Food and Feeding Habits of Three Ecologically Important Fish Species in Lake Hawassa, Ethiopia

Teshome Belay[1, 3*], Elias Dadebo[1], Girma Tilahun[1] and Degsera Aemro[2]

ABSTRACT

Understanding the feeding behavior of fish species is crucial for evaluating ecosystem health, trophic relationships, and resource availability in aquatic environments. This study investigated the feeding habits of three fish species in Lake Hawassa, Ethiopia, during two rainy and two dry months in 2024: the straightfine barb [*Enteromius paludinosus* (Peters, 1852)], the stone-lapping minnow [*Garra quadrimaculata* (Rüppell, 1835)], and the black lampeye [*Aplocheilichthys antinorii* (Vinciguerra, 1883)]. A total of 1,795 specimens were collected using beach seines and hand nets. Gut content analysis was conducted using frequency of occurrence, volumetric contribution, and index of preponderance methods. A high degree of dietary overlap (C>60%) was observed across size classes in all species, with some exceptions. Seasonal variation in prey availability was reflected in the frequency and volume of consumed items. *E. paludinosus* consumed seven main prey categories, including phytoplankton, detritus, macrophytes, zooplankton, fish eggs, and nematodes. *G. quadrimaculata* ingested all these items, while *A. antinorii* consumed all except nematodes. Phytoplankton dominated the diet of all three species, with the highest frequency of occurrence (87.17%, 63.18%, and 84.10%), volumetric contribution (84.24%, 46.38%, and 59.88%), and index of preponderance (85.94%, 47.71%, and 63.16%) for *E. paludinosus*, *G. quadrimaculata*, and *A. antinorii*, respectively. Seasonal variations in diet composition were significant, while intraspecific dietary overlap remained consistently high (C>60%) across size classes. The results indicate that all three species exhibit omnivorous feeding habits.

Keywords: Dietary overlap, Feeding habit, Lake Hawassa, Omnivorous

INTRODUCTION

Understanding the feeding habits of fish species is essential for assessing ecosystem health, trophic interactions, and resource availability within aquatic environments. Fish play a crucial role in structuring food webs, influencing nutrient cycling, and maintaining ecological balance. However, research has disproportionately focused on commercially important species, leaving ecologically significant but non-commercial fish species understudied. These species contribute to ecosystem stability, serve as prey for large fish, and may compete for resources with economically valuable species. Assessing their feeding habits is therefore critical to understanding their ecological roles, particularly in the context of habitat degradation, overfishing, and climate variability.

Despite their ecological importance, non-commercial fish species remain poorly studied in Ethiopian inland waters. While extensive research

[1]Department of Aquatic Sciences, Fisheries and Aquaculture, College of Natural and Computational Sciences, Hawassa University, Hawassa, Ethiopia
[2]Department of Fisheries and Aquatic Sciences, School of Fisheries and Wildlife, College of Agriculture and Environmental Sciences, Bahir Dar University, Bahir Dar, Ethiopia
[3]Department of Animal Sciences, College of Agriculture and Natural Resource, Dilla University, Dilla, Ethiopia
*Corresponding author. E-mail address: teshimeansc@gmail.com
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has documented the biology of commercially important fish species (Tilahun *et al*., 2021), studies on ecologically significant species remain limited. Their distinct habitat preferences and limited interest from fishers contribute to this research gap, as these species often require specialized sampling methods (Tekle-Giorgis *et al*., 2016a). Recent studies have emphasized the need to investigate the biological parameters of ecologically significant fish species to better understand their roles in maintaining ecosystem health (Lakew *et al*., 2024). For instance, studies on *Enteromius paludinosus* (Peters, 1852) in Lake Ziway (Dadebo *et al*., 2013), and Lake Hawassa (Desta *et al*., 2008), and *Garra quadrimaculata* (Rüppell, 1835) in the Awash River (Temesgen *et al*., 2023), Debbis River (Tirfessa *et al*., 2017), and Lake Hawassa (Tekle-Giorgis *et al*., 2016a), have revealed that these species exhibit generalist feeding habits, consuming both plant- and animal-based food sources.

Lake Hawassa, located in the Central Ethiopian Rift Valley, supports six distinct fish species. Among these, *E. paludinosus*, *G. quadrimaculata*, and *Aplocheilichthys antinorii* (Vinciguerra, 1883) are considered ecologically important but lack commercial value (Dadebo, 2000). Most research on Lake Hawassa has focused on commercially important species such as Nile tilapia [*Oreochromis niloticus* (Linnaeus, 1758)], African catfish [*Clarias gariepinus* (Burchell, 1822)], and African big barb [*Labeobarbus intermedius* (Rüppell, 1836)] (Tilahun *et al*., 2021), while little attention has been given to the smaller, ecologically important species. These fish serve as prey for larger, commercially valuable species, including *C. gariepinus* (Dadebo, 2000; Desta *et al*., 2007; Tekle-Giorgis *et al*., 2016b), and *L. intermedius* (Admasu and Dadebo, 1997). Additionally, *A. antinorii* has been identified as prey for the larger *E. paludinosus* in Lake Hawassa (Desta *et al*., 2008).

These species are commonly found in non-permanent habitats, such as shoreline areas dominated by macrophytes (Desta *et al*., 2008), which are increasingly threatened by human activities. Urban farming, shoreline modifications for investment purposes, macrophyte harvesting for domestic use (Tadesse *et al*., 2015), and pollution from both point and non-point sources (Tilahun, 2023) contribute to habitat degradation. Understanding their feeding habits is therefore crucial for assessing the ecological consequences of habitat loss and predicting potential shifts in fish community structure.

In addition to their ecological significance, smaller non-commercial fish species may influence the feeding dynamics of larger, economically important species (Jawad, 2021). Recent studies from Lake Hawassa indicate a decline in major prey items for larger fish, such as macroinvertebrate (Wondmagegn and Mengistou, 2020) and plankton biomass (Beyene *et al*., 2022a; 2022b). Overfishing of *O. niloticus* has significantly reduced its availability as a food source for *C. gariepinus* (Tekle-Giorgis *et al*., 2016b), leading to a dietary shift from carnivory (Dadebo, 2000) to omnivory, with increased reliance on plankton (Tekle-Giorgis *et al*., 2016b). These changes highlight the need for updated research on smaller fish species to assess dietary competition and support trophic modeling efforts.

