1 INTRODUCTION

Entire food webs can be restructured if trophic levels differ in their responses to climate warming (Voigt et al., 2003). In aquatic food webs, such variation in thermal responses often increases the biomass of higher trophic levels as temperatures warm (O’Connor et al., 2009; Sastri et al., 2014; Shurin et al., 2012; Symons & Shurin, 2016; Velthuis et al., 2017; Yvon-Durocher et al., 2011). One
explanation is that warming disproportionately increases the velocity at which consumers attack their resources (Dell et al., 2011), resulting in greater grazing and predation pressure (Kratina et al., 2012; O’Connor et al., 2009). Prey may be less sensitive to warming because they are always under stronger selection to avoid being captured (Dell et al., 2011). Organisms at the base of food webs may also become disproportionately smaller as waters warm (Forster et al., 2012; Yvon-Durocher et al., 2011). Consumers will therefore have to ingest more resources to obtain the biomass they need to support their metabolism, and thereby result in relatively larger reductions in the numerical abundance of lower trophic levels (Yvon-Durocher et al., 2011).

The consequences of warming-induced changes in food web structure for the long-term population dynamics of different trophic levels remain poorly understood in lakes. Such changes may be particularly important in lakes because all but a very few taxa, like birds and otters, are ectotherms that are highly sensitive to changes in their thermal environment (Forster et al., 2012). In one of the few observational studies that was long enough to detect impacts of warming, keystone *Daphnia* grazers could not track the earlier onset of peak diatom abundance in Lake Washington, USA, resulting in their population decline over 40 years (Winder & Schindler, 2004). By contrast, *Daphnia* populations increased over the last 60 years in Lake Baikal, correlating more strongly with warmer temperatures than algal biomass (Hampton et al., 2008). These contrasting responses can have at least three explanations. First, asynchronous changes in phenology may depend on the timing of warming, such as if it occurs at a time of year that promotes one trophic level over another (Adrian et al., 2006; Straile et al., 2015; Wagner & Benndorf, 2007). Second, higher trophic levels like grazers can also fail to track warming-induced changes in primary production if they are recruited in spring from resting eggs that respond more to photoperiod than temperature (Domis et al., 2007). Resources will be tracked more closely where consumers maintain free-swimming populations year-round (e.g. Straile, 2000). Finally, warming might be outweighed by changes in trophic state, such as oligotrophication that limits primary productivity (Stich & Brinker, 2010; Thackeray et al., 2008). The two studies highlighted above also analysed only plankton, even though differences in higher trophic levels including fish can influence food web structure (Hampton et al., 2008; Winder & Schindler, 2004). Both multi-year and within-year datasets across multiple trophic levels are therefore required to determine the effects of warming on food web structure.

Testing how warming influences lake food webs also requires disentangling it from other changes that arise over the decadal timescale on which climate changes. Notably, changes in trophic state have coincided with warming in many lakes worldwide (Adrian et al., 2009). In north temperate regions, lake water phosphorus concentrations have often been reduced to reverse the unwelcome symptoms of cultural eutrophication (Jeppesen et al., 2005), and can thus counter the positive effects of climate warming on primary production (Stich & Brinker, 2010; Verbeek et al., 2018). Fishing efforts may have also changed over time. There are surprisingly little temporal data on fishing efforts in lakes, but catches have been rising worldwide (Bartley et al., 2015). Any overharvesting could offset the direct benefits to higher trophic levels from climate warming.

Here we report how warming lake temperatures have primarily restructured the pelagic food web of an iconic European lake from 1981 to 2008. We exploited a monthly plankton dataset across and within three trophic levels and yearly fisheries data from two higher trophic levels. Our approach used structural equation modelling (SEM) to separate the influence of inter-correlated processes (e.g. Jeziorski et al., 2015), namely climate and oligotrophication, on the abundance and biomass of individual populations. Warming and oligotrophication occurred during different time periods, allowing us to disentangle their effects on the food web despite not using an experimental approach. Using SEM, we tested the hypotheses that changes in the pelagic food web arose because (a) higher trophic levels benefitted more from lake warming and (b) temperature exerted greater control over all trophic levels than other environmental changes, such as in trophic state. We predicted that, in the planktonic food web, warming temperatures would be more directly associated with abundances of zooplanktivores than with lower trophic levels. Consequently, we expected a decline in grazers from predation that could outweigh any benefits they received from warmer waters, such as through longer growing seasons or more food availability. We also tested a third hypothesis to explain changes in the lake food web: (c) warming indirectly benefited predatory zooplankton by favouring the expansion of a warm but dark metalimnion (Manca & DeMott, 2009), which others have suggested reduces daytime predation by zooplanktivorous fish (Yan et al., 2001; Yan & Pawson, 1998).

We advance past work, namely of Manca and DeMott (2009), which only tested how this third indirect hypothesis could influence predatory zooplankton without considering the direct effects of climate warming and wider changes in food web structure, for example, fish predation. We specifically compared all our hypotheses about the direct and indirect effects of climate warming on the food web in a single analysis using SEM. Our work was also novel because we modelled a longer and high-resolution (intra-annual) timescale than Manca and DeMott (2009), allowing for more realistic instantaneous and time-delayed responses of organisms.

