



Lake morphometry predicts the degree of habitat coupling by a mobile predator

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Habitat coupling is an ecosystem process whereby semi-discontinuous habitats are connected through the movement of energy and nutrients by chemical, physical or biological processes. One oft-cited example is that of littoral–pelagic coupling in lakes. Theory has argued that such habitat coupling may be critical to food web dynamics, yet there have been few empirical studies that have quantified ecological factors that affect the degree of habitat coupling in ecosystems. Specifically, the degree to which habitat coupling occurs across important physical gradients has largely been ignored. To address this, we investigate the degree of littoral habitat coupling (i.e. the degree to which a top predator lake trout, *Salvelinus namaycush*, derives energy from the littoral zone) along a gradient of lake shape, where lake shape modifies the relative quantity of coupled epilimnetic benthic and pelagic habitats within each lake. Herein we demonstrate that littoral habitat coupling is intensified in simple circular lakes compared to their reticulate counterparts in seven Canadian Shield lakes. Although the more reticulate lakes had larger areas of epilimnetic benthic habitat, littoral food sources comprised 11% compared to 24% of lake trout diet in reticulate and circular lakes, respectively. This heightened interaction in circular lakes also appears to translate into increased omnivory in more circular lakes compared to reticulate lakes such that lake trout of circular lakes have a significantly lower trophic position than lake trout of reticulate lakes ($F_{1,5} = 6.71$, $p = 0.05$). These results suggest that it is the accessibility of littoral production via thermal refugia, and not the amount of littoral production, that determines the degree to which lake trout couple littoral and pelagic habitats in lakes.

The littoral zone has recently been highlighted as an important component of lake community structure and function (Vadeboncoeur et al. 2002, Sierszen et al. 2003, Babler et al. 2008). While some studies have argued for the independent functioning of littoral and pelagic habitats (France 1995, Bertolo et al. 2005), the emerging consensus is that littoral and pelagic zones are connected through physical, chemical and biological processes (Schindler et al. 1996, Benoy and Kalff 1999, Vander Zanden et al. 1999a, Rooney et al. 2003). The degree of this littoral–pelagic coupling will, however, vary among lakes. Hypotheses addressing the factors that influence the degree of littoral–pelagic coupling have been proposed, but remain untested empirically (Schindler and Scheuerell 2002).

From a trophodynamic perspective, littoral–pelagic habitat coupling can be thought of as the integration of energy and nutrients from otherwise discontinuous food chains by the movement and foraging of mobile predators (Schindler and Scheuerell 2002). This food web structure of coupled energy channels has been observed in a variety of food webs (Vander Zanden and Vadeboncoeur 2002, Rooney et al. 2006, 2008). Recently, the strength of habitat coupling by mobile predators has been shown to be a major factor in governing the stability of food webs (Post et al.

2000a, McCann et al. 2005, Rooney et al. 2006). Thus, determining the factors that influence the degree of habitat coupling in ecosystems has emerged as a priority in aquatic food web ecology.

Several factors may influence the relative degree to which mobile top predators are able to couple littoral and pelagic habitats. For example, eutrophication promotes pelagic productivity, which could result in a relative increase in the amount of energy that a top predator derives from phytoplankton production (Vadeboncoeur et al. 2003), thus lessening the degree of littoral habitat coupling (defined as the proportion of total energy derived from the littoral zone) by mobile pelagic predators. From a food web perspective, the presence of smallmouth bass *Micropterus dolomieu* in freshwater food webs has been shown to competitively limit lake trout *Salvelinus namaycush* access to littoral resources (Vander Zanden et al. 1999a). While the aforementioned factors incorporated biogeochemical and biological factors, the influence of lake morphometry on habitat coupling may rank among the most important.

Schindler et al. (1996) predicted that lakes with relatively larger littoral zones should exhibit higher levels of littoral habitat coupling by mobile predators due to the relative

increase in productive littoral space (sensu Schoener 1989). This idea was elaborated by Schindler and Scheuerell (2002) who proposed that ecological interactions between (littoral) benthic and pelagic habitats should be most important in lakes with high perimeter:area ratios (P:A ratios). Among lake variation of the P:A ratio can be driven by two factors. The first factor is simply lake area, as smaller lakes will have larger P:A ratios, all else being equal. Secondly, and independent of lake size, lakes with high degrees of shoreline convolution will also tend to have higher P:A ratios. Early empirical evidence suggests that, indeed, smaller freshwater ecosystems exhibit a higher degree of littoral habitat coupling and omnivory, compared to food webs in larger freshwater bodies (Post et al. 2000b, Gunn 2002, Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005). In contrast to the number of studies examining the influence of lake size on littoral habitat coupling, the prediction that shoreline convolution influences littoral habitat coupling as proposed by Schindler et al. (1996) and Schindler and Scheuerell (2002) remains untested.

Whereas Schindler and Scheuerell (2002) predicted that the amount which littoral foraging contributes to mobile predator energetics ought to be a positive function of the degree of lake convolution, there exists at least one alternate hypothesis in north temperate lakes. MacRae and Jackson (2001) note that thermal refugia may be afforded to warm water tolerant prey when their predator, a cold water species, is restricted to the cold water zones of a lake during the warm summer months. For example, the cold water predator lake trout has been documented foraging in the littoral zone when water temperatures are well above its physiologically preferred range (Bergstedt et al. 2003). As such, it is not surprising that littoral warm water foraging is normally restricted to short temporal bouts on the order of 5–15 minutes (Morbey et al. 2006). This suggests that only littoral habitat that is in close proximity to thermally optimal cold water pockets of a lake is accessible to lake trout during the summer months. Conversely, littoral habitat that is distant from the cold water area is likely to function as a refuge for littoral prey (Fig. 1).

