Seasonal changes in icefish diel feeding patterns in Lake Chaohu, a large shallow eutrophic lake of China

Guo, L.*; Xie, P.; Deng, D.; Yang, H.; Zhou, Q.

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Abstract

Seasonal changes in the diel feeding patterns of the zooplanktivorous icefish (*Neosalanx taihuensis*), which is an endemic species of China, were studied in the large, shallow eutrophic Lake Chaohu of China during the autumn of 2002 and summer of 2003. The results of the diel feeding rhythm indicate that icefish is a visual particulate feeder. There were large differences in diet composition and the selection indices of certain prey by icefish. In general, icefish fed more on calanoids than on cyclopoids, and fed more on larger cladocerans (i.e., *Daphnia*, *Moina*, *Leptodora*) than smaller cladocerans (i.e., *Bosmina*, *Ceriodaphnia*). Icefish is highly selective of individual food items, with prey selection also being dependent on fish size. There was no significant difference in the prey selection between male and female icefish. This study provides the first report of diel feeding rhythm in icefish, and is the first comparative study on prey selection between male and female icefish.

Keywords: Icefish, Diel feeding patterns, Diet composition, Prey selection, Zooplankton, Lake Chaohu

Donghu Experimental Station of Lake Ecosystems, State Key Laboratory for Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, P.R. China

* Corresponding author's email: longgen@ihb.ac.cn

Introduction

The diet of fish usually changes as they grow, which is often associated with changes in diel and seasonal patterns. These changes may arise in response to morphological changes at different ontogenetic phases of maturation, such as the increase in mouth size and improvements in locomotory and sensory abilities (Gerking, 1994; Wootton, 1998). In addition, changes in diel and seasonal dietary patterns probably reflect changes in fish activity, prey vulnerability, and/or the life-history patterns of prey organisms (Wootton, 1998; Gill, 2003; Anastácio et al., 2011). There have been many studies on the feeding ecology of fish, both in a field and experimental framework. However studies remain limited with respect to understanding the feeding mechanisms of fish (Vinyard et al., 1976; Wright and O'Brien, 1984; Henderson and Northcote, 1985; Lazzro, 1987; Hambright and Hall, 1992; Wanzenböch, 1992; Guthrie and Muntz, 1993; Gerking, 1994; Wootton, 1998; Gill, 2003).

Icefishes (Salangidae) originate from the Chinese Yellow Sea, and are distributed in China, Korea, Japan, Vietnam, and Russia. Across species, there is a wide range of prey items, despite the fish exhibiting high levels of environmental sensitivity. These species develop quickly and have short life cycles for 1 year, with discrete generations, high fecundity, and wide fluctuations in population numbers (Wang 1996; Wang et al. 2002). The icefish, *Neosalanx taihuensis*, is primarily distributed in the pelagic zone of freshwater lakes along the middle and lower reaches of the Yangtze, Huaihe, and Oujiang rivers in China (Wu, 1979; Li and Chen, 1984; Xie and Xie, 1997). It is of commercial importance in the freshwater fisheries of China (Liu, 2001). For this reason, the icefish has been introduced into many lakes and reservoirs outside of its native range since the 1980s, which has had significant ecological impacts on native fishes in some plateau lakes (Yang, 1994).

Lake Chaohu is the fifth largest freshwater lake (775 km^2) in China, and has had a productive icefish fishery since the 1950s. It is a shallow lake, without summer oxygen or temperature stratification, but with a high water temperature ranging 5-34^{o}C. In addition, the lake has been subject to serious levels of eutrophication during recent decades, because of high nutrient loading as a result of large amounts of domestic sewerage discharge from surrounding cities (Jin et al., 1990). Due to the high eutrophication in this lake, there have been dense cyanobacterial blooms (mainly composed of *Microcystis* and *Anabaena*) during the warm seasons (June to September) of each year since the 1970s (Jin et al., 1990; Deng, 2004). These blooms may affect the structure of the fish population, which would endanger the sustainable management of this fishery resource. A survey in 1963 recorded the presence of 94 fish species in this lake, of which four were species of icefish, *Hemisalanx prognathus* Regan, *H. brachyrostrialis* Fang, *Protosalanx hyalocranius* Abbott and *Neosalanx taihuensis* Chen (Institute of Aquatic Science of Anhui Province & Nanjing Institute of Geography and Limnology, 1963). The annual production of fish exceeded 5500 tons since 1985, and reached over 9000 tons in 2003 and the icefish (*N. taihuensis*) has been commercially exported since the 1970s. Recently, the catch production of icefish (dominated absolutely by *N. taihuensis*) comprises about 5% of total fish yield, and up to 30% of economic value. Hence, it is essential to improve our understanding of the feeding patterns of this fish species in a natural eutrophic lake, as well as to evaluate the impact of introducing icefish to lake ecosystems.

