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SPECIAL SECTION

Native Lampreys: Research and Conservation of Ancient Fishes

Pacific Lamprey and Western River Lamprey marine ecology: Insight from new ocean collections

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Abstract

Objective: Little is known about the marine ecology of anadromous Pacific Lamprey *Entosphenus tridentatus* and Western River Lamprey *Lampetra ayresii*. This information is needed to determine how marine life regulates adult abundances and to identify management actions that may benefit declining populations.

Methods: To address this deficit, we compiled historic data, collected lamprey from marine stock assessment surveys and commercial fisheries, and documented fish with Pacific Lamprey wounds.

Result: Pacific Lamprey were most commonly caught by midwater trawls targeting Pacific Hake *Merluccius productus* along the continental shelf break from northern California to northern Washington. Pacific Lamprey ranged in size from 115 mm total length (TL) and 2.9 g to 714 mm TL and 655 g ($n = 1912$) and were expected to represent multiple ocean ages. The vast majority (93%) of Pacific Lamprey were small (≤300 mm TL) and thus were likely in their first year in marine waters. Growth for small Pacific Lamprey was estimated as 0.37 mm/day and 0.13 g/day over the summer. Gut fullness for Pacific Lamprey was high (5.5% of body weight [BW]), but it was highly variable for larger individuals (range = 0–55% BW). Our results suggest that there is a positive relationship between calendar day and lamprey length and condition factor in most years, while the effect of latitude varies by life stage. We documented Pacific Lamprey wounds on 240 individual fish representing 16 species, of which six species are newly identified as lamprey hosts. We had comparably few records for Western River Lamprey ($n = 72$; mean length = 285.5 mm TL), which were primarily found in surface waters on the continental shelf from northern California to southern British Columbia.

Conclusion: Our results have implications for both fisheries and conservation management, including development of best practices for lamprey caught by net fisheries and the use of new marine information to inform conservation actions.

KEYWORDS

distribution, gut fullness, marine ecology, Pacific Lamprey, Western River Lamprey

INTRODUCTION

Impact statement

We show that native Pacific Lamprey are widespread in marine waters along the U.S. West Coast. They are caught as bycatch in Pacific Hake and other commercial fisheries, requiring development of methods to ensure that Pacific Lamprey released from fisheries survive to ensure the continued existence of this ancient fish.

The Pacific Lamprey *Entosphenus tridentatus* and Western River Lamprey *Lampetra ayresii* are ancient anadromous fishes that are native to the eastern North Pacific Ocean and its adjacent river basins (Beamish 1980; Renaud et al. 2009). Like native lampreys around the world, the Pacific and Western River lampreys face many common threats that have resulted in declining abundances and substantial extinction risks to some populations (Clemens et al. 2010, 2021). Recent status assessments indicate that the range of the Pacific Lamprey has contracted and that most extant populations along the west coast of the continental United States are at risk of biological extinction (U.S. Fish and Wildlife Service [USFWS] 2019); many populations currently receive protection under state statutes (Clemens and Wang 2021). In British Columbia, Canada, Pacific Lampreys are considered "secure" (defined as "common, widespread, and abundant"), although the abundance or trends for many Canadian populations are not known (Renaud et al. 2009; Clemens et al. 2021). The distribution, abundance, and trends for most Western River Lamprey populations are poorly documented, partly due to their smaller adult size and lack of subsistence, traditional, or commercial uses. The status of the Western River Lamprey is "apparently secure" (defined as "uncommon but not rare") or "secure" in some British Columbia watersheds, but this species is expected to be declining along the U.S. West Coast and also receives some protection from state statutes (Moyle et al. 2009; Renaud et al. 2009; Clemens and Wang 2021; Clemens et al. 2021).

Anadromous lampreys, including the Pacific and Western River lampreys, have complex life cycles. They are characterized by a protracted larval stage (synonymous with "ammocoete"; Clemens 2019) that dwells in and consumes riverine sediments; transformation, with the growth of eyes, an oral feeding disc, and the ability to osmoregulate in seawater; and a parasitic or predatory juvenile marine phase (Beamish 1980; Beamish and Youson 1987; Hardisty 2006; Clemens et al. 2010; Dawson et al. 2015).

Relatively little is known about the marine ecology of most Pacific and Western River lampreys (Clemens et al. 2010, 2019; Wade and Beamish 2016; Quintella et al. 2021). In general, Pacific Lampreys enter the ocean in winter to early spring, primarily during freshets (Beamish 1980; Beamish and Levings 1991; Weitkamp et al. 2015; Clemens et al. 2019). Adult Pacific Lampreys generally return to freshwater in winter and spring after 3–7 years in the ocean (Beamish 1980; Hess et al. 2022). Pacific Lampreys have been documented in marine waters from Baja California and Japan in the eastern and western Pacific Ocean, respectively, to the Bering and Chukchi seas in the north, which mirrors their freshwater distribution (Mecklenburg et al. 2002; Orlov et al. 2009; Renaud et al. 2009; Clemens et al. 2019). Depth distributions of Pacific Lampreys are highly variable but generally range from 0 to 500 m and are shallower (31–100 m) in the Strait of Georgia (Beamish 1980, 2014; Orlov et al. 2008; Wade and Beamish 2016).

Compared to the Pacific Lamprey, Western River Lampreys have a shorter marine phase (<5 months) and remain higher in the water column, typically within 30 m of the surface (Beamish 1980, 2014; Bond et al. 1983; Beamish and Neville 1995). Most Western River Lampreys enter marine waters in spring and early summer and return to freshwater in the late summer and fall of the same year (Beamish 1980; Beamish and Youson 1987; Beamish and Neville 1995; Weitkamp et al. 2015). Outside of the Strait of Georgia, the marine distribution of Western River Lampreys is poorly documented but is expected to mirror their freshwater distribution, which ranges from Southeast Alaska (Taku River) to San Francisco Bay (Sacramento and San Joaquin rivers; Hart 1973; Mecklenburg et al. 2002).

Anadromous lampreys are parasitic (consume blood and body fluids) or predatory (consume flesh) in marine waters (Quintella et al. 2021). Pacific Lampreys are categorized as parasitic and predatory, and Western River Lampreys are categorized as predatory (Beamish 1980; Quintella et al. 2021). Identification of hosts or prey is typically based on the presence of (1) circular wounds where parasitic lampreys have attached using the oral disc or (2) irregular flesh wounds caused by predatory lampreys (Beamish 1980; King 1980; Orlov et al. 2009; Siwicke and Seitz 2015; Weitkamp et al. 2015). Clemens et al. (2019) listed 32 species of fish and marine mammals that are known to serve as Pacific Lamprey hosts in marine waters, and those authors characterized Pacific Lampreys as "opportunistic generalists." Common fish hosts include Walleye Pollock *Gadus chalcogrammus*, Pacific Cod *G. macrocephalus*, Greenland Halibut *Reinhardtius hippoglossoides*, and Pacific Halibut *Hippoglossus stenolepis* in the Bering Sea and the Gulf of Alaska; Pacific Hake *Merluccius productus* off the U.S. West Coast; and all Pacific salmonids *Oncorhynchus* spp. (Beamish 1980;

Siwicke and Seitz 2015; Orlov 2016). Common marine prey for Western River Lampreys tend to be smaller bodied and include Pacific Herring *Clupea pallasii*, Northern Anchovy *Engraulis mordax*, and juvenile Pacific salmon (Beamish 1980; Beamish and Neville 1995; Wade and Beamish 2016). Both parasitic and predatory lampreys can cause high mortality among their common hosts and prey (Beamish and Neville 1995; Simpkins et al. 2021).

Many ecological questions about lamprey marine ecology remain unanswered but are foundational for managing conservation risk and implementing successful mitigation measures for these species. In particular, detailed information on marine distributions, movements, feeding behavior and host selection, growth rates, duration in marine waters, and overall survival is needed for both Pacific and Western River lampreys (Clemens et al. 2010, 2019; Quintella et al. 2021). Given the currently limited understanding of lamprey marine ecology, assessments relating marine conditions to adult lamprey abundance must rely heavily on speculation in the absence of better information (e.g., Murauskas et al. 2013; Wade and Beamish 2016).

In the United States, Pacific Lampreys have received substantial conservation and research attention from a 2012 conservation agreement signed by tribes and federal, state, and other natural resource agencies, including the National Marine Fisheries Service (NMFS; USFWS 2019). Among the signatories to this agreement, NMFS is uniquely positioned to research lamprey marine ecology. Under the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act (2006), NMFS regulates marine fisheries and conducts surveys that catch anadromous lampreys as bycatch. The law also requires commercial fishing vessels to carry fisheries observers; these observers opportunistically collected lamprey specimens and recorded fish with Pacific Lamprey wounds specifically for the present study. Here, we greatly expand what is known about the marine ecology of Pacific Lampreys and coastal Western River Lampreys by providing a compilation of historical lamprey catch records and analyses of new marine collections from stock assessment surveys and fisheries in coastal waters from northern British Columbia to southern California. Although both species were found to be relatively rare in marine waters, these results help to inform fisheries practices and conservation management for anadromous lampreys.

METHODS

We compiled data on Pacific and Western River lampreys and their hosts in marine areas along the west coast of North America. These data came from records of lampreys caught during stock assessment surveys conducted by the NMFS Northwest Fisheries Science Center (NWFSC), actual lamprey specimens collected during NWFSC surveys and by fisheries observers on commercial vessels, and records (including photographs) of fish with characteristic round Pacific Lamprey wounds. We conducted analyses to look for patterns in size; feeding success; and the time, location, and depth of recovery for these two lamprey species.

