



Trophic ecology of moonfish in southwest Taiwan: Insights from stable isotopes and stomach content approach in connection to marine environmental factors

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ABSTRACT

Moonfish (*Mene maculata*) has been recognized as a prospective commercial species in Taiwanese waters; however, its diet and trophic ecology remain poorly understood. It was hypothesized that diet composition and trophic position (TP) vary with body size and monsoonal environmental changes. This study presents the first investigation of its feeding ecology in southwest Taiwan (SWT), focusing on seasonal and ontogenetic variation. A total of 2329 individuals collected from September 2021 to May 2024 were analyzed using stomach content analysis (SCA) and stable isotope analysis (SIA). Eight zooplankton prey groups were identified, with feeding intensity found to be higher during the northeast (NE) monsoon, likely for energy restoration during gametogenesis, and reduced during the southwest (SW) monsoon, coinciding with spawning. Immature individuals exhibited a more diverse diet, particularly during the NE monsoon (e.g., Decapoda: 58.6 % IRI; Euphausiida: 14.2 % IRI), while Decapoda dominated (>90 %) across all size classes during the SW monsoon. PERMANOVA confirmed significant effects of size, season, and their interaction on diet ($R^2 = 93.17\%$, $p < 0.001$). Isotopic values ranged from -18.0% to -16.24% for $\delta^{13}\text{C}$ and 6.57% – 11.92% for $\delta^{15}\text{N}$, confirming a mid-level carnivorous role. Generalized additive models (GAMs) revealed that dissolved silicate, nitrate, and phosphate were key environmental predictors of TP. Broader isotopic niches were observed during the NE monsoon, suggesting greater dietary plasticity. These findings illustrate how nutrient-driven environmental variability influences trophic dynamics and support ecosystem-based fisheries management (EBFM) strategies in Taiwan's coastal ecosystems. By elucidating the feeding adaptability of moonfish, this study contributes valuable insights for predicting how climate-induced shifts in monsoonal regimes may affect food web stability and fishery sustainability.

1. Introduction

Studying trophic ecology is crucial for the better understanding of its prey requirements, inter-specific interactions, and its overall role within an ecosystem (Brodeur et al., 2017). The influence of predators on prey productivity and dynamics is partially contingent upon the

geographical, temporal, and abundance-related variations in prey selection and consumption (Turschwell et al. 2019). Moreover, considering the evident intra-specific geographical, temporal, and ontogenetic heterogeneity in fish diets (Sánchez-Hernández et al. 2019), it is essential to delineate the trophic ecology of a species over these dimensions.

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In marine and aquatic ecosystems, the structure and function of food webs are shaped by both bottom-up (resource-driven) and top-down (predator-driven) processes (Lynam et al., 2017). The feeding behaviour of forage fish, such as *Mene maculata*, is strongly influenced by both prey availability and predator presence, which vary spatially and temporally. Bottom-up regulation occurs when environmental factors such as nutrient availability and primary production influence higher trophic levels, while top-down control involves predators shaping the abundance and behaviour of lower trophic groups (Antell and Saupe, 2021). Forage fish serve as critical intermediaries in these dynamics, linking primary producers with apex consumers. These small to medium-sized schooling fish are typically fast-growing, short-lived, highly fecund, and abundant, making them essential dietary components for a wide range of marine predators including fishes, seabirds, and mammals (Pikitch et al. 2014; Essington and Munch, 2014). They occupy diverse trophic roles, consuming prey ranging from detritus to small fish, and facilitate energy and nutrient transfer both within and across marine food webs (Nelson et al. 2013). In high-productivity systems—particularly pelagic upwelling zones—limited taxonomic diversity among forage fish can create a “wasp-waist” trophic structure, where a few mid-trophic species mediate both bottom-up and top-down pressures, leading to complex bi-directional regulation (Griffiths et al. 2013). In contrast, forage fish in nearshore subtropical regions often exhibit higher taxonomic and dietary diversity (Camp et al. 2019), supporting more stable and resilient food webs. Yet, in tropical and subtropical ecosystems, especially in subtropical regions, where the preservation of prey diversity is essential for enhancing trophic resilience, functional redundancy, and the ability of food webs to withstand environmental fluctuations and perturbations (O’Connor et al., 2017; Nagelkerken et al., 2023).

Previous research on moonfish (*Mene maculata*), the only species in the Menidae family (Feng et al., 2012), in the southwestern waters of Taiwan (SWT) has concentrated on catch rates, reproductive biology, and the impact of environmental factors on their distribution. The primary distribution of moonfish is primarily in the deeper coastal areas of SWT. This slender coastal forage fish, residing at depths of 20–100 m, has recently gained economic significance in Taiwan. They are essential in the energy transfer to apex predators (Lan et al., 2012). In the subtropical waters of SWT, prey selection in moonfish is largely driven by seasonal shifts in oceanographic conditions, such as nutrient availability, water temperature, and current patterns, which influence prey community composition (Griffiths et al., 2013; Chen et al., 2021). Seasonal shifts between the NE and SW monsoons create distinct environmental conditions that lead to varying prey availability, which in turn affects the feeding intensity and dietary composition of moonfish (Essington and Munch, 2014; Camp et al., 2019). For example, during the NE monsoon, increased primary productivity and prey availability support a broader, more diverse diet, whereas in the SW monsoon, food availability declines, and moonfish primarily consume Decapoda, reflecting top-down regulation from predator-prey interactions (Sánchez-Hernández et al., 2019). Geographic variability also plays a critical role, with inshore populations exhibiting more diverse prey types compared to those in offshore pelagic zones, which experience stronger bottom-up controls (Turschwell et al., 2019). Understanding these dynamics is crucial for improving fisheries management strategies, as fluctuations in prey diversity and abundance can have significant implications for ecosystem-based management (EBFM), especially in regions subject to monsoonal shifts and nutrient fluxes. Nevertheless, there exists a significant research gap in the literature regarding the trophic ecology of moonfish in this region.

The southwest coastal waters of Taiwan, located in the western Pacific Ocean, experience strong seasonal environmental variability driven by a subtropical monsoon climate. Taiwan has abundant marine resources characterized by the influence of warm tropical marine air masses from the southwest (SW) during the summer months (May to September, SW monsoon) and cold continental air masses from

northeast (NE) in the winter (October to April, NE monsoon) (Chan et al. 2022). In summer, the Kuroshio Current (KC) and South China Sea Warm Current (SCSWC) transport warm water masses from the south, promoting water column stratification and reduced nutrient upwelling. The China Coastal Current (CCC) predominates in this region during winter, transporting a low-temperature water mass from the northern continental waters via the Taiwan Strait (TS) (Liao et al. 2018), leading to enhanced vertical mixing and primary productivity. The NE wind, in conjunction with CCC and Taiwan’s “cold dome,” leads to enhanced upwelling during winter, resulting in increased primary productivity compared to summer (Liu et al. 2014), producing distinct faunal compositions. This seasonal alternation generates marked variability in temperature, salinity, and nutrient concentrations, shaping phytoplankton dynamics and consequently, food web structure in Taiwanese coastal ecosystems. These hydrographic dynamics are especially relevant for coastal forage fishes like moonfish, which serve as key mid-trophic connectors between planktonic prey and upper-level predators. Given their ecological role and the pronounced monsoonal influence on nutrient and prey availability, we hypothesize that the dietary composition and TP of moonfish vary seasonally, reflecting both bottom-up environmental forcing and ontogenetic feeding shifts. However, the extent to which these monsoonal regimes impact forage fish trophodynamics in Taiwanese waters remains poorly documented, highlighting the need for integrated, seasonally resolved trophic studies in this region.

Stomach content analysis (SCA) and stable isotope analysis (SIA) serve as methodologies to deduce basal carbon sources, trophic interactions, and food web structure. SCA provides taxonomic information regarding prey items, including their abundance, weight, and occurrence. However, SCA provides only a recent snapshot of ingested prey (within hours to days) and may be influenced by varying digestibility among the targeted items (Hyslop, 1980). Predators incorporate the carbon and nitrogen isotopic compositions of their prey into their tissues, making SIA a valuable tool for understanding dietary habits over extended periods (ranging from days to months, depending on the tissue), which reflects the prey assimilated (Fry, 2006). However, SIA does not provide precise information regarding the diversity and identity of prey items. The association of SCA and SIA leverages their complementarity, enabling the calculation of complementary metrics (Petta et al. 2020). SIA often examines the concept of isotopic niche through various metrics that assess food web structure, including resource use and trophic position (TP) among organisms, populations, or trophic groups (Sturbois et al., 2022a). Trophic niche variability is influenced by the availability of food resources, habitat utilization, behaviours, and distributions within ecosystems (Yang et al. 2024). The intraspecific niche illustrates opportunistic or specialist feeding behaviours within a species’ functional diversity, while the interspecific niche indicates competition or resource partitioning strategies among populations.

This study aims to address the paucity of regional data on moonfish by combining SCA and SIA to assess how monsoon-driven environmental variability influences their feeding ecology in the coastal waters of SWT. The research focuses on seasonal variation in diet composition, TP, food source assimilation, trophic niche width, and inter-size-class niche overlap between immature and mature individuals during NE and SW monsoons. We hypothesize that fluctuations in oceanographic variables and nutrient concentrations—common during monsoonal shifts—exert strong bottom-up control over the trophic behaviour of moonfish. Specifically, the NE monsoon is expected to be associated with increased feeding activity, broader trophic niches, and higher overlap across size classes, likely linked to reproductive energy demands as breeding begins in early spring. While studies on moonfish trophic ecology remain sparse, recent work on forage fishes in the SCS and Pacific Ocean has shown that seasonal nutrient fluxes and current-driven productivity have significant effects on fish diet and isotopic signatures (Wang et al., 2025; Mammel et al., 2024). Investigations from adjacent regions have also emphasized how SIA and SCA integration

improves detection of dietary shifts and niche plasticity in response to environmental forcing (Tsai et al., 2015). However, few studies have examined these effects across maturity stages or considered both short-term and long-term dietary indicators under monsoon regimes. By filling this gap, our study not only clarifies the trophic role of moonfish in Taiwan's coastal ecosystem but also contributes to the knowledge base essential for EBFM in subtropical marine systems.

2. Methods

2.1. Sampling area and moonfish sampling

A cumulative total of 2329 ice-frozen samples of moonfish were procured from the Taiwan Fishery Agency under a monthly pattern on random different dates throughout a three-year duration, spanning from September 2021 to May 2024 (Fig. 1) from Kaohsiung, Tainan, Taichung, Penghu, and Taoyuan. However, no samples were received during July, and samples are lacking for some site*date. In the laboratory, all specimens were measured using a Vernier caliper (fork length/FL to the nearest 0.1 mm), weighed (body weight/BW to the nearest 0.001 g) before evisceration. To assess ontogenetic dietary diversity, immature (FL < 140 mm) were differentiated from mature individuals (FL > 140 mm) considering 140 mm to be the length at first maturity (L_m) for moonfish according to a recent study by Villanueva (2018). This classification allows for comparison of feeding strategies before and after the onset of reproductive maturity. The size-frequency distribution of sampled individuals is shown in Fig. S1, confirming a balanced representation across size classes. Furthermore, individuals from each class

were evenly distributed across monsoonal seasons (NE and SW) and geographic sampling sites, ensuring robustness in comparisons of dietary and isotopic variation by length, location, and climate regime.

2.2. Data analysis

2.2.1. SCA

A total of 2329 stomachs were analyzed. When present, prey items were sorted under an Olympus BX35 binocular microscope into their lowest possible taxonomic group, counted and weighed (Hyslop, 1980). Identification of prey, including Decapoda, Calanoida, and Euphausiids, was based on established identification keys and marine planktonic invertebrate taxonomic guides (Newell and Newell, 1977; Boltovskoy, 1979; Castellani and Edwards, 2017). Fully digested prey and unidentified material were discarded from the study according to Costalago et al. (2015). The chi-square test (χ^2) was employed to ascertain potential proportional disparities between empty and full stomachs. The Kruskal–Wallis test was applied to look for differences between size and season. These two tests were selected due to the non-normal distribution of the data in all instances. Dunn's post hoc test was utilized to ascertain significant differences among the seasonal groups. A significance threshold of $p < 0.05$ was applied to all tests. A cumulative prey curve was created to determine if enough samples were collected to characterize the diet (Ghosh et al. 2021). The "specaccum" function (Oksanen et al. 2013) was used to create the curve using the "random" technique by randomising the test samples 100 times. The average and standard deviation of cumulative prey items per stomach were plotted based on the number of stomachs studied. We employed permutational

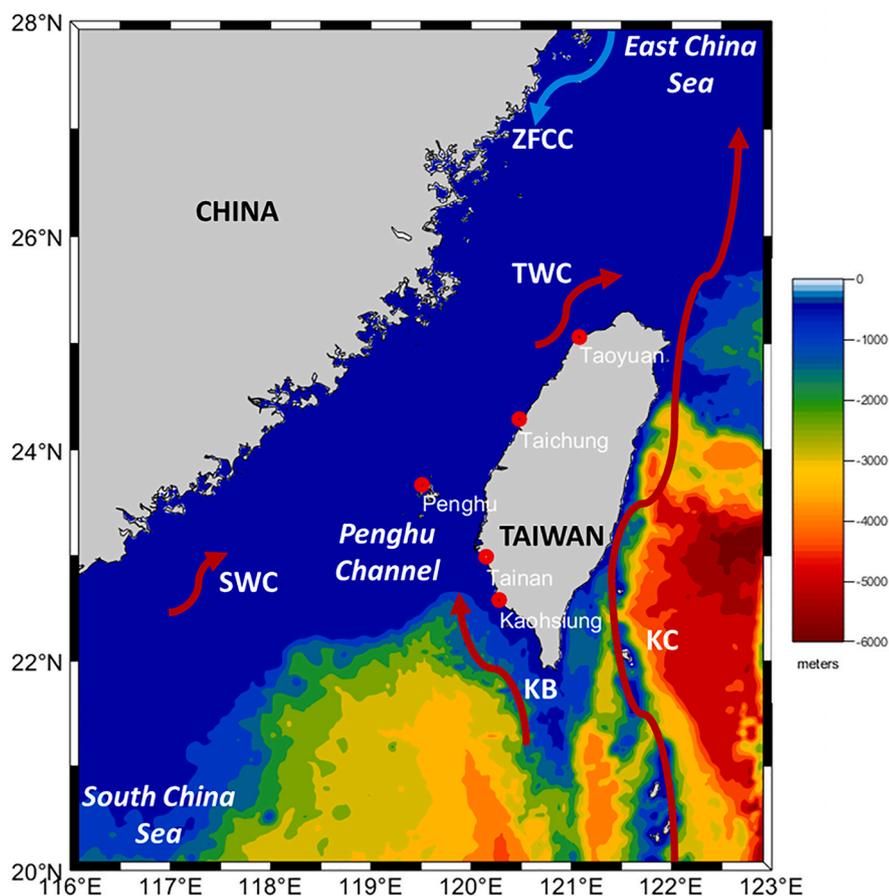


Fig. 1. The study area depicting the regions from where monthly moonfish samples were received for the study (red dots). The solid, red, arrowed lines denote warm currents originating from the south, comprising the Kuroshio Current (KC), the Kuroshio branch (KB), the South China Sea Warm Current (SCSWC), and the Taiwan Warm Current (TWC). The solid, light blue, arrowed line represents the China Coastal Current (CCC) originating from the north. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

multivariate analysis of variance (PERMANOVA) to assess differences in diet composition among FL and across seasons. Both tests were computed with the Vegan R package (Oksanen et al. 2013). Feeding intensity and the fullness index for each specimen were calculated using the following equations (Herbold, 1986):

$$\text{Fullness index} = \frac{\text{Weight of fish stomach content}}{\text{Body weight of fish}} \times 100 \dots \dots \dots (\text{Eq. 1})$$

$$\text{Feeding intensity} = \left(\frac{\text{Weight of full stomach} / \text{Weight of empty stomach}}{\text{Fish body weight}} \right) \times 100 \dots \dots \dots (\text{Eq. 2})$$

