

Impact of environmental and innate factors on the food habit of Chinese perch *Siniperca chuatsi* (Basilewsky) (Percichthyidae)

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Abstract

Laboratory and field investigations were conducted to study the food habit of Chinese perch *Siniperca chuatsi* (Basilewsky) from first feeding through adult stage. Only fish larvae were consumed by Chinese perch larvae (2–21 days from hatching), and the presence of zooplankton did not have any significant effect on their survival rate. The ability of Chinese perch to feed on zooplankton is clearly limited by some innate factor. Instead of gill rakers, Chinese perch larvae have well-developed sharp teeth at the first feeding stage, and are well adapted to the piscivorous feeding habit unique to the larvae of Chinese perch, e.g. they bite and ingest the tails of other fish larvae. At the first feeding stage (2 days from hatching), daily rations were both very low, either in light or complete darkness. Although early-staged Chinese perch larvae (7–17 days from hatching) could feed in complete darkness, their daily rations were always significantly higher in light than in complete darkness. Late-staged Chinese perch larvae (21 days from hatching) were able to feed in complete darkness as well as in light, similar to the case of Chinese perch yearlings. Chinese perch yearlings (total length, 14–16 cm) consumed prey fish only and refused shrimp when visual cues were available (in light), but they consumed both prey when visual cues were not available (in complete darkness), suggesting that prey consumption by Chinese perch yearlings is affected by their sensory modality in predation. Both prey were found in the stomachs of similar-sized Chinese perch (total length, 14–32 cm) from their natural habitat, suggesting that shrimp are consumed by

Chinese perch at night. Prey selection of Chinese perch with a length >38 cm, which consumed only fish in the field, appears to be based upon prey size instead of prey type. These results suggest that although environmental factors (e.g. light intensity) affect prey detection by Chinese perch, this fish is anatomically and behaviourally predisposed to prey on live fish from first feeding. This makes it a difficult fish to cultivate using conventional feeds.

Keywords: *Siniperca chuatsi*, food habit, first feeding, sensory modality, feeding organ, carnivorous fish

Introduction

Food habits can develop with learning experience (Brown 1985; Warburton 2003). Although environmental factor is probably a large component of the behavioural change seen with learning experience, the impact of predisposed factor must also be considered (Montgomery & Sutherland 1997; Poling & Fuiman 1997; Carvalho, Noltie & Tillitt 2004; Jackson, Rundle, Attrill & Cotton 2004; Peña, Dumas, Saldivar-Lucio, García, Trasviña, Hernández-Ceballos 2004; Snickars, Sandström & Mattila 2004; Stoner 2004; Carton 2005; Hara 2006). In contrast with learning experience, unlearned predispositions should be extremely important to the formation of the species-specific food habit of different fish.

Chinese perch *Siniperca chuatsi* (Basilewsky) (Percichthyidae) or mandarin fish is one of the most valuable food fish native to the freshwaters of China

and the River Amur along the Russian borderlands. Because of water pollution and overfishing, the natural resources of Chinese perch have been depleted. Chinese perch has great aquaculture potential due to its large size, rapid growth and delicious flesh. Artificial reproduction, fry and fingerling rearing and commercial fish culture of Chinese perch have been successful both in China and in Russia (Jia, Wang, Song, Song & Zhou 1974; Xiao & Wang 1983; Strebkova & Shabalina 1984). Chinese perch have been acclimatized and cultivated in brackish water with salinity below 1.4‰, and were found to grow faster than striped bass *Morone saxatilis* Walbaum in the same pond (Strebkova & Shabalina 1984).

However, Chinese perch have very peculiar food habits. In its natural habitat, the Chinese perch is an absolute carnivore (consuming both fish and shrimp), and was found to capture live fry of other fish species from the first feeding stages (Chiang 1959). Under cultivation conditions, Chinese perch were found to consume live prey fish only and refuse shrimp, dead fish or artificial diets. Live fry and fingerlings of other farmed fish are used as the sole source of food in intensive culture of Chinese perch. Problems with a large stable supply of live prey fish, essential for commercial Chinese perch production, currently present a bottleneck to mass culture (Liang, Oku, Ogata, Liu & He 2001).

