Indian J. Fish., 69(4): 65-72, 2022
DOI: 10.21077/ijf.2022.69.4.124228-08

Habitat selection behaviour of *Pungitius kaibarae* (Gasterosteidae) in the presence of the visual predator *Anguilla japonica* (Anguillidae)

JEONG-SOO GIM[1], SANG-BIN LEE[2], HYO GYEOM KIM[1], DONG-KYUN KIM[3], SEOK-NAM KWAK[4], GEA-JAE JOO[1] AND HYUNBIN JO[1, 5]
[1]*Department of Integrated Biological Science, Pusan National University, Busan, Republic of Korea*
[2]*Fort Lauderdale Research and Education Center, Entomology and Nematology Department, University of Florida Fort Lauderdale, Florida, United States*
[3]*K-water Research Institute, Daejeon, Republic of Korea*
[4]*Environ-Ecological Engineering Institute Co. Ltd., Busan - 48058, Republic of Korea*
[5]*Institute for Environment and Energy, Pusan National University, Busan, Republic of Korea*
e-mail: kjs1@pusan.ac.kr; 1004kyeom@gmail.com

ABSTRACT

Our study deals with how the short nine-spine stickleback *Pungitius kaibarae* uses visual cues to select among habitats, thereby reducing predation pressure from the Japanese eel *Anguilla japonica*. We examined the behaviour of *P. kaibarae* in selecting four habitats (water weed, sandy, rocky and open water) under the presence/absence of *A. japonica*. Using video tracking technology, we found that in the presence of *A. japonica*, sticklebacks preferred specific refuge patches, such as water weed and rocks, over open water with a sandy bottom. Thus, our investigation demonstrated the importance of habitat structures in evoking escape behaviour. We discuss the importance of this bold behaviour patterns of the prey fish.

Keywords: Bold behaviour, Stickleback, Eel, Swimming speed, Video tracking

Introduction

Habitat selection is a fundamental feature exhibited by animals, but we still do not wholly understand the nature of the evolutionary forces that drive selection behaviour (Rosenzweig, 1981; Rosenzweig, 1991). Habitat selection behaviour has been well-documented in sessile and facultative sessile invertebrates (Wilson, 1952; Fairchild, 1981). However, habitat selection is present in mobile species, including, for example, amphibians (Strijbosch, 1979), reptiles (Pringle *et al*., 2003), fish (Hugie and Dill, 1994), birds (Hilden, 1965) and mammals (Geier and Best, 1980). In fishes, for instance, members of the Gobiidae prefer rocky habitats that provide protection from the physical threat of rapid flow. Of course, those places also provide refuge from predators (VittatuS, 2008). Habitat patch selection (HPS) has drawn research focus for cognition and behaviour studies in fish (Brown *et al*., 2008; DeBoom and Wahl, 2013; Sowersby *et al*., 2016). HPS can affect foraging, predator-prey interactions, and fish growth rate (Webster and Hart, 2006; Brehmer *et al*., 2013; Jo *et al*., 2016; 2019). HPS is a major factor in modifying fish behaviour in response to predatory attacks (Huntingford and Wright, 1989). In earlier studies, to assess the effects of predation on prey behaviour, prey fish have been exposed to visual (Hojesjo *et al*., 2015; Kelley and Magurran, 2003a) and chemical cues (Brown and Smith, 1998; Kopack *et al*., 2015) reflecting predator presence.

Chemical cues are suggested for studying the olfactory mechanism of prey using particles and the odour of predators (Webster *et al*., 2007). However, chemical signals transfer through diffusion, which affects all areas, therefore, it is difficult to impact only particular areas (Webster and Weissburg, 2009). Visual cues are more easily recognised by stimulation in the experiment of habitat choice than chemical cues for characin fish (Brown and Magnavacca, 2003; Kovalenko *et al*., 2010; Figueiredo *et al*., 2015). Visual cues were considered efficient in an HPS experiment where prey responded to intimidation by predators (Preisser *et al*., 2005). Compared to studies on chemical cues, those using visual cues were relatively scarce due to difficulties in the experimental set-up (Sorensen and Wisenden, 2015). For example, presenting dummies is recognised insufficiently by prey organisms (lure; Kelley and Magurran, 2003a, animated images; Ahmed *et al*., 2012). Therefore, we designed an experimental set-up for visually presenting a live predator.

Recognising and responding to potential predation risk to prey depends either on the type of microhabitat derived by HPS or on swimming speed based on predation cues (Poulin and FitzGerald, 1989; Abrahams, 1995). HPS and swimming speed are indicators of escape responses because repeated use of a habitat type could result in the selection of traits that favour anti-predator for that specific habitat type (Rodewald and Foster, 1998; Lehtiniemi, 2005). Specifically, gasterosteid fishes are well suited to test the hypothesis that behavioural patterns are affected by visual cues such as escape, reproduction and prey-predator interaction (Rowland, 1999; Nilsson and Nilsson, 2000; Odling-Smee and Braithwaite, 2003; Huntingford and Ruiz-Gomez, 2009; Candolin and Selin, 2012; Hojesjo, *et al*., 2015). These studies include five major temperament trait categories *viz*., shyness-boldness, avoidance-exploration, activity, sociability and aggressiveness (Ward *et al*., 2004; Dzieweczynski and Crovo, 2011; Fürtbauer *et al*., 2015). Despite numerous attempts, these studies lacked measurement of how behaviour changes when various habitats exist.

