

**Lake Michigan hydrodynamics: *Mysis* and larval fish interactions**

**by**

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## ABSTRACT

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I studied the interactions between Lake Michigan hydrodynamics (the spring thermal bar) and *Mysis*, deepwater sculpin, and burbot larvae. The thermal bar is a zone of sinking 4 °C water that separates warmer inshore water from colder offshore water. *Mysis* was a major bycatch of sampling for larval fishes. The density of *Mysis* did not differ statistically between inshore (about 6° C) and offshore of the thermal bar, but the percentage of *Mysis* that were newborns was significantly higher inshore (P = 0.007). These “early start” coastal *Mysis* may have an advantage in growth and survival, but with the risk that, unless they drift offshore, they will be at bottom depths that are ultimately inhospitable. The thermal bar period, and shortly thereafter, may be the only time that *Mysis* and the invasive *Hemimysis anomala* significantly overlap spatially. The most important impact of these newborn *Mysis* may be for newly free-swimming and free-feeding Age-0 lake trout (*Salvelinus namaycush*) which, for coastal reefs, emerge from spawning reefs during the period of thermal bar dynamics. The density of larval deepwater sculpin was higher inside of the thermal bar. For four out of nine sampling dates, inshore deepwater sculpin were significantly ( $p < 0.05$ ) larger. While the density of

*Limnocalanus* copepods density did not differ between inside vs. outside of the thermal bar, the larvae inshore consumed significantly ( $p < 0.038$ ) more prey (*Limnocalanus* copepods). Subsequent analysis using daily growth rings suggested that inshore larvae had significantly ( $p < 0.05$ ) higher daily growth rates than offshore larvae, which could result in larger body size and better ability of catching prey and avoiding predators. After the pelagic period, deepwater sculpin larvae need to go back offshore and become demersal. If inshore larvae can't return offshore and settle, they wouldn't contribute to the recruitment. However, from the perspective of growth, the deepwater sculpin larvae benefit from being inside of the thermal bar. Burbot *Lota lota* exhibit four previously known reproductive strategies in the Great Lakes region. The four known, shallow-water strategies are as follows: (1) spawning by self-sustaining, landlocked populations, (2) spawning in tributaries in winter and the exit of larvae to a Great Lake, (3) spawning by residents in a spawning stream with access to a Great Lake, and (4) spawning on unconsolidated and rocky areas in shallow water in winter in the lake. I did not find any burbot larvae during the spring thermal bar period. However, I did report a new spawning strategy for burbot--spring and summer spawning at deep reefs, where there is probably cobble or boulder habitat. The evidence comes from midlake reefs in Lake Michigan: I collected adult burbot at midlake reefs in Lake Michigan; and I collected many burbot larvae (many of which were newly hatched) from Lake Michigan in June –August. An important question remains, namely, which life history strategy provides the highest recruitment success for this species.

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## **Chapter 1**

### **Introduction**

#### **Match and mismatch hypothesis**

Fish survival can be affected by both biotic (i.e. prey abundance; predation intensity) and abiotic factors (such as light, water clarity, and temperature) and their interactions. There is strong evidence that the availability of food resources during the larval stage is a critical regulator of recruitment (Kallasvuo et al. 2010). The young-of-year (YOY) fish probably experience high rates of size-dependent mortality primarily as a result of starvation and predation (Miller et al. 1988; Houde, 1997, 2002; Höck et al. 2007). After the yolk is absorbed, the fish larvae change from internal to external feeding and the variation in the availability of plankton can result in variability of larval survival (Hjort, 1914; Lasker, 1975; Cushing, 1990). Prey limitation can directly affect larval mortality through starvation or indirectly through slow growth, which leads to more vulnerability to predation (Durant et al, 2007).

Among the classic fish stock-recruitment theories such as density-dependent theory and young fish mortality theory, none had taken particular account of the events intervening between stocking and recruitment, especially during the early life stages (Rothschild, 1986). At the dawn of fishery research, Hjort proposed that the timing of spawning relative to timing of the onset of spring production of phytoplankton might be an important mechanism in the success or failure of a year class (Hjort, 1914). The idea of a “critical period”, the early life stage during which larvae and young fish experience high rates of mortality, is also first implied by Hjort (1914). He suggested that if there is a

lapse between availability of food and the critical period when larvae first require external nourishment, an enormous larval mortality would result.

In 1975, Cushing formalized the match/mismatch hypothesis (MMH hereafter). Cushing (1975) suggested that marine larval fish survival and eventual recruitment depend on the varying availability of suitable prey in time and space. Larva transported into nursery grounds with more favorable temperature and enriched nutrients encounter favorable feeding conditions and would develop more rapidly.

MMH has been supported by the case studies of many fishery biologists. Leggett et al. (1994) constructed a model of capelin (*Mallotus villosus*) recruitment based on the evolutionary choice of the onshore winds by the larvae: a good year class depends on onshore north-easterly winds, in which larvae emerge in good conditions: warm water with high zooplankton and few predators. Brander et al. (2001) reported that the interannual variability in *Calanus* spp. egg production had a significant effect on cod recruitment in the Irish Sea and around Iceland. The work of Platt et al. (2003) showed that the survival of the larval haddock depends on the timing of the local spring bloom of phytoplankton. The model by Hinckley (2009) provided both spatial and temporal evidence to support MMH for walleye pollock (*Theragra chalcogramma*) production in Shelikof Strait. The young pollock that were transported to the coastal area between the Semidi Islands and the Shumagin Islands early in the year tended to have poor development because the levels of major prey nauplii were consistently low. MMH has also been tested experimentally by a few studies (Durant et al. 2007). For example, Gotceitas et al. (1996) investigated the MMH by exposing Atlantic cod larvae to 1 of 5 different food treatments, mimicking the different mismatch possibilities. Their result

revealed that a mismatch and its timing can significantly influence the growth and survival of cod larvae: larvae reared under match conditions (high food treatment) grew faster, achieved a larger size-at age, and showed a tendency for better survival than those reared under simulated mismatch conditions.

MMH has also been applied to the Laurentian Great Lakes. Rice et al.'s (1987) work on bloater (*Coregonus hoyi*) was one of the first studies that supported MMH in fresh water systems. Rice et al. (1985) found that although more eggs were produced in 1982, there were more age-0 larvae produced in 1983, which they attributed to the earlier occurrence of spring warm up. However, details such as chlorophyll and zooplankton concentration were not reported in that study.

### **The importance of thermal cycle in Lake Michigan**

In temperate regions, many lakes undergo seasonal overturn due to the changes in water density with temperature (Boehrer and Schultze, 2008). The density of freshwater changes with water temperature. Fresh water reaches its maximal density at 4 °C. As spring approaches, the lake starts to warm up. As the solar radiation absorbed decreases with depth, the lake heats from the surface down, which in turn, results in an arising of density gradients. The warm water is less dense than the colder water below, resulting in a layer of warm water (epilimnion) that floats over the cold water (hypolimnion). These two layers are separated by the thermocline, where temperature changes rapidly with the depth. This phenomenon with three distinct layers is called stratification.

Lake Michigan is the largest freshwater lake in the United States and it has a surface area of 58,000 km<sup>2</sup>. Around mid-December, autumnal cooling and increasing wind action

destroy summer stratification and to bring the temperature of the whole water mass down to near 4°C (Mortimer, 2004). Lake Michigan becomes well mixed from top to bottom (Beletsky and Schwab, 2001). This winter/early spring mixing is ecologically important because as the lake mixes from top to bottom, nutrients such as nitrogen and phosphorus are expected to be delivered to the euphotic zone (Millie et al. 2000). Therefore, resuspension coupled with optimal nutrient/light conditions might provide for development of spring bloom of phytoplankton in Lake Michigan (Millie et al., 2000). The spring bloom can contribute up to half of the lake's annual primary production (Fahnenstiel and Scavia 1987; Gardner et al. 1990, Brooks and Edgington, 1994).

Spring warm-up occurs during early spring from the coast (since heating is faster) towards the center (Holland et al. 2001). Freshwater reaches its maximum density at 4°C. The denser water sinks to the bottom; at the same time, a vertical front separating warmer (greater than 4°C) inshore water from cooler offshore (less than 4°C) water (Stoermer, 1968; Bukreev and Gavrilov, 2010) is formed. This phenomenon is called the "thermal bar" (Fig.1). This phenomena occurs regularly in the Great Lakes (Rao and Schwab 2007), and was first reported by Rodgers (1968) in Lake Ontario. The thermal bar progressively, but erratically, moves offshore (Mortimer, 1988). The timing of thermal bar varies from year to year. This event has importance in regulating physical, chemical, and biological processes in Lake Michigan in spring (Mortimer, 1988; Moll et al., 1993). Chlorophyll is more concentrated inshore of the thermal bar than offshore, and there is a typically a peak at the 4 °C isotherm (Tarapchak & Stoermer, 1976; Moll et al. 1993; Mortimer 1988; Consi et al. 2009; Wang et al. 2012). Hence, inshore water is believed to benefit coastal zooplankton (Brandt 1993).

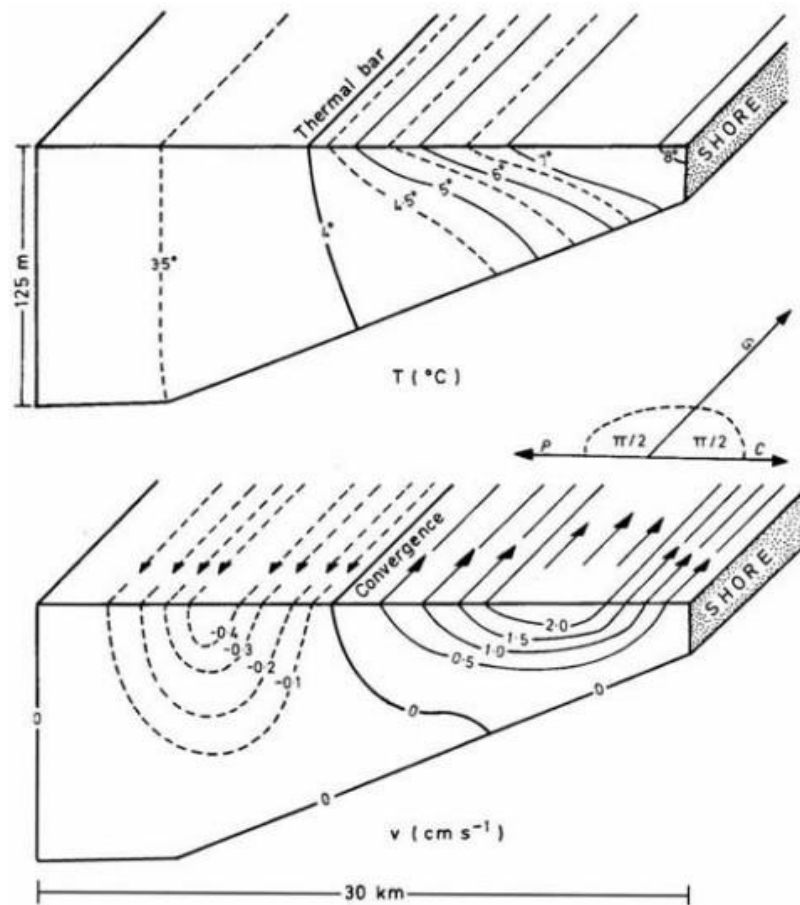


Figure. 1 Schematic diagram of the spring thermal bar (From Henderson-Sellers, 1984).

The timing of larval fish emergence varies from year to year. For those larvae hatching around later winter to early spring, finding an ideal nursery ground with preferable temperature and sufficient available nutrients is important. Failure to do so can be fatal. Since the swimming ability of larvae can be negligent during the early stage, the distribution of larvae is mainly determined by currents (Bishai, 1960). This difference in distribution by the currents can lead to different fates. During the time of the spring thermal bar, fish larvae transported to inside of the thermal bar can benefit from an

increase in either phyto- or zooplankton and temperature, which in turn, results in better survival.

