

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



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Introduction

Macroinvertebrate assemblage 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 assemblage 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 assemblage 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 assemblage structure. Excessive amounts of fine sediment interfere with leaf and detrital processing and may also affect macroinvertebrates by impairing the periphyton assemblage (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 in 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 1st to 4th 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 spanned 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. Substrate models were developed and validated with data from 496 sites. A set of 50 sites was randomly set-aside for independent validation, leaving 446 sites for model calibration (Figure 1). Temperature models were developed and validated with data from 328 sites. A set of 50 sites was randomly set-aside for independent validation, leaving 278 sites for model calibration (Figure 2).

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.

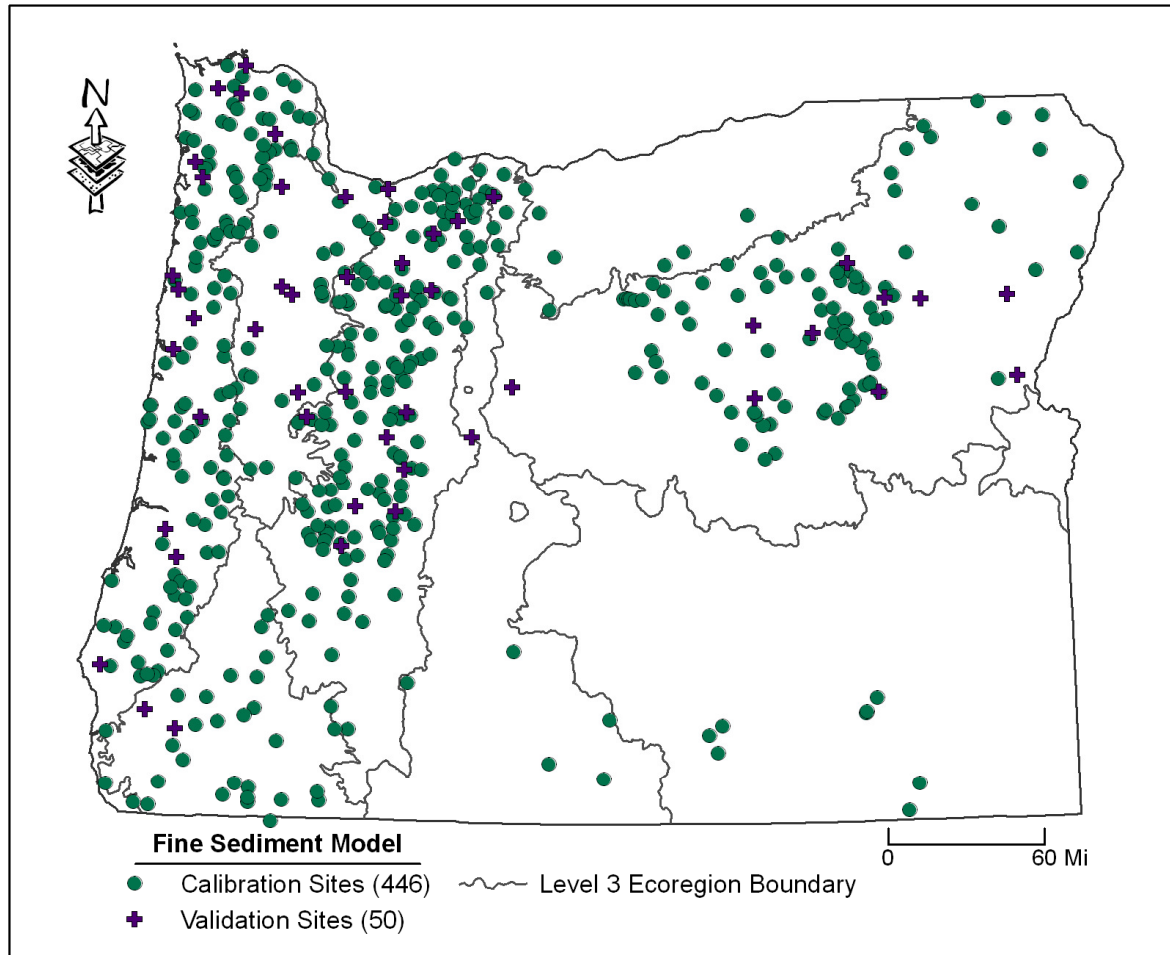


Figure 1. The locations of calibration and validation sites for fine sediment inference models are shown on a map of Oregon. Grey lines delineate the nine Level 3 ecoregions (Thorsen et al. 2003) that occur in Oregon.

