel; 80.0 60 = black line, bottom panel. MOCNESS mean number of species with 95% confidence intervals at station 108 from 0-200m depth (red point with error bars), and from 0-600m depth (blue point with error bars).

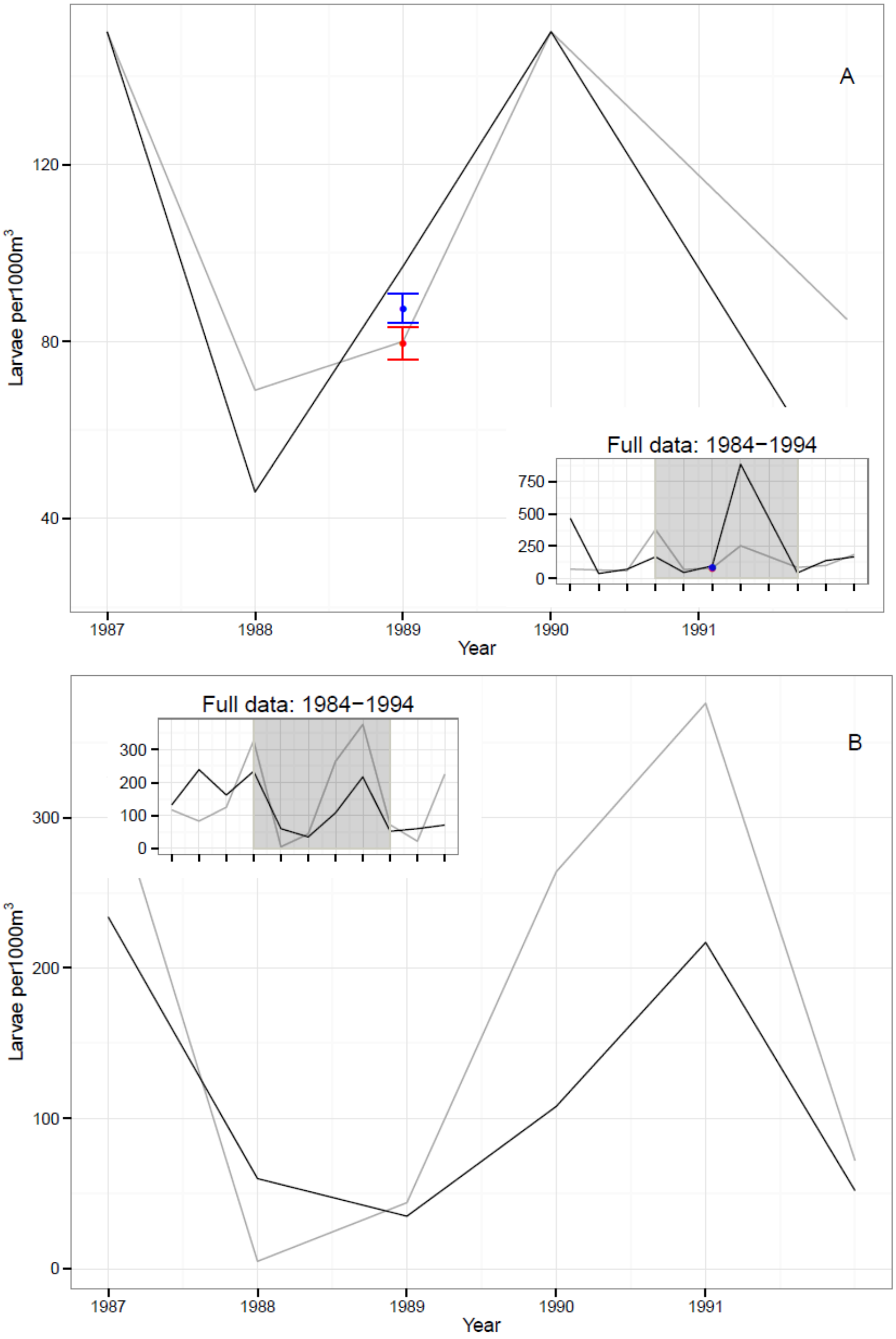

Figure 5:
CalCOFI time series of mesopelagic fish larval abundance at four stations from 1987-1991 (main graphs A and B) and 1984-1994 (inset graphs A and B). Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey line, bottom panel; 80.0 60 = black line, bottom panel. MOCNESS mean larval abundance with 95% confidence intervals at station 108 from 0-200m depth (red point with error bars), and from 0-600m depth (blue point with error bars).

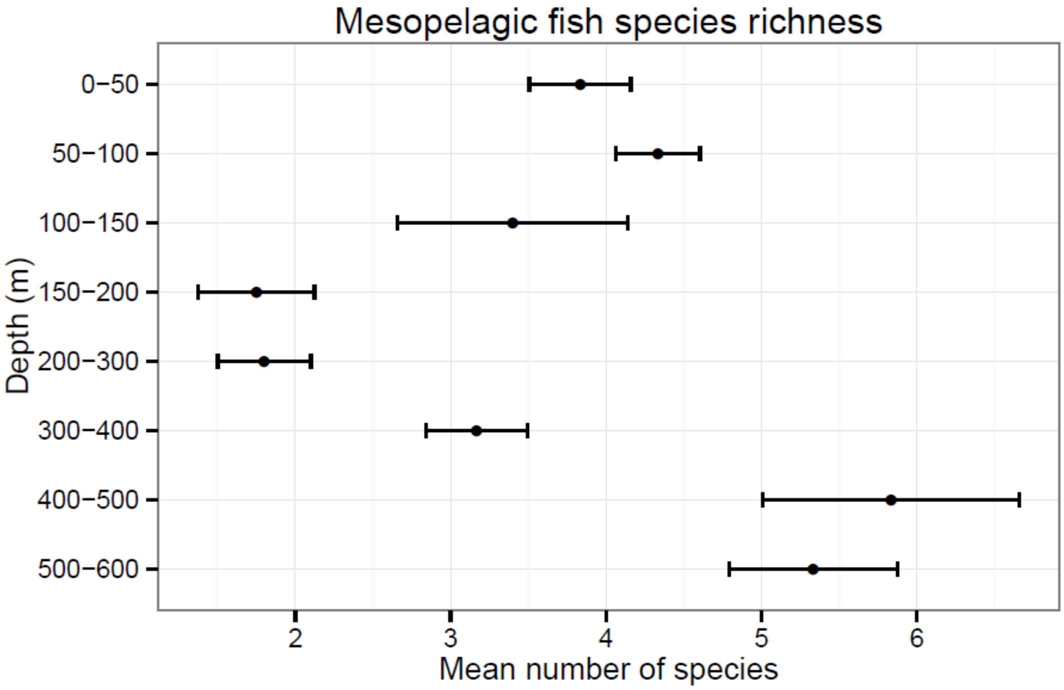

Figure 6:
Mean number of mesopelagic fish species collected in each of the eight depth strata for six MOCNESS tows at station 108 (day and night samples combined) with 95% confidence intervals.

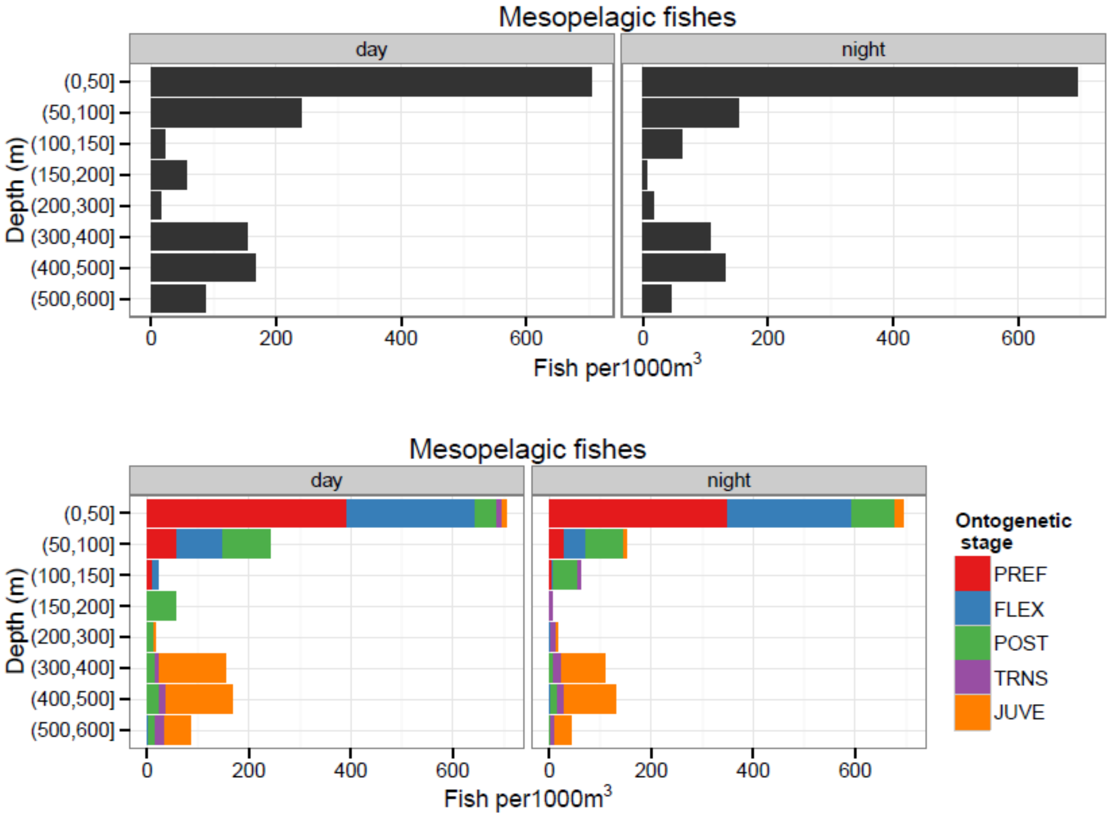

Figure 7:
Distribution and abundance of mesopelagic fishes collected from day and night MOCNESS samples from Station 108 (top panel). Stage-specific distribution and abundance of all mesopelagic fishes collected in the day and night MOCNESS samples from Station 108 (bottom panel). PREF=preflexion, FLEX=flexion, POST=postflexion, TRNS=transformation, JUVE=juvenile.

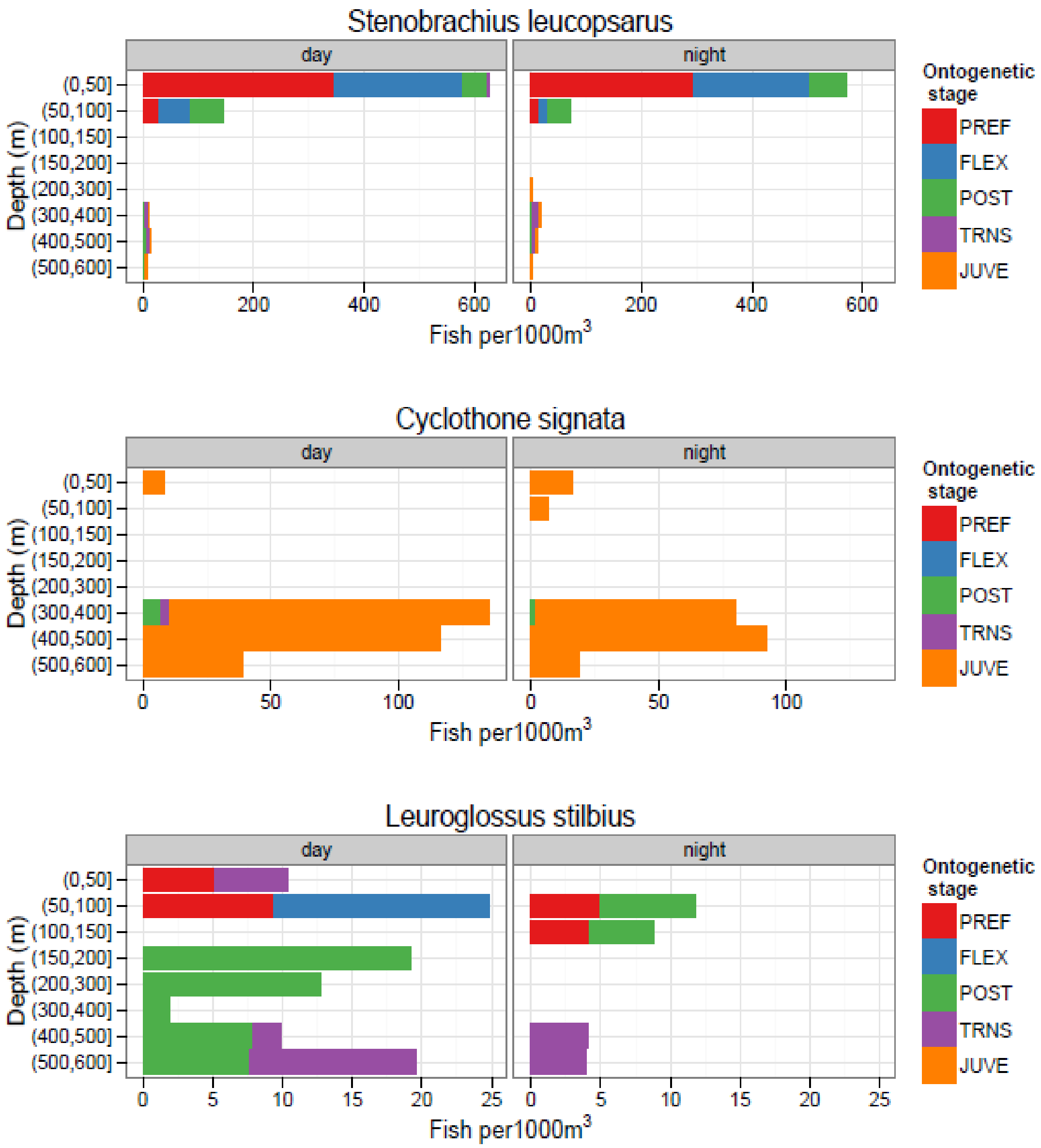

Figure 8:
Stage-specific distribution of the most abundant species of mesopelagic fish (*Stenobrachius leucopsarus*), the second most abundant species (*Cyclothone signata*), and the third most abundant species (*Leuroglossus stilbius*) collected in the day and night MOCNESS samples from Station 108.

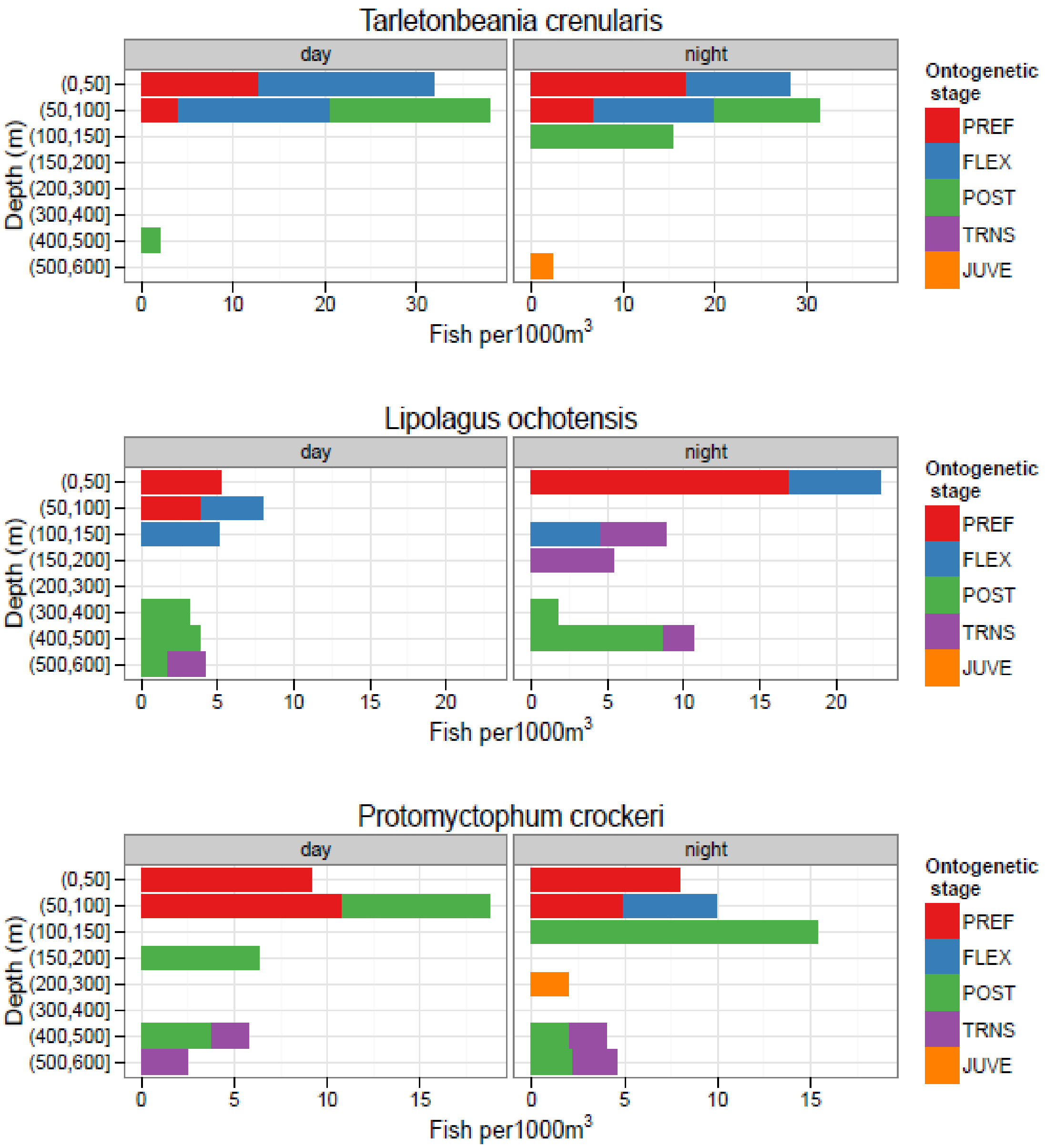

Figure 9:
Stage-specific distribution of the fourth most abundant species of mesopelagic fish (*Tarletonbeania crenularis*), the fifth most abundant species (*Lipolagus ochotensis* and *Protomyctophum crockeri*) collected in the day and night MOCNESS samples from Station 108.

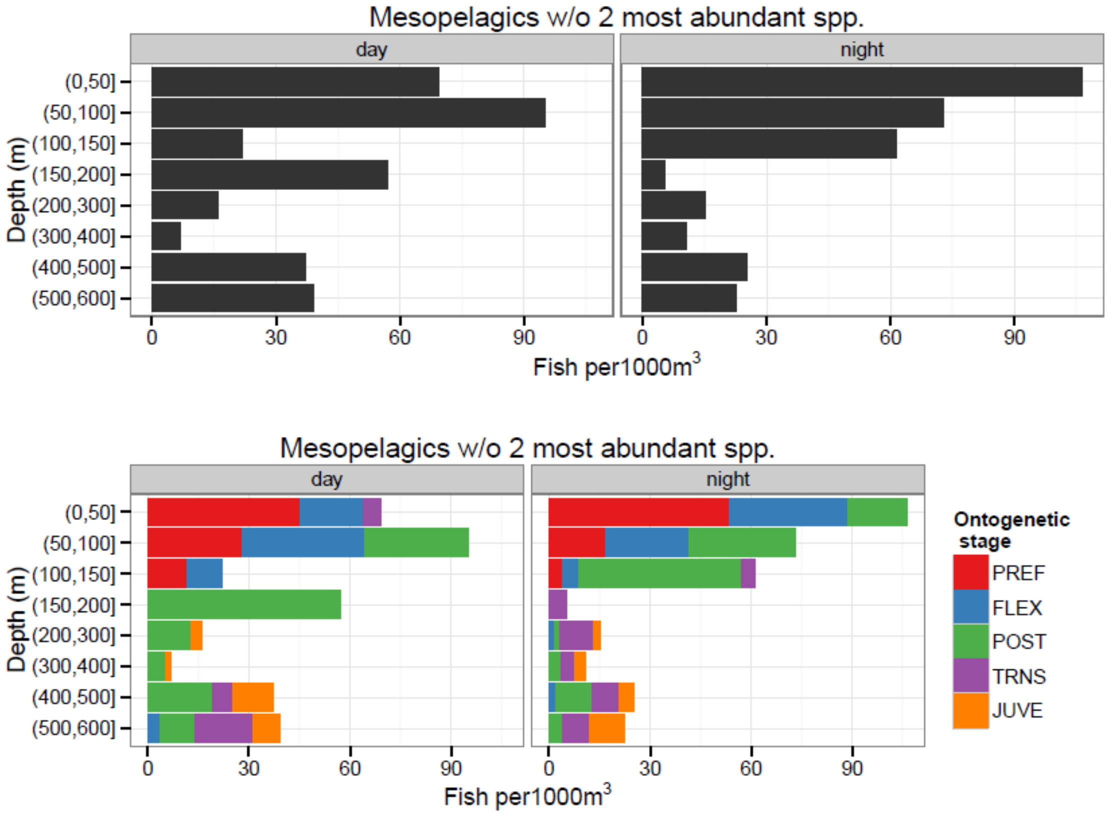

Figure 10:
Distribution of all but the two most abundant mesopelagic fishes collected from day and night MOCNESS samples from Station 108 (top panel). Stage-specific distribution and abundance of all but the two most abundant species of mesopelagic fishes collected in the day and night MOCNESS samples from Station 108 (bottom panel).

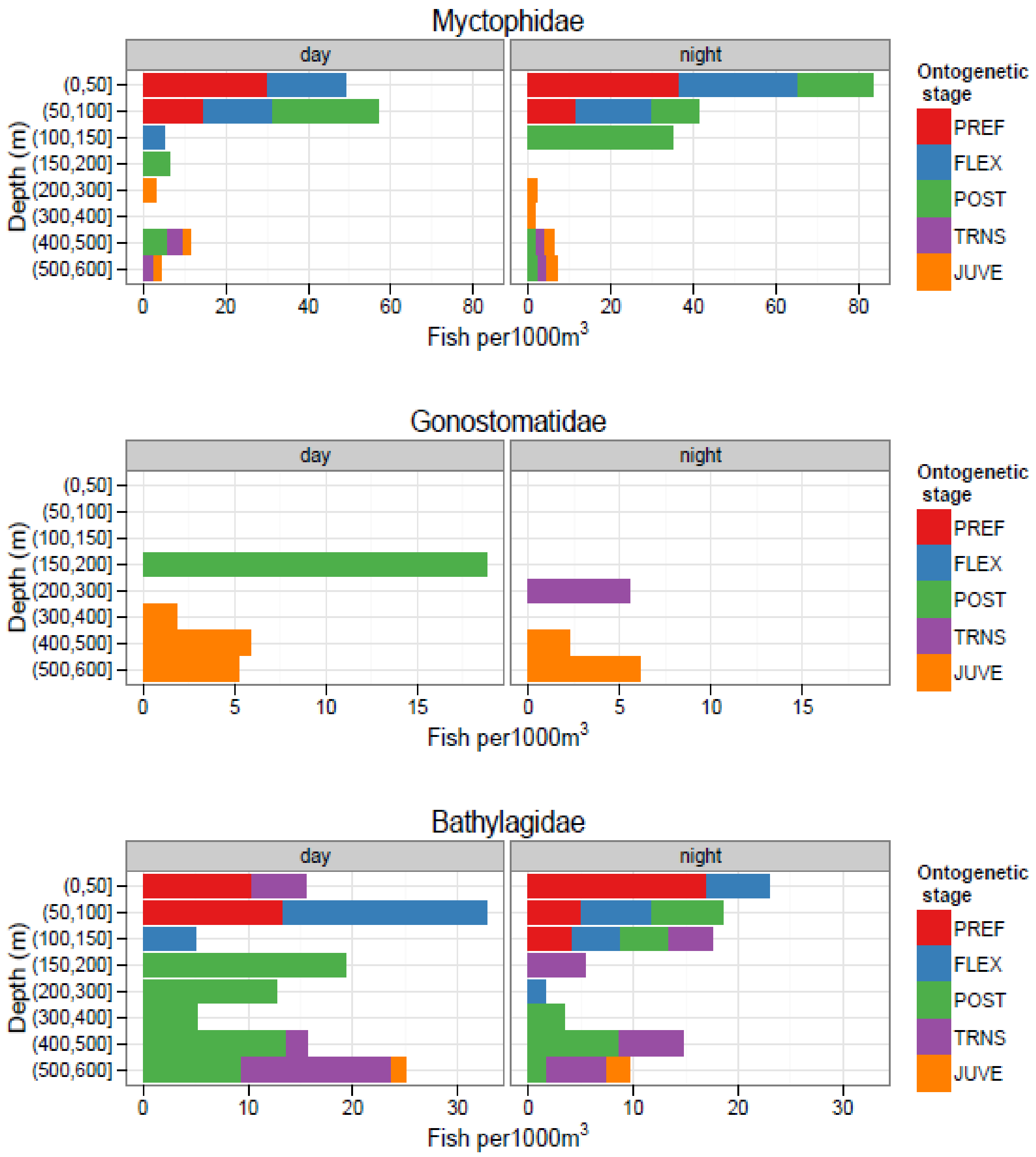

Figure 11:
Stage-specific distribution of all species of families Myctophidae, Gonostomatidae, and Bathylagidae except for *Stenobrachius leucopsarus* and *Cyclothone signata*, collected in the day and night MOCNESS samples from Station 108.

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APPENDIX A: Model Output Summary Tables

Table 1:
Species Richness model from equation (1): $E(count_{\#spp}) \sim depth\ stratum * time\ of\ day$

```
Call:
glm(formula = spp ~ as.factor(stratum) * as.factor(light), family =
gaussian,
    data = freq.stage.counts.stratum)

Coefficients:
                                          Estimate Std. Error t value
Pr(>|t|)
(Intercept)                                 4.0000     0.8440   4.739
5.65e-05 ***
as.factor(stratum)2                         0.3333     1.1936   0.279
0.7821
as.factor(stratum)3                        -2.0000     1.3344  -1.499
0.1451
as.factor(stratum)4                        -2.0000     1.1936  -1.676
0.1049
as.factor(stratum)5                        -2.5000     1.3344  -1.873
0.0715 .
as.factor(stratum)6                        -1.3333     1.1936  -1.117
0.2734
as.factor(stratum)7                         3.0000     1.1936   2.513
0.0180 *
as.factor(stratum)8                         2.0000     1.1936   1.676
0.1049
as.factor(light)night                      -0.3333     1.1936  -0.279
0.7821
as.factor(stratum)2:as.factor(light)night   0.3333     1.6880   0.197
0.8449
as.factor(stratum)3:as.factor(light)night   2.6667     1.7904   1.489
0.1475
as.factor(stratum)4:as.factor(light)night  -0.6667     2.0673  -0.322
0.7495
as.factor(stratum)5:as.factor(light)night   0.8333     1.7904   0.465
0.6452
as.factor(stratum)6:as.factor(light)night   1.3333     1.6880   0.790
0.4362
as.factor(stratum)7:as.factor(light)night  -2.0000     1.6880  -1.185
0.2460
as.factor(stratum)8:as.factor(light)night  -1.0000     1.6880  -0.592
0.5583
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.136905)

    Null deviance: 160.545  on 43  degrees of freedom
Residual deviance:  59.833  on 28  degrees of freedom
AIC: 172.39
Number of Fisher Scoring iterations: 2
```

Table 2:

Overall abundance of fishes within the depth strata, equation (2):

$E(count_{all\ spp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * time\ of\ day)$

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) * 
    as.factor(day), family = poisson, data = abund8904.new.mp)

Coefficients:
                                    Estimate Std. Error z value 
Pr(>|z|)    
(Intercept)                         -0.35684    0.09206  -3.876 
0.000106 ***
as.factor(stratum)2                 -1.94973    0.22017  -8.856  < 2e-
16 ***
as.factor(stratum)3                 -2.36647    0.29223  -8.098 5.59e-
16 ***
as.factor(stratum)4                 -4.86675    1.00422  -4.846 1.26e-
06 ***
as.factor(stratum)5                 -3.92904    0.34581 -11.362  < 2e-
16 ***
as.factor(stratum)6                 -1.93157    0.15945 -12.114  < 2e-
16 ***
as.factor(stratum)7                 -1.72159    0.15686 -10.976  < 2e-
16 ***
as.factor(stratum)8                 -2.21940    0.23684  -9.371  < 2e-
16 ***
as.factor(day)1                      0.19913    0.12417   1.604 
0.108795    
as.factor(stratum)2:as.factor(day)1  0.53324    0.27322   1.952 
0.050977 .  
as.factor(stratum)3:as.factor(day)1 -1.37778    0.58510  -2.355 
0.018534 *  
as.factor(stratum)4:as.factor(day)1  1.99810    1.06138   1.883 
0.059761 .  
as.factor(stratum)5:as.factor(day)1 -0.78692    0.57143  -1.377 
0.168480    
as.factor(stratum)6:as.factor(day)1 -0.01399    0.21553  -0.065 
0.948259    
as.factor(stratum)7:as.factor(day)1  0.10455    0.20845   0.502 
0.615971    
as.factor(stratum)8:as.factor(day)1  0.64817    0.28887   2.244 
0.024845 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 8.6810e+02  on 15  degrees of freedom
Residual deviance: 3.7303e-14  on  0  degrees of freedom
AIC: 112.43
Number of Fisher Scoring iterations: 3
```

Table 3:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$
Stenobrachius leucopsarus, Day samples:
Coefficients:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp292.8904.day)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-5.7306  -0.0001  -0.0001  -0.0001   2.7807

Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                     -2.3760     0.1459 -16.289  < 2e-16 ***
as.factor(stratum)2             -1.8502     0.3349  -5.524 3.32e-08 ***
as.factor(stratum)3            -22.2149  5442.4598  -0.004 0.996743
as.factor(stratum)4            -22.1502  5442.4598  -0.004 0.996753
as.factor(stratum)5            -23.4097  5442.4598  -0.004 0.996568
as.factor(stratum)6            -23.2925  5442.4598  -0.004 0.996585
as.factor(stratum)7            -23.1322  5442.4598  -0.004 0.996609
as.factor(stratum)8            -22.5474  5442.4598  -0.004 0.996694
stagePOST                       -1.6529     0.3639  -4.543 5.55e-06 ***
stagePREF                        0.3983     0.1886   2.112 0.034656 *
stageTRNS                       -3.8501     1.0106  -3.810 0.000139 ***
stageJUVE                      -22.0541  5442.4598  -0.004 0.996767
as.factor(stratum)2:stagePOST    1.8200     0.5479   3.322 0.000895 ***
as.factor(stratum)3:stagePOST    1.6529  7696.8004   0.000 0.999829
as.factor(stratum)4:stagePOST    1.6529  7696.8004   0.000 0.999829
as.factor(stratum)5:stagePOST    1.6529  7696.8004   0.000 0.999829
as.factor(stratum)6:stagePOST   20.5500  5442.4598   0.004 0.996987
as.factor(stratum)7:stagePOST   20.9555  5442.4598   0.004 0.996928
as.factor(stratum)8:stagePOST   20.5500  5442.4598   0.004 0.996987
as.factor(stratum)2:stagePREF   -0.8503     0.5190  -1.639 0.101316
as.factor(stratum)3:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)4:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)5:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)6:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)7:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)8:stagePREF   -0.3983  7696.8004   0.000 0.999959
as.factor(stratum)2:stageTRNS  -16.7517  5442.4599  -0.003 0.997544
as.factor(stratum)3:stageTRNS    3.8501  7696.8005   0.001 0.999601
as.factor(stratum)4:stageTRNS    3.8501  7696.8005   0.001 0.999601
as.factor(stratum)5:stageTRNS    3.8501  7696.8005   0.001 0.999601
as.factor(stratum)6:stageTRNS   23.1527  5442.4599   0.004 0.996606
as.factor(stratum)7:stageTRNS   23.1527  5442.4599   0.004 0.996606
as.factor(stratum)8:stageTRNS    3.8501  7696.8005   0.001 0.999601
as.factor(stratum)2:stageJUVE    1.4523  7696.8004   0.000 0.999849
as.factor(stratum)3:stageJUVE   22.0541  9426.6169   0.002 0.998133
as.factor(stratum)4:stageJUVE   22.0541  9426.6169   0.002 0.998133
as.factor(stratum)5:stageJUVE   22.0541  9426.6169   0.002 0.998133
as.factor(stratum)6:stageJUVE   40.2581  7696.8005   0.005 0.995827
as.factor(stratum)7:stageJUVE   40.2581  7696.8005   0.005 0.995827
```

Table 3:
Ontogenetic habitat (depth) distribution differences, equation (3), *Stenobrachius leucopsarus*, Day samples: continued

```
as.factor(stratum)8:stageJUVE   40.9512  7696.8005   0.005 0.995755
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 979.99  on 119  degrees of freedom
Residual deviance: 127.15  on  80  degrees of freedom
AIC: 292.01
Number of Fisher Scoring iterations: 17
```

Table 4:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Stenobrachius leucopsarus, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp292.8904.night)

Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                     -2.6152     0.1644 -15.908  < 2e-16 ***
as.factor(stratum)2             -2.9102     0.6003  -4.848 1.25e-06 ***
as.factor(stratum)3            -21.9756  5442.4598  -0.004  0.99678
as.factor(stratum)4            -21.9110  5442.4598  -0.004  0.99679
as.factor(stratum)5            -23.1705  5442.4598  -0.004  0.99660
as.factor(stratum)6            -23.0533  5442.4598  -0.004  0.99662
as.factor(stratum)7            -22.8929  5442.4598  -0.004  0.99664
as.factor(stratum)8            -22.3081  5442.4598  -0.004  0.99673
stagePOST                       -1.1260     0.3322  -3.390  0.00070 ***
stagePREF                        0.2809     0.2178   1.290  0.19714
stageTRNS                      -21.8149  5442.4598  -0.004  0.99680
stageJUVE                      -21.8149  5442.4597  -0.004  0.99680
as.factor(stratum)2:stagePOST    1.9733     0.7659   2.577  0.00998 **
as.factor(stratum)3:stagePOST    1.1260  7696.8004   0.000  0.99988
as.factor(stratum)4:stagePOST    1.1260  7696.8004   0.000  0.99988
as.factor(stratum)5:stagePOST    1.1260  7696.8004   0.000  0.99988
as.factor(stratum)6:stagePOST   19.3300  5442.4599   0.004  0.99717
as.factor(stratum)7:stagePOST   19.3300  5442.4599   0.004  0.99717
as.factor(stratum)8:stagePOST    1.1260  7696.8004   0.000  0.99988
as.factor(stratum)2:stagePREF   -0.6864     0.9385  -0.731  0.46456
as.factor(stratum)3:stagePREF   -0.2809  7696.8004   0.000  0.99997
as.factor(stratum)4:stagePREF   -0.2809  7696.8004   0.000  0.99997
as.factor(stratum)5:stagePREF   -0.2809  7696.8004   0.000  0.99997
as.factor(stratum)6:stagePREF   -0.2809  7696.8005   0.000  0.99997
as.factor(stratum)7:stagePREF   -0.2809  7696.8004   0.000  0.99997
as.factor(stratum)8:stagePREF   -0.2809  7696.8004   0.000  0.99997
as.factor(stratum)2:stageTRNS    2.5123  7696.8005   0.000  0.99974
```

Table 4:
Ontogenetic habitat (depth) distribution differences, equation (3), *Stenobrachius leucopsarus*, Night samples: continued

```
as.factor(stratum)3:stageTRNS   21.8149  9426.6169   0.002  0.99815
as.factor(stratum)4:stageTRNS   21.8149  9426.6169   0.002  0.99815
as.factor(stratum)5:stageTRNS   21.8149  9426.6169   0.002  0.99815
as.factor(stratum)6:stageTRNS   41.9648  7696.8005   0.005  0.99565
as.factor(stratum)7:stageTRNS   41.1175  7696.8005   0.005  0.99574
as.factor(stratum)8:stageTRNS   21.8149  9426.6169   0.002  0.99815
as.factor(stratum)2:stageJUVE    2.5123  7696.8004   0.000  0.99974
as.factor(stratum)3:stageJUVE   21.8149  9426.6168   0.002  0.99815
as.factor(stratum)4:stageJUVE   21.8149  9426.6168   0.002  0.99815
as.factor(stratum)5:stageJUVE   40.0189  7696.8005   0.005  0.99585
as.factor(stratum)6:stageJUVE   40.0189  7696.8005   0.005  0.99585
as.factor(stratum)7:stageJUVE   40.7120  7696.8005   0.005  0.99578
as.factor(stratum)8:stageJUVE   40.0189  7696.8005   0.005  0.99585
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 755.66  on 119  degrees of freedom
Residual deviance: 129.65  on  80  degrees of freedom
AIC: 278.2
Number of Fisher Scoring iterations: 17
```

Table 5:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Cyclothone signata, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp78.8904.day)

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2           -3.979e-01  2.092e+04   0.000    1.000
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                     -1.852e-10  2.092e+04   0.000    1.000
stagePREF                     -1.849e-10  2.092e+04   0.000    1.000
stageTRNS                     -1.916e-10  2.092e+04   0.000    1.000
stageJUVE                      2.090e+01  1.479e+04   0.001    0.999
as.factor(stratum)2:stagePOST  1.821e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePOST  1.875e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST  1.814e-10  2.959e+04   0.000    1.000
```

Table 5:
Ontogenetic habitat (depth) distribution differences, equation (3), *Cyclothone signata*, Day samples: continued

```
as.factor(stratum)5:stagePOST  1.764e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST  2.130e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  2.264e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePOST  1.940e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stagePREF  1.817e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePREF  1.868e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePREF  1.813e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePREF  1.760e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePREF  1.513e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stagePREF  2.263e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePREF  1.940e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageTRNS  1.882e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  1.939e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageTRNS  1.881e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS  1.741e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stageTRNS  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stageTRNS  2.329e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stageTRNS  2.008e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stageJUVE  3.367e+00  2.092e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.367e+00  2.092e+04   0.000    1.000
as.factor(stratum)8:stageJUVE  2.351e+00  2.092e+04   0.000    1.000
(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 650.747  on 119  degrees of freedom
Residual deviance:  25.211  on  80  degrees of freedom
AIC: 154.03
Number of Fisher Scoring iterations: 19
```

Table 6:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Cyclothone signata, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp78.8904.night)

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2           -3.979e-01  2.092e+04   0.000    1.000
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
```

Table 6:
Ontogenetic habitat (depth) distribution differences, equation (3), *Cyclothone signata*, Night samples: continued

```
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                      3.635e-10  2.092e+04   0.000    1.000
stagePREF                      3.635e-10  2.092e+04   0.000    1.000
stageTRNS                      3.588e-10  2.092e+04   0.000    1.000
stageJUVE                      2.090e+01  1.479e+04   0.001    0.999
as.factor(stratum)2:stagePOST -3.664e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePOST -3.645e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST -3.642e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePOST -3.566e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST -3.656e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePOST -3.596e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stagePREF -3.663e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePREF -3.641e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePREF -3.636e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePREF -3.564e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePREF -3.544e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stagePREF -3.656e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePREF -3.595e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageTRNS -3.618e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stageTRNS -3.595e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageTRNS -3.593e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -3.430e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stageTRNS -3.507e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stageTRNS -3.627e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stageTRNS -3.564e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -6.931e-01  2.092e+04   0.000    1.000
as.factor(stratum)3:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stageJUVE  3.068e+00  2.092e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.091e+00  2.092e+04   0.000    1.000
as.factor(stratum)8:stageJUVE  1.504e+00  2.092e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 479.835  on 119  degrees of freedom
Residual deviance:  30.992  on  80  degrees of freedom
AIC: 152.87
Number of Fisher Scoring iterations: 19
```

Table 7:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Leuroglossus stilbius, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
```

Table 7:
Ontogenetic habitat (depth) distribution differences, equation (3), *Leuroglossus stilbius*, Day samples: continued

```
   stage, family = poisson, data = sp72.8904.day)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.82574  -0.00003  -0.00003  -0.00003   1.23784

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2            2.090e+01  1.479e+04   0.001    0.999
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.607e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                     -5.953e-07  2.092e+04   0.000    1.000
stagePREF                      2.020e+01  1.479e+04   0.001    0.999
stageTRNS                      2.020e+01  1.479e+04   0.001    0.999
stageJUVE                     -3.921e-07  2.092e+04   0.000    1.000
as.factor(stratum)2:stagePOST -2.130e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stagePOST  5.953e-07  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST  2.130e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stagePOST  2.181e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stagePREF -2.061e+01  1.479e+04  -0.001    0.999
as.factor(stratum)3:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)8:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)2:stageTRNS -4.151e+01  2.092e+04  -0.002    0.998
as.factor(stratum)3:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stageTRNS  3.350e-07  2.092e+04   0.000    1.000
as.factor(stratum)8:stageTRNS  1.946e+00  2.092e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -2.130e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageJUVE  3.920e-07  2.959e+04   0.000    1.000
as.factor(stratum)4:stageJUVE  3.915e-07  2.959e+04   0.000    1.000
as.factor(stratum)5:stageJUVE  3.911e-07  2.959e+04   0.000    1.000
as.factor(stratum)6:stageJUVE  3.921e-07  2.959e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.350e-07  2.959e+04   0.000    1.000
as.factor(stratum)8:stageJUVE  7.440e-07  2.959e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)
```

Table 7:
Ontogenetic habitat (depth) distribution differences, equation (3), *Leuroglossus stilbius*, Day samples: continued

```
    Null deviance: 129.219  on 119  degrees of freedom
Residual deviance:  26.974  on  80  degrees of freedom
AIC: 153.29
Number of Fisher Scoring iterations: 19
```

Table 8:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Leuroglossus stilbius, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp72.8904.night)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.15470  -0.00002  -0.00002  -0.00002   0.92946

Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                  -2.743e+01  2.439e+04  -0.001    0.999
as.factor(stratum)2          -3.979e-01  3.449e+04   0.000    1.000
as.factor(stratum)3          -1.607e-01  3.449e+04   0.000    1.000
as.factor(stratum)4          -9.606e-02  3.449e+04   0.000    1.000
as.factor(stratum)5          -1.356e+00  3.449e+04   0.000    1.000
as.factor(stratum)6          -1.238e+00  3.449e+04   0.000    1.000
as.factor(stratum)7          -1.078e+00  3.449e+04   0.000    1.000
as.factor(stratum)8          -4.932e-01  3.449e+04   0.000    1.000
stagePOST                     1.954e-09  3.449e+04   0.000    1.000
stagePREF                     1.958e-09  3.449e+04   0.000    1.000
stageTRNS                     1.941e-09  3.449e+04   0.000    1.000
stageJUVE                     1.947e-09  3.449e+04   0.000    1.000
as.factor(stratum)2:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)3:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)4:stagePOST -2.004e-09  4.878e+04   0.000    1.000
as.factor(stratum)5:stagePOST -1.738e-09  4.878e+04   0.000    1.000
as.factor(stratum)6:stagePOST -1.979e-09  4.878e+04   0.000    1.000
as.factor(stratum)7:stagePOST -2.208e-09  4.878e+04   0.000    1.000
as.factor(stratum)8:stagePOST -1.939e-09  4.878e+04   0.000    1.000
as.factor(stratum)2:stagePREF  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)3:stagePREF  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)4:stagePREF -2.008e-09  4.878e+04   0.000    1.000
as.factor(stratum)5:stagePREF -1.744e-09  4.878e+04   0.000    1.000
as.factor(stratum)6:stagePREF -1.983e-09  4.878e+04   0.000    1.000
as.factor(stratum)7:stagePREF -2.212e-09  4.878e+04   0.000    1.000
as.factor(stratum)8:stagePREF -1.947e-09  4.878e+04   0.000    1.000
as.factor(stratum)2:stageTRNS -2.471e-09  4.878e+04   0.000    1.000
as.factor(stratum)3:stageTRNS -2.515e-09  4.878e+04   0.000    1.000
```

Table 8:
Ontogenetic habitat (depth) distribution differences, equation (3), *Leuroglossus stilbius*, Night samples: continued

```
as.factor(stratum)4:stageTRNS -1.991e-09  4.878e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -1.727e-09  4.878e+04   0.000    1.000
as.factor(stratum)6:stageTRNS -1.965e-09  4.878e+04   0.000    1.000
as.factor(stratum)7:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stageJUVE -2.490e-09  4.878e+04   0.000    1.000
as.factor(stratum)3:stageJUVE -2.524e-09  4.878e+04   0.000    1.000
as.factor(stratum)4:stageJUVE -1.997e-09  4.878e+04   0.000    1.000
as.factor(stratum)5:stageJUVE -1.733e-09  4.878e+04   0.000    1.000
as.factor(stratum)6:stageJUVE -1.973e-09  4.878e+04   0.000    1.000
as.factor(stratum)7:stageJUVE -2.200e-09  4.878e+04   0.000    1.000
as.factor(stratum)8:stageJUVE -1.931e-09  4.878e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 46.555  on 119  degrees of freedom
Residual deviance: 12.033  on  80  degrees of freedom
AIC: 108.03
Number of Fisher Scoring iterations: 20
```

Table 9:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Tarletonbeania crenularis, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp299.8904.day)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.63299  -0.00003  -0.00003  -0.00003   1.85891

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -4.840e+00  5.000e-01  -9.680   <2e-16
***
as.factor(stratum)2           -3.979e-01  7.071e-01  -0.563    0.574
as.factor(stratum)3           -2.175e+01  1.479e+04  -0.001    0.999
as.factor(stratum)4           -2.169e+01  1.479e+04  -0.001    0.999
as.factor(stratum)5           -2.295e+01  1.479e+04  -0.002    0.999
as.factor(stratum)6           -2.283e+01  1.479e+04  -0.002    0.999
as.factor(stratum)7           -2.267e+01  1.479e+04  -0.002    0.999
as.factor(stratum)8           -2.208e+01  1.479e+04  -0.001    0.999
stagePOST                     -2.159e+01  1.479e+04  -0.001    0.999
stagePREF                     -2.877e-01  7.638e-01  -0.377    0.706
stageTRNS                     -2.159e+01  1.479e+04  -0.001    0.999
stageJUVE                     -2.159e+01  1.479e+04  -0.001    0.999
as.factor(stratum)2:stagePOST  2.159e+01  1.479e+04   0.001    0.999
```

Table 9:
Ontogenetic habitat (depth) distribution differences, equation (3), *Tarletonbeania crenularis*, Day samples: continued

```
as.factor(stratum)3:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)4:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  4.179e+01  2.092e+04   0.002    0.998
as.factor(stratum)8:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stagePREF -1.099e+00  1.354e+00  -0.811    0.417
as.factor(stratum)3:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)4:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)5:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)6:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)7:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)8:stagePREF  2.877e-01  2.092e+04   0.000    1.000
as.factor(stratum)2:stageTRNS -8.345e-12  2.092e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)4:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stageTRNS  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stageJUVE -6.250e-12  2.092e+04   0.000    1.000
as.factor(stratum)3:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)4:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stageJUVE  2.159e+01  2.562e+04   0.001    0.999
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 109.134  on 119  degrees of freedom
Residual deviance:  24.536  on  80  degrees of freedom
AIC: 126.4
Number of Fisher Scoring iterations: 19
```

Table 10:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Tarletonbeania crenularis, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp299.8904.night)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.41421  -0.00002  -0.00002  -0.00002   0.92946
```

Table 10:
Ontogenetic habitat (depth) distribution differences, equation (3), *Tarletonbeania crenularis*, Night samples: continued

```
Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -5.533e+00  7.071e-01  -7.825 5.08e-15
***
as.factor(stratum)2           -3.979e-01  1.000e+00  -0.398    0.691
as.factor(stratum)3           -2.206e+01  2.439e+04  -0.001    0.999
as.factor(stratum)4           -2.199e+01  2.439e+04  -0.001    0.999

as.factor(stratum)5           -2.325e+01  2.439e+04  -0.001    0.999
as.factor(stratum)6           -2.314e+01  2.439e+04  -0.001    0.999
as.factor(stratum)7           -2.298e+01  2.439e+04  -0.001    0.999
as.factor(stratum)8           -2.239e+01  2.439e+04  -0.001    0.999
stagePOST                     -2.190e+01  2.439e+04  -0.001    0.999
stagePREF                      4.055e-01  9.129e-01   0.444    0.657
stageTRNS                     -2.190e+01  2.439e+04  -0.001    0.999
stageJUVE                     -2.190e+01  2.439e+04  -0.001    0.999
as.factor(stratum)2:stagePOST  2.190e+01  2.439e+04   0.001    0.999
as.factor(stratum)3:stagePOST  4.420e+01  3.449e+04   0.001    0.999
as.factor(stratum)4:stagePOST  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)5:stagePOST  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stagePOST  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)7:stagePOST  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stagePOST  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stagePREF -1.099e+00  1.528e+00  -0.719    0.472
as.factor(stratum)3:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)4:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)5:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)6:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)7:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)8:stagePREF -4.055e-01  3.449e+04   0.000    1.000
as.factor(stratum)2:stageTRNS  6.037e-12  3.449e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)4:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)5:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)7:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stageTRNS  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stageJUVE  5.983e-08  3.449e+04   0.000    1.000
as.factor(stratum)3:stageJUVE  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)4:stageJUVE  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)5:stageJUVE  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stageJUVE  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)7:stageJUVE  2.190e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stageJUVE  4.310e+01  3.449e+04   0.001    0.999
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 77.555  on 119  degrees of freedom
Residual deviance: 12.033  on  80  degrees of freedom
AIC: 118.65
Number of Fisher Scoring iterations: 20
```

Table 11:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Lipolagus ochotensis, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) * 
    stage, family = poisson, data = sp68.8904.day)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-1.15470  -0.00003  -0.00003  -0.00003   1.31445  

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2            1.981e+01  1.479e+04   0.001    0.999
as.factor(stratum)3            2.004e+01  1.479e+04   0.001    0.999
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                      3.190e-07  2.092e+04   0.000    1.000
stagePREF                      2.020e+01  1.479e+04   0.001    0.999
stageTRNS                      2.114e-07  2.092e+04   0.000    1.000
stageJUVE                      2.067e-07  2.092e+04   0.000    1.000
as.factor(stratum)2:stagePOST -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stagePOST -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stagePOST -3.190e-07  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePOST -3.191e-07  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stagePREF -2.020e+01  1.479e+04  -0.001    0.999
as.factor(stratum)3:stagePREF -4.041e+01  2.092e+04  -0.002    0.998
as.factor(stratum)4:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)8:stagePREF -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)2:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageTRNS -2.114e-07  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -2.114e-07  2.959e+04   0.000    1.000
as.factor(stratum)6:stageTRNS -1.975e-07  2.959e+04   0.000    1.000
as.factor(stratum)7:stageTRNS -2.557e-07  2.959e+04   0.000    1.000
as.factor(stratum)8:stageTRNS  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stageJUVE -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageJUVE -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -2.067e-07  2.959e+04   0.000    1.000
as.factor(stratum)5:stageJUVE -2.067e-07  2.959e+04   0.000    1.000
as.factor(stratum)6:stageJUVE -1.927e-07  2.959e+04   0.000    1.000
as.factor(stratum)7:stageJUVE -2.510e-07  2.959e+04   0.000    1.000
```

Table 11:
Ontogenetic habitat (depth) distribution differences, equation (3), *Lipolagus ochotensis*, Day samples: continued

```
as.factor(stratum)8:stageJUVE -4.617e-07  2.959e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 55.492  on 119  degrees of freedom
Residual deviance: 19.200  on  80  degrees of freedom
AIC: 117.81
Number of Fisher Scoring iterations: 19
```

Table 12:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Lipolagus ochotensis, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp68.8904.night)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.41421  -0.00002  -0.00002  -0.00002   0.92946

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -6.226e+00  1.000e+00  -6.226 4.78e-10
***
as.factor(stratum)2           -2.160e+01  2.439e+04  -0.001    0.999
as.factor(stratum)3           -1.607e-01  1.414e+00  -0.114    0.910
as.factor(stratum)4           -2.130e+01  2.439e+04  -0.001    0.999
as.factor(stratum)5           -2.256e+01  2.439e+04  -0.001    0.999
as.factor(stratum)6           -2.244e+01  2.439e+04  -0.001    0.999
as.factor(stratum)7           -2.228e+01  2.439e+04  -0.001    0.999
as.factor(stratum)8           -2.170e+01  2.439e+04  -0.001    0.999
stagePOST                     -2.120e+01  2.439e+04  -0.001    0.999
stagePREF                      1.099e+00  1.155e+00   0.951    0.341
stageTRNS                     -2.120e+01  2.439e+04  -0.001    0.999
stageJUVE                     -2.120e+01  2.439e+04  -0.001    0.999
as.factor(stratum)2:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)3:stagePOST  1.098e-06  3.449e+04   0.000    1.000
as.factor(stratum)4:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)5:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stagePOST  4.241e+01  3.449e+04   0.001    0.999
as.factor(stratum)7:stagePOST  4.379e+01  3.449e+04   0.001    0.999
as.factor(stratum)8:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stagePREF -1.099e+00  3.449e+04   0.000    1.000
as.factor(stratum)3:stagePREF -2.230e+01  2.439e+04  -0.001    0.999
as.factor(stratum)4:stagePREF -1.099e+00  3.449e+04   0.000    1.000
as.factor(stratum)5:stagePREF -1.099e+00  3.449e+04   0.000    1.000
as.factor(stratum)6:stagePREF -1.099e+00  3.449e+04   0.000    1.000
```

Table 12:
Ontogenetic habitat (depth) distribution differences, equation (3), *Lipolagus ochotensis*, Night samples: continued

```
as.factor(stratum)7:stagePREF -1.099e+00  3.449e+04   0.000    1.000
as.factor(stratum)8:stagePREF -1.099e+00  3.449e+04   0.000    1.000
as.factor(stratum)2:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)3:stageTRNS  2.120e+01  2.439e+04   0.001    0.999
as.factor(stratum)4:stageTRNS  4.241e+01  3.449e+04   0.001    0.999
as.factor(stratum)5:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)7:stageTRNS  4.241e+01  3.449e+04   0.001    0.999
as.factor(stratum)8:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)3:stageJUVE  1.312e-11  3.449e+04   0.000    1.000
as.factor(stratum)4:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)5:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)7:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 68.327  on 119  degrees of freedom
Residual deviance: 16.427  on  80  degrees of freedom
AIC: 119.65
Number of Fisher Scoring iterations: 20
```

Table 13:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Protomyctophum crockeri, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = sp288.8904.day)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.15470  -0.00003  -0.00003  -0.00003   1.31445

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2           -3.979e-01  2.092e+04   0.000    1.000
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
```

Table 13:
Ontogenetic habitat (depth) distribution differences, equation (3), *Protomyctophum crockeri*, Day samples: continued

```
stagePOST                      7.504e-10  2.092e+04   0.000    1.000
stagePREF                      2.090e+01  1.479e+04   0.001    0.999
stageTRNS                      7.399e-10  2.092e+04   0.000    1.000
stageJUVE                      7.461e-10  2.092e+04   0.000    1.000
as.factor(stratum)2:stagePOST  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)3:stagePOST -7.476e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stagePOST -7.511e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST -7.536e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stagePOST  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stagePOST -9.424e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stagePREF -1.131e-09  2.092e+04   0.000    1.000
as.factor(stratum)3:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)8:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)2:stageTRNS -1.123e-09  2.959e+04   0.000    1.000
as.factor(stratum)3:stageTRNS -7.350e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageTRNS -5.966e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -7.409e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stageTRNS -7.490e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stageTRNS  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stageTRNS  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stageJUVE -1.120e-09  2.959e+04   0.000    1.000
as.factor(stratum)3:stageJUVE -7.406e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageJUVE -6.059e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageJUVE -7.462e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stageJUVE -7.452e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stageJUVE -8.810e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stageJUVE -9.370e-10  2.959e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)
```

Table 14:
Ontogenetic habitat (depth) distribution differences, equation (3):
$E(count_{sp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$
Protomyctophum crockeri, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) * 
    stage, family = poisson, data = sp288.8904.night)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-0.81650  -0.00002  -0.00002  -0.00002   0.92946  

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
```

Table 14:
Ontogenetic habitat (depth) distribution differences, equation (3), *Protomyctophum crockeri*, Night samples: continued

```
(Intercept)                  -2.743e+01  2.439e+04  -0.001    0.999
as.factor(stratum)2           2.081e+01  2.439e+04   0.001    0.999
as.factor(stratum)3          -1.607e-01  3.449e+04   0.000    1.000
as.factor(stratum)4          -9.606e-02  3.449e+04   0.000    1.000
as.factor(stratum)5          -1.356e+00  3.449e+04   0.000    1.000
as.factor(stratum)6          -1.238e+00  3.449e+04   0.000    1.000
as.factor(stratum)7          -1.078e+00  3.449e+04   0.000    1.000
as.factor(stratum)8          -4.932e-01  3.449e+04   0.000    1.000
stagePOST                     2.095e-06  3.449e+04   0.000    1.000
stagePREF                     2.120e+01  2.439e+04   0.001    0.999
stageTRNS                     8.685e-07  3.449e+04   0.000    1.000
stageJUVE                     8.736e-07  3.449e+04   0.000    1.000
as.factor(stratum)2:stagePOST -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)3:stagePOST  2.230e+01  4.225e+04   0.001    1.000
as.factor(stratum)4:stagePOST -2.095e-06  4.878e+04   0.000    1.000
as.factor(stratum)5:stagePOST -2.116e-06  4.878e+04   0.000    1.000
as.factor(stratum)6:stagePOST -2.095e-06  4.878e+04   0.000    1.000
as.factor(stratum)7:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stagePOST  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stagePREF -2.120e+01  2.439e+04  -0.001    0.999
as.factor(stratum)3:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)4:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)5:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)6:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)7:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)8:stagePREF -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)2:stageTRNS -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)3:stageTRNS -1.134e-06  4.878e+04   0.000    1.000
as.factor(stratum)4:stageTRNS -8.685e-07  4.878e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -8.899e-07  4.878e+04   0.000    1.000
as.factor(stratum)6:stageTRNS -8.685e-07  4.878e+04   0.000    1.000
as.factor(stratum)7:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)8:stageTRNS  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)2:stageJUVE -2.120e+01  4.225e+04  -0.001    1.000
as.factor(stratum)3:stageJUVE -1.139e-06  4.878e+04   0.000    1.000
as.factor(stratum)4:stageJUVE -8.736e-07  4.878e+04   0.000    1.000
as.factor(stratum)5:stageJUVE  2.120e+01  4.225e+04   0.001    1.000
as.factor(stratum)6:stageJUVE -8.736e-07  4.878e+04   0.000    1.000
as.factor(stratum)7:stageJUVE -1.030e-06  4.878e+04   0.000    1.000
as.factor(stratum)8:stageJUVE -9.996e-07  4.878e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 57.170  on 119  degrees of freedom
Residual deviance: 17.578  on  80  degrees of freedom
AIC: 119.58

Number of Fisher Scoring iterations: 20
```

Table 15:
Overall abundance of fishes within the depth strata, after removing the two most abundant species, equation (2): $E(count_{all\ spp}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * time\ of\ day)$

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) * 
    as.factor(day), family = poisson, data = abund8904.mp.wo78.292)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-2.5406  -0.8507   0.0000   0.6647   2.7793  

Coefficients:
                                    Estimate Std. Error z value
Pr(>|z|)    
(Intercept)                          -3.3358     0.2357 -14.153  < 2e-
16 ***
as.factor(stratum)2                  -0.8034     0.3727  -2.156  
0.03111 *  
as.factor(stratum)3                  -0.4862     0.3640  -1.336  
0.18165    
as.factor(stratum)4                  -2.9864     1.0274  -2.907  
0.00365 ** 
as.factor(stratum)5                  -2.1665     0.4249  -5.099 3.42e-
07 ***
as.factor(stratum)6                  -2.3370     0.4714  -4.958 7.14e-
07 ***
as.factor(stratum)7                  -1.4835     0.3727  -3.981 6.87e-
05 ***
as.factor(stratum)8                  -0.9857     0.3827  -2.576  
0.01001 *  
as.factor(day)1                      -0.1823     0.3496  -0.522  
0.60201    
as.factor(stratum)2:as.factor(day)1   0.7419     0.5032   1.475  
0.14034    
as.factor(stratum)3:as.factor(day)1  -0.9963     0.6702  -1.487  
0.13710    
as.factor(stratum)4:as.factor(day)1   2.3795     1.1105   2.143  
0.03214 *  
as.factor(stratum)5:as.factor(day)1  -0.2877     0.6687  -0.430  
0.66706    
as.factor(stratum)6:as.factor(day)1  -0.5108     0.7888  -0.648  
0.51725    
as.factor(stratum)7:as.factor(day)1   0.6419     0.5081   1.263  
0.20652    
as.factor(stratum)8:as.factor(day)1   0.9625     0.5048   1.907  
0.05655 .  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 204.15  on 47  degrees of freedom
```

Table 15:
Overall abundance of fishes within the depth strata, after removing the two most abundant species, equation (2): continued

```
Residual deviance:  64.70  on 32  degrees of freedom
AIC: 229.84

Number of Fisher Scoring iterations: 5
```

Table 16:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Bathylagidae, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = bathylagidae.8904.day)
Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.00000  -0.00003  -0.00003  -0.00003   1.52242

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                    -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2             2.119e+01  1.479e+04   0.001    0.999
as.factor(stratum)3             2.004e+01  1.479e+04   0.001    0.999
as.factor(stratum)4            -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5            -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6            -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7            -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8            -4.932e-01  2.092e+04   0.000    1.000
stagePOST                       1.283e-07  2.092e+04   0.000    1.000
stagePREF                       2.090e+01  1.479e+04   0.001    0.999
stageTRNS                       2.020e+01  1.479e+04   0.001    0.999
stageJUVE                       3.260e-07  2.092e+04   0.000    1.000
as.factor(stratum)2:stagePOST -2.159e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stagePOST -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stagePOST  2.130e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stagePOST  2.159e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stagePOST  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  2.215e+01  2.562e+04   0.001    0.999
as.factor(stratum)8:stagePOST  2.200e+01  2.562e+04   0.001    0.999
as.factor(stratum)2:stagePREF -2.118e+01  1.479e+04  -0.001    0.999
as.factor(stratum)3:stagePREF -4.110e+01  2.092e+04  -0.002    0.998
as.factor(stratum)4:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)8:stagePREF -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)2:stageTRNS -4.179e+01  2.092e+04  -0.002    0.998
as.factor(stratum)3:stageTRNS -4.041e+01  2.092e+04  -0.002    0.998
as.factor(stratum)4:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
```

Table 16:
Ontogenetic habitat (depth) distribution differences, equation (4), Bathylagidae, Day samples: continued

```
as.factor(stratum)6:stageTRNS -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)7:stageTRNS  1.587e-07  2.092e+04   0.000    1.000
as.factor(stratum)8:stageTRNS  2.197e+00  2.092e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -2.159e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageJUVE -2.020e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -3.262e-07  2.959e+04   0.000    1.000
as.factor(stratum)5:stageJUVE -3.260e-07  2.959e+04   0.000    1.000
as.factor(stratum)6:stageJUVE -3.260e-07  2.959e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.947e-08  2.959e+04   0.000    1.000
as.factor(stratum)8:stageJUVE  2.020e+01  2.562e+04   0.001    0.999

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 166.598  on 119  degrees of freedom
Residual deviance:  36.477  on  80  degrees of freedom
AIC: 174.06
Number of Fisher Scoring iterations: 19
```

Table 17:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Bathylagidae, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = bathylagidae.8904.night)

Deviance Residuals:
    Min        1Q    Median        3Q       Max
-1.41421  -0.30216  -0.00006  -0.00006   1.31445

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -6.226e+00  1.000e+00  -6.226 4.78e-10
***
as.factor(stratum)2           -3.979e-01  1.414e+00  -0.281    0.778
as.factor(stratum)3           -1.607e-01  1.414e+00  -0.114    0.910
as.factor(stratum)4           -1.930e+01  8.973e+03  -0.002    0.998
as.factor(stratum)5           -1.356e+00  1.414e+00  -0.959    0.338
as.factor(stratum)6           -2.044e+01  8.973e+03  -0.002    0.998
as.factor(stratum)7           -2.028e+01  8.973e+03  -0.002    0.998
as.factor(stratum)8           -1.970e+01  8.973e+03  -0.002    0.998
stagePOST                     -1.920e+01  8.973e+03  -0.002    0.998
stagePREF                      1.099e+00  1.155e+00   0.951    0.341
stageTRNS                     -1.920e+01  8.973e+03  -0.002    0.998
stageJUVE                     -1.920e+01  8.973e+03  -0.002    0.998
as.factor(stratum)2:stagePOST  1.920e+01  8.973e+03   0.002    0.998
```

Table 17:
Ontogenetic habitat (depth) distribution differences, equation (4), Bathylagidae, Night samples: continued

```
as.factor(stratum)3:stagePOST  1.920e+01  8.973e+03   0.002    0.998
as.factor(stratum)4:stagePOST  1.920e+01  1.554e+04   0.001    0.999
as.factor(stratum)5:stagePOST -1.184e-07  1.269e+04   0.000    1.000
as.factor(stratum)6:stagePOST  3.910e+01  1.269e+04   0.003    0.998
as.factor(stratum)7:stagePOST  3.979e+01  1.269e+04   0.003    0.997
as.factor(stratum)8:stagePOST  3.841e+01  1.269e+04   0.003    0.998
as.factor(stratum)2:stagePREF -1.099e+00  1.826e+00  -0.602    0.547
as.factor(stratum)3:stagePREF -1.099e+00  1.826e+00  -0.602    0.547
as.factor(stratum)4:stagePREF -1.099e+00  1.269e+04   0.000    1.000
as.factor(stratum)5:stagePREF -2.030e+01  8.973e+03  -0.002    0.998
as.factor(stratum)6:stagePREF -1.099e+00  1.269e+04   0.000    1.000
as.factor(stratum)7:stagePREF -1.099e+00  1.269e+04   0.000    1.000
as.factor(stratum)8:stagePREF -1.099e+00  1.269e+04   0.000    1.000
as.factor(stratum)2:stageTRNS  2.475e-08  1.269e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  1.920e+01  8.973e+03   0.002    0.998
as.factor(stratum)4:stageTRNS  3.841e+01  1.269e+04   0.003    0.998
as.factor(stratum)5:stageTRNS  2.475e-08  1.269e+04   0.000    1.000
as.factor(stratum)6:stageTRNS  1.920e+01  1.554e+04   0.001    0.999
as.factor(stratum)7:stageTRNS  3.951e+01  1.269e+04   0.003    0.998
as.factor(stratum)8:stageTRNS  3.951e+01  1.269e+04   0.003    0.998
as.factor(stratum)2:stageJUVE  1.709e-08  1.269e+04   0.000    1.000
as.factor(stratum)3:stageJUVE  1.709e-08  1.269e+04   0.000    1.000
as.factor(stratum)4:stageJUVE  1.920e+01  1.554e+04   0.001    0.999
as.factor(stratum)5:stageJUVE  1.708e-08  1.269e+04   0.000    1.000
as.factor(stratum)6:stageJUVE  1.920e+01  1.554e+04   0.001    0.999
as.factor(stratum)7:stageJUVE  1.920e+01  1.554e+04   0.001    0.999
as.factor(stratum)8:stageJUVE  3.841e+01  1.269e+04   0.003    0.998
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 102.50  on 119  degrees of freedom
Residual deviance:  39.55  on  80  degrees of freedom
AIC: 166.62
Number of Fisher Scoring iterations: 18
```

Table 18:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Gonostomatidae, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = gonostomatidae.8904.day)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.02855  -0.00003  -0.00003  -0.00003   2.20415
```

Table 18:
Ontogenetic habitat (depth) distribution differences, equation (4), Gonostomatidae, Day samples: continued

```
Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2           -3.979e-01  2.092e+04   0.000    1.000
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                      2.677e-09  2.092e+04   0.000    1.000
stagePREF                      4.903e-10  2.092e+04   0.000    1.000
stageTRNS                      2.168e-10  2.092e+04   0.000    1.000
stageJUVE                      2.090e+01  1.479e+04   0.001    0.999
as.factor(stratum)2:stagePOST -2.659e-09  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePOST -2.756e-09  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST  2.130e+01  2.562e+04   0.001    0.999
as.factor(stratum)5:stagePOST -2.686e-09  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST  2.130e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST -2.663e-09  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePOST -2.671e-09  2.959e+04   0.000    1.000
as.factor(stratum)2:stagePREF -5.058e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePREF -5.701e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePREF -5.619e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePREF -4.990e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePREF -5.035e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stagePREF -4.871e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePREF -4.877e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageTRNS -2.183e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stageTRNS -2.997e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageTRNS -3.391e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS -2.267e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stageTRNS  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stageTRNS -2.092e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stageTRNS -2.151e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)3:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stageJUVE  3.384e+00  2.092e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.418e+00  2.092e+04   0.000    1.000
as.factor(stratum)8:stageJUVE  2.485e+00  2.092e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 688.778  on 119  degrees of freedom
Residual deviance:  35.281  on  80  degrees of freedom
AIC: 167.52
Number of Fisher Scoring iterations: 19
```

Table 19:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Gonostomatidae, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = gonostomatidae.8904.night)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.30869  -0.00003  -0.00003  -0.00003   2.99210

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -2.643e+01  1.479e+04  -0.002    0.999
as.factor(stratum)2           -3.979e-01  2.092e+04   0.000    1.000
as.factor(stratum)3           -1.607e-01  2.092e+04   0.000    1.000
as.factor(stratum)4           -9.606e-02  2.092e+04   0.000    1.000
as.factor(stratum)5           -1.356e+00  2.092e+04   0.000    1.000
as.factor(stratum)6           -1.238e+00  2.092e+04   0.000    1.000
as.factor(stratum)7           -1.078e+00  2.092e+04   0.000    1.000
as.factor(stratum)8           -4.932e-01  2.092e+04   0.000    1.000
stagePOST                     -7.525e-11  2.092e+04   0.000    1.000
stagePREF                     -4.311e-10  2.092e+04   0.000    1.000
stageTRNS                     -2.597e-10  2.092e+04   0.000    1.000
stageJUVE                      2.090e+01  1.479e+04   0.001    0.999
as.factor(stratum)2:stagePOST  1.063e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePOST  3.499e-11  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePOST  9.069e-11  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePOST  7.583e-11  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePOST  2.020e+01  2.562e+04   0.001    0.999
as.factor(stratum)7:stagePOST  7.647e-11  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePOST  6.262e-11  2.959e+04   0.000    1.000
as.factor(stratum)2:stagePREF  4.530e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stagePREF  4.218e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stagePREF  4.564e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stagePREF  4.307e-10  2.959e+04   0.000    1.000
as.factor(stratum)6:stagePREF  3.901e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stagePREF  4.379e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stagePREF  4.320e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageTRNS  2.850e-10  2.959e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  2.452e-10  2.959e+04   0.000    1.000
as.factor(stratum)4:stageTRNS  2.776e-10  2.959e+04   0.000    1.000
as.factor(stratum)5:stageTRNS  2.090e+01  2.562e+04   0.001    0.999
as.factor(stratum)6:stageTRNS  2.131e-10  2.959e+04   0.000    1.000
as.factor(stratum)7:stageTRNS  2.622e-10  2.959e+04   0.000    1.000
as.factor(stratum)8:stageTRNS  2.534e-10  2.959e+04   0.000    1.000
as.factor(stratum)2:stageJUVE -6.931e-01  2.092e+04   0.000    1.000
as.factor(stratum)3:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)4:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)5:stageJUVE -2.090e+01  2.562e+04  -0.001    0.999
as.factor(stratum)6:stageJUVE  3.068e+00  2.092e+04   0.000    1.000
as.factor(stratum)7:stageJUVE  3.114e+00  2.092e+04   0.000    1.000
```

Table 19:
Ontogenetic habitat (depth) distribution differences, equation (4), Gonostomatidae, Night samples: continued

```
as.factor(stratum)8:stageJUVE  1.792e+00  2.092e+04   0.000    1.000

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 489.78  on 119  degrees of freedom
Residual deviance:  33.56  on  80  degrees of freedom
AIC: 159.07
Number of Fisher Scoring iterations: 19
```

Table 20:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Myctophidae, Day samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) * 
    stage, family = poisson, data = myctophidae.8904.day)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-2.00000  -0.00006  -0.00006  -0.00006   1.85891  

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                   -4.840e+00  5.000e-01  -9.680   <2e-16 
***
as.factor(stratum)2           -3.979e-01  7.071e-01  -0.563    0.574
as.factor(stratum)3           -1.547e+00  1.118e+00  -1.384    0.166
as.factor(stratum)4           -2.069e+01  8.973e+03  -0.002    0.998
as.factor(stratum)5           -2.195e+01  8.973e+03  -0.002    0.998
as.factor(stratum)6           -2.183e+01  8.973e+03  -0.002    0.998
as.factor(stratum)7           -2.167e+01  8.973e+03  -0.002    0.998
as.factor(stratum)8           -2.108e+01  8.973e+03  -0.002    0.998
stagePOST                     -2.059e+01  8.973e+03  -0.002    0.998
stagePREF                      5.596e-01  6.268e-01   0.893    0.372
stageTRNS                     -2.059e+01  8.973e+03  -0.002    0.998
stageJUVE                     -2.059e+01  8.973e+03  -0.002    0.998
as.factor(stratum)2:stagePOST  2.100e+01  8.973e+03   0.002    0.998
as.factor(stratum)3:stagePOST  1.386e+00  1.269e+04   0.000    1.000
as.factor(stratum)4:stagePOST  3.979e+01  1.269e+04   0.003    0.997
as.factor(stratum)5:stagePOST  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)6:stagePOST  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)7:stagePOST  4.089e+01  1.269e+04   0.003    0.997
as.factor(stratum)8:stagePOST  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)2:stagePREF -8.473e-01  9.880e-01  -0.858    0.391
as.factor(stratum)3:stagePREF -1.976e+01  8.973e+03  -0.002    0.998
as.factor(stratum)4:stagePREF -5.596e-01  1.269e+04   0.000    1.000
as.factor(stratum)5:stagePREF -5.596e-01  1.269e+04   0.000    1.000
as.factor(stratum)6:stagePREF -5.596e-01  1.269e+04   0.000    1.000
```

Table 20:
Ontogenetic habitat (depth) distribution differences, equation (4), Myctophidae, Day samples: continued

```
as.factor(stratum)7:stagePREF -5.596e-01  1.269e+04   0.000    1.000
as.factor(stratum)8:stagePREF -5.596e-01  1.269e+04   0.000    1.000
as.factor(stratum)2:stageTRNS -1.670e-07  1.269e+04   0.000    1.000
as.factor(stratum)3:stageTRNS  1.386e+00  1.269e+04   0.000    1.000
as.factor(stratum)4:stageTRNS  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)5:stageTRNS  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)6:stageTRNS  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)7:stageTRNS  4.049e+01  1.269e+04   0.003    0.997
as.factor(stratum)8:stageTRNS  4.049e+01  1.269e+04   0.003    0.997
as.factor(stratum)2:stageJUVE  1.268e-07  1.269e+04   0.000    1.000
as.factor(stratum)3:stageJUVE  1.386e+00  1.269e+04   0.000    1.000
as.factor(stratum)4:stageJUVE  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)5:stageJUVE  3.979e+01  1.269e+04   0.003    0.997
as.factor(stratum)6:stageJUVE  2.059e+01  1.554e+04   0.001    0.999
as.factor(stratum)7:stageJUVE  3.979e+01  1.269e+04   0.003    0.997
as.factor(stratum)8:stageJUVE  3.979e+01  1.269e+04   0.003    0.997
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 171.039  on 119  degrees of freedom
Residual deviance:  50.408  on  80  degrees of freedom
AIC: 176.08
Number of Fisher Scoring iterations: 18
```

Table 21:
Ontogenetic habitat (depth) distribution differences, equation (4):
$E(count_{family}) \sim g^{-1}(offset(\log(water\ volume)) + depth\ stratum * stage)$

Myctophidae, Night samples:

```
Call:
glm(formula = count ~ offset(log(T.VWS)) + as.factor(stratum) *
    stage, family = poisson, data = myctophidae.8904.night)

Deviance Residuals:
    Min        1Q    Median        3Q       Max
-1.82574  -0.00003  -0.00003  -0.00003   1.60987

Coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                      -4.6167     0.4472 -10.323   <2e-16
***
as.factor(stratum)2              -0.9087     0.7303  -1.244    0.213
as.factor(stratum)3             -21.9741 14794.1413  -0.001    0.999
as.factor(stratum)4             -21.9095 14794.1395  -0.001    0.999
as.factor(stratum)5             -23.1690 14794.1396  -0.002    0.999
as.factor(stratum)6             -23.0518 14794.1397  -0.002    0.999
```

Table 21:
Ontogenetic habitat (depth) distribution differences, equation (4), Myctophidae, Night samples: continued

```
as.factor(stratum)7             -22.8914 14794.1393  -0.002    0.999
as.factor(stratum)8             -22.3066 14794.1398  -0.002    0.999
stagePOST                        -0.5108     0.7303  -0.699    0.484
stagePREF                         0.1823     0.6055   0.301    0.763
stageTRNS                       -21.8134 14794.1391  -0.001    0.999
stageJUVE                       -21.8134 14794.1411  -0.001    0.999
as.factor(stratum)2:stagePOST     0.1054     1.1690   0.090    0.928
as.factor(stratum)3:stagePOST    22.6607 14794.1413   0.002    0.999
as.factor(stratum)4:stagePOST     0.5108 20922.0727   0.000    1.000
as.factor(stratum)5:stagePOST     0.5108 20922.0728   0.000    1.000
as.factor(stratum)6:stagePOST     0.5108 20922.0729   0.000    1.000
as.factor(stratum)7:stagePOST    20.7148 14794.1394   0.001    0.999
as.factor(stratum)8:stagePOST    20.7148 14794.1398   0.001    0.999
as.factor(stratum)2:stagePREF    -0.5878     1.0954  -0.537    0.592
as.factor(stratum)3:stagePREF    -0.1823 20922.0740   0.000    1.000
as.factor(stratum)4:stagePREF    -0.1823 20922.0727   0.000    1.000
as.factor(stratum)5:stagePREF    -0.1823 20922.0728   0.000    1.000
as.factor(stratum)6:stagePREF    -0.1823 20922.0729   0.000    1.000
as.factor(stratum)7:stagePREF    -0.1823 20922.0726   0.000    1.000
as.factor(stratum)8:stagePREF    -0.1823 20922.0729   0.000    1.000
as.factor(stratum)2:stageTRNS     0.5108 20922.0724   0.000    1.000
as.factor(stratum)3:stageTRNS    21.8134 25624.2021   0.001    0.999
as.factor(stratum)4:stageTRNS    21.8134 25624.2010   0.001    0.999
as.factor(stratum)5:stageTRNS    21.8134 25624.2011   0.001    0.999
as.factor(stratum)6:stageTRNS    21.8134 25624.2012   0.001    0.999
as.factor(stratum)7:stageTRNS    42.0174 20922.0723   0.002    0.998
as.factor(stratum)8:stageTRNS    42.0174 20922.0726   0.002    0.998
as.factor(stratum)2:stageJUVE     0.5108 20922.0739   0.000    1.000
as.factor(stratum)3:stageJUVE    21.8134 25624.2032   0.001    0.999
as.factor(stratum)4:stageJUVE    21.8134 25624.2022   0.001    0.999
as.factor(stratum)5:stageJUVE    42.0174 20922.0740   0.002    0.998
as.factor(stratum)6:stageJUVE    42.0174 20922.0741   0.002    0.998
as.factor(stratum)7:stageJUVE    42.0174 20922.0738   0.002    0.998
as.factor(stratum)8:stageJUVE    42.0174 20922.0741   0.002    0.998
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 158.017  on 119  degrees of freedom
Residual deviance:  36.443  on  80  degrees of freedom
AIC: 170.19

