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UNIVERSITY OF CALIFORNIA SAN DIEGO

Diet and Maternal Investment in Larval *Sebastes* spp. – Implications for Growth and Survival

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Kamran Aidan Walsh

Committee in charge:

Professor Brice X. Semmens, Chair
Professor Moira Décima
Professor Colleen M. Petrik

2023

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University of California San Diego

2023

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LIST OF ABBREVIATIONS

| | |
|---------|---|
| CalCOFI | California Cooperative Oceanic Fisheries Investigations |
| CCE | California Current Ecosystem |
| CI | Confidence interval |
| IRI | Index of Relative Importance |
| RG | Recent Growth |
| SCB | Southern California Bight |
| SL | Standard Length |
| WAIC | Watanabe Akaike Information Criterion |

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ABSTRACT OF THE THESIS

Diet and Maternal Investment in Larval *Sebastes* spp. – Implications for Growth and Survival

by

Kamran Walsh

Master of Science in Marine Biology

University of California San Diego, 2023

Professor Brice X. Semmens, Chair

Survival through the larval phase greatly affects the population dynamics of most fishes, and both diet and maternal investment have long been hypothesized as important contributors to

interannual recruitment variability. This study examines the feeding ecology of larval *Sebastes* spp. rockfishes with respect to ontogeny, selectivity, and the respective influences of diet and maternal investment on size and growth. Prey selection was calculated from larval gut contents, maternal investment was estimated using otolith core radii, and recent growth was derived from outer increment widths. Bayesian multilevel models were used to describe independent and interactive effects of diet and core on length and growth. Larval rockfishes were observed to primarily select for Calanoid nauplii and copepodites, modulating feeding with ontogeny and in response to prey availability. Models that accounted for maternal investment and prey specificity more effectively predicted length and growth than models that only accounted for total gut content biomass. Calanoid copepodite gut content carbon biomass was generally more correlated with length and growth than gut content carbon biomass of other taxa, but older and younger larvae experienced different growth rates in association with different prey. Positive relationships between core and both length and age suggest that maternal provisioning increases the likelihood of larval survival. These findings provide evidence of selective feeding throughout larval Sebastidae development, support the notion that maternal investment may positively influence larval survivorship across coastal *Sebastes* species assemblages, and emphasize the importance of taxonomical prey preference in facilitating growth and survival of larval rockfishes.

INTRODUCTION

While survival of marine fishes through the larval stage of development is generally thought to play an important role in driving adult populations, the specific factors that drive larval performance remain largely unresolved (Lasker, 1981; Robert et al., 2014; Hare 2014). Understanding the role of different environmental factors in mediating larval growth, fitness and survival is therefore a critical part of efforts to connect early life history to fisheries recruitment and population dynamics. The capacity of larvae to feed on preferred prey is likely a major factor that influences growth and survival, and has long been hypothesized to mediate year-class strength. In fact, this notion serves as the foundation of the “critical period” and match-mismatch hypotheses, wherein the strength of the spatio-temporal match between larvae and prey is theorized to determine year-class success (Hjort, 1914; Hjort, 1927; Anderson, 1988; Cushing, 1990). The role of preferred prey in determining survival falls within the context of the widely accepted “growth-mortality” hypothesis (Anderson, 1988), which frames larval recruitment variability within the context of surviving starvation and predation through fast growth and early recruitment. As dictated in the “stage duration” and “bigger is better” complementary hypotheses, larvae without access to adequate prey are more likely to exhibit slower growth rates, which may increase the likelihood of starvation, predation and subsequently mortality (Chambers and Leggett, 1987; Houde, 1987). Slower growing larvae remain in smaller size ranges for extended periods of time, and thus remain vulnerable to a wider range of ichthyoplankton predators than faster growing larvae that quickly exit the high-mortality larval stage (Shepherd and Cushing, 1980; Miller et al., 1988). The accompanying “growth-selective predation” hypothesis suggests that slow growing larvae exhibit decreased escape responses

when encountering predators due to the inherent physiological drawbacks of being in poor condition (Houde, 2008). As a consequence, larger, faster growing larvae have a selective advantage over slower growing individuals (Hare & Cowen, 1997). However, conclusive *in situ* evidence supporting these hypotheses in relation to prey abundance is limited (Leggett & Dublois, 1994).

Given the suite of studies that have failed to produce the expected positive relationships between bulk zooplankton biomass and recruitment success (Agostini et al., 2007; Irigoien et al., 2009), it is apparent that more studies investigating larval diet selectivity as a driver of recruitment are needed (Robert et al. 2014) . Those few existing studies that have resolved prey taxonomy generally show positive relationships between preferred prey and parameters of fitness (e.g., Beaugrand et al., 2013; Murphy et al., 2012). Energetic mechanisms behind prey preference manifest in tradeoffs between energetic input gained from consumption and output required for capture. However, some studies have indicated that the prey types most conducive to growth and survival are not necessarily those most strongly selected for by larval fishes (Burns et al., 2021), and that low abundances of preferred prey may result in other prey taxa becoming alternatively selected (Ivlev, 1961). Shifts in zooplankton community composition and timing in response to changing oceanographic conditions may thus induce changes in diet, with negative consequences to growth and fitness (Anderson, 1994). Despite the clear importance of evaluating larval feeding ecology and its impact on recruitment success, a conclusive understanding of the degree to which prey selection influences larval growth and survival remains elusive.

The role of maternal investment has also emerged as a potentially critical contributing factor in determining survival throughout the larval stage. Studies have found size variation in eggs and larvae to be largely of maternal condition (Chambers & Leggett, 1996). Strong positive

relationships between parental size and both larval size and condition have been documented in haddock (*Elanogrammus aeglefinus*) (Hislop, 1988), while correlations between otolith hatch check diameter –a proxy for size-at-birth– and survival duration have been documented in European sardine (*Sardina pilchardus*) (Garrido et al., 2014). Similar relationships have been found between the age of the mother and both growth and median time to starvation in offspring of rockfishes *Sebastes* spp., the latter, in particular, attributed to increased provisioning of endogenous triacylglycerol (TAG) energy stores (Berkeley et al., 2004). However, studies that simultaneously account for the contributions of both maternal investment and larval feeding ecology to growth and survival are limited.

Rockfishes are a genus of ovoviviparous Scorpaeniformes abundant in North Pacific waters and throughout the California Current Ecosystem (CCE). The genus *Sebastes* is diverse in morphology, size, habitat, and behavior, ranging from larger species heavily targeted in commercial and recreational fisheries to smaller counterparts that, while not fisheries targets, are common as bycatch and important prey for higher trophic level predators (Love et al. 2002; Field et al., 2007). Due to the long lifespans, relatively low fecundity, and slow growth of many rockfishes, they are highly vulnerable to overexploitation and stocks of several species have suffered dramatic declines over the past century (Love et al. 1998). Many have been shown to be responsive to conservation efforts including spatial closures (Thompson et al. 2017). In addition, two recent studies provided important insight on conditions that facilitate rockfish recruitment. First, Schroeder et al (2019) found that recruitment for multiple species of rockfishes correlated with the exposure of adults to cold, high oxygen, high nutrient, low salinity Pacific subarctic water (California Current water) in the months prior to recruitment. Second, Fennie et al (submitted) demonstrated that females spawn larger larvae when bathed in Pacific subarctic

water during gestation and that size at birth accurately predicts rates of survival. Here, we build on these findings to evaluate the role of larval prey on condition and survival. Larval rockfishes are known to prey on copepod eggs, nauplii, and copepodites, as well as euphausiid nauplii, diatoms, and protists (Sumida & Moser, 1984; Burns et al, 2021). However, the degree to which they select for these prey items, whether preference involves the active selection of specific prey taxa or passively selecting organisms based on their relative abundances in the surrounding environment, and the predictive power of gut content biomass on their size and growth is unknown.

In this study, we examine larval rockfish feeding ecology and maternal investment with respect to changes in diet and feeding selectivity with ontogeny. We also investigate the impacts of gut content carbon biomass and maternal investment on larval size and recent growth through integrated Bayesian inference. The primary objectives of this study are to (i) describe the diet of *Sebastes* larval assemblages in the contemporary oceanographic conditions of the CCE, (ii) examine ontogenetic trends of niche breadth, prey preference, and active/passive selection, and (iii) determine the degree to which maternal investment and the consumption of different prey taxa contribute to size, growth and survival. The intent of our study is to leverage field, laboratory and statistical techniques to holistically understand how prey selection and parental investment influence larval growth and fitness in temperate coastal regions.

METHODS

Sample Collection

Larval *Sebastes* were collected along seven inshore California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling locations (Line/Station 85-42.9, 86.7-33, 90-30, 90-35, 90-37, 93.3-28, and 93.3-35) in the Southern California Bight during the Winter and early Spring of 2021 (Figure 1). Stations 93.3-28 and 90-30 were sampled in both Winter and Spring, station 86.7-33 was sampled only in Winter, and all other stations were sampled only in Spring. Samples were collected via oblique tows from the upper 30 m of the water column using a 90cm dual bongo (bongo-90) frame with 505 μ m synthetic nylon mesh nets (Kramer et al 1972). The volume filtered was determined using a mechanical flowmeter centered in the mouth of the starboard net. Upon collection, the cod end of the bongo nets were immersed in a saltwater ice slurry for one minute to increase stomach content retention of the captured larvae (larvae can excavate their guts when immediately placed in preservative). Following this, the samples were immediately concentrated using cold, unfiltered seawater through a 300 μ m sieve and fixed in 95% tris-buffered ethanol (EtOH).

To characterize the prey field of each sample station, a second bongo with 202 μ m mesh and 53 μ m mesh nets was deployed shortly after each 505 μ m haul. A second flowmeter was centered in the mouth of the 202 μ m (starboard) side of the frame. The contents of both nets were filtered through sieves, and samples from each net were fixed in 3.7% formalin to ease identification of small zooplankton.

Larval Identification

Rockfish larvae were sorted from the 505 μ m samples under a dissecting microscope, photographed, and identified to either preflexion (after yolk sac absorption and before start of notochord flexion), flexion (start of notochord flexion to notochord tip angle $\sim 45^\circ$) or postflexion (completion of notochord flexion) stage. Following this, standard length (SL) was measured from the tip of the lower jaw to the tip of the notochord in preflexion larvae, and to the base of the notochord in flexion and postflexion larvae.

Because most rockfish larvae are indistinguishable to species based on morphology (Moser 1996), they were genetically identified via Sanger Sequencing as described in Thompson et al. (2016). Briefly, tissue samples were taken from the eye of the larvae, and chelex-based boiling was used to extract genomic DNA from each sample (Hyde et al. 2005). The target genomic region was amplified by polymerase chain reaction (PCR) using the primers GLURF2-5' and CB3RF2-5' (Hyde et al. 2008). Each PCR was conducted in 10 μ l volumes with buffer (67mM Tris-HCl pH 8.8, 16.6mM [NH₄]₂SO₄, 10mM β -mercaptoethanol, 2mM MgCl₂), 800 μ M dNTP, 0.4 μ M of each primer, 0.5mg ml⁻¹ bovine serum albumin, 0.5 units Taq DNA polymerase (New England Biolabs), and 1 μ l of chelex supernatant containing DNA template. The thermal profiles of the PCRs were: denature at 92°C for 2 h and 30 min; followed by 40 cycles of 94°C for 30 min, 55°C for 90 min, 70°C for 90 min; then a final extension of 72°C for 3h. Negative, no template controls were run for each PCR to monitor for possible contamination. PCR products were enzymatically cleaned using ExoSap-IT (Affymetrix). The resultant products were sequenced using the internal primer CBINR3 (5'-ATG AGA ART AGG GGT GGA AGC T-3') and BigDye v.3.1 Dye Terminator chemistry following manufacturer's protocols. The

sequenced products were analyzed using an ABI3730 Genetic Analyzer (Life Technologies). Finally, the sequences were edited and aligned using Sequencher v.4.9 (GeneCodes), aligned with templates from reference adult rockfishes (Hyde & Vetter 2007), and identified by creating Neighbor Joining phylogenetic trees with MEGA v11 (Tamura et al, 2021).

Stomach Content Analysis

The entire digestive tract (both hindgut and foregut) were removed from 170 larvae and dissected under a dissecting microscope. The stomach contents were identified, photographed, and measured to the nearest 0.2 μ m using an eyepiece micrometer. All recovered prey items were identified to the taxonomic class or order level due to the partially digested condition that many were in when recovered from the stomach. Many prey items lacked morphologically distinguishing features such as appendages and urosome spines in copepods, and those that could not be reliably identified to a class level were not included in subsequent analyses. To measure relative carbon (C) biomass contributions of respective prey taxa, carbon biomass weights in μ g C were estimated for each recovered prey item using length-weight conversion factors from existing literature (Table 2) (Menden-Deuer and Lessard, 2000), (Robert et al, 2008), (Shiroza et al, 2021). The total carbon biomass consumed by each larva was used as a proxy for feeding success.

Zooplankton Identification and Enumeration

In situ plankton community samples from the 202 μ m mesh nets were analyzed via ZooScan digital scanning and image analysis (Gorsky et al, 2010). Subsamples were taken for each jar and were split into small (202-999 μ m), large (1000-4999 μ m), and extra large (5000-999999 μ m) sizes using a 1mm and 5mm mesh sieve. Two aliquots of the small size range, one aliquot of the large size range, and one aliquot of the extra large size range were scanned at 2400 dpi resolution (four scans per sample). 29,137 vignettes were classified by a machine learning algorithm using Random Forest classification and regression tree methods, and all images were reexamined manually to correct misidentifications. Ten individuals of each prey taxa identified from the gut contents of larval *Sebastes* spp. from each subsample size at each station were randomly selected and body length (prosomal length for copepodites) and width measured to the nearest 0.001 μ m using ImageJ image processing software.

Due to limitations of the optical resolution of the ZooScan machine for reliably identifying organisms smaller than 200 μ m, *in situ* plankton samples from the 53 μ m mesh nets were identified and enumerated manually under a dissecting microscope. 15ml subsamples were taken from the 53 μ m jars and diluted to 80ml, then 0.5-3ml aliquots were taken depending on the zooplankton concentration of the sample. Taxa counts of each aliquot were extrapolated to the total volume filtered through the corresponding haul to calculate abundance m^3 . Approximately 30 individuals of each commonly consumed prey taxa and approximately 10 individuals of all other taxa from each station were randomly selected and measured to the nearest μ m using an eyepiece micrometer. All plankton identifications in Zooscan and manual microscopy processed samples were made using regional taxonomic literature, with taxa identified to the class or order

level consistent with the taxonomic resolution of the stomach contents. *In situ* zooplankton carbon weights from both were estimated using the same length-weight conversion factors as previously described (Table 2) (Menden-Deuer and Lessard, 2000), (Robert et al, 2008), (Shiroza et al, 2021). Taxon-specific Abundance per m³ and C biomass in µg C per m³ was calculated for the four sample stations in which larval feeding selectivity was calculated, both to compare gut contents to and to gain a sense of spatial and temporal plankton community variation.

Data from the 200 µm (Zooscan) and 53 µm (microscopy) tows were compared to determine size cutoffs based on the respective capture efficiencies of each mesh size net for assessing plankton abundance within different length and width ranges. Size cutoffs were made by comparing the abundances of each taxa and developmental stage at a given length or width range in the 200µm samples to the abundances of the same taxonomic group and size range in the 53µm samples (Table 3). Taxa categories of a given size range with greater abundances in one mesh size than the other were used for subsequent analyses. Two different data sheets were used for respective length and width selectivity measurements, the former with the length cutoffs and the latter with the width cutoffs.

