Ph. D. Thesis

Conservation of Arctic lamprey and its fishery culture in Japan

Division of Science for Bioproduction and the Environment
Graduate School of Bioresources and Environmental Sciences
Ishikawa Prefectural University

Hiroaki Arakawa

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General introduction

Lampreys

Lampreys (order *Petromyzontiformes*), a group of jawless fishes without bones, have persisted on Earth for at least 430 million years (Forey & Janvier, 1993). Morphological characters of lampreys typically suggest *cyclostome* paraphyly including hagfishes, that is, that lampreys are the sister group to the jawed vertebrates (superclass *Gnathostomata*) and that hagfishes represent an earlier offshoot from the vertebrate family tree (Docker et al. 2016). *Cyclostome* is taxonomically classified lampreys as a vertebrate and hagfishes as an invertebrate (Nelson 2006). The fossil of an ancestral group of lampreys was of recorded from the Late Devonian period and the Carboniferous period in the Paleozoic era (Janvier 1996; Gess et al. 2006). A fossil record of morphological features similar to anatomically modern lampreys from the late Mesozoic era demonstrates that modern lamprey groups were present by the era (Chang et al. 2006). Lampreys are considered to be primitive vertebrates and have survived at least four of five mass extinction events historically (Docker et al. 2016). The ancestral groups of our vertebrates contribute to providing the resolution for learning the evolution of vertebrates (Oisi et al. 2013; Kuratani et al. 2016).

Lifecycle

Life history phase of lamprey includes 1) larval stage (ammocoete), 2) metamorphosis stage (microphthalmia), and 3) adult stage (Evans et al. 2018). Lamprey species are classified into two different lifecycles; parasitic-anadromous species and nonparasitic-fluvial species, depending on feeding and migrating behavior after metamorphosis (Fig.1, Yamazaki & Goto 2000). Both groups spawn in rivers, and the larvae develop in sand and silt for 3-7 years in fresh water and feed on fine organic matter as filter feeder (Dawson et al. 2015). Metamorphosized juveniles of parasitic-anadromous species migrate downstream to lakes or the ocean where they begin the parasitic stage and back to freshwater for spawning (Moser et al. 2020). In contrast, nonparasitic-fluvial species spend their entire life in fresh water and have a non-trophic during adult stage until spawning (Docker & Potter 2019).

Species

Eighteen parasitic-anadromous species and 23-27 nonparasitic fluvial species are found in the world (Docker and Potter 2019). The earlier lampreys were likely to live in the coastal ocean of fluctuating salinity and prepare them for the subsequent invasion of freshwater following the development of more inland areas (Docker & Potter 2019). From the morphological comparison of parasitic and nonparasitic species, both species possess functional mucosal folds around the inner layer of the intestine, indicating adaptive features for feeding after the metamorphosis stage and these findings suggest that speciation in nonparasitic lamprey speciated from ancestral stocks of parasitic species (Yamazaki et al. 2001). As an intraspecific variation, the freshwater residential or landlocked form (praecox form) occurs in the population of some kind of anadromous species constantly (Docker and Potter 2019). Geographical isolation by physical barriers promotes reproductive isolation in the anadromous population having the landlocked form and establish lamprey speciation (Yamazaki & Goto 2015). In Japan, Arctic lamprey *Lethenteron camtschaticum* (Fig.2), Pacific lamprey *Entosphenus tridentatus*, nonparasitic-fluvial L. sp. N, L. sp. S, Siberian lamprey *L. kessleri* are distributed (Yamazaki and Goto 2016). The Far Eastern brook lamprey *Lethenteron reissneri* was recognized as one species until the 1990s and recently studies taxonomically classified it into two cryptic species (*L.* sp. N, *L.* sp. S) lacking a hybridization (Yamazaki and Goto 1996; Yamazaki and Goto 2000). The freshwater residential Arctic lamprey also has been found in Fukushima and Iwate. This fluvial population in Fukushima is a consequence of geographical isolation following dam construction (Yamazaki et al. 2011).

Ecological importance

Lampreys are important ecologically in the freshwater and ocean ecosystem through their lifecycle. In the freshwater, larva and adult have roles of ecological engineering and contribute to bioturbation. Larval lampreys stay in sediment for most of the life stage in the freshwater (Dawson et al. 2016). Hatched prolarva burrow into sediment and feed on fine organic matter such as leaf litter, algae, and diatom (Appegate 1950; Sutton &Bowen 1994; Shirakawa et al. 2009). Their burrowing and feeding behavior promote physically softer sediment, increase oxygen in interstitial water, and FPOM on the streambed surface (Shirakawa et al. 2013; Boeker & Geist 2016). The chemical and microbial condition also change due to the aerobic condition via larval behavior, including an increase in nitrate concentrations and domination of aerobe bacteria (Boeker & Geist 2016). The nest-building activity on streambeds by spawing adult create patch mound where less cover of fine sediment and reduction in embeddedness and have an effect on benthic invertebrates (Hogg et al. 2014). In addition, the carcass of adult lampreys contributes to supply additional marine-derived nutrients to the terrestrial areas (Weaver et al. 2018; Dunkel et al. 2020).

Lampreys are important food resources in freshwater, brackish water, ocean ecosystem. Through the lifecycle, they exposed to predation by a variety of predators, including mammals (American Mink *Mustela vision*, Pacific harbor seal *Phoca vitulina richards*i, sea lions *Zalophus californianus*, *Eumetopias jubatus*), birds (Great Blue Heron *Ardea Herodias*, goosander *Mergus merganser*, Gulls *Larus* spp. Caspian terns *Sterna caspia*, Double-crested cormorants *Phalacrocorax auritus*), and fishes (White Sturgeon *Acipenser transmontanus*, burbot *Lota lota*) (Fig.3, Beamish 1980; Clemens et al. 2019; Close et al. 1995; Collis et al. 2002; Condit & Le Boeuf 1984; Sjöberg 1980; Wolf & Jones 1989). In some region, native lampreys have been preyed by the introduced exotic species such as Brown trout *Salmo trutta*, European catfish *Silurus glanis*, Northrn Pikeminnow *Ptychocheilus oregonensis*, Smallmouth Bass *Micropterus dolomieu* (Boulêtreauet al. 2020; Hasegawa et al. 2007; Porter 2013; Schultz et al., 2017). Adult lampreys have higher caloric value than salmonids (*Onchorynchus* species), ranging from 5.92~6.34 kcal/g wet mass (Whyte et al. 1993) whereas salmon average 1.26~2.87 kcal/g wet mass (Stewart et al. 1983). Lampreys are slower and easier to capture than salmon and could provide an important predation buffer for upstream migrating adult salmon from sea mammals and downstream migrating juvenile salmon from avian and fish predators (Close et al. 2002).

Cultural importance

Lampreys have historically been important culturally and valued for food (Docker et al. 2015). The consumption area spread worldwide including Europe, North America, New Zealand, Japan. Especially in Europe, the economic value of Sea lamprey *Petromyzon marinus* is higher. The total catch of sea lamprey is estimated at 140 tons (15,4 million FF) in French at the end of the 20th century (Castelnaud 2000) and were 57 tons (the highest during 1986-2011) in the Iberian Peninsula (Araújo et al. 2016). European river lamprey *Lampetra fluviatilis* is also popular in northern Europe. The total catches of European river lamprey were 130 tons (2.7-3.0 million individuals) in Finland in the early 1970s and 147 tons in Latvia during 1974-1979 (Sjöberg 2011). Pacific lamprey *Entosphenus tridentatus* is important as a food resource and ceremonial purposes for native American tribes in the western United States for thousands of years (Close et al. 2002; Petersen Lewis 2009; Docker et al. 2015). In New Zealand, Pouched lamprey *Geotria australis* is an important food source for the indigenous Māori (Stewart & Baker 2012). In Japan, Arctic lamprey is captured throughout Hokkaido Island to the middle of Japan and along the Sea of Japan (Kataoka et al. 1980; Murano et al. 2008; Arakawa et al. 2018). Due to its rich content of Vitamin A (MEXT 2015), Arctic lamprey has been used as Chinese medicine for preventing night blindness and an important food resource for residents in rural area "*satoyama*" (Arakawa et al. 2018).

Population Decline

Lampreys are at risk due to an anthropogenic pressure and the conservation status of 33 species (75%) has been assessed at a global scale (Fig.4, Maitland et al. 2015). In the northern hemisphere, one species Miller Lake lamprey *Lampetra minima* had been extinct by poisoning with ichthyocides during the 1950s (Miller et al. 1989; Renaud 1997). The magnitude of lamprey extinction observed since 1500 is at least 42–1400 times the magnitude observed during the K–Pg mass extinction and this estimation suggests that extinction of all lampreys might occur in 627–19,494 years (McCallum 2015).

Anadromous lampreys are recognized as important food resources for human beings, but their population have decline seriously (Clemens et al. 2017; Mateus et al. 2012). Eleven threats to these anadromous lampreys have been identified: climate change, shifting oceanographic regimes, artificial barriers, low water quantity/flow management, habitat degradation, poor water quality, reduced habitat availability, host and prey availability, predation, overharvest, and disease (Clemens et al. 2020). Especially, artificial barriers such as dams, weirs and culverts are key and critical threat since they impede upstream migrating by spawning adult and downstream emigrating by larvae and juveniles (Clemens et al. 2020; Moser et al. 2020) The fishways built next to the dams are designed for ascending salmon and most Pacific lampreys cannot ascend the fishways

(Moser et al. 2002). Mataus et al. (2012) estimate that 80% of accessible habitat in the Iberian Peninsula has been lost by artificial barriers (dams and weirs). The probability of occurrence of Arctic lamprey in Hokkaido, Japan, is reduced above dam (over 5m height) (Fukusima et al. 2007). From tagging and tracking monioring for spawning European river lamprey, the passage rate is low even in low-headed weirs (lower 5m height) and spawning sites are are limited to downstream (Lucas et al. 2009). In addition, these low-headed weirs cause a delay in migration (mean: 6.3 days per obstacle) and a significant reduction of migrants upstream of each impoundmen (Silva et al. 2019). To improve connectivity between segregated habitats, the more-acceptable fish passages have been tested, installed and the upper population has been increased (Almeida et al. 2002; Moser et al., 2011; Pacific Lamprey Technical Workgroup 2017). The negative impact of large artificial barriers on anadromous lamprey is undeniable but the biological information (migrating pattern and behavior) and ecological information (spatial distribution and suitable spawning habitat) are insufficient to conserve and manage these species.

Arctic lamprey in Japan

Arctic lamprey is one of the anadromous lamprey species. Species distribution is in the Arctic Ocean, North Pacific, and associated freshwater drainages in Canada, the United States (Alaska), Japan, and Russia (Clemens et al. 2020). In Japan, its distribution range in Japan is the coast of the Sea of Japan from Hokkaido to Shimane and the coast of the Pacific Ocean from Hokkaido to Ibaraki (Kawanabe and Mizuno 2001). Arctic lamprey has mainly been caught in the Ishikari River, Hokkaido, where it has been used for general consumption by the local population and sustains the local lamprey festival (Murano et al. 2008). In Noto Peninsula, Ishikawa in central Japan, arctic lamprey has been caught predominantly in spring using a specialized fishing gear called “Kanko” (Arakawa et al. 2018). However, this species has been designated as a vulnerable species in the Red Data Book of Japan due to serious population decline (Ministry of the Environment 2007). Management actions have included artificial propagation, adult translocation, larval habitat restoration, and outreach (Hokkaido Government Ishikari Sub-prefectural Bureau, 2007, Kataoka, 1985, Kataoka and Hoshino, 1983, Takeuchi et al., 2007). The latest resource management for Arctic lamprey was in 2006 in Hokkaido but even after that, the management has not conducted in Japan.

Threats to Arctic lamprey

Threats to Arctic lamprey are not well understood, but likely include climate change, oceanographic regimes, interactions between climate change and oceanographic regimes, artificial barriers, water quantity/quality, habitat degradation, decreased water quality, host/prey availability, overharvest, and predation (Clemens et al. 2020).
Japan is located at its southern limit of the distribution. Rising temperatures due to global warming greatly influence populations of cold-water organisms living in the southern portions of their ranges (Meisner 1990). However, the basic thermal tolerance of larval Arctic lamprey and microhabitat in the river located in the southern limit are not well characterized.

In addition, upstream migration is interrupted by artificial barriers, the distribution of Arctic lamprey is limited to areas downstream of the structure (Fukusima et al. 2007; Murano et al. 2008). Because warm temperature promotes the maturation of adult lamprey (Clemens et al. 2009), lampreys in warmer areas may spawn earlier and further downstream. The interaction between the limited distribution to downstream areas and warming river temperature could affect the maintenance of the population at the southern limit of their range. The spatial distribution pattern of larva and adult of in river is necessary to assess the impact of artificial barriers and river modification. However, these information are shortage throughout Japan.

Overharvest is also one threat to Arctic lamprey. Information about the harvest and the fishery culture are collected from only Hokkaido and Ishikawa (Arakawa et al. 2018; Murano et al. 2008). These locally restricted records could complicate resource management. Acquisition of data on the distribution and abundance in freshwater is needed for all anadromous lamprey management. (Clemens et al. 2020). Inland biodiversity in Japan had been affected by anthropogenic impact including dam construction and river modification after the 1960s (rapid economic growth) (Goto 1997). Therefore, dynamics of distribution and abundance prior (past) and posterior (present) the 1960s may provide a insight for assessing current situation. However, freshwater fishery statistics in Japan have only been monitored in the last 1 to 3 decades and provide insufficient information (Katano and Matsuzaki 2012). Historical information about the lower-concerned Arctic lamprey is very limited and distribution, abundance, and dynamics are unknown. These information gaps prohibit the management progress.

Objectives

This study main objective is to collect ecological and ethnobiological data of endangered species "Arctic lamprey" to conserve species and its fishery culture. First, we interviewed with inland fishery cooperatives (FC) to organize information about Japanese lamprey fishing including distribution of fishing ground, method (gear, season), and ecological knowledge (**Chapter 1**). To determine the river and where arctic lamprey were historically caught and its geographical characteristics before river modification projects occurred, we conducted the estimation using the two information resources (scientific data: fishery statics, ethnobiological data: inland fisherman) (**Chapter 2**). Historical habitat potential in Japan for Arctic lamprey and its decline sicario due to global warming were predicted using information from inland fisherman by species distribution model (**Chapter 3**). To reveal thermal tolerance (incipient lethal temperature, sub-lethal temperature), we conducted two rearing experiment using young of year larvae (**Chapter 4**). In Noto peninsula located at the southern limit, 3 lamprey species (Arctic lamprey, *L.* sp. N, *L.* sp. S) are distributed. To reveal the distribution pattern and the interspecific difference in microhabitat in summer, we conducted larvae sampling and environmental measurements from downstream to headwater (**Chapter 5**). To evaluate the spatial distribution of adult Arctic lamprey and impact of low-head barriers in spawning season, we conducted eDNA analysis and compared eDNA concentration longitudinally and among two different seasons (**Chapter 6**). Exotic species introduced into freshwater ecosystem have impact on native species population and original biodiversity. Larval lamprey also exposed to threat of these exotic predator, but the impact is unknown and assessing method is not established. To evaluate the predation threat to larvae, rearing experiment was conducted using larval Pacific lamprey and Western brook lamprey as preys and various native and non-native fishes from the Columbia River Basin species as predators in confined tanks (**Chapter 7**). To improving assessing method for lampreys in prey-predator relationship, we analyzed stomach contents consisted by larvae from predatory fishes and evaluate whether the lamprey genera/species and their parents could be determined for any of the consumed larval lampreys (**Chapter 8**).

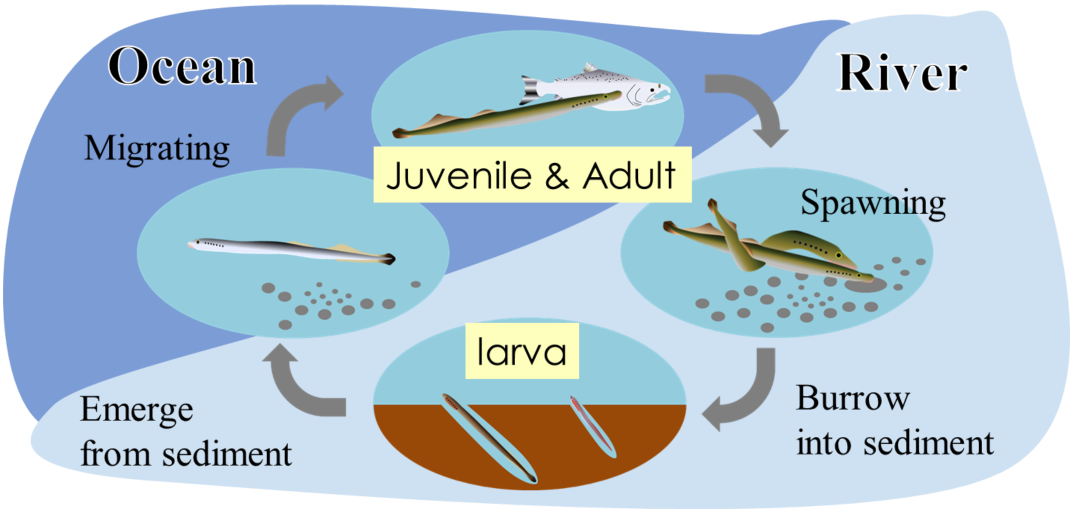


Fig. 1 Lifecycle of anadromous lampreys

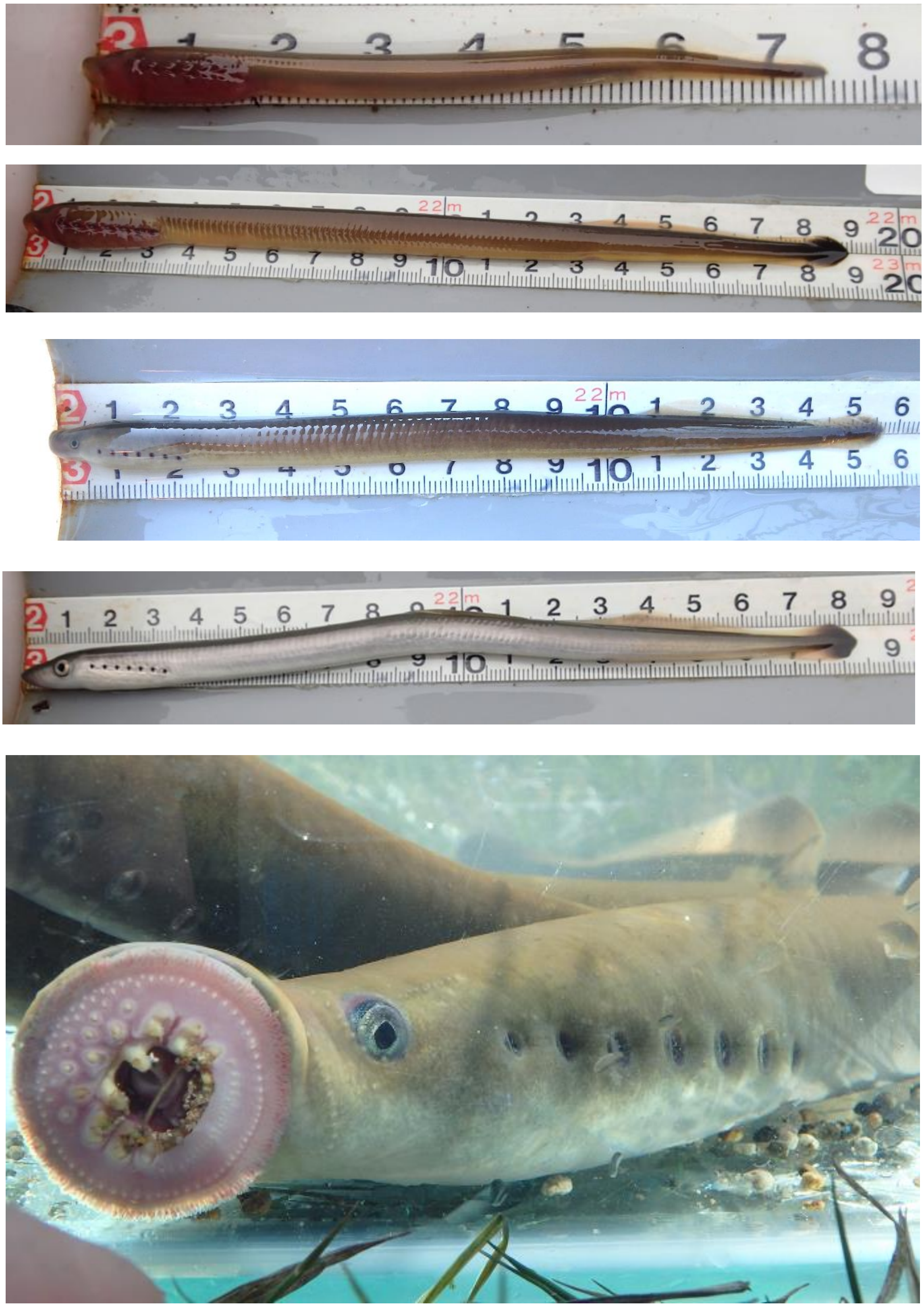


Fig. 2 Arctic lamprey (in order; small larva, large larva, transforming larva, transformed microphthalmia, adult)

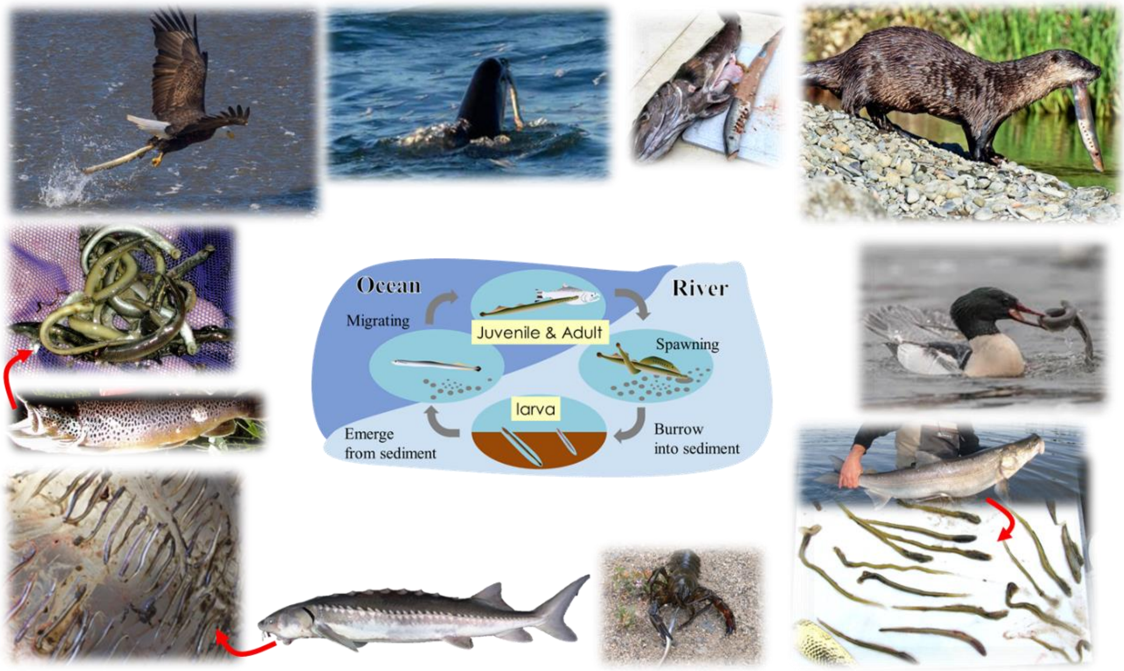


Fig. 3 Various predator species of lampreys throughout their lifecycle

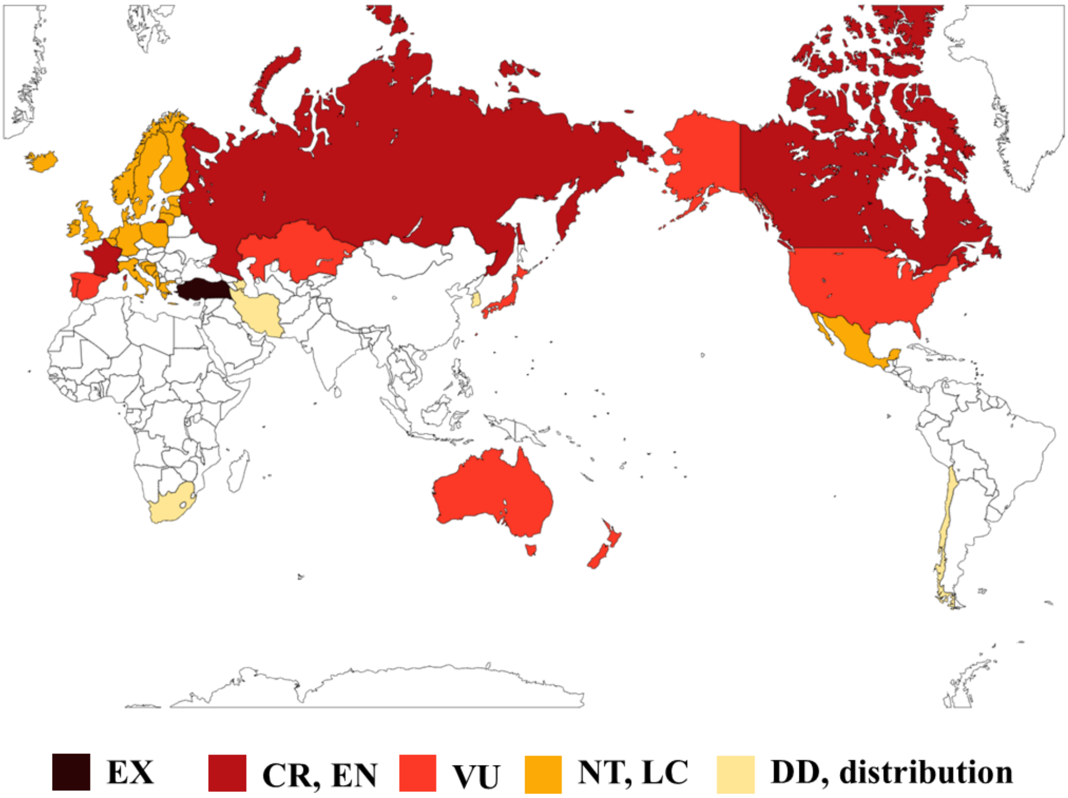


Fig. 4 Species status of lamprey species in the world

Chapter 1 Traditional fishing for Arctic lamprey (*Lethenteron camtschaticum*) along the Sea of Japan Coast

Introduction

Arctic lamprey (*Lethenteron camtschaticum*) is an anadromous parasitic lamprey species distributed in Japan, Russia, and Alaska, where it is harvested and consumed (Kawanabe and Mizuno, 1989; Orlov et al., 2014). In Alaska, residents along the Innoko and Yukon Rivers harvest this species by ice-fishing and use it as source of food, oil, and skin (Brown et al., 2005). Traditional fishing and food cultures are found in Hokkaido and Ishikawa, Japan (Murano et al., 2008; Arakawa et al., 2018). However, the Arctic lamprey catch in Japan has decreased and it is listed as vulnerable in the Red Data Book of Japan (Ministry of the Environment, 2007; Arakawa et al., 2018). A further decline could threaten the sustainability of the local fisheries.

Traditional ecological knowledge is defined as the general cumulative body of knowledge, practices, and beliefs acquired by adaptive processes and handed down through generations by cultural transmission, about the relationships of living beings (including humans) with one another and their environment (Berkes et al., 2000). For fishing, these local practices can provide insight into the conservation of biodiversity and sustainable resource management. Information on aquatic organisms can be obtained from sources, such as indigenous people (Petersen, 2006; Sheoships, 2014) and local fishers (Lopes et al., 2019). Information from the latter resource is known as local or fishers' ecological knowledge (LEK or FEK) and is used to estimate fish distributions (Lopes et al., 2019). By using fisher's memories, their ecological knowledge can provide critical information for the management of fishery resources, including interannual, seasonal, lunar, diel, tide-related, and habitat-related differences in the behavior and abundance of target species (Johannes et al., 2000). However, several studies have reported that the loss of local and indigenous knowledge driven by globalization, modernization, and market integration is likely to threaten the conservation of biodiversity (Aswani et al., 2018).

Information about the traditional lamprey fisheries in Japan has not been organized and the ecological knowledge developed through fishing might be lost. From scientific research, the occurrence of Arctic lamprey in rivers is limited to downstream of dams (Fukushima et al., 2007) and artificial barriers, including dams, culverts, weirs, and tide gates, threaten all anadromous lampreys (Clemens et al., 2020; Moser et al., 2020).

Therefore, knowledge of their spawning migration behavior in freshwater is essential for restoring river connectivity for species conservation. However, the spatial distribution and the migration pattern are not known due to a shortage of long-term monitoring. Therefore, the ethnographical fishery relationship between inland fishers and spawning Arctic lamprey has the potential to provide critical, supplemental information for resource management.

This study interviewed members of inland fishery cooperatives (FCs) to organize information about Japanese lamprey fishing, including the distribution of fishing grounds, methods (gear and season), and practical knowledge. The FCs comprise local organizations of fishers. We interviewed fishers in the FCs since their information reflects the fishery status within each area. Arakawa et al. (under review, Chapter 2) examined the distribution of Arctic lamprey and its changes based on fisher's knowledge and historical inland fishery statistics. This current study describes the fishing methods and fishers' ecological knowledge to understand lamprey behavior and contribute to species management. We obtained details of the fishers' knowledge and temporal changes in the harvest and the number of fishers from face-to-face interviews and demonstrations on the fishing grounds.

Materials and Methods

We conducted structured interviews with representatives of 109 inland FCs (63 river basins) along the Sea of Japan coast and 25 inland FCs (15 river basins) along the Pacific Ocean coast by telephone. A fisher or staff in each FC was asked about 1) the presence of fishing activity for Arctic lamprey in the past and present and 2) fishing methods (gear, fishing grounds, and season) if they reported fishing activity. Arakawa et al. (under review, Chapter 2) analyzed quantitative data to assess the historical distribution. Here, we organized qualitative data to classify Japanese lamprey fishing based on its characteristics. Additional face-to-face interviews were conducted with fishers of 10 FCs with active lamprey fishing. We asked the fishers about 1) the detailed techniques used and their knowledge of lamprey fishing, as a qualitative question, and 2) the total catch and the number of lamprey fishers in the past and present, in semi-constructed interviews. For six of the 10 FCs, we accompanied members while lamprey fishing. Both interview were conducted throughout 2019.

Results

Arctic lamprey fishing

Along the Sea of Japan coast, Artic lamprey fisheries were recorded at 62 (30 river basins) of 109 FCs (61 river basins) in the past, while active fisheries had decreased to 15 FCs (nine river basins, Fig. 1). Along the Pacific coast, Arctic lamprey fishery was recorded at three (three river basins) of 25 FCs (61 rivers), in the past only. Of the FCs reporting past fishery activity, 35 FCs confirmed the fishing methods and the other 27 FCs were not sure (Fig. 2).

Of the 35 FCs, 16 FCs harvested lampreys by set net fishing using "*Dou*" (cone tubes), fyke nets, and baskets (Fig. 2) and 22 FCs caught lampreys using hooks, by hand, or with fishing nets (Fig. 2). Multiple methods were used in some FCs. The fishing grounds for set net fishing were mainly in the lower and middle reaches of large rivers (Figs. 1 and 2). The target in set-net fishing was harvesting migrating lampreys.

There were two fishing grounds for catching lamprey: at artificial barriers such as weirs or at spawning beds in the upper-middle reaches and tributaries. Ten FCs caught lampreys below barriers while 16 FCs caught lampreys in spawning beds. Accidental lamprey catches while fishing for other species were reported in four FCs. We did not classify the accidental catches as fishing for lamprey since they did not reflect continuous fishing activity and did not involve a long-term relationship between fishers and lamprey. Fishing for Arctic lamprey was classified into 1) set-net fishing or catching lamprey at 2) artificial barriers or 3) spawning beds. Details of the fishing methods and knowledge of lamprey fishing are described in the next section based on 10 face-to-face interviews.

Three types of lamprey fishing

Type 1

The Iwamigawa FC is downstream in the Omono River, Akita, and has harvested lampreys from the estuary near the sea by longline fishing using multiple cone tubes. The trap consists of 60 plastic cone tubes [large diameter (LD) 39 cm, opening diameter (OD) 3 cm, length (L) 100 cm, Fig. 3a) connected to a 200 m mainline by 3 m branch lines. This trap was set across the river and the cone tubes opened downstream. The traps were checked once every 4 to 7 days. In the past, the cone tubes were made of bamboo (LD 30 cm, OD 3 cm, L 120 cm, Fig. 3b). The fishing season is from October to next February (main season Oct–Dec). A local fisher said that Arctic lamprey was rarely caught when water was clear or at low tide, while there were many lampreys in the traps after rain. In the past, 60 lampreys/fisher·day (L/F·D) were harvested, and the traps were checked every day; at present, 10 L/F·D are collected. The total catch during the main 3-month season was 6000 L/F in the past and 50–100 L/F at present. The catch fell below 1000 L/FM in 2000 and has been decreasing since then. While there were previously eight fishers, there are only three at present.

The Senboku Seibu FC also conducts longline fishing, but in the middle of the mainstream of the Omono River, Akita. They use 20-30 cone tubes (LD 30 cm, OD 3 cm, L 70 cm) made of polycarbonate resin connected to the mainline (Fig. 4). The fishing season is from October to the next April (main season Oct–Nov). The line is installed in

1-m-deep water, with the traps at a depth of about 0.5 m. A fisher said that if the cone tubes were placed on the bottom of the river, they would fill with sediment. In the past, the fishers used cone-shaped woven-rush mats filled with willow branches. However, since there was no funnel-shaped entrance, the fishers had to lift the traps carefully so that the lampreys would not escape. There were numerous lampreys in the traps when river flow increased, but the flow could be too high for fishing. The daily catch was 200–300 L/F·D in the past and 10 L/F·D at present. The total catch during the season reached 2000–4000 L/F. In the past, there were more than 30 fishers, while there is one at present. In a conservation effort, the FC releases some of the harvest above the weir in spring.

The Mogamigawa Dai Hachi FC is in the middle reach of the Mogami River, Yamagata, and conducts lamprey fishing using cone tubes made of plants. The cone tubes are not connected to a longline, but are roped to poles. The fishers work from a boat to place the traps into the river and collect them the next day. There are two fishing seasons: from September to the next spring and from April 10 to May 5. The daily catch was 200–300 L/F·D in the past and is 10 L/F·D at present. There were over 30 fishers in the past and only two at present. As a conservation effort, for 60 years the FC has released larvae they propagate.

The Iwakigawa FC fishing ground is the middle and lower mainstream of the Iwaki River, Aomori. In the past, the fishers used cone tubes made of plants, but now use metal trapezoidal baskets (LD 30–40 cm, OD 3 cm, L 70 cm). The entrance to the basket is square and it narrows to a 3 cm quadrangle at the opening. Baskets are roped to poles and installed on the river bottom at a depth of around 60 cm. The entrance faces downstream and the opposite end is inclined upward to buffer the water. The fishing season is from the end of April to May. The daily catch was 300–400 L/F·D in the past and is 4–5 L/F·D at present. In the past, type 3 fishing using hooks was also conducted and the catch exceeded 100 L/F·D. Presently, there are 5–10 fishers, while there were many (both type 1 and 3) in the past.

The Matsuhama FC harvests lamprey using a fyke net in the Agano River Estuary, Niigata. The fyke net consists of a guide net and bunt attached to a pole fixed in the riverbed in water 3–3.5 m deep. The traps face downstream. All of the fishing work is done from a boat (Fig. 5). The fisher said that the traps should be placed on an inclined riverbed, since lampreys prefer this geographical feature for migration. The fishing season is from December to the middle of January. The fisher said that they could harvest many lampreys at night with a new moon, but not with a full moon. The daily catch was 100–150 L/F·D in the past and is presently 5-6 L/F·D. There were 10–20 fishers in the past and only one at present.

The Teradomari FC fishes for lamprey in the estuary in the Ookoudzu flood control channel of the Shinano River. The fisher places an “*Otoshidamo*”, a kind of fyke net without a guide net, from the riverside (Fig. 6). The entrance frame is a 2-m-high, 0.5-m-wide rectangle and the bunt is composed of multiple 8-m-long funnels. This trap needs to be placed at an appropriate site and depth due to the lack of a guide part. The fisher said that the traps were set beside the riverbank, since lampreys tended to migrate nearer the bank than in the line of maximum depth. The depth of the fishing ground was 3–4 m and the traps were set at a depth of 1.5–2 m. In the past, they also harvested lampreys by sinking a scoop net in the river for several tens of minutes. The fisher said that many lampreys were captured at night when the water was choppy, but very stormy weather limited the placing of the traps safely. There were two fishing seasons: from October to the next January and from March to April 10 (main season Oct–Dec). In the past, the size of the catch was unknown, but so many lampreys were harvested that they were crushed in the traps due to the high physical pressure. The present daily catch was only 10 L/F·D. There were 4–5 fishers in the past and only one at present. As a conservation measure, the FC released 20% of the harvest in the mainstream of the Shinano River.

Type 2

The Senboku FC is located in the middle mainstream of the Omono River, Akita. The fishers catch lampreys at weirs using hooks. The river is around 100 m wide and high water volumes prevent fishers from entering the river. Therefore, fishers use a 3-m-long rig made of three fishhooks and a fishing pole (Fig. 7). The fishers stand at the riverside of the lower weir and jig the hooks up and down at night. The fishing season is from October to the next May. Many lampreys have been captured at night with a new moon or when the river water rose and became muddy. In the past, fishers worked from 17 PM to 4 AM, but with the decreasing lamprey harvest, they now work from 17 PM to 21 PM. The daily catch was 150 L/F·D in the past and is presently 20 L/F·D. There were 20–30 fishers in the past and are 2–3 at present. As a conservation effort, the FC has released part of the harvest in the upper reaches of tributaries.

The Yanagida Kasen FC catches lampreys in the middle mainstream of the Machino River, Ishikawa. The fishers used a 3-m-long “Kanko” hook made of wood and hooked piano wire. At night, they stand above the weir in the river and jig for lampreys below the weir (Fig. 8). The fishing season is from December to the next March. A fisher said that lampreys were caught when the temperature started to get warmer and the river flow rose due to rain. The daily catch was 100 L/F·D in the past. At present, they sometimes harvest a few lampreys (1–2 L/F·D). There were 20~30 fishers in the past and are 1–2 at present. In the past, type 3 fishing was also conducted using a short version of the same type of hook (length 1 m). The spawning beds are found in riffles in knee-deep water. The type 3 fishing is done from dusk to 19-20 PM. To find spawning lamprey, the fishers walk in the river holding a carbide lamp.

The Akagawa FC used a unique fishing technique in the lower mainstream of the Aka River. In the past, the fishers got into the water up to their shoulders below the groundsill at night, facing downstream. They waited for a lamprey to attach to their bodies and grabbed them by hand with cotton or rubber gloves. A wooden board was also used to weaken the river flow and attract lampreys by holding it in front of them. Since the fishing was conducted in the cold-water season (autumn to early winter), the fishers warmed at a fire beside the river and by drinking alcohol. This method is no longer used. Now fishers do not get into the river, but grab lampreys at shallow sites close to the shore using wooden boards (Fig. 9). There are two fishing seasons: from September to November and from April to May 10. Lampreys are not harvested with bright moonlight or after agrochemical spraying upstream. The fishing is done for 2–3 hours after sundown. The daily catch averaged 500 (max 1000) L/F·D in the past and is 20–30 (max 100) L/F·D at present. There were more than 10 fishers in the past and three at present.

Type 3

The Anigawa FC is one of a few FCs still conducting Type 3 fishing. The fishing ground is in the tributaries of the Yoneshiro River. The fishers catch spawning lampreys by hand or with hooks. The 1–1.4-m-long hooks are made of cedar wood or plastic (a ski pole) with a metal hook. The 1.4-m-long hooks are used from a boat with a boxed water glass to jig for lampreys on the bottom of the river at depths over 1 m. In shallow water at depths of around 15 cm, fishers wearing waders walk closer to spawning beds and jig using a 1-m-long hook or grab lampreys by hand. A fisher said that the lamprey spawning beds tended to be at the heads of riffles and they needed to catch male lampreys before catching female lampreys because the males dispersed if the females were collected first. The fishing season is from middle April to May at present and was from June to July in the past. The catch throughout the season was 300 L/F/hour in the past and 200–300 L/F at present. There were 30–40 fishers in the past who rarely had boats and there is only one at present.

Summary of the three fishing types

The harvest had decreased in all FCs, with the maximum declines in the Iwamigawa, Iwakigawa, and Yanagidakasen FCs to 1% of past levels and the minimum decline in Senboku FC to about 10%. The number of lamprey fishers has also decreased, and few members remain in each FC. Four FCs also conducted conservation efforts independently. One FC artificially propagated and released larvae and three FCs released some of the adult lampreys in the upper reaches or tributaries

Prefectural species Status and fishery regulation

In 2000s, Arctic lamprey were designated as Critical Endangered (CR, EN) in 1 prefecture (pref. as follow, 6%), Vulnerable (VU) in 2 pref. (13%), Lower Risk (LR, NT) in 1 pref. (6%), data deficient (DD) in 2 pref. (13%), and not listed in 9 pref (56%, Table1).The prefectures located in southern area such Fukui, Hyogo, Shimane, were tended to list Arctic lamprey as an endangered species. 11 prefecture (69%) treated Artic lamprey as not-endangered species designating DD or not-listing. In contrast, in 2010s, Arctic lamprey were designated as CR in 4 pref. (25%), VU in 5 pref. (38%), LR in 3 pref. (19%), DD in 2 pref. (13%), and not listed in 1 pref. (6%, Table1). The status of threatened and Lower risk had increased to 81 % (12 pref.). The status of DD or not-listing had decreased to 19% (4 pref.)

According to the latest version of inland fishery adjustment regulation, Arctic lamprey fishing was regulated in only 3 pref. (13%) of Hokkaido, Yamagata, and Niigata (Table1). Lamprey fishing in Hokkaido was regulated by selling fishing right and limiting fishing season. In Niigata Prefecture, the license from prefectural government were needed for the fishing. In Yamagata, the fishing during spawning season (May 10-June 30) and capturing small individual (TL under 30 cm) was prohibited.

Discussion

Characteristics of Japanese lamprey fishing

A variety of lamprey fishing methods has been used along the Sea of Japan coast as determined by river size, the aquatic environment, and lamprey behavior. Type 1 set net fishing was conducted in the lower and middle mainstream reaches by longline fishing with cone tubes, fyke nets, and baskets. The same method using cone tubes and basket traps or *Dou* is common for Arctic lamprey fishing in Hokkaido, Japan (Murano et al., 2008). Set-net fishing using fyke nets is common in the Scandinavian Peninsula, Baltic States, and Iberian Peninsula (Sjöberg, 2013; Araújo et al., 2016). Historically, small baskets made of plants were used in Finland but, since 2000, these have been replaced by large metal and plastic fishing gear, such as fyke nets (Sjöberg, 2011). In Japan, the use of large fyke nets was less common than the use of cone tube traps because of geographical restrictions. Rivers in mountainous areas of Japan flow rapidly due to the steep topography. In addition, the inland fishing season for lamprey is from winter to spring when the water volumes are increased because of the melting snow. These features restrict the use of large set net fishing gear. By contrast, cone tubes fixed by longlines and floats are easy to manage, which might promote their utilization downstream and in mainstreams. The depths at which the nets are set can be controlled by weights in the traps and the water current (Nashimoto and Sato, 1985). Sea lampreys do not migrate in the surface layer (< 1 m) (Holbrook et al., 2015). At the bottom of the streambed, the fishing efficiency deteriorates due to debris flow. In Hokkaido, lamprey traps are set at intermediate depths (Murano et al., 2008). Japanese type 1 set-net fishing has developed in accordance with the topography to harvest lampreys efficiently.

In type 2 fishing, fishers catch lampreys concentrated below artificial barriers in the middle reaches, and in second-class rivers with smaller water volumes. Similarly, indigenous people on the west coast of the USA and New Zealand catch lampreys concentrated at falls by hand or with nets (Close et al., 2002; Jellyman et al., 2002). The Japanese lamprey fishing grounds are at weirs constructed for irrigation and flood control. The type 2 fishing gear mainly consists of a rod and fishhooks. The shapes of the hook are similar, but the rod lengths differ depending on the environment in the fishing ground. Hooks are also used for type 3 fishing, but are shorter (1 m) for use in shallower rivers. In the Iberian Peninsula, wounding gear called "*Galheiro*" is used, with longer versions for jigging from riverbanks and smaller ones for use in the water (Araújo et al., 2016). Shorter hooks are also used in the Klamath River Estuary, in the USA, to hook Pacific lampreys by casting from the shore (Petersen, 2006). The Japanese gear used for catching Arctic lamprey was developed depending on the river size and environment.

Type 3 fishing to catch lampreys in spawning beds was conducted in the upper reaches and tributaries. However, fishing at spawning beds is not common in other countries because harvesting spawning lampreys has a negative impact on their reproduction and lampreys caught in spawning beds taste different from those captured in estuaries. The energy is expended as the anadromous lamprey migrate upstream and spawn (William and Beamish, 1979). A sensory evaluation of migrating chum salmon reported that their flavor deteriorated with a corresponding decrease in lipid content (Hatano et al., 1987). After a long migration, lampreys also consume body lipid contents and might be preferred less. However, Arctic lamprey contains many essential fatty acids (DHA and EPA) and vitamins and was described as medicine for preventing night blindness in a book published in 1712 (Yazawa, 2007). In Japan, marine stingrays were eaten historically in mountain areas because they were nutrient-rich, and not perishable when transported inland (Tomioka et al., 2010). Therefore, Arctic lampreys that migrate upstream might be important food resources throughout river basins. The fishers interviewed said that Arctic lampreys containing less fat after swimming in rivers were easy to eat and more delicious. Residents of the Noto Peninsula, Ishikawa, consumed spring Arctic lampreys as seasonal food (Arakawa et al., 2018). Therefore, Arctic lamprey with different tastes might be enjoyed as medicines or as traditional dishes.

Fishers' ecological knowledge of lampreys

Seasonal cycle

There were two main fishing seasons for types 1 and 2 fishing: from autumn to winter, and in spring. Arctic lampreys have two migrating populations: a fall-run that enters rivers in fall, overwinters there, and spawns the next spring and a spring-run that enters rivers in spring and spawns immediately (Savvaitova et al., 2007; Sakashita, 2010). Yamazaki et al. (2014) investigated the population genetic structure of Arctic lamprey distributed from Japan to Russia, but the difference between the two run populations is unknown. The fishers' knowledge indicates the presence of a two-run population and it is necessary to exam their population structure and migrating behaviors for effective resource conservation in the future.

Lunar cycle

Lamprey fishers said that few Arctic lampreys were caught under a full moon. The migration activity of the European river lamprey is negatively associated with the night-time light intensity of the moon (Aronsuu, 2015) and fishers in Sweden reported low migratory activity near the full moon (Asplund and Sodergren, 1974). By contrast, the lunar cycle does not predict the migratory activity of sea lamprey. Low night-time light levels increase the migratory activity of lampreys (Hardisty and Potter, 1971). Cloud cover with a nearly full moon correlate positively with the European lamprey catch (Aronsuu, 2015). Lamprey migration activity might be regulated by the night-time light level and synchronized with the lunar cycle. We found that Arctic lamprey appear to be regulated by night-time illumination. Therefore, in rivers flowing through the urban areas, the influence of artificial light on migration behavior is a concern.

Diel cycle

The fishers set traps or caught lampreys at night. Lampreys actively migrate upstream in freshwater at night (Keefer et al., 2011; Arakawa et al., 2019, Chapter 6), while they rest under rocks or along riverbanks from dawn to dusk (Hardisty and Potter, 1971; Almeida et al., 2002). Larval lampreys in freshwater follow the same diel pattern, and are active and change habitat at nighttime (Derosier et al., 2007). The nocturnal migration behavior of spawning lampreys could be related to the protection from predation afforded by darkness (Moser et al., 2015). In rivers, numerous predators consume spawning lampreys, including birds and large fish (Close et al., 2002). While adult Arctic lampreys show nocturnal migration behavior but it is not known what species consume Arctic lamprey there.

Habitat-related differences

The Arctic lamprey catch increased when the river flow increased and became muddy. In other lamprey species, the number of spawning lampreys increases below artificial barriers when the river flow increases (Binder et al., 2010; Keefer et al., 2011;

Foulds and Lucas, 2013). By contrast, high flow limits the passage of river lampreys, which spend more time attached to substrate surfaces to hold their position (Keefer et al., 2013). The Arctic lamprey has a poor ability to ascend even small differences (20 cm) in water depth upstream and downstream of a weir (Arakawa et al., 2019, Chapter 6). High flow conditions allow lampreys to pass low barriers by minimizing the depth difference (Moser et al., 2020). A decline in the quantity of light within rivers due to a rise in water depth and muddy water also regulates the migration behavior. Therefore, high flow conditions might be important for assessing the migration behavior of Arctic lamprey.

The fishers find the spawning beds of Arctic lampreys in riffles. The spawning beds of Arctic lamprey are about 30 cm in diameter (Murano et al., 2008) and constructed at the head of shallow, flat riffles where the riverbed is composed of pebbles and gravel (Shiraishi et al., 2018). The fishers' knowledge is consistent with field research and provides insight into the historical distribution of spawning sites. The original spawning habitat is difficult to assess at present since existing artificial barriers prevent natural migration. Therefore, information about the spawning site from fishers' memories can contribute to understanding the ecology of the lamprey life cycle and their historical distribution in freshwater.

Decline of the fishery and future conservation

The mean catch of Arctic lamprey has decreased to 1–10% of previous levels in coastal Honshu along the Sea of Japan. In the Ishikari River, Hokkaido, the catch began to decline in the 1980s and dropped to 1% after 2000 (HRO, unpublished data). A consistent reduction in the catch has been observed throughout Japan.

Overharvest is one threat to anadromous lampreys (Clemens et al., 2020). Ten Japanese inland FCs caught lamprey at artificial barriers, which prevent migration and have created new fishing grounds where many lampreys concentrate. Fishing in these areas has the potential for overharvesting. In Latvia, traditional lamprey fishing "*Pata*" is regulated and river traps are allowed to span only one-third of the river width (Sjöberg, 2011). The harvesting of spawning individuals has a negative impact on reproduction. To conserve fishery resources and preserve fishing culture sustainability, appropriate management, regulation, and conservation efforts are needed. However, only Hokkaido, Yamagata, and Niigata Prefectures regulate lamprey fishing at present. While Arctic lamprey fishing occurred along the coast of Japan widely in the past, there is a gap between utilization and resource management. Our study suggests two reasons why Arctic lamprey fishing is not regulated sufficiently.

First, little is known of the use of Arctic lamprey in Japan. Residents of the Noto Peninsula, Ishikawa, harvested Arctic lamprey for their own consumption (Arakawa et al., 2018). We found that lamprey fishing was limited by geographical features, but a variety of types of fishing have developed using gear that accommodates the river environment. The relatively small fishing culture might delay its management.

