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Within-lake habitat heterogeneity mediates community response to warming trends

Rachel A. Hovel,[1,3] James T. Thorson,[2] Jackie L. Carter,[1] and Thomas P. Quinn[1]

[1]*School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, Washington 98105 USA*
[2]*Fisheries Resource Assessment and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd East, Seattle, Washington 98112 USA*

Abstract. Climate change is rapidly altering many aquatic systems, and life history traits and physiological diversity create differences in organism responses. In addition, habitat diversity may be expressed on small spatial scales, and it is therefore necessary to account for variation among both species and locations when evaluating climate impacts on biological communities. Here, we investigated the effects of temperature and spatial heterogeneity on long-term community composition in a large boreal lake. We used a five-decade time series of water temperature and relative abundance of fish species captured in the littoral zone throughout the summer at 10 discrete locations around the lake. We applied a spatial dynamic factor analysis (SDFA) model to this time series, which estimates the sensitivity of each species to changing water temperature while accounting for spatiotemporal variation. This analysis described the trend in community composition at each sampling location in the lake, given their different trends in temperature over time. The SDFA indicated different magnitude and direction of species responses to temperature; some species increased while others decreased in abundance. The model also identified five unique trends in species abundance across sites and time, indicating residual dynamics in abundance after accounting for temperature effects. Thus, different regions in the lake have experienced different trajectories in community change associated with different rates of temperature change. These results highlight the importance of considering habitat heterogeneity in explaining and predicting future species abundances, and our model provides a means of visualizing spatially-explicit temporal variation in species' dynamics.

Key words: boreal lake; climate change; fish community; habitat heterogeneity; life history; spatial dynamic factor analysis; water temperature.

Introduction

Species commonly respond to climate change in different ways, due to varied habitat use, life history traits, physiological limits, and other attributes (Parmesan 2006). Climate change literature frequently addresses biological responses at the individual- or species-level, and knowing life histories and physiological tolerances of individual taxa is often useful in predicting biological responses to observed and projected habitat changes (Mackenzie et al. 2007, Portner and Farrell 2008). However, in situ organisms experience climate change effects within the context of other biological dynamics, including complex interactions with other individuals and other species. Therefore, evaluating biological response on the community level can offer an important framework for identifying and predicting changes (Walther 2010). Many biological interactions can be difficult to measure or incorporate into modeling approaches, and describing community responses to climate change depends on identifying and accounting for community-level dynamics that are separate from climate effects. This community-level perspective can effectively capture the diversity of responses to climate change (Harley et al. 2006), but this approach is presently underrepresented in climate change literature and uncertainty remains in how future communities might look.

Existing community-level analyses have indicated assemblage restructuring and idiosyncratic responses to climate change (Le et al. 2008). Some research suggests that changing climate will lead to novel communities, but if mobile species undergo range shifts together then communities as a whole might experience little change (Lyons 2003). Currently, predictive ability is lacking on an assemblage-wide level, and even less work has assessed community response on finer scales, especially in systems where species range shifts are restricted by physical limitations. In part, this is because many analytic approaches to date cannot effectively capture both spatial and temporal variation for multivariate species abundance and community composition data. Moreover, many terrestrial and aquatic communities have already been altered by non-native species, habitat modification,

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[3] E-mail: rhovel@u.washington.edu

and other processes, making empirical studies of climate effects difficult to disentangle from the effects of other anthropogenic changes.

Habitat heterogeneity is an ecosystem feature that promotes life history diversity, can buffer fluctuations in population abundance, and maintains stability of multiple ecosystem components, thereby preserving system functions in scenarios of landscape-level changes to the environment (Oliver et al. 2010, Schindler et al. 2010, Stirnemann et al. 2015). Benefits of fine-scale heterogeneity have been recognized in terrestrial landscapes as functions of vegetation cover and small-scale topographical features (Ford et al. 2013) and in rivers due to dendritic structure and landscape gradients (Brown 2003, Thompson and Townsend 2005), but lakes have received less attention as systems with spatial heterogeneity on scales relevant to mobile organisms. Failure to recognize and account for this heterogeneity within lakes can mislead our understanding of biological responses to environmental changes (Luoto and Heikkinen 2008).

