

CHAPTER SEVENTEEN

TRENDS IN THE CATCHES OF RIVER AND PACIFIC LAMPREYS IN THE STRAIT OF GEORGIA

JOY WADE AND RICHARD BEAMISH

Introduction

Pacific lamprey (*Entosphenus tridentatus*) and river lamprey (*Lampetra ayresii*) are anadromous fishes that enter and feed in the Strait of Georgia British Columbia, Canada. The Strait of Georgia is the body of water between Vancouver Island and British Columbia mainland that has been an area of study of juvenile Pacific salmon (*Oncorhynchus* spp.) survival (Beamish et al. 1998, 2012) Because of the recent interest in understanding factors affecting Pacific lamprey abundances in the Columbia River (Murauskas et al. 2013), we use incidental catches of lampreys from studies focused on juvenile salmon in the Strait of Georgia to improve our understanding of marine survival. Specifically, it is hypothesized that population abundance of Pacific lamprey and river lamprey is regulated by prey availability which in turn is highly influenced by environmental conditions as has been found for Pacific salmon (Ruggerone & Goetz 2004; Duffy & Beauchamp 2011; Beamish et al. 2010; Swain et al. 1991).

It is difficult to get information on Pacific lamprey and river lamprey during their marine life as trawl nets are designed to catch juvenile salmon and not to retain lamprey, as well, some investigators are reluctant to handle the ones that are retained. The intent of this paper is to use information collected through the study of other species such as Pacific salmon (*O. spp.*), Pacific herring (*Clupea pallasii*) and groundfish, to help understand the early marine survival of Pacific and river lamprey within the Strait of Georgia.

Pacific lamprey

In British Columbia, Pacific lamprey are considered common and have been found in most large freshwater rivers as well as small rivers which empty into large rivers (R. Beamish, personal observations). Beamish (1980) notes that Pacific lamprey are widespread in British Columbia and have a greater distribution than previously thought as they have been observed in all the commercially important fishing areas off the west coast of Canada. Globally, they are found from the Sea of Japan to the Bering Sea to the eastern North Pacific Ocean south to Mexico (Mecklenburg et al. 2002; Renaud 2011).

One of the sources of Pacific lamprey that enter the Strait of Georgia is the Nicola River, a major tributary of the Thompson River, British Columbia. Pacific lamprey from the Nicola River spend approximately 4 or 5 years as ammocoetes with young adults migrating downstream beginning in September (Beamish & Levings 1991). Ammocoetes and young adults sampled from the Fraser River were aged using statoliths (Beamish & Levings 1991). The oldest ammocoetes were age 6, recently metamorphosed lamprey ranged in age from 4 to 8 years (Beamish & Levings 1991). Ammocoete ages were also determined by Beamish and Northcote (1989) from data collected before and after a dam was constructed on the outlet of Elsie Lake, British Columbia. It was possible to estimate the age of Pacific lamprey ammocoetes to be approximately 7 years because lamprey spawning was prevented after the construction of the dam. (Beamish & Northcote 1989). The average length of young adult Pacific lamprey collected from the Fraser River in the spring of 1985 was 12.1 cm; 10.6 cm from the period March to May 1986 and; 12.3 cm from early April to early May 1987 (Beamish & Levings 1991). The time from metamorphosis to sea water entry has been reported to take up to one year (Beamish & Levings 1991) however, recently metamorphosed individuals may begin feeding in freshwater or in salt water by mid-October (Beamish 1980). Feeding in freshwater is most likely temporary as it has not been possible to keep metamorphosed anadromous Pacific lamprey in the laboratory in freshwater for their entire adult life span (Clark & Beamish 1988). Reports of freshwater feeding are for a short period of time after metamorphosis (Beamish & Northcote 1989) or in one case, a new species (Beamish 1982). Pacific lamprey from the Fraser River enter the Strait of Georgia over a protracted period of time, from March until the end of July (Beamish & Levings 1991). They return to freshwater either in the spring or fall and begin their upstream migration (Beamish 1980). Those lamprey populations that return in the spring tend to migrate farther upstream than

fall returning fish, however, both spawn between April and July the following year (Beamish 1980).

