

# The effects of experimental whole-lake mixing on horizontal spatial patterns of fish and Zooplankton

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**Abstract** We examined horizontal spatial patterns of fish densities and zooplankton biomass at a fine spatial scale of 50 m across seasons before, during, and after an experimental lake destratification to determine how interacting trophic levels may respond to alteration of thermal stratification. We used semivariogram analysis to calculate maximum distances of autocorrelation for fish and zooplankton separately, and cross variograms to determine whether relationships between fish and zooplankton are positive or negative. Fish became more dispersed during the manipulation, likely due to a flight response with the loss of preferred cold water habitat. There were no changes in zooplankton horizontal distributions with mixing, but we detected seasonal trends in distribution and biomass. We detected positive relationships between fish densities and zooplankton biomass for portions of the year, but did not detect any negative relationships. There was no effect of lake mixing on spatial interactions between fish and zooplankton. Our

results indicate that external factors, such as seasonal wind patterns, may drive whole-lake zooplankton distributions, and that fish respond horizontally to change in vertically structured processes, especially when reliant on depth-dependent variables such as cold water.

**Keywords** Autocorrelation · Hydroacoustics · Semivariogram

## Introduction

In a variety of ecosystems, interacting abiotic and biotic processes create a heterogeneous environment resulting in patchy distributions of organisms (Folt and Burns 1999; Turner et al. 2001; Rinke et al. 2009). Spatial heterogeneity influences population dynamics and predator–prey interactions, mediates species coexistence, and increases species' persistence (Hanski 1981; Pinel-Alloul 1995, Hastings 1988; Brentnall et al. 2003). In lakes, spatial heterogeneity also increases biomass and production rate of both predator and prey populations (Rovinsky et al. 1997). Therefore, in order to fully understand lake ecosystem functions, we must also understand spatial distributions of organisms, their underlying causes, and their potential ramifications.

Planktivorous fishes and zooplankton represent two spatially autocorrelated trophic levels of pelagic lake food webs whose horizontal heterogeneous distributions are the result of physical and biological components interacting across a wide range of spatial and temporal scales (Pinel-Alloul 1995; Rinke et al. 2009). However, many limnological monitoring programs focus exclusively on vertical gradients. Considering the patchy nature of fish and zooplankton in lakes, monitoring that overlooks horizontal patterning may miss information on overall ecosystem level

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variability. In order to gain a more thorough understanding of spatial ecology of lakes, we must consider horizontal patterning of these organisms and the processes involved in their interactions. Few studies have examined the interactions among fish, zooplankton, and abiotic processes that affect horizontal distributions at a whole-lake spatial scale and even fewer studies span more than one season (George and Winfield 2000; Thackeray et al. 2004; Blukacz et al. 2009; Rinke et al. 2009).

The “Multiple Driving Forces Hypothesis” (Pinel-Alloul 1995) suggests that there is a multifactorial suite of variables acting to dictate aggregations of zooplankton and fish. These variables include wind-induced water movements, temperature, predatory avoidance, prey selectivity, and basin morphology (Rose and Leggett 1990; Pinel-Alloul 1995; George and Winfield 2000). Furthermore, the intensity of variables driving distributions depends heavily on the spatial and temporal scales at which parameters are measured (Pinel-Alloul 1995; Rinke et al. 2009). Blukacz et al. (2009) found that large-scale, whole-lake zooplankton patchiness is driven mainly by wind-induced water circulations. However, others have found factors acting at smaller scales, such as predator avoidance and feeding behavior, may also affect zooplankton distributions (Ragotzkie and Bryson 1953; George and Winfield 2000). Additionally, distributions may be species and size-specific, and patterns and drivers are likely to vary across systems (George and Winfield 2000; Ahrenstorff et al. 2013).

Thermal stratification is an abiotic factor with a strong influence on large-scale spatial heterogeneity in lakes. Thermal stratification structures heterogeneous physical habitat, and has far-reaching effects on rates of chemical and biological processes, phenology of aquatic animals, species distribution, and predator-prey interactions (Sommer et al. 1986; Tessier et al. 1991; MacPhee et al. 2011; Tessier et al. 2011). A great body of limnological research relies on assumptions that mixing and stratification are central to cyclical biological events (Sommer et al. 1986; Wetzel 2001). Experimental prevention of stratification would allow assessment of the role of stratification in regulation of spatial structuring of fish and zooplankton populations. Such a manipulation would reveal responses of horizontal patterning to removal of vertical structure. Manipulation would also aid in determination of ultimate causes of spatial distributions of multiple trophic levels at a whole-lake scale.

A team of physical, biological and chemical scientists completed a whole-lake manipulation of Crystal Lake in Vilas County, WI, USA resulting in complete thermal destratification in two summer seasons (Lawson et al. 2015). This experiment provided an opportunity to examine changes in horizontal spatial distributions of fish and zooplankton in response to mixing and loss of vertical spatial

heterogeneity. By comparing pre-, during, and post-manipulation data, we addressed three main questions: (1) How does prevention of stratification affect the scales of spatial autocorrelation for both fish and zooplankton populations? (2) How do spatial interactions between fish and zooplankton change with prevention of stratification? (3) Are spatial patterns in fish and zooplankton distributions determined by physical–chemical mechanisms, predator–prey interactions or both? We used hydroacoustic data, and semivariogram and covariogram analyses to examine horizontal spatial relationships between fish and zooplankton, before (2010–2011), during (2012–2013), and after (2014) mixing. This research will aid in determining the role of stratification in food web interactions, yield information regarding physical and biological coupling, and indicate lake responses to a disturbance regime induced by mixing.

## Materials and methods

### Study site and thermal manipulation

Crystal Lake is a 37 hectare oligotrophic seepage lake located in Vilas County, WI, USA. The lake has a maximum depth of 20.5 m, a pre-manipulation average Secchi depth during the ice-free period of 8 m, and a well-oxygenated ( $6\text{--}7\text{ mg}\cdot\text{l}^{-1}$ ) hypolimnion that has a mean temperature of  $5\text{--}7\text{ }^{\circ}\text{C}$  during the summer (Magnuson et al. 2006). The littoral habitat is sandy with little coarse woody habitat, and few macrophytes. Crystal Lake is also a North Temperate Lakes Long Term Ecological Research lake, and has over 30 years of abiotic and biotic limnological data available (NTL-LTER). Historically, Crystal Lake was dominated by yellow perch (*Perca flavescens*) until the invasion of rainbow smelt (*Osmerus mordax*) in 1985. After invading, rainbow smelt became the dominant species in Crystal Lake. Numerically, smelt comprise about 99 % of the pelagic fish community in Crystal Lake. We used monthly 24-h gill netting events using stretch mesh sizes of 19, 25, 32, 51, 64, and 89 mm to obtain species composition information (NTL-LTER).