The second reason is related to the limited ecological information and lack of artificial propagation methods. If an inland fishery resource species were to be regulated, the FCs would have been required to conduct conservation efforts, such as releasing juveniles. However, the artificial propagation of this species was not well established until recently (Lampman et al., 2020; Arakawa and Yanai, 2018, 2019). Some FCs in Japan did perform artificial insemination and reintroduction independently. However, releasing propagated juveniles could cause a loss of genetic diversity and adaption in the population (Taniguchi, 2007). Habitat and river connectivity need to be restored for long-term conservation. In the future, we need to use our ecological knowledge to establish a conservation plan and adaptive management for Arctic lamprey and traditional fishing culture.

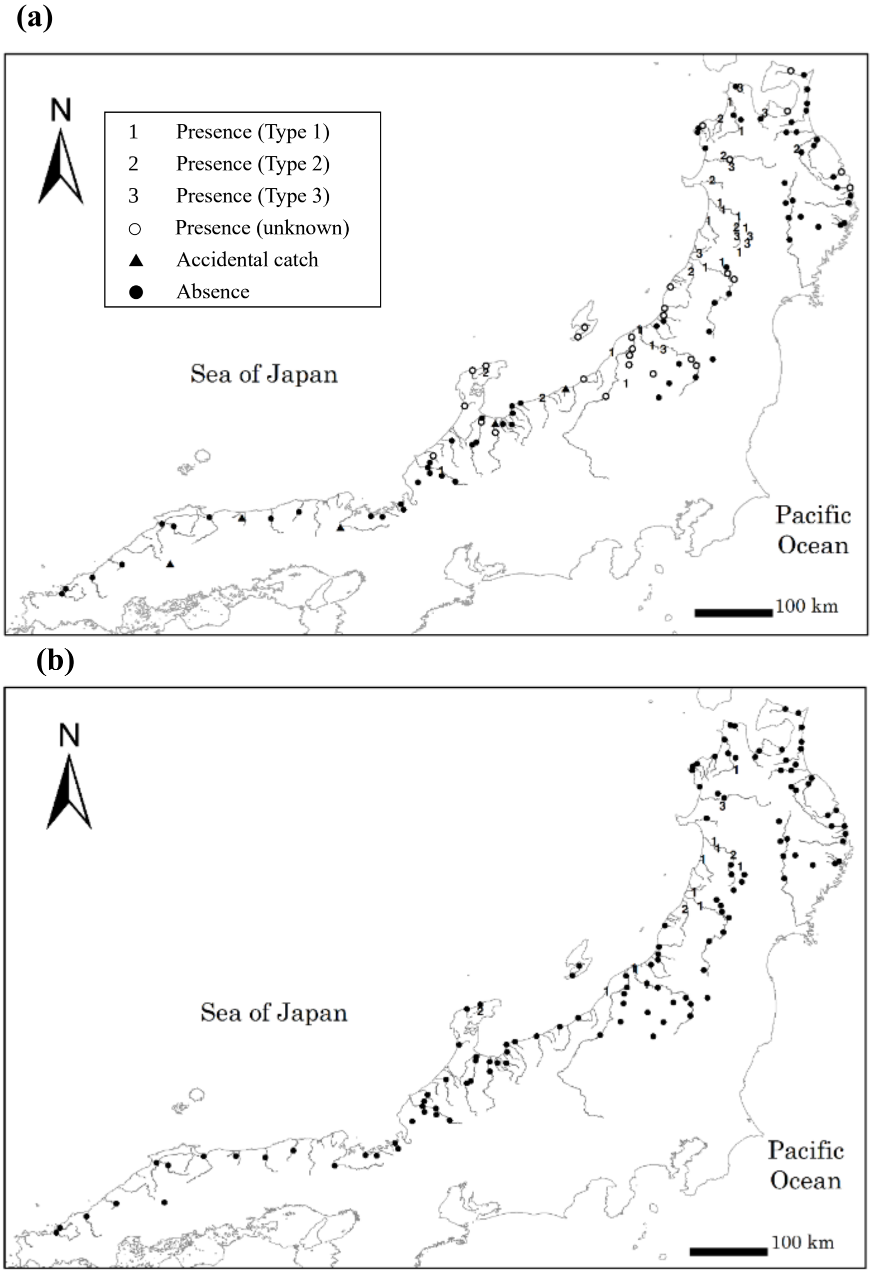


Fig.1 Distributions of Arctic lamprey fishing in the FCs in the (a) past and (b) present. Fishing areas along the Pacific coast are also marked (Arakawa et al. under rev.)

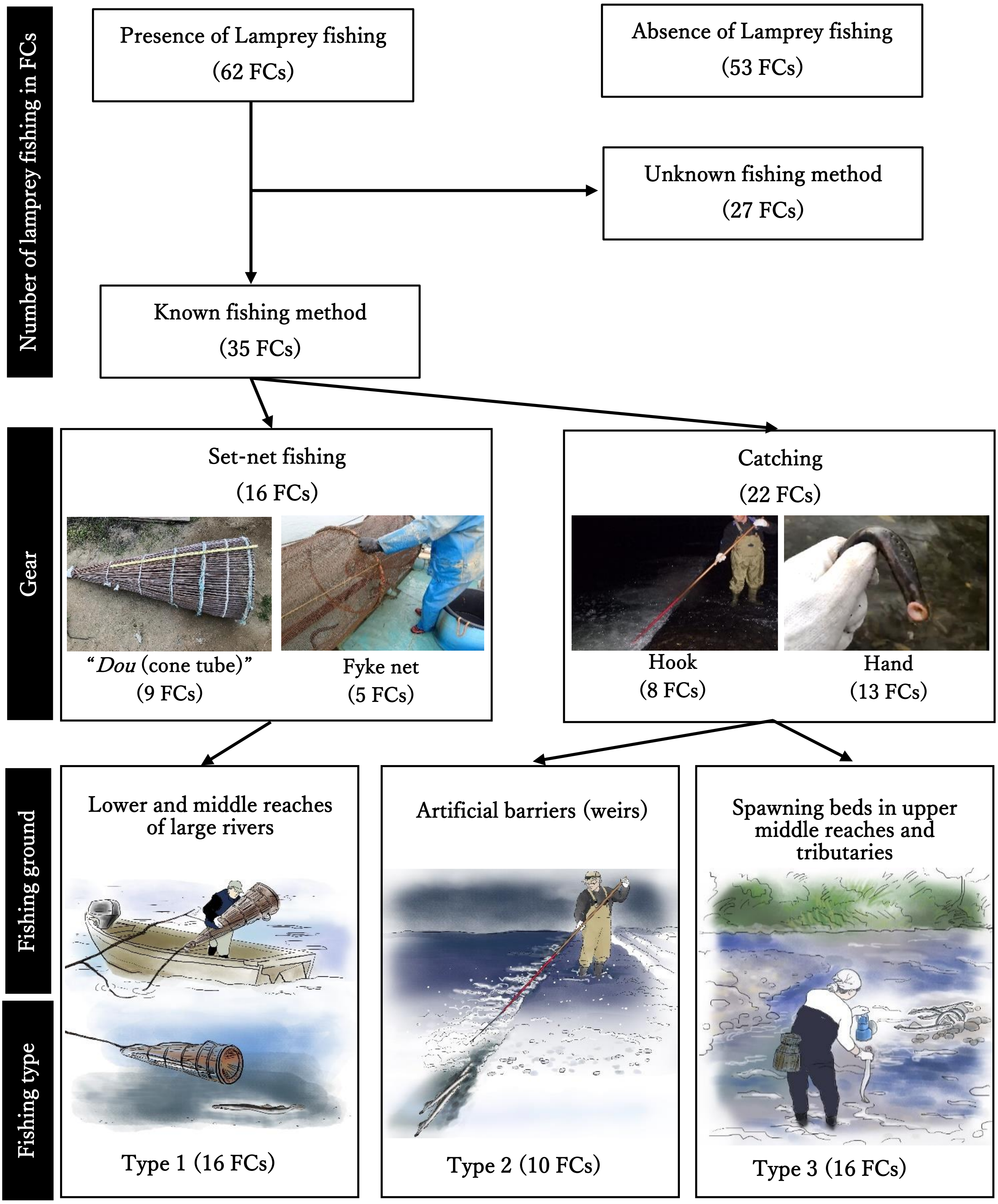


Fig.2 Flowchart classifying Japanese lamprey fishing in the inland FCs. The mismatched numbers between all FCs and gear used by FCs arises because some FCs use multiple fishing

Fig.3 Present (a) and past (b) cone tubes. 11 December 2019. Photo: Hiroaki Arakawa

Fig.4 Longline fishing using cone tubes.
10 December 2019. Photo: Hiroaki Arakawa

Fig.5 Fyke net fishing.
30 January 2019. Photo: Hiroaki Arakawa

Fig.6 “*Otoshidamo*” fyke net without a guide net. 29 January 2019. Photo: Seiji Yanai

Fig.7 A hook for type 2 fishing. 10 December 2019.
Photo: Hiroaki Arakawa

Fig.8 Jigging lampreys at a weir.
30 March 2015. Photo: Seiji Yanai

Fig.9 Grabbing lampreys from behind a board.

23 March 2019. Photo: Hiroaki Arakawa

Table 1. Species Status in the 2000s and the 2010s and latest fishery regulation of prefectures along the Sea of Japan

Prefecture	Status				Fisehry reguration
	2000s		2010s		
Hokkaido	2001	LP	2017	LR, NT	○
Aomori	2006	—	2020	LR, NT	
Akita	2002	—	2016	CR, EN	
Yamagata	2002	—	2018	VU	○
Niigata	2001	LR, NT	2015	VU	○
Fukushima	2002	—	2017	DD	
Nagano	2003	—	2015	—	
Toyama	2002	—	2012	CR, EN	
Ishikawa	2009	—	2020	VU	
Fukui	2002	VU	2016	VU	
Kyoto	2002	DD	2015	VU	
Hyogo	2003	CR, EN	2017	CR, EN	
Tottori	2002	—	2012	DD	
Shimane	2004	VU	2014	VU	
Yamaguchi	2002	DD	2019	CR, EN	

Chapter 2 Historical distribution of Arctic lamprey (*Lethenteron camtschaticum*) in Japanese rivers and its change estimated from fishery statistics and local ecological knowledge

Introduction

Inland water areas including rivers and lakes, provide habitats for 312 fish species or subspecies in Japan (Kawanabe and Mizuno 2001). Inland fisheries incorporate both fishing and aquaculture. Inland fisheries produce 34 × 103 tons/year of product, which represented 0.7% of the output from marine fisheries and aquaculture in 2011 before the East Japan great earthquake and tsunami (Katano et al. 2015). Although the freshwater harvest is recognized as having a lower economic value than the harvest from marine fisheries, inland fisheries not only provide an important food resource to inland residents but also contribute to human health, local likelihoods, and tourism (Lynch et al. 2016). However, biodiversity in freshwater systems has substantially declined due to human activities, including river management and the introduction of exotic species (Goto 1997; Natsumeda et al. 2010). A total of 169 fish species has been designated as endangered species (CR: critical endangered, EN: endangered, VU: vulnerable) in the Red Data Book of Japan (Ministry of the Environment: http://www.env.go.jp/press/107905.html "Accessed 11 Aug 2020"). Dams are one of the main factors that have a negative impact on biodiversity by preventing migration and promoting habitat fragmentation and changes in genetic structure (Morita et al. 2000; Morita and Yamamoto 2002; Fukushima et al. 2007; Kitanishi et al. 2012). Dams (less than 100 m high) for electric power supply were built in Japan before the 1940s (Hirose and Yanagida 1992). Since the 1950s, many huge dams (larger than 100 m height) were built due to the increased demand for electric power for socioeconomic recovery, which was facilitated by technological innovations in concrete materials and heavy machinery after the Second World War (Inamatsu 1982; Nagayama 1994). After the 1960s, some river banks were concreted, and check dams were constructed for erosion control and water utilization as a result of rapid economic growth, which resulted in extensive urbanization and industrialization (Goto 1997). Dams prevent the freshwater migration of anadromous species and cause habitat fragmentation and reductions in genetic diversity (Yamamoto et al. 2004; Fukushima et al. 2007). To preserve these fish species and the overall freshwater biodiversity, there is a need to set management goals or baselines according to the distribution or population size of aquatic species prior to the large impact of dams after the 1950s.

Fishery statistics may provide a powerful tool for quantifying long-term population changes and human impacts, and can be used to establish a baseline from which to assess current ecosystem conditions and biodiversity status (Lotze and Worm 2009). However, freshwater fishery statistics in Japan have only been monitored in the last 1 to 3 decades and provide insufficient information (Katano and Matsuzaki 2012). In a recent study, the distribution range of anadromous *Oncoryncus masou ishikawae* in the 1930s was described based on historical fisheries statistics throughout the enormous range of Japanese rivers (Kishi and Tokuhara 2019). Historical fishery statistics have the potential to evaluate past species distributions and biodiversity dynamics in freshwater systems.

Anadromous lampreys have been historically used as an important food resource for cultural and economic reasons worldwide (Docker et al. 2015; Almeida et al. under rev.). Arctic lamprey is a traditional and important food resource that is captured in Japanese inland waters (Murano et al. 2008; Arakawa et al. 2018). Its distribution range in Japan is the coast of the Sea of Japan from Hokkaido to Shimane and the coast of the Pacific Ocean from Hokkaido to Ibaraki, while internationally its range extends up to Alaska and Russia (Kawanabe and Mizuno 2001). Arctic lamprey has mainly been caught in the Ishikari River, Hokkaido, where it has been used for general consumption by the local population and sustains the local lamprey festival (Murano et al. 2008). In Noto Peninsula, Ishikawa in central Japan, Arctic lamprey has been caught predominantly in spring using a specialized fishing gear called "*Kanko*" (Arakawa et al. 2018). However, this species has been designated as a vulnerable species (VU) in the Red Data Book of Japan due to serious population decline (Ministry of the Environment: http://www.env.go.jp/press/107905.html "Accessed 11 Aug 2020"). Clemens et al. (in press) suggests that the threats to anadromous lampreys include climate change, oceanographic regimes, land developments (artificial barriers, water quantity/stream flow, habitat degradation, and decreased water quality), and species interactions (host/prey availability, predation, disease, and overharvest). The population reduction of Arctic lamprey has caused a decline in the traditional lamprey culture in Japan. Despite conservation and restoration efforts by the Hokkaido government from 2004 to 2007 to protect traditional food resources (Hokkaido Government Ishikari Sub-prefectural Bureau http://www.ishikari.pref.hokkaido.lg.jp/ss/sis/grp/yatume2.pdf "Accessed 11 Aug 2020") , the population has not yet recovered. The size of Arctic lamprey harvest in the Ishikari River and the Shiribetsu River has been continuously recorded since the 1980s (Almeida et al. under rev.); however, historical fishery information and statistics are limited and the baseline for conservation and restoration is not well-known.

Various types of nets, traps, and angling equipment used in the inland fishery have traditionally been developed in each local region (Katano et al. 2015). The information accrued due to the relationship between humans and their environment is defined as traditional ecological knowledge (TEK). TEK evolves by adaptive processes and has been handed down through generations by cultural transmissions, including cumulative bodies of knowledge, practices, and beliefs (Berkes et al. 2000). Because of their in-depth knowledge of the land, aboriginal people have a particularly important role to play in environmental monitoring and distinguishing project-related changes from natural changes in the environment (Stevenson 1996; Huntington 2000). Lampreys are utilized by native residents in the northwest United States, Alaska, and New Zealand and the relationship between humans and lamprey has developed over time (Close et al. 2002; Brown et al. 2005; Stewart and Baker 2012). Studies of the TEK of native residents related to lampreys have revealed a population reduction and the impacts of human activity (Petersen 2009).

It is not only native indigenous people that are a source of information; local fishermen are also a useful resource. Recent studies have reported that the fishers' ecological knowledge (FEK) of fishing resources held by fishermen has the potential to improve fishery management by providing new information about the ecology, behavior, and abundance of fish and other aquatic animals (Silvano, and Valbo-Jørgensen 2008).

The FEK from local fishermen has the potential to be an alternative information resource for freshwater management and environmental assessment. On the other hand, it is estimated that all inland fishermen belonging to Japanese fishery cooperatives (FCs) would be 0 until 2035 – 3036 due to aging and changes in people's life cycles (Nakamura 2017). The FEK could possibly be lost due to the decreasing number of individual fishermen and cooperative unification. Arctic lamprey is consumed in certain local areas, where it has contributed to the regional culture (Arakawa et al. 2018), and some traditional fishing cultures have been reported at the prefectural scale. However, fishery information and statistics about Arctic lamprey have not been accumulated or systematized throughout Japan. The local knowledge of Arctic lamprey held by inland fishermen has the potential to fill in gaps in our knowledge of the species ecology, such as changes in its historical distribution.

To determine the river and where Arctic lamprey were historically caught and its geographical characteristics before river modification projects occurred, two information resources were obtained. First, the rivers for which harvest information was available were analyzed to determine their latitude, river length and river gradient based on fishery statistics published in the 1930s as scientific data. Secondly, we conducted a survey of Arctic lamprey fishing activity by inland FCs as an ethnobiological data throughout Honshu, Japan. To determine the status of fishing activities in the area, we asked them whether fishing was conducted in the past and if it was still conducted in the present (i.e., 2019–2020). In this study, the information from inland FCs was defined as FEK not TEK. Olsson and Folke (2001) suggest that FEK differs from TEK in lacking a sense of historical and cultural continuity of resource use and is knowledge held by a specific group of people about their local ecosystems. Because Japanese local FC has developed recently and conduct fishing within a part of the river as a fishing ground, we treated all information from FCs as FEK. To evaluate the effectiveness of the FEK of inland fishermen for estimating historical species distribution as a pilot study, we compared the actual harvest in rivers and the southern limit of the harvest between the fishery statistics and FEK from FCs.

Materials and Methods

Fishery statistics as historical scientific data

To establish the historical distribution of Arctic lamprey, we used inland fishery statistics, "*Kasen Gyogyo* (Fisheries Bureau, the Department of Agriculture and Forestry 1930–1934, 1937)" according to Kishi and Tokuhara (2019). These fishery statistics consisted of six volumes, with data for 327 – 371 rivers in Japan. Volumes 1 (data for 1927), 2 (data for 1928), 3 (data for 1929), 4(data for 1930), and 5(data for 1931) listed the size of the harvest for the major fish species captured in each river. Volumes 4 and 6 (data for 1932) listed the names of the fish species captured in each river. All fish species were described using a Japanese name. The scientific name for Arctic lamprey was not used in Volume 1, but it was described as *Entospheus japonicus* Martens (Cyclostomata) from Volume 2 onward. The Japanese name for Arctic lamprey is "*kawayatsume*" although "*yatsume unagi*" and "*yatsume*" are also used (Kawanabe and Mizuno 2001). We extracted these Japanese names from the fishery statistics and treated them as harvest information. Volumes 1–5 contained quantitative harvest information, but details of the catch, such as method, area, and period, were not provided. Therefore, we treated all harvest information from these sources simply as presence data.

The rivers in the fishery statistics were divided into five coastal zones: the Sea of Okhotsk, the Sea of Japan, the Pacific Ocean, the Seto Inland Sea, and the East China Sea. The Arctic lamprey harvest was recorded in the coastal rivers of the Sea of Japan, except for two rivers along the Sea of Okhotsk. To establish the spatial distribution of the species, we extracted 116 rivers along the Sea of Japan for statistical analyses. In addition, some of the 116 rivers were listed in only one volume. The limited amount of data could lead to the reporting of a false negative. We extracted 97 rivers that were listed in more than three of six volumes to improve data credibility. The presence of a harvest was determined based on whether a harvest was recorded in one volume.

Ethnobiological data obtained by interviewing FCs

To establish the distribution of Arctic lamprey from FEK, we conducted a structured interview with the inland FCs along the rivers located in Honshu from the Tohoku to Chugoku regions and enquired about the presence of Arctic lamprey fishing activity. The FCs have fishery rights for designated fish species within a part of a river as a fishing ground. We interviewed multiple FCs within the same river basin to establish an accurate spatial distribution. The survey objective area was Honshu, which is an area that is not well known for Arctic lamprey fishing. There were 109 FCs in 61 rivers from Aomori to Yamaguchi in the coastal area of the Sea of Japan and 25 FCs in 15 rivers from Aomori to Iwate in the coastal area of the Pacific Ocean. The structured interview was conducted telephonically once for each FC. All fishermen were asked quantitative and qualitative question formats to 1) if they had conducted fishing activity for Arctic lamprey in the past and were still currently active, and 2) which fishing method they used if they were active. A structured interview by telephone is used to gain quantitative and qualitative data from fishermen operating within a specific area (Rees et al. 2013). The fishing methods used for Arctic lamprey were classified into three types; 1) set net fishing (Type 1), 2) fishing below cross river structures (Type 2), and 3) fishing at the spawning beds (Type 3), (Almeida et al. under rev.). The presence of fishing activity was confirmed if they had one of the three types of fishing or the specified fishing for Arctic lamprey which detailed method was unknown. Accidental catches of Arctic lamprey while fishing for other fish were not treated as the presence of a harvest because this type of catch did not reflect continuous fishing activity and an annual fluctuation could not be determined. The details of past harvests were not recorded and this information was dependent on the memory of fishermen. All historical information regarding the presence of Arctic lamprey was defined as the past period.

Statistical analysis

A generalized linear model (GLM) was performed to clarify the geographical factors explaining the distribution of Arctic lamprey along the Sea of Japan, according to Kishi and Tokuhara (2019). The response variable was the catch of Arctic lamprey, which followed a binomial distribution (1: present, 0: absent). The explanatory variables were the latitude at the river mouth, river length, and river gradient. The latitude at the river mouth was obtained from the website of the Geographical Survey Institute. The river length was calculated based on river data from digital national land information (https://nlftp.mlit.go.jp/ksj/jpgis/datalist/KsjTmplt-W05.html ”Accessed 11 Aug 2020”) using geographic information system (GIS). The river gradient (GW: gradient of the whole reach) was calculated by dividing the elevation of the headwater, obtained from the website of the Geographical Survey Institute, by the river length. Larval Arctic lampreys distribute areas composed of the fine sediment in the lower and middle reaches as their preferred habitat (Shirakawa et al. 2009; Arakawa and Yanai 2017). Therefore, the river gradient of one-third of the lower reach (GL: gradient of the lower reach) was calculated and used as the explanatory variable. To prevent multicollinearity between GW and GL, the best model was selected from the use of two other explanatory variables and each river gradient to minimize the Akaike's information criterion (AIC). A probability of a harvest of more than 0.5 (less than 0.5) was defined as the presence (absence)of Arctic lamprey and the precision of the best model was verified. To determine the southern limit of the Arctic lamprey harvest, the latitude and 95% confidence interval when the probability of a harvest was 0.5 were estimated by substituting the median values of the selected explanatory variables for all 97 rivers into the best model.

A GLM was performed to select the geographical factors explaining the spatial distribution of Arctic lamprey along the Sea of Japan in the past and present periods according to the harvest information from 109 FCs. The response variable was the presence of fishery activity for Arctic lamprey, which followed a binomial distribution (1: present, 0: absent). The explanatory variables were river length, two river gradients (GW, GL), latitude, and elevation of the FC offices. Most of the actual fishing locations could not be determined by the interviews. River length and river gradient were used as basic geographical variables, providing river-scale information. The latitude and elevation of FC offices were alternative variables that indicated the approximate location of fishing grounds, because they were located within or near the actual grounds. River length and two river gradients were calculated, and the results matched the data in the fishery statistics. Latitude and elevation of FCs were obtained from the website of the Geographical Survey Institute. The models for which the explanatory variables minimized the Akaike's information criterion (AIC) for the past and present periods, respectively, were selected as the best models. A probability of a harvest more than 0.5 (less than 0.5) was defined as the presence (absence) of fishery, and the precision of the best model was verified. In addition, to determine the southern limit of the Arctic lamprey fishery distribution, the latitude and 95% confidence interval when the probability of a harvest was 0.5 were estimated by substituting the median of the selected explanatory variables for all 109 FCs into the best model. All statistical analyses were performed using the ‘glm’ function in the Status Package by R ver. 3.5.1 (Venables and Ripley 2002).

Result

Estimating the historical distribution from fishery statistics

The harvest information of Arctic lampreys was recorded in 48 of 97 rivers along the Sea of Japan from 1927 to 1392 (Fig. 1, Table 1). In northern Hokkaido, harvest records were available for more than half of the rivers, with the most northerly being Teshio River (43.9643ºN, 142.8808ºE). In Honshu, the presence of a harvest was recorded in 35 of 71 rivers. There was no harvest recorded in Kyushu. The most southerly river with a harvest was the Maruyama River (35.1727ºN, 134.7842 ºE).

In the best GLM, the latitude at the river mouth, GL, and river length were selected to explain the presence of an Arctic lamprey harvest (Table 2). Latitude was selected in all six models being at the smallest AIC. Comparing the GW and GL river gradients of, GL was selected in the best, second, and sixth best models, while GW was selected in the third and fifth best models. In the best model, latitude and river length were positively correlated with the presence of a harvest, while GL was negatively correlated with the presence of a harvest. The mean (minimum–maximum) river length and GL in rivers with a harvest were 80.1 km (9–372 km) and 1/981 (1/5054–981), respectively.

Positive and negative harvest estimates were made at 42 and 55 rivers, respectively, by substituting the explanatory variables of all rivers into the best model (Fig. 2a). Correct estimations were made for 68% (66 rivers) of rivers, while incorrect estimations were made for 32% (31 rivers) of rivers. The false positives were the 13 rivers of Furubira, Amano, Ishizaki, Oyobe, Shiriuchi, Moheji, Akaishi, Miomote, Hakui, Kuzuryu, Yura, Hii, and Gouno. The false negatives were the 18 rivers of Atsumi, Syounaioguni, Iso, Oo, Tainai, U, Kakizaki, Seki, Shiraiwa, Jintsuu, Shou, Kawarada, Konmachi, Oono, Sai, Tedori, Daishouji, Maruyama. Ishizaki, Oyobe, Shiriuchi, Moheji, Akaishi, Miomote, Hakui, Kuzuryu, Yura, Hii, and Gouno. The latitude when the probability of a harvest was 0.5 was estimated to be 37.3299º N (95% CI: 35.9669º N - 38.3882º N) in Wajima City in the Noto Peninsula, Ishikawa and Kashiwazaki City, Niigata as the southern limit of the Arctic lamprey fishery distribution (Fig.3a).

Estimating past and present distributions from FCs

Arctic lamprey fishery activity in the past period was recorded at 56 of 109 FCs in 30 of 61 rivers along the Sea of Japan and at 3 of 25 FCs in 3 of 15 rivers along the Pacific Ocean (Fig. 4, Table 1). Accidental catches of Arctic lamprey while fishing for other fish were recorded in 5 FCs within the southern rivers of Kuwaori, Jintsu, Yura, Tenjin, and Gouno (Table 1). Fishery activity in 2019–2020 had decreased to 14 FCs in 10 rivers along the Sea of Japan and there was no activity along the Pacific Ocean coast. The southernmost active FC changed from Fukui in the past period to Niigata in the present. We obtained details of the detailed fishing method for Arctic lamprey from 33 FCs within 17 rivers and these were classified into three types (i.e., 1. set net fishing, 2. fishing below cross river structures, and 3. fishing at the spawning beds; see Almeida et al. under rev.). There were 25 FCs in 16 rivers that fished specifically for Arctic lamprey using methods that were unknown. The presence of a harvest within the rivers was determined from fishery statistics and the information from FCs for 73% (33 rivers) of the estimates (Table 1).

In the GLM that explained the presence of fishery activities, river length, GL, latitude, and elevation of FC were selected for both the past and present periods (Table 3). Latitude and river length were positively correlated with the presence of a harvest activity, and GL and elevation were negatively correlated with the presence of a harvest activity. There were changes in the geographical variables associated with the active FCs from the past to present periods. The mean river length (minimum–maximum) increased from 149 km (7–372 km) to 172 km (34–372 km, Fig. 5a). The mean elevation decreased from 54 m (0.8–347 m) to 21 km (0.8–62 m, Fig. 5b). The mean GL decreased from 1/501 (1/6038–1/99) to 1/987 (1/5054–1/208, Fig. 5c).

From the best model for the past period, positive and negative harvest estimates in the rivers were made for 54 and 55 FCs, respectively, by substituting the explanatory variables of all FCs and rivers into the best model. Correct estimations were achieved for 81% of FCs (89 FCs, Fig. 2b). From the best model for the present period, positive and negative harvest estimates in the rivers were made for 6 and 103 FCs, respectively. Correct estimations were achieved for 83% of FCs (91 FCs, Fig. 2c). The latitude when the probability of fishery activity was 0.5 was estimated to be 36.6225° N (95% CI:

35.6213 º N -37.2805º N) at Kanazawa city, Ishikawa, being the southern limit of the distribution in the past period (Fig.3b). For the southern limit in the present period, the latitude was estimated to be 42.5130º N (95% CI: 40.8209 º N -) at Kudou gun, Hokkaido (Fig. 3c).

Discussion

Use of FEK to estimate the historical Arctic lamprey distribution

The presence of a historical harvest in Japanese rivers and the southern limit of Arctic lamprey along the coast of the Sea of Japan was estimated according to two information resources from fishery statistics and inland FCs. These geographical distributions based on two sets of scientific data and ethnobiological information were largely identical. Ethnobiological information provided by fishermen is sufficient to predict the distribution of species for which past scientific data are lacking, and results can be obtained that are similar to those acquired from the use of scientific data collected from the field and bibliographic sources (Silvano and Begossi 2010; Lopes et al. 2019). Local ecological knowledge is an alternative information source that can be used to reconstruct historical trends, including temporal and geographical variation in the distribution of aquatic species (Azzurro et al. 2011; Turvey et al. 2013). The Arctic lamprey has been utilized in the broad coastal area along the Sea of Japan, but there is a lack of historical ecological records. Local ecological knowledge is an information source that can be used to estimate the distribution and population fluctuation of this species. It is interesting that information regarding the presence of past harvests of Arctic lamprey from the FCs agreed with the available data for information in 1927–1932, i.e., prior to the majority of the river improvement work. Historically, a variety of fishing methods for Arctic lamprey fishing has been developed in accordance with season, river size and aquatic environment through the coastal area of the Sea of Japan (Murano et al. 2008; Arakawa et al. 2018). This wide distribution of a common fishing culture adapted to each regional environment is related to the cultural and resource value of Arctic lamprey and contributes to the credibility of the information. Therefore, by taking into account aspects of qualitative information about the fishery and cultural linkages, as well as the presence of harvest, FEK from FCs provides a helpful insight into the conservation measures required to ensure the diversity of aquatic species and local cultures.

However, anecdotal information from living memory can be used for making scientific inferences but its use to improve estimations or predictions is debatable (Lotze and Worm 2009). Fishing carrying capacity and the perceived population baseline fishery resources differ among age groups (Pauly 1995). Older fishermen have more experience and detailed knowledge of local fisheries and can provide information that complements the current and past knowledge of species and environmental conditions (Damasio et al. 2015). Previous FEK research regarding marine fish in coastal sea areas, has indicated the need to compile occurrence data for individual fishing grounds in various locations. Many inland FCs operating in Japanese rivers have compartmentalized their fishing grounds. Therefore, information from the FCs provides details of the spatial distribution of species within river basins. In our study, FCs were interviewed once to obtain the harvest information as a pilot study. To improve estimation fishery resources and preserve FEK from fishermen, the number of samples for interviewing needs to increase. However, when applied to other fish species, telephone interview should not be recommended because individual interviews are likely to be burdensome to fishery cooperatives. Therefore, establishing a framework for collecting information from FCs efficiently is required for the development of sustainable use of fishery resources in the freshwater while utilizing information fishermen have.

Historical harvest records of Arctic lamprey in 1927-1932

There were harvest records of Arctic lamprey in 1927–1932 for 48 of 97 rivers along the Sea of Japan, but there were no harvest records along the Pacific Ocean. This spatial distribution of Arctic lamprey in rivers was consistent with the marine spatial distribution. Long-tern trawl surveys have indicated that an abundance of Arctic lamprey has been captured in the Sea of Okhotsk near the continental coast of the northwestern Sea of Japan (Orlov et al. 2014). By contrast, an extremely low density of Arctic lamprey has been recorded in the Pacific Ocean on the eastern coast of Kamchatka (Sviridov et al. 2007; Orlov et al. 2014). In terms of the seasonal changes in the distribution of Arctic lamprey, catch numbers in the northwestern Sea of Japan and near western Kamchatka were high between June and August and then decreased as the fish migrated to the northwestern Sea of Okhotsk and their spawning rivers (Orlov et al. 2014). In addition, the size of the Arctic lamprey harvest differed between the coastal area of the Sea of Japan and the Pacific Ocean. According to the inland fishery statistics, "*Kasen Gyogyo*" used in our study, the Arctic lamprey had the second-largest harvest of all fish species after the chum salmon (*Oncorhynchus keta*) in the Ishikari River and the largest harvest in the Shiribetsu River, which enters the Sea of Japan (Fisheries Bureau, the Department of Agriculture and Forestry 1931, 1932) . By contrast, it was interesting that there was no harvest information along the Pacific Ocean coast. The migration route and its mechanisms are not well known but it is considered that Arctic lamprey migrate to rivers along the Sea of Japan for spawning and are captured as an inland aquatic food resource.

Kawanabe and Mizuno (2001) reported that Arctic lamprey was distributed along the Pacific Ocean coast between Hokkaido and Ibaraki, whereas our study suggested there was no harvest along the Pacific Ocean in 1927–1932. Larval and adult Arctic lamprey have not been caught along the Pacific coast south of Akita since 2010, according to National Census on River Environments (Ministry of Land, Infrastructure and Transport http://www.nilim.go.jp/lab/fbg/ksnkankyo/ "Accessed 11 Aug 2020"). Because information regarding anadromous Arctic lamprey is very limited for the Pacific coast of Miyagi, and Ibaraki, this species is designated as data deficient on the prefectural Red List (Ibaraki Prefecture https://www.pref.ibaraki.jp/seikatsukankyo/shizen/tayousei/redbook/ibaraki_redbook.html "Accessed 11 Aug 2020"; Miyagi Prefecture https://www.pref.miyagi.jp/soshiki/sizenhogo/red-book2016.html "Accessed 11 Aug 2020"). A fluvial non-parasitic Arctic lamprey inhabits locations in Iwate and is designated as critically endangered species (Iwate Prefecture http://www2.pref.iwate.jp/~hp0316/rdb/06tansuigyo/index.html "Accessed 11 Aug 2020"). This fluvial population is also found in the upper reach of the Agano River, which is a consequence of geographical isolation following dam construction (Yamazaki et al. 2011). Arctic lamprey with a fluvial non-parasitic lifecycle occur in all populations and have been found in Asia and North America (Docker and Potter 2019). Rising seawater temperatures due to climate change could promote a northward latitudinal shift in the migration route of anadromous populations and causing a fluvial non-parasitic population to occur in the southern area (Yamazaki et al. 2011). The limited available information for anadromous Arctic lamprey and the habitat data for the fluvial non-parasitic population along the Pacific Ocean could indicate a historically smaller abundance compared to that in the Sea of Japan, even before river modification. Therefore, the absence of harvest records should be interpreted to indicate that a small population has the potential to return to the rivers, although the fishery activity has not occurred due to the limited resources.

Geographical factors limiting the presence of fisheries

Latitude was selected as a significant explanatory variable in the harvest information from the inland fishery statistics in 1927–1931 and the survey of FCs. The southern limits of the fishery distribution in the past period were estimated to be 37.3299º N (95% CI: 35.9669 º N -38.3882º N) from the inland fishery statistics and 36.6225º N (95% CI: 35.6213 º N -37.2805º N) from the information held by the FCs. Both results indicated that Ishikawa was located at the historical southern limit for an Arctic lamprey fishery. Larval Arctic lamprey inhabit the Noto Peninsula in Ishikawa, and traditional fishing for this species occurs in the area (Arakawa and Yanai 2017; Arakawa et al. 2018). We found literature describing a harvest north of the southern limit but there was no harvest information for the area south of the limit. Two old documents" *Kefukisou*" and "*Ruisen*" published in the 17th century in Japan reported that Niigata was famous for the harvest of lampreys (Satake 2000). Kataoka (1980) reported Arctic lamprey were captured in the river at Niigata. However, accidental catches of Arctic lamprey were observed by 4 FCs south of the limit, while only 3 FCs specifically fished for Arctic lamprey in this area. This accidental catch information corresponded to the distribution reported between Hokkaido and Shimane along the Sea of Japan by Kawanabe and Mizuno (2001). Some populations of Arctic lamprey might migrate to the rivers the south of the southern limit, but their numbers were not sufficient to enable the formation of a specific fishery, as was case in the coastal Pacific Ocean.

There were no harvest records of Arctic lamprey in some rivers located north of the southern limitation. As significant geographical variables other than latitude, the river length and GL were selected to estimate the presence of an Arctic lamprey harvest. According to a previous study of *Oncorhynchus masou ishikawae* using "*Kasen Gyogyo*", river length has a positive effect on the presence of salmon, because this variable represents the amount of potential habitat available in a river (Kishi and Tokuhara 2019).

In our study, the presence of Arctic lamprey also increased in large rivers. Because the river length reflects the quantitative capacity of the habitat in rivers, it is considered that the amount of available resources will be larger in large rivers. The GL was negatively correlated with the presence of Arctic lamprey. River gradient determines the depositional and erosional areas, water depth, and velocity in river and can be considered a surrogate variable to describe the optimal larval habitat (Young et al. 1990). Larval lampreys burrow in fine sediment accumulations as a habitat in the river (Shirakawa et al. 2009; Dawson et al. 2015; Arakawa and Yanai 2017). The abundance of larval pacific lamprey (*Entosphenus tridentatus*) is higher in reaches with a low gradient where fine sediments tend to accumulate (Torgersen and Close 2004). In addition, organic matter accumulates more in low gradient reaches than in steep reaches (Dawson et al. 2015). Arctic lamprey feed on fine organic matter by filter-feeding and their abundance is high where organic matter is rich (Sutton et al. 1994; Shirakawa et al. 2009). In Alaskan rivers, larval Arctic lampreys do not inhabit the upper reaches, which tend to have a steep gradient, but are rather distributed from the middle to lower reaches that provide appropriate habitat and food conditions (Sutton 2017). Because the river gradient is related to the qualitative habitat potential for larvae, the river gradient of the lower reaches is an effective environmental variable for determining the presence of Arctic lamprey. Therefore, even in rivers north of the southern limit, if the geographical quantitative and qualitative potential is low, there could be an absence of harvest information due to the narrow and unsuitable habitat conditions.

Decline of fishery activity and implications for conservation

The southern limit of the harvest in the past period was estimated to be 36.6225 ºN (95% CI: 35.6213–37.2805ºN) from the information held the FCs. However, the latitude of the southern limit in the present period was estimated to be 42.5130ºN (95% CI: 40.8209ºN–) and shifted further north. This is likely the influence of global warming on the Arctic lamprey population. Climate change has had an impact on the lamprey population and its interspecific relationships including prey fish and predators through oceanographic regime changes (Clemens et al. 2020). In the ocean, Arctic lamprey migrate from the Sea of Japan to the Bering Sea (Orlov et al. 2014; Siwicke and Seitz 2015), while preying mainly on juvenile salmonids (Shink et al. 2019). The return rate of spawning chum salmon significantly negatively correlated with coastal seawater temperature (Kim et al. 2017). The warming seawater temperature has affected a change in the distribution and abundance of Arctic lamprey due to its thermal preference and interspecific predator–prey relationships. In freshwater systems, the distribution of larval lamprey is limited to downstream areas due to the presence of artificial barriers blocking the spawning migration (Mateus et al. 2012; Clemens et al. 2017; Fukushima et al. 2007). The relatively warm river water in estuaries restricts the abundance of larval pacific lamprey at the southern end of its distribution range along the Pacific coast (Goertler et al. 2020). Air temperature in the 2010s at the Wajima observation station near the southern limit in the past period has increased by 1.2°C compared to the 1930s (Japan Meteorological Agency 2020 https://www.data.jma.go.jp/obd/stats/etrn/index.php "Accessed 11 Aug 2020"). The river temperature in the lower reach near the observation station exceeds the upper lethal temperature (29.3ºC) for larval Arctic lamprey (Arakawa and Yanai 2020, Chapter 4). Our research conducted by tracing fishery activity suggests that the distribution has shifted to the north. Climate change has had a serious impact on the sustainability of the Japanese traditional lamprey culture, and we recommend an assessment of its impact on the Arctic lamprey population.

The number of Arctic lamprey fisheries has decreased from 56 FCs in the past to 14 FCs in 10 rivers in 2019. In the past, Arctic lamprey fisheries were observed in the inland upper reaches of the Agano River up to 200 km from the river mouth. The fluvial non-parasitic Arctic lamprey is present in this reach due to geographical isolation following the dam construction (Yamazaki et al. 2011). The presence of anadromous lamprey suggests that gene flow historically occurred between anadromous and fluvial populations. However, a few fisheries were active only in the downstream areas of large rivers. The spatial distribution of lamprey is limited to the downstream areas below cross river structures (Mateus et al. 2012; Clemens et al. 2017). Arctic lamprey has a limited ability to ascend vertical structures (Arakawa et al. 2019, Chapter 6), and the occurrence of this species is therefore lower in the upper reaches (Fukushima et al. 2007). Dams in Japan have adversely affected native freshwater fishes by blocking their migration routes, favoring non-native fishes, or altering existing habitats. The scales of and changes in the historical and spatial distribution of Arctic lamprey are unknown due to the limited number of distribution surveys. Historical upstream distribution of lamprey species provides key information necessary to guide management and habitat restoration efforts (Hamilton et al. 2011). Our results indicate that a decline of fishery activity has occurred in the upper reaches of rivers, which is consistent with the available scientific data. Therefore, the knowledge held by FCs has the potential to fill the gaps in our understanding of the original spatial distribution and its changes within river basins.

However, the recent decline in the Arctic lamprey harvest might be related to the decrease in the number of inland fishermen. The number of the full-time inland fishermen was only 1/10 to 1/12 of the number of fishermen in 1945 and inland fishing mainly provided a seasonal supplementary income (Nakamura 2017). In inland areas, agriculture has developed due to land improvement and the number of full-time agricultural workers has increased in the period after the Second World War. In recent years, the social structure has substantially changed, with the population now concentrated in cities. These changes in the environment and social structure have reduced the dependence on inland fisheries, for which income is not stable and reliable. The membership of Japanese inland FCs is expected to decrease exponentially (Nakamura 2017). Therefore, comparisons between different periods between which the number of active fishermen has changed may underestimate the harvest information in the present period. However, the Arctic lamprey harvest per a fisherman in Noto Peninsula, Ishikawa has decreased to one out of 100 comparing the 1980s (Arakawa et al. 2018). All inland fishery resources, including lamprey, have clearly decreased. These losses in aquatic biodiversity have reduced the economic value of fisheries and may promote a vicious cycle affecting inland FCs. To restore fishery resources that support the traditional fishing culture within the inland area, it is necessary to collect and systematize the losses experienced by inland fishermen and ensure sustainable management of the inland freshwater system.

Our study revealed that the historical distribution, geographical characteristics of Arctic lamprey before environmental changes to rivers, and changes in the species distribution are expected to contribute to the establishment of a baseline for conservation plans of this endangered species and the development in monitoring tool to improve the conservation of inland biodiversity.

Table 1 Information used to determine the presence of an Arctic lamprey harvest in rivers obtained from fishery statistics “Kasen Gyogyo” in the 1930s and the inland FCs. S1 means the result obtained using fishery statistics. F1 and F2 mean the presence of fishery activity in the past and present periods, respectively. Circles indicate the presence of fishery harvest and horizontal bars indicate the absence of a fishery harvest. Blanks indicate no information. The numbers of rivers correspond to those in Fig. 1

Side of the Sea of Japan																									**Side of the Pacific Ocean**				
No.	River	S_1	F_1	F_2	No.	River	S_1	F_1	F_2	No.	River	S_1	F_1	F_2	No.	River	S_1	F_1	F_2	No.	River	S_1	F_1	F_2	No.	River	S_1	F_1	F_2
1.	**Teshio**	○			26.	Noheji		○	-	51.	Miomote	-	○	-	**76.**	**Oyabe**	○	-	-	101.	Iinashi	-			114.	Koipe		-	-
2.	**Enbetsu**	○			27.	Nonai		○	-	**52.**	**Ara**	○	○	-	**77.**	**Machino**	○	○	-	102.	Hii	-	-	-	115.	Oippe		-	-
3.	**Haboro**	○			28.	Tsutsumi		-	-	**53.**	**Tainai**	○	-	-	**78.**	**Kawarada**	○	○	-	103.	Kando	-	-	-	116.	Takase		-	-
4.	**Obirashibe**	○			29.	Imabetsu		○	-	**54.**	**Kaji**	○	-	-	**79.**	**Konmachi**	○			104.	Sizuma	-			117.	Okuirise		-	-
5.	Horo	-			30.	Masukawa		-	-	**55.**	**Agano**	○	○	○	80.	Hakui	-	○	-	105.	Gouno	-	△	-	118.	Mabuchi		○	-
6.	Kungetsu	-			**31.**	**Iwaki**	○	○	○	**56.**	**Shinano**	○	○	○	**81.**	**Oono**	○			106.	Sufu	-	-	-	119.	Araida		-	-
7.	**Ishikari**	○			32.	Nakamura		○	-	57.	Kokufu		○	-	**82.**	**Sai**	○			107.	Takatsu	-	-	-	120.	Akka		○	-
8.	**Yoichi**	○			33.	Akaishi	-			58.	Hamochi		○	-	**83.**	**Tedori**	○	-	-	108.	Ooi	-	-	-	121.	Omoto		○	-
9.	Furubira	-			34.	Oirase	-	○	-	**59.**	**Sabaishi**	○			**84.**	**Kakehasi**	○			109.	Abu	-	-	-	122.	Settai		-	-
10.	Yobetsu	-			35.	Agatsuma		-	-	**60.**	**U**	○			**85.**	**Daishouji**	○	○	-	110.	Awano	-			123.	Tashiro		-	-
11.	**Horikappu**	○			36.	Sasanai		-	-	**61.**	**Kakizaki**	○	○	-	86.	Kuzuryuu	-	○	-	111.	Naka	-			124.	Hei		-	-
12.	**Shiribetsu**	○			37.	Mase	-	-	-	**62.**	**Seki**	○			87.	Shouno	-			112.	Onga	-			125.	Ootsuchi		-	-
13.	**Shubuto**	○			**38.**	**Yoneshiro**	○	○	○	**63.**	**Kuwatori**	○	△	-	88.	Mimi	-	-	-	113.	Matsuura	-			126.	Kozuchi		-	-
14.	Baba	-			**39.**	**Babame**	○	○	-	64.	Nou	-			89.	Hayase	-								127.	Unozumai		-	-
15.	**Shiribeshitoshibetsu**	○			**40.**	**Omono**	○	○	○	65.	Haya	-			90.	Kita	-	-	-						128.	Kitakami		-	-
16.	**Futoro**	○			**41.**	**Koyoshi**	○	○	○	66.	Hime	-	○	-	91.	Saburi		-	-										
17.	**Assabu**	○			42.	Shirayuki	-			67.	O		○	-	92.	Yura	-	△	-										
18.	Amano	-			**43.**	**Gakkou**	○			68.	Kurobe	-	-	-	93.	Takno	-												
19.	Ishizaki	-			**44.**	**Nikkou**	○	○	○	69.	Katakai	-	-	-	94.	Sanotani	-												
20.	Oyobe	-			**45.**	**Mogami**	○	○	○	70.	Hayatsuki	-			**95.**	**Maruyama**	○												
21.	**Fukushima**	○			46.	Aka		○	○	71.	Kamiichi		-	-	96.	Yada	-	-	-										
22.	Shiriuchi	-			**47.**	**Iso**	○			72.	**Shiraiwa**	○	-	-	97.	Sendai	-	-	-										
23.	Moheji	-			**48.**	**Atsumi**	○			73.	Jyouganji	-			98.	Tenjin	-	△	-										
24.	Noushi		-	-	**49.**	**Syounaioguni**	○			74.	**Jintsuu**	○	△	-	99.	Yura	-												
25.	Oohata		○	-	**50.**	Oo	○	○	-	75.	**Shou**	○	○	-	100.	Hino	-	-	-										

Table 2 Coefficients of the variables in models that were selected to explain the harvest distribution of arctic lamprey along the coast of the Sea of Japan from1927 to 1931 in 97 rivers in Japan

Model	Coefficients					AIC	ΔAIC
	Intercept	Latitude	River length	GW	GL		
1	-13.7 ***	0.37 ***	$5.7e^{-3}$		-207.2 **	102.8	0
2	-13.1 ***	0.37 ***			-233.9 ***	104.8	2.0
3	-10.6 **	0.28 **	$9.6e^{-3}$	-36.14 .		106.7	3.8
4	-10.7 ***	0.25 **	$5.8e^{-3}$ *			106.8	4.0
5	-9.7 **	0.28 ***		-53.26 **		114.6	11.8
6	-21.7 ***	0.32 ***	$2.2e^{-3}$		-153.5 ***	116.5	13.7

Table.3 Coefficients of the variables in models that were selected to explain the harvest distribution of arctic lamprey along the coast of the Sea of Japan based on the results of a survey of FCs

Model	Coefficients					
	Intercept	FC		River		
		Latitude	Elevation	Length	GW	GL
Past	-20.89 ***	0.56 ***	-0.0078 ***	0.0072 *		-203.7 *
Present	-16.68 .	0.41 .	-0.028 *	0.0059 .		-476.0 .

