

AN ABSTRACT OF THE THESIS OF

Abel Forest Brumo for the degree Master of Science in Fisheries Science presented on September 22, 2006.

Title: Spawning, Larval Recruitment, and Early Life Survival of Pacific Lampreys in the South Fork Coquille River, Oregon

Abstract approved:

Douglas F. Markle

Recently, there has been concern over the decline of the Pacific lamprey, *Lampetra tridentata*, in the northwestern United States. However, effective management has been impeded by data gaps in basic biology, especially in the early life stages. Consequently, in 2004 and 2005 I examined reproductive ecology, larval recruitment, and lamprey monitoring methods in the South Fork Coquille River, a coastal Oregon stream.

In Chapter 2 I monitored spawning populations at large (9.2 km) and small (focal area) scales. Relationships between adult counts at the two spatial scales and adult and redd counts at the large scale were analyzed. Weekly adult, redd, and carcass counts and tagging were also used to describe spawning and residence times, movement, size, and sex of mature adults. Large-scale adult and redd counts were highly correlated (2004, $r^2 = 0.867$; $P = 0.0069$; 2005, $r^2 = 0.877$; $P = 0.0002$); as were large-scale and focal area adult counts over both years combined ($r^2 = 0.690$, $P = 0.0001$) and in 2004 ($r^2 = 0.753$, $P = 0.0250$), but not in 2005 when densities were much lower ($r^2 = 0.065$, $P = 0.5069$).

Average residence time in spawning areas was less than a week for males and shorter for

females, since >90% of recaptured fish were male. Two-thirds of dead fish (2:1) were male, versus only one-half of live fish (1:1), indicating additional sex-specific differences in postspawning behavior. No seasonal or spatial patterns in sex ratio or adult length were detected. Both adult and redd counts have inherent errors related to observer variability, movement during surveys, night spawning, and variable visibility due to weather and flow. To make adult and redd counts more useful for population monitoring their errors need to be better quantified and their relevance to life-cycle dynamics better understood.

In Chapter 3 I monitored intra-annual cohorts of spawning adults and emergent larvae at a single spawning area to examine annual and seasonal patterns of spawning, larval recruitment, and early life survival. In 2004 spawning occurred from April 6–June 3 (59 d) and larval emergence occurred from May 6–June 28 (54 d). In 2005 both spawning and emergence were later and more protracted, from April 25–July 3 (70 d) and May 15–July 25 (71 d), respectively. Over both years, larval recruitment was highly variable and only marginally correlated with spawning stock ($r^2 = 0.149$, $P = 0.0512$). Survival until larval emergence was significantly related to spawning stock size, discharge during spawning, and their interaction. Survival generally declined with increasing spawning stock and decreasing discharge, both apparently related to negative density-dependent effects, which resulted in highly variable early life survival. For example, in April 2004, 65% of larvae were produced by 28% of spawners, while in May, 35% of larvae were produced by 70% of spawners. Egg predation by speckled dace, *Rhinichthys osculus*, increased with temperature, but contrary to expectations, had no detectable effect on survival until emergence.

This study provided justification for a multi-life stage approach to monitoring Pacific lamprey populations and understanding their dynamics. Application of this approach can provide insight into density-dependent survival and the roles of biotic and abiotic factors in larval production. Applied to the South Fork Coquille, Pacific lamprey larval production appeared to have an upper limit related, in part, to spawner density.

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Spawning, Larval Recruitment, and Early Life Survival of Pacific Lampreys in the South
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by

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Abel F. Brumo, Author

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CONTRIBUTION OF AUTHORS

Steve Namitz and Leo Grandmontagne assisted with study design and data collection for Chapter 2. Dr. Douglas Markle assisted with data analysis and interpretation of Chapters 2 and 3.

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CHAPTER 1

GENERAL INTRODUCTION

The Pacific lamprey, *Lampetra tridentata*, is a culturally and ecologically important, anadromous fish that spawns and rears in Northern Hemisphere streams flowing into the temperate Pacific Ocean (Hubbs and Potter 1971; Byram 2002; Close et al. 2002; Close et al. 2004; Peterson 2006). In recent years, state, federal, and tribal agencies have expressed concern at the apparent decline of lamprey populations in the Northwestern United States (Close et al. 2002, Moser and Close 2003; CRBLTW 2005; ODFW 2006). Widespread anecdotal accounts of decreased Pacific lamprey spawning and carcasses have been supported by a substantial reduction in counts of migrating individuals at dams since the late 1960's (Moser and Close 2003; Nawa 2003).

The root causes of lamprey population decline are unknown, but in all likelihood, multifaceted. Due to similarity in habitat requirements and life histories between the Pacific lamprey and anadromous salmonids, as well as a near parallel in population collapse, it is likely that many of the same factors are limiting their survival. Dewatering of streams, obstruction of migration routes, predation by non-indigenous species, degradation of spawning and rearing habitats, and changes in ocean conditions, among others, have been theorized as sources of lamprey decline (Moser et al. 2002; Close et al. 2003, Nawa 2003, ODFW 2006).

A 2003 petition by twelve conservation organizations for Endangered Species Act (ESA) protection of four western United States lamprey species, including Pacific lamprey and western brook lamprey, *L. richardsoni*, galvanized region-wide efforts to

improve understanding of the biology and status of these fishes (Nawa 2003). Although the United States Fish and Wildlife Service (USFWS) halted species status review in a Dec. 27, 2004 "90-day-finding" (U.S. Office of the Federal Register 2004), efforts to list Pacific lamprey are anticipated to resume in the future. Meanwhile, the status of this species remains a concern to Native American tribes, conservation organizations, and state, federal, and tribal scientists across the region.

There have been several comprehensive investigations of Pacific lamprey biology (Pletcher 1963; Kan 1975; Beamish 1980; Beamish and Levings 1991), plus a concerted effort in recent years to improve our understanding of freshwater distribution (Graham and Brun 2005; Luzier and Silver 2005; Cochnauer et al. 2006), habitat (Torgersen and Close 2004; Gunckel et al. 2006), migration timing (van de Wetering 1998; Bayer et al. 2000), dam passage (Moser et al. 2002), phylogeny and stock-structure (Docker et al. 1999; Goodman et al. 2006), and status (Close et al. 1995; Kostow 2002; Moser and Close 2003). Despite these recent advances, effective management and recovery continue to be hindered by a lack of basin-specific information on distribution, life-history, population dynamics, and factors limiting survival (Kostow 2002; Moser and Close 2003; CRBLTW 2005; ODFW 2006). Most research has taken place in the Columbia River Basin, with little targeted research elsewhere. Furthermore, information on the egg incubation period and early larval stages is especially scarce: with few exceptions (Meeuwig et al. 2005), research on Pacific lamprey has focused on adults, juvenile outmigrants, and older size-classes of larvae.

Understanding biotic and abiotic factors controlling survivorship and recruitment of early larvae is a key element in successful fisheries management and recovery (Houde

1987; Magnuson 1991; Pepin 2002). Because mortality rates of fish eggs and larvae are naturally high and variable, survival during these stages is especially important in shaping eventual adult recruitment (Hjort 1914; Rice et al. 1987; Leggett and DeBlois 1994; Johnston et al. 1995; Houde 2002; Pepin 2002). Recruitment level is initially dependent on the number of spawning adults, but other factors such as predation, disease, and starvation can obscure that relationship and ultimately be more important in determining recruitment (Elliot 1989; Leggett and DeBlois 1994; Houde 2002).

A fundamental step in evaluating recruitment limitations and understanding population dynamics, especially in a species as little-studied as the Pacific lamprey, is collection of clear and consistent data on spawning populations. In most river basins, however, there is an absence of reliable annual monitoring data (Kostow 2002). Until recently, the primary means for monitoring lamprey populations has been counts of upstream migrants at mainstem dams (Kostow 2002; Moser and Close 2003). Because these surveys are designed for monitoring salmonids, they have inherent weaknesses when used for lampreys (Moser and Close 2003). Although they can be useful for evaluating long term population trends, dam counts do not provide information on when or where passing fish will spawn.

Adult and redd counts on spawning grounds offer more accurate data on timing and spatial distribution of spawners, but the majority of these data are collected irregularly or are incidental to steelhead monitoring (Kostow 2002). Implementation of standardized monitoring protocols is necessary to fully comprehend the meaning of spawning survey data. Likewise, knowledge on spatial and temporal patterns in spawning activity, sex ratio, length frequency, and the relationship between adults and

redds is imperative for accurate interpretation of spawning survey data, as well as for understanding patterns in larval recruitment.

The overall goal of this study was to describe Pacific lamprey reproductive ecology and larval recruitment patterns in a Northwest coastal river system—with an emphasis on assessment of monitoring methods. Both spawning adult and emergent larval populations were monitored regularly on the South Fork Coquille River during 2004 and 2005 spawning seasons. Chapter 2 evaluates the utility of adult and redd counts for gauging spawning activity; compares timing of spawning on small and larger spatial scales; and documents temporal and spatial trends in length frequency and sex ratio of spawning adults in relation to interpretation of monitoring data. Chapter 3 describes variation in spawning time and larval production between and within years; evaluates the relationship between spawning stock and larval production; and documents and describes potential limitations to early life survival. Chapter 4 presents a summary of findings as they relate to species management and future research needs.

STUDY LOCATION

The river name “Coquille” is thought to be derived from the Chinook Jargon (a widely used trade language across the Northwest) words “scoquel” or “coquel,” meaning eel, which is a commonly used vernacular term for Pacific lamprey (Byram 2002). This name, along with historical accounts and interviews with tribal elders from the area, suggest that Pacific lampreys were once extremely abundant in the basin and one of the most important trade items for the Coquille Indians (Byram 2002).

At 2743 km², the Coquille River Basin is the largest river system originating in Oregon's coastal range. The South Fork Coquille River is a 4th order stream originating in the Rogue-Siskiyou National Forest and draining roughly 746 km², or 27% of the Coquille catchment area. The annual discharge pattern is typical of a Northwest coastal river system, with peak flows in winter and minimum flows in late summer. Mean monthly discharges for the South Fork Coquille River for January, April, and August from 1917–2004 were 1808±107.6 cfs, 918± 55.1 cfs, and 35±1.5 cfs, respectively (mean±SE; USGS gauge # 14325000 at river km 105.4). A flashy system, the South Fork Coquille is subject to rapid, order of magnitude changes in discharge during the early portion of Pacific lamprey spawning season.

In addition to Pacific and western brook lampreys, native fish species present in the Coquille River include: speckled dace (*Rhinichthys osculus*), largescale sucker (*Catostomus macrocheilus*), three-spined stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*C. aleuticus*), riffle sculpin (*C. gulosus*), reticulate sculpin (*Cottus perplexus*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), winter steelhead (*O. mykiss*), and coastal cutthroat trout (*O. clarki clarki*). Known non-indigenous species, found primarily in lower gradient reaches near the mainstem Coquille River, include yellow bullhead (*Ameiurus natalis*), largemouth bass (*Micropterus salmoides*), striped bass (*Morone saxatilis*) and American shad (*Alosa sapidissima*).

PACIFIC LAMPREY LIFE HISTORY

Pacific lamprey spawning can take place from March through July depending on water temperature and the river system (Pletcher 1963; Kan 1975). During spawning, eggs are deposited into a gravel redd where they hatch after approximately 15 days and spend another 15 days until they emerge into the drift at night. These eyeless larvae, or ammocoetes, settle out and burrow into downstream depositional areas, in which they spend a protracted filter-feeding larval phase (4–10 years) prior to undergoing metamorphosis into an eyed adult (Pletcher 1963; Moore and Mallatt 1980; van de Wetering 1998). After metamorphosis, these smolt-like individuals, or macrophthalmia, migrate to the ocean between fall and spring to feed parasitically on marine fishes (Richards and Beamish 1981; Beamish and Levings 1991; van de Wetering 1998). Pacific lampreys are thought to remain in the ocean for approximately 18–40 months before returning to freshwater as immature adults between April and July on the Oregon coast and in southwestern Canada (Kan 1975; Beamish 1980). In the Klamath and Columbia rivers, they have been reported to enter freshwater year round (Kan 1975; Larson and Belchik 1998). After remaining inactive under boulders or similar substrate throughout the winter (Bayer et al 2000) Pacific lampreys come out the following spring as sexually mature adults to spawn. Like Great Lakes sea lampreys, *Petromyzon marinus*, Pacific lampreys do not necessarily home to natal spawning streams (Bergstedt and Seelye 1995; Goodman et al. 2006). Instead, it is thought that migratory lamprey species select spawning location based on presence and concentration of a pheromone-like substance secreted by ammocoetes (Bjerselius et al. 2000; Vrieze and Sorensen 2001).

CHAPTER 2

PATTERNS OF PACIFIC LAMPREY SPAWNING TIME, LENGTH, AND SEX-RATIO IN A COASTAL OREGON STREAM: IMPLICATIONS FOR MONITORING

INTRODUCTION

There have been several comprehensive investigations of the Pacific lamprey, *Lampetra tridentata*, in the Northwestern United States (Kan 1975) and British Columbia (Pletcher 1963; Beamish 1980; Beamish and Levings 1991), yet there is little basin-specific information on their life history, distribution, and basic biology (CRBLTW 2005). Due to the diversity in size, climate, and ecology among river systems in the Pacific lamprey's expansive range, there is potential for geographic variation in life history, ecological roles, and demographic processes. Successful management and protection of this species requires documentation and better understanding of such geographic differences.

Since a proposed Endangered Species Act (ESA) listing in 2003 (Nawa 2003), most Pacific lamprey research and management activities have occurred within the Columbia River Basin (Torgersen and Close 2004; CRBLTW 2005; Graham and Brun 2005; Howard et al. 2005; Luzier and Silver 2005; Meeuwig and Bayer 2005; Meeuwig et al. 2005; Cochnauer et al. 2006), with little work occurring elsewhere in the Pacific Northwest. Southwestern Oregon is no exception. Although the region has a diversity of river sizes and is in a transitional zoogeographic zone, its Pacific and western brook lamprey, *L. richardsoni*, populations have been largely ignored. For this reason, a primary goal of this research was to describe the biology and evaluate survey

methodologies of spawning stage Pacific lampreys in South Fork Coquille River, a major tributary in the Coquille River Basin (Figure 2.1). Preliminary investigations carried out by Leo Grandmontagne (Wild Fish for Oregon) and Steve Namitz (United States Forest Service) beginning in 1997 provided insight into spawning distribution, ecology and behavior in the basin and set the foundation for this project.

Recently the Columbia River Basin Lamprey Technical Workgroup (CRBLTW 2005) documented the need for institution of standardized protocols aimed at monitoring population size and documenting life history attributes. Monitoring temporal trends in spawning population abundance is an especially important aspect of understanding species status and instituting recovery plans, yet accurate assessment of these trends can be difficult (Dunham et al. 2001; Al-chokhachy et al. 2005). Counts of mature adults and redds on spawning grounds are one the most widely used approaches for monitoring Pacific lamprey populations (Kostow 2002; Gunckel 2006) but in many cases these data are collected haphazardly or as byproducts of surveys designed to monitor steelhead populations (Kostow 2002). Compounding this problem, there is little information on the relationship between the two count types and no understanding of seasonal and annual differences in sex ratio and length frequency. Improved understanding of these factors is necessary for designing effective survey protocols and understanding population-level implications of survey data.

Spatial and temporal variations in adult and redd counts, sex ratio, and length can greatly complicate data interpretation (Dunham et al. 2001; Al-chokhachy et al. 2005). For example, using adult counts in the absence of information on sex ratio could result in overestimation of effective spawning population size if the population is heavily skewed

towards males. Similarly, if sex ratio varies over the spawning season or between spawning areas, a single monitoring survey to gauge sex ratio could lead to erroneous conclusions. Because larger females produce more eggs (Malmqvist 1986), female size differences over time and space can also confound interpretation of adult count data.

Redd counts are often assumed to be linearly related to adult counts when used to survey seasonal and annual patterns in spawner abundance of anadromous fishes (Dunham et al. 2001; Al-chokhachy et al. 2005). However, seasonal and interannual differences in the ratio of redds to spawning adults are largely undescribed. Variation in redd size, superimposed spawning, multiple redds per adult, multiple adults per redd, and difficulty in aging redds can all compromise interpretation of monitoring data (Dunham et al. 2001; Gunckel 2006).

A final variable that should be considered when designing adult and redd count surveys is the scale of observation. If spawning populations are patchily distributed in space or time, surveying too small an area or on an infrequent basis could result in flawed conclusions about population size (Dunham et al. 2001). The importance of scale is especially critical when there are limited resources and there is a need for the highest quantity and quality of data for the least amount of work.

We examined adult and redd count data at two spatial scales on the South Fork Coquille River: a large-scale section and a single spawning site near the downstream end of the large-scale section to: 1) describe timing, distribution, size, and sex of spawning adults; 2) compare patterns in these variables over spatial, seasonal, and annual scales; 3) evaluate pros and cons of adult and redd counts and their utility for monitoring Pacific and western brook lamprey spawning populations.

METHODS

STUDY SITE

The large-scale survey took place in a 9.2 km river section of the South Fork Coquille River between Yellow Creek (42° 56' 57" N, 124° 05' 58" W) at river kilometer 90.0, and Baker Creek (42° 54' 21" N, 124° 06' 40" W) at river kilometer 99.2 (Figure 2.1). The large-scale section was chosen to encompass a river segment that was floatable in a single day and known to include comparatively high densities of suitable Pacific lamprey spawning and rearing habitats. Small-scale surveys took place at a single spawning ground (30x30 m), designated the focal area, which was roughly 1000 m downstream from the downstream end of the large-scale section (42° 57' 22" N, 124° 06' 21" W). Located at river kilometer 88.6, the focal area was selected based on its reputation for being a heavily used spawning area, as well as ease of access for more frequent observations.

ABIOTIC VARIABLES

Water temperature was monitored at 30 minute intervals at the focal area from April 27–July 13, 2004 and from April 4–August 3, 2005 using an Onset Optic Stowaway Temp Logger® placed in a shaded area at the river bottom. From April 6–April 27, 2004 water temperature was recorded daily with a bulb thermometer and daily mean temperatures were estimated based on bulb temperature at time of observation in relation to diel temperature trends in early May, 2004. On-site discharge data were obtained from a U.S. Geological Survey (USGS) gauging station located at Powers, OR (“POWO3”; 42

53'31" N, 124 4'16" W), 5.4 river km upstream of Baker Creek. No significant tributaries enter the river section between the gauge and the large-scale survey section.

LARGE-SCALE SURVEYS

Using inflatable pontoon boats, adult and redd surveys were conducted on the large-scale section on a weekly basis from April 29 through June 2, 2004 and April 21 through June 30, 2005 (Table 2.1). Surveys normally began around 1000 hours and lasted until 1600-1800 hours; though on three occasions in 2004, when adult densities were high, surveys required two days. In 2004, due to logistical problems, large-scale surveys did not begin until roughly 3 weeks after spawning was initially observed in the focal area. In 2005 high flow events prevented surveys from occurring on a regular 7 day interval, resulting in irregular survey timing.

The large-scale river section was divided into five river reaches as defined by Oregon Department of Fisheries and Wildlife (Table 2.2; Figure 2.1), and all spawning areas in each reach were surveyed by wading or floating. All visible adult Pacific lampreys were systematically captured by hand with cloth gloves or a modified dip net. All adult lampreys captured were mature, spawning stage fish. Before release, live fish were measured and sexed, then tagged with week and reach-specific, colored, ½" T-Bar floy tags to avoid recounting in subsequent survey weeks. Tagging also provided insight into tag retention, movement between reaches, and duration on spawning grounds. Visible carcasses were also recovered, measured, sexed, examined for tags, and cut in half to avoid recounting. Differences in mean lengths of both live males and live females among large-scale reaches and between sampling dates were investigated using ANOVA

and significance was determined using Bonferroni intervals. Lastly, Pacific lamprey redds estimated to have been built within the previous week, based on redd integrity and color, were enumerated for each reach and survey. The relationship between Pacific lamprey adult and redd counts was analyzed using simple linear regression of survey counts.

FOCAL AREA SURVEYS

Adult counts at the focal area (Figure 2.1) were obtained by systematically wading through the spawning ground during 38 surveys carried out between March 28 and July 12, in 2004, and 46 between April 5 and July 17, in 2005. To avoid disruption of spawning and potential introduction of error into estimates of larval production and survival (see Chapter 3), fish were not captured or tagged in the focal area. When visibility permitted, counts were made in late afternoon and separated by no more than 4 days during the spawning season. Relationships between spawning activity in the large-scale section and the focal area were evaluated for both years using the total number of adults per weekly large-scale survey, the total number of adults per reach in each survey, and the mean number of adults per survey in the focal area for each week.

During 2004 and 2005 spawning seasons, regular observations and notes were taken on spawning activity, habitat utilization, and ecological interactions between Pacific lampreys and other organisms in the large-scale section and focal area based on wading, snorkeling, underwater photography, and video. Counts and observations of western brook lampreys were also recorded during Pacific lamprey focal area spawning surveys.

RESULTS

ABIOTIC VARIABLES

Discharge during the lamprey spawning season in 2004 was marked by a single, mid-April high-flow event, which peaked on April 21 at 4840 cfs (Figure 2.2). In contrast three substantial discharge events (> 2000 cfs) occurred early in the 2005 spawning season and smaller events (851 and 1030 cfs) occurred later in the season (Figure 2.2). During April–July spawning periods daily mean stream discharge was inversely related to daily mean water temperature (2004 and 2005 combined; $r^2 = 0.865$; $P < 0.0001$; Figures 2.2, 2.3). Average water temperature from April 6–July 13 was warmer in 2004 (16.3°C) than in 2005 (14.0°C) in 2005. In both years, water temperature rose gradually during spring, but diel fluctuations of up to 8°C occurred (Figure 2.3).

LARGE-SCALE ADULT COUNTS

During six weekly large-scale surveys in 2004, 446 Pacific lampreys were captured, measured, and tagged—8.1 fish per total kilometer surveyed (Tables 2.3, 2.4). An additional 54 live individuals were seen but not captured due to water depth or human error: a catch success rate of 89%. Peak catch was 169 fish on May 13, with numbers dropping off dramatically after May 19 (Figure 2.4). The highest number of fish was captured in Rowland reach, followed by Long Tom, Whiskey, Yellow, and Beaver (Figure 2.1; Table 2.4). When adjusted for reach length, adult density (fish per kilometer) was greatest in Whiskey, the furthest upstream reach, and decreased downstream, with the lowest density in Yellow reach (Table 2.4).

Only 140 Pacific lampreys were captured and tagged during nine surveys in 2005. Fish per total kilometer surveyed was 1.7, 79% less than 2004 (Table 2.4). Thirty-one live fish were seen but not captured in 2005: a catch success rate of 82%. Peak catch was bimodal, with a peaks of 52 on May 5 (52) and a peak of 40 on June 1 (Figure 2.5). Highest abundance and density of fish were in Long Tom reach, followed by Rowland, Whiskey, Yellow, and Beaver (Figure 2.1; Table 2.5).

LARGE-SCALE CARCASS RECOVERY

A total of 373 Pacific lamprey carcasses were collected during 2004 surveys (Table 2.3). Few carcasses were found early in the season, but the number gradually increased and peaked on May 27 (Figure 2.6). Peak carcass counts lagged peak adult counts by about 1–2 weeks (Figures 2.4, 2.6). The highest number of carcasses was collected in Rowland reach (138), followed by Long Tom (119), Yellow (83), Beaver (17), and Whiskey (16) reaches (Figure 2.6). Only 17 carcasses were collected from the 9.2 kilometer survey section in 2005 (Table 2.3). In both years, carcasses were concentrated in areas of low water velocity: long, slow pools or large back-eddies. Carcass recovery again appeared to lag adult counts by roughly 1–2 weeks (Figure 2.7).

ADULT VS. REDD COUNTS

In 2004, 1,759 Pacific lamprey redds were counted, with a peak of 791 on May 5 (Table 2.5; Figure 2.8). Total redd density was 31.9 per kilometer (Table 2.5). Redd density in 2004 was highest in Long Tom, followed by Whiskey, Yellow, Beaver, and Rowland reaches (Figure 2.1; Table 2.5). In 2005, 1,169 redds were counted, with the

two highest peaks occurring on May 5 (299) and June 1 (384) (Figure 2.9). Total redd density was 14.1 per kilometer and was highest in Long Tom; followed by Whiskey, Rowland, Beaver, and Yellow (Figure 2.1; Table 2.5).

Although peak redd counts preceded peak adult counts by about a week in 2004, the two counts were significantly correlated ($r^2 = 0.867$; $P = 0.0069$; Figures 2.4, 2.8, 2.10). Approximately four redds were counted for every live adult observed in 2004 (Tables 2.4, 2.5) and there was no indication of a temporal pattern in redds counted per adult (Figure 2.11). In 2005 both redd and adult counts were bimodal and significantly correlated ($r^2 = 0.877$; $P = 0.0002$; Figures 2.5, 2.9, 2.10). More than eight redds were counted for each live adult (Tables 2.4, 2.5). In 2005 the number of redds counted per adult appeared to increase seasonally (Figure 2.11).

FOCAL AREA ADULT COUNTS

In 2004, 233 adult Pacific lampreys were counted in the focal spawning area, first detected on April 6, and last seen on June 3 (Figure 2.12). Mean number per survey during this period was 8.32 ± 1.24 (SE). The maximum number of fish counted was 27, on May 4 (Figure 2.12) and 95% of adult observations occurred by May 17. A large spring freshet in mid-late April precluded observations during this period (Figures 2.2, 2.12).

In 2005, 85 fish were counted in the focal area, with a mean of 2.65 ± 0.50 (SE) fish per survey during the spawning period. Spawning began later and occurred over a more prolonged period than in 2004, from April 25 through July 3, with 95% of observations occurring by June 6 (Figure 2.13). Peaks in 2005 adult spawning activity

were bimodal, with one in late April and the other from late May to early June (Figure 2.13). The maximum number of fish counted was nine, on April 26 (Figure 2.13). Five high discharge events during the 2005 spawning season precluded observations during these periods (Figures 2.2, 2.13).

LARGE-SCALE VS. FOCAL ADULT COUNTS

Adult counts from weekly large-scale surveys were significantly correlated with weekly mean focal area adult counts over the two years combined ($r^2 = 0.690$, $P = 0.0001$) and in 2004 ($r^2 = 0.753$, $P = 0.0250$); but not in 2005 ($r^2 = 0.065$, $P = 0.5069$) when densities were low (Table 2.6; Figure 2.14). Adult counts from each reach in the large-scale section were also significantly correlated with each other, total large-scale survey counts, and with weekly mean focal area counts (Table 2.6).

TAGGING RECAPTURES, RESIDENCE TIME, AND MOVEMENT

Eleven of 446 fish (2.5%) tagged in 2004 were recaptured alive (Table 2.7). In 2005, none of the 140 tagged fish were recovered dead or alive. Ten of 11 fish tagged in 2004 were male and all were found one week after tagging (Table 2.8). Four males were caught upstream of the reach where they were tagged, two downstream, and four in the same reach (Table 2.8). The recaptured female was caught one day after being tagged, three reaches downstream of the tagging location (Table 2.8). Percentage of tagged individuals recapture after one week generally declined as the spawning season progressed (Table 2.9). Since only 10 of 446 (2.2%) adults tagged in 2004, all of which were males, were recaptured alive after one week (Table 2.8), residence time on

spawning grounds must typically be less than one week—and is probably shorter for females than males.

Thirty-five of 446 tagged fish were recovered dead with tag intact during large-scale surveys in 2004 (Table 2.7). Over 77% (27 of 35) of recovered carcasses were male, while the remaining 8 were female. Twenty-nine (83%) of the recovered carcasses were found in reaches downstream from their tagging locations. Two, both of which were male, were found upstream, while the remaining four were located in the same reach where they were tagged. All carcasses were found within 9 days of their last tagging date.

ADULT LENGTH

Lengths of mature adults (live and dead) collected from spawning areas in the large-scale section in 2004 ranged from 35.5 to 60.0 cm, with a mean of 48.0 ± 0.147 cm (mean \pm SE; Table 2.3; Figure 2.15). Males (50.0 ± 0.173 cm) were significantly longer than females (45.4 ± 0.175 cm) in 2004 by about 10% (Table 2.3). In 2005 mature adults ranged from 31.0 to 58.0 cm, with a mean length of 46.9 ± 0.394 cm (Table 2.3; Figure 2.15). Again, in 2005, males (48.3 ± 0.491 cm) were significantly longer than females (45.2 ± 0.574 cm) by approximately 6%. Males were significantly shorter in 2005 compared to 2004, but females were not (Table 2.3).

In both years, there was not a statistically significant difference between mean lengths live males or live females between large-scale survey reaches (2004 males: $F_{4,212} = 1.69$, $P = 0.1523$; 2004 females: $F_{4,224} = 0.21$, $P = 0.9312$; 2005 males: $F_{4,69} = 0.17$, $P = 0.9552$; 2005 females: $F_{4,58} = 1.96$, $P = 0.1125$). Additionally, in both years mean

lengths of live males or females were not statistically significantly different among survey dates (ANOVA: 2004 males: $F_{4,212} = 0.62$, $P = 0.6479$; 2004 females: $F_{5,223} = 0.18$, $P = 0.9700$; 2005 males: $F_{5,68} = 1.73$, $P = 0.1395$; 2005 females: $F_{4,58} = 2.45$, $P = 0.0562$; Figure 2.16). In 2005 there was a significant difference between live female lengths on two dates, April 28 (N = 5) and May 25 (N = 20) (Figure 2.16).

SEX RATIO

In 2004 the sex-ratio of live fish was 0.94:1 (217 male and 229 female), but that of carcasses was 2:1 (233 males and 116 female). Sex could not be determined for 24 of the 373 carcasses collected in 2004 (Table 2.3). In 2005, the sex ratio of live fish was 1.15:1 (75 male and 65 female) and sex ratio of dead fish was 1.13:1 (9 male and 8 female; Table 2.3). In both years, there was no evidence for a seasonal pattern in sex ratio (Figure 2.17).

SPAWNING AND ECOLOGICAL OBSERVATIONS

Most Pacific lampreys observed in spawning areas were digging redds or resting in and around redd gravels, but very few daytime spawning events were observed in either year. Greater spawning activity was occasionally witnessed after dark during other research activities (See Chapter 3). While monogamous spawning was more frequently observed, polygamous events with two or more females and a male spawning in a single redd were observed on several occasions. Pacific lampreys spawned in gravel/cobble (about 4–15 cm) embedded in finer gravel/sand at depths from 0.3–1.0 m, building a variety of nest-types, ranging from isolated, circular nests to 20 m long communal

trenches. Such trenches, as well as evidence of superimposed spawning, were generally observed during periods of higher spawning activity.

During and after lamprey spawning, large numbers of speckled dace, *Rhinichthys osculus*, and smaller numbers of salmonids were observed feeding on eggs in and around redds—particularly in 2004 (see Chapter 3). In addition, snorkeling observations revealed that vigorous movement of stones by Pacific lampreys during redd construction dislodged stream insects. Salmonid parr and larger cutthroat trout (*O. clarki clarki*) were commonly observed “stacking-up” and feeding immediately downstream of actively digging lampreys. At night, cutthroat trout were also observed resting within low-flow refuges offered by lamprey redds.

