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Upwelling enhances planktivory in a benthic-feeding omnivorous damselfish on subtropical reefs

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ABSTRACT: Reef ecosystems are fueled by both benthic and pelagic pathways, yet how the contribution of these sources varies across spatial and temporal scales remains a central question in reef ecology. Most research has focused on tropical coral reefs, whereas subtropical systems, defined by stronger oceanographic variability, have received far less attention. Coastal upwelling amplifies this variability and delivers nutrient-rich pelagic subsidies that may reshape food web dynamics, although their effects on reef trophic interactions remain largely unknown. Here, we investigated the influence of upwelling on multiple dimensions of the trophic niche by increasing plankton subsidies to the benthic-feeding omnivorous damselfish *Stegastes pictus*, integrating foraging behavior, diet composition, and stable isotope analysis in subtropical reefs of the Southwestern Atlantic, under contrasting non-upwelling and upwelling conditions. Although benthic feeding prevailed in both conditions, plankton feeding increased markedly during upwelling, with bite rates nearly tripling and dietary contribution rising from 0.1 to almost 20%. Stable isotope data and Bayesian mixing models indicated a consistent contribution of both benthic and pelagic sources across periods, reflecting longer-term pelagic integration. These findings reveal that upwelling creates transient windows of trophic opportunity, promoting pelagic food resource use and trophic niche expansion in benthic-feeding omnivorous fishes such as *S. pictus*. Environmental variability in subtropical systems thus provides high-quality pelagic resources that support generalist species with flexible diets, enhancing trophic connectivity, resilience, and the overall stability of subtropical reef food webs.

KEY WORDS: Trophic niche · Food web · Diet shift · Foraging behavior · Stable isotope analysis · *Stegastes pictus* · Yellowtip damselfish · Southwestern Atlantic

1. INTRODUCTION

Reefs are among the most productive and biodiverse ecosystems on Earth, supporting high abundance and biomass across trophic levels (Odum & Odum 1955, Shakya & Allgeier 2023, Morais et al. 2025). Clarifying the origins and pathways of energy and nutrients through reef food webs is key to understanding the mechanisms that sustain such exceptional productivity (Bierwagen et al. 2018, Palola et al. 2025). Historically, high productivity was attributed to efficient endogenous recycling within the benthic compartment, via algae, zooxanthellate corals, filter-feeding invertebrates, detritus-associated microorganisms, and the production of eggs and larvae (Odum & Odum 1955, Hatcher 1988, Allgeier et al. 2018). However, reefs are embedded in dynamic seascapes where water movement transports subsidies

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across large spatial and temporal scales, promoting substantial pelagic inputs among habitats (Hamner et al. 1988, Shakya & Allgeier 2023, Morais et al. 2025, Palola et al. 2025). Increasing evidence highlights the significant contribution of pelagic pathways to reef food webs and secondary productivity, supporting organisms across multiple trophic levels, including top predators (Hamner 1988, Morais & Bellwood 2019, Morais et al. 2021, Siqueira et al. 2021, Skinner et al. 2021, Richardson et al. 2025). Benthic recycling and pelagic subsidies are complementary to sustain reef productivity, with their relative contributions shaped by the communities and environmental conditions (Shakya & Allgeier 2023).

Although still limited, existing research on reef productivity has primarily focused on tropical coral systems, while the role of benthic and pelagic processes in sustaining food webs on subtropical reefs remains poorly understood. Subtropical reefs are characterized by pronounced oceanographic variability and unpredictability, exhibiting wide seasonal fluctuations in water temperature, turbidity, and nutrient availability (Ferreira et al. 1998b, Beger et al. 2014, Cordeiro et al. 2020, Toth et al. 2021, Wu et al. 2025). These systems experience chronic disturbance regimes across multiple temporal scales (Beger et al. 2014), in contrast to the relative environmental stability of tropical coral reefs (Toth et al. 2021, Wu et al. 2025). Among the environmental variables that shift seasonally, temperature plays a dominant role due to its direct influence on the metabolic and feeding rates of ectothermic organisms (Barneche et al. 2009, Nunes et al. 2021, Zaú et al. 2025). Some subtropical reefs are often subject to coastal upwelling, which intensifies temperature variability by delivering cold water (Kämpf & Chapman 2016, Liu et al. 2025). Acute drops in ambient temperature can therefore have physiological and behavioral consequences for fish, impairing locomotion and foraging, reducing energy intake, and potentially leading to starvation or other negative impacts on health and fitness (Donaldson et al. 2008). At the same time, upwelling acts as an important source of pelagic subsidies, thereby increasing overall reef productivity (Menge et al. 2003, Kämpf & Chapman 2016, Cordeiro et al. 2020, Liu et al. 2025). This duality creates a challenge in disentangling the potential negative effects of cooling from the beneficial trophic enrichment driven by upwelling in these dynamic ecosystems.

Upwelling events transport large amounts of plankton, organic matter, and nutrients from cold, deep waters to the surface, enhancing local productivity and attracting species across multiple trophic levels, thereby transforming upwelling areas into potential biodiversity hotspots (Chavez & Messié 2009, Kämpf & Chapman 2016). Although coastal upwelling tends to follow seasonal patterns, its temporal and spatial dynamics are highly variable due to unpredictability in meteorological–oceanographic interactions, causing fluctuations in frequency, duration, and intensity (Ferreira et al. 1998b, Kämpf & Chapman 2016, Fernandes et al. 2017). Upwelling influences reef food webs by supplying pelagic subsidies (upwelled zooplankton and organic matter) and dissolved nutrients that alter trophic structure and intensify the pace of feeding interactions within marine ecosystems (Polis et al. 1997, Menge et al. 2003, Palumbi 2003, Kämpf & Chapman 2016). These processes shape spatial and temporal variability in plankton communities, modifying zooplankton composition and increasing its abundance, thereby attracting planktivorous fishes and their predators (Palumbi 2003, Guenther et al. 2008, Rosa et al. 2016, 2023). Upwelling inputs also impact the reef benthos, where dissolved nutrients enhance algal productivity and affect the benthic community structure, in terms of composition, abundance, and growth (Menge et al. 2003, Corbisier et al. 2014, Cordeiro et al. 2020, Spring & Williams 2023). The ecological significance of upwelled oceanic inputs is increasingly recognized as a critical driver in sustaining reef food webs and buffering thermal stress imposed by climate change (Menge et al. 2003, Spring & Williams 2023, Richardson et al. 2025). However, most evidence comes from tropical reefs, whereas in subtropical reefs, marked by pronounced oceanographic variability and serving as biogeographic boundaries for tropical species (Beger et al. 2014), the role of upwelling subsidies remains poorly understood.

Fish play a central role in reef trophic dynamics, acting as keystone consumers that drive nutrient transport and internal recycling to sustain high ecosystem productivity (Odum & Odum 1955, Allgeier et al. 2014, Brandl et al. 2019). Their rapid behavioral responses to environmental change make reef fishes sensitive indicators of shifts in ecosystem parameters (e.g. Ferreira et al. 1998b, Mendes et al. 2009, Goldstein et al. 2017, Zaú et al. 2025). Upwelling delivers pulses of plankton, organic matter, and dissolved nutrients, particularly enriched in nitrogen and phosphorus, that are typically limited in oligotrophic waters and benthic habitats (Kämpf & Chapman 2016). Yet few studies have assessed whether reef fishes actively switch feeding strategies to exploit these sporadic subsidies. Pelagic contributions detected from stable isotope signatures in benthic-feed-

ing species have generally been attributed as shifts in benthic prey nutritional quality enhanced by nutrient input rather than in prey type, as observed in herbivore and detritivores on subtropical reefs (Wyatt et al. 2012, Cardozo-Ferreira et al. 2023) and omnivores on temperate, macroalgae-dominated reefs in Chile (Docmac et al. 2017). In contrast, direct evidence of increased upwelled plankton consumption has only been reported for economically important demersal fishes inhabiting soft-sediment habitats (Hamaoka et al. 2014, Bauer & Fischer 2024). Thus, the extent to which upwelling-driven pelagic subsides directly influences the feeding ecology of reef-associated fishes remains largely unexplored.