A collaborative research project between China and the United States aimed at training Chinese perch to accept artificial diets (Wu & Hardy 1988) first demonstrated the apparent absolute carnivorous nature of this fish. Since then, a series of studies have been conducted on the sensory basis and feeding behaviour of Chinese perch to elucidate the main reasons for the fish refusing artificial diets (Wu & Hardy 1988; Liang 1994; Liang, Zeng & Wang 1994; Liang 1996a, b; Liang, Liu & Huang 1998). Based on the first work of Wu and Hardy (1988), a specific training procedure was designed to wean Chinese perch onto artificial diets successfully in small net cages (Liang *et al.* 2001), but this method cannot work in pond culture of Chinese perch, which is the major cultivation form for the commercial production of this fish. The present study was conducted to elucidate the impact of environmental and innate factors on the food habit of Chinese perch through laboratory investigations on food consumption of Chinese perch larvae and yearlings fed with only one potential prey type (pond zooplankton, shrimp or fish) under a light or a dark condition, as well as field investigations in their natural habitat.

Materials and methods

Source and acclimatization of fish

Newly hatched larvae of Chinese perch were obtained from the Guangdong Mandarin Fish Farm (Nanhai, Guangdong Province, China). They were produced by artificial propagation using broodstock from the Yangtze River (Qianjiang, Hubei Province, China). Ten larvae were kept in a 1000 mL beaker, containing 500 mL of aerated dechlorinated tap water. The water temperature ranged from 25 to 26 °C. The photoperiod was 12L:12D. Lighting was provided by fluorescent lights. The fish were acclimatized to the laboratory conditions for 1–2 days before the start of the experiment. During acclimatization, the Chinese perch larvae were fed twice daily with an excess of live newly hatched larvae of mud carp *Cirrhina molitorella* (Cuvier and Valenciennes) when they were over 3 days from hatching.

Yearlings of Chinese perch were caught by seining in the Yangtze River at Jinkou, Hubei Province, China. They were held in concrete indoor pools. Each pool had several stones on the bottom to form crevices for the fish to use as refuges. The water temperature ranged from 23 to 26 °C. The photoperiod was 12L:12D. Lighting was provided by fluorescent lights. The fish were acclimatized to the laboratory conditions for a month before the start of the experiment. During acclimatization, they were fed once daily with an excess of live minnow *Pseudorasbora parva* (Temminck and Schlegel).

Feeding experiments on Chinese perch larvae

In experiment 1, Chinese perch larvae without feeding experience (3 days from hatching) were divided into three groups. Ten larvae were kept in a 1000 mL beaker as described before, and six beakers were assigned to each group. The three groups were fed with live newly hatched mud carp larvae, zooplanktons and no food (control) respectively. The zooplanktons were obtained from a pond in Jinan University (Guangzhou, Guangdong Province, China), and were used in the experiments at once. The composition of the zooplanktons was 50% cladocera, mainly *Diaphanosoma brachyurum* (Liéven), 40% copepod, mainly *Thermocyclops taihokuensis* Harada, 3% rotifer and 7% other planktons. After 3 days, the survival rate for each beaker was determined. Data of six beakers were used as replicates for statistical analysis ($N = 6$). There were 12 other beakers (containing 120 Chinese perch larvae)

assigned to the zooplankton group, and 40 Chinese perch larvae (from four beakers) were sampled and preserved in 7% formalin each day during the 3-day experiment. The stomach contents of the Chinese perch larvae were then examined under a dissecting microscope (Olympus SZX7, Tokyo, Japan).

In experiment 2, 10 larvae of the same developmental stage (2, 7, 12 or 17 days from hatching) were kept in a 1000 mL beaker. The 2-day Chinese perch larvae had no feeding experience. 7-, 12- and 17-day Chinese larvae were reared as described in the previous acclimatization section, and were starved for 24 h before being used in the experiment. They were fed with live mud carp larvae of suitable size. Six beakers of Chinese perch larvae at each developmental stage (2, 7, 12 or 17 days from hatching) were placed indoor under an illumination of about 200 lx (197–220 lx), and six other beakers of Chinese perch larvae at the same stage were placed in complete darkness. The feeding experiment was terminated after 20 h for the 2-day Chinese perch larvae, and after 5 h for other larvae by adding formalin in each beaker at a final concentration of 7%. The number of prey fish eaten was counted for each beaker, and the daily ration of Chinese perch larvae at the four different stages under either a light or a dark condition was then calculated. Data of six beakers were used as replicates for statistical analysis ($N = 6$).

