Local and Cumulative Influences of Docks on Littoral Habitat Structure

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Abstract

Littoral habitat is a critical component of lake ecosystems. Aquatic macrophytes and coarse woody structure provide refuge, foraging area, and spawning substrate for many fish species. The expansion of residential development along Minnesota lakeshores has led to substantial habitat modification, and is considered a threat to lake fish communities. Previous studies have linked lakeshore development to reductions in abundance of aquatic vegetation and coarse woody structure; however, few studies have quantified the specific influence of docks on aquatic habitat structure. We assessed coarse woody structure and three measures of macrophyte abundance across three scales of development in 11 Minnesota lakes, using docks as an index of development. All four structural habitat components were significantly influenced by distance to the nearest dock structure. Coarse woody structure and emergent and floating-leaf vegetation were reduced at sites where docks were present. Site-level abundance of coarse woody structure and presence of emergent species were significantly and negatively related to lake-wide dock density, indicating that these habitat components are particularly vulnerable to development. These findings suggest that management of lake fish habitat should address both local and lake-wide scales of development. In addition, dock size restrictions could minimize impacts to critical habitat structure.

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Introduction

Littoral habitat complexity supports lake fish communities by providing critical structure for fish assemblages and their prey. More complex, structurally heterogeneous habitats generally support higher species diversity across lakes (Eadie and Keast 1984) and within lakes (Weaver et al. 1997, Jennings et al. 1999, Pratt and Smokorowski 2003). Large substrate particles and coarse woody structure (CWS; Newbrey et al. 2005) increase surface area for colonization by bacteria, periphyton, and macroinvertebrates (Schmude et al. 1998), and serve as spawning substrate for many northern freshwater fishes (Smokorowski and Pratt 2007). CWS with complex branching patterns offers refuge for small and juvenile fishes (Newbrey et al. 2005). High densities of submerged wood support fish species richness and centrarchid abundance (Barwick 2004). Similarly, the diverse array of growth forms exhibited by emergent, submerged, and floating-leaf macrophytes enhances spawning, refuge, and foraging opportunities for littoral fishes. Young-of-the-year fish, in particular, rely on densely vegetated areas for protection (Weaver et al. 1997). By influencing prey densities (Crowder and Cooper 1982) and predator-prey interactions (Savino and Stein 1982), macrophyte abundance plays an important role in fish growth.

Reductions in littoral habitat structure have been associated with negative impacts to fish communities. A number of studies have examined the effects of littoral CWS depletion on fish community structure (Sass et al. 2006, Roth et al. 2007), lake food web interactions (Helmus and Sass 2008, Ahrenstorff et al. 2009), and black bass *Micropterus spp.* nest site selection (Hunt and Annett 2002; Lawson et al. 2011). The removal of littoral CWS exerts complex effects on lake food webs by affecting prey availability, mortality rates, and reproductive success across multiple trophic levels. Several studies proposed that reductions in littoral CWS due to increased lakeshore development drove observed changes in fish productivity and spatial distribution. CWS loss was attributed to decreased growth of bluegill *Lepomis macrochirus* (Schindler et al. 2000) and largemouth bass *Micropterus salmoides* (Gaeta et al. 2011), reduced nest success among largemouth bass (Wagner et al. 2006), and increased dispersion of littoral fishes (Scheuerell and Schindler 2004). Recent evidence suggests that changes to fish communities associated with littoral CWS removal are not easily reversed by CWS addition (Sass et al. 2012).

Studies documenting the effects of large-scale macrophyte removal on fish communities have largely focused on lakes dominated by invasive plant species, such as Eurasian watermilfoil *Myriophyllum spicatum* (Olson et al. 1998; Valley and Bremigan 2002, Kovalenko et al. 2009); thus, it is less clear how widespread macrophyte removal affects fish populations among lakes with diverse native plant communities. Two studies in Minnesota observed minimal changes in fish abundance and growth in response to widespread chemical removal of submerged aquatic vegetation (Radomski et al. 1995, Pothoven et al. 1999). Nevertheless, aquatic macrophytes contribute to habitat heterogeneity within lakes, and are particularly important in areas lacking other forms of habitat structure.

Previous studies have established that lakeshore residential development modifies littoral habitat through direct and indirect mechanisms. CWS is highly vulnerable to lakeshore residential development because natural recruitment from riparian forest succession is a slow process (Christensen et al. 1996). The clearing of upland trees, as well as direct removal of CWS from the near-shore area rapidly deplete littoral CWS along developed shorelines (Christensen et al. 1996, Jennings et al. 2003, Francis and Schindler 2006, Marburg et al. 2006), and ultimately limit the potential for natural CWS input in the future.

Macrophyte communities are also affected by lakeshore development. Reduced coverage of emergent and floating-leaf macrophytes has been attributed to lakeshore development in Wisconsin (Jennings et al. 2003), Minnesota (Radomski and Goeman 2001, Radomski 2006), Iowa (Bryan and Scarnecchia 1992), and Ontario, Canada (Hicks and Frost 2011). Although submerged macrophyte abundance is generally not affected by lakeshore development (Jennings et al. 2003; Hicks and Frost 2011), overall macrophyte species richness has been shown to decline as lakeshores become more developed (Hatzenbeler et al. 2004, Hicks and Frost 2011).

Past research in this area has typically relied on the presence of a residential cabin, or cabin density, as indices of lakeshore development, whereas other studies defined ‘developed’ shoreline more loosely, as shoreline that has been altered from its natural condition (e.g. Bryan and Scarnecchia 1992). Although cabins provide a clear indication of human presence on the shore, they can be difficult to monitor remotely and are often disconnected from the aquatic zone. In contrast, docks physically occupy the littoral zone and are readily identified from aerial imagery. Due to their association with in-water recreational activities, docks likely represent ‘loci’ of lakeshore development, or areas of highly concentrated disturbance (Radomski et al. 2010). Landowners may intentionally remove littoral CWS and aquatic vegetation to improve swimming and boating conditions near the dock. Unintentional vegetation removal may result from dock shading (Garrison et al. 2005, Campbell and Baird 2009) and motorized water sports (Asplund and Cook 1997). Motorboats, in particular, can limit vegetation by reducing water clarity and physically damaging plants (Liddle and Scorgie 1980, Asplund and Cook 1997).

Few studies have specifically investigated the influence of docks or other in-water recreational structures on littoral habitat. Although previous research has confirmed that docks effectively block sunlight and directly limit aquatic plant growth in Wisconsin (Garrison et al. 2005) and Florida (Campbell and Baird 2009), these studies did not investigate impacts extending beyond the footprint of the dock structure. The only study to quantify dock-related impacts to littoral habitat on Minnesota lakes derived vegetation data from aerial photographs (Radomski and Goeman 2001). To date, no field investigations have defined the influence of residential dock structures on surrounding aquatic habitat.

We assessed four components of littoral habitat structure (CWS and three measures of macrophyte abundance) in relation to lakeshore development, which was defined by the presence of an in-water dock. Relationships were examined across three spatial scales (*proximity, site-level,* and *lake-wide*) to meet the following objectives:

1) *Proximity*: Define the relationship between aquatic habitat structures and distance to the nearest dock. 2) *Site-level:* Compare littoral habitat structure between developed and undeveloped sites. 3) *Lake-wide:* Investigate relationships between lake-wide development density and littoral habitat structure.

This research is part of a larger project investigating the cumulative impacts of lakeshore residential development on macrophyte and fish communities across a larger group of Minnesota lakes. Thus, I will relate my findings to the broader context of the project, as well as other relevant studies.

Methods

Lake selection

Lakes with similar limnological and watershed characteristics were chosen to isolate the effects of lakeshore development on littoral habitat structure. We selected lakes managed by the Minnesota Department of Natural Resources (MN DNR) which had fish and aquatic plant survey data collected within the past five years. Candidate lakes were located within the Northern Lakes and Forests (NLF) Ecoregion of Minnesota (Figure 1), a lake-rich area with widespread lakeshore development. We selected relatively small (40-200 ha) and mesotrophic lakes with at least 80 percent forested watersheds; these criteria are characteristic of recreational development lakes within the NLF Ecoregion (Heiskary and Wilson 2005). We used geo-referenced aerial imagery from the U. S. Department of Agriculture Farm Service Agency to estimate dock densities across all candidate lakes in the region. Dock density was calculated by dividing lake-wide dock counts by shoreline length. The lakes were ordered from undeveloped (< 1 dock/km shoreline) to highly developed (70 docks/km) and binned by quintiles. Six lakes were drawn from each grouping to obtain a set of 30 lakes spanning a range of development densities. These 30 lakes were involved in the larger research project assessing fish and plant communities. A representative subset of 12 lakes was selected for this study (Table 1). The study lakes belong to similar ecological lake classes with fish communities dominated by northern pike *Esox lucius* and bluegill (Schupp 1992). Two of the study lakes were undeveloped; therefore, dock-related habitat sampling was conducted on only 10 lakes. After the completion of lake selection and the commencement of the field season, we determined that one of the 12 study lakes did not meet all of the selection criteria. Located in a different region of the state and belonging to a dissimilar lake class, South Twin was inadequate for comparison with the other study lakes; hence, we eliminated it from the study. Sample sizes reported in the remainder of the manuscript were adjusted to reflect this change.

Field site selection

We used ArcGIS to divide the shoreline of each study lake into 20m segments, or "sites." Recent aerial photographs were used to classify shoreline sites as "developed" or "undeveloped". Candidate developed sites contained docks which were simple in shape and relatively isolated (at least 20m from a neighboring dock) to avoid sampling in areas influenced by an adjacent dock. Candidate undeveloped sites were also located at least 20m from neighboring dock structures. From these candidate sampling sites, we randomly selected five developed sites from each of the 9 developed study lakes. Five additional dock sites were sampled within the two largest developed lakes (Gilbert and Girl). In total, 55 developed sites were chosen for habitat sampling. Because undeveloped sites were expected to exhibit more variation than developed sites, we randomly selected a minimum of 10 undeveloped sites within each of the 11 study lakes. Fourteen undeveloped sites were selected from Gilbert and Girl. Thus, we selected a total of 118 undeveloped sites for sampling.

Field methods

Habitat sampling: Developed sites

Habitat data were collected during July and August of 2012. We navigated to each pre-determined site location using a handheld GPS unit and documented habitat structure along transects spaced at fixed distances from the dock (Figure 2). Transects were oriented parallel to the dock and extended from the shoreline to the end of the dock; thus, transect length was equivalent to the length of the dock over the water. Sampling transects began at the edge of the dock (distance = 0m) with subsequent transects spaced every meter until a distance of eight meters was reached. If a boat lift, boat, or other structure extended from the edge of the dock proper, sampling began at the edge of the ancillary structure. As a result, transects were not always linear, but conformed to the unique shape of the recreational structure. Nine transects were surveyed on each side of the dock, for a total of 18 transects per developed site.