Sources of lamprey specimens and data

The NWFSC conducts surveys for Pacific Hake and other groundfish to provide fishery-independent abundance estimates for stock assessments and fisheries management (Keller et al. 2017; Berger et al. 2019). It also conducts annual juvenile salmon surveys in marine waters off the coasts of Washington and Oregon (Peterson et al. 2010). In these surveys, all retained fish and invertebrates were identified to species, enumerated, and weighed by species (groundfish and Pacific Hake surveys) or were individually measured for length (juvenile salmon survey). Lampreys were either released (all surveys) or retained (frozen) in U.S. waters beginning in 2017 (Pacific Hake and groundfish surveys). Survey staff also examined and documented fish with Pacific Lamprey marks (i.e., circular wounds) starting in 2014.

We used historic records primarily to document the seasonal presence and location of Pacific and Western River lampreys. To the extent possible, we also used reported size data. Specifically, in cases where two lampreys were weighed together, we used the mean weight as the individual weight; when more than two lampreys were represented by a single weight, we discarded the weight record (but kept the location and date information). We briefly describe the Pacific Hake, groundfish, and juvenile salmon surveys here, but detailed descriptions of the surveys are provided by Berger et al. (2019; Pacific Hake survey), Keller et al. (2017; groundfish survey), and Peterson et al. (2010; juvenile salmon survey).

Pacific Hake survey

Since 2001, the Joint U.S.–Canadian West Coast Pacific Hake Integrated Acoustic and Trawl Survey (hereafter, “Pacific Hake survey”) has been conducted biennially in U.S. and Canadian waters to estimate the abundance and distribution of age-2 and older Pacific Hake. The survey's maximum spatial extent is Dixon Entrance (54.5°) to Point Conception (34.17°; Berger et al. 2019; Edwards et al. 2022). East–west-aligned transects spaced 18.5–37.0 km apart are surveyed acoustically at water depths from roughly 50 to 1500 m. Midwater trawls (Aleutian wing trawl 24/20, cod end liner mesh size = 3.2 cm [1.25 in]) are conducted opportunistically to determine the species composition of acoustically observed fish congregations and to collect measurements and samples (Berger et al. 2019). Approximately 90 hauls (tow duration = 10–60 min, covering 0.1–2.6 km) are made during the survey.

West Coast Groundfish Survey

The West Coast Groundfish Survey (hereafter, "groundfish survey") uses bottom trawls to target a diverse community of demersal fishes and invertebrates (Keller et al. 2017; Pacific Fishery Management Council 2022). Since 2003, the groundfish survey has sampled shelf and slope habitat from the Canada–USA border (48.5°) to the USA–Mexico (32.5°) border, conducting two full passes from approximately mid-May to late October. In a typical year, 500–700 randomly selected sites are sampled. Bottom trawls using an Aberdeen-type trawl with a 3.8-cm (1.5-in) cod end liner are deployed at depths of 55–1280 m. Tow duration is 15 min (measured once the net contacts the bottom).

Juvenile salmon survey

Since its inception in 1998, the Juvenile Salmon and Ocean Ecosystem Survey (hereafter, "juvenile salmon survey") has used a Nordic 264 trawl towed at the surface to sample juvenile salmon and associated nekton at a series of fixed stations from near Cape Flattery (48.25°) to Newport, Oregon (44.68°; Peterson et al. 2010). Two surveys are conducted each year (late May and late June), with a September cruise occurring in 1998–2012. The average number of hauls completed each year has varied from 130 during 1998–2012 (3 cruises/year) to 71 during 2013–2022 (2 cruises/year). The net has variable mesh from 162.6 cm in the throat to 8.9 cm in the cod end, with a 0.8-cm (0.31-in) knotless cod end liner (Peterson et al. 2010).

As part of this larger study, two smaller projects caught lampreys that were included in the data set. For the first project, gear trials using the Nordic 264 trawl towed at the surface were conducted near the mouth of the Columbia River during the summers of 2011, 2014, and 2015 (Wainwright et al. 2019). The other project deployed fine-mesh purse seines (228–304 m long × 12–18 m deep, with 1-cm mesh) in shallow water (4–35 m deep) near the mouth of the Columbia River in July–September 2012 (L. A. Weitkamp, unpublished data).

Commercial fisheries

Fisheries observers are trained scientists deployed by the NWFSC on board U.S. West Coast commercial fishing vessels to document fishing effort, sample the catch, monitor for protected species, and collect samples as needed (Somers et al. 2018, 2021). Observers deployed in the "at-sea" Pacific Hake fishery, groundfish limited-entry trawl sector, and pink shrimp *Pandalus jordani* fishery opportunistically collected lampreys for this study starting in 2017. As time permitted, lampreys were collected, labeled with the date and catch location, and immediately frozen. Observers in the at-sea Pacific Hake fishery also identified and photographed characteristic round Pacific Lamprey wounds on fish beginning in 2017. Although observer lamprey collections were opportunistic, we have no reason to believe that they were biased in ways that would influence our results or conclusions (e.g., more collections in some regions or times than others). Observer coverage for both the at-sea Pacific Hake fishery and the groundfish limited-entry trawl sector is 100%, whereas coverage is lower for the pink shrimp fishery (median = 14%; Somers et al. 2018, 2021).

The at-sea Pacific Hake fishery uses midwater trawls (minimum cod end mesh size = 7.5 cm) to target semi-pelagic Pacific Hake (Pacific Fishery Management Council 2022). The fishery operates between May 15 and November and mainly occurs north of 42° N (the Oregon–California border) in U.S. waters (Table 1). We also received five individual lamprey specimens collected by observers from the limited-entry trawl sector of the groundfish fishery; for convenience, these fish were included in the groundfish survey. The pink shrimp fishery uses fine-mesh trawls over mud- and mud–sand-bottom habitats from British Columbia to California (Hannah et al. 2018). In U.S. waters, the commercial season is open from April 1 to October 31.

Fish with Pacific Lamprey wounds

Scientists on board the NWFSC surveys and the at-sea Pacific Hake vessels opportunistically identified and photographed characteristic round Pacific Lamprey wounds (King 1980; Siwicke and Seitz 2015). Our objectives for this data set were to identify fish with wounds, characterize wound location on the body, and summarize the gear type and capture locations (latitude, bottom depth) of the fish. Because this effort was opportunistic, it is not a systematic survey of fish wounds (e.g., Siwicke and Seitz 2015). Information accompanying photographs included fish species, location (latitude, longitude), date, and sometimes fish length or weight. Because severe wounds were

TABLE 1 Sources of historic records (Rec) and collected specimens (Coll) of Pacific and Western River lampreys used in our analysis. Abbreviations: BC, British Columbia; Comm., Commercial; NWFSC, Northwest Fisheries Science Center.

Source	Type	Trawl location in water column	Geographic extent	Range of years		Pacific Lamprey		Western River Lamprey	
				Lampreys recorded	Lampreys collected	Rec	Coll	Rec	Coll
NWFSC Pacific Hake survey	Survey	Midwater	Northern BC to Point Conception	1998–2019	2016–2019	650	18	11	0
NWFSC groundfish survey	Survey	Bottom	USA–Canada border to USA–Mexico border	2003–2021	2017–2021	45	14	4	0
NWFSC juvenile salmon survey	Survey	Surface	Northern WA to Newport, OR	1999–2018	–	12	0	53	3
At-sea Pacific Hake fishery	Comm. fishery	Midwater	USA–Canada border to OR–CA border	–	2017–2022	0	1805	0	1
Shrimp fishery	Comm. fishery	Bottom	Northern WA to northern CA	–	2017–2022	0	75	0	0

more likely to be noticed than mild or healed wounds (i.e., scars), we did not attempt to categorize wounds by severity or degree of healing. We recorded the location of wounds using six body areas (Orlov et al. 2009; Siwicke and Seitz 2015): head (anterior to dorsal and pectoral fins), tail (posterior to the dorsal and anal fins), and on the sides of the body anterior or posterior to the anterior end of the anal fin above or below the lateral line (i.e., anterior dorsal, anterior ventral, posterior dorsal, and posterior ventral). Possible wounds created by flesh-eating Western River Lampreys are much less distinctive and easily confused with net damage (Beamish and Neville 1995; Weitkamp et al. 2015; Weitkamp, personal observation) and therefore were not recorded.

Processing of specimens

All collected lampreys were labeled, bagged, and frozen in the ship's freezers and remained frozen during transport to the NWFSC laboratory in Newport, Oregon. In the lab, lampreys were thawed, identified to species based on dentition (Renaud 2011), and measured (total length [TL] to the nearest 1 mm; weight [W] to the nearest 0.1 g); the gut was dissected out (see below), and the body was refrozen. Fin clips were also collected for genetic analysis (Hess et al. 2021, 2022). To explore variation in fish shape, we calculated Fulton's condition factor (CF) for each fish as $\mathrm{CF} = 100{,}000 \times W/(\mathrm{TL}^3)$ (Murphy and Willis 1996). We did not calculate CFs for any Pacific Lampreys with estimated length or weight values (see below).

