Whole-lake influences of littoral structural complexity and prey body morphology on fish predator–prey interactions


Abstract – We used a longline tethering method to examine the relationship between prey refugia, prey body morphology and the location and magnitude of predation mortality within an individual lake and among three lakes that differed in coarse woody habitat (CWH) and aquatic macrophyte abundances. Predation events were lowest in the macrophyte and/or CWH refuges, peaked at or just beyond the refuge edge and declined in pelagic portions of the lakes. Predation risk at the refuge edge and just beyond was positively correlated with the abundance of littoral refuge. In contrast, predation events within the refuge and in the pelagic zone were negatively correlated with littoral refuge abundance. Deep-bodied and spiny prey morphologies were less vulnerable to predation than fusiform prey lacking fin spines. The structural complexity of littoral zones and prey fish body morphology may influence the outcome of predator–prey interactions and ultimately determine fish species assemblages in lakes.

Introduction

Elucidating how refuge habitats, such as coarse woody habitat (CWH) and macrophytes, influence fish communities and predator–prey interactions is of fundamental and applied concern as humans continue to alter the dynamics that occur at the terrestrial–aquatic interface of aquatic ecosystems. For example, CWH and aquatic macrophyte abundances are negatively correlated with lakeshore residential development in northern Minnesota and Wisconsin lakes (Christensen et al. 1996; Radomski & Goeman 2001; Jennings et al. 2003; Sugden-Newbery 2004). Critical habitat loss has been implicated in the extirpation of a diverse range of plant and animal taxa across the world’s ecosystems (Tilman et al. 1994; Chapin et al. 2000). A decrease in size-specific fish growth rates and changes in fish community spatial distribution along an increasing development gradient are examples of patterns that emerge from simplification of littoral zone habitats in lakes (Werner et al. 1977; Schindler et al. 2000; Scheuerell & Schindler 2004).

Structural complexity in aquatic environments mediates predator–prey interactions by providing refuge for small fishes. Within many lakes, littoral habitats vary from sand/gravel substrates with little vegetation or submerged logs and branches, to densely vegetated areas with abundant woody habitat. Predation rates may then vary with respect to the spatial variation in habitat structure. For example, macrophytes and CWH afford refuge by lowering the encounter rate between predators and prey (Anderson 1984). Structure causes visual interference, thus preventing predators from seeing potential prey (Savino & Stein 1982). Small fishes are also better able to move through interstices than large predators.
Table 1. Summary of the location, physical characteristics, mean coarse woody habitat (CWH) and mean aquatic macrophyte characteristics of the three lakes examined in this study.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Surface area (ha)</th>
<th>Maximum depth (m)</th>
<th>Secchi depth (m)</th>
<th>CWH density (no. per km)</th>
<th>Macrophyte density (stems m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crampton (WI/MI)</td>
<td>24</td>
<td>15</td>
<td>4.3</td>
<td>965</td>
<td>100</td>
</tr>
<tr>
<td>Bay (MI)</td>
<td>69</td>
<td>12</td>
<td>4.3</td>
<td>442</td>
<td>30</td>
</tr>
<tr>
<td>Little Rock (WI)</td>
<td>18</td>
<td>10</td>
<td>3.8</td>
<td>344</td>
<td>5</td>
</tr>
</tbody>
</table>

Physical and CWH characteristics as reported in Christensen et al. (1996) and Schindler et al. (2000). No dwellings were present on any of the lakes.

Methods

Study area

Bay (Gogebic County, MI) and Crampton (border of Gogebic and Vilas County, WI) lakes are located within the University of Notre Dame Environmental Research Center (UNDERC) property where public access and fishing is prohibited (Carpenter & Kitchell 1993). Little Rock Lake (Vilas County) is also closed to public access and fishing (Frost et al. 1999). The lakes are oligotrophic, similar in limnological characteristics and have no lakeshore residential development (Table 1). The dominant piscivore in all three lakes, and the only top predator in Crampton and Little Rock lakes, is largemouth bass. Bass densities in Crampton and Little Rock lakes were similar in 2001 [Crampton = 33 bass ha⁻¹ (95% confidence interval 20–83); Little Rock = 59 bass ha⁻¹ (95% confidence interval 47–78)]. No largemouth bass population estimate was available for Bay Lake; however, a 2001 electrofishing survey of Bay Lake resulted in 22 largemouth bass per hour of electroshocking, seven smallmouth bass (Micropterus dolomieu, Lacepede 1802) per hour and zero northern pike (Esox lucius, Linnaeus 1758) per hour. Whole-lake CWH densities in Bay and Crampton lakes were taken from Christensen et al. (1996). Briefly, CWH abundances were measured in five to 13 randomly selected 40-m transects along the 0.5-m depth contour of the lake (Christensen et al. 1996). All CWH >5 cm in diameter that intersected the transect line were counted and measured with a caliper (Christensen et al. 1996). Measurements of CWH abundance were relative and represented a standardised subset of the total CWH (Christensen et al. 1996). We measured whole-lake CWH for Little Rock Lake and at specific sites in Crampton Lake in the summer of 2001 using the same protocol as Christensen et al. (1996). CWH in Crampton approached some of the highest densities observed in regional lakes, while Bay and Little Rock lakes had intermediate densities (Christensen et al. 1996; Sugden-Newbery 2004). We used 1 m² quadrats to measure the aquatic macrophyte stem density at the 0.5-m depth contour of each site. Crampton Lake had a two- to threefold higher abundance of littoral refuge than Bay or Little Rock lakes (Table 1).
Tethering