Coarse woody structure (CWS) was defined as any piece of wood ≥ 10cm in diameter anywhere along the trunk and ≥ 60cm in length. We counted every piece of CWS intersecting each transect and assigned each piece a qualitative complexity score from 1 to 5. A “1” indicates the simplest structural type, typically a simple log with no branches. A “5” indicates a highly complex, branchy tree exhibiting fourth-order branching patterns (e.g. Newbrey et al. 2005) along the majority of the trunk. If a single piece of CWS crossed more than one transect line, it was documented each time; however, we also obtained CWS counts within the entire site.

We recorded water depth, substrate type (i.e. sand, cobble, etc.), and visual macrophyte biovolume estimates at points along each sampling transect using a buoyant circular sampling ring (50cm diameter) constructed from foam pipe insulation. The sampling points began at the shoreline and were spaced every 3m from shore until the end of the dock was reached. Therefore, docks over 6m long received sampling along more than three points per transect. Most docks were sampled at three or four depths, with the deepest sampling points aligned with the end of the dock. Macrophyte biovolume was estimated for each of three structural categories: emergent, submerged, and floating-leaf. Emergent biovolume was assigned integer values from 0 to 5 based on the following stem counts: 0: absent (0), 1: sparse (< 4 stems), 2: 4-9 stems, 3: 10-19 stems, 4: 20-30 stems, 5: dense (>30 stems). Submerged biovolume was recorded as a percentage from 0 to 100 in increments of 5 percent, based on the density of vegetation within the water column. In areas where vegetation was sparse, 1 percent biovolume was reported. Coverage of floating-leaf vegetation was recorded as the percentage of the sampling ring covered by floating leaves. Estimates of floating-leaf cover could range from 0 to 100 percent in increments of 5 percent, although 1 percent was noted for areas with minimal cover.

Habitat sampling: Undeveloped sites

The sampling approach at undeveloped sites was similar to that used at developed sites, in which macrophyte sampling was conducted along transects oriented perpendicular to the shoreline. To reduce bias, the first sampling transect was placed at the GPS location and subsequent transects were located to the right of the first transect. Three macrophyte sampling transects were spaced approximately 6.7m apart and extended from 0.3 to 0.9m water depth. Macrophyte sampling points were placed along each transect at depths of 0.3, 0.6, and 0.9m. Macrophyte biovolume was visually estimated in each of the three structural categories following the methods described for developed sites. We counted each piece of CWS within the sampling area defined by the macrophyte transects, which covered approximately 20m of shoreline.

Near-shore Fish Sampling

As part of the larger research project, near-shore fish assemblages were sampled in 29 lakes during the summers of 2011 and 2012. Thirteen lakes were sampled in 2011, and the remaining 16 lakes were sampled in 2012. Fish were collected following the sampling protocol as per the fish-based index of biotic integrity for Minnesota lakes (Fish IBI; Drake and Pereira 2002, Drake and Valley 2005). Each lake was sampled at 10 or more random sites spaced equal distances around the shoreline. At each site, fish were collected along 30m of shoreline using a combination of electroshocking and shoreline seining. We made two passes with a backpack electroshocker parallel to shore, each covering a width of about 1.5m. One pass was made in shallow water, close to the shoreline; the second pass was made in deeper water (approximately 75-100 cm), adjacent to the first sampling pass. Where possible, a 15ft or 50ft bag seine was hauled along 30m of shoreline and out to the length of the seine from shore or maximum wadeable depth (approximately 1.3m). Sites with soft bottoms or steep drop-offs were sampled by electroshocking from the boat. The abundance of each fish species was recorded for each site.

Near-shore fish abundance data were compiled with the most recent fish biomass data from standardized gillnet and trapnet surveys collected by the MN DNR. These data were used to calculate a Fish IBI score for each study lake.

Statistical Analyses

Overview

A number of statistical models were used to examine the influences of development and other non-anthropogenic factors on near-shore habitat structure at the local scales (Table 2). Each structural habitat component (CWS, emergent, submerged, floating-leaf biovolume) was included as a response variable in at least one model. All mixed models included random effects, which were used to account for variation between the sampling units; these random effects are associated with the model's error term (Zuur et al. 2009). Generalized linear mixed models (GLMMs) and generalized linear models (GLMs) were used for response variables with specific distributions, such as presence/absence data (binomial) and count data (Poisson). Generalized models use link functions to relate the explanatory variables to the response variable. Other data transformations, square-root and ln(+1), were applied to linear mixed model (LMM) responses to satisfy the analytical assumptions, which were verified by graphical inspection of residual plots.

Models were generated for five different response variables relating to aquatic habitat structure: presence/absence of coarse woody structure (pCWS), abundance of coarse woody structure (CWS_Total), presence/absence of emergent biovolume (pEm), submerged biovolume (Sub) and floating-leaf biovolume (Float). The two binary response variables, pCWS and pEm, were examined because both CWS and emergent vegetation were infrequently observed near docks; only 6 percent of the dock sampling transects contained CWS, and emergent species were present in 31 percent of the transects. The second CWS response variable, “CWS_Total,” corresponded to site-level CWS abundance. CWS structural complexity was not examined because the majority of documented CWS consisted of simple logs (complexity=1). Submerged and floating-leaf biovolume were treated as numeric variables.

The three explanatory variables used in CWS models were related to development: distance to the nearest dock (Dist), site type (Type), and lake-wide dock density (Docks_km). Dist and Docks_km were treated as continuous, numeric variables. Type was a two-level factor consistent with the shoreline site classification in which sites were “developed” or “undeveloped”. Macrophyte models incorporated development characteristics, as well as several other covariates, to explain variation in the responses. Measures of macrophyte presence or abundance, pEm, Sub, and Float, were included as predictors to examine potential competitive or mutualistic interactions between macrophyte structural types. Water depth (Depth) and substrate texture (Substrate) were included as other potential sources of variation. Depth, recorded in meters, was treated as a numeric variable. Substrate was analyzed as a four-level factor based on gross particle size differences (coarse, mix, sand, fine) among substrate types; for example, boulder, gravel, and cobble substrates were considered “coarse”, whereas substrates such as silt, clay, and muck were classified as “fine.” Combinations of coarse and fine substrates (e.g., cobble and silt) were designated as “mix.” Sand was distinguished from other fine substrates not only because it is associated with a distinct macrophyte community, but also because it is a highly desirable substrate for lakefront property.

Aquatic Habitat Structure and Proximity to Docks

A binomial GLMM was used to investigate the relationship between presence of coarse woody structure (pCWS) and distance to the nearest dock. A nested random effect was used to account for variation between sampling sites within study lakes.

Mixed models were used to examine relationships between aquatic macrophyte responses (pEm, Sub, Float) and distance to the nearest dock (Dist). A binomial GLMM was used to model pEm, and LMMs were used to model Sub and Float, which were square-root transformed. All three models included a nested random effect.

We also applied mixed models to identify key drivers of local macrophyte abundance. Each of the three macrophyte responses were modeled in response to a suite of physical, biological, and development characteristics. For example, the full model for pEm response included the following five explanatory variables: Dist, Sub, Float, Substrate, and Depth. Each model was refined via backward elimination, which uses Akaike's Information Criterion (AIC) and *P*-values to arrive at the best model.

Site-Level Comparisons of Habitat Structure

We used nonparametric statistics and mixed models to compare aquatic habitat structure between developed and undeveloped sites. Developed sites were standardized for comparison to undeveloped sites by eliminating samples from water depths less than 0.3m or greater than 0.9m. Mean submerged and floating-leaf biovolume was calculated for each site. We compared CWS_Total, Sub, and Float responses across Type using the Mann-Whitney *U*-test. Two high outliers (CWS_Total > 90) from Portage lake were removed from the CWS analysis to facilitate site-level comparisons. LMMs were used to examine Sub and Float in relation to Type and Substrate; these models included a random lake effect. Both macrophyte responses were transformed by ln(+1). Sub and Float were compared across substrate categories using the Kruskal-Wallis test.

Presence of emergent vegetation (pEm) was analyzed using Chi-square contingency tables. We constructed a 2x2 contingency table to examine pEm across Type. A 2x8 contingency table was used to examine pEm across unique combinations of Substrate and Type (e.g. coarse/undeveloped, fine/developed).

Cumulative Effects of Lake-wide Development on Habitat Structure

We used analysis of covariance (ANCOVA) to investigate cumulative effects of lake-wide development on site-level aquatic habitat structure (Table 3). Data from all 11 study lakes were used to examine trends across dock densities ranging from 0.3 to 46 docks per shoreline kilometer. Models were constructed for each of four response variables: abundance of coarse woody structure (CWS_Total), presence of emergent vegetation (pEm), mean submerged biovolume (Sub), and mean floating-leaf cover (Float). Each initial model included an interaction between site type (Type) and dock density (Docks_km). If the interaction term was not statistically significant ($\alpha = 0.05$), we eliminated the interaction term and fitted a model with both individual explanatory variables.

Results

Aquatic Habitat Structure and Proximity to Docks

Presence of CWS was positively related to distance to the nearest dock (Z= 3.32, P= 0.001; Figure 3), indicating that the probability of CWS presence increased with separation from docks. The model intercept was also statistically significant (Z= -9.46, P <0.001), suggesting that at the edge of a dock (Dist = 0m), the probability of CWS was significantly different from zero.

Presence of emergent species exhibited a positive and significant relationship with distance to the nearest dock (Z= 11.76, P <0.001; Figure 4A). The model intercept was significantly different from zero (Z= -7.43, P <0.001), indicating a 9 percent likelihood of emergent species occurrence at the edge of a dock.

Submerged and floating-leaf biovolume were significantly related with distance to the nearest dock. Submerged biovolume had a slight, positive relationship with distance (t= 8.01, df=3177, P <0.001; Figure 4B). The model intercept was significantly different from zero (t= 11.41, df=3177, P <0.001), and estimated to equal 2.3 percent biovolume. Floating-leaf biovolume was also positively associated with distance to the nearest dock (t= 13.00, df=3177, P <0.001; Figure 4C). The model intercept was not significantly different from zero (P= 0.16).

