



Corrigenda

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Dynamics of Laterality in Relation to the Predator–prey Interaction Between the Piscivorous Chub “*Hasu*” and its Prey “*Ayu*” in Lake Biwa

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A Japanese piscivorous chub, “*hasu*” (*Opsariichthys uncirostris*), and its main prey, “*ayu*” (*Plecoglossus altivelis*), both have laterally asymmetric bodies, similar to other fishes; each population consists of righty morphs and lefty morphs. This antisymmetric dimorphism has a genetic basis. Temporal changes in the ratios of laterality (i.e., frequency of righty morphs in a population) of these predator and prey fish species were investigated for a 20-year period at a pelagic site in the southwestern area of Lake Biwa, Japan. The dimorphism of each species was maintained dynamically throughout the period, and the ratio of laterality was found to change periodically in a semi-synchronized manner. Direct inspection of the relationship between the ratios of laterality of the two species indicated that the ratio of *ayu* followed that of *hasu*, suggesting that the predator–prey interaction was responsible for the semi-synchronized change. Stomach contents analysis of each *hasu* revealed that cross-predation, in which righty predators catch lefty prey and lefty predators catch righty prey, occurred more frequently than the reverse combination (parallel-predation). This differential predation is presumed to cause frequency-dependent selection on the two morphs of the predator and prey, and to drive semi-synchronized changes in the laterality of the two species. Some discussion pertaining to the atypical form of the semi-synchronized change in laterality found in this study is presented from the viewpoint of predator–prey interaction in fishes.

Key words: *Opsariichthys uncirostris*, *Plecoglossus altivelis*, predator–prey interaction, cross-predation, semi-synchronized oscillation

INTRODUCTION

Behavioral and sensory lateralization is widely recognized in various vertebrates (Roger and Andrew, 2002). Studies of lateralization have focused primarily on humans and higher vertebrates; they have mainly examined cerebral lateralization and related behavioral or sensory differentiation between right and left sides of the body. However, morphological asymmetry (e.g., differences between the right and left sides of behavioral or sensory organs) has not been explored in detail (Matsui et al., 2013). Notably, some recent studies of laterality in fish have revealed that behavioral laterality is always associated with morphological asymmetry, which is characteristically represented as dimorphism in populations; thus, each population is composed of both

righty morphs (“righty”) and lefty morphs (“lefty”) at different proportions (e.g., Hori et al., 2017). This morphological asymmetry in animals is categorized as antisymmetry and can be distinguished from fluctuating or directional asymmetry (sensu Palmer and Strobeck, 1986).

Antisymmetric laterality in fish was first discovered in the scale-eating cichlid fish of Lake Tanganyika (Liem and Stewart, 1976; Hori, 1993), which attacks other fish and snatches some scales from the victim’s trunk. In the scale-eating cichlids, each population consists of righty morphs and lefty morphs. In righty morphs, the right side of the body is more developed than the left side, and the mouth opens twisted to the left. Lefty morphs exhibit the reverse morphology. This asymmetry is associated with lateralized attacking behavior, such that righty morphs attack the right trunk of prey and lefty morphs attack the left trunk (Hori, 1993; Takahashi et al., 2007; Takeuchi et al., 2012). This antisymmetric dimorphism is called laterality. After its discovery in

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the scale-eating cichlid, laterality was discovered in various other fish species (Nakajima et al., 2004; Takeuchi and Hori, 2008; Takeuchi et al., 2010; Hata et al., 2011; Yasugi and Hori, 2012); it was eventually shown that all extant fish, including agnathan and cartilaginous fish, share the characteristic of laterality (Hori et al., 2017). The laterality of fish has a genetic basis (Seki et al., 2002; Hori et al., 2007; Stewart and Albertson, 2010; Hata and Hori, 2012; Hata et al., 2012). A stomach contents analysis of the largemouth bass (*Micropterus salmoides*), which preys mainly on freshwater goby (*yoshinobori* in Japanese) (*Rhinogobius* sp.) in Lake Biwa, suggested that the laterality is maintained by the predator–prey interaction (Yasugi and Hori, 2011). This viewpoint was supported by simultaneous sampling of individual scale-eating fish and their prey in Lake Tanganyika (Hori et al., 2019).