High-latitude lakes are very sensitive to climate change and warming temperatures, especially in regard to seasonal regulation of biological processes (De Stasio et al. 1996, Smol et al. 2005). In these systems, climate change has led to longer annual ice-free periods, warmer average and peak water temperatures, and higher productivity due to longer growing seasons and metabolic processes of primary producers (Schindler 2009). Freshwater biota, including fishes, respond strongly to these changes (Parmesan 2006, Keller 2007, Adrian et al. 2009). Earlier ice breakup dates may alter the timing in life history or reproductive cycles (Schneider and Hook 2010, Hovel et al. 2017) or influence species distribution and behavior, including competition (Abrey 2005, Schindler et al. 2005, Rich et al. 2009). Increased water temperatures can differently affect the distribution and phenology of fishes because species vary in thermal preference and tolerance (Edwards and Cunjak 2007). Warming temperatures generally increase metabolic rate (Clarke and Johnston 1999) and, with unrestricted prey and thermal limits, many species will experience faster growth or maturation with a longer, warmer growing season (Magnuson et al. 1990, Schindler et al. 2005). However, physiological limits and thermal optima varies widely among taxa, and some species may undergo thermal stress and declining growth due to increasing metabolic costs (Beitinger and Fitzpatrick 1979). Destabilization has been observed in freshwater plankton communities with increased temperatures (Winder and Schindler 2004, Carter and Schindler 2012), and increased metabolic demands and shifts in niche exploitation may affect the behavior and ecological interactions of planktivorous fish and other higher-trophic organisms (Beisner et al. 1997). Together, these species reactions ultimately shape community responses to climate change in lakes.

Here, we investigated the community-level effects of climate warming on littoral zone fishes in an oligotrophic, high-latitude Alaskan lake, using a data set of methodologically consistent sampling conducted annually for 52 yr. This yearly sampling included repeated assessment of fish abundance and water temperature at multiple sites in the lake. In contrast to studies where biological responses to climate are complicated by concurrent anthropogenic influences (Schindler 2011), this study offers a rare opportunity to examine long term changes in an entirely native freshwater fish community largely unaffected by direct human activity in the watershed. These fishes represent diverse life histories, including anadromous and resident, and spring and fall spawning periods. These data are also well suited to illustrate a recently developed multivariate method that accounts for spatio-temporal community dynamics while estimating the impact of environmental covariates on site-specific abundance for each species. Goals of our analysis were to: (1) test whether within-lake spatial heterogeneity explains differences in community composition over time, and (2) estimate the effect of temperature on species abundance, while accounting for residual variation in dynamics for each species (attributed to unmeasured factors). Our data and analytic methods permit a community-level approach to testing the effect of within-lake heterogeneity on biological response to climate change.

Methods

Study site

Lake Aleknagik is a large oligotrophic lake with mean depth of 43 m and surface area of 83 km^2 (Hartman and Burgner 1972), and is the farthest downstream of five interconnected lakes that drain into the Wood River, Bristol Bay, Alaska (Fig. 1). Located north of the 59th parallel, this system has a short season of biotic productivity and is ice-covered for up to 8 months of the year (Hartman and Burgner 1972, Schindler et al. 2005). The lake experiences thermal stratification between mid-June and mid-September of most years, and mean epilimnetic (0–20 m depth) August water temperatures range from 10°C to 12°C. Data collection has been standardized in this system since 1963, and since then significant trends have been observed in timing of ice breakup (average of 10 d earlier) and average lake water temperature, with taxa-specific effects on the zooplankton community (Carter and Schindler 2012). These changes have been attributed to the combined influences of global warming and the switch from a cool to warm phase of the Pacific Decadal Oscillation during the study period (Mantua et al. 1997, Schindler et al. 2005).

The Wood River watershed is largely unaffected by anthropogenic activities aside from salmon fishing (e.g., no shoreline development, logging, agriculture, dams or water diversions), and habitat and fish communities have remained intact throughout our period of study. Lake Aleknagik supports an entirely native community of