This study aimed to investigate how benthic and pelagic pathways contribute to the food web of subtropical reefs subjected to upwelling, through a benthic-feeding omnivorous fish. Among reef fish assemblages, damselfishes (Pomacentridae) are ubiquitous across reefs globally, spanning a range of trophic strategies, from benthic territorial herbivory and omnivory to planktivory and intermediate modes (Frédérich et al. 2009, 2016, Gajdzik et al. 2016). Thus, they are important reef representatives and suitable model species for trophic studies (Barneche et al. 2009). We used an integrative approach to assess the feeding ecology of the yellowtip damselfish *Stegastes pictus* (Castelnau, 1855) on subtropical rocky reefs of the southwestern Atlantic, influenced by seasonal coastal upwelling. The species' trophic niche dimensions were examined using complementary approaches: bite rate to quantify foraging behavior, gut content analysis for diet composition, and stable isotope analysis to trace nutrient assimilation pathways. We hypothesized that upwelling events, by delivering nutrient- and protein-rich pelagic subsidies, promote a trophic niche expansion for fish through the exploitation of ephemerally abundant planktonic resources.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted on subtropical rocky reefs off the southeastern coast of Brazil, at Arraial do Cabo (22° 58′ S, 42° 02′ W), located in the Southwestern Atlantic (Fig. 1). This system comprises an isthmus and 2 main islands that enclose a sheltered bay, mostly surrounded by rocky reefs that support high reef-associated biodiversity (Ferreira et al. 2001, Cordeiro et al. 2020, Cord et al. 2022). The area is strongly characterized by seasonal upwelling events driven by prevailing NE and N winds, occurring mainly in austral spring and summer, known as the Cabo Frio Upwelling System (Gonzalez-Rodriguez et al. 1992, Valentin 2001, Rosa et al. 2023). These events bring cold, nutrient-rich waters to the surface, boosting productivity and, consequently, local zooplankton biomass (Valentin 1984, Rosa et al. 2023). Two sampling campaigns were carried out under contrasting oceanographic conditions. The first was conducted in March 2023, during the austral summer—autumn transition, defined here as the non-upwelling condition, characterized by warm waters. The second occurred in Sep-

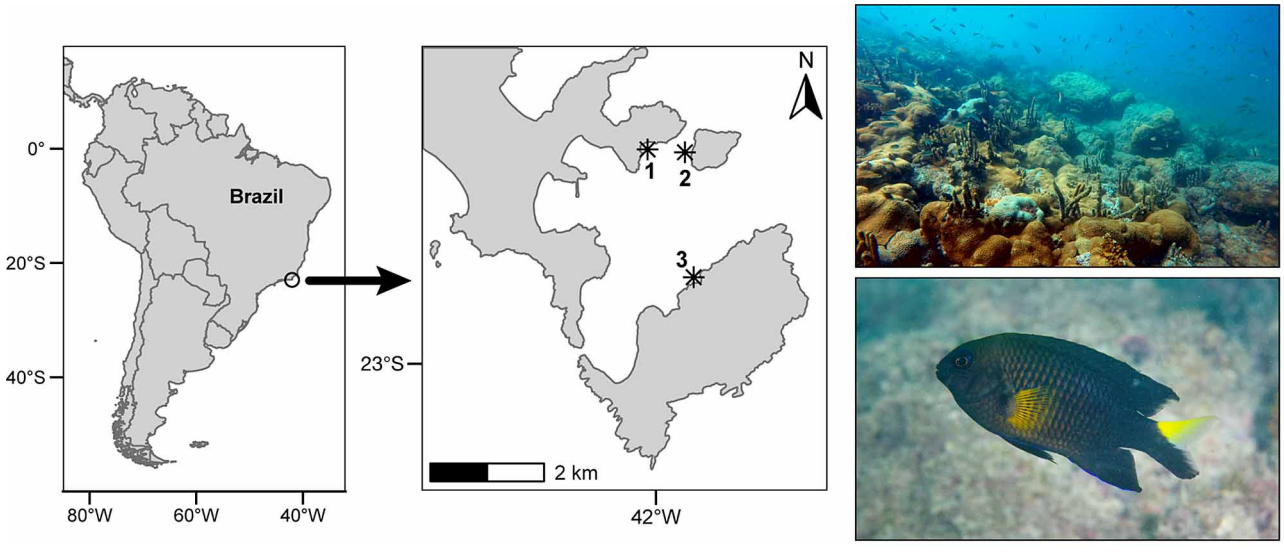

Fig. 1. Study area on subtropical reefs off Arraial do Cabo, Brazil, with photographs detailing the Porcos reef site and *Stegastes pictus*. Asterisks: sampled sites (1: Cardeiros; 2: Porcos; 3: Pedra Vermelha). Photos by Jaqueline Toledo and João Paulo Krajewski

tember 2023, during the austral winter–spring transition, and is defined here as the upwelling condition. This sampling encompassed both an active upwelling event and the subsequent days when cold, upwelled waters mixed with warmer waters (Rosa et al. 2023). The active upwelling period was inferred from NE winds and *in situ* measurements of minimum water temperatures (<18°C) at 1 and 6 m depths, as recorded in real time by the Aqualink buoy 'Farol Island Beach' (Aqualink, https://aqualink.org/sites/984, accessed 10 December 2025). In each campaign, we used SCUBA diving to sample 3 sites within the sheltered bay, where *Stegastes pictus* occurs in high densities.

S. pictus is an endemic Brazilian damselfish characterized by generalist habitat use and feeding plasticity (Fig. 1). It occurs from shallow to mesophotic reefs along most of the Brazilian coast and oceanic islands, tolerating variable oceanographic conditions in tropical, subtropical, and temperate-warm regions (Floeter et al. 2007, de Oliveira Soares et al. 2018, Chaves et al. 2021). Although previously described as omnivorous (Ferreira et al. 2001, Floeter et al. 2007), herbivorous (de Oliveira Soares et al. 2018), or invertivorous (Chaves et al. 2021), no study to date has evaluated its diet and the use of resources from benthic and pelagic compartments.

2.2. Foraging behavior

To assess the foraging behavior of *S. pictus*, we conducted focal-animal observations (Lehner 1992) on 212 individuals during SCUBA dives: 93 in non-upwelling conditions and 119 during upwelling. *S. pictus* exhibits a patchy spatial distribution, typically forming high-density aggregations, with each individual maintaining a well-defined territory. Within each aggregation, 2–3 individuals, separated by sufficient distance to ensure independent foraging observations, were selected along with additional solitary individuals. Each focal fish was observed for 5 min to quantify absolute bite rates in 2 foraging compartments: benthic (i.e. bites on the substrate) and pelagic (i.e. bites in the water column). In total, 17.6 h of behavioral observations were conducted. To minimize diver interference on fish behavior, observers maintained a distance of 2–3 m from individual territories and allowed a 2 min acclimation period before sampling began. Only adult individuals (i.e. total length of >6 cm and lacking the black ocellus on the dorsal fin) were sampled to avoid ontogenetic variability. Water temperature at each focal individual territory was measured using dive computers. From the bite rate data, we calculated the relative bite rate in each compartment, i.e. the percentage of total bites per fish that occurred in each compartment, thereby standardizing feeding across fish regardless of variation in absolute bite rate counts.

