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**Landscape Allometry of Oligohaline
Tidal Channels of the Lower Chehalis River, Washington**

William Gregory Hood

**A dissertation submitted in partial fulfillment of the
requirements for the degree of**

Doctor of Philosophy

University of Washington

2000

Program Authorized to Offer Degree: School of Fisheries

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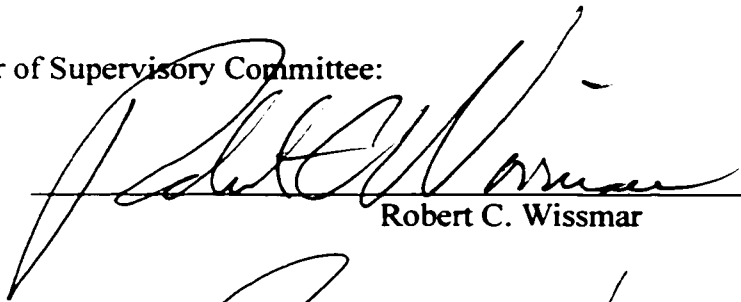
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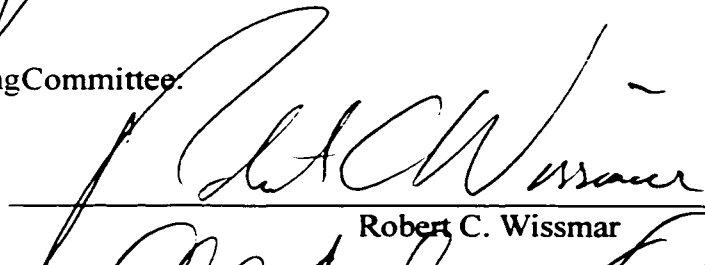
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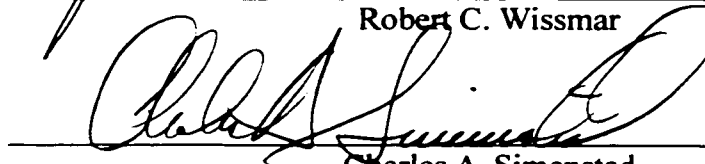


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Abstract

Landscape Allometry of Oligohaline
Tidal Channels of the Lower Chehalis River, Washington

William Gregory Hood

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The fractal geometry of landforms implies that landscapes can be viewed as systems of related rates of change between various geomorphic features of the landscape. Consequently, biological patterns and processes associated with landscape features may also be described by related rates of change, i.e., exhibit landscape-scale allometry. The goals of this dissertation were [1] to examine this hypothesis in a system of oligohaline tidal channels (sloughs) in the Chehalis River (Washington) delta; and [2] to suggest practical applications of landscape allometry in the management and restoration of estuarine sloughs to benefit juvenile Pacific salmon (*Oncorhynchus* spp.).

The Chehalis sloughs exhibited allometric form with respect to length, perimeter, surface area, and outlet width and depth. Ebb surface flow velocity was correlated with slough size, as was exit time and export of tiny drogues used to model floating allochthonous detritus. Consequently, the percent organic matter in slough sediments depended on slough size and channel width, as did surface deposit feeder biomass.

In contrast, a slough excavated to mitigate port improvements did not resemble the allometric forms of natural sloughs. This resulted in high retention of allochthonous inputs, sediment accretion, and headcutting. Additionally, intertidal sedge habitat abundance and distribution in large sloughs did not conform to the allometric patterns seen in smaller sloughs, suggesting that sedge habitat in large sloughs has been destroyed by past log storage and transportation.

A model relating slough size to tidal export of riparian inputs, showed close agreement between model predictions and observed net export of spruce needles. Differences between observed and modeled aphid and chironomid export could be explained by fish predation. The model indicated that small sloughs export a greater proportion of riparian input than do large sloughs. Thus, landscape allometry supplements other theories of landform influences on tidal export.

Landscape allometry has several practical implications: [1] natural allometric templates suggest restoration and mitigation design criteria, realistic goals given project constraints, and standards for measuring project success; [2] slough size becomes a covariate, allowing replication of reference sites; [3] historical disturbances can be inferred; and [4] predicted fish distributions in sloughs suggest restoration priorities.

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PREFACE

The research presented in this dissertation had several motivations. I was primarily interested in developing a theoretical framework for studying landscape ecology, which I call landscape allometry. This conceptual model of landscape ecology assumes that abiotic factors are important in determining ecological patterns and processes. It further assumes that landscape form is one of these important abiotic factors. Perhaps the most easily modeled and generalizable aspect of landscape form is geometry. Fractal geometry has been used extensively to describe landscape geometry (e.g. Church & Mark 1980, Mandelbrot 1983, Rodriguez-Iturbe & Rinaldo 1997, see also Woldenberg 1966, Bull 1975). The success of the fractal model implies that landscape form can be viewed as a system of related rates, e.g., when the relative rate of change of one part of a system (y) is proportional to the relative rate of change of another part of the system (x), or of the whole system then

$$\frac{dy}{y} \frac{1}{dt} = b \frac{dx}{x} \frac{1}{dt} \quad (1)$$

where b is a proportionality constant. On multiplying by dt and integrating, one obtains the log-linear function, $\log(y) = \log(a) + b \log(x)$, which is equivalent to the power function, $y = ax^b$ (Woldenberg 1966).

Rather than focus on fractal dimension, per se, I have chosen to focus on the related rates of change between various geomorphic features of the landscape, and thus, correlated rates of change between various biological patterns and processes associated with those landscape features. Therefore, I have chosen to use the terminology of allometry which I feel better reflects this focus, even though allometry and fractal geometry are the same phenomenon (Mandelbrot 1983, pp. 156 & 350).

There were also practical motivations which further narrowed the focus of the research. My research assistanceship brought me to a system of oligohaline tidal channels (sloughs) in the floodplain of the lower Chehalis River, where the mandate was to compare a natural slough to one excavated by the US Army Corps of Engineers as mitigation for dredging impacts to salmon habitat. There is considerable regional interest in the value of estuarine sloughs as habitat for juvenile Pacific salmon (*Oncorhynchus* spp.) during their seaward migration. Estuarine sloughs are likely zones of physiological transition for out-migrating juveniles, and they may provide juvenile salmon with temporary refuge from predation until they can outgrow their size-related vulnerability to predators (Iwata & Komatsu 1984, Levings et al. 1989). Furthermore, estuarine wetlands are thought to be areas of high productivity and therefore areas which may provide an abundance of prey to juvenile salmon (Reimers 1973, Levy & Northcote 1979, Healey 1982, Simenstad & Wissmar 1983). In many Pacific Northwest slough systems, insect flotsam is the dominant component of the

diets of juvenile salmon (Congleton 1978, Northcote et al. 1979, Levy & Northcote 1982, Tschaplinski 1988, Miller & Simenstd 1997, personal observations). “Insect flotsam” denotes insects that are found floating at the water’s surface, which do not have any particular adaptations to existence at this surface, but instead are adapted to existence elsewhere (Cheng & Birch 1978). Consequently, my dissertation research focused on estuarine sloughs and insect flotsam.

The dissertation consists of four chapters in journal article form. The first chapter mainly provides evidence for allometric slough form and discusses the significance for habitat restoration. The second chapter demonstrates allometric correlations between slough form and ecosystem processes and pattern. The third chapter describes a model of tidal export, further illustrating ecological correlates of slough size, i.e., rates of input and export of insect flotsam and spruce needle detritus. The last chapter reviews and discusses literature that illustrate the possibility of applying landscape allometry to other systems.

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CHAPTER 1**Application of Landscape Allometry
to Restoration Ecology****INTRODUCTION**

Replication is problematic for a variety of ecosystem- or landscape-scale studies (Carpenter 1989, 1990, Eberhardt & Thomas 1991, Underwood 1994). One of the constraints on replication is the availability of suitable replicates, and one aspect of suitability concerns the size of the experimental unit. For example, large and small lakes or streams would not appear to be comparable due to the physical and biological consequences of lake or stream size. Thus, suitable replicates would be of relatively uniform size.

However, models of landscape geomorphology show that landforms are allometric, or fractal (Woldenberg 1966, Bull 1975, Church & Mark 1980, Mandelbrot 1983, Rodriguez-Iturbe & Rinaldo 1997). This suggests that landscape form can be viewed as a system of related rates of change between various geomorphic features of the landscape (Woldenberg 1966), and thus, one might expect correlated rates of change between various biological patterns and processes associated with those landscape features. Put another way, the boundaries of ecosystem compartments can be described by allometric models analogous to those used in organismal biology. Process models of material and energy fluxes

across these boundaries can be linked to the allometric description of landscape form to create an allometric description of ecosystem processes. In this way, landscape form and ecological pattern and process can be linked on a landscape scale, so that size becomes less of a constraint on replication of large-scale studies.

The objective of this chapter is to illustrate the concept of landscape allometry and its application in restoration ecology by comparing an artificial oligohaline tidal channel (slough) to a suite of nearby natural sloughs, which dissect the floodplain of the lower Chehalis River, Washington. The artificial slough was excavated by the US Army Corps of Engineers (USACE) in 1990 as mitigation for dredging impacts to salmon habitat. An allometric perspective on this comparison provides several insights into important issues for habitat restoration and mitigation, such as project design and assessment, inference of historical conditions, the influence of landscape form on ecosystem function, as well as replication in large-scale studies.

By providing a physiological transition zone, refuge from predation, and source of abundant prey, oligohaline sloughs and other estuarine habitats in the Pacific Northwest are thought to enhance the growth and survival of juvenile salmon (Levy & Northcote 1982, Simenstad et al. 1982, Wissmar & Simenstad 1988). The salmon species most reliant on estuarine wetlands are, in decreasing order of dependence, chinook, chum, and coho (*Oncorhynchus tshawytscha*, *O. keta*, and *O. kisutch*, respectively); pink and sockeye (*O. gorbuscha* & *O. nerka*) are less dependent on

estuaries (Healey 1982, Simenstad et al. 1982). The most important salmonid prey in the Chehalis river sloughs consist primarily of terrestrial and semi-terrestrial insects, especially aphids (Homoptera), adult chironomids (Diptera), and other adult diptera. From late April to early June, aphids comprise 25% to 90% of the diet of juvenile coho and from 25% to 70% for juvenile chinook, while adult chironomids may comprise 20% to 50% of the diets of coho and 15%-55% for juvenile chinook (Simenstad et al. 1992, 1993, 1997, Miller & Simenstad 1997). Less prominent prey items include mysid shrimp, copepods, and clam siphons.

Casual observations of various sloughs suggested that the density of allochthonous detritus floating on the slough surface waters (flotsam) might be greater in smaller sloughs than larger ones. A thin, whitish surface film, pocked with spruce needles and tiny insects was clearly visible in smaller sloughs but less apparent in large ones. This observation, led to the hypothesis that the availability to juvenile salmon of insect prey, such as aphids and adult chironomid flies, varies with slough size. This would be consistent with the hypothesis that slough perimeter and surface area are allometrically related. If allochthonous insect abundance is a function of perimeter, then insect density (prey availability) would be related to perimeter/area scaling. Additionally, if slough form is allometric, then the amount of intertidal sedge habitat within a slough may also vary with slough size. This is significant for foraging salmon, because the intertidal sedges host a large population of aphids.

The USACE has chosen a single reference slough to evaluate the similarity of their artificial slough to natural ones, with regard to salmon usage and salmon prey production. However, if biological patterns and processes vary with slough size, then the slough excavated by the USACE could be compared to a suite of estuarine sloughs rather than only a single, similarly-sized slough. Slough size could be treated as a covariate, allowing broader selection of replicate reference sloughs.

STUDY SITE DESCRIPTION

A detailed description of the USACE-excavated slough has been previously published (Miller & Simenstad 1997). In general, the estuarine sloughs of the lower Chehalis River are found in a relatively undisturbed floodplain that is bordered to the north by the southern flank of the Olympic mountains and to the south by the Willapa Hills (Fig. 1). The estuarine reach of the floodplain is generally 2.5 km wide and stretches along the river for 15 km from the downstream cities of Aberdeen and Cosmopolis to diked farmlands upstream (Fig. 2).

The floodplain consists of Sitka spruce- (*Picea sitchensis*)-dominated forested freshwater wetlands that are now rare in Washington and Oregon, but still abundant in coastal British Columbia and Alaska. Understory vegetation is dominated by

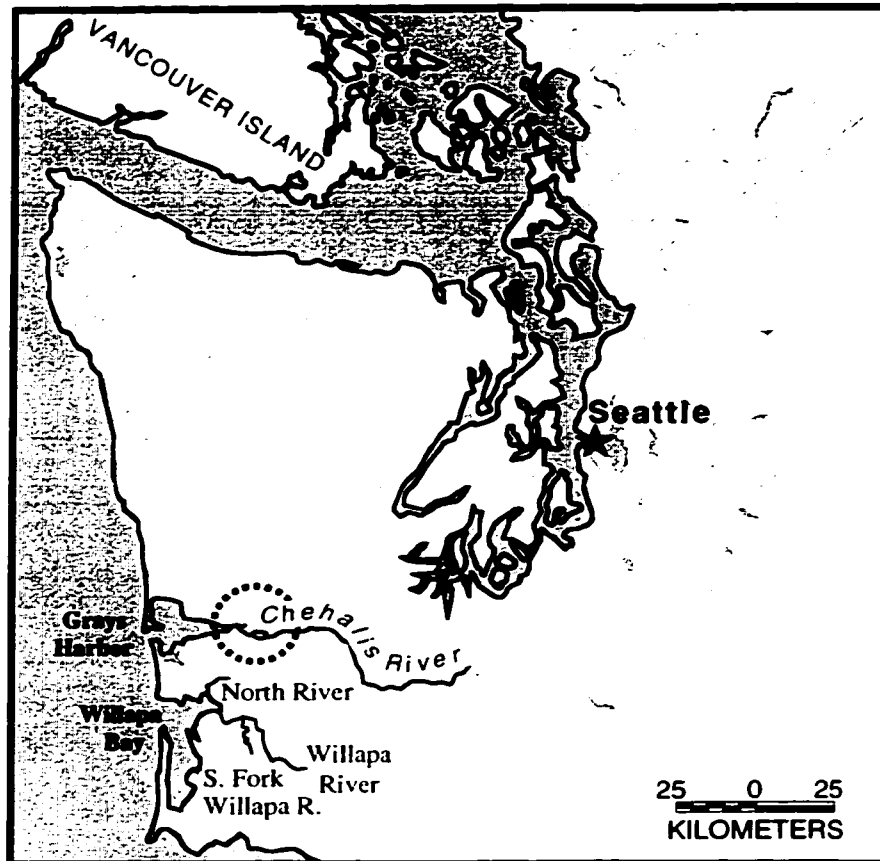


FIGURE 1. Study Site Location. Circled area is the general location of the estuarine sloughs of the lower Chehalis River.

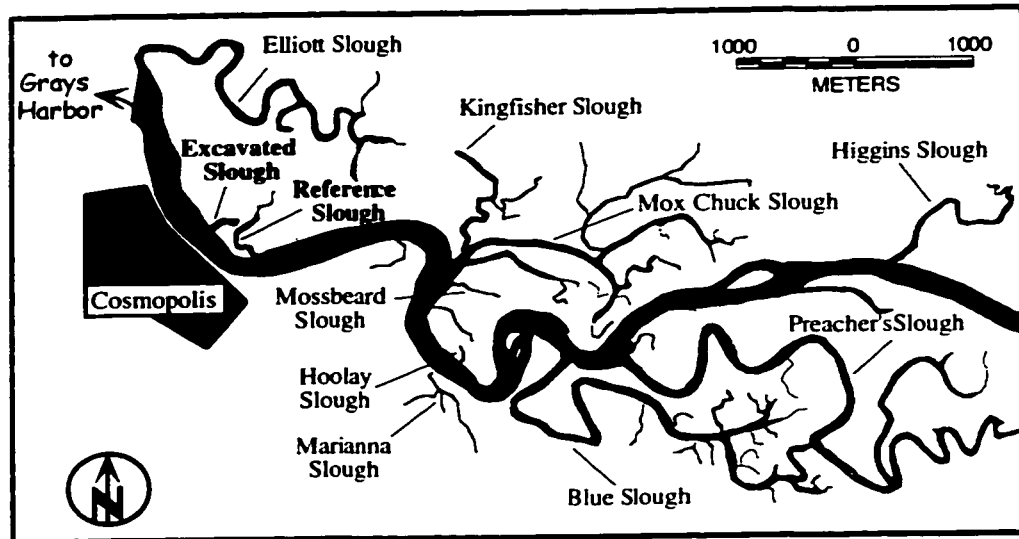


FIGURE 2. Sloughs of the lower Chehalis River

salmonberry (*Rubus spectabilis*), black twinberry (*Lonicera involucrata*), cascara (*Rhamnus purshiana*), red-osier dogwood (*Cornus stolonifera*), willows (*Salix* spp.), slough sedge (*Carex obnupta*) and skunk cabbage (*Lysichitum americanum*). The floodplain is dissected by sloughs containing two intertidal habitats, mudflats and marsh (Fig. 3). The marsh habitat is usually a monoculture of Lyngby's sedge (*C. lyngbyei*). Smaller sloughs are almost completely drained on low tides.

METHODS

Sloughs were chosen for study based on the following criteria: they had to [1] be located within the tidal and oligohaline reach of the Chehalis river floodplain; [2] be part of a set of sloughs that spanned as large a range of sizes as possible; [3] have similar riparian vegetation (i.e., bordered mostly by Sitka spruce); and [4] be accessible (e.g., not obstructed by fallen trees). These sloughs ranged from river-km 0 (Elliott Slough) to near river-km 13.7 (Higgins Slough) with most of them concentrated between river-kms 6 and 10 (Fig. 2).

Landform Allometry

To investigate the potential allometry of the Chehalis River sloughs, I used digitized aerial photos of 1:2400 scale (USACE-SD) to

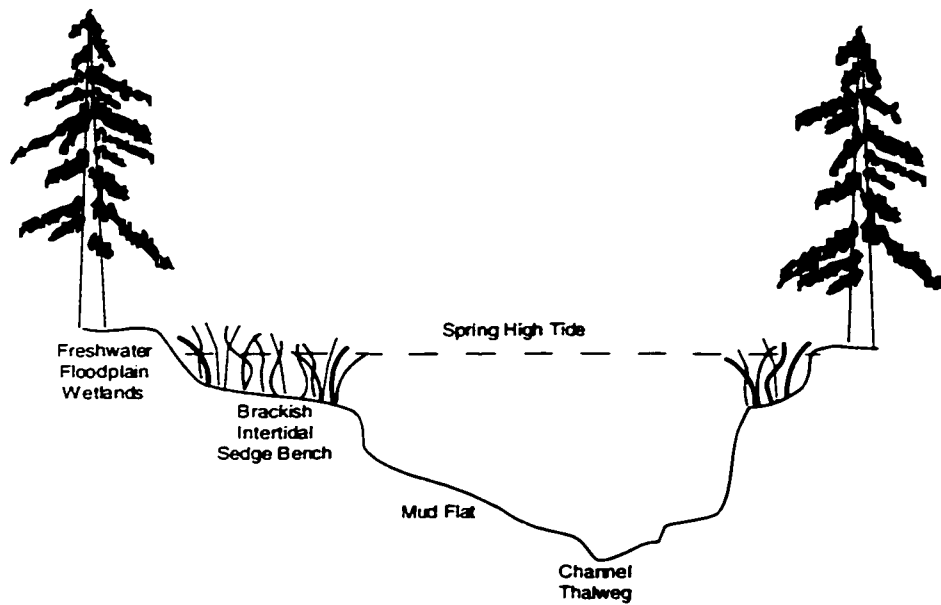


FIGURE 3. Schematic representation of a channel cross-section for a small slough, showing major habitat features. Not to scale.

measure slough length, width, perimeter, and surface area. Length was measured along the mainstem of a slough and did not include the lengths of tributaries. Width was measured at the slough outlet. Perimeter and surface area values included major tributaries to the sloughs. The perimeter was defined as the border between floodplain vegetation and intertidal vegetation or mud. Forest cover prevented delineation of the smallest sloughs and slough tributaries.

To determine whether slough geometry varied between slough systems, I used 1:20,000 scale aerial photos (US Department of Agriculture Soil Conservation Service, 1965) to make similar measurements for sloughs of the North River, Willapa River, and the South Fork of the Willapa River, which all empty into Willapa Bay (Figs. 1 & 4). These systems were chosen because each contained a sufficient number and range of sloughs to employ regression analysis. Additionally, limiting the geographic range to Willapa Bay would make detection of allometric differences between slough systems all the more remarkable given an expectation for low geomorphic variation due to presumably similar large-scale geological influences (e.g., tectonic and seismic history, sediment sources, tidal wave modification by the bay). More geographically diverse systems would presumably have greater variation than any found between the Willapa systems.

Slough depth was measured with a plumb line to the nearest 15 cm by taking the deepest of several soundings at slough outlets at a standardized tidal elevation (+2.0 m, determined from tide

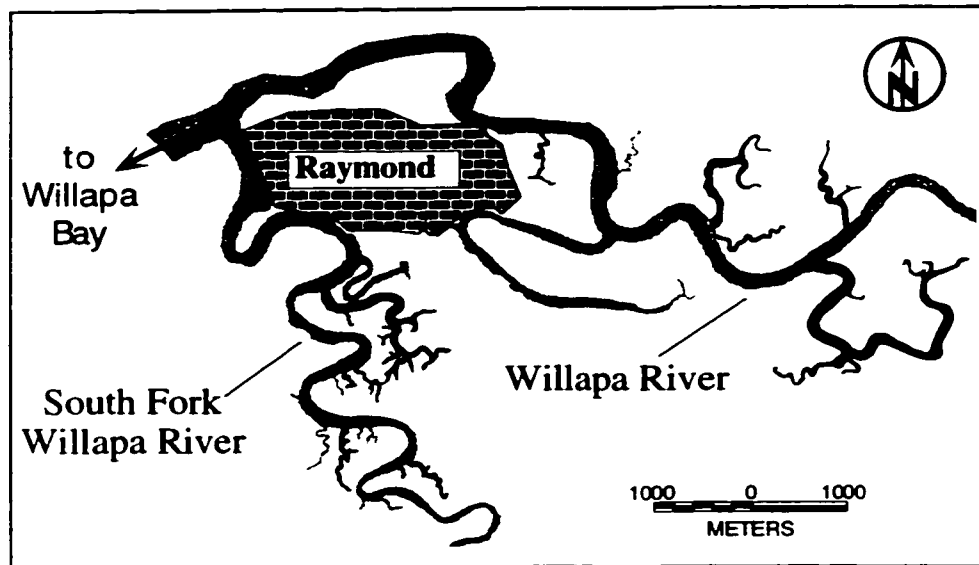
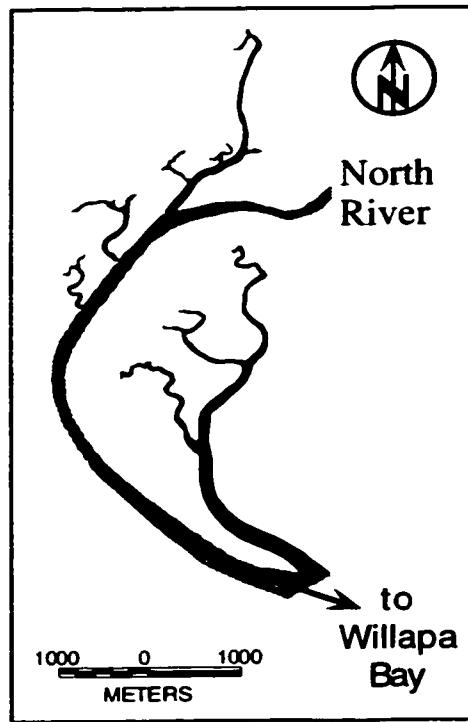


FIGURE 4. Sloughs of the North River, Willapa River, and South Fork Willapa River. Measured sloughs are shaded.

tables). Depth soundings for all sloughs were made within a 30 minute sampling window spanning high slack tide. The first of the series of sloughs measured was sounded again at the end of the sampling sequence to correct for changes in depth during the ebbing tide.

The extent of intertidal sedge habitat was sampled by measuring the width of sedge habitat at 3-m intervals along 100-m transects parallel to the shoreline. Depending on slough size, 5 to 29 such transects were randomly selected for each slough. Sedge habitat width was measured perpendicular to the channel with a tape measure to the nearest 0.1 m. Slough channel widths in the vicinity of the sampled transects were measured from aerial photographs, which were ground truthed for smaller channels. Similar measurements of intertidal sedge habitat width were also made for oligohaline reaches of the Chehalis River. A second approach measured sedge bench widths at the slough outlets, a single measurement on each bank. This approach provided a single standard location for sedge bench width measurements which facilitated comparisons between sloughs. Since the river itself is generally lined by a sedge bench, the measurements for each slough outlet were located inland from the river by a distance equal to the width of the river's sedge bench.

Detrital Insect Outflux

To test the hypothesis that salmonid prey availability scales with slough size, detrital flotsam was collected during May and June of 1993 and 1995 on ebb tides using 0.5-mm mesh nets that resemble oil-spill containment booms (Fig. 5). The booms were placed across slough outlets at high slack tide and sampled until low slack tide. Outflux flotsam was skimmed by the booms from the surface of the ebbing water (to a depth of 25 cm), subsampled with a dip-net, and sorted through a series of sieves of 13-mm, 5.6-mm, and 0.5-mm mesh. Detrital insects were identified to the family level, counted, and weighed (blotted wet weight) to the nearest 0.1 mg.

Statistical Analyses

Linear regression analysis was employed extensively in this study. Dependent and independent variables were log transformed for two reasons: [1] to equalize variance in the residuals; and [2] to fit power functions, because it was hypothesized that slough form and ecological processes associated with form exhibit scaling analogous to organismal allometry.

Model 1 linear regression was used in the analysis of the allometry of slough form even though the independent variables were random (i.e., subject to error) because the coefficients of determination (r^2) were very high (>0.9) and under these

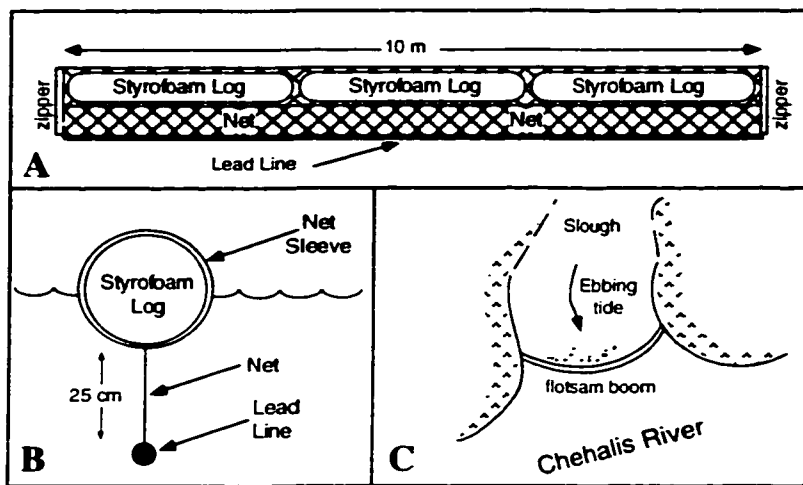


FIGURE 5. Schematic of net used to sample insect flotsam export from sloughs: (A) side view of a single module of the net; (B) cross-section of the net; (C) typical net placement at slough outlet.

circumstances differences between model 1 and model 2 regression are insignificant (Mark & Church 1977). Following the guidance of Sokal & Rohlf (1995, Table 14.3), model 1 linear regression was also used in the analysis of insect flotsam allometry because a causal relation was assumed between slough size (i.e., length of perimeter) and insect outflux abundance.

