Environmental Biology of Fishes (2006) 75:395–407
DOI 10.1007/s10641-005-5150-8

Quantifying littoral vertical habitat structure and fish community associations using underwater visual census

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Received 8 October 2004 Accepted 5 November 2005

Key words: community ecology, lake, microhabitat, quadrat sampling, canonical correspondence analysis, vertical structure, littoral

Synopsis

We developed and tested a new visual census technique to quantify the importance of vertical habitat structure on the associated fish assemblages in the littoral zone of a freshwater lake. We demonstrated that the primary environmental gradient, accounting for the most variation in the species data, represented a temporal gradient of seasonal characteristics. The secondary environmental gradient was related to the vertical structure at the sampling locations, showing the importance of the vertical component of the environment on fish community structure. Characterizing the vertical component at different resolutions provided different interpretations. The primary difference was the strength of influence of woody material on community structure. Woody material had a stronger influence on community structure throughout the water column when a single vertical unit defined the fish data. The appropriateness of defining the data by either multiple vertical strata or by a single vertical one would be dependent on the objectives of the study, as neither approach was found to explain substantially more variation in the species data. The current study demonstrates that fish are closely associated with particular elements of habitat structure in the littoral zone, even in the absence of major piscivorous predators. We provide a novel study quantifying the vertical multiple habitat structures and habitat use by fish in the water column of a freshwater lake. The new vertical visual census technique can be used to more comprehensively sample the three-dimensional environment of lake littoral zones, and quantify the fish–habitat spatial relationships across a range of abiotic and biotic habitat features.

Introduction

Aquatic ecosystems are naturally complex, making it difficult to understand the processes that structure communities (Jackson et al. 2001). To discern the processes that influence community structure, the differential responses of assemblages and individual species to environmental factors must be examined (Weaver et al. 1996). To understand the relationship between habitat and fish distribution, it is necessary to characterize and quantify aspects of the environment that are important to fishes. Considering spatial and temporal changes on a microhabitat scale may help to unravel some of the complexity of aquatic ecosystems.

Habitat complexity or heterogeneity has been shown to influence fish distribution in the littoral zone of freshwater lakes (e.g. Pratt & Smokorowski 2003). Fish distribution has been linked to environmental variables including the presence or diversity of macrophytes (e.g. Pratt & Smokorowski 2003), shoreline aspect and substrate composition (Gido et al. 2002), distance from shore, and lake morphological features including lake size, lake depth and the associated thermal stratification. However, whereas studies of other aquatic and terrestrial systems have long recognized the importance of vertical habitat complexity and heterogeneity (e.g. Catsadorakis 1997, Grossman et al. 1998), lake studies have lacked a similar focus on the three-dimensional aspect of the environment.

Habitat structure in freshwater lakes has often been measured by considering the amount and distribution of macrophytes. Studies have relied on removing sections of vegetation from natural lake habitat to determine the importance of macrophyte composition (e.g. Weaver et al. 1997). However, more traditional approaches of quantifying the vertical component of vegetation involve the visual inspection of macrophytes to estimate their relative abundance in an area of interest (e.g. Tonn & Magnuson 1982) or to classify aquatic plants as submerged, emergent, or floating types. Estimating the percentage cover of vegetation has not always been the best measure of habitat structure because the vertical component of the vegetation is often ignored. In such instances, two very different types of vegetative structure may be given the same weight in the analysis related to fish community structure.

Macrophytes are the most commonly measured element of habitat structure in the littoral zone of freshwater lakes. Additional physical habitat features such as woody material, also referred to as woody debris or necromass, may influence fish distribution in the littoral zone but have received limited attention (e.g. Mallory et al. 2000). There is a need for improved knowledge of a broader base of habitat structures and their relation to fish distribution; a comprehensive quantitative method of sampling habitat and fish associations is the most valuable approach. Quantifying woody debris and fish use of woody structure, other than that associated with predator–prey interactions, would be valuable for enhancing the current state of knowledge of the role that woody debris plays in structuring littoral zone fish communities.

Visual census

To understand fish community structure, both the habitat and the fish must be sampled. Many methods of fish sampling have limitations and biases associated with them (Jackson & Harvey 1997). Visual census is a commonly used technique for observing fish habitat and fish species associations in aquatic systems. The technique involves either snorkeling or using SCUBA to remain in the water for extended periods of time, using quadrats, point-abundance sampling, or strip counts to sample a variety of sites.

Our study developed and tested a new quadrat-based, visual-census technique that quantified the vertical-habitat structure and vertical habitat use by fish. To most effectively test this technique, we chose a small lake, Poorhouse Lake, which had no development on the shoreline and lacked major littoral predators such as bass, *Micropterus* species, or pike, *Esox lucius*. The lack of major predators resulted in a lake system with a large number of cyprinids that did not display predator-escape behaviour in the presence of a snorkeling observer (MacRae and Jackson 2001). The lack of shoreline development ensured undisturbed littoral-zone habitat and suggested the presence of a natural fish community, unaffected by introduced or invading species. Within Poorhouse Lake, we sampled 20 sites; we quantified both the habitat structure and fish associations in three-dimensions.