Number of Fisher Scoring iterations: 19
```

CHAPTER 3:

Ontogenetic habitat shifts and the development of diel vertical migration in mesopelagic fishes off Central and Southern California

INTRODUCTION

The process of habitat selection is often described as a trade-off between growth rate and predator avoidance (Werner and Gilliam 1984, Werner and Anholt 1993). Environmental factors affecting these often vary throughout ontogeny. For example, early life history stages of fishes need to select habitats where densities of prey of the appropriate type and size are high enough to avoid starvation and enable growth (Houde 1997). Optimal habitats for food resources can often be co-located with predators which dictates that fishes exhibit life history strategies that strike the correct balance between survival and foraging success throughout development (Dahlgren and Eggleston 2000, Job and Bellwood 2000).

Mesopelagic fishes provide an interesting model system to study questions about the ontogeny of habitat selection because of the deceptively complex variety of habitats they use throughout their life histories. Depth stratification of an array of environmental factors, as well as the abundance of adults of most species are well-documented. In addition, adults of many species are known to undergo daily vertical migrations between productive surface waters where they are vulnerable to visual predators and deeper waters with fewer predators but where food is less common (Lampert 1989, Sutton 2013). However, much less is known regarding the behavior and depth distribution of their early life history stages. In general, mesopelagic fishes begin life as pelagic eggs near the surface in the epipelagic zone. Upon hatching, like other new larvae, they must locate and capture prey soon after their yolk-sacs are depleted. At some point during ontogeny, these larval mesopelagic fishes move deeper in the water column to their juvenile and adult habitats, and in some species, establish their vertical migration behavior. While some studies have found that depth occurrence of some mesopelagic fish species is associated with size or developmental stage, it is still unclear if the progression from the surface waters is gradual or abrupt and at what life history stage(s) the transitions begin and are completed (Sassa et al. 2007). In addition it is often assumed that these earlier life history features and behaviors are consistent with families (Moser 1996, Sassa et al. 2007) but this assumption has not been widely tested.

The present study documents the depth distributions of early life history stages of common mesopelagic fishes in the California current system. This analysis is based on discrete depth samples of fish larvae identified to species from multiple cruises over multiple years.

METHODS

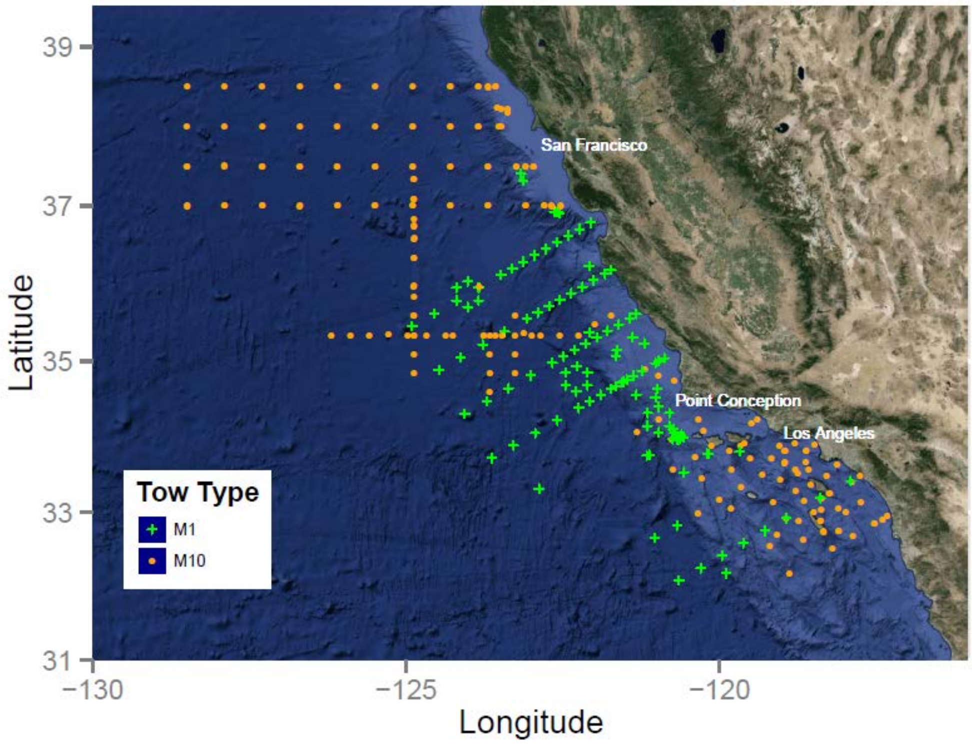


Figure 1:
Map of study area. Two types of MOCNESS were used off central and southern California. The 1 m^2 MOCNESS (M1) tows are represented by green crosses and the 10 m^2 MOCNESS (M10) are represented as filled orange circles.

Field Sampling & Laboratory Work

This study is based on ten oceanographic cruises conducted between the years of 1987 and 2001 off central and southern California (Figure 1, Table 1). Each of these cruises was conducted with different research goals but they all employed a Multiple Opening/Closing Net Environmental Sensing System (MOCNESS) (Wiebe 1976). Five cruises used a MOCNESS with a 1 m^2 mouth opening and the other five cruises used the 10 m^2 mouth opening, fitted with nets with different mesh sizes, for a total of 342 tows. Both types of MOCNESS were consistently towed at a speed of 2-2.5 knots with an angle of stray of 45°±8°, but the discrete samples were collected from a variety of depth strata. For all cruises, volume of filtered seawater and depth data were collected by the

MOCNESS. Once onboard, all nets were washed and samples were preserved in 5% buffered formalin solution.

All fishes were sorted, enumerated, identified to the lowest possible taxon, and assigned to a life-history stage as defined by Kendall (1984). In this study yolk-sac larvae were not included in the analysis due to the paucity of specimens at this earliest larval stage. Preflexion (PREF), flexion (FLEX), postflexion (POST), transformation (TRNS), and juvenile (JUVE) stages were all included in the analysis for all mesopelagic species captured.

Data Analysis

Given the spatial, temporal, frame size, and net size differences in the MOCNESS samples from the ten cruises, each sampling unit was defined as the mesopelagic fishes collected from each MOCNESS tow combining all depth strata (nets), further divided by each life-history or ontogenetic stage. More specifically, for each species, at each stage, we calculated the depth of center of mass (z_{cm}) of the vertical distribution sampled by the MOCNESS at each station. The z_{cm} calculations are based on Röpke et al. (1993) and Irisson et al. (2010).

$$z_{cm} = \sum_i A_i * z_i \qquad (1)$$

where z_i is the mean depth range in meters sampled by each individual MOCNESS net i, and A_i is the relative concentration of fish collected in each net i. These relative concentrations are standardized to account for the sampling effort of each MOCNESS net:

$$A_i = \frac{C_i * \ h_i}{\sum_i C_i * h_i} \qquad (2)$$

where C_i is the concentration of fish in each net i, and h_i is the depth range sampled by each net in meters.

$$C_i = \frac{f_i}{v_i} \qquad (3)$$

where f_i is the raw number of fish in net i and v_i is the volume of water filtered by net i. All depths of center of mass calculations (z_{cm}, Eq. 1) from the ten cruises were included in this study. For the statistical analysis of these data, each sampling unit was defined as the z_{cm} for each species, at each ontogenetic stage, collected from each MOCNESS station.

A generalized linear mixed model was built to test the hypothesis that mesopelagic fishes exhibit a downward shift in their vertical distribution as they progress through ontogeny with day and night differences.

For this hypothesis we set the following model with two fixed effects and one random effect,

$$z_{cm_{spp}} \sim stage + time\ of\ day + stage * time\ of\ day,\ \sim 1|cruise, \qquad (4)$$

where $z_{cm_{spp}}$ is the depth of center of mass for each mesopelagic fish species from each sample, $stage$ is the fixed effect of the respective ontogenetic stage, and $time\ of\ day$ is a binary fixed effect indicating if the samples were collected at night or during the day. The operator * indicates that the two fixed effects variables were fit with interactions as in a two-way ANOVA model. The random effect of the MOCNESS cruise on the intercept of the model is represented by $cruise$. The model was fit using a Log-normal error distribution for the response variable using penalized quasi-likelihood (PQL) estimation to account for non-normality and the unbalanced sampling design (Bolker et al. 2009). Wald tests were used to determine the importance of the fixed effects in the model fit for each species. These generalized linear mixed effects models were fit with the MASS package (Venables and Ripley 2002) developed for R statistical software (R Core Team 2015).

A post-hoc multiple comparison test was performed to determine the level of significance between all stages and times of day for each species (Bretz et al. 2010). The multiple comparison procedures were conducted using the multcomp package (Hothorn et al. 2008) developed for R statistical software (R Core Team 2015).

RESULTS

Laboratory Work

A total of 114,815 fishes were collected from the 342 MOCNESS tows (2,237 nets). Pelagic species from seven families (pelagic and coastal pelagic species) accounted for 23% of the fishes (26,710 individuals), and demersal species from 24 families (demersal, reef, rocky bottom, and kelp forest species) accounted for 10% (11,289 individuals) of the fishes (Table 2). Of the total fishes, only 48 individuals were in too poor of condition to be identified to family. The remaining 67% or 76,766 specimens were mesopelagic species from 33 families, of which 76,011 individuals were identified to species, 296 individuals identified to genus, and 459 individuals identified to the family level (Table 2 and Table 3). For the remainder of the paper, only those mesopelagic fishes identified to species are considered. The two most abundant species, *Stenobrachius leucopsarus* (Myctophidae) and *Cyclothone signata* (Gonostomatidae) exceeded the abundance of all other species by an order of magnitude and together accounted for 50% of the total number of mesopelagic specimens. The next 12 most abundant species in decreasing order of abundance were *Leuroglossus stilbius* (Bathylagidae), *Lipolagus ochotensis* (Bathylagidae), *Merluccius productus* (Merluccidae), *Tarletonbeania crenularis* (Myctophidae), *Nannobrachium ritteri* (Myctophidae), *Protomyctophum crockeri* (Myctophidae), *Cyclothone acclinidens* (Gonostomatidae), *Chauliodus macouni* (Stomiidae), *Diaphus theta* (Myctophidae), *Cyclothone pseudopallida* (Gonostomatidae), *Triphoturus mexicanus* (Myctophidae), and *Bathylagus pacificus* (Bathylagidae), and together accounted for 40% of the mesopelagic specimens. The remaining 10% included 85 species from 32 families.

Juvenile stage fishes were the most abundant (45% of all individuals), followed by preflexion (21.5%), postflexion (17.5%), flexion (13%), and transformation (3%) stages. The majority of the juvenile stage fishes (17,772/34,848 or 51%) were *C. signata*, the second most abundant species. The most abundant of the preflexion stage was *S. leucopsarus* (5,734/16,415 or 35%) (Table 3). Nighttime tows yielded more mesopelagic fishes than daytime tows by at least a factor of 1.2 for every ontogenetic stage (Table 4).

Statistical Analysis

For the statistical analyses we chose a subset of the mesopelagic species collected in the MOCNESS samples. The goal was to select species that were relatively abundant in each stage, from each of the five most abundant families, however only three families were sufficiently abundant. Three species were chosen from the family Myctophidae: *S. leucopsarus*, *T. crenularis*, and *P. crockeri*. Three species were chosen from the family

Bathylagidae: *L. stilbius*, *L. ochotensis*, and *B. pacificus*. *Chauliodus macouni* was the only stomiid with sufficient counts in each stage to be included in the analysis. Although very abundant overall, the gonostomatids collected in these samples had relatively few representatives in the early ontogenetic stages, thus species of this family were not chosen for further analysis. *Merluccius productus* was the only species collected from the family Merluccidae, and similar to the gonostomatids, there were too few specimens from each ontogenetic stage to include in the analyses. In total, generalized linear mixed models were fit for seven mesopelagic species.

Results of a Wald Chi-Square Test on the global importance of the fixed effects in the model indicate that both ontogenetic stage, time of day, and the interaction between both variables influence the depth of center of mass of these fishes (Table 5). These results for each species show that ontogenetic stage is more influential on the depth of center of mass than time of day. However, time of day and the interaction between ontogenetic stage and time of day also influence the depth of center of mass for all selected species except for *B. pacificus* and *C. macouni*.

The generalized linear mixed effects model results provide a more specific analysis of the fixed effects while accounting for the random effect of the cruise variable. For each species all stages except for the flexion stage were significantly different ($p<0.05$), while very few of the results for time of day or the interaction between the fixed effects differed significantly (Appendix A, Tables 1-7). However, given the appearance of differences from the plotted distributions of the depths of center of mass for each species (Figures 2-8) we conducted post hoc Tukey multiple comparison tests to determine the difference between all combinations of stage and time of day for each species (Appendix B, Tables 1-7). Preflexion and flexion stage fishes did not differ in their depths of center of mass regardless of the time of day for all species. Differences between postflexion, transformation, and juvenile stages, both during the day and at night, were present for most species. Below we describe the observed vertical patterns of distribution in the epipelagic (0-200m) and mesopelagic (200-1,000m) individually for each species to better understand the habitats these fishes occupy throughout their ontogeny.

Myctophidae

Stenobrachius leucopsarus preflexion and flexion larvae had very similar day and night vertical distributions with depths of center of mass almost entirely restricted to the upper epipelagic zone and none occurred below 242 m (Figure 2). For both of these earliest larval stages, the median nighttime distribution of depth of center of mass was slightly deeper than that during the day (day = 46 m and 39 m, night = 61 m and 59 m, respectively). During the postflexion stage, the vertical distribution range of the depths of center of mass extended from the upper epipelagic down to the mesopelagic (z_{cm}: day = 12 – 501 m, night = 13 – 586 m). During this mid-ontogenetic stage, the median nighttime depth of center of mass (72 m) was shallower than that during the day (83 m). During the transformation stage the day and night distributions of the depths of center of mass were much different than those seen in the earlier stages. Daytime distributions of the depths of center of mass were restricted to the mesopelagic zone (225 – 629 m) while the nighttime distributions extended from the epipelagic to the mesopelagic (12 – 512 m), with a median depth shallower (401 m) than that during the day (430 m). During the juvenile stage, we observed the most drastic difference between the day and night distributions. The distribution ranges were similar (day = 53 – 900 m, night = 12 – 898 m), however the median depths of center of mass were significantly different (median z_{cm}: day = 399 m, night = 122 m).

Tarletonbeania crenularis preflexion and flexion larvae also had their vertical distribution of depths of center of mass in the upper epipelagic, with an indistinguishable difference between day and night within and between these two stages (Figure 3). Even though flexion stage median depths of center of mass were similarly shallow during the day and at night (74 m and 73 m, respectively), some of these early larvae had centers of mass as deep as 717m. The postflexion distribution ranges of the depths of center of mass extended from the epipelagic to the mesopelagic (z_{cm}: day = 24 – 501 m, night = 23 – 536 m) with a deeper median daytime depth (median z_{cm}: day = 126 m, night = 89 m). Daytime depths of center of mass of transformation larvae were largely restricted to the mesopelagic (286 – 902 m), including the deepest depth sampled, with a slightly deeper median daytime depth than at night (median z_{cm}: day = 497 m, night = 450 m). The nighttime distribution range was the greatest of all stages, extending from the upper epipelagic to the maximum depth sampled (z_{cm} = 38 – 903 m). The juvenile stage distributions were dramatically different in their daytime and nighttime median depths of center of mass (422 m and 75 m, respectively). During the day, juveniles were mostly in the mesopelagic, and at night, they were mostly in the upper epipelagic.

Protomyctophum crockeri preflexion and postflexion larvae were almost entirely in the epipelagic (Figure 4). Day and night distributions of the depths of center of mass of preflexion larvae were similar (z_{cm}: day = 22 – 251 m, night = 19 – 256 m), while flexion larvae had a slightly deeper median depth during the day than at night (median z_{cm}: day =

99 m, night = 75 m). Postflexion larvae had a broader depth of center of mass distribution range (z_{cm}: day = 25 – 450m, night = 29m – 421m) with similarly deeper median depths (median z_{cm}: day = 147 m, night = 137 m). Transformation larvae were mostly in the mesopelagic with a deeper nighttime median depth of center of mass (495 m) than during the day (390 m). Juveniles were found between the lower epipelagic and upper mesopelagic with a deeper median daytime depth of center of mass (300 m) than at night (225 m).

Myctophid preflexion and flexion larvae of all three focal species had similar depth of center of mass distribution patterns. The median depths for both day and night were all in the upper epipelagic with negligible differences between day and night within each species. Of these three myctophids, *S. leucopsarus* preflexion and flexion larvae had the shallowest depth of center of mass distributions with median daytime depths of 46 m and 39 m, respectively, and 61 m and 59 m, respectively, at night. *Tarletonbeania crenularis* and *P. crockeri* preflexion larvae had similar depth of center of mass distributions with equally similar median values. All three myctophids exhibited an expansion in their range of depth of center of mass in the postflexion stage, with deeper median values. Again, *S. leucopsarus* at this stage had the shallowest median daytime and nighttime depths (median z_{cm}: day = 83 m, night = 72 m), while *T. crenularis* was deeper (median z_{cm}: day = 126 m, night = 89 m) and *P. crockeri* was the deepest (median z_{cm}: day = 147 m, night = 137 m). During transformation all three myctophids were found much deeper in the water column and with daytime depth of center of mass distributions almost entirely restricted to the mesopelagic. Day and night differences in median values were much greater during transformation for *S. leucopsarus* and *P. crockeri*, and less so for *T. crenularis*. All three species showed the greatest differences in day and night distributions and median depths of center of mass during the juvenile stage with similar qualitative patterns of being deeper during the day and shallower at night.

Bathylagidae

Leuroglossus stilbius day and night depth of center of mass distribution ranges for preflexion (z_{cm}: day = 46 – 499 m, night = 14 – 200 m) and flexion larvae (z_{cm}: day = 25 – 240 m, night = 19 – 192 m) were mostly in the epipelagic (Figure 5). However, the preflexion median depth during the day (83 m) was slightly shallower than the corresponding nighttime median value (89 m), while the opposite was true for the flexion larvae (median z_{cm}: day = 123 m, night = 92 m). During postflexion larvae had a larger vertical range (z_{cm}: day = 36 – 652 m, night = 13 – 502 m) as well as a greater difference between the median depth of center of mass during the day (238 m) and at night (125 m). Transformation and juvenile stages were similar in their depth of center of mass distributions with the most dramatic difference between their median values during the day (median z_{cm}: TRNS = 448 m, JUVE = 449 m) and at night (median z_{cm}: TRNS = 124 m, JUVE = 104 m).

Lipolagus ochotensis preflexion and flexion larvae had similar depth of center of mass vertical distribution patterns during the day (z_{cm}: PREF= 23m – 240m, FLEX= 14m – 361m) and at night (z_{cm}: PREF= 20m – 379m, FLEX= 12m – 175m) with daytime medians (z_{cm}: PREF = 86m, FLEX = 87m) slightly deeper than those at night (z_{cm}: PREF=81m, FLEX = 76m) (Figure 6). Postflexion larvae exhibited much deeper depth distributions in the water column both during the day (z_{cm} = 25m – 500m) and at night (z_{cm} = 14m – 550m), with a deeper daytime median (z_{cm} =147m), in contrast to the nighttime median (z_{cm} = 92m). Transformation larvae occurred deepest in the water column, with their daytime depth of center of mass distribution restricted to the mesopelagic (z_{cm} = 252m – 893m) and exhibited a greater contrast between their median depths during the day (z_{cm} = 497m) and at night (z_{cm} = 352m). During the juvenile stage they exhibited their most dramatic contrast between day and night median depths (z_{cm} = 498m and 99m, respectively).

Bathylagus pacificus preflexion larvae had similar daytime and nighttime median depths of center of mass in the lower epipelagic (161 m and 163 m, respectively) with diel distributions that extended well into the mesopelagic (z_{cm}: day = 23 – 401 m, night: 64 – 454 m) (Figure 7). Flexion larvae had a slightly deeper median daytime depth of center of mass (176 m) than at night (150 m). The range of depths of center of mass of postflexion larvae was shifted during the day (179 – 448 m) and at night (124 – 502 m), with a median depth considerably deeper in the water column during the day than at night (median z_{cm}: day = 321 m, night = 184 m). Transformation larvae exhibited a drastic downward shift in their day and night distributions (z_{cm}: day = 435 – 900 m, night = 435 – 901 m), with their daytime median shallower (644 m) than at night (900 m). Juvenile distributions of depth of center of mass were higher in the water column, with their nighttime range (124 – 902 m) extending into the epipelagic, while maintaining the same median depths during the day and at night (median z_{cm}: day = 501 m, night = 500 m).
Of the three bathylagids selected for analysis, *L. stilbius* and *L. ochotensis* exhibited nearly identical depth of center of mass distribution patterns at each ontogenetic stage, with slightly different daytime and nighttime median values. This pattern consisted of roughly the same day and night distributions during preflexion, slightly shallower at night

during flexion, and an expansion of the distribution during postflexion while occurring deeper during the day than at night. During the transformation stage these fishes exhibited a dramatic shift deep into the mesopelagic during the day in contrast to shallower nighttime depths of center of mass. Finally juveniles showed a clear separation between depths: deep during the day and shallow at night. *Bathylagus pacificus* depth of center of mass distribution patterns, although deeper, were similar to those of *L. stilbius* and *L. ochotensis* during preflexion, flexion, and postflexion. However, the transformation and juvenile stage depth distribution patterns were very different compared to the other two bathylagids. Transformation depths of center of mass were much deeper and did not extend into the epipelagic as observed for *L. stilbius* and *L. ochotensis.* And although juvenile *B. pacificus* occurred higher in the water column, there was no difference between their daytime and nighttime median depths.

Stomiidae

Chauliodus macouni preflexion larvae had similar depth of center of mass distribution patterns during the day (25 – 274 m) and at night (26 – 299 m), ranging from the upper epipelagic and into the mesopelagic (Figure 8). Flexion larvae had a more compact depth range (z_{cm}: day = 69 – 225 m, night = 21 – 223 m) and were slightly deeper in the water column during the day (median z_{cm} = 99 m) than at night (median z_{cm} = 76 m). Postflexion larvae occurred deeper and had greater depth of center of mass ranges both during the day (26m – 485m) and at night (17m – 402m). Transformation larvae occurred still deeper in the mesopelagic (z_{cm}: day = 413 – 622 m, night = 169 – 501 m) with a slightly deeper median depth of center of mass during the day (454 m) than at night (432 m). Juveniles had similar depth distributions during the day and at night

(z_{cm}: day = 227 – 693 m, night = 125 – 581 m) and nearly identical median depths (median z_{cm}: day = 435 m, night = 436 m), with ranges similar to the transforming larvae.

DISCUSSION

Investigation of the depths of center of mass (z_{cm}) revealed that there are differences in vertical distribution throughout ontogeny for each species analyzed in this study. In general these mesopelagic fishes spend their earliest larval stages in the upper epipelagic, gradually shift deeper into the mesopelagic as they develop, and either maintain diel depth differences, or remain in the depths in their later stages. These results are consistent with descriptions of ontogenetic shifts to deeper habitats within the water column by mesopelagic fishes off California and Baja California (Ahlstrom 1959), in the North Central Pacific Gyre (Loeb 1979), the Western North Pacific (Sassa et al. 2007), the Florida Current region (Cha et al. 1994), and in the Indian Ocean sector of the Southern Ocean (Moteki et al. 2009).

The process of habitat selection involves finding a balance between prey availability and predator avoidance (Werner and Gilliam 1984, Werner and Anholt 1993). Early larvae of fishes move slowly but have some nutritional reserves in their yolk-sacs. As they resorb their natal reserves, they develop better swimming abilities, increasing prey capture efficiency, while decreasing predation vulnerability (Hunter 1984). Ontogenetic shifts to deeper habitats by mesopelagic fishes have most often been interpreted as the optimization of potential prey intake and predation avoidance (Fortier and Harris 1989). After the yolk-sac is depleted, larvae need to consume prey frequently and they are limited to what they can successfully locate, capture, and fit in their relatively small mouths. Suitable concentrations of small prey items such as phytoplankton, protozoans, and copepod nauplii are most abundant in the upper epipelagic (Houde 2001). Preflexion and flexion larvae for all species analyzed were found in the upper epipelagic both during the day and at night. This behavior may suggest that these early larvae remain in the surface waters where feeding conditions are optimal in terms of prey size, prey density, and light intensity, as has been described for other temperate fish species (Munk et al. 1989).

The majority of all mesopelagic fish larvae have been described as being located in the upper 100 m of the water column in association with the upper mixed layer and thermocline (Ahlstrom 1959, Loeb 1979). We observed that the two earliest larval stages of the species analyzed in this study have their median depths of center of mass (z_{cm}) in the upper 100 m. However, the median depths of center of mass of postflexion and transformation larvae of these species are well below 100 m, with the exception of *S. leucopsarus* postflexion larvae. The distribution ranges of the depths of center of mass for the later larval stages of these species extend deep into the mesopelagic (Figures 2-8). These patterns can be interpreted as consistent with the idea that as larvae progress through ontogeny and they become more efficient at capturing larger prey, they also improve their ability to move out of the surface waters where they are more susceptible to visually oriented predators (Margulies 1989).

We also observed contrasting general trends both within and between the families Myctophidae and Bathylagidae. Of the three myctophids analyzed in this study, *T. crenularis* and *P. crockeri* (subfamily Myctophinae) had depths of center of mass deeper than *S. leucopsarus* (subfamily Lampanyctinae) at every ontogenetic stage (Figures 2-4).

This pattern between the subfamilies has been observed in the North Pacific Central Gyre (Loeb 1979) and in the Southern California Bight (Moser 1996). These findings are also consistent with the relative depth occurrences of myctophid larvae in the Western North Pacific (Sassa et al. 2007).

Within the Myctophidae, all three species had negligible differences in distribution between their preflexion and flexion stages, which were mainly in the epipelagic both during the day and at night. During postflexion, all three species exhibited an expansion in their distribution ranges, deepening their median depths of center of mass, with only slight diel differences. All three had dramatically deeper distributions during transformation, however, *S. leucopsarus* and *T. crenularis* had distinct diel differences in their distribution ranges. Both species’ daytime depth of center of mass distributions were restricted to the mesopelagic, while their nighttime depth minimums were both within 40m of the surface and extending deep into the mesopelagic. Juvenile stages of these species increased the difference between their daytime and nighttime depth of center of mass medians and ranges. The distribution patterns of the juveniles are consistent with what we would expect from diel vertically migrating fishes and these two species have been described as diel vertical migrators as adult fishes in the North Eastern Pacific (Paxton 1967, Pearcy et al. 1977, Willis and Pearcy 1982). These data suggest that *S. leucopsarus* and *T. crenularis* may begin their diel vertical migratory behavior during their transformation stage as has been described for other species of myctophids (Loeb 1979, Sassa and Kawaguchi 2006, Sassa et al. 2007). The third myctophid analyzed (*P. crockeri*) did not exhibit a diel vertical migratory pattern during any of its ontogenetic stages which is consistent with the descriptions of the adult stage as being a non-migrator (Pearcy and Laurs 1966, Paxton 1967, Pearcy et al. 1977, Willis and Pearcy 1982, Davison et al. 2015).

In contrast to the myctophids, two of the bathylagids analyzed, *L. stilbius* and *L. ochotensis* exhibited distribution patterns mainly in the epipelagic during preflexion and flexion stages, followed by distinct diel differences in the postflexion stage, and then what appears to be diel vertical migratory patterns in both transformation and juvenile stages. This is consistent with diel vertical migration behavior described for the adults of these species (Ahlstrom 1959, Pearcy and Laurs 1966, Willis and Pearcy 1982, Cailliet and Ebeling 1990). These two bathylagids appear to begin their diel migratory patterns in the postflexion stage, whereas the myctophids observed in this study do not begin this pattern until transformation (Figures 5 and 6). The third bathylagid, *B. pacificus*, did not show patterns of diel vertical migration, which is consistent with the descriptions of adults of this species as a non-migrator (Ahlstrom 1959, Loeb 1979, Willis and Pearcy 1982, Davison et al. 2015).

The only stomiid selected for analysis, *C. macouni*, had a clearly discernible distribution pattern that changed dramatically during larval development. The preflexion and flexion larvae had similarly shallow depth of center of mass distributions, while the postflexion larvae exhibited an expansion in their depth range, similar to the other mesopelagics in this study. The transformation larvae seem to have distinct diel distribution patterns, but the juvenile distribution patterns are clearly the same and do not show the diel migratory patterns observed for some of the other species. *Chauliodus macouni* is a mesopelagic predator (Moser and Smith 1993) and is described as a species that does not undergo diel vertical migrations as an adult (Loeb 1979, Willis and Pearcy

1982). Although this species is not classified as a vertical migrator, its juvenile depth of center of mass distribution range overlaps with all of the other mesopelagics in this study that are potential prey.

Although the observed patterns for these species appear to be consistent with the accepted descriptions of the presence or absence of vertical migratory behavior in the adults, it is possible that these patterns are affected by net avoidance. The global calculations of the abundance of mesopelagic fishes are considered to be underestimates revealed by the large discrepancies between the consistently higher acoustic estimates compared to estimates made from net tows, due to net avoidance by these taxa (Kaartvedt et al. 2012). It is possible that these fishes are able to avoid nets in their earlier life history stages which would affect the patterns observed in this study, however, we think this is not the case because of the higher occurrence of these fishes at the surface at night, and deeper in the water column during the day, in their later larval stages. The presence of this pattern was described by Pearcy and Laurs (1966) as an indication of diel vertical migration.

Diel vertical migration is a behavior pattern associated with the life history strategies of many mesopelagic taxa (Sutton 2013). It is clear, however, that many deeper-living mesopelagic species do not undergo diel vertical migrations as shown for *P. crockeri*, *B. pacificus*, and *C. macouni* in this and other studies (Ahlstrom 1959, Pearcy and Laurs 1966, Lavenberg and Ebeling 1967, Paxton 1967, Pearcy et al. 1977, Loeb 1979, Willis and Pearcy 1982, Cailliet and Ebeling 1990, Neighbors and Wilson 2006, Davison et al. 2015). There are potentially significant life history strategy tradeoffs associated with this behavior such as the energetic costs required to undertake these vast migrations daily, and increased predation risks when moving into the euphotic zone. Childress (1980) described some of the potential tradeoffs in terms of growth, energy, and reproduction. Relative to non-migrators, vertical migrators were described as growing more slowly and reproducing earlier and more often. Vertical migrators use a considerable amount of energy to make their diel movements, but they are feeding in much more productive waters with potentially higher prey densities, than if they remained at depth. Migrators are typically small-bodied, which potentially allows for increased energy allocation to reproduction because these fishes spawn on average after 1-3 years. In contrast to the migrator strategy, non-migrators that are deeper-living (such as *C. macouni*) allocate more energy into growing to much larger relative sizes and a delay in reproduction.

We determined that mesopelagic fish species in the study area exhibit a downward shift in the water column as they progress through early ontogeny, a shift that generally occurs in the postflexion stage. We also found that diel vertical migratory behavior may start as early as the postflexion stage in some bathylagids, and the transformation stage in some myctophids. These details indicate that mesopelagic fishes begin establishment of adult habitat use patterns earlier than generally appreciated. However, there is significant variation in these ontogenetic patterns within the families Myctophidae and Bathylagidae, cautioning against generalizing assumptions of such behaviors across families. In addition, studies of the distributions and behaviors of larval mesopelagic fishes identified only to higher taxonomic levels are potentially compromised in light of this variation.

An additional physical constraint both migrators and non-migrators are challenged with is the low oxygen concentrations in the deeper waters below the productive surface layers (Childress and Seibel 1998). The presence of this oxygen minimum zone may be an especially important parameter affecting the survival of the early stages of fish larvae whose circulatory and respiratory systems are incompletely developed (O'Connell 1981). Given the ontogenetic increase in depth distributions of larval mesopelagic fishes documented in this and other studies (Ahlstrom 1959, Loeb 1979, Cha et al. 1994, Sassa et al. 2007, Moteki et al. 2009), the predicted shoaling of oxygen minimum zones (Bograd et al. 2008, Netburn and Koslow 2015) will likely have a larger impact on these fishes than previously recognized.

Chapters 2, 3, and 4, in part, are currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of the material in all chapters of this dissertation.

Table 1:
Summary of the ten MOCNESS sampling schemes used for this study. M1 = 1 m^2 MOCNESS; M10 = 10 m^2 MOCNESS.

Cruise Code	Start Date	End Date	MOCNESS Type	# Discrete Nets	Depth Range Sampled (m)	Net Mesh Size (mm)	# of Tows
8701	1987-01-11	1987-02-15	M1	9	0-1186	0.505	20
8904	1989-04-16	1989-05-04	M1	8	0-1200	0.505	17
9104	1991-03-22	1991-05-01	M1	9	0-1219	0.505	51
9107	1991-07-02	1991-07-17	M10	5	0-1000	0.505	47
9203	1992-03-14	1992-04-02	M10	5	0-600	0.505	46
9306	1993-06-26	1993-07-12	M10	5	0-612	0.333	34
9503	1995-03-10	1995-03-27	M1	9	0-315	0.505	30
9504	1995-04-06	1995-05-06	M10	5	0-316	0.333	16
9701	1997-01-10	1997-01-22	M1	9	0-300	0.505	18
0106	2001-06-18	2001-07-14	M10	5	0-200	0.505	63

Table 2:
Counts of individual fishes collected in the MOCNESS samples divided by family, further categorized by habitat type.

Habitat	Family	Total	Habitat	Family	Total
Demersal	Paralichthyidae	4698	Mesopelagic	Myctophidae	31626
	Scorpaenidae	4241		Gonostomatidae	21636
	Pleuronectidae	1936		Bathylagidae	12941
	Gobiidae	139		Merlucciidae	3773
	Sciaenidae	66		Stomiidae	2864
	Blenniidae	30		Sternoptychidae	2117
	Cottidae	25		Melamphaidae	568
	Liparidae	18		Paralepididae	262
	Zoarcidae	15		Trachipteridae	158
	Agonidae	13		Microstomatidae	157
	Hexagrammidae	9		Platytroctidae	133
	Syngnathidae	5		Scopelarchidae	81
	Anoplopomatidae	4		Centrolophidae	73
	Ophidiidae	3		Bythitidae	59
	Bathymasteridae	2		Notosudidae	57
	Ophichthidae	1		Phosichthyidae	54
	Cyclopteridae	1		Howellidae	53
	Chaenopsidae	1		Microstomatidae	40
	Stichaeidae	1		Argentinidae	29
	Pomacentridae	16		Opisthoproctidae	22
	Balistidae	1		Alepocephalidae	21
	Labridae	40		Nemichthyidae	11
	Serranidae	23		Tetragonuridae	6
	Kyphosidae	1		Icosteidae	5
Pelagic	Engraulidae	26343		Anoplogastridae	4
	Clupeidae	126		Macrouridae	3
	Stromateidae	36		Oneirodidae	3
	Scombridae	9		Neoscopelidae	2
	Sphyraenidae	3		Eurypharyngidae	2
	Carangidae	190		Cyematidae	2
	Scomberesocidae	3		Serrivomeridae	2
				Cottidae	2
				Chiasmodontidae	2

Table 3:
Counts of individual mesopelagic fish species with 100 or more individuals collected in the MOCNESS samples, per ontogenetic stage. The distribution of the seven species above the dashed line were analyzed separately.

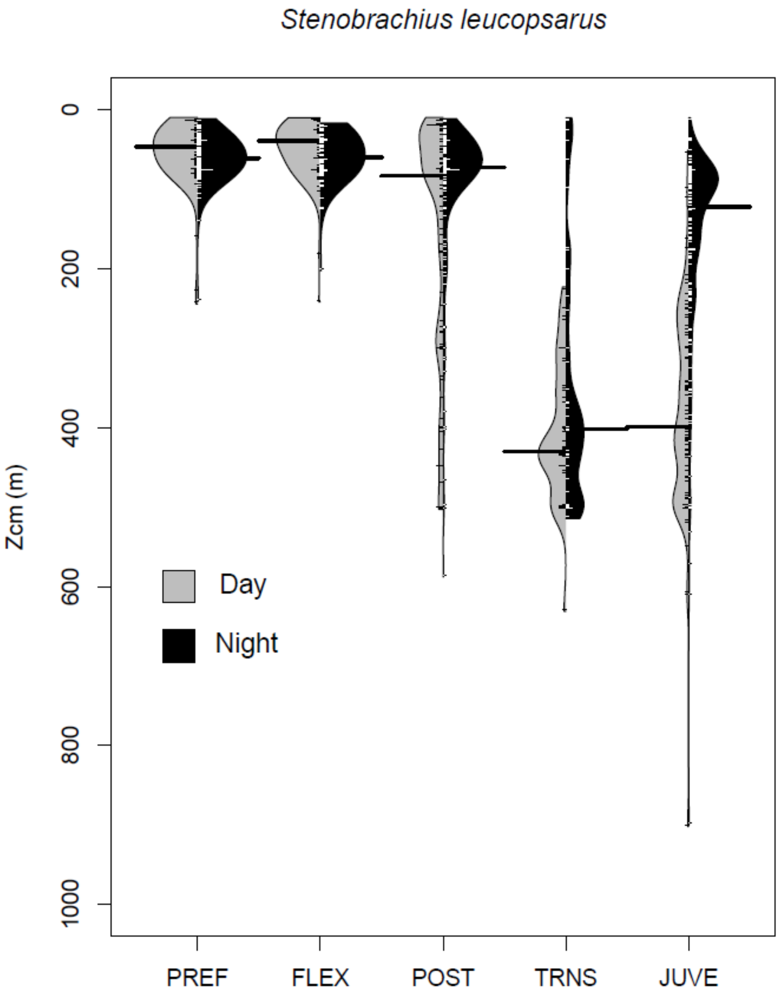
Taxon	PREF	FLEX	POST	TRNS	JUVE	Total
Stenobrachius leucopsarus	5734	4465	5419	568	4199	20385
Leuroglossus stilbius	2835	1154	1264	288	300	5841
Lipolagus ochotensis	2601	1139	1063	192	358	5353
Tarletonbeania crenularis	638	609	1488	242	241	3218
Protomyctophum crockeri	181	193	687	49	774	1884
Chauliodus macouni	106	92	774	66	764	1802
Bathylagus pacificus	717	107	40	28	98	990
Cyclothone signata	4	5	36	53	17772	17870
Merluccius productus	1955	1041	734	9	34	3773
Nannobrachium ritteri	283	173	200	37	1635	2328
Cyclothone acclinidens	0	0	0	0	1818	1818
Diaphus theta	112	201	366	207	490	1376
Cyclothone pseudopallida	0	0	0	1	1252	1253
Triphoturus mexicanus	61	133	229	1	707	1131
Argyropelecus sladeni	3	2	12	68	755	840
Danaphos oculatus	3	8	86	135	360	592
Tactostoma macropus	98	124	136	5	154	517
Cyclothone atraria	0	0	0	0	433	433
Argyropelecus hemigymnus	1	0	3	69	303	376
Idiacanthus antrostomus	0	4	8	1	328	341
Bathylagidae	328	1	2	0	4	335
Nannobrachium regale	73	55	101	10	96	335
Melamphaes lugubris	35	20	105	28	106	294
Bathylagoides wesethi	19	19	30	3	218	289
Ceratoscopelus townsendi	2	7	9	2	219	239
Lestidiops ringens	38	12	93	25	64	232
Symbolophorus californiensis	12	3	77	2	106	200
Nannobrachium sp.	151	6	5	2	15	179
Argyropelecus affinis	3	1	9	32	124	169
Nansenia candida	74	58	24	0	1	157
Trachipterus altivelis	36	61	34	4	12	147
Cyclothone pallida	0	0	0	0	145	145
Pseudobathylagus milleri	75	16	14	4	24	133
Diogenichthys atlanticus	20	7	38	9	59	133
Aristostomias scintillans	0	0	3	0	127	130
Myctophidae	22	17	30	5	50	124
Cyclothone sp.	0	0	0	0	117	117

Table 4:
Counts of individual mesopelagic fish specimens per ontogenetic stage collected in the MOCNESS samples. Time of Day indicates if the specimen was collected during the day or at night.

Time of Day	PREF	FLEX	POST	TRNS	JUVE
day	5989	3184	3899	849	15724
night	10430	6660	9522	1376	19133

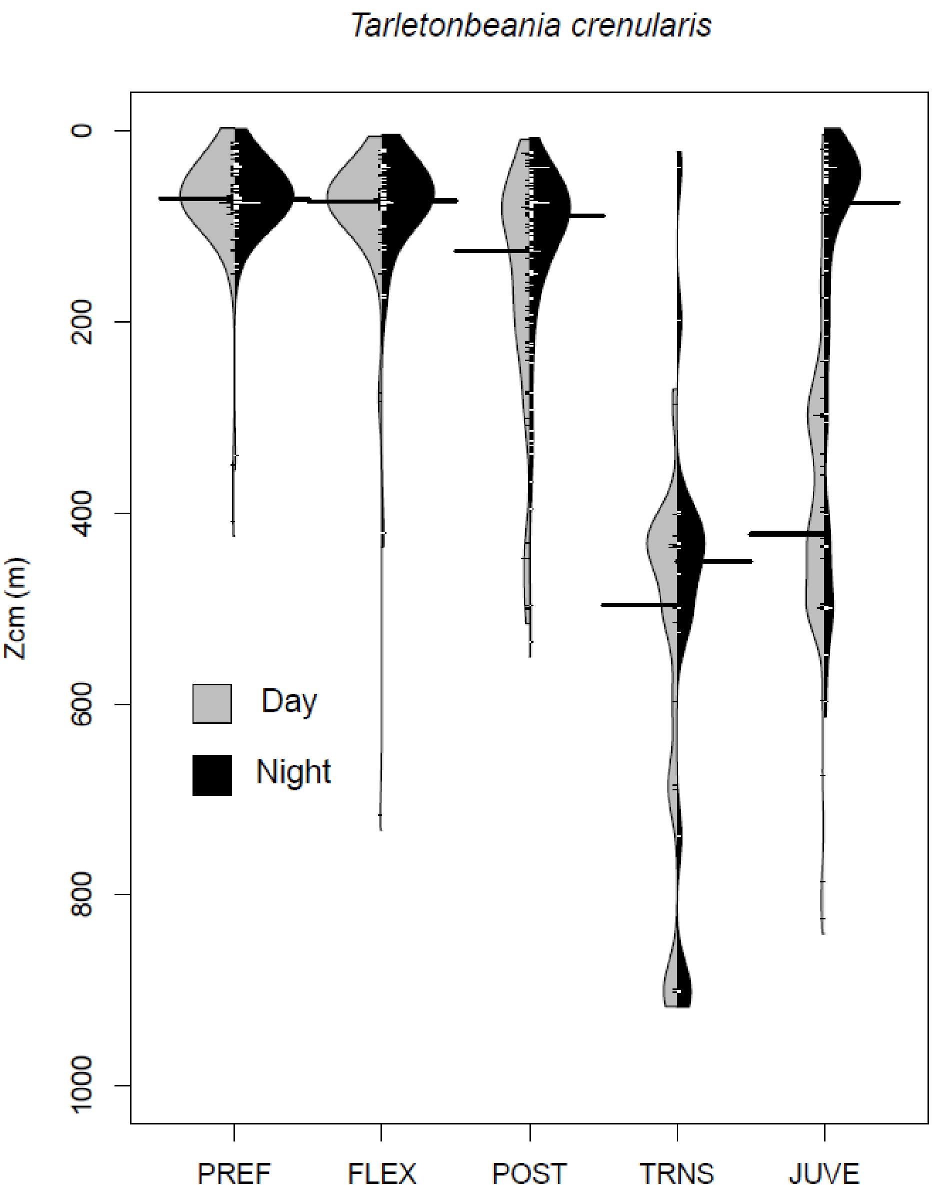
Table 5:
Wald Chi-Square test results indicate the importance of each fixed effect in the generalized linear mixed model. For each test, the test statistic and *p*-value are reported; significant test results are bolded.

	Fixed Effects					
	stage		time of day		stage*time of day	
Species	X^2	p	X^2	p	X^2	p
Stenobrachius leucopsarus	549.34	**< 0.001**	83.405	**< 0.001**	39.908	**< 0.001**
Tarletonbeania crenularis	454.21	**< 0.001**	454.21	**< 0.001**	454.21	**0.001**
Protomyctophum crockeri	873.217	**< 0.001**	4.98	**0.0256**	11.069	**0.0258**
Leuroglossus stilbius	271.002	**< 0.001**	34.227	**< 0.001**	10.512	**0.0326**
Lipolagus ochotensis	551.756	**< 0.001**	82.042	**< 0.001**	90.91	**< 0.001**
Bathylagus pacificus	346.788	**< 0.001**	1.012	0.3143	11.509	**0.0214**
Chauliodus macouni	1071.719	**< 0.001**	1.853	0.174	3.243	0.518



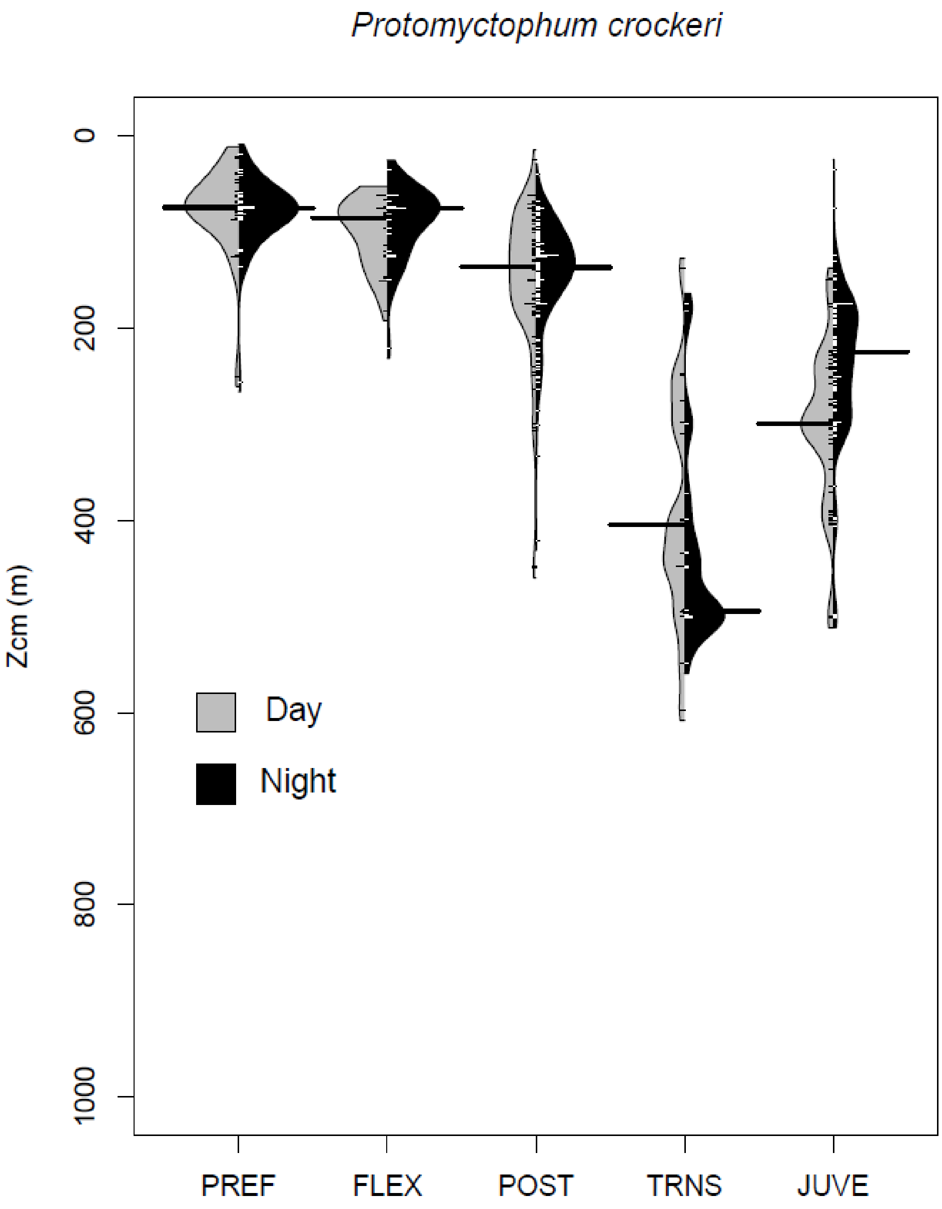
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	85	95	57	78	93	143	42	41	86	156
min (m)	12	13	12	19	12	13	225	12	53	12
max (m)	242	239	240	200	501	586	629	512	900	898
median (m)	46	61	39	59	83	72	430	401	399	122

Figure 2:
Ontogenetic vertical distribution of *Stenobrachius leucopsarus*, family Myctophidae, shown as “beanplots” (modified violin plots) of the probability density function of the day and night vertical distribution of the depth center of mass (z_{cm}) of each ontogenetic stage for each species collected from ten MOCNESS cruises. Each shape is estimated using kernel density for the number of z_{cm} calculations (n) made at each station where each species at each stage was collected. The horizontal axis indicates each of five ontogenetic stages: preflexion (PREF), flexion (FLEX), postflexion (POST), transformation (TRNS), and juvenile (JUVE). The vertical axis is the depth, in meters, of the centers of mass. The table below the beanplots provides a day and night summary of the number of (n), median depth, minimum depth, and maximum depth of center of mass (z_{cm}) calculations for each ontogenetic stage.



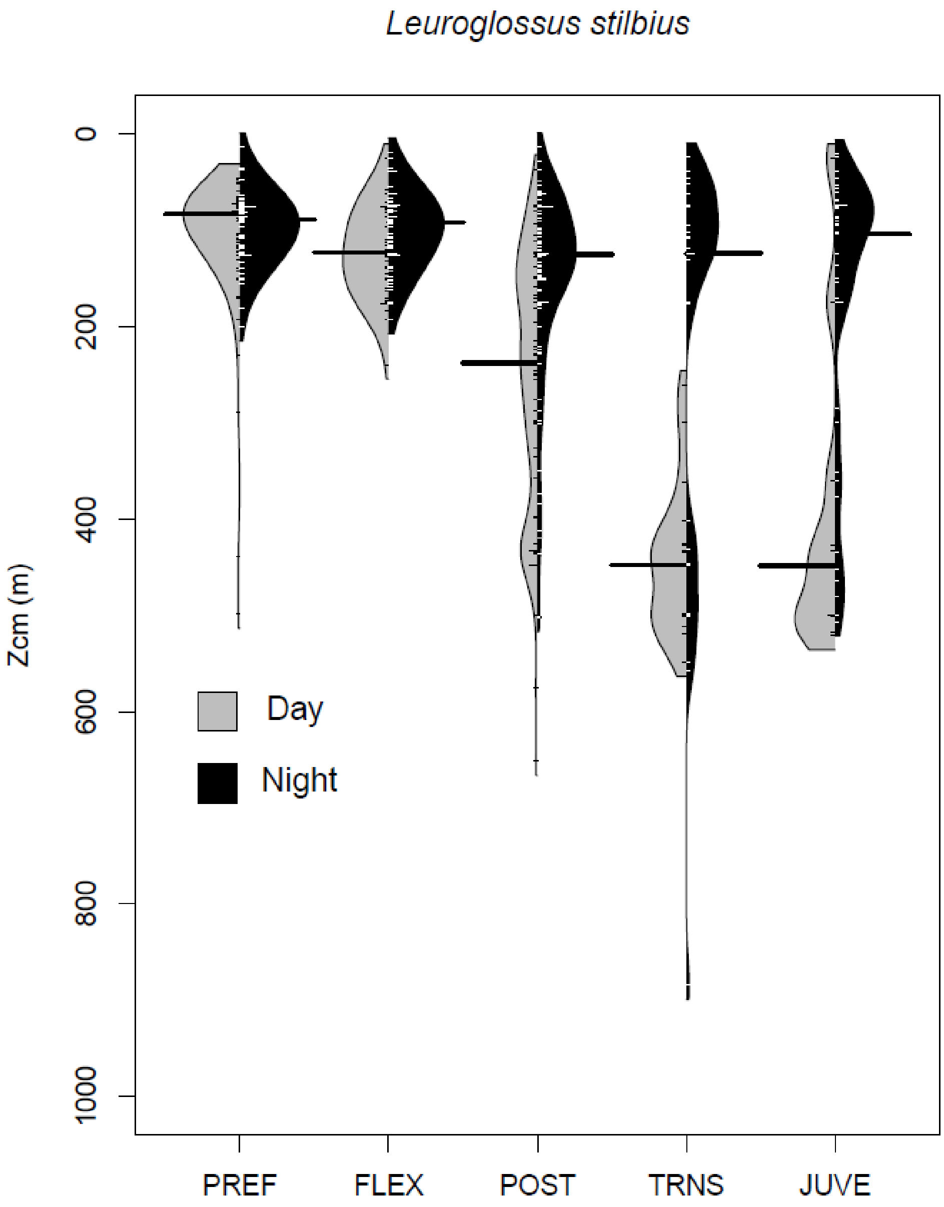
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	59	67	43	42	64	99	17	16	38	47
min (m)	12	13	21	19	24	23	286	38	19	13
max (m)	409	340	717	421	501	536	902	903	825	598
median (m)	71	72	74	73	126	89	497	451	422	75

Figure 3:
Beanplot of the ontogenetic vertical distribution of *Tarletonbeania crenularis*, family Myctophidae. See Figure 2 for description.



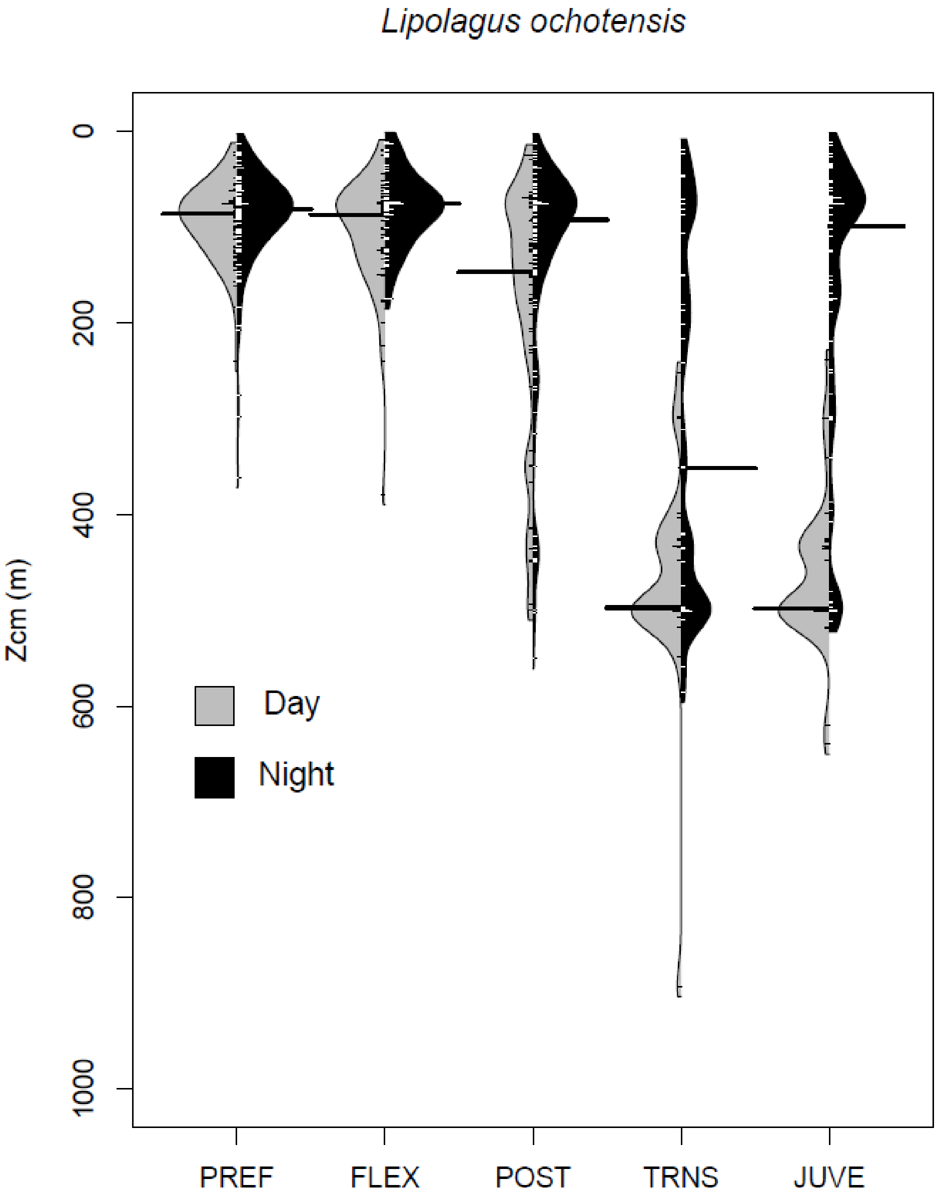
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	30	39	29	29	82	127	17	21	67	87
min (m)	22	19	63	36	25	39	138	175	148	35
max (m)	251	256	182	221	450	421	598	549	502	501
median (m)	75	75	86	75	136	137	405	195	299	225

Figure 4:
Beanplot of the ontogenetic vertical distribution of *Protomyctophum crockeri*, family Myctophidae. See Figure 2 for description.



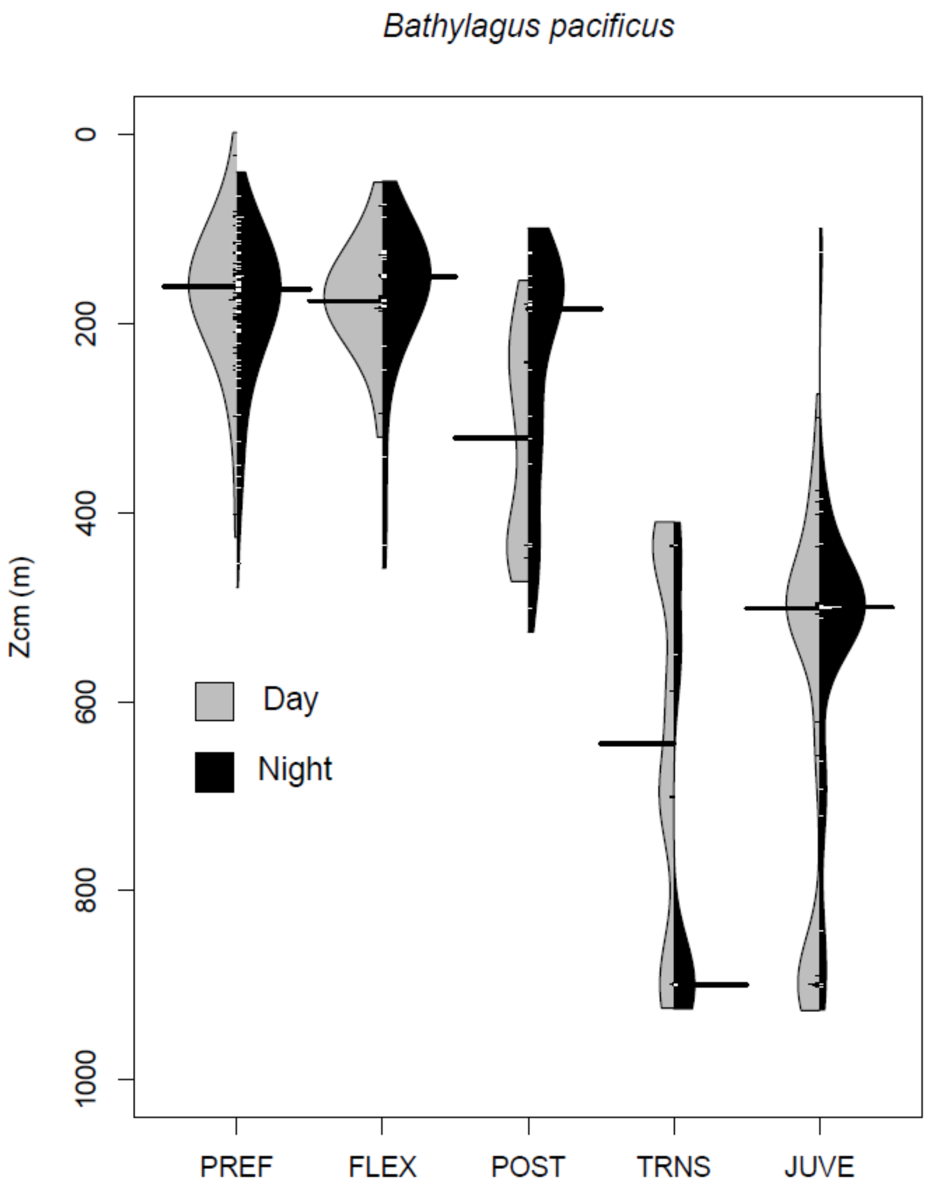
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	57	61	44	63	52	92	17	30	11	43
min (m)	46	14	25	19	36	13	260	24	25	21
max (m)	499	200	240	192	652	502	549	885	521	507
median (m)	83	88	123	92	238	125	448	124	449	104

Figure 5:
Beanplot of the ontogenetic vertical distribution of *Leuroglossus stilbius*, family Bathylagidae. See Figure 2 for description.



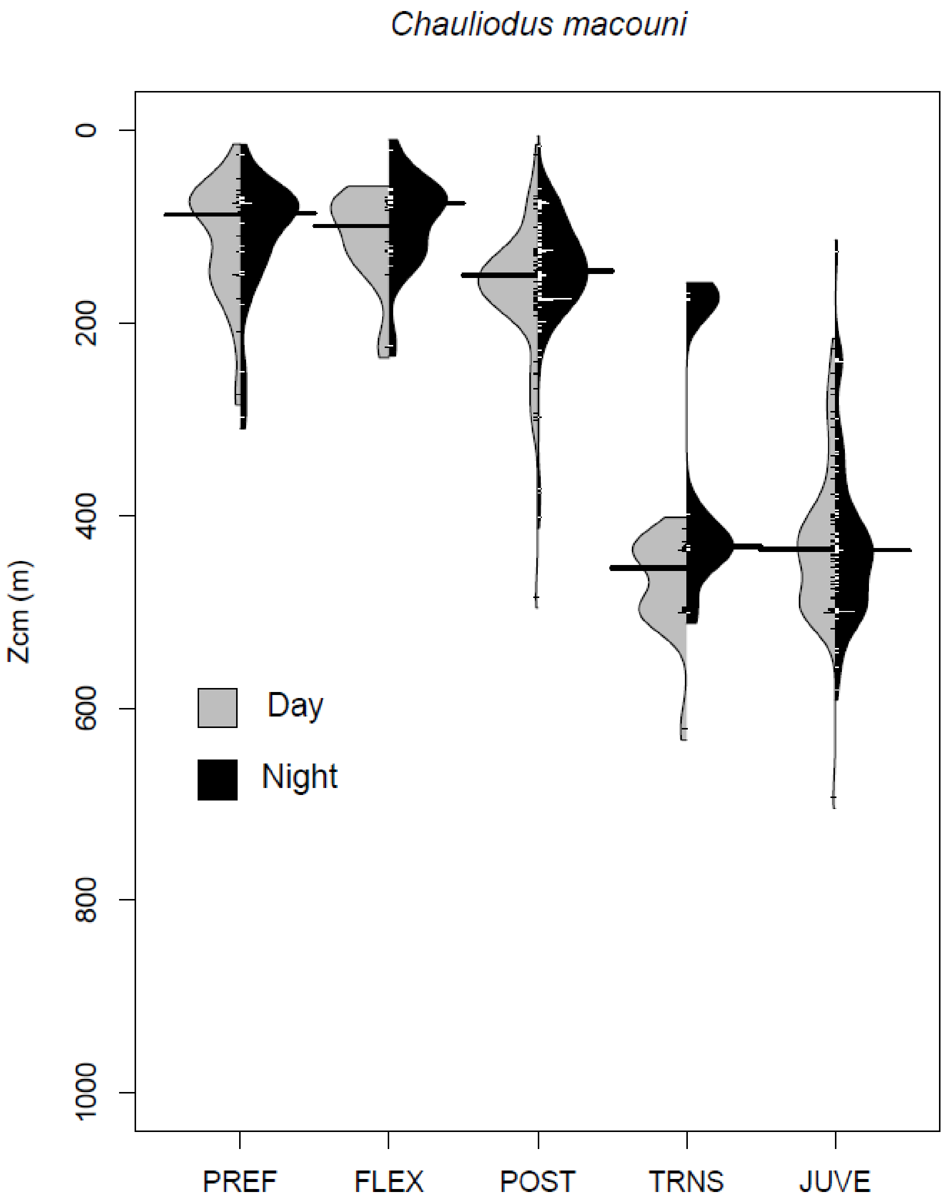
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	79	85	58	73	59	92	26	39	37	64
min (m)	23	14	20	12	25	14	252	19	239	12
max (m)	240	361	379	175	500	550	893	586	640	512
median (m)	86	81	87	76	147	92	497	352	498	99

Figure 6:
Beanplot of the ontogenetic vertical distribution of *Lipolagus ochotensis*, family Bathylagidae. See Figure 2 for description.



	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	42	49	15	20	7	16	8	5	29	27
min (m)	23	64	75	74	179	124	435	435	299	124
max (m)	401	454	295	434	448	502	900	901	902	902
median (m)	161	164	176	150	321	184	644	900	501	500

Figure 7:
Beanplot of the ontogenetic vertical distribution of *Bathylagus pacificus*, family Bathylagidae. See Figure 2 for description.



	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	23	20	10	15	60	107	19	9	58	61
min (m)	25	26	69	21	26	17	413	169	227	125
max (m)	274	299	225	223	486	402	622	501	693	581
median (m)	88	85	99	76	150	146	454	432	436	436

Figure 8:
Beanplot of the ontogenetic vertical distribution of *Chauliodus macouni*, family Stomiidae. See Figure 2 for description.

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APPENDIX A: Generalized Linear Mixed Model Output Summary

Each of the proceeding tables is the summary of the model results for each of the seven mesopelagic species from equation (4):

$$Z_{cm_{spp}} \sim stage + time\ of\ day + stage * time\ of\ day, \sim 1|cruise$$

In each table, $time\ of\ day$ is represented by the variable "light."

Table 1:
Stenobrachius leucopsarus

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.292
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.2895362 98.51739

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                         Value Std.Error  DF   t-value p-value
(Intercept)           3.799937 0.2222436 857 17.098075  0.0000
stageFLEX            -0.090120 0.3321418 857 -0.271328  0.7862
stagePOST             1.085399 0.2118809 857  5.122682  0.0000
stageTRNS             2.039357 0.2058560 857  9.906714  0.0000
stageJUVE             1.963154 0.2036495 857  9.639867  0.0000
lightnight            0.140668 0.2629571 857  0.534946  0.5928
stageFLEX:lightnight  0.039458 0.4209261 857  0.093741  0.9253
stagePOST:lightnight -0.403309 0.2819950 857 -1.430200  0.1530
stageTRNS:lightnight -0.254447 0.2692185 857 -0.945130  0.3449
stageJUVE:lightnight -0.700843 0.2680758 857 -2.614346  0.0091
 Correlation:
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.546
stagePOST            -0.858  0.576
stageTRNS            -0.884  0.593  0.936
stageJUVE            -0.893  0.598  0.942  0.972
lightnight           -0.691  0.462  0.724  0.745  0.754
stageFLEX:lightnight  0.431 -0.788 -0.453 -0.466 -0.470 -0.625
stagePOST:lightnight  0.643 -0.431 -0.747 -0.697 -0.704 -0.932
0.582
stageTRNS:lightnight  0.675 -0.452 -0.708 -0.754 -0.736 -0.977
0.610  0.911
```