WESTERN BROOK LAMPREY

Western brook lampreys and their redds were not effectively monitored from pontoon boats or wading during large-scale surveys due to their small size and time limitations. Thirty-one and 45 sexually mature western brook lampreys (WBL) were seen in the focal area in 2004 and 2005, respectively. In 2004 the first individual was seen on April 9, but peak activity was from mid-May to early June. The last WBL was seen on June 16 (Figure 2.18). As with Pacific lampreys, the observed WBL spawning season started later (May 2) and lasted longer (July 4) in 2005, with peak activity in early to mid-June. In some cases, WBLs built small redds in the center of Pacific lamprey redds; possibly using the low-flow refuge and smaller gravel produced after larger gravel was removed by Pacific lampreys. In several instances individual WBLs were seen

digging in or swimming around redds while Pacific lampreys were spawning in them. Like Pacific lampreys, WBL spawning activity was often observed at night.

DISCUSSION

ADULT COUNTS AND SPAWNING TIME

Overall spawning activity, as measured by adult counts, redd counts, and carcasses, was considerably higher in 2004 (Tables 2.3–2.5). The greater frequency of high discharge events in 2005 made adult undercounts more prevalent in that year. Despite the likelihood of adult undercounts, a threefold decline in larval drift rates in 2005 (see Chapter 3) also suggests lower spawning activity.

Pacific lamprey spawning in the South Fork Coquille River occurred between early April and early June in 2004 (59 d), and over a longer period from late April until early July in 2005 (70 d). The April–July spawning period observed on the South Fork Coquille generally agrees with observations from other coastal systems. Kan (1975) reported coastal Oregon Pacific lampreys spawn from March through May, and on the Smith River in SW Oregon, Gunckel et al. (2006) detected newly built redds between April and June. In British Columbia spawning was been observed between April and July, but typically peaked in June and July (Beamish 1980; Richards 1980; Farlinger and Beamish 1984). Inland and northern populations of Pacific lamprey are thought to initiate spawning later than coastal populations (Kan 1975; Beamish 1980; Richards 1980).

In previous years, spawned out individuals have been recovered in the vicinity of the focal area as early as March 14 (L. Grandmontagne, unpublished data) so it is

possible that some fish spawned before we observed them. Elevated river levels prohibited surveys prior to April in 2004 and late April in 2005. Furthermore, larval drift samples (Chapter 3) indicate that Pacific lampreys successfully spawned much earlier than predicted from adult surveys in 2005. These early spawners were likely associated with low flows and unseasonably high temperatures that occurred in February and March of 2005 (Figure 2.2), which likely resulted in water temperatures warm enough to initiate early spawning. Similarly, the cool conditions caused by recurrent high flow events, beginning in late March 2005, most likely arrested spawning activity until daily mean water temperatures warmed above 11°C in late-April (Chapter 3). A delayed initiation of spawning was also observed in the Smith River, Oregon in spring 2005 (Gunckel et al. 2006). The dependence of fish spawning time on temperature and flow regimes is well established (Pletcher 1963; Hardisty and Potter 1971b; Kempinger 1988; Reichard et al. 2002a; Dahl et al. 2004).

ADULT VS. REDD COUNTS

The linear relationship between adult counts and redd counts suggests both could provide similar information about relative spawning activity over time. However, there was considerable variability in the number of redds counted per adult between surveys and years. The redd to adult ratio was 4:1 in 2004, greater than 8:1 in 2005, and typically much higher in later surveys. The high redd to adult ratios in both years point to underestimation of total spawning population and/or multiple redds per spawning pair. Population underestimation is supported by tagging results, which suggest individuals likely remained on spawning grounds less than the one week separating surveys. If one

redd was built per spawning pair, we would expect a 1:2 ratio of redds to adults. Farlinger and Beamish (1984), who used adult counts to estimate the total Pacific lamprey spawning population and counted all redds in a tributary stream, found a redd to adult ratio of about 1:2. Multiple redds per spawning pair were not directly observed in this study but individual spawners were seen moving rocks in multiple locations within a single spawning ground. Lampreys have been observed beginning redd construction in one location, getting interrupted, and starting construction again in another location (Hardisty and Potter 1971b). Alternatively, if an individual completes a redd, and a receptive spawning partner is not in the area, it may move to another location (Pletcher 1963).

The considerably higher redd to adult ratio observed in 2005 compared to 2004 can be attributed to variability in redd counters between years, higher water depth, lower average visibility, which served to make fish detection and capture relatively more difficult than redd observation. Approximately 20% of observed fish evaded capture in 2005, versus 10% in 2004. In addition to greater depth and poorer visibility, the lower catch success rate in 2005 can be explained by two field workers instead of three in 2004. For the latter reason, a catch-per-unit-effort index could be a more accurate adult survey metric. The general increase in number of redds counted per adult later in the spawning season, especially in 2005 may be explained by shorter adult residence time later in the season or counter error due to accumulation of older redds over time.

Both adult counts and redd counts present logistic difficulties and have no clear-cut way to quantify errors. These problems include: observer variability, movement of lampreys during surveys, greater spawning activity at night, and variable visibility due to

rain, wind, turbidity, water depth, sun angle, and discharge. Standardization of both survey types in relation to weather, discharge, and time of day is possible, but risks inconsistent data collection over the season, which would compromise interannual comparability. Redd and adult count errors are expected to be more consistent from year to year in shallow river systems with low variation in spring discharge. Such systems are rare over much of the Pacific lamprey's range.

Unlike many other fish species, spawning adult Pacific lampreys are not easily spooked from spawning areas and can be caught by hand relatively easily. For this reason, personnel training may be easily standardized for adult counts in clear, shallow systems. However, variable redd shape, size, and age, as well as superimposition, make consistency in redd counts more problematic (Dunham et al. 2001; Al-chokhachy et al. 2005; Gunckel et al. 2006). In this case, we attempted to count all redds perceived to be built within one week of the survey, but this was a subjective judgment. Research on redd count error in bull trout, *Salvelinus confluentus*, suggests that even with significant training, observer variability is substantial, and might be unavoidable (Dunham et al. 2005).

Signs of redd superimposition were observed in early May of 2004, when over 25 spawners and remarkably high redd concentrations were seen in the 30x30 meter focal area (Figure 2.12). Elevated densities of spawning Pacific lampreys and large areas of disturbed spawning substrate (20x5 m) were also seen during weekly large-scale floats in May 2004, making individual redds almost impossible to distinguish. Anecdotal evidence of superimposed spawning by Pacific lampreys has been cited in previous studies (Pletcher 1963; Kan 1975; Close et al. 2003; Gunckel et al. 2006). The potential

for inter-specific redd superimposition with steelhead, *Oncorhynchus mykiss*, should also be noted. In April and May, we observed steelhead spawners and redds in spawning areas used by lampreys. Steelhead redd misidentification has been cited as a source of error in redd counts for inexperienced observers (Gunckel et al. 2006).

Because of potentially high observer error in redd counts and uncertainty in the number of redds produced per adult, redd surveys may only be useful for revealing comparatively large fluctuations in lamprey population abundance. For this reason adult counts might more accurately estimate relative escapement. On the other hand, sizable errors in adult counts could occur if the sampling interval is too long. Due to the short presence of adults on spawning grounds and/or nighttime spawning, counts of more permanent redds may be better when sampling is infrequent or not standardized by time-of-day. Additionally, when population abundance is low, redds may be preferable for detecting presence of spawning due to their greater abundance. Future research should focus on better quantifying these error sources.

SPATIAL SCALE IN ADULT COUNTS

The significant correlations between adult counts in the focal area, large-scale reaches, and the large-scale survey section (Table 2.6; Figure 2.14) suggests seasonal patterns of spawning were independent of spatial scales at these scales. At larger spatial scales and in rivers with greater variability in flow and water temperature, the correlation between spawning activity at small and large scales may not hold. The ability to detect spatial relationships at low densities may require more frequent samples.

Low densities and cooler temperatures appeared to contribute to the lack of correlation between large-scale and focal area surveys in 2005. Cooler temperatures in 2005 might have also restricted the daily duration of spawning activity more than in 2004. Large-scale surveys typically took place between 1000-1500 hours when average water temperatures were below the daily maximum temperature; whereas most focal surveys took place around 1600 hours, a time closer to the daily maximum. Pacific lampreys require 11–13°C to initiate spawning (Pletcher 1963; Kan 1975; Close et al. 2003; see Chapter 3), and these temperatures were not reached until late-afternoon—especially early in the 2005 spawning season. The relatively high correlations between the weekly mean of focal area surveys and counts taken once a week in other reaches (Table 2.6) imply that, when densities are relatively high, similar information about seasonal patterns in spawning may be gained by surveying, either, once per week or multiple times per week.

TAGGING RECAPTURES, RESIDENCE TIME, AND MOVEMENT

The low recovery rate of live, tagged fish in 2004 (2.2%) and 2005 (zero) suggests that adult residence in spawning areas was short—likely less than one week. For this reason, our weekly surveys likely undercounted the total spawning population. In British Columbia, Farlinger and Beamish (1984) estimated Pacific lamprey residence time in spawning areas at about 5 days, while Pletcher (1963) reported a range of 1–14 days between spawning and subsequent death. Although Pacific lamprey residence time is typically short, one individual tagged for practice on the focal area early in 2004 was recaptured in the same area 28 days later. Due to consistently low river levels and clear

water in 2004, it is unlikely that a meaningful portion of tagged fish were present in spawning areas and not detected during surveys. In 2005, comparatively poor visibility during a number of surveys may have contributed to not detecting tagged fish.

The higher proportion of males recovered (90% live, 77% carcasses) indicates a difference in postspawning activity and longer residence time for males, which could help explain the sex ratio difference between live and dead fish (Table 2.3). Farlinger and Beamish (1984) reported that male Pacific lampreys remained on spawning grounds longer than females—for an average of 6.5 versus 4.6 days, respectively. Beamish (1980) reported that river lamprey, *Lampetra ayresi*, females died within a few hours after spawning but males typically survived for about 3 weeks. Although our recapture dataset is small, it also suggests that a substantial portion of males moved between spawning areas: 6 of 10 recaptured live males were found outside of their tagging reach (Table 2.8).

As the spawning season progressed, the percentage of tagged individuals recaptured alive the following week declined, implying that earlier spawning individuals likely survive longer and/or spend more time on spawning areas than those spawning later. Research on residence time of spawning Pacific salmon has also indicated longer residence time for earlier spawning individuals (Neilson and Geen 1981).

Only 35 of 446 tagged fish were recovered as carcasses in 2004 and none were recovered in 2005. It is likely that most tagged individuals died within a week of tagging and their carcasses drifted downstream out of the survey reach, into deep pools where they could not be recovered, or were scavenged by birds or mammals. It is also notable that, during large-scale surveys, apparent post-spawn Pacific lampreys of unknown sex

were commonly observed swimming slowly downstream. Since most (29 of 35) recovered carcasses were found downstream of their tagging location, use of carcasses as a population metric for a given river section may be difficult, especially in a year like 2005 when high-discharge events likely flushed them further downstream than in 2004. Furthermore, although most authors agree that lampreys die after spawning (Pletcher 1963; Beamish 1980; Manion and Hanson 1980; Malmqvist 1986), it is uncertain whether or not a small percentage of Pacific lampreys survive spawning and out-migrate to the ocean, as has been equivocally reported on the Olympic Peninsula (Michael 1980; Michael 1984).

Tag retention was not estimated in this study, but several recovered carcasses retained tags for 14 days, and one individual was recovered alive 28 days later with tag intact. Research on the Deschutes River by Graham and Brun (2005) approximated tag retention at 42.9% for T-Bar floy tags, 72.0% for Single Strand floy tags, and 84.6% for Numbered floy tags. Because the ½” T-bar tags used in our study are considerably shorter than the T-Bar tags used on the Deschutes, it is likely that our tag retention was higher than 42.9%.

ADULT LENGTH

The size range of spawning stage Pacific lampreys collected on the South Fork Coquille River (31.0–60.0 cm) was comparable to, though slightly larger than the 33.2 to 54.2 cm size-range of spawning lamprey measured by Kan (1975) on various Oregon coastal systems. In a tributary to Babine Lake in British Columbia, Beamish (1980)

reported a mean length of 48 cm for Pacific lampreys sampled during the spawning period (sexes combined), with a range of 41–59 cm.

Mean sizes of lampreys (live and dead) 2004 (48.0 cm, 0.15 cm SE) and 2005 (46.9 cm, 0.40 SE) were smaller than those measured on the South Fork Coquille in 2000 (52.0 cm, 0.64 SE) (L. Grandmontagne, unpublished data). Annual differences in size could be due to different sex ratios. However, the smaller mean size in 2005 is likely due to both smaller males (1.7 cm smaller, Table 2.3) and fewer males (1.2:1, male : female in 2005 versus 1.3:1 in 2004; live and dead). Alternatively, an earlier-spawning, larger morphotype observed and measured in previous years was absent in 2004 and 2005.

We found no indication of spatial trends in mean size of live, mature male or female Pacific lampreys collected during large-scale surveys in either year. Therefore, at the reach scale observed, there is expected to be little difference in mean female reproductive potential among spawning areas. Anecdotal observations from this study indicate that larger males and females generally selected larger spawning substrate, which could result in spatial differences in length associated with habitat differences between individual spawning grounds.

In a recent status report, Kostow (2002) reported that size of spawning adult Pacific lampreys on the South Fork Coquille River in 2000 (data from Leo Grandmontagne) tended to decline over the spawning season. However, sex ratio of this sample was not analyzed and it included both live and dead individuals, which undoubtedly spawned at different times. In 2004 and 2005, we found little evidence for temporal trends in length of spawning adults: there was not a statistically significant

difference between mean lengths of live males or females between survey dates in either year.

SEX RATIO

In both years the sex ratio of live adults was approximately 1:1. From a sample of 252 fish collected during the spawning season, Farlinger and Beamish (1984) found a sex ratio of around 1.3 males per female. Similarly, Kan (1975) reported a sex ratio of roughly 1.2 males per female for spawning-stage individuals collected from Oregon streams. Hardisty and Potter (1971) reviewed results from studies on various European and North American species and found that there was almost always an excess of spawning males in both resident and anadromous species; although sex ratio varied between species and years.

In 2004 the male to female ratio of live fish (1:1) was considerable lower than dead fish (2:1). In addition to differences in postspawning behavior, possible explanations for discrepancies in sex-ratio between live and dead fish include differences in longevity or predator preference (Kan 1975). Little or no data on the sex ratio of dead Pacific lampreys exists in the literature. Lorion et al. (2000) noted that samples of mature Miller Lake lamprey (*L. minima*) usually had a 3:1 male bias, except for a large collection of dead fish where they found a 9:1 female bias.

Unlike Pacific salmon species, in which the earlier arrival of males to the spawning grounds is common (Morbey 2000), we found no evidence for protandry in Pacific lampreys spawning in the South Fork Coquille. Despite indications from tagging that males remain on spawning areas longer than females, males did not appear to arrive

on spawning areas earlier and sex ratio did not exhibit a seasonal pattern in either year (Figure 2.17). Farlinger and Beamish (1984) also did not detect a seasonal trend in sex ratio of spawning Pacific lampreys; though Hardisty and Potter (1971) and Malmqvist (1986) cited several examples in which males of various lamprey species preceded females to spawning areas and initiated redd building.

WESTERN BROOK LAMPREY

Western brook lamprey adults and redds were more difficult to detect than Pacific lampreys and they could not be monitored during large-scale surveys due to time limitations and highly variable error with visibility. Float surveys covering less distance, or in smaller streams, and spending more time in each spawning area are recommend for monitoring WBLs. It was possible to make counts of WBL adults on the focal area because of the intensive nature of these surveys and observer familiarity with the spawning ground. Although WBL redds were seen on the focal area in both years, accurate counts were not feasible due to their small size and the high amount of Pacific lamprey redd building activity in the area. More uncertainty exists in WBL adult count data, but we are reasonably confident that onset and peak WBL spawning occurred later than Pacific lampreys in both years. Even with lower visibility in spring 2005, it was also apparent that annual WBL spawning activity was significantly higher in that year than in 2004. Furthermore, it was evident that both the onset and peak of WBL spawning activity occurred later in 2005 than in 2004. As evidenced by redd counts, Gunckel et al. (2006) also found later onset and peak of western brook lamprey spawning activity in

2005 on the Smith River. However, in contrast to the South Fork Coquille, they observed about 20% fewer WBL redds in 2005 than in 2004.

During both years of observation in the focal area and large-scale surveys, we observed considerably more Pacific lamprey spawning activity than western brook lamprey activity. While it was clear that the two species overlapped in spawning habitat and range in the section of the South Fork Coquille River surveyed, it is expected that the western brook lampreys increase in relative abundance further upstream and in smaller order tributaries. Such a species distribution pattern has been reported by both Luzier and Silver (2005) and Gunckel et al. (2006).

CONCLUSIONS

This work evaluated spatial and temporal considerations for Pacific lamprey adult and redd surveys. In addition, spawning time, length frequency, sex ratio, and movement were described in a Southwestern Oregon coastal river system. Use of pontoon boats to monitor spawners and their redds was a suitable approach for describing seasonal patterns of relative spawning abundance. However, because spawner residence time appeared to be less than one week, sample frequency needs to be almost daily to estimate absolute population size. When adult densities were relatively high, seasonal patterns in spawning activity were highly correlated spatially; thus it may be possible to gain comparable information on relative abundance by monitoring a single, high-use spawning area. Annual population monitoring can also be combined with larval emergence data to evaluate reproductive success (see Chapter 3). Additional work on spawning surveys should: (1) better quantify survey error sources, as done by Dunham et al. (2005) on bull

trout—especially observer variability in redd counts, diel variations in spawning time, and differences between streams varying in size and habitat; (2) describe adult residence time, sex ratio, and temporal differences to determine appropriate survey frequency; (3) describe the mean and variance in number of redds produced per adult; and (4) lead to a sampling manual with standardized protocols for adult and redd surveys that provides pros, cons, error sources, and analysis considerations for each.

TABLES

Table 2.1. Dates of large-scale adult and redd surveys in 2004 and 2005.

2004	2005
April 29	§April 21
*May 5–6	April 28
*May 13–14	May 5
*May 19 & 21	†May 14
May 27	May 25
June 2	June 1
	June 10
	June 15
	†June 30

*Survey required more than one day to complete

§Zero fish counted

†Zero fish measured

Table 2.2. Reach information for large-scale surveys, ordered from upstream to downstream (9.2 km total).

Reach	Start Position	End Position	Distance (kilometers)
Whiskey	42 54' 21" N 124 06' 40" W	42 54' 49" N 124 06' 09" W	1.2
Rowland	42 54' 49" N 124 06' 09" W	42 55' 16" N 124 07' 12" W	2.5
Long Tom	42 55' 16" N 124 07' 12" W	42 56' 02" N 124 06' 05" W	2.4
Beaver	42 56' 02" N 124 06' 05" W	42 56' 17" N 124 06' 07" W	0.7
Yellow	42 56' 17" N 124 06' 07" W	42 56' 57" N 124 05' 58" W	2.4

Table 2.3. Abundance (*N*) and mean length of live and dead Pacific lampreys during 2004 and 2005 large-scale surveys; excluding live fish seen but not captured (54 in 2004 and 31 in 2005).

Category	Sex	2004			2005		
		<i>N</i>	Size (cm)	SE	<i>N</i>	Size (cm)	SE
All	Both	819	48.0	0.147	154	46.9	0.394
	Males	450	50.0	0.173	83	48.3	0.491
	Females	345	45.4	0.175	71	45.2	0.574
Live	Both	446	47.4	0.200	140	46.6	0.409
	Males	217	49.6	0.276	75	48.4	0.527
	Females	229	45.4	0.211	65	44.5	0.531
Dead	Both	373	48.6	0.212	17	49.4	1.231
	Males	233	50.4	0.209	9	48.1	1.396
	Females	116	45.4	0.310	8	50.9	2.056
	Unsexed	24	45.8	0.939	0		

Table 2.4. Total number of live adult Pacific lampreys per reach and number per total kilometer surveyed for 2004 and 2005 large-scale surveys. Reaches are ordered from upstream to downstream.

Year	Data Type	Whiskey	Rowland	Long Tom	Beaver	Yellow	Total
2004	Adults/reach	108	126	114	23	75	446
	Adults/km	15.5	8.5	7.8	5.4	5.2	8.1
2005	Adults/reach	15	34	58	5	28	140
	Adults/km	1.4	1.5	2.6	0.8	1.3	1.7

Table 2.5. Total number of Pacific lamprey redds per reach and number per total kilometer surveyed for 2004 and 2005 large-scale surveys. Reaches are ordered from upstream to downstream.

Year	Data Type	Whiskey	Rowland	Long Tom	Beaver	Yellow	Total
2004	Redds/reach	232	405	570	125	421	1759
	Redds/km	33.4	27.2	38.8	29.4	29.1	31.9
2005	Redds/reach	171	295	404	70	229	1169
	Redds/km	16.4	13.2	18.4	11.0	10.5	14.1

Table 2.6. Matrix of r^2 statistics and associated P-values for relationships between weekly adult Pacific lamprey counts in each of the large-scale survey reaches, the entire large-scales section, and the focal area (combined 2004 and 2005 data; N = 15 for all survey types). Survey reaches are ordered from upstream to downstream.

Weekly Adult Count	Result	Focal Area Mean	Large-scale Total	Whiskey Reach	Rowland reach	Long Tom Reach	Beaver Reach	Yellow Reach
Focal area mean	r^2		0.690	0.526	0.584	0.668	0.637	0.702
	P-value		0.0001	0.0022	0.0009	0.0002	0.0004	0.0001
Large-scale Total	r^2	0.690		0.903	0.919	0.874	0.776	0.868
	P-value	0.0001		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Whiskey Reach	r^2	0.526	0.903		0.872	0.697	0.609	0.651
	P-value	0.0022	<0.0001		<0.0001	0.0001	0.0006	0.0003
Rowland Reach	r^2	0.584	0.919	0.872		0.659	0.863	0.708
	P-value	0.0009	<0.0001	<0.0001		0.0002	<0.0001	0.0001
Long Tom Reach	r^2	0.668	0.874	0.697	0.659		0.558	0.828
	P-value	0.0002	<0.0001	0.0001	0.0002		0.0014	<0.0001
Beaver Reach	r^2	0.637	0.776	0.609	0.863	0.558		0.683
	P-value	0.0004	<0.0001	0.0006	<0.0001	0.0014		0.0001
Yellow Reach	r^2	0.702	0.868	0.651	0.708	0.828	0.683	
	P-value	0.0001	<0.0001	0.0003	0.0001	<0.0001	0.0001	

Table 2.7. Number and mean lengths (cm) of tagged Pacific lampreys recaptured or recovered dead from large-scale surveys in 2004.

Category	Sex	Number recaptured	Mean length
All	Both	46	49.9
Live	Both	11	49.8
	Males	10	50.5
	Females	1	42.5
Dead	Both	35	49.9
	Males	27	50.8
	Females	8	46.9

Table 2.8. Tagging and recovery locations and weeks, and movement distance and direction for live Pacific lampreys recaptured during 2004 large-scale surveys.

Sex	Reach Tagged	Reach Found	Direction Moved	Reaches Moved	Week Tagged	Week Found
M	Yellow	Long Tom	upstream	2	1	2
M	Yellow	Whiskey	upstream	4	2	3
M	Yellow	Rowland	upstream	3	2	3
M	Whiskey	Rowland	downstream	1	2	3
M	Long Tom	Long Tom	stayed	0	2	3
M	Yellow	Long Tom	upstream	2	2	3
M	Yellow	Yellow	stayed	0	2	3
M	Yellow	Yellow	stayed	0	2	3
M	Long Tom	Long Tom	stayed	0	3	4
M	Whiskey	Long Tom	downstream	2	3	4
F	Rowland	Yellow	downstream	3	2	2

Table 2.9. Numbers and percent of Pacific lampreys from each tagging date recaptured on spawning grounds alive after one week in 2004; note that a female recaptured after only one day is excluded. Zero fish were recaptured in 2005.

Date Tagged	Number Tagged	Number recaptured alive	Percent recaptured
29-Apr	25	1	4.00
5-May	155	7	4.52
13-May	169	2	1.18
19-May	92	0	0.00
27-May	1	0	0.00
2-Jun	4	0	0.00
Total	446	10	2.24

FIGURES

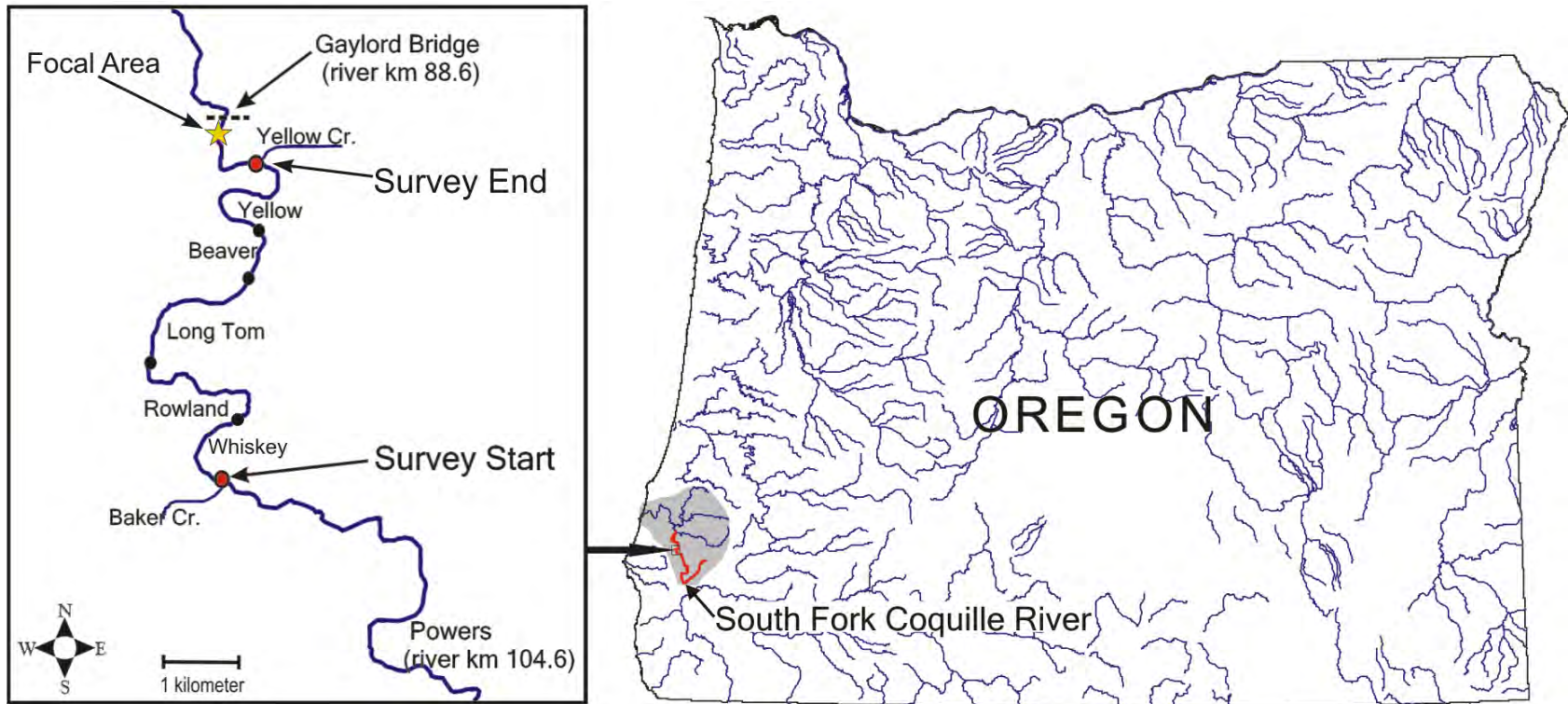


Figure 2.1. Location of the large-scale survey section, study reaches, and the focal area within the Coquille River Basin, Oregon.

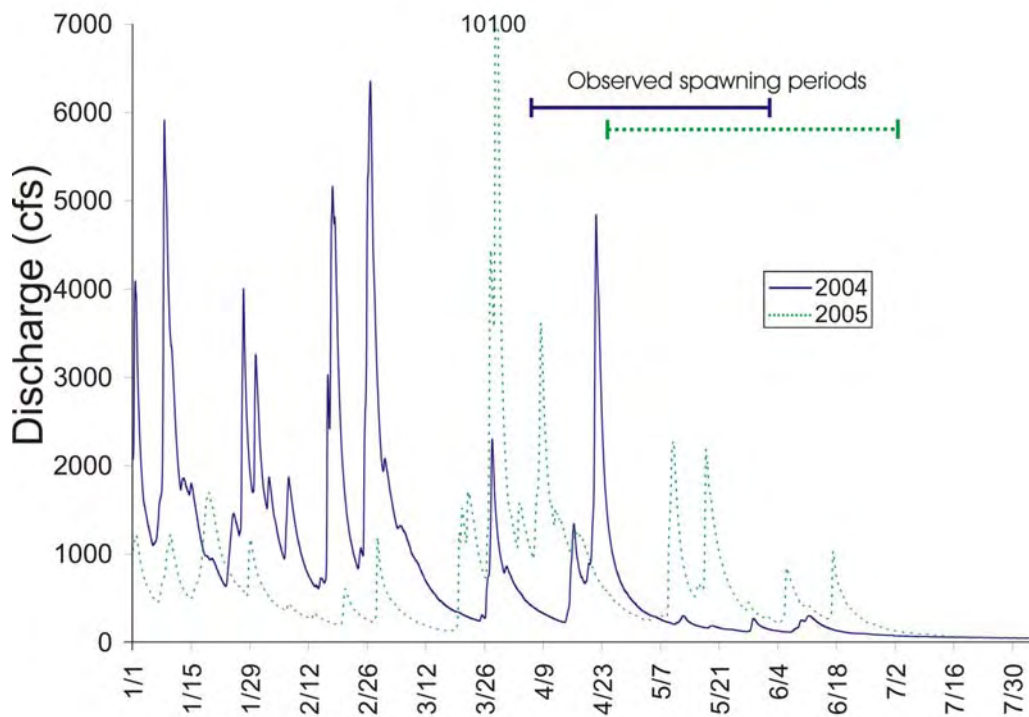


Figure 2.2. 2004 and 2005 discharge (cubic feet per second) on South Fork Coquille River from January 1 to July 30.

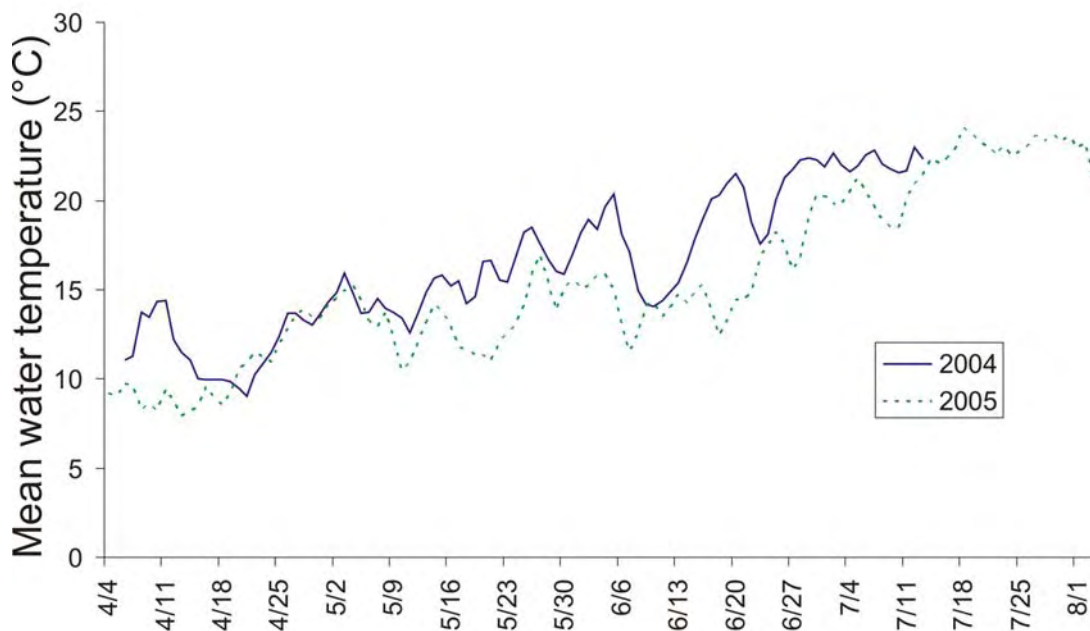


Figure 2.3. Daily mean water temperature at the focal area from April 4 until August 3, 2004 and 2005.

