Physical Constraints to Aquatic Plant Growth in New Zealand Lakes

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ABSTRACT

The nature of aquatic plant communities often defines benthic habitat within oligotrophic and mesotrophic lakes and lake management increasingly recognizes the importance of maintaining plant diversity in order to sustain biological diversity and capacity within lakes. We have developed simple statistical relationships between key physical and vegetation variables that define the habitat requirements, or "habitat-templates", of key vegetation types to facilitate management of plant communities in New Zealand lakes. Statistical relationships were derived from two datasets. The first was a multi-lake dataset to determine the effects of water level fluctuation and water clarity. The second dataset was from a comprehensive shoreline survey of Lake Wanaka, which allowed us to examine within-lake variables such as beach slope and wave action. Sufficient statistical relationships were established to develop a habitat template for each of the major species or assemblages. The relationships suggested that the extent and diversity of shallow-growing species was related to a combination of the extent of water level fluctuation and wave exposure. Upper limits of many deeper-growing species could also be related to wave action exposure. Water clarity set the lower limits for most vegetation types. To test the applicability of the templates we compared predictions with recent surveys of two lakes, Lake Wakatipu and Lake Manapouri, which were not included in the model formula-tion. We found that vegetation variables predicted from water level fluctuation and water clarity provided useful estimates of species diversity and lower depth limits on lake-wide scales. Predictions of finer scale distributions, based on estimates of wave action made using a 200-m resolution shoreline model, with no site-specific wind, slope or aspect data were useful with respect to the presence or absence of vegetation, but poor predictors of the depth ranges of plants. Overall, our analysis showed that the habitat template approach is a valuable tool for estimating the likely distribution, range and composition of vegetation within a lake, but that the spatial resolution within a lake is poor when predictions are based on coarse scale variables.

Key words: wave exposure, water clarity, water level fluctuation, aquatic plant communities, habitat-templates.

INTRODUCTION

There is recognition in New Zealand that aquatic plants are not only significant components of lake ecosystems but also sensitive integrators of environmental change (Schwarz and Hawes 1997, James et al. 1998, Weatherhead and James 2001). Environmental managers also realize that concepts of ecological integrity or health (*sensu* Schofield and Davies 1996) need to be incorporated into guidelines for the management of aquatic systems (ANZECC 2002). In New Zealand this has led to incorporation of criteria for maintenance of aquatic plant communities into lake management objectives and their use in monitoring the extent to which management goals are achieved. For example, in Lake Coleridge, a large, oligotrophic South Island lake modified for hydropower generation, research has shown that the depth
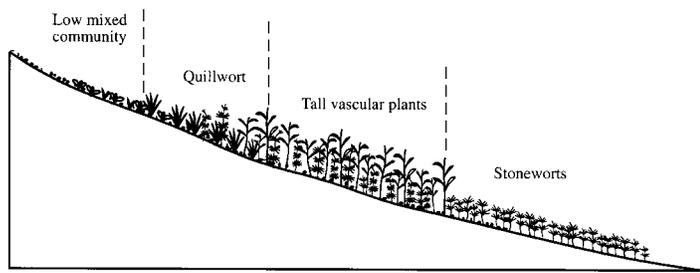
Figure 1. A stylized vegetation profile in a South Island New Zealand lake.

Figure 2. Relationship between water level range (mean monthly range) and the number of species of shallow water plants per lake.

range of the littoral zone is particularly sensitive to water clarity (Schwarz and Hawes 1997), which can be modified in this lake by control of turbid inflows. Most of the lake's invertebrate biomass and diversity is associated with littoral zone plants, (James et al. 1998, Weatherhead and James 2001) and this zone provides 95% of the food resources of an important recreational fishery (Graynoth, E., pers. comm.). Management criteria for water clarity in Lake Coleridge have therefore been set to maintain the bottom depth limits of the littoral zone at 25 m, and an aquatic plant/water clarity monitoring regime put in place to ensure that this goal is achieved.

Applying guidelines for the protection of submerged vegetation within aquatic systems presupposes an understanding of the physical, chemical and biotic factors that affect this community. One approach to gaining this understanding is to develop a series of "habitat templates" - mathematical descriptions that define the requirements of the different components of the submerged flora. There is a strong research base to support this approach, particularly with respect to physical factors. Water clarity is known to set lower limits to many communities (Vant et al. 1986, Middelboe and Markager 1997, Schwarz et al. 2000), littoral slope affects biomass (Margalef 1984, Duarte and Kalff 1986), wave action (Jupp and Spence 1977, Wilson and Keddy 1986, Coops et al. 1994) and water level fluctuation (Riis and Hawes 2002a) affect distribution, biomass and diversity.

In this paper we use new and published information on the physical habitat requirements of New Zealand sub-
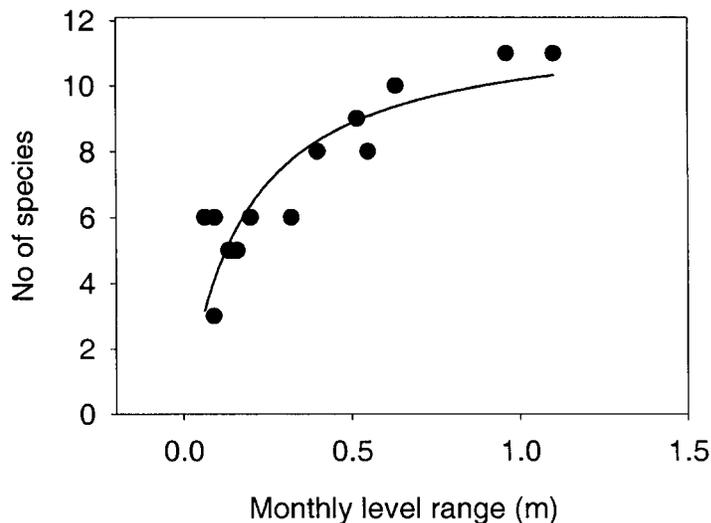
merged plant communities to develop physical habitat templates for different vegetation types. Templates were tested by comparing the predicted vegetation patterns in Lakes Manapouri and Wakatipu with recent vegetation surveys of these two lakes. The purpose of our analysis is to determine whether the physical environment that supports specific plant communities can be sufficiently well quantified to allow the setting of management criteria for their protection or rehabilitation. The aim is therefore to provide a management tool for assessing the optimal vegetation characteristics in a lake. Similar analyses have been attempted for specific problem species with some degree of success (Lehmann and Lachavanne 1998). While our analysis is specific to New Zealand lakes, we suggest that the principles developed may be more widely applicable.