Studies on the diet of the icefish have been conducted for *N. pseudotaihuensis* (Liu, 2001) and for *N. taihuensis* (Liu and Zhu, 1994; Yin et al., 1997; Gong et al., 1999; You et al., 1999; He et al., 2001). However, information is not available about the diel feeding pattern of icefishes, or possible differences in prey selection between males and females. Previous studies on the spawning population and biology of *N. taihuensis* in Lake Chaohu were carried out by Wu (1979), Li and Chen (1984) and Diao (1986). However, more information on the feeding pattern and food consumption by icefish is essential to understand the role of this species on the structure and function of aquatic food webs. Hence, this study aimed to examine seasonal changes in the diel feeding patterns of the icefish *N. taihuensis*, including diet composition, feeding rhythm and prey selection. Finally, we discuss the possible mechanisms that may underlie seasonal variations in the foraging strategies of this species of icefish, and how this relates to its survival in eutrophic lake systems.

Materials and methods

Study site

Lake Chaohu is located in the Anhui Province of east China (117^{o}16’54’’-117^{o}51’46’’E, 30^{o}25’28’’-31^{o}43’28’’N). The surface area of the lake covers 760 km^2, with a mean depth of 2.7 m, and a storage capability of 2.1 billion m^3. The lake belongs to the river system of the left bank in the lower reaches of the Yangtze River, which is connected via the Yuxi River, but landlocked by the Chaohu Dam and the Yuxi Dam, which were constructed in 1960 and 1996, respectively (Fig. 1).

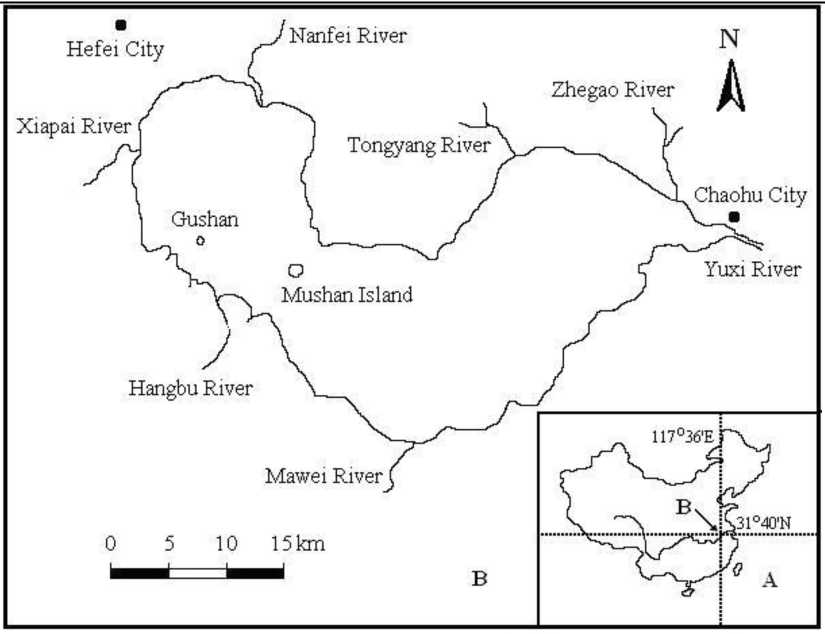

Figure 1: Map of Lake Chaohu and the sampling stations. There are six river inflows around Lake Chaohu, and the Yuxi River is the outflow, which connects to the Yangtze River and is separated by two dams (one dam was built between the Yuxi River and Lake Chaohu in 1960; another was built between the Yuxi River and the Yangtze River in 1966). All fish were sampled in the vicinity of Mushan Island, in the eastern part of Lake Chaohu.

Fish sampling

Icefish were captured by using the trawl boats of fishermen in the eastern part of Lake Chaohu (Fig.1). Seasonal sampling was conducted during the daytime at random 1 to 2 hour intervals on 19 September 2002 (early autumn), 22 November 2002 (late autumn), and 13 January 2003 (winter). Samples for diel feeding patterns of icefish were collected on 30 April to 1 May (spring) and 23-24 July (summer) in 2003 from two trawls on one trawl boat. Each trawling lasted 10-20 min, with sampling at 3 h interval throughout the 24 h cycle. Due to the presence of extremely high air temperatures (35°C), the 15:00 samples on 24 July 2003 could not be collected.

Zooplankton sampling

During the study periods, crustacean zooplankton was sampled simultaneously to the fish sampling protocols. Length-weight regression or individual weights provided by Zhang and Huang (1991) were used to estimate zooplankton biomass.

Fish diet analyses

All fish were immediately preserved in 10% formalin, and returned to the laboratory for measurement (mm) and identification. The entire gut was measured, and then dissected for prey analysis. Because it was often difficult to identify the prey species correctly, due to partial digestion, prey items were usually sorted to the genus level, and grouped into eight taxonomic categories: *Bosmina*, *Moina*, *Daphnia*, *Diaphanosoma*, *Ceriodaphnia*, *Leptodora*, calanoid copepods and cyclopoid copepods.

For each sampling group, the guts of icefish with no food or with only unidentifiable matter were recorded. The relative importance of a prey item was evaluated by the percentage frequency of occurrence (%*F*) (empty guts excluded), percentage of biomass (%*M*), and numerical percentage (%*N*). Prey type selection was determined by using Chesson's preference index (α) (Chesson, 1983). This index is calculated as follows:

$$\alpha = \frac{r_i n_i^{-1}}{\sum_{j=1}^{m} r_j n_j^{-1}}, \; i = 1, \ldots, m$$

where r_i and n_i are the number of prey type i in the gut and in the lake, respectively; m is the number of prey categories (9 in this study). The measure of preference α for a prey type is between 0 (no selection) and 1 (complete selection), while a value of approximately m^{-1} indicates that the predators feed randomly on the prey.

