Wetlands (2012) 32:401–410
DOI 10.1007/s13157-012-0294-8

ARTICLE

Beaver in Tidal Marshes: Dam Effects on Low-Tide Channel Pools and Fish Use of Estuarine Habitat

W. Gregory Hood

Received: 31 August 2011 / Accepted: 16 February 2012 / Published online: 27 February 2012

Abstract Beaver (*Castor* spp.) are considered a riverine or lacustrine animal, but surveys of tidal channels in the Skagit Delta (Washington, USA) found beaver dams and lodges in the tidal shrub zone at densities equal or greater than in non-tidal rivers. Dams were typically flooded by a meter or more during high tide, but at low tide they impounded water, allowing beaver to swim freely while quadrupling pool habitat for fish compared to channels without dams. Seven fish species were caught in low-tide pools, including threatened juvenile Chinook salmon (*Oncorhynchus tshawytscha*), whose densities (by volume) averaged 3.2 times higher in low-tide pools than shallows. Accounting for the total contribution of pools and shallows to juvenile Chinook abundance, beaver pools tripled shrub zone channel capacity for juvenile Chinook salmon at low tide relative to herbaceous zone marsh without beaver pools. Current Chinook recovery efforts focus on restoring herbaceous zone tidal marsh for rearing juveniles, but this focus overlooks presently rare and poorly understood habitat, like tidal shrub marsh, that was historically common and likely important to beaver and small estuarine or anadromous fish.

Keywords *Castor canadensis* · Oligohaline wetlands · Tidal scrub-shrub wetlands · Juvenile salmon · Ecosystem engineer

Introduction

Beaver (*Castor canadensis* and *C. fiber*) are the archetypal ecosystem engineer; they build large and abundant dams that can have multi-decadal or longer effects on river channel form, riverine and floodplain wetlands, riparian vegetation, nutrient spiraling, benthic community structure, and the abundance and productivity of fish and wildlife (Jenkins and Busher 1979; Naiman et al. 1988; Collen and Gibson 2001; Pollock et al. 2003; Rosell et al. 2005). While beaver are known to be able to traverse marine waters to colonize new territories (Anderson et al. 2009), they are perceived as an essentially freshwater, riverine or lacustrine mammal, a fact reflected in an extensive scientific literature in which a mere handful of studies mention beaver in tidal systems (Nolet and Baveco 1996; Rosell and Nolet 1997; Pasternack et al. 2000). Even so, those studies are of microtidal systems where river discharge dominates water level fluctuations. However, the work described in this paper is motivated by observations of beaver in meso- to macro-tidal portions of the Skagit Delta (Puget Sound, Washington, USA), which challenge the conventional view of beaver as residents only of non-tidal, freshwater habitats. This work aims to address the following questions: (1) Are beaver as abundant in the tidal marshes of the Skagit Delta as in non-tidal rivers? (2) Is the distribution of beaver in Skagit Delta tidal marshes affected by the distribution of shrub versus herbaceous vegetation? (3) Do beaver dams in tidal channels have any geomorphic consequences which may affect the distribution or abundance of fish habitat in tidal channels? (4) Does the tidal channel habitat generated by beaver dams have the potential to affect the productivity of estuarine fish? Comparable beaver abundance between tidal marshes and non-tidal rivers would suggest tidal marshes can be important beaver habitat, while low abundance in tidal marshes would suggest beaver only make occasional excursions into marginal habitat. Association of beaver with tidal shrub versus tidal herbaceous vegetation would suggest that historical, anthropogenic loss of tidal shrub habitat has contributed to the paucity of observations of beaver in tidal shrub marshes. Finally, observation of beaver effects on tidal

W. G. Hood (✉)
Skagit River System Cooperative,
P.O. Box 368, LaConner, WA 98257, USA
e-mail: ghood@skagitcoop.org

channel habitat and fish productivity would indicate that the well known effects of ecosystem engineering by beaver in non-tidal rivers may extend to tidal channels as well. This would further imply that historical, anthropogenic losses of tidal shrub marshes or of tidal beaver may have had previously unrecognized impacts on ecosystem processes and functions.

Setting

The 8,544-km^2 watershed of the Skagit River drains the Cascade Mountains of northwestern Washington State and southern British Columbia. Basin elevations range from sea level to 3285 m, while mean annual precipitation ranges from 80 cm in the lowlands to over 460 cm in the mountains The Skagit is the largest river draining into Puget Sound (Washington, USA) with a mean annual discharge of 470 m^{3}s^{-1} that amounts to 34% of the Sound's freshwater inflows. The 327-km^2 Skagit delta is likewise the largest in Puget Sound, though more than 90% of it has been isolated from riverine and tidal influence by dikes and converted to agriculture and other uses (Collins et al. 2003). Most of the remaining undiked tidal wetlands are located at the mouths of the North and South Forks of the Skagit River, the two principal river distributaries, so that these marshes are oligohaline even at their most bayward extents, with soil pore water salinity ranging from 0 to 8 ppt during normal river flow. Tidal marsh vegetation is dominated by *Carex lyngbyei* (sedge) at the lowest elevations and, with increasing elevation, by zones of *Typha angustifolia* (narrow-leaf cattail), *Myrica gale* (sweetgale) shrub thickets, and finally mixed-species thickets of shrubs and trees growing on high distributary levees and large nurse logs (Hood 2007). The mixed-species shrub and tree community is composed primarily of *Salix* spp. (willows), *Lonicera involucrata* (black twinberry), and *Picea sitchensis* (Sitka spruce). Tidal shrub habitat is currently limited to 190 ha in the Skagit Delta (Hood 2007), which amounts to 5% of the 3780 ha occurring prior to Euro-American settlement (Collins et al. 2003). Semi-diurnal tides in the delta have a maximum range of 4.5 m (Yang and Khangaonkar 2009). The current study focuses on the South Fork tidal marsh, which is three times larger than that of the North Fork. However, both marshes are similar in character and qualitative observations in the North Fork marsh indicate study results are representative of both areas.