METHODS

Vegetation types and physical variables

Submerged vegetation types in New Zealand lakes can be grouped into four categories: a shallow water community, characterized by short stature angiosperms and termed the low mixed community (LMC—Johnson and Brooke 1998); a quillwort (*Isoetes alpinus* Kirk) zone; tall vascular plants [originally native water milfoils (*Myriophyllum* spp.) and pondweeds (*Potamogeton* spp.) but now including introduced hydrocharitaceans]; and stoneworts (characeans; Wells et al. 1998). These communities occupy distinct but overlapping depth zones (Figure 1). Our starting assumptions are that physical factors control the boundaries of each community's niche, but recognize that these are modified by competitive interactions between species and vegetation types. We assume that of these physical factors, water level fluctuation (Keddy 1983, Riis and Hawes 2002a), wave exposure (Jupp and Spence 1977, Riis and Hawes 2002b), substrate type, slope (Duarte and Kalff 1986) and water clarity (Schwarz et

TABLE 1. SUMMARY OF THE ANALYTICAL PROCESS USED FOR EACH VEGETATION TYPE TO DETERMINE PHYSICAL HABITAT TEMPLATES IN SUBMERGED AQUATIC VEGETATION. WLF IS MEAN MONTHLY WATER LEVEL INTER-QUARTILE RANGE, SLOPE MEASURED AROUND MEDIAN WATER LEVEL ARE USED FOR ANALYZING SHALLOW WATER PLANT COMMUNITIES AND SLOPE MEASURED FROM 1 M DEPTH TO VASCULAR PLANT LOWER DEPTH LIMIT IS USED FOR ANALYZING DEEP WATER COMMUNITIES. N INDICATES NUMBER OF LAKES OR SITES INCLUDED IN THE ANALYSIS. FOR THE DATA SOURCE COLUMN, APDB INDICATES AQUATIC PLANT DATABASE (DE WINTON 2002), AND WAN A COMPREHENSIVE SURVEY OF LAKE WANAKA (RIIS AND HAWES 2002B).

Physical variable	N	Data source
WLF	11	APDB
$1/K_d$	19-22	APDB
Run-up	35	WAN
Sediment motion depth	35	WAN
Slope	35	WAN

Vegetation variable	Dominant Physical variable	Relationship	R^2	P	N
(A)					
Presence/Absence	Run-up	<0.3 m m^{-1}	N/A	N/A	41
Number of spp	WLF	12.3 x WLF/(WLF+0.182)	0.66	0.01	14
Z_u	Run-up	0.59 – 4.71 x RU	0.38	0.001	25
Z_c	Sediment motion depth	1.1 + 0.2 x SMD	0.47	0.001	26
(B)					
Number of spp	Clarity	$(10.44/K_d)/(2.33+1/K_d)$	0.43	0.001	26
Z_u	No relationship found				
Z_c	Clarity	$4.8/K_d$ - 2.6	0.79	0.001	26

al. 2000) are key variables. These physical variables are known to affect plant distributions and useful in management decisions mediated through mapping and planning packages.

Developing habitat templates

The physical factors listed above have different scales of variability. Water level fluctuation and clarity vary more between than within lakes, whereas substrate type, wave exposure and shoreline slope vary as much or more within lakes. The time scales of variation are also different – water level fluctuations may occur over long or short time scales, affecting plants in different ways, and water clarity may also show temporal variation.

The data we have used for the analysis come from two sources. Lake-specific variables (water clarity, water level fluctuation) are from compilations of data from a range of New Zealand lakes in the New Zealand Aquatic Plants Database (de Winton 2002), some of which have been previously published (Schwarz et al. 2001). Water clarity was determined as
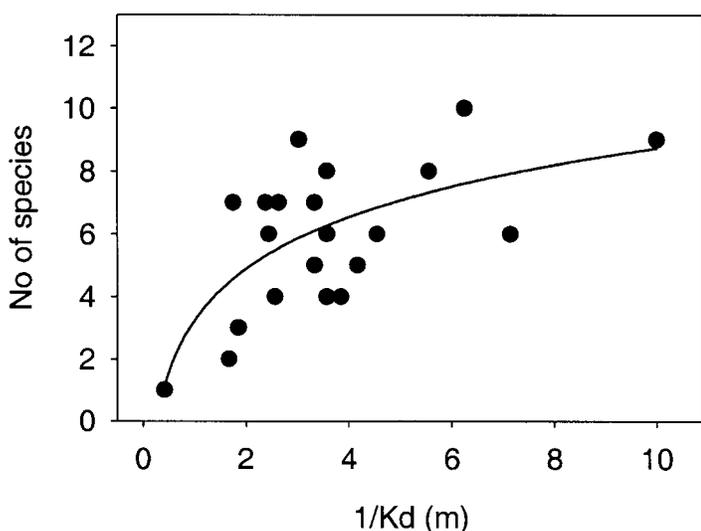
the reciprocal of vertical attenuation coefficient for down welling irradiance $(1/K_d)$, calculated from data obtained by vertical profiling with a LiCor underwater quantum sensor.