Experiment 3 was a repeat of experiment 2, except that 2-, 7-, 8-, 9-, 12- and 21-day Chinese perch larvae (a batch different from that used in experiment 2) were tested for daily food intake under light or dark conditions, and that silver carp *Hypophthalmichthys molitrix* (Cuvier and Valenciennes) larvae were used as prey.

Feeding experiments on Chinese perch yearlings

In experiment 4, eight tanks were divided into two groups. Four tanks of Chinese perch yearlings were placed indoor under an illumination of about 30–50 lx (provided by artificial light), and four other tanks of Chinese perch yearlings were placed in complete darkness. Two uniform-sized yearlings of Chinese perch (total length, 14–16 cm) were placed in each of the eight tanks. Each tank ($58 \times 43 \times 43$ cm) contained 82.3 L of dechlorinated fresh-water, and had six dark plastic holes on the bottom for the fish to use as refuges. The tank was provided with flow-through dechlorinated tap water, and four-fifths of the water was replenished every

day. Aeration was provided and the oxygen content was maintained at more than 5 mg L^{-1} . The water temperature ranged from 20.0 to 22.5 °C. The experimental fish were acclimatized in the tank for a week before the start of the experiment. During acclimatization, they were fed once daily as described previously. During the experiment, 10 live minnow *P. parva* and ten oriental river prawn *Macrobrachium nipponense* of the same length (total length, 2.5–3.0 cm) were simultaneously placed in each of the eight tanks daily in the morning. The number of minnow or oriental river prawn eaten was counted at the same time (08:30 hours) the following day, and the number of minnow or oriental river prawn eaten was then added to each tank. The daily ration in prey (minnow or oriental river prawn) number was calculated for each tank as daily ration = prey number of initial day – that of the next day/Chinese perch number. The experiment lasted for 18 days. The daily ration was the number of prey eaten per Chinese perch per day averaged for all 18 days in each tank. Data of four tanks were used as replicates for statistical analysis ($N = 4$).

Stomach content examination of Chinese perch in the field

A total of 67 specimens of Chinese perch larvae (total length, 5.5–7.0 mm) were collected with larva nets at Jinkou (Hubei Province, China) in the spawning season of Chinese perch (late May to early July 1990). The stomach content examination of the Chinese perch larvae was performed as described previously in experiment 1.

A total of 217 specimens of Chinese perch (total length, 14–62.5 cm) were caught by seining or electrofishing in Fuqiaohe Reservoir (Hubei Province, China) at night between 14 February 1993 and 13 July 1994. The stomachs were immediately dissected and fixed with 10% buffered formalin. The prey items were carefully separated, and identified to the lowest possible taxonomic level. Fish digested beyond visual recognition were counted as unidentified fish. Prey item species and individuals of each taxon were counted for each of the 217 specimens. The total number of each prey species in the stomach of the 217 specimens sampled was calculated as food item amount (if a prey species had more than one individual in the stomach of the same specimen, the number of prey species was counted as the real number in this specimen), or as food item occurrence (if a prey species had more than one individual in the

stomach of the same specimen, the number of the prey species was counted as one).

Statistical analysis

Data were subjected to one-way analysis of variance. Fisher’s Protected Least Significant Difference (STATVIEW 4.51, Abacus Concepts, Berkeley, CA, USA) was used to identify differences among means at $P < 0.05$. Percentage data were arcsin transformed before analysis. Data are reported as mean values \pm SEM.

Results

Feeding experiments on Chinese perch larvae

The most prominent morphological feature of the Chinese perch larva was its well-developed teeth, appearing at the first feeding stage (2–3 days from hatching, dependent on the hatching temperature of the embryo). The first feeding Chinese perch larvae were found to feed on the larvae of other fish by biting at the tail first, swallowing the live prey from the tail gradually and finally ingesting the tail by cutting it with its sharp teeth from the rest of the prey body.