2.3. Diet composition

The diet composition of *S. pictus* was characterized by gut content analysis under both non-upwelling and upwelling conditions. We collected 24 adult individuals per oceanographic condition by spearfishing in the morning, between 08:30 and 12:00 h, following behavior observations that confirmed active foraging during this period. Specimens were immediately frozen to minimize the digestive processes. In the laboratory, total length, standard length, and intestinal length were measured in each specimen. The stomach and the anterior 4 cm of the intestine were dissected and preserved in 4% formalin. Each gut was opened in a Petri dish under a stereomicroscope, and feeding items were separated and identified to the lowest possible taxonomic resolution and classified according to benthic or pelagic origin. Unidentifiable amorphous material was categorized as digested organic matter and, together with plastic debris, excluded from quantitative analysis. This category comprised endogenous gastrointestinal material (e.g. gastric fluids, mucus) and highly digested prey remains that could not be reliably assigned to a taxonomic or functional category, or to a benthic or pelagic origin. We acknowledge that excluding this fraction may lead to an underestimation of pelagic feeding, particularly of soft-bodied or gelatinous planktonic prey. On average, digested organic matter accounted for 64.6 and 76% of gut contents during non-upwelling and upwelling, respectively. Feeding item volumes (mm^3) were measured by compressing each item between the edges of two 1 mm-thick microscope slides over the mm-gridded Petri dish and counting the number of squares, each thus representing 1 mm^3 (Liedke et al. 2016). Diet was quantified by the volumetric index (%V), i.e. the percentage contribution of each feeding item's volume to the total gut content volume per fish; and the frequency of occurrence (%FO), i.e. the percentage of sampled guts in which each item was present, per condition (Liedke et al. 2016). Finally, we calculated the percentage feeding importance index (%IA) for each item category (i) per condition, using the equation $\%IA_i = (\%V_i \times \%FO_i) / \sum (\%V \times \%FO) \times 100$ (Kawakami & Vazzoler 1980).

2.4. Carbon and nitrogen stable isotopes

To trace the origins of assimilated resources in *S. pictus* tissues, we measured stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from the dorsal muscle of the same individuals analyzed for diet and from representative sources from benthic and pelagic compartments. The comparison was made between the 2 sampling periods, i.e. summer–autumn and winter–spring, rather than non-upwelling and upwelling conditions, given that fish tissue turnover exceeds the duration of the sampled upwelling event. The benthic resources were represented by the epilithic algal matrix (EAM), the main benthic substrate targeted by *S. pictus* (authors' pers. obs.). The sampling was conducted in damselfish territories after focal-animal sessions, specifically from areas with high bite rates. A total of 26 EAM samples per condition were scraped from 10 × 10 cm areas, stored in hermetically sealed plastic bags, and immediately frozen. In the laboratory, EAM samples were sorted under a stereomicroscope into Chlorophyta, Ochrophyta, Rhodophyta, and detritus. Due to the small size of EAM components, the 26 samples collected per condition yielded limited material; therefore, some samples of the same component were pooled to obtain sufficient biomass for isotope analysis.

Pelagic resources were collected using a 64 µm mesh plankton net with a mouth diameter of 50 cm, towed horizontally by a SCUBA diver over 100 m at 2–3 m above the reef substrate, within the depth range where *S. pictus* potentially feeds in the water column. The filtered water volume per tow was estimated at 19.63 m^3, using the formula for a cylinder ($V = \pi r^2 h$), based on the net mouth radius (r) and horizontal distance covered (h). Seston samples were collected in triplicate per condition, stored in bottles, and immediately frozen. Samples were thawed in the lab and filtered through a 150 µm mesh to remove larger plankton and retain particulate material at the base of pelagic food webs (i.e. pelagic primary producers). All fish, benthic (algae and detritus), and pelagic (seston) samples were stored at −18°C for subsequent procedures.

The samples were oven-dried at 60°C for 24 h and ground into a fine, homogeneous powder with mortar and pestle. Detritus was split into 2 subsamples: one was acidified with 5% HCl to remove inorganic carbonates not related to diet and avoid bias in $\delta^{13}C$, while the other was left untreated for $\delta^{15}N$ (Schlacher & Connolly 2014). The samples were weighed to the nearest 0.0001 g and packed into tin capsules. The stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were analyzed using a continuous flow isotope ratio mass spectrometer (Flash 2000 Delta V Advantage) coupled to an elemental analyzer (TC/EA) (EA-IRMS ThermoFisher Scientific), at the Centro Integrado de Análises–CIA-FURG. Isotope ratios were expressed as δ in parts per thousand (‰), in relation to international standards. The standard reference materials were Vienna PeeDee Belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. The average analytical precision obtained from internal standards was 0.22 for $\delta^{13}C$ and 0.05 for $\delta^{15}N$. The influence of lipids on $\delta^{13}C$ of fish muscle was evaluated based on the C:N ratio, and values were corrected when they exceeded 3.5 using a normalization equation (Svensson et al. 2014).

2.5. Statistical analysis

All statistical analyses were performed in R software version 4.3.3 (R Core Team 2024). Foraging, diet, and stable isotope data did not meet the assumptions of normality or homogeneity of variances as assessed using Shapiro-Wilk and Levene's tests and were therefore analyzed using non-parametric statistical methods. Water temperatures between non-upwelling and upwelling conditions were compared using the Fisher-Pitman permutation test with 999 permutations (package 'coin'; Hothorn et al. 2008). Foraging behavior was assessed at 2 levels. (1) Overall absolute bite rates were compared between conditions using the Fisher-Pitman permutation test. (2) To evaluate how absolute bite rates in benthic and pelagic compartments were affected by oceanographic condition, a generalized linear mixed model (GLMM) was fitted using 'glmmTMB' package (Brooks et al. 2017), assuming a negative binomial distribution with a log link to account for overdispersed count data. The model included foraging compartment (benthic and pelagic), condition (non-upwelling and upwelling), and their interaction as fixed effects. As each fish contributed one bite rate per compartment, individual fish identity was included as a random intercept to account for the repeated structure of the data set. Model assumptions were validated using residual diagnostics from the 'DHARMa' package (Hartig 2024; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/meps15142_supp.pdf), and post hoc multiple comparisons across fixed-effect pairwise contrasts were evaluated using estimated marginal means from the 'emmeans' package (Lenth 2023).

Diet analysis was based on %V, which enables standardized comparisons among individuals while avoiding biases associated with absolute ingested vol-

umes. Diet was assessed at 3 levels. (1) To test for the effect of condition on diet composition across feeding compartments, an analysis of similarity (ANOSIM) was performed using Bray-Curtis dissimilarities (function 'anosim' in the 'vegan' package; Oksanen et al. 2011). Patterns in diet composition were visualized using non-metric multidimensional scaling (nMDS; function 'metaMDS' in the 'vegan' package). (2) To assess whether the volume contribution of pelagic items differed between conditions, a Fisher-Pitman permutation test was applied. (3) To evaluate the influence of condition on the diet composition across fine-scale taxonomic groups, a second ANOSIM was conducted, followed by nMDS for visualization. A 3-dimensional solution ($k = 3$) was chosen as it reduced the stress to an acceptable level (<0.2).

Stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) of *S. pictus* and its benthic and pelagic food resources were analyzed using 2 approaches. (1) A visual dispersion in an isotopic biplot of $\delta^{13}C$ and $\delta^{15}N$ with average and standard error was used to assess potential shifts between summer–autumn and winter–spring periods. To compare the fish isotopic values between periods, a Kruskal-Wallis test was applied. (2) To estimate the relative contribution of assimilated feeding sources by *S. pictus* between periods, Bayesian stable isotope mixing models were used (package 'simmr'; Parnell et al. 2013), based on the $\delta^{13}C$ and $\delta^{15}N$ of benthic and pelagic resources. Potential food sources for the mixing model were selected from the biplot, prioritizing those with distinct $\delta^{13}C$ signatures (i.e. Chlorophyta, detritus, and seston) to reduce isotopic overlap and improve model discrimination. Benthic resources (algae and detritus) were treated as direct food items (i.e. consumed directly by *S. pictus*); therefore, trophic discrimination factors for herbivorous fish muscle were applied ($\Delta^{13}C = 2.6 \pm 0.6$ and $\Delta^{15}N = 4.5 \pm 0.5$; Stephens et al. 2023). In contrast, seston samples represent pelagic basal primary producers and organic matter, which are not directly consumed. To account for an additional trophic step between these consumers and these basal sources, trophic discrimination factors for carnivorous fish were added for this source ($\Delta^{13}C = 4.3 \pm 0.8$ and $\Delta^{15}N = 5.7 \pm 0.7$; Stephens et al. 2023).

3. RESULTS

3.1. Foraging behavior

Water temperature differed significantly between oceanographic conditions (Fisher-Pitman permutation test; $Z = 13.886$, $p < 0.001$; Fig. S2A), being warm and stable during non-upwelling (24–26°C; mean: 25.1°C) and cooler and more variable during upwelling (18–22°C; mean: 19.6°C). *Stegastes pictus* foraging patterns were also influenced by condition ($Z = 6.222$, $p < 0.01$), with a 42% decrease in bite rate during upwelling (17.7 ± 0.9 bites per 5 min during non-upwelling and 10.2 ± 0.7 bites per 5 min during upwelling; Fig. S2B). Bite rates differed significantly across feeding compartments and oceanographic conditions (negative binomial GLMM; $z = 9.75$, $p < 0.001$; Fig. 2; Tables S1 & S2). During non-upwelling,

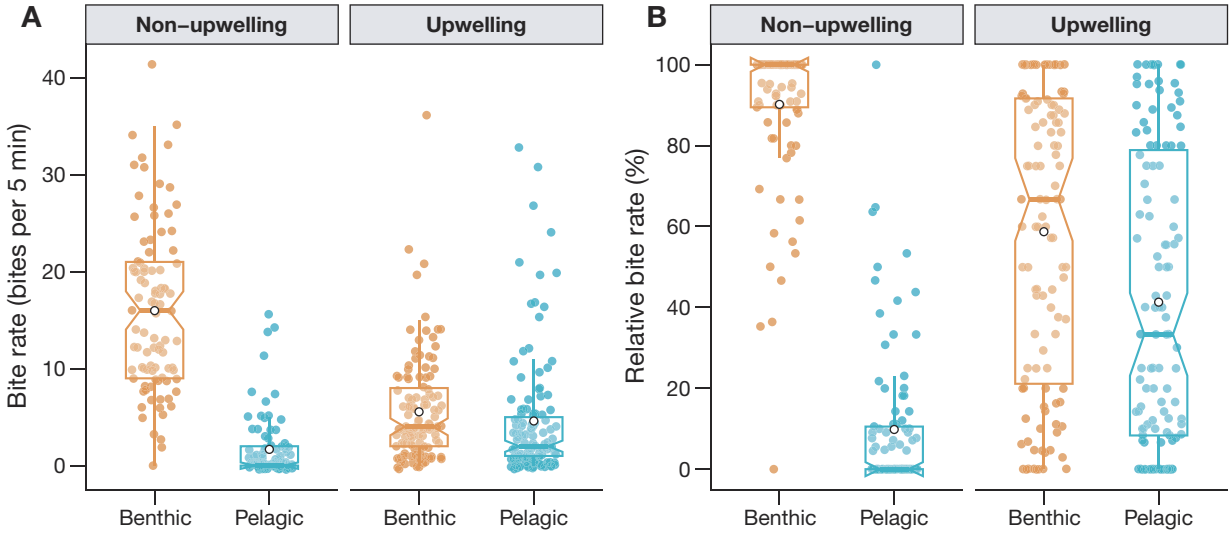

Fig. 2. (A) Absolute bite rate and (B) relative bite rate of *Stegastes pictus* in benthic and pelagic compartments under non-upwelling and upwelling conditions. Dots: individual fish; white circles: mean. Boxplots show the median and interquartile range (Q1–Q3); whiskers represent the minimum and maximum values, excluding outliers

benthic foraging dominated, with almost 10-fold higher bite rates than pelagic feeding (16 ± 0.9 and 1.7 ± 0.3 bites per 5 min, respectively). However, during upwelling, bite rates on benthic substrates declined, while pelagic bite rates increased nearly 3-fold (5.5 ± 0.5 and 4.6 ± 0.6 bites per 5 min, respectively), resulting in a reduced disparity between benthic and pelagic foraging compared to non-upwelling conditions, although they remained statistically distinct (Table S3). The distribution of relative bite rates also differed considerably between conditions (Fig. 2B). Under non-upwelling, most individuals (75%) concentrated their feeding on benthic substrates, directing no more than 10.5% of their bites to plankton (i.e. upper quartile). In contrast, during upwelling, most individuals substantially increased pelagic foraging, with up to 78.9% of their bites directed to planktonic prey.

3.2. Diet composition

The diet of *S. pictus* was dominated by benthic food items under both conditions, but a clear shift in plankton contribution was observed (Fig. 3A; Table S4). Condition significantly influenced diet composition (ANOSIM; R = 0.274, p < 0.001), with planktonic items occurring more frequently — appearing in 90% of all individuals — and with greater %V in upwelling compared to non-upwelling conditions. Consequently, the feeding importance index of planktonic items increased from just 0.1% in the absence of upwelling to 19.7% during its influence (Fig. 3A), revealing a greater relative contribution of planktonic items during upwelling (Fisher-Pitman permutation test; $Z = -2.864$, $p < 0.001$). Upwelling promoted a dietary niche expansion, as shown by the expansion of the convex hull during this condition in the nMDS (Fig. 3B). In the absence of upwelling, diet was largely restricted to benthic items, whereas during upwelling, the polygon not only encompassed the previous dietary space but also expanded due to a more plankton-based diet.

