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Cover: Oil painting of Humpback Whale *Megaptera novaeangliae*. © R. Mahesh.



Dietary assessment of tadpoles of selected rhacophorid frogs (*Polypedates*, *Rhacophorus*, *Zhangixalus*) (Amphibia: Anura: Rhacophoridae) of Kangchup, Manipur, India

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Abstract: Tadpoles are an abundant and diverse component of many freshwater ecosystems, yet little is known about their trophic status and feeding ecology compared to many other consumer groups. This study used gut content analysis to examine the diet patterns of four rhacophorid tadpole species (*Polypedates mutus*, *P. braueri*, *Rhacophorus bipunctatus*, and *Zhangixalus burmanus*) collected from ephemeral pools in Manipur, India. The food spectrum of tadpoles included mostly phytoplankton (diatoms, desmids, algae), followed by zooplankton (crustaceans, rotifers, insects). It was observed that *Phormidium* and *Surirella* were the primary sources of food for *P. mutus*, whereas *Navicula* and *Netrium* were consumed in large quantities by the other three species. Members of the class Bacillariophyceae (*Melosira* sp., *Navicula* sp., *Synedra* sp.) and Zygnematophyceae (*Netrium* sp.) were consistently present in the gut of all the tadpoles examined. These findings suggest that *Netrium* sp. and *Navicula* sp. represent key dietary components within the ecological niche occupied by the species, highlighting their significant role in the trophic dynamics of the habitat. Trophic niche width and overlap were also analysed between the species. Important insights into the ecological dynamics and conservation of tropical amphibian populations and communities can be acquired from studying the diet of amphibian tadpoles.

Keywords: Diet, dietary flexibility, ephemeral pools, feeding ecology, gut analyses, herbivory, microalgae, niche overlap, niche width, zooplankton.

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Author contribution: YSD conducted the field surveys, analyzed the data, and prepared the original manuscript draft. SS supervised the study, provided guidance throughout the research work, and reviewed and proofread the manuscript.

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INTRODUCTION

Tadpoles live in freshwater habitats and are remarkably diverse, occurring in both lotic and lentic ecosystems throughout tropical regions (Inger et al. 1986; Whiles et al. 2006). They play a variety of ecological roles in their ecosystems, have a wide range of microhabitats, and show considerable morphological variation (Altig & Johnston 1989). Saidapur (1989) also highlighted that many Indian anuran species co-breed and use a range of lentic and lotic water bodies, including rivers, streams, ephemeral ponds, wet grounds, temporary puddles, and permanent ponds following the south-west monsoon rains.

A fundamental aspect of tadpole biology involves understanding food and feeding techniques. Since amphibians' diets reflect the availability of food of optimum size, it is generally believed that they are feeding opportunists (Asrafuzzaman et al. 2018). It is crucial to understand the tadpole's diet and feeding habits as the early stages of an amphibian's life depend on the availability of food in their natural environment (Diaz-Paniagua 1985; Inger 1986). Dietary data for anuran larvae have only been published in the last 30 years (Khare & Sahu 1984; Ao & Khare 1986; Sekar 1990; Saidapur 2001; Sinha et al. 2001; Khongwir et al. 2003). The feeding ecology of tadpoles has been poorly studied despite their diversity and abundance in various kinds of freshwater habitats (Altig et al. 2007).

According to Duellman & Trueb (1994), tadpoles are regarded as specialized filter-feeder herbivores since they eat a wide range of algae during their development period (Wickramasinghe et al. 2007). Tadpoles may additionally consume microscopic organisms, fungi, and protozoa that are present in their environment, making them omnivores (Altig & Johnston 1989). Further study shows that tadpoles are more carnivorous than previously believed (Petranka et al. 1998) or that they are nonselective consumers (Seale 1980) with little dietary differentiation (Kupferberg 1997). Despite their high diversity and abundance across a wide range of freshwater habitats, the feeding ecology of tadpoles remains poorly understood and inadequately explored (Altig et al. 2007).

