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[Article]

Nearshore Habitat and Fish Community Associations of Coaster Brook Trout in Isle Royale, Lake Superior

OWEN T. GORMAN* AND SETH A. MOORE[1]

U.S. Geological Survey, Lake Superior Biological Station, 2800 Lake Shore Drive East, Ashland, Wisconsin 54806, USA

ANDREW J. CARLSON[2]

Department of Biological Sciences, Michigan Technological University, 1400 Townsend Drive, Houghton, Michigan 49931, USA

HENRY R. QUINLAN

U.S. Fish and Wildlife Service, Ashland Fishery Resources Office, 2800 Lake Shore Drive East, Ashland, Wisconsin 54806, USA

Abstract.—We characterized the nearshore habitat and fish community composition of approximately 300 km of shoreline within and adjacent to the major embayments of Isle Royale, Lake Superior. Sampling yielded 17 species, of which 12 were widespread and represented a common element of the Lake Superior fish community, including cisco *Coregonus artedi*, lake whitefish *C. clupeaformis*, round whitefish *Prosopium cylindraceum*, lake trout *Salvelinus namaycush*, rainbow smelt *Osmerus mordax*, lake chub *Couesius plumbeus*, longnose sucker *Catostomus catostomus*, white sucker *C. commersonii*, trout-perch *Percopsis omiscomaycus*, ninespine stickleback *Pungitius pungitius*, burbot *Lota lota*, and slimy sculpin *Cottus cognatus*. The presence of brook trout *S. fontinalis* in an embayment was associated with the common species of the Isle Royale nearshore fish community, particularly cisco, longnose sucker, and round whitefish. However, brook trout were present in only five embayments and were common only in Tobin Harbor. Most Isle Royale embayments had broadly overlapping ranges of nearshore habitats. Within embayments, fish were distributed along a habitat gradient from less-protected rocky habitat near the mouth to highly protected habitat with mixed and finer substrates at the head. Embayments with brook trout had greater mean protection from the open lake, greater variation in depth, greater mean cover, and higher mean frequencies of large substrates (cobble, boulder, and bedrock). Within those embayments, brook trout were associated with habitat patches with higher mean frequencies of small substrates (particularly sand and coarse gravel). Within Tobin Harbor, brook trout were associated with midembayment habitat and species assemblages, especially those locations with a mixture of sand, gravel, and cobble substrates, an absence of bedrock, and the presence of round whitefish, white sucker, and trout-perch. Comparison of embayments with the model, Tobin Harbor, showed that six embayments without brook trout had very similar arrays of habitat. However, four embayments with brook trout had relatively different arrays of habitat from Tobin Harbor. These results suggest that there is potential for further recovery of brook trout populations across Isle Royale nearshore habitats.

Brook trout *Salvelinus fontinalis* are native to northern and eastern North America, once ranging from the Great Lakes, the upper Mississippi, eastern Canada and the Hudson Bay drainages into New England and south into the Appalachians and the Great Smoky Mountains (MacCrimmon and Campbell 1969; Scott and Crossman 1973). In marine coastal streams and rivers, some brook trout populations include individuals exhibiting an anadromous life history; these are called "salters." Transplanted populations of brook trout have been successfully established in rivers and streams in at least 10 western and southern states (Cowley 1987; Cummings 1987; De Staso and Rahel 1994; Heft 2006).

The brook trout's native range has been greatly diminished over the past 200 years as a result of massive ecosystem disruption in the wake of the European settlement of North America (Newman and DuBois 1997). Principal perturbations include large-scale clear-cut logging of eastern forests, disruption of natural drainages and stream channels, spread of

* Corresponding author: owen_gorman@usgs.gov
[1] Present address: Grand Portage Band of Lake Superior Chippewas, 27 Store Road, Grand Portage, Minnesota 55605, USA.
[2] Present address: Department of Zoology and Physiology, University of Wyoming, Department 3166, 1000 East University Avenue, Laramie, Wyoming 82071, USA.

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agriculture across large areas, and industrialization and urbanization of critical habitats near streams and lakes (Lenat 1984; Flebbe and Dolloff 1995; Flebbe 1999). Other consequences of European settlement include introduction of exotic salmonids and overfishing to the point of extirpation of many local populations (Mills et al. 1993). To compensate for the decline in native populations, management agencies stocked hatchery strains of brook trout throughout the northern and southern Appalachian region over the past 100 years or more (McCracken et al. 1993; Perkins et al. 1993). Remnant brook trout populations have been impacted by population bottlenecks and by hybridization with stocked hatchery strains in almost every region where brook trout are native (Krueger and Menzel 1979; Webster and Flick 1981; Danzmann et al. 1991; McCracken et al. 1993; Perkins et al. 1993; Kriegler et al. 1995). As a result, unspoiled native brook trout populations are now rare throughout the Appalachian region (Quattro et al. 1990; McCracken et al. 1993; Perkins et al. 1993; Kriegler et al. 1995). In the latter decades of the 20th century, a shift in management has emphasized the restoration of native brook trout populations (e.g., Kriegler et al. 1995).

Within the Lake Superior drainage basin, native brook trout populations are either stream resident or spend all or part of their life history in Lake Superior, the latter being referred to as the "coaster" brook trout life history variant (Becker 1983). Before European settlement in the second half of the 19th century, coaster brook trout were relatively abundant along coastal areas of Lake Superior and supported a world-class fishery. By 1900, after widespread settlement, habitat disturbance, and intense fishing pressure, coaster brook trout were reduced to a few scattered populations (Newman and DuBois 1997). At the present time, coaster brook trout populations are known to exist only in a few locations in Canada and at Isle Royale (Newman and DuBois 1997), and these dwindling populations may be approaching extirpation. Three remnant coaster brook trout stocks have been identified within Isle Royale and these populations have relatively few reproductive fish; the largest, found in Tobin Harbor, has approximately 200 adults (H. R. Quinlan, unpublished data). Previous sampling conducted on Isle Royale indicates that brook trout aggregate around presumptive spawning areas in embayments or near the mouths of streams in the fall. The presence of ripe fish at these locations has enabled managers to collect gametes for broodstock development (Quinlan, personal observation).

Habitat has been defined as the abiotic feature of the spatial environment of an organism needed for life, exclusive of food, predators, and competitors (i.e., physical habitat; Orth and White 1999), but it may include a combination of biotic and abiotic factors that define the place where a fish lives (i.e., physical and biological habitat; Hudson et al. 1992; Hayes et al. 1996). Detailed knowledge of the habitat associations of remnant populations of brook trout in Lake Superior is lacking (Schreiner et al., in press), and that deficiency hampers efforts to develop management actions to protect and restore brook trout populations in Lake Superior.

Isle Royale, a remote large island in Lake Superior and a national park, has a complex shoreline incorporating many embayments, some of which harbor brook trout populations (Newman and DuBois 1997). As such, Isle Royale provides the opportunity to investigate habitat and fish community associations for coaster brook trout. These investigations would also identify additional embayments in Isle Royale where brook trout populations might be reestablished. In response to the need to develop a knowledge base of habitat and fish community associations for coaster brook trout and the opportunity to fulfill this need by focusing on Isle Royale embayments, we addressed the following objectives:

(1) Describe nearshore aquatic habitats across all major Isle Royale embayments.
(2) Describe large-scale patterns of habitat and fish community associations among Isle Royale embayments.
(3) Identify habitat and species associations specific to brook trout at large and small scales.
(4) Identify embayments that have the potential to support brook trout populations.

