







## RESEARCH NOTE

# Trophic level influences larval Shortbelly Rockfish development

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## Abstract

**Objective:** Early life success of fishes is considered one of the most important drivers of recruitment to adult populations, and elucidating the governing mechanisms is important for management efforts. Many hypotheses over the past century have been proposed to explain recruitment fluctuation, with the recently postulated Trophic Efficiency in Early Life (TEEL) hypothesis arguing that a shorter food chain length equals greater energy transfer efficiency from primary producers to larval fishes, thereby reducing early-life mortality and ultimately leading to stronger recruitment. Under TEEL it would then be assumed that feeding low in the food chain would improve growth and body condition, as these are often shown to be associated with increased survival in larval fishes. The objective of this study was to test this aspect of the TEEL hypothesis by quantifying condition, growth, and trophic level of larval Shortbelly Rockfish *Sebastes jordani* collected by the California Cooperative Oceanic Fisheries Investigations program and archived at the Ichthyoplankton Collection.

**Methods:** The trophic level on larval Shortbelly Rockfish was assessed with compound-specific isotopic analysis of amino acids. Their size at age and survival were estimated with otolith microstructure. Their diet was examined through stomach content analysis.

**Result:** Observations indicate that larvae consuming prey at a lower trophic level have greater body weight and exhibit faster growth rates. However, feeding at a lower trophic level did not influence body length. The ingested prey responsible for the lower trophic level within larval rockfish could not be determined.

**Conclusion:** Larval Shortbelly Rockfish consuming prey at a lower trophic level garnered greater body weight and exhibited faster growth rates and provides support for the TEEL hypothesis. However, further research is needed to identify the preferred prey(s) responsible for the more efficient energy transfer.

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## KEYWORDS

compound-specific isotopic analysis of amino acids, CSIA-AA, diet, food chain length, otolith, recruitment, stable isotope

## INTRODUCTION

The adult population sizes for highly fecund fishes are driven by their spawning stock biomass, spawning habitat size, and recruitment (Hare 2014; Robert et al. 2014; Thompson et al. 2016; Fennie et al. 2023a). Of these, recruitment is highly dynamic in short-lived marine fishes, which can fluctuate interannually by many orders of magnitude (Peck et al. 2021), inducing major economic and ecological responses. In the California Current Ecosystem, fluctuations in the abundance of Pacific Sardine *Sardinops sagax* and Northern Anchovy *Engraulis mordax* have been linked to variability in the condition of pinniped pups (McClatchie et al. 2016) and seabirds (Fennie et al. 2023a). Meanwhile, fisheries targeting rockfish *Sebastes* spp. in California have historically exceeded US\$1 billion (Lenarz 1987; Love et al. 1998), but intense commercial and recreational fishing pressure can dramatically reduce their numbers. Subsequent implementation of management plans and marine protected areas coupled with favorable recruitment conditions appeared to help rebuild certain rockfish populations (Thompson et al. 2016). Even so, identifying the factor(s) influencing early life success (the life stage generally considered as the main driver of recruitment and adult population dynamics; Hare 2014) could improve predictions and management strategies.

Many hypotheses over the past century have examined hydrodynamics and mortality to explain recruitment variability, and they can largely be distilled into a single question: are larvae able to feed on prey that bolsters growth and survival (Hjort 1914, 1926; Lasker 1978; Cury and Roy 1989; Cushing 1990)? Past studies focused on the quantity of prey ingested since greater prey abundance generally leads to a faster growth rate (Pepin 1988). However, larval fish are not simply generalist feeders (Pepin et al. 2014), and a recent metadata analysis revealed that a fast growth rate alone does not adequately explain recruitment variability (Robert et al. 2023), suggesting that other factors, such as size at hatch (Fennie et al. 2023a, 2023b) and larval body condition, may also be important. Little is known about the trophic characteristics of fast-growing and fit larvae or their relationship with size at hatch. Recently, the Trophic Efficiency in Early Life (TEEL) hypothesis postulated that a shorter food chain length (or a lower trophic level) through an “optimal” prey results in more efficient energy transfer from primary producers to young fish, thereby increasing

## Impact Statement

Scientists have long sought to explain and predict the variability in adult fish population size. Here, we tested a recently proposed hypothesis and found larval Shortbelly Rockfish that fed on prey from lower trophic levels grew heavier and faster, likely as these prey confer more energy from phytoplankton to the larvae.

larval survival and ultimately leading to a larger adult population (Swailethorp et al. 2023). The TEEL hypothesis appears to have explained most of the variability in the Northern Anchovy population over a 45-year period, but would this pattern also apply to a species that is phylogenetically distinct from Northern Anchovy, such as the viviparous Shortbelly Rockfish *S. jordani*?

