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Corrected version:
Impact of the invasive signal crayfish, *Pacifastacus leniusculus*, on native salmonids, *Oncorhynchus keta* and *Oncorhynchus masou*, in Hokkaido, Japan

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Abstract

The signal crayfish *Pacifastacus leniusculus*, whose habitat in Japan is mainly in Hokkaido, is an invasive species that coexists in certain streams with various salmonid species that migrate to the sea. The present investigation focused on two indigenous salmonid species, chum salmon (*Oncorhynchus keta*) and cherry salmon (*Oncorhynchus masou*), sampled from both signal crayfish-inhabited and non-inhabited zones in the Uguisuzawa Stream in Bihoro, eastern Hokkaido. Generalized linear models were used to identify factors that influence the fork length of age-0 individuals of these two salmonid species.

In locales inhabited by signal crayfish, the estimated mean fork lengths of the two salmonid species were significantly larger than those in non-inhabited locales, and the mode of the distribution also shifted toward larger size classes for the two species in these locales.

We therefore postulate that signal crayfish prey on these two indigenous salmonid species, leading to the depletion of smaller individuals, and the observed augmentation in mean fork length and the heightened peak in length composition distribution may be attributed to this predation-induced size selection. The depletion of small individuals in the Uguisuzawa Stream could potentially lead to a reduction in the proportion of individuals migrating to the sea, which would result in a reduction in the quantity of marine-derived nitrogenous compounds.

Key words: invasive species; alien species; salmonid species; predation; sea-run; stream ecosystem

Introduction

Invasive alien species – organisms introduced outside their natural range – present numerous challenges such as predatory behavior affecting native species, habitat alterations resulting in soil modifications, competition for food and space, hybridization with native species, and the introducion of novel parasites and diseases (Elton 1958; Mack 2000; IPBES 2023).

The signal crayfish (*Pacifastacus leniusculus*) is a freshwater crayfish indigenous to the region spanning from southwestern Canada to the northwestern United States (Lewis 2002). This species was introduced into Japan on at least five separate occasions, with targeted releases occurring at fisheries experiment stations across 29 prefectures and in six or more natural water bodies from 1926 to 1930 (Kawai et al. 2002). In recent observations, this species has been identified in 12 prefectures: Hokkaido, Miyagi, Fukushima, Tochigi, Gunma, Chiba, Tokyo, Niigata, Toyama, Nagano, Fukui, and Shiga (Japan Wildlife Research Center 2019; Hoshino et al. 2023; Fuwa and Inamura 2023, Kanno et al. 2024).

The signal crayfish impacts numerous indigenous species through predation on various organisms, including detritus, algae, and benthos (Guan and Wiles 1998; Crawford et al. 2006; Machida and Akiyama 2013). Numerous researchers have reported on the impact of the signal crayfish on fish species, including

