# Food composition, niche breadth, and overlap of *Cyclocheilichthys armatus* (Valenciennes, 1842) in Diatas Lake, Solok, West Sumatra, Indonesia

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**Abstract**. The food of *Cyclocheilicthys armatus* (Valenciennes, 1842) in Diatas Lake, Solok, West Sumatra, Indonesia was investigated seasonally. The food composition was independent of the season, sizes, sexes, and locations with statistical significance ($p < 0.05$), that were composed of 1) phytoplankton, which consisted of Bacilaryophyceae, Chlorophyceae, and Cyanophyceae, 2) zooplankton, which consisted of Sarcodina, Rotatoria, and Crustacea, 3) Oligochaeta, 4) detritus, and 5) digested food. *C. armatus* is an euryphagic omnivore fish. The largest index of preponderance (IP) values for all sizes, sexes, locations, and seasons was phytoplankton from the class Bacillariophyceae. The main food of *C. armatus* is phytoplankton class Bacillariophyceae, complementary food for Chlorophyceae and Crustacea, and additional food for Cyanophyceae, Sarcodina, Rotatoria, Oligochaeta, and Detritus. The dominant genus in food is *Navicula*. The total length of the body represents 30% of the volume of food in the intestine. The niche breadth of food is classified as medium, which ranges from 0.548 to 0.641. The niche overlap index of food between size and sex is high, ranging from 0.948 to 0.989 in the rainy season and 0.962 to 0.992 in the dry season, indicating a potential for competition if food availability in the waters is limited. The index of electivity (E) ranges from -0.750 to 0.765 in the rainy season, with the largest index in the genus *Ephitemia* and the lowest in *Fragillaria*, while the dry season is -0.803 to 0.601, with the largest index in the genus *Pinnularia* and the smallest in *Fragillaria*. The abundance of food species in the intestine of *C. armatus* had a weak positive correlation with the abundance of plankton in the water.

**Key Words**: diet composition, index of selectivity, index of preponderance, niche breadth, niche overlap.

**Introduction**. Diatas Lake is one of the lakes in West Sumatra. Diatas Lake is located in two sub-districts, namely Lembah Gumanti District and Danau Kembar District, Solok Regency. Diatas Lake is a tectonic lake with an area of 12.3 km², a depth of 44 m, and is located at an altitude of 1,531 m above sea level (Nakano et al 1987). The water source of the Diatas Lake comes from the Aie Mati River and the Batang Galagah River, while the water flows out to the Gumanti River. This lake has several potential resources for improving the community's economy, especially in the fields of tourism and agriculture (DLH 2020).

One of the resources that the Diatas Lake community utilizes to support the local economy is fishing. Diatas Lake boasts a diverse range of fish resources. Atminarso et al (2015) identified 6 species. The potential for fish production in the Diatas Lake ranges from 38 to 57 kg $ha^{-1}$ $year^{-1}$ with an average of 44 kg $ha^{-1}$ $year^{-1}$ or 54 tons $year^{-1}$ (Samuel & Adiansyah 2016). One of the fish species commonly caught in the waters of Diatas Lake is the Catua fish, *Cyclocheilichthys armatus* (Valenciennes, 1842), also known by its Indonesian name, Kampras (Froese & Pauly 2025). These local references provide essential contextual framing for the lake's fisheries and environment and will be linked to up-to-date evidence from tropical Asian freshwater studies to ensure ecological and management relevance (Atminarso et al 2015; DLH 2020).

*C. armatus* is an important capture-fishery species in Diatas Lake and may be increasingly exposed to fishing pressure and environmental change, underscoring the need to clarify its trophic ecology. Prior work documents the role of inland capture fisheries in supporting local livelihoods and suggests that this sector is facing rising pressure associated with regional socio-economic dynamics (Atminarso et al 2015; BPS 2018). Here, we quantify diet composition, niche breadth, and trophic niche overlap of *C. armatus* to generate evidence relevant to inland fisheries management in Diatas Lake. *C. armatus* inhabits medium to large rivers, lakes, reservoirs, and floodplain trenches with weak currents to inundated conditions, favoring surface waters rich in aquatic macrophytes, leaf litter, twigs, and root structures that support an abundance of plankton and crustaceans. It prefers water temperatures of 24-26°C. In Indonesia, the species is found in Java, Sumatra, and Kalimantan, and more broadly across Southeast Asia, from Indonesia to Myanmar. It is native to this region and is not known to occur naturally anywhere else. Reported extra-Asian occurrences lack evidence of native populations. Its distribution includes Sumatra, Kalimantan, Java, Malaysia, Laos, Cambodia, Thailand, Vietnam, Myanmar, and Indochina (Kottelat et al 1993). These habitat preferences and biogeographic patterns provide a priori expectations for diet and potential niche interactions that we test in the Lake Diatas context.

Fish require dietary energy that is allocated to maintenance, growth, and reproduction (Allan et al 2021). In freshwater, energy can be obtained from various foods, such as plants, animals, and detritus. Food is an important component of water, which is an ecological factor, and plays an important role in determining the level of population density, population dynamics, growth, reproduction, and the condition of fish (Lagler 1956).

Information about diet and food habits can help to understand how aquatic fish share limited natural resources in aquatic ecosystems. The study of food and feeding habits of freshwater fish species is a subject of continuous research, and it is very important to study the feeding habits and diet of fish. This is because it makes up a basis for the development of a successful management program on fish capture and culture (Potter et al 2022). Besides, knowledge on the feeding habits and food can be important basic data for fisheries management, evaluating possible environmental impacts due to future economic development or trophic impacts of invasive fish on natural ecosystems (Mahesh et al 2018), in captivity or their natural habitat (Hamid et al 2015). Diet and feeding ecology are commonly inferred from stomach content analysis. Recent freshwater studies recommend transparent reporting of frequency of occurrence ($O_i$), volumetric or numerical contributions (%V/%N), and the index of preponderance (IP), with explicit controls for sampling and identification biases (Amundsen et al 2019). Stomach content data provide insights into behavior, condition, habitat use, energy intake, and inter- and intra-specific interactions (Manko 2016) and underpin evaluations of trophic interactions within aquatic food webs (Mahesh et al 2018).

This study aims to characterize the trophic ecology of *C. armatus* in Diatas Lake. Specifically, we quantified diet composition and the IP, estimated niche breadth and niche overlap, measured relative gut length (RGL) and stomach fullness, evaluated prey selectivity (electivity index), and tested the relationship between stomach volume and body length. The resulting trophic metrics provide baseline evidence to support sustainable management and domestication initiatives for *C. armatus* in this tropical inland lake.

## Material and Method

***Description of the study sites***. Fish samples were collected with the help of fishermen who were taken from six locations or collection stations (Figure 1). Six stations are placed at six locations around the lake, i.e. Pier Station "Dermaga" (St. 1: 1 3' 30,998" S; 100 44' 52,889" E), Bay Dalam Station "Taluak Dalam" (St. 2: 1 3' 49,015" S; 100 45' 19,802" E), Muaro Outlet Station "Muaro" (St. 3: 1 4' 39,949" S; 100 46' 29,766" E), Batanghari Inlet Station Batanghari (St. 4: 1 5' 23,607" S; 100 46' 21,930" E), Mid-Lake Station "Tengah danau" (St. 5: 1 4' 33,232" S; 100 45' 14,205" E) and Bay Kinari Station "Taluak Kinari" (St. 6: 1 4' 53,382" S; 100 44' 50,137" E). Samples from each station were taken twice, namely in the rainy season in November 2018 and the dry season in February 2019.

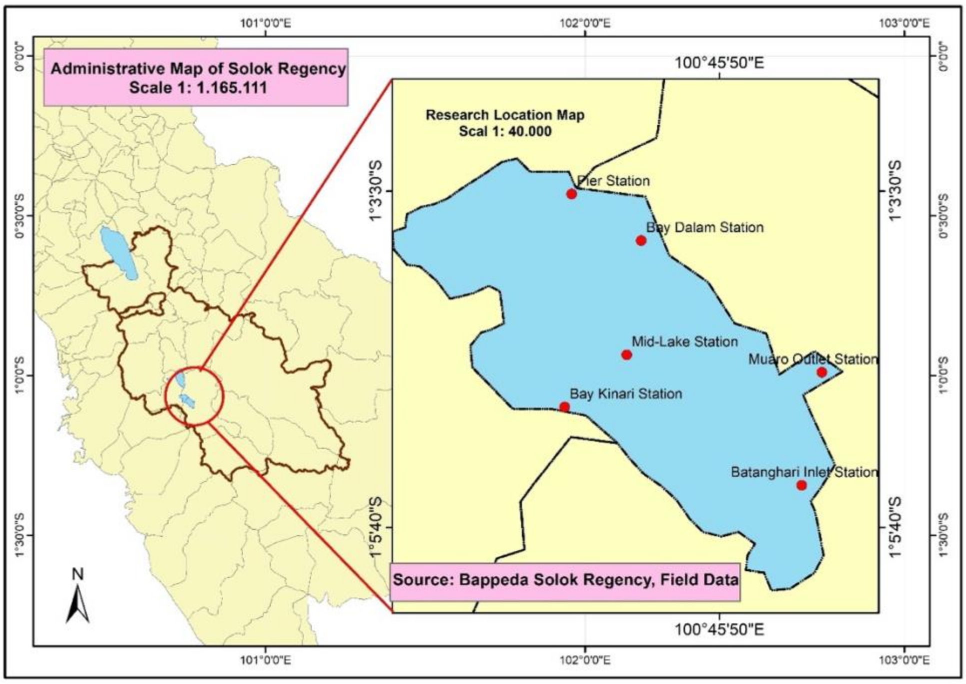


Figure 1. Map of the study area and observation stations.