A mathematical model of a one predator/one prey system (Takahashi and Hori, 1994) predicted that the ratios of laterality in populations of both predator and prey in a simple system exhibit oscillation with a fixed period. Other mathematical computer simulation models consisting of one predator/one prey with three species of each at three trophic levels (Nakajima et al., 2004, 2005) demonstrated virtually the same results. To the best of our knowledge, few field studies have investigated the maintenance and dynamic changes of laterality in predator and prey over a long time period in any fish communities. However, Yasugi and Hori (2011) suggested that the laterality of largemouth bass, *M. salmoides*, and its main prey fish, *yoshinobori*, were maintained temporally and dynamically for 8 years in Lake Biwa. Hori et al. (2019) also demonstrated that the ratios of laterality in populations of two congeneric species of scale-eating cichlids were maintained dynamically for more than 30 years, but the temporal change in laterality of prey fish was not traced in that study. Because littoral fish communities in Lake Tanganyika harbor many fish species, as in other tropical lakes, and the interspecific interactions are very complex (Hori, 1987, 1991, 1997), it is quite difficult to investigate the laterality relationship between any predator and specific prey species. However, this difficulty may be overcome by studying a pelagic fish community in a temporal lake where the composition of the fish community is sufficiently simple that the laterality relationship between a predator and specific prey species can be investigated relatively easily.

In the pelagic area of Lake Biwa, Japan, the food web in the fish community (especially in open water) is relatively simple. Specifically, the predominant predator is the piscivorous chub, *Opsariichthys uncirostris* (Temminck et Schlegel) (*hasu* in Japanese; Cyprinidae), which is originally endemic in Lake Biwa and the River Yodo Water System. And the main prey of *hasu* is *Plecoglossus altivelis* (Temminck et Schlegel) (*ayu* in Japanese; Plecoglossidae) (Tanaka, 1964; Okuda et al., 2013; Maehata, 2020), which is distributed widely in Japan, but the population of Lake Biwa is confined to the lake and its tributaries. This fish depends mainly on plankton in the pelagic zone and partly on epilithic algae on rocks in the littoral zone (Miyadi et al., 1963). It has been proven that the two species exhibit laterality and that each population is composed of righty morphs and lefty morphs (Hori et al., 2017).

One of the purposes of this study was to demonstrate

that the ratios of laterality in both populations (i.e., *hasu* and *ayu*) are maintained dynamically for a long period. The ratios of laterality of the two species were surveyed for 20 years at a fixed pelagic site of Lake Biwa.

Some experimental studies (Nakajima et al., 2007; Yasugi and Hori, 2012) have suggested that the driving force of such dynamism of fish laterality is predator–prey interaction, especially the predominance of “cross-predation.” In situations where all fishes have laterality, two types of predation incidents can be distinguished: 1) a predator catches a prey of the same morph of laterality (righty predator catches righty prey, and lefty morph catches lefty prey; i.e., “parallel-predation”), and 2) a predator catches a prey of the opposite morph (righty predator catches lefty prey, and lefty predator catches righty prey; i.e., “cross-predation”) (Nakajima et al., 2007). Provided that the ratios of laterality in both populations of predator and prey are maintained in any pattern, the predation incidents in an overall community (at a single point in time) are predicted to be biased toward an excess of one type of predation over the other—either cross-predations are predominant over parallel-predations (predominance of cross-predation) or the reverse (predominance of parallel-predation)—but both types of predation are not predicted to occur at a similar frequency (random predation).