In experiment 1, when the Chinese perch larvae (3 days from hatching) were fed with newly hatched mud carp larvae, the survival rate of Chinese perch larvae was 74.5% (Table 1). Chinese perch larvae fed with newly hatched larvae of silver carp or grass carp showed a similar survival rate (data not shown). However, all the larvae died within 3 days (on the sixth day from hatching) when they were fed with pond zooplanktons. This was similar to the case of Chinese perch larvae fed no food (control). Gut content examination of Chinese perch larvae fed with pond zooplankton revealed that only one out of the 120 Chinese perch larvae dissected contained a copepod *T. taihokuensis* Harada in the stomach.

Table 1 Survival rate* of Chinese perch larvae (3 days from hatching) fed two different live foods for 3 days in experiment 1

Food type	Survival rate (%)
Newly hatched mud carp larvae	0.746 \pm 0.08 ^a
Pond zooplanktons	0 \pm 0 ^b
Control (no food)	0 \pm 0 ^b

*Values with the same superscript are not significantly different from each other at the 0.05 level.

In experiments 2 and 3, the effect of illumination and darkness was tested using two different batches of Chinese perch larvae, and is shown in Figs 1 and 2. At the first feeding stage (2 days from hatching), daily rations of the two batches were both very low, either in light or in complete darkness. With the development of the Chinese perch larvae (7–17 days from hatching, Batches 1 and 2), the daily rations of the larvae in complete darkness increased steadily, but the daily rations in light were always significantly higher than those in complete darkness in both experiments 1 and 2 (Fig. 2). In experiment 2, when more developed Chinese perch larvae (21 days from hatching, Batch 2) were further tested, these Chinese perch larvae did not show a significant difference between daily rations in light and in complete darkness (Fig. 2).

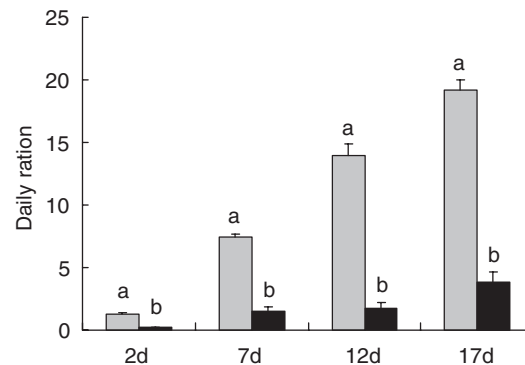


Figure 1 Effect of illumination (200 lx, grey column) and darkness (black column) on the daily ration (number of prey fish eaten per day) of Chinese perch larvae (2–17 days from hatching) fed mud carp larvae in experiment 2.

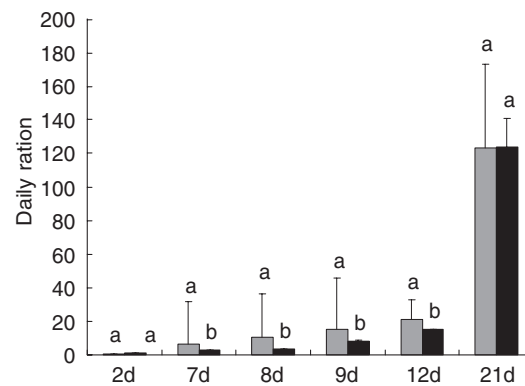


Figure 2 Effect of illumination (200 lx, grey column) and darkness (black column) on the daily ration (number of prey fish eaten per day) of Chinese perch larvae (2–21 days from hatching) fed silver carp larvae in experiment 3.

Feeding experiments on Chinese perch yearlings

In experiment 4, when visual cues were available (in light), Chinese perch yearlings (total length, 14–16 cm) consumed prey fish only and refused shrimp, but when visual cues were not available (in complete darkness), they consumed both prey (Table 2).

Stomach content examination of Chinese perch in the field

During the spawning season of Chinese perch on the flood land of the Yangtze River at Jinkou (Hubei Province, China), Chinese perch larvae were found at the

Table 2 Prey consumption* by Chinese perch (total length, 14–16 cm) fed two kinds of prey (fish or shrimp with a total length of 3.0–3.5 cm) for 18 days in experiment 4

Prey type	Daily ration (number of prey eaten per day)	
	In light	In complete darkness
Fish	2.57 ± 0.11 ^a	2.35 ± 0.24 ^a
Shrimp	0 ± 0 ^b	0.67 ± 0.34 ^c

*Values with the same superscript are not significantly different from each other at the 0.05 level.

water surface, chasing after and attacking the larvae of major cultivated Chinese carps, e.g. silver carp and grass carp. However, from 67 specimens collected, no intact food items could be identified in the stomach of the Chinese perch larvae (total length, 5.5–7.0 mm).