***Sampling method***. Fish sampling was carried out twice, once in the rainy season in December 2018 and once in the dry season in February 2019. Sampling was done seasonally during the rainy season (November 2018) and the dry season (February 2019). Fish samples collected consisted of male and female fish with two size criteria, namely total length (TL > 150 mm and TL 120-150 mm), and juveniles. The determination of juvenile fish was based on a TL of less than 120 mm and undeveloped gonads. The total number of samples observed during the two seasons reached 360 individuals, with six individuals for each size criterion from each observation station. The total samples observed in the two seasons was 360 individuals, with details of 6 individuals for each size criterion from each station. TL was measured using a ruler with an accuracy of 0.1 mm and an electronic digital caliper model DL91300, which has a capacity of 300 mm and an accuracy of 0.01 mm. Body weight was measured using a digital balance model SF-400 with a capacity of 10,000 g (or 353 oz) and an accuracy of 0.01 g. The TL was measured using a ruler with a precision of 0.1 mm, and an electronic digital caliper model DL91300 with a precision of 0.01 mm; the body weight was measured using a digital balance with an accuracy of 0.01 g. Analysis of stomach contents used direct observation methods with surgical techniques (Manko 2016). The digestive tract was removed directly in the field and fixed with 70% alcohol. Gut length (GL) was measured using an electronic digital caliper model RoHS with an accuracy of 0.01 mm. Food weight was measured using a professional digital mini scale model Weighing, which has an accuracy of 0.0001 g and is capable of measuring in units of grams (g), ounces (oz), troy ounces (ozt), pennyweights (dwt), carats (ct), and grains (gn). GL was measured with a caliper accuracy of 0.01 mm, and the weight of food was measured with a digital balance accuracy of 0.0001 g.

***Stomach content studies***. Quantitative analysis of the gastric contents of *C. armatus* employed a combination of the $O_i$ and percentage methods (Effendie 1979). Measurement of the length from the digestive tract and identification of the type of food was done according to instructions (Manko 2016), namely: 1) The digestive tract was excised from the body cavity, and intestinal length was measured from the esophagus to the anus; 2) the contents of each digestive tract were put into a petri dish coated with filter paper; 3) the weight of the food was weighed; 4) the weighed food was placed into a measuring glass filled with 10 mL of distilled water, the addition of the volume of aquadest was recorded as the total volume of contents from the diges tive tract; 5) each sample was observed as much as 1 mL (±20 drops), and the type of food was observed through five fields of view using electric binocular microscope, model Olympus CX21. The gastric contents of each fish were identified to the lowest possible taxon based on Needham & Needham (1962), Pinder & Ohtaka (2004).

***Data analysis***. The IP was calculated following Natarajan & Jhingran (1961).

$$IP = \frac{V_i \ x \ O_i}{\sum_{i=1}^{n}(V_i x \ O_i)} x100$$

or with the formula:

$$IP = \frac{N_i \ xO_i}{\sum_{i=1}^{n}(N_i \ x \ O_i)} x100$$

where: IP is the index of preponderance, $V_i$ is the percentage of the volume of item *i*, $O_i$ is the frequency of occurrence of the given item *i,* and $N_i$ is the percentage of the number of items *i.*

The volume percentage and the type percentage were expressed by calculating the volume or number of similar foods divided by the total volume of food using the formula (Temesgen et al 2022):

$$Vi = \frac{Volume \ of \ food \ types \ i}{Volume \ of \ all \ types \ of \ food} x100$$

$O_i$ was expressed as a percentage and calculated using the Hynes formula (Krebs 2014), namely:

$$Oi = \frac{N_i x}{N} x \ 100$$

$$Ni = \frac{Number \ of \ food \ types \ i}{Amount \ of \ all \ foods} x100$$

where: $O_i$ is the frequency of occurrence of given item *i*. $N_i$ is the percentage of the number of items *i,* and N is the total number of food organisms.

Analysis of the niche breadth reflects the proportion of food resources used by fish and the selectivity of fish between species or individuals in the same species to food resources in certain habitats, using the formula of Levins (Krebs 2014), namely:

$$B = \frac{1}{\sum P \ ij^2}$$

where: B is Levins' measure of niche breadth, and $Pij^2$ is the proportion of individuals found in or using resource state *j*.

Standardization of the value of the niche area is using the formula of Hurlbert (Krebs 2014), namely:

$$Ba = \frac{B-1}{N-1}$$

where: Ba is Levins' standardized niche breadth, B is Levins' measure of niche breadth, and N is the number of possible resource states.

Niche overlap is calculated using the simplified Index of Morisita-Horn (Krebs 2014). The Morisita index value ranges from 0 to 1; $C_H$ = 0.00-0.29 indicates niche overlap or low similarity, 0.30-0.60 = moderate similarity, 0.61-1.00 = high similarity (Krebs 2014).

$$C_H = \frac{2\sum_i^n Pij\ Pik}{\sum_i^n Pij^2 + \sum_i^n Pik^2}$$

where: $C_H$ is Morisita index of niche overlap between species j and species k/percentage overlap species j and k, $P_{ij}$ is proportion resource i is of the total resources used by species j, $P_{ik}$ = proportion resource i is of the total resources used by species k, and *n* is a total number of resource states (i = 1, 2, 3, .... n).

RGL is calculated based on the Montgomery formula (Montgomery 1977), namely:

$$RGL = \frac{GL}{TL}$$

where: RGL is relative gut length, GL is gut length, and TL is total body length.

The index of stomach content (ISC) was calculated following Hyslop (1980):

$$ISC = \frac{SCW}{BW} x\ 100$$

where: ISC is the index of stomach contents (%), SCW is the total weight of stomach contents (g), and BW is the total weight of fish (g).

The electivity of index (E) was calculated using Ivlev's formula (Lechowicz 1982):

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where: $E_i$ is Ivlev's index of electivity, $r_i$ is the relative quantity (portion, percentage) of the food item *i* in the digestive tract content, and $p_i$ is the relative quantity of the food item *i* in the environment.

***Statistical analysis****.* Differences in the food composition of *C. armatus* between the rainy and dry seasons were analyzed using independent-samples t-tests and, as a sensitivity analysis, Mann-Whitney U tests, implemented in IBM SPSS Statistics version 26.0. The relationships between the abundance of food organisms in the stomach of *C. armatus* and the abundance of plankton in the water, as well as the relationship between the volume of food and the total length of *C. armatus*, were determined using linear regression in SPSS version 26.

**Results and Discussion**. The total sample of fish used for the analysis of stomach contents consisted of 360 fish, of which 180 were from the rainy season sample and 180 from the dry season sample. From the total sample used, the composition of the food was obtained. The composition of the stomach content of *C. armatus* is presented in Table 1.

Table 1

Food composition of *Cyclocheilichthys armatus* in Diatas Lake

| *No* | *Food organism* | *Relative abundance (%)* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Rainy season* | | | | *Dry season* | | | |
| | | *Male* | *Female* | *Juvenile* | *Total* | *Male* | *Female* | *Juvenile* | *Total* |
| | | *Phytoplankton* | | | | | | | |
| | Bacillaryophyceae | | | | | | | | |
| 1 | *Amphora* | 3.40 | 3.13 | 3.57 | 3.29 | 3.05 | 2.99 | 3.34 | 3.08 |
| 2 | *Navicula* | 10.78 | 9.13 | 11.75 | 10.09 | 10.26 | 11.80 | 10.98 | 10.79 |
| 3 | *Denticula* | 6.69 | 6.84 | 8.73 | 6.97 | 7.07 | 18.45 | 7.07 | 10.19 |
| 4 | *Diatoma* | 2.97 | 4.04 | - | 3.18 | 4.00 | 7.00 | - | 4.24 |
| 5 | *Ephitemia* | 8.63 | 8.20 | 7.35 | 8.30 | 8.85 | 11.09 | 7.85 | 9.32 |
| 6 | *Fragillaria* | - | 0.71 | - | 0.34 | - | 1.10 | 1.17 | 0.48 |
| 7 | *Gomphonema* | 5.74 | 7.11 | 7.26 | 6.55 | 7.46 | 2.66 | 7.43 | 6.14 |
| 8 | *Melosira* | - | 1.33 | 1.07 | 0.75 | 1.33 | 2.50 | 1.30 | 1.65 |
| 9 | *Cymbella* | 5.45 | 5.75 | 8.45 | 5.90 | 5.60 | 3.59 | 8.34 | 5.45 |
| 10 | *Neidium* | 2.21 | 2.57 | 4.85 | 2.65 | 2.27 | 0.85 | 5.37 | 2.34 |
| 11 | *Nitzschia* | 8.66 | 7.00 | 9.86 | 7.99 | 7.36 | 0.94 | 9.07 | 5.85 |
| 12 | *Pinnularia* | 6.23 | 5.22 | 3.30 | 5.45 | 5.22 | 1.76 | 4.12 | 4.11 |
| 13 | *Surirella* | 4.12 | 4.63 | 1.83 | 4.13 | 4.15 | 1.09 | 3.94 | 3.28 |
| 14 | *Synedra* | 1.56 | 2.12 | 0.98 | 1.77 | 1.37 | 1.20 | 1.49 | 1.34 |
| | Chlorophyceae | | | | | | | | |
| 15 | *Pediastrum* | 3.40 | 4.59 | 2.41 | 3.87 | 4.69 | 2.47 | 2.53 | 3.77 |
| 16 | *Desmidium* | 6.86 | 6.74 | 7.69 | 6.89 | 6.38 | 10.39 | 8.06 | 7.73 |
| 17 | *Staurastrum* | 8.31 | 6.44 | 5.83 | 7.16 | 7.38 | 0.89 | 4.88 | 5.23 |
| 18 | *Oedogonium* | 1.40 | 1.37 | 1.10 | 1.36 | 1.08 | 1.01 | 1.25 | 1.09 |
| 19 | *Closterium* | 2.59 | 2.72 | 1.83 | 2.58 | 2.53 | 0.85 | 1.75 | 1.96 |
| 20 | *Spirogyra* | 2.60 | 2.27 | 2.44 | 2.43 | 2.40 | 0.99 | 2.37 | 2.01 |
| | Cyanophyceae | | | | | | | | |
| 21 | *Oscillatoria* | 1.81 | 1.44 | 1.34 | 1.59 | 1.89 | 1.44 | 1.43 | 1.70 |
| | Subtotal | 93.41 | 93.36 | 91.64 | 93.20 | 94.36 | 85.08 | 93.74 | 91.73 |
| | | *Zooplankton* | | | | | | | |
| | Protozoa | | | | | | | | |
| 22 | *Arcella* | 0.36 | 0.57 | 0.73 | 0.50 | 0.34 | 1.13 | 0.60 | 0.59 |
| | Rotatoria | | | | | | | | |
| 23 | *Brachionus* | 0.74 | 0.89 | 1.07 | 0.85 | 0.74 | 1.89 | 0.78 | 1.06 |
| | Crustacea | | | | | | | | |
| 24 | *Ceriodaphnia* | 1.00 | 0.79 | 1.04 | 0.90 | 0.61 | 2.57 | 0.73 | 1.17 |
| 25 | *Cyclops* | 0.96 | 1.13 | 1.19 | 1.06 | 0.89 | 2.03 | 0.81 | 1.19 |
| 26 | *Nauplius* | 0.99 | 1.14 | 1.22 | 1.08 | 0.93 | 2.03 | 0.86 | 1.22 |
| | Subtotal | 4.05 | 4.52 | 5.25 | 4.40 | 3.51 | 9.65 | 3.78 | 5.23 |
| 27 | Oligochaeta | 1.64 | 1.67 | 1.37 | 1.63 | 1.36 | 3.82 | 1.15 | 2.00 |
| | | *Unidentified* | | | | | | | |
| 28 | Detritus | 0.44 | 0.21 | 0.82 | 0.37 | 0.38 | 0.74 | 0.70 | 0.53 |
| 29 | Digested food | 0.46 | 0.23 | 0.92 | 0.40 | 0.39 | 0.71 | 0.63 | 0.51 |
| | Total | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