Thus, another purpose of the present study was to investigate which type of predation is predominant in the *hasu* and *ayu* predator–prey system. Recently, Yasugi and Hori (2011, 2012, 2016) predicted that cross-predation would be predominant over parallel-predation in a system in which predator fish attack prey fish from behind, as the *hasu* does. To test this prediction, *hasu* were collected only if they were hunting around schools of *ayu*; the combination of laterality between each *hasu* and the *ayu* taken from its stomach was examined.

Overall, the purposes of this study were to demonstrate the long-term dynamics of laterality in the predator and prey fish populations in a simple community, and to investigate whether cross-predation is predominant over parallel-predation in the *hasu* and *ayu* predator–prey system.

MATERIALS AND METHODS

Sampling of *hasu* and *ayu* to monitor temporal changes in the ratios of laterality

A 20-year survey from 1995 to 2014 was conducted on the ratios of laterality in the populations of *hasu* and *ayu* at a pelagic site at Wani Point (35°09'41.86" N, 135°56'01.75" E) in the southwestern area of Lake Biwa (city of Otsu, Shiga Prefecture, Japan; Fig. 1A). In the same season of each year (from the middle of June to early July), fish samples of the two species were purchased from particular fishermen using the traditional settle net (i.e., the “eri-ami” net) (Fig. 1B), which was settled at 400 m off of Wani Point. The settle net was maintained at the same position throughout the study period, although the ownership changed twice. The water depth at the net was 16–18 m. *Ayu* are an annual fish that breed in late summer (from August to October) in Lake Biwa (Miyadi et al., 1963). *Hasu* in the lake breed in summer (from May to August) and mature in the 3rd or 4th season at lengths greater than 16 cm standard length (SL) for males and in the 2nd or 3rd season at lengths greater than 13 cm SL for females (Tanaka, 1970). For this analysis, all obtained *ayu* were used, while only adult *hasu* whose lengths were greater than 16 cm SL for males and 13 cm SL for females were used. In each year, several tens of individuals of each species (for

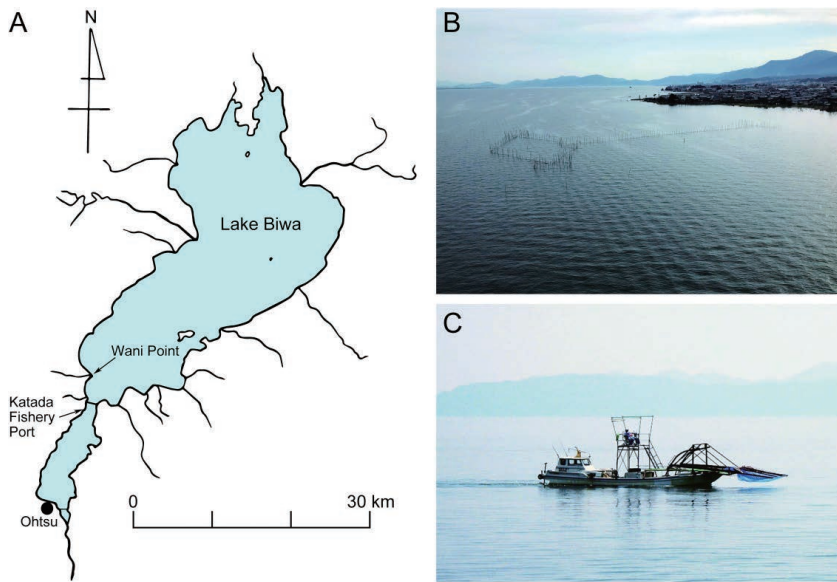


Fig. 1. Study site and two methods of sampling. **(A)** Map of Lake Biwa showing Wani Point, the study site of the populations of *hasu* and *ayu*; **(B)** view of *eri-ami* settle net at Wani Point; and **(C)** *okisukui-ami* fishing boat in operation off Wani Point.