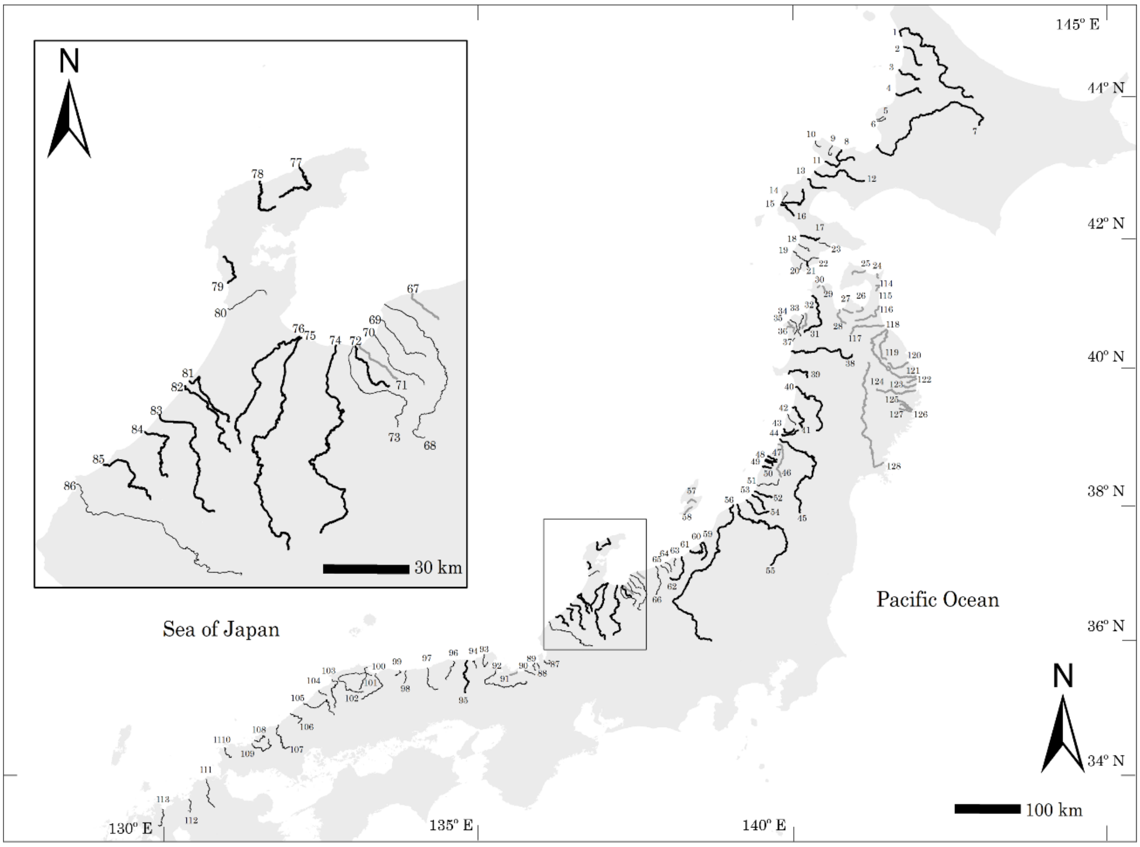


Fig.1 The historical distribution of the Arctic lamprey harvest from fishery statistics "Kasen Gyogyo" in the 1930s and the fishery cooperatives (FCs). The black thick and thin lines indicate the presence and absence, respectively, of a harvest according to the fishery statistics. The numbers beside the rivers correspond to those in Table 1. The gray line indicates the river harvest information obtained from only the FCs, with the result shown in Table 1

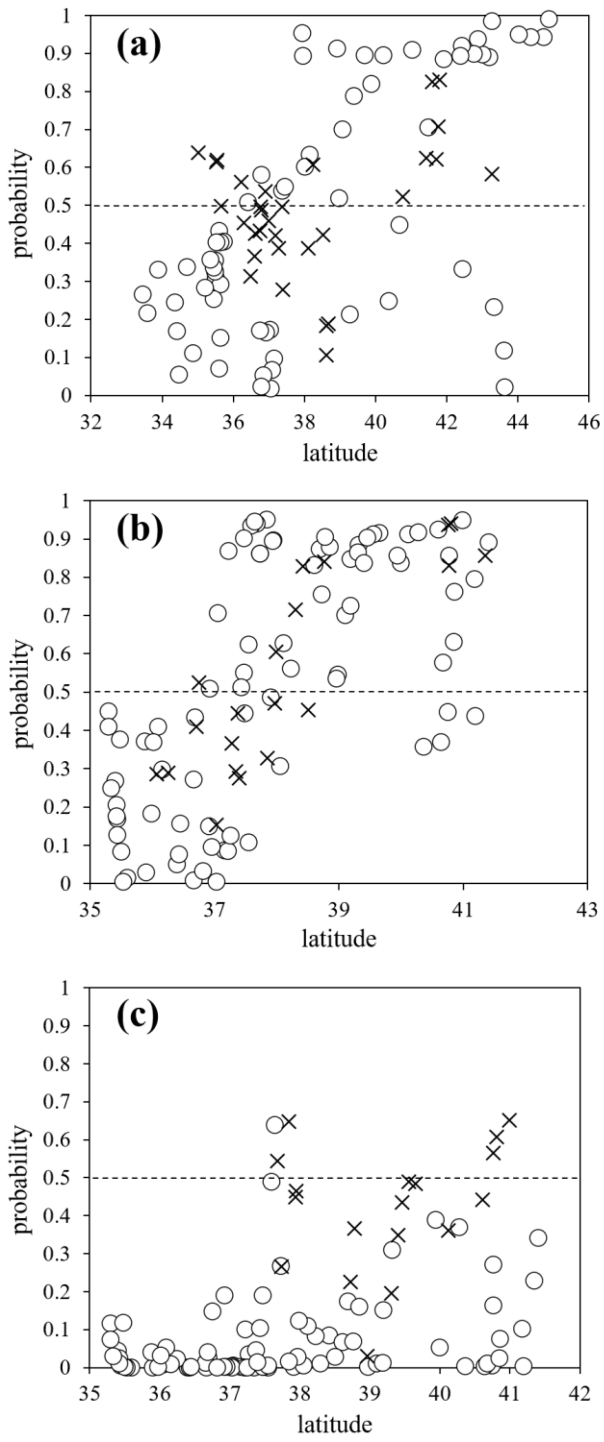


Fig.2 Probability of an Arctic lamprey harvest (presence ≥ 0.5, absence < 0.5) from the fisheries statistics from 1927 to 1931 (a), from the survey of FCs regarding their fishing activity in the past (b) and present (c), calculated from the best-fitted model. Correct classifications and misclassifications are represented by circles and crosses, respectively

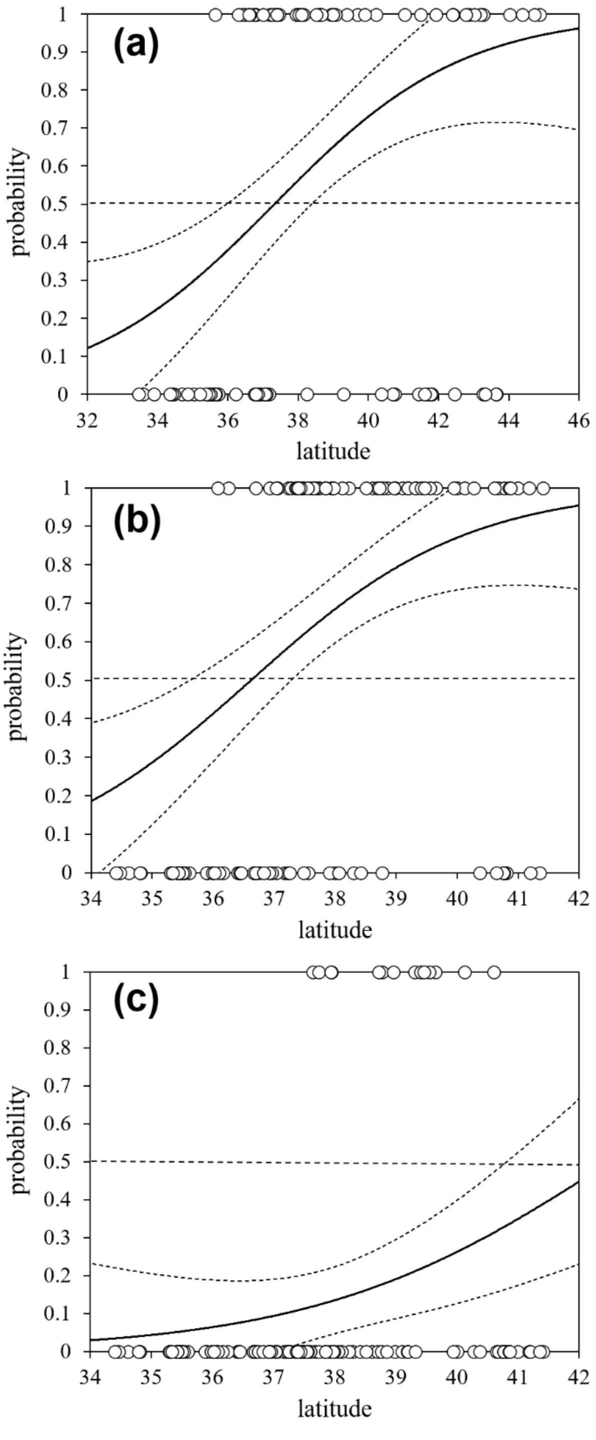


Fig.3 Relationship between the harvest distribution of Arctic lamprey from the fisheries statistics from 1927 to 1931 and the latitude of the river mouth (a), and between the harvest distribution from the survey of FCs regarding their fishing activity in the past (b) and present (c) and latitude at FCs. The relationship in (a) was estimated using the best model by substituting the median river gradient of the lower reach (1/403) and the medium river length (43 km) of 79 rivers. The relationships in (b, c) were estimated using the best model by substituting the median elevation at FCs (28 m), median river length (102 km) and median gradient of lower reach (1/719). When the probability was 0.5, the latitude of the southern limit of the harvest distribution was estimated to be (a) 37.3299ºN (95% CI: 35.9669ºN -38.3882ºN), (b) 36.6225ºN (95% CI: 35.6213ºN -37.2805ºN) and (c) 42.5130ºN (95% CI: 40.8209ºN -). The probability (presence=1, absence=0) for all rivers and FCs are indicated as circles

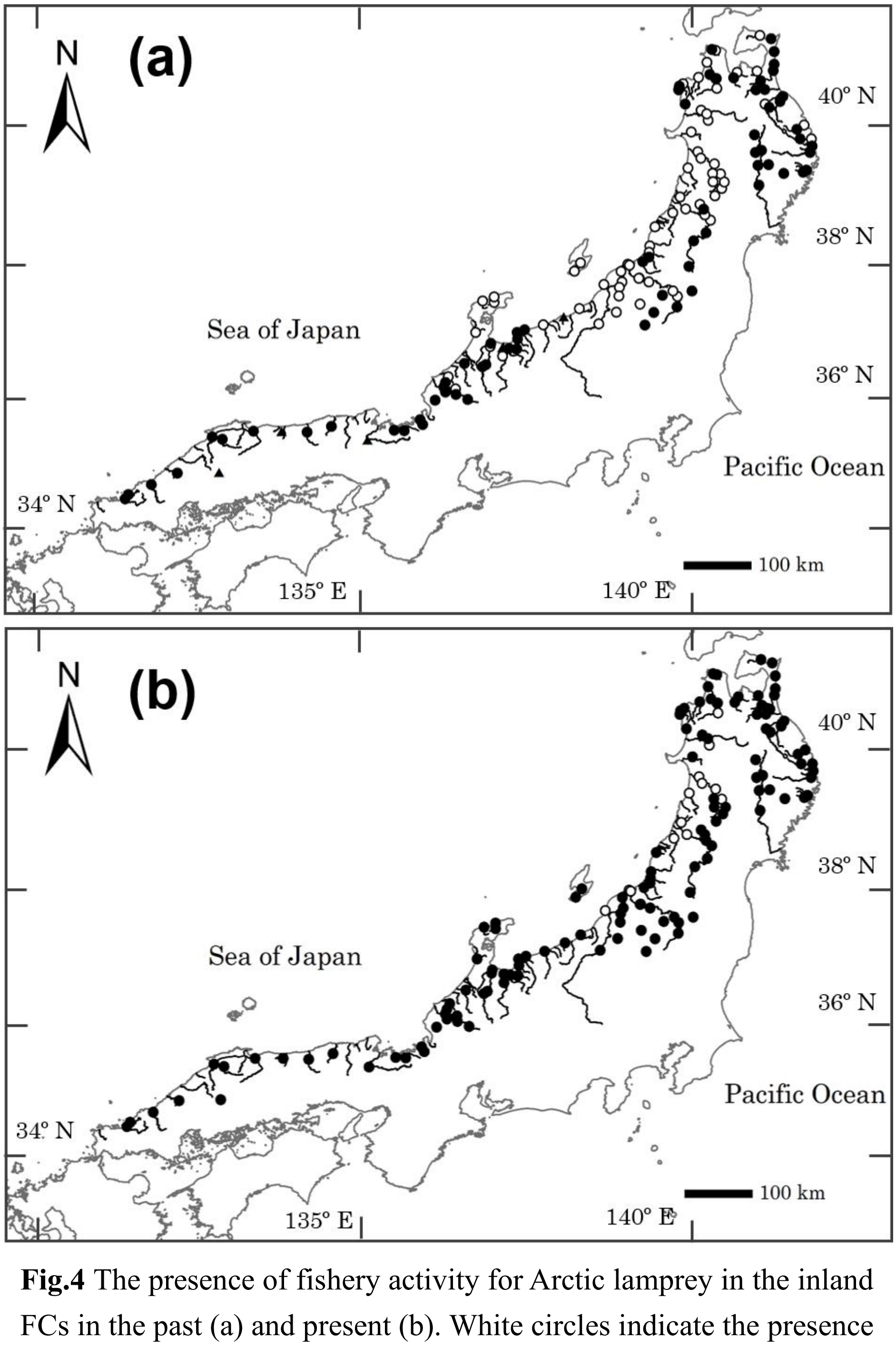


Fig.4 The presence of fishery activity for Arctic lamprey in the inland FCs in the past (a) and present (b). White circles indicate the presence of fisheries and black circles indicate the absence of fisheries

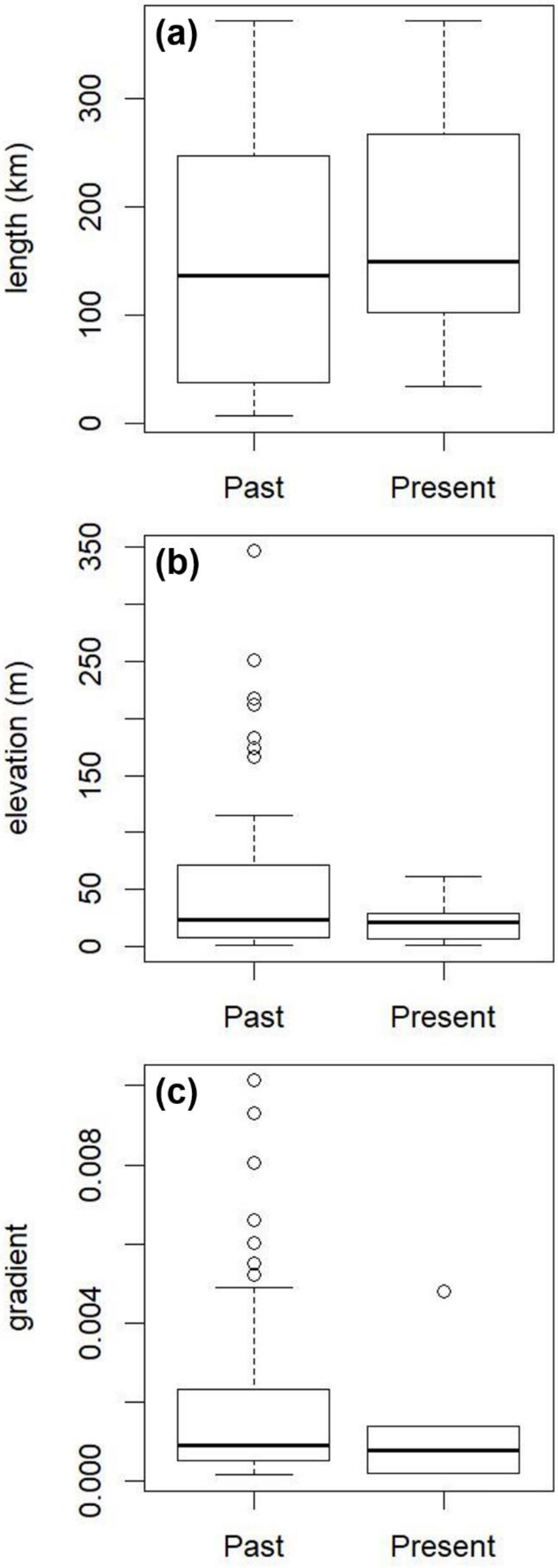


Fig.5 Geographical factors explaining the spatial distribution of Arctic lamprey along the Sea of Japan in the past and present periods according to the harvest information obtained from differences in the river length (a), elevation at fishery cooperative (b) and river gradient of the lower reach (c)

Chapter 3 Estimation of habitat potential for Arctic lamprey (*Lethenteron camtschaticum*) from Fishers' ecological knowledge and prediction of impacts of global warming on the future distribution in Honshu, Japan

Introduction

Maximum Entropy (MaxEnt) model is one of the species' distribution models (SDM) for modeling species geographic distributions with presence-only data (Phillips et al. 2006). Recent researches on SDM have served to place this technique among emerging new approaches relevant to ecology, biogeography, and conservation biology (Petersen et al. 2007). This predicted distribution is critical to predicting the effects of global climate change, evaluate the invasive potential of alien species, and discover new populations (Petersen et al. 2006). In recent studies, fishers' ecological information (FEK) including harvest information from fishermen has applied to SDM as presence-only data to support species conventional management (Silvano and Begossi 2010; Lopes et al. 2017). However, few studies use fishers' knowledge, mostly because this knowledge is considered to be anecdotal, non-methodological, and of limited application among scientists and managers (Bender et al. 2014). Fishermen can identify areas in their own region where target species are, but it is unknown that this local information from FEK can be used to predict species occurrence or niche distribution (Begossi et al. 2016; Lopes et al. 2017). Currently, species distribution predicted from FEK should be assessed the appropriateness of comparing the existing scientific data.

The fishery harvest baselines established according to the information from FEK in the areas differ among the generations. The 'shifting baseline syndrome' has arisen because each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers (Pauly 1995). Many reports suggest that older fishermen who have more experienced have specific and detailed ecological knowledge on the past target species abundance and distribution (Bender et al. 2014; Damasio et al. 2015). When the next generation starts its career, the stocks have further declined, but it is the stocks at that time that serve as a new baseline (Pauly 1995).

Arctic lamprey (*Lethenteron camtschaticum*) is an important fishery resource in Japan, but the catch has been decreased (Arakawa et al. 2018; Arakawa and Yanai under review, Chapter 1). The southern limit of Arctic lamprey harvest from FEK has shifted further north in Japan due to anthropogenic impact (Arakawa et al. under review, Chapter 2). To estimate the habitat potential Arctic lamprey, we should refer to all information including fishery activity which is presently being conducted and out of works. Especially, the fishery activity in the only past time such as losing memory could a potential to improve the SPD.

In this study, we modeled the habitat potential of Arctic lamprey in the Honshu Island, along the Sea of Japan using MaxEnt. To assess the appropriateness for the predicted distribution, we referred to the information about the rivers distributed Arctic lamprey according to the inland fishery statistics in 1927-1931 (Arakawa et al. under review, Chapter 2). As the species present data for Arctic lamprey, we used two information from FEK for testing the improvement in the models. Two species present data were the past harvest information which fishing methods were known and unknown from the Japanese inland fishery cooperatives.

Collions et al. (2003) estimate that the average surface air temperature will rise 2.6 and 4.8 degrees in the end of the 21st century from a baseline period of 1986–2005 depending on the climate change scenario. Rising temperatures due to climate change greatly influence populations of cold-water organisms living in the southern portions of their ranges in the northern hemisphere (Meisner 1990). Species distributions have shifted to higher elevations and to higher latitudes per decade (Chen et al. 2011). Lampreys are vulnerability to the climate change (Wang et al. 2020) and loss of the population in drainage the southern distribution are observed (Reid and Goodman 2016). The impact of climate change on the distribution of Arctic lamprey is now concerned but the concrete spatial distribution map in the present and future are not well established (Arakawa et al. under review; Arakawa and Yanai under review, Chapter 1, 2). Therefore, we predicted the loss of the habitat potential by comparing the original habitat potential due to the global warning.

Materials and Methods

Species presence data

Arakawa and Yanai (under review, Chapter 1) interviewed with the inland fishery cooperatives in the Honshu, along the Sea of Japan to organize the lamprey fishing method (gear, ground, season). The fishermen had traditional specific fishing method for Arctic lamprey depended on the ecological behaviors (Arakawa and Yanai under review, Chapter 1) and the distribution rivers and the southern limit were consistent with the available scientific data (Arakawa et al. under review, Chapter 2). We used this harvest information in the past from the inland fishery cooperatives as species presence data. The harvest information classified into three types of fishing methods and unknown fishing method. The unknown fishing method indicated the presence of Arctic lamprey fishing, but the interviewed person had never experienced to conduct or seen fishing individually. The harvest information known, and unknown fishing method was defined as detailed data (N=39), and ambiguous data (N=25), respectively (Fig.1). As the locational point data, we used the location of the fishing ground. But if we could not obtain the geo-referenced information, we estimate the presence of the species at a point in the river close to the fishery cooperative offices.

Environmental data

The study area was the region across Honshu along the Sea of Japan. To assess the habitat potential, the environmental variables should be hardly variable against anthropogenic environment modification (Inui et al. 2016). We used 4 environmental variables; 1) average slope SLP (º), 2) catchment area CA (km^2) , 3) distance from sea DS (km), and ground water temperature GWT (ºC, Fig.2). These environmental variables were used for predicting species distribution of cool-water species white-spotted char *Salvelinus leucomaenis* (Nakano et al. 1996; Takekawa et al. 2017). The GWT in the 1990s was calculated using altitude and latitude by following formula (Nakano et al. 1996),

$$GWT=56.364-1.120\ Latitude-0.005\ Altitude$$

The southern limit of the distribution for Arctic lamprey estimated by FEK was consistent with the fishery statistics in the 1930s (Arakawa et al. under review, Chapter 2). GWT increases by 0.94 °C when air temperature increases by 1 °C (Nakano et al. 1996). To estimate the GWT during 1900-1949, we referred annual average temperatures in 12 meteorological stations along the Sea of Japan (Suttsu, Aomori, Akita, Yamagata, Niigata, Fushiki, Kanazawa, Fukui, Kyoto, Sakae, Hamada, Simonoseki) during 1900-1949 and in the1990s.

Three-dimensional mesh having rivers was extracted for the analysis. All geographical information was obtained from the Ministry of Land, Infrastructure, Transport, and Tourism (digital national land information; https://nlftp.mlit.go.jp/ksj/) and edited by ArcMap soft ver. 10.7.

Species distribution modeling

We performed two species distribution modeling with two data sets. One was the dataset of only detailed data, and the other dataset was all information of detailed and ambiguous data. The modeling using MaxEnt ver. 3. 3. 3 was used for the modeling. As a setting, the random test percentage was 25, the regularization multiplier was 2 to avoid overfitting (Radosavljevic and Anderson 2014), and the maximum number of background points was 10,000. We ran 5 replicates in both models using random seed.

To predict the impacts of global warming on the future distribution for Arctic lamprey in Honshu, we performed projection layers in MaxEnt. We edited the only GWT in 1900-1949 of the model using all data increase when the air temperature raised by 1, 2, 3, 4 °C.

Results and Discussion

Significant predictors

The results of MaxEnt models showed that the area under the receiver operating characteristic curve statistics (AUC) indicating estimation accuracy were 0.878 for the model using detailed data and 0.854 for the model using all data. The AUC over 0.8 is considered to have sufficient discriminatory (Stress 1988). AUCs higher than 0.8 for both models suggest that models have good agreement with the testing.

In both models, average slope was the strongest predictor for Arctic lamprey distribution with 65 % contribution (Fig.3). In the model using the detailed data, catchment area and ground water temperature in 1900-1949 were the secondary important predictors with 15 % and 12 % contributions, and in the model using all data, ground water temperature in 1900-1949 and catchment area were the secondary important predictors with 15 % and 13 % contributions. The distance from sea was the lowest contributions with 8 % and 7% in both models. The occurrence of Arctic lamprey seems to occur in areas with lower slope, large catchment area, and lower ground water temperature. Especially, the geographical limitation such as river slope is the primary factor to restrict the distribution for Arctic lamprey.

Habitat potential

The area logistic threshold was 0.4297 in the model using the detailed data and 0.4269 in the model using all data. Although overall the predicted habitat potential distributions were the same for both models (Fig.4). The habitat potential of both models distributed at lowlying areas and alluvial fans across the range from Tohoku (north area) to Hokuriku (middle area). Within the range, there were some unsuitable areas including Aomori (Shirakami Mountains) and Toyama (Northern Alps Mountains). These areas are considered to restrict the distribution due to steep geographical characteristics and the absent harvest record in the 1930s from the inland fishery statistics is consisted with this result. However, there were some differences in the prediction between two models, especially in the marginal regions such as southern and inland area. In the model using the detailed data, the habitat potential did not distribute at the western Toyama and the middle reach of the Agano River (Fukushima), whereas the model using all data predated the habitat potential in these areas. According to the inland fishery statistics in the 1930s, the harvest of Arctic lamprey was recorded in the rivers at western Toyama with relative lower river steep downstream, in addition, the fishermen was used to catch Arctic lamprey in the middle and upper reach in the Agano River (Arakawa et al. under review, Chapter 2). The loss of the fishery activity for Arctic lamprey has been obviously occurred in the southern area and higher elevation area (Arakawa et al. under review, Chapter 2). The loss of information about the traditional fishing culture is conserved to corresponded with the decline of fishing activity. Therefore, our study suggests that the model depending on the FEK including harvest information unknown fishing methods defined as ambiguous data could contribute to improvement in predicting potential species distribution. The inland fishermen have the potential to provide the critical ecological information for species management. But the number of inland fishermen belonging to Japanese fishery cooperatives (FCs) is estimated to be 0 until 2035 – 3036 due to aging and changes in people's life cycles (Nakamura 2017). With the loss of information about historical biodiversity and species abundance in the local areas, the associating information should be conducted to establish conservation plan for inland biodiversity.

Impacts of global warming on the future distribution

For the loss of habitat potential with temperature increase, the dominant distribution areas in Hokuriku and downstream at Niigata had been lost in the 1990s, whereas, the upper reach of the Shinano River and the Angano River had the habitat potential. With 1℃ increase, the dominant habitat potential in the upper reach of the Shinano River and the Angano River had been lost. With 2 and 3℃ increases, the dominant habitat potential in the Yamagata and Akita had been lost, sequentially. With 4℃ increases, the habitat potential in Honshu had been lost. The present harvest of Arctic lamprey in the Noto peninsula located in Hokuriku has decreased and consisted with the result (Arakawa et al. 2018). However, the decline similarity in harvest has been occurred through Honshu along the Sea of Japan (Arakawa and Yanai review, Chapter 1). The present decline of harvest cannot be explained with only the impact of warming in the freshwater. Arctic lamprey has lower homing abilities, and the gene flow is observed in the populations in North Pacific Ocean coast between Japan and Russia. The impacts of climate change to anadromous lampreys are not completely understood at specific geographical locations and across life stages (Clemens et al. 2020). In the ocean for migrating juvenile and adult stages, oceanographic regimes and interactions between climate change and oceanographic regimes can limit the distribution and availability of host species (Clemens et al. 2020). Orlov et al. (2014) report the migration of Arctic lamprey in the North Pacific but the long-term dynamics is unknown. To assess the impact of global warming on the Arctic lamprey population, the dynamics and suitable characteristics for all stages in freshwater and ocean should be investigated in the future. Our study provides the basic spatial distribution pattern of Arctic lamprey in Japan located in the southern limit of the distribution and contribute to assess the impact of future global warming.

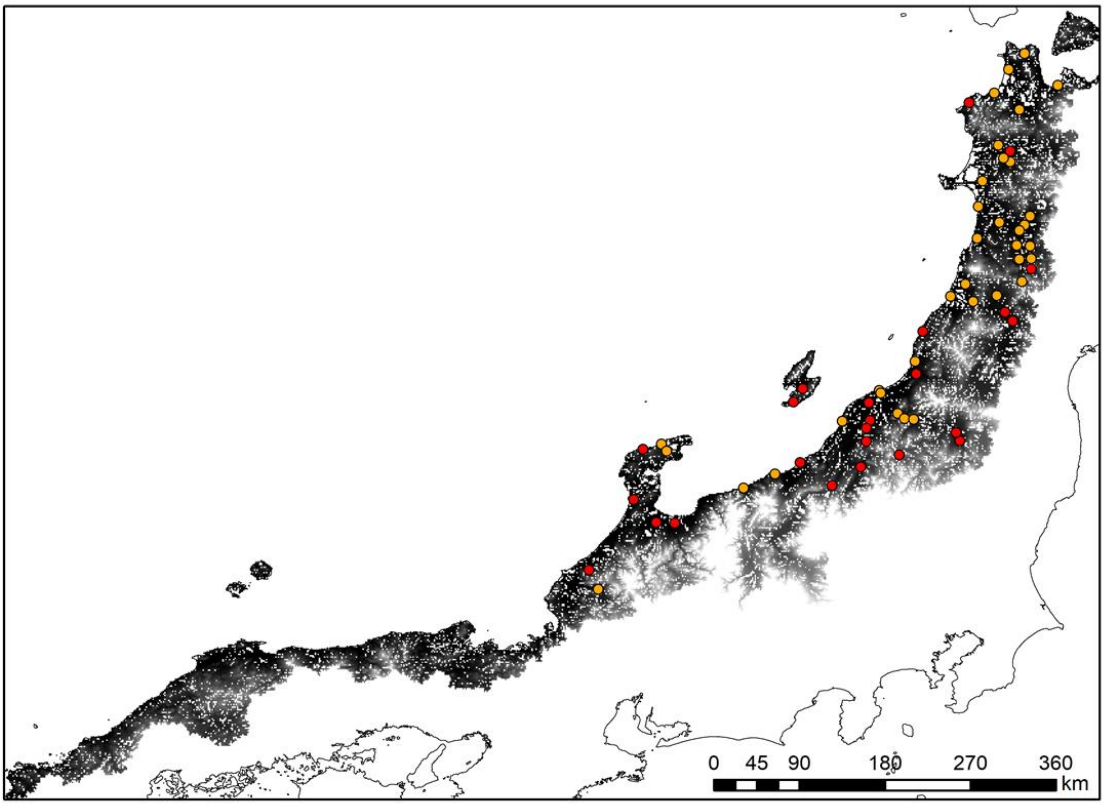


Fig. 1 Point data of species distribution in the past according to the harvest information including detailed fishing method (orange color) and unknown fishing method (red color).

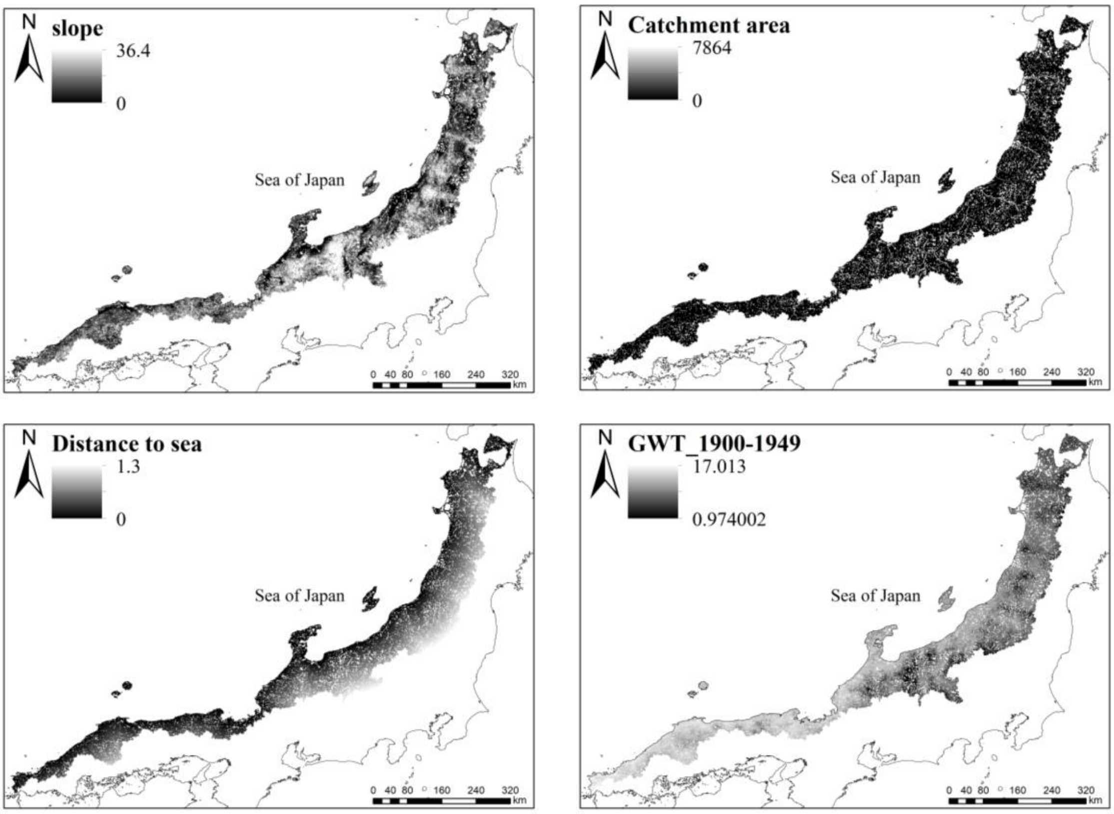
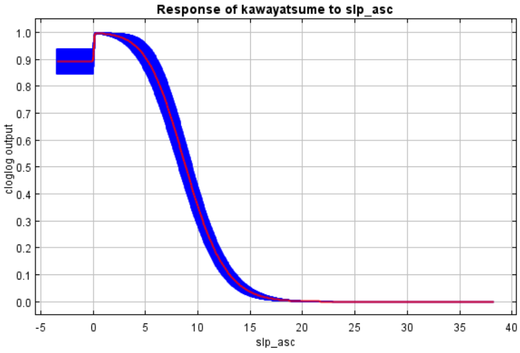
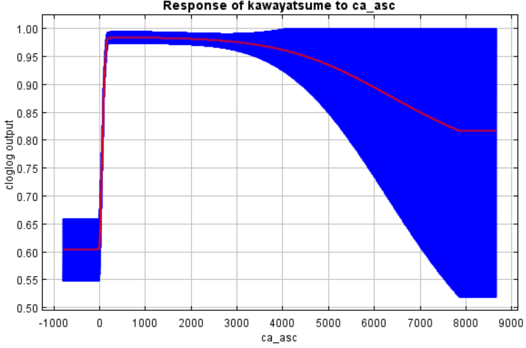


Fig. 2 Layer data of geographical factors for 3 mesh (5×5 km) of mean slope, catchment area, distance to sea, and GWT_1900-1949 (groundwater temperature during 1900-1949)

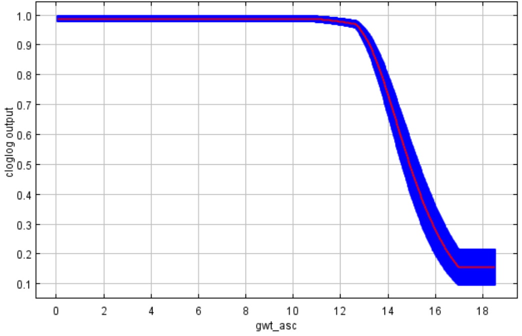
Average slope (65 %)



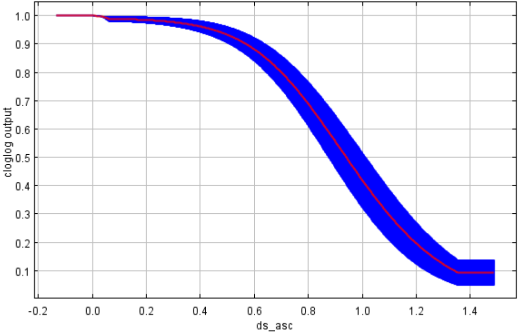
CA (15 %)



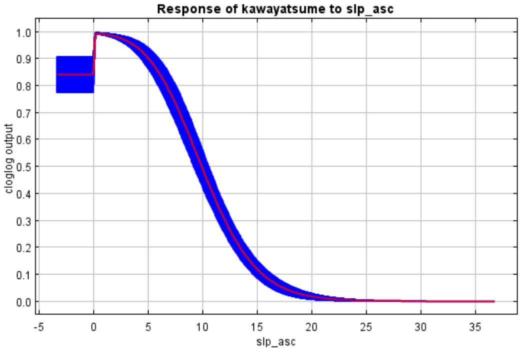
GWT in 1900-1949 (12 %)



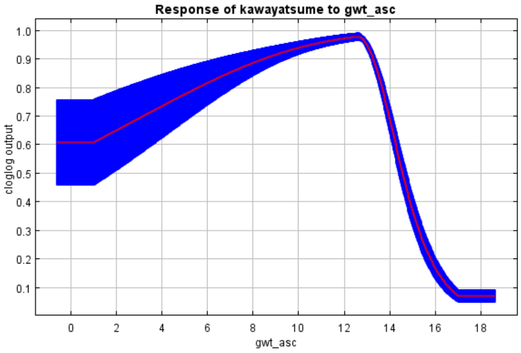
DS (8 %)



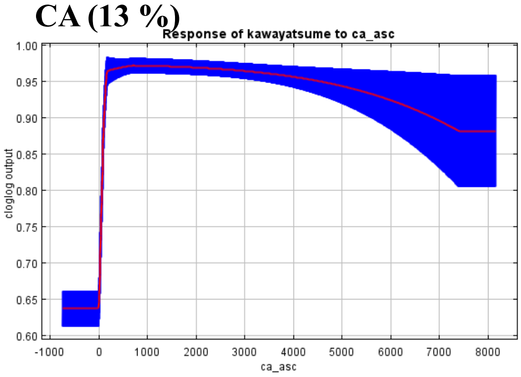
Average slope (65 %)



GWT in 1900-1949 (15 %)



CA (13 %)



DS (7 %)

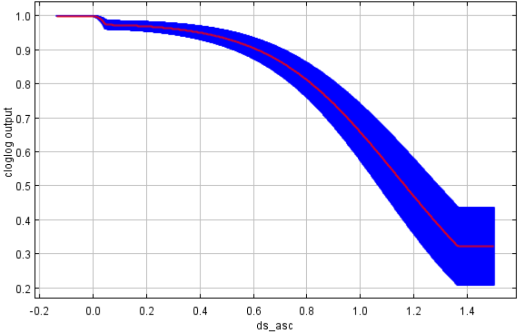


Fig. 3 Species occurrence response of geographical variables (Percent contribution). The order indicates higher contribution to the species distribution models predicted by detailed data (left side) and all data (right side)

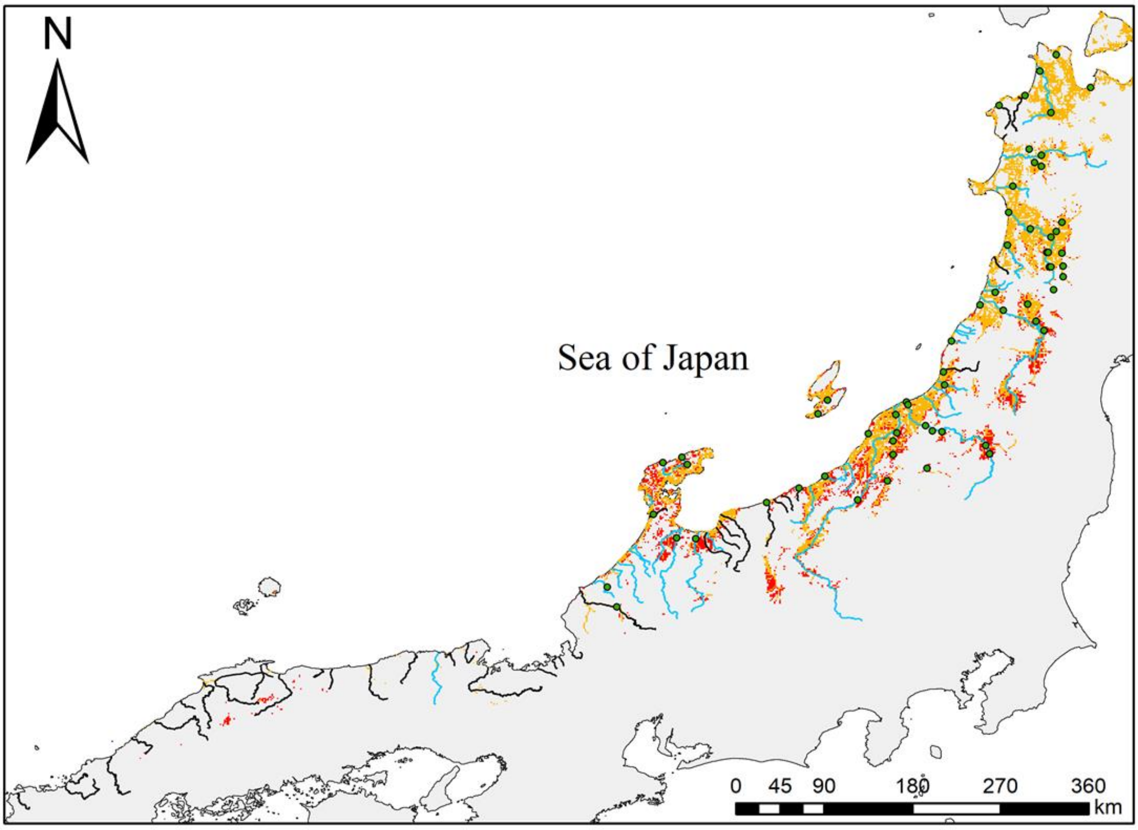


Fig. 4 Habitat potential for Arctic lamprey in the past, which were estimated by the harvest information of only detailed fishing method (orange color) and detailed fishing method and unknown fishing method (red color). Blue lines and black lines indicate the harvest presence and absence from the fishery statistics in 1930s

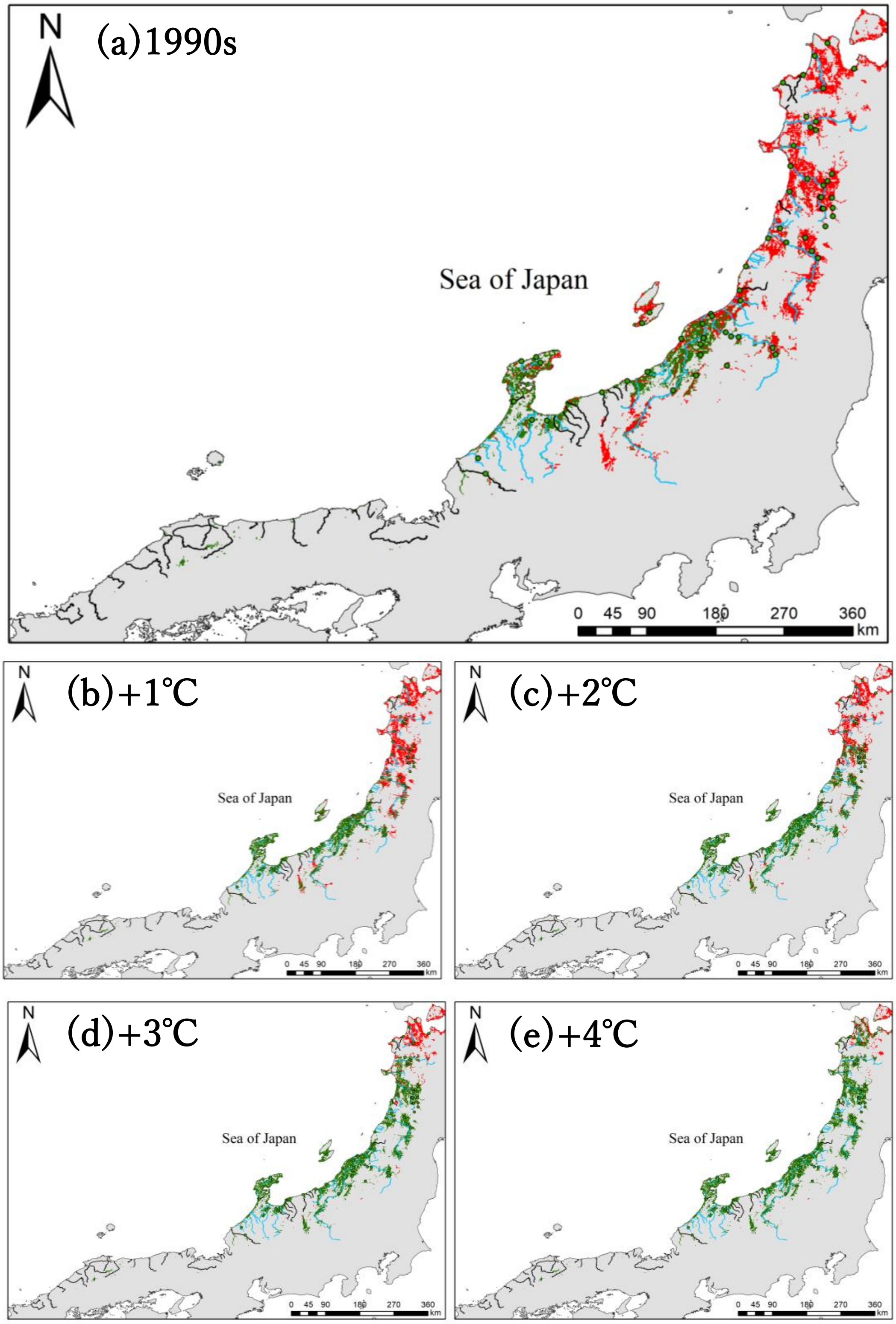


Fig. 5 Habitat potential reduction when air temperature rises (1-4°C) after the 1990s. The red and green areas indicate habitat potential and potential loss. (a) Habitat potential in the 1990s. (b-e) Habitat potential when air temperature rises at 1-4°C. Blue lines and black lines indicate the harvest presence and absence from the fishery statistics in 1930s

Chapter 4 Upper thermal tolerance of larval Arctic lamprey (*Lethenteron camtschaticum*)

Introduction

Arctic lamprey (Lethenteron camtschaticum) is a cool-water jawless vertebrate with a parasitic and migratory lifecycle, which is distributed throughout high and middle latitude regions around the northern Pacific Ocean (Orlov et al. 2014). Alaska and Russia represent the northern limits of its distribution, and Japan is located at its southern limit. In Japan, Arctic lamprey is distributed from Hokkaido to Shimane along the Sea of Japan. However, the abundance of this species has substantially declined due to river modifications, such as dam construction and channelization (Murano et al. 2008). In addition, the southern distribution limit has shifted northward in the past decade, according to the National Census on River Environments (Ministry of Land 2020). Harvest of Arctic lamprey has sharply declined at the southern edge of its distribution range (Arakawa et al. 2018).

Rising temperatures due to global warming greatly influence populations of cold-water organisms living in the southern portions of their ranges (Meisner 1990). For increases of 1.0-4.0ºC in mean annual air temperature, the summer thermal habitat for Dolly Varden trout is reduced by 25.0-74.0% (Kitano et al. 1995). In river ecosystems, water temperature is a major direct threat; it also indirectly limits the habitat of fish (Ferguson 1958). Water temperature has effects on metabolism (Clarke and Johnston 1999), feeding (Takami et al. 1997), growth (Selong et al. 2001), and interspecies competition (Schlosser 1987). For Pacific lamprey (Entosphenus tridentatus), changes in stream temperature and flow regimes can interfere with and create the mismatches in the timing of the seasonal activities of migration, spawning, and embryonic development (Maitland et al. 2015; Clemens et al. 2016). In addition, summertime warm stream temperatures exceeding 20°C cause stress, tissue damage, and potential mortality thorough the lifecycle (Clemens et al. 2016). In contrast, since adult Arctic lamprey spends less than half a year from autumn to spring in freshwater (Kawanabe and Mizuno 1989), summer warm stream temperature has an impact on the larval stage. However, the basic thermal tolerance of larval Arctic lamprey is not well characterized and needs to be estimated to evaluate the impact of rising water temperature due to global warming.

To determine the upper lethal limit of larval Arctic lamprey, we used the incipient lethal temperature (ILT) and the acclimated chronic exposure (ACE) methods. The ILT method involves transferring test fish rapidly from an acclimation temperature to a constant test temperature and measuring tolerance in terms of time to death (Brett 1952). The temperature at which fifty percent of test fish die (LD50) is defined as the ultimate ILT and used as a measure of thermal tolerance. The ILT method allows determination of the temperature tolerance of the target organism within a short period. In addition, because many studies have reported estimates of the thermal tolerances of a variety of fish using the ILT method, this approach can be used for interspecies comparisons. However, the ILT method produces unnaturally rapid changes (Selong et al. 2001). In the ACE method, the temperature of the tank containing the test fish is gradually changed by 1ºC per day until reaching the test temperature (Zale 1984). This slow increase in water temperature minimizes the effects of temperature acclimation and allows evaluation of their growth and survival rates.

We estimated the ultimate ILT of larval Arctic lamprey during a short-term rearing experiment and reared larvae for a long period at temperatures around the ultimate ILT to evaluate the influence of high temperature on their survival and growth rates using the ACE method.

Materials and Methods

Larval lampreys and experiment settings

For the ILT and ACE experiments, we used artificially propagated young-of-year larvae to avoid excessive individual collection from the river. The artificial propagation was conducted on May 5, 2017, using one pair of mature Arctic lampreys (one female and multiple males) captured in the Mogami River, Yamagata, Japan (See Arakawa and Yanai 2018). The hatched larvae were reared in an irrigation canal at Ishikawa Prefectural University, Ishikawa, Japan; they were fed dry yeast, wheat flour, and juvenile fish feed until the start of acclimation. Larvae were collected from the substrate of the irrigation canal by scooping sediment with larvae. Larvae were reared in an aquarium covered with fine sediment from the same habitat, fitted with an aerator and heater. They were acclimated at 18ºC for one week prior to both experiment.

For both experiments, we used three small, replicated plastic containers (15×20.5×16.5 cm) set within a large plastic container (70×40×20 cm). Both containers were filled with water to a depth of 12 cm. A heater was installed in the large container. The water temperature in the small containers was indirectly controlled by the water temperature in the large container. Aerators were placed in each container to agitate the water to stabilize its temperature. Three small containers were used as replicates for each test temperature. The experiments were conducted in a thermostatically shielded room at 17-19ºC and illuminated for a 12:12 hours period. During the experiments, additional water of the same temperature was added into the containers to prevent water depth reduction due to evaporation.

Incipient lethal temperature (ILT) method

For the ILT experiment, the test temperatures were set to 18ºC, 21ºC, 24ºC, 27ºC, 28ºC, 29ºC, 30ºC, and 33ºC. Ten larvae were placed into each replicate container (30 larvae per test temperature). The experimental period except the acclimation period was one week. At the beginning of the experiment, 20 larvae were randomly subsampled and their total length (TL; mm) and wet mass (WM; mg) were measured. These larvae were weighed after removing excessive water using a sponge gently. Mean TL and WM were 27±5 mm and 40±25 mg, respectively. Larvae were immediately transferred from the 18ºC acclimation aquarium to the small containers at each test temperature. Survival rates were observed continuously for the first hour and then mortality and temperature were checked per 24 hours for one week. We observed dead lampreys, which did not move and appeared dusky white in color. The pH, conductivity, and dissolved oxygen were measured at the start and end of the experiment. Dissolved oxygen saturation was calculated from dissolved oxygen, based on the dissolved oxygen content when the chloride ion content of water was 0 mg Cl-/L (Namiki 2014). To measure thermal tolerance, the length of time to 50% survival (LD50) at each test temperature was calculated. Based on the relationship between water temperature and LD50, logistic regression was performed via the least squares method to estimate the water temperature at which the survival rate equaled 50% in one week, representing the ultimate ILT. The experiment was conducted from August 16 to September 9, 2017. Since the survival rates at 28ºC and 29ºC were around 50% in one week, the experimental duration was extended for several days to obtain the LD50.