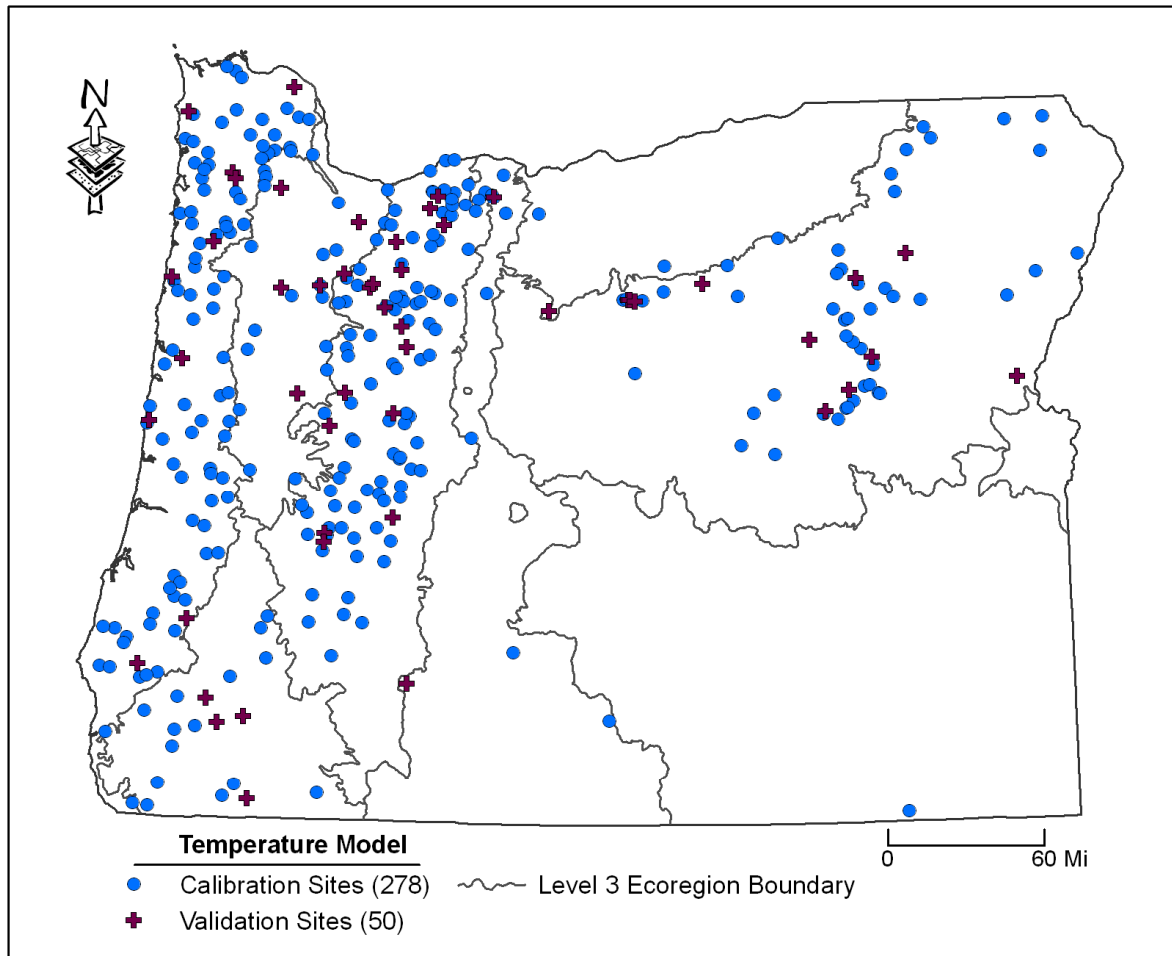


Figure 2. The locations of calibration and validation sites for temperature inference models are shown on a map of Oregon. Grey lines delineate the nine Level 3 ecoregions (Thorsen et al. 2003) that occur in Oregon.

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 study was the average of the daily maximum temperatures for the warmest seven-day period of the season (7-DSMT). This temperature metric corresponds to the state water quality temperature criteria to protect salmonid populations (Oregon Administrative Rules: OAR 340-041-0028).

Substrate data were collected from 21 cross-sectional transects evenly spaced along the sampled stream reach forty times the mean wetted channel width and ranged from 150 to 800 meters (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: $x = \text{Log}_{10} \left(\left(\arcsin \sqrt{b} \right) \left(\frac{2}{\pi} \right) + 1 \right)$, 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 C² 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:

$$\hat{U}_k = \frac{\sum_{i=1}^n y_{ik} x_i}{\sum_{i=1}^n y_{ik}}$$

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

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

where x = the environmental variable, x_i = the value of x in sample i , y_{ik} = the abundance of taxon k in sample i ($y_{ik} \leq 0$) ($i = 1, \dots, n$ sites and $k = 1, \dots, m$ invertebrate taxa). The C² 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:

$$\hat{X}_i = \frac{\sum_{k=1}^m y_{ik} \hat{U}_k}{\sum_{k=1}^m y_{ik}}$$

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 (ter Braak 1988) or inverse regression (ter Braak and Van Dam 1989) may be used to deshrink the estimates. 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.

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 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. Additionally, 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:

$$b = \left[\text{Sine}\left(\frac{\Pi(10^x - 1)}{2}\right) \right]^2, \text{ where } b \text{ is the untransformed value and multiplying by}$$

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 beyond the preferences typically observed in reference assemblages.

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 fine 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 a 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 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 operational taxonomic units (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 constituted 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, constituting only 7% of all OTUs, and included a wide variety of taxonomic resolution ranging from genus to phylum.

