



**Climate change alters the quantity and phenology of habitat
for lake trout (*Salvelinus namaycush*) in small Boreal Shield
lakes**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0190.R2
Manuscript Type:	Article
Date Submitted by the Author:	19-Oct-2016
Complete List of Authors:	Guzzo, Matthew M.; University of Manitoba, Biological Sciences Blanchfield, Paul; Fisheries and Oceans Canada, Freshwater Institute
Keyword:	LAKES < Environment/Habitat, ENVIRONMENTAL CONDITIONS < General, FRESHWATER FISHES < General, HABITAT < General, TROUT < Organisms



1 **Climate change alters the quantity and phenology of habitat for lake**
2 **trout (*Salvelinus namaycush*) in small Boreal Shield lakes**

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15 **Abstract**

16 We analyzed monitoring data (1970–2013) from small Boreal Shield lakes to understand how
17 variations in air temperature and precipitation affect the phenology and amount of habitat for
18 lake trout (*Salvelinus namaycush*). Annual air temperatures increased by ~2 °C (significant in
19 fall and winter). In response, ice-cover was reduced by ~19 d. Despite earlier ice-offs, springs
20 became longer, allowing lake trout longer access to littoral regions when water temperatures
21 were cool. Although summer surface water temperatures increased, the summer did not
22 lengthen. Instead, later spring-warming and fall-cooling of lakes caused summer to shift later in
23 the year, potentially delaying fall spawning. Complete loss of optimal oxythermal habitat volume
24 occurred in all lakes and became more prevalent over time, moreso in the darkest lakes.
25 Although air temperatures did not become more variable, several habitat measures did,
26 including mean summer surface water temperatures, duration of ice-cover, timing of ice-off, and
27 minimum volumes of optimal oxythermal habitat. Our results suggest that future warming will
28 impose greater thermal stress on lake trout, but may be tempered by longer springs.

29

30 **Keywords:** cold-water fish, air temperature, precipitation, thermal stratification, global warming,
31 temperate lake

32 Introduction

33 Cold water with high dissolved oxygen (DO) concentrations (i.e. oxythermal habitat) defines the
34 habitat requirements of cold-water fish (Gibson and Fry 1953, Christie and Regier 1988). As
35 such, the availability of suitable oxythermal habitat is accepted to be a critical factor determining
36 the capacity of lakes to support cold-water fish (Evans et al. 1991, Ryan and Marshall 1994,
37 Wilson and Mandrak 2004, Jacobson et al. 2010). In north-temperate regions, lakes containing
38 cold-water fish typically undergo thermal stratification during summer—a period when suitable
39 oxythermal habitat becomes limited to the hypolimnion (Wetzel 2001). Although thermal
40 stratification represents a period of habitat limitation for cold-water fish, it is a critical feature of
41 north-temperate lakes that preserves suitable oxythermal habitat during summer. Indeed, if
42 lakes were to fully mix during summer they would be unable to support cold-water fish because
43 water temperatures would exceed their thermal requirements (Gibson and Fry 1953, Christie
44 and Regier 1988). Thus, the balance between duration and intensity of thermal stratification
45 should be important for lakes to support cold-water fish. However, with recent evidence that lake
46 surface temperatures have risen globally over the past 30 years (O'Reilly et al. 2015), and the
47 expectation that strong warming and increased frequency of extreme temperatures will continue
48 in north-temperate regions (IPCC 2014), the capacity for some lakes to support cold-water fish
49 could diminish in the future.

50 Lake trout (*Salvelinus namaycush*) is a cold-water stenotherm that occupies oligotrophic
51 lakes of northern North America (Martin and Olver 1980). To survive in cold, unproductive
52 ecosystems, lake trout have evolved a life-history characterized by slow growth, late maturation,
53 and low reproductive output (Martin and Olver 1980). Taken together, narrow temperature and
54 DO requirements, and vulnerable life-history, make lake trout a sentinel species for studying the
55 effects of climate change on north-temperate lakes (Schindler et al. 1996b, Jansen and
56 Hesslein 2004, Plumb et al. 2014). Certainly there is evidence that lake trout populations have
57 gone extinct from central and eastern Ontario lakes where optimum summer habitat was absent

58 or limited (MacLean et al. 1990). Lake trout populations are especially concentrated along the
59 southern edge of the Boreal Shield ecozone near the southern extent of its geographic
60 distribution, where they typically occur in small lakes (75 % of lakes < 500 ha, median size 169
61 ha) that undergo annual thermal stratification (Gunn and Pitblado 2004). Boreal Shield lakes are
62 expected to experience changes in physical and biological properties because of climate
63 change (Keller 2007), which heightens the need to understand how lake trout occupying lakes
64 with marginal habitat near the southern extent of their distribution will be impacted by rising and
65 potentially more variable air temperatures.

66 By the end of this century, annual air temperatures across the Boreal Shield are
67 expected to increase by 4–7 °C with greater frequency of extreme temperatures (Colombo et al.
68 2007, IPCC 2014). Air temperatures have direct and relatively rapid influences on the thermal
69 structure of small Boreal Shield lakes. For example, seasonal air temperature strongly
70 influences surface water temperatures (De Stasio et al. 1996, Stefan et al. 1998), and the
71 phenology of the ice-cover and stratification (Robertson and Ragotzkie 1990, De Stasio et al.
72 1996, Magnuson et al. 2000, Keller 2007, Shuter et al. 2013). Consequently, warmer air
73 temperatures have been predicted to reduce the amount of time that lakes are cold in the spring
74 and early summer (Jansen and Hesslein 2004), and extend the duration of the thermally-
75 stratified and open-water seasons (Keller 2007). As such, the predicted magnitude of warming,
76 and potential impacts of this warming on the thermal structure and phenology of lakes, implies
77 that climate change could have serious implications to lake trout populations across the Boreal
78 Shield.

79 Unlike air temperature, predictions of future precipitation for the Boreal Shield vary in
80 direction regionally, with any increases potentially offset by greater evaporation (Colombo et al.
81 2007, Keller 2007). In small lakes (<500 ha) the volume of oxythermal habitat during
82 stratification is a function of the effect of water clarity on thermocline depth (i.e. clear lakes =
83 deeper thermoclines), which is indirectly controlled by precipitation through its effects on

84 terrestrial runoff of dissolved organic matter (DOM) (Fee and Hecky 1996, Schindler et al.
85 1996a, Stasko et al. 2012). The shallower thermoclines found in darker lakes would be
86 expected to result in larger volumes of cold-water habitat relative to clearer lakes of the same
87 depth and size. However, because DO is consumed through bacterial respiration of DOM in the
88 water column and sediments, darker lakes (i.e. due to increase terrestrial DOM) could be more
89 susceptible to low hypolimnetic DO during summer stratification (Molot et al. 1992, Dillon et al.
90 2003, Couture et al. 2015). These counteractive effects of precipitation on oxythermal
91 habitat highlight the importance of detailed long-term empirical lake temperature and DO data
92 collected during wet and dry periods for understanding how future climate scenarios may
93 alter lake trout habitat in Boreal Shield lakes.

94 Most studies on lake trout habitat in Boreal Shield lakes have focused on volumes of
95 late-summer oxythermal habitat (Schindler et al. 1996a, Dillon et al. 2003, Jansen and Hesslein
96 2004, Herb et al. 2014). But, with increases in air temperature expected to occur across
97 seasons it is likely that changes in the thermal habitat phenology may be profound, and these
98 may modulate changes in lake thermal structure. Here, we use long-term meteorological and
99 limnological monitoring data collected over the past 44 years to quantify how variations in air
100 temperature and precipitation have altered the lake trout habitat in four small Boreal Shield
101 lakes. Our specific objectives were to (1) quantify how variations in air temperature and
102 precipitation relate to the temporal changes in thermal habitat for lake trout, and (2) determine if
103 long-term trends in oxythermal habitat have occurred, and how they relate to air temperature
104 and precipitation.

105

106 **Materials and Methods**

107 *Study site and datasets*

108 This study used long-term monitoring data collected during 1970–2013 within the Experimental
109 Lakes Area (ELA), located in the Boreal Shield of northwestern Ontario, Canada (49°40'N,

110 93°44W). The ELA is a set of 58 lakes and their watersheds closed to the public for conducting
111 aquatic research (Blanchfield et al. 2009a). The forests of ELA are dominated by jackpine
112 (*Pinus banksiana*) and black spruce (*Picea mariana*). Soils are mostly thin (≤ 1 m) and lay over
113 Precambrian bedrock. Thin layers of *Spagnum* moss often cover soil and bedrock. In the small
114 wetlands surrounding lakes, *Spagnum*-derived peat reaches depths in excess of 10 m
115 (Schindler et al. 1996a).

116 As part of the long-term monitoring program at the ELA, daily air temperature and
117 precipitation data have been collected at Environment Canada's Rawson Lake (Lake 239)
118 meteorological station since 1969. Annual dates of winter ice-formation and break-up dates
119 (hereafter ice-on and ice-off dates, respectively) were also monitored at Lake 239 (54 ha). We
120 assumed that ice-on and ice-off dates were the same for all study lakes because the lakes were
121 relatively similar in size and located within ~20 km from one another. The study lakes are all
122 ELA long-term reference lakes that contain native, self-sustaining lake trout populations, but
123 vary in several physical attributes relevant to their response to changes in air temperature and
124 precipitation, including depth, surface area, watershed area, and water clarity (Table 1). Water
125 temperature and DO of the study lakes were monitored every 2–4 weeks during the open-water
126 season for periods ranging from 26 to 45 years (Table 1). Water temperatures were measured
127 using a handheld probe (XRX-620 CTD, RBR, Ottawa, ON, Canada) at 1 m depth intervals, and
128 DO was measured by Winkler titration at 5 m depth intervals (Stainton et al. 1977), from the lake
129 surface to bottom. In 2013, DO data was collected using an optode probe (4330F Aanderaa
130 Data Instruments, Fall River, MA, USA). Sampling and laboratory methods were consistent over
131 the entire study period. When changes in equipment or methods took place, vigorous
132 calibrations were performed to ensure data were comparable (Stainton et al. 1977, Schindler et
133 al. 1996a, Prairie et al. 2009)

134

135 *Air temperature and precipitation*

136 Mean annual and seasonal air temperature and precipitation were estimated using mean daily
137 air temperature and precipitation values collected at the Lake 239 meteorological station.
138 Annual means were calculated as the grand mean of all mean daily air temperature or
139 precipitation values in a given year, with air temperature calculated as a calendar year and
140 precipitation calculated as a water year (November 1–October 31). Seasonal mean air
141 temperature and precipitation for each year were calculated as the grand mean of all mean daily
142 air temperature or precipitation values for each of the following monthly groupings, which
143 roughly correspond to the four seasons at the ELA: March–May (Mar-May), June–August (Jun-
144 Aug), September–November (Sep-Nov), and December–February (Dec-Feb).