Water level fluctuation was quantified using 10 years of water level records prior to lake sampling for vegetation variables. Range was expressed as the inter-quartile range of mean level, and was initially calculated on three time scales—daily mean, monthly mean and annual mean. Early in the analysis it became clear that we could identify two groups of lakes based on the temporal characteristics of water level fluctuation. Most of the lakes were in a group where most fluctuation occurred on a daily and monthly time scale, with little inter-annual variation, while in a small group the inter-annual variation exceeded monthly variation (Riis and Hawes 2002a). The latter group included both hydro lakes and natural lakes with water levels that vary from year to year; extensive bare zones around these lakes suggests that this regime is highly unfavorable for plants. We used only those lakes with short-term fluctuations in this study and in this group of lakes daily and monthly water level fluctuations were tightly correlated. We have therefore used only monthly interquartile range as our measure of water level fluctuation, hereafter termed WLF, in the analysis. We also eliminated Lake Hawea from the analysis; since in some years it has up to 8 m vertical draw down in winter.

For variables with an in-lake variation (slope, wave action) we have used site-specific studies of Lake Wanaka in the South Island of New Zealand (Riis and Hawes 2002b). Lake Wanaka is an oligotrophic lake with a full complement of the vegetation types found in New Zealand lakes, including exotic species (though these may not have spread to their full potential yet) and a complex shoreline giving a range of exposures. The synoptic survey was carried out in February 2001, when 41 sites around the lake were visited. The shoreline slope at each site was measured at two locations - at median water level, using a tape and surveyors level, and below the shelf break, where approximately 1 to 2 m below median level the lakebed steeply dropped away. The drop-off gradient was measured by SCUBA divers using calibrated depth gauges along a marked transect line. The wave exposure indices at each site were calculated using the NARFET model of Smith (1991) and were based on slope, sediment grain size and density, local wind records (for the year preceding the survey) and shoreline shape (Riis and Hawes 2002b). Two statistics were calculated - the maximum depth of sedi-

Figure 3. The relationship between water clarity and the number of species of stoneworts.
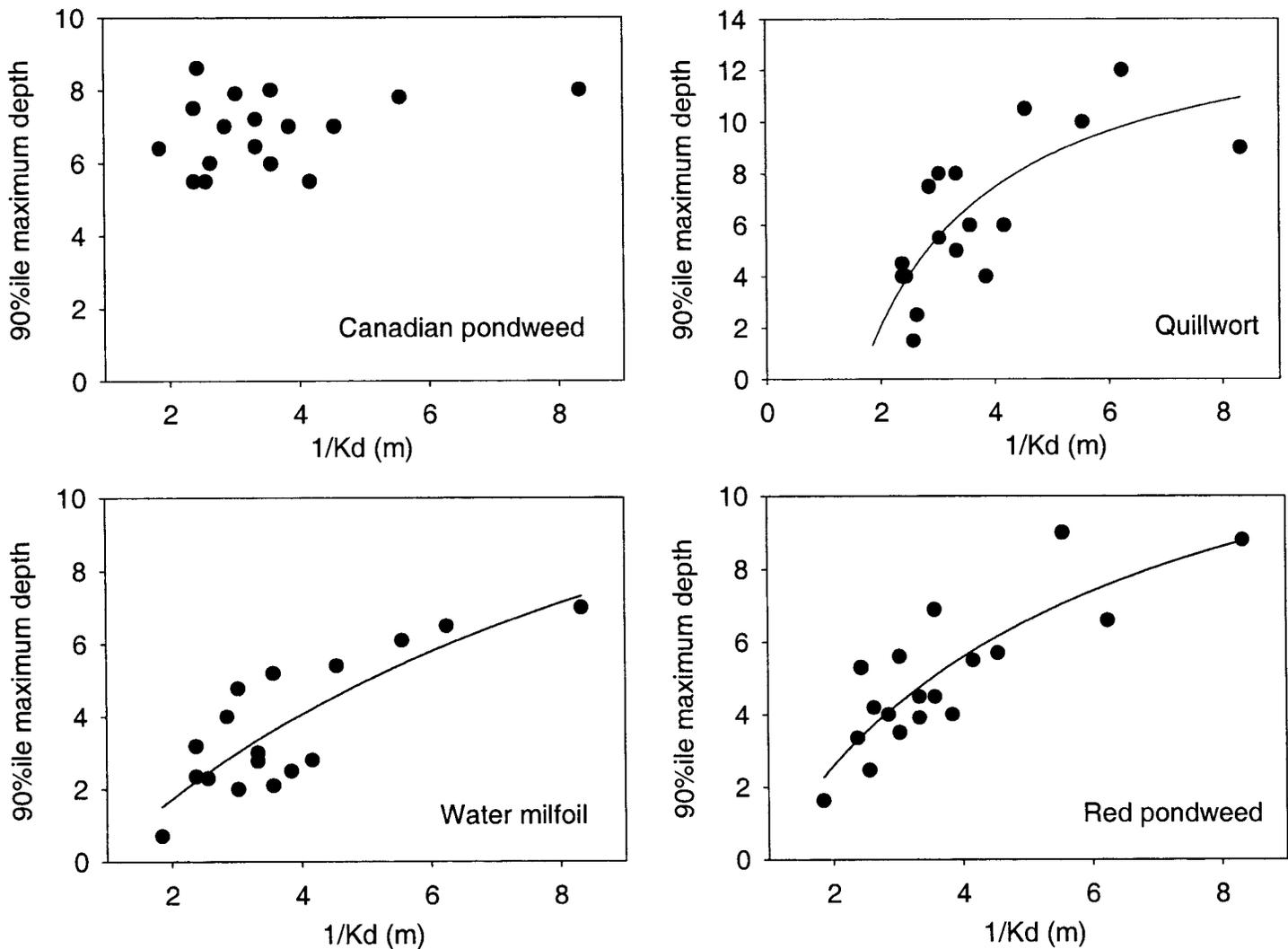
Figure 4. Significant relationships between bottom limit for most common vascular species and water clarity; the latter is expressed as the reciprocal of the attenuation coefficient of downwelling irradiance.

ment motion and the maximum run-up (vertical extension of waves at the shore).

