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Within-lake habitat heterogeneity mediates community response to warming trends

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Variability shapes response to climate

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Abstract

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

49 **Keywords**

50 *Climate change, fish community, spatial dynamic factor analysis, boreal lake, water*
51 *temperature, habitat heterogeneity, life history*

52 **Introduction**
53 Species commonly respond to climate change effects in different ways, due to varied
54 habitat use, life history traits, physiological limits, and other attributes (Parmesan 2006). Climate
55 change literature frequently addresses biological responses at the individual- or species-level,
56 and knowing life histories and physiological tolerances of individual taxa is often useful in
57 predicting biological responses to observed and projected habitat changes (Mackenzie et al.
58 2007, Portner and Farrell 2008). However, *in situ* organisms experience climate change effects
59 within the context of other biological dynamics, including complex interactions with other
60 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

61 biological interactions can be difficult to measure or incorporate into modeling approaches, and
62 describing community responses to climate change depends on identifying and accounting for
63 community-level dynamics that are separate from climate effects. This community-level
64 perspective can effectively capture the diversity of responses to climate change (Harley et al.
65 2006), but this approach is presently underrepresented in climate change literature and
66 uncertainty remains in how future communities might look.

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

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

89 High-latitude lakes are very sensitive to climate change and warming temperatures,
90 especially in regard to seasonal regulation of biological processes (De Stasio et al. 1996, Smol et
91 al. 2005). In these systems, climate change has led to longer annual ice-free periods, warmer
92 average and peak water temperatures, and higher productivity due to longer growing seasons and

93 metabolic processes of primary producers (Schindler 2009). Biota of freshwater systems,
94 including fishes, respond strongly to these changes (Parmesan 2006, Keller 2007, Adrian et al.
95 2009). Earlier ice breakup dates may alter the timing in life history or reproductive cycles
96 (Schneider and Hook 2010, Hovel et al. 2017) or influence species distribution and behavior,
97 including competition (Abrey 2005, Schindler et al. 2005, Rich et al. 2009). Increased water
98 temperatures can differently affect the distribution and phenology of fishes because species vary
99 in thermal preference and tolerance (Edwards and Cunjak 2007). Warming temperatures
100 generally increase metabolic rate (Clarke and Johnston 1999) and, with unrestricted prey and
101 thermal limits, many species will experience faster growth or maturation with a longer, warmer
102 growing season (Magnuson et al. 1990, Schindler et al. 2005). However, physiological limits
103 and thermal optima varies widely among taxa, and some species may undergo thermal stress and
104 declining growth due to increasing metabolic costs (Beitinger and Fitzpatrick 1979).
105 Destabilization has been observed in freshwater plankton communities with increased
106 temperatures (Winder and Schindler 2004, Carter and Schindler 2012), and increased metabolic
107 demands and shifts in niche exploitation may affect the behavior and ecological interactions of
108 planktivorous fish and other higher-trophic organisms (Beisner et al. 1997). Together, these
109 species reactions ultimately shape community responses to climate change in lakes.

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

125 approach to testing the effect of within-lake heterogeneity on biological response to climate
126 change.

127 **Methods**

128 *Study Site*

129 Lake Aleknagik is a large oligotrophic lake with mean depth of 43 m and surface area of
130 83 km² (Hartman and Burgner 1972), and is the farthest downstream of five interconnected lakes
131 that drain into the Wood River, Bristol Bay, Alaska (Figure 1). Located north of the 59th parallel,
132 this system has a short season of biotic productivity and is ice-covered for up to eight months of
133 the year (Hartman and Burgner 1972, Schindler et al. 2005). The lake experiences thermal
134 stratification between mid-June and mid-September of most years, and mean epilimnetic (0-20 m
135 depth) August water temperatures range from 10° C to 12° C. Data collection has been
136 standardized in this system since 1963, and since then significant trends have been observed in
137 timing of ice breakup (average of 10 days earlier) and average lake water temperature, with taxa-
138 specific effects on the zooplankton community (Carter and Schindler 2012). These changes have
139 been attributed to the combined influences of global warming and the switch from a cool to
140 warm phase of the Pacific Decadal Oscillation during the study period (Mantua et al. 1997,
141 Schindler et al. 2005).