The contribution of each prey type to this species' diet was quantified using percentage number (%N), percent weight (%W), and percent frequency of occurrence (%FO) according to Cortes (1997):

$$\%N = (\text{Number of each prey type} / \text{Total number of all prey types}) \times 100 \dots \dots \dots (\text{Eq. 3})$$

$$\%W = (\text{Weight of each prey type} / \text{Total weight of all prey types}) \times 100 \dots \dots \dots (\text{Eq. 4})$$

$$\%FO = \frac{\text{Number of guts containing each prey type}}{\text{Total number of full stomachs}} \times 100 \dots \dots \dots (\text{Eq. 5})$$

The three indicators previously mentioned were incorporated into the index of relative importance (IRI) to more accurately reflect the contribution of each prey item to the diet (Mahesh et al. 2018). IRI values were represented as percentages to facilitate comparisons among prey items (%PSIRI) (Cortes, 1997) according to the equations:

$$\text{IRI} = (\%N + \%W) \times 100 \dots \dots \dots (\text{Eq. 6})$$

$$\%PSIRI = \frac{\text{IRI}}{\sum \text{IRI}} \times 100 \dots \dots \dots (\text{Eq. 7})$$

Costello's (1990) graphical method was employed to illustrate the significance of prey and feeding strategy, namely a plot of %N against %FO. The primary prey items are situated toward the upper right corner. The alternate diagonal pertains to the feeding strategy: prey items with low frequency yet significant in quantity indicate a form of specialization and are situated nearer to the left corner. The dietary diversity for the combined dataset, seasons and length classes individually was assessed using the complement of Simpson's index (D), computed as follows:

$$D = 1 - \sum_i \frac{n_i(n_i - 1)}{N(N - 1)} \dots \dots \dots (\text{Eq. 8})$$

Investigations into length-weight relations are crucial in fisheries research as they provide vital information into fish population dynamics, growth patterns, overall health, and habitat conditions (Mohanraj et al., 2024). Analysis of covariance (ANCOVA) was employed to assess variables, including fish condition (length-weight relationship), prey number, and prey weight, across FL groups and months, utilizing FL as the covariate.

2.2.2. SIA

Small portions of dorsal musculature from 87 moonfish samples having the lowest, median, and highest FL from each sampled month (sometimes more than 3 isotope samples were processed from the same month since they belonged to different harbours from the same date of collection) were examined for bulk carbon and nitrogen stable isotopes (SI). Samples were desiccated at 60 °C in a drying oven for a minimum of 48 h and subsequently ground into a powder. Subsamples (0.8–1 mg) were weighed, encapsulated in tin foil, and subsequently analyzed using a Conflo IV connected into Thermo Electron DeltaPlus IRMS (Beta Analytic Testing Laboratory, Miami, USA). Analyses produced carbon to nitrogen ratios (C:N) and isotopic ratios of ^{13}C : ^{12}C and ^{15}N : ^{14}N for each sample. We presented SI ratios utilizing the traditional delta notation (i.

e., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) referencing Pee Dee belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$, calculated using the following equation:

$$\delta\text{C}^{13} \text{ or } \delta\text{N}^{15} = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) \times 1000 \dots \dots \dots (\text{Eq. 9})$$

A lipid correction curve was implemented for each sample utilizing the C:N ratio derived from the mass spectrometry results. The correction was implemented utilizing the model developed for fish muscle tissue (Logan et al. 2008):

$$\delta\text{C}^{13} \text{ corrected} = \delta\text{C}^{13} - 4.763 + 4.401 \times \ln(\text{C} : \text{N}) \dots \dots \dots (\text{Eq. 10})$$

Student's t-tests were employed to assess differences within moonfish by season, except for seasonal comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in moonfish, which were analyzed using the Wilcoxon ranked sum test due to unequal variances. We utilized trophic enrichment factor (TEF) of 3.4 ‰ for $\delta^{15}\text{N}$ and trophic level of 2 to small zooplankton (<500 µm) to mitigate the effects of variations in the $\delta^{15}\text{N}$ baseline in order to calculate the TP of moonfish from the SIs.

$$\text{TP} = \lambda + \frac{\delta\text{N}^{15}_{\text{Consumer}} - \delta\text{N}^{15}_{\text{Baseline}}}{\text{TEF}} \dots \dots \dots (\text{Eq. 11})$$

The standard ellipse area (SEA, 95 %) and the small sample-corrected standard ellipse area (SEA_C, 40 %) were used to quantify the ecological niche widths of moonfish FL classes across NE and SW monsoons using SI data and the SIBER package to analyze temporal and interspecific variation (Jackson et al. 2011). We calculated the Bayesian SEA (SEA_B) for each FL class in each monsoon period to get the most likely SEA_C estimate (Wedrick and Jelinski, 2017).

$$\text{SEA}_c = \text{SEA} \times (n - 1 / n - 2) \dots \dots \dots (\text{Eq. 12})$$

We used NicheRover to quantify isotopic niche overlap among moonfish FL classes for each monsoon period to examine how monsoon influences interspecific trophic niche interactions (Swanson et al. 2015). Based on SI levels, isotopic niche overlaps measure how similar two groups' ecological roles are. We calculated the degree of overlap between mature and immature moonfish during NE and SW monsoons using the niche region, which is the area where a species is present with 95 % likelihood in a bivariate space. We calculated the 95 % likelihood of one group existing in another's NR and vice versa. We measured species niche overlap using bidirectional overlap values (Quintana et al. 2023).

SI trajectories were studied through the analysis of quantitative geometric properties in two-dimensional δ spaces, frequently augmented by vectors in SI scatter plots and/or circular representations (Agostinho et al., 2020). De Cáceres et al. (2019) demonstrated the efficacy of geometrically based approaches inside the community trajectory analysis (CTA) framework within a selected space of community similarity, without restrictions on the number of dimensions used. In CTA, trajectories are defined as entities consisting of successive segments that are studied and compared using distance- and direction-based metrics inside the selected multivariate space. Building upon the original concept, Sturbois et al. (2022b) proposed a novel Ecological Trajectory Analysis framework termed Stable Isotope Trajectory Analysis (SITA) including trajectory roses and the integration of trajectory metrics into maps or ordination diagrams. SITA necessitates the specification of Ω , characterized by the similarity between pairs of observations, quantified by a dissimilarity coefficient d . SITA relies on dissimilarity values found inside a distance matrix $\Delta = [d]$ (De Cáceres et al. 2019). Here we computed a principal component analysis (PCA), followed by SITA using mean and sd values of SI variables ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C: N, %C, and %N) to study the trophic dynamics among month from January to December and among monsoon seasons. The resulting axes were labeled as "Dim 1" and "Dim 2" in accordance with the default output of the R "factoextra" package; however, these represent PC 1 and PC 2, respectively. Distance-based metrics were calculated. The segment

length is the distance between consecutive months, and the net change is the distance between January and each following month. This approach provided insight into the seasonal and monsoonal dynamics of isotopic niche structure and trophic variability.

Pearson correlation coefficient was employed to examine the association between SIs and FL and different environmental predictors (SST, sea surface salinity: SSS, sea surface height: SSH, mixed layer depth: MLD, sea surface chlorophyll: SSC, euphotic zone depth: EUP, iron: FE, nitrate: NO₃, net primary productivity: NPP, oxygen (O), phosphate (PO₄), phytoplankton concentration (PHY), and dissolved silicate (DSI), the monthly data from 2021 to 2024 were derived from Copernicus Marine Services (Table S1) from the surface layer (0.5 m depth). This depth corresponds to the epipelagic distribution zone of moonfish in coastal marine systems. The climatic regime in Taiwanese waters is governed by alternating monsoons. During winter, the NE monsoon facilitates nutrient-rich cold-water intrusion from the north via the CCC, enhancing productivity through vertical mixing. The SW monsoon, by contrast, results in reduced productivity due to stable stratification from warm currents like KC. These spatiotemporal variations influence prey field dynamics, justifying their inclusion as explanatory variables in our GAM analysis. We employed single parameter generalized additive models (GAMs) to examine the correlations between TP, utilizing the predictor factors. We used 'TP' as a response variable in each model to ascertain the extent to which trends varied between TP. All models employed a Gaussian distribution and identity link function; smoothing parameters were computed using GCV and subsequently simplified with the select function, which efficiently eliminates superfluous smoothers from the model. GAMs were selected due to their flexibility in modeling non-linear ecological relationships (Wood, 2017), and their frequent application in isotopic ecology to assess environmental effects on continuous trophic metrics (Jackson et al., 2011). All statistical analysis was done in R 4.2.3 (R Foundation for Statistical Computing, Vienna, Austria) and MATLAB 2019a.

3. Results

3.1. Population structure of sampled individuals

FL of moonfish showed a broader range during NE monsoon than during SW monsoon as displayed in Table S2. During NE monsoon, BW had a broader range and a larger standard deviation, whereas SW monsoon showed a narrower range and a lower standard deviation. In NE monsoon, the population has a wider size distribution, peaking in the 161–170 mm category, closely followed by the 181–190 mm category as evident in Fig. S1. This indicates a broader diversity of size classes including juvenile and adult individuals following the recruitment. Conversely, during SW monsoon, the size distribution was more homogeneous, with a pronounced peak between the 201–210 mm, indicative of larger, more mature specimens. The lack of smaller size classes during SW monsoon indicates diminished recruitment relative to NE monsoon as well as a smaller sample size. The data indicate that NE monsoon represents a phase of population rejuvenation characterized by a heterogeneous size distribution, whereas SW monsoon was characterized by a more mature population.

3.2. Feeding activity

Among the 2329 moonfish specimens collected, 69.08 % (1609 individuals) had empty stomachs, while only 30.92 % (720 individuals) contained identifiable prey. This high vacuity rate, though consistent with findings in some pelagic fish species, raises potential concerns about the completeness of dietary reconstruction. It suggests that the SCA results are largely driven by a limited subset of the population actively feeding at the time of capture. The ratio of fish with empty stomachs was markedly greater than that of fish which have fed before sampling (chi-square test: $X^2 = 61.564$, $p = 0.00096$). The fullness index

exhibited no significant variation between immature and mature moonfish (Kruskal–Wallis test: $X^2 = 2.78$, $p = 0.257$) but exhibited considerable seasonal fluctuations. Dunn's post hoc test revealed significant differences ($X^2 = 7.32$, $p = 0.011$, Z score = -2.71) throughout NE and SW seasons (Fig. 2). The Kruskal–Wallis outcome strongly suggests that statistically significant variations in feeding intensity exist across the months ($X^2 = 167.31$, $p = 0.0002$) and FL ($X^2 = 225.65$, $p = 0.00025$). Certain months, like January and December, demonstrate elevated feeding intensities and greater variability, whereas others, such as February and March, reveal diminished values and narrower ranges (Fig. 3). The distribution of feeding intensity was wider for the mature group, indicating increased heterogeneity in feeding behavior within this size category. Conversely, the immature group demonstrates a significantly lower feeding intensity ascribing to variations in metabolic requirements, nutritional possibilities/choices, or ecological functions linked to their ontogenetic developmental phases.

3.3. Diet composition

The cumulative curves of prey groups reached an asymptote at 11 and 7 stomachs for NE and SW monsoons respectively (Fig. S2), pointing that the quantity of stomachs analyzed was adequate for the diet characterization of moonfish in our study.

88 stomachs from individuals with FL < 140 mm and 632 stomachs belonging to individuals with FL > 140 mm were analyzed. Eight prey groups were discerned in the diet using SCA (Table 1). In NE monsoon, juvenile moonfish display a varied diet, predominantly consisting of Decapoda (50 % IRI), followed by Mysida (25 %) and Ostracoda (15 %). Decapoda constitutes the predominant prey group for mature moonfish (55 % IRI), while Mysida and Ostracoda account for roughly 20 % and 10 %, respectively. Other prey families, like Euphausiids and Calanoida, contribute insignificantly (<5 %). Conversely, during SW monsoon, the diet undergoes a significant transformation, with Decapoda comprising approximately 90 % IRI in both immature and mature moonfish. All other prey categories, such as Mysida, Ostracoda, and Calanoida, combined account for less than 10 % IRI, pointing to a significant feeding diversity decline. This dietary seasonal variation during SW monsoon may probably happen due to a decreased feeding activity during the reproductive period. The dominance of decapods in the moonfish diet during SW monsoon likely reflects seasonal shifts in shrimp assemblages driven by monsoon-induced environmental changes, which increase decapod availability in the western coastal waters of Taiwan (Chen et al. 2021) that also could be another major explanation.

