

## Basin-scale patterns in the drift of embryonic and larval fishes and lamprey ammocoetes in two coastal rivers

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### Synopsis

We studied the distribution and abundance of drifting embryonic and larval fishes and lampreys in the Smith and Van Duzen rivers of northern California, U.S.A. We collected seven fish species in four families and at least one lamprey species in the drift. All taxa drifted almost exclusively at night. Sculpins, *Cottus aleuticus* and *C. asper*, outnumbered all other taxa, comprising 63% of the catch in the Van Duzen River and 90% of the catch in the Smith River. We estimated that sculpin drift reached  $3 \times 10^7$  individuals  $\text{h}^{-1}$  during the relatively high flow period from late winter through early summer. Most sculpin in these two rivers appeared to drift to the estuaries; we estimated  $2.5 \times 10^9$  sculpin embryos and larvae reached the Smith River estuary in 1995. In contrast to the sculpins, the patterns in the drift of other taxa suggest limited transport to the estuaries. Suckers, *Catostomus occidentalis* in the Van Duzen River, *C. rimiculus* in the Smith River, threespine stickleback, *Gasterosteus aculeatus*, and lamprey, *Lampetra tridentata* and possibly *L. richardsoni*, drifted at much lower rates and later in the year than sculpins. In the Van Duzen River, drift appeared to serve as a dispersal mechanism for only one of three introduced cyprinids. California roach, *Lavinia symmetricus*, drifted at low rates throughout the summer while we captured only seven Sacramento pikeminnow, *Ptychocheilus grandis*, and no speckled dace, *Rhynchichthys osculus*. The information gathered on the drift of early life history phases is germane to both the conservation of native fishes and management of non-indigenous species in coastal rivers.

### Introduction

The drift of early life history phases (sensu Balon (1999)) is recognized as an important component of the ecology of many lotic fishes (e.g. Tyus & Haines 1991, Johnston et al. 1995, Araujo-Lima & Oliveira 1998). For fishes and lampreys in coastal streams, life histories that include embryonic and larval drift could result in downstream transport into salt water in estuaries or the ocean. While some fishes in these systems rely on estuaries for larval and juvenile rearing, obligate freshwater species or anadromous species that rear for some time in fresh water should benefit from life histories that limit the risk of transport into salt

water. Describing the patterns of drift by these species would contribute greatly to our understanding of community structure and population dynamics in coastal streams.

Aside from basic life history questions, another issue of interest to fisheries managers is the potential role of larval drift in the dispersal of introduced species (e.g. Stoeckel et al. 1997). To date, however, published research is rare on the drift in coastal streams of introduced fishes and non-salmonid fishes in general (Mason & Machidori 1976, Harvey et al. 2002). To better understand the life histories and distributions of native and introduced fishes in two unregulated coastal rivers in western North America, we examined

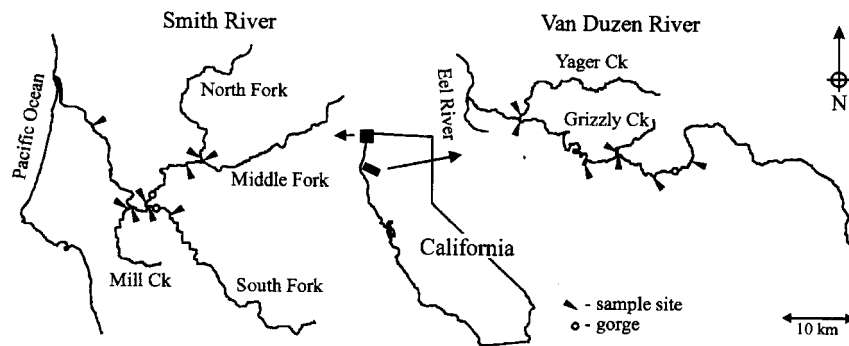


Figure 1. Map of study sites on the Smith and Van Duzen rivers in northwestern California, U.S.A.

basin-scale patterns in the drift of their early life history phases.