The stomach food content of a total of 217 specimens of Chinese perch (total length, 14–62.5 cm) is shown in Table 3. From 217 specimens examined, 134 (61.75%) had food in their stomachs. A total of 296 prey items belonging to two groups (fish and shrimp) were identified. The diet of Chinese perch consisted of at least 18 different species. Fish were the most important prey by amount (62.5%) and occurrence (73.3%). Among the fishes, bighead carp *Aristichthys nobilis* (Richardson) and silver carp made an important contribution to the diet, followed by barcheek goby *Ctenogobius giurinus* (Rutter), bitterling *Rhodeus sinensis* Günther, crucian carp *Carassius auratus* (Linnaeus), grass carp *Ctenopharyngodon idellus* (Cuvier and Valenciennes), black carp *Mylopharyngodon piceus* (Richardson), spiny bitterling *Acanthorhodeus chankaensis* (Dybowsky), thin sharpbelly *Toxabramis swinhonis* Günther, bluntnose bream *Megalobrama amblycephala* Yih, sharpbelly *Hemiculter leucisclus* (Basilewsky) and redbfin culter *Culter alburnus* Basilewsky. The frequency of occurrence of other fish items did not exceed 3.0%. The composition of fish species in the stomach of Chinese

Table 3 Stomach food contents of 217 Chinese perch (total length, 14–62.5 cm) in Fuqiaohe Reservoir (Hubei, China)

Species (Family)	Food item amount		Food item occurrence	
	Number	%	Number	%
Bighead <i>Aristichthys nobilis</i> (Richardson) (Cyprinidae)	63	21.3	31	17.6
Silver carp <i>Hypophthalmichthys molitrix</i> (Cuvier and Valenciennes) (Cyprinidae)	42	14.2	37	21.0
Barcheek goby <i>Ctenogobius giurinus</i> (Rutter) (Gobiidae)	10	3.4	8	4.5
Bitterling <i>Rhodeus sinensis</i> Günther (Cyprinidae)	6	2	4	2.3
Crucian carp <i>Carassius auratus</i> (Linnaeus) (Cyprinidae)	5	1.7	5	2.8
Grass carp <i>Ctenopharyngodon idellus</i> (Cuvier and Valenciennes) (Cyprinidae)	5	1.7	2	1.1
Black carp <i>Mylopharyngodon piceus</i> (Richardson) (Cyprinidae)	4	1.4	4	2.3
Spiny bitterling <i>Acanthorhodeus chankaensis</i> (Dybowsky) (Cyprinidae)	4	1.4	3	1.7
Thin sharpbelly <i>Toxabramis swinhonis</i> Günther (Cyprinidae)	4	1.4	2	1.1
Bluntnose bream <i>Megalobrama amblycephala</i> Yih (Cyprinidae)	2	0.7	2	1.1
Sharpbelly <i>Hemiculter leucisclus</i> (Basilewsky) (Cyprinidae)	2	0.7	1	0.6
Redfin culter <i>Culter alburnus</i> Basilewsky (Cyprinidae)	2	0.7	2	1.1
Minnow <i>Pseudorasbora parva</i> (Temminck and Schlegel) (Cyprinidae)	1	0.3	1	0.6
Spotted steed <i>Hemibarbus maculatus</i> Bleeker (Cyprinidae)	1	0.3	1	0.6
Spiny eel <i>Mastacembelus aculeatus</i> (Basilewsky) (Mastacembelidae)	1	0.3	1	0.6
Northern snakehead <i>Channa argus</i> (Cantor) (Channidae)	1	0.3	1	0.6
Dark sleeper <i>Odontobutis obscura</i> (Temminck and Schlegel) (Eleotridae)	1	0.3	1	0.6
Unidentified fish	31	10.5	23	13.1
Rice shrimp <i>Neocaridina denticulata</i> (Kemp) (Atyidae)	111	37.5	47	26.7
Total	296	100	176	100

Table 4 Stomach prey type (fish or shrimp) and total length of Chinese perch in Fugiaohe Reservoir (Hubei, China)

Stomach prey type	Chinese perch number	%	Total length of Chinese perch (cm)
Only fish	87	40.09	24–62.5
Only shrimp	30	13.82	17–38
Both fish and shrimp	17	7.83	14–32
No food	83	38.25	18.5–59
Total	217	100	14–62.5

perch was almost the same as that in the reservoir, indicating that Chinese perch do not show a strict selection on fish species. Rice shrimp *Neocaridina denticulata* (Kemp) was the second most important prey group by amount (37.5%) and occurrence (26.7%).