In the cold water lakes of Ontario, lake shape (measured as the shoreline development index) tends to be positively correlated to the relative amount of littoral area (unpublished Ontario Ministry of Natural Resources data, $n = 538$; $R^2 = 0.15$; $F_{2,535} = 45.2$, $p < 0.01$). Thus, more reticulate lakes tend to have a greater amount of littoral area relative to pelagic area, and more of the littoral zone will be distant from the cold water habitat of the lake trout. From the viewpoint of littoral prey, therefore, increased shoreline convolution represents the potential for an increase in refugia via both habitat complexity and distance from the thermally optimal habitat of the predator (the hypolimnion; see Fig. 1 for further explanation). Thus, we propose that in our study of cold water Ontario lakes, the degree of shoreline convolution may negatively influence the degree of littoral habitat coupling by mobile predators through restricting predator accessibility to distant warm water littoral productivity.

Two contrasting hypotheses can therefore be identified regarding habitat coupling by cold water mobile predators: 1) the Littoral space hypothesis: an increase in the complexity of lake shape increases littoral habitat coupling, through an

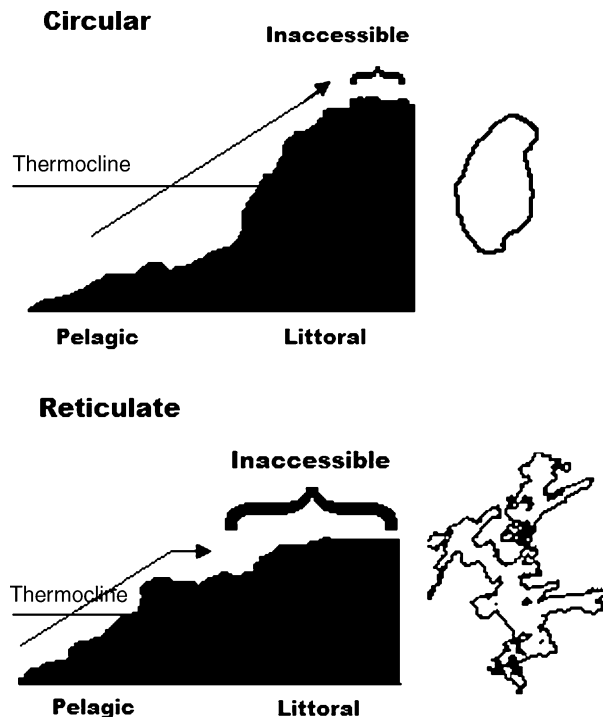


Figure 1. Accessibility hypothesis. In circular lakes, lake trout can quickly move between the pelagic and littoral zone where water temperatures are supra-optimal. As lakes become more reticulate the accessibility of the littoral zone becomes energetically and thermally restricted to lake trout.

increase in available productive littoral space (Schindler et al. 1996, Schindler and Scheuerell 2002). This hypothesis necessarily predicts that the amount of littorally derived energy in a mobile predator's diet will increase as the amount of productive littoral space increases. Alternatively, 2) the Accessibility hypothesis: an increase in the complexity of lake shape decreases littoral habitat coupling by mobile predators, via reduced accessibility (Fig. 1). We tested these contrasting hypotheses by quantifying the degree of littoral habitat coupling by a top predator across a gradient of lake shape in a series of oligotrophic lakes in Algonquin Park, Ontario, Canada; where lake shape correlated positively to the relative amount of epilimnetic benthic habitat (littoral habitat).

Methods

Site selection and lake descriptions

Seven lakes were chosen for food web analysis within Algonquin Provincial Park, Central Ontario, Canada and range from the park's southern ($78^{\circ}11' \text{ W}$; $45^{\circ}11' \text{ N}$) to northern ($78^{\circ}33' \text{ W}$; $46^{\circ}08' \text{ N}$) boundaries. Selected abiotic attributes of the lakes are given in Table 1. Due to the hard igneous and metamorphic rock of the Canadian Shield, few nutrients (e.g. phosphorous, potassium and nitrogen) are leached into the lake by erosion ensuring low productivity (Mackie 2001). Algonquin Park lakes are oligotrophic with total phosphorus concentrations between $5\text{--}15 \mu\text{g l}^{-1}$ (Wissel and Ramacharan 2003). The lakes are also similar

Table 1. Lake morphometric and limnological characteristics from seven study lakes in the central Canadian Shield are shown. Shoreline development index (Dev index) is a measurement of lake shoreline convolution and relative epilimnetic benthic habitat (REB) is the area of the lake above the measured thermocline relative to total lake area. Important lake trout food items and their presence amongst the lakes are also listed. *Mysis relicta* presence/absence is based on the Martin and Chapman 1965 survey (suspected designation implies no new survey has occurred since Martin and Chapman). Lake and Round whitefish presence/absence is based on catch data of this study and a historical OMNR database (OMNR unpublished). **Mysis* presence detected by a 2007 survey (S. Reid pers. comm. 2007).