The analysis of detrital insect flotsam also employed stepwise multiple linear regression with slough perimeter (log-transformed), year of sampling, month of sampling, tidal range during sampling, and sedge width at slough mouth (log-transformed) as independent variables, and the log transformed wet weight of various insect groups as dependent variables. Tidal range was determined from tide tables and defined as high tide elevation minus low tide elevation). The software employed for the statistical analysis was StatView 4.5.1 (Abacus Concepts, Inc., Berkeley, CA). Systat 5.2.1 (Systat, Inc., Evanston, IL) was used for analysis of covariance (ANCOVA) and Tukey's HSD *post hoc* tests. All tests were conducted at a 5% significance level.

RESULTS

Slough Allometry

Width, depth, and area of all natural sloughs were positively correlated with slough length ($n = 14, 11,$ and $10,$ respectively, $p <$

0.0001 in every case) (Fig. 6), with coefficients of determination (r^2) ranging from 0.95 to 0.98. Additionally, slough perimeter and area were strongly correlated with an r^2 of 0.96 ($n = 10$, $p < 0.0001$). Regression analysis of other combinations of these slough parameters had similarly high r^2 's and low p -values (data not shown).

In contrast, the excavated slough fell well outside of the 95% confidence bands for all of the Chehalis slough regression lines (Fig. 6). The excavated slough was wider, deeper, and had greater surface area than natural sloughs of its length, and was actually wider and deeper than most of the longer natural sloughs. Furthermore, when the excavated slough was compared to the nearby slough systems of Willapa Bay, it was similarly anomalous in form (Fig. 7), falling well outside of the 95% confidence bands for all three of the slough systems examined.

Analysis of covariance indicated that the morphological scaling of different slough systems varied significantly for width vs. length, area vs. length, and perimeter vs. area ($F_{3,26} = 9.12$, $p < 0.001$; $F_{3,23} = 3.93$, $p < 0.05$; $F_{3,23} = 3.92$, $p < 0.05$; respectively; Table 1). *Post hoc* comparisons indicated that width-length scaling of sloughs of the South Fork of the Willapa River differed significantly from those of the mainstem Willapa River and the North River ($p < 0.01$). Likewise, the width-length scaling of the Chehalis River sloughs differed significantly from those of the mainstem Willapa River and the North River ($p < 0.01$, $p < 0.025$, respectively), while there were no significant differences between the South Fork and

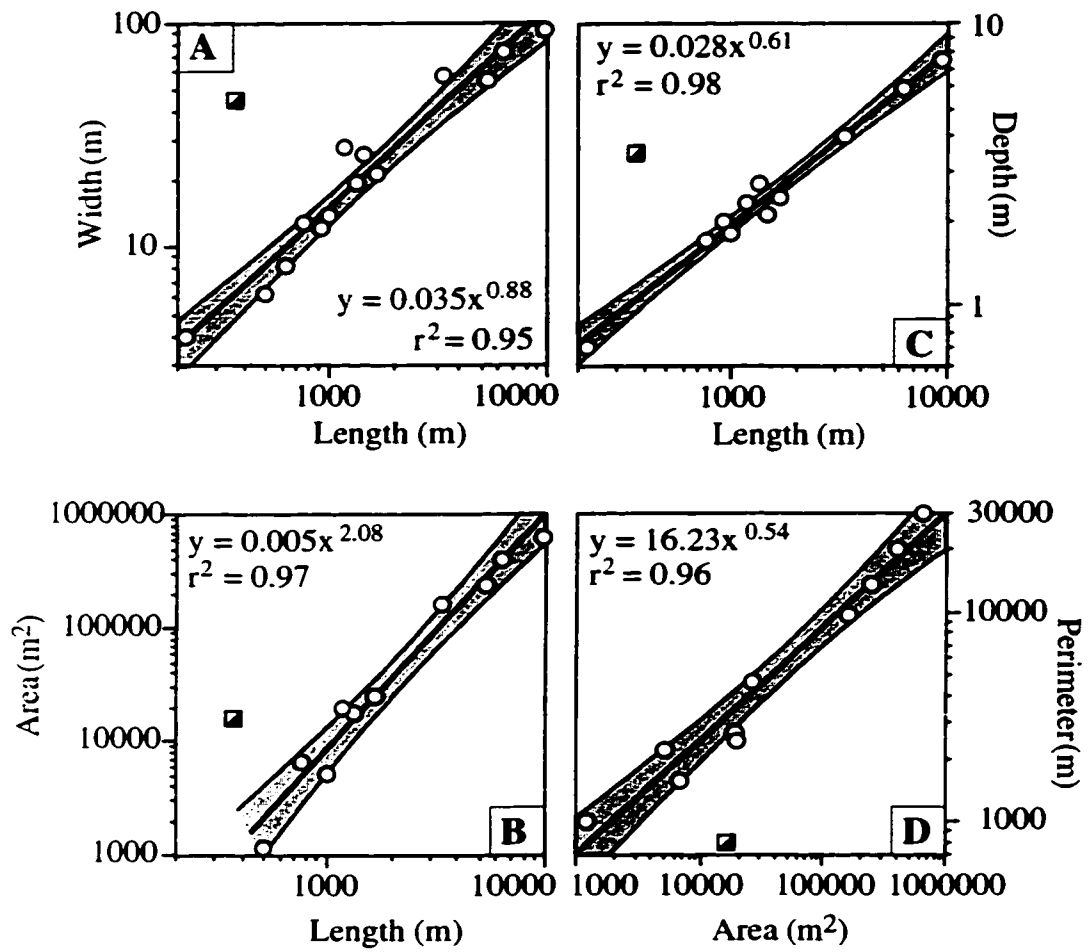


FIGURE 6. Allometry of slough form for Chehalis River sloughs (○). The excavated slough (■) is shown for comparison. Shaded bands are 95% confidence bands.

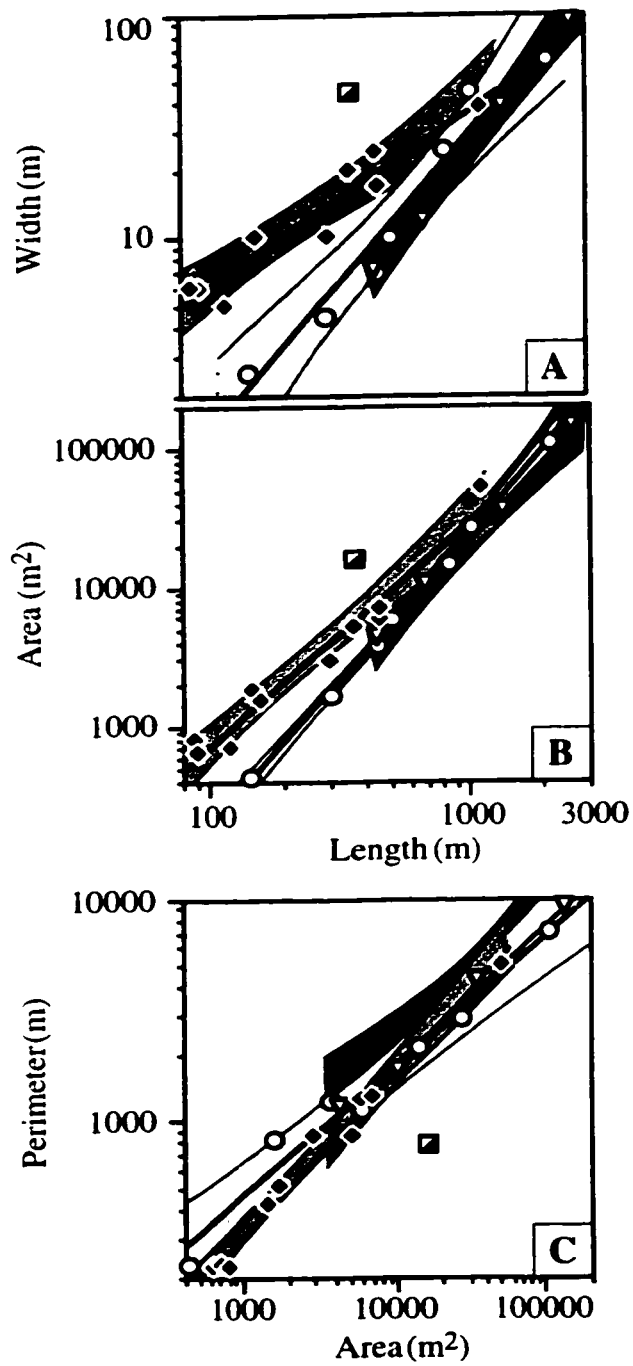


FIGURE 7. Slough form allometry for Willapa River (○), South Fork Willapa River (◆), and North River (▼) sloughs. The excavated slough (■) is shown for comparison. Shaded bands are 95% confidence bands. See Table 1 for details.

Table 1. Slough system comparisons of Length (L), Width (W), Area (A), and Perimeter (P) scaling.

Chehalis River	Willapa River	S. Fork Willapa R.	North River
$W = 0.035L^{0.88}$	$W = 0.003L^{1.35}$	$W = 0.165L^{0.78}$	$W = 0.001L^{1.47}$
$R^2 = 0.95$ n= 14	$R^2 = 0.95$ n= 7	$R^2 = 0.91$ n= 9	$R^2 = 0.99$ n= 4
$A = 0.005L^{2.08}$	$A = 0.012L^{2.09}$	$A = 0.489L^{1.58}$	$A = 0.034L^{1.93}$
$R^2 = 0.97$ n= 7	$R^2 = 0.99$ n= 10	$R^2 = 0.96$ n= 10	$R^2 = 0.99$ n= 4
$P = 8.24A^{0.54}$	$P = 16.23A^{0.58}$	$P = 1.87A^{0.74}$	$P = 6.52A^{0.61}$
$R^2 = 0.96$ n= 10	$R^2 = 0.97$ n= 7	$R^2 = 0.98$ n= 10	$R^2 = 0.99$ n= 4

the Chehalis. Additionally, the South Fork sloughs differed significantly from the mainstem Willapa and Chehalis River sloughs in area-length scaling ($p < 0.05$, $p < 0.025$, respectively) and perimeter-area scaling ($p < 0.05$, $p < 0.01$, respectively). There were no other significant differences between slough systems.

Sedge Bench Allometry

Because the intertidal sedge benches within the sloughs host a large population of aphids that are important components of salmon diets in this system, and because sedge bench formation is due in part to tidal sediment transport, I hypothesized an allometric relationship between sedge bench size and slough size. Mean channel width and mean sedge bench width for the smaller sloughs and the lower Chehalis River were positively correlated. However, the largest slough did not fit this general allometric pattern (Fig. 8a). Blue Slough was the only large slough whose sedge benches were sampled and measured. However, visual inspection of other similarly large sloughs such as Preacher's Slough, Mox Chuck, and Elliott Slough clearly indicated that Blue Slough was representative of other large sloughs regardless of their location on the river. The largest sloughs have considerably narrower sedge benches than would be predicted by the allometric model. The average sedge bench width in the largest sloughs is narrower than those in all but the smallest sloughs.

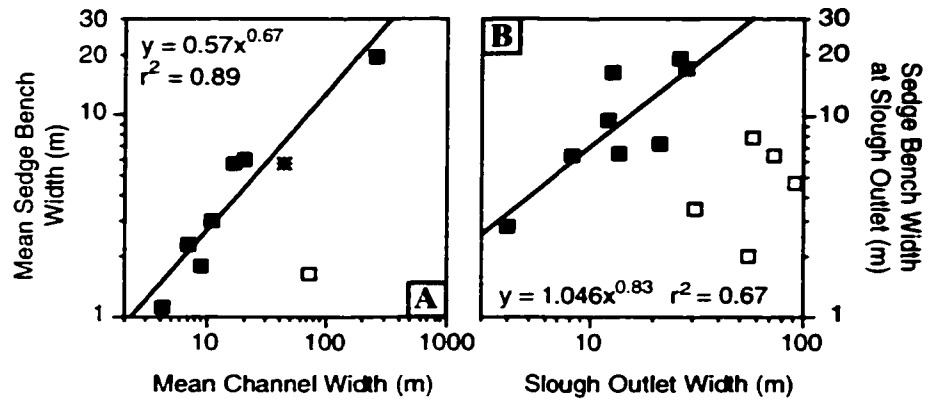


FIGURE 8. Allometry of sedge benches in small sloughs (■) and the lower Chehalis River (◻). Larger sloughs (◻) deviate from this allometry. The excavated slough (*) is shown for comparison.

Sedge bench widths at the slough outlets showed a similar relationship between slough size and sedge bench width (Fig. 8b). Once again, slough size (outlet width) and sedge bench size (width of sedge bench at outlet) were correlated for smaller sloughs, while there was no such relationship for the largest sloughs.

Detrital Insect Export

The most prominent prey in the diets of juvenile coho and chinook salmon were also the most abundant elements of the insect outflux flotsam. Aphids (Homoptera) were the numerically most abundant (30% of all terrestrial insects in the outflux), followed by adult chironomids (Diptera; 29%), and ceratopogonids (Diptera; 6%). "Other Adult Diptera" (mostly Sciaridae, Cecidomyiidae, Empididae, Psychodidae, Ephydriidae, Tipulidae, and Dolichopodidae, in decreasing order of abundance) amounted to 7% of the terrestrial insect outflux. Other insect groups which were not analyzed and which are not common prey of salmonids were generally less abundant. Biomass comparisons resulted in a similar ranking: aphids had the highest biomass (27% of all terrestrial insects by wet weight) followed by chironomids (16%), "Other adult Diptera" (10%), and ceratopogonids (3%).

Stepwise multiple regression indicated that slough perimeter length (log transformed) was the strongest predictor of exported insect biomass, accounting for 40%-55% of the variance in the biomass data, depending on the taxon (Table 2). Year of sampling

Table 2. Summary of stepwise regression results with insect wet weight (log transformed) as the dependent variable and length of slough perimeter, year of sampling, month of sampling, tidal range during sampling (high tide minus low tide elevation), and sedge bench width at slough outlets (log transformed) as independent variables. R^2 is the coefficient of determination for the multiple regression; n is the sample size.

Dependent Variables ^a	Slough ^a Perimeter	Year of Sampling	Month	Tidal Range	Sedge ^a Width	R^2 n
Aphid wet weight	40% ^b <0.0001 ^c 1.14±0.25 ^d	7% <0.05 -0.26±0.12			23% <0.001 1.60±0.41	0.70 24
Chironomid wet weight	44% <0.0001 1.14±0.19	20% <0.005 -0.41±0.09		7% <0.05 0.08±0.03		0.71 27
Cerato-pogonid wet weight	55% <0.0001 1.20±0.18	21% <0.005 -0.37±0.10	6% <0.05 -0.37±0.14			0.82 22
Other Diptera wet weight	48% <0.0005 1.04±0.23	13% <0.05 -0.32±0.12				0.61 24

^a Log transformed data.

^b Percent of variance explained by the independent variable.

^c P-value for the independent variable.

^d Coefficient for the independent variable ± the standard error of the coefficient

was the second most important predictor, except in the case of aphids. Year explained 13%-21% of the biomass variance depending on the type of dipteran. Insect abundance was lower in the 1995 collections than in those of 1993.

Sedge bench width at slough outlets (log transformed) was used as an index of sedge habitat abundance, and it was the second strongest predictor of aphid biomass, accounting for 20% of the variance in biomass. Outlet sedge bench width was not a significant predictor for any of the diptera. Month of sampling during the sampling period was a significant predictor only for ceratopogonids, while tidal range was significant only for chironomids. Neither explained more than 7% of the variance in the data. Highly similar results were obtained with insect numerical abundance rather than biomass as the dependent variable and are therefore not shown.

While detrital insect export increased with slough size (Fig. 9), insect density (biomass/slough surface area) decreased with slough size (Fig. 10). Stepwise multiple regression of the insect density data showed parallel results with those of the previous analysis (Table 3).

The excavated slough did not export flotsam at all. The flotsam nets that were placed across the mouth of the excavated slough consistently bowed into the slough rather than being pushed outward by ebbing currents as was normal in the natural sloughs. Following up on this unexpected observation, colored marshmallows were placed at four locations along the length of the excavated slough during ebb tides, a different color at each location. These

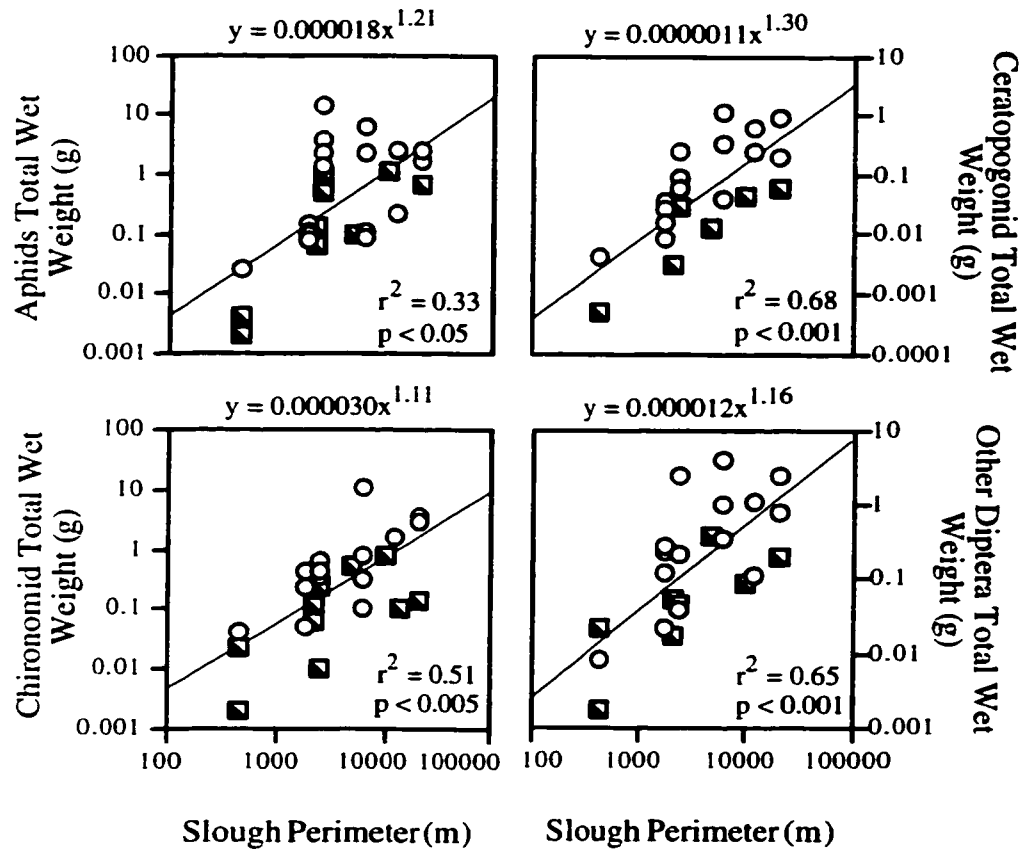


FIGURE 9. Scaling of detrital insect flotsam export with slough size (perimeter) for 1993 (○) and 1995 (■) sampling periods.

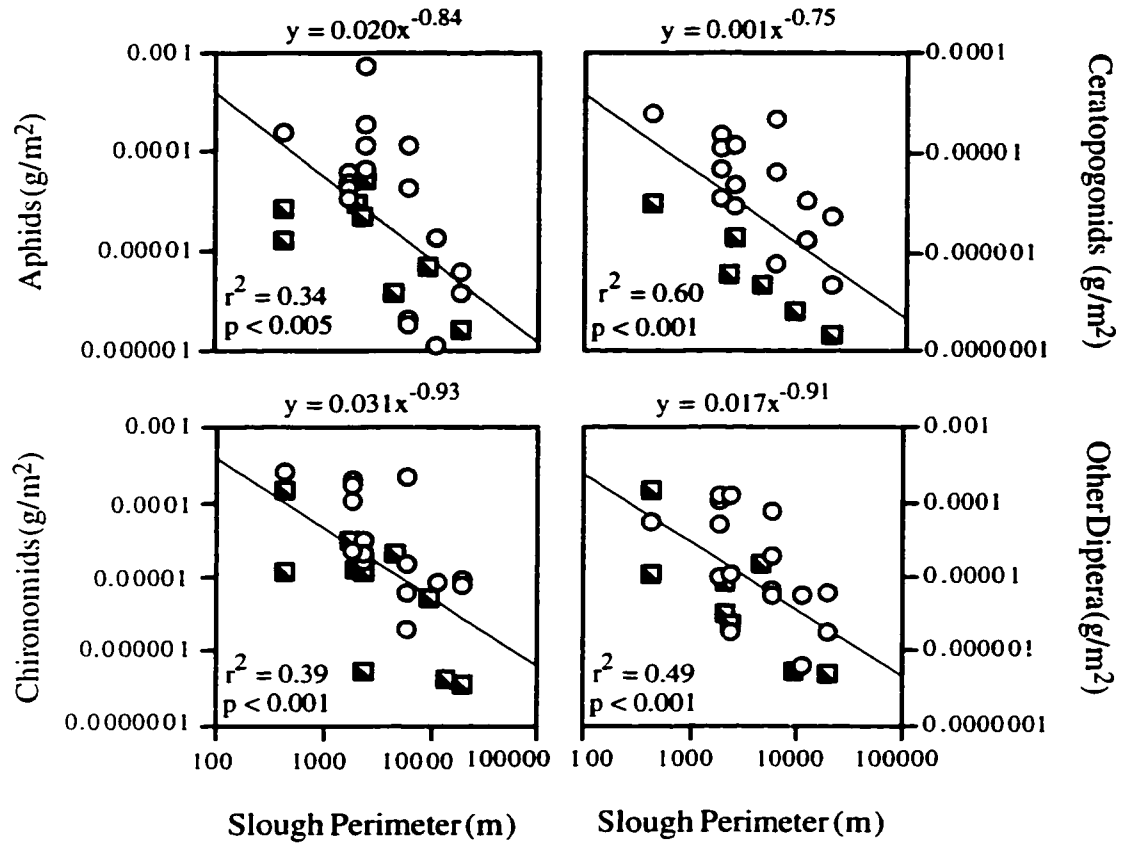


FIGURE 10. Scaling of detrital insect flotsam density (g wet wt/m² slough surface area) with slough size (perimeter) for 1993 (○) and 1995 (■) sampling periods.

Table 3. Summary of stepwise regression results with insect density (wet weight/slough surface area, log transformed) as the dependent variable and length of slough perimeter, year of sampling, month of sampling, tidal range during sampling (high tide minus low tide elevation), and sedge bench width at slough outlets (log transformed) as independent variables. R^2 is the coefficient of determination for the multiple regression; n is the sample size.

Dependent Variables ^a	Slough ^a Perimeter	Year of Sampling	Month	Tidal Range	Sedge ^a Width	R^2 n
Aphid wet wt/area	28% ^b <0.0002 ^c -0.90±0.20 ^d	16% <0.01 -0.28±0.10			20% <0.005 1.07±0.33	0.64 24
Chironomid wet wt/area	34% <0.0003 -0.90±0.21	22% <0.0005 -0.42±0.10		8% <0.05 0.08±0.04		0.64 27
Cerato- pogonid wet wt/area	36% <0.0001 -0.79±0.16	36% <0.0001 -0.46±0.07	9% <0.01 -0.34±0.11			0.81 22
Other Diptera wet wt/area	36% <0.0005 -1.03±0.24	16% <0.05 -0.33±0.12				0.52 24

^a Log transformed data.

^b Percent of variance explained by the independent variable.

^c P-value for the independent variable.

^d Coefficient for the independent variable ± the standard error of the coefficient.

mini-marshmallows acted as miniature biodegradable drogues and served as a simple and easily observed physical model of the movement of insect flotsam. On three separate occasions, in absolutely still wind, these marshmallows moved further into the slough from where they were originally deposited, rather than being exported by the ebbing tide.

DISCUSSION

Allometric scaling of slough form is consistent with models of tidal channel hydraulic geometry (Myrick & Leopold 1963, Hume 1991, Leopold et al. 1993, Zeff 1999) and is likely a consequence of the influences on erosional and depositional processes that shape sloughs, namely tidal prism, river discharge, sediment source and type, and vegetation. Similar investigations have extended the principles of hydraulic geometry to the outlets of large estuaries (e.g., Hume 1991, Hume & Herdendorf 1993). In all of these studies, tidal prism has been correlated with outlet cross-sectional area, depth, and width. The observations of the present study on the allometry of estuarine sloughs are a logical extension of the application of hydraulic geometry to tidal systems, since tidal prism shapes not only the geometry of the slough outlet, but also the geometry of every possible cross-section and thus the geometry of the whole slough. These results are also consistent with similar allometric observations in other geomorphic systems such as

hillslopes, cirques, dolines, and rivers (Faulkner 1974, Bull 1975, Kemmerly 1976, Graf 1978, Church & Mark 1980, Olyphant 1981), and with a general theory of the fractal geometry of landforms (Rodriguez-Iturbe & Rinaldo 1997).

Comparison of the allometry of the Chehalis River sloughs with sloughs of the Willapa River, the South Fork Willapa River, and the North River suggests that there are variations in slough geometry among different river systems. The most striking difference is between Willapa River and South Fork Willapa River sloughs. Even though these two systems are joined at their confluence, and thus share tidal influences, they do not share a common scaling of surface area, perimeter, length, or outlet width. Evidently, differences in their respective watersheds--such as freshwater discharge, gradient, or soils--affect the forces which sculpt sloughs. Even more dramatic differences exist between the Chehalis River sloughs and those of the Minas Basin of the Bay of Fundy in Nova Scotia (personal observations). Although data do not exist to confirm my casual observations, visual inspection of the sloughs of the Minas Basin strongly suggest that they are significantly deeper, wider, and shorter than sloughs of the Chehalis River. This is undoubtedly due to the tremendous tidal range (15 m) for which the Bay of Fundy is famous. By comparison, the maximum tidal range in the Chehalis River system is about 4.8 m. These allometric differences between slough systems suggest that restoration which seeks to mimic the natural template for slough form should take into account the local landscape which will be the

context for the restoration project. Generalization from even nearby systems may not be appropriate as the comparison of the slough systems of the Willapa River and the South Fork Willapa River demonstrate.

Restored or excavated sloughs, such as the one in the Chehalis River, that do not conform to the natural allometric template for local sloughs are unlikely to be morphologically stable over time. The natural forces--tidal sediment transport, riverine sediment transport, sediment source and type, resistance to erosion due to vegetation cover--that interact to form estuarine sloughs, will remold the artificial shapes of such sloughs. Restored or excavated sloughs are likely to move along an unpredictable trajectory toward a form that more closely resembles a natural slough (Fig. 11). Indeed, within four years of construction, the excavated slough in the Chehalis River system began to show significant accumulation of sediment as well as initiating headcutting (Simenstad et al. 1997). More recent observations indicate a dramatic decrease in the depth of the excavated slough, particularly near its outlet where river-borne sediments are first deposited. Thus, the excavated channel is already becoming shallower and longer, and near its outlet it also appears to be narrowing.