We determined the impact of continuous visual cues of predators on HPS (*e.g.,* open *versus* refuge patches) and behavioural patterns (*e.g.,* swimming speed and residence time). Most studies on prey HPS have used temporal visual cues (*i.e.* for a second; 2~3 s) of predator presence (Walters and Juanes, 1993; Hugie and Dill, 1994) and a few studies have been conducted assessing HPS patterns based on continuous visual cues of predators (Savino and Stein, 1989; Webster and Hart, 2006). In this study, we examined residence time, patch type selection and movement speed, and how stickleback's habitat selection behaviour changes when exposed to a continuous visual predator cue. We hypothesise that short nine-spine stickleback (*Pungitius kaibarae*) residence time increased for identifiable refuge habitats (rocks and water weed) and swimming speed from open patches (open water and sandy) to refuge patches when stimulated by a visual cue.

Materials and methods

Study animals and ethics statement

We used the short nine-spine stickleback (*P. kaibarae*), a small gasterosteid fish inhabiting brackish and freshwater environments in far East-Asia (MoE, 2011) and is classified as Near Threatened in Korea and Japan (MoE, 2011). The stickleback adults (Table 1) used in this study were collected from the Ilgwang Stream (35°16'34.5"N; 129°13'48.6"E) using scoop net (mesh size: 5×5 mm) with authorisation from the Ministry of Environment, Republic of Korea. Collected male fish were kept in tanks (45×30×25 cm) in temperature-controlled rooms (16.4±1°C) and exposed to a natural photoperiod. Before starting the experiment, collected fish were given two weeks of acclimation time. Chopped frozen bloodworms (Chironomid larvae, frozen bloodworms, China) were provided as food every day. The test fish were fed each morning throughout the experiment and were returned to their tanks following the completion of the behavioural trials. The Japanese eel (*Anguilla japonica*) was chosen as a predator since the eel typically feeds on Gasterosteidae (Hartley, 1948). One single Japanese eel (250 mm in

Table 1. List of individual's basic information. The identification of sexes as per Chae and Yang (1990) (Male stickleback; Head length/Standard length above 25)

Individual No.	Total Length (mm)	Standard Length (mm)	Head Length (mm)	Weight (g)	Head length/Standard length	Sex
1	53	45	11	0.78	24.4	Female
2	50	42	12	0.73	28.6	male
3	57	49	13	1.09	26.5	male
4	47	39	11	0.57	28.2	male
5	47	42	10	0.63	23.8	Female
6	53	44	12	0.8	27.3	male
7	50	41	11	0.61	26.8	male
8	55	48	14	0.94	29.2	male
9	55	49	13	0.94	26.5	male
10	50	44	12	0.73	27.3	male
11	55	49	13	0.92	26.5	male
12	52	46	12	0.75	26.1	male
13	47	41	12	0.54	29.3	male
14	51	46	13	0.76	28.3	male
15	54	47	13	0.7	27.7	male
16	54	49	13	0.88	26.5	male
17	52	42	11	0.63	26.2	male
18	53	46	11	0.81	23.9	Female
19	55	46	12	0.94	26.1	male
20	55	47	14	0.93	29.8	male
21	45	38	10	0.62	26.3	male
22	51	44	11	0.73	25.0	Female

length) was used for all experiments. As an apex predator, eel is the number one threat to stickleback fish in their natural habitat (brackishwater; Gross, 1978). In addition, our predator (*A. japonica*) was the only potential threat to sticklebacks in the study site. The study complied with the guidelines of the Pusan National University Institutional Animal Care and Use Committee (PNUIACUC, PNU-2018-1787). No fish (stickleback or eel) died during the experiment. All fish were returned to the collection site after competion of the experiments.

