

UNIVERSITY OF CALIFORNIA, SAN DIEGO

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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2016

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Chair

University of California, San Diego

2016

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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ACKNOWLEDGEMENTS

I would first like to thank my advisor, Phil Hastings, for his mentorship, guidance, and patience in helping me learn to become a scientist. Phil has always encouraged me to investigate any aspect of larval fish ecology that I've been interested in throughout my graduate experience. I feel extremely lucky to have had Phil as my advisor because he is a great professor with seemingly limitless knowledge of fish behavior and systematics and he knows how to connect with all types of students to help spark their own quests for knowledge. I truly enjoyed our many brainstorming sessions and appreciated his immediate willingness to admit when he was unfamiliar with a topic and was always enthusiastic to aid in finding the answer or resource needed. Phil is highly respected in the Scripps Institution of Oceanography (SIO) community not just because of his academic success but also because he is good human. I mean that in the most fundamental way. Phil is a caring, thoughtful, and wonderful human being who is deeply interested in science and research but also in his community and society as a whole. I think the latter is the reason we work so well together. We both have similar interests in contributing to society that involves sharing our experiences with the people that haven't yet had the opportunities of exposure to marine science. I am so thankful that Phil has always understood and encouraged me to do science outreach with the community, especially with young students in lower socioeconomic regions.

Phil took a gamble with me because I entered graduate school with a full-time job after taking a seven-year break from school. For this, the reasons above, and many more than I can list here, I am forever indebted to Phil.

I'd also like to thank my committee, Sam McClatchie, Dave Checkley, Tony Koslow, Brice Semmens, and David Holway. Sam was always available to help in any way that I asked which included many general discussions of what I was thinking about my research. He shared his vast knowledge of scientific literature with me regularly. I could stop by his office at any time to discuss a topic and Sam would give me multiple sources to read further on that topic. Sam played a critical role in teaching me how to use the statistical programming language, R. He sat with me for several hours a week for a number of months to get me started. I have greatly benefitted from all that Sam has taught me.

I am thankful that Tony Koslow encouraged me to dig into the literature which prompted many discussions that helped me better define my research questions. Dave Checkley always pushed me to take a step back to think about the broader ecological implications of my work throughout the entire process. I'm deeply appreciative of his constant constructive criticism because it comes from his many years of experience, his own genuine interest in finding answers, and from his tireless desire to help all of his students improve. Brice Semmens was wonderfully patient in helping me on the bumpy road to understanding the appropriate statistical analyses I used in each of my chapters. I am grateful for his ability to explain very complex ideas in a language I could understand. Finally, I'd like to thank David Holway for reminding me of my passion for ecology by encouraging me to keep the fundamental ecological theories in the forefront of my mind throughout the evolution of my doctoral research.

I would also like to thank the three people that have served as unofficial committee members, Bill Watson, Andrew Thompson, and Christian Reiss. Bill Watson

is my supervisor at the Southwest Fisheries Science Center and without his support I never would have been able to keep my job at the Fisheries while being a graduate student at Scripps. Bill has provided scientific, administrative, and emotional support throughout this endeavor. He is a wonderful scientist and supervisor and I'm very proud to be his employee. Andrew Thompson has been a great friend and colleague to me. There were countless times that we sat together in front of the computer to figure out my most recent struggles with statistics and code-writing. We both work for Bill Watson, and I will always be grateful for the countless times the three of us would sit in Bill's office to discuss ideas. Christian Reiss was full of enthusiastic support for me throughout this journey. He continuously helped keep me grounded the many times I felt that I was in over my head. He'd help me step back, clear my head, and talk through my ideas. Even though Bill, Andrew, and Christian were not officially on my committee, I'm confident that their participation in my dissertation research and in my life has directly contributed to my success.

During my second year I had the wonderful opportunity to participate on the UC Ship Funds graduate student led cruise, CalECHOES, where I collected many ichthyoplankton samples. I am very thankful for the help of two fantastic volunteers, Wendy Lee and Casey Bogan, for spending hundreds of hours with me, sorting those samples under the microscope.

I am also thankful for the help, encouragement, and support of my Southwest Fisheries Science Center family including Russ Vetter, Dale Sweetnam, Rose Sanford, Juan Zwolinski, Vicki Pease, Dawn Graham, Kevin Stierhoff, Sue Manion, Dave Griffith, Amy Hays, Dave Ambrose, Elaine Acuna, Sherri Charter, Emily Gardner,

Kelsey Gilmore, Megan Human, Anne Friere, Dereka Chargualaf, Jessica Lipsky, Meghan Donahue, Robin Schnug, and John Hyde.

Thank you to the SIO graduate office staff, past and present, for all of their administrative support. Denise Darling, Josh Reese, Krystle Shertz, Gilbert Bretado, Adam Petersen, Maureen McCormack, Maureen McGreevy, Satomi Saito, all provided guidance and help navigating through the PhD process. All of these wonderful people tirelessly provide the essential infrastructure and behind the scenes work that keeps the graduate programs at SIO running.

I have made so many wonderful friends at SIO, many of which I consider to be as close as family. Several members of the 2009 cohort that I was so lucky to be a part of were absolutely essential in helping me to make it through the critical period of the first year. Thank you to Levi Lewis, Mindi Summers, Lauren Shipp, Joe Campanale, Jill Harris, Matt Leslie, Cotton Rockwood, Liz Vu, Christian Briseño, Jenan Karbush, Kait Fraiser, Kerri Seger, and Bonnie Ludka for including me as part of the team struggling through the first year together. My wonderful officemate, Grant Galland was very much like a big brother to me in helping me navigate through the graduate student life. Karli Merkens and Aly Fleming stepped in as my student-mentors whose guidance has been absolutely critical to my success. Thank you to my wonderful friends Summer Martin and Emily Kelly for helping to guide me through the final steps of the PhD. I'm very thankful to have met my wonderful partner, Will Hutchison, in the final year of graduate school. His friendship, love, support, patience, kindness, and comic-relief, was such a wonderful suite of gifts wrapped into one remarkable human being. I happy that we were together as I finished my PhD and I am thankful and elated that we are planning our future together.

Finally I am honored to thank my family, Lyndon, Nickey, Ethan, Kelly, Jacob, and Matthew for their love, support, and encouragement. My parents worked hard and sacrificed a lot to provide for my brother and me. In doing so they instilled the extremely solid work ethic that enabled me to successfully maintain my full-time job while in pursuit of a PhD at SIO. In addition they taught me integrity and self-respect, two essential characteristics that helped me throughout the PhD marathon. My wonderful brother has always given me strength through the loving bond that only siblings have. My sister-in-law and my sweet nephews constantly reminded me that there was so much family fun to look forward to in the future. I cannot say enough about my family, if they didn't love, teach, support, and encourage me in the ways that they did throughout my life, I'm sure this PhD would never have been part of my reality.

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

University of California, San Diego, 2016

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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 1m² 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 Niño event in 1997-1998 followed by the La Niña 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/m³), 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 (Percy 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 1m² 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 1m² MOCNESS from the same station during both day and night.

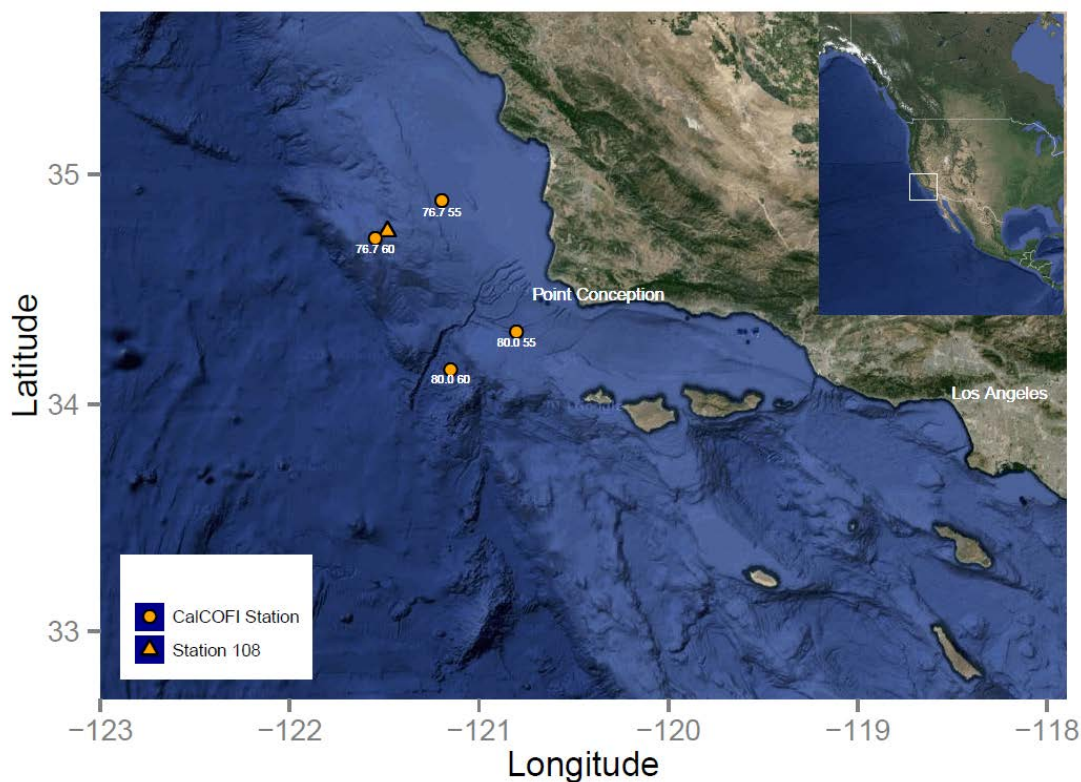


Figure 1:

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 m² 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 $45^{\circ} \pm 8^{\circ}$. 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 $45^{\circ} \pm 8^{\circ}$ 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 ($^{\circ}\text{C}$), salinity (psu), potential density (kg m^{-3}), chlorophyll-a concentration ($\mu\text{g/L}$), 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,

$$E(\text{count}_{\#spp}) = \text{depth stratum} + \text{time of day} + \text{depth stratum} * \text{time of day}, \quad (1)$$

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,

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

where $count_{all\ spp}$ 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).

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

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.

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

The Poisson distribution was used for all models in which the response variable was counts, as recommended for biological census data (Kabacoff 2011). The Gaussian 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 *Stenobranchius 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 *Stenobranchius 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
<i>Stenobrachius leucopsarus</i>	128	98	50	17	9	302
<i>Cyclothone signata</i>	0	0	4	1	238	243
<i>Leuroglossus stilbius</i>	5	3	19	13	0	40
<i>Tarletonbeania crenularis</i>	8	12	10	0	1	31
<i>Lipolagus ochotensis</i>	5	4	9	5	0	23
<i>Protomyctophum crockeri</i>	6	1	10	5	1	23
<i>Cyclothone acclinidens</i>	0	0	0	0	9	9
Myctophidae	2	4	1	0	0	7
<i>Bathylagus pacificus</i>	0	2	2	1	0	5
<i>Chauliodus macouni</i>	1	0	3	0	1	5
<i>Danaphos oculatus</i>	0	0	3	2	0	5
<i>Diogenichthys atlanticus</i>	0	0	3	1	0	4
<i>Melamphaes lugubris</i>	0	0	4	0	0	4
<i>Nannobrachium ritteri</i>	0	0	0	0	4	4
<i>Argyrolepecus sladeni</i>	0	0	0	3	0	3
<i>Bathylagoides wesethi</i>	0	0	1	0	2	3
<i>Argyrolepecus affinis</i>	0	0	0	1	1	2
<i>Argyrolepecus hemigymnus</i>	0	0	1	0	1	2
<i>Cyclothone pseudopallida</i>	0	0	0	0	2	2
<i>Nannobrachium regale</i>	2	0	0	0	0	2
<i>Sagamichthys abei</i>	0	1	1	0	0	2
<i>Argyrolepecus lychnus</i>	0	0	0	1	0	1
<i>Diaphus theta</i>	0	0	0	0	1	1
<i>Holtbyrnia latifrons</i>	0	1	0	0	0	1
<i>Microstoma</i> sp.	1	0	0	0	0	1
<i>Scopelarchus analis</i>	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.

Depth (m)	DAY			NIGHT		
	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 1m² 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 1m² 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 (equation 3; 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). *Stenobranchius 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 1m² 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 (Kaaertvedt 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 coarse 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.

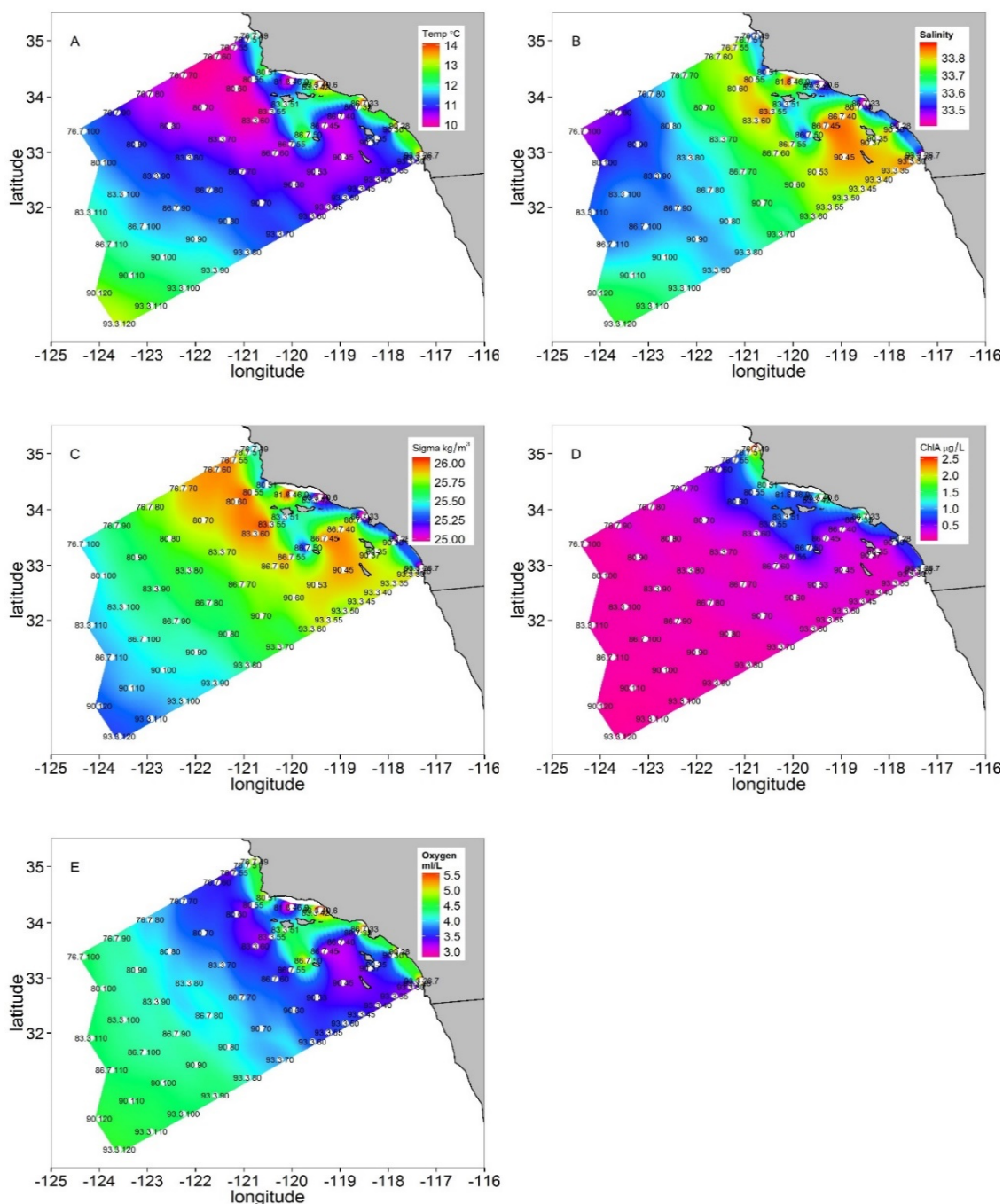


Figure 2:
CTD casts from the spring CalOFI surveys integrated over the water column for each cast, for each of five physical variables: temperature (A), salinity (B), potential density (C), chlorophyll-a concentration (D), and oxygen concentration (E), averaged over the ten year period 1984-1994.

