Detecting Shifts in Macroinvertebrate Community Requirements:
Implicating Causes of Impairment in Streams

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Introduction

Macroinvertebrate community analysis is perhaps the most sensitive tool available for accurately assessing the effect of anthropogenic disturbance on aquatic ecosystems (Gray 1989, Schindler 1987). Macroinvertebrate communities are an ecologically relevant indicator because their responses can be extrapolated to the whole system through mechanisms such as cascading changes in food web dynamics, competition and predation (Attrill and Depledge 1997). The impact of an array of environmental stressors (*sensu* Odum 1985) is integrated through a broad range of physiological tolerances, feeding modes and trophic interactions over the course of many generations. Major approaches to detecting biological impairment in aquatic systems thus far, however, have used either predictive models that generate expected taxa lists in the absence of human disturbance (Wright et al.1993, Moss et al. 1999) or indices based on the response of communities across gradients of human disturbance (Karr 1981, Barbour et al. 1996). These methods satisfy many of the criteria for biological monitoring listed by Schindler (1987) and Karr (1991), but do not quantitatively address the potential causes of impairment.

The objective of this work is to use weighted average (WA) inference models to reveal shifts in community composition that implicate either substrate degradation (i.e. fine sediment pollution) or temperature pollution (Cairns 1967) as causes of impairment in streams. An empirical basis for evaluating the relative condition of test sites is to use sites that are minimally affected by human activities as a reference (Bailey et al. 1998, Reynoldson and Wright 2000). The divergent characteristics of “disturbed” versus “undisturbed” assemblages indicate shifts in community composition that may discriminate stressor effects.

WA inference models (Birks et al. 1990) that use optima and tolerances (see Huff et al. 2005) to characterize the mean environmental requirements of macroinvertebrate communities allow specific stressors to be quantified. Inferences of environmental conditions using WA have been shown to correspond to observations with organisms such as lake macroinvertebrates (Brodersen et al. 1998), stream macroinvertebrates (Hamalainen and Huttunen 1996, Larsen et al. 1996), diatoms in streams (Pan et al. 1996), diatoms in lakes (Birks et al. 1990) and lentic chironomids (Walker et al. 1991, Olander et al. 1999, Larocque et al. 2001). A variety of environmental gradients such as temperature (Walker et al. 1991, Olander et al. 1999, Larocque et al. 2001), trophic status (chlorophyll [a]) (Christie and Smol 1993, Jones and Juggins 1995, Brodersen et al. 1998), pH (Birks et al. 1990, Pan et al.1996), acidity (Hamalainen and Huttunen 1998), total phosphorus (Hall and Smol 1992, Pan et al. 1996), conductivity (Gasse et al. 1995), dissolved organic carbon (Kinston and Birks 1990), turbidity (Pan et al. 1996) and salinity (Zeeb and Smol 1995) have been modeled as well.

Many benthic macroinvertebrates show a remarkably high affinity for a particular substrate type and respond negatively to increased levels of sedimentation (Brusven and Prather 1974, McClelland and Brusven 1980, Lemly 1982). Fine sediments can fill interstitial spaces and disrupt filter feeding (Lemly 1982), increase drift (Bournaud 1963, Waters 1972), and impede foraging and mobility (McClelland and Brusven 1980). High variability in taxa-specific responses to the substrate caused by erosion and deposition of sediments can result in notable changes in community structure. Excessive amounts of fine sediment interfere with leaf and detrital processing and may also affect macroinvertebrates by impairing the periphyton community (Cummins 1974).

The distribution of macroinvertebrates is strongly temperature dependent (Magnuson et al. 1979, Vannote and Sweeney 1980, Hawkins et al. 1997). Their thermal niche is influenced by physiological processes (Moulton et al. 1993), and biotic processes such as food availability (Sweeney and Vannote 1986) and niche partitioning (Hildrew et al. 1979, Ward and Stanford 1982). High summer water temperatures are especially critical for many macroinvertebrate populations because the maximum temperature attained during summer low-flow conditions may limit the incidence of certain species (Vannote and Sweeney 1980). Temperature has a principal role in determining diversity, distribution and abundance patterns of aquatic macroinvertebrates, therefore, persistent alterations in water temperature are reflected in the composition of macroinvertebrate communities.

Study objectives

1) We quantitatively identified macroinvertebrate *indicator taxa* that show a strong relationship to fine sediment and/or temperature gradients and quantified their requirements. The indicator taxa identified here can be used to calculate tolerant/intolerant metrics for use Indices of Biotic Integrity (IBIs).

2) We generated WA inference models for temperature and sediment for use as screening tools to detect stress in wadeable streams throughout Oregon. Inferred values at a test site can be compared to conditions observed at regional reference sites to see if there is a difference in assemblage-level preferences for temperature or fine sediment.

Methods

Study Sites

Macroinvertebrate, temperature and substrate data were collected during the summer months (June through September) from 1998-2003 from 1^{st} to 4^{th} order streams (Strahler 1964) on 1:100,000 scale maps. Sample reach length was forty times the mean wetted channel width (Lazorchak et al. 1998) and ranged from 150 to 800 meters. Sites included a wide range of wadeable stream types and span all of the major ecoregions in Oregon. Sampling locations were chosen either randomly with a spatially systematic component (Herlihy et al. 2000) or were purposely chosen because they were determined to be minimally affected by anthropogenic disturbance. The drainage areas of all random and hand-picked sites were then screened using digital maps for human disturbance factors in their drainage areas such as high road density, urban and agricultural use, active or recent logging and presence of cattle grazing. Site visits were also made to identify reach-level disturbance factors such as channel modification and land use activities within 10m of the stream bank (roads, mining activity, buildings, etc.). Reach level and drainage area assessments were combined into an overall human disturbance score for each sampling site, and all sites were assigned a disturbance grade based on a 5-level scale (see Drake 2004). Sites with a low disturbance score were considered “reference” for the purposes of this analysis and were used for comparison to test sites. All reference and non-reference sites with both macroinvertebrate and environmental parameter data were used for inference model calibration. A total of 320 sites were used for substrate model calibration and 269 sites used for temperature model calibration (Figure 1).