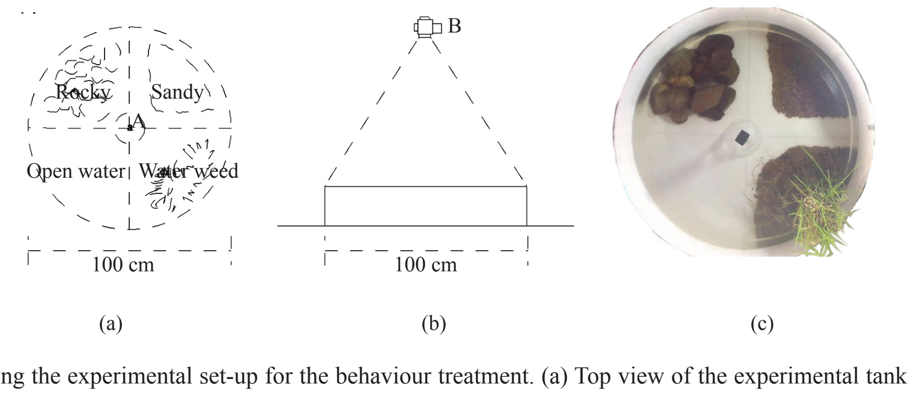
Behavioural experiments

The experimental tank (1.0×1.0×0.35 m, circular shape) was subdivided into four quarters, three containing water weed (*Zizania latifolia*), sandy (particle size: 1.4±0.5 mm), or rocky (particle size: 168.5±18.4 mm) substratum, the fourth quarter was intentionally left as open water, representing completely exposed area (Fig. 1. a and c). Experimental tank walls were covered with opaque white paper to prevent disturbance during the experiment. The sticklebacks were introduced into the experimental tank. Then, an open-ended Erlenmeyer flask containing the predator was placed centrally inside the experimental tank (with predator, WP). In control tank (no predator, NP), empty flask was placed in the tank at exactly the same position as with WP (Fig. 1. a, c). A camera (Logitech cx900, Logitech, Republic of Korea) was mounted on top of the tank and video tracking was carried out for three hours (Fig. 1a,b). Individual sticklebacks were observed for three hours and recorded behaviour in the presence (WP) or absence of the predator (NP). Experiments were carried out from 21. 00 hrs to midnight when the predators (*A. japonica*) were known to be active to test the effect of predator presence (Wang *et al*., 2011). This time is also the individual activity time for gasterosteid fish (Reebs *et al*., 1984). Twenty replications each for the presence and absence of a predator were undertaken.

Data measurement

Three different parameters, residence time [s], patch selection [n] and movement speed [cm s^{-1}] including directions were quantified using the video files. To assess patch selection, a beaker (500 ml) with a short nine-spine stickleback was placed in the centre of the experimental tank. To ensure that the study animal was calm, we allowed 5 min period for the animal to acclimatise before we started the experiment. Patch selection was measured from beginning to select the first patch until moving to another patch. For instance, if a stickleback chose a rocky patch as the first patch, and moved to water weed, we counted the number of patch selections as 1 rocky and 1 water weed. Residence time measured the total time spent in each of the microhabitats during the experimental trial. Across the number of selected patches, residence time was counted whenever fish moved from one patch to another.

The frame rate was 4 frames per s (4 f/s) and each captured picture was determined to be 0.25 s. Movement speed which can be a representative factor among anti-predation behaviours as boldness was measured using Image J software (http://imagej.nih.gov/ij/). From these we calculated the swimming speed (distance/time), expressed as cm s^{-1}. We measured the moving distance with the residence patch as its starting point. If the sample moved 4.0 cm for 1.0 second from rocky to water weed, movement speed was calculated as 4 cm s^{-1}. Water weeds and rocky were classified as refuge patches, while the other patches (*i.e.,* open water and sandy) were classified as open patches. We also measured four directions of movement (from open patches to refuge patches in NP; from refuge patches to open patches in NP; from open patches to refuge patches in WP; from refuge patches to open patches in WP). Furthermore, we assigned a score of '0' when individual fish stopped while moving to another patch.



(a) (b) (c)

Fig. 1. Diagram showing the experimental set-up for the behaviour treatment. (a) Top view of the experimental tank showing area of the four habitats (rocky, sandy, water weed and open water); (b) Side view of the experimental tank showing the position of the camera used to record patch selection; (c) Photo of the experimental tank. A: Starting point for the stickleback and position of the flask in the predator trial; B: Digital camera

Statistical analysis

Data was log-transformed before the analysis in order to satisfy assumptions in the parametric test. Residence time and the number of patch selections were subjected to two-way ANOVA (α=0.05) with the presence or of absence of predators (2 treatments) and patches (4 types; rocky, sandy, water weed and open water). Tukey's HSD was carried out to discern statistical differences among patches. Concerning the speed of movement change, student's t-test was used to compare statistical differences between NP and WP. All Statistical values were normally distributed and were considered significant at p≤0.05. All analyses were performed using SPSS version 21.0 for Windows (SPSS Inc.).

Results and discussion

Overall, stickleback fish spent less time in open patches (sandy and open water) when the predator was present and spent more time in water weed and rocky patches than in sandy or open water patches. The average resident time significantly decreased from 395.3 to 110.0 s in the open-water patch. Average residence time was significantly different based on patch type (F=24.801; df=3, p<0.001), presence or absence of predator (F=27.782, df=1, p<0.0001) as well as the interaction (F=2.833, df=3, p=0.040) (Fig. 2a).