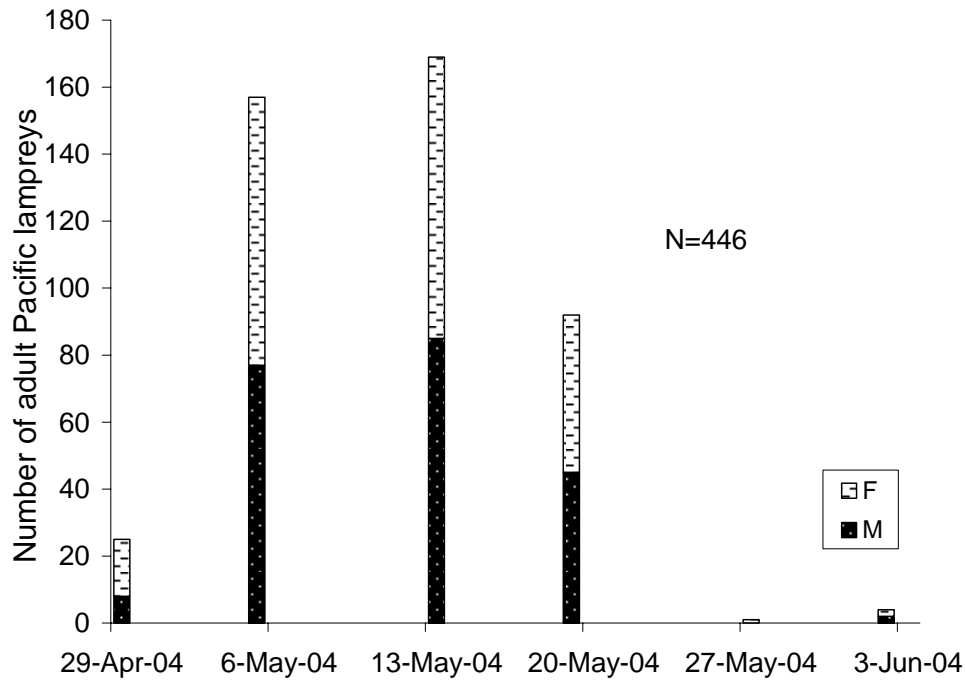


Figure 2.4. Number of live adult male and female Pacific lampreys observed on spawning areas during 2004 large-scale surveys (all reaches combined).

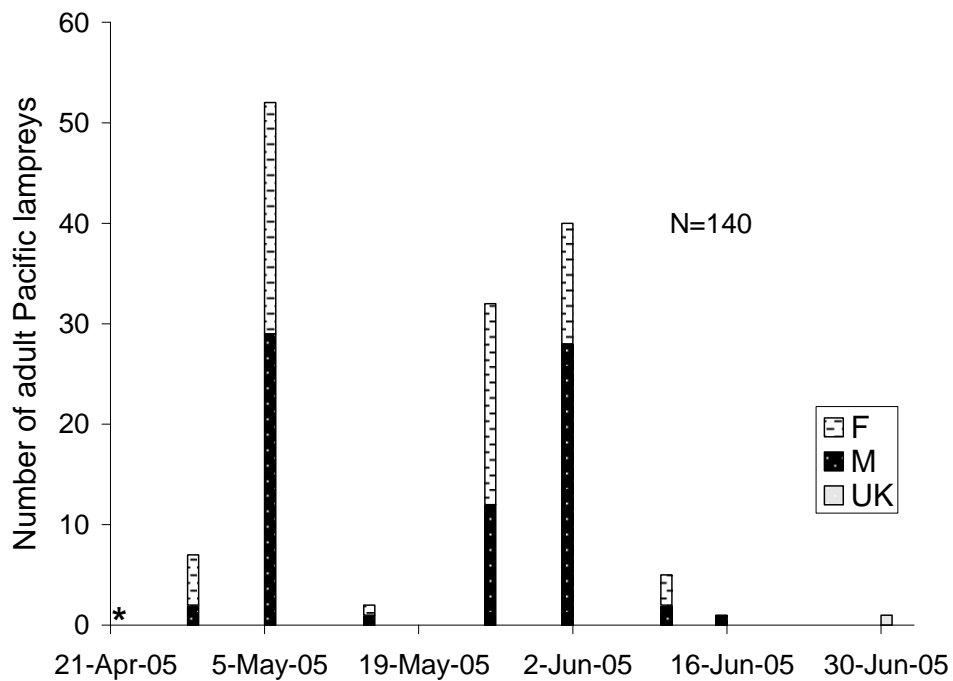


Figure 2.5. Number of live adult male and female Pacific lampreys observed on spawning areas during 2005 large-scale surveys (all reaches combined). The star represents a survey in which zero fish were seen. Note difference in scale of y-axis between Figures 2.4 and 2.5.

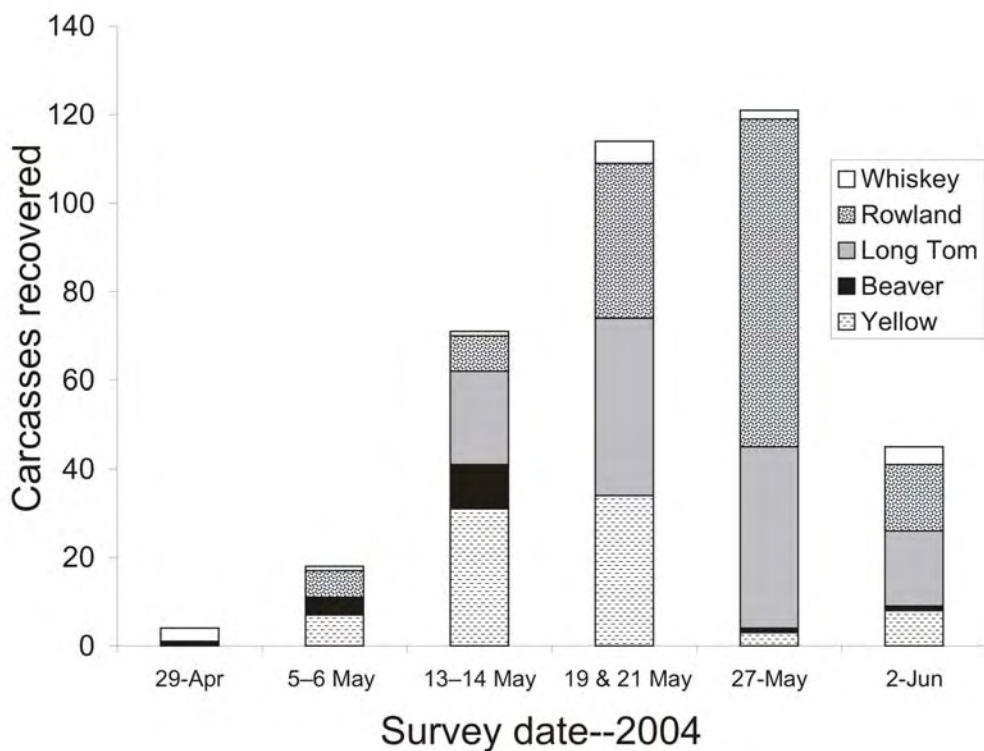


Figure 2.6. Number of carcasses recovered in large-scale reaches during 2004 surveys. Reaches are ordered from upstream (Whiskey) to downstream (Yellow).

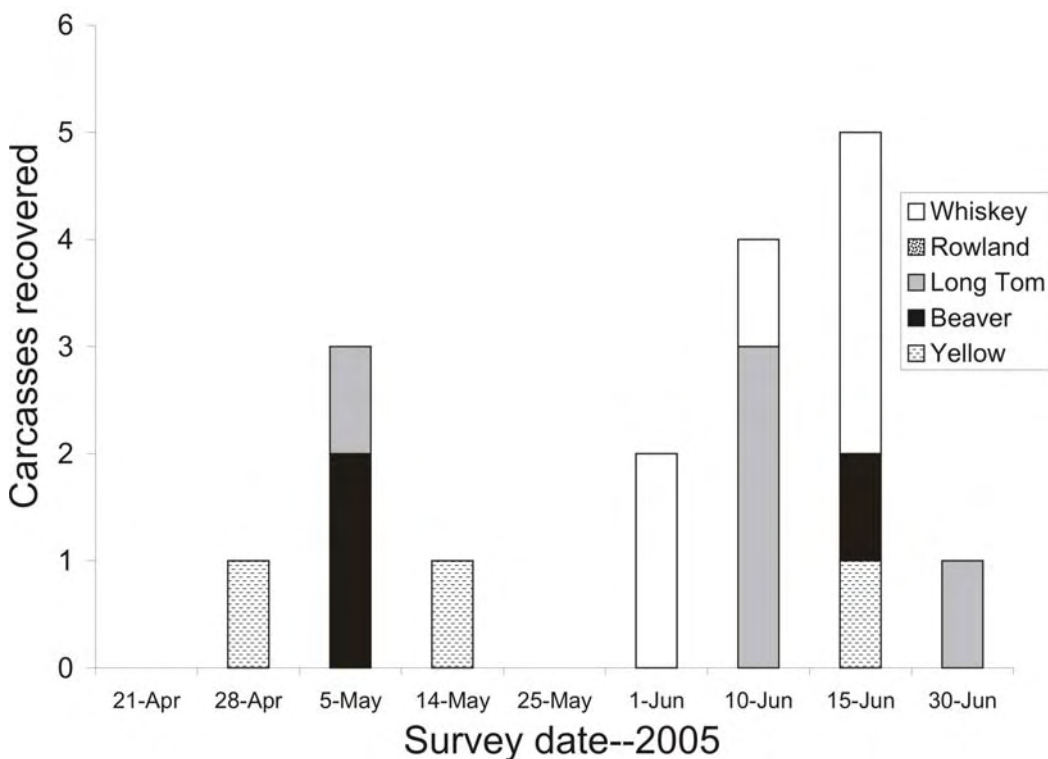


Figure 2.7. Number of carcasses recovered in large-scale reaches during 2005 surveys. Reaches are ordered from upstream (Whiskey) to downstream (Yellow).

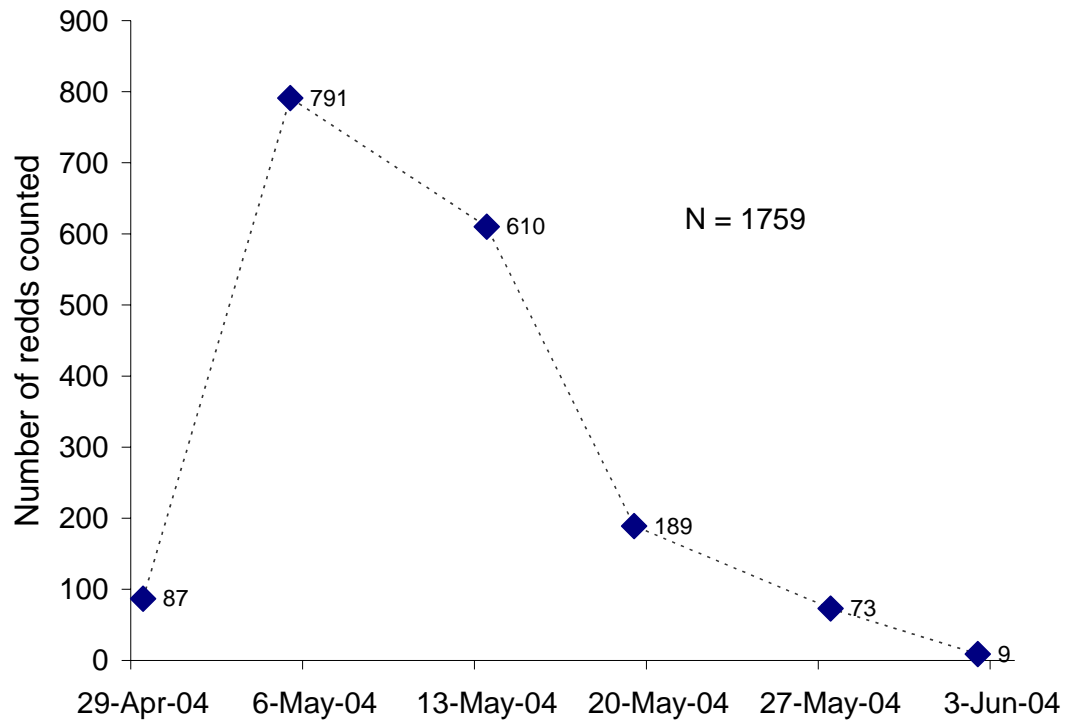


Figure 2.8. Number of Pacific lamprey redds counted during 2004 large-scale surveys (all reaches combined).

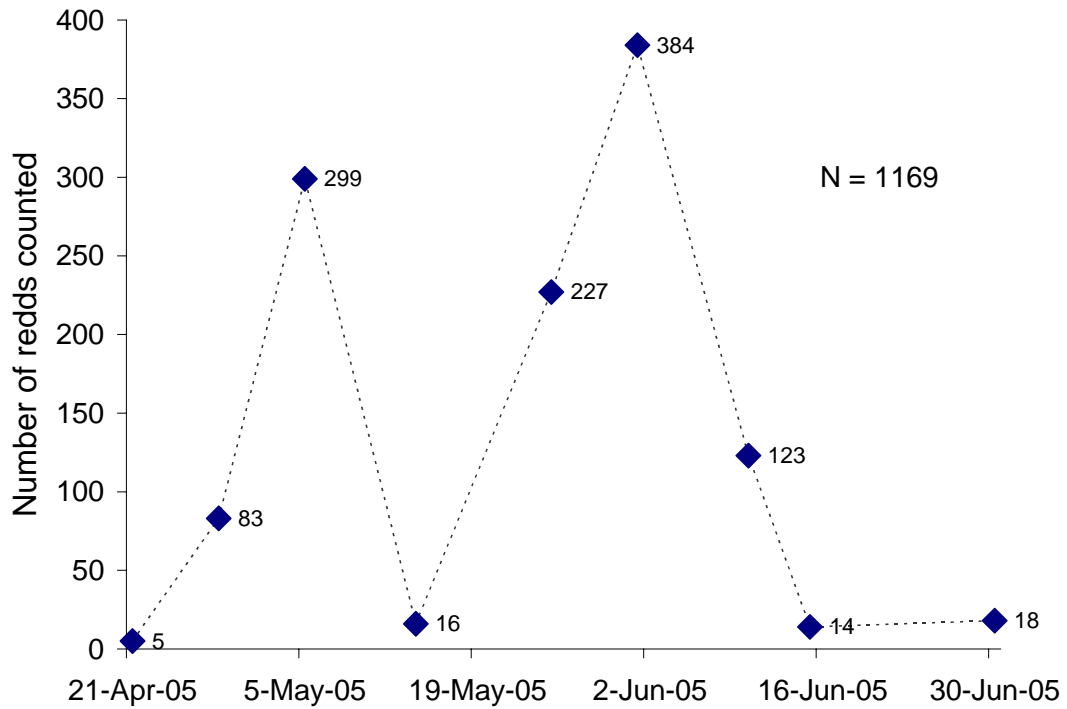


Figure 2.9. Number of Pacific lamprey redds counted during 2005 large-scale surveys (all reaches combined).

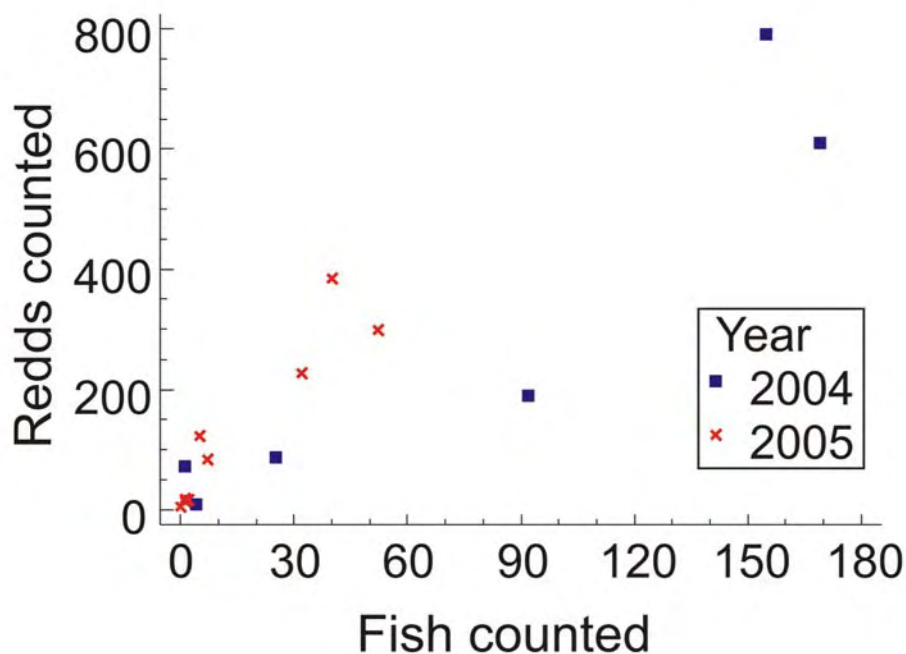


Figure 2.10. Number of redds counted versus number of live adult Pacific lampreys captured during weekly large-scale surveys.

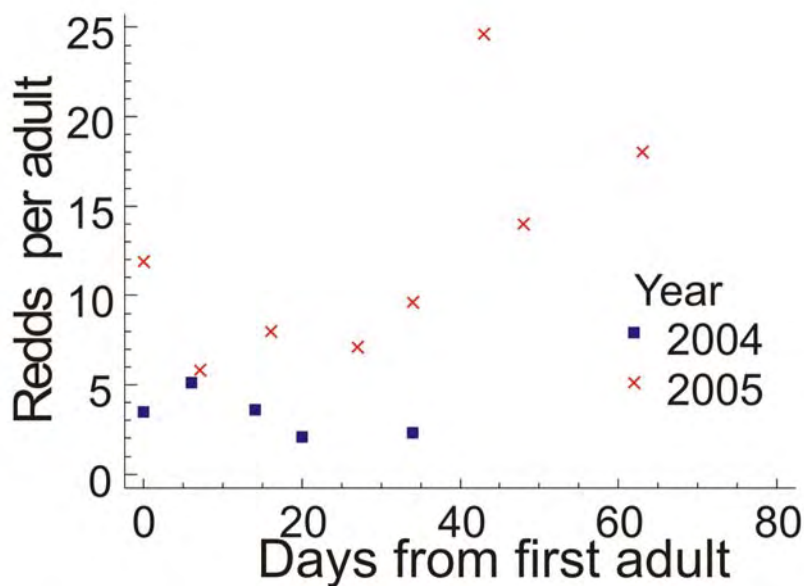


Figure 2.11. Number of redds counted per adult versus days from the first adult was observed in large-scale surveys. A 5/27/04 observation of one fish and 73 redds, 28 days from the first adult observation, was omitted.

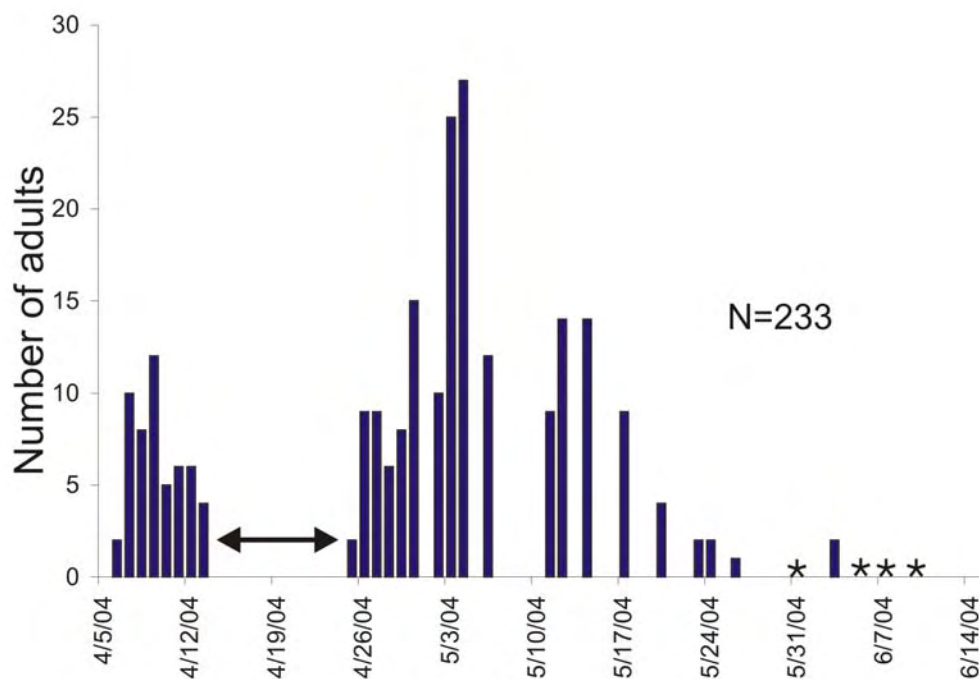


Figure 2.12. Seasonal distribution of adult Pacific lampreys in the focal area in 2004. The arrow indicates a period of high discharge when sampling was not possible. Stars represent observations when zero fish were seen.

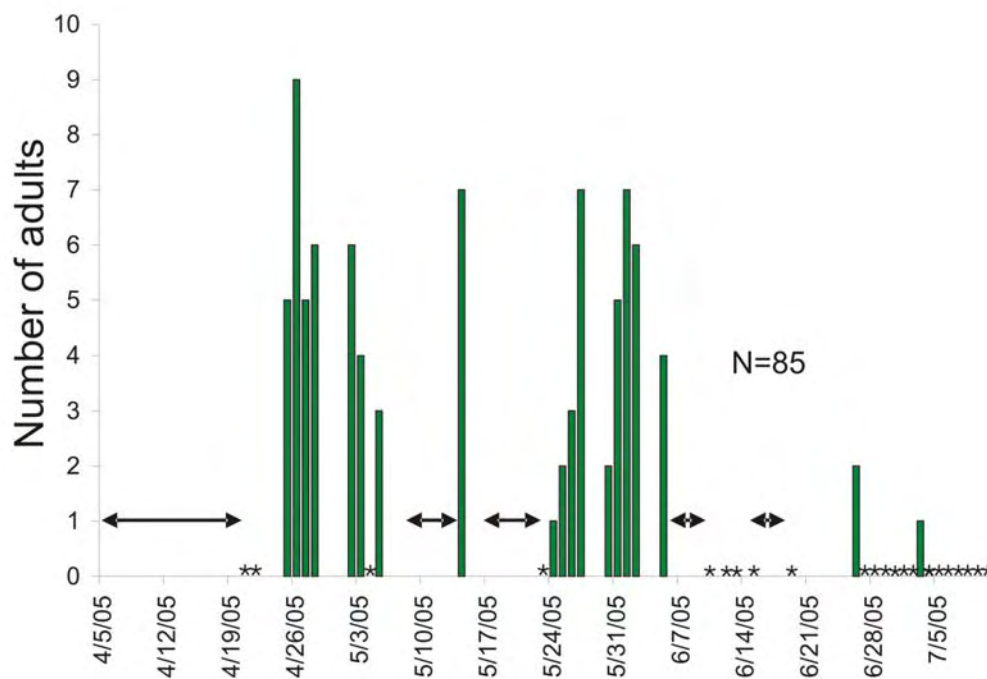


Figure 2.13. Seasonal distribution of adult Pacific lampreys in the focal spawning area in 2005. Arrows indicate periods of high discharge when sampling was not possible. Stars represent observations when zero fish were seen. Note the difference in y-axis scale between Figures 2.12 and 2.13.

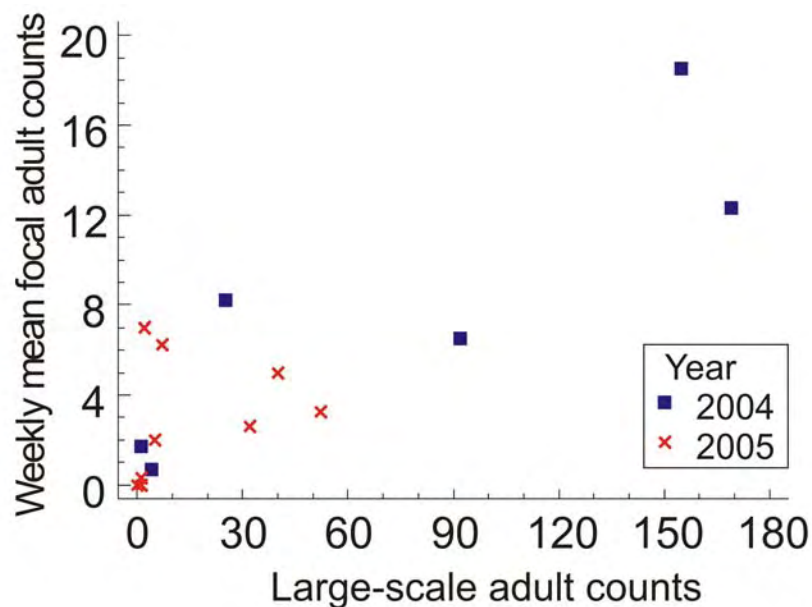


Figure 2.14. Weekly mean focal adult counts (fish per observation) versus number of live adult Pacific lampreys captured during weekly large-scale surveys.

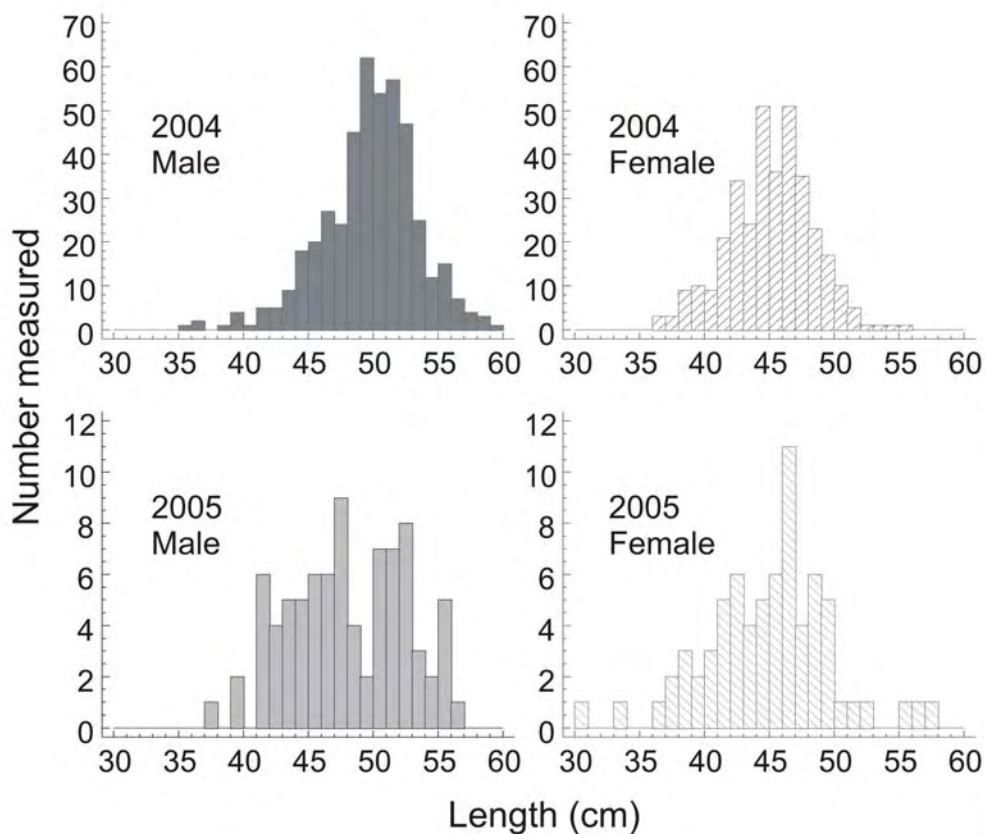


Figure 2.15. Length frequencies of all male and female mature adult Pacific lampreys sampled in 2004 and 2005 (live fish and carcasses included).

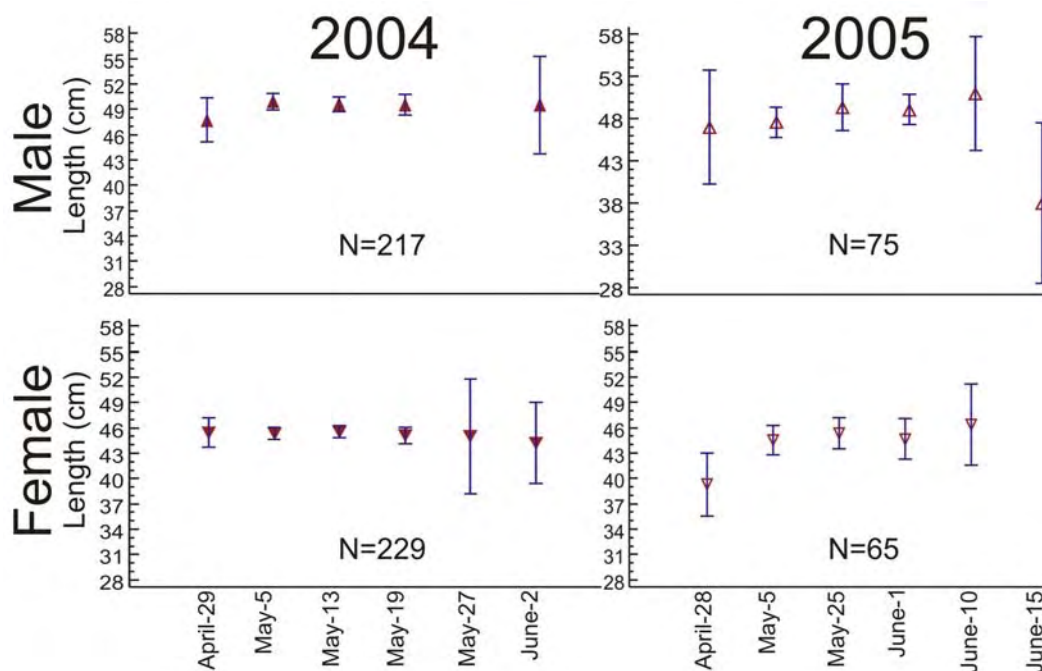


Figure 2.16. Mean lengths of live mature adult Pacific lampreys collected from spawning areas on large-scale survey dates when fish were measured in 2004 and 2005. No males were measured on May 27, 2004 and no females were measured on June 15, 2005. Bars represent Bonferroni intervals from multiple comparison procedures. There were no statistically significant differences in length between any of the spawning groups in either year, except for females between April 28 and May 25, 2005.