Mechanisms related to larval development can influence long-term demographics by regulating their survival. While quantitative understanding of how water mass dynamics affect passive fish transport continues to be a fundamental problem for fishery scientists, advances in hydrodynamic and coupled physical-biological models have made it possible to begin to examine population-level implications of environmental processes, especially in marine environments (Werner et al. 1997). Many studies have been done to link variation in hydrodynamics to variability of marine fish recruitment, population distribution, and abundance during the early life history stages (Werner et al. 1997). Wilderbuer et al. (2002) reported an above-average recruitment of flatfish due to wind-driven advection of larvae to favorable nursery grounds in the Eastern Bering Sea through the use of an ocean surface current simulation model (OSCURS). In freshwater lake ecosystems, the study of spring thermal bar dynamics on the early life history of larvae could help predict recruitment of fish species that emerge during this time period, and furthermore, the whole food web and fish community. This could benefit fishery managers in establishing sustainable patterns of exploitation and providing new approaches to regulation of fish population.

### ***Mysis* and larval fish phenology in Lake Michigan**

Variability in fish recruitment has long been linked to the overlap in space and time between larval and juvenile fish and their prey (Durant et al. 2007). Cushing's (1975) MMH is often used to explain annual variations in recruitment in both marine and freshwater ecosystems (Durant et al. 2007). The MMH proposes that in temperate waters, larval fish survival and eventual recruitment is determined by the degree of overlap between the larval period and the peak abundance of their suitable prey in time and space (Cushing 1990, Cushing 1996). A match between emergence of larval fish and peak prey abundance can result in higher survival rates, which in turn, leads to higher recruitment. However, the role of spring thermal bar in survival and development variability has not been well explored.

Deepwater sculpin (*Myoxocephalus thompsonii*) and burbot (*Lota lota*) were sampled, with *Mysis diluviana* (henceforth *Mysis*) as a by-catch, for this study because these are the two deepest benthic fishes in the Great lakes with pelagic larvae. Larvae of deepwater sculpin emerge from offshore deep water (Madenjian et al. 1983), while that of burbot are founded from both inshore and offshore water (Nash and Geffen 1991; Madenjian et al. 1983).

### ***Mysis***

*Mysis* is an important food source for a diverse range of Great Lakes fishes and its importance may have increased following the decline of *Diporeia* spp. in the four Great Lakes invaded by dreissenid mussels (Hondorp et al., 2005; Pothoven and Madenjian, 2008). *Mysis* generally reside at depths greater than 100 m in the daytime in the Great

Lakes, partially due to their preference for low light levels, and at night they ascend to depths determined in part by light intensity, but modified by other factors (Boscarino et al. 2007, 2009). However, during summer upwelling events, *Mysis* can be as shallow as 7 m bottom depth; they are in the water column at night but during the day they are commonly under rocks (John Janssen scuba obs. 1978 to present).

There has been little Great Lakes coastal (<20 m) sampling for *Mysis* during spring. The shallowest reported occurrence in Lake Michigan was by Reynolds and DeGraeve (1972) who sampled via bottom sled from 9 to 130 meters during daytime. They found no *Mysis* shallower than 20 m during April and May, but *Mysis* could occur shallower during winter and upwelling events in summer. In Lake Ontario, *Mysis* was collected at night in depths less than 10 m during the end of May (Johannsson, 1995).

Chlorophyll is more concentrated inshore of the thermal bar than offshore (Mortimer 1988, Moll et al. 1993, Consi et al. 2009); hence, inshore water is believed to benefit coastal zooplankton (Brandt 1993). *Mysis* feed on larger phytoplankton and zooplankton (Bowers and Grossnickle 1978, Nero and Sprules 1986, Nordin et al. 2008) so an increase in either phyto- or zooplankton should be a benefit.

Here I report on the relative density and age composition (as expressed as percent juvenile) of *Mysis* juveniles inshore vs. offshore of the thermal bar for three successive spring warm-ups.

### **Deepwater sculpin**

The deepwater sculpin, *Myoxocephalus thompsonii*, has historically been an important food source for the native top predators lake trout (*Salvelinus namaycush*) and burbot

(*Lota lota*) in lakes Michigan (Day 1983; Fratt et al., 1997; Madenjian et al. 2002; Murray et al. 2003), Superior (Dryer et al., 1965), Ontario (Dymond, 1928) and Huron (Riley et al., 2008) and thus plays a major role in coupling nutrients from energy rich benthic invertebrates to top-level predators (O'Brien et al., 2009). However, it is one of the most poorly known freshwater fishes in North America (Girard 1852, Parker 1988). The adult deepwater sculpin is a cold-water and bottom dwelling fish that spawns in offshore deep water (>~70m) (Deason, 1939). The majority of deepwater sculpin larvae hatch in offshore deepwater in early spring (late-February to mid-March), and become pelagic shortly thereafter (Mansfield et al. 1983; Geffen and Nash, 1992). During the pelagic stage, the deepwater sculpin larvae are dispersed by currents due to the winter lake-wide mixing, so that some fraction of the population is transported inshore. Geffen and Nash (1992) found some of the larvae in inshore water in Lake Michigan before stratification, which suggested transportation prior to spring warm-up. They found the largest deepwater sculpin larvae in May at their shallowest (15m) station in SE Lake Michigan. These fish were all post-yolk sac, while 90% of the larvae at their deepest station (50 m) had yolk sacs. These deepwater sculpin larvae were possibly the largest because that they were inside of the thermal bar, thus benefiting from the relatively warmer water and an increase in prey availability inside of the thermal bar.

The primary prey of larval deepwater sculpin is copepods (Mansfield et al., 1983; Roseman et al., 1998). In inshore water, the more concentrated phytoplankton is expected to foster zooplankton growth (Brandt 1993). Another more subtle impact is that where phytoplankton is concentrated the zooplankton feeding on them are likely to have a greater nutrition value (Reitan et al., 1997). Skiftesvik et al. (2003) argued that one way

to benefit larval fish was probably to increase the nutritional quality of zooplankters. His hypothesis has been supported by a number of recent works. For example, Villar-Argaiz & Sterner (2002) found phytoplankton quality affected the development of a diaptomid calanoid copepod: nauplii fed on phosphorus-deficient algae failed to develop into adults while nauplii fed on phosphorus-sufficient algae developed into adults that successfully reproduced. Twombly et al. (1998) had similar results for a cyclopoid copepod: individuals fed on low-quality phytoplankton developed more slowly and were smaller at maturity than those reared on high-quality phytoplankton.

The deepwater sculpin population has undergone significant decreases in several Great Lakes. Such declines in Lake Michigan, Huron, and Ontario are likely related to the dramatic ecosystem change that has occurred due to invasive species such as dreissenid mussels, and the species may be further threatened by future environmental change. Restoration of deepwater sculpin in Great Lakes requires a better understanding of early life development of deepwater sculpin larvae.

### **Burbot**

Burbot is a cold water, benthic freshwater species (Pääkkönen et al. 2000). It is the only freshwater member of the cod family (*Gadidae*) (Bonar et al. 2000). In Lake Michigan, Huron, Erie and Ontario, burbot populations collapsed between 1930 and the early 1960 and the collapses in Lakes Michigan, Huron, and Ontario have been attributed to predation by sea lamprey (*Petromyzon marinus* L.) (Stapanian et al. 2008). Burbot population recovered from 1960-2000 due to sea lamprey control in Lakes Michigan, Huron, and Ontario after near extirpation (Stapanian et al. 2006, 2008). However, shortly

after that, burbot populations sharply declined again (CWTG 2008; Stapanian et al. 2008). Several studies suggested that recruitment failure was the most likely cause of collapse (Stapanian et al. 2008; CWTG 2008; Paragamian et al. 2000, 2005).

The spawning strategies of burbot include: winter spawning over rubble or sand bottoms on shoals or reefs in lakes (Muth 1973; McCrimmon 1959; Clady 1976; Bailey 1972); winter spawning in streams (Mansfield et al., 1983). The stream spawned larvae could stay in stream or could enter the lake. If the latter ones encounter the spring thermal bar in Lake Michigan, their early life-stage development may vary depending on their distribution relative to the thermal bar position. The objective of this study is to provide a better understanding of burbot spawning strategies and burbot recruitment. Here I examined the distribution of burbot during spring thermal bar formation and during spring stratification on the Lake Michigan Mid-lake Reef Complex (MLRC hereafter), and document a new spawning behavior in hypolimnetic waters in spring-summer.

### **Overview of rationale**

A summary of the rationale is that larval fish/juvenile *Mysis* fortunate enough to encounter warmer prey-rich waters are more likely to survive and thus, contribute to recruitment. By the best evidence thus far available, recruitment in fishes that have pelagic larvae is strongly affected by events they experience in the few days or weeks after hatching when they have little control over finding their nursery habitat. The “fortunate” offshore originating young are probably those that encounter the warm, prey-rich patches. The fortunate inshore originating young are probably those that remain within warm, prey-rich patches.

## Chapter 2

### METHODOLOGY

#### **Larval fish, zooplankton and *Mysis* sampling and statistics**

Larval fish (deepwater sculpin and burbot) were sampled at night during the thermal bar period in spring from 2007 to 2009 in western Lake Michigan near Milwaukee WI from the University of Wisconsin, Milwaukee's R/V Neeskay. The sampling was along an inshore to offshore transect crossing the thermal bar. Since the thermal bar is a mobile physical structure, the initial location of sampling was determined with respect to the center of the 4 °C isotherm. I limited the sampling to inshore and offshore at these two stations. The thermal bar was located via a continuously recording calibrated sonde (YSI model 6600ZDS-M) which rested in a PVC pipe with continuous fresh water flow pumped from about 2 meters below the surface. The offshore station was about 2-3 km offshore of the thermal bar, in water less than 4 °C, and the inshore station was at a location near 6 °C. As the thermal bar moved offshore, the sampling stations moved offshore as well.

At each station, larvae were captured with a 1.4 m wide by 2 m deep rectangular Tucker trawl equipped with a 500 micron mesh net. The sampling procedures followed Rice et al. (1997) and Geffen & Nash (1992). The sampling was at night and stepwise. Towing speed was 2 knots. Tows began at 10 m (+/- about 1m) deep and rose every 3 minutes in stages, approximately 1 m toward the surface by pulling in on the winch cable. Tow direction was into the wind and waves to maximize control of the vessel and trawl depth. Depth was recorded by a Reefnet SensusPro depth logger. Flow data from a General

Oceanics calibrated flowmeter attached to the center of the Tucker trawl mouth was used to estimate the volume of water sampled (following Nash & Geffin, 1991). Samples were stored in 95% ethanol immediately after capture. In the laboratory, all larvae were separated from the zooplankton and counted. The preserved total length of all larvae was measured to closest 0.1 mm under dissection microscope.

For diet analysis, the stomachs were dissected using a dissecting microscope. Prey items were identified to genera and enumerated. For partially digested prey items, I considered the head capsules of copepods as evidence that one prey item was consumed.

The density, size, prey consumption, and daily growth rate of larval deepwater sculpin were compared individually with two-way mixed-model ANOVA. In all analysis, I used location as the fixed effect and date as the random effect. In all analyses,  $MS_{\text{location} \times \text{date}}$  was error variance for testing the location effect (Zar, 1984). All analysis except density used  $MS_{\text{error}}$  as error variance for testing date effect. The density analysis differed because the other analyses provided replications for further analysis. Since date effect was not the one I was interested in, it was tested using  $MS_{\text{remainder}}$  in density test, while assuming there was no significant interaction effect (Zar, 1984).

*Mysis* were sampled following the same procedure as larval fish sampling. The densities of *Mysis* were compared between inshore and offshore using paired t-test with date being the replicate. The percent juvenile was compared using an analysis of covariance (ANCOVA) with sampling location (inshore vs. offshore of the thermal bar) and year as group variables and date since April 15 (arbitrary starting date) as a covariate. A two-

sample t-test was used for comparison of the length of juveniles between inshore and offshore samples.

Vertical temperature structure and surface fluorescence were continuously recorded at three buoyed stations via a near surface sonde (YSI model 6600ZDS-M) and thermister strings (Consi et al. 2009) (Fig.2). The buoys were anchored at 20m, 40m, and 60m (2.2 km, 6.0km, and 12.0 km (Fig.2) from shore respectively and within a few km of our sampling transect (see Consi et al. for details). Buoys were deployed over a period of about three weeks, with the shallowest buoy deployed first and the deepest buoy deployed last.

Surface zooplankton was collected at the beginning of larvae collections with a 0.5 m diameter 63  $\mu$ m mesh net (3m long). A General Oceanics flowmeter was used to record the total filtered volume. The net was deployed at the surface and slowly released until it reached a 15 m depth. Three replications were taken at each station. Each deployment was followed by a 5 min interval to retrieve and clean the net. Zooplankton was preserved immediately in 95% ethanol after capture. Samples were subsequently sorted, enumerated and analyzed in the laboratory. The abundance of zooplankton was examined using two-way mixed-model ANOVA with dates and locations as factors.