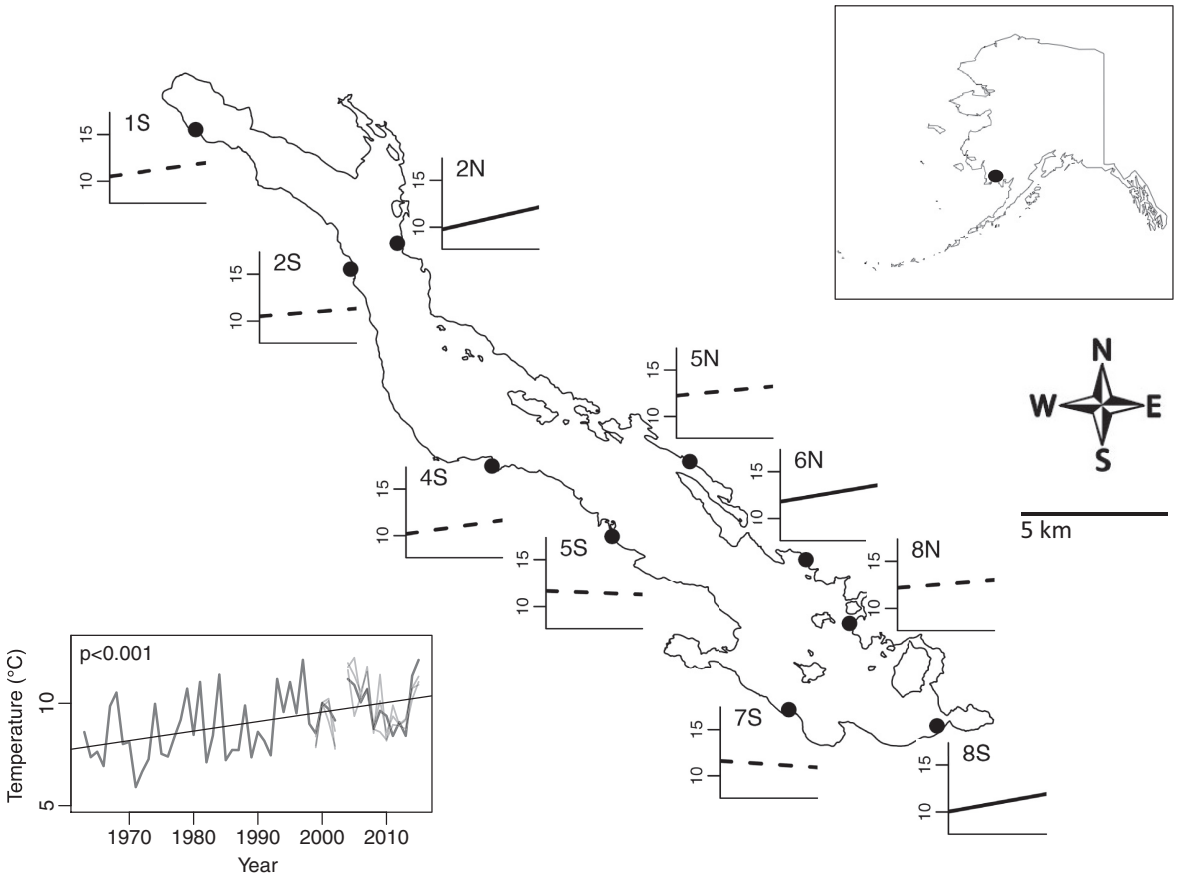

FIG. 1. Map of Lake Aleknagik, Alaska. Black dots indicate beach seine sample locations, and adjacent plots display linear model fit for surface water temperature across years (*y*-axis shows temperature in °C and the line is solid where trend is significant). The bottom left inset shows annual mean values and linear model fit of July epilimnetic water temperature (years 1963–2014, black line); gray lines show site-specific limnetic temperatures where records are available.

both anadromous and non-anadromous fishes. Dominant taxa in the lake are juvenile sockeye salmon (*Oncorhynchus nerka*) rainbow trout (*O. mykiss*), Arctic char (*Salvelinus alpinus*), northern pike (*Esox lucius*), threespine stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), sculpins (*Cottus* spp.), Alaska blackfish (*Dallia pectoralis*), and whitefish species (Coregonidae). Arctic char and whitefish species rear in littoral habitats of the lake as juveniles, and threespine and ninespine sticklebacks and sculpin species comprise the remainder of the numerically dominant members of the littoral community as both juveniles and adults. Other Pacific salmon, including coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*) and Chinook (*O. tshawytscha*) are present in the system in small numbers, as they migrate quickly to sea and do not represent a significant part of the lake community in relative abundance or duration of residence.

Sockeye salmon are the numerically dominant anadromous species, and feed as juveniles in Lake Aleknagik from when they emerge after overwintering in gravel nests in tributary streams until they migrate to sea in early summer (Quinn 2005). Juvenile sockeye salmon primarily occupy littoral habitat during the summer after emergence (Rogers 1987) but move offshore by mid to late summer (Abrey 2005); over 90% of the juvenile sockeye in this system spend one full year in the lake (the remainder stay for two years). The Wood River system is a major tributary to the Nushagak River and annually accommodates 1 million or more returning adult sockeye salmon, after large-scale commercial fisheries operate in marine waters. Natural variation in abundance exceeds that related to fishing, such that there are often more salmon even after fishing in some years than would return without fishing in other years. Density-dependent competition for breeding space in streams plays an important role in determining the abundance of juvenile sockeye salmon entering the lake (Quinn 2005), and this strongly mitigates the effect of the fishery on abundance of juvenile sockeye salmon in the lake. The commercial fisheries are well-regulated to meet biological escapement goals (Hilborn 2006) and the recreational fisheries on rainbow trout and Arctic char are predominantly catch-and-release.

Sample collection

Beach seining.—The littoral zone fish community was sampled with beach seine nets at 10 locations along the north and south shores of Lake Aleknagik (Fig. 1). The sites were chosen to not only encompass the entire circumference of the lake, but also because they differ in exposure to wind, gradient, substrate, vegetation, proximity to streams, and thermal regime (Appendix S2: Table S1). From years 1963 to 2014, sampling occurred every ~7 d between approximately the first week in June (shortly after ice breakup) and the first week in August (Rogers et al. 2002). After early August, catches diminish as juvenile sockeye salmon, Arctic char, and threespine stickleback move to the limnetic zone of the lake (Abrey 2005). Seining was carried out by deploying a 30-m beach seine (6-mm mesh) using a boat, and manually returning the net to shore. All fish captured (or a random subset of the catch if prohibitively large) were identified to species (except for sculpins and whitefish, identified to genus) and enumerated. If the catch was sub-sampled, counts for each species were expanded by the sample fraction to reflect the number of fish captured.