	Lake						
	Gilmour	Canoe	Three Mile	Catfish	White Partridge	Burntroot	Hogan
Long. (DMS)	78°29'W	78°43'W	78°54'W	78°33'W	78°06'W	78°40'W	78°30'W
Lat. (DMS)	46°04'N	45°32'N	45°59'N	45°55'N	45°50'N	45°51'N	45°52'N
Area (km ²)	1.66	3.74	4.16	5.35	5.85	11.54	12.57
Perimeter (km)	5.43	27.58	20.9	46.99	14.92	61.95	60.4
Max depth (m)	24	37	37	22	47	25	31
Mean depth (m)	9.1	11.6	11	5.5	16.7	6.3	6.5
Dev index	1.19	4.02	2.89	5.73	1.74	5.14	4.81
Thermocline depth (m)	7	8	6	9.5	8.5	7.9	6.8
Secchi depth (m)	4.7	4.36	3.8	3.26	4.84	3.62	3.2
Relative epilimnetic benthic habitat	0.43	0.49	0.33	0.79	0.32	0.68	0.59
Lake whitefish (<i>Coregonus clupeaformis</i>)	absent	present	absent	present	absent	present	present
Round whitefish (<i>Prosopium cylindraceum</i>)	absent	present	absent	present	absent	absent	absent
<i>Mysis relicta</i>	suspected	absent	present*	absent	present	absent	suspected

in oxygen concentration, glacial and geochemical history and species assemblages. Wetland and bog habitats are present but their area does not exceed 20% of the drainage basin in any of the study lakes. Lakes were chosen based on known presence of similar food web composition (e.g. presence of lake trout, and the pelagic forage fish cisco, *Coregonus artedii*). Species presence was estimated using a historical OMNR database (OMNR unpubl.). In addition, only some lakes contained the zooplankton predator *Mysis relicta*, lake whitefish *Coregonus clupeaformis* and round whitefish *Prosopium cylindraceum*; Table 1. Three lakes (Three Mile, Canoe and Gilmour) contained smallmouth bass *Micropterus dolomieu* at different stages of invasion. Canoe Lake has an established cottage industry and an easily accessible boat launch, resulting in moderate fishing pressure. White Partridge Lake has limited motorized boat access resulting in elevated fishing pressure compared to other interior park lakes. Fishing pressure in all other lakes is low due to reduced accessibility (canoe only, no motorized boat access).

Determination of lake morphometry

The protocol outlined in Hulsman et al. (2001) was followed to create bathymetric maps of the study lakes. Bathymetric information for White Partridge and Canoe lakes were also collected following Hulsman et al. (2001) but were provided by the OMNR (G. Betteridge, OMNR pers. comm. 2007).

A Garmin GPSMAP 492 chart-plotter receiver was used to collect depth sounding information, which was recorded using the Bathymetric Automated Survey System 2.0. Digital maps were created using ArcMap 9.1 software (ESRI ver. 9.1. 2007). Bathymetric information was used to determine the shoreline development index, total area, and the relative amount of epilimnetic benthic habitat above the thermocline in each lake.

The degree of shoreline convolution (a proxy for the amount of littoral space, and accessibility) was estimated using the shoreline development index (Dev index). Dev index estimates the degree of shoreline convolution for a lake of given size, related to a perfect circle of the same size, and was calculated according to Kent and Wong (1982):

$$\text{Dev index} = \text{perimeter} / 2 \times \text{SQRT}(\text{PI} \times \text{area}) \quad (1)$$

Dev index was not correlated with lake total area in any of the study lakes, and so further manipulations of the shape metric were not required (Kent and Wong 1982). In order to ensure that the shoreline development index would function as a gross measure of accessibility, we developed the metric relative epilimnetic benthic habitat (REB):

$$\text{REB} = \text{EB} / \text{A} \quad (2)$$

where EB represents the area of epilimnetic benthic habitat that lies above the thermocline (standardized among lakes to the 10°C isocline) and A is the total lake area.

Collection of organisms

All lakes were sampled between 15 June – 5 August 2007. For each lake, lake trout, cisco, littoral forage fish (*Luxilus cornuta*, *Lepomis gibbosus*, *Semotilus atromaculatus*, *Perca flavescens*), littoral grazing snails (*Campeloma decisum*), unionid mussels (*Elliptio complanata*) and littoral benthic invertebrates (*Odonata* and *Ephemeroptera*) were collected. Thermocline depth measurements were recorded using a Quanta Hydrolab.

Live minnow traps baited with bread were used to capture 8–10 littoral forage fish individuals per lake. Three traps per lake were set for 12 to 24 h haphazardly in optimal littoral forage fish habitat. Lake trout and cisco were captured using multi-panel size-specific gill nets. All nets were 60.8 m long and comprised of four 15.2 m long by 2.4 m high panels. Both trout and cisco nests had double knotted monofilament mesh with 51, 64 mm and 32, 45 mm stretched mesh

sizes, respectively. The ratio of mesh sizes per panel was 1.73:1. Nets were set perpendicular to shore when targeting lake trout, and parallel to the shoreline when targeting cisco. Net sets varied in all aspects, from time of day, set duration, depth and number of net sets per lake. Evening and overnight sets had the highest yield, consistent with increased lake trout activity (Martin and Oliver 1980). The depths of the net sets ranged from 4–15 m and only rarely were very deep (> 20 m) sets required to catch lake trout.

The number of lake trout caught per lake varied from 8 to 20. When feasible, only specimens over 41 cm (fork length) long were used in the analysis to eliminate differences in diet due to ontogenetic factors (Martin and Oliver 1980). However, in White Partridge Lake only 8 trout greater than 41 cm (fork length) were caught and so two additional individuals of 39 cm were analyzed. These individuals did not appear as outliers and were therefore used in the further analysis.