Methods

Marsh Habitat Mapping

Tidal marsh vegetation was mapped in a geographic information system (ArcGIS 9.3) from false-color infrared orthophotos flown at an altitude of 1850 m on 30 August 2004 during a low tide of −0.3 m mean lower low water (MLLW) at a scale of 1:12,000 with 15-cm pixels. Two broad types of tidal marsh vegetation communities were distinguished: tidal herbaceous vegetation, with *C. lyngbyei* and *T. angustifolia* predominating, versus tidal shrub vegetation, which could be further resolved into monospecific thickets of *M. gale* and mixed species thickets of shrubs with occasional trees. The tidal shrub photosignatures were easily distinguishable from the tidal herbaceous vegetation by differences in color and texture. Photo interpretations were extensively groundtruthed to confirm their characterization (Hood 2007).

Tidal Channel Surveys

Low-tide pools were defined as tidal channel areas more than 20 cm deep at low tide; the remaining areas were termed shallows. Previous field experience suggested this criterion—most flat channel bottoms tend to be less than 15 cm deep at low tide, while most pool-like channel depressions or impoundments formed by bank slumps or logs tend to be at least 20 cm deep. Tidal channel bottom elevations, relative to the tidal frame, were high enough that pools and shallows were present for about 2 h before and after low tide.

Tidal channels were chosen for survey and sampling based on their accessibility. Some channels were inaccessible by boat at low tide and too distant to reach on foot, survey, and return to the boat before the flood tide. However, every effort was made to distribute the surveys evenly across the South Fork marsh. Channels were surveyed by walking the length of the channel, starting from the channel mouth. A hip chain was used to determine distance traveled, the start and end of pools, locations of beaver dams and lodges, and locations of major tributary junctions. Hip chain measurement errors were corrected by comparing tributary junction locations measured in the field with GIS measurements of aerial photos. Laminated aerial photos (1:700 scale) were an additional field navigation and mapping aid, with channel bends, tributary junctions, distinctive vegetation patches, and large logs providing abundant landmarks. A stadia rod was used to measure water depth at low tide, channel depth from bank top to thalweg bottom, channel width, and dam width. Water depth was calculated from the mean of three to ten representative measurements in the channel thalweg, a larger number of measurements for larger pools. The maximum water depth was noted while wading in the deepest portion of the pool. The dam head was defined as the difference in the water surface elevations immediately upstream and downstream of a beaver dam. This was measured by extending the stadia rod horizontally downstream from the water surface above the dam, leveling the rod with a hand level, and measuring the distance from the underside of the rod to the water surface below the dam with a metal tape measure. The presence of Great Blue Herons (*Ardea herodias;*

GBH) or their tracks in channel bottoms was noted in the course of tidal channel surveys, referenced to hip chain measurements, and mapped in the field on the laminated aerial photos. GBH are an abundant predator of small fish in the Skagit tidal marshes. Their occurrence was mapped to determine if, as suspected from casual observation, they were preferentially associated with tidal herbaceous rather than tidal shrub channels; if so, this would suggest tidal shrub channels could provide juvenile salmon a refuge from GBH predation.

Fish Sampling

Fish sampling occurred from early March to late June to coincide with the peak period of juvenile salmon migration through the delta. Channel segments were isolated using two blocking nets, while a 2.5-m wide, 1.5-m tall seine with 0.3-cm knotless nylon mesh was used to catch fish. Each channel segment was seined repeatedly till depletion of the fish population, with the catch noted for each seining. Seining was repeated three to five times, depending on catch size and depletion rate. Fish population sizes in sampled channel segments were estimated using the method of Zippin (1958). Eighteen channel segments were sampled for each combination of vegetation zone (tidal herbaceous vs. tidal shrub marsh) and channel habitat (low-tide pool vs. shallows), for a total of 72 samples. Channel segment length, mean width, and mean depth were measured with a stadia rod at the time of sampling. Sampled low-tide pools and shallows were similar in depth, length, and volume between the tidal shrub and tidal herbaceous vegetation zones (Table 1). Fish abundance was standardized by channel segment water volume, which minimized differences in fish densities between tidal channel shallows versus pools, but which also reflected true fish density; abundances standardized by surface area confound the effects of differences in channel segment volume and possible differences in volumetric density and would have accentuated density differences between shallows and pools, i.e., density differences by surface area could occur without volumetric density differences simply because of the greater volume of pools versus shallows.

Table 1 Mean (standard deviation) water depth, length and volume in channel segments sampled for fish during low tides

	Tidal Shrub Zone	Tidal Herbaceous Zone
Depth		
Pools	0.43 m (0.12)	0.33 m (0.08)
Shallows	0.14 m (0.06)	0.09 m (0.04)
Length		
Pools	5.36 m (1.52)	5.71 m (1.22)
Shallows	4.78 m (1.39)	6.49 m (3.22)
Volume		
Pools	4.51 m^3 (2.94)	4.21 m^3 (2.32)
Shallows	0.83 m^3 (0.61)	0.93 m^3 (0.79)

Statistical Analysis

The frequency of fish occurrence in four habitat types (herbaceous marsh pools, herbaceous marsh shallows, shrub marsh pools, and shrub marsh shallows) was evaluated separately for each of the seven most commonly encountered species using a test for comparing more than two proportions (Zar 1984, pp. 400-402). Fish density was analyzed separately for each species by non-parametric two-factor analysis of variance (ANOVA) using the Kruskal-Wallis test (Zar 1984). One factor was vegetation zone (tidal herbaceous vs. tidal shrub marsh), while the other was channel habitat (low-tide pool vs. shallows). Traditional parametric ANOVA was inappropriate because of the large proportion of null samples for most of the fish species and the generally non-normal distribution of the data.

Because the Kruskal-Wallis tests were repeated for each of seven species of fish, Bonferroni-type multiple comparison procedures were used to determine significance thresholds (α) that would avoid inflated risk of Type I inference error. Multiple comparison procedures guard against Type I errors at the expense of Type II errors, i.e., at the expense of statistical power. With this in mind, a multiple comparison procedure was used which prioritized statistical power (Benjamini and Hochberg 1995) to off-set the generally lower power of the non-parametric Kruskal-Wallis tests compared to parametric ANOVA. The more conservative Holm-Bonferroni method (Holm 1979) was used for the tests of proportions, because the power of this test was not an issue.