The Pacific lamprey population in the US Pacific Northwest has been reported to be in decline in recent years (Luzier et al. 2011; Murauskas et al. 2013; Mayfield et al. 2014). In 2003, the US Fish and Wildlife Service petitioned to list Pacific lamprey, among other lamprey species, as threatened or endangered under the Endangered Species Act of 1973 (Hayes et al. 2013). The petition was denied, in part, because of a lack of specific population information such as distribution, abundance and population structure (Klamath-Siskiyou Wildlife center and ten other conservation organizations, 2003). As a result of this determination, a range-wide conservation initiative was undertaken (Luzier et al. 2011), and an assessment was performed which found that Pacific lamprey populations have declined and many are at risk of extirpation (Hayes et al. 2013).

River lamprey

River lamprey are distributed from the Sacramento River in California north to Juneau, Alaska (Scott & Crossman 1973; Renaud 2011). In British Columbia, river lamprey have most frequently been reported from larger rivers such as the Fraser River (Beamish 1980; Beamish & Northcote 1989; Beamish & Neville 1995) where it has been shown to be the dominant organism by weight in the sediments of the 160 km section of the river from Hope, British Columbia to the mouth of the Fraser River (Beamish & Youson 1987). Beamish (2010) also reports samples of river lamprey from the Nass River, Knight Inlet (Klinaklini River) and Puget Sound. It is now known that some river lamprey in Puget Sound originate from several rivers flowing into the sound (Hayes et al. 2013) indicating that they also occur in smaller rivers.

Metamorphosis begins in July but river lamprey do not enter the Strait of Georgia until the following year, from May to July (Beamish 1980; Beamish & Youson 1987). Metamorphosis is not complete until the oesophagus is open in the spring of the year following the onset of metamorphosis which delays salt water entry. Once the oesophagus opens, the lamprey can osmoregulate in salt water (Beamish & Youson 1987). They return to freshwater from September until late winter with spawning occurring in freshwater from April to June (Beamish 1980). The lifespan from metamorphosis to death of a river lamprey is approximately two years (Beamish 1980).

Based on the results of a survey conducted in 1975, river lamprey abundance in the Strait of Georgia was estimated at 667,000 (Beamish & Williams 1976). Although the major prey of river lamprey entering the Strait of Georgia is Pacific herring, Pacific salmon remain an important component of the diet (Beamish & Neville 1995). In efforts to understand the potential causes of the marine mortality of salmon, Beamish and Neville (1995) estimated that river lamprey from the Fraser River killed a minimum of 20 million juvenile Chinook salmon (*O. tshawytscha*) and 2 million juvenile coho salmon (*O. kistutch*) in 1990 and; 18 million juvenile Chinook salmon and 10 million coho salmon in 1991. In 1991 alone, this equated to 65% and 25% of the total Canadian hatchery production of coho and Chinook salmon, respectively (Beamish & Neville 1995).

Methods

Temperature data

Temperature data have been compiled from 1969 to 2011 from the central Strait of Georgia, British Columbia. Oceanographic data including sea level height, sea surface temperature and salinity are taken at lighthouses in the Strait of Georgia and managed by the Department of Fisheries and Oceans Canada's Institute for Ocean Sciences. Methodology for daily sea surface temperature and salinity have remained unchanged since the beginning of the time series and are described in Fissel et al. (1991).

Trawl catches

Lampreys were captured in trawls that were fished using the Government of Canada research vessel, *W.E. Ricker*. Standardized trawl surveys were performed as described in Beamish et al. (2000). Standardized trawl surveys were used to study the ocean life of juvenile Pacific salmon in the Strait of Georgia (Beamish et al 2000). A model 250/350/14 trawl (Cantrawl Pacific Ltd., Richmond, BC) was fished. The front end was 54m long with large meshes (ranging < 2 m to > 3.8 m wide). The intermediate section of the net contained mesh ranging from 1.6 m to 20 cm; the cod end meshes were 10 cm with a 1 cm liner in the last 7.6 m.