Following ice-out and prior to the onset of late spring stratification in 2012 and 2013, thermal manipulation of Crystal Lake began. Gradual Entrainment Lake Inverters (GELIs; Read et al. 2011) were used to continuously mix the lake, increase heat flux into the lake, and prevent stratification. GELIs are large, 8-m diameter trampoline-like discs consisting of a membrane bound to a stainless steel frame. GELIs contain a central air bladder which received air from an on-shore air supply through underwater tubing. Air delivery was controlled via commands from a central computer station located at the center of six GELIs arranged in a circular pattern in the deeper basin of Crystal

Lake (Fig. 1). Inflating the air bladder caused GELIs to rise through the water column. At the surface GELIs expelled air, deflated, and descended to the bottom. Constant cycling of GELIs created a large amount of surface drag throughout the water column. By mixing cold water from the bottom with warmer top waters, GELIs formed a homogenous temperature throughout the entire water column (Lawson et al. 2015).

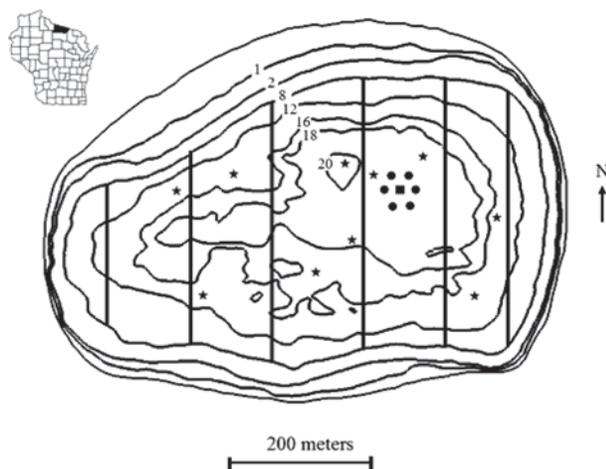
Crystal Lake was fully destratified during manipulation years (2012 and 2013) (Lawson et al. 2015). In pre and post manipulation years, stratification set up in the spring and persisted through the summer until fall turnover. During manipulation, the temperature was similar throughout the entire water column during the season and isothermic at peak temperatures by August (Lawson et al. 2015). Maximum lake temperatures during manipulation exceeded most critical temperatures for smelt, including preferred (12 °C), upper avoidance (15 °C), and lethal temperatures (22 °C) (Ferguson 1965; Wismer and Christie 1987; Lantry and Stewart 1993; Lawson et al. 2015). In 2012 and 2013 the maximum temperatures achieved were 21.6 and 20.8 °C, respectively (Lawson et al. 2015).

### Hydroacoustic data

Hydroacoustic surveys were conducted on Crystal Lake every other week from late May to early November during years of pre-manipulation (2010 and 2011), manipulation (2012 and 2013), and 1 year post-manipulation (2014). We collected data in pelagic regions (>8 m

depth) at night (at least 1 h after sunset) to ensure fish schools were dispersed. Schooling in fish and swarming in zooplankton, which commonly occur during the day, introduce error in hydroacoustic estimates (Appenzeller and Leggett 1992; Parker-Setter et al. 2009). Furthermore, diet analyses indicate the primary planktivore, rainbow smelt (*Osmerus mordax*), actively feeds at night, suggesting that encounters with food resources occur at low light levels (Hrabik et al. 1998). Thus, we sampled at night to reduce error in spatial measures of acoustic backscatter specifically caused by schooling and zooplankton swarming to identify overall spatial patterning in each trophic level. We acknowledge that by sampling at night we are not capturing schooling and swarming behavior, but more general behavioral dynamics that occur at night when these very small scale visually driven patterns are reduced. We used a Biosonics DTX echosounder with 123- and 430-kHz split-beam transducers mounted to a tow body (Biofin, Biosonics Inc.) and towed next to the boat at 0.5 m depth with a vessel speed not exceeding 3mph (2.6 knots). The 123-kHz transducer was used to measure backscatter from fish targets with low interference from zooplankton, and the higher frequency 430-kHz transducer was used to measure backscatter from zooplankton within the water column.

We verified the accuracy of transducer calibration during every sampling event using standard tungsten-carbide spheres to ensure that the received target strengths did not vary from expected target strengths for each sphere ( $< \pm 1$  dB) on any date. We used GPS concurrently with hydroacoustic sampling to obtain latitude and longitude. Acoustic transects on Crystal Lake in 2010, 2011, and 2012 were conducted in a zig-zag pattern. Transects during 2013 and 2014 were composed of 6 parallel lines running north-south (Fig. 1). We changed transect design to adapt for greater spatial coverage part way through the study because we were allowed to use gas powered motors over electric powered motors, which were required by lake regulations early in the study. Based on overall patterning we observed in our analysis, we do not feel this directly influenced our results. We used a pulse duration of 0.4 ms at 3 pulses per second, and a minimum threshold for raw echo inclusion of  $-70$ dB for 123 kHz and  $-100$ dB for 430 kHz using  $20\log R$  echo integration. The nearfield for the 123 kHz transducer was 1.2 and 0.41 m for the 430 kHz transducers (Parker-Setter et al. 2009). Crystal Lake was equipped with a profiling buoy to obtain average water column temperatures, which we used to calculate the sound speed through water. Hydroacoustic data were analyzed using Echoview software (v.4.1).



**Fig. 1** Hydroacoustic survey transects on Crystal Lake (Vilas County, WI, USA) for 2013 and 2014 (vertical black lines), location of Wisconsin net and hydroacoustic zooplankton sampling for linear regression (filled star), location of GELIs (filled circle), and location of GELI control center (filled square). Depth contours are in meters (Lake District Bathymetry, NTL-LTER)

### Fish densities

Post-processing of acoustic data included a series of steps to ensure that only high-quality data were analyzed. We removed bottom echoes from each sample date by excluding 0.5 m from the bottom. We did not perform vertical binning of samples because we sampled only pelagic waters. The bulk of fish and zooplankton biomass was located at 3–12m in depth, regardless of the stage of manipulation. Also, considering nearfield and bottom deadzones associated with hydroacoustic surveys (Simmonds and MacLennan 2006; Parker-Stetter et al. 2009), the contribution of warm epilimnetic areas to backscatter was minimal. Over 99 % of the pelagic gillnet catch biomass in Crystal Lake is one species, rainbow smelt, and the distribution of smelt was associated with similar vertical layers pre- and post-manipulation although they were slightly shallower post mixing. Stratifying layers smaller than 10 m may lead to significant process errors in hydroacoustic data, and vertical binning would consequently be more appropriate in larger, deeper lakes (Simmonds and MacLennan 2006). The vertical bin structure would have also varied on each date and possibly introduced processing error into our analyses. We therefore chose to analyze for only horizontal spatial patterning with no vertical binning.