The relationship of stomach prey type and Chinese perch length is shown in Table 4. Among the 134 Chinese perch with food in the stomach, 87 Chinese perch (total length, 24–62 cm) consumed only prey fish, 17 Chinese perch (total length, 14–32 cm) consumed both prey fish and shrimp and the other 30 Chinese perch (total length, 17–38 cm) consumed only shrimp. From the results, it was deduced that larger Chinese perch with a length more than 38 cm were not found to consume any shrimp, and smaller Chinese perch with a length less than 38 cm did not show a strict selection on prey type (fish or shrimp).

Discussion

In the present study, the size of zooplankton appears to be suitable to be captured by newly hatched Chinese perch larvae. Newly hatched Chinese perch larvae were found to respond to nearby zooplanktons by approaching and biting at them. This was similar to the feeding behaviour elicited by prey fish larvae. With the development of Chinese perch larvae, this behaviour towards zooplankton became less frequent. Meanwhile, gut content examination and survival rate results showed that zooplanktons were not consumed by Chinese perch larvae. Apparently, with learning experience during development, Chinese perch larvae gradually knew how to recognize and capture their preferred prey, other fish larvae rather than zooplankton. Although the learning process appeared to be similar to the case of other fish larvae that consume zooplankton (Brown 1985; Noakes & Godin 1988; Warburton 2003), the learning ability of

Chinese perch larvae to feed on zooplanktons was clearly limited by some predisposed factor.

One such predisposed factor could be the specific developmental mode of feeding organs (gill rakers and teeth) in this fish. Usually at the first feeding stage, other fish larvae feed on zooplanktons of suitable size when they have several gill rakers developed. These gill rakers are important for the larval fish to consume zooplankton prey and they appeared in all the first-feeding larvae studied, e.g. eight gill rakers in Nile tilapia *Oreochromis niloticus* (Linnaeus) (Hu & Zhang 1983), five gill rakers in blunt snout bream *M. amblycephala* Yih (Meng & Tang 1986), four to nine gill rakers in bighead carp *A. nobilis* (Richardson) (Liu, Chui, Li, Sun & Zhu 1992) and four to eight gill rakers in silver carp *H. molitrix* (Cuvier and Valenciennes) (Liu, Li, Li & Zhu 1993). However, no gill rakers were found in Chinese perch larvae until this fish reached a total length of 9.4 mm (Tang & Fan 1993). Instead of gill rakers, Chinese perch larvae had well-developed sharp teeth at the first feeding stage. This adapts well to the piscivorous feeding habit unique to the larvae of Chinese perch, which bite and ingest the tails of other fish larvae using these sharp teeth. This is also the likely reason why no intact food items could be identified in the stomach of the wild Chinese perch larvae from the Yangtze River in the present study.

The present study shows that with the development of Chinese perch larvae, daily rations of the larvae in complete darkness increased steadily, indicating that the non-visual sense must have developed quickly during this developmental stage. In addition, late-staged Chinese perch larvae (21 days from hatching) were found to be able to feed in complete darkness as well as in light, suggesting that their non-visual sense is already well developed and had the same important role as vision at this stage. These results are consistent with results of previous studies on the sensory basis of feeding behaviour in Chinese perch yearlings, which demonstrated the importance of vision and lateral-line mechanoreception for Chinese perch to capture prey (Liang *et al.* 1998; Wu & Hardy 1988). This specific developmental mode of the sensory modality in the feeding behaviour of Chinese perch larvae contrasts with the case of zooplanktivorous fish larvae, for these larvae cannot feed in complete darkness (Noakes & Godin 1988). Furthermore, it is known that only certain fish species with a well-developed lateral-line system can feed on live prey in complete darkness via lateral-line mechanoreception after the larval stage (Appelbaum

& Schemmel 1983; Janssen, Jones, Whang & Oshel 1995; Janssen 1996; Janssen, Sideleva & Biga 1999; New & Kang 2000; New, Fewkes & Khan 2001). The importance of lateral-line mechanoreception for Chinese perch larvae to capture prey can be well explained by its peculiar hunting strategy. Because the tail of prey fish larvae is the major source of vibration among the whole body, Chinese perch larvae can capture the tail of other fish larvae through the perception of mechanical information.