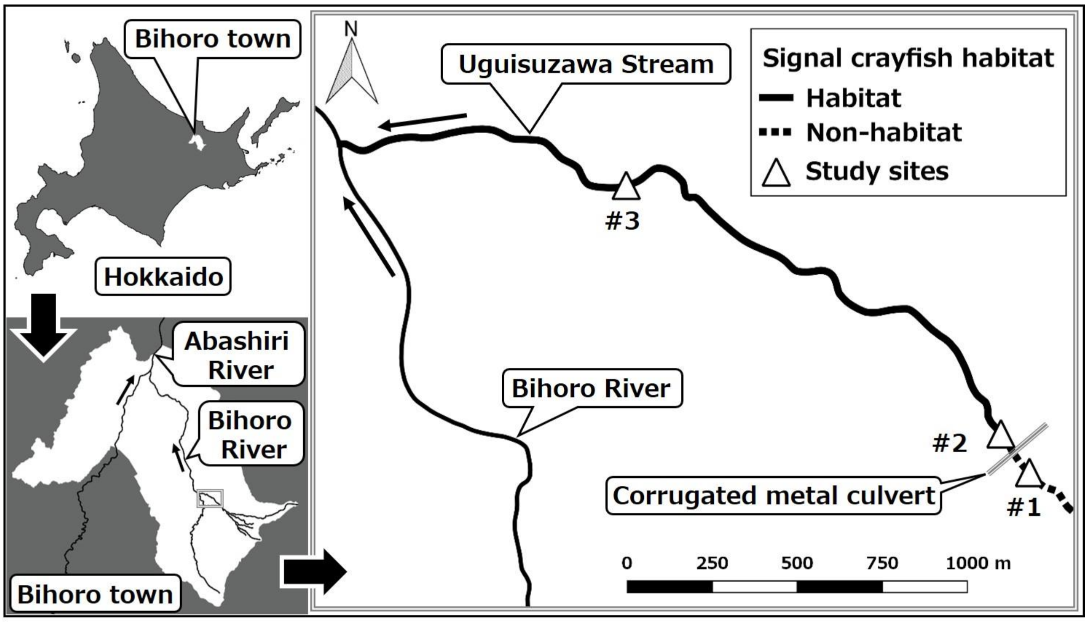

Fig. 1. Map of the study sites. The solid line indicates signal crayfish habitat and the dotted line indicates a non-habitat. Triangles indicate the study sites. Arrows indicate the direction of flow.

a reduction in the density of stone loach (*Barbatula barbatula*) and bullhead (*Cottus gobio*) populations (Guan and Wiles 1996) and predation upon Atlantic salmon (*Salmo salar*) eggs (Findlay et al. 2015). Additionally, there have been reports of the disappearance of small benthic fishes and a decline in the abundance of age-0 salmonids (Galib et al. 2021). In Hokkaido, the principal habitat of signal crayfish in Japan, several salmonid species such as chum salmon (*Oncorhynchus keta*), cherry salmon (*Oncorhynchus masou*) and white-spotted char (*Salvelinus leucomaenis leucomaenis*) migrate from the sea to spawn, and some of them coexist with signal crayfish in a single locale. Nevertheless, information regarding the impact of signal crayfish on salmonid species in Japan is scarce.

The change in size composition can be caused by predation and competition from invasive species (e.g., Takahashi 2002), and such changes serve as crucial indicators for indirectly understanding ecologically significant impacts that are challenging to observe directly (e.g., Rozzi et al. 2023). An investigation into the impacts of signal crayfish on the length composition of fish has yet to be conducted in the world. In addition, invasive species can also have an impact on the ecosystem (e.g., Mile et al. 2023), an understanding of which would be important for the management of these species.

In the present study, we investigated the fork length composition of native salmonid species to understand the impact of signal crayfish on these species. The use of experimental animals adhered to the guidelines of Tokyo University of Agriculture (https://www.nodai.ac.jp/application/files/4316/8966/0320/44.pdf, last accessed on 11 October 2023).

Materials and Methods

Data sampling

Data for this investigation were procured from three study sites along the Uguisuzawa Stream in the Furuume district of Bihoro town in eastern Hokkaido (Fig. 1). The signal crayfish population in this stream is notably influenced by the presence of a corrugated metal culvert (length 5 m) installed beneath a forest road (Fig. 2). The crayfish mainly inhabit the downstream area of the metal culvert (Onimaru and Machida 2009). The observation of salmonid species (chum salmon, cherry salmon, and white-spotted char)

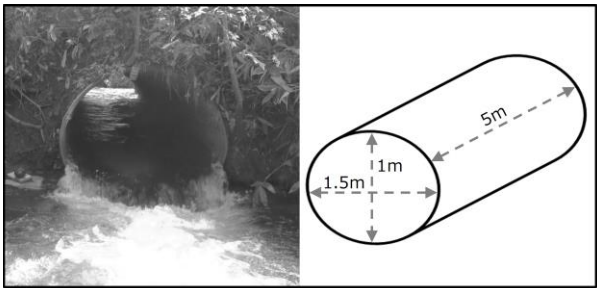

Fig. 2. Corrugated metal culvert in the Uguisuzawa Stream. The photo shows the corrugated metal culvert. The right panel shows a schematic diagram of the culvert.