Burbot larvae were also sampled at the mid lake reef complex (MLRC hereafter) station on Lake Michigan. Sampling was conducted during the day at two locations with similar bottom depth: coastal (55-62 m deep; 43°01.5703' N-87°42.4820'W to 43°01.6125' N-87°43.1299'W) vs. East Reef (55-60m deep; 43 °01.5703'N-87 °21.1581'W) from 2007-2009. Reef locations were about 27 km offshore of the coast. East Reef, composed of

bedrock with cobble and sand veneer, rises from a depth of 100 m or greater (see Janssen et al. 2006 for bathymetry of its western face). I used the same Tucker trawl and sampling steps and procedures as used for thermal bar transect sampling. Sampling was conducted on six dates: 25 June and 6 July 2007, 23 June and 1 July 2008, 18 June and 14 July 2009. Two-way ANOVA was used with date and locations as factors to compare burbot larvae density, size and diet between these two locations.

### **Otolith Analysis**

Growth rate corresponding to different water temperatures between inshore and offshore of the thermal bar were determined from daily growth increments of sagittal otoliths from age-0 deepwater sculpin collected in the tucker trawl. Otoliths were removed by teasing them from stored deepwater sculpin larvae. Dissected sagittal otoliths were cleaned in deionized water to remove the adhering tissue and allowed to dry. They were transferred to a clean glass slide by picking them up on the end of a fine dissecting needle wetted with immersion oil (Brothers et al. 1976). The pair of otoliths were mounted with one to two drops emersion oil and covered with 0.17 mm coverslip. No additional preparations such as polishing was needed since larval otoliths were thin and clear enough to allow a total count and measurement of the daily increment. Sagittae were observed under DIC Leica DMR microscope using HCX DL APO 63x 1.20 Water objective. It has been suggested by Brothers (1976) that the observation in oil can reduce resolution when a larval otolith is examined. Daily growth rate was calculated by measuring the outermost four complete daily increments. Only the outermost four rings were measured for three reasons. First, the exact age determination of deepwater sculpin might not be possible since the exact timing of the initiation of daily growth ring formation varies from species

to species and must be determined for each one independently (Brothers et al. 1976).

Second, the otolith was thick enough that it was impossible to measure each individual growth ring. Last, looking only at the last four days would increase the probability of only examining rings representing a time that the larvae spent in the same location (relative to the thermal bar) as where they were caught.

## Chapter 3

### Results

#### *Mysis*

In 2007 for the 20, 40 and 60 meter stations the first onset of the thermal bar occurred on 21 April, 1 May, and 5 May respectively. In 2008 the onset occurred on 14 April, 20 April, and April 29 for the three stations respectively. First onset of the thermal bar occurred on 20 April, 29 April, and 9 May in 2009. Temperature profiles from buoys show the passage of the thermal bar and the onset of stratification progressing from shallow to deeper water in 2009 (Fig. 2). The surface chlorophyll concentration at the 40 m buoy increased during the time interval of 5-9 May 2009 as the water warmed to about 8°C (Fig.2). Consi et al. (2009) reported that chlorophyll was more concentrated inshore of the thermal bar than offshore. The dynamic nature of the thermal bar and the fluctuation in its position is illustrated in Fig. 2. For example, between the period of 5-9 May 2009 the thermal bar was offshore of the 40 m buoy and there was a brief period in which there was a thermocline (Fig. 2). The thermal bar, or wedge, even migrated briefly past the 60 m buoy around 9 May. The surface chlorophyll concentration at the 40 m buoy increased during the time interval of 5-9 May as the water warmed to about 8° C (Fig. 3). Mixing due to a wind event then weakened the thermocline and diluted the surface chlorophyll.

Reynolds and DeGraeve (1972) used 11 mm as the cutoff to separate juvenile and adult *Mysis*. My measurements should a bimodal length distribution with the gap at about 10

mm; consequently, I used 10 mm as my criterion to separate “juvenile” and “large” (Fig.4).

I collected *Mysis* in 6° C surface water as shallow as 17 m bottom depth and consistently over 20-25 m bottom depth (Fig. 5). Data from two nights with a full moon were excluded due to the low numbers of *Mysis* at both inshore and offshore stations. Mean density of *Mysis* inshore was 0.150/m<sup>3</sup>, while offshore was 0.313/m<sup>3</sup> (Fig. 5) but there was no consistent pattern regarding whether *Mysis* densities were higher offshore vs. inshore (paired  $t_9 = 1.37$ ,  $P=0.205$ ). However, when I excluded juveniles from the counts there were significantly higher densities of large *Mysis* at the offshore stations (paired  $t_9 = 3.3$ ,  $P=0.011$ ).

The overall size distribution (Fig. 5) should a tendency for juvenile *Mysis* to be at the shallow stations. This was confirmed by the statistical analyses; the percent of the sample that was juveniles was greater for inshore vs. offshore stations (Fig. 6;  $F_{1,13} = 8.7$ ,  $P = 0.011$ ). Neither the year effect nor the time covariate (days since April 15) effect was statistically significant ( $F_{2,13} = 1.9$ ,  $P = 0.19$  and  $F_{1,13} = 2.1$ ,  $P = 0.17$  respectively).

Further examination of the length distribution using only the juvenile size class suggests that those from the shallow stations are slightly larger than those from the deeper station (Fig. 5). A statistical analysis considering all factors was highly unbalanced because there were frequently low numbers of juvenile *Mysis* at the offshore stations, so the number of replicate dates is small. However, when I pooled all dates to compare lengths for inshore vs. offshore juvenile *Mysis*, juvenile *Mysis* were statistically larger than those

collected offshore. (inshore: 7.1 mm ( $s = 1.64$ ) vs. offshore: 6.4 mm ( $s = 2.04$ );  $t_{175} = 2.35$ ,  $P = 0.020$ ).

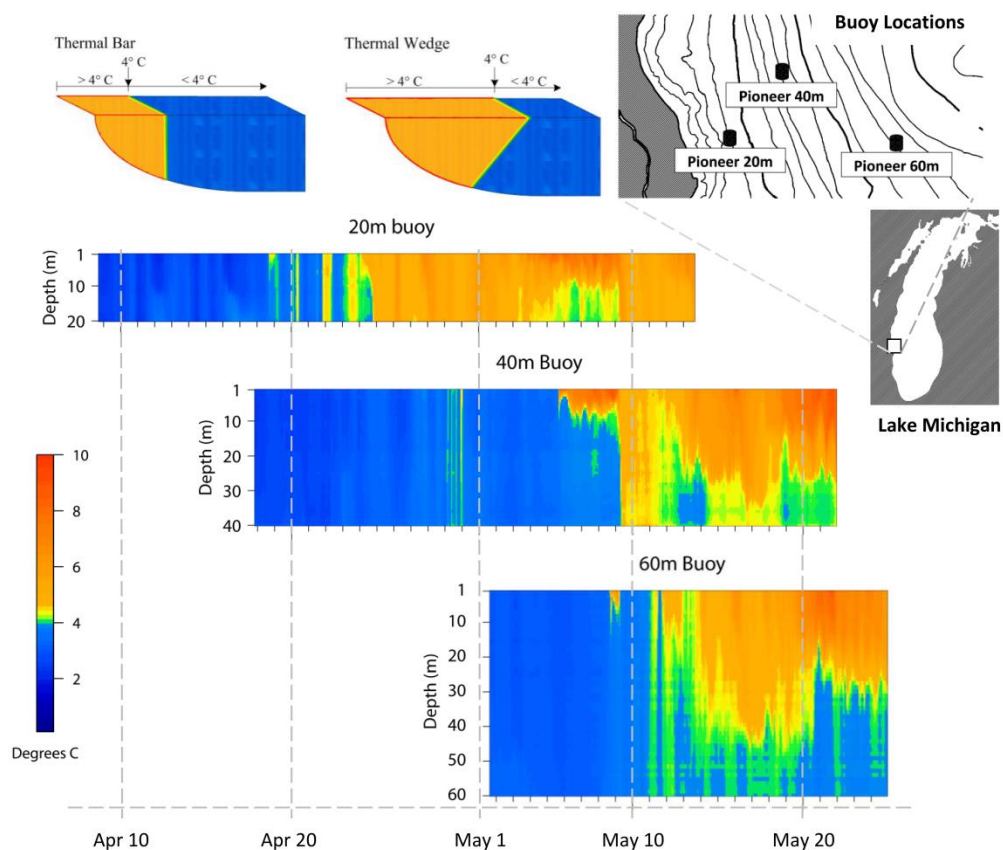


Figure 2. Spring thermal bar/thermal wedge evolution. In the idealized evolution (without strong winds), water warms close to shore and when it reaches 4°C it sinks, with warmer, less dense water towards shore and less dense colder water offshore. As the coastal water continues to warm, the 4°C zone migrates offshore. The water shoreward of the 4°C water can begin to stratify, forming a thermal wedge. Time series of the temperature strings for buoys at 20 m, 40 m, and 60 m. The first date of 4°C water was Apr. 19 (20 m), Apr. 29 (40m), and May 9 (60 m). Note the actual thermal bar evolution is much more dynamic than the ideal diagram because of winds and currents. Also note that vertical temperature profiles are erratic meaning that the thermal wedge is dynamic in its shape.

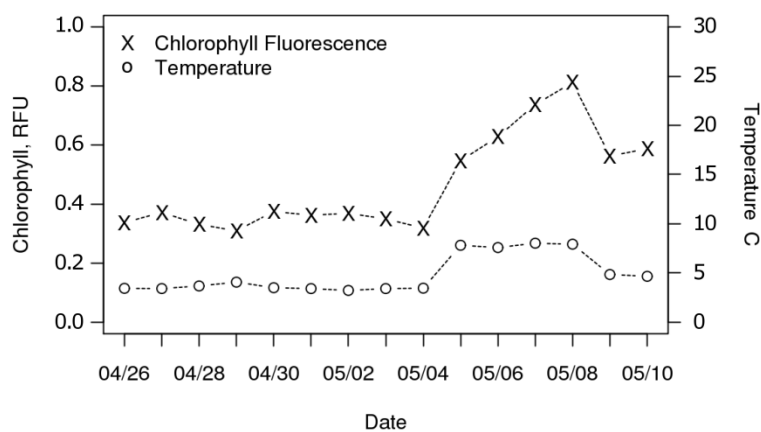


Figure 3. Surface temperature and chlorophyll relative concentration measured in relative fluorescence units (RFU) at the 40 m buoy during 2009. From about 5-9 May the thermal bar was offshore of the buoy, then returned closer to shore. There was a spike in chlorophyll concentration as the coastal water was at the buoy.

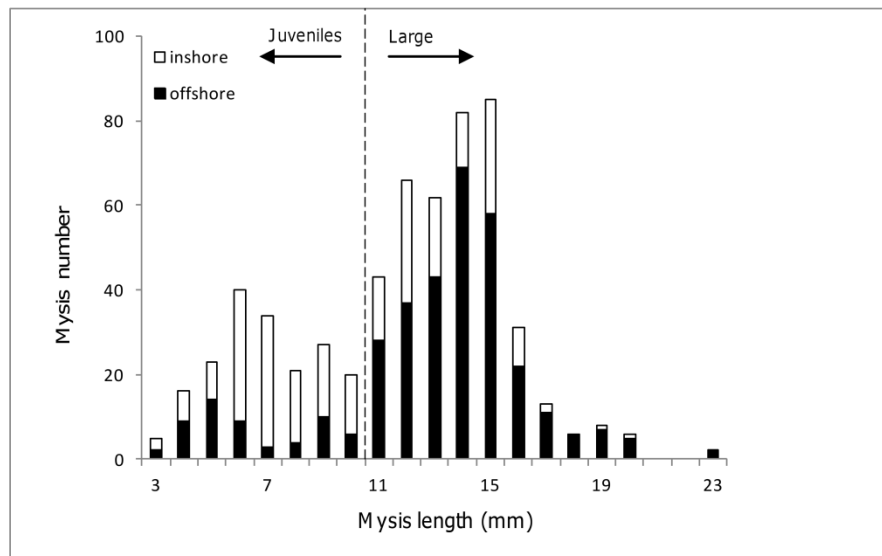


Figure 4. Length distribution of *Mysis* at stations inshore vs. offshore of the thermal bar during spring thermal period from 2007 to 2009 in Lake Michigan. Lengths are rounded to the nearest integer. The dotted bar at 10 mm represents the operational definition of juvenile vs. large length.