Isotopic analysis

Stable isotope analysis of carbon signatures has become a useful tool for studying food web interactions among individuals and species. Particularly useful is that carbon isotopes fractionate differentially between the littoral and pelagic habitats of lakes so that diet origin can be revealed (Vander Zanden and Rasmussen 1999). Carbon is also ideal as it does not significantly magnify as it is transferred up the food web (Post 2002). Typically, littoral carbon signatures are enriched 4–5‰, compared to pelagic signatures (littoral carbon signatures range from $\delta^{13}\text{C}$ of -22 to -25 in the study lakes, compared to pelagic carbon signatures of $\delta^{13}\text{C}$ -25 to -33). Thus we are able to discriminate between the amount of littoral and pelagic-derived energy of lake trout among lakes (France 1995, Post 2002). In addition, isotopic signatures represent assimilated prey energy and reflect a time-integrated measure of predation, as opposed to a snap-shot view of un-assimilated material from diet analysis (Post 2002).

Following Post (2002) tissue samples were taken (~ 1 g) from unionid mussels (*Elliptio complanata*, $n = 8$ per lake) and littoral grazing snails (*Campeloma decisum*, $n = 1$ –8 depending on lake) to estimate baseline carbon and nitrogen isotopic signatures in the pelagic and littoral food chains respectively. Due to low snail abundance in some lakes, littoral grazing benthic invertebrate specimens (*Odonata* and *Ephemeroptera*, $n = 6$ –8 per lake) were incorporated into the littoral carbon baseline signature. All littoral benthos and littoral grazing snails were captured between 0.2 and 1.0 m depth within all lakes, thus eliminating any depth-related effect in the carbon signature.

From each lake a 1–3 g sample of dorsal musculature was taken from eight to ten lake trout and ten cisco per lake, as well as a total of eight littoral forage fish per lake (from amongst: *Luxilus cornuta*, *Lepomis gibbosus*, *Semotilus atromaculatus*, *Perca flavescens*). All samples were freeze-dried for 24 h and ground. Analysis of carbon and nitrogen stable isotopes were carried out in the Finnigan-Mat Delta Plus interface via continuous flow to an NC2500 elemental analyzer by staff at the Canadian Rivers Institute, NB.

Stable carbon isotope values are expressed in terms of their deviation from a standard in parts per thousand:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (3)$$

where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard reference for $\delta^{13}\text{C}$ was Pee Dee Belemnite limestone (Canadian Rivers Institute Isotopic Analysis Lab 2007). Replicate samples were completed on 10% of the samples and the mean standard deviation between replicates was 0.08.

Using C:N ratios, all samples were standardized for differences in lipid concentration using the equation:

$$\delta^{13}\text{C} \text{ normalized} = \delta^{13}\text{C} \text{ untreated} - 3.32 + 0.99 \times \text{C:N} \quad (4)$$

as described in Post et al. (2007). Standardizing tissues for differences in lipid concentration removes potential variances in the carbon signature due to a higher fractionation rate of $\delta^{13}\text{C}$ during lipid formation.

Individual lake trout diets were estimated using the multi-end mixing model Isosource (Phillips and Gregg 2003). Isosource assumes a carbon fractionation of 0‰ and nitrogen of 3.4‰, and the lakes herein had a tolerance (the deviation allowed between the actual unknown diet and that estimated by the program) of 3 or 4, depending on the lake. For each individual lake trout, Isosource was used to estimate diet composition using four known sources, in this case: cisco, zooplankton, littoral forage fish, and littoral benthos. Isosource thus produces an estimate of individual lake trout diet composition based on the known food sources' isotopic signature contributing to that of the individual lake trout isotopic signature. A whole lake average of lake trout foraging was determined by averaging individuals within a lake. Zooplankton isotopic signatures were estimated by removing 3.4‰ from the nitrogen signature of cisco, and assuming a carbon signature equal to that of the pelagic base. Zooplankton isotopic signatures were not determined directly due to potential changes in their isotopic signatures as a result of differing sampling times among lakes. All values are standardized for among lake differences in baseline carbon and nitrogen signatures following Post (2002).

Trophic position was calculated using the following equation:

$$\text{TP} = 2 + (\alpha_{\text{C}} + \alpha_{\text{Z}}) \times (\delta\text{N}_{\text{T}}^{15} - \delta\text{N}_{\text{PB}}^{15}) + (\beta_{\text{FF}} + \beta_{\text{I}}) \times (\delta\text{N}_{\text{T}}^{15} - \delta\text{N}_{\text{LB}}^{15}) \quad (5)$$

where α_{C} , α_{Z} represent the dietary contributions of cisco, and zooplankton as estimated by Isosource. While β_{FF} , β_{I} represent the Isosource estimated contribution of forage fish and benthic invertebrates, respectively, to lake trout diet. T = trout, PB = pelagic base and LB = littoral base.

Statistical analysis

Linear regression models were used to quantify among-lake variation in littoral and pelagic derived energy of lake trout diet, explained by the predictor variables: surface area, Dev index and REB. Isotopic diet data did not meet tests of normality and was transformed using arcsine of the square

root to account for a binomial distribution which is common among proportional data. ArcC (arcsine of the square root percent cisco contribution to lake trout diet) and ArcZ (zooplankton) were used to estimate the amount of pelagic foraging by trout. ArcFF (forage fish) and ArcB (littoral benthos) were used to estimate littoral habitat foraging by lake trout. Un-transformed data is available in Appendix 1.