both upstream and downstream of the culvert suggests that the culvert does not impede the migration of these salmonid species. Study site #1 (Fig. 1) was located immediately upstream from the culvert, encompassing a 55-m section of the stream where signal crayfish had not previously been reported and did not inhabit during our investigation. Study site, #2 (Fig. 1), a 13-m section, was located at 30 m downstream from the culvert, and study site, #3 (Fig. 1), a 90-m section, was located 2.5 km downstream. Habitats of signal crayfish were found and observed only at sites #2 and #3.

Although samples of the above three salmonid species were collected in the Uguisuzawa Stream, the present paper focuses solely on chum salmon and cherry salmon due to the limited number of white-spotted char samples obtained. The survey was conducted in May and June 2016, during early summer when salmonid species typically develop into fry, and when signal crayfish are also more active; preliminary surveys showed that fry had not surfaced prior to May. An electric fisher (Smith-Root, Inc., Vancouver, WA, USA; Model LR-20, DC50-990V, 2600W, 100V, Max 60A), a push net, and a landing net were used to catch the fish samples. The fork length of samples were measured to the nearest millimeter under anesthesia induced by clove oil (NOW Foods, USA) (Soto and Burhanuddin 1995). Once the captured fish recovered, they were released back into the stream.

To identify environmental differences that may affect the growth of salmonid fish, water temperature, water depth, and flow speed were also measured. Since it was impractical to measure the environment of each captured individual, survey areas were set to include both rapids and pools. Water temperature, water depth and flow speed were measured utilizing a water temperature gauge, a tape measure and a propeller-type current meter respectively at six locations within each of the three study sites, i.e. both sides and the center of the stream at the upper and lower limits of each site.

Data analysis

A number of researchers have reported that the stock depletion of salmonid species in freshwater environments predominantly occurs during their early life stage (e.g., Elliott 1986). This vulnerability has been attributed to the limited swimming abilities of alevins, the immediate post-hatch stage, making them more susceptible to predation (Lister and Genoe 1970; Moore and Gregory 1988; Nagata et al. 2002; Urabe 2015). Since the capacity for instantaneous swimming in typical salmonid species increases with body growth (Blaxter and Dickson 1959; Okuma et al. 1998), young fry are also more susceptible to predation.

The present investigation thus focused on small individuals from hatching to approximately one year. For cherry salmon, individual fork lengths of 78 mm or less were categorized as age-0, employing teardown analysis, using the EM algorithm, under the assumption that the natural logarithm of fork length adheres to a multivariate normal distribution (Fig. 3).

Model selection for generalized linear models was applied to identify factors that influence the fork length of each species. The logarithm of fork length served as the response variable that varied with normal distribution. Study sites, presence of signal crayfish, months, the logarithm of the total catch of chum salmon or cherry salmon at the survey site, and the logarithm of the survey zone length were used as

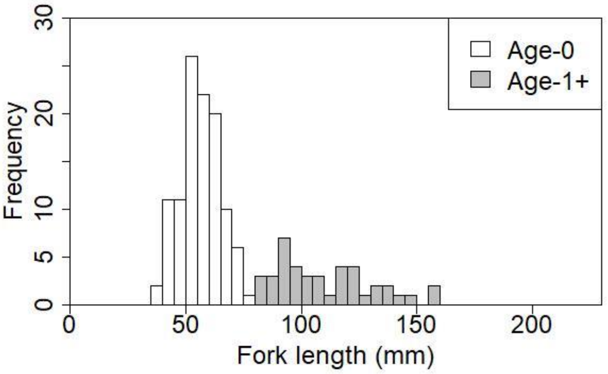

Fig. 3. Histogram of fork length frequency for cherry salmon. Gray and white bars indicate the two estimated cohorts, age-0 and age-1+, respectively.