Macrophyte responses were not only affected by proximity to docks, but other local physical and biological factors as well. We used AIC to compare the simple proximity models to the more complex local models and found that for each macrophyte response, the complex models, which included Substrate and Depth, accounted for more variation in the response. However, Dist remained a significant explanatory variable in each of the models. Presence of emergent vegetation was significantly related to distance to the nearest dock, floating-leaf cover, substrate texture, and water depth (Table 6). Presence of emergent species was positively related to distance to the dock (Z= 13.35, P <0.001) and negatively associated with floating-leaf cover (Z= -3.03, P= 0.002) and water depth (Z= -17.37, P <0.001). Presence of emergent species was also affected by substrate particle size; emergent species were most common in fine substrates and least common in coarse substrates.

Submerged biovolume was significantly and positively related to distance to the nearest dock (t= 8.92, df=3171, P <0.001; Table 7), presence of emergent species (t= 2.46, df=3171, P <0.001), floating-leaf cover (t= 2.15, df=3171, P= 0.01), and water depth (t= 27.08, df=3171, P <0.001). Submerged vegetation was most abundant in fine substrates and least abundant in coarse substrates.

Floating-leaf biovolume was positively and significantly related to distance to the nearest dock (t= 12.79, df=3171, P <0.001; Table 7), submerged biovolume (t= 7.73, df=3174, P <0.001) and water depth (t= 7.68, df=3171, P <0.001). Floating-leaf cover was negatively related to presence of emergent vegetation (t= -2.98, df=3171, P= 0.003). Floating-leaf biovolume was highest in fine substrates; interestingly, the model coefficients relating to the other three substrate categories (coarse, mix, and sand) were not significantly different from zero ($P \geq 0.05$; Table 7).

Site-level Comparisons of Aquatic Habitat Structure

Site-level CWS abundance was quite variable among study lakes (Table 4). Portage Lake had particularly high CWS densities, with a mean of 14 pieces per site and a maximum of 91 pieces observed at one site. However, the grand mean CWS abundance across all 11 study lakes was 3.2 pieces per site. CWS abundance was significantly related to site-level development, with undeveloped sites exhibiting higher CWS abundance than developed sites (Mann-Whitney *U*-test, *W*=2137, *P*=0.04). Mean CWS abundance was 0.73 (SE, 0.15) at developed sites and 1.72 (SE, 0.27) at undeveloped sites (Figure 5).

The presence of emergent species varied significantly with site type (X^2= 8.47, df= 1, *P*= 0.004). Whereas emergent species were present at only 53% of developed sites, they were present at 74% of undeveloped sites (Figure 6). Presence of emergent vegetation was also significantly related to a combination of substrate texture and site type (X^2= 64.05, df =7, *P* <0.001; Figure 7). Emergent species were most commonly observed at undeveloped sites with fine substrates (1.0), and absent from developed sites with coarse substrates. Among developed sites, the highest frequency of emergent species was observed at those with fine substrates (0.82). Although presence of emergent species varied greatly with substrate texture, emergent species were more frequently observed at undeveloped sites than developed sites.

Abundance of submerged and floating-leaf macrophytes also varied with site-level development (Figure 8). Mean submerged biovolume was 4.84 (SE, 0.35) at developed sites and 5.96 (SE, 0.40) at undeveloped sites; however, this difference was not statistically significant (Mann-Whitney *U*-test; *U*= 2201, *P*= 0.10). Floating-leaf cover varied significantly with site type (Mann-Whitney *U*-test; *U*= 1791, *P*= 0.001) with developed sites averaging 5.47 (SE, 1.53) percent cover and undeveloped sites averaging 13.50 (SE, 1.72) percent cover. Substrate texture was an important source of variation in macrophyte abundance (Figure 9). Both macrophyte forms were most abundant at undeveloped sites with fine substrates and least abundant at developed sites with coarse substrates. The highest mean submerged biovolume was 6.76 (SE, 0.45); the lowest mean biovolume was 2.45 (SE, 0.45), which was observed at developed sites with coarse substrate. Submerged biovolume was significantly different across the four substrate categories (Kruskal-Wallis test; H= 52.77, df= 3, $P < 0.001$). The highest floating-leaf cover was 12.20 (SE, 0.91) at sites with fine substrates, which was higher than the mean coverage for the other three substrate categories, even among undeveloped sites (range 1.07 to 2.90). The estimate of mean floating-leaf cover at developed sites with coarse substrates was effectively zero (P= 0.72). Floating-leaf cover varied significantly across all four substrate groupings (Kruskal-Wallis test; H= 76.21, df= 3, $P < 0.001$).

Cumulative Effects of Lake-wide Development on Habitat Structure

Site-wide abundance of coarse woody structure (CWS) was significantly related to the interaction of site type (developed/undeveloped) and lake-wide dock density (Figure 10); CWS abundance within undeveloped sites decreased as lake-wide development increased. The model indicated that at moderately high development densities, approximately 25 docks per kilometer, CWS abundance within undeveloped sites equaled that within developed sites.

Probability of presence of emergent vegetation was affected by a combination of site type and lake-wide dock density (Figure 11). Both site types were negatively related to dock density (Z= -2.14, P= 0.03); however, probability of emergent presence was approximately 0.07 higher at undeveloped sites than developed sites regardless of lake-wide development density.

Submerged and floating-leaf biovolume were not related to either the interaction term, Type*Docks_km, or dock density (P >0.05), suggesting that these growth forms may be less sensitive to development than emergent macrophyte species.

Discussion

Local Effects of Docks on Habitat Structure

Human activities associated with residential docks significantly influence natural aquatic habitat structure. Reductions in the presence and abundance of critical habitat components were documented as far as eight meters from docks in this study. Presence of CWS and emergent vegetation, as well as abundance of submerged and floating-leaf macrophytes, were reduced within this 8m zone. These findings are consistent with the 7.6m 'habitat impact zone' suggested by Radomski et al. (2010), which was based on vegetation removal guidelines for recreational development lakes in Minnesota. Dock impacts to habitat could extend beyond eight meters; however, our sampling efforts did not allow us to determine the full extent of the influence. Nevertheless, our findings suggest that habitat impacts may increase with dock size; assuming natural structure is limited beneath the dock footprint, our localized habitat models imply that increasing dock width would expand the total area of influence. This inference is supported by Radomski and Goeman (2001), who documented reduced coverage of emergent and floating-leaf vegetation in plots with larger docks; however, we did not explicitly test this hypothesis.

Other local factors, such as substrate texture and water depth, were also key drivers of macrophyte biovolume. Presence of emergent species and coverage of submerged and floating-leaf vegetation was consistently highest in areas with fine substrates. Dock-related impacts to aquatic vegetation are likely to be highest at sites with fine substrates simply because aquatic plants are naturally more abundant in such areas. Floating-leaf vegetation was particularly abundant in sites with fine substrates. Substrate is an important feature of lakefront properties; whereas muck is a highly undesirable substrate type, sand is very appealing to potential landowners. Landowners may even augment natural substrates with sand to create artificial beaches (Engel and Pederson 1998). We found that a majority (61%) of the developed sites sampled had sandy substrates; however, a large proportion of undeveloped sites (42%) also contained sand. Although sand was not associated with the highest macrophyte abundance, sandy substrates typically supported higher macrophyte coverage than coarse and mixed substrates. If landowners preferentially develop sandy sites, naturally vegetated areas will be limited, particularly in highly developed lakes. Widespread reductions in macrophyte cover could negatively affect the survival of juvenile fishes, as well as intolerant north temperate fish species, such as the blackchin shiner *Notropis heterodon*, blacknose shiner *Notropis heterolepsis*, and banded killifish *Fundulus diaphanus*, which are strongly associated with dense beds of vegetation (Valley et al. 2010). Although the preferential development of sandy sites could spare impacts to densely-vegetated boggy sites, macrophyte species favoring sandy substrates, such as emergent hardstem bulrush *Scirpus acutus*, would remain at risk. Reductions in the coverage of hardstem bulrush could limit nesting habitat for fishes such as black crappie *Pomoxis nigromaculatus* which are closely associated with the species (Reed and Pereira 2009).

Our findings also suggested that macrophyte structural types are somewhat partitioned by depth zones. Emergent species tend to occupy shallower areas and become less frequent as water depth increases. Conversely, abundance of floating-leaf species increased with water depth. The negative associations between presence of emergent species and floating-leaf biovolume suggest that these growth forms may compete for sunlight. Low-growing, shade-tolerant submerged macrophytes were positively associated with the presence of emergent species and abundance of floating-leaf cover, and became more abundant as water depth increased. This partitioning of macrophyte structural types by depth could influence the sensitivity of macrophyte growth forms to shoreline disturbance. Because emergent species tend to colonize areas nearest the shoreline, they are likely the most vulnerable to development impacts.

Cumulative Effects of Lake-wide Development on Habitat Structure

Our analyses indicated that lake-wide development had a cumulative impact on some forms of aquatic habitat structure. Abundance of CWS, in particular, was significantly related to the interaction between site type and lake-wide dock density such that CWS abundance at undeveloped sites declined with as dock densities increased. CWS abundance at developed sites increased with dock density, although at a slightly lower rate. The reduction in CWS abundance at undeveloped sites could be attributed to land use changes around the lake. For instance, the clearing of shoreline trees for access roads may have limited the natural recruitment process. Additionally, riparian CWS could be depleted by lakeshore residents collecting firewood (Marburg et al. 2006). The increase in CWS abundance in relation to site-level and lake-wide development is puzzling; however, this result may reflect our ability to detect CWS, rather than an accurate pattern of abundance. Whereas detection was particularly difficult in densely-vegetated sites, which were generally undeveloped, CWS was easily observed at developed sites that were cleared of vegetation. Nevertheless, increases in lake-wide development are likely to cause reductions in the overall availability of CWS throughout the littoral zone. Estimates of CWS density, projected from mean abundances for each site type (Table 4), suggested lake-wide CWS density declined rapidly with small increases in lakeshore development. CWS density dropped dramatically between zero and five docks per shoreline kilometer, then remained fairly constant as development increased (Figure 12). Our estimates of lake-wide CWS density were consistent with previous estimates for lakes of similar development densities in Wisconsin (Christensen et al. 1996, Marburg et al. 2006), and upper Michigan (Francis and Schindler 2008). Large-scale reductions to littoral CWS have been attributed to declines in yellow perch *Perca flavescens* (Sass et al. 2006), as well as dietary shifts and reduced growth among largemouth bass (Ahrenstorff et al. 2009). Reduced yellow perch abundance was attributed to limited recruitment and high mortality rates associated with loss of spawning substrate and refuge (Sass et al. 2006, Roth et al. 2007, Helmus and Sass 2008). It is possible that docks offer surrogate habitat structure in the absence of natural CWS; however, a recent study by Lawson et al. (2011) found that largemouth bass nests were consistently located nearer to CWS than they were to docks, even in highly developed lakes with low CWS densities. Reed and Pereira (2009) observed that nest site selection by largemouth bass and black crappie were influenced by development practices along the shore; although nests were rarely found near developed shores, they were located in deeper water than nests adjacent to undeveloped sites. These results, together with our findings, suggest the influences of docks on fish communities are largely negative.