145

146 *Oxythermal habitat and lake surface temperatures*

147 Daily estimates of oxythermal habitat for each open-water season were obtained using water
148 temperature and DO profiles collected from each of the four study lakes (Fig. 1). Measured
149 water temperature and DO values were linearly-interpolated between sampling dates to obtain
150 daily profiles at each measurement depth. Next, we linearly-interpolated each of the daily water
151 temperature and DO profiles to 0.1 m depth intervals to obtain daily profiles at 0.1 m resolution.
152 For years where a lake was not sampled or had an insufficient number of summer sampling
153 dates, data from that lake were excluded. The daily 0.1 m resolution water temperature and DO
154 profiles were then used to calculate daily depths of ecologically-relevant isotherms and
155 oxyclines—the deepest depth at which a specific temperature or shallowest depth at which a
156 specific DO concentration were found in the water column. Isotherms and oxyclines represented
157 the theoretical upper thermal and lower oxygen habitat boundaries for lake trout, respectively.
158 For all years of data available from each lake, we calculated the daily depths of each isotherm
159 and oxycline representing optimal and usable lake trout habitat during each open-water season.
160 Optimal oxythermal habitat for lake trout was considered to be the volume of water bound
161 between temperatures $<10\text{ }^{\circ}\text{C}$ and $\text{DO}>6\text{ mg}\cdot\text{L}^{-1}$, while usable habitat was bound between

162 temperatures $<15\text{ }^{\circ}\text{C}$ and $\text{DO}>4\text{ mg}\cdot\text{L}^{-1}$ (Ferguson 1958, Coutant 1977, Evans et al. 1991, Ryan
163 and Marshall 1994, Evans 2007). The daily depths of isotherms and oxyclines corresponding to
164 optimal and usable habitat boundaries were converted to daily habitat volumes using lake-
165 specific bathymetry, and were presented as proportions of total lake volume that met the optimal
166 or usable habitat criteria. Specifically, we presented the oxythermal habitat volumes and
167 corresponding isotherm and oxycline depths when lake trout habitat was at its minimum each
168 year, typically occurring in late-summer or fall. When DO boundaries were shallower than
169 temperature boundaries, optimal or usable habitat was considered to be absent (eliminated).
170 Mean summer (Jun–Aug) surface water temperatures for each lake were calculated using daily
171 water temperatures at 1 m depth from the interpolated water temperature profile data.

172

173 *Thermal habitat phenology*

174 The phenology of key events defining the transitions between thermal habitat periods for lake
175 trout were defined using the existence of usable water temperatures ($<15\text{ }^{\circ}\text{C}$) for lake trout and
176 the presence of ice-cover (Fig. 1). For each year of data for each lake, four thermal habitat
177 periods, each representing a distinct ecological period for lake trout, were defined (Fig. 1). We
178 designated these four thermal periods for lake trout as: (1) Winter – a period of cold
179 temperatures ($1\text{--}4\text{ }^{\circ}\text{C}$), low light, and low lake production, defined as the days between fall ice-
180 on and the following spring ice-off; (2) Spring – a period of cool temperatures ($4\text{--}15\text{ }^{\circ}\text{C}$) when
181 lake trout feed heavily in the littoral zone of Boreal Lakes, defined as the period following spring
182 ice-off and lasting until the lake surface water temperatures reached $15\text{ }^{\circ}\text{C}$; (3) Summer – a
183 period of thermal stratification when water temperatures in the littoral zone exceed the usable
184 limit for lake trout, defined as the period when lake surface water temperatures are $\geq 15\text{ }^{\circ}\text{C}$; and,
185 (4) Fall – the period occurring as lake temperatures cool to $<15\text{ }^{\circ}\text{C}$ and lasting until fall ice-on.
186 This is the period when lake trout spawn. We were unable to directly assess changes in
187 seasonal lake trout habitat based on optimal water temperatures ($<10\text{ }^{\circ}\text{C}$) because lakes often

188 had already reached 10 °C by the time spring sampling began. Furthermore, Plumb and
189 Blanchfield (2009) have shown that the 15 °C better defines the depth use of lake trout in these
190 small lakes. Nevertheless, we found moderate–strong correlations between the dates that
191 surface water temperatures reached 10 °C and when they reached 15 °C for all lakes (Pearson
192 correlation: $r=0.48-0.60$, all $p<0.1$, allowing findings from changes in seasonality based on
193 usable thermal habitat to be generalized to optimal thermal habitat.

194

195 *Statistical analyses*

196 We used Mann-Kendall tests to determine if long-term, monotonic trends occurred in time-series
197 of annual and seasonal air temperatures and various lake trout habitat measures (Mann 1945,
198 Kendall 1955). Mann-Kendall tests were not applied to precipitation data because we knew *a*
199 *priori* that precipitation at the ELA followed a ~30 y cycle (Prairie et al. 2009). Where Mann-
200 Kendall tests indicated significant time-series trends, corresponding slopes were estimated
201 using Sen's slope (Sen 1968). We used a Levene's mean test of equal variance to determine if
202 variability in annual and seasonal estimates of air temperature and precipitation as well as lake
203 trout habitat measures changed over the course of the study, based on data from our longest
204 studied lake, Lake 239. Levene's tests involved comparing estimates of each measure taken
205 during the first (1970–1991) and second (1992–2013) halves of the 44 year study period. If a
206 monotonic trend was found for a given measure, we used the residuals in the Levene's test to
207 ensure the trend did not impact the analysis. Where a Levene's test indicated a significant
208 difference, we presented the change in variation between the first and second half of the study
209 as the standard deviation (SD) in the results. We used analysis of covariance (ANCOVA) to test
210 if seasonal air temperatures or annual precipitation had an effect on the phenology of thermal
211 habitat, minimum volumes of oxythermal habitat, and lake surface water temperatures within
212 each study lake. Finally, we tested if the probability that the complete elimination of optimal lake
213 trout habitat was increasing over time in each lake using logistic regression.

214 Assumptions of statistical models were tested as outlined in Zuur et al. (2010). Where
215 necessary, variables were transformed to meet assumptions of each statistical test. Due to the
216 inherently high variability of climate and limnological data, and the interpolations necessary to
217 produce our working dataset, we accepted a higher chance of type-1 error and considered
218 $p < 0.1$ as statistically significant for all analyses. All data processing, analyses, and figures were
219 completed in R (Version 3.2.1, R Development Core Team 2015).

220

221 Results

222 *Air temperature and precipitation*

223 Annual air temperatures at the ELA increased at a rate of $0.043 \text{ }^\circ\text{C}\cdot\text{y}^{-1}$ from 1970 to 2013,
224 representing a $1.84 \text{ }^\circ\text{C}$ increase in mean temperature, from $1.77 \text{ }^\circ\text{C}$ to $3.61 \text{ }^\circ\text{C}$ (Fig. 2a). Annual
225 temperatures were quite variable over the study period, ranging by $4.37 \text{ }^\circ\text{C}$, with a minimum of
226 $0.86 \text{ }^\circ\text{C}$ and maximum of $5.23 \text{ }^\circ\text{C}$, but this variability did not increase over the study period ($F_{1,42}$
227 $= 0.66$, $p = 0.42$). Changes in air temperature were most pronounced for Sep-Nov and Dec-Feb,
228 where they increased significantly at rates of $0.039 \text{ }^\circ\text{C}\cdot\text{y}^{-1}$ and $0.078 \text{ }^\circ\text{C}\cdot\text{y}^{-1}$, respectively. Air
229 temperatures during Mar-May and Jun-Aug periods did not show evidence for monotonic trends
230 over the study period (Fig. 2b). None of the seasonal air temperatures became more variable
231 over the study period (Spring $F_{1,42} = 0.58$, $p = 0.45$, Summer $F_{1,42} = 0.17$, $p = 0.68$, Fall $F_{1,42} = 0.73$,
232 $p = 0.40$, Winter $F_{1,42} = 0.58$, $p = 0.45$).

233 Unlike air temperature, annual precipitation did not exhibit a monotonic trend over time
234 (Fig. 2c), and was consistent with previous studies (Prairie et al. 2009) indicating that ELA
235 precipitation is part of a ~ 30 year cycle of wet and dry periods. During the study period, annual
236 precipitation ranged by $1.45 \text{ mm}\cdot\text{d}^{-1}$, from a minimum of $1.33 \text{ mm}\cdot\text{d}^{-1}$ to a maximum of 2.78
237 $\text{mm}\cdot\text{d}^{-1}$ (Fig. 2c). Generally, the climate was drier at the ELA during late 1970s and 1980s and
238 considered to be in a wet period during 1990s through the 2000s. Annual precipitation rates did
239 not become more variable over the study period ($F_{1,42} = 0.25$, $p = 0.62$) and neither did spring, fall,

240 or winter precipitation rates (Spring $F_{1,42}=0.50$, $p=0.48$, Fall $F_{1,42}=2.53$, $p=0.12$, Winter $F_{1,42}=1.41$, $p=0.24$). We did, however, find evidence that summer precipitation rates were more
241 variable in latter half of the study ($F_{1,42}=5.71$, $p=0.02$), where the SD of summer precipitation
242 increased from 0.53 to 0.95 mm•d⁻¹.
243

244

245 *Thermal habitat phenology*

246 The average length of the winter ice-covered season decreased over time, becoming 19 d
247 shorter in 2013 than it was in 1970 (Fig. 3). The length of winter also became more variable
248 during the second half of the study ($F_{1,42}=3.78$, $p=0.06$), where the SD of winter length was 4.35
249 d greater than in the first half of the study (Fig. 3). There was marginal, but non-significant
250 evidence that spring ice-off dates became earlier over time ($slope=-0.21$ d•y⁻¹, $p=0.11$). Ice-off
251 dates ranged by 42 d, with the earliest being on April 5, 2012 and latest on May 17, 1996. Six of
252 the seven earliest spring ice-off dates have occurred since 1999. Ice-off dates also become
253 more variable over time ($F_{1,42}=4.15$, $p=0.04$); the SD of ice-off dates increased by 3.80 d in the
254 second half of the study. In contrast, there was strong evidence that fall ice-on dates became
255 later over time ($slope=0.21$ d•y⁻¹, $p=0.002$), increasing by since 1970. Seven of the eight latest
256 ice-on dates have occurred since 1999. Fall ice-on dates ranged by 31 d, with the earliest on
257 November 4, 1991 and latest on December 1, 2009, but did not become more variable in the
258 second half of the study ($F_{1,42}=0.01$, $p=0.93$).