Data were analyzed in 50 m horizontal bins. For each horizontal bin we calculated areal density ( $\rho_{as}$ ) of number of fish per  $m^2$ . We used a proportion of number of specimens in each species ( $p_s$ ) of 1 because we were interested in all fish rather than specific species.

We first calculated the weighted mean backscattering cross-section ( $\overline{\sigma_{bs}}$ )

$$\overline{\sigma_{bs}} = \sum \left( p_s * 10^{\frac{TS_s}{10}} \right) \quad (1)$$

where  $TS$  is the species specific mean target strength. We then calculated volumetric density ( $\rho_{vs}$ )

$$\rho_{vs} = \frac{P_s}{\overline{\sigma_{bs}}} * s_v \quad (2)$$

where  $s_v$  is the linear mean volume backscattering strength for each cell, which is calculated from the echo integration file of the echogram. Finally, we calculated fish areal density ( $\rho_{as}$ ):

$$\rho_{as} = \rho_{vs} * T \quad (3)$$

where  $T$  is the thickness of the bin (m).

### Zooplankton biomass hydroacoustic regression

We developed a regression to convert 430 kHz acoustic data to estimate zooplankton biomass. We incorporated data from three separate oligotrophic lakes in order to

ensure adequate range in zooplankton biomass and facilitate development of a more general and predictive relationship between zooplankton biomass and acoustic information for oligotrophic lakes. We sampled Crystal Lake and Sparkling Lake, an oligotrophic seepage lake which is very similar to Crystal Lake but is slightly more productive. We also incorporated previously gathered zooplankton biomass/acoustic measurements from Lake Superior (Holbrook 2011). These data were obtained using the same methods employed in our study. Combining these three lakes which span a range of oligotrophic lake conditions and their associated zooplankton communities facilitated the development of a more robust backscatter to biomass relationship.

Zooplankton were collected at ten pelagic locations on Crystal (Fig. 1) and Sparkling (Fig. A1) Lakes during one night sampling event (July 9, 2014). A 0.5 diameter, 153  $\mu$ m mesh size Wisconsin net was towed from 1.5 m above the lake bottom to the surface. Two replicates were taken at each site. Samples were preserved in glass jars in 90 % ethanol. Acoustic sampling with the 430 kHz transducer was completed at the exact location of each of the ten different pelagic sample locations on each lake. In the laboratory, zooplankton were sorted to species, except *Diatomus spp.*, and cyclopoid and calanoid copepods. We subsampled three 1 ml aliquots, and ensured at least 100 individuals were counted. All individuals were identified and counted in each aliquot. Five individuals in each species/taxon were measured for length. *Cladocera* were measured from the top of the head to the base of the caudal spine and *Copepoda* were measured from the top of the head to the insertion of spines on the caudal ramus (GLNPO 2003).

To convert Wisconsin net data to biomass, a basic length-mass model was used:

$$\ln(w) = \ln(a) + b \ln(L) \quad (4)$$

where  $\ln(w)$  is the natural logarithm of estimated dry weight ( $\mu$ g),  $a$  and  $b$  are species-specific constants, and  $\ln(L)$  is the mean of natural log transformed lengths measurements (mm) of species within each sample (GLNPO 2003).

We then developed a regression to convert acoustic backscatter to biomass. We used the Area Backscatter Coefficient (ABC) from acoustic data, which is the strength of backscattering per meter:

$$ABC = 10^{\frac{S_v}{10}} T [m^2 m^{-2}] \quad (5)$$

where  $S_v$  is the mean volume backscattering strength of the domain being integrated, and  $T$  is the thickness of the domain being integrated (average depth within each horizontal bin).

Fish targets were eliminated manually in Echoview during post-processing prior to formal analysis. ABC was

analyzed down to 1.5 m from the bottom of the lake in the 20logR domain for echo integration. ABC was regressed against zooplankton dry weight biomass estimates (mg) from the Wisconsin nets in order to establish a relationship between the two variables. We used the regression to estimate zooplankton biomass for each sampling date, and did not apply the 95% confidence intervals to the estimates.

### Semivariogram analysis

Although acoustic sampling was most often completed every other week, some survey dates were lacking GPS coordinates due to intermittent equipment failure. Other data sets showed signs of interference by large insect hatches. We chose to omit these sample dates in order to use only the most accurate and robust data for analysis.

We developed semivariograms for each sampling date for fish and zooplankton. We tested for geometric anisotropy using directional semivariograms. The directional semivariograms did not show evidence of anisotropy, and we therefore only considered isotropic semivariograms.

Semivariance ( $\gamma$ ) represents the sums of squared differences between measurements at sample points separated by distances ( $h$ ):

$$\gamma(h) = \frac{1}{2n(h)} \sum_i [Z(x_i) - Z(x_i + h)]^2 \quad (6)$$

where  $n$  is the number of pairs of sample points separated by distance  $h$ , and  $Z(x_i)$  is the density (fish) or biomass (zooplankton) estimate at point  $x_i$ , and  $Z(x_i + h)$  is the density or biomass estimate at various distances (Pastor et al. 1998; Durance et al. 2006). Semivariograms assume samples are stationary. In our study we assume our samples were stationary relative to the movement of the boat at the time of sample, where the speed of the boat was much higher than the speed of the organism.

Geostatistical data are typically spatially autocorrelated, where samples that are located close together are more similar than samples farther apart from each other. Semivariograms indicate how autocorrelation decreases with increasing distance (ESRI 2015). Semivariogram models depict rising semivariance until a certain distance, then stabilizes. The distance at which the semivariance stabilizes is called the range, which indicates the distance beyond which samples are no longer autocorrelated and become independent. Samples collected at distances below the range are autocorrelated and are not spatially independent. Range values also give insight regarding size of areas with similar densities. The semivariance value reached at the range is referred to as the sill (Durance et al. 2006). Theoretically, at lag separation distances of zero, there should be zero semivariance. However, semivariograms often have a value greater than zero for semivariance at distance zero. Values greater than

zero indicate the “nugget effect,” suggesting there is spatial variability at scales smaller than those used for analysis (ESRI 2015). Therefore, low nugget values indicate adequate sample resolution while higher nugget values would necessitate exploring finer spatial scales (Durance et al. 2006). We used spherical semivariogram models because they provided the most accurate predictions. For virtually all sampling dates, spherical modeling performed better than the other models (ESRI 2015).