Food composition of moonfish was strongly affected by season, FL, and FL*season, the latter accounting for the largest proportion of variation (PERMANOVA: 93.17 %, $R^2 = 0.9317$, $F = 26.39$, $p = 0.00091$). The season alone contributed to 0.369 % of the variance ($F = 16.5$, $p = 0.00036$), showing a significant seasonal variation in diet. FL accounts for 5.15 % of the variance ($F = 13.3$, $p = 0.00031$), underscoring size-dependent feeding behavior. The size class exerts a minor but statistically significant influence (0.038 % variance, $F = 3.7$, $p = 0.0043$), although BW*season is not significant ($p = 0.3$). The ANCOVA results indicated that the substantial F-values for both months ($F = 15.5$, $p = 0.00055$) and BW ($F = 9.3$, $p = 0.0009$) demonstrate that both variables considerably affect the correlation between FL and BW (Fig. 4). The interplay of these factors over the months reveals clear linear patterns in the FL-BW relation for various months indicating temporal fluctuations in the condition of moonfish, perhaps affected by seasonal variables.

Fig. 5 further indicates that the number and weight of prey in moonfish were affected by FL, month, and their interaction. The FL category did not significantly affect prey number ($F = 0.184$, $p = 0.1$), suggesting that both immature and mature individuals consume a comparable quantity of prey overall. Nevertheless, month has a substantial impact on prey abundance ($F = 1.970$, $p = 0.017$), and FL*month is also noteworthy ($F = 2.768$, $p = 0.021$), indicating that seasonal fluctuations in prey abundance vary between the two size

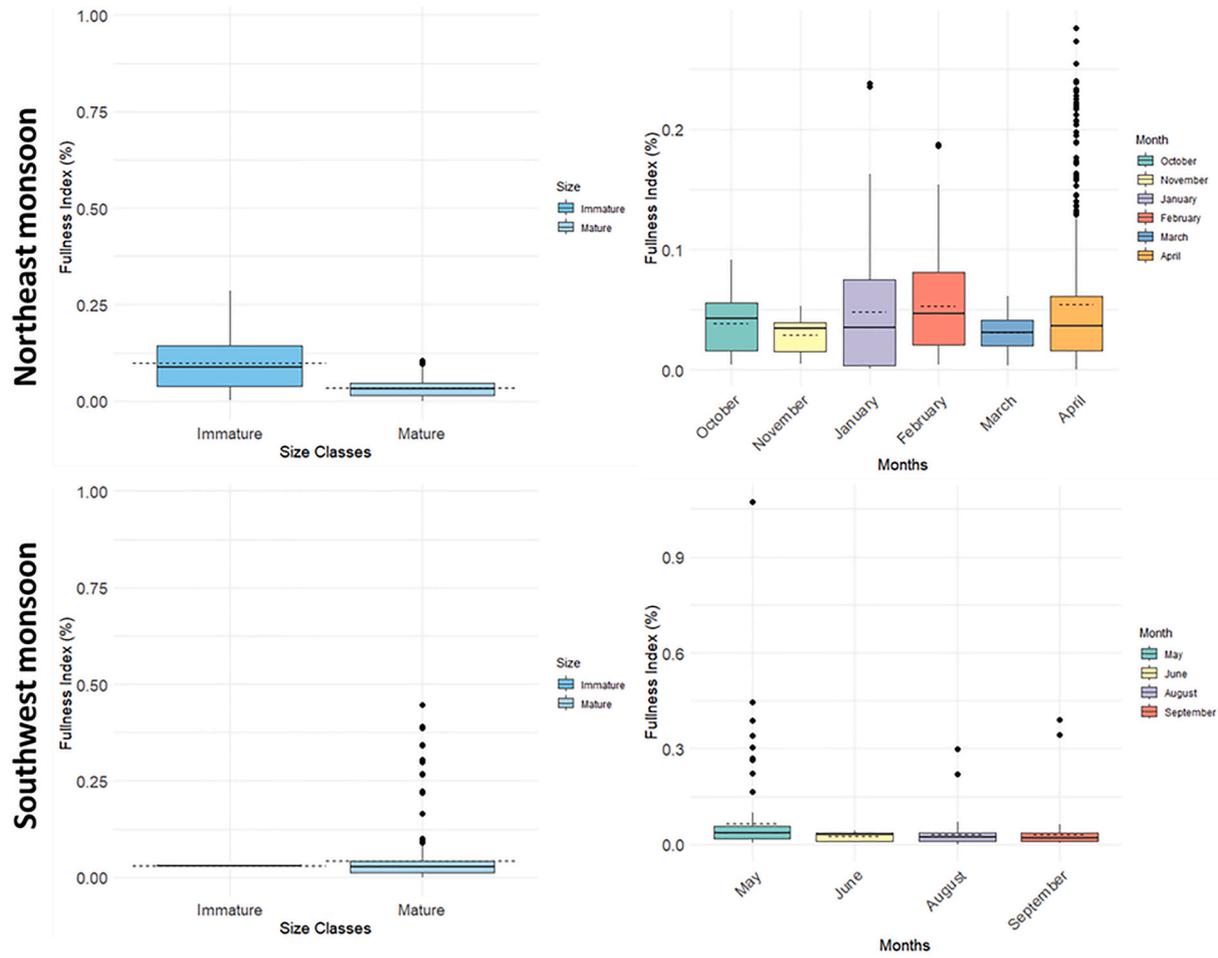


Fig. 2. Differences in fullness index according to the NE and SW monsoons of moonfish in SWT. The dotted line denotes the mean, the horizontal line signifies the median, the box illustrates the quartiles, the vertical lines indicate the 10th and 90th percentiles, the black dots represent outliers, and the whiskers (bars) depict the standard deviations.

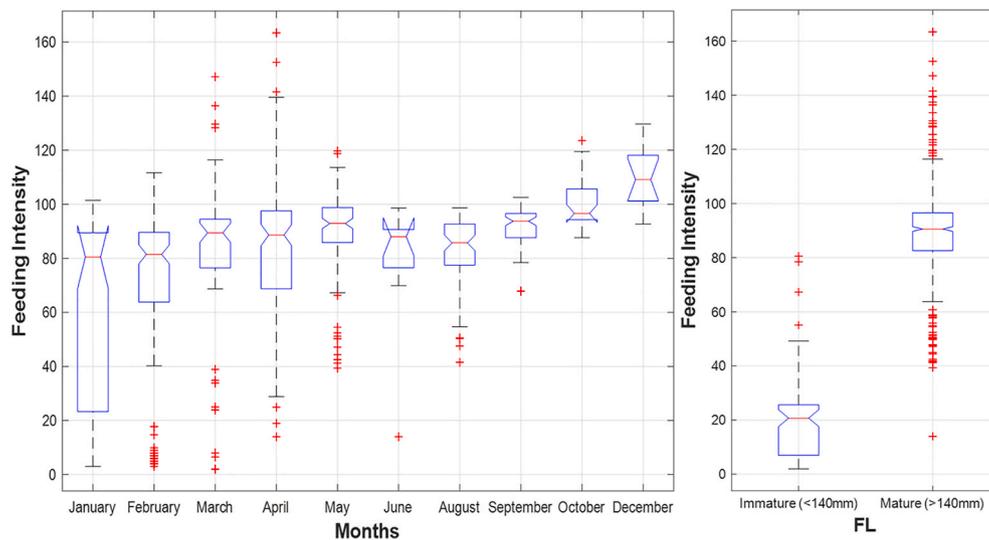


Fig. 3. Differences in feeding intensity of moonfish across months and FL in SWT. The dotted line denotes the mean, the horizontal line signifies the median, the box illustrates the quartiles, the vertical lines indicate the 10th and 90th percentiles, the black dots represent outliers, and the whiskers (bars) depict the standard deviations.

Table 1

The whole dietary content of moonfish is represented by N, % abundance; FO, % frequency of occurrence; and IRI, % index of relative importance.

Northeast monsoon						
Immature (FL < 140 mm)			Mature (FL > 140 mm)			
Prey group	%N	%FO	% IRI	%N	%FO	% IRI
Amphipoda	5.34	1.17	0.79	6.87	1.99	2.32
Calanoida	4.85	0.88	0.67	1.56	0.5	0.087
Decapoda	33.5	8.5	41.7	36.2	10.5	58.6
Euphausiida	17	3.81	9.54	18.6	5.38	14.2
Mysida	30.8	9.38	45.5	20.4	5.79	19.1
Ostracoda	8.5	1.47	1.77	11.8	3.15	5.42
Heteropoda	–	–	–	2.42	0.828	0.197
Stomatopoda	–	–	–	2.19	0.745	0.176
Southwest monsoon						
Immature (FL < 140 mm)			Mature (FL > 140 mm)			
Decapoda	100	4.55	100	79.2	28.9	95.7
Calanoida	–	–	–	5.51	1.72	0.306
Euphausiida	–	–	–	1.43	0.66	0.032
Mysida	–	–	–	10	3.83	1.29

categories. Immature individuals have elevated prey counts, peaking in April, whereas mature individuals display a more consistent trend with minor peaks in June and December. FL significantly influences prey weight ($F = 9.194, p = 0.0025$), with immature individuals ingesting larger amount of prey, especially from January to April. The prey weight was significantly affected by month ($F = 4.925, p = 0.00094$), however FL*season was not significant ($F = 1.846, p = 0.1183$), suggesting uniform seasonal trends in prey weight across both FL categories. Overall, the data indicates that juvenile moonfish demonstrated greater seasonal fluctuations in feeding behavior and prefer larger prey, whereas adult moonfish exhibited more stable feeding patterns with smaller prey throughout the seasons.

Fig. 6 elucidates that Decapoda was the predominant prey group, comprising a substantial portion of the diet with %N > 50 %, underscoring its essential function as the principal food source. Conversely, Mysida and Euphausiida were often ingested (with %FO nearing 100) yet account for a little proportion of the overall prey populations (%N < 15 %), indicating their function as ancillary prey categories in the moonfish diet. Likewise, less prevalent Ostracoda (%FO ~80 %) functions as a secondary dietary element. Infrequently ingested prey, including Amphipoda, Calanoida, Heteropoda, and Stomatopoda (%FO < 10 %, %N < 5 %), play a negligible role in the diet, possibly indicating opportunistic or incidental consumption rather than intentional foraging.

3.4. Diet diversity and niche width

Fig. 7 presents Simpson’s Index (D) across various size classes (FL < 140 mm and FL > 140 mm), monsoon seasons (NE and SW monsoons), and a combined dataset. D, which quantifies dietary dominance, reveals that individuals with FL < 140 mm demonstrate marginally greater diversity (mean = 0.75 ± 0.1) than those with FL > 140 mm (mean = 0.65 ± 0.1), suggesting increased evenness in the diets of smaller fish. Diversity is greater during NE monsoon (mean = 0.80 ± 0.1) compared to SW monsoon (mean = 0.55 ± 0.1), indicating a reduction in prey specialization and an increase in diet variability during the NE monsoon. The combined dataset demonstrates moderate diversity, with a mean of 0.70 ± 0.1 .

3.5. SIA

Table 2 presents the $\delta^{13}C$ and $\delta^{15}N$ readings for moonfish. The $\delta^{13}C$ values varied from -18‰ to -16.24‰ , with a mean of $-17.82 \pm 0.37 \text{‰}$ and $\delta^{15}N$ values varied from 6.57 ‰ to 11.92 ‰, with a mean of $9.62 \pm 0.87 \text{‰}$ for $n = 87$.

The Pearson correlation analysis revealed no correlation between $\delta^{15}N$ and $\delta^{13}C$ with FL and BW ($p = 0.06$) (Fig. S3). The t-tests and Wilcoxon rank sum tests revealed no statistically significant variations in isotopic values ($\delta^{13}C$ and $\delta^{15}N$) between seasons, FL, or BW in moonfish. Although these differences were not statistically significant, the observed overlap patterns in ellipse plots suggest potential similarities in trophic strategies and habitat utilization within size classes and across seasons. However, these interpretations should be treated cautiously given the statistical limitations. Fig. 8 illustrates the $\delta^{13}C$ - $\delta^{15}N$ biplot with 95 % standard ellipses for immature and mature moonfish during the NE and SW monsoons indicating isotopic niche widths. During the NE monsoon, ellipses for both immature (red) and mature (blue) individuals are relatively wider and show considerable overlap, indicating a more diverse resource use. In contrast, during the SW monsoon, ellipses for immature (green) and mature (orange) fish are narrower and show less overlap, implying reduced trophic diversity and more focused foraging behavior. This supports our interpretation that NE monsoon offers greater trophic opportunities, possibly due to increased primary productivity and prey availability. The density distribution of moonfish TP, derived from $\delta^{15}N$ values, reveals clear ontogenetic and seasonal differences (Fig. 9). Mature individuals during NE monsoon exhibit a right-shifted and sharper TP peak compared to immature fish, indicating a higher and more consistent trophic status. Immature individuals during the NE monsoon also show broader

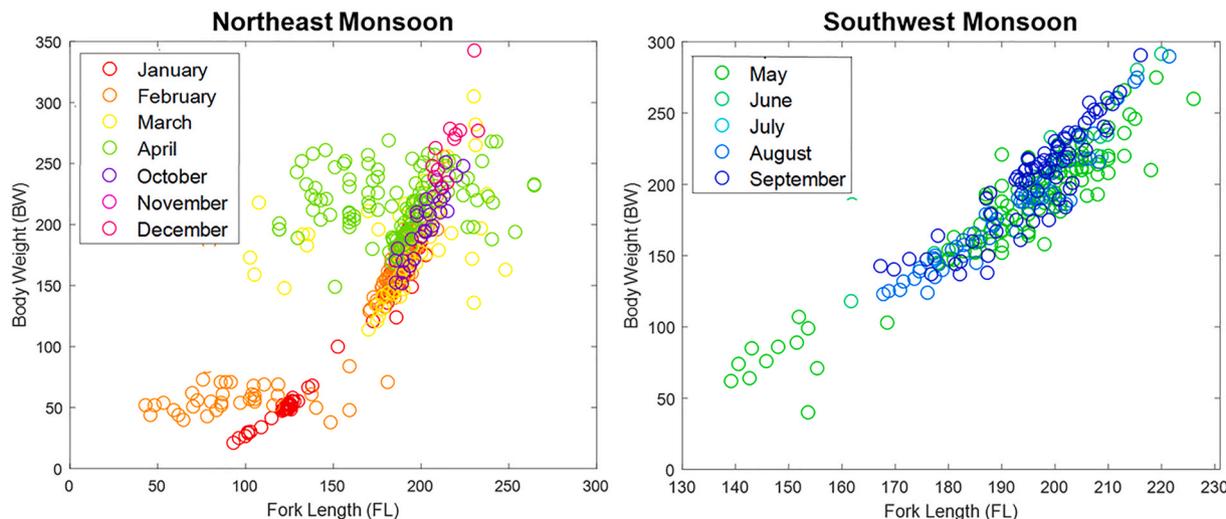


Fig. 4. ANCOVA between BW and FL categorized by month.