Because historical records provided length or weight but not both, we estimated the missing values from length–weight relationships developed from specimens; these estimates were primarily used for graphical rather than analytical purposes. For Pacific Lampreys, we used the length–weight relationship from all specimens ($n = 1899$) as $\ln(\text{weight}) = 3.007 \times \ln(\text{length}) - 12.952$ ($r^2 = 0.966$, $p < 0.05$). For Western River Lampreys, we used the average CF (0.183) from the four ocean-caught specimens to calculate missing length or weight measurements.

We measured gut fullness as an indicator of recent feeding success for Pacific Lampreys. Like other jawless fishes (agnathans), lampreys have no true stomach; instead, the esophagus attaches directly to the intestine (Hardisty 2006). Accordingly, the entire intestine (i.e., gut) of each Pacific Lamprey was removed by dissection. The complete intestine (lining plus contents) was weighed to the nearest 0.01 g, individually bagged, and refrozen. Gut contents were not extruded from the lining so as to maximize their usefulness for subsequent genetic analyses of contents (i.e., Shink et al. 2019). To correct estimates of gut fullness for the weight of the intestinal lining, the weights of the lining and the contents were measured separately for 63 individuals (whole-fish W range = 4.4–567.0 g; gut lining weight [LW] range = 0.06–6.35 g). A relationship between whole-fish W (g) and LW (g) was developed: $\ln(\mathrm{LW}) = [1.83 \times \ln(W)] - [0.11 \times \ln(W)^2] - 5.57$ ($r^2 = 0.95$, $p < 0.05$). Estimated LW was then subtracted from complete intestine weight to determine gut content weight (GW). We then estimated gut fullness (expressed as a percentage of body weight [% BW]) as

$$\text{Gut fullness}\ (\%\,\mathrm{BW}) = 100 \times \frac{\mathrm{GW}}{W - \mathrm{GW}}.$$

We did not dissect or measure gut fullness for Western River Lampreys because we had so few specimens ($n = 4$) that it would have been difficult to draw any meaningful conclusions.

Statistical analysis

Pacific Lamprey records and specimens were divided into two size categories (small and large) based on date-adjusted length and weight thresholds reflecting clear gaps between sizes of fish. This size cutoff increased from 235 mm and 31 g for lampreys caught prior to June 15 to 300 mm and 100 g for those caught after August 5, as the size of lampreys increased over the summer. It was assumed that small lampreys (those below the cutoff size) were in their first summer in marine waters because they overlapped with reported sizes of downstream migrants (e.g., Beamish 1980; Beamish and Levings 1991; Weitkamp et al. 2015). We assumed that larger lampreys had spent one or more winters in marine environments; we did not attempt to assign ocean ages (OAs) to larger individuals, due to a continuous size range and the lack of methods for age determination in juvenile lampreys (Pelekai et al. 2023, this special section). No size categories were assigned for Western River Lampreys because this species only spends a single summer in marine waters (Beamish and Neville 1995; Weitkamp et al. 2015).

We used generalized linear models to examine sources of variation in Pacific Lamprey size, CF, and gut fullness; separate models were constructed for each response. Data from small and large lampreys were analyzed independently because small lampreys were much more numerous than large lampreys (small individuals constituted >90% of all Pacific Lampreys), making detection of potentially subtle trends for large lampreys difficult. Because many years in our data had few samples (<10) and we were interested in exploring interannual variability, we restricted the modeling portion of our analysis to only include data from 2016 to 2022 (these years only included Pacific Lamprey data from the Pacific Hake survey and fishery [i.e., considered one group] and the shrimp fishery). We used a Gaussian response family for models of CF and ln(length), and we fit models using maximum likelihood in the R package glmmTMB (Brooks et al. 2017; R Development Core Team 2022). Gut fullness was recorded as a proportion and included zeros. As such, we modeled gut fullness with zero-inflated beta regression using maximum likelihood and the R package mgcv (Wood 2011).

For all models, we considered the following potential covariates: day of year (referred to as “day,” either as a linear or quadratic predictor), year (either as a numeric or factor variable), latitude (either as a linear or quadratic predictor), fishery/survey (factor variable), and depth (numeric continuous). To allow for potential variability across years, we also allowed factor covariates to include linear interactions with the year variable. Finally, as some samples consisted of multiple fish, we used ln(count) as an offset to account for unequal sample sizes. The relative data support between models was compared using Akaike's information criterion (AIC; Akaike 1973), and models with the lowest AIC value were selected.

RESULTS

Pacific Lamprey

We assembled historical catch records for and obtained specimens of 2685 Pacific Lampreys caught in marine waters (Table 1); these consisted of records for 707 Pacific Lampreys caught by NWFSC surveys beginning in 1998 and 1912 lamprey specimens opportunistically collected from commercial fisheries and NWFSC surveys in 2016–2022. Most records and specimens were recorded or collected between mid-May and late November, when fishing effort and survey effort were highest. Over 100 individual lampreys were collected each year during 2017 ($n = 735$), 2018 ($n = 601$), 2020 ($n = 374$), and 2021 ($n = 108$), and 9–43 lampreys were collected annually in 2016, 2019, and 2022 as a result of variable sampling effort.

Overall, lamprey specimens ranged in size from 115 mm TL and 2.9 g to 714 mm TL and 655 g (Figure 1). The vast majority (92.9%; $n = 1777$) of Pacific Lamprey specimens were small (<300 mm TL and <40 g by late summer; see Methods), with the remainder classified as large ($n = 135$; Figure 1). Small lampreys averaged 193.8 mm and 19.9 g, with a CF of 0.251, while large lampreys averaged 498.7 mm TL and 328.4 g, with a CF of 0.231 (Figures 1, 2). We measured gut fullness for 1844 Pacific Lampreys that were caught during 2016–2022 (Figure 2). Gut fullness averaged 5.35 ± 2.37% BW (mean ± SD) for small lampreys ($n = 1708$) and 6.77 ± 10.42% BW for large

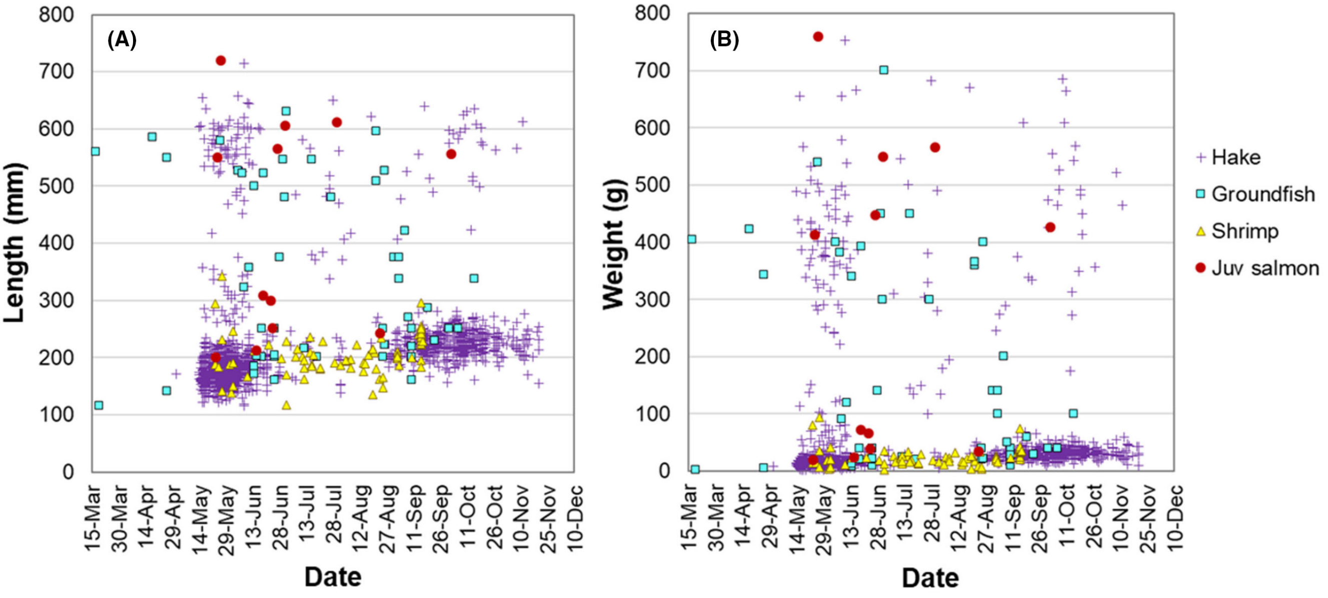

FIGURE 1 (A) Length and (B) weight of Pacific Lampreys by day of year for all years (1998–2022) combined. The source of the lampreys (Pacific Hake survey and fishery [Hake], groundfish survey [Groundfish], shrimp fishery [Shrimp], or juvenile salmon survey [Juv salmon]) is indicated.