In choosing a horizontal bin size for spatial analyses, there is a tradeoff between fine scale resolution and minimizing bins with zero fish that result in zero density estimates. Further, Parker-Stetter et al. (2009) recommend using bin sizes less than half of the range value estimates from semivariogram analysis. We tested bin sizes of 25, 50, and 75 m and found that 25 m often resulted in empty bins, and chose to use the smallest bin size with a sufficient number of targets for density estimates (50 m). Although 50 m is greater than half the range for some sample dates (Tables 3, 4), we chose to use 50 m bin sizes to decrease zero density estimates. Use of 50 m bin sizes also resulted in low to no presence of the nugget effect.

We determined autocorrelation between fish and zooplankton aggregations for each sampling date by calculating cross variograms:

$$\gamma_{ab}(h) = \frac{1}{2n(h)} \sum_i \sum_j \{Z_a(x_i) - Z_a(x_j)\} \{Z_b(x_i) - Z_b(x_j)\} \quad (7)$$

where  $n$  is the number of pairs of observations separated by distance  $h$  for the first variable,  $Z_a$ , and the second variable,  $Z_b$ , at points  $x_i$  and  $x_j$ .

We tested for effects of season and mixing on range values from semivariogram and cross variogram analysis. We defined spring as any date on or prior to June 30 (fish  $N=4$ , zooplankton  $N=5$ ), summer as dates ranging July 1–August 31 (fish  $N=12$ , zooplankton  $N=12$ ), and fall as September 1 and later (fish  $N=7$ , zooplankton  $N=5$ ).

On dates where we found significant autocorrelation between fish and zooplankton from semivariogram analysis, we further examined potential positive and negative relationships by plotting zooplankton density against fish density for each 50 m bin within the sample date. We analyzed the relationship for significance and whether the slope was positive or negative using linear regression ( $\alpha=0.05$ ). A significant positive slope would indicate fish are aggregating in areas of high zooplankton biomass, and a negative slope would indicate that zooplankton are aggregating as a predatory avoidance tactic, or that fish are initially drawn to an area of high zooplankton biomass and then deplete the biomass through consumption.

We log-transformed fish and zooplankton data to make the density data more normally distributed. Also, it is more

likely to detect spatial autocorrelation with log-transformed data (Rivoirard et al. 2008). We used Kruskal–Wallis tests to analyze for significant effects of season and mixing on semivariogram estimates using an alpha level of 0.05.

### Wind analysis

We collected wind data from an instrumented raft on nearby Sparkling Lake as a means of testing the hypothesis that wind is a major driving force of zooplankton distributions (NTL-LTER). If wind is truly a major driver, we would expect the manipulation to have minor effects on zooplankton distributions. The raft uses meteorological sensors to measure wind speed at 2 m height every 20 min. We calculated average daily wind speed for each day, assigning seasons the same as with our semivariogram analysis. We used Kruskal–Wallis tests to determine whether average daily wind speed was related to season. We also examined occurrence of dates with prolonged events, defined by a 48 h period with less than 10% change in wind direction. To determine if wind is the major driving force of zooplankton distributions, we tested for effects of season on prolonged wind events, and whether zooplankton range values were related to prolonged wind events using Kruskal–Wallis tests ( $\alpha=0.05$ ).

## Results

### Zooplankton biomass hydroacoustic regression

The Crystal Lake, Sparkling Lake, and Lake Superior Wisconsin net zooplankton samples contained variable proportions of taxonomic groups (Fig. 6, see Holbrook 2011

for Lake Superior data). Crystal Lake consisted mainly of cyclopoid copepods, daphnids, and other cladocera with a small proportion of calanoid copepods. Sparkling Lake consisted mainly of cyclopoid and calanoid copepods. Lake Superior largely consisted of calanoid copepods with some cyclopoid copepods and daphnids. In general, all three lakes contained species typically found in oligotrophic lakes.

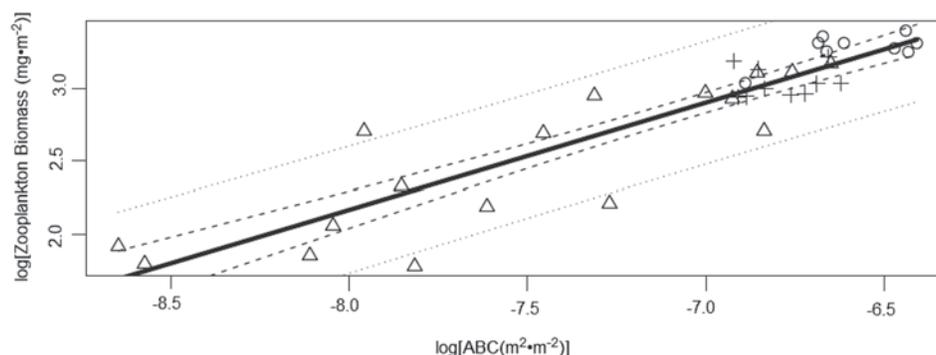
We found a significant linear relationship ( $p<0.0001$ ) between log transformed zooplankton biomass estimates from Wisconsin nets ( $\text{mg}/\text{m}^2$ ) and ABC ( $\text{m}^2/\text{m}^2$ ) despite differences in species compositions across lakes (Fig. 2). The relationship was:

$$\begin{aligned} \log[\text{ZooplanktonBiomass}(\text{mg m}^{-2})] \\ = 0.73 * \log[\text{ABC}(\text{m}^2 \text{m}^{-2})] \\ + 8.04? (N = 36, F = 118.1, \\ R^2 = 0.83, p < 0.0001). \end{aligned} \quad (8)$$

There was no difference in the zooplankton biomass vs. ABC relationship among lakes (Homogeneity of Slopes test,  $p>0.5$ ,  $F<0.6$ ,  $df=30$  for lake and lake/ABC interaction). Therefore, the regression equation was applied to the acoustic data to estimate zooplankton biomass for subsequent spatial analyses.