Shortbelly Rockfish are capable of explosive population growth fueled by extremely high annual recruitment (Schroeder et al. 2019), and they serve as an important forage species for fishes, seabirds, and marine mammals in the California Current Ecosystem (Love et al. 2002; Field et al. 2007). Shortbelly Rockfish can impact fishery management despite not being commercially targeted. For example, Shortbelly Rockfish are sometimes taken as bycatch in the Pacific Hake *Merluccius productus* fishery off Oregon and Washington, but prior to 2018 they were scarce in this region and the bycatch limit was set at a very low level. However, record-high recruitment from 2013 to 2016 in California (Schroeder et al. 2019) induced a surge in population size, and warm water caused a northward expansion of Shortbelly Rockfish (Stern-Pirlot et al. 2021, 2022). As a result, the Shortbelly Rockfish bycatch limit of the Pacific Hake fishery was exceeded within the first week of the fishing season near coastal Oregon and threatened to (but ultimately did not) prematurely close the fishery (Free et al. 2023). As climate change continues to alter marine ecosystem dynamics, scenarios such as the one described above may become more frequently encountered. This highlights the need to understand the mechanism(s) driving recruitment dynamics, which has remained a fundamental issue in fisheries science despite over a century of research (Hjort 1914; Hare 2014).

The TEEL hypothesis proposes that trophic efficiency is a critical component in recruitment dynamics. To test

this hypothesis, we required the ability to extract feeding history from archival larval fish samples captured within relatively close geographical proximity and across multiple years. Such archival samples often are not accompanied by their prey items, which would be needed in traditional stable isotopic analysis to establish the source nitrogen (N) level. In contrast, the use of compound-specific isotope analysis of amino acids (CSIA-AA) allows for the sampling of both trophic level and source N level solely from the consumer's tissues. Using a combination of CSIA-AA, otolith microstructure, and gut content analysis, this study provides observations on whether trophic level and size at hatch may be important for the growth and body condition of larval Shortbelly Rockfish.

## METHODS

### Sample collection

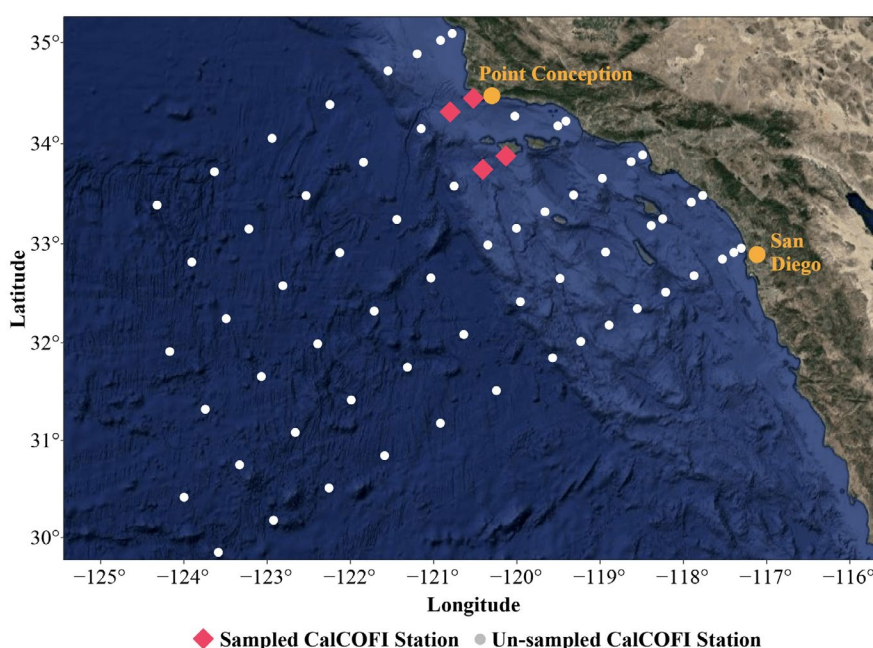
Larval rockfish (preserved in 95% ethanol) were collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program and archived at the Ichthyoplankton Collection curated by the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center (La Jolla, California). Shortbelly Rockfish were identified via mitochondrial cytochrome *b* gene sequencing (Thompson et al. 2017). To reduce variability, we selected larval Shortbelly Rockfish of comparable size