Otolith Analysis

Sagittal otoliths from both the right and left side of a subset of 61 flexion and postflexion larvae were extracted and removed under a dissecting microscope and mounted on a microscope slide. Individuals were selected to represent all seven sample stations. Otoliths were photographed using an oil immersion microscope at 100x magnification and rendered via HeliconFocus v8.1.2. Due to a lack of substantial evidence indicating variation in otolith

microstructure between left and right sagittae, the otolith image with the clearest resolution was selected for further analysis. Otolith microstructure was measured using the RFishBC package in R. Core radius was measured from the center of the otolith outwards to the first visible band, age was measured by the number of daily increments from the first visible band to the outer edge of the otolith, and recent growth (RG) was estimated by the average widths of the three outermost complete daily increments-at-age. Multiple reads were taken and compared with known length-at-age relationships for larval and early juvenile *Sebastes hopkinsi* (Laidig et al., 2008), an abundant SCB rockfish species.

Data Analysis - Diet, Feeding Niche, Prey Preferences

Relative C contributions of prey taxa were calculated for all individual larvae in each growth stage and at each sample station to capture ontogenetic and spatial variability in diet. Dietary indices, taxonomic niche breadth, and feeding selectivity were evaluated using the Index of Relative Importance (%IRI), Levins' standardized niche breadth (\hat{B}_A), and Chesson's selectivity index (α), respectively. Dietary indices and niche breadth were calculated for each larval developmental stage based on the twelve prey taxa most common in the gut contents of larval rockfishes: Calanoida nauplii, Cyclopoida nauplii, other Copepoda Nauplii, Cladocerans (Podonidae), Calanoida copepodites, Cyclopoida copepodites, Poecilostomatoida copepodites, other Copepoda copepodites, Diatoms/Protists, eggs, Euphausiid nauplii and Euphausiid juveniles. For the initial diet composition analyses, 'Other Copepodites' included Harpacticoida copepods and copepods not identifiable to a higher taxonomic resolution. For Chesson's selectivity index, the categories were reduced to the eight most commonly observed prey taxa.

Nauplii unidentified to a higher taxonomic resolution than Copepoda were removed for purposes of higher taxonomic resolution in assessing prey preference. Cladocerans were removed due to insufficient abundances from three of the four stations analyzed for selectivity. Poecilostomaoids were included in the ‘Other Copepodites’ category.

IRI was estimated using the percentage of each prey taxa’s total abundance and C biomass contribution over the total abundance or C biomass of all prey items ($\%C_i$), and the percentage of larvae with non-empty guts that had ingested that prey item ($\%FO_i$). The equation was $IRI_i = \%C_i \times \%FO_i$ and presented as: $\%IRI = IRI_i / \sigma IRI$, where σIRI is the sum of all IRIs from all twelve prey categories i . Levins’ standard niche breadth \hat{B}_A was calculated from the following equation:

$$\hat{B}_A = \frac{\hat{B} - 1}{n - 1}, \quad \hat{B} = \frac{1}{\sum p_i^2}$$

where \hat{B} reflects niche breadth, p_i is the proportion of larvae with a given prey category i , and n is the total number of prey categories observed. High \hat{B}_A values are an indication of a wide taxonomic feeding niche, indicating generalist feeding behavior, while low values reflect a narrow niche and specialist feeding behavior.

Four selectivity calculations were taken to describe prey preference across ontogeny. Selectivity of all individuals from all stations was pooled to gain a sense of general trends in prey preference, selectivity within each sample station was calculated to compare spatial differences in feeding preference, and selectivity within prey size ranges was calculated using logarithmic size intervals, consisting of ten length classes (length midpoint (μm) - 119, 168, 237, 335, 473, 668, 944, 1334, 1884, 2661, corresponding length ranges - 101-141, 142-200, 201-282, 283-400, 401-562, 563-800, 801-1122, 1123-1585, 1586-2239, 2240-3162) and nine width classes (width

midpoint (μm) - 84, 119, 168, 237, 335, 473, 668, corresponding width ranges - 72-100, 101-141, 142-200, 201-282, 283-400, 401-562, 563-800) using measurements from the Zooscan and manual microscopy measurements. Chesson's α -selectivity index was calculated from the following equation, as described in (Chesson, 1978):

$$\alpha_i = \frac{d_i/z_i}{\sum(d_i/z_i)}, \text{ for } i = 1 \dots N$$

where d_i is the abundance of prey type i in the guts, z_i is the abundance of that prey item i in the environment, (d_i/z_i) is the ratio of gut content to *in situ* abundance for all prey categories, and N refers to the number of prey categories i . A threshold of 12.5% ($(1/\text{prey categories } N) * 100$) was estimated as neutral preference for measures of taxa selection, with smaller values indicating negative (weak) selection and larger values indicating positive (strong) selection. For size range categories, a threshold of $(1/\text{prey categories } N_p \times \text{prey size categories } N_s)$ was estimated as neutral preference. α_i values were calculated for each individual larva and averaged by developmental stage. Differences in bulk gut content C biomass, number of prey, and size of prey between developmental stages was calculated via one-way analysis of variance (ANOVA) in R version 4.2.1. Differences in C biomass of consumed prey and selectivity towards prey taxa between growth stages and stations were calculated using permutational multivariate ANOVA in Primer v6.1.7 (Primer, LTD) on a Bray-Curtis similarity matrix with 999 permutations. For comparisons between stations, growth stages were nested within station to assess spatial variation in diet and selectivity for each growth stage. Prey abundances were square root-transformed and prey C biomasses were log-transformed prior to testing. Similarity percentage (SIMPER) analysis was performed to determine prey taxa and stations responsible for driving

observed dissimilarity between groups. For all selectivity and feeding niche calculations, samples from the Winter and Spring of 93.3-28 were pooled due to low larval abundances in the Winter sample and a low average dissimilarity in plankton community abundance between the Winter and Spring tows.

Data Analysis – Influence of Diet and Maternal Investment

Diet and maternal investment data were integrated into Bayesian hierarchical models to explore the relative effects of age, different diet parameters, and maternal investment on size and growth when multiple predictors were combined into the same model. A total of four models were fit, two with standard length and two with recent growth as response (y). For each of the two models per response, a model containing only total C biomass and age as predictors was compared to one containing multiple diet parameters, age, and core radius. Four Hamiltonian Markov chains with 1000 iterations each were used. Due to the data having been standardized, a mean of 0 and standard deviation of 1 were initially included as informative priors. Normally distributed posterior distributions were summarized using central tendencies and variance, in this case mean and standard deviation. The models were fit using the following equations:

Integrated Diet, Maternal Investment, and Age Model:

$$y_i = \text{Normal}(\mu_i, \sigma_i)$$

$$\mu_i = \alpha_{[station]} + \beta_r r_i + \beta_w w_i + \beta_j j_i + \beta_e e_i + \beta_n n_i + \beta_o o_i + \beta_{rj} r_i j_i + \beta_{re} r_i e_i + \beta_{rn} r_i n_i \\ + \beta_{ro} r_i o_i$$

$$\alpha_{[station]} = \text{Normal}(0, \alpha_\sigma)$$

$$\sigma_i = \text{Exp}(1)$$

$$\alpha_\sigma = \text{Exp}(1)$$

Total Carbon Biomass and Age Model:

$$y_i = \text{Normal}(\mu_i, \sigma_i)$$

$$\mu_i = \alpha_{[station]} + \beta_r r_i + \beta_c c_i + \beta_{rc} r_i c_i$$

$$\alpha_{[station]} = \text{Normal}(0, \alpha_\sigma)$$

$$\sigma_i = \text{Exp}(1)$$

$$\alpha_\sigma = \text{Exp}(1)$$

Table 1: parameters used in modeling framework.

| Parameter | Description | Units |
|-----------|--|---------------------|
| y | Standard Length, Recent Growth | mm, m |
| a | Intercept | |
| station | Sample station | Categorical integer |
| r | Age | Days post-extrusion |
| c | Total gut content carbon biomass | $\mu\text{g C}$ |
| w | Otolith core radius, radius from center to extrusion check | μm |
| j | Calanoid copepodite gut content carbon biomass | $\mu\text{g C}$ |
| e | Euphausiid gut content carbon biomass | $\mu\text{g C}$ |
| n | Calanoid and Cyclopoid nauplii gut content carbon biomass | $\mu\text{g C}$ |
| o | All other prey taxa gut content carbon biomass | $\mu\text{g C}$ |

In all models, sample station number was entered as a random effect to account for any spatial differences in environmental conditions, maternal investment, and prey field biomass or community composition. Carbon biomass and age were entered as fixed effects in the total C biomass model, while core radius, Calanoid Copepodite C biomass, Euphausiid C biomass, Calanoid and Cyclopoid Nauplii C biomass, and other prey taxa C biomass were entered as fixed effects in the integrated model. All diet parameters were log-transformed and standardized. Interactions between age and each diet parameter were integrated into the model to account for expected increases in C biomass uptake with age. Interactions between core and age were not included as the degree of maternal investment is not affected by the age of the progeny. The fit of each integrated model was compared to its accompanying single variable model using

Watanabe Akaike Information Criterion (WAIC). Predictive accuracy of the models to the observed data was determined using posterior predictive distributions, and MCMC convergence diagnostics were graphically computed using traceplots. Prior sensitivity analysis was conducted by modifying priors from (0,1) to (0,0.1) and assessing how change in prior affected model convergence, posterior distributions of (y) and each parameter estimate B, and posterior parameter estimates. The modeling framework was coded in the R 'rethinking' package, and all data used for this project is available upon request to the corresponding author.

RESULTS

Rockfish Species, Size, and Spatial Assemblages

170 larval rockfish in intact condition were analyzed for gut content, encompassing twenty (20) different species in a subsample of 121 sequenced individuals that represent a vast range of sizes, morphologies, habitat types, and degrees of fishing pressure (Table 4). The most abundant species were *Sebastes semicinctus* (halfbanded rockfish), *S. hopkinsi* (squarespot rockfish), and *S. saxicola* (stripetail rockfish), all three of which are primarily non-targeted species that are encountered by fishers as bycatch. The species present in the most sample stations were *S. hopkinsi*, *S. simulator* (pinkrose rockfish), *S. jordani* (shortbelly rockfish), and *S. ensifer* (swordspine rockfish), also primarily nontargeted species. Due to the low sample sizes present for many species across the assemblage, we opted to lump all individuals into a single group for analysis (*Sebastes* spp.); that is, we make the simplifying assumption that larval rockfishes are trophically and functionally similar across species. This assumption is supported by past observations of early juvenile rockfishes feeding within the same trophic levels within years, and high overlap in diet between some species in early life (Bosley et al, 2014). In addition, the cohabitation of numerous species of rockfish larvae in the same immediate pelagic environment observed in this study and in Thompson et al, 2016 suggests that larval rockfishes of numerous species are subject to similar degrees of prey availability that govern selection. Further, although annual recruitment can fluctuate by orders of magnitude, recruitment tends to be highly synchronous among species, suggesting that larvae from different species experience similar environmental or maternal conditions (Rlaston et al, 2013; Schroeder et al., 2019). The ontogenetic distribution of the assemblage consisted of 61 preflexion stage (mean SL = 4.61 mm

± 0.77 (standard deviation unless otherwise noted)), 64 flexion stage (mean SL = 6.51 mm ± 1.26), and 45 postflexion stage (mean SL = 9.47 mm ± 1.92) larvae. Observed size ranges between preflexion (3.76-6.59 mm SL), flexion (3.99-9.22 mm SL) and postflexion (6.42-15.42 mm SL) stages exhibited considerable degrees of overlap with one another. While the larvae were selected in an effort to provide uniformity in ontogenetic distributions representative of variability between sample stations, this was constrained by uneven spatial abundances of respective growth stages (Table 5).

Abundance and Biomass of Ambient Plankton Communities

Stations on the same transect lines (Figure 1) tended to be more similar in abundance contributions of different zooplankton taxa (Table 6) (mean dissimilarity within line = 16.32%) than stations sampled on different transects (mean dissimilarity between lines = 21.08%) and on different seasons (mean dissimilarity within seasons = 16.62%, mean dissimilarity between seasons = 22.29%). This trend was concurrent with the dissimilarity trends apparent in plankton community biomass (Table 7), with much larger dissimilarity observed between stations on different transects (mean dissimilarity = 32.23%) than in other comparisons. Station 93.3-28, the only station sampled during both Winter and Spring, had a relatively low average dissimilarity in both abundance (17.40%) and biomass (15.65%).

The most abundant taxa in all stations were diatoms and protists, also accounting for the highest biomass in two of the four stations in which average diatom size was much larger than in the other stations. However, the nets used were not ideal for quantifying these organisms as many are smaller than the mesh diameter or are destroyed. Calanoid copepodites and nauplii

were more abundant than Cyclopoids on transect line 90 and in station 93.3-28 (Winter), with the opposite true in the remaining stations. Euphausiids accounted for the highest carbon biomass per organism. Contributions of Poecilostmatoids such as *Corycaeus* spp., other copepodites (primarily Harpacticoids and copepods unidentified to a higher taxonomic resolution), and Cladocerans to total community abundance and biomass were relatively minor, with the latter taxa only present in station 90-35. The taxa accounting for the greatest dissimilarity in community abundance between Winter and spring tows were diatoms and protists, which were more abundant during the Winter. Other zooplankton taxa present in the original samples but excluded from here due to relative or complete absences in the larval gut contents included larval bivalves, Polychaetes, Pteropods, Dinoflagellates, Appendicularians, Rhizarians, Chaetognatha, Cnidarians, and other larval fishes, primarily Northern Anchovy (*Engraulis mordax*).

Otolith Microstructure, Age in relation to Core

Otoliths were extracted from 30 flexion and 31 postflexion larvae, with an average age of 23.81 days post-extrusion \pm 10.36 SD and an age range of 7-48 days post-extrusion. The average core radius was $15.9\mu\text{m} \pm 4.0$, with a range of 6.81 - 24.4 μm . The mean of the averaged three outer bands' widths was $2.55\mu\text{m} \pm 1.2$, with a range of 0.952 - 0.639 μm . Core radius had a positive, significant relationships with age ($R = 0.54$, $p < 0.001$). The residuals of the linear model were normally distributed. For purposes of graphical comparison, values in Figure 2 were standardized prior to regressions being run.

Larval Diet and Carbon Biomass Contributions

A total of 3,629 prey items were recovered from 170 larvae. Empty guts were present in only 11 individuals, consisting of one flexion larva and 10 preflexion larvae (SL: 3.54-5.68 mm). The average prey size was $0.328 \text{ mm} \pm 0.21$ and the average number of prey items per individual was 25.22 ± 22.63 . There were significant differences in the total number ($df=2$, $F=52.68$, $p<0.001$), size ($df=2$, $F=149.2$, $p<0.001$), and total carbon biomass ($df=2$, $F=205.5$, $p<0.001$) of prey consumed in different stages of ontogeny. Larval gut contents contained prey of increasing size (preflexion= $206.0 \mu\text{m} \pm 92.0$, flexion= $261.1 \mu\text{m} \pm 130.4$, postflexion= $407.1 \text{ mm} \pm 261.0$), quantity (preflexion = 6.10 ± 5.37 , flexion= 22.85 ± 15.55 , postflexion= 39.89 ± 25.45), and carbon biomass (preflexion = $0.162 \mu\text{g} \pm 0.257$, flexion = $0.346 \mu\text{g} \pm 1.69$, postflexion = $1.53 \mu\text{g} \pm 7.76$) as larvae grew, with a 6.9x increase in average number of prey items contained in gut between early preflexion and late postflexion stages.