Statistical analyses

Data analyses were performed with the Statistic f Software packet (StatSoft Institute, Version 6.0). For the comparison of prey consumed among seasons, data were analyzed primarily by analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) multiple comparisons. The Student's t-test was used to establish prey categories within zooplankton.

Results

Seasonal feeding patterns

During the study period, a total of 530 icefish were collected, ranging between 20.0 mm and 87.0 mm in size (Table 1). The average length of captured fish varied significantly across different sampling dates (one-way ANOVA, *F*-test, $P < 0.001$).

Table 1: The number of icefish that were examined, including total length measurements (TL, mm) and the percentage of empty guts.

Season	No. of fish examined	Mean ± SD of TL (Range)	Empty guts (%)
Early autumn	41	63.5 ± 5.3 (52.0-74.0)	4.9
Late autumn	87	74.1 ± 6.7 (41.0-87.0)	21.8
Winter	60	74.8 ± 7.0 (43.0-85.0)	21.7
Spring	227	52.8 ± 13.0(20.0-87.0)	22.9
Summer	115	49.9 ± 9.3 (23.0-66.0)	51.3

The number of prey items and the relative weight of gut contents indicated that icefish fed actively throughout all seasons (Fig. 2). The total number of prey in the guts (excluding the empty guts) varied significantly across seasons (one-way ANOVA, *F*-test, *P* < 0.001), and was significantly higher in late autumn (November) compared to other seasons (Tukey's HSD test, P < 0.05). However, the gut content weight was highest in spring (April-May) and lowest in winter (January). Eight groups of crustacean zooplankton were found in the guts of *N. taihuensis* during the study period (Fig. 3).

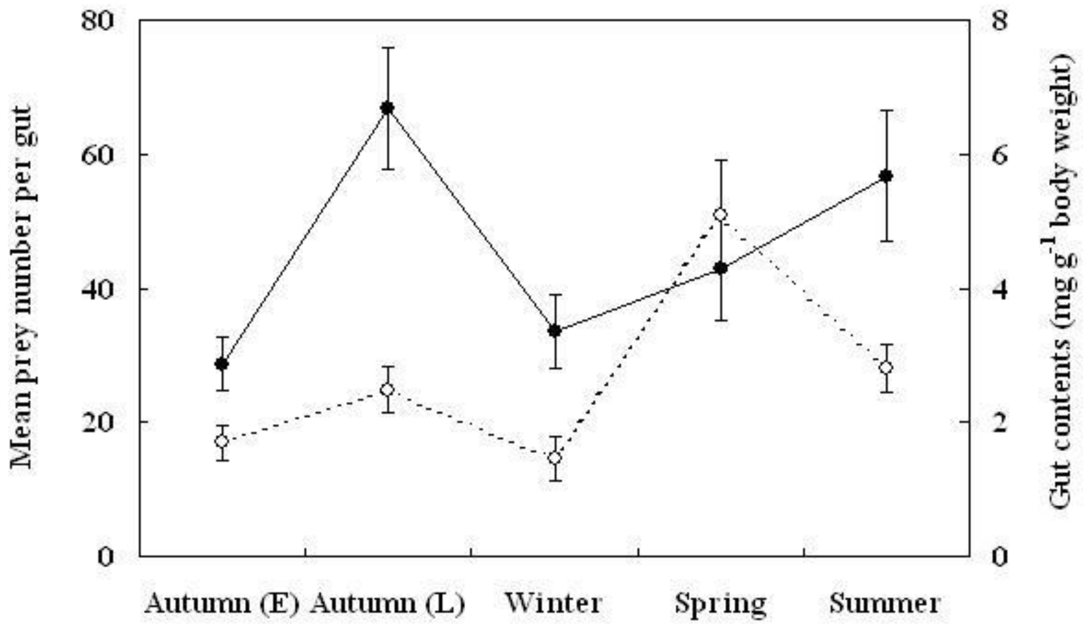

Figure 2: Seasonal changes in the mean number of prey per gut (solid line) and the mean weight of gut contents (mg. g $^{-1}$ body weight; broken line) of icefish in Lake Chaohu. Vertical bars are the standard error.

