The Effects of Natural Turbulence on Diurnal Fish Community Assemblages, Distribution, and Habitat Selection

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Abstract
The study of fish community assemblages and the myriad factors that determine their makeup, including wind-driven turbulence on lakes, is of great importance to fisheries resource management and policy. Studies done on coral reefs have concluded that morphology differences play important roles in the way fish react to turbulence. Translating this concept to a freshwater system, this study looked at turbulence on South Fishtail Bay, Douglas Lake, Michigan, and its effects on fish distributions and assemblages. Based on the morphological measure of body depth, it was hypothesized that deeper-bodied species, such as sunfish and perch, would show a greater aversion to turbulence than would shallow-bodies species, such as minnows. Data was limited and was sufficient only to corroborate the notion that yellow perch (*Perca flavescens*) and smallmouth bass (*Micropterus dolomieui*) do indeed seek refuge from turbulence in deeper waters, though results regarding the other species were inconclusive. A more thorough, all-encompassing method of data collection and analysis is a critical next step in assessing the relationship between turbulence and fish communities.

Introduction
Fisheries benefit from long-term studies of their fish assemblages, as information regarding fish development, community composition, and community stability in relation to physical variables can be gathered and utilized in various aspects of management and policy (Gido et al. 2000). In the case of turbulence, with global climate change expected to alter the frequency and intensity of storm events (and thus wave turbulence) in the near future, gaining a better understanding of the effects of turbulence on fish communities in lakes is crucial to fisheries management (Rose 2000).

Turbulence, a physical factor that describes unstable eddying flow, along with temperature, dissolved oxygen, and physical habitat, exerts an influence by challenging the physical capabilities of fishes, and thus helps to determine their fundamental niches. Turbulence exerts its influence on multiple levels. Turbulence can occur over a large range of energies, and thereby creates a challenge for fishes to maintain stability (Denny 1988; Webb 2006a). Turbulence further causes increased oxygenation and nutrient uptake into the water, increasing productivity that is beneficial (Webb 2006a). Wind can also cause vertical mixing, a process which serves to resuspend benthic matter, including diatoms, and affect plankton distributions (Demers et al. 1987; MacKenzie et al. 1994; Montgomery et al. 2000). For all of these reasons, turbulence is increasingly recognized for its relevance to fish behavior, habitat use, and distribution (Potts 1970; Webb 2006a).

Other physical variables, such as vegetation, habitat complexity, and temperature are known to exert influences on fish assemblages. Biotic factors include predation and interspecific competition (Mittelbach 1988; Wikramanayake 1990; Hinch et al. 1991; Diehl
Among the other major drivers of fish movements and assemblage composition are diel changes in fish behavior, which are believed to occur not only for resource partitioning purposes but also to facilitate thermoregulation, spawning, foraging, and predator avoidance (Wurtsbaugh & Li 1985; Wikramanayake 1990; Shoup et al. 2004).

In moving bodies of water, fish have been observed to occupy turbulent areas in response to habitat requirements, but also to utilize areas of lower turbulence among those suitable and to furthermore seek out both coarse and fine scale current refuges (Cotel et al. 2006; Webb 1998; Webb 2006b). On coral reefs, where wind is the major driver of turbulence, fish community assemblages and distributions have been shown to depend on wave exposure, particularly the swimming power of various species based on fin morphology, as quantified by the measure of fin aspect ratio (Bellwood & Wainwright 2001).

It is the aim of this study to assess the effects of wind-driven-wave turbulence on the fish assemblage characteristics of South Fishtail Bay, Douglas Lake, in northern Lower Michigan, particularly by looking at the levels of turbulence sensitivity for several fish. With a fish base including several species of centrarchids, percids, and cyprinids, it provides a good model for such a study. Cyprinids are physically better built for stabilization than are centrarchids and percids, which are better built for generating power. While both spiny-rayed centrarchids and percids, and soft-rayed cyprinids possess pectoral fins located high on their side to facilitate stability and maneuverability (Cailliet et al. 1986; Webb 2006b), the deeper-bodied centrarchids and percids are subjected to more roll-inducing forces, making the maintaining of stability a more costly process in energetic terms. Cyprinids are better able to handle turbulence without being rolled, and thus will likely remain in more turbulent areas during storms. Based on prior studies of turbulence (Fulton & Bellwood 2002; Bellwood & Wainwright 2001) and its impacts on fish communities, it is believed that as turbulence levels increase, fish assemblages will change accordingly, with deep-bodied species, including the centrarchids and percids, moving to deeper, less-turbulent water and cyprinids remaining in the more turbulent shallows.