We developed a longline tethering system to quantify where predation mortality occurs as a function of depth, distance from shore, littoral zone structure and prey fish body morphology. Longlines consisted of a length of rope attached to shore, extended perpendicularly and anchored with 5-kg weights. The longline was buoyed at the surface by regularly spaced plastic floats and each prey item was tethered below each float on either a 0.75 or 1 m length of monofilament fishing line as described below. Therefore, each prey item was tethered at ≤0.75 or 1 m below the surface of the water. Each tether ended with a snap-swivel for prey attachment and was deployed for 1 h. Each prey item was attached to the tether by puncturing the skin just posterior to the dentary bone (i.e., lower jaw) with the open snap-swivel and then closing the snap-swivel. We assumed that the absence of a prey fish or physical damage to the body or fins of any remaining prey, after 1 h corresponded to a predation event at that tether.

Quantifying predation mortality – within lake

We conducted tethering trials in Crampton Lake from June to August 2001 to determine the influence of habitat type (CWH, macrophyte, sand/gravel) and prey fish body morphology on patterns of predation. Each longline was 40 m long with 0.75 m long tethers spaced at 5-m intervals for a total of 11 tethers. Yellow perch ranging in size from 80 to 110 (mean = 92; S.D. = 9.07) mm total length, and fathead minnow from 50 to 80 (mean = 61; S.D. = 7.18) mm were used as prey items. Tethered bluegill/pumpkinseed sizes ranged from 60 to 80 (mean = 74; S.D. = 6.49) mm total length, and pumpkinseed from 60 to 90 (mean = 76; S.D. = 7.00) mm total length. We used a generalised linear model (GLM) to compare predation mortality among habitats and body morphologies. We used predation event as our response variable (binary) and refuge (binary), edge (binary) and prey fish species (categorical) as predictor variables ($\alpha = 0.05$). We also examined all interactions of the predictor variables. Interaction terms were dropped from the final models if $P > 0.05$. Location within the refuge was at the 4-m position and the refuge edge at the 12-m tether position. Average refuge edge distance (distance to edge of aquatic macrophytes and/or CWH) was 10 m from shoreline and was the mean refuge edge distance across all sites.

Quantifying predation mortality – among lakes

During August of 1999 and 2001, we conducted a total of two tethering trial replicates at eight sites for Crampton and Bay lakes ($N = 16$ longlines, 176 tethers) and two replicates at 12 sites for Little Rock Lake ($N = 24$ longlines, 264 tethers). Tethering sites were distributed at regularly spaced intervals throughout the littoral zone of each lake to provide a whole-lake perspective of fish predator–prey interactions. Each longline was 51 m long with 1-m long tethers spaced at 5-m intervals for a total of 11 tethers. Yellow perch ranging in size from 80 to 110 (mean = 92; S.D. = 9.07) mm total length were used as prey items. We used a GLM to identify factors influencing patterns in predation among lakes. We used predation event (Crampton, $N = 176$; Bay, $N = 176$; Little Rock, $N = 264$) as our binary response variable and macrophyte stem density (no. per m$^2$), depth of the lake at the tether position (m), yellow perch total length (mm), refuge (binary) and edge (binary) as predictor variables ($\alpha = 0.05$). CWH abundance was not used as a predictor variable in the models because values were based on whole-lake estimates and thus did not differ between tethering sites within each lake (Table 1). In models with multiple significant predictors, all interactions were examined and removed from the model if $P > 0.05$. We used a Kolmogorov–Smirnov test to check for potential differences in the distributions of perch predation mortality (no. consumed/no. tethered) among lakes ($\alpha = 0.05$) (Sokal & Rohlf 1995).