142 The Wood River watershed is largely unaffected by anthropogenic activities aside from
143 salmon fishing (e.g., no shoreline development, logging, agriculture, dams or water diversions),
144 and habitat and fish communities have remained intact throughout our period of study. Lake
145 Aleknagik supports an entirely native community of both anadromous and non-anadromous
146 fishes. Dominant taxa in the lake are juvenile sockeye salmon (*Oncorhynchus nerka*) rainbow
147 trout (*O. mykiss*), Arctic char (*Salvelinus alpinus*), northern pike (*Esox lucius*), threespine
148 stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), sculpins
149 (*Cottus* spp.), Alaska blackfish (*Dallia pectoralis*) and whitefish species (Coregonidae). Arctic
150 char and whitefish species rear in littoral habitats of the lake as juveniles, and threespine and
151 ninespine sticklebacks and sculpin species comprise the remainder of the numerically dominant
152 members of the littoral community as both juveniles and adults. Other Pacific salmon, including
153 coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*) and Chinook (*O. tshawytscha*) are
154 present in the system in small numbers, as they migrate quickly to sea and do not represent a
155 significant part of the lake community in relative abundance or duration of residence.

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

171 *Sample collection*

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

185 Lake temperature and habitat: Site-specific water temperature was recorded during each
186 beach seine sample event using a hand-held thermometer at a depth of approximately 10 cm.
187 Over this time period, limnological sampling was also conducted every 10 days from the end of

188 June through early September at six fixed mid-lake locations along the length of the lake. At
189 three of the six locations, a vertical temperature profile up to 60 m in depth was recorded using a
190 YSI (Yellow Springs, Inc.) thermister or, in earlier decades, at discrete depths with thermometer
191 measurements from water bottle samples. Additional habitat variables were also measured at
192 each sample location (details and data presented in Appendix S2).

193 Statistical methods

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

204 Site-specific surface water temperatures were averaged over the season at each beach
205 seine sample location, tested for autocorrelation (trend in residuals), and plotted with linear
206 model fits to show trends in average summer surface temperature at each site. July epilimnion (0-
207 20 m) temperatures were averaged over the three limnology sites, tested for autocorrelation of
208 residuals, and plotted with linear model fit.

209 Temporal trends in assemblage composition

210 We applied a spatially-explicit dynamic factor analysis model to describe changes in fish
211 assemblages at each of the 10 sample locations. Similar to a traditional dynamic factor analysis,
212 SDFA identifies one or more latent trends in a set of time series data, and can also partition
213 structure in the time series to covariates such as environmental variables. This spatial dynamic
214 factor analysis (SDFA) model (Thorson et al. 2016) was chosen for multiple reasons: because
215 each factor includes both correlation among sites in a given year (“spatial autocorrelation”) and
216 correlation among years at a given site (“temporal autocorrelation”), and it therefore controls for
217 both spatial and temporal autocorrelation in density (i.e. spatially-explicit abundance) for each
218 species; because log-density for each species is a linear combination of different factors, and the
219 loadings of each species on each factor represents shared responses to unmeasured

220 environmental factors (“correlation among species”); and because SDFA can estimate the impact
221 of measured environmental variables on density for each species while controlling for residuals
222 that co-vary in complicated ways (e.g., spatial, temporal, and among-species correlations).
223 We treated samples as arising from a Poisson distribution while including lognormal
224 overdispersion for each sample (i.e., used a lognormal-Poisson distribution).

225 Using the species abundance data for each sample date at each site across years from
226 1963-2014, we ran a suite of SDFA models with varying numbers of estimated factors. We
227 included site-specific water temperature as a covariate in each model, and estimated a separate
228 linear effect of temperature on log-abundance for each species. We selected the number of
229 estimated factors based on the criterion that each factor explains no less than 5% of total
230 variance, and used a varimax rotation to visualize the estimated loadings of species onto factors.
231 The rotated loadings matrix therefore groups species based on residuals that vary similarly across
232 sites and over time (after controlling for species-specific responses to temperature). Models were
233 run in R (R Core Team 2016) using Template Model Builder (TMB) for parameter estimation
234 (Kristensen et al. 2016) and the R-INLA package for computing a finite-element mesh used in an
235 approximation to spatial correlations (Lindgren and Rue 2015). Further details on the SDFA
236 model and its interpretation can be found in Appendix S1.