The three most commonly consumed prey taxa across all stages of larval development were Calanoida nauplii, Cyclopoida nauplii, and Calanoida copepodites, which in total accounted for 82.2% of the number of prey items and 66.3% of the total carbon biomass. Calanoida nauplii were the single most common prey type (36.8%), and Calanoida copepodites comprised the largest portion of gut content carbon biomass (33.5%). The remainder of the diet consisted primarily of other Copepoda copepodites and nauplii, Copepod eggs, Euphausiid nauplii and juveniles, diatoms and protists, and Cladocerans.

Carbon biomass contributions of prey taxa differed significantly between developmental stages ($df=2$, $F=73.14$, $p<0.001$). The degree of dissimilarity between preflexion/flexion (69.10%) and flexion/postflexion (66.85%) larval C biomass content was similar. Preflexion to

flexion shifts were characterized by increased consumption of Calanoid nauplii, which accounted for 17.76% dissimilarity in gut content C biomass between preflexion and flexion larvae. The prevalence of Calanoid copepodites in the diet increased with development, accounting for the greatest abundance of prey in postflexion larvae and the highest proportion of Carbon biomass in both postflexion and flexion larvae (Figure 3a,c). Euphausiids were also in the gut contents of many of the larger larvae, contributing to much of the carbon biomass unaccounted for by Calanoids in postflexion larvae. When taking %IRI dietary indices into account, the relative contributions of Calanoid nauplii and Copepodites to the diet generally became more pronounced in the index while that of Euphausiids diminished. The low contribution of Euphausiids to the %IRI indicates that relatively few larvae fed on Euphausiids, despite the high energy content of these prey (Figure 3b,d).

Carbon biomass contributions of different prey taxa also differed significantly between growth stages compared across stations ($df=15$, $F=3.60$, $p=0.001$). Dissimilarities in C biomass contributions of prey groups between stations was primarily driven by Calanoid copepodite C biomass, on average accounting for 26.19% dissimilarity between stations, and were more pronounced spatially than temporally. Taxa also responsible for C dissimilarities were Calanoid nauplii and copepod eggs. Slightly higher dissimilarities were observed between stations on different transect lines sampled at the same time of year (71.60%) than between stations on the same transect lines sampled at different times of year (67.61%).

Taxonomic Niche Breadth and Prey Preferences

Feeding niche generally narrowed with increased development (Figure 4). While flexion and postflexion larvae fed on a larger total number of prey types than their respective preceding developmental stages (Figure 3a), a larger proportion of their diet consisted of fewer prey taxa than observed earlier in ontogeny. However, the degree to which this occurred was inconsistent spatially and there was no significant difference in \hat{B}_A between sample stations.

Taxonomic preference and feeding selectivity also changed with ontogeny (Figure 5) and in response to prey availability in the surrounding environment. There were significant differences in preference across sample stations (Table 8) ($df=4$, $F=4.32$, $p=0.001$) indicating modulation of selection in response to changing abundances of prey taxa in ambient zooplankton communities. Significant differences in preference between flexion and postflexion larvae were observed in two of the stations (90-37: $p = 0.002$, 93.3-35: $p = 0.001$), but no significant differences between preflexion and flexion larvae were observed in any stations. The general trend in diet was driven by a strong selection towards copepod eggs and nauplii in first feeding larvae, with decreased consumption and selection of these prey types with ontogeny but inclusion of larger prey types such as calanoid copepodites (Table 8). Greater dissimilarity in preference between flexion and postflexion larvae (66.22%) was observed than between preflexion and flexion larvae (52.99%). Selection towards calanoid nauplii was strong across all sample stations and growth stages, while selection towards cyclopoid nauplii was more prevalent in preflexion and flexion larvae. Calanoid Copepodites, the largest contributor to gut content C biomass, became increasingly selected for during ontogeny and were preferred by postflexion larvae. However, strong selection towards Calanoid copepodites in the preflexion stage was

limited to stations 93.3-28 and stations 90-37. Selection towards eggs was strongest in station 93.3-35, with this trend observed in preflexion and postflexion larvae. Consumption of other copepodites also increased with ontogeny, but taxa such as Cyclopoida and Poecilostomatoida remained selected against. Euphausiid nauplii and juveniles went from being absent from the gut contents in first feeding larvae to prevalent in the guts of flexion and postflexion larvae, but nevertheless also remained selected against.

Larvae also exhibited strong preferences towards specific size ranges of their prey, but the degree to which selection was centered around specific length and width ranges differed between growth stages. When selection was calculated for each logarithmic length and width range (Tables 7a and 7b), preflexion larvae generally selected for prey within a narrower range of length midpoints than width midpoints. The opposite was true in flexion and postflexion larvae, with both growth stages exhibiting stronger selection towards specific width classes and weaker selection across a wider range of length midpoints. While the preferred size ranges of prey increased with ontogeny, size ranges within the most strongly selected for prey groups did not dramatically increase as expected. Rather, selection generally followed copepod developmental history, with the strongest selection across different growth stages for given prey groups falling within relatively similar size ranges. Larger larvae began to incorporate larger size ranges in their feeding, but nevertheless displayed considerable overlap in size range of prey with preceding growth stages. Width class selection for all three growth stages was strongest in the 142-200 μ m range, and length class selection was strongest in the 201-282 μ m range. Preference towards cyclopoid nauplii size classes was more constrained by length than width, while the opposite was observed in preference towards size classes of calanoid nauplii and calanoid copepodites. Other pronounced size range increases with ontogeny occurred as the

result of inclusion of different prey groups into the diet of late stage larvae, with postflexion larvae introducing Euphausiid nauplii, Euphausiid juveniles, and other copepodites into their feeding.

Integrated Model Output, Comparison and Fit

The integrated diet and maternal investment mixed effects model predicting standard length (referred to thereafter as mSL1) fit the data better than the model only accounting for total gut content C biomass (referred to thereafter as mSL2) (WAIC mSL1 = 73.1, SE=10.34, pWAIC = 12.8, weight = 0.86; WAIC mSL2 = 76.7, SE=13.84, pWAIC = 9.5, weight = 0.14). The effect sizes reported from mSL1 were consistent with the linear regression analyses, with Calanoid copepodite gut content C biomass biomass (bJ) having the largest effect on standard length (mean = 0.44 ± 0.09 , 89% posterior confidence interval (CI), = 0.31-0.57) (Figure 6). The parameter with the second largest effect size was age (mean = 0.24 ± 0.08 , 89% CI = 0.10-0.37), followed by core radius (mean = 0.15 ± 0.07 , 89% CI = 0.05-0.25). Naupliar biomass was found to have a small effect on length (mean = -0.05 ± 0.06 , 89% CI = -0.14-0.05), as well as other prey C biomass and interactions between each diet parameter and age. In mSL2 both total gut content C biomass (mean = 0.59 ± 0.10 , 89% CI = 0.44-0.74) and age (mean = 0.38 ± 0.09 , 89% CI = 0.24-0.52) were found to have large positive effect sizes on standard length, with minimal influence of the interaction between the two. Effect sizes of random groupings did not follow a clear trend and there was low strength of evidence for sampling location having a large effect in either model, with the most pronounced effect sizes observed in a[3] and a[6], stations 93.3-35 and 93.3-28 (Spring), respectively. A negative relationship with length was associated with both

stations. Relatively high uncertainty was present in the random effect groups and in Euphausiid gut content C biomass.

For the models predicting recent growth, the integrated diet and maternal model (mRG1) also fit the data better than its equivalent only accounting for total C biomass (mRG2) (WAIC mRG1 = 151.2, SE=12.09, pWAIC = 12.5, weight = 0.99; WAIC mRG2 = 159.7, SE=14.13, pWAIC = 6.5, weight = 0.01). Effect sizes for mRG1 were also fairly consistent with those of the linear regression models, with additional parameter inclusions adding new information to the relationships present between diet and size (Figure 7). Calanoid copepodite gut content C biomass also produced the strongest effect on recent growth of larvae (mean = 0.73 ± 0.17 , 89% CI = 0.44-1.0), as well as the interactive effect between Euphausiid gut content C biomass and age (mean = 0.62 ± 0.18 , 89% CI = 0.33-0.90). Strong negative effect sizes with high uncertainty were observed with Euphausiid gut content C biomass when treated independently from age (mean = -0.73 ± 0.33 , 89% CI = -1.24 - (-0.20)), as well as the interaction between Calanoid copepodite gut content C biomass and age (mean = -0.60 ± 0.18 , 89% CI = 0.33-0.90). Effect sizes of random effects did not follow a clear trend in either recent growth model. The most pronounced effects of sample station in mRG1 were a positive effect on recent growth in a[1], station 90-35 and a negative effect in a[6] 93.3-28 (spring), while variation between stations in mRG2 was less clearly evident.

Counterfactual plots were used to visualize the age-dependent effects of Euphausiid gut content biomass on recent growth described by these interactions (Figure 9). At an age of (-)1.96 (mean standardized age - 2SD) representative of younger larvae in the subsample, the relationship between Euphausiid biomass and growth was strongly negative. At an age of 1.96 (mean standard age + 2SD), the relationship between Euphausiid biomass and growth was

positive. When examining the counterfactual effect of Calanoid copepodite gut content biomass on recent growth, the opposite trend was apparent. The relationship between copepodite biomass and recent growth was positive in younger fish, and negative in older fish. In contrast, the counterfactual effects of euphausiid and calanoid biomass on standard length displayed similar trends in both younger and older larvae (Figure 10).

Model fit was validated using posterior predictive checks for each of the four models, and the models were observed to fit the data well (Figure 8). Convergence diagnostics indicated good mixing of Markov chains. Prior sensitivity analyses yielded different results between the length models mSL1, mSL2 and recent growth models mRG1, mRG2. Both models predicting standard length exhibited high robustness with respect to model convergence, posterior distributions, and posterior estimates. Models predicting recent growth were moderately sensitive to changes in prior. Convergence was largely unaffected, but posterior distributions shifted and posterior estimate effect sizes were compressed when prior standard deviations were regularized. This was particularly evident when examining the impact of interactive effects in mRG1, namely those that produced the largest effect sizes in the posterior estimates.

DISCUSSION

Larval growth is governed by a confluence of abiotic and biotic factors that interact with one another to shape the likelihood of an individual successfully recruiting to the adult population. Variability in growth has been long hypothesized to heavily influence larval survival and fluctuations in year-class strength, with slower-growing larvae generally believed to be more vulnerable to mortality in early life (Chambers and Legget, 1987; Houde; 1987; Miller et al., 1988; Hare & Cowen, 1997; Houde, 2008). While many studies have previously documented the diet composition of larval stages of fishes, the degree to which larval fitness is shaped by the consumption of preferred prey has not been well studied (Robert et al, 2014). Thus, improving knowledge of how larval feeding ecology influences ontogeny and growth in wild fishes is essential for gaining a more mechanistic understanding of the ecological drivers of the “critical period” hypothesized over a century ago (Hjort, 1914). In similar fashion, while maternal investment has emerged as a common driver of variation in size-at-birth and size-at-age in larvae (Garrido et al., 2014; Fennie et al., in review), studies investigating the joint impacts of maternal investment and feeding ecology on larval ontogeny and fitness are limited. In this study, larval rockfishes were observed to shift diet and selection towards specific prey taxa with ontogeny and exhibit active selection in response to prey availability in the surrounding environment. Models that integrated maternal investment and gut content carbon biomass contributions of individual prey taxa were observed to better predict size and growth distributions than total gut content biomass, with certain prey types generating larger effect sizes than others. Lastly, the degree to which different prey taxa affected recent growth differed between age classes of larvae. Here, we discuss these results in the context of zooplankton ecology, regional oceanography, and previous

early life history studies, with particular attention given to the challenges associated with interpreting causal mechanisms responsible for governing diet, size and growth in the larval stage.

Ontogenetic Shifts in Diet and Feeding Selectivity

Larval rockfishes were observed to shift their diet in response to ontogeny (Figure 3), with significant differences in the size of prey, number of prey, C biomass contributions of prey, and species diversity of prey taxa consumed between growth stages. These results are consistent with previous studies that observed strong ontogenetic shifts in larval feeding (Murphy et al., 2012; Malca et al, 2022; Shiroza et al, 2022; Llopiz, 2013). While feeding selectivity also changed with ontogeny, more pronounced changes in preference were observed between flexion and postflexion larvae. This observation suggests that increased changes in selection occur late in larval ontogeny, but it remains uncertain if larval fishes truly become more selective as they grow or if individuals that feed selectively early in ontogeny are more likely to survive to late larval stages. While older, larger larvae have better swimming ability than younger, smaller larvae and subsequently have better foraging capabilities (Fisher & Bellwood, 2005; Majoris et al., 2019), variability in survival during the larval stage has also been attributed to selective mortality facilitated by unequal distributions of phenotypic traits important for survival (Johnson et al., 2014). Prey selection early in ontogeny may dictate the proportion of larvae that survive to late larval stages, with observed feeding niche and selectivity trends in older larvae potentially being driven by the survival of individuals that had exhibited stronger selection for certain prey taxa earlier in life. However, due to insufficient data in this study to support the latter paradigm,

we make the assumption that larval selection in our sample is plastic and older larvae experience greater changes in selection. Ontogenetic shifts in prey type remained within a narrower range of widths (Table 10) than lengths (Table 9), indicating that prey width may be a greater limiting factor in selection than length. Selection towards developmental stages of copepod taxa remained within similar width ranges across ontogeny. This may be a function of esophagus width, which was not analyzed in this study but may influence size ranges of consumed prey and play a greater role in limiting consumption than mouth gape (Shiroza et al, 2021). Size ranges of prey in guts might also be reflective of *in situ* abundances of different size ranges within copepod development, with larvae selecting for size ranges found in the highest quantities in their environment.

Prey Availability Regulates Feeding Selectivity

Rather than indiscriminately feeding on whatever was available in their environment, larval rockfish diet was centered around the selective consumption of various life stages of copepods, particularly Calanoids. While larvae of all growth stages preyed upon and selected for Cyclopoid nauplii to varying degrees, consumption and selection for copepodites was primarily centered around Calanoids. Calanoids of various life stages have been documented as a major food source of some *Sebastes* species (Sumida & Moser, 1984; Nagasawa & Domon, 1997; Swalethorp et al, 2015), but evidence of selection towards this prey type within *Sebastes* has been limited to studies of Atlantic redfish (Anderson 1994). Calanoids are known to be preferred by the larvae of numerous species from other families (Govoni et al, 1983; Llopiz, 2013; Robert et al, 2014), with periods of low calanoid density resulting in larvae shifting to other prey taxa

believed to be less conducive for survival and strong recruitment (Ivlev, 1961; Paradis et al., 2012). Selection towards Calanoids is likely driven by the energetic tradeoff between energy gained by consumption and energy expended for capture. Abundance of prey facilitates increased encounter rates by predators, and Calanoids are characteristically highly abundant in temperate ocean regions worldwide (Kozak et al, 2014). Historical species compositions of Calanoid populations have remained stable in the region throughout 60-year CalCOFI survey periods (Rebstock, 2001). Their stable abundance is attributed to their robustness to changing oceanographic regimes, with *C. pacificus* in particular observed to be tolerant to warm water regimes such as the recent marine heatwaves in the SCB (Ashlock et al., 2021). While Calanoid populations have fluctuated in response to El Niño events, they have also exhibited rapid recovery rates and high resilience to such perturbations (Rebstock, 2002; Lilly & Ohman, 2018).