(total length [mean  $\pm$  standard error, SE] =  $6.56 \pm 0.23$  mm; dry weight =  $0.28 \pm 0.03$  mg) and CalCOFI stations (L80 [line], S51 [station]; L80, S55; L83.3, S51; and L83.3, S55) sampled during winter cruises in the years 2004, 2005, 2006, 2008, 2010, 2012, and 2013 (Figure 1). Altogether, 18 of 30 samples were successful in both otolith dissection and CSIA-AA analysis. Unfortunately, seven samples were lost during otolith microdissection, and nine samples were lost during CSIA-AA processing or discarded due to insufficient mass (four samples had both issues).

### Morphometric, otolith, and gut analysis

Shortbelly Rockfish were imaged with a DSLR camera (Nikon D7000) under a compound microscope (Leica DMLB) for standard length (SL) measurements. Sagittal otoliths and digestive organs were dissected for the respective analyses. The remaining portion of each larval Shortbelly Rockfish was frozen at  $-80^{\circ}\text{C}$  for 24 h, freeze-dried for 24 h, weighed on a microscale for dry weight (without the otolith and gut), and then returned to storage at  $-80^{\circ}\text{C}$  until CSIA-AA processing.

Dissected otoliths were imaged across focal planes (Z-stack imaging) under a compound microscope (1000 $\times$ ; Leica DMLB) and then were focus-stacked (Helicon Focus version 8.0.4). Images were analyzed in R (R Core Team 2020) using the R package RFishBC (Ogle 2022) to obtain the otolith core size (from the center to the



**FIGURE 1** California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling stations and the sampling site for this experiment. To reduce variability, we selected larval Shortbelly Rockfish of comparable size collected at comparable CalCOFI sampling stations during winter cruises in the years 2004, 2005, 2006, 2008, 2010, 2012, and 2013.

postrostral edge of the extrusion check) and age and increment widths (the number and width, respectively, of daily rings beginning at the first growth increment) by two readers (Supplemental Figure 1 available separately online). Within-reader precision was assessed using the R package FSA (Ogle et al. 2020) to calculate the average percent error (2.089%) and the coefficient of variation (2.954%) between the two readers. Unfortunately, 3 of the 18 aged otoliths were not included in the within-reader precision due to data loss that occurred during one co-author's switch to another institution (though the data were recorded and they were independently read by two readers).

Digestive tracts were dissected, and stomach contents were identified, photographed, and measured to the nearest 0.5  $\mu\text{m}$  with an eyepiece micrometer. Recovered prey were categorized by taxonomic grouping; growth stage; average length, width, and number found within rockfish larvae with non-empty guts; percent numerical contribution to the diet; average carbon (C) weight; and percent C biomass contribution to the diet. For copepodites, length was measured as prosome length, while total length was measured for all other prey groups. Carbon weights ( $\mu\text{g}$ ) were estimated using conversion factors from existing literature (Supplemental Table 1 available separately online).

## CSIA-AA

The CSIA-AA protocol follows the procedures detailed by Swalethorp et al. (2020). Larvae were hydrolyzed in 0.5 mL of 6-N HCl for 24 h at 90°C, dried under vacuum in a Labconco centrifugal evaporator at 60°C, redissolved in 0.5 mL of 0.1-N HCl, and filtered through an IC Nillix-LG 0.2- $\mu\text{m}$  hydrophilic polytetrafluoroethylene filter. Samples were redried before redissolving in 100  $\mu\text{L}$  of 0.1% trifluoroacetic acid in Milli-Q water, and they were stored at  $-80^\circ\text{C}$  until amino acid separation. We used an Agilent 1200 Series high-performance liquid chromatography (HPLC) system equipped with a degasser (G1322A), a quaternary pump (G1311A), an autosampler (G1367B), and a Realtek fixed flow splitter (5:1), which directed the flow to an analytical fraction collector (G1364C) and an evaporative light-scattering detector (385-ELSD; G4261A), respectively. Amino acids were separated on a reverse-phase semi-preparative scale column (Primesep A; 10  $\times$  250 mm, 100- $\text{\AA}$  pore size, 5- $\mu\text{m}$  particle size; SiELC Technologies Ltd.) using a 120-min ramp solvent program with 0.1% trifluoroacetic acid in Milli-Q water (aqueous phase) and HPLC-grade acetonitrile (organic phase). The fraction collector collected glutamic acid (Glu) and phenylalanine (Phe) in 7-mL glass tubes based on elution time. Collection quality was assessed by comparing chromatograms with set