From Table 1, it can be seen that the food composition of *C. armatus* in the rainy season and dry season includes: 1) phytoplankton, which consists of Bacilaryophyceae, Chlorophyceae, and Cyanophyceae, 2) zooplankton, which consists of Sarcodina, Rotatoria, and Crustaceans, 3) Oligochaeta, 4) detritus, and 5) digested food. This composition indicates that the dietary pattern of *C. armatus* is classified as euryphagic. The phytoplankton is more abundant in the stomach of the collected fish during the dry season. This condition is in line with the abundance of phytoplankton in the waters. This condition is in line with the abundance of phytoplankton in the waters, which is also more abundant in the dry season than in the rainy season. Fluctuations in the availability of natural fish food organisms in water are influenced by the season and nutrient content in the waters (Que et al 2021). The existence and abundance of phytoplankton species in waters are strongly influenced by water quality (Essa et al 2024).

Food composition (Table 1) describes the food habits of *C. armatus* as similar to the food habits of other fish in the Cyprinidae family (Nyanti et al 2021). The type of food of *C. armatus* varies with the dietary composition of *C. apogon* in the Murum river Serawak, which consists of phytoplankton, zooplankton, worms, insects, detritus, and aquatic plants (Nyanti et al 2021), *Barbonymus gonionotus* and *Cyprinus carpio* in the Mekong River

(Saowakoon et al 2021), and *C. armatus* in Khlong Luang Rachalothorn Reservoir, Thailand, which is dominated by macroalgae, oligochaetes and aquatic insects (Thong-Ngok et al 2022), and *C. apogon* in the Temengor and Bersia Reservoir, Malaysia (Hamid et al 2015), and in the Murum river, Serawak (Nyanti et al 2021) which animals, including Oligochaeta, Chironomidae, and detritus dominate.

Given the variety of food types (Table 1), *C. armatus* can be classified as a fish with an euryphagic diet. Based on the number of variations in food, fish are grouped into euryphagic, namely eating various kinds of food, stenophagic, eating a few types of food, and monophagic, eating one type of food (Pratiwy et al 2023). The same results were found in other species of *Cyclocheilicthys*, namely *C. apogon* (Hamid et al 2015; Nyanti et al 2021).

Descriptive statistics indicated that the mean diet composition of *C. armatus* was virtually identical between the rainy and dry seasons across all sex-size strata, with negligible absolute differences (e.g., Juveniles: 3.448 vs 3.448; Table 2). This consistency in means and dispersion indicates no seasonal shift in dominant resources during the study period, aligning with evidence from Indonesian highland lakes where Cyprinidae rely on benthic-periphytic/detrital resources and show notable niche overlap (Sathyananta et al 2024) and with other tropical lake studies reporting seasonally stable diets (Andi et al 2020).

Seasonal comparisons of diet composition indicated no significant differences between rainy and dry periods across all sex-size strata, with homogeneous variances (all Levene's $p > 0.05$) and confidence intervals for mean differences spanning zero, supporting the inference of seasonal trophic stability in *C. armatus* and a relatively constant resource supply over the sampling window. This pattern is consistent with regional evidence that many Southeast Asian cyprinids in tropical highland lakes and other lentic systems maintain opportunistic, benthic-periphytic, and detritus-based feeding with notable niche overlap and limited seasonal displacement, as documented for *Osteochilus vittatus* and *Barbodes binotatus* in Lake Tamblingan (Sathyananta et al 2024), and for lacustrine assemblages in Matano (though non-cyprinids; Andi et al 2020). Complementary studies from Indonesian reservoirs and rivers likewise portray cyprinids as flexible generalists that track locally abundant resources, and *O. wandersii* in the Lenggang headwaters (Febryanti et al 2021), while broader syntheses emphasize environmental and behavioral drivers of feeding in tropical fishes (Pratiwy et al 2023). Taken together, these sources align with our finding of negligible seasonal shifts: even though the frequency and distribution of specific food items may vary slightly by size class and sex, the aggregate composition remains statistically indistinguishable between seasons, consistent with a generalist feeding strategy buffered by relatively stable basal resources in tropical highland lake environments.

Table 2

Descriptive statistics of diet composition by season and strata with independent-samples t-test results (including Levene's test)

| Combined descriptive + t-test (rainy vs dry) | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Strata* | *N rainy* | *Mean rainy* | *SD rainy* | *N dry* | *Mean dry* | *SD dry* | *Levene F* | *Levene p* | *t* | *df* | *P (2-tailed)* | *Mean diff (rainy−dry)* | *SE diff* | *95% CI lower* | *95% CI upper* |
| Juvenile | 29 | 3.448 | 3.689 | 29 | 3.448 | 3.189 | 0.068 | 0.795 | 0.000 | 56 | 1.000 | 0.000 | 0.861 | -1.725 | 1.725 |
| Male 120-150 mm | 27 | 3.703 | 2.940 | 28 | 3.574 | 3.197 | 0.096 | 0.758 | 0.156 | 53 | 0.877 | 0.129 | 0.829 | -1.534 | 1.792 |
| Male > 150 mm | 27 | 3.703 | 2.940 | 28 | 3.572 | 2.786 | 0.051 | 0.822 | 0.170 | 53 | 0.866 | 0.131 | 0.772 | -1.418 | 1.680 |
| Male total (TL ≥ 120 mm) | 27 | 3.704 | 3.034 | 28 | 3.571 | 2.952 | 0.001 | 0.981 | 0.165 | 53 | 0.870 | 0.133 | 0.807 | -1.486 | 1.752 |
| Female 120-150 mm | 29 | 3.448 | 2.872 | 29 | 3.448 | 2.870 | 0.002 | 0.969 | 0.000 | 56 | 1.000 | 0.000 | 0.754 | -1.510 | 1.511 |
| Female > 150 mm | 29 | 3.448 | 2.617 | 29 | 3.448 | 2.558 | 0.047 | 0.830 | 0.000 | 56 | 1.000 | 0.000 | 0.679 | -1.361 | 1.361 |
| Female total | 29 | 3.448 | 2.707 | 29 | 3.448 | 4.249 | 0.749 | 0.391 | 0.000 | 56 | 1.000 | 0.000 | 0.936 | -1.874 | 1.874 |
| All (RA total) | 29 | 3.000 | 3.000 | 29 | 3.000 | 3.000 | 0.006 | 0.938 | 0.000 | 56 | 1.000 | 0.000 | 0.773 | -1.547 | 1.548 |

Note: N denotes the sample size for each group; Mean and SD represent the arithmetic mean and standard deviation, respectively; F and p refer to Levene's test for equality of variances; t represents the independent-samples t statistic; df denotes degrees of freedom; p (two-tailed) indicates the significance level; Mean diff refers to the difference between rainy and dry season means (rainy − dry); SE diff denotes the standard error of the mean difference; and CI represents the 95% confidence interval of the mean difference.

Table 3

Mann-Whitney U test results (rainy vs. dry)

| *Mann-Whitney U test (rainy vs dry)* | | | | | |
|---|---|---|---|---|---|
| *Strata* | *U* | *Z* | *p (2-tailed)* | *r = Z/sqrt(N)* | *N total* |
| Juvenile | 390.500 | -0.467 | 0.461 | -0.061 | 58 |
| Male 120-150 mm | 349.000 | -0.488 | 0.625 | -0.066 | 55 |
| Male > 150 mm | 360.500 | -0.295 | 0.768 | -0.040 | 55 |
| Male Total TL ≥ 120 mm | 361.500 | -0.278 | 0.781 | -0.038 | 55 |
| Female 120-150 mm | 414.500 | -0.093 | 0.926 | -0.012 | 58 |
| Female > 150 mm | 414.000 | -0.101 | 0.919 | -0.013 | 58 |
| Female total TL ≥ 120 mm | 375.000 | -0.708 | 0.479 | -0.093 | 58 |
| Total (all combined) | 412.000 | -0.132 | 0.895 | -0.017 | 58 |

Note: U denotes the Mann–Whitney U statistic; Z represents the standardized test statistic; p (two-tailed) indicates the significance level; r is the effect size calculated as Z/√N; N refers to the total sample size.

Nonparametric sensitivity analysis Mann-Whitney tests corroborated the parametric findings: no seasonal differences in diet distributions across all strata, with trivial effect sizes (e.g., Juveniles: U = 390.500, Z = -0.467, p = 0.641, r = -0.061; Table 3). This cross-method agreement indicates the null effect is not an artifact of parametric assumptions.