Although some studies have investigated the trophic status of smaller fish species in Lake Hawassa, comprehensive information remains scarce. For example, both *E. paludinosus* (Desta *et al*., 2008), and *G. quadrimaculata* (Tekle-Giorgis *et al*., 2016a) have been identified as omnivorous. These studies indicate dietary overlap, with both species consuming similar prey items such as plankton and insects, which are also key food sources for larger, economically important fish. Such overlap may contribute to interspecific competition for food. Moreover, the study by Desta *et al*. (2008) provided only limited information on the feeding habits of *E. paludinosus* in Lake Hawassa, focusing primarily on mercury concentration rather than seasonal dietary compositions.

To date, no studies have documented the feeding habits of *A. antinorii* in Lake Hawassa. Therefore, the present study aims to address this knowledge gap by providing a comprehensive analysis of its diet, contributing to a broader understanding of trophic interactions and ecosystem dynamics within the lake.

MATERIALS AND METHODS

Description of the study area

Lake Hawassa is one of the Central Rift Valley Lakes of Ethiopia, located approximately 275 km south of the capital, Addis Ababa. It lies between latitudes 6°58′ to 7°6′N and longitudes 38°22′ to 38°30′E (Figure 1). The lake covers a surface area of approximately 91.87 km^2 and has a maximum depth of 23.58 m (Menberu *et al.*, 2021). Although the Tikur Wuha River contributes inflow to the lake, it lacks a defined outflow, rendering it an endorheic system (Menberu *et al.*, 2021). Lake Hawassa experiences substantial nutrient mixing, particularly during the dry season when wind-driven turbulence enhances vertical water column dynamics (Tilahun and Ahlgren, 2010).

The lake supports a rich assemblage of aquatic organisms, including hundreds of phytoplankton species (Kebede *et al.*, 1994) and 22 species of zooplankton, with rotifers being the dominant group (Beyene *et al.*, 2022a). It also habors a diverse community of macro-invertebrate, which constitutes one of its ecological strengths (Wondmagegn and Mengistou, 2020). The shoreline is fringed with abundant submerged and emergent macrophytes (Desta *et al.*, 2007).

The ichthyofauna of Lake Hawassa consists of six distinct fish species (Dadebo, 2000). Among them, *O. niloticus*, *C. gariepinus*, and *L. intermedius* are of commercial importance, while *A. antinorii*, *G. quadrimaculata*, and *E. paludinosis* play essential ecological roles as prey for larger predatory species such as *C. gariepinus* (Dadebo, 2000).

In recent years, the lake has faced increasing anthropogenic pressure from both point and non-point sources of pollutant, posing significant threats to its aquatic biodiversity (Tilahun, 2023).

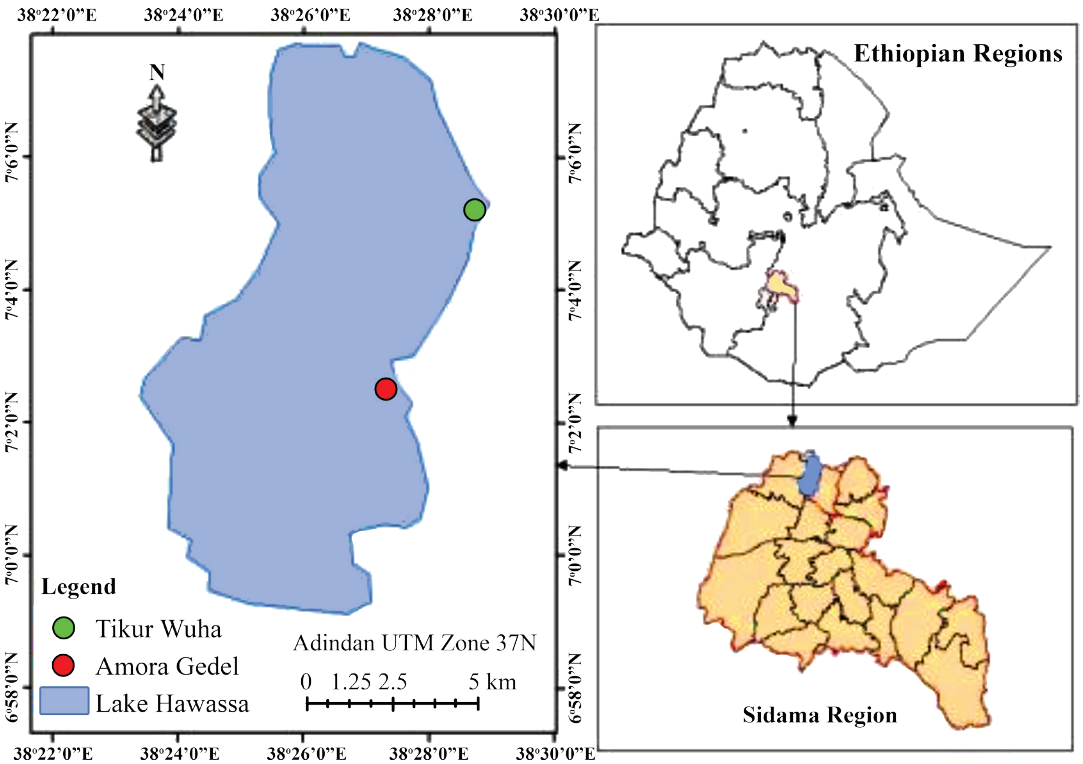

Figure 1. Geographic locations of Lake Hawassa.

Sample collection

All specimens used in this study were collected from the littoral and sub-littoral zones of the lake using a beach seine and a hand net. The beach seine was 30 m in length with a mesh size of 6 mm, and it was deployed and retrieved with the assistance of experienced fishers. To ensure the collection of individuals across different size classes, an additional hand net with a mesh size of 0.6 mm was used in the littoral zones, with the support from a reed boat fisher.

Following collection, the specimens were immediately placed in an ice box and transported to the Fisheries Laboratory at Hawassa University for further analysis. The samples were subsequently stored in a deep freezer to preserve their condition until morphometric measurements and dietary composition analyses were performed.

Morphometric measurements

In the laboratory, the total length of each specimen was measured to the nearest 0.1 cm using a measuring board. Total body weight was determined using a precision balance following a two-step approach. Larger specimens of *G. quadrimaculata* and *E. paludinosus* were weighed to the nearest 0.01 g. In contrast, smaller specimens, including *A. antinorii* and juvenile *G. quadrimaculata* and *E. paludinosus*, were weighed using an electronic balance with a sensitivity of 0.0001 g to ensure precise measurement.

Following morphometric measurements, the specimens were dissected for sex identification. The gut contents were then extracted and preserved in a 5% formalin solution for subsequent dietary composition analysis.