collection times, and they were accepted only when at least 99% of the peak areas fit within the collection windows. Whole larval samples were injected into the column to collect amino acids for N isotope analysis ( $\geq 1 \mu\text{g N}$ ). Collected amino acids were dried in the centrifugal evaporator at 60°C, dissolved in 40  $\mu\text{L}$  of 0.1-N HCl, and transferred to tin capsules (Costech; 3.5  $\times$  5.0 mm). Capsules were then dried overnight in a desiccator under vacuum.

Amino acid N isotopic analyses were performed at the Stable Isotope Laboratory, University of California Santa Cruz, on a Nano-EA-IRMS system designed for small sample sizes (0.8–20.0  $\mu\text{g N}$ ). The automated system is composed of a Carlo Erba CHNS-O EA1108 elemental analyzer connected to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer via a Thermo Finnigan GasBench II with an N trapping system.

The  $\delta^{15}\text{N}$  values were corrected for size effects and instrument drift by using Indiana University acetanilide, USGS41 Glu and Phe standards, and protocols (<https://es.ucsc.edu/~silab>) based on Fry et al. (1992). The  $\delta^{15}\text{N}$  values of Glu and Phe are not significantly affected by ethanol preservation (Swalethorp et al. 2020). The 18 larval Shortbelly Rockfish with both CSIA-AA and otolith measurements were divided into two groups based on their differences in  $\delta^{15}\text{N}$  between the trophic amino acid Glu and the source amino acid Phe ( $\delta^{15}\text{N}_{\text{Glu-Phe}}$ ) values. The nine larvae with higher  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  were sorted into the high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  group (mean  $\pm$  SE =  $13.82 \pm 0.40\text{‰}$ ), and the remaining nine larvae with lower  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  were sorted into the low group ( $9.68 \pm 0.74\text{‰}$ ).

## Statistical analysis

All analyses were performed using R version 4.0.3. Age and  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  effects on the SL and mass of larval Shortbelly Rockfish were analyzed with Bayesian hierarchical models encoded with the R package “rethinking” (McElreath 2020). Four Hamiltonian Markov chains with 1000 iterations were used. Bayesian inference is considered to lend advantages over frequentist methods when analyzing small sample sizes due to inclusion of prior information, which increases robustness by incorporating current knowledge of expected outcomes into the model (McNeish 2016). Since all variables were standardized, a mean of 0 and a standard deviation of 1 were included as informative priors for each predictor variable. Normally distributed posterior distributions were summarized using central tendencies and variance—in this case, the mean and 89% compatibility interval of each predictor variable. The effect of  $\delta^{15}\text{N}_{\text{Phe}}$  on  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  was determined by using a hierarchical model, with sample station and year as random effects, as fitted to equations 1–8 (Supplemental Table 2). Sample station and year were also