Research objectives

The primary objective of the current study was to develop and test a new visual-census technique for quantifying the vertical component of habitat structure and fish use of habitat in the littoral zone of a freshwater lake. We used multiple, discrete vertical strata to quantify vertical habitat structure and fish position in the water column. We employed multiple approaches for integrating or pooling the data to determine how differences in the resolution of vertical stratification affected the pattern of fish–habitat interactions. Our approach can vertically quantify both fish and habitat structure whereas to date there has been a lack of focus on the three-dimensional arrangement of habitat in lakes.

Methods

Study area

We chose Poorhouse Lake for this study based on the following criteria: the accessibility of the lake, the absence of major predators, high numbers of cyprinids and known species composition (Jackson 1992), adequate water clarity for visual census, and heterogeneity of the littoral zone habitat. Poorhouse Lake, (45°22′ N latitude and 78°45′ W longitude) has an area of 29.4 ha and a depth of 12.5 m at its deepest point, although this study focused on the littoral zone.

Site selection

We first surveyed the entire shoreline to determine the range of habitat types, from simple to complex. We selected 20 sites around the perimeter of Poorhouse Lake, each at approximately 1 m depth within the littoral zone, for sampling throughout the summer of 2001. We selected 15 of the 20 sites based on the relative occurrence of particular habitat types within the lake, and we chose five sites at random. We selected each sampling site by choosing a section representative of the general area within each habitat type. We marked quadrat sites with a short length (2–3 cm) of flagging tape tied to a nail pushed into the sediment. The sites chosen ranged from simple sandy sites to complex sites, consisting of various combinations of woody and rocky structures with vegetation, and a variety of substrates. We mapped all sites to confirm the habitat type within a radius of approximately 2 – 3 m of the quadrat marker.

We followed a standard protocol for collecting habitat details at all sites. We set a temperature logger at each site on 30 May, which remained in the water until 29 September. Loggers were placed at least 3 m from each quadrat center to prevent the logger from becoming part of the three-dimensional habitat of the site at locations lacking vertical relief. Depth of the water column at all quadrat markers was initially recorded in May and monitored each month throughout the summer. We measured the distance to shore from each quadrat center once in May and once in August, and set minnow traps at different times throughout the summer to verify species identification.

For each trial, we approached the site slowly from at least 5 m away by snorkeling and placed a quadrat at the marker. Small fishing bobbers tied to the ends of fishing line attached at each corner floated to the surface and held the line vertical in the water (Figure 1a). The lines were stratified vertically, at 25 cm intervals and were numbered consecutively from the lower most to the top. The activity trial began 3–5 min after the quadrat was in place so that the fish were acclimated to the presence of the motionless swimmer and quadrat. We recorded the following details underwater on a clear Plexiglass slate, every minute for 10 min: the abundance of each species of fish present in the quadrat, the behaviour and activity exhibited by each species, and the vertical position of the fish in the water column. When more than 50 fish were present at the site, single-minute observations could not be made. In these cases, we recorded the following information: total number of fish ob-

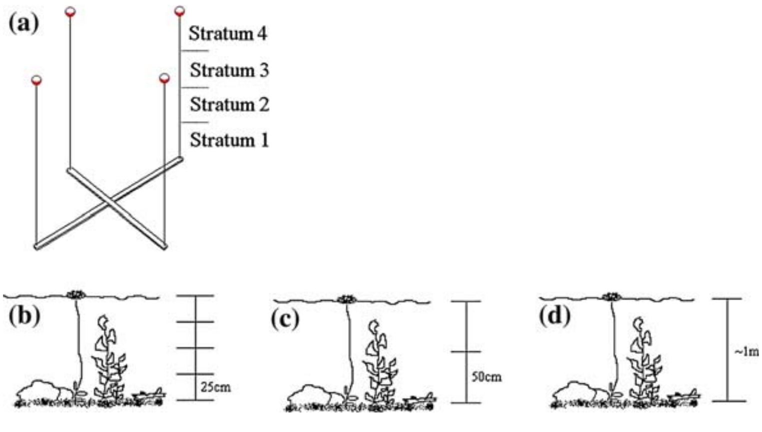

Figure 1. Quadrat used to quantify vertical and horizontal habitat structure (1 m^2) in Poorhouse Lake littoral zone (a), and the three resolutions of vertical stratification used for data organization: 25 cm strata (b), 50 cm strata (c), and the full water column as a single vertical unit (d).

served, an estimated percentage of each species present, and the activity, behaviour, and position of each species. To minimize disturbance to the fish and habitat, there was little fin or arm movement by the observer throughout each trial; a position was chosen for observation that would avoid casting a shadow onto the site. After the trial, we recorded the amount of wood, rock, and vegetation within each stratum using a modified Domin scale (Kershaw 1973). Environmental data collected included surface water temperature, air temperature, time of day, and weather conditions; the Beaufort wind scale was used to estimate wind speed. Additional notes were made on the fish observed in the general area and conditions specific to that day and trial. We determined substrate type using a modified Wentworth scale (Cummins 1962); we estimated percentage cover of each substrate type using the modified Domin scale, at the end of the summer sampling period. In May through August, we sampled Poorhouse Lake twice per month. Within each sampling period, we ran two sets of trials for all 20 sites. In September, we sampled Poorhouse once with one set of trials.