Ordination

All sites with paired macroinvertebrate samples and environmental variables were used to assess the strength of the relationships between assemblage structure and seasonal maximum temperature and fine sediment. The NMS results summarized in Table 1 indicate strong assemblage 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 (≥ 10) 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 3; 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 4. 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 (≥ 18.9), but showed definitive stress caused by fine sediment with mean values (22 and 27) well above the reference benchmark (9). Big Creek and Wolf Creek showed slight stress to both temperature and fine sediments. Sixes Creek showed stress to fine sediments (11) slightly above the reference benchmark (9). However, the TS for Sixes Creek (22.6) was much higher than the reference benchmark (19.8). 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

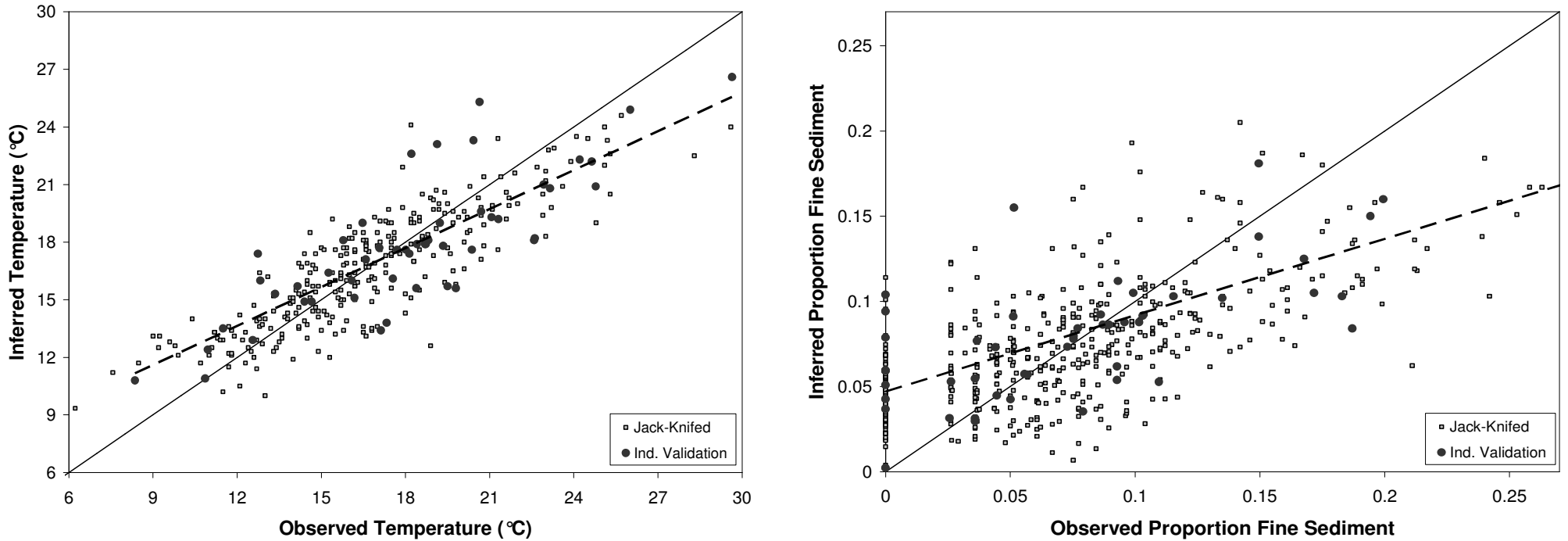


Figure 3. The relationship between observed and macroinvertebrate inferred temperature (top) and sediment (bottom) values is shown with a jackknifed validation dataset (squares) and an independent validation dataset (circles). The diagonal solid line was drawn with a 1 to 1 ratio. The dashed line is a linear trendline generated using the independent validation dataset (50 sites for each model). Proportional fine sediment values (x) are transformed such that:

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

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.

Operational Taxonomic Unit	Sites	r	Optima	Upper Tolerance
Temperature				
<i>Prosimulium</i>	18	-0.346	12.2	14.8
<i>Baetis bicaudatus</i>	12	-0.323	12.3	15.2
<i>Neothremma</i>	37	-0.334	12.9	15.8
<i>Zapada columbiana</i>	86	-0.584	12.9	15.6
<i>Parapsyche elsis</i>	62	-0.493	13.5	15.7
<i>Caudatella</i>	62	-0.453	13.6	16.8
<i>Megarcys</i>	51	-0.470	13.6	16.3
<i>Visoka</i>	77	-0.496	13.7	16.2
<i>Epeorus grandis</i>	69	-0.420	14.2	17.2
<i>Yoraperla</i>	135	-0.570	14.2	17.2
<i>Ephemerella</i>	77	-0.365	14.4	18.1
<i>Despaxia</i>	84	-0.335	14.5	17.0
<i>Drunella coloradensis/flavilinea</i>	58	-0.336	14.5	17.0
<i>Doroneuria</i>	97	-0.408	14.5	17.0
Turbellaria	115	-0.486	14.6	17.9
<i>Ironodes</i>	122	-0.376	14.9	17.6
<i>Ameletus</i>	120	-0.395	15.2	18.3
<i>Drunella doddsi</i>	160	-0.450	15.2	18.3
<i>Rhyacophila Brunnea</i> group	159	-0.333	15.5	18.6
<i>Cinygmula</i>	169	-0.342	15.5	18.2
<i>Micrasema</i>	145	-0.365	15.6	18.8
<i>Dipheter hageni</i>	174	0.405	17.9	21.4
<i>Antocha</i>	114	0.322	18.3	22.0
<i>Hydropsyche</i>	146	0.443	18.5	21.7
<i>Juga</i>	95	0.377	18.6	21.4
Chironomini	149	0.562	18.8	22.0
<i>Zaitzevia</i>	159	0.595	19.0	22.5
<i>Optioservus</i>	132	0.639	19.6	22.9
<i>Dicosmoecus gilvipes</i>	28	0.371	20.6	24.2

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

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.