The spatial prey abundance data collected in this study indicates that Calanoid abundance and biomass may vary on fine spatial scales (Tables 6 and 7). This, coupled with known seasonal shifts in Calanoid abundance (Landry et al., 1994) may result in larvae needing to shift to other prey taxa in order to survive. Indeed, postflexion larvae were observed selecting strongly for Euphausiids and copepod eggs in station 93.3-35 (Table 8), a sample station which both had relatively low abundances of Calanoid copepodites and postflexion larvae. Changes in selection in response to changes in Calanoid availability have been reported for *Sebastes* in the North Atlantic, with poor larval condition and delayed metamorphosis associated with increased consumption of *Oithona* spp. Cyclopoids (Anderson, 1994). Timing and intensity of Spring phytoplankton blooms are also critical in shaping larval survival, forming a core supporting basis for the “match-mismatch” hypothesis that entails a need for larval development to coincide with prey availability (Cushing, 1969). Timing of prey availability and small-scale spatial variability

may subsequently explain, to some degree, how interannual variability in recruitment strength may be linked to diet, despite the relative stability of Calanoid copepod populations in the California Current Ecosystem.

Active Selection and Proposed Ecological Mechanisms

Significant variation in selection between prey groups across sample stations indicates active selection occurring in larval rockfishes. Active selection indicates changes being made by larvae in response to shifting prey group proportions in the surrounding environment (Shiroza et al, 2022). If selection were passive, selection would have remained constant across all sample stations irrespective of planktonic community composition. Larvae were observed to select for calanoids even at sample stations with higher abundances of other prey, including similar sized copepod species such as Cyclopoids. While the fitness benefits of active selection remain unclear, it is likely a potential function of some energetically favorable outcome associated with pursuing a particular prey type. (Swalethorp et al, in review). Indeed, Swalethorp et al found that northern anchovy *Engraulis mordax* populations boomed when larvae consumed energetically efficient prey and busted when the prey base shifted to species less conducive to energy transfer. Calanoids are likely energetically favorable due to the confluence of their aforementioned abundance and relative population stability (Rebstock et al., 2012), high energy content (Paradis et al., 2012), and availability in a wide variety of size ranges from small eggs to nauplii to copepodites. While copepod eggs were not identified to the Calanoid level due to difficulties in accurately identifying copepod eggs through morphological characteristics (Makino et al., 2013), it is likely that a large percentage of identified eggs were Calanoids due to known abundances of

later Calanoid developmental stages in the gut contents and *in situ* samples. Cyclopoids also generally carry their egg sacs (Kiørboe & Sabatini, 1994), whereas Calanoids are the only major order of Copepoda known to be free spawners (Webb & Weaver, 1998). Individual, free drifting eggs are thus more likely to be Calanoids.

Potential explanatory mechanisms for other prey taxa being selected differently than Calanoid nauplii and Copepodites draw upon physiological, ecological, and behavioral characteristics. Euphausiids became selected for in late developmental stages and are known prey of early juveniles and even the adults of species such as *Sebastes jordani*, but were largely avoided by early larvae and preyed upon in lower quantities by older larvae (Chess et al., 1988; Bosley et al., 2014). While more energy rich than copepods and potentially a good food source if acquired (Bachiller et al., 2018), Euphausiids generally hatch at larger sizes and fall outside of the length and width ranges most commonly selected for by rockfish larvae across ontogeny, particularly in early developmental stages (Tables 9 & 10). Euphausiids were also less abundant than copepods in all stations in which they were encountered and are also known to have far patchier distributions closely linked to upwelling events (Lilly & Ohman, 2021). Diatoms and protists are highly abundant compared to other plankton taxa (Table 6) and through sheer abundance account for a high biomass comparable or exceeding that of other trophic levels (Table 7), but are not particularly energy rich on an individual level due to their small size and are subsequently unlikely to be energetically favorable for larger larvae.

Similarly sized copepod taxa such as *Oithona* spp. Cyclopoids, Poecilostomatoids, and Harpacticoids were generally selected against. Cyclopoid nauplii were strongly selected for in naupliar stages, but largely avoided in copepodite stages. Mechanisms potentially responsible for copepodites such as Cyclopoids and Harpacticoids being relatively uncommon in larval gut

contents may not only involve the lower relative energy content of these taxa (Bachiller et al., 2018), but anatomical and behavioral characteristics that may make them more difficult to handle as prey. This may be in part due to their decreased motility, as Cyclopoids are primarily raptorial feeders that experience long periods of inactivity between strikes when compared to the highly motile suspension feeding often exhibited by Calanoids (Paffenhöfer et al, 1982; Williams & Muxagata, 2006). While counterintuitive, studies have suggested that larval strike rates may be triggered by more motile prey, potentially due to more active prey movement facilitating increased visibility in turbid conditions and potentially increasing encounter rates (Sullivan et al., 1983; Buskey et al., 1993). Harpacticoid copepodites such as the abundant *Microsetella norvegicus* were largely absent from the gut contents despite being among the largest contributors to the *in situ* “Other Copepodites” category. Harpacticoids not only have long spines extending from their urosomes that may deter predators, but are characteristically particle-associated and may also be more difficult for larval fishes to detect (Koski et al., 2005). While these characteristics of different taxa may be partially responsible for certain taxa being preferred over others in the larval stage, more research is needed to solidify understanding of the explanatory mechanisms driving feeding and selectivity in larval fishes.

Ecological and Maternal Drivers of Fitness and Growth

Analysis of diet and maternal investment yielded results that may solidify understanding of the factors that influence variability in larval size and growth. Different prey items were associated with different fitness responses. Calanoid copepodite gut content C biomass consistently displayed the largest positive effect size in the standard length and recent growth

multilevel models accounting for specificity in diet parameters (mSL1, mRG1) (Figure 6,7), suggesting that Calanoid copepodite consumption may drive relationships between larval diet and fitness. Both integrated models that included diet specificity predicted the data better than either model accounting only for total C biomass and age, supporting the notion that accounting for taxonomic prey preferences rather than bulk prey biomass may be essential when predicting the effects of diet on size, growth, and subsequently recruitment (Mayer & Wahl, 1997; Castonguay, 2008; Malca et al, 2022). The additional observation that Calanoid copepodite C biomass and gut content C biomass had larger positive relationships with standard length than age was unexpected, supporting the notion that larval size is closely linked to food intake, and suggesting that feeding capacity may influence observed variability in size at age in larval fishes. However, age validation in larval rockfishes is limited (Laidig et al, 2008) and variation in size-at-hatch and growth documented in larval fishes may be responsible for the observed variation in length-at-age in our sample (Garrido et al, 2014). This is particularly relevant when considering the diverse species assemblage present in this study. However, the strong positive effect of Calanoid biomass in turn suggests that Calanoid consumption may predict size and growth more effectively than age across *Sebastes* spp. assemblages with interspecific variation in size-at-age and growth rates.

The positive correlation between core and age (Figure 2) suggests that maternal investment increases survivorship, as individuals with larger cores survive to later ages. These results are consistent with trends observed in recent studies, in which core size was positively correlated with age, size, and condition in fishes with very different adult life history traits (Garrido et al., 2015; Fennie et al., in review; Robidas et al., 2022). Core size may subsequently act as a driver of selective mortality in larval rockfishes. Variability in maternal investment is

generally attributed to being the result of parental condition, with numerous studies showing that older, larger females produce better quality offspring more resistant to starvation (Berkeley et al., 2004, Sogard et al., 2008, Rodgveller et al., 2012). Larger adults are also more abundant in locations far from fishing ports, in areas with minimal fishing pressure, and in rockfish conservations areas closed to fishing (Bellquist & Semmens, 2016; Keller et al., 2019). More recently, maternal investment has been observed to also be heavily influenced by oceanographic conditions experienced by the parents, with exposure to oxygen and nutrient-rich pacific upper subarctic water (PUSW) resulting in offspring with larger core widths (Fennie et al., in review). Effects of maternal investment from non targeted species have been observed to be more pronounced further from fishing ports, and the increased transport of PUSW to offshore banks in the CCE may suggest that oceanographic conditions play a likely role in facilitating improved maternal condition.

Larger larvae with bigger cores may be able to successfully overcome hydrodynamic feeding constraints imposed by low Reynolds' Numbers (China & Holzman, 2014), and observed increases in larval size attributed to maternal investment may provide a selective advantage both post-extrusion and throughout the larval stage by increasing prey capture efficiency. The high nutrient content of PUSW positively associated with increased maternal investment also supports higher zooplankton biomass and more energy-rich zooplankton, potentially facilitating improved feeding conditions for larvae that also coincide with regions of better parental condition (Chelton et al., 1982; Miller et al., 2017). In the multilevel models, while model support was higher for the integrated models containing core measurements than models that excluded them, the magnitude of core radius' positive relationship with standard length was found to be smaller than that of Calanoid copepodite gut content C biomass, total C

biomass, and age in the standard length models. No discernible positive effect of core radius was present when predicting recent growth in either the regressions or multilevel model. This suggests that maternal provisioning may be a less reliable predictor of size than diet, and that the effects of maternal provisioning are not directly manifested in recent growth rates in late stage larvae. As a result, its influence on survivorship may be more pronounced in younger larvae. Prior sensitivity analyses indicated that the models predicting recent growth were more sensitive to prior specification than those predicting standard length, indicating that prior information may be a critical component of predicting recent growth in larval fishes in future studies.

Diet consistently displayed stronger effect sizes on standard length than maternal investment, but examining how diet impacts length is difficult in wild-caught fishes due to difficulties in evaluating causal influences of either parameter on the other. While maternal investment is unaffected by events that occur post-extrusion, reconciling causal pathways between diet and size is more challenging. Diet affects size by facilitating growth, but larger fish are also able to consume more food due to increased stomach volume and improved foraging capabilities (Pirhonen et al., 2019). We attempted to determine the degree to which expected increases in food uptake by older fish accounted for observed responses by accounting for interactions between each diet parameter and age in multilevel models. The examined relationships between diet and size were found to generally be robust to this measure implemented to reduce and identify influences of age, with multilevel model interactions between diet and age generally having minimal effect sizes on standard length.

Interactive effects played a greater role in determining outcomes of recent growth models mRG1 and mRG2 than standard length models mSL1 and mSL2, which may shed light on how consumption of different prey types impacts growth at different points in larval development and

strengthens the case for selectivity shaping larval survival. The strong negative effect of euphausiid gut content C biomass on recent growth but large positive effect of its interaction with age suggests that euphausiid consumption is more advantageous for growth in older postflexion larvae, while the opposite effect observed in the interaction between Calanoid gut content C biomass and age suggests that increased consumption of Calanoids is more favorable for growth in younger larvae (Figure 9). In contrast, the effects of these diet parameters on standard length were largely independent of age (Figure 10), indicating that relationships observed between these diet parameters and length is unlikely to be driven by larvae within a particular age class. Younger larvae in the subsample modeled were flexion stage larvae, the stage observed to begin feeding heavily on copepodites compared to first-feeding individuals. These results support the notion that feeding upon Calanoid copepodites earlier in life may be advantageous for larval survival. Feeding on Euphausiids earlier in life may be energetically costly for younger larvae despite their high energy content, potentially due to the energy output required to acquire larger, less abundant Euphausiids. However, feeding on the most energy-rich prey in their environment may provide an energetic benefit to older, larger larvae able to more effectively capture larger prey (Rønnestad et al, 2013; Leech et al, 2021).

The strength of evidence suggesting that specific prey items were better predictors of size and growth than others followed a trend similar to that recently observed in atlantic redfish (Burns et al., 2021), in which consumption of the dominant and preferred prey, in this case *C. finmarchicus* eggs, had a weaker relationship with recent growth than naupliar stages of the same copepod species. The results of this study differ in that Calanoid copepodites were the prey group most strongly associated with parameters indicative of larval success, while naupliar Copepods were associated with no significant response. A key difference between the rockfish

assemblage used in this study and Burns et al (2021) was the age range of the larvae analyzed, which encompassed much older larvae in this study (7-48 days vs. 1-19 days). The shift towards copepodites and later euphausiids being positively associated with length and recent growth in different phases of larval development indicates that the effects of prey composition on size and growth modulate throughout the larval stage.

Based on the positive relationships observed between certain diet parameters and both length and growth despite the measures implemented to reduce and identify age bias, we argue that there is evidence for standard length and recent growth being impacted by gut content biomass in our sample. Although size at a given point in time is unlikely to be the result of growth induced by gut content biomass at that same moment in time, gut content biomass in larval fishes may be reflective of recent feeding conditions experienced over a span of days or even weeks. This notion is strengthened by the known sensitivity of larval fishes to food-poor conditions (Ivlev, 1961; Rice et al., 1987; Shan et al, 2008), with rapid starvation occurring in periods as short as several days or less without food (Yin & Blaxter, 1987; Garrido et al, 2015). A lengthy body of evidence also indicates that larval dispersal occurs in conjunction with other plankton community inhabitants of the surrounding water parcel in response to physical features such as ocean currents and eddies (Govoni et al., 2010; Gerard et al., 2022), suggesting that successful larvae may have existed in the same prey field throughout the early weeks of their lives. While the long-held paradigm describes larval dispersal as passive and their ability to swim horizontally against ocean currents limited (Scheltema, 1971), recent studies have provided increased evidence suggesting the ability for larvae to exhibit some degree of at least active horizontal dispersal (Paris & Cowen, 2004; Fisher et al., 2005), although the ecological mechanisms driving this and the degree to which it is either influenced by or impacts foraging

ability and prey encounter rates remain largely unresolved (Leis, 2006; Leis, 2007). The strong relationships found between diet parameters –namely consumption of Calanoid copepodites in younger larvae– and recent growth solidify the notion that gut content biomass may be reflective of foraging patterns over longer time scales than the period of time in which the gut contents were accumulated. This is supported by evidence suggesting that larval growth rates at a given moment in time are influenced by growth rates earlier in life, which may be tied to feeding success (Tanaka et al, 2010). Increased otolith increment width coinciding with periods of increased predation on preferred prey taxa has also been observed in other species of larvae (Malca et al., 2022). Examining the stations responsible for the greatest random effects variance in the recent growth data provides further evidence of preferred prey availability in the surrounding environment being favorable for recent growth and survival, as the station grouping with the most pronounced positive effect size on growth (90-35) was also the station with the highest Calanoid copepodite and Euphausiid gut content and *in situ* abundance and biomass, as well as the station with the highest postflexion larvae abundance (Tables 5a and 5b). The stations with the largest negative effect sizes (stations 93.3-35 and 93.3-28) had much lower biomasses and abundances of these prey types and lower numbers of postflexion larvae. However, a larger time series of data describing spatial changes in diet, larval abundance, and plankton community abundance and composition is needed to strengthen evidence for these observations.