Acclimated chronic exposure (ACE) method

For the ACE experiment, the test temperatures were 18ºC, 26.5ºC, 28ºC, 29.5ºC, and 31ºC. The optimum temperature for various larval lamprey species was estimated at around 18ºC (Holmes and Lin 1994; Meeuwig et al. 2005). Therefore, we assumed that 18ºC was the ideal temperature for larval Arctic lamprey and compared the survival and growth rates at 18ºC with those at other test temperatures.

To rear larval lampreys, we provided fine sediment (particle size of less than 0.25 mm) to a depth of 3 cm in the small containers as burrowing habitat; we also provided feed. When larvae are fed without flow, water quality decreases because not all of the food is consumed. A reportedly effective method for culturing without flow consists of feeding 250 mg/week of food per 1 L water and replacing 30% of the water in the aquarium twice weekly (Moser M. L., NOAA, private communication). In our experiment, the water volume of the small containers was 2.76 L and the amount of feed was 690 mg/week of mixed food (dry yeast and salmonid food at 4:1). Feeding was conducted twice weekly. Water replacement of 30% was carried out once per week. The TL and WM were measured for all larvae used in the experiment. Ten larvae (30 larvae per test temperature) were introduced into the small containers set to the initial temperature of 18ºC. To reach each test temperature, the temperature was raised by 1ºC per day and timed such that the test temperature was reached at the same time by all containers. The temperature increase began on September 21, 2017; all containers reached their test temperatures on October 4, 2017. Subsequently, larvae were reared at each test temperature for one month. We observed dead lampreys, which appeared dusky white in color, on top of the sediment once daily throughout the experiment. Water temperature, pH, conductivity, and dissolved oxygen were measured at the same frequency as in the ILT experiment. In addition, we measured oxidation-reduction potential in the fine sediment as a sediment environmental condition when water quality conditions were measured. After one month, we removed all sediment from the containers into a wide metallic tray and collected the surviving larvae for calculation of survival rates and measurement of the TL and WM of all surviving larvae.

Differences in the initial TL and WM of individuals among containers used in the ACE experiment were determined using one-way analysis of variance with the anova function. Differences in survival rates in the ILT and ACE experiments among test temperatures were determined using the Kruskal-Wallis test via the kruskal.test function. The growth rates of TL and WM in the ACE experiment were compared among test temperatures using the Tukey-Kramer test with the TukeyHS function. Differences were considered statistically significant at $P < 0.05$; all statistical analyses were conducted using R version 3.5.1.

Results

ILT method

During the ILT experiments, temperature variations at 18-28ºC and 33ºC were less than 0.5ºC. The test temperatures of 29ºC and 30ºC reached 30.1ºC on the 6th day and 29.1-29.2ºC on the 3rd and 4th days. The pH ranged between 7.89 and 8.90, with no differences between the start and end points or among test temperatures. Conductivity initially showed no difference among test temperatures (0.250-0.276 mS/cm), but eventually increased at warmer test temperatures (0.303-0.562 mS/sm). Dissolved oxygen was saturated at all test temperatures throughout the experiment (97-108%).

The mean survival rates in one week were 96-100% at 18-28ºC, 63% at 29ºC, 30% at 30ºC, and 0% at 33ºC (Fig. 1a). The mean survival rates differed significantly among test temperatures ($X2 = 20.2$, $P < 0.05$). The median survival times (LD50) were 144-304 hours at 29ºC, 12-96 hours at 30ºC, and 0.5 hours at 33ºC. The correlation between water temperature and LD50 was significant (Fig. 2, $R^2=0.66$). Based on the regression formula, the ultimate ILT of larval Arctic lamprey for 7 days of culture was estimated to be 29.3ºC (95% CI: 28.2-30.2ºC).

ACE method

The mean TL and WM of larvae at the start of the ACE experiment were 30.3-31.9 mm and 53.00-63.5 mg, with no significant difference among test temperatures ($F = 0.109$, $P = 1$). During the experiment, temperature variations at 18ºC and 26.5ºC were less than 0.5ºC. However, at the test temperature set to 28ºC, 27.1ºC was recorded on the 12th day; at the test temperature set to 29.5ºC, 28.9ºC was recorded on the 18th day; and at the test temperature set to 31ºC, 30.0ºC, 30.2ºC, and 30.2ºC were recorded on the 6th, 12th, and 25th days, respectively. The pH and dissolved oxygen values were 7.36-8.79 and 93-129% respectively, with no differences among test temperatures. At the end of the experiment, conductivity had increased (start: 0.209-0.235 mS/cm, end: 0.397-0.899 mS/cm) and oxidation-reduction potential had decreased at warmer test temperatures (start: 230-268 mV, end: -234-37 mV).

The survival rates were 97-100% at 18ºC, 26.5ºC, and 28ºC; 60% at 29.5ºC; and 3.3% at 31ºC (Fig. 1b). Above 29.5ºC, the survival rate decreased with a significant difference among test temperatures (X2 = 13.0, $P < 0.05$). The growth rates based on TL and WM of the larvae were higher at cooler test temperatures than at warmer test temperatures (Fig. 3a, b). The highest growth rates of TL and WM were 33% and 114% at 18ºC. The lowest growth rates were 0% for TL and a reduction of 17% for WM at 29.5ºC. The growth rate of TL at 18ºC was significantly different from the growth rates at all other test temperatures. The growth rate of WM at 18ºC was significantly different from the growth rates at 28ºC and 29.5ºC.

Discussion

The present study demonstrated that the ultimate ILT (one week) of young-of-year larval Arctic lamprey was 29.3ºC (95% CI: 28.2-30.2ºC), which is comparable to the thermal tolerances of other larval lampreys, e.g. 31.4ºC for Sea lamprey and 29.2-29.4ºC for Brook lamprey (Lampetra planeri) (Potter and Beamish 1975). The upper thermal tolerance of lamprey species is within the range of 29-31ºC. In the ACE experiment where larvae were reared in water temperatures of 29.5ºC and 31ºC, survival rates were significantly lower than those at the optimal temperature of 18ºC. Survival in a habitat above the upper lethal temperature is difficult for larval Arctic lampreys. In addition, inhibition of growth in terms of TL and WM occurred at 28ºC, which is below the lethal temperature. The growth rates of cool-water fish are reduced at sublethal temperatures, compared to the optimal thermal range (Takami et al. 1997, Selong et al. 2001). Because the availability of food was greater in the rearing aquarium than in the natural environment, the impact of sublethal warm temperature could markedly limit the survival of larval Arctic lampreys in natural freshwater habitats.

In the Machino River (Ishikawa, Japan), which is located at the southern limit of the distribution range of Arctic lamprey, the maximum daily river temperature in summer was above 30ºC, exceeding the upper lethal temperature (Arakawa H., unpublished data). Cool-water fish prefer thermal habitats that are cooler than upper lethal and sublethal temperatures (Christine and Regier 1988). For example, Bull Trout (Salvelinus confluentus), which shows significant vulnerability to warm water, is distributed where the maximum temperature is below 13-14ºC and daily mean temperature is in the range of 8-10ºC in summer (Rieman and Chandler 1999). Due to global warming, the habitats of cool-water fish at the southern limits of their distributions will be limited to cooler upstream areas in the Northern Hemisphere (Nakano et al. 1996). Therefore, fish must migrate upstream to utilize the optimal thermal habitat available in mountain areas, and this process depends on the swimming ability of the species. Lampreys are anadromous and exhibit downstream migration of larvae and the upstream spawning migration of adults (Hardisty and Potter 1971). The maximum swimming speed of large larval Sea lamprey has been estimated at 0.45 m/sec (Thomas 1962). Larval lampreys cannot move against rapid currents and are transported downstream by river flow and flooding (Hardisty 1944; Hardisty and Potter 1971; Derosier et al. 2007). Therefore, the upstream spawning migration of adults dictates the thermal range that will be experienced by larvae. However, Arctic lamprey show poor ascending ability at weirs with slight water depth differences (Arakawa et al. 2019, Chapter 6). When upstream migration is interrupted by a dam or weir, the distribution of Arctic lamprey is limited to areas downstream of the structure (Murano et al. 2008), and lampreys cannot reach upper watershed areas in the appropriate thermal range. In addition, because warm temperature promotes the maturation of adult lamprey (Clemens et al. 2009), lampreys in warmer areas may spawn earlier and further downstream. The interaction between the limited distribution to downstream areas and warming river temperature could affect the maintenance of the population at the southern limit of their range.

However, Arctic lamprey larvae were distributed in rivers where maximum water temperature exceeds their upper thermal tolerance (Arakawa H., unpublished data); thus, they might somehow avoid the metabolic problems caused by lethal warm water. Larval lampreys burrow in fine sediment during the daytime and emerge from the sediment to move to a new habitat at night (Derosier et al. 2007). Therefore, the water temperature within the sediment must be measured to evaluate the impact of lethal temperature on larval density. Sediment provides a thermal gradient, becoming cooler at deeper levels during the warm season (Evans et al. 1995). In rivers fed by spring water, the temperature in the sediment is more strongly influenced by spring water than river water (Kawanishi and Inoue 2018). Spring water areas have small-scale temperature dynamics that provide thermal refuge for cool-water fish when the river temperature rises during the day (Ebersole et al. 2003). Research regarding the relationship between cool-water fish and their sediment habitat is very limited, and further studies are needed. Fine sediment rich with organic matter provides food resources and is important habitat for larval lampreys (Potter et al. 1986; Shirakawa et al. 2009). However, warm river water promotes anaerobic decomposition of organic content in fine sediment under low-flow conditions, leading to critical oxygen shortage (Ryan 1991). Arakawa and Yanai (2017) reported that larval Arctic lampreys avoided anaerobic sediment in the river located at the southern limit of their range. Evaluation of sediment as a thermal refuge and the indirect effects of the chemical environment in the sediment on larval habitat is essential. A better understanding of the thermal tolerance of larval Arctic lamprey will contribute to the development of conservation and management plans, prediction of present habitat potential and loss in freshwater systems caused by climate change in the future.

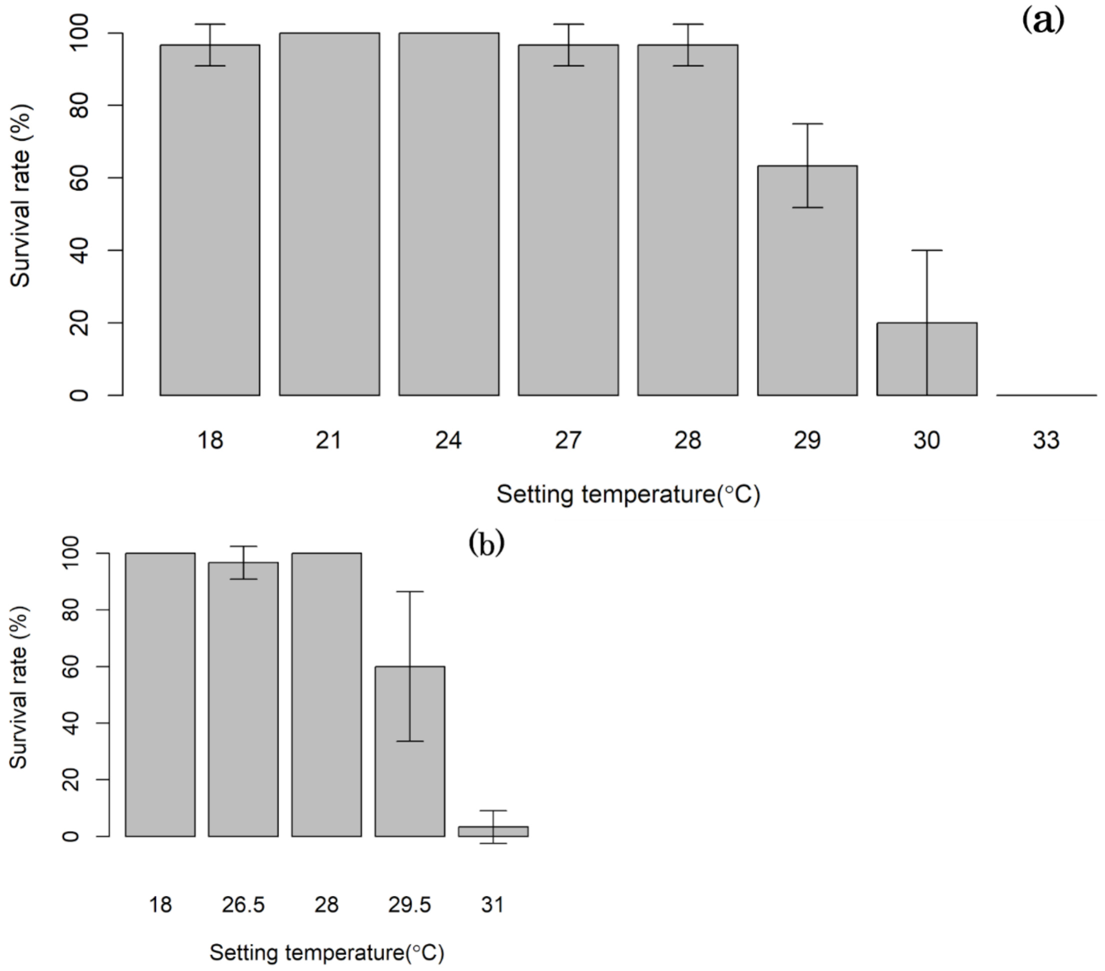


Fig. 1 Average survival rates on each test temperatures in the DAE experiment (**a**) and the ACE experiment (**b**). Bars indicate standard deviations. Significantly difference occurred among the test temperatures using Kruskal-Wallis test (DAE: X^2=20.2, $P < 0.05$, ACE: X^2=13.0, $P < 0.05$)

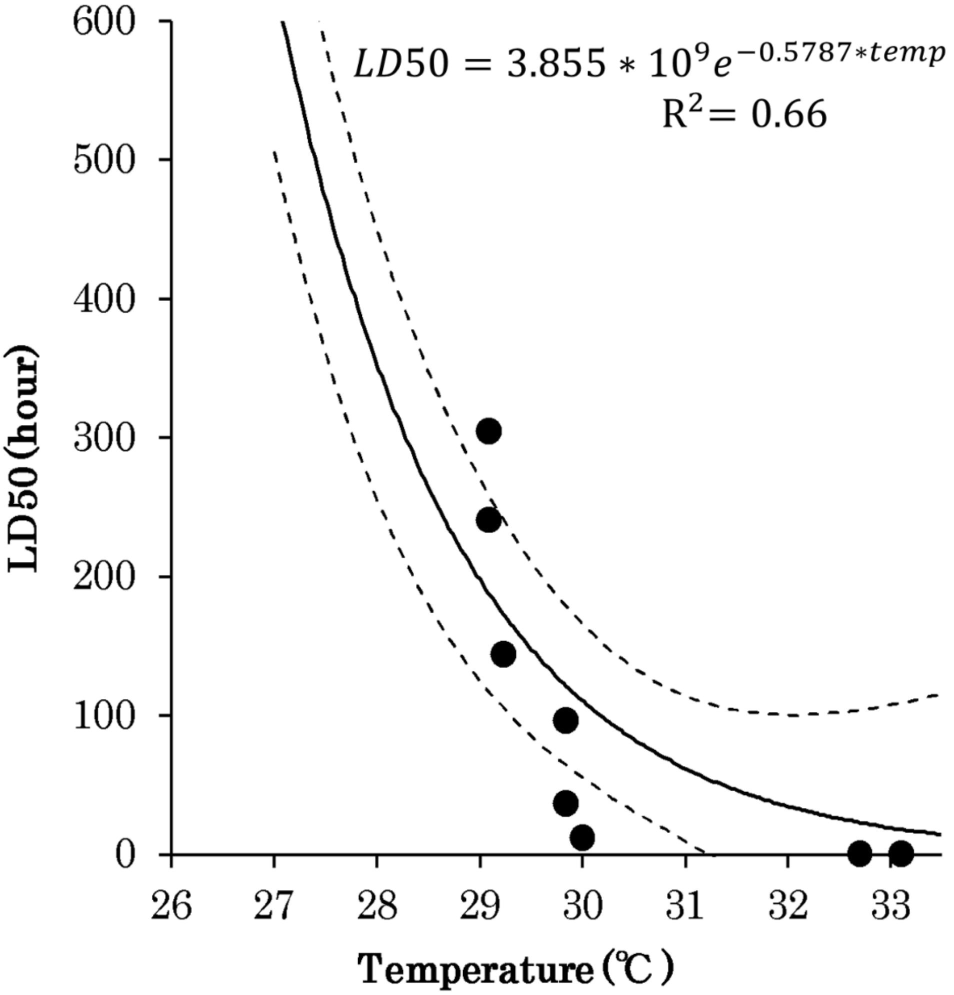


Fig. 2 Relationship between the exposed test temperature and LD50 (time to 50% survival). Dotted lines indicate the 95% confidence interval of regression line

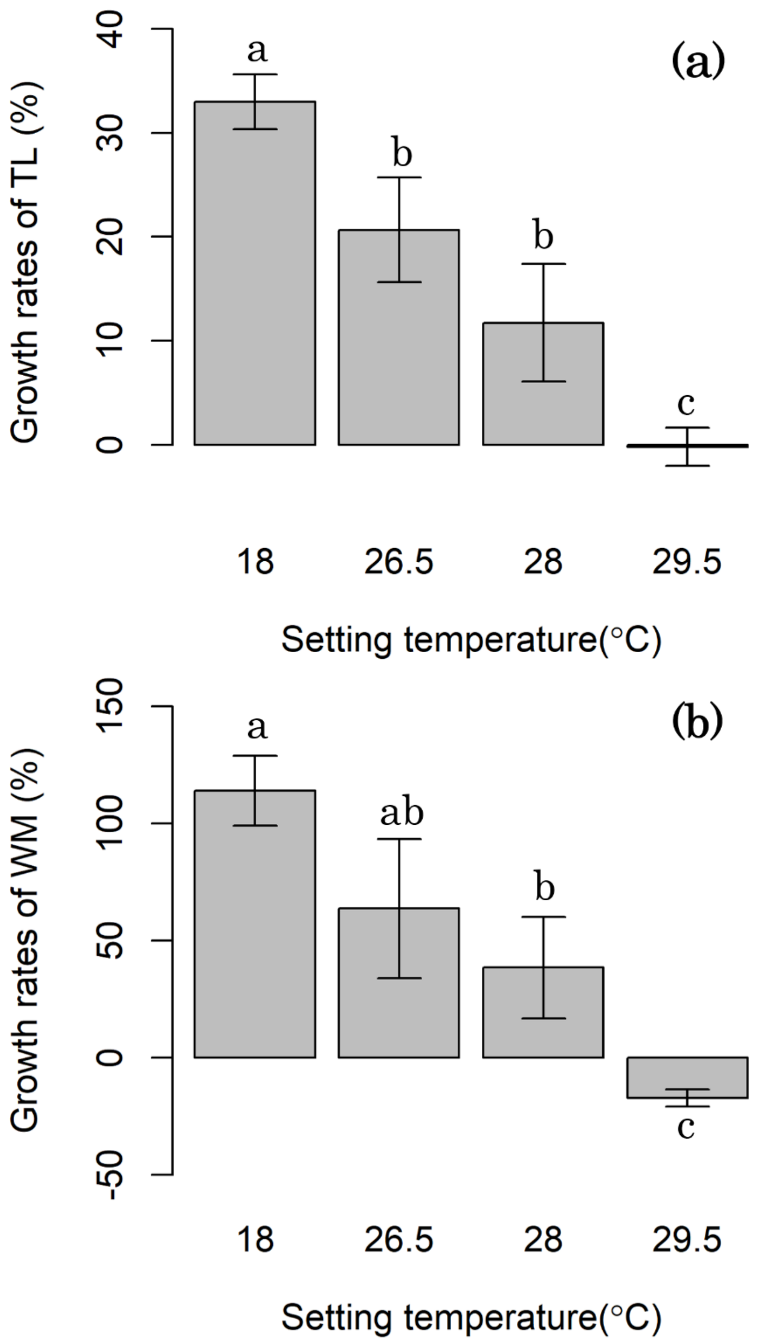


Fig. 3 Average growth rates of larval length (**a**) and wet mass (**b**) on each temperature treatments. Bars indicate standard deviations. Alphabets indicate that the significantly differences between the test temperatures using a multiple comparison; Tukey-Kramer test ($P < 0.05$)

Chapter 5 Differences in distribution and microhabitat of larval three lamprey species (*Lethenteron* spp.) in a sympatric river, Ishikawa, Japan

Introduction

Lamprey (*Petromyzontiformes*) is one of the oldest and primitive groups of vertebrates (Docker et al. 2016). Lamprey species are classified into two types of groups: parasitic-anadromous and nonparasitic-fluvial species, depending on feeding and migrating behavior after metamorphosis (Yamazaki and Goto 2000). Both groups spawn in rivers, and the larvae develop in sand and silt for a few years in the river and feed on fine organic matter as filter feeder (Dawson et al. 2015). At a larval stage in the river, they contribute to ventilate the streambed by their burrowing and feeding behavior (Boeker and Geist 2016; Shirakawa et al. 2013). Metamorphosized juveniles of parasitic-anadromous species migrate downstream to lakes or the ocean where they begin the parasitic stage and back to freshwater for spawning (Moser et al. 2020). The spawning individuals contribute to the freshwater ecosystem by physical disturbing caused by nest-building activity on streambeds and providing additional nutrients via their carcass (Hogg et al. 2014; Weaver et al. 2018; Dunkel et al. 2020). In contrast, nonparasitic-fluvial species do not show migrating behavior downstream and stay in rivers until spawning.

Eighteen parasitic-anadromous species and 23-27 nonparasitic fluvial species are found in the world (Docker and Potter 2019). In Japan, parasitic-anadromous Arctic lamprey *Lethenteron camtschaticum*, Pacific lamprey *Entosphenus tridentatus*, nonparasitic fluvial *L*. sp. N, *L*. sp. S, Siberian lamprey *L. kessleri* are distributed (Yamazaki and Goto 2016). The Far Eastern brook lamprey *Lethenteron reissneri* was recognized as one species until the 1990s and recent studies taxonomically classified it into two cryptic species (*L*. sp. N, *L*. sp. S) lacking a hybridization (Yamazaki and Goto 1996; Yamazaki and Goto 2000). Distributions of these species are partly overlapped but mainly northern Japan for *L*. sp. N and southern Japan for *L*. sp. S (Yamazaki et al. 1999). Parasitic-anadromous lamprey is important food resource culturally and Arctic lamprey has been captured by traditional fishing and consumed in the coastal Japan along the Sea of Japan (Almeida et al. under rev.; Arakawa and Yanai under rev., Chapter 1). However, Arctic lamprey population have been declined caused by primarily threat including climate change, oceanographic regimes, interactions between climate change and oceanographic regimes, artificial barriers, water quantity/quality, habitat degradation, and overharvest (Clemens et al. 2020; Yamazaki and Goto 2015; Arakawa et al. under rev.; Arakawa and Yanai under rev., Chapter 1, 2). In the Red Data Book of Japan, Arctic lamprey, *L.* sp. N, and *L.* sp. S are listed as endangered species; vulnerable (Ministry of the Environment 2007).

Artificial barriers prevent adult anadromous lampreys from migrating to upstream spawning habitat (Clemens et al. 2020). Therefore, it is necessary to understand the spatial distribution of lampreys in river basin for establishment of conservation plan and promotion of sustainable harvesting. Previous study reports the negative impact by large barriers (over 5 m height) on the distribution of Arctic lamprey (Fukushima et al. 2007). Not only large dam but small-head barriers such as weirs may also have a potential to limit their distribution of Arctic lamprey. It is reported that negative impact by weirs on the migration of Ayu P*lecoglossus altivelis altivelisin* and eels *Anguilla japonica*, *A. marmoratain* in the Japanese rivers (Aino et al. 2018; Itakura et al. 2020). Artificial barriers also decrease gene flow of *L.* sp. N into upstream populations and played consistently higher lower genetic diversity are displayed in upper stream from the barriers (Yamazaki et al. 2011). However, the spatial distribution in basin-scale of *Lethenteron* spp. and the restriction of small-head barriers are unknown.

In the southern limit of lamprey’s distribution along the east coastal the Pacific Ocean, the larval habitat in the downstream is degraded by warm air and river temperature (Goertler et al. 2020). The southern limit of Arctic lamprey distribution is estimated at Ishikawa Prefecture, middle of Japan, along the coastal the Sea of Japan (Arakawa et al. under rev., Chapter 2). In these areas, the maximum river temperature in summer exceeds over the lethal temperature of 29.3 °C for larval Arctic lamprey (Arakawa and Yanai 2020, Chapter 4). In addition, L. sp. N is considered to be an ice age relic species and inhabits in spring water area (Hirano et al. 2020; Mukai et al. 2011). The larval distribution range might be potentially restricted by future climate change. However, the relationship between distribution reach and river temperature is not clear.

River modification and dredging are also major threats promoting loss of accumulated sediment for suitable larval habitat (Yamazaki and Goto 2016). Particle size of sediment is essential environmental factor relating burrowing behavior and maintaining burrow (Smith et al. 2011a). *Lethenteron* spp. larvae also prefer the habitat where fine sediment accumulates (Arakawa and Yanai 2017; Shirakawa et al. 2009; Sugiyama and Goto 2002; Sutton 2017; Yamazaki 2007). Because interspecific difference in microhabitat limits the distribution in sympatric area, the optimal microhabitat for larval *Lethenteron* spp. and the interspecific difference can contribute to establish flexible conservation plan. However, the interspecific microhabitat for *Lethenteron* spp. has not been investigated enough yet. Yamazaki (2007) reports that both *L*. sp. N and *L*. sp. S larvae select the fine sediment as a habitat and the interspecific microhabitat is not observed. In survey design, if sampling quadrat set at regular interval length, not suitable coarse sand habitat can be included in sampling site and the preference for microhabitat except particle size can be underestimated.

Our study objectives is to reveal the distribution pattern and the interspecific difference in microhabitat of larvae of the endangered 3 *Lethenteron* species (*L. camtschaticum*, *L*. sp. N and *L*. sp. S). We conducted larvae sampling and environmental measurements at multiple sites where fine sediment accumulated in a river from downstream to headwater. The distribution ranges for each species were estimated by logistic regression using distance from the river mouth and effect of artificial barrier and riverside modification were evaluated. Non-parastic fluvial lamprey such as *L*. sp. N migrate to tributary and upper reach for spawning (Hirano et al. 2020). The connectivity from distribution range of mainstream to tributaries were evaluated. The study river is located in the southern limit of the distribution for *L. camtschaticum*, *L*. sp. N. Therefore, the environmental factor in summer, may limit their habitat utilization. To reveal interspecific difference in microhabitat during summer when temperaute get close to lethal temperature, we conducted survey in daytime in July to August and measured environmental factors including habitat temperature in river and sediment.

Materials and Methods

Study site

The study was conducted in the Machino River (stream length: 21 km, drainage area: 169 km^2) at Noto Peninsula, Ishikawa, which located in the middle of Japan along the coastal Sea of Japan (Ishikawa Prefecture 2002). In the Machino River, three lamprey species including Arctic lamprey, *Lethenteron* sp. N, and *L*. sp. S distribute (Arakawa and Yanai 2017; Sakai and Yamazaki 2011). These species are designated as endangered species in the prefectural Red Data Book in 2020. Historically, the flood had occurred frequently in this river and the revetment had been applied by using concrete through most of the sections from the downstream to the upstream from 1951 to 1991. Paddy fields spread in the lower-middle reaches where multiple weirs locate for irrigation and intake. The local fishermen and residents harvest Arctic lampreys concentrated downstream of these weirs using the traditional fishing hook to catch (Arakawa et al. 2018). The upstream flow through a mountainous area where the forest was widespread and terraced rice fields were scattered along the river. Sakai and Yamazaki (2011) have confirmed the habitat of L. sp. N. at the upper reaches of this river. Therefore, the survey section was about 22 km section from the mainstream at the confluence of the Suzuya River to Nakazai as the most upper reach where the L. sp. N inhabited. The downstream from the confluence of the Suzuya River tributary was excepted for the survey section since the water depth was too deep to collect larval lampreys. In the survey section, we confirmed the accumulation area of fine-grained sediment generally preferred by larvae for setting survey stations near the riverbank (area: 0.15-2.25 m2). Accumulations were confirmed only within the accessible area by walking. in total 54 stations, larvae collection and environmental measurements were conducted (Fig.1).

Larval lampreys collection and measuring environmental condition measurement

In every study site, we first collected larval lampreys using an Electrofisher Model 12 (Smith-root, USA) and dip nets for about 10 minutes. The electrofisher applied a 3:1 burst pulse train with 250-300 V for larvae emergence from the substrate. Total length (TL) and wet mass (WM) of collected larvae were measured to the nearest 0.1 cm and 1 g using a scale and EJ-200 (A&D Company, Limited, Japan). To identify species between Arctic lamprey and two residential lampreys, Arctic lamprey has a black pigment on the dorsal fin (Nazarov et al. 2011). However, larval L. sp. N and L. sp. S could not be identified morphologically. A small piece of the dorsal fin was clipped from each individual and fixed in 70 % ethyl alcohol to transport to the laboratory for morphological analyze. If we collected over 11 individuals, 10 of them selected randomly were measured for TL and collected for morphological samples. For smaller individuals (TL smaller than 5 cm), black pigment on the tail was undeveloped not to be identified and the fin size was too small to clip without any damage safely. Therefore, the smaller individuals was designated as *Lethenteron* sp.

In the study station after larvae collection, we measured four environmental variables of current velocity, water depth, sediment depth, and oxidation reduction potential (ORP) in sediment. Current velocity was measured at 60 % depth using a portable velocity meter (VR-301, KENEK Corporation, Japan). Water depth and sediment depth were measured using aluminum staff 2 m (Sinwa, Japan) to the nearest 1cm. Aluminum staff was inserted into the bottom sediment until it stopped, and the depth of substrate covered on the bottom sediment was defined as sediment depth. ORP was measured by electrode inserting into subsample in plastic bottle grabbed from sediment in the study site using a portable pH/ORP meter (D-72, Horiba, Japan). The larvae collection and the environmental measurements were conducted on July 26-27 and August 9 2018.

To ideal particle size of sediment, sediment samples were collected from every study site using a plastic bottle to transport to the laboratory. The sediment samples dried in a vacuum oven at 105 °C for 24 hours were sieved into five particle size classes (0.125 mm, 0.25 mm, 0.5 mm, 1 mm, 2 mm) and each size classed were weighed to the nearest 0.01 g to calculate median particle diameter.

As thermal habitat on study sites, we measured water temperature above the sediment and in sediment in the other days. The thermal measurements were conducted during AM 11:00 and PM 15:00 on on August 10-11 2018. Water temperature was measured using portable thermo meter (CT-422 WR, Custom, Japan) at three different vertical points of 50 % of river depth as river temperature, within 3 cm depth of sediment, and at bottom sediment. Because thermo meter was capable to measure at 20 cm of sediment, the bottom sediment was measured up to the 20 cm. The river temperature verified among upper area from downstream. To generalize the thermal habitat in the sediment, decrement of water temperature were calculated by subtracting the temperature within 3 cm depth of sediment and at bottom sediment from river temperature as $\varDelta Te_{3cm}$ and $\varDelta Te_{bottom}$

Genetic identification

A total of 80 L. spp. over 5 cm TL were collected from the field survey. Since 20 and 12 L. spp. were collected in st.36 and st.37, 10 were selected randomly and analyzed for morphological identification. A total 67 samples were analyzed for the identification. Genomic DNA of the samples fixed with ethyl alcohol was extracted using DN-sure tissue mini kit (Integrale, Japan). PCR protocol for identifying *L*. sp. N and *L*. sp. S was referred to Yamazaki et al. (2003). DNA amplification for multiplex PCR was performed using four primers (LmpL6860: 5'-GGCTTTGGCAACTGACTTGTACC-3', L7143: 5'-AACCTCCAACTATAACAAAG-3', LmpL7461: 5'-AATGGCTATCGGACTATTACGA-3', LmpH7933: 5'-CATGTAGTGTATGCATCAGGGTARTC-3'). Gotaq® Green Master Mix 2X (Promega, USA) was used for PCR. PCR reactions were performed in 20 L volume of GoTaq Green Master Mix 10 µl (1x), four primers 0.5 µl (0.05 µM), DNA template 1 µl, and nuclease-free water 7 µl. The thermal cycling procedure for PCR was followed by 35 cycles of 94 ºC for 30 s, 45 ºC for 30 s, and 72 ºC for 60 s. PCR products were electrophoresed on a 1.5% agarose gel and stained with ethidium bromide. The species-specific bands on the gel were observed using ultraviolet trans-illumination.

Statical analysis

To estimate the longitudinal distribution range for each species, a logistic regression analysis was performed using a general linear model (GLM) using glm function in stats package. The response variable was presence of inhabited larvae in the station following a binomial distribution (1: present, 0: absent). The explanatory variable was river length from the river mouth to the stations. Linear function and quadratic function of were performed as regression formula to demonstrate logistic curve and peak curve, respectively. We selected the effective function as a best model to explain the species distribution to minimize the Akaike's information criterion (AIC) for each species. More than 0.5 probability of a species occurrence was defined as the distribution range. In addition, to evaluate the relationship between the distribution range and the river condition including connectively to upper region and tributaries and revetment on the riverside, the location of weirs and tributary confluences and information about riverside (concreted or natural) were obtained by conforming at the field and using an aerial photograph. The weirs in the study reach were up to 2 m height and considered to be defined as low-head barrier.

To evaluate the interspecific difference in microhabitat and the suitable environment variables for each larva, the study stations within the distribution ranges for each species were used for the statistical analysis. First, multiple comparisons using bonferroni adjustments were carried out to compare the environmental variables in inhabited stations for each species within the distribution ranges. Pairwise.t.test function in stats package was used for the multiple comparison. Secondly, GLM was paformed to the suitable environment variables to explain the larval dencity for each species using glm.nb function in MASS package. The response variable was the number of larvae offset by area in all study stations within the distribution range following a negative binomial distribution. The explanatory variables were 1) length from the river mouth to the study as spatial variations, 2) current velocity, 3) depth, 4) median particle diameter, 5) sediment depth, 6) ORP as environmental factors, 7) river temperature, 8) $\varDelta \mathrm{Te}_{\mathrm{bottom}}$ as thermal factors. To avoid a multicollinearity in models, only $\varDelta \mathrm{Te}_{\mathrm{bottom}}$ was used and $\varDelta \mathrm{Te}_{3\mathrm{cm}}$ was not used for the analysis. In addition, a multicollinearity among the environment variables for each species was confirmed by cor function in stats package. Correlation coefficient over 0.7 was defined as a multicollinearity. In the model for *L*. sp. N, a multicollinearity between depth and ORP was confirmed therefore ORP was used for the analysis. All statistical were performed using R 3.5.1.

Results

Collected larvae

A total of 131 larvae were collected in the present survey. Of them, 39 were Arctic lamprey, 24 were *L*. sp. S, 44 were *L*. sp. N, 12 were *L*. spp. with TL over 5 cm collected in St. 36 and 37 not analyzed genetically, and 12 were smaller *L*. spp. with TL smaller than 5 cm. Since all analyzed 20 individuals from St. 36 and 37 were identified as *L*. sp. N, 12 *L*. spp. (TL over 5 cm) were treated as *L*. sp. N as below analysis. The mean (minimum-maximum9) of TL and WM for each species were 13.5 cm (7.5-20 cm) and 4.51g (0.66-11.85 g) for Arctic lamprey, 11.8 cm (7.2-16.1 cm) and 3.24 g (0.68-7.46 g) for *L.* sp. S, 9.19 cm (5.0-15.5 cm), 1.81g (0.31-7.01 g) for *L.* sp. N. From the histogram of TL, the peak of cumulative larval number differed among species (Fig.2). The peaks indicating isochronic populations were relatively larger in the order of Arctic lamprey, *L.* sp. S, and *L.* sp. N. The minimum and maximum size of 12 small individuals (TL under 5 cm) were 2.2 cm and 4.6 cm. The larval densities for each species were ranged in 0.5-3.5 larvae/m^2 for Arctic lamprey, 0.5-6 larvae/m^2 for *L.* sp. S, and 0.5-21 larvae/m^2 for *L.* sp. N.

Distribution range

From the logistic regression analysis, the functions in the best model to minimize AIC were linear function for Arctic lamprey and *L.* sp. N and quadratic function for *L.* sp. S (Table 1). In the best models for all species, the river length from the river mouth were selected as a significant variable to explain the presence of inhabited larvae. From the probability over 0.5 estimated by the best models, the distribution ranges were located downstream for Arctic lamprey, in the middle reach for *L.* sp. S, and the upper reach for *L.* sp. N. and were not overlapped among species (Fig.3). The distribution range for Arctic lamprey were estimated from 0 km (river mouth) to 11.3 km (95%CI: 10.9-11.6 km). In the distribution range, all riversides were covered by concrete, five weirs existed, and all sections enclosed by weirs connected to the tributaries. In 4 km reach upper from the limitation of the upper distribution, ten weirs were existed. The distribution range for *L.* sp. S were estimated from 14.9 km (95%CI: 13.2-17.3 km) to 22.8 km (95%CI: 20.3-24.5 km). In the distribution range, all riversides were covered by concrete, 15 weirs existed, and three of 15 section enclosed by weirs connected to the tributaries. The distribution range for *L.* sp. N were estimated from 28.0 km (95%CI: 27.6-28.4 km) to 31.5 km (close to the headwater). In the distribution range, the riversides were partially covered by concrete but most riverside were not concreted and natural, and weir did not exist. The lower reach from 26.5 km were all concreted and the probability for *L.* sp. N was 0.16 (95%CI: 0.07-0.25) extremely low value.

Depending on the probability including 95% confidence interval for each species, the distribution range was defined as 7.8 km reach from 3.8 km (the confluence to the Suzuya River) to 11.6 km for Arctic lamprey, 11.3 km reach from13.2 km to 24.5 km for *L.* sp. S, and 2.5 km reach from 27.6 km to 31.5 km for *L*. sp. N. The number of study stations within the distribution ranges was 16 stations for Arctic lamprey, 19 stations for *L*. sp. S, and 15 stations for *L*. sp. N. All 14 stations where Arctic lamprey inhabited were within the distribution range (lower and upper station: 3.8 – 11.6km). 9 stations where *L*. sp. S inhabited were within the distribution range, 3 stations were lower (10.1, 10.2, 11.6km), and 1 station was upper (25.3km) 9 stations where *L*. sp. N inhabited were within the distribution range, 1 station was lower (26.8 km) where riverbank was natural.

Microhabitats of 3 Lethenteron spp.

From the multiple comparison among species for the microhabitat where larvae inhabited, the significant difference were confirmed in river length, water temperature, ⊿Te$_{\mathrm{3cm}}$, ⊿Te$_{\mathrm{bottom}}$, and ORP. The river length was significantly different among all species (p<0.05, Fig.4). Water temperature, ⊿Te$_{\mathrm{3cm}}$, and ⊿Te$_{\mathrm{bottom}}$, were significantly different between *L*. sp. N and the other species (p<0.05, Fig.4). The river temperature was the coolest at 19.4±2.0℃. The decrements (⊿Te$_{\mathrm{3cm}}$, ⊿Te$_{\mathrm{bottom}}$) were the smallest among species, -0.2±0.4℃ within 3 cm depth, and -0.2±0.9° C at bottom sediment. The river temperature where the other species larvae inhabited were warmer 29.2±0.3˚C for Arctic lamprey and 28.4±2.3˚C, for *L*. sp. S. However, ⊿Te$_{\mathrm{3cm}}$, and ⊿Te$_{\mathrm{bottom}}$ were larger, -1.9±-2.0˚C and -4.1±-3.1˚C for Arctic lamprey, and –1.4±-0.7˚C and -3.9±-2.9˚C for *L*. sp. S. ORP was differed between Arctic lamprey and *L*. sp. S significantly (p<0.05, Fig.4). The ORP was anaerobic -32±-77 mV for Arctic lamprey, aerobic 71±83 mV for *L*. sp. N, and medium 35±120 mV for *L*. sp. S. The other environmental variables were not differed among species, current velocity was 2.3-4.9 cm/s, depth was 11-18 cm, sediment depth was 9-15 cm, and median particle diameter was 477-970μm.

In the best models to explanin the larval density for each species by GLM, river length from the mouth, depth and ORP were selected for Arctic lamprey (Table 2). The larval density of Arctic lamprey correlated to river length from the river mouth, depth negatively (dinstance from river mouth: estimate = -0.18, p<0.01; depth: estimate = -0.13, p<0.05), and ORP weaker positively (estimate = 0.004, p=0.13). For *L*. sp. S, river length from the river mouth, sediment depth, mediam particle diameter, and ORP were selected. The larval density of *L*. sp. S correlated to river length from the river mouth, sediment depth, ORP positively (dinstance from river mouth: estimate = 0.12, p=0.12; sediment depth:

estimate = 0.10, $p=0.05$; ORP: estimate = 0.006, $p<0.1$), and medium particle diameter negatively (estimate = -0.004, $p<0.01$). For *L*. sp. N, the larval density correlated to only $\varDelta Te_{bottom}$ negatively (estimate = -0.82, $p<0.01$).

Discussion

Longitudinal distribution of larval lampreys

The distribution of three larval *Lethenteron* spp. in the Machino river, were differed among species longitudinally. The distribution was located downstream for Arctic lamprey, in the middle reach for *L*. sp. S, and the upper reach for *L*. sp. N. In Alaskan, the larval density of *Lethenteron* spp. including Arctic lamprey increase in a downstream due to the increase in suitable habitat in a downstream direction (Sutton 2017). Our study also demonstrated the similarity of the increase in density of Arctic lamprey at the lower reach within the distribution range. Residential *L*. sp. N and S larvae were distributed at upper reach than anadromous Arctic lamprey. Mukai et al. (2011) reported that *L*. sp. N and S larvae were distributed through the river basin from plain to mountain area. The difference in microhabitat between these species is not observed and they inhabit sympatrically (Yamazaki et al. 2007). In addition, the sympatric distribution by Arctic lamprey and *L*. sp. N are observed in Hokkaido (Maeda 2017). Therefore, the differences in the distribution range in our study suggest that the differences in lifecycle and the environmental factors may limit the habitat segregation among species.

The occurrence of Arctic lamprey larvae decreased in the upper reach and was below 0.5 at 11.3 km (95%CI: 10.9-11.6 km) from the river mouth as the limit distribution range. In contrast, the upper reach from the limit distribution range were dominated by *L*. sp. S larvae and Arctic lamprey was not collected. There was no difference in microhabitat exept the river length from the river mouth between Arctic lamprey and *L.* sp. S. Therefore, the upper reach from the limit distribution of Arctic lamprey has a habitat potential patchily, but the biased distribution restricted to the lower reach may cause by the loss of connectivity to upper habitat for spawning adults through artificial barriers. Artificial barriers are a well-recognized threat for anadromous lamprey (Clemens et al. 2020). The present study reports the distribution of larval Arctic lampreys including lamprey is limited to downstream due to the presence of artificial barriers with over 5 m height (Fukushima et al. 2007). In contrast, the artificial barriers in this study reach have a low head with a lesser 2 m height. In the freshwater, the spawning European river lamprey *Lampetra fluviatilis* shows a lower passage rate at low-headed weirs (lesser 5 m) and utilize the lower area for spawning not suitable (Lucas et al. 2009). In addition, the passing efficiency increases at low-headed weirs, and the rate of arrival at the upstream is significantly reduced (Silva et al. 2019). Hydraulic experiments show that the successful ascent rate is significantly reduced at vertical and gauging weirs with 20-30 cm height (Russon et al. 2011; Arakawa et al. 2019, Chapter 6). Within 4 km reach located at the upper reach from the limit distribution of Arctic lamprey, 10 low-headed weirs were continuously present. This loss of connectivity to the upper reach may delay the passing time and promote the utilization downstream by larvae. However, the spawning habitat potential in the upper reach and the migrating behavior after entering freshwater is known. The future study should examine the ecology of spawning individuals in the freshwater ecosystem.

The distribution range of *L*. sp. S located in the middle reaches, and the larval density tended to be higher in the upstream direction within the distribution range. in general, Residential lampreys inhabit and spawn in upper reaches and smaller streams and tributaries (Gunckel et al. 2009; Levin et al. 2016). Lamprey larvae disperse downstream from the spawning habitat by seasonal flooding. (Dawson et al. 2015; White and Harvey 2003). *L*. sp. S is considered to have spawned in small rivers or in the upper reaches and inhabited the middle mainstream after dispersing downstream. Since there was no difference in the microhabitat comparing to Arctic lamprey, the area in the mainstream with fine sediment can provide a habitat for *L*. sp. S

In the distribution section of the southern species of L. sp. S, 12 of 15 section enclosed by weirs did not connect to the tributaries. The spawning environment is depended on body size and is different between anadromous Arctic lamprey and non-parasitic lampreys. Small non-parasitic species spawn at the area where current velocity is slow, depth is shallow, and riverbed material consisted of fine gravel (Johnson et al. 2015). The TL of L. sp. S is 99-146 mm (Yamazaki and Goto 2000), which is about one-third of TL od 352-431 mm Arctic lamprey (Yamazaki and Goto 1998). In this study river, the distribution range has a relatively large river scale but has the potential to be inhibited to move upstream or to tributaries by continuous weirs. As Arctic lamprey, it is suggested that continuous low-headed dams may cause low reproduction efficiency. The ecology of non-parasitic lamprey has not been investigated. The spawning habitat and the migration behavior of non-parasitic lampreys should be examined in future studies.

Difference in microhabitats among 3 Lethenteron species

As for the riverside type, all distribution range for Arctic lamprey and *L*. sp. S were concreted revetment and they inhabited where fine sediment deposited after the channelization. In contrast, *L*. sp. N was distributed only in the upstream area with a natural riverbank where the riverside was not channelized. Comparing the thermal habitats of the distribution range for *L*. sp. N and *L*. sp. S, the river temperature for *L*. sp. N was 19.4 ± 2.0 °C, which was significantly lower than that of *L*. sp. S at 28.4 ± 2.3 °C, and the temperature within sediment was always below 20 ° C even though the decrement of water temperature within sediment was smaller than the other two species. *L*. sp. N is dependent on spring water for larval habitat and considered to be a species remaining from the ice age (Hirano et al. 2020; Mukai et al. 2011). It has been reported that the distribution of larval lamprey is limited by air and water temperature in the southern limit of distribution (Goertler et al. 2020). Therefore, the downstream dispersion of *L*. sp. N may be restricted by the water temperature. In Japan, the agricultural field improvement project including concrete revetments and channelization has been conducted to improve the efficiency even in mountainous areas. However, the loss of spring water due to the loss of continuity between the river channel and the surrounding environment can lead to the extinction of spring-dependent cold-water species (Jinguji et al. 1999). Rising water temperature due to climate change may cause deterioration of the habitat of *L*. sp. N population and revetment work are also concerned to promote habitat degradation for species which is considered to be vulnerable to fluctuations in water temperature.

Comparing the microhabitat among the species, the water temperature, ΔTe3cm, and ΔTebottom differed between *L*. so. N and the other two species. ORP was also different between Arctic lamprey and *L*. so. N. The differences in these environmental variables for each species partly reflect the preference for suitable habitat. However, the differences in water temperature and ORP differ from downstream to upstream within the river-basin scale, which also reflects the differences in the longitudinal distribution ranges.

In addition, ORP correlated positively with the larval density of Arctic lamprey and the *L*. sp. S. The burrowing behavior by larval lampreys in the sediment make river water flow into the sediment, create an aerobic environment and increase the redox potential (Boeker and Geist 2016; Shirakawa et al. 2013). Shirakawa et al. (2013) also report that ORP in the sediment shows a positive correlation with the dissolved oxygen. The larval stage of lampreys consumes less oxygen than metamorphic individuals and adults (Lewis and Potter 1977) and is generally tolerant of stagnant or hypoxic water (Lampman et al. 2020). The rate of oxygen consumption varies between stages of life history, but the increase in water temperature increases oxygen consumption by larvae (Lewis and Potter 1977). The thermal tolerances of larval Arctic lamprey are estimated at 29.3°C as upper lethal temperature and the growth rate reduces significantly higher than 26°C comparing to the optimal temperature at 18°C (Arakawa and Yanai 2020, Chapter 4). In the present study, the average water temperature at the bottom within sediment was 25.1 °C, which was equivalent to the water temperature at which the growth rate decreased. These results suggest that the possibility that the oxygen consumption of the larvae increases due to the high metabolism activity defected by warmer temperature in the sediment. Therefore, larval Arctic lamprey and *L*. sp. S, which inhabit the warmer reaches comparing to *L*. sp. N, prefer to use aerobic sediment with higher oxygen concentration. In contrast, ORP was not selected as a limiting factor for L. sp. N. Since the upper reach where *L*. sp. N inhabit provide cooler thermal habitat around 20 ° C aerobic sediment, the ORP are not an ineffective limiting factor for *L*. sp. N. In our study, the differences in microhabitat among three *Lethenteron* species were observed. These differences depend on the physiological characteristics of each species such as thermal tolerance and oxygen consumption, but the longitudinal and spatial differences could limit the microhabitat for each species.

Conservation of lampreys

Arctic lamprey is consumed as food in Japan but the harvest in this river has decreased to less than 1/100 (Arakawa et al. 2018). Arakawa and Yanai (under review, Chapter 1) mention the necessity to conduct the conservation effort to protect this fishery resources. Our study reveals that Arctic lamprey larvae are distributed downstream lower than the reach where the low-headed weirs exist continuously. It is reported that larval abundance was negatively related to the number of artificial barriers and distance upstream (Goodwin et al. 2008). In addition, it is concerned that the migration to the upstream and tributaries for spawning by L. sp. S is restricted by the continuous low-headed weirs. To promote the expansion of inhabitable upper reach, the reconnection in the river for natural migration for lampreys are needed. As conservation for lamprey species, the improvement of fish passage for specific lamprey and reintroduction of adults into upper reaches have been conducted (Close et al 2009; Moser et al. 2011; Pereira et al. 2019). Additional research for *Lethenteron* spp. needs to collect ecological information such as migration behavior of adults, and the status of larval and spawning habitat in the upstream reach to implement the conservation and management for each species.

It is also important to protect and improve the existing habitat in order to conserve the populations. Our study suggested that, the northern species of Asiatic Brook Lamprey is dependent on the cool water habitat and inhabits the upper area, which is considered to be the most vulnerable species to habitat degradation due to the revetment work and climate change. Therefore, we should pay the utmost attention to the anthropogenic impact on the population when the artificial modification is carried out within the distribution range. Arctic lamprey and L. sp. S larvae inhabited aerobic sediment. In order to provide suitable habitat, creating diverse river environments will lead to an increase in the abundance of available habitats. Our result provides basic information about the distribution and microhabitat of three *Lethenteron* larvae that can contribute to improving conservation and management.