Materials and Methods
Location & Lake
Douglas Lake, located in Cheboygan County, Michigan (T37N, R03W), is a 1,374 hectare natural lake consisting of seven separate basins with a maximum depth of 80 feet (Cwalinski 2004). Douglas Lake is considered mesotrophic with limited oligotrophic characteristics (Cwalinski 2004). The various substrate types include sand, rock, marl, and gravel, with the most prevalent substrate being sand (Cwalinski 2004). The limited emergent aquatic vegetation in Douglas Lake consists of various rushes and lilies (Cwalinski 2004). Within the littoral zone there is a much higher diversity of aquatic flora. Several fish studies conducted over the past century in Douglas Lake have revealed the presence of numerous species of fish (Table 1).

Table 1. Fish species of Douglas Lake, collected between 1912-2007. While not collected in the most recent survey, occasional angler reports of walleye in Douglas Lake have been received.
<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>American brook lamprey</td>
<td><em>Lampetra lamottei</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>bowfin</td>
<td><em>Amia calva</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Cwalinski 2004</td>
</tr>
<tr>
<td>brown trout</td>
<td><em>Salmo trutta</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>brook trout</td>
<td><em>Salvelinus fontinalis</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>lake herring</td>
<td><em>Coregonus artedii</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>grass pickerel</td>
<td><em>Esox americanus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>northern pike</td>
<td><em>Esox lucius</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>mudminnow</td>
<td><em>Umbra limi</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>northern redbelly dace</td>
<td><em>Phoxinus eos</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>hornyhead chub</td>
<td><em>Nocomis biguttatus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>golden shiner</td>
<td><em>Notemigonus crysoleucas</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>river shiner</td>
<td><em>Notropis blennius</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>common shiner</td>
<td><em>Luxilus cornutus</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>blacknose shiner</td>
<td><em>Notropis heterolepis</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>spottail shiner</td>
<td><em>Notropis hudsonius</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>spotfin shiner</td>
<td><em>Notropis spilopterus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>sand shiner</td>
<td><em>Notropis stramineus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>mimic shiner</td>
<td><em>Notropis volucellus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>bluntnose minnow</td>
<td><em>Pimephales notatus</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914</td>
</tr>
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<td>blacknose dace</td>
<td><em>Rhinichthys obtusus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>creek chub</td>
<td><em>Semotilus atromaculatus</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915</td>
</tr>
<tr>
<td>white sucker</td>
<td><em>Catostomus commersonii</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915; Cwalinski 2004</td>
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<tr>
<td>brown bullhead</td>
<td><em>Ameiurus nebulosus</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>banded killifish</td>
<td><em>Fundulus diaphanus</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>brook stickleback</td>
<td><em>Culaea inconstans</em></td>
<td>Webb &amp; Schrank, in proc.</td>
</tr>
<tr>
<td>trout perch</td>
<td><em>Percopsis omiscomatus</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915</td>
</tr>
<tr>
<td>Fish</td>
<td>Scientific Name</td>
<td>Authors</td>
</tr>
<tr>
<td>--------------</td>
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</tr>
<tr>
<td>rock bass</td>
<td><em>Ambloplites rupestris</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>pumpkinseed</td>
<td><em>Lepomis gibbosus</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>bluegill</td>
<td><em>Lepomis macrochirus</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>smallmouth bass</td>
<td><em>Micropterus dolomieui</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Cwalinski 2004</td>
</tr>
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<td>largemouth bass</td>
<td><em>Micropterus salmoides</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>black crappie</td>
<td><em>Pomoxis nigromaculatus</em></td>
<td>Webb &amp; Schrank, in proc.; Cwalinski 2004</td>
</tr>
<tr>
<td>yellow perch</td>
<td><em>Perca flavescens</em></td>
<td>Webb &amp; Schrank, in proc.; Colbert 1914; Reighard 1915; Cwalinski 2004</td>
</tr>
<tr>
<td>walleye</td>
<td><em>Sander vitreus</em></td>
<td>Webb &amp; Schrank, in proc.; Cwalinski 2004</td>
</tr>
<tr>
<td>Iowa darter</td>
<td><em>Etheostoma exile</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>Johnny darter</td>
<td><em>Etheostoma nigrum</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>log perch</td>
<td><em>Percina caprodes</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
<tr>
<td>mottled sculpin</td>
<td><em>Cottus bairdi</em></td>
<td>Webb &amp; Schrank, in proc.; Reighard 1915; Colbert 1914</td>
</tr>
</tbody>
</table>