237 **Results**

238 July epilimnetic (0-20 m) water temperatures have increased significantly over time
239 (Figure 1, inset) at the offshore sampling locations. However, significant heterogeneity existed
240 among surface temperature trends for the different nearshore sampling locations (Figure 1,
241 Appendix S2; Table S1). Temperatures at three sites increased significantly over time with
242 different slope values (2N, 6N, 8S), and sites on the south shore of the lake generally
243 experienced slower warming. Other habitat features that varied across beach seine sample
244 locations included direction of exposure and vegetation (Appendix S2; Table S1).

245 *Temporal trends in community structure*

246 From 1963-2014, a total of 2,724,739 individuals were captured of the 13 fish species
247 retained for SDFA analysis. This catch was numerically dominated by threespine stickleback
248 (45%) and juvenile sockeye salmon (44%). Ninespine sticklebacks (5%), sculpin (3%), and
249 Arctic char (2%) were the next most abundant, and the least frequently encountered species
250 made up 1%.

251 An advantage to using spatio-temporal models is the ability to generate estimates of
252 effect sizes for covariates, while controlling for the confounding effect of other unmeasured
253 drivers of community structure that otherwise cause covariation among species, sites, and years.
254 Surface water temperatures at each beach seine site were used as a covariate in the SDFa model,
255 and allowed us to estimate the percent change in species abundance expected for each 1° C
256 increase in temperature (Table 1). Most species *increased* in abundance in the littoral zone as
257 temperature increased: threespine stickleback, ninespine stickleback, Alaska blackfish, whitefish
258 species, Arctic char, rainbow trout, and Chinook, chum and coho salmon all increased between
259 0.4% and 11.9%. Catches of sockeye salmon, sculpin species, pink salmon and Arctic grayling
260 *declined* with temperature increases. The temperature effect was significant for ninespine
261 stickleback, threespine stickleback, sockeye salmon, Alaska blackfish, whitefish species and
262 sculpin species.

263 After using the model covariate to account for the temperature effect for each species, the
264 latent trends in species abundance (representing unmeasured variables) were grouped into
265 “factors”. The model also generated estimates showing how different species are associated with
266 each of the varimax-rotated factors (Figure 2). We selected a final model with 5 estimated
267 factors, where the final factor explained 6.3% of total variance prior to varimax rotation. Factor 1
268 was positively associated with the abundance of threespine and ninespine stickleback and
269 sockeye salmon. Factor 2 was primarily associated with Alaska blackfish and whitefish species
270 (positive), and pink salmon (negative); Factor 3 was positively associated with Arctic char and
271 sculpin species. Factor 4 was most associated with Chinook salmon and coho salmon (positive)
272 and Alaska blackfish (negative), and Factor 5 had a positive relationship with coho salmon
273 abundance. Most of the variation accounted for by latent trends was described by threespine
274 stickleback, ninespine stickleback and sockeye salmon (Factor 1; 33.4%), and by Chinook
275 salmon and coho salmon (Factor 4; 30.3%). Factors 2, 3 and 5 respectively explained 20.0%,
276 6.3%, and 10.0% of the variance.

277 Each factor was associated with different locations in the lake, suggesting differences in
278 community structure across sampling sites, and each factor had a different trajectory over time
279 (Figure 3). The numerically dominant threespine and ninespine sticklebacks and sockeye salmon
280 (represented by Factor 1) had highest values at sites on the far north and east ends of the lake
281 (1S, 6N, 8N), and this trend declined steadily over time, consistent with an overall decline in
282 catches of juvenile sockeye salmon across years. The Alaska blackfish, whitefish and pink

283 salmon of Factor 2 were dominant at the lake outlet (site 8S); the latent trend for these species
284 declined overall until an apparent increase starting in 2004. Arctic char and sculpins (Factor 3)
285 dominated at the ends of the lake (2N, 2S, 7S), with a more gradually declining trend. Factor 4,
286 dominated by Chinook salmon, was weakly associated with sites throughout the lake and
287 relatively stable over time, with a peak around 2005. The trend for coho salmon (Factor 5) was
288 concentrated at sites 2N and 7S, and peaked in 1995 before declining.