Conclusion and Future Directions

In the present study, the feeding habits of developing rockfish larvae were investigated at sample stations throughout the nearshore SCB. Particular attention was given to examining

ontogenetic shifts in diet and selection, the effects of prey availability and community composition on feeding, and how diet and maternal investment contributed to responses of size and recent growth when examined both as singular units and in direct comparison with one another. The observations that larval rockfishes actively select for specific prey taxa in relation to changes in ontogeny, that larvae modulate their feeding and selection in response to prey availability in the surrounding environment, that preferred prey consumption's positive relationships with size and growth is driven by specific taxa selected for in late stage larvae, that Calanoid copepodite gut content C biomass is more strongly correlated with standard length and recent growth than C biomass of other prey types, age, and core size, and that different prey taxa produce varying growth responses in different stages of larval development provide new insights into the complex mechanisms that govern larval growth and survival. Future studies should center around solidifying causal relationships between diet and size/growth in wild caught larvae to overcome challenges in interpreting how diet affects size. Evaluating species-specific variation in diet is also critical to determine the degree to which diet and preference are regulated by species, and if different rockfish species are affected differently by environmental factors that alter plankton community composition (Bosley et al., 2014). Larger sample sizes of different *Sebastes* spp. are critical to allow for direct comparisons of diet and selectivity between species. It is also important to examine how ecological drivers of diet and maternal investment change in response to oceanographic regime shifts, particularly with regard to how larval success is affected in a warming ocean and how recent patterns of recruitment have confounded past understanding of how species fare in response to such changes (Jacox et al, 2016; Thompson et al, 2022). Given the increasingly recognized role of southward PUSW transport in facilitating enhanced maternal provisioning and potentially favorable feeding conditions, comparisons of

inshore and offshore *Sebastes* spp. larval assemblages may also be valuable (Schroeder et al., 2019; Fennie et al, in review).

Future studies should also improve the mechanistic understanding of why certain prey taxa are selected for over others. A higher taxonomic resolution of prey taxa is also needed in future feeding studies, in order to assess which species of prey account for the greatest contributions to diet. Ecosystems such as the California Current Ecosystem with variable within-order copepod diversity make species-level identifications challenging, particularly when examining copepod nauplii, which can be extremely difficult to morphologically identify to a species level in plankton communities that experience levels of high diversity (Hernandez-Trujillo & Suarez-Morales, 2000; Kiesling et al., 2002). Prey taxa are also frequently recovered from gut contents in partially or completely digested states that confound species-level identifications (Aguilar et al., 2016). Genetic techniques such as metabarcoding and environmental DNA bear great potential to not only expedite sampling procedures in stomach content analyses, but to overcome limitations of morphological examinations (Snider et al., 2021; Satterthwaite et al. 2023). Metabarcoding stomach contents serves as a means to overcome sampling bias within and between studies, and improve identification of prey items with either few morphological distinguishing characteristics from kin or those recovered from stomachs in degraded states (Mychek-Londer et al., 2020). Utilization of novel methods to improve sampling strength and confidence of prey identification will help subsequently solidify relationships between prey abundance and larval condition by more accurately honing in on particular species that are preferred, improving the collective understanding of how diet and selectivity influence recruitment success.

FIGURES AND TABLES

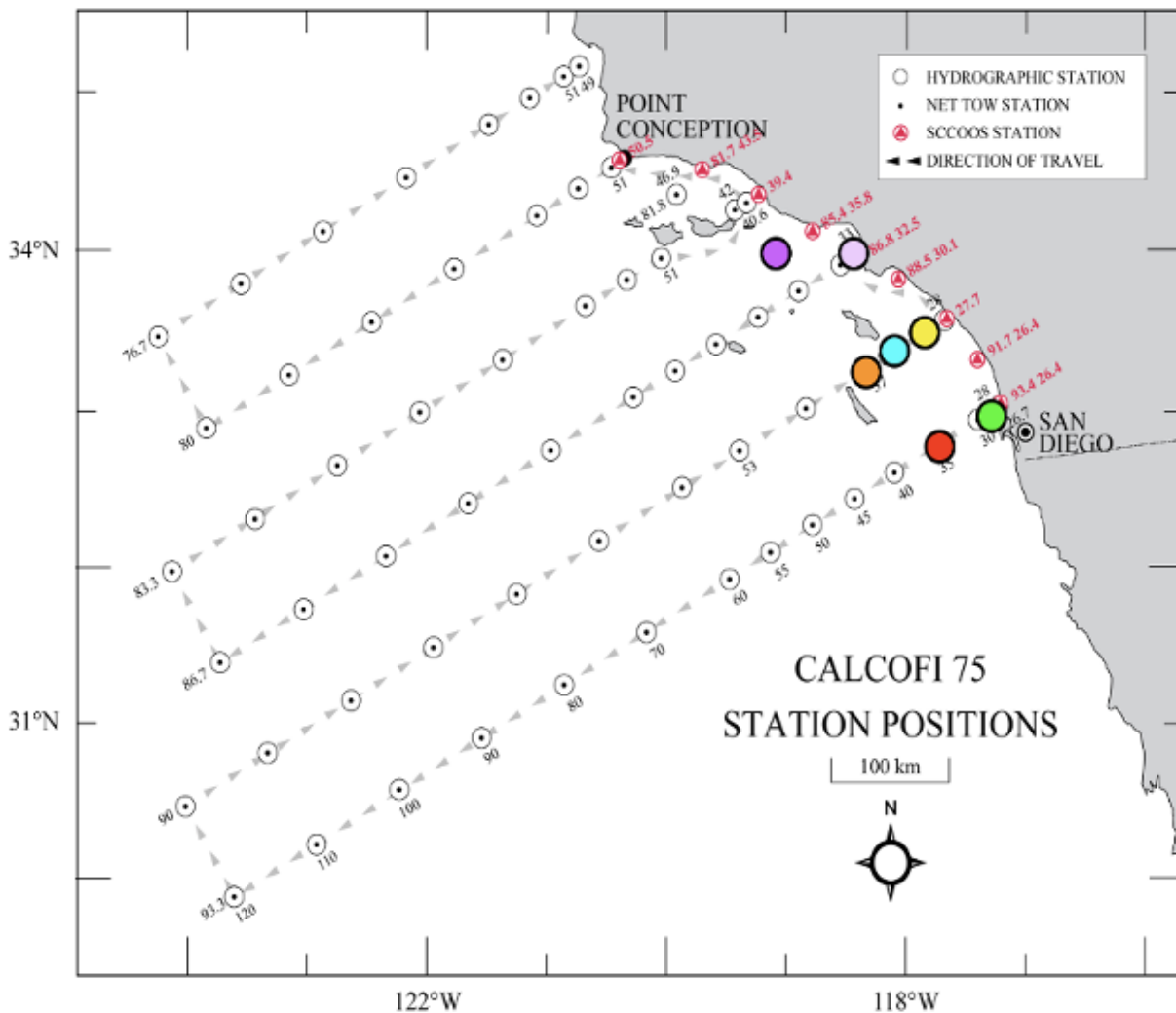


Figure 1: Schematic of CalCOFI transects and sample stations of ichthyoplankton and prey field collection in the SCB.

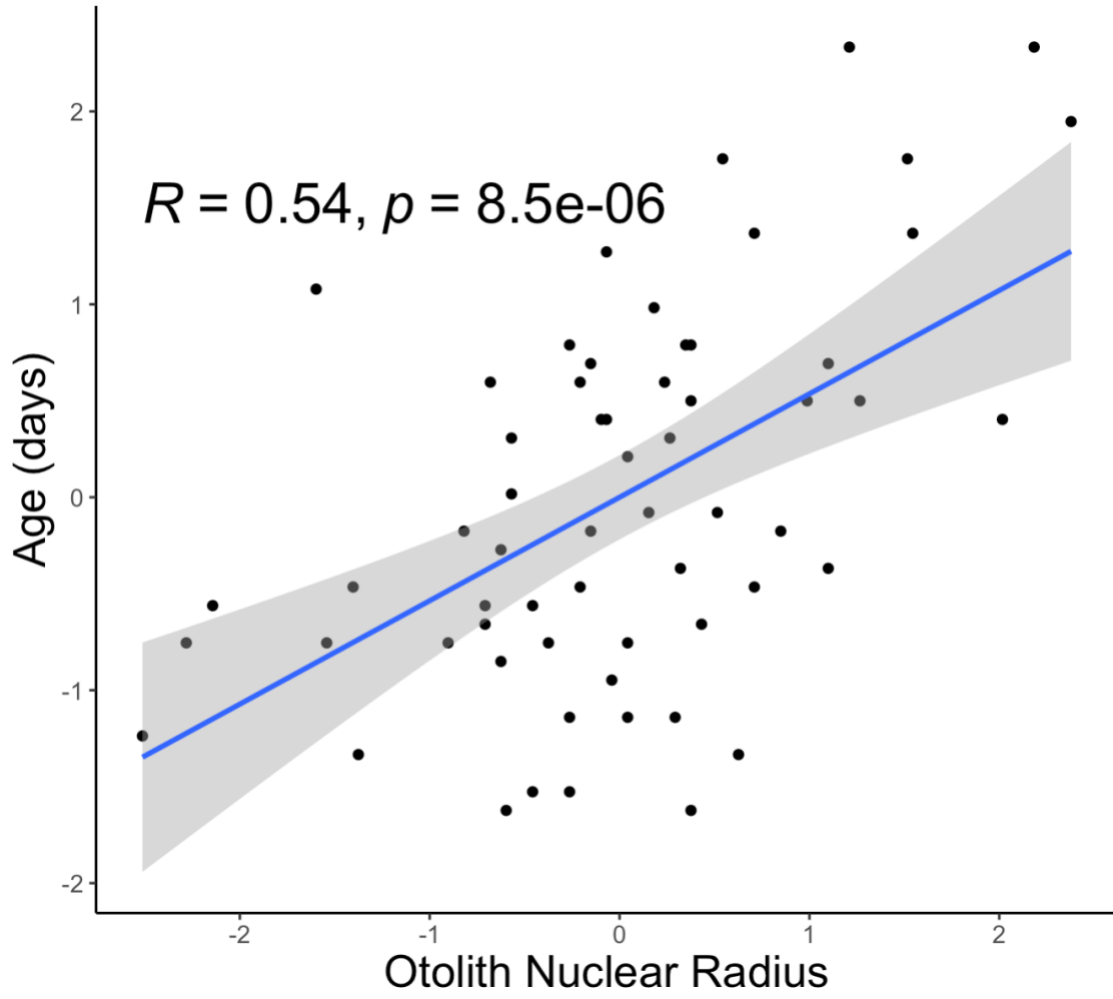


Figure 2: Standardized core width plotted against age (days).

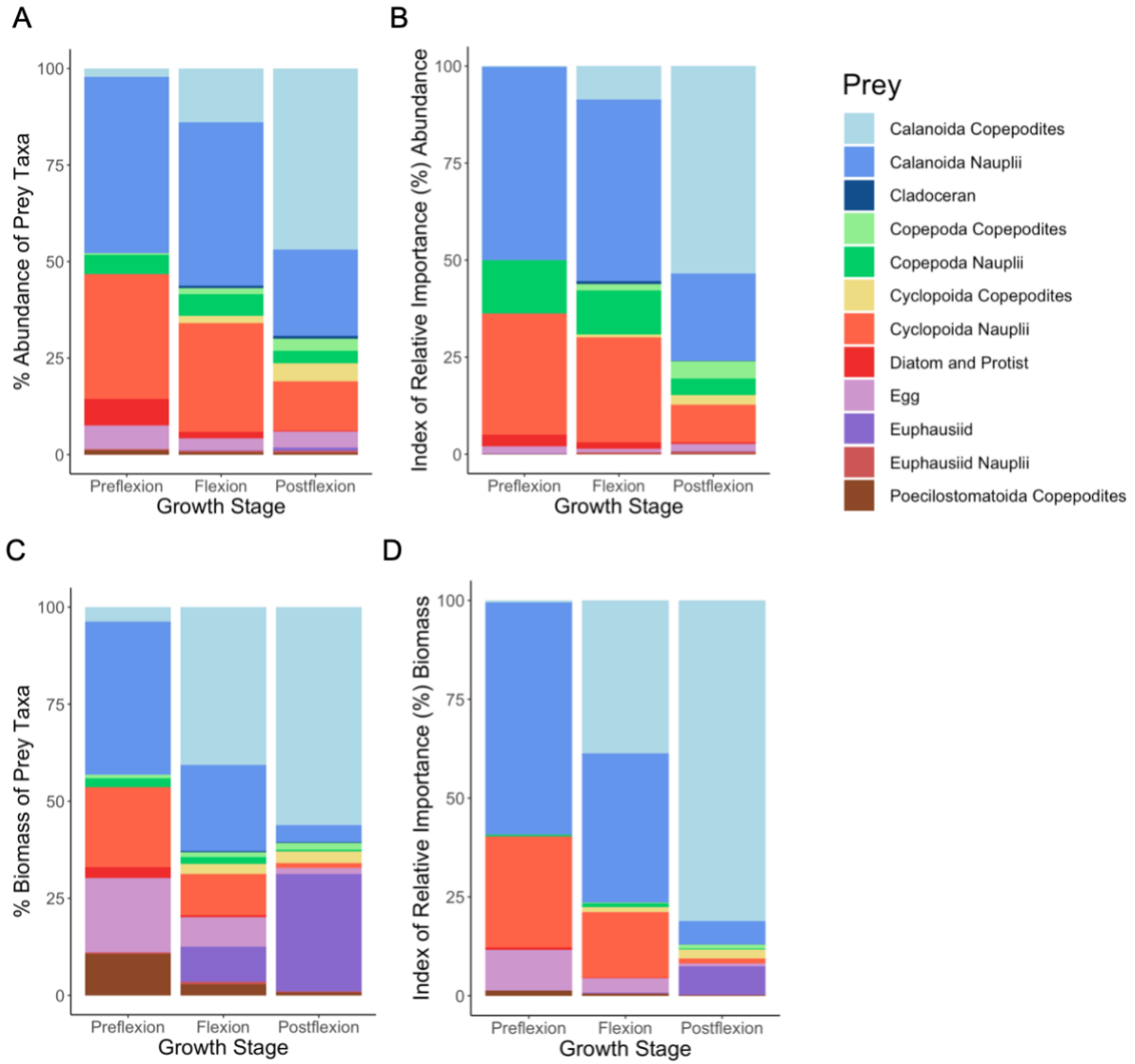


Figure 3: Proportions and %IRI of the 12 most commonly consumed prey taxa by abundance within the gut contents (A, B) and gut content carbon biomass (C, D).