**Study Site**

Water turbulence and fish assemblages were assessed at the University of Michigan Biological Station, at a near-shore site along South Fishtail Bay on Douglas Lake, which is typically downwind of storms due to the dominant west winds in the area (Colbert 1914; Gannon & Fee 1970). The study site of interest consisted primarily of sandy substrate, roughly 65% of which classifies as “medium sand,” with 30% considered “fine sand,” and varying sand types comprising the remainder. Vegetation increases with depth as the dropoff is approached, and does so quickly, but is not so dense as to cause any large edge effects. With an average vegetation density of about 2% at a depth of 30cm, vegetation does not begin to become prevalent until a depth of approximately 1m, where average vegetative cover is about 30%, and from there quickly reaches levels as high as 85% cover over the dropoff. The site consisted of a 100m long lakeside plot, which was arbitrarily divided into 5m increments (+50m → -50m) to denote relative position. The site
was generally devoid of obstructions or large sources of cover, excepting a small (2m) seasonal dock platform located at approximately -17m.

**Measuring Physical Habitat**

A 100m length of sandy shoreline formed one boundary of the sample site, with the parallel boundary formed by the steep dropoff beginning roughly 12m offshore. Samples of macrophytes within the plot were assessed by counting the percent cover at 10m intervals along the plot at depths of 30cm, 1m, and over the dropoff (~2 - 2.5m). Two acoustic Doppler velocimeters (ADV) and two wave probes were set at different depths (offshore=115cm depth, ADV 15cm below surface, sample volume=20cm below surface; inshore=25cm depth ADV, 17cm below surface, sample volume=22cm below surface) perpendicular to shore to measure changes in turbulence levels in all directions. With the use of ADV software and Excel, data from these instruments was collected and transformed for appropriate use in statistical analysis, including correlation analysis and chi-square tests.

**Sampling Fishes**

Data was collected using a variety of surveying techniques to minimize gear bias, among them snorkeling/above-water wading, underwater video, seining, and trapping (i.e., minnow traps and fyke nets). Other variables, including habitat characteristics, substrate, water temperature, and time of day were measured, as were fish location, size, and species. Two transects, one at a depth of 30 cm and the other at 1m, were swam every eight hours (at 0600h, 1400h, and 2200h) almost daily in order to survey fish visually and to check the traps. This method allowed for real-time data collection, and movements could be specifically recorded with respect to time of day and location along the experimental plot, allowing for such variables to be considered during subsequent data analysis. When feasible, wading was done, mainly to assess the habitat in depths under 10cm, which was impossible to snorkel but contained literally thousands of small (<2cm) sand shiners. A line of four Aqua-Vu underwater video cameras were set out to record fish movements. Video was utilized to observe these movements and characterize their direction, either inshore or offshore. Within the experimental array, a line of eight minnow traps were set out from shore every 3.3m. The first four were set on the bottom, with the fifth and all subsequent traps suspended under a float vertically (Figure 1).
Three Fyke nets, one oriented longitudinally, one facing inshore, and one facing away from shore, were used to collect larger individuals and to characterize the direction of their movements. Seining, though implemented late in the experiment, was used to characterize fish from a depth of 1m to the shoreline, and was accomplished by making four runs with a 5m bag seine at four consistent, obstacle-free locations within the plot. Measures of abundance (catch per unit effort, CPUE), were used to characterize fish communities. Data was analyzed using a variety of correlation matrices and other descriptive statistics. Fish morphology (e.g., body depth) was also considered. Results of the study describe the effects of turbulence on fish community assemblages in lakes, and should provide useful information for future research and management on this and physically similar lakes.