289 **Discussion**

290 *Temperature variability*

291 From 1963 to 2014, mid-lake water temperatures consistently increased in Lake
292 Aleknagik, but rates of temperature increase varied among shoreline sample locations and some
293 sites even declined in temperature over this period (Figure 1). The sites that became cooler (5S
294 and 7S) are located at the southeast end of the lake, where they are exposed to prevailing wind
295 and wave action. Littoral habitat may be increasingly inundated with water from below the
296 thermocline when the lake undergoes wind-related vertical mixing, especially during seiche
297 events (Lisi and Schindler 2015). Other sites vary in beach slope, substrate size, and exposure,
298 but the sites with most rapid warming over our period of observation are shallower and generally
299 south or west-facing. Small-scale habitat heterogeneity has been shown to mediate the effects of
300 climate change in terrestrial (Scherrer and Karner 2009) and riverine systems (Isaak et al. 2010),
301 and affects how organisms experience climate change (Potter et al. 2013). The importance of
302 habitat heterogeneity is less commonly appreciated in lakes, and we show here that variability in
303 littoral zone habitat, associated with shoreline features and landscape position, corresponds to
304 substantial variation in surface water temperature trends. This thermal variability explains
305 differences in how fish assemblages throughout the lake respond to regional warming.

306 *Temperature effects and temporal patterns in community structure*

307 To explicitly test the variability in space and time for species assemblage composition,
308 we extended the spatial dynamic factor analysis model, a recently developed tool for spatio-
309 temporal community analysis (Thorson et al. 2016), to include measured covariates (i.e.
310 temperature). We found that different taxa had widely varying temperature effects, with some
311 increasing and others declining with increasing temperature. The five factors in our selected
312 model explained all but a small amount of the spatio-temporal variance that remained after
313 accounting for temperature, and each of these factors was represented at different locations in the
314 lake and associated with different species assemblages and trends. The temporal trends in fish

315 assemblages correspond to larger climate trends observed in this system; Lake Aleknagik
316 temperature observations are consistent with the noted switch from the cool to warm phase
317 Pacific Decadal Oscillation (PDO) in the mid-1970s and the marked warming trends observed in
318 the Bristol Bay region in subsequent decades (Mantua and Hare 2002, Rich et al. 2009, Carter
319 and Schindler 2012). Together, the covariate effects and factors generated by the S DFA model
320 allow the results to be biologically interpreted according to species life histories.

321 Interpreting changes in species abundance using the temperature covariate allows our
322 model to inform changes to the fish community using climate projections. Under a moderate
323 emissions scenario, the IPCC temperature projection for southwest Alaska forecasts a 2.3° C air
324 temperature increase between 1990-1999 and 2090-2099 (Christensen et al. 2007). Developing
325 air-to-water temperature relationships would allow the temperature effect parameter to be
326 extrapolated to predict abundance changes in the future, as these effect sizes indicate percent
327 change in abundance with each 1° C change in water temperature. Predicted abundance varies
328 widely by taxa. Threespine and ninespine sticklebacks were among the taxa with the largest
329 positive temperature effect, with up to 11% increase per 1° C (Table 1). These species can
330 tolerate warmer temperatures than salmonids or other coldwater fishes (Beauchamp et al. 1989,
331 Hovel et al. 2015), and with a sufficiently long and warm growing season threespine sticklebacks
332 can spawn multiple times (Brown-Peterson and Heins 2009, Hovel et al. 2017). Alaska blackfish,
333 which increased almost 9% with for each 1°C increase in water temperature, are unique in their
334 ability to tolerate warm water and hypoxic conditions at spawning locations (Lefevre et al.
335 2014). Whitefish species also tended to increase with warming temperatures; life histories vary
336 somewhat within this genus, but the pattern is likely driven by productivity of small-bodied lake
337 residents (McPhail and Lindsey 1970). In contrast, sockeye salmon declined 11% with every 1°
338 C, and sculpin species also had a significant negative association with temperature. While none
339 of the fishes in Lake Aleknagik are likely experiencing temperatures near their thermal maxima,
340 more warm-adapted species appear to be benefitting from warming water temperatures, and in
341 the future will likely have greater relative abundance in littoral habitats of the lake.