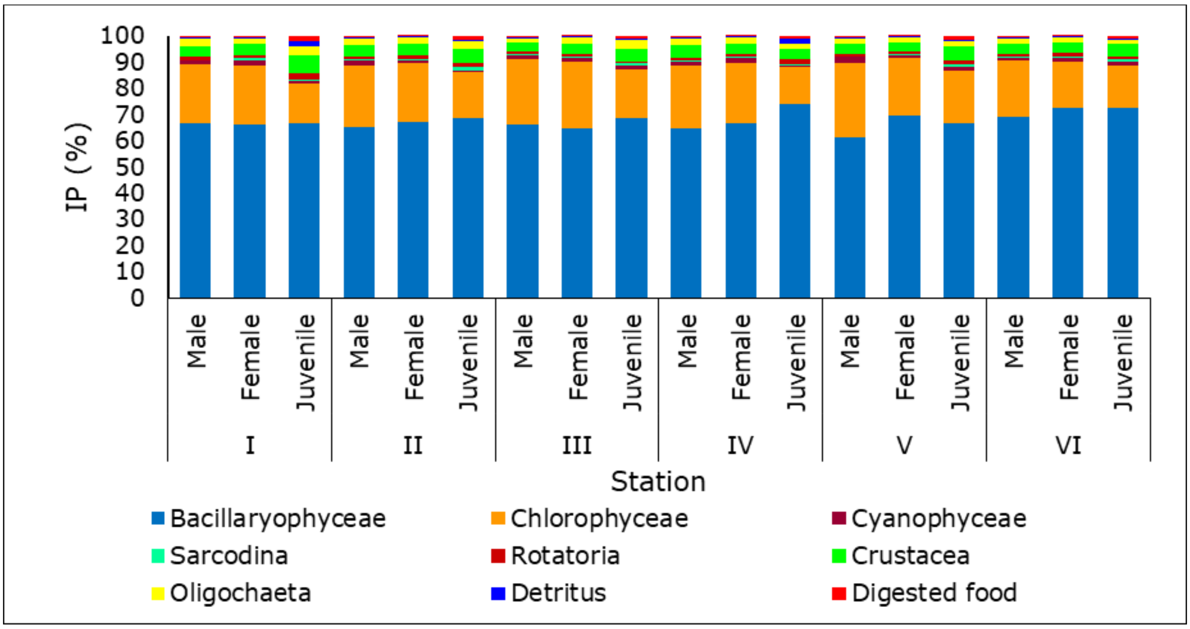


Figure 2. Food composition of *C. armatus* by sex, developmental stage (male, female, juvenile), and sampling station during the rainy season.

Figure 2 shows the percentage of Bacillariophyceae in the intestines of *C. armatus* males, females, and juveniles at each station during the rainy season. Bacillariophyceae were also found as the dominant phytoplankton in the stomachs of *O. vittatus* and *B. binotatus* (Sathyananta et al 2024). The percentage of Bacillariophyceae in the intestines of male fish ranged from 61.05 to 69.12% which was dominated by the Navicula genus, and female 64.81 to 72.63% dominated by the Navicula genus, except for station VI which was dominated by the genus Ephitemia and juvenile fish 60.45 to 73.81% which were dominated by the genus Denticula except for stations I and IV which were dominated by the genus Navicula. Phytoplankton of the class Bacillariophyceae are the most abundant organisms found in the intestine of *C. armatus* males, females, and juveniles. This shows that the aquatic environment of Diatas Lake strongly supports the life of Bacillariophyceae.

Sulastri (2018) stated that Bacillariophyceae are phytoplankton with cell walls from silicates, some of which can adapt by attaching to the substrate, but generally have the nature of floating in water. However, the abundance and distribution are not always the same, especially in relatively cold waters, and the presence of diatoms in all kinds of aquatic ecosystems, their ability to reach a high number of species even in small areas, including polluted and clean waters, and easy sampling are why they are preferred for comparing aquatic ecosystems with each other (Aykut et al 2021).

The high percentage of Bacillariophyceae found in the intestines of *C. armatus* was due to observations of the types of plankton found in the waters, showing that the species from the Bacillariophyceae class were the dominant organisms found in all these locations, resulting in fish *C. armatus* consuming more of these types of organisms. The phylum Bacillariophyceae (diatom) life histories (frequent asexual cycles plus sex to reset size) and physiological adaptations explain dominance and rapid bloom formation and are in the most tolerant group of phytoplankton so that it can adapt to various water conditions (Behrenfeld et al 2021), so the numbers are very abundant in the waters result in very abundant numbers in the water, besides that their small size can enter the mouth of small fish, therefore Bacillariophyceae tends to be chosen by fish as the food.

The dominant presence of the genus Navicula in the natural food composition of *C. armatus* is because Navicula is a unicellular diatom and has a small size, so it fits the mouth of all sizes of *C. armatus*, and it is widely eaten. Whether or not a type of food organism is eaten by fish is determined by many factors, including (1) food size, (2) food availability, (3) food color, and (4) the fish's appetite for food (Lubis et al 2021). Furthermore, Potter et al (2022) stated that the marked selectivity for prey was related to certain prey and predator traits, i.e. size category of prey species, and prey located above the substrata, either permanently or at frequent intervals, and to visual acuity and a fast-swimming angled attack by the predator.

Navicula cell size ranges from 6 to 42 μm in length and from 1 to 4 μm in width (Sulastri 2018; Genkal & Komulaynen 2024). In addition to the suitable size, Navicula is also abundant in the waters, as the environmental conditions of Diatas Lake are suitable for its life, including low temperatures, high alkalinity, and oligotrophic water types. Navicula is found in oligotrophic to eutrophic type lake waters, with a temperature of 18.23-27.44°C, pH 7.16-7.23, and alkalinity ($CaCO_3$) 70.94-219.31 mg $L^{-1}$ (Sulastri 2018).

Figure 3 shows a high percentage of Bacillariophyceae in the intestines of *C. armatus* males, females, and juveniles at each station during the dry season. The distribution of IP values in Figure 3 also shows that the main diet of males, females, and juveniles at each station in the dry season is the same as in the rainy season (Figure 2), namely, the class Bacillariophyceae. This is evident from the percentage of Bacillariophyceae in the intestine at all stations, which exceeds 40%. The percentage of Bacillariophyceae in male fish ranged from 66.22 to 69.54%, and each station was dominated by the genus Navicula except station II, which was dominated by the genus Denticula; in female fish ranged from 65.54 to 70.05% which was dominated by the genus Navicula, except station V which was dominated by the genus Ephitemia and station VI was dominated by the genus Denticula, and juvenile fish, ranging from 70.92 to 74.02%, which was dominated by the genus Navicula except station II which was dominated by the genus Denticula. This proves that fish tend to forage in areas that are rich in preferred food resources (Ebrahim et al 2020), with foraging rates positively correlating with local food abundance and habitat selection being driven by prey availability. This proves that fish tend to forage in areas that are rich in preferred food resources (Nikolsky 1963).

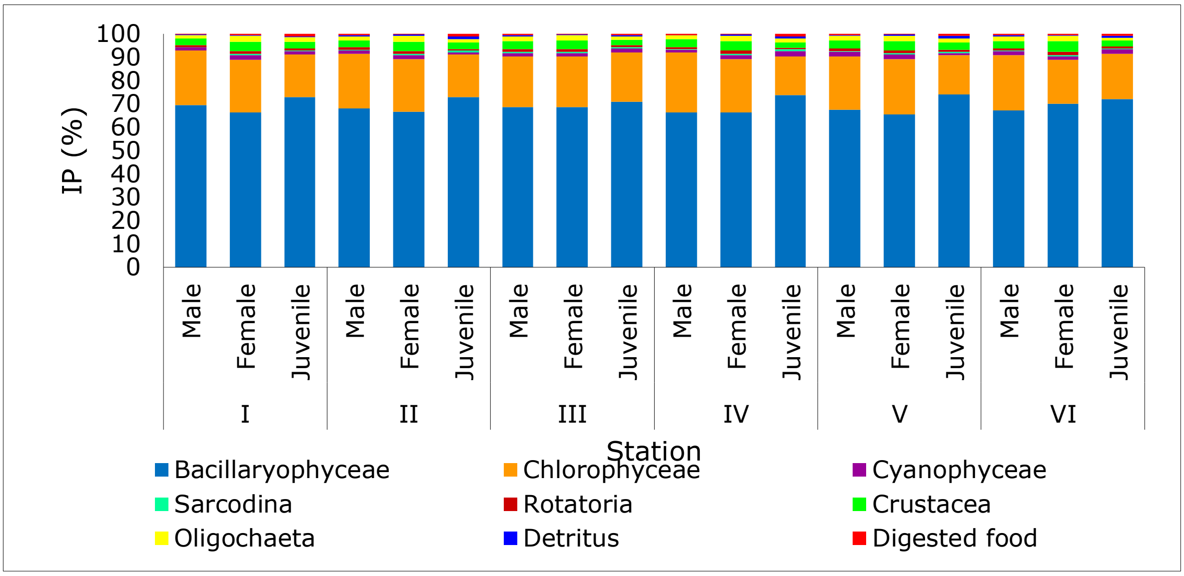


Figure 3. Food composition of *C. armatus* based on sex, developmental stage (male, female, juvenile), and sampling station in the dry season.

The distributions of IP values in Figures 2 and 3 indicate that the food composition of *C. armatus* is broadly similar among stations in both rainy and dry seasons. Across sex and life stages (male, female, juvenile), phytoplankton consistently yielded the highest IP values, with Bacillariophyceae dominating and exceeding the "main food" threshold at most stations and in both seasons. Comparable phytoplankton dominance has been reported for several cyprinids, including *Rasbora lateristriata* and *Puntius binotatus* (Elinah et al 2016), and *O. wandersii* (Febryanti et al 2021).

