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A food web model of Lake Garda as a management tool within the context of climate changes

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Abstract

Freshwater ecosystems support enormous biodiversity and provide key ecosystem services. However, alteration of natural flow regimes, nutrient loading and climate forcing have resulted in major impacts on water quality, food webs and productivity. Lake Garda, the largest of the deep southern subalpine lakes, experienced, during the last 40 years, a significant tendency to an increase of phosphorus content and water temperatures (0.035 °C/year in the upper 50 m layer). The objective of the thesis was to characterize trophic interactions and energy fluxes within the Lake Garda food web and to evaluate their temporal dynamics, considering effects of fisheries and climate change, using an Ecopath with Ecosim (EwE) mass-balanced model composed by 22 functional groups. According to the model outputs, ecotrophic efficiency is generally higher for fish groups and lower for zooplankton and primary producers, indicating that bottom-up control is the dominant pattern in the lake. At the current status, primary production required for total catch is 88.43 t/km², which corresponds to 4.23% of total primary production (2090 t/km²/year). Dynamic simulations based on temperature increase scenarios show that, with constant primary production, effects on the different groups in terms of relative biomass are mixed, whereas, with increased primary production, effects are significantly positive for most groups, with an increase in the total biomass of the system up to 20%.

1. Introduction

Freshwater ecosystems are considered among the most threatened on the planet. Alteration of natural flow regimes and pollution from cities and agriculture, especially nutrient loading, have resulted in declines in water quality, major impacts on freshwater biota and the loss of essential ecosystem services (IPCC, 2014). As a direct consequence of these and other impacts, freshwaters have some of the highest rates of extinction of any ecosystem for those species groups assessed for the IUCN Red List (estimated as much as 4% per decade for some groups, such as crayfish, mussels, fishes, and amphibians in North America). This is a particular concern given that freshwater habitats support 6% of all described species, including approximately 40% of the world's fish diversity and a third of the vertebrate diversity (Strayer and Dudgeon, 2010). However, climate change will have significant additional impacts, such as altered thermal regimes, altered precipitation and flow regimes (IPCC, 2014).

In particular, lake ecosystems are vital resources for aquatic species and human needs, holding a large majority of earth's liquid freshwater, supporting enormous biodiversity, and providing key provisioning and cultural ecosystem services (O'Reilly et al., 2015). Thus, any alteration of their environmental quality and water renewal rates has wide ecological and societal implications (Vincent, 2009). As a result of the increasing accumulation of greenhouse gases in the atmosphere from human activity, mean air surface temperatures showed an increase of about 0.85 °C since the late 19th century, and current global circulation models predict a further increase up to 4.8 °C by the end of the 21st century, combined with large changes in the regional distribution and intensity of precipitations (IPCC, 2013). These shifts in climate forcing have begun to affect the structure, functioning, and stability of lake ecosystems throughout the world, and much greater impacts are likely in the future. The resulting changes in the physical, chemical, and biological properties of lakes are affecting their ability to maintain the current biological communities, and their capacity to provide ecosystem services such as safe drinking water and inland fisheries (Vincent, 2009; Sahoo et al., 2011).

The ecological status of many lakes in Europe has changed dramatically over the last 30 years. Many of these changes are the result of anthropogenic influences in the catchment but some are also driven by changes in the regional climate (George, 2010). Rising temperatures between 0.01 and 0.1 °C/yr in the well-mixed surface waters have been observed in many temperate lakes both in situ and from satellite (Shimoda et al., 2011). Increased surface temperatures affect stratification and seasonal convective mixing, with increased duration and stability of the thermocline during summer, and result in reduced periods of ice formation (Schmid et al., 2014; IPCC, 2014). Changes in temperature and stratification further affect biological and geochemical processes. For instance, they are projected to cause a shift in dominance to smaller phytoplankton and cyanobacteria, especially in those ecosystems experiencing high anthropogenic loading of nutrients (Winder et al., 2009; Wagner and Adrian, 2009), with impacts to water quality, food webs, and productivity (Shimoda et al., 2011). Moreover, oxygen concentrations may decrease in deep stratified lakes and increase in ice-covered lakes. Changes in the fish assemblage composition have already been observed, while more complex interactions between physical and biological processes, such as a disruption of the linkage between different trophic levels need further investigation (Jeppesen et al., 2012; Schmid et al., 2014). The various impacts and threats differ substantially between biomes and among geographical regions, and even within regions, hydrological factors and catchment properties will be major determinants of the responses of lakes ecosystems to climate change (Adrian et al., 2016).

As largely closed systems, lakes are ideal systems to studying climate-induced effects, through changes in temperature, hydrology and ice cover, as well as through biological communities (phenology, species and size distribution, food-web dynamics, life-history traits, growth and respiration, nutrient dynamics and ecosystem metabolism). These freshwater ecosystems are strongly sensitive and respond rapidly to climate forcing, due to fast turnover times from the scale of organisms to entire lake ecosystems (Adrian et al., 2009). In fact, studies of lake ecosystems have provided some of the earliest indications of the impact of current climate change on ecosystem structure and function (Adrian et al., 2016). Therefore, lake ecosystems are excellent sentinels for current climate change, as they provide indicators of climate change either directly or indirectly through the influence of climate on the catchment. The indicators are measurable response variables, such as water temperature, dissolved organic carbon, or phytoplankton composition (Adrian et al., 2009). In addition to respond directly to climate change and incorporate the effects within the catchment, lakes are particularly good sentinels for current climate change for several other reasons: they are well-defined ecosystems and persistently studied; they integrate responses over time, filtering out random noise; they are distributed worldwide and cover many different geographic locations and climatic regions. However, the large range in lake morphology, geographic location, and catchment characteristics means that broad statements about the ability of lakes to capture the impacts of the current, rapidly changing climate must be made with caution (Adrian et al., 2016). The aim of this introductory chapter is to describe the current understanding about climate change impacts on lake systems, focusing on temperate regions. It is structured as follows: section 1.1 deals with climate change effects on physical aspects, such as temperature and stratification; section 1.2 describes effects on chemical aspects, such as nutrients and oxygen; section 1.3 focus on responses of lake biota and ecosystem structure and dynamics; lastly, section 1.4 details the specific objectives of this thesis.

1.1 Climate change impacts on lake physics

There is evidence of a strong relationship between atmospheric conditions, such as air temperature and wind patterns, and lake thermal structure. Generally, the thermal properties of aquatic ecosystems are more directly governed by the climatic and large-scale oceanic fluctuations than the thermal properties of terrestrial ecosystems. Specifically, there is evidence of changes in the onset of stratification, thermocline depth, mean epilimnetic temperature, turnover date, and the duration of ice cover. Additionally, the influence of macroscale atmospheric processes and the persistence of their signals vary substantially among lakes with different sizes and mixing regimes, even under similar climatic conditions (Shimoda et al., 2011).

One of the most important physical parameters in any lacustrine system is the temperature of the lake since it reflects meteorological forcing in a direct and sensitive way (George, 2010). Key drivers of surface water temperature include absorbed solar irradiance and heat exchange with the atmosphere, which is controlled by air temperature, solar radiation, humidity, ice cover, and wind but is also mediated by local factors such as lake surface area, volume and depth (Schmid et al., 2014). In temperate regions, the highest surface water temperatures in winter are recorded in deep lakes that retain heat and the lowest in shallower lakes that lose more heat to the atmosphere (George, 2010). Warmer air temperatures result in warmer surface waters via conduction, although this may be dampened in part by increased evaporation rates (Vincent, 2009). Moreover, as

morphometric factors vary enormously across lakes, and recent rates of change in climate variables are also spatially heterogeneous, patterns of lake warming are expected to be highly variable (O'Reilly et al., 2015). During the last few decades, lakes worldwide have become warmer and lakes in mid- to high latitudes of the Northern Hemisphere are warming particularly fast. For example, from 1985 to 2009, the summer surface temperature of lakes across northern and central Europe has increased at rates of 0.6–0.8 °C per decade (Schneider and Hook, 2010).

Schmid et al. (2014) estimated the effects of climate change, as predicted by six climate models, on lake surface temperatures on a global scale, using the lake surface equilibrium temperature as a proxy. Interactions between different forcing variables and the sensitivity of lake surface temperatures to these variables were evaluated, as well as differences between climate zones. Lake surface equilibrium temperatures are predicted to increase by 70 to 85 % of the increase in air temperatures. On average, air temperature resulted the main driver for changes in lake surface temperatures, and its effect is reduced by ~10% by changes in other meteorological variables. However, the contribution of these other variables to the variance is ~40% of that of air temperature, and their effects can be important at specific locations.

A recent synthesis of in situ and satellite lake data (O'Reilly et al., 2015) shows that lake summer surface water temperatures (LSSWT) are warming significantly, with a mean trend of 0.34°C/decade, across 235 globally distributed lakes between 1985 and 2009 (Fig. 1). This warming rate is consistent with the rapid annual average increase in air temperatures (0.25°C/decade) and ocean surface temperatures (0.12°C/decade) over a similar time period (1979-2012).

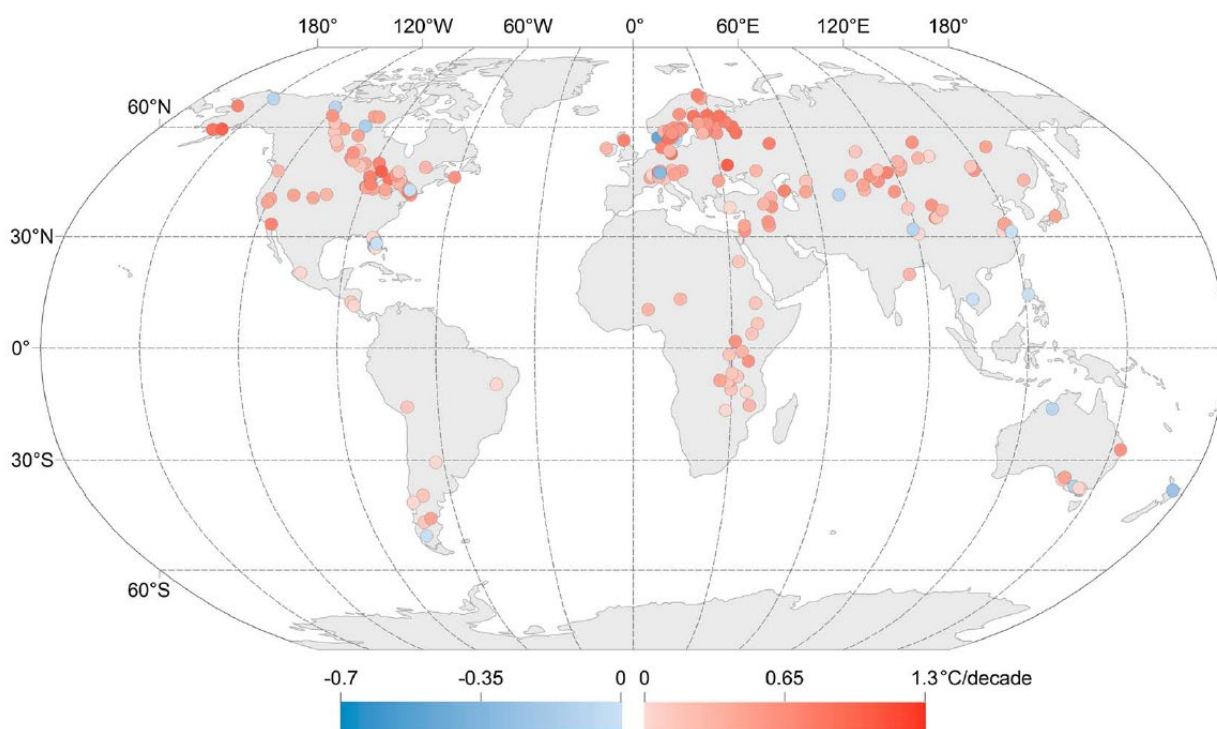


Fig. 1 Map of trends in lake summer surface temperatures from 1985 to 2009, showing that the vast majority of lakes is warming. The magnitudes of warming and cooling are not the same, and there is a large spatial heterogeneity in lake trends (O'Reilly et al., 2015).

However, despite a broad global coherence in air and lake temperature trends, for individual lakes air and lake temperature trends often diverged (**Fig. 2**). Thus, a similar response of lake temperatures to air temperatures cannot be assumed, emphasizing the importance of the various factors controlling lake heat budgets.

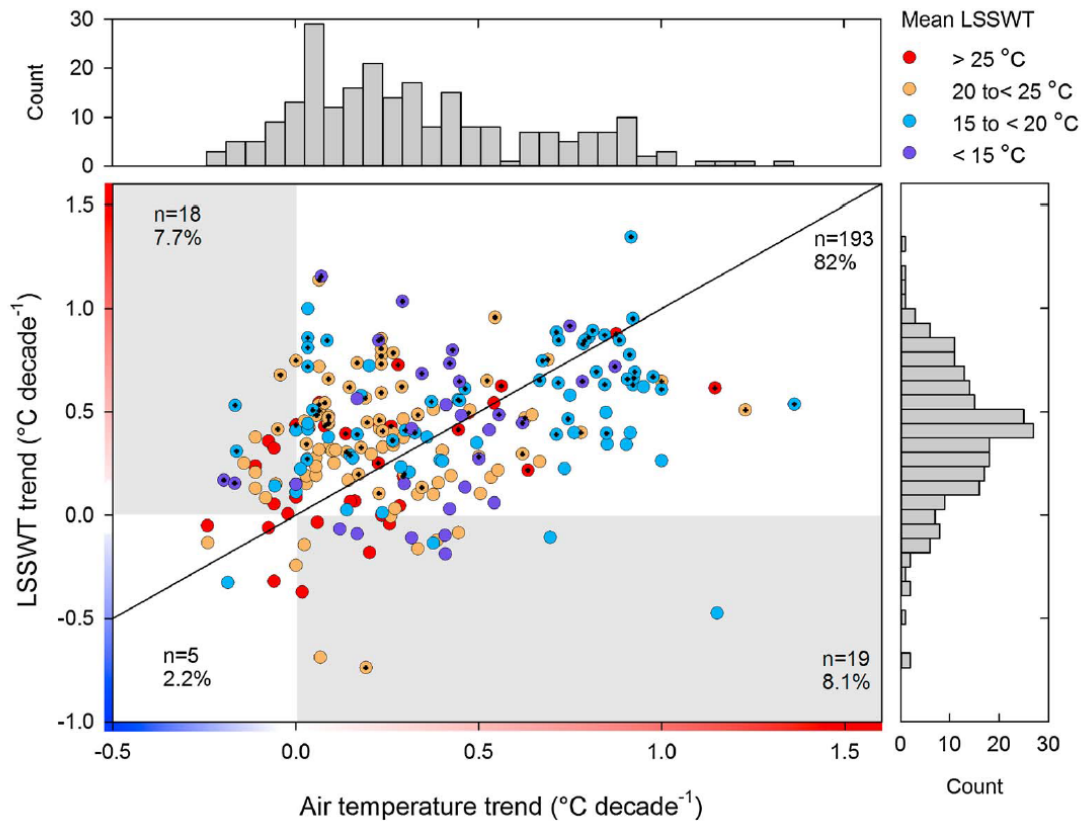


Fig. 2 Linear regression between lake surface water temperature (LSSWT) trends and air temperature trends. Although the slope of the regression line was not significantly different from 1, there was wide variation in both air and lake temperature trends. Black central dots within a data point indicate LSSWT trends significant at $p < 0.1$. The 1:1 line and counts (n) and % in each quadrant are also included. Histograms show distribution of data along that axis (O'Reilly et al., 2015).

Although warming is widespread, LSSWT trends range from -0.7 to $1.3^{\circ}\text{C}/\text{decade}$ and show clear regional variation. However, no single geographic (latitude and elevation) or morphometric factor (depth, volume, and surface area) adequately explained this variation, since correlations between these geomorphic factors and LSSWT were weak (< 0.2) to moderate (< 0.4). For instance, warming and cooling trends occurred in high-latitude lakes (e.g., Alaska) and in nearby lakes within several regions (e.g., Central Europe and Tibetan Plateau). Moreover, in both the Laurentian Great Lakes region and in Northern Europe, lakes were warming significantly faster than the global average, whereas lakes in south-eastern North America were warming significantly more slowly than the global average. This large heterogeneity in LSSWT trends is associated with different geomorphic and climatic factors, including increases in air temperatures, shifts in cloud cover and type, and increases or decreases in solar radiation at various locations. However, winter ice cover appears to be a key factor influencing LSSWT trends. In fact, on average, ice-covered lakes are warming significantly faster than lakes that do not experience ice cover (ice-covered median $0.48^{\circ}\text{C}/\text{decade}$; warm-winter median $0.25^{\circ}\text{C}/\text{decade}$) (O'Reilly et al., 2015). Moreover, among ice-covered lakes, LSSWT trends were related to both geomorphic characteristics and cloud cover trends, whereas LSSWT trends in ice-free lakes were more closely associated with trends

in air temperature and solar radiation. This is also consistent with theoretical predictions based on the psychrometric properties of air and water, which find that long-term rates of temperature change should be lower for lakes than air (Schmid et al., 2014).

Therefore, the high level of spatial heterogeneity in lake warming rates found in O'Reilly et al. (2015) shows that warming rates are dependent on combinations of climate and local characteristics, rather than just lake location, countering the common assumption of regional consistency in lake warming. This underscores the importance of considering interactions among climate and geomorphic factors that are driving lake responses and prevents assumptions that any individual lake has warmed concurrently with air temperature or that all lakes in a region are warming similarly.

Although the evidence that global climate change is probably an important driver of these warming trends, lake temperatures track other medium-term (decadal time scale) climatic variation, including climatic oscillations such as the North Atlantic Oscillation (NAO) or the East Atlantic Pattern (EA) (Dokulil, 2014; Lepori and Roberts, 2015). These long distance climatic forcings affect the processes that regulate the summer dynamics of the lakes, including the onset, timing and duration of thermal stratification, the depth and intensity of mixing and the heat content. In fact, in temperate regions, lake surface water temperatures (LSWT) are closely correlated with the air temperature at all elevations, but both variables are strongly influenced by the North Atlantic Oscillation (NAO), especially during winter and spring. Some example of this kind of correlations include Lake Neusiedler in the eastern part of Austria and two lakes from the Carinthian lake-district south of the Alps. Moreover, the temperature records of Lake Neusiedler have been compared with the Mediterranean Oscillation Index (MOI), an index commonly used to analyse weather patterns in the Mediterranean region. In this case, the MOI resulted a better predictor of summer and early autumn water temperatures in Lake Neusiedler, suggests that the "Mediterranean" influences could be important there, but the NAO still has a significant effect on the LSWT in winter (George, 2010).

Therefore, any attributions of lake warming to global warming would be uncertain without an assessment of the relative contribution by climatic oscillations. However, as the oscillation periods do not usually exceed 60-80 years, if climatic oscillations have been (and will continue to be) the main drivers, the warming trends may revert spontaneously in the future. By comparison, as global climate change arises to a greater extent from a human-induced accumulation of greenhouse gases in the atmosphere, if global climate change has influenced (or will influence) lake temperatures, the warming trends may not revert until the emission of these gases is reduced (Lepori and Roberts, 2015). Regardless of when such reduction might be achieved, the influence would be long-lasting because, globally, temperature is expected to rise for at least another century (IPCC, 2013).

Across Europe, climatic conditions and the increase in surface atmospheric temperature (AT) reported during the 20th century are variable. For instance, in Northern Europe, atmospheric temperature increased by 0.3-1.0°C in Fennoscandia and by 0.5-0.8°C for different parts of the Mediterranean. Climate warming was even more pronounced in the greater perialpine region, where air temperatures have increased by almost 2°C, twice the global average. Nevertheless, impacts on physical properties of inland waters, such as temperature and the timing of ice-out, are surprisingly coherent, both regionally and vertically (Dokulil, 2014).

In the western part of Europe, LSWT increased by 1.4 °C in Lake Windermere, English Lake District, between 1960 and 2000 and by 0.7°C in Lough Feeagh, Western Ireland, between 1960 and 1997 (George et al. 2007). Mean lake temperature of Lake Zurich, Switzerland, increased at a rate of 0.16°C/decade from 1950 to 1990, whereas the decadal increase was 0.1°C in Lake Constance, Switzerland, at approximately the same time (Shimoda et al., 2011; Dokulil, 2014). Epilimnetic temperature increased in July in the majority of the European

lakes between 0.5 and 0.6 °C/decade, ranging from 0.2 °C/decade in Greifensee, Switzerland, to 0.9 °C per decade in Lake Vättern, Sweden. An exceptionally high increase of 1.6 °C/decade was reported from Lake Stensjön, Sweden (Adrian et al., 2009).

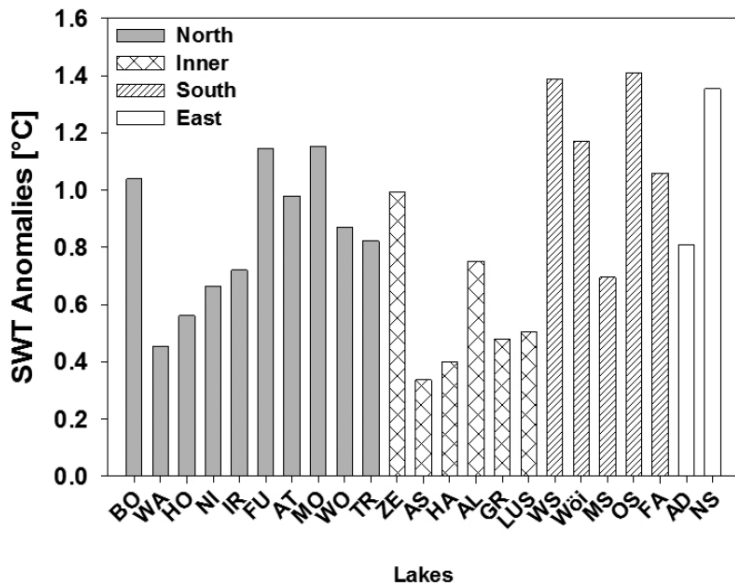


Fig. 3 Surface water temperature (SWT) anomalies as temperature difference in °C between the 1991-2010 period and the 1961-1990 base period for 23 Austrian lakes. The lakes are grouped into lakes north of the Alps, inner alpine lakes, lakes south of the Alps and lakes in the eastern plains (Dokulil, 2014).

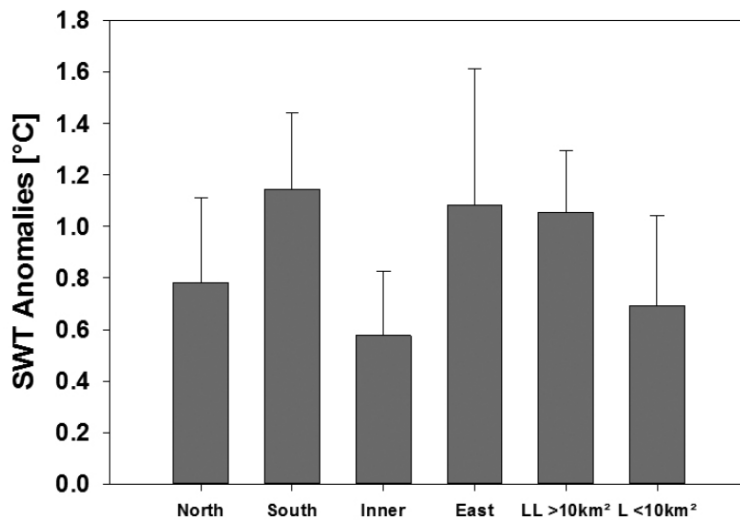


Fig. 4 Mean and standard deviation of SWT anomalies summarised for lakes north, south, and in and east of the Alps. Lakes are additionally grouped into lakes larger and smaller than 10 km² (Dokulil, 2014).

Long-term trends in LSWT of 19 European lakes from Finland, UK, Austria, and Switzerland were summarized by George (2010). The average decadal increase between 1940 and 2000 in 16 lakes north of the Alps was 0.17°C for the winter season and 0.25°C for both spring and summer. The average rate of change in the autumn was 0.07°C/decade but there were large differences between the individual lakes (-0.31 to 0.21). The average increase in LSWT in 3 middle sized lakes south of the Alps was very similar to that north of the Alps but absolute values were smaller and less variable at all seasons. Mean summer SWT increase per decade was 0.29 °C in Switzerland, 0.35 °C in UK, 0.38 °C in Finland, and 0.43°C in Austria. In the 9 Austrian lakes larger than 10 km², Dokulil (2014) reported increments of LSWT ranging from 0.4 to 0.66°C/decade for June to September 1965-2010, whereas 4 of the 9 lakes increased on average by more than 0.6 °C per decade. Warming rates were further analysed for 23 Austrian lakes of varying size and location, and in almost all cases, long-term monthly mean AT are closely related to monthly mean SWT (Dokulil, 2014). The relation of SWT to AT ranged from 0.90 to 1.52. The average SWT anomaly from the base period 1961-1990 was 0.86 °C for the 1991-2010 time window (Fig. 3; range 0.14-1.41 °C), increasing to 0.93 °C when the time frame was changed to the 10-year period 2001–2010. The greatest deviation from the base period of 1.41 °C occurred in the 5 lakes south of the Alps, and the average increase was 0.78 °C in the 10 lakes north of the Alps (Fig. 4).

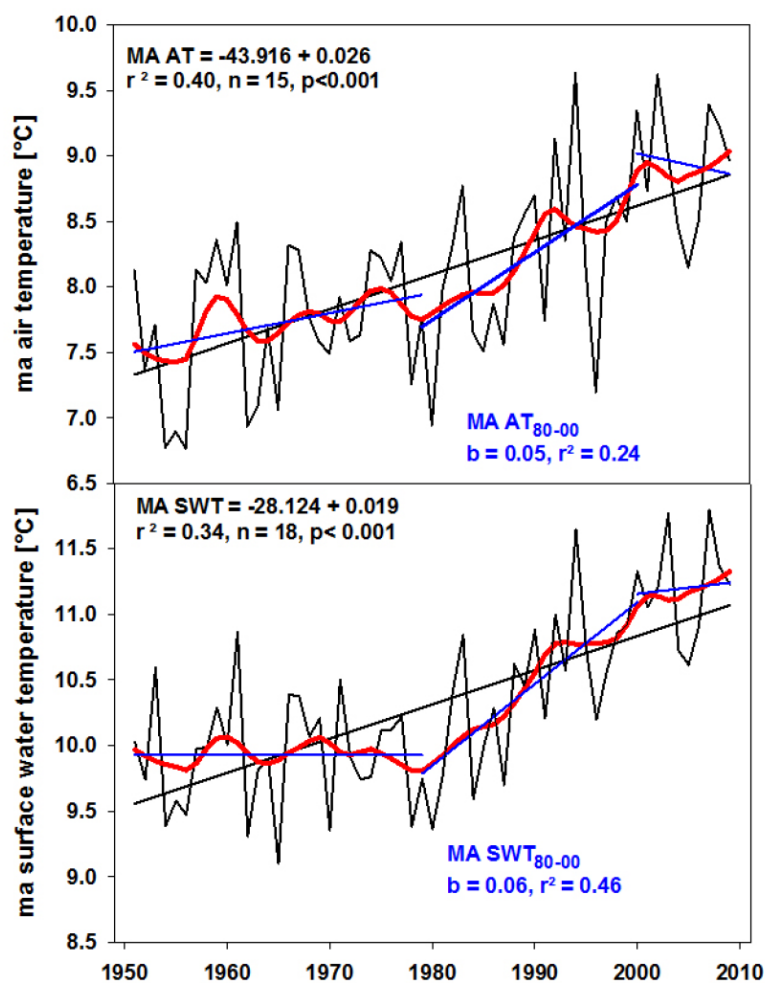


Fig. 5 Time series of mean annual (MA) air temperature (AT) for 15 stations close to the lakes (upper panel) and mean annual surface water temperatures (SWT) for 18 lakes (lower panel) for 1953–2010 (Dokulil, 2014).

Monthly long-term median SWT anomalies for the winter half year (Oct–Mar) were significantly correlated with positive indices of the NAO anomalies, while the summer half year (Apr–Sep) was not significantly related to negative indices (Dokulil, 2014). AT and SWT of Austrian lakes were significantly determined by the NAO winter index except for lakes isolated in alpine narrow valleys or south of the Alps. On a larger scale, however, lakes respond coherently to a long-distance climatic signature across Europe. In fact, average long-term records of AT and SWT for 18 Austrian lakes show at least 3 phases of temperature increments between 1950 and 2010 (**Fig. 5**). In the first phase from 1950 to 1980, average AT increased by 0.2°C/decade and mean SWT remained constant. In the second phase from 1980 to 2000, both temperatures increased at a rate of 0.5 and 0.6°C/decade respectively. The 10-year period 2000–2009 is characterised by reduced warming, with AT decreasing by 0.02 °C per year and average SWT remained almost constant, similar to global observations (Dokulil, 2014).

