

Effect of landscape factors on fish distribution in arctic Alaskan lakes

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SUMMARY

1. The distribution of species is affected by many factors operating at a variety of temporal and spatial scales in a heterogeneous landscape. In lakes, fish communities are dynamic, influenced by landscape-level factors that control colonisation and extinction.
2. We used classification and regression tree (CART) analyses to quantify the importance of landscape-level factors in determining the distribution of fish species in 168 arctic Alaskan lakes. Factors including lake size, depth, outflow gradient, distance to other lakes, lake order, altitude, river drainage and age of glacial surface were analysed. These factors could affect either access of fish to a lake (colonisation variables), or their survival in a lake that already had been colonised (extinction variables).
3. The presence of a species was predicted accurately in 78.4% ± 10.5% (mean ± SD) of cases, and absence in 75.0% ± 6.1% of cases. The relative importance of extinction versus colonisation variables varied with species. Extinction variables were most important for lake trout (*Salvelinus namaycush*) and slimy sculpin (*Cottus cognatus*), a mixture of extinction and colonisation variables was important for arctic char (*Salvelinus alpinus*), and colonisation variables were most important for arctic grayling (*Thymallus arcticus*) and round whitefish (*Prosopium cylindraceum*).
4. Ecological differences among species account for much of the difference in relative importance of colonisation versus extinction variables. In addition, stream piracy events have occurred over geologic time scales, which have resulted in lakes that are currently inaccessible but support relict fish populations.
5. Climate warming, currently occurring in the arctic, is likely to alter further the stream network, which could have dramatic effects on fish distributions by affecting access to isolated lakes or isolating lakes that are currently accessible.

Keywords: arctic fish, classification and regression tree analyses, extinction versus colonisation, landscape factors, stream piracy

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Introduction

Ecological patterns and processes are influenced by factors that occur across temporal and spatial scales. Hierarchy theory provides insight into how finer-scale ecosystem patterns and processes are constrained by events and processes that occur at larger spatial and temporal scales, recognising that ecosystems are nested within others in the landscape (see Ahl & Allen, 1996). For example, Richards *et al.* (1997) predicted life history and behavioural characteristics of stream insects using physical properties occurring at catchment and reach scales. Palik, Buech & Egeland (2003) found that the glacial landform had the greatest influence over the abundance of seasonal wetlands in an upland forest.

Landscape-level approaches have been used to study the distribution of organisms between lakes. For example, lake area and depth affect the richness of fish (Tonn & Magnuson, 1982; Tonn *et al.*, 1990; Magnuson *et al.*, 1998) and zooplankton communities (Dodson, 1992; O'Brien *et al.*, 2004). Landscape features affect biotic distributions either directly (Tonn *et al.*, 1990; Magnuson *et al.*, 1998; Hershey *et al.*, 1999; Lewis & Magnuson, 2000), or indirectly through control of water chemistry (e.g. Schindler, 1977, 1978; Vanni & Findlay, 1990; Kratz *et al.*, 1997; Soranno *et al.*, 1999), thereby functioning as filters through which species pass in order to exist in a given system (Tonn *et al.*, 1990; Poff, 1997).

Landscape position describes the spatial relationship among lakes within a region, which may affect physical, chemical and biological attributes of a lake. Kratz *et al.* (1997) described a lake's landscape position as its hydrologic position within the local to regional flow system, and its spatial position relative to nearby lakes. They showed that lake area, conductivity and fish species richness increased with increasing surface water inputs. Lake order, defined by Riera *et al.* (2000), is a measure of the degree of surface water connections to the stream network. In north-central Wisconsin, lake order explained 12–56% of the variation in 21 of 25 variables examined (Riera *et al.*, 2000). Within a catchment, snail species richness was lower in isolated negative order highland lakes than in positive order, stream-connected, lowland lakes (Lewis & Magnuson, 2000). In Adirondacks lakes, drainage lakes (positive order) were phosphorus (P) limited, whereas seepage lakes (0 or negative order),

which were stained, were either nitrogen (N) or N + P limited (Saunders, Shaw & Bukaveckas, 2000).

An important process that alters spatial patterns in landscapes is 'stream piracy', or the capture of all or part of one drainage system by another system (see Mackin, 1936; Woodruff, 1977). Such events reroute drainage basins, thereby altering the physical and biological processes that are linked to basin hydrology. Advance and retreat of glaciers is one cause of stream piracy (Hamilton, 2002). In such cases, it is important to consider the landscape on a geological timescale in order to understand contemporary spatial patterns.

The geomorphic-trophic hypothesis for arctic lakes (Hershey *et al.*, 1999) postulates that lake trophic structure is influenced by the geomorphic template. In this paper, we examine the role of landscape criteria, which operate at different scales, in controlling the distribution of fishes among lakes. Previously, we demonstrated that fish affect benthic and pelagic invertebrate communities in arctic lakes (Hershey, 1985, 1990; Cuker, McDonald & Mozley, 1992; Goyke & Hershey, 1992; Tate & Hershey, 2003; O'Brien *et al.*, 2004). Consequently, if the landscape exerts control on fish distribution, it should indirectly affect invertebrate communities (see Hershey *et al.*, 1999).

We consider features that affect the access of fish to lakes (colonisation variables); and that affect survival in a lake that has already been colonised (extinction variables). We hypothesised that the relative importance of various colonisation and extinction variables would vary with fish species, depending on life history characteristics. The colonisation variables selected were river drainage, age of till since glaciation of the catchment, lake order, maximum outflow stream gradient (maximum gradient), average hillslope gradient to the next downslope lake or major river system (direct gradient), distance to the next downslope lake or major river system (direct distance), and altitude.

River drainage should affect fish distribution because species may have had unequal abilities to move between drainages over geological time, either through forays into the arctic ocean or because of stream capture events. Age of till (ranging from Late Tertiary to Late Wisconsin), could affect fish distribution because glacial advance and retreat alters stream courses and thus fish access to a lake. Higher order lakes, which are more connected to the stream network, might be more accessible, and lake order should have greatest effect on fishes that migrate

through rivers. We expected that poorer swimmers would be restricted from lakes with higher maximum gradient along their outflow streams. Average direct gradient could affect fish colonisation differently from maximum gradient because the former accounts for historical barriers to fish migration that may have been altered with changing stream course. Greater values of direct distance might restrict some species of fish, especially poorer swimmers, because fish cannot overwinter in most streams. Finally, altitude could affect fish access by integrating the effects of gradient, distance and till age. Stream fish assemblages are often nested along altitudinal gradients (Cook *et al.*, 2004).

Extinction variables we considered were depth, perimeter and shoreline development factor (SDF, *sensu* Riera *et al.*, 2000). Depth should be very important, because only deeper lakes have a sufficient volume of oxygenated water for fish to overwinter under ice cover. Also, epilimnetic temperatures are generally warmer (McDonald, Hershey & Miller, 1996) than is optimal (about 10 °C for most species present; Scott & Crossman, 1973), so deeper lakes also provide more summer habitat. Perimeter, a measure of lake size, could restrict fish distribution because smaller lakes offer less habitat, especially for larger fishes which require more foraging area per individual. SDF measures the irregularity of lake shorelines (Riera *et al.*, 2000), which could determine the habitat and nearshore refugia for small fish from predators (e.g. McDonald, Cucker & Mozley, 1982; McDonald, Hershey & O'Brien, 1992).