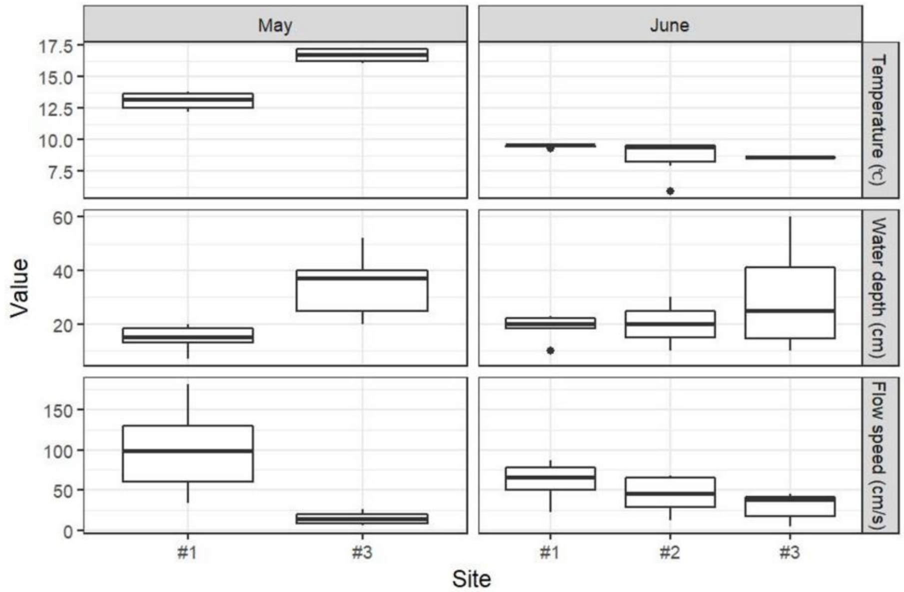

Fig. 4. Data showing water temperature, water depth, and flow speed.

explanatory variables in the models. Akaike Information Criterion (AIC) was then used to select the optimal model. The least squared mean, calculated using the optimal models, yielded estimated values for fork length. A comparative analysis of fork length compositions at the study sites was subsequently conducted. In addition, the Skillings-Mack test was used to examine whether water temperature, water depth, and flow speed differed between locations.

The statistics software R ver. 4.1.2 (R Core Team 2021) was used for all statistical analyses in this investigation.

Results

The recorded temperatures, depths, and flow speeds are detailed in Fig. 4. A total of 304 salmonid individuals were captured in this survey: 65 chum salmon and 49 cherry salmon at #1, 4 chum salmon and 42 cherry salmon at #2, and 84 chum salmon and 60 cherry salmon at #3 (Table 1).

Model selection for chum salmon

Presence of signal crayfish and month were used as explanatory variables in the optimal model for determining the fork length of the age-0 chum salmon (Table 2).

The estimated fork length values for May were 42.06

Table 1. Catch number of each salmonid species by study site and age. (No chum salmon of age-1+ was caught).

Study site	chum salmon	cherry salmon	
	age-0	age-0	age-1+
#1	65	36	13
#2	4	34	8
#3	84	39	21
Total	153	109	42

Table 2. Estimated values of fork length for the optimal model by fish species.

Species	Variable	Estimate	Std. error	t value	p value
Chum salmon	Intercept	4.01	0.11	37.75	< 0.00
	Presence of crayfish	-0.07	0.02	-3.91	< 0.00
	Month	-0.04	0.02	-2.07	0.04
Cherry salmon	Intercept	3.63	0.22	16.51	< 0.00
	Presence of crayfish	-0.13	0.04	-3.18	< 0.00
	Month	0.25	0.06	3.91	< 0.00
	Total catch	-0.29	0.11	-2.65	0.01

mm at the signal crayfish habitats (sites #2 and #3) and 45.01 mm at the non-habitat (site #1), while for June, the values were 40.37 mm and 43.20 mm, respectively.