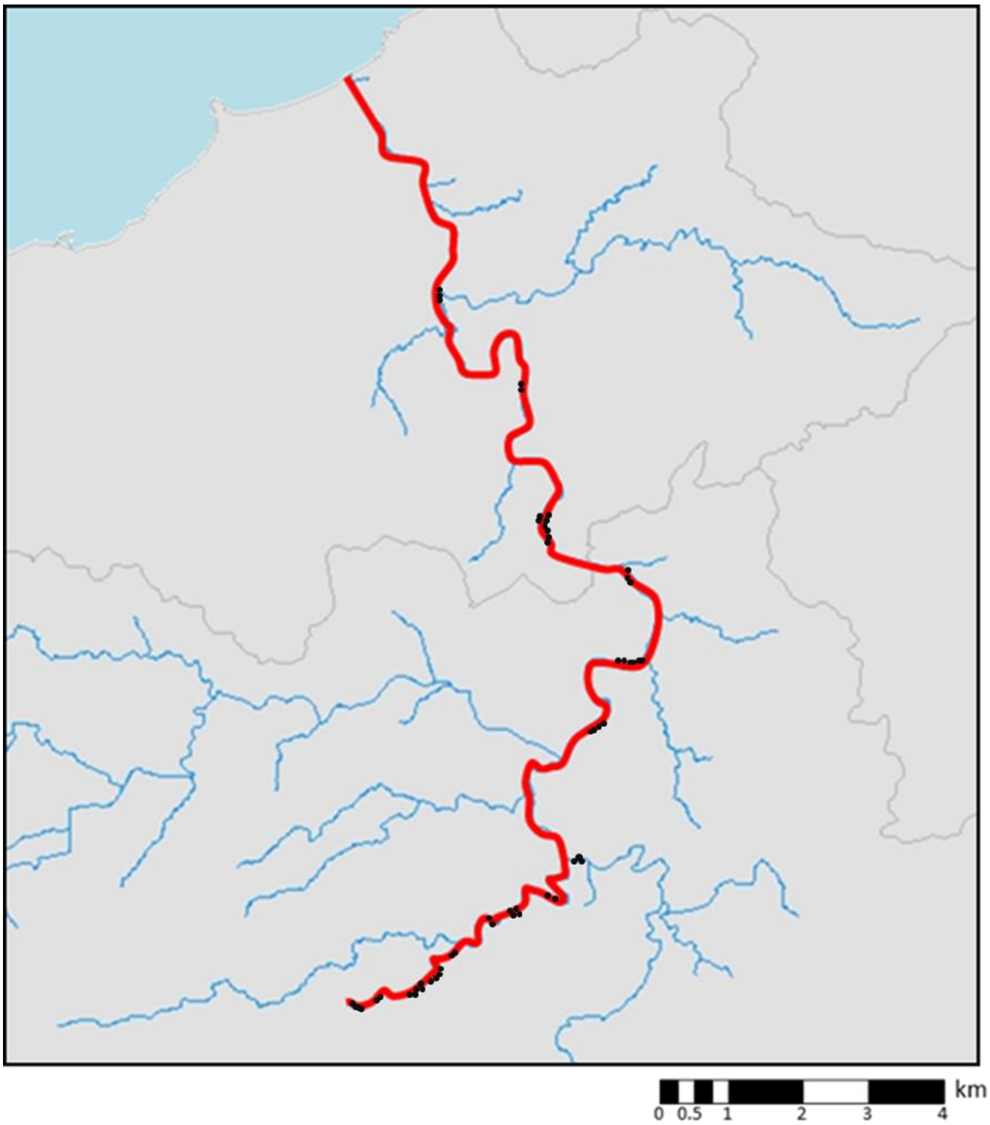


Figure 1 Study reach (red line) and 54 study stations (black circles) in the Machino River, Ishikawa, Japan.

Table. 1 Regression coefficient of river length from the river mouth in the best model

species	**formula**	**Coefficient**			**AIC**	**Δ AIC**
		intercept	**river length^2**	**river length**		
L. camtschaticum	Linear	14.4**	-	-1.24**	22.0	0
	quadratic	3.10	-0.07	0.51	23.6	1.6
L. sp. S	quadratic	-10.9**	-0.03**	1.21**	52.7	0
	Linear	-1.05	-	0.0001	65.8	13.1
L. sp. N	Linear	-22.9*	-	0.80*	23.2	0
	quadratic	-11.2	0.02	-0.25	25.2	2.0

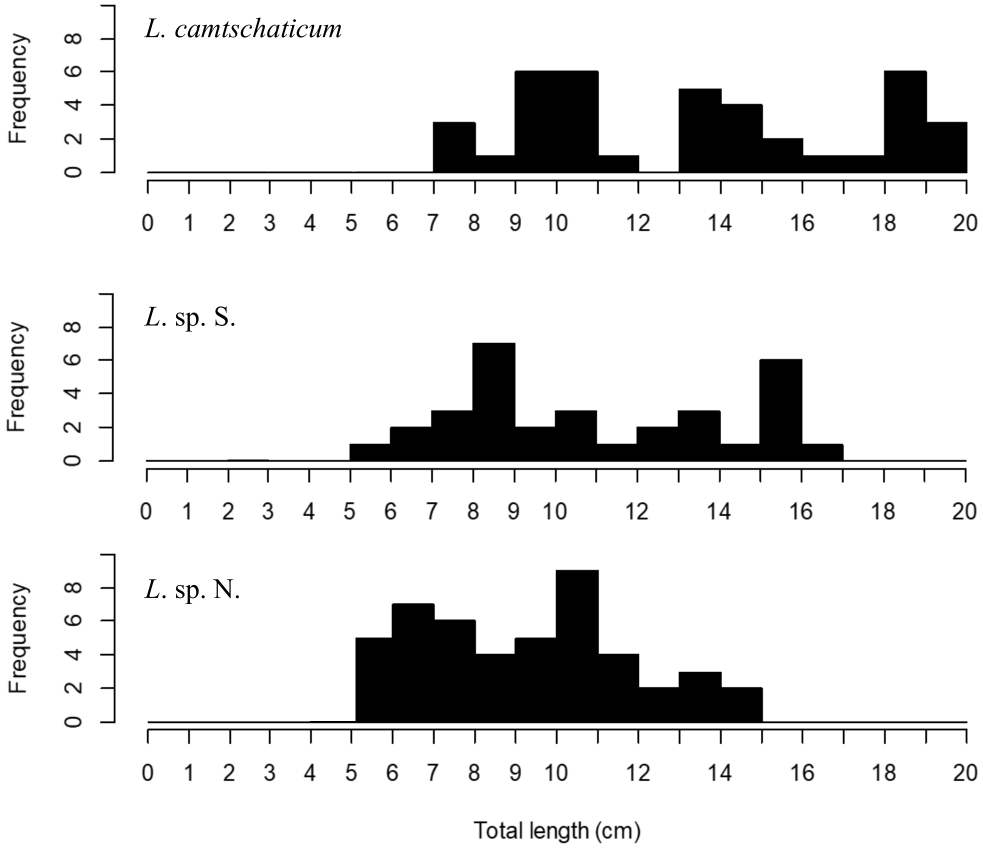


Fig.2 Histogram of TL for larval three Lethenteron species

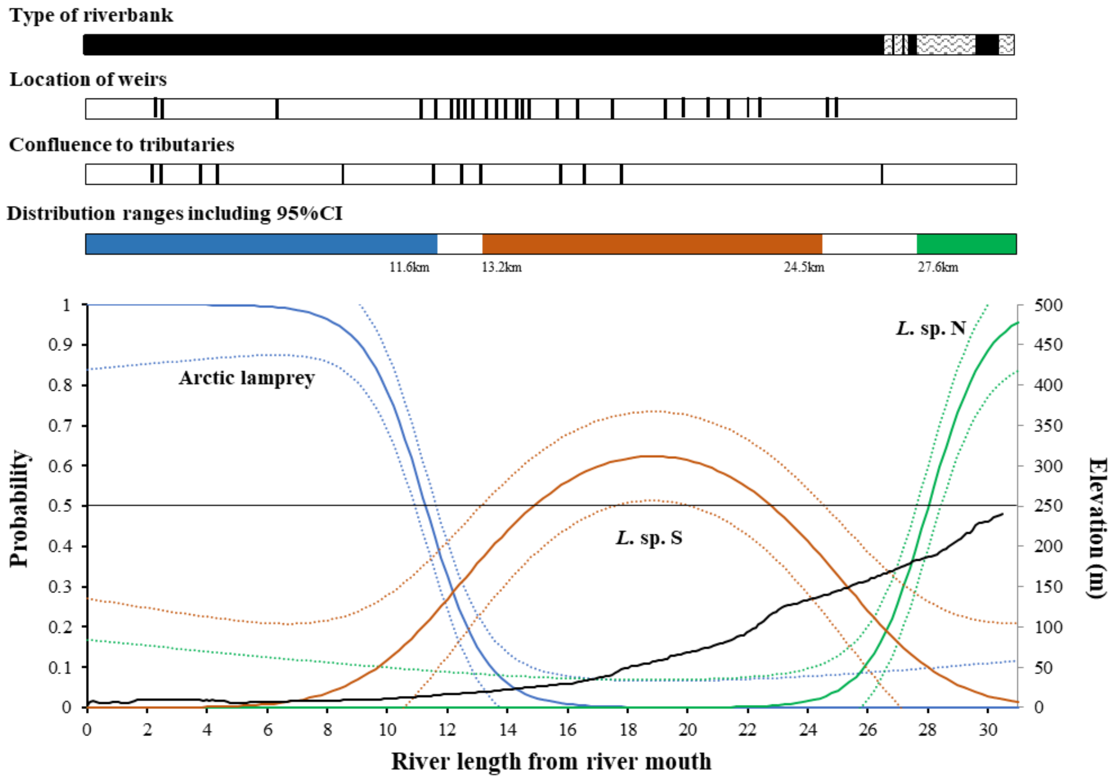


Fig. 3 Species distribution of larval 3 *Lethenteron* spp. along the study river from river mouth to head water. Top bars indicates type of riverbank (black bar: concreted, wavy bar: natural river bank), location of weir (lower 5 m height), and connection to tributaries.

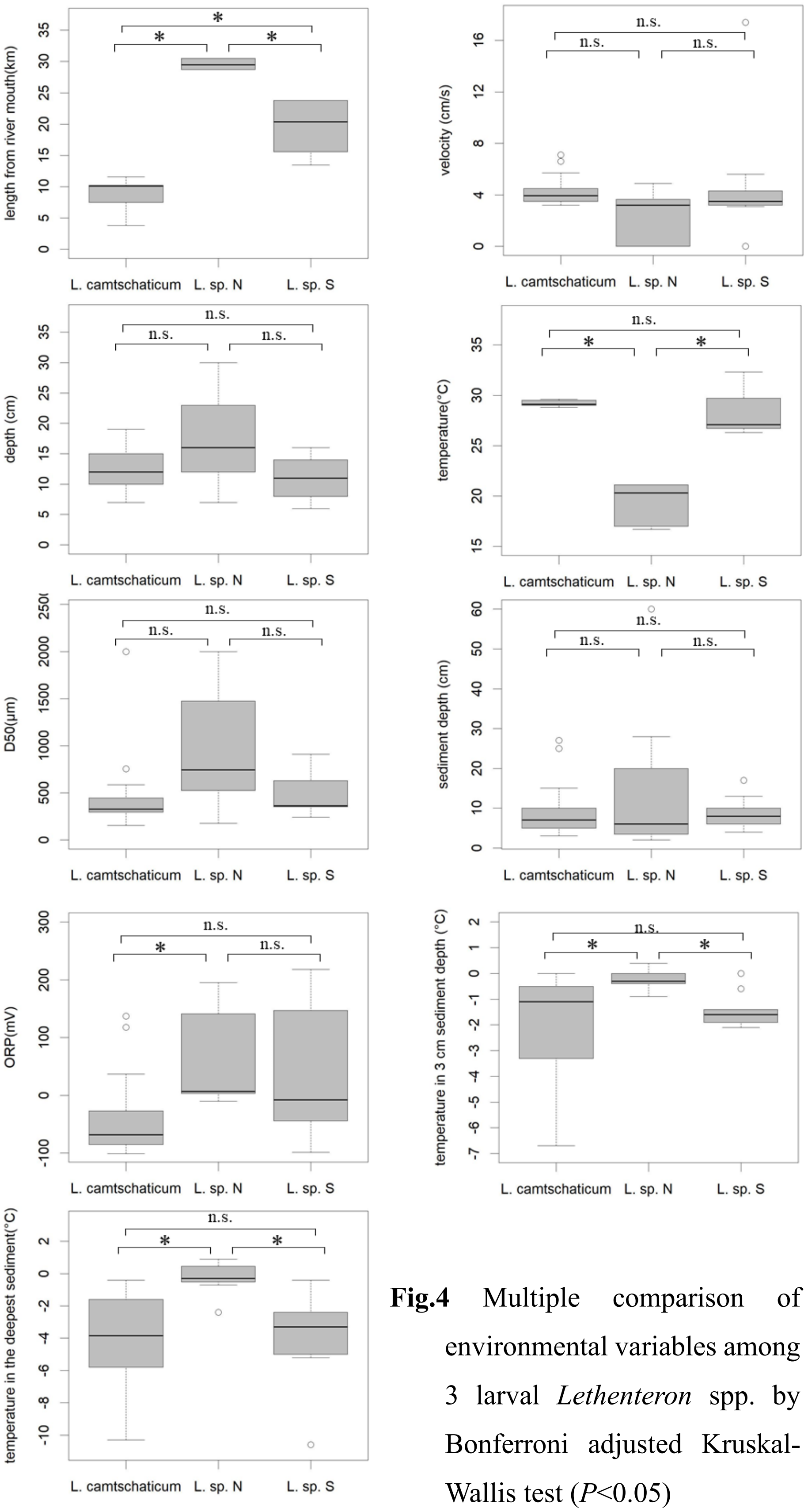


Fig.4 Multiple comparison of environmental variables among 3 larval *Lethenteron* spp. by Bonferroni adjusted Kruskal-Wallis test ($P<0.05$)

Table. 2 Regression coefficients of environmental variables in the best model for 3 *Lethenteon* spp.

Species	AIC	Coefficients (SE)								
		Intercept	River lengh from mouth	Current velocity	Water depth	Water temperature	Sediment depth	Mediun particle diameter	ORP	Δ Wt_{deep}
L. camtschaticum	68.4	3.63 (1.02)***	-0.18 (0.07) **		-0.13 (0.05) *				0.004 (0.003)	
L. sp. N.	64.1	1.17 (0.27) ***								-0.82 (0.28) **
L. sp. S.	51.8	-1.46 (2.11)	0.12 (0.08)		-		0.10 (0.06)	-0.005 (0.002) **	0.006 (0.003) .	

Chapter 6 Factors that Affect Arctic lampreys' Ascent Behavior on Fishway Weirs

Introduction

Lampreys are the most primitive group of vertebrates, with a suckermouth lacking jaws (Yamazaki and Goto, 2000). They are classified as Agnatha and have anadromous migration life cycle. During the larval period, their eyes are hidden under the skin and they have a funnel-shaped mouth. Arctic lamprey (Lethenteron japonicum) larvae burrow and stay in sediment of fine particles and organic matter in freshwater (Shirakawa et al., 2009; Arakawa and Yanai, 2017). The larval period lasts two to five years (Kataoka, 1985). The larvae feed on detritus and organic matter in sediment (Moore and Mallatt, 1980; Sutton and Bowen, 1994). The larvae metamorphose during autumn and winter. They then go to sea during May and June of the next year. Adult lampreys parasitize fishes including Osmeriformes, Clupeiformes and Trachiniformes in the sea and suck the blood of these fishes (Shink et al., 2019).

L. japonicum migrate across shallow-depth areas (less than 100 m deep) from the Sea of Japan to the northwestern Bering Sea (Potter and Hilliard, 1987; Orlov *et al.*, 2014; Siwicke and Seitz, 2017). They migrate in the sea for about three years. Then, they ascend rivers from the late summer to the early spring. They overwinter near spawning areas (midstream) in the river. They spawn in spring and die after spawning.

Two genera and five species of lampreys, including *L. japonicum*, are distributed in Japan (Hubbs and Potter, 1971; Yamazaki and Goto, 2000). The population sizes and distribution ranges of these species have dramatically decreased mainly because of artificial disturbances (Renuad, 1997). *L. japonicum* has been selected as a vulnerable species (that is, VU) by the Ministry of the Environment because of the rapid decrease of population size and distribution. *L. japonicum* has abundant fat and vitamins. Thus, this species has been used for fishery harvests (Murano *et al.*, 2008; Arakawa and Yanai, 2018). However, the harvest is in danger of disappearance because of the rapid decrease of lamprey populations (Murano *et al.*, 2008).

The main reasons causing the decrease of lampreys are (i) concrete-lining the shores of rivers (Sugiyama and Goto, 2002; Smith *et al.,* 2011), (ii) artificial structures such as dams in rivers (Moser *et al.,* 2002; Keefer *et al.*, 2012) and (iii) degradation of water quality (Myllynen *et al.*, 1997). Especially, artificial structure is critical because it restricts lampreys' spawning area and habitat (Mateus *et al.,* 2012).

Many dams have been constructed along the Columbia River. The fishways built next to the dams are designed for ascending salmon. Most *Entosphenus tridentatus* cannot ascend the fishways (Moser *et al.,* 2002). In fishway with low efficiancy of ascent rate by lamprey, it needs to design lamprey-specific passage structures additionally (Moser *et al.,* 2006). Therefore, fishways suitable for *E. tridentatus* ascents have also been constructed (Moser *et al.,* 2011; Pacific Lamprey Technical Workgroup, 2017). Similarly, fishways suitable *L. japonicum* ascents should be constructed in Japanese rivers. To design fishway accomodating passage by diverse fish communities, there is need to evaluate species-specific fish performance and behavior systematically (Keefer *et al.,* 2010). However, the information on the ascent ability of *L. japonicum* is limited and the optimal design of fishways has not been identified.

This study conducted laboratory experiment to identify the optimal fishway design and environmental conditions suitable for *L. Japonicum* ascents.

Materials and Methods

Information about adult lampreys

Five lampreys with a standard length of 400-460 mm were used for the first experiment in 2015. These lampreys were captured using fish hooks in Omou, Yanagida, Noto-cho, Ishikawa Prefecture, in the middle reach of the Machino River. The lampreys were stocked in a water tank at 11–15°C for 2–3 weeks. Subsequently, they were used for the ascent experiments.

For the second experiment in 2017, five lampreys measuring 450–490 mm standard length were used. These lampreys were captured using a basket-shape net in Mogami River in Yamagata Prefecture. These lampreys were stocked in a water tank at the same temperature as the experimental temperature for 1 week. They were then used for the ascent experiments.

Laboratory experiment design

Three types of fishway-weirs were used in our study: (1) sharp-crested weir, (2) inclined sharp-crested weir, and (3) broad-crested weir (Figure 1). All weirs were 0.5 m wide and 0.3 m in perpendicular height. The inclined sharp-crested weir had a 45° incline upstream. All weirs were made using 24-mm-thick plywood. The uppers edges of the sharp-crested and inclined sharp-crested weirs had a 24-mm-radius curve. The broad-crested weir had a 10-cm horizontal region on the upper edge, a 100-mm-radius curve in the middle and a 20-cm vertical region at the lower end. All weirs and the bottom of flume were painted black using a synthetic resin. A net wall was set at 1 m downstream from the weir to prevent fish escaping. A net trap was set at 1 m upstream from the weir to catch the fish that ascended the weir.

The ascent experiments are shown in Table 1. The three weir types were used. The difference in water depth upstream and downstream of the weir (Δh) was set at three different levels (11, 18 and 24 cm). The ascent experiments were conducted separately for daytime (9:00–17:00, for 8 hours) and night (19:00–5:00, for 10 hours). The lampreys were put in the downstream pool of the weir when the experiment started (9:00 or 19:00). Flow volume was constant at 5.3L/s through all experiments. Critical water depth (h_c) was calculated from the flow volume (Q: 5.3 L/s), width of weir (B: 0.5 m) and gravity acceleration (g: 9.8). Critical velocity (V_c) at the overflow section of all weirs was calculated at 0.47 m/s as follows,

$$h_c = \sqrt[3]{\frac{Q^2}{gB^2}} \qquad (1)$$

$$V_c = \frac{Q}{h_c B} \qquad (2)$$

The burst speed of *L. japonicum* has not been measured. However, Kemp *et al.*, (2011) reported that European river lamprey (*Lampetra fluviatilis*) classified in the same family to *L. japonicum* did not pass the weir when maximum velocities were as high as 1.66 m/s. In this experiment, it was presumed that the critical velocities of the weirs were lower than the burst speed of *L. japonicum*.

Lampreys' ascent behavior was recorded using video camera. In the daytime experiments, HD video camera (Sony Co.,Ltd. type: HDR-GW66V) was used. The movie was recorded continuously for 8 hours. In the night experiments, interval movies were taken using a night-vision camera (BMC Software Inc., type: SG560P-8M) for 30 seconds per 15-minute interval, or using the other camera (CAMS Co. Ltd., type: LTL-5210B) for 60 seconds per 5-minute interval. Later, moves were extracted for 30 seconds per 15-minute interval. Then, the lampreys' ascent behaviors were analyzed using these movies. Ascent challenge behavior was defined as the behavior when the lamprey's head was thrust from the water surface toward the overflow area on weir. Successful ascent behavior was recored when a lamprey went through the weir and non-successful ascent behavior when a lamprey failed to go through the weir. The frequency of ascent challenge behavior was calculated by summing the numbers of successful and non-successful ascent behavior. The successful ascent rate (%) was calculated as the frequency of successful ascent behavior divided by the frequency of ascent challenge behavior.

Water depths upstream and downstream of the weir, water temperature, dissolved oxygen level (DO), pH, and electric conductivity (EC) were measured when each experiment started and finished. Illumination was measured in 2-hour intervals only in the daytime experiments. Water depth was measured using a steel scale. Water temperature was measured using a digital thermometer (SATO KEIRYOKI MFG. Co. Ltd., type: SK-1260 with SK-S102T sensor). Portable meters (OM-51-2, Twin pH B-712, and Twin Cond B-173, HORIBA, Ltd.) were used to measure DO, pH, and EC. Discharge in the flume was measured using a point gauge when each experiment started and finished.

Statistical analysis

Regression analysis was conducted using a generalized linear mixed model to estimate the most suitable weir-shape and time period for lamprey ascents. A matrix comprising the numbers of successful and non-successful ascending individuals was used as a response variable. This matrix was made using R-software's cbind-function according to Kubo (2012). The error distribution of the objective variable was assumed as a binomial. Weir type, Δh, and time period were used as explanatory variables. Weir type and time period were defined as categorical variables and Δh was defined as the numerical variable. The tolerance values of these explanatory variables were over 0.5 and above the criteria of Cohen *et al.*, (2003). Therefore, we considered multicollinearity among explanatory variables so weak that it could be ignored. However, chemical environmental variables (pH, DO and electric conductivity) and hydraulic variables (flow velocity and water depth) were not used as explanatory variables because multicollinearity among experimental variables was too strong (tolerance values were lower than 0.2) to conduct the analysis.

We made and examined all possible models. The model with the lowest AIC was defined as the best model. Following that, we calculated ΔAIC, which is the difference in AICs between a given model and the best model. $\Delta AIC < 2$ indicated that the model was almost equivalent to the best model (Burnham and Anderson, 2002); these models were defined as candidate models. Additionally, ΔAIC can be used to compute the Akaike's weights of each model, which is a measure of the likelihood that a model is the best one. We calculated the relative importance values (RI) of each explanatory variable using Akaike's weight. The relative importance value is defined as the sum of the Akaike's weights of the models including an explanatory variable. The RI value is between 0 and 1. It increases as the importance of the explanatory variable increases.

R 3.1.1 software (R Development Core Team, 2014) was used for all analyses. We used the glm function for logistic regression analysis, the tolerance function (Aoki, 2004) for calculating tolerance values and the dredge function from the MuMIn package to make and select models.

Results

Arctic lampreys' Ascent Behavior

Lampreys successfully ascended all weirs when Δh was 11 cm and the sharp-crested weir when Δh was 18 cm (Figure 2). No lamprey succeeded to ascend the all weir when Δh was 24 cm. The frequency of ascent challenge behavior taken using video cameras was shown in Figure 3. In this figure, the results of the experiments with 0% successful ascent rate (experiments 5, 6, 17 and 18) were compared because the number of lampreys that stayed in the downstream pool was constant in these experiments. In experiment 5 (daytime), lampreys were challenged in their ascent only twice between 10:15 and 10:45. In experiment 6 (night), the number of challenges continued and increased between 20:15 and 2:45. In experiment 17 (daytime), lampreys were challenged in their ascents only twice between 16:30 and 17:00. In experiment 18 (night), they were continuously challenged between 22:00 and 4:30. Therefore, they were challenged more frequently at night than daytime. The numbers of successful and non-successful ascending individuals and the means of standard lengths were shown in Table 2. Average length individuals ascended the sharp－crested and broad- crested weirs when Δh was 11 cm. However, larger individuals ascended the inclined sharp-crested weir when Δh was 11 cm and the sharp-crested weir when Δh was 18 cm. The water temperature, water quality, and illumination were shown in Table 3. The water temperature was 13.1-18.7°C. The ranges of DO and pH were below the criteria of Japan Fisheries Resource Conservation Association (2005), so that water was safe enough for lampreys.

Factors that affect ascent behavior

The results of regression analysis indicated that the difference in water depth upstream and downstream of the weir (Δh) was selected as an explanatory variable in the best model except weir type and time period to estimate the successful rates of ascended lamprey (Table 4). RI value of Δh was 0.784 and much higher than time period (0.313) and weir type (0.156) (Table 5). From the regression coefficient of the best model, Δh negatively affected the number of successful ascending individuals; Lampreys successfully ascended more when Δh was smaller (Table 6).

Discussion

Our results indicated that Δh negatively and strongly affected the number of successful ascending individuals. Especially, no lamprey ascended when Δh was 24 cm. These results suggest that weirs with lower Δh are more suitable for lamprey ascents. Arctic lampreys may have relatively low swimming and jumping ability and high Δh may interfere with their ascents. Ichion *et al.,* (2015) reported that Medaka (*Orizias* sp.) ascended fishways with 6 cm Δh more often than those with 9 cm Δh. Medaka has small body and thus low swimming and jumping ability. Therefore, Δh is likely to affect the successful ascent rate of species with low swimming ability, such as Arctic lamprey and Medaka. In our experiment, we observed Arctic lampreys propelled themselves forward by shaking the caudal fin in the pool when they challenged to ascent the weir (Figure 4).

When Δh was larger, they could not get enough driving force since their caudal fin did not reach to the pool sufficiently. To create optimal fishways for Arctic lamprey, it is necessary to design step or Δh smaller and modify the fishway structure.

Keefer *et al.,* (2010) showed that vertical steps and sharp-edged corners in a fishway interfered with Pacific lamprey (*Entosphenus tridentatus*) ascents and stated that vertical steps should be removed or modified. In our experiment, inclined sharp-crested weir with a 45° ramp was used as the modification to vertical sharp-crested weir. However, our modification did not contribute to Arctic lamprey ascents because weir type did not affect ascents. Further study is needed to appropriately modify weir design. The weir with a gentler slope than 45° might be better. Indeed, Reinhardt *et al.,* (2008) indicated that Pacific Lamprey ascended a fishway with an 18° ramp more often than that with a 45° ramp. Additionally, Moser *et al.,* (2002) indicated that Pacific Lampreys ascended fishways with a 40° ramp more often than that with a 45° ramp.

Lamprey advanced on the slope weir by "burst and attach" locomotion repeating cycles of attaching to the weir by their sucker mouths, bending their bodies into a W shape, and then rapidly straightening their body to propel themselves up the weir, with a simultaneous brief release of suction (Reinhardt *et al.*, 2008). We expected that broad-crested weir serves as the attachment place for their mouths (Figure 5). However, the results indicated that this weir type was not better than the other two types. It is reported that the burst and attach locomotion at flows with greater velocities is inefficient and lamprey passage is likely unsuccessful (Keefer *et al.*, 2010; Kirk *et al.*, 2016; Pacific Lamprey Technical Workgroup, 2017). In this experiment, broad-crested weir did not contribute to the increase of lamprey ascent rate since the critical velocity of the weir might be greater than the swimming speed to burst and attach for Arctic lamprey. There is also a possibility that the swimming behavior differs in lamprey species. In future research, other shapes and settings should be tested to provide such an attachment place.

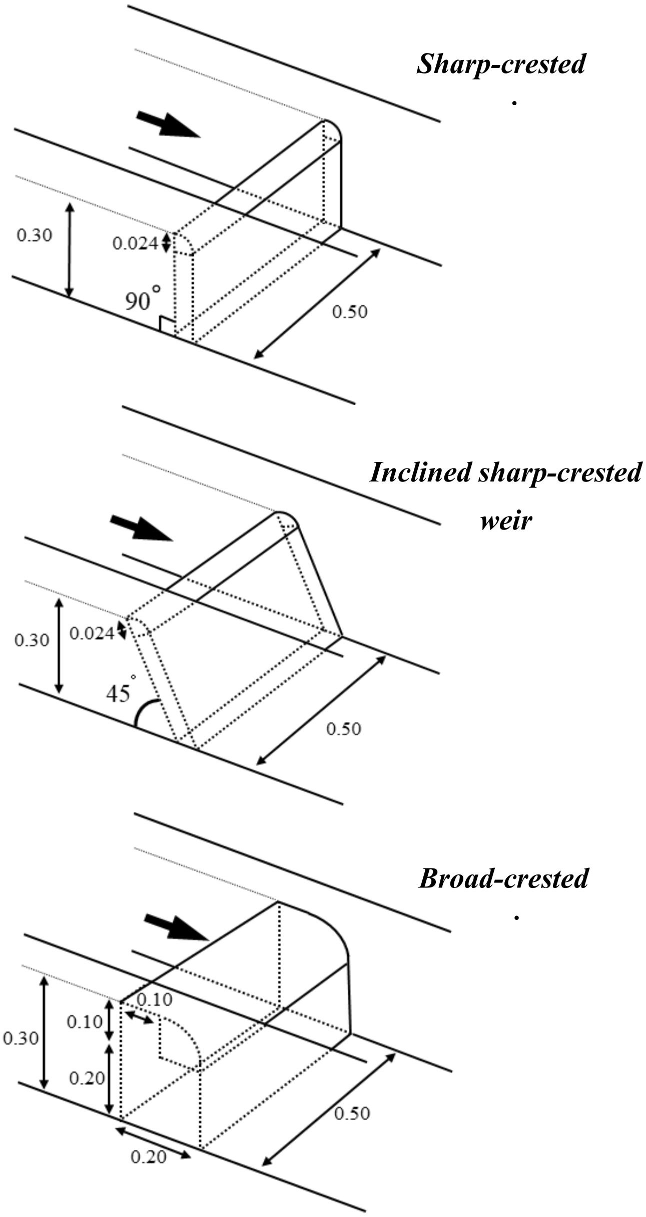
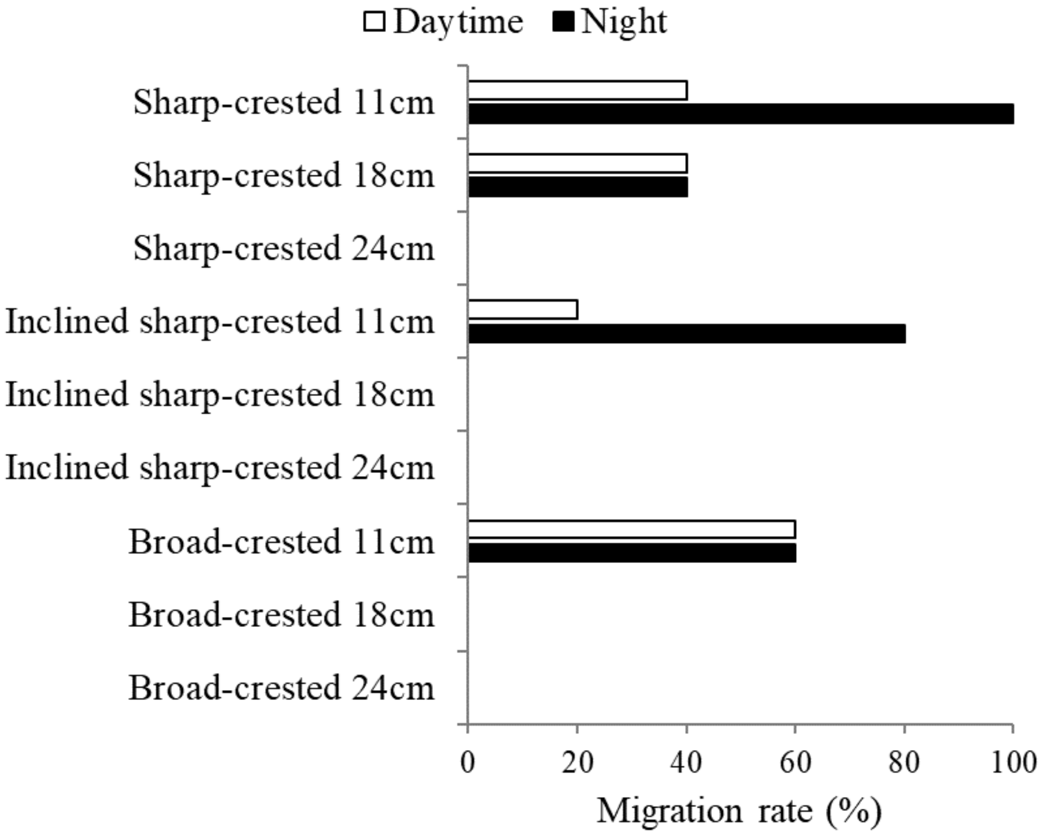


Figure 2: Ascent rates in each types of fishway-weirs, Δh and time period



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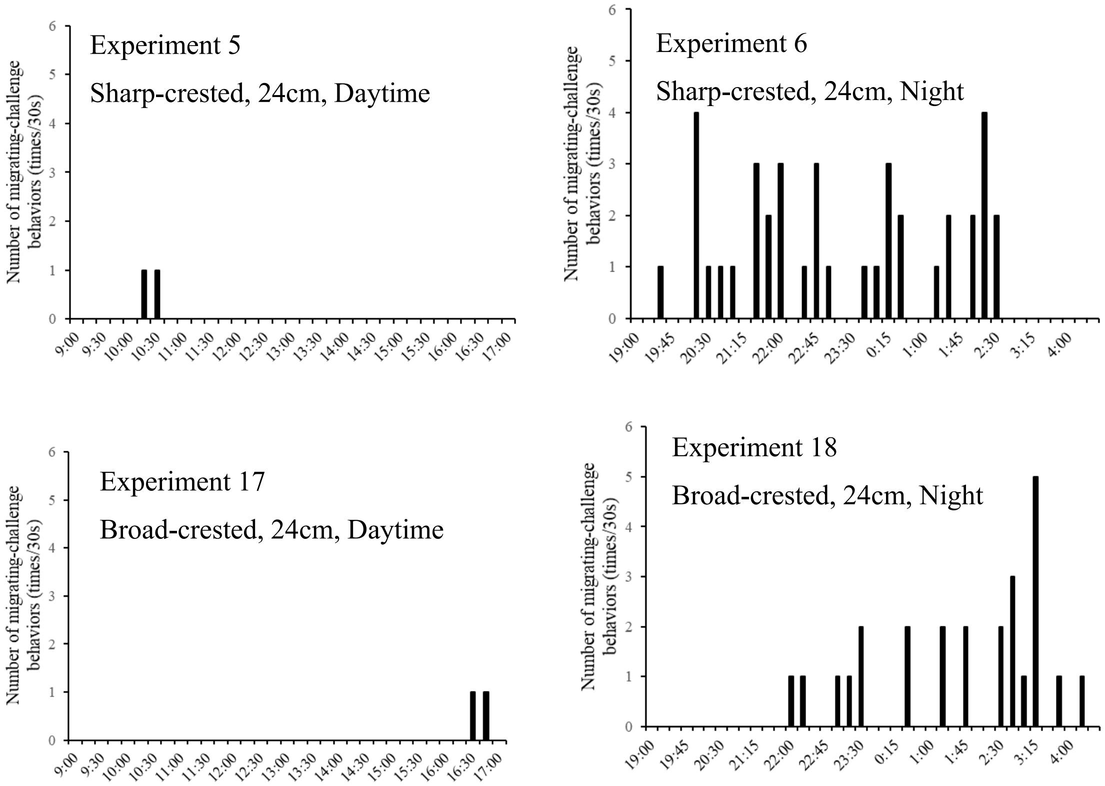

Figure 3: Frequency of ascent challenge behavior

Table 2: Population, mean length and standard deviation of migrated and non-migrated fish

No	Migrated fish			Not migrated fish		
	Population	Average	SD	Population	Average	SD
1	2	430	28	3	437	32
2	5	444	19	0	-	-
3	2	479	16	3	459	19
4	2	474	8	3	462	24
5	0	-	-	5	434	27
6	0	-	-	5	434	27
7	1	440	0	4	434	26
8	4	443	17	1	405	0
9	0	-	-	5	467	19
10	0	-	-	5	467	19
11	0	-	-	5	435	22
12	0	-	-	5	435	22
13	3	467	14	2	468	32
14	3	467	14	2	468	32
15	0	-	-	5	467	19
16	0	-	-	5	467	19
17	0	-	-	5	467	19
18	0	-	-	5	467	19

Table 3: Water temperature, water quality and mean illumination

No.	Temperature（°C）	DO (mg/L)	pH	EC (mS/cm)	Illumination (lux)
1	17.7	7.22	7.7	0.23	1,070
2	17.4	7.69	7.7	0.23	N/A
3	17.7	7.68	8.2	0.28	970
4	18.8	7.35	8.1	0.28	N/A
5	18.7	7.48	7.9	0.23	1,070
6	18.3	7.41	7.8	0.23	N/A
7	15.8	7.73	7.8	0.23	1,088
8	16.6	7.32	7.8	0.23	N/A
9	18.9	7.55	8.0	0.27	910
10	19.5	7.41	8.0	0.28	N/A
11	13.1	9.14	7.5	0.23	1,098
12	14.6	8.38	7.6	0.23	N/A
13	19.6	7.39	8.2	0.28	974
14	20.4	7.21	8.2	0.29	N/A
15	20.1	7.25	8.0	0.28	830
16	19.6	7.34	8.2	0.29	N/A
17	19.3	7.81	8.0	0.28	968
18	19.3	7.76	8.1	0.28	N/A

Table 4: Candidate model

Rank	Explanatory variable	ΔAIC	weight
1	Δh	0.00	0.452
2	Δh + time period	1.55	0.209
3	Null	2.51	0.129
4	Δh + type	3.36	0.084
5	time period	4.20	0.055
6	Δh + time period + type	4.89	0.039
7	type	5.97	0.023
8	time period + type	7.65	0.010

Table 5: Relative importance (RI level)

Explanatory variable	RI
Δh	0.784
Type	0.156
Time period	0.313

Table 6: Regression coefficient of water level differences (Δh) of the best model

Explanatory variable	Regression coefficient	Standard error	*p-value*
(Intercept)	1.531	0.625	0.0143
Water level difference (Δh)	-0.07	0.0322	0.0365

Figure 4: Lamprey shaking the caudal fin in the pool.

Figure 5: Lamprey ascent behavior on broad-crested weir.

Chapter 7 An experimental study to evaluate predation threats on two native larval lampreys in the Columbia River Basin, USA

Introduction

Lampreys (*Petromyzontiformes*), a group of jawless fishes without bones, have persisted on Earth for at least 430 million years (Forey & Janvier, 1993). The Western Brook Lamprey, *Lampetra richardsoni*, is considered a "a species of concern" and "sensitive species" in the states of Washington and Oregon, USA (USFWS, 2011; ODFW, 2019), but very little is known about their ecology and long-term population viability. The Pacific Lamprey, *Entosphenus tridentatus*, is a very important species both culturally (for the Pacific Northwest Native American tribes) and ecologically (Close, Fitzpatrick, & Li, 2002). Population numbers and the distribution range of Pacific Lamprey have decreased substantially in the past several decades in the Columbia Basin (CRITFC, 2011) and range wide (USFWS, 2018). Many questions remain regarding the extension and severity of threats that these two lamprey species face (Kostow, 2002; Clemens et al., 2017).

The Pacific Lamprey has an anadromous life cycle whereas the Western Brook Lamprey is a resident species (ODFW, 2019). Larval lampreys burrow in the fine sediment of streams and rivers as filter and deposit feeders after hatching in freshwater (Mallatt, 1983). For Pacific Lamprey, this life stage lasts 3-8 years (Dawson, Quintella, Almeida, Treble, & Jolley, 2015) until they metamorphose into juveniles (McGree, 2005). Afterwards, juvenile Pacific Lamprey begin their downstream migration towards tidal waters and the ocean (Beamish, 1980; Close et al., 2002), and parasitic feeding commences whereby they feed on other fishes' blood and body fluids (Clemens et al., 2019). By contrast, Western Brook Lamprey metamorphose directly from a larva to an adult and spawn several months later (Pletcher, 1963).

One of the most obvious causes of decline for anadromous Pacific Lamprey is upstream passage barriers. Many existing artificial structures (i.e. hydro and diversion dams, etc.) hinder them from reaching their preferred spawning grounds (Moser, Almeida, Kemp, & Sorensen, 2015a). While adult passage has received research focus in the Columbia River Basin (Moser et al., 2015a), very little is known about the migration behavior and survival of larval and juvenile lamprey moving downstream (Luzier et al., 2011; Moser, Jackson, Lucas, & Mueller, 2015b; Liedtke et al., 2019). Many other knowledge gaps still remain for Pacific Lamprey, including the threat from predation (Close et al., 2002; Cochran, 2009; Clemens et al., 2017). This threat may impact lamprey population dynamics substantially by influencing their survival across many life stages.

When spawning in rivers and streams, Pacific Lamprey are susceptible to predation by a variety of predators such as *Pinipids, Mustelidae, Accipitriformes,* and *Acipenseridae* (Beamish, 1980; Wolf & Jones, 1989; Close, Fitzpatrick, Parker, Hatch, & James, 1995; Close et al., 2002). Pacific Lamprey eggs are also consumed by a variety of native freshwater fishes in the Columbia River (Pfeiffer & Pletcher, 1964; Close et al., 1995; Brumo, 2006). However, little is known about the characteristics of predators that feed on larval lampreys and their role in the food chain of rivers and streams. Larval lampreys are often observed at high densities relative to other life stages and are concentrated in their specialized habitat, which are fine sediment areas in slow water (Hardisty, 1944). Although not readily evident due to their highly cryptic nature of burrowing in the fine sediment, the biomass of lamprey larvae is estimated to be potentially one of the highest of all fish fauna in some river systems, such as Lower Fraser River (Beamish, 1980). As a result, larvae may potentially face a high risk of predation in streams and rivers in their specialized habitat or during their downstream migration (Cochran, 2009).

Non-native and invasive predator fishes have a large impact on local river ecosystems and population dynamics of native fishes such as salmonids (*Oncorhynchus* spp.) in the Northwestern USA (ISAB, 2008). Predation by invasive and/or non-native fishes has become a serious problem in the Columbia River Basin (Zimmerman, 1999; Fritts & Pearsons, 2004; Carey, Sanderson, Friesen, Barnas, & Olden, 2011). The vast majority of predation studies in the Columbia River Basin have focused on the predation of juvenile salmonids. For example, Smallmouth Bass (*Micropterus dolomieu*) were estimated to consume approximately ~200,000 salmonids on average during March to June in the Yakima River (Fritts & Pearsons, 2004). In the Columbia River near Richland (WA, USA), each Smallmouth Bass and Northern Pikeminnow (*Ptychocheilus oregonensis*) were estimated to consume 1.0-1.4 and 0.3-0.6 salmonids daily, respectively (Tabor, Shively, & Poe, 1993). A recent research from Southern Oregon suggested that Smallmouth Bass poses a high predation threat to lamprey larvae and negatively impacts the lamprey population (Schultz et al., 2017). However, information on the extent and magnitude of larvae predation by various fishes is still very limited.

In our study, we used native and non-native fishes to evaluate the predation threat to larvae, using confined, experimental tanks with two durations. While investigating this question, we also assessed the roles of other key potential variables on larvae survival. Our research questions included 1) the role of fine sediment in providing a predation refuge; 2) difference in preference by predators for consuming live and dead lampreys as well as two lamprey species; and 3) size relationships between consumed larvae and predator fishes. Although the actual impact of predation in their natural habitat cannot be projected or estimated from this pilot study, our main goal was to assess the "potential" of various fishes in consuming various sizes and species of larvae, which will provide an important context for future predation research to follow.

Materials and Methods

Larval Lampreys

The relative predatory threats were examined over four sets of binary factors, including: 1) short (2-day) or long (7-day) duration, 2) presence/absence of fine sediment, 3) live or dead larvae, and 4) species of lampreys. We used two durations for the predation study including a short-term study and a long-term study with sediment and without sediment. Four size classes of live larva and one size class of dead larva were used in the short-term study (Table 1). We used artificially propagated Pacific Lamprey (see Lampman et al., 2016) for young-of-the-year (YOY) and small size classes, which were considerably more difficult to obtain from the wild. Medium and large size class larvae were all collected from dewatered irrigation diversions in the Yakima and Wenatchee subbasins (WA, USA) using ABP-2 electrofishers (ETS Electrofishing System, Madison, WI, USA) and held for up to three years before the start of the study. For medium and large size classes, the species composition was 50% Pacific Lamprey and 50% Western Brook Lamprey to test the effect of lamprey species on predation. All larvae were fed a diet of primarily active dry yeast and wheat flour three times a week until the start of each experiment (Lampman et al., 2016). For dead larvae, we used a mix of Pacific Lamprey (both wild and hatchery origin) and Western Brook Lamprey (wild origin) that were preserved frozen from mortality events that occurred at hatchery or dewatering events at irrigation diversions. For the long-term study, we focused on slightly larger larvae sizes and only used three alternate size classes of live larvae (Table 1). Similar to the short-term study, we used approximately 30 mm size increments, with the size thresholds increased by 10 mm.

Predator Fishes

We used seven native and three non-native fish species in our study (Table 2). Native predators were Northern Pikeminnow, Chiselmouth (*Acrocheilus alutaceus*), Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), Torrent Sculpin (*Cottus rhotheus*) and White Sturgeon. Due to the difficulty in obtaining wild White Sturgeon and Coho Salmon, we acquired hatchery origin fishes reared at Marion Drain Hatchery and Prosser Fish Hatchery, respectively (WA, USA). The other native fishes were captured from dewatered irrigation diversions within the Yakima Subbasin, including Wapato, Sunnyside, Chandler, and Wapatox diversions (WA, USA) between mid-October and late November, 2016. Non-native predator fishes were Smallmouth Bass, Common Carp (*Cyprinus carpio*) and Yellow Bullhead (*Ameiurus natalis*); all were caught in the Chandler Diversion using electrofishing in late November, 2016. Efforts were made to reduce the holding period as short as possible to minimize the potential influence on their natural feeding behavior, but extended up to 35 days. Based on their feed preferences, predator fishes were fed a variety of natural feed while being held, including isopods (*Asellota* spp.), gammarids (*Gammaridae* spp.), algae (primarily *Hydrodictyon* spp.), and fish meat (frozen, bite-size pieces) with the goal of providing 3-9% of their body weight per day with larger fishes generally receiving lower percentage (New, 1987; Craig, Helfrich, Kuhn, & Schwarz 2017). The fish meat consisted of rainbow trout and Channel Catfish *Ictalurus punctatus* captured from the Chandler Diversion during dewatering salvage operations and were preserved frozen; the former died directly as a result of dewatering and the latter were euthanized intentionally. Three to four individuals of one fish species were used per experiment to minimalize the variability by individual fish.

Predation Experiments

All of our studies were conducted at Prosser Fish Hatchery using double wall, foam filled insulated plastic containers (100 × 113 × 78 cm; Bonar Plastic Inc., West Chicago, IL, USA) as the experimental tanks. The tank tops were covered by a black fine mesh net (6.35 mm mesh with 70% opening; AgroFabric, Canby, OR, USA) to allow some natural sunlight to infiltrate the tanks while preventing predation by animals from outside. Both short- and long-term studies had two distinct periods; the first period with fine sediment and the second period without fine sediment. At the start of each study, the bottom of the tanks were covered partially with fine sediment (<540 micron, 4 cm in depth) and the surface area of the fine sediment was adjusted based on number of predator fishes to maintain the same density of larvae per sediment surface area (64 lamprey/m^2). In natural settings, density of Pacific Lamprey larvae can reach 100 lamprey/m^2 or higher in some habitats (Torgersen & Close, 2004; Beals & Lampman, 2016; Beals & Lampman, 2017).

Water flow and depth were maintained at 6-8 L/min and 40 cm, respectively, and water volume was 460 L. Throughout both studies, the water temperature was kept between 13-15 ˚C using pathogen-free well water. The length of each larva and the total combined weight of all larvae were measured prior to placement into the experimental tanks. A group of predator fish were added to the tank at least ten minutes after placing larvae into the tanks to ensure larvae had an opportunity to burrow in the sediment first. Both predator fish and lamprey larvae were held in the same water source and temperature as the new tank prior to the start of the study to minimize the acclimation period. We conducted the experiment separately for each predator fish group, containing three to four individuals per experiment and their fork length (FL) and wet mass (WM) were measured before the placement (Table 2). The smallest group among native fishes was Torrent Sculpin [FL=62 ± 3 mm (± SD), WM=2 ± 0.3 g]. White Sturgeon (large) had the largest size (FL=398 ± 73 mm, WM=444 ± 312 g). The density level we used for White Sturgeon (1.18 kg/m^2) is still considered acceptable based on the rearing densities suggested by Fajfer, Meyers, Willman, Carpenter, & Hansen (1999) for Lake Sturgeon *Acipenser fulvescens* (1.35-3.75 kg/m^2).

For the short-term study, all experiments took place between December 5, 2016, and February 15, 2017. We conducted the experiment once with sediment and once without sediment for each predator fish under equal conditions. Ten larvae (two live larvae from each of the four size classes, and two dead larvae) were added for each predator fish to ensure that the same number of larvae were available per each individual predator fish (Table 1). Two nights after adding the larvae and predator fish, we temporarily removed all predator fish and larvae from the tank.

To separate larvae from the fine sediment, we siphoned water, sediment, and larvae together into a nylon mesh screen basket (<540 micron) which sat inside a water bath. Following careful sifting, most of the fine sediment (<540 micron) deposited under the mesh, allowing us to collect any remaining larvae efficiently on the mesh screen basket. No fresh mortalities were observed during this sifting process. Given the relatively short duration of our experimental trials and the lack of escape routes within the tanks and sifting screens, we assumed that the absence of lampreys after each trial represented mortality associated with predation.