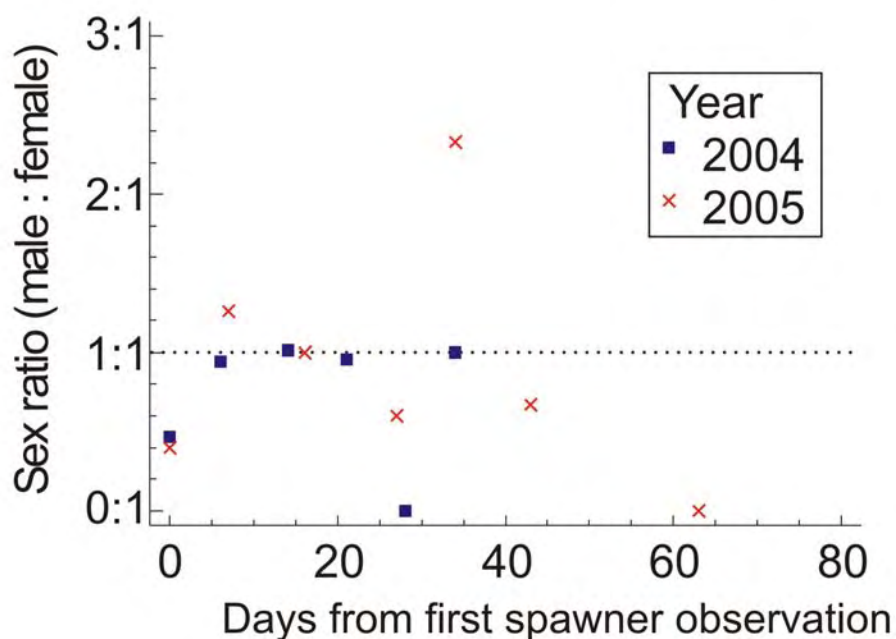


Figure 2.17. Sex ratio of live adult Pacific lampreys on spawning grounds versus days since the first mature adult was observed in 2004 and 2005 large-scale surveys.

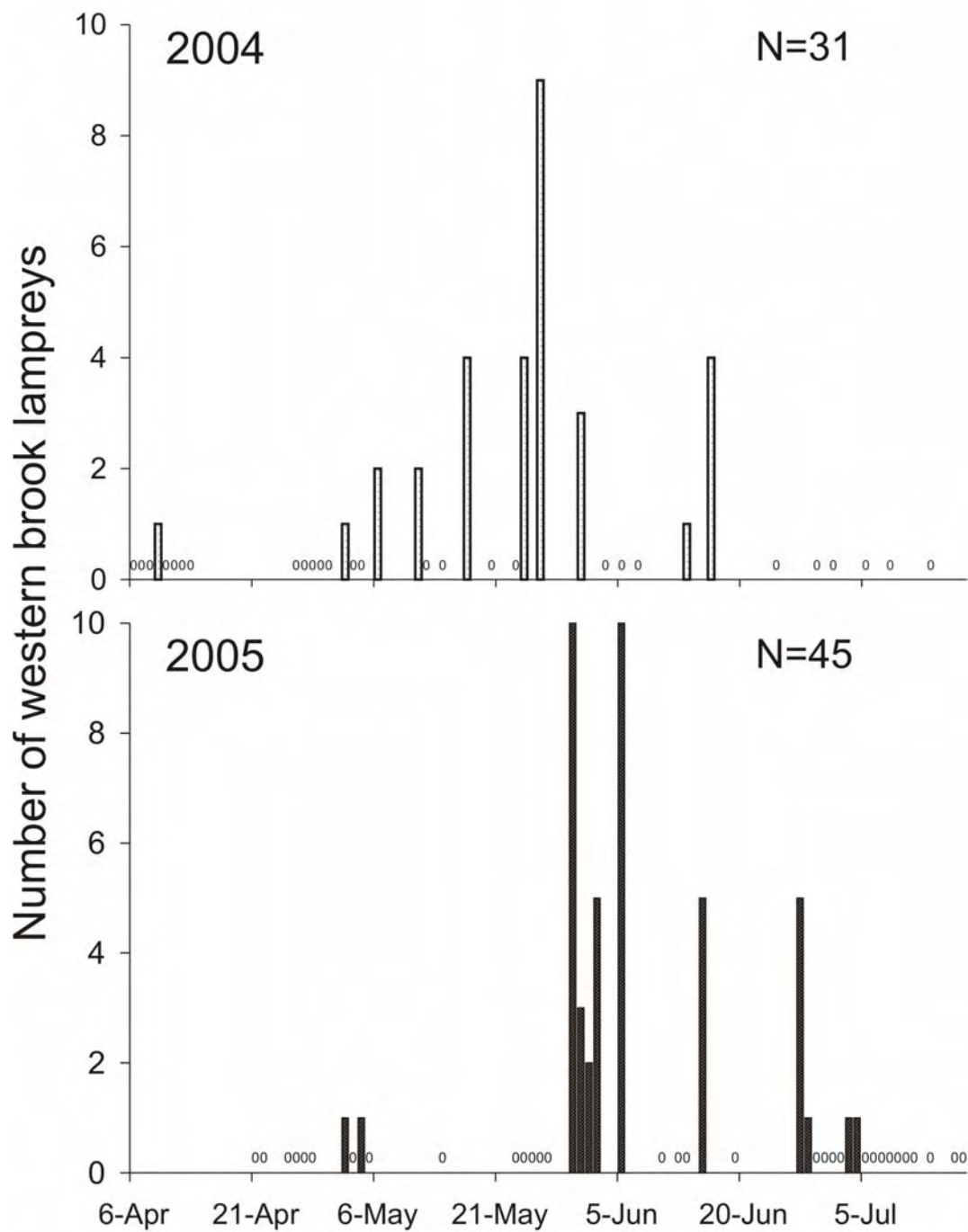


Figure 2.18. Number of mature western brook lampreys observed in the focal area in 2004 and 2005. Zeros denote observations in which no fish were counted.

CHAPTER 3

ANNUAL AND INTRA-ANNUAL PATTERNS IN PACIFIC LAMPREY SPAWNING, LARVAL RECRUITMENT, AND EARLY LIFE SURVIVAL IN A COASTAL OREGON STREAM

INTRODUCTION

Egg and larval survival in riverine fishes tends to be low and unpredictable compared to other life stages (Houde 1987; Kempinger 1988; Magnuson 1991; Bjorkstedt 2000; Pepin 2002). For this reason, differences in mortality during these stages can have important consequences for year-class success and eventual adult recruitment (Hjort 1914; Rice et al. 1987; Elliot 1989; Leggett and DeBlois 1994; Johnston et al. 1995; Houde 2002). Spawning stock size or total egg production sets the upper potential for larval recruitment, but realized recruitment is lowered due to limiting biotic and abiotic factors occurring during development (Corbett and Powles 1986; Elliot 1989; Leggett and DeBlois 1994; Houde 2002). Clarifying the relationship between spawning stock size and larval recruitment and identifying mechanisms underlying variability in early life survival are essential steps in modeling fish populations and implementing successful monitoring and recovery plans.

Despite its recognized importance in fish population dynamics, the period from spawning until larval emergence remains the least understood part of many species' life cycles. The Pacific lamprey, *Lampetra tridentata*, is no exception. Excluding a laboratory study investigating the effects of temperature on developing embryos (Meeuwig et al. 2005), research has focused on adults and older size-classes of larvae, while neglecting the critical incubation period. Therefore, the overall goal of this study

was to describe patterns of Pacific lamprey larval recruitment and early life survival in the wild.

An extremely fecund species, Pacific lampreys lay between 98,000 and 240,000 eggs (Kan 1975); though, only a minute fraction are expected to survive to maturity. For the Great Lakes sea lamprey, *Petromyzon marinus*, only 14% of a female's eggs were estimated to reach the redd gravels, but up to 90% of these survived until hatching (13–15 days; Manion and Hanson 1980). Manion (1968) estimated that, on average, only 6.3% of a female's eggs survive until hatching. Comparatively low densities of age-0 lampreys in rearing habitats additionally indicate that only a small percentage of individuals survive until the larval, or ammocoete, stage (Jones and Derosier 2002; Torgersen and Close 2004). Mortality of ammocoetes in the substrate, however, is thought to be relatively low, declining with increasing size (Pletcher 1963, Manion 1968; Hardisty and Potter 1971a; Potter 1980). As a result, survival between time of spawning and ammocoete settlement into rearing substrates is hypothesized to be central in determining outmigrant production (see Chapter 1 for a full life history description).

Among the most important factors that influence survival and recruitment during early life stages are spawning time, density of spawning adults, discharge, water temperature, and predation. There is strong selective pressure for linking timing of spawning and emergence with ecological conditions favorable for early-life survival (Flecker 1992; Frank and Leggett 1994; Dahl et al. 2004). In most temperate river systems, environmental stochasticity is the norm, and many fish species have evolved to spawn over a prolonged period as a way of hedging their bets against such variation (Quinn and Adams 1996; Humphries et al. 1999). Pacific lampreys spawn over a period

of 3–4 months (Kan 1975; Richards 1980; current study) and offspring of earlier spawning individuals can be exposed to a suite of environmental conditions that differ markedly from those experienced by offspring of later spawning individuals. For this reason substantial seasonal and annual differences in spawning time and egg and larval survival are expected.

Understanding the relationship between spawning stock and larval recruitment is essential for evaluating early life survival, yet the stock-recruit relationship has not been described for the Pacific lamprey. In highly fecund fishes, there is typically a non-linear relationship between the number of spawning adults and the number of young produced (Hjort 1914; Houde 1987; Bjorkstedt 2000). Investigations into sea lamprey population dynamic, for example, show a high amount of density-independent variation in recruitment to age-1, but a general reduction in recruitment at highest spawner densities (Jones et al. 2003; Haesker et al. 2003). Because lampreys spawn in limited benthic habitats, density dependent mechanisms may influence their survival and recruitment. Lowered recruitment of lotic fishes at higher spawner densities can result from redd superimposition by later spawning adults (Manion and Hanson 1980; Van den Berghe 1989; Fukushima et al. 1998; Jones et al. 2003), and intraspecific competition for limited food or habitat resources during juvenile stages (Elliot 1989; Weise and Pajos 1998; Partridge and DeVries 1999).

Discharge during spawning and development has also been shown to influence early life survival of lotic fish (Kempinger 1988; Scrivener et al. 1989; Johnston 1995; Fukushima et al. 1998; Mion 1998), but the effects of discharge on Pacific lamprey are unknown. We hypothesized that high flow events, which are common in Northwest

coastal rivers during the lamprey spawning season, would result in lowered cohort survival due to decreased egg deposition, scouring of eggs and prolarvae from redd gravels, and desiccation of redds associated with rapidly dropping river levels following these events.

As with other fishes (Alderdice and Velsen 1978; Hamel et al. 1997; Benoît and Pepin 1999; Pitlo 2002), water temperature is also a crucial parameter in development and survival of lamprey embryos (Pletcher 1963; Rodríguez-Muñoz et al. 2001; Meeuwig et al. 2005). In a laboratory setting, Meeuwig et al. (2005) found a sharp decline in survival of both “fertilization-to-hatch” and “hatch-to-larvae” stages as rearing temperature increased from 18°C to 22°C. Embryos reared at 22°C were also shown to be approximately six times more likely to have developmental abnormalities than those reared at lower temperatures (Meeuwig et al. 2005). The impact of water temperature on Pacific lamprey reproductive success has also not been evaluated in the wild and may differ from laboratory studies because of fluctuating temperatures and ecological interactions. Based on the results of Meeuwig et al. (2005) we anticipated that water temperatures in excess of 18–22°C during spawning and egg development may reduce larval survival.

Predation is a final source of early life mortality thought to be important in Pacific lamprey early life survival and recruitment. Numerous fishes, including rainbow trout, sculpin, stickleback, and dace have been observed feeding on eggs in lamprey redds during and after spawning (Pletcher 1963; Manion 1968; Hardisty and Potter 1971a). Preliminary observations from our study site indicated high densities of speckled dace (*Rhinichthys osculus*) in and around Pacific lamprey redds during and after spawning.

For this reason, we hypothesized that egg predation could be a significant factor in lamprey spawning success. Although it is clear that fish readily consume lamprey eggs, the recruitment consequences of this predation are unknown.

A challenge in studies of early life mortality and larval recruitment involves selecting an appropriate time scale for observation. Ecological conditions occurring before, during, and after spawning can influence reproductive success and should be considered when investigating recruitment processes (Rice et al. 1987; Kempinger 1988; Houde 2002; Pitlo 2002). This within-season variability is often overlooked when evaluating recruitment on an annual basis. An alternative to annual assessment of fish populations is analysis of intra-annual cohorts in relation to environmental variation occurring within spawning and development seasons (Rice et al. 1987; Elliot 1989; Mion 1998; Partridge and DeVries 1999; Hoffman and Olney 2005). Such an approach may help reveal mechanisms underlying variability in year class strength.

In this study we examined intra-annual cohorts of Pacific lamprey spawning adults and their larvae during 2004 and 2005 on the South Fork Coquille River to address the following questions: 1) How does spawning time and ammocoete production vary between and within years and in relation to environmental conditions? 2) What is the relationship between spawning stock and larval recruitment? And 3) how are spawning stock, temperature, discharge, and egg predation related to cohort survival until larval emergence?

METHODS

SAMPLING SITE

The primary sampling site, designated the focal area, encompassed a single Pacific lamprey spawning area (ca. 30x30m) and a riffle-pool sequence immediately downstream. The focal area was located about 200 m upstream of Gaylord, OR (42° 57' 22" N, 124° 06' 21" W) at river kilometer 88.6, and was selected based on its reputation for being a heavily used spawning area and for ease of nighttime access (Figure 3.1). The closest Pacific lamprey spawning area was approximately 300 m upstream, immediately below which was a long pool with substantial depositional habitat.

ABIOTIC VARIABLES

Water temperature was monitored at 30 minute intervals from April 27–July 13, 2004 and from April 4–August 3, 2005 using an Onset Optic Stowaway Temp Logger® placed in a shaded area at the river bottom directly downstream of the focal area. From April 6–April 27, 2004 water temperature was recorded daily with a bulb thermometer and daily mean temperatures were estimated based on bulb temperature at time of observation in relation to diel temperature trends in early May, 2004. Daily mean water temperature during periods before April 6 in 2004 and April 4 in 2005 were predicted using year-specific multiple linear regression models with maximum daily air temperature at Powers and \log_e of discharge as explanatory variables (2004, $R^2 = 0.863$, $P < 0.0001$; 2005, $R^2 = 0.918$, $P < 0.0001$).

On-site discharge data were obtained from a U.S. Geological Survey (USGS) gauging station located at Powers, OR, 14.5 river km upstream of the focal area

("POWO3"; 42 53'31" N, 124 4'16" W). No significant tributaries enter the river section between the gauge and the focal area. Lunar phase and fraction of moon illuminated, defined as illuminated area of the moon's apparent disk divided by total disk area, were obtained from the US Naval Observatory web page (<http://aa.usno.navy.mil/data/docs/moonphase.html>).

SPAWNING ACTIVITY

Pacific lamprey spawning activity in the focal area was monitored in 2004 and 2005 using counts of mature adults as an index of spawning activity. Counts were obtained by systematically wading through the focal area on 38 days between March 28 and July 12, in 2004, and on 46 days from April 5 until July 17, in 2005. When visibility permitted, counts were made in late afternoon and separated by no more than 4 days during the spawning season.

LARVAL PRODUCTION

Abundance of age-0 ammocoetes was monitored every three or four days (biweekly samples) from April 11 to July 14, 2004 and April 25 to July 28, 2005 at a site on the downstream margin of the focal area. Emergent ammocoetes from these samples were used as surrogates for intra-annual cohorts. Beginning and ending sampling dates encompassed the period of larval emergence predicted from observed spawning times, estimated incubation time, and water temperature. Drift sampling ceased after no emergent ammocoetes were caught for 4–5 consecutive samples. Biweekly samples were collected using a 500 μm mesh zooplankton-drift net [0.70 x 1.5 m opening; 2.5 m long;

“large net”] fastened to steel posts driven into the substrate, 27 m downstream of the focal area boundary. Each sample was collected between 2 and 3 hours after civil twilight (time sun is 6° below horizon; U.S. Naval Observatory web page: <http://aa.usno.navy.mil/>) in 2004 and approximately 3 hours after civil twilight in 2005. Net position relative to stream width was within 2 m of the thalweg (6–12 m from the stream margin) except during periods of high water when the net had to be set closer to the stream margin. With few exceptions, the net covered the entire water column depth. Depending on flow conditions and concentrations of net-clogging detrital matter, each net was fished for 7–16 minutes. A TSK mechanical flowmeter was centrally mounted in the net opening to estimate water velocity and volume filtered. Variation in net efficiency across sample dates due to clogging was assumed negligible for age-0 ammocoetes because of their poor swimming ability. High river levels limited access to the net-site on two dates in 2004 and five in 2005 and an alternate site approximately 200 m upstream had to be used. Of these alternate samples, only the last three in 2005 contained age-0 ammocoetes and were included in analyses of larval production from the focal area.

Net samples were rinsed into the cod-end using a battery powered wash-down pump. Contents were treated with rose bengal bioactive staining agent to facilitate sorting and preserved in 5% formalin. Age-0 ammocoetes were sorted and counted in the laboratory under magnification and measured to the nearest 0.1 mm total length using a dissecting scope equipped with an ocular micrometer. For samples containing more than 100 age-0 ammocoetes, a random subsample of 100 individuals was measured. Emergent ammocoetes were defined as individuals >7.9 mm and < 9.1 mm (“8–9” mm). The emergent size range was based on lengths from early season samples—when all

individuals were expected to be emergent—and lengths of larvae hatched in captivity (M. Meeuwig, USGS, personal communication). A pilot project, in which eggs were reared in situ until emergence, verified emergence in the 8–9 mm size range (see Appendix I). We assumed that the emergent size range did not change across sampling dates and years. Female size influences size of offspring (Elliott and Hurley 1998; Benoit and Pepin, 1999), but no temporal differences were detected in size of Pacific lamprey females in the South Fork Coquille River (see Chapter 2).

Age-0 ammocoetes larger than 9.0 mm were assumed to represent upstream production and not emergent larvae from the focal area. Larvae smaller than 8.0 mm were excluded from analyses of Pacific lamprey larval production due to the possibility they were western brook lampreys. Prior research indicates that both mean egg diameter and emergent larval length of western brook lampreys are significantly smaller than those of Pacific lampreys (Pletcher 1963; Meeuwig et al. 2004).

Seasonal comparisons of larval abundance were based on a standardized drift rate, defined as individuals drifting past the wetted-width cross section per minute, which was calculated as: individuals per m³ H₂O * discharge (m³ H₂O/second) * 60 seconds/minute. This measure of larval abundance was selected to adjust for variable stream discharge between samples. However, there was a strong correlation between drift rate (individuals per minute) and drift density (individuals per m³ H₂O) and similar results were obtained using either measure ($r^2 = 0.963$; $P < 0.0001$).

For calculations of drift rate, we assumed that density of drifting ammocoetes was uniform across the stream during the sample period and tested this assumption using smaller, paired drift nets (0.30 m x 0.45 m opening, 1 m long; 500 μm mesh; “small

nets”) set on either side of, equidistant from, and concurrent with biweekly nets. Each pair of nets consisted of a top and bottom net stacked to cover the water column, the contents of which were combined into a single net sample for analysis. Volume of water filtered was estimated from area of the net opening, time fished, and water velocity, which was measured using a pole-mounted TSK flowmeter held stationary in each net center for 1 minute. These “spatial” samples were taken on three occasions in 2004. Differences in age-0 ammocoete drift density between net positions across the wetted-width were not significant (ANOVA: $F_{2,6} = 0.02$, $P = 0.98$). For seasonal comparisons of larval production, we also assumed that the percentage of total drifting larvae caught at the biweekly net position was consistent across sampling dates.

Drift samples were collected throughout 24-hour cycles to investigate diel patterns in ammocoete drift behavior and assess whether biweekly samples collected 2 and 3 hours after sunset were representative of relative drift abundances on sample dates. Diel samples were collected on 6–7 June and 28–29 June in 2004, and 13–14 June and 5–6 July in 2005 using paired small nets stacked to cover the water column. In 2004, samples were taken concurrently at the biweekly net-site, and a site immediately upstream of the focal area, resulting in two diel cycle samples for each sample date. In 2004 samples were collected at 1–4 hour intervals at 0800, 1200, 1600, 2000, 2100, 2200, 2300, 0000, 0200, 0400, 0500, and 0600 hours. Nets were fished for 20 minutes during daylight and 10 minutes during dusk, dawn, and darkness. In 2005 paired diel nets were set at the biweekly net site for 15 minutes, at 2100, 2200, 2300, 0000, 0200, 0400, 0500, and 0600 hours. No daylight samples were taken in 2005 because 2004 diel samples verified that ammocoetes seldom move during these times. Volume of water filtered was

estimated as described above. Because river discharge was essentially constant during 24-hour sample cycles, results were expressed as standardized drift densities (individuals per m^3 H_2O filtered). Drift densities from each net were normalized by expressing them as a percent of the total density captured during a 24-hr sample cycle. Over the six diel sampling events, hourly differences in percent of total daily drift density were compared using One-way ANOVA. Bonferroni's multiple comparison procedure was employed to determine significance among sample times.

EGG PREDATION

Speckled dace and other likely egg predators were surveyed qualitatively in the focal area by sight, under water photography, and video and categorized into the following feeding activity levels: Level 1, a non-feeding observation, when speckled dace were absent or scattered and in low densities relative to lamprey redds; Level 2, when dace were aggregated in and behind spawning lampreys or active redds in comparatively high densities, but not seen feeding aggressively; and Level 3, feeding-frenzy, when high densities of dace (~ 100 per m^3) were congregated in or behind recently spawned-in redds and actively feeding on eggs.

To verify that speckled dace were indeed consuming lamprey eggs, a small number were collected during apparent feeding events, anesthetized, and preserved in 10% formalin for inspection of stomach contents. Stomach contents were dissected from individual dace and examined under a dissecting microscope. Probable Pacific lamprey eggs were compared to a sample of fertile eggs obtained from a manually spawned pair (Appendix I).

DATA ANALYSES

Linking Larval Drift Samples with Corresponding Adult Counts

Spawning dates for emergent ammocoete cohorts were estimated by backcalculating from the capture date to the date required to achieve 300.7 effective degree-days (EDD). This EDD estimate was based on temperature units required to reach larval stage 18 (Piavis 1961), which was calculated from a USGS laboratory study on Pacific lamprey eggs reared at constant water temperatures of 10, 14, 18, and 22°C (Meeuwig et al. 2005; Table 3.1). Effective degrees for each day were calculated by subtracting the theoretical temperature for zero development, 4.85°C (Meeuwig et al. 2005), from the daily mean water temperature. The predicted spawning date for each emergence date was the date at which cumulative EDD was closest to 300.7 (Table 3.1). Duration of embryonic development was the number of days between emergence and the estimated spawning date. The predicted spawning period for each larval cohort was the period corresponding to the day before a larval drift sample to the day after a larval drift sample, which ranged from 2–5 days. The sum of adult counts during this period was used as an estimate of spawning stock in analyses.

Because adult counts were not available for all days in spawning periods corresponding to each emergence date, we generated estimates of adult counts for all missing days (Appendices IV, V). Based on previous research (Pletcher 1963; Kan 1975; Close et al. 2003) and observations from the current study, adult spawning activity was assumed to be zero on days with daily mean water temperature below 11°C. Missing adult counts were estimated from simple linear regressions of actual counts on daily mean water temperature from April 6–May 19 in 2004 ($r^2 = 0.356$, $P = 0.0034$) and April

5–June 5 in 2005 ($r^2 = 0.217$; $P = 0.0287$). Temperature-predicted regression estimates for missing dates were then adjusted based on the residuals of actual adult counts on the two adjacent dates. The residuals were weighted based on proximity of actual counts to the missing dates, and the sum of the two weighted residuals were added to the regression estimate for the missing date. For example, if actual adult counts on May 9 and May 11, were 10 and 20, but temperature-predicted regression estimates were 12 and 14, respectively, then the regression estimate for May 10 would be adjusted by +2, or 50% of the residual from May 9 (-1) plus 50% of the residual from May 11 (+3). Spawning activity after May 19 in 2004 and June 5 in 2005 were not described by linear temperature models; therefore adult estimates were generated using simple linear interpolation between actual adjacent adult counts.

In analyses of stock-recruitment and survival until emergence, we only included data points in which both emergent larvae and corresponding spawners were present ($N=26$). These points consisted of all larval drift samples from May 13–June 24, 2004 ($N=13$) and May 30–July 14, 2005 ($N=13$), which constituted 99.8% and 97% of seasonal larval production, respectively. Of these 26 spawning periods, only two spawning stock estimates, both in 2005, were comprised entirely of predicted adult counts.

There are a number of error sources to consider when linking intra-annual larval cohorts with spawning adults. First, duration of the incubation period until emergence can differ between laboratory-reared eggs and those reared in situ. In this case, days from fertilization to larval emergence in the wild may not be equivalent to days from fertilization to larval stage 18 in the lab (burrowing stage; Piavis 1961; Meeuwig et al.

2005), which was used as proxy for emergence. Designation of stage 18 involves inspection of level of yolk extrusion from the gut and is a rather qualitative assignment (M. Meeuwig, USGS, personal communication). Furthermore, naturally fluctuating temperature regimes in the field can lead to different development rates than eggs reared at constant temperatures in controlled laboratory studies (Alderdice and Velsen 1978; Hamel et al. 1997). Derosier (2001) found that it took 8.6% and 38.6% more cumulative degree days for 50% larval emergence to occur for sea lampreys in two Lake Huron tributaries, than for 50% of individuals reared at constant temperature in laboratory experiments to reach the burrowing stage (Stage 18; Piavis 1961). On the contrary, Bestgen and Williams (1994) found little difference in time of hatch between fluctuating and constant temperatures over a range of mean development temperatures for Colorado pikeminnow, *Ptychocheilus lucius*. Notably, light intensity (John and Hasler 1956), oxygen concentration (Shumway et al. 1964; Hamor and Garside 1976), and photoperiod (Hamel et al. 1997) have also been shown to influence fish development rate and each of these factors could change over time and differ between field and laboratory settings.

A second potential error source in linking larvae with their parents involves variation in time of larval emergence from a single redd. Our in situ incubation pilot project showed that larvae from eggs fertilized on the same date emerged over a period of nearly two weeks, with 70% emerging over a 5-day period (Appendix I). This result suggests that either, there was substantial variation in development rate, or larval emergence timing was controlled in part by factors other than developmental stage. Derosier (2001) concluded that sea lamprey larvae from like-nests emerged over a period

of 3–14 days; although her sampling design almost certainly caught larvae originating from multiple nests.

Third, multiple methods can be used to predict spawning time based on water temperature, and error is introduced from the temperature-development model selected (Hamel et al. 1997). We used a cumulative effective degree-day model to match intra-annual cohorts of drifting larvae with corresponding spawning periods. The degree-day model is relatively simple and assumes a linear increase in developmental rate with temperature. Although it has been criticized for its lack of application outside a central range of temperatures (Alderdice and Velsen 1978), Hamel et al. (1997) showed that, for white sucker, *Catostomus commersoni*, the degree-day model was at least as accurate as several more complex models. At the moderate range of temperatures experienced by most developing embryos in this study, it is safe to assume that the degree-day model was reasonably accurate in its prediction of incubation time (Hamel et al. 1997). Using this model, the last newly-emerged larvae collected in both years were within 3–4 days of dates predicted from water temperature and adult observations. Moreover, 50% of larvae reared in the in situ egg incubator, at a mean temperature of approximately 15°C, emerged within 3–4 days of the time predicted using the degree day model (Appendix I).

In spite of the potential drawbacks of using a temperature-development equation obtained from laboratory data, our results suggest the methods employed were adequate to predict spawning time at the temporal resolutions considered. If consistent across temperatures, these error sources are unlikely to alter our conclusions about relative survival and stock-recruitment.

The relationship between adult counts and actual spawning can also be questioned as a potential bias when linking intra-annual larval cohorts with their parents. Even though the majority of fish observed in the focal area were not in the act of spawning, we believe presence of adults was an accurate surrogate for spawning activity. First, nearly all of adult Pacific lampreys observed were either in the process of redd-digging or were resting in the vicinity of a redd. Secondly, all adults examined exhibited characteristics of ripe fish: enlarged dorsal and caudal fins, engorged false anal fins in females, or running ripe with eggs or milt. Finally, results from a tagging study (See Chapter 2) suggest that the period of residence on spawning grounds is typically not more than one week. Farlinger and Beamish (1984) also estimated that Pacific lampreys remain on spawning grounds for about 5 days.

Stock – recruitment

The relationship between spawning stock and downstream larval recruitment was evaluated using a simple linear regression model of \log_e of emergent larval recruitment (drift rate) versus \log_e of spawning stock. A Ricker stock-recruitment model was fit to the same data for comparative purposes using the following equation (Ricker 1975):

$$\mathbf{Equation\ 1:} \quad R = \alpha * S * e^{-\beta * S}$$

where R is larval recruitment, S is corresponding spawning stock, α is the coefficient of density-independent mortality, and β is the coefficient of density-dependent mortality.

The parameters α and β were obtained from the exponentials of the intercept and the slope, respectively, of a simple linear regression of \log_e larval recruitment per spawning stock versus spawning stock.

Survival until Larval Emergence

Relative Pacific lamprey reproductive success, or survival until larval emergence, was assessed by comparing larval production per spawning adult between and within 2004 and 2005 spawning seasons. Annual survival was contrasted using a “Relative Survival Index,” calculated by dividing total annual drift rate of emergent larvae by the estimated annual number of spawners. Monthly indices of survival until emergence were calculated for each spawning month, by dividing the percent of total annual emergent larval production by the percent of annual spawners in that month. Survival until emergence was assessed for each intra-annual cohort as emergent larval production per spawner. We assumed that average fecundity, which is related to female length (Malmqvist 1986), was unchanged throughout the spawning season since there were no significant differences in mature female lengths between sampling dates (see Chapter 2).

Explaining Survival until Larval Emergence

Simple linear regression was employed to examine relationships between cohort survival until emergence and the following variables: mean water temperature during the development period (MWTD), number of days daily mean water temperature exceeded 20°C during development (DMWT20+), mean water temperature during the spawning period (MWTS), stream discharge during each drift sample (discharge), mean discharge during the development period (MDD), number of days daily mean discharge exceeded 1000 cfs during development (DMD1000+), mean discharge during the spawning period (MDS), fraction of the moon illuminated during each drift sample (FMI), number of adult Pacific lamprey present during each corresponding spawning period (SS), duration of the

development period (DDP), and Year (Table 3.2). Where necessary, data were \log_e transformed before regression to meet conditions of normality and constant variance, or to improve linearity. Conditions occurring during periods of high and low survival were also evaluated using two sample t -tests to compare mean values of each explanatory variable between cohorts with the highest 50% of survival values, and those with the lowest 50% of survival values.