Increments in SWT are transmitted by convection and turbulence to deeper layers in the water column and eventually affect hypolimnetic water temperatures (HWT). For instance, in Lake Maggiore, Northern Italy, water temperatures had increased at all depths during 1963–1998, but particularly in the deep water below 300 m (Ambrosetti and Brabanti, 1999). Similar increases were found in several other northern Italian lakes, such as Lake Garda, where Salmaso (2005) reported HWT warming of 0.7 °C per decade from 1990 to 2003. Results from 12 lakes across Europe showed that HWT had increased by about 0.1–0.2°C/decade during the last half of the 20th century. In 10 of the 12 lakes, HWT was significantly related to the winter NAO index (Dokulil, 2014).

Increased warming may lead to a complete change in lake stratification and mixing regime (Vincent, 2009). Summer warming will cause increases in the frequency and the duration of stratification events in polymictic lakes, which mix throughout the year. In the long run, lakes currently polymictic or dimictic, which mix twice per year, may become monomictic in the future, i.e. mixing once per year, if they are then free of ice during winter (George, 2010). Deep lakes that are already monomictic will experience individual years in which some form of stratification persists throughout the year, reducing the intensity of mixing and inhibiting deep-water renewal. Thus, some deep monomictic lakes may show a tendency towards becoming oligomictic, i.e. will not mix fully every year (Adrian et al., 2016). For example, in the very deep Italian lakes south of the Alps was found

a reduction of winter mixing over the last 40 years and, consequently, the deeper layers have become less affected by seasonal variations. In such deep lakes, complete circulation becomes increasingly difficult affecting lake hydrodynamics, turnover, deep water chemistry and dissolved gases. Mixing events then require more energy, that is more wind, to re-establish initial thermal conditions (Ambrosetti et al., 2003). Deep polar lakes are usually cold monomictic, i.e. they remain stratified under the ice through most of the year, and then mix at temperatures less than 3.98°C (the temperature of the maximum density of water) throughout their summer period of open water conditions. However, if the water temperatures warm above 3.98°C in summer, the lake will become stratified, and therefore dimictic, with periods of mixing before and after this summer period. This shift from cold monomixis to dimixis is a critical threshold that allows the retention of heat in the surface waters (Vincent, 2009).

Modelling studies on strictly dimictic lakes which are ice-covered in winter suggest that surface temperatures will increase faster than deep-water temperatures as a result of climate change. In monomictic lakes, the divergence between surface and deep-water temperatures is likely to be less strong as a result of heat carry-over in winter (Adrian et al., 2016). However, even in such lakes historical data show that near-surface water temperatures are increasing faster than deep-water temperatures, which implies an increase in thermal stability leading to an increase in the duration of stratification in summer and a corresponding decrease in the duration of homothermy in winter and spring (Adrian et al., 2016). Moreover, for north temperate lakes, the increased duration of ice-free conditions will allow increased warming of the surface waters by sensible heat transfer (conduction) and by radiative transfer (penetration of solar radiation into the water column). These effects in turn cause changes in the density structure of lakes, with a layer of warmer, lighter water at the surface that prevents the transport of heat via turbulent mixing to deeper parts of the lake. This retention of heat in the upper waters acts as a positive feedback mechanism, and with increasing heating the thermal stratification becomes stronger and more resistant to wind-induced mixing. By trapping more heat in the surface-mixed layer, less is available for heating the lower column, and deep waters can become cooler as a result of climate warming (Vincent, 2009). An example of this strong effect on water temperature is the current trend in Lake Superior, Canada-USA. The summer surface water temperatures of this lake increased by 2.5°C over the period 1979–2006, well in excess of the air temperature increase over the same period. This has been primarily attributed to earlier ice break-up and the earlier onset of stratification and warming each year. This differential effect is not apparent in tropical lakes that lack winter ice cover, and such waters appear to be more closely tracking the regional trend in air temperatures (Vincent, 2009).

1.2 Climate change impacts on lake chemistry

Since many of a lake's specific chemical properties are representative of the terrestrial landscape, impacts of climate change on inland waters are essentially a catchment-related problem (Adrian et al., 2009, Dokulil, 2014). Climate affects many landscape properties, including vegetation and soils, which in turn exert a strong influence on water quality and quantity in the receiving lake basin. In fact, changes in weather patterns within the watershed, such as increased temperatures and precipitation, and especially changes in frequency and intensity of extreme events (e.g. heavy rainfalls, storms, and extremely warm or mild seasons), may lead to increased rock weathering, thereby affecting solute composition and concentrations in the runoff (Vincent, 2009, Dokulil, 2014). In addition, global warming is expected to increase evapotranspiration, thereby intensifying the

hydrological cycle, causing also alterations in glacial melting and amount of ice and snow cover in the catchment, which will indirectly impact all water resources (Dokulil, 2014). As a consequence of these changes in terrestrial export related to climatic influences on weathering rates, precipitation, runoff, fire frequency, or terrestrial primary productivity, nutrient concentrations and ratios in lakes are likely to be altered, with cascading effects on nutrient cycling (Jeppesen et al., 2009). The pH, ionic strength, ionic composition, and conductivity are also very sensitive and can be used as indicators of changes in weathering rate or water balance (Adrian et al., 2009). Abrupt changes in AT can strongly change biogeochemical processes in the catchment, thus altering water chemistry and causing ecosystems to become more sensitive to further changes in precipitation (Dokulil, 2014).

The chemical composition of lake waters is affected by the hydraulic residence time of a lake (the time required to completely replace all water in a lake by its river, groundwater and rainfall inputs), as it controls the time available for biogeochemical and photochemical processes to operate, the accumulation and loss of dissolved and particulate materials, and the duration of biogeochemical interactions with the lake sediments and littoral zone (Vincent, 2009). For instance, reduced precipitation and inflows can result in a prolonged residence time, causing an increase in phosphorus accumulation and eutrophication. Conversely, in regions that experience increased precipitation and water flow, the increased flushing of nutrients and phytoplankton may result in reduced algal production, even though this effect may be offset by increased catchment erosion and transport of nutrient-rich soils (Vincent, 2009).

In northern temperate regions, higher annual nutrient loading to lakes is expected due to the higher runoff from the catchment and more extreme events. However, this may not necessarily lead to higher annual mean lake concentrations because the nutrient concentrations in the inlet water are predicted to decline due to dilution (Jeppesen et al., 2009). In southern Europe, the projected increase of winter precipitation will increase nutrient loading to lakes and contribute to a climate-induced eutrophication. The impact will be proportional to external loading and the in-lake nutrient concentration and therefore will be more pronounced in waters of lower trophic (Dokulil, 2014). Several variables, such as winter air and spring SWT, spring epilimnetic phosphorus (P), and hypolimnetic oxygen, varied coherently in several deep lakes south of the Alps (Garda, Iseo, Como, Lugano, and Maggiore). The synchronization originated from effects of the winter climate triggered by atmospheric modes relevant for the Mediterranean (East Atlantic and East Mediterranean pattern) rather than the NAO. Spring water renewal and nutrient replenishment were of prime importance for the interannual variation of the lakes (Salmaso et al. 2014).

Increased temperatures, increased rainfall intensity, and changes in winter rainfall are expected to enhance the P loading to freshwaters in the temperate zone and the Arctic and to reduce the loading, but not the concentrations, in streams and lakes in the Mediterranean region (Jeppesen et al., 2009). In addition, as discussed in the previous section, with higher temperatures, in deep summer-stratified lakes, the thermocline often occurs at lower depth and the duration of stratification increases, whereas polymictic lakes may become temporarily stratified. The stronger and more prolonged stratification of lake waters is likely to lead to more pronounced gradients in chemical variables through the water column. In particular, this enhances the risk of oxygen depletion below the thermocline, triggering the shift from oxygenated to anoxic conditions in the bottom waters. Crossing this threshold is typically accompanied by major upshifts in the concentrations of various toxic compounds, such as hydrogen sulfide (H₂S), and release of algal nutrients from the sediment, including P (Vincent, 2009; Jeppesen et al., 2009; Adrian et al., 2009). An analysis of five summer-stratified Danish lakes, monitored from 1989 to 2003, showed strong interannual variations in oxygen and nutrients in the hypolimnion,

depending on summer temperature (**Fig. 6**). In the years with the highest summer temperatures, the depth where the minimum oxygen concentrations in the hypolimnion passed below 3 and 2 mg/L during the stratification period was lower than the average for the study period and much higher in the colder years. This also means that areas with low oxygen concentrations often, depending on lake morphometry, are larger in warm than in cold years. Maximum ortho-phosphate concentrations in the hypolimnion were overall higher in warm years, likely as a response to the lower oxygen concentrations leading to release of iron-bound phosphate. Total phosphorus responded more strongly to changes in external loading and tends to be lower in cold years (Jeppesen et al., 2009). Higher temperatures also imply a lower oxygen capacity in the water, enhancing the risk of oxygen depletion in the lakes, even though temperature increases much less in the hypolimnion than in the epilimnion with warming. In shallow, non-stratified lakes, P release may also be stimulated by the higher temperature (**Fig. 7**) (Jeppesen et al., 2009). Anoxia can also lead to increased nitrogen losses from the ecosystem by denitrification, the bacterial process that converts nitrate to nitrogen gas (Vincent, 2009).

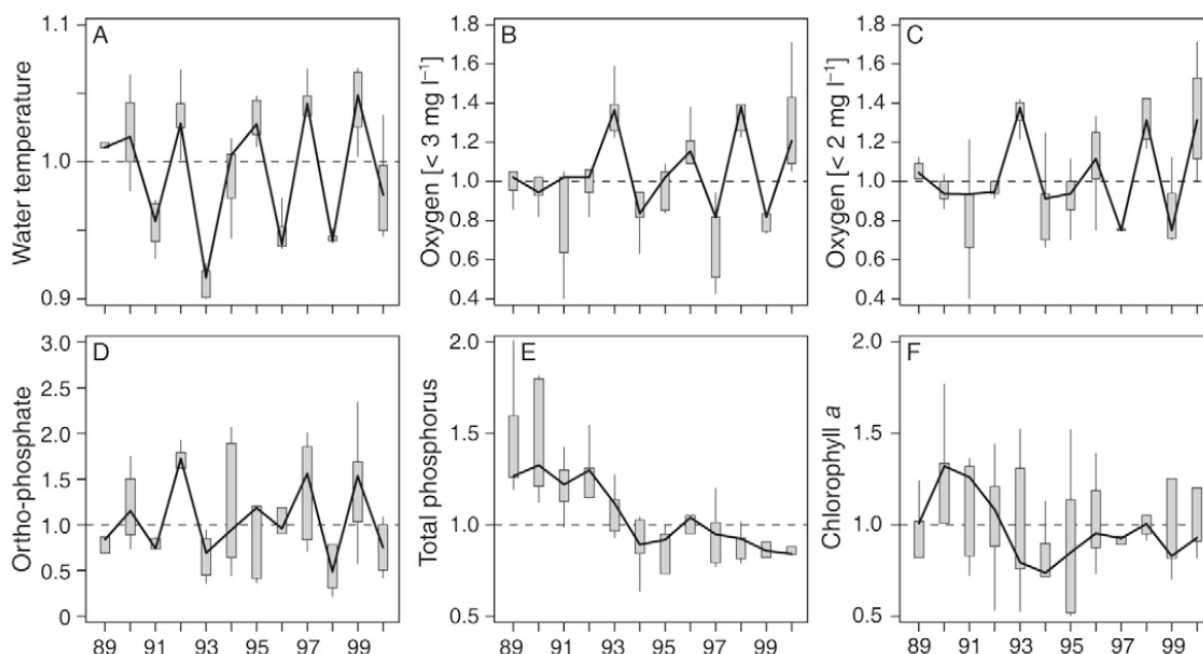


Fig. 6 Boxplot of various variables in each year normalized to the means for the period 1989 to 2003 in five stratified, eutrophic Danish lakes. The variables are interpolated summer mean temperatures in the epilimnion (A), minimum depth where oxygen passes below 3 mgO₂/L (B), and 2 mgO₂/L (C), respectively, at any sampling date during stratification, maximum ortho-P (D), summer mean epilimnion concentration of TP (E), and chlorophyll a (F) (Jeppesen et al., 2009).

Nevertheless, the concentration of nitrate in most European waters has increased in recent years as well, resulting in several problems, such as the acidification of lakes and changes in the qualitative composition of phytoplankton (George, 2010). The factors affecting the atmospheric deposition of nitrate and its transformations in the soil have been intensively studied, but less attention has been dedicated to the effects of weather changes on the transfer of nitrate from terrestrial to aquatic systems. These processes are very different from those that control the supply of phosphate, as nitrate ions are not so tightly bound to the soil matrix and are more readily mobilised by rain. Moreover, the relationship between the quantity of nitrate leached from the catchment and that measured in the lake is quite complex and can be influenced by the depth of a lake, its residence time and the growth of different functional groups of phytoplankton (George, 2010). In Europe,

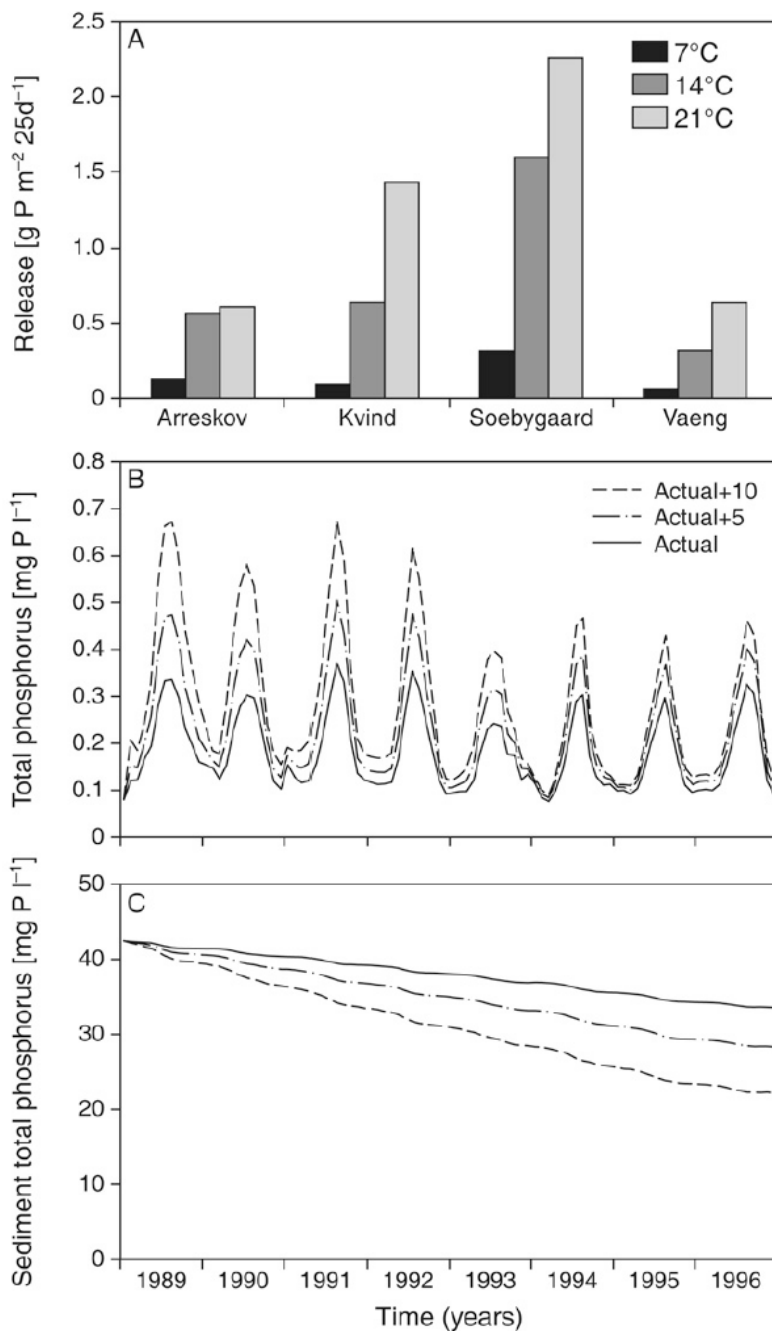


Fig. 7 Short-term experiments showing release of phosphorus (P) at three different temperatures in four shallow Danish lakes (A); simulated changes in P in shallow Lake Dons, Denmark, after nutrient loading reduction, during the period 1989-1996: water P concentrations (B) and change in the P pool in the upper 20 cm of the sediment (C) under three temperature scenarios (Jeppesen et al., 2009).

historical analyses summarized in [George \(2010\)](#) indicate that the factors regulating the flux of nitrate were different in the lakes of two climatic regions. In Finland, the key factor was the change in the snow pattern, which has a major effect on the seasonal dynamics of nitrate and is, in turn, regulated by the soil and air temperature. In particular, the controlling factors are believed to be the depth of snow, the timing of spring snow melt and the hydrological characteristics of the catchment. In fact, a net mineralization of nitrogen under snow has been reported, and alternate periods of freezing and thawing, a feature of mild winters, result in a net increase in the leaching of nitrate. In contrast, in UK, the most important factor was the projected increase in the winter rainfall, which may lead to a progressive increase in the winter load of nitrate, even if this trend could be reversed if increasing amounts of nitrate are retained by biological uptake in the catchment. Increased terrestrial uptake of nitrate in mild winters was assumed to be an additional factor ([George, 2010](#)).

Despite the small fraction of the earth surface occupied by inland waters, they play a substantial role in the global carbon (C) cycle and thus potentially affect climate as well. In fact, the consumption and production of carbon dioxide (CO_2), methane, and nitrous oxide by microorganisms influences the concentrations of these greenhouse gases (GHG) in the atmosphere and thereby affects the atmospheric

heat budget. Recent analyses have shown that lakes are extremely active sites for transport, transformation, and storage of considerable amounts of C received from the terrestrial environment and therefore may have an effect that is disproportional to their spatial extent ([Tranvik et al., 2009](#)). Dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) are the predominant carbon inputs to most lakes, followed by particulate organic carbon (POC) and particulate inorganic carbon, with their relative importance varying with lake location

and hydrology (Tranvik et al., 2009). However, the continuing alterations in the biogeochemical processes in watersheds and within lakes, and alterations in the occurrence and geographic distribution of lakes (e.g., by loss in regions where the climate will become dryer), will change the future role of lakes with regard to carbon cycling and climate (Tranvik et al., 2009). DOC loading is particularly responsive to climate change, through the leaching and erosion of soils, changes in microbial transformation rates of particulate and dissolved organics, and through changes in catchment vegetation (Vincent, 2009). DOC is an important constituent of many natural waters. It is generated by the partial decomposition of organic matter and may be stored in soils for varying lengths of time before transport to surface waters. DOC imparts a characteristic brown colour to the water due to the absorption of visible light by these compounds, thus influencing light penetration into surface waters, as well as their acidity, nutrient availability, metal transport and toxicity (Kernan et al., 2011).

Alterations in precipitation patterns as a result of shifts in climate will likely affect the inputs of carbon to aquatic systems from the watershed. Carbon loading to lakes, in particular, will be influenced by the impacts of hydrological patterns on terrestrial primary production. DOC integrates multiple responses within the lake, such as water transparency (particularly in the ultraviolet range), heat absorption, and lake metabolism, as well as changes observed in the catchment related to increased run-off, permafrost melting, shifts in vegetation, and changes in wetlands, and increased CO₂ concentrations (Adrian et al., 2009). In some cases, increased drought has been associated with increased DOC inputs to lakes through the exposure of previously water-logged peat to oxygen, thereby triggering microbial degradation and mobilization of DOC. In contrast, other analyses indicate that drier climates yield lower concentrations of DOC in lakes as a result of increased water retention times and, hence, more time for degradation processes to occur. Wetter climates result in more export of DOC to lakes and higher standing stocks, first by increasing the proportion of DOC-rich water derived from organic soils and secondly by reducing water residence time, and hence DOC removal by degradation (Tranvik et al., 2009; Kernan et al., 2011).

Increases in watershed net primary production are likely to result in higher DOC concentrations, bacterial production, bacterial respiration, and emission of CO₂ to the atmosphere in subarctic lakes. In addition, decomposition of soil organic matter induced by warming, especially in arctic and subarctic soils, will result in greater transport of allochthonous DOC to lakes that previously received low inputs (Tranvik et al., 2009). In fact, experimental data suggest that rates of soil DOC production are increased under higher temperatures and in response to a shift from anaerobic to aerobic conditions in saturated soils (Kernan et al., 2011). Allochthonous DOC concentrations can be a key indicator of catchment processes, particularly in boreal catchments, where DOC is generally dominated by allochthonous material, and increasing inputs associated with climate change are having strong effects on lake ecosystems (Adrian et al., 2009). Increases in nutrient input from watershed processes may also increase the autochthonous production of DOC, whose sources include extracellular release by phytoplankton, release by grazers, and lysis of plankton (Tranvik et al., 2009). During the past two decades, rising DOC concentrations have been observed across much of the lakes in the British Isles, large areas of Fennoscandia, parts of Central Europe, and northeastern North America, widely interpreted as evidence of climate-change impacts on terrestrial carbon stores (Kernan et al., 2011).

Many lakes are oversaturated with CO₂ emitted to the atmosphere, often attributed to the oxidation of DOC in the lake. However, data from 20 lakes and 26 years showed that CO₂ is also directly delivered from inflowing streams and not only produced by lake degradation, suggesting that CO₂ emission to the atmosphere is not necessarily a symptom of heterotrophic lake ecosystems but a reflection of the productivity of the catchment. Thus, any alterations in catchment management and concomitant effects of global warming will affect future

CO₂ concentrations in lakes and their emissions to the atmosphere (Dokulil, 2014). With an increase in the relative importance of autochthonous DOC compared to that of allochthonous DOC, the evasion of CO₂ to the atmosphere is expected to decrease (Tranvik et al., 2009).

1.3 Climate change impacts on lake ecosystem dynamics

The changes in the physical and chemical properties directly and indirectly affect the physiology, distribution, life cycle, and the development of the aquatic organisms, and those of lake systems are particularly sensitive because of the relatively static nature of the lacustrine environments (Adrian et al., 2009).

Responses of lake biota to climate change are complex and often species-specific, because of multiple interactions of different factors such as resource availability, density dependence, and predation (Adrian et al., 2009; Vincent, 2009). However, some widespread climate-related changes of lake biota have emerged, and the mechanisms involved are becoming better understood. The great variety of direct and indirect effects operates at multiple scales, from changes in whole ecosystem structure and dynamics, to physiological responses at the individual level (Vincent, 2009).

For instance, phytoplankton and zooplankton communities, which respond rapidly to subtle thermal changes, have been relatively well-documented in many lakes over extended time periods. Therefore, their records are useful for extracting climate-related responses (Adrian et al., 2009). In particular, changes in spring and early summer phenology can provide a good reflection of climatic shifts for fast-growing plankton. For longer-lived organisms with a complex life cycle, climate warming can accelerate ontogenetic development, which can cause a shift in growth rates, abundance, and species composition. In fact, given sufficient resource availability, increasing temperatures generally accelerate growth and development rates of individual organisms, although changes in absolute abundances tend to be species-specific (Adrian et al., 2009). In addition, stronger vertical stratification induced by climate can cause shifts in phytoplankton species composition, especially among those taxonomic groups that are sensitive to temperature and mixing, such as cyanobacteria, diatoms, and flagellates. In particular, at higher temperatures, bloom-forming cyanobacteria have a competitive advantage over other phytoplankton groups. Changes in fish-species distributions, abundance, and community structure are also a consequence of climate effects, particularly as available habitat for cold-water species contracts (Adrian et al., 2009).

In fact, at the broadest scale, the potential of climate change to radically alter the physical structure of lake ecosystems can cause the extinction or alteration of aquatic biota. For example, the contraction of large shallow lakes can induce major habitat loss, and even in deep lakes relatively small fluctuations in water level may result in the loss of important ecological features (Vincent, 2009).

Changes in ice cover, stratification, and mixing, and thereby the vertical gradients in lake properties, will have significant effects on pelagic communities. In fact, the resulting changes in light and nutrients will affect phytoplankton production, and therefore the availability of food to high trophic levels. However, while for some high-latitude systems decreased ice cover and stronger stratification may allow for increased irradiance supply and rates of primary production, in temperate lakes earlier summer stratification results in a higher nutrient limitation of algal growth, due to the shorter period of nutrient mixing from deep waters into the euphotic

zone. A prolonged ice-free period can be also an advantage for some fish species, as it can reduce oxygen depletion of the hypolimnion and the resulting “winter kill” of fish stocks (Vincent, 2009).

Changes in light and nutrient availability will also have a qualitative effect on species composition and diversity at the primary producer level, which in turn may impact on higher trophic levels. A major concern at temperate latitudes is the possible shift in phytoplankton composition toward dominance by species of cyanobacteria that form harmful blooms, thereby creating many water quality problems, including production of various toxins, disruption of zooplankton feeding and oxygen depletion (Vincent, 2009; Shimoda et al., 2011).

Fish play a key role in the trophic dynamics of inland waters. Complex changes in fish assemblage structure may be expected with climate warming due to direct effects of temperature and indirect effects operating through eutrophication, water level changes and stratification (Dokulil, 2014). Many fish species are sensitive to even small changes in the temperature of their surroundings, and the warming trend associated with climate change is likely to cause a shift in the geographic distribution of many taxa. Some cold water species may become extinct in some lakes because their thermal tolerance is exceeded, while other species may be able to colonize new habitats as a result of warmer conditions (Vincent, 2009). In European lakes, profound changes were reported during recent decades in fish assemblage composition (e.g. higher dominance of eurythermal species), body size and/or age structure, associated with an increase in temperature of about 0.15-0.3 °C/decade (Jeppesen et al., 2012). Climate change may also affect the migratory behaviour of some fish species. For example, migration of species from arctic lakes to sea, e.g. arctic char, are projected to decrease if lakes become more productive as a result of climate change, even though this may result in individuals of smaller size (Vincent, 2009).

The combined effects of the global climate change and the other anthropogenic stressors are profoundly altering freshwater biological processes. Several biogeochemical studies have shown the effects of lake temperatures and water chemistry changes on individual organism physiology, population abundance, community structure, and food-web dynamics. These structural shifts may be more severe in aquatic environments with strong seasonality, where growth and reproduction of many species are usually restricted to short time windows over the annual cycle and prey–predator interactions are largely determined by synchronies in space and time. In fact, climate change has different effects on various taxonomic groups/trophic levels, thus can also decouple species from favourable food conditions, a process referred as the match-mismatch hypothesis (Shimoda et al., 2011).

1.3.1 Phytoplankton

Phytoplankton are at the base of aquatic food webs. They are the dominant primary producers in many aquatic ecosystems, are critical to global biogeochemical cycling and of global importance for ecosystem functioning and services (Winder and Sommer, 2012; Rühland et al., 2015). Phytoplankton closely tracks both short- and long-term environmental changes in lake ecosystems (Salmaso, 2010). In fact, the dynamics of these photosynthetic cells are linked to annual fluctuations of temperature, water column mixing, resource availability, and consumption (Winder and Sommer, 2012). Nutrients represent one of the main environmental dimensions defining fundamental and realised algal niches, but other factors, essentially mediated by lake physiography, hydrology and food web structures, also have a major influence on the development of algal communities (Salmaso, 2010). Climate can modify these environmental factors and affects phytoplankton both directly through physiology and indirectly by changing fundamental aquatic ecosystem processes, such as water

column stratification, resource availability or grazing by heterotrophs (Winder and Sommer, 2012). In fact, substantial differences are recognisable in algal communities when the effects of latitude, and therefore climate, on phytoplankton composition and abundance are considered (Salmaso, 2010). Thus, recent anthropogenic warming within lakes can alter the seasonal development of phytoplankton growth, structure and taxonomic composition, e.g. favouring species traits best adapted to changing condition (Winder and Sommer, 2012). In all lakes, the response of algal communities is most evident and striking when climate-mediated ecological thresholds are passed (Rühland et al., 2015).

Knowledge on the effects of warming on plankton species diversity and food webs is still limited respect to those on terrestrial environments. One of the reasons is that direct effects of temperature increase in aquatic ecosystems tend to be muted by the high specific heat of water and the key dependence of primary production on nutrients rather than temperature. In addition, in deep lakes, the role played by climatic fluctuations and anthropogenic nutrient alterations on phytoplankton may be confounded by the effects of spring lake overturn on surface nutrient enrichment (Salmaso, 2010).