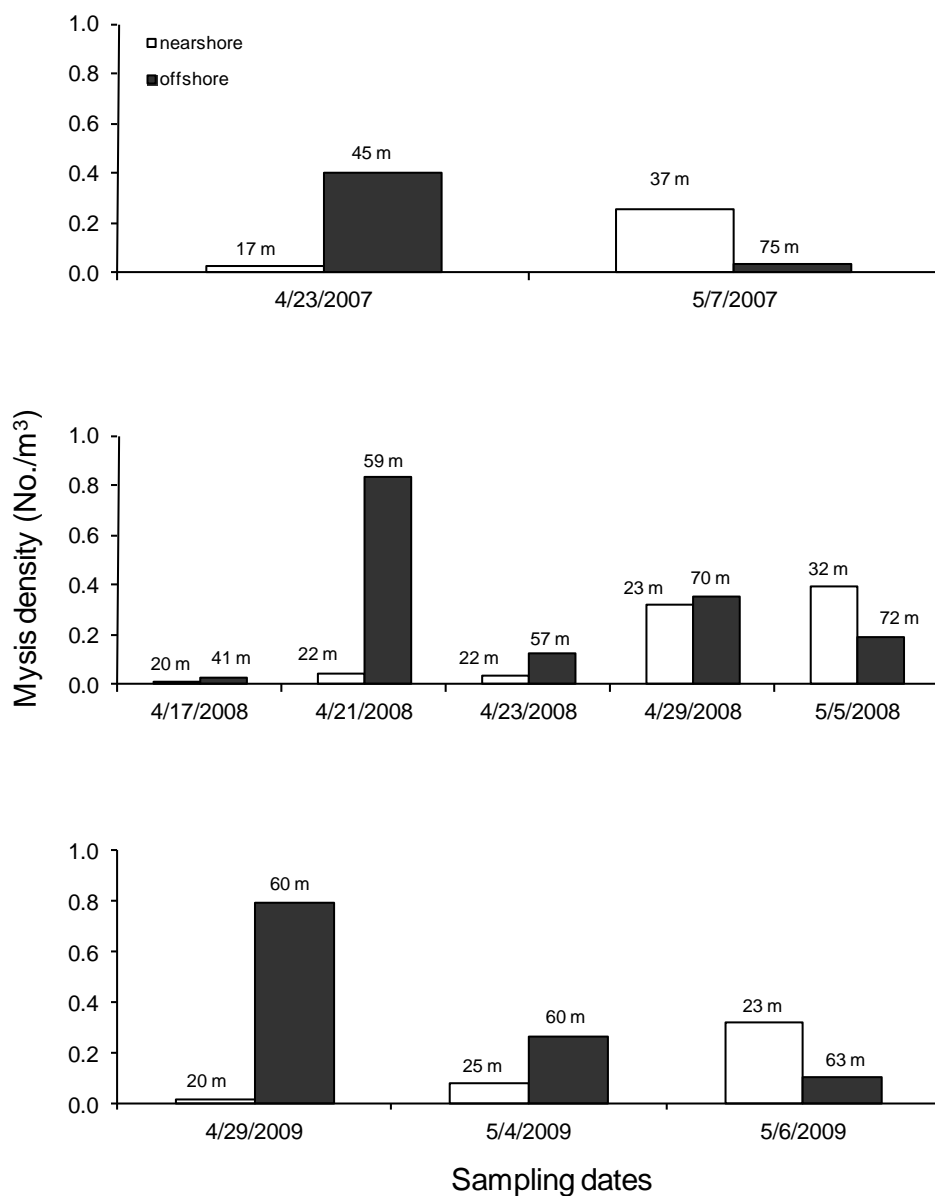


Figure 5. Mysis density (No./m<sup>3</sup>) at stations inshore vs. offshore of the thermal bar during spring thermal bar period from 2007 to 2009 in Lake Michigan. Inshore tows were at about 6°C and offshore tows were about 2-3 km offshore of the thermal bar. All samples presented and analyzed were collected when the moon was not full.

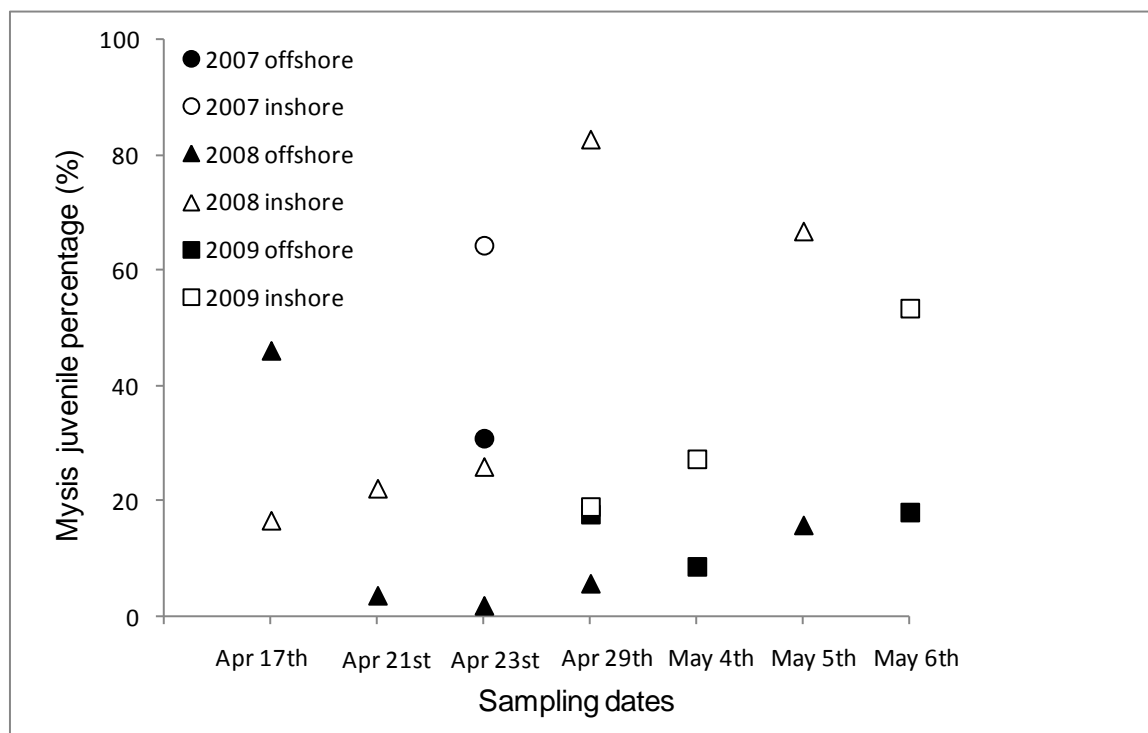


Figure 6. *Mysis* juvenile (< 10 mm) percentage in both inshore (inshore of the thermal bar) and offshore (offshore of the thermal bar) waters in Lake Michigan during thermal bar dynamics from 2007 to 2009. Filled symbols represent offshore. Open symbols represent inshore.

### Larval deepwater sculpin

A total of 171 larvae were collected with size ranging from 9 to 23 mm. Deepwater sculpin larvae were present at both inshore and offshore stations (Fig. 7). The density (number/1000m<sup>3</sup>) of larval deepwater sculpin inside vs. outside of the thermal bar was compared using two-way mixed-model ANOVA with location being the fixed factor and sampling date being the random factor (Fig. 7). The densities of deepwater sculpin larvae were log transformed before the analysis. The ANOVA showed that the date was not significant ( $F_{9,9} = 0.643$ ,  $p=0.74$ ). The location was significant ( $F_{1,9} = 13.019$ ,  $p=0.006$ ), indicating that there were higher densities of deepwater sculpin larvae inside of the thermal bar.

The diets of inshore and offshore larval deepwater sculpin were analyzed using two-way mixed-model ANOVA. Samples collected on 7 May 2007, 17 April 2008, and 4 May 2009 were accidentally lost and excluded for the analysis. Sampling location was the fixed effect and date was the random effect. The main effect location was statistically significant ( $F_{1,6} = 5.87$ ;  $p < 0.038$ ). This indicated that inshore larvae consumed statistically more copepods than offshore larvae during spring thermal bar period. The other main effect, date, is not significant ( $F_{6,100} = 0.502$ ,  $p=0.806$ ).

*Limnocalanus* copepod density was compared between inshore and offshore during spring thermal bar using two-way ANOVA. Both main effects were not significant (location effect:  $F_{1,8} = 1.272$ ,  $p > 0.05$ ; date effect  $F_{8,42} = 1.609$ ,  $p = 0.151$ ), suggesting there is no difference of *Limnocalanus* copepods inshore vs. offshore during sampling time.

The total length of deepwater sculpin inside and outside of the thermal bar was compared using two-way mixed-model ANOVA (Fig. 8). The mixed model included two factors: location being the fixed effect, and sampling date being the random effect. The total lengths were log transformed before analysis. The interaction between location and date was significant ( $F_{8, 131} = 3.848, p < 0.001$ ). Thus, the two main effects cannot be interpreted because the impact of one effect depends on the level of the other effect. Subsequent Dunnett's test ( $\alpha = 0.05$ ) was performed to compare 9 pairs (9 sampling dates) of inshore versus offshore total lengths. For two out of nine sampling dates (3-4 May 2007; 5 May 2008), deepwater sculpin larvae from inshore station were significantly larger than offshore larvae ( $q' = 2.62, p < 0.05$ ;  $q' = 3.932, p < 0.05$ ). During 4 May 2009, inshore larvae were marginally significantly larger than offshore larvae ( $q' = 2.631$ ; the critical  $q$  value is 2.69). For samples from 23 April 2007, deepwater sculpin larvae from offshore station were significantly larger ( $q' = 4.19, p < 0.05$ ). And for the other five sampling dates, there was no significant difference between inshore and offshore larvae.

The average of the four outermost daily rings of inshore and offshore deepwater sculpin larvae (Fig. 9) were compared using two-way mixed-model ANOVA with two effects: temperature was the fixed effect and sampling date was the random effect. Based on the measurement of daily growth rings, the location effect was statistically significant ( $F_{1,6} = 4.88, p < 0.05$ ). This difference in location suggested that larval deepwater sculpin in the inshore zone grew faster than those in the offshore zone during the spring thermal bar period. The other main effect, sampling date, was not significant ( $F_{6, 82} = 2.01, p = 0.074$ ). The daily rings and total length analyses together suggested that the region inside of the thermal bar provided advantages for inshore deepwater sculpin larvae: they grew faster,

thus had larger body size than offshore larvae during spring thermal bar dynamics; consequently, they likely had better survival than offshore ones.

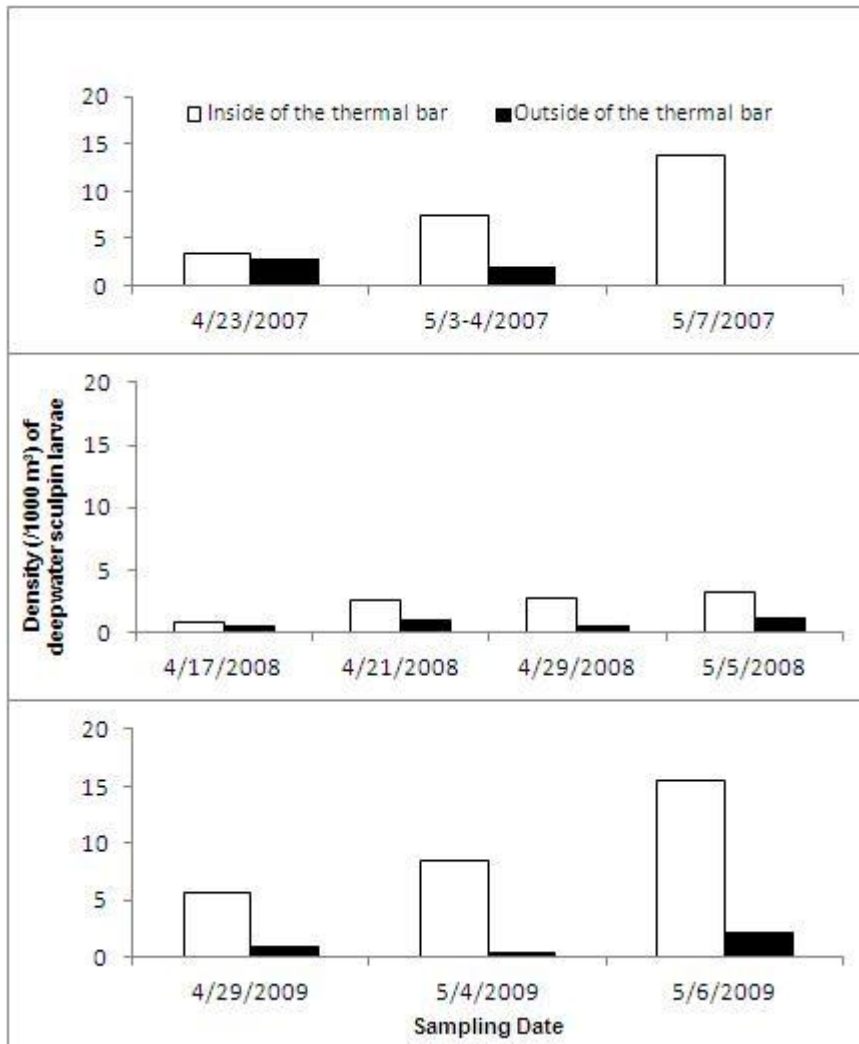


Figure.7 Number of larval deepwater sculpin collected at the inshore and offshore locations (GPS are approximately 43°05', 87°50'-43°05', 87°42') during the spring thermal bar from 2007 to 2009.