Across stations and in both seasons, Bacillariophyceae yielded the highest mean IP values for males, females, and juveniles, consistently exceeding 40%, indicating that diatoms constitute the primary diet of *C. armatus* in Diatas Lake. Using the standard IP thresholds (IP > 40% primary; 4-40% secondary; < 4% incidental (Nikolsky 1963; Febryanti et al 2021), this pattern classifies Bacillariophyceae as the main food item. Comparable phytoplankton dominance has been reported for several cyprinids, like in *O. hasseltii* (Munfaridzi et al 2020), and *R. lateristriata* and *P. binotatus* (Elinah et al 2016).

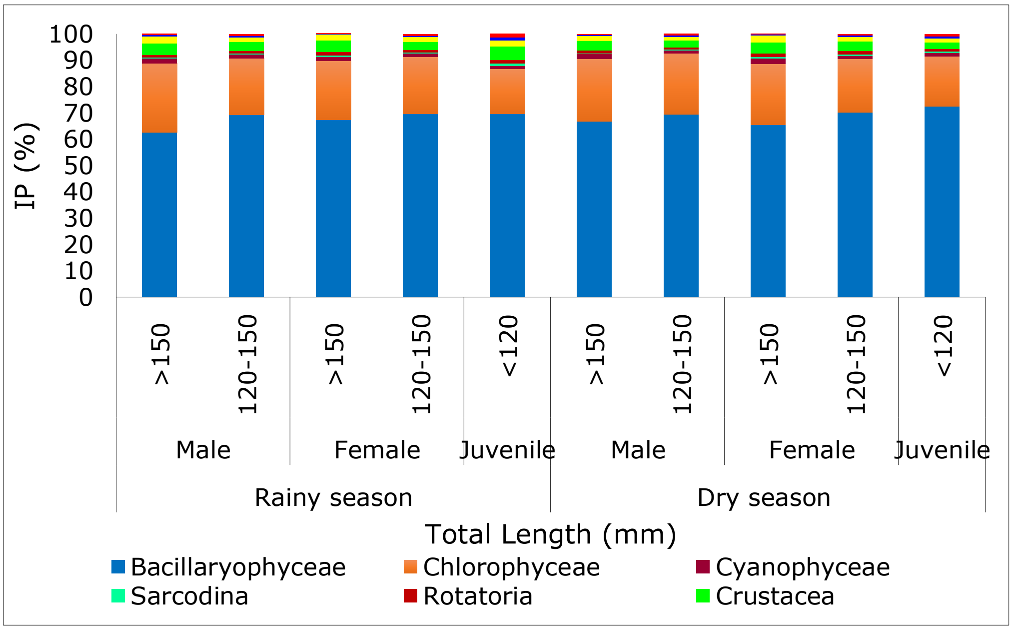


Figure 4. Food composition of *Cyclocheilichthys armatus* based on sex, developmental stage (male, female, juvenile), and total length.

Figure 4 shows the variation in the percentage of the main food (Bacillariophyceae) in the diet of male, female, and juvenile fish from each body size group in the rainy and dry seasons. The percentage of the principal dietary component, the main food of *C. armatus* in the rainy season, is the male fish, ranging from 62.60 to 69.26%, female 36 to 69.55%, and juvenile 69.65%, while in the dry season, male fish ranged from 66.78 to 69.48%, female 65.53 to 70.13%, and juvenile 72.41%. Figure 4 also shows the change in the IP value of the main diet of male and female fish in both seasons, where the IP value of the main food of fish with TL < 120 mm is greater than TL 120 to 150 m, and TL 120 to 150 mm is greater than TL > 150 mm in both seasons for both male and female fish. This suggests a tendency for the value to decrease with increasing body length. This suggests a tendency for the value to decrease with increasing body length. The increase in body length is related to the level of gonad development (Moon et al 2024). The longer the body length, the larger the gonads will also become. Consequently, the large size of the gonads will suppress the digestive tract, providing less space in the stomach, which in turn will decrease the eating power of the fish (Yagnesh & Hitesh 2022). The feeding intensity of adult fish decreases during the spawning season, compared to the non-spawning season. The increase in body length is related to the level of gonad development. The longer the body length, the size of the gonads will also increase, and then the large size of the gonads will suppress the digestive tract, so that the eating power of fish will decrease. The feeding intensity of adult fish decreases during the spawning season, compared to the non-spawning season, and variations in feeding intensity were greater in females than in males because the ovaries occupy more space than the testes (Mukhopadhyay et al 2020).

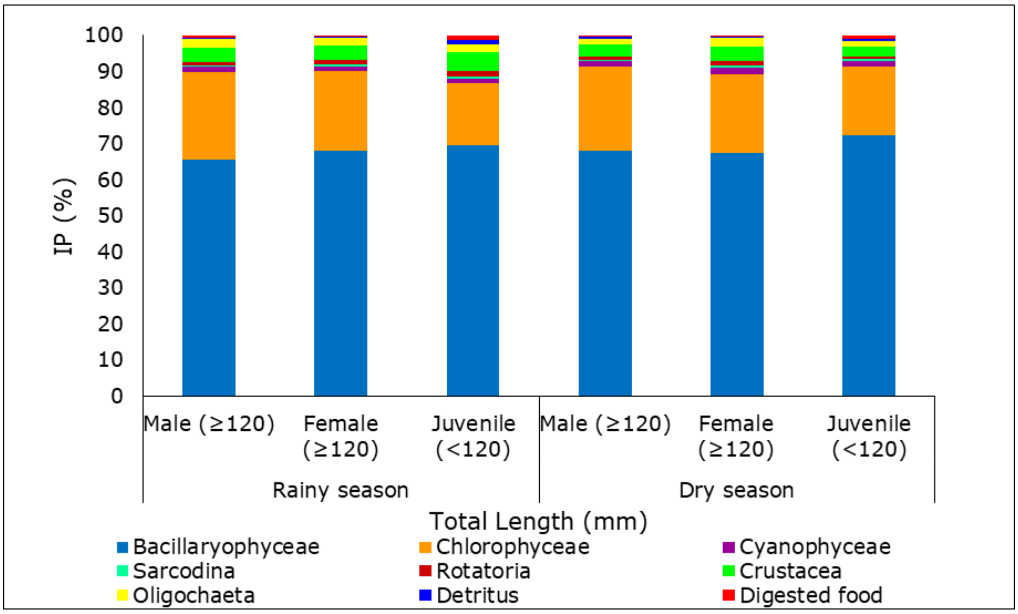


Figure 5. Food composition of *Cyclocheilichthys armatus* based on sex, developmental stage (male, female, juvenile), and size.

Figure 5 presents the average IP for male, female, and juvenile fish during the rainy and dry seasons. The IP value for male fish was 65.58% in the rainy season, lower than the value of 67.97% observed in the dry season. Conversely, the IP for female fish was higher during the rainy season (67.96%) than in the dry season (67.40%). Juvenile fish exhibited the highest IP values, reaching 72.41% in the rainy season compared to 69.65% in the dry season. These IP values indicate the relative dominance of different food types in the diet of each demographic group across seasonal variations. Furthermore, the results demonstrate a consistent pattern where the dietary IP for male fish is generally lower than that of females, which in turn is lower than that of juvenile fish.

Food types for *C. armatus* male, female, and juvenile are relatively the same; both are dominated by phytoplankton from the classes Bacillariophyceae and Chlorophyceae (Figures 2 and 3). Based on the size and level of development of the fish found, the higher the size and level of development, *C. armatus* tended to eat more zooplankton (Crustacea) and Oligochaeta (Figure 2); this may be related to meeting protein requirements for gonad development. The composition of the diet also depends on various factors, such as the size of the fish and the prey, the behaviour of the fish, the home range of the fish, and the availability of food (Trkov et al 2024), and the types of food eaten by a fish species usually depend on preferences for a particular food type size, age, season, habitat, and the availability of food type in nature (Yazıcı et al 2025), and also the physiological adaptations of the fish such as the length of intestine, the nature and physiological conditions of digestion (Duque-Correa et al 2024).

The composition of zooplankton and Oligochaeta in the diet of female fish from male fish is also related to protein requirements for egg development, where fish need more protein for egg yolk formation. The IP value of zooplankton in juveniles was found to be higher than that of male and female fish. This is probably because juvenile fish need a lot of protein for growth, and also because the development of digestive organs is not yet complete, like adult fish, so they are more likely to choose foods that are easy to digest. Research confirms that juvenile fish have "high protein and low fat requirements at the starter stage, while the higher growth rates and organogenesis require higher quantities of protein". This increased protein demand is directly related to incomplete digestive development, as "pepsin excretion as the primary pyloric proteolytic enzyme begins on 29 dph" (Javid Rahmdel & Falahatkar 2021), indicating that digestive capacity is still developing during juvenile stages. Consequently, juvenile fish preferentially select easily digestible prey items, as low-moving, easily digested, and small zooplankton as well as benthic organisms are commonly the first foods consumed by various fishes (Genelt-Yanovskaya et al 2023). This preference is particularly evident in cyprinid species, where "small metazooplankton like rotifers form an important food source mainly for fish larvae (e.g., larvae of cyprinids)" (Declerck & de Senerpont Domis 2022). Experimental evidence further supports this selectivity pattern, demonstrating that "the fish showed strong selectivity for crustaceans, including copepodites and adults of copepods" (Nakamura et al 2024). Bitterlich & Ganaiger (1984) found that silver carp (*Hypophthalmichthys molitrix*) prefer detritus and zooplankton with low abundance as the potential energy source compared to phytoplankton with higher abundance in the waters, because detritus and zooplankton are more easily digested by fish belonging to these stomachless fish, such as silver carp.