Both shore distance and temperature range data were log-transformed to approximate normal distributions and improve linearity between variables; we performed square transformations on depth and water temperature data. We used principal coordinates analysis (PCoA; Legendre & Legendre 1998) with the Euclidean distance coefficient to summarize the gradient among the eight substrate variables used in data collection. A gradient of coarse substrate types (e.g., boulder) to fine substrate (organic silt) was summarized along the first PCoA axis. We replaced the eight different substrate variables by this single substrate variable, which summarized a gradient from fine to coarse substrate.

Fish species presence–absence data were organized into three different resolutions of vertical stratification (Figure 1b–d) to better elucidate the effectiveness of the new technique in capturing community interactions. The finest level of resolution treated the data as it was collected in the field: the data was defined by vertical strata 25 cm high, from the substrate to the surface, with each site having four or five strata in total depending on the site depth. The coarser level of resolution used pooled data so that the water column was divided into only two strata: the first extended from the substrate to 50 cm above it, and the second extended from 50 cm above the substrate to the water's surface. The final, coarsest resolution used pooled fish data that was defined by the single vertical unit of the full water column (i.e. each site had only one set of observations per survey). However, in this final consideration of the data, the vertical habitat measurements of wood, rock and vegetation were included as separate variables so that the role of these habitat structures could be considered in the four vertical strata (25 cm) of the water column. At this coarsest resolution, the fish data were defined by the full water column but the physical habitat attributes were still considered in multiple vertical units. This approach allowed a comprehensive evaluation of the influence of individual habitat structures throughout the water column on fish distribution.

We used correspondence analysis to summarize species association relationships at each of the three resolutions of vertical stratification. Biplot scaling was used, with a symmetric focus. We excluded samples in which no fish were observed from the analysis, as these cannot be included in a CA approach. In total, we included 17 species and classifications of fish in the analyses (Table 1).

Canonical correspondence analysis (CCA) was used with each vertical resolution of data to quantify the relative importance of vertical habitat structure in influencing community structure, compared to other environmental variables. As in the CA, biplot scaling was used with a symmetric focus, and only samples in which fish were observed were included. To assess the importance of the vertical component of habitat structure, stratum designation was included as an environmental variable at the two finest vertical resolutions. In total, 10 environmental variables were included in the CCA analysis of two out of the three levels of data organization: data defined vertically at 25 cm stratification and 50 cm stratification. When data were pooled to represent the full water column, vertical-habitat measurements were included to evaluate the role of habitat structure in specific sections of the water column: the percentage of cover provided by vegetation, rock, and wood was recorded for each stratum and treated as a separate environmental variable. In total, 15 environmental variables were included. Certain

Table 1. Species list and codes for the 17 species and classifications of fish included in the analyses and graphical results.

Species code	Common name	Scientific name
bln-dc	Blacknose dace	*Rhinichthys atratulus*
blt-ns	Bluntnose minnow	*Pimephales notatus*
brk-sb	Brook stickleback	*Culaea inconstans*
cmn-sn	Common shiner	*Luxilus cornutus*
crk-cb	Creek chub	*Semotilus atromaculatus*
fat-hd	Fathead minnow	*Pimephales promelas*
“fry”	Very small fish that could not be visually identified while in the water	
gld-sn	Golden shiner	*Notemigonus crysoleucas*
pkn-sd	Pumpkinseed	*Lepomis gibbosus*
rbl-dc	Northern redbelly dace	*Phoxinus eos*
Trout	Brook trout	*Salvelinus fontinalis*
Ukn	Last year’s young-of-the-year	*N/A*
ukn-cyp	Unidentified cyprinid	*Cyprinidae*
ukn-sn	Unidentified shiner	*Cyprinidae*
ylw-pr	Yellow perch	*Perca flavescens*
yoy	This year’s young-of-the-year	*N/A*
ypkn-sd	Young-of-the-year pumpkinseed	*Lepomis gibbosus*

environmental variables were measured at a single point in time for each observation. As such, the data collected for these variables did not accurately reflect the potential influence of the variables on the habitat; they were therefore included as covariables in all CCA analyses. In total, five covariables were included in the analysis: cloud cover, wind strength, wind–gust strength, time, and air temperature. By making these five variables covariables, any confounding effects on the remaining environmental variables or the fish species patterns were removed.

Results

Correspondence analysis

Ordination plots illustrated the physical separation between the young and adult fish at all three levels of data organization (Figures 1b–d). The general pattern was the same across the three resolutions of data (Figures 2a–c); the two young species classifications grouped together, the adults grouped at the opposite end of the same axis, and the “fry” (denotes very small fish that could not be visually identified while in the water) aligned with the alternate axis, separated from both groups. The percentage inertia represents the percentage of the total species inertia explained by each axis, a measure similar to variance. The percentage of inertia of species data explained (Table 2) increases from the finest resolution of four vertical strata (14.1 and 13.4% for axis 1 and 2, respectively) to the coarsest level of resolution, the full water column (17.4 and 16.2% for axis 1 and 2, respectively). However, note that the total inertia decreases substantially from the four strata vertical component to the combined data format due to the reduction in the size of the data matrix. Therefore, as the total amount of variation explained by the species relationships decreases from the level of four strata (4.006) to the full water column (2.645) each axis’ eigenvalue represents a greater percentage of that smaller total. The 6.1% difference in the amount of variation explained by the first two axes from the finest to the coarsest vertical resolution was not substantial enough to determine which resolution was the better method of considering the data given the associated change in the size of the matrices being considered.