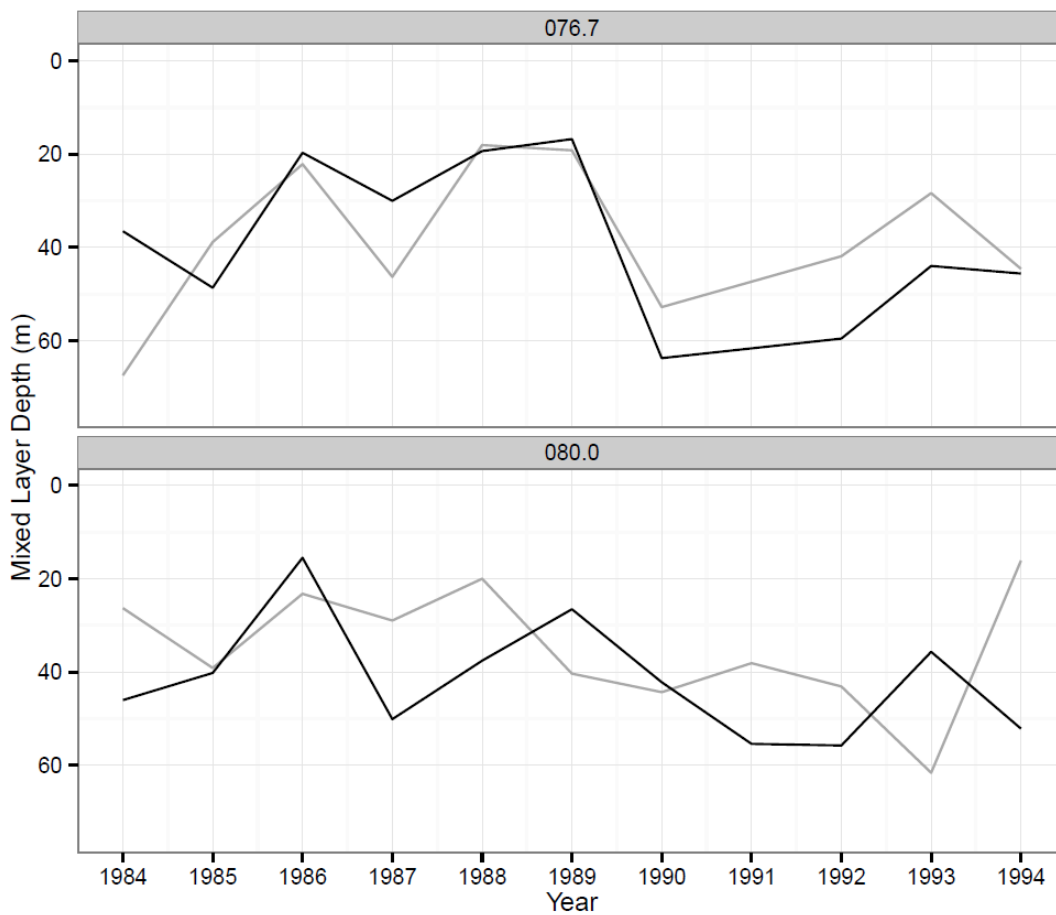


Figure 3:
CalCOFI time series of mixed layer depth at four selected stations from 1984-1994.
Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey
line, bottom panel; 80.0 60 = black line, bottom panel.

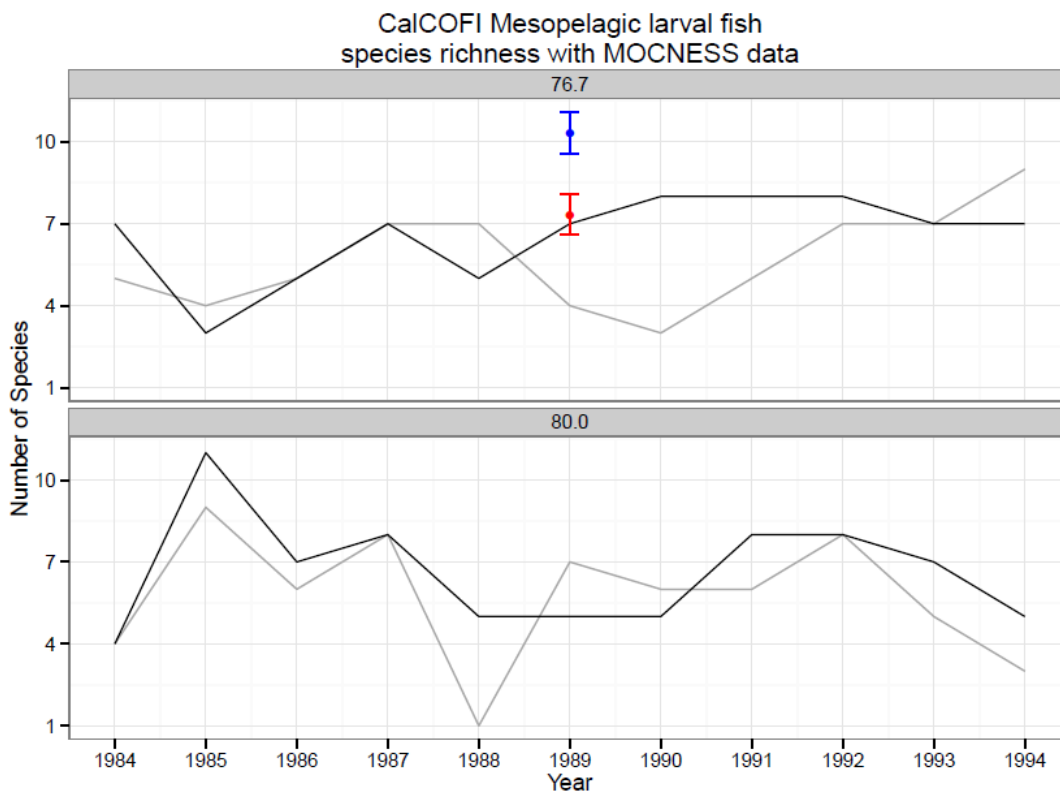


Figure 4:
CalCOFI time series of the number of mesopelagic fish larvae species at four stations from 1984-1994. Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey line, bottom panel; 80.0 60 = black line, bottom panel. MOCNESS mean number of species with 95% confidence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

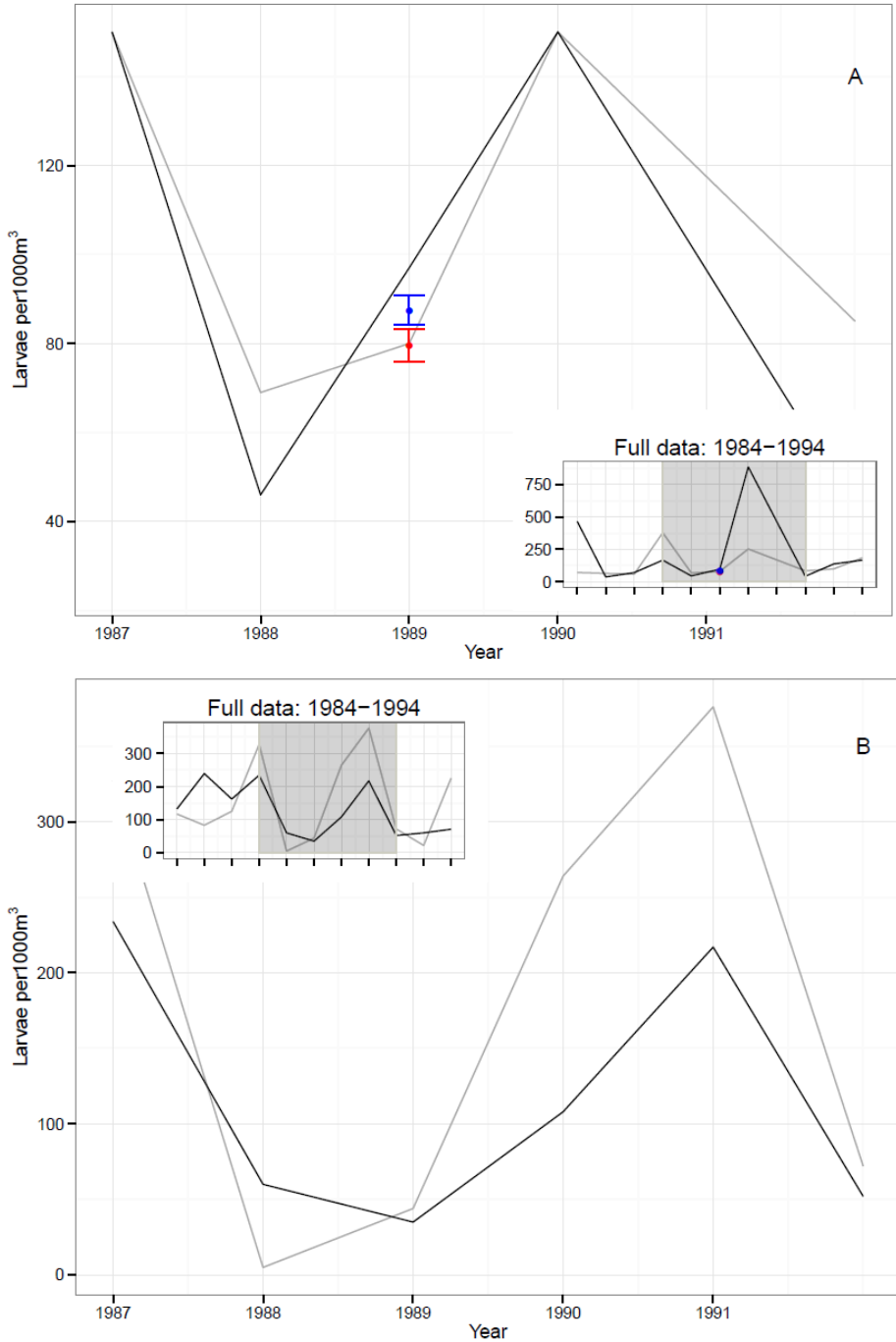


Figure 5:
 CalCOFI time series of mesopelagic fish larval abundance at four stations from 1987-1991 (main graphs A and B) and 1984-1994 (inset graphs A and B). Stations: 76.7 55 = grey line, top panel; 76.7 60 = black line, top panel; 80.0 55 = grey line, bottom panel; 80.0 60 = black line, bottom panel. 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).

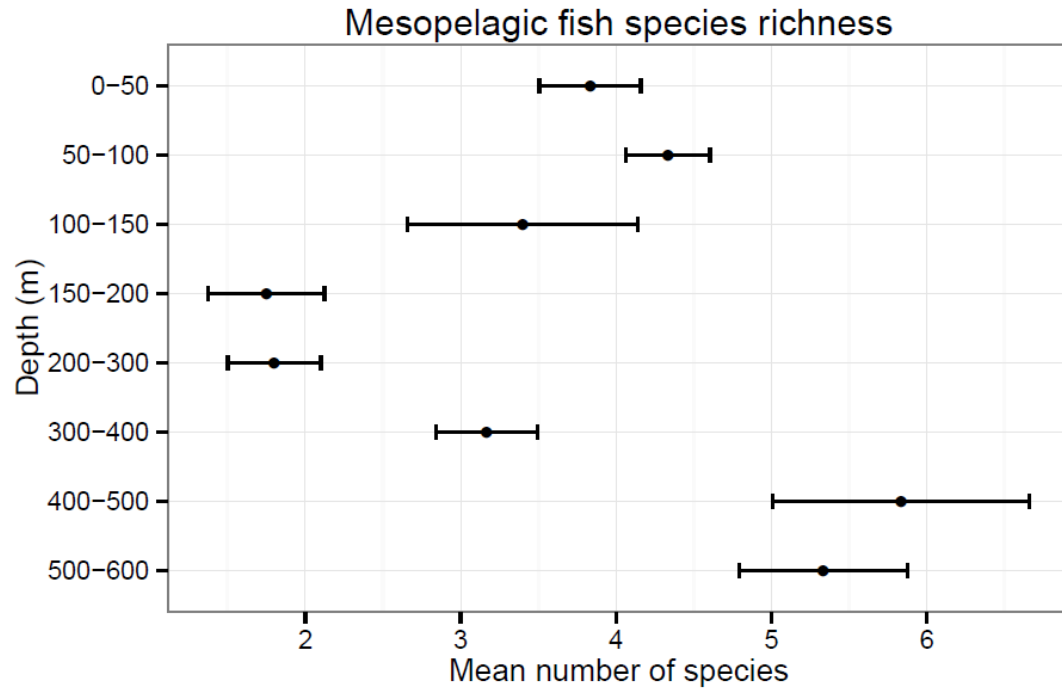


Figure 6:
Mean number of mesopelagic fish species collected in each of the eight depth strata for six MOCNESS tows at station 108 (day and night samples combined) with 95% confidence intervals.

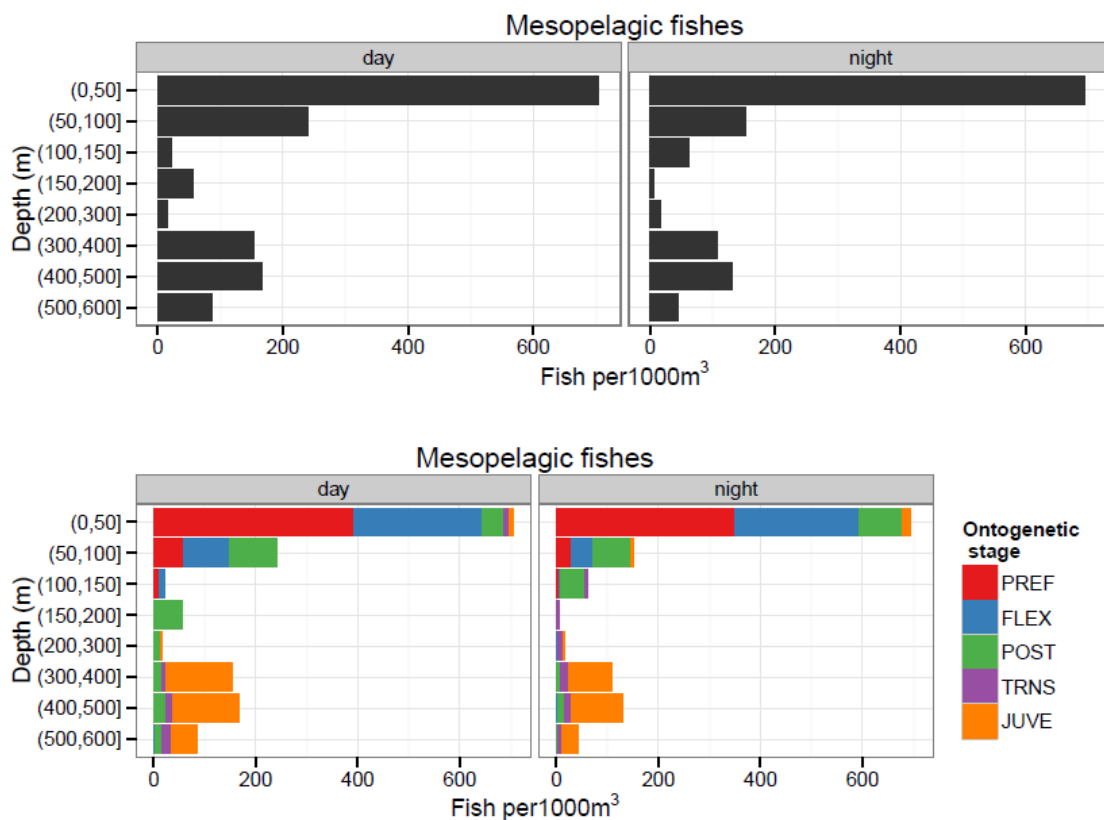


Figure 7: Distribution and abundance of mesopelagic fishes collected from day and night MOCNESS samples from Station 108 (top panel). Stage-specific distribution and abundance of all mesopelagic fishes collected in the day and night MOCNESS samples from Station 108 (bottom panel). PREF=preflexion, FLEX=flexion,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

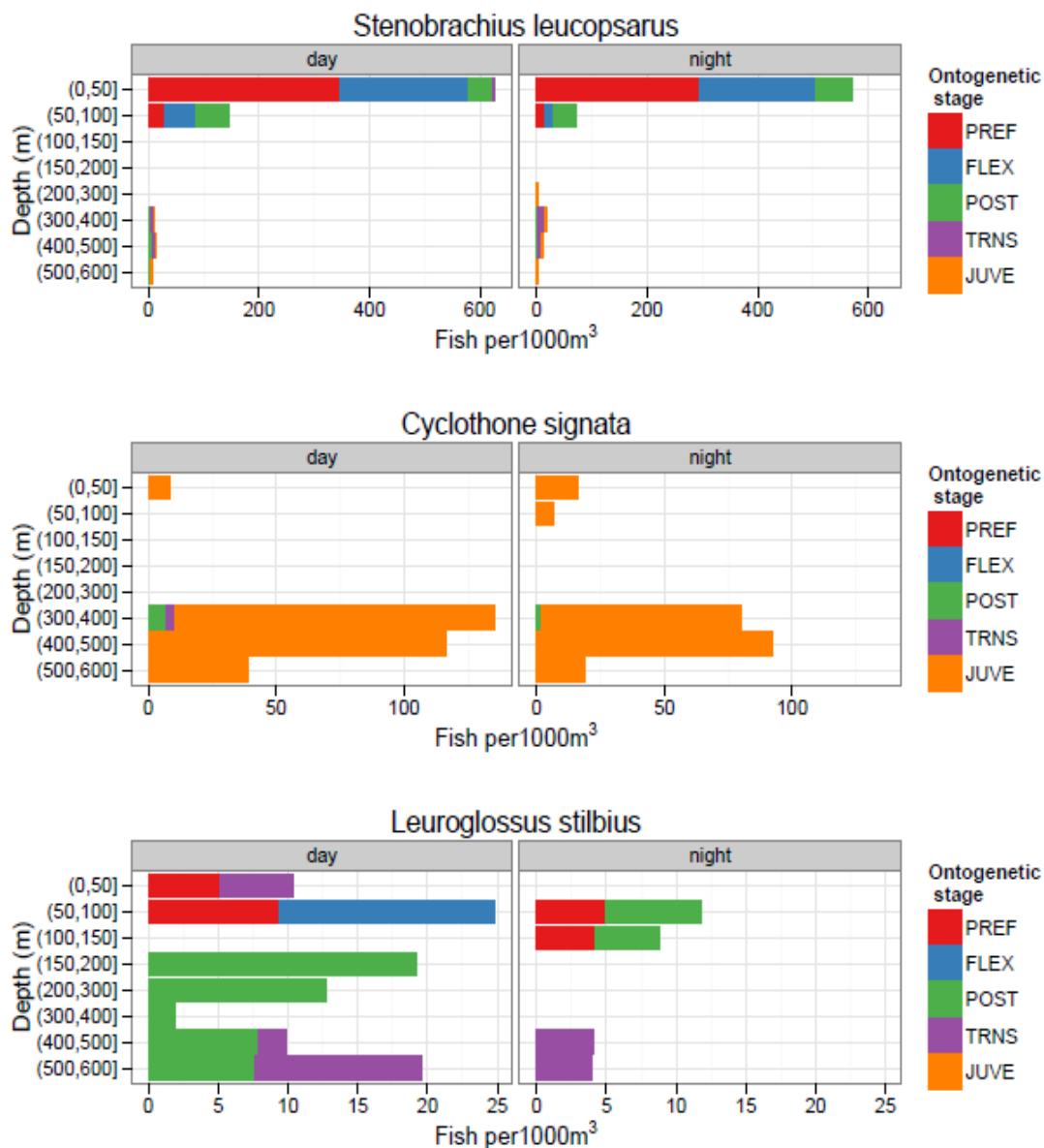


Figure 8: Stage-specific distribution of the most abundant species of mesopelagic fish (*Stenobranchius leucopsarus*), the second most abundant species (*Cyclothone signata*), and the third most abundant species (*Leuroglossus stilbius*) collected in the day and night MOCNESS samples from Station 108.