Results
Richness and Gear Bias
Between all fish collection and observation methods utilized in this study, a total of 11 species were observed. Most commonly among them were the sand shiner and yellow perch, though smallmouth bass, bluegill, and common shiners were all caught frequently. Among the four methods used heavily (i.e., snorkeling/wading, minnow traps, fyke nets & seining), the greatest number of different fish species was observed through the combination of snorkeling and wading (Figure 2).
Snorkeling and wading accounted for all 11 species seen during the course of this experiment. Conversely, minnow traps showed the least richness, generally catching multiple individuals of three or four species. Even very limited seining managed to sample a wider range of species than did the minnow traps. Gear bias between sampling methods was apparent, given the differences in catch per unit effort (CPUE) for different fish species caught by each (Figure 3).
Figure 3. Variation in CPUE for various sampling methods at a depth of 1m. YP=yellow perch, SMB=smallmouth bass, BG=bluegill, CS=common shiner, SS=sand shiner. Fyke net data not included due to different classification for sampling depths.

While snorkeling and wading combined seemed to result in seeing many yellow perch and smallmouth bass, seining seemed to favor both common and sand shiners alike, while minnow traps captured bluegill at a much higher rate than other methods. Regarding the fyke nets, their catches were similar to those of the minnow traps, with slightly larger sizes caught on occasion. The one exception occurred early in the study, when a 75cm bowfin was caught in the inshore-facing net. Integration of the entire range of data was made difficult due to variations in the equations used to calculate CPUE for different methods.

**Turbulence and CPUE**

Finding the best proxy for turbulence requires one to decide between values for Beaufort scale, turbulence intensity (TI), wave height, and current speed, the latter three of which have both near- and offshore components. As Beaufort values were collected for the duration of the study with everything else measure only toward the latter half of the study, a way of connecting Beaufort values to those of TI would be convenient, though a comparison of the two yields a weak negative correlation, less than 0.012 in both cases (Figure 4).

![Figure 4. Relationship between Beaufort measures and near- and offshore TI measures.](image)

The effects of turbulence, here measured as turbulence intensity, for both near-shore and offshore locations, seem to only weakly correlate with distribution patterns for any of
the prominent fish species. Looking at near-shore TI, no species of fish responded significantly to changes in TI. General trends included negative correlations for common shiner ($m= -0.004$, $r^2=0.007$), yellow perch ($m= -0.004$, $r^2=0.015$), smallmouth bass ($m= -0.062$, $r^2=0.076$), and bluegill ($m= -0.002$, $r^2=0.039$). Only sand shiner proportions tended to increase with increased shallow turbulence, though not to a significant degree ($m=0.328$, $r^2=0.157$). Similar trends are observed using offshore TI and fish distributions at a depth of 1m and beyond the dropoff. Although nothing correlates significantly, both negative and positive trends are seen. The same occurs when CPUE is compared with Beaufort scale measures. Categorization of the Beaufort values into “low” (0-1.5) and “high” (2+) categories in a chi-squared test, however, yields significant results. For both yellow perch ($X^2=123.2$, df=2) and smallmouth bass ($X^2=105.3$, df=2), there is a significant difference between the observed and expected values to allow rejection of the null hypothesis that turbulence plays no role in driving fish movements. Chi-squared tests, unfortunately, are not appropriate for bluegill, common shiner and sand shiner data, as the data for these three species produces expected values less than five.

**Diel Effects**

There appears to be multiple relationships between time of day and the location of different kinds of fishes (Figure 5).