Cumulative percentage variation of species data was low in the CCA results for all three resolutions of vertical stratification (Table 3). CCA can produce low percentage inertia of species data because data can be very noisy, especially presence–absence data (ter Braak 1998), or because the fish community is not structured along the variation in the environmental conditions. Nearly three quarters (73.8%) of the explained variation was

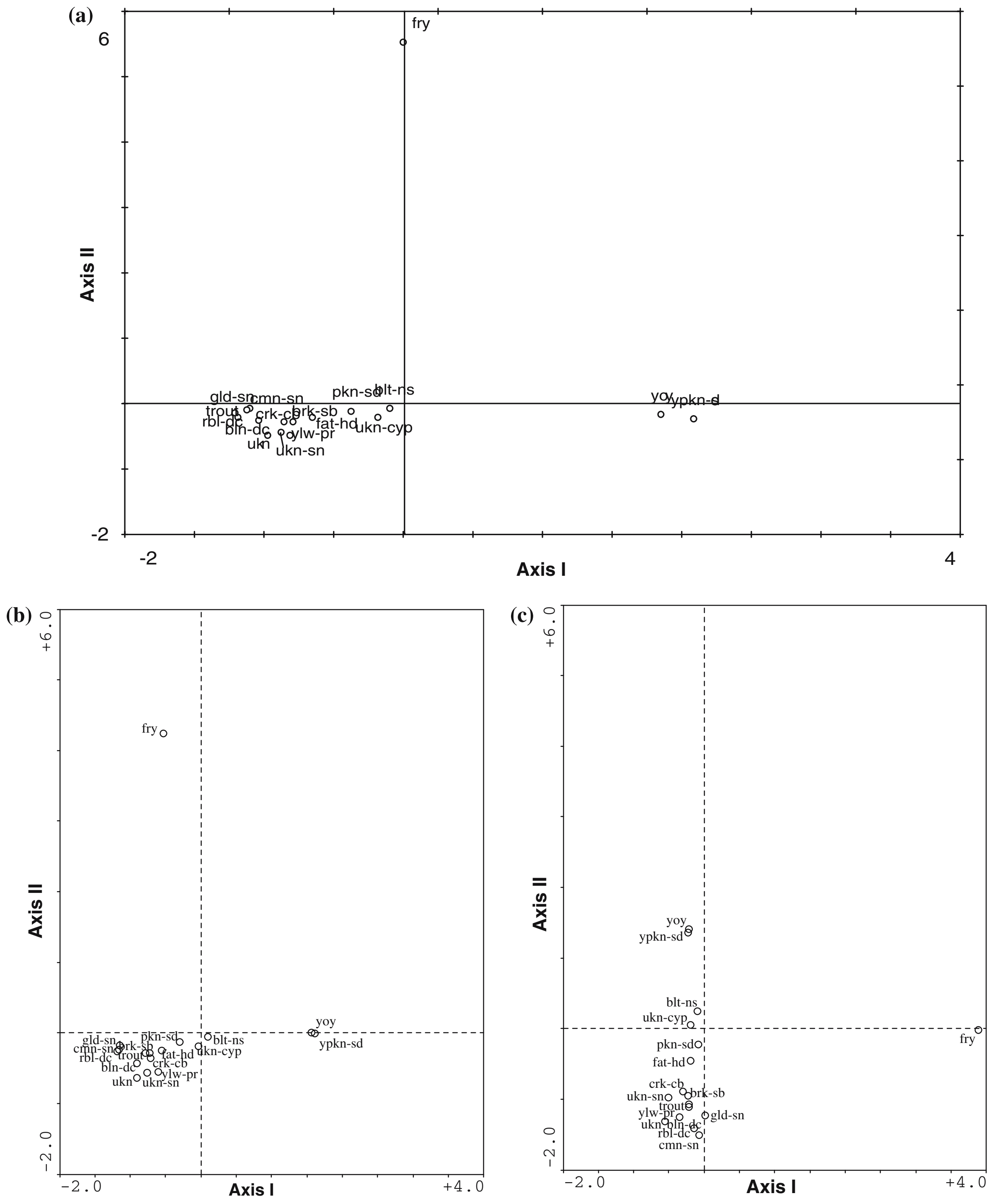

Figure 2. Correspondence analysis axes one and two, showing the association of fish species based on presence–absence data defined by (a) 25 cm vertical stratification, Axis I and II summarized 14.1 and 13.4%, respectively, of the variation in the species data, (b) 50 cm vertical stratification, Axis I and II summarized 15.3 and 14.7%, respectively, of the variation in the species data and (c) the single vertical unit of the full water column, Axis I and II summarized 17.4 and 16.2%, respectively, of the variation in the species data.

Table 2. Eigenvalues and percentages of variation from correspondence analyses of species presence–absence data at three resolutions of vertical stratification; the number of samples in the fully collapsed data is not half that of the two strata vertical component because not every site had fish present in the second strata and therefore, when it was collapsed the sample number only reduced by the number of samples that had fish present in the second strata (i.e. 124 samples).