259 We did not find that summer for lake trout was starting (development of the 15 °C
260 isotherm) earlier over time in any of the study lakes (Fig. 4a), which is in agreement with the fact
261 that Mar-May air temperatures had not increased over time (Fig. 2b). We did find that the end of
262 summer (breakdown of the 15 °C isotherm) was persisting later into the fall (Fig. 4b),
263 corresponding to increases found in Sep-Nov air temperature (Fig. 2b). All study lakes showed
264 evidence that the end of the summer period was becoming later, and for the longest studied
265 lake, Lake 239, summers for lake trout were on average ending one week later in 2013 than in

1970 (Fig. 4b). Despite the summer lasting later into the year, we did not find that summers were getting longer over time (Fig. 3, 4c). This corresponded to our finding of the spring period becoming longer over the study (Fig. 3), and indicates that the summer for lake trout was shifting later into the year, but not getting longer (Fig. 4). Despite warming fall air temperatures, the fall season for lake trout did not get longer over time (Fig. 3). We found no evidence that the length of the spring ($F_{1,42}=1.35$, $p=0.25$) or fall ($F_{1,42}=0.02$, $p=0.89$) periods became more variable in the latter half of the study and only marginal, but non-significant evidence ($F_{1,42}=2.65$, $p=0.11$) that summer lengths became more variable during the second half of the study.

Spring ice-off and fall ice-on dates were strongly related to air temperatures experienced during their respective seasons (Fig. 5a, d). Overall, Mar-May and Sep-Nov air temperatures accounted for 75 % and 61 % of the variation in ice-off and ice-on dates, respectively. Ice-off was 4.38 d earlier for every 1 °C increase in average Mar-May air temperature (Fig. 5a). In contrast, warmer Sep-Nov air temperatures meant later ice-on dates, where ice formed 3.64 d later for every 1 °C increase in average Sep-Nov air temperature (Fig. 5d). The slopes (Lake x Spring: $F_{3,126}=0.57$, $p=0.63$) and intercepts (Lake: $F_{3,129}=0.39$, $p=0.76$) of the relationship between Mar-May air temperature and the warming of lakes to ≥ 15 °C (i.e. the start of the summer) did not differ among lakes. The start date of summer was significantly predicted by Mar-May air temperature ($est=-2.51$, $se=0.33$, $r^2=0.30$, $p<0.001$; Fig. 5b) and began 2.51 d earlier for every 1 °C increase in Mar-May air temperature. The number of days the lake was cool (<15 °C) following ice-off (i.e. length of the spring) was significantly predicted by Mar-May air temperature ($est=1.82$, $se=0.40$, $r^2=0.13$, $p<0.001$) and the slopes (Lake x Spring: $F_{3,126}=0.62$, $p=0.60$) and intercepts (Lake: $F_{3,129}=0.66$, $p=0.58$) did not differ among lakes. The spring period for lake trout became longer by 1.82 d for every 1 °C increase in Mar-May air temperature (Fig. 5c). Interestingly, the length of spring only decreased by 0.59 d for each day that the ice retreated later into spring ($est=0.59$, $se=0.07$, $r^2=0.35$, $p<0.001$, meaning in years

292 when ice-off occurred earlier, the lake took longer to reach 15 °C. The length of spring periods
293 greatly varied in the four study lakes, ranging from less than one week (5 d) to almost two
294 months (59 d) (Fig. 5c). In the fall season, the slopes (Lake x Fall: $F_{3,126}=0.25$, $p=0.86$) and
295 intercepts (Lake: $F_{3,129}=0.60$, $p=0.62$) of the relationship between the end of summer/start of fall
296 and Sep-Nov air temperature did not differ among lakes. The end of the summer (breakdown of
297 the 15 °C isotherm) was significantly predicted by Sep-Nov air temperatures ($est=1.77$, $se=0.38$,
298 $r^2=0.14$, $p<0.001$), where summer lasted 1.77 d longer for every 1 °C increase in Sep-Nov air
299 temperature (Fig. 5e). The length of fall was also significantly predicted by Sep-Nov air
300 temperature ($est=2.14$, $se=0.43$, $r^2=0.15$, $p<0.001$); the slopes (Lake x Fall: $F_{3,126}=0.27$, $p=0.84$)
301 and intercepts (Lake: $F_{3,129}=0.43$, $p=0.73$) of this relationship did not differ among lakes (Fig. 4f).
302 The fall period for lake trout lasted 38–74 d, and increased in length by 2.15 d for every 1 °C in
303 Sep-Nov air temperature (Fig. 5f).

304

305 *Summer surface water temperatures*

306 We found an increase in mean summer surface water temperature of 0.03 °C·year⁻¹ in the
307 longest sampled lakes (39–43 y), while those sampled for shorter time periods (the last 26–27
308 y) showed no trends (Fig. 6a). The surface water temperatures of all lakes were highly related to
309 Jun-Aug air temperatures, which explained 78 % of the variation in summer surface water
310 temperature (Fig. 6b). Because of the similarly strong relationships between Jun-Aug air
311 temperature and summer surface water temperature, we expect that Lake 373 and Lake 442
312 would have shown similar increases in surface water temperature if monitored for longer
313 periods. We also found that surface water temperatures in Lake 239 were more variable during
314 the latter half of the study period ($F_{1,42}=3.48$, $p=0.07$) where the SD was 0.52 °C greater than
315 observed during the first half of the study. Although the length of summer was not found to
316 increase over time, this variable was only weakly correlated to Jun-Aug air temperature (Fig.
317 6c). Instead we found that the length of summer was better predicted by Mar-May and Sep-Nov

318 air temperatures, which promote the development and breakdown of the 15 °C isotherms that
319 define the start and end of summer for lake trout (Fig. 4b, e).

320

321 *Oxythermal habitat*

322 We did not test for monotonic trends in the maximum extent of isotherm, oxyclines, or minimum
323 habitat volumes because these measures are highly dependent on precipitation and watershed
324 processes that were cyclic over the study period (Fig. 2c, d, Fig. 7). Qualitative observation of
325 Figure 7, specifically the longest datasets from Lake 239 and Lake 224, suggest that the depth
326 of thermal barriers for lake trout were deepest (most intense) when precipitation was low in the
327 late 1980s and shallowest (i.e. least intense) in the 1990s and 2000s during wet cycles (Fig. 2c,
328 d). This was corroborated by the fact that annual maximum depths of the 10 °C and 15 °C
329 isotherms were significantly predicted by annual precipitation in three of four study lakes (Table
330 2). The maximum depths of the 10 °C isotherm were less variable (SD decrease of 0.31 m) in
331 the latter half of the study ($F_{1,38}=3.95$, $p=0.05$); however, this was not the case for the 15 °C
332 isotherm ($F_{1,38}=1.26$, $p=0.26$).

333 Generally, differences in isotherm depths among lakes were predicted by water
334 transparency; the clearest (Lake 224) and darkest (Lake 442) lakes had the deepest and
335 shallowest isotherms, respectively (Fig. 7a, Table 1). Because of the control of precipitation on
336 runoff, annual precipitation predicted the depths of the annual maximum 10 °C and 15 °C
337 isotherms in three study lakes, Lake 239 being the exception. For the 10 °C isotherm, the
338 slopes of the relationships with annual precipitation did not differ (Lake x Precipitation:
339 $F_{3,102}=0.95$, $p=0.42$), while intercepts did (Lake: $F_{3,105}=55.59$, $p<0.001$) among lakes. For the 15
340 °C isotherm, slopes of the relationships with annual precipitation differed among lakes (15 °C
341 isotherm: Lake x Precipitation: $F_{3,102}=3.00$, $p=0.03$). These differences in slopes and intercepts
342 indicated that individual linear regressions should be run for each lake to individually assess the
343 relationship between maximum isotherm depths and annual precipitation (see Table 2).

344 The annual maximum extent (i.e. minimum depths) of the $6 \text{ mg}\cdot\text{L}^{-1}$ and $4 \text{ mg}\cdot\text{L}^{-1}$
345 oxyclines were relatively constant over the study period, except for the $4 \text{ mg}\cdot\text{L}^{-1}$ oxycline in Lake
346 239, which was highly variable throughout. Similar to trends observed in maximum isotherm
347 depth, minimum oxyclines were shallowest (i.e. largest low oxygen zones) during wet periods
348 and deepest (i.e. smallest low oxygen zones) during dry periods of the precipitation cycle (Fig.
349 2c, d, Fig. 7b). The maximum extent of the $6 \text{ mg}\cdot\text{L}^{-1}$ oxycline became more variable over the
350 study ($F_{1,38}=2.93$, $p=0.09$), where its SD increased by 1.42 m. In contrast, the maximum extent
351 of the $4 \text{ mg}\cdot\text{L}^{-1}$ oxycline was not more variable during the second half of the study ($F_{1,38}=0.08$,
352 $p=0.78$).