## Methods

### Study areas

We studied the drift of embryonic and larval fishes and lampreys in the Smith and Van Duzen rivers in northwestern California, U.S.A. ( $40^{\circ}$ – $41^{\circ}50'$  N,  $123^{\circ}50'$ – $124^{\circ}10'$  W) (Figure 1). The Smith River, the northern-most coastal river in California, flows undammed through a  $1950\text{ km}^2$  catchment composed primarily of coniferous forest and mixed hardwood–coniferous forest. Roughly  $150\text{ km}$  south of the Smith River, the Van Duzen River empties into the lower Eel River  $10\text{ km}$  from the estuary. The Van Duzen River flows undammed through a  $750\text{ km}^2$  catchment, composed primarily of coniferous forest, oak woodland and pastureland. Climate in the region is marked by wet winters and dry summers: average annual rainfall is approximately  $250\text{ cm y}^{-1}$  in the Smith River catchment and  $150\text{ cm y}^{-1}$  in the Van Duzen River catchment, with  $>75\%$  falling from November through May. Discharge in the wet season averages  $170\text{ m}^3\text{ s}^{-1}$  in the lower Smith River and  $45\text{ m}^3\text{ s}^{-1}$  in the lower Van Duzen River. Dry season (June through October) flows average  $20\text{ m}^3\text{ s}^{-1}$  in the Smith River and  $2\text{ m}^3\text{ s}^{-1}$  in the Van Duzen River. Water temperatures are typically  $6$ – $10^{\circ}\text{C}$  in winter and  $18$ – $23^{\circ}\text{C}$  in summer.

Historically, similar fish assemblages probably occupied the two rivers, comprised largely of anadromous salmonids (chinook salmon, *Oncorhynchus tshawytscha*, coho salmon, *O. kisutch*, coastal cutthroat trout, *O. clarki clarki*, and steelhead, *O. mykiss*) and

few year-round residents. Resident species included prickly sculpin, *Cottus asper*, coastrange sculpin, *C. aleuticus*, suckers (Klamath smallscale sucker, *Catostomus rimiculus*, in the Smith River; Sacramento sucker, *C. occidentalis*, in the Van Duzen River), threespine stickleback, *Gasterosteus aculeatus*, resident rainbow trout, *O. mykiss*, and resident coastal cutthroat trout. Pacific lamprey, *Lampetra tridentata*, were probably common in both rivers.

In contrast to the Smith River, the Van Duzen River now contains established populations of introduced fishes (Brown & Moyle 1997). Sacramento pikeminnow, *Ptychocheilus grandis*, and California roach, *Lavinia symmetricus*, both native to the Sacramento–San Joaquin Drainage and several coastal rivers to the south, are among the most abundant fishes in the Van Duzen River. The speckled dace, *Rhynchichthys osculus*, a species native to much of the western U.S.A., is apparently restricted to a  $25\text{ km}$  reach between steep gorges in the Van Duzen River.

### Sampling

We sampled drift of embryonic and larval fishes and lampreys in the Smith River bi-weekly from 1 March 1995 to 30 August 1995 at nine sites dispersed throughout the basin (Figure 1). We located sites both upstream and downstream of two bedrock gorges that were potential barriers to upstream movement by adult fishes (Figure 1). To describe diel patterns in drift, every 4 wk we collected samples over a 24-h period at the site on the Middle Fork Smith River just upstream of the confluence with the South Fork Smith River (and also once, in June, at the most downstream site). We sampled eight additional tributaries (three downstream of the gorges

and five upstream) once each over the course of the 6-mo study period.

We sampled drift of embryonic and larval fishes and lampreys in the Van Duzen River bi-weekly or monthly from 4 February 1997 to 29 October 1997 at seven sites (Figure 1), five in the mainstem and two in large tributaries (Yager and Grizzly creeks). We located sites both upstream and downstream of a bedrock gorge (Figure 1). We sampled three additional tributaries once over the course of the 9-mo study period.

To collect embryos and larvae, we used paired drift nets (30 × 45 cm rectangular mouth, 363- $\mu$ m mesh) anchored to the stream bed with steel stakes. We positioned the nets in stream margins where they captured the entire water column. The two nets fished abreast, usually separated by 1–2 m. At the beginning of each set, we recorded the depth and measured the velocity at the mouth of each net. We fished the nets for 36 min on average. Times ranged from 10–152 min, with shorter sets in faster water and/or when debris clogged nets. Volume fished averaged 92 m<sup>3</sup> per net. We completed all collections within 6 h after nightfall, except for the diel samples, which were collected for a minimum of 15 min (average 60 min) separated by at most 4 h over the 24-h period. We fixed all samples in the field in buffered 5% formalin.

In the laboratory, we separated fish and lamprey embryos and larvae from debris and other organisms under dissecting microscopes. For samples with large amounts of debris, we used a plankton splitter to obtain more manageable portions (usually one half or one quarter of the original). We used characteristics provided in Wang<sup>1</sup> to identify individuals to species for all taxa except sculpins and lampreys, which we identified to genus. For each taxon within a sample, we recorded the total count and measured the total length (TL  $\pm$  0.1 mm) of individuals using an ocular micrometer. When the total count for a taxon exceeded 50, we measured a sample of 50 individuals.