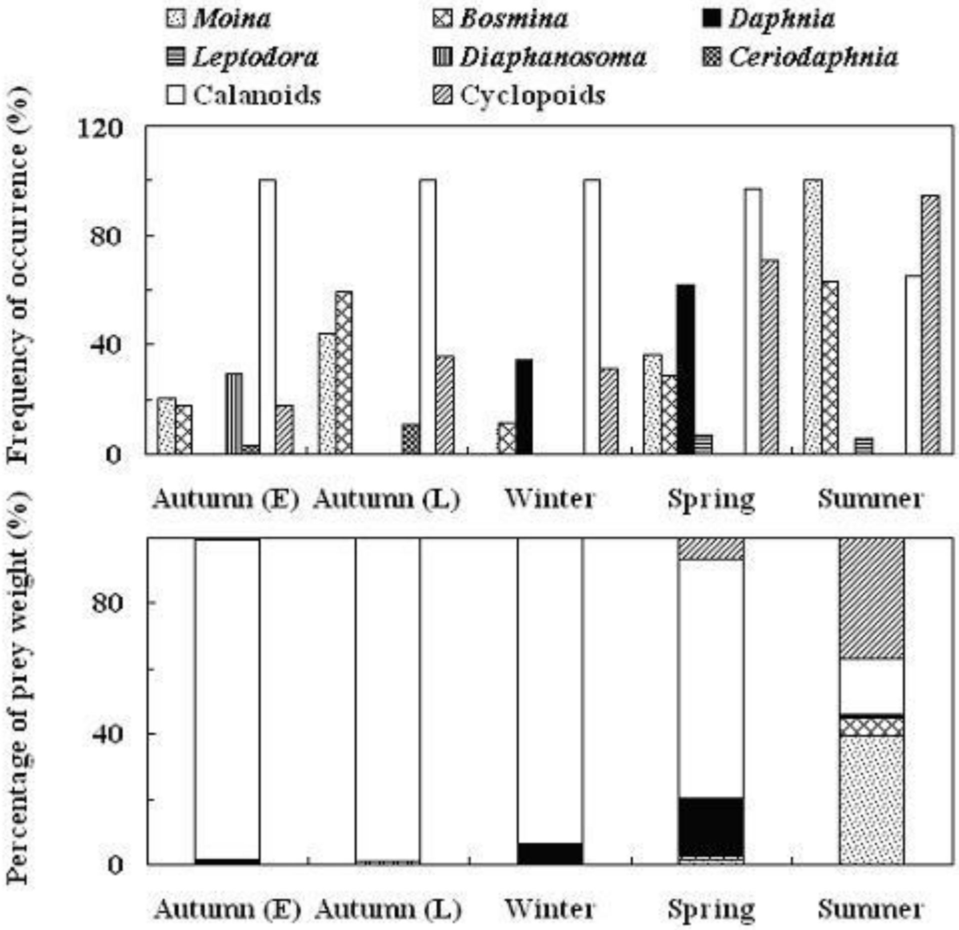

Figure 3: Seasonal variation in the diet of icefish in Lake Chaohu. Frequency of occurrence and percentage of prey weight in the early (September) and late autumn (November) of 2002 and the winter (January), spring (April-May), and summer (July) of 2003.

The major prey categories of the icefish diets were the cladoceran *Moina*, *Bosmina*, *Daphnia*, *Leptodora*, *Diaphanosoma*, and *Ceriodaphnia*, in addition to calanoids and cyclopoids. Calanoids were the prominent prey item of the icefish diets from autumn to spring, but the percentage weight of this prey was at its minimum in the summer. In comparison, the prey weights of both cyclopoids and *Moina* were at their maximum in the summer. *Daphnia* was a dominant prey item in winter and spring, but absent in summer. *Leptodora* appeared in the fish diets in spring and summer, but only minimally. *Bosmina* were preyed on by the icefish throughout the seasons, but at low proportions in the fish diets, with a maximum of 4.9% in the summer. *Diaphanosoma* and *Ceriodaphnia* were occasional prey items across the study period.

Diel feeding patterns

The diel feeding patterns in various seasons showed that the icefish fed only in the daytime. For example, a high percentage of empty guts were recorded between dusk and dawn, while much greater prey numbers per gut were recorded in the daytime. The mean prey number per gut in the daytime remained similar across all seasons (Fig. 4).