After evaluating univariate relationships, a list of prospective multiple linear regression models was selected from a subset of predictor variables (Table 3.2) and narrowed-down using the information-theoretic approach (Burnham and Anderson 1998). Initially the “regression selection” feature of STATGRAPHICS was employed to fit all possible one to five variable combinations of nine potential explanatory variables, including an interaction term between SS and MDS, and an indicator variable for Year (Table 3.2). This procedure resulted in a preliminary list of 382 models. A matrix of correlations was used to identify high correlation between independent variables (Appendix VI). Models having highly correlated variables were inspected for serious multicollinearity by calculating Variance Inflation Factors (VIF) of their parameters using STATGRAPHICS. Only models containing parameters with VIFs less than 5 were retained. Additionally, models containing the interaction term but not both interacting variables were eliminated, resulting in 145 candidate models.

Akaike Information Criterion (AIC) values with a small sample size correction (AIC_c; Hurvich and Tsai 1989) were calculated for the 145 remaining models using Equation 2 (Burnham and Anderson 1998; p. 51) and subsequently arranged in ascending order of AIC_c value.

Equation 2:
$$AIC_c = -2 \log[\mathcal{L}(\hat{\theta})] + 2K \left(\frac{n}{n - K - 1} \right)$$

The first term in Equation 2 measures goodness of fit of the model, and the second term represents a penalty for increasing numbers of parameters (Burnham and Anderson 1998). $\log(\mathcal{L}(\theta))$ represents the log-likelihood estimator, K represents the number of parameters in the model, and n equals sample-size. The log-likelihood estimator was approximated as $\log(\mathcal{L}(\theta)) = -\frac{1}{2}n \log(\hat{\sigma}^2)$ (Burnham and Anderson 1998; p. 17). The multiplication of the term $2K$ by $n/n-K-1$, a small sample size correction factor, is recommended when the ratio of $n-K$ is less than 40 (Burnham and Anderson 1998).

Models with smaller AIC_c values provide a more parsimonious explanation of variation in the dependent variable than models with larger values (Burnham and Anderson 1998).

ΔAIC_c , or the difference in AIC_c values between each model and the model with the smallest AIC_c value (“top model”), were calculated to assist in model evaluation. Models with ΔAIC_c values ≤ 2.0 were considered competing with the top model (Burnham and Anderson 1998) and received consideration in the discussion. Akaike weights (w) were also calculated for each model to aid in their comparison using Equation 3 below (Burnham and Anderson 1998; p. 124).

Equation 3:
$$w_i = \frac{\exp(-\frac{1}{2}\Delta AIC_c_i)}{\sum \exp(-\frac{1}{2}\Delta AIC_c_i)}$$

ΔAIC_c_i equals AIC_c for the i th model minus the AIC_c value for the top model. Finally, relative importance values for each explanatory variable were then computed from the

145 candidate models by summing w_i for all models in which a given variable appeared. Importance values offer a means of evaluating each explanatory variable's relative weight in explaining the variability in the response.

Lastly, a stepwise linear regression model selection technique was employed with the same explanatory variables using Splus (Table 3.2). This technique consisted of alternating forward selection and backward elimination steps until no explanatory variables could be added or removed. Stepwise regression acted as a separate means for selecting a suitable model from the pool of available explanatory variables (Table 3.2), as well as a substantiation of variables selected using AIC_c .

Dace activity level during spawning was excluded from regression models due to a small sample size in periods corresponding to intra-annual cohort spawning periods ($N = 16$). Instead, differences in mean lamprey survival until emergence at each dace feeding level were examined using a one-way ANOVA. To better understand observed patterns of dace activity, factors hypothesized to influence dace feeding level, such as water temperature and density of spawning Pacific lampreys, were also investigated using one-way ANOVA.

RESULTS

ABIOTIC VARIABLES

Discharge during the 2004 lamprey spawning season was marked by a single, mid-April high-flow event, which peaked on April 21 at 4840 cfs (Figure 3.2). In 2005 three substantial high-flow events (> 2000 cfs) occurred early and two smaller events

(851 and 1030 cfs) occurred later in the spawning season (Figure 3.2). During the April–July spawning periods stream discharge was inversely related to water temperature (2004 and 2005 combined; $r^2 = 0.865$; $P < 0.0001$; Figures 3.2, 3.3). Average water temperature from April 6–July 13 was about 15% higher in 2004 (16.3°C) than in 2005 (14.0°C). In both years, water temperature rose gradually during spring, but diel fluctuations of up to 8°C occurred (Figure 3.3). Full moons occurred near the beginning of each month in 2004 and towards the end of each month in 2005.

SPAWNING ACTIVITY

In 2004, 233 adult Pacific lampreys were counted in the focal spawning area between April 6 and June 3 (Figure 3.4), with 95% observed by May 17. The maximum number counted per day was 27, on May 4 (Figure 3.4), and mean number per day during the spawning period was 8.32 ± 1.24 (mean \pm SE). A large spring freshet in mid–late April precluded observations (Figures 3.2, 3.4).

In 2005, 85 fish were counted in the focal area, with a mean of 2.65 ± 0.50 fish per survey during the spawning period. Spawning began later and occurred over a more prolonged period than in 2004, from April 25 through July 3, with 95% of observations occurring by June 6 (Figure 3.5). Spawning activity was bimodal, with peaks in late April and from late May to early June (Figure 3.5). The maximum number counted per day was nine, on April 26 (Figure 3.5). The five moderate to high flow events in 2005 precluded adult observations (Figures 3.2, 3.5).

Mean water temperature during both spawning seasons was approximately 15°C, with mature adults observed at a daily mean temperature ranged from 11.1–19.7 °C

(Figure 3.6). Spawning activity generally exhibited a curvilinear relationship with water temperature. In both years, the number of adults observed peaked between 13°C and 16 °C, declining at temperatures above and below this range (Figure 3.6). Mature adults were observed at the focal area at daily mean discharges of 124–932 cfs, with maximum spawning activity occurring from around 200–500 cfs (Figure 3.7).

Water temperature during spawning was highly correlated with both mean temperature ($r^2 = 0.768$; $P < 0.0001$) and discharge ($r^2 = 0.615$; $P < 0.0001$) during egg and larval development. In contrast, discharge during spawning was only moderately related to mean water temperature ($r^2 = 0.283$; $P = 0.0017$) and discharge ($r^2 = 0.274$; $P = 0.0021$) during development.

LARVAL PRODUCTION

In 2004, 74 drift samples (26 biweekly and 48 diel) were taken between April 11 and July 14 (Table 3.3). A total of 6901 age-0 ammocoetes were captured in the 26 biweekly samples. Fifty-five percent of these individuals were newly-emerged (8–9 mm size-class), 43% were greater than 9 mm, and 2% were less than 8 mm. Early season biweekly nets in 2004 caught predominately 8–9 mm individuals, with the proportion of older and larger age-0 larvae increasing as the season progressed (Figure 3.8).

Emergent ammocoetes occurred in the drift for a 54 day period in 2004, from May 6 until June 28—30 days after the first, and 25 days after the last adult was detected in the focal area (Figures 3.4, 3.8). Emergent ammocoete abundance averaged 353.3 ± 141.6 (mean \pm SE) fish per minute, peaking in mid-May at 2131.9 fish per minute.

Approximately 60% of emergent ammocoetes were captured by May 24, and 99% by

June 21. The median emergence date, when 50% of the annual abundance was captured, occurred between May 20 and 24.

During the emergence period in 2004 (May 6 – June 28), abundance of emergent ammocoetes was significantly correlated with abundance of age-0 ammocoetes larger than 9 mm ($r^2 = 0.501$; $P = 0.0022$; \log_e - \log_e model). Abundance of larger (>9 mm) ammocoetes peaked at 610.2 per minute in early June, and remained high throughout the month (Figure 3.8). A low number of larvae <8 mm, likely western brook lampreys, were caught between May 27 and June 21, peaking on June 10 at 57.1 fish per minute (Figure 3.8).

In 2005, 43 drift samples (27 biweekly and 16 diel), were collected between April 25 and July 28 (Table 3.3; Figure 3.8). A total of 2,854 age-0 ammocoetes were collected in biweekly samples, of which approximately 48% were newly-emerged, 50% were greater than 9 mm, and 2% were less than 8 mm. Emergent ammocoete drift rate during 2005 was about a third lower than in 2004, with a mean of 112.1 ± 34.9 individuals per minute. Emergent ammocoetes were present in the drift over 71 days in 2005—from May 15, 20 days after initial adult detection, to July 25, 22 days after final adult detection (Figures 3.5, 3.8). Emergent ammocoete drift rate exhibited two distinct peaks in 2005; the first and largest (550.9 fish per minute) around mid-June, and the second (405.2 fish per minute) in early July (Figure 3.8). Approximately 60% of emergent ammocoete production occurred by June 18, about half way through the observed emergence period. The median emergence date occurred between June 12 and June 15 in 2005.

Unlike 2004, during the emergence period in 2005 (May 15 – July 25) abundance of emergent ammocoetes was only weakly correlated with abundance of age-0

ammocoetes larger than 9 mm ($r^2 = 0.148$; $P = 0.0572$; \log_e - \log_e model). Ammocoetes >9 mm were captured in three main peaks in 2005: early, mid, and late June (Figure 3.8). In contrast to 2004, a relatively high number of larger age-0 ammocoetes were present in early season samples—sometimes in numbers greater than the emergent size-class (Figure 3.8). A few smaller larvae (<8 mm) were caught between May 26 and July 17, with drift rate peaking at 58.2 fish per minute on June 22.

Mean water temperature during development of larval cohorts ranged from 12.55°C to 18.26°C in 2004, and from 11.81°C to 21.85°C in 2005 (Figure 3.9). Duration of the development period (DDP), or number of days between spawning date and emergence date, which was estimated from effective degree-days, ranged from 21–42 d in 2004 and 18–49 d in 2005. In both years, peak larval production occurred at mean development temperatures of approximately 13–16°C, with 69.2% of larvae developing within that range (Figure 3.9). Above mean development temperatures of 16°C, recruitment generally declined with increasing water temperature (Figure 3.9). Water temperature during development increased seasonally, and later emerging larvae were generally exposed to higher development temperatures than earlier larvae (Figure 3.10). During development of larvae emerging after June 15, 2004 and June 29, 2005, daily mean water temperatures commonly surpassed 20°C—the level predicted to be detrimental to larval survival (Meeuwig et. al 2005; Figure 3.3).

Mean water temperature during development was inversely related to mean discharge during development ($r^2 = 0.793$; $P < 0.0001$). In both years, mean discharge during development declined seasonally (Figure 3.10). Developing larvae were exposed to mean discharges ranging from 152–685 cfs in 2004 and 71–841 cfs in 2005 (Figure

3.11). Larval production displayed a weak curvilinear relationship with mean development discharge; generally increasing with discharge up to 600 cfs, and decreasing with discharge above 600 cfs (Figure 3.11).

DIEL PERIODICITY IN LARVAL DRIFT

In diel drift samples, maximum abundance of age-0 ammocoetes occurred during the darkest hours of night, with negligible drift occurring between dawn and dusk (Figure 3.12). Averaged over the six diel sample cycles, peak drift of all age-0 ammocoetes occurred between 2300 and 0200 hours, with no significant differences between those times (Figure 3.12). Size-specific differences in age-0 larval drift timing were evident, with smaller larvae more likely to drift later. Abundance of emergent ammocoetes was significantly higher at 0000 and 0200 hours than at 2300 and 0400 hours (Figure 3.12). In contrast, larger ammocoetes (>9 mm) drifted slightly earlier, with peak density between 2300 and 0000 hours and fewer at 0200 and 0400 hours (Figure 3.12). Smaller ammocoetes (<8 mm) had a diel drift pattern similar to emergent Pacific lampreys (8–9 mm).

STOCK – RECRUITMENT

Emergent ammocoete recruitment over both years was weakly correlated with spawning stock, as measured by the estimated number of adults in the corresponding spawning period ($r^2 = 0.149$, $P = 0.0512$, $N = 26$; Figure 3.13). When years were considered independently, there was little evidence for a correlation between spawning stock and larval recruitment (2004: $r^2 = 0.127$, $P = 0.2328$, $N = 13$; 2005: $r^2 = 0.098$; $P =$

0.2968, $N = 13$; Figure 3.13). Though highly variable across the range of stock sizes observed, emergent larval recruitment appeared to level out, or even decline, at higher spawning stocks. However, over both years combined a Ricker stock-recruit model had an even weaker fit to the data ($r^2 = 0.107$).

SURVIVAL UNTIL LARVAL EMERGENCE

Total ammocoete production from the focal area was nearly three times higher in 2004 than in 2005, but annual larval production per spawning adult (relative survival until emergence) was only slightly higher in 2004 (Table 3.4). Within years, relative survival until emergence varied markedly between intra-annual cohort spawning periods. In 2004, early spawning fish were generally more successful than those spawning later (Figure 3.14). Only 28% of 2004's spawners were observed in April, but they produced nearly 65% of the year's emergent ammocoetes (Figure 3.14, Table 3.5). In contrast, over 70% of the season's spawners were observed in May, but they produced only 35% of emergent ammocoetes (Figure 3.14, Table 3.5). Few fish spawned in June, 2004 (~1%) and they produced only a small number of emergent larvae (Table 3.5).

In 2005 middle and late season spawners were typically more successful than those spawning earlier (Figure 3.15). As in 2004, about a quarter (26%) of spawners were observed in April, but they produced only 7% of 2005's larvae (Figure 3.15; Table 3.5). Highest spawning success occurred in May, when 47% of the season's spawners accounted for almost two-thirds of annual larval production (Table 3.5). In June, 27% of the year's adults produced 27% of the larvae. Less than one percent of spawning observations occurred in July, resulting in an insignificant fraction of emergent larvae.

Univariate Models

Of the 10 explanatory variables analyzed by simple linear regression, mean discharge during the spawning period (MDS) explained the highest percentage of variability in survival until emergence as measured by emergent larval drift rate per adult ($r^2 = 0.307$; $P = 0.0033$; $df = 25$; Table 3.6). Over the range of discharges observed in 2004 and 2005, survival until emergence generally increased with increasing discharge during spawning, but was highly variable below 600 cfs (Figure 3.16). Both mean discharge during development (MDD) and number of days mean discharge surpassed 1000 cfs during development (DMD1000+) were not significantly related to survival (MDD, $P = 0.675$; DMD1000+, $P = 0.649$; Table 3.6). Discharge during drift samples also had no significant association with survival (Table 3.6).

Number of spawners (SS) had the second highest linear correlation with survival until emergence (Table 3.6). For periods when both larval drift rate and number of spawners were >0 , emergent larval drift rate per adult was negatively related to spawning stock, but more variable at moderately high stock sizes ($r^2 = 0.252$; $df = 25$; $P = 0.0091$; Figure 3.17).

Water temperature during spawning (MWTS) and egg incubation (MWTD and DMWT20+) did not have a significant linear relationship with survival until emergence within temperature ranges observed ($P = 0.104$, 0.7378 , and 0.544 , respectively; Table 3.6). There was, however, a weak tendency for survival to decrease with increasing temperature during spawning (Figure 3.18). Fraction of the moon illuminated during drift samples (FMI), duration of the development period (DDP), and *Year* were also not significantly related to survival until emergence (Table 3.5).

Of the variables examined, only mean discharge during spawning (MDS) and spawning stock (SS) were significantly different between cohorts with the highest 50% of survival values and those with the lowest 50% of survival values (Table 3.7). The mean value for MDS for high survival cohorts (674.24 cfs) was significantly higher than for low survival cohorts (318.55 cfs) (two-sample *t*-test: $P = 0.0342$; Table 3.7; Figure 3.19). Mean spawning stock size was significantly lower for high survival cohorts (9.43 spawners) than for low survival cohorts (25.28 spawners) (two-sample *t*-test: $P = 0.0310$ Table 3.7; Figure 3.20).

Multiple Linear Regression Models

Of the 145 regression models examined using Akaike's Information Criteria, the most parsimonious model ("top model"), explaining 43.5% of Pacific lamprey survival until emergence included the variables: spawning stock (SS) and mean discharge during the spawning period (MDS) (Table 3.8; Model 1). Two of the 144 remaining models had AICc values within 2.0 units of the top model and were considered contending models (Table 3.8). Of particular interest is Model 3, which contained an interaction term between SS and MDS (Table 3.8). Importance value rankings confirmed that variables included in the top model, MDS and SS, were comparatively most influential of those considered in the 145 candidate models (Table 3.9). The remaining independent variables had relatively less weight in explaining variation in survival until emergence (Table 3.9). Model selection using stepwise regression further attested to the relative importance of SS and MDS in explaining survival. This technique selected SS, MDS, and *Year* (AICc Model 2; Table 3.8) as predictor variables in the final model.

Egg Predation

Visual observations, together with underwater videos and photographs, clearly demonstrated speckled dace feeding in high densities (~ 100 individuals per m^3) in and around recent Pacific lamprey redds (Figures 3.21, 3.22). Lamprey eggs were positively identified in three of seven dace stomachs collected and preserved immediately during an obvious egg predation event. Other stomach contents that were not preserved immediately did not contain identifiable Pacific lamprey eggs.

During Pacific lamprey spawning periods, mean dace activity level on the focal area was significantly higher in 2004 (1.85 ± 0.18) than in 2005 (1.37 ± 0.11) (mean \pm SE; two-sample *t*-test: $P = 0.0276$). In general, feeding activity increased as spawning seasons progressed, with highest egg predation occurring after April (Figure 3.23).

Water temperature appeared to be a key factor controlling level of dace egg predation activity. No dace feeding events were observed at daily mean water temperatures under 14°C —even when both spawning lampreys and dace were present in considerable numbers. During lamprey spawning periods over both years, daily mean water temperature was significantly lower during non-feeding dace activity observations (Level 1) than during feeding observations (Levels 2 and 3) (two sample *t*-test: $P = 0.0064$). There was not a statistically significant difference in daily average water temperature between dace feeding levels 2 and 3 (two sample *t*-test: $P = 0.2692$). Although speckled dace were only observed feeding in the presence of recent spawning activity, level of dace activity did not appear to be related to abundance of Pacific lampreys in the focal area. During periods of lamprey presence there was not a

significant difference in the mean number of adult lampreys across dace activity levels (ANOVA: $F_{2,41} = 1.39$, $P = 0.2603$).

Despite observations of substantial dace predation on lamprey eggs, mean lamprey survival until emergence was not significantly different among levels of dace egg predation (ANOVA: $F_{2,14} = 0.33$, $P = 0.7248$). Likewise, dace predation level was not significantly different between high survival and low survival cohorts (Table 3.7).

DISCUSSION

SPAWNING ACTIVITY

Pacific lampreys in the South Fork Coquille River spawned between early April and early June in 2004 (59 d), and over a considerably longer period, from late April until early July in 2005 (70 d). Estimates of beginning and ending dates of spawning seasons were similar whether based on adult observations or presence and absence of emergent ammocoetes; the later always about 20–30 days after initial and final spawner detection. The April–July spawning period observed on the South Fork Coquille generally agrees with a March–July season reported in other coastal systems (Kan 1975; Beamish 1980; Richards 1980; Gunckel et al. 2006). Inland and northern Pacific lamprey populations are thought to initiate spawning later than coastal populations (Kan 1975; Beamish 1980; Richards 1980; Close et al. 2003).

In previous years, spawned out individuals have been recovered in the vicinity of the focal area as early as March 14 (L. Grandmontagne, Wild Fish for Oregon, personal communication) so it is probable that a small number of fish spawned before we observed

them. Elevated river levels prohibited adult surveys prior to early April in 2004 and late April in 2005. Furthermore, presence of 9–12 mm age-0 ammocoetes in early season drift samples in 2005 (Figure 3.8) indicate that Pacific lampreys successfully spawned upstream earlier than predicted from adult surveys. These early spawners were likely associated with low flows and unseasonably high temperatures that occurred in February and March of that year (Figure 3.2). This dry and warm late-winter weather likely resulted in water temperatures warm enough to initiate early spawning. Similarly, the cool conditions caused by recurrent high flow events, beginning in late March 2005, most likely arrested spawning activity until daily mean water temperatures warmed above 11°C in late-April. Delayed initiation of Pacific lamprey spawning was also observed in the Smith River in spring 2005 (Gunckel et al. 2006). The dependence of fish spawning time on temperature and flow regimes is well established (Pletcher 1963; Hardisty and Potter 1971b; Kempinger 1988; Reichard et al. 2002a; Dahl et al. 2004).

The finding that Pacific lamprey spawning activity peaked at daily mean water temperatures between 13°C and 16 °C is consistent with the range of spawning temperatures cited in the literature (Pletcher 1963; Kan 1975; Close et al. 2003). The strong correlations between water temperatures during spawning, water temperature during development, and discharge during development suggests that embryonic development conditions may impose strong selective pressure on Pacific lamprey temperature preference and spawning time. Disruption of these relationships through alteration of spring temperature and flow regimes could result in a mismatch between spawning time and conditions for successful embryonic development.

LARVAL PRODUCTION

Nearly three times as many emergent ammocoetes were produced in 2004 than in 2005. Although number of spawning adults appears to be a poor predictor of larval production (Figure 3.13), it is highly likely that lowered production in 2005 was at least partially due to the three-fold decline in spawners between years.

In both spawning seasons, date of initial and final larval emergence observed from drift samples largely agreed with that predicted from focal area spawning observations and degree-days required for emergence. As was expected from cooler spring water temperatures and prolonged adult spawning in 2005, duration of larval emergence was more than two weeks longer (71 d) compared to 2004 (54 d). Emergence peaked around mid-May in 2004 and mid-June in 2005. The greater part of larval production occurred when mean water temperature during development was 13–17°C and mean discharge was 150–700 cfs. The lowered larval production associated with higher water temperatures and lower discharges during development may have been partially due to decreased embryonic survival, but appeared to be primarily seasonal since these conditions occurred during the end of the spawning season when few adults spawned.

Young of the year ammocoetes drifted during darkest hours of night, peaking from 2300 until 0200 hours. Emergent ammocoetes (8–9 mm) drifted, on average, later than larger and older age-0 larvae (>9 mm), which was likely due to behavioral differences in drift initiation or spatial differences in point of entry into the drift. The majority of the 8–9 mm ammocoetes likely originated from redd gravels in the focal area, whereas older individuals presumably entered the drift from transitory daytime habitats further upstream. Results from our diel samples concur with previous research showing

that ammocoetes display a circadian pattern of drift. In the Great Lakes, drift of emergent sea lamprey was shown to occur predominately during darkest hours, declining sharply as dawn approached (Bennett and Ross 1995; Derosier 2001). Similar trends were detected in drift patterns of mixed age-0 size-classes of *Lampetra* species (most likely Pacific lampreys) in Northwest river systems (Pletcher 1963; Gadomski and Barfoot 1998; White and Harvey 2003). Drifting at night is theorized to be an adaptive response to reduce exposure to visual predators (Muth and Schmulbach 1984; Harvey 1991; Flecker 1992).

There are a number of error sources associated with our estimates of seasonal production of Pacific lamprey larval from the focal area based on drift samples. First, a portion of 8–9 mm larvae collected in biweekly nets likely originated from spawning areas upstream of the focal area. However, the impact of these individuals on our results is considered negligible because of the existence of significant depositional, rearing areas between the focal spawning area and the nearest upstream spawning area. Furthermore, adult spawning activity in the 9.2 river kilometers upstream was highly correlated with focal area spawning activity (see Chapter 2), suggesting that the relative influence of emergent ammocoetes originating upstream was likely unchanged over time. Similarly, White and Harvey (2003) found that seasonal trends in ammocoete drift rate were comparable longitudinally within two Northern California coastal basins.

Second, since spawning western brook lampreys were seen in the focal area in both years (see Chapter 2), some of their emergent larvae were most likely captured in the drift. A small pulse of 6–7.5 mm individuals observed in later samples corroborates this belief (Figure 3.8). Attempts to identify larvae using caudal pigmentation (Richards

et al. 1982) and various morphological measurements failed. It is thought, however, that species contamination error was small due to exclusion of individuals shorter than 8.0 mm from analyses. A small percentage of western brook lamprey larvae could have been larger than 8.0 mm, particularly in later season samples after earlier emerging individuals had grown. Nonetheless, the influence of these individuals on our results is believed to be inconsequential due to low numbers of spawning western brook lampreys observed in conjunction with the extremely high fecundity of Pacific lampreys (Kan 1975). A small number of ammocoetes less than 8.0 mm could have also been Pacific lampreys, but the percentage of these individuals in each sample was assumed to be constant over time, having negligible impact on temporal comparisons of larval production.

A third potential error source in comparing larval production among intra-annual cohorts is variation in diel drift timing between sample dates. In our analysis of diel drift, samples taken closest to 3 hours post-sunset (0000 hours) caught, on average, 34.4% of daily emergent ammocoete drift—but the value ranged from 13.7% to 52.5% among the six sample dates. It is possible that seasonally varying factors such as moon illumination, water clarity, or cloud cover affected diel timing. Reichard et al. (2002b) found that drift density of larval cyprinids was negatively correlated with light intensity. We assumed that variation in proportion of total daily drift caught during 3 hours post-sunset was considerably lower than variation in total drift abundance among sampling dates. Reichard (2004) found that variation in drift abundance of various cyprinids within a night was typically much less than variation among sampling dates.

Replicate drift sampling during each sample period has been recommended by various authors because it provides a more accurate approximation of daily, relative drift

abundance (Allan and Russek 1985; Franzin and Harbicht 1992). In this case, however, a particularly large drift net [70 x 150 cm opening] was used, which was equivalent to setting 7.7 typically-sized drift nets [30 x 45 cm opening] simultaneously. Others studies on drifting invertebrates and fish have shown that a single sample taken near estimated peak drift time is sufficient to predict total drift from the 24-hr period (Allan and Russek 1984; Zitek et al. 2004).

Finally, our analyses of larval production assumed that observed seasonal drift patterns corresponded to actual seasonality, not short term fluctuations in emergence timing. A test comparing drift rate variability of nets set on several consecutive nights to variability between weekly samples would help substantiate this sampling assumption. Reichard et al. (2002a) used such a strategy and found no significant differences in drift densities of several cyprinid species between five successive nights.

Nighttime drift samples have advantages and disadvantages relative to adult and redd surveys. When adult surveys are impractical due to river size, visibility, or access; drift nets used in conjunction with a temperature logger and known degree days required for emergence are an effective way to pinpoint spawning times and provide a continuous picture of upstream larval production. In rivers where abundance of spawners is low, drift nets could be used to demonstrate upstream presence when visual adult observations might not. It is best to sample rare species during parts of the life cycle when their numbers are great, individuals are vulnerable to quantitative sampling gears, and individuals can be found over large areas (McDonald 2004). Because of the high fecundity of Pacific lampreys and associated high larval drift densities, the early life stages meet these criteria better than other stages.

Data on relative larval abundance in the drift can also aid in identification of productive spawning tributaries and assignment of basinwide conservation priorities without implementation of spawning surveys. In basins where little information exists, these techniques allow for rapid collection of diverse information on multiple life stages and can be used to monitor annual and intra-annual spawning success. In addition to providing data on various size classes of target lamprey species (Appendices II and III), drift nets can be used to concurrently collect larval production data on other fish species (Johnston et al. 1995; White and Harvey 2003). We collected data on five other fish genera. Disadvantages of drift samples include nighttime work hours, laboratory time, taxonomic identification problems, difficulty quantifying catches in fluctuating discharge conditions, and lack of information gained on initial egg production (Allan and Russek 1985; Franzin and Harbicht 1992).

STOCK-RECRUITMENT AND EARLY SURVIVAL

Pacific lamprey spawning success and early mortality was highly variable over time; as has been documented in numerous other fishes (Kempinger 1988; Hjort, J. 1914; Harvey 1991; Bestgen and Williams 1994), including lampreys (Hardisty and Potter 1971a; Manion 1968; Derosier 2001; Haesker et al. 2003). On average, number of larvae produced per spawning adult was similar between years, but there were striking survival differences relative to spawning time (Tables 3.4, 3.5). Early spawning fish were generally more successful in 2004 and later spawning fish were more successful in 2005 (Figures 3.14, 3.15). The order of magnitude differences observed in survival between offspring of early and late spawners is characteristic of highly fecund fishes spawning in

unpredictable environments (Houde 1987; Kempinger 1988; Legget and DeBlois 1994; Pepin 2002). These discrepancies in early life survival were likely due, in part, to different discharge and water temperature regimes between the two years (Mion et al. 1998; Pitlo 2002; Reichard 2002a), which influenced spawning time, adult density, egg predation, and interactions among these and other ecological variables affecting egg and larval survival (Harvey 1991; Johnston et al. 1995; Houde 2002).

At the spawner densities observed in the present study, production of larvae was positively related to spawning stock on an intra-annual basis. However, spawning stock explained less than 15% of the variability in larval production, indicating that the remaining variability can be attributed to embryo mortality after egg deposition. Low and intermediate abundances of spawners sometimes produced as many or more larvae as high numbers of spawners (Figures 3.13–3.15). Because of this variability, it is unlikely that spawning stock can be used to accurately predict year class success until emergence. Similarly, it is unknown if larval production gives a reliable indication of future recruitment of out-migrating juveniles, or most importantly returning spawners. Though higher abundance of newly-hatched larval fish sometimes equate to higher abundance of older age-classes (Johnston et al. 1995); more commonly, there is little if any relationship between the two (Partridge and DeVries 1999; Pepin 2002; Pitlo 2002).

The apparent plateau in larval production at higher stock sizes indicates that habitat saturation may have limited early survival. Results from both univariate (Tables 3.6, 3.7) and AIC_c regression model selection (Tables 3.8, 3.9) showed that density of spawning adults was a significant predictor of variability in survival until emergence. Survival declined with increasing numbers of spawners (Figures 3.18, 3.19), suggesting

that density dependence may have limited survival until emergence at elevated spawner densities through superimposition, or enhanced survival at lower spawner densities via compensatory mechanisms acting within the redd (Frank and Leggett 1994; Jones et al. 2003). Other potential mechanisms explaining a decline in survival until emergence at higher spawner densities are density-dependent egg predation or disease. Density-dependent survival until emergence has not been otherwise documented for Pacific lampreys. For sea lampreys, Jones et al. (2003) found that recruitment of young-of-the-year ammocoetes was consistently diminished at large stock sizes, but was widely variable at low to intermediate stock sizes.

Lowered spawning stock sizes may also trigger compensatory mechanisms after ammocoetes emergence. Shifts in larval sex ratio towards more females (Zerrenner and Mardsen 2005), increased larval production and growth rate (Weise and Pajos 1998), and earlier age at metamorphosis (Jones et al. 2003) have all been cited as examples of post-swimup compensation in sea lamprey populations following eradication programs. Increased growth of older Pacific lamprey ammocoetes with decreasing density has also been documented (Mallat 1983),

While the effects of superimposition have not been directly documented in Pacific lampreys, they may have contributed to low survival at high spawner densities. Indication of redd superimposition by later spawning lampreys was observed in early May of 2004, when, on two occasions, over 25 spawners and remarkably high redd concentrations were seen in the 30x30 m focal area (Figure 3.4). High densities of spawners and large areas of disturbed spawning substrate (20x5 m) were also witnessed during weekly large-scale surveys in May 2004 (see Chapter 2), making individual redds

virtually impossible to distinguish. Anecdotal evidence of superimposed spawning by Pacific lampreys has been cited in previous studies (Pletcher 1963; Kan 1975; Close et al. 2003; Gunckel et al. 2006). Redd superimposition is well recognized as an influential factor in recruitment of both sea lampreys (Manion and Hanson 1980; Jones et al. 2003) and anadromous salmonids (Van den Berghe 1989; Fukushima et al. 1998), which spawn in habitats nearly identical to Pacific lampreys. The potential for inter-specific superimposition with steelhead, *Oncorhynchus mykiss*, should also be noted because of overlap in the species' spawning seasons. In April and May, we observed steelhead spawners and redds in the focal area and other lamprey spawning sites.