Methods

Field studies.—Research was conducted within embayments and along adjacent shorelines of Isle Royale, an approximately 66-km-long island situated in upper central Lake Superior and oriented along a southwest-to-northeast axis from 47°50′N, 89°20′W to 48°11′N, 88°25′W (Figure 1). Field research was conducted at Isle Royale during early summer (mid-June) and early fall (early October) in 2001–2003. Based on previous experience by one of us (H.R.Q.), the timing of early fall sampling was before the brook trout spawning period in Isle Royale. During mid-June of 2001, 2002, and 2003, we conducted standardized surveys of Tobin Harbor, which included single-pass nighttime electrofishing of the harbor shoreline and setting fyke nets at 20 locations. During early October 2001, 2002, and 2003, we conducted single-pass nighttime electrofishing along shorelines inside and

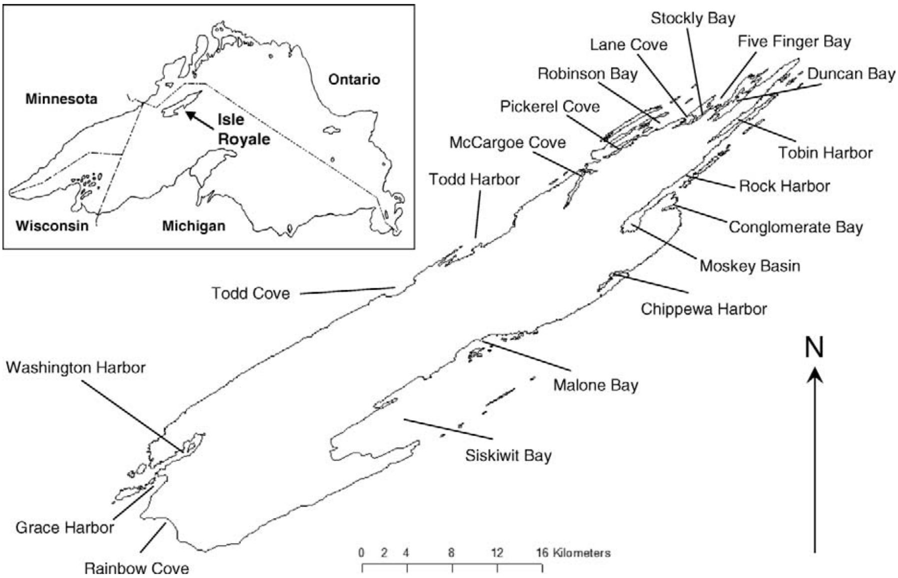

FIGURE 1.—Isle Royale, Lake Superior. Shown are embayments and subembayments where brook trout were sampled in 2001–2003.

adjacent to the following 18 embayments and subembayments: Duncan Bay, Five Finger Bay (including Stockly Bay), Robinson Bay, Lane Cove, Pickerel Cove, McCargoe Cove, Todd Harbor (including Todd Cove), Washington Harbor (including Grace Harbor), Rainbow Cove, Siskiwit Bay (including Malone Bay), Chippewa Harbor, Conglomerate Bay, and Rock Harbor (including Moskey Basin). Shoreline habitat in Tobin Harbor was surveyed in June 2002 and was surveyed in other areas in conjunction with October electrofishing. The rationale for more intensive summer sampling in Tobin Harbor was to describe small-scale habitat and fish community associations outside of the fall spawning season. Sampling of other embayments during the fall prespawning period was intended to describe large-scale habitat and fish community associations. Fall sampling increased the likelihood of capturing brook trout in an embayment, as fish aggregated near spawning areas at this time, and these aggregations have been targets for collecting gametes in Isle Royale for broodstock development (Quinlan, personal observation).

In Tobin Harbor and all other areas surveyed in Isle Royale, single-pass nighttime electrofishing was conducted to include the entire perimeter of an embayment and adjacent Lake Superior shorelines near the mouth and effectively sample fish in a zone 0–6 m from shore to a maximum depth of about 3 m. We used a pulsed-DC electrofisher (Smith-Root Model GPP) mounted to a 6.1-m-long aluminum hull vessel equipped with two boom anodes holding 10 droppers each; the boat hull functioned as the cathode. Output voltage was adjusted to maintain 2–4 A at settings of 60 or 120 pulses/s. Fish observations and captures were tallied for every interval between habitat sampling grids (0.4 km in Tobin Harbor and 1.0 km in other areas). We attempted to capture all brook trout observed but only took vouchers of other species. For each fish sampling interval, we estimated relative abundances by visual observation as absent, rare ($n = 1$–3), common ($n = 4$–20), or abundant ($n > 20$). Our assessment of relative abundance of other species by visual observation was possible because of the high clarity of the water and the experience of the observers. Thus, specimens captured by electrofishing represented a subset of the fish observations for each sampling interval.

In Tobin Harbor, fyke nets (1.2-m $\times$ 1.8-m opening, 12-mm mesh) were set in a stratified-random manner at locations of habitat sampling grids around the perimeter of the embayment. Sampling locations ($N = 43$) were numbered and divided between the northern ($N = 22$) and southern ($N = 21$) sides of the embayment. With the aid of a random number table, 10 locations were selected for each side of the embayment. On the first day of sampling, nets were set at the first five randomly chosen locations for each side. We set nets as close as possible to locations of habitat sampling grids. Each fyke net was set with the lead tied to shore and stretched perpendicularly out to a distance of 10–15 m. Depending on water depth and shoreline conditions, each fyke net sampled fish from a zone between 0 and 10–15 m from shore with a maximum depth of 3–4 m. After 24 h, we lifted and reset nets at the next five randomly chosen locations so that 20 locations were sampled in 2 d of sampling (10 on each side of the embayment). For each net location, we recorded date, latitude and longitude, surface water temperature, maximum water depth, and times of set and lift. For each year of sampling (2001, 2002, 2003), a new set of sampling locations was selected with the use of the above stratified-random design.

All brook trout captured in fyke nets and by electrofishing were measured to the nearest millimeter total length (TL); weighed to the nearest gram; sampled for scales; examined for fin clips, tags, scars, marks, and deformities; and then tagged, photographed, and released near the point of capture. Up to 25 of each species captured in fyke nets were enumerated and measured to the nearest millimeter TL.

Habitat measures were collected following methods described in Gorman and Karr (1978) and Gorman and Stone (1999). To summarize, we used a point-based sampling method whereby data were collected at intersections of 2-m × 2-m cells within a grid 20 m long and 4 m wide that was oriented perpendicular to shore. In Tobin Harbor, habitat sampling grids were spaced at 0.4-km intervals, whereas grids were spaced at 1.0-km intervals in other embayments and along adjacent shorelines exposed directly to Lake Superior. Grids were spaced at regular intervals around the perimeter of embayments to allow detection of a gradient in habitat characteristics from protected areas at the head to sites at the mouth that were exposed to the open lake. At each sample point, depth, substrate, and cover variables were recorded (Gorman and Stone 1999). Depth was measured to the nearest centimeter. Substrate type at each sample point was categorized according to a modified Wentworth scale (Gorman and Karr 1978): 0 = silt, 1 = fine or silty sand, 2 = coarse sand, 3 = small gravel, 4 = large gravel, 5 = small cobble, 6 = large cobble, 7 = small boulder, 8 = large boulder, and 9 = bedrock. At each point, substrate contacting or overlapping a 5-cm radius was inspected; the dominant substrate type had the greatest areal coverage within the 5-cm radius, and subdominant substrate types were listed in order of decreasing areal coverage (Gorman and Stone 1999). Categories of organic secondary substrates included submerged vegetation, woody debris, detritus, algae, roots, leaves, and emergent vegetation. A cover value for each sample point in the grid was generated from structural habitat features present (Gorman and Stone 1999). High-cover values were returned for points with high vertical structure (>50% change in slope within 1 m), emergent edge within 50 cm, submerged log (>20 cm diameter), overhead shade (>50% coverage), overhead ledge, and overhead log.

Analysis of data.—Tabulation of species presence and relative abundance allowed us to characterize fish community composition across the Isle Royale embayments. For each embayment, mean relative abundances were calculated for each species and reflected relative dominance. We then summed species mean relative abundances for each embayment to provide a measure of overall fish abundance. Across all embayments, the grand mean relative abundance for each species reflected that species' relative abundance in Isle Royale nearshore waters. We judged mean values of 0.25 or greater to indicate common species and values greater than 1.0 to indicate dominant species within and across embayments. The proportion of embayments where a species had a relative abundance of 0.25 or greater indicated that species' prevalence as widespread and common in Isle Royale nearshore waters.

Measurement of habitat features at points within grids permitted detection of other variables, including distance from shore, bottom slope, variation in bottom slope, variation in depth, and generation of frequency counts for substrates and cover types (Gorman and Stone 1999). Across the 30 sample points in each grid, we determined the mean and SD in depth (avDPH, stdDPH) and primary and secondary substrate size (avSUB1, avSUB2, stdSUB1, stdSUB2). For each grid, mean and SD in degrees of slope (avSLOPE, stdSLOPE) were calculated from changes in depth between each point along the three rows of sample points perpendicular to shore. Standard deviation in depth and slope provided indicators of bottom roughness and vertical structure. Overall slope for the grid (shoreline slope), expressed in degrees, was calculated from the distance to shore from the maximum depth of outermost points (maxSLOPE). Positive angular variation in the bottom, expressed in degrees, was calculated for each point in the grid from the greatest positive change in depth among adjacent points in the grid, or from an emergent edge 200 cm or less away. Adjacent points of decreased depth generated positive values (positive vertical angle; PVA). Mean PVA (avPVA) for each grid provided a measure of bottom variation. Frequency of occurrence of the 10 modified Wentworth substrate categories (Freq0 through Freq9) provided detailed information on substrate composition in each grid. Overall cover in a grid was reflected by the mean cover (avCVR).