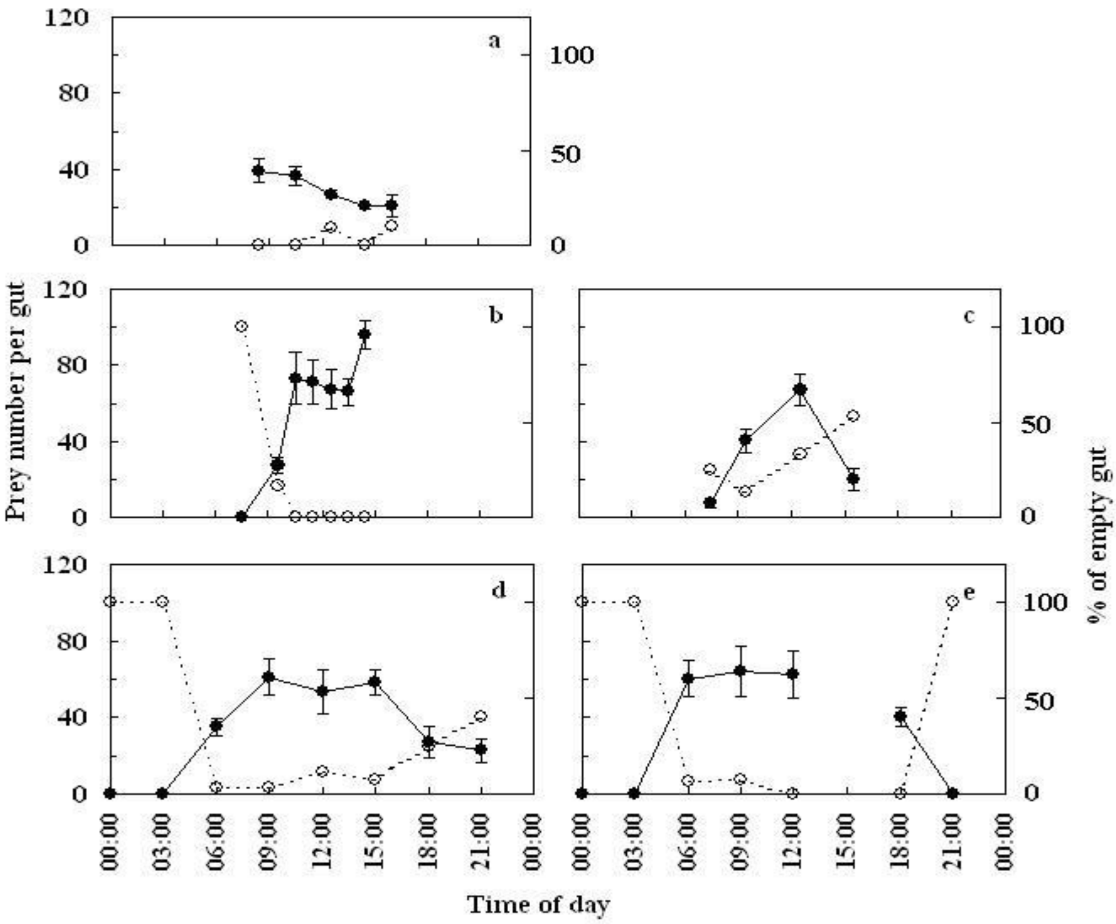

Figure 4:Seasonal variation in diel feeding activity of icefish showed by total prey number (solid line) and the percentage of empty guts (broken line): (a) September 2002, (b) November 2002, (c) January 2003, (d) April-May 2003, and (e) July 2003. Vertical bars are the standard error.

The diel variation in prey composition of the icefish in different seasons is shown in Fig. 5. Except for July, calanoids primarily dominated the prey biomass of gut contents in all months. *Daphnia* were also an important prey item in the diet of spring samples (Fig. 5D). In summer, the dominance of calanoids was replaced by a combination of *Bosmina*, *Moina* and calanoids (Fig. 5E).

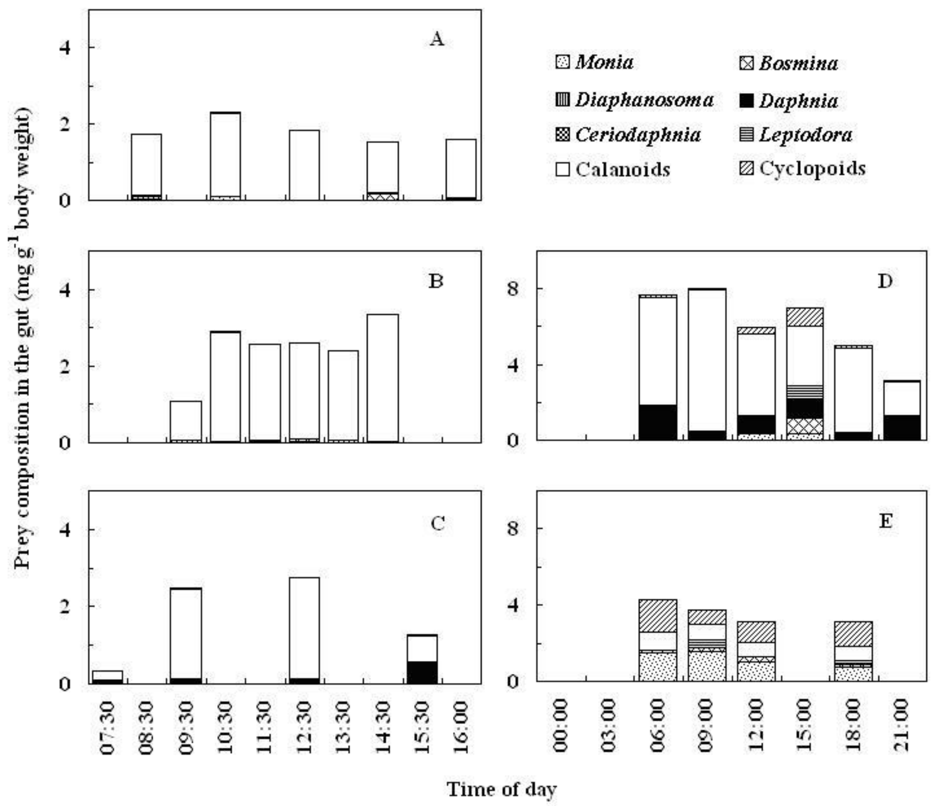

Figure 5: Diel variation in prey composition of the gut contents (mg g^{-1} body weight) of icefish in 2002-2003: (a) September 2002, (b) November 2002, (c) January 2003, (d) April-May 2003, and (e) July 2003.

Effects of body length and sex on prey composition

As many as 90.3% of the individuals collected in the spring were mature adults, indicating that spring is the spawning season for *N. taihuensis*. However, it should be noted that a small number of mature fish (0.11%) were also found in the autumn samples. The effects of body length and sex on the gut contents of the icefish in spring are shown in Fig. 6-7. There were significant differences in prey occurrence and the percentage composition of prey weight among the seven body length groups. The large-sized cladoceran (*Daphnia*) were more important prey items of larger icefish than for smaller icefish, while icefish smaller than 40 mm did not have any *Daphnia* in their gut contents. *Moina* and cyclopoids were found in the fish of large body length groups (III-VII). *Leptodora* were only found in the largest body length group. Sexual differences in prey composition of the icefish were not significant in the spawning season. *Daphnia*, calanoids and cyclopoids were the major prey items of both males and females in terms of the frequency occurrence and average prey weight.