342 Most of the spatio-temporal variation was explained by Factors 1 and 4, which
343 correspond to different locations throughout the lake and represent species with a range of life
344 histories. Factor 1 was associated most strongly with threespine stickleback, ninespine
345 stickleback and sockeye salmon, and the highest values for this factor consistently occurred at
346 warmer, more protected sites. Threespine and ninespine stickleback are small resident fish, with

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

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

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

391 In particular, spatial dynamic factor analysis represents a compromise between
392 mechanistic and phenomenological approaches to analyzing community dynamics. On the one
393 hand, a “mechanistic” approach to community dynamics might estimate the matrix of species
394 interactions, representing the impact of 1% increase in density for species A on per-capita
395 productivity of species B for every pair of species. This is what recent time-series and spatio-
396 temporal models have sought to do (Ives et al. 2003, Thorson et al. 2017). However, this
397 mechanistic approach requires estimating an n by n matrix of species interactions (where n is the
398 number of species), and is not likely to be parsimonious (or even computationally feasible) for
399 many species, or when analyzing data from uncommon species in an assemblage (e.g. Lake
400 Aleknagik whitefish). By contrast, a phenomenological approach like nonmetric
401 multidimensional scaling (NMDS) provides insight on the relationship between community
402 dynamics and environmental drivers only through performing post-hoc comparisons, and such
403 comparisons risk doing “statistics on statistics”. In particular, analyzing output from a
404 dimension-reduction algorithm (e.g., NMDS) as if it were data in a secondary statistical model
405 precludes the use of model diagnostics to assess fit to observation-level data (Warton et al.
406 2015), calculation of data-level variance explained by each individual factor, or estimates of
407 statistical significance for environmental covariates (e.g., temperature) while accounting for
408 spatial autocorrelation (Dormann et al. 2007). We note, however, that there are many other ways
409 to construct parsimonious representations of community associations and interactions (Kissling

410 et al. 2012), and recommend that future research expand the range of available options for
411 spatiotemporal community analysis. Further developing and implementing these techniques will
412 have important implications for conservation concerns, and also for our understanding of how
413 ecological interactions and fine-scale habitat heterogeneity shape ecosystem responses to large
414 scale disturbances.

415

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426

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586

587 **Tables**

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

593

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 <i>spp.</i>	0.056	0.019	2.957	0.003
Sculpin <i>spp.</i>	-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

594

595

596 Fig. 1

597 Map of Lake Aleknagik, Alaska. Black dots indicate beach seine sample locations, and plots
 598 adjacent to each display linear model fit for surface water temperature across years; black lines
 599 indicate a significant model fit, and the y-axis values are °C. The bottom left inset shows mean
 600 annual values and linear model fit of July epilimnetic water temperature from 1963-2014 (black
 601 line); gray lines show site-specific limnetic temperatures where records are available.