To gauge the relative degree of protection of each grid from the influence of the open lake, we calculated an embayment exposure index (EEI) as the ratio of (1) the distance in kilometers from a grid location to the mouth of the bay to (2) the width at the mouth of the bay. Values less than 4 indicated grids that were relatively open to the lake (unprotected), values of 4–7 grids with intermediate protection, and values greater than 7 highly protected grids at the head of long, narrow embayments.

We used descriptive statistics, one-way analysis of variance, and two-sample *t*-tests that assuming unequal variances to discern univariate differences among habitat associations. Multivariate analyses were used to test hypotheses addressing the effects habitat and fish community associations have on brook trout presence at a large scale (between embayments) and a small scale (within embayment). Stepwise discriminant function analysis (DFA) was used to develop classification models that identified variables most useful for predicting the presence or absence of brook trout (Williams 1983; Gauch 1982). In a forward and backward stepwise analysis, we used $\alpha = 0.15$ to enter and remove variables; if the *P*-value of the model did not improve when a variable was added, it was removed. We included prior probabilities in the brook trout distribution so that we could evaluate our model based on the actual ratio of brook trout present. A matrix of cross-validation classification rates was generated to determine the level of correct classification of the a priori presence/absence groups based on variables entered in the model. We selected models with the highest overall cross-validation classification rate. Univariate means for each variable entered into the model were useful for showing how habitat variables differed in areas with and without brook trout. Principal components analysis (PCA) was used to summarize habitat and species associations among and within embayments. For PCAs used to assess the effect of brook trout presence/absence, the correlation matrix was used to assess patterns without reference to preassigned presence/absence groups. For descriptive statistics and multivariate analyses, JMP (SAS Institute 2003) and SYSTAT 11 (SYSTAT 2004) software were used.

Large-scale brook trout habitat associations.—The 19 embayments and subembayments sampled in this study included 7 where brook trout were present and 11 where they were absent (we were unable to sample fish in 1 embayment, Chippewa Harbor). To judge the large-scale habitat effects on brook trout presence or absence, we scored all fish sampling intervals in an embayment as brook trout present if brook trout were captured within any fish sampling interval in that embayment or were known to occur there, and habitat characteristics were summarized by sample grid. We then used DFA to identify habitat variables that were most useful for predicting the presence or absence of brook trout in an embayment. This approach identified the large-scale (macrohabitat) features of embayments that were associated with the presence or absence of brook trout. To summarize brook trout habitat associations among embayments, we conducted a PCA of mean habitat variables for 14 embayments (including 5 subembayments) and a posteriori identified embayments as brook trout present or absent. In essence, we used PCA to graphically describe differences among embayments based on habitat variables.

Large-scale brook trout and fish community associations.—To determine those species that were associated with brook trout presence across the embayments, we scored all sampling intervals in an embayment as having brook trout present if brook trout were captured at any interval in that embayment or were known to occur there. We then used species presence/absence data by sampling interval as independent variables in a stepwise DFA to identify fish species associated with brook trout presence in an embayment. To summarize brook trout community associations among embayments, we conducted a PCA of mean abundances for 13 embayments (including 5 subembayments) where fish were sampled and a posteriori identified embayments as brook trout present or absent. In essence, we used PCA to graphically describe differences among embayments based on community composition.

Large-scale community and habitat associations.—To evaluate large-scale habitat and species associations independent of brook trout presence, we performed a PCA of mean habitat variables for the 17 species listed in Table 1 across all embayments. Mean habitat variables were calculated by averaging the values for habitat variables listed in Table 2 over the sampling intervals where each species was present across all embayments. In essence, this PCA described the relative segregation among species of the nearshore fish community by habitat associations across all embayments.

Small-scale brook trout habitat associations.—The higher density of sampling intervals and higher relative abundance of brook trout in Tobin Harbor provided the opportunity to investigate small-scale habitat associations. We used stepwise DFA to identify habitat variables that were most useful for predicting the presence or absence of brook trout by sampling interval. We then used PCA to summarize those habitat variables that were associated with brook trout presence and absence in Tobin Harbor.

Small-scale brook trout and fish community associations.—The Tobin Harbor data set allowed analysis of brook trout species associations at the within-embayment scale. We used species presence/absence data by sampling interval from Tobin Harbor in a stepwise

TABLE 1.—Fish community composition and relative abundances of species captured in major embayments of Isle Royale, 2001–2003. Species relative abundance by sampling interval was recorded as absent ($n = 0$), few ($n = 1$–3), common ($n = 4$–20), or abundant ($n > 20$). Represented are mean relative abundances; values 0.25 and greater reflect common species and values greater than 1.0 reflect dominant species within and between embayments. Row means reflect species relative abundance across all embayments, and prevalence is the proportion of embayments where a species had a relative abundance of 0.25 or more. Column sums reflect the relative abundances of all fish species in an embayment. Species are burbot *Lota lota* (BUR), coaster brook trout (CBT), coho salmon *Oncorhynchus kisutch* (COS), cisco *Coregonus artedi* (LAH), lake chub *Couesius plumbeus* (LCH), lake trout *Salvelinus namaycus* (LKT), longnose sucker *Catostomus catostomus* (LNS), lake whitefish *Coregonus clupeaformis* (LWF), northern pike *Esox lucius* (NOP), ninespine stickleback *Pungitius pungitius* (NSS), rainbow trout *O. mykiss* (RBW), round whitefish *Prosopium cylindraceum* (RWF), rainbow smelt *Osmerus mordax* (SMT), slimy sculpin *Cottus cognatus* (SSC), trout-perch *Percopsis omiscomaycus* (TRP), white sucker *Catostomus commersonii* (WHS), and yellow perch *Perca flavescens* (YEP). Values in bold italics indicate relative abundances >0.25.

	Embayment														
Species	Conglom-erate	Duncan	Five Finger	Lane	Mc-Cargoe	Pickerel	Rain-bow	Rob-inson	Rock	Siskiwit	Tobin	Todd	Wash-ington	Mean	Preva-lence
BUR	0	***2.05***	***2.82***	***1.82***	0.11	***1.63***	***1.00***	***1.61***	***0.74***	***1.5***	0.19	***2.23***	***1.69***	***1.33***	***0.77***
CBT	0	0	0	0	0	0	0	0	0.03	0.05	***0.50***	0.03	0	0.02	0.08
COS	0	0	0	0	0	0.13	0	0.11	0.08	0.02	0	0.17	0.16	0.05	0.00
LAH	***0.5***	***0.91***	***0.41***	0	0	***0.25***	0	0	**0.54**	0.12	***0.38***	***0.27***	0.06	***0.25***	***0.62***
LCH	***1.00***	***2.86***	***2.65***	***2.09***	***1.67***	***2.13***	***0.33***	***2.17***	***1.36***	***0.95***	***1.35***	***2.57***	***2.03***	***1.74***	***1.00***
LKT	0.17	***0.95***	***1.18***	***0.55***	0.11	0	***0.33***	***0.39***	***0.59***	0	0.04	***1.83***	***0.28***	***0.5***	***0.62***
LNS	***0.33***	0	0.18	***0.27***	0	0	0	0.06	***0.46***	0.05	***0.53***	***1.5***	***0.31***	***0.28***	***0.46***
LWF	0	0.09	***0.76***	0.18	***0.83***	***0.38***	***0.67***	***0.33***	0.23	***0.62***	0.70	***0.8***	***0.28***	***0.43***	***0.62***
NOP	0	***1.23***	***0.29***	0	***1.11***	0.13	0	0	0	0.05	0	0	0	0.22	0.23
NSS	0	***0.59***	***0.59***	0.09	***0.39***	***0.5***	0	0	0.08	0	0.09	0.2	0	0.19	***0.31***
RBW	0	0	0	0	0	0	0	0.06	0.1	0.05	0.00	***0.27***	***0.72***	0.09	0.15
RWF	0	0	0.12	***0.64***	***0.56***	0.13	***1.00***	***0.67***	***1.85***	***0.86***	***0.55***	***1.47***	***1.47***	***0.71***	***0.69***
SMT	0	***1.41***	***0.47***	0.09	***0.28***	0.13	0	0	***0.36***	0.21	***0.29***	0	0	***0.25***	***0.38***
SSC	***0.33***	***2.73***	***2.76***	***1.82***	***1.5***	***1.63***	***1.00***	***1.56***	***1.32***	***1.43***	***0.81***	***1.3***	***0.59***	***1.41***	***1.00***
TRP	0	***0.95***	***0.76***	0.18	***0.72***	0.13	0	0.06	0.13	0	***1.15***	0.17	***0.91***	***0.36***	***0.38***
WHS	0	***0.77***	***0.88***	0	***1.28***	***1.25***	0	0.17	0.05	***0.5***	***1.60***	***0.9***	***1.03***	***0.63***	***0.62***
YEP	0	0.23	0.06	0	***0.78***	0	0	0	0	0	0	0	0	0.08	0.08
Sum	2.33	***14.77***	***13.93***	7.73	***9.34***	8.42	4.33	7.19	7.92	6.41	8.17	***13.71***	***9.53***	8.54	
No. of species	5	12	14	10	12	12	6	11	15	13	14	14	12		

DFA to identify fish species (independent variables) associated with brook trout presence and absence.