Results

Tidal Channel Surveys

Surveys covered 11.9 km of channels in the tidal herbaceous vegetation zone and 13.1 km in the tidal shrub zone of the South Fork delta. Surveyed tidal channels were 1.4±0.3 m (standard deviation) deep, while beaver dams averaged 41± 21 cm tall. Consequently, beaver dams were flooded by a meter or more at high tide; pools were formed by dams only at low tide. Channels without dams typically had water less than 10 cm deep at low tide. No beaver dams or lodges were found in tidal herbaceous zone channels, but 125 beaver dams and 14 lodges were found in 8.6 km (66%) of channels surveyed in the tidal shrub zone (Fig. 1). Of the 125 dams, 117 were functional with a mean water surface head of 19 cm (range 7 to 50 cm) while 8 were in disrepair with no head. Dams averaged 1.9 m wide (range 0.3 to 6.0 m) and all were made of sticks and mud, sometimes incorporating bank

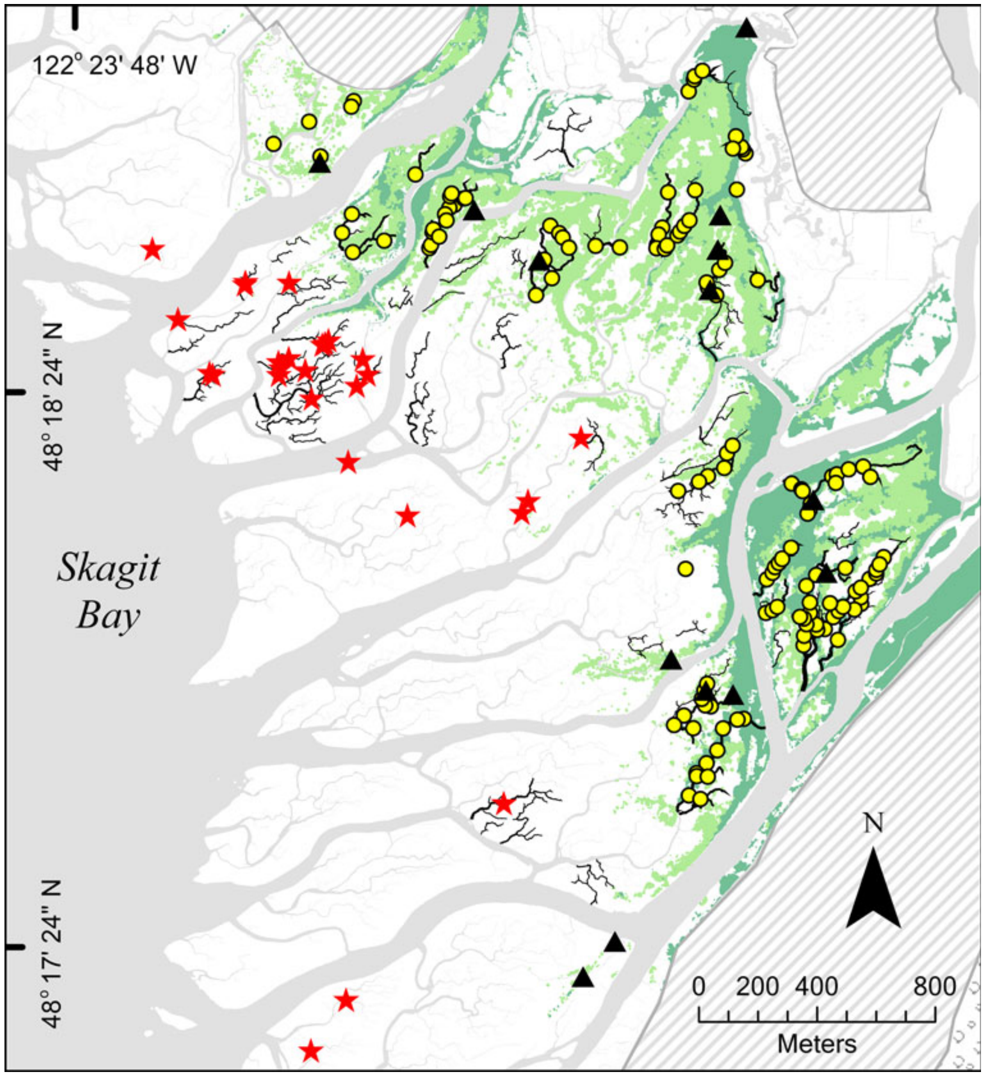

Fig. 1 Location of intertidal beaver dams (*yellow circles*) and lodges (*black triangles*) in the South Fork Skagit River delta. White areas are herbaceous tidal marsh; light green areas are *Myrica gale* thickets; dark green are mixed species tidal shrub habitat; hatched areas are farmland. Surveyed tidal channels are in black; red stars are Great Blue Heron observations

slumps (Fig. 2). No dams were made exclusively of mud nor of mud mixed with herbaceous vegetation. The preponderance of woody material in the dams indicates dependence on tidal shrub vegetation for construction material. Dam density was 8.9 km^{-1} of shrub zone tidal channel. Lodge density was 10.2 km^{-2} of tidal shrub marsh, a conservative estimate because beaver lodges were usually located in dense, nearly impenetrable shrub thickets where lodges were well hidden. GBH or their tracks were observed on 28 occasions during channel surveys, exclusively in the tidal herbaceous vegetation zone.

Most low-tide pools were associated with beaver dams, bank slumps, logs, meander bends, tributary junctions, and channel outlets. Low-tide pools comprised 65.5% of channel length in tidal shrub marsh versus 16.4% in tidal herbaceous marsh. Beaver dam pools amounted to 47.7% of tidal shrub channel length, while 17.8% were pools formed by other means—similar to the 16.4% in tidal herbaceous channels. Thus, the difference in pool abundance between the two vegetation zones was due entirely to beaver dam pools. Beaver-dam pools were three times longer than other pools (mean=44.9 m vs. 14.2 m; Kruskal-Wallis test chi-square=67.5, df=1, $p<0.0001$; Fig. 3), indicating the greater size of beaver-dam pools accounted for most of the observed differences in low-tide pool abundance between vegetation zones.