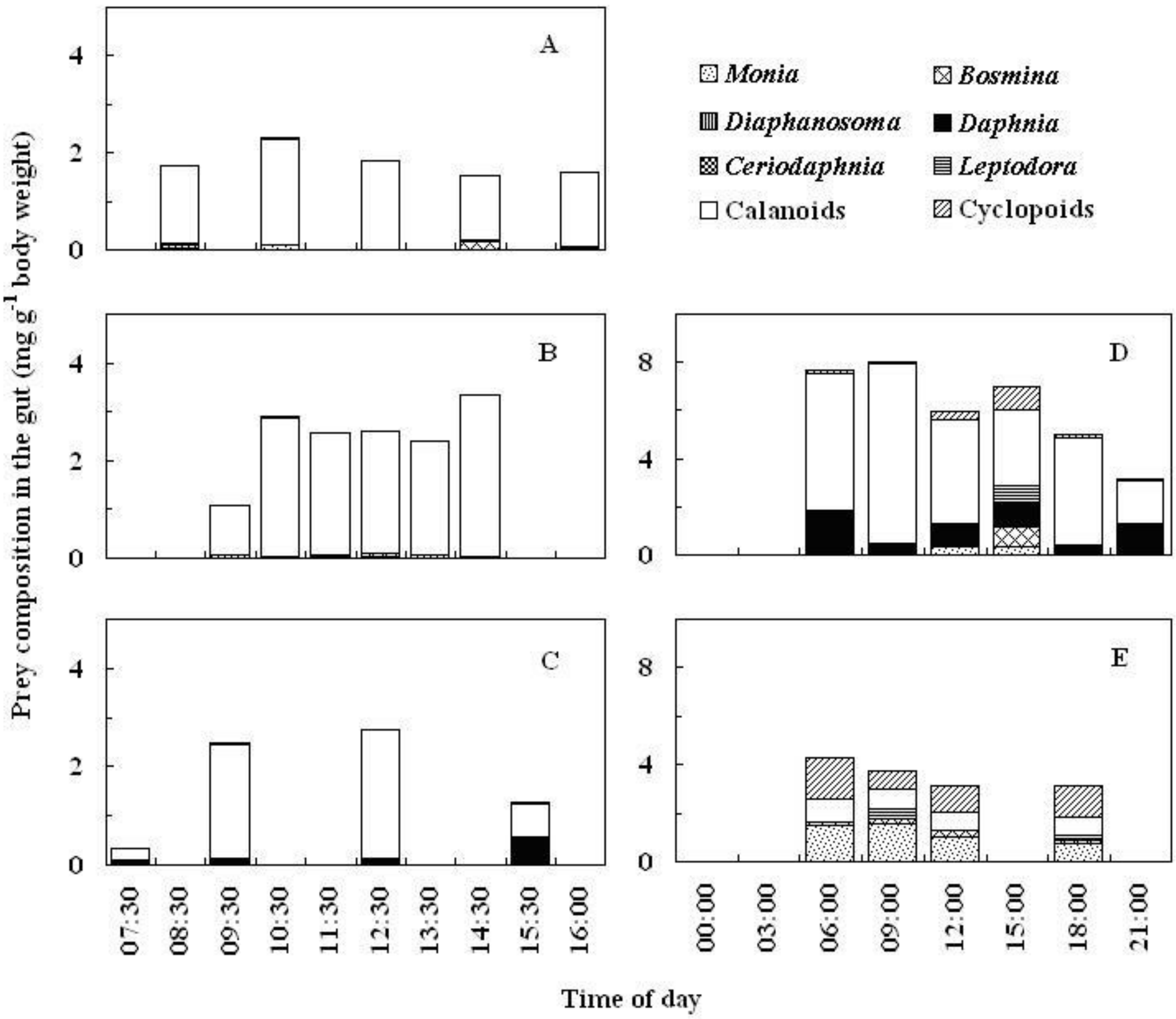

Figure 6: Variation in the frequency of occurrence of prey and percentage composition of prey weight in the diets of various sized icefish in the spring of 2003. The fish were divided into seven size groups: I (20-29 mm), II (30-39 mm), III (40-49 mm), IV (50-59 mm), V (60-69 mm), VI (70-79 mm), and VII (80-89 mm).