Discharge during spawning (MDS), or some correlated variable, also played an important role in Pacific lamprey early life survival in 2004 and 2005: MDS had the highest relative importance of the predictor variables considered (Table 3.9). Contrary to the hypothesis that high discharge during spawning would reduce relative survival via scour or decreased egg deposition, embryo survival generally increased at higher discharges—even for individuals spawning during spring freshets. For example, larval production resulting from relatively few fish spawning on the front end of a mid-April 2004 high-water event was among the highest recorded during the period of study (Figures 3.2, 3.14). Notably, though cohort survival was generally higher at higher discharges during spawning, it was highly variable below 600 cfs, which suggests that the relationship was not adequately modeled with linear regression at lower discharges.

Increased survival at high discharges during spawning also questions the population-level consequences of redd desiccation following high discharge events. In both years, a number of dried-out Pacific lamprey redds were observed in spawning

gravels exposed to the air during rapidly declining river levels following spring freshets. While these events unquestionably caused extreme mortality for individual redds, their impact on overall larval cohort survival was not detected and may have been offset by beneficial factors coupled with high discharge during spawning.

The mechanisms by which discharge during spawning influences Pacific lamprey spawning success are unclear. Higher flows could elevate survival indirectly due to lowered water temperature, better interstitial water quality, decreased egg predation, or reduced redd superimposition resulting from increased size of spawning areas (Johnston et al. 1995). The latter theory was supported by the significance of the SS*MDS interaction term in the second ranking regression model (Table 3.8). Survival decline at the upper range of observed spawner densities suggests that Pacific lampreys in the South Fork Coquille River may, at times, approach the carrying capacity of available spawning habitat. If this is the case, increasing available spawning substrate could significantly bolster larval recruitment. Likewise, if density-dependent recruitment is a generalizable phenomenon, increased inundation of spawning gravels in the spring may be a viable management option in regulated rivers.

The apparent unimportance of discharge during development in larval survival (MDD; Tables 3.7, 3.9) implies that once eggs were safely deposited in redd gravels, they were relatively unaffected by discharges experienced during this study. Fukushima et al. (1998) showed negligible loss of eggs from pink salmon redds exposed to freshets after spawning ceased. Others, however, have documented increased early-life mortality with increasing discharge (Scrivener et al. 1989; Mion 1998). Since egg size, adhesiveness,

and substrate size all interact with flow conditions, the post-spawning relationship between flow and survival is likely complex and variable over time and between species.

In both years, water temperature tended to increase and discharge declined over spawning and development periods (Figure 3.10). In spite of the fact that water temperatures during spawning and development were not significantly correlated with larval survival at the temperatures ranges observed in this study, the impacts of temperature on Pacific lamprey early life survival in the wild merit further study. First, relationships between survival until emergence and water temperature during spawning and development were not easily modeled using linear regression. Second, even though survival was highly variable with spawning temperature, only low survival values were observed at high spawning temperatures (Figure 3.18). There is also evidence that eggs and larvae of later spawners were exposed to adverse temperature conditions—particularly in 2004 when daily mean water temperatures commonly surpassed 18°C and daily maximums exceeded 25°C (Figures 3.3, 3.14). These temperatures are considerably higher than those shown to be detrimental to lamprey embryos in the lab (Meeuwig et al. 2005). Even so, if other factors such as spawner density, discharge, egg predation, or interactions between these variables reduced survival to a greater magnitude than temperature, the temperature-related decline in embryo survival observed in a controlled laboratory setting might not be detected in the wild (Hamor and Garside 1976; Harvey 1991; Pepin 2002).

Although, linear population effects of water temperature were not found, developing Pacific lamprey embryos in southern parts of their range, as well as in arid, inland river systems, can be exposed to water temperatures much higher than those

observed on the South Fork Coquille (Ruiz-Campos and Gonzalez-Guzman 1996; Close et al. 2003). Adverse water temperatures may play a more crucial role in early life survival in these systems.

Water temperatures during spawning and incubation may also have delayed consequences that diminish performance and survival of ammocoetes after emergence, when they become established in depositional habitats. Rodriguez-Munoz et al. (2001) demonstrated survival rates of sea lamprey embryos reared until the burrowing stage were similar at 15°C, 19°C and 23°C; but after 3 months of exogenous feeding in a common thermal environment survival was best at 15°C, significantly lowered at 19°C, and close to zero at 23°C. Meeuwig et al. (2005) also showed higher rates of developmental abnormalities for Pacific and western brook lamprey embryos reared at 22°C than those reared at 18°C, 14°C, and 10°C. These abnormalities would presumably result in delayed mortality in the wild. Such post swim-up mortality due to delayed temperature effects is missed when sampling emergent larvae in the drift. Monitoring age-0 ammocoetes in depositional habitats in the fall, after these delayed effects have occurred, is an alternative approach. However, because of variability in larval growth rates and lack of daily growth rings in lamprey aging structures (Beamish and Medland 1988), it would be nearly impossible to distinguish age-0 intra-annual cohorts after settlement.

Low water temperatures have also been shown to decrease survival in developing lampreys. Rodriguez-Munoz et al. (2001) found that sea lamprey embryos incubated at 7°C died early in development, and those reared at 11°C did not reach the burrowing stage. We found no evidence that Pacific lamprey were exposed to adversely low water

temperatures. Because Pacific lamprey spawning is not initiated until water temperatures reach 11–12°C and occurs in the spring under a progressively warming temperature regime, cold water temperatures are unlikely to limit survival in coastal Oregon streams. Moreover, Pacific lampreys tolerate much lower temperatures regime for spawning and development than do sea lampreys (Rodriguez-Munoz et al. 2001; Meeuwig et al. 2005).

Developing embryos in this study experienced incubation durations ranging from 18–49 days. Following the logic of the stage duration hypothesis (Leggett and DeBlois 1994), we predicted that longer incubation time would decrease survival by amplifying the probability of mortality from egg predation, dislodging flows, superimposition, siltation, or other factors acting on developing embryos. However, our results did not support this hypothesis: duration of development period (DDP) had no demonstrable effect on survival until the larval stage over the range of development durations observed (Table 3.6). On an annual basis Johnston et. al (1995) found no significant effect of incubation period on year class strength of various freshwater fishes. In contrast, other studies have cited longer incubation as a root cause of variability in embryo survival (Rice et al. 1987; Kempinger 1988).

Predation on eggs and larvae is also recognized as a major source of early life mortality, but its impact is difficult to detect and quantify in the field (Kempinger 1988; Houde 2002). Though speckled dace were observed feeding in high densities on Pacific lamprey eggs—particularly later in the 2004 spawning period—we did not detect a significant influence of predation on relative survival of larval cohorts (Table 3.7). Other factors acting on survival within the redd may have rendered population-level effects of dace predation undetectable. Even in the absence of predation, many eggs never reach

redd gravels (Manion and Hanson 1980), and dace may have been primarily focused on these eggs. Still, our visual observations of dace feeding suggest they actively burrowed into redd gravels in search of eggs, even 3–6 hours after spawning ceased.

Notably, dace predation on Pacific lamprey eggs was observed only above 14°C and appeared to increase in intensity with increasing water temperature. Speckled dace have also been shown to initiate spawning activity after temperatures were increased from 15°C to 18°C (Kaya 1991). Through its alteration of dace metabolic activity, temperature is likely a key variable mediating ecological interactions between the two species. This conclusion is in tune with research demonstrating that interspecific interactions between fishes can be governed by water temperature (Baltz et al. 1982; Reeves et al. 1987). Despite the apparent insignificance of dace egg predation on larval cohort survival, it may be influential under certain conditions and further inquiry into this subject would be valuable. More frequent and quantitative dace feeding observations across a range of environmental conditions, as well as quantification of egg consumption are recommended.

Pacific lamprey eggs and carcasses have an exceptionally high caloric content (Whyte et al. 1993) and may be crucial for productivity of oligotrophic coastal river systems during the spring and summer growth periods (Wipfli et al. 1998; Chaloner et al. 2002). Our observations indicate that lamprey eggs might be an important source of nourishment for gamete development and post-spawning recovery of speckled dace, which spawn in spring to early summer (Kaya 1991). Young of the year salmonids and aquatic invertebrates were also observed feeding on lamprey eggs and carcasses, respectively. Investigation into the role of marine derived nutrients supplied by

anadromous lampreys is lacking, but vital for understanding the ecological consequences of their population decline.

In addition to the explanatory variables considered here, unmeasured factors such as oxygen concentration, water chemistry (Myllnen et al. 1997), siltation (Kempinger 1988; Meyer 2003), fungal infection (Kempinger 1988; Close 2002), and predation within the redd (Meyer 2003) may also influence survival until the larval stage. For example, in coho salmon spawning in similar habitat, Meyer (2003) found that the amount of fine sediment in the lower half of the egg pocket, which may be related to presence of a fish egg-eating oligochaete, was a strong predictor of egg survival until hatching. Research on the European river lamprey, *L. fluviatilis*, in Finland showed that hatching success declined markedly with increasing concentrations of iron and aluminum (Myllinen et al. 1997). The same study showed significant declines in hatching success and survival of newly hatched ammocoetes at pH levels below 5.5 and 5.0, respectively. Though adverse water quality has the potential to critically limit Pacific lamprey reproductive success in systems altered by human activities, its effects on developing eggs and larvae are unknown.

CONCLUSIONS

Results of regression models employed in this study should be viewed with caution when drawing inferences about variability in Pacific lamprey early life survival and recruitment. The explanatory variables shown to be significant are not necessarily causally related to survival until emergence, but may be correlated to other unknown factors that are. Likewise, care should be taken when applying conclusions from this

study to management of lamprey populations. It is expected that factors important in determining larval recruitment vary geographically, among habitats, and between years with dissimilar ecological conditions. Nonetheless, this study offers an important first step in generating hypotheses about Pacific lamprey stock-recruitment and factors bearing on early life survival.

Although larval production, stock-recruitment, and early life survival are typically evaluated on an annual basis (Magnuson 1991; Johnston et al. 1995; Bjorkstedt 2000; Haeseker 2003), the greater number of data points obtained here by using biweekly cohorts was advantageous because long term annual data were not available. Using intra-annual cohorts also allowed us to gain insight on reproductive ecology and factors related to survival that would not be possible with interannual studies. First, we demonstrated that timing and magnitude of both, Pacific lamprey spawning and ammocoete production varied considerably between and within years, and were likely reliant on discharge and temperature conditions. Second, level of larval production was only marginally explained by the number of spawning adults, highly variable over the range of stock sizes observed, and generally diminished at the highest stock sizes. Third, relative survival until emergence varied greatly between cohorts and was most associated with discharge conditions during spawning, spawning stock, and an interaction between the two variables.

These results, along with signs of redd superimposition, suggest that, at higher stock sizes, larval survival and production may be limited, in part by the amount of available spawning habitat or other factors related to density-dependence. Because of the high fecundity of Pacific lampreys and potential for density-dependent compensation

(Jones et al. 2003), increases in larval populations may be achieved relatively quickly by modest gains in spawning and rearing habitats. Conversely, destruction of spawning habitats is expected to have especially severe consequences by increasing chances of superimposed spawning. Due to the apparent lack of homing and population subdivision in Pacific lampreys (Goodman et al. 2006), larval production from a particular river system is not anticipated to set the baseline for future adult returns of that cohort. However, through its amplification of the concentration of pheromone-like migratory attractor substances secreted by ammocoetes (Bjerselius et al. 2000; Vrieze and Sorensen 2001), increased larval production could give rise to improved adult returns on a shorter time-scale.

Our findings advise against using adult or redd counts as a singular measure of reproductive success because of the weakness in correlation between spawning stock and larval recruitment. Spawning surveys are informative with respect to timing and distribution of reproduction, but they can be misleading because larval production resulting from a few spawners is sometimes substantially higher than that resulting from a large number of spawners. Though there are considerable errors associated with sampling emergent larvae, the technique provides valuable information on intra-annual and annual larval recruitment than cannot be obtained from spawning surveys. Because they can be taken in situations when adult counts are not possible, drift samples may paint a more complete picture of temporal patterns in spawning activity. When feasible, the multi-life stage approach implemented in this study is recommended because it provides insight into population-level processes and factors limiting early life survival that would not be possible when considering adult or larval data independently.

TABLES

Table 3.1. Calculation of mean effective degree days (EDD) until the larval stage (stage 18, see Piavis 1961) from laboratory data on Pacific lamprey eggs reared at four constant temperatures. Effective temperature was calculated by subtracting the theoretical temperature for zero development (4.85°C) from rearing temperature.

Rearing Temperature (°C)	Effective Temperature (°C)	Days Until Larval Stage	EDD
10	5.15	56	288.4
14	9.15	35	320.3
18	13.15	23	302.5
22	17.15	17	291.6
mean			300.7

Note: days until the larval stage and the theoretical temperature for zero development were obtained from Meeuwig et al. (2005).

Table 3.2. Variables employed in simple and multiple linear regression models explaining \log_e larval drift rate per adult (survival until emergence) for intra-annual cohorts and associated symbols.

Explanatory Variable	Symbol
Number of adult Pacific lamprey present in spawning period ^{1,2}	SS
Mean water temperature during development period ^{1,2}	MWTD
Number of days daily mean water temperature exceeds 20°C ¹	DMWT20+
Mean water temp during spawning period ^{1,2}	MWTS
Discharge during drift sample ¹	Discharge
Mean discharge during development period ^{1,2}	MDD
Number of days daily mean discharge exceeded 1000 cfs ¹	DMD1000+
Mean discharge during spawning period ^{1,2}	MDS
Fraction of moon illuminated during drift sample ^{1,2}	FMI
Duration of development period ^{1,2}	DDP
Year (indicator variable) ^{1,2}	Year
SS*MDS Interaction Term ²	SS*MDS

¹Denotes variable used in simple linear regression.

²Denotes variable used in multiple linear regression model selection.

Table 3.3. Total number of age-0 ammocoetes caught at focal area in biweekly and diel samples by size-class in 2004 and 2005; N = number of net samples. Net samples from small nets consisted of two small nets stacked to cover the water column.

Sample Type	Gear	N	2004			2005			
			<8 mm	8–9 mm	>9 mm	N	<8 mm	8–9 mm	>9 mm
Biweekly	Large Net	26	110	3791	3000	27	67	1355	1432
Diel	Small Nets	48	213	837	192	16	64	583	380
	Total	74	323	4628	3192	43	131	1938	1812

Table 3.4. Relative annual survival until the larval phase for Pacific lampreys in 2004 and 2005. *Total Annual Larval Production* equals the annual sum of emergent ammocoete drift rates from all biweekly nets. *Number of Spawners* is the estimated number of mature adults present in the focal area during spawning periods corresponding to biweekly larval cohorts. *Relative Survival Index* equals *Total Annual Larval Production* divided by *Number of Spawners*.

Measure	2004	2005
Total Annual Larval Production	5652.5	2017.8
Number of Spawners	369.8	177.7
Relative Survival Index	15.3	11.4

Table 3.5. Percent of Pacific lampreys spawning in each month, percent of larval production resulting from each month's spawners, and monthly Index of Survival (calculated by dividing percent of larvae by percent of spawners) for 2004 and 2005. Within each year, Index of Survival values greater than 1.0 are considered above average and lower than 1.0 below average.

Spawning Month	2004			2005		
	Percent of Spawners	Percent of Resultant Larvae	Index of Survival	Percent of Spawners	Percent of Resultant Larvae	Index of Survival
March	0.0	0.0	na	0.0	0.1	na
April	27.9	64.6	2.3	25.9	7.3	0.3
May	70.8	35.0	0.5	46.6	65.6	1.4
June	1.3	0.3	0.3	26.7	26.9	1.0
July	0.0	0.0	na	0.7	0.0	0.0

Table 3.6. Results of simple linear regression models explaining survival until emergence (\log_e larval drift rate per adult; $df = 25$). Note: r^2 values and coefficient values are only listed for models with $P < 0.15$. See Table 3.1 for description of variable symbols.

Variable	P	r^2	Coefficient Value
SS ^{ln}	0.0091	0.251	-0.583
MWTD	0.7378		
DMWT20+	0.5435		
MWTS	0.1041	0.106	-0.246
Discharge ^{ln}	0.7259		
MDD ^{ln}	0.6752		
DMD1000+	0.6492		
MDS	0.0033	0.307	0.002
FMI	0.3986		
DDP	0.9576		
Year	0.7238		

^{ln} Denotes variable \log_e transformed before regression.

Table 3.7. Comparison of mean values of explanatory variables between the highest 50% (N=13) and lowest 50% (N=13) of intra-annual-cohort survival values from 2004 and 2005 combined data. P -values were derived from two sample t -tests. See Table 3.1 for description of variable symbols.

Variable	Low Survival		High Survival		P -Value
	Mean value	SE	Mean Value	SE	
*SS	25.28	6.407	9.43	2.599	0.0310
MWTD	15.38	0.553	14.97	0.508	0.5874
DMWT20+	1.38	0.781	1.23	0.579	0.8756
MWTS	14.60	0.529	13.41	0.538	0.1285
Discharge	194.31	29.091	290.15	66.416	0.1987
MDD	364.54	64.036	448.15	59.416	0.3480
DMD1000+	2.15	0.933	2.92	0.880	0.5543
*MDS	318.55	32.744	674.24	154.943	0.0342
FMI	0.47	0.084	0.30	0.093	0.2053
DDP	28.54	1.509	29.54	1.444	0.6364
Dace Activity Level	1.69	0.249	1.56	0.258	0.7323

*Significantly different between low and high survival levels

Table 3.8. Top ten linear regression models describing relative Pacific lamprey survival until emergence; selected from AIC_c analysis. Akaike weight was calculated from all 145 candidate models (N = 26 for all models).

Model: Survival ^{ln} = function of:	$\mathcal{L}(\theta)$	K	AIC _c	ΔAIC_c	e^{\wedge} ($-\frac{1}{2}\Delta\text{AIC}_c$)	Akaike weight (w)	R^2
1) SS ^{ln} , MDS	-2.496	4	14.897	0.000	1.000	0.102	0.435
†2) SS ^{ln} , MDS, Year	-1.180	5	15.359	0.462	0.794	0.081	0.489
†3) SS ^{ln} , MDS, SS*MDS	-1.561	5	16.122	1.225	0.542	0.055	0.474
4) SS ^{ln} , MDS, FMI	-2.169	5	17.339	2.441	0.295	0.030	0.449
5) MDS	-5.134	3	17.358	2.461	0.292	0.030	0.307
6) SS ^{ln} , MDD ^{ln} , MDS	-2.304	5	17.607	2.710	0.258	0.026	0.443
7) SS ^{ln} , MDS, DDP	-2.365	5	17.729	2.832	0.243	0.025	0.440
8) MDS, FMI	-4.008	4	17.920	3.022	0.221	0.023	0.365
9) SS ^{ln} , MWTS, MDS	-2.468	5	17.937	3.039	0.219	0.022	0.436
10) SS ^{ln} , MWTD, MDS	-2.496	5	17.992	3.095	0.213	0.022	0.435

^{ln} Denotes variable log_e transformed before regression.

† considered competing with top model.

Table 3.9. Relative importance values of variables used to predict survival until emergence. Calculated from Akaike weights of the 145 candidate models. See Table 3.1 for description of variable symbols.

Model Parameter	Relative Importance Value
MDS	0.850
SS	0.765
Year	0.327
FMI	0.256
MWTS	0.239
DDP	0.174
SS*MDS	0.169
MDD	0.152
MWTD	0.127

FIGURES

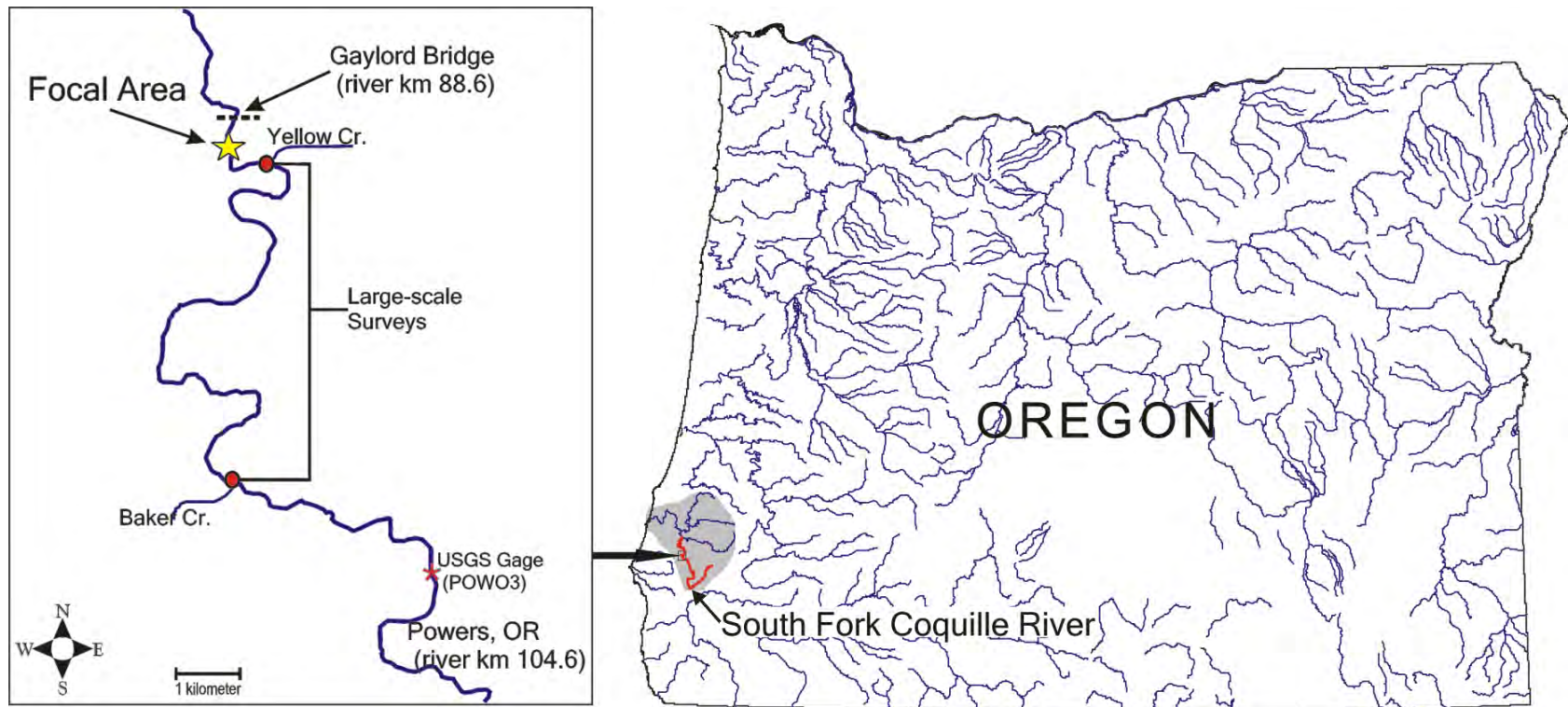


Figure 3.1. Location of focal spawning area in relation to the large-scale survey section (see Chapter 2) and the Coquille River Basin, Oregon.

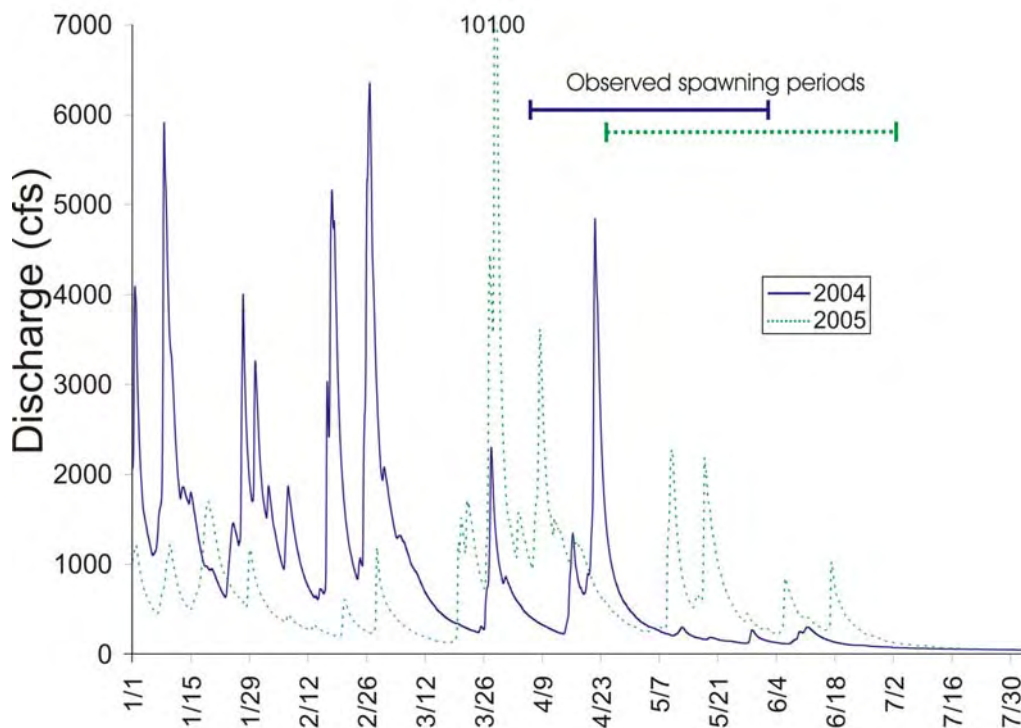


Figure 3.2. 2004 and 2005 discharge (cubic feet per second) on South Fork Coquille River from January 1 to July 30.

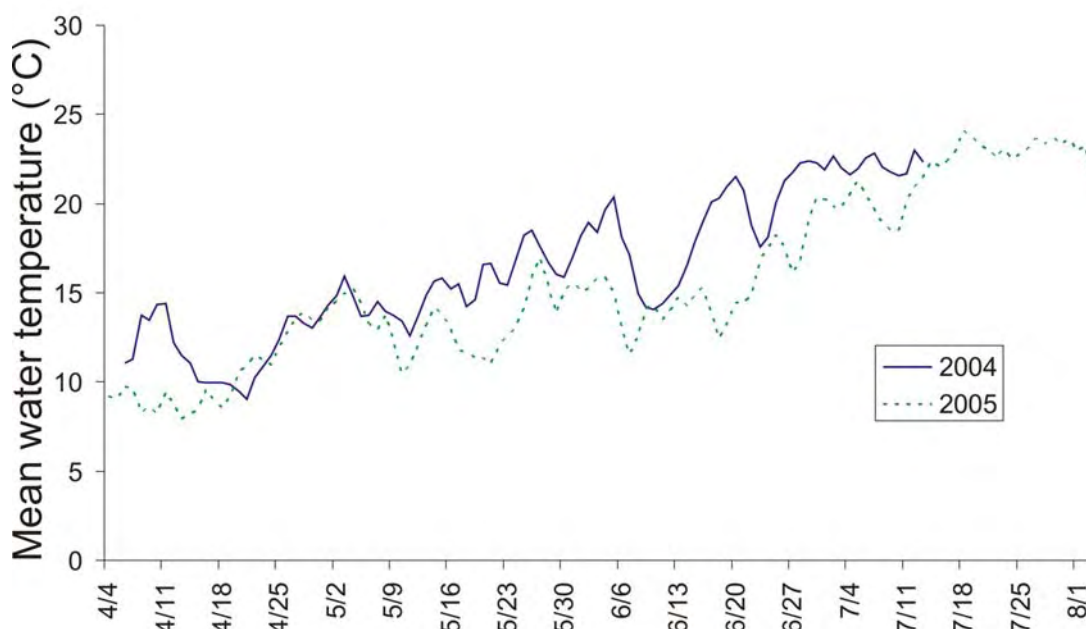


Figure 3.3. Daily mean water temperature at the focal area from April 4 until August 3, 2004 and 2005.

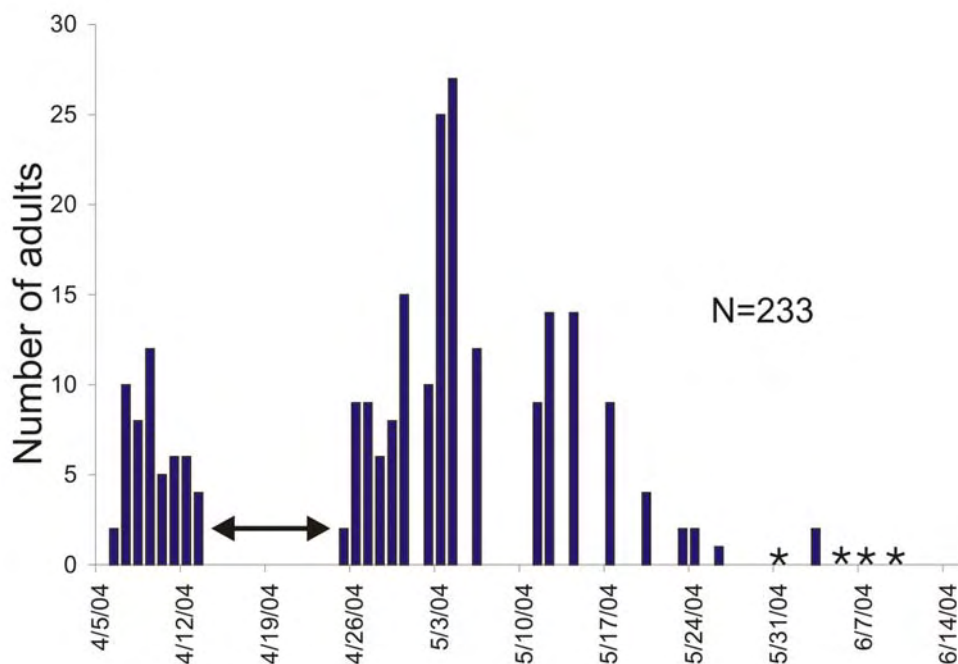


Figure 3.4. Seasonal distribution of adult Pacific lampreys in the focal spawning area in 2004. The arrow indicates a period of high discharge when sampling was not possible. Stars represent observations when zero fish were seen.

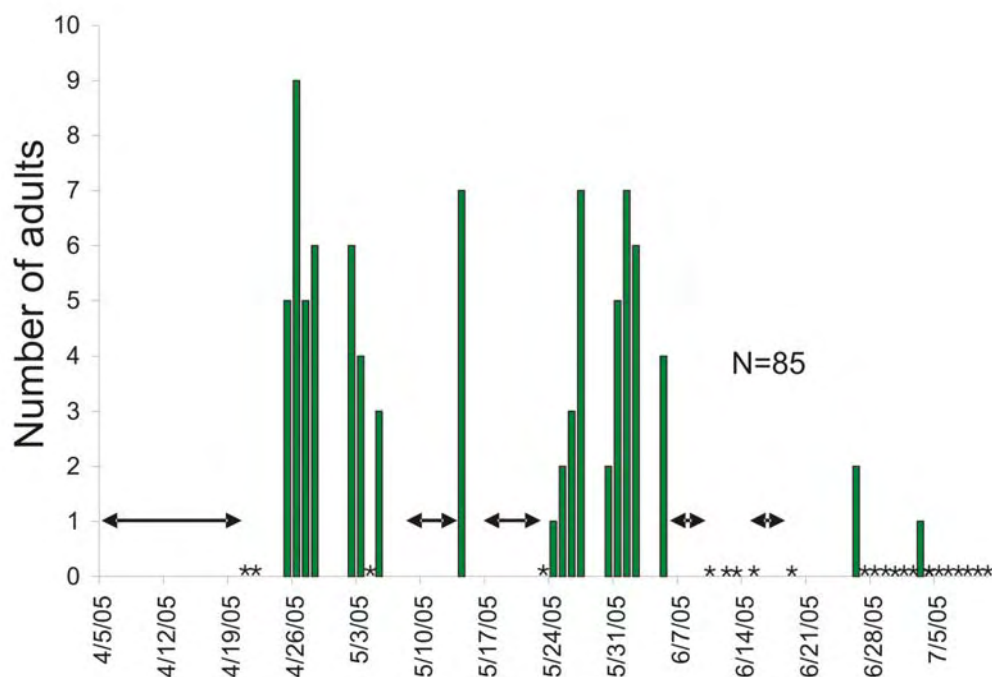


Figure 3.5. Seasonal distribution of adult Pacific lampreys in the focal spawning area in 2005. Arrows indicate periods of high discharge when sampling was not possible. Stars represent observations when zero fish were seen. Note the difference in y-axis scale between Figures 3.4 and 3.5.