The patch selection, on average (±SE), significantly decreased in the presence of a predator (Rocky: 23.6±5.1 to 10.2±3.6; Sandy: 28.4±10.2 to 13.5±4.4; Water weed: 30.4±9.0 to 11.3±3.5; Open water: 23.4±4.5 to 7.2±2.7). Although the full patch selection decreased when the predator was present (105.8±27.6 to 42.3±14.0), there was no tendency to prefer specific habitats. The presence or absence of predators also significantly affected the number of patch selections (F=55.539, df=1, p<0.0001). There was, however, no statistical difference in the number of patch selections defined by habitat type (F=1.118, df=3, p=0.344) as well as in its interactions (F=0.364, df=3, p=0.779) (Fig. 2b). As a result, they were reducing the number of patch selection and increasing the residence time of specific patch (water weed).

Movement speed from open patches to refuge patches in WP was significantly faster than from open patches to refuge patches in NP (head for refuge patches: t=-3.951, df= 158, p<0.001). Furthermore, the fish in the WP treatment showed faster movement into refuge patches (water weed and rocky) and slower movement into the open patches (sandy and open water) than in the NP treatment (Fig. 3).

Our study showed that the stickleback increased residence time for the water weed and swimming speed from open water to Water weed in response to predator

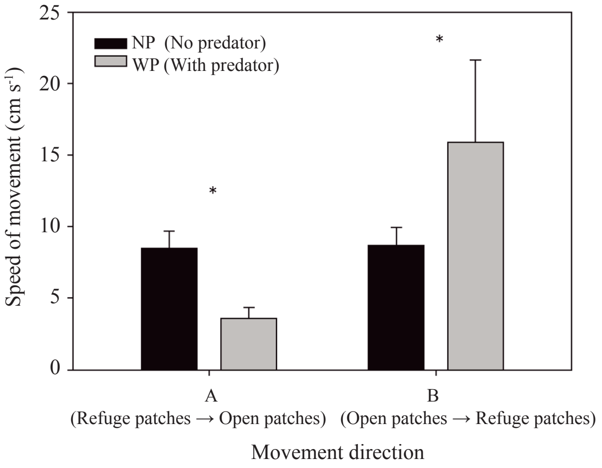
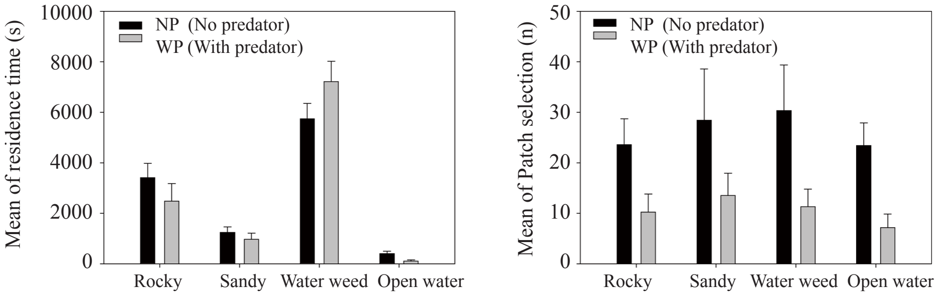


Fig. 3. Speed of movement (mean±SD) of the study animals in open patches (open water and sandy) and refuge patches (rocky and waterweed) without a predator (no predator; NP) and with a predator (WP; *, p<0.05). A: Direction of movement from refuge patches to open patches; B: Direction of movement from open patches to refuge patches



(a) (b)

Fig. 2. The mean±SE of residence time in different habitat patches and number of patch selection by the sticklebacks in the presence or absence of a predator. (a) Mean of residence time of patch; (b) Mean of patch selection. The different lower case and upper case letters indicate significant difference by Tukey's HSD (honestly significant difference)

presence. When a prey fish encounters a predator, the prey fish exhibits anti-predation behaviours (such as fast movements, hiding, protective colourations and bursting). Among the anti-predation behaviours, boldness such as quick movements and bursting are effective anti-predator mechanisms and are interpreted as risking predation for increased resources, especially foraging gains. To decrease predator intimidation, therefore, the disposition of anti-predation and boldness behaviours can be applied to the stickleback' conservation plan (Brown and Magnavacca, 2003; Kelley and Magurran, 2003b; Vamosi and Schluter, 2004; Brown *et al*., 2008; Marras *et al*., 2015).

Structurally complex habitats such as water weeds and rocky patches have been considered a factor in reducing predation risk to various aquatic prey species (Heck *et al*., 1997; Crowder and Cooper, 1982; Savino and Stein, 1982). Gasterosteid fish are also known to prefer water weed habitats, with slow-flow areas such as depositional patches (Prenda *et al*., 1997). In addition to habitat preference, stickleback reproduction primarily occurs in water weeds (Park and Lee, 1999). Our results agree with previous studies showing that the stickleback spend more time in water weed patches than other patches and spend significantly less time in the open water patch.