To test our hypotheses, we surveyed the distribution of fish species in 168 pristine and oligotrophic arctic Alaskan lakes. We then used classification and regression tree (CART) analyses (Breiman *et al.*, 1984; Magnuson *et al.*, 1998) to determine the relative importance of each of the landscape level variables studied. Our analysis was restricted to geomorphic factors and did not consider lake chemistry because the lakes are chemically relatively similar in terms of factors that typically restrict fish species.

Methods

Site and community description

The lakes were near Toolik Field Station (68°38'N, 149°38'W) on the North Slope of the Brooks Range in

arctic Alaska. The land surface near Toolik Lake was not covered by a continental glacier during the Illinoian or Wisconsin glaciations, but was influenced by four major advances of alpine glaciers from the Central Brooks Range (Hamilton, 2002) dating from the late Tertiary and early Pleistocene through about 11.5 kyr. These advances resulted in considerable land surface heterogeneity, and altered stream courses through stream piracy (e.g. Mackin, 1936; Woodruff, 1977; Easterbrook, 1993; Hamilton, 2002). The approximately 18 000-km² study area (Fig. 1) includes portions of all of these advances.

Lakes in the region are ultraoligotrophic to oligotrophic with spatially heterogeneous limitation by N and P (Whalen & Alexander, 1986; O'Brien *et al.*, 1992; Levine & Whalen, 2001). Fish species richness in the region is biogeographically constrained by the Brooks Range to the South and the Arctic Ocean to the North, such that only six species of fish occur [lake trout *Salvelinus namaycush* (Walbaum), arctic char *Salvelinus alpinus* (Linnaeus), arctic grayling *Thymallus arcticus* (Pallas), round whitefish *Prosopium cylindraceum* (Pallas), slimy sculpin *Cottus cognatus* Richardson, and burbot *Lota lota* (Linnaeus)].

Lake surveys

We surveyed fish presence in 168 arctic lakes in the general vicinity of Toolik Lake (Fig. 1) during the ice-free season, beginning in late June and continuing through early August 1998–2003. Fish generally reside year-round in lakes because most streams freeze solid in winter. Thus, the sampling date or year should not impact the results. The possible exception is the arctic grayling, that migrates into streams for spawning, although this would have been completed before our surveys began each summer. Some grayling remain in the streams for the summer, but grayling also summer in lakes. Some grayling also make summer forays into shallow lakes (which freeze solid during the winter).

Fish were assessed by a variety of methods although effort was not uniform among lakes for two reasons. First, only six species occur in the area and we could survey for only five of them (see below). Once a species was sampled, we did not continue to look for it. Secondly, prior information guided our work. Lakes that are shallow enough to freeze solid and are not connected directly to a

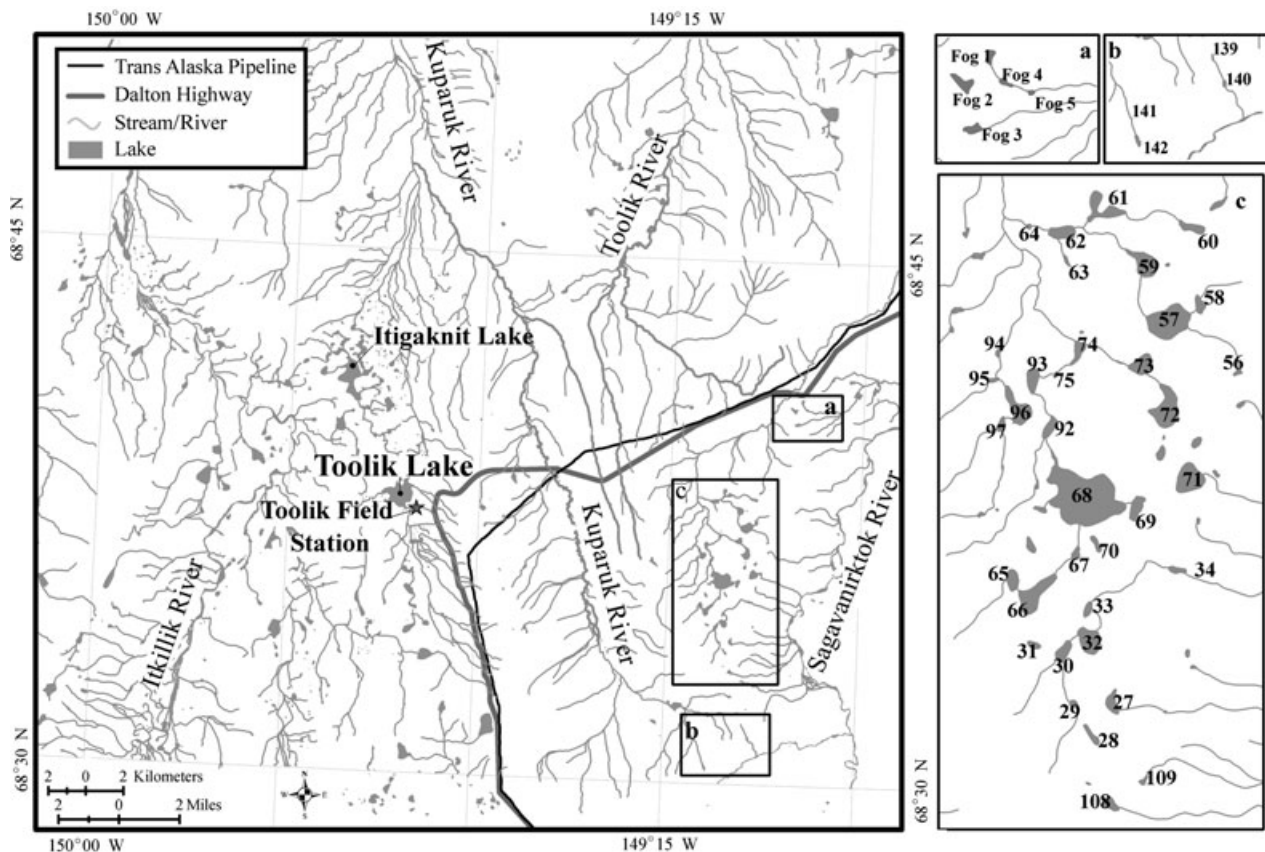


Fig. 1 Map of the study area in the vicinity of the Toolik Lake field stations. Inserts show areas where: (a) and (b) stream piracy has altered stream gradient such that lakes are inaccessible to fish, but relict populations occur; and (c) lakes are highly interconnected and lake trout and arctic char often coexist.

deeper lake or river could not support fish. We expended a minimum effort (3 gill net hours and shoreline dip netting and seining) looking for fish in such shallow lakes in case the lake had a deep area that we missed with our sonar transects (see below), or an intermittent stream connection that was dry during our survey. Similarly, lakes with very large zooplankton species, such as fairy shrimps (*Anostraca*), do not support fish (O'Brien *et al.*, 2004), and we expended the same minimum effort looking for fish in those lakes. Our previous studies also showed that most species are found in large lakes, and thus we expended more effort there until satisfied that we had found all the fish that were present (i.e. no additional fish species captured after an additional night of gillnetting, 3 days of trapping, and several hours of angling). Finally, our previous studies and observations (Hershey *et al.*, 1999) showed that grayling and sculpin were more wide-

spread than the other species. Thus, if we captured any of the other species in a lake, but not grayling or sculpin, we expended more effort in that lake in order to decrease the likelihood of falsely concluding that those species were absent (see Angermeier, Krueger & Dolloff, 2002).