The tadpoles of India, especially those from the northeastern region, are very poorly documented. A great deal of studies on amphibians have focused on the Western Ghats, a biodiversity hotspot, with little research done in other parts of India (Aravind & Gururaja 2011). In the present study, the diet of tadpoles of four Rhacophorids (*Polypedates mutus*, *P. braueri*,

Rhacophorus bipunctatus, *Zhangixalus burmanus*) of Gosner stage 32–36 (Gosner 1960), were investigated based on the hypothesis that species that dwell in the same microhabitat must share similar food resources. By documenting the food items consumed during their developmental stages, it was aimed to gain insights into their feeding behaviour and to quantify niche width and niche overlap amongst tadpoles to assess the extent of resource partitioning.

MATERIALS AND METHODS

Sample collection

Tadpoles were collected from ephemeral pools during the month of June–September (2023–2024) from 1100 h to 1600 h from the foothills of Kangchup, Manipur (24.859° N, 93.810° E) located in Imphal–west District by visual encounter survey using dip-net (1 × 1 m). Pools were sampled for approximately 15 minutes. Dip-net sweeps were performed systematically along the margins and open water of each pool to ensure representative sampling. Collected tadpoles (N = 10 for each species of Gosner stage 32–36) were euthanised using tricaine methane sulphonate (5 g/L MS-222). After which, they were preserved in 10% formalin immediately after collection to prevent the complete digestion of food particles they had consumed. Tadpoles were deposited in the laboratory of Assam Don Bosco University.

Identification

The identification of tadpoles was based on the morphology observed, which includes colour pattern, pigmentation, body shape, position of the spiracles, vent tube, eyes, nostrils, and morphometric relations (Inger 1986; Sahu 1994; Grosjean 2001; Malkmus et al. 2002). Further, tadpoles were matched with syntopic adults based on partial sequences of the mitochondrial 16S rRNA gene.

Gut analyses

The entire length of the alimentary canal of each tadpole was removed through a longitudinal incision from mouth to anus. The gut contents were collected on a Petri plate and were stored in 10% formalin. Each sample was analysed in six replicates on glass slides using a Leica DMLS2 light microscope at 10× magnification, and when necessary, 40× magnification was used. The food items were quantified as the number of individuals per field of view over 10 observations per slide, and classified to the lowest possible taxonomic level following Needham

& Needham (1962), van der Valk (2012), and Thorp et al. (2014).

Data analyses

The items ingested by tadpoles were expressed as proportional utilization (% PU) and occurrence frequency (% OF). Further, prey-specific abundance (%) was calculated following Costello (1990) and the modified model of Amundsen et al. (1996).

The Shannon-Wiener index (H') was used to determine diet diversity for all four species, and Levins' measure (B) to determine the niche width for different types of food items consumed (Krebs 1999). Niche overlap was calculated following Pianka (1973). Venn diagrams showing the shared and unique food items between the taxonomically related pairs were created using R software (version 4.4.3).

RESULTS

Around 23 different food items were identified from *Polypedates mutus* tadpoles, 14 food items from *Polypedates braueri*, 13 from *Zhangixalus burmanus*, and 15 from *Rhacophorus bipunctatus*. The total amount of food items ingested by tadpoles varied markedly. Of the four species studied, *P. mutus* consumed different food items but in smaller amounts, while *R. bipunctatus* preferred limited food items but in larger amounts.

Five food items were consistently present in the diets of all four species examined: *Melosira* (diatoms), *Navicula* (diatoms), *Synedra* (diatoms), *Netrium* (desmids), and *Phormidium* (blue-green algae). In addition to these, *Meridion* (diatoms), *Gomphonema* (diatoms), *Diatoma* (diatoms), *Closterium* (desmids), and *Dileptus* (protozoans) were commonly found in the diets of *R. bipunctatus* and *Z. burmanus*. While, *Gyrosigma* (diatoms), *Ophiocytium* (green algae), *Oscillatoria* (blue-green algae), *Monostyla* (rotifers) and *Euglena* (protozoans) were commonly present in the diet of *P. mutus* and *P. braueri* (Table 1). *Rotaria* (16.66%), *Cyclops* (16.66%), and *Penium* sp. (14.28%) were the rare food items.

Certain prey items were species specific: *Euastrum* (desmids) was only consumed by *Z. burmanus*. Likewise, *Achnanthes* (diatoms), *Cocconeis* (diatoms), *Eunotia* (diatoms) and egg parasites were unique to *R. bipunctatus*; *Penium* (desmids), *Rotaria* (rotifers), *Cyclops* (crustaceans), and *Spirulina* (blue-green algae) to *P. mutus*; *Epithemia* (diatoms), *Amphora* (diatoms), *Surirella* (diatoms), *Pediastrum* (green algae),

Mougeotia (green algae), *Microspora* (green algae), *Euchlanis* (rotifers), *Coelosphaerium* (blue-green algae), *Selenastrum* (green algae), and *Crucigenia* (green algae) to *P. braueri*.