Temperature directly affects metabolism of primary producers, which consists of both photosynthetic and respiratory activity. However, it is expected that global warming increases light-saturated rates of photoautotrophic production, but not light-limited ones, which are insensitive to temperature (Winder and Sommer, 2012). Moreover, compared to photosynthesis rates, the metabolism of heterotrophic organisms is more sensitive to temperature. Consequently, warming should increase consumption by herbivores more strongly than primary production, thus strengthening top-down control over primary production (Winder and Sommer, 2012).

However, the most significant climatic effects on phytoplankton species composition will very likely be related to changes in thermal stratification patterns such as vertical mixing processes (**Fig. 8**), usually accompanied by changes in availability of light and nutrients, and largely determined by meteorological variables. Enhanced water column stratification suppresses the upward flux of nutrients from deep-water layers through vertical mixing, resulting in more nutrient-depleted conditions in surface waters. This results in the competitive advantage of specific algal cell types that are better competitors for nutrients. Moreover, a change in the intensity or duration of thermal stratification has a direct impact on turbulent diffusion and thus phytoplankton cell sedimentation, the major mechanisms causing vertical displacement for non-motile cells. As sinking velocities increase non-linearly with size, smaller and buoyant species have an advantage in an environment where turbulence is not present to resuspend all planktonic species (Winder and Sommer, 2012).

Light, essential for photosynthesis, is also dependent of climatic conditions of temperature, wind, and precipitation, which act on stratification, cloud cover, and transport of suspended solids and dissolved humic substances from land. Therefore, climate change will influence the light availability for phytoplankton in different and contrasting ways. In fact, earlier onset of thermal stratification, earlier ice-melt and reduced mixing depth in summer induced by warming tend to increase light availability. On the other hand, increased windiness will partially counteract this effect, i.e. delay the onset of stratification and increase mixing depth, in addition to increase the resuspension of sediments. Moreover, increased runoff from land will increase the transport of suspended particulate matter or humic matter to lakes, influencing underwater light conditions (Winder and Sommer, 2012).

Despite different interacting processes strongly control abundance, distribution, and size structure of phytoplankton communities, some widespread climate-related responses have emerged. In fact, a large number of

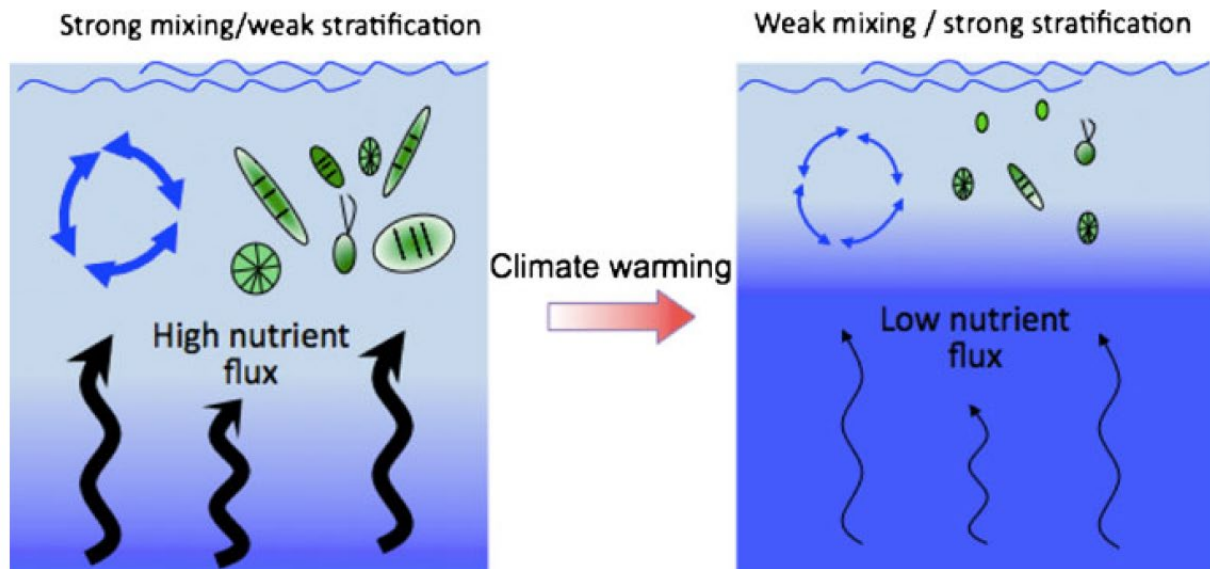


Fig. 8 The effect of increasing temperature on water column stratification (blue arrows), associated nutrient redistribution (black arrows), and phytoplankton production and cell size (Winder and Sommer, 2012).

studies have reported that the timing and magnitude of seasonal plankton blooms are shifting in response to climate change. Plankton blooms are an important source of energy and drive many ecosystems and community processes in seasonal aquatic environments. Timing and magnitude of blooms are controlled by resource dynamics and predator-prey interactions, but they are usually initiated by changes in water temperature and light supply (Winder and Sommer, 2012). Shifts in plankton spring phenology related to climate have been shown in several ecosystems, whereas later in the season the extraction of a clear climate signal is complicated by other factors like biotic interactions. In particular, phytoplankton spring peaks have advanced in a variety of aquatic systems induced by climate warming (Dokulil, 2014), and changes in bloom magnitude have been observed (Winder and Sommer, 2012).

Both empirical evidence and model predictions show that the advancement of the spring phytoplankton bloom timing is an established pattern in north temperate deep lakes regardless of their trophic status. In fact, the spring phytoplankton bloom has advanced on average by 1-2 weeks, responding both to the earlier stratification onset or to a relaxation of turbulent vertical mixing (Shimoda et al., 2011). For example, spring warming advanced the timing of stratification onset and the spring bloom in Lake Washington by 20 days over the last four decades. However, the degree of advance varies among taxonomic groups, with cryptophytes and diatoms showing the strongest response to warming (Winder and Sommer, 2012). An analysis of long term data from a 58-year period (1945–2003) for 4 lakes in the English Lake District showed that the timing of the phytoplankton spring peak not only advanced, but species phenology reacted differently. For instance, the timing of the *Asterionella formosa* maximum advanced but was delayed for *Aulacoseira* spp. and *Cryptomonas* spp. in Lake Windermere, *A. formosa* and *Aulacoseira* spp. advanced with temperature while *Cryptomonas* spp. was significantly delayed in 3 lakes. However, soluble reactive phosphorus concentration had a more consistent effect upon phenology respect to temperature (Dokulil, 2014).

Enhanced water column stratification and subsequently more nutrient-depleted conditions in surface waters is also expected to affect phytoplankton size structure. In these conditions, small-sized algal taxa are expected to be favoured because of their rapid nutrient exchange through the cell surface, lower sinking rates and more rapid division (Winder and Sommer, 2012).

Diatoms are an abundant phytoplankton group in aquatic habitats, contributing between 20 and 25% of global primary production, and an essential link for energy transfer to upper trophic levels, as they are a preferred high-quality food source for primary consumers (Winder et al., 2009; Rühland et al., 2015). In most freshwater lakes, diatom algae are often dominant primary producers, in some cases comprising the majority of a lake's phytoplankton biovolume (Rühland et al., 2015). Individual diatom cells are relatively large, commonly in the range of 10-200 μm , characterized by silicon oxide cell walls, which cause them to sink readily. Therefore, many diatoms benefit from turbulent mixing to remain suspended in euphotic water layers. In temperate systems, diatom population dynamics show strong seasonal patterns and often bloom in spring when growth conditions of mixing, nutrients and light availability are optimal (Winder et al., 2009).

Therefore, as thermal stratification and physical mixing processes are controlled by climatic forcing, it is expected that climate change will particularly affect diatom abundance and community structure. In fact, the vertical thermal and, hence, density gradient affects the energy required to mix nutrient-depleted surface waters with the nutrient-rich deep waters, and suppresses the formation of turbulence, increasing sinking velocities of non-motile species. These physical changes of the water column affect light and nutrients availability of individual cells. Consequently, climate warming is expected to enhance the competitive advantage of cell types that are better competitors for nutrients and able to maintain their vertical position in the euphotic zone, and replace diatoms, which generally have high nutrient requirements and high sinking rates, with other phytoplankton groups best adapted to reduced turbulent mixing (Winder et al., 2009).

However, morphological and physiological traits differ widely among diatom species. In particular, most physiological traits and sinking parameters can be related to cell size: small-sized diatoms with high surface area to volume ratios have small diffusion boundary layers that enable efficient nutrient uptake, higher ability to harvest light, and lower sinking rates respect to large-sized cells with low surface area to volume ratio. Thus, it can be expected that, as a taxonomic group, they may have the capacity to adapt to mixing alterations induced by climate, through the selection of species that are best adapted to enhanced water column stratification (Winder et al., 2009). In fact, both paleolimnological and limnological studies have shown the existence of measurable effects of climate change on the taxonomic structure of diatoms (Salmaso, 2010). Using a long-term diatom dataset (1982-2006), Winder et al., 2009 showed that diatoms were able to maintain their biovolume with increasing water temperature and stratification in Lake Tahoe over the last decades. However, the diatom community structure changed, as small-cell species with lower sinking velocity were selected, particularly within the *Cyclotella* genus. This study shows that within the diverse group of diatoms, small-sized species with a high surface area to volume ratio were able to adapt to a decrease in mixing intensity, supporting the hypothesis that abiotic drivers affect the size structure of planktonic communities and that warmer climate favours small-sized diatom cells.

Among phytoplankton groups, cyanobacteria are in general of major interest because their potential toxicity might have negative effects on the environment, health, economics, and society. In fact, in a warmer world, species-specific responses in cyanobacterial biomass may significantly affect bloom toxicity, biodiversity, and ecosystem functioning (Dokulil, 2014). Bloom-forming cyanobacteria are likely to be favoured in a warming climate by several mechanisms. First, cyanobacteria have a higher maximum specific growth rate compared to other groups, such as diatoms and green algae, at temperatures above 23°C, which makes them strong competitors at high temperatures, as showed by several studies reporting increases in cyanobacteria at higher temperatures in several lakes with different mixing regimes (Salmaso, 2010; Winder and Sommer, 2012). Thus, warmer conditions will favour their more rapid accumulation and dominance. Second, these species can

regulate their position in stable water columns through gas vacuoles that, changing their density, allow them to sink or rise to the optimal depths for photosynthesis or nutrient uptake. This ability to exploit habitats under intensified stratification, provide them a distinct competitive advantage over other phytoplankton taxa at reduced vertical mixing. In fact, increased stratification and water column stability predicted for future climate change scenarios would favour this strategy (Winder and Sommer, 2012). Third, cyanobacteria tend to become increasingly prevalent with increasing degree of phosphorus enrichment, which, as discussed before, will be a consequence of a warmer climate, in terms of both internal and external phosphorus loading (Vincent, 2009). Warmer water temperatures coupled with favourable hydrodynamic conditions will potentially increase the relative contribution of cyanobacteria to the total phytoplankton biomass in nutrient enriched freshwater ecosystems. In particular, there is evidence that the lagged response between phytoplankton and cladocerans abundance peaks provides a window of opportunity for filamentous cyanobacteria to establish dominance after the diatoms in warm springs (Shimoda et al., 2011). Excessively warm and cold AT can alter the biomass of cyanobacteria in either direction (Dokulil, 2014). However, Gallina et al. (2011) found these temperature extremes did not lead to cyanobacterial dominance in 5 perialpine lakes of different trophic status. In these cases, both extreme hot and extreme cold events generated a loss of diversity among cyanobacteria.

Phytoplankton can also influence the thermal structure of lakes by feedback mechanisms. In fact, phytoplankton biomass induces an increase in vertical light attenuation, therefore affecting vertical short-wave radiation. High light attenuation results in higher surface temperatures, stronger stratification and shallower thermoclines (Dokulil, 2014).

Differences in phenological responses among primary producers and consumers, e.g. different degrees of change in phytoplankton peaks and zooplankton growth, can lead to a decoupling of food requirements and peak food availability. This can result in predator-prey mismatches, affecting energy transfer to higher trophic levels, and thus greatly influencing food-web dynamics (Winder and Sommer, 2012).

1.3.2 Zooplankton

Zooplankton are key components of aquatic food webs, as they are the intermediate trophic level between phytoplankton and fish and account for a large proportion of the energy transfer to fish. Zooplankton are also key in the transfer of energy between benthic and pelagic domains (Everett et al., 2017). Therefore, a better understanding of the role of climate change in altering zooplankton dynamics, structure, and function is of high scientific and economic value. As reported in **Fig. 9**, which summarizes the documented and projected direct and indirect effects of climate change on freshwater zooplankton, variation in temperature, precipitation, wind and subsequent floods, droughts, altered mixing regimes all represent major forcing on the abiotic and biotic component. Temperature, however, is one of the most important factors accounting for variation in nearly all biological rates and times, including population growth, life span, developmental time and metabolic rate (Vadadi-Fülöp et al., 2012). The latter, in particular, is known to control ecological processes at all levels of organization. Species' response may be determined by the seasonal timing and rates of warming, in combination with species-specific life-history events mediated by temperature. In particular, in different lake ecosystems, a key variable concerning phenological changes are spring temperatures, which have shown the strongest increases (Wagner et al., 2013).

A central concept when studying the relationship between different components of ecological systems is the match vs. mismatch of the climate-phenology response. In fact, some coexisting species respond to warming at similar rates and thus maintain synchrony (match), whereas for other coexisting species, a loss of synchrony may lead to a decoupling of their interactions (mismatch). Asynchronies in biotic communities induced by climate change are likely to result in a phenological decoupling of trophic relationships, because of the different sensitivity of predators and their preys to physical changes, e.g. increasing time lag between population peaks (Shimoda et al., 2011; Vadadi-Fülöp et al., 2012). It is demonstrated that asynchrony across multiple trophic levels of as little as 2 weeks increases the potential risk of temporal changes in trophic match (Wagner et al., 2013). However, phenotypic adaptations or genetic modifications of populations may optimize the timing of consumers and their ability to effectively access good quality food, ensuring the integrity of the food-web interactions (Shimoda et al., 2011).

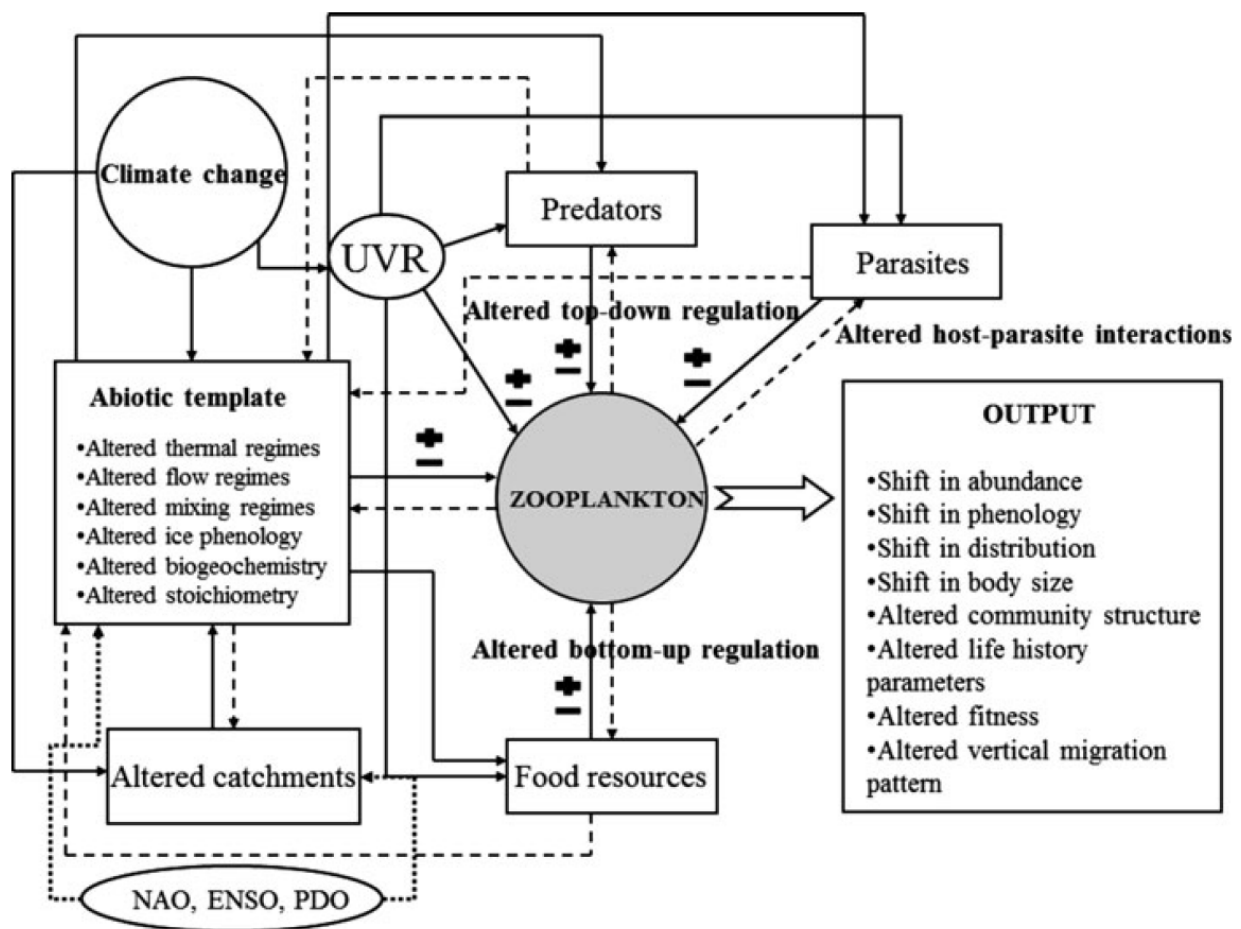


Fig. 9 Conceptual model of the possible direct and indirect effects of climate change on freshwater zooplankton. Solid arrows indicate linkage between components while dashed arrows indicate feedbacks. Dotted lines indicate synchronizing effects of large-scale oceanic fluctuations (NAO, ENSO and PDO). Plus and minus signs indicate potential positive and negative effects on zooplankton (Vadadi-Fülöp et al., 2012).

As increased temperature leads to an earlier peak in phytoplankton, the relative timing of different zooplankton groups is also changed (Shimoda et al., 2011; Dokulil, 2014). For instance, this decoupling was reported in Lake Washington, where, following an advancement of the spring phytoplankton bloom, the rotifer *Keratella cochlearis* appeared to adapt its phenology, whereas *Daphnia pulicaria* was not able to do so and declined in abundance. This mismatch may be explained by the different life history strategy and thus the different hatching

cues used by the cladoceran (Vadadi-Fülöp et al., 2012). Other observed shifts in zooplankton phenology ranged from 1 week in *Bosmina sp.* and *Keratella sp.* to 3 months in *Bythotrephes longimanus*, and theoretical studies also suggest that phenological events in freshwater zooplankters will advance considerably (Vadadi-Fülöp et al., 2012).

Daphnia species play a key role in the food web of temperate freshwater systems (Wojtal-Frankiewicz, 2012; Wagner et al., 2013), and the factors determining spring biomass levels of daphnids have recently received considerable attention. Climate warming can influence *Daphnia* population dynamics, altering predator-prey interactions and algal biomass control. Several studies indicate that warming has direct and indirect effects on *Daphnia* biology and ecology through its influence on their metabolism, growth and reproduction, and the properties of their habitats (Wojtal-Frankiewicz, 2012). The adaptive response of daphnids is generally high and includes phenotypic plasticity and changes in genotypes, although it also depends on the strength of selection and the available genetic variation. The seasonal timing and magnitude of temperature increases are important for seasonal biomass fluctuations of *Daphnia*, thus influencing the potential synchrony of daphnids and phytoplankton succession. Even a minor warming during critical seasonal periods can disturb *Daphnia* population dynamics and destabilize lake food webs by decoupling trophic interactions (Wojtal-Frankiewicz, 2012). In fact, the mechanism through which climate warming affect the timing of growth of *Daphnia* populations are different respect to phytoplankton. While the earlier transition from strong to weak vertical mixing is decisive for phytoplankton development, for *Daphnia* growth the increase in water temperature is more important. A mismatch in timing of the two processes may thus interrupt food web interactions in spring (Dokulil, 2014). For instance, in Lake Washington a long-term decline in daphnids populations was associated with a growing temporal mismatch with the spring diatom bloom, and this shift to their diet has been hypothesized to have strong ramifications on food-web interactions (Shimoda et al., 2011). Moreover, the early summer period of algal suppression by herbivores resulting in a clearwater phase, a regular and distinct feature in temperate lakes, has advanced by approximately 2 weeks in some central European lakes within the last 30 years (Dokulil, 2014).

Both winter and spring are important critical periods for determining seasonal fluxes of daphnids and, consequently, the occurrence and duration of their midsummer decline. Moreover, winter conditions may also affect the impact of fish predation on daphnids during summer (Wojtal-Frankiewicz, 2012). Thus, it's clear that the different responses of daphnids to climate anomalies depend on both biotic (e.g., predator abundance and seasonal phytoplankton succession) and abiotic (e.g., hydrodynamics, intensity and duration of thermal stratification, trophic state, and geomorphology) factors of lakes, which are directly influenced by weather changes. As discussed before, reduced vertical mixing favours small-sized species, species with buoyancy regulation (e.g. cyanobacteria) and motile flagellates over diatoms and green algae with higher sinking velocities, thus altering community structure of phytoplankton. This is of crucial importance for consumers, as diatoms are known as high-quality food for zooplankton because of their high content of HUFA (highly unsaturated fatty acids), whereas increased cyanobacteria dominance does not favour herbivorous zooplankton and may have several negative effects on grazers. In fact, cyanobacteria are poor-quality food for zooplankton, their filaments cause mechanical interference with the feeding apparatus of filter feeders, and they can be toxic for consumers. However, small zooplankters (cyclopoid copepods, small-bodied cladocerans, and rotifers) can also benefit from cyanobacteria dominance, for instance by escaping from competition with large-bodied herbivores, e.g. *Daphnia*. Moreover, calanoid copepods have found to be better suited to cyanobacterial blooms than cladocerans (Vadadi-Fülöp et al., 2012).

Since increased stratification and reduced mixing can cut nutrient flux from deeper layers, the consequent decrease in phytoplankton production can also lead to the starvation of zooplankton. For instance, the strongly reduced *Daphnia* abundance in Esthwaite Water, England, was assumed to be the result of food limitation because shallow mixing hampered algal growth through nutrient depletion. However, Daphnids may also benefit from stratification through a direct positive response to increased water temperatures and/or, indirectly, via increased phytoplankton productivity (Vadadi-Fülöp et al., 2012).

These are all examples of food-web related bottom-up effects of climate change from a zooplankton perspective. Regarding top-down effects, the study of Manca and DeMott (2009) is an example of how climate warming-related change in habitat structure can induce strong cascading effects in pelagic food webs. This study showed that in Lake Maggiore, Italy, the earlier establishment of thermal refuge from fish predators, linked with climate warming, allowed the predatory cladoceran *Bythotrephes longimanus* to strongly increase in abundance and suppress the population of *Daphnia hyalina galeata*. Warming can also increase the risk of predation by prolonging the period of predators spending in the open water. For example, *Leptodora kindtii* predation on *Daphnia galeata* advanced by 13 days per degree warming in Bautzen reservoir, Germany (Vadadi-Fülöp et al., 2012).

However, climate warming may allow increased predation pressure on zooplankton due to improving growing conditions and decreasing winter mortality of fish. Furthermore, fish may become smaller and more omnivorous with increasing temperatures implying higher predation on zooplankton and constraining vertical migration (Jeppesen et al. 2010). This means that high densities of planktivorous fish and related strong predation pressure have the potential to mask the direct effect of climate change on zooplankton. For instance, it has been showed that, although warming during spring increased both the net recruitment and the consumptive mortality of *Daphnia* populations, the latter increased to a much higher extent, thus reducing the population stability during summer. Consumptive mortality may be forced by changes in fish communities towards a dominance of planktivorous fish, induced by a direct effect of warming on juvenile stages or by a superior competitive ability of the warm-adapted species (e.g. cyprinids). Since planktivorous fish are typically characterized by highly selective predation on large grazers, this can cause complex changes in ecosystem processes (Wagner et al., 2013). Therefore, in general, global warming may change the habitat overlap between planktivorous fish and their prey both spatially and temporally, but the outcome of this predator-prey interaction may vary with species and places.

Wagner et al. (2013) performed a field study in Saldenbach Reservoir, Germany, a dimictic, temperate reservoir to understand how warming during a sensitive period alters trophic interactions of three key species: *Daphnia* (primary consumer), the predatory cladoceran *Leptodora kindtii* (secondary consumer, feeding on *Daphnia*), and *Perca fluviatilis* (tertiary consumer, feeding on *Daphnia* and *Leptodora*). *Leptodora* is a key species in many temperate freshwater systems. It preys upon different zooplanktonic crustaceans, including *Daphnia*, and it is dynamically coupled to the vertebrate *Daphnia* predators. In contrast to their original hypothesis and to some other lake studies, it resulted that warming exceeding a critical mean temperature during May (14° C) increases the stability of the *Daphnia* population during summer. This result suggests that predicting the consequences of climate warming for plankton dynamics may require the knowledge of lake-specific differences in timing and rates of trophic interactions. In fact, elevated May temperatures shortened the period of matching of predation on *Daphnia* by *P. fluviatilis* and *L. kindtii* by up to 1 month, and a lower match index correlated to high *Daphnia* biomass during summer (Fig. 10a). By contrast, low *Daphnia* biomass occurred when the synchronised predation was extended until the end of August in cold-May years. In addition, total predation losses of

Daphnia in July also decreased significantly at elevated May temperatures (**Fig. 10b**), because the positive temperature effect on *Leptodora* growth and consumption resulted to be less important compared to the indirect cascading effect of *P. fluviatilis* which may control the dynamics of *Leptodora* during summer. Consequently, the indirect effects of higher trophic levels stabilised the *Daphnia* population during summer. This study indicates that the effect of spring warming on the population stability of *Daphnia* was related to differences in timing and rates of the cascading effect of *P. fluviatilis* on *Leptodora* rather than to the direct top-down control of fish on *Daphnia* or to temperature effects on reproduction of *Daphnia*.

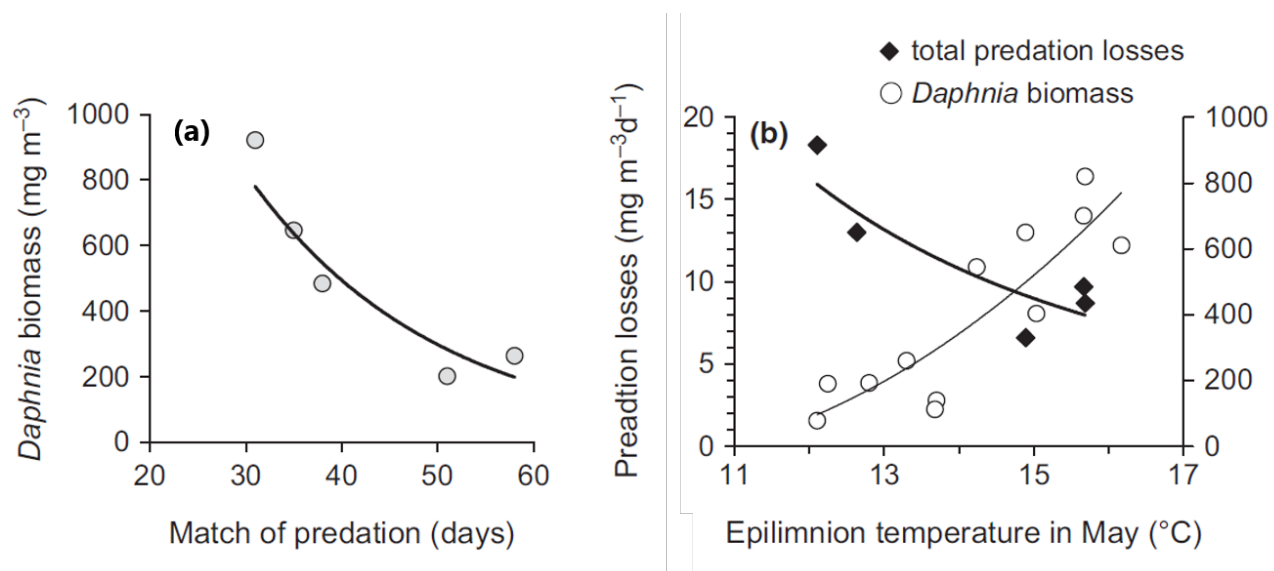


Fig. 10 Temperature-driven changes in the duration of matching of predation by *Leptodora* and *P. fluviatilis* on *Daphnia* biomass during August (a); impact of epilimnetic temperatures during May on predation losses of *Daphnia* (b, black quadrate) and consequences for *Daphnia* summer dynamics (b, white circles) (Wagner et al., 2013).