353 Temporal changes in minimum annual oxythermal habitat volumes, reported as a
354 proportion of total lake volume that met optimal or usable habitat requirements of lake trout,
355 generally followed the cyclic pattern of precipitation (Fig. 7c). At their annual minimum, usable
356 habitat for lake trout generally accounted for 20 % to 50 % of lake volume (Fig. 7c). All study
357 lakes had complete loss of optimal habitat during the study period, but it occurred most
358 frequently in the two darkest lakes (Lakes 442 and 239). In the longest studied lake, Lake 239,
359 complete elimination of optimal habitat became more prevalent over time (Logistic regression:
360 $est=0.07$, $se=0.03$, $z=2.22$, $p=0.03$), but not in Lakes 442, 224 or 373 (Fig. 8). Optimal habitat
361 for lake trout in Lakes 442 and 239 were eliminated for periods ranging from one week up to 75
362 and 100 d, and in Lake 442, optimal habitat has been completely eliminated each year since
363 1995 (Fig. 8). The minimum amount of optimal oxythermal habitat available to lake trout each
364 year was more variable (SD increase of 6 % total lake volume) in the latter half of the study ($F_{1,38}$
365 $=4.38$, $p=0.04$), but this was not the case for usable habitat ($F_{1,38}=2.11$, $p=0.17$).

366

367

368 **Discussion**

369 We demonstrate that lake trout habitat in small Boreal Shield lakes undergoes distinct changes
370 in quantity and phenology as air temperature increases and precipitation rates vary. Most
371 notably, we show that despite summer surface water temperatures increasing, the length of
372 summer (i.e. period when lake surface temperatures exceed 15 °C), did not expand over time.
373 Instead, evidence of earlier ice-offs, longer springs, and the cooling of lakes to <15 °C occurring
374 later in the fall, suggests that the summer period has shifted later into the year. Due to the later
375 onset of fall, ice-on became delayed, and paired with earlier ice-offs, the winter ice-covered
376 period became shorter over time. Moreover, we show that the elimination of optimal habitat
377 occur in all study lakes to various degrees, but most commonly in darker lakes. Elimination of
378 optimal habitat also became more common over time in the longest studied lake. Lastly, the
379 minimum volume of optimal oxythermal habitat available for lake trout during the late-summer
380 became more variable over time, while usable oxythermal habitat did not, suggesting optimal
381 habitat may be more sensitive to climate change. Together our results suggest that the warmer
382 and more extreme air temperatures forecasted should impact the ecology of lake trout in Boreal
383 Shield lakes, which is heavily tied to seasonal variations in water temperature (Martin 1952,
384 1970, Blanchfield et al. 2009b, Plumb and Blanchfield 2009). Moreover, for lakes with marginal
385 suitable habitat, especially those near the southern extent of lake trout's distribution, warmer
386 conditions may result in more frequent elimination of optimal oxythermal habitat during late-
387 summer, potentially impacting the ability of these lakes to support lake trout.

388 Our findings of increasing annual air temperatures were expected, as these data were
389 extensions of those previously published (Schindler et al. 1996a, Prairie et al. 2009), and are in
390 agreement with long-term data from the northeastern Boreal Shield (Keller 2007). Increases in
391 annual air temperature were driven by warmer seasonal air temperatures during Dec-Feb and
392 Sep-Nov, which provide a likely explanation for corresponding trends found in ice phenology.
393 Higher air temperatures in late winter increase the rate of snow melt, which acts to insulate ice.
394 Once snow is removed, light penetrates and warms water below the ice, rapidly degrading it

395 (Gao and Stefan 1999, Wetzel 2001, Jansen and Hesslein 2004, Shuter et al. 2013). Although
396 not significant, marginal evidence for a monotonic trend in Mar-May temperatures (Mann
397 Kendall $p=0.18$), suggests that temperatures during this period could also be increasing at more
398 variable rate than those observed in Sep-Nov and Dec-Feb, but still contributing to the
399 increasing the rate of ice melt and advance the timing of ice-off dates (Shuter et al. 2013). In
400 contrast, warmer Sep-Nov air temperatures delay the cooling of lakes, resulting in later fall
401 turnover and cooling of surface waters to 0 °C, slowing ice-formation (Raymond Hesslein
402 *unpublished data*, Gao and Stefan 1999, Shuter et al. 2013). Mean depth has also been found
403 to be a predictor of ice-phenology (Shuter et al. 2013), although not relevant to our study of the
404 same lakes over time, it suggests that deeper lakes may have more delayed ice-formation due
405 to the larger volume of water to be cooled. Indeed, the changes in ice-phenology observed here
406 are in agreement with several studies that have found warming air temperatures to expedite
407 spring ice-melt and delay fall ice-formation, resulting in longer open-water seasons in north-
408 temperate regions (Schindler et al. 1990, Magnuson et al. 2000, Futter 2003, Keller 2007,
409 Latifovic and Pouliot 2007, Benson et al. 2012, Sharma and Magnuson 2014, Sharma et al.
410 2016). Winter (i.e. period of ice-cover) is often recognized to be a period when cold water
411 temperatures slow metabolic processes and limit growth (Kerr 1971); however, indication that
412 lake trout feed almost exclusively on fish during this period (Martin 1954), and evidence that
413 lake trout may grow during this period (Eck and Wells 1986), suggests that winter may be
414 underappreciated growth period in small lakes lacking pelagic prey fish, such as our study lakes
415 (Blanchfield et al. 2009b).

416 Spring periods for lake trout became longer over time. This unexpected extension of the
417 spring period during years with earlier ice-offs was likely caused by the differential impact of
418 spring air temperature on ice-off dates (start of spring) and heating of surface waters to 15 °C,
419 signifying the start of summer for lake trout (Plumb and Blanchfield 2009). Although the start
420 dates of both spring and summer were negatively correlated to spring air temperature (i.e.

421 spring and summer started both earlier during warmer springs), the slope of the relationship for
422 the start date of summer was lower than for the start date of spring. Consequently, spring
423 periods were longer in years with earlier ice-offs and warmer air temperatures. We suspect this
424 observation is because when the ice comes off the lake earlier in spring, air temperatures are
425 relatively cooler, with a greater chance for cold night temperatures than if ice were to come off
426 later in spring, where air temperatures would be greater. Furthermore, differences in sun angle
427 and the longer day lengths that occur later in spring would also promote more rapid heating of
428 lakes in years with later spring ice-off (Shuter et al. 2013). These findings of longer springs are
429 contrary to the modelling study by Jansen and Hesslein (2004), which indicated that increases
430 in air temperature would reduce the number of days during spring and early summer when lakes
431 were cool. This extension of the spring period is particularly important for lake trout occupying
432 lakes without pelagic prey fish (Vander Zanden and Rasmussen 1996). In these lakes, lake trout
433 are highly dependent on their ability to access to littoral forage fish (i.e. minnows) and benthic
434 invertebrates when surface water temperatures are cool to achieve sufficient growth for
435 reproduction in fall (Martin 1952, 1970, Plumb et al. 2014). Moreover, King et al. (1999) found
436 that in years when thermal stratification was earlier, lake trout had reduced growth, likely due to
437 reduced access to littoral energy without thermal consequence. This is further supported by
438 evidence that lake trout typically occupy the upper portions of the water column until surface
439 waters reach 15 °C (Plumb and Blanchfield 2009) and achieve lower growth with reduced use of
440 littoral habitat (Plumb et al. 2014). Therefore an expansion of the spring period could be
441 important for tempering the effects of future warming in lakes where littoral prey fish are the
442 main source of energy for lake trout.

443 Our finding that the summer period has not lengthened over time is likely a result of
444 changes occurring to its shoulder seasons. The observed delay in the onset of fall was only long
445 enough to offset the lengthening of spring that came as a result of earlier ice-offs, in turn
446 preventing a lengthening of the summer period. This finding is contrary to studies that have

447 predicted longer stratified periods with warming (Robertson and Ragotzkie 1990, De Stasio et
448 al. 1996); however, this disconnect could be because we looked at the existence of an
449 ecologically relevant water temperature (15 °C) to define summer, not a planar thermocline. A
450 recent study by Kraemer et al. (2015), which evaluated long-term stratification data from 26
451 lakes from various latitudes, suggested that deep lakes should be more susceptible to longer
452 stratified periods. The lakes studied here were relatively shallow compared to most lake trout
453 lakes, suggesting longer stratified period may be less of a concern to these lake types. Another
454 potential explanation for the lack of trend in the length of the summer period could be that fall air
455 temperatures were not always correlated to spring temperatures within a given year. However,
456 as air temperatures continue to rise and spring ice-off continues to become earlier, the number
457 of days where lake surface water temperatures exceed the useable limit for lake trout may
458 inevitably increase, especially if summer air temperatures in the Boreal Shield increase, as
459 predicted by some recent climate models (Colombo et al. 2007, IPCC 2014).

460 Increases in Sep-Nov air temperatures corresponded to lakes cooling to <15 °C later
461 and delaying the onset of the fall season for lake trout. Therefore, the shift of the summer
462 period, caused by longer springs and later arrival of fall conditions could also have biological
463 implications to lake trout. Lake trout is a fall spawner whose migration onto shoals is triggered
464 when water temperatures reach 12 °C or lower (Redick 1967). Therefore, later fall cooling of
465 lakes would delay spawning of lake trout. Indeed, there is evidence that the peak of lake trout
466 spawning in several ELA lakes is now occurring 10 days later than it was in the late 1970s
467 (Michael Rennie, *unpublished data*). This delay in the timing of spawning and evidence for
468 shorter ice-covered periods could result in fry being less developed in spring. This reduction in
469 development and the potential for earlier spring phytoplankton blooms (Peeters et al. 2007),
470 may lead to mismatches between feeding ability of fry and peak food availability, potentially
471 reducing recruitment (Cushing 1969, 1990).

472 Variations in minimum optimal and usable oxythermal habitat followed cyclic variations in
473 precipitation, where deeper maximum thermal barriers (10 °C and 15 °C isotherms) occurred in
474 years with reduced precipitation. The link between the depth of usable and optimal isotherms
475 and annual rates of precipitation suggests that future changes (either increases or decreases) in
476 precipitation for the Boreal Shield will alter the thermal barriers for lake trout (Fee and Hecky
477 1996, Schindler et al. 1996a). But these precipitation induced changes will also depend on the
478 magnitude of precipitation changes and potential increases in evaporation (Colombo et al. 2007,
479 Keller 2007). The three study lakes that had smallest watershed areas (Lakes 224, 442, 373) all
480 responded relatively rapidly to annual changes in precipitation (i.e. on an annual basis);
481 however Lake 239, which has a watershed 2–4 larger than the other study lakes, did not show a
482 similar response. Additionally, the Lake 239 watershed has three sub-basins each containing
483 wetlands that increase the memory of the watershed and delay the response of the lake to
484 precipitation (Schindler et al. 1996a). Potential decreases in late-summer isotherm depth that
485 may occur if precipitation increases may also be offset by the shift of the stratified period later
486 into fall, which will promote habitat-limiting isotherms to become deeper and potentially reach
487 deeper maximum depths. Further, the delayed timing of fall turnover may result in a greater
488 extent of low DO in the future, which will pose additional constraints on the volume of optimal
489 habitat for lake trout (Fig. 6). Together, larger low DO zones and potentially deeper late-season
490 maximum thermal barrier depths may increase the exposure of lake trout to non-optimal
491 conditions.