Akaike's information criterion (AIC) was calculated to compare models of lake trout diet and trophic position as a function of lake size or lake shape. A delta AICc (small sample size) of zero indicates the best model, and the weighted criterion (ω_i) shows the weight of evidence for one model over another (Burnham and Anderson 2002).

Results

Littoral habitat coupling

Relative epilimnetic benthic habitat (REB) and Dev index values for each lake are given in Table 1. REB was positively

and significantly related to Dev index in our lakes ($F_{1,5} = 15.6$, $p = 0.01$).

Pooled lake trout isotopic data ($n = 8-10$) among lakes revealed that Dev index is a good predictor of the degree of littoral habitat coupling by lake trout (Fig. 2a-b). In more reticulate lakes, the percent of littoral forage fish in lake trout diet tended to be lower (Fig. 2a; $F_{1,5} = 5.81$, $p = 0.061$) compared to circular lakes. Similarly, the percent of pelagic forage fish in lake trout diet was significantly higher among reticulate lakes (Fig. 2b; $F_{1,5} = 9.84$, $p = 0.026$) compared to circular lakes. In agreement with the accessibility hypothesis, lower REB values were significantly correlated to a higher degree of total (ArcFF + ArcB) littoral habitat coupling ($F_{1,5} = 8.5$, $p = 0.031$).

A diagram of the consumption trends from a circular (White Partridge) and a reticulate (Catfish) lake are shown in Fig. 3 for comparative purposes. This diagram represents untransformed dietary proportions using lakes of similar size (5.85 and 5.35 ha, respectively). Notably, littoral forage fish consumption was 13% higher in the circular compared to reticulate lake. Figure 3 also shows that plankton and littoral benthos consumption was greater in the circular

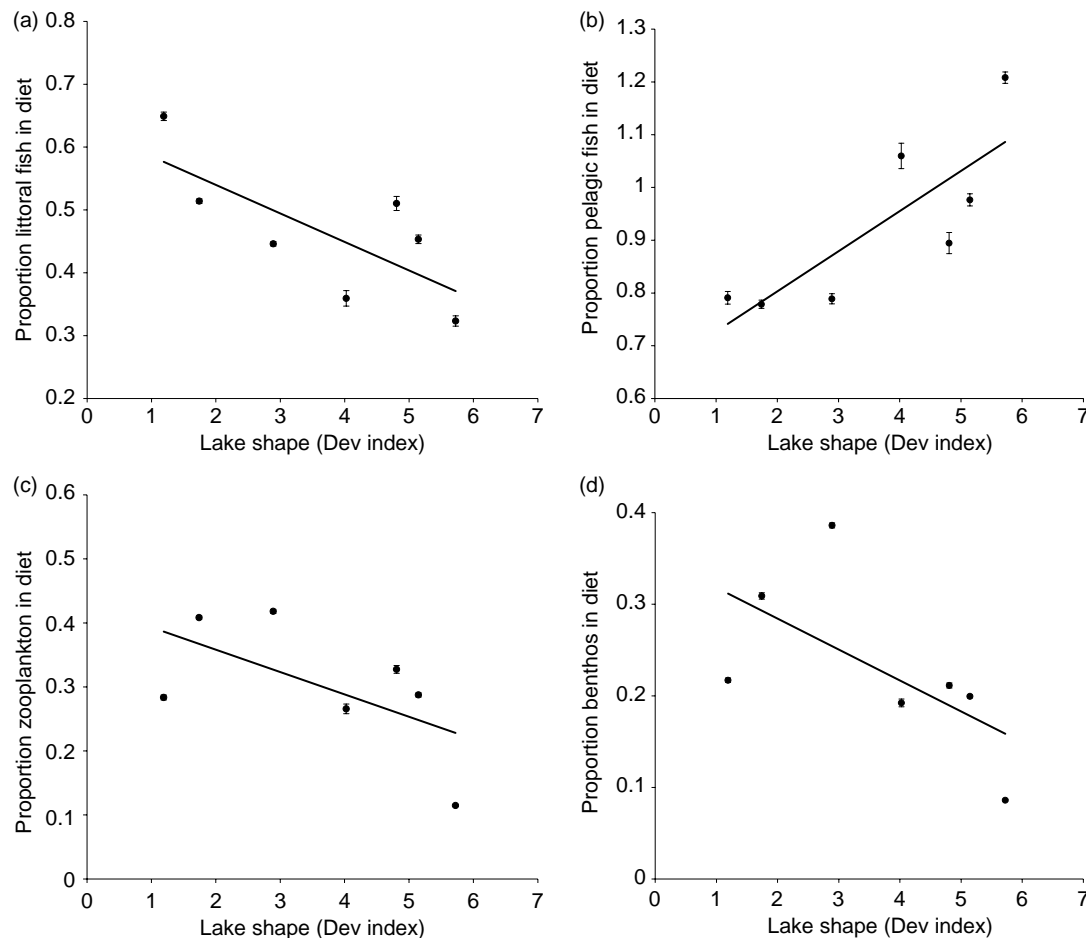


Figure 2. Among lake differences in lake trout ($n = 8-10$ per lake) habitat coupling. Arcsine square root of the proportion of lake trout diet from (a) littoral forage fish (perch, creek chub, pumpkinseed and common shiner), (b) pelagic forage fish (cisco), (c) zooplankton, and (d) littoral benthos. Error bars show the standard error of the mean (and are sometimes obscured by the data point). Reticulate lakes have a high development index. Diet proportions were estimated using carbon and nitrogen stable isotopes in the mixing model Isosource (Phillips and Greg 2003). Significance and r^2 values are listed in Table 2a.