We initially speculated that rocky patches might play a similar role as water weeds. Since we tested eel as predator, which are known to inhabit rocky habitats (Acou *et al*., 2011), it is likely that the stickleback avoided the rocky patches. When prey fish tend to hide in rocky shelters to avoid predators, there is a concordant increase in the residence time of rocky patches due to the presence of a substrate-dwelling predator (Preisser *et al*., 2005). We did not find any statistical differences between rocky and sandy habitats. Although sandy and open patches have higher relative predation risks than rocky patches, the sandy patch lacks selection and residence time (Fig. 2). Those fish choosing sediments are known to possess an adaptive colouring that matches the colour in choice trials (Ryer *et al*., 2008) and lateralisation (Cantalupo *et al*., 1995). Cryptic colouring is used for colours similar to the microhabitat (sandy and rocky) in the patch selection for predator avoidance (Main, 1987; Ryer *et al*., 2008). Therefore, sandy and rocky patches may have similar roles as habitats for the stickleback.

In the current study, it is noteworthy that the number of patch selections was not significantly different among habitat patches. Predator presence, however, has a significant effect on the number of patch selections. This is because frequent habitat change may be more vulnerable to predation risk (Gilliam and Fraser, 1987; Abrahams, 1995). In our study, we focused on one species of predator; however, to be comprehensively descriptive, further research is needed on the influence of multiple predators on the prey species

Bursting (increased swimming speeds over a short distance, such as critical swimming speed; U crit) is a behavioural strategy used by some prey species to avoid predators (Garenc *et al*., 1999; Fu, 2015). Bursting is defined as increased swimming speeds over a short distance and does not define exact figures for the speed. Wardle and He (1988) described 5.5 m s^{-1}, but this speed applies only to *Scomber scombrus* L. species (Wardle and He, 1988). Therefore, we defined bursting speed as "significantly higher than other movement speed (above 10 m s^{-1})". This swimming speed is often used as an indicator of fitness as a response to the influence of the surrounding environment (Guderley *et al*., 2001). However, there is little empirical evidence quantifying bursting in response to different habitat patches and our study revealed that there is a significant difference in movement speed in response to predators as well as habitat patches. Swimming to the shelters (rocky and water weed) can be challenging because it is exposed to predators as soon as it moves (Klefoth *et al*., 2012). High rates of bursting to shelters seem to result from the distribution of bold individuals.

However one drawback of our experiment is that it focuses on common behaviours (*i.e.* habitat selection and swimming speed). It might overlook stickleback reactions to rare occurrences that might also reflect individuality, for example, responses to predators or novel environments (*i.e.,* boldness-shyness and exploration-avoidance). Shyness-boldness is an individual's reaction to any risky situation, but not new situations and includes response to risky situations, such as predators (Reale *et al*., 2007). Exploration-avoidance is an individual's reaction to a new situation and includes behaviour towards a new habitat, new food, or novel objects (Slipogor *et al*., 2016). For further study, therefore experiments have to consider significant temperament trait categories such as shyness-boldness and exploration-avoidance.

In conclusion, our present study demonstrated that predatory visual pressure significantly impacts residence time, the number of patch selections and movement speed, including the direction of stickleback fish. The information generated by this study can help to understand the behavioural strategies of stickleback fish in different habitats and response to predators. While perceiving fish habitat selection behaviour it is essential to understand natural habitat preferences, that is helpful in informing the aquaculture industry about the ways to reduce stress for a target species.

Acknowledgments

This research was funded by the National Research Foundation of Korea, Grant No. NRF-2020R1C1C10090 66.

References

Abrahams, M. V. 1995. The interaction between antipredator behaviour and antipredator morphology: Experiments with fathead minnows and brook sticklebacks. *Can. J. Zool.*, 73(12): 2209-2215. DOI:10.1139/z95-261.

Acou, A., Rivot, E., Van Gils, J. A., Legault, A., Ysnel, F. and Feunteun, E. 2011. Habitat carrying capacity is reached for the European eel in a small coastal catchment: Evidence and implications for managing eel stocks. *Freshw. Biol.*, 56(5): 952-968. DOI:10.1111/j.1365-2427.2010.02540.x.

Ahmed, T. S., Gerlai, R. and Fernandes, Y. 2012. Effects of animated images of sympatric predators and abstract shapes on fear responses in zebrafish. *Behaviour*, 149(10-12): 1125-1153. DOI:10.1163/1568539X-00003011.

Brehmer, P., Laugier, T., Kantoussan, J., Galgani, F. and Mouillot, D. 2013. Does coastal lagoon habitat quality affect fish growth rate and their recruitment? Insights from fishing and acoustic surveys. *Estuar. Coast. Shelf. Sci.*, 126: 1-6. DOI:10.1016/j.ecss.2013.03.011.

Brown, C., Laland, K. and Krause, J. 2008. *Fish cognition and behaviour.* John Wiley and Sons, New Jersey, USA.