Finally, we helped to explain the SEM results using metrics of plankton phenology and population growth. We focused these analyses on the predatory spiny water flea (*Bythotrephes longimanus*) and grazers in the *Daphnia longispina–galeata* complex. These taxa were numerically most abundant in their respective trophic levels in our study lake and they are known to have large impacts on food web structure and dynamics (Azan et al., 2015; Lampert, 2011). Furthermore, both taxa showed the strongest temporal changes in our dataset and were monitored at high frequency (up to weekly intervals), providing enough resolution to test changes in phenology over the 28-year study period. Consistent with theory and experimental studies (Gauthier et al., 2014; Hansson et al., 2013; Shurin et al., 2012; Voigt et al., 2003), our novel analyses of high-resolution time series collectively show how warming can strengthen top-down structuring of lake food webs in nature.


2 | METHODS

2.1 | Study site

Lake Maggiore is a large deep lake bordering Italy and Switzerland (area: 213 km²; fetch: 54 km; mean depth: 171 m; max depth: 370 m). The pelagic food web is generally characterized by five trophic levels (Visconti et al., 2014): (a) primary producers, (b) grazers, of which there are three main crustacean taxa: the D. longispina-galeata group (which requires molecular markers for full species-level identification; Keller et al., 2008), *Bosmina* (mainly *Eubosmina longispina* and *Diaphanosoma brachyurum*, in addition to rotifers; (c) predatory zooplankton, of which there are the two cladoceran species *B. longimanus* and *Leptodora kindtii*, cyclopoid copepods (*Cyclops abyssorum* and *Mesocyclops leuckarti*), and diaptomid copepods (*Mixodiaptomus laciniatus* and *Eudiaptomus spp.*); (d) zooplanktivorous fish, which in pelagic surface waters are primarily coregonids (*Coregonus spp.*), shad (*Alosa agone*) and bleak (*Alburnus alburnus alborella*; Volta et al., 2013, 2018); and (e) predatory fish, which are almost exclusively *Sander lucioperca* and *Salmo trutta* in pelagic surface waters (Volta et al., 2018). Within the predatory zooplankton, *Bythotrephes* has been found to occupy a similar trophic position as zooplanktivorous fish during much of the year (Visconti et al., 2014).

The lake has undergone three main changes in recent decades. First, oligotrophication since the 1980s accompanied reduced nutrient loads (Manca & Ruggiu, 1998). Second, incomplete mixing and a limited response to daily changes in surface heat content have made Lake Maggiore more sensitive to long-term warming air temperatures than other lakes in continental climates (Ambrosetti & Barbanti, 1999). Bottom layers deeper than 300 m have warmed by about 10% since the 1970s (Ambrosetti & Barbanti, 1999), with a 6% increase alone below 200 m between 2007 and 2016 (Rogora et al., 2018). Finally, densities of the native predatory cladoceran *B. longimanus* have increased 10-fold since the 1980s in part due to changes in trophy and climate (Manca et al., 2007), but the relative importance of these changes within the food web remains poorly understood.

2.2 | Sampling

From 1981 to 2008, we sampled physical and chemical characteristics of Lake Maggiore at the point of maximum depth (45°58′30″N; 8°39′09″E). This central site is generally representative of spatial patterns across the pelagic zone in physical (e.g. temperature), chemical (e.g. total phosphorus [TP], pH) and biological (e.g. plankton community composition) parameters (Table S1; Figure S1; Bertoni et al., 2004; Caroni et al., 2012; de Bernardi et al., 1988; Poma et al., 2014). Monthly water temperatures were averaged over 0–20 and 0–50 m, respectively, corresponding to the euphotic zone that hosted most phytoplankton and grazers (Callieri & Piscia, 2002; de Bernardi et al., 1988; Manca et al., 2000), and the epilimnetic zone where *Bythotrephes* and other zooplanktivores were mainly distributed (Manca & DeMott, 2009). Vertical temperature profiles were also used to calculate the thickness of refuge from fish predation as the difference between the depth of the top of the hypolimnion and the bottom of the euphotic zone (Yan & Pawson, 1998). The top of the hypolimnion was where temperatures decreased by <1°C/m or fell beneath the maximum vertical gradient (Manca & DeMott, 2009). Hypolimnion depths were zero when the lake was not stratified, generally between November and March. The bottom of the euphotic zone was estimated as 1.6 times the Secchi depth measured alongside water temperatures (Manca & DeMott, 2009). Concentrations of both TP and chlorophyll a were determined monthly using spectrophotometry from a volume-weighted sample at 0, 5, 10 and 20 m depths. For 46 of 322 observations without TP values, we imputed missing values using Kalman smoothing on a structural time series model fitted by maximum likelihood with the imputeTS package in R v3.5 (Moritz & Bartz-Beielstein, 2017). Imputation was necessary to avoid excluding missing observations in our SEM.