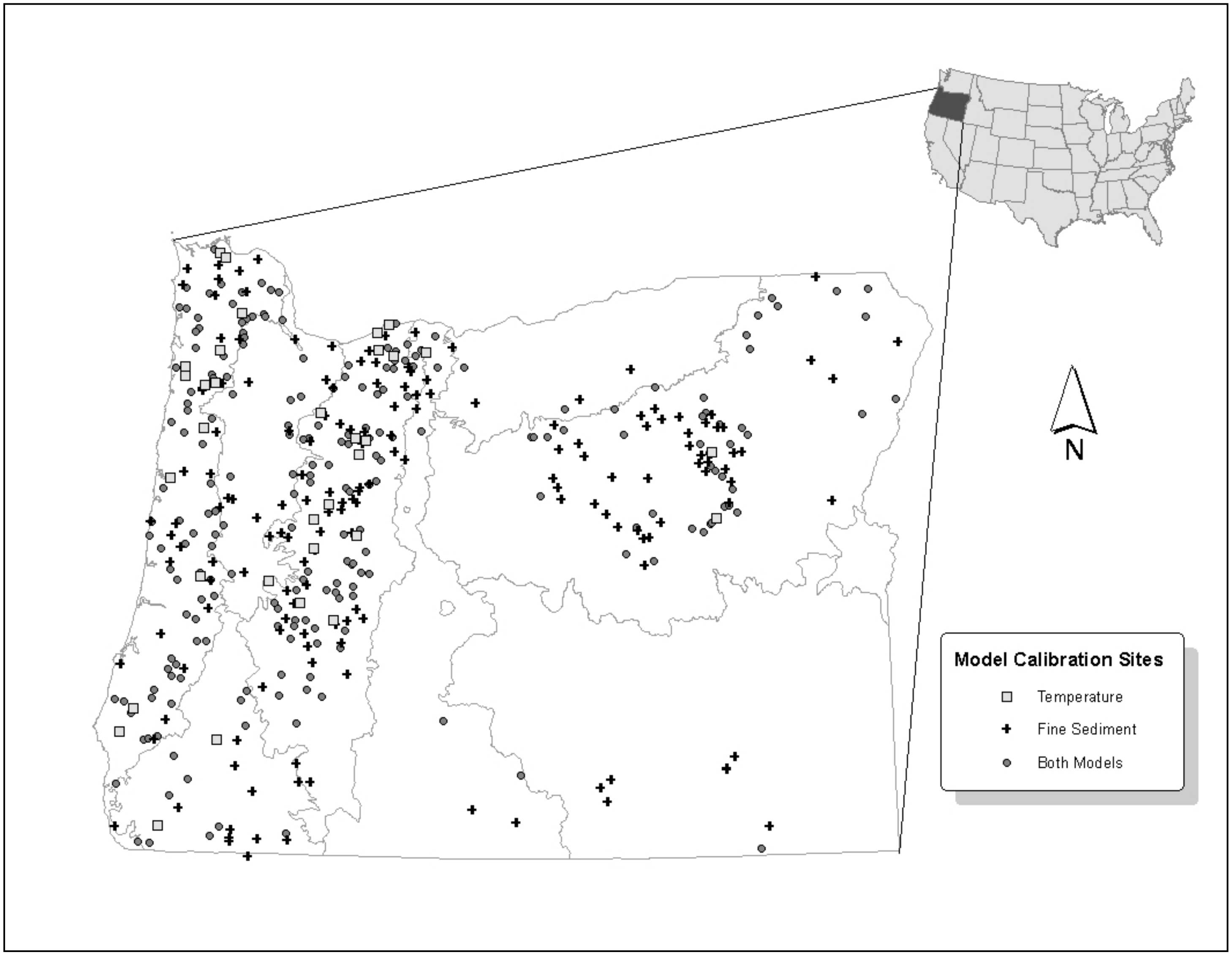
Macroinvertebrate Data

We used macroinvertebrate assemblage data collected from composite kick-net samples obtained from riffle habitats. Samples were sorted and sub-sampled to 500 individuals and were identified to the lowest possible taxonomic level (usually genus). Full details of macroinvertebrate sampling are given by Waite et al. (2000) and Klemm et al. (2003). Because the models required a consistent level of taxonomy, we either aggregated taxa to a higher taxonomic category (e.g. species were grouped within one genera) or we excluded individuals identified to a higher taxonomic category, such as order, when most others were identified to a lower level. This exercise resulted in a list of operational taxonomic units (OTUs) that varied in their level of taxonomic resolution, but were unique from one another.

Temperature and Substrate Data

Continuous temperature data were recorded at 30-minute intervals using VEMCO® temperature loggers. We deployed data loggers at study sites from late May to early July and removed them from September to October. They were placed in a well-mixed, shaded location to avoid thermal stratification or heating by direct solar radiation (ODEQ 1997). The temperature metric used for this

Figure 1. The locations of calibration sites are shown on a map of Oregon for both temperature and fine sediment inference models. Grey lines delineate the nine Level 3 ecoregions (Thorsen et al. 2003) that occur in Oregon.



study was the average of the daily maximum temperatures for the warmest seven-day period of the season (7-DSMT).