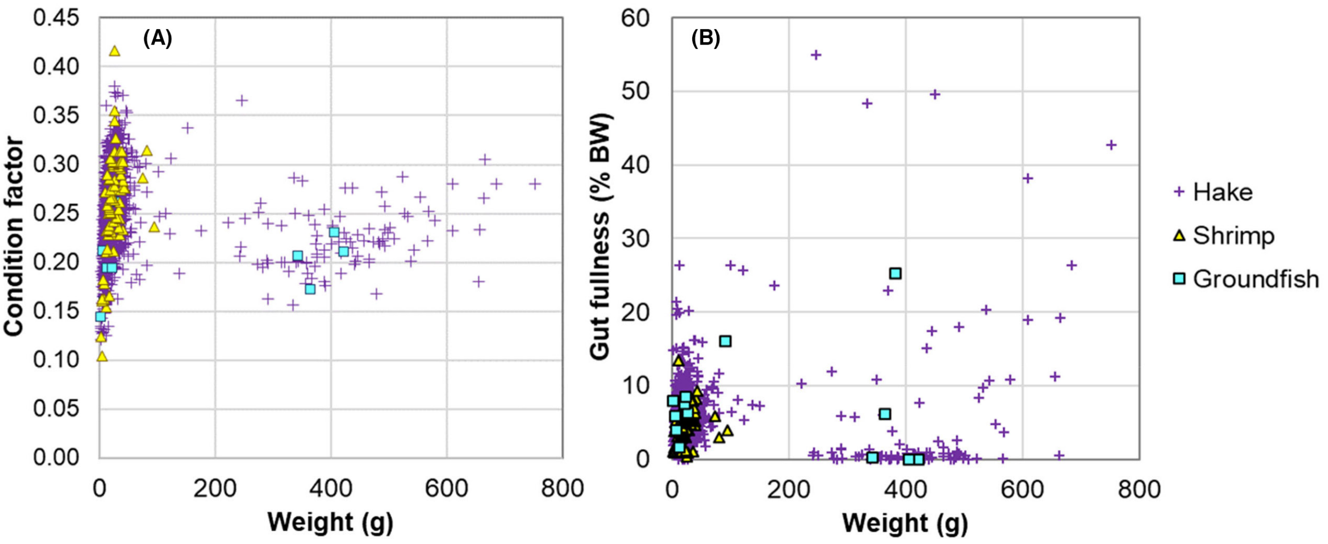

FIGURE 2 (A) Fulton's condition factor and (B) gut fullness (expressed as a percentage of body weight [BW]) of individual Pacific Lampreys plotted against total weight (g). The source of the lampreys (Pacific Hake survey and fishery [Hake], groundfish survey [Groundfish], or shrimp fishery [Shrimp]) is indicated.

lampreys ($n = 136$). Twenty-five lampreys (1.35%) had empty guts (defined as ≤0.05% BW), while one small lamprey and 10 large lampreys had gut fullness exceeding one-quarter of their body weight, with a maximum value of 54.9% BW. Gut fullness was statistically similar regardless of whether lampreys were caught in midwater trawls (mean ± SD = 5.44 ± 3.61% BW; $n = 1765$), shrimp trawls (5.22 ± 2.15% BW; $n = 60$), or bottom trawls (8.82 ± 8.00% BW; $n = 19$).

Historic records and collections indicated that most Pacific Lampreys were caught by midwater trawls targeting Pacific Hake ($n = 2473$; 94.4%), some were caught by bottom trawls for groundfish or shrimp ($n = 134$; 5.1%), and very few were caught in surface trawls targeting juvenile salmon ($n = 12$; 0.5%; Table 1). The relative number of small or large Pacific Lampreys caught in these fisheries and surveys varied widely: the vast majority (92–95%) of individuals caught by midwater and shrimp trawls were small, the two sizes were equally represented in the groundfish survey (30 small lampreys; 29 large lampreys), and the juvenile salmon survey caught twice as many large individuals (8) as small individuals (4). These individuals

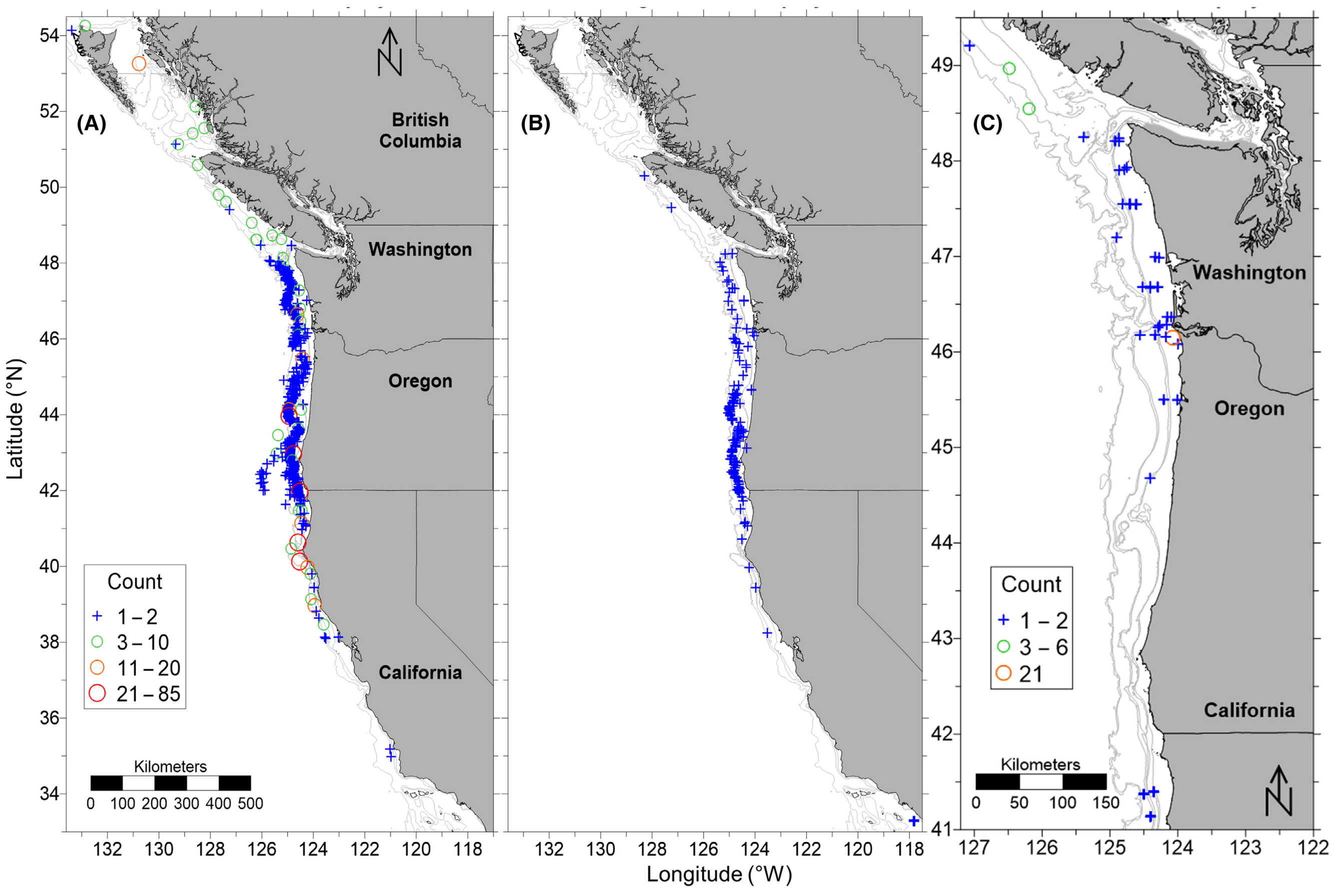

FIGURE 3 Locations of (A) small Pacific Lampreys, (B) large Pacific Lampreys, and (C) all sizes of Western River Lampreys caught along the west coast. Contours indicate the 100-, 200-, and 1000-m isobaths.

were widely distributed along the west coasts of British Columbia and the continental United States, from the north side of Haida Gwaii (54.25°, −132.87°) to extreme southern California (33.07°, −117.4°), representing a distance of over 2600 km (Figure 3). However, the vast majority of Pacific Lampreys were caught between 41° N and 48° N, whereas only three individuals were caught south of 38° N and 24 individuals were caught north of 52° N.

Fishing and bottom depths where lampreys were caught depended on gear type. Fishing depths for lampreys caught by midwater trawls (which fish above the bottom) averaged 238.3 ± 65.6 m (mean ± SD) in water averaging 466.7 ± 348.9 m deep. Fishing depth (i.e., bottom depth) was shallower for lampreys caught in bottom trawls for groundfish (312.0 ± 137.2 m) and shrimp (151.6 ± 38.3 m), while bottom depth was shallower still (69.0 ± 39.9 m) for lampreys caught in surface trawls (fishing depth = 0–20 m).

Results of model fits for length, CF, and gut fullness indicated several important sources of variation, particularly day and latitude. The best statistical model (lowest AIC) of length for small Pacific Lampreys showed that day, year, and latitude were important covariates but fishery and depth were not (Tables S1–S6 available in the Supplementary Information in the online version of this article). Specifically, length and weight of small individuals increased linearly with day from a mean of 171.8 mm TL and 12.33 g on May 15 to 227.9 mm and 32.08 g on October 15, which represents an increase of 0.366 mm/day and 0.13 g/day. The change in length also varied by year and was highest in 2017 (0.448 mm/day; 0.151 g/day) and much lower in both 2016 (negative slope) and 2019, when sample sizes were small ($n \leq 60$) and confidence intervals were large (Figure 4; Tables S1–S6.). The length of small lampreys also decreased with latitude (−0.8 mm/degree latitude). The best model of length for large lampreys also included terms for date and year but not for latitude or interactions (Table S2).