Small-scale community and habitat associations.—To evaluate small-scale habitat and species associations independent of brook trout presence, we conducted a PCA using mean habitat variables for 11 species present at 4 or more of 43 sampling intervals in Tobin Harbor. Mean habitat variables were calculated by averaging the values for the habitat variables listed in Table 2 over the sampling intervals where each species was present. This analysis described the relative segregation of nearshore species by habitat associations within Tobin Harbor.

Results

Description and Distribution of Habitats of the Nearshore Zone of Isle Royale

Habitat surveys and fish sampling were completed in 13 embayments (including 5 subembayments) and the adjacent Lake Superior shoreline around Isle Royale (Figure 1; Table 2). We were only able to survey habitat in Chippewa Harbor because sea conditions prevented transport of the electrofishing vessel to this remote area. Of the embayments sampled, brook trout are known to be present in Tobin Harbor, Rock Harbor, Siskiwit Bay, and Washington Harbor (Quinlan, unpublished). With the exception of Washington Harbor, we found brook trout to be present in these embayments and also in Todd Harbor.

We characterized the nearshore habitat from 307 habitat sample grids distributed across approximately 300 km of shoreline within 14 embayments (including 5 subembayments) and adjacent Lake Superior shoreline around the perimeter of Isle Royale (Table 2). The average slope calculated across the first 20 m perpendicular from shore ranged from 0.1° to 45.0° and averaged 7.2° for the 307 sample grids. Mean depth for the 307 habitat sample grids was 1.28 m with a SD of 0.98 m. Variation in depth within grids (as reflected by mean SD of depth for 307 grids) was 0.68 m, which is less than among grids (0.98 m).

In low-slope areas (<9°), there was a bimodal distribution of substrate types present; the dominant substrate types were sand (present at 19.8% of the

TABLE 2.—Summary of habitat characteristics of the major embayments of Isle Royale, 2001–2003. Values expressed are grand means of habitat measures for habitat grids from embayments. Embayment exposure index (EEI) grand means of 2.0 or less indicate that a large proportion of habitat is relatively exposed to the open lake and values greater than 4.0 indicate that most habitat is relatively well protected. For the point measure of relative cover (CVR, nearby vertical structure, overhanging banks, logs, trees, etc.), values less than 1.0 indicate low cover and values greater than 2.0 indicate high cover. The mean positive vertical angle is indicated as avPVA, avSLOPE and stdSLOPE are the mean and SD of degrees in slope between habitat sample points perpendicular to shore, avDPH, maxDPH, and stdDPH are the mean, maximum, and SD of depth in centimeters, and SUB1 and SUB2 are primary and secondary substrate size following a modified Wentworth scale (Freq; 1–9). Five Finger Bay includes Stockly Bay, Rock Harbor includes Moskey Basin, Siskiwit Bay includes Malone Bay, Todd Harbor includes Todd Cove, and Washington Harbor includes Grace Harbor.

	Embayment													
Variable	Chippewa	Conglomerate	Duncan	Five Finger	Lane	McCargoe	Pickerel	Rainbow	Robinson	Rock	Siskiwit	Tobin	Todd	Washington
grids	9	6	22	17	11	18	8	3	18	39	42	43	30	32
EEI	4.5	0.67	6.23	0.73	2.71	5.97	5.25	0.19	4.01	11.47	2.74	4.99	1.34	2.56
avCVR	3.68	4.02	1.1	1.6	0.8	1.08	1.79	1.67	1.41	1.61	2.81	0.76	2.6	2.07
maxSLOPE	15.13	5.10	8.82	9.39	10.28	110.94	14.38	7.61	11.59	6.62	3.11	9.95	6.75	8.31
avPVA	15.19	7.42	8.48	10.02	9.8	10.56	14.3	12.51	11.52	8.01	4.06	10.15	9.98	8.89
avSLOPE	16.72	3.63	6.89	7.82	8.71	7.64	11.36	5.19	9.36	5.34	3.11	8.52	6.57	6.93
stdSLOPE	12.49	2.27	3.85	6.85	6.36	5.83	8.51	6.48	5.16	4.39	2.21	5.19	4.63	5.32
avDPH	288.76	77.87	129	156.39	118.69	137.15	112.75	91.94	112.92	98.39	56.98	166.95	120.81	130.06
maxDPH	515.56	153.5	277.91	318.71	243.18	289.72	284.38	242.67	253.83	203.9	101.71	326.19	220.8	276.63
stdDPH	161.51	39.62	80.9	99.73	75.58	86.38	82.57	57.45	79.89	57.88	28.75	108.8	63.81	77.49
avSUB1	7.05	6.4	4.08	4.67	2.99	3.71	4.97	6.3	4.57	5.09	5.62	3.91	6.88	5.43
stdSUB1	1.27	0.9	1.41	1.21	1.24	1.48	1.74	0.43	1.4	1.23	1.29	1.54	0.94	0.91
avSUB2	5.27	5.59	3.18	2.94	2.64	4.17	3.16	5.53	3.76	5.08	4.81	4.4	6.28	5.34
stdSUB2	1.27	0.94	1.7	2.06	1.73	1.28	1.84	0.97	1.9	1.15	1.03	1.52	0.85	0.86
Freq1	0.22	0.00	7.41	5.41	4.00	7.39	5.00	0	2.39	0.97	2.36	3.72	1.30	1.50
Freq2	6.00	3.17	7.36	8.29	15.64	10.67	6.25	1.67	5.83	10.92	6.52	16.07	3.37	7.69
Freq3	1.33	4.83	8.50	3.41	6.00	8.44	2.88	6.67	2.72	6.31	3.62	2.09	2.73	3.47
Freq4	3.67	5.67	6.05	4.06	4.73	2.39	3.75	10.33	6.17	6.03	7.86	5.56	3.23	6.25
Freq5	2.22	11.50	7.45	9.53	6.09	3.33	9.25	7.67	10.72	9.21	11.21	7.23	7.30	9.22
Freq6	1.78	19.17	4.50	9.65	3.73	3.72	7.38	10.33	8.83	8.67	10.81	4.09	11.50	11.41
Freq7	3.00	9.50	3.09	5.82	1.55	3.72	4.00	4.00	3.50	6.26	4.69	2.16	11.20	11.19
Freq8	1.67	0.33	0.14	0.06	0.09	0.78	0.13	1.33	0.06	2.26	0.29	0.47	9.47	2.84
Freq9	18.22	6.50	4.14	3.47	0.27	3.39	2.00	10.00	1.83	6.15	8.48	4.26	11.10	2.13

points in the grid) and small boulders (21.1%). In high-slope areas (>9°), the dominant substrates included gravel–cobble (32.3%) and boulder–bedrock (31.3%). Subdominant substrates in both high- and low-slope areas were boulder–cobble (48% and 45.9%, respectively). Substrate variability across all habitat sample grids was 2.25 Wentworth classification units. For example, mean substrate size classified as sand (classification unit = 2) typically varied from silty sand (1) to gravel (3). The mean within-sample grid substrate-size variability across the 307 grids was 0.68 Wentworth units, much lower than the among-location variability. This result indicates that substrates within grids were more similar than among grids.

Only 5% of the 307 habitat sample grids contained organic secondary substrate; the most common type was woody debris, which was found in 60% of the grids that had organic substrate present. Detritus, submerged vegetation, and algae were also common organic substrates. High-cover values were recorded for 2.7% of the sample grids, and the most common type of cover was vertical structure, which occurred in 44.4% of the sites with cover present. Other common cover types included emergent edge (14.5%), submerged logs (9.8%), and overhead shading (8.0%).