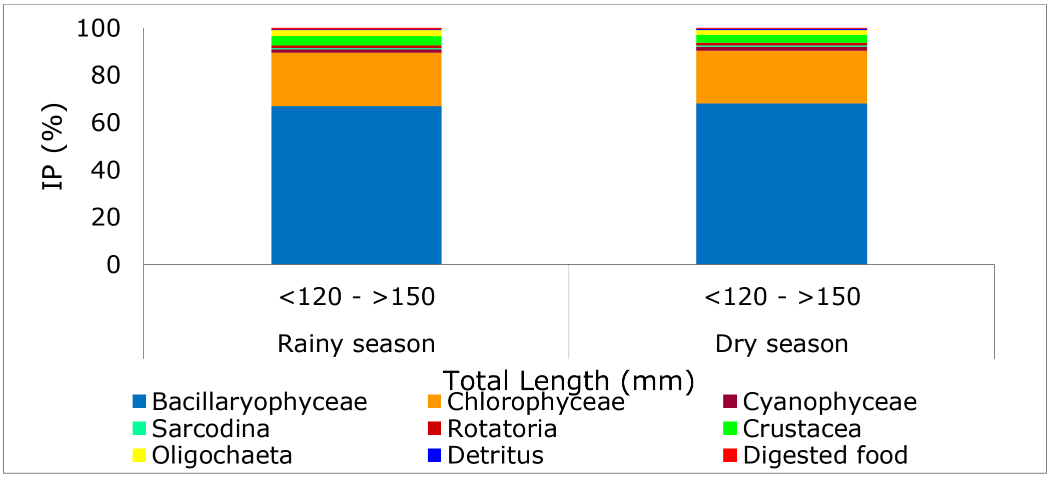


Figure 6. Food composition of *Cyclocheilichthys armatus* based on season.

From Figure 6, it can be seen that the largest percentage of food in both seasons is the Bacillariophyceae class. The percentage of Bacillariophyceae in the rainy season is 66.97% lower than in the dry season, which is 68.12%. This is related to the availability of food in the waters, which is also higher in the dry season. Differences in food strategies are determined by habits in using and choosing food and availability of food in waters, gender, and differences in activity levels (Feraco et al 2024). Recent research confirms that fish "significantly adjusted their time spent far and close to its food (anemone) depending on the tide, status, and the presence of eggs" (Wong et al 2022), demonstrating how environmental and social factors influence feeding behavior. Food availability in aquatic environments directly affects feeding strategies, as "changes in the fishery community structure and the decline in the abundance of primary prey resources have led the Greater lizardfis (*Shaurida tumbil*) population in the Beibu Gulf, South China Sea to diversify their prey species" (Yang et al 2024). Furthermore, habitat characteristics play a crucial role, where "larger littoral habitat led to an increased reliance on littoral-derived macroinvertebrates in the diet" (Berthelsen et al 2023). Species-specific feeding preferences are evident, as some fish "exhibits specialized feeding preferences" while others demonstrate "a more generalist approach" (Lilkendey et al 2024). The relationship between prey density and feeding behavior is also well-established, with studies showing "a nearly linear increase in feeding rate as function of prey density" (Khrizman et al 2024). The fish species in nature have a very close relationship with the presence of their food; the fish can survive if there is the type of food they like, which is further supported by evidence that many Arctic fish species "are generalist feeders that demonstrate wide dietary niches" (Wight et al 2023).

Table 4

Index of preponderance of food organisms from *Cyclocheilichthys armatus*

| *Food organism* | *Index of preponderance (%)* | | | | | |
|---|---|---|---|---|---|---|
| | *Rainy season* | | | *Dry season* | | |
| | *Male* | *Female* | *Juvenile* | *Male* | *Female* | *Juvenile* |
| Bacillariophyceae | 65.58 | 67.96 | 69.65 | 67.97 | 67.40 | 72.41 |
| Chlorophyceae | 24.11 | 22.13 | 17.12 | 23.40 | 21.93 | 18.96 |
| Cyanophyceae | 1.65 | 1.39 | 1.15 | 1.59 | 1.62 | 1.48 |
| Protozoa | 0.35 | 0.58 | 0.77 | 0.29 | 0.64 | 0.52 |
| Rotatoria | 0.94 | 1.14 | 1.47 | 0.92 | 1.20 | 0.84 |
| Crustacea | 4.03 | 3.85 | 5.09 | 3.16 | 4.03 | 2.60 |
| Oligochaeta | 2.26 | 2.23 | 2.35 | 1.77 | 2.44 | 1.51 |
| Detritus | 0.50 | 0.33 | 1.06 | 0.43 | 0.36 | 0.78 |
| Undigested food | 0.58 | 0.40 | 1.35 | 0.46 | 0.38 | 0.90 |

Value of the largest IP of foods *C. armatus* male and female and juveniles as a whole can be grouped into phytoplankton (Bacillariophyceae, Chlorophyceae, and Cyanophyceae), zooplankton (Sarcodina, Rotatoria and Crustacea), Oligochaeta, detritus, and digested food (Table 4 and Figure 2), According to Nikolsky (1963) the main food of a fish species if the largest share IP is 40%, the complementary food for the IP value is range 4-40% and additional food if the IP < 4%. This classification system has been consistently applied in recent fish diet studies, with explicit confirmation that IP > 40% = main food, IP 4-40% = complementary food, IP < 4% = additional food" (Hasibuan et al 2025). Based on this, *C. armatus* Diatas Lake of all sexes and sizes obtained the same main diet, namely phytoplankton from the class Bacillariophyceae. Complimentary food for males and juveniles in the rainy season and females in the dry season is phytoplankton from the Chlorophyceae class and zooplankton from the subphylum Crustacea, while for females in the rainy season and males and juveniles in the dry season, only Chlorophyceae. Additional food for females in the rainy season and males and juveniles in the dry season consists of Cyanophyceae, Sarcodina, Rotatoria, Crustacea, Oligochaeta, and detritus, while males and juveniles in the rainy season and females in the dry season are Cyanophyceae, Protozoa, Rotatoria, Oligochaeta, and detritus.

The number of zooplankton (Sarcodina, Rotatoria, and Crustacea), Oligochaeta, and detritus in the dietary composition of *C. armatus* Diatas Lake of all sizes and sexes is low and on average is classified as a supplementary food. The same thing was also found in *Hampala dispar* and *Mystacoleucus marginatus* in the Uboltrana reservoir, Thailand (Kakkaeo et al 2004). Similar dietary patterns have been documented in other Southeast Asian cyprinids, where environmental factors significantly influence feeding behavior and species composition in tropical lake systems (Rahman & Fathi 2022).

The status of crustaceans in the food composition of *C. armatus* Diatas Lake, in the group of males and juveniles in the rainy season and females in the dry season, is classified as a complementary food, whereas females in the rainy season and males and juveniles in the dry season are classified as a supplementary food. The same was found in the dietary composition of *C. apogon* in the Temengor and Bersia reservoirs, Malaysia (Hamid et al 2015). Similar seasonal feeding variations have been documented in other Asian cyprinids, where silver carp showed seasonal variation in feeding selectivity based on prey availability (Xia et al 2022).

Total body length (TL) and RGL are presented in Table 5. The value of intestinal length is relatively low in smaller-sized fish and tends to increase with fish growth to a certain size, and the relative intestinal length of male fish tends to be longer than that of female fish. The value of the RGL obtained indicates that *C. armatus* fish is herbivorous and tends to lead to omnivores. The same was found in *C. apogon* in the Temengor and Bersia reservoirs, Malaysia (Hamid et al 2015).

Table 5

Average of relative gut length of *Cyclocheilichthys armatus* based on sexes, developmental stage (male, female, juvenile), and total length

| *Gender* | *Total length (mm)* | *Relative gut length* | | | | | |
|---|---|---|---|---|---|---|---|
| | | *Rainy season* | | | *Dry season* | | |
| | | *Range* | *Average* | *SD* | *Range* | *Average* | *SD* |
| Male | 120-150 | 1.197-1.207 | 1.2 | 0.002 | 1.190-1.211 | 1.202 | 0.005 |
| | > 150 | 1.085-1.213 | 1.2 | 0.02 | 1.193-1.293 | 1.205 | 0.016 |
| Female | 120-150 | 1.170-1.194 | 1.183 | 0.005 | 1.176-1.195 | 1.183 | 0.005 |
| | > 150 | 1.172-1.189 | 1.183 | 0.004 | 1.145-1.191 | 1.182 | 0.007 |
| Juvenile | < 120 | 1.116-1.174 | 1.129 | 0.014 | 1.116-1.141 | 1.125 | 0.007 |

Note: SD represents the standard deviation.

From Table 5 and Figure 7, it can be seen that the RGL of *C. armatus* between the male, female, and juvenile rainy and dry seasons is relatively the same. The RGL of male and female fish between groups of size 120-150 mm total length, with >150 mm, is relatively the same. The RGL of the juvenile is shorter than that of males and females. This indicates the increase in gut length follows the increase in body length. The average relative length of the gut as a whole exceeds the total length of the body; this indicates that the diet of *C. armatus* is omnivorous. This is also indicated by the various types of food in the intestines of *C. armatus*, which consist of phytoplankton, zooplankton, Oligochaeta, and detritus. Nikolsky (1963) stated that the RGL for carnivorous fish is < 1, for omnivorous fish between 1-3, while for herbivorous fish is > 3. In addition to Kramer & Bryant (1995), the intestinal length range for carnivorous fish is 0.5-2.4 times their body length, omnivorous fish are 0.8-5 times their body length, and herbivorous fish have intestinal lengths between 2-21 times their body length. The same results were found in other types of Cyprinidae, such as the RGL value of *C. apogon*, which ranged from 0.984 to 1.376 (Hamid et al 2015).

Diet represents the primary factor influencing RGL variations in fish, with this relationship well-documented in Asian cyprinid systems where fish with similar RGLs show considerable gut microbiome similarity and metabolic specialization (Liu et al 2022). Studies of Asian cyprinids from Dianchi Lake demonstrate that feeding habits determine digestive morphology, with herbivorous species like *Ctenopharyngodon idellus* showing distinct intestinal adaptations, including longer gut lengths compared to carnivorous and omnivorous species (Jiao et al 2023). This pattern is consistent across cyprinid radiations globally, as demonstrated by Garra species, where periphyton feeders possess longer guts compared to zoophagous ecomorphs, illustrating the universal relationship between diet and gut morphology in cyprinids (Komarova et al 2022). The correlation between RGL and diet in cyprinids reflects broader evolutionary patterns where herbivorous fish require longer intestines to process high-fiber plant materials with specialized gut microbiomes, while carnivorous species maintain shorter guts optimized for protein digestion (Jiao et al

2023). Environmental changes and food availability in Asian freshwater systems drive morphological adaptations in cyprinid digestive systems, with RGL serving as an ecological indicator that reflects dietary preferences and adaptive responses to local resource availability rather than simply body size constraints (Duque-Correa et al 2024). These findings support the concept that RGL in Asian cyprinids, including species like Cyclocheilichthys, represents a functional trait shaped primarily by diet and ecological adaptation to available food resources in tropical freshwater environments.