The most dominant food items in the gut of *P. mutus* tadpoles were *Phormidium* sp. (39.9%) and *Surirella* sp. (25.4%); *Navicula* sp. (47.4%) and *Netrium* sp. (17.8%) in *P. braueri*; *Navicula* sp. (37.2%) and *Netrium* sp. (27.8%) in *Z. burmanus*; *Navicula* sp. (55.5%) and *Netrium* sp. (27.6%) in *R. bipunctatus*, respectively (Figure 1). Two genera, namely *Navicula* sp. and *Netrium* sp., dominated the food spectrum.

Tadpoles of *P. mutus* consumed *Synedra* sp., *Phormidium* sp., *Navicula* sp. and *Coelosphaerium* sp., with an occurrence frequency of 100% in their diet (Table 2). The least occurring food items were *Melosira* sp., *Epithemia* sp., *Gyrosigma* sp., *Cyclops*, *Netrium* sp., and *Rotaria* (16.66%). In the congeneric species *P. braueri*, *Meridion* sp., *Netrium* sp., *Melosira* sp., *Synedra*

Table 1. Food items identified from the intestine of anuran tadpoles: PM—*Polypedates mutus* | PB—*Polypedates braueri* | RB—*Rhacophorus bipunctatus* | ZB—*Zhangixalus burmanus* | +—present | --absent.

Class	Genus	PM	PB	ZB	RB
Bacillariophyceae	<i>Melosira</i> sp.	+	+	+	+
	<i>Navicula</i> sp.	+	+	+	+
	<i>Synedra</i> sp.	+	+	+	+
	<i>Meridion</i> sp.	+	-	+	+
	<i>Gomphonema</i> sp.	-	+	+	+
	<i>Diatoma</i> sp.	-	-	+	+
	<i>Achnanthes</i> sp.	-	-	-	+
	<i>Gyrosigma</i> sp.	+	+	-	+
	<i>Cocconeis</i> sp.	-	-	-	+
	<i>Eunotia</i> sp.	-	-	-	+
	<i>Epithemia</i> sp.	-	+	-	-
	<i>Amphora</i> sp.	-	+	-	-
	<i>Surirella</i> sp.		+		
Zygnematophyceae	<i>Netrium</i> sp.	+	+	+	+
	<i>Closterium</i> sp.	-	-	+	+
	<i>Euastrum</i> sp.	-	-	+	-
	<i>Penium</i> sp.	+	-	-	-
	<i>Ophiocytium</i> sp.	+	+	-	-
	<i>Mougeotia</i> sp.	-	+	-	-
Cyanophyceae	<i>Phormidium</i> sp.	+	+	+	+
	<i>Spirulina</i> sp.	+	-	-	-
	<i>Oscillatoria</i> sp.	+	+	-	-
	<i>Microspora</i> sp.	-	+	-	-
Monogononta	<i>Monostyla</i> sp.	+	+	+	-
	<i>Euchlanis</i> sp.	-	+	-	-
	<i>Rotaria</i> sp.	+	-	-	-
Litostomatea	<i>Dileptus</i> sp.	+	-	+	+
Euglenophyceae	<i>Euglena</i> sp.	+	+	+	-
Chlorophyceae	<i>Pediastrum</i> sp.	-	+	-	-
	<i>Coelosphaerium</i> sp.	-	+	-	-
	<i>Selenastrum</i> sp.	-	+	-	-
	<i>Crucigenia</i> sp.	-	+	-	-
Crustacea	<i>Cyclops</i> sp.	+	-	-	-
Insecta	Eggs of parasites	-	-	-	+
	Miscellaneous invertebrates	-	+	+	-