An experimental gill net was set in each lake for several hours or, when catch was low or zero but fish were expected, overnight. Nets were set from shore, extending out into deep water, in order to cover the range of habitats that might be used by catchable species. Gill nets are the most reliable method for capturing lake trout, arctic char, grayling and round whitefish, but are not effective for sculpin and burbot. We fished nets often to remove and release live fish, and did not leave nets longer than necessary to document fish presence. Gill netting was supplemented by angling, visual inspection (often we could see and positively identify fish in

nearshore areas), trapping, seining and dip netting (see below).

To catch sculpin, we used clear jar traps with clear funnel inserts (McDonald *et al.*, 1982), wire minnow traps, collapsible minnow traps, visual inspection, seining, and dip netting. A minimum of 18 traps were set for a minimum of 8 h in each lake, or until sculpin were found by another method. If sculpin were strongly suspected based on the presence of other fish and the absence of large-bodied zooplankton, traps were left in for up to 3 days unless helicopter support did not permit a return trip to the lake. Those lakes were revisited on another occasion for the specific purpose of detecting sculpin.

Burbot were not susceptible to gill nets. They were only rarely collected in traps or by angling, and these methods did not consistently sample burbot even in lakes where we knew they occurred (especially Toolik Lake). Thus, we abandoned our attempt to assess burbot presence in surveys because logistic constraints prevented us from expending sufficient effort to be confident of assessing their absence.

Finally, we examined our dataset prior to the 2003 field season for lakes that appeared to be outliers in some respect, such lake trout present without sculpin or grayling, or the sole presence of sculpin. We then revisited these lakes to increase our confidence in the data. Thus, with the exception of burbot, we made every reasonable effort to find all the species in a lake. If a species was not found (except burbot), it was judged absent.

Landscape data

Landscape variables included in our analyses are described in Table 1. Lakes were sampled within the Sagavanirktok, Kuparuk, Toolik and Itkillik River drainages (Fig. 1). The Toolik River is a major tributary of the Kuparuk River, but the others drain independently from the Brooks Range to the Arctic Ocean. Although it might be possible for fish from a study lake in the Toolik River drainage to colonise a lake in the Upper Kuparuk River drainage by swimming to the confluence, it is a long distance (approximately 250 straight line kilometre, but through braided channels), and there are few lakes suitable for overwintering for most of that distance. Thus, such colonisation events would be expected to be rare.

Table 1 Landscape variables considered in the classification tree (CART) analysis of fish distribution in arctic lakes. Variables were grouped according to whether they were expected to affect fish access to a lake (colonisation variables) or survivorship in the lake once it had been colonised (extinction variables).

Colonisation variables

River system – major river into which the lake drains (Sagavanirktok, Kuparuk, Toolik, Itkillik)

Till age – rank age of the underlying glacial surface on which a lake occurs (Table 2)

Lake order – measure of connection of a lake to the stream network (after Riera *et al.*, 2000)

Maximum effective gradient – the maximum gradient between a lake and the nearest connected downstream lake or large river. If unconnected to the drainage, the maximum gradient along a straight line to the nearest downslope lake

Average direct gradient – the average gradient along a straight line to the nearest downslope lake or large river

Direct distance (m) – the distance along a straight line to the nearest downslope lake or large river

Altitude (m) – the altitude of the lake based on the United States Geological Survey (USGS) 1 : 63 000 topographic map

Extinction variables

Depth (m) – maximum depth of lake

Perimeter (m) – distance around lake digitised from USGS 1 : 63 000 topographic maps

Shoreline development factor = $\text{perimeter}/[2\sqrt{(\pi \times \text{area})}]$ (after Riera *et al.*, 2000)

Age of till was determined by overlaying the lake map with the glacial surface maps created by Hamilton (2002). These surfaces range in age from Late Wisconsin to Late Tertiary. For many of our study lakes, the surface age was given as a broad range rather than an approximate date (see Hamilton, 2002). To simplify our analysis of the effect of surface age, we assigned rank ages to the glacial surfaces underlying each lake (Table 2).

Lake order was assigned according to Riera *et al.* (2000), except that we used 1 : 63 000 United States Geological Survey (USGS) maps rather than 1 : 24 000 because the latter are not available for the study region. At this scale, lake order ranged from –3 to 3. Order –3 lakes have no inflow or outflow. Order –2 lakes are connected to the surface drainage by a wetland. Order –1 lakes have temporary stream connections to the surface drainage. Order zero lakes have an outflow but no permanent inflow. First order lakes have a permanent inflow and outflow. Second order lakes have a second order outflow stream (i.e. have a second order inflow and/or multiple first order inflow streams). Third order lakes have a third

Table 2 Assignment of lakes to glacial surfaces was based on maps provided by Hamilton (2002). In cases where a lake or its catchment spanned two surfaces, proportional ranks were given, but these are rounded to the nearest whole number in the column indicating number of lakes of each rank.

Approx. geologic period	Glacial advance	Approximate age (kyr)	Rank age	No. lakes	Comments
Late Wisconsin	Itkillik II readvance	12.8–11.4	1	32	Also includes lakes that appear to be on Holocene surfaces
Late Wisconsin	Itkillik II	25–11.5	2	40	Combines phase A and B
Late Pleistocene	Itkillik I	120–55	3	56	Combines phase A and B
Middle Pleistocene	Sagavanirktok late phase	780–125	4	7	These surfaces are distinct on the maps but age separation is not given
Middle Pleistocene	Sagavanirktok main phase		5	14	

order outflow stream (see Riera *et al.*, 2000). None of the survey lakes had a lake order of -2 .

Direct distance was calculated by digitising a straight line between the two nearest points on the edges of a lake and the nearest down slope lake (or river, if there was no lake down slope). We chose to use direct distance rather than stream distance because the former recognises that stream courses change over time, and stream distance recognises only the current distance that a fish must travel between lakes.