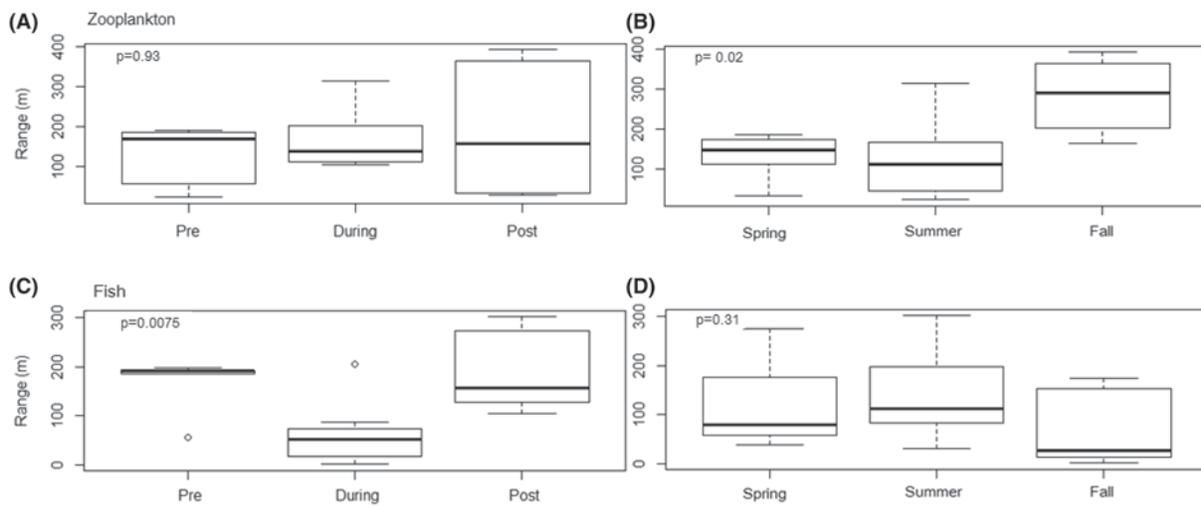
### Zooplankton spatial analysis

Mixing did not have a significant effect on average zooplankton biomass (Table A1, Kruskal–Wallis,  $H=2.8$ ,  $df=2$ ,  $p=0.24$ ), but there was a significant seasonal effect on biomass (Kruskal–Wallis,  $H=11.3$ ,  $df=2$ ,  $p=0.003$ ). Range estimates (m) for zooplankton populations were not significantly affected by mixing (Fig. 3a, Kruskal–Wallis,



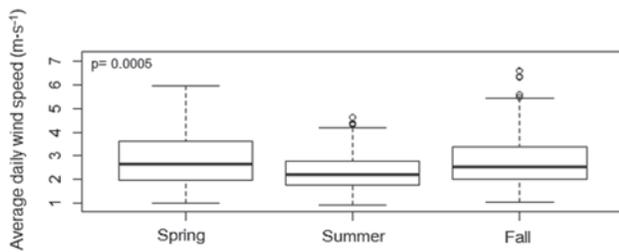
**Fig. 2** Linear relationship between site-specific log zooplankton biomass estimates ( $\text{mg m}^{-2}$ ) from Wisconsin net tows and 430 kHz log hydroacoustic backscatter (ABC, Area Backscatter Coefficient,  $\text{m}^2 \text{m}^{-2}$ ) ( $N=36$ ). The innermost solid line represents the ordinary least squared regression trend line, inner dashed lines represent the

95% confidence intervals, and the outer dotted lines represent 95% prediction intervals. (Circle) indicates Crystal Lake, (plus) indicates Sparkling Lake, and (triangle) indicates Lake Superior (Lake Superior data are from Holbrook 2011)



**Fig. 3** Box plots for range values (m) from zooplankton semivariograms **a** for each stage of the manipulation (Pre: N=6, During: N=10, Post: N=6), **b** for each season, (Spring: N=5, Summer: N=12, Fall: N=5) 2010–2014, and from fish variograms, **c** for each stage of the manipulation (Pre: N=7, During: N=12, Post: N=6)

and **d** for each season (Spring: N=4, Summer: N=12, Fall: N=6). Dark bars indicate median range values, top and bottom of boxes indicate 25th and 75th quartiles, lower and upper capped bars indicate minimum and maximum calculated range values, and hollow circles indicate outliers



**Fig. 4** Average daily wind speed ( $\text{m s}^{-1}$ ) for each season (Spring: N=287, Summer: N=310, Fall: N=381). Dark bars indicate median average daily wind speed values, top and bottom of boxes indicate 25th and 75th quartiles, lower and upper capped bars indicate minimum and maximum calculated average daily wind speed values, and hollow circles indicate outliers

$H=0.14$ ,  $df=2$ ,  $p=0.93$ ). However, we found significant seasonal effects on zooplankton range values (Fig. 3b, Kruskal–Wallis,  $H=7.5$ ,  $df=2$ ,  $p=0.02$ ). The range estimates for zooplankton in spring and summer were  $130 \pm 56$  m (95% CI) and  $127 \pm 57$  m (95% CI), respectively. This distance increased in the fall to  $282 \pm 87$  m (95% CI). We regressed zooplankton biomass estimates against range values to determine if low zooplankton biomass in the fall were causing variability around average range values, and found no significant effect of biomass estimates on the range values ( $N=18$ ,  $F=2.25$ ,  $p=0.15$ ,  $R^2=0.1$ ).

We tested for effects of wind on zooplankton range values, and found that wind varied significantly across season (Fig. 4, Kruskal Wallis,  $H=39.16$ ,  $df=2$ ,  $p<0.0005$ ), where summer average daily wind speed during our

sampling period (2010–2014) was significantly lower than spring and fall average daily wind speed. We found no effect of prolonged wind events on zooplankton range values (Kruskal Wallis,  $H=0.52$ ,  $df=1$ ,  $p=0.4689$ ).