We also sampled the pelagic food web. Fortnightly throughout the year, we took integrated phytoplankton samples for biovolume and density through the 0–20 m layer (Morabito et al., 2012). Zooplankton were collected weekly to fortnightly in spring/summer of most years, and at least monthly at other times, with a 76 μm Clarke-Bumpus plankton sampler using sinusoidal hauls from 0 to 50 m (Manca & DeMott, 2009; Manca et al., 2007). Few zooplankton generally occur in waters deeper than 50 m in this lake during daytime (de Bernardi et al., 1988; Manca & DeMott, 2009; Tonelli, 1969) because they become constrained by low temperatures and food availability (Manca et al., 2000). Samples were fixed and counted entirely for zooplankton. Cyclopoid and diaptomid counts were missing from 35 and 38 of 322 observations, respectively, so we imputed values as for TP. We excluded microplankton (rotifers and nauplii) from our analyses because they would have been under-sampled with our 76 μm net (Chick et al., 2010; Thomas et al., 2017). Finally, we calculated whole-lake fish catch per unit effort (CPUE) as per standard approaches for the three zooplanktivorous and two piscivorous fish taxa in the pelagic zone (Volta et al., 2013). We divided the annual biomass of these groups caught by commercial fisheries by the daily square kilometres of gillnets deployed across each year. In principle, fisheries have only used nylon monofilament gillnets and with unchanged choice of target species during the study period (Volta et al., 2013). Although fish were only monitored annually, we found that size distributions did not change across months for coregonids, the dominant zooplanktivores in Lake Maggiore (Figure S2). Total biomass may therefore be representative of the sum of individual consumption rates, which scale with body size (Yodzis & Innes, 1992). There was also much more inter- than intra-annual variation in CPUE than in zooplankton densities, supporting our decision to analyse this timescale (Figure S3).

2.3 | Has warming changed Lake Maggiore?

We first asked whether the lake warmed and abundances of different trophic levels changed over time. As monthly time series are confounded by seasonality and random noise, we decomposed them
into an underlying trend using locally weighted polynomial regression with the stplus function in R. We then determined whether the estimated trends changed monotonically over time with Mann–Kendall rank correlation tests. Mann–Kendall tests are widely applied to detect trends in hydro-meteorological time series because they do not require strictly linear responses, are distribution-free, and tolerate censored data (Hipel & McLeod, 1994; Yue et al., 2002). We used Mann–Kendall tests on the raw data for fish as only annual catch data existed and so no seasonal decomposition of the time series could be performed.

2.4 | Does a greater sensitivity to warming at higher trophic levels re-structure the lake food web?

We tested our hypothesis that temperature ultimately controlled trophic structure, with predators responding most strongly to warming, by estimating the strength and direction of effects in a hypothesized model of food web interactions. In this network, we allowed the amount of food available to primary consumers to vary with monthly water temperatures, total monthly precipitation and solar radiation recorded at a lakeshore meteorological station in Verbania Pallanza (45.924°N, 8.548°E), and TP both at the time of spring mixing (i.e. March) and in each study month. Spring TP was used because it can be associated with seasonal phytoplankton standing stocks (Manca & Ruggiu, 1998; Morabito et al., 2012). Although food availability could not be directly measured because it is an abstraction of many aspects of diet choice and both phytoplankton quality and quantity, it could be parameterized from observed data by treating it as a latent variable. Latent variables are increasingly applied in ecology to represent theoretical, multifaceted concepts that are reflected by, and thus can be estimated from, measured variables (Grace et al., 2010). We specifically defined food availability as proportional to monthly chlorophyll a concentrations, total phytoplankton biovolume and the density of diatoms, which were the lake’s dominant phytoplankton group and sensitive to both trophic state and temperature (Morabito et al., 2012). We then tested how food availability influenced monthly abundances of the grazers Daphnia, Bosmina and Diaphanosoma. This timescale was necessary to align food web sampling with physical and chemical data that were collected monthly, averaging across fortnightly plankton measurements where applicable. We used a first-order autoregressive process to account for temporal autocorrelation, that is, populations in each month depended on those in previous months, and a Poisson error structure as the data were counts.

We compared the effect of food availability in our network of trophic interactions to the direct effects of monthly water temperature and predation. For grazers, predation was inferred from the abundances of Bythotrophes, Leptodora and adult cyclopoid copepods two months prior to that being modelled because cross-correlation coefficients between predator and prey time series were more negative over a 2- than 1-month lag. Diaptomid copepodes are suspension-feeders that mainly consume rotifers and phytoplankton so were not considered cladoceran predators (Brandl, 2005). To infer fish predation, we used the annual biomass of zooplanktivores standardized by fishing effort, that is, CPUE. Focusing on biomass rather than abundance was preferable for fishes. Fish have orders of magnitude more variation in body size among individuals, and thus feeding rates, than in zooplankton consumers, where we analysed densities, that is, population counts. Zooplankton densities were also very closely correlated with biomass in a subset of months with both measurements (Figure S4).

We also compared the effects of temperature and predation on predatory zooplankton. For cyclopoids and diaptomids, we modelled their abundances by summing copepodites and adults, counted in each month. Predation was estimated separately for each predatory zooplankton group from the CPUE of zooplanktivorous and piscivorous fish. For cyclopoids and diaptomids, we also considered predation from Bythotrophes densities two months prior. Bythotrophes consume copepods (Schulz & Yurista, 1998; Strecker & Arnott, 2008) and can indirectly reduce their food availability (Kerfoot et al., 2016). For diaptomids, we also let abundances vary with food availability as these taxa consume phytoplankton alongside rotifers (Brandl, 2005; Kerfoot et al., 2016). Cyclopoid copepods in our study were not modelled from phytoplankton because they are grasping predators that primarily consume zooplankton, even as copepodites (van den Bosch & Santer, 1993; Williamson, 1986). Furthermore, while we used annual fish biomass as a predictor of zooplankton in these analyses, we could not model it against temperature. Fish have multiple age classes that are responding to temperature in different ways over different timescales (van Dorst et al., 2019), so the absence of detailed age-structure data precluded further analyses. We instead estimated how predation by fish on lower trophic levels could be modified indirectly by changes in fishing effort or warming that increased the size of refuge (see below).