To evaluate basin-scale patterns in the drift of each taxon, we plotted monthly mean drift rates at each site on maps of the two rivers. For each taxon collected at a site on a particular date, we calculated drift rates (individuals h<sup>-1</sup>) by multiplying the mean density (individuals m<sup>-3</sup>) for the paired nets by the estimated

river discharge (m<sup>3</sup> h<sup>-1</sup>) at the site. For these calculations, we assumed equal density of drifting larvae across the channel. We estimated river discharge at the sample sites using data from U.S. Geological Survey (U.S.G.S.) stream gages. For one site in each river close to an existing gage, we used gage flows directly. Three other sites lie close to defunct U.S.G.S. gages, which enabled us to estimate flow at those sites using relationships between the old and existing gages. For ungaged sites, we determined a ratio of flow at the existing gage to flow at the sites based on the ratio of the catchment areas weighted by mean annual precipitation. At the three sites with historic discharge data, the two methods we used for estimating flows differed by  $\leq 5\%$ .

To examine diel patterns in drift, we divided the day into four time periods. Rather than restrict the time periods to hours on the clock, we divided both the hours of darkness and the hours of daylight in half to compensate for changing day lengths over the 6-mo study period. We then summarized the data by presenting the proportion of the total catch for each taxon in each of the four time periods.

## Results

In the Smith River, we collected about 13 750 fish and lamprey embryos and larvae at the nine primary sites and 785 embryos and larvae in three of the eight additional tributaries we sampled. We captured a total of 705 embryos and larvae during 24-h sampling. In the Van Duzen River, we collected about 19 250 embryos and larvae at the seven primary sites but none in the three additional tributaries we sampled.

Overall, we collected seven fish species in four families and one or two lamprey species in the drift. Coastrange and prickly sculpin, suckers, threespine stickleback, and lamprey (Pacific lamprey and possibly western brook lamprey, *Lampetra richardsoni*) drifted in both rivers. Sacramento pikeminnow and California roach drifted in the Van Duzen River.

Sculpins greatly outnumbered other taxa, comprising 90% of the total catch in the Smith River and 63% in the Van Duzen River. Sculpins drifted at high rates from mid-winter through early summer with no distinct peaks (Figure 2). We calculated a maximum drift rate of  $1.0 \times 10^7$  individuals h<sup>-1</sup> (density = 8.1 individuals m<sup>-3</sup>) at the lower Smith River site on 12 April, and  $1.0 \times 10^5$  individuals h<sup>-1</sup> (density = 7.4 individuals m<sup>-3</sup>) at the lower Van Duzen River site on 19 March. Drift rates decreased with distance upstream (Figure 2).

<sup>1</sup> Wang, J.C.S. 1986. Fishes of the Sacramento-San Joaquin estuary and adjacent waters, California: a guide to the early life histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary, Technical Report 9, Department of Water Resources, Sacramento. 400 pp.

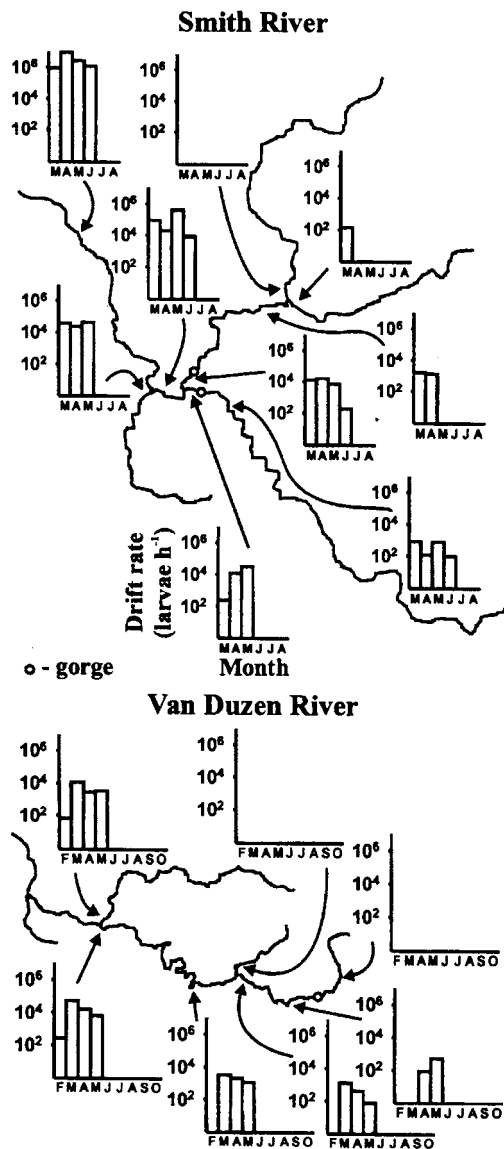


Figure 2. Drift rates of sculpin embryos and larvae in the Smith and Van Duzen rivers. Bars represent means of two sample trips per month except for March and August in the Smith River and April in the Van Duzen River (three trips), and July through October in the Van Duzen River (one trip). Drift rates apply to the first 6 h after dark.