The average direct gradient was calculated for all lakes as the difference between the altitudes of a lake and that of the nearest down slope lake (or river, if there was no lake down slope), divided by the direct distance. Maximum gradient was determined by estimating the steepest portion along the outflow streams (or down slope to the nearest lake or river if there was no outflow stream). Estimates were made using 5-m contour intervals generated by the digital elevation model (DEM). The difference in altitude between the top and bottom of this section was divided by the length of the segment to calculate gradient. All measurements were performed in ARC VIEW.

Extinction variables included lake depth, perimeter and SDF. Depth values were taken as the maximum depth observed during lake sonar transects conducted from rafts. The number of transects varied depending on lake size, ranging from one transect in very small lakes to up to four transects in larger lakes. Perimeter was digitised from spatially rectified 1 : 63 000 USGS maps. Area was digitised from the same map as was perimeter. However we did not use area as a landscape variable in the analyses presented below because area and perimeter are geometrically inter-

dependent, highly correlated ($r = 0.95$ for our data set), and are both directly related to lake size. We chose perimeter for the practical reason that it provided slightly better models than did area. Although other pairs of variables in the dataset were also not independent (see Table 3), all variables selected measured distinct landscape constraints on fishes.

Data analysis

We constructed a Pearson's correlation matrix to examine relationships among all continuous numeric variables. We developed classification trees using CART (Breiman *et al.*, 1984; McCune & Grace, 2002; Salford Systems, 2002) to predict fish species presence and absence, and species richness, from the landscape variables described above. This approach was recently used by Magnuson *et al.* (1998) to describe fish distribution in Wisconsin and Finnish lakes, but using a different set of landscape constraints, and predicting fish community types rather than distribution of individual species. Classification trees built with CART are nonparametric recursive models that create hierarchical trees in which observations (e.g. lakes) are sorted with respect to a target variable (e.g. the presence of a particular fish species). At each step in model construction, the algorithm selects a value of a single predictor variable (e.g. maximum depth >4 m) that best sorts the observations according to the target variable. CART continues to sort the observations using other predictor variables or alternate values of the initial variable until final unsplitable groups of observations are achieved. The approach is robust to nonlinear data and interactions among variables, and accepts categorical and continuous variables. Interactions among variables are not problematic because

Table 3 Pearson's correlations between landscape variables, including those used in CART analyses and area, which was not included in CART because of its close relationship with perimeter. Variables are described in Table 1. Note that correlations were not calculated for river drainage which is not numerical, or for lake order and till age, which are not continuous.

	Z	Area	Perimeter	SDF	DirectDist	MaxEff gradient	Ave gradient	Altitude
Z*	1							
Area	0.39	1						
Perimeter	0.45	0.95	1					
SDF [†]	0.15	0.40	0.58	1				
DirectDist [‡]	0.07	0.01	-0.02	-0.10	1			
MaxEff gradient [§]	0.14	-0.08	-0.10	-0.10	0.43	1		
Ave gradient [¶]	0.08	-0.14	-0.14	-0.15	-0.12	0.23	1	
Altitude	0.08	-0.03	-0.04	-0.06	0.10	0.10	0.08	1

*Z, maximum depth; [†]SDF, shoreline development factor; [‡]Direct Dist, Direct Distance; [§]MaxEff gradient, maximum effective gradient; [¶]Ave gradient, average gradient.

only the single best predictor is selected at each branch, although other predictors may still be selected at other branches. The path of predictor variables used to create the splits forms the tree, which is similar to a dichotomous key (McCune & Grace, 2002). In our case, the tree classified lakes according to the likelihood of a fish species being present or absent, based on the values of the landscape variables. Classification accuracy was assessed using cross-validation by repeatedly subdividing the data in a Monte Carlo fashion to generate bootstrapped estimates of accuracy (McCune & Grace, 2002).

The CART output also provides relative importance values for each of the variables considered in a given tree, with and without surrogates (Salford Systems, 2002). Surrogate variables are those that could substitute for those used in the model, but were not used in construction of a best tree (McCune & Grace, 2002). For example, a tree might divide the dataset initially into two branches using the variable 'perimeter'. If a slightly less accurate division could be made using the variable 'depth', then depth would be considered a surrogate for perimeter. In ranking the relative importance of the variables, depth would be included even if it did not appear on the tree, because it could serve almost as well as perimeter. In this manner, CART includes correlated variables by identifying as surrogates the next best variables to those selected (McCune & Grace, 2002; Salford Systems, 2002).

In constructing the best tree, CART selects the tree that minimises costs (trade-off between prediction success and statistical over fitting of the model) by 'pruning' branches, or simplifying an over-fitted tree, but also provides a cost curve that allows the investigator to examine and select alternate trees

(McCune & Grace, 2002). For each tree, we examined the cost curves and reviewed pruning decisions made by the software. In one case we chose to prune a tree because the CART model appeared to be an overfit (see Results).

The CART analyses were performed using CART version 5.0 Salford Systems. Models were constructed using both the Gini and Entropy splitting methods, and with the assumption of equal prior probabilities or with prior probabilities calculated from the data. In all cases, models using the Gini splitting method and the assumption of equal prior probabilities provided higher prediction success. Therefore, we only report those results.

To use CART for predicting fish species richness, we eliminated the one lake from our dataset that had an observed richness of five. CART uses a v-fold cross-validation method, which takes the original data and randomly subdivides it into 10 subsets. Recursively, nine of the subsets are used as a learning dataset and the observations in the remaining subset are then classified using the tree generated with the learning dataset. This process is repeated until all of the subsets have been used as the test sample. The misclassification percentages reported are calculated from the cumulative classification success of these iterations. As there was only one lake with richness = 5, the cross validation could not be performed (i.e. the model would be trying to classify a five with a tree that only went up to four).

Results

Correlation coefficients among landscape variables used in the CART models are shown in Table 3. Direct

distance and maximum gradient were the only colonisation variables that were fairly closely correlated ($r = 0.43$). Among extinction variables, perimeter was positively correlated with depth ($r = 0.45$) and SDF ($r = 0.58$). Note that area and perimeter were highly correlated (0.95; Table 3), reflecting that they were essentially measuring the same thing.

Among fish species, CART was most successful in predicting arctic char distribution and least successful in predicting arctic grayling distribution (Table 4). Successful prediction of fish presence, or the percentage of the lakes where a fish was found that it was also predicted to be present, ranged from 68% to 92% (mean \pm SD = 78.4% \pm 10.5%; see Table 4). Absence was correctly predicted with 75.0% \pm 6.1% (mean \pm SD) accuracy, and ranged from 66% to 83%. Patterns of prediction success were not significantly related to the number of lakes in which species occurred (Table 4) or to the complexity of the trees produced by CART (comparison of Figs 2–6, and Table 4). Across species, extinction variables were slightly more important than colonisation variables, although the relative importance of colonisation and extinction variables differed among species. Depth and perimeter were the most important extinction variables, and altitude and lake order were the most important colonisation variables.

