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Major shift in the phenology of crustacean biomass in western Lake Superior associated with temperature anomaly

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ABSTRACT

Variable weather patterns during the early months of 2014 and 2015 resulted in differences between years in spring and summer surface water temperatures in the offshore areas of western Lake Superior. Zooplankton were collected in western Lake Superior during several cruises from late spring to early fall in 2014 and 2015 to test the hypotheses that colder summer water temperatures in 2014 were correlated with reduced zooplankton biomass, later peaks in zooplankton biomass, and a smaller contribution of warm-water taxa to the zooplankton assemblage. The total amount of zooplankton biomass from early June through early October did not differ greatly between years. Of the taxonomic subcategories (large-bodied calanoids, small-bodied calanoids, cyclopoids, nauplii, and herbivorous cladocerans) however, cyclopoid and cladoceran biomass was somewhat smaller in 2014 compared to 2015, providing some support for the hypothesis that warm-water taxa contribute less to offshore zooplankton biomass in colder years. The timing of peak biomass for cladocerans, small-bodied calanoids, and cyclopoids did not differ between years, but peaks in the biomass of copepod nauplii and large-bodied calanoids (primarily *Limnocalanus macrurus*) occurred several weeks later in 2014 than 2015 which was evidence for phenological delay during a year with unusually cold spring and summer surface water temperatures. Though this study only evaluates the role of temperature in driving zooplankton biomass and phenology in Lake Superior, it does provide insight into the potential effects of climate variability on the Lake Superior food web.

Introduction

It is well understood that temperature is one of the primary drivers of zooplankton phenology in both freshwater and marine ecosystems (Gerten and Adrian, 2002; Richardson, 2008). In recent years, concern over the effects of climate change on food webs and ecological processes has led to increased interest in the effect of temperature on the phenology of zooplankton and many other organisms (Edwards and Richardson, 2004). In the Laurentian Great Lakes, average surface water temperatures are rising and it is thought that annual weather patterns in the region will become more variable and extreme (Reavie et al., 2017; Kretschmer et al., 2017). While numerous studies have described zooplankton life history and seasonal patterns in zooplankton community assemblages in the Great Lakes, few studies have done this during consecutive years with strongly contrasting weather patterns. Such information would be valuable as weather becomes more variable.

In Lake Superior, the largest and coldest of the Great Lakes, zooplankton have received less research attention in recent decades compared to the other Great Lakes. This is due in part to the fact that the food web of Lake Superior has been more stable than in the other Great Lakes and remains the most intact (Gamble et al., 2011; Barbiero et al., 2012). Previous studies demonstrated that the timing of life history events (e.g., reproduction and instar advancement) for many zooplankton species occurs a month or more later in Lake Superior than in the other, warmer Great Lakes (Selgeby, 1975; Watson and Wilson, 1978; Sprules et al., 1990). Past work also indicated that peak zooplankton biomass in Lake Superior was correlated with peak surface water temperature (Watson and Wilson, 1978; Munawar and Wilson, 1978; Zhou et al., 2001; Yurista et al., 2009). These patterns suggest that the timing of peak zooplankton biomass and the quantity of biomass at the peak may be both responsive to temperature and likely to occur earlier and be larger, respectively, in warmer years. However, prior work has also shown that peaks in zooplankton biomass are correlated with peaks in primary production in Lake Superior, suggesting that zooplankton may also be resource limited (Patalas, 1972; Munawar and Wilson, 1978; Zhou et al., 2001; Yurista et al., 2009). If true, zooplankton may not show direct or pronounced responses in phenology or biomass

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to variation in weather patterns unless primary production also changes.

Year-to-year changes in the crustacean zooplankton in Lake Superior may manifest differently along taxonomic or life-history lines. In the offshore areas of Lake Superior, zooplankton biomass is dominated by calanoid copepods, particularly *Limnocalanus macrurus* and *Leptodiaptomus sicilis* (Johnson et al., 2004; Barbiero et al., 2012; Oliver et al., 2014). Both of these copepod species prefer cool, offshore water (Balcer et al., 1984) and though the life histories of these taxa in Lake Superior have been described in a variety of studies, it is unclear how much these life histories vary between years with warmer or cooler water temperatures (Selgeby, 1975; Conway, 1977; Watson and Wilson, 1978). Other cold-adapted calanoid species such as *Calanus finmarchicus*, which dominates zooplankton biomass in the North Atlantic, advance through instars more rapidly in warmer years but begin to grow more slowly once temperatures rise above 11 °C (Møller et al., 2012; Weydmann et al., 2017). In Lake Superior, *L. macrurus* and *L. sicilis* may also mature more rapidly in warmer years assuming they can also track their preferred temperatures as the summer progresses. Other taxa, such as cladocerans and cyclopoids, tend to prefer warmer water and generally develop first in the nearshore regions of Lake Superior in the early summer and later appear offshore as surface temperatures there rise (Watson and Wilson, 1978; Link et al., 2004). This suggests that the absolute and/or relative abundances of these warm-water taxa may be smaller in offshore regions of the lake in colder years. However, predicting the effect of variable water temperature on the relative amounts of different taxa requires caution because cladocerans, calanoid copepods, and cyclopoid copepods are all also influenced by the quantity and quality of food (McNaught, 1975; Gannon and Stemberger, 1978; Munawar and Wilson, 1978).