Analysis of long-term zooplankton time series suggests that increased climate variability may either increase or decrease long-run population growth rates. Simulations show that the amplitude of fluctuations of herbivorous zooplankton increases with temperature while the mean biomass and minimum values decrease. In fact, the mean densities of all interacting species in a community subject to environmental stress will be determined by the sensitivity of all species and the indirect effects of species interactions (Vadadi-Fülöp et al., 2012).

Climate warming may have both direct and indirect effects on body size. It has been shown that increasing temperatures shifted the zooplankton assemblage toward smaller forms, even though some studies have not supported these findings (Vadadi-Fülöp et al., 2012). However, a recent meta-analysis on ectotherm aquatic organisms including also zooplankton provides an evidence of decreasing body size both at the community and individual levels in response to climate change (Daufresne et al. 2009). Among several explanations proposed, the most important is that higher temperatures are coupled with increasing metabolic costs. Furthermore, it has been suggested that even cyanobacterial toxins can cause a reduction in adult size of *Daphnia* (Vadadi-Fülöp et al., 2012).

Another significant component of global environmental change is the establishment of non-native species, which is particularly influenced by altered thermal regimes. One of the most striking and well-documented examples of climate change-related invasions in freshwater zooplankton is the that of *Daphnia lumholtzi* in southern US reservoirs, which, however, is not expected to have a major impact on the native zooplankters

(Vadadi-Fülöp et al., 2012). In contrast, as a result of *Bythotrephes longimanus* invasion, species richness, abundance, and diversity of native zooplankton, particularly cladocerans, strongly declined in some North American and European lakes. In the case of Lake Maggiore, abundance and invasion success of *B. longimanus* were linked to the duration and thickness of a deep, warm-water refuge from planktivorous fish, associated with variation in lake thermal properties (Manca and DeMott 2009).

1.3.3 Fish

Fish play a key role in the trophic dynamics of lakes, promoting cascading effects through predation on zooplankton (thus increasing phytoplankton biomass), and linking littoral, benthic and pelagic zones through nutrient translocation. Climate change will expose fishes to new habitats through different mechanisms, which will probably not operate independently, but in synergy between them (Ficke et al., 2007). Changes in fish habitat suitability in response to climate change have been already documented by numerous studies, mainly focused on cold-water species such as salmonids, because of their ecological, economic and cultural importance, and because they might be more prone to respond than other tolerant species, especially in the early decades of climate alteration (Comte et al., 2013).

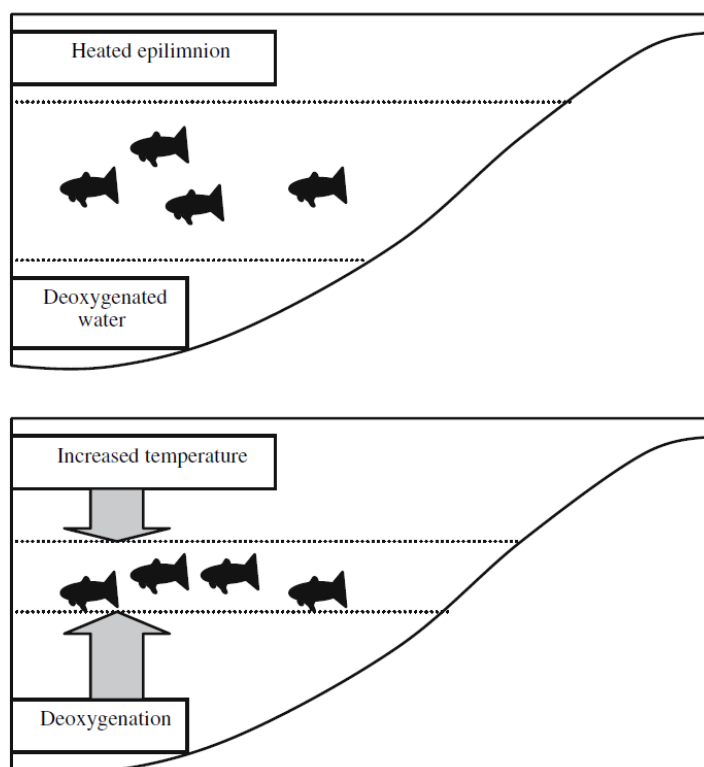
Climate warming can induce changes in fish community structure through direct and indirect effects on fish metabolism, biotic interactions and geographical distribution, with potential major changes in ecosystem functioning (Jeppesen et al., 2010; Jeppesen et al., 2012). In general, warmwater fish are stimulated by climate warming while cold-water and cool-water fish are negatively affected, even though the response of cool-water species could be more variable (Comte et al., 2013). Fish communities in temperate regions are usually dominated by cold-water species with physiological optima below 20°C. These communities are vulnerable to displacement by invasive non-native cool water species (optima 20-28°C) or even warm water species (optima >28 °C) when temperatures rise (Dokulil, 2014).

Since all freshwater fishes are exotherms, i.e. they cannot regulate their body temperature through physiological means, but only by moving to different areas, they are constrained by the range of temperatures available in the environment (Ficke et al., 2007; Jeppesen et al., 2010; Jeppesen et al., 2012). Therefore, different physiological functions such as growth, food consumption or reproduction, which depends on body temperature, can be affected by increasing global temperature, through a variety of mechanisms including cardiac inefficiency and increased cost of repairing heat-damaged proteins. As a consequence, fish population can increase or decrease in abundance, experience range expansions or contractions, or face extinction, depending on their temperature tolerance ranges, according to which species are classified as stenothermal (narrow thermal range), e.g. *Salvelinus alpinus*, or eurythermal (wide tolerance range), e.g. *Cyprinus carpio* (Jeppesen et al., 2010; Jeppesen et al., 2012). Other important factors are also the region they inhabit, the magnitude and rate of the thermal change in the ecosystem, and the opportunities to move to areas with appropriate thermal conditions. In fact, endemic species in small lakes or in rivers with impassable barriers may not be able to move to avoid lethal conditions (Ficke et al., 2007).

Moreover, since oxygen solubility in water has an inverse relationship with water temperature, and metabolic rates of most cold-blooded aquatic organisms increase with temperature, an increase in temperature will both decrease the dissolved oxygen supply (through reduced saturation concentrations relative to air) and increase the biological oxygen demand. In addition, as global temperatures rise, stratification in temperate zone lakes will be strengthened and prolonged, making more difficult the mixing process, which is essential for the movement of oxygen to the hypolimnion. Therefore, fishes can face situation where the decreased supply of oxygen

cannot meet the increased demand (Ficke et al., 2007, Jeppesen et al., 2010). Concentration of dissolved oxygen below 2-3 mg/L are considered hypoxic for most aquatic organisms. In particular, this can compromise the suitability of the hypolimnion, an important refuge from high summer water temperatures for numerous cold-water stenothermal fishes, such as *Salvelinus spp.* and *Coregonus spp.* As shown in **Fig. 11**, fishes are then confined to shrinking habitats whose boundaries are defined by the warm temperatures in the epilimnion and the low levels of dissolved oxygen in the hypolimnion. The smaller volumes of these thermal refugia are characterized by rapid oxygen depletion, low prey availability, stress, and increased probability of disease transmission. Decreased levels of dissolved oxygen can reduce the growth and reproductive success of individual fishes, which will become smaller, less fecund and less likely to survive. Acclimation and adaptation to lower levels of dissolved oxygen are possible but with limitations, depending on other environmental stressors (Ficke et al., 2007).

Fig. 11 Climate change may restrict pelagic habitat availability for many species, due to their different temperature and oxygen requirements. Increased solar radiation will thicken the epilimnion, and increased fish metabolism will result in decreased concentrations of dissolved oxygen (Ficke et al., 2007).



However, increased strength and duration of thermal stratification could increase access to prey for cool- and cold-water species, by decreasing the ability of a prey species to use the epilimnion as a refuge. Moreover, warm- and cool-water fishes, such as *Perca spp.*, may experience an increase in thermal habitat because of increased global temperatures (Ficke et al., 2007).

Longer periods of stratification also create favourable conditions for cyanobacteria, inedible to most species of zooplankton consumed by planktivorous fishes. Therefore, such a shift in phytoplankton composition can negatively affect fisheries productivity. In addition, some species of cyanobacteria (e.g. *Anabaena flos-aquae*) produce alkaloids that are toxic to fish or their prey items (Ficke et al., 2007).

Increases in lake trophic states, likely resulting from increased temperatures through altered external and internal nutrient loading and evaporation rates, often negatively affect fish communities through direct effects on macroinvertebrate prey and through effects on the algal community that support the zooplankton. Therefore, eutrophication in temperate lakes appears to replace economically important species such as salmonids

with smaller and less desirable species such as cyprinids (Ficke et al., 2007, Jeppesen et al., 2010). Eutrophication also favours the reduction of oxygen levels in the hypolimnion in stratified lakes, which may further stimulate a shift in fish community composition in deeper lakes (Jeppesen et al., 2010).

Fishes inhabiting temperate and polar regions areas will be particularly affected by temperature change. In temperate ecosystems, a slight increase in water temperature could be beneficial for fish currently limited by temperatures below the species optimum, because of the extension of the growing season, i.e. summer months, and the increase in over-winter survival. However, for cold- and cool-water (e.g. *Salvelinus spp.* and *Coregonus spp.*) fish growth rates are predicted to increase only if the food supply can sustain the increased metabolic demand. At temperatures above a species' optimal temperature, feeding activity is depressed (Ficke et al., 2007). Therefore, cold-adapted species, such as salmonids, will likely be extremely affected, in particular in eutrophic lakes where oxygen levels in the hypolimnion are low. Future local extinctions and distribution contractions are projected as a result of the decline in the number and size of areas of suitable habitat for most cold-water fish species (Comte et al., 2013). *Salvelinus alpinus* populations are already declining, for instance, in Lake Elliðavatn, Iceland, where a major reduction was recorded from 1987 to 2006 after a significant warming of the lake, with increase in monthly mean temperatures of 0.8-2.7 °C over February-September, due to rising air temperature (Jeppesen et al., 2010). However, some studies have also found that in some North American lakes, climate change could result in an increase in suitable thermal habitats for all thermal guilds, including cold-water species (Comte et al., 2013). In general, the potential responses of cool- and warmwater species to future climate change show greater variation and often depend on the location and the climate change scenario used. In some cases, cool-water species are likely to follow the same general trend as cold-water species (i.e. a decline of suitable habitat) but to a lesser degree, even though some studies have also suggested that they could experience an increase in suitable lake habitat. Regarding warm-water species, most studies are consistent in finding that they may benefit from future climate warming and experience an increase in their suitable thermal habitat and their distribution (Comte et al., 2013).

Many temperate freshwater fish species are limited by cold water temperatures at the highest latitudes and altitudes of their range, and by warm water temperature at the lowest latitudes and elevations of their range. Therefore, a global warming trend would result in the northward expansion of warm- and cool-water species, which would compete for space with native species. In fact, range shifts will occur at the species level, but not necessarily at the community or ecosystem level, as fishes (and other organisms) in the same community may not share the same thermal optima and tolerance limits. This raises the possibility that ecosystem components like food webs, interspecific competition, and host-parasite interactions will be altered. Moreover, the shift in dominance of the fish community may not only be a direct effect of temperature on the most sensitive stages (typically the juvenile stage), but could be also a result of reduced competition with more warm-adapted species (Ficke et al., 2007, Jeppesen et al., 2010). Percids are expected to move northward in the absence of dispersal limitations and may be favoured at the expense of coregonids and other salmonids. Further warming may also benefit cyprinids in Europe and centrarchids in North America (Jeppesen et al., 2010). Expansions beyond the currently known spatial distribution of several fish species have already been reported, promoting the colonisation or establishment of non-native species. For instance, climate warming allowed an invasive species, *Morone americana*, to invade the Great Lakes, thus potentially endangering native populations. Similarly, the spatial distribution of the *Rhodeus amarus* appears to have recently expanded in Eastern Europe, probably due to a combination of factors including rising air temperature (Comte et al., 2013).

A comparison of fish populations in Europe has shown that lower-latitude fish species are often smaller, grow faster, mature earlier, have shorter life spans and allocate less energy to reproduction than populations at higher latitudes (Jeppesen et al., 2010; Jeppesen et al., 2012). A higher growth rate and an earlier age at maturity at lower latitudes are probably determined mainly by longer growing seasons, higher temperatures, and stability of resources, potentially increasing fish fecundity. Moreover, spawning starts earlier and last longer with decreasing latitude, likely due to an adaptive response to the shorter growing seasons at high latitudes. Analyses on the age structure of *Perca fluviatilis* and *Rutilus rutilus* in 50 Swedish lakes also showed that the proportion of young fish increase from north to south. It was argued that such changes in size/age structure along a latitude gradient are a result of a long-term evolution and adaptation to the climate conditions. Data from 200 Danish lakes collected in the period 1989-2006 confirmed this hypothesis for *Perca fluviatilis* and *Abramis brama*, which showed a fast response to increasing temperature in May-July, with a higher proportion of small (<10 cm) fish, while *Rutilus rutilus* was not affected by temperature (Jeppesen et al., 2010). Climate warming seems also to affect feeding habits of fish. It was found a greater contrast between size of fish at the upper and lower ends of food chains with increasing latitude, and therefore a greater contrast in

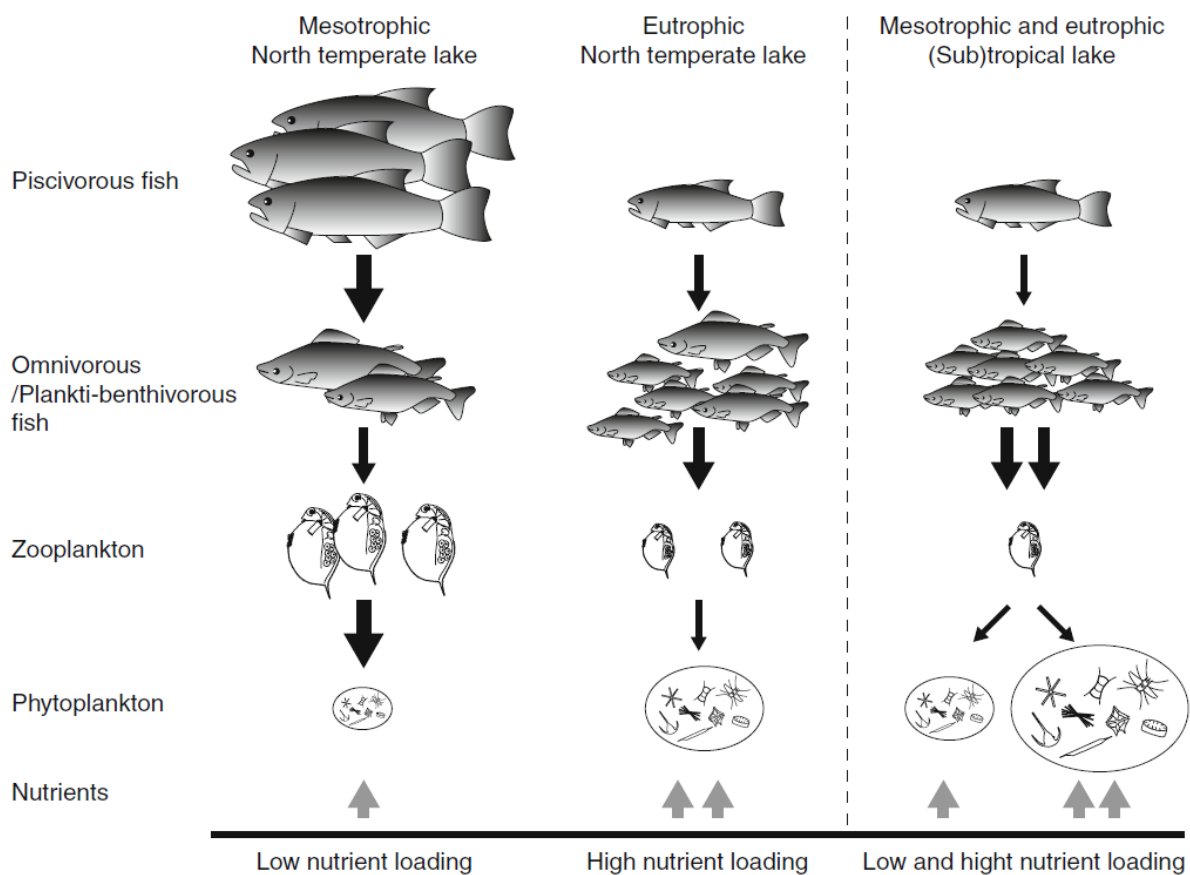


Fig. 12 Conceptual model showing trophic structure changes in sensitivity to nutrient loading in mesotrophic and eutrophic lakes. In north temperate mesotrophic lakes, plankti-benthivorous fish are controlled by piscivorous fish, which release the predation on large-bodied zooplankton (*Daphnia* spp.). Therefore, grazing on phytoplankton is relatively high and the lakes are only moderately sensitive to small increases in nutrient loading. When such lakes become eutrophic, the control of piscivores is reduced and the number of cyprinids feeding on large-bodied zooplankton increases. Accordingly, there are few *Daphnia* and the grazing on phytoplankton is low. Such lakes are extremely sensitive to additional nutrient loading which is channelized directly into phytoplankton growth. In subtropical lakes, however, lakes are dominated by numerous small omnivorous fish and grazing zooplankton is scarce in both mesotrophic and eutrophic lakes, in contrast to similar temperate lakes. Accordingly, warm lakes are all highly sensitive to addition of nutrients (Jeppesen et al., 2010).

diet. In fact, fish communities in warm climates appear to be characterised by a high proportion and richness of omnivorous species. An analysis of 137 lakes where only native species were present found that the proportion of fish species consuming plant material was higher (>25%) in warm lakes than temperate lakes (0-25%), whereas in Arctic and Subarctic lakes none of the fish species consumed plant material. This is consistent with other studies, which found that in 84 European lakes the top-down control of plankton by benthivorous fish weakened from North to South Europe. Moreover, in subtropical lakes there is a predominance of omnivorous planktivorous fish, with few large strict or facultative piscivorous species. Therefore, the trophic cascading effects from piscivorous fish on phytoplankton appear more likely to occur in cold-temperate lakes than in warm lakes, as illustrated in **Fig.12** (Jeppesen et al., 2010).

The decreasing proportion of piscivores and the higher dominance of zooplanktivorous and omnivorous fish implies increased predation on zooplankton and, consequently, less grazing on phytoplankton with increasing temperatures. In European lakes, it was found that the ratio of fish biomass to zooplankton biomass increased from North to South and that the zooplankton/phytoplankton biomass ratio decreased substantially. Moreover, data from Danish lakes indicate a decrease in the average size of cladocerans and copepods with increasing temperature, which usually suggests enhanced predation by fish (Jeppesen et al., 2009).

Moreover, a shift towards stronger benthic-planktivorous and omnivorous fish dominance induced by climate will likely promote a stronger energy flux from the littoral and benthic zones to the pelagic zone, thus increasing nutrients available to primary producers (Jeppesen et al., 2010).

Jeppesen et al. (2012) reviewed long-term fish data series from 24 European lakes, which experienced, along with an annual temperature increase of about 0.15-0.3 °C per decade, profound changes in fish assemblage composition, body size and/or age structure during recent decades. The cold-stenothermic *Salvelinus alpinus* has been particularly affected and decreased in abundance in the majority of the lakes where it was present. Coregonids and *Osmerus eperlanus* showed a different response depending on lake depth and latitude. *Perca fluviatilis* has apparently been stimulated in the north, but its abundance has declined in Lake Maggiore, Italy. Eurythermal species such as *Abramis brama*, *Sander lucioperca* and/or *Alosa spp.* are apparently increasing in several lakes. Specific results for 5 of the lakes considered in the analysis of Jeppesen et al. (2012) are now reported.

In lakes Vänern and Vättern, Sweden, two deep oligotrophic lakes, the increase in water temperature was significant since 1955, and more pronounced during the last 20 years, inducing several marked changes in the commercial catch for the key fish species. While there is no trend in total catch over time, in Lake Vänern the catches of *Sander lucioperca* have increased over time, whereas in Lake Vättern the catches of *Salvelinus alpinus*, the traditionally most important species, have declined steadily from the mid-1950s, negatively correlated with an increase in mean temperature. In Lake Vänern also resulted that long ice winters, where the ice lasted until the beginning of March or longer, yielded a strong recruitment of *Coregonus albula*. (Jeppesen et al., 2012).

Lake Constance (Austria/Germany/Switzerland), the second largest peri-alpine lake in Europe, after a pronounced eutrophication during the twentieth century, became oligotrophic by the beginning of the twenty-first century and undergone an average water temperature increase in the upper 20 m of 0.22 °C per decade between 1965 and 2009. Annual commercial yields peaked during the 1970s at around 30 kg/ha and declined to pre-eutrophication levels (17 kg/ha) during the 2000s. Commercial harvests of *Salvelinus alpinus* increased markedly in the 2000s, suggesting that lake oligotrophication has improved its conditions, counteracting the effect of increasing temperature. Moreover, an effect of the temperature increase on the harvest of the

dominant fish species, coregonids and *Perca fluviatilis*, could not be detected, likely because this deep lake always provides cold-water refuges, even though such an effect might occur in the future under persisting oligotrophic conditions (Jeppesen et al., 2012).

In the deep and eutrophic Lake Geneva, France/Switzerland, the mean temperature has increased by 0.17 °C per decade since 1986. The most important change in the fish assemblage over the past decades has been a major increase in commercial catches of coregonids, positively correlated with mean temperature and negatively with total phosphorus, mainly interpreted as the result of changes in lake trophic state following nutrient loading reduction. However, the lake warming was also favourable for coregonids recruitment, as the change in seasonal dynamics of primary production provided an earlier availability of food for the fish larvae. In contrast, *Salvelinus alpinus* was negatively impacted by the lake warming, with catches negatively related to both mean temperature and total phosphorus. Moreover, warming induced a mismatch between *Perca fluviatilis* juveniles and *Rutilus rutilus* larvae as a food resource, thus favour the dynamics of *R. rutilus*, which avoids predation from *P. fluviatilis* juveniles (Jeppesen et al., 2012).

Lake Maggiore is a large oligomesotrophic pre-alpine lake, situated in north-western Italy, which undergone eutrophication since the mid-1960s, followed by a recovery period since the mid-1970s. During recent decades the effects of climate warming have become also particularly evident, with significant increases in water temperatures both in the hypolimnion and the epilimnion. Since the 1980s, the total fishing yield has decreased significantly from 45 kg/ha to the current 8 kg/ha, and species contribution to the catches has changed markedly, reflecting the changes in lake fish assemblages, induced by multiple stressors. In particular, coregonids and *Salmo trutta* harvests have decreased significantly, while *Alburnus arborella* has almost disappeared. In contrast, eurythermal species such as *Alosa agone* and *R. rutilus* recently became abundant in the catches. Harvests of coregonids, *S. trutta* and *P. fluviatilis* were all negatively correlated with hypolimnetic temperature (Jeppesen et al., 2012).

1.4 Objective of the thesis

The aim of this thesis is to implement a dynamic food-web model for Lake Garda, a deep sub-alpine lake, built in Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Christensen et al., 2008), explicitly accounting for the effects of water temperature increase on the system components. The application of ecosystem modelling represents a useful tool to better understand aquatic ecosystem dynamics, test future scenarios and assess possible management strategies in systems vulnerable to climate change effects. Despite being characterized by an inherent uncertainty, the EwE mass balance modelling approach is a well-known method to quantitatively describe external impacts on ecosystems. EwE models have been extensively applied to many ecosystems worldwide, in particular open seas and coastal areas, but rather rarely to freshwater ecosystems, especially in Europe.

Therefore, the final goals of the thesis are: describing the ecological structure of Lake Garda, quantifying food-web interactions and trophic flows, and gaining a better understanding of the dynamics taking place in the system and the direction towards which it can evolve, by obtaining a future outline of the lake, representative of the end of 21st century.

The following chapters are structured as follows: chapter 2 is composed by five main sections, which present a detailed description of the study area (section 2.1), formulations of the EwE modelling approach (section 2.2),

an illustration of the different functional groups included in the food-web model (section 2.3), methodologies and literature sources used to derive the key parameters required by the EwE model (section 2.4), and methodologies used to perform dynamic simulations based on temperature increase scenarios (section 2.5); chapter 3 illustrates the main results obtained by the analysis, including steady-state model (section 3.1) and dynamic simulations (section 3.2); chapter 4 presents a discussion of the results and possible limitations related to the methodology; lastly, chapter 5 contains a summary and concluding remarks.

2. Materials and methods

2.1 Study site

Lake Garda is the largest of the deep southern subalpine lakes (which include also Lakes Orta, Maggiore, Lugano, Como, Iseo and Idro, with depths ranging from 120 to 410 m and an overall volume of over 124 km³), with a surface of 368 km², a maximum depth of 350 m and a volume of 49 km³, representing over 30% of freshwater volume stored in the natural and artificial Italian basins (Salmaso and Decet, 1998; Salmaso et al., 2002). Located in one of the most densely populated and productive Italian areas, Lake Garda is a renowned interest location for tourism, in addition to being an important resource for fishing and water supply for both drinking and irrigation purposes. Management and protection of this important natural and economic resource require a careful and qualified study of its physical, chemical and biological characteristics. However, due to the absence of environmental emergencies and to the apparently better water quality in comparison to the other deep southern subalpine lakes, continuous limnological studies in Lake Garda began only at the end of the 1980s (Salmaso, 2002).

On the basis of its bathymetry, Lake Garda can be divided into a western (W) and an eastern (E) basin, separated by an underwater ridge connecting the Sirmione peninsula with Punta S. Vigilio (**Fig. 13**). The western basin is the larger and deeper of the two: in its northern part the shores descend at steep slopes and the bottom covers over 20 km at depths from 300 to 350 m (maximum depth). In the eastern basin, the maximum depth is around 80 m and the shape is nearly conical. Despite its extent, the eastern basin represents only around 7% of the lake's overall volume (Salmaso and Decet, 1998; Salmaso, 2002; Salmaso, 2005).

The drainage basin covers 2260 km² (including the lake) and is mainly alpine, with about 28 km² covered by glaciers, reaching a maximum altitude of 3556 m a.s.l. (M. Presanella). Most of the area is formed by sedimentary rocks (limestones, dolomites, marly and dolomitic limestones, morainic and fluvial deposits). Igneous (granites, granodiorites, quartz diorites, quartz porphyries) and metamorphic rocks (quartz phyllites, mica schists and paragneisses) are abundant only in a limited area of the northwestern part of the drainage basin (Salmaso and Decet, 1998).

The main inflow is River Sarca, at the northern edge of the lake. Other tributaries are of less importance and mainly flow towards the western and northern shores. The outflow is River Mincio, at the southern edge of the lake, with an average discharge of about 58 m³/s. This value is low if compared with those of the other two

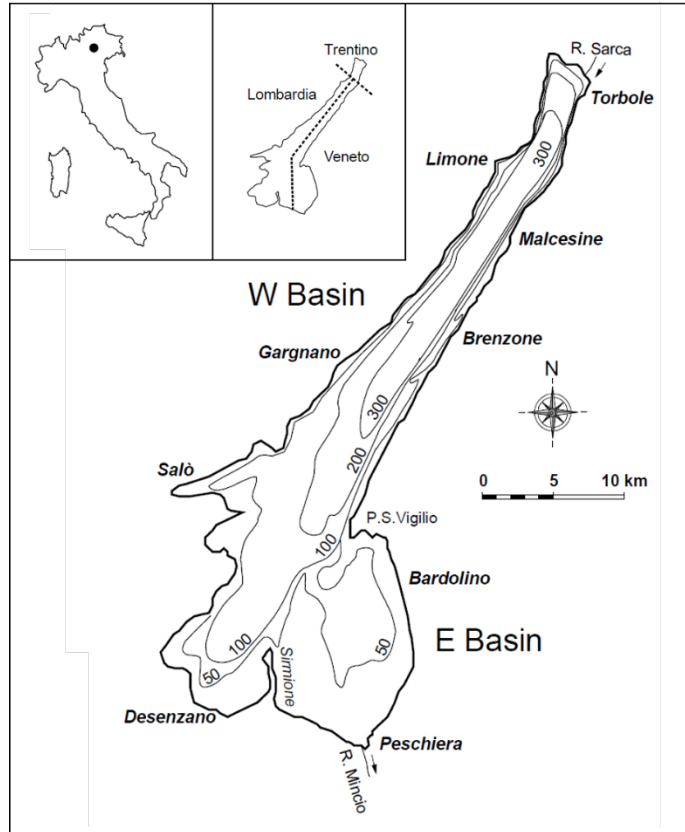


Fig. 13 Location and bathymetric map of Lake Garda (modified from Salmaso, 2002).

largest subalpine lakes (Maggiore, 296 m³/s, and Como, 158 m³/s), and is due to the Lake Garda's small catchment (lake included)/lake surface ratio (around 6) and to a low annual rainfall in the catchment area (790-1150 mm). As a consequence, the Lake Garda's theoretical water renewal time of about 27 years for the whole basin is the longest among the deep southern subalpine lakes (Salmaso and Decet, 1998; Salmaso, 2002).