Table 1:
Stenobrachius leucopsarus, continued

```
stageJUVE:lightnight  0.675 -0.454 -0.712 -0.733 -0.755 -0.980
0.613  0.916  0.958

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.4697828 -0.4321124 -0.0629099  0.2929729  6.6154382

Number of Observations: 876
Number of Groups: 10
```

Table 2:
Tarletonbeania crenularis

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.299
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.3301373 114.9159

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                         Value Std.Error  DF   t-value p-value
(Intercept)           4.170164 0.2303203 472 18.105933  0.0000
stageFLEX             0.250337 0.2726830 472  0.918051  0.3591
stagePOST             0.805318 0.2212381 472  3.640050  0.0003
stageTRNS             2.011130 0.2109412 472  9.534077  0.0000
stageJUVE             1.696233 0.2095170 472  8.095923  0.0000
lightnight           -0.048118 0.2826595 472 -0.170234  0.8649
stageFLEX:lightnight -0.152190 0.4125059 472 -0.368940  0.7123
stagePOST:lightnight -0.077311 0.3093925 472 -0.249879  0.8028
stageTRNS:lightnight  0.008925 0.2926796 472  0.030494  0.9757
stageJUVE:lightnight -0.503118 0.2991022 472 -1.682093  0.0932
 Correlation:
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.639
stagePOST            -0.789  0.678
stageTRNS            -0.826  0.712  0.889
stageJUVE            -0.833  0.715  0.893  0.941
lightnight           -0.609  0.517  0.635  0.667  0.671
stageFLEX:lightnight  0.418 -0.653 -0.435 -0.458 -0.459 -0.684
```

Table 2:
Tarletonbeania crenularis, continued

```
stagePOST:lightnight  0.555 -0.476 -0.696 -0.617 -0.620 -0.913
0.625
stageTRNS:lightnight  0.587 -0.499 -0.612 -0.685 -0.648 -0.965
0.660  0.882
stageJUVE:lightnight  0.569 -0.489 -0.601 -0.633 -0.673 -0.944
0.646  0.864  0.913

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.3881043 -0.5059887 -0.1023704  0.1419174  5.4023837

Number of Observations: 491
Number of Groups: 10
```

Table 3:
Protomyctophum crockeri

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.288
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.1893478 65.01991

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                         Value Std.Error  DF   t-value p-value
(Intercept)           4.214863 0.1695115 509 24.864755  0.0000
stageFLEX             0.279539 0.1995311 509  1.400979  0.1618
stagePOST             0.690274 0.1651585 509  4.179465  0.0000
stageTRNS             1.683944 0.1630786 509 10.325968  0.0000
stageJUVE             1.405209 0.1607213 509  8.743144  0.0000
lightnight            0.051232 0.2059827 509  0.248719  0.8037
stageFLEX:lightnight -0.152330 0.2749383 509 -0.554053  0.5798
stagePOST:lightnight -0.012342 0.2158537 509 -0.057180  0.9544
stageTRNS:lightnight -0.021489 0.2130851 509 -0.100845  0.9197
stageJUVE:lightnight -0.202330 0.2096085 509 -0.965277  0.3349
 Correlation:
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.733
```

Table 3:
Protomyctophum crockeri, continued

```
stagePOST            -0.888  0.751
stageTRNS            -0.902  0.761  0.922
stageJUVE            -0.913  0.773  0.941  0.948
lightnight           -0.711  0.603  0.728  0.738  0.748
stageFLEX:lightnight  0.534 -0.727 -0.547 -0.555 -0.562 -0.750
stagePOST:lightnight  0.675 -0.575 -0.762 -0.704 -0.714 -0.954
0.716
stageTRNS:lightnight  0.692 -0.584 -0.705 -0.765 -0.723 -0.968
0.727  0.922
stageJUVE:lightnight  0.696 -0.592 -0.716 -0.724 -0.757 -0.982
0.737  0.938  0.949

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.69332231 -0.51920757 -0.09738994  0.46915972  4.23077672

Number of Observations: 528
Number of Groups: 10
```

Table 4:
Leuroglossus stilbius

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.72
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:    0.383533 89.09074

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                         Value Std.Error  DF   t-value p-value
(Intercept)           4.576676 0.1627378 451 28.123015  0.0000
stageFLEX             0.084228 0.1527031 451  0.551583  0.5815
stagePOST             0.853353 0.1174417 451  7.266178  0.0000
stageTRNS             1.235054 0.1213686 451 10.176061  0.0000
stageJUVE             1.246765 0.1254691 451  9.936825  0.0000
lightnight           -0.127336 0.1591869 451 -0.799915  0.4242
stageFLEX:lightnight  0.001247 0.2272320 451  0.005489  0.9956
stagePOST:lightnight -0.190338 0.1754094 451 -1.085109  0.2785
stageTRNS:lightnight  0.010480 0.1774715 451  0.059050  0.9529
```

Table 4:
Leuroglossus stilbius, continued

```
stageJUVE:lightnight -0.342181 0.1860869 451 -1.838825  0.0666
 Correlation:
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.437
stagePOST            -0.584  0.618
stageTRNS            -0.568  0.596  0.832
stageJUVE            -0.541  0.567  0.779  0.771
lightnight           -0.414  0.442  0.574  0.554  0.535
stageFLEX:lightnight  0.289 -0.667 -0.403 -0.390 -0.373 -0.698
stagePOST:lightnight  0.373 -0.400 -0.624 -0.511 -0.491 -0.906
0.634
stageTRNS:lightnight  0.367 -0.399 -0.518 -0.616 -0.482 -0.898
0.628  0.818
stageJUVE:lightnight  0.345 -0.374 -0.482 -0.467 -0.635 -0.855
0.596  0.778  0.774

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-4.20643308 -0.54255846 -0.07627991  0.41203771  5.14216265

Number of Observations: 470
Number of Groups: 10
```

Table 5:
Lipolagus ochotensis

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.68
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.2835307 99.18657

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                        Value Std.Error  DF   t-value p-value
(Intercept)          4.357463 0.1542619 593 28.247184  0.0000
stageFLEX            0.129575 0.1734744 593  0.746941  0.4554
stagePOST            0.745461 0.1417592 593  5.258641  0.0000
stageTRNS            1.646697 0.1299426 593 12.672493  0.0000
stageJUVE            1.649231 0.1279748 593 12.887150  0.0000
```

Table 5:
Lipolagus ochotensis, continued

```
lightnight            0.020649 0.1674368 593  0.123324  0.9019
stageFLEX:lightnight -0.259752 0.2558362 593 -1.015305  0.3104
stagePOST:lightnight -0.143530 0.1948295 593 -0.736698  0.4616
stageTRNS:lightnight -0.355184 0.1796170 593 -1.977450  0.0485
stageJUVE:lightnight -0.707510 0.1835371 593 -3.854863  0.0001
 Correlation: 
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.539                                   
stagePOST            -0.665  0.607                            
stageTRNS            -0.723  0.662  0.821                     
stageJUVE            -0.735  0.672  0.832  0.906              
lightnight           -0.565  0.501  0.612  0.667  0.678       
stageFLEX:lightnight  0.367 -0.672 -0.403 -0.440 -0.447 -0.654
stagePOST:lightnight  0.480 -0.432 -0.707 -0.577 -0.586 -0.858
0.563
stageTRNS:lightnight  0.522 -0.467 -0.570 -0.698 -0.632 -0.931
0.609  0.800
stageJUVE:lightnight  0.503 -0.457 -0.554 -0.605 -0.671 -0.912
0.598  0.787  0.851

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-3.3146723 -0.4555012 -0.1273523  0.2790805  4.8581697 

Number of Observations: 612
Number of Groups: 10
```

Table 6:
Bathylagus pacificus

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.69 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.1531219 107.4755

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: Zcm ~ stage * light 
                         Value Std.Error  DF  t-value p-value
(Intercept)           5.151450 0.1183755 201 43.51787  0.0000
```

Table 6:
Bathylagus pacificus, continued

```
stageFLEX             -0.073910 0.1973204 201 -0.37457  0.7084
stagePOST              0.431544 0.1727770 201  2.49769  0.0133
stageTRNS              1.082782 0.1320867 201  8.19751  0.0000
stageJUVE              1.273090 0.1174983 201 10.83497  0.0000
lightnight             0.097597 0.1300443 201  0.75049  0.4538
stageFLEX:lightnight -0.024260 0.2525798 201 -0.09605  0.9236
stagePOST:lightnight -0.318385 0.2146115 201 -1.48354  0.1395
stageTRNS:lightnight  0.084972 0.1593848 201  0.53313  0.5945
stageJUVE:lightnight -0.220318 0.1397715 201 -1.57627  0.1165
 Correlation: 
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.445                                   
stagePOST            -0.545  0.349                            
stageTRNS            -0.706  0.461  0.593                     
stageJUVE            -0.789  0.504  0.634  0.839              
lightnight           -0.635  0.386  0.433  0.568  0.638       
stageFLEX:lightnight  0.324 -0.760 -0.230 -0.308 -0.344 -0.516
stagePOST:lightnight  0.387 -0.237 -0.713 -0.356 -0.395 -0.605
0.313
stageTRNS:lightnight  0.511 -0.320 -0.356 -0.653 -0.532 -0.818
0.430  0.496
stageJUVE:lightnight  0.596 -0.369 -0.417 -0.548 -0.672 -0.928
0.480  0.563  0.760

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-5.18385453 -0.38853479 -0.06277608  0.36987159  2.99499313 

Number of Observations: 218
Number of Groups: 8
```

Table 7:
Chauliodus macouni

```
Linear mixed-effects model fit by maximum likelihood
 Data: allfish.ctr.mass.156 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | cruise
        (Intercept) Residual
StdDev:   0.1663972 64.16207

Variance function:
 Structure: fixed weights
```

Table 7:
Chauliodus macouni, continued

```
Formula: ~invwt
Fixed effects: Zcm ~ stage * light
                         Value Std.Error  DF  t-value p-value
(Intercept)           4.655093 0.1305800 363 35.64936  0.0000
stageFLEX            -0.007403 0.2172614 363 -0.03407  0.9728
stagePOST             0.394210 0.1304881 363  3.02104  0.0027
stageTRNS             1.421141 0.1252129 363 11.34979  0.0000
stageJUVE             1.367089 0.1223232 363 11.17604  0.0000
lightnight           -0.009052 0.1750433 363 -0.05172  0.9588
stageFLEX:lightnight -0.138162 0.3055672 363 -0.45215  0.6514
stagePOST:lightnight -0.074965 0.1880338 363 -0.39868  0.6904
stageTRNS:lightnight -0.114989 0.1884421 363 -0.61021  0.5421
stageJUVE:lightnight -0.000310 0.1771834 363 -0.00175  0.9986
 Correlation:
                     (Intr) stFLEX stPOST stTRNS stJUVE lghtng
sFLEX: sPOST: sTRNS:
stageFLEX            -0.492
stagePOST            -0.818  0.504
stageTRNS            -0.854  0.528  0.891
stageJUVE            -0.875  0.538  0.909  0.952
lightnight           -0.606  0.372  0.624  0.651  0.666
stageFLEX:lightnight  0.347 -0.709 -0.359 -0.375 -0.383 -0.573
stagePOST:lightnight  0.561 -0.348 -0.690 -0.612 -0.625 -0.932
0.535
stageTRNS:lightnight  0.557 -0.346 -0.580 -0.649 -0.619 -0.929
0.533  0.871
stageJUVE:lightnight  0.600 -0.368 -0.617 -0.644 -0.677 -0.988
0.566  0.921  0.918

Standardized Within-Group Residuals:
       Min         Q1         Med          Q3         Max
-2.9234579 -0.5266989  0.0378202  0.4872463  4.8082488