After all measurements were taken, we supplemented live and dead larvae to restore the original numbers at the beginning of the study, substituting any consumed larvae with new lamprey from the same size classes. To reduce variability by individual fish, the same individuals of predator fish were placed back into the tank to begin the second half of the study, this time without any fine sediment. The experiment was terminated two nights after the start of the second half of the study, and the same measurements taken at the end of the first half without sediment were remeasured. In addition to those data, the height and width of each predator fish's mouth were also measured at the end of the experiment to calculate the mouth size (area) to the nearest millimeter. The number of unconsumed live and dead larvae, the combined total weight of remaining live larvae, and the size classes that were consumed by predators were assessed. The ratio of the final to initial counts of larvae (for live and dead lamprey groups separately) was calculated as the probability of survival and served as a proxy for the predation threat.

The long-term study took place between December 28, 2016, and February 20, 2017, using two species of native predator fishes and two species of non-native predator fishes that consumed a higher number of larvae in the short-term study. The tank conditions and protocols were similar to the short-term study. However, a total of eight live larvae (two larvae from small and large size classes and four larvae from medium size class) were added for each predator fish and no dead larvae were used for this experiment due to the high degree of deterioration expected at the end of the study. Protocols for measurements of larvae and predator fishes before and after the experiment were the same as the short-term study, except that the duration was extended to 14 nights (seven days with sediment and seven days without sediment).

Data Analysis

We employed the generalized linear mixed model (GLMM) using glmmML package (Broström & Holmberg, 2011) in R statistical software (R Core Team, 2018) to select the best model in estimating the predation rates of live larvae by predator fishes in the short-term study. GLMM was used due to two reasons; 1) the predation rates as the response variable displayed a Poisson distribution; and 2) the need to incorporate interspecific difference as a random effect. The explanatory variables included in this analysis were 1) fine sediment presence/absence (categorical), 2) species - native or non-native (categorical), 3) average predator fork length (continuous), and 4) interaction between fine sediment presence/absence and the other variables. We used only predator fork length and did not use the wet mass and mouth area of predators as explanatory variables due to multicollinearity. We also compared the frequencies of the predation rates between larvae of Pacific Lamprey and Western Brook Lamprey when sediment was absent during the short-term study by Fisher's test using fisher.test function in R statistical software.

To evaluate the effects of predators' morphological features on predation rates in the absence of sediment, a correlation between average fork length of predator fishes and average and maximum sizes of consumed larvae was examined. Pearson's correlation coefficient and a regression line (least squares method) was calculated for both the average and maximum sizes of preyed larvae. We also estimated the average weight of larvae consumed as a percentage of the average predator weight.

Finally, principal component analysis (PCA) was conducted to analyze, compare, and classify the characteristics of predator fishes preying on larvae. R statistical software (R Core Team, 2018) with prcomp function (Venables & Ripley, 2002) was used to perform the statistical analyses. We included four response variables; predation rates of live and dead larvae, with and without sediment. Contribution rates, cumulative proportion, and factor loadings of the were calculated.

Results

Short-Term Study

The predator fishes preyed on live lamprey larvae substantially more frequently when fine sediment was absent during the short-term study (Figure 1a). Average ± SD predation rates were 5 ± 4% (range: 0-9%) with sediment and 47 ± 28% (range: 0-92%) without sediment. Without sediment, the highest predation rates were 92 and 88 % by Common Carp and White Sturgeon (large), respectively. With sediment, their predation rates were 0 and 4%, respectively. Salmonid species (Chinook and Coho Salmon and rainbow trout) behaved differently from most other species in that they fed on very few live larvae when sediment was present or absent. The average predation rates among non-salmonid native fishes (four species) were 4 ± 3% with sediment (3 ± 5% for salmonids) and 38 ± 28% without sediment (3 ± 3% for salmonids). Average predation rates by non-native fishes (three species) were 5 ± 5% with sediment and 66 ± 18% without sediment. No significant difference was observed between the predation rates of Pacific Lamprey and Western Brook Lamprey (Fisher's-test, P=0.591, Figure 2). Based on GLMM analysis, there was a significant difference in predation rates between treatments with and without sediment (z=4.843, P<0.0001; Table 3). The average predator FL was also selected as one of the best predictor variables and positively correlated with the predation rates when sediment was absent (z=3.817, P<0.001).

In contrast, the predation rates of dead larvae did not vary based on the presence/absence of sediment (Figure 1b). Torrent Sculpin consumed dead larvae in neither treatments and Northern Pikeminnow (small, large) and Smallmouth Bass (large) consumed less than half of all dead larvae overall. In contrast, all salmonid groups ate 100% of the dead larvae under at least one of the two sediment treatments. The average predation rates of dead larvae among native fishes were 67 ± 39% with sediment and 59 ± 44% without sediment. The average predation rates by non-native fishes were 80 ± 45% with sediment and 72 ± 34% without sediment.

With sediment, most predator fishes only consumed YOY size larvae; exceptions were Northern Pikeminnow (small), rainbow trout and Yellow Bullhead (small), which also ate small and/or medium size larvae (Figure 3). Without sediment, a wide range of larva sizes were consumed by the predator fishes. However, only four groups of predators, namely

Northern Pikeminnow (large), White Sturgeon (large), Common Carp and Yellow Bullhead (large) consumed large size larvae (Figure 3). Average predator fork length (P_{fl}) and maximum (A_{max}) and average (A_{ave}) size of consumed larvae were positively correlated ($R^2=0.67$, $P<0.05$ and $R^2=0.61$, $P<0.05$, respectively; Figure 4). Some species of predators consumed larvae that were roughly the same size as themselves; the maximum size of larvae consumed by predators were 101% and 95% of their average FL for Smallmouth Bass (small) and Torrent Sculpin, respectively (Figure 5). In addition, Yellow Bullhead (small), Yellow Bullhead (large) and Northern Pikeminnow (small) consumed larvae that were 81%, 68% and 57% of their own fork lengths.

For the principal component analysis, the contribution rates of the first component (PC1) and second component (PC2) were 0.45, 0.25, respectively, and the cumulative proportion was 0.69. The variables with the highest eigenvector for PC1 were the predation rates of dead larvae with sediment (0.66) and without sediment (0.65). For PC2, the predation rates of live larvae without sediment was the variable with the highest eigenvector (0.98). PC1 could be interpreted as the predation rate of dead larva and PC2 could be interpreted as the predation rates of live larvae without sediment. Based on these components, all predators were classified into four groups (Figure 6). Group A including all three salmonids displayed positive loading on PC1 and negative loading on PC2, indicating that these species consumed a lot of dead larvae but relatively few live larvae without sediment. Group B including Northern Pikeminnow (small, large), Torrent Sculpin, and Smallmouth Bass (large) displayed negative loading on PC1 and positive loading on PC2, indicating that these species consumed a lot of live larvae without sediment but relatively few dead larvae. Group C including Chiselmouth (small, large), White Sturgeon (small), Smallmouth Bass (small), and Yellow Bullhead (small) displayed positive loading on PC1 and intermediately positive loading on PC2, indicating that these species consumed a lot of dead larvae and moderate quantity of live larvae without sediment. Finally, Group D included White Sturgeon (large), Common Carp, and Yellow Bullhead (large) displayed positive loading on PC1 and PC2, indicating that these species consumed a lot of live larvae without sediment as well as dead larvae.

Long-Term Study

We compared the predation rates of larvae over two 7-day periods using four groups of predator fishes with and without sediment (Figure 7). All four groups consumed 100% of the larvae when sediment was absent at this extended duration. When sediment was present, the predation rates by Northern Pikeminnow (large) and Smallmouth Bass (large) did not increase significantly in comparison with those rates from the short-term study. However, the predation rates by Common Carp and White Sturgeon with sediment present increased considerably at this extended duration. The predation rates during the short-term and long-term studies by White Sturgeon was 4% and 62%, respectively. Predation rates of Common Carp during the short-term and long-term studies were 0% and 17%, respectively.

Discussion

Importance of sediment and other variables

Close et al. (1995) indicated that indigenous predators, such as White Sturgeon and Northern Pikeminnow, as well as exotic predators, such as Channel Catfish, can feed on larval Pacific Lamprey. Our study results indicated that a variety of fish species, both native and non-native, large and small, had a high propensity to prey on larvae when fine sediment was absent. Species, such as Yellow Bullhead, sculpin, Chiselmouth, and Common Carp, which are typically not considered a high risk predator for salmonids due to their small size and/or feeding behavior showed a high propensity to feed on lamprey larvae in the enclosed tank environment. However, considerable differences were observed in their feeding preferences in relation to both lamprey condition (live vs. dead) and sediment condition (presence vs. absence).

Our study demonstrated innate ability of lamprey larvae to evade predation by burrowing into fine sediment. Numerous studies suggest the importance of fine sediment for lamprey larvae as rearing habitat in the rivers and streams (Hardisty, 1944; Malmqvist, 1980; Sugiyama & Goto, 2002; Smith, Welsh, & Turk, 2011a). A study using larval Least Brook Lamprey (*Lampetra aepyptera*) concluded that predation risk decreased significantly when fine sediment (0.125–0.500 mm) were available compared to coarse sand (0.500–1.400 mm) or a silt/clay mix (Smith et al., 2011a). It is evident that fine sediment habitat provides larvae not only a rearing habitat for feeding, but also a refuge habitat to hide from various predator fishes. However, larvae are likely to face risks of predation when they move out of the sediment to change habitat (Cochran, 1986; Cochran, 2009). Sea Lamprey, *Petromyzon marinus*, emerge from sediment predominantly at night (Potter, 1980; Derosier, Jones, & Scribner, 2007), which likely reduces their risk of encountering potential predators.

In our study, Smallmouth Bass (small) were able to consume a lamprey larva that was 101% of their own size. Similarly, sculpin and Yellow Bullhead (small) consumed larvae that were 95% and 81% of their own size, respectively. Predation studies in the Columbia Basin have concluded that Smallmouth Bass consumed salmonids that were on average 19-29% of their total length and none were over 50% (Tabor et al., 1993; Fritts & Pearsons, 2006). Similarly, Northern Pikeminnow consumed salmonids that were on average 11~31% of their own size (Tabor et al., 1993). A study in a northwestern Washington lake concluded that Smallmouth Bass consumed prey including juvenile salmonids, crayfish, and sculpins, whose sizes were 18 to 34% of their own (Pflug & Pauley, 1984). These results suggest that these predator fishes can consume relatively larger lampreys (in terms of length) compared to other prey fishes. Prey body depth is also an important factor in the selection of prey by piscivores (Gillen, Stein, & Carline, 1981). Hambright (1991) reported that Largemouth Bass (*Micropterus salmoides*) never consumed prey of body depth greater than their own mouth width. Because lampreys maintain a slim morphology with no bone structure, it allows predator fishes to consume and digest these larger prey. As a result, even older larvae (5~8 years old) are susceptible to predation from medium size predators (150-200 mm).

Predator groups of larval lampreys

In our study, predator fishes were classified into four groups using principle component analysis based on feeding behavior and preference. Juvenile salmonids (Group A) had the lowest predation rates of live lamprey larvae when sediment was absent whereas piscivorous predators (Groups B) and benthic predators (Group D) displayed the highest rates. However, juvenile salmonids and benthic predators displayed a strong feeding inclination for dead larvae. Other smaller-sized predator fishes (Group C) displayed intermediate characteristics compared to the other three groups. The larger-sized individuals of these same species were classified as piscivorous predators (Groups B) or benthic predators (Group D), indicating the specialized species-specific predatory behavior is more evident only in the larger-sized fishes.

Juveniles salmonids (Chinook Salmon, Coho Salmon, and rainbow trout) did not consume many live lamprey larvae compared to the other predator fishes we examined. Pfeiffer, and Pletcher (1964) reported larvae were rarely found in the stomachs of salmonid fry. O'Rouke (2014) reported that younger and smaller Brown Trout (*Salmo trutta*) fry were less ichthyophagous, and displayed a greater preference for aquatic insects than older and larger fry. In our study, smaller and younger juvenile salmonids were used and it was possible that the small size of the juvenile salmonids might have affected the low predation rates of live larvae. In contrast, juvenile salmonids readily consumed dead larvae. Lamprey larvae may have a distasteful skin due to their discharging of a noxious substance from club cells and granular cells (Pfeiffer & Pletcher, 1964; Lethbridge & Potter, 1980). In our study, we observed some live larvae that survived attacks by other predators (including from juvenile salmonids) with obvious bite marks on their skin, alluding to the hypothesis of distasteful skin. Indeed, juvenile salmonids may have been able to consume more dead larvae due to the cessation of noxious substance discharge from being dead and/or once frozen. However, salmonids are known to feed on eggs of Pacific Lamprey (Pfeiffer & Pletcher, 1964; Close et al., 1995; Brumo, 2006) and adult Brown Trout are known to prey on transformed far eastern brook lamprey (*Lethenteron* spp.) in the spring (Hasegawa, Adams, & Maekawa, 2007). As a result, salmonids may be more prone to prey on lampreys in other life stages, including eggs and transformers, which were not examined in our study.

Northern Pikeminnow (small, large), Smallmouth Bass (large) and sculpin were classified together as Group B and showed high predation rates for live lamprey larvae without sediment and the lowest predation rates for dead larvae. Northern Pikeminnow is a native species, but has caused a serious predation issue in the Columbia River Basin for other native species (Porter, 2011). Smallmouth Bass is an invasive non-native species in the Western United States and is known as a ferocious predator of native species, including juvenile salmonids and sculpin species (Pflug & Pauley, 1984). These piscivorous predators tend to feed on prey in response to motion (Howick & O'Brien, 1983; Irvine & Northcote, 1983), and this may explain why they showed a higher preference for live larvae compared to dead ones in our experiment. Piscivorous predators such as Smallmouth Bass are not necessarily specialized for preying on lamprey larvae in sediment but have the potential to consume larvae emerging from the sediment. Schultz et al. (2017) estimated that a Smallmouth Bass population consumed 1,911 lamprey larvae in a 1.1 km segment of Elk Creek (OR, USA) during a 3-month period between July and September. This suggests that predation by Smallmouth Bass could still pose a serious threat to native lamprey populations.

Predation rates of both live and dead lamprey larvae were higher in Group D species [White Sturgeon (large), Common Carp, and Yellow Bullhead (large)] than the other groups in our short-term study. In addition, the predation rates of larvae in fine sediment by White Sturgeon increased dramatically from 4% to 63% when we extended the study duration from two to seven nights. White Sturgeon are known to feed on benthic prey such as Burrowing Shrimp *Neotrypaea californiensis* (Dumbauld, Holden, & Langness, 2008), and can potentially feed on all life stages of Pacific Lamprey (Close et al., 2002). Common Carp are also known as a benthic predator, preying on species such as Zebra Mussels *Dreissena polymorpha* (Tucker, Cronin, Soergel, & Theiling, 1996). Brown Bullheads, closely related to Yellow Bullheads, have an omnivorous feeding habit and their diet include aquatic invertebrates and detritus (Keast & Webb, 1966; Kline & Wood, 1996). This feeding habit is in accord with our results, which demonstrated that Yellow Bullhead preyed heavily on both dead and live larvae. Because bullheads siphon sediment containing small invertebrates and detritus (Keast & Webb, 1966), they have a high likelihood of encountering lamprey larvae in the sediment. Smith, Welsh, & Turk (2011b) reported that Yellow Bullhead showed high lamprey larva predation rates even in silt/clay and coarse sand. Both Common Carp and Yellow Bullhead are invasive species in the Northwestern USA and the additional predation threats imposed by these benthic predators potentially pose a serious threat for lamprey populations in regions where their distribution overlap considerably.

Conservation of lamprey species

Our experimental study evaluated the predation threat of various predator fishes on lamprey larvae within a confined laboratory setting. Although these results may not shed light directly on the predation risks for larvae within their natural environment, it provides important context for exploring this topic further. In the future, other prey species besides larval lampreys could potentially be added to the confined tanks to assess the preference of predator fishes in prey selection. In addition, further research is warranted on the predation threat of other widely distributed species within the Columbia River Basin which were not tested in our study, including Walleye (*Sander viteus*), American Shad (*Alosa sapidissima*), sucker (*Catostomidae* spp.), and Mountain Whitefish (*Prosopium williamsoni*). Furthermore, to assess the preference of predator fishes in prey selection, other prey fishes besides lamprey larvae could potentially be added to the experimental design.

Predation research in the Columbia River Basin has so far focused primarily on a select number of predator species, such as Smallmouth Bass and Channel Catfish, primarily due to the focus on salmonid predation (Tabor et al., 1993; Fritts & Pearsons, 2006). Our study indicated that benthic predators, such as White Sturgeon, Common Carp and Yellow Bullhead are especially adept at preying on lamprey larvae within fine sediment. When considering lamprey predation as a whole, there is a need to evaluate the impact of many other species. To successfully manage and restore Pacific Lamprey populations within the Columbia River Basin, we need to understand the potential threats from non-native and invasive predators that have become so prevalent across the region. The threat of predation on lamprey species remains a critical knowledge gap for many of the native lamprey species regionally and locally. With the emergence of global climate change and its influence on various fish communities across the region, including potential and suspected increases in abundances of non-native invasive species (Hellmann, Byers, Bierwagen, & Dukes, 2008; Rahel & Olden, 2008), more research on predation is warranted to help understand the population dynamics and conservation needs of these imperiled species.

TABLE 1. Summary data of larval lampreys used in the short-term and long-term studies

Study	Condition	Size class	TL range (mm)	Lamprey species	Origin	Tag
short term	live	YOY	< 30	Pacific	hachery	untagged
		small	30 - 59	Pacific	hachery	untagged
		medium	60 - 89	Pacific, Western Brook	wild	untagged
		large	90 - 130	Pacific, Western Brook	wild	untagged
	dead		20 - 40	Pacific, Western Brook	hatchery, wild	untagged
long term	live	small	40 - 69	Pacific	hachery	VIE, untagged
		medium	70 - 99	Pacific	wild	VIE, PIT, untagged
		large	100 - 130	Pacific	wild	PIT, untagged

TABLE 2. Summary data of predator fish species evaluated in the short-term and long-term studies

Name	**Scientific name**	**Short name**	**Size class**	**#**	**Short term**	**Long term**	**Fork Length (mm)**		**Wet Mass (g)**		**Mouth area (cm^2)**	
							Mean	**Range**	**Mean**	**Range**	**Mean**	**Range**
Native fish												
Northern Pikeminnow	*Ptychocheilus oregonensis*	NPM (S)	small	4	○	×	138	124-150	28	21-35	1.1	0.7-1.4
		NPM (L)	large	4	○	○	264	235-282	203	155-248	5.1	3.6-8.0
Chiselmouth	*Acrocheilus alutaceus*	Chisel (S)	small	3	○	×	111	104-116	14	11-16	0.3	0.3-0.4
		Chisel (L)	large	3	○	×	191	177-214	79	51-123	0.8	0.4-1.1
Chinook Salmon	*Oncorhynchus tshawytscha*	Chinook		4	○	×	107	94-121	14	8-21	0.7	0.5-0.9
Coho Salmon	*Oncorhynchus kisutch*	Coho		3	○	×	120	107-129	20	12-26	1.1	0.7-1.4
rainbow trout	*Oncorhynchus mykiss*	RBT		4	○	×	155	124-187	40	17-62	1.1	0.9-1.3
Torrent Sculpin	*Cottus rhotheus*	Sculpin		3	○	×	62	60-65	2	2-3	0.4	0.4-0.5
White Sturgeon	*Acipenser transmontanus*	Sturgeon (S)	small	3	○	×	276	255-287	126	112-141	1.5	1.2-1.7
		Sturgeon (L)	large	3	○	○	398	343-481	444	240-804	3.5	2.6-4.6
Non-native fish												
Smallmouth Bass	*Micropterus dolomieu*	SMB (S)	small	4	○	×	73	70-76	5	4-5	0.5	0.4-0.6
		SMB (L)	large	3	○	○	304	276-356	435	301-668	8.3	5.9-10.8
Common Carp	*Cyprinus carpio*	Carp		3	○	○	284	254-304	439	312-549	4.0	3.2-4.6
Yellow Bullhead	*Ameiurus natalis*	Bullhead (S)	small	3	○	×	97	94-103	9	8-11	0.7	0.7-0.8
		Bullhead (L)	large	3	○	×	187	171-201	72	51-89	3.7	3.1-4.1

TABLE 3. Variables selected by the Generalized Linear Mixed Model (GLMM) for estimating predation rates of live larvae during the short-term study. The explanatory variables have significant effect at *P < 0.05, **P < 0.01 and ***P< 0.001

Action	**Variable**	**Coefficient**	**Std. Error**	***z* Value**	***Pr* (>|*z*|)**
	Intercept	1.055	0.502	2.102	0.035
	With sediment	-	-	-	-
	Without sediment	1.432	0.295	4.843	*P*<0.0001***
With sediment (Interaction)	Native predator	-	-	-	-
	Non-native predator	0.810	0.773	1.048	0.295
	Predator fork length	-0.001	0.001	-1.010	0.312
Without sediment (Interaction)	Native predator	-	-	-	-
	Non-native predator	1.263	0.735	1.717	0.085
	Predator fork length	0.002	0.001	3.817	*P*<0.001***

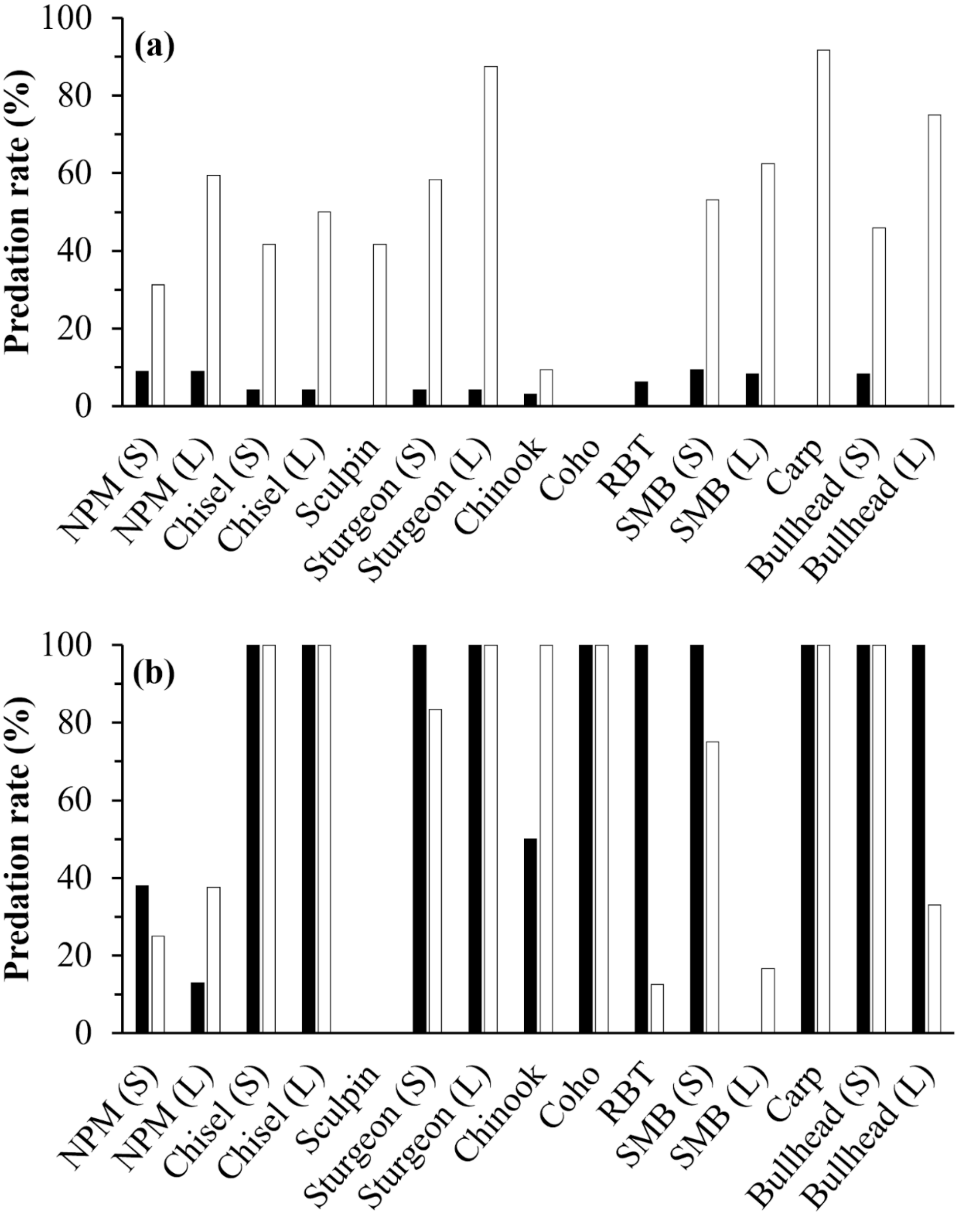

FIGURE 1 Predation rates of (a) live and (b) dead larval lampreys from the short-term study. The solid and open bar indicate the results with sediment and without sediment, respectively

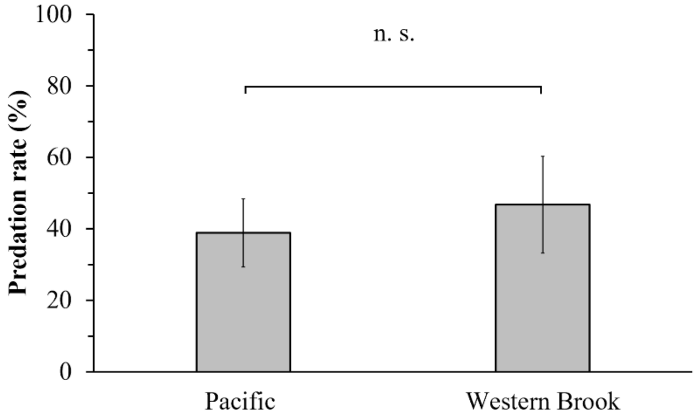

FIGURE 2 Predation rates of Pacific Lamprey and Western Brook Lamprey larvae during the short-term study (Fisher's test, $P<0.05$). Mean differences are significant at "*" $P< 0.05$ and not significant "n. s." $P>0.05$

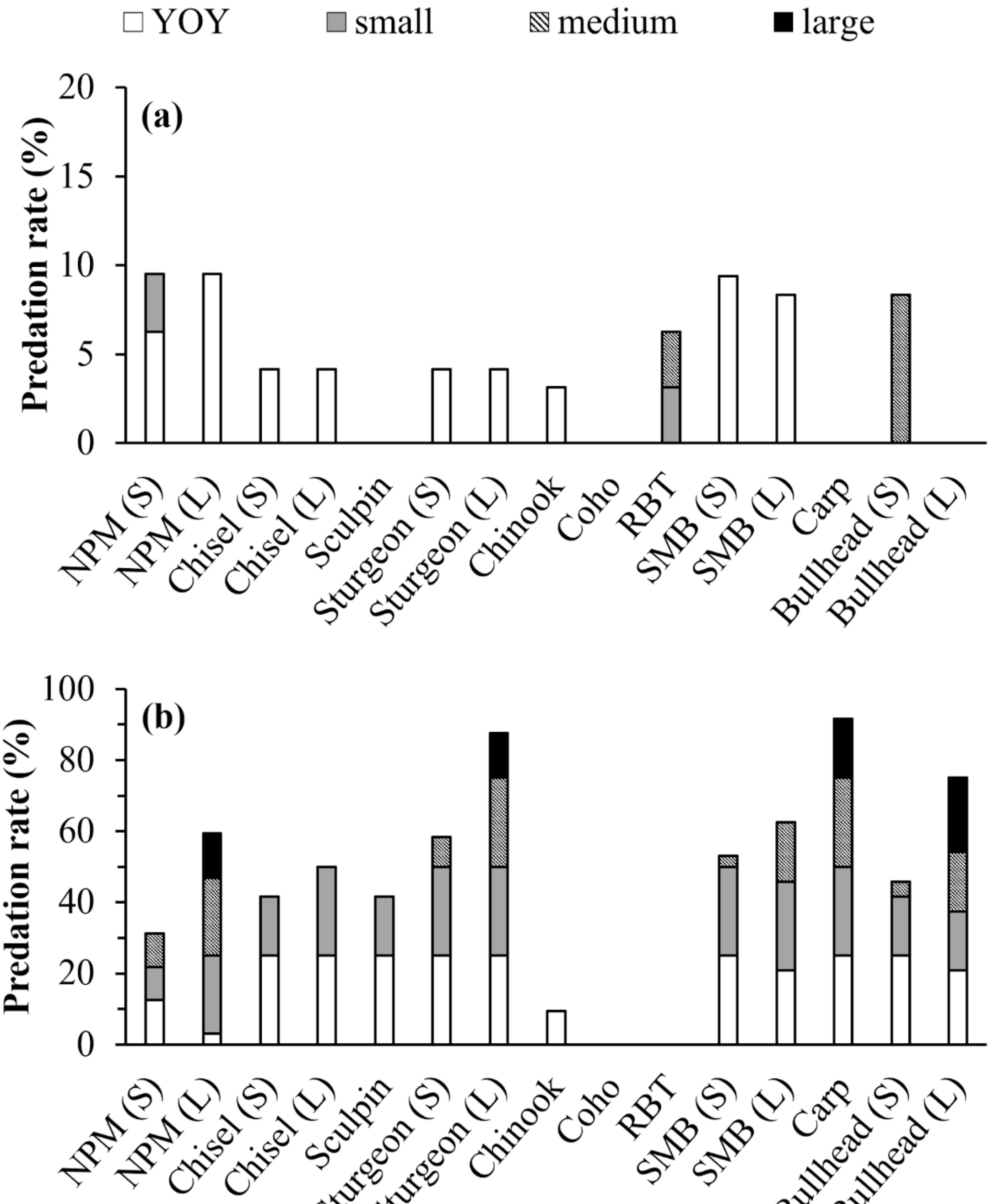

FIGURE 3 Predation rates of larval lampreys of each size class when fine sediment was (a) present and (b) absent during the short-term study

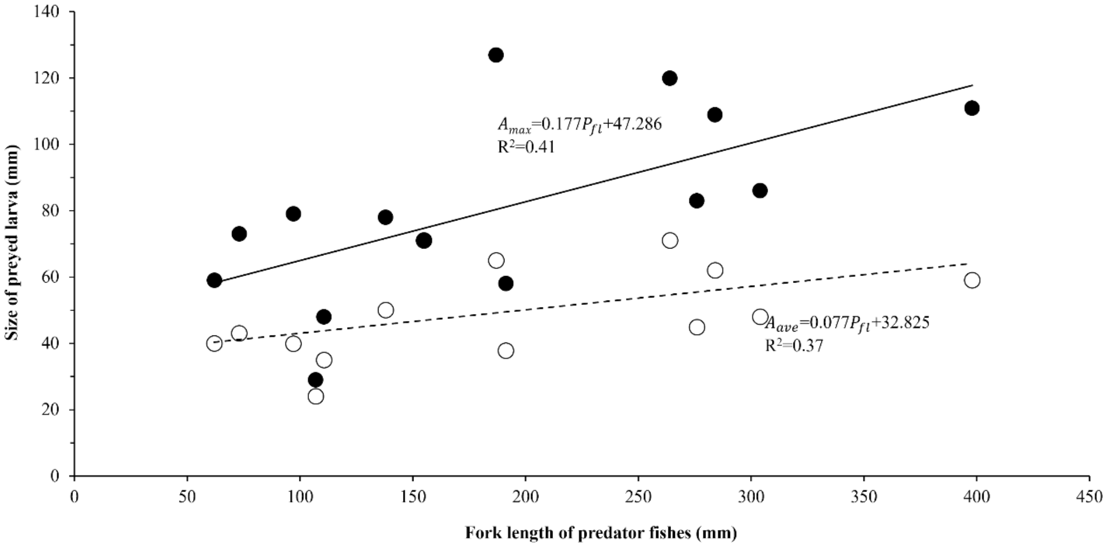

FIGURE 4 Relationships between average fork length of predator fishes (Pfl) and sizes of consumed larvae. The solid circles and line display the maximum sizes of consumed larvae (Amax) and its trend line, whereas open circles and the dotted line display average sizes of consumed larvae (Aave) and its trend line

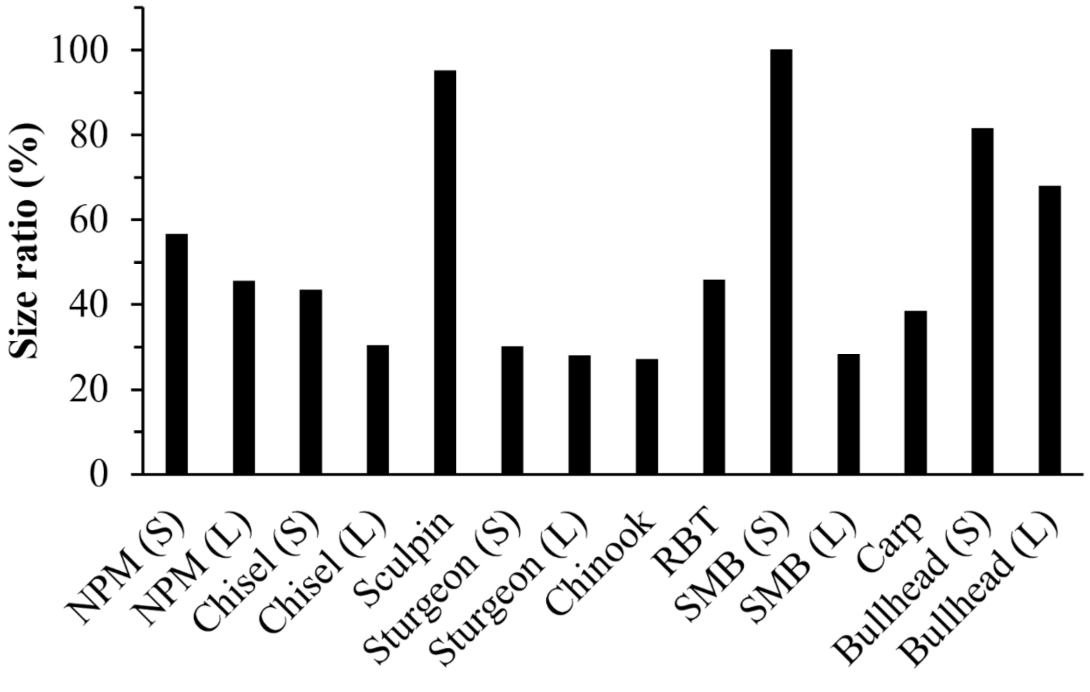

FIGURE 5 Ratio of the maximum size of larva consumed to the average predator FL during the short-term study

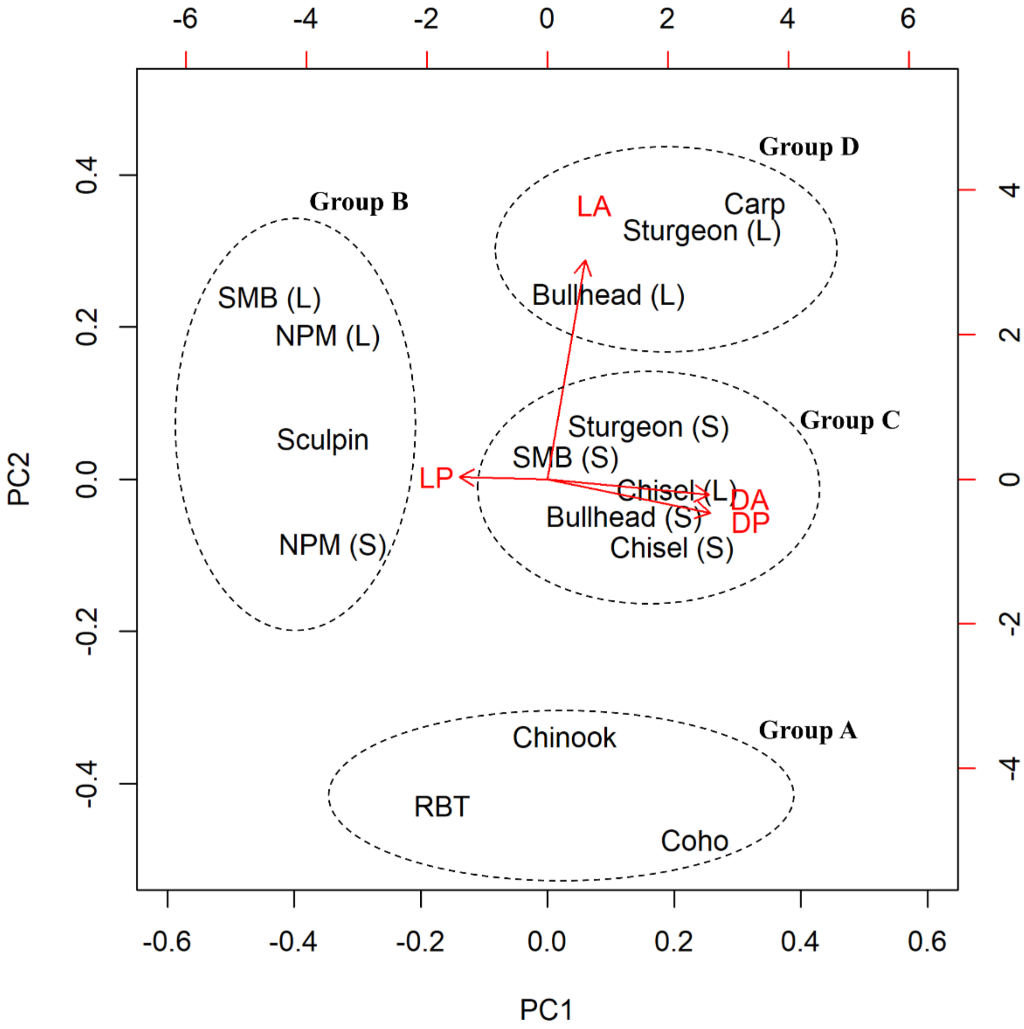

FIGURE 6 Predator fishes were distinguished according to their larval lamprey consumption traits using principal component analysis. The principal components included the predation rates of live larvae with sediment (LP), without sediment (LA), the predation rates of dead larvae with sediment (DP) and without sediment (DA)

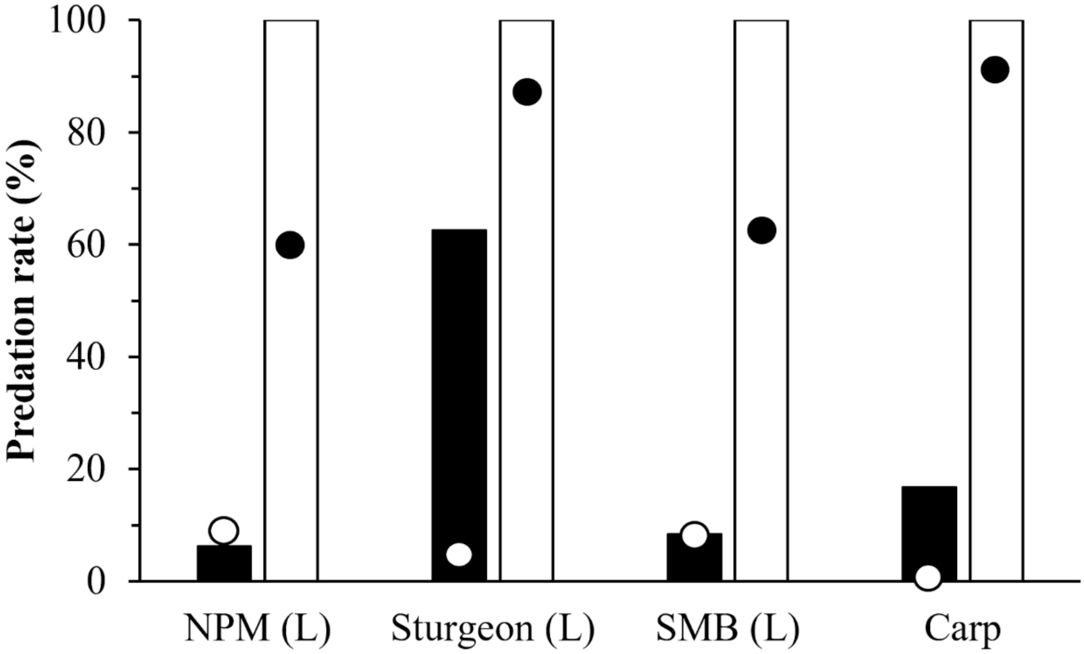

FIGURE 7 Predation rates of larval lampreys over seven days during the long-term study and two days during the short-term study. Solid and open bars display results from the long-term study with sediment and without sediment, respectively, whereas the open and solid circles display the results from the short-term study with sediment and without sediment, respectively

Chapter 8 Whose kids did you eat? Genetic identification of species and parents of larval lampreys in fish predator guts

Introduction

Lampreys (order: *Petromyzontiformes*) are among the earliest known fish species, dating back at least 430 million years in fossil record, relatively unchanged from its primordial form (Forey and Janvier 1993; Gess et al. 2006). The Pacific Lamprey (*Entosphenus tridentatus*) is a very important species both ecologically (CRITFC 2011; Dunkle et al. 2020) and culturally (Close et al. 2002; Wicks-Arshack et al. 2018), inhabiting the streams, rivers, and coastal waters of the Pacific Rim. However, population numbers and distribution range have decreased severely in the past several decades in the Columbia Basin (CRITFC 2011) and range wide (USFWS 2018). In addition to passage and habitat related threats, predation may potentially pose a serious threat for larval and juvenile lampreys migrating downstream (Cochran 2009; Arakawa and Lampman 2020, Chapter 7), especially with the recent trend in more widespread distribution and increased abundances of non-native, invasive fish species in many tributary and mainstem environments (Hellmann et al. 2008; Rahel and Olden 2008). While diagnostic bones are often used to identify prey fish species from the predator's stomach (Hansel et al. 1988; Buckland et al. 2017), identification (ID) of soft-bodied organisms lacking bones, such as lampreys, from stomach contents are much more challenging via traditional methods that depend primarily on diagnostic, morphological observation (Nakamoto and Harvey 2003; Sakaguchi et al. 2017). Further, because lampreys are composed of cartilaginous, non-calcified internal skeletons (Kaucka and Adameyko 2019) and their skins are scaleless (Hardisty 1954), the true numbers of larval/juvenile lampreys contained in the stomach of predator fishes may be substantially underestimated due to their rapid assimilation in the predators' stomach. Consumed lampreys in the digestive systems are often fully digested and decomposed prior to stomach content analysis, making ID to genera or even life stages (larval vs. juvenile) extremely difficult (Schultz et al. 2017;

Arakawa and Lampman 2020, Chapter 7).

In recent years, molecular techniques have been developed and applied for estimating prey items and diet diversity, and these studies have demonstrated that they can be very effective in detecting various prey items compared to traditional morphological methods (Symondson 2002; Carreon-Martinez et al. 2011; Sakaguchi et al. 2017). Further, genetic analysis is also increasingly being applied to fisheries management through the use of parentage-based tagging (PBT) to determine the age and origin of sampled fish (Hess et al. 2016; Steele et al. 2019; Hess et al. 2020a). Parentage-based tagging makes use of large numbers of genetic markers to identify the offspring from a dataset of candidate parents; as a result, the offspring can be effectively aged and their natal origins determined when the year and sites in which the parents spawned are known. The ability to age is a very useful tool for lamprey species particularly because accuracy in aging is considerably limited using statolith structures compared to those with otolith structures (Meeuwig and Bayer 2005).

Given these new levels of information that PBT can provide, molecular techniques such as these have the potential to vastly improve our understanding of lampreys as a prey species. We conducted an experimental predation study in the laboratory using a variety of commonly observed native and non-native fish species from the Columbia River Basin that had a high likelihood of consuming larval lampreys (see Arakawa and Lampman 2020, Chapter 7). As part of this study, in addition to visual, morphological detection, genetic analysis of deteriorated and decomposed tissues from predator fishes' gastrointestinal tracts were conducted to evaluate whether the lamprey genera/species and their parents could be determined for any of the consumed larval lampreys.

Materials and Methods

Experimental Setup of Feeding Studies

We held various predator fishes with larval Pacific Lamprey and *Lampetra* spp. (e.g. Western Brook Lamprey [*Lampetra richardsoni*]) in double wall, foam filled insulated plastic tanks (100 × 113 × 78 cm) at Yakama Nation (YN) Prosser Fish Hatchery (WA, USA) for two nights (short-term) or seven nights (long-term). For both durations, the tanks received well water (6-8 L/min, 13-15 ˚C), water depth was at 40 cm, and a semi-porous mesh covered the tank to simulate natural lighting. We used a variety of larval lamprey size classes ranging from under 30 mm to 130 mm. We used artificially propagated Pacific Lamprey for young-of-the-year and small size classes (propagated in 2016 and 2014, respectively; see Lampman et al. 2016). Medium and large size class larvae were a combination of Pacific Lamprey and *Lampetra* spp., which were collected from dewatered irrigation canals in the Yakima and Wenatchee subbasins (WA, USA) using ABP-2 electrofishers (ETS Electrofishing System, Madison, WI, USA) and identified based on caudal fin characteristics (Lampman 2018). Predatory fishes (three or four individuals of one species per experiment) were comprised of the following native (n=5) and non-native (n=3) fish species: Chinook Salmon (*Oncorhynchus tshawytscha*, mean total length ± SD = 107 ± 11 mm), two size classes of Chiselmouth (*Acrocheilus alutaceus*, small: 110 ± 6 mm, large: 191 ± 20 mm), two size classes of Northern Pikeminnow (*Ptychocheilus oregonensi*s, small: 138 ± 11 mm, large: 263.5 ± 21 mm), two size classes of White Sturgeon (*Acipenser transmontanus*, small: 276 ± 18 mm, large: 398 ± 73 mm), Torrent Sculpin (*Cottus rhotheus*, 62 ± 3 mm) as native species, Common Carp (*Cyprinus carpio*, 284 ± 27 mm), Smallmouth Bass (*Micropterus dolomieu*, 73 ± 3 mm), and two size classes of Yellow Bullhead (*Ameiurus natalis*, small: 97 ± 5 mm, large: 187 ± 15 mm) as non-native species. Common Carp, Northern Pikeminnow (Large), and White Sturgeon (Large) were used for the long-term study and the other predatory fishes were used for the short-term study. The experiment was conducted with some other native species (Coho Salmon *Oncorhynchus kisutch* and rainbow trout *Oncorhynchus mykiss*), but these species were excluded from the analysis due to the lack of live larval lamprey consumption during the short-term study. Each of the aforementioned groups of predator fishes were tested separately and held with the allocated number of larvae (eight larvae per predator fish) for either two or seven nights for the short- and long-term studies, respectively. The short- and long-term studies took place between 5 December 2016 and 15 February 2017 and between 28 December 2016 and 20 February 2017, respectively. See Arakawa and Lampman (2020, Chapter 7) for more details on the study design and protocols. and protocols.

Analysis of the Digestive Tract Contents

At the end of both studies, we counted remaining unconsumed larval lampreys in the tank and from this we determined the number of consumed larvae. Remnants of larvae from the predator fishes' digestive tract were extracted by euthanizing the group of predator fish immediately after the experiment using 4-5 times the regular anesthetic dosage of MS-222 for euthanasia and dissecting their peritoneal cavity. The contents were obtained from four regions of the digestive tract: esophagus, stomach, fore intestine, and hind intestine; in the case of cyprinid predators (namely Northern Pikeminnow, Chiselmouth, and Common Carp) only three regions were available due to the lack of a true stomach. First, we identified the contents from esophagus and stomach visually; unassimilated individuals that could be identified as larval lamprey morphologically were counted (Figure 1). Second, we also subsampled one small mass from each of the predator's digestive tract (up to one from each region) which contained remnants (of various degradation levels) for genetic analysis. The remnants of the digestive tract ranged from a small piece of larval tissue to a liquefied black fragment (Table 1). All samples (N=53) were separated and dried on Whatman filter paper, sent to the Columbia River Inter-Tribal Fish Commission Hagerman Genetics Lab (Hagerman, ID, USA) for analysis.

DNA sequencing analysis was conducted on all samples to verify whether the remnants of the digestive tract could be positively identified as lampreys. DNA was extracted from larval tissue using nondenatured Chelex (Sigma-Aldrich), and genotyped using 308 single nucleotide polymorphism (SNP) loci and protocols for Genotyping in Thousands by sequencing (GT-seq). The GT-seq method is a high throughput method that uses Illumina sequencers to rapidly genotype thousands of individual samples at hundreds of loci for less than ¼ the cost of previously used TaqMan assays (Campbell et al. 2015).

The GT-seq panel includes four SNPs designed for species ID (two redundant SNPs [LampSD_478 and LampSD_700] distinguish *Entosphenus* from *Lampetra* spp.; two redundant SNPs [LampSD_1589 and LampSD_327] further discriminate *L. pacifica* from *L. richardsoni* / *L. ayresii* within *Lampetra* spp.). Additionally, there are 304 SNPs developed specifically for Pacific Lamprey population genetic and parentage analysis (Hess et al. 2020b). The GT-seq panel has been designed to a maximum of 75 bp to allow for inexpensive sequencing runs on an Illumina NextSeq 500. For any Pacific Lamprey individuals that passed a quality control threshold of > 90% genotype success across 308

SNPs, we performed parentage analysis using the program SNPPIT (Anderson 2012) using a baseline of candidate parents that had either artificially propagated in the laboratory (N=158, propagated between 2012 and 2016) or were translocated and released in the Yakima River basin (N=1562, translocated between 2012 and 2016). We used a strict threshold log likelihood ratio (LOD) score ~≥ 14 and false discovery rate (FDR) < 0.1 for accepting parent assignments. *Lampetra* individuals typically do not genotype successfully at more than approximately 50% of the 308 SNPs even from a well preserved genetic tissue sample, but are possible to identify to species using the species ID SNPs. For definitive species ID of *Lampetra* individuals, we needed at least one of the two redundant species ID markers (i.e. either LampSD_478 or LampSD_700) to genotype successfully; a homozygote genotype (i.e., both alleles are the same) of the "G" allele identifies *Lampetra* individuals, whereas a homozygote genotype for the alternate allele ("A" or "T", for LampSD_478 and LampSD_700, respectively) indicates *Entosphenus* individuals. Heterozygote genotypes (i.e., one copy of each of the two alleles) have not been observed to date, but would be possible if hybridization between *Lampetra* and *Entosphenus* were to occur; the fact that we did not observe any "hybrid" species ID genotypes in this study helped to provide some degree of confidence that we were collecting genotypes from single individuals.

Results

Number of consumed larvae

During the short-term study (two nights), Chinook Salmon only consumed three larval lamprey, which was considerably less compared to the other predators, which all consumed 10-18 larvae. During the long-term study (seven nights), all three groups of predator species, namely Common Carp, Northern Pikeminnow (Large), and White Sturgeon (Large), consumed 100% of the larvae provided. Despite the relatively high consumption rates of larvae, no larvae were visually detected within the digestive tracts of three cyprinid species (Northern Pikeminnow, Chiselmouth, Common Carp) and White Sturgeon (Small). Digestive remnants were detected and obtained from the esophagus and stomach of Chinook Salmon, Smallmouth Bass, Torrent Sculpin, and Yellow Bullhead (Small, Large) in the short-term study, and White Sturgeon (Large) in the long-term study. The remnants were only obtained from the intestinal regions for Northern Pikeminnow

(Large), Chiselmouth (Small, Large), and White Sturgeon (Small). No remnants were obtained from any of the digestive tracts of Common Carp and Northern Pikeminnow (Small).