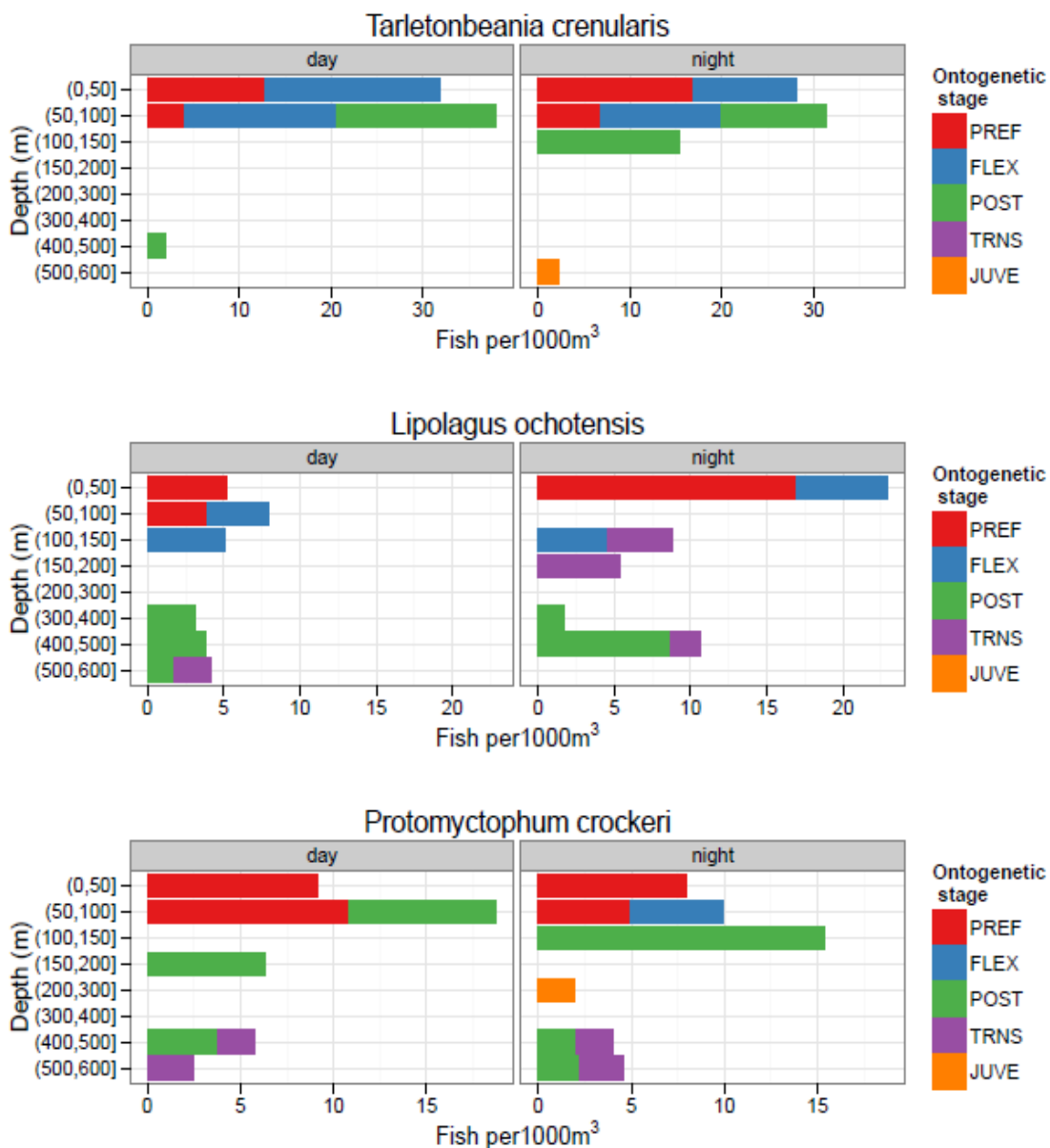


Figure 9:
 Stage-specific distribution of the fourth most abundant species of mesopelagic fish (*Tarletonbeania crenularis*), the fifth most abundant species (*Lipolagus ochotensis* and *Protomyctophum crockeri*) collected in the day and night MOCNESS samples from Station 108.

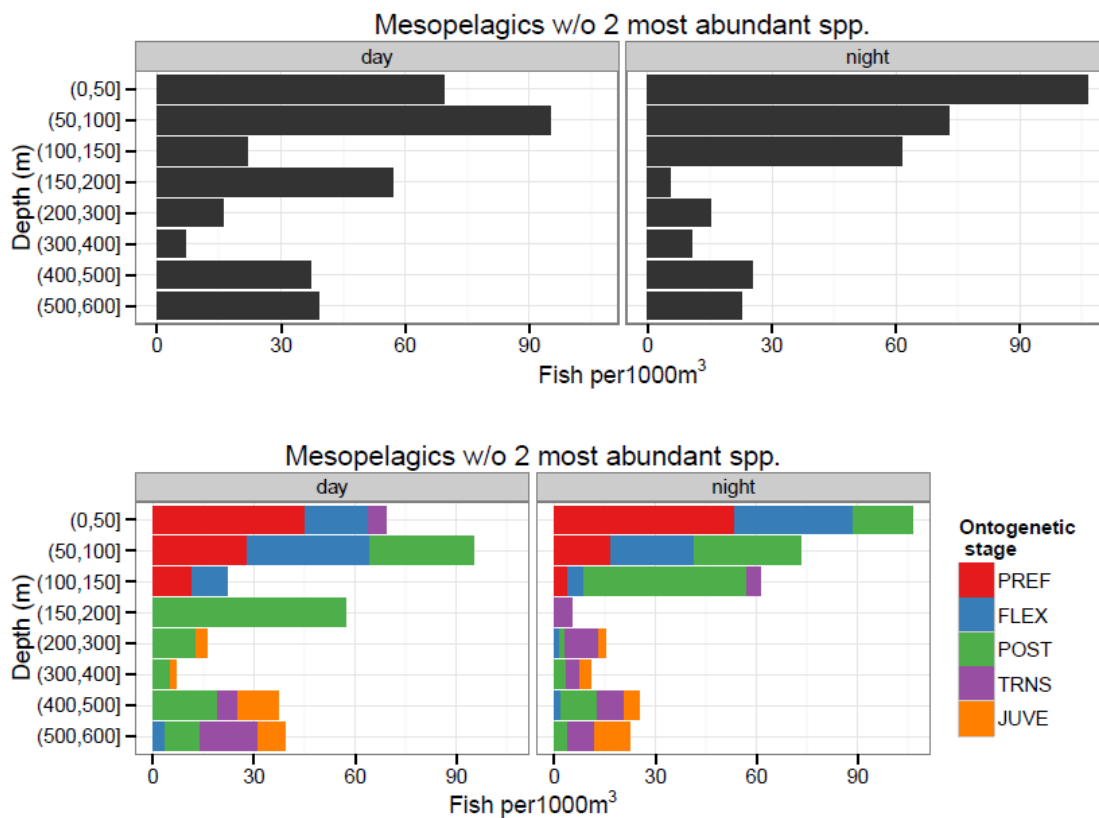


Figure 10:

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).

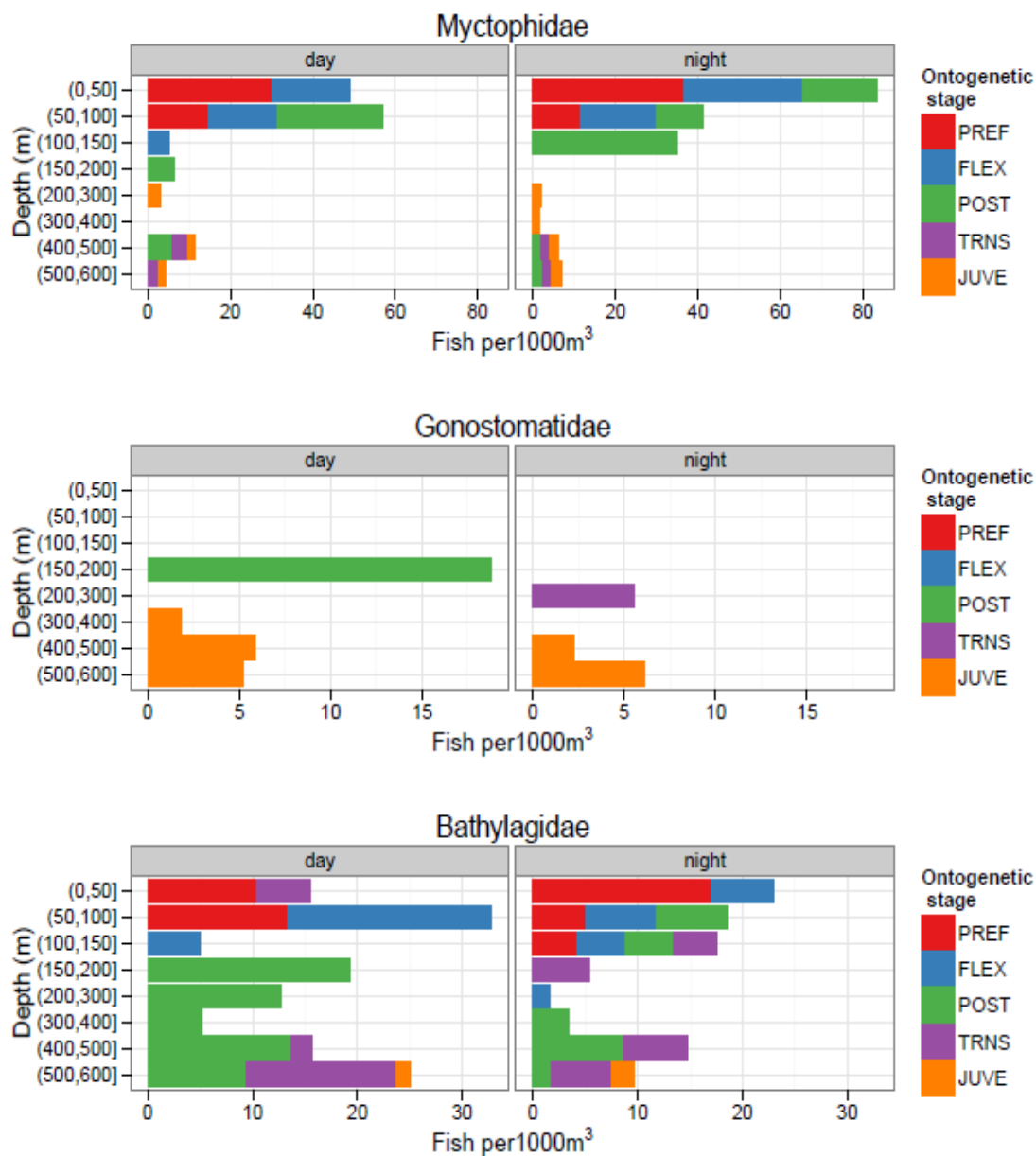


Figure 11: Stage-specific distribution of all species of families Myctophidae, Gonostomatidae, and Bathylagidae except for *Stenobranchius leucopsarus* and *Cyclothone signata*, collected in the day and night MOCNESS samples from Station 108.

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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):

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

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):

$$E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

Stenobranchius 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), *Stenobranchius 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):
 $E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

Stenobranchius 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):
 $E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):
 $E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):
 $E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):

$E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):
 $E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):

$$E(count_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

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):

$E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):

$E(\text{count}_{sp}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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

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):

$$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

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):

$$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

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):

$$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

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)6: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):

$$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$$

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):

$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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):

$E(\text{count}_{family}) \sim g^{-1}(\text{offset}(\log(\text{water volume})) + \text{depth stratum} * \text{stage})$

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

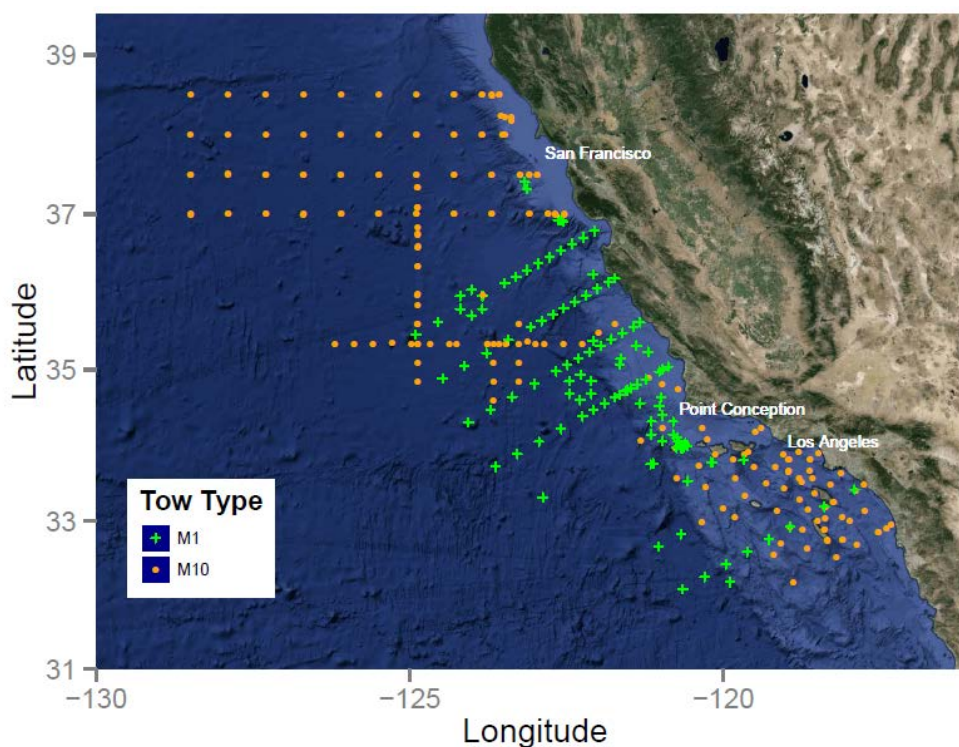


Figure 1:
Map of study area. Two types of MOCNESS were used off central and southern California. The 1 m² MOCNESS (M1) tows are represented by green crosses and the 10 m² MOCNESS (M10) are represented as filled orange circles.

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 m² mouth opening and the other five cruises used the 10 m² 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 $45^{\circ} \pm 8^{\circ}$, 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).

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

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:

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

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.

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

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,

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

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,

Stenobranchius 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), *Nannobranchium 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

Stenobranchius 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 ($z_{cm} = 92\text{m}$). Transformation larvae occurred deepest in the water column, with their daytime depth of center of mass distribution restricted to the mesopelagic ($z_{cm} = 252\text{m} - 893\text{m}$) and exhibited a greater contrast between their median depths during the day ($z_{cm} = 497\text{m}$) and at night ($z_{cm} = 352\text{m}$). During the juvenile stage they exhibited their most dramatic contrast between day and night median depths ($z_{cm} = 498\text{m}$ 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, Percy et al. 1977, Willis and Percy 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 Percy 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, Percy and Laurs 1966, Lavenberg and Ebeling 1967, Paxton 1967, Percy et al. 1977, Loeb 1979, Willis and Percy 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 m²
 MOCNESS; M10 = 10 m² MOCNESS.