Brown, G. E. and Magnavacca, G. 2003. Predator inspection behaviour in a characin fish: An interaction between chemical and visual information? *Ethology*, 109: 739-750. DOI:10.1046/j.1439-0310.2003.00919.x.

Brown, G. E. and Smith, R. J. F. 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): Conditioning hatchery-reared fish to recognise chemical cues of a predator. *Can. J. Fish. Aquat. Sci.*, 55: 611-617. DOI:10.1139/f97-261.

Candolin, U. and Selin, M. 2012. Density-dependent habitat selection in a growing threespine stickleback population. *Int. J. Zool.*, 2012: 1-6. DOI:10.1155/2012/378913.

Cantalupo, C., Bisazza, A. and Vallortigara, G. 1995. Lateralisation of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia*, 33(12): 1637-1646. doi:10. 1016/0028-3932(95)00043-7.

Chae B. S. and Yang, H. J. 1990. Sexual dimorphism in eightspine stickleback, *Pungitius sinensis:* Gasterosteidae. *Korean J. Zool.*, 33(3): 260-265.

Crowder, L. B. and Cooper, W. E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63: 1813-1892. DOI:10.2307/1940122.

DeBoom, C. S. and Wahl, D. H. 2013. Effects of coarse woody habitat complexity on predator-–prey interactions of four freshwater fish species. *Trans. Am. Fish. Soc.*, 142: 1602-1614. DOI:10.1080/00028487.2013.820219.

Dzieweczynski, T. L. and Crovo, J. A. 2011. Shyness and boldness differences across contexts in juvenile three□spined stickleback *Gasterosteus aculeatus* from an anadromous population. *J. Fish Biol.*, 79(3): 776-788.

Fairchild, G. W. 1981. Movement and microdistribution of *Sida crystallina* and other littoral Microcrustacea. *Ecology*, 62: 1341-1352. DOI:10.2307/1937297

Figueiredo, B. R., Mormul, R. P. and Thomaz, S. M. 2015. Swimming and hiding regardless of the habitat: Prey fish do not choose between a native and a non-native macrophyte species as a refuge. *Hydrobiologia,* 746(1): 285-290. DOI:10.1007/s10750-014-2096-x.

Fu, S. J. 2015. Flow and stress acclimation both enhance predator avoidance in a common cyprinid fish. *Aquat. Biol.*, 24: 1-8. DOI:10.3354/ab00633.

Furtbauer, I., Pond, A., Heistermann, M. and King, A. J. 2015. Personality, plasticity and predation: Linking endocrine and behavioural reaction norms in stickleback fish. *Funct. Ecol.*, 29(7): 931-940.

Garenc, C., Couture, P., Laflamme, M. A. and Guderley, H. 1999. Metabolic correlates of burst swimming capacity of juvenile and adult threespine stickleback (*Gasterosteus aculeatus*). *J. Comp. Physiol. B.*, 169: 113-122. DOI:10.1007/s003 600050201.

Geier, A. R. and Best, L. B. 1980. Habitat selection by small mammals of riparian communities: Evaluating effects of habitat alterations. *J. Wildl. Manage.*, 16-24. DOI:10.2307/3808346.

Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: A test of a model with foraging minnows. *Ecology*, 68(6): 1856-1862. DOI:10.2307/1939877.

Gross, H. P. 1978. Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L. *Can. J. Zool.*, 56(3): 398-413. DOI:10.1139/ z78-058.

Guderley, H., Leroy, P. H. and Gagne, A. 2001. Thermal acclimation, growth and burst swimming of threespine stickleback: Enzymatic correlates and influence of photoperiod. *Physiol. Biochem. Zool.,* 74(1): 66-74. DOI: 10.1086/319313.

Hartley 1948. Food and feeding relationships in a community of fresh-water fishes. *J. Anim. Ecol.*, 1-14. DOI:10.2307/1604.

Heck, K., Nadeau, D. A. and Thomas, R. 1997. The nursery role of seagrass beds. *Gulf Mex. Sci.*, 15: 50-54. DOI:10.18785/ goms.1501.08.

Hilden, O. 1965. Habitat selection in birds: A review. In: *Annales Zoologici Fennici. Finnish Zoological and Botanical Publishing Board*, 2(1): 53-75. https://www.jstor.org/stable /23730835.

Hojesjo, J., Axelsson, M., Dahy, R., Gustavsson, L. and Johnsson, J. I. 2015. Sight or smell? Behavioural and heart rate responses in subordinate rainbow trout exposed to cues from dominant fish. *Peer J.*, e1086. DOI:10.7717/peerj.1169.

Hugie, D. M. and Dill, L. M. 1994. Fish and game: A game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.*, 45: 151-169. DOI:10.1111/j.1095-8649.1994.tb01090.x.