Finally, temperature indirectly influences the volume of suitable habitat in addition to its direct physiological effects on organisms. We therefore let abundances vary with the depth of the euphotic zone (for grazers) and with the size of the refuge from fish predation (for zooplanktivores) to separate the two potential mechanisms of temperature-driven change. Including the thickness of the daytime refuge from fish predation allowed us to test the hypothesis that warming influences zooplanktivorous predation on lower trophic levels by expanding a warm, dark metalimnion (Manca & DeMott, 2009). We further estimated how the size of this refuge varied with water temperature and rainfall, which may increase turbidity by exporting more organic matter from the surrounding catchment. Overall, our analysis allowed for both instantaneous and time-delayed responses within and among each zooplankton group by modelling their abundances in relation to trophic interactions in the corresponding month and abundances in the preceding month.

The model was fitted using Hamiltonian Monte Carlo sampling by calling RStan v2.19 from R (Carpenter et al., 2017). Convergence
was determined using standard approaches and there was no evidence of missing linkages or model misspecification (Methods S1). To infer effects, we calculated posterior means and 95% credible intervals (CIs) for each parameter by drawing a subset of 1,000 simulations. We rejected hypotheses if 95% CIs for their associated effects overlapped zero. All estimated coefficients were standardized to a mean of 0 and SD of 1 to compare the relative importance of different effects. Full model details are given in Methods S1 with reproducible R code in Data S1.

2.5 How is temperature associated with population dynamics?

We tested the effect of temperature on plankton phenology and population growth to understand better its association with the modelled network of food web structure. We first asked whether populations at different trophic levels peaked at different temperatures and could thereby uncouple predator-prey dynamics. Using all weekly/fortnightly data (i.e. not just a single measurement aligning with monthly water sampling), we found the Julian date in each year when *Daphnia* and *Bythotrephes* abundances peaked. We fitted a linear model to test the association between these dates and lake temperature averaged from April to June, when peaks typically occurred, allowing for differences between species (i.e. statistical interaction between temperature and species). Similarly, we asked if warmer mean annual temperatures were associated with a greater number of instances of positive population growth between successive weeks in each year using Pearson’s correlations. Finally, we confirmed *Daphnia* were responding to *Bythotrephes* rather than both groups positively covarying with warmer temperatures. We did so by estimating the strength with which *Bythotrephes* tracked *Daphnia* from the number of days between when both groups reached peak densities in each year. We then used Pearson’s correlation tests to relate this measure to the timing and size of peak densities in *Daphnia*. We expected that if top-down control increased, such as if *Bythotrephes* benefited more from warmer temperatures and peaked relatively earlier, *Daphnia* should have slower population growth and consequently take longer to reach peak densities.

3 RESULTS

3.1 Long-term trends

Lake Maggiore underwent marked changes in climate and trophic state between 1981 and 2008. Mean monthly epilimnetic (0–20 m) temperatures increased by 0.05°C/year (\(r = 0.54, p < .001\)), with a smaller 0.02°C/year increase in deeper (0–50 m) waters, when accounting for temporal autocorrelation within years due to seasonality (\(r = 0.51, p < .001\); Figure 1a). These increases were larger during the spring to early-summer period that is important for the annual development of plankton communities, with mean annual 0–20 and 0–50 m temperatures increasing from c. 10 to 12°C (\(r = 0.51, p < .001\)) and 8 to 9°C (\(r = 0.46, p < .001\)) across the 28 years, respectively. Epilimnetic (0–20 m) TP also declined in monthly measurements between 1981 and 2008 by 0.22 µg L\(^{-1}\) year\(^{-1}\), with a trend from c. 13 to 7 µg/L (\(r = -0.55, p < .001\); Figure 1b). TP at the time of spring mixing in each year showed a similar decrease (\(r = -0.45, p < .001\)). There was no long-term trend in fishing effort over the study period (\(r = -0.22, p = .143\); Figure 1c).

The lake food web shifted as climate warmed and TP declined between 1981 and 2008. Phytoplankton biovolume declined from values that regularly exceeded 2 mm\(^3\)/m\(^3\) to <2 mm\(^3\)/m\(^3\) (\(r = -0.58, p < .001\); Figure 2a). *Daphnia* abundances correspondingly declined from 1981 to 1996 (\(r = -0.69, p < .001\)). Although numbers increased thereafter with warmer temperatures (\(r = 0.49, p < .001\)), they did not reach peak densities observed in the early 1980s of >10,000 individuals/m\(^3\) (Figure 2b). *Bosmina* showed a similar but less pronounced pattern as *Daphnia* over each of the two time periods (\(r = -0.32, p < .001\) and \(r = 0.32, p < .001\), respectively; Figure 2c). By contrast, *Dianthus* steadily increased in abundance from a median of about 10 to 140 individuals/m\(^3\) after accounting for seasonality (\(r = 0.54, p < .001\); Figure 2d).