Regarding the taxonomic composition of dietary prey, *S. pictus* exhibited an omnivorous feeding strategy, based mainly on crustaceans and algae in both conditions (Fig. 4A). However, when dietary items were analyzed at the lowest taxonomic resolution possible, upwelling significantly influenced diet composition (ANOSIM; R = 0.248, p < 0.001; Table S3). This differentiation was also evident in the nMDS ordination (Fig. 4B), where the dietary composition of individuals from each condition formed distinct, non-overlapping polygons. The polygon representing the diet during upwelling was larger and extended towards pelagic-origin resources, also suggesting an expansion of the trophic niche driven by upwelling. The main contributors to the increased importance of planktonic items for the diet of *S. pictus* were crustaceans and mollusks (Fig. 5). No pelagic crustaceans were recorded in the diet during the non-upwelling condition. In contrast, holoplanktonic copepods (Calanoida and Cyclopoida), planktonic ostracods, and decapod lar-

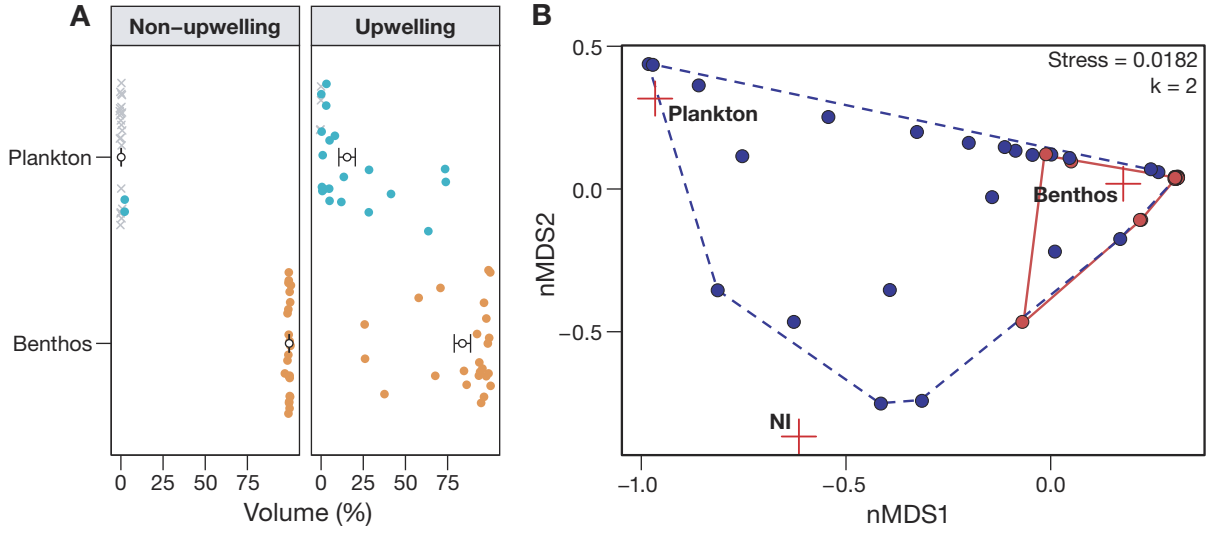

Fig. 3. (A) Relative contribution of benthic (orange) and pelagic (turquoise) resources to the diet volume of individual *Stegastes pictus* (dots). Crosses: zero values; white circles: mean ± SE. (B) Non-metric multidimensional scaling (nMDS) of diet composition (% volume) of individual fish (dots) in relation to resource compartment (red crosses) under non-upwelling (solid red line, red dots) and upwelling (dashed blue line, blue dots). Polygons enclose the variation in individual diets within each condition. NI: items with unidentified compartment origin

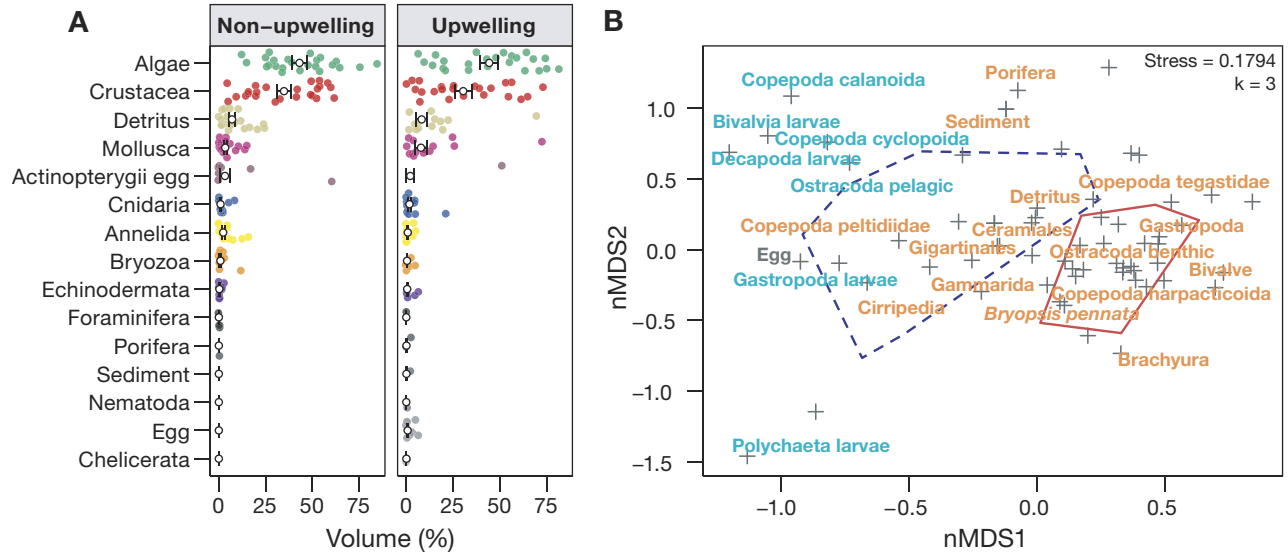

Fig. 4. (A) Relative contribution of major taxonomic groups to the diet volume of individual *Stegastes pictus* (dots). White circles: mean ± SE. (B) Non-metric multidimensional scaling (nMDS) of diet composition at finer taxonomic resolution (crosses) under non-upwelling (solid red line) and upwelling (dashed blue line) conditions. Polygons enclose the variation in individual diets within each condition. Labels indicate benthic (orange) and pelagic (turquoise) items, displaying only the most relevant taxa, in terms of volume. Gray labels: items with unidentified origin

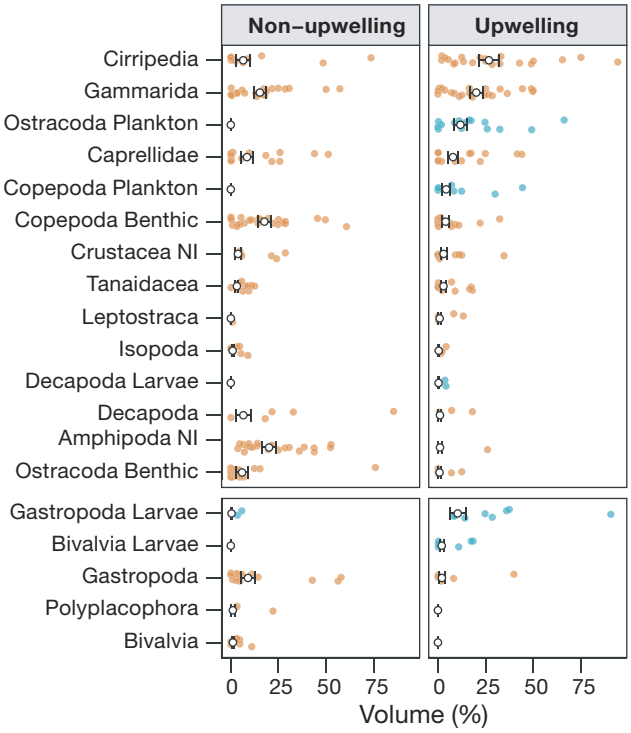

Fig. 5. Contribution of Crustacea (top) and Mollusca (bottom) to the diet of *Stegastes pictus*. Percentages were calculated considering only invertebrate categories (standardized to 100% of the invertebrate fraction, excluding other dietary components). Categories are ordered by decreasing mean relative volume (%) under upwelling conditions. Dots: percentage contribution of each category to individual fish (orange: benthic invertebrates; turquoise: pelagic invertebrates). White circles: mean ± SE. NI: not identified

vae were found exclusively during upwelling, occurring in almost 80% of the guts analyzed (i.e. 19 out of 24 guts). Consequently, when evaluating the feeding importance of crustaceans alone, pelagic forms increased from 0 to 34% during the upwelling. Pelagic-phase larvae of gastropod and bivalve were also predominantly observed during upwelling and occurred in high abundances when present. Some fish guts contained large volumes of gastropod larvae, representing over 25% of the total diet volume, while others contained more than 100 individual bivalve larvae.