Two-way ANOVAs testing the relation between marsh vegetation zone and pool type on pool depth had to omit beaver pools (found only in tidal shrub zone channels) and tributary junction pools (found only in tidal herbaceous zone channels). For the remaining pool types, mean pool depth was greater in tidal shrub zone channels than in tidal herbaceous zone channels (45.6 cm vs. 37.8 cm; $F_{1,221}=7.35$, $p<0.01$; Fig. 4), although there was no relationship between maximum pool depth and vegetation zone ($F_{1,167}=3.65$, NS). In comparison, two-sample t-tests indicated beaver dam pools had greater mean and maximum depths than other tidal shrub zone pools (60.8 cm vs. 45.5 cm mean depth; $t=5.05$, df=144, $p<0.0001$; 65.5 cm versus 56.2 cm maximum depth; $t=2.03$, df=49, $p<0.05$). Mean and maximum pool depths were correlated ($R=0.82$; Fig. 5).

Fig. 2 Two examples of beaver dams at low tide. The author's daughter in the foreground of the top frame is 1.10 m tall. At high tide the marsh surface would be flooded by 30 cm and the dam (and girl) would be submerged. Similar tidal flooding occurs over the dam of the bottom frame

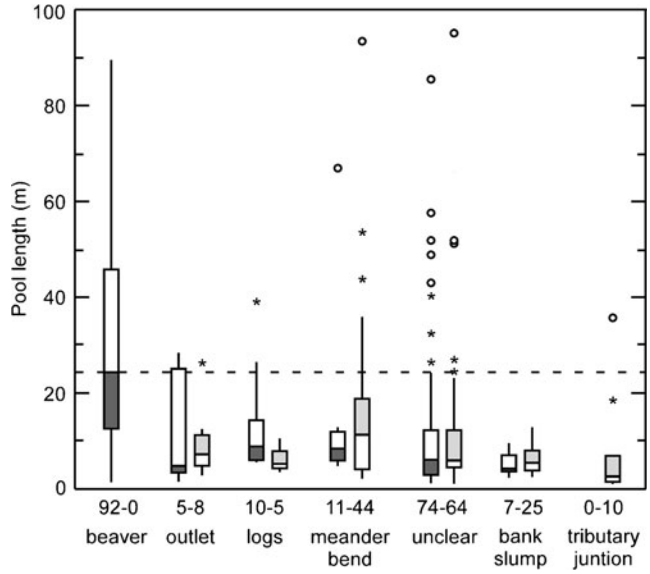

Fig. 3 Box-and-whiskers data distribution plots of low tide channel pool lengths relative to formative agent. Top box edge=third quartile, bottom box edge=first quartile, box split=median, vertical bars=one standard deviation (SD), *=points within two SD, o=outliers. Boxes whose lower sections are darkly shaded refer to tidal shrub zone channels; boxes whose upper sections are lightly shaded refer to tidal herbaceous zone channels. The dashed horizontal reference line marks the median length of pools associated with beaver dams. Sample sizes appear below each box plot

Fish Surveys

Seven fish species were caught during low-tide channel sampling (Table 2). The most frequent was three-spine stickleback (*Gasterosteus aculeatus*), in 76% of samples. Juvenile Chinook salmon (35–65 mm fork length) was the next most common, in 29% of samples. Sticklebacks were also the most abundant fish, occurring in densities (m^{-3}) two orders of magnitude greater than any other species. Sticklebacks, Chinook, prickly sculpin (*Cottus asper*), and juvenile (transforming) river lamprey (*Lampetra ayresi*) showed similar occurrence patterns. For each species, occurrence frequency was greater in low-tide pools than in shallows ($p<0.001$ for all species); vegetation zone had no influence except for sticklebacks, which were more common in tidal shrub shallows than in herbaceous shallows ($p<0.001$). Chum salmon (*O. keta*) occurred mostly in tidal herbaceous pools ($p<0.001$), with no differences among other habitats. Other species were encountered too rarely to exhibit distribution patterns.

Stickleback, Chinook, and prickly sculpin had 2.2-, 3.2-, and 7.5 times higher densities (m^{-3}), respectively, in low-tide pools than in shallows ($p<0.0001$ for each). Density differences standardized by surface area, as is more customary, were 5.1-, 8.0-, and 64.4 times higher, respectively, in pools versus shallows. Similarly, juvenile lamprey were only encountered in low-tide pools. Depletion seining was not conducive to estimating lamprey abundance; juvenile lamprey bury themselves in sediment so catches were small in the initial seining but increased as subsequent seinings disturbed the sediments. No volumetric density differences between pools or shallows were detected for the other fish species.

Vegetation zone only affected volumetric densities of sticklebacks (higher in the tidal shrub zone, $p<0.02$) and staghorn sculpin (*Leptocottus armatus*) (higher in the tidal herbaceous zone, $p<0.05$). Stickleback volumetric densities were 11.4 times higher in tidal shrub shallows than in tidal herbaceous shallows, but only 1.2 times higher in tidal shrub pools as herbaceous pools. Likewise, the pool/shallows density ratio was 12 in tidal herbaceous zone vegetation, but only 1.3 in tidal shrub zone vegetation. Chum were uniquely more abundant in low-tide herbaceous pools than in any other habitat ($p<0.03$).

Patterns in fish length could only be investigated for the most abundant and frequently occurring species. Chinook lengths were similar for pools in both vegetation zones (Fig. 6), as were growth rates inferred from the slopes of the length vs. time regressions (0.125 mm/day). Chinook in shallows were too rare to analyze. In contrast, sticklebacks were 8%