Axes	1	2	3	4	Total inertia
Four strata vertical component ($n = 676$)					
Eigenvalues	0.564	0.539	0.304	0.29	4.006
% Variation of species data	14.1	13.4	7.6	7.3	
Cumulative % of species data	14.1	27.5	35.1	42.4	
Two strata vertical component ($n = 426$)					
Eigenvalues	0.5	0.48	0.26	0.24	3.274
% Variation of species data	15.3	14.7	7.9	7.3	
Cumulative % of species data	15.3	30	37.9	45.2	
Collapsed data-full water column ($n = 302$)					
Eigenvalues	0.459	0.43	0.215	0.19	2.645
% Variation of species data	17.4	16.2	8.1	7.2	
Cumulative % of species data	17.4	33.6	41.7	48.9	

represented by the species–environment relations of the first two axes portrayed for the finest vertical resolution of 25 cm strata. The amount of variation decreased slightly at the level of 50 cm strata to 73.2%. When data were collapsed and the water column was treated as a single vertical unit, the cumulative percentage variation of species–environment relations for the first two axes dropped to 63.6%. Similar to the CA results, the total inertia was smaller at the coarsest level of vertical resolution: 2.645 versus 4.006 for the finest resolution.

The Monte Carlo test of significance of the first canonical axis and the test of significance of all canonical axes illustrated that the relationship between the species and the environmental variables was highly significant ($p = 0.005$) for the three vertical resolutions used to study the community structure.

The community structure at each resolution of vertical stratification can be depicted by CCA ordination diagrams. The finest resolution of stratification was 25 cm stratum, with four or five strata per site, depending on site depth. The first axis of the ordination diagram at this resolution represented a seasonal gradient (Figure 3a). The depth, water temperature, and date variables were closely aligned with the first axis and strongly correlated with each other, as indicated by the small angles between the vectors.

The second axis summarized a gradient in the vertical habitat across sites. Vegetation was correlated with fine substrate, increasing shore distance and decreasing stratum level, suggesting that vegetation was found more in the lower part of the water column, growing in fine substrate, and at sites that were found on the gentler sloping shores of the lake

Table 3. Eigenvalues and percentages of variance from canonical correspondence analyses of species presence–absence and environmental data at three resolutions of vertical stratification; Monte Carlo significant probabilities are shown in italics.

Axes	1 (p)	2	3	4	Total inertia
Four strata vertical component ($n = 676$)					
Eigenvalues	0.313 (*0.005*)	0.072	0.04	0.032	4.006
Cumulative percentage variance of species–environment relation	59.9	73.8	81.4	87.4	
Two strata vertical component ($n = 426$)					
Eigenvalues	0.29 (*0.005*)	0.072	0.033	0.025	3.274
Cumulative percentage variance of species–environment relation	58.7	73.2	80	85.1	
Collapsed data-full water column ($n = 302$)					
Eigenvalues	0.268 (*0.005*)	0.075	0.046	0.038	2.645
Cumulative percentage variance of species–environment relation	49.8	63.6	72.1	79.1	