Lake temperature and habitat.—Site-specific water temperature was recorded during each beach seine sample event using a hand-held thermometer at a depth of approximately 10 cm. From 1963–2014, limnological sampling was also conducted every 10 d from the end of June through early September at six fixed mid-lake locations along the length of the lake. At three of the six locations, a vertical temperature profile up to 60 m in depth was recorded using a YSI (Yellow Springs, Inc., Yellow Springs, OH, USA) thermister or, in earlier decades, at discrete depths with thermometer measurements from water bottle samples. Additional habitat variables were also measured at each sample location (details and data presented in Appendix S2).

Statistical methods

We used counts of each species observed in beach seine catches from 1963 to 2014, reflecting the period over which standardized, consistent sampling occurred at each location. Extremely rare species (observed in <5% of the samples) were removed from the data set, leaving 13 species or genera remaining: threespine stickleback, ninespine stickleback, sculpin, Alaska blackfish, sockeye salmon, Chinook salmon, coho salmon, chum salmon, pink salmon, rainbow trout, Arctic char, Arctic grayling, and whitefish. Sculpins (Cottidae) and whitefish (Coregonidae) were aggregated at genus level, to avoid identification discrepancies over the years. Two sculpin and two whitefish species are present: coastrange sculpin (*Cottus aleuticus*) and slimy sculpin (*C. cognatus*), and pygmy whitefish (*Prosopium coulteri*) and round whitefish (*P. cylindraceum*).

Site-specific surface water temperatures were averaged over the season at each beach seine sample location, tested for autocorrelation (trend in residuals), and plotted with linear model fits to show trends in average summer surface temperature at each site. July epilimnion (0–20 m) temperatures were averaged over the three limnology sites, tested for autocorrelation of residuals, and plotted with linear model fit.

Temporal trends in assemblage composition.—We applied a spatially-explicit dynamic factor analysis model to describe changes in fish assemblages at each of the 10 sample locations. Similar to a traditional dynamic factor analysis, SDFA identifies one or more latent trends in a set of time series data, and can also partition structure in the time series to covariates such as environmental variables. This spatial dynamic factor analysis (SDFA) model (Thorson et al. 2016) was chosen for multiple reasons: because each factor includes both correlation among sites in a given year ("spatial autocorrelation") and correlation among years at a given site ("temporal autocorrelation"), and it therefore controls for both spatial and temporal autocorrelation in density (i.e., spatially-explicit abundance) for each species; because log-density for each species is a linear combination of different factors, and the loadings of each species on each factor represents shared responses to unmeasured environmental factors ("correlation among species"); and because SDFA can estimate the impact of measured environmental variables on density for each species while controlling for residuals that co-vary in complicated ways (e.g.,, spatial, temporal, and among-species correlations). We treated samples as arising from a Poisson distribution while including log-normal overdispersion for each sample (i.e., used a log-normal-Poisson distribution).

Using the species abundance data for each sample date at each site across years from 1963 to 2014, we ran a suite of SDFA models with varying numbers of estimated factors. We included site-specific water temperature as a covariate in each model, and estimated a separate linear effect of temperature on log-abundance for each species. We selected the number of estimated factors based on the criterion that each factor explains no less than 5% of total variance, and used a varimax rotation to visualize the estimated loadings of species onto factors. The rotated loadings matrix therefore groups species based on residuals that vary similarly across sites and over time (after controlling for species-specific responses to temperature). Models were run in R (R Core Team 2016) using Template Model Builder (TMB) for parameter estimation (Kristensen et al. 2016) and the R-INLA package for computing a finite-element mesh used in an approximation to spatial correlations (Lindgren and Rue 2015). Further details on the SDFA model and its interpretation can be found in Appendix S1.

Results

July epilimnetic (0–20 m) water temperatures have increased significantly over time (Fig. 1, inset) at the

offshore sampling locations. However, significant heterogeneity existed among surface temperature trends for the different nearshore sampling locations (Fig. 1; Appendix S2: Table S1). Temperatures at three sites increased significantly over time with different slope values (2N, 6N, 8S), and sites on the south shore of the lake generally experienced slower warming. Other habitat features that varied across beach seine sample locations included direction of exposure and vegetation (Appendix S2: Table S1).

Temporal trends in community structure

From 1963 to 2014, a total of 2,724,739 individuals were captured of the 13 fish species retained for SDFA analysis. This catch was numerically dominated by threespine stickleback (45%) and juvenile sockeye salmon (44%). Ninespine sticklebacks (5%), sculpin (3%), and Arctic char (2%) were the next most abundant, and the least frequently encountered species made up 1%.