Diet composition analysis

Preserved gut contents were extracted and measured using graduated cylinders with volumes of 5 mL, 10 mL, and 15 mL, marked with increments ranging from 0.1 to 1 mL. The total gut content volume for each specimen was recorded after extraction. To ensure uniformity, the contents were thoroughly mixed by continuous shaking prior to analysis. Larger food particles were examined and identified under a dissecting microscope (LEICA MS) at 10× magnification, while smaller prey items, including plankton, were analyzed under a compound microscope (LEICA DME) at 100× magnification. For the identification of microscopic prey items, three sub-samples were taken from the homogenized gut contents and mounted on microscopic slide. The percentage occurrence of each prey item in each sub-drop was recorded, and the average value was used for further analysis.

These standard methods were employed for gut content analysis: the frequency of occurrence method (Hyslop, 1980), the volumetric contribution method (Bowen, 1983), and the index of preponderance method (Natarajan and Jhingran, 1961).

Frequency of occurrence

The frequency of occurrence of specific prey items was determined based on non-empty fish guts. In this method, the number of times a particular prey item appeared was recorded to assess its prevalence among all non-empty gut samples analyzed. The occurrence of each prey item was expressed as a percentage (Hyslop, 1980) using the formula:

$$\%FO = (TNS_i / TNSP_i) \times 100 \qquad (1)$$

where: %FO = frequency of occurrence of a specific prey item from non-empty fish guts; TNS_i = total number of fish containing prey item i; $TNSP_i$ = total number of non-empty gut samples examined for dietary analysis.

Volumetric contribution

The volumetric contribution of each food item was calculated as a percentage of the total volume of gut contents from non-empty samples, following Bowen (1983), using the formula:

$$V_i\% = \frac{V_s\, P_s}{V_f\, N_g} \times 100 \qquad (2)$$

where: $V_i\%$ = volumetric contribution of prey item i (expressed as a percentage); V_sP_s = volume of a specific prey item found in all specimen; V_fN_g = total volume of all food items found in all non-empty guts.

Index of preponderance

The index of preponderance (IoP%) was calculated to integrate frequency of occurrence and volumetric contribution into a single metric. It was calculated following Natarajan and Jhingran (1961) as:

$$IoP\% = \frac{V_i \times F_i}{\sum_i^n (V_i \times F_i)} \times 100 \quad (3)$$

where: F_i = frequency of occurrence of prey item i; V_i = volumetric percentage of prey item i; n = total number of prey types.

The IoP values were expressed as percentages (IoP%) to facilitate interspecific and intraspecific comparisons.

Ontogenetic dietary shifts and dietary overlap analysis

To assess ontogenetic dietary shifts, specimens were grouped into different size classes based on species-specific body length. *E. paludinosus* and *G. quadrimaculata* were categorized into 2 cm intervals, while *A. antinorii* was grouped into 0.5 cm intervals. The significance of the ontogenetic dietary shifts between size classes was analyzed using Schoener's dietary overlap index (Schoener, 1970). The volumetric contributions of major prey items were allocated to each size class and visualized using stacked bar charts expressed as percentages. Intraspecific competition and dietary shifts were assessed through size class comparisons, with major prey items analyzed for cross-comparison. Dietary overlap was calculated using Schoener's dietary overlap index as follows:

$$C = 1 - \frac{1}{2}\left(\sum |p_{xi} - p_{yi}|\right) \quad (4)$$

where: C = Schooner's dietary overlap index; P_{xi} and P_{yi} = proportions of prey item i in the diets of species x and y, respectively.

Seasonal variation

The diet composition was categorized based on rainy and dry months using meteorological data. The same methodological approaches–frequency of occurrence, volumetric contribution, and index of preponderance—were applied to analyze seasonal dietary variations. To test for significant seasonal differences in diet composition, the chi-square (χ^2) test was used for frequency of occurrence, and the independent sample t-test was applied for volumetric contributions. Major prey item variations were cross-checked using statistical comparisons.

Data analysis

Diet composition data were organized in Microsoft Excel. Statistical tests were applied to determine variations in feeding habits between seasons: the chi-square (χ^2) test was used to assess significant differences in the frequency of occurrence of prey items between rainy and dry months; the independent sample t-test was used to test for significant differences in volumetric contributions; and Schoener's dietary overlap index was used to evaluate intraspecific competition, with values above 0.6 considered biologically significant.

RESULTS

Diet compositions

A total of 824 specimens of *E. paludinosus* (total length: 3.1–11.0 cm) were analyzed to assess feeding habits in Lake Hawassa. Among these, 68 individuals (8.3%) had completely empty guts. The remaining 756 individuals (91.7%) had non-empty guts containing seven major prey items in varying proportions (Table 1).

Phytoplankton was the dominant food item, with a high frequency of occurrence (87.17%), volumetric contribution (63.18%), and index of preponderance (84.10%). Non–filamentous algae, particularly blue-green algae and diatoms, were the most commonly consumed phytoplankton taxa (Table 1). Detritus ranked second, with a frequency of occurrence of 37.83%, a volumetric contribution of 18.9%, and an index of preponderance of 10.97%. Macrophytes were the third most consumed food item (24.74% occurrence, 10.48% volume, 3.96% preponderance), followed by zooplankton (12.96% occurrence, 3.35% volume, and 0.66% preponderance). Other prey items, including fish eggs, insects, and nematodes, were consumed less frequently (Table 1).

Among the insect taxa, Ephemeroptera was the most commonly ingested, found in 3.04% of the non-empty guts, with a volumetric contribution of 0.85% and a preponderance index of 0.04%. Other insect groups (Diptera, Odonata, and Hemiptera) were rarely consumed and had negligible preponderance values (Table 1).

For *G. quadrimaculata*, 176 samples (total length: 3.7–13.1 cm) were examined. Of these, 11 individuals (6.3%) had completely empty guts, while the remaining 165 individuals (93.7%) contained gut contents comprising seven major prey categories. Phytoplankton, detritus, and macrophytes were the most frequently consumed items, with occurrence rates of 87.17%, 37.8%, and 24.74%, respectively. Their corresponding volumetric contributions were 63.18%, 18.98%, and 10.48%, and their indices of preponderance were 84.10%, 10.97%, and 3.96%, respectively. Zooplankton, fish eggs, and insects

Table 1. Frequency of occurrence (FO), volumetric contribution (Vol), and index of preponderance (IP) of food items found in the gut contents of *Enteromius paludinosus* collected from Lake Hawassa (N = 756).