Model selection for cherry salmon

Presence of crayfish, month, and total catch were also used as explanatory variables in the optimal model for determining the fork length of age-0 cherry salmon (Table 2). When the total catch was averaged based on actual measurements, the estimated fork length values for May were 48.29 mm at the signal crayfish habitats and 55.44 mm at the non-habitat, while for June, the values were 51.93 mm and 59.57 mm, respectively.

Environmental differences between study sites

While no significant differences were observed in water depth and flow speed, significant differences were observed in water temperature.

Discussion

In the two habitats occupied by signal crayfish (sites #2 and #3), the estimated mean fork lengths of age-0 individuals for the two salmonid species as estimated by the optimal models were notably larger than those in the non-habitat (site #1). The mode of the length composition distribution for both chum salmon and cherry salmon, as sampled in this study, shifted toward larger size classes at the signal crayfish habitats compared to the non-habitat across both May and June (Figs. 5 and 6).

The physical downstream movement of individuals was initially considered as a potential factor contributing to variation in fork length. This movement occurs when fish are carried through the corrugated metal culvert by the river current and do not return. Smaller individuals, due to their lower resistance against the flow (Okuma et al. 1998), are predicted to exhibit a larger average fork length upstream if there is a significant impact from the physical downstream movement of fish. In the present study, however, we observed a smaller average fork length upstream than downstream (Figs. 5 and 6), indicating limited influence from physical downstream movement.

We then considered differences in growth attributed to environmental variations between sites. It has been reported that differences in water temperature affect the growth of salmonid fish fry, i.e. growth rates are reportedly the highest for chum salmon when the water temperature is below 14 °C and for cherry salmon when it is below 16.83 °C (Koshiishi 1980; Jiang et al. 2007). Those conditions were met except at #3 in May. Furthermore, water temperatures at the survey sites in May were highest at #3, followed by #1, and in June, the highest water temperature was at #2, followed in order by #1 and #3. Therefore, while significant differences existed between sites, no single site consistently showed a tendency for higher water temperatures, and differences in estimated fork length thus could not be explained by water temperature.

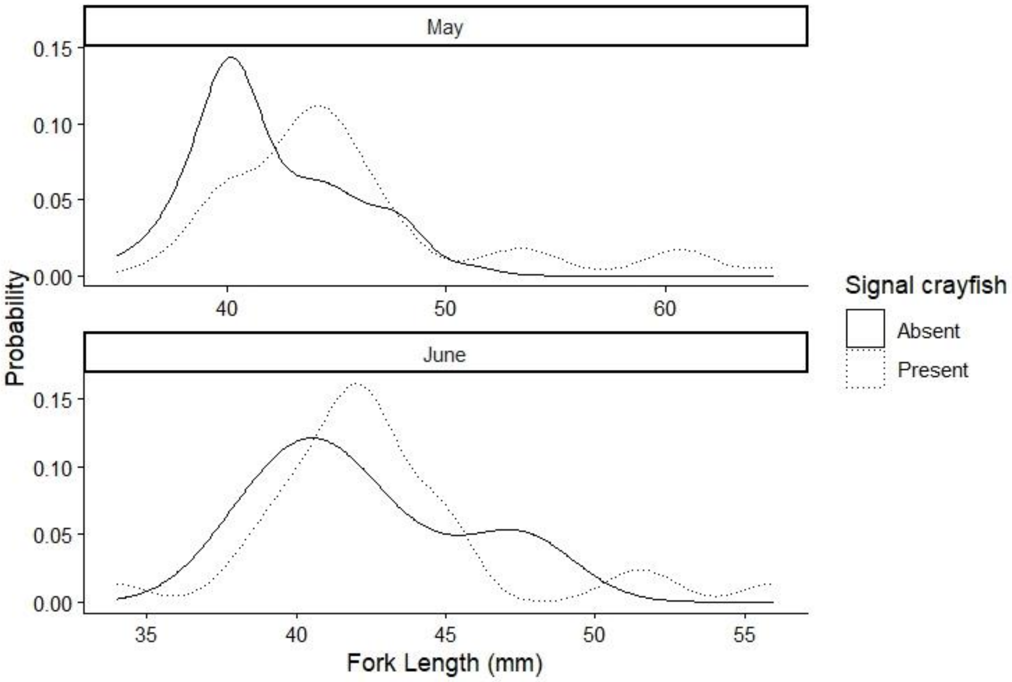

Fig. 5. Density plot of fork length frequency for chum salmon by study site and month. The solid line indicates data at the non-habitat of signal crayfish (#1) and the dotted line indicates data at habitats (#2 and #3).