Morphological identification

Among all the consumed larvae by predators, the mean ± SD percent of individuals that could be morphologically identified as lampreys based on the contents of the digestive tracts (which only occurred in esophagus and stomach tracts) were 13 ± 16% in the short-term study and 3 ± 5% in the long-term study (Table 1). All samples recovered from the esophagus and a subset of samples from the stomach region (50.0%) contained visually identifiable lampreys (based on lamprey specific features, including its gills, filter feeding mouth, elongated body with scaleless skin; [A] and [B] in Figure 1) without the help of a microscope or other special equipment. In contrast, larvae from the intestinal regions were dissolved and deliquesced, preventing any morphological ID as lampreys. Multiple larvae (two to three) were visually identifiable in the stomach region of individual predatory fish species, including Torrent Sculpin, White Sturgeon (Large) and Yellow Bullhead (Small, Large) (see [A] and [B] in Figure 1). The maximum and minimum morphological detection rates in the short-term study were 33% and 0%, respectively, indicating that 67-100% of the consumed larvae were already decomposed within two nights and could not be identified visually as lampreys. However, it is important to note that the times of consumption were completely unknown and as a result those that were identifiable might have been consumed much more recently than two nights prior. Similarly, the maximum and minimum detection rates in the long-term study were 8% and 0%, respectively, indicating that 92-100% of the larvae were severely decomposed within seven nights.

Molecular identification

The percent of samples that were successfully genotyped for at least one of the two redundant species ID SNPs by respective digestive tracts are listed in Table 2. Species ID was successful for the majority of samples from the stomach region (83%), whereas the rates were much lower in other regions (< 8%). Furthermore, none of the samples from the hind intestine or esophagus regions were genotyped successfully for species ID.

Although samples from the stomach of three Smallmouth Basses ([C] in Figure 1), one Yellow Bullhead (Small), two Yellow Bullheads (Large, [D] in Figure 1) were not morphologically identifiable, genetic species ID of these samples were successful. In contrast, stomach samples from one Torrent Sculpin and one Yellow Bullhead (Small) were visually identifiable as a larval lamprey but were not genotyped to species successfully. From the fore intestine region, only one sample (8.3%; from a White Sturgeon [Large]) was successfully genotyped to species ([E] in Figure 1). There was only one sample extracted from the fore intestine of a cyprid species (Chiselmouth [Small]), which lack true stomach; however, genetic ID was not possible ([F] in Figure 1).

As a more variable quantitative measure of DNA quality, we also reported the percent of all 308 SNP loci in the GT-seq panel that were successfully genotyped for each individual. The mean ± SD percent genotype success of samples from the stomach and esophagus regions were relatively high (74.5 ± 34.0% and 37.2 ± 24.6%, respectively, Table 2), whereas that of samples from the fore and hind intestine regions were low (5.7 ± 18.2% and 0.7 ± 3.4%, respectively). Three individuals from stomach were identified as *Lampetra*, and the mean percent genotyping was 43.6 ± 12.2% (N=3). If we only considered individuals with positive species ID and analyzed *Entosphenus* separately, the mean percent genotype success for stomach and fore intestine were 86.4 ± 27.6% (n=7) and 63.3% (n=1), respectively.

Parentage

Of the eight Pacific Lamprey individuals that were genotyped successfully for species ID, five of them were also successfully genotyped at >90% of all SNPs. These five individuals were used to perform parentage assignment to candidate parents. Three (from the stomach of one Torrent Sculpin and two Yellow Bullheads [Small]) were confirmed to be offspring of artificially propagated parents (two crosses of four unique parents spawned in late April and mid-May, 2014), and as a result were confirmed to be 2.5-year-old larvae during this study. One larva from the stomach of a Yellow Bullhead (Large, [A] in Figure 1) was confirmed to be an offspring of translocated parents: Two adults released in Naches River (river km 4.7) on 12 September 2013 as part of a radio telemetry adult passage study. Because these adults were immature at the time of release and likely spawned the following year (during spring/summer), we presume this larva to be 2.5 years old as well. One larva with > 90% genotyping success from White Sturgeon (Large) did not assign to any candidate parents ([B] in Figure 1). However, baseline genetic data are not available from parents of volitional migrants, and it is possible that this larva was derived from those parents.

Discussion

Consuming behaviors of various predator fish

In our experimental study, a portion of larval lampreys from the stomach of piscivorous predators, such as Torrent Sculpin, Smallmouth Bass, and Yellow Bullhead, were identifiable visually and morphologically. In contrast, no larvae were morphologically detected in cyprinid species (i.e. Northern Pikeminnow, Chiselmouth, and Common Carp) despite these species consuming an equivalent number of larvae as the aforementioned predators. Although some studies have reported the predation potential of larval lampreys by cyprinid species, including Northern Pikeminnow (Close et al. 1995) and Common Carp (Arakawa and Lampman 2020, Chapter 7), these studies are far and few between. Cyprinid species use pharyngeal teeth to consume rigid food sources, including Mullusca hard shells (French III 1993). Brandenburg and Gido (1999) suggested that predation by cyprinid species were likely underestimated due to rapid digestion and potential shredding by these pharyngeal teeth. Furthermore, Tabor et al. (1993) concluded that gut contents of Northern Pikeminnow were considerably more challenging to identify based on external features compared to those of Smallmouth Bass and often required the presence of diagnostic bones. Evaluation of the experimental Northern Pikeminnow removal program in the Columbia River concluded that salmon and juvenile lamprey made up the highest percentage of prey fish species consumed by this predator (Porter 2013); however, juvenile lamprey were identified primarily by regurgitation and in some cases the presence of lamina (i.e. lamprey teeth) and rarely an entire lamprey were detected within the predator’s gut. Considering the unique feeding behavior of cyprinid species, our study as well as past studies strongly suggest that alternative methods are needed to accurately assess the predation potential of larval lampreys.

Detections of lamprey larvae

Reliance on visual and morphological ID alone would have been largely ineffective for our study given that the majority of consumed larval lampreys (average of 88% with a range of 67-100%) were diminished to a deliquesced state within two nights, and it was likely that the few that were identifiable were preyed upon much more recently than 48 hrs. Our study confirmed that detecting species of larval lampreys from the stomach content of predators using DNA sequencing was very successful, even when morphological ID was unattainable. Molecular diet analysis was effective in quantifying the predation on the early life stages of lake sturgeon *Acipenser fulvescens*, which were significantly underestimated by the standard gut content analysis (Waraniak et al. 2018). Furthermore, Michel et al. (2018) concluded that differing effects of predator species on juvenile salmon were determined based on standard predator density monitoring and molecular based diet estimates; the molecular genetic gut contents analysis provided unique insights in assessing the predation potential by non-native species. As a result, we conclude that molecular and other alternative methods for detecting rapidly digestible larval lampreys from the gut content of non-native and invasive predators will be valuable and advantageous in improving our understanding of their predation.

Recently, DNA metabarcoding was used qualitatively to characterize species composition of the diet of Arctic lamprey (*Lethenteron camtschaticum*) in the ocean (Shink et al. 2019), and this same technology could potentially be useful in detecting consumed larvae in the guts of lamprey predators (Amundsen and Sánchez-Hernández 2019). Moreover, we show that genotyping-by-sequencing technology can deliver not only qualitative presence/absence results that are similar to DNA metabarcoding studies but also more detailed information at the individual level of the prey based on parentage analysis. This level of detail affords age and natal-rearing sites for the offspring of candidate parents that were genetically tagged, and thus provides a novel and profoundly intimate way of characterizing fish predation behavior than has ever been shown before. Expansion of this work to predator fishes caught in natural environments would potentially allow us to reconstruct age and approximate locations of lamprey larvae that predators are utilizing preferentially based on the baseline of candidate parents. This in turn could provide insights for larvae's differential risk to predation pressure related to age, locations, and even down to the level of individual spawning pairs. For instance, if offspring from a certain origin (e.g., a certain tributary or brood year) are disproportionately being detected through molecular analysis, this additional data on particularly vulnerable segments of the populations can potentially help direct relevant management and conservation actions.

When conducting predator gut content and other predation studies, it is important to consider incorporating new methods such as molecular technologies to help improve detections of lamprey larvae in predation studies given the high probability of underestimation with the exclusive use of morphological methods, given that they are digested quickly and lack bone structures. For many of the native lamprey species both regionally and locally, predation related threats remain a critical knowledge gap. Increases in abundances of non-native invasive species is projected as a result of global climate change and its influence on fish communities across the region (Hellmann et al. 2008; Rahel and Olden 2008). As such, predation will be a key knowledge gap to fill to further our understanding of population dynamics and conservation needs of these imperiled species.

TABLE 1. Numbers and rates of visually and morphologically identifiable larval lampreys in the digestive tracts of predators in comparison to the overall number of consumed larval lampreys from the short and long-term studies (Eso = esophagus, Sto. = stomach, F. Int. = fore intestine, H. Int. = hind intestine). Species names with asterisks denote non-native species in the Columbia Basin. Hyphens signify that the three cyprinid predators (Northern Pikeminnow, Chiselmouth, and Common Carp) all lack a true stomach.

Experimental period	**Predatory fish**		**# of preyed larvae**	**# of the individuals having remnants in each tract**				**# of visually identified larvae**	**Detection rates (%)**
	Species (size class)	**#**		**Eso.**	**Sto.**	**F. int.**	**H. int.**		
2 days (short-term)	Chinook Salmon	4	3	1	0	0	3	1	33
	Chiselmouth (Small)	3	10	0	-	1	3	0	0
	Chiselmouth (Large)	3	12	0	-	0	2	0	0
	Northern Pikeminnow (Small)	4	10	0	-	0	0	0	0
	Smallmouth Bass*	4	17	1	3	3	4	1	6
	Torrent Sculpin	3	10	0	2	1	2	3	30
	White Sturgeon (Small)	3	14	0	0	0	3	0	0
	Yellow Bullhead* (Small)	3	11	0	3	2	3	3	27
	Yellow Bullhead* (Large)	3	18	0	3	3	3	2	11
	Total and mean for detection rates	**30**	**105**	**2**	**11**	**10**	**23**	**10**	**12**
7 days (long-term)	Common Carp*	3	24	0	-	0	0	0	0
	Northern Pikeminnow (Large)	4	32	0	-	0	1	0	0
	White Sturgeon (Large)	3	24	0	1	2	3	2	8
	Total and mean for detection rates	**10**	**80**	**0**	**1**	**2**	**4**	**2**	**3**

TABLE 2. Genetic detection rates of larval lampreys (Pacific Lamprey or Western Brook Lamprey) from the gastrointestinal tracts of predator fishes. Mean and maximum values of %GT (percent genotyped) display the percentage of 308 SNP loci that were successfully genotyped as Pacific Lamprey from each of the four digestive tracts averaged across all predator species. Species names with asterisks denote non-native species in the Columbia Basin. Numbers in parentheses with an asterisk indicate the numbers identified as *Lampetra*. Hyphens signify that no remnants or tissues were found.

Experimental period	**Species (size class)**	**Esophagus**	**Stomach**	**Fore intestine**	**Hind intestine**
2 days (short-term)	Chinook Salmon	0/1	-	-	0/3
	Chiselmouth (Small)	-	-	0/1	0/3
	Chiselmouth (Large)	-	-	-	0/2
	Smallmouth Bass*	0/1	3/3 (1*)	0/3	0/4
	Torrent Sculpin	-	1/2	0/1	0/2
	White Sturgeon (Small)	-	-	-	0/3
	Yellow Bullhead* (Small)	-	2/3	0/2	0/3
	Yellow Bullhead* (Large)	-	3/3 (2*)	0/3	0/3
7 days (long-term)	Northern Pikeminnow (Large)	-	-	-	0/1
	White Sturgeon (Large)	-	1/1	1/2	0/3
	Species ID rates (%)	0/2 (0 %)	10/12 (83 %)	1/12 (8 %)	0/28 (0 %)
	Mean ± SD %GT (all samples)	37.2 ± 24.6	74.5 ± 34.0	5.7 ± 18.2	0.7 ± 3.4
	Mean ± SD %GT (positive for *Entosphenus*)		86.4 ± 27.6	63.3	
	Max %GT	54.6	99.7	63.3	17.9

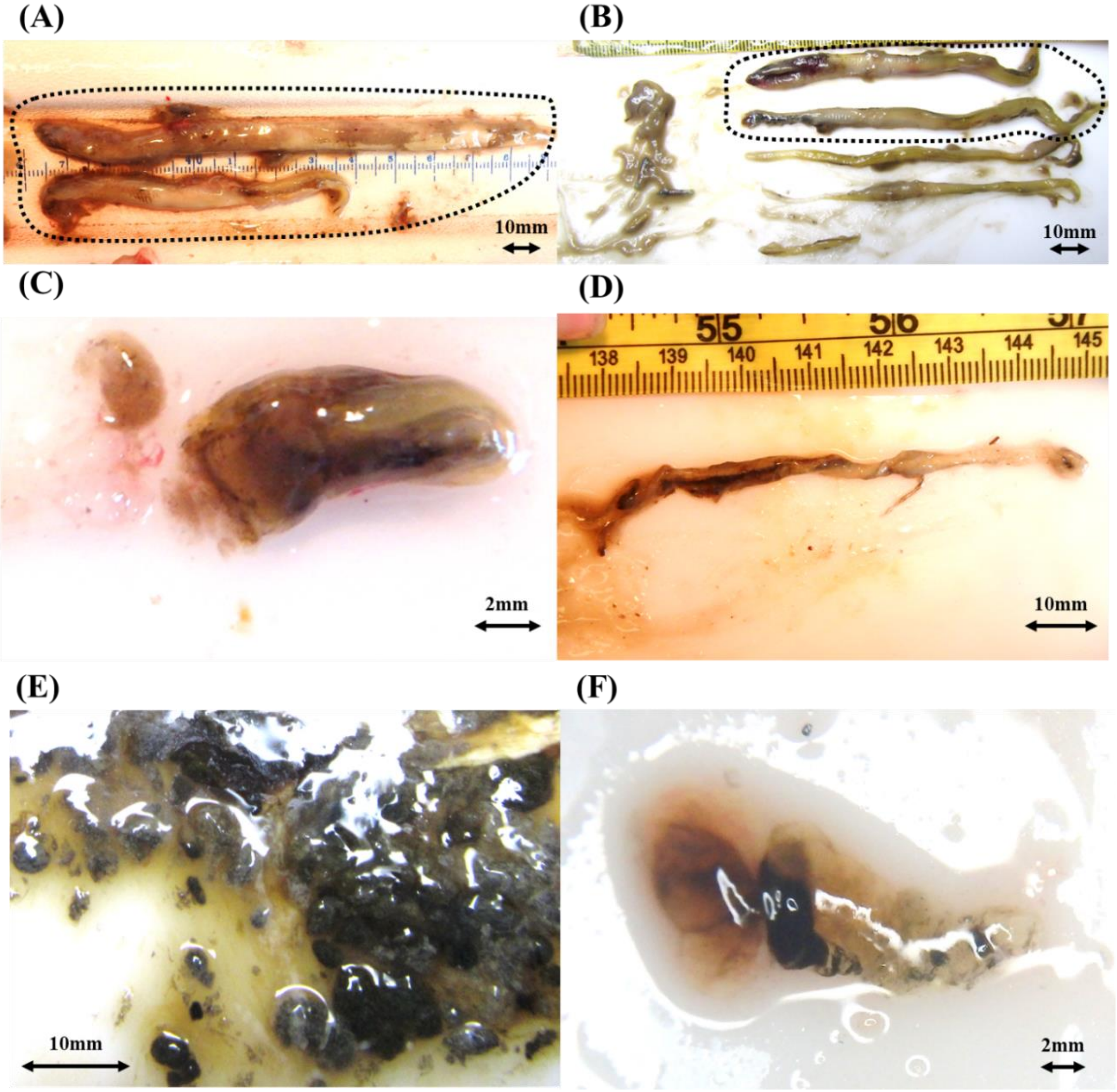

FIGURE 1. Remnants of larval lampreys from the stomach of a Yellow Bullhead (Large) (**A**), White Sturgeon (Large) (**B**), Smallmouth Bass (**C**) and Yellow Bullhead (Large) (**D**) and the fore intestine of a White Sturgeon (Large) (**E**) and Chiselmouth (Small) (**F**). Those that were successfully identified morphologically are circled (dotted line) in (**A**) and (**B**). Species genotyping was successful for samples from (**A**), (**B**), (**C**), (**D**), and (**E**).

General discussion

Fishing culture

Traditional Arctic lamprey fishing culture has distributed in the entire basin from estuaries to tributaries along the Sea of Japan coast from Tohoku to Hokuriku Region. Japanese inland fishers have harvested Arctic lamprey thorough their entire migrating period in the freshwater by developing fishing methods and gear in accordance with river size, the aquatic environment, and lamprey's behavior. Depended on the characteristics of fishing (gear, lamprey's behavior), fishing for Arctic lamprey was classified into 3 types including 1) set-net fishing, 2) catching lamprey at artificial barriers, 3) catching lamprey at spawning beds. Type 1 set-net fishing catch Arctic lamprey using cone tubes, fyke nets, and baskets in the estuaries and middle mainstream reaches. In the middle reaches, as Type 2 fishing, the fishers catch lampreys concentrated below artificial barriers. Type 3 catching lampreys in spawning beds was conducted in the upper reaches and tributaries.

This wide distribution of fishing culture suggests the cultural importance of Arctic lamprey as food resources historically. Lampreys have been fished in their distribution in Europe, Russia, North America, Oceania, and Asia, and formed the traditional culture (Almeida et al. under review). The story of lamprey utilization has long history and back 2000 in Roma Docker et al. (2015). The value of lampreys as food are important commercially for European and ceremonially for native people in North America and New Zealand (Close et al. 2002; Jellyman et al. 2002; Docker et al. 2015). In Japanese dishes for Arctic lamprey, grilled "*kabayaki*", raw "*sashimi*", and flied lampreys are consumed in the Ishikari River Basin (Murano et al. 2008, Fig.1). In Tohoku Region, lampreys have been appreciated as grilled and boiled dishes (Inuzuka 2003; Kometani 1996, Fig.2-4). In Akita, miso soup baked in the shell of a clam or pot called "*kaiyaki*" is traditional dish using lamprey as a seasonal ingredient (Akita Prefecture http://common3.pref.akita.lg.jp/aktshoku/aji/index.html?article_id=20, Fig.5). In central Japan, rivers in Niigata were famous for the harvest of lampreys (Kataoka 1980; Satake 2000), and lampreys are dried and wrapped win straw for preservation (Fig.6). Residents in Noto Peninsula has traditional fishing culture and consumed lampreys as seasonal food (Arakawa et al. 2018).

Most of Japanese fishers catch lampreys for self-consumption (Arakawa et al. 2018, Chapter 6; Murano et al. 2008). From our study, catching by hand or hooks in relative small-scale fishing was popular upper middle reaches. These small fishing can provide an appropriate amount for self-consumption within local areas. Small-middle class rivers and steep topography through the rivers in mountainous areas might restrict the commercial harvest. These local consumptions in the entire basins might prevent associating information about the fishing culture and the utilization in Japan.

For nutrition of Arctic lamprey, it contains many essential fatty acids (DHA and EPA) and vitamins (Yazawa, 2007), and vitamin A level is the highest among any fish or animal (Higashi et al. 1958). It is served in a number of different ways in restaurants and are highly valued as a medicine against night blindness and was described as medicine for preventing night blindness in a book published in 1712 (Renaud 2011; Yazawa, 2007).

Arctic lamprey has been important food resources for traditional dishes and as medicine along the North and central Sea of Japan coast, and historically formed local fishing culture fishers' ecological knowledge developed in accordance with the topography to harvest lampreys efficiently.

However, the number FCs having active fishing has decreased from 56 in the past to 14 at present. The mean catch has also decreased to 1–10% of previous levels through the coastal Honshu along the Sea of Japan. In the Ishikari River, Hokkaido, the catch began to decline in the 1980s and dropped to 1% after 2000 (HRO, unpublished data). A consistent reduction in the catch has been observed throughout Japan and occurred seriously in the marginal regions such as southern and inland areas. The southern limits of the fishing culture distribution have shifted further north from 36.62 ºN (Ishikawa) to 42.51ºN (Hokkaido). In the past, Arctic lamprey fisheries were observed in the inland upper reaches with higher 100 m elevation, as Arctic lamprey fisheries were observed in the Agano River up to 200 km from the river mouth. However, the fishing existed in the area with a lower 100 m elevation at present.

Importance of FEK

The historical distribution of Arctic lamprey was estimated from two information resources of fishery statistics published in the 1930s as scientific data and fishers' ecological knowledge (FEK) provided by inland fishery cooperatives as ethnobiological data. The distribution patterns (geographical characteristics, southern limitation latitude) in the past estimated using FEK were largely consistent with one estimated by the scientific data. The habitat potential predicted by the same FEK was largely identical with the distribution of rivers from the scientific data.

Ethnobiological information provided by fishes is sufficient to predict the distribution of species for which past scientific data are lacking, and results can be obtained that are similar to those acquired from the use of scientific data collected from the field and bibliographic sources (Silvano and Begossi 2010; Lopes et al. 2019). Local ecological knowledge is an alternative information source that can be used to reconstruct historical trends, including temporal and geographical variation in the distribution of aquatic species (Azzurro et al. 2011; Turvey et al. 2013). Therefore, the FEK about Arctic lamprey has the potential to fill in the gaps in ecological information and contribute to conservation.

However, the underestimation in the prediction for habitat potential was observed when the species distribution models depended on only the FEK having detailed fishing memory. whereas additional ambiguous memory into the model improved predicting the marginal regions such as southern and inland area. Many reports suggest that older fishers who have more experienced have specific and detailed ecological knowledge on the past target species abundance and distribution (Bender et al. 2014; Damasio et al. 2015). The biodiversity and abundance in Japanese rivers have been decreased dramatically after the 1960s due to the river modification works as a result of rapid economic growth (Goto 1997). In the present days, the FEK from the older fishers who have more past experiences could contribute to estimating the distribution which is consistent with the old fishery statistics in the 1930s. However, the loss of fishing culture and memory has occurred obviously in the marginal regions of distribution. The number of inland fishermen belonging to Japanese fishery cooperatives (FCs) is estimated to be 0 until 2035 – 3036 (Nakamura 2017). The FEK is an effective alternative information resource for species management but the future information loss due to the decline of fishing culture can make estimating the original distribution more difficult and underestimating.

Distribution pattern

Arctic lamprey fishing distributed along the Sea of Japan Coast, but there were few harvest records along the Pacific Ocean Coast. Some studies reveal that an abundance of Arctic lamprey has been captured in the Sea of Okhotsk near the continental coast of the northwestern Sea of Japan, by contrast, an extremely low density in the Pacific Ocean on the eastern coast of Kamchatka (Sviridov et al. 2007; Orlov et al. 2014). The migration route and its mechanisms are not well known but this spatial distribution in rivers relates to the spatial distribution in the ocean and oceanographic regimes.

Latitude was the most significant explanatory variable to predict Arctic lamprey distribution, and the southern limits of the fishery distribution in the past were estimated to be 37.32º N (95% CI: 35.96 º N -38.38º N) from the inland fishery statistics and 36.62º N (95% CI: 35.62 º N -37.28º N) from FEK. We found literature describing harvest records near the limit (Satake 2000; Kataoka 1980), but there was no harvest information south of the limit. In our study, accidental catches were observed by 4 FCs south of the limit. These areas are within the species distribution from Hokkaido to Shimane according to Kawanabe and Mizuno (2001). Therefore, some populations migrate into the rivers in the south of the southern limit, but their numbers are not sufficient to enable the formation of fishing culture, as is the case in the coastal Pacific Ocean.

As significant geographical variables other than latitude, the river length and gradient of the lower reach were also selected. River length reflects the quantitative capacity of the habitat in rivers. And the river gradient is related to the qualitative habitat potential such as the depositional and erosional areas for larvae. The river gradient of the lower reaches was a more effective environmental variable than the gradient of the whole reach, which is considered to be related to the species distribution in the rivers. In Alaskan, larvae do not inhabit the upper reaches, which tend to have a steep gradient, but are rather distributed from the middle to lower reaches (Sutton 2017). The species distribution model using FEK predicted that the habitat potential distributed at low-lying areas and alluvial fans. This habitat potential can demonstrate that the river gradient of the lower reaches is more effective to explain the distribution. The historical distribution has been unknown ever due to the shortage of long-term monitoring and research, but our study results can contribute to the management and conservation of this species.

Threats and Conservation

Overharvesting and Fishing regulation

Overharvest is one threat to anadromous lampreys (Clemens et al., 2020). Ten Japanese inland FCs caught lamprey at artificial barriers, which prevent migration and have created new fishing grounds where many lampreys concentrate. The harvesting of spawning individuals also has a negative impact on reproduction. Appropriate management as fishing regulation should be performed to conserve sustainable fishery resources. However, the fishing was regulated in only Hokkaido, Yamagata, and Niigata Prefectures at present. In the cases of the other countries, the fishing using obstructed traps across rivers are allowed to span at least one-third to half of the river width (Araújo et al. 2016; Sjöberg, 2011). And technical controls stipulating fishing season, areas, gears (net dimensions), and minimum landing has been mainly performed. By contrast, the utilization hidden in Japanese local and shortage of scientific research for Arctic lamprey might delay the insufficient regulation. If an inland fishery resource species is regulated, the FCs would have been required to conduct conservation efforts. Recently, the artificial propagation technique of lampreys has been developing (Lampman et al., 2020; Arakawa and Yanai, 2018, 2019). Aquacultural technique development and the Japanese fishing culture study enable conservation efforts.

Artificial barriers and River reconnection

The fishing culture has declined seriously in inland areas. In freshwater systems, the distribution of larval lamprey is limited to downstream areas due to the presence of artificial barriers blocking the spawning migration (Mateus et al. 2012; Clemens et al. 2017; Fukushima et al. 2007). The previous study reports the negative impact of large barriers (over 5 m height) on the spawning migration of Arctic lamprey (Fukushima et al. 2007). In the Machino River, the occurrence of Arctic lamprey larvae decreased in the upper reach and the distribution range was decided to extend from the river mouth to the meddle reach with 11.3 km (95%CI: 10.9-11.6 km) length. However, from the species distribution model, the habitat potential distributed in the whole basin due to the flat topography consisted of a low mountain area in the Noto Peninsula. At the upper limit of the longitudinal distribution, 10 low-headed weirs with a lesser 2 m height are continuously present within 4 km. Recently, and even low-headed weirs decrease passage efficiency, and the multiple weirs reduce the rate of arrival at the upstream (Lucas et al. 2009; Silva et al. 2019). From the experiment to assess the Arctic lamprey ascent behavior, the difference in water depth upstream and downstream of the weir strongly affected the number of successful ascending individuals. No lamprey ascended the fishway-weir with a 24 cm difference. These results suggest the Arctic lamprey in the risk of artificial barriers including low-head weirs and the need for reconnection through the rives. As conservation for lamprey species, the improvement of fish passage for specific lamprey and reintroduction of adults into upper reaches have been conducted (Close et al 2009; Moser et al. 2011; Pereira et al. 2019). The habitat potential can contribute to deciding the conservation reach in the river and an additional filed survey is needed to confirm the present habitat status prior to the action.

Global warming and Utilization of upper reach

The southern limits of the fishing culture distribution have shifted further north. This is likely the influence of global warming on the Arctic lamprey population is now concerned. The upper lethal temperature for larval Arctic lamprey was estimated at 29.3ºC (95% CI: 28.2-30.2ºC). The river temperature within the distribution range in the Machino rivers located at the southern limits in the past was recorded at warmer temperatures than the lethal temperature during the summer. Arctic lamprey larvae might avoid the lethal temperature by burrowing into cooler sediment as a refuge. The larvae slightly preferred the aerobic sediment, which suggests the possibility that the oxygen consumption of the larvae increases due to the high metabolism activity defected by warmer temperature in the sediment. From the simulation, the habitat potential loss responding to the air temperature rise will antecedently occur downstream comparing to the upper reach. To conserve the populations near the southern limit, promoting the expansion of inhabitable cooler upper reach is needed by reconnection in the river for natural migration for lampreys. By contrast, the dynamics of migrating patterns in the ocean are unknown. To assess the impact of global warming on the Arctic lamprey population, the dynamics and suitable characteristics for all stages in freshwater and the ocean should be investigated in the future.

Information gap and outreach

The absence of recreational and commercial fisheries on lampreys creates a paradigm where funding is unavailable to monitor and manage them, thus perpetuating a lack of awareness and scientific understanding (Clemens et al. 2020). To increase awareness of lampreys, outreach is essential to species conservation. In the United States, Oregon Zoo exhibits Pacific lamprey to introduce its ecological and cultural importance (Oregon Zoo https://www.oregonzoo.org/discover/animals/pacific-lamprey). In Japan, the exhibition of Arctic lamprey has been conducted in Niigata City Aquarium and Aquarium and Ishikawa Zoo (Fig.6). We took the initiative to carry out the latter exhibition and explain the interests in biology and cultural importance in the Noto Peninsula using a panel (Fig.7). In addition, we conducted collaborative conservation activity with the local junior high school students and local fishers, and residents. First, we demonstrated artificial insemination in the local community center with the residents (Fig.8). The fertilized eggs and adult lampreys were transported to the junior high school to held till hatching for observation (Fig.8). After hatching, we held the presentation for the students and residents to introduce the ecology of lamprey, threat (Fig.9), traditional fishing culture. Because funding for science and research for low-concern species is limited, management action collaborative with the diverse associations is needed. Our study suggests the local fishers' ecological knowledge is effective for species adaptive management, and these cumulative bodies of knowledge and practices should be handed down to the next generations through the actions to conserve species and its traditional culture.

Fig.1 Broiled lamprey with soy sauce “*kabayaki*” (left) and raw lamprey “*sashimi*” (right) in Hokkaido

Fig.2 Grilled lamprey with salt and pepper “*shioyaki*” in Akita

Fig.5 Grilled lamprey with salt and pepper “*shioyaki*” in Aomori

Fig.3 Lamprey in miso soup with welsh onion and soybean curd “*kaiyaki*” in Akita

Fig.5 Boiled lamprey with soy sauce (right) cooked frozen lamprey (left) in Aomori

Fig.5 Dried Arctic lamprey wrapped in straw (right) after drying (left) in Niigata

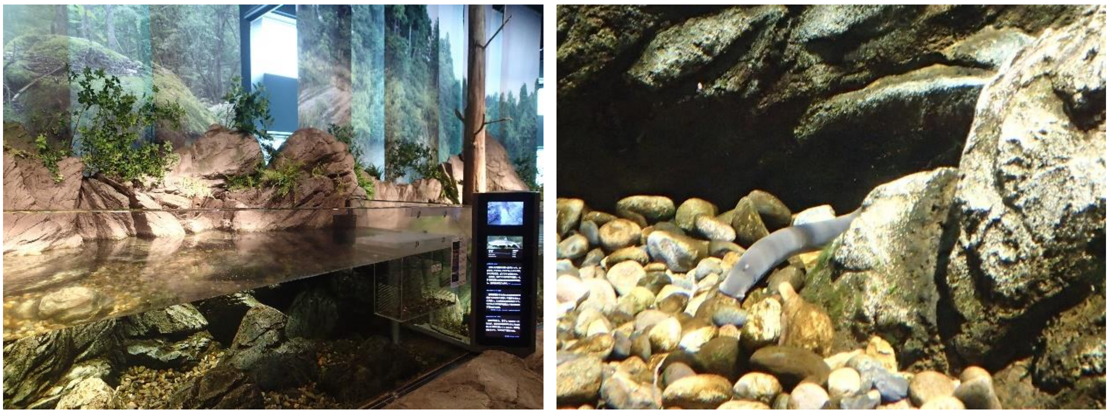

Fig.6 Exhibition of Adult Arctic lampreys at Niigata City Aquarium

Fig.7 Exhibition of Adult Arctic lampreys at Ishikawa Zoo

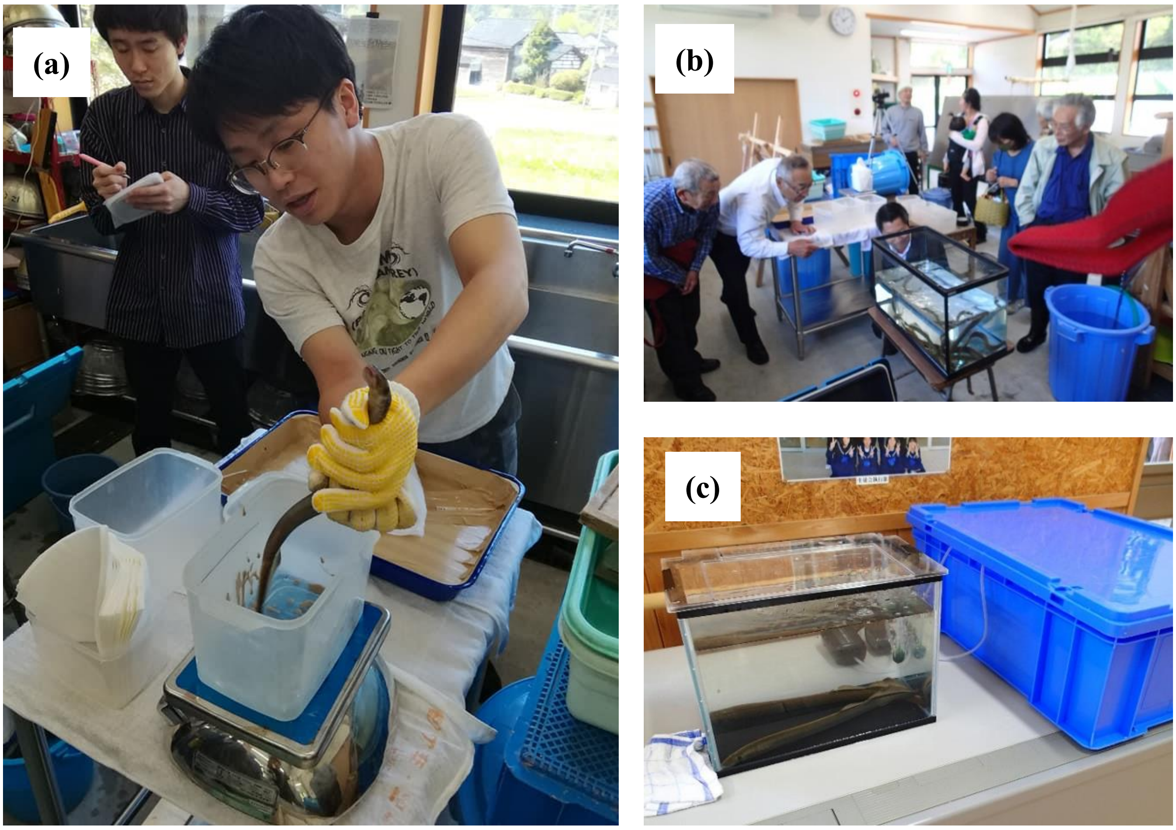

Fig.8 Artificial propagation event in Noto, Ishikawa (a,b), exhibition of adult Arctic lampreys and fertilized eggs at junior high school in Wajima, Ishikawa (c)

Fig.9 Educational evet at Wajima, Ishikawa, including the contents of demonstrating traditional fishing culture by local fisher (a), explaining the ecology and threats for Arctic lamprey (b), introducing the lamprey research in US (c), and releasing hatched larvae by the students (d).

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Reference

Aino S., Yodo T., Yoshioka M. (2018) Influence of a weir on the upward migration of ayu Plecoglossus altivelis altivelis in the Shonai River, Central Japan. Aquaculture Science 66(3):185-192

Almeida P, Arakawa H, Aronsuu K, Baker C, Blair SR, Beaulaton L, Belo A, Kitson J, Kucheryavyy A, Kynard B, Lucas M, Moser M, Potaka B, Romakkaniemi A, Staponkus R, Tamarapa S, Yanai S, Zhuang P (under review) Lamprey fisheries: history, trends and management. J Great Lakes Res.

Almeida P. R., Quintella B. R., Dias N. M. 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). In Aquatic Telemetry (pp. 1-8). Springer, Dordrecht.

Amundsen, P. A., J. Sánchez-Hernández. 2019. Feeding studies take guts–critical review and recommendations of methods for stomach contents analysis in fish. Journal of Fish Biology 95:1364–1373.

Anderson, E. C. 2012. Large-scale parentage inference with SNPs: an efficient algorithm for statistical confidence of parent pair allocations. Statistical Applications in Genetics and Molecular Biology 11:1544-6115.

Aoki, S. (2004): Check of multicollinearity (Tolerance and VIF). http://aoki2.si.gunma-u.ac.jp/R/tolerance.html (in Japanese). Accessed 14 June 2017.

Arakawa H, Ichion E, Nakano M, Yanai S (2019) Factors that Affect Arctic lampreys' Ascent Behavior on Fishway Weirs. J Rainwater Catchment Syst 25:15–21

Arakawa H, Shima Y, Yanai S (2018) Reginal culture for Arctic lamprey and its harvest change in rural rivers of Noto Peninsula, Ishikawa Prefecture, Japan. Departmental Bulletin Paper of Ishikawa Pref Univ 1:11–21 (In Japanese)

Arakawa H, Yanai S (2017) Autumn microhabitat for larvae of endangered Arctic lamprey (*Lethenteron japonicum*) in Noto Peninsula, Ishikawa Prefecture, Japan. Ecology and Civil Engineering, 20:11–24 (In Japanese)

Arakawa H, Yanai S (2018) Maturation and artificial propagation of Arctic lamprey *Lethenteron japonicum*. Report of the Noto Marine Center 24:29–39 (In Japanese)

Arakawa H, Yanai S (2020) Upper thermal tolerance of larval Arctic lamprey (*Lethenteron camtschaticum*). Ichthyol Res. doi: doi.org/10.1007/s10228-020-00757-

3

Arakawa H., Kishi D., Yanai S. (under review) Historical distribution of Arctic lamprey (*Lethenteron camtschaticum*) in Japanese rivers and its change estimated from fishery statistics and local ecological knowledge. Fisheries Science.

Arakawa H., Yanai S. 2019. Optimal sediment particle size and rearing method for hatched larval Arctic lamprey (*Lethenteron camtschaticum*). Report of the Noto Marine Center, 25: 9-18.

Arakawa, H., and R. T. Lampman. 2020. An experimental study to evaluate predation threats on two native larval lampreys in the Columbia River Basin, USA. Ecology of Freshwater Fish 29:611–622.

Araújo M. J., Silva S., Stratoudakis Y., Gonçalves M., Lopez R., Carneiro M., ... Antunes C. 2016. Sea lamprey fisheries in the Iberian Peninsula. Jawless fishes of the world, 2: 115-148.

Aronsuu, K. 2015. Lotic life stages of the European River lamprey (*Lampetra fluviatilis*): anthropogenic detriment and rehabilitation. Jyväskylä studies in biological and environmental science: 301.

Asplund C., Sodergren S. 1974. The spawning migration of River Lampreys (*Lampetra fluviatilis*) in the River Rickleå. Zoologisk Revy, 36: 111-119.

Aswani S., Lemahieu A., Sauer W. H. 2018. Global trends of local ecological knowledge and future implications. PLoS One, 13(4): e0195440.

Azzurro E, Moschella P, Maynou F (2011) Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. PLoS One. doi: doi.org/10.1371/journal.pone.0024885

Barron J. M., Hanson K. C., Headley R. R., Hawke K. A., Twibell R. G., Gannam A. L. 2020. Evaluation of effluent waste water from salmonid culture as a potential food and water supply for culturing larval Pacific lamprey *Entosphenus tridentatus*. Aquaculture, DOI: doi.org/10.1016/j.aquaculture.2019.734791

Beals, T., & Lampman, R. (2016). Yakima Subbasin larval lamprey distribution, occupancy, and index site monitoring report (2009-2015). Appendix C1 in Yakama Nation Pacific Lamprey Project 2015 Annual Progress Report. Project No. 2008-470-0070. U.S. Department of Energy, Bonneville Power Administration, Portland.

Beals, T., & Lampman, R. (2017). Wenatchee Subbasin larval lamprey monitoring report, 2016. Appendix C4 in Yakama Nation Pacific Lamprey Project 2016 Annual Progress Report. Project No. 2008-470-00. U.S. Department of Energy, Bonneville Power Administration, Portland.

Beamish, R. J. (1980). Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentate*) from the Pacific coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences, 37, 1906–1923.

Begossi, A., Salivonchyk, S., Lopes, P. F., Silvano, R. A. (2016). Fishers' knowledge on the coast of Brazil. Journal of ethnobiology and ethnomedicine, 12(1), 20.

Bender, M. G., Machado, G. R., de Azevedo Silva, P. J., Floeter, S. R., Monteiro-Netto, C., Luiz, O. J., Ferreira, C. E. (2014). Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. PLoS One, 9(10), e110332.

Berkes F., Colding J., Folke, C. 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecological applications, 10(5): 1251-1262.

Binder T. R., McLaughlin R. L., McDonald D. G. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. Transactions of the American Fisheries Society, 139(3): 700-712.

Brandenburg, W. H., and K. B. Gido. 1999. Predation by nonnative fish on native fishes in the San Juan River, New Mexico and Utah. The Southwestern Naturalist 44:392–394.

Boeker, C., Geist, J. (2016). Lampreys as ecosystem engineers: burrows of *Eudontomyzon* sp. and their impact on physical, chemical, and microbial properties in freshwater substrates. Hydrobiologia, 777(1), 171-181.

Boulêtreau, S., Carry, L., Meyer, E., Filloux, D., Menchi, O., Mataix, V., & Santoul, F. (2020). High predation of native sea lamprey during spawning migration. Scientific Reports, 10.

Brett JR (1952) Temperature Tolerance in Young Pacific Salmon,Genus Oncorhynchus. J Fish Res Board Can 9:265–323

Broström, G., & Holmberg, H. (2011). Generalized linear models with clustered data:

Fixed and random effects models. Computational Statistics and Data Analysis, 55, 3123-3134. https://doi.org/10.1016/j.csda.2011.06.011

Brown C, Burr J, Elkin K, Walker RJ (2005) Contemporary subsistence uses and population distribution of non-salmon fish in Grayling, Anvik, Shageluk, and Holy Cross. Alaska Department of Fish and Game, Juneau

Brumo, A. F. (2006). Spawning, larval recruitment, and early life survival of Pacific lampreys in the South Fork Coquille River, Oregon. Master's Thesis, Oregon State University, Corvallis, OR, USA

Buckland, A., R. Baker, N. Loneragan, and M. Sheaves. 2017. Standardising fish stomach content analysis: The importance of prey condition. Fisheries Research 196:126–140.

Burnham, K.P., Anderson, D.R. (2002): Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York, 487p.

Campbell, N. R., S. A. Harmon, and S. R. Narum. 2015. Genotyping-in-Thousands by sequencing (GT-seq): A cost effective SNP genotyping method based on custom amplicon sequencing. Molecular ecology resources 15: 855-867.

Campbell, N. R., S. A. Harmon, and S. R. Narum. 2015. Genotyping-in-Thousands by sequencing (GT-seq): A cost effective SNP genotyping method based on custom amplicon sequencing. Molecular ecology resources 15:855–867.

Carey, M. P., Sanderson, B. L., Friesen, T. A., Barnas, K. A., & Olden, J. D. (2011). Smallmouth bass in the Pacific Northwest: a threat to native species; a benefit for anglers. Reviews in Fisheries Science, 19, 305-315. https://doi.org/10.1080/10641262.2011.598584

Carreon-Martinez, L., T. B. Johnson, S. A. Ludsin, and D. D. Heath. 2011. Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. Journal of Fish Biology 78:1170–1182.

Carreon-Martinez, L., T. B. Johnson, S. A. Ludsin, and D. D. Heath. 2011. Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. ournal of Fish Biology 78:1170-1182.

Castelnaud, G. (2000) Fishing location, fishermen and production of migratory species fisheries in the French rivers. Bulletin Français de la Pêche et de la Pisciculture, (357-360), 439-460.

Chang, M. M., Zhang, J., & Miao, D. (2006). A lamprey from the Cretaceous Jehol biota of China. *Nature*, *441*(7096), 972-974.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333(6045), 1024-1026.

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893–905

Clemens BJ, Arakawa H, Baker C, Coghlan S, Kucheryavyy A, Lampman R, João Lança M, Mateus CS, Miller A, Nazari H, Pequeño G, Sutton TM, Yanai S (2020) Management of anadromous lampreys: Common threats, different approaches. Journal of Great Lakes Research.

Clemens BJ, Beamish RJ, Kelly CC, Docker MF, Jason BD, Gray AE, Hess JE, Jolley JC, Lampman RT, McIlraith BJ, Moser ML, Murauskas MG, Noakes DLG, Schaller HA, Schreck CB, Starcevich SJ, Streif B, van de Wetering SJ, Wade J, Weitkamp LA, Wyss LA (2017) Conservation challenges and research needs for Pacific Lamprey in the Columbia River Basin. Fisheries. doi: doi.org/10.1080/03632415.2017.1305857

Clemens BJ, Schreck CB, Sower SA, van de Wetering SJ (2016) The potential roles of river environments in selecting for streamand ocean-maturing Pacific Lamprey, *Entosphenus tridentatus* (Gairdner, 1836). In: Orlov AM, Beamish RJ (ed) Jawless fishes of the world, volume 2. Cambridge Scholars Publishing, New Castle upon Tyne. pp 299–322

Clemens BJ, Van De Wetering S, Kaufman J, Holt RA, Schreck CB (2009) Do summer temperatures trigger spring maturation in Pacific lamprey, *Entosphenus tridentatus*? Ecology of Freshwater Fish, 18:418–426

Clemens, B. J., Weitkamp, L., Siwicke, K., Wade, J., Harris, J., Hess, J., . . . & Orlov, A. M. (2019) Marine biology of the pacific lamprey Entosphenus tridentatus. Reviews in Fish Biology and Fisheries, 1-22. https://doi.org/10.1007/s11160-019-09578-8

Close D. A., Currens K. P., Jackson A., Wildbil, A. J., Hansen J., Bronson P., Aronsuu K. 2009. Lessons from the reintroduction of a noncharismatic, migratory fish: Pacific lamprey in the upper Umatilla River, Oregon. In American Fisheries Society Symposium, 72: 1-21.

Close D. A., Fitzpatrick M. S., Li H. W. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. Fisheries, 27(7): 19-25.

Close, D. A., Fitzpatrick, M., Li, H., Parker, B., Hatch, D., & James, G. (1995). Status report of the Pacific lamprey (Lampetra tridentata) in the Columbia River Basin. Report. Project No. DOE/BP-39067-1, U.S. Department of Energy, Bonneville Power Administration, Portland.

Cochran, P. A. (1986). The daily timing of lamprey attacks. Environmental Biology of Fishes, 16, 325-329. https://doi.org/10.1007/BF00842989

Cochran, P. A. (2009). Predation on lampreys. In L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish & P. B. Moyle (Eds.), Biology, management, and conservation of lampreys in North America (pp. 139-151). Bethesda, USA: American Fisheries Society.

Cohen, J., Cohen, P., West, S.G., Aiken, L.S. (2003): Applied multiple regression/correlation analysis for the behavioral sciences. 3rd ed. L. Erlbaum Associates, Mahwah, 703p.

Collis, K., Roby, D. D., Craig, D. P., Adamany, S., Adkins, J. Y., & Lyons, D. E. (2002). Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society, 131(3), 537-550.

Collins M, Knutti R, Arblaster J, Dufresne JL, Fichefet T, Friedlingstein P, Gao X, Gutowski WJ, Johns T, Krinner G, Shongwe M, Tebaldi C, Weaver AJ, Wehner M (2013) Long-term climate change: projections, commitments and irreversibility. In Climate Change 2013-The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1029-1136). Cambridge University Press.

Condit, R., & Le Boeuf, B. J. (1984). Feeding habits and feeding grounds of the northern elephant seal. Journal of Mammalogy, 65(2), 281-290.

Craig, S., Helfrich, L. A., Kuhn, D., & Schwarz, M. H. (2017). Understanding fish nutrition, feeds, and feeding. Publication. Virginia Cooperative Extension - Virginia Tech, Blacksburg, VA, USA.

CRITFC (Columbia River Inter-Tribal Fish Commission). 2011. Tribal Pacific lamprey restoration plan for the Columbia River Basin. Report. Columbia River Inter-Tribal Fish Commission, Portland, Oregon. Available: http://www.critfc.org/wp-content/uploads/2012/12/lamprey_plan.pdf.

Damasio, L. D. M. A., Lopes, P. F., Guariento, R. D., & Carvalho, A. R. (2015). Matching fishers' knowledge and landing data to overcome data missing in small-scale fisheries. PLoS One. doi: doi.org/10.1371/journal.pone.0133122

Dawson, H. A., Quintella, B. R., Almeida, P.R., Treble, A.J., & Jolley, J.C. (2015). Ecology of larval and metamorphosing lampreys. In M. F. Docker (Eds.), Lampreys: Biology, Conservation and Control, Fish & Fisheries (pp. 75–137). Dordrecht Germany: Springer Science+Business Media.

Derosier A. L., Jones M. L., Scribner K. T. 2007. Dispersal of sea lamprey larvae during early life: relevance for recruitment dynamics. Environmental Biology of Fishes, 78(3): 271-284.

Docker, M. F., & Potter, I. C. (2019). Life history evolution in lampreys: alternative migratory and feeding types. In: Docker MF (eds) Lampreys: biology, conservation and control. Springer, Dordrecht, pp 287–409

Docker, M. F., Hume, J. B., & Clemens, B. J. (2015). Introduction: a surfeit of lampreys. In: Docker MF (eds) Lampreys: biology, conservation and control. Springer, Dordrecht, pp 1–34

Dumbauld, B. R., Holden, D. L., & Langness, O. P. (2008). Do sturgeon limit burrowing shrimp populations in Pacific Northwest Estuaries?. Environmental biology of fishes, 83, 283–296. https://doi.org/10.1007/s10641-008-9333-y

Dunkle, M. R., R. T. Lampman, A. D. Jackson, and C. C. Caudill. 2020. Factors affecting the fate of Pacific lamprey carcasses and resource transport to riparian and stream macrohabitats. Freshwater Biology 65:1429–1439.

Ebersole JL, Liss WJ, Frissell CA (2003) Cold water patches in warm streams: physicochemical characteristics and the influence of shading. Journal of the American Water Resources Association, 39:355–368

Evans EC, Greenwood MT, Petts GE (1995) Thermal profiles within river beds. Hydrol Process 9:19–25

Evans, T. M., Janvier, P., & Docker, M. F. (2018). The evolution of lamprey

(*Petromyzontida*) life history and the origin of metamorphosis. Reviews in Fish Biology and Fisheries, 28(4), 825-838.