Vegetation variables measured at each site were species present, upper (Z_u) and lower (Z_c) depth limits. These were recorded by SCUBA divers working from the bottom upwards and by wading for shallower plants. The number of species and depth ranges of vegetation used in the analysis of lake-specific variables were derived from 25 to 50 transects swum by SCUBA divers, evenly spaced around the lake. We used the 90 percentile values of Z_u and Z_c in our models. Use of these rather than maximum-maximum or median-maximum limits was designed to eliminate both occasional extreme depth records that may have been due to single plants outside the normal depth range and biasing from transects in regions where deep penetration is prevented by stochastic factors (such as fallen trees or subsidence of substrate).

Although substrate type is clearly a powerful factor, we do not address it in this analysis. All of the vegetation types we describe rely on a rooting medium for growth so an overriding variable determining habitat suitability is the presence of soft sediments, either as the dominant substrate or as part of a mosaic. To date insufficient information is available to determine the spatial requirements for establishment of communities in patchy habitats. Use of substrate type is further complicated by its close relationship with wave exposure. In our experience, depositional shorelines are usually restricted to those with low wave action, whereas erosional shorelines more often have coarse substrata but also higher wave exposure. We therefore expect that substrate type and stability may be at least partly captured by estimates of wave exposure.

Statistical approach

The approach used has been to develop three types of univariate model of individual physical factors (or derivatives of these factors) against vegetation variables. The three types are 1) threshold models, which accept the possibility that a critical value for a variable may exist beyond which a plant community is unlikely to occur, 2) simple linear mod-
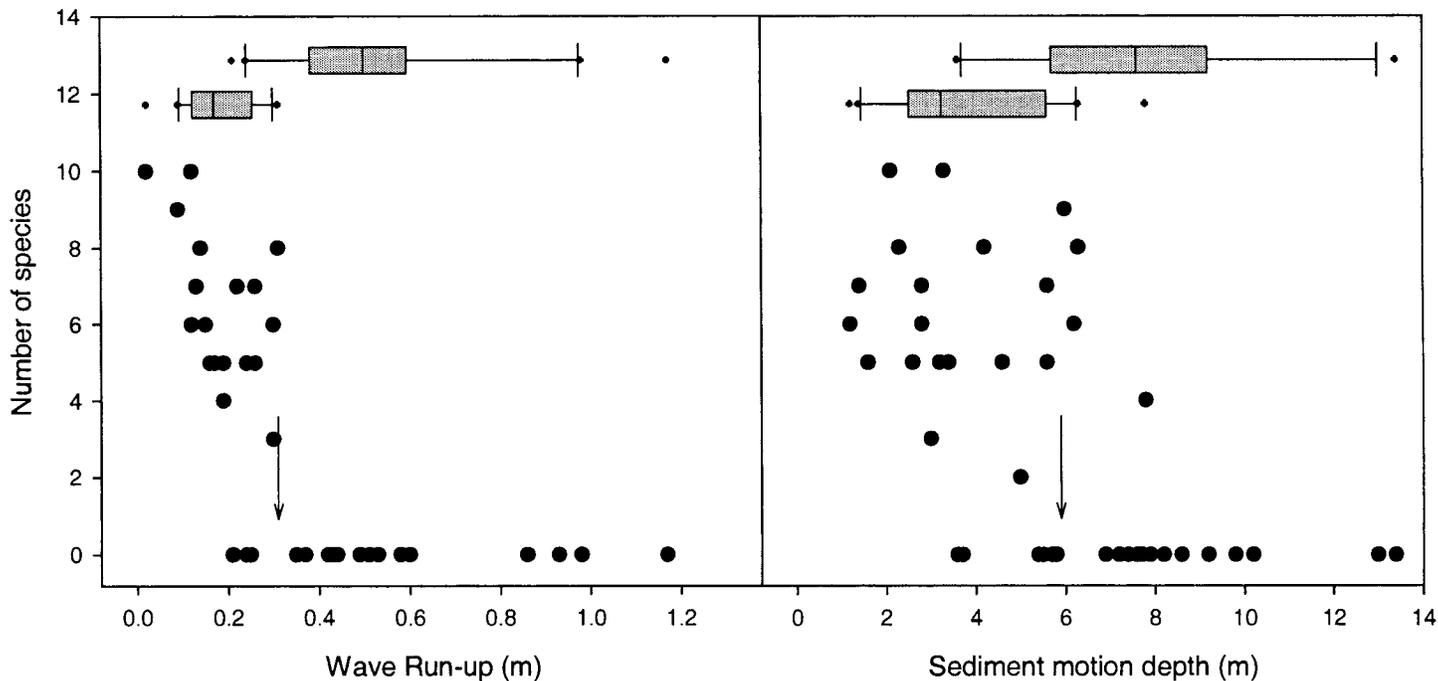
Figure 5. The relationship between wave exposure variables of wave run-up and sediment motion depth, and LMC species number. The horizontal box-whisker plots show the range, inter-quartile and median values of each exposure variable at sites with and without the LMC. Arrows designate "threshold values" for the point at which LMC becomes probable and improbable.