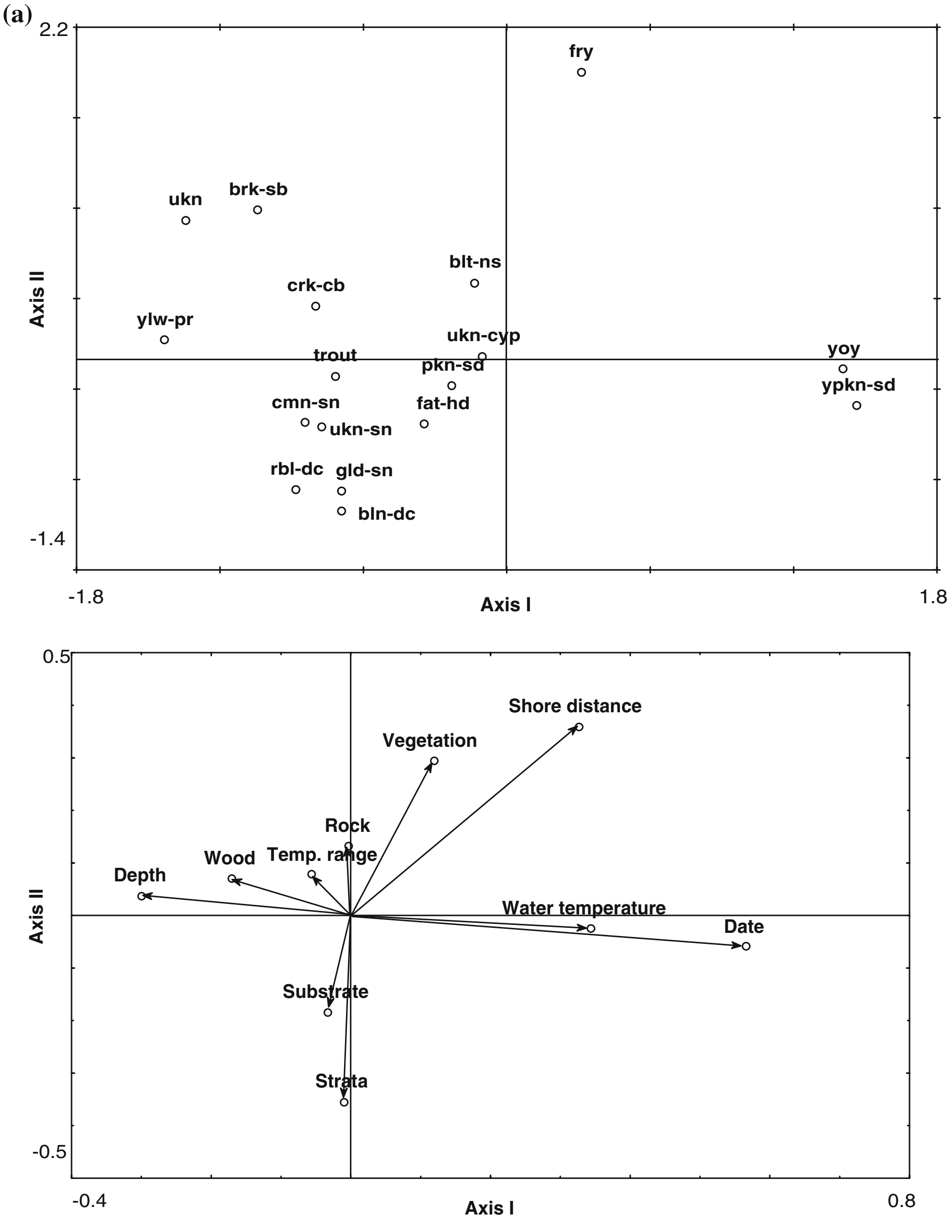

Figure 3. Canonical correspondence analysis axis one and two, showing the association of fish species and habitat characteristics based on presence–absence and environmental data defined by (a) 25 cm vertical stratification, Axis I and II summarized 8.1 and 1.9%, respectively, of the variation in the species data, (b) 50 cm vertical stratification, Axis I and II summarized 9.3 and 2.3%, respectively, of the variation in the species data, and (c) the single water-column stratum, Axis I and II summarized 10.7 and 3.0%, respectively, of the variation in the species data.

(therefore were further from shore at ~1 m depth). "Fry" and bluntnose minnows, *Pimephales notatus*, were most strongly associated with the vertical gradient. Wood was not correlated with the vertical component, but the amount of wood increased in deeper sites, even though the variation in depth among sites was relatively limited. The environmental variables most strongly associated with community structure were shore distance, date, vegetation, water temperature, and vertical stratum.