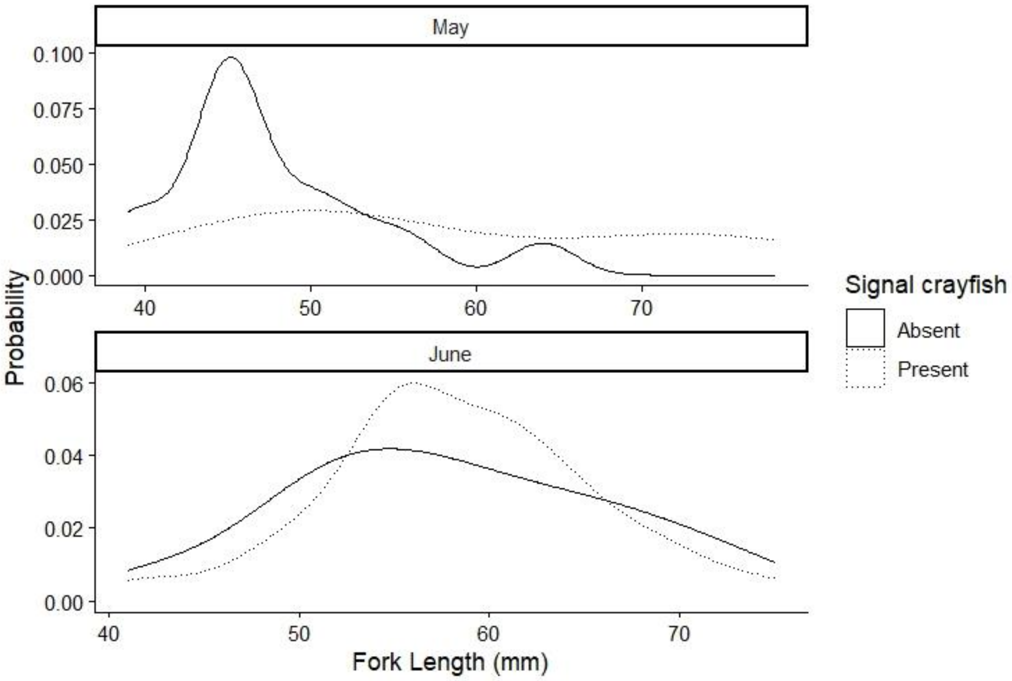

Fig. 6. Density plot of fork length frequency for cherry salmon by study site and month. The solid line indicates data at non-habitat of signal crayfish (#1) and the dotted line indicates data at habitats (#2 and #3).

Fish that are able to withstand a fast-flowing current are generally larger individuals with their more developed swimming ability (e.g., Onitsuka et al. 2009). Although significant differences in flow speed were not observed between survey sites, we initially predicted that #1 with its faster maximum flow, would be more suitable for use by larger individuals, and that #2 and #3, with a slower maximum flow, would be more suitable for smaller individuals. However, the estimates fork length was smaller in individuals collected at #1, indicating that estimated fork length could not be explained by the speed of water flow.

Water depth has been reported to increase juvenile feeding success rates and utilization frequency in deeper areas (Harvey and White 2017; David and Stiling 2024). Although no differences in water depth were observed between survey sites, the larger size of individuals at sites #2 and #3, which had the greatest maximum water depth, aligns with the aforementioned report. On the other hand, the reduction or disappearance of small individuals at #2 and #3 slightly conflicted with earlier research suggesting high fry utilization. In particular, at #2 and #3 in May, the fork length distributions for both salmonid species exhibited a pattern that suggested the disappearance of smaller individuals compared to site #1 where there were no signal crayfish (Fig. 5: around 40 mm for chum salmon; Fig. 6: around 45 mm for cherry salmon).