Nearshore Fish Assemblages

Across the nearshore waters of 13 embayments and 5 subembayments sampled for fish, we captured 17 species, of which 12 were widespread and relatively common (Table 1). Dominant and widespread nearshore species (mean relative abundance and prevalence >0.25) included burbot, cisco, lake chub, lake trout, longnose sucker, round whitefish, lake whitefish, ninespine stickleback, rainbow smelt, slimy sculpin, trout-perch, and white sucker. Of these species, burbot, lake chub, and slimy sculpin were the most abundant and widespread. Higher relative abundances of fish were encountered in Duncan, Five Finger, McCargoe, Todd, and Washington embayments. The species with restricted distributions (i.e., found in five or fewer embayments) included brook trout, rainbow trout, northern pike, and yellow perch. Rainbow trout was a common species in Washington and Todd harbors.

TABLE 3.—Large-scale and small-scale habitat characteristics of embayments in Isle Royale with and without brook trout 2001–2003. Large-scale date include data from 298 habitat grids distributed across 17 embayments sampled in Isle Royale for habitat. The presence of brook trout in an embayment was determined by capture during this study and from recent historical records. Small-scale data include data from 43 habitat sample grids in Tobin Harbor. The *F*-ratios and probabilities are for one-way analysis of variance testing the effect of presence of brook trout. Significant differences ($P < 0.05$) are indicated by asterisks; nearly significant differences ($P < 0.10$) are indicated by tildes. Refer to Table 2 for definitions.

	Large scale				Small scale			
Variable	Present	Absent	*F*	*P*	Present	Absent	*F*	*P*
EEI	***4.98***	***3.76***	***4.95***	***0.0269****	5.74	3.95	3.90	0.055~
avCVR	***1.87***	***1.46***	***7.06***	***0.0083****	***0.49***	***1.15***	***7.39***	***0.010****
maxSLOPE	***6.88***	***9.83***	***15.74***	***<0.0001****	9.47	10.62	0.36	0.553
avPVA	***8.10***	***10.12***	***7.77***	***0.0057****	9.35	11.25	1.03	0.317
avSLOPE	***6.07***	***7.79***	***7.61***	***0.0062****	8.27	8.86	0.11	0.739
stdSLOPE	***4.28***	***5.49***	***5.70***	***0.0177****	4.49	6.15	1.59	0.214
avDPH	114.54	124.32	1.05	0.3075	161.54	174.48	0.14	0.709
maxDPH	***225.53***	***267.23***	***4.05***	***0.045****	309.12	349.89	0.36	0.538
stdDPH	67.97	79.80	2.83	0.0938	104.23	115.14	0.20	0.658
avSUB1	***5.24***	***4.45***	***8.45***	***0.0039****	***3.08***	***5.06***	***13.44***	***0.001****
stdSUB1	1.23	1.31	0.92	0.3386	1.52	1.58	0.06	0.809
avSUB2	***5.07***	***3.65***	***51.74***	***<0.0001****	***4.03***	***4.90***	***4.14***	***0.049****
stdSUB2	***1.13***	***1.63***	***41.20***	***<0.0001****	1.41	1.68	1.82	0.185
Freq1	***2.13***	***4.77***	***8.70***	***0.0034****	***6.12***	***0.39***	***4.76***	***0.035****
Freq2	9.65	7.84	1.97	0.1614	***19.12***	***11.83***	***5.98***	***0.019****
Freq3	***3.56***	***5.79***	***7.93***	***0.0052****	2.68	1.28	3.96	0.053~
Freq4	5.73	5.29	0.40	0.5284	5.44	5.72	0.05	0.817
Freq5	8.83	8.06	0.69	0.4052	7.04	7.50	0.07	0.794
Freq6	8.79	7.55	1.50	0.2222	3.96	4.28	0.06	0.814
Freq7	***6.36***	***4.43***	***4.61***	***0.0327****	***1.04***	***3.72***	***3.41***	***0.072****
Freq8	***2.59***	***0.51***	***9.63***	***0.0021****	0.08	1.00	2.22	0.144
Freq9	***6.41***	***3.31***	***8.34***	***0.0042****	***2.04***	***7.33***	***7.28***	***0.010****
Number	186	112			25	18		

Coho salmon was relatively rare but widespread (found in six embayments). Brook trout were absent or rare in all embayments, except for Tobin Harbor, where 41 were captured across 25 of 43 sampling intervals. Brook trout captures in other embayments included 4 in four sampling intervals in Siskiwit Bay, 1 in Rock Harbor, and 1 in Todd Harbor.

Large-Scale Brook Trout Habitat Associations

Univariate comparisons of habitat in embayments with and without brook trout revealed significant differences (Table 3). We did not include Chippewa Harbor in these comparisons because no fish sampling was conducted there. Embayments with coaster brook trout were more protected (higher mean EEI), provided higher mean cover (avCVR), had larger primary and secondary substrates (avSUB1, avSUB2), and had higher frequencies of small and large boulders and bedrock (Freq7, Freq8, Freq9). Embayments with brook trout had lower measures of slope (maxSLOPE, avPVA, avSLOPE, stdSLOPE), smaller maximum depth (maxDPH), less variation in secondary substrate (stdSUB2), and lower frequencies of silty sand and gravel (Freq1, Freq3). Classification models detected differences in habitat among embayments with and without brook trout (ANOVA: $F = 19.13$; df = 13, 248; $P < 0.0001$). Variables selected by the DFA that best predicted the presence of brook trout were maxSLOPE, maxDPH, stdSUB2, Freq3, Freq8 (all negative), and EEI, stdDPH, avSUB1, avSUB2, Freq1, Freq2, Freq4 (all positive). Predictive modeling averaged an overall cross-validation classification rate of 91% for the 13 Isle Royale embayments and 5 subembayments where we sampled habitat and fish. Brook trout presence was classified at a rate of 91% correctly and absence was classified at 79% correctly. Overall, brook trout were present in embayments with greater protection from the open lake, larger primary and secondary substrates, greater variation in depth, greater cover, and increased frequencies of silty sand, sand, and coarse gravel substrates. The lower percent absence classification suggests that habitat in some embayments without brook trout was similar to habitat in embayments with brook trout.

To summarize the large-scale habitat differences among embayments, we conducted a PCA of mean habitat variables from Table 2. This was intended to provide a graphical presentation of unweighted habitat measures and identify those variables that contrast differences among embayments, particularly in regard to the presence/absence of brook trout (Figure 2). In this analysis, we included Chippewa Harbor to

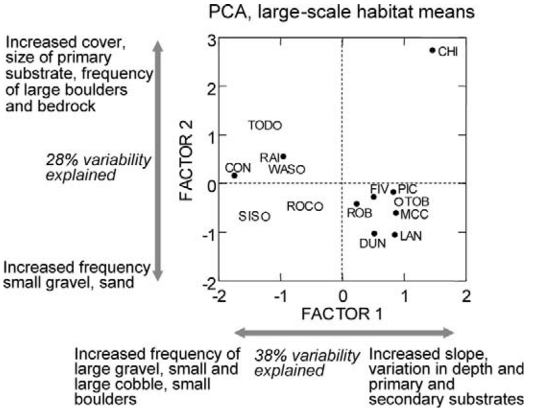

FIGURE 2.—Principal components analysis (PCA) of large-scale habitat characteristics among Isle Royale embayments based on mean habitat variables, 2001–2003. Labels for embayments are as follows: Chippewa Harbor (CHI), Conglomerate Bay (CON), Duncan Bay (DUN), Five Finger Bay (FIV), Lane Cove (LAN), Pickerel Cove (PIC), McCargoe Cove (MCC), Rainbow Cove (RAI), Robinson Bay (ROB), Rock Harbor (ROC), Siskiwit Bay (SIS), Tobin Harbor (TOB), Todd Harbor (TOD), and Washington Harbor (WAS). Open circles denote embayments where brook trout are present.

compare its habitat profile with other Isle Royale embayments. Of the five embayments where there was evidence of brook trout presence, the first principal components (PC) axis failed to resolve differences, and although the second PC axis provided some separation, that difference was driven by the unusually high amount of bedrock found in Chippewa Harbor. These results suggest that most of the Isle Royale embayments examined contain overlapping ranges of near-shore habitats that include specific habitats associated with brook trout presence, as shown in the univariate analysis and classification modeling above. Because Tobin Harbor contains the metapopulation of brook trout in Isle Royale, more weight should be given to its position relative to other embayments. Six embayments from the northeastern end of Isle Royale where brook trout were not found in our surveys were clustered with Tobin Harbor (Figure 1). This result suggests that these embayments (Duncan Bay, Five Finger Bay, McCargoe Cove, Lane Cove, Pickerel Cove, Robinson Bay) contain ranges of habitat that overlap considerably with those in Tobin Harbor.