492 All lakes experienced complete loss of optimal oxythermal habitat for lake trout at least
493 once during the study. In most years, optimal habitat was nearly or completely eliminated from
494 some of the study lakes and this became more common over time in the longest study lake.
495 Large reductions or elimination of habitat can force lake trout to occupy habitat outside of their
496 thermal or DO optima, which can have metabolic implications (Gibson and Fry 1953, Evans
497 2007). The importance of optimal habitat is highlighted from the fact that several lake trout

498 populations have become extinct from central and eastern Ontario lakes where optimum
499 summer habitat volumes were absent or limited (MacLean et al.1990), and that lake trout
500 productivity declines as volume of suitable thermal habitat decreases (Christie and Regier
501 1988). We suspect that the presence of *Mysis* in our study lakes provides an important energy
502 subsidy allowing lake trout to survive in lakes with marginal habitat. In other studies of lake trout
503 occupying small lakes, lake trout have been found to use zooplankton as an alternative food
504 source during thermal stratification (Martin 1952, Konkle and Sprules 1986, VanderZanden and
505 Rasmussen 1996).

506 Recent studies have suggested that greater temperature variation and shifts in
507 skewness towards warmer temperatures may amplify or have greater impacts on the metabolic
508 function of ectotherms than increases in mean temperature alone (Deutsch et al. 2008,
509 Paaijmans et al. 2013, Vasseur et al. 2014). We did not find evidence that air temperatures,
510 annually or seasonally, became more variable over time. The lack of evidence for increasing air
511 temperature variation may be because we used grand means of daily mean air temperatures
512 calculated over large scales (e.g. year or four month periods), which may have dampened any
513 increases in variation occurring at shorter scales (e.g. days or weeks). Furthermore, our study
514 did not evaluate if changes in maximum or minimum temperatures occurred, which would be a
515 valuable avenue for future work. Interestingly, despite inconclusive findings for air temperature,
516 we show that variability in some temperature-driven measures of lake trout habitat did increase
517 over time. The length of winter (ice-cover), ice-off dates and summer surface water
518 temperatures were all more variable during the latter half of the study. Interestingly, minimum
519 optimal oxythermal habitat became more variable over time, while usable oxythermal habitat did
520 not, suggesting that optimal habitat may be more sensitive to climate change. With evidence
521 that lake trout behaviour in these lake types follows usable habitat (Plumb and Blanchfield
522 2009), this suggest that lake trout growth, which is maximized at 10 °C (Christie and Regier
523 1988), may be more impacted by warming than metabolic function, which is maximized at 15 °C

524 (Kelly et al. 2014). Moreover, this greater year-to-year variability in the amount and phenology of
525 habitat suggests that lake trout will need to be highly adaptable in their use of littoral habitat and
526 prey to minimize exposure to warm water (Plumb et al. 2014, Tunney et al. 2014). Indeed,
527 temporal studies evaluating how individual populations adjust their resource use in response to
528 changes in habitat availability will be important for understanding how the growth and
529 abundance of lake trout and other cold-water fish respond to future warming.

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531 **Acknowledgments**

532 The authors thank the many students and staff who have attributed to the ELA's long-term
533 database, the International Institute for Sustainable Development, Experimental Lakes Area
534 (IISD-ELA) and Fisheries and Oceans Canada for providing access to data. We thank Ken
535 Beaty and Ray Hesslein for valuable discussions while preparing the manuscript and two
536 anonymous reviewers whose comments improved the manuscript. This work was funded by
537 NSERC, The W. Garfield Weston Foundation, Fish Futures Manitoba, DeBeers Canada, and
538 the University of Manitoba.

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714 **Table 1.** Physical characteristics of study lakes, including surface area (A_s ; ha), volume (V ; m^3), maximum depth (Z_{max} ; m), watershed
 715 area (A_w ; ha), watershed to surface area ratio (A_w/A_s), light attenuation coefficient ($mE_{inst} \cdot m^{-1} \cdot sec^{-1}$), and secchi depth (m).

Lake	Period sampled	A_s	V	Z_{max}	A_w	A_w/A_s	Attenuation coefficient ¹	Secchi depth ¹
224	1974–2013	25.9	3.0×10^6	27.4	97.5	3.8	0.29	6.5
239	1970–2013	54.3	5.7×10^6	30.4	393.3	7.2	0.65	4.0
373	1986–2013	27.3	3.0×10^6	20.8	80.6	3.0	0.38	6.3
442	1987–2013 ²	16.0	1.4×10^6	17.8	161.0	10.1	0.56	4.5

716 ¹ Average of all data available for each lake which includes data for all seasons, but only limited data from winter. ² Dissolved oxygen

717 data with sufficient resolution only collected 1995 onwards.

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718 **Table 2.** Results of linear regressions testing for relationships between the annual estimates of the maximum depth of the thermal
 719 barrier for lake trout and mean annual precipitation. Individual regressions were performed because significant differences because,
 720 significant differences in slopes or intercepts were found for both isotherm measures (see Results for ANCOVA statistics).

Lake	Measure	<i>Estimate</i>	<i>Standard error</i>	<i>df</i>	<i>t-value</i>	<i>p-value</i>	<i>r</i> ²
224	15 °C isotherm	-1.92	0.37	28	-5.16	<0.001	0.47
	10°C isotherm	-1.95	0.67	28	-1.50	0.007	0.20
239	15 °C isotherm	-0.54	0.36	37	-3.93	0.14	0.03
	10 °C isotherm	-0.54	0.53	37	-4.85	0.32	0.00
373	15 °C isotherm	-1.35	0.34	21	-2.90	<0.001	0.40
	10 °C isotherm	-1.56	0.95	21	-1.02	0.08	0.10
442	15 °C isotherm	-1.29	0.27	16	-1.79	<0.001	0.57
	10 °C isotherm	-1.16	0.53	16	-2.17	0.04	0.18

721 **Bold** values are significant at $p < 0.1$.

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722 **Figure captions**

723 **Figure 1.** Schematic illustrating the seasonal phenology of usable lake trout habitat in Boreal
724 Shield lakes, as defined in the current study. Winter was the period of ice-cover, when lake
725 temperatures are between 1 and 4 °C. Fall and spring were the periods before and after ice-
726 cover when lake surface water temperatures are <15 °C. Summer is the period between spring
727 and fall, when lake surface water temperatures are ≥15 °C. During fall, winter, and spring, cool
728 water temperatures allow lake trout to access littoral prey sources without thermal
729 consequence. During summer, littoral zone temperatures are above the usable threshold for
730 lake trout (≥15 °C) and deep water is low in dissolved oxygen (DO; <4 mg L⁻¹), forcing lake trout
731 to reduce use of the littoral zone and deep hypolimnetic regions to avoid unusable habitat. Low
732 DO zones also occur during winter, but this is less constraining as no upper thermal boundary
733 exists. Low DO zones are replenished when lake waters mix during spring and fall turnovers.

734
735 **Figure 2.** Long-term variations in (a) mean annual air temperature, (b) seasonal air
736 temperatures (c) mean annual precipitation, and (d) seasonal precipitation since 1970 collected
737 at the meteorological station within the Experimental Lakes Area, northwestern Ontario,
738 Canada. For air temperature, a linear trend line and corresponding slope estimate are present in
739 plots where a Mann-Kendall test indicated a significant monotonic trend at $p < 0.1$. Because
740 precipitation follows ~30 year cycle in the region, a loess curve has been used to visualize cyclic
741 patterns in precipitation.

742
743 **Figure 3.** Long-term variations in the proportion of each thermal season (as defined in Fig. 1)
744 for lake trout based on our longest studied lake, Lake 239, located within the Experimental
745 Lakes Area. Trend lines and corresponding Sen's slope estimate are present in plots where a
746 Mann-Kendall test indicated a significant monotonic trend at $p < 0.1$.

747

748

749 **Figure 4.** Long-term variations in the phenology of lake trout thermal habitat constraint in four
750 small boreal shield lakes within the Experimental Lakes Area, including (a) start date of summer
751 (i.e. date that the 15 °C isotherm develops), (b) the end date of summer (i.e. date that the 15 °C
752 isotherm breaks down),, and (c) length of summer (i.e. number of days with a 15 °C isotherm). A
753 trend line and corresponding Sen's slope estimate are present in plots where a Mann-Kendall
754 test indicated a significant monotonic trend at $p < 0.1$. The label on the left of each plot indicates
755 the individual study lake. The y-axes of among lakes are scaled the same so that differences in
756 magnitude can be compared.

757

758 **Figure 5.** Relationships between spring and fall air temperature and timing of important
759 limnological events in four small Boreal Shield lakes located within the Experimental Lakes Area
760 during 1970–2013. Panels a–c are relationships between spring air temperature and (a) end
761 date of winter (i.e. spring ice-off date), (b) start date of summer (i.e. date that the 15 °C isotherm
762 develops), (c) length of spring (i.e. number of days between end of winter and start of summer).
763 Panels d–e are relationships between fall air temperature and (d) start date of winter (i.e. fall
764 ice-on date), (e) end date of summer (i.e. date that the 15 °C isotherm breaks down), (f) length
765 of fall (i.e. number of days between end of summer and start of winter).

766

767 **Figure 6.** Long-term variations in (a) surface (1 m depth) water temperature and relationships
768 between summer air temperature and (b) surface water temperature and (c) summer length, in
769 four small boreal shield lakes within the Experimental Lakes Area. A trend line and
770 corresponding statistics are present in plots where a Mann-Kendall test or regression indicated
771 a significant relationship at $p < 0.1$.