3.3. Carbon and nitrogen stable isotopes

The stable isotope biplot of $\delta^{13}C$ and $\delta^{15}N$ of *S. pictus* showed no distinct values between sampling periods (Fig. 6). Neither $\delta^{13}C$ nor $\delta^{15}N$ values differed significantly between conditions (Kruskal-Wallis; $\chi^2 = 1.52$, df = 1, p = 0.217; $\chi^2 = 0.44$, df = 1, p = 0.506, respectively). The $\delta^{15}N$ values of *S. pictus* ranged from 12.4 ± 0.1‰ in summer–autumn to 12.5 ± 0.12‰ during winter–spring. Moreover, the stable isotope Bayesian mixing model revealed consistent relative contributions of benthic and pelagic compartments to the diet of *S. pictus*, with almost no visual differences between sampling periods (Fig. 7). During summer–autumn sampling, benthic sources accounted for an average of 64.5% of the total dietary source, with algae

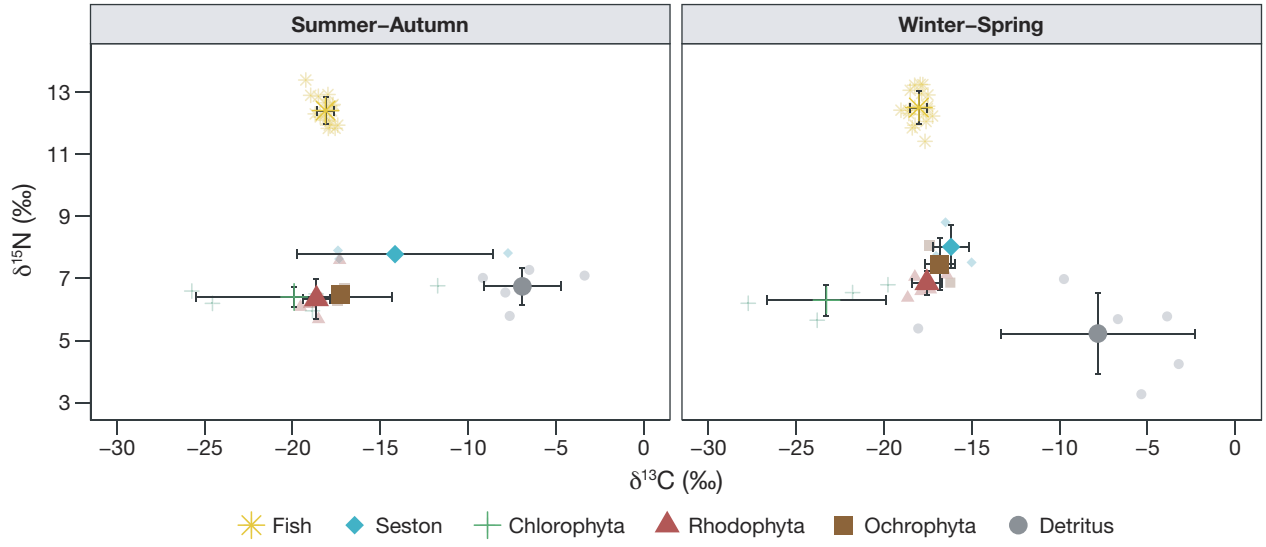

Fig. 6. $\delta^{13}C$ and $\delta^{15}N$ values of *Stegastes pictus*, benthic resources (Chlorophyta, Ochrophyta, Rhodophyta, and detritus), and pelagic resources (seston) between summer–autumn and winter–spring periods. Larger, darker symbols: mean ± SD; smaller, lighter symbols: individual fish or resource samples

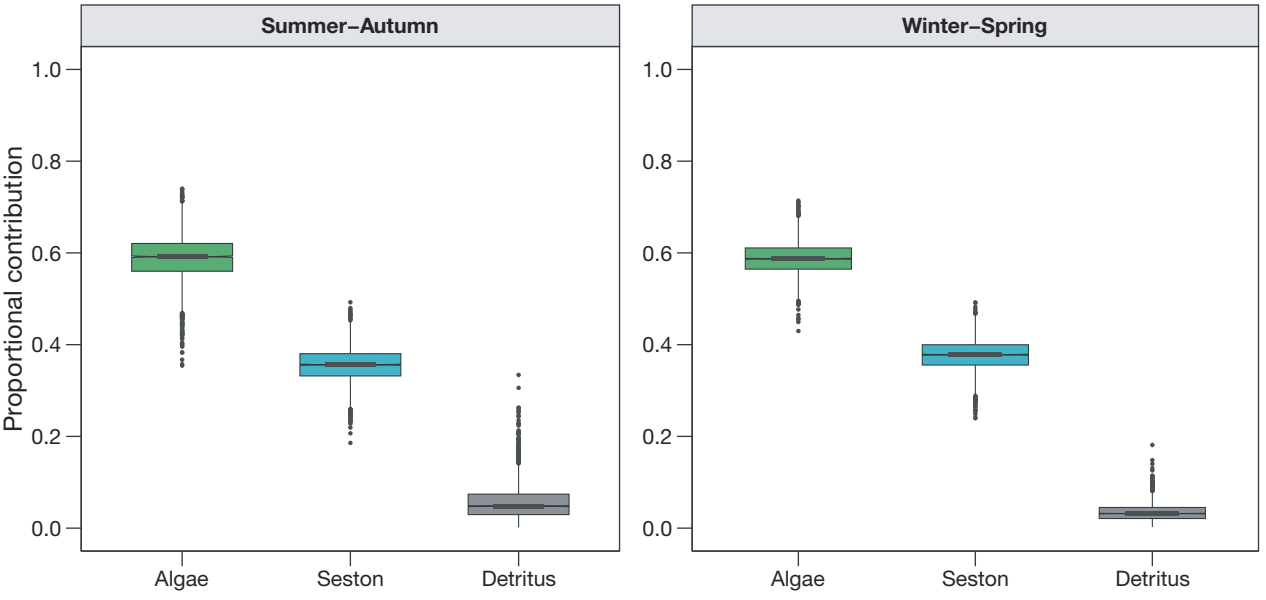

Fig. 7. Estimated contribution of benthic (algae and detritus) and pelagic (seston) sources to the diet of *Stegastes pictus* between summer–autumn and winter–spring periods, based on Bayesian stable isotope mixing models (SIMMR). Boxplot parameters as in Fig. 2

comprising 58.9% (48.2–67.9 at 95% credible interval) and detritus 5.6% (1–14.9%), whereas pelagic sources (seston) comprised 35.5% (28.1–42.2%). A similar pattern was observed during winter–spring, where benthic sources contributed an average of 62.2%, with algae comprising 58.7% (52.2–65.3%) and detritus 3.5% (0.8–7.8%), whereas pelagic sources (seston) comprised 37.8% (31–43.8%).