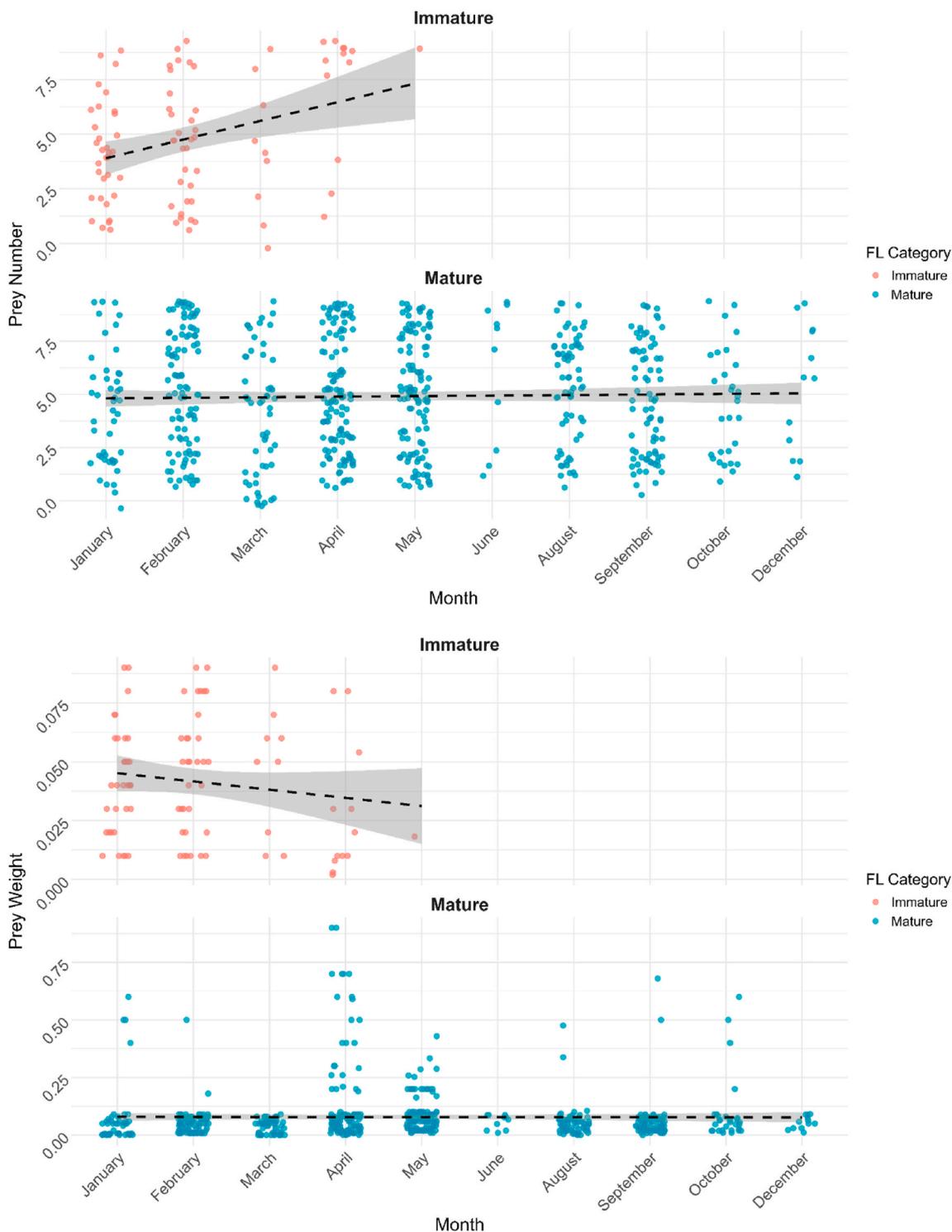


Fig. 5. ANCOVA of prey number and prey weight respectively with FL and month.

variability in TP. During SW monsoon, all groups—especially immature fish—display lower and broader TP distributions, suggesting reduced foraging efficiency or lower trophic prey availability in this season.

Fig. 10a presents SITA across months, with node size indicating net isotopic change. This figure reveals distinct seasonal phases. For example, January and June are marked by high $\delta^{15}\text{N}$ variability, while February–May cluster together, suggesting consistent feeding patterns. September appears distinct, possibly reflecting a post-reproductive dietary shift. Fig. 10b shows the PCA biplot, the first two principal components (PCA 1 and PCA 2), which explained 50.47 % and 24.0 % of the

total variance respectively, were used as the ordination space for SITA. Segment length values show a higher trophic variability in the second part of the study period (Fig. S4). Net change value increased at the beginning of the study period showing some differences in trophic metrics values compared to the January, and then stabilize despite variation of segments length values. That indicates an alteration of departing and recovering segments from the values observed in January. Net changes values start to decrease at the end of the study period after a maximum value but do not recover to trophic metrics values like January.

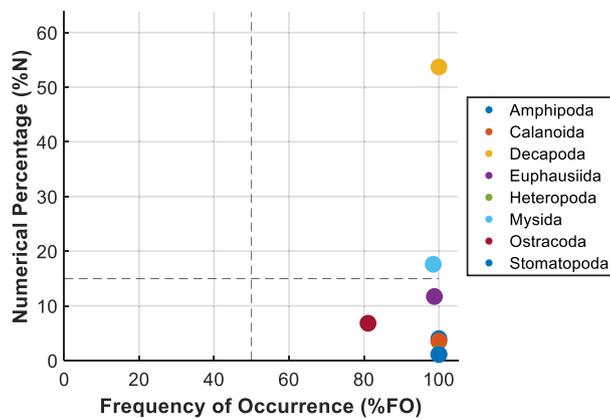


Fig. 6. Relationship between percentage number (%N) and occurrence frequency (%FO) of primary food items in the diet.

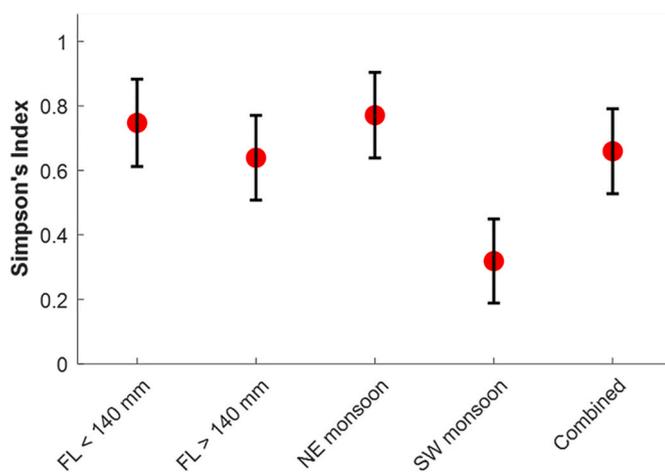


Fig. 7. The niche breadth was analyzed using Simpson's index (D) in relation to FL and season, respectively. Statistical significance was established at $P < 0.05$.

Table 2
SI variations of moonfish during NE and SW monsoons.

Season	Total n = 87	Northeast monsoon n = 39	Southwest monsoon n = 48
$\delta^{13}\text{C} \text{ ‰}$	Mean \pm SD	-17.82 \pm 0.37	-17.35 \pm 0.36
	Range	-18 to -16.24	-18 to -16.54
		-18 to -16.54	-18 to -16.54
$\delta^{15}\text{N} \text{ ‰}$	Mean \pm SD	9.62 \pm 0.87	9.5 \pm 0.96
	Range	6.57 to 11.92	8.71 to 11
		6.57 to 11.92	6.57 to 11.92

"n" indicates the moonfish sample size.

3.6. Correlation between SI and environmental factors

Analysis of Copernicus satellite-derived oceanographic data (0.5 m depth) revealed clear monsoonal patterns in environmental parameters relevant to trophic dynamics (Fig. S5a–b). During SW monsoon (May–September), the region exhibited elevated SST, reduced MLD, and lower concentrations of nutrients such as NO_3 , PO_4 , and DSI, indicative of stratified water conditions. In contrast, NE monsoon (October–April) was associated with deeper MLD, higher oxygen levels, and greater nutrient availability—conditions likely driven by intensified upwelling due to the interaction of CCC and prevailing NE winds. These hydroclimatic transitions provide an ecologically relevant backdrop for

understanding observed seasonal shifts in the trophic position and dietary composition of moonfish in southwest Taiwanese seas.

Fig. 11 displays heatmaps showing Pearson correlations between isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and four environmental variables (SST, SSS, SSH, MLD) across the two monsoons. During the SW monsoon, $\delta^{15}\text{N}$ shows strong negative correlations with SST ($r = -0.51$) and SSH ($r = -0.48$), and a positive correlation with SSS ($r = 0.53$), all statistically significant. These relationships suggest that trophic position (linked with $\delta^{15}\text{N}$) is sensitive to upper-ocean stratification and salinity gradients in this period. In the NE monsoon, only MLD shows a significant negative correlation ($r = -0.32$), indicating limited isotopic response to physical drivers.

Fig. 12 demonstrates seasonal variation in the relationship between isotopic values and nutrient concentrations (e.g., nitrate, phosphate, iron, silicate). During the SW monsoon, $\delta^{15}\text{N}$ strongly correlates positively with productivity proxies (e.g., SSC, NPP, PO_4), and negatively with Fe, NO_3 , and DSI—indicating that higher trophic levels correspond with increased productivity but reduced nutrient concentrations in the water column, possibly due to uptake. During the NE monsoon, these relationships are weaker or nonsignificant, further highlighting the seasonal decoupling between nutrients and isotope-based trophic structure.

Fig. 13 and Table 3 show the partial effects of environmental variables on the TP of moonfish from GAMs. Key predictors include month, NO_3 , PO_4 , DSI, and SSC. For instance, TP increases with higher SSC and PO_4 , while showing non-linear responses to NO_3 and MLD. Notably, DSI displays a significant negative effect, implying that increased silicate levels may reduce the trophic level, possibly by influencing prey composition. These curves emphasize the dynamic influence of both nutrient and physical variables on trophic structure over time. Among the environmental predictors analyzed, DSI, NO_3 , and PO_4 explained the highest deviance in moonfish TP, indicating their substantial ecological influence. DSI, for instance, is essential for the growth of diatoms—siliceous phytoplankton that often dominate during periods of high productivity (Yoshikawa et al., 2022). Elevated DSI may lead to diatom blooms, which support zooplankton communities (e.g., copepods and euphausiids) with specific isotopic characteristics and lower $\delta^{15}\text{N}$ signatures. Consequently, higher DSI could result in lower moonfish TP values due to a shift toward herbivorous or primary-consuming prey. Similarly, elevated NO_3 and PO_4 concentrations enhance phytoplankton biomass and primary productivity, enriching the food base for mesozooplankton, such as decapods and mysids (Fripiat et al., 2023). These prey taxa form a major part of moonfish diet, especially during high-feeding NE monsoon periods. Therefore, increased nutrient availability may elevate moonfish TP by promoting trophic upwelling and facilitating access to nitrogen-enriched secondary consumers. The GAM models also indicated strong seasonal effects, emphasizing that temporal nutrient cycling and water column mixing events influence prey community structure and availability. This supports the view that moonfish are responsive to bottom-up trophic forces mediated by environmental nutrient dynamics.

4. Discussion

4.1. Main hypothesis and study rationale

Moonfish, the only member of the Menidae family, is widely distributed in Indo-West Pacific tropical waters (Du et al., 2012). Our study was motivated by the limited knowledge of moonfish feeding ecology and recent indications of population declines in some areas (Hwang, 1984). We hypothesized that moonfishes have an opportunistic, broad diet that shifts with fish size (ontogeny) and varies by environmental context. This hypothesis stems from the general importance of diet in influencing fish distribution and habitat use (Wang et al., 2025). For instance, prior work has shown that feeding habits and prey availability can shape fish feeding grounds and migration patterns

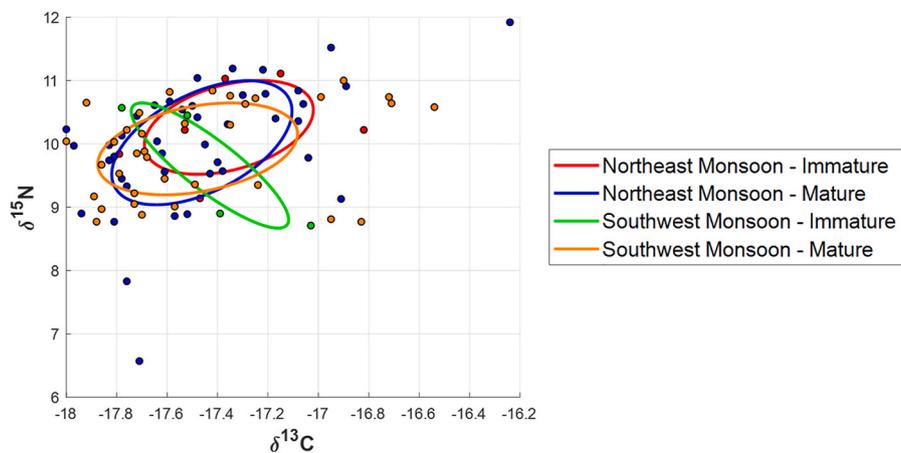


Fig. 8. SI ratios and standard ellipses of moonfish categorized by FL and season adjusted for sample size.

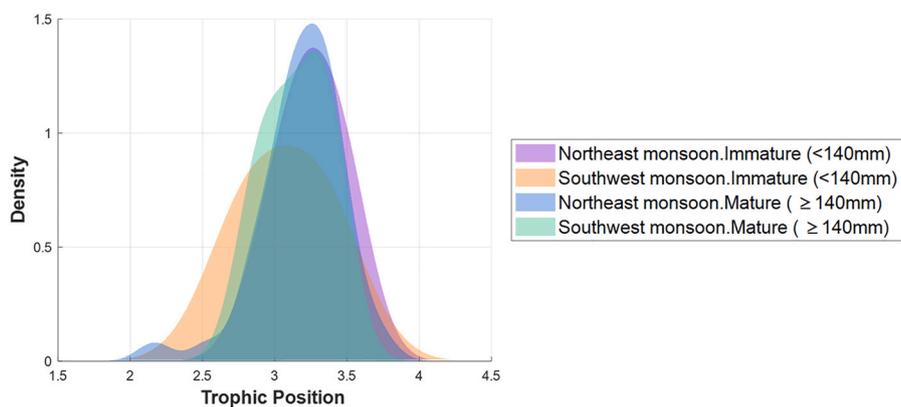


Fig. 9. Density map illustrates the trophic position (TP) of moonfish spanning two monsoon seasons and FL categories.