As part of the larger research project, we calculated Fish IBIs for 29 lakes, including the 11 lakes from this study. Macrophyte-based IBIs (Beck et al. 2010) were also calculated for the 11 lakes. IBIs provide a standardized approach for assessing the biological integrity of ecosystems. IBI metrics were selected to be for their sensitivity to anthropogenic disturbance; thus, we expected IBI scores to decrease with dock density. Fish IBI was significantly and negatively related to dock density within the 11 study lakes (Figure 13); for every 1-unit increase in dock density, Fish IBI was predicted to decline by 0.6. Although the larger set of lakes followed a similar trend, the relationship was not statistically significant (P= 0.82). The decline of the Fish IBI across the 11 study lakes was due to an increase in the relative biomass of omnivorous fishes, most commonly bullheads *Ameiurus spp*. Omnivore biomass from trap-net catches was a significant predictor of Fish IBI (R^2= 0.65, P= 0.002); Fish IBI declined with increased omnivore biomass. Omnivore biomass was positively correlated with dock density (Spearman's rho=0.80, P= 0.003). CWS density was not correlated with omnivore biomass, which suggests that other factors associated with development, such as loss of vegetation, reduced water clarity, or fishing pressure could be driving the increase in omnivore productivity. Macrophyte IBI scores were not significantly related to lake-wide dock density; however, we documented significant reductions in the presence of emergent macrophyte species.

The presence of emergent macrophyte species declined with dock density, regardless of whether the site was developed or undeveloped. Abundance of submerged and floating-leaf macrophytes was not significantly related to dock density, suggesting that local factors exert a stronger influence over the coverage of these growth forms. Interestingly, substrate characteristics may account for the lack of response in floating-leaf vegetation. Floating-leaf species dominated sites with fine substrates, which are undesirable for lakefront property; therefore, impacts to floating-leaf cover may have been minimized by development preferences. Submerged macrophytes were least affected by development; site-level development did not significantly affect the abundance of submerged vegetation. This could indicate that submerged growth forms are more tolerant of disturbance than other macrophyte types. Alternatively, submerged species may be overlooked by landowners because they are less conspicuous than highly-visible emergent and floating-leaf species. Similar shifts in macrophyte communities have been reported in Canadian Shield lakes (Hicks and Frost 2011), where declines in emergent and floating-leaf macrophyte coverage were accompanied by increased coverage of submerged vegetation. The loss of emergent vegetation across highly developed lakes could have negative implications for species such as black crappie and other species which nest near emergent macrophyte species.

Conclusion

We documented reduced aquatic habitat complexity across three scales of lakeshore residential development. Our findings illustrate the importance of managing fish habitat across multiple scales. The site-level and lake-wide relationships between docks and habitat structure are consistent with the results of previous studies, which used cabins, rather than docks, as indicators of lakeshore development. This study was the first to quantify relationships between habitat structure and proximity to a dock. Coarse woody structure, presence of emergent species, and floating-leaf cover were significantly related to both local scales of analysis (*proximity* and *site-level*). CWS and emergent species appear to be particularly vulnerable to development; both were negatively related to lake-wide dock density. Reduced natural habitat structure associated with docks may limit the reproductive potential of fishes requiring CWS and/or emergent vegetation, such as black crappie, largemouth bass, and yellow perch. Finally, the distribution and size of docks may play a role in determining fish habitat availability in near-shore areas. Because the same measure of dock density can be achieved through multiple configurations, future research should explore impacts relating to the spatial arrangement of docks. Additional research linking shoreline management practices (e.g. vegetation removal, dock size) to biological outcomes is needed to inform lake management policies.

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Appendix: Tables and Figures

Table 1. Limnological and development characteristics of 11 study lakes. "% WS Disturbed" includes urban, agricultural, and mining land cover types (2001 National Land Cover Dataset).

Lake Name	Lake Class[a]	Surface Area (ha)	% Littoral	Max. Depth (m)	Mean TP (ppb)	Secchi Depth (m)	% WS Disturbed	Devel. Density (Docks/km)
Elk[b]	23	122	23.9	28.4	21	4.0	0.7	0.4
Thistledew[b]	23	130	22.4	13.7	19	5.0	2.8	0.8
Upper Cullen	29	174	69.0	12.2	26	3.0	13.1	7.3
Portage	23	111	34.3	25.6	14	8.0	7.4	13.4
Eagle	25	169	38.7	23.5	19	3.0	10.1	20.3
Gilbert	25	159	56.9	13.7	32	4.5	10.9	20.7
Horseshoe	23	104	30.7	15.5	38	5.0	7.8	24.8
Hand	25	116	48.4	17.4	23	4.0	4.3	24.9
Gladstone	29	175	55.8	11	18	4.0	3.7	34.4
Bass	23	77	22.3	16.8	15	5.0	3.6	39.1
Girl	25	171	63.5	24.7	18	4.0	4.8	46.0

[a] Schupp (1992)
[b]Undeveloped lake included as a reference condition.

Table 2. Summary of mixed models used in local-scale analyses. Presence/absence of coarse woody structure (pCWS), CWS abundance (CWS_Total) and presence/absence of emergent macrophytes (pEm) were examined using generalized linear mixed models (GLMMs) from the lme4 package (Bates et al. 2012). Submerged macrophyte biovolume (Sub), and cover of floating-leaf macrophytes (Float) were examined using linear mixed models (LMMs) in the nlme package (Pinheiro et al. 2012). Explanatory variables included distance to the nearest dock (Dist), site type (Type), categorical substrate texture (Substrate), and water depth (Depth). All models were created in R version 2.15.2.

Response	Explanatory Variables	Model	R Package	Family	Link	Random Effect	# Lakes
pCWS	Dist	GLMM	lme4	Binomial	logit	Lake/Site	9
CWS_Total	Type	GLMM	lme4	Poisson	ln	Lake	9
pEm	Dist	GLMM	lme4	Binomial	logit	Lake/Site	9
	Dist, Float, Substrate, Depth	GLMM	lme4	Binomial	logit	Lake/Site	9
Sub	Dist	LMM	nlme	Gaussian	ln(+1)	Lake/Site	9
	Dist, pEm, Float, Substrate, Depth	LMM	nlme	Gaussian	ln(+1)	Lake/Site	9
	Type, Substrate	LMM	nlme	Gaussian	ln(+1)	Lake	9
Float	Dist	LMM	nlme	Gaussian	sqrt	Lake/Site	9
	Dist, pEm, Sub, Substrate,Depth	LMM	nlme	Gaussian	sqrt	Lake/Site	9
	Type, Substrate	LMM	nlme	Gaussian	sqrt	Lake	9

Table 3. Summary of ANCOVA models used to investigate lake-wide impacts of docks on habitat structure. Response variables examined were: coarse woody structure abundance (CWS_Total), presence/absence of emergent species (pEm), submerged biovolume (Sub), and floating-leaf biovolume (Float). All responses were measured at the site scale. Explanatory variables were both development indices: site type (Type), and dock density, measured in docks per kilometer of shoreline (Docks_km). The asterisk (*) denotes an interaction between two variables. All models were created in R version 2.15.2.

Response	Explanatory Variables	Model	R Package	Family	Link	# Lakes
CWS_Total	Type*Docks_km	GLM	lme4	Poisson	ln	11
pEm	Type*Docks_km	GLM	lme4	Binomial	logit	11
pEm	Type, Docks_km	GLM	lme4	Binomial	logit	11
Sub	Type*Docks_km	LM	nlme	Gaussian	sqrt	11
Sub	Type, Docks_km	LM	nlme	Gaussian	sqrt	11
Float	Type*Docks_km	LM	nlme	Gaussian	sqrt	11
Float	Type, Docks_km	LM	nlme	Gaussian	sqrt	11

Table 4. Site-level and estimated lake-wide density of coarse woody structure (CWS; mean ± SE) for each study lake. Undeveloped (U) sites (n= 10-14 per lake) were located at least 20m from a dock. Each developed (D) site (n= 5 per lake) was centered around a residential dock.

Lake Name	Dock Density (docks/km)	CWS (U) (pcs/site)	CWS (D) (pcs/site)	CWS density (pcs/km)
Elk	0.4	5.70 ± 1.26	NA	284
Thistledew	0.8	8.40 ± 1.24	NA	411
Upper Cullen	7.3	0.30 ± 0.21	0.00 ± 0.00	13
Portage	13.4	21.90 ± 11.58	0.20 ± 0.20	948
Eagle	20.3	1.22 ± 0.62	0.40 ± 0.24	51
Gilbert	20.7	1.79 ± 0.49	0.60 ± 0.22	71
Horseshoe	24.8	1.00 ± 0.37	1.40 ± 0.60	55
Hand	24.9	1.60 ± 0.76	0.80 ± 0.58	73
Gladstone	34.4	0.80 ± 0.49	0.00 ± 0.00	23
Bass	39.1	2.40 ± 0.86	0.20 ± 0.20	74
Girl	46.0	2.07 ± 1.00	1.90 ± 0.48	99

Table 5. Macrophyte biovolume characteristics summarized for each of the 11 study lakes. Emergent biovolume (Em) was measured on a scale of 0-5 in increments of 1. Submerged biovolume (Sub) and floating-leaf cover (Float) were reported to range from 0 to 100 in increments of 5. Undeveloped (U) sites (n=10-14 per lake) were located at least 20m from a residential dock. Each developed (D) site (n=5 per lake) was centered around a residential dock.