The likely instability of non-conforming sloughs has several implications for restoration design and planning. For example, the excavated slough in the Chehalis River system was mandated as mitigation for impacts to subtidal salmon habitat from the dredging of a turning basin for shipping in the lower river. The regulatory

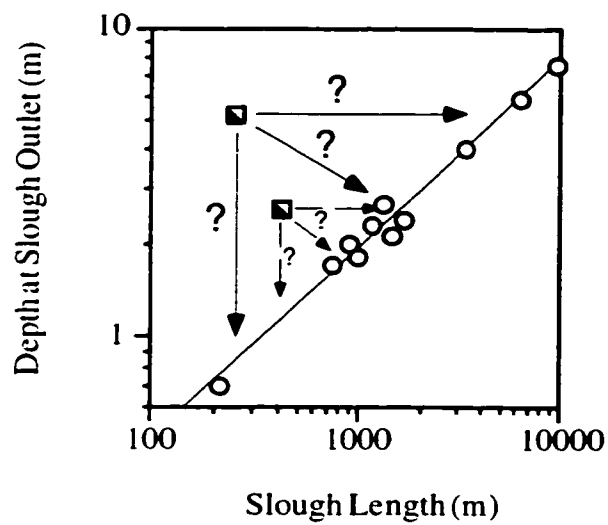


FIGURE 11. Illustration of potential design uncertainty and instability associated with excavated sloughs (■) which deviate to varying degrees from the allometry of natural Chehalis River sloughs (O). Larger question marks and longer arrows represent greater uncertainty for the future trajectory of the unstable slough form.

requirements for the slough design included: [1] a 2:1 minimum mitigation ratio, which mandated the excavation of 1.6 ha of slough to compensate for the destruction of 0.73 ha of subtidal habitat, and [2] subtidal habitat had to be present in the excavated slough, i.e. it had to be deep. Additional constraints were the availability and suitability of property, and a desire to avoid impacting forested wetlands. Consequently, human constraints on design were foremost, and natural (i.e. allometric) constraints were generally overlooked.

A mitigation ratio greater than 1:1 is generally required by regulators to compensate for the relatively high uncertainty of mitigation success. Size and shape of the project are only one component of success. Habitat productivity, resistance to invasive species, biodiversity, are also crucial elements of success. A mitigation design that accounts for landscape allometry and more closely mimics natural landforms is more likely to provide design stability and remove some of the uncertainty of mitigation success (Fig. 11). Such geomorphic stability would provide more confidence that a mitigation ratio would be an enduring one that could, hopefully, compensate for potential biological failures.

In retrospect, it is now clear that in the context of slough allometry the regulatory objective of providing subtidal habitat in such a short slough, i.e. on a small parcel of property, was unrealistic. Subtidal habitat no longer exists in the slough due to sedimentation. According to the allometric pattern observed in the natural sloughs, a slough with persistent subtidal habitat would

have to be at least 3 km long, about 8 times longer than the excavated slough. This illustrates that landscape allometry can be used not only for stable mitigation design but also to inform decision makers about realistic goals within design constraints.

Sedge Bench Allometry

Because of strong allometric relationships among slough length, perimeter, surface area, outlet depth, and outlet width, I predicted a similar allometry for slough sedge bench size. Indeed, except for extremely large sloughs, two different measures of sedge bench allometry fit my prediction. Furthermore, the lower Chehalis River itself has a mean sedge bench width and a mean channel width that are also consistent with the allometric pattern of the smaller sloughs. So why do the larger sloughs not fit the pattern? A possible explanation is that the larger sloughs used to have wider sedge benches, but no longer do as a result of historical human disturbance. Aerial photographs of the area by the US Army as early as 1942 and 1944 (the earliest available) and by the US Department of Agriculture-Soil Conservation Service during the 1960's and 1970's clearly show that large sloughs were used extensively as log storage areas. State environmental regulations prohibited water transportation and storage of logs in 1978 and photos during the 1980's do not show rafts of logs in the Chehalis River or in any large sloughs. Evidently, prior to 1978 rafts of logs were commonly floated down the Chehalis River and temporarily

stored in the large sloughs. The earliest records of floated or rafted logs in the Chehalis River go back to 1904 (Sedell & Duval 1985). These records also indicate that from 1940 to 1960 a half billion board feet of timber were floated annually down the Chehalis River. Pilings, which assisted in anchoring log rafts and in guiding their movement, are still present in all of the large sloughs. In Blue Slough, structures used for rolling logs into the slough from nearby hillsides are also still visible. Thus, large sloughs served as part of a log transportation system as well as a storage area. Such log storage was not observed in photos of smaller sloughs, nor are any pilings present in the smaller sloughs. If larger sedge benches were present in the larger sloughs, they may have been destroyed by log storage. Log handling and storage in intertidal areas is known to severely impact emergent vegetation by (1) scouring soils and plants during groundings, (2) decreasing light penetration in the water column by direct shading and by increased turbidity from suspended wood fibers, and (3) smothering vegetation through the deposition of bark and wood debris (Sedell & Duval 1985). After the sedges were killed the soil beneath them could have eroded away.

There is some visible evidence in Blue Slough to support this hypothesis. Many of the narrow sedge benches in Blue Slough are bordered on either side along the shore or further into the channel by lower elevation benches which are vegetated by a small rush, *Eleocharis* sp., instead of sedges. These *Eleocharis* benches are not found in the smaller sloughs or along the banks of the Chehalis

River. Thus, the larger sloughs appear to have been left with narrow remnant sedge benches and the eroded remains of sedge benches which have been colonized by *Eleocharis*.

An additional observation consistent with this hypothesis is that while slough sedge benches are very small or non-existent throughout most of the lower two-thirds of Blue Slough, they are much wider in the narrower, upstream portion of the slough where pilings are not found and thus, presumably, where log storage did not occur. This pattern is contrary to small, presumably unimpacted, sloughs where sedge bench width declines as the slough narrows.

This example suggests that landscape allometry can provide insight into historical conditions. Estuarine sloughs, in particular, have been frequently modified by human activity. Some have been dredged for greater log storage as in the case of sloughs near timber mills in the towns of Cosmopolis and Raymond, Washington (USA). In others, the tidal prism has decreased due to construction of causeways, dikes, and tide-gates, with consequent changes in sediment transport and slough form. Some sloughs have completely disappeared due to agricultural or industrial development, e.g. sloughs of the lower Duwamish River in what is now an industrial port for Seattle (US Dept. Interior 1897, Bortleson 1980). The probable destruction of sedge benches by log storage in sloughs is a comparatively subtle human impact on slough habitats and it might have never been suspected without an allometric investigation. Thus, allometric analysis of landscape form can

contribute to historical reconstruction of altered sloughs and thereby provide some design criteria for habitat restoration.

Detrital Insect Flotsam Export

The effect of sedge bench width on aphid export from the sloughs would not have been discernible if the large sloughs had had undamaged sedge benches, because auto-correlation of slough size and sedge bench width would have confounded attempts to separate their effects. Only aphids were significantly correlated with sedge bench widths due to their greater dependence on this habitat combined with their lower mobility relative to chironomids, ceratopogonids and other diptera which rear in mudflats and floodplain wetlands as well as among intertidal sedges (Simenstad et al. 1997). Aphids are abundant in the intertidal sedge habitat and easily transported to the slough waters during high tides. Mudflats are obviously not a source of aphids and those that rear in the floodplain wetlands are not easily transported to the slough waters because aphids generally do not have wings or fly during the period of sampling. The absence of any effect by sedge bench width on the abundance of dipterans suggests that although there is considerable production of dipterans in the intertidal sedge habitat, other sources of dipterans contribute significantly to insect tidal outflux.

Another line of reasoning supports this inference. Approximately 16% of the insects caught in emergence traps placed

among intertidal sedges are adult chironomids (Simenstad et al. 1993, 1997). If intertidal sedges were the only, or even the predominant, source of chironomids in the slough outflux then the expected proportion of chironomids in the outflux flotsam would be equal to or less than 16%. Actually, because the outflux flotsam nets catch insects that the emergence traps do not (e.g. aphids, coleoptera, and other non-flying insects) there is even more reason to expect a chironomid proportion less than 16% in the outflux flotsam. Instead, 30% of the terrestrial insects found in outflux flotsam were adult chironomids. This suggests that many chironomids are coming from another source, probably the adjacent floodplain wetlands.

Fewer insects were caught in the slough outflux in 1995 than in 1993. This was true regardless of species. Furthermore, the difference between years were relatively similar for each taxon. It is likely that differences in weather, which can affect the rate of insect growth, reproduction, or mortality, were responsible for the interannual differences in insect outflux.

The declining density of detrital insects with increasing slough size may potentially affect the behavior of fish that feed on these insects. Because of higher encounter rates, fish might preferentially forage in smaller sloughs, in the smaller segments of large sloughs, or if in larger sloughs they may more actively seek out favorable microhabitats such as eddies behind fallen logs or along shoreline irregularities where insect flotsam might accumulate.

The deviation of the excavated slough from the norm of the natural sloughs may benefit foraging fish that occupy it. Because of its non-conforming shape, the excavated slough does not export detrital insects during ebb tides. It serves instead as a trap for detrital flotsam, which suggests that detrital prey items might be of greater density in the created slough than in a natural slough of similar size--as measured by width. However, a natural slough of comparable surface area would be less than half as wide, so that differences in the density of detrital prey items between the excavated slough and a natural slough of comparable surface area would likely be much less. Ann's slough (Fig. 2) was chosen as a reference site by the USACE-SD and the US Fish and Wildlife Service to evaluate the success of the mitigation slough. The reference slough is 33% less wide, 33% less deep, and has approximately 20% more surface area than the excavated slough. Salmon diets in the two sloughs have been shown to be comparable, but stomach fullness was greater in the reference slough than in the excavated one (Miller & Simenstad 1997). While the lower stomach fullness of salmon in the excavated slough may have been due to differences in perimeter/area ratios, it may also have been due to the inhibitory effect of piscine predators that were more common in the excavated slough as a result of its greater depth (Miller & Simenstad 1997). Unfortunately, sampling for detrital insect flotsam in the excavated slough was problematic so direct comparisons of flotsam density could not be made.

Reference Sites and Replication

These comparisons raise an interesting question. What is the appropriate reference slough for the excavated slough, one of similar width, depth, or surface area? Or alternatively, which of the natural sloughs might the excavated slough most resemble, a small one or a large one? A mitigation design consistent with a natural allometric template would make this question moot, because such a slough could be compared to a suite of natural reference sloughs regardless of their size. By using slough size as a covariate, all of the natural sloughs become appropriate reference sloughs. In this way, an allometric approach to landscape ecology reduces the constraints on choosing replicate reference sites that may serve as natural standards for mitigation or restoration designs. Another advantage of this approach is that mitigation or restoration projects are explicitly evaluated within a larger landscape context, which helps to avoid a myopic focus on one or a few sites.

Caveats

Many biological patterns may not correlate strongly with landscape geometry. As previously mentioned, salmonid abundance may not scale with slough size because foraging behavior may change instead. Other behaviors may also change due to biotic interactions such as competition, predation, disease, and social behaviors. Relative to the geometric and physical

foundation for ecological patterns, these biological interactions are emergent properties of the system. Populations vulnerable to density-independent effects such as insects may be unlikely to scale with landscape form due to their high variability.

Nevertheless, this study and others (Bach 1980, 1984, Risch 1981, Kareiva 1983, 1985) provide successful examples of insect-landscape allometry. Finally, while power functions are useful for describing pattern over a wide range of scales, precise prediction is problematic due to correlation of variance with means at arithmetic scales.

SUMMARY

Mitigation and restoration projects in estuarine slough systems, and probably in other systems as well, should strive to emulate the natural landforms in which the project will be located when mimicry of natural ecosystem function is a goal of the project. Tidal prism, river discharge and other factors affecting sediment transport sculpt allometric slough forms. This results in an allometry of intertidal sedge habitat which interacts with slough geometry to affect the density of allochthonous insect flotsam. This, in turn, may potentially affect the distribution or behavior of fish that feed on the insects. Thus, restored or created sloughs should conform to the natural allometric template of the local system in

order to maximize the probability of mimicing natural slough processes.

Approaching mitigation and restoration planning from the perspective of landscape allometry will also allow greater confidence in the predictability of the design in a dynamic environment, which in turn provides greater confidence in meeting design goals for an enduring period of time. Furthermore, landscape form is probably the easiest variable to control in mitigation projects, given the enormous capability of earth-moving equipment. A landscape allometry approach to restoration and mitigation planning can also assist in reconstructing historical conditions, thereby providing design goals or criteria for project success. Once the project is completed, replication of reference sites is facilitated since system size can be controlled statistically as a covariate.

CHAPTER 2**Landscape Allometry:****From Hydraulic Geometry to Benthic Ecology****INTRODUCTION**

It has been argued that the problem of scale is at the heart of ecological theory (Levin 1992, Levin & Pacala 1997). Many approaches to this problem search directly for scaling patterns in biological phenomena (e.g. O'Neill et al. 1986, Wiens 1989, Russell et al. 1992, Peterson et al. 1998, Underwood & Chapman 1998). This paper, however, pursues another approach which begins with the well established scaling of geomorphological structure (Horton 1945, Church & Mark 1980, Rodriguez-Iturbe & Rinaldo 1997) and assumes a linkage between landscape form and landscape ecology, i.e. a landscape-scale structure-function relationship. Thus, the conceptual model which motivates this paper begins with a foundation of geomorphic scaling which is hypothesized to result in a parallel scaling of the overlying ecological systems. Consequently, this approach, for the sake of simplicity, ignores influences such as stochastic climatic events, disturbance, and biological processes such as predation, competition, and disease, which have the potential to dampen the influence of landscape form on ecosystems. This paper will use the term, "landscape allometry," to refer to the

hypothesized parallel scaling between landscape form and landscape ecology.

From a practical perspective, there is good reason to investigate the linkage between landform and ecological processes. Humans have been dramatically modifying landforms for many centuries, most notably in the reclamation of land from the sea by the Dutch, the excavation of immense surface mines, and in engineering large river systems and their floodplains. The advent of powerful earth-moving equipment has made landform modification easier and perhaps more common. Recently, landform modification has been undertaken in order to restore or mitigate previously altered landscapes. Landscape allometry may perhaps provide a useful tool for planning landform modifications and evaluating their ecological consequences (Chapter 1).

This paper investigates the potential utility of an allometric approach to landscape ecology in a system of estuarine sloughs (oligohaline tidal channels) which drain the floodplain of the lower Chehalis River near the Pacific coast of Washington (Fig. 12). These sloughs have been previously shown to exhibit allometric form: slough length, width and depth at the outlet, surface area, and perimeter are all highly correlated ($r^2 > 0.90$) (Chapter 1). This allometry is a logical consequence of tidal channel hydraulic geometry (Myrick & Leopold 1963, Hume 1991, Hume & Herdendorf 1993, Friedrichs 1995, Zeff 1999).

The objective of this paper is to investigate whether there is a parallel scaling of ecological patterns and processes in the sloughs.

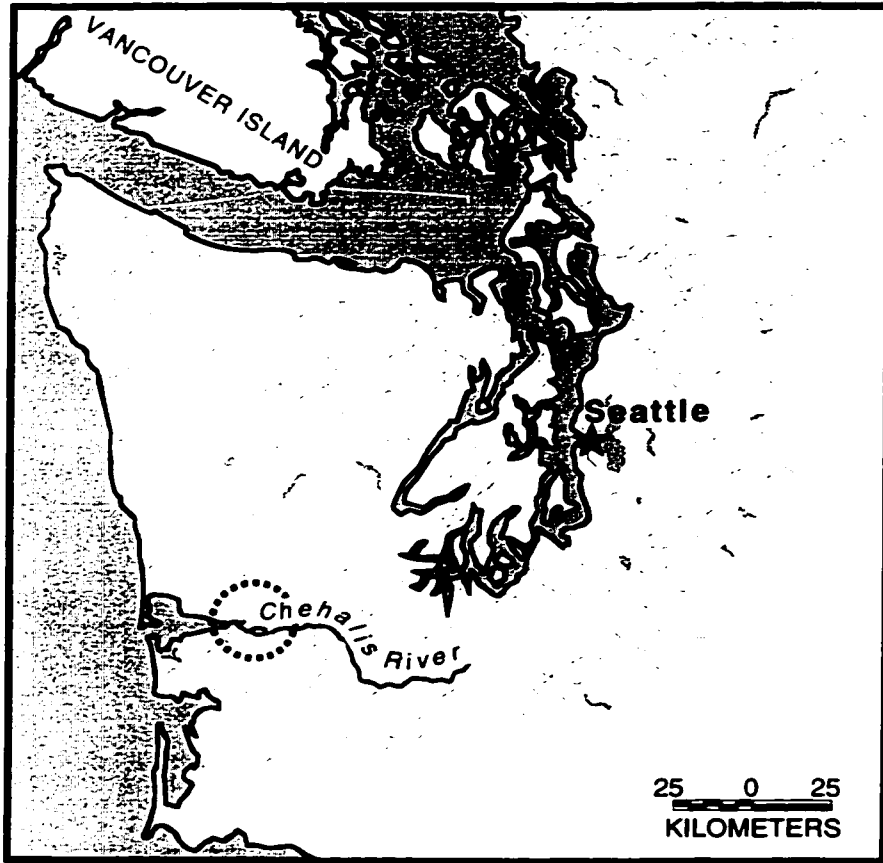


FIGURE 12. Study Site Location. Circled area is the general location of the estuarine sloughs of the lower Chehalis River.

To this end, data are presented on the relationships between slough size and the following variables: the velocity of slough surface currents during ebb tides, the exit time and probability of export of allochthonous detritus which floats on the surface of the slough waters, the accumulation of organic material in the slough sediments, and the composition of the benthic communities in the sloughs. Allochthonous detritus was chosen for investigation due to interest in the importance of terrestrial subsidies to the diets of juvenile salmon (Chapters 1 & 3).

METHODS

Study Site Description

The estuarine sloughs of the lower Chehalis River are found in a tidal floodplain that is bordered to the north by the Olympic mountains and to the south by the Willapa Hills. The floodplain is generally 2.5 km wide and stretches along the river for 15 km from the cities of Aberdeen and Cosmopolis to diked farmlands upstream (Fig. 13). Most of the floodplain is relatively undisturbed by human impacts despite proximity to cities and farmlands.

The floodplain is characterized by sitka spruce (*Picea sitchensis*) wetlands, with scrub-shrub vegetation dominated by salmonberry (*Rubus spectabilis*), black twinberry (*Lonicera involucrata*), cascara (*Rhamnus purshiana*), red-osier dogwood

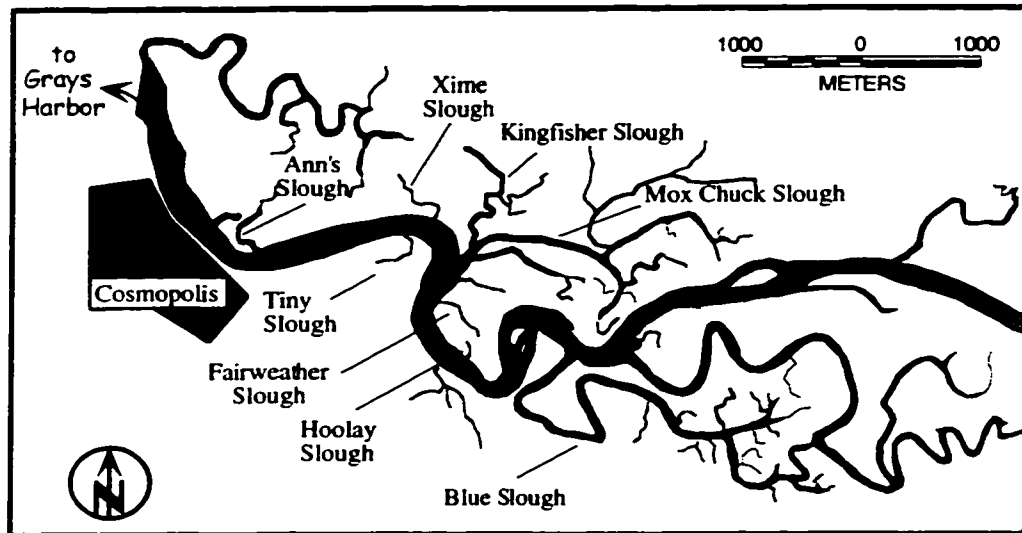


FIGURE 13. Estuarine Sloughs of the Lower Chehalis River.

(*Cornus stolonifera*), and willows (*Salix* spp.). Understory vegetation is dominated by slough sedge (*Carex obnupta*) and skunk cabbage (*Lysichitum americanum*). The floodplain is dissected by oligohaline sloughs which contain two intertidal habitats, mudflats and a fringe of marsh which is usually a monoculture of Lyngby's sedge (*C. lyngbyei*).

Salinity in the sloughs varies seasonally, and with slough depth and distance from the ocean. Typical values over the study area range from about 1 to 14 parts per thousand (ppt). Salinities are stratified near slough outlets, but are usually well-mixed further up the sloughs. The estuary is mesotidal, although maximal tide ranges can approach 4.5 m. Tides are semidiurnal.

Surface Flow Velocity Measurements

Casual observations suggested that surface flow velocity might be correlated with slough size. If so, this would likely affect the rate at which floating detrital insects, such as aphids and adult chironomids, are exported from different sloughs. This, in turn, could affect salmon distribution in the sloughs, because these insects are the primary components of the diets of juvenile salmon in this habitat (Miller & Simenstad 1997).

All measurements of surface flow velocity were made with a hand-held velocity meter (Swoffer 2100) on ebb tides just inland of the slough outlets in the center of the channels. Six to seven sloughs were sampled sequentially over the course of one hour on

each of three different occasions, 25 October 1992, 1 November 1992, and 21 May 1996. Sampling began approximately two hours after the beginning of ebb flow. However, the 25 October 1992 sampling date included an additional sampling period which began approximately four hours into the ebb tide. In order to account for acceleration or deceleration of the flow due to sinusoidal tidal velocity patterns, the first slough sampled was sampled again at the end of each hour long sampling period. Changes in surface velocity between the start and end of the sampling period were insignificant, less than 0.02 m/sec. Large and small sloughs were alternated during the course of a sampling period in order to avoid confounding possible temporal trends with the effects of slough size.

On 21 May 1996, measurements of surface velocity were also made along a 5000 m longitudinal transect of Blue Slough, the second largest slough in the tidal floodplain system. Sampling began three hours after the onset of ebb flow and required one hour to complete. The first and last measurements were made at the slough outlet to control for velocity changes during the sampling period. Once again, the change in velocity was negligible, i.e., 0.03 m/sec.

Exit Time of Floating Detritus

Small ($\sim 0.6 \text{ cm}^3$) biodegradable drogues (colored mini-marshmallows), were used to simulate the movement of organic

flotsam such as, spruce needles and allochthonous terrestrial insects in the slough surface waters. Marshmallows were sorted by color and deployed at four different distances from the slough outlet at high slack tide in each slough sampled. Two to four thousand marshmallows were deployed at each location. Exit time of allochthonous detritus in the slough surface waters was estimated as the mean time required for the marshmallows to move from the point of deployment to the slough outlet on the ebbing tide

Visual observations indicated that marshmallow movement was not affected by wind. Instead, ebb currents determined marshmallow movement. Visual comparisons with ordinary allochthonous detritus indicated that movements were similar in speed and trajectory. Recovery rates of marshmallows (about 90% over the course of three sequential ebb tides, i.e., 31 hrs) in preliminary trials indicated that fish consumption of marshmallows was not significant.

Sediment Organic Matter

Sediment samples were taken with a 5-cm diameter corer to a depth of 5 cm along longitudinal transects in Blue, Kingfisher, and Hoolay sloughs, representing large, medium, and small sloughs respectively (Fig. 2). Samples were taken at low tide from mudflat habitat located approximately 0.5 m lower in elevation than the

fringing intertidal marsh habitat. Samples were chilled with ice during transport to the lab.

In the lab, 10 g subsamples were taken from the homogenized sediment cores and dried for one day at 105° C, then cooled in a desiccator for 1 hr, weighed to the nearest 0.001 g, heated in a combustion furnace at 600° C for 2 hrs, cooled in a desiccator for 2 hrs and weighed again. The proportion of total volatile solids in the sediments was calculated as the amount of weight lost after combustion divided by the weight of the dried subsample, with this value estimating the proportion of organic matter (Plumb 1981).

Benthic Community Structure

Benthic organisms were sampled with a 5-cm diameter sediment corer to a depth of 5 cm. Seven to ten samples per slough were taken at low tide from mudflat habitat that was approximately 0.5 m lower in elevation than the fringing intertidal marsh habitat. Samples were preserved in 10% buffered formaldehyde, stained with rose-bengal, sieved in the lab, sorted by taxonomic family, counted, and blotted and weighed (wet weight) to the nearest 0.0001 g. Sampling occurred in September of 1999 along longitudinal transects in Blue, Mox Chuck, Kingfisher, Xime, and Hoolay sloughs (Fig. 2).

Statistical Analysis

The software employed for regression analysis was StatView 4.5.1 (Abacus Concepts, Inc., Berkeley, CA). Regression variables were log transformed to equalize variance in the residuals. Systat 5.2.1 (Systat, Inc., Evanston, IL) was used for analysis of covariance (ANCOVA) and Tukey's HSD *post hoc* tests. One-tailed t-tests were used for hypothesis tests of regression slopes when there were *a priori* directional expectations. All tests were conducted at a 5% significance level.

RESULTS

Ebb Surface Flow Velocity

Surface flow velocities scaled similarly with outlet width on all dates (Fig. 14). ANCOVA indicated that the slopes of the regression lines were homogeneous ($F_{3,17} = 0.58$, NS), with a common slope of 0.45. However, regression elevations were significantly different ($F_{3,20} = 57.8$, $p < 0.001$). Tukey's HSD indicated that the 25 Oct 92 measurements taken two hours into the ebb tide differed significantly from all other groups ($p < 0.001$ for each comparison). The 25 Oct 92 measurements taken four hours into the ebb tide also differed from all other groups ($p < 0.005$ vs 21 May 96, $p < 0.05$ vs 1 Nov 92).

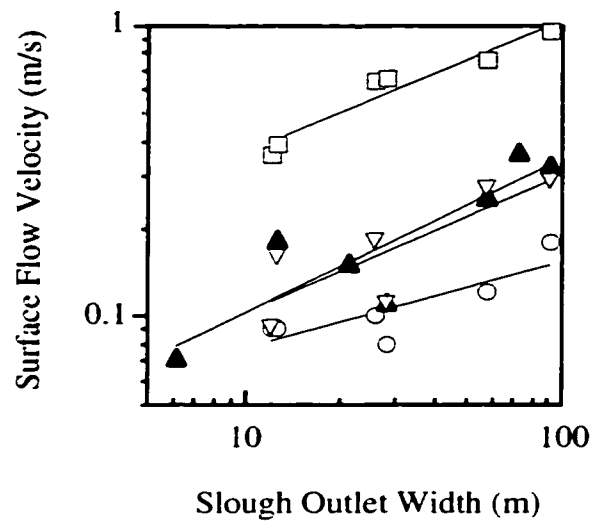


FIGURE 14. Scaling of slough surface flow velocity with slough outlet width. Data taken two hours after the onset of spring tide ebb flow (Oct 1992, □), neap tide ebb flow (Nov 1992, ▽, May 1996, ▲), and four hours after the onset of spring tide ebb flow (Oct 1992, ○).