We captured drifting sculpin upstream of both gorges in the Smith River but none upstream of the gorge in the Van Duzen River (Figure 2). The three Smith River tributaries where we captured drifting sculpin (Mill (one of the bi-weekly sample sites), Peacock and Myrtle creeks) lie downstream of the gorges. Though

sampled on consecutive trips (late April–early May), drift densities in Peacock and Myrtle creeks differed substantially, with Peacock Creek (catchment area = 6 km<sup>2</sup>, slope = 2%) yielding 18 000 individuals h<sup>-1</sup> and Myrtle Creek (catchment area = 14 km<sup>2</sup>, slope = 6%) only 1000 individuals h<sup>-1</sup>. The lengths of drifting sculpin varied little (Smith River: mean TL = 5.8 mm, range 4.9–7.0 mm, *n* = 2095; Van Duzen River: mean TL = 6.0, range 4.7–7.0 mm, *n* = 2071), with no apparent differences over time or among sites within basins.

Suckers constituted 2% of the total catch in the Smith River and 6% in the Van Duzen River. We captured suckers beginning in June in the Smith River and May in the Van Duzen River (Figure 3). Drift of suckers continued into July or August in both rivers, with apparent peak rates in June in the Smith River and May in the Van Duzen River (Figure 3). The maximum drift rate for the Smith River, approximately 28 000 individuals h<sup>-1</sup> (density = 0.1 individuals m<sup>-3</sup>) at the lower Smith River site on 21 June, is probably an overestimate, reflecting the expansion of a measured density of 0.1 fish m<sup>-3</sup> (actual catch = 4 individuals) by a relatively high discharge of 64 m<sup>3</sup> s<sup>-1</sup>. The maximum for the Van Duzen River reached only about 900 individuals h<sup>-1</sup> (density = 1.9 individuals m<sup>-3</sup>) at one of the middle mainstem sites on 29 May. Except for a longer window of occurrence at some of the upriver sites, drift rates of suckers showed no clear longitudinal pattern within either basin (Figure 3). We did not capture suckers in Smith River tributaries. Klamath smallscale suckers in the Smith River averaged 14.0 mm TL (range 7.7–21.4 mm, *n* = 313) while Sacramento suckers in the Van Duzen River averaged 14.8 mm TL (range 12.0–22.0 mm, *n* = 541). We observed no apparent differences in sucker lengths over time or among sites within basins.

Threespine stickleback rarely occurred in the drift in the Smith River (only 32 individuals in our regular sampling) but constituted 17% of the total catch in the Van Duzen River. In the Van Duzen River, drift of stickleback began in May and continued into August, with peak rates in June (Figure 4). We calculated a maximum drift rate of nearly 4500 individuals h<sup>-1</sup> (density = 7.3 individuals m<sup>-3</sup>) at the lower Van Duzen River site on 24 June. Drift rates decreased with distance upstream and we captured no stickleback upstream of the gorge (Figure 4). Stickleback in the Van Duzen River averaged 7.4 mm TL (range 6.0–14.0 mm, *n* = 926) with no apparent differences in lengths over time or among sites.