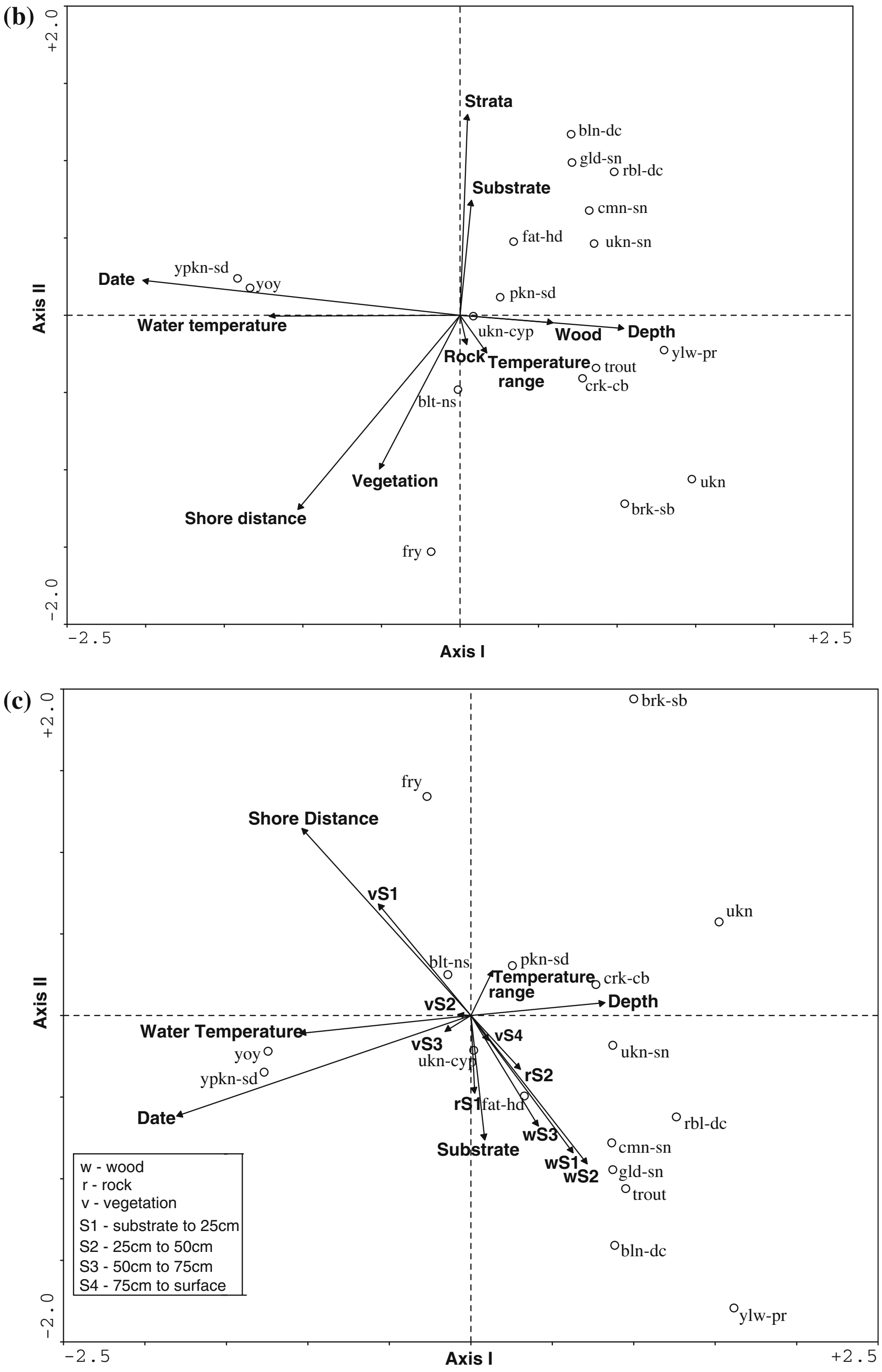

Figure 3. Continued

The ordination diagram for the data defined more coarsely at two 50 cm, vertical strata (Figure 3b) illustrated similar patterns of community structure as those found at the finer resolution. A seasonal gradient was observed along the first axis, and a vertical gradient was observed along the second axis. The following differences in environmental associations were observed: wood and depth were more strongly (positively) correlated with each other and negatively correlated with water temperature and date; however, water temperature showed a weaker association with date than at the finer resolution. Temperature range and rock cover were more closely correlated, but both had shorter vectors relative to the vectors of the other environmental variables, suggesting they were not strongly associated with the community structure extracted from the data included in this study. Vegetation and shore distance were more strongly positively correlated, as were stratum and substrate.

Species associations were very similar as those observed at the finer resolution with the exceptions that brook trout, *Salvelinus fontinalis*, and creek chub, *Semotilus atromaculatus*, were more closely associated with each other and with yellow perch, *Perca flavescens*; all three species were associated with deeper, woodier sites, although the yellow perch were most closely aligned with the depth vector. The shiner group showed a weaker correlation with the depth vector than at the finer vertical resolution. Fathead minnows, *Pimephales promelas*, showed stronger association with the shore distance and vegetation vectors in this analysis, but were closer to the origin than either the shiner group or dace-shiner group; therefore, the fathead minnow association with non-vegetated sites close to shore was weaker than that observed for the two groups. Both the shiner and dace-shiner groups, as well as the fathead minnows, showed a stronger association with the vertical gradient in this analysis than in the previous, finer vertical resolution analysis. The dace-shiner group exhibited a correlation with the upper strata, whereas the shiner group and fathead minnows showed an association with strata lower in the water column.

The CCA results of community relationships at the full water column data set depicted different patterns than those detected when data were defined by finer vertical components (Figure 3c). The primary difference when the fish data from different strata were combined was the increased influence of woody cover on community structure. Shore distance, date, and woody structure appeared to have the strongest association with the community structure when the data included the habitat structural components measured at each section of the water column.

The seasonal characteristics were again correlated: water temperature and date were positively related to each other, but negatively with depth. A complexity gradient was observed in the grouping of most of the remaining environmental variables, although the gradient did not align with either axis. Shore distance was positively correlated with vegetation in the first stratum; the first stratum vegetation vector (vS1) was the longest of all vegetation vectors, which suggested that vegetation closest to the substrate had the most influence on the community structure of the four vertical vegetation components observed.

The species most strongly associated with the vertical woody structure were the larger bodied species, including common shiners, *Luxilus cornutus*, and golden shiners, *Notemigonus crysoleucas*, brook trout and yellow perch. The smaller-bodied blacknose dace, *Rhinichthys atratulus*, was also associated with the vertical woody structure. Wood and depth were more weakly associated at this coarsest vertical resolution; this weaker association illustrated the yellow perch's correlation to wood and the creek chub's correlation to depth. These correlations were not discerned at the finer vertical resolutions. Northern redbelly dace, *Phoxinus eos*, did not exhibit as strong a response to shore distance or vegetation at this resolution but were still weakly associated with the vertical gradient.

When fish data were organized by the single vertical component of the full water column, both the rock and wood vectors showed different trends than when the vertical component was defined on a finer scale. At the coarsest vertical resolution, rocky structure was positively correlated with coarseness of substrate and negatively correlated with temperature range; previously, it was associated with finer substrate and increased temperature range. The length of the rock vector, however, indicates that rocky cover did not have a strong association with the community structure extracted in this analysis, whereas woody structure did. Woody structure was strongly positively related to increased rock cover and coarse substrate, but was negatively related to shore distance and vegetation. When data were defined by finer vertical components in the previous two analyses, woody structure was only very weakly related to either rock or vegetation cover.