Level 3 Ecoregion	n	Temperature Score			Fine Sediment Score		
		Median	75 th Percentile	Maximum	Median	75 th 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

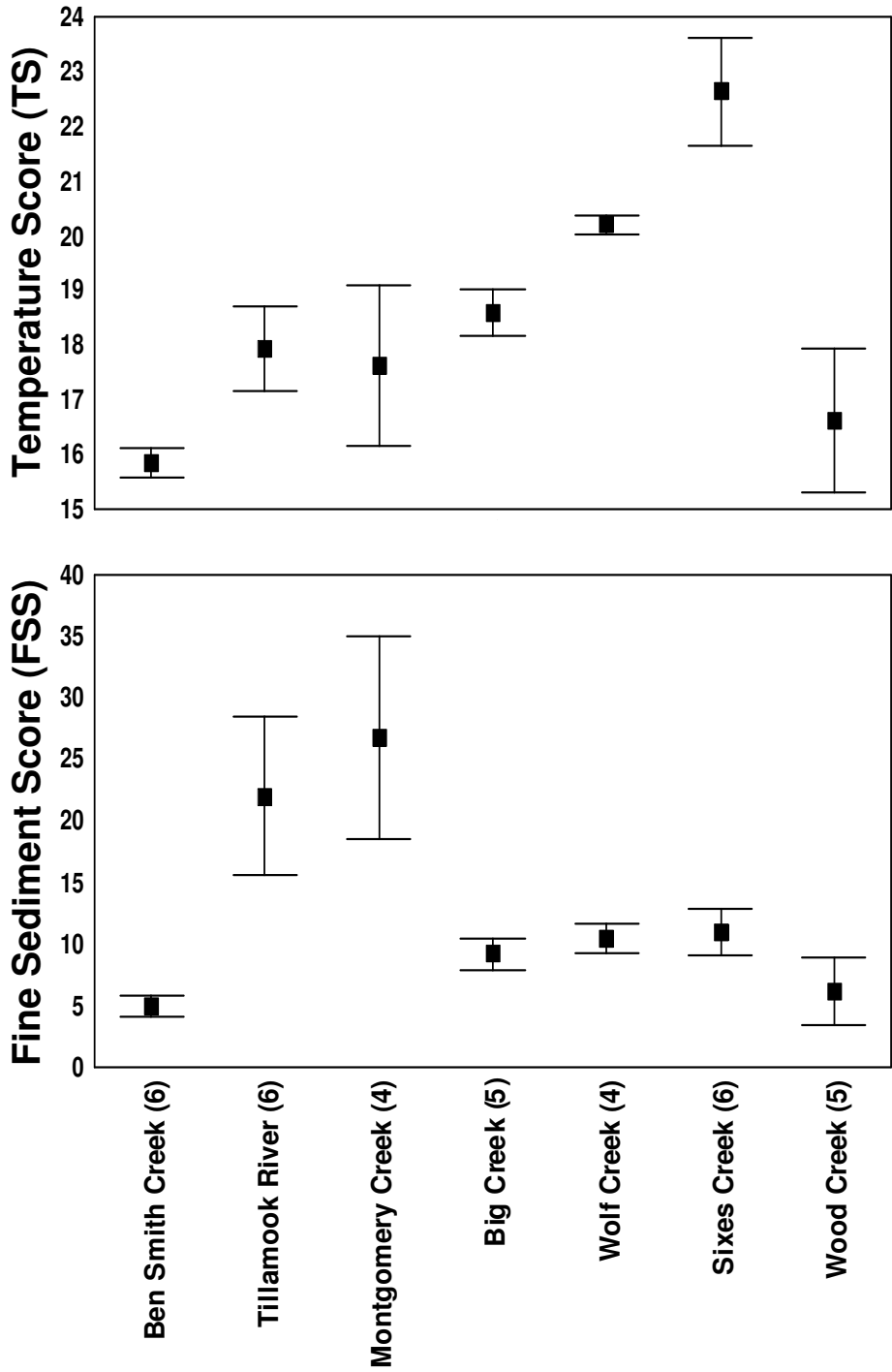


Figure 4. Mean temperature and sediment scores for seven annually repeated sites in the Coastal Coho ESU. Error bars represent 85% confidence intervals about the mean. The number of yearly samples between 1998 and 2004 is shown in parentheses.