Cruise		MOCNESS		# Discrete	Depth Range	Net Mesh	
Code	Start Date	End Date	Type	Nets	Sampled (m)	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		Melamphidae	568
	Liparidae	18		Paralepididae	262
	Zoarcidae	15		Trachipteridae	158
	Agonidae	13		Microstomatidae	157
	Hexagrammidae	9		Platyroctidae	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
<i>Stenobranchius leucopsarus</i>	5734	4465	5419	568	4199	20385
<i>Leuroglossus stilbius</i>	2835	1154	1264	288	300	5841
<i>Lipolagus ochotensis</i>	2601	1139	1063	192	358	5353
<i>Tarletonbeania crenularis</i>	638	609	1488	242	241	3218
<i>Protomyctophum crockeri</i>	181	193	687	49	774	1884
<i>Chauliodus macouni</i>	106	92	774	66	764	1802
<i>Bathylagus pacificus</i>	717	107	40	28	98	990
<i>Cyclothone signata</i>	4	5	36	53	17772	17870
<i>Merluccius productus</i>	1955	1041	734	9	34	3773
<i>Nannobranchium ritteri</i>	283	173	200	37	1635	2328
<i>Cyclothone acclinidens</i>	0	0	0	0	1818	1818
<i>Diaphus theta</i>	112	201	366	207	490	1376
<i>Cyclothone pseudopallida</i>	0	0	0	1	1252	1253
<i>Triphoturus mexicanus</i>	61	133	229	1	707	1131
<i>Argyropelecus sladeni</i>	3	2	12	68	755	840
<i>Danaphos oculatus</i>	3	8	86	135	360	592
<i>Tactostoma macropus</i>	98	124	136	5	154	517
<i>Cyclothone atraria</i>	0	0	0	0	433	433
<i>Argyropelecus hemigymnus</i>	1	0	3	69	303	376
<i>Idiacanthus antrostomus</i>	0	4	8	1	328	341
<i>Bathylagidae</i>	328	1	2	0	4	335
<i>Nannobranchium regale</i>	73	55	101	10	96	335
<i>Melamphaes lugubris</i>	35	20	105	28	106	294
<i>Bathylagoides wesethi</i>	19	19	30	3	218	289
<i>Ceratoscopelus townsendi</i>	2	7	9	2	219	239
<i>Lestidiops ringens</i>	38	12	93	25	64	232
<i>Symbolophorus californiensis</i>	12	3	77	2	106	200
<i>Nannobranchium sp.</i>	151	6	5	2	15	179
<i>Argyropelecus affinis</i>	3	1	9	32	124	169
<i>Nansenia candida</i>	74	58	24	0	1	157
<i>Trachipterus altivelis</i>	36	61	34	4	12	147
<i>Cyclothone pallida</i>	0	0	0	0	145	145
<i>Pseudobathylagus milleri</i>	75	16	14	4	24	133
<i>Diogenichthys atlanticus</i>	20	7	38	9	59	133
<i>Aristostomias scintillans</i>	0	0	3	0	127	130
<i>Myctophidae</i>	22	17	30	5	50	124
<i>Cyclothone sp.</i>	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.

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

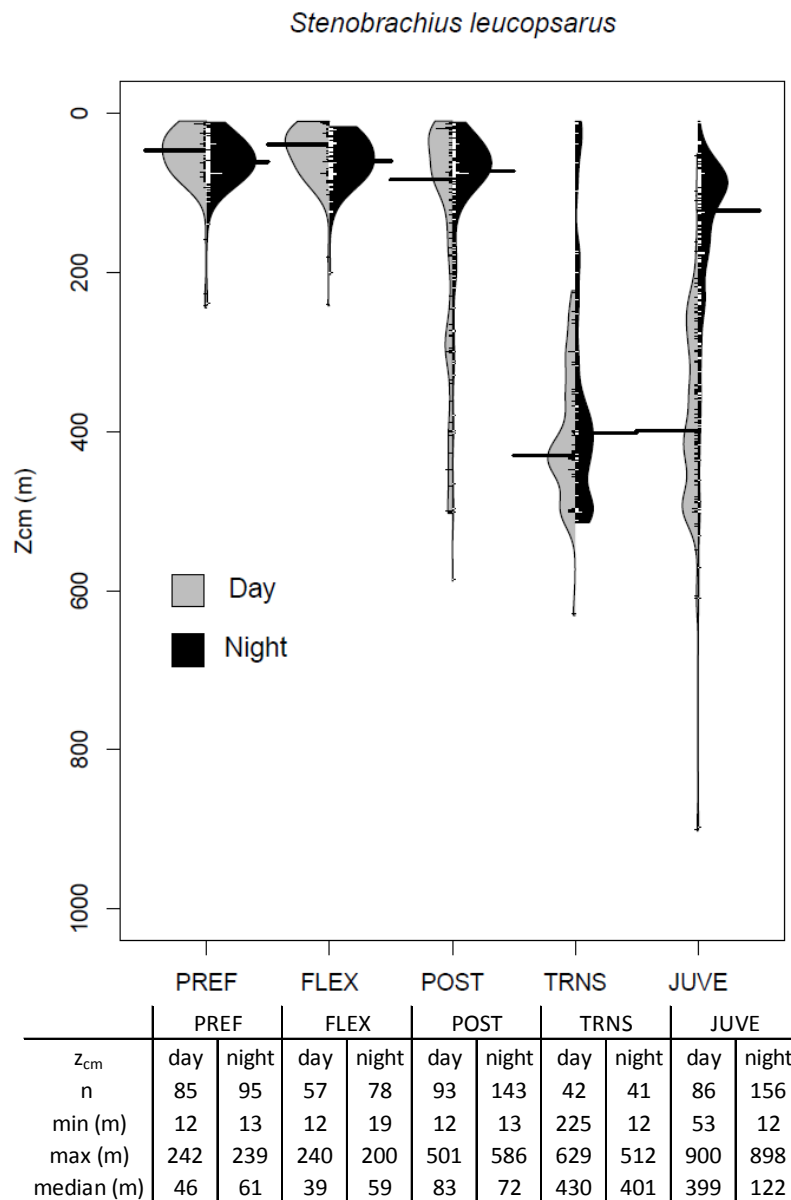
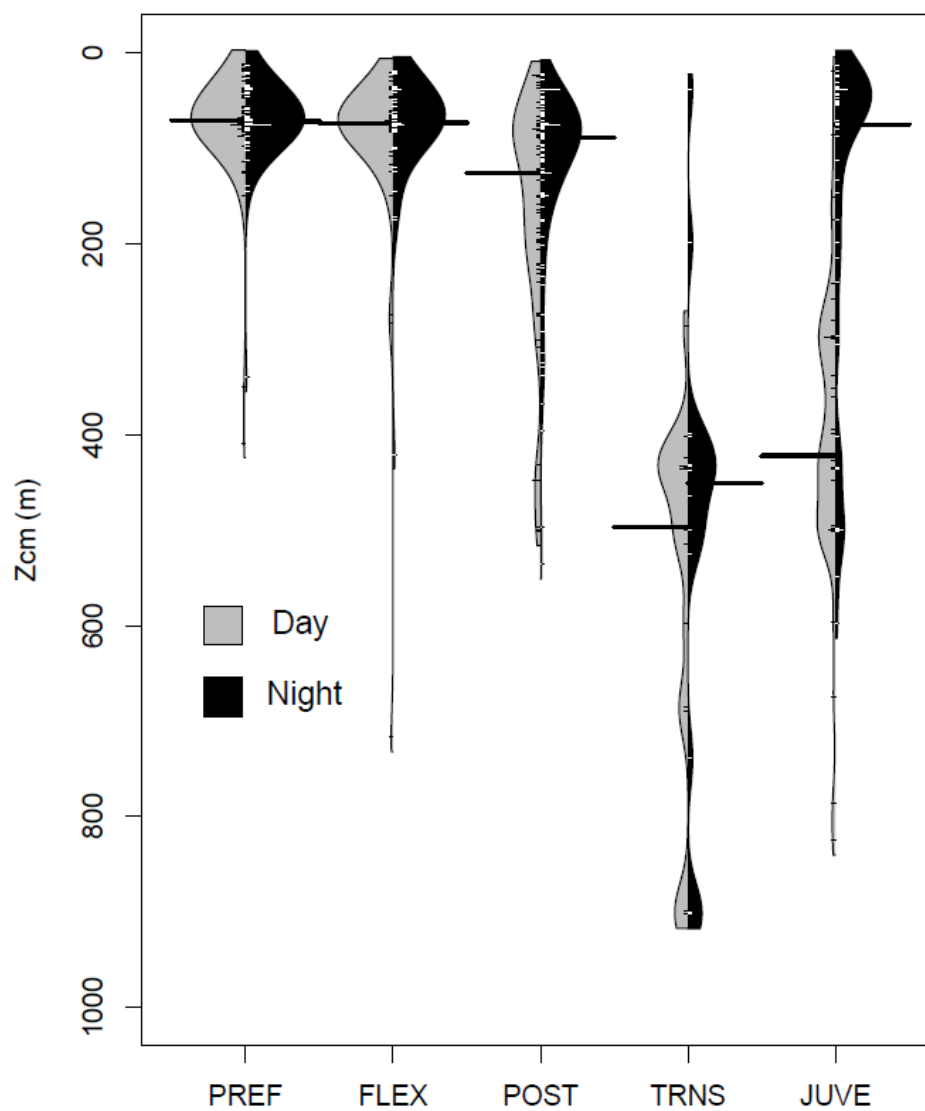


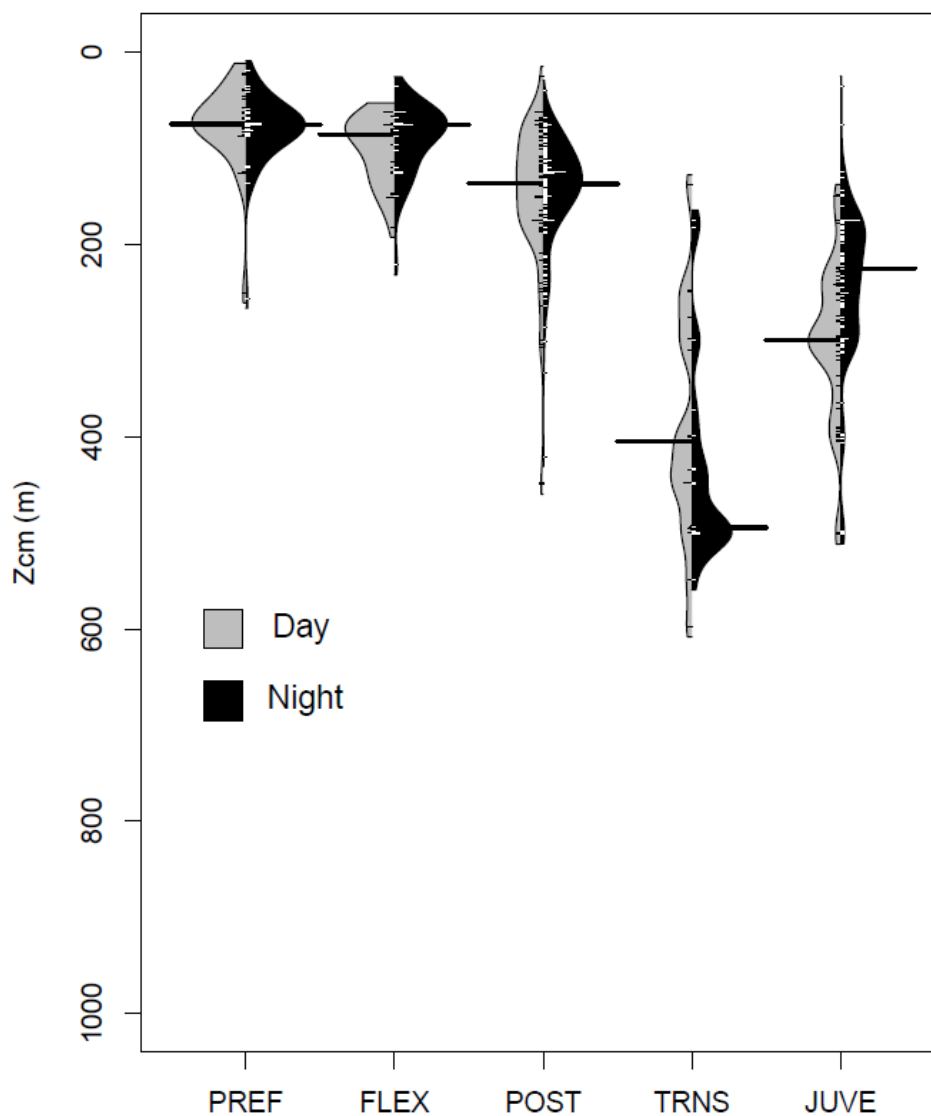
Figure 2:

Ontogenetic vertical distribution of *Stenobranchius 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.

Tarletonbeania crenularis

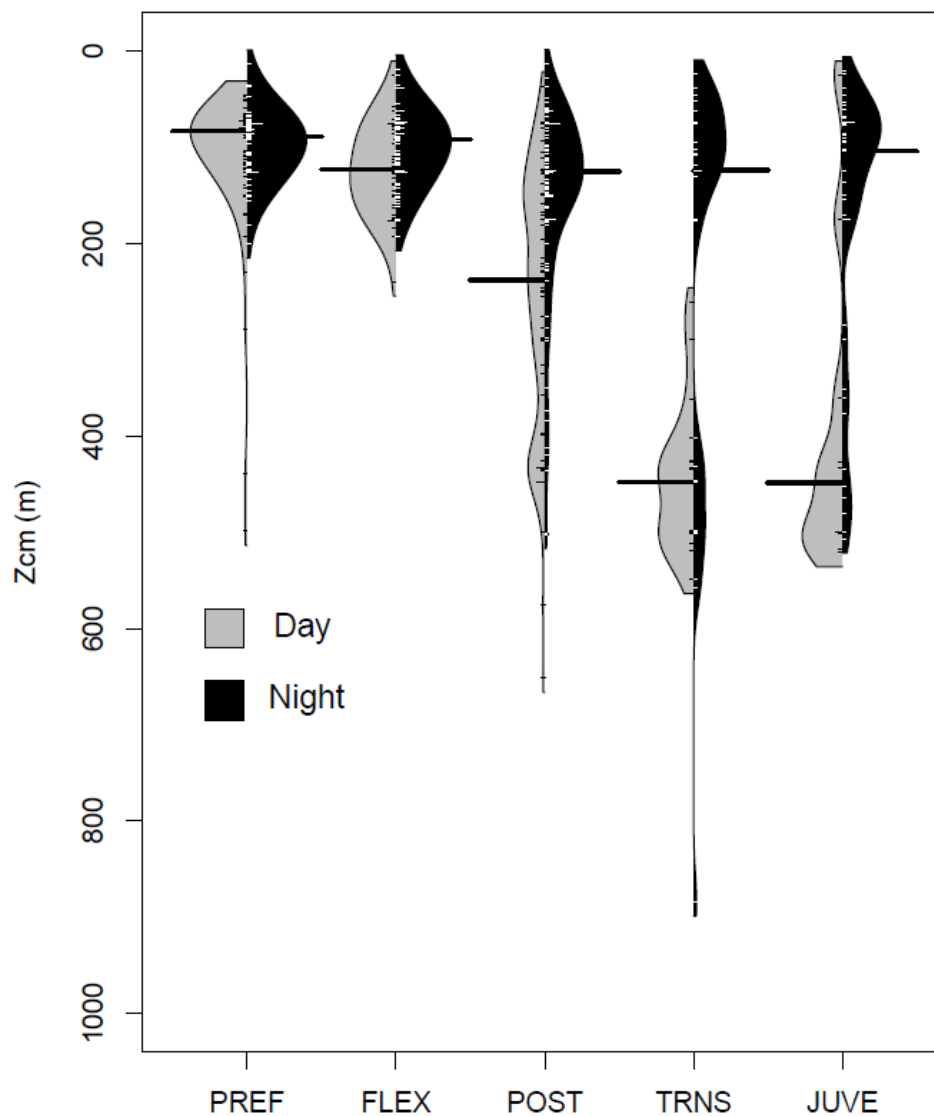
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	59	67	43	42	64	99	17	16	38	47
min (m)	12	13	21	19	24	23	286	38	19	13
max (m)	409	340	717	421	501	536	902	903	825	598
median (m)	71	72	74	73	126	89	497	451	422	75

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

Protomyctophum crockeri

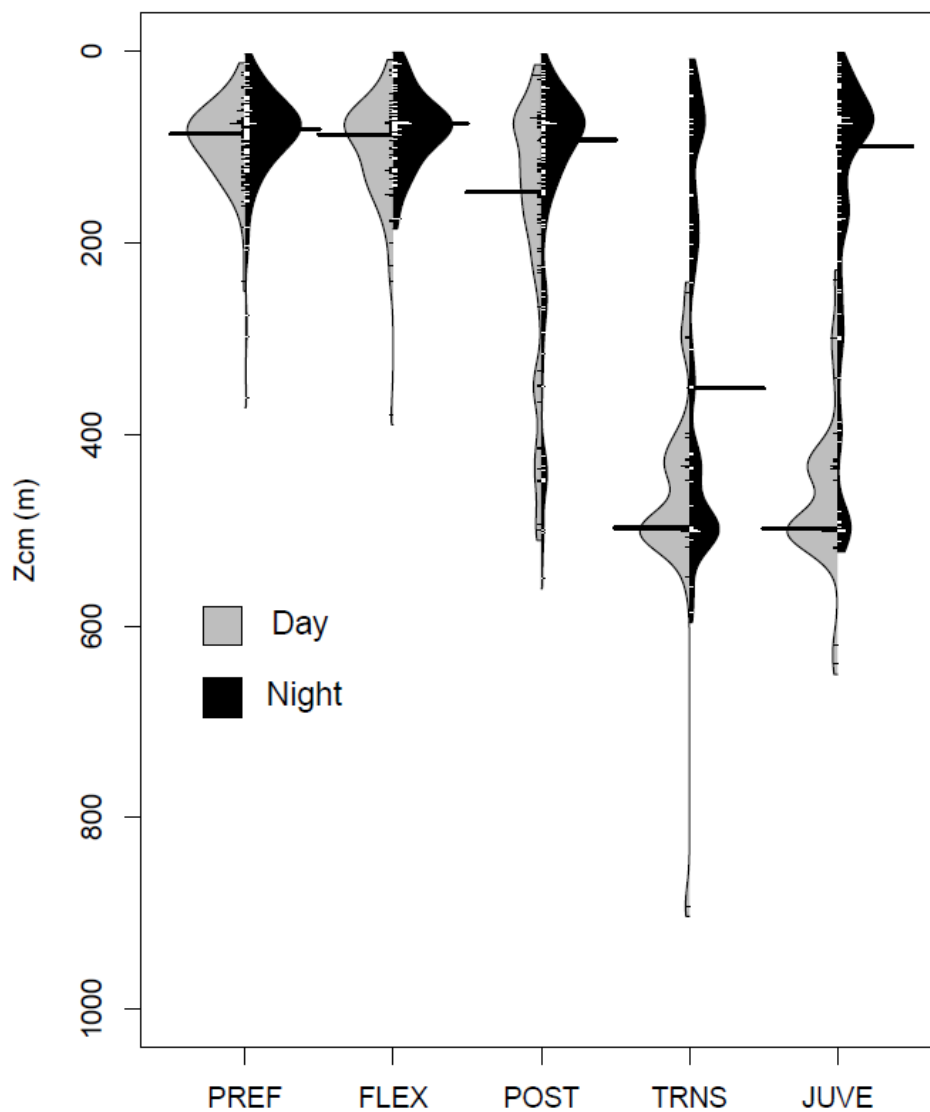
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	30	39	29	29	82	127	17	21	67	87
min (m)	22	19	63	36	25	39	138	175	148	35
max (m)	251	256	182	221	450	421	598	549	502	501
median (m)	75	75	86	75	136	137	405	195	299	225