Fig. 2. Example of stomach contents analysis. Dissection revealed that the adult female *hasu* (*Opsariichthys uncirostris*, TL: 155 mm) had preyed on one subadult *ayu* (*Plecoglossus altivelis*, TL: 51 mm). The predation incident had occurred immediately before collection of the *hasu*, as the *ayu* remained at the anterior division of the intestine and had not undergone digestion.

hasu: range, 30 to 247; average, 87; for *ayu*: range, 47 to 355; average, 116) were collected to gain reliable ratios of laterality.

The laterality of the fish was assessed by means of the method used by Hori et al. (2019). Briefly, the laterality of each fish was judged from the direction of the mouth opening when the fish's abdomen was held upward; its mouth was opened by insertion of a small spatula and the mandible was lifted forward. The mandible of righty fish opens in a twisted position, generally leftward, while the mandible of the lefty fish opens rightward. Morphologically, the asymmetric mouth opening is due to a three-dimensional position differential between the right and left joints of the mandible to the

suspensorium (e.g., right joint taking a position frontward, ventrally, and outside compared to the opposite side) (Liem and Stewart, 1976; Hata et al., 2013). A rightward twist indicates that the left side of the head and flank are more developed, in comparison to the right side (Hata et al., 2013; Hori et al., 2017). The functional morphology and quantitative measurement of the asymmetric mouth opening have been explored in previous works (Yasugi and Hori, 2011; Hata et al., 2013; Hori et al., 2017). The periodicity in the ratio of laterality of the two species was analyzed using Fourier transformation by means of the method described in the Supplementary Material in Yasugi and Hori (2011).

Sampling of *hasu* containing fresh prey fish in the stomach to assess the combination of laterality at each predation event

The combination of laterality of each predator fish and the prey fish it has eaten can be determined by a stomach contents analysis of the predator fish. However, fish caught by *eri-ami* (settle net) are not suitable for this examination because the fish are left alive in the net for up to two days and the stomach contents are nearly fully digested. In contrast, *hasu* foraging on *ayu* can be obtained as a bycatch of “*okisukui-ami*” fishing, in which a special fishing boat equipped with a large scooping net at the bow rushes toward and scoops a shoal of *ayu* at the surface of the pelagic area of the lake (Fig. 1C). The fish caught are then kept on ice in the boat. Samples of *hasu* were purchased from fishermen conducting *okisukui-ami* fishing at the Katada Fishery Cooperative, whose fishing area covers Wani Point, two or three times in the month of July (mainly in 2003, 2004, and 2007; small numbers of samples were also added in 2005, 2006, and from 2008 to 2012). At each time, supplementary samplings of *hasu* were also conducted using a casting net in the shallow area of the mouth of the Wani River, where adult *hasu* sometimes forage for *ayu*. However, the samples acquired by casting net only occasionally contained *ayu* in the stomach. The *hasu* caught by casting net were fixed immediately by immersion in cold water with ice.

These samples of *hasu* for the stomach content analysis were kept frozen in the laboratory until examination. In total, more than 600 *hasu* were collected. The samples were dissected, and prey fish, if any, were taken from the stomach (Fig. 2). Nearly all prey fish

found in the *hasu* were *ayu*; 60 *ayu* (in total) with little damage from digestion were taken. Prey fish with mouth parts in which digestion-related damage prevented definition of laterality were excluded from the analysis. The laterality of both the *hasu* and *ayu* were identified based on the direction of mouth opening; the combinations of their laterality were examined. Typically, each *hasu* had one *ayu* in its stomach, but three *hasu* individuals each had two *ayu* individuals. In these instances, only the *ayu* taken first (i.e., the *ayu* found in a deeper position of the stomach) was used as the prey in the analysis; this avoided duplication of data. Additionally, a second incidence of predation could have been affected by a first

incidence of predation. To determine whether cross-predation or parallel-predation was predominant in these samples, a statistical test was performed using the odds ratio with a 95% confidence limit.

These treatments were performed in accordance with the Regulations on Animal Experimentation at Kyoto University.