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 assemblage 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 results 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 assemblage 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 assemblage 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 assemblage 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 assemblage 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 provide a method by which a single macroinvertebrate sample may be used to identify 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 be both time consuming and expensive. A single macroinvertebrate sample can be collected quickly in the field (< 2 hours) and processed at a relatively small cost per sample (\$180-\$250). With appropriate sample replication at the individual site or region scale, and coupled 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. For an example of how these models have been used by ODEQ staff, see Hubler (2008b).

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Appendix. Optima and tolerances for all taxa used to construct the weighted average inference models for seasonal maximum temperature and fine sediments.

Taxon	Temperature				Fine sediment			
	n	r	optima	tolerance	n	r	optima	tolerance
Miscellaneous								
Nematoda	150	-0.059	16.5	3.8	231	0.162	11	4
Prostoma	5	0.107	20.6	4.2	6	0.123	14	2
Turbellaria	115	-0.486	14.6	3.3	158	-0.049	8	3
Hirudinea	2	0.128	21.3	8.2	4	0.102	15	3
Oligochaeta	220	0.048	16.9	4.1	361	0.301	10	5
Trombidiformes	238	-0.058	16.6	3.7	383	0.175	9	4
Crustacea								
Gammarus	8	0.134	19.5	4.2	12	0.231	28	7
Talitridae					1	0.059	72	3
Hyaella	5	0.139	19.9	3.6	15	0.225	27	9
Asellidae	7	0.062	17.5	3.1	12	0.117	21	9
Ostracoda	65	-0.088	15.7	4.5	93	0.32	17	4
Gastropoda								
Ferrissia	9	0.224	22.1	2.8	14	0.135	17	6
Lymnaeidae	3	0.249	19.1	4.5	11	0.257	18	6
Physa	11	0.319	21.1	4.0	28	0.39	21	7
Planorbidae	7	0.11	17.8	4.5	17	0.215	19	4
Fluminicola	22	0.191	20.2	3.5	32	0.154	16	3
Juga	95	0.377	18.6	2.8	132	0.253	15	5
Valvata					1	-0.013	2	3
Corbicula	1	0.054	25.3	3.2	2	0.122	27	1
Margaritifera	4	0.087	20.8	2.3	5	0.041	17	3
Sphaeriidae	103	0.175	17.7	3.7	176	0.528	21	6
Pristinicola	14	-0.121	13.5	3.4	28	0.085	12	2
Coleoptera								
Amphizoa	2	-0.076	13.3	2.4	3	0.055	14	2

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Curculionidae	2	-0.083	12.1	0.3	1	0.044	41	3
Helichus	1	0.184	21.4	3.2	15	0.177	12	5
Dytiscidae	35	0.175	18.2	2.3	64	0.21	17	6
Ampumixis	42	-0.157	15.8	2.2	59	-0.208	3	2
Cleptelmis	41	0.064	18.5	2.8	76	0.231	16	4
Dubiraphia	3	0.149	23.3	2.6	7	0.192	25	5
Heterlimnius	177	-0.265	15.8	2.6	259	-0.212	7	3
Lara	62	-0.113	15.8	2.6	105	0.055	11	6
Microcylloepus	2	0.206	26.3	4.7	9	0.167	17	6
Narpus	72	0.136	17.5	2.6	109	0.01	9	4
Optioservus	132	0.639	19.6	3.3	236	0.382	12	4
Ordobrevia	19	0.191	19.8	3.4	37	-0.027	1	2
Zaitzevia	159	0.595	19	3.5	274	0.241	9	4
Haliplidae	8	0.092	19.2	4.1	8	0.178	28	3
Hydraena	13	0.095	18.5	4.7	27	0.187	15	5
Ochthebius	3	-0.088	16.8	1.9	5	0.069	15	3
Hydrophilidae	20	0.059	16.3	2.6	46	0.201	16	4
Acneus	7	-0.055	15.5	1.3	10	-0.043	2	2
Eubrianax edwardsii	20	0.127	19.1	2.0	36	-0.035	3	2
Psephenus	14	0.309	23.3	4.4	22	0.146	6	2
Diptera								
Atherix	20	0.229	22.1	3.5	28	0.059	5	4
Dolichopodidae	2	0.045	18.2	3.6	10	0.054	20	6
Chelifera/Metachela	95	0.051	16.5	3.3	165	0.012	8	3
Clinocera	49	-0.139	15.6	3.5	73	-0.152	5	3
Hemerodromia	8	0.135	21.3	5.1	1	-0.021	0	3
Oreogeton	26	-0.227	13.6	2.8	36	-0.113	3	2
Wiedemannia	9	-0.134	15.8	3.2	10	-0.064	4	1
Ephydriidae	4	0.054	20	3.9	11	0.136	10	7
Muscidae	5	0.133	20	4.8	10	0.15	21	5
Glutops	77	-0.243	15.3	2.8	124	-0.1	8	3
Sciomyzidae	1	-0.041	14	3.2				