602

603 Fig. 2

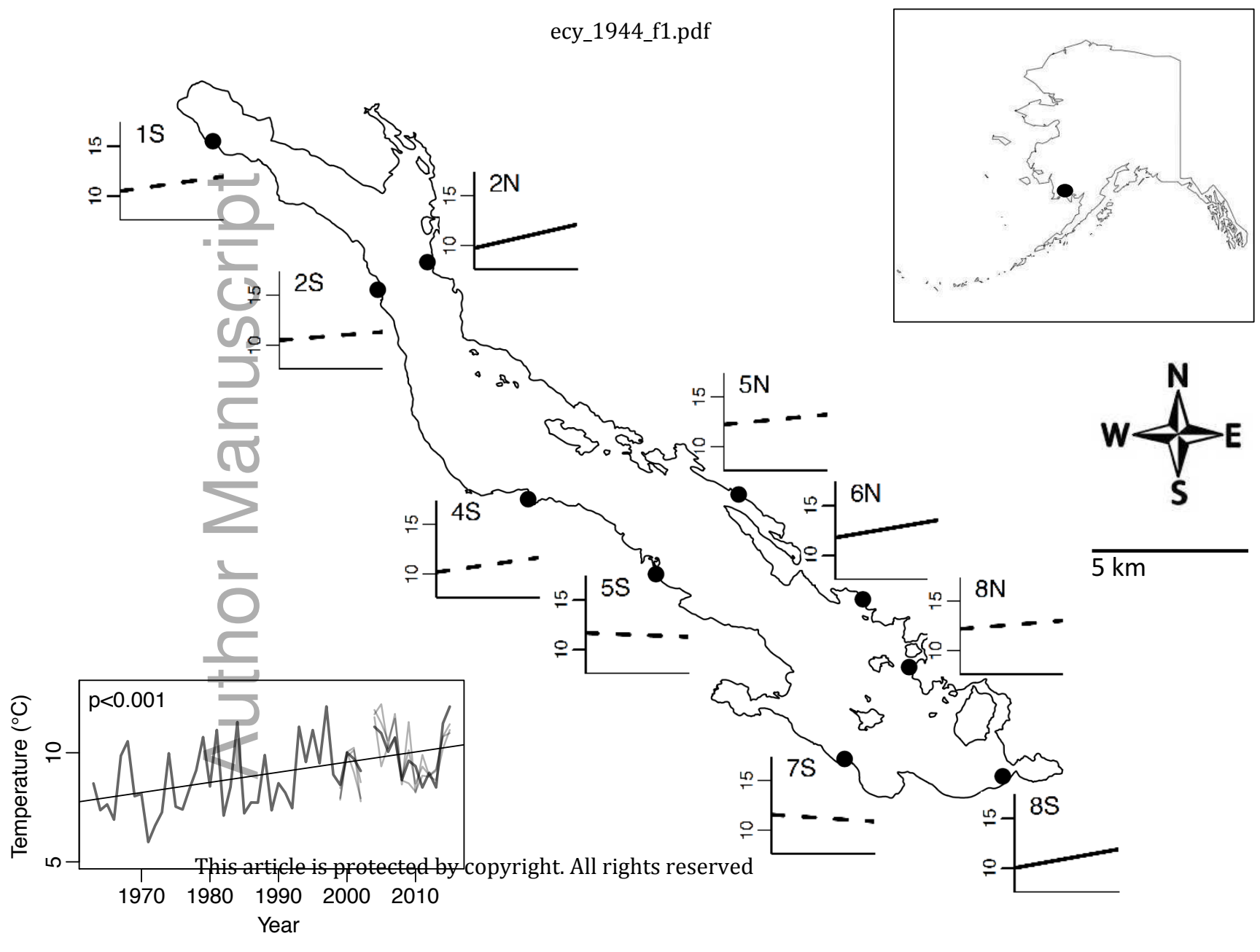
604 Factor loadings for each of 13 fish species, indicating the direction and strength of species
 605 association with each of five factors in the selected model after varimax rotation in the SDFa.

606

607 Fig. 3

608 For each of five factors, the right panel indicates the trend over time at each site (gray lines) and
609 the mean trend across all sites (black line). In the left panel, colored dots indicate the mean factor
610 values associated with each site. Warm colors (red = maximum) indicate high values and high
611 association and cool colors (dark blue = minimum) indicate low values. See Figure 2 for species
612 associations with each factor.