els, which link quantitative changes in physical and vegetation variables, and 3) hyperbolic models, where an upper value of a plant variable exists. While multivariate approaches can often explain a higher degree of variation within a given dataset (Lehmann 1998, Lehmann and Lachavanne 1998), they have the disadvantage of weaker applicability outside that dataset. We have also avoided non-parametric techniques; while they are powerful methods for identifying relationships, they are less useful as predictive tools. Table 1 summarizes the physical and vegetation variables used in each of the vegetation types and the analytical approach taken. With the exception of threshold models, models were fitted using the curve fitting function of Sigmaplot Version 7 (SPSS Science, Chicago Il.). Fitting of threshold models was primarily by eye, and was used when there was a clear difference between sites supporting a vegetation type and those not. This difference was always checked as significant ($p < 0.05$) using a t-test of the independent variable. Where a linear or a hyperbolic relationship could be fitted, the model that explained the greatest amount of variation, indicated by the highest value of r^2, was elected as the "best" descriptor.
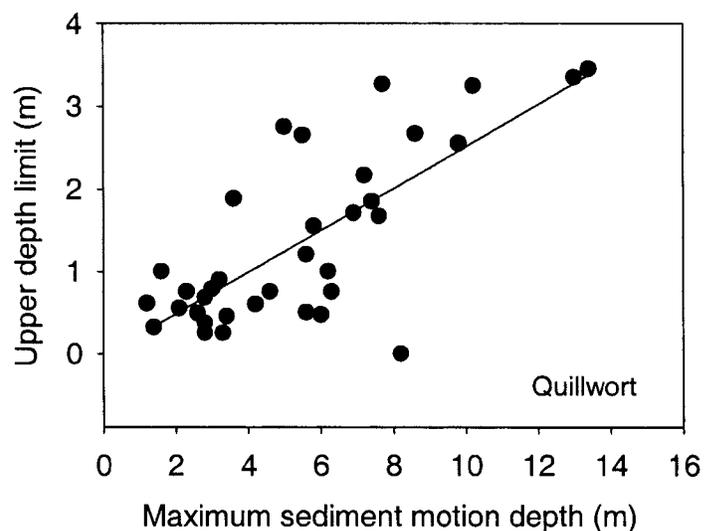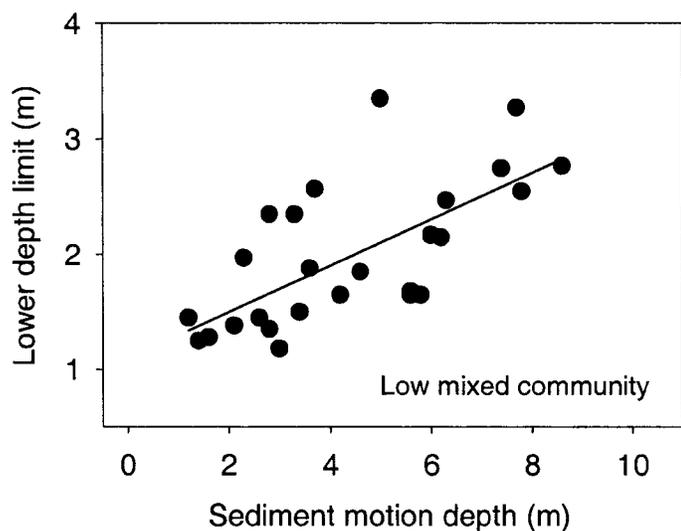

Figure 6. The relationships between (a) lower limit of LMC and (b) upper limit of quillwort vegetation and sediment motion depth.

TABLE 3. SUMMARY OF THE PHYSICAL HABITAT TEMPLATES DERIVED FOR THREE SPECIES OF AQUATIC PLANTS. NO RELATIONSHIPS COULD BE ESTABLISHED FOR CANADIAN PONDWEED. ONLY THE STRONGEST RELATIONSHIP BETWEEN A PHYSICAL VARIABLE AND EACH VEGETATION VARIABLE IS GIVEN. Z_u AND Z_c ARE UPPER AND LOWER DEPTH LIMITS.

Species	Vegetation variable	Dominant Physical variable	Relationship	R^2	P	N
Quillwort	Z_u	Sediment motion depth	$0.25 + 0.18 \times SMD$	0.54	0.001	35
	Z_c	Clarity	$[(50/K_d)/(0.67+1/K_d)]-36$	0.58	0.002	16
Red pondweed	Z_u	Sediment motion depth	$1.77 + 0.28 \times SMD$	0.29	0.001	33
	Z_c	Clarity	$[(18.1/K_d)/(4.1+1/K_d)]-3.4$	0.70	0.001	17
NZ Water milfoil	Z_u	Sediment motion depth	$0.46 + 0.29 \times SMD$	0.53	0.001	34
	Z_c	Clarity	$[(19.1/K_d)/(9.46+1/K_d)]-1.1$	0.66	0.001	16

RESULTS AND DISCUSSION

Between-lake variables

Water level fluctuation

We found an asymptotic relationship between WLF and species number for the LMC in the 16 lakes with short-term water level fluctuations (Figure 2). In a more comprehensive analysis elsewhere we reported a similar relationship for the LMC (Riis and Hawes, 2002a). The relationship showed an increase in species richness with increasing WLF up to 1 m, but indicated that more than 12 species were unlikely to be found (Table 2). Outliers to the relationship in Figure 2, excluded from curve fitting, include one hydro lake with extreme monthly water level range, and two that have recently undergone devegetation due to abnormally high turbidity. Species number was abnormally low in all outliers. Water level fluctuations could not be related to Z_u or Z_c for the LMC, quillwort, tall vascular or stonewort vegetation, nor species number for the last vegetation type.