Fajfer, S., Meyers, L., Willman, G., Carpenter, T., & Hansen, M. J. (1999). Growth of juvenile lake sturgeon reared in tanks at three densities. North American Journal of Aquaculture, 61, 331-335. https://doi.org/10.1577/1548-8454(1999)061<0331:GOJLSR>2.0.CO;2

Ferguson RG (1958) The Preferred Temperature of Fish and their Midsummer Distribution in Temperate Lakes and Streams. J Fish Res Board Can 15:607–624

Fisheries Bureau, the Department of Agriculture and Forestry (1930) Kasen Gyogyo Volume 1 (Data for 1927). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Fisheries Bureau, the Department of Agriculture and Forestry (1931) Kasen Gyogyo Volume 2 (Data for 1928). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Fisheries Bureau, the Department of Agriculture and Forestry (1932) Kasen Gyogyo Volume 3 (Data for 1929). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Fisheries Bureau, the Department of Agriculture and Forestry (1933) Kasen Gyogyo Volume 4 (Data for 1930). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Fisheries Bureau, the Department of Agriculture and Forestry (1934) Kasen Gyogyo Volume 5 (Data for 1931). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Fisheries Bureau, the Department of Agriculture and Forestry (1937) Kasen Gyogyo Volume 6 (Data for 1932). Fisheries Bureau, the Department of Agriculture and Forestry, Tokyo (in Japanese)

Forey, P., and P. Janvier. 1993. Agnathans and the origin of jawed vertebrates. Nature 361:129–134.

Foulds W. L., Lucas M. C. 2013. Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*). Ecological Engineering, 58: 423-433.

French III, J. R. 1993. How well can fishes prey on zebra mussels in eastern North America? Fisheries 18:13–19.

Fritts, A. L., & Pearsons, T. N. (2004). Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. Transactions of the American Fisheries Society, 133, 880–895. https://doi.org/10.1577/T03-003.1

Fritts, A. L., & Pearsons, T. N. (2006). Effects of predation by nonnative smallmouth bass on native salmonid prey: The role of predator and prey size. Transactions of the American Fisheries Society, 135, 853–860. https://doi.org/10.1577/T05-014.1

Fukushima M., Kameyama S., Kaneko M., Nakao K., Ashley Steel E. 2007. Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan. Freshwater Biology, 52(8): 1511-1524.

Gess, R., M. I. Coates, and B. S. Rubidge. 2006. A lamprey from the Denovian period of South Africa. Nature 443:981–984.

Gillen, A. L., Stein, R. A., & Carline, R. F. (1981). Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. Transactions of the American Fisheries Society, 110, 197–209. https://doi.org/10.1577/1548-8659(1981)110<197:PBPTMO>2.0.CO;2

Goertler PA, Shakya AW, Seesholtz AM, Schreier BM, Matica SZ, Holley KS (2020) Lamprey (*Entosphenus* sp. and *Lampetra* sp.) estuarine occupancy is regionally variable and constrained by temperature. J Fish Biol, 96:527–532

Goodwin, C. E., Dick, J. T. A., Rogowski, D. L., Elwood, R. W. (2008). Lamprey (*Lampetra fluviatilis* and *Lampetra planeri*) ammocoete habitat associations at regional, catchment and microhabitat scales in Northern Ireland. Ecology of Freshwater Fish, 17(4), 542-553.

Goto A (1997) Conservation of the Natural Environments and Fish Biodiversity in Japanese Rivers. Assoc Wildlife Hum Soc 2:127–133 (in Japanese)

Gunckel, S. L., Jones, K. K., Jacobs, S. E. (2009). Spawning distribution and habitat use of adult Pacific and western brook lampreys in Smith River, Oregon. In American Fisheries Society Symposium, 72:173-189.

Hambright, K. D. (1991). Experimental analysis of prey selection by largemouth bass: Role of predator mouth width and prey body depth. Transactions of the American

Hamilton JB, Curtis GL, Snedaker SM, White DK (2005) Distribution of anadromous fishes in the upper Klamath River watershed prior to hydropower dams—a synthesis of the historical evidence. Fisheries 30:10–20

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of American Fisheries 117:500–508.

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of American Fisheries 117:500–508.

Hardisty M. W., and I. C. Potter. 1971. The general biology of adult lampreys. Pages 127–206 in M. W. Hardisty and I. C. Potter, editors. The biology of lampreys. Academic Press, New York

Hardisty MW, Potter IC (1971) The behaviour, ecology and growth of larval lampreys. In: Hardisty MW, Potter IC (ed) The Biology of Lampreys Volume 1. Academic Press, London. pp 85–125

Hardisty, M. W. (1944). The life history and growth of the brook lamprey (*Lampetra planeri*). Journal of Animal Ecology, 13, 110–122. https://www.jstor.org/stable/1444

Hardisty, M. W. 1954. Permeability to water of the lamprey integument. Nature 174:360–361.

Hasegawa, K., Adams, R., & Maekawa, K. (2007). Predation on native lamprey species by nonnative brown trout in Hokkaido, Japan. Aquaculture Science, 55, 651–52. https://doi.org/10.11233/aquaculturesci1953.55.651

Hatano M., Takahashi K., Takama S., Nakajima T. 1987. Sensory Evaluation of Fresh Quality of Fall Chum Salmon. Hokkaido University Collection of Scholarly and Academic Papers, 38(3): 311-321.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. Conservation Biology, 22, 534-543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22:534–543.

Hess, J. E., J. J. Smith, N. Timoshevskaya, C. Baker, C. C. Caudill, D. Graves, M. L. Keefer, A. P. Kinziger, M. L. Moser, L. L. Porter, G. Silver, S. L. Whitlock, S. R. Narum. 2020b. Genomic islands of divergence infer a phenotypic landscape in Pacific lamprey. Molecular Ecology 29:3841-3856.

Hess, J. E., M. W. Ackerman, J. K. Fryer, D. J. Hasselman, C. A. Steele, J. J. Stephenson, J. M. Whiteaker, S. R. Narum. 2016. Differential adult migration-timing and stock-specific abundance of steelhead in mixed stock assemblages. ICES Journal of Marine Science 73: 2606–2615.

Hess, J. E., N. R. Campbell, M. F. Docker, C. Baker, A. Jackson, R. Lampman, B. McIlraith, M. L. Moser, D. P. Statler, W. P. Young, A. J. Wildbill, and S. R. Narum. 2014. Use of genotyping by sequencing data to develop a high-throughput and multifunctional SNP panel for conservation applications in Pacific lamprey. Molecular Ecology Resources 15: 187-202.

Hess, J. E., R. L. Paradis, M. L. Moser, L. A. Weitkamp, T. A. Delomas, S. R. Narum. 2020a. Robust recolonization of Pacific lamprey following dam removals. Transactions of the American Fisheries Society. DOI: 10.1002/tafs.10273

Higashi, H., Hirano, S., Yamada, J., Kikuchi, R. (1958). Vitamin contents in the lamprey, Entosphenus japonicus Martens. The Journal of vitaminology, 4(2), 88-99.

Hirose T, Yanagida T (1992) Historical Development of Concrete Dams. Journal of Japan Society of Civil Engineers, 451:13–19 (in Japanese)

Hokkaido Government Ishikari Sub-prefectural Bureau 2007. Arctic lamprey in Ishikari River, http://www.ishikari.pref.hokkaido.lg.jp/ss/sis/grp/yatume2.pdf, 20 May 2019.

Holbrook C. M., Bergstedt R., Adams N. S., Hatton T. W., McLaughlin R. L. 2015. Fine-scale pathways used by adult sea lampreys during riverine spawning migrations. Transactions of the American Fisheries Society, 144(3): 549-562.

Holmes JA, Lin P (1994) Thermal niche of larval sea lamprey, Petromyzon marinus. Canadian Journal of Fisheries and Aquatic Sciences, 51:253–262

Howick, G. L., & O'Brien, W. J. (1983). Piscivorous feeding behavior of largemouth bass: an experimental analysis. Transactions of the American Fisheries Society, 112, 508-516. https://doi.org/10.1577/1548-8659(1983)112<508:PFBOLB>2.0.CO;2

Hubbs, C.L., and Potter I.C. (1971): Distribution, phylogeny and taxonomy. In “The

Biology of Lampreys vol. 1" (Hardisty, M.W., and Potter, I.C., eds), pp. 1-65, Academic Press, London.

Huntington HP (2000) Using traditional ecological knowledge in science: methods and applications. Ecol Appl 10:1270–1274

Ichion, E., Maeda, K., Yamamoto, S., Nakano, S., Chono, S., and Fujihara, Y. (2015): Factors that affect ascending rate in weir of upstream-inclined weir fishway. Journal of Rainwater Catchment Systems 20 (2), pp. 85-92, (in Japanese).

Inamatsu (1982) Denryoku Doboku no Rekishi – Kaku Kasen Suiryoku Kaihatu no Hensen (in Japanese). Papers of the Research Meeting on the Civil Engineering History in Japan 2:154–164 (in Japanese)

Hirano, Y., Kidera, N., Kondo, N. I., & Nishihiro, J. (2020). Habitat characteristics and size structure in a population of an endangered lamprey, *Lethenteron* sp. N, in an urbanized area of Japan. Ichthyological Research, 1-7.

Hogg, R. S., Coghlan Jr, S. M., Zydlewski, J., Simon, K. S. (2014). Anadromous sea lampreys (*Petromyzon marinus*) are ecosystem engineers in a spawning tributary. Freshwater biology, 59(6), 1294-1307.

Inui, R., Akamatsu, Y., Hiraki, R., Takemura S. (2016) Potential distribution of Willows in western Japan.-Toward suitable management of forestation in rivers-. Doboku Gakkai B1, 72(4):1051-1056

Inuzuka K. (2003) Mogamigawa no dentou gyorou. Mogamigawa bunka kenkyu, 1:43-58.

Irvine, J. R., & Northcote, T. G. (1983). Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Canadian journal of fisheries and aquatic sciences, 40, 1745-1749. https://doi.org/10.1139/f83-202

ISAB (Independent Scientific Advisory Board). (2008). Non-native species impacts on native salmonids in the Columbia River Basin. Council Document No. ISAB 2008-4. ISAB, Portland.

Itakura, H., Wakiya, R., Gollock, M., & Kaifu, K. (2020). Anguillid eels as a surrogate species for conservation of freshwater biodiversity in Japan. Scientific Reports, 10(1), 1-12.

Janvier, P. (1996) Early Vertebrates. Clarendon, Oxford, UK.

Japan Fisheries Resource Conservation Association (2005): Criteria of water quality of fisheries (2005 version). http://www.kanhokyo.or.jp/keieinet/1_jouhou/1148_suisan_yousui_kijun.html . Accessed 19 February 2019.

Jellyman D. J., Glova G. J., Sykes J. R. E. 2002. Movements and habitats of adult lamprey (*Geotria australis*) in two New Zealand waterways. New Zealand Journal of Marine and Freshwater Research, 36(1): 53-65.

Jinguji H., Kondo T., Sawata A., Mori S. (1999) Habitat conditions and preservation of the Ninespine Stickleback, Pungitius pungitius in small springs. Ecological Civil of Engineering, 2(2): 191-198.

Johannes R. E., Freeman M. M., Hamilton R. J. 2000. Ignore fishers' knowledge and miss the boat. Fish and Fisheries, 1(3): 257-271.

Johnson, N. S., Buchinger, T. J., Li, W. (2015). Reproductive ecology of lampreys. In Lampreys: biology, conservation and control (pp. 265-303). Springer, Dordrecht.

Katano O, Hakoyama H, Matsuzaki SIS (2015) Japanese inland fisheries and aquaculture: status and trends. In Craig JF (eds) Freshwater Fisheries Ecology. Wiley-Blackwell, New York City, pp 231–240

Katano O, Matsuzaki SIS (2012) Biodiversity of freshwater fish in Japan in relation to inland fisheries. In Nakano S et al. (eds) The Biodiversity Observation Network in the Asia-Pacific Region. Springer, Tokyo, pp 431–444

Kataoka T, Hosoya H, Emura K (1980) Study on the Propagation of Lampreys , *Entosphenus japonicus* (MARTENs)-I. Niigata Prefecture Inland Fisheries Experimental Station, Niigata (in Japanese)

Kataoka, T. (1985): Study on the Propagation of Lampreys, *Entosphenus japonicus* (MARTENs)-IV. Scientific reports of the Nigata Prefecture Freshwater Fisheries Research Institute, 12: pp.23-28, (in Japanese).

Kaucka, M., and I. Adameyko. 2019. Evolution and development of the cartilaginous skull: From a lancelet towards a human face. Seminars in Cell and Developmental Biology 91: 2-12.

Kaucka, M., and I. Adameyko. 2019. Evolution and development of the cartilaginous skull: From a lancelet towards a human face. Seminars in Cell and Developmental Biology 91: 2–12.

Kawanabe H, Mizuno N (1989) Freshwater fishes of Japan. Yama to Keikoku-sha, Tokyo (In Japanese)

Kawanabe H, Mizuno N (2001) Freshwater fishes of Japan. Yama to Keikoku sha, Tokyo (in Japanese)

Kawanishi R, Inoue M (2018) Hyporheic zone as a fish habitat: ecological significance of vertical hydrological connectivity. Journal of Groundwater Hydrology, 60:157–167

Keast, A., & Webb, D. (1966). Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. Journal of the Fisheries Research Board of Canada, 23, 1845–74. https://doi.org/10.1139/f66-175

Keefer M. L., Caudill C. C., Clabough T. S., Jepson M. A., Johnson E. L., Peery C. A., ... Moser M. L. (2013). Fishway passage bottleneck identification and prioritization: a case study of Pacific lamprey at Bonneville Dam. Canadian Journal of Fisheries and Aquatic Sciences, 70(10): 1551-1565.

Keefer M. L., Peery,C. A., Lee S. R., Daigle W. R., Johnson E. L., Moser M. L. 2011. Behaviour of adult Pacific lamprey in near-field flow and fishway design experiments. Fisheries Management and Ecology, 18(3): 177-189.

Keefer, M.L., Boggs, C.T., Peery, C.A., and Caudill, C.C. (2012): Factors affecting dam passage and upstream distribution of adult Pacific lamprey in the interior Columbia River basin. Ecology of Freshwater Fish 22(1), pp. 1-10.

Keefer, M.L., Daigle, W.R., and Peery, C.A. (2010): Testing adult pacific lamprey performance at structural challenges in fishways. North American Journal of Fisheries Management 30(2), pp. 376-385.

Kemp, P. S., Russon, I. J., Vowles, A. S., and Lucas, M. C. (2011): The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. River Research and Applications 27(4), pp. 488-498.

Kim S, Kang S, Kim JK, Bang M (2017) Environmental variability and chum salmon production at the northwestern Pacific Ocean. Ocean Science Journal, 52(4), 549–562.

Kirk, M. A., Caudill, C. C., Johnson, E. L., Keefer, M. L., and Clabough, T. S. (2015):

Characterization of adult Pacific lamprey swimming behavior in relation to environmental conditions within large dam fishways. Transactions of the American Fisheries Society 144 (5), pp. 998-1012.

Kishi D, Tokuhara T (2019) Distribution of anadromous red-spotted masu salmon *Oncorhynchus masou ishikawae* from 1927 to 1931 evaluated from data published in “River Fishery” by the Fisheries Agency, Ministry of Agriculture and Forestry, Japan. Japanese Journal of Ichthyology. DOI: doi.org/10.11369/jji.19-011 (in Japanese with English abstract)

Kitanishi S, Yamamoto T, Edo K, Higashi S (2012) Influences of habitat fragmentation by damming on the genetic structure of masu salmon populations in Hokkaido, Japan. Conservation genetics, 13(4), 1017–1026.

Kitano F, Nakano S, Maekawa K, Ono Y (1995) Effect of stream temperatures on longitudinal distribution of fluvial Dolly Varden and potential habitat loss due to global warming. Wildl Conserv Jpn 1:1–11 (In Japanese)

Kline, J. L., & Wood, B. M. (1996). Food habits and diet selectivity of the brown bullhead. Journal of Freshwater Ecology, 11, 145–51. https://doi.org/10.1080/02705060.1996.9663473

Kostow, K. (2002). Oregon lampreys: natural history, status, and analysis of management issues. Salem, USA: Fish Division, Oregon Department of Fish and Wildlife.

Kubo, T. (2012): Statistical modeling introductory guide for data analyses—generalized linear model, hierarchical Bayesian model, and MCMC. Iwanami Shoten, Tokyo, 272p, (in Japanese).

Kometani K. (1996) Kiki kaki aomorikennai no naisuimen gyogyou.

Kuratani, S., Oisi, Y., & Ota, K. G. (2016). Evolution of the vertebrate cranium: viewed from hagfish developmental studies. Zoological science, 33(3), 229-238.

Lampman R., Maine A. N., Moser M. L., Arakawa H., Nease F. B. 2020. Lamprey Aquaculture Successes and Failures: A Path to Production for Control and Conservation. Journal of Great Lakes Research.

Lampman, R. 2018. Columbia Basin Lamprey Identification Guide. In Yakama Nation Pacific Lamprey Project 2018 annual report (Appendices 4.3 / L1, Cooperative Agreement No. R15AC00044 / Project No. 2008-470-00). Prepared for the U.S. Dept.

of Interior, Bureau of Reclamation, Boise, ID, and U.S. Dept. of Energy, Bonneville Power Administration, Portland, OR, 3 pp. Available: https://www.fws.gov/pacificlamprey/Documents/ Identification%20Guides/ 2017%20Lamprey%20Identification%20Guide%20Final.pdf.

Lampman, R., M. Moser, A. Jackson, R. Rose, A. Gannam, and J. Barron. 2016. Developing techniques for artificial propagation and early rearing of Pacific lamprey (*Entosphenus tridentatus*) for species recovery. Pages 160-194 in A. Orlov and R. Beamish, editors.Jawless Fishes of the World, Vol. 2. Cambridge Scholars Publishing, Newcastle upon Tyne, U.K.

Lethbridge, R. C., & Potter, I. C. (1980). Quantitative studies on the skin of the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Journal of morphology, 164, 39-46. https://doi.org/10.1002/jmor.1051640104

Levin, B. O. R. I. S., Ermakov, A. N. D. R. E. Y., Ermakov, O., Levina, M., Sarycheva, O., & Sarychev, V. (2016). Chapter Three Ukrainian Brook Lamprey *Eudontomyzon mariae* (Berg): phylogenetic position, genetic diversity, distribution. Jawless fishes of the world, 1, 58-82.

Lewis, S. V., & Potter, I. C. (1977). Oxygen consumption during the metamorphosis of the parasitic lamprey, *Lampetra fluviatilis* (L.) and its non-parasitic derivative, *Lampetra planeri* (Bloch). Journal of Experimental Biology, 69, 187-198.

Liedtke, T. L., Lampman, R. T., Deng, D. Z., Beals, T. E., Porter, M. S., Hansen, A. C., . . . Monk, P. (2019). Movements of juvenile Pacific Lamprey (*Entosphenus tridentatus*) in the Yakima and Columbia Rivers, Washington, 2018—A pilot study using acoustic telemetry. Report. Project No. 2019-1058. US Geological Survey, Reston.

Lopes P. F. M, Verba J. T., Begossi A., Pennino M. G. 2019. Predicting species distribution from fishers' local ecological knowledge: a new alternative for data-poor management. Can J Fish Aquatic Sci 76:1423-1431

Lotze HK, Worm B (2009) Historical baselines for large marine animals. Trends Ecol Evol 24:254–262

Lucas, M. C., Bubb, D. H., JANG, M. H., Ha, K., & Masters, J. E. (2009). Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. Freshwater Biology, 54(3), 621-634.

Luzier, C. W., H. A. Schaller, J. K. Brostrom, C. Cook-Tabor, D. H. Goodman, R. D. Nelle, K. Ostrand, and B. Strief. (2011). Pacific Lamprey (Entosphenus tridentatus) assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, Oregon.

Lynch AJ, Cooke SJ, Deines AM, Bower SD, Bunnell DB, Cowx IG, Nguyen VM, Nohner, Kaviphone Phouthavong K, Riley B, Rogers MW, Taylor WW, Woelmer W, Youn S, Beard Jr. TD (2016) The social, economic, and environmental importance of inland fish and fisheries. Environ Rev 24:115–121

Maitland PS, Renaud CB, Quintella BR, Close DA, Docker MF (2015) Conservation of native lampreys. In Docker MF (ed) Lampreys: biology, conservation and control. Springer, Dordrecht. pp 375–428

Mallatt, J. (1983). Laboratory growth of larval lampreys (Lampetra (*Entosphenus*) *tridentate Richardson*) at different food concentrations and animal densities. Journal of Fish Biology, 22, 293-301. https://doi.org/10.1111/j.1095-8649.1983.tb04753.x

Malmqvist, B. (1980). Habitat selection of larval brook lampreys (*Lampetra Planeri, Bloch*) in a South Swedish stream. Oecologia, 45, 35–38. https://doi.org/10.1007/BF00346704

Mateus, C.S., Rodríguez-Muñoz, R., Quintella, B.R., Alves, M.J., and Almeida, P.R. (2012): Lampreys of the Iberian Peninsula: distribution, population status and conservation. Endangered Species Research 16(2), pp. 183-198.

McGree, M. (2005). Timing and stages of metamorphosis in Pacific Lamprey (*Lampetra tridentata*). Master's Thesis, University of Portland, Portland, OR, USA.

McCallum, M. L. (2015). Vertebrate biodiversity losses point to a sixth mass extinction. Biodiversity and Conservation, 24(10), 2497-2519.

Meeuwig MH, Bayer JM, Seelye JG (2005) Effects of temperature on survival and development of early life stage Pacific and western brook lampreys. Trans Am Fish Soc 134:19–27

Meeuwig, M. H., and J. M. Bayer. 2005. Morphology and aging precision of statoliths from larvae of Columbia River Basin lampreys. North American Journal of Fisheries Management 25:38–48.

Meisner JD (1990) Effect of climatic warming on the southern margins of the native range of brook trout, Salvelinus fontinalis. Can J Fish Aquat Sci 47:1065–1070

MEXT (Ministry of Education, Culture, Sports, Science and Technology), 2015. Food Composition Database, Fish, Mollusks and Crustaceans/Fish/lamprey, raw. MEXT. Tokyo, Japan

Michel, C. J., Smith, J. M., Demetras, N. J., Huff, D. D., and Hayes, S. A. 2018. Non-native fish predator density and molecular-based diet estimates suggest differing impacts of predator species on juvenile salmon in the San Joaquin River, California. San Francisco Estuary and Watershed Science 16. DOI: 10.15447/sfews.2018v16iss4art3.

Miller, R. R., Williams, J. D., & Williams, J. E. (1989). Extinctions of North American fishes during the past century. Fisheries, 14(6), 22-38.

Ministry of Land (2020) River Environmental Database. Electronic version, updated 15 January 2020. http://www.nilim.go.jp/lab/fbg/ksnkankyo/. Accessed 27 January 2020

Ministry of the Environment 2007. Red Lists/red data books of fishes, https://www.env.go.jp/press/files/jp/9944.pdf, 15 September 2019

Moore, J.W., and Mallatt, J.M. (1980): Feeding of larval lamprey. Canadian Journal of Fisheries and Aquatic Sciences, 37(11), pp. 1658-1664.

Morita K, Yamamoto S (2002) Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conserv Biol 16:1318–1323

Morita K, Yamamoto S, Hoshino N (2000) Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. Can J Fish Aquatic Sci 57:1300–1306

Moser, M. L., Almeida, P. R., King, J. J., & Pereira, E. (2020). Passage and freshwater habitat requirements of anadromous lampreys: Considerations for conservation and control. Journal of Great Lakes Research.

Moser M. L., Matter A. L., Stuehrenberg L. C., & Bjornn T. C. 2002. Use of an extensive radio receiver network to document Pacific lamprey (Lampetra tridentata) entrance efficiency at fishways in the Lower Columbia River, USA. In Aquatic Telemetry (pp. 45-53). Springer, Dordrecht.

Moser, M. L., Jackson, A. D., Lucas, M. C., & Mueller, R. P. (2015b). Behavior and potential threats to survival of migrating lamprey larvae and macrophthalmia. Reviews in Fish Biology and Fisheries, 25, 103-116. https://doi.org/10.1007/s11160-

014-9372-8

Moser, M. L., Ogden, D. A., Cummings, D. L., and Peery, C. A. (2006): Development and Evaluation of a Lamprey Passage Structure in the Bradford Island Auxiliary Water Supply Channel, Bonneville Dam, 2004. Report of research to Portland District U.S. Army Corps of Engineers, pp. 1-27.

Moser, M.L., Keefer, M.L., Pennington, H.T., Ogden, D.A., and Simonson, J.E. (2011): Development of Pacific lamprey fishways at a hydropower dam. Fisheries Management and Ecology 18(3), pp. 190-200.

Moser, M.L., Ocker, P.A., Stuehrenberg, L.C., and Bjornn, T.C. (2002): Passage Efficiency of Adult Pacific Lampreys at Hydropower Dams on the Lower Columbia River, USA. Transactions of the American Fisheries Society 131(5), pp. 956-965.

Mukai T., Ikeya K., Koya Y., Onaka T., Takagi M., Tsukahara K., Teramachi S., Yoshimura T. 2011. Distribution of two cryptic species of *Lethenteron* lamprey in Gifu Prefecture, Japan. Bulletin of the Biogeographical Society of Japan 66:203–209.

Murano N, Yagi C, Sawada T, Nagatsu M, Kojima E (2008) Japanese Lamprey *Lethenteron japonicum* in the Ishikari River : Field work and the creation of a supplemental guide book. Bulletin Paper of Rakunou Gakuen Univ 32:183–220 (in Japanese)

Myllynen, K., Ojutkangas, E., and Nikinmaa, M. (1997): River Water with High Iron Concentration and Low pH Causes Mortality of Lamprey Roe and Newly Hatched Larvae. Ecotoxicology and Environmental Safety 36(1), pp. 43-48.

Nagayama I (1994) Dam. Concrete Journal 32:6–10 (in Japanese)

Nakamoto, R. J., and B. C. Harvey. 2003. Spatial, seasonal, and size-dependent variation in the diet of Sacramento pikeminnow in the Eel River, northwestern California. California Fish and Game 89:30–45.

Nakamura T (2017) Annual changes and predictions of the membership of the inland fishery cooperatives in Japan. Aquac Sci 65:97–105 (in Japanese with English abstract)

Nakano S, Kitano F, Maekawa K (1996) Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. Freshw Bio 36:711–722

Namiki H (2014) Testing methods for industrial wastewater JIS K 0102:2013. Japanese Standards Association, Tokyo (In Japanese)

Nashimoto K., Sato O. 1985. Lamprey Fish pots used in the Ishikari River. Bulletin of the Faculty of Fisheries Hokkaido University, 36(1): 28-34.

Natsumeda T, Tsuruta T, Iguchi K (2010) An evaluation of the ecological features of endangered freshwater fish commonly distributed in Japan. Nippon Suissan Gakkaishi 76:169–184 (in Japanese with English abstract)

Nelson J. S. (2006) Fishes of the world, 4th edition. Wiley Hoboken, USA.

New, M.B. (1987). Feeds and feeding of fish and shrimp - a manual on the preparation and presentation of compound feeds for shrimp and fish in aquaculture. Rome, Italy: Food and Agriculture Organization of the United Nations and United Nations Environment Programme.

O' Rouke, P. M. (2014). Diet composition of wild brown trout and stocked rainbow trout in a coldwater tailwater fishery in North Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies, 1, 83–88. Retrieved from http://www.seafwa.org/13ORouke_83-88.pdf#search='Diet+composition+of+wild+brown+trout+and+stocked+rainbow+trout+in+a+coldwater+tailwater+fishery+in+North+Georgia.'

ODFW (Oregon Department of Fish and Wildlife). (2019). Coastal, Columbia, and Snake Conservation Plan for Lampreys in Oregon. Retrieved from https://www.dfw.state.or.us/agency/commission/minutes/19/12_Dec/H/Attachment%204_Conservation%20Plan%20for%20Lampreys.pdf

Oisi, Y., Ota, K. G., Kuraku, S., Fujimoto, S., & Kuratani, S. (2013). Craniofacial development of hagfishes and the evolution of vertebrates. Nature, 493(7431), 175-180.

Olsson P, Folke C (2001) Local ecological knowledge and institutional dynamics for ecosystem management: a study of Lake Racken watershed, Sweden. Ecosystems 4:85-104

Orlov A. M., Baitalyuk A. A., Pelenev D. V. 2014. Distribution and size composition of the Arctic lamprey *Lethenteron camtschaticum* in the North Pacific. Oceanology, 54(2): 180-194.

Orr, A. J., Banks, A. S., Mellman, S., Huber, H. R., DeLong, R. L., Brown, R. F. (2004). Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids. Fishery Bulletin, 102(1), 108-117.

Pacific Lamprey Technical Workgroup. (2017): Practical guidelines for incorporating adult Pacific lamprey passage

Pauly D (1995). Anecdotes and the shifting baseline syndrome of fisheries. Trends in ecology & evolution 10:430

Petersen RS (2009) Yurok and Karuk traditional ecological knowledge: insights into Pacific lamprey populations of the lower Klamath Basin. In Brown LR et al. (eds) Biology, management, and conservation of lampreys in North America. American Fisheries Society, Bethesda, pp 1–39

Petersen, R. S. 2006. The role of traditional ecological knowledge in understanding a species and river system at risk: Pacific lamprey in the lower Klamath basin. Master thesis of Oregon State University.

Pfeiffer, W., & Pletcher, T. F. (1964). Club cells and granular cells in the skin of lamprey. Journal of the Fisheries Board of Canada, 21, 1083–1088. https://doi.org/10.1139/f64-098

Pflug, D. E., & Pauley, G. B. (1984). Biology of smallmouth bass (*Micropterus Dolomieui*) in Lake Sammamish, Washington. Northwest Science, 58, 118–130. Retrieved from http://www.mercergov.org/files/21%20-%20Biology%20of%20Smallmouth%20Bass.pdf#search='Biology+of+smallmouth+bass+%28Micropterus+Dolomieu%29+in+Lake+Sammamish%2C+Washington'

Phillips, S. J., Anderson, R. P., Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. Ecological modelling, 190(3-4), 231-259.

Pletcher, F. T. (1963). The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. Doctoral dissertation, University of British Columbia, Vancouver, Canada.

Porter, R. (2011). Report on the predation index, predator control fisheries, and program evaluation for the Columbia River Basin experimental Northern Pikeminnow management program. 2011 Annual report. Project No. 1990-077-00. U.S. Department of Energy, Bonneville Power Administration, Portland.

Porter, R. 2013. Report on the predation index, predator control fisheries, and program evaluation for the Columbia River Basin experimental Northern Pikeminnow management program. 2012 Annual Report prepared in cooperation with Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife for the U.S. Department of Energy, Bonneville Power Administration, Project #1990-077-00, Portland, Oregon.

Potter IC, Beamish FWH. (1975) Lethal Temperatures in Ammocoetes of Four Species of Lampreys. Acta Zool 56:85–91

Potter IC, Hilliard RW, Bradley JS, McKay RJ (1986) The influence of environmental variables on the density of larval lampreys in different seasons. Oecol 70:433–440

Potter, I. C. (1980). Ecology of larval and metamorphosing lampreys. Canadian Journal of Fisheries and Aquatic Sciences, 37, 1641-1657. https://doi.org/10.1139/f80-212

Potter, I.C., and Hilliard, R.W. (1987): A proposal for the functional and phylogenetic significance of differences in the dentition of lampreys (*Agnatha: Petromyzontiformes*). Journal of Zoology 212(4), pp. 713-737.

Radosavljevic, A., Anderson, R. P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of biogeography, 41(4), 629-643.

Rahel, F. J., Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. Conservation Biology, 22, 521-533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533.

R Development Core Team (2014): R: A language and environment for statistical computing. Vienna, Austria.

Rees SE, Rodwell LD, Searle S, Bell A (2013) Identifying the issues and options for managing the social impacts of Marine Protected Areas on a small fishing community. Fish Res 146:51-58

Reid, S. B., Goodman, D. H. (2016). Pacific Lamprey in coastal drainages of California:

occupancy patterns and contraction of the southern range. Transactions of the American Fisheries Society, 145(4), 703-711.

Reinhardt, U.G., Eidietis, L., Friedl, S.E., and Moser, M.L. (2008): Pacific lamprey climbing behavior. Canadian Journal of Zoology 86, pp. 1264-1272.

Renaud C. B. (2011) Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. FAO Species Cat Fish Purp 5, FAO, Rome

Rieman BE, Chandler GL (1999) Empirical evaluation of temperature effects on bull trout distribution in the Northwest. Final report. U.S. Forest Service, Rocky Mountain Research Station, Boise, Idaho

Russon, I. J., Kemp, P. S., & Lucas, M. C. (2011). Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. Fisheries Management and Ecology, 18(3), 201-210.

Ryan PA (1991) Environmental effects of sediment on New Zealand streams: a review. New Zeal J Mar Fresh 25:207–221

Sakaguchi, S. O., S. Shimamura, Y. Shimizu, G. Ogawa, Y. Yamada, K. Shimizu,... and K. Takishita. 2017. Comparison of morphological and DNA-based techniques for stomach content analyses in juvenile chum salmon Oncorhynchus keta: a case study on diet richness of juvenile fishes. Fisheries science 83:47-56.

Sakai K., Yamazaki Y. (2011) Distribution of two cryptic species of lampreys, *Lethenteron* sp. (*Lethenteron* sp. N) and *Lethenteron* sp. 2 (*Lethenteron* sp. S), at the Noto Peninsula, Ishikawa Prefecture, based on the mitochondrial DNA analysis. Report of the Noto Marine Center, 17: 1-6.

Satake F (2000) Nihon no Tansuigyo – Sono Daihyousyu to Syokuyou no Rekisi. Food Science Journal 268:18–30 (in Japanese)

Savvaitova K. A., Pavlov D. S., Kuzishchin K. V., Gruzdeva M. A., Kucheryavyi A. V. 2007. Ecological analogies in the Pacific lamprey *Lethenteron camtschaticum* and the mykiss P*arasalmo mykiss* in Kamchatka. Journal of Ichthyology, 47(5): 341-347.

Schlosser IJ (1987) The Role of Predation in Age- and Size-Related Habitat Use by Stream Fishes. Ecology 68:651–659

Schultz, L. D., M. P. Heck, B. M. Kowalski, C. A. Eagles-Smith, K. Coates, and J. B. Dunham. 2017. Bioenergetics models to estimate numbers of larval Lampreys consumed by Smallmouth Bass in Elk Creek, Oregon. North American Journal of Fisheries Management 37:714-723.

Selong JH, McMahon TE, Zale AV, Barrows TB (2001) Effect of Temperature on Growth and Survival of Bull Trout, with Application of an Improved Method for Determining Thermal Tolerance in Fishes. Trans Am Fish Soc 130:1026–1037

Sheoships G. 2014. Pacific lamprey *Entosphenus tridentatus*: integrating traditional ecological knowledge and contemporary values into conservation planning, and stream substrate associations with larval abundance in the Willamette River Basin, Oregon, USA.

Shink, K. G., Sutton, T. M., Murphy, J. M., and López, J. A. (2019): Utilizing DNA metabarcoding to characterize the diet of marine-phase Arctic lamprey (*Lethenteron camtschaticum*) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences.

Shiraishi H., Toyobe T., Kanaya M. 2018. Civil Engineering Research Institute for Cold Region. https://thesis.ceri.go.jp/db/files/12256825095d22d6d61d6ec.pdf

Shirakawa H, Yanai S. Kouchi K (2009) Habitat selection of fluvial lamprey larvae *Lethenteron japonicum* change with growth stage. Ecol Civil Eng 12:87–98 (In Japanese)

Shirakawa H., Yanai S., & Goto A. 2013. Lamprey larvae as ecosystem engineers: physical and geochemical impact on the streambed by their burrowing behavior. Hydrobiologia, 701(1): 313-322.

Shirakawa H., Yanai S., Goto A. 2012. Spawning redds selection of Arctic lamprey *Lethenteron japonicum* in the Ishikari River. Ecology and Civil Engineering, 15(1): 71-79.

Silva, S., Barca, S., Vieira-Lanero, R., & Cobo, F. (2019). Upstream migration of the anadromous sea lamprey (Petromyzon marinus Linnaeus, 1758) in a highly impounded river: Impact of low-head obstacles and fisheries. Aquatic Conservation: Marine and Freshwater Ecosystems, 29(3), 389-396.

Silvano RA, Valbo-Jørgensen J (2008) Beyond fishermen's tales: contributions of fishers' local ecological knowledge to fish ecology and fisheries management. Environ Dev Sustain 10:657

Silvano RAM, Begossi A (2010) What can be learned from fishers? An integrated survey of fishers' local ecological knowledge and bluefish (*Pomatomus saltatrix*) biology on the Brazilian coast. Hydrobiologia 637:3–18

Siwicke KA, Seitz AC (2015). Interpreting lamprey attacks on Pacific cod in the eastern Bering Sea. T Am Fish Soc 144:1249–1262

Siwicke, K.A., and Seitz, A.C. (2017): Spatial differences in the distributions of Arctic and Pacific lampreys in the eastern Bering Sea. Transactions of the American Fisheries Society 147(1), pp. 111-127.

Sjöberg, K. 2011. River lamprey *Lampetra fluviatilis* (L.) fishing in the area around the Baltic Sea. Journal of Northern Studies, 5(2): 51-86.

Sjöberg, K. 2013. Fishing Gear Used for River Lamprey *Lampetra fluviatilis* (L.) Catches: Documenting Rivers that Flow into the Baltic Sea. Part II, Finland, Latvia and Estonia. Journal of Northern Studies, 7(2): 7-74.

Smith, D. M., Welsh, S. A., & Turk, P. J. (2011b). Available benthic habitat type may influence predation risk in larval lampreys. Ecology of Freshwater Fish, 21, 160–163. 10.1111/j.1600-0633.2011.00532.x

Smith, D.M., Welsh, S.A., & Turk, P.J. (2011a). Selection and preference of benthic habitat by small and large larvae of the least brook lamprey (*Lampetra aepyptera*). Environmental Biology of Fishes, 91, 421–428. https://doi.org/10.1007/s10641-011-9800-8

Steele, C. A., M. Hess, S. Narum, and M. Campbell. 2019. Parentage-Based Tagging: Reviewing the Implementation of a New Tool for an Old Problem. Fisheries 44:1-11.

Stevenson MG (1996) Indigenous knowledge in environmental assessment. Arctic 49:278–291

Stewart M, Baker CF (2012) A sensitive analytical method for quantifying *petromyzonol sulfate* in water as a potential tool for population monitoring of the southern pouched lamprey, *Geotria australis*, in New Zealand streams. J Chem Ecol 38:135–144

Sugiyama, H., & Goto, A. (2002). Habitat selection by larvae of a fluvial lamprey, *Lethenteron Reissneri,* in a small stream and an experimental aquarium. Ichthyological Research, 49, 62–68. https://doi.org/10.1007/s102280200006

Sutton TM (2017) Distribution and ecology of lampreys *Lethenteron* spp. in interior

Alaskan rivers. J Fish Biol 90:1196–1213

Sutton TM, Bowen SH (1994) Significance of organic detritus in the diet of larval lampreys in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences, 51:2380–2387

Sviridov VV, Glebov II, Starovoytov AN, Sviridova AV, Zuev MA, Kulik VV, Ocheretyanny MA (2007) Wounding of Pacific salmon in relation to the spatio-temporal variation in distribution patterns of important predatory fishes in the Russian economic zone. North Pacific Anadromous Fish Commission Bull 4:133–144

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. Science, 240(4857), 1285-1293.

Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. Molecular Ecology 11:627–641.

Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. North American Journal of Fisheries Management 13:831–838.

Takami T, Kitano F, Nakano S (1997) High water temperature influences on foraging responses and thermal deaths of Dolly Varden *Salvelinus malma* and white-spotted charr S. leucomaenis in a laboratory. Fish Sci 63:6–8

Takegawa, Y., Kawaguchi, Y., Mitsuhashi, H., Taniguchi, Y. (2017). Implementing species distribution models to predict the impact of global warming on current and future potential habitats of white-spotted char *Salvelinus leucomaenis* for effective conservation planning in Japan. Japanese Journal of Conservation Ecology, 22, 121-134.

Takeuchi, K., Maruoka, N., Daimon, S., 2007. Nature restoration plan for the lower reaches of the Ishikari River. Report of Riverfront Japan Research Institute 18, 33–40.

Taniguchi N. 2007. Studies on conservation and utilization of genetic divergence in fish and shellfish population. Nippon Suisan Gakkaishi, 73(3): 408-420.

Thomas MLH (1962) Observations on ecology of ammocoetes *Petromyzon marinus* L. and *Entosphenus lamottei* (Le sueur). Thesis, Univ of Tronto, Ontario

Tomioka N., ohta A., Shigaki H., Fukumoto T., Fujita T., Mizutani R. 2010. Regional consumption of the Stingray in Japan. The Japan Society of Cookery Science, 43(2): 120-130.

Torgersen C E, Close DA (2004) Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biol 49:614–630

Tucker, J. K., Cronin, F. A., Soergel, D. W., & Theiling, C. H. (1996). Predation on zebra mussels (Dreissena polymorpha) by common carp (Cyprinus carpio). Journal of Freshwater Ecology, 11, 363–372. https://doi.org/10.1080/02705060.1996.9664459

Turvey ST, Risley CL, Moore JE, Barrett LA, Yujiang H, Xiujiang Z, Kaiya Z, Ding W (2013) Can local ecological knowledge be used to assess status and extinction drivers in a threatened freshwater cetacean?. Biol Conserv 157:352–360

USFWS (U.S. Fish and Wildlife Service). (2011). Species Fact Sheet Western brook lamprey *Lampetra richardsonii*. Retrieved from https://www.fws.gov/wafwo/species/Fact%20sheets/WesternBrookLamprey_final.pdf

USFWS (U.S. Fish and Wildlife Service). (2018). Pacific Lamprey *Entosphenus tridentatus* Assessment. U.S. Fish and Wildlife Service, Portland.

Venables, W. N., & Ripley, B. D. (2002). Modern Applied Statistics with S 4th. New York, USA: Springer verlag.

Wang, C. J., Schaller, H. A., Coates, K. C., Hayes, M. C., Rose, R. K. (2020). Climate change vulnerability assessment for Pacific Lamprey in rivers of the Western United States. Journal of Freshwater Ecology, 35(1), 29-55.

Waraniak, J. M., E. A. Baker, and K. T. Scribner, 2018. Molecular diet analysis reveals predator–prey community dynamics and environmental factors affecting predation of larval lake sturgeon Acipenser fulvescens in a natural system. Journal of Fish Biology 93:616–629.

Weaver, D. M., Coghlan Jr, S. M., & Zydlewski, J. (2018). Effects of sea lamprey substrate modification and carcass nutrients on macroinvertebrate assemblages in a small Atlantic coastal stream. Journal of Freshwater Ecology, 33(1), 19-30.

White, J. L., Harvey, B. C. (2003). Basin-scale patterns in the drift of embryonic and larval fishes and lamprey ammocoetes in two coastal rivers. Environmental Biology of Fishes, 67(4), 369-378.

Wicks-Arshack A., M., Dunkle, S. Matsaw, and C. Caudill. 2018. An ecological, cultural and legal review of Pacific lamprey in the Columbia River Basin. Idaho Law Review 54:45-99.

William F., Beamish H. 1979. Migration and spawning energetics of the anadromous sea lamprey, Petromyzon marinus. Environmental Biology of Fishes, 4(1): 3-7.

Wolf B. O., Jones S. L. 1989. Great blue heron deaths caused by predation on Pacific lamprey. The Condor, 91(2), 482-484.

Yamamoto S, Morita K, Koizumi I, Maekawa K (2004) Genetic differentiation of white-spotted charr (Salvelinus leucomaenis) populations after habitat fragmentation: spatial–temporal changes in gene frequencies. Conserv Genet 5:529–538

Yamazaki, Y. (2007). Microhabitat use by the larvae of cryptic lamprey species in *Lethenteron reissneri* in a sympatric area. Ichthyological Research, 54(1), 24-31.

Yamazaki, Y., Goto, A. (1996). Genetic differentiation of *Lethenteron reissneri* populations, with reference to the existence of discrete taxonomic entities. Ichthyological Research, 43(3), 283-299.

Yamazaki, Y., Goto, A. (1998). Genetic structure and differentiation of four *Lethenteron* taxa from the Far East, deduced from allozyme analysis. Environmental Biology of Fishes, 52(1-3), 149-161.

Yamazaki, Y., Goto, A. (2000). Breeding season and nesting assemblages in two forms of *lethenteron reissner*i, with reference to reproductive isolating mechanisms. Ichthyological Research, 47(3-4), 271-276.

Yamazaki, Y., & Goto, A. 2016. Moolecular phylogeny and speciation of East Asian lampreys (genus Lethenteron) with reference to their life-history diversification. Pages 17-57 in A. Orlov and R. Beamish, editors.Jawless Fishes of the World, Vol. 1. Cambridge Scholars Publishing, Newcastle upon Tyne, U.K.

Yamazaki, Y., Goto, A., Byeon, H. K., & Jeon, S. R. (1999). Geographical distribution patterns of the two genetically divergent forms of *Lethenteron reissneri* (Pisces: Petromyzontidae). Biogeography, 1, 49-56.

Yamazaki, Y., Goto, A., Nishida, M. (2003). Mitochondrial DNA sequence divergence between two cryptic species of *Lethenteron*, with reference to an improved identification technique. Journal of Fish Biology, 62(3), 591-609.

Yamazaki, Y., Yamano, A., & Oura, K. (2011). Recent microscale disturbance of gene flow in threatened fluvial lamprey, *Lethenteron* sp. N, living in a paddy water system. Conservation genetics, 12(5), 1373.

Yamazaki Y, Yokoyama R, Nagai T, Goto A (2011) Formation of a fluvial non-parasitic population of Lethenteron camtschaticum as the first step in petromyzontid speciation. J Fish Biol 79:2043–2059

Yamazaki Y., Yokoyama R., Nagai T., Goto A. 2014. Population structure and gene flow among anadromous Arctic lamprey (Lethenteron camtschaticum) populations deduced from polymorphic microsatellite loci. Environmental biology of fishes, 97(1): 43-52.

Yamazaki, Y., Goto, A. 2016. Moolecular phylogeny and speciation of East Asian lampreys (genus Lethenteron) with reference to their life-history diversification. Pages 17-57 in A. Orlov and R. Beamish, editors.Jawless Fishes of the World, Vol. 1. Cambridge Scholars Publishing, Newcastle upon Tyne, U.K.

Yamazaki, Y., Goto, A., Nishida, M. (2003). Mitochondrial DNA sequence divergence between two cryptic species of Lethenteron, with reference to an improved identification technique. Journal of Fish Biology, 62(3), 591-609.

Yamazaki, Y., Yamano, A., & Oura, K. (2011). Recent microscale disturbance of gene flow in threatened fluvial lamprey, Lethenteron sp. N, living in a paddy water system. Conservation genetics, 12(5), 1373.

Yazawa Y. 2007. Seasonal Change of Essential FFA and β-lipoprotein Contents in Lamprey, Lampetra japonica. Reports of Taisetsuzan Institute of Science, 41: 49-54.

Young RJ, Kelso JRM, Weise JG (1990) Occurrence, relative abundance, and size of landlocked sea lamprey (Petromyzon marinus) ammocoetes in relation to stream characteristics in the Great Lakes. Can J Fish Aquatic Sci 47:1773–1778

Zale AV (1984) Applied aspects of the thermal biology, ecology, and life history of the blue tilapia, Tilapia aurea (Pisces: Cichlidae). Doctoral dissertation, Univ of Florida, Gainesville

Zimmerman, M. P. (1999). Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society, 128, 1036–1054. https://doi.org/10.1577/1548-8659(1999)128<1036:FHOSBW>2.0.CO;2

Publications

Publications (First author)

1. **Arakawa H.**, Yanai, S. 2017. Autumn microhabitat for larvae of endangered Arctic lamprey (L*ethenteron japonicum*) in Noto Peninsula, Ishikawa Prefecture, Japan. ***Ecology and Civil Engineering***, 20: 11-24 (**in Japanese**)
2. **Arakawa H.**, Yanai S. 2018. Maturation and Artificial Propagation of Arctic lamprey *Lethenteron japonicum*. ***Noto Marine contact center research report***, 24: 29-39 (**in Japanese**)
3. **Arakawa H.**, Shima Y., Yanai S., 2018. Regional culture for Arctic lamprey and its harvest change in rural rivers of Noto Peninsula, Ishikawa Prefecture, Japan. ***Bulletin of Ishikawa Prefectural University***, 1: 11-21 (**in Japanese**)
4. **Arakawa H.**, Yanai S. 2019. Optimal sediment particle size and rearing method for hatched larval Arctic lamprey (Lethenteron camtschaticum). ***Noto Marine contact center research report***, 25: 9-18 (**in Japanese**)
5. **Arakawa H.**, Ichion E., Nakano E., Yanai S. 2019. Factors that affect Arctic lampreys' ascent behavior on fishway weirs. ***Journal of Rainwater Catchment System***, 25: 15-21.
6. **Arakawa H.**, Yanai S. 2020. Upper thermal tolerance of larval Arctic lamprey (*Lethenteron camtschaticum*). ***Ichthyological Research***, DOI: doi.org/10.1007/s10228-020-00757-3
7. **Arakawa H.**, Lampman R. T. 2020. An experimental study to evaluate predation threats on two native larval lampreys in the Columbia River Basin, USA. ***Ecology of Freshwater Fish***. DOI: doi.org/10.1111/eff.12537

Publications (Not first author)

8. Clemens B. J., **Arakawa H.**, Baker C., Coghlan S., Kucheryavyy A., Lampman R., Lanuca M. J., Mateus C. S., Miller A., Nazari H., Pequeño G., Sutton T., Yanai S. 2020. Management of anadromous lampreys: Common threats, different approaches. ***Journal of Great Lakes Research***.
9. Lampman R., Maine A. N., Moser M. L., **Arakawa H.**, Nease F. B. Accepted. Lamprey Aquaculture Successes and Failures: A Path to Production for Control and

Conservation. ***Journal of Great Lakes Research***.

10. Matsumoto T., **Arakawa H.**, Murakami T., Yanai S. Accepted. Settlement patterns of two *Sesarmid* megalopae in the Sai River Estuary, Ishikawa Prefecture, Japan. ***Plankton and Benthos Research***.

Papers under review

1. **Arakawa H**., Kishi D., Yanai S. Under review. Historical distribution of Arctic lamprey (*Lethenteron camtschaticum*) in Japanese rivers and its change estimated from fishery statistics and local ecological knowledge. *Fisheries Science.*
2. **Arakawa H.**, Yanai S. Under review Traditional Fishing for Arctic lamprey (*Lethenteron camtschaticum*) in the costal Sea of Japan. *Bulletin of Ishikawa Prefectural University*
3. **Arakawa H.**, Lampman R., Hess J. Under review. Whose kids did you eat? Genetic identification of species and parents of larval lampreys in fish predator guts. *Transaction of American Fisheries Society*.
4. Almeida P., **Arakawa H.**, Aronsuu K., Baker C., Blair S.R., Beaulaton L., Belo A., Kitson J., Kucheryavyy A., Kynard B., Lucas M., Moser M., Potaka B., Romakkaniemi A., Staponkus R., Tamarapa S., Yanai S., Zhuang P. Accepted. Lamprey fisheries: history, trends and management. ***Journal of Great Lakes Research***.