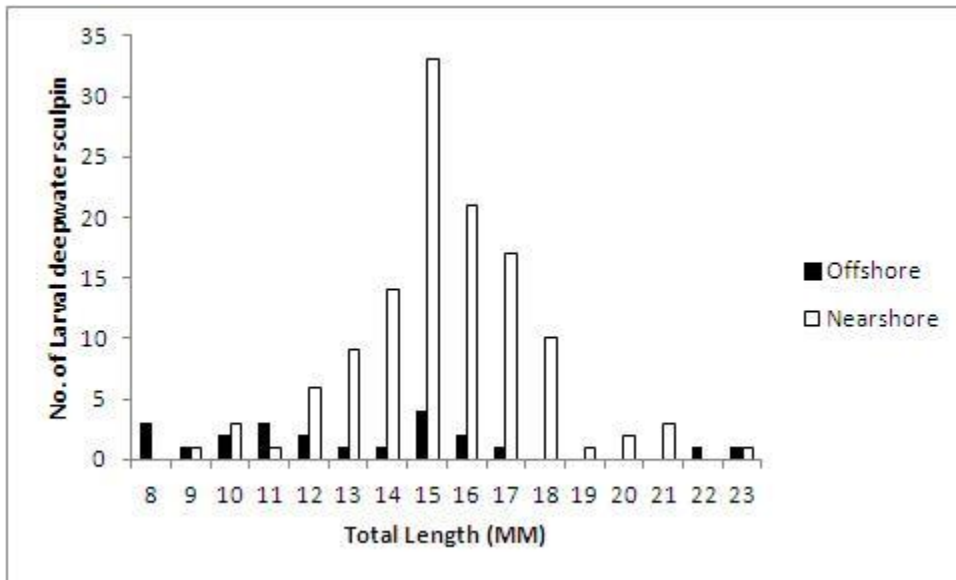


Figure.8 Total length of larval deepwater sculpin collected at the inshore and offshore locations (GPS are approximately 43°05', 87°50'-43°05', 87°42') during spring thermal bar from 2007 to 2009.

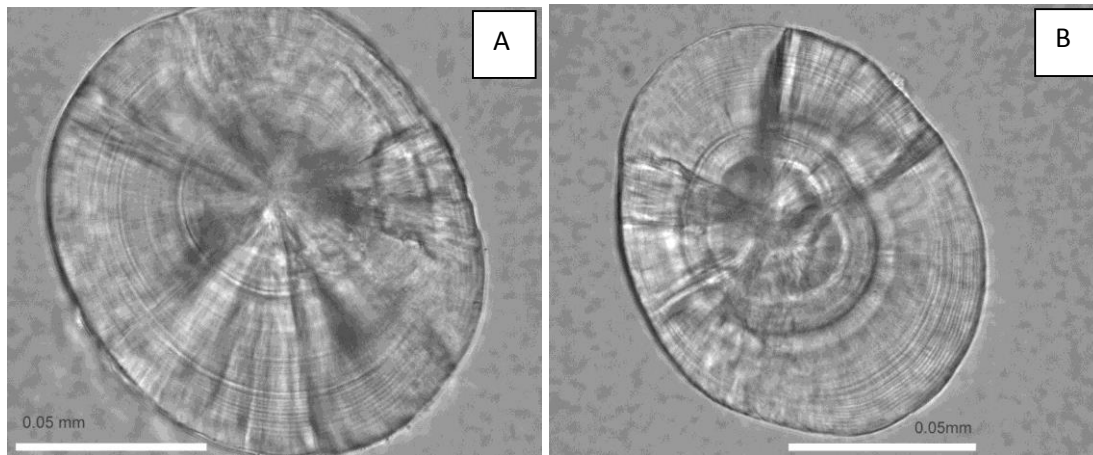


Figure 9. Otolith comparison of deepwater sculpin inshore versus offshore. A. Sagittal otolith of deepwater sculpin inshore deepwater sculpin larvae from 29 April 2009, with total length being 16.2 mm. B. Sagittal otolith of offshore deepwater sculpin larvae from 29 April 2009, with total length being 16.1 mm.

## Burbot

*Adult burbot at the MLRC-* During 6 August 2009, I extracted 13 adult burbot from dense, multilayered boulder cover in an area approximating 1,500 m<sup>2</sup>. This density (about 130/ha) should be considered as minimal because burbot was not targeted species; sampling the area was not spatially comprehensive, and we could only see burbot affected by the electroshocker. Burbot resting in recesses in piled cobbles or boulders that provided extensive overhead cover would not be visible to the video camera (Boyer et al. 1989). Burbot observed via ROV on Julian's Reef (23-41 m deep) in southern Lake Michigan had a similar density of 139/ha (Edsall et al. 1993).

*Larval burbot distribution during thermal bar formation* — I sampled for larval burbot during spring along the western side of Lake Michigan off Milwaukee, WI during thermal bar formation. Inside the thermal bar, sampling depths increased from 17 to 37 m (2.4 to 10.0 km from shore) as the bar moved offshore. Depths of offshore locations increased from 39 to 78 m (8.0 km to 18.9 km from shore). Sampling occurred within and outside the bar three to four times during 17 April- 14 May 2007-2009 to determine if thermal conditions and prey densities favored survival of burbot larvae. No burbot were collected during the spring thermal bar time in my study, despite collecting 11 samples (5.5 he of sampling effort), suggesting no spawning occurred in the local tributaries to Lake Michigan on the western side. Becker (1983) reported no resident burbot populations exist in these streams either.

*Larval burbot distribution around the MLFC--*I also collected 4,074 larval burbot (length range: 3.4 -14 mm) (Fig. 10) in Tucker trawls on six sampling dates after stratification

from 2007-2009 at two locations: coastal (54-60m bottom depth) and on reef at similar bottom depth (55-60 m). Many burbot larvae were newly hatched. I aged eight burbot larvae that were 3-4 mm and found that they averaged 3 days old. Burbot density (Fig. 11) was log transformed before comparing the abundance using the two-way ANOVA analysis. The interaction between sampling date and location was not significant ( $F_{5,6}=0.327, p=0.880$ ). The larval burbot density on MLRC was significantly greater ( $F_{1,6}=6.854, p=0.04$ ) than that of the coastal location. Burbot total length (Fig.10) was log transformed and compared with two-way ANOVA analysis. The interaction between date and location was significant ( $F_{5,302}=2.842, p=0.016$ ). The data was re-analyzed as a one way ANOVA with 12 (6 dates x 2 sites) independent sampling cases ( $F_{11,302}=8.698, p<0.001$ ), followed by a subsequent Tukey test. The Tukey result showed that, for one (14 July 2009) out of six dates, larval burbot captured from coastal location were significantly larger ( $p=0.008$ ) than those from MLRC location.

*Larva burbot stomach content analysis around the MLFC*— I compared the stomach contents of burbot (Fig. 12) between the two sampling locations. The analysis showed a tendency that burbot larvae on the reef fed more on *Limnocalanus* copepods than those from coastal location. The two-way ANOVA with date and location as factors showed a significant interaction between these two factors ( $F_{11,302}=3.121, p=0.009$ ), so the main effects (date and location) were not interpretable. Therefore, I re-analyzed as a one way ANOVA with 12 independent sampling cases ( $F_{11,302}=23.99, p<0.001$ ) to generate the error mean square for a subsequent Tukey multiple comparison analysis of the 12 location/date combinations. This generates 66 ( $12!/10!2!$ ) pairwise comparisons. This result showed that, for five out of the six dates larval burbot collected on the reef had

significantly more *Limnocalanus* in their stomachs than coastal ones ( $p < 0.001$ ). For one of these dates there was no significant difference between the two locations.

The stomach content analysis also suggested that coastal larvae fed more dreissenid veligers than did those on the reef. One way ANOVA with 12 sampling cases supported this tendency ( $F_{11,302} = 6.655$ ,  $p < 0.001$ ). The subsequent Tukey test showed that, on two out of six dates (June 18<sup>th</sup> 2009 and July 14<sup>th</sup> 2009), coastal larval burbot had significantly more veligers in their stomach than those on the reef. For the other four sampling events, no such difference was found.

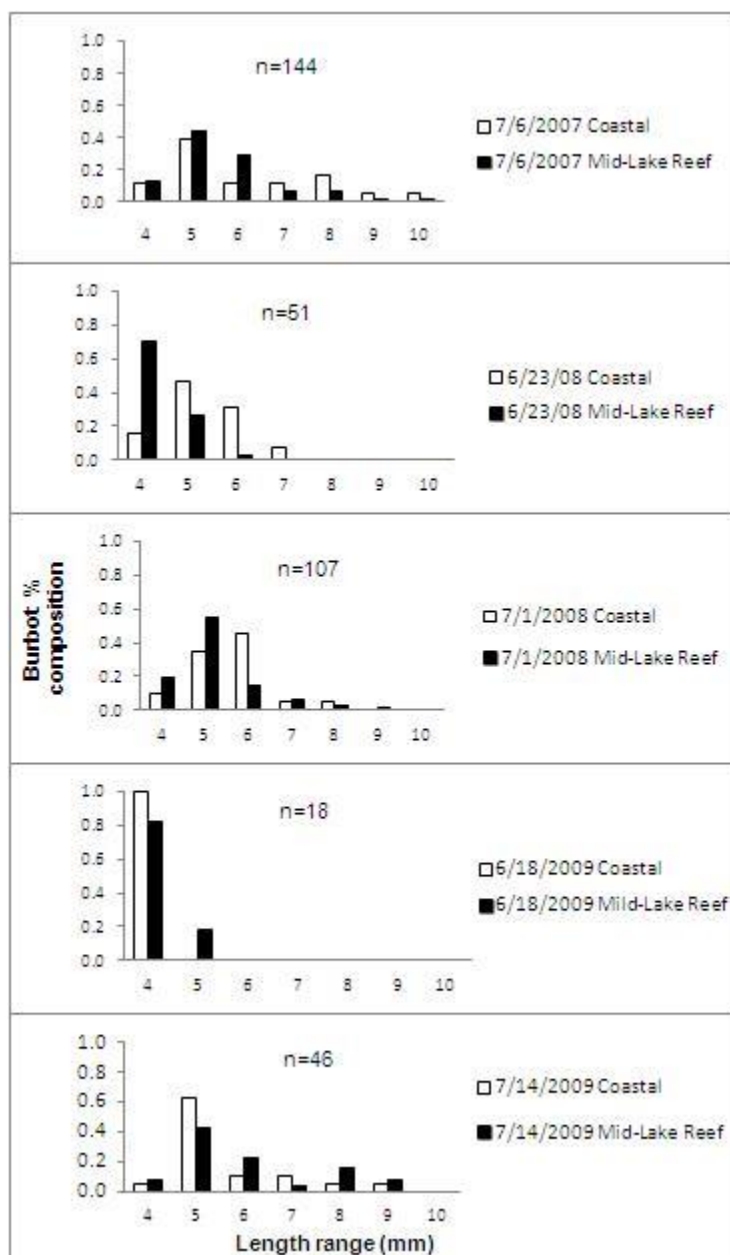


Figure 10. Length-frequency histograms for larval burbot collected during 2007-2009 for coastal and mid-lake reef sites.