Number of Observations: 382
Number of Groups: 10
```

APPENDIX B: Multiple Comparison Post Hoc Test Results

A block comparison table was constructed to represent the results of the multiple comparisons test with significance levels represented by *** (p<0.001), ** (p<0.01), and * (p<0.05). Cases when there weren't significant differences between levels have a value of zero.

Table 1:
Stenobrachius leucopsarus

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	***	**	***	***	***	***
PREF Night	-	-	0	0	***	**	***	***	***	***
FLEX Day	-	-	-	0	***	*	***	***	***	***
FLEX Night	-	-	-	-	***	*	***	***	***	***
POST Day	-	-	-	-	-	***	***	***	***	**
POST Night	-	-	-	-	-	-	***	***	***	***
TRNS Day	-	-	-	-	-	-	-	0	0	***
TRNS Night	-	-	-	-	-	-	-	-	0	***
JUVE Day	-	-	-	-	-	-	-	-	-	***
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 2:
Tarletonbeania crenularis

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	**	*	***	***	***	***
PREF Night	-	-	0	0	***	*	***	***	***	***
FLEX Day	-	-	-	0	0	0	***	***	***	***
FLEX Night	-	-	-	-	0	0	***	***	***	***
POST Day	-	-	-	-	-	0	***	***	***	0
POST Night	-	-	-	-	-	-	***	***	***	**
TRNS Day	-	-	-	-	-	-	-	0	*	***
TRNS Night	-	-	-	-	-	-	-	-	*	***
JUVE Day	-	-	-	-	-	-	-	-	-	***
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 3:
Protomyctophum crockeri

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	***	***	***	***	***	***
PREF Night	-	-	0	0	***	***	***	***	***	***
FLEX Day	-	-	-	0	*	*	***	***	***	***
FLEX Night	-	-	-	-	**	**	***	***	***	***
POST Day	-	-	-	-	-	0	***	***	***	***
POST Night	-	-	-	-	-	-	***	***	***	***
TRNS Day	-	-	-	-	-	-	-	0	***	***
TRNS Night	-	-	-	-	-	-	-	-	***	***
JUVE Day	-	-	-	-	-	-	-	-	-	**
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 4:
Leuroglossus stilbius

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	***	***	***	***	***	***
PREF Night	-	-	0	0	***	***	***	***	***	***
FLEX Day	-	-	-	0	***	***	***	***	***	***
FLEX Night	-	-	-	-	***	***	***	***	***	**
POST Day	-	-	-	-	-	***	***	*	***	0
POST Night	-	-	-	-	-	-	***	***	***	0
TRNS Day	-	-	-	-	-	-	-	0	0	***
TRNS Night	-	-	-	-	-	-	-	-	0	**
JUVE Day	-	-	-	-	-	-	-	-	-	***
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 5:
Lipolagus ochotensis

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	***	***	***	***	***	***
PREF Night	-	-	0	0	***	***	***	***	***	***
FLEX Day	-	-	-	0	***	*	***	***	***	***
FLEX Night	-	-	-	-	***	***	***	***	***	***
POST Day	-	-	-	-	-	0	***	***	***	0
POST Night	-	-	-	-	-	-	***	***	***	*
TRNS Day	-	-	-	-	-	-	-	***	0	***
TRNS Night	-	-	-	-	-	-	-	-	***	***
JUVE Day	-	-	-	-	-	-	-	-	-	***
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 6:
Bathylagus pacificus

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	0	0	***	***	***	***
PREF Night	-	-	0	0	0	0	***	***	***	***
FLEX Day	-	-	-	0	0	0	***	***	***	***
FLEX Night	-	-	-	-	0	0	***	***	***	***
POST Day	-	-	-	-	-	0	***	***	***	***
POST Night	-	-	-	-	-	-	***	***	***	***
TRNS Day	-	-	-	-	-	-	-	0	0	0
TRNS Night	-	-	-	-	-	-	-	-	0	0
JUVE Day	-	-	-	-	-	-	-	-	-	0
JUVE Night	-	-	-	-	-	-	-	-	-	-

Table 7:
Chauliodus macouni

	PREF Day	PREF Night	FLEX Day	FLEX Night	POST Day	POST Night	TRNS Day	TRNS Night	JUVE Day	JUVE Night
PREF Day	-	0	0	0	*	0	***	***	***	***
PREF Night	-	-	0	0	0	0	***	***	***	***
FLEX Day	-	-	-	0	0	0	***	***	***	***
FLEX Night	-	-	-	-	*	0	***	***	***	***
POST Day	-	-	-	-	-	0	***	***	***	***
POST Night	-	-	-	-	-	-	***	***	***	***
TRNS Day	-	-	-	-	-	-	-	0	0	0
TRNS Night	-	-	-	-	-	-	-	-	0	0
JUVE Day	-	-	-	-	-	-	-	-	-	0
JUVE Night	-	-	-	-	-	-	-	-	-	-

CHAPTER 4:

Effects of El Niño on the ontogenetic distribution and abundance of mesopelagic fishes off southern California

INTRODUCTION

Studies of larval fish assemblages have provided critical insights into our understanding of marine ecosystem dynamics (e.g., Adams 1980, Hsieh et al. 2005, Ciannelli et al. 2014, Asch 2015). These and similar studies often do not make a distinction between early life history stages and instead view fish larvae as one demographic unit. However, fishes undergo tremendous changes in development during the larval period (e.g., Hubbs and Blaxter 1986, Fuiman and Magurran 1994, Fisher et al. 2000) and thus potentially require different habitats for survival and successful growth through the larval state. Knowledge of the abundance and distribution of each early life history stage of fish species could provide critical information on their changes in ontogeny and habitat requirements, and their responses to these changes, leading to a deeper understanding of community dynamics.

Early life history stages of fishes may be especially sensitive to environmental variation (Miller and Kendall 2009), including variation associated with changing climate conditions. A potential source of insight into these dynamics may be found in larval fish abundance and distribution patterns observed during extreme conditions such as El Niño and La Niña events.

The El Niño Southern Oscillation (ENSO) phenomenon is a climate signal dependent upon the coupled interactions between ocean and atmospheric dynamics. El Niño is the warm phase of ENSO which follows the relaxation and reversal of the westward winds in the western equatorial Pacific (Cane 1983, Trenberth 1997). These winds generate Kelvin waves that propagate from the western tropical Pacific along the equator toward the South American coast, then continue north and south as trapped coastal waves (Wyrtki 1975). In the waters off California, these Kelvin waves result in anomalous warming, a deepening of the thermocline, low nutrient levels in the surface waters, and lower than average primary productivity (Chavez 1996). La Niña is the cool phase of ENSO and is associated with low surface air pressure and high westward winds resulting in intensified upwelling off California (Hayward et al. 1999)

The 1997-1998 El Niño was one of the strongest on record and resulted in anomalously warm conditions and low zooplankton biomass in the California Current system (Bograd et al. 2000). This extreme warm phase was followed by the 1999-2002 La Niña event producing cool water conditions and an increase in upwelling and productivity.

The ichthyoplankton samples collected during the quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises off southern California during these years provide an ideal model for studying changes in larval fish distribution and abundance during these environmental extremes. The present study documents these changes with a focus on the ontogeny of the mesopelagic fish larvae and their potential correlation with the changing environment.

METHODS

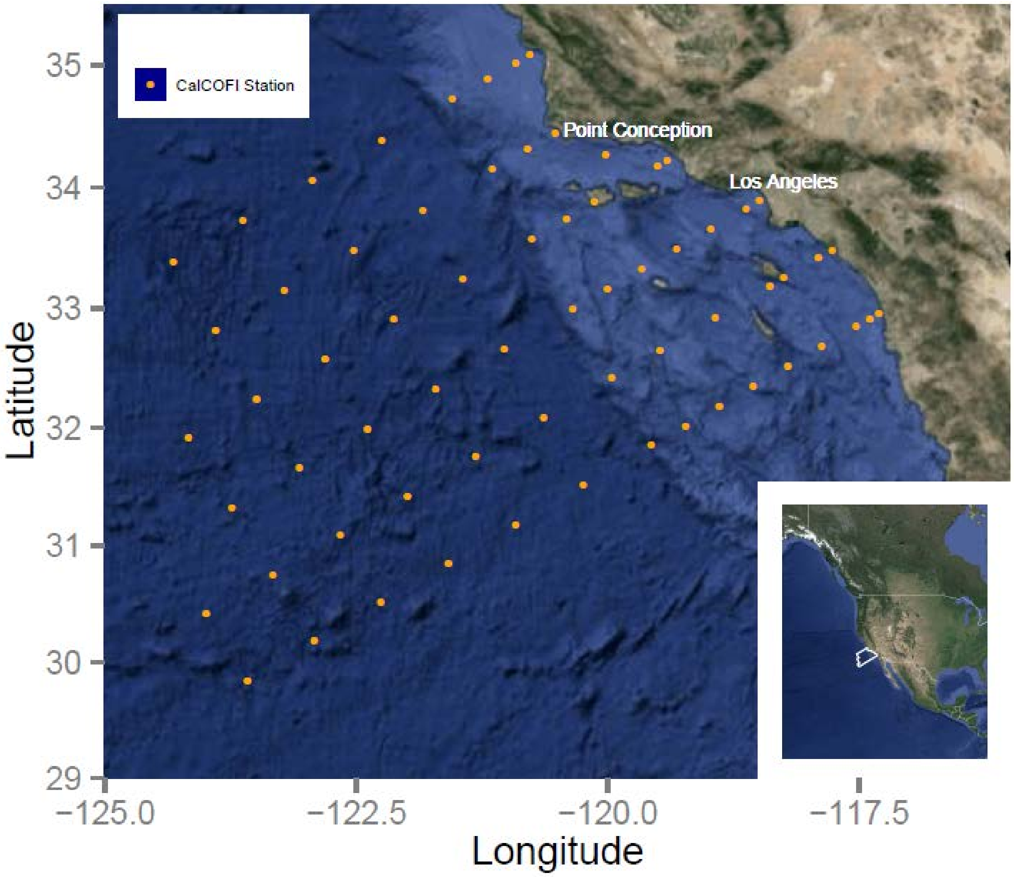


Figure 1:
Map of study area. Filled orange circles indicate sampling sites in the core CalCOFI pattern (66 stations).

Field Sampling & Laboratory Work

This study is based on ichthyoplankton and hydrographic samples collected from twelve oceanographic research cruises that were part of the California Cooperative Oceanic Fisheries Investigation surveys (CalCOFI; Hewitt 1988) in winter, spring, summer, and fall during 1997, 1998, and 1999. Ichthyoplankton samples were collected using a 0.71-meter-diameter bridleless bongo frame fitted with 0.505 mm mesh nets lowered to approximately 200 meters or within 10 meters of the bottom in shallow areas, towed at a 45°±8° angle at an ascent rate of 20 meters per minute as described by Kramer et al. (1972) and Smith and Richardson (1977). Once onboard, all nets were washed and samples were preserved in 5% formalin buffered with sodium borate. Hydrographic samples were collected by CTD Seabird SBE-19 vertical casts to 500 meters or within 10 meters of the bottom in shallow areas. In this study, ichthyoplankton and hydrographic samples were analyzed from the core CalCOFI pattern (Figure 1) (McClatchie 2013).

All fish larvae were sorted, enumerated, identified to the lowest possible taxon, and assigned to a life-history stage as defined by Kendall et al. (1984). Yolk-sac and transformation stage larvae were not included in the analysis due to the paucity of specimens at these stages. Ichthyoplankton samples also included fish eggs; those that are reliably identifiable to species were included in the laboratory enumeration and identification process. Eggs (EGGS), preflexion (PREF), flexion (FLEX), and postflexion (POST) stages were all included in the analysis for all identifiable mesopelagic species captured.

Data Analysis

Generalized linear models were built to test the hypothesis that there is a difference in the relative abundance of each mesopelagic fish species at each stage between seasons and years during 1997, 1998, and 1999. For this hypothesis we set the following model,

$$glm(abund_{spp.stage} \sim season + year + season * year), \tag{1}$$

where $abund_{spp.stage}$is the abundance of each mesopelagic fish species at a particular life history or ontogenetic stage under 10 m^2 of sea surface area, $season$ is a factor indicating which of the four seasons (winter, spring, summer, or fall) the samples were collected, and $year$ is a factor indicating whether the samples were collected in 1997, 1998, or 1999. The operator * indicates that the two main effects variables were fit with interactions as in a two-way ANOVA model. The model was fit using a negative-binomial error distribution for the response variable to account for the large number of zeros in these count data using the MASS package (Venables and Ripley 2002) developed for R statistical software (R Core Team 2015).

To investigate the potential presence of inter-annual changes in the spatial distribution of mesopelagic fishes at different ontogenetic stages within seasons during the 1997-1999 time period, calculations of the distance between centroids of the distribution of each species at each stage in a given season between years, were analyzed. Centroid calculations were made based on samples where the relative abundance of a species at a certain stage was at least ten individuals under 10 m^2 of sea surface area. These calculations were performed using the aspace package (Bui et al. 2012) developed for R statistical software (R Core Team 2015).

Predictions of the interannual seasonal abundance and centroid locations for each of the mesopelagic fishes were made based on CalCOFI ichthyoplankton time series analyses of ecological and biogeographical information. Moser (2001) analyzed larval fish species distribution patterns to infer the likely regional spawning season based on the timing and location of peaks in larval abundance in the core CalCOFI area. Hsieh et al. (2005, 2009) provided a classification for the mesopelagic fishes in the California Current region from analyses of the CalCOFI ichthyoplankton time series that indicated a particular species' affinity for warm, cold, or broad temperature conditions, as well as the affinity for coastal or oceanic environments. Based on these classifications it was predicted that the cold-water species would be most abundant in the CalCOFI area during their spawning seasons before and after the El Niño (1997 and 1999), warm-water species most abundant in their spawning seasons during the El Niño (1998), and species with a broad temperature affinity to be equally abundant during their spawning seasons for all three years. The centroid locations for each species were predicted based on their affinities for temperature and habitat (distance from shore). Both warm-water and cold-water species with an affinity for oceanic habitats were predicted to be offshore in the pre-El Niño year (1997) and during La Niña (1999), and inshore during El Niño (1998). The cold-water, coastal-oceanic species were predicted to have centroids inshore during all three years. The oceanic species with broad temperature affinities were predicted to have centroids located offshore during all three years.

Generalized linear mixed models were built to test the hypothesis that the relative abundance of each species at each stage is affected by environmental changes with a focus on the extreme El Niño event in 1997-1998 followed by the strong La Niña event in 1999. The environmental variables included in this study are the CTD data from the core CalCOFI stations, including temperature, salinity, density, oxygen concentration, and chlorophyll-a concentration integrated over the 200 meter water column that was sampled in conjunction with the bongo samples collected at each station. These environmental variables are correlated with each other, therefore they were transformed using a principal components analysis to reduce the data into an uncorrelated linear set of variables for use in the generalized linear mixed models (Lande and Arnold 1983).

The following generalized linear mixed model was fit with three fixed effects and one random effect,

$$glmmPQL(abund_{spp.stage} \sim depth + PC1 + PC2 + year,\ \sim 1|season), \tag{2}$$

where $abund_{spp.stage}$ is the abundance of each mesopelagic fish species at each ontogenetic stage under 10 m^2 of sea surface area, $depth$ is the fixed effect of the numeric value of the bottom depth in meters of each station, $PC1$ and $PC2$ are the fixed effects of the principal components calculated from the environmental data collected by the CTD at each station, and $year$ is the fixed effect of the year in which the cruises were conducted. The random effect of the season in which each of the CalCOFI cruises took place are represented by $season$. The model was fit using a quasi-Poisson distribution for the overdispersed count data response variable (Hoef and Boveng 2007) using penalized quasi-likelihood (PQL) estimation (Bolker et al. 2009) with the MASS package (Venables and Ripley 2002) developed for R statistical software (R Core Team 2015).

RESULTS

Laboratory Work

Totals of 54,846 larval fishes and 152,748 fish eggs were collected from 736 bongo tows from twelve CalCOFI cruises during 1997, 1998, and 1999. Pelagic species from ten families accounted for 40% of the larvae (22,029 individuals) and 31% of the identifiable eggs (47,374 individuals), while demersal species from 22 families accounted for 5% of the larvae (2,686 individuals) and 0% of the eggs. Of the total larvae only five individuals were in too poor of condition to be identified to family. Of the specimens that were in good condition but unidentifiable, there were only 20 individual larvae, but there were 65,705 eggs in this category. The remaining 55% of larvae (30,106 individuals) and 26% of eggs (39,669 individual eggs) were mesopelagic species from 26 and 10 families, respectively, for a total of 27 mesopelagic families (Table 1). Of the mesopelagic larvae, 29,457 individuals (98%) were identified to species, 618 individuals identified to genus, and 31 individuals identified to the family level (Table 1 and Table 2). For the remainder of the paper, only those mesopelagic fishes identified to species are considered. The two most abundant mesopelagic species for larvae and eggs combined, *Vinciguerria lucetia* (Phosicthyidae) and *Leuroglossus stilbius* (Bathylagidae) together accounted for 50% of the total number of larvae and 76% of the eggs. The next nine most abundant species of larvae in decreasing order of abundance were *Merluccius productus* (Merluccidae), *Bathylagoides wesethi* (Bathylagidae), *Stenobrachius leucopsarus* (Myctophidae), *Lipolagus ochotensis* (Bathylagidae), *Ceratoscopelus townsendi* (Myctophidae), *Triphoturus mexicanus* (Myctophidae), *Cyclothone signata* (Gonostomatidae), *Protomyctophum crockeri* (Myctophidae), and *Diogenichthys atlanticus* (Myctophidae), and together accounted for 40% of the mesopelagic larval fish specimens. The remaining 10% of larvae included 69 species from 21 families. The remaining 24% of the mesopelagic fish eggs were represented by the following ten species in decreasing order of abundance: *Merluccius productus* (Merluccidae), *Bathylagoides wesethi* (Bathylagidae), *Lipolagus ochotensis* (Bathylagidae), *Argentina sialis* (Argentinidae), *Tetragonurus cuvieri* (Tetragonuridae), *Trachipterus altivelus* (Trachipteridae), *Chauliodus macouni* (Stomiidae), *Microstoma* sp. (Microstomatidae), *Nansenia candida* (Microstomatidae), and *Icichthys lockingtoni* (Centrolophidae).

Statistical Analysis

A subset of the mesopelagic species collected in the CalCOFI bongo samples was chosen for the statistical analyses. Species that were relatively abundant in each stage from three families were chosen. Four species were selected that were sufficiently abundant in eggs and most larval stages: *Vinciguerria lucetia*, the only species from the family Phosichthyidae, and three species from the family Bathylagidae: *L. stilbius, B. wesethi*, and *L. ochotensis*. Eight species with enough specimens in the larval stages were chosen from the family Myctophidae: *S. leucopsarus, C. townsendi, T. mexicanus, P. crockeri, D. atlanticus, S. californiensis, N. ritteri,* and *T. crenularis.* Eggs are not reliably identifiable to the species level for myctophids in these samples, therefore they are not included in the analysis. In total, generalized linear models and generalized linear mixed models were fit for twelve mesopelagic species.

Principal components one and two (PC1 and PC2) for the environmental variables together accounted for 93% of the variance in the analysis (Table 3). PC1 was positively associated with water of high salinity, high density (SigmaTheta), low temperature, and low oxygen concentration (Figure 2). PC2 was negatively associated with water high in temperature and high in salinity (Figure 3). During winter, spring, and summer 1997, the warm, high oxygen, low salinity water (dark blue and purple in figure 2) was far offshore. By fall 1997 through summer 1998 this warmer mass of water was more inshore and dominated the core CalCOFI area. Beginning in fall 1998 through fall 1999, the colder, higher salinity, and lower oxygen water became dominant in the upper 200 meters of the core CalCOFI area (light blue, green, and yellow in Figure 2). In addition to the results of PC1, PC2 highlights the warmer, saltier water along the coast in winter 1998 and in the southwestern corner of the core CalCOFI area in summer and fall 1998 (dark blue and purple in Figure 3).

The generalized linear models built to test for differences in the relative abundance of each mesopelagic fish species at each stage between seasons and years produced mixed results; some combinations produced significant differences, some were not significant, and for some the model would not converge (Appendix A, Tables 1-40). This is most likely due to the low proportion of positive samples in this dataset (Table 4). The interannual centroid distribution pattern for these mesopelagic species provided a spatial element to the abundance patterns. Centroid locations were compared within season between years for each combination of species and stage where samples were sufficiently abundant. Although the model results were mixed, interesting patterns of abundance and centroid distribution emerged.

Peak abundances generally occurred during the described spawning seasons for most species and stages for all three years, with the exception of two species with an affinity for cold, oceanic habitats (Figures 4-6). *Protomyctophum crockeri* is described as a winter spawner, but some of the highest peaks in abundance for all three larval stages occurred during the spring and summer. *Tarletonbeania crenularis* with a described spawning season of winter through spring, had high spikes in abundance for the earliest larval stage (preflexion) during the summer.

Within each species abundance pattern, the earliest stages were typically at least twice as abundant as the subsequent ontogenetic stage. For the four species with reliably identifiable eggs (*V. lucetia*, *L. stilbius*, *L. ochotensis,* and *B. wesethi*), this earliest stage was often an order of magnitude more abundant than preflexion, flexion, and postflexion larvae (Figure 4). For all eight myctophids in this study, preflexion larvae were much more abundant than flexion and postflexion larvae (Figures 5 and 6).

Overall abundance for each species was generally highest during the years that corresponded to their described temperature affinities. Five of the seven species with an affinity for cold temperature conditions (*L. stilbius*, *B. wesethi*, *L. ochotensis*, *N. ritteri*, and *T. crenularis*) were most abundant during the cooler conditions in either the pre-El Niño (1997) or La Niña (1999) years, and least abundant during the warm conditions of the El Niño (1998) (Figures 4-6). Of the two remaining cold-water species, *P. crockeri* was relatively equally abundant during all four years, and *S. californiensis* was most abundant during the El Niño (Figure 6). All three warm-water species, *V. lucetia*, *D. atlanticus*, and *T. mexicanus* were most abundant during the El Niño (Figures 4 and 5). The two species with an affinity for broad temperature conditions showed opposite patterns: *C. townsendi* was most abundant during the warm El Niño conditions, and *N. ritteri* was most abundant during the cooler pre-El Niño conditions (Figures 5 and 6).

The most common pattern of centroid locations was offshore during the pre-El Niño conditions, inshore during El Niño, and offshore during La Niña. This pattern was observed for three of the cold, oceanic species (*B. wesethi*, *P. crockeri*, and *S. californiensis*; Figures 9, 16, and 17), two of the warm, oceanic species (*V. lucetia* and *T. mexicanus*; Figures 7 and 13), and one of the broad temperature, oceanic species (*N. ritteri*; Figure 15). There were two cold, coastal-oceanic species (*L. stilbius* and *L. ochotensis*) that had centroids inshore during the pre-El Niño and El Niño conditions, and offshore during the La Niña (Figures 8 and 10). Two species exhibited offshore centroid locations during all three years: a broad temperature, oceanic species (*C. townsendi*, Figure 10), and a warm, oceanic species (*D. atlanticus*, Figure 14). One of the cold, oceanic species (*S. leucopsarus*), exhibited a mixed pattern; centroids inshore during the pre-El Niño conditions, offshore and inshore during El Niño, and offshore during La Niña (Figure 11). The remaining cold, oceanic species (*T. crenularis*) had insufficient data to calculate centroid locations for comparisons (Figure 18). Additionally, in most seasons and years, all stage-specific centroids for a given species were within the same vicinity (inshore or offshore) but generally exhibited some geographic separation (Figures 7-18).

The overall predictions of relative abundance and centroid locations based on the described affinities for temperature and coastal or oceanic environments were 72.9% accurate (Table 5). The average prediction accuracy for centroid location was higher (81.8%) than for that of the interannual seasonal abundance (63.9%).

Station depth, PC1, PC2, and the year were the main effects in the generalized linear mixed model (Equation 2). Overall, the station depth and year did not significantly affect the abundance of each species at each ontogenetic stage (Table 6). However, PC1 and PC2 were highly significant for the majority of the models fit (Table 6). A general pattern emerged from these models: the earlier ontogenetic stages were better correlated with the environment than were the later stages (Figure 19). With the exception of *B. wesethi*, the relative abundance of preflexion stage larvae was best predicted by the environmental variables. For *B. wesethi*, the egg abundance was more highly correlated with the environment than was the abundance of preflexion stage larvae. However this was not true for the other three species for which there were reliably identified eggs (*V. lucetia, L. stilbius, and L. ochotensis*). Generally, the correlation between the environmental variables and the relative abundance of early life history stages decreased with increasing ontogeny.

DISCUSSION

Fish larvae are often considered as a homogeneous demographic but considerable morphological, physiological, and neurological differences are evident between these early life history stages (Margulies 1989, Leis 2006, Miller and Kendall 2009). Results from this study confirm the observations of others (e.g., Ahlstrom 1959, Loeb 1979, Sassa et al. 2007, Chapter 3) that the distribution, abundance, and ecology of early life history stages of mesopelagic fishes may change significantly during the larval period. In addition, this is the first study to include time series information of stage-specific observations of mesopelagic fish larvae, including the egg stage, in the waters off southern California.