Lake Name	Docks/km	Em (U)	Em (D)	Sub (U)	Sub (D)	Float (U)	Float (D)
Elk	0.4	1.96 ± 0.34	NA	4.61 ± 0.28	NA	4.24 ± 2.38	NA
Thistledew	0.8	1.32 ± 0.29	NA	5.56 ± 0.99	NA	3.17 ± 1.11	NA
Upper Cullen	7.3	2.30 ± 0.14	0.96 ± 0.22	5.91 ± 1.00	5.05 ± 0.25	21.79 ± 5.09	2.68 ± 0.46
Portage	13.4	0.57 ± 0.22	0.17 ± 0.11	3.57 ± 0.56	3.33 ± 0.38	0.17 ± 0.12	0.19 ± 0.19
Eagle	20.3	2.13 ± 0.31	0.65 ± 0.46	11.73 ± 1.51	6.20 ± 0.83	23.63 ± 6.15	7.65 ± 1.32
Gilbert	20.7	2.18 ± 0.47	0.29 ± 0.12	5.91 ± 0.59	4.60 ± 0.97	9.09 ± 2.25	5.88 ± 4.54
Horseshoe	24.8	0.77 ± 0.26	0.50 ± 0.45	4.31 ± 0.43	3.44 ± 0.49	4.63 ± 3.20	4.59 ± 4.59
Hand	24.9	0.94 ± 0.18	0.80 ± 0.33	6.26 ± 0.60	5.41 ± 0.37	34.47 ± 7.89	21.25 ± 10.30
Gladstone	34.4	2.81 ± 0.38	0.91 ± 0.67	5.36 ± 0.82	5.82 ± 1.95	13.72 ± 5.19	1.36 ± 0.74
Bass	39.1	0.08 ± 0.04	0.00 ± 0.00	2.76 ± 0.43	2.77 ± 0.72	1.07 ± 0.48	0.00 ± 0.00
Girl	46.0	1.10 ± 0.24	0.68 ± 0.31	7.74 ± 1.63	6.00 ± 0.99	15.10 ± 3.04	5.36 ± 2.91

Table 6. Parameter estimates from the binomial generalized linear mixed model examining presence of emergent species (logit-transformed) in relation to distance to the nearest dock in meters (Dist), floating-leaf macrophyte cover (Float), substrate texture (Substrate: coarse, mix, sand, fine), and water depth in meters (Depth).

	Estimate	SE	*Z*	*P*
Intercept	-2.63	0.44	-5.88	<0.001
Dist	0.32	0.02	13.35	<0.001
Float	-0.02	0.01	-3.03	0.002
Substrate:fine	3.13	0.54	5.80	<0.001
Substrate:mix	1.71	0.34	4.98	<0.001
Substrate:sand	1.64	0.33	5.00	<0.001
Depth	-4.05	0.23	-17.37	<0.001

Table 7. Parameter estimates from linear mixed models examining responses of submerged biovolume (Sub) and floating-leaf macrophyte cover (Float) in relation to a suite of local factors, including distance to the nearest dock in meters (Dist), presence/absence of emergent species (pEm), substrate texture (Substrate: coarse, mix, sand, fine), and water depth in meters (Depth). Submerged biovolume responses were transformed using ln(+1), and floating-leaf cover responses were square-root transformed.

Response	Predictor	Estimate	SE	df	*T*	*P*
Sub	Intercept	0.24	0.113	3171	2.09	0.04
	Dist	0.03	0.004	3171	8.92	<0.001
	pEm	0.07	0.028	3171	2.46	<0.001
	Float	0.002	0.001	3171	2.15	0.014
	Substrate:fine	0.59	0.088	3171	6.73	0.031
	Substrate:mix	0.36	0.055	3171	6.58	<0.001
	Substrate:sand	0.50	0.041	3171	10.1	<0.001
	Depth	0.84	0.031	3171	27.08	<0.001
Float	Intercept	-0.58	0.20	3171	-2.82	0.005
	Dist	0.13	0.01	3171	12.79	<0.001
	pEm	-0.23	0.08	3171	-2.98	0.003
	Sub	0.08	0.01	3171	7.73	<0.001
	Substrate:fine	1.48	0.24	3171	6.03	<0.001
	Substrate:mix	0.30	0.15	3171	1.97	0.049
	Substrate:sand	0.02	0.14	3171	0.13	0.894
	Depth	0.68	0.09	3171	7.68	<0.001

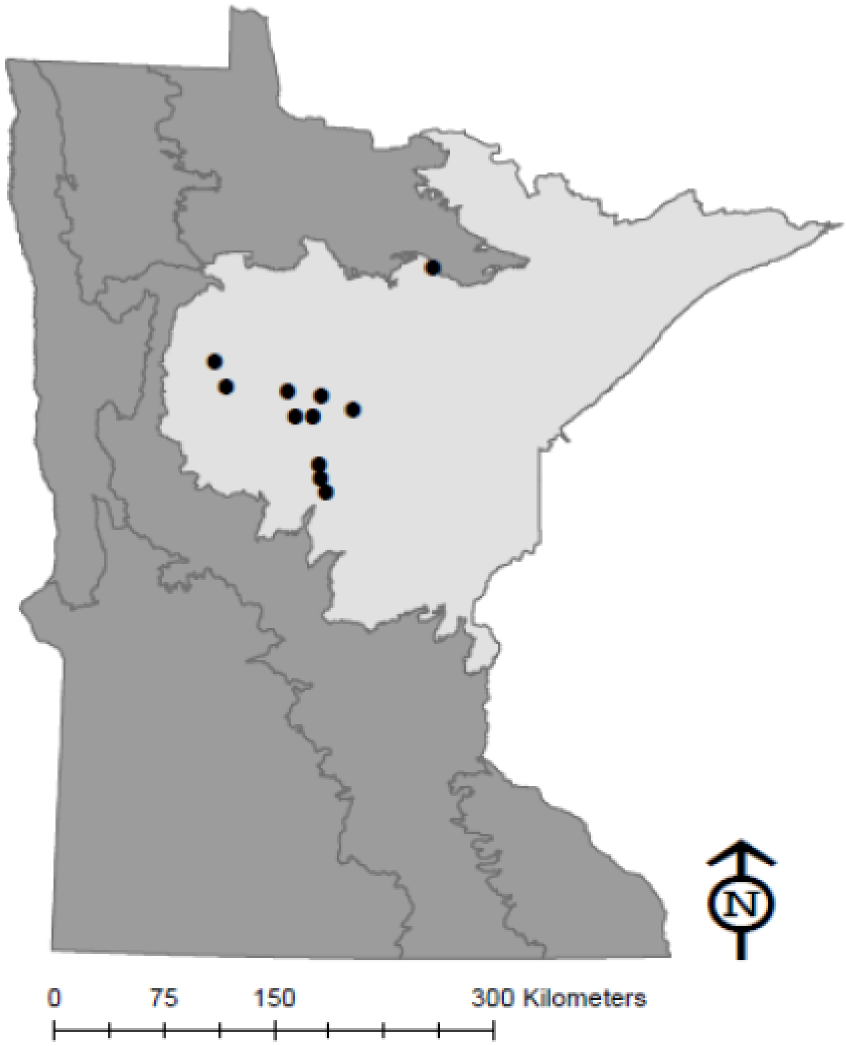

Figure 1. Locations of the 11 study lakes (black circles) within the Northern Lakes and Forests Ecoregion of Minnesota (light gray area).

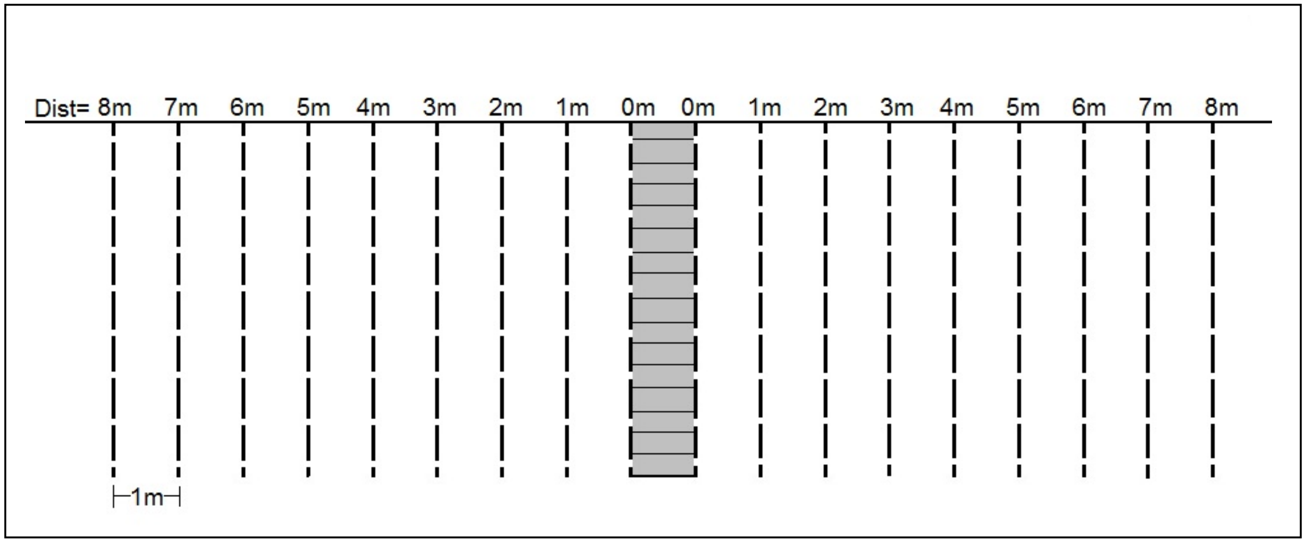

Figure 2. Example habitat sampling scheme with the shoreline located at the top of the figure. Nine sampling transects (dashed lines) were sampled on each side of the residential dock (gray rectangle). Transects began along the edges of the dock (Distance= 0m) and were spaced at 1m intervals until a distance of 8m was reached on either side.

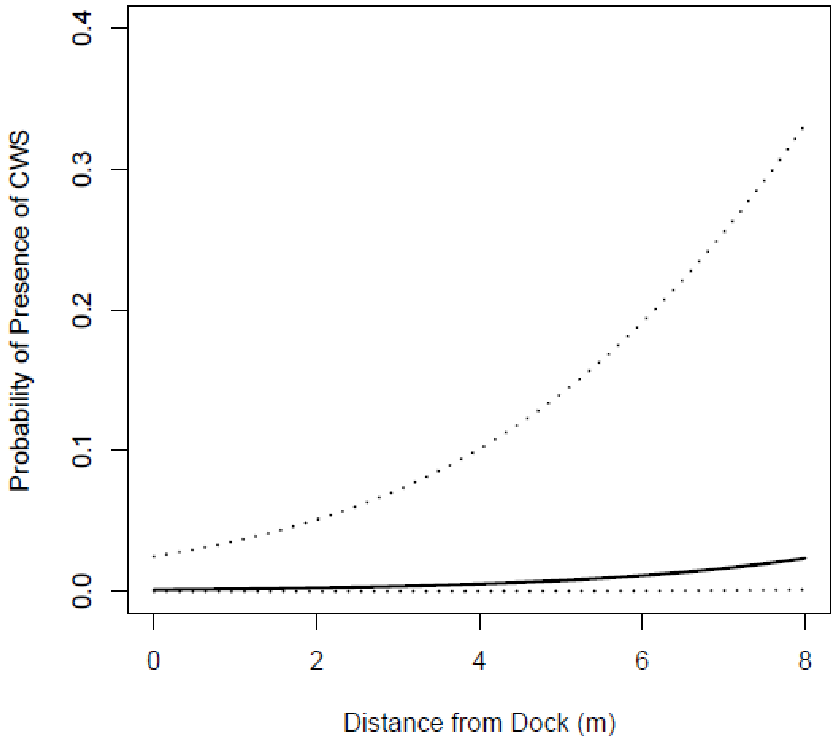

Figure 3. Predicted probability of CWS presence, pCWS, increases with distance to the nearest dock. The mean response is shown by the solid line, and dotted lines indicate 95% confidence intervals.