Huntingford, F. A. and Ruiz-Gomez, M. L. 2009. Three-spined sticklebacks *Gasterosteus aculeatus* as a model for exploring behavioural biology. *J. Fish Biol.*, 75(8): 1943-1976. DOI:10.1111/j.1095-8649.2009.02420.x.

Huntingford, F. A. and Wright, P. J. 1989. How sticklebacks learn to avoid dangerous feeding patches. *Behav. Processes*, 19(1-3): 181-189. DOI:10.1016/0376-6357(89)90040-5.

Jo, H., Jeppesen, E., Ventura, M., Buchaca, T., Gim, J. S., Yoon, J. D., Kim, D.H. and Joo, G. J. 2019. Responses of fish assemblage structure to large-scale weir construction in riverine ecosystems. *Sci. Total Environ.*, 657: 1334-1342. DOI:10.1016/j.scitotenv.2018.11.446.

Jo, H., Yoon, J., Kim, J. H., Jeong, K. S., Do, Y. and Joo, G. J. 2016. Diet shifts and delayed piscivorys, specialisation during the ontogenesis of the largemouth bass *Micropterus salmoides* (Lacepede, 1802) in the Nakdong River and Upo Wetlands, South Korea. *Indian J. Fish.*, 63(4): 48-54. DOI:10.21077/ijf.2016.63.4.58221-08.

Kelley, J. L. and Magurran, A. E. 2003a. Effects of relaxed predation pressure on visual predator recognition in the guppy. *Behav. Ecol. Sociobiol.*, 54: 225-232. DOI:10.1007/s00265-003-0621-4.

Kelley, J. L. and Magurran, A. E. 2003b. Learned predator recognition and antipredator responses in fishes. *Fish Fish.*, 4(3): 216-226. DOI:10.1046/j.1467-2979.2003.00126.x.

Kim, I. S. 1997. *Illustrated encyclopedia of fauna and flora of Korea vol. 37, Freshwater fishes.* Ministry of Education, Sejong, South Korea.

Klefoth, T., Skov, C., Krause, J. and Arlinghaus, R. 2012. The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behav. Ecol. Sociobiol.*, 66(4): 547-559. DOI:10.1007/s00265-011-1303-2.

Kopack, C. J., Broder, E. D., Lepak, J. M., Fetherman, E. R. and Angeloni, L. M. 2015. Behavioral responses of a highly domesticated, predator naive rainbow trout to chemical cues of predation. *Fish. Res.*, 169: 1-7. DOI:10.1016/j.fishres.2015.04.005.

Kovalenko, K. E., Dibble, E. D., Agostinho, A. A. and Pelicice, F. M. 2010. Recognition of non-native peacock bass, *Cichla kelberi* by native prey: Testing the naivete hypothesis. *Biol. Invasions*, 12: 3071-3080. DOI:10.1007/s10530-010-9698-7.

Lehtiniemi, M. 2005. Swim or hide: Predator cues cause species specific reactions in young fish larvae. *J. Fish Biol.*, 66(5): 1285-1299. DOI:10.1111/j.0022-1112.2005.00681.x.

Main, K. L. 1987. Predator avoidance in seagrass meadows: Prey behavior, microhabitat selection and cryptic coloration. *Ecology*, 68(1): 170-180. DOI:10.2307/1938817.

Marras, S., Noda, T., Steffensen, J. F., Svendsen, M. B., Krause, J., Wilson, A. D., Kurvers, R. H., Herbert-Read, J., Boswell, K. M. and Domenici, P. 2015. Not So Fast: Swimming behaviour of sailfish during predator-prey interactions using high-speed video and accelerometry. *Integr. Comp. Biol.*, 55: 719-727. DOI:10.1093/icb/icv017.

MoE. 2011. *Red Data Book of Endangered Fishes in Korea*. Econature, Incheon, South Korea.

Nilsson, S. O. and Nilsson, G. E. 2000. Free choice by female sticklebacks: Lack of preference for male dominance traits. *Can. J. Zool.*, 78(7): 1251-1258. DOI:10.1139/z00-051.

Odling-Smee, L. and Braithwaite, V. A. 2003. The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Anim. Behav.*, 65(4): 701-707. DOI:10.1006/anbe.2003.2082.

Park, S. R. and Lee, J. S. 1999. Territorial behaviour of eightspine sticleback, *Pungitius sinensis kaibarae* in Korea. *J. Ecol. Nat. Environ.*, 22: 163-167.

Poulin, R. and FitzGerald, G. J. 1989. Risk of parasitism and microhabitat selection in juvenile sticklebacks. *Can. J. Zool.*, 67(1): 14-18. DOI:10.1139/z89-003.

Preisser, E. L., Bolnick, D. I. and Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86: 501-509. DOI: 10.1890/04-0719.

Prenda Marín, J., Armitage, P. D. and Grayston, A. 1997. Habitat use by the fish assemblages of two chalk streams. *J. Fish. Biol.*, 51: 64-79. DOI:10.1111/j.1095-8649.1997.tb02514.x.