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

Leuroglossus stilbius

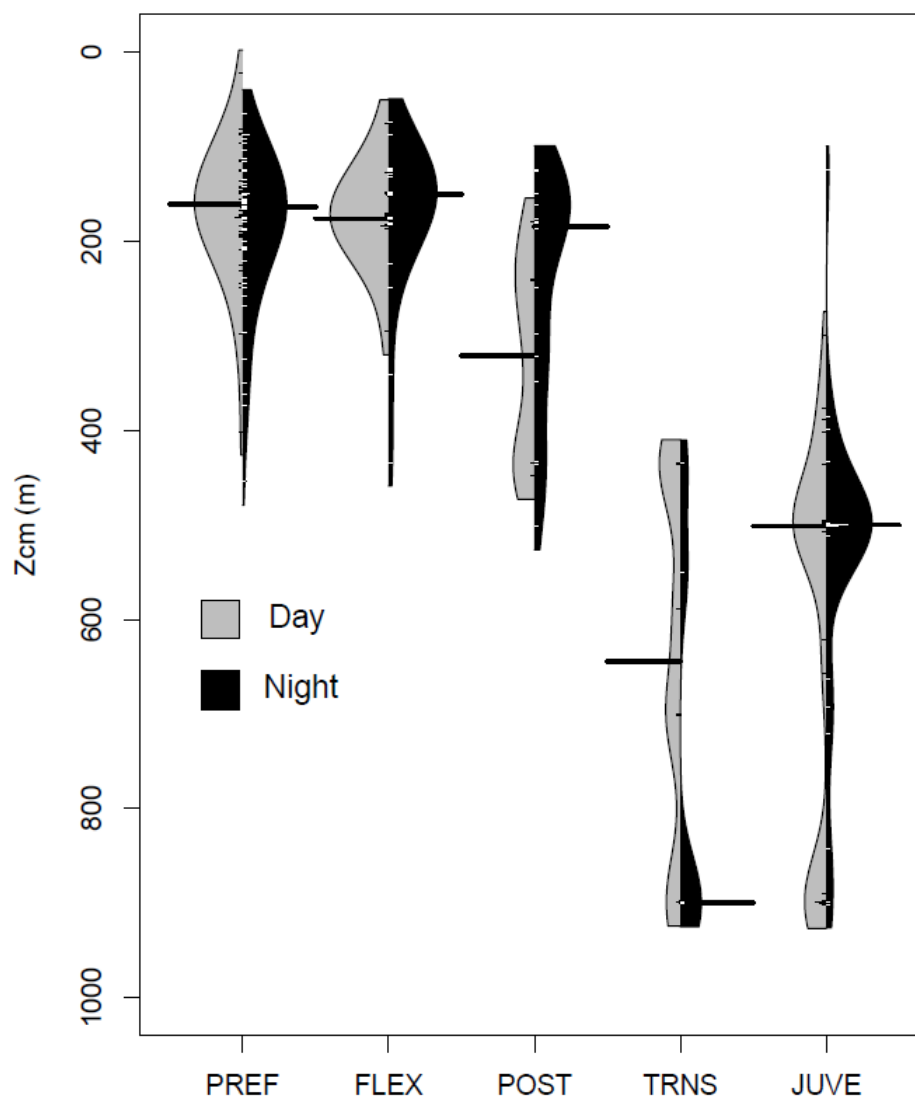
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	57	61	44	63	52	92	17	30	11	43
min (m)	46	14	25	19	36	13	260	24	25	21
max (m)	499	200	240	192	652	502	549	885	521	507
median (m)	83	88	123	92	238	125	448	124	449	104

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

Lipolagus ochotensis

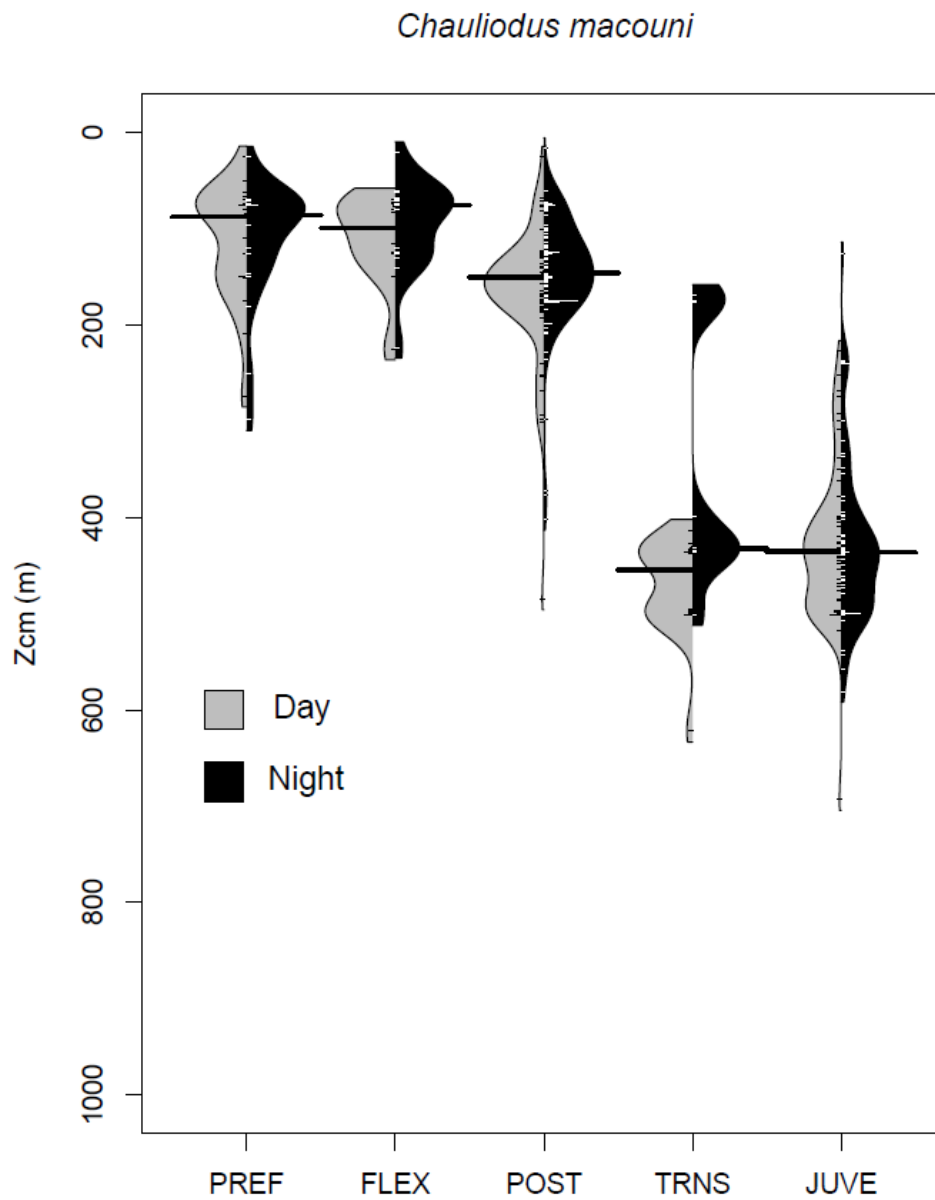
	PREF		FLEX		POST		TRNS		JUVE	
z_{cm}	day	night	day	night	day	night	day	night	day	night
n	79	85	58	73	59	92	26	39	37	64
min (m)	23	14	20	12	25	14	252	19	239	12
max (m)	240	361	379	175	500	550	893	586	640	512
median (m)	86	81	87	76	147	92	497	352	498	99

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

Bathylagus pacificus

	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):

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

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:
Stenobranchius 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	-	-	-	-	-	-	-	-	-	-

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 (Wyrki 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

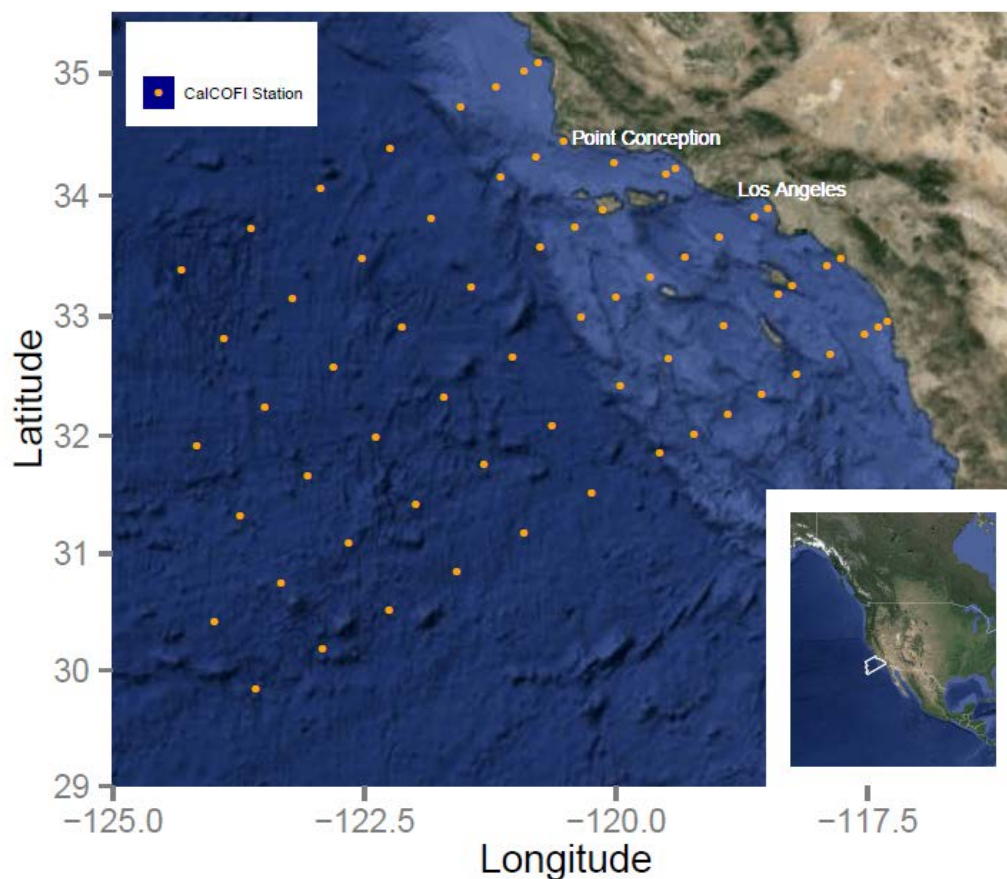


Figure 1:
Map of study area. Filled orange circles indicate sampling sites in the core CalCOFI pattern (66 stations).

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 $45^{\circ} \pm 8^{\circ}$ 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,

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

where $abund_{spp.stage}$ is the abundance of each mesopelagic fish species at a particular life history or ontogenetic stage under 10 m² 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 m² 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,

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

where $abund_{spp.stage}$ is the abundance of each mesopelagic fish species at each ontogenetic stage under 10 m² 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* (Phosichthyidae) 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), *Stenobranchius 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 ($\Sigma\theta$), 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, Kobylansky 1985 cited by Moser 1996). In addition, all of the species in this study undergo diel vertical migrations (Percy 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	
	Sphyrnaenidae	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
<i>Vinciguerria lucetia</i>	18586	9785	1209	2469	74	32123
<i>Leuroglossus stilbius</i>	11653	1247	126	53	2	13081
<i>Bathylagoides wesethi</i>	2524	942	102	25	2	3595
<i>Lipolagus ochotensis</i>	1004	496	54	29	0	1583
<i>Stenobranchius leucopsarus</i>	0	1396	155	135	1	1687
<i>Ceratoscopelus townsendi</i>	0	800	115	138	0	1053
<i>Triphoturus mexicanus</i>	0	800	97	81	2	980
<i>Protomyctophum crockeri</i>	0	272	103	240	2	617
<i>Diogenichthys atlanticus</i>	0	392	70	146	1	609
<i>Symbolophorus californiens</i>	0	287	55	39	1	382
<i>Nannobranchium ritteri</i>	0	269	26	35	1	331
<i>Tarletonbeania crenularis</i>	0	57	12	11	0	80
<i>Merluccius productus</i>	4528	4469	134	24	0	9155
<i>Cyclothone signata</i>	0	299	135	239	1	674
<i>Argentina sialis</i>	499	29	3	2	0	533
<i>Tetragonurus cuvieri</i>	468	52	10	3	0	533
<i>Nannobranchium</i> sp.	0	308	4	0	0	312
<i>Diogenichthys laternatus</i>	0	154	21	56	0	231
<i>Idiacanthus antrostomus</i>	0	100	32	53	1	186
<i>Trachipterus altivelis</i>	170	8	2	1	0	181
<i>Lestidiops ringens</i>	0	89	10	20	0	119
<i>Chauliodus macouni</i>	45	21	8	33	0	107
<i>Diaphus</i> sp.	0	53	5	39	3	100
<i>Melamphaes lugubris</i>	0	53	17	26	2	98
<i>Sphyræna argentea</i>	0	83	2	0	0	85
<i>Icichthys lockingtoni</i>	72	8	1	2	1	84
<i>Argyropelecus sladeni</i>	0	66	5	9	0	80
<i>Microstoma</i> sp.	52	16	7	4	0	79
<i>Nansenia candida</i>	53	15	3	1	0	72
<i>Hygophum reinhardtii</i>	0	42	6	12	0	60
<i>Sternoptyx</i> sp.	0	43	7	6	1	57
<i>Stomias atriventer</i>	0	25	13	11	3	52
<i>Danaphos oculatus</i>	0	12	6	30	1	49
<i>Cyclothone</i> sp.	0	24	9	14	0	47
<i>Cyclothone acclinidens</i>	0	4	10	31	0	45
<i>Myctophum nitidulum</i>	0	41	2	2	0	45
<i>Nannobranchium regale</i>	0	22	11	7	0	40
<i>Vinciguerria poweriae</i>	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

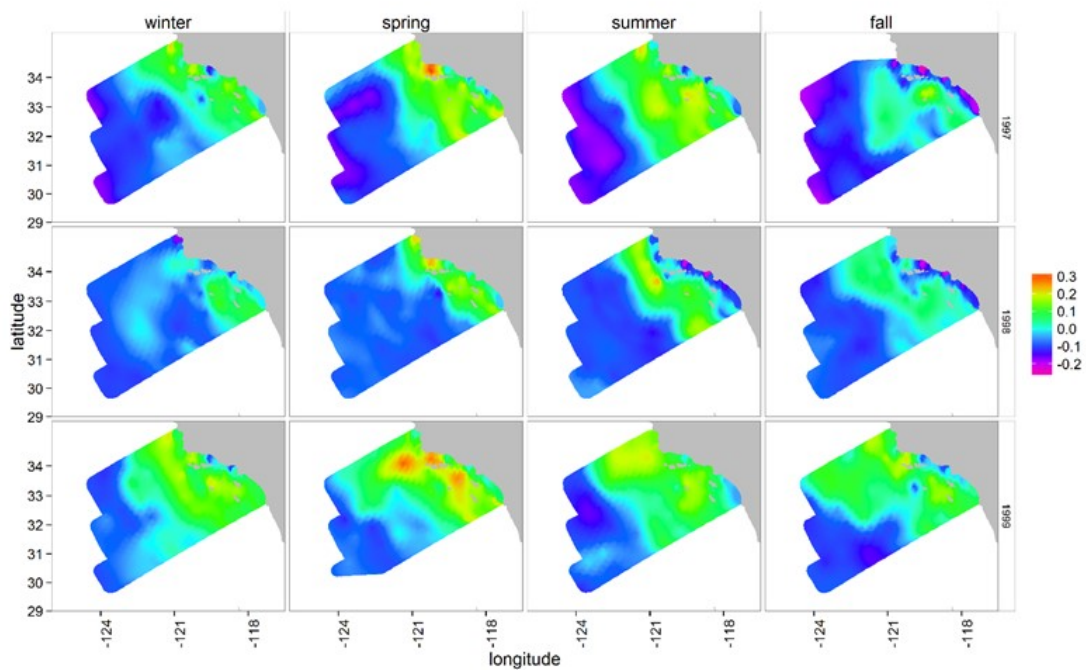


Figure 2:
Graphical representation of principal component 1 (PC1) calculated from the hydrographic data collected from the quarterly CalCOFI cruises during 1997, 1998, and 1999.