The only non-significant comparison was between the 1 Nov 92 and 21 May 96 dates, both sampled two hours into the ebb tide. Four sloughs measured on both dates had velocity measurements that were nearly identical on both occasions, despite being measured in different seasons and different years. Both dates were neap tides with tidal ranges of only 1.1 and 1.5 meters, respectively. In contrast, the 25 October 1992 measurements were made during a spring tide with a tidal range of 4.1 meters. On this occasion surface flow velocities observed two hours into the tide were almost four times faster than those observed in the neap tides. In every case, whether measured on spring or neap tides, early in the tide or later--the larger the slough, the faster the flow. Stepwise multiple regression analysis ruled out sequence of measurement and distance of the slough outlet from the coast (which affects tidal amplitude) as factors affecting slough surface velocities for any of the sampling dates.

Surface flow velocities measured along a 5000 m longitudinal transect in Blue Slough declined with increasing distance from the slough outlet (Fig. 15A). At 4000 m from the outlet, there is a large tributary to the slough. Measurements along a 500 m transect up the tributary indicated that tributary surface flow was dramatically lower compared to the main channel of Blue Slough. Surface flow velocities scaled with channel width, when the data for the mainstem and the tributary were lumped together ($r^2 = 0.87$, $F_{1,6} = 41.1$, $p < 0.001$; Fig. 15B). Multiple regression indicated that

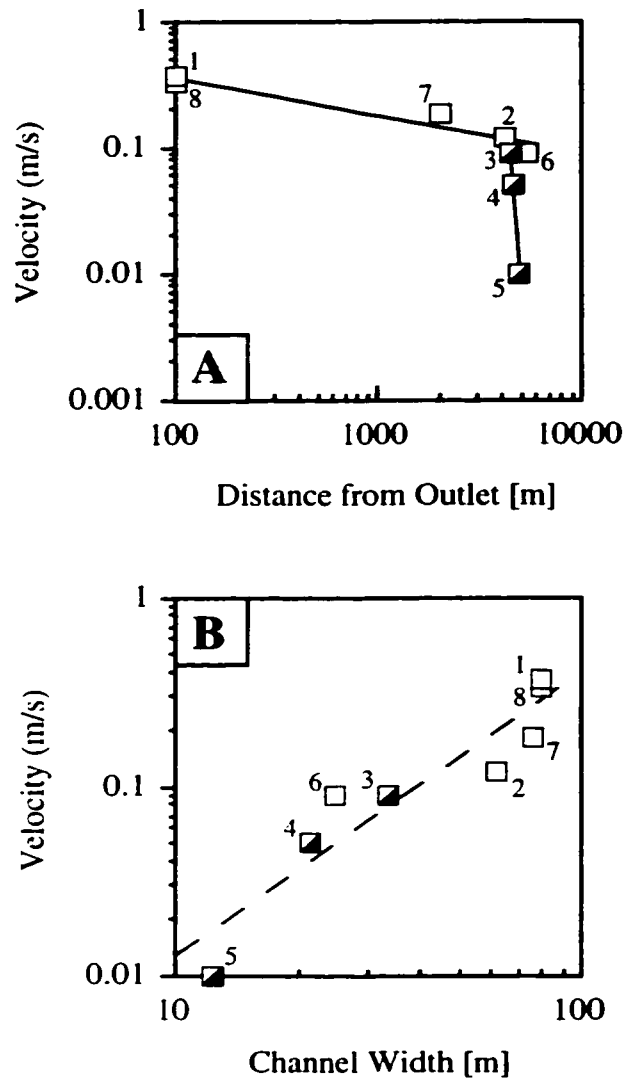


FIGURE 15. Ebb flow surface velocity for Blue Slough (□) and its largest tributary (■) vs. distance from the outlet [A]. Fitted lines are visual guides only, due to small sample size. [B] Ebb flow surface velocity versus channel width for Blue Slough (□) and its largest tributary (■), $y = 152x^{0.58}$, $r^2 = 0.87$, $F_{1,6} = 41.1$, $p < 0.001$. Numbers adjacent to the data points indicate the sequence in which the measurements were made.

temporal sequence of measurement was not a significant predictor ($t = 0.282$, NS, $df = 5$). Furthermore, the first and last measurements were made at the same place near the slough outlet, and they differed by less than 9%, which suggests that error due to asynchronous measurements was less than 9%.

Exit Time Scaling

Marshmallow drogue exit time varied with the distance from the slough outlet at which the drogues were deployed. The slopes of the regression lines describing this scaling were heterogeneous on different dates for Ann's Slough ($F_{3,7} = 5.73$, $p < 0.05$, Fig. 16A), but post hoc tests found differences only between the September and August data. ANCOVA that omitted the September data showed no significant difference in the elevations of the regressions ($F_{2,7} = 3.70$, NS). ANCOVA that omitted the August data showed a significant difference ($F_{2,7} = 19.9$, $p < 0.001$), and post hoc tests indicated that the September data differed from the other dates ($p < 0.01$ vs July, $p < 0.005$ vs May). The two sampling dates for Mox Chuck Slough did not have significantly different slopes ($F_{1,2} = 0.46$), but elevations were different ($F_{1,3} = 12.4$, $p < 0.05$). Exit time was approximately 40% greater in May vs. July (Fig. 16B). The sampling dates for Blue Slough (Fig. 16C) did not have significantly different slopes ($F_{2,2} = 0.16$) or elevations ($F_{2,4} = 2.70$).

Between-slough comparisons (Fig. 17A) showed no significant differences in the scaling of exit time with distance from slough

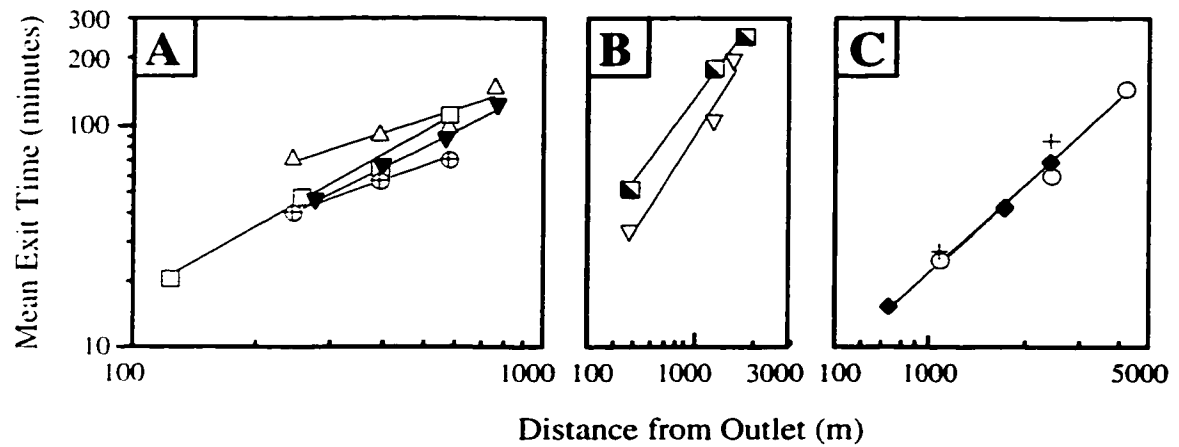


FIGURE 16. Scaling of mean marshmallow drogue exit time with distance from slough outlet for [A] Ann's Slough (□ 14 August 1994; △ 13 September 1994; ● 18 May 1996; ▼ 10 July 1996), [B] Mox Chuck (■ 13 May 1996; ▽ 11 July 1996), and [C] Blue Slough (○ 16 June 1995; ◆ 16 May 1996; + 2 July 1996).

outlet ($F_{3,25} = 2.76$), but there were differences in elevations ($F_{3,28} = 80.8$, $p < 0.001$). Post hoc tests indicated that the only non-significant comparison was between Fairweather Slough and Mox Chuck. Fairweather differed from Ann's Slough at $p < 0.005$, while all other comparisons differed at $p < 0.001$. Additionally, there was a tendency for regression elevations to be correlated with slough size (Fig. 17B) and with the mean of the November 1992 and May 1996 ebb flow surface velocities (Fig. 17C). In general, exit time was shorter for larger sloughs than for smaller ones.

Marshmallows deployed far into the sloughs had lower recovery rates than those deployed closer to the slough outlets. Recovery data fit a negative exponential model (Fig. 18A). There were no detectable statistical differences in regression slopes ($F_{3,19} = 0.78$) or elevations ($F_{3,22} = 2.76$, $p < 0.07$) between sloughs. However, the distance from the slough outlet at which drogues had a 50% probability of export (Dist_{50}) was correlated with slough length (Fig. 18B).

Observation of marshmallow drogue trajectories in a large slough suggested the likely fate of unrecovered marshmallows. Marshmallows were deployed at four locations in Blue Slough at approximately high slack tide and followed during their ebb tide outflux (Fig. 19). In the first trajectory, nine thousand marshmallows were deployed approximately 4.7 km into the slough. There was considerable dispersion along their trajectories, but most traveled about 1.5 km at a mean velocity of 0.1 m/s before being stranded on the muddy banks of the slough. The

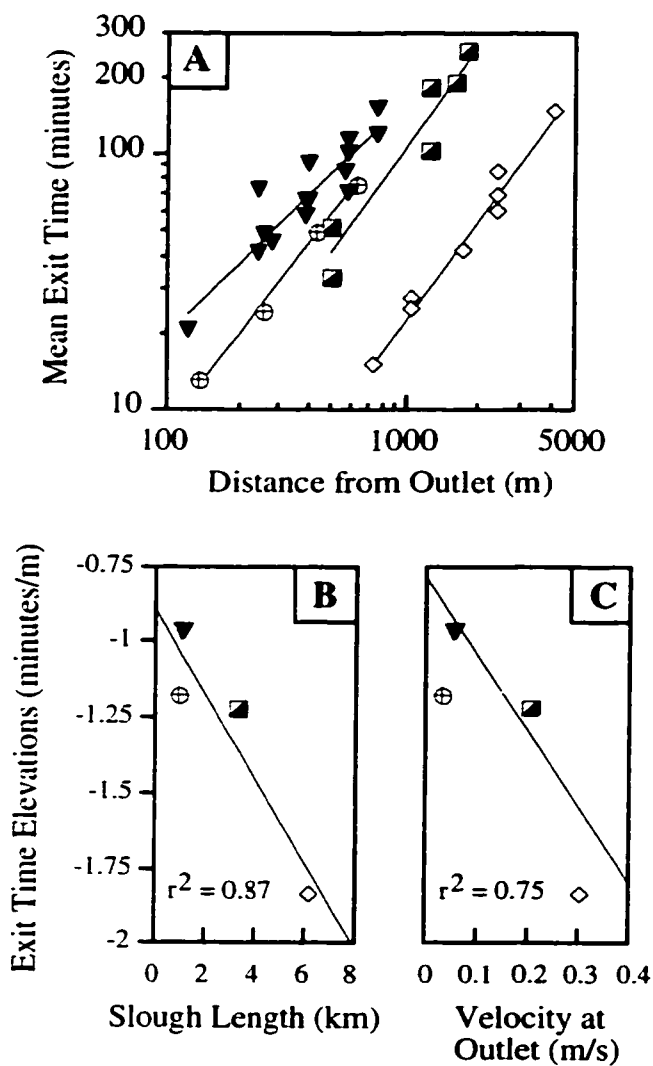


FIGURE 17. Scaling of mean marshmallow drogue exit time for Ann's Sl. (\blacktriangledown , $y = 0.31x^{0.90}$, $r^2 = 0.84$), Fairweather Sl. (\bullet , $y = 0.034x^{1.20}$, $r^2 = 0.99$), Mox Chuck (\blacksquare , $y = 0.011x^{1.33}$, $r^2 = 0.91$), and Blue Sl. (\blacklozenge , $y = 0.003x^{1.28}$, $r^2 = 0.98$) [A]. Relationship between the elevations of the regression lines in Figure 17A and slough length [B], or surface flow velocity at slough outlets [C].

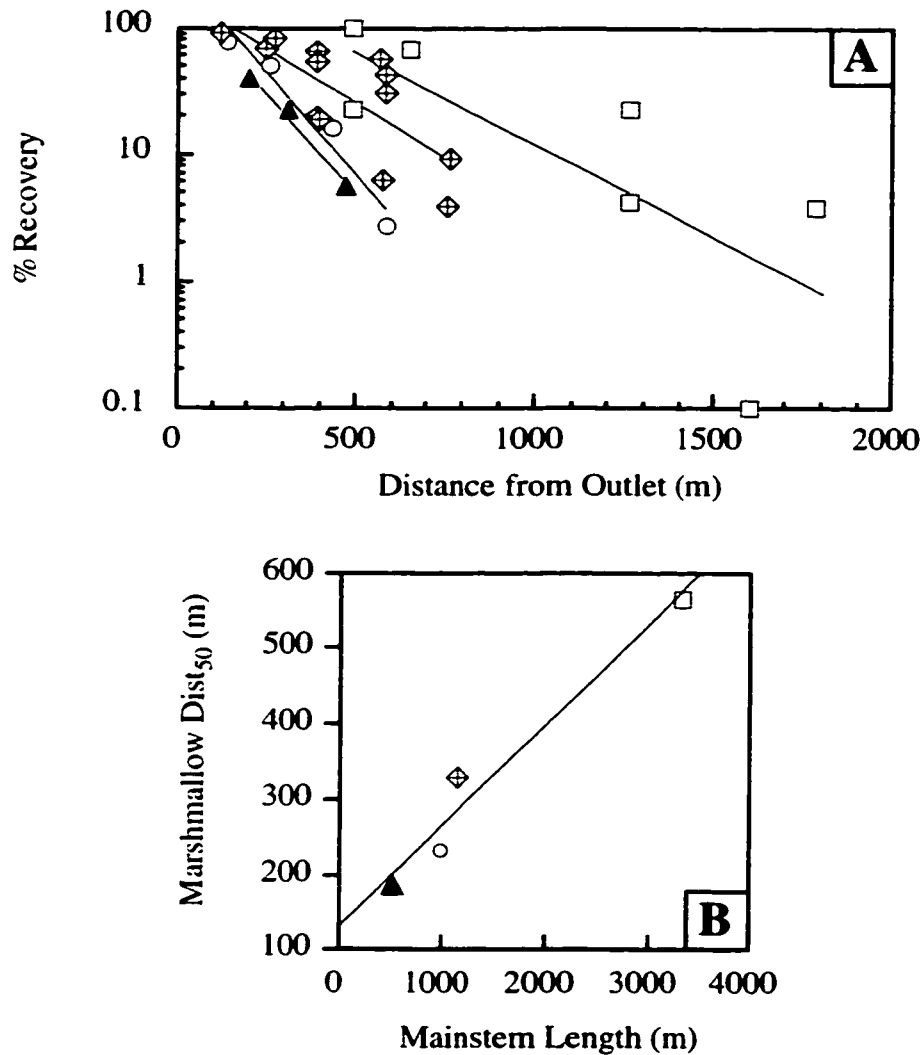


FIGURE 18. [A] Percentage of marshmallow drogues recovered vs distance from slough outlet of initial deployment, for Mox Chuck (\square , $y = 332e^{-0.0034x}$, $r^2 = 0.59$, $F_{1,5} = 7.1$, $p < 0.05$), Ann's Slough (\diamond , $y = 186e^{-0.0040x}$, $r^2 = 0.57$, $F_{1,11} = 14.7$, $p < 0.005$), Fairweather Sl. (\circ , $y = 284e^{-0.0075x}$, $r^2 = 0.96$, $F_{1,2} = 42.8$, $p < 0.05$), and Tiny Sl. (\blacktriangle , $y = 188e^{-0.0073x}$, $r^2 = 0.99$, $F_{1,1} = 88.8$, $p < 0.07$). [B] Distance from outlet where drogues had 50% probability of export ($Dist_{50}$) vs slough size (mainstem length) for the sloughs in Figure 18A ($y = 0.134x + 126$, $r^2 = 0.99$, $F_{1,2} = 58.7$, $p < 0.05$).

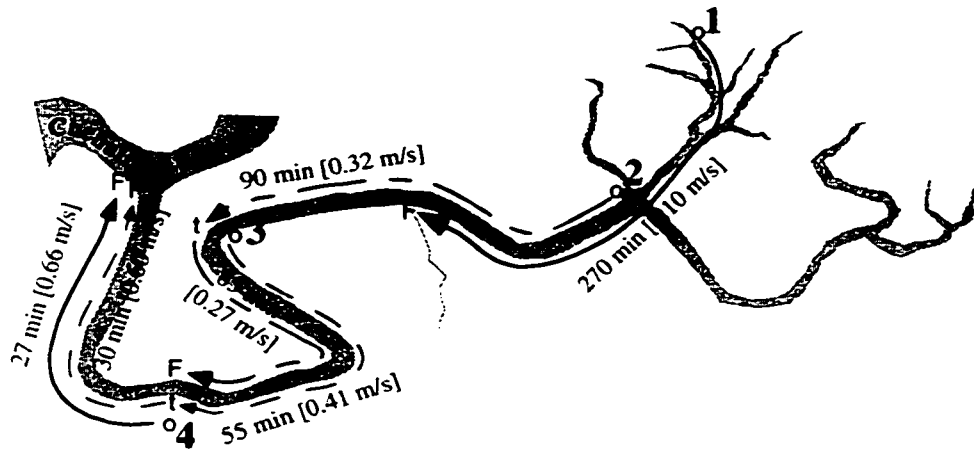


FIGURE 19. Marshmallow drogue trajectories in Blue Slough, 2 July 1996. Each trajectory is numbered; points of initial drogue deployment (o), intermediate points of observation (t), and final location at low slack tide (F) are connected by arrows of different line patterns for each trajectory.

second trajectory began about 4.1 km into the slough with approximately 2000 marshmallows. They traveled approximately 2.7 km at a mean velocity of 0.30 m/s before stranding on the muddy slough banks. Once again there was considerable dispersion of the drogues along this trajectory with many becoming stranded earlier in the trajectory. The third trajectory began about 2.5 km into the slough with approximately 1600 marshmallows. These traveled 2.5 km at a mean velocity of 0.51 m/s. Most of these drogues escaped the slough, however there was some dispersion along this trajectory and a few drogues were stranded on the slough banks. The final trajectory began about 1.25 km into the slough with approximately 1100 marshmallows. Virtually all of these drogues escaped the slough, traveling at a mean velocity of about 0.66 m/s. Two patterns are apparent in these observations: [1] drogues deployed further into the slough had slower mean velocities to their final destinations; [2] drogues deployed further into the slough were less likely to escape the slough before the tide reversed. These patterns are consistent with the preceding observations on surface flow velocity and drogue recovery rates. These patterns also suggest that allochthonous detrital inputs are more likely to be retained in small sloughs and in the smaller and more distal portions of large sloughs, where they will either be consumed or eventually sink and accumulate in the sediments. To test these predictions the organic content of slough sediments were measured on longitudinal slough transects as were the benthic communities of several sloughs. Sediment Organic Content

The percentage of organic material in slough sediments increased exponentially with distance from the slough outlet; the smaller the slough, the more rapid the increase (Fig. 20A). Within Blue Slough, there was a sharp increase in the amount of organic material in a tributary's sediments. This sharp increase mirrors the pattern of surface flow velocity in the slough, which is apparent when sediment organic content is compared to the inverse of velocity ("slowness") (Fig. 20A).

The percentage of organic material in slough sediments declined with channel width, and each slough comprised a relatively distinct set of points (Fig. 20B). Slopes were significantly different ($F_{2,22} = 4.21$, $p < 0.05$), and a post hoc test indicated that Blue Slough differed from Hoolay Slough ($p < 0.05$). In general, the smaller the slough the more rapid the decrease in sediment organic content with increasing channel width. Additionally, for a given channel width the sediment organic content was greater in a longer slough than in a shorter one.

Spruce Needle Sedimentation

Accumulation of spruce needles in slough sediments was examined because needles were abundant in slough flotsam as well as in benthic samples and thus were an important allochthonous input. Additionally, spruce needles are more refractory to

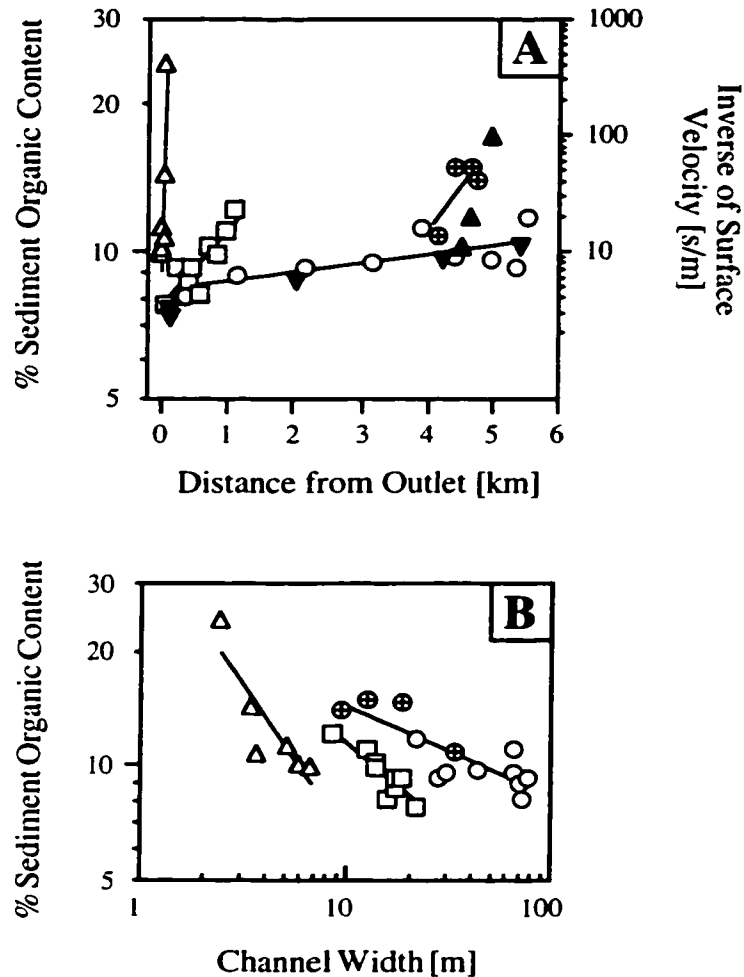


FIGURE 20. [A] Sediment organic matter content vs. distance from slough outlet for (in increasing order of slough size) Hoolay Slough (Δ , $y = 2.15e^{0.015x}$, $r^2 = 0.60$, $p < 0.05$), Kingfisher Sl. (\square , $y = 2.05e^{0.00036x}$, $r^2 = 0.76$, $p < 0.005$), and Blue Sl. (\circ , $y = 2.12e^{0.000042x}$, $r^2 = 0.50$, $p < 0.05$) and its largest tributary (\bullet , $y = 0.69e^{0.00043x}$, $r^2 = 0.56$, NS). The inverse of surface velocity (“slowness”) is plotted for Blue Sl. (\blacktriangledown) and its tributary (Δ) on the right axis for comparison. [B] Scaling of slough sediment organic matter content with channel width for Hoolay Sl. (Δ , $y = 39.5x^{-0.78}$, $r^2 = 0.77$, $p < 0.05$), Kingfisher Sl. (\square , $y = 33.5x^{-0.47}$, $r^2 = 0.81$, $p < 0.001$), and Blue Sl. and its largest tributary (\circ & \bullet , respectively; $y = 24.6x^{-0.24}$, $r^2 = 0.70$, $p < 0.01$).

decomposition or consumption than allochthonous insects and thus are more likely to be encountered in benthic cores.

In general, as channel width increased needle density in channel sediments decreased (Fig. 21A). The only exception was Blue Slough, the largest slough, for which no pattern was apparent. Slopes for the regressions were heterogeneous ($F_{4,29} = 4.05$, $p < 0.01$). Since, the regression of the Blue Slough data did not have a slope significantly different from zero ($F_{1,4} = 0.46$, NS), a second ANCOVA omitted the Blue Slough data. This second ANCOVA indicated that slopes were homogeneous for the remaining four sloughs ($F_{3,25} = 1.36$, NS) with a common slope of -0.13 , while elevations were heterogeneous ($F_{3,28} = 3.46$, $p < 0.05$), with significant differences for Mox Chuck vs. Kingfisher ($p < 0.05$), Xime ($p < 0.05$), and Hoolay ($p < 0.05$) sloughs. In general, between slough comparisons at similar channel widths show a consistent pattern of higher needle abundance in longer sloughs.

Spruce needle density in slough sediments generally increased with distance from the slough outlet (Fig. 21B). ANCOVA indicated that the slopes for the regressions were heterogeneous ($F_{4,29} = 3.20$, $p < 0.05$). Since, the regression of the Blue Slough data did not have a slope significantly different from zero ($F_{1,4} = 1.82$, NS), a second ANCOVA omitted the Blue Slough data. This analysis indicated that slopes were homogeneous for the remaining four sloughs ($F_{3,25} = 2.77$, NS) with a common slope of 0.94 , while regression elevations were heterogeneous ($F_{3,28} = 8.62$, $p < 0.001$), with significant differences for Mox Chuck vs. Xime ($p < 0.005$) and

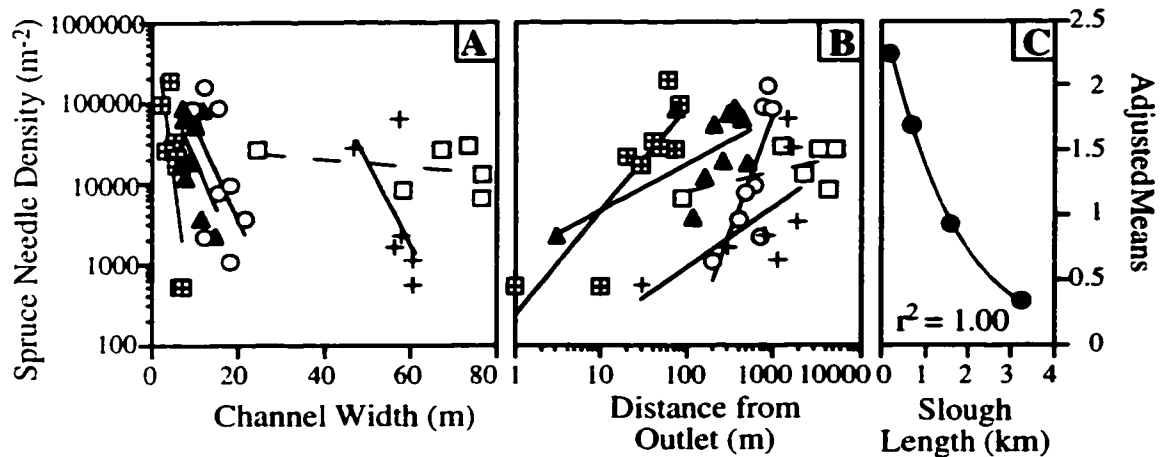


FIGURE 21. [A] Relationship between spruce needle density in slough sediments and distance from the slough outlet for, in order of increasing slough size, Hoolay Sl. (\blacksquare , $y = 232x^{1.29}$, $r^2 = 0.74$, $p < 0.005$), Xime Sl. (\blacktriangle , $y = 1220x^{0.57}$, $r^2 = 0.43$, $p < 0.05$), Kingfisher Sl. (\circ , $y = 0.0001x^{2.94}$, $r^2 = 0.63$, $p < 0.05$), Mox Chuck (+, $y = 19x^{0.83}$, $r^2 = 0.46$, $p < 0.10$), and Blue Sl. (\square , $y = 2500x^{0.24}$, $r^2 = 0.31$, NS). Solid lines = significant regressions, dashed lines = non-significant regressions. [B] Relationship between spruce needle density in slough sediments and slough channel width for Hoolay Sl. (\blacksquare , $y = 15.9e^{-1.32x}$, $r^2 = 0.55$, $p < 0.01$), Xime Sl. (\blacktriangle , $y = 12.8e^{-0.29x}$, $r^2 = 0.31$, $p < 0.05$), Kingfisher Sl. (\circ , $y = 13.5e^{-0.27x}$, $r^2 = 0.32$, $p < 0.10$), Mox Chuck (+, $y = 21.1e^{-0.23x}$, $r^2 = 0.37$, $p < 0.10$), and Blue Sl. (\square , $y = 10.3e^{-0.011x}$, $r^2 = 0.10$, NS). Solid lines = significant regressions, dashed lines = non-significant regressions. [C] Correlation of adjusted mean needle density- from Figure A with mainstem slough length.

vs. Hoolay ($p < 0.001$) sloughs, and for Kingfisher vs. Xime ($p < 0.05$) and vs. Hoolay ($p < 0.01$) sloughs, according to Tukey's HSD.