Large-Scale Brook Trout and Fish Community Associations

Of the 16 other species captured in Isle Royale embayments, 9 species showed significant associations with the presence or absence of brook trout (Table 4). Increased presence of rainbow trout and round whitefish was associated with the presence of brook trout, while increased presence of burbot, lake chub, lake trout, northern pike, ninespine stickleback, slimy sculpin, and yellow perch were associated with brook trout absence (*t*-test with unequal variances: $P \leq 0.0001$). Classification models detected differences in fish community composition among embayments with and without brook trout (ANOVA: $F = 17.07$; df $= 11, 276$; $P < 0.0001$). Of the 16 other species detected in electrofishing sampling, brook trout presence in an embayment was best predicted by increased frequency of occurrence of cisco, longnose sucker, rainbow trout, round whitefish, rainbow smelt, white sucker, and decreased frequency of occurrence of lake chub, lake trout, northern pike, ninespine stickleback, and slimy sculpin. Validation of the model gave 78% correct classification rates for the distribution of brook trout, 83% for brook trout presence and 73% for absence. This pattern of association suggests that brook trout were not associated with species more commonly found in highly exposed habitat near the mouth of embayments (lake chub, lake trout) nor were they associated with species more commonly encountered in the highly protected head of embayments (northern pike, ninespine stickleback). The positive association of brook trout with coregonids, longnose and white suckers, and rainbow smelt is probably a reflection that all of these species are more commonly encountered in midembayment habitats.

A classification model based on species with overall mean abundance and prevalence of 0.25 or more (Table 1) was developed to investigate the associations with common, widespread species and also revealed significant differences in composition among embayments with and without brook trout (ANOVA: $F = 22.58$; df $= 6, 281$; $P < 0.0001$). Brook trout presence was associated with the presence of cisco, longnose sucker, and round whitefish and the absence of lake chub, lake trout, and slimy sculpin. Validation of the model gave 74% correct classification rates for the distribution of brook trout, 81% for brook trout presence and 66% for absence. The lower percent absence classification suggests that brook trout were absent in some areas where significant predictor species were present.

To summarize the patterns of species associations by embayment, we conducted PCA with mean relative species abundances (unweighted measure of relative abundance) from Table 1. The first axis in a PCA including all 17 species provided some separation of embayments with and without brook trout, but most embayments with brook trout clustered to the left of PC space (Figure 3). Duncan Bay and Five Finger Bay, located in the northeastern end of Isle Royale, were

TABLE 4.—Large-scale and small-scale effects of brook trout presence on the relative abundance of fish species in Isle Royale embayments, 2001–2003. Large-scale data include data from 291 fish sampling intervals distributed across 17 embayments sampled in Isle Royale for fish and habitat. The presence of brook trout in an embayment was determined solely by capture during this study. Small-scale data include data from 43 sampling intervals in Tobin Harbor. Mean abundance was derived from records of relative abundance by sampling interval: absent ($n = 0$), rare ($n = 1$–3), common ($n = 4$–20), or abundant ($n > 20$). Small-scale comparisons were made only for species that were present in more than four sampling intervals. Statistics are for *t*-tests (assuming unequal variances) testing the effect of brook trout presence. Significant differences ($P < 0.05$) are indicated by asterisks; nearly significant differences ($P < 0.10$) are indicated by tildes. Refer to Table 1 for species abbreviations.

	Large-scale mean abundance				Small-scale mean abundance			
Species	Present	Absent	*t*	*P*	Present	Absent	*t*	*P*
BUR	***0.97***	***1.7***	***5.5***	***<0.0001****	0.2	0.056	1.03	0.31
COS	0.06	0.07	0.17	0.87				
LAH	0.23	0.3	0.95	0.34	0.24	0.11	0.79	0.43
LCH	***1.31***	***2.17***	***5.88***	***<0.0001****	0.7	1.08	1.05	0.30
LKT	***0.2***	***0.87***	***6.68***	***<0.0001****				
LNS	0.37	0.36	0.08	0.94	0.48	0.61	0.47	0.64
LWF	0.4	0.48	0.95	0.34	0.44	0.33	0.49	0.64
NOP	***0.13***	***0.4***	***5.38***	***<0.0001****				
NSS	***0.03***	***0.3***	***4.61***	***<0.0001****				
RBW	***0.21***	***0.03***	***4.27***	***<0.0001****				
RWF	***1.11***	***0.57***	***4.61***	***<0.0001****	0.52	0.28	0.85	0.40
SMT	0.22	0.35	1.7	0.09~	***0.48***	***0***	***2.75***	***0.01****
SSC	***0.93***	***1.79***	***6.4***	***<0.0001****	0.4	0.33	0.25	0.81
TRP	0.4	0.42	0.28	0.78	0.74	0.61	0.47	0.64
WHS	0.74	0.68	0.57	0.57	1.4	1.28	0.3	0.77
YEP	***0***	***0.15***	***3.28***	***0.001****				
Number	159	132			25	18		

positioned higher along factor 1, and Todd Harbor, located on the northern side of Isle Royale, was positioned high on factor 2. We interpreted this pattern to be driven by embayments with considerable shallow and weedy heads (Duncan Bay, Five Finger Bay) and accompanying common species, particularly ninespine stickleback, northern pike, and rainbow smelt. When a PCA was restricted to the dominant and prevalent species (listed in Table 1), embayments with brook trout clustered more tightly in the center of the PC space. Again, the assemblages of Duncan Bay and Five Finger Bay were relatively distinct from those where brook trout were present. Embayments without brook trout but with similar assemblage structure to those with brook trout included Lane Cove, McCargoe Cove, Pickerel Cove, and Robinson Bay. These embayments are clustered around Tobin Harbor, which contains the brook trout metapopulation and are all located in the northeastern end of Isle Royale (Figures 1, 3). These results suggest that at the embayment level, nearshore fish assemblages in many of Isle Royale's embayments are relatively similar (8 of 13 compared, including subembayments) and, of these, 4 contained brook trout. When results of PCA are compared with univariate analyses and classification models, brook trout presence appears to be broadly associated with the common species of the Isle Royale nearshore fish community but has more specific associations with a subset of that community, particularly fish assemblages in embayments containing an abundance of cisco, longnose sucker, and round whitefish.

Large-Scale Community and Habitat Associations

We used PCA to summarize the habitat associations for 17 species distributed across 13 embayments and 5 subembayments on Isle Royale (Figure 4). Along the first PC axis, species were separated along a gradient of high protection and fine substrates to low protection and large substrates, which coincided with the head-to-mouth embayment array of habitats. The second axis further separated species from shallow habitats with low slope to deeper habitats with high slope. Most of the common and prevalent species were clustered in the center of the PC space. Outliers ranged from yellow perch associated with areas of high protection, fine substrates, and shallow water (typically found at heads of embayments) to longnose sucker associated with areas of low protection, large substrates, deep water, and steep slopes (typically found at mouths of embayments). Brook trout clustered closely with species associated with habitat intermediate along PC axis 1, indicative of midembayment areas. Examination of separation along PC axis 3 showed that brook trout were more distinctly associated with sandy substrates than other species (Figure 4). Brook trout habitat associations were not a result of the dominance of

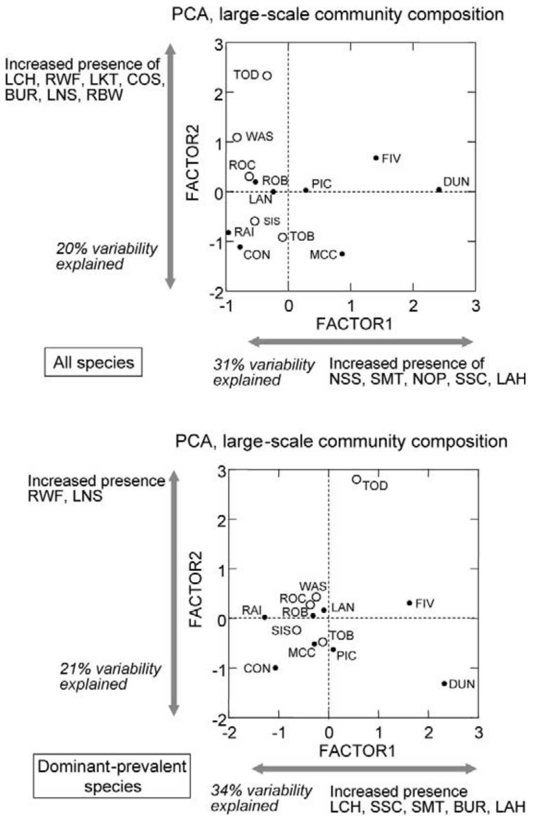

FIGURE 3.—Principal components analysis (PCA) of large-scale fish community composition among Isle Royale embayments based on the mean relative abundances of fishes, 2001–2003. Refer to Figure 2 for the embayment abbreviations and Table 1 for the species abbreviations. Open circles denote embayments where brook trout were present. The upper panel shows the results for all 17 species listed in Table 1 and the lower panel the results for the dominant–prevalent species, that is, those with a grand mean abundance and prevalence greater than 0.25 as listed in Table 1.