A fixed survey design using track lines was used for these juvenile salmon surveys in the Strait of Georgia (Fig. 17-1) (Beamish et al. 2000). The survey area was 5,899 km² and encompassed approximately 93% of the total area of the Strait of Georgia (Beamish et al. 2000). Surveys were

normally conducted in July and September. Most sets were in the top 45m, and the proportion of deeper sets was consistent among surveys.

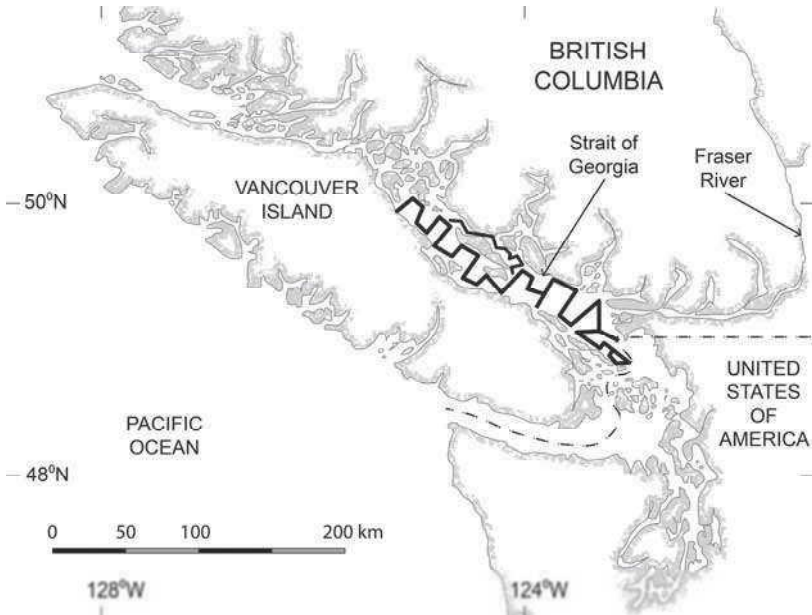


Figure 17-1. Standard track lines (bold) for trawl surveys in the Strait of Georgia. Sets were evenly spaced along these lines.

Catches of lampreys were standardized to 30 minute sets and summed for each depth strata. After 2011 the research cruises were staffed differently than had been done in previous years. Thus our data on catches from the trawl survey terminate after 2011 except for some specific reports where we are confident of the identifications. Catch data by depth strata are presented to demonstrate the depths over which lamprey have been captured in the Strait of Georgia. The depth data for river lamprey were only available for July and September 1997 to 2002 and July 2004. Catch per unit effort (CPUE) was calculated as the number of fish captured per set. CPUE for river lamprey was calculated for 1998 to 2011 with the exclusion of 2003 as only the September trawl data were available. It is probable that the lamprey catches, and subsequently CPUE, are low because the survey methods and net were not designed for the capture of lamprey.

A species distribution survey provided relative abundance estimates of Pacific hake (*Merluccius productus*) and walleye pollock (*Gadus chalcogrammus*). These research surveys were in addition to the July and September surveys performed for salmonid research however, the same fishing methodologies applied. Catches of Pacific hake and walleye pollock include young-of-the-year, juvenile and mature fish at different depths. Sets were made at varying depths from the bottom to the surface throughout the Strait of Georgia. This allowed for the determination of species composition throughout the water column within a small area.

Results

Temperature

There was a warming trend from 1969 to 2003 followed by a cooling trend to 2011 (Fig. 17-2). The warming trend that was evident from the beginning of the time series in 1969 changed to a cooling trend in the early 2000's. From 1969 to 2003 the average annual increase was 0.98°C at the surface and 0.94°C at 10m. From 2004 to 2011 there was a decrease in surface temperature of 0.63°C and a decrease of 1.25°C at 10m.

Pacific lamprey

Total catch of Pacific lamprey in the Strait of Georgia (1998-2011) from trawl surveys was highest in 1998 (n=28) and declined until 2005 (n=0) with catches increasing beginning in 2008 to 12 individuals in 2011 (Table 17-1). Pacific lamprey CPUE was highest in 1998 at 0.15 and lowest in 2005 and 2008 at 0 (Fig. 17-3).