Adjusted means were correlated with slough size (Fig. 21C). In general, the smaller the slough the higher the abundance of spruce needles at a given distance from the slough outlet.

Benthic Community Structure

The benthos of the sampled sloughs was dominated numerically by nematodes (63.6% of all organisms), oligochaetes (9.6%), *Coulana canadensis* (Copepoda-Harpacticoida, 8.7%), and ostracods (8.7%). In terms of biomass, the dominant groups were nereid polychaetes (46.8%), *Hobsonia floridana* (Polychaeta, 23.5%), *Corophium salmonis* (Amphipoda, 8.8%), oligochaetes (7.5%), and nematodes (5.5%). The gravimetrically dominant feeding groups were predators (47.5%, essentially nereids, but also occasional ceratopogonid and empidid [Diptera:Insecta]) larvae, surface deposit feeders (35.4%, primarily *H. floridana*, and *C. salmonis*, but also Ostracoda and *Manyunkia esturina* [Polychaeta], and to a much lesser degree harpacticoid copepods and chironomid [Diptera]) larvae, and buried deposit feeders (12.9%, nematodes and oligochaetes).

There were significant relationships between slough channel width and blotted wet weight for only one category, surface deposit feeders (Fig. 22A). Negative exponential functions were better fits to the data than power functions, and biomass decreased as channel

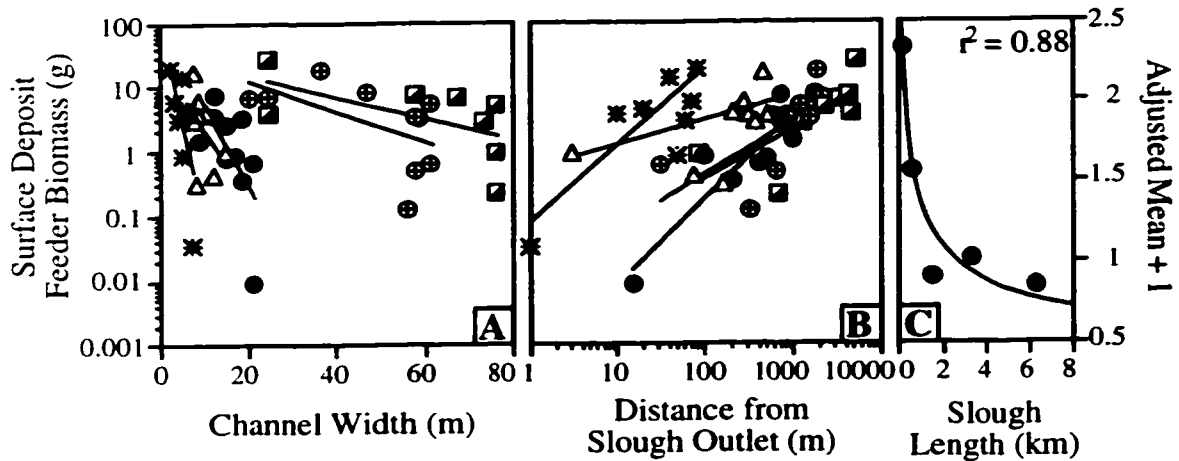


FIGURE 22. [A] Relationship between surface deposit feeder biomass and distance from slough outlet for, in order of increasing slough size, Hoolay Slough (\ast , $y = 0.070x^{1.11}$, $r^2 = 0.67$, $p < 0.01$), Xime Sl. (Δ , $y = 0.24x^{0.43}$, $r^2 = 0.28$, $p < 0.10$), Kingfisher Sl. (\bullet , $y = 0.0004x^{1.32}$, $r^2 = 0.82$, $p < 0.001$), Mox Chuck (\odot , $y = 0.009x^{0.83}$, $r^2 = 0.50$, $p < 0.05$), and Blue Sl. (\blacksquare , $y = 0.010x^{0.77}$, $r^2 = 0.53$, $p < 0.05$). [B] Relationship between benthic surface deposit feeder biomass and slough channel width for Hoolay Sl. (\ast , $y = 4.63e^{-0.75x}$, $r^2 = 0.41$, $p < 0.05$), Xime Sl. (Δ , $y = 3.08e^{-0.24x}$, $r^2 = 0.23$, $p < 0.10$), Kingfisher Sl. (\bullet , $y = 4.59e^{-0.30x}$, $r^2 = 0.39$, $p < 0.05$), Mox Chuck (\odot , $y = 3.46e^{-0.05x}$, $r^2 = 0.29$, $p < 0.10$), and Blue Sl. (\blacksquare , $y = 3.41e^{-0.04x}$, $r^2 = 0.35$, $p < 0.10$). [C] Correlation of adjusted mean biomass from Figure A with mainstem slough length.

width increased. Slopes were homogeneous with a common estimate of -0.024 ($F_{4,35} = 2.58$, NS). Elevations were heterogeneous ($F_{4,39} = 2.76$, $p < 0.05$), with significant differences for Kingfisher Slough vs. Blue and vs. Mox Chuck sloughs. In general, at similar channel widths, between slough comparisons show a consistent pattern of higher biomass in longer sloughs.

Surface deposit feeder biomass increased with increasing distance from the slough outlet (Fig. 22B), paralleling the results for spruce needles. There was no significant difference in the slopes of the regression lines ($F_{4,35} = 1.63$); the common slope (or exponent in the power function) was 0.86. There were significant differences in the elevations of the regressions ($F_{4,39} = 7.26$, $p < 0.001$), and Tukey's HSD revealed that Hoolay Slough differed from Blue, Mox Chuck, and Kingfisher sloughs ($p < 0.001$), as well as from Xime Slough ($p < 0.05$). Additionally, Xime Slough differed from Kingfisher Slough ($p < 0.05$). Adjusted means were correlated with slough size (Fig. 22C).

DISCUSSION

Landscape allometry assumes that abiotic factors are important in determining ecological patterns and processes, and that landscape form is one of these important abiotic factors. Fractal models of landscape form (e.g. Church & Mark 1980, Mandelbrot 1983, Rodriguez-Iturbe & Rinaldo 1997) imply that

landscapes can be viewed as systems of related rates (e.g., Woldenberg 1966, Bull 1975). Thus, rather than focus on fractal dimension, *per se*, landscape allometry focuses on related rates of change between various geomorphic features of the landscape, and corresponding related rates of change between various biological patterns and processes associated with those landscape features. Therefore, the terminology of allometry is used to reflect this focus, even though allometry and fractal geometry are similar phenomena (Mandelbrot 1983).

Surface Flow Velocity

Two fundamental patterns emerged from measurements of ebb tide surface flow velocity: [1] surface flow velocity was greater for larger sloughs (between-slough comparisons at slough outlets), and [2] surface flow velocity decreased further into the slough (within-slough longitudinal comparisons). In both cases velocity declined considerably as channel depth and width declined. This allometric scaling between ebb surface velocity and landscape form was the likely underlying foundation for the scaling of drogue exit time, accumulation of sediment organic material, and surface deposit feeder biomass with slough size.

Scaling of ebb surface flow velocity with slough size was constant for all sampling dates and for measurements taken early in the ebb tide as well as late in the tide. This somewhat surprising result can be explained as follows: assume that a sine function

approximates tidal flow so that for a set of sloughs $\{S_1, S_2, \dots, S_n\}$, $v_n = m_n \sin t$, where $v_n =$ surface flow velocity for S_n , $t =$ time, and m_n is a variable that affects the amplitude of the sine curve such that m_n is correlated with slough size. Since $v = aW^z$, where $W =$ slough outlet width and a and z are constants, then $m \sin t = aW^z$ or $m = a'W^z$. Additionally, since $v_1 = m_1 \sin t$ and $v_2 = m_2 \sin t$, then $v_1/v_2 = m_1/m_2$. Similarly, $v_1' = m_1 \sin (t+x)$ and $v_2' = m_2 \sin (t+x)$, then $v_1'/v_2' = m_1/m_2$. Thus, $v_1/v_2 = cv_1'/cv_2'$, where c is a constant. Since $v = aW^z$, $cv' = aW^z$ so that $v' = (a/c)W^z$, i.e. the scaling exponent, z , is constant regardless of t . Only the elevation of the regression line changes. This argument explains why the measurements of surface flow velocity taken on 25 Oct 92 two hours after high slack tide scale similarly to those taken four hours afterwards. The likely explanation for the similar scaling on different dates during different seasons and on spring and neap tides is that differences in tidal velocity due to differences in tide range can be accounted for by a variable, k , such that $v_n = km_n \sin t$, so that the preceding arguments still hold. Since $m = a'W^z$, then $km = ka'W^z$, so that only the elevation of the power function is changed.

Real data may differ slightly from the preceding ideal arguments because: [1] sine functions are only an approximation of tidal velocity patterns; and [2] data for each slough were not collected simultaneously, but rather in as short a period of time as was practical. Hence, while some error and variation in scaling

could be expected, such variation was not large enough to be detected statistically.

Export Probability

The exit time of marshmallow drogues was correlated with slough size as well as surface flow velocity. Two other factors, which probably affect exit time and also scale with slough size, are the amount of shoreline intertidal vegetation where detritus and drogues can be detained (Chapter 1), and the number and size of eddies caused by fallen logs (Montgomery et al. 1995). Drogue exit time varied between dates. However, between-slough differences were greater than between-date differences within sloughs. This suggests that slough size and factors that vary with slough size are the predominate influences on exit time.

Differences in tidal range or river discharge would seem to be the most likely explanation for between-date differences. However, neither is related to exit time. For example, Mox Chuck exit times were significantly different on two dates, yet the tidal ranges were identical. Conversely, on three sampling dates, Blue Slough tides had ranges of 2.5 m, 3.6 m, and 3.9 m, but there were no differences in exit time. Similar observations were made for Ann's Slough. This non-correlation with tidal range appears particularly problematic since ebb surface flow velocity, which presumably influences drogue exit time, differed between spring and neap tides. However, the spring tide range in that comparison was 4.1 m

while the neap tide ranges were 1.1 and 1.5 m, so the differences in tide range were more than 2.4 times greater for the velocity measurements than for the exit time measurements.

Data on river discharge for the lower Chehalis River were not available, so data from two large tributaries, the Satsop (gage #12035000) and Wynoochee (gage #12036000) rivers, were used instead. Both drain the southern flanks of the Olympic mountains and contribute significantly to the total discharge of the Chehalis river. Blue Slough mean exit times, were similar on two dates, while river discharge differed 2-fold. Likewise, mean exit times for Ann's Slough were similar on two dates, while river discharge differed more than 5-fold. Thus, the cause of the between date differences in mean exit time is unclear.

Drogue recovery, or export probability, decreased exponentially with distance from slough outlet. While ANCOVA did not detect significant differences in recovery rates, regression of $Dist_{50}$ with slough length indicated that $Dist_{50}$ was greater for larger sloughs. These contrasting results suggest that there was insufficient power for ANCOVA to detect significant differences. The regression results suggest that small sloughs were more efficient at retaining the drogues, probably for the same reasons that exit time was related to slough size, i.e. between slough scaling of surface flow velocity, area of intertidal vegetation, and numbers of fallen trees and logs. The scaling of export probability with slough size and distance from slough outlet is consistent with the geohydrologic continuum concept (Dame et al. 1992, Dame 1994),

except that landform geometry is explicitly the underlying cause of pattern.

Sediment Organic Content

Sediment organic content was greatest in the more distal and narrow portions of sloughs, where surface flow velocities were lowest and retention of marshmallow-drogues was greatest. At a given distance from their outlets, smaller sloughs had more sediment organic content than larger ones. Conversely, smaller sloughs had less sediment organic content at a given channel width than did large sloughs.

Allochthonous detritus that falls into sloughs is less likely to be exported from small sloughs than large sloughs, and less likely to be exported from the more distal and narrow portions of sloughs. This retained detritus eventually sinks to the sediments or is deposited there on a low tide and adheres to the mud. The combined influence of surface flow velocity and distance from the slough outlet means that allochthonous inputs to large sloughs 1000m from the outlet quickly escape the slough due to high ebb surface flow velocity, while slower velocity in smaller sloughs makes it less probable that allochthonous inputs at the same distance escape before the tide reverses. Hence, there was lower organic content in larger sloughs than smaller ones when the comparison was made at similar distances from the slough outlets. Conversely, a segment of a large slough that is of similar width to a

segment of a small slough will be more distant from the slough outlet. Thus, allochthonous materials falling into these slough segments may be moving at similar velocities, but they must travel a longer distance to escape the larger slough and thus are more likely to be retained by the larger slough and to eventually sink to the sediments. Finally, there is one additional influence on the amount of organic material in slough sediments: floodtide inputs are funnelled into narrowing channels thereby concentrating floating detritus in the more distal portions of sloughs.

Spruce Needles & Surface Deposit Feeders

Data from benthic samples are notoriously variable (Allan 1984). Nevertheless, patterns in spruce needle and surface deposit feeder abundance in the slough sediments paralleled those of sediment organic content. Spruce needle numbers and surface deposit feeder biomass were higher in the more distal and narrow reaches of the sloughs. They were also higher in smaller than larger sloughs at a given distance from the slough outlets. Likewise, as channel width increased spruce needle density and surface deposit feeder biomass in the channel sediments decreased. In general, at similar channel widths, spruce needle density and surface deposit feeder biomass were higher in longer than shorter sloughs.

Surface deposit feeders were the only feeding group that exhibited these patterns, probably because they are most directly

and immediately affected by sedimentation of detritus. Benthic predator density did not covary with potential prey density, i.e. surface deposit feeders, probably because there are many highly mobile pelagic predators such as Crangonid shrimp and fish that may compete with or prey on benthic predators.

SUMMARY

Scaling of slough ebb surface flow velocity, drogue exit time and export probability, sediment organic content, density of sedimented spruce needles, and surface deposit feeder biomass with distance from slough outlet and channel width show consistently similar patterns between sloughs of different sizes as well as consistently similar longitudinal patterns within sloughs. These consistently similar patterns suggest a chain of cause and effect. Allometric slough form (Chapter 1) results in scaling of ebb surface flow velocity, which in turn contributes to scaling of the exit time and export probability of floating detritus (e.g., spruce needles and terrestrial insects), which leads to scaling of the sedimentation rate of this detritus, and thus to scaling of the proportion of sediment that is organic material, scaling of the number of spruce needles in the sediments, and to scaling of benthic surface deposit feeder density.

These scaling patterns have potential implications for fish usage of the sloughs. Sticklebacks (*Gasterosteus aculeatus*), which

are abundant in sloughs, and juvenile coho and chinook salmon (*Oncorhynchus kisutch* and *O. tshawytscha*, respectively) feed extensively on terrestrial insects, especially aphids, that fall into the slough surface waters (Simenstad et al. 1992, 1993, 1997, Miller & Simenstad 1997, personal observations). Thus, the scaling of flotsam exit time and export probability suggest that prey resources for fish feeding at the surface will be more abundant in smaller sloughs and in the more distal and narrow portions of sloughs, which suggests that such fish would have greater success foraging in these areas. Similarly, epibenthic prey of juvenile salmon, sticklebacks, and peamouth (*Mylocheilus caurinus*) consist mostly of chironomid larvae and *Corophium salmonis*, both of which are surface deposit feeders. Hence, epibenthic-feeding fish may also have greater feeding success in smaller sloughs and in more distal, smaller slough segments. Finally, these could be optimal feeding areas where energy expenditure to maintain position is minimized due to lower current velocities while energy gain is maximized due to high concentration of prey.

The effect of predation on fish distribution is less clear, but it could be argued that the small fish that have been mentioned would be less vulnerable in smaller sloughs and smaller reaches. In shallow waters the fish would be vulnerable to great blue herons. However, in deeper waters potential predators include large fish, kingfishers, mergansers, osprey, and river otters.

Previous studies on the longitudinal patterns of fish use of two estuarine sloughs in the Fraser River (British Columbia) delta

(Levy et al. 1979, Levy & Northcote 1981) support the hypothesis that fish distributions in sloughs may scale with slough size.

Stickleback density increased with distance from slough outlets, in agreement with allometric predictions. Juvenile chinook, chum, and pink salmon (*O. gorbuscha*) had bimodal distributions with one density peak near the mouth and then a longitudinal increase in density with distance from the slough outlet.

From the perspective of habitat protection or restoration, these results suggest that bigger is not necessarily better. Small sloughs and the smaller reaches of large sloughs may be relatively important habitats for management targets like salmon and for ecosystem functions like secondary production. Diking of intertidal marshes has cut off many of these smaller channels from the estuary with consequences for fish that are likely to be disproportionate to the size of the channels (Simenstad et al. 2000).

CHAPTER 3

A Simple Model of Allochthonous Detritus Export from Oligohaline Tidal Channels, Motivated by Landscape Allometry

INTRODUCTION

Juvenile coho and chinook salmon (*Oncorhynchus kisutch* and *O. tshawytscha*) feed extensively on aphids and adult chironomids in oligohaline tidal channels (sloughs) which dissect the floodplain of the lower Chehalis River, Washington (Miller & Simenstad 1997, Simenstad et al. 1992, 1993, 1997). Aphids fall into the slough surface waters from intertidal sedges (*Carex lyngbyei*) that border the slough banks, while adult chironomids fall into the surface waters after their brief lifespan (< 2-3 weeks; Oliver 1981). Some proportion of these insects are exported from the sloughs by ebb tides. The remainder are retained in the slough where they may be consumed by predators or detritivores. This paper addresses two questions: [1] what proportion of aphid and chironomid inputs to the sloughs are exported to the river versus retained in the slough, and [2] does this proportion vary with slough size? An additional goal of this chapter was to develop a simple and intuitive model to investigate the role of landscape allometry (i.e. slough size and variables correlated with sloughs size) in tidal export of aphids,

chironomids and spruce needles from the Chehalis River estuarine sloughs.

Outwelling (tidal export of materials) has been a subject of considerable debate. Some estuarine systems have been shown to be net exporters, others net importers, and yet others neither, depending on the materials measured (Nixon 1980, Odum 1980, Dame et al. 1992). Several hypotheses have been proposed to explain variance in outwelling. The geohydrologic continuum hypothesis (Dame et al. 1992, Dame 1994) suggests that young tidal creeks tend to be net importers of all materials, while mid-aged systems tend to be net importers of particulate and exporters of dissolved constituents, and mature creeks are net exporters of everything. Geological age, in this case, is correlated with distance from the ocean shore (Dame et al. 1991). Odum et al. (1979) suggested that geomorphometry of coastal bays, tidal amplitude, and the magnitude of freshwater inputs interact to cause outwelling or inwelling.

Tidal export of aphids and chironomids were examined due to their importance in the diets of juvenile salmon. Spruce needles were examined as a non-edible contrast to the insects and because they were the most abundant constituent of the particulate organic matter export (POM). The goals for the model were that it should make predictions that agree with observations, be as simple as possible, be generalizable to sloughs of various sizes, and require minimum effort for reasonable estimates of its parameters.

METHODS

Study Site Description

The estuarine sloughs of the lower Chehalis River are located in a tidal floodplain that is bordered to the north by the Olympic mountains and to the south by the Willapa Hills. The estuarine reach of the floodplain is generally 2.5 km wide and stretches along the river for 15 km from the downstream cities of Aberdeen and Cosmopolis to diked farmlands upstream (Figs. 23 & 24). Most of the floodplain is relatively undisturbed by human impacts despite proximity at its downstream limit to several cities and to diked farmlands at its upstream limit.

The floodplain consists of Sitka spruce (*Picea sitchensis*) forested wetlands, with scrub-shrub components of the wetland dominated by salmonberry (*Rubus spectabilis*), black twinberry (*Lonicera involucrata*), cascara (*Rhamnus purshiana*), red-osier dogwood (*Cornus stolonifera*), and willows (*Salix* spp.). Understory vegetation is dominated by slough sedge (*Carex obnupta*) and skunk cabbage (*Lysichitum americanum*). The floodplain is dissected by oligohaline sloughs that generally contain two intertidal habitats, mudflats and a fringing marsh "bench" that is usually a virtual monoculture of Lyngby's sedge (*C. lyngbyei*). Salinity in the sloughs ranges from about 1 to 14 parts per thousand (ppt) depending on river discharge, slough depth and distance along the estuarine gradient. The estuary is mesotidal;

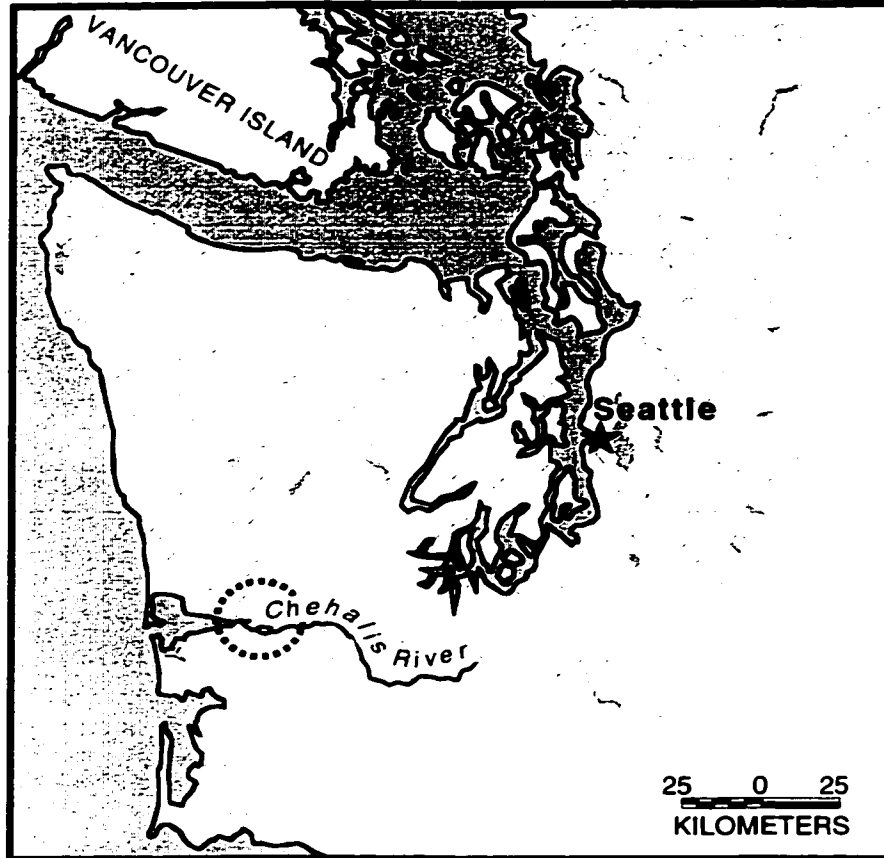


FIGURE 23. Study Site Location. Circled area is the general location of the estuarine sloughs of the lower Chehalis River.

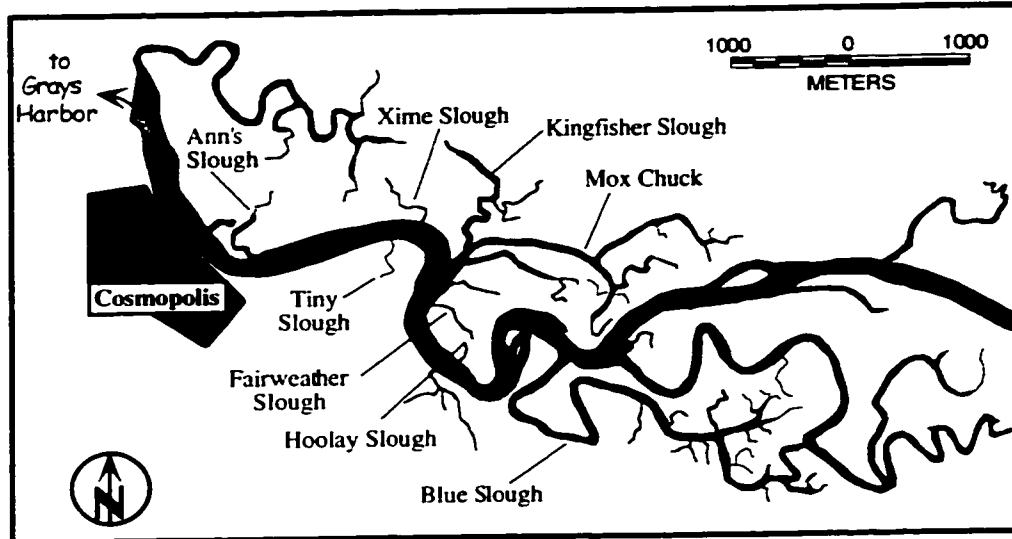


FIGURE 24. Estuarine Sloughs of the Lower Chehalis River.

maximal tide ranges can approach 4.5 m in some sloughs. Tides are mixed semidiurnal. Smaller sloughs are almost completely drained on low tides.

Initial Model

Export of floating allochthonous detritus from a point, P , in a slough depends on the rate of allochthonous input (input) at that point and the probability of tidal export (*probexp*) from the slough at that point. Thus:

$$\text{Export}_P = (\text{input}_P)(\text{probexp}_P) \quad [1]$$

Total export is the sum of all such products for every point, P_i , along the length of the slough at a distance D_i from the slough outlet. Thus:

$$\text{Total Export} = \int_0^L (\text{input}_{P_i})(\text{probexp}_{P_i})dD \quad [2]$$

where L is the length of the slough. Export probability is known to depend on distance from the slough outlet as well as slough length (Chapter 2). Input rates were estimated by sampling.

Materials that are not exported (i.e., $(\text{input}_P)(1-\text{probexp}_P)$) have various possible fates, including consumption by predators or detritivores within the sloughs, and sedimentation. The model does

not distinguish between these possible fates. They are implicitly aggregated in the *probexp* term.

Spruce Needle and Chironomid Input Rates

Rectangular plastic trays (55 x 37 x 12 cm) were placed in intertidal sedge habitat on transects perpendicular to the shoreline. Tall plastic (PVC) pipes were inserted into the ground at each side of the trays to allow them to float on the high tide, but not move from the transect. The trays were filled with a dilute solution (20-30%) of unscented household ammonia, that served as a preservative for any insects which fell into the trays. It was assumed that the strong smell of ammonia would be aversive to chironomid flies, or at least not an attractant, so that capture rates would represent passive collection of senescing flies. Trays were collected three to five days after deployment, depending on the abundance of insects in the trays.

Transects were established in three locations: Hoolay Slough, where the channel was 5.4 m wide and the transect 1.8 m long; Ann's Slough, where the channel was 24 m wide and the transect 6 m long and the Chehalis River near the outlet of Mox Chuck, where the river channel was 215 m wide and the transect was 73 m long. Each transect was sampled on three occasions in 1996; June 2-5, June 22-29, and July 31 to August 4.