The present oligo-mesotrophic character of Lake Garda contrasts with its original oligotrophic status. In fact, at the end of the 19th century this lake was characterised by a very low abundance of fish. Moreover, paleolimnological analyses estimated, for a period at the beginning of the 20th century, a very low annual production for Lake Garda, indicative of oligo- or ultra-oligotrophic conditions. The long-term studies carried out from the 1970s showed an increase of the phosphorus content in the water column, with concentrations of TP generally below or around 12 µg/l in the 1970s and mid-1980s, and 17-20 µg/l at the end of the 1990s. This increase is associated with the resident population rise and the strong development of tourism. The changes in the phytoplankton community were difficult to report because of the scarcity of available works and of the different methodologies adopted in the field and laboratory, especially in the investigations before the 1970s (Salmaso, 2002). In the upper catchment, in Trentino region, the lake receives discharge from sewage treatment plants, whereas a ring trunk sewer along the western and eastern shores, in Lombardia and Veneto regions, carries waste waters around the lake. The inadequacy of the ring trunk sewer in controlling nutrient loads, due to insufficient size and operational problems, as highlighted by a few surveys, has apparently contributed to the increase of phosphorus concentrations in the lake (Salmaso, 2010).

2.1.1 Physical and chemical aspects

Lake Garda and the other deep lakes located south of the Alps should be classified as warm monomictic, i.e. they circulate completely once a year in the winter at or above 4 °C and are stably stratified for the remainder of the year. However, owing to their great depth, they are typically characterised by variable temporal periods of incomplete mixing, interspersed with occasional events of complete mixing during cold, windy winters, a situation known as oligomixis (Salmaso et al., 2002).

The lake presents a marked stratification from June to September, due to a pronounced heating of the upper water column during summer, with a maximum deepening of the thermocline to 30-45 m (Salmaso et al., 1997a; Salmaso, 2002) (Fig. 14). The course of thermal stratification follows a similar pattern in the two basins. However, in some years, particularly in 1999 and 2000, the establishment of the thermal stability in the deepest and large W basin appeared delayed in comparison to the shallower east basin, due to the greater thermal inertia of the W basin and its elongated shape, which favours the action of strong winds and wave action (Salmaso, 2002). The highest temperatures reach 22-25 °C at the surface in July and August, whereas the lowest reach 8.3-9.0 °C from February to early April. In the two basins, the layer 0-20 m shows a complete thermal mixing between the end of September and October. In the deeper layers, temperatures vary between 8.17-8.66 °C (100 m), 8.00-8.26 °C (200 m) and 7.97-8.14 °C (bottom, 340 m). Minimum thermal gradients in the whole water column are reached between March and April (Salmaso et al., 1997a, Salmaso, 1998). The analysis of hypolimnetic temperatures allowed to identify episodes of cooling in spring 1991, 1999-2000 and 2004-2006, associated with complete mixing events. In the deepest layer (300 m to bottom), the decrease of the

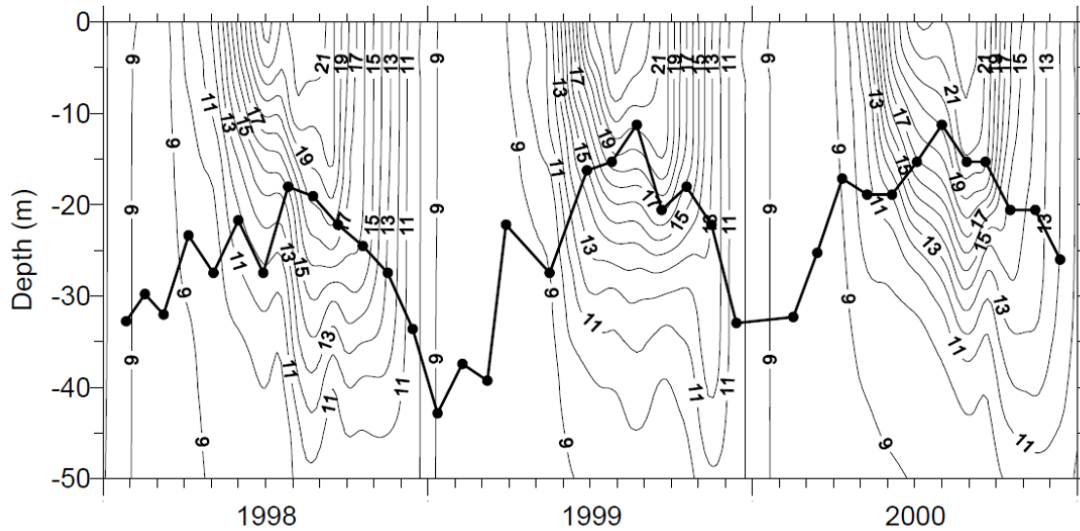


Fig. 14 Isoleths of temperatures (°C) with superimposed seasonal variations of the euphotic depth (m) in the western basin (Salmaso, 2002).

temperature values on these occasions ranged from 0.18 °C (1991) to 0.378 °C (1999) (Salmaso et al, 1997b; Salmaso, 2005; 2010). At present, the periods of partial or complete mixing appear to be strictly determined by the evolution of the climate. In fact, in the years of complete circulation in 1991, 1999 and 2000, the water column experienced its greatest cooling after a decrease in the mean winter (December-February) air temperatures of around 2 °C compared to previous years (Salmaso et al., 2002). In the period between the cooling episodes, the hypolimnion underwent progressive significant warming. In the layer comprised between 200 m and the bottom, the temperature increase followed a linear trend with an average increase of about 0.1 °C/year. At 100 and 150 m the annual thermic cycle was still evident, but there was a tendency toward higher average temperatures (Salmaso et al., 1997b; Salmaso, 2005; 2010). The alternation of periods of gradual warming with short events of cooling is strongly linked to the long-term evolution of the winter climatic conditions, as can be observed by the temporal evolution of the mean winter air temperatures and minimum mean values of temperature recorded in the lake from 0 to 100 m (Fig. 15). Since the 0-100 m layer underwent homogeneous cooling every year, it may be considered to represent the part of the lake that is most affected by the climatic events during the limnological winter (Salmaso, 2005).

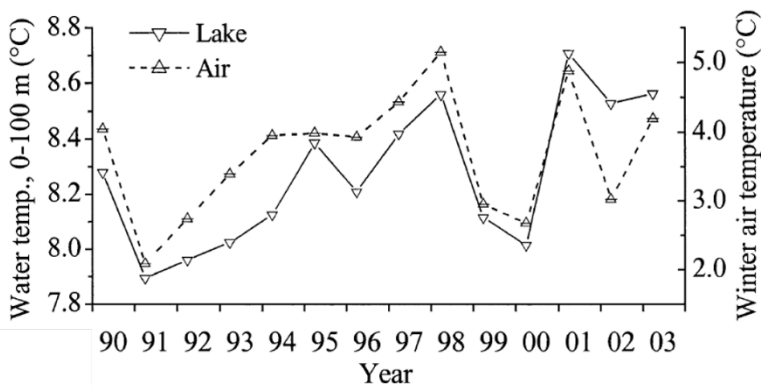


Fig. 15 Volumetrically weighted spring minimum lake temperatures between 0 m and 100 m (continuous line) and average winter (December-February) air temperatures (dashed line) from 1990 to 2003 (Salmaso, 2005).

During the last 40 years, Lake Garda experienced a significant tendency to an increase of water temperatures, in line with the warming recorded in other deep lakes at the southern and northern border of the Alps, strictly linked to annual mean air temperatures, which showed a significant increase from 1984 to 2007, at a rate of

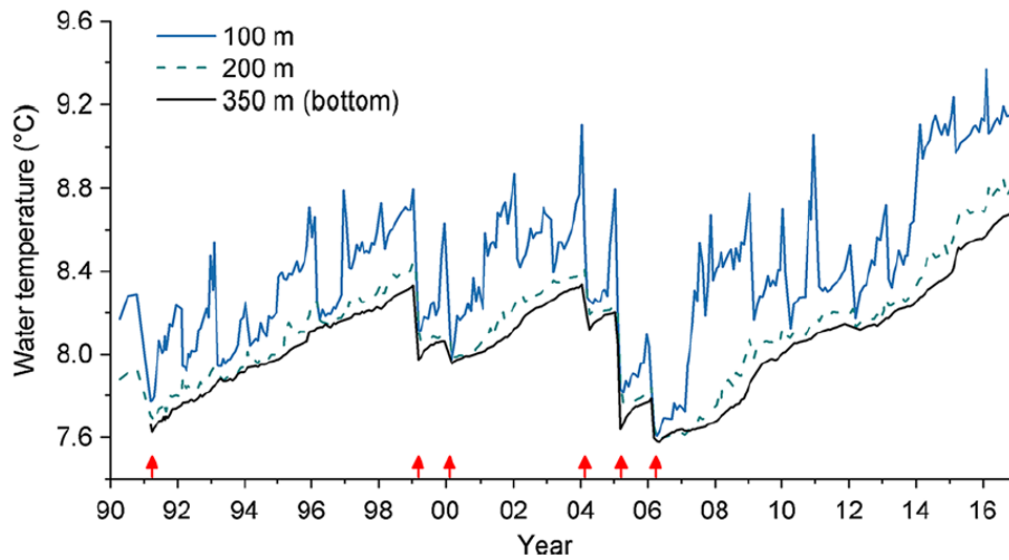


Fig. 16 Temporal variations of hypolimnetic temperatures from April 1990 to December 2016. The red arrows indicate complete cooling and mixing (Salmaso, 2018).

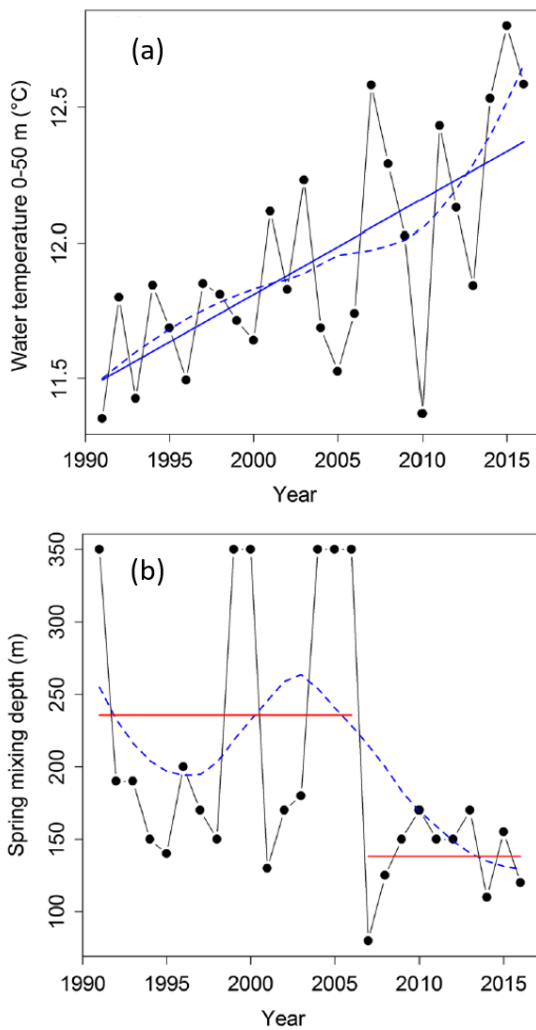


Fig. 17 Long-term development of the annual mean water temperature between the surface and 50 m depth (a) and spring mixing depth (b), since 1991 (Salmaso, 2018)

around $0.6\text{ }^{\circ}\text{C}$ per decade (Salmaso, 2010). The most recent temperature data recorded (Salmaso et al., 2018) confirmed the alternation between periods of warming and sudden cooling episodes observed at the end of the winter months, strongly linked to the average winter air temperatures (Fig. 16). Besides 1991 and 1999-2000, the most recent cooling of the lake water column was observed between 2004 and 2006. The analysis revealed that, since the last overturn episodes, the lake continued to show a warming trend of hypolimnetic waters, at a rate of around $0.1\text{ }^{\circ}\text{C}/\text{year}$. The tendency of the lake to warm is confirmed by the temporal development of the mean annual water temperature measured in the 0-50 m layer (Fig. 17a), showing an increasing trend at a rate of $0.035\text{ }^{\circ}\text{C}/\text{year}$, which is equivalent to a $0.91\text{ }^{\circ}\text{C}$ increase since 1991. As shown by the red arrows in Fig. 16, the strong cooling episodes coincided with a complete or more extended mixing of the water column. After the last complete full spring mixing events (2004-2006), the lake experienced a long period of reduced spring mixing ($<170\text{ m}$), with a shift after 2006 detected by the changepoint analysis (Fig. 17b).

In a two years study (1995-1996) the lowest Secchi disk readings (around 6 m) were recorded in August in connection with the higher algal density, and the highest transparencies were measured in winter and spring with a maximum of 27.5 m on April 1996 (Salmaso and Decet, 1998). After

the end of the 1990s, there was a quite sharp decrease of water transparency, with a clear change in annual mean values from 11.7 m to 9.5 m between 1992-1999 and 2000-2016, but a little tendency to increase after 2007 (Salmaso et al., 2018). The trend of the corresponding euphotic depth varied between 11 and 45 m in the W basin (Fig. 14), and between 10 and 30 m in the E basin. In particular, the lower limit of the euphotic depth, during summer, ranged between 15 and 25 m from 1995 to 1998 and between 11 and 20 m in 1999 and 2000. The euphotic depth is generally similar or greater than the mixing depth from May-June to September (Salmaso, 2002; 2003).

Annual mean values of the euphotic depth showed a decrease from the middle of the 1990s to 2007 (Fig. 18) (Salmaso, 2010).

In the study by Salmaso and Decet (1998), spring salinity values were reported to increase beginning from 120-150 m in 1995 and around 200 m in 1996, even though the differences were small, with values in the ranges 183-189 mg/l in 1995 and 185-191 mg/l in 1996 within the whole water column (0-340 m). The density differences from 50 m to the bottom were equal to 2.8×10^{-5} and 0.93×10^{-5} g/cm³ in 1995 and 1996, respectively (0.34×10^{-5} and 0.40×10^{-5} g/cm³ considering the contribution of salinity alone). In 1995 and 1996 the isopycnic mixed layers extended up to about 140 m and 200 m, respectively.

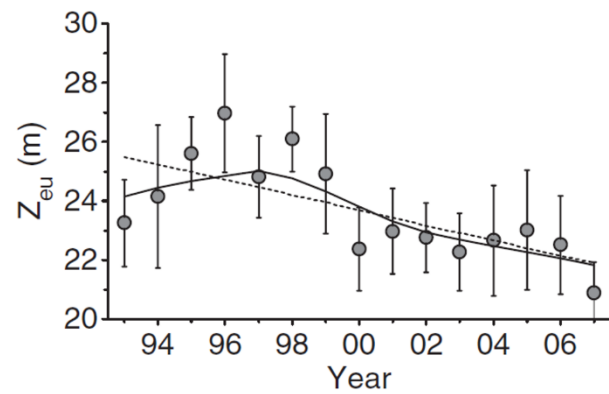


Fig. 18 Annual mean values of the euphotic depth in the period 1993-2007 (Salmaso, 2010)

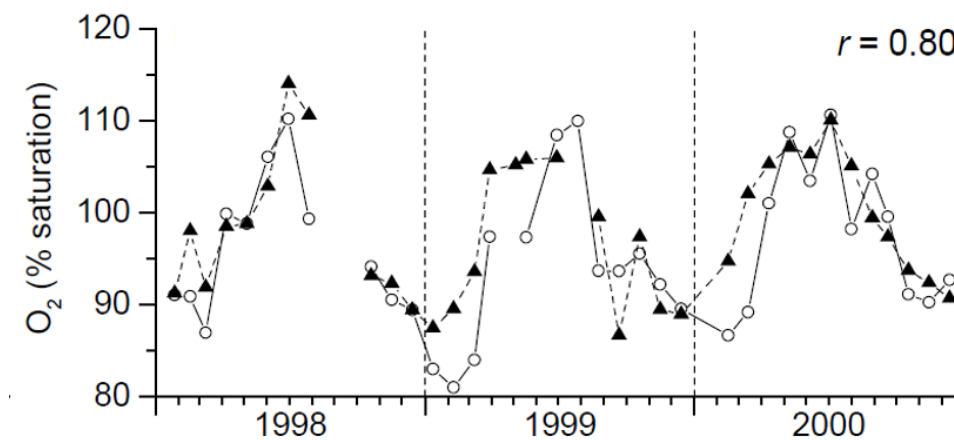


Fig. 19 Temporal variations of oxygen (percent saturation) in the layer 0-21 in the western (continuous line) and eastern (dashed line) basins (Salmaso, 2002).

The seasonality of the chemical variables is associated to the higher phytoplankton biomass and activity during the stratification months and to the vertical mixing of the water column from late autumn to early spring (Salmaso, 2002). In the surface layers, O₂ concentrations show a slight undersaturation in the coldest months (10-11 mg/l, 85-100% in early April, during maximum overturn; Fig. 19). The decrease of oxygen concentrations from May to August is associated with surface warming, but the values remain around or a little above the equilibrium (95-115% at 0.5 m and 90-95% at 19.5 m) due to increased phytoplankton abundance and activity. There is a clear O₂ gradient with depth, with a particularly different oxygenation between the layers at 300 and 200 m. In the period 1994-1996, concentrations were in the range 5.5-7.1 mg/l (47-71%) at the bottom and 6.6-7.3 mg/l (56-62%) at 300 m, indicating a separation of these layers from those above. The values at 200 m increase in spring during the maximum overturn, but are near the equilibrium (around 10 mg/l) with the upper layers only in early April 1996. In 1996 the mean decrease of O₂ in the hypolimnion of the W basin (40-350 m)

was around 1.0 mg/l from April to the end of October (when a minimum average value of 8.4 mg/l was found) (Salmaso et al., 1997a; Salmaso and Decet, 1998). In the period 1991-1996, at 100 m, during the maximum spring overturn, O₂ always reached concentration equivalent with those at the surface. These data indicated that the layer interested by mixing was comprised, starting at least from 1993, between 100 and 200 m. In particular, the O₂ profiles obtained with the multiparameter probe allowed to identify a complete mixing event in 1991, whereas in the following years the circulation reached a maximum depth of about 180 m in 1992-1993, 150 m in 1994, 140 m in 1995 and 200 m in 1996 (Salmaso et al., 1997b). During the period 1996-2003, average concentrations in the deep hypolimnion (200 m-bottom) were always greater than 6 mg/l, indicating a satisfactory level of oxygenation (Fig. 20). However, from 1996 to 1998, and during 2001, the water column was characterised by the presence of marked concentration gradients, while in the biennium 1999-2000 oxygen was evenly distributed along the water column during the spring overturn. These situations were the result of the incomplete vertical cooling and consequent partial overturn of the water column from 1996 to 1998 and in 2001, and by the complete cooling and circulation of the lake in 1999 and 2000, between February and March (Salmaso, 2002; 2005; Salmaso et al., 2002). Since the shallower E basin undergoes a complete overturn every year from January to March, O₂ concentrations are homogeneous over the whole water column (10-11 mg/l; 85-90% saturation) (Salmaso et al., 1997a; Salmaso and Decet, 1998).

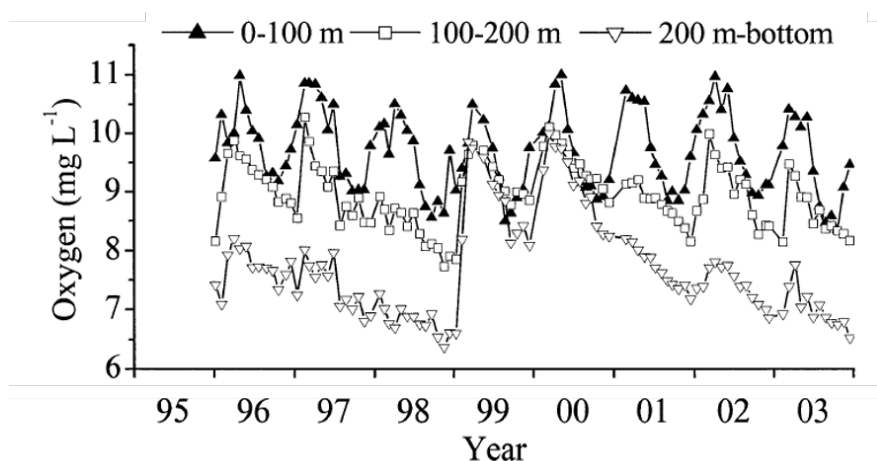


Fig. 20 Average oxygen concentrations (in mg/l) from January 1996 to December 2003 in three selected layers (0-100 m; 100-200 m; 200 m-bottom) (Salmaso, 2005).

Oligomixis in Lake Garda has a major effect on the vertical distribution of algal nutrients and, consequently, on their supply in the superficial, euphotic layers. In fact, in years of incomplete mixing, the concentrations of nutrients in the layer from 100 m to the bottom were 2-3 times as high as those measured in the layer 0-100 m, whereas, during years characterized by a complete overturn, concentrations assumed homogeneous values in the whole water column in spring, reaching their maximum values in the euphotic zone (Salmaso et al., 2002). The consequences of vertical mixing appear evident in the temporal distribution of total and reactive phosphorus (RP), nitrate and reactive silica within the water column in the years 1994-1996 (Fig. 21). The supply of nutrients to the superficial layers, after their depletion by the phytoplankton community during the growing season, was more evident in spring 1996, in coincidence with a larger mixing layer. However, unlike RP and silica, nitrate concentrations have minor differences in the deep hypolimnion, with values at 300 m slightly greater or coincident with that at 100-200 m (Fig. 21c) (Salmaso and Decet, 1998). In the period 1995-2003, epilimnetic phosphorus concentrations never exceed 21 µg/l (TP) and 11 µg/l (RP), with annual average concentrations of 10 and 2 µg/l for TP and RP respectively. Considering the period 1995-2007, annual mean epilimnetic concentrations of TP varied between 8 and 14 µg/l (Fig. 22a) (Salmaso, 2010). No seasonal trend for phosphorus compounds is observable (Fig. 21a,b), but there is an evident replenishment from deeper strata

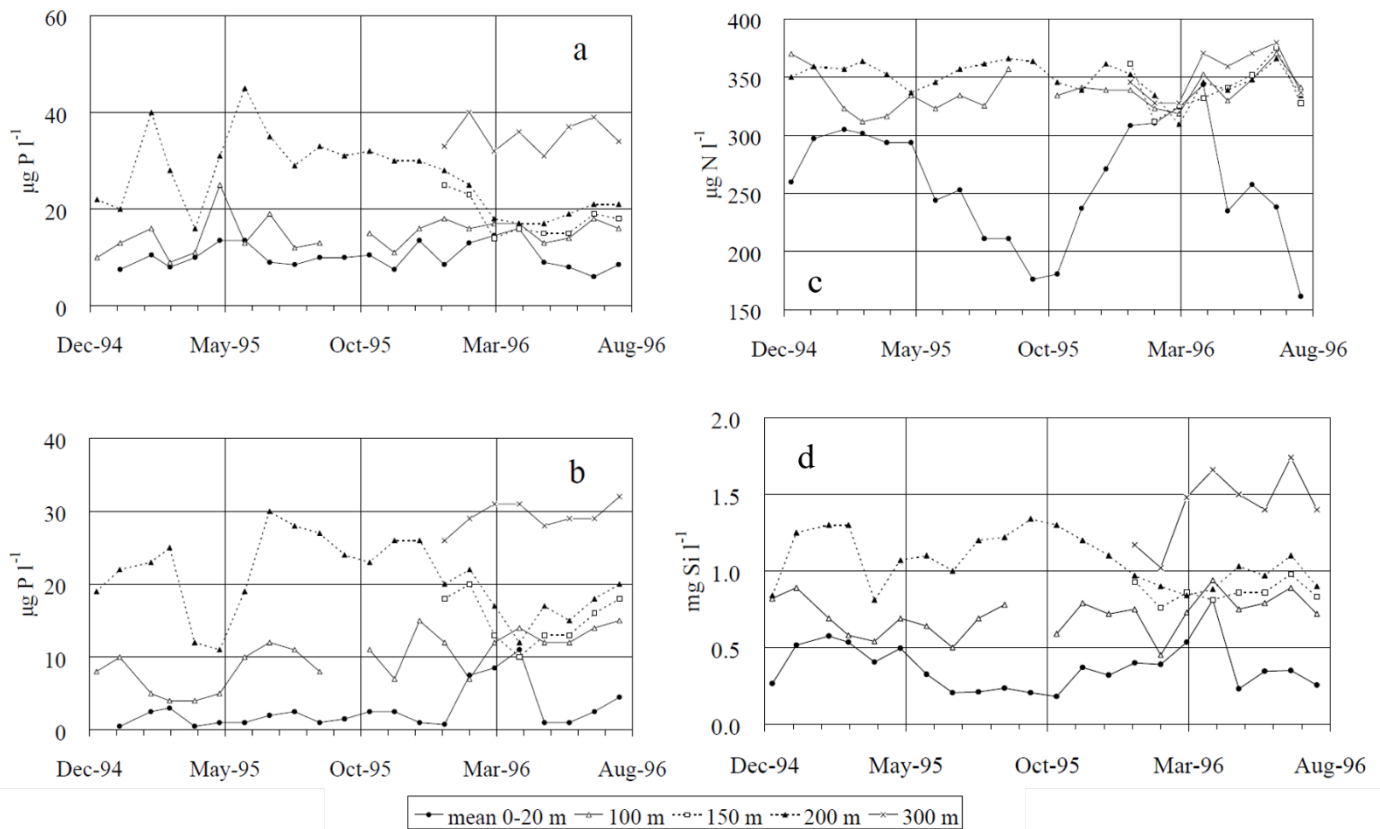


Fig. 21 Total (a) and reactive (b) phosphorus, nitrate nitrogen (c) and reactive silica (b) concentrations in the western basin (Salmaso et al., 1997a).