The CART predicted that lake trout would be found in relatively deep, large lakes, consistent with our observations. CART resulted in a three-node tree for lake trout using the extinction variables of depth and perimeter as the decision criteria (Fig. 2). Without consideration of surrogate variables, depth was most important, and perimeter was about 69% as important as depth (Table 5). Minor importance was also assigned to SDF, altitude and maximum gradient. However, when surrogate variables were considered, the relative order of importance of the two primary

Table 4 Prediction success for each fish species using CART analysis. See text for details

Fish species	Number of lakes present	% correct presence	% correct absence
Lake trout	48	85	75
Arctic char	25	92	83
Slimy sculpin	82	79	74
Arctic grayling	81	68	66
Round whitefish	22	68	77
Mean \pm SD		78.4 \pm 10.5	75.0 \pm 6.1

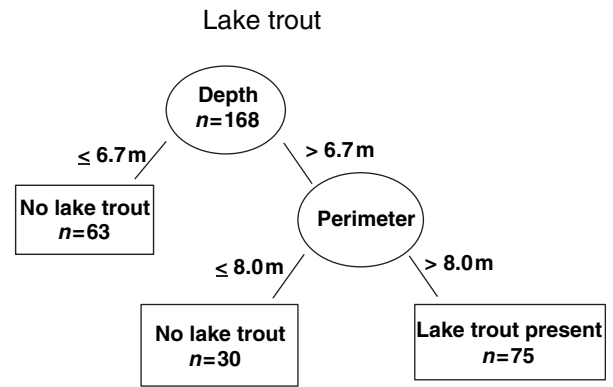


Fig. 2 Classification and regression tree (CART) analysis for lake trout. Ovals show variables used as decision points, and values of decision criteria are indicated along diagonal lines. Rectangles show nodes used in tree construction. Lake trout are predicted to be absent in cases to the left of a decision point if there are no further decision points, and present in cases to the right of a decision point if there are no further decision points.

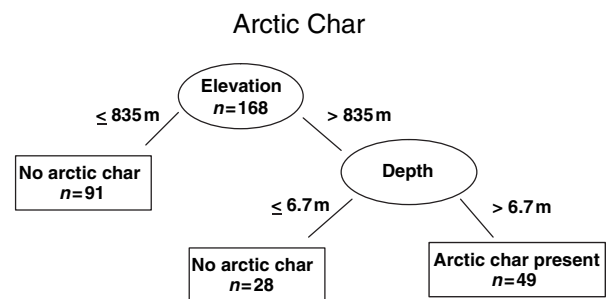


Fig. 3 Classification and regression tree (CART) analysis for arctic char. See legend Fig. 2.

variables reversed; perimeter was most important, and depth was 84% as important as perimeter. SDF, altitude, till age, river drainage and maximum effective gradient were included in the model but of lower importance (Table 5).

In the arctic char CART analysis, both extinction and colonisation variable groups had similar importance. CART predicted that arctic char would be found in high altitude, deep lakes, especially in the Sagavanirktok and Itkillik River systems (Fig. 3). Without consideration of surrogates, altitude was the most important variable, with depth, river system and perimeter contributing about 70%, 18% and 14% importance, respectively (Table 5). Consideration of surrogates reversed the importance of depth and altitude, increased the relative weight of

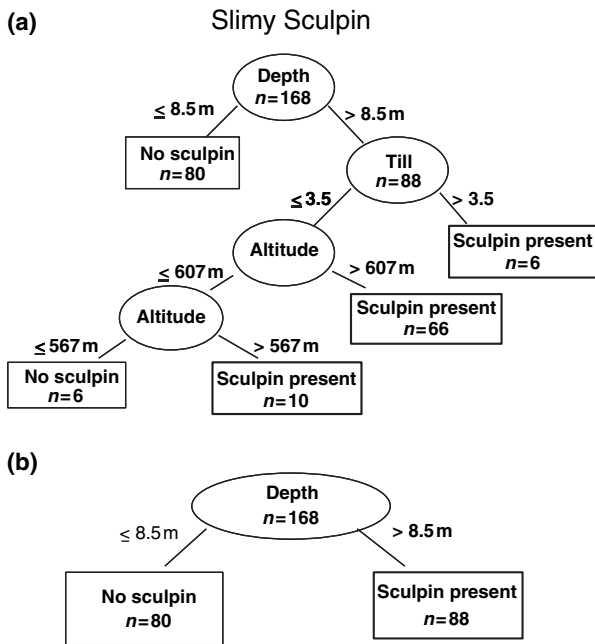


Fig. 4 Classification and regression tree (CART) analysis for slimy sculpin. (a) Results from unpruned tree, which appears to be a statistical over fit to the data (see text for Discussion). (b) Pruned tree which sacrifices some prediction accuracy but does not statistically over fit the data (see text for Discussion). See legend Fig. 2.

river system and perimeter, and added lake order to the model.

Both extinction and colonisation variables also were important for predicting sculpin distribution, although the extinction variable depth was overwhelmingly most important (Table 5). CART initially

produced a five-node tree for sculpin (Fig. 5a). Sculpin were predicted to be present in the six lakes that are deep and occur on till of rank age >3.5 . However, this prediction was not very successful, erring in five of the six cases. Of deep lakes on younger till, two levels of altitude were used to describe sculpin distribution further. Sculpin were predicted to occur in relatively high altitude lakes (>607 m), and this criterion was successful in 58 of 66 cases. Among the remaining 16 lakes that occurred at lower altitude, sculpin were predicted to be present in those of >567 m and absent from lower altitude lakes. Only one of these 16 lakes was correctly classified.

We viewed the five node tree for sculpin as an over fit because the two altitude criteria did not seem ecologically reasonable. Pruning resulted in a two-node tree that used depth as a single criterion (Fig. 5b); sculpin were predicted in lakes deeper than 8.5 m. Pruning sacrificed some prediction success; sculpin were correctly predicted as absent in 74% of cases rather than 87%. However, prediction success for presence improved from 74% to 79%. In this model, depth was the only variable of importance when surrogates were not considered (Table 5). When surrogates were included, till age (41%) and perimeter (25%) were also important. Altitude contributed only 3% importance to the model.

Colonisation variables contributed more importance to the CART model for arctic grayling than did extinction variables, regardless of whether surrogate variables were included. The tree for arctic grayling

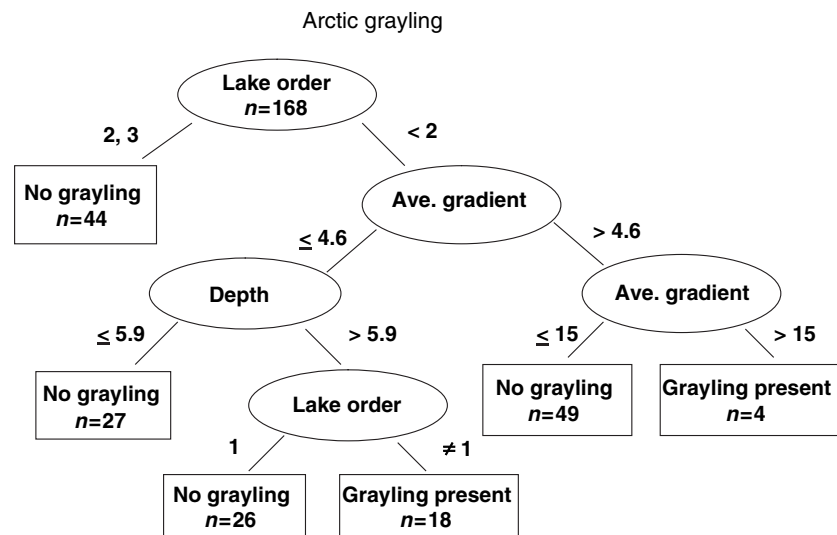


Fig. 5 Classification and regression tree (CART) analysis for arctic grayling. See legend Fig. 2.