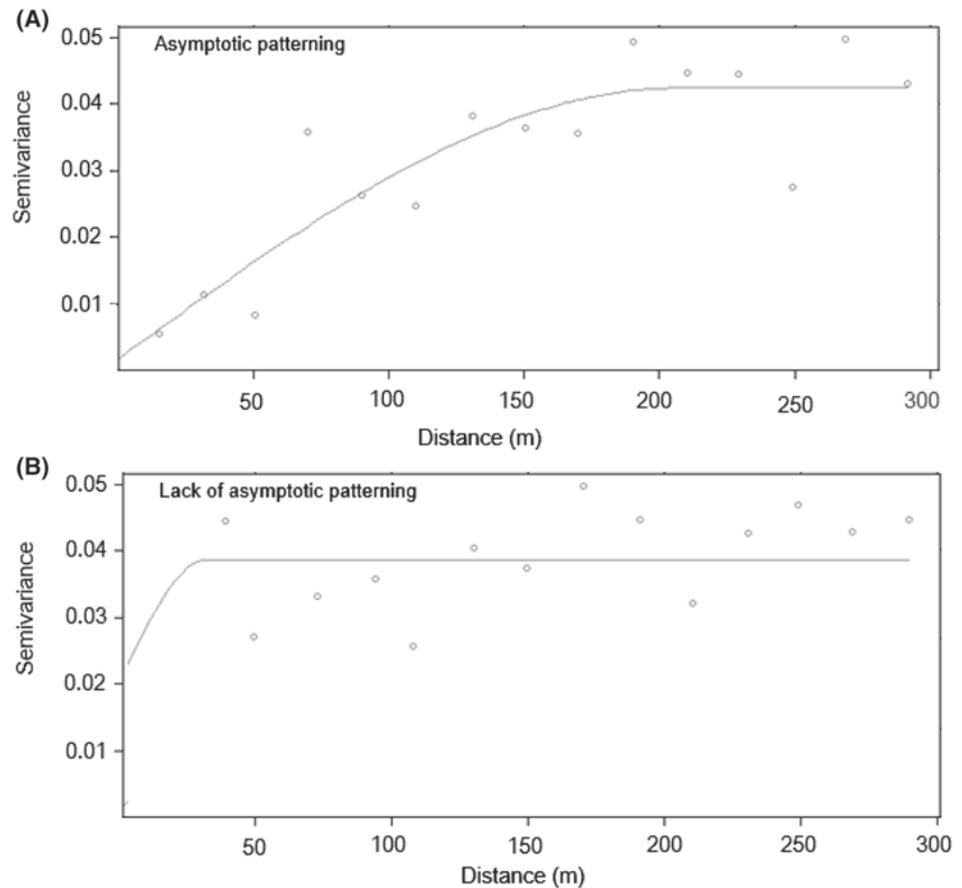
### Fish spatial analysis

We found no significant seasonal effect on the range estimates for fish (Fig. 3d, Kruskal–Wallis  $H=2.3$ ,  $df=2$ ,  $p=0.31$ ), or seasonal effect on fish areal densities (Table 2, Kruskal–Wallis  $H=5.7$ ,  $df=2$ ,  $p=0.58$ ). There was a significant effect of lake mixing on fish range values (Fig. 3c, Kruskal–Wallis,  $H=9.8$ ,  $df=2$ ,  $p=0.0075$ ). During pre-manipulation years autocorrelation for fish occurred at distances less than  $171 \pm 52$  m (95% CI). During the mixing phase of the experiment, the range decreased to an average of  $68 \pm 32$  m (95% CI). Post-manipulation autocorrelation range estimates increased to  $192 \pm 62$  m (95% CI) and were not different from pre-manipulation range values.

### Interactions between fish and zooplankton

We identified significant cross variograms by those fitting the standard semivariogram curve, where semivariance sample points increase with distance and then level off (Fig. 5a), and non-significant cross variograms as semivariograms with no asymptotic pattern in sample points (Fig. 5b). Cross-variograms showed significant spatial autocorrelation between fish and zooplankton at range values of 80–315m, averaging 188 m or less (Table 4). All but one sample date indicate spatial correlation at ranges

**Fig. 5** Example (a) from Oct. 31 2010 of a cross variogram for fish and zooplankton indicating spatial autocorrelation at range value 156 m (sample points with asymptotic patterning). Example (b) from July 16 2013 of a cross variogram for fish and zooplankton indicating no autocorrelation (sample points with no asymptotic patterning)



from 156 m–315 m (Table A3). There was no significant relationship between cross variogram range values and mixing (Kruskal–Wallis,  $H=1.3$ ,  $df=2$ ,  $p=0.52$ ) or season (Kruskal–Wallis,  $H=0.49$ ,  $df=2$ ,  $p=0.78$ ). For significantly autocorrelated cross-variograms, our linear regressions indicated a positive relationship between fish and zooplankton. We did not detect negative relationships between fish and zooplankton in any of our sample dates (Table 1).

## Discussion

### Zooplankton spatial distributions

The experimental mixing drastically altered internal biological and physical features of Crystal Lake previously found to affect zooplankton distributions (e.g. Hanski 1981; Folt and Burns 1999; Ware and Thomson 2005). Manipulation resulted in elimination of stratification, and altered zooplanktivorous fish behavior (Fig. 3c). Nonetheless, seasonal patterns in horizontal distributions of zooplankton persisted. Prey behavioral movements in response to change

in predator behavior may be more likely to be observed on scales smaller than those used in our analysis (~1 m) (Folt and Burns 1999; Thackeray et al. 2004). Furthermore, any short-term movement zooplankton undergo in response to predatory avoidance is likely to be overridden by larger scale physical processes (Thackeray et al. 2004; Blukacz et al. 2009).

Persistent seasonal trends in zooplankton spatial organization despite changes within the ecosystem suggest that horizontal distributions are driven by external forces, such as wind and wind-induced water movements, which did not change as a result of our manipulation (George and Winfield 2000; Blukacz et al. 2009, Rinke et al. 2009). Our consistently high range estimates across seasons and lack of change during the mixing phase of the experiment support previous research findings that large scale abiotic processes such as wind-induced water movements are major drivers of horizontal zooplankton distributions (George and Winfield 2000; Thackeray 2004; Blukacz et al. 2009).

Seasonal differences in wind show that average daily wind speed is greater in the spring and fall than in the summer. The increased wind speed appears associated with increased zooplankton spatial correlation range.

**Table 1** Linear regression results used to determine positive or negative relationships between fish and zooplankton

Sample date	Slope	Intercept	p-value
June 04 2010	0.07249	3.4	0.12
July 13 2010	0.035	3.23	0.07
Oct 31 2010	0.202	2.35	<0.001*
July 28 2011	0.09411	3.14	<0.01*
May 31 2012	0.058	3.32	<0.01*
June 30 2012	0.016	3.59	0.36
Aug 06 2012	0.056	3.4	0.38
Oct 11 2012	0.12	2.3	<0.001
Nov 08 2012	0.167	2.2	<0.001
July 02 2013	-0.002	4.25	0.88
July 16 2013	0.215	3.03	<0.001*
Aug 15 2013	-0.2211	4.4	0.12
June 17 2014	-0.0133	3.65	0.56
July 09 2014	-0.014	3.64	0.5
July 31 2014	0.0506	2.95	0.02*
Aug 06 2014	0.211	2.5	<0.001*
Sept 20 2014	0.257	2.11	<0.001*
Oct 11 2014	0.18	2.5	<0.001*

Only dates with significantly autocorrelated cross-variograms were used for linear regression analysis

\*Significant positive relationships at the alpha level of 0.05

Increased range values and apparent patch size occurred when wind tended to cause unidirectional increases in zooplankton on the windward side of the lake, particularly in fall. We did not observe a similar correlation with higher wind speeds in spring. In this case, lower total biomass values and lower sample size likely reduced the probability of detecting range differences during the spring season. Our results are consistent with several other studies that show high wind speeds result in zooplankton redistribution and higher range values (Blukacz et al. 2009; Rinke et al. 2009; George and Winfield 2000). When compared to previous studies, however, our study lake is small and protected by surrounding forest, which may reflect the lower overall effect of wind on our spatial analyses (Blukacz et al. 2009; Rinke et al. 2009; George and Winfield 2000). Furthermore, seasonal patterns in horizontal distributions of zooplankton did not appear associated with seasonal changes in sunlight intensity. However, because there is lower overall zooplankton biomass in spring relative to other seasons, it is difficult to disentangle the influence of light with other factors such as wind that vary among season.