In the July 2013 survey in the Strait of Georgia an exceedingly large catch of Pacific lamprey (n=132) was landed off the central Strait of Georgia at a depth of 45 m (Table 17-2). In this same set, 464 walleye pollock were captured, many with lamprey scars (Fig. 17-4, centrefold, page iii). This many Pacific lamprey in one set was the largest ever recorded during these surveys.

Figure 17-2 (next page). Average annual temperature from the Strait of Georgia for surface and 10m from 1969 to 2011 showing the warming trend to about 2003 followed by a cooling trend.

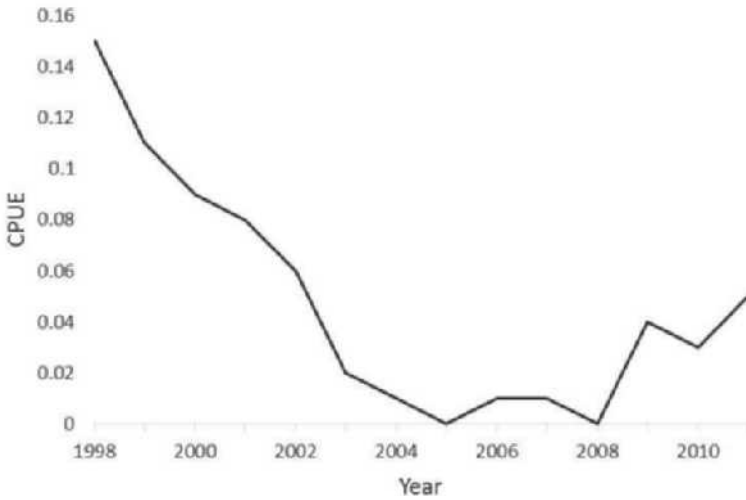
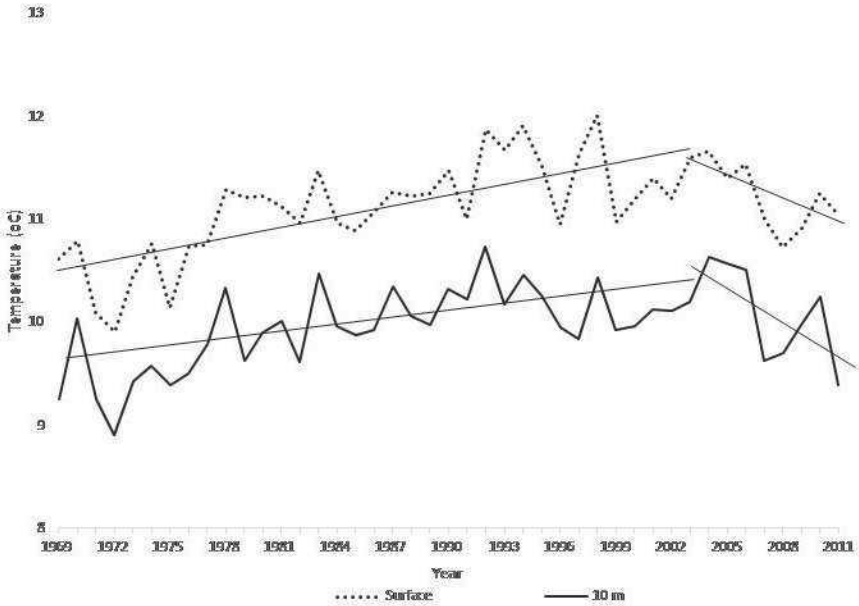


Figure 17-3. Pacific lamprey CPUE showing a declining trend from 1998 to 2008 followed by an increasing trend after 2008.

Table 17-1. Number of Pacific lamprey caught in trawl surveys (1998-2011).

Year	Catch
1998	28
1999	20
2000	15
2001	15
2002	10
2003	2
2004	1
2005	0
2006	2
2007	2
2008	0
2009	6
2010	7
2011	12

Table 17-1. Catch of Pacific lamprey off central Strait of Georgia in late June/ early July 2013.