Substrate data were collected from 21 cross-sectional transects evenly spaced along the sampled stream reach (Lazorchak et al. 1998). Systematic “pebble” counts gave whole reach substrate characterizations by calculating percentages of observations within stated size classes (Kaufmann et al. 1999). We used proportional fine sediment (particles <0.06 mm diameter) values (x) transformed such that: $x = \mathrm{Log}_{10}\left(\left(\left(\arcsin\sqrt{b}\right)\left(\frac{2}{\Pi}\right)\right)+1\right)$, where b is the untransformed value, to characterize substrate quality for the sample reach. This transformation was performed to improve the normality of the data set.

Identifying Indicator Taxa

We used non-metric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976) to relate macroinvertebrate assemblage patterns in the WA model calibration datasets to the temperature and fine substrate gradients using PC-Ord software (McCune and Mefford 1999). The abundance value for a taxon at each site (x) was transformed to log(x+1) to stabilize the variance of the data set and downweight dominant taxa (Thorn et al. 1999). We used Bray-Curtis distance to calculate the similarity matrix (Bray and Curtis 1957) and sample units were assigned to random starting configurations for NMS using a random number generator. The appropriate number of dimensions was determined when plots of final stress versus the number of dimensions showed that a greater number of axes resulted in small reductions in “stress” (i.e. departure from monotonicity in the plot of distance in the original dissimilarity matrix and distance in the reduced ordination space). We calculated instability as the standard deviation in stress over the preceding 10 iterations. When instability reached a level of 0.00001, iterations were stopped and the solution was considered final. The stability of the solutions was also examined by plotting stress versus number of iterations.

When we plotted the final solution, we rotated the point cloud to maximize the correlation of temperature or fine sediment with the horizontal axis (Mather 1976). The strength of the relationship between the temperature and substrate values and the ordination scores was determined by calculating Pearson’s correlation coefficient (r) (Clarke and Ainsworth 1993).

Indicator taxa were chosen by calculating r for each species against the previously rotated horizontal NMS axis. The positions of species on the plot were compared to their abundances at a given site. Species were considered to have a strong relationship with the environmental variables if they were among the thirty highest ranked absolute r-values. Histograms of these taxa abundances were examined to ensure an adequate sampling coverage across the possible environmental ranges that a taxon may inhabit (see Huff et al. 2005).

Weighted Average Inference Models and Stressor Scores

We estimated taxa optima using a weighted-average (WA) method with the C^2 software (Juggins 2003). Taxa with an optimum closest to a given value will tend to be more abundant at locations close to that value than in locations where the optimum is distant from the value (Ter Braak and Barendregt 1986). An ecologically sound estimate of a taxon's optima is therefore the mean value for all the sites where it is found, weighted by its log transformed abundance at each site. A taxon's tolerance is one standard deviation from the mean of the value, weighted by the taxon's log transformed abundance (Birks et al. 1990).

The WA estimate of a taxon's optima, or weighted mean, $\hat{u}_k$, (Birks et al. 1990) is:

$$\hat{u}_k = \sum_{i=1}^{n} y_{ik} x_i \Big/ \sum_{i=1}^{n} y_{ik}$$

Taxon tolerance, $\hat{t}_k$, or weighted standard deviation is:

$$\hat{t}_k = \left[\sum_{i=1}^{n} y_{ik} (x_i - \hat{u}_k)^2 \Big/ \sum_{i=1}^{n} y_{ik} \right]^{\frac{1}{2}}$$

where x = the environmental variable, x_i = the value of x in sample i, y_{ik} = the abundance of taxon k in sample i ($y_{ik} \leq 0$) (i = 1, … n sites and k = 1, …m invertebrate taxa). The C^2 software corrected bias in the tolerance value by adjusting for the estimated effective number of occurrences of a taxon (Hill 1973).

The estimated optima were used to infer an environmental parameter from the benthic macroinvertebrate assemblage by:

$$\hat{x}_i = \sum_{k=1}^{m} y_{ik} \hat{u}_k \Big/ \sum_{k=1}^{m} y_{ik}$$

where y_{ik} is the abundance of taxon k in sample i, $\hat{u}_k$ is the optima of taxon k and $\hat{x}_i$ is the *initial* inferred parameter.

Shrinkage of the range of inferred parameter values occurs because averages are taken twice, once in the regression step and once in the calibration step (Birks et al. 1990). Classical or inverse regression may be used to deshrink the estimates where the initial inferred $\hat{x}_i$ is regressed on the observed $\hat{x}_i$ of the calibration set:

Initial $\hat{x}_i$ = a + b *observed* $\hat{x}_i$

and

final $\hat{x}_i$ = *(initial* $\hat{x}_i$ -a)/b for classical deshrinking (ter Braak 1988), where *a* is the intercept and *b* is the slope of the linear regression. For inverse deshrinking (ter Braak and Van Dam 1989), where the observed x_i is regressed on the initial inferred $\hat{X}_i$:

$$final\ \hat{X}_i = a + b\ initial\ \hat{X}_i$$

where *a* and *b* are the coefficients of the deshrinking regression. Both types of deshrinking models were generated and evaluated. WA calibration can also be performed by down-weighting a taxon's optima by the inverse of the squared weighted standard deviation of the optima (Birks et al. 1990). Tolerance down-weighted models were evaluated as well.