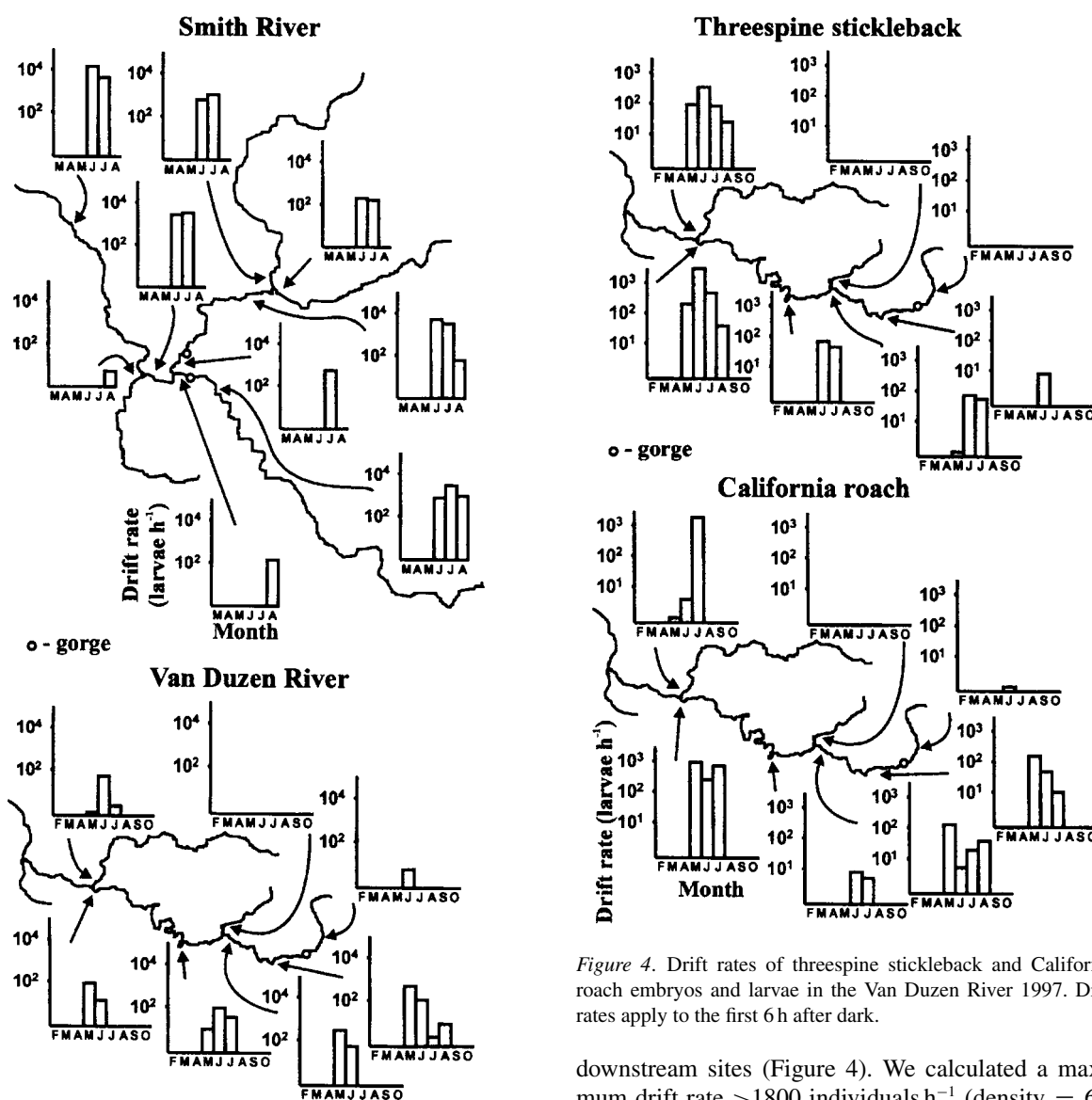


Figure 3. Drift rates of Klamath smallscale sucker embryos and larvae in the Smith River and Sacramento sucker larvae in the Van Duzen River. Drift rates apply to the first 6 h after dark.

Of the three introduced cyprinids in the Van Duzen River, only California roach constituted a significant portion of the total catch (10%). We captured only seven Sacramento pikeminnow and no speckled dace. California roach first appeared in the drift in May and were present until August, with no clear peaks in abundance. We captured California roach throughout the basin, though they drifted at the highest rates at the

Figure 4. Drift rates of threespine stickleback and California roach embryos and larvae in the Van Duzen River 1997. Drift rates apply to the first 6 h after dark.

downstream sites (Figure 4). We calculated a maximum drift rate >1800 individuals h<sup>-1</sup> (density = 6.7 individuals m<sup>-3</sup>) in Yager Creek on 8 July. California roach in the Van Duzen River averaged 7.9 mm TL (range 6.5–10.5 mm,  $n = 701$ ) with no apparent differences in lengths over time or among sites. We captured the seven Sacramento pikeminnow (never >1 per net) in late May through early August at the four middle-to upper-mainstem sites in the Van Duzen River.

Lamprey embryos and larvae (ammocoetes) constituted 8% of the total catch in the Smith River (the second most abundant taxon) and 4% in the Van Duzen River. We captured ammocoetes in every month we sampled in both rivers (Figure 5). Ammocoetes drifted at moderate rates compared to other taxa,