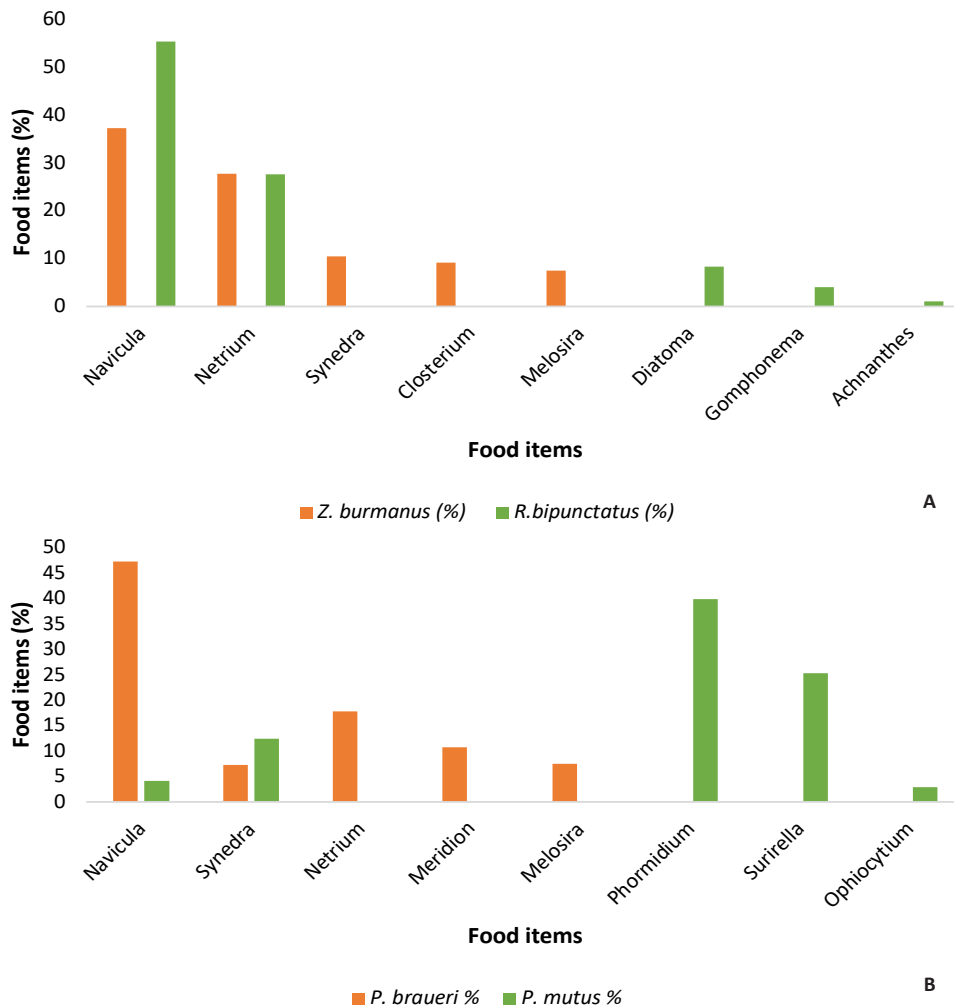


Figure 1. Five most abundant food items of each species of taxonomically related pairs and of the congeners: A—*Zhangixalus burmanus* and *Rhacophorus bipunctatus* | B—*Polypedates mutus* and *P. braueri*.

sp., *Navicula* sp., and *Phormidium* sp. were ingested by the tadpoles, with a 100% occurrence frequency in their diet (Table 3). The least occurring food items of this species were *Penium* sp. and *Oscillatoria* sp. (14.28%).

Tadpoles of *R. bipunctatus* consumed *Navicula* sp., *Netrium* sp., *Gomphonema* sp., *Achnanthes* sp., *Diatoma* sp., *Melosira* sp., and *Cocconeis* sp. with an occurrence frequency of 100% in their diet (Table 4). The least occurring food items were *Synedra* sp. (0.46%) and *Gyrosigma* sp. (0.22%). While, in the congeneric species *Z. burmanus*, most of the food items were ingested by the tadpoles with an occurrence frequency of 100% and 75% except for *Euglena* sp. with 25% occurrence frequency (Table 5).

Phormidium sp. showed the highest Pi value (39.84) among all the food items ingested by *P. mutus* tadpoles, suggesting that it is both frequently consumed and a highly dominant component. *Navicula* sp. also

exhibited the highest Pi value (47.37) in the diet of *P. braueri* tadpoles, indicating that it is a significant dietary component. It was observed that members of *Navicula* sp. dominated the food spectrum of *R. bipunctatus* (Pi: 55.49) and *Z. burmanus* (Pi: 37.23).