Before the models were calibrated, fifty samples were randomly extracted from the calibration data and set aside for validation. The performance of the inference models was assessed by evaluating the root mean-squared error (RMSE) and correlation coefficient (r^2) of the observed versus inferred values for the calibration set, a jackknifed validation data set and the 50 independent validation samples. Models that produced high r^2 and low RMSE were considered better models. Because the inferred value of the environmental variable for a calibration site was derived from the calibration set which included the inferred site, the apparent r^2 for observed versus inferred values may not be realistic for assessing the predictive power of the models (Cumming et al. 1995, Reavie et al. 1995). Therefore, independent validation and cross validation with leave-one-out jackknifing was used to validate the apparent r^2 (ter Braak and Juggins 1993). Jackknifing infers the environmental value for a site by using all the sites except the inferred site to derive an estimated value, thereby avoiding possible circularity in the model evaluations. The largest absolute value of mean bias for 10 equal parts of the environmental sampling interval (maximum bias) for apparent and validation datasets was used to evaluate systematic model error (ter Braak and Juggins 1993).

Inferred fine sediment values were converted to a stressor score (fine sediment score = FSS) by untransforming the inferred values (*x*) by:

$b = \left[\mathrm{Sine}\left(\frac{\prod (10^{x} - 1)}{2} \right) \right]^2$, where *b* is the untransformed value and multiplying by 100 to generate integer values. Temperature scores (TS) are simply equal to the inferred temperature values rounded to tenths of degrees Celsius.

We established screening criteria for temperature and/or fine sediment stress by comparing an individual site score to reference sites in the same Level 3 ecoregion (Thorsen et al. 2003). Sites with temperature and fine sediment scores higher than the 75th percentile of the ecoregion reference site distribution would be considered to show a significant shift in assemblage-level preferences for fine sediment and/or temperature.

Annually Repeated Sites

Seven annually repeated sites in the Coast Range ecoregion were evaluated to examine year to year variability in the model inference scores at different sites with varying levels of disturbance. Additionally, these annual re-visits were used to see if the models were independent of each other (e.g., can a site show temperature stress without exhibiting fien sediment stress, and vice versa). These sites are in largely forested catchments. Ben Smith Creek is a medium sized (Bank Full Width = 7.7m) stream at mid elevation (208m) in the north coast; the geology is volcanic and land use is predominantly low intensity logging. The Tillamook River is a medium sized (Bank Full Width = 5.5m) stream at low elevation (44.2m) in the north coast; the geology is siltstone and land use is a mix of low and high intensity logging with dairy land adjacent to the sampled reach. Montgomery Creek is a small (Bank Full Width = 3.1m) stream at low elevation (19.5m) in the mid-north coast; the geology is sandstone and land use is predominantly high intensity logging. Big Creek is a large (Bank Full Width = 20.2m), low elevation (4.3m) stream in a mid-coast wilderness area; the geology is volcanic. Wolf Creek is a medium sized (Bank Full Width = 11.1m) stream at mid elevation (116m) near the southern coast; the geology is sandstone and land use is mix of low and high intensity logging. Sixes Creek is a large (Bank Full Width = 18.8m) stream at low elevation (51m) in the south coast; the geology is sandstone and land use is mix of predominantly moderate intensity logging. Wood Creek is a small (Bank Full Width = 5.4m) stream at high elevation (487m) in the south coast; the geology is primarily volcanic and land use is dominated by moderate and high intensity logging.

Results

Macroinvertebrate Taxa

We used 242 OTUs across both models. Of these, the temperature model calibration dataset included 234 OTUs and the sediment model calibration dataset included 240 OTUs. The majority of the OTUs were identified to the genera level (60%), followed by species level (15%), family level (12%), and species groups (7%). Levels of taxonomy higher than family comprised less than 3% of the OTUs (phylum = 1 OTU, class = 2, and subclass = 3). All chironomidae OTUs were at the subfamily level, except for the chironominae which were modeled at the tribe level. Non-insect OTUs (primarily of mollusks, amphipods and annelids) were relatively uncommon, comprising only 7% of all OTUs, and comprised a wide variety of taxonomic resolution ranging from genus to phylum.

Ordination

All sites with paired macroinvertebrate samples and environmental variables were used to asess the strength of the relationships between community structure and seasonal maximum temperature and fine sediment. The NMS results summarized in Table 1 indicate strong community relationships to both temperature ($r^2 = 0.64$) and fine sediment ($r^2 = 0.35$).

Indicator Taxa

Optima and upper tolerance bounds are shown in Table 2. Interestingly, there didn't appear to be much difference in tolerances between less taxonomically resolved OTUs with fewer potentially unresolved species versus more potentially unresolved species. Only *Dubiraphia* was dropped from the sediment indicator list because it failed to occur at enough sites to adequately represent its potential sediment gradient. No taxa were dropped from the temperature indicator taxa list. The taxon with the lowest temperature optimum was *Prosimulium* (12.2°C) and the highest optimum was *Physa* (21.1°C). The lowest fine sediment optimum was *Arctopsyche* (2%) and the highest optimum was for Coenagrionidae (25%). Twelve of the taxa (40% of each indicator list) were common indicators for both fine sediment and temperature.

Weighted Average Inference Model Performance

Among the various choices of weighted averaging temperature models there were few substantial differences between inverse and classic deshrinking and tolerance down-weighted options (Table 3). The inverse deshrinking temperature model had a slightly lower independent validation and jackknifed RMSE than the other options with an intermediate level of bias. Independent validation r^2 values were roughly equivalent for all four temperature models, while the jackknifed r^2 values were lower for the 2 tolerance down-weighted models. The inverse deshrinking model was chosen as the best model (independent validation $r^2 = 0.66$). The inverse deshrinking sediment model had a lower independent validation RMSE and a higher independent validation r^2 than the other sediment model options. It was therefore chosen as the best model.