The temporal changes in grazers coincided with changes in higher trophic levels. *Bythotrephes* went from being virtually absent to averaging densities of 10 individuals/m\(^3\) (\(r = 0.40, p < .001\); Figure 2e). *Leptodora* similarly increased in abundance over time (\(r = 0.27, p < .001\)), but by much less than their *Bythotrephes* competitors, with mean density trending from 1 to 3 individuals/m\(^3\).

![FIGURE 1](image-url) Long-term trends in Lake Maggiore. Monthly (a) mean lake temperatures (0–20 m), (b) total phosphorus (0–20 m) and (c) fishing effort determined by multiplying the km\(^2\) of gillnets deployed per day by the number of fishing days. Solid lines show statistically significant trends that were smoothed after decomposition of the corresponding time series, with dotted lines denoting initial and final values. In (b), imputed values are shown in light grey and were excluded from Mann–Kendall trend tests.
FIGURE 2 Restructuring the Lake Maggiore food web. Monthly (a) phytoplankton biovolume, abundances of (b) Daphnia, (c) Bosmina, (d) Diaphanosoma, (e) Bythotrephes, (f) Leptodora, (g) cyclopoid copepods, (h) diaptomid copepods and (i) annual commercial harvests of coregonids, shad, and bleak standardized per fishing effort (km² gillnets deployed across all fishing days in a year). Solid lines show statistically significant trends that were smoothed after decomposition of the corresponding time series, with dotted lines denoting initial and final values. In (g) and (h), imputed values are shown in light grey and were excluded from Mann–Kendall trend tests.

(Figure 2f). Cyclopoid copepods also increased in abundance from around 1,200 individuals/m² to regularly exceeding 2,000 individuals/m² after 1997 ($r = 0.15, p = .001$), having undergone declines from 1981 to 1996 like Daphnia and Bosmina ($r = −0.41, p < .001$; Figure 2g). Diaptomid copepods showed no temporal trends ($r = −0.05, p = .138$; Figure 2h). Finally, CPUE of zooplanktivorous fish declined from >10 to <2 tonnes km⁻² year⁻¹ despite regularly reaching high values ($r = −0.42, p = .001$; Figure 2i). Piscivorous fish, which accounted for between 0.4% and 10.7% of total fish CPUE, were unchanged over time ($r = −0.03, p = .813$).

3.2 Drivers of change

As predicted, the restructuring of the pelagic food web in Lake Maggiore was primarily attributable to warming. Effect sizes associated with temperature were more important (i.e. wider arrows in Figure 3), and more beneficial for higher trophic levels (i.e. darker green arrows in Figure 3), than effects associated with oligotrophication or fishing (Table 1; Table S2). For example, a 1°C increase in water temperature above the long-term mean directly increased the mean abundance of Daphnia from 95 to 134 individuals/m³ (95% CI for increase: 8.7–69.2 individuals/m³). Bosmina abundance increased similarly from 61 to 97 (95% CI: 14.1–59.4) individuals/m³. This effect was stronger than the depth of the euphotic zone for Bosmina (95% CIs for difference: 0.27–1.53 and −0.14 to 1.09, respectively). In Leptodora and Bythotrephes, an identical 1°C increase in water temperature was associated with relatively larger increases in abundances from 1 to 4 (95% CI: 0.8–5.4) and 2 to 6 (95% CI: 2.2–6.0) individuals/m³, respectively, at mean values of all other predictors. Diaphanosoma was also strongly promoted by warmer temperature despite being a grazer (Figure 4). This result may have arisen because its absolute abundance was much smaller than other grazers and so food resources may have not been limiting, resulting in a stronger response to warming (Figure S5). A 1°C increase in water temperature above the long-term mean increased Diaphanosoma abundance from only 5 to 15 (95% CI: 5.3–15.8) individuals/m³. By contrast, copepods, which were the most numerically abundant, had the weakest responses to temperature (Figure S5), with neither cyclopoid nor diaptomid abundances increasing with warmer water temperatures (Figures 3 and 4; Table S2).

Warmer temperatures also reduced food available to grazers, defined by strong positive associations with chlorophyll a concentrations, phytoplankton biovolume and diatom concentrations (Figure 3; Table 1). This effect could be offset by more solar radiation and rainfall that both promoted food availability (Figure 3). Importantly, temperature had weaker absolute effects on food availability than it did on cladoceran predators (95% CIs for differences in effects <0), and thus less control over the food web from the bottom-up. Neither TP in the month of measurement nor during spring mixing were associated with food availability (Figure 3), potentially because of the relatively limited range of concentrations observed over time (Figure 1b).

In addition to its direct effects, temperature also indirectly restructured the food web by favouring higher trophic levels and thereby increasing predation. The main effects of predation linked to temperature were declines in Daphnia and copepods from Bythotrephes (Figure 3; Table 1). Given the strong positive effect of temperature on Bythotrephes, a 1°C increase in water temperature was enough to reduce Daphnia indirectly by a mean of 8 (95% CI: 1.5–15.7) individuals/m³. The 95% CI for the change...
in Daphnia abundance with 1°C warming subsequently overlapped zero (−11.5 to 47.9 individuals/m$^3$) when summed across both the direct temperature, food availability and Bythotrephes pathways in Figure 3. We also found that abundances of Bythotrephes and Diaphanosoma were negatively associated with zooplanktivorous fish CPUE (Figure 3; Table 1). However, in contrast to our predictions, these effects did not depend on refugia from predation when accounting for other drivers of population change (Figure 3). Although we lacked detailed age-class data for fish, so we could not appropriately model their temperature responses, we found no long-term trend in harvests during the period coinciding with warming lake temperatures (Figure 1c). Thus, predation by fish has likely remained relatively consistent despite fewer fish being caught per unit effort in years with more fishing (Figure 3). Together, these results suggest that reduced predation on Bythotrephes, either direct or mediated through temperature-dependent thickening of refugia, cannot explain their recent population expansion (Figure 2e).