The analysis revealed a high trophic niche overlap value (0.92) between the tadpoles *R. bipunctatus* and *Z. burmanus*, suggesting potential competition for shared food resources. In contrast, the low overlap value between *P. braueri* and *P. mutus* (0.18) suggests minimal trophic overlap and reduced competition, indicating clear resource partitioning despite their congeneric and sympatric occurrence (Figure 2).

Niche width was found to be the lowest in *P. mutus* tadpoles (0.27) indicating that the species has a narrow ecological niche while niche width was highest in *Z. burmanus* (1.81) suggesting a wide range of ecological niche among the four tadpole species examined.

Table 2. Proportional utilization, occurrence frequency and prey-specific dominance of different food items in the tadpoles of *Polypedates mutus*.

<i>Polypedates mutus</i>	Proportional utilization	Occurrence frequency (%)	Prey specific dominance pi (%)
<i>Microspora</i> sp.	0.009	66.666	1.340
<i>Synedra</i> sp.	0.124	100	12.388
<i>Phormidium</i> sp.	0.398	100	39.843
Rotifers	0.005	50	1.052
<i>Melosira</i> sp.	0.009	16.666	5.797
<i>Navicula</i> sp.	0.041	100	4.129
<i>Epithemia</i> sp.	0.002	16.666	1.538
<i>Gomphonema</i> sp.	0.012	33.333	4.347
Miscellaneous invertebrates	0.015	83.333	1.827
<i>Gyrosigma</i> sp.	0.002	16.666	1.538
<i>Pediastrum</i> sp.	0.003	33.333	1.056
Cyclops	0.001	16.666	0.813
<i>Mougeotia</i> sp.	0.004	33.333	1.212
<i>Amphora</i> sp.	0.001	16.666	0.769
<i>Coelosphaerium</i> sp.	0.022	100	2.232
<i>Oscillatoria</i> sp.	0.008	50	1.690
<i>Selenastrum</i> sp.	0.011	66.666	1.672
<i>Netrium</i> sp.	0.017	16.666	11.538
<i>Ophiocytium</i> sp.	0.029	83.333	3.363
<i>Rotaria</i> sp.	0.001	16.666	0.729
<i>Surirella</i> sp.	0.253	66.666	35.303
<i>Euglena</i> sp.	0.019	66.666	2.643
<i>Crucigenia</i> sp.	0.008	33.333	2.027

Rhacophorus bipunctatus tadpoles have moderately narrow niche width (1.08) and *P. braueri* has an intermediate (1.37) niche width (Table 6).

DISCUSSION

The present study revealed that the food diversity of four tadpole species includes various microalgae, mainly from three classes namely, Bacillariophyceae, Zygnematophyceae, and Cyanophyceae. Bacillariophyceae have been identified as the most commonly ingested food item in the diets of various lentic tadpoles (Rossa-Feres et al. 2004; Echeverría et al. 2007; Bionda et al. 2012; Huckembeck et al. 2016; Mohapatra et al. 2017; Rout et al. 2018), suggesting that high diatom concentrations in tadpole intestinal contents could be considered a widespread occurrence. Sengupta

Table 3. Proportional utilization, occurrence frequency and prey-specific dominance of different food items in the tadpoles of *Polypedates braueri*.

<i>Polypedates braueri</i>	Proportional utilization	Occurrence frequency (%)	Prey specific dominance pi (%)
<i>Meridion</i> sp.	0.108	100	10.807
<i>Netrium</i> sp.	0.178	100	17.794
<i>Melosira</i> sp.	0.075	100	7.532
<i>Synedra</i> sp.	0.073	100	7.314
<i>Penium</i> sp.	0.001	14.285	0.917
<i>Spirulina</i> sp.	0.009	85.714	1.168
<i>Navicula</i> sp.	0.474	100	47.379
<i>Monostyla</i> sp.	0.004	42.850	1.142
<i>Phormidium</i> sp.	0.036	100	3.602
<i>Oscillatoria</i> sp.	0.001	14.285	0.917
<i>Dileptus</i> sp.	0.009	42.850	2.244
<i>Euglena</i> sp.	0.003	42.850	0.810
<i>Ophiocytium</i> sp.	0.018	71.428	2.387
<i>Gyrosigma</i> sp.	0.007	42.850	1.601

Table 4. Proportional utilization, occurrence frequency and prey-specific dominance of different food items in the tadpoles of *Rhacophorus bipunctatus*.