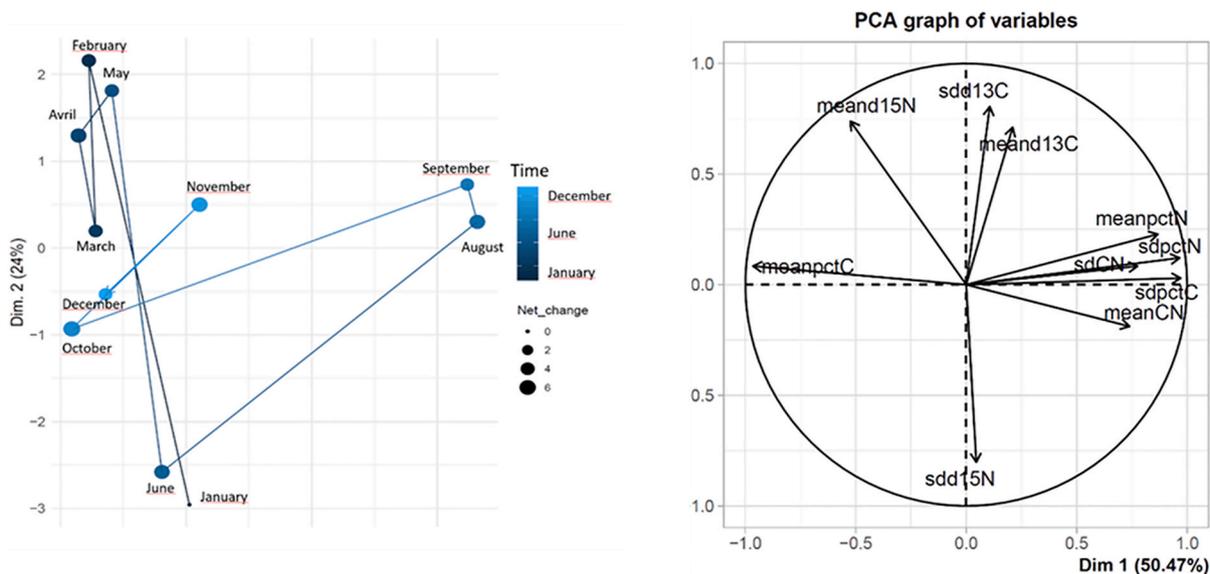


Fig. 10. a) SITA of variable changes across months, represented in a two-dimensional space. Node size corresponds to net changes, while connecting lines depict transitions between months (i.e. segment length) and b) Principal Component Analysis (PCA) biplot of variables, showing the contributions of different metrics along the first two principal components (Dim 1: 50.47 %). Arrows indicate the direction and strength of variable loadings, with closely aligned vectors representing correlated variables.

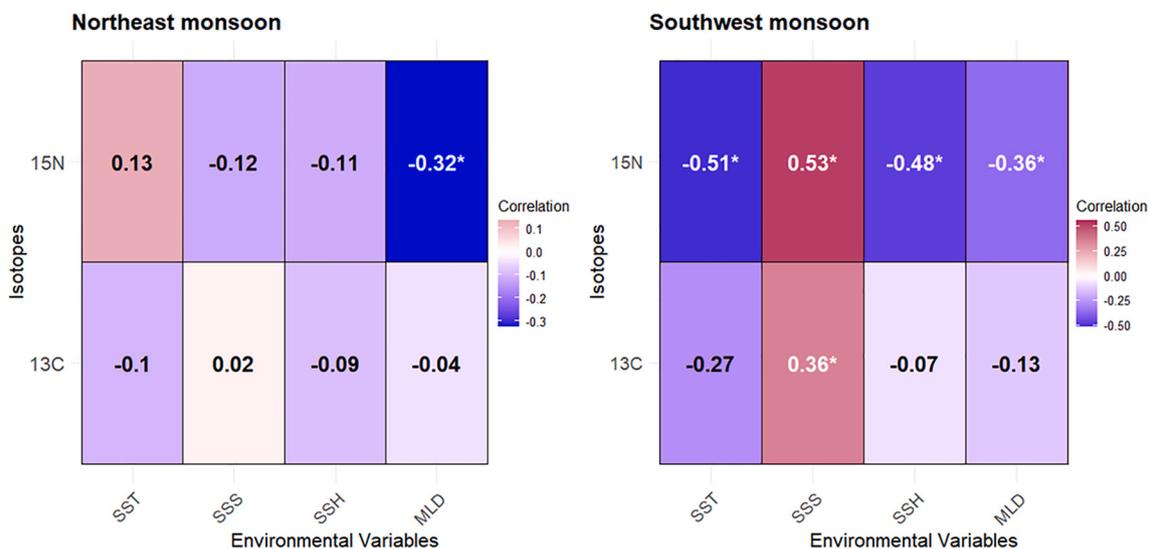


Fig. 11. Correlation coefficients between SI and essential environmental indicators in SWT. *p < 0.05; **p < 0.01.

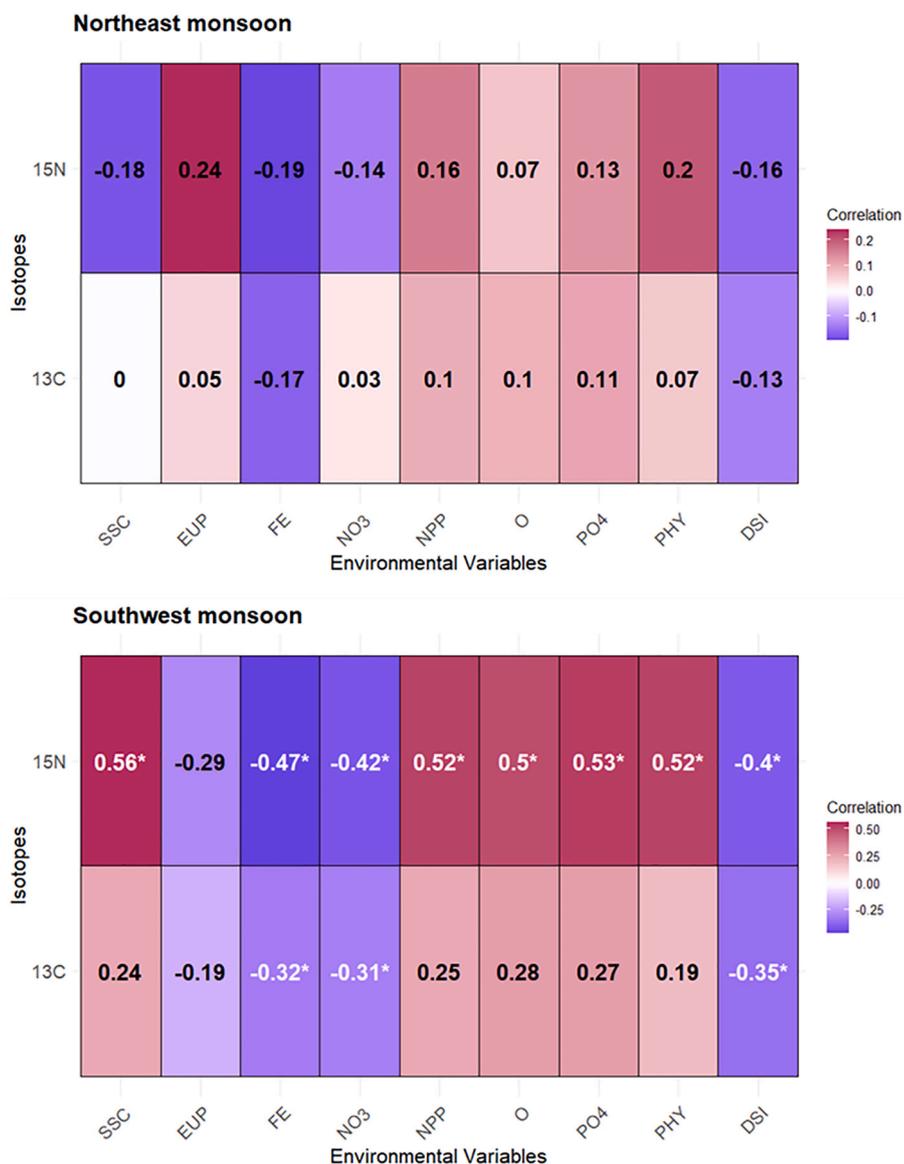


Fig. 12. Correlation coefficients between SI and essential nutrient indicators in SWT. *p < 0.05; **p < 0.01.

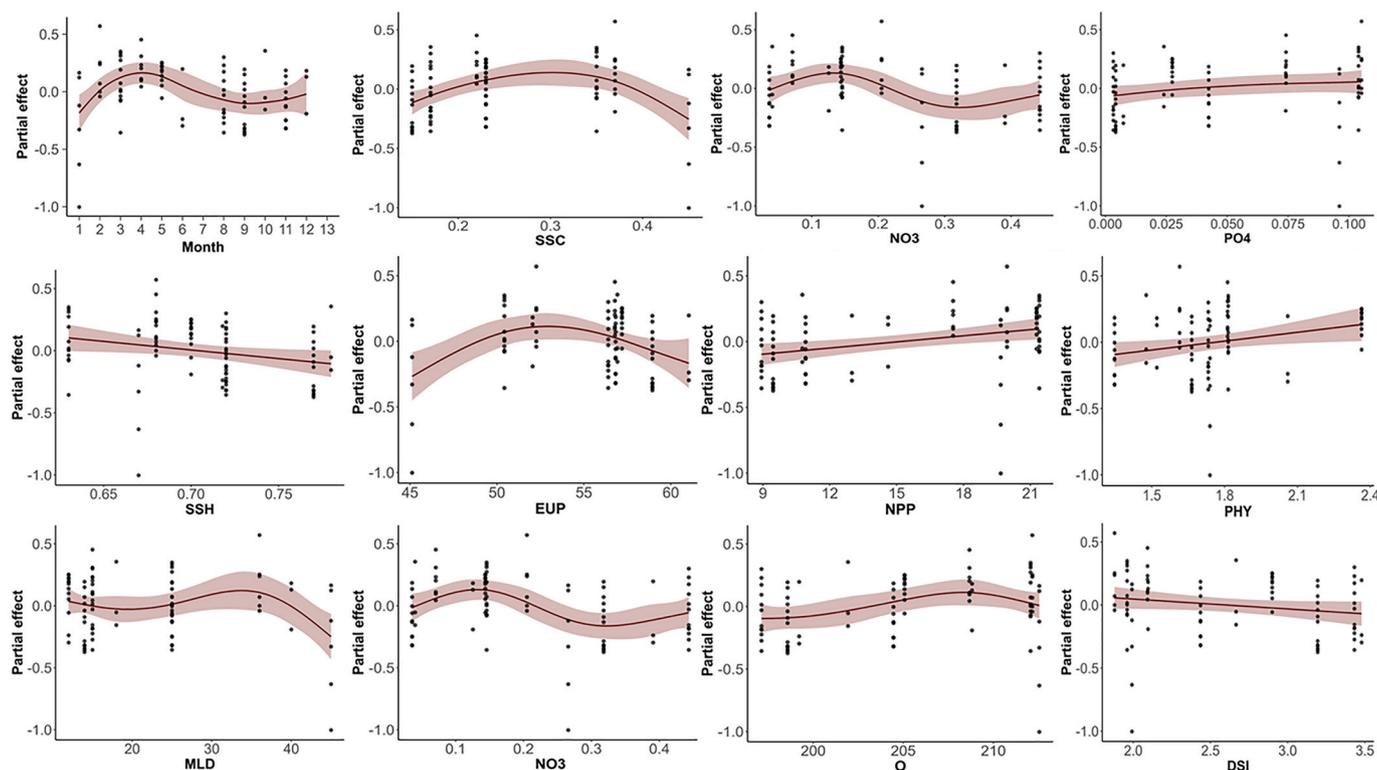


Fig. 13. The influence of fluctuations in anticipated drivers on TP of moonfish with a p value < 0.5. Plots illustrate correlations as determined by the optimal GAM. Smoothed functions are represented by solid lines, peach shading signifies confidence level, and grey circles designate observed data.

Table 3

Outcomes of GAM evaluating the effect of different predictors on the TP of moonfish in SWT.

Metrics	Adjusted R ²	Deviance explained (%)	GCV	P value
Month	0.256	32.6	0.053	***
FL	0.0579	8.07	0.067	.
SST	0.0659	9.07	0.062	.
SSS	0.0766	10.3	0.061	.
SSH	0.0466	5.58	0.063	*
MLD	0.103	13.9	0.06	*
SSC	0.177	20.2	0.055	***
EUP	0.185	24.1	0.057	**
FE	0.114	15.6	0.06	*
NO3	0.254	31	0.052	***
NPP	0.0914	10.2	0.059	**
O	0.231	29.6	0.054	***
PO4	0.258	30.6	0.051	***
PHY	0.195	25.5	0.056	**
DSI	0.239	31.7	0.055	***

Significance codes: '****' 0.001 '***' 0.01 '**' 0.05 '.' 0.1.

(Wang et al., 2025). We expected that moonfish feeding would reflect the most available prey in its environment, and that larger individuals might consume larger prey types than juveniles. To test these ideas, we analyzed stomach contents of moonfish across different size classes and seasons. This stomach content approach was chosen as a direct way to identify prey items and assess short-term diet composition, providing a foundation to understand when and on what these fish feed. The justification for this approach lies in its ability to reveal specific trophic interactions – information critical for fisheries management and conservation, given the moonfish’s role in the marine food web as both predator and prey (Viswambaran et al., 2019). Our analysis aimed to elucidate the main feeding patterns of moonfish and to see if those patterns support our hypothesis of size-related and temporal diet shifts.