RESULTS

Temporal changes in the laterality of *hasu* and *ayu*

At Wani Point, both lateral morphs (righty and lefty) of *hasu* and *ayu* were maintained for 20 years (Fig. 3 and see Supplementary Table S1). The ratios of laterality (frequency of righty morphs in the total number of fish collected in each year) of each species changed temporally around a value of 0.5, but nearly always remained within the range of 0.4 to 0.7. Fourier transform analysis showed a significant 4.2-year periodicity of the cycle of the ratio of *hasu* ($P < 0.001$), indicating that the ratio of *hasu* oscillated with a period of 4.2 years throughout the 20 years. In contrast, the analysis showed no significant periodicity for *ayu* ($P > 0.1$), although the ratio of *ayu* exhibited some cyclic change similar to that of *hasu*; more specifically, it appeared to change in accordance with the oscillation of the ratio of *hasu*.

The relationship of the cyclic change of laterality between the two fish species was examined by directly plotting the ratio of *ayu* against that of *hasu* (Fig. 4 and see Supplementary Figure S1). The plots were scattered in a counterclockwise pattern of rotation, suggesting that the ratio of *ayu* followed nearly 1 year behind the oscillation of the ratio of *hasu*. The rotation did not occur around the equilibrium point (i.e., the coordinate [0.5, 0.5]), but around the coordinate (0.52, 0.54), calculated as the average of all of the data points for both species. This suggests that the periodic changes of laterality of both populations were maintained such that righties tended to outnumber lefties slightly during the entire period.

Correspondence of fish laterality between each *hasu* and its *ayu* prey

In total, 60 individual *hasu* were collected with an individual *ayu* in the stomach that exhibited minimal digestion-related damage. Because the number of samples per year

was not large, the data were pooled for analysis. The predator-prey relationship between each *hasu* and its *ayu* prey exhibited a significant bias toward cross-predation (Table 1 and see Supplementary Table S2). The odds ratio was 7.62 (95% confidence limit; 2.44–23.71), indicating that cross-predation occurred significantly more frequently than

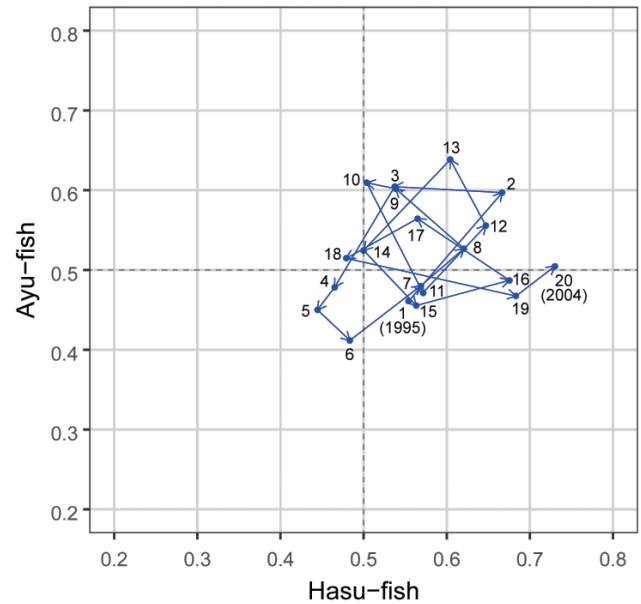


Fig. 4. Relationship of ratios of laterality between *hasu* and *ayu* from 1995 to 2014 at Wani Point. Each dot is numbered in order from the first year (1995) to the last year (2014) of the survey.

Table 1. Correspondence of morph type between each *hasu* and each prey *ayu*.