Finally, we identified a biomass/ABC regression using backscatter from 430 kHz acoustic data for three

oligotrophic lakes. Building a lake-specific relationship would require sampling during extreme periods of zooplankton abundance, a range which is spanned by the cross-lake analyses. Although Crystal Lake, Sparkling Lake, and Lake Superior have slightly different zooplankton species compositions, all lakes are dominated by Copepods which have similar scattering properties (Stanton et al. 1996). The compositional differences did not cause significant deviations in our regression, suggesting the relationship is robust and broadly representative of variable species compositions in similar oligotrophic lakes. Our regression provides a means to quickly measure zooplankton biomass over a large spatial scale at a fine resolution in oligotrophic lakes. Acoustic estimates of zooplankton biomass are less time intensive than traditional methods of zooplankton sampling, such as Wisconsin nets, and are less influenced by naturally patchy distributions of zooplankton.

### Fish spatial distributions

Our results suggest the shift in the scale of aggregation for fish was a plastic behavior in response to mixing-induced changes in thermal habitat. The change in the scale of aggregation is consistent with changes in behavior observed by Lawson et al. (2015) during the manipulation. In this case, rainbow smelt were occasionally observed near shore and at the surface of the lake during the day. We hypothesize this shift is likely due to a behavioral response to altered thermal habitat. Change in behavior may indicate searching behavior for more suitable thermal conditions. This stress response hypothesis is further supported by an observed decrease in smelt body condition during the manipulation, which indicates a decline in population performance (Neumann and Willis 1996; Lawson et al. 2015). We observed a crash in smelt population density, and although we did find smelt in our horizontal near-shore gillnets, it was not enough to account for the drop in densities and we still observed most of them in deeper areas (Lawson et al. 2015). We therefore do not expect on-shore movement to have affected our spatial analysis.

Our results are consistent with other studies on the effects of increasing water temperature on stenothermic fish. Cold water fish often abandon normal behavior and exhibit searching behavior in an attempt to decrease physiological imbalances (Breau et al. 2011). These "flight," or searching responses often override other behaviors such as schooling and feeding (Robinson and Pitcher 1989; Breau et al. 2011). It is possible that our

manipulation induced such a flight response in rainbow smelt, where fish began to swim separately in smaller aggregations in order to reduce intraspecific competition for resources required for increased metabolism, and to seek out cooler water (Berman and Quinn 1991; Robinson and Pitcher 1989; Breau 2011). Furthermore, our observations were made during low light conditions when schooling behavior in fish and swarming behavior by zooplankton are reduced. While we do not have the data to examine small scale (0–10 m) patterns driven by visually mediated behaviors, we would expect them to be prevalent during high light periods. Future studies adopting school detection in fish and higher resolution sampling with remote sampling techniques for zooplankton may reveal differences in spatial structuring in high light versus low light periods in aquatic ecosystems.

### Spatial relationships and interactions between fish and zooplankton

Our cross variogram results indicate fish and zooplankton are autocorrelated, on average, at distances less than approximately 190 m with most ranges falling between 156–315 m. During dates when spatial autocorrelation was significant, fish and zooplankton were always positively correlated, suggesting fish were aggregating in areas of high zooplankton density. We did not detect any negative relationships between fish density and zooplankton density. Our results indicate fish are concentrating in areas of higher zooplankton biomass during portions of the year. If prey species are highly mobile, predation avoidance may result in a negative correlation between plankton and their predators (Krebs 1978; Rose and Leggett 1990). However, if prey are relatively less mobile and do not have access to refuge areas, positive spatial correlation is likely to occur (Sih 1984). In oligotrophic systems such as Crystal Lake, zooplankton are likely to remain in high-risk regions in order to maximize their feeding opportunities because they are food-limited (Lampert 1989; Dodson 1990). The absence of top-down effects of fish on zooplankton aggregations may also indicate that these top down interactions are occurring at scales we did not measure or could not detect with this set of spatial analyses. Future studies that increase sample density several fold may be better able to detect these scale dependent phenomenon.

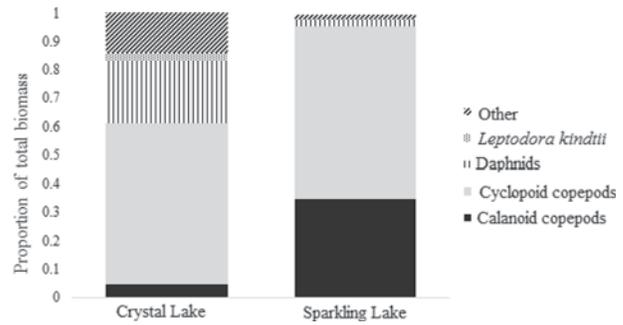
Lack of fish-zooplankton spatial correlation on some dates may also indicate dietary shifts in fish. Rainbow smelt have diverse diets that vary seasonally (Isaac et al. 2012). Although we did not detect seasonal effects on

correlations in fish, it is possible fish were selecting for different prey that were not well-measured by our backscatter data during some of the sample dates (e.g. Chironomid pupae). Examinations of prey selection are ongoing and may shed light on changes in feeding on zooplankton and potential influences on spatial covariation between zooplankton and fish.

Another possibility for a lack of fish/zooplankton spatial correlation is that our general measure of zooplankton biomass may not be solely representative of the zooplankton that fish are selecting for consumption. Zooplanktivorous fish are primarily visual predators, and therefore select the largest zooplankton that are most visible (Brooks and Dodson 1965, Lathrop et al. 2002). Our 430 kHz acoustic/biomass regression measured total zooplankton biomass and not size or species specific scattering. Our results were most consistent with those of Rinke et al. (2009) who found a bottom-up relationship between overall zooplankton biomass and fish density. If the planktivore was a generalist, strong spatial covariation between fish and zooplankton would be expected regardless of season. In our case, we know rainbow smelt to be a selective predator and that prey selection varies seasonally (Hrabik et al. 1998). Some of the hypotheses related to size selection and spatial patterning might be addressed in the future through the use of size-specific approaches such as optical plankton counters in combination with the sampling approach used here.

We have identified that spatial patterning by fish and zooplankton may respond differently to environmental disturbance and seasonal change, but that there are periodic strong positive spatial correlations between fish and zooplankton. This is the first study that has concurrently examined horizontal spatial relationships of each trophic level at a relatively fine resolution in a small lake across seasonal and yearly timescales. In our study, lake mixing caused spatial correlation in fish to break down at all spatial scales. Our results suggest fish may respond to disturbance of vertically structured processes, especially when fish are reliant on depth-dependent factors such as cold water. Furthermore, because patterns of fish and zooplankton distributions occur at different spatial scales and result from different processes, it is important to measure each group at the appropriate scale. Geostatistics, such as the semivariogram analysis used in this study, provide a means to guide hypothesis testing and subsequent management decisions by indicating distances at which samples are spatially independent and determining relative importance of variables across scales.