### 3.3 | Population responses to warming

Warmer temperatures re-structured the food web partly by advancing the onset and extending the duration of population growth. Using high-frequency sampling, we found that Daphnia and Bythotrephes densities peaked earlier in the growing season by c. 50 and 60 days, respectively, by the end of 28-year study period (Figure 5). The Julian date of peak densities advanced as it was preceded in the same year by warmer spring to early-summer water temperatures across 0–20 and 0–50 m depths for Daphnia and Bythotrephes ($t_{52} = \sim 2.02, p = .049$ and $t_{52} = \sim 3.64, p = .001$, respectively; Figure 6a). This correlation was absent in Daphnia when we used temperatures in the 0–50 m range where all zooplankton were collected, as expected if individuals were mostly concentrated in the euphotic zone (0–20 m) during daytime sampling ($t_{52} = \sim 1.45, p = .154$). Bythotrephes also advanced their peak at a faster rate than Daphnia (difference in slopes: $t_{50} = 2.31, p = .025$; Figure 6a).

Consistent with the earlier peak densities, we found three times more instances of positive population growth between subsequent...
Bythotrephes counts in years that were generally warmer ($r = .77$, $p < .001$; Figure 6b). Years with more instances of positive population growth consequently reached peak densities earlier ($r = -.55$, $p = .002$). The probability of detecting positive population growth was independent of density when we fitted a generalized linear model with binomial error structure to the presence–absence of positive population growth between successive weeks given the initial population density ($z_{48} = -.33, p = .742$). By contrast, we found no association between warming and positive population growth for Daphnia ($r = .18, p = .349$), as might be expected if their earlier onset was under strong top-down control from the growing Bythotrephes population (Figure 6b).

Further evidence for strong top-down control of Daphnia was suggested by the observation that Bythotrephes tracked the earlier emergence of their Daphnia prey largely irrespective of spring to early-summer or annual temperature ($r = -.33, p = .090$ and $r = -.35$, $p = .066$, respectively; Figure 6c). This observation was not solely because warming similarly impacted both species. Daphnia peaked at lower densities and took longer to do so when they were more closely tracked by Bythotrephes ($r = -.24$, $p = .07$ and $r = -.17$, $p = .021$, respectively; Figure 7ab). By contrast, Bythotrephes reached higher densities where they more closely tracked Daphnia ($r = .50$, $p = .007$). As Daphnia generally peaked in density earlier than Bythotrephes, this result also meant there was less disparity between the timing of peak
densities when *Bythotrephes* were more abundant (Figure 7c), as expected if strong predation delayed peak *Daphnia* densities.

4 | DISCUSSION

We found that warming temperatures have more strongly restructured the food web of a large European lake than changes in trophic state or fishing efforts by analysing exceptionally long time series of multiple trophic levels. These findings provide rare validation from nature for mesocosm and whole-lake experiments that predict more positive responses of higher trophic levels to future climate warming (Gauthier et al., 2014; Hansson et al., 2013; Shurin et al., 2012; Yvon-Durocher et al., 2011). We also found that the strong thermal response of the zooplanktivore *B. longimanus* resulted in earlier population peaks as the lake warmed and longer periods of positive population growth. However, advances in the timing and size of peak *Bythotrephes* densities were ultimately dependent on changes in the timing and size of prey populations. This

![Figure 4](image-url) **Figure 4** Warmer waters generally promoted abundances across trophic levels. Curves are estimated posterior densities for effect of monthly water temperature on numerical abundances of each taxonomic group and estimated food availability. Only direct effects are considered, that is, without indirect pathways of predation and food for consumers. Shaded area contains 95\% of the probability mass and vertical line is median

![Figure 5](image-url) **Figure 5** Phenology has advanced in Lake Maggiore zooplankton over the last three decades. Julian day corresponding with peak densities of *Daphnia* (grey boxes) and *Bythotrephes* (purple circles) decreases across the 28-year period ($r = -0.42, p = .002$ for both)

![Figure 6](image-url) **Figure 6** *Bythotrephes* benefit from lake warming from 1981 to 2008. (a) Julian day corresponding with peak densities of *Daphnia* (grey boxes) and *Bythotrephes* (purple circles) decreases with mean spring to early-summer lake temperatures (0–20 and 0–50 m depths, respectively), in each sampling year. Shaded triangles show slopes that are significantly different between species ($t_{49} = 2.31, p = .025$). (b) Per cent of observations (\% obs) where zooplankton abundances increased between subsequent sampling weeks is positively related to mean annual lake temperature for *Bythotrephes* but not *Daphnia*. (c) Number of days after *Daphnia* that *Bythotrephes* peak in density is not related to the mean annual 0–50 m lake temperature
4.1 Lake warming benefits higher trophic levels and strengthens top-down control