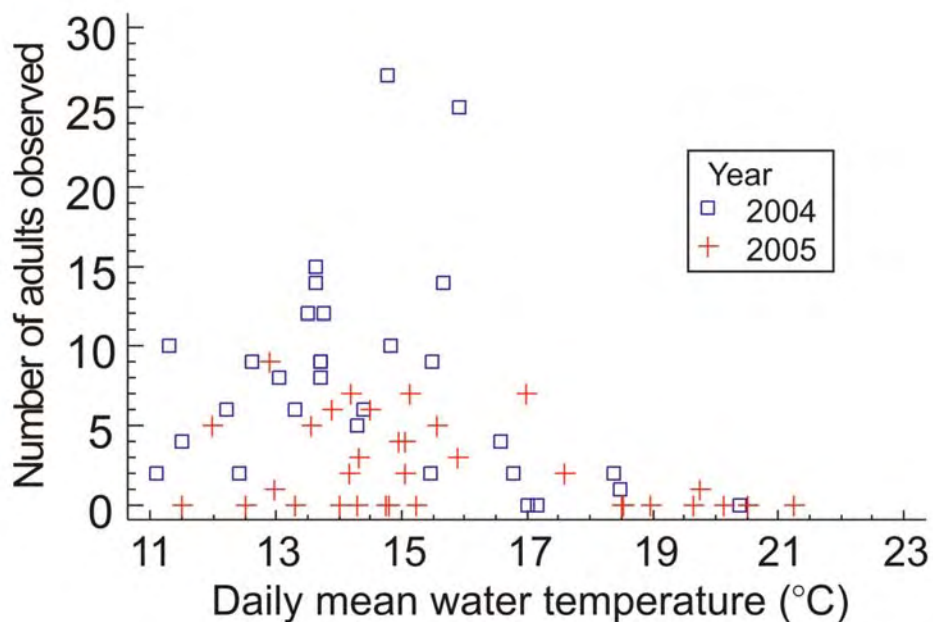


Figure 3.6. Number of mature adult Pacific lampreys on the focal area versus daily mean water temperature in 2004 and 2005.

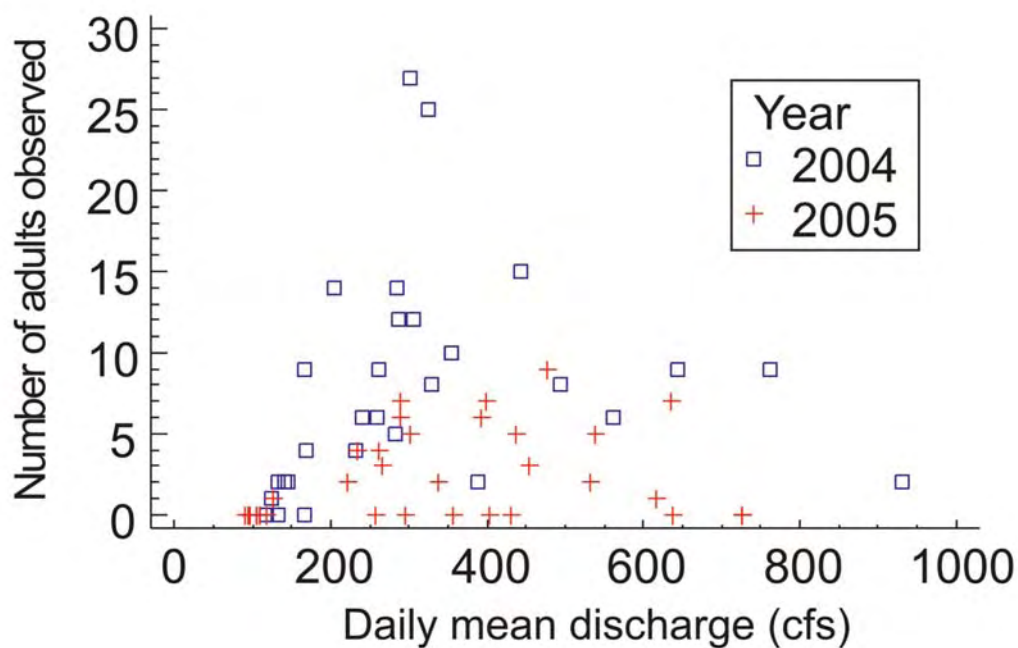


Figure 3.7. Number of mature adult Pacific lampreys on the focal area versus daily mean discharge during observations in 2004 and 2005.

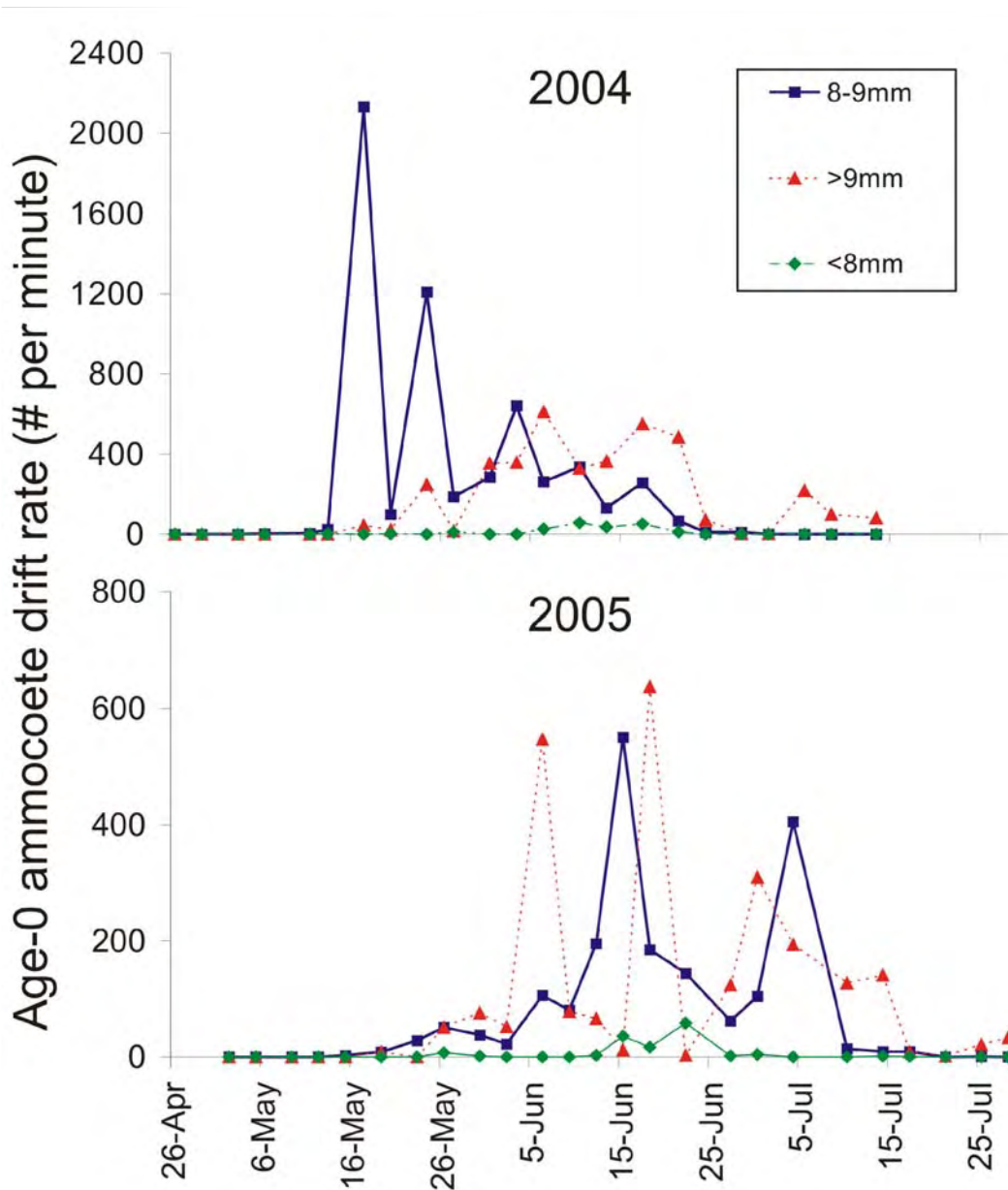


Figure 3.8. Age-0 lamprey drift rates in 2004 and 2005 for emergent ammocoetes (8–9 mm), ammocoetes greater than 9 mm, and those less than 8 mm. Note the difference in the y-axis scale between years.

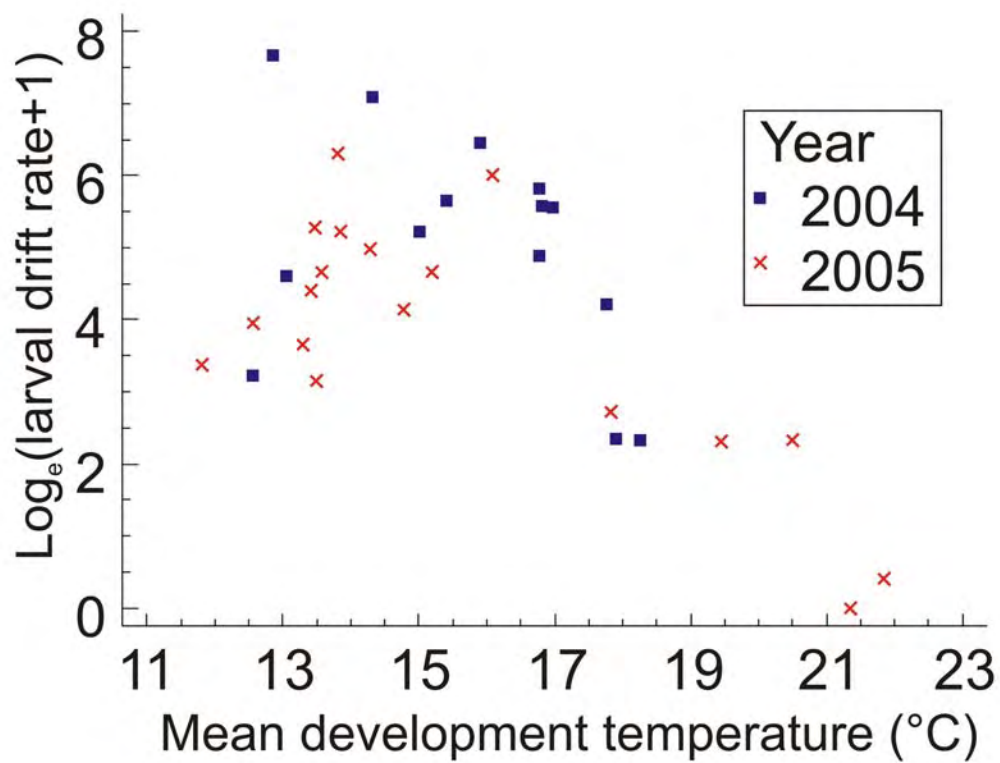


Figure 3.9. Log_e 8–9 mm larval drift rate (number per minute) versus mean water temperature during development.

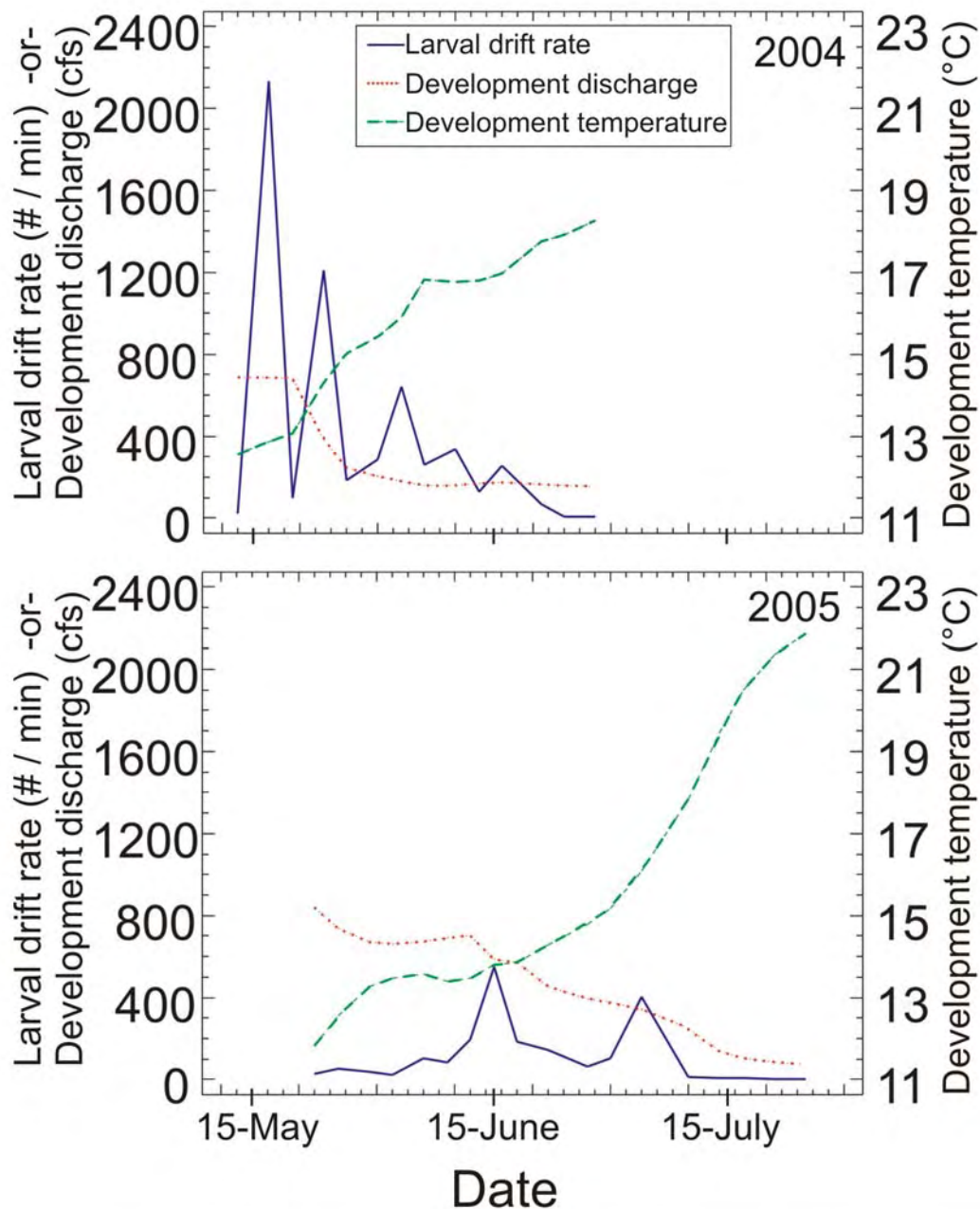


Figure 3.10. Seasonal production of emergent larvae (number per minute) and mean water temperature and discharge during corresponding developmental periods in 2004 and 2005.

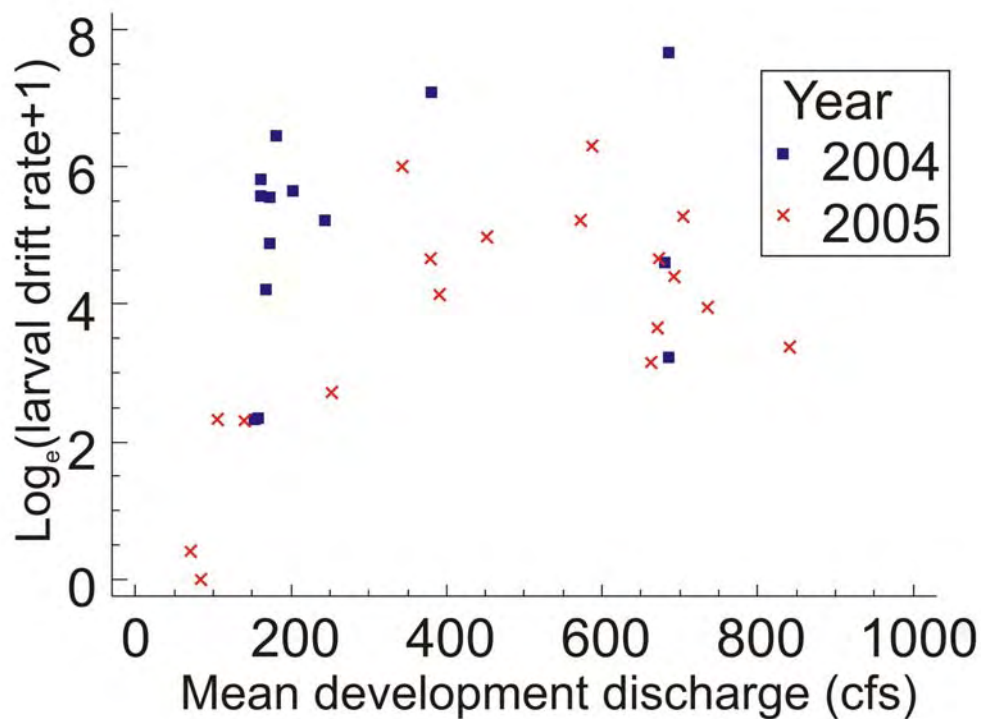


Figure 3.11. Log_e 8–9 mm larval drift rate (number per minute) versus mean discharge during development.

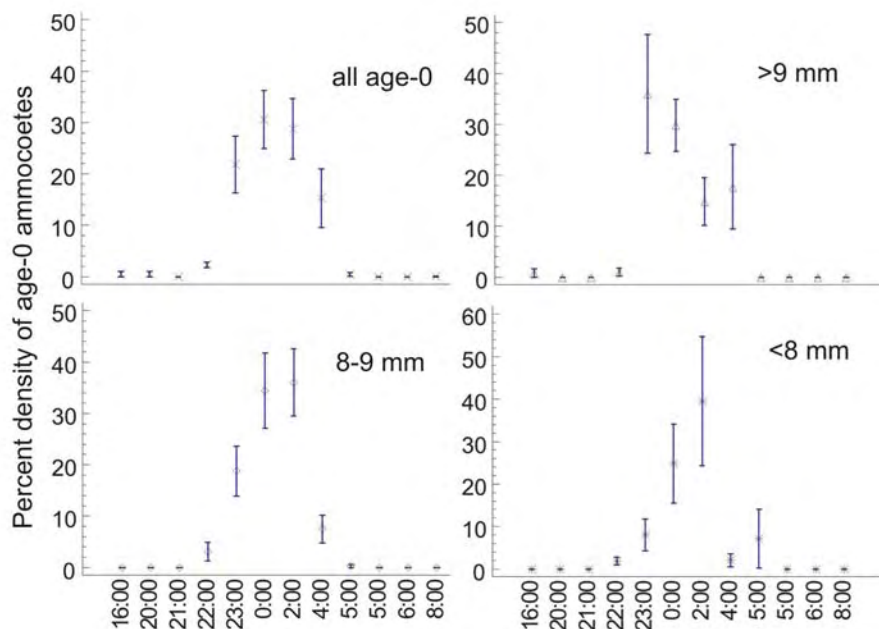


Figure 3.12. Percent drift density at each net-time for age-0 ammocoetes captured during diel samples. Averaged over 6 sampling cycles; 2004 and 2005 samples combined. Bars represent standard errors.

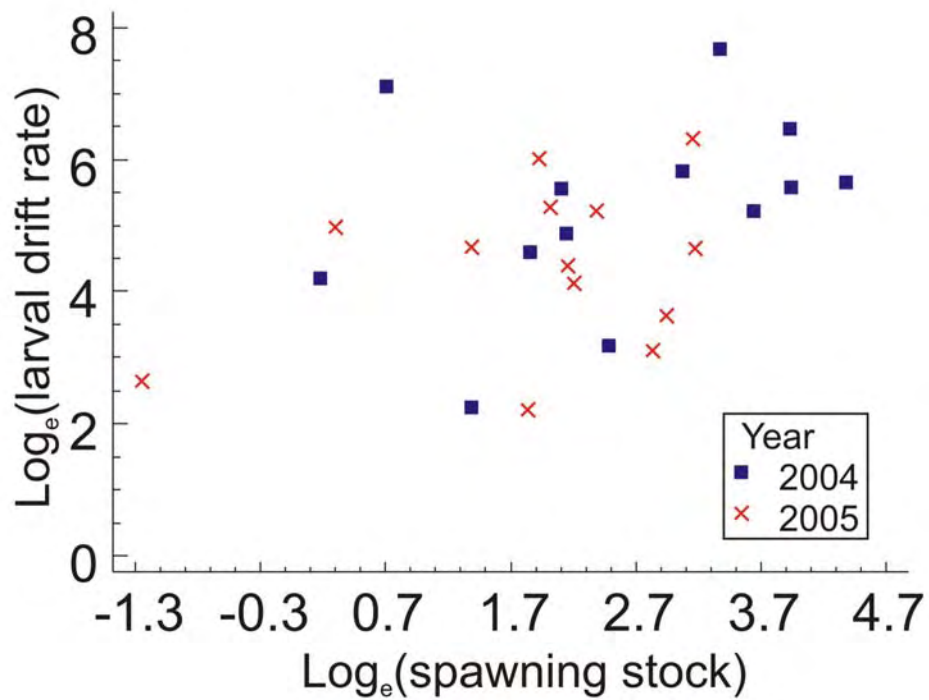


Figure 3.13. Relationship between larval production (8–9 mm ammocoete drift rate) and spawning stock (adult count estimates from corresponding spawning period).

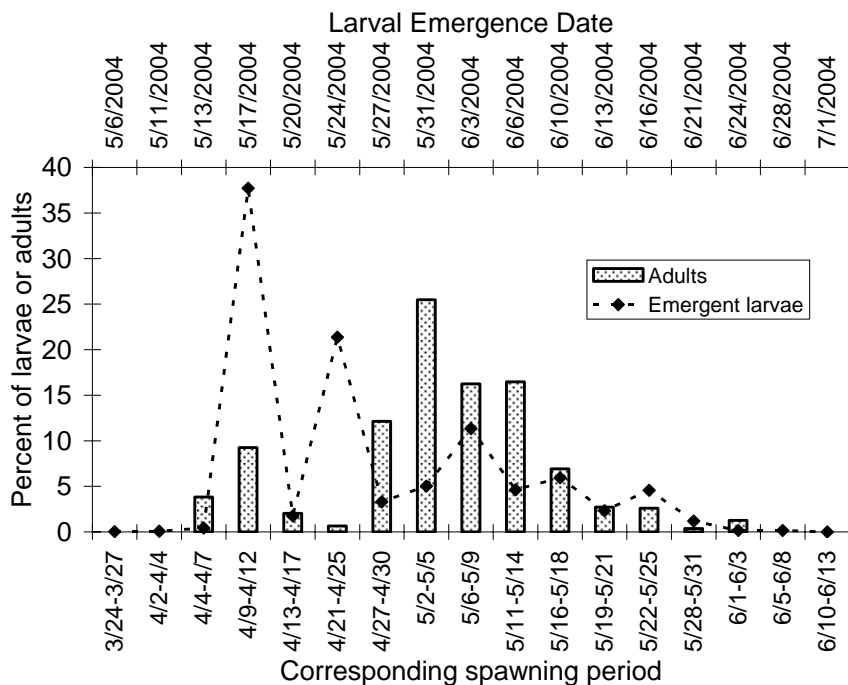


Figure 3.14. Percent of 2004 emergent larval production collected during drift samples overlaid on percent of annual adult observations from corresponding spawning periods. Differences between magnitude of percent adults and percent emergent larvae represent relative survival until emergence.

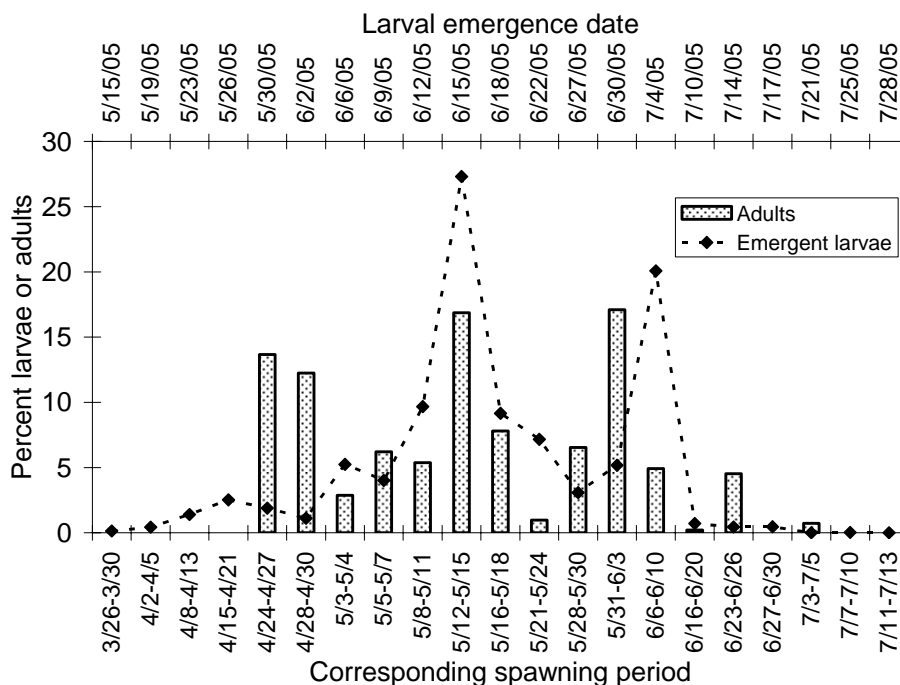


Figure 3.15. Percent of 2005 emergent larval production collected during drift samples overlaid on percent of annual adult observations from corresponding spawning periods. Differences between magnitude of percent adults and percent emergent larvae represent relative survival until emergence.

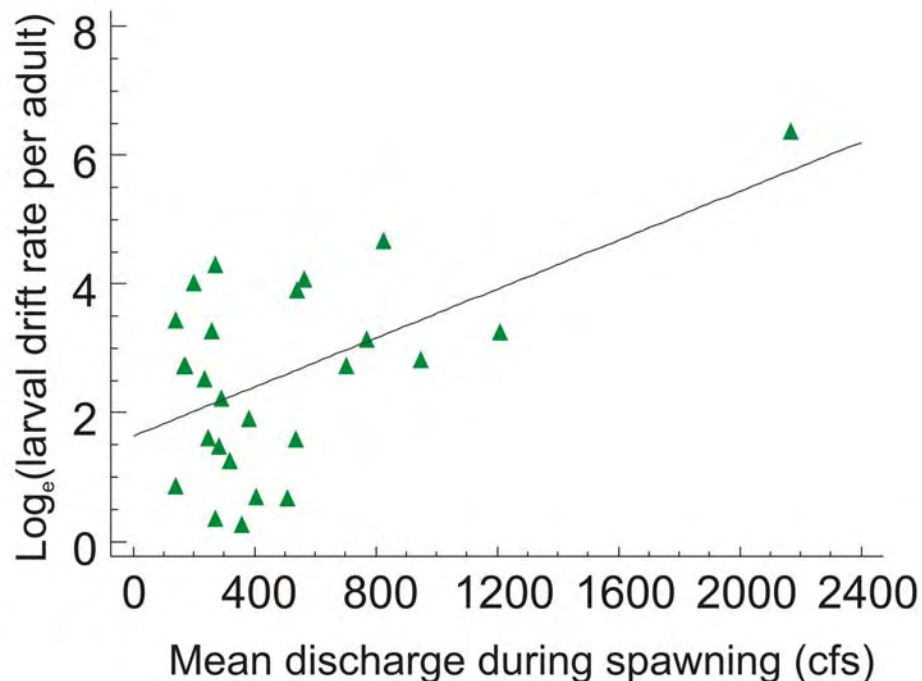


Figure 3.16. Relationship between relative survival until emergence (emergent larval drift rate per corresponding adult) and mean discharge during the spawning period ($r^2 = 0.307$; $P = 0.0033$; $N = 26$).

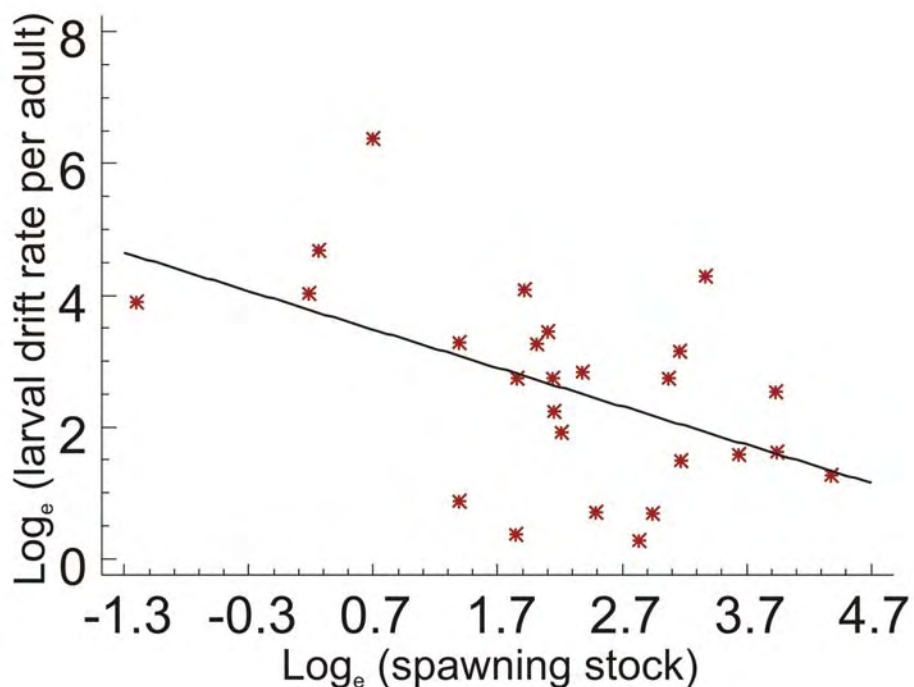


Figure 3.17. Relationship between relative survival until emergence (emergent larval drift rate per corresponding adult) and number of adults present in the corresponding spawning period ($r^2 = 0.252$; $P = 0.0091$; $N = 26$).