Both temperature (Inverse DS) and fine sediment (Inverse DS) models showed strong correlations between macroinvertebrate inferred and observed values (Figure 2; Table 3). The temperature model showed a more even distribution about the 1:1 line, while the sediment values were skewed toward the lower end of the range. Inferred fine sediment values tended to underestimate observed values at the higher end of the range and overestimate at the lower end. To a lesser degree, similar results were observed with the inferred temperature values. The temperature model yielded better predictability than the sediment model, which corresponded with strength of the relationship of the variables to the NMS ordination scores shown in Table 1.

Temperature and Fine Sediment Scores were calculated for reference sites from each of the Level 3 ecoregions in Oregon. The distribution of stressor scores in each ecoregion were used to establish a benchmark for determining whether the assemblage-level inferences for temperature or fine sediment were similar to those observed at regionally appropriate reference sites (Table 4). The benchmark for each ecoregion was calculated as the 75th percentile (upper 25th percentile) of reference site scores.

Annually Repeated Sites

Annually repeated measurements of temperature and fine sediment scores for seven sites in the Coast Range ecoregion are shown in Figure 3. Sites with mean stressor scores greater than the Coast Range ecoregion reference benchmarks (TS = 18.9 and FSS = 9) were considered stressed. Sites with mean values less than the benchmark, but upper 85% confidence intervals (CIs) exceeding the benchmark were considered slightly stressed. Two sites, Ben Smith Creek (mean TS and FSS scores, 15.9 and 5) and Wood Creek (16.6 and 6), showed no signs of temperature or fine sediment stress (means and upper CIs were less than the reference benchmarks. Tillamook River and Montgomery Creek showed similar levels of stress to temperature and fine sediment. Both sites showed slight levels of temperature stress, but showed definitive stress caused by fine sediment with mean values (22 and 27) well above the reference benchmark. Big Creek showed slight stress to both temperature and fine sediments. Wolf Creek and Sixes Creek both showed stress to fine sediments, but their mean FSS scores (10 and 11, respectively) were only slightly above the reference benchmark. However, both sites showed much higher mean TS (20.2 and 22.6, respectively) than the reference benchmarks. These results suggest that the two WA inference models are able to independently assess stress to macroinvertebrate assemblages caused by seasonal maximum temperature and fine sediments.

Table 1. Summary statistics and NMS ordination results for fine sediment and temperature. Fifty randomized Monte Carlo tests were run. Relation to the environmental variable is the amount variation along a single rotated axis (gradient maximized) that is explained by each environmental variable. Axis variance is the cumulative proportion of variance represented by each axis and is based on the r^2 between distance in the rotated ordination space and the distance in the original space. Fine sediment values are the percent of substrate <0.06 mm in diameter.

	Fine Sediment	Temperature
Number of sites	496	328
Number of taxa	243	245
Minimum value	0%	6.2°C
Median value	7%	16.6°C
Mean value	13%	16.8°C
Standard deviation	18%	3.8°C
Maximum value	98%	29.6°C
NMS Relation (r^2) to environmental variable	0.35	0.64
Number of NMS dimensions	3	3
NMS Monte Carlo test result (p)	0.02	0.02
NMS Iterations	189	129
NMS Final stress	17.4	17.4
NMS Axis variance (r^2)	0.80	0.78

Figure 2. The relationship between observed and macroinvertebrate inferred temperature (top) and sediment (bottom) values is shown with a jackknifed validation dataset (squares) and an independent validation dataset (circles). The diagonal solid line was drawn with a 1 to 1 ratio. The dashed line is a linear trendline generated using the independent validation dataset (50 sites for each model). Proportional fine sediment values (x) are transformed such that:

$x = \mathrm{Log}_{10}\left(\left(\left(\mathrm{arcsine}\sqrt{b}\right)\left(\frac{2}{\Pi}\right)\right)+1\right)$, where b is the untransformed value.