		Ayu	
		Righty	Lefty
Hasu	Righty	7	20
	Lefty	24	9
		Total: 60	

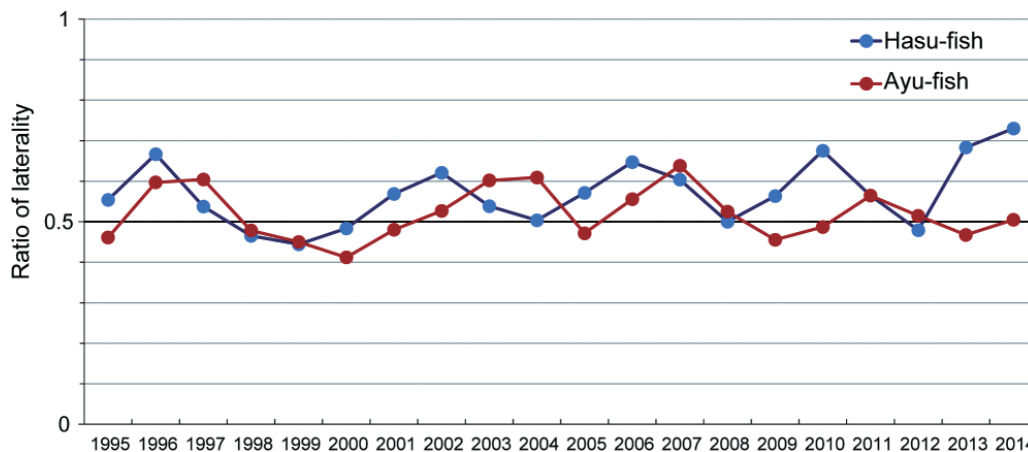


Fig. 3. Temporal changes in the ratios of laterality of *hasu* and *ayu* from 1995 to 2014 in a pelagic area offshore from Wani Point, Lake Biwa. The ratios of laterality indicate the frequency of righty morphs in the total number of fish collected in each year.

parallel-predation (Mantel-Haenszel test; $P < 0.001$).

DISCUSSION

Our results showed that the laterality in the populations of *hasu* and *ayu* was maintained throughout the study period. Notably, the ratios of laterality of the two species changed in a cyclical manner with a similar amplitude throughout the study period. Such cyclic changes suggest that some negative frequency-dependent selection was in effect. The results of stomach contents analysis showed that righty *hasu* predominantly succeeded in capturing lefty prey over righty prey, whereas lefty *hasu* predominantly succeeded in capturing righty prey over lefty prey. A statistical test based on the common odds ratio revealed a significant probability, suggesting that cross-predation was 2.8-fold more frequent than parallel-predation. Under such a situation, the majority morph of *hasu* at a given time, say righty, will exploit the lefty of *ayu*, and then the righty of *ayu* will attain higher fitness, i.e., minority advantage, and increase their frequency after a particular time span has elapsed, which will then favor the lefty morph of *hasu*.

Some empirical studies, such as those of Yasugi and Hori (2011) and Hori et al. (2019), have suggested that cross-predation is a critical factor in the resulting oscillations. Nakajima et al. (2004) constructed a mathematical model of population dynamics of one predator/one prey systems with antisymmetric laterality, which indicated that a predominance of cross-predation over random-predation can exert a strong negative frequency-dependent selection for both populations of predator and prey; this should cause cyclic changes in the ratios of laterality in both populations. The high level of predominance of cross-predation found in *hasu* seemed to sufficiently explain the oscillation of laterality observed in the populations of *hasu* and *ayu*. Furthermore, the negative frequency-dependent selection for antisymmetric dimorphism involves a time lag, because the minority advantage exerted by the predation and the resultant increase in progeny presumably requires at least one generation. This time lag effect should cause semi-synchronized cyclic changes in the ratios of laterality in predator and prey populations.

The ratios of laterality of *hasu* and *ayu* showed similar cyclic changes with a periodicity of approximately 4 years. Fourier transform analysis indicated that the ratio of *hasu* oscillated with a period of 4.2 years during the 20-year study period. However, the ratio of *ayu* showed no significant periodicity throughout the study period. Fourier transform analysis attempts to detect any fixed periodicity. Thus, if the period of any involved oscillation changes during the research period, the analysis may fail to detect the periodicity. In the dynamics of laterality of interacting species, there is no logical reason that ratios of laterality should oscillate with a fixed periodicity. Using a mathematical model, Takahashi and Hori (1994) suggested that the periodicity is a function of the development rates of the interacting species. Thus, if the development rates change because of some factors, such as mean annual temperature, the periodicity of cyclic change may be altered. Furthermore, the impact of annual temperature on the development ratio may be large for annual fish (i.e., *ayu*).