An advantage to using spatio-temporal models is the ability to generate estimates of effect sizes for covariates, while controlling for the confounding effect of other unmeasured drivers of community structure that otherwise cause covariation among species, sites, and years. Surface water temperatures at each beach seine site were used as a covariate in the SDFA model, and allowed us to estimate the percent change in species abundance expected for each 1°C increase in temperature (Table 1). Most species *increased* in abundance in the littoral zone as temperature increased: threespine stickleback, ninespine stickleback, Alaska blackfish, whitefish species, Arctic char, rainbow trout, and Chinook, chum and coho salmon all increased between 0.4% and 11.9%. Catches of sockeye salmon, sculpin species, pink salmon and Arctic grayling *declined* with temperature increases. The temperature effect was significant for ninespine stickleback, threespine stickleback, sockeye salmon, Alaska blackfish, whitefish species and sculpin species.

TABLE 1. Species-specific estimates for the water temperature covariate included in SDFA. Estimate values indicate percent change in abundance for each species per each 1°C increase in temperature (e.g., ninespine stickleback increase by 11.9% for each 1°C temperature increase whereas sockeye salmon decrease by 11.8%). Values in bold indicate species with significant effects.

Species	Estimate	Standard error	*z*-value	*P*-value
Ninespine stickleback	**0.119**	**0.009**	**13.393**	**<0.001**
Alaska blackfish	**0.089**	**0.020**	**4.538**	**<0.001**
Threespine stickleback	**0.082**	**0.010**	**8.350**	**<0.001**
Whitefish spp.	**0.056**	**0.019**	**2.957**	**0.003**
Sculpin spp.	**−0.047**	**0.007**	**−6.724**	**<0.001**
Sockeye salmon	**−0.118**	**0.013**	**−9.076**	**<0.001**
Coho salmon	0.050	0.050	0.995	0.320
Chinook salmon	0.042	0.034	1.241	0.215
Arctic char	0.015	0.010	1.560	0.119
Chum salmon	0.011	0.059	0.187	0.851
Rainbow trout	0.004	0.069	0.056	0.956
Pink salmon	−0.007	0.030	−0.245	0.806
Arctic grayling	−0.052	0.102	−0.515	0.607

After using the model covariate to account for the temperature effect for each species, the latent trends in species abundance (representing unmeasured variables) were grouped into "factors". The model also generated estimates showing how different species are associated with each of the varimax-rotated factors (Fig. 2). We selected a final model with five estimated factors, where the final factor explained 6.3% of total variance prior to varimax rotation. Factor 1 was positively associated with the abundance of threespine and ninespine stickleback and sockeye salmon. Factor 2 was primarily associated with Alaska blackfish and whitefish species (positive), and pink salmon (negative); Factor 3 was positively associated with Arctic char and sculpin species. Factor 4 was most associated with Chinook salmon and coho salmon (positive) and Alaska blackfish (negative), and Factor 5 had a positive relationship with coho salmon abundance. Most of the variation accounted for by latent trends was described by threespine stickleback, ninespine stickleback and sockeye salmon (Factor 1; 33.4%), and by Chinook salmon and coho salmon (Factor 4; 30.3%). Factors 2, 3, and 5 respectively explained 20.0%, 6.3%, and 10.0% of the variance.

Each factor was associated with different locations in the lake, suggesting differences in community structure across sampling sites, and each factor had a different trajectory over time (Fig. 3). The numerically dominant threespine and ninespine sticklebacks and sockeye salmon (represented by Factor 1) had highest values at sites on the far north and east ends of the lake (1S, 6N, 8N), and this trend declined steadily over time, consistent with an overall decline in catches of juvenile sockeye salmon across years. The Alaska blackfish, whitefish and pink salmon of Factor 2 were dominant at the lake outlet (site 8S); the latent trend for these species declined overall until an apparent increase starting in 2004. Arctic char and sculpins (Factor 3) dominated at the ends of the lake (2N, 2S, 7S), with a more gradually declining trend. Factor 4, dominated by Chinook salmon, was weakly associated with sites throughout the lake and relatively stable over time, with a peak around 2005. The trend for coho salmon (Factor 5) was concentrated at sites 2N and 7S, and peaked in 1995 before declining.