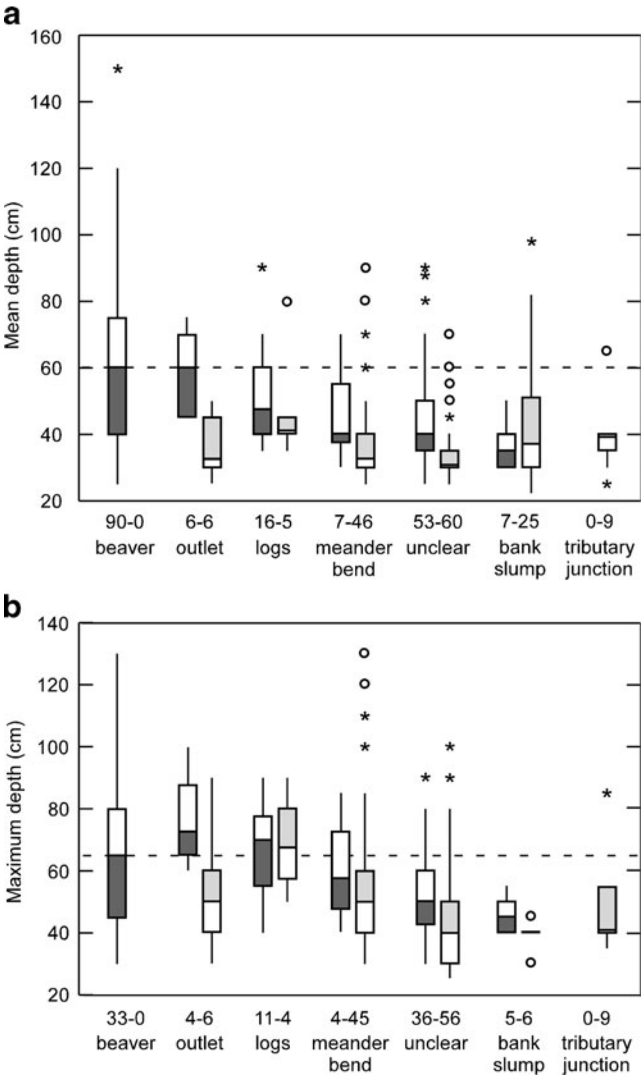

Fig. 4 Box-and-whiskers data distribution plots of low tide channel pool mean (**a**) and maximum (**b**) depths relative to formative agent. Top box edge=third quartile, bottom box edge=first quartile, box split=median, vertical bars=one standard deviation (SD), *=points within two SD, o=outliers. Boxes whose lower sections are darkly shaded refer to tidal shrub zone channels; boxes whose upper sections are lightly shaded refer to tidal herbaceous zone channels. The dashed horizontal reference line marks the median depth values of pools associated with beaver dams. Sample sizes appear below each box plot

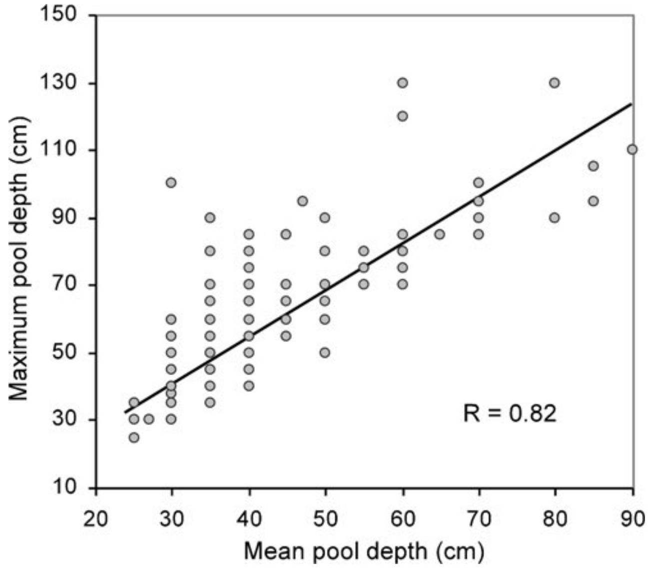

Fig. 5 Correlation between mean and maximum depth of low tide pools. Depths were measured to the nearest 5 cm

longer in tidal herbaceous pools than in tidal shrub pools from early April to late June (paired by date sampled, t=3.58, df=17, p<0.002) even though growth rates were similar in both vegetation zones. Stickleback length did not differ between pools and shallows (paired t=1.37, df=10, p<0.25). Stickleback were caught in herbaceous and shrub zone shallows on the same date only three times, too few for statistical testing.

The effects of beaver dams on potential fish production should also be considered from a landscape-scale perspective. Beaver dams quadrupled pool density (per unit length) in the tidal shrub zone compared to the tidal herbaceous zone; pools increased low-tide juvenile Chinook density 12.2-fold (per unit length) relative to shallows. Accounting for the total contribution of pools and shallows to juvenile Chinook abundance at low tide, beaver pools nearly tripled total low tide channel capacity for juvenile Chinook salmon in the tidal shrub marsh relative to tidal herbaceous marsh without beaver pools ([65.5% pool * 12.2+34.5% shallows]:[17.8% pool * 12.2 +82.2% shallows]=2.8:1). Similarly, stickleback density was 6.5-fold higher in low tide pools than shallows, so beaver pools increased total low-tide shrub zone channel capacity for sticklebacks by 2.3-fold relative to the herbaceous zone.

Discussion

Beaver dam density in the Skagit tidal shrub zone (8.9 km^{-1}) was comparable to densities in non-tidal North American rivers (Leidholt-Bruner et al. 1992; Suzuki and McComb 1998; Pollock et al. 2003; MacCracken and Lebovitz 2005) after accounting for sampling effort (surveyed channel length); high dam densities scaled with low sampling effort in the reviewed literature (Fig. 7), suggesting sampling bias is common. Tidal shrub zone lodge density, 10.2 km^{-2}, contrasts with colony densities in non-tidal North American rivers ranging from 0.2–0.9 km^{-2} (Pollock et al. 2003). A beaver colony can construct several lodges, so direct comparison of colony and lodge densities is inappropriate. However, Skagit delta beaver would have to build at least 11 lodges per colony to have a colony density comparable to those of non-tidal rivers. This degree of redundant lodging seems an unlikely expenditure of effort; a simpler alternative is that beaver density in the Skagit delta is much greater than in non-tidal

Table 2 Frequency of occurrence (%, upper cell values) and density (m^{-3}, lower cell values in italics) of fish sampled in tidal channel segments at low tide, followed by test statistics (upper cell values: Chi-square for frequency test, *H* for two-factor Kruskal-Wallis density test) and p-values (lower cell values in italics)