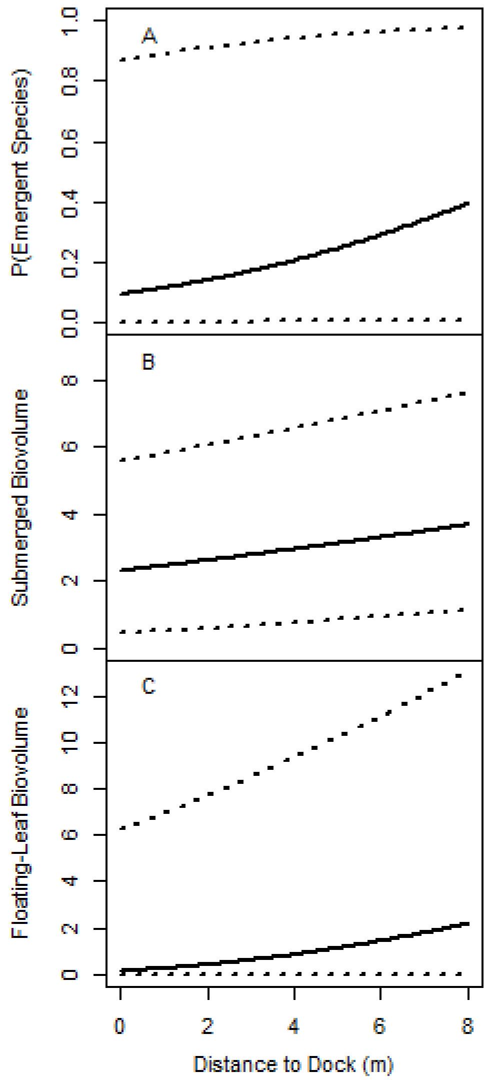

Figure 4. Presence of emergent species (A), submerged biovolume (B), and floating-leaf cover (C) in relation to distance to the nearest dock structure. The solid black lines indicate the model estimates and the dotted lines represent 95% confidence intervals.

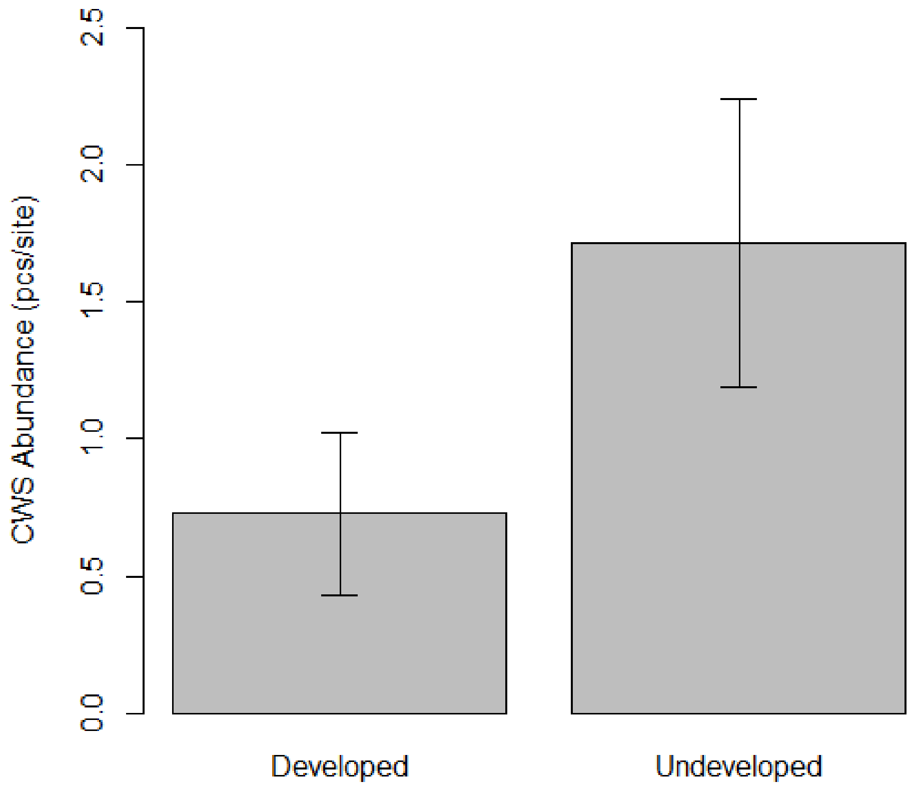

Figure 5. Mean abundance of coarse woody structure (CWS) varied significantly between site types. The mean abundance at developed sites was 0.73 (SE, 0.15) and 1.72 (SE, 0.27) at undeveloped sites. Whiskers indicate 95% confidence intervals.

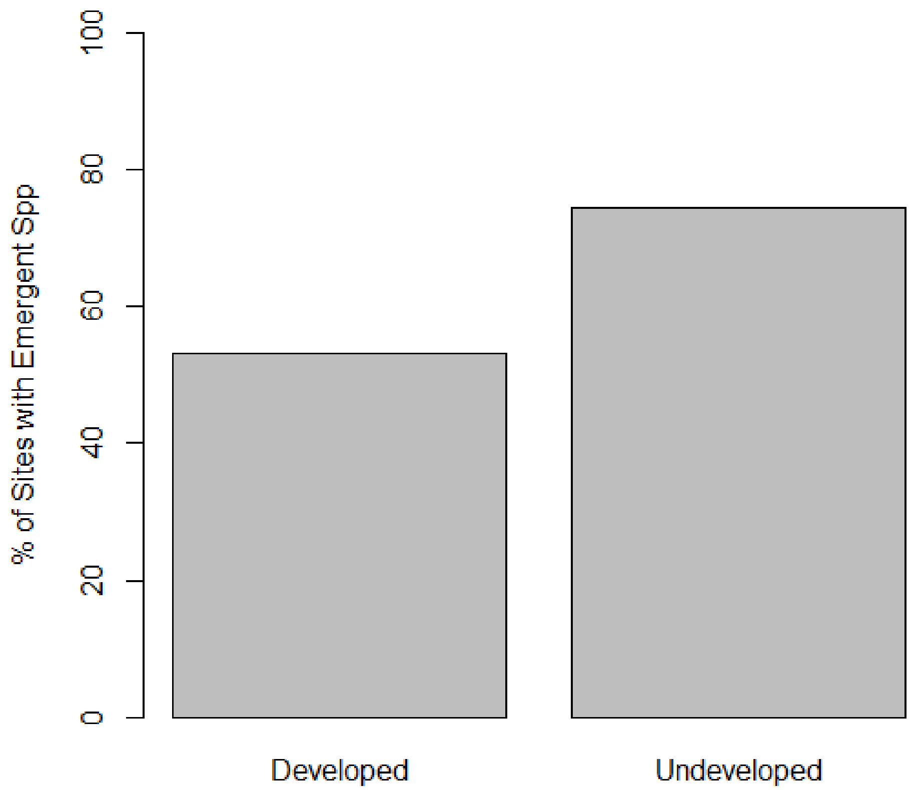

Figure 6. The presence of emergent species varied significantly with site type. Whereas emergent species were present at only 53% of the developed sites sampled, they were present at 74% of undeveloped sites.

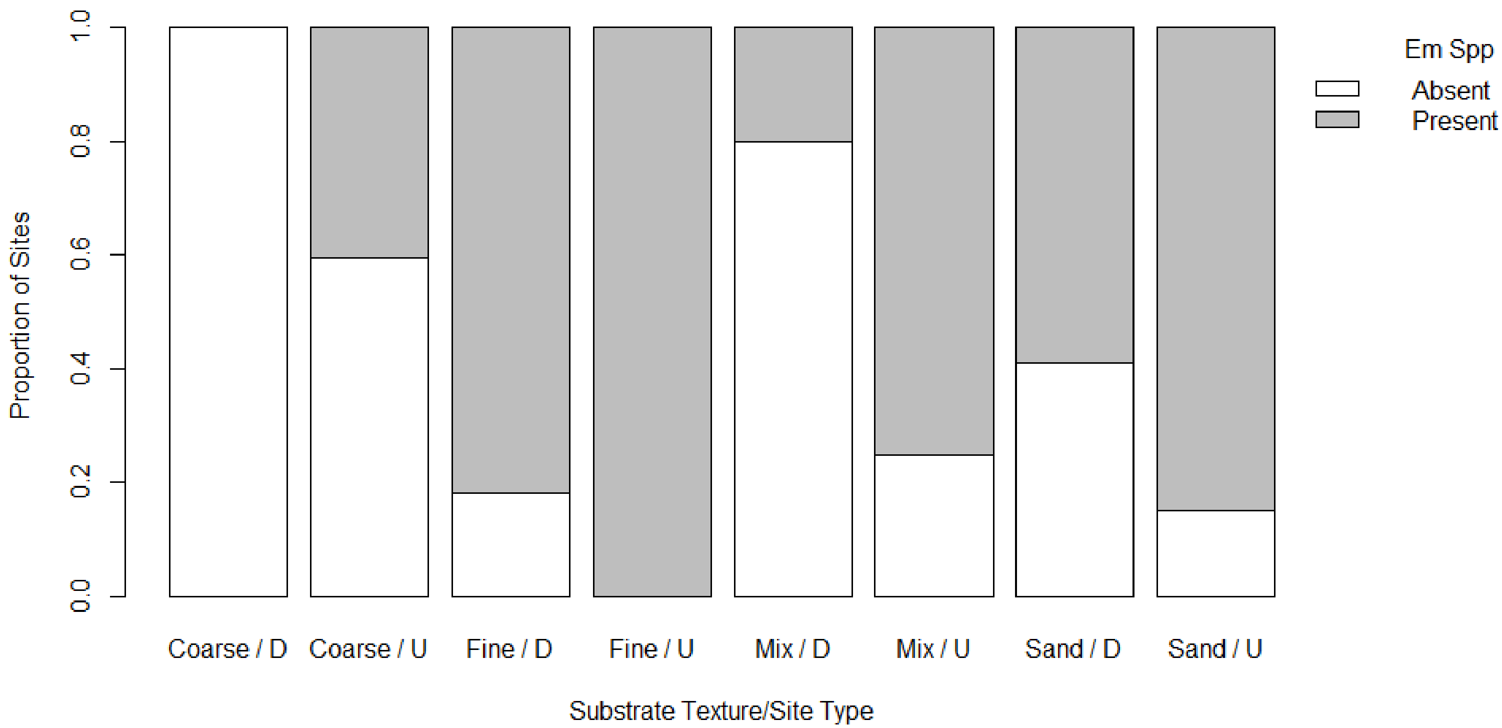

Figure 7. Presence of emergent species varied greatly with substrate texture and site type. Emergent species were present (gray) at all sites with fine substrates, and absent (white) from all sites with coarse substrates. Although presence of emergent species varied with substrate texture, emergent species were more frequently observed at undeveloped (U) sites than developed (D) sites.