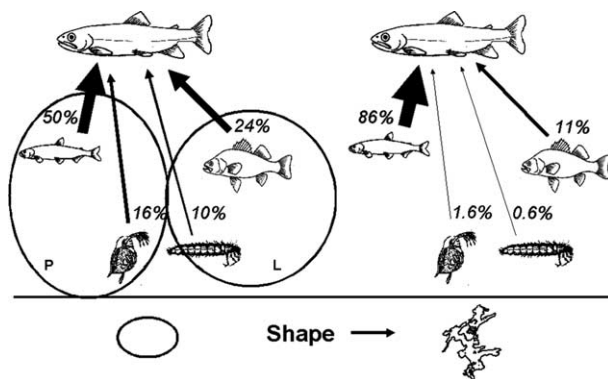


Figure 3. Lake trout foraging between a circular (Dev index = 1.74) and reticulate (Dev index = 5.73) lake. Lake trout in circular lakes couple the littoral and pelagic habitats more so than in reticulate lakes; lake trout littoral foraging amounted to 24% of total diet in a circular lake, compared to 11% in the reticulate lake. Lake trout in circular lakes also tended to be more omnivorous; zooplankton and benthic invertebrate foraging is ~10% higher in circular lakes. P=pelagic food chain, L=littoral food chain (Sketches courtesy of G. L. Mackie).

compared to reticulate lake (16 and 10% compared to 1.59 and 0.6%, respectively). Significance values and best fit estimates of Area, Dev index and REB are compared for all variables in Table 2a.

Omnivory

Lake trout consumption of zooplankton and benthic invertebrates tended to be lower as Dev index increased (Fig. 2c–d; $F_{1,5} = 2.85$ and 3.14 , and $p = 0.15$ and 0.14 , respectively). While the statistical support for the trend is modest, the result is consistent with the pattern observed for trophic position. The average trophic position of lake trout among lakes was positively and significantly related to Dev

index, indicating that lake trout omnivory decreased with Dev index (Fig. 4. $F_{1,5} = 6.71$, $p = 0.049$).

Lake size versus shape

In order to ensure that the above results were not merely a function of ecosystem size, we compared the predictive power of lake surface area and Dev index for the measured response variables. Lake shape was consistently chosen as the best model (compared to lake size) to explain all response variables of lake trout diet and trophic position as shown by Akaike's information criterion (delta AICc and weighted model estimates; Table 2b). Model fits using lake shape are also shown to be clearly superior to models using lake size in predicting these ecological characteristics (Table 2a).

Discussion

By using isotopic diet data to quantify the degree of littoral habitat coupling among seven lakes, we were able to discriminate between the littoral space hypothesis and the accessibility hypothesis. The data strongly suggest that lake trout littoral habitat coupling is determined by lake morphometry as predicted in the accessibility hypothesis counter to the predictions of the productive littoral space hypothesis. Specifically, lakes with a lower shoreline development index (e.g. more circular lakes) and small relative epilimnetic benthic habitat (REB) show greater coupling by lake trout to the littoral-based food chain (e.g. an increase in the consumption of littoral forage fish and benthos; Fig. 2). The positive relationship between REB and Dev index is critical; it indicates that in our lakes, the relative amount of epilimnetic benthic habitat increases and the degree of accessibility to littoral production tends to decrease as lakes become more reticulate in shape.

It is worth noting that the most productive area of a littoral zone is often found in less than 3 m depth in

Table 2. (a) Significance and best fit estimates for predictor variables Area, Dev index and REB and (b) a comparison of lake size (Area) and lake shape (Dev index) to predict the degree of littoral habitat coupling by lake trout using Akaike's information criterion (AIC). Isotopic diet data was used to estimate the proportion of each diet source in the mixing model Isosource (Phillips and Greg 2003). ω_i is Akaike's weighted estimate of the best model.

	ArcC	ArcFF	ArcZ	ArcB	Trophic position
(a)					
Area (km ²)					
p-value	0.81	0.87	0.9	0.75	0.13
R ²	0.01	0	0	0.02	0.55
Dev index					
p-value	0.03	0.06	0.15	0.14	0.05
R ²	0.66	0.54	0.36	0.39	0.57
REB					
p-value	0.018	0.26	0.017	0.01	0.36
R ²	0.71	0.24	0.72	0.76	0.17
(b)					
Independent variable					
Area (km ²)					
delta AICc	9.0	5.5	3.2	3.0	1.5
ω_i	0.01	0.06	0.17	0.16	0.32
Dev index					
delta AICc	0	0	0	0	0
ω_i	0.99	0.94	0.83	0.84	0.68

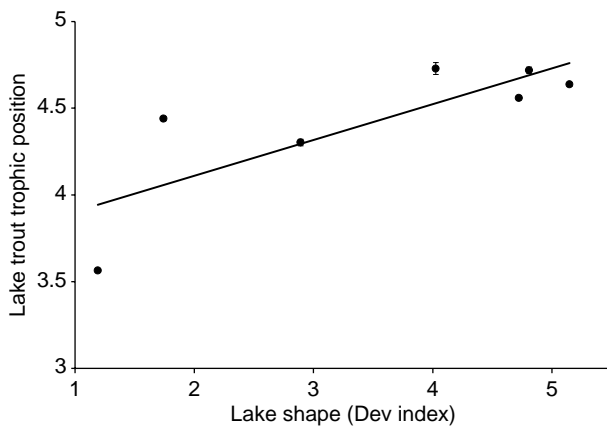


Figure 4. Among lake differences in average lake trout ($n = 8\text{--}10$ per lake) trophic position. Trophic position was calculated based on isotopic diet estimates using Isosource (Phillips and Greg 2003) and Eq. 4. Error bars show the standard error of the mean (and are sometimes obscured by the data point). Significance and r^2 values listed in Table 2a. The logarithmic linear transformation was performed to meet the criteria for a linear regression.

oligotrophic lakes (Keast and Harker 1977). As such, lakes with direct access to the littoral zone (e.g. circular lakes) ought to facilitate access to the most productive habitat of the littoral zone compared to lakes where this productive region would be further from optimal lake trout habitat.