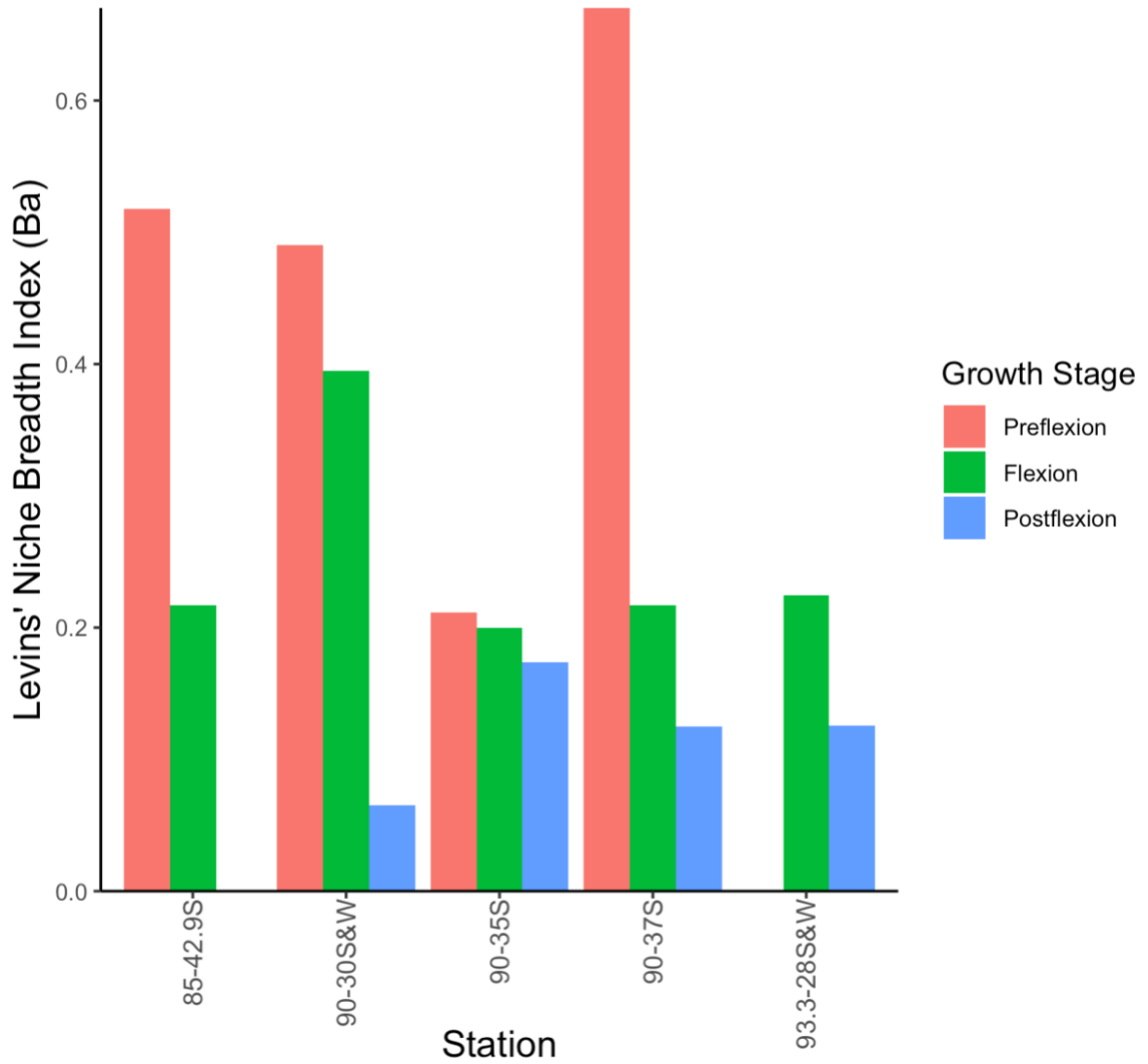


Figure 4: Levins' standardized niche breadth (Ba) illustrating changes in feeding niche between developmental stages across five sample stations. Growth stages of a particular sample stage with $n < 3$ were excluded.

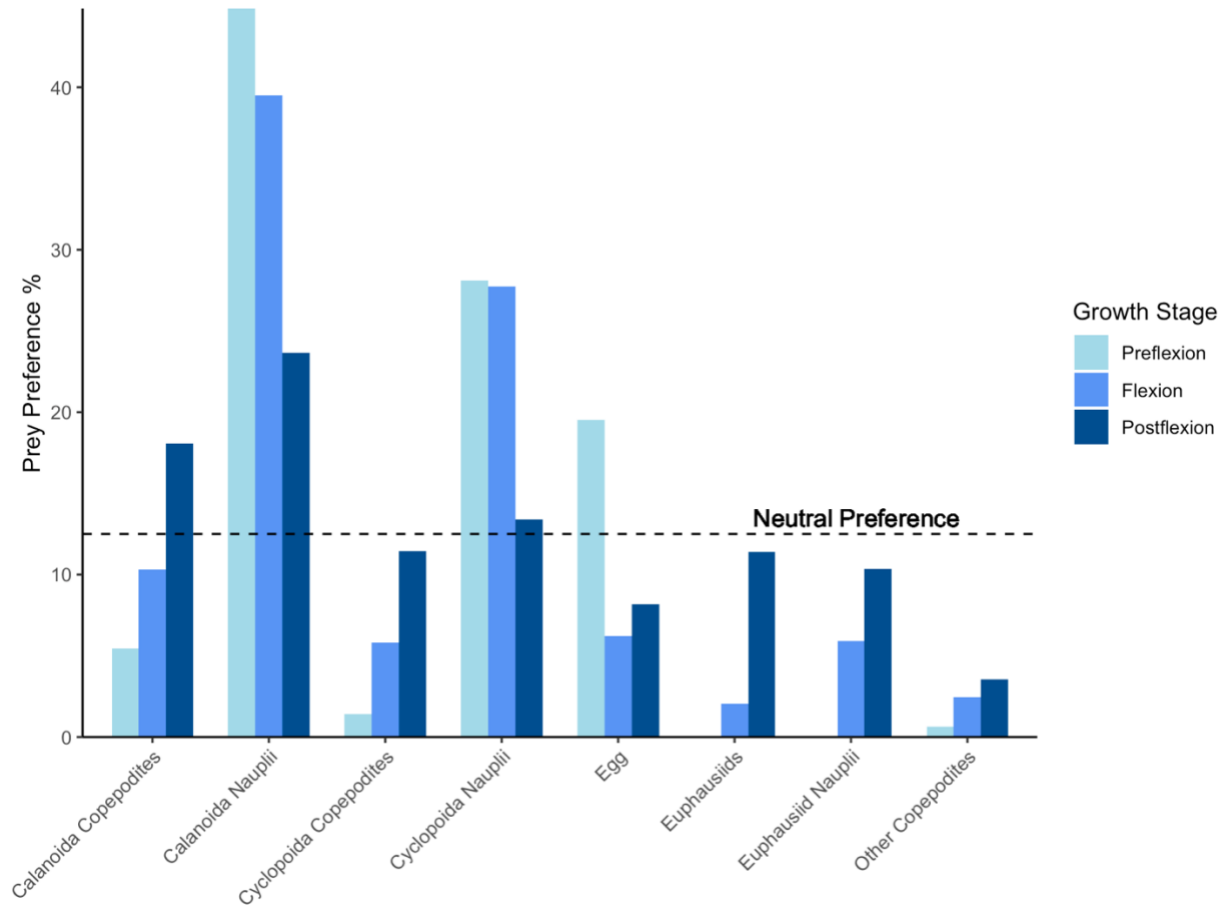


Figure 5: Prey taxonomic preferences of larval rockfish development stages. The dashed line indicates the neutral prey preference % threshold of 12.5%.

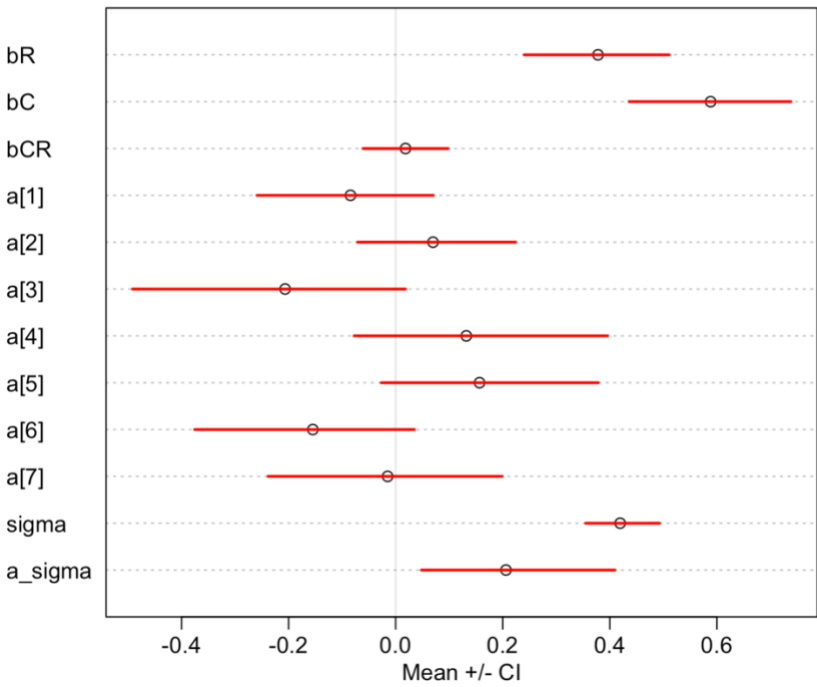
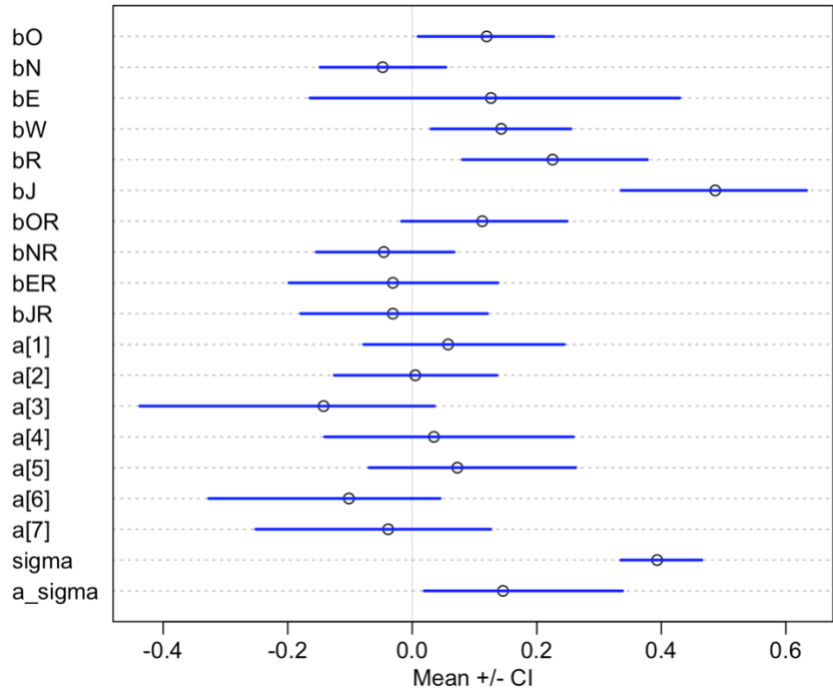


Figure 6: Coefficient plots of Bayesian mixed effects models mSL1 (blue) and mSL2 (red) for standard length, describing mean effect sizes and 89% compatibility interval (CI). Parameters are defined as bO = gut content C biomass of all prey taxa other than Euphausiids, Calanoid copepodites, and copepod nauplii, bN = copepod nauplii gut content C biomass, bE = Euphausiid gut content C biomass, bW = core width, bR = age in days, bJ Calanoid copepodite gut content C biomass, bC = total gut content C biomass of all prey, bOR, NR, ER, JR, CR = interactions of diet parameters with age, $a[1-7]$ = sample stations.

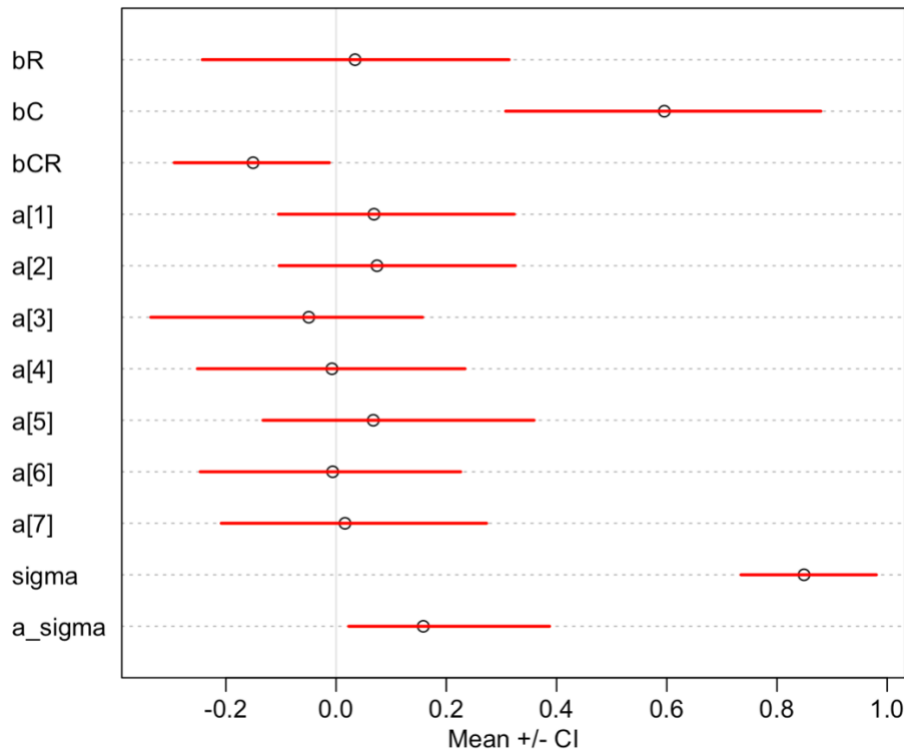
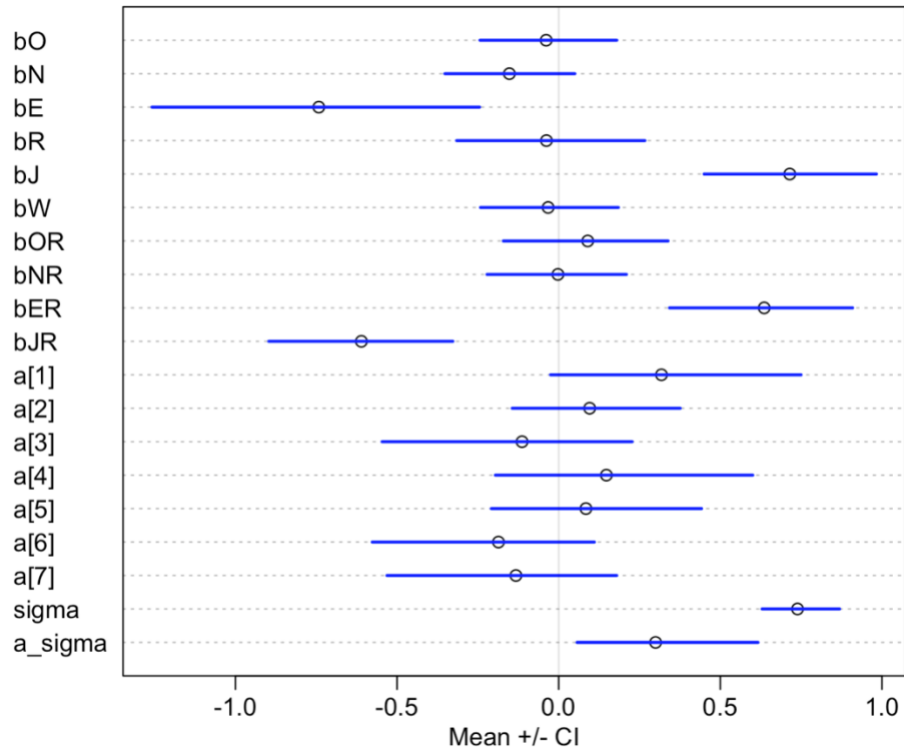


Figure 7: Coefficient plots of Bayesian mixed effects models mRG1 (blue) and mRG2 (red) for recent growth, describing mean effect sizes and 89% CI. Parameters are defined as in Figure 6.