<i>Rhacophorus bipunctatus</i>	Proportional utilization	Occurrence frequency (%)	Prey specific dominance pi (%)
<i>Navicula</i> sp.	0.555	100	55.493
<i>Netrium</i> sp.	0.276	100	27.638
<i>Dileptus</i> sp.	0.003	71.428	0.422
<i>Synedra</i> sp.	0.001	28.571	0.464
<i>Gomphonema</i> sp.	0.041	100	4.085
<i>Achnanthes</i> sp.	0.010	100	1.021
<i>Gyrosigma</i> sp.	0.001	28.571	0.219
<i>Diatoma</i> sp.	0.084	100	8.387
<i>Melosira</i> sp.	0.006	100	0.588
<i>Meridion</i> sp.	0.007	85.714	0.785
<i>Cocconeis</i> sp.	0.006	100	0.649
<i>Closterium</i> sp.	0.002	57.142	0.449
<i>Phormidium</i> sp.	0.002	71.428	0.308
Eggs of parasites	0.003	85.714	0.320
<i>Eunotia</i> sp.	0.003	42.850	0.595

et al. (2013) observed seven different food items in the gut of five species of tadpoles of Basistha stream in Assam, India with diatoms (class Bacillariophyceae) being the most abundant food items consumed by tadpoles, which was also observed in this study.

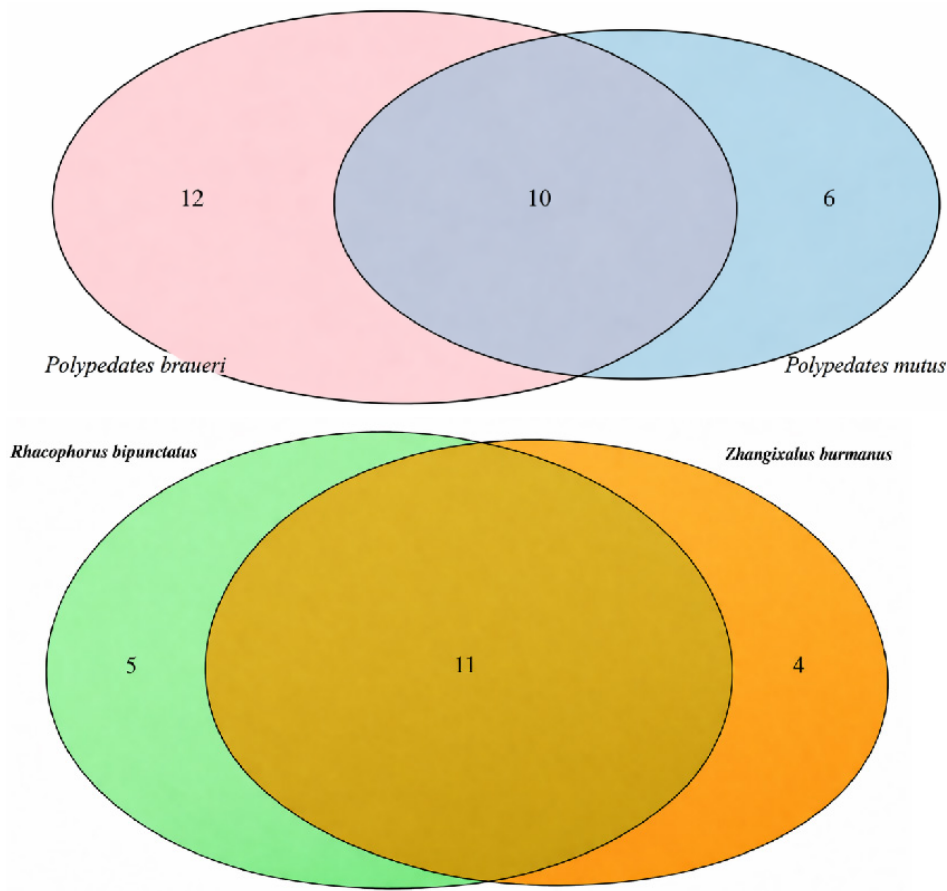


Figure 2. Venn diagram showing shared and unique food items between: a—*Polypedates braueri* and *P. mutus* | b—*Rhacophorus bipunctatus* and *Zhangixalus burmanus*. The overlapping region represents food items consumed by both species, and the non-overlapping region represents species-specific items.