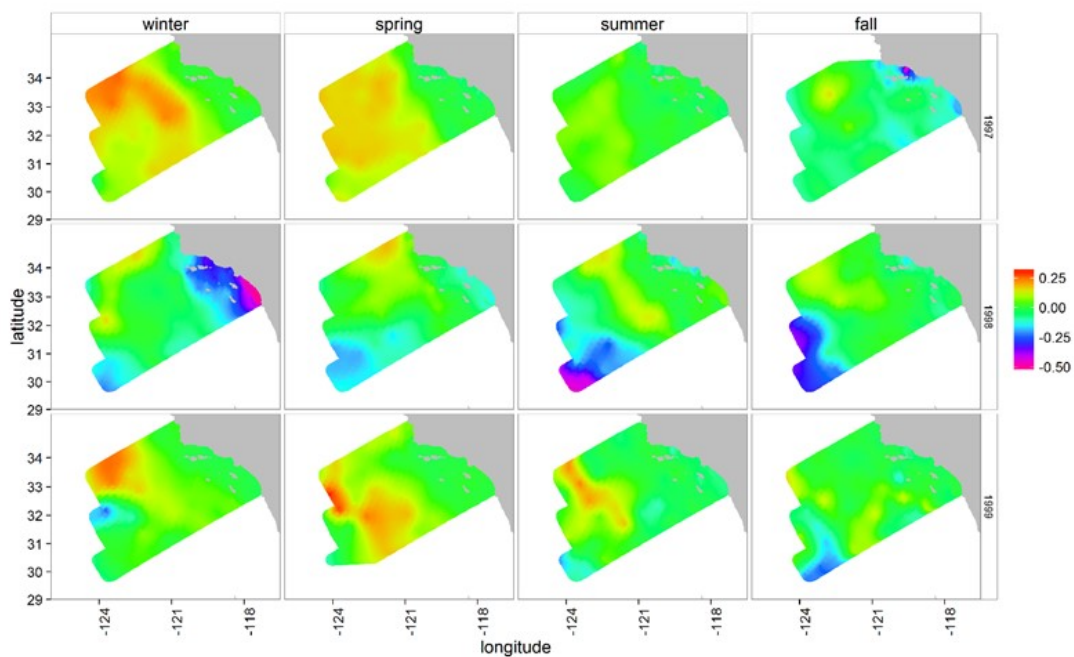


Figure 3:
Graphical representation of principal component 2 (PC2) calculated from the hydrographic data collected from the quarterly CalCOFI cruises during 1997, 1998, and 1999.

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

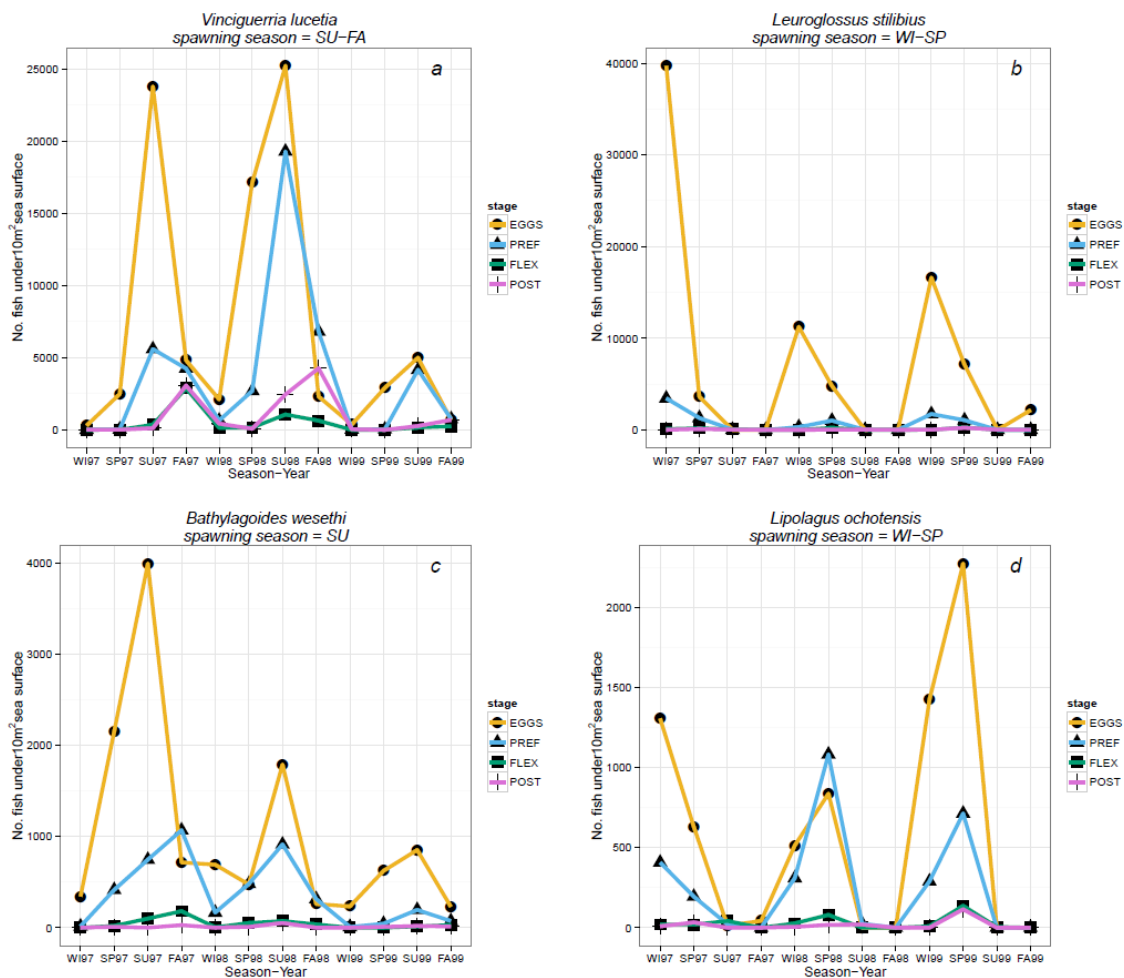


Figure 4:

Graphical representation of the abundance (number of fish under 10 m² 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.

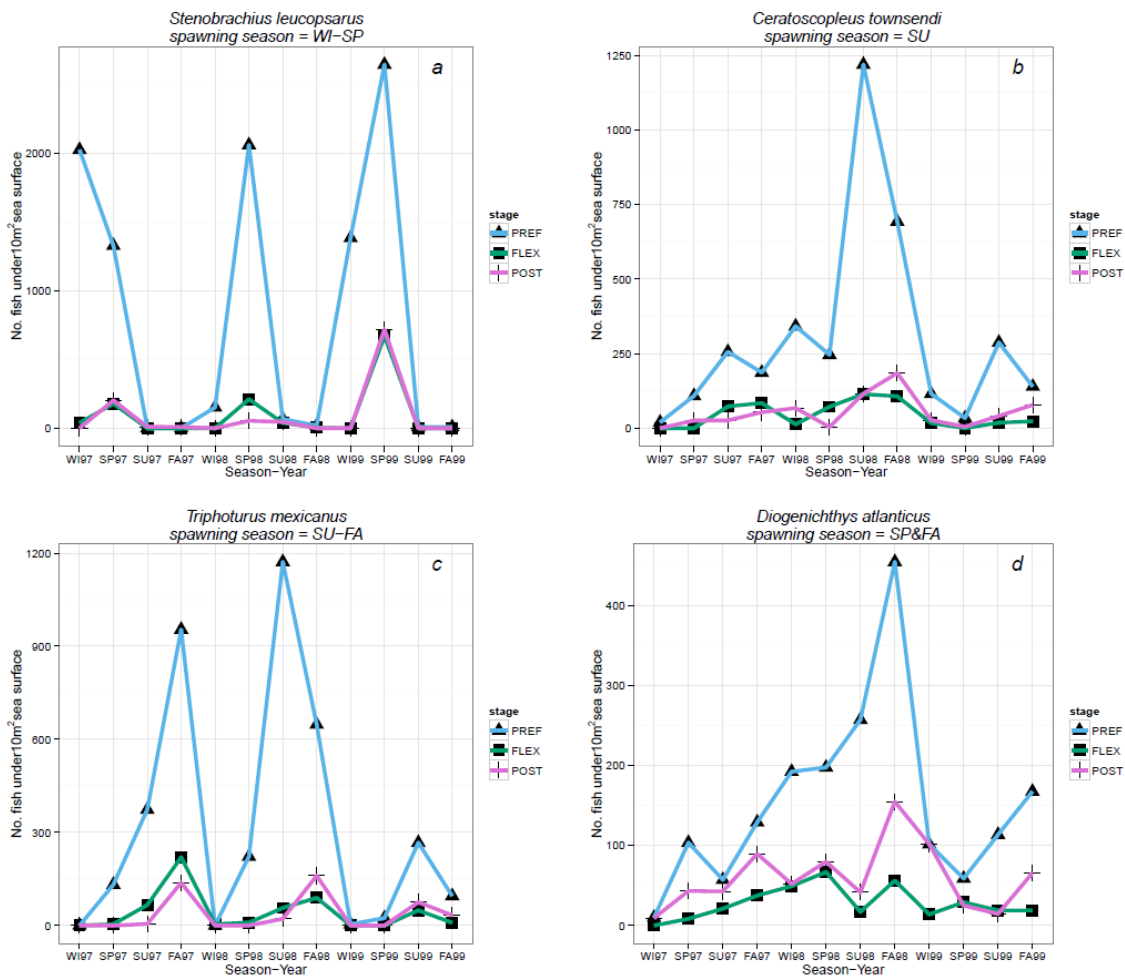


Figure 5:

Graphical representation of the abundance (number of fish under 10 m² 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) *Stenobranchius leucopsarus*, b) *Ceratoscopeus townsendi*, c) *Triphoturus mexicanus*, d) *Diogenichthys atlanticus*. Note differences in y-axis scales.

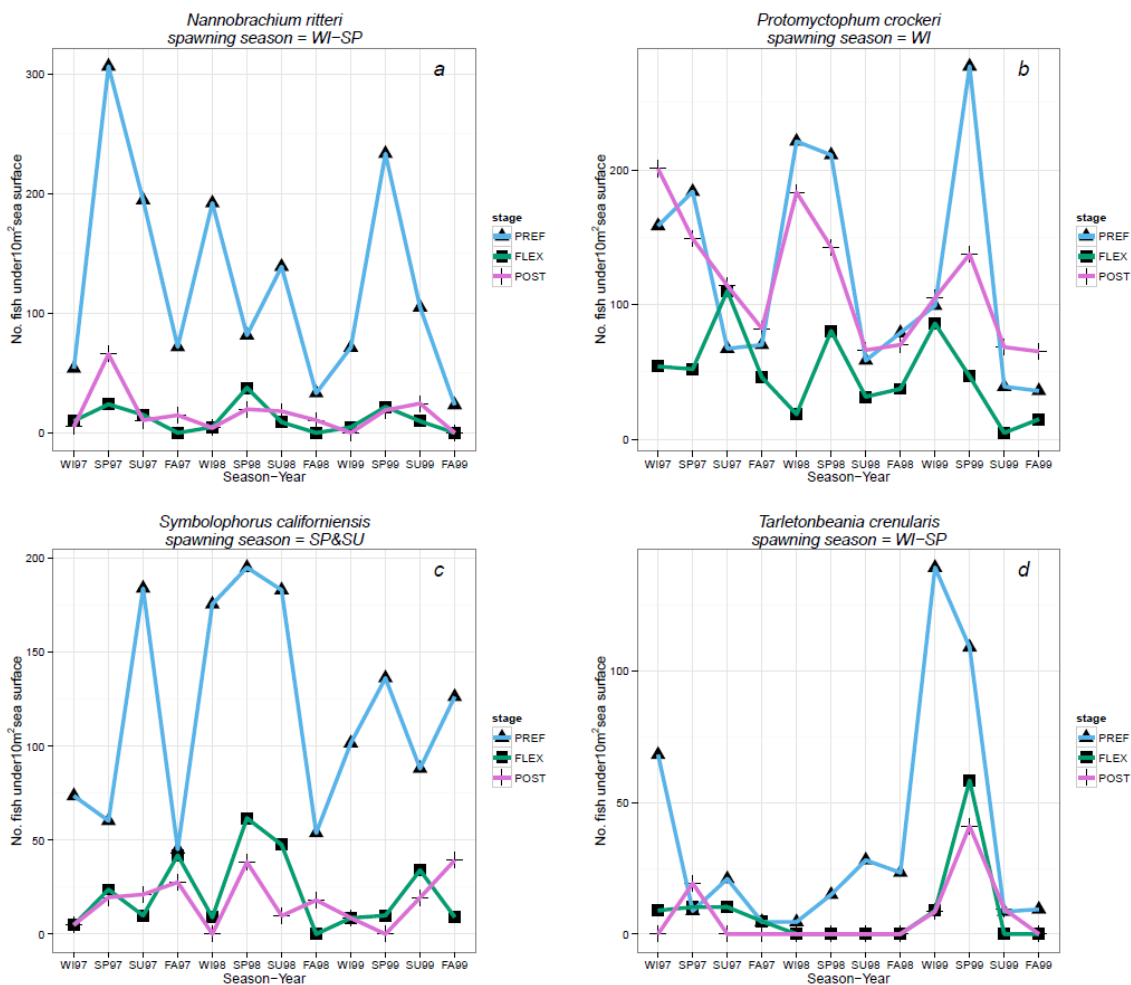
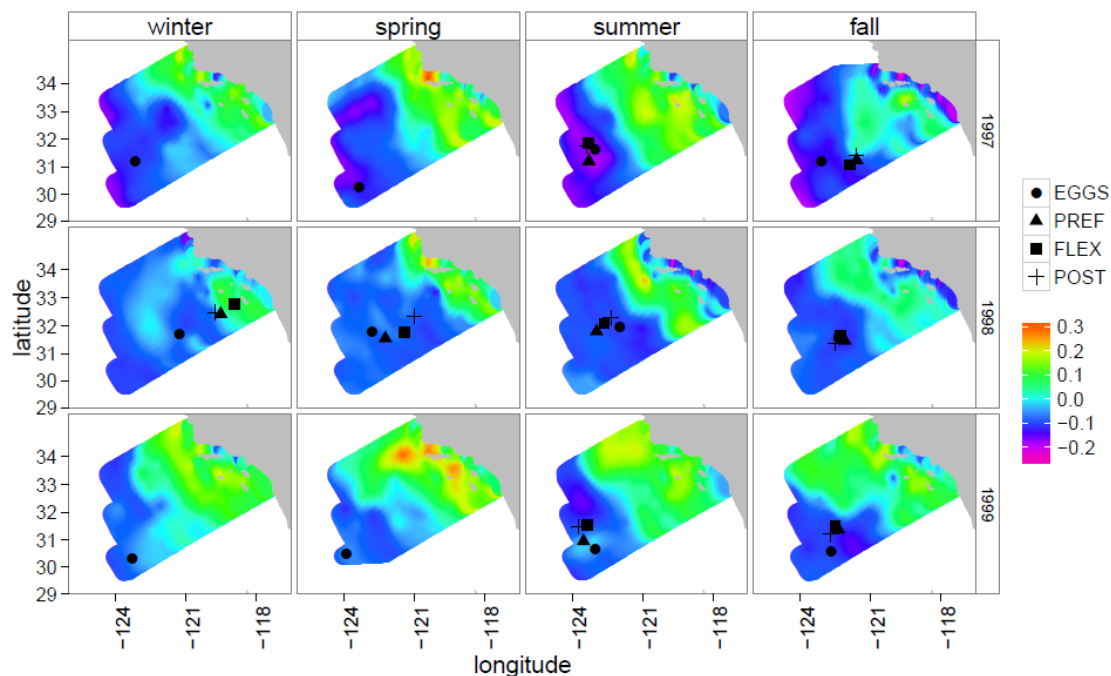


Figure 6:

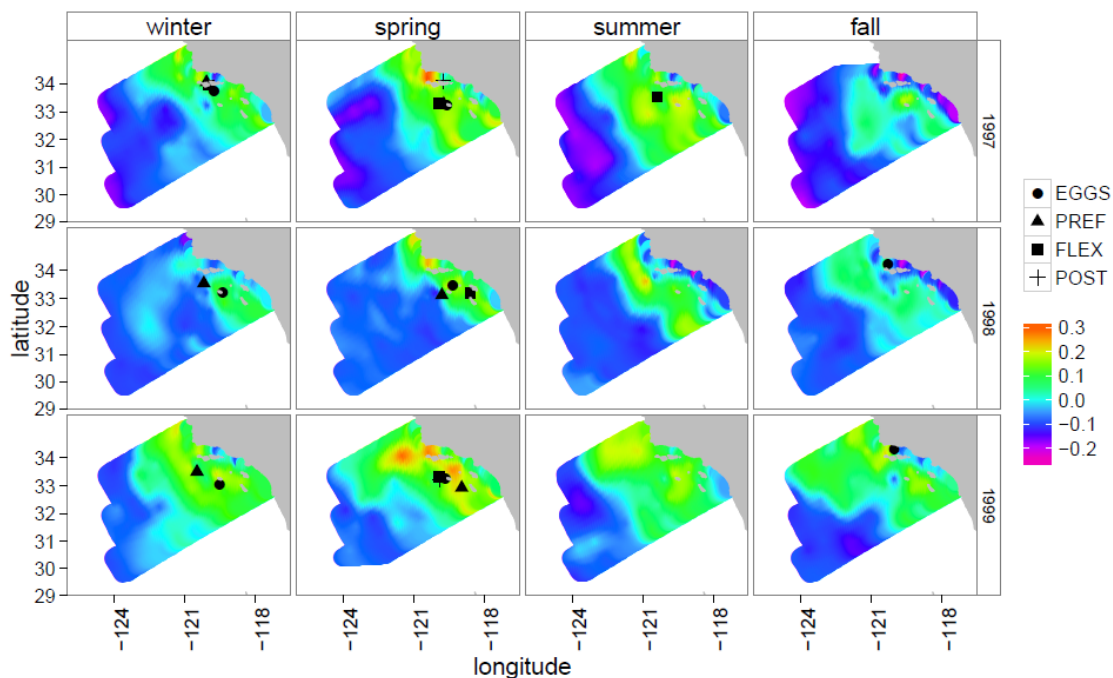
Graphical representation of the abundance (number of fish under 10 m² sea surface area) of four species of myctophids, separated by ontogenetic stage, in CalCOFI bongo samples collected during winter (WI), spring (SP), summer (SU), and fall (FA) cruises in 1997, 1998, and 1999. Each species' spawning season is indicated at the top of each panel. Species in each panel: a) *Nannobranchium ritteri*, b) *Protomyctophum crockeri*, c) *Symbolophorus californiensis*, d) *Tarletonbeania crenularis*. Note differences in y-axis scales.