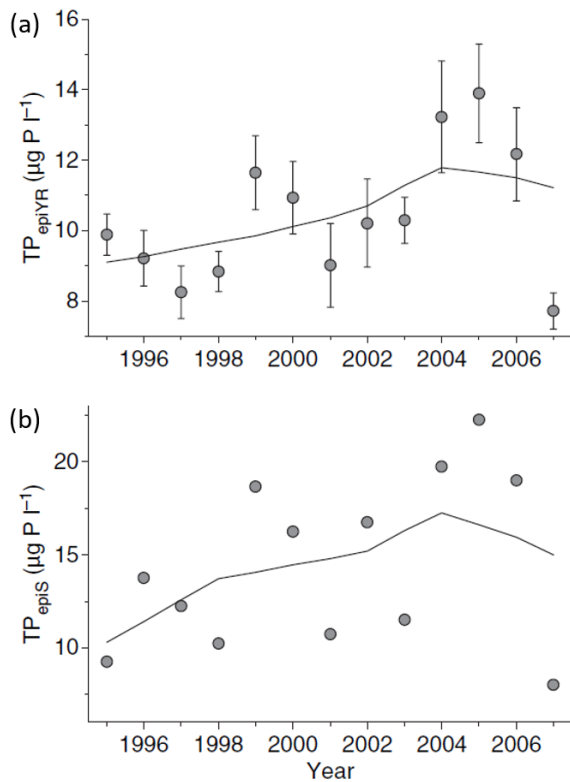


Fig. 22 Annual average concentrations of TP (a) and peaks of TP at maximum overturn (between February and March) (b) in the trophogenic layer (0–20 m) from 1995 to 2007 (Salmaso, 2010).

in January-February and soon after the period of maximum overturn (March-April) (Salmaso et al., 1997a). During incomplete overturn, the mean spring TP concentrations remained $<15 \mu\text{g/l}$ with the exclusion of 2002. Higher concentrations of TP were found in 1999 and 2000 (up to 20 and 17 $\mu\text{g/l}$, respectively) and 2004–2006 (up to 25 $\mu\text{g/l}$) (Fig. 22b), due to the different extent of the spring vertical mixing, which determined, in the whole basin, a major recycling of TP from the deepest layers to the surface during the years (1999–2000 and 2004–2006) of complete overturn (Salmaso, 2005; 2010). This was confirmed by Salmaso (2018), who reported that during the last three mixing episodes (2004–2006), TP concentrations in the 0–100 m layer were around or higher than 20 $\mu\text{g/l}$, whereas in the successive years they decreased to 15 $\mu\text{g/l}$ or below (Fig. 23). In the period 1998–2000, RP concentrations reached 13–17 $\mu\text{g/l}$ recorded during complete spring circulation (Salmaso, 2002; 2003). The TP concentrations at 100 m (Fig. 21a) are a little higher or similar to those found

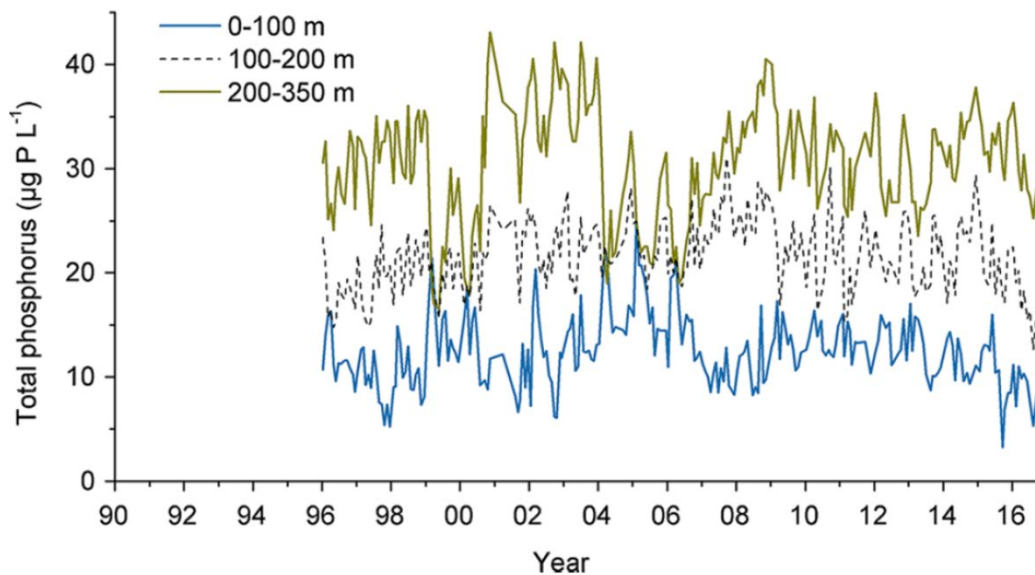


Fig. 23 Concentrations of TP from January 1996 to December 2016 in the mixolimnetic (0-100 m), and upper (100-200 m) and deep hypolimnetic (200-350 m) layers (Salmaso, 2018).

in the upper strata, while TP concentrations at 200 m (16-45 µg/l) and 300 m (31-40 µg/l) are considerably higher. A comparable pattern is observable for RP (**Fig. 21b**), with concentrations ranging between 4-15, 10-20, 11-30 and 26-32 µg/l at 100, 150, 200 and 300 m respectively. Minor differences along the water column are present only during the short period of maximum water mixing when TP and RP concentrations were homogeneous down to 100 m (10-11, 3-4 µg/l for TP and RP respectively) in 1995 and to 200 m (16-17, 10-14 µg/l) in 1996 (Salmaso et al., 1997a). In the period 1995-2007, depending on the extent of spring water mixing, the annual mean values of TP in the 100-200 m layers were between 18 and 25 µg/l (Salmaso, 2010). In years of incomplete mixing, the annual average concentrations of TP in the layer from 200 m to the bottom were 27 µg/l (1996-1998), 33 µg/l (2001-2003) and 28 µg/l (2007-2016), more than threefold as high as those measured in the layer from 0 m to 20 m (9.5 ± 0.4 µg/l). In contrast, during years with a complete overturn, TP concentrations at the end of the winter months assumed homogeneous values in the whole water column (Salmaso, 2005, Salmaso et al., 2018). As can be observed in **Fig. 23**, there was a slight but substantial tendency of phosphorus to increase in the hypolimnetic layers until 2004. This tendency was particularly evident considering

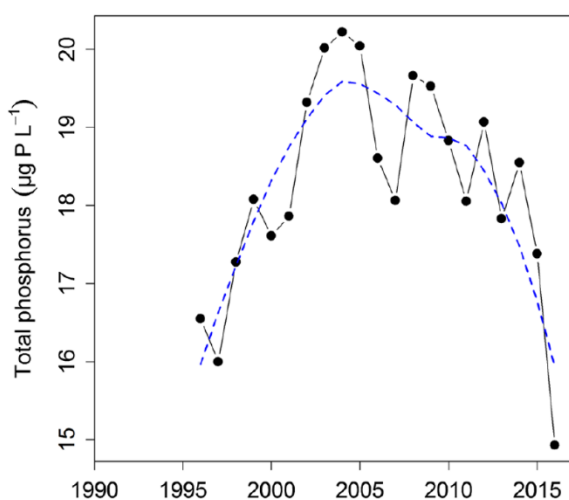


Fig. 24 Annual mean concentrations of TP in the whole water column since 1996 (Salmaso, 2018).

the mean concentrations of TP before and after the two overturn episodes in 1999-2000 in the layers from 100 m to 200 m (19.3 ± 0.4 and 22.5 ± 0.5 µg/l, respectively) and from 200 m to the bottom (30.8 ± 0.5 and 36.0 ± 0.6 µg/l, respectively). This increasing trend of phosphorus in the lake was confirmed by the temporal evolution of the mean concentrations of TP in the whole water column from 1996 to 2004, with a significant increase from 16-17 up to 20 µg/l, i.e. at a rate of 0.4-0.5 µg/l/yr (Salmaso, 2005). However, in 2005-2006 the mean annual concentrations of TP showed a stabilisation and, subsequently, started to decline (Salmaso, 2010). The recent analysis by Salmaso (2018) reported a clear a tendency of

TP to peak in the first half of 2000s, revealed by the temporal pattern of annual mean TP in the whole water column between 1995 and 2016 (**Fig. 24**).

Nitrate and reactive silica are also characterized by steep concentration gradients, but with a greater homogeneity in the water column during the maximum overturn. Moreover, some differences and a pronounced seasonal periodicity of surface concentrations in comparison with phosphorus compounds were observed, with a clear decrease during the summer months ([Salmaso et al., 1997a](#); [Salmaso and Decet, 1998](#)). In the period 1995-2007, annual mean epilimnetic concentrations of dissolved inorganic nitrogen (DIN) ranged between 180 and 260 $\mu\text{g/l}$, showing a slight tendency to decrease, with a more pronounced trend during the summer months (**Fig. 25**).

Mean summer concentrations in the first metres (0–2 m) were below 100 $\mu\text{g/l}$ in 1999-2000 and in the period 2003-2007 ([Salmaso, 2010](#)). Nitrate was almost the exclusive form of nitrogen, as in the whole water column ammonium and nitrite never exceed 40 and 6 $\mu\text{g/l}$ respectively. In the period 1994-1996, a strong reduction of nitrate in the warmest months was particularly evident in the 0-2 m layer, with values ranging from 100 to 175 $\mu\text{g/l}$ in July-October 1995 and reaching a minimum value of 86 $\mu\text{g/l}$ in July 1996, whereas concentrations below 100 m (**Fig. 21c**) ranged between 309-380 $\mu\text{g/l}$. Overall, in the period 1996-2016, nitrate concentrations from the surface to the bottom ranged between 280 and 350 $\mu\text{g/l}$, without any apparent long-term trend ([Salmaso, 2010](#); [Salmaso et al., 2018](#)). Reactive silica concentrations range between 0.06-0.85 mg/l in the surface strata, whereas the highest concentrations are found in the deepest waters (300 m: 1.02-1.74 mg/l). Annual average values in the whole water layer were between 0.7 and 0.9 mg/l. As in the case of nitrate, lower values are found in the warmest months (**Fig. 21d**) ([Salmaso et al., 1997a](#); [Salmaso, 2010](#)). In the period 1998-2000, minimum values of nitrate and silica in the 20-m layers were comprised between around 50-120 $\mu\text{g/l}$ and 0.1-0.2 mg/l, respectively, and a clear influence of the extent of the vertical water mixing was not evident for these two nutrients. Nitrite concentrations were always below 20 $\mu\text{g/l}$ and contributed only secondarily to the amount of the measured nitrogen pool ([Salmaso, 2002](#)).

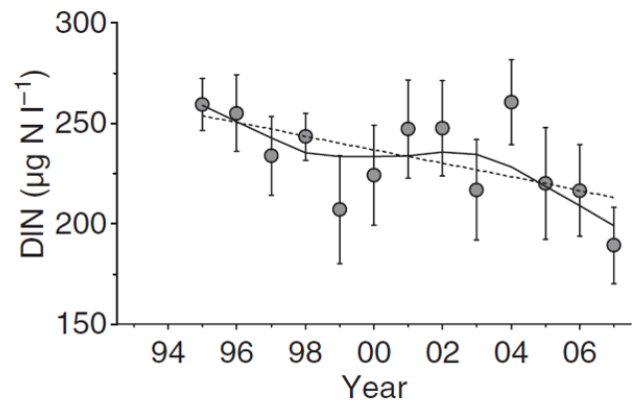


Fig. 25 Annual average concentrations of dissolved inorganic nitrogen in the trophogenic layer (0–20 m) ([Salmaso, 2018](#)).

2.1.2 Biological aspects

The significant increase in phosphorus content in the water column and the tendency to an increase of water temperatures in Lake Garda during the last 40 years have been coupled with significant modifications to the composition and structure of the phytoplankton community ([Salmaso, 2010](#)). Annual mean concentrations of chlorophyll-a, in the period 1993-2007, ranged between 2.3 and 4.0 $\mu\text{g/l}$ (**Fig. 26a**), with higher values in 1999-2000 and, subsequently, a tendency to decrease. Annual mean concentrations of algal biovolumes were instead characterised by a continuous and significant increase, showing a negative correlation with euphotic depth, but a clear positive correlation with chlorophyll-a only considering the monthly observations. A changepoint

analysis performed by [Salmaso et al. \(2018\)](#) identified two periods characterized by rather homogeneous biovolumes between 1993 and 2004 (816 mm³/m³), and 2005 and 2015 (1137 mm³/m³) (**Fig. 26b**). In **Fig. 27** are reported the variations of the annual mean values of the biovolumes of the dominant algal orders from 1993 to 2007, whereas the list of the dominant taxa is reported in **Table 2**. The most abundant algal groups in Lake Garda were chlorophytes, diatoms and cyanobacteria. Among the chlorophytes, *Mougeotia sp.* (the unique Zygnematales) was the dominant taxon until 2004, when the population underwent a sudden collapse and recovered only partially in the successive years, with annual average biovolumes ranging between 86 and 190 mm³/m³ (**Fig. 27a**). Chlorococcales represent a further important order among the chlorophytes, mainly composed by small green spherical colonial algae, *Coelastrum polychordum*, *C. reticulatum* and *Ankyra judayi*, and characterized by an overall decreasing trend of the annual averages of biovolume (**Fig. 27h**). The most abundant cyanobacteria were the Oscillatoriales, mainly composed by *Planktothrix rubescens* and, secondarily, *Planktolyngbya limnetica* and Limnotrichoideae, showing a constant and significant increase and becoming the most abundant algal order after 2004, following the decrease of *Mougeotia* (**Fig. 27b**).

The annual mean values of the biovolume of cyanobacteria ranged between 50 and 150 mm³/m³ until 2004 and increased dramatically (240-360 mm³/m³) between 2005 and 2007, due to a higher increase of *Planktothrix rubescens*. Since then, excluding a peak in 2014, it decreased to values between 80 and 170 mm³/m³. Overall, from 2005 to 2015, cyanobacteria were characterized by an increase in their annual mean biovolumes, and by an increase in interannual variability (**Fig. 28a**) ([Salmaso et al., 2018](#)). Pennate diatoms in Lake Garda are principally composed by *Fragilaria crotonensis*, with maximum development in spring and autumn, whereas the other species, mainly *Asterionella formosa*, *Tabellaria fenestrata* and *Diatoma tenuis*, are present almost exclusively from late autumn to early spring. Centric diatoms are dominated by the large and heavy *Aulacoseira granulata*, *A. islandica* and *Stephanodiscus sp.* (late winter and early spring), and the small and light *Cyclotella spp.* (summer and early autumn). No significant annual trend was observed in the two diatom orders until 2007 (**Fig. 27c,d**), but centric diatoms showed a tendency to increase since 2003 (**Fig. 27d**). Excluding a couple of peaks, from 1993 to 2007 annual mean biovolumes of diatoms were around or below 250 mm³/m³, whereas after 2007, excluding a lower value in 2013, biovolumes were between 290 and 600 mm³/m³ (**Fig. 28b**). This increase was mostly due to an increase of *F. crotonensis* (from 120 before to 253 mm³/m³ after 2007), concurrently with a strong drop of *Tabellaria fenestrata* and *Aulacoseira islandica* (from 8-10 to <0.5 mm³/m³) ([Salmaso et al.,](#)

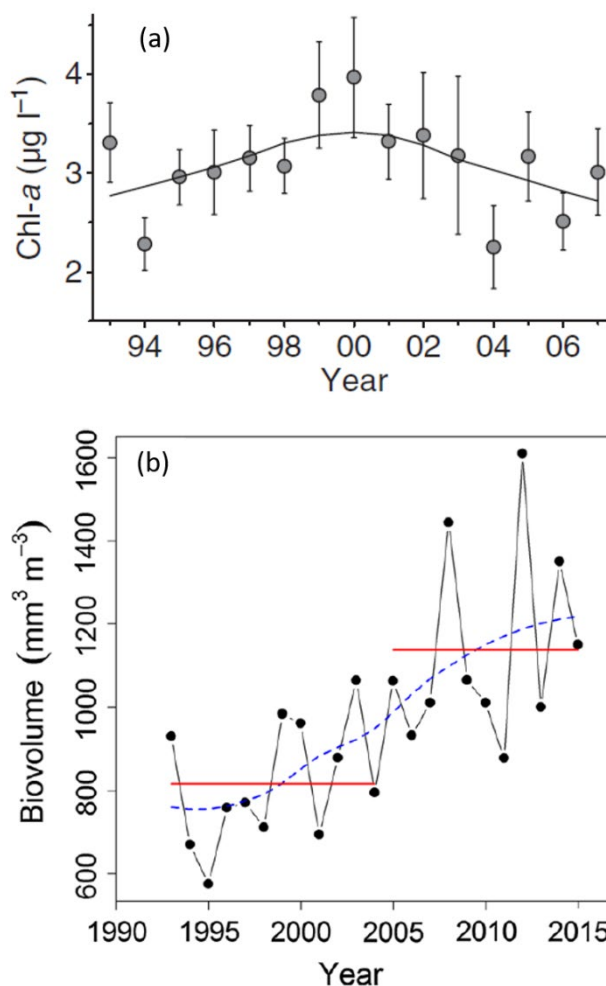


Fig. 26 Annual average concentrations of chlorophyll-a (a) and total phytoplankton biovolume (b) in the trophogenic layer (0–20 m) since 1993 ([Salmaso, 2010; 2018](#)).

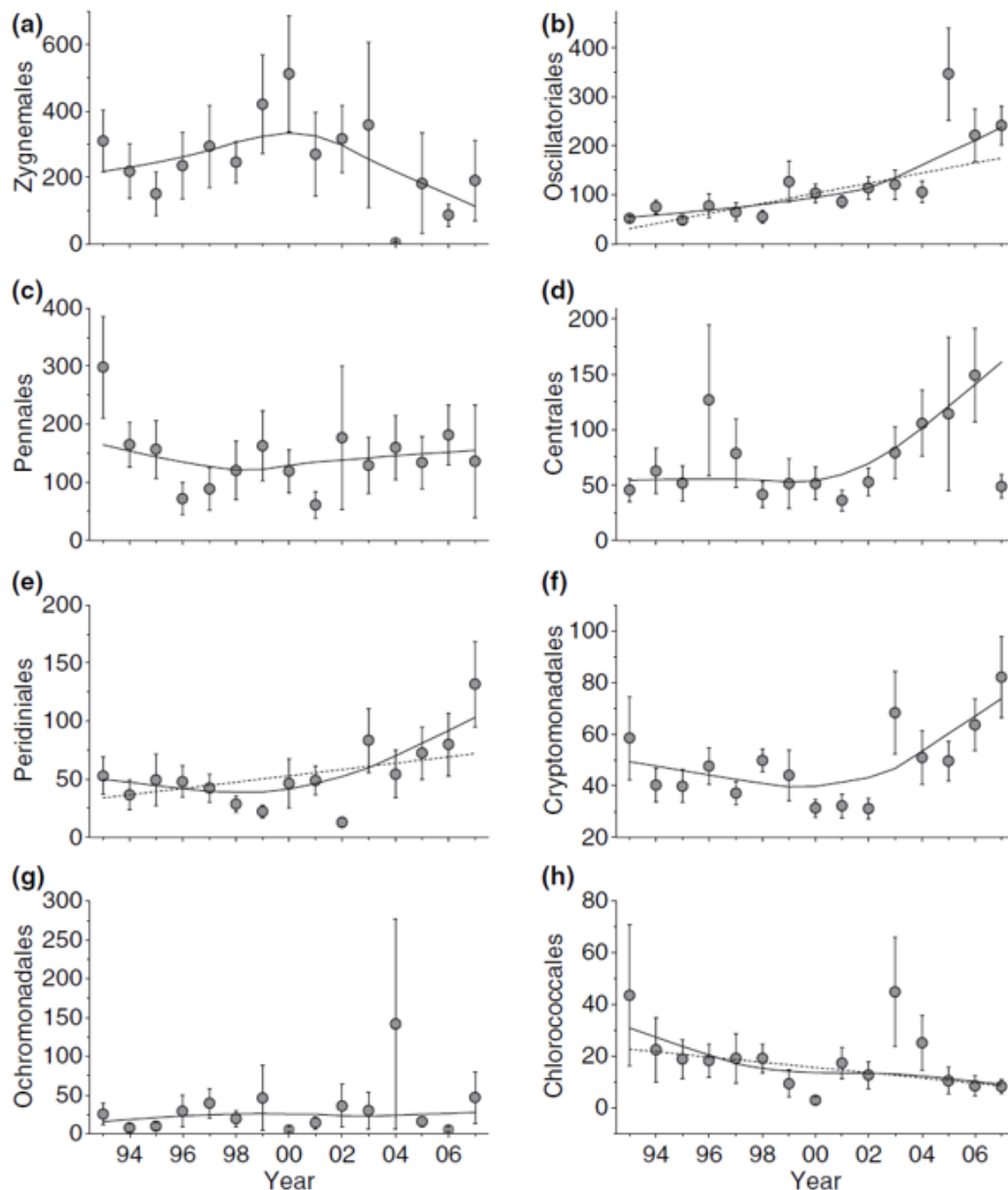


Fig. 27 Annual average concentrations of the most abundant algal orders in the trophogenic layer (0–20 m) (Salmaso, 2010).

2018). The analysis of sediment cores by Milan et al. (2015) revealed that during oligotrophic conditions of Lake Garda before the 1960s small *Cyclotella* species were the almost only constituent of diatom assemblages, whereas the following shift towards oligo-mesotrophic and mesotrophic conditions was characterized by the abrupt increase of larger species, including *F. crotonensis*, still present in the phytoplankton community of Lake Garda. Regarding the remaining orders, Peridinales showed a tendency to increase (Fig. 27e), whereas Ochromonadales and Cryptomonadales did not show any significant trend (Fig. 27f,g), even if in the latter group larger biovolumes were recorded in the last years of observation. Among the less abundant algal orders, significant temporal annual trends were detected in the Chroococcales (Cyanobacteria). Moreover, the first blooms of *Anabaena lemmermannii* (Nostocales) observed at the beginning of the 1990s represent one of the most dramatic changes in the phytoplankton of Lake Garda, even if biovolumes of this cyanobacterium in the whole study period remained always low ($<25 \text{ mm}^3/\text{m}^3$) (Salmaso, 2010).

Major temporal trends and interannual variations of the different phytoplankton groups and species in Lake Garda were essentially related to the long-term variations in the availability of TP in the water column, to the

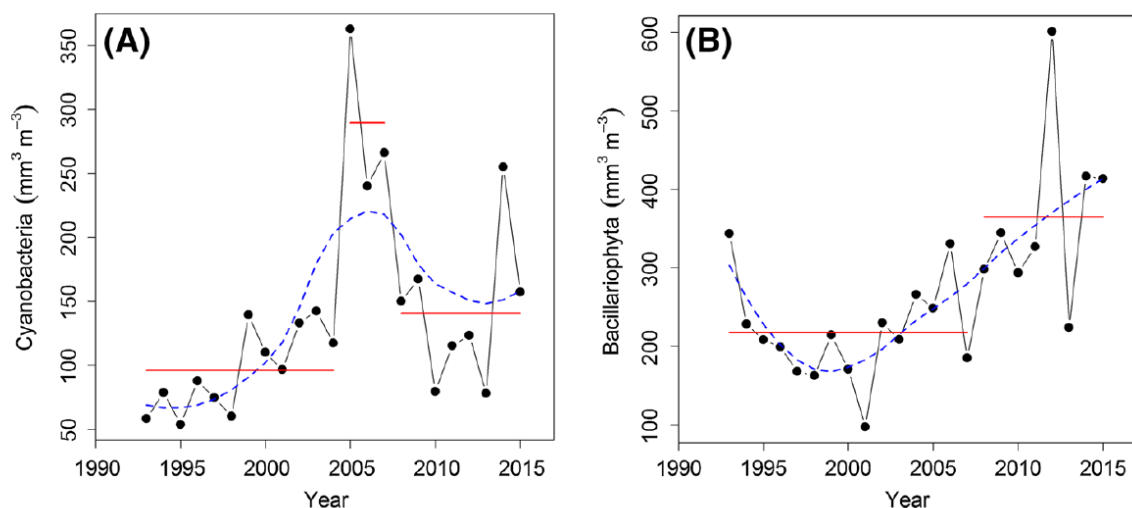


Fig. 28 Long-term development of the annual mean values of biovolume of Cyanobacteria (a) and Bacillariophyta (diatoms, b), (Salmaso, 2018).

spring epilimnetic replenishment of TP, and to the interannual variations of temperature. Analyses by Salmaso (2010) indicated a strong impact of nutrient fertilisation at spring overturn on the phytoplankton development, in particular diatoms and cyanobacteria, with the major influence due to TP compared with DIN and Si. Correlations between the epilimnetic concentrations of TP and phytoplankton orders were only marginally evident for pennate and centric diatoms, but they were larger excluding the contribution of the small *Cyclotella*. A clear positive link with the overall content of TP in the water column was instead documented for the Oscillatoriales, the large spring centric diatoms and the Pennales (Salmaso, 2010). Recent analyses revealed that the impact of the higher TP availability in the trophogenic layers during the years of complete overturn was particularly apparent in the case of cyanobacteria, which showed their maximum development in the period 2005-2007. The following meromictic period of the lake, with the corresponding decrease of TP in the trophogenic layers, was associated with the collapse of cyanobacteria between 2008 and 2013, coinciding also with a strong reorganization of the group (Salmaso et al., 2018). According to results by Salmaso (2010), a few algal orders showed a clear link with the interannual variations of thermal regime. In fact, Cryptomonadales showed a significant positive correlation with the epilimnetic water temperature, Peridinales showed a marginal positive correlation, whereas Desmidiaceae were negatively correlated. The recent regression analysis by Salmaso (2018) concluded that total phytoplankton biovolumes, cyanobacteria and diatoms showed a positive relationship with both water temperature and availability of TP in the mixolimnetic layer. Therefore, all recent observations were fully consistent with the strong and well-known impact of both water temperature and TP on phytoplankton development, even though in this typology of deep lakes the direct effects of temperature may be less important when compared with the larger, indirect effects on the dominant species mediated through winter climatic oscillations and spring fertilisation (Salmaso, 2010). Therefore, as noted in Salmaso (2018), if the tendency of phosphorus in the mixolimnetic layers of Lake Garda will continue to decrease, and if the warming scenarios will be confirmed, we could expect further shifts in algal assemblages, for instance a decline of *F. crotonensis* and other large diatoms in favour of small and lighter *Cyclotella*. Contrary to cyanobacteria and diatoms, dinoflagellates and cryptophytes showed a positive relationship with water temperature, and not with nutrients. In fact, these two groups are represented by flagellate species, which are capable to optimize their position in the water column relative to temperature, light and nutrient gradients and are favoured by high-temperature levels and water stability. Their competitive abilities in warmer and low nutrient environments can

explain the higher importance that dinoflagellates took on in Lake Garda in the last decade, which also gave rise to extended brownish water blooms visible at naked eye on the northern area of the lake. Cryptophytes also showed a tendency to increase abundances in the last decade, even though its correct interpretation requires to consider the trophic relationships within the food web, including grazing by large zooplankton, such as *Daphnia*, which can severely constrain their growth in the early summer period (Salmaso et al., 2018). As mentioned before, zooplankton is an important constituent of the food web in pelagic ecosystems, as they feed on the phytoplankton, bacteria and other zooplankton species, and are preyed by almost all freshwater fish. The traits and composition of zooplankton of Lake Garda, evidenced since the first studies carried out from the beginning of 20th century, are typical of deep lakes with moderate productivity, where the calanoid copepods constitute the main component in comparison with cladocerans and smaller rotifers (Salmaso and Naselli-Flores, 1999). The studies carried out in 1995 and 1997 in Lake Garda have revealed an assemblage of 30 zooplankton taxa, dominated, as number of species, by rotifers (21 taxa), whereas Cladocera and Copepoda were found with 3 and 6 taxa, respectively (**Table 1**). The three species of Copepoda appear to maintain an unaltered coexistence in all the studies carried out with modern criteria since 1957-1958. The calanoid *Copipodiptomus steueri*, the most representative member, is a typical species identified also in other deep and shallow lakes of Northern Italy and of the hinterland of the central Adriatic Region. Despite being absent in a 1960s study, *Mesocyclops leuckarti* is considered, together with the other two copepods, a constant and typical constituent of Lake Garda (Salmaso and Naselli-Flores, 1999; Salmaso, 2002). Regarding cladocerans, the main difference among the studies is due to the disappearance, beginning from the end of the '50s, of *Sida crystallina*, whose causes, although difficult to establish, are possibly related to the introduction of allochthonous fishes, such as *Coregonus lavaretus*. Some problems resulted in the taxonomy of *Daphnia*, which was reported as *D. longispina* until 1960s and *D. hyalina* afterwards. In the study by Salmaso and Naselli-Flores (1999), the identification of *D. hyalina* was further complicated by the appearance, principally during the warmest months, of morphotypes with characteristics resembling those of *D. galeata*. As a consequence, at present *Daphnia sp.* is included in the *D. hyalina-galeata* group. Moreover, the species of the genus *Bosmina*, reported as *Bosmina (Eubosmina) coregoni* in previous studies, after closer investigations, was subsequently identified as *B. (Eub.) longicornis kessleri*. Despite the composition of rotifers may be greatly influenced by the sampling strategy, and changes observed must be interpreted with caution, the genera reported in **Table 1**, were found in all the previous studies, except for *Brachionus*, sporadically identified only after the '70s. The most consolidated modifications within this group are the appearance of the new species *Keratella quadrata* and *Lecane lunaris* since the '70s, and *Euchlanis dilatata* since the second half of the '80s.