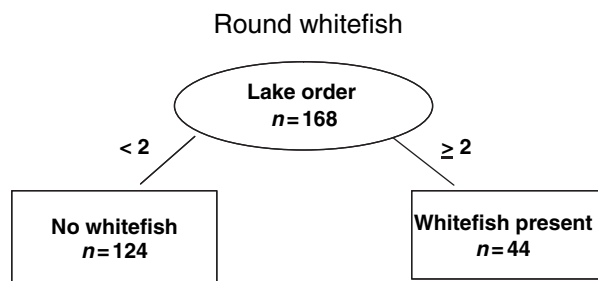


Fig. 6 Classification and regression tree (CART) analysis for round whitefish. See legend Fig. 2.

consisted of six nodes (Fig. 5). CART predicted arctic grayling to be present in low order, high gradient lakes, or lower gradient, deep lakes, except first order lakes. Without use of surrogate variables, lake order was most important, but average gradient (61%) and depth (26%) were also important variables in the CART model (Table 5). When surrogate variables were considered, all variables except till age and river system contributed at least 11% importance to the model (Table 5).

The colonisation variable lake order was most important in the CART model for round whitefish (Table 5). CART used lake order as the single decision criterion, predicting their presence only in high order lakes (Fig. 6). Model success was 77% correct at predicting absence and 68% correct at predicting presence (Table 4). Surrogate variables

(Table 5) that were also important relative to lake order included maximum gradient (21%), average gradient (12%), altitude (32%), perimeter (24%) and SDF (37%).

Both colonisation and extinction variables were important for prediction of fish species richness, although the extinction variable depth was most important regardless of whether surrogate variables were considered. Prediction of fish species richness involved a complex eight-node tree (Fig. 7). The highest richness value was predicted for deep (>6.7 m), low gradient ($\leq 1.2\%$) lakes that were not in the Itkillik River drainage. High richness values were also predicted for lakes with higher stream gradient but low direct distance (<341 m), or large lakes (perimeter >1578 m) on older till. Depth was the most important variable in the model, regardless of whether surrogate variables were used (Table 5). Important variables relative to depth (Table 5) were river drainage (47%), lake order (38%), altitude (33%), direct distance (30%) and perimeter (30%). When surrogates were considered, all landscape variables were important. Till age was only 5% as important as depth, but all other variables were at least 24% as important in the model as depth (Table 5).

In general, fish species richness was not predicted as successfully as the distribution of individual species (Table 6). Prediction success was highest for lakes with high richness ($S = 4$; 58%) and for fishless

Table 5 Importance values for extinction and colonisation landscape variables as determined by CART analyses. Variable importance is given separately for each fish and for richness, with and without consideration of surrogates. Importance values are relative to a score of 100, assigned to the most important variable in the model (CART version 5.0 Salford Systems).

	Lake trout		Arctic char		Slimy sculpin		Arctic grayling		Round whitefish		Richness	
	w/ surr*	w/out surr [†]	w/ surr	w/out surr	w/ surr	w/out surr	w/ surr	w/out surr	w/ surr	w/out surr	w/ surr	w/out surr
Extinction												
Perimeter	100	69	33	14	25		28	6	24	5	24	30
Z [‡]	84	100	100	70	100	100	35	26			100	100
SDF [§]	18	5	7		7		31	3	37	6	37	
Colonisation												
Altitude	17	1	82	100	3		15	1	32	8	32	33
Lake Order			18	2			100	100	100	100	85	38
Till age					41						5	
River	6		46	18			1				47	47
Max Gradient	10	1	1				11	3	21	5	42	
Average Gradient					4		64	61	12	3	39	
Direct Distance					1		21	1			40	30

*w/surr, with surrogates; [†]w/out surr, without surrogates; [‡]Z, maximum depth; [§]SDF, shoreline development factor.

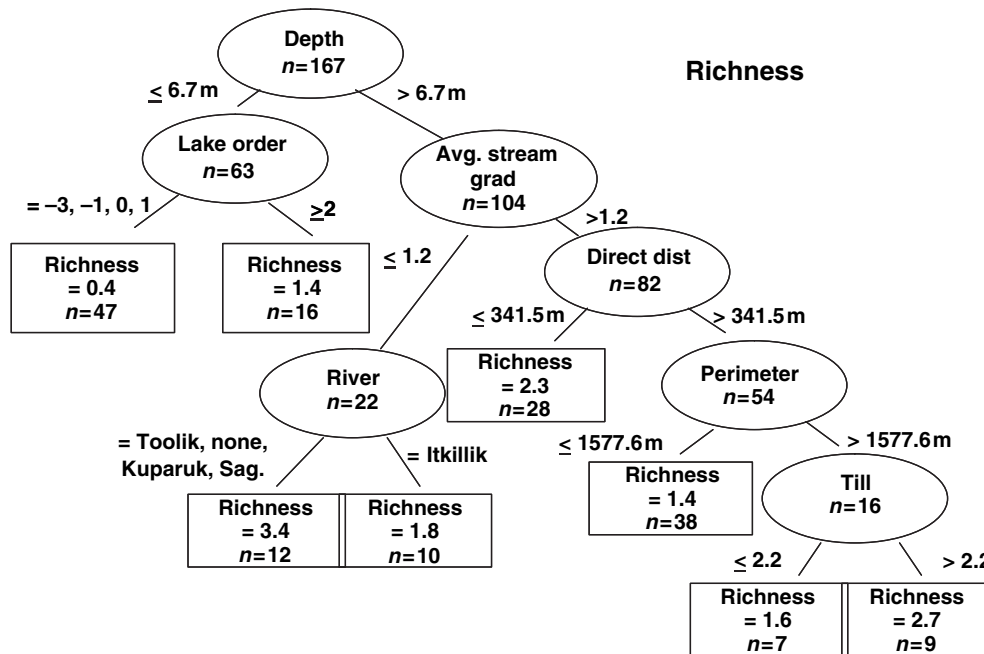


Fig. 7 Classification and regression tree (CART) analysis for fish richness. See legend Fig. 2. However, nodes show predicted richness for each set of decision criteria. Prediction success is shown in Table 6. Designation of ‘none’ for river reflects that one lake was perched between two drainage basins and had no outflow.

lakes (56%), lowest for single species lakes (11%), and intermediate for two- (41%) and three-species (35%) lakes (Table 6). Most misclassified lakes were classified as having one more or one less species than observed (Table 6).