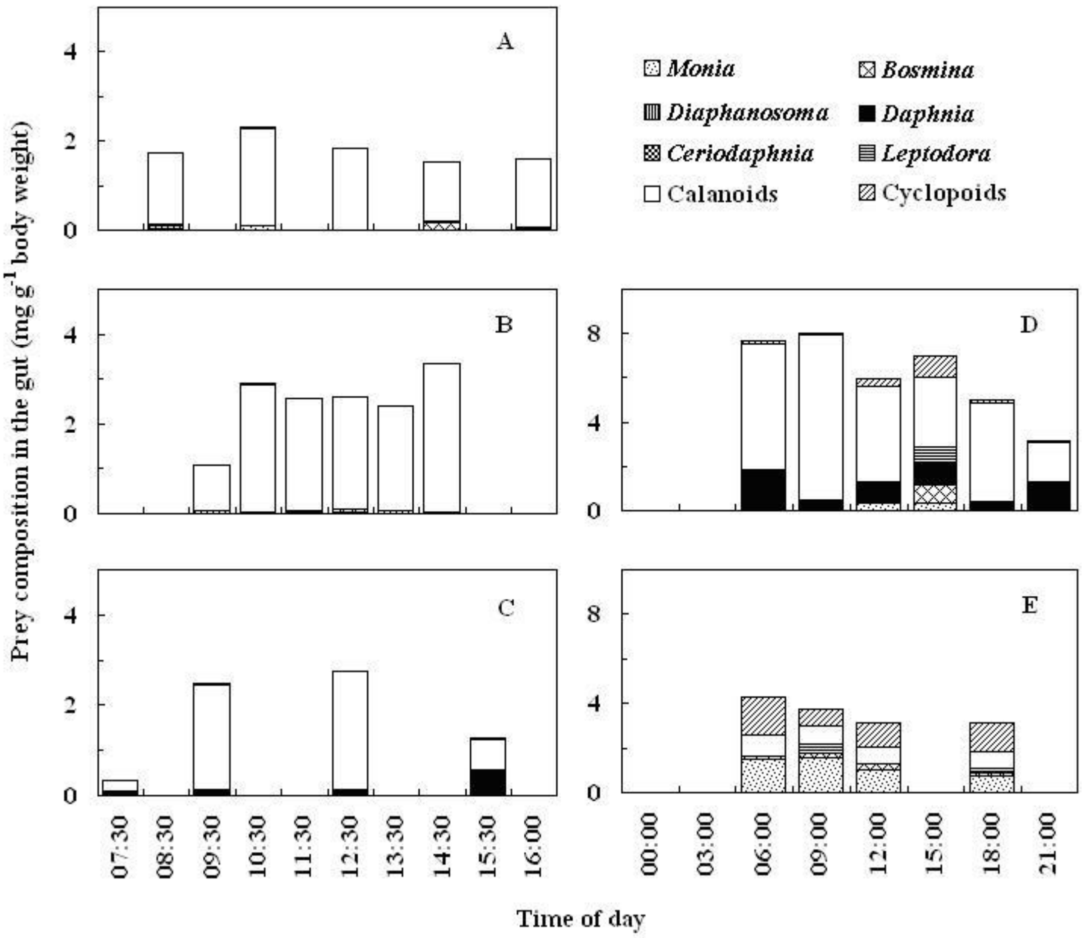

Figure 7: Variation of prey related to sex in the diet of icefish in the spring of 2003.

Prey selection

In general, icefish preferred calanoids to other groups during the study period (one-way ANOVA, $P < 0.01$) (Table 2). *Moina* were preferentially selected during the summer, while *Daphnia* were preferentially selected in winter. There was a weak selection for *Leptodora* and cyclopoids in spring. The icefish preferentially selected for calanoids in the autumn, but showed negative selection for this group in the summer (Tukey's HSD test, $P < 0.01$). Neither *Bosmina* nor *Ceriodaphnia* was selected by the icefish, although they were the dominant species in the lake during the study period.

Table 2: Seasonal variation in Chesson's index (α) of the major prey categories of icefish during the early autumn of 2002 and summer of 2003. An α value of 0.125 indicates random feeding, and "–" indicate that no individual of a particular prey item was found in the diet.

Season	*Moina*	*Bosmina*	*Daphnia*	*Leptodora*	*Ceriodaphnia*	Calanoids	Cyclopoids
Autumn (E)	0.018	0.001	-	-	0.034	0.891	0.055
Autumn (L)	0.047	0.005	-	-	0.001	0.94	0.008
Winter	-	0.026	0.633	-	-	0.356	0.002
Spring	0.283	0.009	0.039	0.221	-	0.293	0.260
Summer	0.878	0.005	-	0.021	-	0.031	0.022

Discussion

The results of the current study indicate that icefish showed a large increase in body length during spring and autumn, but was delayed in summer. A delay in the growth rate of icefish during summer has also been reported at Lake Wanghu, and was attributed to inhibition caused by high temperatures, as icefish are originally sub-cold water fish (Yin et al., 1997). At Lake Chaohu, heavy toxic cyanobacteria blooms occurred in the summer, which may also be an important factor in delaying the growth of the icefish, since high microsystin contents were detected in the fish tissues from the lake (Xie et al., 2005). In addition, the scarcity of preferred prey items (*e.g.* larger cladocerans and calanoids) (Deng, 2004) during summer may also contribute to the reduction in growth rates during this period.