Water Clarity

It has previously been found that depth distributions of stoneworts in New Zealand lakes are linked to water clarity (Schwarz et al. 1996, 2000, 2001). We found the same relationship in the current analysis (we were using a subset of the same data) and we also found that water clarity was correlated with the lower depth limits of tall vascular plants and quillwort reconfirming previous findings in New Zealand lakes (Vant et al. 1986) and overseas studies (Middelboe and Markager 1997; Table 3). We found no reason to alter the linear relationship between water clarity and maximum depth of stoneworts in South Island lakes developed by Schwarz et al. (1996). This relationship finds the bottom limit of this vegetation type to be at approximately 2% surface irradiance. We also found that the species richness of the stonewort community increased with increasing water clarity, towards an asymptote of approximately 9 species (Figure 3).

We found that much better prediction of lower limits was possible if tall vascular species were examined separately, rather than as a group. The three most frequently encountered native plants, red pondweed (*Potamogeton cheesemanii* A. Bennett), New Zealand water milfoil (*Myriophyllum triphyllum* Orch.) and quillwort, showed good relationships to water clarity, though bottom limits of New Zealand water milfoil were consistently shallower than those of red pondweed and quillwort (Figure 4). There was no good relationship for the widespread exotic species Canadian pondweed (*Elodea canadensis* Michaux; Figure 4), which was able to reach 10 m when water clarity permitted only 3.5% of light to reach this depth.

The observation of a simple linear relationship between water clarity and stoneworts, but a hyperbolic relationship to vascular plants has been noted before (Middelboe and Markager 1997); however a satisfactory explanation is lacking. The implication is that the light requirement at Z_c increases with increasing water clarity for vascular plants, but not for stoneworts in the same lakes. The common suggestion that hydrostatic pressure prevents vascular plants from growing at more extreme depths does not appear to be the case (Dale 1981, 1984), though the possibility that pressure places an increas-

TABLE 4. PREDICTED AND OBSERVED CHARACTERISTICS FOR LAKES MANAPOURI AND WAKATIPU, BASED ON THE HABITAT-TEMPLATES DESCRIBED IN TABLE 2.

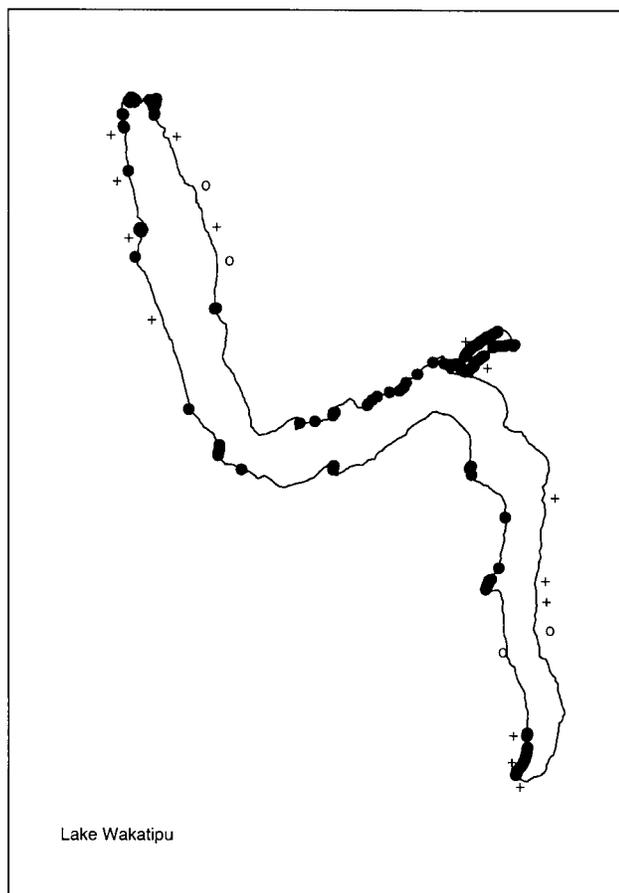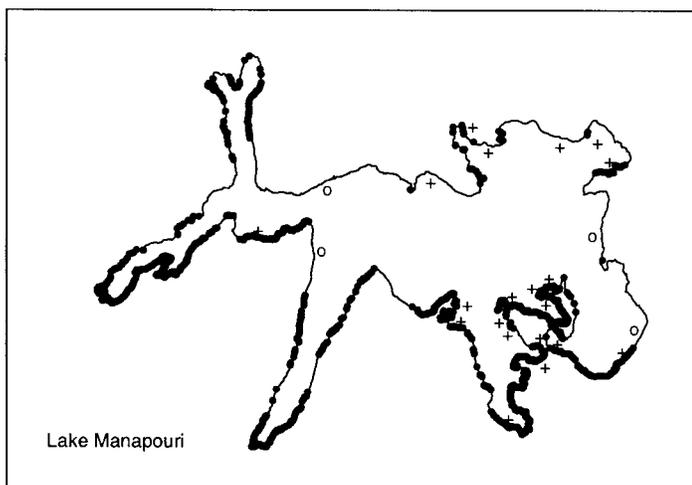| Vegetation type	Vegetation variable	Lake Wakatipu		Lake Manapouri	
		Prediction	Observed	Prediction	Observed
LMC	Number of spp	8	8	10	11
Quillwort	Z_c	10.3	8	4.9	3.6
Red pondweed	Z_c	8.8	9.8	4.3	3.6
Canadian pondweed	Z_c	8	8.5	7	6.6
NZ Water milfoil	Z_c	7.9	4.8	v3.6	3.6
Stoneworts	Number of spp	8	8	6	6
	Z_c	37	34	15	13