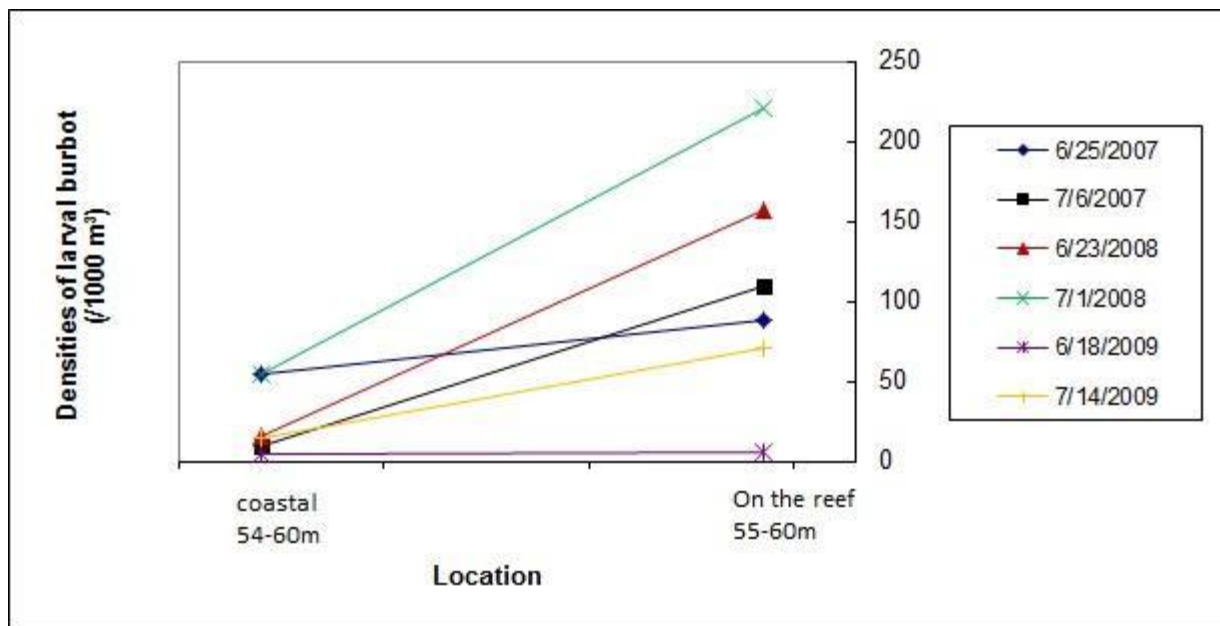


Figure 11. Densities of burbot larvae at about 50-60m bottom depth along the western coast and on East Reef (Mid-Lake Reef Complex, June-July 2007-2009, depth range: 52-83m) in southern Lake Michigan. The two locations are separated by about 27 km and the bottom depth adjacent to East Reef is > 100m.

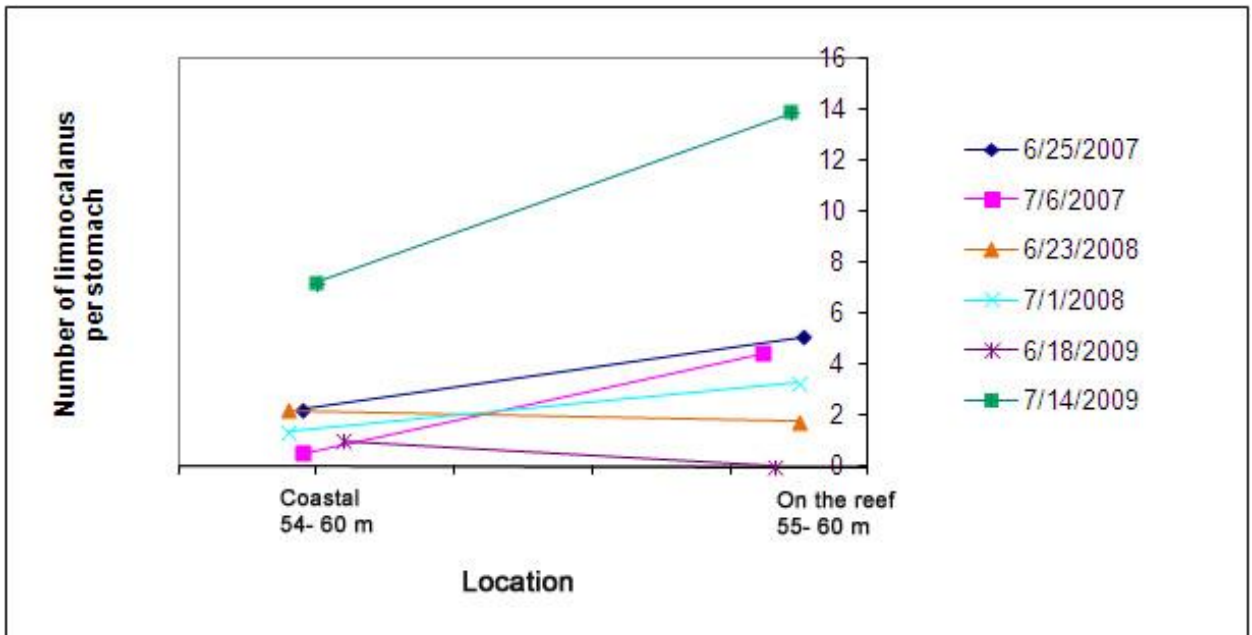


Figure 12: Number of *Laminocalanus* copepod in the stomachs of larval burbot sampled from 2007-2009 along the western coast and Mid-Lake Reef Complex.

## Chapter 4

### Discussion

#### *Mysis*

While information on *Mysis* was the byproduct of my larval fish project, my results justify more intensive study of *Mysis* in regards to thermal bar dynamics. A particularly interesting time is during thermal bar development, when temperature structure is mostly horizontal rather than the better studied vertical structure of summer. I propose that *Mysis* interactions with these physical structures and benthic organisms will likely parallel that of euphausiids, which are marine analogs to *Mysis*. Genin et al. (1988) found predation by bottom-associated fishes on vertically migrating euphausiids advected into shallow water with consequent intensification of euphausiid patchiness. The ability to ascertain parallel dynamics for the Great Lakes will require better bathymetry maps and a better understanding of coastal hydrodynamics. My work shows that *Mysis* can occur shallow enough for diverse dynamics analogous to those described by Genin et al. (1988).

Prior to my study the shallowest depth that *Mysis* had been collected in spring (April-May) for Lake Michigan was at 37 meters (none at 27 m) (Reynolds & DeGraeve, 1972); I consistently collected *Mysis* from 12-15 m, and at other depths shallower than 37 m. Johansson (1995) found *Mysis* at shallow depths comparable to ours in Lake Ontario. Johansson did not report temperatures, so it is not known what water mass (inside vs. outside of the thermal bar) they were in. However, her sampling occurred in the last week

of May. So, if warming was comparable to my Lake Michigan work, the spring thermal bar period was over.

I suggest that *Mysis* were advected prior to thermal bar initiation into shallow water by strong winter/early spring currents when the lake has negligible thermal structure.

Reynolds & DeGraeve (1972) found *Mysis* in December and January at a depth of 27 m (but none at 18 m). They found *Mysis* as shallow as 18 m during summer upwelling events, presumably advected along with the hypolimnetic water. In Lake Ontario, *Mysis* was reported at 12.5m bottom depth in November (Johannsson, 1995). Movement of *Mysis* into shallow regions was attributed to upwelling events (Johannsson, 1992). Lake Michigan currents can be very strong; even during late spring and summer Lake Michigan currents can account for offshore advection of larval yellow perch in the epilimnion (Beletsky et al., 2007).

Ascertaining the significance of *Mysis* in shallow coastal water will require further work, which will be a technological challenge. It is likely that my Tucker trawl did not sample the entire vertical extent of *Mysis*, and, because *Mysis* vertical distribution is affected by light levels, temperature, predators, prey, and *Mysis* size (Boscarino et al. 2007, 2009), the vertical distribution likely differed between offshore vs. inshore stations. At inshore stations, some *Mysis* may have stayed so close to the bottom that no towed net technique would sample them. The western coast of Lake Michigan is predominantly rocky with irregular depths (Janssen et al. 2005) so trawling close to the bottom is hazardous due to the high risk of snagging. The best sampling strategy is likely via quantitative bioacoustics on very dark nights.

There is an inherent bias in my sampling related to potentially missing the deepest part of the *Mysis* layer in my samples. However, I think that the bias would favor finding a higher percentage of larger *Mysis* inshore. Assuming that light was the major factor affecting nighttime depth of *Mysis*, I would expect decreased light penetration inshore of the thermal bar because of increased chlorophyll concentrations. Therefore, the depth range of the inshore *Mysis* layer would be shallower in the water column than those offshore where light penetration is greater. As a thought experiment, I assume equal densities for inshore and offshore *Mysis* layers. A shift upward of the entire *Mysis* layer at the inshore site due to less light penetration would increase the number of larger individuals shallow enough to be captured by the trawl. The smaller individuals are also shallower, but their vulnerability to the trawl has not changed. Hence the percent juveniles captured is expected to be less for the inshore site. This expectation is contrary to my results. But, because so many factors affect vertical distribution (Boscarino et al. 2007, 2009) and because the thermal structure as well as other factors differ so greatly between inshore and offshore sites I suspect that the actual vertical distribution would be difficult to predict and an excellent test of Boscarino et al.'s (2007, 2009) models of vertical distribution.

Advection to shallow water during winter and early spring, when inshore temperatures are not warm, may be important for interactions with the newly invasive *Hemimysis anomala*, a mysid that is associated with coastal rocky areas (Walsh et al., 2010).

Unmanned submersible and scuba diver observations at an artificial reef in fall (2009 and 2010) showed high densities of *Hemimysis* at the base of the reef at 15 m, not much shallower than my shallowest *Mysis* samples. I did re-examine my samples for this

project and found no *Hemimysis*. *Hemimysis* did not become common in Lake Michigan until after my study. Although the depth distribution of *Hemimysis* is not well known, my study demonstrates there is a potential for *Mysis* and *Hemimysis* to overlap spatially.

Genin et al. (1988) argued that advection of vertically migrating zooplankton into shallow water can be an important energy subsidy for bottom associated fishes. One particularly important Great Lakes example might be lake trout (*Salvelinus namaycush*) whose first feeding fry emerge from winter incubation during the thermal bar period. *Mysis* was more than 50% (by volume) of the first food of coastal lake trout fry collected over bottoms less than 10 m at the only well-studied Lake Superior nursery (Hudson et al. 1995). These first-feeding lake trout were caught mainly in April and May, the time that Auer and Gatzke (2004) found thermal bar development for Lake Superior. Increased recruitment by invasive lake trout in Flathead Lake, Idaho was attributed to the introduction of *Mysis* (Ellis et al. 2011). Unfortunately, almost nothing is known about lake trout spawning and nursery areas in this and other mountain lakes in which *Mysis* and lake trout have been introduced.

Much of what I have learned about *Mysis* vertical distribution has been driven by its interaction with vertically migrating planktivorous fishes such as alewife (*Alosa pseudoharengus*; e.g. Boscarino et al. 2010). I propose that cross-shelf dynamics are important for interactions between *Mysis* and near-bottom predators. For example, *Mysis* horizontal distribution is affected by upwelling/downwelling events (Morgan and Grossnickle 1979). Price et al. (2003) reported similar movements by lake whitefish (*Coregonus clupeaformis*), a coastal benthopelagic species that feeds on *Mysis* (Pothoven

and Madenjian, 2008). It may be that the lake whitefish are not tracking temperature *per se*, but are tracking *Mysis* horizontal distribution.

There is at least one possible physical explanation for smaller individuals being relatively more abundant at my shallow stations. Because smaller *Mysis* tend to rise shallower than larger ones at night (Beeton and Bowers 1982), they are more likely to be advected into shallow water if the larger individuals remain on or near bottom.