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Stratiomyidae	2	0.174	17.6	8.2	9	0.171	12	4
Tabanidae	12	0.196	20.8	3.5	26	0.182	16	8
Blephariceridae	13	0.073	17.1	2.8	19	-0.083	3	1
Ceratopogoninae	135	0.024	17	3.2	200	0.148	11	4
Forcipomyiinae	42	-0.057	15.8	2.9	62	-0.001	6	3
Chironomini	149	0.562	18.8	3.2	260	0.272	10	5
Pseudochironomini					2	0.082	5	4
Tanytarsini	270	0.071	16.8	3.7	426	0.171	8	4
Diamesinae	95	-0.088	16.8	4.1	1	-0.025	2	3
Orthocladiinae	277	-0.229	16.5	3.8	444	0.103	8	4
Podonominae	5	-0.085	13.5	4.9	8	0.091	13	7
Prodiamesinae	5	0.091	19.4	2.9	8	0.119	41	20
Tanypodinae	164	0.256	17.3	3.8	279	0.519	12	6
Deuterophlebia	1	0.066	21.1	3.2	112	-0.156	5	3
Dixa	86	-0.156	15.4	3.5	5	0.014	13	6
Dixella	8	0.034	17	2.1	122	0.104	11	4
Meringodixa	14	-0.031	15.6	1.8	26	0.035	10	3
Maruina	36	0.114	17.7	3.4	52	0.044	6	2
Pericoma/Telmatoscopus	39	-0.087	16.9	4.0	70	0.082	10	3
Psychoda					2	-0.014	9	1
Ptychopteridae	8	0.056	16.5	1.4	12	0.121	31	5
Prosimulium	18	-0.346	12.2	2.6	35	-0.018	7	2
Simulium	201	0.317	17.4	3.2	303	-0.025	8	5
Thaumalea	17	-0.163	13.4	3.0	28	-0.031	5	1
Antocha	114	0.322	18.3	3.7	187	-0.044	5	3
Cryptolabis	10	0.045	17.9	2.2	9	0.011	14	3
Dicranota	160	0.01	16.2	3.1	53	0.151	9	4
Gonomyia	1	0.058	20.7	3.2	18	0.01	10	3
Hesperoconopa	11	-0.062	14.7	5.8	21	-0.116	3	2
Hexatoma	108	0.114	17.2	3.3	176	-0.064	8	3
Limnophila	17	0.094	17.4	2.7	42	0.09	14	6
Limonia	5	-0.036	15.9	4.2	12	0.112	9	2

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Molophilus					2	0.052	24	4
Ormosia	1	-0.161	6.23	3.2	1	-0.06	12	3
Pedicia	8	0.02	16.4	1.8	10	0.116	21	5
Pilaria	3	-0.053	15.5	3.5	5	-0.042	2	3
Pseudolimnophila	2	-0.008	16.3	5.3	2	-0.023	4	9
Rhabdomastix	13	-0.037	16.4	1.8	21	-0.101	7	3
Tipula	14	0.047	17.2	4.1	34	0.219	25	9
Ephemeroptera								
Ameletus	120	-0.395	15.2	3.1	184	-0.183	6	3
Acentrella insignificans	3	0.107	22.2	4.7	9	0.001	4	4
Acentrella turbida	21	0.187	19.6	3.5	36	-0.001	5	3
Baetis alius	2	-0.023	17.8	0.3	3	0.031	9	6
Baetis bicaudatus	12	-0.323	12.3	2.9	17	-0.166	6	1
Baetis flavistriga	10	0.141	21.3	2.4	17	0.029	6	4
Baetis notos	11	0.127	20	2.5	15	0.071	10	2
Baetis tricaudatus	254	-0.012	16.6	3.4	398	-0.391	6	4
Callibaetis	2	0.109	23.2	2.2	2	0.14	63	7
Centroptilum	1	0.025	20.1	3.2	6	0.141	21	22
Dipheter hageni	174	0.405	17.9	3.5	250	0.108	9	5
Labiobaetis	2	0.04	16.5	0.7	1	-0.012	10	3
Procloeon					2	0.082	5	1
Attenella	31	0.071	17	2.8	49	-0.043	7	2
Caudatella	62	-0.453	13.6	3.2	90	-0.287	4	2
Drunella coloradensis/flavilinea	58	-0.336	14.5	2.5	134	-0.224	4	2
Drunella doddsi	160	-0.45	15.2	3.1	83	-0.348	3	2
Drunella grandis	18	0.018	18.1	5.4	240	-0.581	3	2
Drunella pelosa	1	-0.017	16.2	3.2	25	-0.087	5	3
Drunella spinifera	33	-0.216	14.8	2.4	65	-0.079	6	2
Ephemerella	77	-0.365	14.4	3.7	97	-0.018	9	3
Serratella teresa	10	-0.085	14.6	4.2	20	-0.049	6	1
Serratella tibialis	109	-0.174	16.1	3.1	170	-0.237	5	2