Date	Depth (m)	Catch
27 June	45	132
30 June	60	10
2 July	15	1
2 July	60	1
3 July	60	1
4 July	45	3
4 July	60	16
4 July	0	2
5 July	0	2
6 July	15	1
Total		169

Pacific lamprey were captured throughout the water column, between the surface (0-15 m) and 500 m depth (Table 17-3). The greatest number of Pacific lamprey captured per set (CPUE) was 3.6 at 31-100 m depth followed by 2.4 at 101-500 m depth. The smallest CPUE was at the surface (1.3) and 16-30 m (2.2) depth.

Table 17-3. Catch of Pacific lamprey by depth (1994 to 2002).

Depth	Catch	Number of sets	CPUE
0-15 m	78	60	1.3
16-30 m	20	9	2.2
31-100 m	93	26	3.6
101-500 m	47	20	2.4
Total	238	115	
Average			2.4

River lamprey

Catches of river lamprey were higher in July (n=559) than in September (n=154) (Table 17-4). CPUE was lowest in 2005 at 0.13 and were the largest in 1999 at 1.75 (Fig. 17-5). Overall, there was a declining trend with a low CPUE from 2005 to 2011 ranging from 0.13 to 0.72 (Fig. 17-5).

Table 17-4. Catch of river lamprey (1998-2011) (* only total catches available for these years).

Year	Catch		
	July	September	Total
1998	153	18	171
1999	308	13	321
2000	124	30	154
2001	286	16	302
2002	117	9	126
2003		9	9
2004	271	7	278
2005	16	4	20
2006	37	4	41
2007	64	12	76
2008	68	12	80
2009	103	20	123
2010*			59
2011*			74
Total	559	154	1834

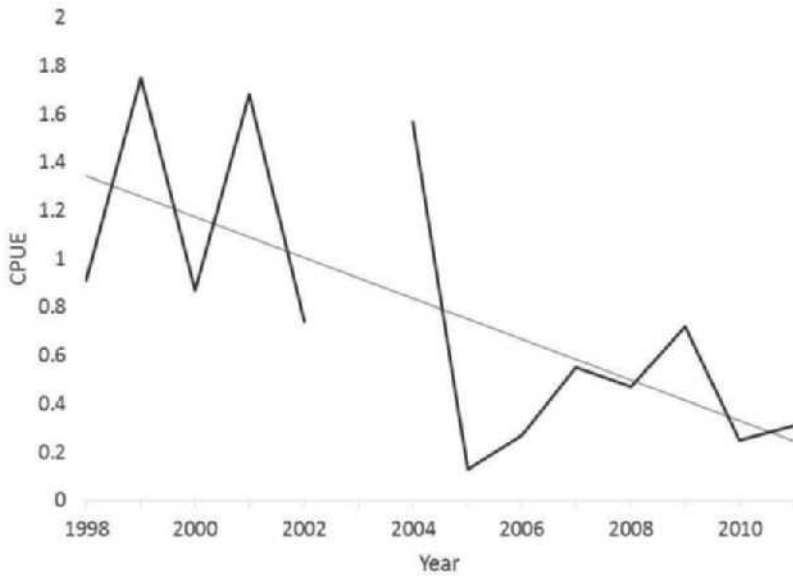


Figure 17-5. River lamprey CPUE in the Strait of Georgia (1998-2011) showing a declining trend. There was no survey in July 2003.

The majority of river lamprey (98%) were caught in the top 30 m. The CPUE for river lamprey, 4.9, was highest at the surface (0-15 m), 1.2 at 16-30 m and 1.3 at 31-100m (Table 17-5). A total of 46 river lamprey were captured at depths greater than 30 m in a total of 33 sets for a combined CPUE of 1.4.

Table 17-5. Catch of river lamprey by depth (1997 to 2002 July and September; July 2004).