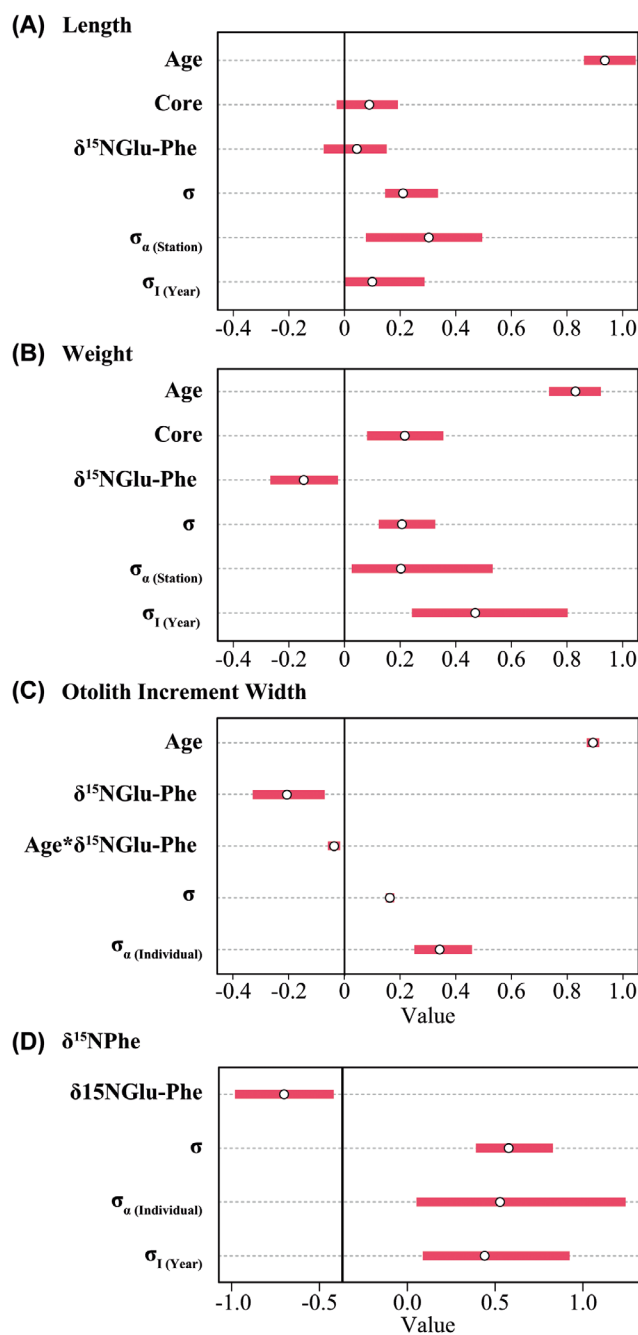
included as random effects (varying intercept) in SL and body weight models, which were fitted to equations 9–18 (Supplemental Table 2). Posterior predictive checks were used to examine the predictive accuracy of the models, and model convergence was confirmed graphically using traceplots (Supplemental Figure 2). To test growth in relation to  $\delta^{15}\text{N}_{\text{Glu-Phe}}$ , another Bayesian hierarchical model in the rethinking package was fitted to the data, with otolith increment width as the dependent variable and  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  and increment number as independent variables. The interactive effect of increment number and  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  was also included as an independent variable, with individual larvae included as a random intercept, as denoted in equations 19–26 (Supplemental Table 2).

## RESULTS AND DISCUSSION

We used  $\delta^{15}\text{N}$  values for the trophic amino acid Glu minus the source amino acid Phe as an indicator of trophic level. Published trophic discrimination factors (TDFs) are exclusively based on adult or juvenile fish. Compared to young larvae, these later life stages of fish exhibit slower growth and metabolic rates, both of which impact isotopic turnover (Bradley et al. 2014). Using TDF values from Bradley et al. (2015), we estimated unrealistically low trophic levels, down to 1.3 in some larvae, indicating that adult TDFs may not be appropriate for use with larvae.

The  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  of larval Shortbelly Rockfish averaged  $11.75 \pm 0.65\text{‰}$  (mean  $\pm$  SE;  $N=18$ ) and ranged from 5.31‰ to 16.38‰ (Supplemental Table 3). As expected, age strongly influenced larval length and weight, indicating that older larval Shortbelly Rockfish were both longer and heavier than their younger counterparts (Figure 2A,B). Feeding on prey with lower  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  did not affect larval length (Figure 2A) but strongly increased larval weight (Figure 2B). This was not surprising: fish condition corresponds to its weight at given length, forming the premise of Fulton's condition factor (Froese 2006). Moreover, rationing experiments in adult fish (Pangle et al. 2004) and larval fish (Letcher and Bengtson 1993; Martínez et al. 2003) indicate that weight gain greatly depends on feeding conditions, whereas length can increase despite suboptimal feeding conditions. This suggests that the condition of Shortbelly Rockfish is related to the trophic level of larval prey and, by extension, the efficiency with which energy is transferred from the base of the food chain up to the larvae and assimilated by the larvae (Swailethorpe et al. 2023).

Since  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  integrates feeding history over the first days or weeks of life, we next examined the otolith microstructure of larval Shortbelly Rockfish (1–25 days postextrusion) to assess whether trophic efficiency affected otolith size at age and growth rate.