Salmaso and Naselli-Flores (1999) and Salmaso (2002) found that the temporal evolution of zooplankton assemblage in Lake Garda, in particular cladocerans and copepods, is characterized by the presence of a distinct seasonal component, with higher densities during the spring-summer months and/or autumn months (**Fig. 29-30**). Moreover, the analysis found also interannual differences in the amplitude of zooplankton cycles. In fact, in 1995 cladocerans showed a more pronounced development, whereas in 1997 and 1998 rotifers were dominated by a strong number of *Conochilus*. The seasonal evolution of copepods is almost entirely determined by *C. steueri*, as confirmed also by other studies (e.g. Barbato, 1988). The species reached densities of 25.000-55.000 ind/m³ in summer and autumn months in 1995, whereas in 1997 two period of high development were observed in spring and during summer (up to 40.000 ind/m³). Cyclopoids presented lower densities of individuals respect to *C. steueri*. The most abundant species is *M. leuckarti*, with the maximum development observed in a limited period between the summer and autumn months (up to 6500 ind/m³ in 1995 and 1800

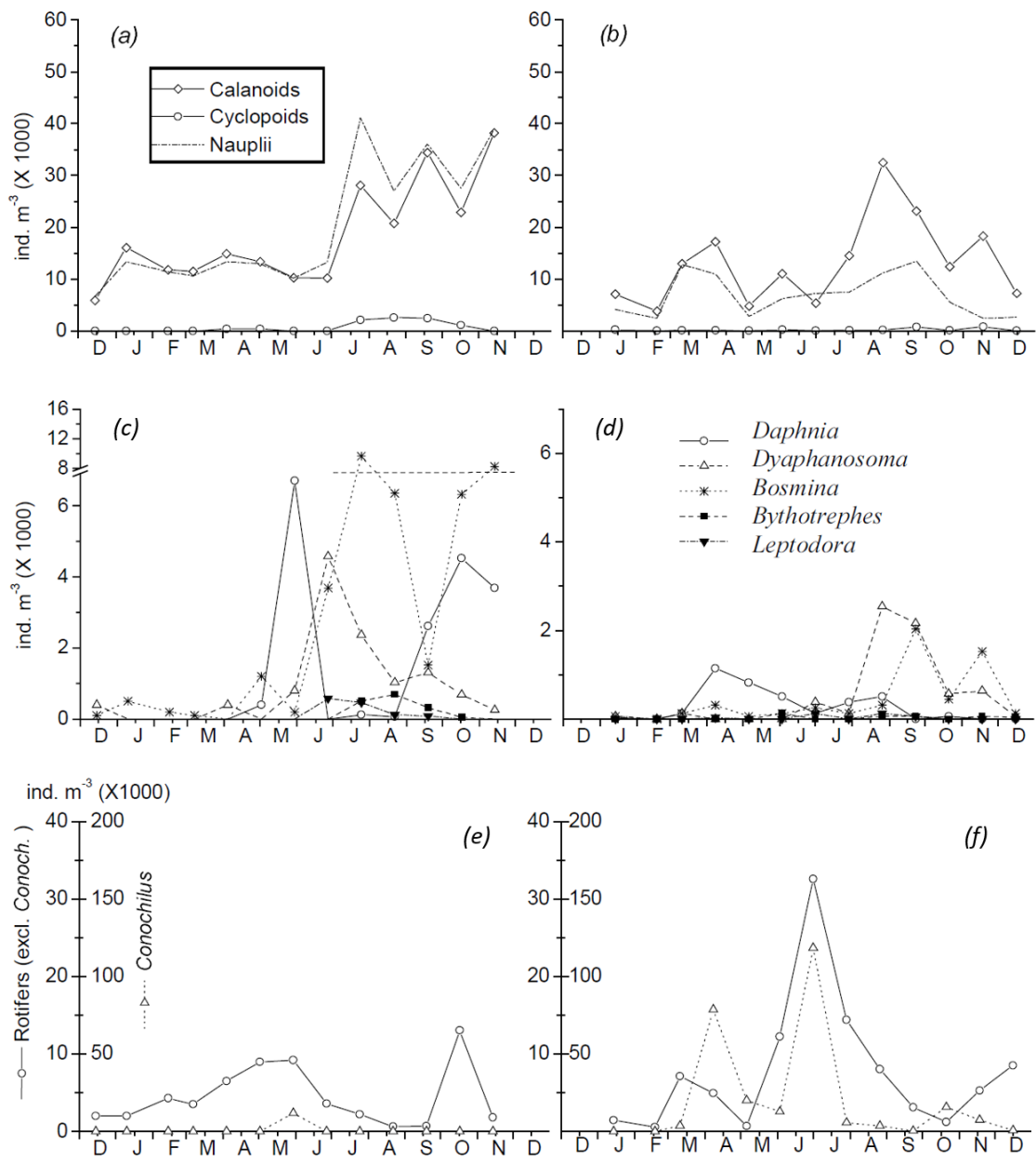


Fig. 29 Density variations of calanoids (*Copipodiaptomus*), cyclopoids (*Mesocyclops*, *Cyclops*) and nauplii (a, b), cladocerans (c, d) and rotifers (e, f) in 1995 (left panels) and 1997 (right panels) (Salmaso and Naselli-Flores, 1999).

ind/m³ in 1997). By contrast, the development of *Cyclops abyssorum* appeared mainly limited to the cold and mild months (autumn-spring), with densities generally below 500 ind/m³ (Salmaso and Naselli-Flores, 1999). The numerical prevalence of *Mesocyclops* over *Cyclops* was also reported by Barbato (1988), whereas in analyses carried out in the beginning of the '70s the relative importance of these two cyclopoids appeared inverted in favour of *Cyclops*. In this case, the daily vertical migration behaviour may be a particularly important aspect to consider during samples. In fact, the populations of *C. abyssorum* which live in the subalpine, large and deep lakes prefer the deeper water layers (40-60 m depth) during daytime, migrating to the surface only during the night, whereas *M. leuckarti* appears confined, in the daytime, in the strata between 0-25 m. The three most frequent cladocerans (*Daphnia* spp., *Diaphanosoma brachyurum* and *B. (Eub.) l. kessleri*) showed their maximum densities only from spring to early autumn. In particular, *Daphnia* is characterised by a clear spring pulse, between April and June, whereas in the other months densities are generally lower (Salmaso and Naselli-Flores,

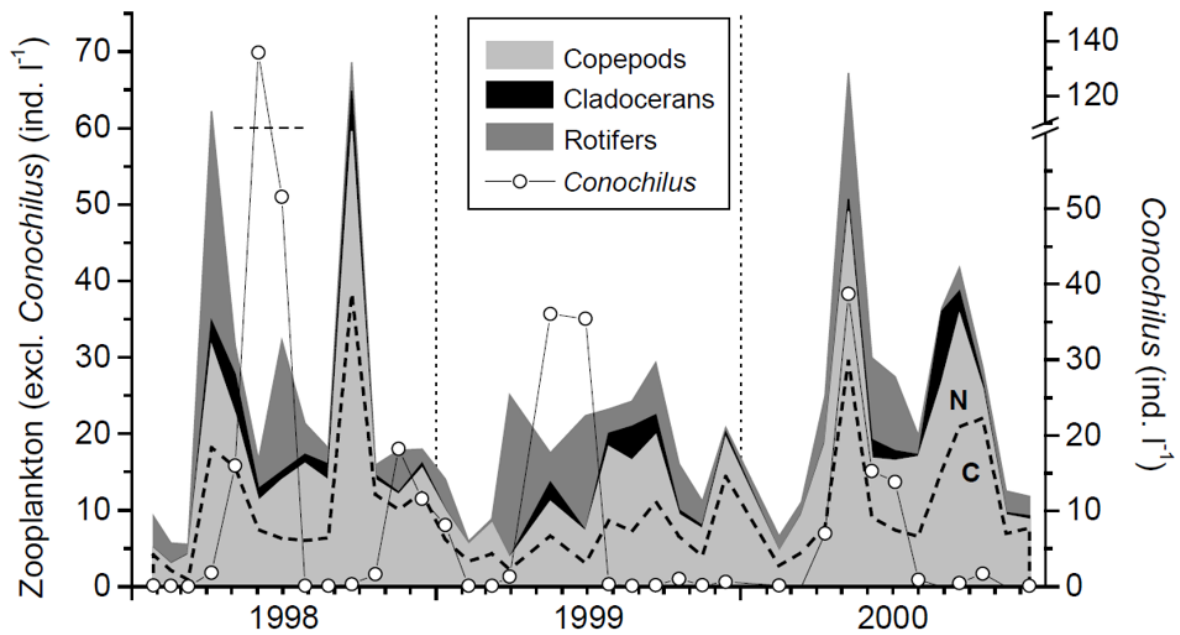


Fig. 30 Density variations of copepods (mainly *Copipodiaptomus steueri*), cladocerans, *Conochilus* and the remaining rotifers in the years 1998-2000. Among copepods, the contribution of nauplii (N area) and copepodites and adults (C area) has been highlighted (Salmaso, 2002).

1999; Salmaso, 2002). In 1995 and 1997, *D. brachyurum* and *B. (Eub.) I. kessleri* showed their maximum development in summer and autumn, but the density of *Bosmina*, differently from *Diaphanosoma*, appears to increase earlier, during the spring development of *Daphnia* (Salmaso and Naselli-Flores, 1999). Analyses in the period 1998-2000 confirmed that *B. (Eub.) I. kessleri* showed its maximum development in coincidence with that of *Diaphanosoma*, but with some irregular peaks also from April and mid-June (Salmaso, 2002). Previous studies also reported a clear correspondence in the spring development of both *Daphnia* and *Bosmina*, with a successive maximum of *Diaphanosoma*, possibly related to competitive mechanisms or selective predation. In fact, *D. hyalina* resulted the preferred food for planktivorous fishes or for *Bythotrephes* and *Leptodora*, whereas *Bosmina* and *Diaphanosoma* do not contribute to the fish diet, but are caught by the invertebrate predators. *L. kindtii*, a warm-stenothermal species, was found in samples between April and September (with maximum densities up to 1600 ind/m³), while *B. longimanus* between June and December (up to 700 ind/m³) (Salmaso and Naselli-Flores, 1999). Among the Rotifera, the most abundant species are represented by *Conochilus*, which, in 1997 and 1998, reached density peaks during summer of 110.000-190.000 ind/m³, and by *A. ovalis*, *E. dilatata*, *K. longispina*, *Polyarthra spp.* (with maximum densities ranging from 7000 to 13.500 ind/m³). The maximum densities reported in the previous studies carried out in pelagic stations are comprised in the range of maximum values found in the period 1995-2000 by Salmaso and Naselli-Flores (1999) and Salmaso (2002). However, regarding *Conochilus*, density peaks with values comparable to those observed in 1997-1998 were recorded only in the investigations in the beginning of the '70s. The maximum development of *Conochilus* in 1997-1998 could be interpreted with a lower development of *Leptodora* and *Bythotrephes*, which contribute significantly to the summer depletion of the rotifer.

Up to the middle of 20st century, the fish assemblage of Lake Garda did not differ substantially from that of the other large and deep lakes of Northern Italy, except for the presence of *Salmo carpio*, an endemic species of Lake Garda, and *Gobio gobio*. In particular, suitable conditions for the survival of salmonids are presents in almost all of the water column of Lake Garda, slightly reducing just in the summer period due to the temperature increase of the surface layers. However, changes in trophic conditions differentiated the population

abundance between the lakes, inducing in Lake Garda firstly an increase in productivity, due to higher food availability, and subsequently, starting from 1960s, a decline of salmonids (such as *Salmo trutta* and *Salmo carpio*), associated with an increase of percids and cyprinids (Regione Lombardia, 2013).

The most relevant changes in species composition of Lake Garda reported in the literature are the definitive disappearance of *Lampetra zanandreae* and some allochthonous species previously introduced in the lake, such as *Lucioperca stizostedion*, *Oncorhynchus kisutch* and *Salvelinus fontinalis*. Moreover, the presence of *Orthrias barbatulus*, *Phoxinus phoxinus*, *Gasterosteus aculeatus* and *Leuciscus souffia* is no longer reported, which suggests a possible local extinction (Regione Lombardia, 2013).

Due to its high depth, reaching 350 m in the western basin, Lake Garda can be subdivided in a littoral and a pelagic region, each with a different fish species composition. The pelagic fish assemblage is prevalent in terms of biomass, but the number of species is considerably higher in the littoral region. Pelagic species include, among salmonids, *Coregonus lavaretus*, particularly abundant, *Salmo Carpio*, *Salmo trutta* and *Oncorhynchus mykiss*, currently particularly rare (Regione Lombardia, 2013). *Coregonus lavaretus*, introduced in Lake Garda in 1918, is a strictly pelagic species, living mainly in the upper 20 m layer (at greater depths during summer months) and stationing near the shore only for reproduction, which usually occurs between December and January. It feeds on zooplankton, in particular cladocerans, actively selecting *Bythotrephes*, *Leptodora* and *Daphnia* respect to *Diaphanosoma* and copepods. Food consumption is particularly high from spring to autumn, whereas in the reproductive period the stomachs were found with very low contents or empty (Arlati, 1984; Giarola, 1986). *Salmo carpio* is a planktivorous endemic species of Lake Garda, which, differently from other salmonids, is capable of two spawning periods, a long one in winter (from December to February) and a shorter one in summer (from July to August), generally at depths between 80 and 200 m. Regarding the trophic spectrum, it was found that *Salmo carpio* is mainly planktivorous, with an active selection for *Bythotrephes*, even though in some period it feeds on benthic crustaceans, such as gammarids and asellids. Similarly to *Coregonus lavaretus*, stomachs were often found empty during the reproductive periods (Melotto, 1990). In the pelagic region are also present *Alosa agone*, with a high abundance, and *Alburnus arborella*, which is established in the pelagic area just for a few months and is increasingly scarce. Two eco-phenotypes of *Alosa Agone* are recognised, a landlocked and a migratory form, but in Lake Garda only the landlocked form is currently present, representing one of the main autochthonous planktivorous species. It is diffused in the whole pelagic region of the lake, but temporary also in the littoral region, mainly during winter and the spawning season, which extends from May to July, with some cases of reproduction in August. The diet of *Alosa Agone* is composed mostly of cladocerans and copepods, but there is a seasonal variation of the two components. In fact, copepods prevail in the diet from November/December to March/April, while cladocerans are the main component from April/May to October (Oppi and Novello, 1986; Bianco, 2002). The littoral fish assemblage

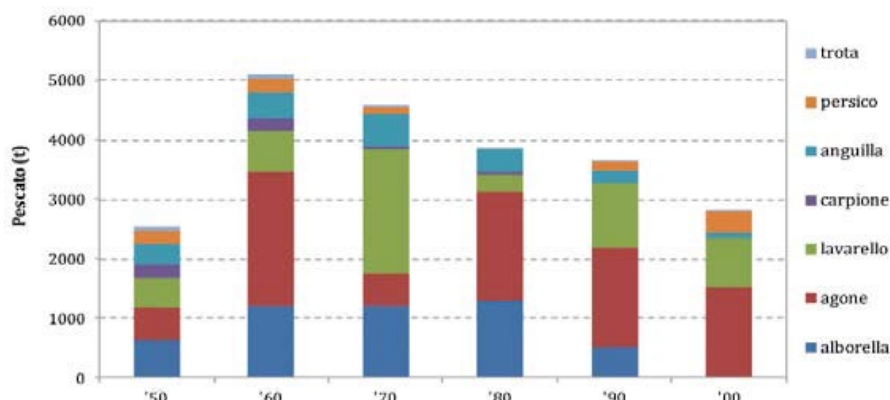


Fig. 31 Evolution of the total catch (in tonnes) of the most interesting species for fisheries in Lake Garda between 1950s and the first decade of 21st century (Regione Lombardia, 2013).

includes notable populations of *Perca fluviatilis*, *Esox lucius*, *Scardinius erythrophthalmus*, *Rutilus erythrophthalmus*, *Leuciscus cephalus* and *Tinca tinca*. According to Oppi (1989), the presence of *Perca fluviatilis* was not particularly relevant until the middle of the last century, when the population started to grow rapidly, possibly due to restocking actions. The spawning occurs from April to June. During the juvenile stage, individuals feed mainly on plankton, whereas adults feed also on small fishes and benthic fauna.

During the first half of 20th century the most important species for fisheries were *Alburnus arborella*, *Alosa agone*, *Anguilla anguilla* and *Coregonus lavaretus*, followed by *Perca fluviatilis*, *Salmo trutta* and *Salmo carpio*. In fact, up to the beginning of the last century, *Alburnus arborella* made up 35-40% of total catch, whereas during 1950s *Perca fluviatilis* made up 6-8%. The catch of *Coregonus lavaretus* increased significantly during the century, from 0.05% in 1926 to 12-13% at the beginning of 1970s. Conversely, the catch of *Salmo carpio* showed a marked decrease from 4-8% in the first half of the century to <1% starting from 1968. Similarly, *Salmo trutta* showed a consistent drop in the catch starting from 1960s, from 5-10% at the beginning of the century to <0.4% in the 1970s. **Fig. 31** shows the total catch variation of the most interesting species for fisheries between 1950s and the first decade of 21st century. In **Fig. 32** are reported the annual catch values, from 1988 to 2010, of the main fish species. As can be observed, catches of *Salmo carpio* present, in this period, generally low values (<4 tonnes/year, in comparison to an average value of 23 tonnes/year in the period 1952-1967), with a positive trend from 1997 to 2006, followed by a sudden drop. *Perca fluviatilis* showed a notable increase starting from the second half of 1990s, reaching catches of 50 tonnes/year, with an exactly opposite trend respect to *Alburnus arborella*, which showed a progressive reduction in the catch and is still undergoing

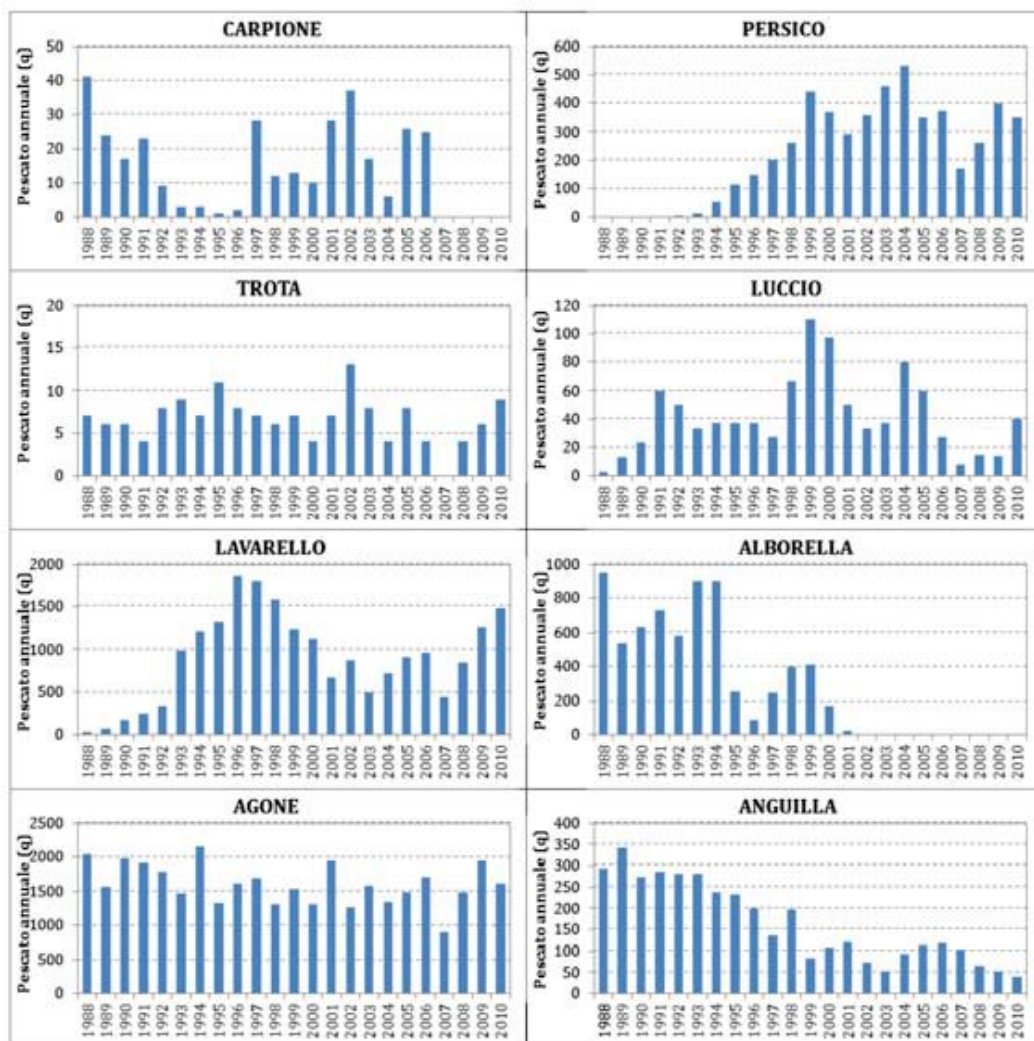


Fig. 32 Annual catch values (x 100 kg), from 1988 to 2010, of the main fish species of Lake Garda (Regione Lombardia, 2013).

a period of sharp crisis. The catches of *Salmo trutta*, in the last 20 years, have been particularly low, even though stable (between 0.5 and 1 tonne/year), whereas *Esox lucius* showed marked oscillations. Still representing one of the most abundant and most commonly caught species, *Coregonus lavaretus* suffered a clear decline starting from the late 1990s, but showed a recovery in the last years. Conversely, *Alosa agone* showed both a good stability and abundance, being the species with the highest catches in Lake Garda, with values between 150 and 200 tonnes/year, representing in 2010 almost 50% of total catch, as can be clearly observed in **Fig. 33**.



Fig. 33 Weight percentage composition of mean annual catch in the period 1988-2010 (Regione Lombardia, 2013).

2.2 Model description

A mass-balanced model was constructed using Ecopath with Ecosim (EwE) software (Christensen and Walters, 2004; Christensen et al., 2008; freely available at www.ecopath.org), to evaluate trophic interactions and energy fluxes within the Lake Garda food web. Since its original development in the early 1980s, EwE modelling has been extensively used in aquatic ecology and ecosystem-based management to quantify ecosystem attributes and to examine the relative role of various ecological processes or stressors (Collèter et al., 2015).

EwE is commonly described as a quantitative ecosystem model, based on processes and species, and representing trophic flows in the ecosystem. In fact, it is designed for the construction, parameterization and analysis of mass-balance trophic models of aquatic and terrestrial ecosystems, with a focus on fisheries management and a suite of tools included for this aim. Hundreds of EwE models representing mainly aquatic ecosystems (but also some terrestrial) have been developed and published world-wide (Christensen and Walters, 2004; Christensen et al., 2008; Collèter et al., 2015).

The Ecopath mass-balance modelling system is built on an approach initially presented by Polovina (1984a; 1984b) for the estimation of the biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem, and subsequently combined with various approaches from theoretical ecology, for the analysis of flows between the elements of ecosystems. The system has been optimized for direct use in fisheries assessment as well as for addressing environmental questions through the inclusion of a temporal dynamic model, Ecosim, and a spatial dynamic model, Ecospace. In many cases, the period considered is a given year, but the state and rate estimates used for model construction may refer to different years. Thus,

models can also represent a decade or more, during which little changes have occurred. Otherwise, when ecosystems have undergone massive changes, two or more models may be needed, representing the ecosystem before, during, and after the changes (Christensen et al., 2008).

As mentioned, EwE has three main components:

1. Ecopath – a static, mass-balanced snapshot of the system;
2. Ecosim – a time dynamic simulation module for policy exploration;
3. Ecospace – a spatial and temporal dynamic module primarily designed for exploring impact and placement of protected areas.

Therefore, the EwE software package can be used to different purposes: address ecological questions, evaluate ecosystem effects of fishing, explore management policy options, evaluate impact and placement of marine protected areas or evaluate effect of environmental changes.

The foundation of the EwE suite is the Ecopath model (Christensen and Pauly, 1992; Pauly et al., 2000), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass “pools”, consisting of a single species, or species groups representing ecological guilds. Pools may be further split into ontogenetic linked groups (e.g. larvae, juvenile, spawners, etc.).

In its present implementation (version 6.5), Ecopath bases the parameterization on an assumption of mass balance over an arbitrary period, usually a year. In particular, models are parameterized by Ecopath based on two master equations, one to describe the production term and one for the energy balance of each group.

The first Ecopath equation describes how the production term for each group (i) can be split in components, implemented with the equation:

$$\text{Production} = \text{catches} + \text{predation mortality} + \text{biomass accumulation} + \text{other mortality} \quad (\text{Eq. 1})$$

or, more formally:

$$P_i = Y_i + B_i M_{2i} + E_i + BA_i + P_i(1 - EE_i) \quad (\text{Eq. 2})$$

where P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), M_{2i} is the total predation rate for group (i), B_i the biomass of the group, E_i the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for (i), while EE_i is ecotrophic efficiency, the proportion of the production that is utilized in the system. The term $P_i(1 - EE_i)$ is an expression of “other mortality”, M_{0i} , representing mortality other than that caused by predation and fishing.

Eq. 2 can be re-expressed as:

$$B_i \left(\frac{P}{B}\right)_i - \sum_{j=1}^n B_j \left(\frac{Q}{B}\right)_j DC_{ji} - \left(\frac{P}{B}\right)_i B_i(1 - EE_i) - Y_i - E_i - BA_i = 0 \quad (\text{Eq. 3})$$

$$B_i \left(\frac{P}{B}\right)_i EE_i - \sum_{j=1}^n B_j \left(\frac{Q}{B}\right)_j DC_{ji} - Y_i - E_i - BA_i = 0 \quad (\text{Eq. 4})$$

where, for each group (i), P/B is the production/biomass ratio, Q/B is the consumption/biomass ratio of predator (j), and DC_{ji} is the fraction of prey (i) in the average diet of predator (j).

In Eq. 3, the term referring to production rate, P_i , is calculated as the product of B_i , the biomass of (i), and $(P/B)_i$, the production/biomass ratio for group (i), which corresponds, under most conditions, to the total mortality rate, Z . The production term describing predation mortality, $M2_i$, has the function to link predators and prey, and it is calculated as:

$$M2_i = \sum_{j=1}^n Q_j DC_{ji} \quad (\text{Eq. 5})$$

where the summation is over all (n) predator groups (j) feeding on group (i), Q_j is the total consumption rate for group (j), and DC_{ji} is the fraction of predator (j)'s diet contributed by prey (i). Q_j is calculated as the product of B_j , the biomass of group (j), and $(Q/B)_j$, the consumption/biomass ratio for group (j).

In an EwE model, the energy input and output of each group must be balanced, considering also other flows in addition to the production term expressed by Eq. 1. After mass balance is achieved between groups, and possible "missing" parameters have been estimated, energy balance is ensured within each group using the equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (\text{Eq. 6})$$

In this case, the energy balance is performed so as to estimate respiration from the difference between consumption and the production and unassimilated food terms, in order to reflect the focus on fisheries analysis, where respiration rarely is measured while the other terms are more readily available.

As mentioned before, the groups of a system may be ecologically, or taxonomically, related species, single species, or size/age groups, i.e., they must correspond to what is generally known as "functional groups". Using single species as the basic units has an advantage if estimated or published consumption and mortality rates are available, without having to average between species. On the other hand, if one has information on all the components of the group, averaging is advantageous and should lead to unbiased estimates. In this case, the input parameters of the combined groups should be the means of the component parameters, weighted by the relative biomass of the components.

EwE allows to create a set of biomass groups representing life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates (M0, predation, fishing) and diet composition are assumed to be similar for individuals within each stanza. In this case, one must enter baseline estimates of total mortality rate Z and diet composition for each stanza, then biomass, Q/B , and BA for one "leading" stanza only. For Ecopath mass balance calculations, the total mortality rate Z entered for each stanza-group is used to replace the Ecopath P/B for that group. Further, the B and Q/B for all stanza-groups besides the leading stanza are calculated before entry to Ecopath, according to the following assumptions:

- 1) body growth for the species as a whole follows a von Bertalanffy growth curve with weight proportional to length-cubed;
- 2) the species population as a whole has had relatively stable mortality and relative recruitment rate for at least a few years, and so has reached a stable age-size distribution.

Under the stable age distribution assumption, the relative number of age "a" animals is given by $l_a / \sum l_a$, where the sum is over all ages, and l_a is the population growth rate-corrected survivorship:

$$l_a = e^{-\left(\sum Z_a - a \frac{BA}{B}\right)} \quad (\text{Eq. 7})$$

where the sum of Z's is over all ages up to "a" and the BA/B term represents effect on the numbers at age of the population growth rate.

Further, the relative biomass, b_s , of animals in stanza s is given by:

$$b_s = \frac{\sum_{a \text{ in } s} l_a w_a}{\sum_{\text{all } a} l_a w_a} \quad (\text{Eq. 8})$$

where $w_a = (1 - e^{-ka})^3$ is the von Bertalanffy prediction of relative body weight at age a .

Knowing the biomass, B , for one leading stanza, and the b_s for each stanza s , the biomasses for the other stanzas are calculated by first calculating population biomass as:

$$B = \frac{B_{\text{leading}}}{B_{\text{leadings}}} \quad (\text{Eq. 9})$$

then setting $B_s = b_s B$ for the other stanzas. Q/B estimates for non-leading stanzas are calculated with a similar approach, assuming that feeding rates vary with age as the 2/3 power of body weight. The internal calculations of survivorship and biomass are actually done in monthly age steps, so as to allow finer resolution than one year in the stanza biomass and mortality structure.