4.2. Comparative feeding ecology across regions

The feeding ecology of moonfish exhibits notable spatial variability influenced by local prey availability, seasonal oceanography, ontogenetic shifts, and interspecific interactions. While most diet studies on moonfish focus on the taxonomic composition of prey items, it is equally critical to interpret feeding patterns considering prey size preference, stomach fullness (indicative of feeding intensity or satiety), and potential trophic interactions with co-occurring predators. Although species-specific diet studies for moonfish remain limited, recent efforts, particularly from southwestern Taiwan, provide foundational insights into its feeding ecology. Our study from SWT aligns with the findings of Wang et al. (2025), who reported that moonfish exhibits a distinct ontogenetic dietary shift, transitioning from a diet dominated by small planktonic crustaceans (e.g., Calanoida and Mysida) in juveniles to increased piscivory and consumption of larger prey such as *Benthosema pterotum* in adults. This pattern of increasing prey size with body size is consistent with established principles of fish trophic ontogeny, where increased gape size and swimming ability allow larger individuals to access more energetically rewarding prey (Sánchez-Hernández et al., 2019). In our dataset, this shift was evident with immature individuals (FL < 140 mm) consuming mostly Mysids (up to 80.9 % by number), while mature individuals increasingly consumed Decapods (up to 79.2 % by number), particularly during SW monsoon. Similar prey-size driven trophic changes have been reported in other mid-trophic fishes such as *Decapterus maruadsi* and juvenile *Thunnus albacares*, supporting a shared ecological strategy among coastal pelagic species. The consistently high %FO of multiple prey taxa, especially in mature individuals across both monsoonal regimes, suggests regular and active foraging. However, recent studies have also documented high proportions of empty stomachs in moonfish collected from Taiwanese waters (Wang et al., 2025), potentially attributable to gear-related biases, diurnal feeding periodicity, or post-capture regurgitation. These findings reinforce the need for synchronized sampling efforts and the inclusion of stomach fullness

indices to more accurately represent feeding intensity, a methodological gap common in diet studies of mesopelagic and coastal pelagic fishes. The dietary overlap between moonfish and other small pelagic fishes suggests that interspecific competition may occur under conditions of prey scarcity. Species such as juvenile tunas, mackerels, and sardines—which also rely heavily on mysids, euphausiids, and small decapods—are likely to occupy similar trophic positions in coastal food webs. Though direct interaction studies are lacking for moonfish, such overlap has been demonstrated in related taxa where competition is modulated by niche partitioning strategies, including vertical segregation, diel feeding shifts, and prey selectivity (Gao et al., 2022). Moonfish, known to inhabit midwater columns and display less or moderate swimming agility, may avoid direct competition by exploiting temporal or spatial foraging windows distinct from more mobile pelagic predators.

4.3. Factors influencing feeding behavior

The investigation of feeding behavior demonstrated a notably elevated prevalence of empty stomachs, also encountered in previous studies on other species (Nolan and Britton, 2018) ascribing to many circumstances such as mismatched timing of fishing with the feeding periods (Huang et al. 2025), stress caused by fishing gear leading to the regurgitation of captured prey (Flores-Martínez et al. 2017) the interval between the capture and extraction of stomach contents (Buckland et al. 2017). Season is the primary element affecting the fullness index of fish, rather than size. Moonfish exhibit heightened feeding activity in NE monsoon compared to SW monsoon. Variations in precipitation between two seasons result in alterations in the availability of food sources (Kwiecien et al. 2022) further associated with the reproductive cycle and its energy demands: during reproduction that commences in spring and reaches its maxima during SW monsoon (June–August), food intake diminishes, resulting in a reduction in feeding intensity. After this interval, upon depleting energy stores, it initiates vigorous feeding during NE monsoon (autumn and winter), aligning with the gametogenesis phase (Kumar et al. 2023).

4.4. Diet composition

Moonfish in SWT is a generalist zooplanktivorous species, primarily consuming decapods and mysids predominating through both NE and SW monsoons. During SW monsoon, overall feeding activity diminishes across all prey categories, indicating seasonal limitations on food availability and diminished feeding intensity during the reproductive period. The accurate representation, derived using the Costello graphical approach signifies a specific feeding strategy aimed at selecting those prey groups, especially during heightened feeding activity like the NE monsoon. Nevertheless, several prey groups have reduced occurrence and numerical proportions, indicating opportunistic feeding on less prevalent or secondary prey items.

The Costello graphical approach classifies prey groups according to their %N and %FO into specific quadrants, offering insights into the feeding habits of moonfish. Decapoda and Mysida occupy this quadrant as crucial prey groups, consistently ingested and substantially contributing to the diet, indicating a selective feeding behavior favouring them. The lower right quadrant signifies prey categories (Amphipoda, Calanoida, and Euphausiida) exhibiting a high %FO but a low %N, suggesting a generalist feeding style, indicating that these prey groups are commonly devoured yet contribute minimally to the overall diet. This underscores moonfish's adaptability in exploiting available prey resources without specializing in any group outside Decapoda. The upper left quadrant, indicating prey with low %FO and high %N, is vacant in this instance, implying that moonfish do not depend on infrequent yet numerically significant prey. Moonfish often include Ostracoda and Stomatopoda as supplemental food components, but their numerical contribution is minimal, indicating a smaller dietary importance.

Understanding the feeding behaviour of moonfish necessitates consideration of seasonality, the primary source of variation, as evidenced in numerous marine fish species (Visser et al. 2020) like the findings of Hure and Mustač (2020) showing that the feeding patterns of European pilchard (*Sardina pilchardus*) fluctuate with seasonal variations, indicating resilience to altering environmental conditions. Furthermore, studies on small pelagic fish in the shallow Wadden Sea indicate that species such as herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) display opportunistic feeding patterns closely associated with the benthic environment (Maathuis et al. 2024).

The comparable abundances of small genera of decapod crustaceans in the diets of moonfish is a significant observation considering the decadal-scale alterations in the zooplankton community in SWT (Molinero et al. 2018). These observations indicate towards the abundance and diversity of small decapods in the Northwest Pacific, whereas the abundance of larger genera, especially the lipid-rich calanoids, has either fluctuated or diminished on regional scales that could be due to metal pollution (Ju et al. 2019) or climate-driven changes (Ashlock et al., 2021). Consequently, we remain uncertain whether the prevalence of these smaller decapod genera in the diet of moonfish in SWT is a reaction to their relatively high availability or the rapidly changing hydrography of the region. The low lipid content of moonfish (2.62 %) indicates a diet predominantly consisting of low-fat prey, implying a dietary preference that emphasizes energy economy (Bharadhirajan et al. 2014). Although lipid-rich Calanoida are plentiful in SWT, moonfish do not predominantly depend on them as a key food element. Calanoida are small prey that yield lesser caloric returns in comparison to larger prey such as Decapoda or Mysida, which are more energy efficient. Secondly, the opportunistic feeding behavior of moonfish may result in the unintentional consumption of Calanoida rather than deliberate selection, elucidating their high %FO yet low %N. The energy requirements of moonfish, particularly for adult specimens during growth and reproduction, likely prioritize larger prey with greater biomass and caloric density, consistent with their low lipid content and dependence on energy-dense food sources.

4.5. Seasonal and ontogenetic dietary shifts

The findings and data about the feeding and trophic ecology of moonfish in SWT indicate ontogenetic dietary shifts in their feeding behavior revealing variations in prey composition and feeding intensity between juvenile and mature moonfish, indicating size-dependent dietary alterations during growth. This signifies a dietary shift towards prey that could be larger or more energy dense, corresponding with the heightened metabolic and reproductive requirements of adult fish. This seasonal consistency among sizes indicates restricted prey availability during this time, surpassing ontogenetic dietary variations that likely indicate a confluence of ecological factors, including prey size selection and habitat usage, alongside biological requirements, such as development and reproduction, as moonfish go from immature to adult phases. Research on small pelagic fish in the Black Sea indicates that species such as anchovy, sprat, and horse mackerel have considerable ontogenetic and seasonal dietary changes (Saglam and Yildiz, 2019). Juvenile anchovies mostly ingest copepods; however, adults have a more varied diet that includes larger crustaceans and small fish. SI metrics simultaneously indicate that the primary carbon source at the foundation of the food web for moonfish is comparable for both mature and immature individuals, as demonstrated by significant overlap in isotopic niche. During the NE monsoon, mature moonfish appeared to display a broader trophic niche than immature counterparts, potentially signifying more diverse diet use. However, since statistical tests did not confirm these differences as significant, such interpretations should be considered exploratory and subject to validation through expanded sampling. This may indicate enhanced foraging adaptability or access to a broader prey spectrum by adult individuals during this season. Conversely, during SW monsoon, both mature and young moonfish exhibit smaller and more

overlapping ellipses, indicating a restricted trophic niche and diminished food diversity. This pattern corresponds with diminished prey availability during SW monsoon, compelling both size classes to depend significantly on analogous prey resources. The diminished isotopic variability and overlap between the ellipses of the two monsoons underscore the impact of seasonal environmental fluctuations on moonfish feeding behaviour, with NE monsoon offering enhanced ecological opportunities for trophic differentiation relative to SW monsoon.

4.6. Isotopic evidence of seasonal variations in moonfish feeding ecology

The marine environment surrounding oceanic islands has a higher abundance of primary producers and nutrients, with the $\delta^{13}\text{C}$ ratio of these producers diminishing as the distance from shore decreases (Troina et al. 2020). The average $\delta^{13}\text{C}$ value for moonfish across all samples suggest dependence on carbon supplies from analogous primary producers in both seasons. While the mean $\delta^{13}\text{C}$ value appeared slightly higher during the NE monsoon than the SW monsoon, and $\delta^{15}\text{N}$ values showed a marginal increase, these differences were not statistically significant. Therefore, although trends may suggest seasonal shifts in the contribution of carbon sources or prey trophic level, such ecological inferences should be interpreted with caution. The consistency in $\delta^{15}\text{N}$ across groups supports a stable mid-trophic role, but minor variations observed could warrant further investigation with a larger sample size. This corresponds with increased feeding behavior during the NE monsoon, as moonfish restore their energy reserves during gametogenesis. Conversely, diminished $\delta^{15}\text{N}$ levels during the SW monsoon may indicate decreased feeding activity or a dietary transition towards lower trophic level species. The variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ readings during each monsoon season indicates differences in individual feeding behaviors, demonstrating dietary adaptability and responsiveness to seasonal prey availability although they were not statistically significant that could possibly be due to the low sampling size. The isotopic variations highlight the impact of monsoonal cycles on the feeding ecology of moonfish, revealing substantial changes in food composition and trophic dynamics between the NE and SW monsoons. This seasonal oscillation is probably influenced by environmental variations, including precipitation, productivity, and prey availability, linked to the monsoonal hydrography of SWT. This investigation underscores the significance of abiotic factors, especially nutrient availability and water quality, in influencing the trophic placement of moonfish in SWT. The substantial importance of variables like DSI, NO_3^- , and PO_4^{3-} highlights the pivotal role of biogeochemical processes in trophic ecology within this area (Fig. S6).

4.7. Monsoonal hydrography and environmental variability in SWT

The seasonal monsoon system strongly influences the hydrography and biogeochemistry of SWT. Boxplot analyses demonstrated clear differences between NE (October–April) and SW (May–September) monsoons in key environmental variables. NE monsoon months were characterized by deeper MLD, lower SST, and elevated levels of NO_3^- , PO_4^{3-} , and DSI. These hydroclimatic conditions are associated with increased nutrient upwelling driven by northeasterly winds and the influence of CCC, promoting primary productivity and enriching lower trophic levels. In contrast, SW monsoon months featured higher SST, reduced MLD, and suppressed nutrient concentrations due to water column stratification driven by KC and SCSWC. These shifts potentially reduce prey abundance and diversity, impacting energy availability and dietary flexibility of moonfish. Such seasonal contrasts in oceanographic conditions are strongly aligned with observed variations in moonfish TP, niche width, and feeding intensity. The elevated nutrient input and enhanced productivity during the NE monsoon correspond with broader isotopic niches and more active foraging, especially in mature individuals undergoing gametogenesis. Meanwhile, reduced prey diversity and lower nutrient levels during the SW monsoon may constrain

feeding and result in dietary convergence across ontogenetic stages. These findings reaffirm the need to consider climate-driven hydrographic cycles when interpreting trophic ecology and support their integration into dynamic models of EBFM in subtropical pelagic systems.

4.8. Methodological considerations and limitations of the study

It is important to assess how our methodological choices – and those of other studies – might influence the results and their interpretation. A key limitation of our SCA is the high proportion (69 %) of empty stomachs observed across samples. This introduces potential bias, as the dietary composition and diversity indices derived from SCA may disproportionately reflect individuals captured during active feeding windows and may not fully represent the population-wide dietary patterns. Such a bias can affect both seasonal comparisons and the detection of ontogenetic dietary shifts. The high vacuity may be attributed to capture-induced regurgitation, diel feeding rhythms, or stress which we suspect is largely an artifact of sampling gear and timing (Wang et al., 2025). The fish were collected using purse seines during daytime operations; such capture methods can cause regurgitation or may simply occur outside the peak feeding period for moonfish. Indeed, prior observations speculated that moonfish feed mainly in the early morning or at specific times not coinciding with typical fishing hours (Mammel et al., 2024). Thus, capture during non-feeding periods would naturally result in many empty stomachs. This potential bias underscores a limitation: our snapshot of feeding intensity may underestimate true feeding activity. By contrast, studies that sampled moonfish during active feeding times or preserved specimens immediately have reported much lower empty stomach rates. For instance, an analysis of moonfish from the Arabian Sea noted virtually no empty stomachs (<1 % empty) when fish were examined soon after capture (Viswambaran et al., 2019). This discrepancy highlights how methodology can affect the perceived “stomach fullness index.” It is advisable in future studies to incorporate dedicated sampling at dawn/dusk or other known feeding times to get a more accurate picture of feeding intensity. We also suggest using a standardized stomach fullness index (e.g. volume or weight of stomach contents relative to body size) in future research to quantitatively compare feeding intensity across studies (Amundsen and Sánchez-Hernández, 2019). In our case, although many stomachs were empty, those with food often contained substantial quantities of prey, indicating that moonfish can feed voraciously when conditions are suitable. To mitigate this limitation, we interpreted SCA results in conjunction with SIA, which integrates longer-term dietary assimilation and provides a more robust assessment of trophic patterns.