One question remaining unanswered is whether there are benefits for juvenile *Mysis* emerging from inshore of the thermal bar. Juvenile *Mysis* may have increased growth shoreward of the thermal bar. Smaller *Mysis* are more dependent on phytoplankton for food than are larger individuals (Lasenby and Landford 1973, Branstrator et al. 2000). Moreover, *Mysis* feeding rate increases with temperature until about 10-12° C (Chippis 1998). The slightly larger inshore juvenile *Mysis* may reflect increased growth as a consequence of increased coastal temperature and phytoplankton abundance (Fig.2). The same question can also be applied to the deepwater sculpin larvae. However, the use of fish otoliths allowed me to resolve this problem one step further.

### **Deepwater sculpin**

My work showed that larval deepwater sculpin passively dispersed to the water inside of the thermal bar grew faster, and thus may contribute better to recruitment. The spring thermal bar corresponded to the pelagic period of larval deepwater sculpin in Lake Michigan, a time marked by high mortality (Geffen and Nash 1992). The swimming speed of deepwater sculpin larvae is slow enough that it can be seen as negligible

comparing to the currents. Thus the distribution of deepwater larvae is mainly determined by the currents. Geffen and Nash (1992) reported the presence of deepwater sculpin larvae in both inshore and offshore waters during early spring in Lake Michigan. My study reported a total of 171 deepwater sculpin larvae in both inshore and offshore water during the spring thermal bar. The densities of deepwater sculpin were low, 0-16 larvae/1000 m<sup>3</sup>.

Higher numbers of *Limnocalanus* were found in the stomachs of deepwater sculpin larvae inside the thermal bar. This can be explained by two hypotheses. First, it suggested that inshore deepwater sculpin larvae encountered higher prey availability. Second, it suggested that inshore larvae could catch prey more successfully than offshore larvae, possibly due to higher growth rates. The zooplankton analysis did not support the first explanation, showing no difference in zooplankton density inshore versus offshore. The subsequent otolith analysis supported the second hypothesis by showing wider daily growth rings for inshore larvae, indicating higher growth rates. Since the rate of larval development is related to their size, not their age, faster growth ensures that larvae develop faster (Kristiansen et al. 2011). Faster development rates reduce the transition time from larvae to juvenile (Kristiansen et al. 2011) and reduce larval vulnerability to predators (McGurk 1986). This pattern is known as the “bigger is better” hypothesis (Leggett and DeBlois 1994).

Lake Michigan has a long history of non-indigenous introductions that have caused significant ecological change (Fahnenstiel et al., 2010). Over the past 30-40 years, nonindigenous species, whether through invasion, intentional stocking, or accidental translocation, have affected all major food web components and ecosystem functions in

Lake Michigan (Madenjian et al., 2002; Cuhel and Aguilar 2012). The most significant introduction during this time frame has been the establishment of dreissenid mussels, especially quagga mussels (*Dreissena rostriformis bugensis*), which have had a much greater impact than the preceding zebra mussels. These mussels have exerted devastating effects on commercial and sport fisheries through ecosystem structure modification-including the decline of primary production (Fahnenstiel et al. 2010; Cuhel and Aguilar 2013). Quagga mussels first appeared in shallow areas of Lake Michigan in 2000 (Nalepa et al. 2001) and as soon as in spring of the 2002, they spread to offshore and were observed in the Mid-lake reef complex (MLRC), which rises out of a 150 m basin to shoals of 40-60 m (Janssen et al. 2006). As the voracious benthic filter-feeding quagga mussels compete with zooplankton for 5  $\mu\text{m}$ -size phytoplankton, the availability of herbivorous zooplankton food for young fish may be in seriously decline (Fahnenstiel et al. 2010).

One of the primary determinants of deepwater sculpin abundance in Lake Michigan is predation by burbot on adults, and by alewife on larvae (Madenjian et al. 2005). The population of deepwater sculpin has been decreasing since 2005, and biomass declined 74% between 2003 and 2007 (Bunnell and Madenjian 2009). The densities of larval deepwater sculpin from our field samples were lower than those (5-78 larvae/1000  $\text{m}^3$ ) reported by Mansfield and Jude (1983) 20 years ago and before the invasion of dreissenids. However, this is unlikely due to alewife since the population has not increased during recent years (Bunnell and Madenjian 2009). Early life constraints may have become increasingly important in regulating deepwater sculpin dynamics, especially following the dreissenid mussel-induced changes in the Great Lakes (Fahnenstiel et al.

2010). Further study and monitoring of the physical and biological factors during spring thermal bar period is necessary for fishery management in order to better understand the ecological influences of *Dreissenid* mussels on deepwater sculpin recruitment.

The quality of copepods (indicated by the mean size) is one biological parameter that was not measured in our study, but could affect the survival and growth rate of larval deepwater sculpin. Beaugrand et al.'s study (2003) on Atlantic cod (*Gadus morhua* L.) showed that cod survival was mainly related to changes in the mean size of calanoid copepods. For future studies, both the quantity and quality of copepod should be considered as prey availability to study the effect on larval deepwater sculpin survival.

During the past few decades, there has been some scientific attention to the ecological influence of the spring thermal bar. Previous studies were mainly focused on the relationship between primary productivity and plankton production. They suggested that the spring thermal bar divides inshore and offshore water as areas of favorable and less favorable physical conditions for plankton growth (Bolgrien et al., 1995; Brett and Goldman, 1996; Botte & Kay 2000). However, knowledge of the ecological effect of the spring thermal bar on larval fish early life stage is limited. My study revealed the interaction between spring thermal bar and larval fish development in Lake Michigan. Deepwater sculpin larvae transported inside of the thermal bar were exposed to better feeding conditions (warmer temperature within preferred range) as shown in our study, thus, they grew more rapidly and bigger. This faster growth increases survival potential by reducing the pelagic duration (Suthers 1998). Different mortality among locations during the early growing season could also dramatically alter the relative number of recruits (Houde 1987, Höök et al. 2007). During early life, fish probably experience high

rates of size-dependent mortality primarily as a result of two processes: starvation and predation (Miller et al. 1988; Leggett and DeBlois.1994). Larger body size renders inshore deepwater sculpin larvae less vulnerable to their predators due to greater swimming speeds. The resultant greater swimming speed, greater energy reserves, as well as reduced mass-specific metabolic rates, make starvation less likely (Miller et al. 1998, Höök et al. 2007). These advantages can lead to greater survival and ultimately higher recruitment to the adult population.

After the pelagic period, deepwater sculpin larvae need to go back to offshore deep water habitat, complete the settlement and become demersal. A prerequisite for population persistence is connectivity among habitats by successive life stages, allowing the survivors to mature and return to the spawning grounds to reproduce successfully (Sinclair, 1988). Although inshore water is a relatively more ideal nursery ground, if inshore larvae can't return offshore and settle, they wouldn't contribute to the recruitment. Geffen and Nash's study (1992) found deepwater sculpin larvae at the size of settlement (30 mm in length) distributed throughout the lower water column from the 15- 100 m depth, and the successful settling of YOY deepwater sculpin was concentrated between the 50 and 75 m depth contours. We did not sample deepwater sculpin in bottom trawl to track their demersal settling. If the inshore deepwater sculpin larvae from our study settled in shallow water (<50 m), they may not recruit and therefore play no future part in the dynamics of the parent population--- this is proposed as "adverse advection" by Hjort (1926). However, from the perspective of growth rate, larval deepwater sculpin benefit from being inside of the thermal bar. The combined work of Dettmers et al. (2005) and Beletsky et al. (2004) found that larval yellow perch were quickly transported

offshore from inshore spawning sites (along the western shoreline of Lake Michigan) by hydrodynamic drift. Hence, some larval deepwater sculpin may also be subject to such drift and return offshore to become demersal.

Climate change has occurred at an unprecedented rate during the last century, with mean temperature increases exceeding two degrees in certain areas of the temperate and arctic climate zones (Houghton et al., 2001). It has resulted in earlier spring and later autumn in temperate regions (Møller, 2002). Moreover, climate change can disrupt preexisting synchrony between interacting species in the seasonal timing of their life-history events (Reed et al., 2013). A shift in synchrony between trophic levels due to climate change has been demonstrated for migratory bird species, in which a growing disjunction between phenology in overwintering areas and their summer breeding grounds occurred (Inouye et al. 2000, Both and Visser 2001, Thomas et al. 2001), and thus they arrive at an inappropriate time to match peak food availability (Winder and Schindler 2004). Many studies have provided mounting evidence that many insectivorous birds are advancing their laying date in association with climatic warming (Both et al., 2004; Crick & Sparks 1999; Dunn & Winkler, 1999; Dunn and Winkler, 2011). However, if the food (such as caterpillars) peak shifts more than the bird's laying date, it will cause a mismatch between the offspring's needs and the peak date in food availability, which in turn would lead to a lower reproductive output (Grøten et al., 2009). Dunn et al. (2011) suggested that climate change is making the current cues for breeding (photoperiod, temperature, and food availability) poorer predictions of food supply and therefore the optimal time for breeding.

In aquatic systems, seasonal changes in temperature lead to a predictable succession of physical processes, as well as phytoplankton and zooplankton growth, in pelagic ecosystems (Sommer et al. 1986). Differences in the temporal and spatial match between predator and prey thus generate variability in predator survival rates (MMH [Cushing 1974]). Climate change affects the relative timing of food requirement and food availability for various organisms and thus influences their survival (Durant et al. 2007). Changes in phenology and resulting trophic mismatch have been reported for the North Atlantic plankton community where the level of response differs throughout the community and the seasonal cycle, resulting in a mismatch of trophic levels and functional groups (Beaugrand et al., 2003; Platt et al., 2003; Edwards and Richardson, 2004). This trophic mismatch finally affected fish stock recruitment, as reported for the North Sea Cod/*Calanus finmarchicus* interaction (Durant et al. 2005). Climate change may also affect the duration of winter/early spring mixing of nutrients. In Lake Michigan, summer stratification blocks the supply of nutrients from lower layers to the surface (Mortimer, 2004). Around mid-December, autumnal cooling has allowed wind action to destroy summer stratification and brings the temperature of the whole water mass down to near 4°C (Mortimer, 2004). Lake Michigan becomes well mixed from top to bottom (Beletsky and Schwab, 2001). This winter/early spring mixing is ecologically important because, as the lake mixes from top to bottom, nutrients such as nitrogen and phosphorus are expected to be delivered to the euphotic zone (Miller et al. 2000). Re-suspension coupled with optimal nutrient and light conditions might provide for development of spring bloom in Lake Michigan (Millie et al., 2000). The spring bloom can contribute up to half of the lake's annual primary production (Fahnenstiel and Scavia 1987; Gardner et

al. 1990, Brooks and Edgington, 1994). Climate change can cause an earlier onset of spring thermal bar in Lake Michigan and reduce the duration of winter mixing. Given that plankton play a central role in trophic transfers through aquatic food webs (Winder and Schindler, 2004), I may expect a decrease in fish population and recruitment due to climate change. Our study showed strong justifications for studying the temporal association between the emergence of pelagic fish larvae and the spring thermal bar event. This information may be crucial to predict the long-term consequence of climate changes on fish recruitment in freshwater systems.

### **Burbot**

With potential larval burbot sources ranging from tributaries to extreme depths there is an interesting question of which is the source of larval burbot recruits, and where and how water temperatures affect this relationship. Because burbot inhabit a wide range of habitats with very different annual temperature regimes, it is not surprising that the composite spawning season is quite long, perhaps in excess of half a year. The geographic variation in the temperature regimes has certain surprises. For example, for East Reef the warmest time of year at its 50-m summit is late November (7-8°C as the thermocline descends (Janssen et al. 2007). Consider the fate of a burbot larva in a coastal stream flushed into the main basin in spring. For the four deepest Great Lakes (Superior, Michigan, Huron, and Ontario) coastal water begins warming partially fed by tributaries, which warm more quickly. Offshore temperature is < 4°C and the inshore water is physically separated from the coastal water by the thermal bar. Coastal water is

both warmer and more fertile than offshore water, so larvae in it are likely to grow faster. The thermal bar transitions first into a “thermal wedge” as the lake warms; finally full-lake stratification is a consequence of local warming and offshore movement of the warmer coastal water. For Lake Michigan the thermal bar generally is initiated in April and stratification may not be complete for a month. Note that a burbot larva originating in a tributary prior to the thermal bar period could be either flushed by lake currents well offshore into offshore water in which warming is well delayed, or stay inshore and experience much earlier warming within the thermal bar. The thermal bar does not reach as far as the Lake Michigan MLRC so that burbot larvae emerging in the coastal zone must wait for complete stratification before transport to offshore deep water.