We generally found support for our prediction that changes in the pelagic food web arose because higher trophic levels benefited more from lake warming. Metabolic reactions, such as ingestion rates, can increase by relatively more in consumers because of warmer temperatures (Dell et al., 2011, 2014), and would explain why we found abundances of higher trophic levels were more positively associated with temperature (MacLennan et al., 2012). Increased metabolism may have also simultaneously intensified selection for larger consumer body sizes that correlate with larger clutch sizes (Branstrator, 2005; Lynch, 1980), and thus potential population growth. Both zooplankton grazers and predators are known to evolve larger body sizes to avoid *Bythotrephes* and gape-limited zooplanktivorous fish (Gillis & Walsh, 2017; Manca et al., 2008; Straile & Hälbich, 2000). Our results, however, suggest that the benefits of warmer temperatures may partly depend on population density. Metabolic rates can slow because of density-dependent competition and food limitation (DeLong et al., 2014; Quévreux & Brose, 2019), and would explain why we found temperature responses were weakest in copepods that were the most numerically abundant taxa. Schindler et al. (2005) estimated that density-dependent reductions in growth of a zooplanktivorous fish were only halved by improved growing conditions under a warmer climate. An alternative explanation for the weak responses in copepods is that their relatively longer life cycles makes them more sensitive to changes in the length rather than total heat content of the growing season (Adrian et al., 2006; Carter & Schindler, 2012).

By contrast, we found no benefit of lake warming on primary producers and a negative association between temperature and food availability, the latter defined by phytoplankton biovolume, chlorophyll *a* concentrations and diatom density. As all the defining measures of food availability were positively associated with mean phytoplankton cell volume (Spearman’s $\rho = 0.55–0.65$, $p < .001$ for all), warmer temperatures also resulted in smaller cells. We could exclude grazing as an explanation for this result because copepods rather than cladocerans tend to release small phytoplankton from grazing (Sommer & Sommer, 2006), and they were not strongly associated with food availability in our model. Instead, by hastening growth, warmer temperatures can place phytoplankton under selection to forgo somatic growth for reproducing before their competitors, resulting in smaller cells. Phytoplankton can also receive a larger competitive advantage than heterotrophs from being smaller because their growth depends more on the rate of diffusion of CO$_2$ and nutrients (Atkinson et al., 2003; Yvon-Durocher et al., 2011). As warming reduces gas solubility and increases nutrient demand from metabolism (Gillooly et al., 2001), smaller cells (i.e. higher surface area to cell volume) maintain greater resource supply relative to metabolic demand.
We also found that *Bythotrephes* and zooplanktivorous fish, but not other predators, had strong top-down effects on the food web. *Bythotrephes* can function like fish because both are visual predators (Azan et al., 2015), and recent evidence shows that zooplanktivorous fish stock prey from further distances under warmer temperatures (Gliwicz et al., 2018). *Bythotrephes* may also outcompete other zooplanktivores like *Leptodora* for food because they mature faster (Kim & Yan, 2010; Vrijverberg & Koelweijn, 2004), and access prey earlier with shorter handling times (Branstrator, 2005). Rapid developmental times can also establish a large sediment egg bank that provides a constant source of recruitment if thermal conditions change and become less favourable (Walsh et al., 2016). These differences, along with resulting changes in prey community composition and size structure, have contributed to the replacement of *Leptodora* in lakes invaded by *Bythotrephes* (Foster et al., 2012; Kerfoot et al., 2016; Lehman & Cáceres, 1993; Weisz & Yan, 2011). Our findings around phenology also add new insights into this process and raise the risk that introduced *Bythotrephes* might outcompete native predators under a warming climate in relatively cool lakes like Maggiore. By contrast, *Bythotrephes* but not *Leptodora* can be numerically reduced by zooplanktivorous fish because they are much more apparent to visual predators (Branstrator, 2005). For copepods, we may have found no effect of cyclooids on lower trophic levels because they were controlled by *Bythotrephes* (Kerfoot et al., 2016), whereas diaptomids can rely much more on littoral resources and terrestrial detritus (Grey et al., 2001; Visconti & Manca, 2011). Experimental tests are now needed for how differences in the life history of *Bythotrephes* and other zooplanktivores influence their population dynamics under different warming scenarios.

*Bythotrephes* may have had a particularly strong effect on lower trophic levels because lake warming released them from top-down control. Fish catches have been shown to have negative or mixed responses to warming in 23 of 31 worldwide lakes, depending on the study species and fishing methods (Kao et al., 2020). Older cohorts of Eurasian perch (*Perca fluviatilis*) were also less productive with warming across Northern European lakes (van Dorst et al., 2019). Although we could not directly model changes in fish abundance with temperature, we found temporal declines in zooplanktivorous fish without corresponding increases in fishing effort, rejecting overharvesting as an explanation for our results. This decline could have also released *Diaphanosoma* from predation (Herzig, 1995). Where fishing pressure has increased, we suggest climate warming could act alongside overexploitation to release predators occupying middle trophic positions, that is, mesopredators like *Bythotrephes*, from top-down control (Baum & Worm, 2009). More generally, our study is one of the first to identify explicitly the potential for mesopredator release in freshwater lakes (Ritchie & Johnson, 2009). We caution, however, that predation by zooplanktivorous fish can vary within years, such as because of seasonal changes in water temperatures (Walsh et al., 2017). Coupling bioenergetic modelling with size structure data would enable a more robust test of temporal changes in fish predation.