Strongly contrasting weather patterns during the early months of 2014 and 2015 offered an opportunity to observe the sensitivity of crustacean zooplankton biomass, phenology, and assemblage structure in Lake Superior to inter-annual variation in temperature. The early months of 2014 were unusually cold and ice persisted well into the spring while the winter and spring of 2015 were comparatively milder and the extent of ice cover was considerably less (NOAA, 2018). Summer surface temperatures in Lake Superior are strongly influenced by the amount of ice cover in the preceding winter (Austin and Colman, 2007), and because of this, zooplankton in Lake Superior presumably experienced a later peak in surface temperature during 2014 than in 2015. We conducted crustacean zooplankton surveys from late spring to early fall during 2014 and 2015 in the offshore areas of western Lake Superior and evaluated relationships between water temperature, zooplankton phenology, biomass, and assemblage structure. We hypothesized that colder temperatures in 2014 would 1) support reduced crustacean zooplankton biomass, 2) cause later peaks in zooplankton biomass, and 3) disfavor warm-water taxa in comparison to 2015.

Materials and methods

Sample collection

Zooplankton and temperature profiles were collected in offshore areas of the western arm of Lake Superior from the *R/V Blue Heron* during four months in both 2014 and 2015. The sampling dates and number of stations visited during each month sampled are summarized in Table 1. Station depths ranged from 77 to 276 m and the location and depth of each station is available in Pawlowski et al. (2017). We estimated total zooplankton biomass in the water column at each station from 60 m vertical net tows using a conical net with a 1 m diameter opening, 1:4 aspect ratio (opening to length), and 153 μm aperture mesh. Triplicate net tows were collected at all stations starting during August of 2014. We chose 60 m as a target depth for net tows because several recent studies have demonstrated that 90% or more of the zooplankton biomass in Lake Superior exists in the upper 50 m of water during day and night and across seasons (Yurista et al., 2009; Oliver et al., 2014). Additionally, standardizing the depth of net tows at stations with different depths ensured that differences in the estimated densities and biomasses between stations were not the result of sampling to different depths and thus eliminated depth of net tow as a confounding factor in the estimates of average density and biomass models described below. The mesh size (153 μm) was chosen as a standard mesh size commonly used for zooplankton research throughout the Great Lakes (GLNPO, 2016; Barbiero et al., 2012; Rudstam et al., 2015). This net does not retain the smallest nauplii, and thus our net tows underestimated naupliar biomass. However, this study was not designed to fully quantify nauplii, especially because the length of time in between sampling events could have missed naupliar biomass dynamics.

Zooplankton assemblage composition, biomass, and phenology

Detailed information on zooplankton sample processing and enumeration can be found in Pawlowski et al. (2017). Zooplankton were identified to species level according to Balcer et al. (1984) except for

Table 1
Average monthly volumetric densities (individuals m^{-3}) for all zooplankton taxa present in 60 m net tows in 2014 and 2015 from all sample locations combined. Values in parentheses indicate standard error.

	June 3–6, 2014	July 23–25, 2014	Aug. 11–19, 2014	Oct. 3–6, 2014	May 20–22, 2015	July 15–17, 2015	Sept. 8–10, 2015	Oct. 5–7, 2015
Sites sampled (n)	5	3	10	13	5	4	4	7
Cladocerans								
Bosmina longirostris	0 (0)	0 (0)	23.3 (18.0)	0.1 (0.06)	0 (0)	3.6 (2.9)	0.2 (0.2)	3.8 (3.0)
Daphnia mendotae	1.1 (0.7)	0 (0)	60.2 (24.8)	74.7 (13.7)	0.01 (0.01)	8.2 (4.0)	151 (38.6)	258 (103.3)
Holopedium gibberum	0 (0)	0 (0)	2.5 (2.2)	4.8 (3.7)	0 (0)	1.2 (0.7)	3.3 (3.2)	4.2 (4.0)
Bythotrephes longimanus	0 (0)	0 (0)	0.41 (0.3)	0.04 (0.03)	0 (0)	0.07 (0.06)	0.02 (0.02)	0.07 (0.07)
Leptodora kindtii	0 (0)	0.01 (0.01)	0.03 (0.01)	0 (0)	0 (0)	0.02 (0.01)	0 (0)	0 (0)
Small-bodied calanoids								
Leptodiaptomus copepodites	58.6 (17.9)	33.4 (26.1)	1493 (402)	804 (164)	36.9 (8.2)	578 (202)	1269 (160)	770 (173)
Leptodiaptomus sicilis adult	211 (43.9)	218 (15.1)	400 (61.9)	421 (102)	211 (20.4)	195 (9.7)	199 (21.2)	772 (212)
Epischura lacustris	0 (0)	0 (0)	7.3 (3.6)	2.9 (1.1)	0 (0)	1.4 (0.9)	8.7 (5.0)	13.0 (4.1)
Nauplii (all)	124 (28.6)	569 (229)	1033 (223)	44.6 (14.0)	67.5 (12.2)	1026 (438)	85.2 (19.6)	47.8 (15.8)
Large-bodied calanoids								
Limnocalanus macrurus	52.5 (24.8)	192 (33.8)	283 (39.2)	252 (23.9)	102 (13.2)	323 (64.1)	257 (69.2)	245 (50.8)
Senecella calanoides	0.4 (0.4)	2.0 (1.1)	3.7 (1.3)	4.3 (1.4)	0.3 (0.1)	4.2 (0.9)	8.7 (3.4)	9.0 (2.8)
Cyclopoids								
Diacyclops copepodite	22.1 (8.1)	9.4 (6.8)	364 (151)	422 (68.8)	4.69 (1.7)	316 (174)	194 (101)	923 (304)
Diacyclops thomasi adult	81.8 (9.8)	50.2 (31.4)	79.3 (28.3)	27.2 (6.3)	106 (21.6)	117 (81.6)	81.7 (34.7)	96.1 (34.5)

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