Our results further indicate that lake morphometry influences the degree of littoral habitat coupling (via accessibility) more so than lake size alone (Table 2b). Previous studies (Post et al. 2000b, Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005) have suggested that habitat coupling strongly relates to an increase in lake size. On a broad scale, as lake size increases, lake complexity (shape) increases because there is a fractal relationship between these variables (Kent and Wong 1982). Since size correlates to more reticulate lake shapes with larger littoral zones, then larger lakes ought to dramatically reduce the accessibility of littoral zones to thermally restricted predators. Thus, it is not surprising that in the aforementioned studies, lake size was shown to influence the degree of habitat coupling. Herein we demonstrate that lake shape can influence the accessibility of habitats by teasing apart the influence of lake size and shape in lakes where they are not correlated.

Accessibility, as predicted by lake shape, may be enhanced by physical limnological attributes. Cold hypolimnetic water intrusions into the littoral zone could facilitate increased littoral foraging by lake trout. Such intrusions occur in lakes as a result of either hypolimnetic water 'pile-up' or sustained thermocline oscillation due to prevailing strong winds (Kalff 2000). In lakes with a lower shoreline development index (e.g. circular lakes) and thus less littoral area (Kent and Wong 1982), these cold water intrusions may very well expose relatively more littoral area in these lakes compared to lakes with higher shoreline development index (e.g. reticulate lakes).

It has been hypothesized that changes in ecosystem productivity could alter food chain length and food web structure (Yodzis 1984, Jenkins et al. 1992, Kaunzinger and Morin 1998). Recently, Post et al. (2000b) found little evidence that productivity influenced food chain length in

freshwater systems, including lake trout lakes. The lakes investigated herein are all oligotrophic with negligible differences in total phosphorous. This suggests that a productivity-driven generalized diet seems unlikely to be influencing lake trout foraging. Thus, while lake productivity certainly plays a role in food web dynamics, it does not appear to clearly manifest itself at the higher trophic levels in our study lakes. Furthermore, there should be a clear tendency for higher littoral benthos production in reticulate lakes because depositional zones tend to occur above the thermocline more often than in circular lakes (Rasmussen and Rowan 1997). Our results illustrate that despite this tendency, lake trout are unable to exploit this potential increase in productivity in reticulate lakes as shown by a lower amount of littoral benthos in their diet compared to circular lakes. The increased benthic production of depositional zones in reticulate lakes may be largely unavailable to lake trout due to thermal inaccessibility (Fig. 2d).

Interestingly, we observed a weak negative trend between the average number of lake trout per lake, and body weight. These results may suggest that circular lakes harbor a larger amount of smaller, more omnivorous trout, while reticulate lakes may yield fewer, larger, less omnivorous trout. These observations, while weakly supported, suggest an interesting opportunity to evaluate changes in life history characteristics of an organism across critical ecosystem gradients.

Omnivory, lake size and lake shape

Recent theoretical work has argued that ecosystem size plays a fundamental role in governing the dynamics of ecosystems. Specifically, McCann et al. (2005) notes that mobile generalist predators experience increased interaction strengths and an increased ability to couple relatively discrete habitats in small ecosystems (McCann et al. 2005). An increase in interaction and coupling strength translates into greater top down pressure in smaller ecosystems such that top predators reduce their prey and, in doing so, release their prey's prey to flourish (e.g. the heightened habitat coupling drives an apparent trophic cascade). Theory suggests that such cascades enhance the profitability of omnivory since the amount of prey two trophic levels below increases relative to the predators' preferred prey. Consistent with these theoretical predictions, small lakes show a pronounced increase in omnivory relative to large lakes (Post et al. 2000b, McCann et al. 2005).

Here, we found that lake trout in circular lakes tended to show increased amounts of habitat coupling relative to more reticulate lakes. Following theory we would expect then that these strongly coupled circular lakes to display increased amounts of omnivory (McCann et al. 2005). Our results again were consistent with these predictions (Fig. 4). Nonetheless, other correlated mechanisms may be driving omnivory. Post et al. (2000b) have argued, for example, that reduced omnivory in large lakes may be due to increased heterogeneity and refugia for prey. The increase in refugia and heterogeneity lead to increased densities of preferred prey and so encourage specialization reducing omnivory. Clearly, this mechanism, or both mechanisms, may be operating in our reticulate lakes. Regardless, it is clear that ecosystem size is not solely driving our changing

food web length, a result that deviates from the interesting contributions of Post et al. (2000b). As a final note, the presence of the glacial relict predatory zooplankton, *Mysis relicta* in our study lakes does not appear to increase the trophic position of lake trout (see Class 3 lake description Vander Zanden and Rasmussen 1996).