Food item	Frequency of occurrence		Volumetric contribution		Index of preponderance	
	FO	%FO	Vol (mL)	%Vol	IP	%IP
Phytoplankton	**659**	**87.17**	**190.29**	**63.18**	**5,507.12**	**84.10**
Diatoms	410	54.23	66.76	22.17	1,202.11	18.36
Green algae	294	38.89	33.21	11.02	428.75	6.55
Blue-green algae	422	55.82	64.03	21.26	1,186.62	18.12
Dinoflagellates	108	14.29	11.52	3.83	54.65	0.83
Euglenoids	131	17.33	14.77	4.90	84.97	1.30
Zooplankton	**98**	**12.96**	**10.10**	**3.35**	**43.49**	**0.66**
Cladocerans	28	3.70	1.50	0.50	1.84	0.03
Rotifers	40	5.29	3.44	1.14	6.05	0.09
Copepods	50	6.61	5.17	1.72	11.35	0.17
Insects	**33**	**4.37**	**5.18**	**1.72**	**7.51**	**0.11**
Odonata	4	0.53	0.66	0.22	0.11	0.00
Zygoptera	1	0.13	0.36	0.12	0.02	0.00
Anisoptera	3	0.40	0.30	0.10	0.09	0.00
Hemiptera						
Naucoridae	2	0.26	0.16	0.05	0.01	0.00
Ephemeroptera	23	3.04	2.55	0.85	2.58	0.04
Diptera (Adult)	6	0.79	1.81	0.60	0.48	0.01
Detritus	**286**	**37.83**	**57.17**	**18.98**	**718.10**	**10.97**
Macrophytes	**187**	**24.74**	**31.56**	**10.48**	**259.21**	**3.96**
Nematodes	**5**	**0.66**	**0.15**	**0.05**	**0.03**	**0.00**
Fish eggs	**43**	**5.69**	**6.74**	**2.24**	**12.73**	**0.19**
∑Total				**100.00**	**6,548.20**	**100.00**

were categorized as intermediate prey items, with occurrence frequencies of 16.97%, 11.52%, and 9.7%, respectively. Nematodes were the least frequent, found in only 1.21% of the non-empty guts.

Among zooplankton, rotifers were the most frequently consumed (7.27% occurence), followed by cladocerans and copepods, each contributing equally (6.06%). Among insects, Ephemeroptera was the most frequent (6.06% occurence), while adult Diptera and Odonata were the second and third most frequently consumed insect taxa, respectively (Table 2). Fish eggs ranked fourth in volumetric contributions at 5.05%, whereas insects, zooplankton, and nematodes had the lowest volumetric contributions.

In the case of *A. antinorii*, 795 specimens (total length: 2.8–5.8 cm) were examined. Of these 82 individuals (10.3%) had completely empty guts. This species predominantly inhabits the shoreline areas of Lake Hawassa. The remaining 713 individuals (89.7%) had non-empty guts, containing six major prey items: phytoplankton, detritus, macrophytes, zooplankton, insects, and fish eggs (Table 3). Phytoplankton was the most frequently consumed prey item, occurring in 85.9% of guts, followed by detritus (58.51%) and macrophytes (40.79%), making them the top three ingested food items. Zooplankton was an intermediate food source, occurring in 18% of gut contents, while insects and fish eggs were consumed less frequently (Table 3). Volumetrically, phytoplankton was also dominant (47.71%), followed by detritus (27.32%) and macrophytes (16.76%).

Table 2. Frequency of occurrence (FO), volumetric contribution (Vol), and index of preponderance (IP) of food items found in the gut contents of Garra quadrimaculata collected from Lake Hawassa (N = 165).

Food item	Frequency of occurrence		Volumetric contribution		Index of preponderance	
	FO	%FO	Vol (mL)	%Vol	IP	%IP
Phytoplankton	**139**	**84.24**	**110.10**	**46.38**	**3,906.84**	**59.88**
Diatoms	111	67.27	44.30	18.66	1,255.26	19.24
Green algae	76	46.06	22.02	9.27	427.20	6.55
Blue-green algae	86	52.12	31.35	13.20	688.22	10.55
Dinoflagellates	21	12.73	5.77	2.43	30.94	0.47
Euglenoids	27	16.36	6.66	2.81	45.93	0.70
Zooplankton	**28**	**16.97**	**5.43**	**2.29**	**38.81**	**0.59**
Cladocera	10	6.06	1.97	0.83	5.03	0.08
Rotifers	12	7.27	1.67	0.70	5.10	0.08
Copepod	10	6.06	1.79	0.76	4.58	0.07
Insects	**16**	**9.70**	**6.38**	**2.69**	**26.05**	**0.40**
Ephemeroptera	10	6.06	3.22	1.36	8.23	0.13
Odonata	4	2.88	0.86	0.36	1.05	0.02
Zygoptera	1	0.61	0.12	0.05	0.03	0.00
Anisoptera	3	1.82	0.74	0.31	0.57	0.01
Diptera (Adult)	5	3.03	2.29	0.97	2.93	0.04
Detritus	**105**	**63.64**	**75.90**	**32.18**	**2,047.82**	**31.39**
Macrophytes	**65**	**39.39**	**27.41**	**11.33**	**446.39**	**6.84**
Nematodes	**2**	**1.21**	**0.19**	**0.08**	**0.10**	**0.00**
Fish eggs	**19**	**11.52**	**12.00**	**5.05**	**58.21**	**0.89**
∑Total				100.00	6,524.21	100.00

Table 3. Frequency of occurrence (FO), volumetric contribution (Vol), and index of preponderance (IP) of food items found in the gut contents of *Aplocheilichthys antinorii* collected from Lake Hawassa (N = 713).

Food item	Frequency of occurrence		Volumetric contribution		Index of preponderance	
	FO	%FO	Vol (mL)	%Vol	IP	%IP
Phytoplankton	**611**	**85.94**	**93.26**	**47.71**	**4,099.58**	**63.16**
Diatoms	344	48.38	28.46	14.56	704.36	10.85
Green algae	277	38.96	20.66	10.57	411.71	6.34
Blue-green algae	326	45.85	32.20	16.47	755.26	11.64
Dinoflagellates	69	9.70	4.70	2.41	23.35	0.36
Euglenoids	100	14.06	7.24	3.70	52.06	0.80
Zooplankton	**128**	**18.00**	**11.02**	**5.64**	**101.49**	**1.56**
Cladoceras	45	6.33	2.88	1.47	9.33	0.14
Rotifers	52	7.31	3.90	1.99	14.58	0.22
Copepods	62	8.72	4.22	2.16	18.83	0.29
Insects	**21**	**2.95**	**4.18**	**2.14**	**6.31**	**0.10**
Diptera						
Chironomidae larvae	2	0.28	0.50	0.26	0.07	0.00
Hemiptera						
Naucoridae	2	0.28	0.52	0.27	0.07	0.00
Ephemeroptera	15	2.11	2.75	1.40	2.96	0.05
Odonata						
Anisoptera	2	0.28	0.41	0.21	0.06	0.00
Detritus	**416**	**58.51**	**53.42**	**27.32**	**1,598.66**	**24.63**
Macrophytes	**290**	**40.79**	**32.77**	**16.76**	**683.75**	**10.53**
Fish eggs	**9**	**1.27**	**0.85**	**0.43**	**0.55**	**0.01**
∑Total				**100.00**	**6,490.33**	**100.00**