Visual foraging is an effective strategy in limnetic systems, because vision provides a greater search volume and offers more precise orientation to prey than other sensory systems (Guthrie and Muntz, 1993; Gerking, 1994; Wootton, 1998). It is known that particulate feeding is dependent on light intensity, and that many particulate feeders stop feeding after sunset when natural light intensity is almost zero (Lazzaro, 1987). The present study is the first to report the presence of a diel feeding rhythm in icefish. Our results indicate that icefish are visual particulate feeders that primarily forage during the daytime. Although crepuscular (dawn and dusk) feeding was also recorded, all activity stopped at night. Many studies have also examined visual feeding by zooplanktivores, and have obtained similar results (Vinyard and O'Brien, 1976; Confer et al., 1978; Wright and O'Brien, 1984; Henderson and Northcote, 1985). Particulate-feeding planktivorous fishes exhibit high selection of individual food items (Lazzaro, 1987). The present results indicate that, the icefish of Lake Chaohu showed a stronger selection for calanoids than for cyclopoids. Similar results have also been reported from other water bodies (Liu and Zhu, 1994; Gong et al., 1999; He et al., 2001; Liu, 2001). In the present study, icefish showed low selectivity for the small-sized *Bosmina*, which supports previous studies (Liu and Zhu, 1994; Liu, 2001). The low selection of the icefish on *Ceriodaphnia* in the present study is similar to the results found at Lake Dianchi (Liu and Zhu, 1994). However, in the current study, the icefish were in general highly selective for larger the cladocerans *Moina*, *Daphnia* and *Leptodora*. There are also reports that icefish strongly select for *Diaphanosoma*, *Daphnia* and *Leptodora* in Xujiahe reservoir of China (Liu, 2001; Liu and Hu, 2001), and for *Diaphanosoma* and *Daphnia* in Lake Dianchi (Liu and Zhu, 1994). Prey abundance does not seem to be a determinant factor for prey selection by icefish. For example, while *Bosmina* were the most dominant crustacean zooplankton in the present study, icefish showed a low selection for this group throughout the seasons. In addition, Liu and Zhu (1994) also reported a similar phenomenon at Lake Dianchi. Gill (2003) reported that there is no variation in the time cost of smaller prey, but that they are generally of a lower profitability value to fish. Accordingly, the optimal foraging theory assumes that fish should aim to maximize their benefits and minimize costs during feeding activities. The results of the present study indicate that icefish probably use this prey selection strategy, due to the size of available prey in the lake environment.

Most ontogenetic changes probably reflect changes in morphology and maturation (*e.g.* mouth size) (Gerking, 1994; Wootton, 1998; Anastácio et al., 2011). The present study indicates that the food selection of icefish is dependent on individual fish size and the size of their prey. For example, larger icefish selected more large-sized cladocerans *(e.g. Daphnia*) than smaller icefish. Nevertheless, at Lake Dianchi, a calanoid, *Diaptomus*, comprised over 95% of the icefish diet, with the total body length of fish ranging from 21 to 70 mm (Liu and Zhu, 1994). In our study, *Daphnia* and *Leptodora* were only predated by icefish larger than 40 mm and 80 mm, respectively. He et al. (2001) reported that the mouth width of icefish increased from 1.55 mm at a body length of 20.7 mm to 2.32 mm at a body length of 41.32 mm, and to 2.85 mm at a body length of 62 mm. You et al. (1999) also reported that the crevice of the gill rake in *N. taihuensis* varied from 0 to 138.9 µm, and that icefish of 37.8 mm in body length can filter prey of about 100µm in size, while larger prey items of 173 µm could be filtered by fish of 75 mm body length. These observations implied that the diet shift of icefish in our study lake generally reflects the structural change of their mouths, which suggests that the capture efficiency of icefish improves with increasing fish size, which supports previous studies. For example, Wanzenböch (1992) concluded that the capture efficiency of three larval and juvenile fish (roach, bleak and blue bream) for cyclopoids increased with the increasing fish size. In addition, Hambright & Hall (1992) found that the ingestion rate of pumpkin seeds by copepods increased with fish size.

Moreover, there was no difference in the prey composition between male and female icefish during the study period (Fig. 7). Wang (1996) reported an almost complete cessation in growth of *N. pseudotaihuensis* due to gonad development and spawning from December to March of the following year in a reservoir, but provided no information on feeding behavior. At Lake Chaohu, two spawning colonies were found in the spring and early autumn, respectively (Diao, 1986), with spawning colonies mainly forming in early summer during the study period. The results indicate that the changes in maturation of icefish do not seem to affect feeding activities in the spring. The reason for this in part may be due to the formation of algal blooms in the warm season of each year.

In conclusion, the results of the present study, showing the diel feeding rhythm in icefish, indicates that they are visual particulate feeders, with no difference in prey selection between males and females in shallow eutrophic lakes. Both the present and previous studies indicate that 1) there are large seasonal variations in the diet composition of icefish, and in the selection indices of certain prey by icefish, which probably occurs as a result of variable zooplankton abundance in Lake Chaohu during the study period, 2) in general, icefish preferentially feed on calanoids than on cyclopoids, and that they feed more on larger cladocerans (*e. g. Daphnia*, *Leptodora*, *Moina*, *Diaphanosoma*) than smaller cladocerans (*e. g. Bosmina*, *Ceriodaphnia*), and 3) prey selection is also dependent on the body length of icefish. Nevertheless, the information provided by the current study confirming both diel and seasonal rhythms in food consumption by icefish provides a baseline from which to determine their predation pressure on zooplankton and other ecosystem communities in the subtropical shallow eutrophic lake.

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