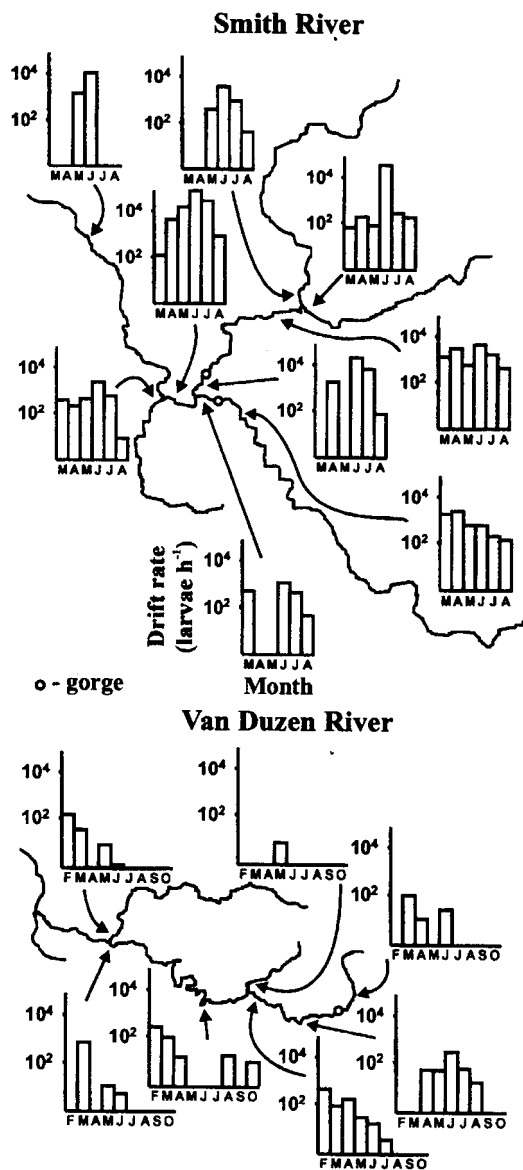


Figure 5. Drift rates of lamprey ammocoetes in the Smith and Van Duzen rivers. Drift rates apply to the first 6 h after dark.

with apparent peaks in June for the Smith River and February in the Van Duzen River. We calculated a maximum drift rate of about 90 000 ammocoetes h<sup>-1</sup> (density = 1.4 individuals m<sup>-3</sup>) at the mainstem Smith River at Mill Creek site on 7 June and approximately 1500 ammocoetes h<sup>-1</sup> (density < 0.1 individuals m<sup>-3</sup>) at the lowest Van Duzen River site on 4 March. Lamprey ammocoetes drifted at similar rates longitudinally

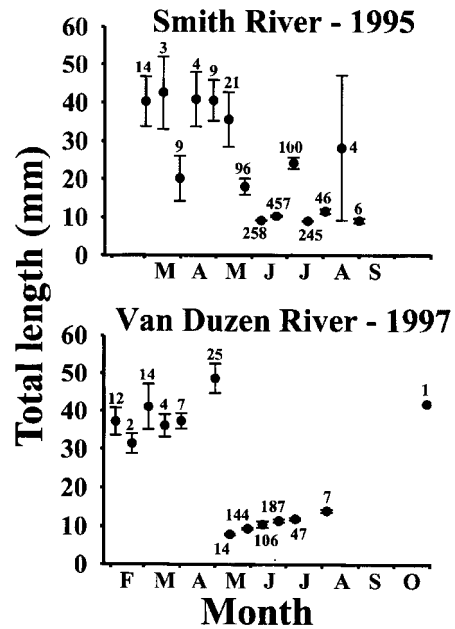


Figure 6. Average length ( $\pm 1$  SE) of drifting lamprey ammocoetes in the Smith and Van Duzen rivers. Numbers associated with each point indicate sample sizes.

within each basin (Figure 5). We captured a total of nine ammocoetes in two of the eight additional tributaries to the Smith River. Both of these tributaries lie upstream of the gorges. Although we found no evidence of longitudinal differences in size, average length of ammocoetes differed over time in both rivers (Figure 6). Ammocoetes averaged 39 mm TL from winter to late spring and 12 mm in summer.

Drift of embryonic and larval fishes and lamprey ammocoetes occurred almost exclusively at night (Figure 7). In the diel sampling in the Smith River, we captured 699 embryos and larvae at night and only six during the day. Most sculpin drifted in the first half of the night while Klamath smallscale suckers drifted in higher numbers later at night (Figure 7).

**Discussion**

We found large numbers of embryonic and larval fishes and lampreys drifting throughout the spring and summer in two coastal basins in northern California. The extremely high number of sculpin drifting in the Smith River merits particular attention. The densities we recorded in the lower Smith River (average 11

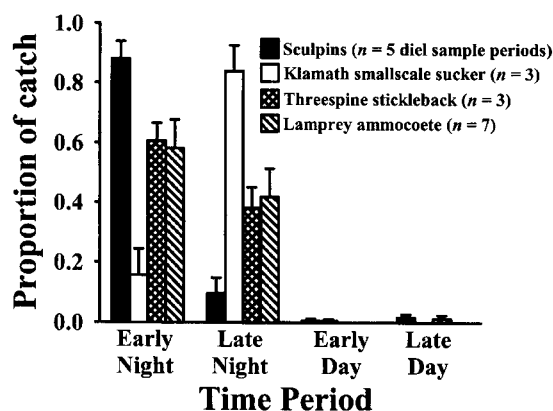


Figure 7. Proportion (with SEs) of total catch by taxon and time period for diel drift samples taken every 4 wk in the Smith River from March through August, 1995. Time periods are the hours of daylight and hours of dark divided in half. Sample sizes (the number of diel sampling periods in which each taxon occurred) are in parentheses.