Conclusions

Habitat coupling theory has allowed recent food web research to highlight the role of littoral and benthic habitats in lake structure and function (Vadeboncoeur et al. 2002, Sierszen et al. 2003, Babler et al. 2008). Specifically, many studies have investigated the influence of habitat coupling by mobile predators foraging on multiple energy channels (France 1995, Brett and Goldman 1996, Vander Zanden et al. 1999b, Polis et al. 2000, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Bertolo et al. 2005, Rooney et al. 2006). Yet the results are not consistent. Evidence for the coupling of littoral and pelagic habitats via predatory feeding is common (Vander Zanden et al. 1999b, Polis et al. 2000, Schindler and Scheuerell 2002), however, some have found little evidence for this coupling (France 1995, Bertolo et al. 2005). These differences may simply reflect that some species are habitat specialists (e.g. northern pike; *Esox lucius*) and some are habitat generalists (e.g. lake trout). Curiously however, little of this research has explored the intensity of the relationship between littoral and pelagic habitat across important gradients (e.g. lake size, shape).

Here, we have expanded on earlier results to show that the degree of habitat coupling by a mobile predator (lake trout) changes along a gradient of lake shape. Specifically, our results suggest that lake shape reflects the accessibility of the littoral habitat and so modifies the degree of littoral habitat coupling by lake trout. More circular lakes provide greater connections between the discontinuous littoral and pelagic food chains and facilitate littoral habitat coupling, particularly when a species exhibits a thermal restriction. In reticulate lakes, however, the littoral food chain is less accessible to lake trout. This is the first study to examine lake food web structure along a gradient of littoral habitat coupling by mobile predators. Given that the degree of habitat coupling influences food web stability and dynamics (Rooney et al. 2006), our empirical results suggest that lake shape, like size (McCann et al. 2005), may reflect a gradient in food web stability.

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Appendix 1. Untransformed dietary data output from the multi-end mixing model Isosource (Phillips and Gregg 2003).

Lake	%Cisco	%FF	%Zoo	%benth	TP calc
	Avg	Avg	Avg	Avg	
Gilmour	0.407	0.452	0.085	0.057	3.670081
	0.409	0.391	0.123	0.077	3.495599
	0.683	0.263	0.035	0.019	3.635687
	0.459	0.378	0.102	0.06	3.514376
	0.518	0.369	0.072	0.041	3.568241
	0.586	0.335	0.051	0.028	3.560581
	0.534	0.363	0.066	0.038	3.574447
Canoe	0.445	0.377	0.112	0.066	3.493934
	0.933	0.038	0.02	0.009	5.119523
	0.923	0.043	0.023	0.011	4.960149
	0.962	0.023	0.01	0.005	5.009878
	0.87	0.072	0.039	0.02	4.895684
	0.74	0.14	0.078	0.042	4.72477
	0.408	0.299	0.188	0.105	4.274988
ThreeMile	0.782	0.118	0.065	0.035	4.779279
	0.533	0.25	0.14	0.077	4.460229
	0.445	0.29	0.171	0.094	4.337983
	0.654	0.131	0.116	0.099	4.60072
	0.592	0.154	0.136	0.117	4.475704
	0.493	0.191	0.169	0.146	4.279451
	0.489	0.193	0.171	0.147	4.273209
Catfish	0.469	0.2	0.177	0.153	4.232807
	0.314	0.258	0.23	0.198	3.927409
	0.489	0.193	0.171	0.147	4.274705
	0.434	0.214	0.189	0.163	4.166115
	0.504	0.187	0.166	0.143	4.304289
	0.599	0.152	0.134	0.115	4.489736
	0.872	0.103	0.017	0.009	4.62048
White P	0.969	0.028	0.003	0	4.648195
	0.634	0.283	0.053	0.03	4.397493
	0.915	0.07	0.01	0.005	4.483275
	0.915	0.07	0.01	0.005	4.484182
	0.881	0.095	0.015	0.008	4.61702
	0.929	0.06	0.008	0.003	4.634691
	0.818	0.144	0.025	0.013	4.454703
Burntroot	0.836	0.13	0.002	0.011	4.697761
	0.52	0.231	0.15	0.099	4.50242
	0.437	0.27	0.176	0.117	4.367846
	0.485	0.248	0.161	0.107	4.449959
	0.565	0.209	0.136	0.009	4.397461
	0.469	0.255	0.16	0.11	4.405711
	0.495	0.243	0.158	0.105	4.463095
Hogan	0.671	0.159	0.103	0.068	4.74707
	0.446	0.266	0.173	0.115	4.381637
	0.457	0.261	0.17	0.113	4.405067
	0.385	0.285	0.198	0.132	4.276066
	0.822	0.112	0.045	0.021	4.764885
	0.608	0.241	0.101	0.05	4.570141
	0.491	0.305	0.137	0.069	4.456612
	0.664	0.207	0.087	0.042	4.623148
	0.796	0.127	0.052	0.025	4.741483
	0.701	0.185	0.077	0.037	4.656058
	0.743	0.159	0.066	0.032	4.693341
	0.715	0.176	0.073	0.036	4.667442
	0.602	0.244	0.103	0.051	4.566071
	0.554	0.277	0.118	0.051	4.684183
	0.494	0.306	0.139	0.06	4.618422
	0.71	0.182	0.076	0.032	4.813648
	0.68	0.201	0.084	0.035	4.788519
	0.835	0.106	0.043	0.017	4.919371
	0.556	0.276	0.117	0.05	4.685801
	0.429	0.322	0.172	0.076	4.518194