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Spatial synchrony in cisco recruitment

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ABSTRACT

We examined the spatial scale of recruitment variability for disparate cisco (*Coregonus artedi*) populations in the Great Lakes ($n = 8$) and Minnesota inland lakes ($n = 4$). We found that the scale of synchrony was approximately 400 km when all available data were utilized; much greater than the 50-km scale suggested for freshwater fish populations in an earlier global analysis. The presence of recruitment synchrony between Great Lakes and inland lake cisco populations supports the hypothesis that synchronicity is driven by climate and not dispersal. We also found synchrony in larval densities among three Lake Superior populations separated by 25–275 km, which further supports the hypothesis that broad-scale climatic factors are the cause of spatial synchrony. Among several candidate climate variables measured during the period of larval cisco emergence, maximum wind speeds exhibited the most similar spatial scale of synchrony to that observed for cisco. Other factors, such as average water temperatures, exhibited synchrony on broader spatial scales, which suggests they could also be contributing to recruitment synchrony. Our results provide evidence that abiotic factors can induce synchronous patterns of recruitment for populations of cisco inhabiting waters across a broad geographic range, and show that broad-scale synchrony of recruitment can occur in freshwater fish populations as well as those from marine systems.

1. Introduction

Separate populations of the same species are frequently observed to fluctuate synchronously (Post and Forchhammer, 2002), yet the mechanisms contributing to these patterns are often unclear. Understanding the spatial scale of synchrony can provide insight into the processes involved because different forcing mechanisms often operate at different spatial scales. For example, biotic factors (e.g., predation and competition) are generally believed to operate at local scales, while many abiotic factors (e.g., climate) operate at broader scales. The synchronizing effect of environmental factors is referred to as the "Moran effect" (Hudson and Cattadori, 1999). Moran's theorem states that the spatial correlation of population variation will equal the spatial correlation of environmental variation for those species whose dynamics are driven by similar environmental cues (Moran, 1953).

Sources of recruitment variation in fish populations have been the subject of much debate (Houde, 2008). Analyses by Myers et al. (1997) suggested the spatial scale of recruitment synchrony for marine fishes is approximately 500 km compared to only 50 km for freshwater fishes. Myers et al. (1997) concluded that biotic interactions regulated recruitment of freshwater species while abiotic factors were more important for marine species. While local biotic interactions certainly influence freshwater fish recruitment, the effects of abiotic factors like climate cannot be dismissed. For example, several studies have reported that indices of water temperature were correlated with patterns of walleye (*Sander vitreus*)

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year-class strength (Koonce et al., 1977; Busch et al., 1975; Schupp, 2002). In addition, Phelps et al. (2008) found that climatic variability synchronized recruitment of common carp (*Cyprinus carpio*) across a 175-km^2 area in the Midwestern United States. Marjomäki et al. (2004) analyzed time-series of vendace (*Coregonus albula*) from 21 lakes in Finland (surface areas < 1100 km^2) and found significant positive correlations among lakes in both recruitment and spawner indices for populations separated by 100–300 km. Bunnell et al. (2010) studied the upper Great Lakes (>50,000 km^2) and found bloater (*Coregonus hoyi*) recruitment was synchronized at 600–800 km. These authors concluded that dispersal of bloater likely contributed to within-lake synchrony, but climate likely led to synchrony found across lakes because the dispersal mechanism seemed implausible. The inferences of Bunnell et al. (2010) were based on catches of 95–130 mm (age-0 and age-1) bloater, and thus dispersal of smaller bloater from natal areas to other sites in the same lake could not be ruled out. Collectively, these examples provide evidence that the spatial scale of synchrony in freshwater populations often exceeds 100 km, suggesting climate can influence fish recruitment in lacustrine environments.

Climate variables are strongly correlated over broad spatial scales (e.g., >1000 km), especially in terms of mean annual values (Koenig, 2002). However, the magnitude of fish recruitment can be set in short time windows (Cushing, 1990). It follows that measuring spatial synchrony of abiotic factors using mean values that integrate too long a time period may mask the Moran effect. Marjomäki et al. (2004) found that vendace population indices and mean air temperature during the month following ice break-up were anisotropic, meaning patterns of synchrony were more evident along east-west axes than north-south axes. This observation highlights the influence of prevailing weather patterns and their movement across the landscape and also underscores the need to consider both the spatial and temporal aspects of plausible bottlenecks when attempting to understand how climate may influence recruitment.