Another methodological aspect is the technique of diet analysis itself. We relied on morphological identification of prey, which is a classical approach with well-documented protocols (Wang et al., 2025). One inherent challenge is that some prey items (e.g. soft-bodied gelatinous zooplankton or well-digested fish) could not always be identified to species or even class. This means our diet composition might under-represent such items. Modern DNA-based dietary analyses could potentially detect those cryptic prey remains, offering a more complete prey list. In addition, SIA could complement our study by indicating assimilated diet over longer integration periods, thus smoothing out the short-term emptiness issue; yet isotopes only give coarse taxonomic resolution (e.g. “trophic level” or broad prey category) and cannot replace the detailed prey-specific insights from SCA (Amundsen and Sánchez-Hernández, 2019). Recent reviews advocate a combined approach: using visual methods for taxonomic detail and fullness estimates, alongside complementary techniques for otherwise undetectable diet components (Amundsen and Sánchez-Hernández, 2019). In our study, the use of the %PSIRI index mitigated some methodological concerns by balancing numeric and gravimetric importance of prey (Hyslop, 1980). Different studies employ different diet metrics (e.g. simple frequency of occurrence vs. IRI); these choices can affect conclusions. We followed the latest recommendations to use prey-specific

indices, which avoid overemphasizing either very small but frequent prey or very large but rare prey (Wang et al., 2025). Overall, while acknowledging limitations, our methodological approach is robust and in line with those used in comparable studies. Differences in findings between studies (e.g. emptiness rates, minor prey components) often trace back to methodological differences such as sampling time, gear selectivity, and diet quantification technique. We have strived to account for these factors in interpreting our results and caution that direct comparisons across studies should consider these methodological contexts.

The size range of the specimens in this study was limited and it also excluded age classes. Future studies on the food web in the SWT should prioritize the collection of specimens from different age groups and the analysis of the carbon and nitrogen composition of environmental components. Examining different size classes in other regions of Taiwanese seas might either corroborate or contradict the consistent TP throughout moonfish body sizes in that area.

Although our sampling encompassed five major Taiwanese fishing harbors (Kaohsiung, Tainan, Taichung, Penghu, and Taoyuan), we did not analyze spatial variation in diet composition. This decision was based on several limitations: inconsistent monthly coverage across harbours, unbalanced sample sizes, and the primary focus of our study on monsoonal and ontogenetic patterns. While environmental heterogeneity and prey assemblages may vary locally, the relatively small geographic scale of Taiwan and its highly dynamic, connected marine systems suggest that spatial trophic differences in moonfish may be less pronounced than in larger or more topographically complex regions. Nonetheless, future studies should consider spatially stratified sampling designs and test whether localized oceanographic differences contribute to dietary variation across Taiwan's coastal gradients.

The comprehensive impact of overall trophic structure and baseline isotopic dynamics, alongside size variations, could not be entirely evaluated in this context; however, significant disparities in nutrient availability between the seasons may elucidate the $\delta^{15}\text{N}$ and TP variations of moonfish between the NE and SW monsoons. Furthermore, the spatial and temporal variability of these monsoons warrants further investigation through SIA, incorporating the effects of differing baselines. A notable limitation in our SIA is the assumption of fixed baseline $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, using small zooplankton as a proxy for the base of the food web. Although this approach aligns with conventional practices, it does not fully account for potential seasonal or spatial variability in isotopic baselines, which may arise due to changes in nutrient inputs, phytoplankton assemblages, or water column dynamics. As such, TP estimates should be interpreted with caution. Future work should include direct measurements of baseline organisms, such as particulate organic matter, suspension-feeding bivalves, or representative zooplankton, sampled concurrently with consumers, to provide more accurate and site-specific baseline corrections for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Considering that sufficient nutrition is essential for individual growth, reproduction, and survival, future studies should focus on evaluating population health to enhance comprehension of their dynamics and environmental interactions. By clarifying ecological trophic structure, shifts in forage fish diets across pelagic systems in response to anthropogenic influences (e.g., fishing pressure) may be more accurately predicted and comprehended. Therefore, comprehensive investigations, including long-term time series analyses, are essential to comprehend the dynamic alterations in trophic interactions.

4.9. Management implications

Our findings and the comparative perspective lead to several management implications. First, the strong linkage between moonfish diet and local prey availability means that ecosystem changes can directly affect moonfish conditions and abundance. If a key prey group declines, moonfish may have to switch prey or suffer reduced nutritional intake. This is particularly relevant under scenarios of climate change. Warming

ocean conditions and shifting currents can alter plankton communities and the distribution of small pelagic prey. Studies have shown that changes in sea temperature and oceanographic features (like KC) already influence moonfish catch rates and distribution range (Wang et al., 2025). As global warming progresses, the zooplankton base of the food web is expected to change significantly. Recent climate-ecosystem models project that tropical oceans will see a decline in nutritious zooplankton such as copepods and krill, accompanied by an increase in gelatinous plankton (salps, jellyfish, etc.) (Heneghan et al., 2023). This shift could force small planktivorous fish like moonfish to consume more gelatinous, lower-quality food. In fact, a global study predicted that the diet quality of small pelagic fishes may drop by up to ~10 % as their diets become “jellyfish salads” instead of crustacean-rich meals. Such a change is metaphorically akin to “replacing a rib-eye steak with a bowl of jelly” in terms of nutritional value for the fish (Heneghan et al., 2023). For moonfish, which rely on energy-rich zooplankton (and in some regions fish eggs or larvae) (Viswambharan et al., 2019), a reduction in prey quality could affect growth, reproduction, and survival. Lower body condition in moonfish might also impact the predators that feed on them, potentially rippling up to affect local fisheries of larger species.

Given these potential shifts, fisheries management and conservation strategies should adopt a precautionary, ecosystem-based approach for moonfish. Monitoring zooplankton populations and composition in moonfish habitats could serve as an early warning for changes in food availability. If warming trends lead to fewer copepods/euphausiids and more gelatinous prey, moonfish stocks might experience declines in productivity, suggesting a need for adjusting harvest levels or protecting critical feeding grounds during vulnerable periods. Additionally, high percentages of empty stomachs observed (in our study and others) point to specific feeding times – management could consider time-area closures for certain fishing gears if moonfish are known to feed intensely at times of day, to ensure they can fulfill their dietary needs without interference. The plastic ingestion noted in moonfish from the Arabian Sea (Viswambharan et al., 2019) also raises concern: moonfish feeding on plankton near urbanized coasts can ingest microplastics, which may reduce gut feeding space or cause sublethal effects. Reducing marine plastic pollution is thus part of safeguarding the food quality for species like moonfish.

Finally, our study underlines the importance of continuing research on moonfish diet under changing conditions. We recommend future work to investigate how seasonal and long-term environmental changes (e.g. marine heatwaves, shifts in plankton blooms) affect moonfish feeding success. This could include comparing historical diet data to present findings or using biochemical indices (like fatty acids or isotopes) to detect if moonfish are getting fewer essential nutrients when plankton communities change (Heneghan et al., 2023). From a fisheries perspective, moonfish is often a lower value catch (used as bait or dried fish) (Wang et al., 2025), but it plays a significant trophic role. Any management plan for coastal pelagic ecosystems in the Indo-Pacific should consider moonfish as both predator and prey. For example, if climate change leads to zooplankton declines or community shifts, moonfish populations might decline or move, which could in turn affect the predators (tunas, billfishes) that fishermen target (Chang et al., 2022). Thus, conserving the base of the food web (zooplankton productivity) is indirectly a way to preserve higher fisheries yields. In summary, ensuring healthy zooplankton populations and mitigating climate impacts on the ocean food chain will be crucial for the future of moonfish and their associated fisheries. Our study provides baseline knowledge of the moonfish's diet and feeding behavior against which future changes can be measured, and it emphasizes that proactive measures (like habitat protection, climate adaptation strategies, and pollution control) will be needed to maintain the delicate balance of this tropical marine food web in a warming world.

5. Conclusion

This study integrates SCA and SIA to examine the trophic ecology of moonfish, considering factors such as length, season, and relevant marine environmental characteristics in Taiwanese waters. The GAM results indicated the influence of marine environmental factors on TP of moonfish, with DSI, NO_3^- , PO_4 , O, EUP, and SSC exhibiting the highest deviance explained among the nutrients, while MLD showed the highest deviance explained among the physical environmental factors. Therefore, the combination of SIA and SCA is more effective than SCA alone for monitoring variability in the dietary composition of moonfish. The results demonstrated that the TPs of moonfish varied according to length and season, indicating an ontogenetic dietary shift. The elevated $\delta^{15}\text{N}$ values and corresponding TP estimates underscore the significant ecological function of moonfish as a mid-level predator within coastal ecosystems. The research indicates that moonfish in Taiwanese waters are generalist and opportunistic predators, consuming a variety of available zooplankton prey species. Future research should incorporate climate-related data and examine the potential impacts on the distribution and abundance of prey species within their habitats.

CRediT authorship contribution statement

Aratrika Ray: Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. **Anthony Sturbois:** Writing – review & editing, Visualization, Software, Investigation, Formal analysis. **Sandipan Mondal:** Writing – review & editing, Visualization, Validation, Software, Investigation. **Sawai Gwyneth Navus:** Writing – review & editing, Validation, Supervision, Software. **Quang-Huy Lu:** Visualization, Supervision, Software, Methodology, Investigation. **Ming-An Lee:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Yi-Chen Wang:** Writing – review & editing, Visualization. **Jia-Sin He:** Visualization, Validation, Supervision, Investigation.

Ethical Approval

This study did not involve live animal experimentation. All fish samples were obtained post-mortem from authorized commercial fisheries via the Taiwan Fishery Agency. Therefore, ethical approval was not required.

Data availability statements

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107358>.

Data availability

Data will be made available on request.

References

- Agostinho, K.F.F., Monteiro, L.R., Benedito, A.P.M.D., 2020. Individual niche trajectories in nesting green turtles on Rocas Atoll, Brazil: an isotopic tool to assess diet shifts over time. *Biota Neotropica* 21 (1), e20201099. <https://doi.org/10.1590/1676-0611-BN-2020-1099>.
- Amundsen, P.A., Sánchez-Hernández, J., 2019. Feeding studies take guts—critical review and recommendations of methods for stomach contents analysis in fish. *J. Fish. Biol.* 95 (6), 1364–1373. <https://doi.org/10.1111/jfb.14151>.
- Antell, G.T., Saupe, E.E., 2021. Bottom-up controls, ecological revolutions and diversification in the oceans through time. *Curr. Biol.* 31 (19), R1237–R1251. <https://doi.org/10.1016/j.cub.2021.08.069>.
- Ashlock, L., García-Reyes, M., Gentemann, C., Batten, S., Sydeman, W., 2021. Temperature and patterns of occurrence and abundance of key copepod taxa in the Northeast Pacific. *Front. Mar. Sci.* 8, 670795. <https://doi.org/10.3389/fmars.2021.670795>.
- Bharadhirajan, P., Periyasamy, N., Murugan, S., 2014. Nutritional evaluation of the moonfish *Mene maculata* (Bloch and Schneider, 1801) from Parangipettai, southeast coast of India. *J. Coast. Life Med.* 2 (1), 53–58.
- Boltovskoy, D., 1979. Zooplankton of the south-western Atlantic. *South Afr. J. Sci.* 75 (12), 541–544.
- Brodeur, R.D., Smith, B.E., McBride, R.S., Heintz, R., Farley Jr., E., 2017. New perspectives on the feeding ecology and trophic dynamics of fishes. *Environ. Biol. Fishes* 100 (4), 293–297. <https://doi.org/10.1007/s10641-017-0594-1>.
- Buckland, A., Baker, R., Loneragan, N., Sheaves, M., 2017. Standardising fish stomach content analysis: the importance of prey condition. *Fish. Res.* 196, 126–140. <https://doi.org/10.1016/j.fishres.2017.08.003>.
- Camp, E.V., Ahrens, R.N., MacDonald, T.C., Thompson, K.A., Lorenzen, K., 2019. Identifying forage populations of concern: a new perspective based on predator recruitment considerations. *Fish. Res.* 219, 105319.
- Castellani, C., Edwards, M., 2017. *Marine Plankton: a Practical Guide to Ecology, Methodology, and Taxonomy*. Oxford University Press.
- Chang, Y.C., Chiang, W.C., Madigan, D.J., Tsai, F.Y., Chiang, C.L., Hsu, H.H., et al., 2022. Trophic dynamics and feeding ecology of skipjack tuna (*Katsuwonus pelamis*) off Eastern and Western Taiwan. *Molecules* 27 (3), 1073. <https://doi.org/10.3390/molecules27031073>.
- Chan, H.Y., Chang, Y.W., Chen, L.S., Nishida, K., Shao, Y.T., 2022. The effect of environmental factors on spatial-temporal variation of heterobranch sea slug community in northern Taiwan. *Front. Mar. Sci.* 9, 1042961. <https://doi.org/10.3389/fmars.2022.1042961>.
- Chen, H.S., Chen, K.S., Chen, C.Y., Hung, C.C., Meng, P.J., Chen, M.H., 2021. Spatiotemporal distribution of shrimp assemblages in the western coastal waters off Taiwan at the tropic of cancer, Western Pacific Ocean. *Estuar. Coast Shelf Sci.* 255, 107356. <https://doi.org/10.1016/j.ecss.2021.107356>.
- Cortes, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 54 (3), 726–738. <https://doi.org/10.1139/f96-316>.
- Costalago, D., Garrido, S., Palomera, I., 2015. Comparison of the feeding apparatus and diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological implications. *J. Fish. Biol.* 86 (4), 1348–1362. <https://doi.org/10.1111/jfb.12645>.
- Costello, M.J., 1990. Predator feeding strategy and prey importance: a new graphical analysis. <https://doi.org/10.1111/j.1095-8649.1990.tb05601.x>.
- De Cáceres, M., Coll, L., Legendre, P., Allen, R.B., Wiser, S.K., Fortin, M.J., Condit, R., Hubbell, S., 2019. Trajectory analysis in community ecology. *Ecol. Monogr.* 89 (2), e01350. <https://doi.org/10.1002/ecm.1350>.
- Essington, T.E., Munch, S.B., 2014. Trade-offs between supportive and provisioning ecosystem services of forage species in marine food webs. *Ecol. Appl.* 24 (6), 1543–1557. <https://doi.org/10.1890/13-1403.1>.
- Feng, B., Hou, G., Lu, H., Yan, Y., 2012. Age and growth of moonfish, *Mene maculata* from mouth of the Beibu Gulf, South China Sea. *J. Fish. China* 36 (4), 576–583. <https://doi.org/10.3724/SP.J.1231.2012.27745>.
- Flores-Martínez, I.A., Torres-Rojas, Y.E., Galván-Magaña, F., Ramos-Miranda, J., 2017. Diet comparison between silky sharks (*Carcharhinus falciformis*) and scalloped hammerhead sharks (*Sphyrna lewini*) off the south-west coast of Mexico. *J. Mar. Biol. Assoc. U. K.* 97 (2), 337–345. <https://doi.org/10.1017/S0025315416000424>.
- Fripiat, F., Sigman, D.M., Martínez-García, A., Marconi, D., Ai, X.E., Auderset, A., et al., 2023. The impact of incomplete nutrient consumption in the Southern Ocean on global mean ocean nitrate $\delta^{15}\text{N}$. *Glob. Biogeochem. Cycles* 37 (2), e2022GB007442. <https://doi.org/10.1029/2022GB007442>.