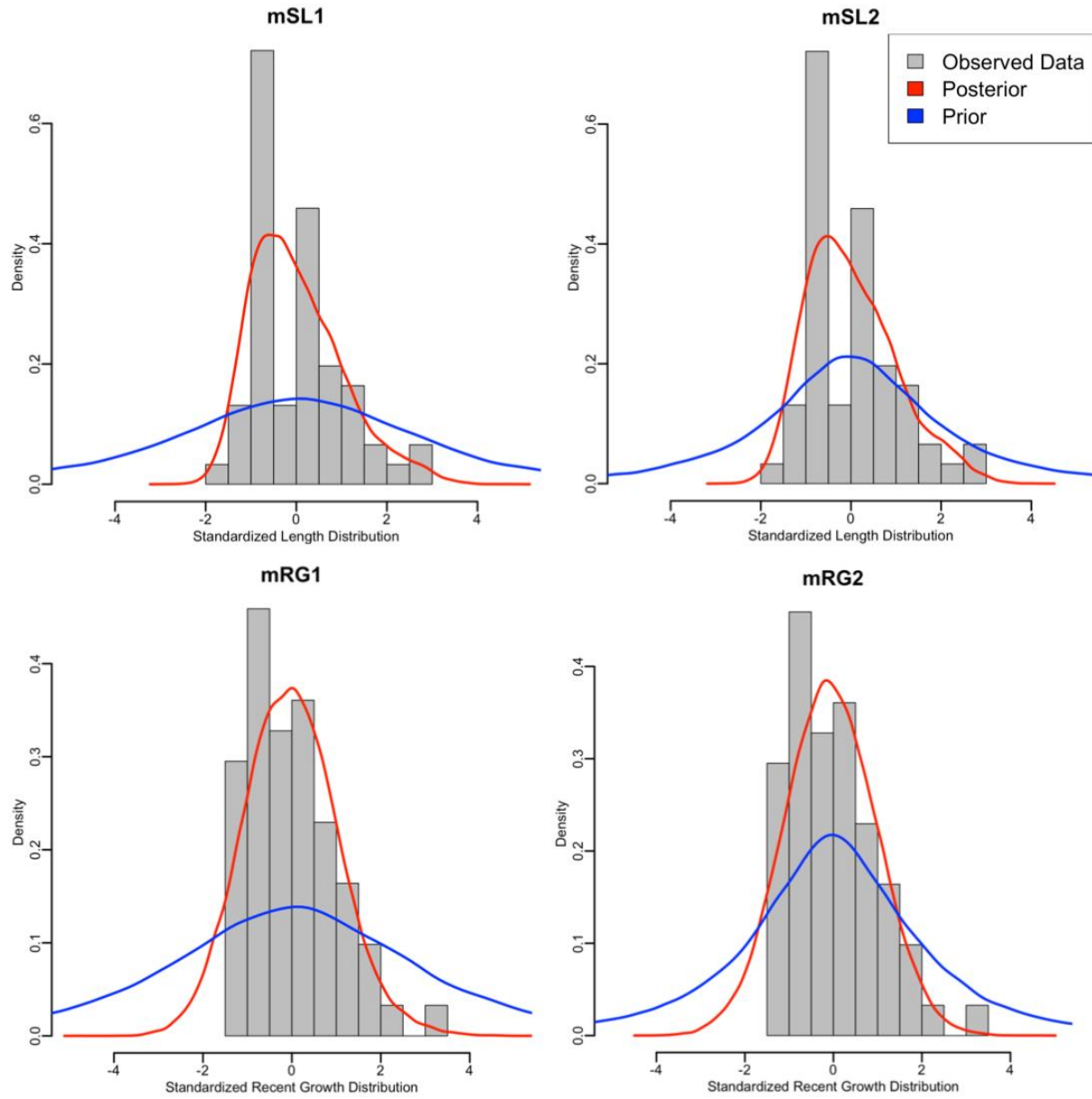


Figure 8: Posterior predictive checks for standard length models *mSL1*, *mSL2*, and recent growth models *mRG1*, *mRG2* containing displaying observed length and recent growth distributions overlaid with posterior (red) and prior (blue) distributions.

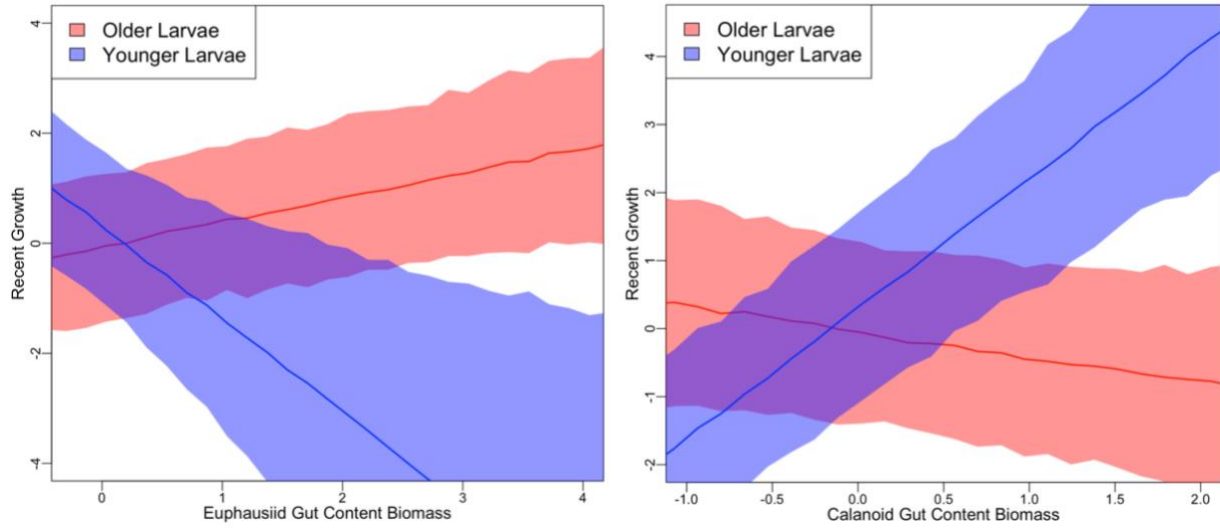


Figure 9: Counterfactual plots describing the relationship between standardized Euphausiid gut content biomass in $\mu\text{g C}$ (left) and standardized Calanoid copepodite gut content biomass in $\mu\text{g C}$ (right) with standardized recent growth in younger larvae (age = mean - 2SD) and older larvae (age = mean + 2SD). Shaded regions represent 89% confidence intervals.

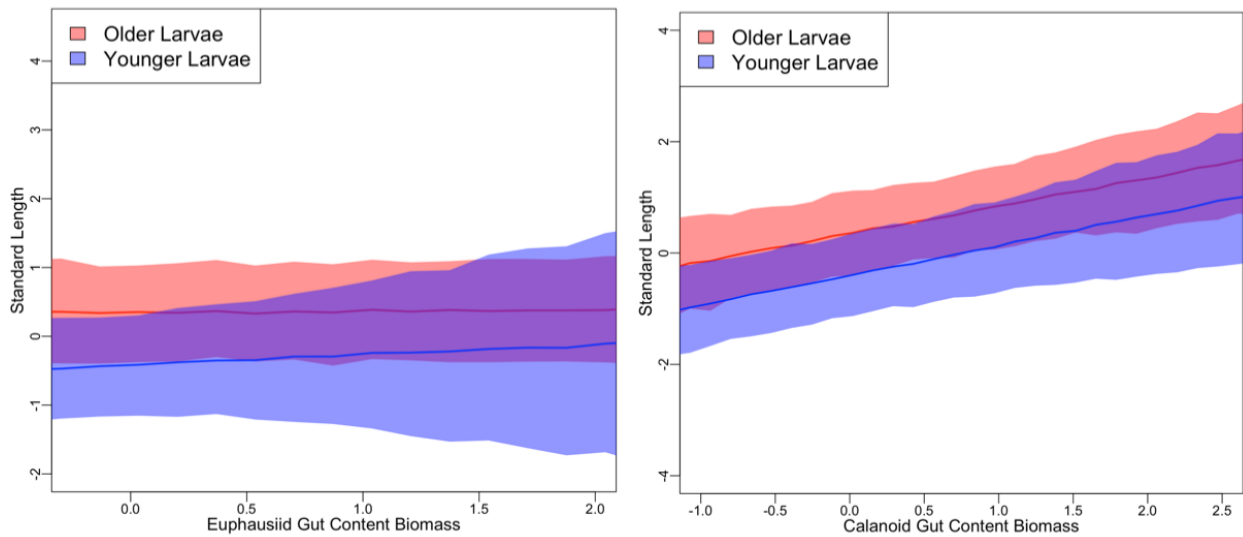


Figure 10: Counterfactual plots describing the relationship between standardized Euphausiid gut content biomass in $\mu\text{g C}$ (left) and standardized Calanoid copepodite gut content biomass in $\mu\text{g C}$ (right) with standardized standard length in younger larvae (age = mean - 2SD) and older larvae (age = mean + 2SD). Shaded regions represent 89% confidence intervals.

Table 2: Length (L) to dry weight (DW) to carbon (C) conversion factors for prey taxa of larval rockfishes.

| Prey Group | Equation | C:DW | Reference |
|------------------------|--|------|-------------------------|
| Calanoida Copepodite | $\ln(\mu\text{g C}) = 2.74 \times \ln(L_{\mu\text{m}}) - 16.41$ | 0.45 | Chisholm and Ruff 1990 |
| Cyclopoida Copepodite | $\log_{10}(\mu\text{g C}) = 3.16 \times \log_{10}(L_{\mu\text{m}}) - 8.18$ | 0.45 | Hopcroft et al., 1998 |
| Copepoda Nauplii (all) | $\ln(\mu\text{g C}) = 2.74 \times \ln(L_{\mu\text{m}}) - 16.41$ | | Satapoomin, 1999 |
| Diatoms and Protists | $\log_{10}(\mu\text{g C}) = (-0.639 + 0.984 * \log_{10}(((L_{\text{mm}}/4)^2 * (L_{\text{mm}}/3)))) / 1E6$ | | Putt and Stoecker, 1989 |
| Cladocerans | $\log_{10}(\mu\text{g C}) = 2.88 \times \log_{10}(L_{\mu\text{m}}) - 8.0767$ | | Shiroza et al., 2021 |
| Euphausiid Nauplii | $\mu\text{g C} = 19.032 \times L_{\text{mm}}^{1.484}$ | | Gorsky et al., 2010 |
| Euphausiid juveniles | $\mu\text{g C} = 19.032 \times L_{\text{mm}}^{1.484}$ | | Gorsky et al., 2010 |
| Copepod Egg | $\mu\text{g C} = 1.4E^{-10} \times V_{\mu\text{m}^3}$ | | Kjørboe et al., 1985 |

Table 3: Size range cutoffs for length and width measurements from 53 μ m and 200 μ m nets. '53 μ m max' represents the maximum size range in which abundances of each taxa in the 53 μ m net were higher than in the 200 μ m, while '200 μ m min' represents the minimum size range in which abundances in the 200 μ m net were higher than in the 53 μ m.

| Length | | | Width | | |
|----------------------|----------------------|-----------------------|----------------------|----------------------|-----------------------|
| Prey Taxa | 53 μ m max. size | 200 μ m min. size | Prey Taxa | 53 μ m max. size | 200 μ m min. size |
| All copepodites | 562 | 563 | All copepodites | 200 | 201 |
| All nauplii | 282 | 283 | All nauplii | 282 | 283 |
| Euphausiid juveniles | - | All | Euphausiid juveniles | - | All |
| Diatom/ Protists | All | - | Diatoms/Protists | All | - |
| Cladocerans | - | All | Cladocerans | - | All |
| Eggs | 282 | 283 | Eggs | 200 | 201 |

Table 4: Scientific and common names of larval rockfishes analyzed for gut content, degree of fishing pressure typically received, proportion of larval abundances within the samples, and proportion of stations where a species was present.

| Species | Common Name | Fishing Pressure | % of Total | % of Stations Present |
|--------------------------|--------------------|-------------------------|-------------------|------------------------------|
| <i>S. semicinctus</i> | Halfbanded | Low | 31.933 | 100.000 |
| <i>S. macdonaldi</i> | Mexican | Low | 0.840 | 14.286 |
| <i>S. simulator</i> | Pinkrose | Low | 9.244 | 71.429 |
| <i>S. hopkinsi</i> | Squarespot | Low | 15.966 | 85.714 |
| <i>S. jordani</i> | Shortbelly | Low | 8.403 | 57.143 |
| <i>S. saxicola</i> | Stripetail | Low | 2.521 | 42.857 |
| <i>S. ensifer</i> | Swordspine | Low | 4.202 | 57.143 |
| <i>S. melanostomus</i> | Blackgill | High | 3.361 | 42.857 |
| <i>S. rufus</i> | Bank | High | 7.563 | 71.429 |
| <i>S. mystinus</i> | Blue | High | 1.681 | 28.571 |
| <i>S. aurora</i> | Aurora | Moderate | 0.840 | 14.286 |
| <i>S. miniatus</i> | Vermilion | High | 1.681 | 14.286 |
| <i>S. wilsoni</i> | Pygmy | Low | 2.521 | 28.571 |
| <i>S. serriceps</i> | Treefish | Moderate | 0.840 | 14.286 |
| <i>S. paucispinis</i> | Boccaccio | High | 0.840 | 14.286 |
| <i>S. rosenblatti</i> | Greenblotched | Moderate | 0.840 | 14.286 |
| <i>S. moseri</i> | Whitespeckled | Low | 3.361 | 28.571 |
| <i>S. diploproa</i> | Splitnose | Moderate | 0.840 | 14.286 |
| <i>S. helvomaculatus</i> | Rosethorn | Moderate | 0.840 | 14.286 |
| <i>S. chloristicus</i> | Greenspotted | Moderate | 0.840 | 14.286 |

Table 5: spatial distributions of rockfish larvae growth stages.

| Station No. & Season | No. Preflexion | No. Flexion | No. Postflexion | Total per Station: |
|---------------------------------|-----------------------|--------------------|------------------------|---------------------------|
| 90-35 Spring | 10 | 10 | 10 | 30 |
| 90-30 Spring | 10 | 10 | 19 | 39 |
| 86.7-33 Winter | 14 | 5 | 0 | 19 |
| 93.3-35 Spring | 7 | 7 | 2 | 16 |
| 93.3-28 Spring & Winter | 6 | 11 | 5 | 22 |
| 90-37 Spring | 4 | 10 | 7 | 21 |
| 85-42.9 S Spring | 10 | 11 | 2 | 23 |
| Total Per Growth Stage | 61 | 64 | 45 | 170 |