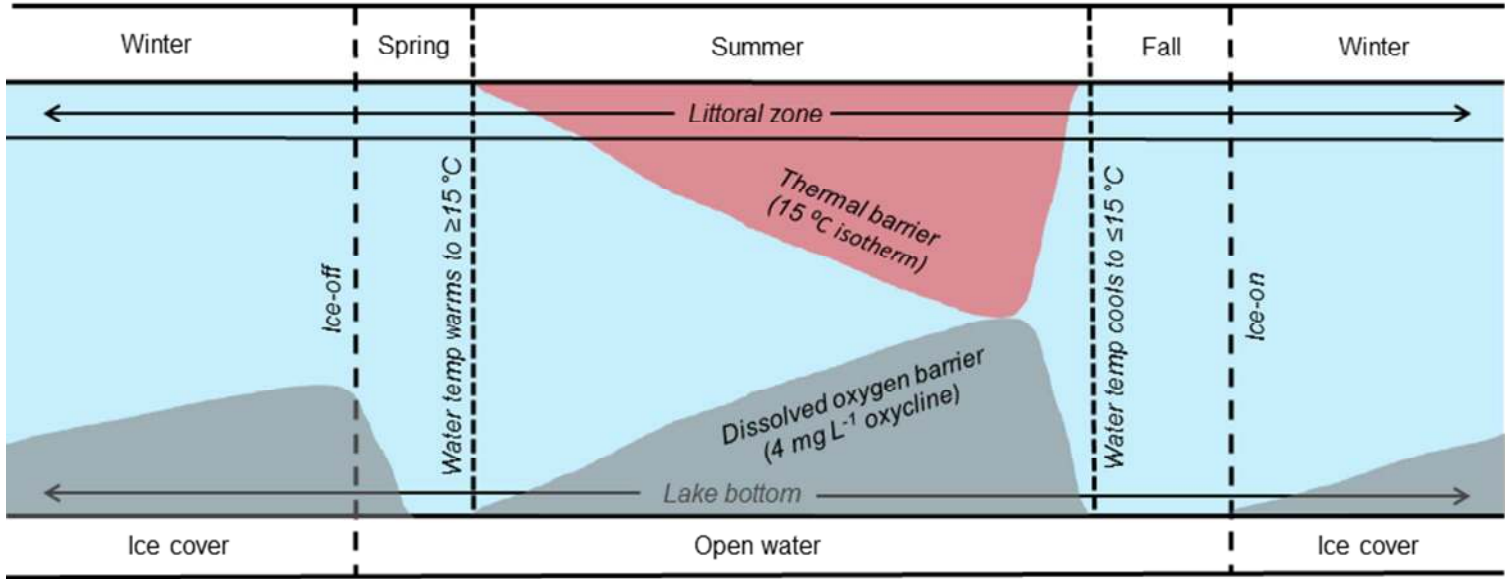
772

773 **Figure 7.** Long-term variations in theoretical thermal and dissolved oxygen habitat boundaries
774 that correspond to the maximum extent of habitat oxythermal constraint for lake trout in four
775 small boreal shield lakes within the Experimental Lakes Area during 1970–2013. Solid lines and
776 points refer to theoretical usable lake trout thermal habitat (panel a - 15 °C isotherm) and
777 dissolved oxygen (panel b - 4 mg•L⁻¹ oxycline) boundaries and corresponding habitat volumes
778 (panel c). Dashed lines and hollow points refer to theoretical optimal lake trout thermal habitat
779 (panel a - 10 °C isotherm) and dissolved oxygen (panel b - 6 mg•L⁻¹ oxycline) boundaries and
780 corresponding habitat volumes (panel c). Horizontal dot-and-dash lines on panel “b” indicate the
781 bottom of each lake and in panel “c” indicate zero lake volume meeting usable or optimal habitat
782 criteria.

783

784 **Figure 8.** Variations of the number of days each year where optimal summer oxythermal habitat
785 (water temperatures <10 °C and DO >6 mg•L⁻¹) for lake trout was eliminated in four small Boreal
786 Shield lakes within the Experimental Lakes Area.

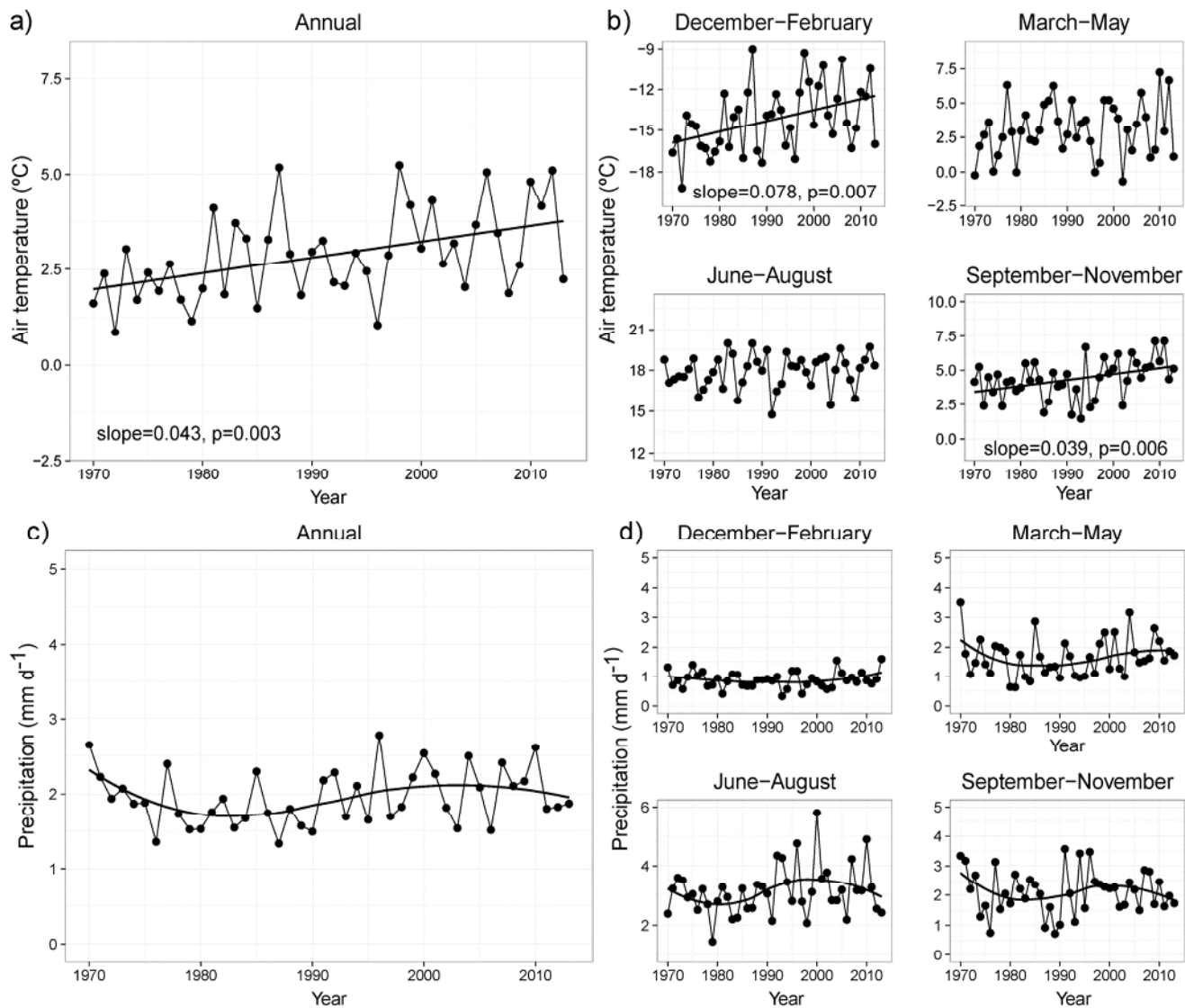
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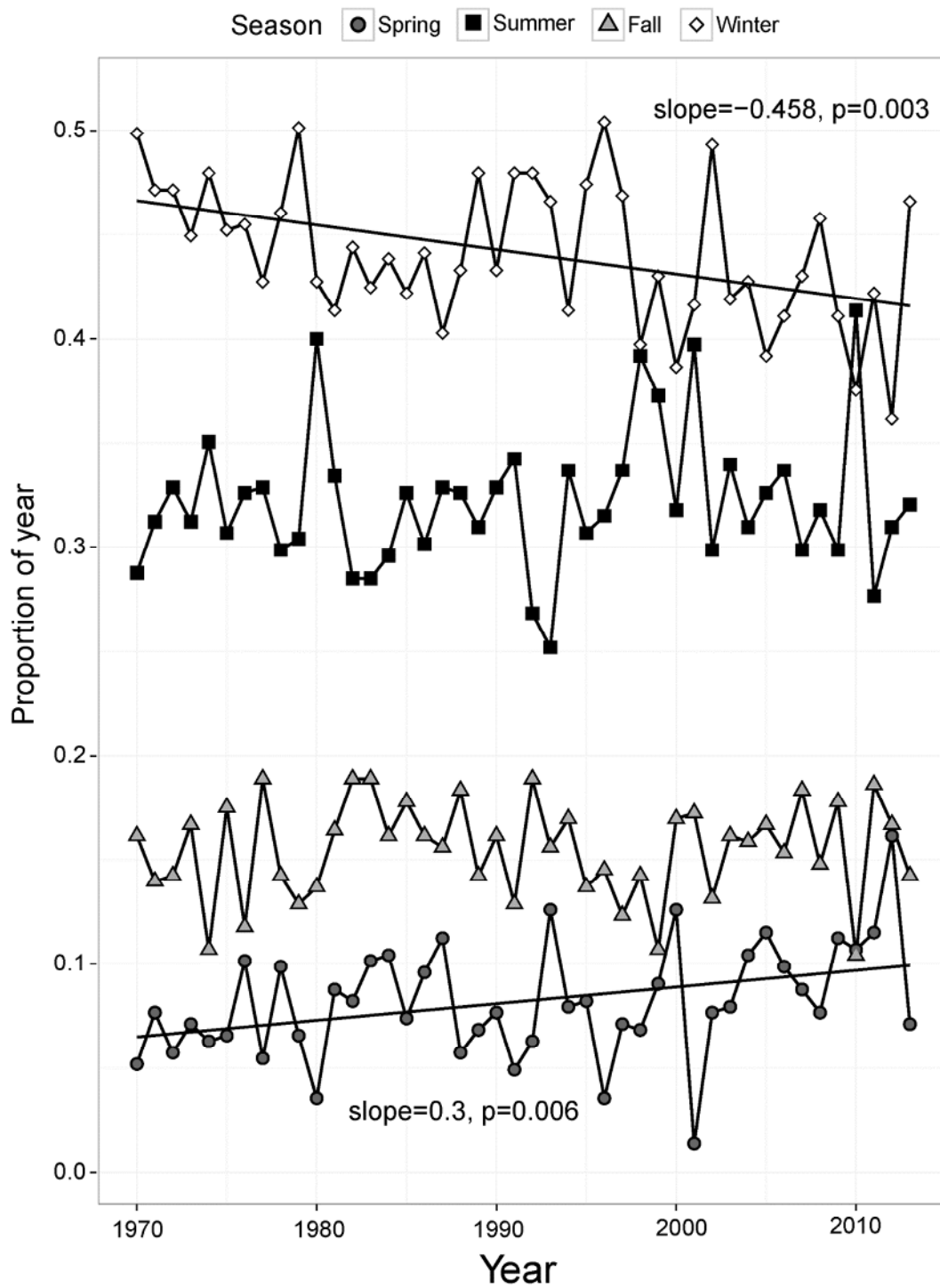
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789 Figure 1.