Impact from other organisms such as density-dependent growth and size-dependent predation could potentially influence the composition of fork length. For cherry salmon, catch numbers were also selected as a factor explaining fork length, indicating that estimated mean fork length decreased when catch numbers were high. This result suggested a trend that was also described in previous studies, i.e. that the growth rate of salmonid fry declines under high-density conditions (e.g., Imre et al. 2005). Furthermore, the presence of signal crayfish was selected as a factor explaining fork length for both chum salmon and cherry salmon, indicating that those fork lengths increased in habitats with signal crayfish. If there was an impact from predation by signal crayfish, it could be anticipated that the predation rate on younger individuals with less developed swimming abilities would be higher. As a result, downstream, there would be minimal impact on the range of fork lengths, and the peak of the average fork length would either increase due to the presence of larger individuals, or the distribution of smaller individuals would decrease, leaving only larger individuals and a narrower range of fork lengths. In this study, the former scenario aligned with our observations for chum salmon in May and June, and cherry salmon in May, while the latter scenario was more consistent for cherry salmon in June. Signal crayfish have been reported to prey on salmonid species (Edmonds et al. 2011), and the increase in the average fork length downstream observed in this study was highly likely influenced by predation from signal crayfish.

Following the invasion of largemouth bass (*Micropterus salmoides*), Nakazawa et al. (2007) observed an increase in the size of the indigenous Isaza goby (*Gymnogobius isaza*). Takahashi (2002) reported on increases in the size of Japanese smelt (*Hypomesus nipponensis*), topmouth gudgeon (*Pseudorasbora parva*), swamp moroko gudgeon (*Gnathopogon elongatus elongatus*), gengorou crucian carp (*Carassius cuvieri*), and northern snakehead (*Channa argus*), as well as a case of size reduction in the Japanese dace (*Tribolodon hakonensis*). Tsunoda (2008) demonstrated an increase in the size of native crucian carp (*Carassius* spp), and size reductions in the Japanese weather loach (*Misgurnus anguillid-caudatus*) and freshwater goby (*Rhinogobius* spp). The findings in our study align with those of earlier research. In addition, our findings that smaller individuals with less developed swimming abilities have a higher predation rate align with those reported by Hasegawa et al. (2021). Although the results of our survey indicate only an indirect impact of signal crayfish on fish, it is important to convey the urgency of the situation suggested by the results. Furthermore, a comprehensive exploration of the signal crayfish's alimentary patterns and an isotopic analysis would enhance our understanding of the crayfish's impact on salmonid species.

Miles et al. (2023) reported that invasive salmonids with overlapping niches may have impacted the behavior of native salmonids and may thus have ecosystem-level implications. The length composition of salmonid species, exemplified by cherry salmon and white-spotted char, is a pivotal determinant influencing the hierarchical arrangement of individuals within a population and, consequently, shapes the entirety of each individual's life cycle. Existing scholarship posits that individuals manifesting larger early growth opt for freshwater-resident forms, while those exhibiting smaller initial growth opt for sea-run alternatives (Morita and Morita 2007). It is often the slower-growing, smaller individuals that adopt the sea-run strategy. Therefore, the depletion of small age-0 individuals by crayfish predation could reduce the proportion of fish migrating to the sea. This would, in turn, decrease the flow of marine-derived nutrients brought back by spawning adults, potentially impacting the entire stream ecosystem productivity (e.g., Gende et al. 2002).

The present study has focused on identifying the impact of signal crayfish on salmonid species with emphasis on predation. In future studies, we would like to broaden the scope of alien species management to encompass the entire ecosystem inhabited by these crayfish and indigenous species and examine it in greater detail.

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