The fluctuations in the observed patterns indicate that there are interannual differences in abundance within the life history stages of the twelve species analyzed. The abundance of eggs (of the four identifiable species) and the preflexion stages are much higher than that of the flexion and postflexion stages for all species analyzed. These differences plausibly result from at least three factors. First, although the bongo net used to sample the CalCOFI ichthyoplankton samples is designed to capture the early life history stages of larvae in the epipelagic zone (Ohman and Smith 1995), it is possible that there is an unknown degree of net avoidance at the latest larval stages. However, it is unlikely that net avoidance would account for the major discrepancies in abundance observed between the earliest and latest larval stages of all species. Second, it is likely that this pattern is primarily the result of the occurrence of high natural mortality and predation at the earliest life history stages (Houde 1997). The abundance of eggs was at least an order of magnitude greater than that of the larval stages (for the four species with identifiable eggs), and the earliest larval stage was at least twice as abundant as the subsequent larval stages for the remaining eight species in this study. Although the magnitude of larval mortality for mesopelagic fishes is poorly known (Moser and Ahlstrom 1974, Neighbors and Wilson 2006), these differences in abundance between the ontogenetic stages are generally consistent with the stage abundance differences for other pelagic species (Houde and Zastrow 1993, Lo et al. 1995). Third, and most interestingly, the relatively low abundance of later-stage larvae may result from the movement of late stages to depths beyond that sampled by the net (200 m). This is likely a significant factor for the species in this system exhibiting an ontogenetic shift in depth of occurrence which has been documented for five of the species in this study (*S. leucopsarus*, *P. crockeri*, *T. crenularis*, *L. stilbius*, and *L. ochotensis*; Chapter 3). This implies that the CalCOFI sampling protocol underrepresents to an unknown extent the abundance of larvae of the dominant species of mesopelagic fishes in this system. However, it is unknown if this shift to deeper depths during early ontogeny occurs in the remaining seven species in this study.

The results of the principal components analysis are consistent with the descriptions of the development of the El Niño and subsequent La Niña in the southern California region.

From spring to early summer in 1997 the El Niño developed quickly and intensely resulting in the initiation of anomalous warming in the eastern North Pacific. Regional wind anomalies in the North Pacific added to the intensity of the El Niño during November 1997 – April 1998 in the waters off California (Lynn et al. 1998). By May

1998 the El Niño conditions significantly weakened due to the intrusion of cool subsurface waters moving eastward from the western Pacific (Hayward et al. 1999). This expansion ushered in the beginning of the cool phase, or La Niña. The physical influence of El Niño in the waters off California weakened during summer and fall 1998. The transition between the El Niño and La Niña conditions in the north east Pacific occurred during winter 1998 through spring 1999, and the cool conditions persisted into winter 2002 (Bograd et al. 2000, Schwing et al. 2002, Venrick et al. 2003).

Although there are no other studies of the abundance of early life history stages of mesopelagic fishes in the California Current region for comparison, the observed abundance and centroid patterns were mostly consistent with expectations conjectured from the combination of the biogeographic classifications and the timing of the 1997-98 El Niño and 1999 La Niña events (Table 5). Most species in this study have an affinity for oceanic habitats and were predicted to be offshore during the pre-El Niño conditions, inshore during El Niño, and offshore during the La Niña. Peak abundances were predicted to occur during a species' inferred spawning season, with the highest peaks corresponding to the most favorable temperature conditions. The prediction accuracy was 63.9% for abundance patterns and 81.8% for centroid patterns. Discrepancies between the expected and observed patterns suggest that the relationship between larval abundance and the environment is more complex than previously thought. The inconsistencies in the predictions may be due to the large geographic ranges of these species that extend well beyond the core CalCOFI region (Wisner 1976, Kobyliansky 1985 cited by Moser 1996). In addition, all of the species in this study undergo diel vertical migrations (Pearcy and Laurs 1966, Paxton 1967) and daily are exposed to extreme changes in the physical features of the water column (e.g., temperature, pressure, salinity). As a consequence, it is likely that they have higher tolerances for environmental variability than what was observed in the CalCOFI region during the 1997-1999 time period.

The anomalously warmer conditions produced by El Niño events have been described as the likely source of expansions of range and spawning area for some species (MacCall and Prager 1988, Lea and Rosenblatt 2000). This was one proposed explanation for the much higher abundance of warm-water mesopelagic fish larvae during an El Niño in the eastern tropical Pacific (Fuenes-Rodriguez et al 2006). This could explain, for example, the marked increase in abundance of *V. lucetia* eggs and larvae during the 1998 El Niño conditions (Figure 4). This warm-water species typically spawns in the summer in the southwest corner of the CalCOFI region (Moser 2001) and it is likely that the adults of this species expanded their range during the El Niño resulting in egg and larval centroids much closer to shore. The presence of the high abundance of eggs and the location of the egg centroids during the El Niño support the idea that this species was spawning farther east than is generally observed during ‘normal’ conditions. In the absence of egg data, these changes in larval abundance and distribution would more likely have been interpreted as the result of advection, not a change in spawning location.

The decreased correlation with environmental variables through ontogeny may imply selection of preferred spawning conditions by adults and potential changes in preference with development or reduced ability of larvae to track preferred environments (Figure 19).

The differences in larval fish abundance throughout development described in this study indicate the importance of the study of ontogenetic stages at a finer scale than is typically undertaken. Many studies use larval fish abundance as an indicator of adult biomass (e.g., Hewitt 1988, Moser et al. 2001, Hitchman et al. 2012) based on the abundance of all larval stages as one demographic group. The abundance of early stages (eggs and preflexion larvae) is more likely to be indicative of critical habitats for spawning than is the abundance of later stages. While it is much more difficult to identify early stage specimens to species than later stages (Hernandez et al. 2013), the expanded effort may be required to more accurately identify critical spawning habitats for mesopelagic fishes.

Chapters 2, 3, and 4, in part, are currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of the material in all chapters of this dissertation.

Table 1:
Number of eggs and larvae of demersal, pelagic, and mesopelagic families of fishes collected and identified in the CalCOFI bongo samples.

Habitat	Family	Total Larvae	Total Eggs	Habitat	Family	Total Larvae	Total Eggs
Demersal	Scorpaenidae	1803	0	Mesopelagic	Phosichthyidae	13587	18586
	Paralichthyidae	378	0		Myctophidae	6720	0
	Gobiidae	68	0		Merlucciidae	4648	4528
	Cottidae	64	0		Bathylagidae	3118	15181
	Pleuronectidae	64	0		Gonostomatidae	772	0
	Blenniidae	60	0		Stomiidae	328	45
	Pomacentridae	51	0		Sternoptychidae	272	0
	Sciaenidae	40	0		Melamphaidae	170	0
	Labridae	33	0		Paralepididae	159	0
	Serranidae	32	0		Tetragonuridae	65	468
	Hexagrammidae	21	0		Scopelarchidae	56	0
	Cynoglossidae	14	0		Microstomatidae	47	105
	Stichaeidae	14	0		Argentinidae	34	499
	Agonidae	12	0		Howellidae	25	0
	Chaenopsidae	11	0		Chiasmodontidae	23	0
	Haemulidae	7	0		Ophidiidae	22	0
	Labrisomidae	4	0		Notosudidae	13	0
	Liparidae	4	0		Centrolophidae	12	72
	Kyphosidae	2	0		Trachipteridae	11	170
	Synodontidae	2	0		Oneirodidae	7	0
	Centriscidae	1	0		Gigantactinidae	6	0
	Macrouridae	1	0		Bythitidae	4	0
Pelagic	Clupeidae	13037	8105		Bathymasteridae	3	0
	Engraulidae	7713	25703		Opisthoproctidae	2	0
	Carangidae	875	11588		Nomeidae	1	0
	Scombridae	296	1978		Ceratiidae	1	0
	Sphyraenidae	85	0		Icosteidae	0	15
	Bramidae	10	0				
	Scomberesocidae	9	0				
	Atherinopsidae	2	0				
	Coryphaenidae	1	0				
	Exocoetidae	1	0				

Table 2:
Counts of individual mesopelagic fish species with 40 or more individuals collected in the CalCOFI bongo samples, per ontogenetic stage. The twelve species above the dashed line were analyzed separately.

Taxon	EGGS	PREF	FLEX	POST	TRNS	Total
Vinciguerria lucetia	18586	9785	1209	2469	74	32123
Leuroglossus stilbius	11653	1247	126	53	2	13081
Bathylagoides wesethi	2524	942	102	25	2	3595
Lipolagus ochotensis	1004	496	54	29	0	1583
Stenobrachius leucopsarus	0	1396	155	135	1	1687
Ceratoscopelus townsendi	0	800	115	138	0	1053
Triphoturus mexicanus	0	800	97	81	2	980
Protomyctophum crockeri	0	272	103	240	2	617
Diogenichthys atlanticus	0	392	70	146	1	609
Symbolophorus californiens	0	287	55	39	1	382
Nannobrachium ritteri	0	269	26	35	1	331
Tarletonbeania crenularis	0	57	12	11	0	80
Merluccius productus	4528	4469	134	24	0	9155
Cyclothone signata	0	299	135	239	1	674
Argentina sialis	499	29	3	2	0	533
Tetragonurus cuvieri	468	52	10	3	0	533
Nannobrachium sp.	0	308	4	0	0	312
Diogenichthys laternatus	0	154	21	56	0	231
Idiacanthus antrostomus	0	100	32	53	1	186
Trachipterus altivelis	170	8	2	1	0	181
Lestidiops ringens	0	89	10	20	0	119
Chauliodus macouni	45	21	8	33	0	107
Diaphus sp.	0	53	5	39	3	100
Melamphaes lugubris	0	53	17	26	2	98
Sphyraena argentea	0	83	2	0	0	85
Icichthys lockingtoni	72	8	1	2	1	84
Argyropelecus sladeni	0	66	5	9	0	80
Microstoma sp.	52	16	7	4	0	79
Nansenia candida	53	15	3	1	0	72
Hygophum reinhardtii	0	42	6	12	0	60
Sternoptyx sp.	0	43	7	6	1	57
Stomias atriventer	0	25	13	11	3	52
Danaphos oculatus	0	12	6	30	1	49
Cyclothone sp.	0	24	9	14	0	47
Cyclothone acclinidens	0	4	10	31	0	45
Myctophum nitidulum	0	41	2	2	0	45
Nannobrachium regale	0	22	11	7	0	40
Vinciguerria poweriae	0	23	5	12	0	40

Table 3:
Principal components analysis of environmental variables collected in the CalCOFI hydrographic samples integrated over the water column from 0-200 meters.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	0.0899	0.0204	0.0084	0.0033	0.0000
Proportion Explained	0.7362	0.1675	0.0692	0.0269	0.0002
Cumulative Proportion Explained	0.7362	0.9037	0.9729	0.9998	1.0000
	PC1	PC2	PC3	PC4	PC5
Temperature_200m	-0.9923	-0.7815	0.1363	-0.1121	-0.0303
Salinity_200m	1.4780	-0.8873	-0.1694	0.1689	0.0090
Oxygen_conc_200m	-1.5639	-0.0246	-0.4198	0.3110	0.0008
SigmaTheta_200m	1.1588	0.4324	-0.1674	0.1410	0.0363
Chlorophyll_a_200m	0.1213	-0.0287	-0.6355	-0.3116	0.0001

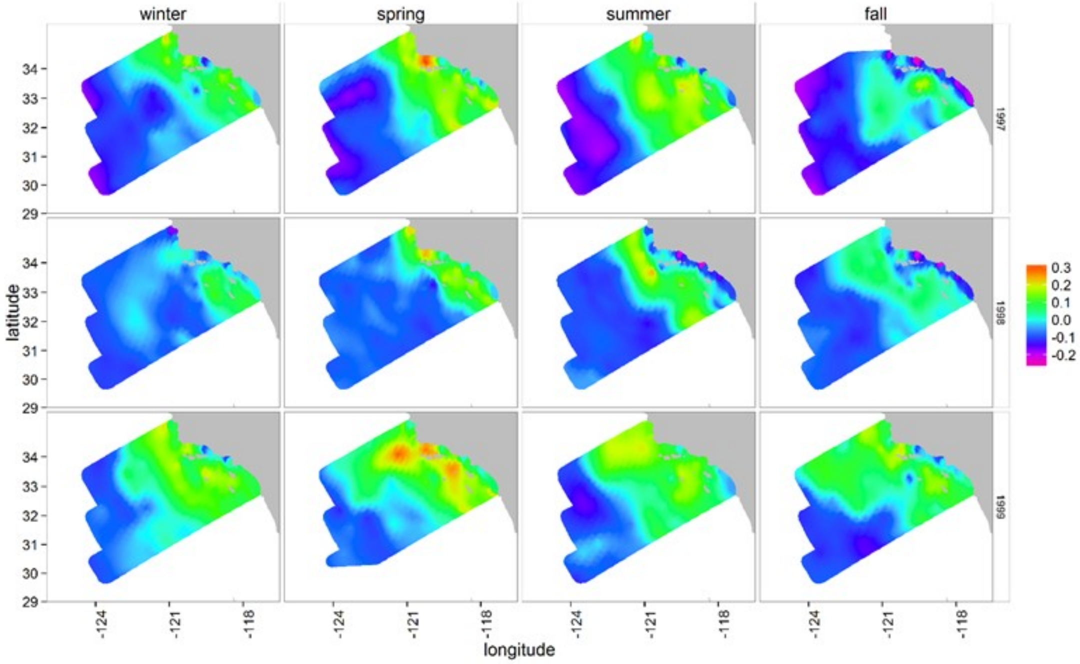


Figure 2:
Graphical representation of principal component 1 (PC1) calculated from the hydrographic data collected from the quarterly CalCOFI cruises during 1997, 1998, and 1999.

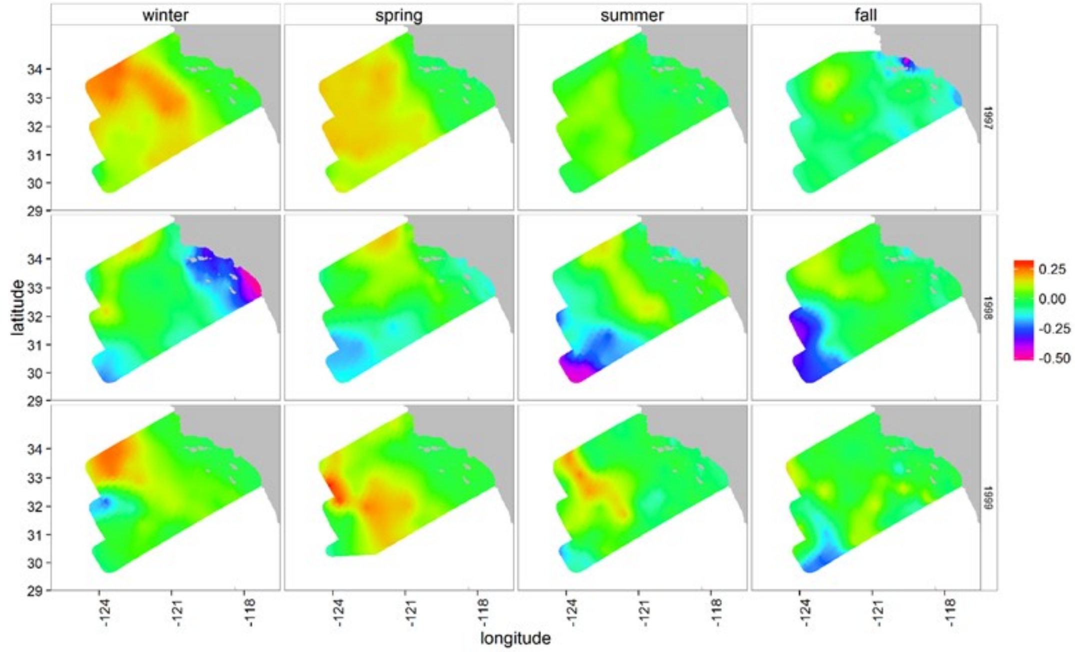


Figure 3:
Graphical representation of principal component 2 (PC2) calculated from the hydrographic data collected from the quarterly CalCOFI cruises during 1997, 1998, and 1999.

Table 4:
Proportion of positive samples at each ontogenetic stage in the CalCOFI bongo tows used for analysis in the generalized linear model fit to predict the relative abundance (Equation 1). The corresponding model results are represented by * (p<0.05), NS (not significant), or NC (model failed to converge.

species	EGGS	model result	PREF	model result	FLEX	model result	POST	model result
Bathylagoides wesethi	0.2745	NS	0.2323	*	0.0815	*	0.0285	*
Leuroglossus stilbius	0.2826	*	0.2418	*	0.0910	NS	0.0530	NC
Lipolagus ochotensis	0.1726	NS	0.1929	NS	0.0421	NC	0.0285	NS
Vinciguerria lucetia	0.3111	*	0.2826	*	0.2065	*	0.2595	*
Ceratoscopelus townsendi	-	-	0.2255	*	0.0734	*	0.1033	NS
Diogenichthys atlanticus	-	-	0.2188	*	0.0707	*	0.1182	*
Nannobrachium ritteri	-	-	0.1861	NS	0.0272	NC	0.0394	*
Protomyctophum crockeri	-	-	0.2147	NS	0.1141	NS	0.2079	NS
Stenobrachius leucopsarus	-	-	0.2853	NS	0.0747	NS	0.0815	NC
Symbolophorus californiensis	-	-	0.1875	NS	0.0625	NS	0.0476	NS
Tarletonbeania crenularis	-	-	0.0571	NS	0.0149	NC	0.0136	NC
Triphoturus mexicanus	-	-	0.2785	*	0.0870	*	0.0679	*

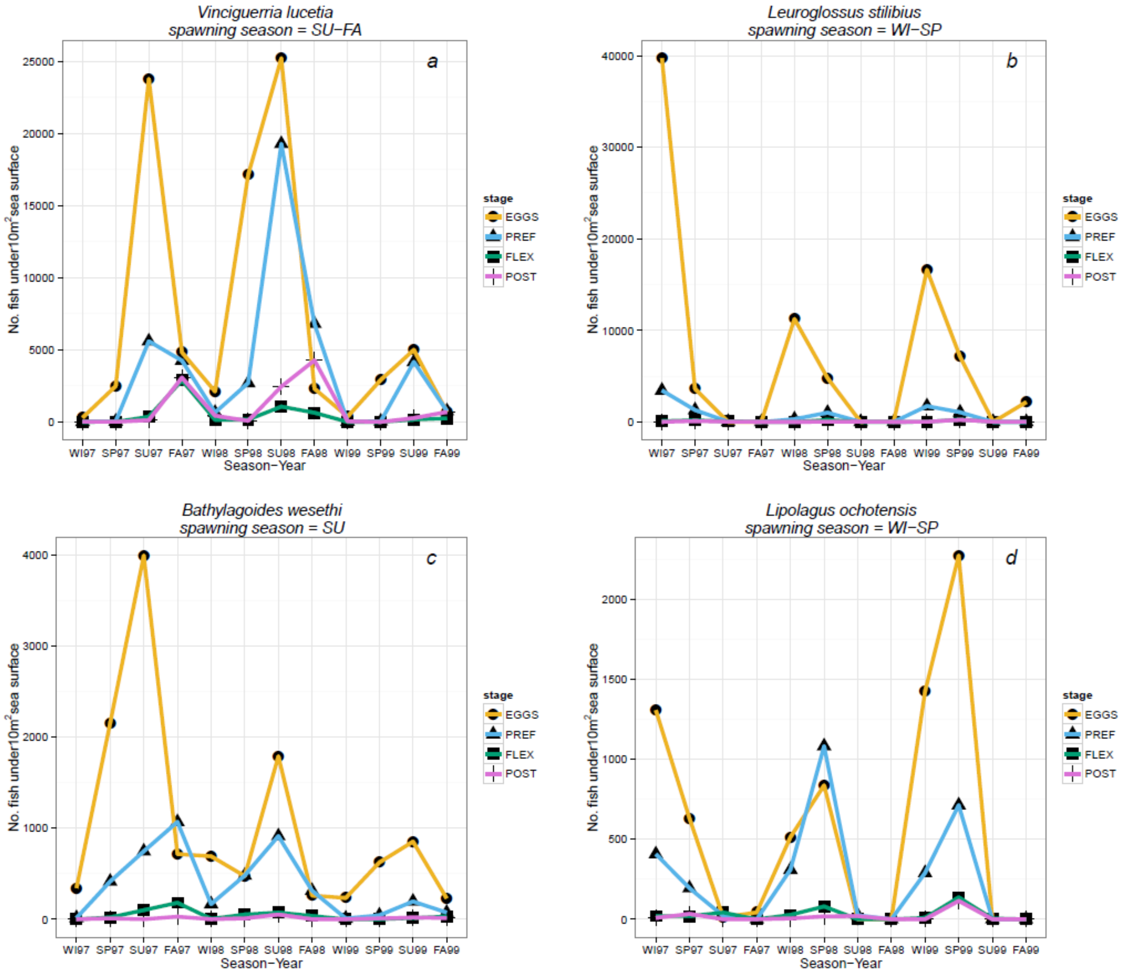


Figure 4:
Graphical representation of the abundance (number of fish under 10 m^2 sea surface area) of four species whose eggs were identified (one species of gonostomatid and three species of bathylagids), separated by ontogenetic stage, from the CalCOFI bongo samples collected during winter (WI), spring (SP), summer (SU), and fall (FA), cruises in 1997, 1998, and 1999. Each species' spawning season is indicated at the top of each panel. Species in each panel: a) *Vinciguerria lucetia*, b) *Leuroglossus stilbius*, c) *Bathylagoides wesethi*, d) *Lipolagus ochotensis*. Note differences in y-axis scales.

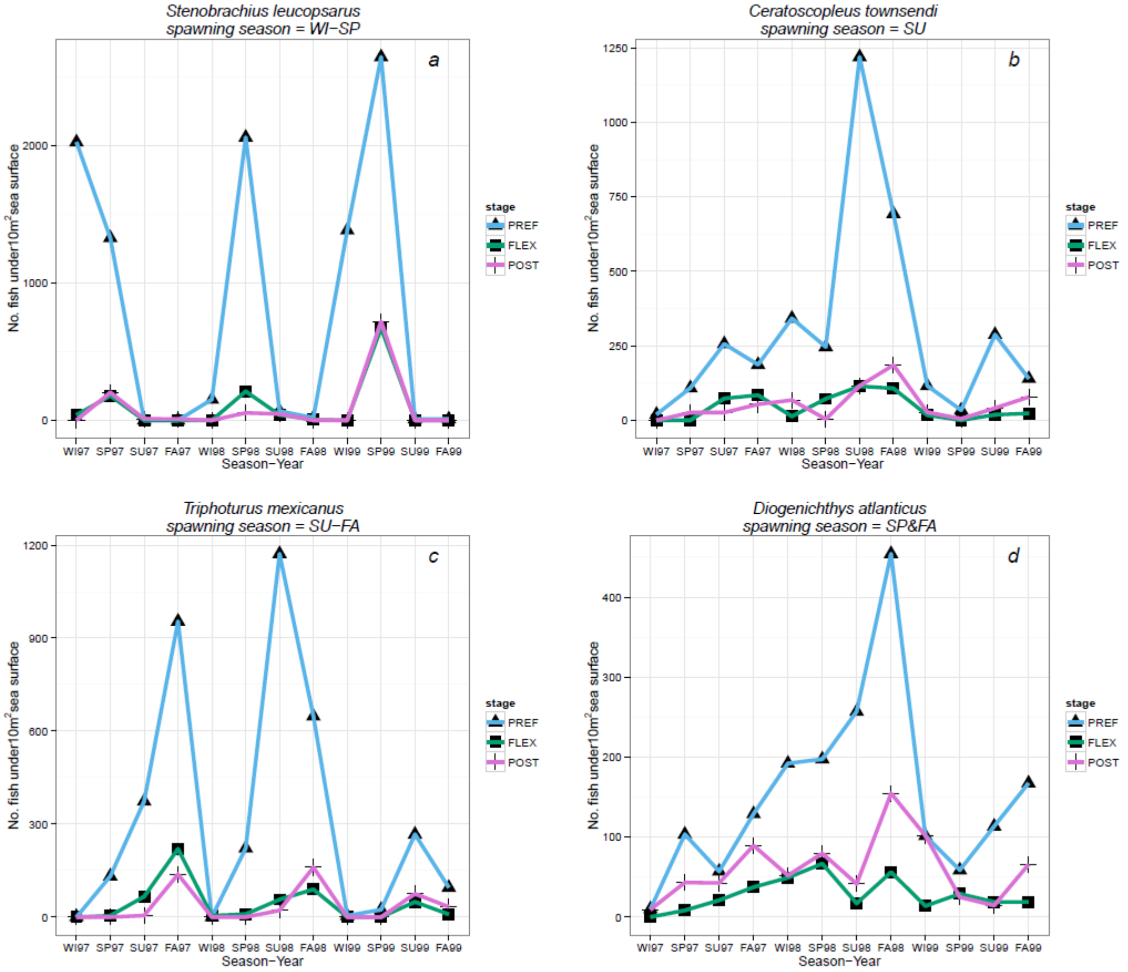


Figure 5:
Graphical representation of the abundance (number of fish under 10 m^2 sea surface area) of four species of myctophids, separated by ontogenetic stage, in CalCOFI bongo samples collected during winter (WI), spring (SP), summer (SU), and fall (FA), cruises in 1997, 1998, and 1999. Each species' spawning season is indicated at the top of each panel. Species in each panel: a) *Stenobrachius leucopsarus*, b) *Ceratoscopeuls townsendi*, c) *Triphoturus mexicanus,* d) *Diogenichthys atlanticus*. Note differences in y-axis scales.

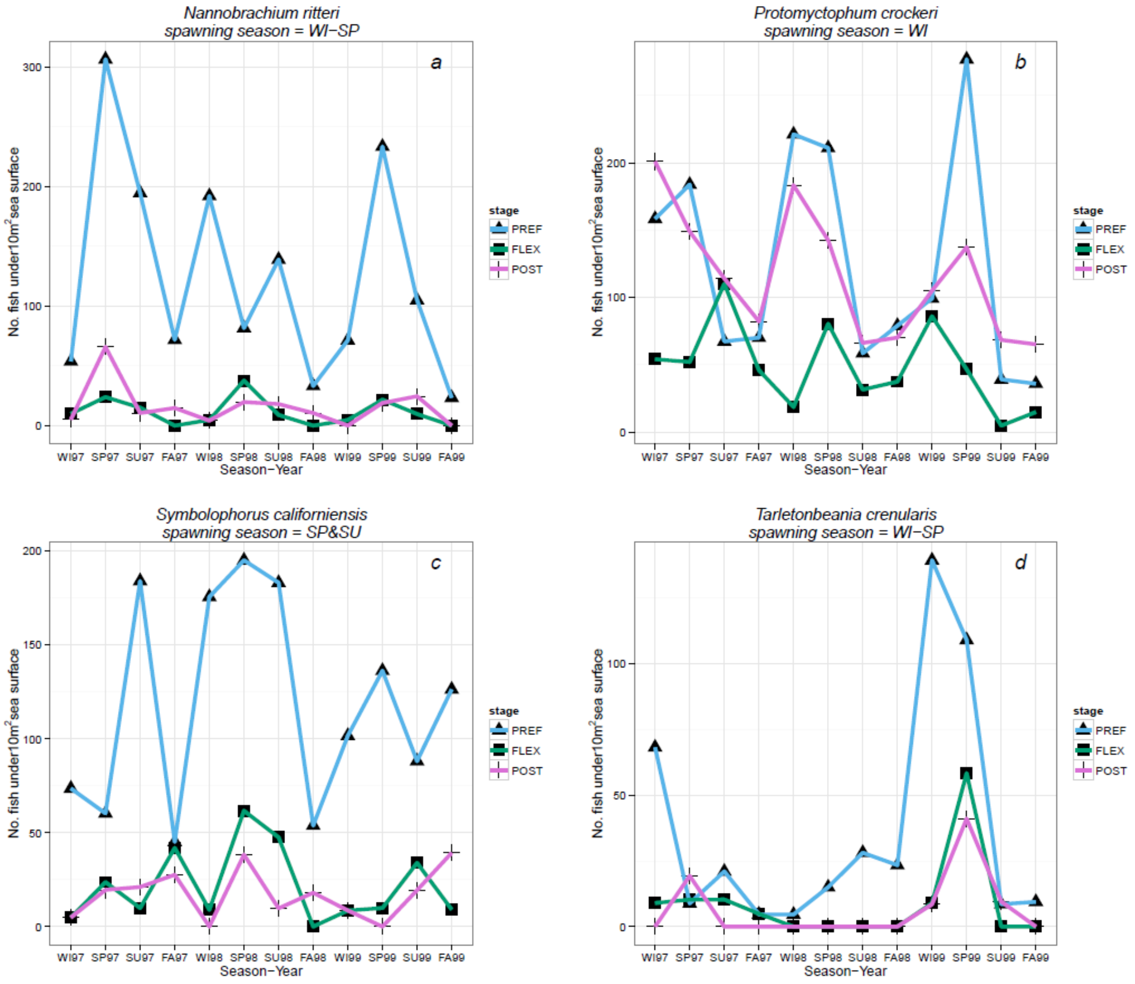
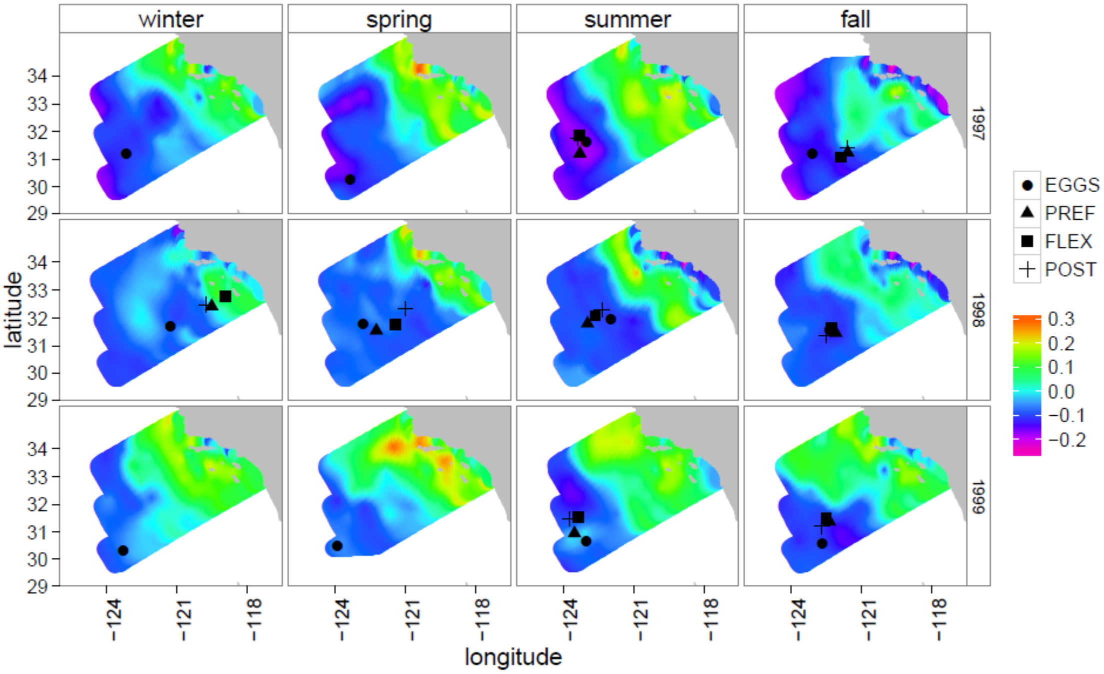
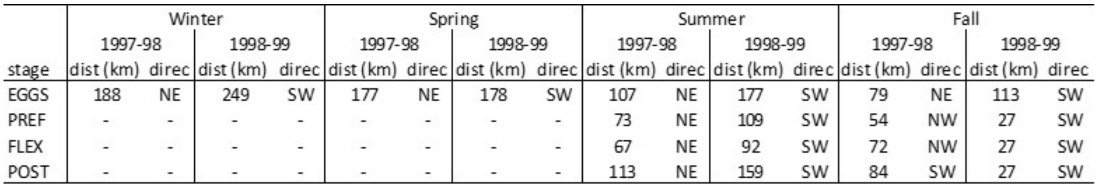


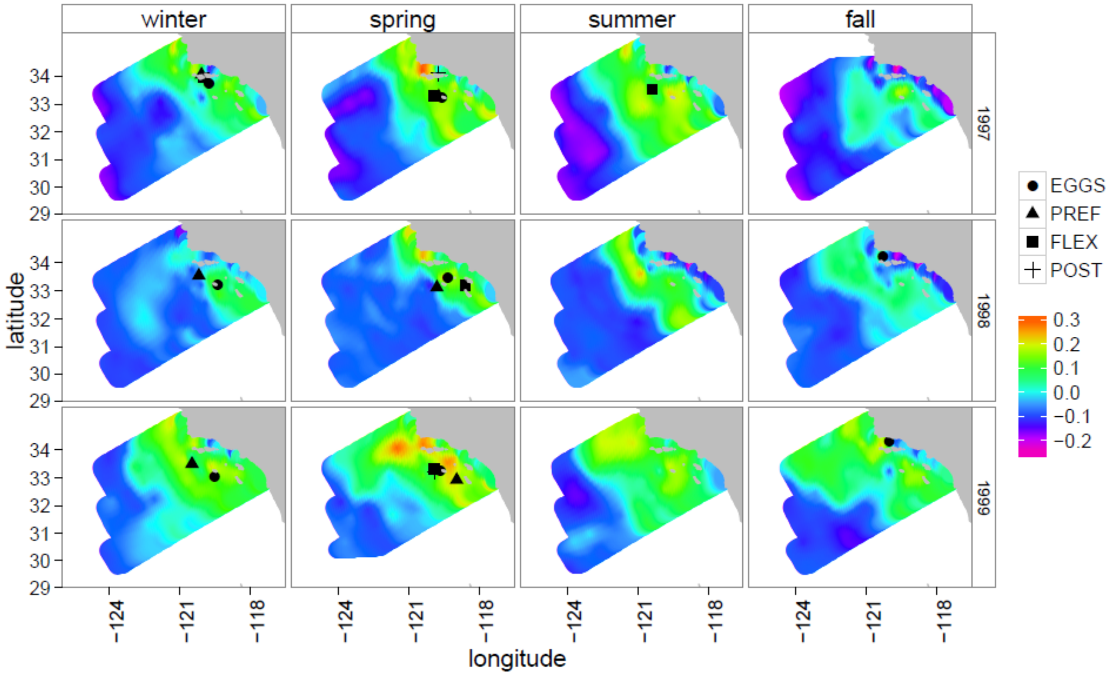
Figure 6:
Graphical representation of the abundance (number of fish under 10 m^2 sea surface area) of four species of myctophids, separated by ontogenetic stage, in CalCOFI bongo samples collected during winter (WI), spring (SP), summer (SU), and fall (FA), cruises in 1997, 1998, and 1999. Each species' spawning season is indicated at the top of each panel. Species in each panel: a) *Nannobrachium ritteri*, b) *Protomyctophum crockeri*, c) *Symbolophorus californiensis*, d) *Tarletonbeania crenularis*. Note differences in y-axis scales.

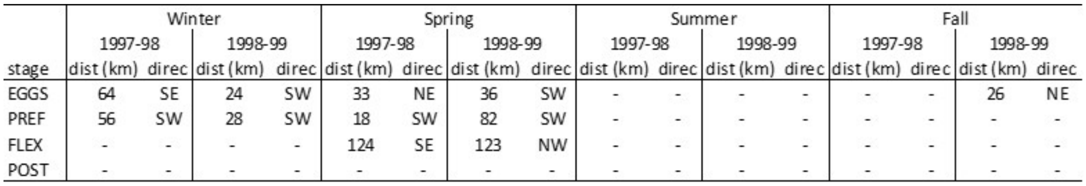




	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
EGGS	188	NE	249	SW	177	NE	178	SW	107	NE	177	SW	79	NE	113	SW
PREF	-	-	-	-	-	-	-	-	73	NE	109	SW	54	NW	27	SW
FLEX	-	-	-	-	-	-	-	-	67	NE	92	SW	72	NW	27	SW
POST	-	-	-	-	-	-	-	-	113	NE	159	SW	84	SW	27	SW

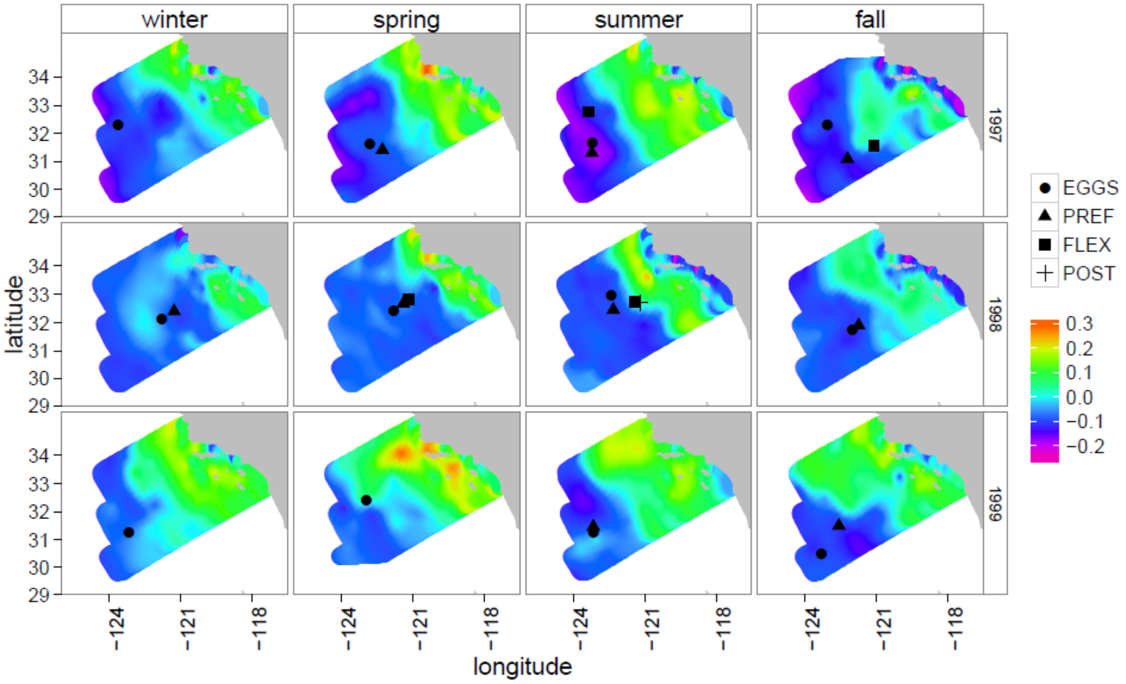
Figure 7:
Vinciguerria lucetia distribution centroid locations plotted over maps of PC1 for each ontogenetic stage divided by season (each column) and year (each row). Centroid locations were compared within season between years for each combination of species and stage where samples were sufficiently abundant. Within each season (column), centroid location differences in distance were calculated between years (rows). Changes in distance (in kilometers) and direction are listed in the table below the centroid location plots. Directions are abbreviated; N = north, S = south, E = east, W = west. Comparisons with insufficient sample sizes are indicated by a dash (-).





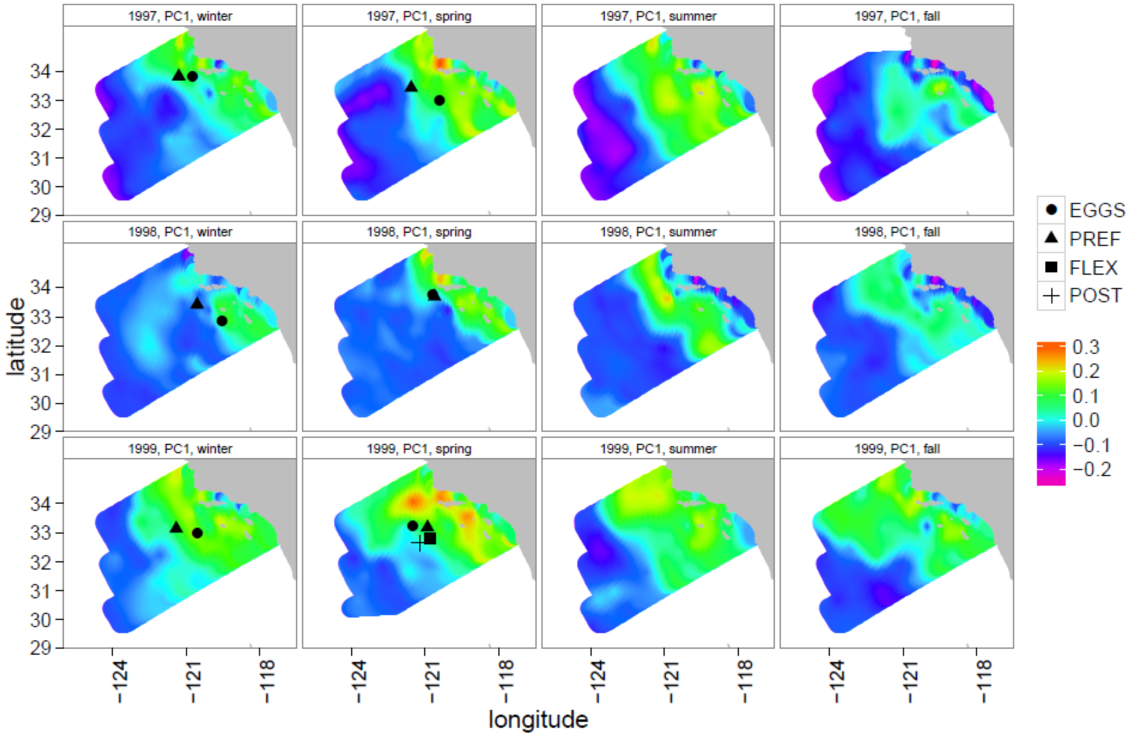
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
EGGS	64	SE	24	SW	33	NE	36	SW	-	-	-	-	-	-	26	NE
PREF	56	SW	28	SW	18	SW	82	SW	-	-	-	-	-	-	-	-
FLEX	-	-	-	-	124	SE	123	NW	-	-	-	-	-	-	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 8:
Leuroglossus stilbius distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage is below the plots. See figure 7 for explanation.



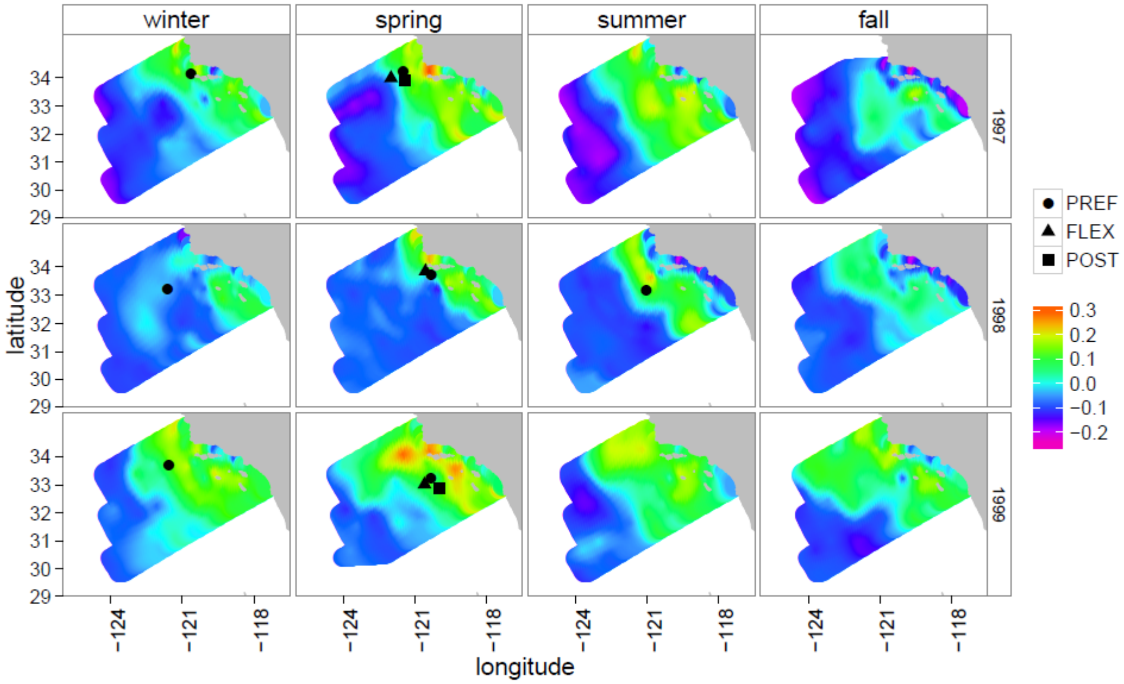
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
EGGS	174	SE	165	SW	128	NE	110	NW	165	NE	205	SW	118	SE	188	SW
PREF	-	-	-	-	162	NE	-	-	153	NE	136	SW	101	NE	91	SW
FLEX	-	-	-	-			-	-	180	SE	-	-	-	-	-	-
POST	-	-	-	-			-	-	-	-	-	-	-	-	-	-

Figure 9:
Bathylagoides wesethi distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



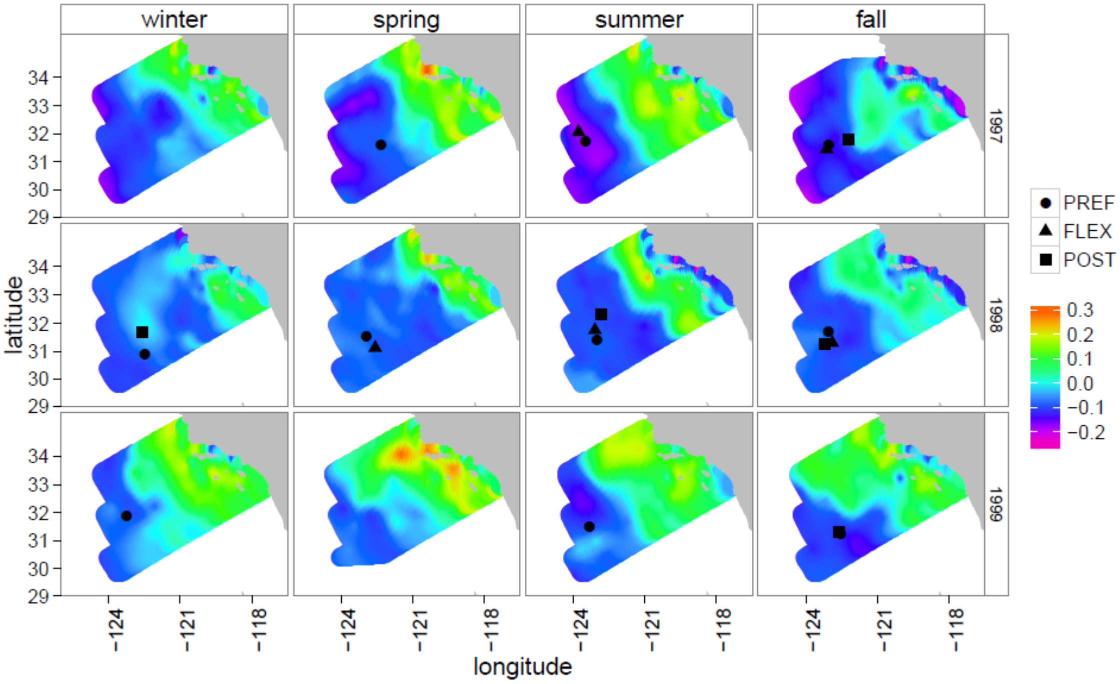
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
EGGS	153	SE	96	NW	91	NW	97	SW	-	-	-	-	-	-	-	-
PREF	83	SE	85	SW	93	NE	61	SW	-	-	-	-	-	-	-	-
FLEX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 10:
Lipolagus ochotensis distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



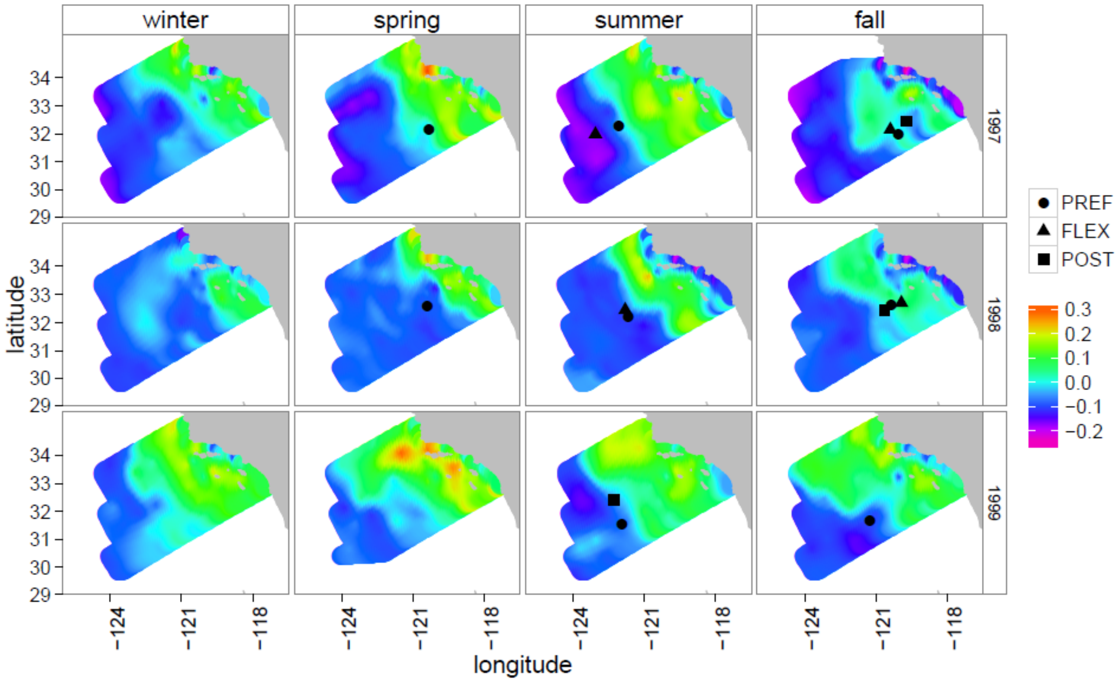
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	133	SW	49	NE	122	SE	56	SW	-	-	-	-	-	-	-	-
FLEX	-	-	-	-	135	SE	93	SW	-	-	-	-	-	-	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 11:
Stenobrachius leucopsarus distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



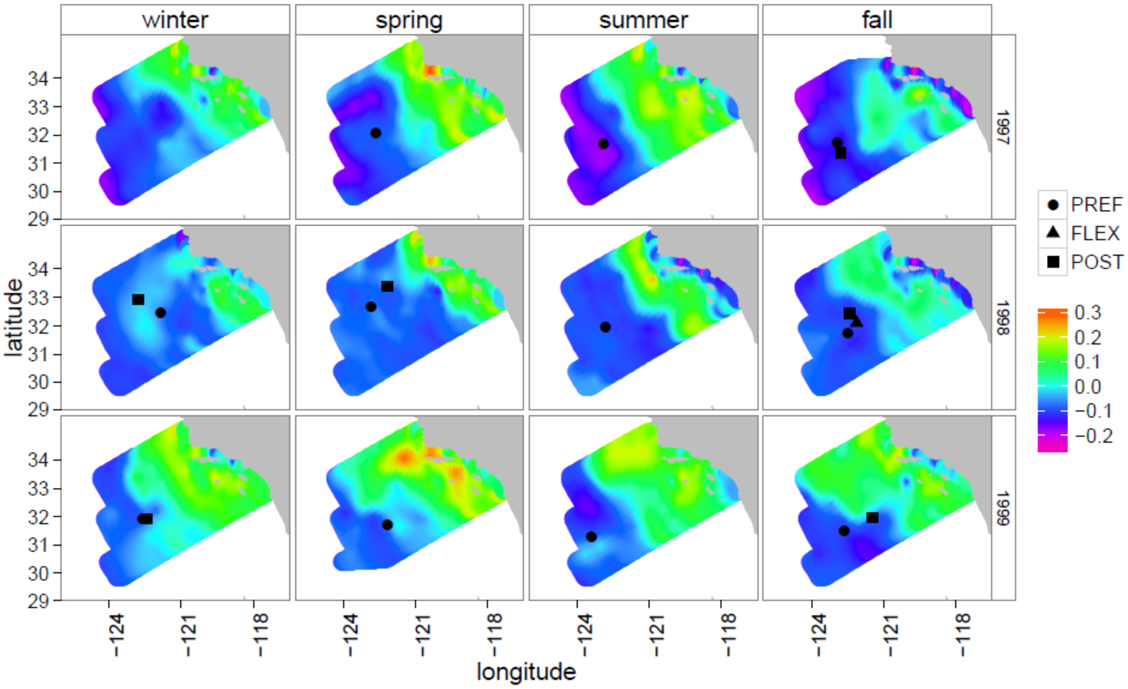
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	-	-	130	NW	58	SW	-	-	58	SE	31	NW	12	NW	71	SE
FLEX	-	-	-	-	-	-	-	-	74	SE	-	-	28	SE	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	111	SW	56	NE

Figure 12:
Ceratoscopelus townsendi distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



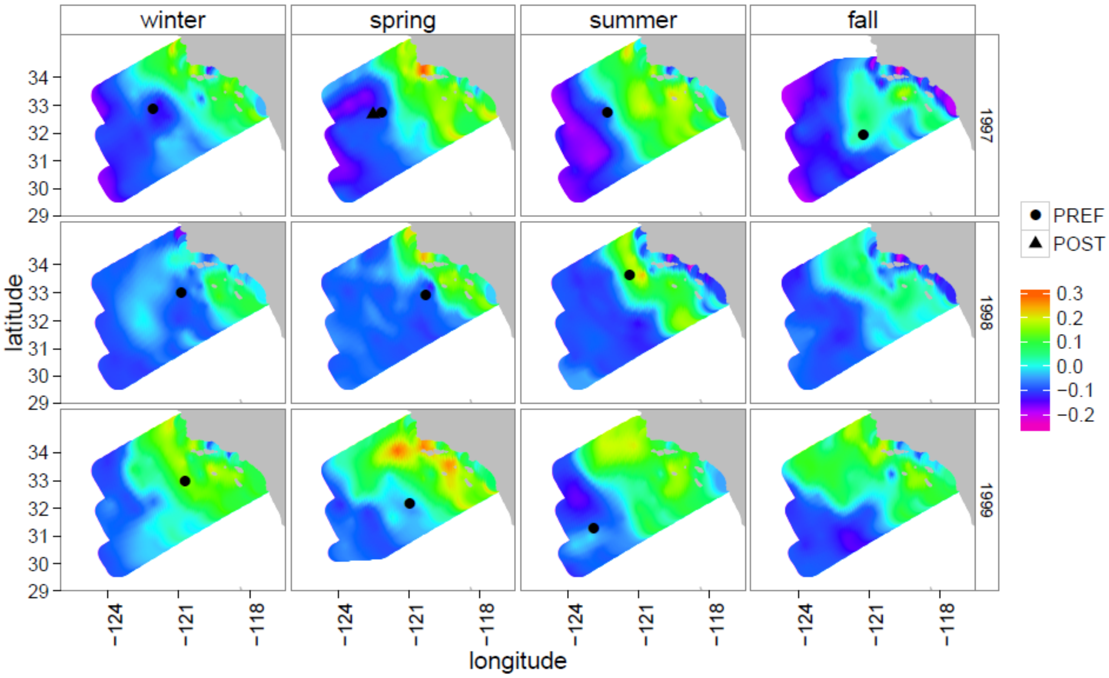
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	-	-	-	-	48	NW	-	-	37	SE	77	SW	-	-	137	SW
FLEX	-	-	-	-	-	-	-	-	129	NE	-	-	75	NE	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	87	NW	-	-

Figure 13:
Triphoturus mexicanus distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



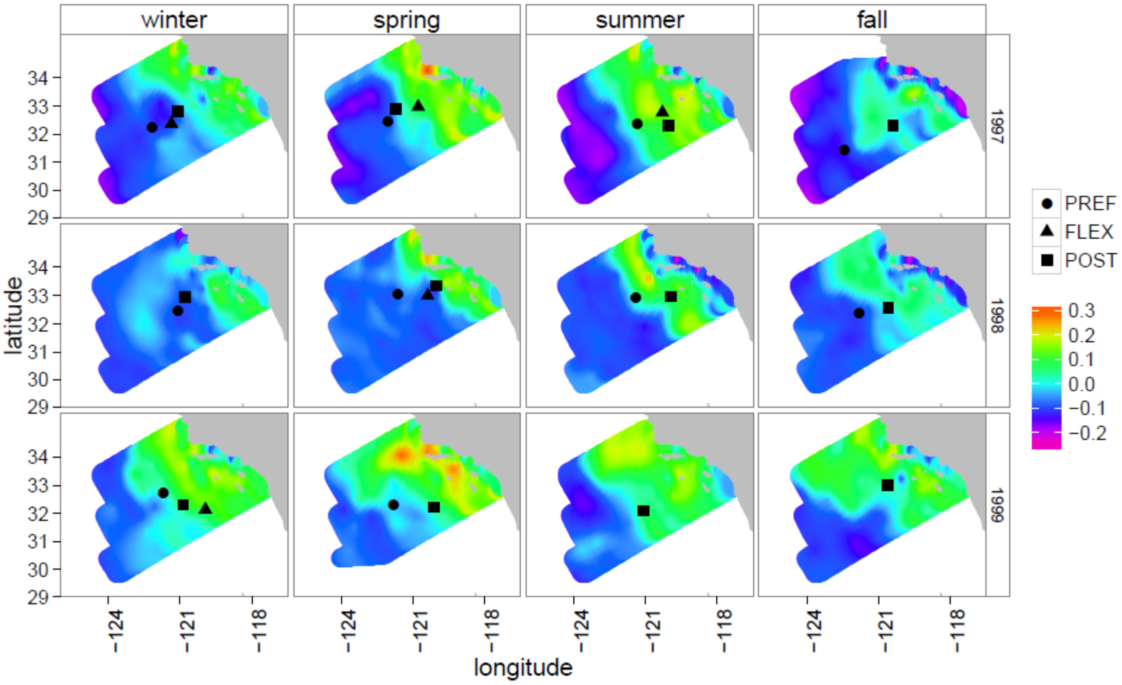
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	-	-	95	SW	68	NW	123	SE	30	NE	92	SW	41	SE	30	SW
FLEX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POST	-	-	117	SE	-	-	-	-	-	-	-	-	127	NE	104	SE

Figure 14:
Diogenichthys atlanticus distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



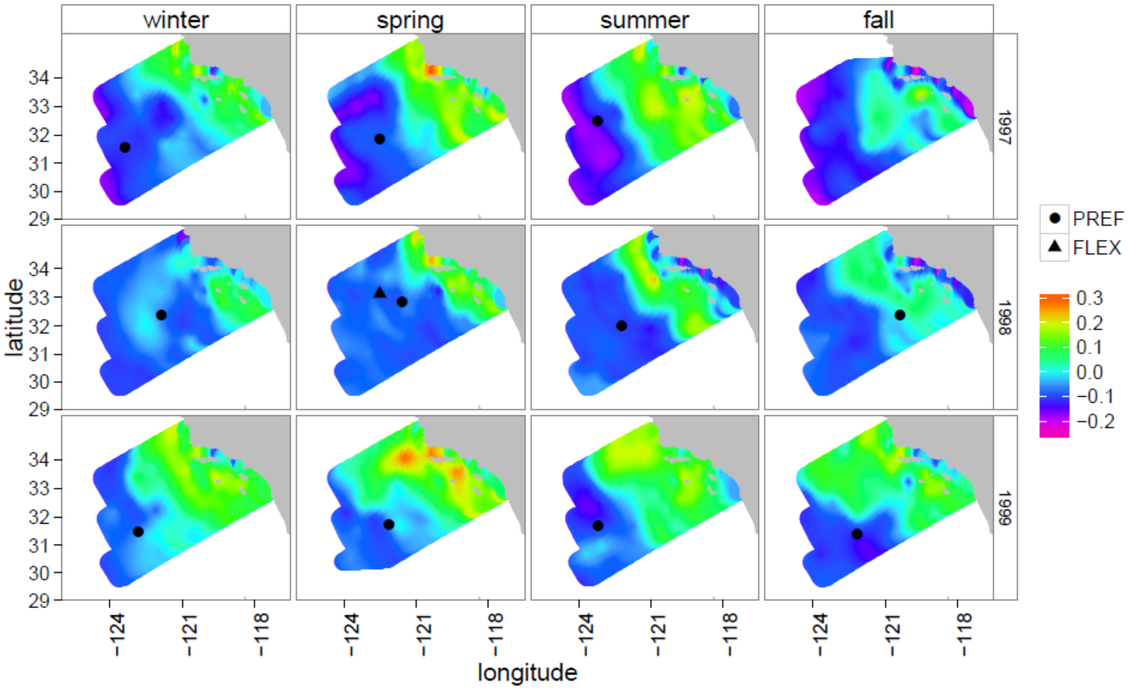
	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	112	NE	15	SE	176	NE	106	SW	132	NE	297	SW	-	-	-	-
FLEX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 15:
Nannobrachium ritteri distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	104	NE	66	NW	79	NE	85	SW	60	NW	-	-	117	NE	-	-
FLEX	-	-	-	-	37	NE	-	-	-	-	-	-	-	-	-	-
POST	29	NE	70	SW	166	NE	124	SW	73	NE	145	SW	32	NW	47	NW

Figure 16:
Protomyctophum crockeri distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
stage	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	169	NE	137	SW	140	NE	135	SW	109	SE	101	SW	-	-	201	SW
FLEX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 17:
Symbolophorus californiensis distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.

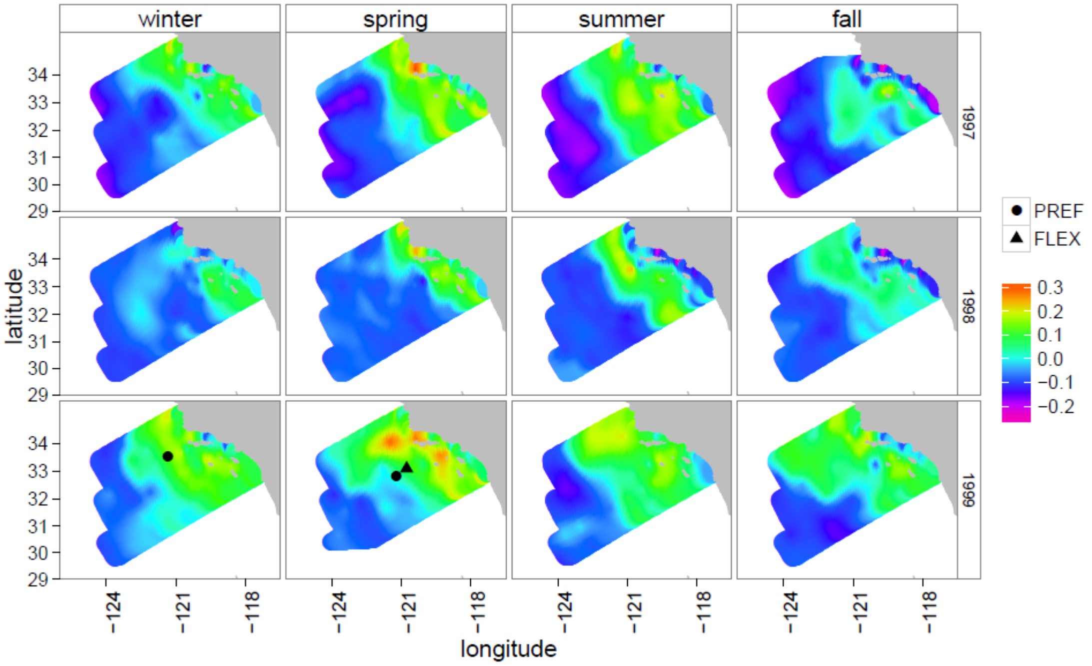


Figure 18:
Tarletonbeania crenularis distribution centroid locations plotted over maps of PC1. A centroid location comparisons table is absent for this species due to insufficient data.

Table 5:
Predicted and observed abundances and centroid locations based on species classifications of affinities for temperature conditions, coastal or oceanic environments, and spawning season. Observations consistent with predictions are indicated in bold. The prediction accuracies (number of correct predictions out of total outcomes) are listed beneath each column of observed outcomes, with the total accuracy below. Abbreviations: abund = abundance, temp affinity = temperature affinity, dist from shore = affinity for coastal (inshore) or oceanic (offshore) environments. Comparisons with insufficient sample sizes are indicated by a dash (-). The * indicates the presence of a mixed pattern.

				Predicted						**Observed**					
				Pre-El Niño		El Niño		La Niña		Pre-El Niño		El Niño		La Niña	
species	temp affinity	dist from shore	spawning season	abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location
Bathylagoides wesethi	cold	oceanic	SU	High	offshore	Low	inshore	High	offshore	**High**	**offshore**	**Low**	**inshore**	Low	**offshore**
Leuroglossus stilbius	cold	coastal-oceanic	WI-SP	High	inshore	Low	inshore	High	inshore	**High**	**inshore**	**Low**	**inshore**	**High**	offshore
Lipolagus ochotensis	cold	coastal-oceanic	WI-SP	High	inshore	Low	inshore	High	inshore	Low	**inshore**	**Low**	**inshore**	**High**	offshore
Vinciguerria lucetia	warm	oceanic	SU-FA	Low	offshore	High	inshore	Low	offshore	High	**offshore**	**High**	**inshore**	**Low**	**offshore**
Ceratoscopelus townsendi	broad	oceanic	SU	High	offshore	High	offshore	High	offshore	Low	**offshore**	**High**	**offshore**	Low	**offshore**
Diogenichthys atlanticus	warm	oceanic	SP & FA	Low	offshore	High	inshore	Low	offshore	**Low**	**offshore**	**High**	offshore	**Low**	**offshore**
Nannobrachium ritteri	broad	oceanic	WI-SP	High	offshore	High	offshore	High	offshore	**High**	**offshore**	Low	inshore	**High**	**offshore**
Protomyctophum crockeri	cold	oceanic	WI	High	offshore	Low	inshore	High	offshore	**High**	**offshore**	High	**inshore**	**High**	**offshore**
Stenobrachius leucopsarus	cold	oceanic	WI-SP	High	offshore	Low	inshore	High	offshore	**High**	inshore	High	*	**High**	**offshore**
Symbolophorus californiens	cold	oceanic	SP & SU	High	offshore	Low	inshore	High	offshore	**High**	**offshore**	High	**inshore**	Low	**offshore**
Tarletonbeania crenularis	cold	oceanic	WI-SP	High	offshore	Low	inshore	High	offshore	Low	-	**Low**	-	**High**	-
Triphoturus mexicanus	warm	oceanic	SU-FA	High	offshore	Low	inshore	High	offshore	**High**	**offshore**	High	**inshore**	Low	**offshore**
									Accuracy	0.6667	0.9091	0.5833	0.7273	0.6667	0.8182
									Abundance	0.6389					
									centroid location	0.8182					
									Total	**0.7286**					

Table 6:
Generalized linear mixed model results fixed effects summary table. Significant results ($p<0.05$) are in bold. The four cases where the model did not converge are represented by NC.

		p-value				
species	stage	depth	PC1	PC2	year (97-98)	year (98-99)
Bathylagoides wesethi	EGGS	0.518	**<0.001**	**<0.001**	**0.018**	**0.002**
	PREF	**0.008**	**<0.001**	**0.020**	0.870	**<0.001**
	FLEX	0.486	**<0.001**	**0.002**	0.078	**<0.001**
	POST	0.664	0.125	0.165	0.402	0.550
Leuroglossus stilbius	EGGS	**0.012**	**<0.001**	0.075	0.702	**<0.001**
	PREF	**0.006**	**<0.001**	**<0.001**	0.266	**<0.001**
	FLEX	0.959	**<0.001**	0.611	0.817	0.191
	POST	0.701	**<0.001**	**0.030**	0.200	**0.012**
Lipolagus ochotensis	EGGS	0.401	**<0.001**	**<0.001**	0.316	**<0.001**
	PREF	0.768	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	FLEX	0.950	0.064	**<0.001**	0.388	0.066
	POST	NC	NC	NC	NC	NC
Vinciguerria lucetia	EGGS	**0.004**	**<0.001**	**0.011**	0.337	0.063
	PREF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.700
	FLEX	**<0.001**	**<0.001**	**0.006**	**0.009**	**<0.001**
	POST	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.005**
Ceratoscopelus townsendi	PREF	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	FLEX	**0.033**	**<0.001**	**<0.001**	0.161	0.556
	POST	**0.010**	**<0.001**	**<0.001**	**<0.001**	**0.003**
Diogenichthys atlanticus	PREF	**0.005**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	FLEX	0.343	**<0.001**	0.959	**0.009**	0.078
	POST	**0.037**	**0.001**	0.951	0.176	0.304
Nannobrachium ritteri	PREF	0.826	**0.014**	**<0.001**	0.840	0.530
	FLEX	0.568	0.156	**0.024**	0.775	0.989
	POST	0.888	0.275	**0.003**	0.615	0.171
Protomyctophum crockeri	PREF	0.540	**0.001**	**0.001**	0.249	0.323
	FLEX	0.814	0.153	**0.008**	0.230	0.060
	POST	0.738	0.165	**<0.001**	0.807	0.141
Stenobrachius leucopsarus	PREF	0.616	**<0.001**	**<0.001**	**0.013**	0.151
	FLEX	0.645	**<0.001**	**0.001**	0.740	**0.003**
	POST	0.265	**0.005**	**0.006**	0.169	**<0.001**
Symbolophorus californiensis	PREF	0.783	**<0.001**	0.345	**0.014**	**<0.001**
	FLEX	0.054	**<0.001**	0.082	0.177	0.845
	POST	0.728	**0.039**	**0.008**	0.876	0.774
Tarletonbeania crenularis	PREF	0.870	**0.002**	**<0.001**	0.199	**0.004**
	FLEX	0.816	**0.050**	**0.003**	0.999	0.180
	POST	0.248	**0.026**	0.104	0.999	**0.040**
Triphoturus mexicanus	PREF	NC	NC	NC	NC	NC
	FLEX	NC	NC	NC	NC	NC
	POST	NC	NC	NC	NC	NC

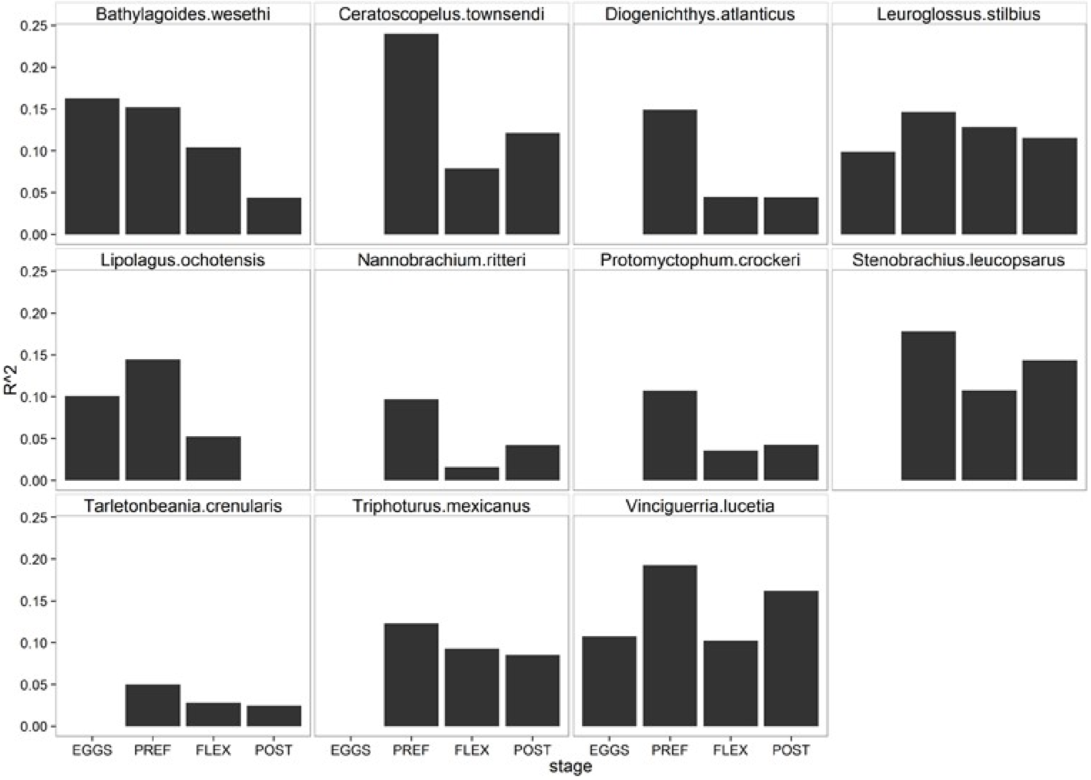


Figure 19:
Graphical representation of generalized linear mixed model fits for early life history of eleven mesopelagic fish species.

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APPENDIX A: Generalized Linear Model Output Summary

Each of the proceeding tables in the summary of the model results for each of the twelve mesopelagic species from equation (1):

$$Abund_{spp.stage} \sim season * year$$

Table 1:

Bathylagoides wesethi, ontogenetic stage = Eggs