Aphid Input Rate

Gentle breezes and small waves can rustle intertidal sedges, causing them to brush against each other and dislodge aphids. To estimate this input of aphids to slough surface waters, square meter plots of intertidal sedges were enclosed at low tide by 0.5 mm mesh netting attached to PVC poles. At high tide, insects floating on the water within the enclosures were collected with a small dip net, taking care not to dislodge any insects from the sedges. Five sample plots per slough were located in sedge habitat that was immediately adjacent to slough channels. This area is lower in elevation than sedge habitat closer to shore, more exposed to channel flow, and thus more likely to contribute aphids to slough surface waters. Nearshore sedges are rarely completely inundated by high tides, while channel edge sedges are frequently completely inundated.

Slough Morphometry

The relationship between channel width and distance from slough outlet was estimated from measurements of aerial photos of 1:2400 scale (US Army Corps of Engineers-Seattle District, 1990). Likewise, the location and length of channel shoreline bordered by intertidal sedges was estimated from the same photos, and later verified by field measurements.

Tidal Export and Import of Detrital Flotsam

Detrital flotsam (floating terrestrial insects and vegetation) was collected on spring tides during May and June using 0.5-mm mesh nets that resemble oil-spill containment booms (Chapter 1). The booms were placed across slough outlets at high slack tide and sampled for flotsam export until low slack tide. Influx was sampled similarly on the following flood tide. Flotsam was skimmed by the booms from the surface of the flowing water (to a depth of 25 cm), subsampled with a dip-net, and sorted through a series of sieves of 13-mm, 5.6-mm, and 0.5-mm mesh. Sampled sloughs, in order of decreasing size, included Blue, Elliott, Peel's, Mox Chuck, Kingfisher, Ann's, Fairweather, Mossbeard, and Hoolay sloughs.

Mathematical and Statistical Analysis

Mathematica 3.0 (Wolfram 1991) was used to evaluate integrals in the model. The software employed for regression analysis was StatView 4.5.1 (Abacus Concepts, Inc., Berkeley, CA). Regression variables were log transformed to equalize variance in the residuals. Systat 5.2.1 (Systat, Inc., Evanston, IL) was used for analysis of covariance (ANCOVA) and Tukey's HSD *post hoc* tests. All statistical tests were at the 5% significance level.

RESULTS

Observed Tidal Export and Import

Detrital export consisted overwhelmingly of spruce needles. However, that portion which was composed of terrestrial insects was dominated by aphids and adult chironomids. Aphids comprised 29.8% of all terrestrial insects by frequency and 27.0% by weight; chironomid adults were 29.1% by frequency and 16.0% by weight; Psocoptera (bark lice) were 13.2% by frequency and 15.8% by weight. The dominant insect order was the Diptera, with 17 families--principally adult Chironomidae, Ceratopogonidae, Sciaridae, Psychodidae, Empididae, and Tipulidae. Homoptera were the next most important due primarily to the abundance of Aphidae, but Cicadellidae, Cercopidae, and Delphacidae were also present. Hymenopteran parasitoids consisted of numerous families, with the two most abundant being Braconidae and Ichneumonidae. Twenty-one families of terrestrial Coleoptera were encountered, of which the Carabidae, Coccinellidae, and Curculionidae were the most abundant. Additionally, spiders and millipedes were notable.

Regression slopes did not differ for samples taken in 1993 vs 1995 for either outflux or influx of spruce needles ($F_{1,7} = 0.01$ and 0.78 , respectively), or aphids ($F_{1,6} = 0.11$ and 0.05 , respectively). Chironomid export also did not differ between years ($F_{1,5} = 0.32$), but import did ($F_{1,5} = 11.5$, $p < 0.05$). Likewise, adjusted means did not differ for export or import for spruce needles ($F_{1,6} = 0.81$ and

0.87, respectively) or aphids ($F_{1,7} = 0.09$ and 0.29 , respectively), nor for chironomid outflux ($F_{1,6} = 0.46$). The significant between-year difference in the scaling of chironomid influx was likely due to a Type I error since there were no differences in the three other between-year comparisons. Thus, 1993 and 1995 data were combined for the following comparisons. Export and import scaled similarly with slough length for spruce needles (Fig. 25A; $F_{1,18} = 0.01$ NS) chironomids (Fig. 25B; $F_{1,14} = 0.36$ NS), and aphids (Fig. 25C; $F_{1,17} = 0.11$ NS). Needle export was 3.4 times greater than import (paired sample $t = 3.9$, $df = 9$, $p < 0.005$) while chironomid export was 4.5 times greater (paired sample $t = 4.1$, $df = 8$, $p < 0.005$), and aphid export was 2.3 times greater (paired sample $t = 3.45$, $df = 9$, $p < 0.01$).

Probability of Export (probexp)

Probexp, was estimated from previous research (Chapter 2), where very small biodegradable drogues (mini-marshmallows) were used to simulate slough flotsam export and provide estimators of the probability of flotsam export for four sloughs: Mox Chuck ($y = 3.32e^{-0.0034D}$), Ann's Slough ($y = 1.86e^{-0.0040D}$), Fairweather Slough ($y = 2.84e^{-0.0075D}$), and Tiny Slough ($y = 1.88e^{-0.0073x}$), where y = probability of export and D = distance from slough outlet. Analysis of covariance (ANCOVA) did not find significant differences in equation elevations or exponents (Chapter 2), so that one estimate of export probability for all sloughs was:

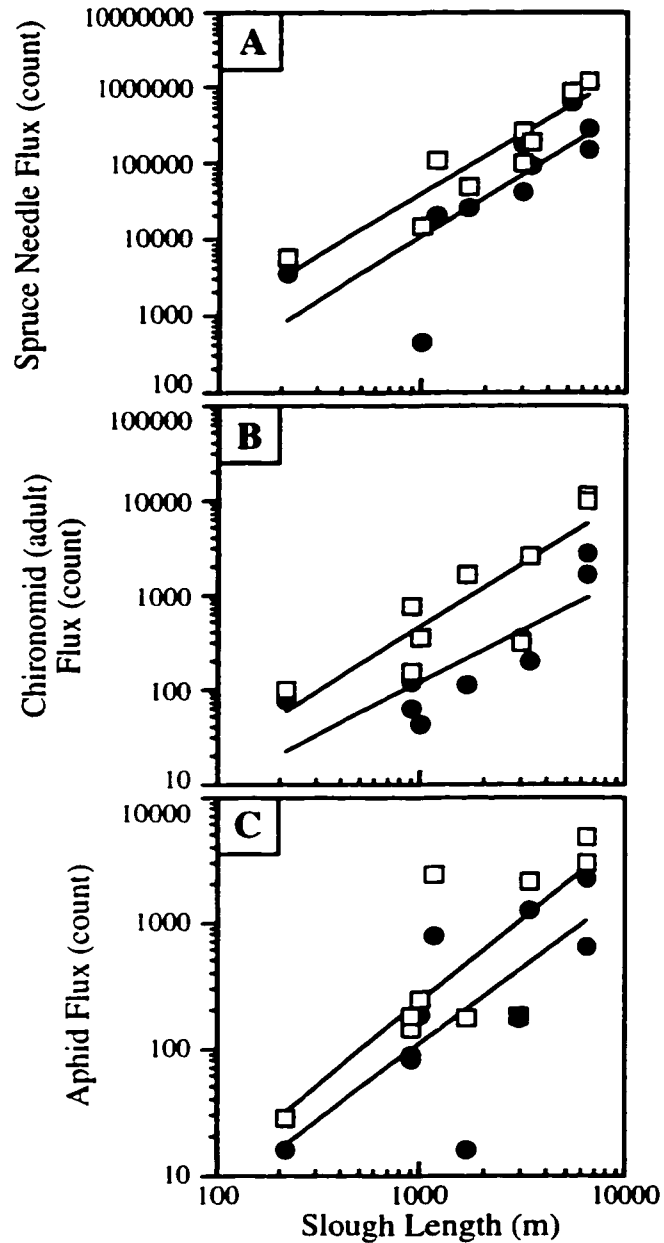


FIGURE 25. [A] Spruce needle outflux (\square , $y = 0.55x^{1.62}$, $r^2 = 0.87$, $F_{1,8} = 53$, $p < 0.001$) and influx (\bullet , $y = 0.11x^{1.67}$, $r^2 = 0.64$, $F_{1,8} = 14.4$, $p < 0.005$) from oligohaline tidal sloughs. [B] Chironomid outflux (\square , $y = 0.044x^{1.34}$, $r^2 = 0.73$, $F_{1,7} = 18.4$, $p < 0.005$) and influx (\bullet , $y = 0.065x^{1.08}$, $r^2 = 0.67$, $F_{1,7} = 14.0$, $p < 0.01$). [C] Aphid outflux (\square , $y = 0.017x^{1.33}$, $r^2 = 0.74$, $F_{1,8} = 22.5$, $p < 0.001$) and influx (\bullet , $y = 0.014x^{1.27}$, $r^2 = 0.64$, $F_{1,9} = 16.0$, $p < 0.005$).

$$\text{probexp} = 174e^{-0.0038D} \quad [3]$$

However, there was a weak correlation between slough length (L) and equation elevations (Fig. 26A; $y = 0.0046L + 1.79$, $r^2 = 0.63$) and exponents (Fig. 26B; $y = ([0.0022]\ln L - 0.021)D$, $r^2 = 0.65$), so the ANCOVA may not have had sufficient power to detect size-related differences in equation parameters. This assumption led to three alternative estimates, where the equation parameters for *probexp* depend on slough size:

$$\text{probexp} = (0.00046L + 1.79)e^{([0.022]\ln L - 0.021)D} \quad [4]$$

$$\text{probexp} = 174e^{([0.022]\ln L - 0.021)D} \quad [5]$$

$$\text{probexp} = (0.00046L + 1.79)e^{-0.0038D} \quad [6]$$

When each alternative was used to calculate the probability of export from slough termini and these values were plotted against slough size, only equation 6 exhibited a consistent decline in export probability with increasing slough size (Fig. 27A). All other equations made the unlikely prediction that slough termini export probability declines with slough size up to a point--and then suddenly increases with slough size. Thus, equation 6 was chosen as the best estimate of export probability.

Setting *probexp* = 1 in equation 6 and solving for *D* produces a value, D_1 , which represents the distance from the slough outlet at which the probability of export is 100%. Any further distance from

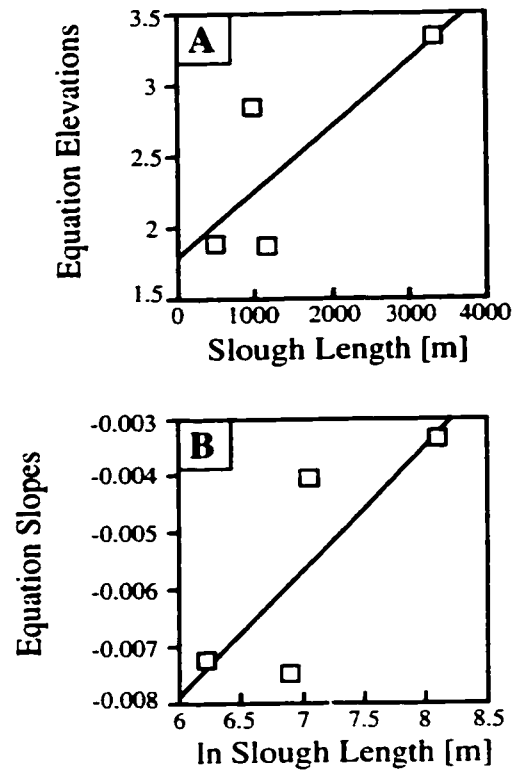


FIGURE 26. Relationship between slough length and [A] the elevation, and [B] the exponent of fitted equations for observed drogue export probability (see Chapter 2).

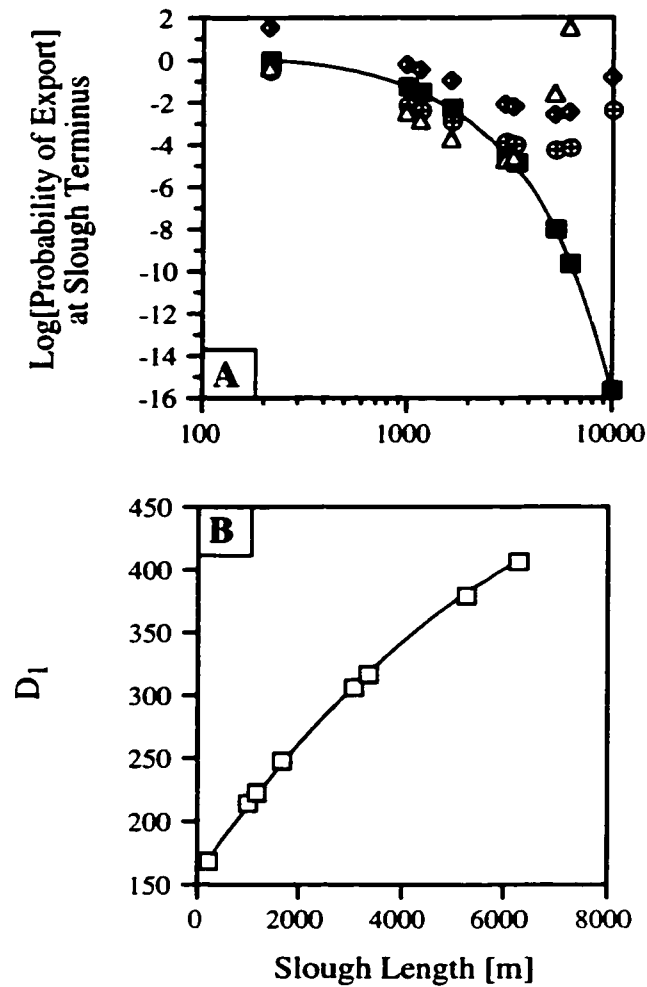


FIGURE 27. [A] Flotsam export probabilities from slough termini predicted by four alternative equations; Δ , $y = 174e^{-0.0038x}$; \oplus , $y = (0.00046x + 1.79)e^{([0.022]\ln x - 0.021)x}$; \blacklozenge , $y = 174e^{([0.022]\ln x - 0.021)x}$; \blacksquare , $y = (0.00046x + 1.79)e^{-0.0038x}$ [B] Distance from the slough outlet at which the probability of export equals 100% vs slough length, as predicted by equation 6 (see text for details).

the outlet and *probexp* declines. Because *probexp* cannot exceed 1, every point between the slough outlet and D_1 also has a 100% probability of exporting detritus. For equation 6, D_1 depends on slough size (Fig. 27B) and is best described as:

$$D_1 = 2.88 \times 10^{-6} L^2 + 0.057L + 158 \quad [7]$$

Spruce Needle, Chironomid, and Aphid Input

Needle input declined with distance from the shoreline for the Chehalis River and Ann's Slough sampling sites (Fig. 28A). There were no between date-differences in rates of decline for the Chehalis River ($F_{2,15} = 1.31$, NS) or Ann's Slough ($F_{2,8} = 1.68$, NS) sites. Thus, date was ignored as a factor for further comparisons. Between-site comparisons showed similar rates of needle input decline along the transects for the Chehalis River and Ann's Slough sites ($F_{1,23} = 0.58$, NS), with a common exponent (slope of log-transformed data) of -1.07. Adjusted means were significantly different between the two sites ($F_{1,24} = 17.2$, $p < 0.001$). For Hoolay Slough, there were also no between-date differences ($F_{2,3} = 2.47$, NS), but needle input was constant with shoreline distance. However, this does not necessarily signify that the pattern of Hoolay Slough needle input was inconsistent with that observed for the other two sites. It is likely that the traps in Hoolay Slough were catching significant input from both banks, because the slough is very narrow. Thus, overlapping patterns of input from each bank

would give the appearance of constant input even though, for each bank separately, input may be declining with distance. Input into a small slough was assumed to be similar to that of a larger slough so that $y = ax^{-1.07}$, where y = needle input, x = distance from the shore, and -1.07 is estimated from the Ann's Slough and Chehalis River sampling sites. Total input across the width of Hoolay Slough is the product of the observed mean rate of input and the width of the channel, or 41.4 needles per tide. This also equals $2 \int_1^{540} ax^{-1.07}$, where the constant accounts for input from both banks and the upper limit of integration is the width of the channel (cm). Solving for a yields the following equation for Hoolay Slough needle input: $y = 5.1x^{-1.07}$, which is depicted as a dashed line in Figure 28A. Thus, the pattern of needle input was similar for all three sites. However, total input from both banks, integrated across the width of the channels, increased linearly with channel width (Fig. 28B; $r^2 = 1.00$) so that

$$ninput = 6.6W \quad [8]$$

where $ninput$ = spruce needle input and W = channel width.

In contrast, there were no consistent patterns in chironomid input (Fig. 28C). Input rates did not vary across the transects between dates for the Chehalis River ($F_{2,15} = 3.61$, NS), Ann's Slough ($F_{2,8} = 1.62$, NS), or Hoolay Slough ($F_{2,3} = 0.52$, NS), so date was ignored. Distance from shore was significant for Chehalis River

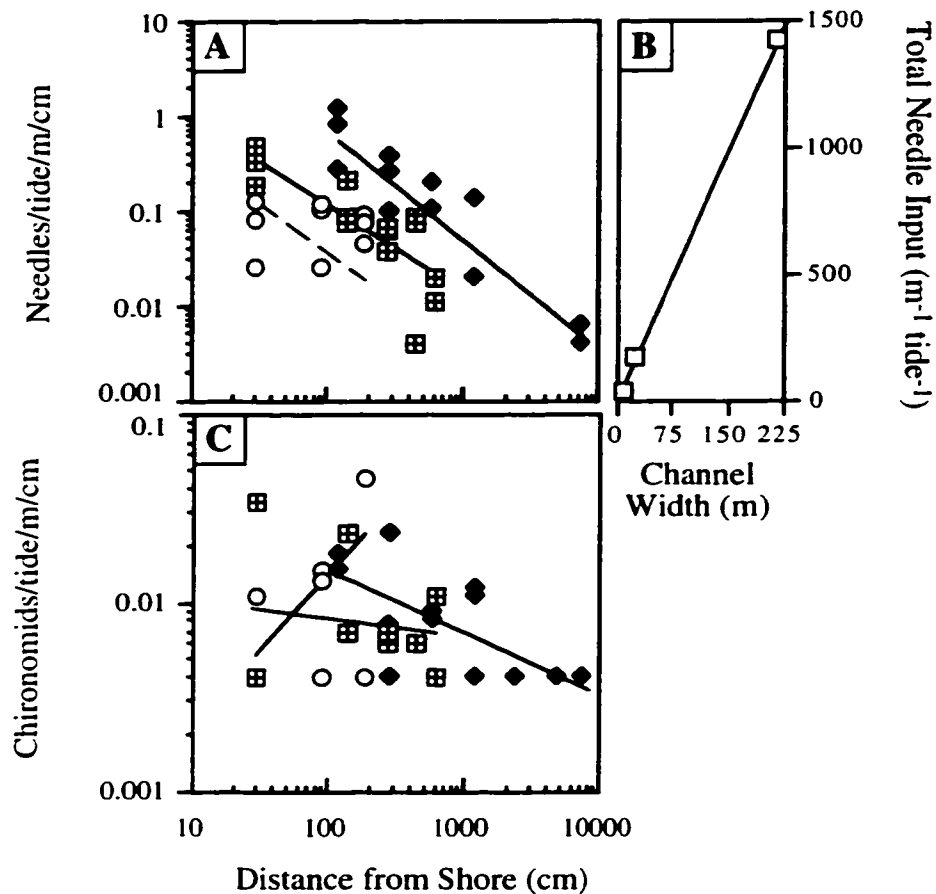


FIGURE 28. [A] Spruce needle input along transects perpendicular to the shores of the Chehalis River (\blacklozenge , $y = 137x^{-1.15}$, $r^2 = 0.77$, $F_{1,19} = 77$, $p < 0.001$), Ann's Slough (\boxtimes , $y = 8.7x^{-0.94}$, $r^2 = 0.63$, $F_{1,12} = 20$, $p < 0.001$), and Hoolay Slough (\circ). Values are per m of shoreline per cm of transect per ebb tide. The dashed line is a theoretical extrapolation, not a statistical fit. [B] Total needle input, calculated by integrating equations fitted to transect data across the width of the channels. [C] Input of adult (senescing) chironomids.

input ($r^2 = 0.52$, $F_{1,14} = 0.58$, $p < 0.005$) but not for Hoolay Slough ($r^2 = 0.25$, $F_{1,5} = 1.65$, NS) or Ann's Slough ($r^2 = 0.02$, $F_{1,8} = 0.19$, NS). Slopes were not significantly different between sloughs ($F_{2,38} = 0.04$, NS) nor were adjusted means ($F_{2,40} = 2.06$, NS). Mean chironomid input (*cinput*) for all sloughs was 0.99 per m of shoreline per m of transect per tide, i.e.,

$$\text{cinput} = 0.99W \quad [9]$$

Aphid input did not vary significantly between sloughs (one-way ANOVA, (Fig. 29; $F_{7,28} = 0.70$, NS). Mean aphid input, *ainput*, for all samples was 19 aphids/m²/tide. Thus,

$$\text{ainput} = 19 \quad [10]$$

Slough Morphometry

Sloughs taper at similar rates regardless of size (Fig. 30A; $F_{7,53} = 0.50$, NS; common slope = -0.0115). The y-intercepts for the regression equations describing this tapering are related to slough length (Fig. 30B; $y = 0.013L^{1.00}$, $r^2 = 0.95$), because the y-intercepts estimate outlet width, which scales with slough length (Chapter 1). Thus, a general equation for the rate of slough tapering is:

$$W = -0.0115D + 0.013L \quad [11]$$

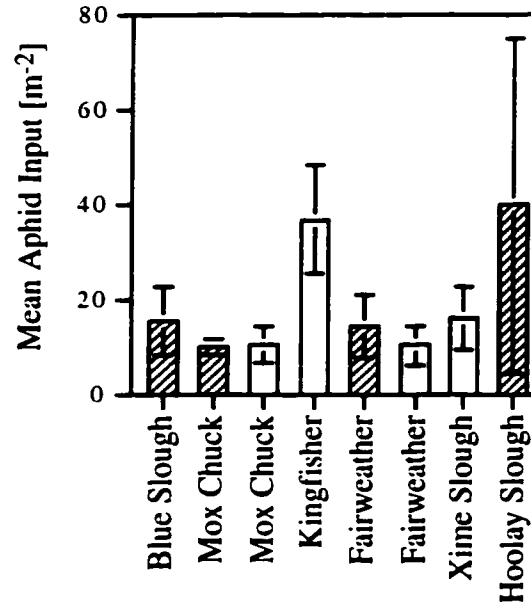


FIGURE 29. Mean aphid input to slough surface waters from square meter plots of intertidal sedges. Hatched bars are July 1995 samples, open bars are July 1996. Error bars are 1 standard error; $n = 5$ for each sample. Sloughs are arranged in order of decreasing size from left to right.

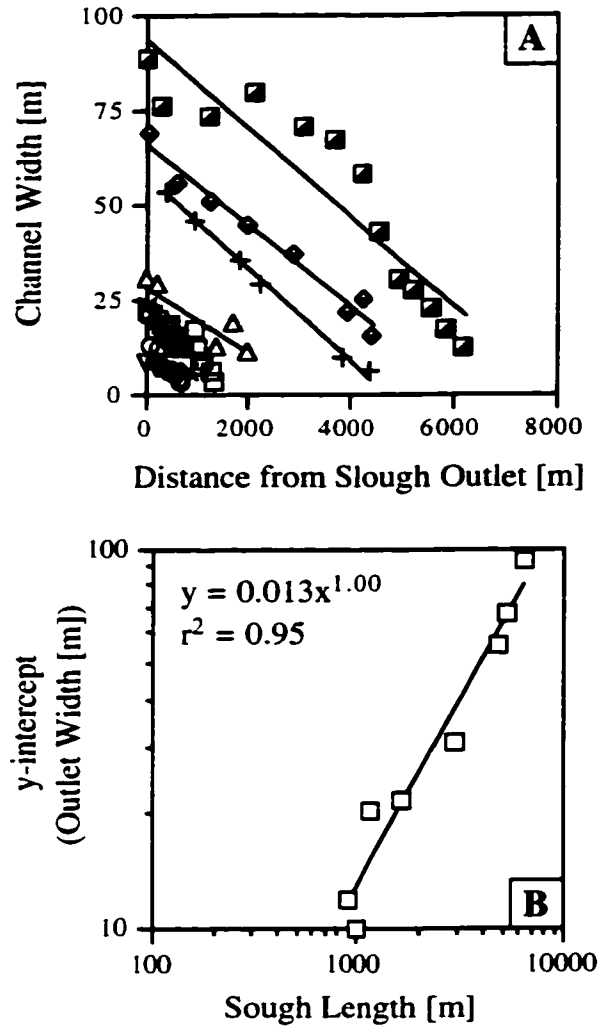


FIGURE 30. Slough width vs. length. [A] Rate of slough tapering for Blue (■), Elliott (◆), Peel's (+), Higgins (▲), Kingfisher (□), Ann's (×), Mossbeard (○), and Fairweather (▽) sloughs. [B] Relationship between y-intercepts for equations fitted to data in Figure 7A and slough length. The y-intercepts estimate outlet width.

Intertidal sedge habitat was found in predictable locations within sloughs, e.g., in depositional areas near slough outlets and on the point bars of slough meanders. A topological simplification of slough form was used to model this pattern in terms of distance from slough outlet (Fig. 31A). The distance of the first sedge patch from the slough outlet was designated S_1 ; the distance of the end of that patch was S_2 ; the distance of the next patch was S_3 ; the distance at which it ended was S_4 ; etc. Thus, $S_2 - S_1$ is the length of the first sedge patch and $S_3 - S_2$ is the length of channel between the first and second sedge patches. When S-values were standardized by slough length (i.e. S_i/L) the resulting regressions describing the spacing of sedge patches had similar slopes ($F_{4,13} = 1.98$, NS) and elevations ($F_{4,17} = 1.58$, NS) for most sloughs (Fig 31B) so that a single equation described sedge spacing ($y = 0.08x + 0.10$) and standardized S-values coincided for sloughs of different sizes. The only exception was Blue Slough. Blue Slough and other large sloughs have been shown to have deviant patterns of sedge habitat compared to smaller sloughs, possibly due to historical impacts from log transportation and storage (Chapter 1).