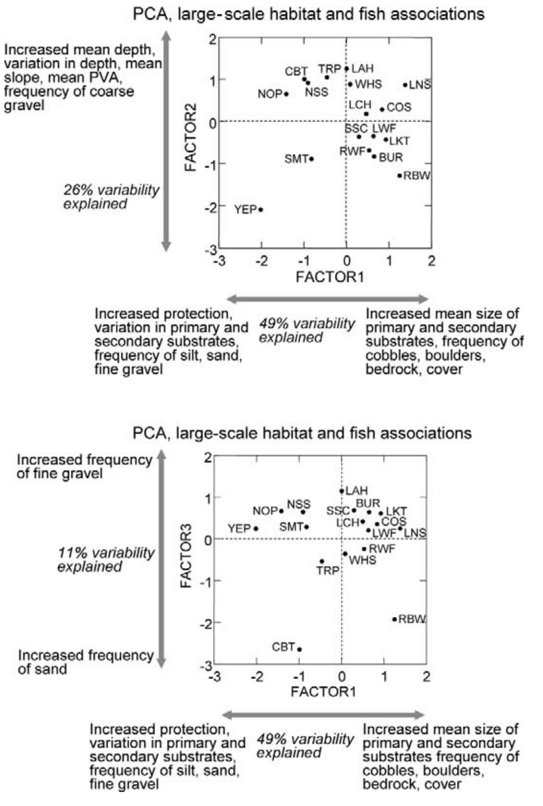

FIGURE 4.—Principal components analyses (PCAs) of large-scale habitat and fish associations across Isle Royale embayments based on mean habitat variables for the 17 species listed in Table 1, 2001–2003.

Tobin Harbor samples in calculation of habitat means; among the habitat variables listed in Table 2, Tobin Harbor brook trout differed significantly from other embayments only in maxDPH, avDPH, stdDPH, avSLOPE, stdSUB1, stdSUB2, and Freq1 (t-test with unequal variances; $P \leq 0.01$), whereas comparisons with other variables yielded higher P-values ($P > 0.10$). These differences would primarily affect the outcome of brook trout on PC axis 2, which provided little separation from other species. Overall, these results indicate that there was considerable overlap in habitat associations among species inhabiting Isle Royale embayments and corroborate classification models that addressed species associations conditioned by presence and absence of brook trout.

Small-Scale Brook Trout Habitat Associations

The Tobin Harbor data set allowed us to discern small-scale habitat associations for brook trout because of the relatively high density of habitat sampling grids (400-m versus 1-km intervals for the rest of the island) and the most brook trout captures of all embayments sampled. The sampling intervals where brook trout were present had significantly smaller mean primary and secondary substrates than intervals without brook trout and significantly higher mean frequencies of silty sand and sand substrates (Table 3). Intervals with brook trout had higher mean protection (EEI) and frequency of gravel substrate, though these comparisons had probabilities of less than 0.10. Sampling intervals without brook trout had significantly higher cover values and frequencies of bedrock.

Using DFA to develop a classification model based on all habitat variables, we detected differences in habitat among sampling intervals with and without brook trout in Tobin Harbor (ANOVA: $F = 7.20$; df $=$ 8, 34; $P < 0.0001$). The presence of brook trout in a

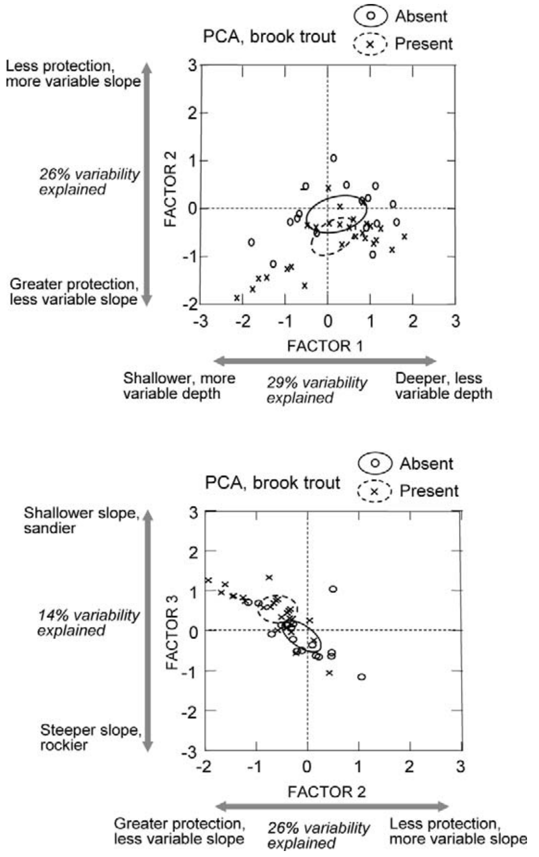

FIGURE 5.—Principal components analyses (PCAs) of small-scale habitat associations for brook trout from Tobin Harbor, 2001–2003. Each point represents a sampling interval and is denoted as brook trout present or absent. Shown are 95% confidence centroids for the bivariate means of presence and absence.

sampling interval was associated with increased frequency of silty sand (Freq1), gravel (Freq3), and large cobble (Freq6), and the absence was associated with increased slope (avSLOPE), cover (avCVR), variation in slope (stdSLOPE), frequency of small cobble (Freq5), and frequency of bedrock (Freq9). Predictive modeling averaged an overall cross-validation classification rate of 77%; brook trout presence was classified at a rate of 76% correctly and absence was classified 78% correctly.

We examined the frequencies of substrates separately to further discriminate habitat characteristics of locations in Tobin Harbor with or without brook trout. Classification models based on substrate frequencies identified differences associated with the presence and absence of brook trout among sampling intervals (ANOVA: $F = 6.33$; df = 4, 34; $P < 0.001$). Brook trout presence in a sampling interval was associated with increased frequency of gravel (Freq3) and decreased frequency of large gravel (Freq4), small boulders (Freq7), and bedrock (Freq9). Classification rates averaged 70% correctly; 72% correctly classified brook trout presence and 67% correctly classified brook trout absence. The lower percentage of brook trout absence classifications suggests that brook trout were not present in all suitable habitats, a likely outcome of low population size.

A PCA was used to summarize the variation in habitat characteristics among the 43 sample grids in Tobin Harbor and to identify principal habitat differences between intervals where brook trout were present and absent. The first three PC axes explained 69% of the total variation (Figure 5). Brook trout present and absent locations completely overlapped along the first PC axis, as indicated by positions of 95% confidence centroids. The second PC axis provided some separation of present and absent locations; brook trout were more often present at locations further from the mouth of the bay (greater protection or high EEI value). The third PC axis showed that brook trout were more often present at locations with lower slope and sandier substrates. Taken together, our univariate analyses, classification models, and PCAs of brook trout capture and habitat data from Tobin Harbor suggest that brook trout were present in locations with a wide range of depths and bottom roughness, but tended to occupy areas further away from the mouth of the embayment that were characterized by lower and less variable slope, presence of sandy gravel and cobble substrates, and the absence of bedrock.