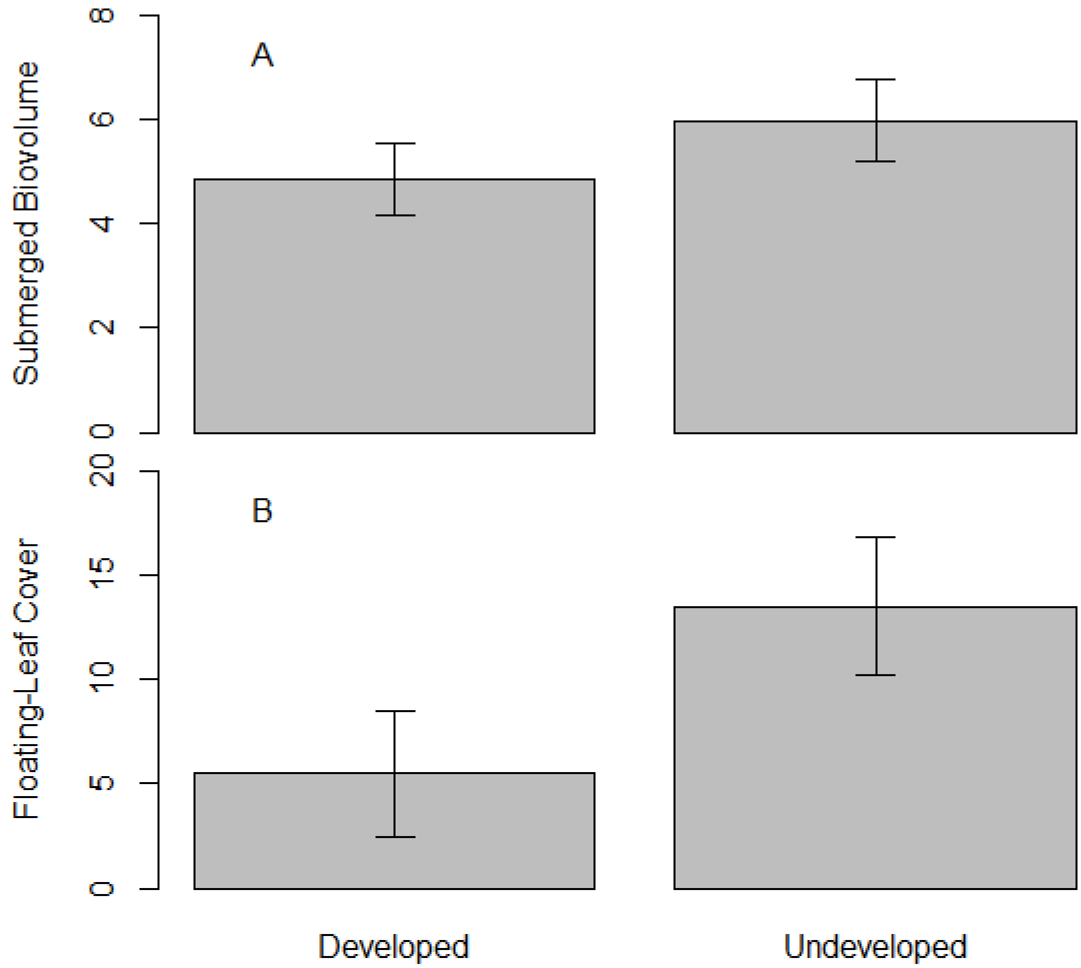

Figure 8. Mean abundance of submerged biovolume (A) did not differ across site type (*P*= 0.10). Floating-leaf cover (B) was more variable across site type, with undeveloped sites exhibiting significantly higher mean biovolume than developed sites. Whiskers represent 95% confidence intervals.

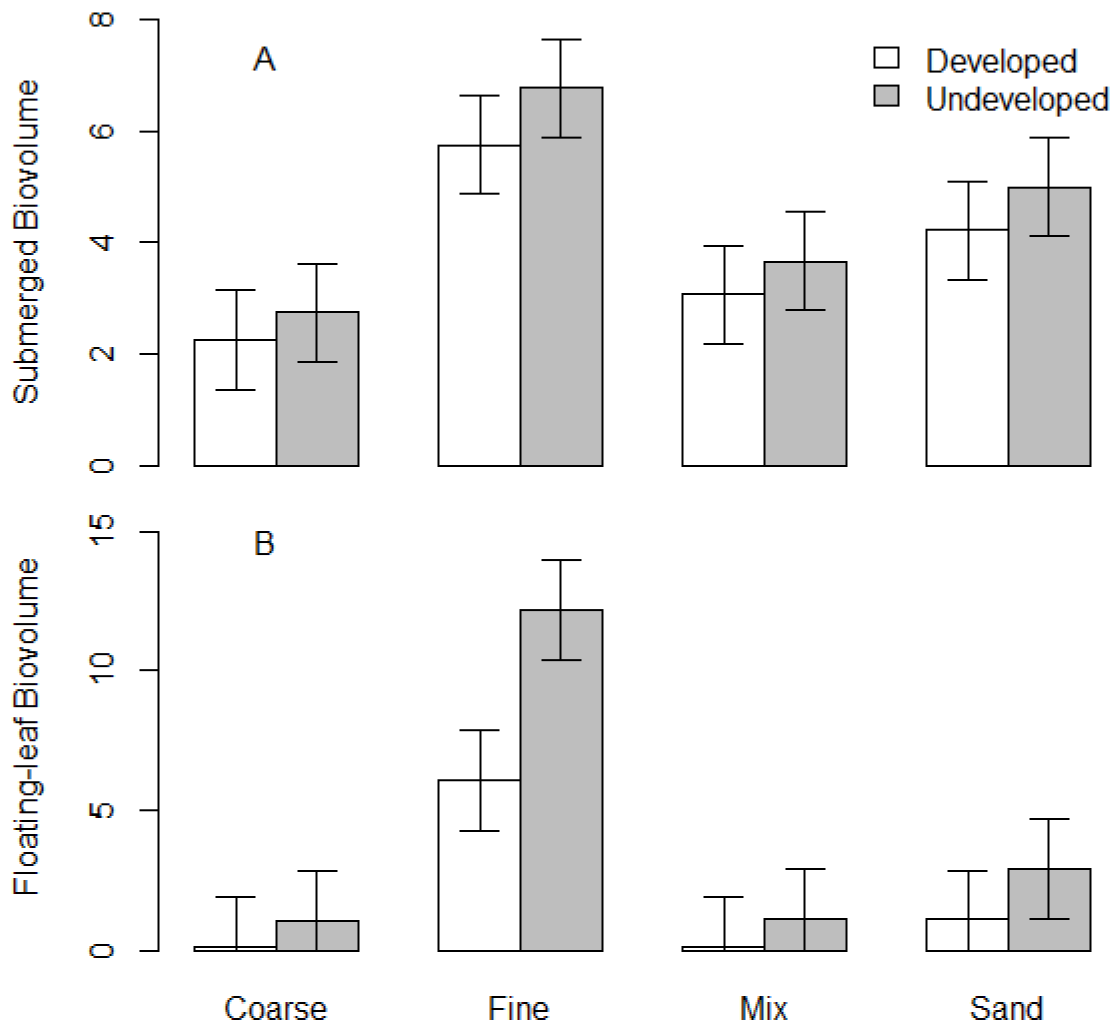

Figure 9. Submerged (A) and floating-leaf (B) biovolume varied as a function of both site type and substrate texture. Undeveloped sites (gray) consistently exhibited higher mean biovolume than developed sites (white). Whereas fine substrates supported the greatest abundance of submerged and floating-leaf vegetation, coarse substrates were associated with the lowest macrophyte abundances. Whiskers indicate 95% confidence intervals. Submerged and floating-leaf biovolume varied significantly across the four substrate categories.

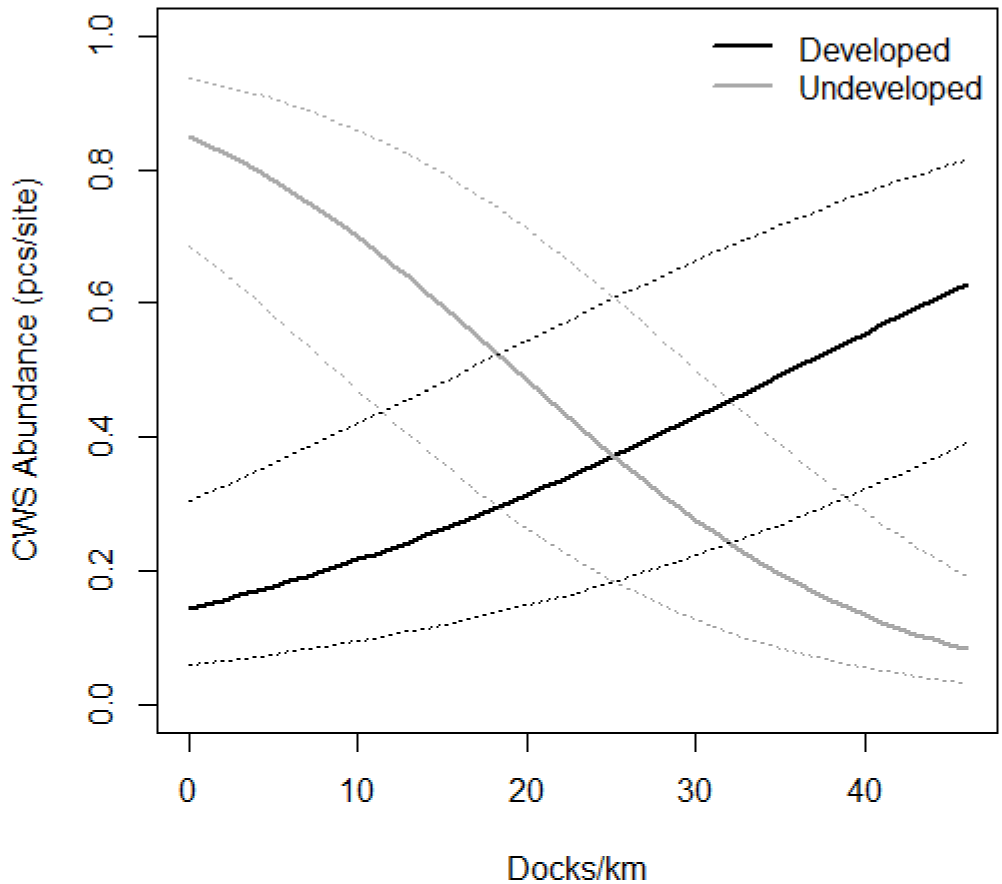

Figure 10. Site-wide abundance of coarse woody structure (CWS) was related to the interaction between site type (developed/undeveloped) and lake-wide dock density, in which expected CWS abundance within undeveloped sites (gray line) decreased as lake-wide development increased. The model indicated that at moderately high development densities, approximately 25 docks per kilometer, CWS abundance within undeveloped sites equaled that within developed sites (black line). Dotted lines represent 95% confidence intervals.