Species	All sites	Shrub pools	Shrub shallows	Herbaceous pools	Herbaceous shallows	Frequency test	Kruskal-Wallis ANOVA		
							Herbaceous vs. shrub	Pools vs. shallows	Interaction
Three-spine Stickleback	76.4	100.0	72.2	100.0	33.3	30.116	5.454	17.691	0.843
Gasterosteus aculeatus	*38.1*	*57.0*	*44.3*	*47.0*	*3.9*	*< 0.0001*	*< 0.02*	*< 0.0001*	*NS*
Chinook Salmon	29.2	55.6	5.6	50.0	5.6	19.550	0.016	16.776	0.002
Oncorhynchus tshawytscha	*0.27*	*0.36*	*0.20*	*0.48*	*0.06*	*< 0.0002*	*NS*	*< 0.0001*	*NS*
Chum Salmon	18.1	11.1	5.6	50.0	5.6	16.789	5.370	7.492	4.988
O. keta	*0.23*	*0.03*	*0.03*	*0.83*	*0.06*	*< 0.001*	*< 0.02*	*< 0.006*	< 0.03
Coho Salmon	8.4	11.1	5.6	16.7	0	3.630	0.000	2.744	0.797
O. kisutch	*0.19*	*0.07*	*0.07*	*0.63*	*0*	*NS*	*NS*	*NS*	*NS*
Prickly Sculpin	27.8	61.1	5.6	44.4	0	23.817	0.412	20.383	0.000
Cottus asper	*0.44*	*0.37*	*0.20*	*1.17*	*0*	*< 0.0001*	*NS*	*<< 0.0001*	*NS*
Staghorn Sculpin	18.1	11.2	5.6	38.9	16.7	7.777	4.839	2.234	0.949
Leptocottus armatus	*0.526*	*0.07*	*0.08*	*1.21*	*0.74*	*NS*	*< 0.03*	*NS*	*NS*
Starry Flounder	9.8	11.2	11.2	11.2	5.6	0.472	0.108	0.094	0.173
Platichthys stellatus	*0.248*	*0.02*	*0.29*	*0.30*	*0.38*	*NS*	*NS*	*NS*	*NS*
River lamprey[a]	12.5	27.8	0	22.2	0	10.437	–	–	–
Lampetra ayresi	–	–	–	–	–	*< 0.02*			

[a] Densities were not estimated for river lamprey. Juvenile or transforming lamprey bury themselves in sediments, which each sweep of the seine increasingly disturbs, leading to increasing lamprey catches rather than depletion

rivers. Beaver colonies in the Mackenzie Delta (Northwest Territories, Canada) reach a density of 2.6 km^{-2} (Aleksiuk 1968); to match this colony density Skagit Delta beaver would have to build four lodges per colony, which suggests colony density is higher in the temperate Skagit Delta than the arctic Mackenzie Delta, but both deltas appear to support higher colony densities than non-deltaic river systems. Perhaps large river deltas with their extensive floodplain wetlands, distributary networks, and tidal channels provide better beaver habitat than comparatively 1-dimensional fluvial systems.

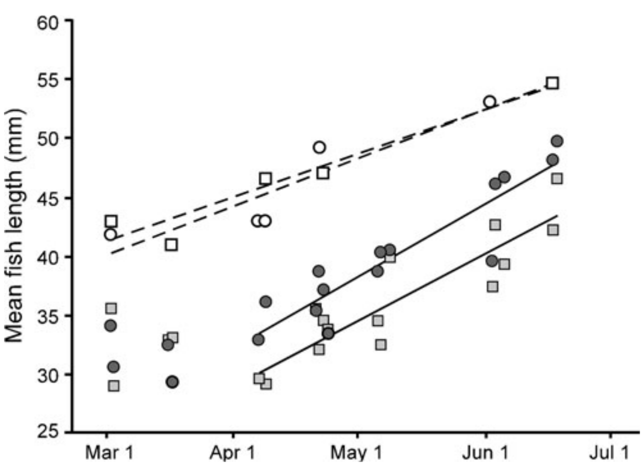

Fig. 6 Mean length of Chinook salmon (*white symbols*) and three-spine stickleback (*gray symbols*) sampled in low-tide pools in tidal shrub (*squares*) and tidal herbaceous (*circles*) vegetation zones. Regression equations: Chinook in tidal herbaceous zone pools, y=0.13x–5183 (R^2=0.82); in tidal shrub zone pools, y=0.12x–4735 (R^2=0.93); sticklebacks in tidal herbaceous zone pools, y=0.20x–7774 (R^2=0.85); in tidal shrub zone pools, y=0.18x–7173 (R^2=0.81)

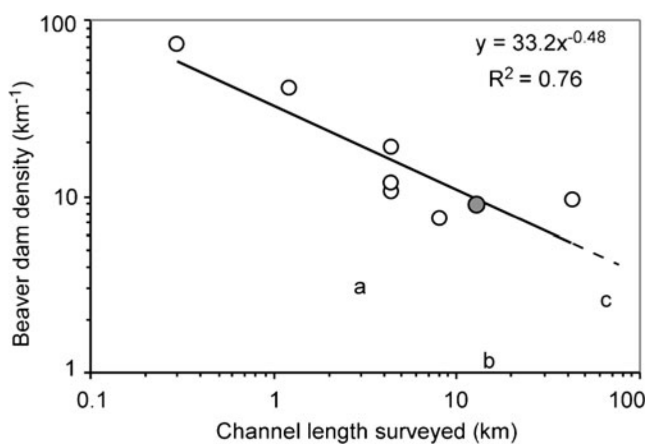

Fig. 7 Beaver dam density versus survey effort. The regression relationship is derived from literature reviewed by Pollock et al. (2003) for riverine systems in North America (*open circles*). The dam density for tidal shrub zone channels in the Skagit delta (*dark circle*) is comparable to the regression, as is point *c* for western Oregon rivers (Suzuki and McComb 1998), but not points *a* and *b* (Leidholt-Bruner et al. 1992; MacCracken and Lebovitz 2005) for rivers in western Washington and Oregon, respectively

In non-tidal rivers, beavers build dams to flood low-lying lands and convert them to open water and marsh (Naiman et al. 1988). Open water areas facilitate safe movement for beaver while the marsh provides herbaceous summer forage and shrubby winter browse. In the Skagit Delta, tidal marshes are extensive and provide abundant food for beaver, including shrubs, sedges and forbs. Thus, the role of beaver dams in Skagit tidal channels is not to produce marsh habitat, but to prevent tidal channels from draining completely at low tide—to allow beaver to swim freely in the partially flooded channels and to keep lodge entrances under water at all times. At high tide dams are typically flooded by a meter or more, making them unnecessary for beaver mobility. Large, deep tidal channels that remain partially flooded at low tide are always accessible to beaver and thus do not have any dams. Because beaver dams only occur in small tidal channels in the Skagit Delta, the dams are generally small compared to those found in non-tidal rivers.