Sinha et al. (2001) conducted qualitative analyses of the food spectrum of five species of anuran tadpoles (*Bufo melanostictus*, *Rhacophorus maximus*, *Amolops afghanus*, *Rana danieli*, and *Euphlyctis cyanophlyctis*) from Arunachal Pradesh, India. They found that diatoms and Chlorophyta were present in all five species. In the present study, diatoms were consumed by all four tadpoles' species, whereas green algae and crustaceans were consumed exclusively by *P. braueri* tadpoles. In accordance with studies conducted by Sinha et al. (2001) and Lalremsanga et al. (2013), the predominant prey category in the diets of *P. maculatus* tadpoles was found to be members of the class Bacillariophyceae. This study also revealed similar findings.

Rotifers, crustaceans, protozoans, and other miscellaneous invertebrates have also been documented in the diets of other species (Candiotti 2005; Dutra & Callisto 2005; Heinen & Abdella 2005; Pfennig et al. 2006; Sousa Filho et al. 2007; Wickramasinghe et al. 2007). In the present study, the diets of the examined tadpoles

were also found to contain these groups. Additionally, the consumption of eggs of the parasitic worm by *R. bipunctatus* tadpoles demonstrates dietary flexibility, shifting from herbivory to omnivory, as observed by Jacobson et al. (2019) in *Tripurion petasatus*. The high nutritional value of invertebrates, particularly in terms of protein and energy, is noteworthy (Bowen et al. 1995). Heinen & Abdella (2005) also suggested that tadpoles require animal food items during their developmental stage for faster growth.

Apart from a large amount of debris ingested accidentally, gut content analysis revealed that the tadpoles' diet consisted primarily of desmids and diatoms, which does not align with the findings of Lajmanovich (2000) and Rossa-Feres et al. (2004), where diatoms and microalgae were the most predominant food items. Bacillariophyceae members are more convenient to eat than filamentous algae, and they may be the richest source of food in their environment (Kupferberg 1997).

Table 5. Proportional utilization, occurrence frequency and prey-specific dominance of different food items in the tadpoles of *Zhangixalus burmanus*.

<i>Zhangixalus burmanus</i>	Proportional utilization	Occurrence frequency (%)	Prey specific dominance pi (%)
<i>Melosira</i> sp.	0.074	100	7.470
<i>Navicula</i> sp.	0.372	100	37.235
<i>Netrium</i> sp.	0.278	100	27.794
<i>Closterium</i> sp.	0.092	100	9.214
<i>Phormidium</i> sp.	0.025	100	2.568
<i>Synedra</i> sp.	0.104	100	10.423
<i>Meridion</i> sp.	0.006	75	0.778
<i>Euastrum</i> sp.	0.019	100	1.888
<i>Monostyla</i> sp.	0.006	100	0.604
<i>Gomphonema</i> sp.	0.007	100	0.755
<i>Diatoma</i> sp.	0.007	100	0.755
<i>Dileptus</i> sp.	0.005	75	0.715
<i>Euglena</i> sp.	0.001	25	0.327

Tadpoles live in microhabitats where they can readily access resources and food (Inger et al. 1986; Horat & Semlitsch 1994). As adaptive omnivores rather than specialized feeders, tadpoles are unlikely to differentiate themselves by food partitioning (Hoff et al. 1999). Considering that food conditions vary depending on habitat, anuran larval dietary patterns should correspond to its distribution pattern; a species may have evolved to be more successful with the nutrient conditions that exist in its ideal habitat, or a species may select the habitat where its appropriate food is abundant (Iwai & Kagaya 2005). Understanding the dietary and feeding habits of tadpoles is crucial because the early stages of an amphibian's existence depend on the food resources in their environment (Sinha et al. 2001).

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Table 6. Niche width (B) and Shannon-Weiner diversity index (H') of the diet of tadpoles in the ephemeral pools of Kangchup, Manipur, India.

Species	B	H'
<i>Polypedates mutus</i>	0.27	1.89
<i>Polypedates braueri</i>	1.37	1.66
<i>Zhangixalus burmanus</i>	1.81	1.71
<i>Rhacophorus bipunctatus</i>	1.08	1.25

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