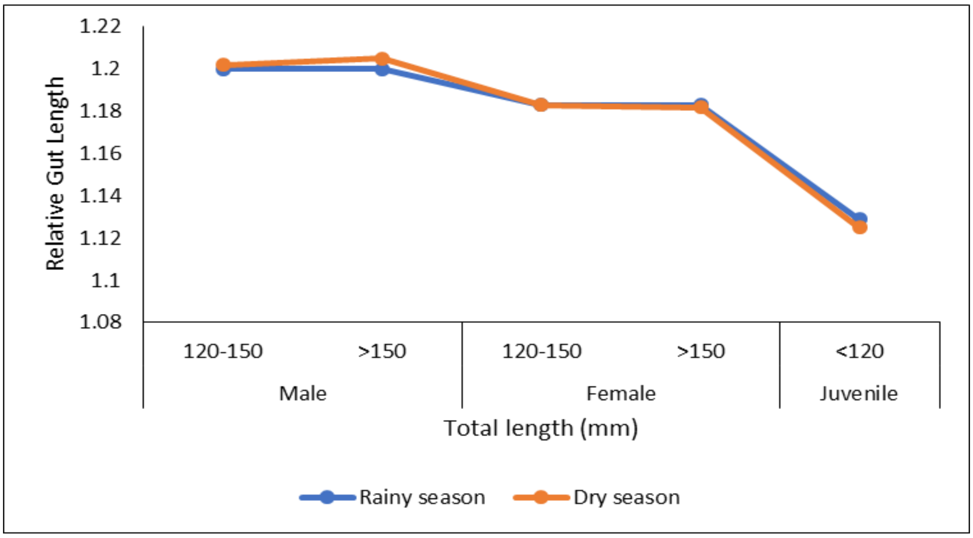


Figure 7. Average RGL of *Cyclocheilichthys armatus* in Diatas Lake during the rainy and dry seasons.

Table 6 shows that the r² of the relationship model between food volume *C. armatus* and TL ranges from 0.028 to 0.305, indicating a weak positive correlation between food volume and TL. Body length can represent a food volume of less than 50%.

Table 6

Relationship between volume of food and total length of *Cyclocheilichthys armatus*

| *Organism* | *a* | *b* | *$r^2$* | *Model* | *Explanation* |
|---|---|---|---|---|---|
| Total | 0.06841 | 0.00137 | 0.305 | Vm = 0.06841 + 0.00137TL | Body length describes the volume of food at 30.5% |
| Male | 0.00188 | 0.04070 | 0.267 | Vm = 0.00188TL – 0.04070 | Body length describes the volume of food at 26.7% |
| Female | 016354 | 0.00098 | 0.162 | Vm = 0.16354 + 0.00098TL | Body length describes the volume of food at 16.2% |
| Juvenile | 009055 | 0.00115 | 0.028 | Vm = 0.09055 + 0.00115TL | Body length describes the volume of food at 2.8% |

Note: a represents the intercept of the regression model; b denotes the slope coefficient describing the rate of change in food volume with total length; r² indicates the coefficient of determination, reflecting the proportion of variance in food volume explained by total length; Vm refers to the volume of stomach contents; and TL denotes total length.

Table 7
Niches breadth of food of *Cyclocheilichthys armatus* during the rainy season and dry season

| *Organism* | *Total length (mm)* | *Niche breath* | | | |
|---|---|---|---|---|---|
| | | *Dry season* | | *Rainy season* | |
| | | *B* | *Ba* | *B* | *Ba* |
| Male | > 150 | 17.643 | 0.616 | 16.688 | 0.603 |
| | 120-150 | 15.788 | 0.548 | 15.514 | 0.558 |
| Female | > 150 | 18.941 | 0.641 | 18.795 | 0.636 |
| | 120-150 | 17.391 | 0.585 | 17.364 | 0.584 |
| Juvenile | < 120 | 15.915 | 0.552 | 15.101 | 0.542 |
| Total of males | 120- >150 | 16.878 | 0.611 | 16.317 | 0.589 |
| Total of females | 120- >150 | 18.330 | 0.619 | 18.273 | 0.617 |
| Male + female | > 150 | 18.387 | 0.621 | 17.953 | 0.605 |
| Male + female | 120-150 | 16.682 | 0.560 | 16.658 | 0.559 |
| Male + female | 120- >150 | 17.680 | 0.596 | 16.658 | 0.559 |
| Male + female + juvenile | < 120- >150 | 17.609 | 0.593 | 17.346 | 0.584 |

Note: Ba is Levins' standardized niche breadth; B is Levins' measure of niche breadth.

From Table 7, it can be seen widely recessed value of food fish *C. armatus* is based on size and sex. Niche breadth analysis of *C. armatus* in Diatas Lake demonstrates feeding patterns consistent with other cyprinid species in Southeast Asian freshwater systems. The values ranging from 0.542-0.636 (rainy season) to 0.548-0.641 (dry season) reflect seasonal adaptations in feeding behavior observed across Asian cyprinids, where trophic niche breadths show significant seasonal variation related to resource availability (Sartimbul et al 2023). Gender differences with females showing higher niche breadth than males indicate more generalist feeding strategies, a pattern that reflects individual trophic niche variation commonly observed in Asian freshwater fish communities (Zhang et al 2024). The selective feeding behavior of male fish, indicated by smaller niche areas, demonstrates resource partitioning strategies that facilitate coexistence in tropical Asian waters where resource competition may be intense (Vejrík et al 2023). Ontogenetic differences between juvenile (0.542-0.552) and adult fish (0.559-0.596) reflect developmental changes in feeding ecology typical of Southeast Asian cypriniform species, where juveniles often utilize different food sources and feeding strategies compared to adults (Medo et al 2023). The seasonal pattern with lower niche breadth during the rainy season (0.584) compared to the dry season (0.593) may reflect monsoon-influenced resource dynamics characteristic of Indonesian freshwater systems, where seasonal precipitation patterns significantly affect food availability and fish feeding behavior. These findings align with patterns documented in related cyprinid species such as *C. apogon*, confirming consistent ecological strategies across the Cyclocheilichthys genus in tropical Asian waters.

Stomach content indices show seasonal variation with higher values during the dry season (Table 8) and size-dependent patterns where smaller fish exhibit greater feeding intensity due to higher weight-specific metabolic rates (Figure 8), and increased energy demands for growth (Dinh et al 2022). Diet changes are closely related to physiological changes during fish life cycles, particularly during reproductive phases when feeding patterns shift according to gonadal maturation stages and spawning requirements (Torsabo et al 2022). Gender differences in stomach content indices reflect size-specific energy demands, with females in the 120-150 mm size class showing higher feeding intensity during gonadal stages 1-2 for egg development, while males dominate in larger size classes, demonstrating that spawning fish require increased energy input with food consumption influenced by multiple factors including fish size, reproductive condition, environmental temperature, and food availability (Syandri et al 2023).

Table 8

Index of stomach content of *Cyclocheilichthys armatus* based on total length

| *Gender* | *Total length (mm)* | *Index of stomach content* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Rainy season* | | | | *Dry season* | | | |
| | | *N* | *Range* | *Average* | *SD* | *N* | *Range* | *Average* | *SD* |
| Male | 120-150 | 36 | 0.590-1.367 | 0.898 | 0.166 | 36 | 0.698-1.183 | 0.957 | 1.128 |
| | > 150 | 36 | 0.237-0.947 | 0.592 | 0.156 | 36 | 0332-0.836 | 0.596 | 0.116 |
| Female | 120-150 | 36 | 0.726-1.180 | 0.918 | 0.11 | 36 | 0.666-1.147 | 0.943 | 0.125 |
| | > 150 | 36 | 0.357-0.852 | 0.536 | 0.093 | 36 | 0.371-0.785 | 0.565 | 0.115 |
| Juvenile | < 120 | 36 | 1.376-2.382 | 1.924 | 0.255 | 36 | 1.368-2.577 | 1.85 | 0.261 |

Note: N denotes the sample size for each group; SD represents the standard deviation.

Different feeding strategies in cyprinid fish are influenced by species-specific food selection patterns and resource availability, as demonstrated in Indonesian waters where fish exhibit adaptive behavioral responses to environmental conditions (Wang et al 2019). Gender differences play a crucial role in feeding behavior and activity levels, with distinct patterns observed in Indonesian cyprinids, including Cyclocheilichthys species, where males and females show different habitat use and foraging strategies (Zak et al 2020). The timing of sampling during different seasons is particularly important for Indonesian freshwater fish studies, as *C. armatus* in Diatas Lake demonstrates specific reproductive patterns closely linked to monsoon cycles, with gonad maturation stages (GMS I-II) occurring from January to May and August to November, and spawning peaks at the end of the rainy season in July and December, reflecting the adaptation of Indonesian cyprinids to tropical seasonal patterns (Widiana et al 2020). This pattern is consistent with other Indonesian freshwater fish species that show peak reproductive activity when environmental conditions are optimal following monsoons.