The best models of CF for small and large lampreys included day, source (the shrimp fishery versus the Pacific Hake fishery and survey), and latitude (small lampreys only) but not year or depth (Tables S3–S4). Small and large lampreys caught by the shrimp fishery had higher CFs (0.257 and 0.276, respectively) than lampreys from the Pacific Hake fishery and survey (0.251 and 0.230, respectively), with higher CFs observed for more southerly

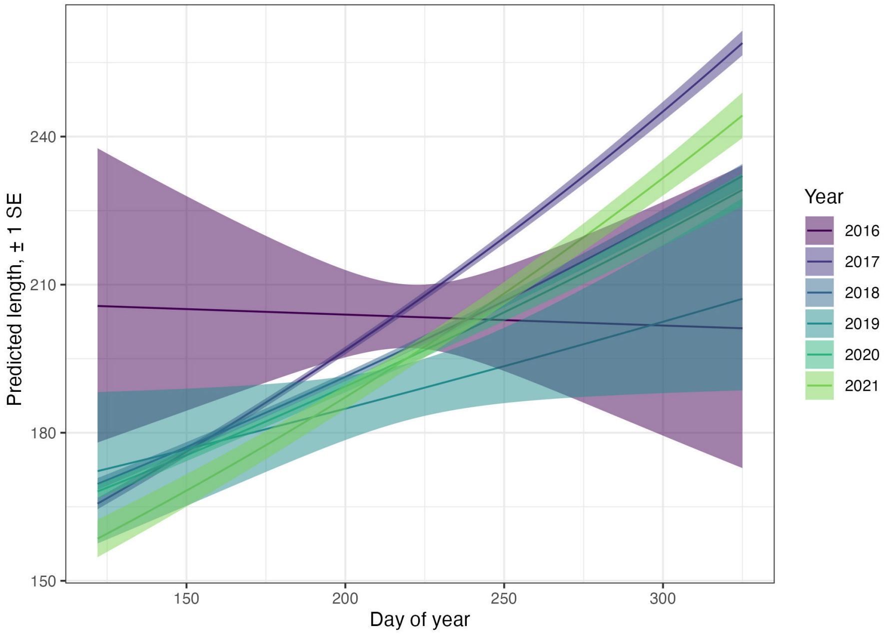

FIGURE 4 Predicted lengths of small Pacific Lampreys, showing year-specific growth rates.

small lampreys. Finally, gut fullness for both small and large lampreys was influenced by latitude and year but not by source or day, with fullness in 2017 being significantly lower (4.5% BW; $n=657$) for small lampreys and higher (11.5% BW; $n=29$) for large lampreys (Tables S5 and S6). Gut fullness in small lampreys decreased by 0.14% BW/degree latitude, while fullness increased by 0.97% BW/degree latitude for large lampreys.

Western River Lamprey

We obtained catch records for 72 Western River Lampreys caught from marine waters between May 22 and September 22 in 2003–2021. Most were caught near the surface with either surface trawls ($n=51$) or purse seines ($n=4$), but records also included individuals caught in midwater trawls by the Pacific Hake survey and fishery ($n=12$) and in bottom trawls by the groundfish survey ($n=4$; Table 1). The mean size of Western River Lampreys was 285.5 mm TL (range = 115–346 mm TL; $n=57$; Figure 5) and 30.7 g (range = 1.65–51.00 g; $n=10$). There was no statistical increase in length with date of capture ($p<0.05$), although the two smallest individuals (115 and 154 mm TL) also had the earliest capture dates (May 22 and 25, respectively). The length of Western River Lampreys caught in surface trawls and purse seines (mean ± SD = 285.4 ± 45.9 mm TL) was greater than that of individuals from the groundfish survey (219.6 ± 50.9 mm TL); only one individual (295 mm TL) was measured in the Pacific Hake survey. Four fish had both length and weight measurements, and their mean CF was 0.183 (range = 0.108–0.213).

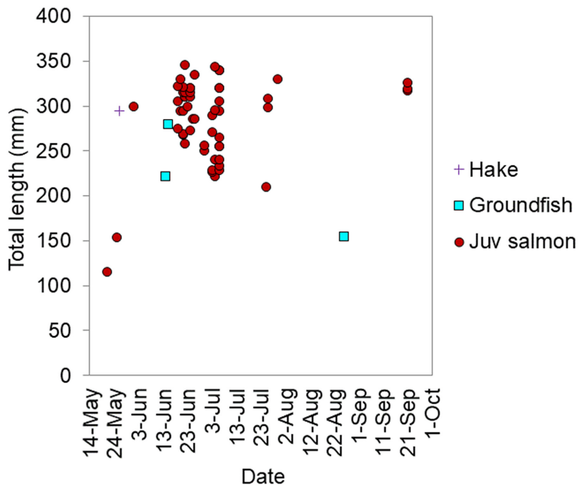

FIGURE 5 Total length (mm) of Western River Lampreys by day of year for all years (2007–2021) combined. The source of the lampreys (Pacific Hake survey and fishery [Hake], groundfish survey [Groundfish], or juvenile salmon survey [Juv salmon]) is indicated.

Western River Lampreys were widely distributed from Trinidad Head, California (41.1°), to Estevan Point on Vancouver Island, Canada (49.2°), at an average distance of 20.7 km from shore (range = 1.9–62.3 km; Figure 3). Nearly half of the Western River Lampreys were caught near the mouth of the Columbia River, which was also an area with large research effort. Water depth at capture was greater for individuals caught by the Pacific Hake survey and fishery (mean ± SD = 262.3 ± 123.3 m) and the groundfish survey (266.7 ± 165.3 m) than for individuals caught

TABLE 2 Numbers and sizes of fish recorded with lamprey wounds and the source(s) of the observations; species denoted by an asterisk have not previously been identified as lamprey hosts (Clemens et al. 2019). Abbreviations: AD, anterior dorsal; AV, anterior ventral; H, head; PD, posterior dorsal; PV, posterior ventral; T, tail.

Species	Number with wounds	Mean length (cm; *n*)	Location(s) of wounds	Source(s)[a]
Pacific Hake *Merluccius productus*	194	44 (182)	H, AD, PD, AV, PV	1, 2, 3
Lingcod *Ophiodon elongatus*	18	73 (2)	AV, PD, PV	3
Widow Rockfish *Sebastes entomelas*	12	42 (10)	AD, PD, AV	1, 2
Jack Mackerel *Trachurus symmetricus*	3	46 (1)	AV, PV	1, 2
Sablefish *Anoplopoma fimbria*	2	–	AV, PV	3
American Shad *Alosa sapidissima**	1	–	–	1
Arrowtooth Flounder *Atheresthes stomias*	1	–	AV	3
Bigfin Eelpout *Lycodes cortezianus*	1	–	AV	3
Chilipepper *Sebastes goodei**	1	–	PV	3
Dover Sole *Microstomus pacificus**	1	–	H	3
Flathead Sole *Hippoglossoides elassodon*	1	38 (1)	AD	3
Pacific Cod *Gadus macrocephalus*	1	57 (1)	H	3
Petrale Sole *Eopsetta jordani*	1	–	AV	3
Ragfish *Icosteus aenigmaticus**	1	–	AV	1
Shortbelly Rockfish *Sebastes jordani**	1	22 (1)	AV	2
Splitnose Rockfish *Sebastes diploproa**	1	–	AV	3

[a] Sources: 1 = observers on commercial Pacific Hake vessels; 2 = Northwest Fisheries Science Center (NWFSC) Pacific Hake survey; 3 = NWFSC groundfish survey.

by either surface trawls (53.2 ± 31.5 m) or purse seines (74.6 ± 40.9 m).

Fishes with Pacific Lamprey wounds

We had photographs and records of presumed Pacific Lamprey wounds on 240 fish representing 16 species, including four rockfish and four flatfish species (Table 2; Figure 6). Most fish with lamprey wounds were Pacific Hake ($n = 194$), Lingcod ($n = 18$), or Widow Rockfish ($n = 12$). Most fish just had a single wound, but several Lingcod and Pacific Hake had two or three wounds on their bodies. The latitude of fish collected with lamprey wounds stretched over 1500 km: from 35.6° (near Point Piedras Blancas, California) to 48.40° (Cape Flattery, Washington; Figure 7). In most cases, only a few (<5) fish with wounds were identified from a single haul. However, 42 Pacific Hake and nine Lingcod with wounds were reported in single hauls by the Pacific Hake and groundfish surveys, respectively. The mean size of fish with lamprey wounds ranged from 22 cm for a single Shortbelly Rockfish to 73 cm (range = 60–87 cm) for Lingcod (Table 2). We had the most measurements for Pacific Hake, which ranged in size from 25 to 64 cm (mean = 44 cm).

Most lamprey wounds were located on the sides of the fish (86%), slightly more common above (47%) than below (41%) the lateral line and more frequently anterior (53%) than posterior (35%) to the anus. A few fish had wounds on their heads (11%), and only three individuals (1%) had wounds on their tails. Wounds were generally severe (deep pits with the musculature fully visible and little healing), although some were comparatively benign (skin only partially broken, but the attachment point was descaled; Figure 6) and included healed wounds.