- Fry, B., 2006. *Stable Isotope Ecology*, vol 521. Springer, New York, p. 318. <https://link.springer.com/content/pdf/10.1007/0-387-33745-8.pdf>.
- Gao, X., Gong, Y., Chen, X., Li, Y., 2022. Dietary shifts and niche partitioning throughout ontogeny reduce intraspecific competition in a pelagic generalist predator. *Mar. Ecol. Prog. Ser.* 692, 81–97. <https://doi.org/10.3354/meps>.
- Ghosh, S., Mamidi, S., Munivenkatappa, M.H., Rohit, P., Median, A.E., Achamveetil, G., 2021. Observations on feeding habits of the common dolphinfish, *Coryphaena hippurus* (Linnaeus 1758) from the western Bay of Bengal. *Aquat. Living Resour.* 34, 24. <https://doi.org/10.1051/alr/2021022>.
- Griffiths, S.P., Olson, R.J., Watters, G.M., 2013. Complex wasp-waist regulation of pelagic ecosystems in the Pacific Ocean. *Rev. Fish Biol. Fish.* 23, 459–475. <https://doi.org/10.1007/s11160-012-9301-7>.
- Heneghan, R.F., Everett, J.D., Blanchard, J.L., Sykes, P., Richardson, A.J., 2023. Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nat. Clim. Change* 13 (5), 470–477. <https://doi.org/10.1038/s41558-023-01630-7>.
- Herbold, B., 1986. An alternative to the fullness index. In: *Contemporary Studies on Fish Feeding: the Proceedings of GUTSHOP'84: Papers from the Fourth Workshop on Fish Food Habits Held at the Asilomar Conference Center, Pacific Grove, California, USA, December 2–6, 1984*. Springer, Netherlands, pp. 315–320. https://doi.org/10.1007/978-94-017-1158-6_27.
- Huang, M., Zhou, Y.G., Yang, X.G., Gao, Q.F., Chen, Y.N., Ren, Y.C., Dong, S.L., 2025. Optimizing feeding frequencies in fish: a meta-analysis and machine learning approach. *Aquaculture* 595, 741678.
- Hure, M., Mustać, B., 2020. Feeding ecology of *Sardina pilchardus* considering co-occurring small pelagic fish in the eastern Adriatic Sea. *Mar. Biodivers.* 50 (3), 40. <https://doi.org/10.1007/s12526-020-01067-7>.
- Hwang, S.Y., 1984. Study on maturity and fecundity of moonfish, *Mene maculata*, in adjacent waters of Taiwan. *Bull. Taiwan For. Res. Inst.* 37, 93–100.
- Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. *J. Fish. Biol.* 17 (4), 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER—stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80 (3), 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Ju, Y.R., Lo, W.T., Chen, C.F., Chen, C.W., Huang, Z.L., Dong, C.D., 2019. Effect of metals on zooplankton abundance and distribution in the coast of southwestern Taiwan. *Environ. Sci. Pollut. Control Ser.* 26, 33722–33731. <https://doi.org/10.1007/s11356-018-2169-x>.
- Kumar, P., Babita, M., Kailasam, M., Muralidhar, M., Hussain, T., Behera, A., Jithendran, K.P., 2023. Effect of changing environmental factors on reproductive cycle and endocrinology of fishes. *Outlook Clim. Change Fish Nutrition* 377–396. https://doi.org/10.1007/978-981-19-5500-6_25.
- Kwiecien, O., Braun, T., Brunello, C.F., Faulkner, P., Hausmann, N., Helle, G., et al., 2022. What we talk about when we talk about seasonality—A transdisciplinary review. *Earth Sci. Rev.* 225, 103843. <https://doi.org/10.1016/j.earscirev.2021.103843>.
- Lan, K.W., Kawamura, H., Lee, M.A., Lu, H.J., Shimada, T., Hosoda, K., Sakaida, F., 2012. Relationship between albacore (*Thunnus alalunga*) fishing grounds in the Indian Ocean and the thermal environment revealed by cloud-free microwave sea surface temperature. *Fish. Res.* 113 (1), 1–7. <https://doi.org/10.1016/j.fishres.2011.08.017>.
- Liao, E., Oey, L.Y., Yan, X.H., Li, L., Jiang, Y., 2018. The deflection of the China Coastal Current over the Taiwan Bank in winter. *J. Phys. Oceanogr.* 48 (7), 1433–1450. <https://doi.org/10.1175/JPO-D-17-0037.1>.
- Liu, X., Dong, C., Chen, D., Su, J., 2014. The pattern and variability of winter Kuroshio intrusion northeast of Taiwan. *J. Geophys. Res.: Oceans* 119 (8), 5380–5394. <https://doi.org/10.1002/2014JC009879>.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcavage, M.E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 838–846. <http://www.jstor.org/stable/20143256>.
- Lynan, C.P., Llope, M., Möllmann, C., Helouët, P., Bayliss-Brown, G.A., Stenseth, N.C., 2017. Interaction between top-down and bottom-up control in marine food webs. *Proc. Natl. Acad. Sci.* 114 (8), 1952–1957. <https://doi.org/10.1073/pnas.1621037114>.
- Maathuis, M.A., Tulp, I., Valk, S., van den Brink, X., Couperus, A.S., Keur, M.C., et al., 2024. Small pelagic fish in the shallow Wadden Sea show opportunistic feeding with a strong benthic link. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 81 (8), 1521–1535. <https://doi.org/10.1093/icesjms/fsae096>.
- Mahesh, V., Ambarish, G., Rekha, N.J., 2018. Stomach content analysis techniques in fishes. *ICAR Sponsored Winter School Recent Adv. Fish. Biol. Tech. Biodiver. Eval. Conserv.* 104–115.
- Mammal, M., Lee, M.A., Wang, Y.C., Ghosh, A., Chen, Y.K., Matilda, M.V., Navus, S.G., 2024. Unraveling the feeding strategies of the greater amberjack: insights into size-dependent dietary patterns and environmental influences in Taiwanese waters. *Fish. Sci.* 90 (6), 931–952. <https://doi.org/10.1007/s12562-024-01808-8>.
- Mohanraj, T., Rajathy, T.J., Cross, S.S., 2024. Length-weight relationship, condition factor, and diet analysis of thresher sharks (Family: Alopiidae) along the southern coast of India. *Fish. Res.* 277, 107067. <https://doi.org/10.1016/j.fishres.2024.107067>.
- Molinerio, J.C., Tseng, L.C., Abbate, C.L., Ramirez-Romero, E., Hwang, J.S., 2018. Interannual changes in zooplankton echo subtropical and high latitude climate effects in the southern East China Sea. *PLoS One* 13 (5), e0197382. <https://doi.org/10.1371/journal.pone.0197382>.
- Nagelkerken, I., Allan, B.J., Booth, D.J., Donelson, J.M., Edgar, G.J., Ravasi, T., et al., 2023. The effects of climate change on the ecology of fishes. *PLOS Clim.* 2 (8), e0000258. <https://doi.org/10.1371/journal.pclm.0000258>.
- Nelson, J.A., Stallings, C.D., Landing, W.M., Chanton, J., 2013. Biomass transfer subsidizes nitrogen to offshore food webs. *Ecosystems* 16, 1130–1138. <https://doi.org/10.1007/s10021-013-9672-1>.
- Newell, G.E., Newell, R.C., 1977. *Marine Plankton—a Practical Guide*. Hutchinson & Co. Publ. Ltd, London.
- Nolan, E.T., Britton, J.R., 2018. Diet of invasive pikeperch *Sander lucioperca*: developing non-destructive tissue sampling for stable isotope analysis with comparisons to stomach contents analysis. *Knowl. Manag. Aquat. Ecosyst.* 419, 49. <https://doi.org/10.1007/s10641-024-01599-y>.
- O'Connor, M.I., Gonzalez, A., Byrnes, J.E., Cardinale, B.J., Duffy, J.E., Gamfeldt, L., et al., 2017. A general biodiversity–function relationship is mediated by trophic level. *Oikos* 126 (1), 18–31. <https://doi.org/10.1111/oik.03652>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., et al., 2013. Community ecology package. R Package Version 2 (0), 321–326. <https://sortie-admin.readyhosting.com/lme/R%20Packages/vegan.pdf>.
- Petta, J.C., Shipley, O.N., Wintner, S.P., Cliff, G., Dicken, M.L., Hussey, N.E., 2020. Are you really what you eat? Stomach content analysis and stable isotope ratios do not uniformly estimate dietary niche characteristics in three marine predators. *Oecologia* 192, 1111–1126. <https://doi.org/10.1007/s00442-020-04628-6>.
- Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., et al., 2014. The global contribution of forage fish to marine fisheries and ecosystems. *Fish. Res.* 15 (1), 43–64. <https://doi.org/10.1111/faf.12004>.
- Quintana, Y., Keppeler, F.W., Winemiller, K.O., 2023. Does invasion by armored catfish shift trophic ecology of native fishes? Evidence from stable isotope analysis. *Ecology* 104 (5), e4024. <https://doi.org/10.1002/ecy.4024>.
- Saglam, H., Yildiz, I., 2019. Temporal and ontogenetic variation in the diet of three small pelagic fish in the Black Sea of Turkey. *Mar. Biodivers.* 49 (4), 1799–1812. <https://doi.org/10.1007/s12526-019-00944-0>.
- Sánchez-Hernández, J., Nunn, A.D., Adams, C.E., Amundsen, P.-A., 2019. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. *Biol. Rev.* 94, 539–554. <https://doi.org/10.1111/brv.12468>.
- Sturbois, A., Cozic, A., Schaal, G., Desroy, N., Riera, P., Le Pape, O., et al., 2022a. Stomach content and stable isotope analyses provide complementary insights into the trophic ecology of coastal temperate benthic-demersal assemblages under environmental and anthropogenic pressures. *Mar. Environ. Res.* 182, 105770. <https://doi.org/10.1016/j.marenvres.2022.105770>.
- Sturbois, A., Cucherousset, J., De Caceres, M., Desroy, N., Riera, P., Carpentier, A., Quillien, N., Grall, J., Espinasse, B., Cherel, Y., Schaal, G., 2022b. Stable I isotope T trajectory A nalysis (SITA): a new approach to quantify and visualize dynamics in stable isotope studies. *Ecol. Monogr.* 92 (2), e1501.
- Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., Reist, J.D., 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* 96 (2), 318–324. <https://doi.org/10.1890/14-0235.1>.
- Troina, G.C., Dehairs, F., Botta, S., Di Tullio, J.C., Elskens, M., Secchi, E.R., 2020. Zooplankton-based $\delta^{13}C$ and $\delta^{15}N$ isotopes from the outer continental shelf and slope in the subtropical western South Atlantic. *Deep Sea Res. Oceanogr. Res. Pap.* 159, 103235. <https://doi.org/10.1016/j.dsr.2020.103235>.
- Tsai, C.N., Chiang, W.C., Sun, C.L., Shao, K.T., Chen, S.Y., Yeh, S.Z., 2015. Stomach content and stable isotope analysis of sailfin (Istiophorus platypterus) diet in eastern Taiwan waters. *Fish. Res.* 166, 39–46. <https://doi.org/10.1016/j.fishres.2014.10.021>.
- Turschwell, M.P., Stewart-Koster, B., King, A.J., Pusey, B., Crook, D., Boone, E., et al., 2019. Flow-mediated predator–prey dynamics influence fish populations in a tropical river. *Freshw. Biol.* 64 (8), 1453–1466.
- Villanueva, J.A., 2018. Assessment of commercially important small pelagic fishes in Davao Gulf CY 2004–2013. <https://doi.org/10.31398/tjpf/25.1.2017C0013>.
- Visser, A.W., Brun, P., Chakraborty, S., Dencker, T.S., van Denderen, P.D., van Gemert, R., et al., 2020. Seasonal strategies in the world's oceans. *Prog. Oceanogr.* 189, 102466. <https://doi.org/10.1016/j.pocean.2020.102466>.
- Viswambharan, D., Rohit, P., Sasikumar, G., Thomas, S., Joshi, K.K., Shenoy, L., Jaiswar, A.K., 2019. Occurrence and abundance of plastic particles in razor moonfish along the eastern Arabian Sea. *J. Mar. Biol. Assoc. India* 61 (2), 27–33. <http://mbai.org.in/php/journalload.php?id=2520&bkid=123>.
- Wang, Y.C., Lee, M.A., He, J.S., 2025. Feeding habits of *Mene maculata* (Teleostei: Menidae) in the Southwestern waters of Taiwan, Western Pacific Ocean. *Fishes* 10 (4), 182. <https://doi.org/10.3390/fishes10040182>.
- Weldrick, C.K., Jelinski, D.E., 2017. Seasonal dynamics in a nearshore isotopic niche and spatial subsidies from multi-trophic aquaculture. *Can. J. Fish. Aquat. Sci.* 74 (9), 1411–1421. <https://doi.org/10.1139/cjfas-2016-0372>.
- Wood, S.N., 2017. Generalized Additive Models: an Introduction with R. Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>.
- Yang, L., Liao, C., Ji, X., Chen, X., Guo, M., Zhang, G., et al., 2024. Trophic niche variation driven by water level fluctuations facilitates the co-occurrence of invasive tilapia species in a subtropical reservoir in China. *J. Fish. Biol.* <https://doi.org/10.1111/jfb.16019>.
- Yoshikawa, C., Ogawa, N.O., Chikaraishi, Y., Makabe, A., Matsui, Y., Sasai, Y., et al., 2022. Nitrogen isotopes of sinking particles reveal the seasonal transition of the nitrogen source for phytoplankton. *Geophys. Res. Lett.* 49 (17), e2022GL098670. <https://doi.org/10.1029/2022GL098670>.