Results

Predation mortality – within lake

The strongest incidence of predation was observed at or just beyond the edges of macrophyte and CWH sites for all three prey morphologies in Crampton Lake. Predation risk increased rapidly with distance

<table>
<thead>
<tr>
<th>Site</th>
<th>Edge distance (m)</th>
<th>CWH density (no. per km)</th>
<th>Macrophyte density (stems·m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWH1</td>
<td>4.3</td>
<td>2900</td>
<td>15</td>
</tr>
<tr>
<td>CWH2</td>
<td>4.9</td>
<td>1900</td>
<td>28</td>
</tr>
<tr>
<td>CWH3</td>
<td>1.2</td>
<td>1600</td>
<td>20</td>
</tr>
<tr>
<td>CWH4</td>
<td>0.8</td>
<td>1700</td>
<td>0</td>
</tr>
<tr>
<td>MP1</td>
<td>7.3</td>
<td>600</td>
<td>151</td>
</tr>
<tr>
<td>MP2</td>
<td>5.5</td>
<td>1300</td>
<td>120</td>
</tr>
<tr>
<td>MP3</td>
<td>6.4</td>
<td>300</td>
<td>77</td>
</tr>
<tr>
<td>MP4</td>
<td>8.2</td>
<td>1000</td>
<td>61</td>
</tr>
<tr>
<td>SG1</td>
<td>1.5</td>
<td>200</td>
<td>16</td>
</tr>
<tr>
<td>SG2</td>
<td>0.8</td>
<td>300</td>
<td>0</td>
</tr>
<tr>
<td>SG3</td>
<td>0</td>
<td>600</td>
<td>0</td>
</tr>
<tr>
<td>SG4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 2. Summary of the coarse woody habitat (CWH) and macrophyte stem densities within and among individual CWH, macrophyte (MP) and sand/gravel sites in Crampton Lake and associated refuge edge distances.
from shore, peaked at or just beyond the CWH and macrophyte refuge edge, and decreased into the pelagic zone (i.e., beyond the refuge edge) (Fig. 1). Prey location within the CWH (GLM, \( N = 250, \text{d.f.} = 1,248, f = 21.2, P < 0.001 \)) or macrophyte (GLM, \( N = 250, \text{d.f.} = 1,248, f = 28.1, P < 0.001 \)) refuge significantly decreased predation risk and location on the CWH edge increased predation risk (GLM, \( N = 250, \text{d.f.} = 1,248, f = 4.4, P < 0.001 \)). Mortality in sand/gravel sites was generally lower than CWH or macrophyte sites and uniform at all distances from shore for each prey morphology (Fig. 1).

In general, fin spines and body depth decreased predation risk; yellow perch were least vulnerable, followed by pumpkinseed/bluegill and then fathead minnow. Discrete separations in species vulnerability were observed in the sand/gravel sites, but were less obvious in CWH and macrophyte sites (Fig. 1).

**Predation mortality – among lakes**

Structural complexity, depth and location of the tethered perch influenced predation mortality across the gradient of lakes. In Crampton Lake, increased macrophyte abundances and depth reduced the frequency of predation events, while location at the refuge edge increased predation events (GLM, \( N = 176, \text{d.f.} = 3,172, f = 14.4, P < 0.001 \)). Perch mortality was also positively correlated with locations on or near the refuge edge in Bay Lake (GLM, \( N = 176, \text{d.f.} = 1,174, f = 14.8, P < 0.001 \)). No significant predictors were found to explain predation mortality in Little Rock Lake (GLM, \( N = 264, \text{nonsignificant constant, } P > 0.05 \)).

Distributions of predation mortality as a function of distance from shore were different among lakes. Proximity to the shoreline provided refuge and mortality peaked immediately adjacent to the refuge edge in each lake (Fig. 2). Crampton Lake offered the safest refuge, whereas Bay and Little Rock were less safe (Fig. 2). Unlike Little Rock Lake, high mortality did not persist into the pelagic zones of Crampton and Bay lakes (Fig. 2). The distributions (i.e., distance from shore) of predation mortality among lakes were significantly different between Crampton and Little Rock lake (K–S test, \( P = 0.017 \)) and Bay and Little Rock lake.
Rock lake (K–S test, \( P = 0.003 \)), but not between Crampton and Bay lake (K–S test, \( P > 0.05 \)).