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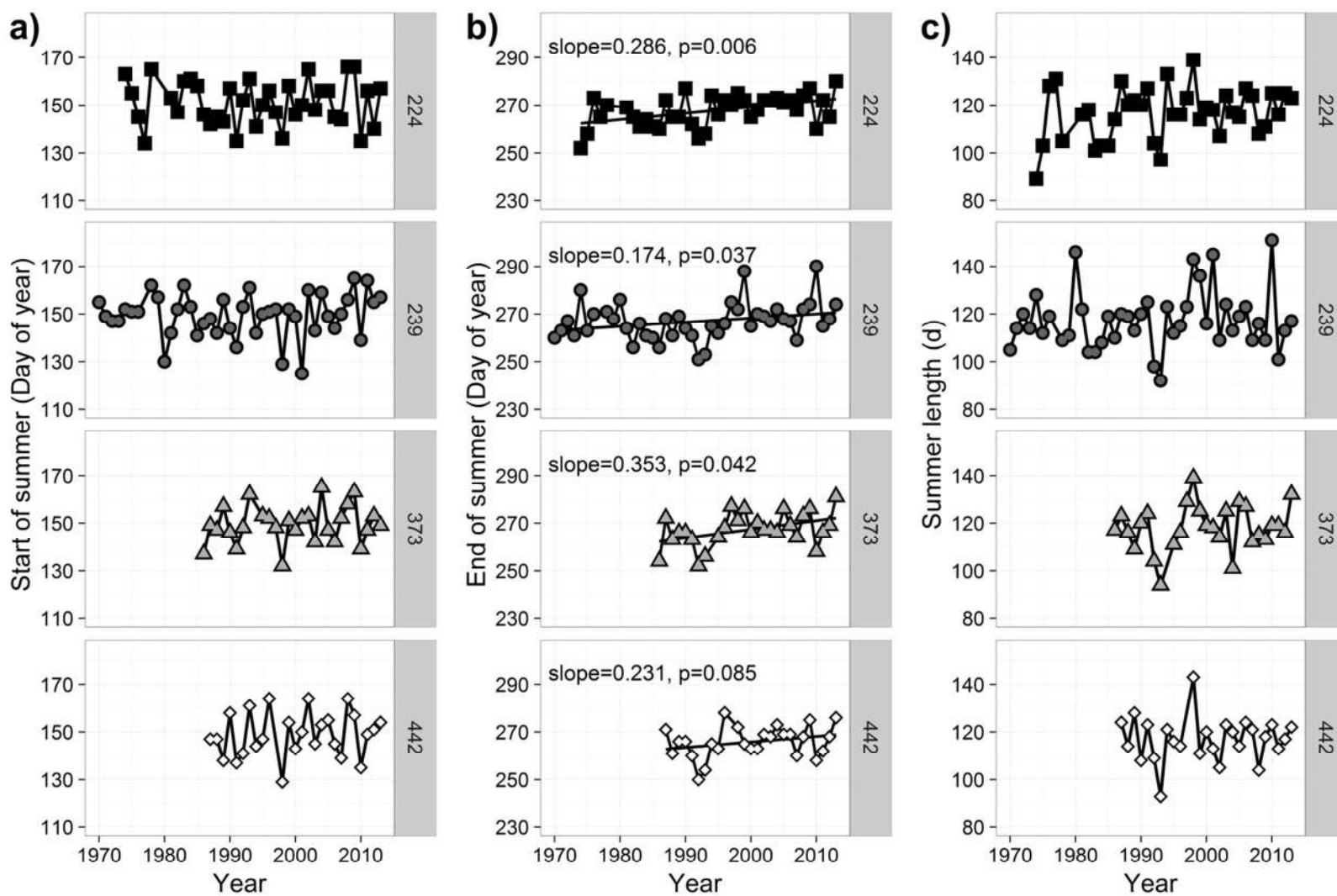


790 Figure 2



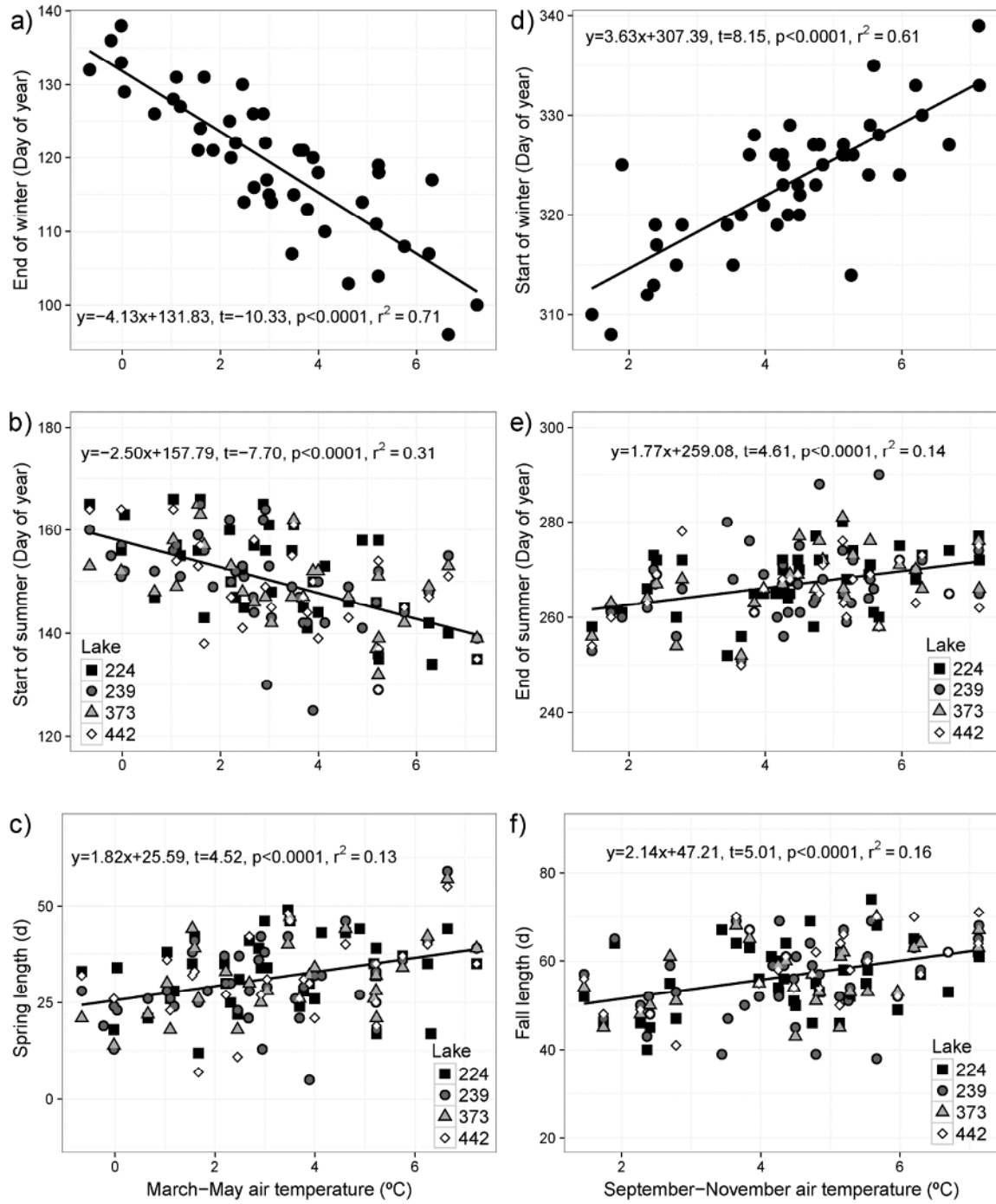
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792 Figure 3