Ontogenetic dietary shift and dietary overlap

The feeding habits of *E. paludinosus* from Lake Hawassa exhibit a clear ontogenetic dietary shift with increasing body size (Figure 2a). In the smallest size class (<5.0 cm total length), the primary prey items were phytoplankton (68.29%), detritus (12.95%), macrophytes (8.99%), and zooplankton (5.36%), while fish eggs, insects, and nematodes contributed minimally. As *E. paludinosus* increased in size, the relative contributions of phytoplankton and zooplankton declined sharply, whereas detritus and macrophytes became more prominent (Figure 2a). Comparisons of Schoener's dietary dietary overlap index (C) indicated biologically significant dietary shifts between the smallest and largest size classes(<5.0 cm vs ≥9.0 cm; and 5.1 cm–6.9 cm and ≥9.0 cm). In contrast, dietary composition remained relatively stable across intermediate size classes, suggesting high intraspecific dietary overlap and potential competition (Table 4).

In *G. quadrimaculata*, prey composition also varied with size class (Figure 2b). Zooplankton was an important dietary component in smaller individuals (<5.0 cm), but its contribution declined in larger size classes. Conversely, the proportion of phytoplankton and detritus increased with body size. Despite these changes, no biologically significant ontogenetic dietary shift was observed, as dietary overlap indices remained high (C>60%), indicating strong intraspecific competition across size classes (Table 4).

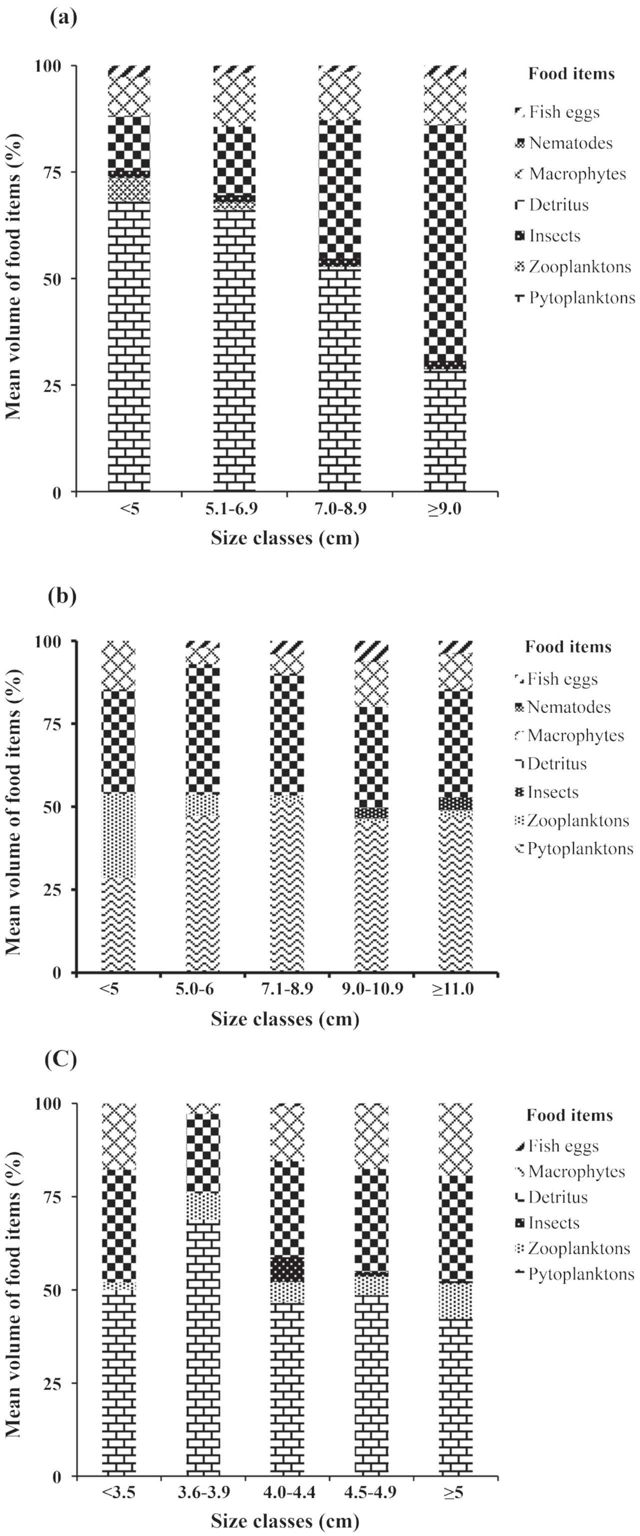

Figure 2. The ontogenetic dietary shift of *Enteromius paludinosus* (a), *Garra quadrimaculata* (b), and *Aplocheilichthys antinorii* (c) collected from Lake Hawassa.

For *A. antinorii*, no substantial ontogenetic dietary shift was observed across most size classes, with dietary overlap values exceeding 0.6 (Figure 2c). A slight shift was noted between the 4.0–4.4 cm and ≥5.0 cm size classes. In the smallest individuals (<4.0 cm), insects contributed minimally to the diet compared to larger size classes. However, overall dietary composition remained consistent across size classes, indicating strong overlap and similar feeding preferences (Table 4).

Seasonal variations in diet compositions

Seasonal variations in the diet of *E. paludinosus* revealed significant differences in the occurrences of major prey items –including zooplankton, insects, and fish eggs–between the rainy and dry seasons (χ^2, $p<0.05$). Phytoplankton and insects showed a slight increase during the dry season, whereas detritus and macrophytes were more prevalent during the rainy season (Table 5). Zooplankton declined during the dry season, and nematodes were absent during this period. The volumetric contributions of phytoplankton, detritus, and macrophytes also differed significantly between seasons (t-test, $p<0.05$), with phytoplankton (64.23%) and detritus (21.84%) being more abundant in the dry season. Conversely, the volumetric contributions of zooplankton, insects, macrophytes, and fish eggs were slightly higher

Table 4. Dietary overlap index (C) among different size classes of three fish species from Lake Hawassa.