Assembling the Model

The model for slough flotsam export can be assembled from its constituent equations, beginning with equations 2 and 6:

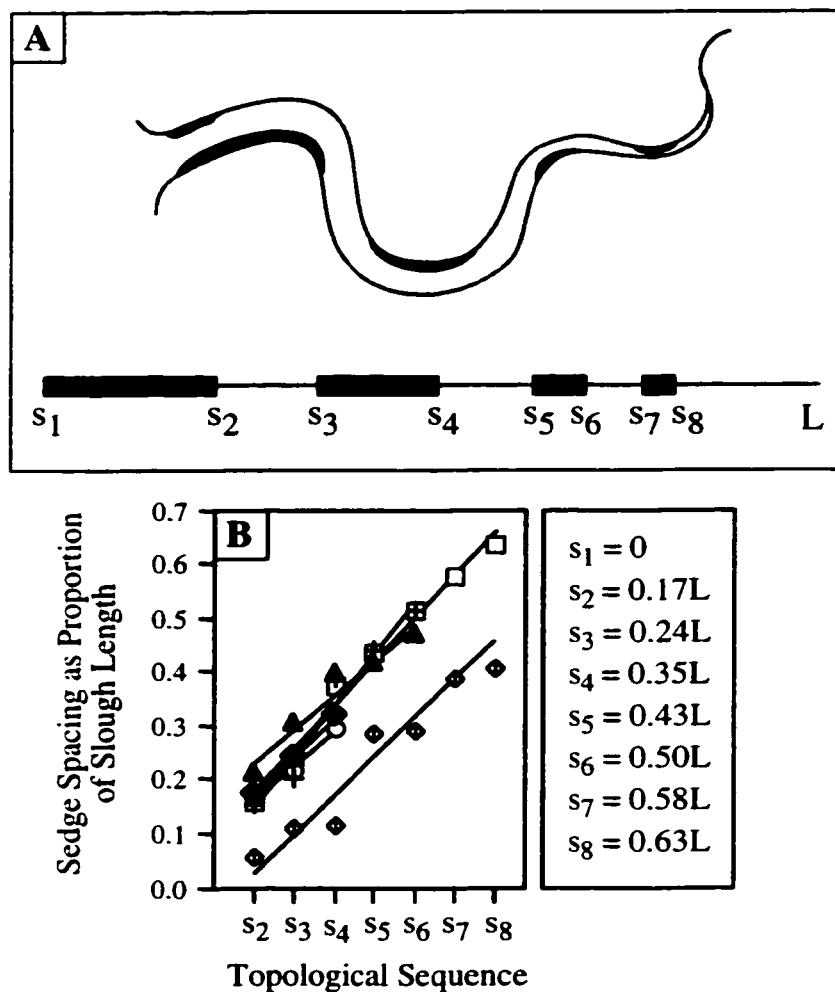


FIGURE 31. Sedge habitat distribution. [A] Schematic of typical sedge habitat distribution in smaller sloughs, with a topological representation for comparison. s_1, s_2 , etc., represent distances from the slough outlet. L = the length of the slough. [B] Standardized sedge habitat distribution for, in order of decreasing slough size, Blue (\diamond), Kingfisher (\blacktriangle), Ann's (\square), Fairweather (\circ), Xime (+), and Hoolay (\blacklozenge) sloughs.

$$\text{Export} = \int_0^L (\text{input})(0.00046L + 1.79)e^{-0.0038D} dD \quad [12]$$

However, equation 7 shows that probability of export = 1 for an initial distance from the slough outlet, D_1 , so that equation 12 has to be modified:

$$\text{Export} = \int_0^{D_1} (\text{input}) + \int_{D_1}^L (\text{input})(0.00046L + 1.79)e^{-0.0038D} dD \quad [13]$$

The input functions for spruce needles (equation 8), chironomids (equation 9), and aphids must be modified by equation 11 to substitute distance and length terms for width:

$$n_{\text{input}} = 0.086L - 0.076D \quad [14]$$

$$c_{\text{input}} = 0.0129L - 0.0114D \quad [15]$$

These equations can be substituted into equation 13 and the integrals solved to yield the following equation for spruce needles

$$\begin{aligned} \text{Export} = e^{-0.0038D} & (-0.01038L^2 - 22.68L - 20.1) \Big|_{D_1}^L \\ & + (0.086L - 0.076)D \Big|_0^{D_1} \end{aligned} \quad [16]$$

and chironomids

$$\text{Export} = e^{-0.0038D}(-0.001558L^2 - 3.4L - 3) \Big|_{D_1}^L + (0.013L - 0.011)D \Big|_0^{D_1} \quad [17]$$

so that export can be evaluated for each slough of a given length, L . Similar calculations were done for aphid export except that the S -values which denoted limits of each sedge habitat patch determined the limits of integration.

Model Predictions vs Empirical Data

Model predictions for spruce needle export were similar to empirical observations of net needle export (Fig. 32A). Slopes were not significantly different ($F_{1,14} = 1.20$), nor were elevations ($F_{1,15} = 0.78$). In contrast, model predictions of chironomid export were 13.5 times higher than observed net export. Slopes were not significantly different ($F_{1,12} = 1.67$), but elevations were ($F_{1,13} = 50.7$, $p < 0.001$). Likewise, model predictions for net aphid export were on average 24.5 times greater than observed (Fig. 32B; paired- $t = 5.4$, $df = 7$, $p < 0.001$). ANCOVA, which omitted Blue Slough due to its atypical sedge habitat spacing, indicated that slopes were not significantly different between the model predictions and observed net export for the remaining sloughs ($F_{1,7} = 0.95$).

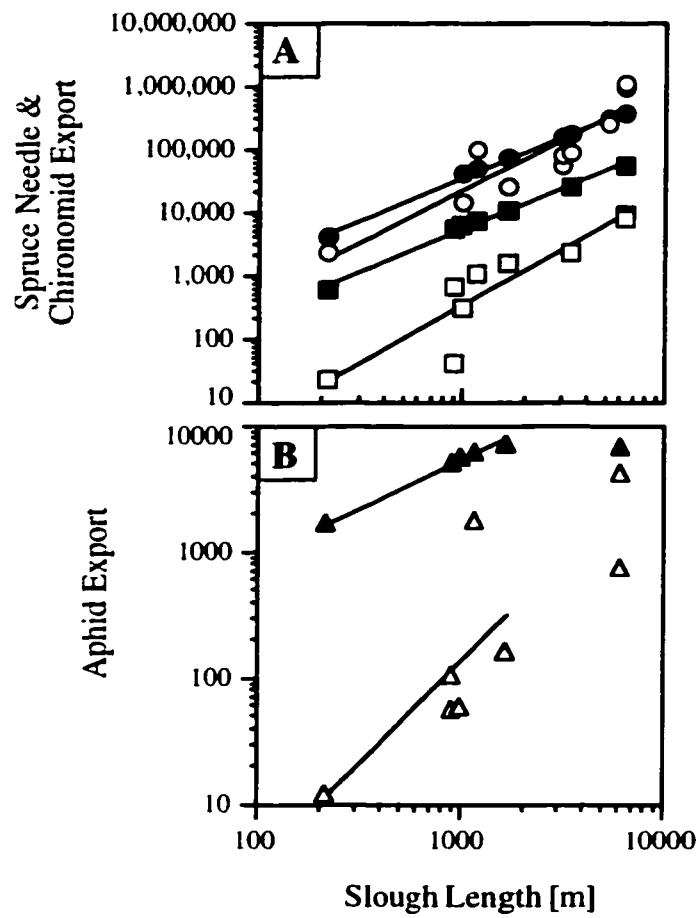


FIGURE 32. Comparisons of model predictions (shaded symbols) and observed net export (open symbols) for [A] spruce needles (squares) and adult chironomids (circles), and [B] aphids.

Total input of spruce needles, chironomids, and aphids from riparian and intertidal vegetation was estimated by setting $probexp = 1$ for the entire lengths of the sloughs. Predicted export divided by predicted input estimated the proportion of input that could be exported by the sloughs (I/E). These estimates were identical for needles and chironomids due to the similar nature of their input. I/E declined with slough length for needles-chironomids and aphids (Fig. 33). However, I/E for small sloughs was nearly 100%, which seemed unrealistic given previous research that found significant accumulation of organic material in the sediments of small sloughs (Chapter 2). The likely source of these high I/E estimates were overestimates of D_I , especially for small sloughs. Thus, the estimate of $probexp$ (equation 6) was modified to reduce this overestimate for small sloughs to a greater degree than for large sloughs. An additional requirement was that D_I for a slough of length, 0, should be 0. The following equation satisfied these requirements (Fig. 34) and entailed the least modification of the original estimate of $probexp$:

$$probexp = (0.00046L + 1.005)e^{-0.0038D} \quad [18]$$

The constant, 1.005, is not significantly different from the original term ($t = 1.72$, $df = 2$).

Predictions by the modified model for spruce needle export were again similar to empirical observations of net needle export (Fig. 35A). Slopes were not significantly different ($F_{1,14} = 0.74$), nor

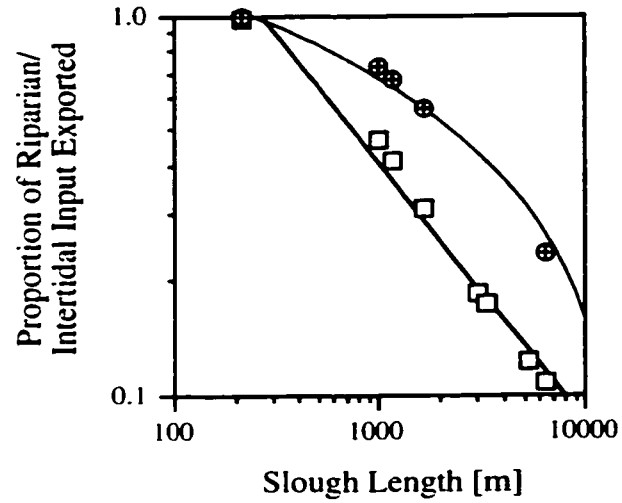


FIGURE 33. Model predictions of the proportion of riparian and intertidal inputs of spruce needles and chironomids (□), and aphids (⊙) exported by sloughs of different sizes.

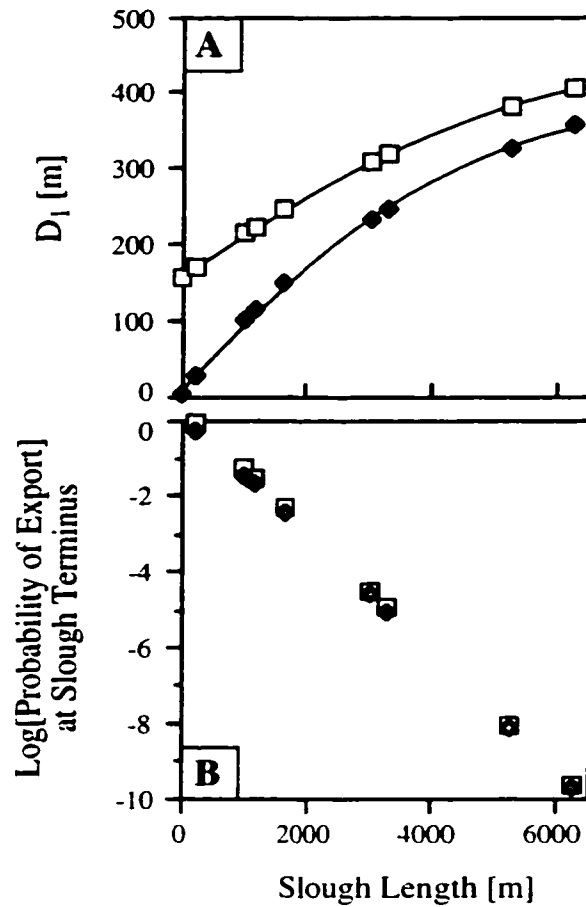


FIGURE 34. Comparison of [A] D_1 and [B] flotsam export probabilities from slough termini, predicted by the original (\square , $\text{probexp} = [0.00046L + 1.79]e^{-0.0038D}$) and a modified (\blacklozenge , $\text{probexp} = [0.00046L + 1.005]e^{-0.0038D}$) estimate of flotsam export probabilities.

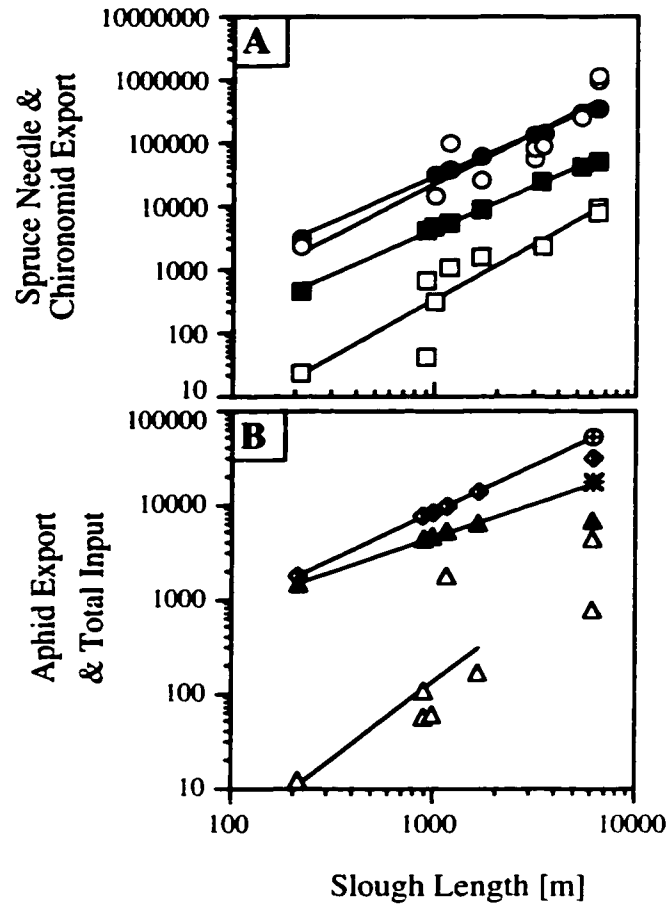


FIGURE 35. [A] Comparisons of modified model export predictions (shaded symbols) and observed net export (open symbols) for spruce needles (squares) and adult chironomids (circles). [B] Similar comparisons for aphids (triangles); and comparison of Blue Slough predictions using observed sedge habitat spacing (\blacklozenge , input; \blacktriangle , export) vs extrapolation from small slough pattern (\oplus , input; \blackstar , export).

were elevations ($F_{1,15} = 0.08$). Differences in slopes were reduced relative to the original model, due to greater reductions in the estimates of export from smaller sloughs. Likewise, the modified model for chironomid export also resulted in greater reductions of export for smaller sloughs so that already insignificant differences in slopes between model predictions and empirical data were further reduced ($F_{1,12} = 1.24$, NS) and model predictions for chironomid export were now only 11 times higher than observed net export ($F_{1,13} = 44.7$, $p < 0.001$). Predictions by the modified model for net aphid export were little changed, on average 21.6 times greater than observed (Fig. 35B; paired-t = 5.3, $df = 7$, $p < 0.001$).

Sedge habitat spacing data and measurements of sedge habitat width (Chapter 1) suggest that Blue Slough sedge habitat has been impacted by human activity. Therefore, a comparison was made of model predictions for aphid input and export for Blue Slough using observed sedge habitat spacing versus predictions consistent with results for smaller sloughs (Fig. 35B). If sedge habitat spacing in Blue Slough were similar to that in smaller sloughs, there would be almost 20,000 more aphids input to Blue Slough surface waters per ebb tide and almost 10,000 more aphids exported from the slough. The modified model produced more reasonable estimates of I/E for small sloughs, while estimates for larger sloughs were relatively unchanged (Fig. 36). The general form of the relationship between I/E and slough length was unchanged by the modified model.

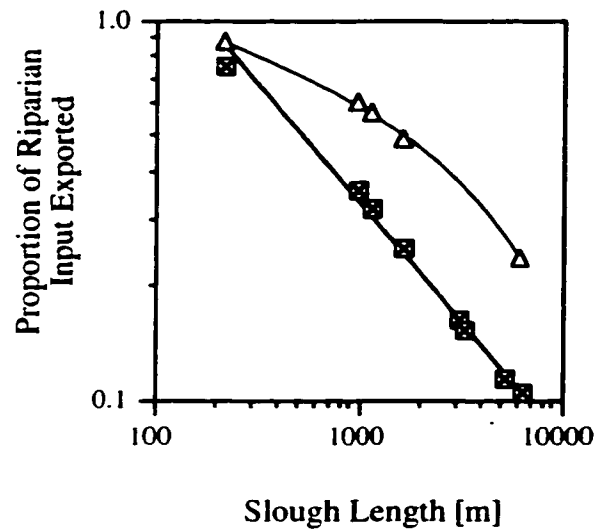


FIGURE 36. Modified model predictions of the proportion of riparian and intertidal input of spruce needles and chironomids (\boxtimes), and aphids (Δ) exported by sloughs of different sizes.

DISCUSSION

The close agreement between model predictions and observed net export of spruce needles was surprising, considering that an imprecise and static estimate of flotsam export probability was used in the model. In fact, flotsam export probability from a given point in a slough must decline over the course of the ebb tide simply because there is less time to reach the slough outlet before the tide reverses. That a static estimate, measured from the beginning of the ebb tide, was sufficient to predict net export suggests that most of the export occurs early in the tide, probably within the first two hours of ebb flow. Indeed, field observations support this supposition. The first few hours of export sampling were required frequent sampling from the flotsam nets due to the large volumes of flotsam accumulating behind the nets, while the last few hours were calm due to low accumulation. This is because the greatest input occurs in the widest parts of the slough channel which are also closest to the slough outlet.

In contrast to spruce needles, observed and modeled aphid and chironomid export differed greatly. There are two possible explanations: [1] aphid and chironomid input were overestimated, or [2] predators consumed the difference. The model assumed that only a 1 m-wide swath of intertidal sedge habitat bordering slough channels contributed aphid input. Since the model overestimated export by 21.6 times, a reduction of input by the same factor would imply that the width of sedge habitat producing the input is less

than 5 cm, an unlikely figure. On the other hand, the average stickleback (*Gasterosteus aculeatus*) eats approximately 56 aphids per ebb tide (unpublished data, $n = 14$). Accordingly, as few as 25-100 sticklebacks could account for the difference between model predictions and observed export, depending on slough size. Intensive sampling of Ann's Slough has shown that stickleback catches for the slough average about 136 individuals per ebb tide, but have ranged as high as 945 (Simenstad et al. 1992, 1993, 1997). Thus, stickleback predation alone can account for the observed differences. Furthermore, coho and chinook salmon also consume an average of 5 and 12 aphids each, respectively, per ebb tide (Miller & Simenstad 1997, Simenstad et al. 1992, 1993, 1997), further bolstering the argument for predation.

It is less clear whether fish predation alone can account for the differences in predicted and observed chironomid export for Ann's Slough. Coho and chinook are the most significant piscine consumers of adult chironomids in the slough (approximately 4.8 and 6.0 individuals per fish per ebb tide, respectively) followed by sticklebacks (0.9 individuals per fish per ebb tide). At mean fish population abundances these rates of consumption only account for 20% of the difference in chironomid export. However, fish catches are highly variable. Maximum estimated fish populations can be seven times larger than average populations and could account for the difference. Waterstriders (Hemiptera: Gerridae), which are very abundant in the sloughs, may also account for a sizable proportion of chironomid consumption. The alternative

explanation, that adult chironomids may be attracted to trays containing dilute ammonia, seems unlikely. The rate of chironomid input into the trays was less than 0.5 individuals per day per tray. If the trays were a particularly attractive feature, one would expect a greater rate of input.

The model indicates that small sloughs export a greater proportion of riparian and intertidal input than do large sloughs. In large sloughs, much of the slough is too distant from the outlet to effectively export flotsam (Chapter 2). This is illustrated by size-based comparisons of the probability of export from slough termini (Fig. 34) where Hoolay Slough (215 m long) had an 83% chance of exporting flotsam from its terminus while Blue Slough (6300 m long) had ten billionths of 1 percent chance of exporting material from its terminus. While all of Hoolay Slough had an 83% or greater chance of exporting flotsam, a large proportion of Blue Slough had an 83% or less chance of export. Thus, landscape allometry (slough size) can be added to the geohydrologic continuum (= distance from outlet: Dame et al. 1991, 1992) and geomorphometry (Odum et al. 1979) as landform influences on tidal export.

The more landward portions of large sloughs may be important rearing areas for juvenile salmon (and sticklebacks) due to retention and concentration of food resources-aphid and chironomid flotsam (Levy & Northcote 1981, 1982). Aerial photos of slough systems in Washington state indicate that these are also areas that historically have been frequently diked or obstructed with tide gates in order to facilitate agricultural development

(personal observation). Thus, habitat restoration efforts should consider assigning priority to these areas.

Landscape allometry posits that ecological processes scale with landscape geometry. In the present example, spruce needle, chironomid, and aphid export scaled with slough size. The proportion of riparian and intertidal input that was exported scaled negatively with slough size. Needle input varied with channel width probably due to greater wind in wider channels. Chironomid input varied linearly with channel width simply due to a constant rate of input per m^2 or per m-width of channel. Finally, aphid input was proportional to the length of intertidal sedge habitat, while export depended on habitat spacing along the length of the sloughs. Sedge habitat length and spacing were constant proportions of slough length. Meander length, mean radius of curvature, and channel width are all related in non-tidal streams. Similar relationships for tidal channels would account for the predictability of sedge habitat length and spacing, because sedge habitat is most extensive on the depositional side of meander bends.

Landscape allometry was a successful organizing principle that motivated and guided the construction of the export model. The concept may be applicable to other ecological systems, such as rivers or lakes, where there are precedents for landscape allometry (Chapter 4).

CHAPTER 4**Landscape Allometry:
Scaling Landscape Form and Ecological
Pattern and Process in Rivers and Lakes****INTRODUCTION**

The issue of scale is fundamental to landscape ecology (Turner 1989, Turner et al. 1989, Levin 1992, Levin & Pacala 1997). Many landscape-scale ecological patterns and processes can be linked to geomorphological patterns, which exhibit fractal geometry (e.g. Kent & Wong 1982, Frontier 1987, Rodriguez-Iturbe & Rinaldo 1997). Fractal models of landscape form imply that landscapes can be viewed as systems of related rates (e.g., Woldenberg 1966, Bull 1975, Church & Mark 1980). When the relative rate of change of one part of a system, y , is proportional to the relative rate of change of another part of the system, x , then

$$\frac{dy}{y} \frac{1}{dt} = b \frac{dx}{x} \frac{1}{dt} \quad [1]$$

where b is a proportionality constant. On multiplying by dt and integrating, one obtains the log-linear function, $\log(y) = \log(a) + b \log(x)$, which is equivalent to the power function, $y = ax^b$ (Woldenberg 1966).

Related rates of change between various geomorphic features of the landscape suggest corresponding related rates of change between various biological patterns and processes associated with those landscape features. This hypothesized parallel scaling between geomorphic and ecological patterns and processes is landscape allometry. More practically, descriptions of landscape features and their boundaries (*e.g.*, lake shorelines) by allometric models can be coupled to descriptions of ecosystem processes (*e.g.*, fluxes of energy, nutrients, or organisms across ecosystem/landscape boundaries) to generate predictions of landscape-scale biological patterns from local-scale biological investigations.

Although landscape allometry is rooted in the fractal geometry of landforms, it does not focus on calculating fractal dimensions. Instead it focuses on relationships between ecological and geomorphological patterns and processes. Fractal dimension relates measures of one variable to the spatial or temporal scale of measurement, *e.g.* the dividers method, the grid method, the Korcak method, the variogram method, time series techniques, and other related approaches (Sugihara & May 1990, Chase 1992, Hastings & Sugihara 1993). However, ecosystem ecologists may often be interested in the relative extent of one compartment of an ecosystem versus another, for example lake epilimnion volume vs. littoral zone area, or stream volume vs. hyporheic volume (*i.e.* the subterranean portion of streamflows). An allometric approach, not concerned with estimating fractal dimension, focuses on the

relationships between two or more variables that describe the extents of ecosystem compartments, which can then be linked to the ecosystem fluxes between those compartments. Since landscape form is allometric and landscape boundaries are important zones of ecological fluxes (Wiens et al. 1985, Frontier 1987, Holland & Risser 1991, Shachak & Jones 1995), ecosystem fluxes are likely to scale in tandem with the landscape boundaries with which they are associated.

There are two precedents in ecology which suggest that a linkage between landscape form and ecosystem processes could be a fruitful approach to landscape ecology. The first is the morpho-edaphic index which was developed to predict fish production in northern temperate lakes from lake depth and total dissolved solids (Ryder 1965), and the second is the river continuum concept which links stream order to the structure and function of biotic communities in the streams (Vannote *et al.* 1980).

LANDSCAPE ALLOMETRY AND THE MORPHO-EDAPHIC INDEX

There has been a long history in limnology of relating lake morphometry, particularly mean lake depth and lake surface area, to lake productivity (Thienemann 1925, Rounsfell 1946, Rawson 1955). Ryder's (1965) correlation of a morpho-edaphic index with fish production attempted to elaborate on earlier morphological work by accounting for edaphic influences of a lake's watershed on the nutrient status of a lake. The morpho-edaphic index is the ratio

of the concentration of total dissolved solids to the mean depth of a lake. In an alternative model by Schindler (1971), the ratio of lake catchment area to lake volume was assumed to be proportional to the concentration of limiting nutrients in a lake, and thus to productivity. The reasoning is that the lake catchment is the source of the nutrients which are washed into the lake by precipitation and then diluted by the volume of the lake. Likewise, Ohle (1965) showed a correlation between primary production and the ratio of drainage area to lake surface area in some European lakes. In yet a third morphometric approach, Fee (1979) related lake primary production to the ratio of epilimnion sediment area to epilimnion volume, the rationale being that nutrient concentration in the epilimnion is related to nutrient input (recycling) from the sediments in contact with the epilimnion and diluted by the volume of the epilimnion. Other indices of lake productivity include the ratio of lake volume to sediment surface area (Strøm 1933), littoral area to volume of the trophogenic layer (Patalas 1980), shoreline length to lake area (Gasith & Hasler 1976), lake surface area to mean depth (Osgood 1988), and littoral area to pelagic volume (Wetzel 1990). This plethora of ratios can be reconciled by a holistic, allometric ecosystem model, because most morphometric features of lakes are interrelated (Tables 4 & 5).

Many components and characteristics of lake ecosystems affect system productivity including: the drainage basin, which is a source of nutrients for the lake (*e.g.* Rasmussen *et al.* 1989, Dillon *et al.* 1993); the littoral zone, which is an area of high nutrient cycling

Table 4. Equations for Lake Landscape Allometry—Physical Variables.