Depth	Catch	Number of sets	CPUE
0-15 m	1942	395	4.9
16-30 m	23	20	1.2
31-100 m	35	27	1.3
101-200 m	11	6	1.8
Total	2011	448	
Average			2.3

In the species distribution survey, the total catch of Pacific hake was 53,918 and 17,241 walleye pollock. CPUE of Pacific hake ranged from a low of 168 in October 2009 to a high of 2035 in September 2012 (Table 17-6). CPUE of walleye pollock ranged from a low of 19 in September 2012 to a high of 1707 in October 2013 (Table 17-6). CPUE was approximately 2.5 times higher for Pacific hake than walleye pollock over this time period.

Table 17-6. Catch of Pacific hake and walleye pollock during species distribution surveys.

Date	Pacific hake			Walleye pollock		
	Catch	Number of sets	CPUE	Catch	Number of sets	CPUE
October 2009	1174	7	168	212	3	71
July 2011	3929	8	491	320	8	40
September 2011	4475	4	1119	1358	3	453
September 2012	24427	12	2035	155	8	19
October 2013	4586	5	917	10245	6	1707
March 2013	15327	16	958	4951	14	354
Total	53918	52		17241	42	
Average			948			441

Discussion

Our study shows that there are trends in the catches of both Pacific lamprey and river lamprey in the Strait of Georgia. Despite the small catches, there is no indication of randomness in the catches. Pacific lamprey catches declined until there was a cooling trend in the Strait of Georgia which we propose resulted in an increase in the walleye pollock abundance, a major prey of Pacific lamprey in the Strait of Georgia. Although our study ends in 2011, we provide catch data from one cruise (2013) that shows that large numbers of Pacific lamprey are associated with schools of walleye pollock. Our species distribution surveys showed that Pacific hake were approximately 2.5 times more abundant than walleye pollock. An assessment in the early 1980s of the relative abundance of Pacific hake and walleye pollock showed that Pacific hake were approximately 16 times more abundant than walleye pollock (Thompson & McFarlane 1982). Thus, walleye pollock may have increased in abundance by about six times relative to Pacific hake abundance. We do not know the absolute abundance of walleye pollock, but it appears that there are more prey available for Pacific lamprey. It is

not known when the abundance of walleye pollock started to increase, but it is possible that it was associated with the beginning of the cooling trend around 2004. An increasing trend in lamprey abundance about 2008 would be consistent with an increasing walleye pollock survival that started approximately 2004. Our observation of an increase in Pacific lamprey catch with increase in preferred prey is similar to the increase in Pacific lamprey catches along the west coast of North America in association with increases in Pacific hake abundances (Murauskas et al. 2013) except that the preferred prey for Pacific lamprey in the Strait of Georgia is walleye pollock and not Pacific hake.

River lamprey catches were mostly in the surface waters as reported here and in Beamish (1980) and Beamish and Neville (1995). The dominant prey of Pacific lamprey are Pacific herring (Beamish & Neville 1995) with young-of-the-year Pacific herring found mostly found in the surface waters of the Strait of Georgia (Beamish et al 2012). Actively feeding river lamprey in schools of Pacific herring is commonly observed in the Strait of Georgia (Beamish 1980).

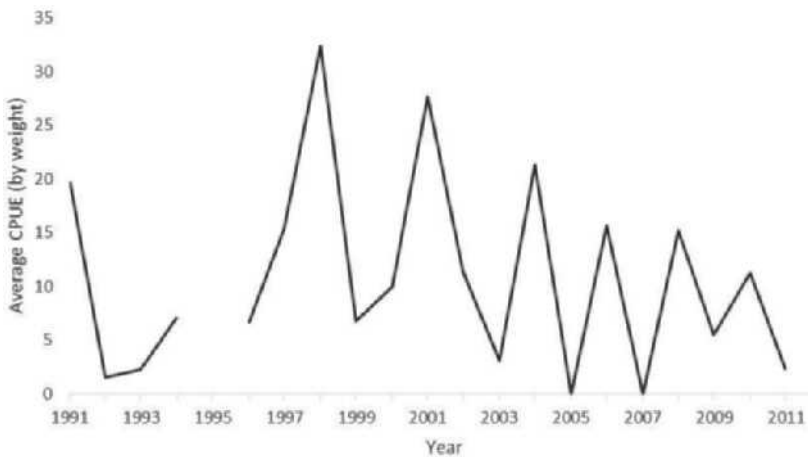


Figure 17-6. Average CPUE (by weight) for age-0 Pacific herring (1991-2011) in the Strait of Georgia showing a declining trend beginning about 1998.