individuals  $m^{-3}$ ) exceed by 1–2 orders of magnitude the total drift density (all species) typically reported in temperate streams (Gale & Mohr 1978, Muth & Schmulbach 1984, Copp & Cellot 1988, Winnell & Jude 1991, Gadomski & Barfoot 1998, Robinson et al. 1998, Marchetti & Moyle 2000); and the maximum density (32 individuals  $m^{-3}$ ) is comparable to that recorded for an assemblage in a warm-water stream in Oklahoma, U.S.A. (Harvey 1991).

The timing of sculpin drift in the Van Duzen and Smith rivers resembles that recorded in another California stream (Marchetti & Moyle 2000). Extending over 4 mo in the spring and early summer, the drift period for sculpins contrasts to drift periods of several weeks or even days typical of other temperate fishes (Clifford 1972, Næsje et al. 1986, Johnston et al. 1995). In the Smith and Van Duzen rivers, the high drift rates over an extended period result in large numbers of sculpin drifting into the estuaries each year. Applying our hourly drift rates to the first half of each night (6 h) from March through June, we estimate  $2.5 \times 10^9$  sculpin embryos and larvae (about 375 kg wet mass) reached the Smith River estuary in 1995.

Our calculations may overestimate total drift rates if our drift samples are not representative of the entire stream. However, in May of 2001 we sampled drift with five nets positioned across the lower Smith River and recorded no cross-channel differences in the density of drifting sculpins. Thus, multiplying the average

density for our near-shore samples by total discharge seems appropriate for sculpins. Unfortunately, we did not capture any other taxa during this sampling effort, so we have no information on their lateral variation in drift density at our study sites. Previous research has revealed lateral variation in the density of drifting larval fishes in some streams (Armstrong & Brown 1985, Harvey 1991, Robinson et al. 1998).

Sculpin embryos and larvae could constitute a substantial portion of the plankton biomass in the Smith River estuary. Prickly sculpin embryos and larvae (probably mixed with coastrange sculpin) are the third most abundant ichthyoplankters in the Columbia River estuary (Misatano 1977), and Yaquina Bay, Oregon (Percy & Myers 1973), outnumbered only by the early life history phases of fishes that spawn in the estuaries (clupeids and gobiids). Sculpin embryos and larvae remain pelagic for 4–5 wk (Krejsa 1967) and could provide food for many organisms in estuaries, including juvenile salmonids.

Probable relationships between the abundance of early life history phases and adults in these two rivers suggest that, for some fish species, drift sampling of early life history phases should be considered where managers or researchers seek to monitor trends in abundance. The lower numbers of sculpin drifting in the Van Duzen River compared to the Smith River are not explained by stream size. Drift densities of sculpin averaged 2.3 individuals  $m^{-3}$  over all sites in the Van Duzen River, 60% of the average density in the Smith River. We recorded a maximum density  $>30$  individuals  $m^{-3}$  in the Smith River, but never  $>10$  individuals  $m^{-3}$  in the Van Duzen River. The difference between the rivers in drift densities of sculpin embryos and larvae probably reflects differences in adult densities. The density of adult sculpins in the Van Duzen River averages  $<1 m^{-2}$  in riffles and runs (Brown et al. 1995), while sculpin density averages  $>5 m^{-2}$  in riffles and runs in the Smith River (White & Harvey 2001). Both differences in habitat (substrate is more embedded in the Van Duzen River) and predation by Sacramento pikeminnow in the Van Duzen River probably contribute to the difference between rivers in density of adult sculpin (White & Harvey 2001).

Similarly, difference between the rivers in drift of threespine stickleback may also reflect a difference in adult densities. Though abundant in the estuary, adult threespine stickleback are uncommon in the Smith River compared to the Van Duzen River. The Van Duzen River contains more aquatic vegetation

and submerged brush than the Smith River, perhaps providing more of the habitat favored by threespine stickleback.