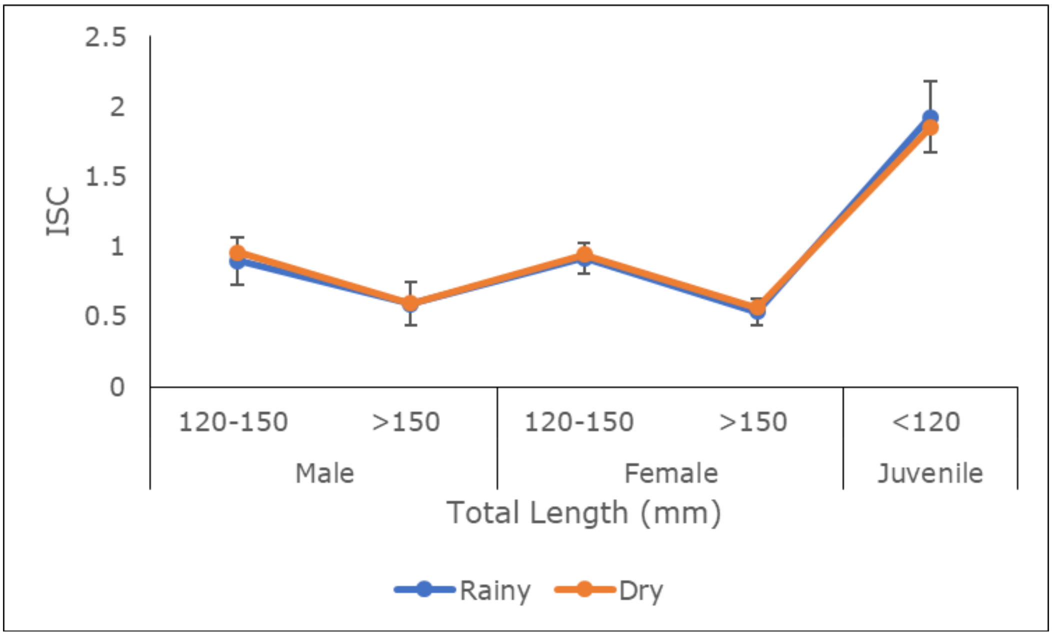


Figure 8. ISC in each group of sizes.

Table 9

Niche overlap of the food resources of *Cyclocheilichthys armatus* during the rainy season

| *Competitive group* | *TL (mm)* | *Male* | | *Female* | | *Male+female* | *Juvenile* |
|---|---|---|---|---|---|---|---|
| | | *>150* | *120-150* | *>150* | *120-150* | *120->150* | *< 120* |
| Male | > 150 | 1 | | | | | |
| Male | 120-150 | 0.981 | 1 | | | | |
| Female | > 150 | 0.982 | 0.970 | 1 | | | |
| Female | 120-150 | 0.985 | 0.974 | 0.989 | 1 | | |
| Male + female | 120 -> 150 | 0.986 | 0.986 | 0.986 | 0.986 | 1 | |
| Juvenile | < 120 | 0.958 | 0.948 | 0.953 | 0.954 | 0.960 | 1 |

Note: TL represents total length.

Table 10

Niche overlap of the food resource of *Cyclocheilichthys armatus* during the dry season

| *Competitive group* | *TL (mm)* | *Male* | | *Female* | | *Male+female* | *Juvenile* |
|---|---|---|---|---|---|---|---|
| | | *>150* | *120-150* | *>150* | *120-150* | *120->150* | *<120* |
| Male | > 150 | 1 | | | | | |
| Male | 120-150 | 0.987 | 1 | | | | |
| Female | > 150 | 0.990 | 0.973 | 1 | | | |
| Female | 120-150 | 0.991 | 0.987 | 0.990 | 1 | | |
| Male + Female | 120 -> 150 | 0.992 | 0.992 | 0.992 | 0.992 | 1 | |
| Juvenile | < 120 | 0.965 | 0.969 | 0.969 | 0.975 | 0.973 | 1 |

Note: TL represents total length.

The value of niches overlaps with C. armatus as a whole, with values close to 1 (one) in both the rainy and dry seasons. Specifically, in the rainy season, the value ranges from 0.948 to 0.989, and in the dry season, it ranges from 0.962 to 0.992 (Table 9-10). High niche overlap values approaching unity indicate similar resource utilization patterns among fish groups, with increased niche breadth and increased niche overlap observed when species share common food sources (Kaymak et al 2023). Resource overlap values demonstrate the quantitative relationship between overlap indices and actual dietary similarity among fish species, with values close to one indicating that different fish groups utilize almost identical food resources. The value of niche overlap shows that overall, both male, female, and juvenile fish in all size groups utilize almost the same type of food. The value of the niche overlap tends to be higher in the dry season than in the rainy season. This seasonal pattern aligns with findings showing that the greatest resource overlap among species occurred in summer, demonstrating seasonal peaks in dietary similarity when resource availability is high (Coulter et al 2019). This is because the amount of food availability in the habitat is higher in the dry season than in the rainy season, causing food (prey) to be easily eaten by fish. This relationship between resource availability and dietary overlap is supported by evidence that the amount of food consumed increased significantly with increasing resource density, and that niche overlap increased until a certain extent of resource density, when species started to segregate more strongly. Overlapping food niches tended to increase with increasing prey abundance because prey was easily preyed upon by all fish, as demonstrated by studies showing that trophic levels peaked during periods of abundant food resources (zooplankton and phytoplankton), indicating that prey abundance directly influences feeding patterns and resource utilization (Quirino et al 2022).

The *Index of electivity* (E) in the rainy season ranges from -0.750 to 0.765, with the largest index in the genus Ephitemia and the lowest in Fragillaria, while the dry season is -0.803 to 0.601, with the largest index in the genus Pinnularia and the smallest in Fragillaria (Table 11). The two genera with the highest IP belong to the Phytoplankton of the class Bacillariophyceae. This shows that *C. armatus* prefers the Bacillariophyceae class, due to the supply of nutrients that support natural feed from the Bacillariophyceae class for breeding. According to Pratiwy et al (2023), fish preference for food is very relative because it is not certain that a type of food that is abundant in waters can be utilized by fish. Several factors can cause this, such as the uneven distribution of organisms as food for fish, the availability of food, the choice of these fish, as well as the presence of physical and chemical factors in the waters that can affect changes in water condition. The lowest IPs in both seasons were found in the genus Fragillaria, which also belongs to the class Bacillariophyceae. This shows that Fragillaria is less favored by *C. armatus*. This is probably because the cells arrange themselves in a ribbon with a length of up to 170 microns, so that it is difficult to digest, and their presence in water is also small because Fragillaria is generally found in eutrophic waters (Sulastri 2018), while Diatas Lake is classified as an oligotrophic lake.

Table 11

The average index of electivity of food *C. armatus*

| *No* | *Food organism* | *Index of electivity (E)* | |
|---|---|---|---|
| | | *Rainy season* | *Dry season* |
| | | Phytoplankton | |
| 1 | *Navicula* | 0.168 | -0.156 |
| 2 | *Denticula* | 0.524 | 0.465 |
| 3 | *Ephitemia* | 0.765 | 0.585 |
| 4 | *Fragillaria* | -0.750 | -0.803 |
| 5 | *Gomphonema* | 0.126 | 0.132 |
| 6 | *Cymbella* | 0.104 | -0.472 |
| 7 | *Nitzschia* | 0.466 | 0.531 |
| 8 | *Pinnularia* | 0.380 | 0.601 |
| 9 | *Pediastrum* | 0.069 | 0.378 |
| 10 | *Staurastrum* | 0.164 | 0.239 |
| 11 | *Spirogyra* | -0.628 | -0.485 |
| | | Zooplankton | |
| 12 | *Arcella* | -0.691 | -0.327 |
| 13 | *Brachionus* | -0.572 | -0.132 |
| 14 | *Ceriodaphnia* | -0.518 | 0.023 |
| 15 | *Cyclops* | -0.503 | -0.026 |
| 16 | *Nauplius* | -0.534 | -0.131 |

Description: low selective level < 1 selective (7 negative choices).

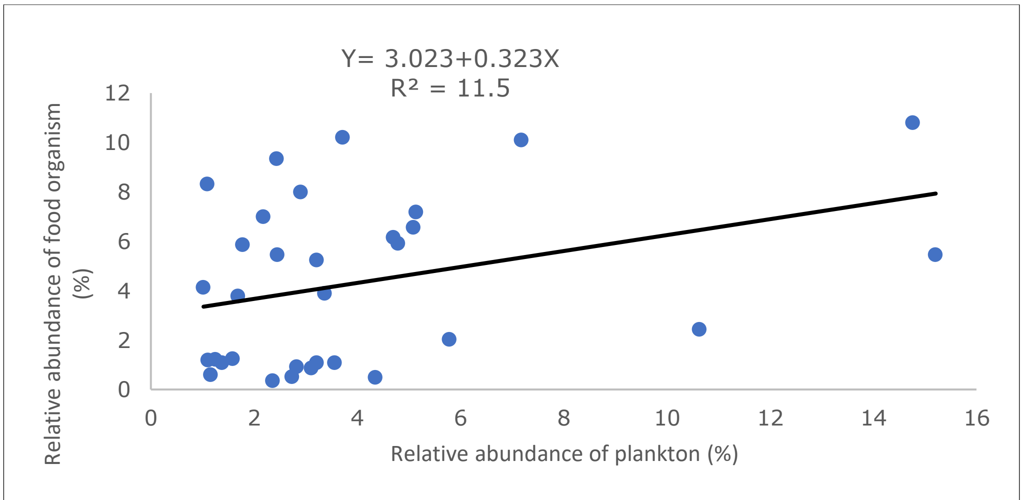


Figure 9. Relationship of food abundance in the intestine of *Cyclocheilichthys armatus* and plankton abundance in the waters.

The form of the relationship between the abundance of food organisms in the intestine of *C. armatus* and the abundance of plankton in the waters is described in the form of Y = 3.023 + 0.323X with $R^2$ = 0.115 (Figure 9). This equation shows that the abundance of food species in the intestine of *C. armatus* has a weak positive correlation with the abundance of plankton in the water.

**Conclusions**. *Cyclocheilichthys armatus* is an omnivorous fish with an euryphagic characteristic, with the main food being phytoplankton from the class Bacillariophyceae, which is dominated by the genus *Navicula*. The types of food used by *C. armatus* were relatively the same between sexes, sizes, places, and locations. The niche breadth tends to increase with the increase in fish size. The niche overlap index for food, by size and sex, and the similarity of the food resources used by C. armatus are high, allowing for competition when food is in limited supply.

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**Conflict of interest**. The authors declare that there is no conflict of interest.

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