Fish species	Size classes (cm)	Dietary overlap index (C)
Enteromius paludinosus	<5 and 5.1–6.9	0.93
	<5 and 7.0–8.9	0.78
	<5 and ≥9.0	**0.54**
	5.1–6.9 and 7.0–8.9	0.83
	5.1–6.9 and ≥9.0	0.60
	7.0–8.9 and ≥9.0	0.76
Aplocheilichthys antinorii	<3.5 and3.5–3.9	0.76
	<3.5 and 4.0–4.4	0.89
	<3.5 and 4.5–4.9	0.95
	<3.5 and ≥5.0	0.90
	3.5–3.9 and 4.0–4.4	0.76
	3.5–3.9 and 4.5–4.9	0.78
	3.5–3.9 and ≥5.0	0.73
	4.0–4.4 and 4.5–4.9	0.94
	4.0–4.4 and ≥5.0	**0.50**
	4.5–4.9 and ≥5.0	0.93
Garra quadrimaculata	<5 and 5.1–6.9	0.71
	<5 and 7.0–8.9	0.68
	<5 and 9.0–10.9	0.74
	<5 and ≥11.0	0.73
	5.1–6.9 and 7.0–8.9	0.93
	5.1–6.9 and 9.0–10.9	0.84
	5.1–6.9 and ≥11.0	0.89
	7.0–8.9 and 9.0–10.9	0.84
	7.0–8.9 and ≥11.0	0.91
	9.0–10.9 and ≥11.0	0.94

Note: Bolded C values indicate comparisons where a biologically significant dietary change was observed.

during the rainy season (Table 5). Based on the index of preponderance, phytoplankton, detritus, and macrophytes ranked as the top three preferred prey items in both seasons. Nematodes, in contrast, played an insignificant dietary role during either season (Table 5).

For *G. quadrimaculata*, the occurrence of detritus, macrophytes, zooplankton, and fish eggs varied significantly between seasons (χ^2, $p<0.05$), whereas nematodes did not show any seasonal variation (χ^2, $p>0.05$) (Table 6). Phytoplankton remained the dominant prey item during both the rainy (81.25%) and dry seasons (90.57%), with diatoms being the most preferred phytoplankton groups (58.93% and 84.91%, respectively). During the rainy season, detritus (68.75%) ranked second in frequency, followed by macrophytes (30.36%) and zooplankton (15.18%). In contrast, during the dry season, macrophytes (58.49%) ranked second, followed by detritus (50.94%) and insects (26.42%). Zooplankton composition also varied seasonally, with cladocerans being dominant in the rainy season (7.14%) and rotifers in the dry season (11.32%). Insect consumption increased during the dry season, particularly for Ephemeroptera. Volumetrically, phytoplankton and detritus were the major dietary components during the rainy

Table 5. Seasonal variation in the diet composition of *Enteromius paludinosus* from Lake Hawassa, based on frequency of occurrence (%), volumetric contribution (%), and index of preponderance (%) of major prey items during the rainy and dry seasons. during the rainy (N = 507) and dry (N = 249) months in.

Food item	Frequency of occurrence (%)		Volumetric contribution (%)		Index of preponderance (%)	
	Rainy	Dry	Rainy	Dry	Rainy	Dry
Phytoplankton	**86.00[a]**	**89.56[a]**	**62.03[a]**	**64.23[a]**	**84.11**	**84.57**
Diatoms	40.39	81.60	13.54	29.64	8.62	35.56
Green algae	37.45	41.20	12.89	9.13	7.61	5.53
Blue-green algae	56.08	54.40	26.23	16.35	23.19	13.08
Dinoflagellates	14.51	13.60	4.22	3.40	0.96	0.68
Euglenoids	16.67	18.40	4.82	4.90	1.27	1.32
Zooplankton	**15.38[a]**	**8.03[b]**	**5.72[a]**	**1.18[b]**	**1.39**	**0.14**
Cladocera	4.54	2.01	0.86	0.16	0.06	0.00
Rotifers	6.31	3.21	1.89	0.45	0.19	0.02
Copepods	8.28	3.20	2.97	0.57	0.39	0.03
Insects	**2.96[b]**	**7.23[a]**	**1.78[a]**	**1.67[a]**	0.08	0.18
Odonata	0.39	0.80	0.30	0.14	0.12	0.00
Anisoptera	0.20	0.80	0.05	0.14	0.00	0.00
Zygoptera	0.20	0.00	0.25	0.00	0.00	0.00
Hemiptera						
Naucoridae	0.39	0.00	0.11	0.00	0.00	0.00
Ephemeroptera	1.97	5.22	1.05	0.66	0.03	0.05
Diptera (Adult)	0.59	1.20	0.32	0.86	0.00	0.02
Detritus	**38.86[a]**	**35.74[b]**	**15.89[b]**	**21.84[a]**	**9.74**	**11.48**
Macrophytes	**25.05[a]**	**24.10[a]**	**10.82[a]**	**10.15[a]**	**4.27**	**3.60**
Nematodes	**0.99[a]**	**0.00[b]**	**0.10[nd]**	**0.00[nd]**	**0.00**	**0.00**
Fish eggs	**7.10[a]**	**2.81[b]**	**3.65[a]**	**0.94[b]**	**0.41**	**0.04**

Note: Different superscript letters in the same row indicate significant differences ($p<0.05$) between seasons. 'nd' denotes values not determined due to zero occurrence.

season (40.49% and 41.03%, respectively), while in the dry season, phytoplankton (55.10%) remained dominant, followed by detritus (18.67%) and macrophytes (14.61%).

In *A. antinorii*, seasonal differences were observed in the occurrences of insects, and macrophytes (χ^2, p<0.05), while phytoplankton, zooplankton, detritus, and fish eggs did not show significant seasonal variation (χ^2, p≥0.05) (Table 7). In both rainy and dry seasons, phytoplankton (86.73% and 85.65%), detritus (55.10% and 66.82%), macrophytes (34.69% and 55.61%), and zooplankton (15.92% and 22.42%) were the most frequently occurring prey items. Insects were consumed at a low frequency during the rainyseason (4.29%) but were absent in the dry season. The occurrence of fish eggs increased slightly during the dry season (Table 7).

Volumetric contributions of phytoplankton and zooplankton differed significantly between seasons (t-test, p<0.05), while other prey items did not show statistical significant differences (t-test, p>0.05). Insects were absent from the dry-season diet but appeared in the rainy season, with Ephemeroptera (2.10%) being the most commonly consumed insect. The index of preponderance ranked phytoplankton, detritus, macrophytes, and zooplankton as the four most important prey items in both seasons (Table 7).

Table 6. Seasonal variation in the diet composition of *Garra quadrimaculata* from Lake Hawassa, based on frequency of occurrence (%), volumetric contribution (%), and index of preponderance (%) of major prey items during the rainy (N = 112) and dry (N = 57) seasons.