stage	Winter		1998-99		Spring		1998-99		Summer		1998-99		Fall		1998-99	
	1997-98	dist (km) direc	dist (km) direc	dist (km) direc	dist (km) direc	dist (km) direc	dist (km) direc	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

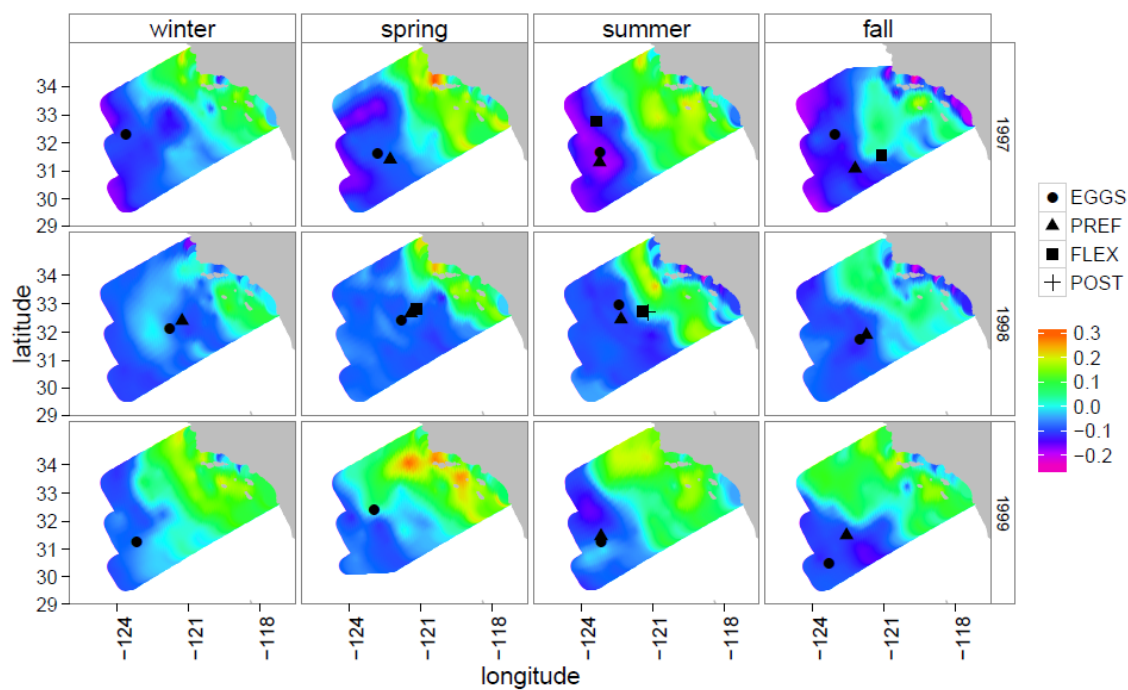
Figure 7:

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 (-).



stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	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	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

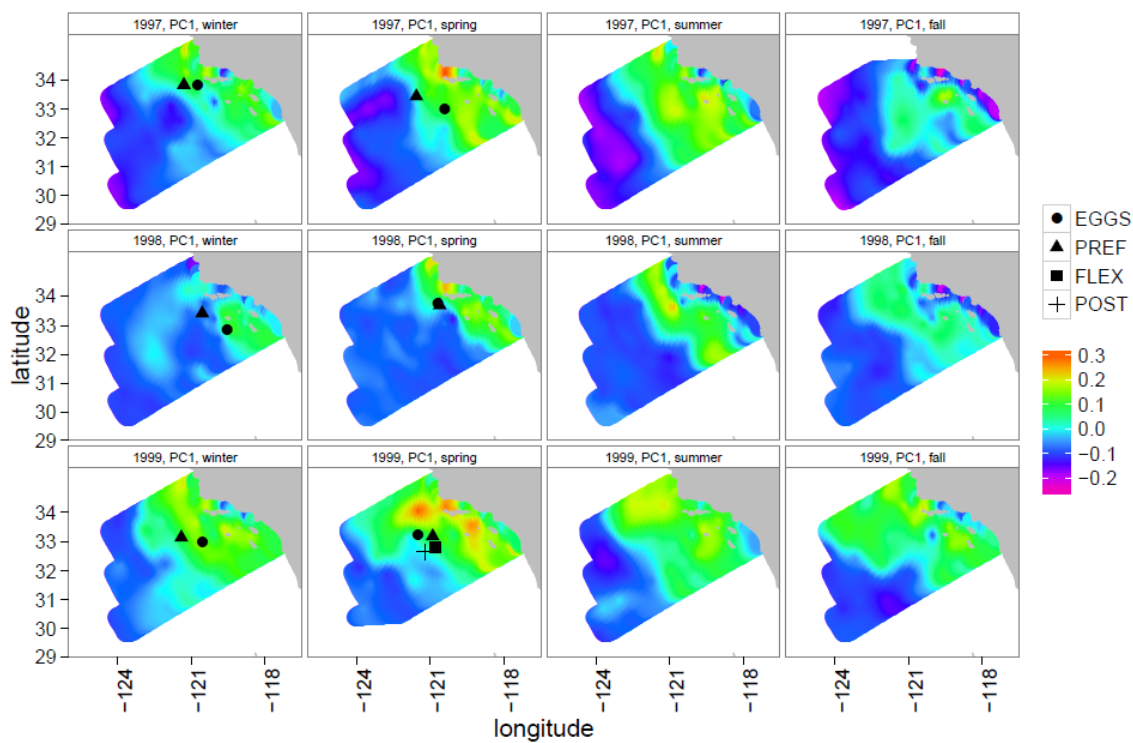
Figure 8:
Leuroglossus stilbius distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage is below the plots. See figure 7 for explanation.



stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	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	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

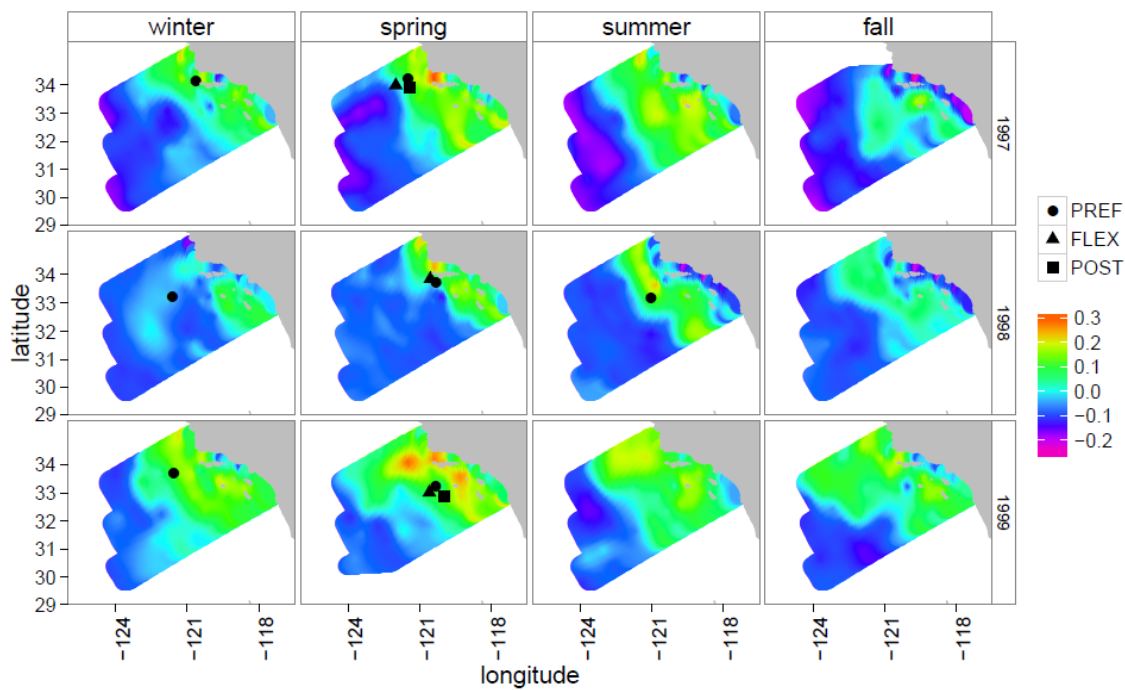
Figure 9:

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.



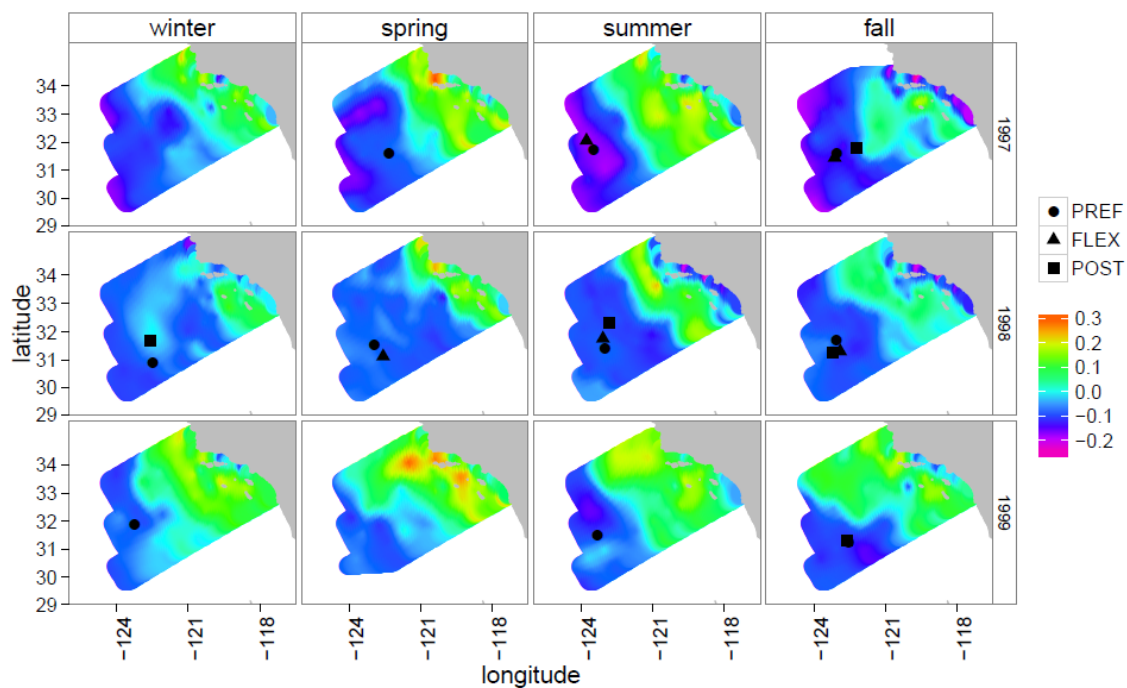
stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
EGGS	153	SE	96	NW	91	NW	97	SW	-	-	-	-	-	-	-	-
PREF	83	SE	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.



stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	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	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

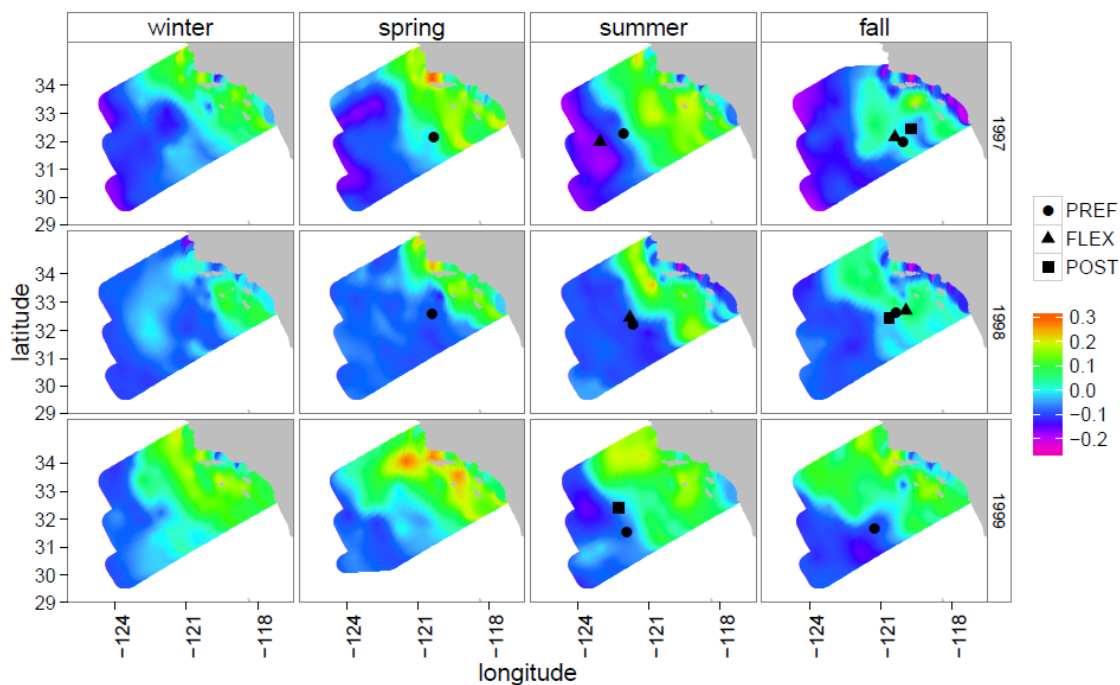
Figure 11:
Stenobranchius leucopsarus distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



stage	Winter		1998-99		Spring		1998-99		Summer		1998-99		Fall		1998-99	
	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99
	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:

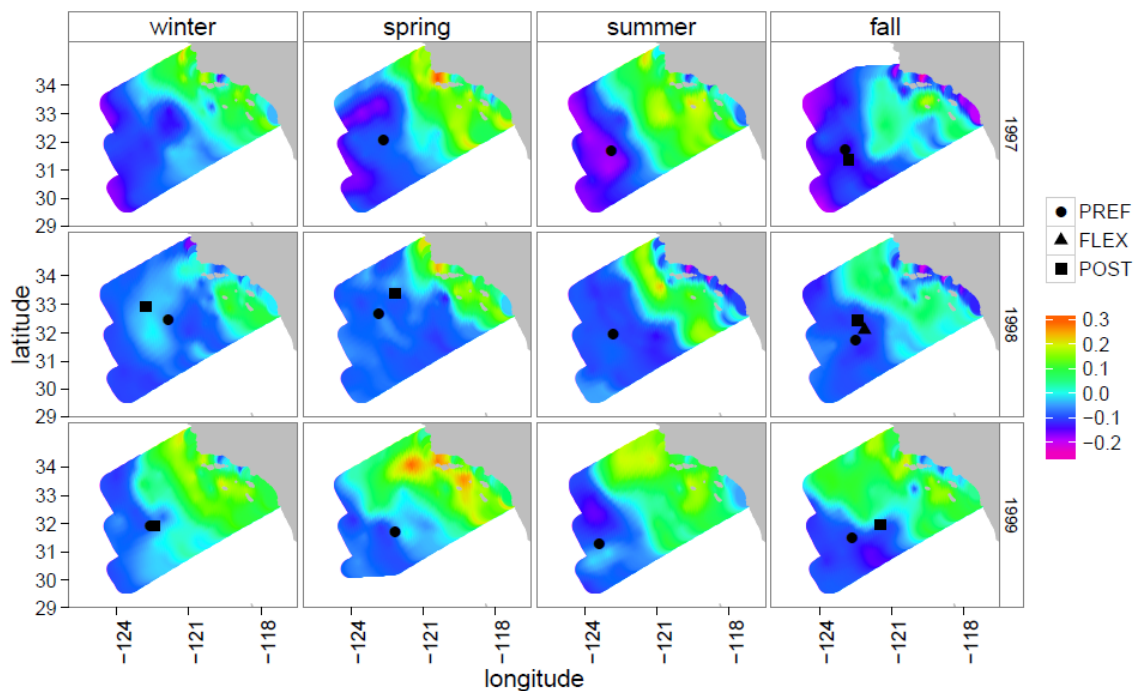
Ceratoscopelus townsendi distribution centroid locations plotted over maps of PC1 with corresponding table of centroid location comparisons within season between years for each combination of species and stage. See figure 7 for explanation.



stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	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	-	-

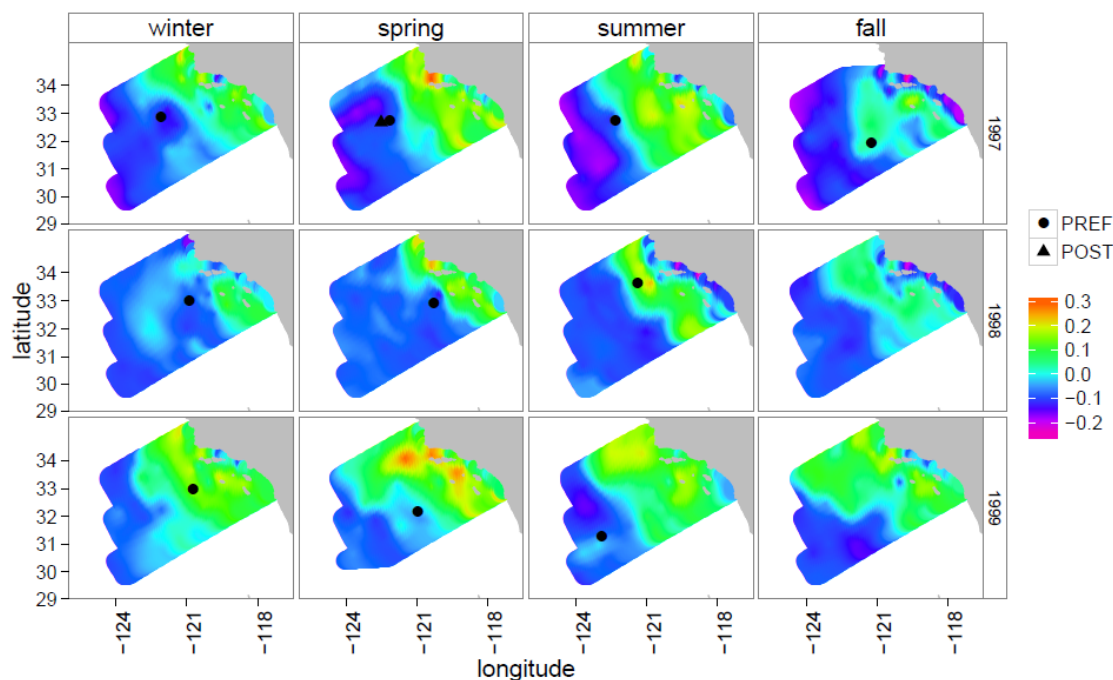
Figure 13:

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.