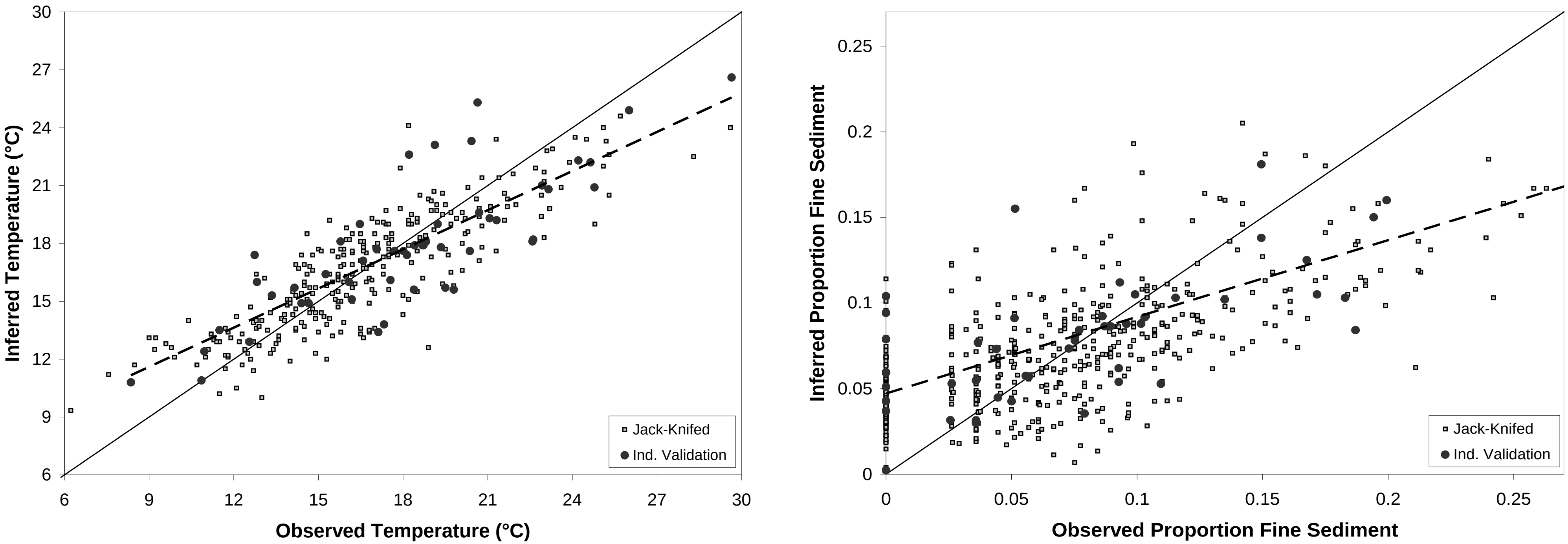


Table 2. Macroinvertebrate indicator taxa. Taxa shown are the top thirty taxa ranked by Pearson's absolute r for temperature and fine sediment against NMS axis 1 (See Table 1). Taxa are listed from lowest to highest optima value for each environmental variable. BPJ = best professional judgement, C = cold, H = high, L = low, U = unknown.

Operational Taxonomic Unit	Sites	r	Optima	Upper Tolerance	BPJ Category
Temperature					
Prosimulium	18	-0.346	12.2	14.8	U
Baetis bicaudatus	12	-0.323	12.3	15.2	C
Neothremma	37	-0.334	12.9	15.8	C
Zapada columbiana	86	-0.584	12.9	15.6	C
Parapsyche elsis	62	-0.493	13.5	15.7	C
Caudatella	62	-0.453	13.6	16.8	U
Megarcys	51	-0.470	13.6	16.3	C
Visoka	77	-0.496	13.7	16.2	C
Epeorus grandis	69	-0.420	14.2	17.2	C
Yoraperla	135	-0.570	14.2	17.2	C
Ephemerella	77	-0.365	14.4	18.1	U
Despaxia	84	-0.335	14.5	17.0	C
Drunella coloradensis/flavilinea	58	-0.336	14.5	17.0	U
Doroneuria	97	-0.408	14.5	17.0	C
Turbellaria	115	-0.486	14.6	17.9	U
Ironodes	122	-0.376	14.9	17.6	U
Ameletus	120	-0.395	15.2	18.3	U
Drunella doddsi	160	-0.450	15.2	18.3	C
Rhyacophila Brunnea group	159	-0.333	15.5	18.6	U
Cinygmula	169	-0.342	15.5	18.2	U
Micrasema	145	-0.365	15.6	18.8	U
Diphetor hageni	174	0.405	17.9	21.4	U
Antocha	114	0.322	18.3	22.0	U
Hydropsyche	146	0.443	18.5	21.7	U
Juga	95	0.377	18.6	21.4	U
Chironomini	149	0.562	18.8	22.0	U
Zaitzevia	159	0.595	19.0	22.5	U
Optioservus	132	0.639	19.6	22.9	U

Dicosmoecus gilvipes	28	0.371	20.6	24.2	U
Physa	11	0.319	21.1	25.1	U
Fine Sediment					
Arctopsyche	72	-0.268	2	4	L
Epeorus grandis	90	-0.414	2	4	U
Rhyacophila Hyalinata group	136	-0.358	3	4	U
Drunella doddsi	83	-0.348	3	5	U
Rhyacophila Angelita group	74	-0.253	3	6	U
Drunella grandis	240	-0.581	3	5	U
Caudatella	90	-0.287	4	6	U
Epeorus longimanus	92	-0.317	4	6	U
Megarcys	70	-0.367	4	6	U
Parapsyche elsis	82	-0.309	4	7	L
Rhyacophila *Brunnea* group	221	-0.423	4	6	U
Rhithrogena	253	-0.473	5	7	U
Rhyacophila Betteni group	272	-0.413	5	8	U
Glossosoma	270	-0.353	5	8	L
Baetis tricaudatus	398	-0.391	6	10	U
Cinygmula	244	-0.295	6	9	U
Zaitzevia	274	0.241	9	12	U
Chironomini	260	0.272	10	15	U
Oligochaeta	361	0.301	10	15	H
Paraleptophlebia	293	0.257	11	16	U
Tanypodinae	279	0.519	12	17	U
Optioservus	236	0.382	12	16	U
Juga	132	0.253	15	20	H
Ostracoda	93	0.320	17	21	U
Hydroptila	43	0.286	17	23	U
Lymnaeidae	11	0.257	18	23	H
Cheumatopsyche	26	0.278	20	24	U
Sphaeriidae	176	0.528	21	26	U
Physa	28	0.390	21	28	H
Coenagrionidae	25	0.336	25	29	U