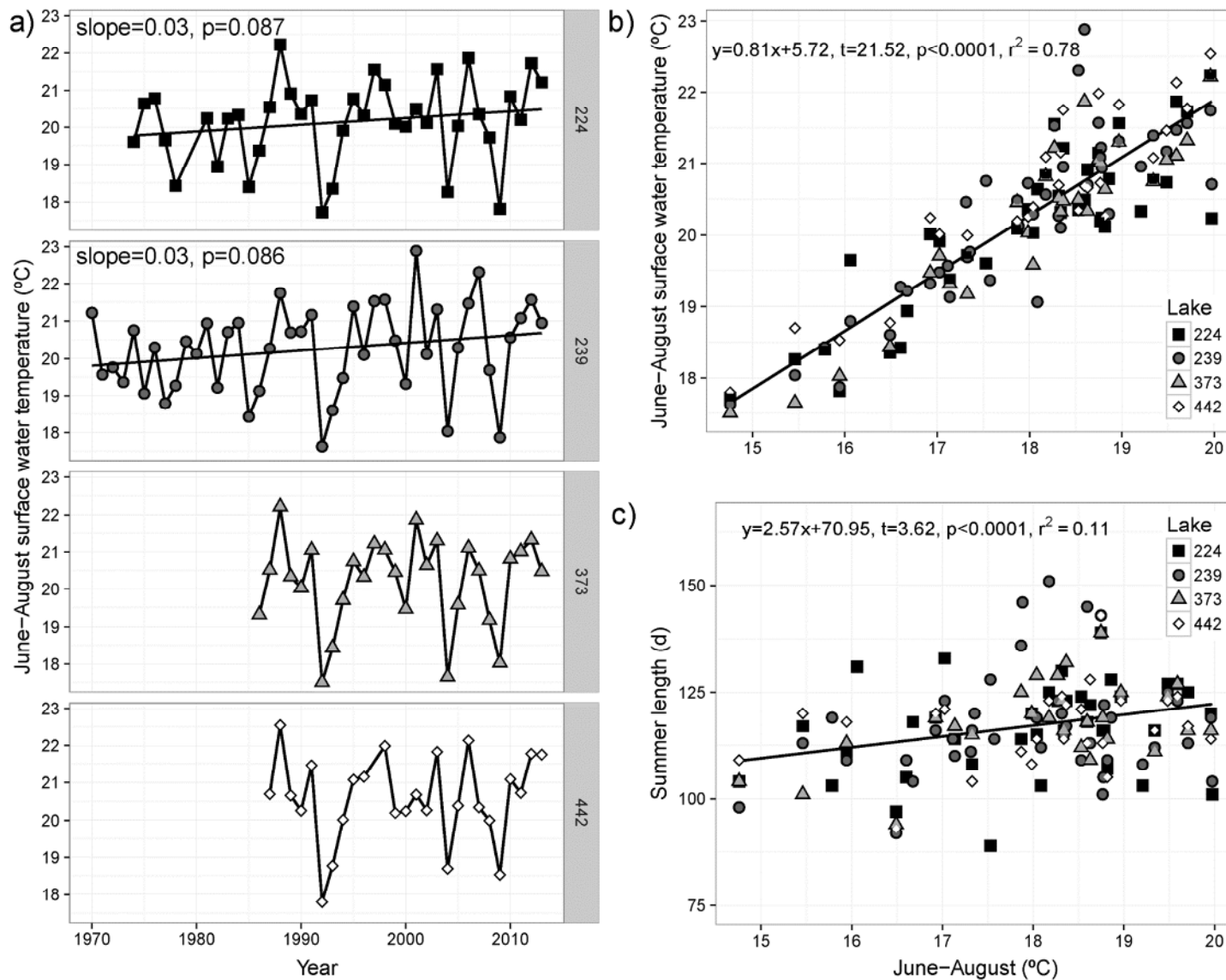
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794 Figure 4

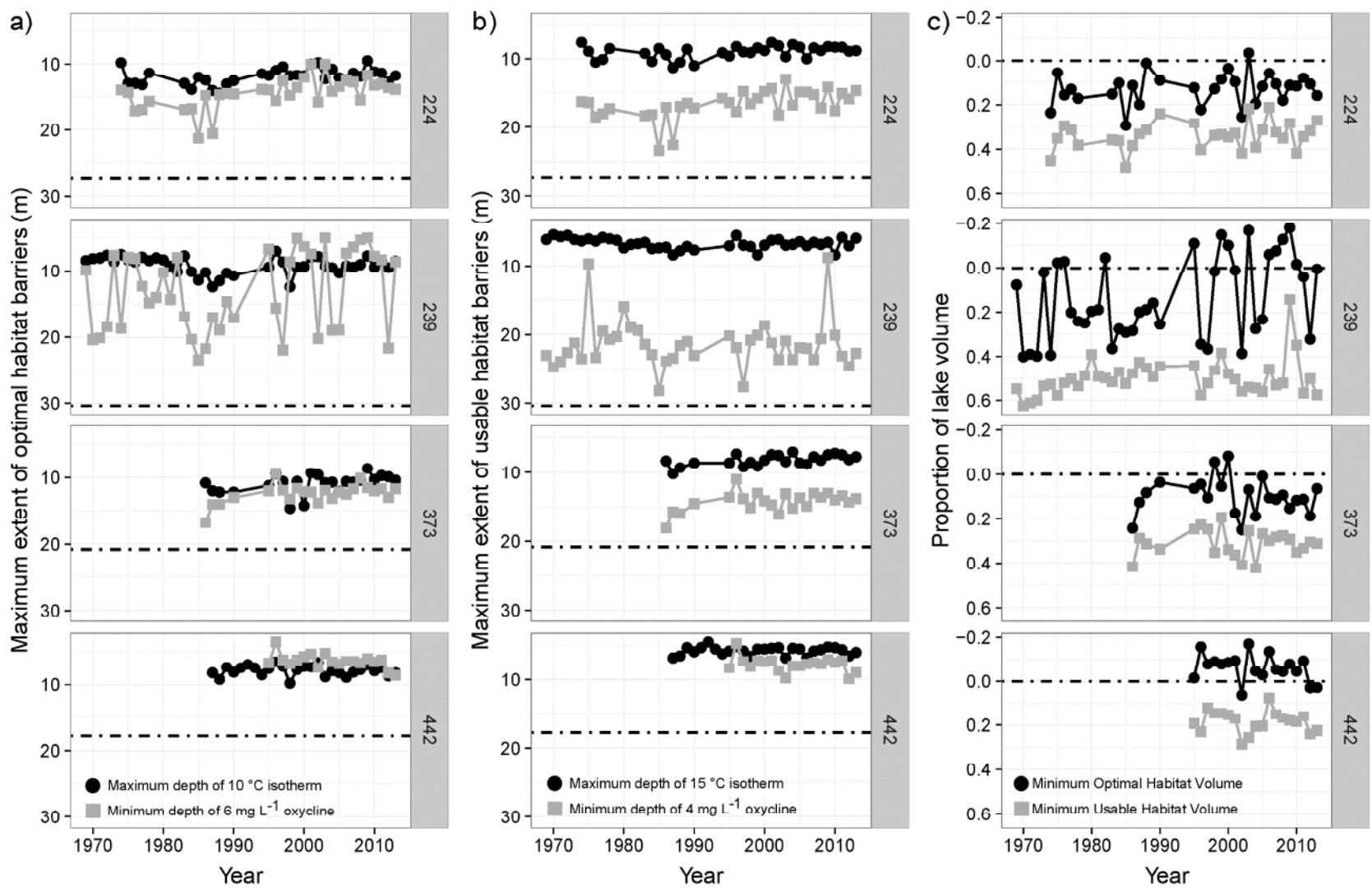


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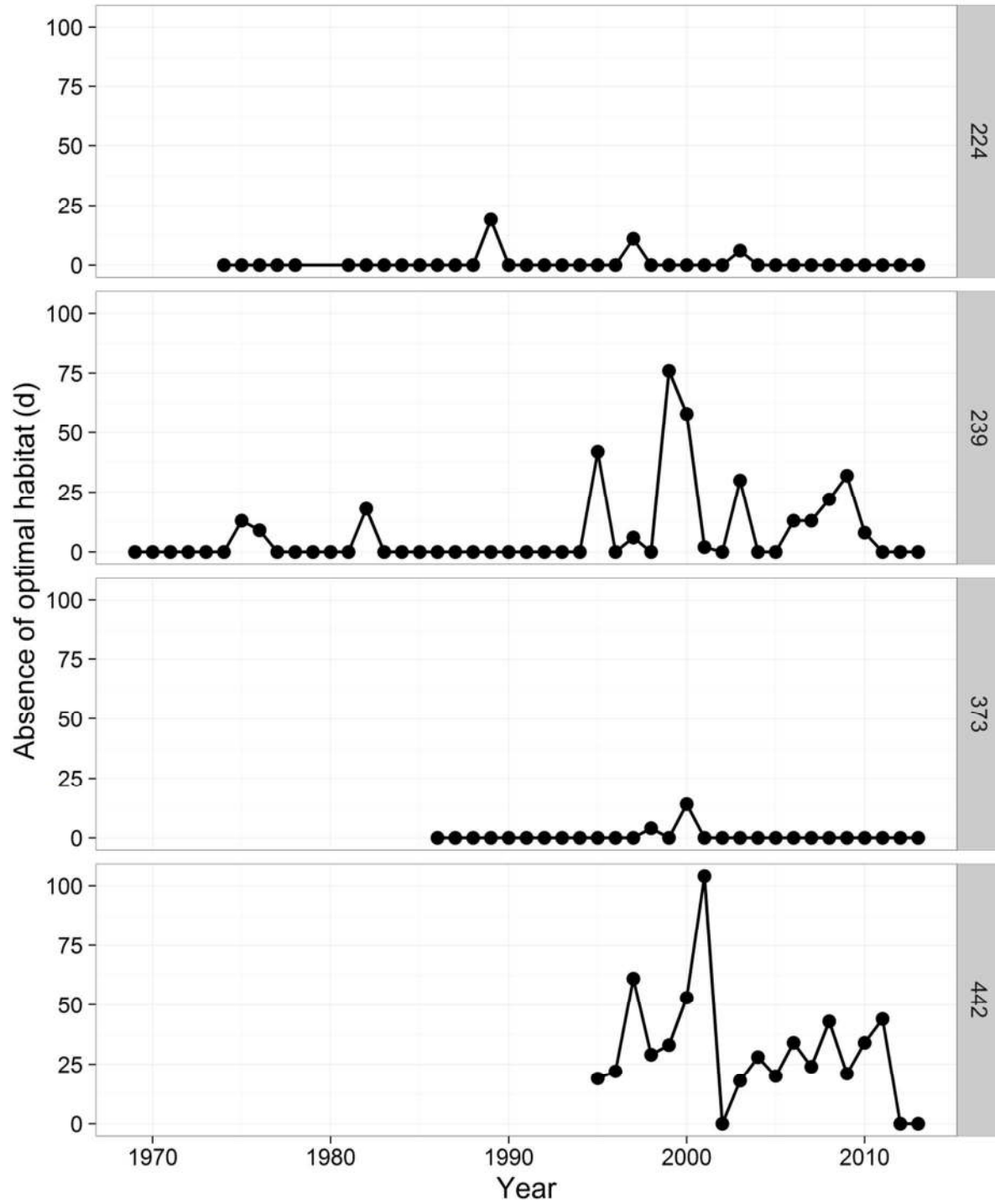
796 Figure 5



797 Figure 6



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799 Figure 7



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801 Figure 8