DISCUSSION

We assembled data for nearly 2700 Pacific and Western River lampreys from marine waters off the west coast of North America over 30 years, including over 1900 lampreys that were collected specifically for this study during 2016–2022. Most Pacific Lampreys were small (<300 mm TL; 100 g; Figure 1) and likely in their first year of marine life based on their overlapping size with transformed

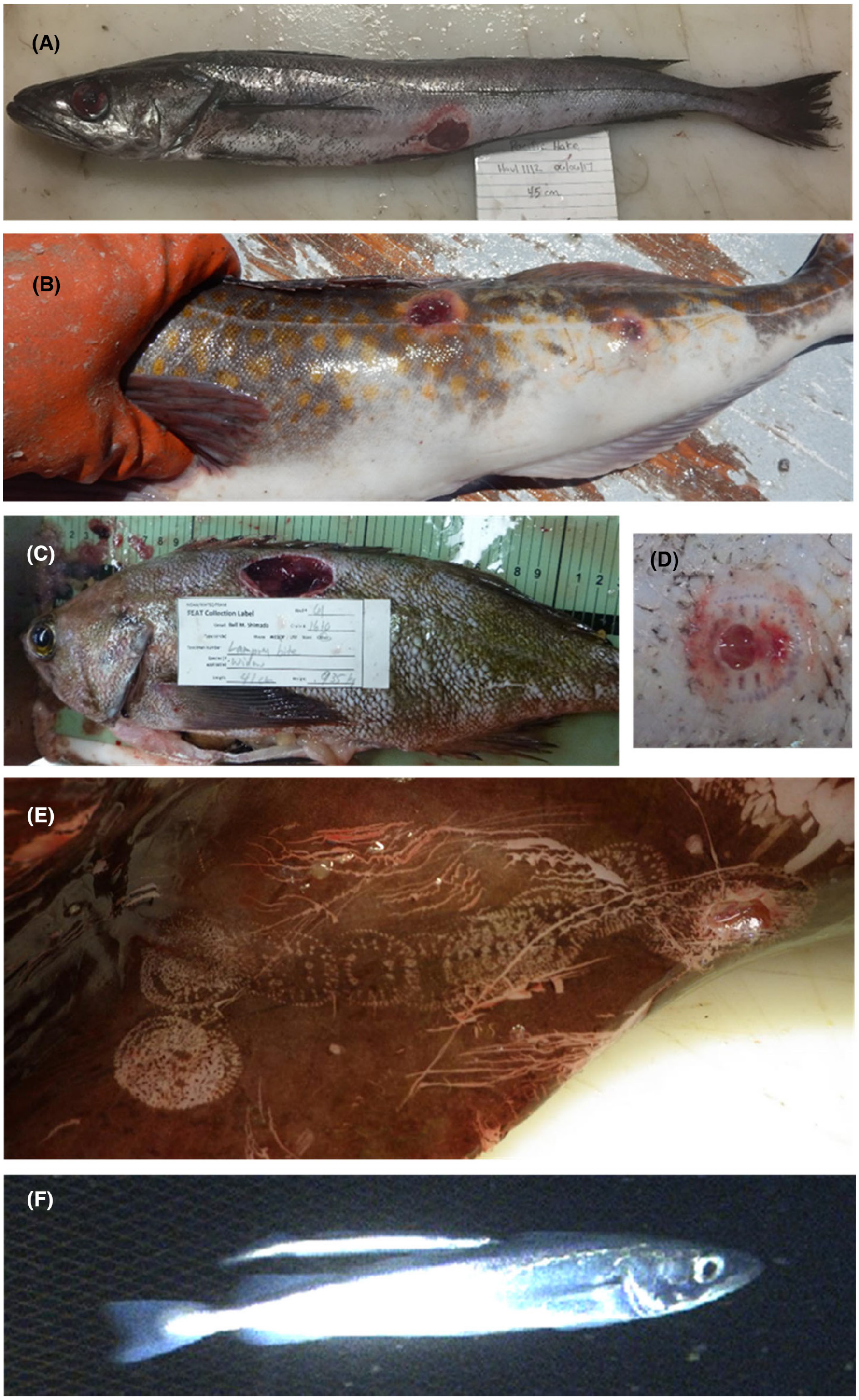

FIGURE 6 Examples of lamprey wounds on fishes and a lamprey attached to a Pacific Hake. Typical lamprey wounds on individual fish are depicted: (A) Pacific Hake, (B) Lingcod, (C) Widow Rockfish, (D) Pacific Hake, and (E) Ragfish. Pacific Lamprey dentition is clearly visible in panels D and E, while panel B shows an unusual double wound. (F) A Pacific Lamprey attached to a Pacific Hake was photographed inside a midwater trawl (approximate depth = 270 m). (Source: National Oceanic and Atmospheric Administration.)

juveniles (macrophthalmia; Clemens 2019) in freshwater (Beamish and Levings 1991; Weitkamp et al. 2015). The largest Pacific Lampreys in our collection (>600 mm TL) were comparable to the size of adults caught in freshwater (reviewed by Clemens et al. 2019), and a few had maturing gonads (mean length = 589 mm TL; range = 523–714 mm TL; $n = 13$), indicating that they were preparing to re-enter freshwater to spawn.

Most Pacific Lampreys had moderate amounts of material (blood, muscle, or digested) in their guts (5.5% BW;

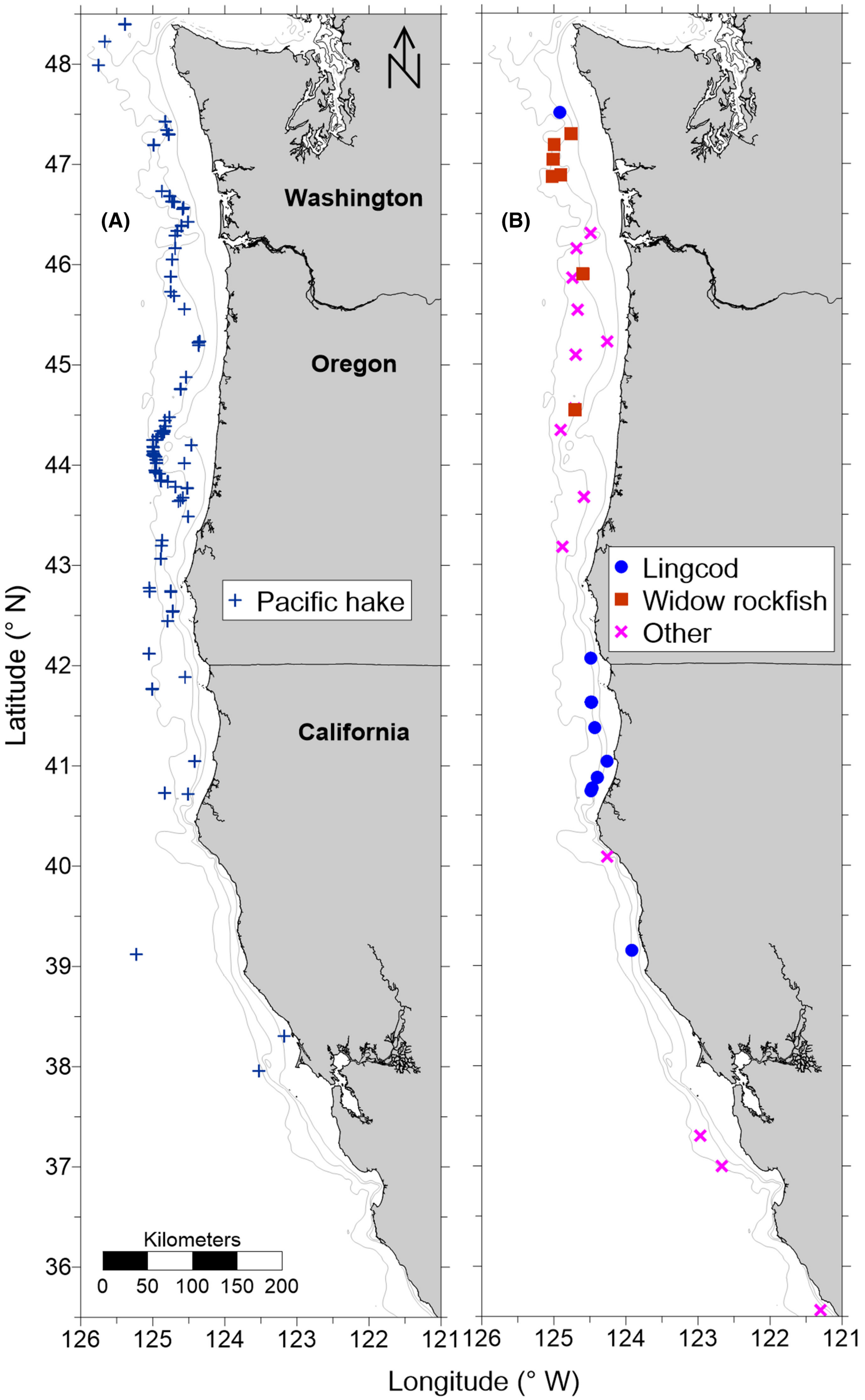

FIGURE 7 Locations of fish identified with characteristic lamprey wounds: (A) Pacific Hake and (B) all other species. Contours indicate the 100-, 200-, and 1000-m isobaths.

Figure 2), and few (<2%) had empty guts, indicating high feeding success. However, some large Pacific Lampreys had truly impressive gut fullness, with contents contributing over one-fourth of their body weight (Figure 2)—something not often observed in marine fishes. In general, gut fullness was highly variable for individual Pacific Lampreys that were caught together in the same tow (mean coefficient of variation [100 × SD/mean] for 35 tows with ≥10 lampreys was 0.36), and gut fullness for lampreys caught in the same haul as extremely full (≥20% BW) individuals was only 4–45% of the extreme value. This indicates that although Pacific Lampreys are often caught with abundant potential hosts, their ability to exploit this resource is highly variable.