```
Call:
glm.nb(formula = as.integer(Bathylagoides.wesethi_EGGS) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.06623963715, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.9505  -0.8453  -0.7822  -0.2107   1.9078
Coefficients:
                    Estimate Std. Error z value Pr(>|z|)
(Intercept)        1198.6985   722.7091   1.659   0.0972 .
seasonspring         45.2805  1009.4526   0.045   0.9642
seasonsummer        207.3702  1024.6260   0.202   0.8396
seasonwinter       -812.6851  1006.6082  -0.807   0.4195
year1                -0.5991     0.3617  -1.656   0.0977 .
seasonspring:year1   -0.0222     0.5052  -0.044   0.9650
seasonsummer:year1   -0.1030     0.5128  -0.201   0.8409
seasonwinter:year1    0.4068     0.5038   0.807   0.4194
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0662) family taken
to be 1)
    Null deviance: 449.52  on 735  degrees of freedom
Residual deviance: 413.34  on 728  degrees of freedom
AIC: 2928.5

Number of Fisher Scoring iterations: 1
              Theta:  0.06624
          Std. Err.:  0.00532
 2 x log-likelihood:  -2910.45300
```

Table 2:

Bathylagoides wesethi, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Bathylagoides.wesethi_PREF) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.07306406362, link
= log)
```

Table 2:
Bathylagoides wesethi, ontogenetic stage = Preflexion, continued

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.9002  -0.7907  -0.6430  -0.5969   1.6860
Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         2776.2483   694.6820   3.996 6.43e-05 ***
seasonspring        -507.6281   972.1189  -0.522   0.6015
seasonsummer       -1645.7896   981.8348  -1.676   0.0937 .
seasonwinter       -2355.5265   978.8090  -2.407   0.0161 *
year1                 -1.3887     0.3477  -3.994 6.49e-05 ***
seasonspring:year1     0.2540     0.4865   0.522   0.6017
seasonsummer:year1     0.8241     0.4914   1.677   0.0936 .
seasonwinter:year1     1.1781     0.4899   2.405   0.0162 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for Negative Binomial(0.0731) family taken
to be 1)
    Null deviance: 422.55  on 735  degrees of freedom
Residual deviance: 367.56  on 728  degrees of freedom
AIC: 2279.8

Number of Fisher Scoring iterations: 1
              Theta:  0.07306
          Std. Err.:  0.00666
 2 x log-likelihood:  -2261.78500
```

Table 3:
Bathylagoides wesethi, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Bathylagoides.wesethi_FLEX) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.04050637625, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.5767  -0.5086  -0.4169  -0.1857   2.8378

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1.872e+03  9.460e+02   1.979   0.0478 *
seasonspring        5.727e+02  1.375e+03   0.417   0.6770
seasonsummer       -2.552e+01  1.350e+03  -0.019   0.9849
seasonwinter       -1.876e+03  1.785e+03  -1.051   0.2934
year1              -9.369e-01  4.735e-01  -1.979   0.0478 *
```

Table 3:
Bathylagoides wesethi, ontogenetic stage = Flexion, continued

```
seasonspring:year1 -2.872e-01  6.881e-01  -0.417   0.6764
seasonsummer:year1  1.266e-02  6.756e-01   0.019   0.9850
seasonwinter:year1  9.369e-01  8.934e-01   1.049   0.2943
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0405) family taken
to be 1)
    Null deviance: 197.63  on 735  degrees of freedom
Residual deviance: 152.23  on 728  degrees of freedom
AIC: 802.18

Number of Fisher Scoring iterations: 1
              Theta:  0.04051
          Std. Err.:  0.00661
 2 x log-likelihood:  -784.17700
```

Table 4:
Bathylagoides wesethi, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Bathylagoides.wesethi_POST) ~ season
*
    year1, data = spstaenvall1, init.theta = 6642.637634, link =
log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.0702  -0.6312  -0.4735   0.0000   7.7366

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1.259e+03  4.387e+02   2.869  0.00412 **
seasonspring       -1.407e+03  6.961e+02  -2.021  0.04331 *
seasonsummer       -2.314e+03  5.462e+02  -4.237 2.26e-05 ***
seasonwinter       -1.296e+03  1.204e+10   0.000  1.00000
year1              -6.307e-01  2.196e-01  -2.872  0.00408 **
seasonspring:year1  7.038e-01  3.484e-01   2.020  0.04340 *
seasonsummer:year1  1.159e+00  2.734e-01   4.238 2.25e-05 ***
seasonwinter:year1  6.307e-01  6.027e+06   0.000  1.00000
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(6642.638) family
taken to be 1)
    Null deviance: 905.08  on 735  degrees of freedom
Residual deviance: 787.33  on 728  degrees of freedom
```

Table 4:
Bathylagoides wesethi, ontogenetic stage = Postflexion, continued

```
AIC: 879.98

Number of Fisher Scoring iterations: 1
```

Table 5:
Leuroglossus stilbius, ontogenetic stage = Eggs

```
Call:
glm.nb(formula = as.integer(Leuroglossus.stilbius_EGGS) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.09030406763, link
= log)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.24304  -1.05277  -0.28876  -0.00003   2.88839

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)        -7.938e+03  9.745e+02  -8.145 3.79e-16 ***
seasonspring        7.264e+03  1.146e+03   6.340 2.29e-10 ***
seasonsummer        7.916e+03  4.783e+06   0.002    0.999
seasonwinter        8.710e+03  1.143e+03   7.620 2.53e-14 ***
year1               3.973e+00  4.877e-01   8.147 3.75e-16 ***
seasonspring:year1 -3.633e+00  5.733e-01  -6.337 2.34e-10 ***
seasonsummer:year1 -3.973e+00  2.394e+03  -0.002    0.999
seasonwinter:year1 -4.356e+00  5.720e-01  -7.616 2.61e-14 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0903) family taken
to be 1)
    Null deviance: 782.59  on 735  degrees of freedom
Residual deviance: 394.65  on 728  degrees of freedom
AIC: 3365.1

Number of Fisher Scoring iterations: 1
              Theta:  0.09030
          Std. Err.:  0.00701
 2 x log-likelihood:  -3347.07100
```

Table 6:
Leuroglossus stilbius, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Leuroglossus.stilbius_PREF) ~ season
*
```

Table 6:
Leuroglossus stilbius, ontogenetic stage = Preflexion, continued

```
    year1, data = spstaenvall1, init.theta = 0.1187923404, link =
log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.1612  -1.0795  -0.2676  -0.1981   3.7174

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)          56.90937 1356.46439   0.042   0.9665
seasonspring        146.95960 1455.09951   0.101   0.9196
seasonsummer       3337.68869 1692.86760   1.972   0.0487 *
seasonwinter        505.43603 1453.37016   0.348   0.7280
year1                -0.03039    0.67891  -0.045   0.9643
seasonspring:year1   -0.07021    0.72828  -0.096   0.9232
seasonsummer:year1   -1.66984    0.84736  -1.971   0.0488 *
seasonwinter:year1   -0.24943    0.72741  -0.343   0.7317
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.1188) family taken
to be 1)
    Null deviance: 710.83  on 735  degrees of freedom
Residual deviance: 367.60  on 728  degrees of freedom
AIC: 2352.4

Number of Fisher Scoring iterations: 1
              Theta:  0.1188
          Std. Err.:  0.0107
 2 x log-likelihood:  -2334.3790
```

Table 7:
Leuroglossus stilbius, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Leuroglossus.stilbius_FLEX) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.06553768017, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.7409  -0.5803  -0.1656   0.0000   3.0684

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         4.506e+03  2.139e+09       0        1
```

Table 7:
Leuroglossus stilbius, ontogenetic stage = Flexion, continued

```
seasonspring       -4.910e+03  2.139e+09       0        1
seasonsummer        5.635e+04  2.299e+09       0        1
seasonwinter       -2.302e+03  2.139e+09       0        1
year1              -2.270e+00  1.070e+06       0        1
seasonspring:year1  2.473e+00  1.070e+06       0        1
seasonsummer:year1 -2.820e+01  1.150e+06       0        1
seasonwinter:year1  1.167e+00  1.070e+06       0        1

(Dispersion parameter for Negative Binomial(0.0655) family taken
to be 1)
    Null deviance: 315.47  on 735  degrees of freedom
Residual deviance: 158.08  on 728  degrees of freedom
AIC: 860.98

Number of Fisher Scoring iterations: 1
              Theta:  0.0655
          Std. Err.:  0.0101
 2 x log-likelihood:  -842.9840
```

Table 8:
Leuroglossus stilbius, ontogenetic stage = Postflexion

```
Model did not converge.
```

Table 9:
Lipolagus ochotensis, ontogenetic stage = Eggs

```
Call:
glm.nb(formula = as.integer(Lipolagus.ochotensis_EGGS) ~ season *
    year1, data = spstaenvall1, init.theta = 0.07466874571, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.9392  -0.8354  -0.3016   0.0000   2.6670

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         4.964e+04  4.473e+07   0.001    0.999
seasonspring       -5.092e+04  4.473e+07  -0.001    0.999
seasonsummer       -1.557e+03  7.274e+07   0.000    1.000
seasonwinter       -5.053e+04  4.473e+07  -0.001    0.999
year1              -2.486e+01  2.240e+04  -0.001    0.999
seasonspring:year1  2.550e+01  2.240e+04   0.001    0.999
seasonsummer:year1  7.789e-01  3.643e+04   0.000    1.000
seasonwinter:year1  2.530e+01  2.240e+04   0.001    0.999
```

Table 9:
Lipolagus ochotensis, ontogenetic stage = Eggs, continued

```
(Dispersion parameter for Negative Binomial(0.0747) family taken
to be 1)
    Null deviance: 494.13  on 735  degrees of freedom
Residual deviance: 265.27  on 728  degrees of freedom
AIC: 1789.9

Number of Fisher Scoring iterations: 1
              Theta:  0.07467
          Std. Err.:  0.00774
 2 x log-likelihood:  -1771.86100
```

Table 10:
Lipolagus ochotensis, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Lipolagus.ochotensis_PREF) ~ season *
    year1, data = spstaenvall1, init.theta = 0.1118756818, link =
log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.0479  -0.8980  -0.3221   0.0000   2.5635

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)        -2.118e+02  9.520e+07       0        1
seasonspring       -1.109e+03  9.520e+07       0        1
seasonsummer        2.280e+03  9.520e+07       0        1
seasonwinter       -2.231e+02  9.520e+07       0        1
year1               9.232e-02  4.765e+04       0        1
seasonspring:year1  5.696e-01  4.765e+04       0        1
seasonsummer:year1 -1.129e+00  4.765e+04       0        1
seasonwinter:year1  1.260e-01  4.765e+04       0        1

(Dispersion parameter for Negative Binomial(0.1119) family taken
to be 1)
    Null deviance: 545.39  on 735  degrees of freedom
Residual deviance: 306.70  on 728  degrees of freedom
AIC: 1721.6

Number of Fisher Scoring iterations: 1
              Theta:  0.1119
          Std. Err.:  0.0117
 2 x log-likelihood:  -1703.6390
```

Table 11:
Lipolagus ochotensis, ontogenetic stage = Flexion

```
Model did not converge.
```

Table 12:
Lipolagus ochotensis, ontogenetic stage = Post

```
Call:
glm.nb(formula = as.integer(Lipolagus.ochotensis_POST) ~ season *
    year1, data = spstaenvall1, init.theta = 0.01703022273, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.3817  -0.2906  -0.2280   0.0000   1.7252

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)        -2.032e+02  5.256e+08       0        1
seasonspring       -1.065e+03  5.256e+08       0        1
seasonsummer       -9.007e+02  5.256e+08       0        1
seasonwinter        3.528e+03  5.256e+08       0        1
year1               8.633e-02  2.631e+05       0        1
seasonspring:year1  5.480e-01  2.631e+05       0        1
seasonsummer:year1  4.650e-01  2.631e+05       0        1
seasonwinter:year1 -1.752e+00  2.631e+05       0        1

(Dispersion parameter for Negative Binomial(0.017) family taken
to be 1)
    Null deviance: 87.001  on 735  degrees of freedom
Residual deviance: 55.189  on 728  degrees of freedom
AIC: 329.96

Number of Fisher Scoring iterations: 1
              Theta:  0.01703
          Std. Err.:  0.00465
 2 x log-likelihood:  -311.96300
```

Table 13:
Vinciguerria lucetia, ontogenetic stage = Eggs

```
Call:
glm.nb(formula = as.integer(Vinciguerria.lucetia_EGGS) ~ season *
    year1, data = spstaenvall1, init.theta = 0.05605672007, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.0108  -0.9274  -0.7980  -0.2709   2.0260
```

Table 13:
Vinciguerria lucetia, ontogenetic stage = Eggs, continued

```
Coefficients:
                     Estimate Std. Error z value Pr(>|z|)  
(Intercept)         1992.4423   781.3618   2.550   0.0108 *
seasonspring       -2148.4401  1092.9400  -1.966   0.0493 *
seasonsummer        -646.6490  1110.1040  -0.583   0.5602  
seasonwinter       -2192.7997  1089.5037  -2.013   0.0442 *
year1                 -0.9955     0.3911  -2.546   0.0109 *
seasonspring:year1     1.0759     0.5470   1.967   0.0492 *
seasonsummer:year1     0.3247     0.5556   0.584   0.5590  
seasonwinter:year1     1.0971     0.5453   2.012   0.0442 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0561) family taken
to be 1)
    Null deviance: 505.40  on 735  degrees of freedom
Residual deviance: 452.65  on 728  degrees of freedom
AIC: 3820.4

Number of Fisher Scoring iterations: 1
              Theta:  0.05606 
          Std. Err.:  0.00408 
 2 x log-likelihood:  -3802.35400
```

Table 14:
Vinciguerria lucetia, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Vinciguerria.lucetia_PREF) ~ season * 
    year1, data = spstaenvall1, init.theta = 0.0577753306, link = 
log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.9572  -0.8924  -0.7969  -0.3628   1.7297  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)  
(Intercept)         1834.5558   769.2095   2.385   0.0171 *
seasonspring       -1927.0545  1077.1561  -1.789   0.0736 .
seasonsummer       -1831.3768  1093.1819  -1.675   0.0939 .
seasonwinter       -2458.2930  1076.2099  -2.284   0.0224 *
year1                 -0.9162     0.3850  -2.380   0.0173 *
seasonspring:year1     0.9638     0.5391   1.788   0.0738 .
seasonsummer:year1     0.9171     0.5471   1.676   0.0937 .
seasonwinter:year1     1.2290     0.5386   2.282   0.0225 *
---
```

Table 14:
Vinciguerria lucetia, ontogenetic stage = Preflexion, continued

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0578) family taken
to be 1)
    Null deviance: 490.57  on 735  degrees of freedom
Residual deviance: 419.07  on 728  degrees of freedom
AIC: 3307.5

Number of Fisher Scoring iterations: 1
              Theta:  0.05778
          Std. Err.:  0.00447
 2 x log-likelihood:  -3289.52800
```

Table 15:
Vinciguerria lucetia, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Vinciguerria.lucetia_FLEX) ~ season *
    year1, data = spstaenvall1, init.theta = 0.06627365719, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.9288  -0.7813  -0.5765  -0.5228   2.7661

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         2522.8639   721.2398   3.498 0.000469 ***
seasonspring       -1340.8868  1029.7969  -1.302 0.192886
seasonsummer       -2017.8727  1024.8280  -1.969 0.048955 *
seasonwinter       -2523.1552  1024.2233  -2.463 0.013759 *
year1                 -1.2614     0.3610  -3.494 0.000475 ***
seasonspring:year1     0.6697     0.5154   1.299 0.193795
seasonsummer:year1     1.0097     0.5129   1.969 0.049002 *
seasonwinter:year1     1.2614     0.5126   2.461 0.013865 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0663) family taken
to be 1)
    Null deviance: 428.86  on 735  degrees of freedom
Residual deviance: 332.90  on 728  degrees of freedom
AIC: 2097.7

Number of Fisher Scoring iterations: 1
              Theta:  0.06627
          Std. Err.:  0.00642
```

Table 15:
Vinciguerria lucetia, ontogenetic stage = Flexion, continued

```
 2 x log-likelihood:  -2079.67400
```

Table 16:
Vinciguerria lucetia, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Vinciguerria.lucetia_POST) ~ season *
    year1, data = spstaenvall1, init.theta = 0.08082926671, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.0618  -0.8519  -0.6022  -0.4720   3.1083

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1576.5573   650.7318   2.423 0.015404 *
seasonspring        -864.3238   955.5152  -0.905 0.365697
seasonsummer       -3137.1370   926.0055  -3.388 0.000705 ***
seasonwinter       -2847.6851   915.1027  -3.112 0.001859 **
year1                 -0.7872     0.3257  -2.417 0.015644 *
seasonspring:year1     0.4303     0.4782   0.900 0.368239
seasonsummer:year1     1.5697     0.4635   3.387 0.000707 ***
seasonwinter:year1     1.4239     0.4580   3.109 0.001878 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0808) family taken
to be 1)
    Null deviance: 537.13  on 735  degrees of freedom
Residual deviance: 401.60  on 728  degrees of freedom
AIC: 2692.2

Number of Fisher Scoring iterations: 1
              Theta:  0.08083
          Std. Err.:  0.00692
 2 x log-likelihood:  -2674.23900
```

Table 17:
Ceratoscopelus townsendi, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Ceratoscopelus.townsendi_PREF) ~
    season * year1, data = spstaenvall1, init.theta =
0.06620941576,
    link = log)
```

Table 17:
Ceratoscopelus townsendi, ontogenetic stage = Preflexion, continued

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.8302  -0.7653  -0.6877  -0.6042   2.2895

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)          367.8349   722.4375   0.509   0.6106
seasonspring         779.9884  1018.0191   0.766   0.4436
seasonsummer        -801.6976  1025.6276  -0.782   0.4344
seasonwinter       -2068.4880  1013.6706  -2.041   0.0413 *
year1                 -0.1833     0.3616  -0.507   0.6123
seasonspring:year1    -0.3909     0.5095  -0.767   0.4429
seasonsummer:year1     0.4015     0.5133   0.782   0.4341
seasonwinter:year1     1.0348     0.5073   2.040   0.0414 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0662) family taken
to be 1)
    Null deviance: 378.34  on 735  degrees of freedom
Residual deviance: 355.79  on 728  degrees of freedom
AIC: 2200.1

Number of Fisher Scoring iterations: 1
              Theta:  0.06621
          Std. Err.:  0.00605
 2 x log-likelihood:  -2182.07800
```

Table 18:
Ceratoscopelus townsendi, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Ceratoscopelus.townsendi_FLEX) ~
    season * year1, data = spstaenvall1, init.theta =
0.02702912935,
    link = log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.4840  -0.4427  -0.3895  -0.3828   2.9808

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1392.8719  1142.2585   1.219   0.2227
seasonspring       -1393.8404  1612.9266  -0.864   0.3875
seasonsummer        -255.9359  1623.3980  -0.158   0.8747
seasonwinter       -4547.4997  1814.5323  -2.506   0.0122 *
```

Table 18:
Ceratoscopelus townsendi, ontogenetic stage = Flexion, continued

```
year1                 -0.6971     0.5717  -1.219   0.2227
seasonspring:year1     0.6971     0.8073   0.864   0.3878
seasonsummer:year1     0.1281     0.8125   0.158   0.8747
seasonwinter:year1     2.2748     0.9081   2.505   0.0122 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.027) family taken
to be 1)
    Null deviance: 149.44  on 735  degrees of freedom
Residual deviance: 132.77  on 728  degrees of freedom
AIC: 761.21

Number of Fisher Scoring iterations: 1
              Theta:  0.02703
          Std. Err.:  0.00448
 2 x log-likelihood:  -743.20800
```

Table 19:
Ceratoscopelus townsendi, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Ceratoscopelus.townsendi_POST) ~
    season * year1, data = spstaenvall1, init.theta =
0.04433383173,
    link = log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.5803  -0.5536  -0.4514  -0.3231   2.4473

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         -350.5893   889.5696  -0.394   0.6935
seasonspring        2382.2319  1412.5559   1.686   0.0917 .
seasonsummer        -373.1758  1272.2172  -0.293   0.7693
seasonwinter       -2320.4620  1293.9647  -1.793   0.0729 .
year1                  0.1757     0.4452   0.395   0.6931
seasonspring:year1    -1.1937     0.7070  -1.688   0.0913 .
seasonsummer:year1     0.1865     0.6367   0.293   0.7696
seasonwinter:year1     1.1607     0.6476   1.792   0.0731 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0443) family taken
to be 1)
    Null deviance: 214.84  on 735  degrees of freedom
```

Table 19:
Ceratoscopelus townsendi, ontogenetic stage = Postflexion, continued

```
Residual deviance: 187.02  on 728  degrees of freedom
AIC: 975.06

Number of Fisher Scoring iterations: 1
              Theta:  0.04433
          Std. Err.:  0.00638
 2 x log-likelihood:  -957.05700
```

Table 20:
Diogenichthys atlanticus, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Diogenichthys.atlanticus_PREF) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.07853043966, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.7982  -0.7753  -0.7042  -0.5479   1.6028  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)  
(Intercept)         -232.6476   665.8402  -0.349   0.7268  
seasonspring         819.0121   937.7125   0.873   0.3824  
seasonsummer        -697.6404   950.9668  -0.734   0.4632  
seasonwinter       -1857.8815   944.7418  -1.967   0.0492 *
year1                  0.1171     0.3333   0.351   0.7252  
seasonspring:year1    -0.4103     0.4693  -0.874   0.3820  
seasonsummer:year1     0.3489     0.4760   0.733   0.4636  
seasonwinter:year1     0.9293     0.4728   1.965   0.0494 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for Negative Binomial(0.0785) family taken 
to be 1)
    Null deviance: 368.92  on 735  degrees of freedom
Residual deviance: 354.85  on 728  degrees of freedom
AIC: 1946.7

Number of Fisher Scoring iterations: 1
              Theta:  0.07853
          Std. Err.:  0.00758
 2 x log-likelihood:  -1928.66800
```

Table 21:
Diogenichthys atlanticus, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Diogenichthys.atlanticus_FLEX) ~ 
    season * year1, data = spstaenvall1, init.theta = 
30789.43963, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-1.2106  -0.9268  -0.7746  -0.7609   8.3912  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)   
(Intercept)          533.1796   247.6626   2.153  0.03133 * 
seasonspring       -1236.6489   377.4159  -3.277  0.00105 **
seasonsummer        -512.6797   424.7832  -1.207  0.22746   
seasonwinter       -1219.2059   413.2402  -2.950  0.00317 **
year1                 -0.2671     0.1240  -2.155  0.03116 * 
seasonspring:year1     0.6188     0.1889   3.276  0.00105 **
seasonsummer:year1     0.2563     0.2126   1.205  0.22807   
seasonwinter:year1     0.6099     0.2068   2.949  0.00319 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(30789.44) family 
taken to be 1)
    Null deviance: 1621.9  on 735  degrees of freedom
Residual deviance: 1584.7  on 728  degrees of freedom
AIC: 1785.7

Number of Fisher Scoring iterations: 1
```

Table 22:
Diogenichthys atlanticus, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Diogenichthys.atlanticus_POST) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.04610215715, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.5886  -0.5577  -0.4883  -0.4279   1.7995  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         3.946e+02  8.731e+02   0.452   0.6513
seasonspring        1.069e+02  1.235e+03   0.087   0.9310
```

Table 22:
Diogenichthys atlanticus, ontogenetic stage = Postflexion, continued

```
seasonsummer        5.568e+02  1.266e+03   0.440   0.6599
seasonwinter       -2.820e+03  1.250e+03  -2.256   0.0240 *
year1              -1.973e-01  4.370e-01  -0.451   0.6517
seasonspring:year1 -5.398e-02  6.182e-01  -0.087   0.9304
seasonsummer:year1 -2.793e-01  6.334e-01  -0.441   0.6592
seasonwinter:year1  1.411e+00  6.254e-01   2.256   0.0241 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0461) family taken
to be 1)
    Null deviance: 223.31  on 735  degrees of freedom
Residual deviance: 209.78  on 728  degrees of freedom
AIC: 1105.5

Number of Fisher Scoring iterations: 1
              Theta:  0.04610
          Std. Err.:  0.00617

 2 x log-likelihood:  -1087.48900
```

Table 23:
Nannobrachium ritteri, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Nannobrachium.ritteri_PREF) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.06742221319, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.7347  -0.7096  -0.6571  -0.4837   1.6782

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1187.1544   758.8451   1.564    0.118
seasonspring        -911.5946  1035.1871  -0.881    0.379
seasonsummer        -677.0185  1053.0189  -0.643    0.520
seasonwinter       -1466.3388  1036.2315  -1.415    0.157
year1                 -0.5945     0.3798  -1.565    0.118
seasonspring:year1     0.4571     0.5181   0.882    0.378
seasonsummer:year1     0.3395     0.5270   0.644    0.519
seasonwinter:year1     0.7344     0.5186   1.416    0.157

(Dispersion parameter for Negative Binomial(0.0674) family taken
to be 1)
```

Table 23:
Nannobrachium ritteri, ontogenetic stage = Preflexion, continued

```
    Null deviance: 327.83  on 735  degrees of freedom
Residual deviance: 309.67  on 728  degrees of freedom
AIC: 1692.6

Number of Fisher Scoring iterations: 1
              Theta:  0.06742
          Std. Err.:  0.00708
 2 x log-likelihood:  -1674.55500
```

Table 24:
Nannobrachium ritteri, ontogenetic stage = Flexion

```
Model did not converge.
```

Table 25:
Nannobrachium ritteri, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Nannobrachium.ritteri_POST) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.01848306838, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.3769  -0.3414  -0.2899  -0.1938   1.8436

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         3516.4107  1713.6896   2.052   0.0402 *
seasonspring       -2272.7668  2189.3603  -1.038   0.2992
seasonsummer       -4461.9662  2229.3893  -2.001   0.0453 *
seasonwinter        -818.7395  2524.3337  -0.324   0.7457
year1                 -1.7612     0.8578  -2.053   0.0401 *
seasonspring:year1     1.1384     1.0959   1.039   0.2989
seasonsummer:year1     2.2338     1.1159   2.002   0.0453 *
seasonwinter:year1     0.4093     1.2636   0.324   0.7460
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0185) family taken
to be 1)
    Null deviance: 91.259  on 735  degrees of freedom
Residual deviance: 76.651  on 728  degrees of freedom
AIC: 431.87

Number of Fisher Scoring iterations: 1
```

Table 25:
Nannobrachium ritteri, ontogenetic stage = Postflexion, continued

```
              Theta:  0.01848
          Std. Err.:  0.00433
 2 x log-likelihood:  -413.87400
```

Table 26:
Protomyctophum crockeri, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Protomyctophum.crockeri_PREF) ~
season *
    year1, data = spstaenvall1, init.theta = 0.08867237036, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.8147  -0.7667  -0.6579  -0.6142   2.0170

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)          696.9246   650.9186   1.071    0.284
seasonspring       -1129.5175   896.7145  -1.260    0.208
seasonsummer        -251.5488   927.3128  -0.271    0.786
seasonwinter        -291.5459   894.8321  -0.326    0.745
year1                 -0.3488     0.3258  -1.071    0.284
seasonspring:year1     0.5659     0.4488   1.261    0.207
seasonsummer:year1     0.1258     0.4641   0.271    0.786
seasonwinter:year1     0.1464     0.4479   0.327    0.744

(Dispersion parameter for Negative Binomial(0.0887) family taken
to be 1)
    Null deviance: 376.85  on 735  degrees of freedom
Residual deviance: 356.53  on 728  degrees of freedom
AIC: 1835.2

Number of Fisher Scoring iterations: 1
              Theta:  0.08867
          Std. Err.:  0.00894
 2 x log-likelihood:  -1817.24700
```

Table 27:
Protomyctophum crockeri, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Protomyctophum.crockeri_FLEX) ~
season *
    year1, data = spstaenvall1, init.theta = 0.04835486685, link
= log)
```

Table 27:
Protomyctophum crockeri, ontogenetic stage = Flexion, continued

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.5940  -0.5271  -0.5233  -0.4211   1.7675

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1118.4736   890.8953   1.255    0.209
seasonspring       -1032.1122  1229.2142  -0.840    0.401
seasonsummer        1916.3961  1308.5547   1.465    0.143
seasonwinter       -1612.5293  1225.4317  -1.316    0.188
year1                 -0.5602     0.4459  -1.256    0.209
seasonspring:year1     0.5169     0.6152   0.840    0.401
seasonsummer:year1    -0.9592     0.6550  -1.465    0.143
seasonwinter:year1     0.8074     0.6133   1.316    0.188

(Dispersion parameter for Negative Binomial(0.0484) family taken
to be 1)
    Null deviance: 218.56  on 735  degrees of freedom
Residual deviance: 206.16  on 728  degrees of freedom
AIC: 1052.6

Number of Fisher Scoring iterations: 1
              Theta:  0.04835
          Std. Err.:  0.00670
 2 x log-likelihood:  -1034.55600
```

Table 28:
Protomyctophum crockeri, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Protomyctophum.crockeri_POST) ~
season *
    year1, data = spstaenvall1, init.theta = 0.08160022012, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.7770  -0.7237  -0.6764  -0.6438   1.8108

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         269.33359  670.39161   0.402    0.688
seasonspring       -216.81246  931.06311  -0.233    0.816
seasonsummer        183.65077  952.08787   0.193    0.847
seasonwinter        333.41273  926.32838   0.360    0.719
year1                -0.13475    0.33553  -0.402    0.688
seasonspring:year1    0.10881    0.46600   0.233    0.815
```

Table 28:
Protomyctophum crockeri, ontogenetic stage = Postflexion, continued

```
seasonsummer:year1   -0.09188    0.47653  -0.193    0.847
seasonwinter:year1   -0.16649    0.46363  -0.359    0.720

(Dispersion parameter for Negative Binomial(0.0816) family taken
to be 1)
    Null deviance: 352.29  on 735  degrees of freedom
Residual deviance: 344.68  on 728  degrees of freedom
AIC: 1791.7

Number of Fisher Scoring iterations: 1
              Theta:  0.08160
          Std. Err.:  0.00826
 2 x log-likelihood:  -1773.72100
```

Table 29:
Stenobrachius leucopsarus, ontogenetic stage = Preflexion
Call:

```
glm.nb(formula = as.integer(Stenobrachius.leucopsarus_PREF) ~
    season * year1, data = spstaenvall1, init.theta =
0.1356239665,
    link = log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.2414  -0.7080  -0.4663  -0.3167   3.2562

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)        -1.397e+03  7.585e+02  -1.842   0.0655 .
seasonspring        7.127e+02  9.044e+02   0.788   0.4306
seasonsummer       -7.215e+01  9.762e+02  -0.074   0.9411
seasonwinter        1.479e+03  9.026e+02   1.639   0.1012
year1               6.982e-01  3.796e-01   1.839   0.0659 .
seasonspring:year1 -3.540e-01  4.526e-01  -0.782   0.4341
seasonsummer:year1  3.664e-02  4.885e-01   0.075   0.9402
seasonwinter:year1 -7.379e-01  4.517e-01  -1.634   0.1023
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.1356) family taken
to be 1)
    Null deviance: 748.89  on 735  degrees of freedom
Residual deviance: 441.44  on 728  degrees of freedom
AIC: 2695.3

Number of Fisher Scoring iterations: 1
```

Table 29:
Stenobrachius leucopsarus, ontogenetic stage = Preflexion, continued

```
              Theta:  0.1356
          Std. Err.:  0.0116
 2 x log-likelihood:  -2677.2500
```

Table 30:
Stenobrachius leucopsarus, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Stenobrachius.leucopsarus_FLEX) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.05061788966, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.7145  -0.4820  -0.3218  -0.1882   3.0082  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)          6.968e+01  1.492e+03   0.047    0.963
seasonspring        -1.414e+03  1.698e+03  -0.833    0.405
seasonsummer        -5.885e+02  1.794e+03  -0.328    0.743
seasonwinter         6.157e+04  1.023e+09   0.000    1.000
year1               -3.679e-02  7.469e-01  -0.049    0.961
seasonspring:year1  7.102e-01  8.499e-01   0.836    0.403
seasonsummer:year1  2.954e-01  8.981e-01   0.329    0.742
seasonwinter:year1 -3.083e+01  5.123e+05   0.000    1.000

(Dispersion parameter for Negative Binomial(0.0506) family taken 
to be 1)
    Null deviance: 282.06  on 735  degrees of freedom
Residual deviance: 139.68  on 728  degrees of freedom
AIC: 768.47

Number of Fisher Scoring iterations: 1
              Theta:  0.05062 
          Std. Err.:  0.00869 
 2 x log-likelihood:  -750.47000 
```

Table 31:
Stenobrachius leucopsarus, ontogenetic stage = Postflexion

```
Model did not converge.
```

Table 32:
Symbolophorus californiensis, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Symbolophorus.californiensis_PREF) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.06710499411, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.7201  -0.6811  -0.6599  -0.5554   2.1167  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)        -1070.8137   739.3937  -1.448    0.148
seasonspring         276.8703  1027.4473   0.269    0.788
seasonsummer        1644.6035  1039.9547   1.581    0.114
seasonwinter         741.6063  1022.3195   0.725    0.468
year1                  0.5360     0.3701   1.448    0.148
seasonspring:year1    -0.1383     0.5142  -0.269    0.788
seasonsummer:year1    -0.8227     0.5205  -1.581    0.114
seasonwinter:year1    -0.3709     0.5117  -0.725    0.469

(Dispersion parameter for Negative Binomial(0.0671) family taken 
to be 1)
    Null deviance: 318.72  on 735  degrees of freedom
Residual deviance: 311.32  on 728  degrees of freedom
AIC: 1677.4

Number of Fisher Scoring iterations: 1
              Theta:  0.06710 
          Std. Err.:  0.00700 
 2 x log-likelihood:  -1659.44100 
```

Table 33:
Symbolophorus californiensis, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Symbolophorus.californiensis_FLEX) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.03004263389, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.4514  -0.4040  -0.3529  -0.2967   1.5410  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         1678.2763  1173.0834   1.431   0.1525
```

Table 33:
Symbolophorus californiensis, ontogenetic stage = Flexion, continued

```
seasonspring        -725.1275  1599.1898  -0.453   0.6502  
seasonsummer       -3097.1209  1623.9666  -1.907   0.0565 .
seasonwinter       -2218.2470  1667.2226  -1.331   0.1834  
year1                 -0.8408     0.5871  -1.432   0.1521  
seasonspring:year1     0.3633     0.8004   0.454   0.6499  
seasonsummer:year1     1.5505     0.8128   1.908   0.0564 .
seasonwinter:year1     1.1099     0.8344   1.330   0.1835  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.03) family taken to
be 1)
    Null deviance: 132.23  on 735  degrees of freedom
Residual deviance: 121.75  on 728  degrees of freedom
AIC: 614.43

Number of Fisher Scoring iterations: 1
              Theta:  0.03004 
          Std. Err.:  0.00576 
 2 x log-likelihood:  -596.43500 
```

Table 34:
Symbolophorus californiensis, ontogenetic stage = Postlexion

```
Call:
glm.nb(formula = as.integer(Symbolophorus.californiensis_POST) ~ 
    season * year1, data = spstaenvall1, init.theta = 
0.02081129173, 
    link = log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-0.4037  -0.3468  -0.3285  -0.2382   1.7448  

Coefficients:
                    Estimate Std. Error z value Pr(>|z|)  
(Intercept)        -354.0533  1312.4020  -0.270   0.7873  
seasonspring       3409.9242  1905.5894   1.789   0.0735 .
seasonsummer        334.6516  1879.0816   0.178   0.8586  
seasonwinter       -407.0970  1957.9887  -0.208   0.8353  
year1                 0.1768     0.6569   0.269   0.7878  
seasonspring:year1   -1.7070     0.9538  -1.790   0.0735 .
seasonsummer:year1   -0.1677     0.9405  -0.178   0.8584  
seasonwinter:year1    0.2028     0.9800   0.207   0.8361  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Table 34:
Symbolophorus californiensis, ontogenetic stage = Postlexion, continued

```
(Dispersion parameter for Negative Binomial(0.0208) family taken
to be 1)

    Null deviance: 99.499  on 735  degrees of freedom
Residual deviance: 91.838  on 728  degrees of freedom
AIC: 501.47

Number of Fisher Scoring iterations: 1
              Theta:  0.02081
          Std. Err.:  0.00445
 2 x log-likelihood:  -483.46900
```

Table 35:
Tarletonbeania crenularis, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Tarletonbeania.crenularis_PREF) ~
    season * year1, data = spstaenvall1, init.theta =
0.0208617396,
    link = log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.4229  -0.3571  -0.3339  -0.3097   1.6466

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         -663.1413  1352.1499  -0.490    0.624
seasonspring       -1923.1371  1887.2622  -1.019    0.308
seasonsummer        1476.9269  1906.2025   0.775    0.438
seasonwinter        -954.6144  1853.6912  -0.515    0.607
year1                  0.3311     0.6767   0.489    0.625
seasonspring:year1     0.9629     0.9446   1.019    0.308
seasonsummer:year1    -0.7390     0.9541  -0.775    0.439
seasonwinter:year1     0.4784     0.9278   0.516    0.606

(Dispersion parameter for Negative Binomial(0.0209) family taken
to be 1)
    Null deviance: 117.73  on 735  degrees of freedom
Residual deviance: 105.88  on 728  degrees of freedom
AIC: 624.92

Number of Fisher Scoring iterations: 1
              Theta:  0.02086
          Std. Err.:  0.00393
 2 x log-likelihood:  -606.91600
```

Table 36:
Tarletonbeania crenularis, ontogenetic stage = Flexion

```
Model did not converge.
```

Table 37:
Tarletonbeania crenularis, ontogenetic stage = Postflexion

```
Model did not converge.
```

Table 38:
Triphoturus mexicanus, ontogenetic stage = Preflexion

```
Call:
glm.nb(formula = as.integer(Triphoturus.mexicanus_PREF) ~ season 
*
    year1, data = spstaenvall1, init.theta = 0.1472763798, link = 
log)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-1.2142  -0.9862  -0.3271   0.0000   2.8886  

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)    
(Intercept)         2.367e+03  4.907e+02   4.824 1.41e-06 ***
seasonspring       -7.589e+02  6.986e+02  -1.086 0.277311    
seasonsummer       -2.296e+03  6.935e+02  -3.311 0.000931 ***
seasonwinter       -5.656e+04  4.965e+08   0.000 0.999909    
year1              -1.184e+00  2.456e-01  -4.820 1.44e-06 ***
seasonspring:year1  3.791e-01  3.496e-01   1.084 0.278176    
seasonsummer:year1  1.149e+00  3.471e-01   3.311 0.000929 ***
seasonwinter:year1  2.829e+01  2.484e+05   0.000 0.999909    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.1473) family taken 
to be 1)
    Null deviance: 665.38  on 735  degrees of freedom
Residual deviance: 419.78  on 728  degrees of freedom
AIC: 2379

Number of Fisher Scoring iterations: 1
              Theta:  0.1473 
          Std. Err.:  0.0129 
 2 x log-likelihood:  -2361.0300 
```