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Timpanoga hecuba	11	0.108	20.3	3.9	14	0.005	6	2
Cinygma	59	-0.139	15.6	2.8	79	0.177	16	5
Cinygmula	169	-0.342	15.5	2.7	244	-0.295	6	3
Epeorus albertae	49	0.254	19.6	4.2	73	0.017	8	3
Epeorus deceptivus	7	-0.212	13.7	2.2	11	-0.185	3	2
Epeorus grandis	69	-0.42	14.2	3.0	90	-0.414	2	1
Epeorus longimanus	60	-0.137	15.2	2.4	92	-0.317	4	2
Ironodes	122	-0.376	14.9	2.7	176	-0.164	6	3
Nixe/Leucocruta	36	0.185	19.6	3.6	55	0.14	10	5
Rhithrogena	174	-0.229	16.1	3.6	253	-0.473	5	3
Paraleptophlebia	187	-0.088	16.4	3.6	293	0.257	11	5
Tricorythodes	6	0.253	23	6.1	15	0.23	10	5
Hemiptera								
Corixidae	2	0.095	19.6	4.7	6	0.108	26	8
Lepidoptera								
Petrophila	3	0.131	24.3	2.9	5	0.098	3	2
Megaloptera								
Corydalidae	15	-0.151	15.2	2.0	7	0.141	22	10
Sialis	15	0.096	17.1	4.0	25	0.141	19	10
Odonata								
Cordulegastridae	1	0.044	20.7	3.2	1	-0.006	6	3
Gomphidae	30	0.199	19.2	3.7	65	0.136	9	4
Libellulidae	1	-0.041	19.7	3.2	2	0.144	21	4
Coenagrionidae	5	0.27	21.9	3.0	25	0.336	25	4
Plecoptera								
Capniidae	19	-0.141	14.4	4.1	33	0.012	10	5
Despaxia	84	-0.335	14.5	2.5	4	0.048	7	0
Moselia	45	-0.252	13.9	2.1	61	-0.026	8	3
Malenka	138	0.026	16.7	2.8	203	0.031	9	4
Nemoura	1	-0.108	7.57	3.2	3	-0.032	4	2
Podmosta	1	0.001	17.3	3.2	1	-0.059	2	3
Prostoia	1	-0.06	13.2	3.2	1	-0.061	0	3

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Soyedina					1	-0.057	2	3
Visoka	77	-0.496	13.7	2.5	109	-0.231	4	2
Zapada cinctipes	170	0.195	17.2	3.3	281	0.216	10	4
Zapada columbiana	86	-0.584	12.9	2.7	104	-0.225	5	2
Zapada frigida	22	-0.147	15.2	3.7	27	-0.08	4	2
Zapada Oregonensis Gr.	45	-0.179	14.8	2.6	65	-0.069	7	2
Taeniopterygidae	8	0.027	13.1	3.0	11	-0.098	8	1
Sweltsa	206	-0.281	15.9	3.4	312	-0.098	8	3
Plumiperla	5	0.071	16.8	1.4	8	-0.036	2	2
Suwallia	12	0.048	16.5	3.4	25	-0.077	5	5
Kathroperla	26	-0.209	14.4	2.4	26	-0.182	3	1
Paraperla	26	-0.065	16.1	2.6	35	-0.075	9	1
Sierraperla	2	-0.114	12.2	4.5	2	-0.087	2	4
Soliperla	23	-0.19	14.8	2.0	33	-0.18	3	2
Yoraperla	135	-0.57	14.2	3.0	190	-0.17	6	3
Calineuria	164	0.259	17.6	3.3	254	-0.176	6	3
Doroneuria	97	-0.408	14.5	2.5	35	-0.054	6	1
Hesperoperla pacifica	101	0.28	17.9	2.5	176	-0.079	7	3
Claassenia sabulosa	2	0.015	18.5	7.1	4	-0.024	5	5
Isoperla	48	-0.089	15.9	3.5	65	0.169	19	5
Megarcys	51	-0.47	13.6	2.7	70	-0.367	4	2
Perlinodes	11	0.103	19.4	4.1	15	-0.032	5	3
Setvena	3	-0.154	10.9	2.9	6	0.003	9	1
Skwala	48	0.144	18.6	4.0	75	0	8	4
Cultus	1	-0.035	12.6	3.2	18	-0.038	5	3
Kogotus/Rickera	9	-0.076	14.2	2.8	14	-0.073	7	2
Diura	1	-0.064	19.7	3.2	278	0.233	10	4
Pteronarcella	14	-0.011	17	3.0	19	0.024	15	3
Pteronarcys	76	-0.173	15.2	3.4	112	-0.237	4	3
Trichoptera								
Arctopsyche	55	-0.093	15.5	2.1	72	-0.268	2	2
Parapsyche almota	25	0.004	16.4	3.0	39	0.07	14	7