Pringle, R. M., Webb, J. K. and Shine, R. 2003. Canopy structure, microclimate and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology*, 84(10): 2668-2679. DOI:10.1890/02-0482.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. and Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82(2): 291-318.

Reebs, S. G., Whoriskey Jr, F. G. and FitzGerald, G. J. 1984. Diel patterns of fanning activity, egg respiration and the nocturnal behavior of male three-spined sticklebacks, *Gasterosteus aculeatus* L.(f. trachurus). *Can. J. Zool.*, 62(3): 329-334. DOI:10.1139/z84-051.

Rodewald, A. D. and Foster, S. A. 1998. Effects of gravidity on habitat use and antipredator behaviour in three-spined sticklebacks. *J. Fish Biol.*, 52(5): 973-984. DOI:10.1111/j.1095-8649.1998.tb00597.x.

Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology*, 62(2): 327-335. DOI:10.2307/1936707.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: The search for mechanism. *Am. Nat.*, 137: S5-S28. DOI:10.1086/285137.

Rowland, W. J. 1999. Studying visual cues in fish behavior: A review of ethological techniques. *Environ. Biol. Fish.*, 56: 285-305. DOI:10.1023/A:1007517720723.

Ryer, C. H., Lemke, J. L., Boersma, K. and Levas, S. 2008. Adaptive coloration, behavior and predation vulnerability in three juvenile north Pacific flatfishes. *J. Exp. Mar. Biol. Ecol.*, 359(1): 62-66. DOI:10.1016/j.jembe.2008.02.017.

Savino, J. F. and Stein, R. A. 1989. Behavior of fish predators and their prey: Habitat choice between open water and dense vegetation. *Environ. Biol. Fish.*, 24: 287-293. DOI: 10.1007/BF00001402.

Savino, J. F. and Stein, R. A. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submerged vegetation. *Trans. Am. Fish. Soc.*, 111: 255-266. DOI:10.1577/1548-8659(1982)111<255:PIBLBA>2.0.CO;2.

Slipogor, V., Gunhold-de Oliveira, T., Tadic, Z., Massen, J. J. and Bugnyar, T. 2016. Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in boldness-shyness, stress-activity and exploration-avoidance. *Am. J. Primatol.*, 78(9): 961-973.

Sorensen, P. W. and Wisenden, B. D. 2015. *Fish pheromones and related cues*. John Wiley and Sons. DOI:10.1007/s10641-015-0466-5.

Sowersby, W., Thompson, R. M. and Wong, B. B. M. 2016. Invasive predator influences habitat preferences in a freshwater fish. *Environ. Biol. Fish.*, 99: 187-193.

Strijbosch, H. 1979. Habitat selection of amphibians during their aquatic phase. *Oikos*, 363-372. DOI:10.2307/3544324.

Vamosi, S. M. and Schluter, D. 2004. Character shifts in the defensive armour of sympatric sticklebacks. *Evolution*, 58: 376-385. DOI:10.1111/j.0014-3820.2004.tb01653.x.

VittatuS, G. 2008. Habitat preferences, distribution, and abundance of *Gobius vittatus* (Gobiidae) in the Kvarner area (northern Adriatic Sea). *Vie. Milieu.*, 58(1): 39-45.

Walters, C. J. and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.*, 50: 2058-2070. DOI:10.1139/f93-229.

Wang, Z. Z., Yang, L., Zhu, W. D., Wang, H. Q. and Shi, J. J. 2011. Study of predation habit of *Anguilla japonica* on *Macrobrachium nipponense*. *Oceanol. Limnol. Sin.*, 1: 16.

Ward, A. J., Thomas, P., Hart, P. J. and Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Socio. Biol.*, 55(6): 561-568.

Wardle, C. S. and He, P. 1988. Burst swimming speeds of mackerel, *Scomber scombrus* L. *J. Fish Biol.*, 32(3): 471-478. DOI:10.1111/j.1095-8649.1988.tb05382.x.

Webster, D. R. and Weissburg, M. J. 2009. The hydrodynamics of chemical cues among aquatic organisms. *Ann. Rev. Fluid Mech.*, 41: 73-90. DOI:10.1146/annurev.fluid.010908.165240

Webster, M. M. and Hart, P. J. 2006. Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): Previous experience and social conformity. *Behav. Ecol. Sociobiol.*, 60: 77-86. DOI:10.1007/s00265-005-0143-3.

Webster, M. M., Atton, N., Ward, A. J. W. and Hart, P. J. B. 2007. Turbidity and foraging rate in threespine sticklebacks: The importance of visual and chemical prey cues. *Behaviour*, 144(11): 1347-1360. DOI:10.1163/156853907782418222.

Wilson, D. P. 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals especially the larvae of *Ophelia bicornis* Savigny. *Annales de l'Institut Oce´anographique*, 27: 49-156.

Date of Receipt : 24.05.2022
Date of Acceptance : 07.12.2022