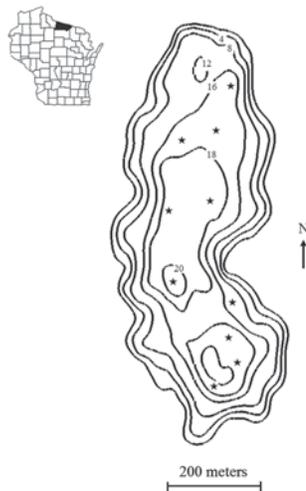
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**Fig. 7** Relative proportion of dry weight (mg) biomass for zooplankton taxonomic groups from Crystal and Sparkling Lakes used to develop regression between 430 kHz hydroacoustic data and zooplankton biomass estimates from Wisconsin tows

**Appendix**

See Figs. 6, 7 and Tables 2, 3 and 4.



**Fig. 6** Locations of Wisconsin net and hydroacoustic zooplankton sampling for linear regression on Sparkling Lake (filled star). Depth contours are in meters (Lake District Bathymetry, NTL-LTER)

**Table 2** Average fish densities and zooplankton biomasses and associated standard deviations for each sample date, estimated via hydroacoustic surveys

Sample date	Average fish density (#·ha <sup>-1</sup> )	Fish standard deviation	Average zooplankton biomass (mg·m <sup>-2</sup> )	Zooplankton standard deviation
June 4 2010	4624	1656	4706	546
June 30 2010	–	–	4165	394
July 13 2010	6919	5848	2152	504
Oct. 31 2010	1461	2755	875	317
July 12 2011	–	–	3248	383
July 28 2011	5639	2406	3143	253
Aug. 15 2011	8446	3180	–	–
May 31 2012	1375	995	3181	339
June 30 2012	4039	4472	4415	258
July 19 2012	4565	3157	5952	1890
Aug. 06 2012	1987	1758	3928	1276
Aug. 22 2012	2544	1600	–	–
Sept. 13 2012	1413	1231	–	–
Sept. 28 2012	487	681	–	–
Oct. 11 2012	1493	2702	867	280
Nov. 08 2012	2907	3569	524	214
July 02 2013	1401	1916	1704	222
July 16 2013	3480	2754	6103	1967
July 29 2013	–	–	3853	1710
Aug. 15 2013	1465	818	5810	2990
June 17 2014	1630	1067	4060	364
July 09 2014	1605	1016	3985	319
July 31 2014	2297	2186	1286	220
Aug. 06 2014	2588	1765	1636	307
Sept. 20 2014	1769	1939	809	382
Oct. 11 2014	967	1000	991	391

Dashes indicate data were not collected on date

**Table 3** Semivariogram results for log fish density and log zooplankton biomass

Sample date	Log fish density				Log zooplankton biomass			
	Maximum distance between points	Nugget	Sill	Range (m)	Maximum distance between points	Nugget	Sill	Range (m)
June 4 2010	488.06	0.00	0.03	66.69	488.06	0.00	0.00	174.24
June 30 2010	–	–	–	–	488.15	0.00	0.00	183.95
July 13 2010	545.33	0.05	0.05	202.30	545.25	0.01	0.00	56.82
Oct. 31 2010	373.98	0.06	0.02	191.48	373.90	0.00	0.01	163.28
July 12 2011	–	–	–	–	534.08	0.00	0.00	189.73
July 28 2011	532.72	0.01	0.02	196.72	532.56	0.00	0.00	22.00
Aug. 15 2011	529.45	0.00	0.05	197.41	–	–	–	–
May 31 2012	531.50	0.13	0.07	38.09	531.78	0.00	0.00	111.67
June 30 2012	488.06	0.06	0.00	78.57	488.15	0.00	0.00	146.59
July 19 2012	515.53	0.02	0.01	90.21	523.31	0.00	0.00	103.50
Aug. 06 2012	518.09	0.19	0.10	62.80	514.22	0.01	0.01	105.28
Aug. 22 2012	480.26	0.00	0.27	30.66	–	–	–	–
Sept. 13 2012	516.68	0.00	0.33	27.53	–	–	–	–
Sept. 28 2012	550.94	0.15	0.05	14.19	–	–	–	–
Oct. 11 2012	495.65	0.87	0.01	11.01	524.93	0.00	0.02	200.72
Nov. 08 2012	520.70	0.00	0.71	26.03	520.90	0.00	0.02	289.59
July 02 2013	556.63	0.06	0.10	96.13	535.81	0.00	0.00	116.70
July 16 2013	520.67	0.00	0.15	208.95	520.34	0.00	0.01	314.51
July 29 2013	–	–	–	–	555.18	0.00	0.04	128.77
Aug. 15 2013	515.49	0.00	0.05	74.80	515.48	0.00	0.04	144.24
June 17 2014	530.28	0.03	0.03	275.65	530.12	0.00	0.00	32.60
July 09 2014	530.28	0.03	0.03	301.87	530.12	0.00	0.00	32.06
July 31 2014	489.62	0.27	0.02	136.35	489.57	0.00	0.01	278.45
Aug. 06 2014	517.88	0.10	0.04	112.58	517.87	0.01	0.00	28.27
Sept. 20 2014	622.80	0.17	0.34	175.01	623.02	0.00	0.08	391.30
Oct. 11 2014	522.07	0.14	0.89	152.70	522.01	0.00	0.04	364.82

Sill values represent the partial sill (actual sill minus the nugget). All semivariogram analysis was conducted using spherical models and a 50 m segment size

**Table 4** Cross variogram results for fish and zooplankton

Sample date	Nugget	Partial sill	Range (m)	Auto-correlation
June 04 2010	0.013	0.016	51.33	–
July 13 2010	0.037	0.0372	31.8	–
Oct. 31 2010	0.023	0.043	156.8	X
July 28 2011	0.01	0.018	315.7	X
May 31 2012	0.07	0.11	31	–
June 30 2012	0.0017	0.0417	206	X
Aug. 06 2012	0.04	0.06	178	X
Oct. 11 2012	0.3	0.45	30.1	–
Nov. 08 2012	0.3	0.36	30	–
July 02 2013	0.04	0.067	35.11	–
July 16 2013	0.03	0.057	31.8	–
Aug. 15 2013	0.06	0.04	142	–
June 17 2014	0.03	0.029	32.3	–
July 09 2014	0.03	0.029	32.3	–
July 31 2014	–0.047	0.083	47.4	–
Aug. 06 2014	0.04	0.0655	29.5	–
Sept. 20 2014	0.15	0.25	81.6	X
Oct. 11 2014	0.098	0.131	25	–

All cross variogram analysis was conducted using spherical models and a 50 m segment size. An “X” under “Autocorrelation” indicates a significant relationship

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