Food item	Frequency of occurrence (%)		Volumetric contribution (%)		Index of preponderance (%)	
	Rainy	Dry	Rainy	Dry	Rainy	Dry
Phytoplankton	**81.25^b**	**90.57^a**	**40.49b**	**55.10^a**	**50.60**	**70.77**
Diatoms	58.93	84.91	17.41	20.75	15.78	24.99
Green algae	33.93	71.70	7.84	11.29	4.09	11.48
Blue Green algae	44.64	67.92	11.02	16.22	7.57	15.63
Dinoflagellates	6.25	26.42	0.78	4.86	0.07	1.82
Euglenoids	12.50	24.53	3.44	1.98	0.66	0.69
Zooplankton	**15.18^b**	**20.75^a**	**2.14^a**	**2.51^a**	**0.50**	**0.74**
Cladocera	7.14	3.77	0.99	0.59	0.11	0.03
Rotifer	5.36	11.32	0.28	1.31	0.02	0.21
Copepods	6.25	5.66	0.86	0.60	0.08	0.05
Insects	**1.79^b**	**26.42^a**	**0.21^b**	**6.32^a**	**0.01**	**2.37**
Ephemeroptera	0.89	16.98	0.06	3.25	0.00	0.78
Odonata	0.89	5.66	0.12	0.60	0.00	0.05
Zygoptera	0.00	1.89	0.00	0.12	0.00	0.00
Anisoptera	0.89	3.77	0.14	0.56	0.00	0.03
Diptera	0.00	9.43	0.00	2.38	0.00	0.32
Detritus	**68.75^a**	**50.94^b**	**41.03^a**	18.67^a	43.38	13.49
Macrophytes	**30.36^b**	**58.49^a**	**9.45^a**	14.61^a	4.41	12.12
Nematodes	**0.89^a**	**1.89^a**	**0.07^a**	0.09^a	0.00	0.00
Fish eggs	**10.71^b**	**13.21^a**	**6.67^a**	2.69^a	1.10	0.50
∑Total			**100.00**	100	100.00	100.00

Note: Major prey items with different superscripts indicate statistically significant differences (p<0.05), while 'nd' denotes prey items that were not detected.

Table 7. Seasonal variation in the diet composition of *Aplocheilichthys antinorii* from Lake Hawassa, based on frequency of occurrence (%), volumetric contribution (%), and index of preponderance (%) of major prey items during the rainy (N = 112) and dry (N = 57) seasons.

Food item	Frequency of occurrence (%)		Volumetric contribution (%)		Index of preponderance (%)	
	Rainy	Dry	Rainy	Dry	Rainy	Dry
Phytoplankton	**86.73**^{a}	**85.65**^{a}	**51.65**^{a}	**39.49**^{b}	68.95	49.77
Diatoms	45.51	56.05	13.58	16.45	9.51	13.57
Green algae	34.69	48.88	10.52	10.59	5.62	7.62
Blue-green algae	54.69	26.91	20.16	8.95	16.97	3.54
Dinoflagellates	13.47	1.79	3.52	0.16	0.73	0.00
Euglenoids	13.67	15.70	3.87	3.34	0.81	0.77
Zooplankton	**15.92**^{a}	**22.42**^{a}	**4.29**^{b}	**8.32**^{a}	1.05	2.74
Cladocera	3.67	12.11	0.90	2.62	0.05	0.47
Rotifers	5.31	11.66	0.85	4.31	0.07	0.74
Copepods	10.61	4.48	2.54	1.38	0.41	0.09
Insects	**4.29**nd	**0.00**nd	**3.19**nd	**0.00**nd	0.21	0.00
Diptera						
Chironomidae larvae	0.41	0.00	0.38	0.00	0.00	0.00
Hemiptera						
Naucoridae	0.41	0.00	0.40	0.00	0.00	0.00
Ephemeroptera	3.06	0.00	2.10	0.00	0.10	0.00
Odonata						
Anisoptera	0.41	0.00	0.31	0.00	0.00	0.00
Detritus	**55.10**^{a}	**66.82**^{a}	**26.28**^{a}	**29.85**^{a}	**22.29**	**29.35**
Macrophytes	**34.69**^{a}	**55.61**^{b}	**14.03**^{a}	**22.16**^{a}	**7.49**	**18.13**
Fish eggs	**0.61**^{a}	**2.69**^{a}	**0.56**^{a}	**0.18**^{a}	**0.01**	**0.01**

Note: Different superscript letters in the same row indicate significant differences ($p<0.05$) between seasons. 'nd' denotes values not determined due to zero occurrence.

DISCUSSION

Food and feeding habits

The present study confirms that *E. paludinosus* is an omnivorous species, consuming seven major prey items, including phytoplankton, detritus, macrophytes, zooplankton, insects, fish eggs, and nematodes, in varying proportions. These findings are consistent with previous reports from African inland water bodies, including Lake Hawassa (Desta *et al*., 2008), Lake Ziway (Dadebo *et al*., 2013), and Lake Chilwa (Bourn, 1974), which also classified *E. paludinosus* as a generalist feeder. Its ability to consume both plant- and animal-based prey reflects a high degree of digestive adaptability, supported by the presence of enzymes such as protease and amylase (Cockson and Bourn, 1973). In Lake Hawassa phytoplankton, detritus, and macrophytes were the dominant food items, consistent with findings from the Kafue River (Welcomme, 1969) and the Nzoia River (Balirwa, 1979), where phytoplankton and detritus were also primary dietary components. In contrast, in Lake Ziway, insects were a major dietary component along with phytoplankton and detritus (Dadebo *et al*., 2013), while in Lake Victoria, ostracods and zooplankton dominated the diet (Welcomme, 1969).

These regional dietary differences likely reflect variation in prey availability, habitat structure, and interspecific competition (Korman *et al*., 2021).

Unlike the findings of Desta *et al*. (2008), fish prey such as *A. antinorii* were not observed in the gut contents of *E. paludinosus* in the present study. This discrepancy may be attributed to differences in fish size; larger individuals tend to consume larger prey (Scharf *et al*., 2000). The maximum fish length analyzed in this study was 11 cm, whereas Desta *et al*. (2008) reported individuals up to 16 cm in total length.

Interestingly, nematodes were detected in the gut contents in the present study, whereas previous studies on the same species in Lake Ziway (Dadebo *et al*., 2013) and Lake Hawassa (Desta *et al*., 2008) did not report their occurrence. These dietary shift may result from differences in prey availability and nutrient requirements (Dorenbosch and Bakker, 2011).