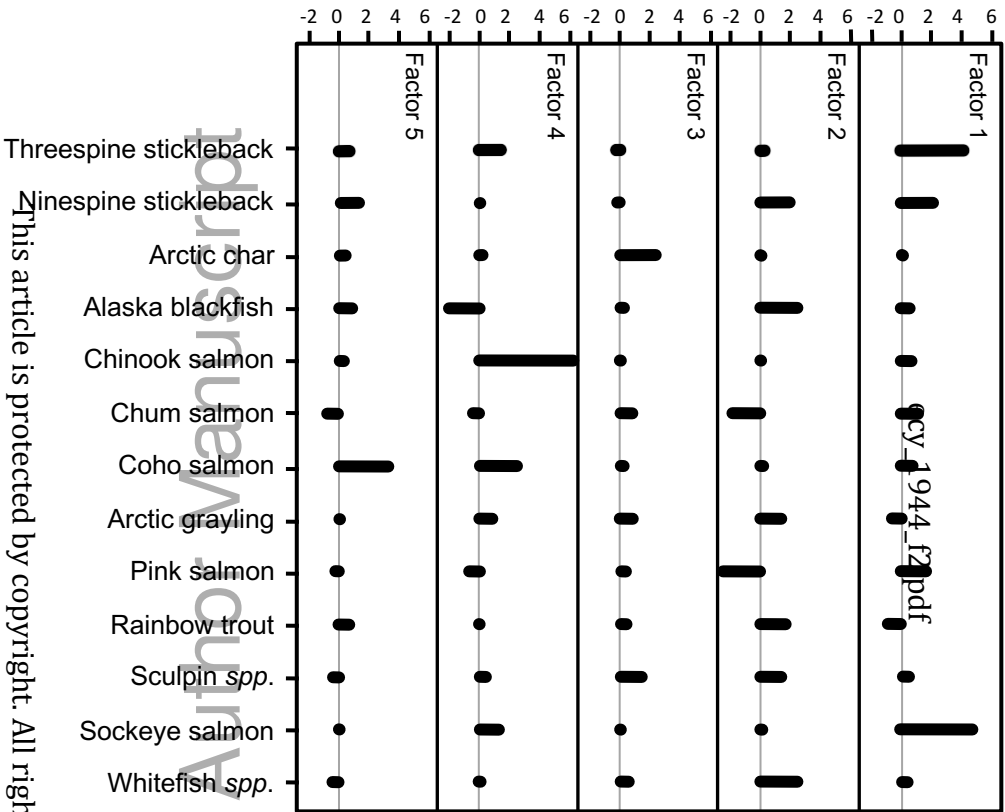
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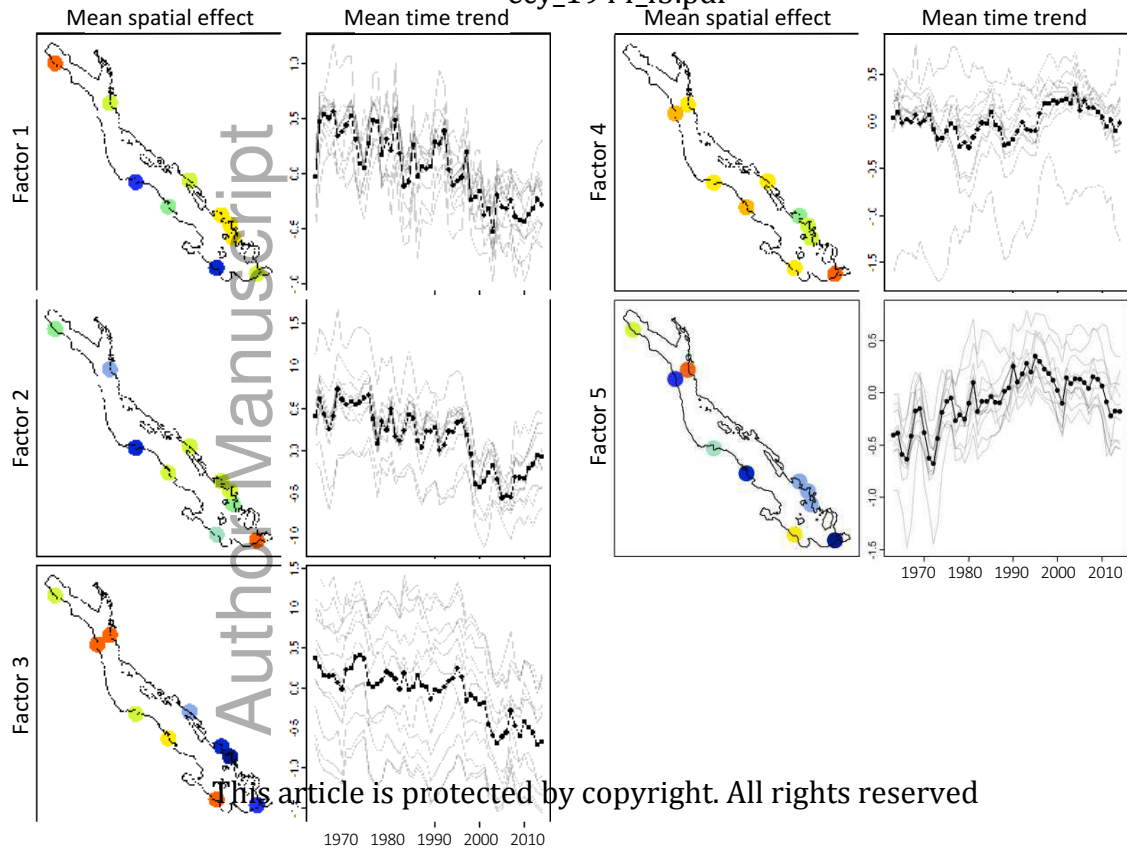


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Estimated species loading





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