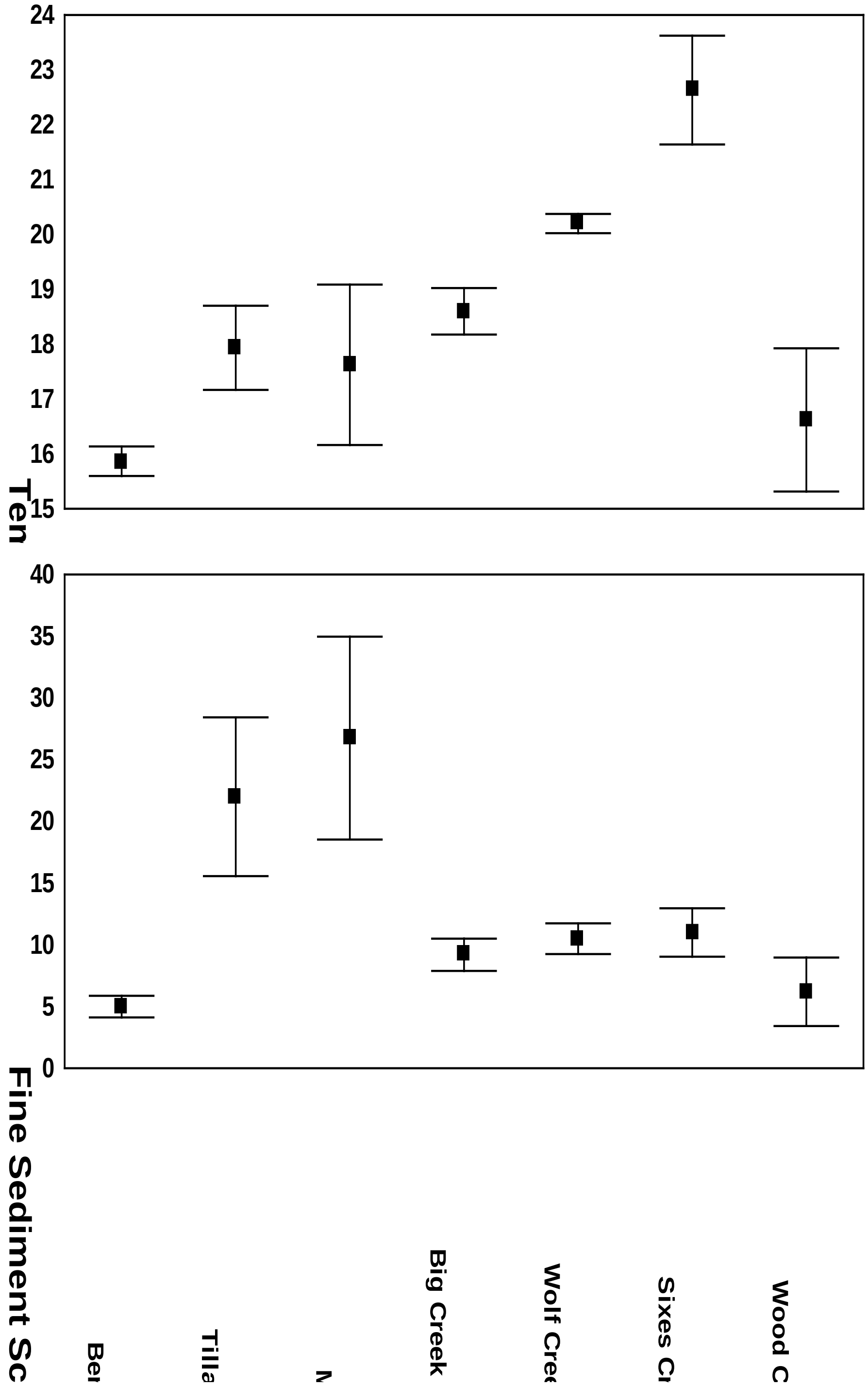
Table 3. Root mean squared errors, correlations and bias estimates for inferred versus observed values and for different temperature and sediment model options. Maximum bias is a measure of systematic error in the predictions (Ter Braak and Juggins 1993). Fine sediment units are untransformed proportions. Values in bold indicate the selected model shown in Figure 2. DS = deshrinking, Tol d/w = tolerance down-weighted, RMSE = root mean squared error, r^2 = Pearson's correlation coefficient.

	Inverse DS	Classic DS	Inverse DS Tol d/w	Classic DS Tol d/w
Temperature (°C)				
Training RMSE	**1.8**	2.0	1.8	2.1
Jackknifed RMSE	**2.0**	2.1	2.2	2.5
Independent Validation RMSE	**2.5**	2.7	2.5	2.6
Training r^2	**0.77**	0.77	0.76	0.76
Jackknifed r^2	**0.72**	0.73	0.65	0.65
Independent Validation r^2	**0.66**	0.66	0.68	0.67
Training Max Bias	**4.2**	1.8	6.7	5.0
Jackknifed Max Bias	**5.7**	3.7	7.4	5.8
Independent Validation Max Bias	**3.1**	3.2	3.3	3.7
Fine Sediment (%)				
Training RMSE	**2**	4	2	4
Jackknifed RMSE	**3**	5	3	5
Independent Validation RMSE	**14**	19	16	24
Training r^2	**0.49**	0.49	0.51	0.51
Jackknifed r^2	**0.41**	0.42	0.40	0.40
Independent Validation r^2	**0.58**	0.52	0.42	0.36
Training Max Bias	**13**	2	12	2
Jackknifed Max Bias	**16**	5	15	4
Independent Validation Max Bias	**19**	22	20	24

Table 4. Distributions of stressor scores at Level 3 ecoregion reference sites. The 75th percentile was chosen as a benchmark for identifying significant shifts in assemblage-level inferences of temperature or fine sediment away from the assemblages observed at reference sites. "n" = the number of reference sites in each ecoregion.

		Temperature Score			Fine Sediment Score		
Level 3 Ecoregion	**n**	**Median**	**75th Percentile**	**Maximum**	**Median**	**75th Percentile**	**Maximum**
Blue Mountains	46	15.5	17.1	27.5	4	8	34
Cascades	131	14.2	16.3	18.4	2	4	19
Coast Range	52	17.8	18.9	21.8	6	9	35
Columbia Plateau	6	19.2	20.5	23.5	9	13	25
Eastern Cascades Slopes and Foothills	16	14.4	15.7	20.4	5	8	22
Klamath Mountains	24	16.9	19.2	21.1	3	6	16
Northern Basin and Range	14	19.2	20.7	23.3	10	17	41
Willamette Valley	13	17.7	18.2	19.8	11	15	19

Figure 3. Mean temperature and sediment scores for seven annually repeated sites in the Coastal Coho ESU. Error bars represent 85% confidence intervals about the mean. The number of yearly samples between 1998 and 2004 is shown in parentheses.