Figure 7. Predictions and observations of the locations where LMC will occur in Lake Manapouri (above) and Lake Wakatipu (below). Black dots indicate predicted occurrence, small crosses sites where LMC was found, and small circles sites where it was not.

ing energetic demand with depth, thus increasing the light requirement, has been discussed by Middelboe and Markager (1997). Canadian pondweed was the only deep growing plant that did not show a relationship between lower depth limit and light, though even this species appeared to have an absolute lower limit of 8 to 9 m (Figure 4). We suspect that the ability of Canadian pondweed to produce a tall, dense

canopy allowed it to circumvent light limitation to some extent by vertical growth. The linear relationship between Z_c and $1/K_d$ among stoneworts can be directly related to the minimum light requirement for net photosynthesis (Schwarz et al. 1996). The increase in species richness in stoneworts in clear lakes, as well as an extension of lower boundary, is a new finding for this community. It is consistent with an increase in microhabitat variation with increasing habitat area, allowing a greater number of taxa to co-exist.

No relationship between water clarity and any attributes of the LMC, or the upper limits of the other communities was found.

Within-lake variables

Wave exposure

Wave action was the primary variable driving the presence, species richness and vertical range of the LMC on shorelines (Riis and Hawes 2002b). Both examined attributes of wave exposure—the maximum depth of sediment motion and the run-up - showed correlations with vegetation variables. Within Lake Wanaka we found a threshold effect of wave action on species number in the shallow water community (Figure 5). Our data suggested that the LMC was likely to be absent where sediment motion depth exceeded 7 m, or when wave run up exceeded 0.3 m. The upper limit of the LMC also tended to be lower on the shore as wave run-up increased (Table 2). We found that increasing wave action deepened the boundary between the shallow community and the quillwort/tall vascular assemblage. This was evidenced by the upper limit of quillwort and tall vascular plants, and by the lower depth limit of the shallow community being deeper with increasing sediment motion depth (Figure 6, Tables 2 and 3). This suggests that removal of competition from quillwort allows the LMC to grow deeper under increasing wave action.

Slope

We were surprised to find that littoral slope was a poor predictor of all vegetation variables. Slope was strongly correlated with run-up and sediment motion depth, but explained no more of the variation than these wave variables on their own. We found no benefit to the predictive powers of the habitat templates for any vegetation variable by including slope.

Testing the habitat templates

The aim of our analysis was to provide a basis for the development of a management tool to assess the optimal vegetation characteristics in a given lake. Predictions must be useful in site-specific applications if they are to be used for management purposes. In this context site may refer to a given lake or a given location within a lake. In our approach, lake-specific variables (WLF and water clarity) are used to predict some vegetation attributes, such as species richness of LMC and stoneworts and maximum depths of deep communities; the site specific exposure variables (run-up and sediment motion depth) recognize that other attributes vary over shorter spatial scales. We tested the applicability of the models by comparing predictions for two contrasting lakes, Lakes Manapouri and Wakatipu, with the results of recent surveys not used in our model development. Both lakes are
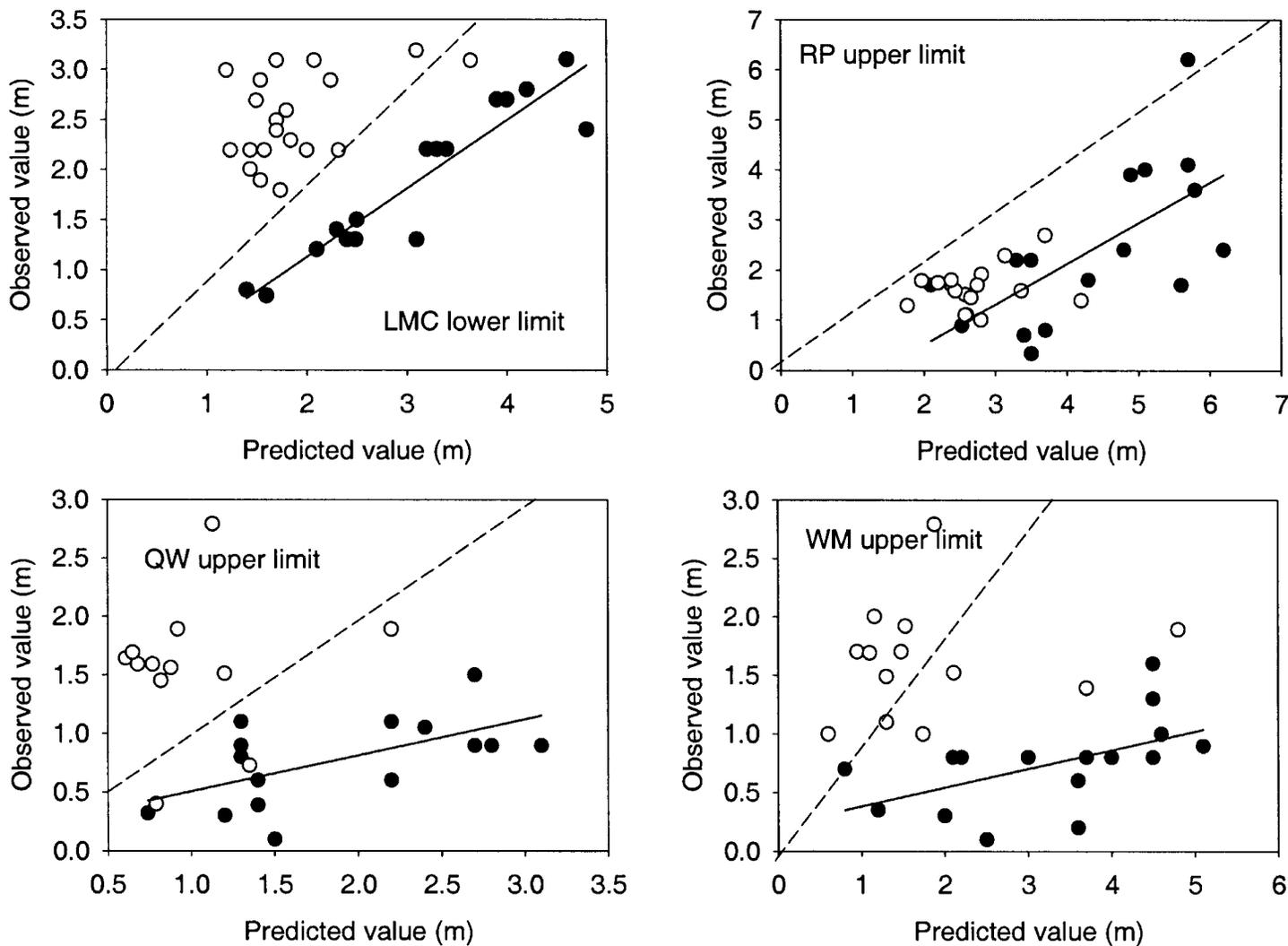
Figure 8. Observed and predicted values for the lower limits of the LMC, and the upper limits of red pondweed (RP), quillwort (QW) and NZ water milfoil (WM). Data shown for Lakes Manapouri (○) and Wakatipu (●). Broken lines show the 1:1 line, solid lines statistically significant regressions (p < 0.05) for the Wakatipu data.