Other predator and prey fishes can also affect the peri-

odicity and amplitude of laterality dynamics. In Lake Biwa, the potential predator fishes are the largemouth bass, which was introduced before 1970 and has recently increased in number, and the biwa salmon (Japanese: *biwamasu*; *Oncorhynchus rhodurus* Jordan et McGregor: Salmonidae). The potential prey fishes are the *yoshinobori* (*Rhinogobius* spp.: Gobiidae), which is widely distributed in freshwater in Japan, and the white goby (Japanese: *isaza*; *Chaenogobius isaza* Tanaka: Gobiidae), which is endemic to Lake Biwa. The diets of these predators have not been sufficiently studied. Yasugi and Hori (2011) investigated the diet of the largemouth bass in Lake Biwa near Wani Point for three summers, and found that very little of the adult fish diet consisted of *ayu* (0.0–4.2%, number basis). Fujioka and Uenishi (2006) studied the diet of *biwamasu* in the northern part of the lake, and reported that adults preyed mainly on *ayu* in deep waters in July. However, the biomass of the *biwamasu* is lower than that of either *ayu* or *hasu*, although there is little reliable information on the comparative biomass of these fish species in Lake Biwa (but see Tanaka, 2011 for *biwamasu*). We infer from their relative biomass that *biwamasu* has a limited effect on laterality dynamics in *ayu*. Tanaka (1964) studied the diet of *hasu*, and reported that adult *hasu* prey mainly on *ayu* (number and weight basis), supplemented by *yoshinobori*, and to a lesser extent by *isaza*. Thus, the effects of these prey fishes on laterality dynamics in *hasu* may also be limited. We conclude that the laterality ratios of *hasu* and *ayu* are mainly influenced by their interactions.

In the investigation of the direct relationship between the ratios of laterality of *hasu* and *ayu*, there was an unexpected result, in that the ratios of laterality of the two species rotated around a point larger than the coordinate (0.5, 0.5). In fact, our mathematical models (Takahashi and Hori, 1994, 1998, 2005; Nakajima et al., 2004) assumed a priori no differences in physical and/or sensory abilities between righty morphs and lefty morphs; the resultant time series of the ratios of laterality in these studies showed that all ratios of predator and prey oscillated around 0.5. Moreover, neither field nor experimental studies of fish have indicated superiority of righty morphs over lefty morphs in terms of abilities to hunt or escape. Therefore, it is difficult to interpret our findings. Abiotic ecological and environmental factors are likely irrelevant because such factors, outside of the animal individuals, cannot affect the antisymmetric abilities of individuals; only interactions among individuals can affect these abilities. Developmental constraints, such as lateralization of the brain or sensory organs, may have some influence; however, this consideration is beyond the scope of the present study.

Notwithstanding the deviation from the even ratio, it remains noteworthy that the ratios of laterality of the predator and prey changed cyclically for a long period of time. Although cyclic change in the ratio of laterality was previously shown in scale-eating cichlids (Hori, 1993; Hori et al., 2019), changes in the ratios of prey populations were not documented. Related cyclic changes in the ratios of laterality of predator and prey fish were suggested in populations of largemouth bass, *M. salmoides*, and its prey, *yoshinobori*, in Lake Biwa by Yasugi and Hori (2011); however, the study period was limited to 8 years and only one cycle was