Burbot exhibit various spawning strategies for overcoming environmental and biological obstacles to survival. Jacob et al. (2010) argued that although burbot experienced drastic reductions in abundance with the invasion of the sea lamprey (Stapanian et al., 2008), complete extirpation was avoided, possibly due to the lack of an extensive commercial fishery. Another possible explanation is that burbot are generalized organisms since they have much more diverse diets (Jacob et al., 2010) while lake trout are specialized organisms. The diet of burbot includes crayfish, alewife, smelt, burbot and so on. Lake trout mainly feed on rainbow smelt and alewife. A third explanation is shown in my study: the extended breeding season allows a longer period of larval production, with more opportunities for a “match”.

Burbot is suspected, in some cases, to influence the recruitment and abundance of valuable fish species and stocking success of fish (Savino & Henry, 1991, Degerman & Sers 1993). Burbot and lake trout are the only two native coldwater piscivores of the

Laurentian Great Lakes (Smith 1968). My study found no presence of larval burbot along the western side of Lake Michigan during the spring thermal bar period. However, burbot larvae were captured from late April through the end of May at high densities near Escanaba, Michigan and the east side of Lake Michigan (Mansfield et al. 1983). This difference could be due to river spawning. Along Green Bay, adult burbot have been observed in the Bark and Ford Rivers in late winter (Mansfield et al., 1983). Along the eastern side, adult burbot have been collected during winter in Muskegon Lake, which connects the Muskegon River and Lake Michigan, and from the St. Joseph River as far upstream as Berrien Springs (Mansfield et al. 1983). Hence this high density of burbot could come from stream spawning, with larvae drifting downstream into Lake Michigan.

Appearance of large numbers of newly hatched burbot on the MLRC in late June-August, argues for spawning there later in the year than what has been documented in the Great Lakes spawning sites and rivers adjoining Lake Michigan: late April-May (Mansfield et al. 1983). Burbot spawning on MLRC may have significance in regulating the lake trout restoration in Lake Michigan. Several studies found that the success of lake trout at refuges is negatively influenced by burbot density due to ecological interaction – predation. Parker et al. (1989) suggested that at the intermediate burbot density (0.33 and 139 burbot/ha.), 10.6 burbot (>450mm) per ha in Tolsona Lake, Alaska, consumed 72,147 (39% of the number stocked) lake trout over 30 days. Jacob et al. found that at the high range of burbot density (139/ha), 946,083 lake trout could be consumed over 30 days, which is over 5 times more lake trout than are stocked annually over Boulder Reef. Edsall et al. (1993) reported that with 139/ha burbot density, no lake trout were seen on Julian's reef, where large numbers of juvenile lake trout have been stocked annually and

temperature on the reef were in the preferred summer temperature range for lake trout. Hence, in order to achieve the success of lake trout reestablishment, the number stocked should exceed the number that potentially be consumed by burbot. My study reported the burbot density at the MLRC is about 130/ha, which is at the high range of reported burbot density. For future lake trout reestablishment at the MLRC, this high burbot density should be taken into consideration to better estimate the minimal number of lake trout yearlings that should be stocked.

I found more larval burbot on the mid-lake reefs than off the reefs during June-July. A possible mechanism for this finding is currents concentrating fish larvae and zooplankton in the area of the reefs. For example, larval deepwater sculpin disappeared from the near shore water column after stratification, a time when larval yellow perch also moved offshore with currents (Dettmers et al. 2005). Lake-wide current studies (Mortimer 2004, Beletsky et al. 2007) clearly showed current patterns and advection of particles from near shore to offshore waters. There are many hydrodynamic factors likely operating at the MLRC that may either render it a profitable place for a larval fish to forage during stratification, or they may physically aggregate larvae. My study did show that burbot larvae on the mid-lake reefs consumed more *Limnocalanus* copepods than those off the reefs, suggesting MLRC is a relatively ideal forage place for burbot larvae. Areas at which strong currents intercept areas of rapid shallowing (termed “abrupt topographics” in the oceanographic literature) can concentrate both zooplankton and fishes (Genin 2004). Where measured, currents at the MLRC can be strong (Gottlieb et al. 1989) and their upwelling is likely responsible for frequent thermal fronts at the MLRC (Ullman et al. 1988). One mechanism discussed by Genin (2004) involved a behavioral response by

zooplankton to swim downward in an upwelling water mass to maintain a favored light-determined, depth preference. This could not only concentrate prey for larval burbot, but, because they vertically migrate, the burbot themselves might be concentrated. Houghton et al. (2010) discussed another mechanism that topographically traps *Mysis* and could facilitate settling of burbot transitioning from the pelagia to benthos.

Dreissenid mussels invaded the Laurentian Great Lakes from the late 1980s through the 1990s (Nalepa et al., 2001). Dreissenids are r strategists with a short maturation time (1-2 years), high fecundity (>1 million eggs produced per female per spawning event), and a remarkable ability for dispersal, aided by a planktonic veliger stage and an adult stage that adheres strongly to most hard surfaces (Ludyanskiy et al. 1993). The energy flow and availability of lower food web resources for fish production in Laurentian Great Lakes have been altered by dreissenid mussels (Vanderploeg et al. 2002). Predation on dreissenid mussels in the Great Lakes has been documented for diving ducks, freshwater drum (*Aphlodinotus grunniens*), yellow perch (*Perca flavescens*), and round goby (French 1993; Morrison et al., 1997; Mitchell et al., 2000; Bunnell et al., 2005). Bunnell et al. (2005) reported annual consumption of dreissenid mussels by the round goby (*Neogobius melanostomus*) population in the central basin of Lake Erie during 1995-2002, even though this consumption had minimal effect on dreissenid mussel population dynamics. During the 2000s in Lakes Michigan and Huron, dreissenid mussels have become an important component of lake whitefish diet, representing up to 80% of the diet for some age groups (Pothoven and Madenjian 2008). However, this change was reported to be consistent with lower lake whitefish condition and growth because dreissenids are lower in energy content than most nonmollusc macroinvertebrates (Hoyle et al. 1999;

Owens and Dittman 2003; Pothoven and Nalepa 2006). Predation on dreissenid mussels by both round goby and lake whitefish are suggested to have a significant effect on dreissenid mussel abundance in the Great Lakes (Lederer et al. 2008; Madenjian et al., 2010).

My study elucidated a trophic link between burbot and dreissenid mussel veligers. Since dreissenid mussels can affect phytoplankton and zooplankton community structure (Fahnenstiel et al. 1995; MacIsaac et al. 1996; Caraco et al. 1997; Johannsson et al. 2000), it was argued that fish that depend on pelagic food pathways may be negatively affected by dreissenid invasions (Fahnenstiel et al. 1995; Johannsson et al. 2000; Strayer et al. 2004). My study showed that larval burbot have adapted to the invasion by including veligers in their diet. Burbot larvae prey selection includes two factors: prey size and taxonomic categories (Ghan and Sprules 1993). The selected prey size increased as the larvae size increased since the first day of feeding and the prey change from rotifer to copepod nauplii to adult copepods and daphnia (Ghan and Sprules 1993). One explanation for the veliger consumption is that veligers do not have diel vertical migration as crustacean zooplankton does. Diel vertical migration is a common behavior pattern in most marine and freshwater zooplankton in which a zooplankton population spends daylight hours deep in a lake and then rise toward the surface for a few hours at night (Niikkelsen et al. 1990). This behavior facilitates escape from light-dependent mortality imposed by visually orienting predators, mostly fish, during daylight hours (Loose and Dawidowicz, 1994). This means during the daytime, as most zooplankton stay deeper in the water column, veligers becomes more selected because they are more abundant, falling in the size selection and easier to handle. The burbot diet result

supported this hypothesis. I found significantly more veligers in the stomachs of coastal burbot larvae than those on the reef.

Studies on adult *Dreissena polymorpha* have found that this invasive mussel represents a lower-quality food item than traditional prey such as fish, clams, and non-mollusc invertebrates (French & Bur, 1996; Nagelkerke & Sibbing, 1996; Magoulick & Lewis, 2002; Pothoven & Madenjian, 2008). However, relatively little research has been conducted on predation on dreissenid veligers by larval fish (reviewed by Molloy et al. 1997). It is important to investigate if burbot larvae are feeding on dreissenids veligers in a cost-effective manner and what is the effect on burbot energy density. Energy density, which is directly related to lipid content, is controlled by two factors, energy content of a fish's diet and feeding rate (Madenjian et al. 2000). Thus, even though the energy content of dreissenids veligers may be lower when comparing to the traditional prey, if the feeding rate of the larvae on the veligers is high enough, the energy density of the burbot larvae may not decrease, or may even increase. Paolucci et al. (2010) found that the shells of *Limnoperna fortunei* veligers represented less than 30% of dry weight, and as they are much slower and clumsier swimmers than crustaceans, their capture times are most probably significantly lower than those of cladocerans and copepods; consequently, veligers represent a higher-quality food in comparison with other prey. Their hypothesis was supported by the fact that feeding on veligers of *L. fortunei* significantly enhanced the growth of 'sábaló, *Prochilodus lineatus* larvae. If this also applies to dreissenid veligers, the predation on veligers will allow higher energy density for burbot larvae, resulting from the higher energy content and/or from the higher feeding rate due to lower energy costs of capturing the prey.

Determining this energy density is important because it provides information on the ability of fish to grow, reproduce, and overwinter (Rottiers and Tucker 1982); it is also a measure of prey quality and quantity, a useful tool to evaluate ecosystem changes after the dreissenid invasion (Madenjian et al. 2000). Moreover, it is also important to study the potential of burbot consumption on dreissenid mussel population control.

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## CURRICULUM VITAE

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**Education**

B.A., Ocean University of China, May 2003

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**Dissertation Title** :Lake Michigan hydrodynamics: *Mysis* and larval fish interactions

**Professional Experience**

May 2006 to June 2006: Ocean University of China

- Field Assistant: Assisted professor with zooplankton field data collection in Yellow Sea; laboratory sample enumeration and data analysis.

Aug 2007 to present: Great Lakes WATER Institute

- Research Assistant: conducted research in freshwater fish ecology in Lake Michigan. Conducted field sampling, collected field data and laboratory data, drafted reports.
- Attended 52<sup>nd</sup> IAGLR Conference: *Bridging Ecosystems & Environmental Health across our Great Lakes* in 2009.
- Attended *Lake Michigan: State of the Lake-6<sup>th</sup> Biennial Conference and Great Lakes Beach Association- 9<sup>th</sup> Annual Meeting* on Sep 29<sup>th</sup>, 2009 and did oral presentation on **Larval burbot distribution around mid-lake reef complex in Lake Michigan**.
- Attended *Physical-biological coupling and fish recruitment in large lakes workshop* in Detroit, Michigan on August 16, 2011

Sep 2009-present: Biology department of UW-Milwaukee

- Teaching Assistant of Survey of Zoology laboratory. Coordinated presentations and demonstrations of animal dissections as part of the lab curriculum.
- Teaching Assistant of Plants of Today's World laboratory. Coordinated presentations and designed experiment for the lab curriculum.
- Teaching Assistant of Anatomy and Physiology 1 Lab. Coordinated presentations and designed experiment for the lab curriculum. Focusing on case studies and hands on activities to motivate students and enhance their critical thinking.
- Teaching Assistant of online courses-Invasive Species & Biology of Women. Grading, developing class assessments, providing students with feedbacks and communicating with students. Worked with major/non-major undergraduate students to foster educational and scientific growth, with an emphasis in learner-centered teaching, promoting active learning, engaging students, and group works. Frequently worked one-on-one with students assisting with laboratory procedures.

May 2013- present: Bryant and Stratton College

- Adjunct Faculty of Ecology: Design curriculum and class activities, focusing on critical thinking skills, active learning, and student motivation. Collaborate with other faculty members across the curriculum.

### **Awards**

April, 2010 - Clifford Mortimer Awards (UW Milwaukee graduate student Scholarship)

April, 2011- Clifford Mortimer Awards (UW Milwaukee graduate student Scholarship)

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### **Publications**

Yu Wang, Tom R. Consi, Tom Hansen, John Janssen. The Relationship Between Coastal Mysis diluviana Abundance and Spring Thermal Bar Dynamics. Journal of Great Lakes Research. Volume 38, Supplement 2, 2012, Pages 68 - 72.

David J. Jude, Yu Wang, Stephen R. Hensler, John Janssen. Burbot Early Life History Strategies in the Great Lakes. Currently under review at Transactions of the American Fisheries Society.