The patterns of drift we observed fit two broadly-defined life history strategies. The first, with early spawning followed by drift of embryos and larvae to the estuaries, applies to the sculpins. Coastrange and prickly sculpin spawn in the late winter and early spring during relatively high river flows and produce small, weak-swimming embryos and larvae that quickly drift down to the estuaries. On several occasions in the Smith River, we used passive traps and kick nets to determine whether sculpin were settling out in the river. We never captured any sculpin using these methods in the river, but did capture benthic larvae in the estuary. The absence of benthic larvae in the river, the narrow range of embryo and larva size in drift samples, and the increasing drift rates with distance downstream with no accompanying gradient in adult densities all support the hypothesis that most sculpin in the Smith and Van Duzen rivers drift to the estuaries. In the comparatively long, low-gradient Eel River, some prickly sculpin appear to settle out upstream (Brown et al. 1995). This upstream recruitment could result from late-spring drift out of cool tributaries into mainstem reaches with declining flow and large expanses of slow water.

The second pattern in drift, low drift rates during declining discharge, suggests that obligate freshwater species in coastal streams have evolved life histories that minimize drift into salt water. For example, Sacramento suckers in the Van Duzen River apparently reproduce 1–2 mo later than Sacramento suckers in two inland California streams, although temperature regimes appear similar (Villa 1985, Marchetti & Moyle 2000). Additionally, the relatively large sucker larvae (generally >12 mm TL) can probably hold place in moderate currents by swimming. Larvae of the Warner sucker, *Catostomus warnerensis*, resist downstream displacement by swimming toward stream edges or quiet water behind obstructions, behavior Kennedy & Vinyard (1997) suggested was an evolutionary response to unreliable downstream habitat. However, the patterns we observed in sucker drift might also be explained by selection to minimize drift away from suitable habitat (rather than to avoid unsuitable habitat downstream).

This study suggests that drift of early life history phases plays a minor role in the dispersal of introduced species in the Van Duzen River. The relative rarity of cyprinid embryos and larvae in the drift

is probably due to a combination of physical conditions in the Van Duzen River and fish behavior. The introduced cyprinids spawn in the late spring and early summer, and the eggs hatch when the Van Duzen River consists primarily of long, shallow pools, with little or no current. Presumably, embryos and larvae settle out or swim to the stream edges in pools and are unlikely to be swept downstream. This scenario may explain the absence of speckled dace from the drift: a series of exceptionally long pools (>500 m long) may have attenuated drift above our most upstream sampling site on the Van Duzen River, which was the only site in the vicinity of the range of adult speckled dace. For the other two cyprinids, the larger size of Sacramento pikeminnow at hatching compared to California roach (Wang<sup>1</sup>) probably leads to greater swimming ability during the embryonic and larval phases and less frequent occurrence in the drift. Like suckers, cyprinids cannot survive exposure to salt water, so a low propensity to drift could particularly benefit populations in coastal streams. However, selection against high drift rates to avoid lethal habitat downstream is not a likely mechanism to explain patterns of drift by cyprinids in the Van Duzen River, because all three cyprinid species have been introduced in the last 30 y. Selection to minimize drift away from suitable habitat may have influenced the relatively low drift rates of both cyprinids and catostomids.

Of the taxa we collected, only the lampreys have a multi-year larval phase, spending up to 7 y in freshwater (Moyle 2002). Drift of ammocoetes in the Great Lakes region of North America primarily occurs at two times, with larger individuals drifting as a result of scouring at high flows during the winter and spring and newly hatched ammocoetes drifting in high numbers in summer (Potter 1980). Drifting lamprey ammocoetes in the Smith and Van Duzen rivers follow a similar pattern, with larger individuals drifting almost exclusively during higher flows in spring, and smaller, presumably newly hatched ammocoetes drifting during the summer. The low to moderate drift rates over narrow windows of occurrence at the downstream-most sites suggest that relatively few ammocoetes drift into the estuaries.

Our observation that fish embryos and larvae and lamprey ammocoetes drift almost exclusively at night during non-flood flows concurs with previous research (Flecker et al. 1991, Harvey 1991, Gadomski & Barfoot 1998, Marchetti & Moyle 2000). Hypotheses proposed to explain the distinct diel periodicity of drift include



predator avoidance (Flecker et al. 1991), and nocturnal disorientation of larvae (Armstrong & Brown 1985). Regardless of the mechanisms involved, our results suggest that embryonic and larval fishes and lampreys may only be available to diurnal drift-feeding organisms at dusk and dawn.

This study indicates that at night throughout the spring and summer, embryos and larvae of fishes and lampreys typically drift in coastal streams at rates exceeding several thousand per hour and sculpins may drift into the estuaries by the millions to tens of millions per hour over a 4-mo period. The movement of such huge numbers of potential prey could be significant for some species of special concern, including some Pacific salmonids. Additionally, the patterns of drift we observed suggest that by reproducing during periods of relatively low flow and/or producing large embryos and larvae that can resist downstream displacement, obligate freshwater species in coastal streams probably face a limited risk of drifting into saltwater. A better understanding of these processes in unregulated rivers should provide useful information for biologists and managers working in regulated systems.

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