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Parapsyche elsis	62	-0.493	13.5	2.2	82	-0.309	4	3
Cheumatopsyche	14	0.268	23.7	1.7	26	0.278	20	5
Hydropsyche	146	0.443	18.5	3.2	248	-0.002	6	3
Dolophilodes	24	-0.152	15.3	3.6	4	0.085	21	15
Wormaldia	144	0.204	17.4	3.3	221	0.044	9	4
Polycentropodidae	10	-0.03	16.1	1.7	18	-0.035	3	2
Psychomyia	5	0.076	18.2	3.0	10	0.045	15	6
Pedomoecus	5	-0.153	14.1	2.0	6	-0.149	5	0
Apatania	43	-0.102	16.1	2.2	71	-0.168	6	3
Amiocentrus	31	0.073	17.9	2.9	56	-0.025	6	2
Brachycentrus	23	-0.033	16.6	3.4	40	-0.051	5	3
Micrasema	145	-0.365	15.6	3.2	223	-0.115	7	3
Heteroplectron	10	0.041	16.5	1.7	14	0.059	11	3
Goera	5	0.106	20.1	2.1	9	0.056	16	3
Goeracea	1	-0.064	9.24	3.2	1	0.024	6	3
Helicopsyche	7	0.227	24.6	5.4	17	0.129	7	6
Lepidostoma	134	0.04	16.6	3.6	195	0.069	7	4
Leptoceridae	4	0.037	17.2	3.3	6	0.079	10	2
Allocosmoecus	2	0.039	18.4	2.6	4	-0.077	2	1
Cryptochia	5	-0.175	12	4.0	24	-0.154	2	1
Dicosmoecus atripes	8	-0.018	17.4	2.1	162	0.012	8	2
Dicosmoecus gilvipes	28	0.371	20.6	3.6	14	-0.045	6	2
Ecclisocosmoecus	6	-0.205	11.5	2.1	11	-0.051	8	1
Ecclisomyia	15	-0.157	13.7	3.0	19	-0.065	3	2
Onocosmoecus	12	0.245	18.4	3.1	19	0.228	25	6
Desmona	1	-0.044	18.9	3.2	1	0	14	3
Psychoglypha	15	-0.035	16.1	4.9	30	0.106	14	6
Hydatophylax	11	0.008	16.7	1.6	10	-0.018	6	5
Philocasca	1	-0.124	13.6	3.2	2	-0.044	3	0
Pseudostenophylax	2	-0.03	18.9	1.4	3	0.158	34	4
Odontoceridae	1	-0.037	14.1	3.2	4	0.003	11	8
Gumaga	9	0.018	16.2	1.7	9	0.098	20	4

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Neophylax occidentalis	3	-0.059	15.5	1.8	5	-0.095	1	1
Neophylax rickeri	46	0.196	17.8	2.2	72	-0.064	5	2
Neophylax splendens	44	-0.126	15.5	3.0	67	-0.141	5	3
Oligophlebodes	24	-0.229	13.1	2.2	31	-0.216	2	1
Farula	2	-0.059	14.2	1.8	2	0.001	22	7
Neothremma	37	-0.334	12.9	2.9	39	-0.066	6	1
Agapetus	25	0.05	18.6	3.6	51	-0.105	4	3
Anagapetus	19	-0.223	14.1	2.5	31	-0.09	4	1
Glossosoma	183	0.046	16.6	3.1	270	-0.353	5	3
Protoptila	1	0.099	23.3	3.2	2	0.019	26	0
Agraylea	4	-0.037	17.4	3.6	7	-0.096	2	2
Hydroptila	18	0.309	21.5	2.7	43	0.286	17	6
Leucotrichia	1	0.066	23	3.2	4	0.072	4	1
Neotrichia	3	0.148	24.6	1.3	6	0.077	4	3
Metrichia	1	0.033	23	3.2	1	0.056	16	3
Ochrotrichia	5	0.04	19.7	1.7	14	0.047	2	1
Palaegapetus	2	-0.094	13.6	3.6	3	-0.004	7	0
Rhyacophila Alberta Gr.	8	-0.124	15	2.1	16	-0.077	7	3
Rhyacophila Angelita Gr.	54	0.055	16.6	2.3	74	-0.253	3	2
Rhyacophila Betteni Gr.	190	-0.293	15.7	3.1	272	-0.413	5	3
Rhyacophila Brunnea Gr.	159	-0.333	15.5	3.1	221	-0.423	4	2
Rhyacophila Coloradensis Gr.	2	0.048	20.7	5.3	5	-0.005	16	3
Rhyacophila Grandis Gr.	14	-0.129	13.5	3.2	19	-0.019	6	4
Rhyacophila Hyalinata Gr.	85	-0.209	15.5	2.7	136	-0.358	3	2
Rhyacophila Iranda Gr	7	-0.122	12.4	3.0	11	-0.095	3	1
Rhyacophila Lieftincki Gr.	14	0.07	17.4	2.7	18	0.035	13	3
Rhyacophila Nevadensis Gr.	4	-0.101	16	5.0	4	-0.093	3	1
Rhyacophila Oreta Gr.	1	0.012	17.5	3.2	1	0.005	2	3
Rhyacophila Rotunda Gr.	1	-0.076	12.2	3.2	2	-0.007	10	0
Rhyacophila blarina	36	0.126	17	2.3	58	0.076	13	5
Rhyacophila narvae	92	-0.253	15.6	3.0	132	-0.163	6	2
Rhyacophila pellisa/valuma	33	-0.262	14.4	3.1	50	-0.16	6	2

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Rhyacophila Vagrita Gr.	13	-0.207	12.8	3.5	14	-0.108	4	2
Rhyacophila Verrula Gr.	6	-0.126	13.2	3.0	17	-0.078	5	3
Rhyacophila Vofixa Gr.	21	-0.183	13.2	4.1	30	-0.145	4	4