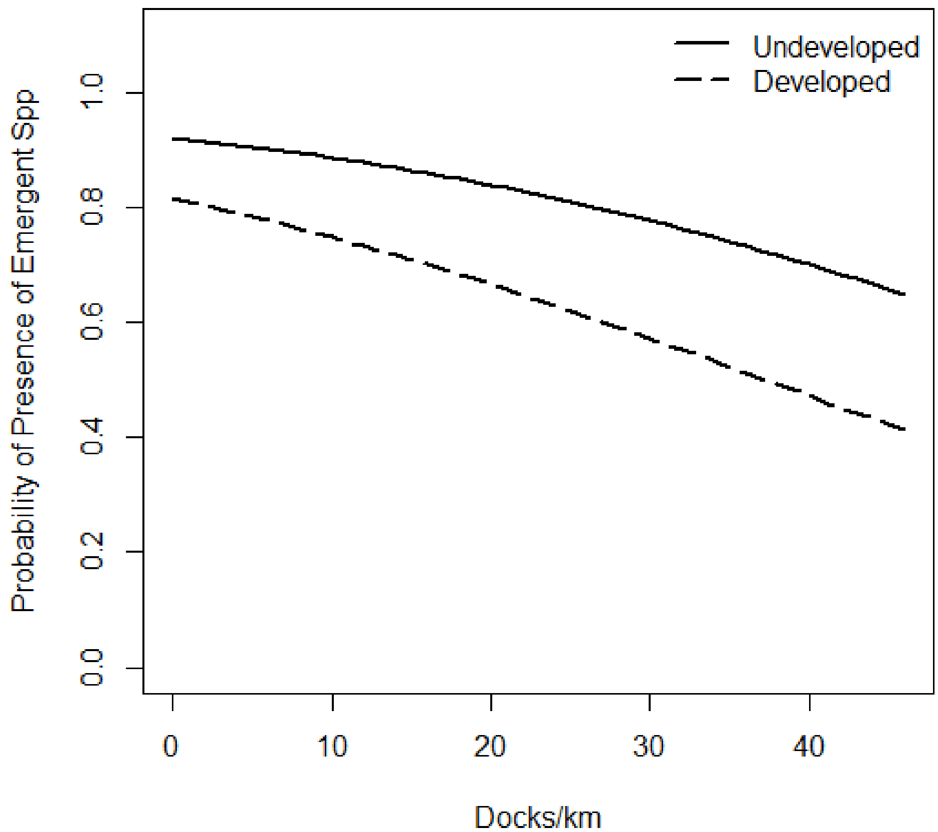

Figure 11. Probability of presence of emergent vegetation was affected by a combination of site type (developed/undeveloped) and lake-wide dock density. Both site types were negatively related to dock density; however, emergent species were more likely to occur at undeveloped sites (solid line) than developed sites (dashed line).

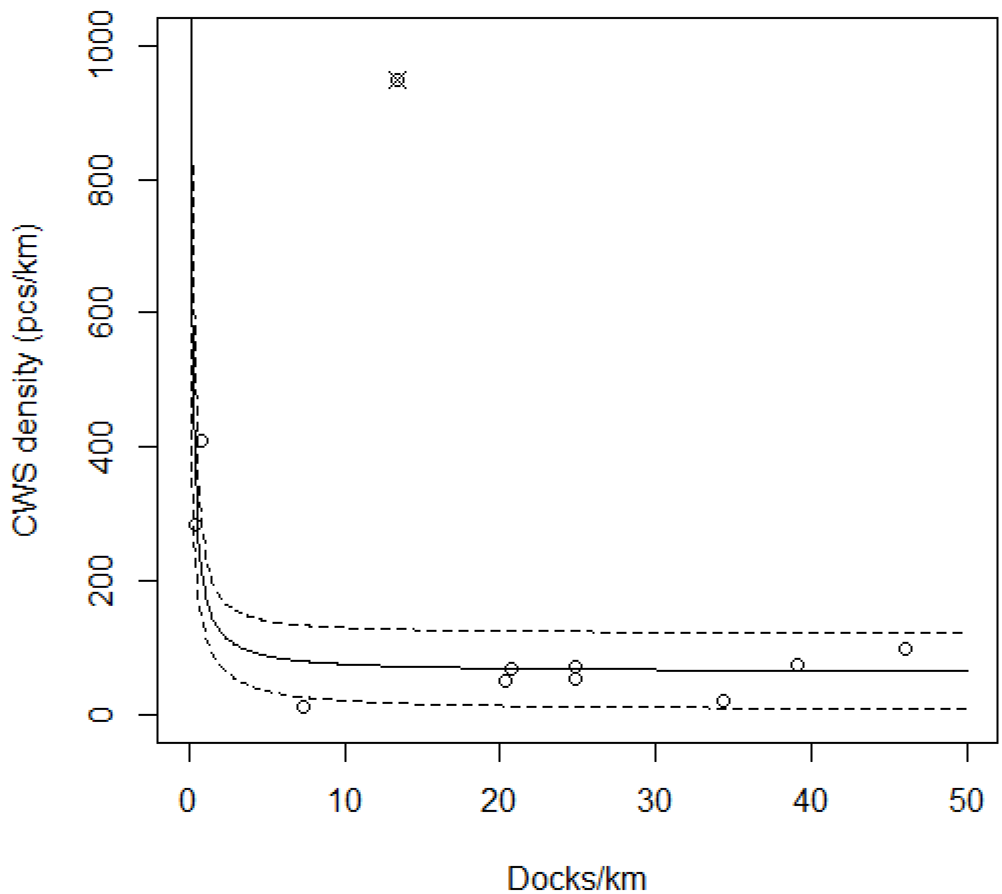

Figure 12. Estimated lake-wide density of coarse woody structure (CWS) declines dramatically as lake-wide dock density increases from 0 to 5 docks per kilometer. Beyond development densities of 5 docks per kilometer, CWS density was relatively constant at approximately 100 pieces per kilometer. The high outlying point with the "x" through the middle corresponds to Portage lake, which was excluded from the model. The model (solid line) explains approximately 60% of the variation in CWS density. Dashed lines represent 95% confidence intervals.

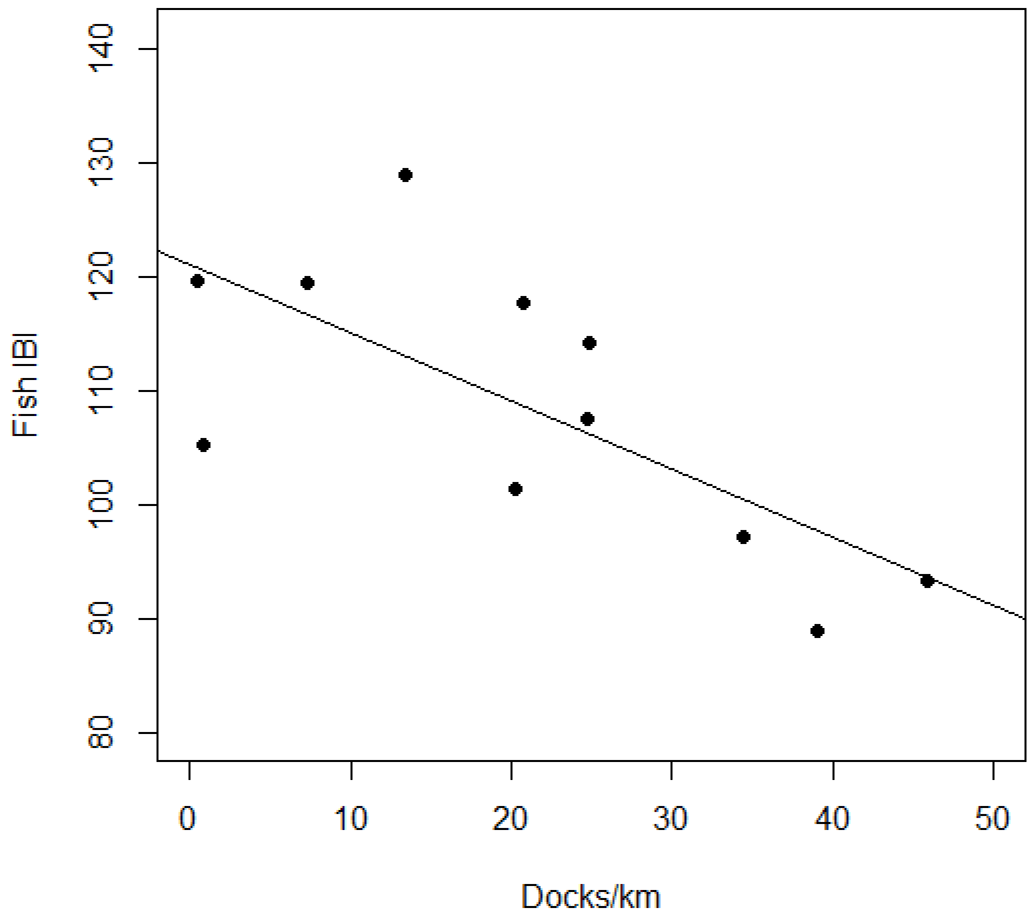

Figure 13. The fish-based Index of Biological Integrity (Fish IBI) was significantly and negatively related to lake-wide dock density within the 11 study lakes. The linear model explains approximately 45% of the variation in Fish IBI scores.