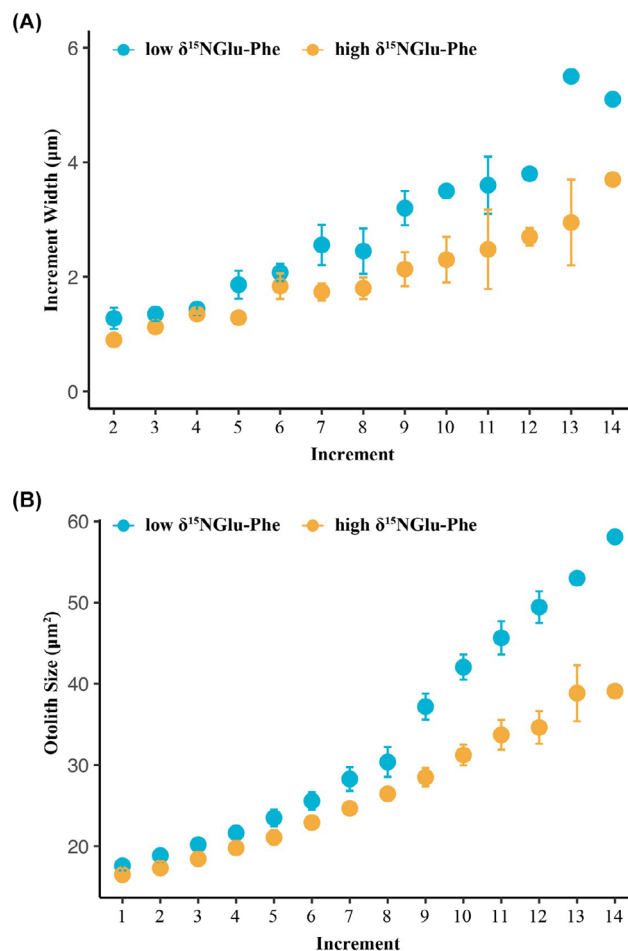
**FIGURE 2** Predictors of larval Shortbelly Rockfish condition. (A) Bayesian hierarchical model output indicates that age is a strong predictor of length, whereas (B) both age and lower  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  are strong predictors of weight. (C) Moreover, age,  $\delta^{15}\text{N}_{\text{Glu-Phe}}$ , their interaction, and individual effects are all strong predictors of otolith increment width. (D) The  $\delta^{15}\text{N}_{\text{Phe}}$  value shows an inverse relationship and substantial effects on  $\delta^{15}\text{N}_{\text{Glu-Phe}}$ . Data represent the mean  $\pm$  89% compatibility interval ( $N=18$ ),  $\sigma$  represents the standard deviation (SD) of the normal distribution estimated by the model,  $\sigma_{\alpha}$  represents the SD of individual random effects, and  $\sigma_{\text{I}}$  represents the SD of year random effects.

Otolith increment width strongly varied across individuals (Supplemental Figure 3). Even so, feeding on lower  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  prey strongly increased the increment width,

and this pattern was amplified with age (Figure 2C). To visualize this, we divided the larval Shortbelly Rockfish into a low  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  group (mean  $\pm$  SE =  $9.68 \pm 0.74\text{‰}$ ;  $N=9$ ) and a high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  group ( $13.82 \pm 0.40\text{‰}$ ;  $N=9$ ). We observed that larval Shortbelly Rockfish feeding on prey with low  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  consistently exhibited faster otolith growth histories (Figure 3A) and larger otolith sizes at age (Figure 3B). Rapid growth is most often found to be an important driver of larval survival. The stage duration hypothesis (Chambers and Leggett 1987) argues that the mortality rate decreases as fish larvae develop because the accelerated growth rate decreases the duration spent in the vulnerable larval stage (Meekan and Fortier 1996; Garrido et al. 2015). Empirically, slower-growing individuals were found to be selectively preyed upon in a variety of fish studies, including studies on the Japanese Anchovy *Engraulis japonicus* (Takasuka et al. 2017) and Quillback Rockfish *S. maliger* (Fennie et al. 2020). Our observations imply that feeding on lower trophic level prey facilitates a larger otolith size at age and faster growth in larval Shortbelly Rockfish.