As shown by the present study, the optimal prey for Chinese perch yearlings is fish, and shrimp were captured only in complete darkness when visual cues of prey were not available, suggesting that the food preference of Chinese perch yearlings was affected by the sensory modality in predation, and that shrimps are likely consumed by Chinese perch in Fuqiaohe Reservoir at night when vision is inhibited or visual acuity is extremely low. Larger Chinese perch (with a total length more than 38 cm) in this reservoir were found to consume only fish, but considering the relative size of the larger Chinese perch and the shrimp (mainly rice shrimp with a total length less than 3 cm), this selection may be based on prey size rather than prey type.

In conclusion, light intensity considerably affects prey detection in early-staged larvae and yearlings of Chinese perch; however, the peculiar food preference of Chinese perch is due to innate or predisposed behaviour, as well as the specific developmental mode of feeding organs (e.g. gill rakers and teeth), which will eventually determine prey availability. These results suggest that although environmental factors (e.g. light intensity) affect prey detection by Chinese perch, this fish is anatomically and behaviourally predisposed to prey on live fish from first feeding. This makes it a difficult fish to cultivate using conventional feeds.

Acknowledgments

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References

- Appelbaum S. & Schemmel C. (1983) Dermal sense organs and their significance in the feeding behavior of the common sole *Solea vulgaris*. *Marine Ecology* **13**, 29–36.
- Brown J.A. (1985) The adaptive significance of behavioural ontogeny in some centrarchid fishes. *Environmental Biology of Fishes* **13**, 25–34.
- Carton A.G. (2005) The impact of light intensity and algal-induced turbidity on first-feeding *Seriola lalandi* larvae. *Aquaculture Research* **36**, 1588–1594.
- Carvalho P.S.M., Noltie D.B. & Tillitt D.E. (2004) Biochemical, histological and behavioural aspects of visual function during early development of rainbow trout. *Journal of Fish Biology* **64**, 833–850.
- Chiang I.K. (1959) On the biology of mandarin fish, *Siniperca chuatsi* of Liang-Tze Lake. *Acta Hydrobiologica Sinica* **3**, 375–385.
- Hara T.J. (2006) Feeding behaviour in some teleosts is triggered by single amino acids primarily through olfaction. *Journal of Fish Biology* **68**, 810–825.
- Hu M. & Zhang Z. (1983) A study on the development of digestive system and feeding habit of fry and juvenile of *Tilapia nilotica*. *Journal of Fisheries of China* **7**, 207–217.
- Jackson A.C., Rundle S.D., Attrill M.J. & Cotton P.A. (2004) Ontogenetic changes in metabolism may determine diet shifts for a sit-and-wait predator. *Journal of Animal Ecology* **73**, 536–545.
- Janssen J. (1996) Use of the lateral line and tactile senses in feeding in four antarctic nototheniid fishes. *Environmental Biology of Fishes* **47**, 51–64.
- Janssen J., Jones W.R., Whang A. & Oshel P.E. (1995) Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 358–363.
- Janssen J., Sideleva V. & Biga H. (1999) Use of lateral line for feeding in two Lake Baikal sculpins. *Journal of Fish Biology* **54**, 404–416.
- Jia C.C., Wang H.Q., Song Z.L., Song R.X. & Zhou Y.C. (1974) Artificial propagation of Chinese perch. *Fisheries Science and Technology Information* **2**, 12–17.
- Liang X.F. (1994) Visual characteristics of mandarin fish (*Siniperca chuatsi*) in relation to its feeding habit: II. general properties of the retina. *Acta Hydrobiologica Sinica* **18**, 376–377.
- Liang X.F. (1996a) The structure and behavioral response of lateral line of *Siniperca chuatsi* in relation to its feeding habit. *Oceanologica et Limnologia Sinica* **27**, 457–462.
- Liang X.F. (1996b) Taste buds in the oropharyngeal cavity of mandarin fish (*Siniperca chuatsi*): scanning electron microscopic and behavioural investigations in relation to fish feeding habit. *Acta Zoologica Sinica* **42**, 22–27.
- Liang X.F., Zeng W.Y. & Wang Y.L. (1994) Visual characteristics of mandarin fish (*Siniperca chuatsi*) in relation to its feeding habit: I. Photo-sensitivity and spectral sensitivity