Discussion

Each organism has a suite of environmental requirements and a history of selective pressures that maximized its survival and fecundity. Deviation from these conditions (i.e. stress) will reduce fitness. Physiological and behavioral adaptation to stress begins at the level of the individual. Better-adapted organisms replace those less suited to current environmental conditions. As stress increases, replacements occur at increasingly higher levels of taxonomic organization (Pearson and Rosenberg 1978). Margalef (1981) stated that: “stress is something that puts into action the mechanism of homeostasis”. When stress is detectable as a shift in the mean requirements of the community it is alarming because it is an indication that homeostasis is failing (Odum 1985). Biotic communities adjust rapidly to changes in an aquatic system and their functional characteristics tend to conform to the mean condition of the system (Vannote et al. 1980). Disturbance over longer time scales will cause changes in life history traits such as growth rate and age at maturity in insect rich macroinvertebrate communities. In contrast to fish, which show great plasticity in these traits, insect growth is determinate with a characteristic adult size (Wootton 1998). As a result, disturbance generally favors insect communities that are dominated by hardy, small-bodied, rapidly reproducing species (Newbold et al. 1980, Woodwell 1983). Detection of shifts in demographic characteristics of the population through macroinvertebrate inference models, therefore, allow interpretation of environmental signals.

Effects of the disruption of the natural thermal regime on macroinvertebrate assemblages are well documented. Bottom-releasing dams cause such changes as static diurnal and seasonal temperatures, and winter warm and summer cold temperatures; this result in lower diversity, increased dominance, and ultimately the development of equilibrium communities with minimal niche overlap (Ward 1976).

The importance of fine sediment as a pollutant that affects endangered fish, including salmonids, has been well recognized (Waters 1995). Loading and storage of fine sediments caused by anthropogenic activities degrade spawning and rearing habitat (Miller et al. 1989, Bisson et al. 1992, Waters 1995) and upsets sustaining food webs which is a major cause of declining stocks (Nehlsen et al. 1991, Frissell 1993). Fine sediment reduces the survival of salmonid embryos by decreasing dissolved oxygen and blocking emerging fry (Chapman 1988). Suttle et al. (2004) showed a shift in assemblages due to increased fine sediment. Assemblages changed from crawler and grazer dominated to burrower dominated. There was no threshold below which fine-sediment addition was harmless. Steelhead growth decreased with increasing fine-sediment concentration which was primarily a result of invertebrate assemblage shifting from available prey organisms to unavailable burrowing taxa.

The difficulty in isolating the impacts of fine sediments from other co-varying physical factors such as flow velocity and turbulence, or channel depth and morphology is neither necessary nor desirable with this method. Although sedimentation is a naturally occurring phenomenon, land-use changes have resulted in an increase in anthropogenically induced fine sediment deposition (Wood and Armitage 1997). Inorganic sedimentation and nutrient addition operate synergistically, affecting a greater number of taxa than one pollutant alone (Lemly 1982).

Inference models relate community structure to environmental gradients by evaluating the ecological limits of taxa. The quantity of individual taxa along the gradient coincides with the distribution of available habitat (Schoener 1974). An accurate environmental inference relies upon the strength of this tendency so that biological community composition may be viewed as an indicator of environmental condition. A reference condition approach (Wright et al. 1993, Bailey et al. 1998) provides a benchmark to measure the degree to which a test site community deviates from the range of conditions found at comparable unimpaired sites. A measure of the variation among many sampled reference site communities may also be used to determine the magnitude of the degradation at a test site.

Ordination results indicate that both temperature and substrate (fine sediment) are important gradients for macroinvertebrate communities. Our results corroborate reports in the literature that these variables are important for structuring macroinvertebrate communities and are therefore good candidates for quantitative environmental inference models (Birks 1998). Temperature however, appears to have a more pervasive influence on aquatic macroinvertebrate community structure than substrate. This is also reflected in the relative performance of the temperature model which outperforms the fine sediment model. This could partially be a consequence of our chosen sampling method or our particular metric (% fines), although preliminary analyses performed by the authors prior to this study revealed that the percent of fines showed as strong of a relationship to macroinvertebrates (and produced at least as strong inference models) as many other sediment composition metrics. The biggest limitation in quantitative environmental reconstructions is the quality and internal consistency of the calibration datasets (Birks 1998). Perhaps one reason the fine sediment inference model shows lower model performance is because sediments are measured across the entire reach, while macroinvertebrate assemblages were sampled exclusively from riffle habitats.

The performance of our temperature and fine sediment models was comparable to those from other published studies (Walker et al. 1991, Olander 1999, Brodersen et al. 1998, Larsen et al. 1996). However, no studies could be located that provided a direct comparison with stream macroinvertebrates and temperature or fine sediment.

The WA inference models presented in this paper of another method by which a single macroinvertebrate sample may be used as a screening tool for determining overall biological condition (Hubler *in prep*) and potential causes of biological impairment. Additionally, the indicator taxa identified in this paper can supplement currently used metrics to examine whether a site is supportive of taxa sensitive and/or tolerant to temperature and fine sediments. Intensive sampling of a stream reach for the full suite of potential stressors (water chemistry, instream and riparian habitat, and biological stressors) can both time consuming and expensive. A single sample can be collected quickly in the field (< 2 hours) and at a relative small cost per sample ($180-$250). With appropriate sample replication at the individual site or region scale, and coupling with a reference condition approach, resource managers could use macroinvertebrate sampling to cost-effectively screen for biological condition and potential causes of impairment. This information could then be used to guide more intensive future monitoring activities with a focus on the most likely stressors.

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