4. DISCUSSION

This study demonstrates that upwelling events can play a key role in expanding the trophic niche of reef fish in subtropical reef systems. By integrating foraging behavior, diet composition, and stable isotope analysis, we show that upwelling-driven subsidies shift the balance between benthic and pelagic forag-

ing for the yellowtip damselfish *Stegastes pictus*. Although benthic prey is the primary food source, our findings reveal a pronounced expansion toward pelagic resource use during upwelling, reflecting an opportunistic response to transient planktonic subsidies and supporting our hypothesis. In subtropical reefs, where oceanographic variability contrasts with the relative stability of tropical systems, upwelling may provide important pulses of pelagic productivity that enhance trophic flexibility and link connectivity along the food webs. Indeed, stable isotope mixing models showed a consistent pelagic contribution irrespective of the sampling periods, reflecting the cumulative incorporation of pelagic material from successive upwelling pulses into fish tissues over time.

Upwelling delivers pelagic subsidies to reef ecosystems by enhancing energy flow with nutrients, organic matter, and plankton availability, thus representing an important link between oceanic and reef environments (Palumbi 2003, Kämpf & Chapman 2016). As a continuous phenomenon that varies in intensity over time (Fernandes et al. 2017, Cardozo-Ferreira et al. 2023), local upwelling can create opportunities for trophic expansion. Despite its ecological significance, few studies have investigated how upwelling influences reef fish trophic niche, apart from temperature variation regulating feeding rates (Ferreira et al. 1998a,b, Mendes et al. 2009). On macroalgae-dominated reefs along the Chilean coast, where the Humboldt Upwelling System ranks among the most intense globally, stable isotope analysis of 7 species of benthic-feeding omnivorous fishes revealed a strong reliance on pelagic-derived material (Docmac et al. 2017). However, this signal was attributed to benthic prey incorporating pelagic inputs rather than to a direct trophic shift in the diet of the fishes — i.e. a shift in feeding from benthic to pelagic food items. In contrast, our study demonstrates a direct shift in damselfish feeding behavior and diet during upwelling, supported by increased planktonic contribution in bite rates and gut content. This finding highlights the opportunistic exploitation of pelagic subsidies when they become temporarily available. Direct trophic shifts have also been observed in sediment habitats, where demersal benthic-feeding fishes shifted their diets toward pelagic fish and crustaceans in response to upwelling (Hamaoka et al. 2014), including examples in our study region (Bauer & Fischer 2024). However, such direct effects of upwelling subsidies on fish trophic pathways in a subtropical reef have not been demonstrated until now.

The trophic niche of *S. pictus* expanded during an upwelling event, with increased bite rates in the water column and a diet composed of a wider and more distinct variety of planktonic prey. Importantly, stable isotope mixing models indicated that pelagic sources contribute nearly 40% of the species' time-integrated diet. Together, these results suggest that the abundance of planktonic organisms delivered during upwelling events represents a substantial energy source that complements the abundant benthic resources. A complementary hypothesis is that plankton may provide an extra source of nitrogen for these consumers. The Cabo Frio Upwelling System is a dynamic seasonal oceanographic feature subject to a mix of intra- and interannual variability that leads to diverse, abundant, and temporally dynamic plankton communities (Valentin 1984, Fernandes et al. 2017, Rosa et al. 2023). Copepods consistently dominate the pelagic community (Valentin 2001, Reis et al. 2025), with shifts in their abundance and species composition during upwelling and increases in opportunistic herbivores following phytoplankton blooms (Guenther et al. 2008, Rosa et al. 2023). The copepod abundance peak occurs between July and September (Rosa et al. 2023), coinciding with the presence of calanoid and cyclopoid pelagic copepods in *S. pictus* gut content. Meroplankton abundance also follows a seasonal pattern, with 2 annual peaks in bivalve larvae: one at the austral summer–autumn transition and another at the austral winter–spring transition (Fernandes et al. 2012). Our results showed that bivalve larvae were present in the yellowtip damselfish diet only during the austral winter–spring transition, attaining high abundance in fish guts when it occurred. Zooplankton have relatively high nutrient quality, as indicated by low average C:N ratios (4.55:1; Gahan et al. 2024), which reflect higher nitrogen content — a key element underpinning consumer growth and productivity. These values are comparable to those of fish prey (4.1:1; Wyatt et al. 2012) and substantially lower than those of turf algae (8.5:1; Purcell & Bellwood 2001) and macroalgae (25:1; Wyatt et al. 2012). Consequently, zooplankton represent a nutritionally valuable resource for reef fishes when available (Wyatt et al. 2012, Gahan et al. 2024). Other zoobenthivorous species may benefit from zooplankton blooms. For example, the cryptobenthic blenny *Parablennius pilicornis* has been observed leaving its refuges to feed on plankton during upwelling events, despite its clearly benthic morphology and limited swimming capacity, thereby expanding its otherwise benthic trophic niche to include planktivory (Ferreira et al. 2023). The occasional availability of these nutrient-rich pelagic resources following upwelling blooms (Rosa et al. 2023) attracts reef fishes from different trophic groups (e.g.

butterflyfish and grunts; C. E. L. Ferreira pers. obs.), driving a temporary expansion of their trophic niche. The overall implications of this opportunistic planktivorous behavior for the trophic dynamics of reef communities present in upwelling regions is a topic that further warrants consideration.

Local upwelling inputs favor not only pelagic organisms but also the benthic community by increasing nutrient availability, which enhances algal primary productivity, the nutritional quality of benthic organisms, and their temporal availability, growth, and abundance (Corbisier et al. 2014, Cordeiro et al. 2020, Spring & Williams 2023). Beyond the direct exploitation of pelagic resources, *S. pictus* may also benefit indirectly from upwelling subsidies through their benthic feeding because the benthic community also incorporates enriched pelagic subsidies (Cardozo-Ferreira et al. 2023). Coupling between pelagic and benthic habitats is known to redistribute nutrients and organic matter through physical and biological processes (Griffiths et al. 2017). These materials are consumed and assimilated by benthic organisms, contributing to nitrogen enrichment of higher-level consumers (Docmac et al. 2017). Although more research is needed to understand how pelagic subsidies interact with endogenous recycling to shape productivity, our findings indicate that upwelling-driven nutrients are integral to *S. pictus*, either in the form of zooplankton prey or through indirect, benthos-mediated pathways.

Subtropical reefs are exposed to the unpredictability of physical conditions and upwelling intensity, driven by dynamic meteorological–oceanographic interactions that shape both intra- and interannual variability beyond simple seasonal patterns (Ferreira et al. 1998b, Beger et al. 2014, Fernandes et al. 2017). In the subtropical reefs studied, recurrent upwelling strongly structures pelagic conditions throughout the year, making pelagic subsidies reaching the reef intrinsically linked to upwelling dynamics (Valentin 1984, Gonzalez-Rodriguez et al. 1992, Guenther et al. 2008, Rosa et al. 2016, 2023, Fernandes et al. 2017). The consistent assimilation of pelagic sources across both sampling periods, revealed by stable isotopic ratios and supported by Bayesian mixing models, confirms that upwelling-derived subsidies continuously contribute to the overall enrichment of the local subtropical reefs. Although pelagic prey incorporated by fishes may originate from sources other than upwelling, including larvae and eggs from benthic origin, the combined evidence from foraging behavior, gut content analysis, and stable isotope patterns further supports enhanced pelagic feeding associated with upwelling-driven increases in plankton availability (Valentin 1984, Rosa et al. 2016, 2023) rather than reliance on baseline pelagic inputs alone. This pattern was also observed in 4 nominally herbivorous fish on the same reefs, which exhibited nearly constant isotopic ratios across seasons, despite dietary shifts primarily driven by fluctuations in algal availability (Cardozo-Ferreira et al. 2023). This was attributed to the continuous nutrient input from upwelling throughout the year, which homogenized the isotopic signatures of both primary producers and consumers, overriding seasonal variability (Cardozo-Ferreira et al. 2023). Our study had a relatively limited sampling scope, yet the combination of short-term (foraging behavior and dietary analyses) and longer-term (stable isotope) approaches provided complementary insights that are essential for understanding the broader trophic role of pelagic subsidies in the ecology of our focal species and may be extended to other omnivorous fishes.