![Figure 5. Fish abundance at 30cm depth in relation to time of day.](image)

While the range of the data is still too great to allow any significant relationships between time of day and fish locations, certain trends, such as an increase in smallmouth bass at 30cm around 1400h is apparent, as is the concurrent increase in sand shiner numbers and the increase in evening (2200-2300h) yellow perch sightings.

**Discussion**

*Richness and Gear Bias*
As expected, each sampling method used in this study presented its own amount of bias. This gear bias is a fundamental aspect of fish biology, and is best handled by employing a variety of sampling techniques (Cailliet et al. 1986). Snorkeling, while fairly effective, was heavily influenced by the amount of vision-obscuring turbidity in the water, and similarly, wading results could easily be obscured by waves on the water surface. Minnow traps proved to be great for catching bluegill, even though all other sampling methods represented bluegill as a smaller part of the overall community. Fyke nets did catch fish, doing so similarly to the way the minnow traps did, though they did not accomplish their true goal of catching large predators in any considerable abundance. Thus, any estimation of potential predation risk, another very important factor in controlling fish distributions (Mittelbach 1988; Wikramanayake 1990; Hinch et al. 1991; Diehl & Eklöv 1995), is impossible. Seining appeared to be promising, but the lateness with which it was undertaken limited the power of the results. In the end, the effect of combining methods was beneficial to give a more widespread picture of the communities present in South Fishtail Bay, though CPUE values had to be analyzed separately for each method. Given a way to factor in turbidity and limited visibility, snorkeling could potentially become a much stronger, less biased method. Even better would be a method for combining the CPUE measures for various methods, though that would undoubtedly be complex.

**Turbulence and CPUE**

While most results were not significant, and often without any trend, there are potential explanations for such results. The lack of correlation between Beaufort measures and TI was unexpected, but could result from the depth at which the TI samples were drawn; while Beaufort measures depend on surface waves, TI is dependent upon samples taken at 20cm and 22cm below the water surface for the offshore and nearshore ADVs, respectively. Turbulence is known to decrease as depth increases, and this could be the reason for the lack of a clear relationship between the two measures of turbulence. On a positive note, the use of chi-squared analysis after categorizing the Beaufort scale into “low” and “high” levels of turbulence yielded two significant results consistent with the hypothesis of this paper. Knowing that both smallmouth bass and yellow perch tend toward deeper water as turbulence increases is a sign that they react to turbulence, though other factors may still be influencing these movements as well.

**Diel Effects**

Although results were not significant, trends came up in the data that are consistent with previously published literature (Shoup et al. 2004) regarding diel fish movements and habitat partitioning. For example, many small (<10cm) smallmouth bass were seen in the shallow (<30cm) parts of the study site during the middle of the day, primarily because they were feeding on the small (<2cm) sand shiners there in great abundance. Yellow perch are harder to analyze due to their ubiquity, but still tended to show a more shallow distribution in the evenings.

**Limits of the Study + Future Goals**

One of the most difficult aspects of a study such as this is dealing with the vast number of physical and biotic variables, many of which are difficult to control for. The ability to
account for various potentially confounding variables is necessary and oversight of such things can lead to incorrect conclusions being reached.

Another shortcoming in this study was an inadequate amount of data, compounded further by occasional ADV malfunctioning that resulted in irrelevant values for TI. The obvious solution is to conduct such a study over a longer period of time, or potentially even over a few seasons. While ambitious, this study could expand on both a spatial and temporal scale, and incorporate inter-annual changes in other variables, making any conclusions more relevant in the dynamic world of fish communities (Rose 2000; Pierce et al. 2001).

**Acknowledgements**

I am indebted to Dr. Paul Webb for his help with the planning and execution of this study; his tutelage was invaluable and allowed a much more thorough study to be conducted. Thanks also are due to Dr. Dave Karowe and Dr. Mary Anne Carroll for their assistance with statistical analysis and logistical considerations. I would be remiss not to thank my volunteer assistants in the field: Danielle Stoermer, Brian Talpos, Christine Trac and Jeff Price. Lastly, I am thankful for the support received from the National Science Foundation’s Research Experience for Undergraduates program and the staff at the University of Michigan Biological Station.

**Literature Cited**