Small-Scale Brook Trout and Fish Community Associations

Electrofishing and fyke-net capture data from Tobin Harbor were used to assess brook trout species associations at the within-embayment scale. Of 10 other species captured at more than 4 of the 43 sampling intervals in Tobin Harbor, only rainbow smelt showed a significant association with the presence of brook trout (Table 4; *t*-test with unequal variances: $P \leq 0.01$). Classification models developed with DFA detected differences in fish community composition among Tobin Harbor sample locations with and without brook trout (ANOVA: $F = 5.88$; df = 4, 36; $P = 0.001$). Using presence/absence data of the 10 other species captured at more than 4 of the 43 sampling locations in Tobin Harbor, brook trout presence was best predicted by presence of lake whitefish, slimy sculpin, and white sucker. Validation of the model classified presence/absence 78% correctly overall, 80% for brook trout presence and 75% for

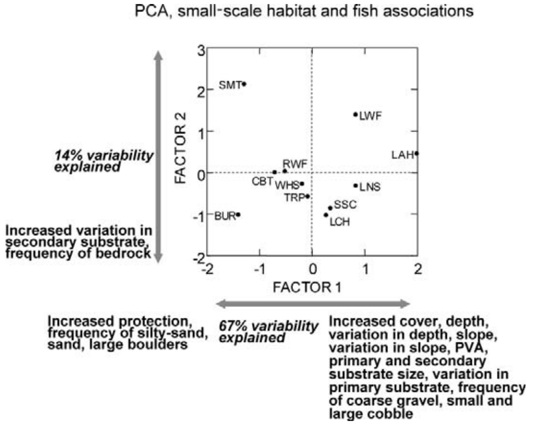

FIGURE 6.—Principal components analysis (PCA) of small-scale habitat and fish associations in Tobin Harbor based on mean habitat variables for 11 species present at 4 or more of the 43 sampling intervals, 2001–2003. Refer to Table 1 for species abbreviations.

absence. Correlates with brook trout presence included the presence of cisco, round whitefish, and rainbow smelt. Correlates with brook trout absence included the presence of lake chub and longnose sucker. Comparison of these results with habitat classification models suggests that fishes are distributed in Tobin Harbor along a habitat and protection gradient from the mouth to the head of the embayment; lake chub and longnose sucker were more frequently associated with less protected rocky habitat near the mouth of embayments, and brook trout, rainbow smelt, round whitefish, and lake whitefish were more frequently associated with more protected habitats at midembayment locations.

Small-Scale Community and Habitat Associations

We used PCA to examine the habitat and species associations of the 11 most common species within Tobin Harbor independent of brook trout presence (Figure 6). The first PC axis represented a gradient of habitat from the protected head of the bay to the relatively unprotected mouth. The second PC axis represented a gradient of habitats dominated by exposed bedrock to those with little bedrock. Brook trout were clustered with round whitefish, white sucker, and trout-perch near the center of PC space, indicative of coexistence in midembayment habitats. Rainbow smelt and burbot were both associated with more protected habitat at the head of the embayment, but burbot differed by its association with areas dominated by bedrock substrate. Cisco, lake whitefish, and longnose sucker were associated with habitats nearer the head of the embayment. These results show considerable overlap in habitat associations among a majority of species present in Tobin Harbor and corroborate classification models that addressed species associations conditioned by presence and absence of brook trout.

Discussion

The rugged geology of Isle Royale was reflected in the characteristics of the nearshore aquatic habitat of embayments and adjacent Lake Superior shorelines. Average depth was highly variable across all habitat sampling grids sampled. Shoreline habitat ranged from low to high slope and substrates from silty sand to bedrock. Predictably, larger substrate particles predominated in high-slope areas and, conversely, smaller substrates predominated in low-slope areas; however, pure silt substrate was nearly absent. Variability in depth and substrate size was consistently lower within sample grids than among sample grids (30–70% less variable), indicating that grids sampled patches of relatively homogeneous habitat. Only a small percentage (5%) of the sites contained organic material, which suggests that very little shoreline in Isle Royale embayments are fully protected from the action of waves and ice scouring. Even shorelines in the well-protected heads of bays showed evidence of seasonal ice scouring—typically, a 1–4-m-wide × 1–2-m-high scour zone extended from the wetted edge to the tree line (O. T. Gorman and S. A. Moore, personal observations). Consistent with this finding is the rarity of cover in the form of overhead shade, logs, and emergent vegetation.

Each embayment provided an array of habitats along a gradient from highly exposed areas near the mouth to highly protected areas near the head. Species composition and habitat changed along these gradients in a predictable manner; across all embayments, species strongly associated with steep, rocky, relatively unprotected habitats near the head of embayments included lake chub, longnose sucker, and lake trout, while species strongly associated with relatively protected midembayment habitats of moderate slope and containing a mixture of substrates included white sucker, trout-perch, ninespine stickleback, and rainbow smelt. In Tobin Harbor, we found that brook trout were closely associated with midembayment habitat and species assemblages, especially those locations with a mixture of sand, gravel, and cobble substrates and the absence of bedrock. Our results suggest that brook trout are relatively selective of habitat patches containing small substrates (particularly sand and gravel) within embayments that are dominated by larger substrates and exposed bedrock.

Nearshore fish assemblages of Isle Royale embayments were characterized by a common element of the

Lake Superior fish community, particularly lake chub, white sucker, longnose sucker, trout-perch, slimy sculpin, burbot, lake trout, round whitefish, lake whitefish, cisco, rainbow smelt, and ninespine stickleback. Brook trout was among the rarest species in Isle Royale embayments, the exception being the island's metapopulation in Tobin Harbor. Many individuals of some open-lake species (e.g., burbot, lake whitefish, round whitefish, cisco, and rainbow smelt) that we captured or observed were small juveniles in the 80–150-mm-TL range (Gorman and Moore, personal observations). This observation underscores the importance of protected embayments as rearing habitat for open-lake species. The coincidence of brook trout and many small-sized species in midembayment habitats is suggestive of a strong predator–prey interaction, particularly in Tobin Harbor where brook trout was a relatively abundant predator.

Our findings were consistent with those of other habitat studies on brook trout in lakes (Mucha and Mackereth 2008, this issue) and streams (Cunjack and Green 1983; Barton et al. 1985; Flebbe 1994; Moore et al., unpublished). Beauchamp et al. (1992) indicated that brook trout presence in Adirondack lakes was associated with prior brook trout stocking, the presence of associated fish species, pH, the presence of competitors, silica, acid-neutralizing capacity, distance to the nearest road, dissolved organic carbon substrate, and downstream access. Although we did not use the predictors of Beauchamp et al. (1992), our results indicate that, at a large scale, there are habitat characteristics, fish species, lack of competitors (Quinlan et al., in press), and remoteness of access (Isle Royale itself) associated with coaster brook trout presence.

Tobin Harbor was used to model small-scale habitat associations because of the presence of the largest brook trout population in Isle Royale, greater sampling effort and number of brook trout captures, and increased density of habitat sampling grids. In Tobin Harbor, the best substrate predictors were silty sand and sand in combination with gravel and cobble substrate and an absence of large boulders and bedrock. Our observation of the association of brook trout presence with sand and gravel substrates has been reported elsewhere (Barton et al. 1985). We found silt substrate (0 on modified Wentworth scale) to be relatively rare in Isle Royale embayments, which may be indicative of high-quality habitat for brook trout. Silt has been shown to reduce the survival and growth rates of juvenile brook trout in stream habitats (Alexander and Hansen 1986; Argent and Flebbe 1999), and brook trout are rarely present in highly silted habitats (Barton et al. 1995; Moore et al., unpublished). Notably missing from Tobin Harbor when compared with literature is the absence of large wood and overhead cover (Flebbe and Dollof 1995; Flebbe 1999; Johnson 1999). We suspect that previously mentioned ice scour removes large wood from nearshore habitats and that the geological roughness of Isle Royale habitat increases hard substrate surface area for colonization by prey items (e.g., Hutchens et al. 2004), which is analogous to how large woody debris contributes to surface area for macroinvertebrate colonization (Gregory et al. 2003).

Our sampling focused on fish that used a narrow band of nearshore habitat, and most fish captures and observations occurred at night. During more than 300 h spent measuring habitat during the day, we found nearshore areas to be notably devoid of fish (Gorman and Moore, personal observations). The relative abundance of fish captured or observed during night electrofishing suggests that most fish reside in deeper waters during the day and move inshore at night. We suspect that the nighttime association of brook trout with small fish in nearshore habitats of midembayment areas may be driven partially by predation opportunity. Thus, despite our sampling a narrow range of available habitat in Isle Royale embayments, our samples do reflect relative measures of the fish community and permit comparisons within and among embayments.

The lower correct percent absence of brook trout compared with presence observed in our classification models suggests that there is suitable unoccupied habitat for brook trout in Isle Royale. This observation is further emphasized by the presence of similar arrays of habitat and species assemblages that we detected across many Isle Royale embayments. Thus, the potential for further recovery of brook trout populations in Isle Royale remains. Embayments with arrays of habitat that were most similar to our model, Tobin Harbor, included Duncan Bay, Five Finger Bay, McCargoe Cove, Lane Cove, Pickerel Cove, and Robinson Bay, all located at the northeastern end of the island. However, the presence of brook trout in other embayments with somewhat different arrays of habitat (e.g., Siskiwit Bay, Washington Harbor, and Todd Harbor) suggests that there is potential for most Isle Royale embayments to support brook trout populations.

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