- of electroretinogram. *Acta Hydrobiologica Sinica* **18**, 247–253.
- Liang X.-F., Liu J.-K. & Huang B.Y. (1998) The role of sense organs in the feeding behavior of Chinese perch. *Journal of Fish Biology* **52**, 1058–1067.
- Liang X.F., Oku H., Ogata H.Y., Liu J. & He X. (2001) Weaning Chinese perch *Siniperca chuatsi* (Basilewsky) onto artificial diets based upon its specific sensory modality in feeding. *Aquaculture Research* **36**, 1588–1594.
- Liu H., Chui H., Li L., Sun C. & Zhu W. (1992) A study on the biology of post-larval development of the filtering apparatus in bighead carp (*Aristichthys nobilis*). *Journal of Dalian Fisheries College* **7**, 1–10.
- Liu H., Li M., Li L. & Zhu W. (1993) A study on the biology of post-larval development of the filtering apparatus in silver carp (*Hypophthalmichthys molitrix*). *Journal of Dalian Fisheries College* **8**, 1–19.
- Meng Q. & Tang Y. (1986) Organ development of blunt snout bream. *Journal of Fisheries of China* **10**, 395–407.
- Montgomery J.C. & Sutherland K.B.W. (1997) Sensory development of the Antarctic silverfish *Pleuragramma antarcticum*: a test for the ontogenetic shift hypothesis. *Polar Biology* **18**, 112–115.
- New J.G. & Kang P.Y. (2000) Multimodal sensory integration in the strike-feeding behaviour of predatory fishes. *Philosophical Transactions of the Royal Society London B* **355**, 1321–1324.
- New J.G., Fewkes L.A. & Khan A.N. (2001) Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of the lateral line and visual sensory systems. *The Journal of Experimental Biology* **204**, 1207–1221.
- Noakes D.L.G. & Godin J.-G.J. (1988) Ontogeny of behaviour and concurrent developmental changes in sensory systems in teleost fishes. In: *Fish Physiology, Volume XI The Physiology of Developing Fish, Part B Viviparity and Posthatching Juveniles* (ed. by W.S. Hoar & D.J. Randall), pp. 345–395. Academic Press, New York, NY, USA.
- Peña R., Dumas S., Saldivar-Lucio R., García G., Trasviña A. & Hernández-Ceballos D. (2004) The effect of light intensity on first feeding of the spotted sand bass *Paralabrax maculatofasciatus* (Steindachner) larvae. *Aquaculture Research* **35**, 345–349.
- Poling K.R. & Fuiman L.A. (1997) Sensory development and concurrent behavioural changes in Atlantic croaker larvae. *Journal of Fish Biology* **51**, 402–421.
- Snickars M., Sandström A. & Mattila J. (2004) Antipredator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. *Journal of Fish Biology* **65**, 1604–1613.
- Stoner A.W. (2004) Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology* **65**, 1445–1471.
- Strebkova T.P. & Shabalina V.N. (1984) Farming of Chinese perch. In: *Marine Fish Culture* (ed. by A.F. Karpevich), pp. 41–52. Vniro Publications, Moscow, USSR.
- Tang Y. & Fan E. (1993) A study on the development of digestive organs of *Siniperca chuatsi* (Basilewsky). *Acta Hydrobiologica Sinica* **17**, 329–336.
- Warburton K. (2003) Learning of foraging skills by fish. *Fish and Fisheries* **4**, 203–215.
- Wu Z.L. & Hardy R.W. (1988) A preliminary ethological analysis on the feeding behavior of mandarin fish. *Freshwater Fisheries* **5**, 18–21.
- Xiao Y.X. & Wang X.S. (1983) Artificial propagation and culture of Chinese perch. *Chinese Journal of Zoology* **18**, 14–16.