Table 39:
Triphoturus mexicanus, ontogenetic stage = Flexion

```
Call:
glm.nb(formula = as.integer(Triphoturus.mexicanus_FLEX) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.06050298559, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.7255  -0.5777  -0.2823  -0.1918   3.1805

Coefficients:
                     Estimate Std. Error z value Pr(>|z|)
(Intercept)         3242.5077   810.7194   4.000 6.35e-05 ***
seasonspring       -1727.8262  1372.7140  -1.259  0.20814
seasonsummer       -3060.0724  1128.0194  -2.713  0.00667 **
seasonwinter       -3246.3472  1639.0140  -1.981  0.04763 *
year1                 -1.6229     0.4058  -4.000 6.35e-05 ***
seasonspring:year1     0.8634     0.6871   1.257  0.20892
seasonsummer:year1     1.5316     0.5646   2.713  0.00667 **
seasonwinter:year1     1.6229     0.8203   1.978  0.04789 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(0.0605) family taken
to be 1)
    Null deviance: 260.88  on 735  degrees of freedom
Residual deviance: 169.00  on 728  degrees of freedom
AIC: 804.83

Number of Fisher Scoring iterations: 1
              Theta:  0.0605
          Std. Err.:  0.0101
 2 x log-likelihood:  -786.8310
```

Table 40:
Triphoturus mexicanus, ontogenetic stage = Postflexion

```
Call:
glm.nb(formula = as.integer(Triphoturus.mexicanus_POST) ~ season
*
    year1, data = spstaenvall1, init.theta = 0.06170641246, link
= log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.7020  -0.5588   0.0000   0.0000   2.2983

Coefficients:
```

Table 40:
Triphoturus mexicanus, ontogenetic stage = Postflexion, continued

```
                    Estimate Std. Error z value Pr(>|z|)    
(Intercept)         1.526e+03  7.629e+02   2.001 0.045421 *  
seasonspring       -1.554e+03  9.310e+07   0.000 0.999987    
seasonsummer       -4.347e+03  1.166e+03  -3.729 0.000192 ***
seasonwinter       -1.554e+03  9.235e+07   0.000 0.999987    
year1              -7.637e-01  3.818e-01  -2.000 0.045481 *  
seasonspring:year1  7.637e-01  4.660e+04   0.000 0.999987    
seasonsummer:year1  2.175e+00  5.833e-01   3.728 0.000193 ***
seasonwinter:year1  7.637e-01  4.622e+04   0.000 0.999987    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for Negative Binomial(0.0617) family taken
to be 1)

    Null deviance: 260.44  on 735  degrees of freedom
Residual deviance: 120.50  on 728  degrees of freedom
AIC: 627.54

Number of Fisher Scoring iterations: 1
              Theta:  0.0617 
          Std. Err.:  0.0111 
 2 x log-likelihood:  -609.5380 
```

APPENDIX B: Generalized Linear Mixed Effects Model Output Summary

Each of the proceeding tables in the summary of the model results for each of the twelve mesopelagic species from equation (2):

$$abund_{spp.stage} \sim depth + PC1 + PC2 + year, \sim 1|season$$

Table 1:

Bathylagoides wesethi, ontogenetic stage = Eggs

```
$Bathylagoides.wesethi_EGGS
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.7006732 8.544886

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std +
year1
                Value Std.Error  DF   t-value p-value
(Intercept)  3.286280 0.6837798 727  4.806050  0.0000
depth.std    0.528445 0.8172020 727  0.646651  0.5181
PC1.std     -6.854189 0.6932040 727 -9.887694  0.0000
PC2.std      3.062734 0.7688040 727  3.983765  0.0001
year12      -0.473385 0.2000083 727 -2.366826  0.0182
year13      -0.750014 0.2360777 727 -3.176978  0.0016
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.077                            
PC1.std   -0.282  0.072                     
PC2.std   -0.796 -0.192  0.022              
year12    -0.286 -0.022 -0.186  0.327       
year13     0.111 -0.195 -0.267 -0.115  0.223

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.46061358 -0.34090456 -0.18564759 -0.08697843 10.67714473 

Number of Observations: 736
Number of Groups: 4 
```

Table 2:
Bathylagoides wesethi, ontogenetic stage = Preflexion

```
$Bathylagoides.wesethi_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.8252555 4.479413

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept)  3.049506 0.5810100 727   5.248629  0.0000
depth.std    1.720824 0.6456154 727   2.665401  0.0079
PC1.std     -6.051369 0.5636681 727 -10.735695  0.0000
PC2.std      1.305466 0.5617790 727   2.323808  0.0204
year12      -0.025005 0.1526869 727  -0.163768  0.8700
year13      -1.474001 0.2875751 727  -5.125623  0.0000
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.036
PC1.std   -0.172  0.045
PC2.std   -0.621 -0.046 -0.130
year12    -0.223 -0.025 -0.251  0.285
year13     0.060 -0.221 -0.187 -0.081  0.231

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.61445370 -0.41147960 -0.20937125 -0.08839121  8.71573369

Number of Observations: 736
Number of Groups: 4
```

Table 3:
Bathylagoides wesethi, ontogenetic stage = Flexion

```
$Bathylagoides.wesethi_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
```

Table 3:
Bathylagoides wesethi, ontogenetic stage = Flexion, continued

```
Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.368491  2.62178

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -1.342907 1.1005515 727 -1.220212  0.2228
depth.std    1.104354 1.5840313 727  0.697179  0.4859
PC1.std     -4.222634 0.8709667 727 -4.848215  0.0000
PC2.std      3.695911 1.1729795 727  3.150875  0.0017
year12      -0.473271 0.2685098 727 -1.762584  0.0784
year13      -1.758451 0.4689470 727 -3.749785  0.0002
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.028
PC1.std   -0.195  0.135
PC2.std   -0.711 -0.176 -0.063
year12    -0.080  0.007 -0.193  0.068
year13     0.110 -0.217 -0.178 -0.131  0.211

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.11707459 -0.28924044 -0.14802749 -0.07118588 12.79606672

Number of Observations: 736
Number of Groups: 4
```

Table 4:
Bathylagoides wesethi, ontogenetic stage = Postflexion

```
$Bathylagoides.wesethi_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    0.907115  2.32552

Variance function:
 Structure: fixed weights
```

Table 4:
Bathylagoides wesethi, ontogenetic stage = Postflexion, continued

```
Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept) -3.004207  1.551793 727 -1.9359590  0.0533
depth.std   -3.284546  7.563190 727 -0.4342805  0.6642
PC1.std     -2.118354  1.379407 727 -1.5356994  0.1250
PC2.std      2.669947  1.920646 727  1.3901294  0.1649
year12       0.441134  0.525605 727  0.8392874  0.4016
year13       0.335687  0.561233 727  0.5981238  0.5499
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.155
PC1.std   -0.415  0.370
PC2.std   -0.804 -0.202  0.019
year12    -0.313  0.075 -0.007  0.127
year13    -0.046 -0.075 -0.203 -0.067  0.537

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-0.42594996 -0.19722451 -0.15229393 -0.09834281 14.86992730

Number of Observations: 736
Number of Groups: 4
```

Table 5:
Leuroglossus stilbius, ontogenetic stage = Eggs

```
$Leuroglossus.stilbius_EGGS
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    2.118956 20.61498

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF   t-value p-value
(Intercept)  -0.709987  1.371642 727 -0.517618  0.6049
depth.std   -14.167281  5.618663 727 -2.521469  0.0119
```

Table 5:
Leuroglossus stilbius, ontogenetic stage = Eggs, continued

```
PC1.std       6.317067  0.630390 727 10.020889  0.0000
PC2.std       1.561749  0.876039 727  1.782739  0.0750
year12        0.104767  0.274159 727  0.382140  0.7025
year13       -0.709092  0.169979 727 -4.171644  0.0000
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.070
PC1.std   -0.420  0.444
PC2.std   -0.478 -0.296  0.179
year12    -0.428 -0.135  0.370  0.638
year13    -0.030 -0.178 -0.147  0.089  0.260

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.92569447 -0.26866071 -0.11461820 -0.03836808 11.08490335

Number of Observations: 736
Number of Groups: 4
```

Table 6:
Leuroglossus stilbius, ontogenetic stage = Preflexion

```
$Leuroglossus.stilbius_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    2.386122 5.875917

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF   t-value p-value
(Intercept)  -3.897317  1.480185 727 -2.632993  0.0086
depth.std   -12.933996  4.665238 727 -2.772420  0.0057
PC1.std       5.296317  0.537052 727  9.861828  0.0000
PC2.std       3.474062  0.895109 727  3.881162  0.0001
year12       -0.248327  0.223236 727 -1.112397  0.2663
year13       -0.662746  0.147276 727 -4.500033  0.0000
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
```

Table 6:
Leuroglossus stilbius, ontogenetic stage = Preflexion, continued

```
depth.std -0.047
PC1.std   -0.370  0.481
PC2.std   -0.455 -0.300  0.262
year12    -0.304 -0.049  0.338  0.472
year13    -0.030 -0.176 -0.158  0.097  0.254

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.10100872 -0.31502810 -0.07194752 -0.02695348  9.91430125

Number of Observations: 736
Number of Groups: 4
```

Table 7:
Leuroglossus stilbius, ontogenetic stage = Flexion

```
$Leuroglossus.stilbius_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.542634 2.660368

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -3.871474 1.3337056 727 -2.902795  0.0038
depth.std   -0.120256 2.3596471 727 -0.050964  0.9594
PC1.std      4.604813 0.6218071 727  7.405534  0.0000
PC2.std      0.632077 1.2446453 727  0.507837  0.6117
year12       0.061139 0.2641812 727  0.231429  0.8170
year13      -0.298630 0.2280745 727 -1.309351  0.1908
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.159
PC1.std   -0.548  0.323
PC2.std   -0.732  0.045  0.405
year12    -0.391  0.024  0.303  0.376
year13    -0.041 -0.060 -0.101 -0.015  0.394
```

Table 7:
Leuroglossus stilbius, ontogenetic stage = Flexion, continued

```
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.49006575 -0.29868702 -0.14615033 -0.07583226 13.89479492 

Number of Observations: 736
Number of Groups: 4
```

Table 8:
Leuroglossus stilbius, ontogenetic stage = Postflexion

```
$Leuroglossus.stilbius_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.214716 2.168778

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std 
+ year1 
                Value Std.Error  DF   t-value p-value
(Intercept) -7.530553  1.722060 727 -4.372992  0.0000
depth.std   -2.192302  5.698313 727 -0.384728  0.7006
PC1.std      5.787901  0.840431 727  6.886827  0.0000
PC2.std      4.117501  1.893369 727  2.174695  0.0300
year12      -0.518765  0.404338 727 -1.282998  0.1999
year13       0.633048  0.250086 727  2.531322  0.0116
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.004                            
PC1.std   -0.693  0.305                     
PC2.std   -0.866 -0.235  0.495              
year12    -0.214  0.042  0.160  0.137       
year13    -0.059 -0.107 -0.102 -0.003  0.401

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.77158586 -0.26030656 -0.12335918 -0.05786236  8.77360591 

Number of Observations: 736
Number of Groups: 4
```

Table 9:
Lipolagus ochotensis, ontogenetic stage = Eggs

```
$Lipolagus.ochotensis_EGGS
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:      1.9241 7.185847

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -5.139429 1.5332366 727 -3.352013  0.0008
depth.std    1.721466 2.0467002 727  0.841093  0.4006
PC1.std      3.253772 0.6848713 727  4.750924  0.0000
PC2.std      5.347742 1.2046205 727  4.439358  0.0000
year12       0.355540 0.3542582 727  1.003619  0.3159
year13       1.004533 0.2409269 727  4.169450  0.0000
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.126
PC1.std   -0.569  0.299
PC2.std   -0.700 -0.013  0.565
year12    -0.356 -0.016  0.260  0.374
year13    -0.095 -0.067 -0.142  0.028  0.490

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.09573116 -0.33583191 -0.08961612 -0.04385143 10.97014821

Number of Observations: 736
Number of Groups: 4
```

Table 10:
Lipolagus ochotensis, ontogenetic stage = Preflexion

```
$Lipolagus.ochotensis_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA
```

Table 10:
Lipolagus ochotensis, ontogenetic stage = Preflexion, continued

```
Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    2.013443 3.822861

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -6.842903 1.3487263 727 -5.073604  0.0000
depth.std   -0.841070 2.8458936 727 -0.295538  0.7677
PC1.std      2.123911 0.5667757 727  3.747357  0.0002
PC2.std      6.807727 0.8543616 727  7.968203  0.0000
year12       1.830661 0.2457055 727  7.450630  0.0000
year13       0.978302 0.2344649 727  4.172487  0.0000
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.148
PC1.std   -0.438  0.445
PC2.std   -0.556 -0.052  0.425
year12    -0.329  0.082  0.211  0.330
year13    -0.093 -0.070 -0.147  0.013  0.661

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.56799671 -0.40551463 -0.09754444 -0.03322378 10.24771246

Number of Observations: 736
Number of Groups: 4
```

Table 11:
Lipolagus ochotensis, ontogenetic stage = Flexion

```
$Lipolagus.ochotensis_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.8703697 2.677793
```

Table 11:
Lipolagus ochotensis, ontogenetic stage = Flexion, continued

```
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -7.230989 1.8467553 727 -3.915510  0.0001
depth.std   -0.170557 2.7307842 727 -0.062457  0.9502
PC1.std      2.023987 1.0914081 727  1.854473  0.0641
PC2.std      6.484373 1.9531338 727  3.319984  0.0009
year12       0.427820 0.4956112 727  0.863217  0.3883
year13       0.740098 0.4024362 727  1.839046  0.0663
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.019
PC1.std   -0.712  0.207
PC2.std   -0.915 -0.128  0.546
year12    -0.354  0.022  0.152  0.246
year13    -0.060 -0.078 -0.158 -0.046  0.520

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-0.85649330 -0.24030221 -0.15066724 -0.08970655 12.79559128

Number of Observations: 736
Number of Groups: 4
```

Table 12:
Lipolagus ochotensis, ontogenetic stage = Post

```
Model did not converge.
```

Table 13:
Vinciguerria lucetia, ontogenetic stage = Eggs

```
$Vinciguerria.lucetia_EGGS
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.114067 25.84346

Variance function:
```

Table 13:
Vinciguerria lucetia, ontogenetic stage = Eggs, continued

```
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  7.820154 0.7472121 727 10.465775  0.0000
depth.std    1.738780 0.6018383 727  2.889114  0.0040
PC1.std     -7.178624 0.7785419 727 -9.220601  0.0000
PC2.std     -1.665974 0.6489682 727 -2.567112  0.0105
year12       0.210236 0.2186195 727  0.961653  0.3365
year13      -0.607026 0.3263110 727 -1.860267  0.0633
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.047
PC1.std   -0.228 -0.013
PC2.std   -0.560  0.024 -0.054
year12    -0.339 -0.024 -0.193  0.456
year13    -0.002 -0.145 -0.256 -0.023  0.345

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.17467480 -0.29454916 -0.15120095 -0.06991159 12.91877715

Number of Observations: 736
Number of Groups: 4
```

Table 14:
Vinciguerria lucetia, ontogenetic stage = Preflexion

```
$Vinciguerria.lucetia_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.271832 13.77888

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept)  6.928846 0.7103207 727   9.754532  0.0000
```

Table 14:
Vinciguerria lucetia, ontogenetic stage = Preflexion, continued

```
depth.std    2.254101 0.5151354 727   4.375746  0.0000
PC1.std     -5.371239 0.5187510 727 -10.354176  0.0000
PC2.std     -3.513924 0.3835830 727  -9.160793  0.0000
year12       0.786684 0.1743087 727   4.513166  0.0000
year13      -0.098587 0.2556744 727  -0.385594  0.6999
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.039
PC1.std   -0.157  0.013
PC2.std   -0.292 -0.048 -0.099
year12    -0.207 -0.036 -0.218  0.259
year13    -0.035 -0.157 -0.264 -0.059  0.498

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.93742888 -0.34001455 -0.17543502 -0.07114016 10.89145907

Number of Observations: 736
Number of Groups: 4
```

Table 15:
Vinciguerria lucetia, ontogenetic stage = Flexion

```
$Vinciguerria.lucetia_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.257645 6.515124

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  4.078147 0.7531817 727  5.414560  0.0000
depth.std    3.442085 0.7552618 727  4.557473  0.0000
PC1.std     -3.797389 0.6203004 727 -6.121854  0.0000
PC2.std     -1.681719 0.6083909 727 -2.764207  0.0059
year12      -0.515266 0.1972130 727 -2.612738  0.0092
year13      -1.731397 0.3717282 727 -4.657696  0.0000
 Correlation:
```

Table 15:
Vinciguerria lucetia, ontogenetic stage = Flexion, continued

```
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.055
PC1.std   -0.102  0.103
PC2.std   -0.409 -0.114 -0.297
year12    -0.139 -0.083 -0.253  0.199
year13     0.043 -0.277 -0.174 -0.059  0.230

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.30315380 -0.26539880 -0.16119027 -0.07015681 16.97583384

Number of Observations: 736
Number of Groups: 4
```

Table 16:
Vinciguerria lucetia, ontogenetic stage = Postflexion

```
$Vinciguerria.lucetia_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.696649  6.74124

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  3.950513 0.9072401 727  4.354429  0.0000
depth.std    3.799064 0.5881701 727  6.459124  0.0000
PC1.std     -3.630227 0.4812469 727 -7.543378  0.0000
PC2.std     -2.301673 0.3961712 727 -5.809793  0.0000
year12       0.816643 0.1512321 727  5.399935  0.0000
year13      -0.754880 0.2664463 727 -2.833140  0.0047
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.067
PC1.std   -0.099  0.097
PC2.std   -0.193 -0.142 -0.229
year12    -0.106 -0.046 -0.271  0.131
year13     0.009 -0.283 -0.221 -0.067  0.420
```

Table 16:
Vinciguerria lucetia, ontogenetic stage = Postflexion, continued

```
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.56404865 -0.34468640 -0.15141095 -0.05222682  9.31070044 

Number of Observations: 736
Number of Groups: 4 
```

Table 17:
Ceratoscopelus townsendi, ontogenetic stage = Preflexion

```
$Ceratoscopelus.townsendi_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.4808316 3.329953

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std 
+ year1 
                Value Std.Error  DF    t-value p-value
(Intercept)  5.194713 0.3447759 727  15.066926   0e+00
depth.std    1.998251 0.4035949 727   4.951132   0e+00
PC1.std     -5.832528 0.4713311 727 -12.374586   0e+00
PC2.std     -4.384522 0.3095138 727 -14.165837   0e+00
year12       1.151480 0.1724158 727   6.678504   0e+00
year13       0.774089 0.2187083 727   3.539366   4e-04
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.060                            
PC1.std   -0.286 -0.015                     
PC2.std   -0.464 -0.008 -0.044              
year12    -0.368 -0.040 -0.269  0.168       
year13    -0.126 -0.075 -0.336 -0.110  0.651

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-3.1828430 -0.4415650 -0.2531235 -0.1170183  8.7403962 

Number of Observations: 736
```

Table 17:
Ceratoscopelus townsendi, ontogenetic stage = Preflexion, continued

```
Number of Groups: 4
```

Table 18:
Ceratoscopelus townsendi, ontogenetic stage = Flexion

```
$Ceratoscopelus.townsendi_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.5327293 2.848692

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  3.469134 0.5598113 727  6.196970  0.0000
depth.std    1.966205 0.9191531 727  2.139149  0.0328
PC1.std     -5.517992 1.0294007 727 -5.360393  0.0000
PC2.std     -3.840858 0.7235496 727 -5.308354  0.0000
year12       0.450132 0.3208250 727  1.403046  0.1610
year13      -0.287372 0.4883655 727 -0.588436  0.5564
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.086
PC1.std   -0.277 -0.027
PC2.std   -0.617  0.020 -0.207
year12    -0.358 -0.063 -0.329  0.226
year13    -0.042 -0.068 -0.301 -0.060  0.459

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.84292540 -0.25005333 -0.15852516 -0.09132197 18.32223609

Number of Observations: 736
Number of Groups: 4
```

Table 19:
Ceratoscopelus townsendi, ontogenetic stage = Postflexion

```
$Ceratoscopelus.townsendi_POST
```

Table 19:
Ceratoscopelus townsendi, ontogenetic stage = Postflexion, continued

```
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:     0.54127 2.643364

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  2.644704 0.5411175 727  4.887486  0.0000
depth.std    2.208553 0.8591289 727  2.570689  0.0103
PC1.std     -4.952467 0.8905714 727 -5.560999  0.0000
PC2.std     -3.759639 0.6307334 727 -5.960742  0.0000
year12       1.149518 0.3308667 727  3.474263  0.0005
year13       1.141190 0.3866792 727  2.951257  0.0033
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.070                            
PC1.std   -0.304  0.028                     
PC2.std   -0.550 -0.052 -0.123              
year12    -0.407 -0.058 -0.295  0.121       
year13    -0.161 -0.083 -0.355 -0.120  0.695

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.61963185 -0.29540201 -0.18174012 -0.09945429 11.71024168 

Number of Observations: 736
Number of Groups: 4 
```

Table 20:
Diogenichthys atlanticus, ontogenetic stage = Preflexion

```
$Diogenichthys.atlanticus_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
```

Table 20:
Diogenichthys atlanticus, ontogenetic stage = Preflexion, continued

```
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.3235037 3.274947

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF   t-value p-value
(Intercept)  0.5923397 0.7467921 727  0.793179  0.4279
depth.std    2.0054378 0.9582788 727  2.092750  0.0367
PC1.std     -2.8480173 0.8875833 727 -3.208732  0.0014
PC2.std      0.0569827 0.9340151 727  0.061008  0.9514
year12       0.4473872 0.3302454 727  1.354711  0.1759
year13       0.3684863 0.3578543 727  1.029710  0.3035
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.068
PC1.std   -0.381  0.134
PC2.std   -0.824 -0.053 -0.019
year12    -0.434 -0.074 -0.102  0.269
year13    -0.101 -0.120 -0.265 -0.026  0.549

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.7896247 -0.3162936 -0.2502522 -0.1712132 11.1066271

Number of Observations: 736
Number of Groups: 4
```

Table 21:
Diogenichthys atlanticus, ontogenetic stage = Flexion

```
$Diogenichthys.atlanticus_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev: 0.000285829 2.407373

Variance function:
 Structure: fixed weights
```

Table 21:
Diogenichthys atlanticus, ontogenetic stage = Flexion, continued

```
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)  0.632826 0.7401114 727  0.855041  0.3928
depth.std    1.188408 1.2520558 727  0.949165  0.3429
PC1.std     -5.955592 1.1773948 727 -5.058280  0.0000
PC2.std     -0.049285 0.9554109 727 -0.051585  0.9589
year12       1.006377 0.3821438 727  2.633502  0.0086
year13       0.774248 0.4380938 727  1.767310  0.0776
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.020                            
PC1.std   -0.333  0.046                     
PC2.std   -0.808 -0.091 -0.095              
year12    -0.468 -0.039 -0.209  0.262       
year13    -0.150 -0.096 -0.297 -0.013  0.616

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-0.7413764 -0.3190961 -0.1851839 -0.1079537 13.5059433 

Number of Observations: 736
Number of Groups: 4 
```

Table 22:
Diogenichthys atlanticus, ontogenetic stage = Postflexion

```
$Diogenichthys.atlanticus_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.3235037 3.274947

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF   t-value p-value
(Intercept)  0.5923397 0.7467921 727  0.793179  0.4279
depth.std    2.0054378 0.9582788 727  2.092750  0.0367
```

Table 22:
Diogenichthys atlanticus, ontogenetic stage = Postflexion, continued

```
PC1.std     -2.8480173 0.8875833 727 -3.208732  0.0014
PC2.std      0.0569827 0.9340151 727  0.061008  0.9514
year12       0.4473872 0.3302454 727  1.354711  0.1759
year13       0.3684863 0.3578543 727  1.029710  0.3035
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.068
PC1.std   -0.381  0.134
PC2.std   -0.824 -0.053 -0.019
year12    -0.434 -0.074 -0.102  0.269
year13    -0.101 -0.120 -0.265 -0.026  0.549

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.7896247 -0.3162936 -0.2502522 -0.1712132 11.1066271

Number of Observations: 736
Number of Groups: 4
```

Table 23:
Nannobrachium ritteri, ontogenetic stage = Preflexion

```
$Nannobrachium.ritteri_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    0.399742 3.711668

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -1.452614 0.8431478 727 -1.722846  0.0853
depth.std   -0.352459 1.5977086 727 -0.220603  0.8255
PC1.std     -1.602546 0.6471022 727 -2.476497  0.0135
PC2.std      4.164426 0.9714048 727  4.287014  0.0000
year12      -0.051059 0.2523767 727 -0.202312  0.8397
year13      -0.153776 0.2449382 727 -0.627817  0.5303
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
```

Table 23:
Nannobrachium ritteri, ontogenetic stage = Preflexion, continued

```
depth.std -0.024
PC1.std   -0.526  0.213
PC2.std   -0.903 -0.146  0.269
year12    -0.382 -0.001  0.047  0.307
year13    -0.016 -0.110 -0.217 -0.032  0.374

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.8039193 -0.3567446 -0.2806851 -0.2011087  8.3016759

Number of Observations: 736
Number of Groups: 4
```

Table 24:
Nannobrachium ritteri, ontogenetic stage = Flexion

```
$Nannobrachium.ritteri_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.5354358 2.766215

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept) -4.579411  2.252474 727 -2.0330589  0.0424
depth.std   -7.814550 13.685607 727 -0.5710050  0.5682
PC1.std     -2.890718  2.034175 727 -1.4210761  0.1557
PC2.std      5.949252  2.623871 727  2.2673569  0.0237
year12       0.190186  0.664355 727  0.2862715  0.7748
year13      -0.008778  0.652022 727 -0.0134633  0.9893
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.182
PC1.std   -0.557  0.470
PC2.std   -0.831 -0.288  0.130
year12    -0.393  0.173  0.087  0.230
year13     0.032 -0.066 -0.223 -0.068  0.373
```

Table 24:
Nannobrachium ritteri, ontogenetic stage = Flexion, continued

```
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-0.47589258 -0.14918579 -0.10656150 -0.08046983 16.43866211

Number of Observations: 736
Number of Groups: 4
```

Table 25:
Nannobrachium ritteri, ontogenetic stage = Postflexion

```
$Nannobrachium.ritteri_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.6194266 2.485244

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept) -4.698648  1.698140 727 -2.7669382  0.0058
depth.std   -0.471322  3.356449 727 -0.1404229  0.8884
PC1.std     -1.357428  1.241209 727 -1.0936335  0.2745
PC2.std      5.870636  1.978831 727  2.9667192  0.0031
year12      -0.232982  0.462881 727 -0.5033310  0.6149
year13      -0.668833  0.487625 727 -1.3716142  0.1706
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.029
PC1.std   -0.552  0.220
PC2.std   -0.924 -0.143  0.311
year12    -0.305  0.026  0.016  0.243
year13     0.073 -0.105 -0.215 -0.106  0.293

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.5511423 -0.2029883 -0.1510609 -0.1099158 13.0307491

Number of Observations: 736
Number of Groups: 4
```

Table 26:
Protomyctophum crockeri, ontogenetic stage = Preflexion

```
$Protomyctophum.crockeri_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    0.456766 3.111835

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF   t-value p-value
(Intercept) -0.5299648 0.6945937 727 -0.762985  0.4457
depth.std    0.6843499 1.1154635 727  0.613512  0.5397
PC1.std     -1.9369426 0.5788371 727 -3.346266  0.0009
PC2.std      2.4976725 0.7628098 727  3.274306  0.0011
year12       0.2620966 0.2270654 727  1.154278  0.2488
year13       0.2164797 0.2188913 727  0.988983  0.3230
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.082
PC1.std   -0.493  0.197
PC2.std   -0.860 -0.066  0.223
year12    -0.468 -0.027  0.052  0.390
year13    -0.086 -0.094 -0.239  0.022  0.463

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.9456135 -0.4184198 -0.3260364 -0.2255741 10.4558658

Number of Observations: 736
Number of Groups: 4
```

Table 27:
Protomyctophum crockeri, ontogenetic stage = Flexion

```
$Protomyctophum.crockeri_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA
```

Table 27:
Protomyctophum crockeri, ontogenetic stage = Flexion, continued

```
Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev: 0.0001175983 2.651293

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                 Value Std.Error  DF    t-value p-value
(Intercept) -2.4628816 0.9192236 727 -2.6793063  0.0075
depth.std    0.4588092 1.9476371 727  0.2355722  0.8138
PC1.std      0.9766960 0.6822219 727  1.4316398  0.1527
PC2.std      2.9178080 1.1027146 727  2.6460229  0.0083
year12      -0.3570943 0.2973063 727 -1.2010991  0.2301
year13      -0.5357119 0.2844894 727 -1.8830648  0.0601
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.055
PC1.std   -0.555  0.263
PC2.std   -0.912 -0.133  0.226
year12    -0.396 -0.019  0.120  0.296
year13    -0.061 -0.114 -0.173  0.022  0.340

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.5377529 -0.3400350 -0.2916391 -0.2380237  9.4508804

Number of Observations: 736
Number of Groups: 4
```

Table 28:
Protomyctophum crockeri, ontogenetic stage = Postflexion

```
$Protomyctophum.crockeri_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
       (Intercept) Residual
StdDev:   0.1251539 3.151421
```

Table 28:
Protomyctophum crockeri, ontogenetic stage = Postflexion, continued

```
Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -2.402328 0.7555345 727 -3.179640  0.0015
depth.std   -0.774796 2.3140928 727 -0.334816  0.7379
PC1.std      0.783790 0.5642785 727  1.389013  0.1653
PC2.std      4.023343 0.8836063 727  4.553321  0.0000
year12       0.054948 0.2248791 727  0.244343  0.8070
year13      -0.330080 0.2238156 727 -1.474786  0.1407
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.094
PC1.std   -0.573  0.338
PC2.std   -0.899 -0.162  0.237
year12    -0.413  0.011  0.124  0.300
year13    -0.067 -0.101 -0.183  0.026  0.392

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.7160570 -0.4318111 -0.3551581 -0.2281818 10.5568661

Number of Observations: 736
Number of Groups: 4
```

Table 29:
Stenobrachius leucopsarus, ontogenetic stage = Preflexion

```
$Stenobrachius.leucopsarus_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.899149 6.059464

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
```

Table 29:
Stenobrachius leucopsarus, ontogenetic stage = Preflexion, continued

```
(Intercept) -6.869700  1.307319 727 -5.254801  0.0000
depth.std   -1.949801  3.890633 727 -0.501153  0.6164
PC1.std      4.775422  0.544220 727  8.774805  0.0000
PC2.std      7.764872  0.917751 727  8.460765  0.0000
year12       0.499502  0.199842 727  2.499480  0.0127
year13       0.221641  0.154044 727  1.438814  0.1506
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.101                            
PC1.std   -0.497  0.510                     
PC2.std   -0.585 -0.213  0.436              
year12    -0.275  0.096  0.267  0.285       
year13    -0.030 -0.154 -0.181  0.038  0.415

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.88854744 -0.35608897 -0.10484853 -0.04182035 10.15179491 

Number of Observations: 736
Number of Groups: 4 
```

Table 30:
Stenobrachius leucopsarus, ontogenetic stage = Flexion

```
$Stenobrachius.leucopsarus_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.561621 4.040893

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1 
                Value Std.Error  DF   t-value p-value
(Intercept) -7.815938 1.9609794 727 -3.985732  0.0001
depth.std    1.250287 2.7083332 727  0.461644  0.6445
PC1.std      3.832191 0.9684430 727  3.957064  0.0001
PC2.std      6.094584 1.9061945 727  3.197252  0.0014
year12      -0.172137 0.5175709 727 -0.332586  0.7395
year13       1.009550 0.3322502 727  3.038525  0.0025
```

Table 30:
Stenobrachius leucopsarus, ontogenetic stage = Flexion, continued

```
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.063                            
PC1.std   -0.737  0.215                     
PC2.std   -0.858 -0.082  0.672              
year12    -0.282  0.004  0.172  0.223       
year13    -0.035 -0.061 -0.156 -0.069  0.459

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.19350836 -0.14301952 -0.07727388 -0.03764028 16.23651508 

Number of Observations: 736
Number of Groups: 4 
```

Table 31:
Stenobrachius leucopsarus, ontogenetic stage = Postflexion

```
$Stenobrachius.leucopsarus_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:    1.904564 3.710002

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std 
+ year1 
                Value Std.Error  DF   t-value p-value
(Intercept) -6.300622  1.866233 727 -3.376117  0.0008
depth.std   -8.235776  7.377120 727 -1.116394  0.2646
PC1.std      2.608034  0.928019 727  2.810323  0.0051
PC2.std      4.985249  1.822402 727  2.735537  0.0064
year12      -0.723371  0.525660 727 -1.376121  0.1692
year13       1.077548  0.295695 727  3.644123  0.0003
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.007                            
PC1.std   -0.616  0.414                     
PC2.std   -0.752 -0.332  0.448              
year12    -0.228  0.081  0.176  0.152       
```

Table 31:
Stenobrachius leucopsarus, ontogenetic stage = Postflexion, continued

```
year13    -0.050 -0.045 -0.139 -0.040  0.404

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.19632026 -0.14044724 -0.06787346 -0.03306484 16.62282031 

Number of Observations: 736
Number of Groups: 4
```

Table 32:
Symbolophorus californiensis, ontogenetic stage = Preflexion

```
$Symbolophorus.californiensis_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a 
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.2683242 3.159059

Variance function:
 Structure: fixed weights
 Formula: ~invwt 
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1 
                Value Std.Error  DF   t-value p-value
(Intercept)  2.239738 0.5301529 727  4.224701  0.0000
depth.std    0.279650 1.0145879 727  0.275630  0.7829
PC1.std     -7.054170 0.7840991 727 -8.996528  0.0000
PC2.std      0.614677 0.6505297 727  0.944887  0.3450
year12       0.583215 0.2366637 727  2.464320  0.0140
year13       0.920216 0.2444661 727  3.764186  0.0002
 Correlation: 
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.004                            
PC1.std   -0.354  0.060                     
PC2.std   -0.826 -0.142 -0.026              
year12    -0.429 -0.019 -0.193  0.320       
year13    -0.081 -0.095 -0.338 -0.010  0.560

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.1680174 -0.4158947 -0.2114770 -0.1127167 12.1451773 
```

Table 32:
Symbolophorus californiensis, ontogenetic stage = Preflexion, continued

```
Number of Observations: 736
Number of Groups: 4
```

Table 33:
Symbolophorus californiensis, ontogenetic stage = Flexion

```
$Symbolophorus.californiensis_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.4003711 2.104396

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -1.017106 0.9228847 727 -1.102095  0.2708
depth.std    1.764621 0.9135560 727  1.931596  0.0538
PC1.std     -4.622574 1.0929860 727 -4.229307  0.0000
PC2.std      1.962621 1.1281986 727  1.739606  0.0824
year12       0.471887 0.3492671 727  1.351077  0.1771
year13       0.078296 0.4013564 727  0.195079  0.8454
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.016
PC1.std   -0.382  0.104
PC2.std   -0.870 -0.113  0.039
year12    -0.410 -0.067 -0.141  0.316
year13    -0.012 -0.196 -0.266 -0.061  0.462

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.6385475 -0.2964011 -0.2001940 -0.1309893 10.2710999

Number of Observations: 736
Number of Groups: 4
```

Table 34:
Symbolophorus californiensis, ontogenetic stage = Postlexion

```
$Symbolophorus.californiensis_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.5703172 2.322854

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF    t-value p-value
(Intercept) -3.229804  1.292947 727 -2.4980170  0.0127
depth.std   -1.429499  4.104651 727 -0.3482633  0.7277
PC1.std     -2.379591  1.150924 727 -2.0675472  0.0390
PC2.std      4.195678  1.583759 727  2.6491899  0.0082
year12       0.066634  0.425220 727  0.1567053  0.8755
year13       0.122460  0.425861 727  0.2875595  0.7738
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std -0.063
PC1.std   -0.452  0.261
PC2.std   -0.875 -0.188  0.129
year12    -0.265  0.032 -0.059  0.152
year13     0.033 -0.078 -0.254 -0.105  0.457

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.5079048 -0.2437255 -0.1843570 -0.1385070 11.7856000

Number of Observations: 736
Number of Groups: 4
```

Table 35:
Tarletonbeania crenularis, ontogenetic stage = Preflexion

```
$Tarletonbeania.crenularis_PREF
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
```

Table 35:
Tarletonbeania crenularis, ontogenetic stage = Preflexion, continued

```
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.1635067 3.201361

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept) -8.832814 1.9132056 727 -4.616762  0.0000
depth.std    0.325635 1.9830579 727  0.164209  0.8696
PC1.std      3.622442 1.1423549 727  3.171031  0.0016
PC2.std      7.956474 2.0225439 727  3.933894  0.0001
year12       0.756342 0.5882358 727  1.285780  0.1989
year13       1.362675 0.4697733 727  2.900707  0.0038
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.036
PC1.std   -0.737  0.167
PC2.std   -0.937 -0.159  0.549
year12    -0.352 -0.007  0.130  0.200
year13    -0.157 -0.083 -0.111 -0.002  0.632

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-0.68845998 -0.23091955 -0.15709948 -0.08505152 10.55563059

Number of Observations: 736
Number of Groups: 4
```

Table 36:
Tarletonbeania crenularis, ontogenetic stage = Flexion

```
$Tarletonbeania.crenularis_FLEX
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.5071938 2.050138

Variance function:
 Structure: fixed weights
```

Table 36:
Tarletonbeania crenularis, ontogenetic stage = Flexion, continued

```
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
(Intercept)   -9.7660         3 727 -3.608900  0.0003
depth.std     -1.1012         5 727 -0.232699  0.8161
PC1.std        3.1110         2 727  1.964722  0.0498
PC2.std        8.6207         3 727  3.015138  0.0027
year12      -996.8687   8600635 727 -0.000116  0.9999
year13         0.6118         0 727  1.343314  0.1796
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.010
PC1.std   -0.812  0.192
PC2.std   -0.953 -0.170  0.661
year12     0.000  0.000  0.000  0.000
year13     0.018 -0.073 -0.182 -0.090  0.000

Standardized Within-Group Residuals:
          Min            Q1           Med            Q3
Max
-7.883453e-01 -1.937403e-01 -9.805408e-02 -2.126633e-17
1.476821e+01

Number of Observations: 736
Number of Groups: 4
```

Table 37:
Tarletonbeania crenularis, ontogenetic stage = Postflexion

```
$Tarletonbeania.crenularis_POST
Linear mixed-effects model fit by maximum likelihood
 Data: sppca2a
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | season
        (Intercept) Residual
StdDev:   0.9540695 1.708481

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects: as.integer(value) ~ depth.std + PC1.std + PC2.std
+ year1
                Value Std.Error  DF   t-value p-value
```

Table 37:
Tarletonbeania crenularis, ontogenetic stage = Postflexion, continued

```
(Intercept)   -8.1490         3 727 -2.994568  0.0028
depth.std      2.1342         2 727  1.155948  0.2481
PC1.std        3.2247         1 727  2.230535  0.0260
PC2.std        4.8366         3 727  1.627744  0.1040
year12      -996.5794   7167335 727 -0.000139  0.9999
year13         0.9751         0 727  2.057375  0.0400
 Correlation:
          (Intr) dpth.s PC1.st PC2.st year12
depth.std  0.184
PC1.std   -0.787  0.026
PC2.std   -0.944 -0.293  0.661
year12     0.000  0.000  0.000  0.000
year13    -0.056 -0.107 -0.142 -0.037  0.000

Standardized Within-Group Residuals:
          Min             Q1            Med             Q3
Max
-6.904064e-01 -1.691494e-01 -8.777452e-02 -1.400235e-17
1.344401e+01

Number of Observations: 736
Number of Groups: 4
```

Table 38:
Triphoturus mexicanus, ontogenetic stage = Preflexion

```
Model did not converge.
```

Table 39:
Triphoturus mexicanus, ontogenetic stage = Flexion

```
Model did not converge.
```

Table 40:
Triphoturus mexicanus, ontogenetic stage = Postflexion

```
Model did not converge.
```

CHAPTER 5:

Conclusions

The relationship between ontogeny and habitat use in mesopelagic fishes has only begun to be studied. Given the global high abundance and biomass of these fishes (Gjøsaeter and Kawaguchi 1980, Lam and Pauly 2005, Irigoien et al. 2014) and their importance in the food web (e.g., Pitman and Ballance 1990, Ohizumi et al. 2003, Field et al. 2007, Potier et al. 2007, Cherel et al. 2008), additional research is needed to more fully understand their changing role in the ecosystem.

Many studies utilize larval fish abundance to represent the communities of adults that produce them (Hsieh et al. 2005), however most such studies only sample the epipelagic zone (0-200 m) to collect the larvae (Smith and Richardson 1977). The results from Chapters 2 and 3 suggest that this type of sampling does not capture the complete distribution of mesopelagic fish larvae and that deeper sampling regimes are needed for a more accurate assessment of species abundances. Additionally, these details indicate that mesopelagic fishes begin establishment of adult habitat use patterns earlier than generally appreciated. This includes the establishment of diel vertical migratory behavior that generally has been assumed to a feature of juvenile and adult mesopelagic fishes (e.g., Pearcy and Laurs 1966, Paxton 1967, Willis and Pearcy 1982, Watanabe et al. 1999). These findings are consistent with the results from Chapter 4 that showed larval abundance of mesopelagic fishes collected in the upper 200 meters of the water column is dominated by the earliest stages of development. Later stages likely were more common beyond the sample depth.

Additional sampling using discrete depth methods deeper in the water column and fine scale taxonomic identifications are both needed to gain a better understanding the ontogenetic patterns of habitat use in early life history (ELH) stages of mesopelagic fish species. This area of research is particularly poignant from a fisheries perspective because these fishes are such a critical component of the forage base. For example, the Pacific Fisheries Management Council, the governing body of the US West Coast commercial fisheries, has identified all species in four families of mesopelagic fishes as species potentially in need of formalized protection and management (Pacific Fisheries Management Council 2014). Management plans for these fishes would most likely include formalized stock assessments which typically use egg and larval abundance estimates (Hewitt 1988). These actions would require a more comprehensive understanding of the relationship between ontogeny and habitat use by the ELH stages of mesopelagic fishes.

Another potential need for a greater understanding of ontogenetic habitat shifts in mesopelagic fishes is related to the predicted shoaling of the oxygen minimum zones (Bograd et al. 2008, Netburn and Koslow 2015). These zones may be an especially important parameter affecting the survival of the early stages of fish larvae whose circulatory and respiratory systems are incompletely developed (O'Connell 1981).

Increasing evidence has indicated that the larvae of marine fishes have much greater behavioral abilities than previously realized. Continued study of stage-specific habitat use by species of mesopelagic fishes will further improve our understanding of their complex roles in the pelagic ecosystem.

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