oligotrophic, but Lake Manapouri is humic-stained (K_d = 0.33 m^{-1}) and Lake Wakatipu has very clear-water (K_d = 0.12 m^{-1}) (Rae et al. 2001). The WLF values for Manapouri are 1.1 m, and for Wakatipu 0.4 m. These values have been used to predict the lake-specific variables (Table 4).

Within lakes, site-specific predictions required estimates of wave exposure, derived from the NARFET model. NARFET requires a number of input variables to obtain maximum depth of sediment motion and run-up height. For depth of sediment motion a wind field, particle size and particle density is required, and for run-up the shoreline slope is also needed. However, it is unrealistic to expect particle size and density and shoreline slope to be known with any degree of spatial resolution for most lakes. We therefore used a standard sediment size and density (0.3 mm, 2.65 g cm^{-3}) for Lakes Manapouri and Wakatipu. The same standard size was used for the Lake Wanaka calculations. For the slope we used the median slope for the Lake Wanaka data set (0.1 m m^{-1}).

The variables in the calculations of wave action then reduce to wind field and shoreline shape. The latter is easy to derive at coarse scales from maps, but wind field is difficult to assess in mountainous regions due to valley funneling effects. Once again, to be practically useful, and acknowledging that site-specific wind data will not be available for most lakes, we approximated wind field in our test lakes. The prevailing strong winds in the South Island of New Zealand are from the SW-NW quadrant, and maximum sustained wind velocities of 30 m s^{-1} are typical (NIWA unpublished database). To assess wave action we assumed that winds would have been funneled from this quadrant according to valley orientation. We therefore estimated run-up and sediment motion depths using 30 m s^{-1} winds oriented according to valley axis, within the 180 to 360° semi-circle. Where more than one wind can be tested, maximum value for each wave action variable at a given site was used. Estimates of site-specific wave exposure therefore reduce to lake morphometry.

The predicted vegetation values derived from inter-lake variables for both Lakes Wakatipu and Manapouri showed good agreement with observed values (Table 4). Predictions of species richness in both the LMC and the stonewort communities were accurate, with only the Manapouri LMC showing one more species found than predicted based on water level fluctuation.

Lower limits predicted for individual species from water clarity were also in good agreement with the observed values (Table 4). The exception was New Zealand water milfoil that was found shallower in Lake Wakatipu than the high water clarity predicted. The reason for this is not clear; it is unlikely to be a hydrostatic effect, since milfoil can reach depths of 7 m (Figure 3). We can thus conclude that, within the bounds of the current model testing, the lake-specific variables provide a good estimate of the lake vegetation that can be expected.

Predictions based on sites within lakes were less successful than the lakewide predictions. The sites in the two lakes where the run-up model predicts that the LMC will occur are indicated in Figure 7. This figure also shows the findings of the actual survey and indicates that at approximately 80% of the sites visited the predictions of presence or absence were accurate. However, predictions of upper and lower limits of wave-sensitive communities failed to fit observed values (Figure 8). For Lake Wakatipu, statistically significant relationships ($p < 0.05$) between observed and predicted values were obtained, but these were not along the 1:1 line. Predicted values were consistently deeper than observed. The predictions for Lake Manapouri were, in contrast, generally shallower than observed values and observations showed no correlation with predictions.

There are many potential reasons for the failure of the site-specific predictions of upper depths. Not only may the wind fields be incorrect, but also the resolution of the topography may be insufficiently precise. During the field survey we noted that different sides of bays can have quite different vegetation characteristics, and in the case of Lake Manapouri the shoreline was highly convoluted at a small scale. Mapping of the wave action was at 200 m resolution, and many bays were considerably smaller than this—sometimes only 20 m. Lake Wakatipu had a simpler shoreline than Lake Manapouri, and here we found that, although the predictions were quantitatively incorrect, observations were correlated with predictions. This suggests that wave exposure was capturing the variability in depth limits of these communities, but that the calibration derived from Lake Wanaka was inaccurate for Lake Wakatipu. It is possible that use of real wind fields and slope characteristics may have reconciled the differences between Lakes Wakatipu and Wanaka.

ACKNOWLEDGMENTS

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