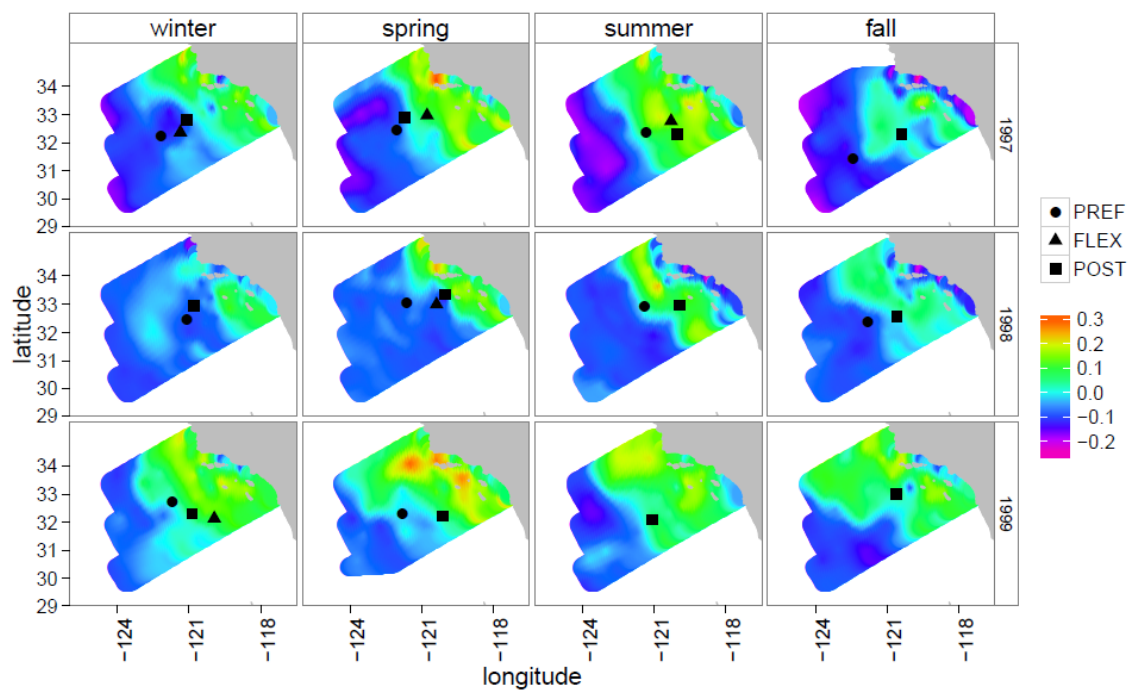
stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	-	-	95	SW	68	NW	123	SE	30	NE	92	SW	41	SE	30	SW
FLEX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



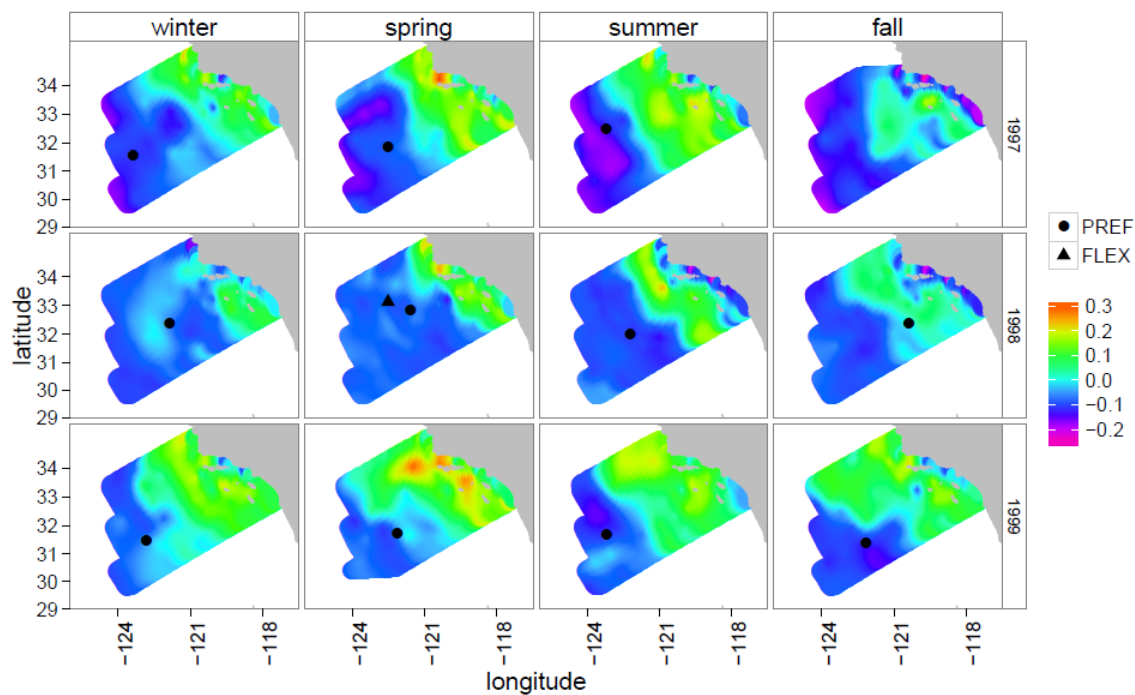
stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc	dist (km)	direc
PREF	112	NE	15	SE	176	NE	106	SW	132	NE	297	SW	-	-	-	-
FLEX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



stage	Winter				Spring				Summer				Fall			
	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	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.



stage	Winter		Spring		Summer		Fall									
	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99	1997-98	1998-99								
	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.

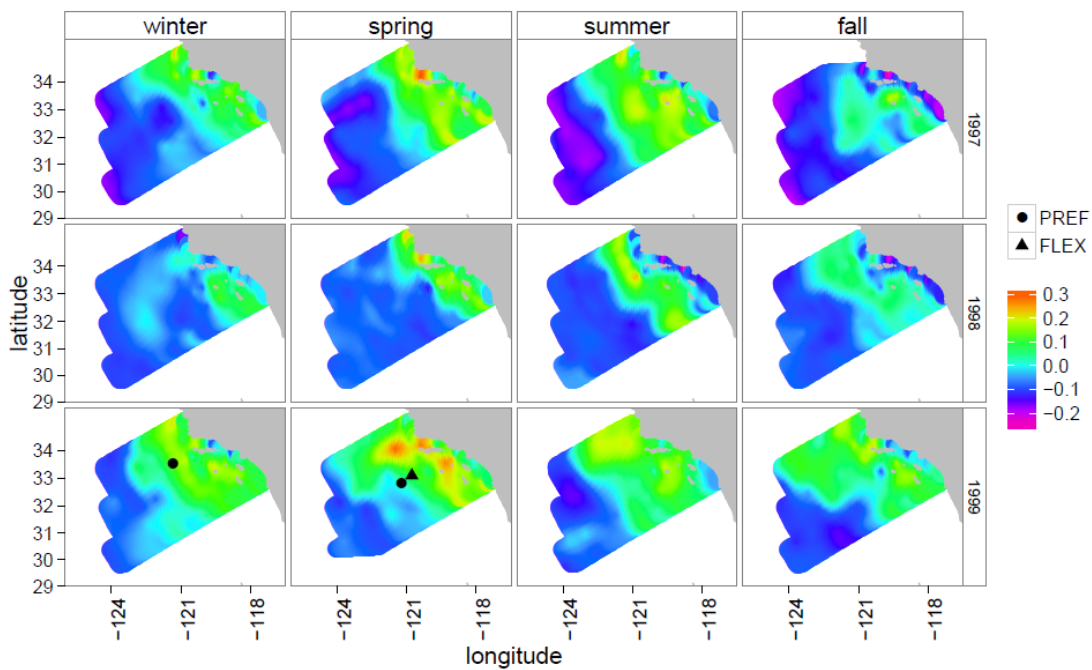


Figure 18:
Tarletonbeania crenularis distribution centroid locations plotted over maps of PC1. A centroid location comparisons table is absent for this species due to insufficient data.

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.

species	temp affinity dist from shore spawning season			Predicted						Observed					
				Pre-El Niño		El Niño		La Niña		Pre-El Niño		El Niño		La Niña	
				abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location	abund	centroid location
<i>Bathylagoides wesethi</i>	cold	oceanic	SU	High	offshore	Low	inshore	High	offshore	High	offshore	Low	inshore	Low	offshore
<i>Leuroglossus stilibius</i>	cold	coastal-oceanic	WI-SP	High	inshore	Low	inshore	High	inshore	High	inshore	Low	inshore	High	offshore
<i>Lipolagus ochotensis</i>	cold	coastal-oceanic	WI-SP	High	inshore	Low	inshore	High	inshore	Low	inshore	Low	inshore	High	offshore
<i>Vinciguerria lucetia</i>	warm	oceanic	SU-FA	Low	offshore	High	inshore	Low	offshore	High	offshore	High	inshore	Low	offshore
<i>Ceratoscopus townsendi</i>	broad	oceanic	SU	High	offshore	High	offshore	High	offshore	Low	offshore	High	offshore	Low	offshore
<i>Diogenichthys atlanticus</i>	warm	oceanic	SP & FA	Low	offshore	High	inshore	Low	offshore	Low	offshore	High	offshore	Low	offshore
<i>Nannobranchium ritteri</i>	broad	oceanic	WI-SP	High	offshore	High	offshore	High	offshore	High	offshore	Low	inshore	High	offshore
<i>Protomyctophum crockeri</i>	cold	oceanic	WI	High	offshore	Low	inshore	High	offshore	High	offshore	High	inshore	High	offshore
<i>Stenobranchius leucopsarus</i>	cold	oceanic	WI-SP	High	offshore	Low	inshore	High	offshore	High	inshore	High	*	High	offshore
<i>Symbolophorus californiens</i>	cold	oceanic	SP & SU	High	offshore	Low	inshore	High	offshore	High	offshore	High	inshore	Low	offshore
<i>Tarletonbeania crenularis</i>	cold	oceanic	WI-SP	High	offshore	Low	inshore	High	offshore	Low	-	Low	-	High	-
<i>Triphoturus mexicanus</i>	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.

species	stage	p-value				
		depth	PC1	PC2	year (97-98)	year (98-99)
<i>Bathylagoides wesethi</i>	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
<i>Leuroglossus stilbius</i>	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
<i>Lipolagus ochotensis</i>	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
<i>Vinciguerria lucetia</i>	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
<i>Ceratoscopelus townsendi</i>	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
<i>Diogenichthys atlanticus</i>	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
<i>Nannobranchium ritteri</i>	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
<i>Protomyctophum crockeri</i>	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
<i>Stenobranchius leucopsarus</i>	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
<i>Symbolophorus californiensis</i>	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
<i>Tarletonbeania crenularis</i>	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
<i>Triphoturus mexicanus</i>	PREF	NC	NC	NC	NC	NC
	FLEX	NC	NC	NC	NC	NC
	POST	NC	NC	NC	NC	NC

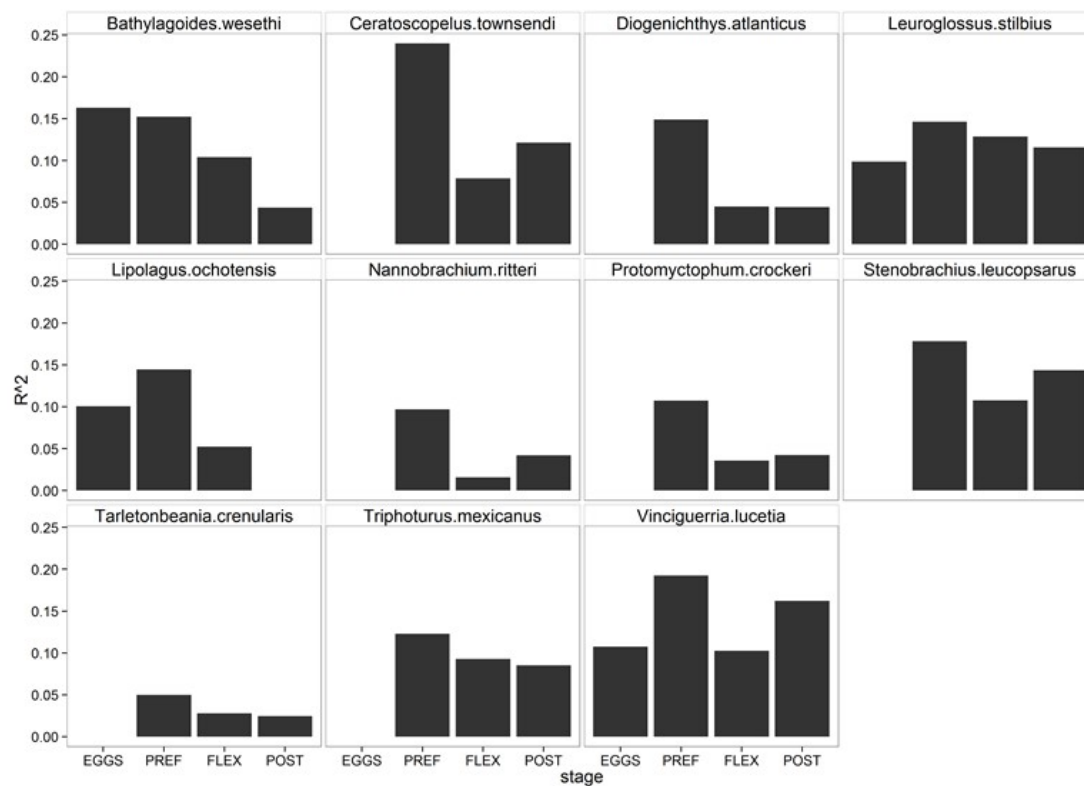


Figure 19:
Graphical representation of generalized linear mixed model fits for early life history of eleven mesopelagic fish species.

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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:

Ceratospelus 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:
Nannobranchium ritteri, ontogenetic stage = Preflexion

Call:

```
glm.nb(formula = as.integer(Nannobranchium.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:

Nannobranchium 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:

Nannobranchium ritteri, ontogenetic stage = Flexion

Model did not converge.

Table 25:

Nannobranchium ritteri, ontogenetic stage = Postflexion

Call:

```
glm.nb(formula = as.integer(Nannobranchium.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:

Nannobranchium 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:

Stenobranchius leucopsarus, ontogenetic stage = Preflexion

Call:

```
glm.nb(formula = as.integer(Stenobranchius.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:

Stenobranchius leucopsarus, ontogenetic stage = Preflexion, continued

```

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

```

Table 30:

Stenobranchius leucopsarus, ontogenetic stage = Flexion

Call:

```

glm.nb(formula = as.integer(Stenobranchius.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:

Stenobranchius 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 = Postflexion

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 = Postflexion, 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

	dpth.s	PC1.st	PC2.st	year12	year13
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
+ year12
              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:
Vinciguerrria lucetia, ontogenetic stage = Eggs
$Vinciguerrria.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:
Ceratospelus townsendi, ontogenetic stage = Preflexion
 \$Ceratospelus.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:
Nannobranchium ritteri, ontogenetic stage = Preflexion

\$Nannobranchium.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:
Nannobranchium 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:
Nannobranchium ritteri, ontogenetic stage = Flexion

\$Nannobranchium.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:
Nannobranchium 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:
Nannobranchium ritteri, ontogenetic stage = Postflexion

\$Nannobranchium.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	PC1.std	PC2.std	year12	year13
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:
Stenobranchius 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:

Stenobranchius leucopsarus, ontogenetic stage = Flexion

\$Stenobranchius.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:
Stenobranchius 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:
Stenobranchius leucopsarus, ontogenetic stage = Postflexion
 \$Stenobranchius.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:

Stenobranchius 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
(Intr) 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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