In non-tidal North American rivers, beaver ponds provide habitat for more than 80 fish species (Pollock et al. 2003), including juvenile salmonids (Leidholt-Bruner et al. 1992; Pollock et al. 2004). Beaver pond attributes favoring fish production include high vegetation cover, high invertebrate prey production, and slow current velocities which allow reduced energy expenditures by foraging fish (Collen and Gibson 2001; Pollock et al. 2003). High fish densities and occurrence in low-tide beaver pools suggest tidal beaver dams likewise provide valuable fish habitat, particularly for juvenile Chinook salmon, sticklebacks, prickly sculpins, and juvenile lamprey. Juvenile coho and chum were not dependent on beaver pools. For coho, this may be the result of low statistical power resulting from their relatively infrequent occurrence in catches; coho were in 8% of catches compared to 29% for Chinook. Chum were found almost exclusively in herbaceous zone pools perhaps because they are less salt-sensitive than Chinook and transition more quickly through oligohaline habitats (Clarke and Hirano 1995).

Several complementary hypotheses for how low-tide beaver pools may benefit fish include: (1) providing refuge from predation by GBH—and potentially other predators found typically in larger channels, such as common merganser (*Mergus merganser*) and belted kingfisher (*Megaceryle alcyon*); (2) providing habitat for invertebrate prey; and (3) allowing fish longer residence time in the delta. Regarding the first point, beaver pools are generally too deep for GBH to wade, while shrub cover over or along tidal shrub zone channels further inhibits GBH access. Stickleback were more abundant and more frequent in tidal shrub zone shallows than tidal herbaceous zone shallows. A similar pattern was observed for juvenile Chinook salmon and prickly sculpin, but their low occurrence frequency in channel shallows impacted statistical power for this comparison. Nevertheless, the differences observed for sticklebacks may reflect lower predation risk for fish in tidal shrub shallows compared to tidal herbaceous shallows due to the cover afforded by shrub thickets. Predation risk is likely greater in distributaries and larger tidal channels at low tide; wide channels are easily accessed by GBH which feed along the margins, while common merganser, belted kingfisher, and large fish feed in deeper waters (personal observations). Beaver dams did not appear to provide significant cover to small fish; beaver food caches, which might provide cover, were not observed. Regarding the second point, seines in beaver pools were consistently filled with detritus and muck, while seines in tidal herbaceous zone pools and shallows were consistently free of debris. Greater detritus abundance in beaver pools should lead to greater abundance of detritivorous fish prey. Finally, low-tide pools allow fish to remain in small tidal channels at low tide rather than being forced to emigrate to river distributaries where they risk river and tidal currents sweeping them prematurely downstream and into the bay. Premature downstream displacement would subject juvenile Chinook to salinity stress and to likely greater predation risk. The risk of premature displacement, and conversely the benefit of beaver pools, likely increases during floods and snow-melt freshets.

Implications for Conservation and Restoration

Since Euro-American settlement in the Skagit Delta, tidal herbaceous marshes have suffered anthropogenic losses of approximately 3200 ha, 65% of their historical extent, but tidal shrub habitat loss has been approximately 3600 ha, 95% of their historical extent (Hood 2007). In other large Salish Sea river deltas, historical tidal shrub habitat has mostly disappeared, while remnant tidal herbaceous marsh still exists (North and Teversham 1984; Collins et al. 2003). These habitat loss patterns are similar to those of other temperate zone deltas, where widespread conversion of historical tidal

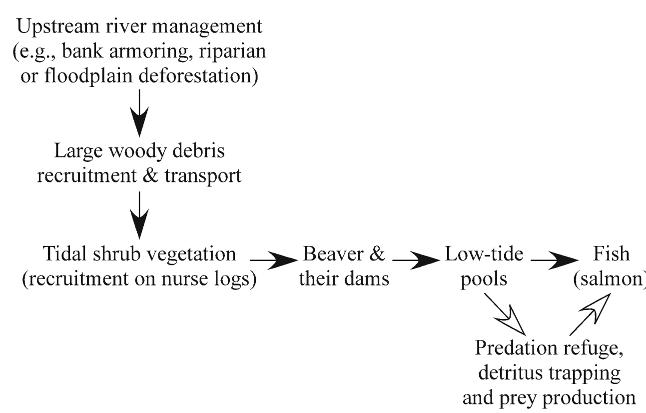

Fig. 8 Diagram of an influence chain illustrating linkage between upstream river management and downstream estuarine ecology with regard to tidal beaver dams and their effects on small fish. Open arrows represent hypothesized linkages

shrub and tidal forest habitat to agricultural, industrial, and urban use occurred much earlier than in the Pacific Northwest (Riera-Mora and Esteban-Amat 1994; Bell and Neumann 1997; Berendsen 1998; Cencini 1998; Ojala and Louekari 2002). Intact historical deltas in North America and Europe potentially supported large populations of intertidal beaver prior to extensive human habitat conversion and the near extinction of beaver by commercial trapping.

Continued persistence of tidal shrub marsh is threatened by global warming which may accelerate sea-level rise beyond the capacity of tidal wetlands to accrete sediment (Kirwan and Murray 2008; Day et al. 2011) while dikes will prevent landward migration of vegetation zones. Thus, the remaining tidal shrub zone could be replaced by tidal herbaceous vegetation as sea level rises, with consequent impacts to beaver, juvenile salmon and other fish. Global warming has already reduced snow pack and caused glacial retreat in the Skagit basin (Pelto 2006; Casola et al. 2009). Continued loss of mountain snow and ice will reduce summer river flows and increase Skagit marsh salinity (Cuo et al. 2009; Mantua et al. 2010), impacting the salt-sensitive tidal shrub zone more than the herbaceous marsh.