Table 6: Spatial abundance distributions of the twelve most commonly consumed zooplankton and phytoplankton prey taxa by larval rockfishes. Abundance is measured in counts per m³.

| Taxa Abundance Counts / m ³ | | | | | |
|--|-----------------------|---------------------|---------------------|-----------------------|-----------------------|
| Taxa Group | 93.3-28 Winter | 90-35 Spring | 90-37 Spring | 93.3-28 Spring | 93.3-35 Spring |
| Calanoida Copepodites | 75.92 | 253.38 | 130.13 | 13.42 | 6.39 |
| Calanoida Nauplii | 99.37 | 82.55 | 14.67 | 15.56 | 12.37 |
| Cladocerans | 0.09 | 8.16 | 2.83 | 0.20 | 0.01 |
| Cyclopoida Copepodites | 42.39 | 13.60 | 11.55 | 23.10 | 10.48 |
| Cyclopoida Nauplii | 58.95 | 42.21 | 14.67 | 24.37 | 16.50 |
| Diatoms & Protists | 18398.63 | 674.91 | 281.90 | 2029.55 | 940.24 |
| Eggs | 16.85 | 5.16 | 0.97 | 33.66 | 9.40 |
| Euphausiid Nauplii | 1.32 | 0.81 | 2.99 | 0.15 | 0.00 |
| Euphausiids | 1.60 | 28.57 | 11.55 | 0.64 | 0.21 |
| Other Copepodites | 11.70 | 32.31 | 11.07 | 8.95 | 7.07 |
| Poecilostomatoida Copepodites | 9.83 | 17.07 | 7.22 | 7.41 | 5.30 |
| Total Abundance m³ | 18716.65 | 1158.74 | 489.56 | 2157.01 | 1007.96 |

Table 7: Spatial biomass distributions of the twelve most commonly consumed zooplankton and phytoplankton prey taxa by larval rockfishes. Biomass is measured in $\mu\text{g C per m}^3$.

| Taxa Group | Taxa Biomass $\mu\text{g C / m}^3$ | | | | |
|-------------------------------|------------------------------------|----------------|----------------|----------------|----------------|
| | 93.3-28 Winter | 90-35 Spring | 90-37 Spring | 93.3-28 Spring | 93.3-35 Spring |
| Calanoida Copepodites | 62.52 | 581.95 | 209.21 | 20.62 | 8.27 |
| Calanoida Nauplii | 8.61 | 12.84 | 2.02 | 1.99 | 1.90 |
| Cladocerans | 0.06 | 14.34 | 3.25 | 0.11 | 0.00 |
| Cyclopoida Copepodites | 13.84 | 3.77 | 8.22 | 8.46 | 2.91 |
| Cyclopoida Nauplii | 5.17 | 3.50 | 1.07 | 1.94 | 1.35 |
| Diatoms & Protists | 645.96 | 127.16 | 81.43 | 2549.31 | 5453.64 |
| Eggs | 16.96 | 2.60 | 0.42 | 30.35 | 11.63 |
| Euphausiid Nauplii | 0.85 | 0.78 | 4.34 | 0.15 | 0.00 |
| Euphausiids | 98.03 | 1299.25 | 667.02 | 15.50 | 17.24 |
| Other Copepodites | 7.03 | 75.10 | 31.89 | 7.20 | 8.85 |
| Poecilostomatoida Copepodites | 1.28 | 4.63 | 2.91 | 2.37 | 5.86 |
| Total Biomass m3 | 860.31 | 2125.92 | 1011.78 | 2637.99 | 5511.65 |

Table 8: Chesson's α -selectivity index calculations for four sample stations with the seven most commonly consumed prey taxa. Values are average $\alpha \pm$ standard error. Bolded values represent taxa and size ranges that are positively selected for. Neutral preference is 3.13%.

| Growth Stage | Prey Taxa | Sample Stations | | | |
|--------------------|-----------------------------------|-----------------------------------|-------------------------------------|------------------------------------|-------------------------------------|
| | | 90-35 | 90-37 | 93.3-28 | 93.3-35 |
| Preflexion | Calanoid Copepodites | 0.4 \pm 1.0 | 2.5 \pm 4.0 | | 0 12.5 \pm 35.0 |
| | Calanoid Nauplii | 50.6 \pm 29.0 | 48.6 \pm 37.0 | 100.0 \pm 0 | 30.6 \pm 21.0 |
| | Cyclopoid Copepodites | | 0 14.1 \pm 20.0 | | 0 0 |
| | Cyclopoid Nauplii | 40.8 \pm 23.0 | 34.7 \pm 14.0 | | 0 15.7 \pm 25.0 |
| | Egg | 6.8 \pm 20.0 | | 0 | 0 41.2 \pm 27.0 |
| | Euphausiid Nauplii | | 0 | 0 | 0 0 |
| | Euphausiids | | 0 | 0 | 0 0 |
| Flexion | Other Copepodites | 1.4 \pm 4.0 | | 0 | 0 0 |
| | Calanoid Copepodites | 7.7 \pm 11.0 | 2.6 \pm 2.0 | 24.4 \pm 29.0 | 0 |
| | Calanoid Nauplii | 46.1 \pm 14.0 | 33.4 \pm 13.0 | 38.6 \pm 29.0 | 40.3 \pm 20.0 |
| | Cyclopoid Copepodites | 9.3 \pm 14.0 | 9.2 \pm 9.0 | 2.1 \pm 4.0 | 0 |
| | Cyclopoid Nauplii | 35.1 \pm 18.0 | 29.9 \pm 15.0 | 0.175 \pm 0.17 | 31.2 \pm 14.0 |
| | Egg | | 0 6.5 \pm 20.0 | 1.6 \pm 5.0 | 28.5 \pm 20.0 |
| | Euphausiid Nauplii | | 0 11.7 \pm 1.0 | 8.8 \pm 21.0 | 0 |
| Postflexion | Euphausiids | | 0 0.3 \pm 1.0 | 6.5 \pm 21.0 | 0 |
| | Other Copepodites | 1.7 \pm 3.0 | 6.4 \pm 8.0 | 0.6 \pm 2.0 | 0 |
| | Calanoid Copepodites | 6.0 \pm 6.0 | 25.0 \pm 34.0 | 37.6 \pm 31.0 | 5.3 \pm 7.0 |
| | Calanoid Nauplii | 24.7 \pm 21.0 | 28.6 \pm 28.0 | 21.7 \pm 44.0 | 5.3 \pm 8.0 |
| | Cyclopoid Copepodites | 8.5 \pm 14.0 | 26.7 \pm 29.0 | 0.5 \pm 1.0 | 0 |
| | Cyclopoid Nauplii | 26.2 \pm 17.0 | 8.5 \pm 12.0 | | 0 0 |
| | Egg | 5.0 \pm 8.0 | | 0 9.1 \pm 15.0 | 50.1 \pm 56.0 |
| Euphausiid Nauplii | 24.8 \pm 40.0 | | 0 | 0 0 | |
| | Euphausiids | 2.8 \pm 7.0 | 3.2 \pm 8.0 | 28.9 \pm 40.0 | 39.4 \pm 56.0 |
| | Other Copepodites | 1.8 \pm 3.0 | 8.0 \pm 9.0 | 2.0 \pm 4.0 | 0 |

Table 9: Chesson's α -selectivity index calculations for ten logarithmic length classes with the seven most commonly consumed prey taxa. Values are average $\alpha \pm$ standard error. Bolded values represent taxa and size ranges that are positively selected for. Neutral preference is 1.25%.

| | | Prey Length Midpoints (μm) | | | | | | | | | |
|---------------|------------------------|---|-----------------------------------|-----------------------------------|-----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|---------------------------------|----------------------------------|
| Flexion Stage | Prey Taxa | 119 | 168 | 237 | 335 | 473 | 668 | 944 | 1334 | 1884 | 2661 |
| Preflexion | Calanoid Copepodites | 0 | 0 | 0 | 0.6 \pm 2.0 | 0.1 \pm <1.0 | 0 | 0 | 0 | 0 | 0 |
| | Calanoid Nauplii | 4.8 \pm 20.0 | 15.0 \pm 27.0 | 15.8 \pm 24.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Copepodites | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Nauplii | 0.8 \pm 3.0 | 4.0 \pm 7.0 | 35.5 \pm 35.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 0 | 21.9 \pm 36.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiid Nauplii | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiids | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Other Copepodites | 0 | 0 | 0 | 0.7 \pm 3.0 | 0.8 \pm 3.0 | 0 | 0 | 0 | 0 | 0 |
| Flexion | Calanoid Copepodites | 0 | 0 | 1.0 \pm 3.0 | 3.2 \pm 9.0 | 2.1 \pm 7.0 | 3.1 \pm 16.0 | 4.1 \pm 17.0 | 0.1 \pm 1.0 | 0.1 \pm 1.0 | 0 |
| | Calanoid Nauplii | 0.8 \pm 5.0 | 11.2 \pm 15.0 | 10.6 \pm 14.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Copepodites | 0 | 0 | 0.7 \pm 2.0 | 1.7 \pm 5.0 | 1.3 \pm 4.0 | 0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Nauplii | 7.7 \pm 17.0 | 4.1 \pm 9.0 | 30.0 \pm 26.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 0 | 5.9 \pm 15.0 | 3.1 \pm 17.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiid Nauplii | 0 | 0 | 1.0 \pm 6.0 | 1.1 \pm 5.0 | 1.5 \pm 9.0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiids | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 \pm 5.0 | 0 | 0 |
| | Other Copepodites | 0 | 0 | 1.4 \pm 7.0 | 0.2 \pm 1.0 | 0 | 0.9 \pm 6.0 | 2.5 \pm 15.0 | 0 | 0 | 0 |
| Postflexion | Calanoid Copepodites | 0 | 0 | 0.1 \pm <1.0 | 1.7 \pm 3.0 | 3.4 \pm 8.0 | 6.5 \pm 21.0 | 8.4 \pm 27.0 | 4.8 \pm 18.0 | 1.7 \pm 7.0 | 2.1 \pm 10.0 |
| | Calanoid Nauplii | 4.8 \pm 3.0 | 15.0 \pm 23.0 | 15.8 \pm 8.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Copepodites | 0 | 0 | 0.1 \pm 1.0 | 0.6 \pm 1.0 | 8.9 \pm 18.0 | 1.1 \pm 4.0 | 0 | 0 | 0 | 0 |
| | Cyclopoida Nauplii | 0 | 1.8 \pm 7.0 | 14.0 \pm 24.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 3.3 \pm 17.0 | 4.1 \pm 13.0 | 1.3 \pm 4.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiid Nauplii | 0 | 0 | 0 | 7.00 \pm 21.0 | 5.7 \pm 20.0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiids | 0 | 0 | 0 | 0 | 0 | 2.5 \pm 11.0 | 0.9 \pm 4.0 | 0.2 \pm 1.0 | <0.1 \pm <1.0 | 0.3 \pm 1.0 |
| | Other Copepodites | 0 | 0 | 0 | 0.4 \pm 1.0 | 0.7 \pm 2.0 | <0.2 \pm <1.0 | 1.3 \pm 7.0 | 3.8 \pm 19.0 | 0 | 0 |

Table 10: Chesson's α -selectivity index calculations for seven logarithmic width classes with the seven most commonly consumed prey taxa. Values are average $\alpha \pm$ standard error. Bolded values represent taxa and size ranges that are positively selected for. Neutral preference is 1.79%.

| | | Prey Width Midpoints (μm) | | | | | | |
|--------------------|-----------------------|--|-----------------------------------|-----------------------------------|----------------------------------|-----------------------------------|-----------------------------------|----------------------------------|
| Flexion Stage | Prey Taxa | 84 | 119 | 168 | 237 | 335 | 473 | 668 |
| Preflexion | Calanoid Copepodites | 0 | 0 | 5.6 \pm 24.0 | 0.2 \pm 1.0 | 0 | 0 | 0 |
| | Calanoid Nauplii | 11.9 \pm 16.0 | 15.1 \pm 32.0 | 20.3 \pm 30.0 | 0 | 0 | 0 | 0 |
| | Cyclopoid Copepodites | 0 | 0 | 0 | 0 | 3.3 \pm 14.0 | 0 | 0 |
| | Cyclopoid Nauplii | 1.2 \pm 3.0 | 17.6 \pm 24.0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 0 | 0 | 23.3 \pm 36.0 | 0 | 0 | 0 | 0 |
| | Euphausiid Nauplii | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Euphausiids | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Flexion | Other Copepodites | 0 | 0 | 0 | 0 | 1.5 \pm 6.0 | 0 | 0 |
| | Calanoid Copepodites | 0.2 \pm 1.0 | 0.3 \pm 1.0 | 1.5 \pm 3.0 | 2.5 \pm 7.0 | 4.9 \pm 15.0 | 3.9 \pm 16.0 | 0.2 \pm 1.0 |
| | Calanoid Nauplii | 16.5 \pm 21.0 | 7.2 \pm 9.0 | 30.1 \pm 30.0 | 0 | 0 | 0 | 0 |
| | Cyclopoid Copepodites | 0 | 0.9 \pm 3.0 | 3.0 \pm 10.0 | 0.5 \pm 2.0 | 0.8 \pm 5.0 | 0 | 0 |
| | Cyclopoid Nauplii | 2.1 \pm 4.0 | 15.5 \pm 18.0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 0 | 0 | 2.9 \pm 9.0 | 0.4 \pm 3.0 | 0 | 0 | 0 |
| | Euphausiid Nauplii | 0 | 0 | 0 | 0 | 0 | <0.1 \pm 0.2 | 0 |
| Postflexion | Euphausiids | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 \pm 0.2 |
| | Other Copepodites | 0 | 0 | <0.1 \pm 0.5 | <0.1 \pm 0.5 | 0 | 0 | 0 |
| | Calanoid Copepodites | 0 | <0.1 \pm 0.2 | 1.4 \pm 3.0 | 2.1 \pm 3.0 | 15.4 \pm 32.0 | 13.5 \pm 25.0 | 2.3 \pm 0.08 |
| | Calanoid Nauplii | 4.3 \pm 8.0 | 2.9 \pm 6.0 | 18.2 \pm 25.0 | 0 | 0 | 0 | 0 |
| | Cyclopoid Copepodites | 0 | 0.3 \pm 2.0 | 1.5 \pm 4.0 | 1.3 \pm 3.0 | 0.5 \pm 3.0 | 0 | 0 |
| | Cyclopoid Nauplii | 1.0 \pm 3.0 | 4.1 \pm 24.0 | 0 | 0 | 0 | 0 | 0 |
| | Egg | 0 | 2.4 \pm 12.0 | 5.3 \pm 18.0 | 2.3 \pm 8.0 | <0.1 \pm <1.0 | 0 | 0 |
| Euphausiid Nauplii | 0 | 0 | 0 | 6.0 \pm 21.0 | 4.0 \pm 16.0 | 0 | 0 | |
| Euphausiids | 0 | 0 | 0 | 2.1 \pm 10.0 | 2.5 \pm 8.0 | 1.8 \pm 6.0 | 1.5 \pm 4.0 | |
| Other Copepodites | 0 | 0.3 \pm 2.0 | 0.2 \pm 1.0 | 0.4 \pm 1.0 | 0.2 \pm 1.0 | 2.7 \pm 1.0 | 0 | |

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