Larval size at age is postulated to positively impact survival, as it influences swimming efficiency, prey capture, and predator evasion (Houde 2008, 2009). Past studies showed that a larger otolith core size (which reflects larval size at hatch/extrusion) was positively correlated with survival (Meekan and Fortier 1996; Garrido et al. 2015; Fennie et al. 2023b), and the effect was magnified with age (Malca et al. 2022). Here, our results suggest that otolith core size did not affect the length of larval Shortbelly Rockfish (Figure 2A) but strongly influenced their weight (Figure 2B). Potential reasons for the lack of effect on larval length may be due to the small sample size. Even so, any advantages related to a larger core size would be inconsequential if there were unsuitable and/or insufficient prey available in the environment.

Next, we sought to identify the low-trophic-level food source responsible for heavier and faster-growing larval Shortbelly Rockfish, as past studies suggested that consuming specific prey taxa can boost larval growth and survival (Murphy et al. 2012; Beaugrand et al. 2013; Burns et al. 2021; Malca et al. 2022). Gut content analysis revealed that the larval Shortbelly Rockfish diet was primarily composed of Calanoida copepodites (41.73%), Calanoida nauplii (17.51%), and unidentified Copepoda copepodites (14.52%; Table 1). Although larvae in the high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  group tended to consume more C mass than the larvae in the low  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  group (Figure 4), their differences were not significant across total prey, Calanoida copepodites, and Calanoida nauplii (Figure 4). This suggests that the trophic level of larval Shortbelly Rockfish may be determined lower in the food chain, possibly impacting prey energy content, and not through prey switching by



**FIGURE 3** The relationship between otolith increment width or otolith size and trophic position. Larval Shortbelly Rockfish with low  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  (mean  $\pm$  standard error [SE] =  $9.68 \pm 0.74\text{‰}$ ) had (A) faster otolith growth histories and (B) larger otolith size at age compared to larvae with high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  ( $13.82 \pm 0.40\text{‰}$ ). Data represent the mean  $\pm$  SE ( $N=9$  fish/treatment).

the larvae. Moreover, our inability to visually identify prey items to species hindered our capacity to determine which prey types optimize energy transfer (Robert et al. 2014).

The observed effects of  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  on larval condition despite similar diet suggest that bottom-up processes could be responsible. To explore this further, we next examined whether  $\delta^{15}\text{N}_{\text{Phe}}$ , which is a source amino acid reflecting  $\delta^{15}\text{N}$  at the base of the larval food chain, showed any relationship with the explored parameters. Although  $\delta^{15}\text{N}_{\text{Phe}}$  did not correlate with time or place of larval capture, length, weight, or otolith growth (not shown), it did affect  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  (Figure 2D). This observation indicates that when  $\delta^{15}\text{N}_{\text{Phe}}$  was high, the larvae fed at a lower trophic level. The value of  $\delta^{15}\text{N}_{\text{Phe}}$  is reflective of (1) changes in inorganic N sources, with deep nitrate characterized by higher  $\delta^{15}\text{N}$  compared to N fixation or recycling near the surface; and (2) changes in primary producers, as different phytoplankton species can fractionate  $\delta^{15}\text{N}$  at

**TABLE 1** Diet metrics for recovered gut contents of Shortbelly Rockfish. Nonpercentage values are presented as mean  $\pm$  standard deviation.