Another important consideration when trying to understand climate effects is the physical characteristics of the lakes under study. Myers et al. (1997) argued that regional weather systems should affect lakes and streams just as they would marine ecosystems. However, freshwater ecosystems vary extensively in size and shape and thus respond to climatic variables at different rates (Magnuson et al., 1997; Gerten and Adrian, 2001; George et al., 2004). Marjomäki et al. (2004) noted that the date of ice-break between Finnish lakes ranged from less than two to greater than four weeks across years, which highlights the variability that can occur in inland lakes, despite their geographic proximity. In contrast, the thermal inertia, internal currents, and hydrologic connectedness of larger systems, such as the Great Lakes, could lead to a more uniform response to climate through space. Thus, the difference in spatial synchrony for vendace and bloater could be interpreted as species-specific dependences on climatic variables or the heterogeneous response of different types of lakes exposed to similar climate regimes. Given the variability associated with freshwater lakes, broad-scale measures of spatial synchrony are an indication of the role of climate but finer-scale measures do not necessarily preclude the influence of climate.

Cisco (*Coregonus artedi*) are a widely distributed freshwater species in the northern regions of North America and can be found in both the Laurentian Great Lakes and deep inland lakes (Scott and Crossman, 1973). In Lake Superior, cisco begin aggregating in October and spawn primarily during November and December (Stockwell et al., 2009). After hatching, cisco larvae spend their early stages of development near the surface in May and June (Stockwell et al., 2009). There is strong evidence indicating that the year-class strength of cisco and other coregonines is established prior to the end of the larval stage (McCormick et al., 1971; Viljanen, 1988; Kinnunen, 1997), with the first few weeks after hatching being especially critical (Rice et al., 1987). Bronte et al. (2003) and Stockwell et al. (2009) showed that year-class strength was synchronized across Lake Superior cisco stocks, and concluded that climate drove these patterns. However, neither analysis provided quantitative estimates of spatial synchrony. Thus, our primary objective was to determine the spatial scale of synchrony for cisco within the Great Lakes, and to explore whether inclusion of populations outside the Great Lakes influenced our findings. To evaluate this objective we gathered data for cisco populations covering a broad spatial scale (>1000 km) occupying a range of lake sizes. We coupled this with an analysis of the spatial correlation of spring meteorological observations from offshore Great Lakes weather buoys, which led to the development of hypotheses regarding the potential influence of climatic variables on cisco recruitment. Although the role of climate in determining Lake Superior cisco recruitment has been speculated (Bronte et al., 2003; Stockwell et al., 2009), Bunnell et al. (2010) highlighted that it is wrong to assume population synchrony is driven solely by climatic events when dispersal of individuals could also explain the phenomenon. To better understand whether dispersal or climate drives cisco synchrony, we examined the inter-annual variability of larval cisco densities at three Lake Superior sites that were separated by 25–275 km. Finding spatial synchrony of larvae that were collected concurrently at separate sites within weeks of emergence would provide evidence that climate, and not dispersal, led to patterns observed by Bronte et al. (2003) and Stockwell et al. (2009).

2. Methods

2.1. Acoustic data collection and sample processing

We sampled 12 cisco populations across the upper Great Lakes region (Fig. 1) including 5 sites in Lake Superior, 2 sites in Lake Huron, 1 site in Lake Michigan, and 4 small lakes in northern Minnesota. Populations in the Great Lakes were assessed during November 2010 when cisco were aggregated for spawning (Yule et al., 2009), while populations in the Minnesota inland lakes were assessed during July and August 2010 (Ahrenstorff et al., 2013). The objective of both the autumn and summer surveys was to measure abundance of yearling and older pelagic fish so combining these datasets was deemed appropriate.

Stockwell et al. (2009) showed that bottom trawl surveys do not adequately describe the age structure, density, or biomass of cisco in Lake Superior. Thus, night hydroacoustic surveys were coupled with netting to estimate abundance and characterize size and age structures of each population. Acoustic data collection and processing followed the Great Lakes standard operating procedure (Parker-Stetter et al., 2009; Rudstam et al., 2009). We collected between 6 and 131 km of acoustic data at each site, with indices of coverage (Aglen, 1983) ranging from 1.2 to 5.0 (Table 1). Using Echoview software version 4.90 (Myriax Pty Ltd., Tasmania, Australia), we defined cells on echograms measuring 10 m in height by 2 km in length and calculated total fish densities (#/ha) in each cell from 3 m below the surface to 0.5 m above the lakebed. Target strength (TS) distribution exports for each cell were used to estimate densities of two sizes of fish: small fish < -35.6 decibels (dB), and large fish ≥ -35.6 dB, coinciding to fish less than and greater than 250 mm, respectively (Yule et al., 2006, 2009). At Drummond Island the acoustic data from 2010 were compromised due to electrical interference, so we used acoustic data gathered during October 2009 for this site.

Midwater trawl catches were used to interpret acoustic data at Lake Superior sites, while gillnets were used at the much shallower Lake Huron, Lake Michigan, and Minnesota inland lake sites