Pacific Lampreys were primarily associated with Pacific Hake, and Pacific Hake were the fish most frequently observed with lamprey wounds, consistent with characterization of Pacific Hake serving as a primary host for Pacific Lampreys along the west coast (Orlov et al. 2009). Given this extremely strong association, Pacific Hake likely play an important role in the dynamics of Pacific Lampreys in coastal waters of the west coast, as suggested by Murauskas et al. (2013). However, parasitizing the fish that supports the largest commercial fishery on the west coast (Edwards et al. 2022) is both beneficial and detrimental to Pacific Lampreys. High abundances of Pacific Hake translate into many potential hosts, which may result in increased growth and survival of lampreys (Murauskas et al. 2013). High Pacific Hake abundances also allow for greater harvest of Pacific Hake, which incidentally capture Pacific Lampreys as bycatch. Clearly, better information on the condition and survival of lampreys caught in commercial fishing nets is needed to develop best practices that minimize potentially negative consequences.

We expected that both Pacific and Western River lampreys would be congregated near the mouths of major west coast rivers, either having recently entered marine waters (small individuals) or preparing for the return to freshwater (large individuals). Instead, lampreys were widely distributed in coastal waters, with few obvious clusters of fish (Figure 3), thus indicating rapid marine dispersal. Most Pacific Lampreys are thought to both enter and leave marine waters in winter to early summer (Beamish 1980; Clemens et al. 2019), while Western River Lampreys enter the ocean in late spring or early summer and return to freshwater in the fall (Beamish 1980; Beamish and Neville 1995; Weitkamp et al. 2015). The distributions we observed indicate that these beginning and end dates for the marine phase likely are widely applicable. Model results indicate that both size and CF decrease with latitude for small Pacific Lampreys, which may reflect earlier ocean entry timing from southern rivers (Moyle et al. 2009). Use of genetic methods to follow Pacific Lamprey families from source rivers across marine waters or to identify regional genetic stocks (e.g., Hess et al. 2021, 2022) will allow for greater characterization of fine-scale oceanic movements.

Pacific Lamprey feeding behavior

Characteristic round wounds made by parasitic lampreys have been used to identify the species of fish that are parasitized by lampreys (e.g., Orlov et al. 2009; Siwicke and Seitz 2015; Simpkins et al. 2021). Our research adds six new species to the list of fishes that are known to serve as Pacific Lamprey hosts (Clemens et al. 2019; Renaud and Cochran 2019; Quintella et al. 2021): American Shad, Chilipepper, Splitnose Rockfish, Shortbelly Rockfish, Dover Sole, and Ragfish (Table 2). In addition, four species (Bigfin Eelpout, Jack Mackerel, Petrale Sole, and Widow Rockfish) that originated from this study were noted by Clemens et al. (2019). The diversity of fishes on this list, which includes pelagic and demersal species as well as several uncommon species (Ragfish and Bigfin Eelpout), confirms that Pacific Lampreys select their hosts opportunistically (Clemens et al. 2019).

Our data and observations also confirm that Pacific Lampreys did indeed make round wounds through their feeding behavior. Three Pacific Lampreys collected by observers on commercial Pacific Hake vessels were noted as being attached to fish when brought on deck: two individuals (162 mm, 9.7 g; and 175 mm, 13.9 g) were attached to Pacific Hake (450 and 410 mm TL, respectively), and one individual (165 mm TL, 9.9 g) was attached to an American Shad (size unknown). We also have images from underwater cameras taken during the Pacific Hake survey, which showed Pacific Hake entering the net with lampreys attached (Figure 6). Finally, in a few cases the lamprey's unique dentition is clearly visible on the fish's skin (Figure 6). Although there will always be round wounds that are questionable in nature, we are confident that most of the wounds we observed were the result of Pacific Lamprey feeding. Future research to identify hosts by using alternative methods, such as DNA metabarcoding of gut contents (e.g., Shink et al. 2019) or trophic biomarker signatures of lamprey and host tissues (e.g., Harvey et al. 2008; Pelekai 2021), is planned.

We expected that feeding success (as indicated by gut fullness) would positively relate to summer growth for small Pacific Lampreys and perhaps Pacific Hake abundances. However, the year with the highest growth rate (2017) had the lowest—not highest—gut fullness for small individuals, and the year with the highest gut fullness (2018; 6.3% BW) had low growth. Gut fullness for small (but not large) Pacific Lampreys was also largely independent of coastwide estimates of Pacific Hake abundance (Edwards et al. 2022). Specifically, in years (2017–2019) with high Pacific Hake abundances (4514×10^3 to 4818×10^3 metric tons), gut fullness for small individuals (5.3% BW; $n=1253$) was similar (5.4% BW; $n=437$) to that in years (2020–2021) with lower Pacific Hake abundances (3633×10^3 to 3770×10^3 metric tons). By contrast, gut fullness for large individuals was generally higher (8.8% BW; $n=63$) in years with more Pacific Hake and lower (5.6% BW; $n=43$) in years with fewer Pacific Hake. These results indicate that the ability of Pacific Lampreys to exploit available resources (i.e., host abundance) is highly variable and likely differs by lamprey life stage.

Relatively few Pacific Lampreys were caught together with groundfishes, but we observed many fish with lamprey wounds that were caught by the groundfish survey, including Lingcod and several species of rockfish (Table 2). Most of the species listed in Table 2 are predatory (versus planktivorous; Field et al. 2006) and could just as easily consume lampreys as lampreys can parasitize the fish. We have observed small lampreys in rockfish stomachs (J. Buchanan, unpublished data) and wounded Pacific Lampreys with clear teeth marks (Weitkamp, unpublished data), suggesting that predatory attacks on lampreys do happen and can be successful.

This vulnerability to predators may limit demersal habitat use by Pacific Lampreys and may explain why few lampreys (especially small individuals) were collected by the extensive groundfish survey and fishery. Fewer large predatory fish reside in pink shrimp habitats (Hannah et al. 2018), and we expected that Pacific Lampreys occupying these demersal habitats would have the lowest gut fullness. However, the "fishery" factor was not a significant source of variation for gut fullness, and lampreys caught by the shrimp fishery had as much material in their guts as those caught with abundant potential hosts. Because Pacific Hake are also voracious predators, we hypothesize that some small lampreys may feed on Pacific Hake or groundfish and then retreat to pink shrimp habitats where predatory fish abundance—and, therefore, predation pressure—are lower.

Analysis assumptions

Our analysis relied on Pacific and Western River lampreys that were caught by using several types of fishing nets (midwater, bottom, surface, and shrimp trawls). Although we deliberately did not calculate lamprey densities from the different gear types, we assumed that catches reflected the relative abundance of lampreys by fishery, location, and size. Clearly, catchability information for different gear types is needed to make this assumption, but such information does not exist. Because lampreys are long and thin, their orientation to the net (headfirst versus sideways) likely influences whether they might easily escape through the mesh (in addition to factors such as tow duration or the total abundance of fish in the net). The mesh size of all Pacific Hake and groundfish nets is large enough (>25 mm) that smaller lampreys can probably escape through the mesh; in contrast, lampreys are unlikely to escape from fine-mesh shrimp trawls. The vast majority (93%) of the Pacific Lampreys for which we had data were small and were caught in midwater trawls targeting Pacific Hake, suggesting that if large numbers of small Pacific Lampreys escaped from these trawls, our ratio of small to large Pacific Lampreys would have been even higher. Although some small lampreys undoubtedly escaped from midwater trawls, many were caught.

Lack of catchability information also makes it difficult to interpret observed patterns, especially when comparing among gear types. In particular, the relatively low catches of lampreys by the groundfish survey and fishery (<5% of total) despite large effort could be due to either (1) a lack of lampreys in those habitats or (2) much lower catchability in bottom trawls relative to midwater trawls. We have no reason to believe that catchability would greatly differ among midwater and bottom trawls, which have similar mesh sizes. The fact that both Pacific Lamprey abundances and fish with lamprey wounds were sparse south of San Francisco Bay leads us to conclude that the abundances of Pacific Lampreys in southern waters were truly low. Furthermore, this low marine abundance parallels precipitously low abundances of Pacific Lampreys in southern California rivers (USFWS 2019), yet it may be an important source for lamprey recolonization of southern rivers (Reid and Goodman 2020).

Absence of intermediate-sized Pacific Lampreys

One puzzling finding was the lack of intermediate-sized Pacific Lampreys—specifically those between 350 and 500 mm TL—either in historic records or among captured specimens (Figure 1). Given expected declines in natural mortality with increasing body size or age (Quinn and Deriso 1999), we would expect a decline in the number of lampreys with increasing size (i.e., lots of small lampreys, some intermediate-sized lampreys, and few large lampreys). Instead, out of 140 specimens that were 350 mm TL or larger, only 16 individuals (15%) were between 350 and 500 mm TL, whereas most ($n = 91$; 85%) were larger than 500 mm TL. We also expected these intermediate-sized fish to be actively feeding and therefore associated with some group of fishes, but their apparent absence from west coast surveys and fisheries suggests that they may have migrated elsewhere.