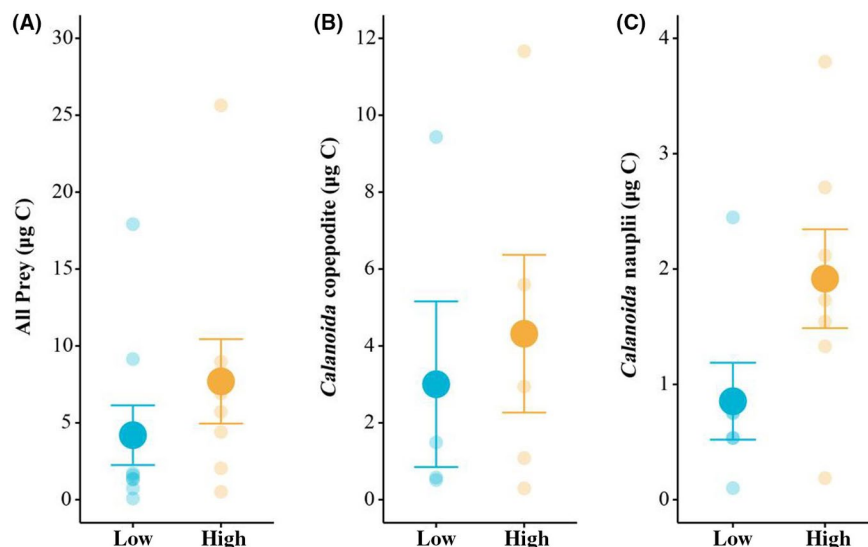
Prey	Average length ( $\mu\text{m}$ )	Average width ( $\mu\text{m}$ )	Average number	Abundance (%)	Average C weight ( $\mu\text{g}$ )	Biomass (%)
Calanoida copepodites	431.58 $\pm$ 155.13	230.72 $\pm$ 88.23	2.92 $\pm$ 4.43	19.94	2.18 $\pm$ 3.94	41.73
Calanoida nauplii	250.76 $\pm$ 68.15	141.96 $\pm$ 43.71	4.21 $\pm$ 4.20	28.77	0.92 $\pm$ 1.02	17.51
Copepoda copepodites	395.11 $\pm$ 125.80	199.54 $\pm$ 42.23	1.17 $\pm$ 2.10	7.98	0.76 $\pm$ 1.45	14.52
Cyclopoida nauplii	201.59 $\pm$ 44.97	107.39 $\pm$ 34.42	3.63 $\pm$ 3.85	24.79	0.45 $\pm$ 0.55	8.64
Eggs	186.68 $\pm$ 75.13	164.82 $\pm$ 29.20	0.46 $\pm$ 1.72	3.13	0.35 $\pm$ 1.45	6.63
Cyclopoida copepodites	440.3 $\pm$ 100.88	212.75 $\pm$ 53.23	0.42 $\pm$ 1.10	2.85	0.33 $\pm$ 0.88	6.22
Other nauplii	192.86 $\pm$ 53.14	124.88 $\pm$ 42.47	1.67 $\pm$ 2.10	11.40	0.19 $\pm$ 0.26	3.72
Others	282.13 $\pm$ 243.74	198.88 $\pm$ 177.04	0.17 $\pm$ 0.38	1.14	0.05 $\pm$ 0.19	1.02

different rates (McMahon and McCarthy 2016; Sigman and Fripiat 2019). Increased upwelling and/or changes in phytoplankton communities could have affected the observed larval trophic changes; however, more research is needed to explore this.

Our results show that Shortbelly Rockfish that fed on prey at lower trophic levels were heavier and grew faster and thereby likely increased their survival. As such, this study lends preliminary support for the TEEL hypothesis (Swalethorp et al. 2023); moreover, our work suggests that TEEL may be applicable to species other than the Northern Anchovy. We cannot rule out prey nutritional quality and larval food assimilation efficiency as having some impact on the observed changes in trophic level (Gaye-Siessegger et al. 2003, 2004; Trueman et al. 2005). Other factors, including maternal investment, size at hatch/extrusion, and species-specific differences in prey, likely also influence larval recruitment and should be explored in future studies. However, our observations suggest that larval performance may be driven by bottom-up processes wherein lower trophic level/higher energy transfer efficiency could be proportional to the amount of energy reaching the larval population. As stated by Lasker (1985), the key to understanding recruitment dynamics is to determine *what* mostly limits recruitment and *when* in the life cycle this occurs. Although limited in scope, our study showcases some of the intricacies between trophic connections and the early life success of fish and highlights the need for more extensive research to connect larval trophic position with prey identity, nutritional quality, and larval performance and to determine its relationship to recruitment in Shortbelly Rockfish and other species that are relevant to fishery management.

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**FIGURE 4** Comparison of carbon (C) weight consumed across larval Shortbelly Rockfish from the low and high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  groups. There was no significant difference in the C weights of (A) total prey ( $t = -1.0402$ ,  $p = 0.3173$ ), (B) Calanoida copepodites ( $t = -0.4412$ ,  $p = 0.6729$ ), and (C) Calanoida nauplii ( $t = -1.9576$ ,  $p = 0.0768$ ) consumed between larvae with low  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  (mean  $\pm$  standard error [SE] =  $9.68 \pm 0.74\%$ ) and those with high  $\delta^{15}\text{N}_{\text{Glu-Phe}}$  ( $13.82 \pm 0.40\%$ ). Data represent the mean  $\pm$  SE.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data are available via Dryad (<http://doi.org/10.5061/dryad.dfn2z3584>).

#### ETHICS STATEMENT

To the best of our knowledge, our work and practices fully comply with the ethics guidelines set by this journal and general scientific and academic standards.

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