Estuarine habitat restoration in Puget Sound has focused almost entirely on restoring tidal herbaceous marshes, while mostly ignoring other historical tidal and delta floodplain habitats. This focus is due in part to poor understanding and underappreciation of ecological relationships within and between diverse historical habitats along the estuarine continuum. As illustrated here, beaver dams are strongly associated with currently rare tidal shrub habitat to the apparent benefit of juvenile Chinook salmon and other small fish. A greater focus on restoration of tidal shrub habitat would not only benefit beaver, it would likely benefit recovery of threatened Chinook salmon as well. However, most shrubs and trees in the tidal shrub marsh are associated with large nurse logs that raise them above mean higher high water, and the nurse logs originate from upstream riparian and floodplain forests (Hood 2007). Consequently, long-term sustainability of tidal shrub marsh and its ecological functions is dependent not only on local-scale marsh conservation, but also on landscape-scale riparian zone management that allows large woody debris recruitment from unarmored riverbanks and adjacent floodplains by freely migrating river channels (Fig. 8). The perhaps surprising abundance of beaver in Skagit Delta tidal shrub marsh suggests greater attention is needed on restoring and protecting the continuum of habitats along the estuarine-riverine gradient in delta landscapes.

Acknowledgements Thanks to Pete Kairis and Jeff Par for help sampling fish, to Eric Beamer for advice on depletion seining. Supported by Environmental Protection Agency Science to Achieve Results (STAR) grant # RD-83301401.

References

Aleksiuk M (1968) Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759–762

Anderson CB, Pastur GM, Lencinas MV, Wallem PK, Moorman MC, Rosemond AD (2009) Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. Mammal Review 39:33–52

Bell M, Neumann H (1997) Prehistoric intertidal archaeology and environments in the Severn Estuary, Wales. World Archaeology 29:95–113

Benjamini Y, Hochberg Y (1995) Controlling false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society, Series B 57:289–300

Berendsen HJA (1998) Birds-eye view of the Rhine-Meuse Delta (The Netherlands). Journal of Coastal Research 14:740–752

Casola JH, Cuo L, Livneh B, Lettenmaier DP, Stoelinga M, Mote PW, Wallace JM (2009) Assessing the impacts of global warming on snowpack in the Washington Cascades. Journal of Climate 22:2758–2772

Cencini C (1998) Physical processes and human activities in the evolution of the Po Delta, Italy. Journal of Coastal Research 14:774–793

Clarke WC, Hirano T (1995) Osmoregulation. In: Groot C, Margolis L, Clarke WC (eds) Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver, pp 319–377

Collen P, Gibson RJ (2001) The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. Reviews in Fish Biology and Fisheries 10:439–461

Collins BD, Montgomery DR, Sheikh AJ (2003) Reconstructing the historical riverine landscape of the Puget Lowland. In: Montgomery DR, Bolton S, Booth DB, Wall L (eds) Restoration of Puget Sound Rivers. University of Washington Press, Seattle, pp 79–128

Cuo L, Lettenmaier DP, Alberti M, Richey JE (2009) Effects of a century of land cover and climate change on the hydrology of Puget Sound basin. Hydrological Processes 23:907–933

Day J, Ibáñez C, Scarton F, Pont D, Hensel P, Day J, Lane R (2011) Sustainability of Mediterranean deltaic and lagoon wetlands with sea-level rise: The importance of river input. Estuaries and Coasts 34:483–493

Hood WG (2007) Large woody debris influences vegetation zonation in an oligohaline tidal marsh. Estuaries and Coasts 30:441–450

Holm S (1979) A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70

Jenkins SH, Busher PE (1979) Castor canadensis. Mammalian Species 120:1–8

Kirwan ML, Murray AB (2008) Ecological and morphological response of brackish tidal marshland to the next century of sea level rise: Westham Island, British Columbia. Global and Planetary Change 60:471–486

Leidholt-Bruner K, Hibbs DE, McComb WC (1992) Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. Northwest Science 66:218–223

MacCracken JG, Lebovitz AD (2005) Selection of in-stream wood structures by beaver in the Bear River, Southwest Washington. Northwestern Naturalist 86:49–58

Mantua N, Tohver I, Hamlet A (2010) Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climate Change 102:187–223

Naiman RJ, Johnston CA, Kelley JC (1988) Alteration of North American streams by beaver. Bioscience 38:753–762
Nolet BA, Baveco JM (1996) Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. Biological Conservation 75:125–137
North MEA, Teversham JM (1984) The vegetation of the floodplains of the lower Fraser, Serpentine and Nicomekl Rivers, 1859 to 1890. Syesis 17:47–66
Ojala E, Louekari S (2002) The merging of human activity and natural change: temporal and spatial scales of ecological change in the Kokemäenjoki river delta, SW Finland. Landscape and Urban Planning 61:83–98
Pasternack GB, Hilgartner WB, Brush GS (2000) Biogeomorphology of an upper Chesapeake Bay river-mouth tidal freshwater marsh. Wetlands 20:520–537
Pelto MS (2006) The current disequilibrium of North Cascade glaciers. Hydrological Processes 20:769–779
Pollock MM, Pess G, Beechie TJ, Montgomery DR (2004) The importance of beaver ponds to coho salmon production in the Stillaguamish River Basin, Washington, USA. North American Journal of Fisheries Management 24:749–760
Pollock MM, Heim M, Werner D (2003) Hydrologic and geomorphic effects of beaver dams and their influence on fishes. American Fisheries Society Symposium 37:213–233
Riera-Mora S, Esteban-Amat A (1994) Vegetation history and human activity during the last 6000 years on the central Catalan coast (northeastern Iberian Peninsula). Vegetation History and Archaeobotony 3:7–23
Rosell F, Bozsér O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35:248–276
Rosell F, Nolet BA (1997) Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). Journal of Chemical Ecology 23:673–689
Suzuki N, McComb WC (1998) Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. Northwest Science 72:102–110
Yang Z, Khangaonkar T (2009) Modeling tidal circulation and stratification in Skagit River estuary using an unstructured grid ocean model. Ocean Modelling 28:34–49
Zar JH (1984) Biostatistical analysis. Prentice Hall, Englewood Cliffs
Zippin C (1958) The removal method of population estimation. Journal of Wildlife Management 22:82–89