DISCUSSION

Temperature variability

From 1963 to 2014, mid-lake water temperatures consistently increased in Lake Aleknagik, but rates of temperature increase varied among shoreline sample

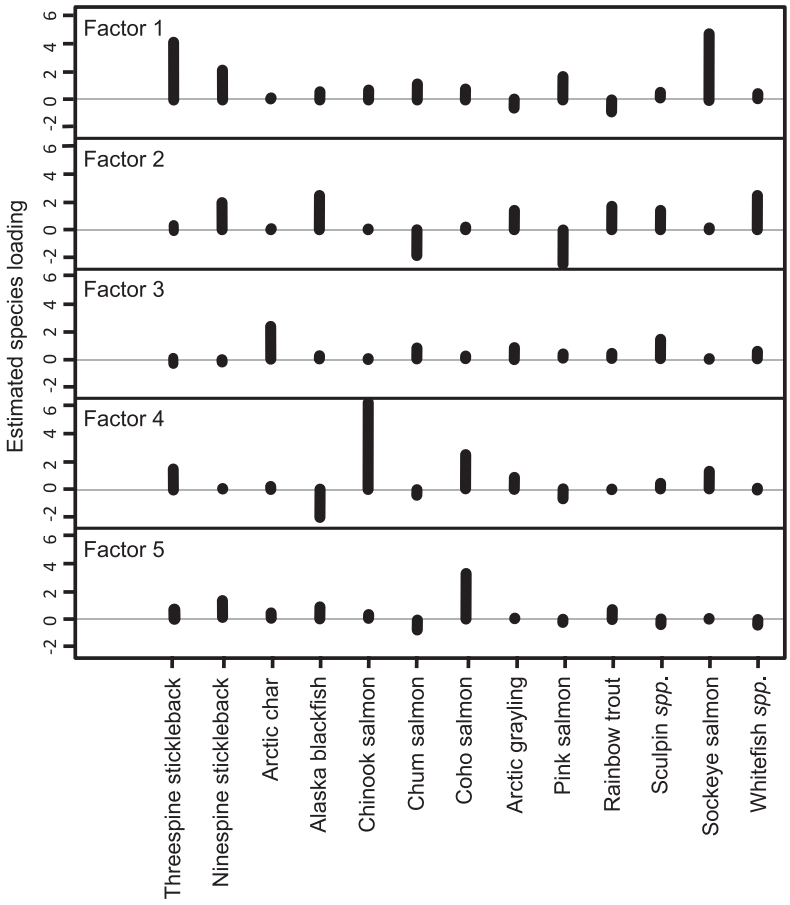

FIG. 2. Factor loadings for each of 13 fish species, indicating the direction and strength of species association with each of five factors in the selected model after varimax rotation in the SDFA.

locations and some sites even declined in temperature over this period (Fig. 1). The sites that became cooler (5S and 7S) are located at the southeast end of the lake, where they are exposed to prevailing wind and wave action. Littoral habitat may be increasingly inundated with water from below the thermocline when the lake undergoes wind-related vertical mixing, especially during seiche events (Lisi and Schindler 2015). Other sites vary in beach slope, substrate size, and exposure, but the sites with most rapid warming over our period of observation are shallower and generally south or west-facing. Small-scale habitat heterogeneity has been shown to mediate the effects of climate change in terrestrial (Scherrer and Karner 2009) and riverine systems (Isaak et al. 2010), and affects how organisms experience climate change (Potter et al. 2013). The importance of habitat heterogeneity is less commonly appreciated in lakes, and we show here that variability in littoral zone habitat, associated with shoreline features and landscape position, corresponds to substantial variation in surface water temperature trends. This thermal variability explains differences in how fish assemblages throughout the lake respond to regional warming.

Temperature effects and temporal patterns in community structure

To explicitly test the variability in space and time for species assemblage composition, we extended the spatial dynamic factor analysis model, a recently developed tool for spatio-temporal community analysis (Thorson et al. 2016), to include measured covariates (i.e., temperature). We found that different taxa had widely varying temperature effects, with some increasing and others declining with increasing temperature. The five factors in our selected model explained all but a small amount of the spatio-temporal variance that remained after accounting for temperature, and each of these factors was represented at different locations in the lake and associated with different species assemblages and trends. The temporal trends in fish assemblages correspond to larger climate trends observed in this system; Lake Aleknagik temperature observations are consistent with the noted switch from the cool to warm phase Pacific Decadal Oscillation (PDO) in the mid-1970s and the marked warming trends observed in the Bristol Bay region in subsequent decades (Mantua and Hare 2002, Rich et al. 2009, Carter and