Equation	Remarks	Source
1. $P = bA^m$	P = lake perimeter, A = lake surface area; $m = 0.75$ $m = 0.58$ for Orinoco dish lakes, $m = 0.71$ for channel lakes	Kent & Wong 1982 Hamilton et al 1992
2. $V = jA^m$	V = lake volume (km^3), A = lake area (ha); $j = -5.4, m = 1.32; r^2 = 0.96$ $j = -4.7, m = 1.42; r^2 = 0.93$ $j = 3.6 \times 10^{-6}, m = 1.32; r^2 = 0.97$ $j = -4.4, m = 1.07; r^2 = 0.88$ $j = -4.5, m = 1.16; r^2 = 0.96$ $j = -4.8, m = 1.44; r^2 = 0.67$	Ryder 1965 Fee 1979 Schneider & Haedrich 1989 LaPerriere 1990 Stewart & Haugen 1990 Dillon <i>et al.</i> 1993
3. $A_L = kA_D^m$	A_L = lake surface area, A_D = drainage area; $k = 0.16, m = 0.99; r^2 = 0.95$ $k = 3.5, m = 0.48; r^2 = 0.66$ $k = 0.47, m = 0.74; r^2 = 0.87$; ELA $k = 0.30, m = 0.93; r^2 = 0.93$; NOLSS	LaPerriere 1990 Dillon <i>et al.</i> 1993 Fee <i>et al.</i> 1996 Fee <i>et al.</i> 1996
4. $V = jZ^m$	V = lake volume; Z = max. lake depth; $m = 1.12; r^2 = 0.77$	Dillon <i>et al.</i> 1993
5. $Z_x = jZ^m$	Z_x = mean lake depth, Z = max. lake depth; $m = 0.940$	Chow-Fraser 1991
6. $E_d = bA^{0.25}$	E_d = depth of thermocline, A = lake surface area	Gorham & Boyce 1989

7. $E_d = bZ^m$	E_d = depth of mixed layer, Z = total depth; $m = 0.61$; $r^2 = 0.83$	Hargrave 1973
8. $N = kA$	N = nutrient input to lake, A = catchment area, k includes edaphic factors & precipitation rate	Schindler 1971
9. $[N] = kAV^{-1}$	$[N]$ = lake nutrient concentration V = volume of lake; k as in #8.	Schindler 1971
10. $F = kZ_x^a$	F = flushing rate (per year), Z_x = mean lake depth; $a = -0.734$; 95% CI = $-1.015 < a < -0.453$	Chow-Fraser 1991
11. $T_r = kV^m$	T_r = water residence time; V = lake volume; $m = 0.40$; $r^2 = 0.46$ $m = 0.58$; $r^2 = 0.31$	Brunskill & Schindler 1971 Paloheimo & Zimmerman 1983
12. $T_r = kZ_x^m$	T_r = residence time; Z_x = mean lake depth; $m = 1.06$; $r^2 = 0.64$ $m = 1.27$; $r^2 = 0.48$	Brunskill & Schindler 1971 Paloheimo & Zimmerman 1983
13. $A_E = kA_L^m$	A_E = epilimnion sediment area, A_L = lake surface area; $m = 1.04$; $r^2 = 0.70$	Zimmerman <i>et al.</i> 1983 Paloheimo & Zimmerman 1983

14. $V_E = kV_L^m$	V_E = epilimnion volume, V_L = lake volume; $m = 0.92$; $r^2 = 0.95$	Zimmerman <i>et al.</i> 1983 Paloheimo & Zimmerman 1983
15. $V_E = kA_S^m$	V_E = epilimnion volume, A_S = lake sediment area, $m = 0.64$; $r^2 = 0.41$	Zimmerman <i>et al.</i> 1983 Paloheimo & Zimmerman 1983
16. $Z_E = kV^m$	Z_E = epilimnion depth, V = lake volume; $m = 0.137$; $r^2 = 0.60$	Fee <i>et al.</i> 1979
17. $Z_E = kA^m$	Z_E = epilimnion depth, A = lake area; $m = 0.191$; $r^2 = 0.58$	Fee <i>et al.</i> 1979

Table 5. Equations for Lake Landscape Allometry—Biological Variables.

Equation	Remarks	Source
1. $P = jD^m$	P = fish production, D = mean lake depth; $j = 22.7$, $m = -0.53$; $r^2 = 0.69$	Ryder 1965
2. $P = j(T/D)^m$	T = total dissolved solids; $j = 2.09$, $m = 0.446$; $r^2 = 0.73$ [NB: T/D only slightly more predictive than D]	Ryder 1965
3. $C_x = kA^m$	C_x = 25-yr mean fish catch, A = lake area; $m = 0.67$; $r^2 = 0.71$	Rawson 1955
4. $[N] = kB$ $B = kA/V$	$[N]$ = nutrient concentration, B = various biotic variables, e.g. phytoplankton biomass, chlorophyll concentration, sediment organic C & N concentration, A = catchment area, V = lake volume	Schindler 1971
5. $Q = CFV^{2/3}$	Q = fish biomass/lake/year, C = conversion efficiency of nutrient to fish, F = flux of limiting nutrient, V = lake volume	Schneider & Haedrich 1989
6. $Q = 20.9A^{0.84}$	Q = fish biomass/lake/year, A = lake surface area; $r^2 = 0.95$, for data from Ryder (1965)	Schneider & Haedrich 1989
7. $C_0 = jZ^d$	C_0 = sed. respiration, Z = mean lake depth; $j = 709$, $d = 0.515$; $r^2 = 0.75$	Hargrave 1973
8. $C_0 = kZ_m^e$	C_0 = sed. respiration, Z_m = mixed layer depth; $k = 85$, $e = 0.71$; $r^2 = 0.64$	Hargrave 1973
9. $P = kZ_x^m$	P = primary production, Z_x = mean lake depth; $m = 0.89$; $r^2 = 0.93$	Fee <i>et al.</i> 1979

10. $P = kV^m$	P = primary production, V = lake volume; $m = 0.446$; $r^2 = 0.80$	Fee <i>et al.</i> 1979
11. $P = kZ_e^m$	P = primary production, Z_e = depth of epilimnion; $m = 1.64$; $r^2 = 0.49$	Fee <i>et al.</i> 1979
12. $S = kA^m$	S = mean sockeye salmon spawning escapement, A = lake area; $m = 1.68$; $r^2 = 0.75$	Burgner 1991

and throughflow from the terrestrial to the aquatic portions of the system, and a nursery area for juvenile fish (reviews by Pieczynska 1990, 1993, Wetzel 1990); the surface microlayer, which is an area of nutrient transformation and atmospheric-aquatic exchange (Parker & Barsom 1970, Wangersky 1976, Dillon *et al.* 1993, Södergren 1993); lake sediments, which are areas of nutrient transformation and exchange (Carlton & Wetzel 1988, Martinova 1993, Van Rees *et al.* 1996); the thickness and volume of the epilimnion, which determines the photosynthetically available irradiance in the mixed layer, the efficiency of nutrient cycling, and the vertical distribution of biota (Fee *et al.* 1996); the residence time of water and nutrients in the various physical compartments of the lake ecosystem; and populations of plankton and fish (*e.g.* Carpenter *et al.* 1992). Landscape allometry provides a conceptual framework for the holistic integration of these various limnological compartments, and it suggests that as a lake is scaled up or down in size the proportional constraints on lake productivity are altered. Ryder (1982) neatly summarizes the quandary that ecosystem ecologists generally face:

...numerous environmental factors influence productivity of natural lakes to some degree; most of these discrete factors also affect one another to collectively influence productivity and, ultimately, fish yield. To measure hundreds of variables, to calculate the degree each is integrated with the others, and to

determine fish yields from all these interactions is usually an intractable task. On the other hand, simplification of natural phenomena into uncomplicated indices may lead to naive conclusions and gross mismanagement of aquatic environments.

An allometric approach to ecosystem studies allows a middle path between naive simplicity and intractable complexity, because very simple models of landscape form can be wedded to detailed models of ecosystem processes at landscape boundaries.

This discussion has focused on lake nutrients and productivity, but a similar rationale applies to lake heat budgets and models of lake ice formation and break-up. Heat fluxes occur at primarily two lake boundaries, sediment-water, and air-water. Advection occurs with precipitation, and stream and watershed discharge. Thus lake volume, surface area, shoreline length, basin area, and discharge, are among the morphometric parameters related to the heat budget (Wetzel & Likens 1979), and all of these parameters interact so that small lakes gain and lose heat more quickly than large ones. Lake depth and volume have been correlated with date of lake ice formation (Stewart & Haugen 1990, Vavrus *et al.* 1996), while Scott (1964, cited in Stewart & Haugen 1990) found that lakes with larger shoreline to area ratios lost their ice sooner, and Palecki & Barry (1986) observed a significant correlation of lake surface area with ice break-up dates.

LANDSCAPE ALLOMETRY AND THE RIVER CONTINUUM CONCEPT

Fish distributions in rivers are affected by several abiotic variables which change from the headwaters to the mouth, including slope, depth, stream order and temperature (Burton & Odum 1945, Huet 1959, Kuehne 1962, Sheldon 1968). Invertebrates also respond to longitudinal changes in substrate, temperature, discharge, and current velocity (Illies & Botosaneanu 1963, Andrews & Minshall 1979). Vannote *et al.* (1980) expanded on this earlier work and proposed in their river continuum concept (RCC) that the geomorphology and hydrology of a river form a template for a continuous longitudinal pattern of community structure and function which is the consequence of longitudinal changes in organic matter loading, transport, utilization, and storage. A prominent theme of the RCC is that stream community structure and metabolism are strongly dependent on riparian vegetation, and the influence of riparian vegetation is strongly dependent on stream size, *i.e.* stream order. As stream order increases, the relative importance of terrestrial organic input decreases, and the importance of autochthonous primary production and organic transport from upstream increases. A test of the RCC by Naiman *et al.* (1987) found that 70% of 73 biological variables examined showed a significant trend with stream order in the 1st-10th order Moisie River drainage.

1985). Johnson *et al.* (1995) suggest that better measures might be the ratio of floodplain width to channel width, the ratio of shoreline length to water surface area in a river reach, or a measure of the average extent and rate of flooding. Kellerhals & Church (1989) recommend drainage area or some characteristic discharge as more meaningful indicators of river size than stream order. All of these alternatives to stream order can be integrated by an allometric approach to lotic ecology. Furthermore, an allometric approach expands the focus of the RCC from riparian-river channel interactions to interactions between the river and other landscape elements such as floodplains or the hyporheic zone.

ALLOMETRY OF THE HYPORHEIC ZONE

River water can be divided into two zones (Triska *et al.* 1989). The channel zone consists of water flowing on the surface. The hyporheic zone consists of subterranean flows of a mixture of river and ground water with the proportion of stream water decreasing with increasing depth of the hyporheic zone. A microbial biofilm, associated with hyporheic sediment particles, mediates a variety of nutrient transformations and is a significant part of a riverine microbial loop (Dahm *et al.* 1987, Gibert *et al.* 1994, Gounot 1994, Stanford *et al.* 1994).

Transport of water and dissolved solutes across the channel-hyporheic interface is through advective exchange, *i.e.*, results from localized pressure variations in the channel that force water into

the subsurface. The depth of advective exchange, and thus of the hyporheic zone, is determined by stream discharge and the roughness, permeability, and morphology of the surface channel. Downwelling of surface water into the hyporheic zone occurs mostly at the upstream end of riffles and point bars, while upwelling occurs at the downstream end (Vaux 1968, Vervier & Naiman 1992, White 1993, Holmes *et al.* 1994, Valett *et al.* 1994). Upwelling zones have been shown to be sources of limiting nutrients and, consequently, associated with high algal productivity (Stanford & Ward 1988, Holmes *et al.* 1994, Valett *et al.* 1994).

Several lines of evidence suggest that hyporheic zones vary with stream size. In rivers with few channel obstructions, river meander length is proportional to mean channel width (Leopold *et al.* 1964). Hence, as river size increases so does the distance between point bars which are associated with meander bends, and so does the distance between riffles which are associated with points of inflection, or crossover, between meanders. In riffle-pool channels in which large woody debris (LWD) forms channel obstructions, riffle-pool spacing decreases with increasing LWD loading (Montgomery *et al.* 1995). For a given debris loading riffle-pool spacing decreases with channel width because large logs may force formation of several pools across a wide channel, whereas only a portion of such logs would be contained in narrower channels. Therefore, in channels obstructed by LWD, both LWD loadings and channel width affect the frequency of riffle-pool complexes. However, there is an inverse relationship between LWD

loading and channel width because logs in larger channels are more readily transported by streamflows. As a result, Montgomery *et al.* (1995) have shown that there are several direct and indirect effects of channel width and LWD loading on riffle-pool spacing.

Because point bar and riffle-pool spacing scale with stream size, downwelling and upwelling frequency should also scale with stream size, with consequent scaling of primary and secondary production associated with nutrient-rich upwelling areas. Benda *et al.* (1992) have shown that the area of salmonid spawning gravels (= riffles) relative to the wetted perimeter of a stream decreases with stream power, which is a function of stream cross-sectional area, velocity, and slope, all of which are functions of stream size. So, it is likely that the sizes of riffles and point bars scale with stream size. Holmes *et al.* (1994) suggest that smaller bars or riffles would have shorter flowpaths and therefore shorter times for nutrient transformations. How does the effect of many small point bars or riffles differ from that of a few large point bars or riffles?

Other physical parameters which scale with stream size also affect the frequency and extent of hyporheic exchange. Flow through sediments is the product of hydraulic conductivity, K , and hydraulic gradient, dh/dl ,

$$v = -K \frac{dh}{dl} \quad [2]$$

where v is specific discharge, or discharge per unit cross-sectional area perpendicular to flow; h is hydraulic head; and l is length of flow path (Freeze & Cherry 1979). Hydraulic conductivity is a function of sediment grain size ($K = Cd^2$, where d is grain particle diameter and C is a constant). Hydraulic head, h , is the sum of elevation head, z , and pressure head, Ψ . Thus, hydraulic gradient, dh/dl , is the sum of elevation gradient (*i.e.*, slope, dz/dl) and pressure gradient, $d\Psi/dl$. Pressure gradient is a function of discharge (*e.g.* Triska *et al.* 1989, Rouch 1992) and local variations in depth (*e.g.* riffle-pool transitions, Vaux 1968).

All of the variables affecting specific discharge scale with stream size. While there is considerable smaller scale heterogeneity, sediment grain size generally decreases with increasing stream size (Leopold *et al.* 1964, Knighton 1980, Creuzé des Châtelliers *et al.* 1994, Ward & Voelz 1994). In addition to specific discharge, sediment particle size also affects biological and chemical reactions. Sediment surface area affects nutrient transformations through microbial biofilms and direct chemical interactions (Triska *et al.* 1989). Due to surface area and volume scaling, there is a negative correlation between sediment particle size and bacterial abundance (Claret & Fontvieille 1997).

The two components of hydraulic gradient, channel slope and pressure gradient, scale in contrasting patterns with stream size. As streams get larger, slope decreases (*e.g.* Leopold *et al.* 1964, Table 6-1), which contributes to decreasing hydraulic gradient. However, discharge increases with stream size (Leopold *et al.*

1964), which increases the pressure gradient and, therefore, the hydraulic gradient. Finally, there is evidence that the depth and width of hyporheic sediments increase with stream size (Perez Filho & Christofolletti 1977, Creuzé des Châtelliers *et al.* 1994, Ward & Voelz 1994). Larger streams have larger basins and valleys which can accommodate greater accumulations of alluvial sediments. Accordingly, the relative discharge of hyporheic and channel waters is likely to change with stream size, because of changes in the relative volumes and flow velocities in each stream compartment (Boulton *et al.* 1998). This would affect stream metabolism and spiraling lengths of nutrients (Triska *et al.* 1989).

In summary, from the headwaters to the estuary there is a pattern of decreasing slope and sediment grain size, increasing stream discharge and volume of alluvial sediments, and increased or decreased spacing of “hotspots” of hyporheic exchange (i.e. point bars and riffle-pool complexes) depending on LWD loading. All of these factors interact to change the amount of hyporheic flow in a stream relative to the channel flow. Due to the contradictory influences of some of these longitudinal patterns of stream geomorphology on hyporheic flow, it seems likely that maximal development of the hyporheic zone relative to stream size may generally occur in mid-order streams (Boulton *et al.* 1998). Hyporheic extent is constrained by shallow depth, width, and low stream discharge in headwater streams, and by low gradient and fine sediments in high order streams. In contrast, White (1993)

argues that hyporheic zones should become increasingly important with stream size, while Munn & Meyer (1988) argue the opposite.

ALLOMETRY OF FLOODPLAINS

Floodplains are areas of high primary production, as well as nursery grounds for many species of juvenile fish and invertebrates, and they have extensive exchanges of sediments and nutrients with rivers during flooding (*e.g.* Welcomme 1979, Edwards & Meyer 1987, Junk *et al.* 1989, Merritt & Lawson 1992, Smock *et al.* 1992, Bayley 1995). However, the river continuum concept omits consideration of floodplains, so some authors have questioned its applicability to rivers with extensive floodplains (Sedell *et al.* 1989, Welcomme *et al.* 1989, Bayley & Li 1992, Johnson *et al.* 1995). While specific predictions by the authors of the RCC may need to be revised to account for floodplain-river interactions, the concept of a size-related continuum of stream form and function is certainly compatible with floodplain-river systems.

Several, mostly informal, or indirect observations suggest that there is an allometric relationship between stream size and floodplain size. Leopold *et al.* (1964, pg 322) have remarked that the width of floodplains is often related to the width of stream channels. Perez Filho & Christofoletti (1977), in one of the few explicit studies of the issue, correlated floodplain width with stream order in 1st through 4th order Amazonian streams, and attributed floodplain development to stream discharge and drainage basin

area. Similarly, Naiman *et al.* (1993) suggest that riparian corridor width and its influence on stream ecology increase with stream size. Welcomme (1979) notes that floodplains tend to increase in width as the slope of the river declines so that there is a progressively greater elaboration of the floodplain as the river flows to the sea. In tropical rivers, drainage basin area and floodplain area are each correlated with fisheries catch; furthermore fisheries production is generally proportional to the extent and duration of flooding (Welcomme 1979). It seems likely that the correlation of fisheries production with floodplain area and flood duration holds along the longitudinal continuum within a river basin as well as between river systems, since flood duration and frequency, as well as floodplain size, increase along the course of a river (Welcomme 1979, Gregory *et al.* 1991).

Interactions between the riparian zone, drainage basin, hyporheic zone and stream channel on stream metabolism should not be neglected. An allometric approach to stream ecology and geomorphology views these various stream ecosystem compartments as linked by related relative rates of change, thus facilitating holistic comparisons between streams of different sizes (Tables 6 & 7). Such an approach also provides a context for the effects of discontinuities in stream structure such as those caused by tributary effects, lakes, sudden breaks in parent geology, or human intervention in stream structure (*e.g.* dams, Ward & Stanford 1995).

Table 6. Equations for Stream Landscape Allometry—Physical Variables.

Equation	Remarks	Source
1. $L = jA^m$	L = stream length, A = drainage area; m varies from 0.6 to 0.7 for NE USA. j averages 1.4 j = 2.29, m = 0.85 for Appalachian karst streams j = 1.78, m = 0.49 for composite data set, which washes out potential regional differences so that m is close to isometric expectation of 0.5	Hack 1957 White & White 1979 Montgomery & Dietrich 1992
2. $Q = jA^m$	Q = discharge, A = drainage area; $0.65 < m < 0.80$	Strahler 1964
3. $w = aQ^b$	Q = discharge, w = stream width	Leopold et al 1964
4. $d = cQ^f$	Q = discharge, d = stream depth	Leopold et al 1964
5. $v = kQ^m$	Q = discharge, v = mean velocity	Leopold et al 1964
6. $G = pQ^j$	G = sediment load (tons/day); $0.8 < j < 1.3$	Leopold et al 1964
7. $s = tQ^z$	s = water surface slope; $-0.49 < z < -1.07$	Leopold et al 1964
8. $n' = rQ^y$	n' = manning roughness coef. y = -0.3	Leopold et al 1964

9. $q_c = kA^m S^n$	q_c = sed. transport capacity, A = drainage area, S = channel gradient	Kirkby 1971
10. $q_s = bA^v$	q_s = sed. supply, A = drainage area	Kirkby 1971
11. $\lambda = jW^m$	λ = meander length, W = channel width; $6.6 < j < 10.9$, $0.99 < m < 1.01$	Leopold et al 1964
12. $A = jW^m$	A = meander amplitude, W = channel width; $2.7 < j < 18.6$, $0.99 < m < 1.1$	Leopold et al 1964
13. $C = 0.05$ $(LWD/m)^{-1.04}$	C = channel widths per pool	Montgomery et al 1996

Table 7. Equations for Stream Landscape Allometry—Biological Variables.

Equation	Remarks	Source
14. $y = 0.95 x^{-1.01}$	y = spawning gravel area/wetted area of stream for a 100 m length of stream, x = stream power, $r^2 = 0.64$ [Stream power = $\rho g A v s$; ρ = mass density of water, g = acceleration due to gravity, A = stream cross-sectional area, v = stream velocity, s = stream slope. Thus stream power is a function of stream size.]	Benda et al 1992
15. $C_n = 0.13A_n^{0.85}$ $C_e = 0.44A_e^{0.90}$	C_n = fisheries catch in African rivers with 'normal' floodplain development, C_e = catch in rivers with 'extensive' floodplains. A = drainage basin area.	Welcomme 1979
16. $C = 10.9A^{0.82}$	C = fisheries catch in various tropical rivers, A = maximum flooded area.	Welcomme 1979, Tables 4.9 & 4.10
17. $B = aL^b$	B = biomass of fish per unit length stream segment. L = length of stream from source to the segment sampled; $a = 0.00183$, $b = 1.177$	Bayley & Osborne 1993

SUMMARY

Fractal models of landscape form imply related relative rates of change between geomorphic features and suggest related relative rates of change with biological patterns and processes associated with these geomorphic features. Process models of materials and energy fluxes across landscape boundaries can be linked to allometric descriptions of these boundaries to form an allometric description of ecosystem processes. In this way form and function can be linked on a landscape scale. Landscape allometry predicts that as lakes and streams change in size, there are correlated size changes in various interacting ecosystem compartments which result in ecological changes as well. However, the adequacy of an allometric model is contingent on the dependent variable having small variability relative to the range of the independent variable (Fig. 37). In other words, allometric models may be too coarse if applied over a narrow range of scales.

In the generic allometric model, $y = ax^b$, the parameter a is a constant of proportionality, or a transfer coefficient. For example, when catchment area is linked to nutrient inputs to a lake or stream, the amount of nutrient input will be proportional to catchment area and to the rate at which nutrients are leached from the catchment soil, which depends on catchment geology, slope, soil temperature and chemistry, and precipitation rates. Thus, while this discussion of ecosystem allometry has heretofore neglected climatic and edaphic variation, these considerations can be included

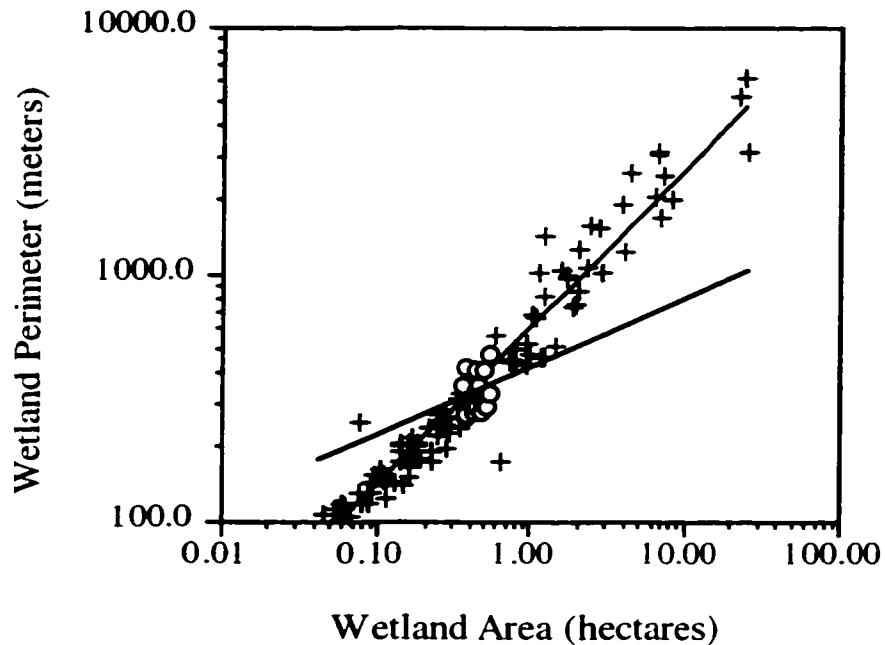


FIGURE 37. Illustration of the effect of scale of observation on results of a simple allometric analysis. Data are dimensions of wetlands from the National Wetlands Inventory of the Montana Valley 7.5 minute Quadrangle. “+” represent a set of 130 wetlands whose areas span 2.7 orders of magnitude and for whom $y = 605x^{0.63}$, $r^2 = 0.95$. “o” represent a subset of 20 wetlands whose areas span 0.2 orders of magnitude and for whom $y = 409x^{0.28}$, $r^2 = 0.06$. The fitted line for the smaller dataset is extended beyond the range of the data for illustrative purposes.

in process models which are linked via transfer coefficients to models of allometric form. Complications such as threshold effects (*e.g.* With & Crist 1995) and landscape discontinuities, *e.g.* tributary effects, may seem to be a challenge to an allometric perspective. However, deviations from allometry may be very informative and interesting. In this respect allometry may provide a useful null model.

Several authors have suggested correlating ecological variables with the fractal dimensions of landscapes in order to develop a "fractal index" of landscape-level ecological processes (Kent & Wong 1982, Frontier 1987, Krummel *et al.* 1987, O'Neill *et al.* 1988), but this approach has been criticized for providing little insight into ecological processes (Cullinan & Thomas 1992). Because ecosystem allometry is based on linking process models of ecological fluxes to allometric structural models of landscape form, it provides an *a priori* linkage of ecological processes to landscape geometry. In other words, rather than starting with a landscape-level fractal dimension and looking for a correlation with various ecological variables, landscape allometry would do the reverse and start with ecological fluxes, linking those fluxes to landscape boundaries, scaling those boundaries and fluxes, and then linking that scaling to a fractal index. No search for correlation is involved, only direct *a priori* linkages. Thus, in addition to providing a holistic view of ecosystem structure and function, ecosystem allometry may also provide a perspective for linking ecosystem processes to fractal indices.

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Publications and Reports

- Simenstad, C. A., **W. G. Hood**, R. M. Thom, D. A. Levy, & D. L. Bottom. 2000. Landscape structure and scale constraints on restoring estuarine wetlands for pacific coast juvenile fishes. *IN: M. P. Weinstein & D. A. Kreeger (eds), Concepts and Controversies in Tidal Marsh Ecology.* Kluwer Academic Publ., Dordrecht.
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Selected Presentations

- Ecosystem allometry: landscape form and ecosystem process. *AT* International Association for Landscape Ecology. Lansing, Michigan. March 1998.
- Landscape allometry: a linkage of landscape form and process. *AT* International Workshop on Ecology and Management of Aquatic-Terrestrial Ecotones, Seattle, February 1994
- Landscape allometry: a model of how form affects function on a landscape scale. *AT* Pacific Estuarine Research Society, Longbeach WA, May 1993. -- best student presentation award.
- Creation of an estuarine slough in the Pacific Northwest: Can we "outdesign" mother nature? *AT* 11th International Estuarine Research Conference, San Francisco, November 1991.

Professional Experience

- 1990-2000 Biological Consultant. Self-employed.
- 1990-1993 Research Assistant, School of Fisheries, University of Washington. Assessment and evaluation of ecosystem functions for a variety of estuarine wetlands.
- 1989-1990 Biologist for David Evans & Associates, Bellevue, WA.
- 1988 Wetland biologist for the City of Auburn, WA.

Teaching Experience

- 1998 Winter Quarter Instructor for CEP 302, Environmental Response Colloquium, Department of Urban Design and Planning, Univ. of Washington.
- 1997 Autumn & Spring TA for FISH 312, Fisheries Ecology, School of Fisheries, Univ. of Washington.
- 1996 Autumn Quarter TA for QSCI 381, Intro. to Probability & Stats., School of Fisheries, Univ. of Washington.
- 1994 Autumn Quarter TA for BIO 201, General Biology Laboratory for majors, Biol. Dept., Univ. of Washington.
- 1990 Autumn Quarter TA for FISH 507, Wetland Ecology, School of Fisheries, Univ. of Washington.
- 1987 Summer Semester Lecturer for Comparative Physiology, Florida State University.
- 1986 Summer Semester Lecturer for General Biology for Majors, Florida State University.

Grants & Awards

NSF Dissertation Improvement Grant, 1994-1996
 W. F. Thompson Award, UW School of Fisheries, 1993-4
 Egtvedt Trust Award, UW School of Fisheries 1993-4
 NSF Graduate Fellowship, 1984-7

Other Skills

Fluent in Spanish and German