Our results suggested *Daphnia* abundances responded weakly to warming-associated increases in food availability because they were limited by predation. Two additional lines of evidence support this conclusion. First, clutch sizes appeared not to be limited by food availability over a subset of our study for which we had additional demographic data. There was a weak correlation between the total number of eggs per ovigerous females counted in monthly hauls between 1983 and 1998 and each sample across the posterior distribution of estimated food availability for the corresponding period (95% CI for Spearman’s rank correlation: \( r = 0.10–0.26, p = .003–0.251 \), as might be expected if more available food increased reproduction. Second, reproduction did not visibly increase to offset mortality. Clutch size and per-capita death rates estimated with long-term demographic data from Manca et al. (2008) were not correlated (\( r = 0.03, p = .695 \)). As *Bythotrephes* select egg-bearing females (Manca et al., 2008), higher *Bythotrephes* abundances with warmer temperatures predation can offset any benefit to *Daphnia* clutch sizes from greater food availability. Together, these observations could explain why *Daphnia* had no net response to temperature when all pathways in our SEM were considered (i.e. sum of predation and food availability). Elsewhere, *Daphnia* have been found to decline in numbers in relatively warm years because predation outweighed higher recruitment from greater food availability (Wagner & Benndorf, 2007). Carter and Schindler (2012) similarly found crustacean zooplankton densities to be unchanged over a 47-year period time, partly because the positive effects of earlier spring ice breakup were masked by greater predation pressure from zooplanktivorous fish (Schindler et al., 2005). Additional experimental tests would help attribute mortality to predation in observational datasets such as ours.

### 4.2 Lake warming more important than trophic state and refugia from predation

Consistent with our predictions, we found that trophic state had weaker effects on food web structure than temperature. One explanation for this result is that the effects of trophy may well depend on the range of observed values. In contrast to other studies where trophy was important (e.g. Stralle & Geller, 1998; Walsh et al., 2017), Lake Maggiore was never eutrophic during our study period. Thus, the decline in TP was relatively limited compared with the increases in temperature. In Lake Constance, oligotrophication during the 1980s to 1990s similarly had weaker effects than temperature on higher trophic levels (Stralle, 2000), until only recently, when soluble reactive phosphorus has become virtually undetectable (Stich & Brinker, 2010). Moreover, any effects of TP on food availability may ultimately depend on winter temperatures that influence vertical mixing and the onset of nutrient upwelling (Manca et al., 2015). Surface waters have received less TP from deeper layers as they have become disproportionately warmer, resulting in more stable and less mixed water columns (Rogora et al., 2018). Therefore, trophy itself may have little direct influence over long-term population dynamics and phenology of higher trophic levels in lakes such as ours where changes in temperature exceed those in nutrient status.

We also found no evidence that the thickness of a daytime refuge from predation by zooplanktivorous fish influenced food web...
structure. Previous work in Lake Maggiore showed that the number of days per year with adult Bythotrephes present and mean annual Bythotrephes abundance increased with the duration of the predation refuge (Manca & DeMott, 2009). As the refuge lasted longer with lake warming (Manca & DeMott, 2009), this effect could have been confounded with the direct effects of temperature on Bythotrephes abundance. Our analysis has now separated the direct and indirect effects of climate, clarifying the underlying causal pathways. We also could not consider refuge duration because it was calculated on an annual rather than the monthly timescale of our analyses. At a monthly scale, refuge thickness may only be important during summer (Yan et al., 2001), when cladoceran prey abundance is highest and/or predation pressure from fish is greatest (Pothoven et al., 2001; Young et al., 2011). Zooplanktivorous fish in Lake Maggiore also rely much more on littoral resources outside of summer (Visconti et al., 2014). Finally, refuge thickness may only correlate with Bythotrephes when they are relatively scarce and before they have displaced other prey of zooplanktivorous fish (Young et al., 2009).

Other food webs are likely to be restructured by mechanisms identified here as lakes tend to respond synchronously to large-scale climate processes across geographical regions (Blenchner et al., 2007; Carter & Schindler, 2012; Rusak et al., 2008). Most lakes are also more sensitive to warming than Lake Maggiore because they are small and lack a permanently cold, deep layer (O’Reily et al., 2015). Sensitivity to warming will further be exacerbated by dark, poorly mixed waters (Rose et al., 2016), which are increasingly common because of climate change (de Wit et al., 2016; Woolway & Merchant, 2019). An outstanding question is how the effects of climate warming may differ from other environmental changes across different lake types. For example, increased nutrient availability may alter food webs more than climate warming in relatively oligotrophic lakes (Alric et al., 2013; Rigosi et al., 2014). By contrast, in Canadian Shield lakes, falling lake water calcium concentrations act alongside climate warming to shift zooplankton community composition (Jeziorcki et al., 2015), though are unimportant in Lake Maggiore where concentrations have exceeded 20 mg/L during our study. Finally, human activities like greater fishing effort or fish stocking can also make predator biomass, and thus their impacts, respectively, more or less vulnerable to climate change (Kao et al., 2020). Future work now needs to focus on improving our understanding of how the magnitude of warming-induced shifts in lake food webs will interact with other drivers of global change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. Equations and code for the structural equation model are available in the supplementary material of this article.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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