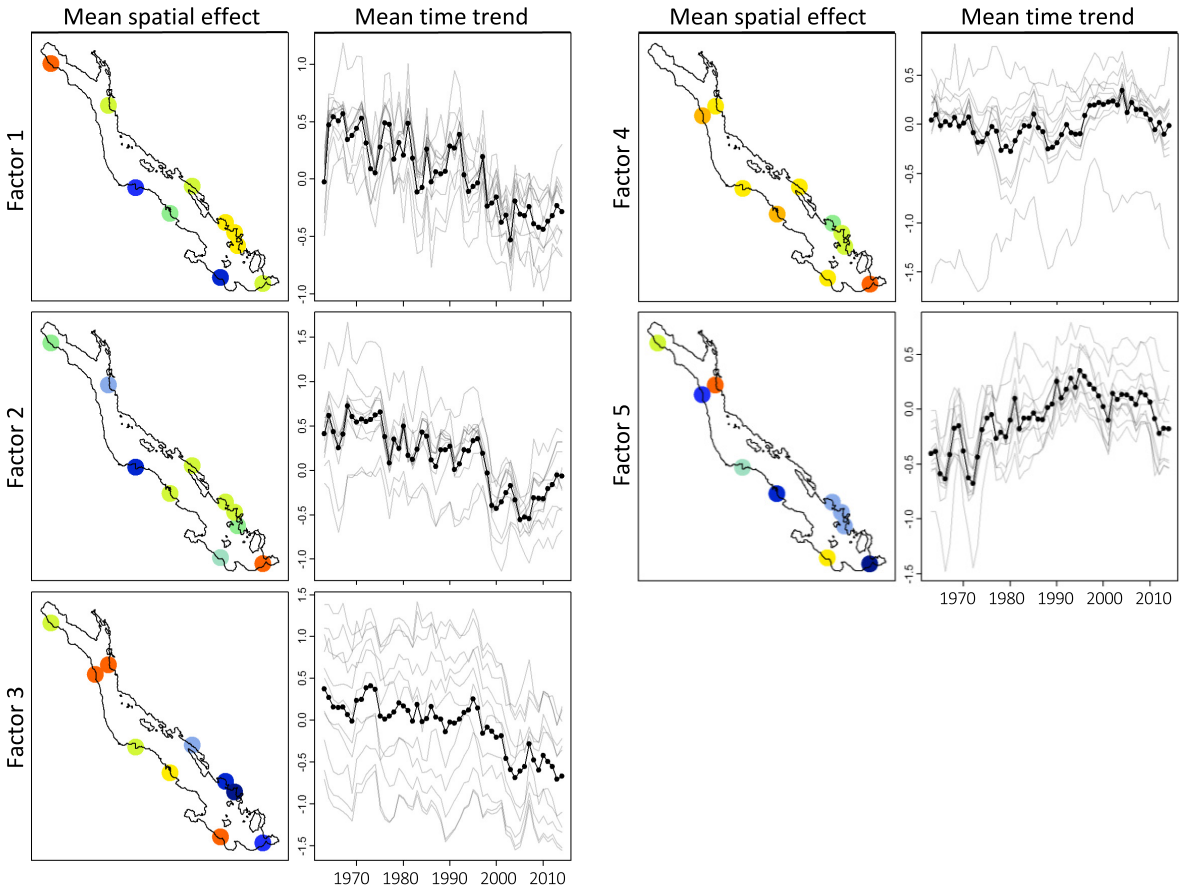

FIG. 3. For each of five factors, the right panel indicates the trend over time at each site (gray lines) and the mean trend across all sites (black line). In the left panel, colored dots indicate the mean factor values associated with each site. Warm colors (red = maximum) indicate high values and high association and cool colors (dark blue = minimum) indicate low values. See Fig. 2 for species associations with each factor. [Color figure can be viewed at wileyonlinelibrary.com]

Schindler 2012). Together, the covariate effects and factors generated by the SDFA model allow the results to be biologically interpreted according to species life histories.

Interpreting changes in species abundance using the temperature covariate allows our model to inform changes to the fish community using climate projections. Under a moderate emissions scenario, the IPCC temperature projection for southwest Alaska forecasts a 2.3°C air temperature increase between 1990–1999 and 2090–2099 (Christensen et al. 2007). Developing air-to-water temperature relationships would allow the temperature effect parameter to be extrapolated to predict abundance changes in the future, as these effect sizes indicate percent change in abundance with each 1°C change in water temperature. Predicted abundance varied widely by taxa. Threespine and ninespine sticklebacks were among the taxa with the largest positive temperature effect, with up to 11% increase per 1°C (Table 1). These species can tolerate warmer temperatures than salmonids or other coldwater fishes (Beauchamp et al. 1989, Hovel et al. 2015), and with a sufficiently long and warm growing season threespine sticklebacks can spawn multiple times (Brown-Peterson and Heins 2009, Hovel et al. 2017). Alaska blackfish, which increased almost 9% with for each 1°C increase in water temperature, are unique in their ability to tolerate warm water and hypoxic conditions at spawning locations (Lefevre et al. 2014). Whitefish species also tended to increase with warming temperatures; life histories vary somewhat within this genus, but the pattern is likely driven by productivity of small-bodied lake residents (McPhail and Lindsey 1970). In contrast, sockeye salmon declined 11% with every 1°C, and sculpin species also had a significant negative association with temperature. While none of the fishes in Lake Aleknagik are likely experiencing temperatures near their thermal maxima, more warm-adapted species appear to be benefitting from warming water temperatures, and in the future will likely have greater relative abundance in littoral habitats of the lake.