A significant ontogenetic dietary shift was observed between smaller and larger size classes, although dietary overlap among larger individuals was not biologically significant. Similar findings were reported in Lake Ziway (Dadebo *et al*., 2013), where dietary overlap between size classes ranged from 91% to 99%. These shifts may be associated with morphological changes, including increased gut size and the development of pharyngeal teeth, which enable larger fish to process harder food items (Golubtsov *et al*., 2005). As *E. paludinosus* grows, gut length increases, and a pH gradient develops along the digestive tract, ranging from 5.4 to 6.2 (mean 5.8) anteriorly to 7.6 to 8 (mean 7.8) posteriorly (Cockson and Bourn, 1973). This pH gradient supports efficient digestion of a wide range of food types, reinforcing its generalist feeding strategy.

Seasonal differences in prey consumption were evident. Phytoplankton was more abundant in the diet during the dry season, while detritus and macrophytes were more prevalent in the rainy season. Similar seasonal patterns were observed in Lake Ziway (Dadebo *et al*., 2013), suggesting that seasonal fluctuations in prey availability and environmental conditions strongly influence feeding behavior (Sánchez–Hernández *et al*., 2019).

The feeding habits of *G. quadrimaculata* in Lake Hawassa also confirm its classification as an omnivore, with phytoplankton (84.24%), detritus (63.64%), and macrophytes (39.39%) as dominant dietary components. These results align with previous studies in the same region, although prey composition and proportions varied (Tekle-Giorgis *et al*., 2016a). In the Debbis River, detritus was reported as the dominant prey for *G. quadrimaculata* (Tirfessa *et al*., 2017), indicating dietary flexibility in response to ecological conditions and prey availability (Stewart *et al*., 2021).

Comparative data on other *Garra* species, such as *Garra gotyla gotyla* in India (Gaur *et al*., 2013), and *Garra rufa* from West Azerbaijan (Ghafouri *et al*., 2023), similarly reported phytoplankton as the primary dietary component. Anatomical features such as adhesive discs and elongated intestines support their adaptation to herbivory and periphyton grazing (Sibbing and Witte, 2005). In this study, dinoflagellates (12.73%) and euglenoids (16.36%) were newly reported among phytoplankton taxa, which were not previously documented by Tekle-Giorgis *et al*. (2016a) in the same study area.

Volumetric analysis indicated that phytoplankton (46.38%), detritus (32.18%), and macrophytes (11.33%) were the dominant prey items for *G. quadrimaculata*. In comparison with earlier studies by Tekle-Giorgis *et al*. (2016a), fish egg and insect consumption declined, potentially due to ecological changes or shifts in prey availability (Stewart *et al*., 2021). High dietary overlap (72–95%) between size classes suggested strong intraspecific dietary competition, which may be influenced by seasonal variations and environmental pressures (Johnson *et al*., 2012).

Seasonal patterns also influence feeding, with phytoplankton more frequently consumed in the dry season (90.57%) than during the rainy season (81.25%). Detritus and macrophytes ranked second and third during the rainy season, while fish eggs and insects consumption increased slightly during the dry season. These shifts may be associated with changes in water levels, prey density, and shoreline vegetation (Glazier *et al*., 2020). Compared to previous reports by Tekle-Giorgis *et al*.

(2016a), a notable decline in insect consumption was observed, possibly due to macroinvertebrate populations declines around Lake Hawassa (Wondmagegn and Mengistou, 2020). Among zooplankton, rotifers were the most frequently consumed, reflecting their stress tolerance to environmental stress and high abundance in polluted systems (Karpowicz *et al*., 2020).

The feeding pattern of *A. antinorii* also reflects omnivory, with six major prey items identified. Phytoplankton (85.94%) dominated the diet, followed by detritus (58.51%) and macrophytes (40.79%). These findings suggest a strong preference for plant-derived food sources, though zooplankton and insects were also consumed. The dominance of phytoplankton likely reflects its abundance in Lake Hawassa (Beyene *et al*., 2022b). Detritus and macrophyte consumption align with the species' habitat preferences for vegetated, shallow shorelines (Naganyal and Saxena, 2019). Although insects were consumed in low proportions, their presence in the diet may be linked to macrophyte-rich habitats that support insect breeding (Petrov, 2022).

While detailed dietary studies on *A. antinorii* are limited, comparisons with related species reveal similar trophic strategies. For instance, *Aplocheilichthys normani* in Guinea displays an omnivorous feeding habit, consuming both plant and animal prey in varying proportions (Romand, 1985). This generalist behavior may be supported by the unique pharyngeal structure of Cyprinodontiformes, which includes rows of caniniform teeth adapted for crushing and chewing a variety of prey types (Hernandez *et al*., 2009).

The predominance of phytoplankton in the diet is likely linked to its high seasonal availability in Lake Hawassa (Beyene *et al*., 2022b). Detritus and macrophytes were also prominent in the diet, likely influenced by the fish's preference for macrophyte-rich, shallow habitats (Prati *et al*., 2021). Although insects were consumed less frequently, they played an important role in macrophyte-dominated habitats where prey diversity is higher (Petrov, 2022). Seasonal fluctuations in prey abundance were evident, with differences between rainy and dry seasons likely due to changes in rainfall, water levels, and habitat structure (Ng'onga *et al*., 2019). Rainy-season flooding of swampy littoral zones may increase prey availability, allowing *A. antinorii* to exploit a broader range of food sources. The observed dietary overlap between smaller and larger size classes suggests strong intraspecific competition, possibly driven by habitat degradation (Tadesse *et al*., 2015).

CONCLUSIONS

Gut content analysis of three ecologically important fish species from Lake Hawassa confirms that all consume both plant- and animal-based prey. However, the occurrence, contribution, and dominance of specific prey items varied seasonally, likely influenced by rainfall and associated environmental changes. Comparisons with earlier studies on *E. paludinosus* and *G. quadrimaculatain* in the same region suggest a decline in the consumption of insects and fish prey (such as *A. antinorii*), while phytoplankton occurrence has increased. This study also provides the first detailed dietary analysis of *A. antinorii*, revealing a strong preference for phytoplankton as its primary food source. High dietary overlap ($C>0.6$) was observed among all three species, with the exception of certain size classes, indicating potential intraspecific competition and resource partitioning.

These findings highlight the importance of detailed studies to better understand nutrient dynamics, food web structures, resource sharing within the lake ecosystem, and potential cascading effects. Given their role as prey for piscivorous fish, these species may also serve as conduits for the transfer of toxic heavy metals and fish parasites to higher trophic levels, including human consumers. As biological indicators, further research is necessary to assess potential ecological risks associated with their feeding habits, ensuring sustainable fish populations in Lake Hawassa. A comprehensive understanding of trophic interactions among fish species in the lake is crucial for ecosystem management and conservation efforts.

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