Discussion

This study illustrated that quantifying the vertical component of habitat structure and habitat use by fish as multiple, discrete units yielded a comprehensive picture of fish community structure and outlined differences in fish distribution and their relationship to habitat differences. Recording the fish and habitat structural data by discrete vertical units is a new visual census approach for quantifying habitat characteristics and fish associations with habitat. The importance of vertical habitat complexity on species diversity and habitat use has been established in several terrestrial systems, as well as in marine and stream systems. When data were recorded using multiple, discrete vertical units in our study, the second strongest influence on the fish community structure was a vertical complexity gradient, following the more influential seasonal gradient. Our study confirms that vertical habitat structure and habitat use by fish could be quantified in lake littoral zones and that vertical habitat structure plays an important role in regulating the fish community.

The organization of environmental and species data at three resolutions illustrated multiple ways of considering the role of the habitat's vertical component. At the two finest resolutions, the data were defined by multiple vertical components, and a separate environmental variable represented the vertical stratification. This direct approach allowed the overall role of vertical habitat, in terms of structure and fish use, to be evaluated. There was very little difference in the community structure when data were defined by either the finest resolution of 25 cm strata, or by the coarser resolution of 50 cm strata. Therefore, either approach could be taken when sampling a littoral zone; the appropriateness of the technique used would likely be a result of the type of question being asked and the system in which it was being studied. In a typical littoral zone, visual census of the habitat and fish community would be simpler using the coarser resolution of 50 cm strata. This reduces the number of boundaries between sampling units, likely reducing the inaccuracy associated with habitat and fish sampled close to those boundaries. However, in highly vertically complex habitats, the finer resolution may be required to distinguish niches of associated fish species.

When habitat was sampled in the field, three structural habitat components (woody debris, rock, and vegetation) were recorded in each stratum. By defining the fish data vertically, the influence of these habitat components at each section of the water column was not directly illustrated. However, when defining the data by the single vertical unit of the full water column, the structural components of wood, rock, and vegetation can be included as individual variables, allowing direct interpretation of their role throughout various parts of the water column. The influence of habitat heterogeneity on fish communities has been a focus within aquatic ecology. Several studies have evaluated habitat heterogeneity or complexity primarily through vegetation density or diversity and substrate type; however, there has been a lack of attention on other elements of the habitat that enhance heterogeneity. When considering the integrated vertical patterns, we were able to address the lack of focus on other habitat structural elements in the water column and the lack of multivariate analysis of fish associations with both environmental variables and vertical habitat components. Defining the fish data by the full water column allowed the evaluation of the individual influence of woody structure, rock, and vegetation on fish distribution in each of the four strata of the water column.

Analysis of fish–habitat interactions at the coarsest vertical resolution revealed that woody structure both on the substrate and throughout the water column, was strongly associated with several species specifically, as well as the overall community structure. This result confirmed that woody debris is a vital component of littoral-zone habitat structure. No major piscivorous predators exist in Poorhouse Lake, but woody structure may have been used by fishes to escape predation from brook trout, large creek chub, common mergansers, *Mergus merganser*, loons, *Gavia immer*, or belted kingfishers, *Ceryle alcyon*, in the littoral zone. While we show the importance of woody habitat, its importance is likely to be much greater in systems containing piscivorous fishes (MacRae & Jackson 2001).

In all three vertical resolutions of data, "fry" was found to be the only species category associated with the heavily vegetated sites in Poorhouse Lake. Conversely, the majority of adult species categories were either associated with sites that lacked vegetation or were not influenced by the presence or absence of macrophytes. This separation of fry and adult individuals may reflect the recognized behaviour of age 0 fish using submerged vegetation for shelter from predation (Werner et al. 1983). Patchy vegetation may offer the best habitat for age 0 fish to gain protection from predation, but it also gives them more immediate access to the open spaces that harbour zooplankton, one of their preferred food resources (Weaver et al. 1997).

The new vertical visual census method described in this study allows data to be evaluated and interpreted at three different vertical resolutions (i.e. 25 and 50 cm strata, and the full water column); assessing the data in this matter allowed a more detailed evaluation of the role of vertical habitat structure in fish communities. The results of this study suggest that no one treatment of the data explains substantially more variation than another. While the choice of which vertical resolution of data to use may depend upon the question being asked, this type of post-collection data flexibility is a strong advantage of the vertical visual sampling technique.

Our study demonstrated that fish are closely associated with habitat structure in the littoral zone even in the absence of major piscivorous predators. As has been established in several terrestrial systems, this study confirmed the integral role of vertical habitat complexity in structuring community interactions. This is the first known study to quantify multiple vertical habitat structures and habitat use by fish in the water column of a freshwater lake. The lack of focus on the three-dimensional environment of lake littoral zones in aquatic community ecology has left a gap of knowledge concerning freshwater fish–habitat interactions. Based on the results of this study, it can be concluded that the new vertical visual census technique presented here can be employed to successfully address that gap. Both researchers and managers can benefit through application of this technique in additional systems, including those containing major piscivorous predators. Researchers can use this method to enhance their understanding of fish–habitat spatial relationships. Managers can gain a more accurate awareness of the implications that development and subsequent habitat structural changes can have on the fish community. In terms of both academia and application, this vertical visual census method of quantifying habitat structure and fish associations provides a valuable tool that can improve our current state of knowledge concerning fish–habitat interactions.

Acknowledgements

Thanks to the Natural Sciences and Engineering Research Council of Canada (NSERC) for a Scholarship to JSM and an NSERC Grant to DAJ. We thank KM Somers for his support during data collection and Z Zommers for her excellent assistance in the field collections.

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