The depth range accounting for the highest total mortality was similar for all lakes, but the magnitude decreased in lakes with less refuge. Depths of 0.5–1.5 m had the highest predation rates of any 1 m depth range. This depth range accounted for 50%, 40% and 26% of the total mortality observed in Crampton, Bay and Little Rock lakes, respectively. The depth ranges that accounted for 90% of the total mortality observed increased in lakes with less refuge (Fig. 3). The depth range for 90% mortality was 0.5–4.0 m in Crampton Lake, 0.5–6.5 m in Bay Lake and 0.5–7 m in Little Rock Lake.

**Discussion**

**Predation mortality – within lakes**

At a local scale, predation mortality in an individual lake was dependent on the complexity of structural refuges and the location of the prey relative to structural refuges. The amount of structural refuge present, particularly macrophytes, showed the strongest effect on predation mortality. Macrophyte assemblages can likely reach higher levels of structural complexity than pieces or aggregations of CWH (Dibble et al. 1996; Valley & Bremigan 2002). Together, the structural complexity of macrophytes and CWH can cause visual interference and, at high densities, decrease predator foraging success to near zero (Crowder & Cooper 1982; Savino & Stein 1982; Gotceitas & Colgan 1989).

Prey survivorship was greater in shallow water and with deeper bottom depths likely as a consequence of prey being able to use the bottom as a refuge in shallow water and the distribution of bass in each system. Some fish tethered within refuge habitats could remain on the bottom, thus preventing detection by predators. Additionally, the distribution of bass predators varied among lakes. In an independent assessment of abundance and distribution for Crampton Lake fishes, none were captured in the pelagic zone (i.e., middle of lake) using vertical gillnets and purse seines or were any observed during pelagic hydroacoustic assessments (Thomas R. Hrabik, unpublished work), which supports the near-shore distribution of predation events observed. In contrast, bass observed during snorkelling surveys (Werner et al. 1977) in Little Rock Lake often used depths greater than 1 m, which may explain high mortality rates into the pelagic zone (Sass 2004).

A perch located on or just beyond the refuge edge had a lower chance of survival than elsewhere in Crampton and Bay lakes. Edge habitats have often been observed as areas of intense fish predator–prey interactions because of decreased refuge for prey.
and increased foraging opportunities for predators (Walters & Juanes 1993; Olson et al. 1998; Walters et al. 2000). Increased edge-related foraging opportunities have also been noted for avian (Estrada et al. 2002), mammalian and reptilian (Chalfoun et al. 2002) predators. In lakes with low amounts of structure, such as Little Rock Lake, predation risk may be intense and widespread throughout the entire lake. In open habitats of otherwise structurally complex lakes, such as sand/gravel areas of Crampton Lake, predation risk may also be widespread. However, small fishes may avoid open habitats leading to fewer piscivores foraging there and an overall decreased risk of predation. In such systems, predators may still key in on more complex habitats despite decreases in prey vulnerability. Structural complexity may serve to concentrate fish predator–prey interactions by attracting both prey and predator fish (Newbrey et al. 2005). In lakes that contain high amounts of structural habitat in the littoral zone, prey fish may avoid open habitats, thus making it unprofitable for predators to forage there. In lakes with an overall lower amount of habitat structure, predator–prey interactions may be distributed more evenly throughout the lake.

Soft-rayed prey was more vulnerable to predation than spiny prey in macrophyte and sand/gravel areas, although this pattern was not observed in CWH habitats. Our results may suggest that predators in CWH areas were not gape limited at the sizes of prey used in this study, but may have been if larger prey were tethered (Moody et al. 1983; Hoyle & Keast 1987; Einfalt & Wahl 1997). High vulnerabilities of fathead minnow were consistent with their fusiform body, lack of spiny rays, small size and ability to release a chemical alarm signal. The release of Schreckstoff [i.e., a chemical alarm substance released by special epidermal cells when the skin is broken that causes conspecifics or closely related fish species to display predator avoidance behaviours (Moyle & Cech 2000)] can warn conspecifics of danger, but can also attract other piscivores leading to increased predation rates (Mathis et al. 1995; Chivers et al. 1996).

High vulnerability to predation and littoral habitat may structure fish species assemblages in lakes. For example, lakes in northern Wisconsin with piscivores generally have few or no cyprinid species, whereas neighbouring lakes with few or no piscivores are dominated by minnow species (Tonn & Magnuson 1982; He et al. 1993). While such distinct assemblages can undoubtedly arise from colonisation processes, our results suggest that small prey may also become increasingly vulnerable to piscivores when refuge habitat is lost. Over time, the removal of littoral habitat may lead to the decline of prey populations that depend on such habitats (Sass 2004).