The relative abundance of young-of-the-year Pacific herring have been determined by the Department of Fisheries and Oceans Canada's Strait of Georgia juvenile herring and nearshore ecosystem survey from 1991 to 2011 (Jennifer Boldt, personal communication). The average CPUE, by

weight, for young-of-the-year Pacific herring follows a distinct pattern of alternating highs and lows with a declining trend beginning in 1998 (Fig. 17-6). The declining trend in CPUE of river lamprey is consistent with the declining trend in CPUE of young-of-the-year Pacific herring.

The declining trend in the survival of young-of-the-year Pacific herring remains to be explained. The alternating pattern of an increased and decreased survival also is not understood. The abundance of adult Pacific herring in the Strait of Georgia is increasing (DFO 2015) and if accurate monitoring of feeding river lamprey could occur, it would be most interesting to see if their abundance increases.

Murauskas et al. (2013) found a correlation between the abundance of returning adult Pacific lamprey and prey in the commercial fisheries off the coast in the United States (US) Pacific Northwest. In contrast, Siwicke (2014) found that there were no significant positive correlations between CPUE of any of the 10 potential hosts and Pacific lamprey examined in trawl studies conducted in the Bering Sea area. However, Pacific cod (*Gadus macrocephalus*) and Greenland halibut (*Reinhardtius hippoglossoides*) had the greatest positive correlation coefficients although still not significant (Siwicke 2014).

Abundances of feeding juvenile lampreys could be related to the number of ammocoetes and to predation on the metamorphosed juveniles when they are in the ocean. Our analysis does not include predation effects but focuses on the changes in the abundances of the major prey of Pacific lamprey and Pacific herring for river lamprey. We know that river lamprey ammocoetes are extremely abundant in the lower Fraser River (Beamish & Youson 1987) and we also know that Pacific lamprey ammocoetes are common to most rivers around the Strait of Georgia (R. Beamish, personal observations). Thus, although ammocoete abundance and predation within the Strait of Georgia can influence the abundance of feeding juveniles, we suggest that the abundances of river lamprey and Pacific lamprey in the Strait of Georgia is closely related to the abundances of their preferred prey.

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References

- Beamish R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1906-1923.
- Beamish R.J. 1982. *Lampetra macrostoma*, a new species of freshwater parasitic lamprey from the west coast of Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 39, 277-287.
- Beamish R.J. 2010. Use of gill pore papillae in the taxonomy of lampreys. *Copeia* 2010, 618-628.
- Beamish R.J., & Levings C.D. 1991. Abundance and freshwater migrations of the anadromous parasitic lamprey, *Lampetra tridentata*, in a tributary of the Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 1250-1263.
- Beamish R.J., Noakes D., McFarlane G., Pinnix W., Sweeting R., King J. & Folkes M. 1998. Trends in coho marine survival in relation to the regime concept. *Canadian Stock Assessment Secretariat Research Document* 98, 1-171.
- Beamish R.J. and Northcote T.G. 1989. Extinction of a population of anadromous parasitic lamprey, *Lampetra tridentata*, upstream of an impassable dam. *Canadian Journal of Fisheries and Aquatic Sciences* 46, 420-425.
- Beamish R.J. & Youson J.H. 1987. Life history and abundance of young adult *Lampetra ayresi* in the Fraser River and their possible impact on salmon and herring stocks in the Strait of Georgia. *Canadian Journal of Fisheries and Aquatic Sciences* 44, 525-537.
- Beamish R.J. & Neville C-E. M. 1995. Pacific salmon and Pacific herring mortalities in the Fraser River plume caused by river lamprey (*Lampetra ayresi*). *Canadian Journal of Fisheries and Aquatic Sciences* 52, 644-650.
- Beamish R.J. & Williams N.E. 1976. A preliminary report on the effects of river lamprey (*Lampetra ayresi*) predation on salmon and herring stocks. *Fisheries and Marine Service Technical Report* 611, 1-26.
- Beamish R.J., McCaughran D., King J.R., Sweeting R.M. & McFarlane G.A. 2000. Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. *North American Journal of Fisheries Management* 20, 369-375.
- Beamish R.J., Neville C., Sweeting R. & Lange K. 2012. A synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser

- River in 2009. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 4, 403-414.
- Beamish R.J., Sweeting R.M., Lange K.L., Noakes D.J., Preikshot D. & Neville C.M. 2010. Early marine survival of coho salmon in the Strait of Georgia declines to very low levels. *Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science* 2, 424-439.
- Clarke W.C. & Beamish R.J. 1988. Response of recently metamorphosed anadromous parasitic lamprey (*Lampetra tridentata*) to confinement in fresh water. *Canadian Journal of Fisheries and Aquatic Sciences* 45, 42-47.
- Duffy E.J. & Beauchamp D.A. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68, 232-240.
- DFO. 2015. Stock assessment and management advice for British Columbia Pacific Herring: 2014 status and 2015 forecast. *DFO Canadian Science Advisory Secretariat Science Advisory Report 2014/060*, 1-21.
- Fissel D.B., Birch, J.R. & Chave R.A.J. 1991. Measurements of temperature, salinity and sound velocity at the Nanoose Bay Naval Underwater Weapons Test Range, 1967-1984: updated March 1991 to include 1985-1989, Appendix 4. Sidney, B.C.: Arctic Sciences Ltd.
- Hayes M.C., Hays R., Rubin S.P., Chase D.M., Hallock M., Cook-Tabor C., Luzier C.W. & Moser, M.L. 2013. Distribution of Pacific lamprey *Entosphenus tridentatus* in watersheds of Puget Sound based on smolt monitoring dHata. *Northwest Science* 87, 95-105.
- Klamath-Siskiyou Wildlands Center and 10 other conservation organizations. 2003. A petition for rules to list: Pacific lamprey (*Lampetra tridentata*); river lamprey (*Lampetra ayresii*); western brook lamprey (*Lampetra richardsoni*) and Kern brook lamprey (*Lampetra hubbsi*) as threatened or endangered under the Endangered Species Act. Ashland, Oregon: Klamath-Siskiyou Wildlands Center.
- Luzier C.W., Schaller H.A., Brostrom J.K., Cook-Tabor C., Goodman D.H., Nelle R.D., Ostrand K. & Streif, B. 2011. Pacific lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. Portland, Oregon: U.S. Fish and Wildlife Service.
- Mayfield M.P., Schultz L.D., Wyss L.A., Clemens B.J. & Schreck C.B. 2014. Spawning patterns of Pacific lamprey in tributaries to the Willamette River, Oregon, USA. *Transactions of the American Fisheries Society* 143, 1544-1554.

- Mecklenburg C.W., Mecklenburg T.A. & Thorsteinson L.K. 2002. Fishes of Alaska. Bethesda: American Fisheries Society.
- Murauskas J.G., Orlov A.M. & Siwicke K.A. 2013. Relationships between the abundance of Pacific lamprey in the Columbia River and their common hosts in the marine environment. *Transactions of the American Fisheries Society* 142, 143-155.
- Renaud C.B. 2011. Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. Rome: FAO.
- Ruggerone G.T. & Goetz F.A. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61, 1756-1770.
- Scott W.B. & Crossmann E.J. 1973. Freshwater Fishes of Canada. *Fisheries Research Board of Canada Bulletin* 184 966pp.
- Siwicke K.A. 2014. Relationships between anadromous lampreys and their host fishes in the eastern Bering Sea. M.S. Thesis. University of Alaska Fairbanks.
- Swain D.P., Riddell B.E. & Murray C.B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kistuch*): environmental versus genetic origin. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 1783-1791.
- Thompson M. & McFarlane G.A. 1982. Distribution and abundance of Pacific hake and walleye pollock in the Strait of Georgia, March 24-May 2, 1981. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 1661, 1-79.