Discussion

All the landscape variables examined had some impact on distribution of at least one species of fish, and all were important in affecting richness. Here we consider how the landscape variables operate differentially, depending on the spatial and temporal scales of the effects and on ecological and life history characteristics of the fishes, to produce the observed pattern of fish distribution on the landscape. It is

necessary also to recognise that many of the variables are not truly independent of the others because they are nested within the drainage basins. However, comparison of CART results with and without surrogates was a mechanism for evaluating whether correlated variables were behaving similarly, and how landscape criteria differentially affect fish species.

Relationships among variables

Distance was not very important in determining distribution of any species, suggesting that distance between lakes was not an insurmountable barrier for fish colonisation. However, connectivity of a lake to the stream network (as indicated by lake order) was important for three of the fishes and for richness. In

Table 6 Success of predicting species richness using CART. For each of the five possible richness values, entries show the total number of lakes for which sampling surveys estimated that value. CART results provide values for percentage of lakes that were correctly classified and the distribution of richness values predicted for each of the observed values.

Observed richness values	Total no. lakes	Percent correct	Richness values assigned by CART				
			0 (n = 43)	1 (n = 22)	2 (n = 42)	3 (n = 32)	4 (n = 28)
0	52	56	29	7	7	5	4
1	37	11	9	4	13	7	4
2	32	41	2	7	13	5	5
3	34	35	3	3	8	12	8
4	12	58	0	1	1	3	7

our dataset, only 13 of our 168 lakes (approximately 8%) had no surface connection, and of these 11 were >2 ha. In northern Wisconsin, connectivity was closely related to lake size, such that 80% of lakes 2 ha or smaller had no surface connection to the stream network (Magnuson *et al.*, 1998). For the one fish species (lake trout) where lake size (as perimeter) was an important surrogate variable, lake order was not included in the model. Similarly, for the two species where lake order was the primary variable, perimeter was not an important surrogate. Thus, although small lakes are somewhat less connected in the landscape than are the larger lakes ($r = 0.21$), lake order and size appear to have distinct and independent effects on fish distribution.

If fish distribution were strongly influenced by the contemporary landscape setting, maximum gradient, which emphasises extant barriers to fish colonisation, should be more important than average gradient, which accounts for historical barriers. However, average gradient was considerably more important for distribution of arctic grayling than maximum gradient, and other species were relatively uninfluenced by either gradient variable. This suggests that contemporary gradient is not a major factor determining current distributions of these fishes. Note that maximum gradient was correlated with distance, but the two gradient variables were not closely correlated with each other and behaved differently in the models. In a relatively low gradient Wisconsin lake district, stream gradient was relatively unimportant in determining distribution of fish assemblages, but was relatively important in segregating fish assemblages in higher gradient Finnish lakes (Magnuson *et al.*, 1998).

Inclusion of surrogate variables in the evaluation of fish distributions changed the relative importance of the first two variables for two fish species, as well as adding variables to the models. For lake trout, the relative importance of depth and perimeter was reversed when surrogates were considered. This partly reflects the fact that both variables represent important habitat requirements. Deep lakes are essential for overwintering beneath ice, but also for providing a summer hypolimnetic temperature refuge for lake trout where epilimnetic temperature may be too warm (McDonald *et al.*, 1996). Large lakes are needed to support a self-sustaining population size for lake trout (e.g. Hershey *et al.*, 1999). Thus, changing the

relative importance of depth and perimeter in the two CART models probably reflects the fact that both variables have major ecological significance to lake trout survival, and also that they were fairly highly correlated among the variable pairs ($r = 0.45$).

The relative importance of depth and altitude was reversed for arctic char when surrogates were included in the CART model. This result is less intuitive because these two variables were not well correlated and would not be expected to have similar ecological effects; depth is an extinction variable, whereas altitude is a colonisation variable. As for lake trout, depth represents an important habitat requirement for char, but the importance of altitude is probably linked to char life history and landscape history. High altitude lakes are associated with landlocked populations, which char could have accessed during glacial recession (Reist, Johnson & Carmichael, 1997, and see The role of stream piracy below), but would not be able to access now.

In addition to accounting for close relationships among variables, surrogate variables also show that factors constraining fish distribution are more complex than the model representations, although the added complexities do not improve model success. Thus, the simplified models (i.e. without surrogates) integrate much of the ecological and biological constraints embedded in the more complex models.

Effect of colonisation versus extinction

In northern Wisconsin and Finnish lakes, extinction factors were more important in determining fish communities than isolation factors (Tonn *et al.*, 1990; Magnuson *et al.*, 1998). Magnuson *et al.* (1998) argue that novel immigration events occur with lower probability than extinctions and, thus, current species composition and richness are more influenced by the 'stamp of extinction'. This necessarily holds for a community within a given lake, which will support the number of species that have colonised less those that have gone extinct since the most recent novel colonisation. The same reasoning does not apply to overall distribution (presence and absence) of a given fish species across the landscape. If a fish species is present in a given lake, clearly there has been one more novel colonisation than extinction event, but if a fish is absent, the numbers of novel colonisation and extinction events have been equal. Thus, fish distri-

bution in the landscape will reflect cases of presence and absence, and there is no a priori reason why extinction events should be of more importance than colonisation events in determining that distribution. For example, if a fish species is present in a lake, extinction may not be very likely because the lake offers suitable habitat (especially true for large, deep lakes). If such a lake is well connected in the landscape, colonisation should occur readily (perhaps continuously), quickly compensating for a local extinction.

In the Alaskan landscape, extinction variables were clearly more important than colonisation variables for lake trout and slimy sculpin, somewhat less so for arctic char and fish species richness, and of low importance for grayling and round whitefish. For lake trout, most of the lakes offer only marginal habitat (i.e. they are small and shallow), such that extinction is likely. Most large lakes that are suitable for lake trout are somewhat better connected with other lakes than are small lakes, but the relationship is weak (Table 3). Thus, for most of the lakes, habitat suitability is a greater barrier for lake trout than is access. Slimy sculpin are small fish which utilise all habitats in arctic lakes, have large populations where they occur (McDonald *et al.*, 1982), and were the most widespread species sampled (Table 4). They should be able to persist in any lake that is deep enough to provide overwintering habitat. Thus, it is not surprising that the extinction variable depth would be of primary importance to predicting their occurrence.