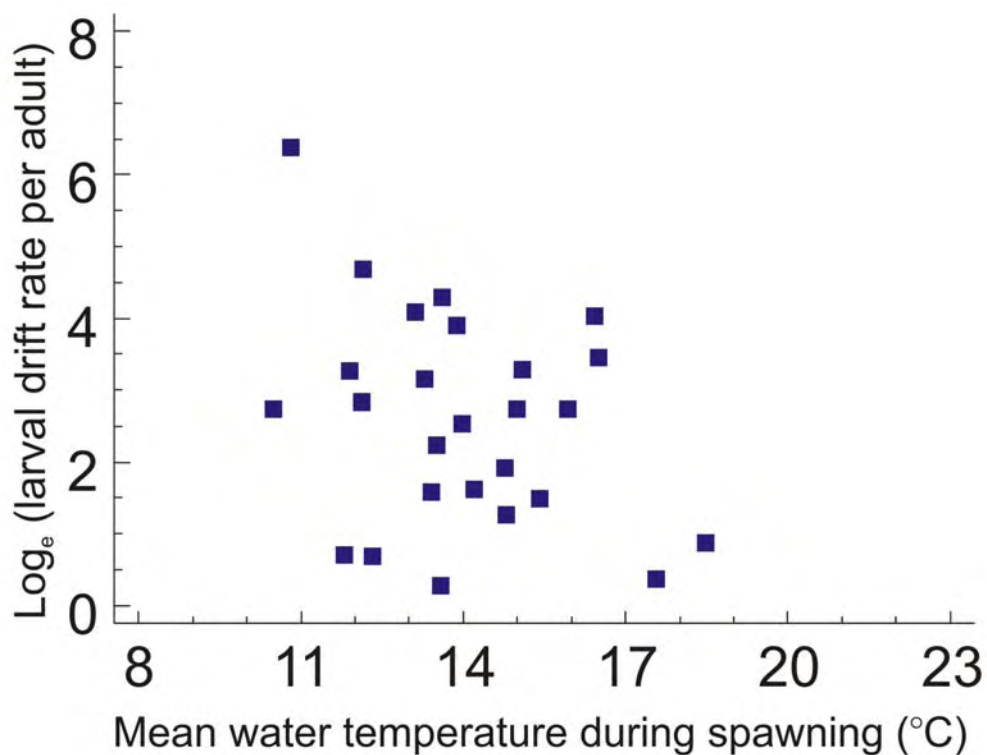


Figure 3.18. Relationship between relative survival until emergence (emergent larval drift rate per corresponding adult) and mean water temperature during the spawning period.

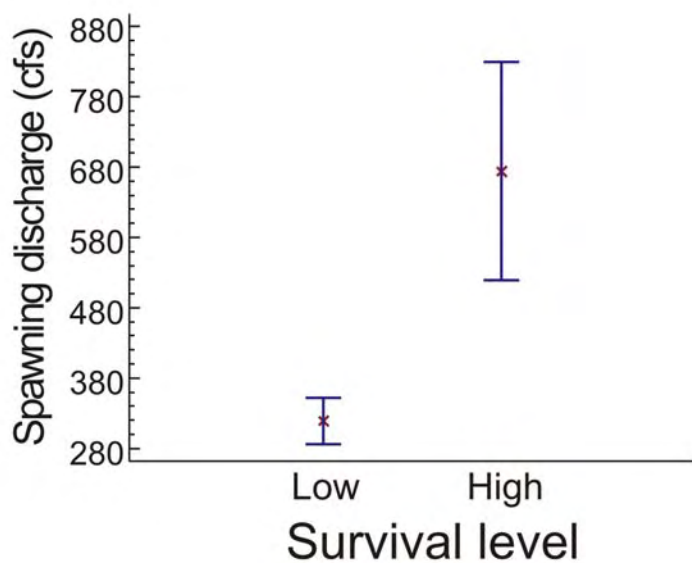


Figure 3.19. Comparison of mean discharge during spawning between the highest 50% (N=13) and lowest 50% (N=13) of intra-annual larval cohort survival values.

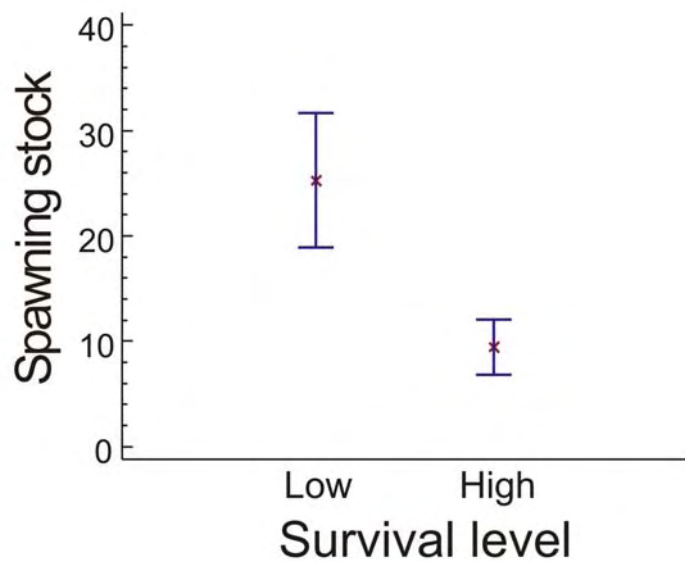


Figure 3.20. Comparison of spawning stock between the highest 50% (N=13) and lowest 50% (N=13) of intra-annual larval cohort survival values.



Figure 3.21. Examples of speckled dace feeding behavior. The photograph on the left illustrates an individual dace burrowing into redd gravels in search of lamprey eggs. The photo on the right was taken immediately downstream of a recently spawned-in Pacific lamprey redd.

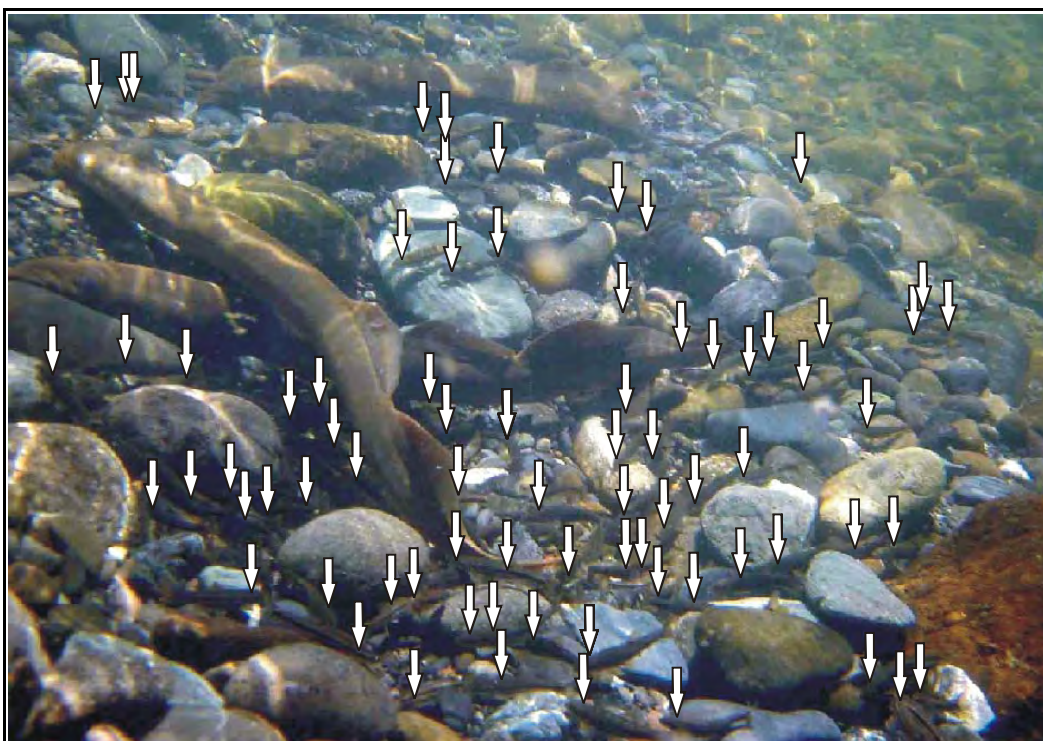


Figure 3.22. Photographic documentation of high densities of speckled dace preying on eggs during Pacific lamprey spawning. Each white arrow represents a visible, individual dace ($N = 76$). The area in the photograph is approximately 1 m^2 .

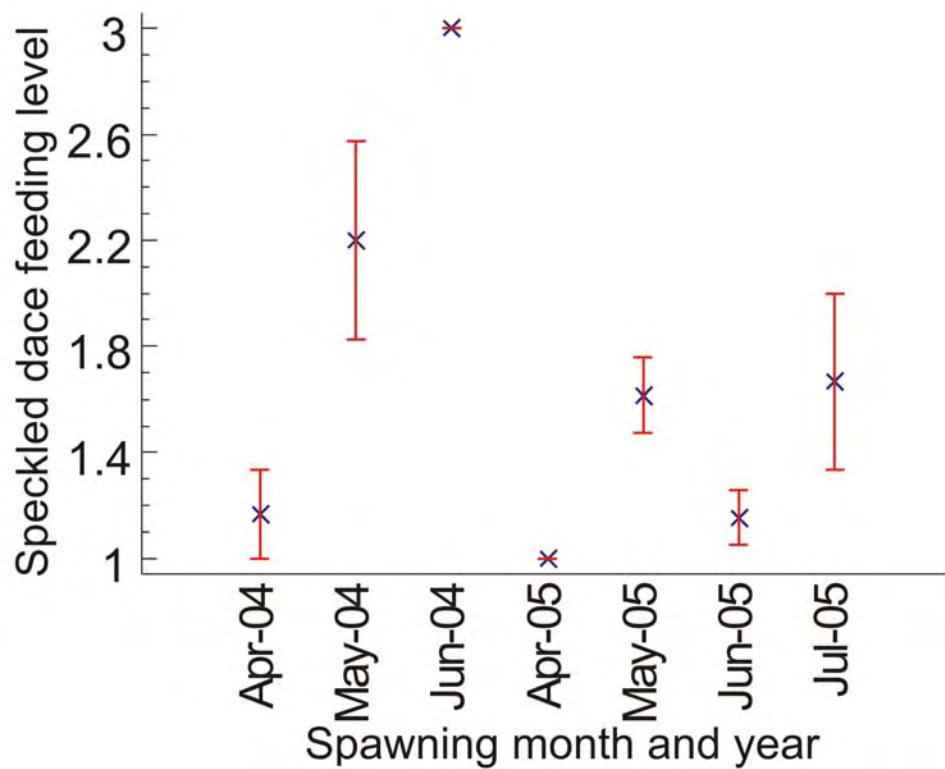


Figure 3.23. Monthly means and standard errors of speckled dace relative feeding level during 2004 and 2005 Pacific lamprey spawning periods.

CHAPTER 4

SUMMARY AND CONCLUSIONS

The 2003 petition for Endangered Species Act (ESA) listing of the Pacific lamprey, *Lampetra tridentata*, has highlighted data gaps in its basic biology and management in the northwestern United States, particularly in early life stages and population monitoring. This study investigated Pacific lamprey spawning and larval recruitment patterns in a coastal Oregon stream in 2004 and 2005.

Chapter 2 evaluated spatial and temporal aspects of adult and redd surveys and documented spawning and residence times, length frequency, sex ratio, and movement in the Coquille River. Residence time on spawning grounds was less than one week and declined as the season progressed. The interpretation of adult data is, therefore, sensitive to the frequency of surveys which, ideally, should be carried out more often than weekly. A more focused tagging study of residence times of both sexes would be valuable for determining the most useful survey frequency.

When spawner abundance was high, seasonal patterns in spawning activity were highly correlated at three spatial scales: a 9.2 km river section, individual reaches within that section, and a single spawning area downstream. Consequently, when resources are scarce it may be better to have more frequent samples of a small area than fewer samples of a large area. However, in this study habitat conditions were comparable among river sections, and such spatial correlations may not hold in other river systems. For this reason, additional evaluations of spawning activity over time and space would be useful for testing assumptions about scale of observation required for informative annual

monitoring. Lastly, adult and redd counts suffer from errors due to observer variability, movement during surveys, night spawning, and variable visibility related to weather and flow. To make spawning surveys more effective tools for population monitoring, these errors need to be better quantified. Since long-term population monitoring is important for understanding species status and response to management actions, future studies should evaluate the meaning of adult and redd count data with respect to both adult escapement and recruitment of future generations.

In Chapter 3 we described seasonal variation in spawning time and larval production, evaluated the stock-larval recruitment relationship, and investigated potential limitations to early life survival. We demonstrated that timing and magnitude of Pacific lamprey spawning and ammocoete production varied greatly between and within years, and were likely dictated by temperature and discharge conditions. Spawning stock explained <15% of the variability in larval production, indicating that gains in egg production at higher stock sizes were offset by increased embryo mortality. As expected, survival until larval emergence varied greatly between intra-annual cohorts. Survival was significantly related to spawning stock size, discharge during spawning, and their interaction and generally declined with increasing spawning stock and decreasing discharge. These relationships could be due to constriction of spawning habitat associated with falling river-levels. These results, as well as investigations into Great lakes sea lamprey population dynamics (Jones et al. 2003; Haesker et al. 2003), point to density-dependent survival and suggest that larval production may be limited by spawning habitat. If this is the case, restoration of degraded spawning habitats or maintenance of flow during the spawning season via dam releases or decreased water withdrawals, could

result in increased larval production. Although density-dependent survival and recruitment is well established for some populations of anadromous salmonids (Van den Berghe 1989; Fukushima et al. 1998) and sea lampreys (Weise and Pajos 1998; Jones et al. 2003; Haesker et al. 2003), more controlled studies of Pacific lamprey populations are needed. Specifically, evaluation of the effect of spawning-stock size on larval production across a range of well-quantified spawning habitat sizes and/or conditions would be valuable. Likewise, longer term studies to monitor spawning populations, emergent larvae, and older age-classes over a range of environmental conditions are needed to better understand recruitment processes. When feasible, the multi-life stage approach implemented in this study is recommended because it allows for greater insight into population dynamics and limiting factors than adult or larval data alone.

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APPENDICES

Appendix I. Methods, Results, and Discussion from an in situ egg incubation pilot project.

Methods

An experimental project using in situ egg fertilization and incubation was carried out in spring 2005 to evaluate sampling assumptions about Pacific lamprey size at emergence and development-time. With assistance from Leo Grandmontagne (*Wild Fish for Oregon*) an “instream egg-incubation chamber” was constructed. The chamber contained four individual compartments with 500 μ m mesh cod-ends on the downstream side for collecting emergent larvae. The chamber bottom was 500 μ m mesh Nytex™, reinforced with stiff screen. Adjustable, overhanging wooden “lips” were mounted on the downstream side of the apparatus to allow regulation of upwelling and flow into cod-ends. Foam tubes were attached for flotation and the apparatus was tied to an overhanging willow upstream, allowing rise and fall with stream level. After securing the chamber in a shaded area on the stream margin, proper sized gravels were arranged in the compartments to mimic natural Pacific lamprey redds. An Onset® temperature logger was placed inside the compartment to be used for incubation.

On May 27, 2005 a ripe male and female pair of Pacific lampreys were captured, anesthetized, and manually spawned in a large glass beaker following methods of Meeuwig et al. (2005). A large amount of fertilized eggs (ca. 1000–10000) were immediately transferred to the gravels and the chamber was covered with a dark cloth to keep developing eggs out of direct sunlight. Due to scarcity of spawning adults, only one pair of lampreys was spawned. During the incubation period, the cod-end was periodically removed and cleansed of detrital matter to maintain adequate water flow through the gravels. Roughly three hours after spawning, 10 eggs were collected to verify successful fertilization. Every 3–6 days until larval emergence, up to ten developing eggs or prolarvae were collected for a developmental sequence. After 25 days, the cod-end was emptied of larvae each morning at 1000 hours until emergent larvae were no longer captured. Fifty days after fertilization of eggs, substrate in the incubator was flushed thoroughly with a wash-down pump, washing any potentially remaining larvae into the cod-end. All larvae were preserved in 5% formalin, counted, and measured to the nearest 0.1 mm with an ocular micrometer.

Results

Of the fertilized eggs initially placed in the incubation chamber, only 81 larvae were collected (in addition to those removed for developmental sequences). Seventy-nine emergent larvae were collected in the cod-end from 30 to 46 days after fertilization, and two larvae were collected 50 days post-fertilization during cleaning of the incubator. The highest number of larvae emerged at 33 days, with approximately 50% emerging by 34 days (Figure Appendix I.1). Mean water temperature in the incubation chamber during this period was 14.61 ± 0.035 (range 10.55–20.33). It took approximately 30.3 days to reach 300.7 cumulative effective degree days, the number of temperature units required to reach the larval stage as predicted from laboratory data (Meeuwig et al. 2005). Only 1.3% of larvae had emerged from the incubator by this time (Figure Appendix I.1).

Lengths of emergent larvae collected from the incubator followed a normal distribution, ranging from 7.5 to 12.5 mm, with a mean of 8.54 ± 0.075 (SE) (Figure

Appendix I.2). Eighty-two percent of larvae collected were greater than 7.9 mm and less than 9.1 mm in length—the size range used to designate emergent larvae caught in drift nets.

Discussion

The instream incubation pilot study offered insight into Pacific lamprey embryonic development, emergence timing, and length frequency under a naturally fluctuating temperature regime. Despite successful incubation of eggs, the apparatus had several drawbacks and did not necessarily represent normal redd conditions. The low survival of larvae (81 of 1000-10,000) in the incubator may be attributed to a number of causes, including disease or suffocation. A high-water event during incubation changed flow conditions in the incubator, introducing clogging organic matter and potentially stagnating water between cleaning events.

Larvae were collected in the cod-end over a 17 day period, suggesting that, either they naturally emerge over a protracted period, or the conditions in the chamber were not natural. The existence of such variation in emergence timing between siblings could be due to microhabitat differences with the redd gravels. Factors such as oxygen concentration and light intensity have been shown to bear on development time. From the evolutionary perspective of an individual female spawning in a highly stochastic, lotic environment, it may be advantageous for her offspring to emerge over an extended period to ensure that a portion are exposed to suitable ecological conditions as they enter the drift. The fact that two individuals remained in the chamber for 50 days, both of whose intestinal tracts showed clear evidence of food ingestion, indicates that the environment within the chamber was suitable for feeding and potentially unnatural. Alternatively, this finding suggests that, a small percentage of larvae may naturally remain in and feed in the safety of redd gravels before emerging.

Furthermore, the incubation apparatus effectively corroborated the size range chosen to delineate newly emerged age-0 ammocoetes from older individuals. The majority of emergent ammocoetes collected were in the 8–9 mm size class. Both individuals over 10 mm in length (Figure Appendix I.2) were collected during removal of the incubator, 50 days post-fertilization, and after exogenous feeding had occurred.

If used during suitable stream conditions, this chamber (or similar equipment) has potential to contribute useful information about fish development and larval behavior in a controlled, semi-natural setting. If the chamber was modified to represent more natural redd conditions and the number of initial fertilized eggs were counted, estimates of survival rate until emergence (in the absence of predators) could be made. Likewise, use of multiple incubation compartments across a range of temperatures would further clarify drift sampling assumptions about emergence timing and size. An alternative approach involves capping lamprey redds immediately after spawning is observed.

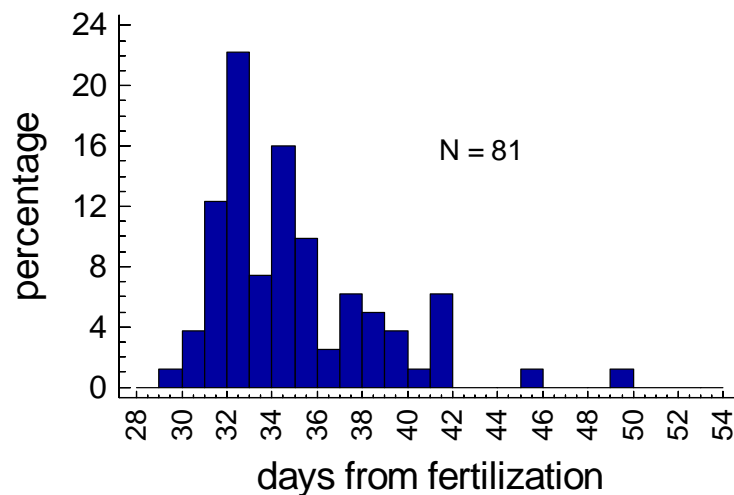


Figure Appendix I.1. Percentage of emergent larvae collected from the incubation chamber at days from fertilization. Fifty percent of emergence occurred at approximately 34.5 days.

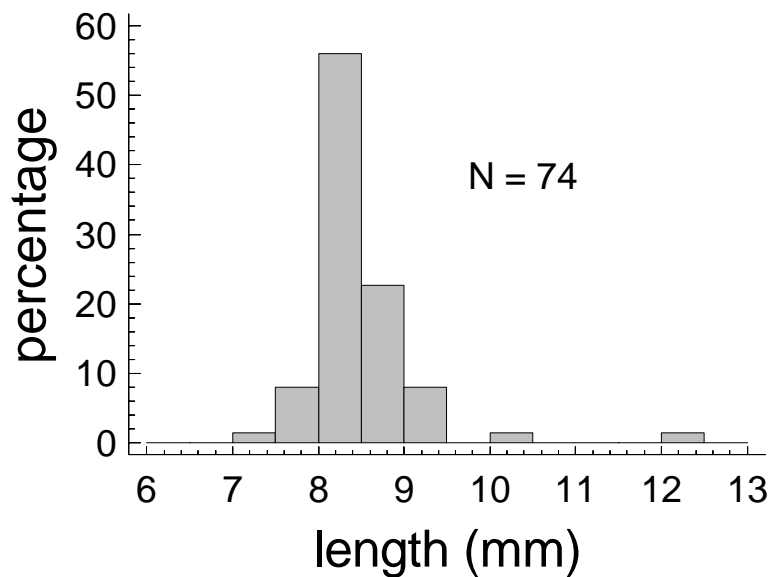
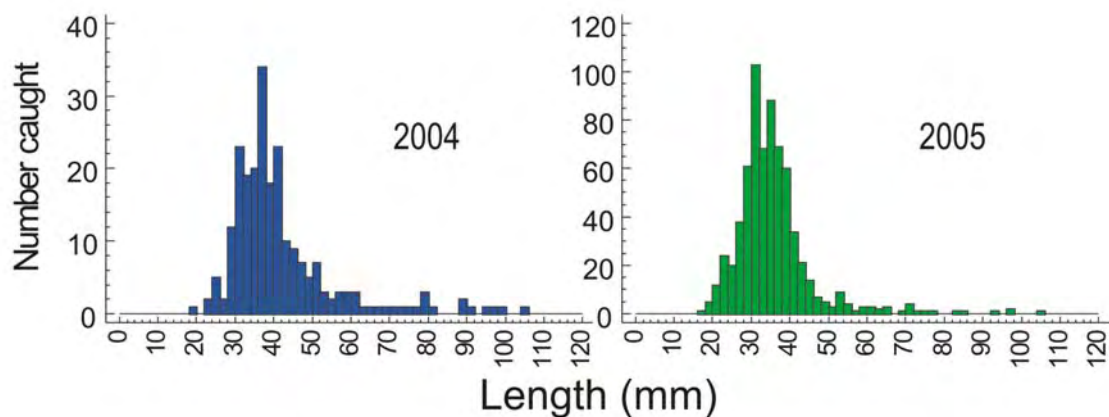
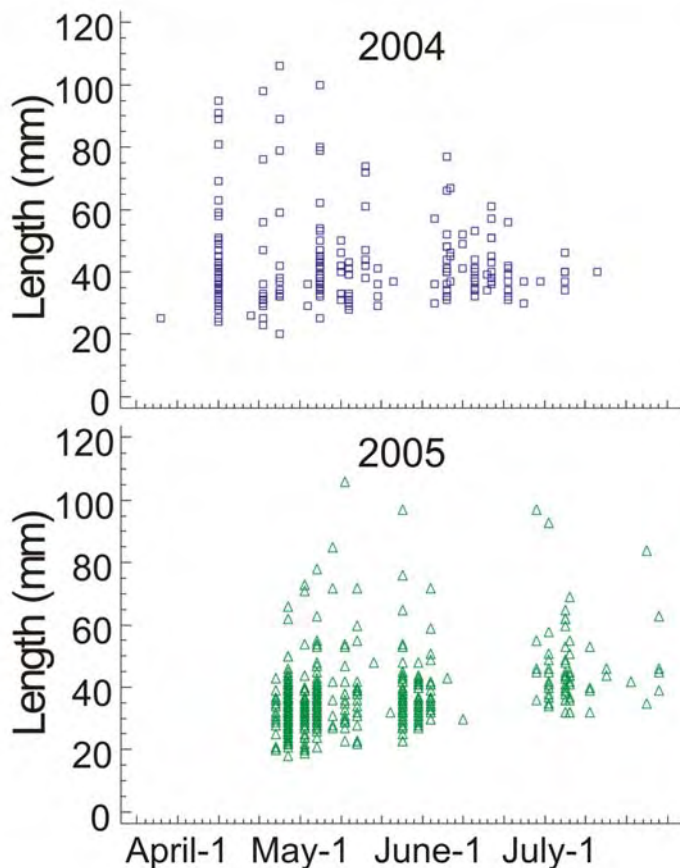


Figure Appendix I.2. Relative frequency histogram of lengths of larvae collected from the instream egg incubation chamber. Six damaged or deformed specimens were excluded.

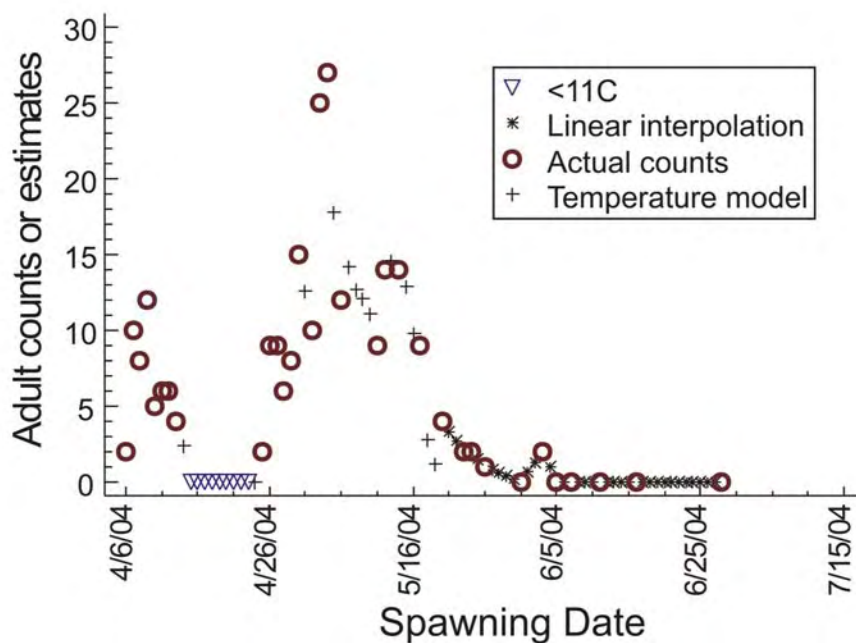
Appendix II. Length frequency of age one and older (>18 mm) ammocoetes collected in biweekly and diel nets set below the focal area (2004: N = 230, 2005: N = 672). Samples could consist of both western brook and Pacific lampreys, but are likely dominated by the latter.



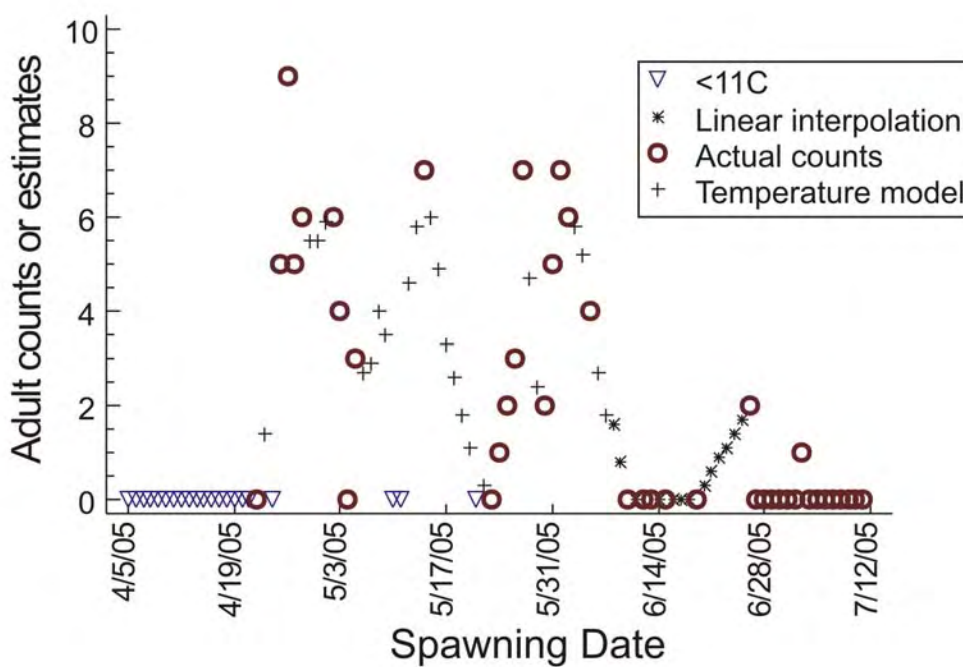
Appendix III. Scatter plot of age one and older (>18 mm) ammocoete lengths across 2004 and 2005 sampling seasons from biweekly and diel drift net samples.



Appendix IV. Actual and estimated focal area adult counts in 2004. Triangles represent dates in which daily mean water temperature was $<11^{\circ}\text{C}$ and spawning activity was assumed to be zero; asterisks are points estimated using linear interpolation between adjacent points; and crosses are temperature-predicted regression estimates.



Appendix V. Actual and estimated focal area adult counts in 2005. Triangles represent dates in which daily mean water temperature was $<11^{\circ}\text{C}$ and spawning activity was assumed to be zero; asterisks are points estimated using linear interpolation between adjacent points; and crosses are temperature-predicted regression estimates.



Appendix VI. Correlation coefficients (top) and *P*-values (bottom) of explanatory variables used in multiple linear regression models explaining relative survival until emergence. Results are for 2004 and 2005 data combined. See Table 3.1 for description of variable symbols.

	SS	MWTD	MWTS	MDD	MDS	FMI	DDP
SS		-0.0209	0.0257	-0.2421	-0.2473	0.5276	-0.0218
		0.9192	0.9008	0.2335	0.2232	0.0056	0.9159
MWTD	-0.0209		0.757	-0.9045	-0.3635	0.1087	-0.9858
	0.9192		<0.0001	<0.0001	0.0679	0.5971	<0.0001
MWTS	0.0257	0.757		-0.6511	-0.6821	-0.0482	-0.7469
	0.9008	<0.0001		0.0003	0.0001	0.8151	<0.0001
MDD	-0.2421	-0.9045	-0.6511		0.3012	-0.2871	0.9356
	0.2335	<0.0001	0.0003		0.1349	0.1551	<0.0001
MDS	-0.2473	-0.3635	-0.6821	0.3012		0.1178	0.3513
	0.2232	0.0679	0.0001	0.1349		0.5666	0.0785
FMI	0.5276	0.1087	-0.0482	-0.2871	0.1178		-0.1458
	0.0056	0.5971	0.8151	0.1551	0.5666		0.4773
DDP	-0.0218	-0.9858	-0.7469	0.9356	0.3513	-0.1458	
	0.9159	<0.0001	<0.0001	<0.0001	0.0785	0.4773	