One possible destination for these intermediate-sized individuals is Alaskan waters, especially the Bering Sea, where Pacific Lampreys appear to concentrate despite the lack of large populations in the region's rivers (Orlov et al. 2008; Siwicke 2014; Orlov and Baitaliuk 2016; USFWS 2019). Several lines of evidence suggest that such an extensive migration by a fish that clearly is not a high-performance swimmer (e.g., Kirk et al. 2016) may indeed be possible. First, Pacific Lampreys collected in the Bering Sea include many individuals in this intermediate (350–500 mm TL) size range (Orlov et al. 2008; Siwicke 2014). Additionally, eight Pacific Lamprey specimens were collected by NMFS surveys in the Gulf of Alaska (51.79–59.33°, −135.39° to −177.69°) and those individuals averaged 384 mm TL (range = 335–610 mm TL). Although far from comprehensive, this indicates that at least some lampreys in northern waters are the size of the "missing" lampreys.

Second, two Pacific Lampreys appear to have made this amazing migration. One was tagged with a PIT tag in the western Bering Sea and was subsequently detected in the Columbia River at Bonneville Dam (Murauskas et al. 2019). The other was caught in the Bering Sea in 2016 and was genetically identified as a full sibling of a lamprey that was collected at Willamette Falls (Columbia River) 2 years later (Hess et al. 2022). This 5000-km-long journey may be facilitated by attaching to gray whales *Eschrichtius robustus*, which also migrate from Baja California and along the west coast to the Bering Sea and back each year. Although Pacific Lampreys have not been documented using gray whales as hosts to the best of our knowledge, they are known to attach to other species of large whale (Clemens et al. 2019).

How long it might take Pacific Lampreys to make this migration is not known, as the aging of juvenile Pacific Lampreys is problematic (Pelekai et al. 2023). If we apply our April–November growth rate (0.37 mm/day [80 mm/year]) for small lampreys to larger individuals, it results in the following size ranges for Pacific Lampreys of OAs 2–5 (years): 300–380 mm TL for OA 2; 380–460 mm TL for OA 3; 460–540 mm TL for OA 4; and 540–620 mm TL for OA 5 (faster [slower] assumed growth rates would result in younger [older] predicted ages). Therefore, 350–500-mm TL Pacific Lampreys in the Bering Sea would be in their second to fourth ocean years, respectively, suggesting that it might take an average of 3 years to travel to and from distant waters. These length-based age estimates are also consistent with new genetic-based estimates showing that ocean life for some Pacific Lamprey populations lasts 5–7 years (Hess et al. 2022). Pacific Lampreys are also present in the Bering Sea throughout the year (including winter; Orlov and Baitaliuk 2016), consistent with an extended stay in northern waters. The possibility that Pacific Lampreys originating from the west coast may reside in the Bering Sea (and therefore comprise a single, widely dispersed population; Murauskas et al. 2016) is an important topic that deserves further investigation for both biological interest and conservation implications.

Western River Lamprey

Most of the catches and records that we had for Western River Lampreys were from surface waters on the continental shelf (Table 1; Figure 3). Especially notable were higher catches near the mouth of the Columbia River, which is not surprising given that Western River Lampreys are often caught in the Columbia River estuary during summer (Weitkamp et al. 2015). These catches likely reflect high effort near the Columbia River mouth rather than reflecting high abundance, as both multi-day gear trials with surface trawls (Wainwright et al. 2019) and nearshore purse seining (Weitkamp, unpublished data) caught nearly one-quarter (23 of 72) of the Western River Lampreys in our records. In contrast, systematic sampling across a grid of stations by the juvenile salmon survey caught Western River Lampreys from Cape Flattery, Washington, to Newport, Oregon, with similar (but not higher) catches on the Columbia River transect. These patterns suggest that Western River Lampreys were widely distributed off the coasts of Washington and northern Oregon in summer.

Our results are also consistent with findings from the Strait of Georgia, where Western River Lamprey marine ecology has been extensively studied (Beamish 1980; Beamish and Neville 1995; Wade and Beamish 2016). Those studies showed that Western River Lampreys were caught in surface waters (especially the Fraser River plume) within the Strait of Georgia from May to September, with a peak in July (Beamish 1980, 2014; Beamish and Neville 1995). Juvenile salmon surveys conducted in late September off the Washington and Oregon coasts during 1998–2012 failed to catch any Western River Lampreys (C. Morgan, Oregon State University, unpublished data), perhaps reflecting their earlier return to freshwater. This timing also matches Western River Lamprey catches from the Columbia River estuary, where Western River Lampreys were present from April through September but were absent by October (Weitkamp et al. 2015).

In the Strait of Georgia, Western River Lampreys preyed extensively on Pacific Herring and juvenile Chinook Salmon *O. tshawytscha*, resulting in high mortality (Beamish 1980; Beamish and Neville 1995). These species were also common prey in the Columbia River estuary (Weitkamp et al. 2015). However, we do not have evidence demonstrating similarly intense predation on these species in coastal waters off Washington and Oregon. We have observed very few Western River Lamprey wounds on juvenile salmon caught in the juvenile salmon survey since 1998 (Weitkamp, unpublished data), even though this survey was the largest source of Western River Lampreys. Unfortunately, no coastal fisheries or surveys consistently catch large numbers of Pacific Herring that could be examined for wounds or scars. Focused efforts to catch Western River Lampreys in marine waters, paired with techniques such as DNA metabarcoding of gut contents (e.g., Shink et al. 2019), are needed to resolve this important aspect of their marine ecology.

Our historic records and catches indicate surprisingly few Western River Lampreys (72 individuals) in coastal waters over nearly 25 years. One interpretation of this low marine abundance is that it simply reflects low overall abundance in freshwater. Unfortunately, the abundance of only one Western River Lamprey population (Fraser River) has been estimated (Beamish 1980; Beamish and Youson 1987; Oregon Department of Fish and Wildlife 2020); therefore, direct comparison of freshwater and marine abundances is not currently possible. However, Western River Lampreys are regularly caught in smolt traps targeting out-migrating juvenile salmon (e.g., Hayes et al. 2013), in coastal estuaries (Bond et al. 1983; Beamish 2010; Weitkamp et al. 2015), and in the Strait of Georgia (Beamish 1980; Beamish and Neville 1995; Wade and Beamish 2016), indicating that they are not exceedingly rare in these habitats. This leads us to conclude that although Western River Lampreys make extensive use of estuaries and inland seas, their use of coastal marine habitats may be quite limited. If true, this greatly reduces the geographic scope for studies of their marine life history and ecology, which should focus instead on estuarine and inland sea habitats.

Although most Western River Lampreys were caught in surface waters on the continental shelf, we also have 14 records and a single specimen of Western River Lampreys that were caught at or near the bottom in 97–434-m-deep water and 23–62 km from shore (Figure 3). This depth and location are much more consistent with Pacific Lampreys, suggesting that some of these fish were misidentified. However, the species of the one collected specimen was confirmed using both dentition and genetics (J. E. Hess, personal observation), and we have high confidence that four of the lampreys that were caught in bottom trawls at depths of 97–435 m were properly identified. Possible explanations for the unusual location and depth are that these individuals were advected offshore and unable to maintain their position high in the water column or they were transported to depth while preying on fish; in either case, they faced an uncertain future. Alternatively, these observations could represent a successful, Pacific Lamprey-like existence for some Western River Lampreys. Clearly, proper identification of ocean-caught lamprey species is essential to understand lamprey marine ecology.

Management implications

Our results provide useful information for fisheries that catch anadromous lampreys and for the conservation management of both Pacific and Western River lampreys. First, our study clearly demonstrates that (1) Pacific Lampreys (but not Western River Lampreys) are caught as bycatch by commercial fisheries targeting Pacific Hake, groundfish, and pink shrimp; and (2) Pacific Hake and several species of groundfish are commonly parasitized by Pacific Lampreys. Although catches of Pacific Lampreys are relatively rare in these large fisheries (Somers et al. 2020), this mortality may have population-level consequences for small lamprey populations.

To minimize the impacts of this interaction, best practices for handling lampreys caught in net fisheries need to be developed. This includes documenting the condition of lampreys when caught in commercial nets (i.e., dead or alive); whether they are retained or released; and, if they are released, the duration between catch and release. With this knowledge, guidance could be provided to maximize the chance that lampreys caught by fisheries have high subsequent survival.

Second, our results inform the management of both species by better defining their geographic distributions, habitat use, and life history parameters, all of which are necessary to develop effective conservation measures. As discussed earlier, our results suggest that Western River Lampreys make limited use of coastal marine habitats and instead are largely restricted to estuaries or inland seas, thus reducing the geographic scope of their marine range. In contrast, we believe that the marine distribution of Pacific Lampreys along the west coast is larger than expected, spanning local coastal waters to the Bering Sea. Accordingly, assessments relating host availability to adult abundances (e.g., Murauskas et al. 2013) will need to consider this entire range. Use of genetic tools with individuals collected in marine waters has refined estimates of the location and duration of the marine phase (Hess et al. 2020, 2022) and should provide resolution of fine-scale movements for individuals with known origins. Overall, our results provide a solid foundation for future research on lamprey marine ecology and should prove useful for informing lamprey conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this analysis are available upon request.

ETHICS STATEMENT

All authors meet the requirements for authorship summarized in the Best Practice Guidelines on Research Integrity and Publishing Ethics. Treatment of all fish used in this analysis followed the current American Fisheries Society policy on the use of fishes in research.

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