A flexible diet may be a key factor in the persistence of species facing the harsh and fluctuating environmental conditions of subtropical reef systems. Upwelling events disrupt these systems across multiple temporal scales (Fernandes et al. 2017), with abrupt temperature changes within hours — a major challenge for ectothermic organisms that must rapidly adjust to these changes (Ferreira et al. 1998b, Donaldson et al. 2008, Zaú et al. 2025). In such chronic disturbance-prone regimes (Beger et al. 2014), pelagic subsidies can bolster ecosystem resilience by supporting food web dynamics. *S. pictus* is an omnivorous damselfish that consumes a broad range of resources, including algae, benthic invertebrates, and detritus, primarily from the EAM. However, a shift in resource origin from benthic to pelagic pathways places this species into a distinct trophic-functional category known as multi-resource omnivory, where feeding resources derive from unrelated basal origins. This type of omnivory is considered a keystone interaction that promotes food web persistence and adaptability (McLeod & Leroux 2021). A comparable mechanism of trophic flexibility was observed by MacDonald et al. (2019), who demonstrated that generalist corallivorous fishes increased their reliance on *Acropora* corals that transitioned from autotrophy to plankton-based heterotrophy at greater depths. This coupling between consumer feeding strategies and prey nutritional plasticity enabled the persistence of both the corals and their associated fishes near their depth distribution limits. Such coupled trophic adjustment enhances consumer-resource stability under environmental stress. This case highlights the ecological

value of trophic flexibility, a strategy that may facilitate the dominance of generalist fishes inhabiting the subtropical reefs of the Southwestern Atlantic (Ferreira et al. 2004), where upwelling-derived pelagic inputs enrich reef food webs. Environmental variability in such systems may be partially mitigated by high-quality pelagic subsidies, which benefit organisms capable of adjusting their diets, promoting multi-resource omnivory and establishing food chains that increase food web persistence and stability (Huxel & McCann 1998, McLeod & Leroux 2021). Pelagic subsidies may thus play a central role in shaping and stabilizing subtropical reef food webs by enhancing trophic connectivity.

The relative contribution of benthic and pelagic pathways to food webs in subtropical reef systems remains poorly understood. Tropical coral reefs are supported by a recently growing body of literature disentangling the importance of pelagic productivity in reef trophic dynamics (Skinner et al. 2021, Shakya & Allgeier 2023, Morais et al. 2025, Palola et al. 2025, Richardson et al. 2025). This reflects the high species richness and biomass production of zooplanktivorous fishes, acting as vectors of pelagic subsidies that underpin the remarkable biodiversity and productivity of reef systems (Hamner et al. 1988, Morais & Bellwood 2019, Morais et al. 2021, Siqueira et al. 2021). In contrast, subtropical rocky reefs in the Southwestern Atlantic support relatively few obligate zooplanktivores, such as *Azurina multilineata*, and are instead dominated by omnivores and mobile invertebrate feeders with primarily benthic diets (Ferreira et al. 2004, Morais et al. 2017). Our findings reveal that upwelling events can drive a dietary shift from benthic to pelagic resources, even in species with a strong benthic association (Ferreira et al. 2023). Nevertheless, generalist species often associated with benthic feeding behavior, such as *Abudefduf saxatilis* and juvenile *Haemulon* spp., are commonly observed foraging on zooplankton in the water column (Pereira et al. 2015, Nunes et al. 2023). Taken together, these observations suggest that pelagic subsidies may play a more substantial role than previously recognized in subtropical reef food webs subject to upwelling, providing transient but significant trophic opportunities. Thus, these systems are not constant 'sweet spots' of productivity like many tropical coral reefs (Morais et al. 2021, 2025). Instead, pelagic inputs and subsidies arise from varying coastal morphology, predominant winds, and currents operating across regional temporal scales, providing episodic yet continuous inputs of enriched food sources that promote trophic niche expansion in generalist species. A recent comparative study of tropical and subtropical reef fish communities in Taiwan further highlighted the contribution of planktivores to subtropical reef productivity and linked their reliance on pelagic subsidies to upwelling occurrence (Liu et al. 2025). While this study used a species-specific trophic niche as a model, accumulated knowledge from the subtropical realm supports a substantial pelagic energy contribution to local food webs (Coutinho & Christofoletti 2024). Yet our understanding of energy flow across these critical transitional oceanographic zones remains limited, underscoring the need for a broader, community-level approach to predict how food web dynamics may respond to climate-driven shifts in species interactions and oceanographic parameters (Beger et al. 2014, Inagaki et al. 2020, Richardson et al. 2025).

5. CONCLUSIONS

Our study demonstrates that upwelling creates transient windows of trophic opportunity for the omnivorous, benthic-feeding damselfish *Stegastes pictus*. This pattern is demonstrated by increased plankton contributions to bite rates and diet composition, driving a significant niche expansion during upwelling. Stable isotope data further indicate that upwelling is frequent enough to yield long-term nitrogen enrichment across the reef community. In subtropical systems characterized by high environmental variability and low ecological stability (Beger et al. 2014), these pelagic subsidies may enhance food web resilience by supporting trophic plasticity and generalist foraging strategies that compensate for harsher conditions (Huxel & McCann 1988, MacDonald et al. 2019). However, climate-driven impacts on oceanographic regimes are expected to warm water temperature (Chaudhary et al. 2023) — as already registered for this study region (Matos et al. 2024) — altering upwelling dynamics (Lübbecke et al. 2014), restructuring plankton communities (Brodeur et al. 2019, Landry et al. 2024), and modifying species distribution (Beger et al. 2014). Such changes could not only lead to more intense and frequent oceanographic disturbances (Harrison et al. 2011) but also affect reef trophic dynamics (Inagaki et al. 2020) and redefine the availability of pelagic subsidies that underpin dietary plasticity (Brodeur et al. 2019). Subtropical reefs are considered potential refugia for tropical species under ocean warming (Beger et al. 2014), and upwelling has been shown to buffer the thermal stress for tropical organisms (Randall et al. 2020, Richardson et al. 2025). Although this can provide a degree of regional pro-

tection to reef communities facing climate change, this buffering capacity is also constrained by thermal limits beyond which ecosystem resilience may collapse (Rodriguez-Ruano et al. 2023). Therefore, further research is essential to understand how these complex linkages between feeding dynamics and multiple environmental drivers will respond to climate change. A deeper understanding of these interactions is critical for informing models that help prioritize biodiversity management and guide the spatial planning of conservation areas under accelerating ocean change (Liu et al. 2025, Richardson et al. 2025).

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