Predation mortality – among lakes

Among lakes, perch survivorship was generally greater in refuge areas and at deeper bottom depths. In all lakes, shallow water (< 0.5 m) or sites close to shore functioned as a refuge for perch regardless of the structural complexity available in the littoral zone. Shallow water provides a refuge for prey species by decreasing the ability of a larger predator to forage successfully, regardless of the level of structural complexity present (Goodyear 1973; Power 1984; Matthews et al. 1986). Increased structural complexity can also lead to safer shallow refuge areas as evidenced by the patterns observed in this study. In lakes with little structural complexity (e.g., Little Rock), shallow water may be the only refuge available. Littoral zone snorkelling surveys (Werner et al. 1977) in Little Rock Lake and gill net assessments have revealed that all perch, regardless of size, are confined to shallow waters less than 0.5 m deep and do not use pelagic areas of the lake (Sass 2004).

The relative safety of the Crampton Lake refuge likely results in heterogenous bass and perch distributions. According to Savino & Stein (1982), largemouth bass foraging success on bluegill decreases and bass foraging tactics change at a threshold level of simulated aquatic vegetation. Bass change from actively foraging to sit-and-wait predators in laboratory experiments as structural complexity of the refuge increases (Savino & Stein 1982). At low structural complexity, predator efficiency may be high and unhindered by the structure. As structural complexity increases, predator efficiency is restricted and, depending on the size-structure of the predator populations (Persson & Crowder 1997; Lundvall et al. 1999), predators may be effectively excluded from refuges at a threshold density of CWH or aquatic macrophytes (Glass 1971; Stein & Magnuson 1976; Savino & Stein 1982). The strong edge effect and lack of pelagic predation in Crampton Lake may suggest that bass are roaming the refuge edge in this system. Bass may be more actively foraging over wider areas and depths in Bay and Little Rock lakes as evidenced by higher pelagic predation rates.

Whole-lake predation mortality

Among all lakes, most predation events occurred at a consistent depth (0.5–1.5 m) that corresponded with the edge of the CWH/aquatic macrophyte refuge; bottom depths were positively correlated with distance from shore in all of our study lakes. The magnitude of total mortality present within this depth range was directly related to the abundance of the refuge habitat. For example, 50% of total perch...
mortality occurred within the 0.5–1.5 m depth range for Crampton Lake. This level of mortality suggests extremely intense predation risk because tethers were only set for 1 h. The first metre of depth beyond the edge of complex refuge habitats may be considered a strong filter through which fish must pass to gain access to the less risky open water (e.g., Crampton). Once in the open water, predation risk at any depth is reduced, but not eliminated. The first filter alone, however, may act to focus the distribution of prey fishes solely within refuge habitats (Werner & Hall 1988; Vander Zanden & Vadeboncoeur 2002). When the amount and complexity of the refuge decreases, this filter (0.5–1.5 m mortality; Bay Lake 40%, Little Rock Lake 26%) may not be as strong and predation risk will remain high into the pelagic zone as evidenced by the depth range of 90% mortality in Bay and Little Rock lakes (Werner & Hall 1988).

Fish predator–prey interactions and refuge loss

We have showed how fish communities interact in unperturbed lakes by using an ecosystem scale study in an environment minimally influenced by humans, which is important to our overall understanding of fish populations and the consequences of anthropogenic change upon them. Residential lakeshore development pressures have reduced the amount of littoral zone CWH and aquatic macrophytes in many lakes (Christensen et al. 1996; Radomski & Goeman 2001; Jennings et al. 2003) with unknown consequences to fish populations. However, a recent whole-lake removal of CWH has caused negative impacts on the abundance of the native prey fish (yellow perch) and growth rates of the native predator (largemouth bass) suggesting a negative effect of habitat loss (Sass 2004). Therefore, refuge in the form of CWH and aquatic macrophytes may influence lake and fish productivity, fish community structure and the persistence of predator and prey populations (Schindler et al. 2000; Vander Zanden & Vadeboncoeur 2002; Scheuerell & Schindler 2004). Perhaps the important role of refuge is most evident in the observation that its presence creates an environment that becomes the focal point and dominant habitat used by fishes in a particular lake. Decreases in the structural complexity of lake littoral zones may cause changes in fish species assemblages as a consequence of newly emerging predator–prey interactions.

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References