revealed. The present study is the first to demonstrate related cyclic changes in the ratios of laterality of predator and prey fish over a long time period; it proves that disproportional attacking success linked to laterality is the driving factor for cyclic changes. However, many studies of lateralized behavior in fish have overlooked the possibility of such cyclic change in the ratio of individuals that perform some lateralized behavior, such as turning mainly rightward in a maze or using the right eye for scouting behavior. Those studies concerning lateralized behavior in fish (e.g., Bisazza et al., 1998; Vallortigara et al., 1999; Vallortigara and Bisazza, 2002) concluded that the behavioral laterality in the population is a fixed property and referred to the laterality at the population level. Few studies have traced the annual change in the ratio of laterality of fish populations in the field, and there may be no logical reason for the ratio of laterality of a fish population to be fixed under natural conditions. Thus, the present study may prompt reconsideration of the proposition that the behavioral laterality in some fish is fixed at the population level.

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COMPETING INTERESTS

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

MH collected the samples, measured specimens, analyzed the data, and wrote the manuscript. JK, MM, and MY collected samples and edited the manuscript. ST analyzed the data and edited the manuscript. All authors read and approved the final manuscript.

SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online. (URL: <https://doi.org/10.2108/zs200155>)

Supplementary Table S1. The number of individuals with each lateral morph in *hasu* (*Opsariichthys uncirostris*) and *ayu* (*Plecoglossus altivelis*).

Supplementary Figure S1. Relationship of ratios of laterality between *hasu* and *ayu* from 1995 to 2014 at Wani Point plotted three-dimensionally.

Supplementary Table S2. Relationship of ratios of laterality between *hasu* and *ayu* in each year.

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Corrigenda

In the article “**Dynamics of Laterality in Relation to the Predator–prey Interaction between the Piscivorous Chub “*Hasu*” and Its Prey “*Ayu*” in Lake Biwa**” by Michio Hori, Jyun-ichi Kitamura, Masayoshi Maehata, Satoshi Takahashi, and Masaki Yasugi, which appeared in *Zoological Science* 38(3): 231–237 (2021), there was an error in the RESULTS section (Page 234, Left, Lines 29–32).

Original sentence: The rotation did not occur around the equilibrium point (i.e., the coordinate [0.5, 0.5]), but around the coordinate (0.52, 0.54), calculated as the average of all of the data points for both species.

Correction: The rotation did not occur around the equilibrium point (i.e., the coordinate [0.5, 0.5]), but around the coordinate (0.57, 0.52), calculated as the average of all of the data points for both species.

There was also an error in Fig. 4 (Page 234). A lettering for sampling year at 20th point should be replaced to “(2014)”. The corrected figure is shown below.

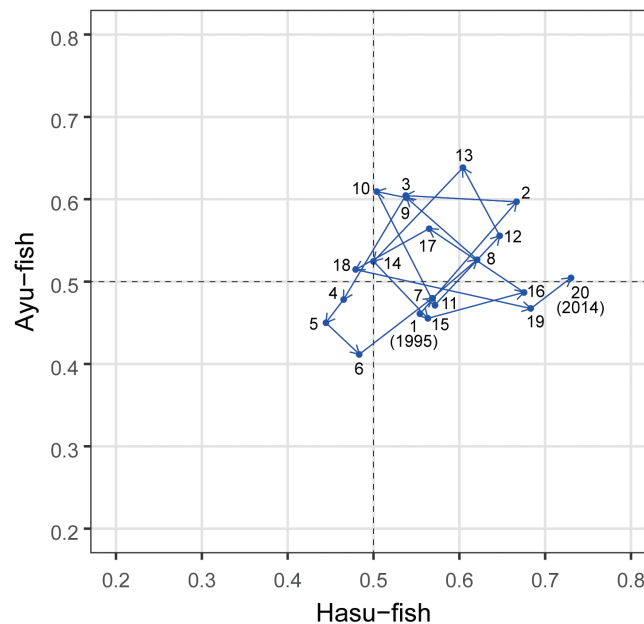


Fig. 4. Relationship of ratios of laterality between *hasu* and *ayu* from 1995 to 2014 at Wani Point. Each dot is numbered in order from the first year (1995) to the last year (2014) of the survey.