Most of the spatio-temporal variation was explained by Factors 1 and 4, which correspond to different locations throughout the lake and represent species with a range of life histories. Factor 1 was associated most strongly with threespine stickleback, ninespine

stickleback and sockeye salmon, and the highest values for this factor consistently occurred at warmer, more protected sites. Threespine and ninespine stickleback are small resident fish, with lake distributions largely regulated by breeding dynamics (McPhail and Lindsey 1970). While threespine stickleback do move offshore and feed in the limnetic zone of the lake in schools (Wootton 1976), the low-plated, small sticklebacks in Lake Aleknagik are not believed to migrate between lake and stream or marine habitats (McPhail and Lindsey 1970). Sockeye salmon respond to conditions in stream and marine habitats beyond the lake, and these conditions may co-vary with lake temperature (Quinn 2005). However, their decline at locations with increasing temperature might also be explained by in-lake conditions; sockeye salmon move from the littoral zone (where they are captured in our sampling) to the pelagic zone of the lake, and this transition is dictated in part by a size threshold (Abrey 2005). In warmer years or locations, more rapid growth might lead to earlier off-shore migration and lower catches in littoral zones. To the extent that this is true, the abundance projection based on littoral zone catches is somewhat paradoxical, as it could occur alongside increasing population abundance. This type of interaction highlights the complex ways in which the life history patterns of species must be considered when interpreting trends and projections.

The Factor 4 trend was more stable over time, weakly associated with sites distributed along the length of the lake, and strongly associated with Chinook salmon and coho salmon. Juvenile coho and Chinook salmon are anadromous after feeding for one or two years in streams and rivers, and the in-lake distributions for both species are likely influenced by stream location and local conditions in streams. Species associations with factors 2, 3 and 5 also appear to be influenced by fish life histories. Alaska blackfish and sculpins are small-bodied benthic or demersal lake residents, and are believed to have localized ranges near to spawning grounds in shallow water (McPhail and Lindsey 1970). As such, abundance of these species at different locations in the lake are likely more related to local ecosystem productivity than migration and habitat selection. Arctic char and whitefish species in seine samples were juveniles, and their distributions were influenced by locations of spawning habitat along the shoreline and in streams (McPhail and Lindsey 1970). Rainbow trout and Arctic grayling are freshwater residents that largely reside in streams and rivers, and use the lake opportunistically for feeding and migration between streams. All Pacific salmon species spawn in tributary streams and rivers on the north and south shores of Lake Aleknagik, and the distributions of pink and chum salmon in particular are likely influenced by stream location and dynamics outside of the lake; both of these species occupy the littoral zone only for brief periods as they migrate to the ocean (Quinn 2005).

Broadly, the SDFA model is a useful tool for quantifying temporal or spatial shifts in in ecological communities across a range of taxa, spatial and temporal scales, and periods of observation. (Thorson et al. 2016). Applied here with an environmental covariate, the SDFA model offers a new probabilistic and predictive approach to multivariate species abundance data that are hierarchical in space and time. It estimates species-specific sensitivity to environmental covariates (e.g., temperature) and partitions remaining spatiotemporal variability into unobserved "factors" that represent positive or negative associations for abundance over time among species within the community. The inclusion of co-variates additionally allows for community shifts to be interpreted according to varying environmental conditions, and facilitates prediction of future species abundance. Developing a method to capture both environmental predictors and residual covariation among sites, species, and years offers a novel way to assess the trajectory of shifts in ecological communities, and contributes an important component in understanding the complexity and nuance of biological responses to climate.

In particular, spatial dynamic factor analysis represents a compromise between mechanistic and phenomenological approaches to analyzing community dynamics. On the one hand, a "mechanistic" approach to community dynamics might estimate the matrix of species interactions, representing the impact of 1% increase in density for species A on per-capita productivity of species B for every pair of species. This is what recent time-series and spatio-temporal models have sought to do (Ives et al. 2003, Thorson et al. 2017). However, this mechanistic approach requires estimating an n by n matrix of species interactions (where n is the number of species), and is not likely to be parsimonious (or even computationally feasible) for many species, or when analyzing data from uncommon species in an assemblage (e.g., Lake Aleknagik whitefish). By contrast, a phenomenological approach like nonmetric multidimensional scaling (NMDS) provides insight on the relationship between community dynamics and environmental drivers only through performing post-hoc comparisons, and such comparisons risk doing "statistics on statistics". In particular, analyzing output from a dimension-reduction algorithm (e.g.,, NMDS) as if it were data in a secondary statistical model precludes the use of model diagnostics to assess fit to observation-level data (Warton et al. 2015), calculation of data-level variance explained by each individual factor, or estimates of statistical significance for environmental covariates (e.g., temperature) while accounting for spatial autocorrelation (Dormann et al. 2007). We note, however, that there are many other ways to construct parsimonious representations of community associations and interactions (Kissling et al. 2012), and recommend that future research expand the range of available options for spatiotemporal community analysis. Further developing and implementing these techniques will have important implications for conservation concerns, and also for our understanding of how ecological interactions and

fine-scale habitat heterogeneity shape ecosystem responses to large scale disturbances.

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