The importance of colonisation versus extinction variables was more equivocal for arctic char. Because arctic char and lake trout are closely related species, and have similar trophic habits and habitat requirements throughout their circumpolar distribution (e.g. see Johnson, 1972, 1976; Sandlund *et al.*, 1992; Snorrason *et al.*, 1994; Riget *et al.*, 2000), they might be expected to occur in the same lakes, unless either colonisation dynamics or interspecific interactions restrict co-occurrence. In our study region, arctic char co-occur with lake trout only in the headwater lakes of Oksrukuyik Creek, a tributary of the Sagavanirktok River (Fig. 1c). In this area, there are several large interconnected lakes, such that recolonisation following extinction events might be fairly common. In contrast, most of the other lakes that support arctic char are more isolated, and currently inaccessible to fish, whereas most of the lakes supporting lake trout

are well connected to the stream network. We suggest that the mixed importance of colonisation and extinction variables is because of two aspects of their biology: (i) arctic char are under the same constraints as lake trout in being restricted to fairly large lakes (i.e. extinction variables are important); and (ii) arctic char are additionally constrained by competition with lake trout. Thus, the presence of char in high altitude lakes is not because these lakes are accessible to char; the char occur there in landlocked relict populations, similar to landlocked char populations in Greenland and Iceland (see Riget *et al.*, 2000), and they could not currently invade. We suggest that they can persist there because lake trout are absent and also cannot invade.

Competitive interactions among salmonid species have often been reported (e.g. Nilsson, 1963; Hindar *et al.*, 1988; Hegge *et al.*, 1989; Donald & Alger, 1993). In much of their Palaearctic distribution, arctic char are found as either the only fish species or in combination with stickleback (Riget *et al.*, 2000). Stocking of salmonids has historically led to negative impact on native salmonids (e.g. Donald & Alger, 1993). We have previously suggested that competitive exclusion is occurring naturally in our study region as lake trout, a more recent invader, replaces arctic char in accessible lakes (Hershey *et al.*, 1999). The additional data reported here strengthen that hypothesis.

For both grayling and whitefish, lake order was overwhelmingly the most important variable in the CART models. However, the biological implications of lake order are different for the two species. For whitefish, gradient variables were important surrogates, as were altitude and perimeter, suggesting that whitefish were excluded from lower order lakes largely because they have difficulty accessing them. Although they occur in rivers, they are primarily lake fish (e.g. Scott & Crossman, 1973). Grayling, however, are more mobile fish, making long migrations through the stream network and breeding in streams (e.g. Bishop, 1971; Craig & Poulin, 1974). The CART model predicted grayling presence in lower order lakes, probably reflecting their high mobility. However, prediction success rate was lower for grayling than any other species. This failure is because the model predicted grayling to be absent in higher order lakes, when, in fact, they are usually present.

Species richness was expected to be more complex than models for individual species because it inher-

ently includes the probabilities for each individual species. Magnuson *et al.* (1998) also found that CART models for predicting fish species richness in Wisconsin and Finnish lakes were more complex than CART models for particular fish assemblages. Species richness is affected by complex array of extinction and colonisation variables because of the differential importance of these variables among the different fish species.

The role of stream piracy

The use of several variables to measure gradient and distance between lakes is a means of accounting for changes in stream courses and drainage systems that could affect fish access to lakes. Two examples of stream piracy events that have clearly affected the distribution of fishes in this region can be seen by examining the Fog Lakes drainage (Hershey *et al.*, 1999) and the Atigun River drainage (Hamilton, 2002). The Fog Lakes (Fig. 1a) drain to the east over a steep slope to the Sagavanirktok River floodplain. However, during the Itkillik II glacial advance, these lakes drained to the northeast along the ice margin and over a much more gradual slope (Hershey *et al.*, 1999). The current stream gradient between the Fog Lakes and the Sagavanirktok River is impassable to all fish, but the ice margin channel would not have been; four of the Fog Lakes support arctic char, grayling and sculpin, while the remaining lake (Fog 4) is shallow and fishless. Thus, it is easy to imagine that the fishless lake, which is lower in the drainage, is frequently colonised from the upstream lake that supports arctic char, grayling and sculpin, but extinction events determined by lack of overwintering habitat maintain it in a fishless condition. In contrast, constraints on colonisation exclude other fish species from the lakes.

An even more dramatic example of stream piracy is illustrated by the Atigun River drainage. Prior to the Itkillik II advances, the Atigun River flowed north from the Brooks Range and formed a tributary to the Kuparuk River (Hamilton, 2002). During the Itkillik II advance, what is now the Atigun Gorge was filled with ice; the Atigun River was diverted into the Atigun Gorge and now flows east through the gorge into the Sagavanirktok River (Fig. 1b). At that time, lakes GTH 139 and GTH 140 (Fig. 1b) were also captured from the headwaters of the Kuparuk River

drainage into the Atigun River drainage (Hamilton, 2002). The implication of this stream capture for our dataset is that GTH 140, which drops over a 200 m waterfall into the Atigun River, supports sculpin (GTH 139 is too shallow to support fish). Sculpin and other fishes are present in GTH 45 and GTH 46 (which remain in the Kuparuk River drainage), but may also have been present in GTH 140 at the time the capture took place. However, GTH 140 is a small lake (approximately 2 ha), thus extinction events would have probably excluded the other fishes if they had been present.

These stream piracy events illustrate that the landscape, and therefore landscape control of fish distributions, is temporally dynamic. The arctic region is warming (e.g. Lachenbruch & Marshall, 1986; McDonald *et al.*, 1996; Comiso, 2003), which is a direct threat to lake trout (McDonald *et al.*, 1996). Warming is also resulting in changing hydrologic patterns (see Rouse *et al.*, 1997). These changes could easily result in increased rates of stream capture (Hansell *et al.*, 1998), isolating lakes that are currently accessible to fish, or providing fish access to lakes that currently support relict populations.

Implications and conclusions

Understanding distribution of fishes in the arctic landscape has both ecological and social implications. Fish have numerous direct and indirect effects on both benthic and pelagic food webs (Shapiro, 1980; Carpenter, Kitchell & Hodgson, 1985; Carpenter, Cottingham & Schindler, 1992; Schindler *et al.*, 1993), are important vehicles for benthic-pelagic coupling (e.g. Vander Zanden & Rasmussen, 1999), and support subsistence, sport and commercial fisheries (Alaska Department of Fish and Game, 2001). In arctic lakes, sport fisheries are an important part of the Alaskan culture and economy, but warming is adversely threatening fish populations (McDonald *et al.*, 1996).

In addition to being of basic ecological and limnological interest, the ability to predict fish species distributions based on easily measured landscape criteria has the potential to provide valuable information for fisheries managers and conservation biologists. For arctic Alaskan lakes, distribution of individual fish species was predictable from landscape characteristics, but the relative importance of

the extinction and colonisation variables varied with fish species, probably because of differences in life history and ecology, as well as landscape dynamics. Ecological differences among species accounted for the difference in relative importance of colonisation versus extinction factors. In addition, stream piracy events have occurred over geologic time scales, which have resulted in lakes that are currently inaccessible, yet support fish. In those instances, the species present are those that were present before isolation, less those that have gone extinct since isolation. Such lakes appear to be important refugia for arctic char, a factor that should be considered by fisheries managers. Climate change is likely to alter the stream network, which also would affect the relative importance of colonisation and extinction variables for the various fish species.

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