The key initial parameters and the linear equations from the base Ecopath model, that describe trophic fluxes in mass-balance, equilibrium assessments of ecosystems, can be re-expressed as differential equations defining trophic interactions as dynamic relationships varying with biomasses and harvest regimes. This approach, called Ecosim, allows to construct dynamic ecosystem models that can be used for dynamic simulation and analysis of changing equilibria, e.g. fishery response dynamics (Walters et al., 1997; Christensen and Walters, 2004; Christensen et al., 2008).

Ecosim uses a system of differential equations that express biomass flux rates among pools as a function of time varying biomass and harvest rates. Predator-prey interactions are moderated by prey behaviour to limit exposure to predation, such that biomass flux patterns can show either bottom-up or top down (trophic cascade) control.

Biomass dynamics represent the basics of Ecosim and are expressed through a series of coupled differential equations derived from the Ecopath master equation and taking the form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \quad (\text{Eq. 10})$$

where dB_i/dt represents the growth rate during the time interval dt of group (i) in terms of its biomass B_i , g_i is the net growth efficiency (production/consumption ratio), M_{0i} the non-predation natural mortality rate ("other mortality"), F_i is fishing mortality rate, e_i is emigration rate and l_i is immigration rate ($e_i B_i - l_i$ is the net migration rate). The two summations estimate consumption rates, the first expressing the total consumption by group (i), and the second the predation by all predators on the same group (i). The consumption rates, Q_{ji} , are calculated based on the "foraging arena" concept.

In fact, Ecosim allows exploring the implications on system dynamics of different views of how the biomass of different groups in the ecosystem is controlled. The two extreme views are "predator control" (or top-down control) and "prey control" (or bottom-up). This is modelled using "vulnerabilities", which represent the degree to which a large increase in predator biomass will induce predation mortality for a given prey. Low vulnerability (close to 1) means that an increase in predator biomass will not cause any noticeable increase in the predation mortality for the given prey. On the contrary, a high vulnerability, e.g. of 100, indicates that if the predator biomass is for instance doubled, it will cause nearly a doubling in the predation mortality it causes for a given prey.

If vulnerabilities are high, the amount of prey consumed by the predator is the product of predator and prey biomass. This may occur in situations where the prey has no refuge, and it is thus always encountered by a predator. Such top-down control, also known as Lotka-Volterra dynamics, easily leads to rapid oscillations of prey and predator biomasses and/or unpredictable behaviour. The opposite situation, bottom-up control, occurs when a prey is protected most of the time, and becomes available to predators only when it leaves the feature that protects it. A bottom-up control usually leads to unrealistically little biomass changes in the prey and predator(s) concerned, but which usually do not propagate through the other elements of a food web.

Therefore, Ecosim is able to represent the predator-prey encounter patterns in nature, which are rarely random in space, but most often associated with behavioural or physical mechanisms that limit the rates at which prey become available to encounters with predators. This is the case, for example, of the flow from phytoplankton in the water column to benthic filter feeders, where only a small fraction of B_i is available to the consumer, limited by physical mixing and sinking processes that bring phytoplankton near the bottom. Another example regards zooplankton, which often show strong vertical migration patterns that limit their availability to planktivorous fish. The latter, in turn, often spend much of their time in behavioural or spatial refuges that limit their encounter rates with piscivores (Walters et al., 1997). More in detail, this aspect of predator-prey interactions is modelled considering the group biomasses (B) on the underlying Ecopath model as consisting of two components, one vulnerable (V_{ij}), the other invulnerable ($B_i - V_{ij}$) to predation (**Fig. 34**). Further, it is assumed that the biomass V_{ij} may exchange fairly rapidly with the unavailable biomass according to the exchange equation:

$$\frac{dV_{ij}}{dt} = v_{ij}(B_i - V_{ij}) - v_{ij}V_{ij} - a_{ij}V_{ij}B_j \quad (\text{Eq. 11})$$

Thus, V_{ij} gains biomass from the currently unavailable pool ($B_i - V_{ij}$) at rate v_{ij} , biomass returns to the unavailable state at rate $v_{ij}V_{ij}$, and biomass is removed from V_{ij} by the consumer at a mass-action encounter rate $a_{ij}V_{ij}B_j$, where a_{ij} represents the instantaneous mortality rate on prey (i) caused by one unit of predator (j) biomass. As can be seen in **Fig. 34**, when v_{ij} is high, the rapid replenishment of vulnerable biomass depleted by predator will rapidly drain the invulnerable part of the biomass, and predation control will be top down. Conversely, if v_{ij} is low, replacement of depleted biomass from the invulnerable to the vulnerable part of the population will be slow, and control is bottom up.

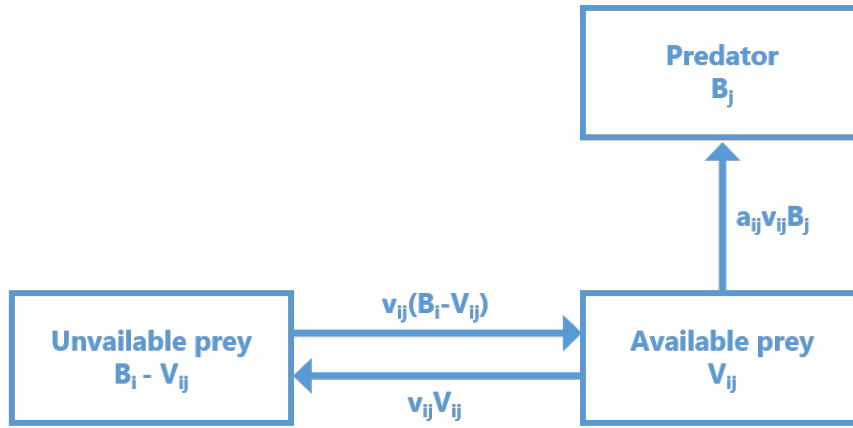


Fig. 34 Diagram representing the flow between available (V_{ij}) and unavailable ($B_i - V_{ij}$) prey biomass, and the flow to predator (j) with biomass B_j in Ecosim. a_{ij} is the predator search rate for prey (i), v_{ij} is the exchange rate between the vulnerable and not-vulnerable state. Based on Walters et al. (1997).

Assuming the exchange process between the two prey states operates on short time scales relative to changes in B_i and B_j , V_{ij} should stay near the equilibrium implied by setting $dV/dt=0$ in Eq. 11, thus getting:

$$V_{ij} = \frac{v_{ij} \cdot B_i}{(2v_{ij} + a_{ij} \cdot B_j)} \quad (\text{Eq. 12})$$

At this equilibrium, the consumption rate for a given predator (j) feeding on a prey (i) is then predicted from:

$$Q_{ij} = \frac{f(T) \cdot a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j}{2v_{ij} + a_{ij} \cdot B_j} \quad (\text{Eq. 13})$$

where, a_{ij} is the effective search rate of predator (j), v_{ij} is the base vulnerability expressing the exchange rate between vulnerable and not-vulnerable state of prey (i), B_i is prey biomass, B_j predator biomass, and $f(T)$ is a forcing function which can be used to modify the predator's search rate in order to account for external drivers that can modify predator's ability to feed on a prey.

Respect to the original Ecosim formulations (Walters et al., 1997), subsequent implementations have led to a more elaborate expression to describe the consumption:

$$Q_{ij} = \frac{f(T) \cdot a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j / D_j} \quad (\text{Eq. 14})$$

where T_i represents prey relative feeding time, T_j predator relative feeding time, S_{ij} user-defined seasonal or long term forcing effects, M_{ij} mediation forcing effects, and D_j represents effects of handling time as a limit to consumption rate:

$$D_j = \frac{h_j \cdot T_j}{1 + \sum_k a_{kj} \cdot B_k \cdot T_k \cdot M_{kj}} \quad (\text{Eq. 15})$$

where h_j is the predator handling time.

For primary producers the production is estimated as a function of the producers' biomass, B_i , from a saturating relationship given by:

$$f(B_i) = \frac{r_i \cdot B_i}{1 + B_i \cdot h_i} \quad (\text{Eq. 16})$$

where r_i is the maximum production/biomass ratio that can be realized (for low B_i 's), and r_i/h_i is the maximum net primary production when the biomass is not limiting to production (high B_i 's).

2.3 Model groups

Data and information obtained from literature allowed to define a food web, representative of the pelagic zone of the lake, composed by 22 functional groups, among which 11 were used to describe fish species, 2 represents crustaceans, 1 insects larvae, 4 zooplankton groups, 3 phytoplankton and 1 detritus. Species found in Lake Garda were placed in the different groups following several criteria, including the importance of the species for fishing activities within the ecosystem, phylogenetic and ecological similarity (based on qualitative behavioural and feeding traits), and the amount of available information for each species. Where biological data were detailed enough, i.e. for fish and crustaceans, the single species were identified as functional groups, whereas the others represent wider ecological categories. The model describes the Lake Garda food web in the period corresponding to the late 90s, where complete data are available for all the main species or groups.

Table 1 List of the functional groups included in the Ecopath model; a description or the species composition of each group and the sources used to derive the basic input parameters are also listed.

No.	Group name	Description/Species included	Data source
1	<i>Esox Lucius</i> (adult)	Esocidae; demersal; piscivorous; adult stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
2	<i>Esox Lucius</i> (juvenile)	Esocidae; demersal; piscivorous; juvenile stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
3	<i>Perca fluviatilis</i> (adult)	Percidae; demersal; piscivorous; adult stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
4	<i>Perca fluviatilis</i> (juvenile)	Percidae; demersal; planktivorous; juvenile stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
5	<i>Scardinius erythrophthalmus</i> (adult)	Cyprinidae; benthopelagic; omnivorous; adult stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)

6	<i>Scardinius erythrophthalmus</i> (juvenile)	Cyprinidae; benthopelagic; omnivorous; juvenile stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
7	<i>Salmo carpio</i>	Salmonidae; demersal; planktivorous; endemic of Lake Garda	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
8	<i>Alburnus alburnella</i> (adult)	Cyprinidae; benthopelagic; omnivorous; adult stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
9	<i>Alburnus alburnella</i> (juvenile)	Cyprinidae; benthopelagic; omnivorous; juvenile stage	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
10	<i>Coregonus lavaretus</i>	Salmonidae; demersal; planktivorous	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
11	<i>Alosa agone</i>	Clupeidae; pelagic; planktivorous	Biomass: Regione Lombardia (2013); P/B: Beverton and Holt (1957); Q/B: Palomares and Pauly (1998)
12	<i>Echinogammarus stammeri</i>	Amphipoda (Crustacea)	P/B: Banse and Mosher (1980), Wetzel (2001); Q/B: Ivleva, (1980), Salomon and Buchholz (2000)
13	<i>Asellus aquaticus</i>	Isopoda (Crustacea)	P/B: Banse and Mosher (1980), Wetzel (2001); Q/B: Ivleva, (1980), Salomon and Buchholz (2000)
14	Chironomida (larvae)	Diptera (Insecta); larval stage	P/B: Banse and Mosher (1980); Q/B: Simcic (2005)
15	Carn. Cladocera	Includes <i>Bythotrephes longimanus</i> and <i>Leptodora kindtii</i>	P/B: Wetzel (2001), Vijverberg et al. (2005), Błędzki and Ryabak (2016); Q/B: Simcic and Brancelj (1997); Błędzki and Ryabak (2016)
16	Herb. Cladocera	Includes <i>Daphnia hyalina-galeata</i> , <i>Bosmina (Eub.) longicornis kessleri</i> and <i>Diaphanosoma brachyurum</i>	Biomass: Barbato (1988); P/B: Wetzel (2001), Vijverberg et al. (2005); Q/B: Simcic and Brancelj (1997); Błędzki and Ryabak (2016)
17	Copepoda	Includes <i>Copipodiaptomus steueri</i> , <i>Cyclops cf. abyssorum</i> and <i>Mesocyclops leuckarti</i>	Biomass: Barbato (1988); P/B: Wetzel (2001), Błędzki and Ryabak (2016); Q/B: Simcic and Brancelj (1997); Błędzki and Ryabak (2016)
18	Rotifera	Includes <i>Brachionus quadridentatus</i> , <i>Keratella cochlearis</i> , <i>Keratella quadrata</i> , <i>Kellicottia longispina</i> , <i>Euchlanis dilatata</i> , <i>Lepadella ovalis</i> , <i>Lecane lunaris</i> , <i>Cephalodella sp.</i> , <i>Trichocerca longiseta</i> , <i>Gastropus stylifer</i> , <i>Ascomorpha ovalis</i> , <i>Synchaeta lackowitziana</i> , <i>Polyarthra major</i> , <i>Polyarthra vulgaris</i> , <i>Ploesoma hudsoni</i> , <i>Asplanchna priodonta</i> , <i>Filinia</i>	P/B: Wetzel (2001); Q/B: Galkovskaya (1995); Gophen (2005); Wallace et al. (2006)

		<i>terminalis</i> and <i>Conochilus unicornis-hippocrepis</i>	
19	Cyanobacteria	Species included are listed in Table 2	Biomass: Gallina et al. (2013); P/B: Guénette (2013)
20	Phytoplankton (large)	Species included are listed in Table 2	Biomass: Gallina et al. (2013); P/B: Guénette (2013)
21	Phytoplankton (small)	Species included are listed in Table 2	Biomass: Gallina et al. (2013); P/B: Guénette (2013)
22	Detritus	Group composed of decaying organic matter	Biomass: Guénette (2013)

In **Table 1** are listed the different components of the functional groups used in the food web model. The fish functional groups of Lake Garda considered in the model include *Alosa agone*, *Coregonus lavaretus*, *Alburnus albolella*, *Salmo carpio*, *Scardinius erythrophthalmus*, *Perca fluviatilis* and *Esox lucius*.

Four species, *Alburnus albolella*, *Scardinius erythrophthalmus*, *Perca fluviatilis* and *Esox lucius*, were divided into bi-stanza groups (juvenile and adult) because the diet composition differs significantly between the two life stages (in the case of *Perca fluviatilis* and *Esox lucius*) or the juvenile individuals constitute a significant fraction of other groups diets (*Alburnus albolella* and *Scardinius erythrophthalmus*), both factors having a great importance in the prey-predator relationships.

Two species of crustaceans were used in the model, i.e. *Echinogammarus stammeri* (Amphipoda) and *Asellus aquaticus* (Isopoda). Chironomida larvae, which represent an important component in the diets of different groups, were also included.

Regarding zooplankton, four major functional groups were considered, represented by the orders Rotifera, Copepoda and Cladocera, with the latter in turn subdivided in a carnivorous group and a herbivorous group. Based on the study carried out by [Salmaso and Naselli-Flores \(1999\)](#), who evaluated the actual zooplankton composition of Lake Garda, has been possible to assign the different zooplankton species to each group. Carnivorous cladocerans group includes *Bythotrephes longimanus* and *Leptodora kindtii*, whereas herbivorous cladocerans group includes *Daphnia hyalina-galeata*, *Bosmina (Eub.) longicornis kessleri* and *Diaphanosoma brachyurum*. Copepods group includes *Copipodiaptomus steueri*, *Cyclops cf. abyssorum* and *Mesocyclops leuckarti*. Rotifers group includes *Brachionus quadridentatus*, *Keratella cochlearis*, *Keratella quadrata*, *Kellicottia longispina*, *Euchlanis dilatata*, *Lepadella ovalis*, *Lecane lunaris*, *Cephalodella sp.*, *Trichocerca longiseta*, *Gastropus stylifer*, *Ascomorpha ovalis*, *Synchaeta lackowitziana*, *Polyarthra major*, *Polyarthra vulgaris*, *Ploesoma hudsoni*, *Asplanchna priodonta*, *Filinia terminalis* and *Conochilus unicornis-hippocrepis*.

Phytoplanktonic component was separated into three groups, based on the morpho-functional classification defined by [Salmaso and Padisàk \(2007\)](#). In this classification, phytoplankton genera were grouped following the criteria of motility, specific nutrient requirement (autotrophy, mixotrophy), size, shape, and presence of gelatinous envelopes. For the model, only the separation of the large and small taxa was considered, with the small taxa group including single cells and small colonies with linear dimension <30-40 µm. In addition, cyanobacteria were included as a third group. The dominant phytoplankton taxa (orders and species) recorded in Lake Garda from 1993 to 2007 and reported in [Salmaso \(2010\)](#) are listed in **Table 2**, grouped into the three groups considered in the model.

Table 2 Composition of the three phytoplankton groups considered in the model, based on the dominant taxa recorded in Lake Garda by Salmaso (2010). Each group is further subdivided according to the morpho-functional groups defined by Salmaso and Padisàk (2007).

Small	Large	Cyanobacteria
Potential mixotrophs (unicellular)	Potential mixotrophs (colonial or unicellular)	<i>Aphanothece sp.</i>
<i>Cryptomonas spp.</i>	<i>Dinobryon divergens</i>	<i>Microcystis aeruginosa</i>
<i>Plagioselmis nannoplanctica</i>	<i>Dinobryon sociale</i>	<i>Snowella cf. aracnoidea</i>
<i>Rhodomonas minuta</i>	Ochromonadaceae	Limnotrichoideae
Small diatoms	<i>Ceratium hirundinella</i>	<i>Planktothrix rubescens</i>
<i>Aulacoseira islandica</i>	<i>Gymnodinium helveticum</i>	<i>Planktolyngbya limnetica</i>
<i>Aulacoseira granulata</i>	<i>Gymnodinium sp.</i>	<i>Anabaena lemmermannii</i>
<i>Cyclotella spp.</i>	<i>Peridinium sp.</i>	
<i>Stephanodiscus sp.</i>	Large diatoms	
Other unicellular	<i>Asterionella formosa</i>	
Chlorococcales	<i>Diatoma tenuis</i>	
<i>Coelastrum reticulatum</i>	<i>Fragilaria crotonensis</i>	
<i>Coelastrum polychordum</i>	<i>Tabellaria fenestrata</i>	
<i>Ankyra judayi</i>	Other unicellular	
<i>Carteria sp.</i>	<i>Closterium aciculare</i>	
	<i>Closterium pronum</i>	
	Other colonies	
	<i>Mougeotia sp.</i>	

2.4 Parameter estimation

In order to parameterize the EwE model, six key data are required for each functional group, i.e. biomass (B) in a certain period of time, production/biomass (P/B), consumption/biomass (Q/B), ecotrophic efficiency (EE), diet composition and catches, but other supplementary parameters can be included such as discards, landings values, and fishing costs.

2.4.1 Biomass

This study aimed at entering biomasses of all fish groups as input to the model. However, direct biomass sampling or surveys were not available in the literature, therefore fish biomass was estimated based on landing data obtained from commercial exploitation of fisheries in Lake Garda from 1988 to 2010 (Regione Lombardia, 2013) and estimated natural mortality, according to the following equation:

$$Z = F + M \quad (\text{Eq. 17})$$

where Z is the total mortality, F is the fishing mortality and M the natural mortality. As at steady states the instantaneous rate of total mortality is equivalent to P/B (Allen, 1971), and fishing mortality can be expressed as $F = C/B$, where C is the annual catch, we get:

$$\frac{P}{B} = \frac{C}{B} + M \quad (\text{Eq. 18})$$

$$B = \frac{C}{\left(\frac{P}{B} - M\right)} \quad (\text{Eq. 19})$$

The natural mortality (M) was estimated using Pauly's empirical equation (Pauly, 1980) linking M , two parameters of the von Bertalanffy Growth Function (VBGF, $L(t) = L_{\infty}(1 - e^{-k(t-t_0)})$, with t_0 being the hypothetical age at which the species has zero length), and mean environmental temperature:

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot T_c^{0.463} \quad (\text{Eq. 20})$$

where L_{∞} is the asymptotic length, the mean length the individuals in the population would reach if they were to live and grow indefinitely (which is calculated from $\log L_{\infty} = 0.044 + 0.9841 \log L_{max}$, where L_{max} is the maximum length in the population), K is the VBGF curvature parameter (expressing the rate at which L_{∞} is approached, and calculated using the empirical relationships in Froese and Pauly, 2018), and T_c is the mean environmental temperature ($^{\circ}\text{C}$). An average temperature of 12°C was used, based on monitoring data by Provincia Autonoma di Trento (2018).

The P/B ratio was also estimated empirically, as described in the next section.

The biomass data for zooplankton groups were calculated based on the most detailed survey available in the literature (Barbato, 1988), which was conducted during a period of 18 months between 1982 and 1983. The biomass of herbivorous Cladocera and Copepoda was estimated at 4.942 t/km^2 and 3.361 t/km^2 , respectively, on a wet weight basis. Concerning the remaining zooplankton groups, carnivorous Cladocera and Rotifera, the estimated biomass resulted too low to be consistent with the trophic requirements of the food web, thus it was calculated by the model, assuming an EE of 0.95 for both groups, due to their expected importance as food source. As mentioned before, EE is the fraction of the production that is used in the system, i.e. either passed up the food web, used for biomass accumulation, migration or export. It varies between 0 and 1 and can be expected to approach 1 for groups with considerable predation pressure.

Phytoplankton biomass was obtained from Gallina et al. (2013), who drew a general picture of the phytoplankton community in peri-Alpine lakes, including Lake Garda, using monthly or bimonthly biomass data recorded from 1997 to 2003 in the layer from 0 to 20 m by state water authorities responsible for lake monitoring and the FEM-IASMA limnological research institute. In the study by Gallina et al. (2013), the species biomass was summed to the genera biomass, and the obtained 233 genera were afterward grouped into the morpho-functional groups defined by Salmaso and Padisak (2007), on which the phytoplankton classification of this model is based. The annual mean biomass obtained was 0.1 g/m^3 for small phytoplankton, 0.7 g/m^3 for large phytoplankton and 0.15 g/m^3 for cyanobacteria. Using the volume of the mean euphotic depth (22 m), these values

were converted to t/km², obtaining 2.2 t/km² for small phytoplankton, 15.4 t/km² for large phytoplankton and 3.3 t/km² for cyanobacteria.

Detritus biomass (D), comprising non-living particulate organic material and detritus associated organisms such as bacteria and microphytobenthos, was calculated using the empirical relationship suggested by Guénette (2013):

$$\log_{10}D = 0.954 \log_{10}PP + 0.863 \log_{10}E - 2.41 \quad (\text{Eq. 21})$$

where PP is primary production in gC/m²/year, and E the euphotic zone depth (set at 22 m). Primary production was estimated from phytoplankton biomass, assuming a P/B of 100/year.

Biomasses of other remaining groups (*Echinogammarus stammeri*, *Asellus aquaticus* and Chironomida larvae) were calculated by the model, due to the lack of data available in the literature.

2.4.2 Production/biomass (P/B)

Production refers to the elaboration of tissue (whether it survives or not) by a group over the period considered, expressed in whatever currency has been selected (Christensen et al., 2008). Total mortality, under the condition assumed for the construction of mass-balance models, equals to production over biomass (Allen, 1971). Therefore, one can use estimates of total mortality (Z) as input values for the production over biomass ratio (P/B) in Ecopath models.

As mentioned before in Eq. 17, production rate is the sum of natural mortality (M = M0 + M2) and fishing mortality (F), i.e. Z = M + F. In this model, Eq. 17 was used in order to calculate fish biomass. Therefore, the P/B estimates for fish groups were based on the equation of Beverton and Holt (1957), who showed that total mortality (Z = P/B), in fish population whose individuals grow according to the von Bertalanffy Growth Function (VBGF), can be expressed by:

$$\frac{P}{B} = \frac{K(L_{\infty} - \bar{L})}{\bar{L} - L_c} \quad (\text{Eq. 22})$$

where L_{∞} is the asymptotic average maximum body size, K is the growth rate coefficient that determines how quickly the maximum is attained (both parameters of the VBGF), L_c is the minimum body length in the catch, and \bar{L} is the average body length of catch. The parameters of the VBGF were calculated using the empirical relationships in Froese and Pauly (2018).

The P/B values were obtained from literature for crustaceans (Banse and Mosher, 1980; Wetzel, 2001), chironomida larvae (Banse and Mosher, 1980), zooplankton (Wetzel, 2001; Vijverberg et al., 2005; Błędzki and Rybak, 2016) and phytoplankton groups (Guenette, 2013).

In some cases, input values were adjusted during the model balancing.

2.4.3 Consumption/biomass (Q/B)

Consumption is the intake of food by a group over the time period considered (Christensen et al., 2008). It is entered as the ratio of consumption over biomass (Q/B). Absolute consumption computed by Ecopath is a flow expressed, e.g., in t/km²/year, while the corresponding Q/B would be year⁻¹.

Analytical methods for obtaining estimates of the Q/B involve estimation of ration, pertaining to one or several size/age classes, and their subsequent extrapolation to a wide range of size/age classes, representing an age-structured population exposed to a constant or variable mortality. The required estimates of ration are obtained from laboratory experiments, from studies of the dynamics of stomach contents in nature, or by combining laboratory and field data (Christensen et al., 2008). In addition, there are existing methods based on empirical regressions for the estimation of Q/B from some easy-to-quantify characteristics of the species for which the Q/B values are required. Palomares and Pauly (1989; 1998), based on a data set of relative food-consumption estimates of marine and freshwater population (n=108 populations, 38 species), described a predictive model for Q/B using asymptotic weight, habitat temperature, a morphological variable and food type as independent variables.

Thus, in this model, the Q/B for fish groups were estimated using the following empirical relationship (Palomares and Pauly, 1998):

$$\log\left(\frac{Q}{B}\right) = 7.964 - 0.204 \log W_{\infty} - 1.965 T' + 0.083 A + 0.532 h + 0.398 d \quad (\text{Eq. 23})$$

where W_{∞} is the asymptotic weight (g), T' is an expression for the mean annual temperature of the water body, expressed using $T' = 1000/\text{Kelvin}$ (Kelvin = °C + 273.15), A is the aspect ratio of the caudal fin, which is closely related to the average level of activity (calculated from $A = l^2/s$, where l is the height of the caudal fin and s is the surface area), h is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores, and 0 for herbivores and carnivores). The mean water temperature was set equal to 12 °C, based on data by Provincia Autonoma di Trento (2018), and the aspect ratio was assumed to be $A=1.32$, based on Froese and Pauly (2018). It was also assumed that the asymptotic weight (W_{∞}) is equal to the weight at L_{∞} , and it was calculated using the length-weight relationships in Froese and Pauly (2018).

The Q/B values were obtained from literature for crustaceans (Ivleva, 1980; Salomon and Buchholz, 2000), chironomida larvae (Simcic, 2005) and zooplankton groups (Galkovskaya, 1995; Simcic and Brancelj, 1997; Gophen, 2005; Wallace et al., 2006; Błędzki and Ryabak, 2016).

In some cases, input values were adjusted during the model balancing.

2.4.4 Diet composition

Diet composition of each group is defined as the fraction of each prey species consumed to the total consumption. The diet matrix was obtained from results of stomach contents analyses available in the literature, selecting information as specific and local as possible (Table 3).

Table 3 Diet composition matrix for the consumer groups in the Lake Garda food web model.

		Predator groups																	
Prey / predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Prey groups	1 <i>Esox lucius</i> (adult)	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2 <i>Esox lucius</i> (juvenile)	0.01	0.08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3 <i>Perca fluviatilis</i> (adult)	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4 <i>Perca fluviatilis</i> (juvenile)	0.02	0.02	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5 <i>Scardinius erythrophthalmus</i> (adult)	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6 <i>Scardinius erythrophthalmus</i> (juvenile)	0.05	0.2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7 <i>Salmo carpio</i>	0.05	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	8 <i>Alburnus arborella</i> (adult)	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	9 <i>Alburnus arborella</i> (juvenile)	0.05	0.2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	10 <i>Coregonus lavaretus</i>	0.04	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	11 <i>Alosa agone</i>	0.2	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	12 <i>Echinogammarus stammeri</i>	0.01	0.05	0.05	0.025	0.15	0.15	0.35	0.05	0.05	0	0	0	0	0	0	0	0	0
	13 <i>Asellus aquaticus</i>	0.01	0.05	0.05	0.025	0	0	0.35	0	0	0	0	0	0	0	0	0	0	0
	14 Chironomida (larvae)	0.01	0.05	0.65	0.9	0.2	0.2	0	0.15	0.15	0.05	0	0.2	0.1	0	0	0	0	0
	15 Carn. Cladocera	0	0	0	0	0	0	0.3	0.1	0.1	0.75	0.6	0	0	0	0	0	0	0
	16 Herb. Cladocera	0	0	0	0.02	0.3	0.3	0	0.4	0.4	0.1	0.2	0	0	0	0.5	0	0	0
	17 Copepoda	0	0	0	0.03	0.1	0.1	0	0.1	0.1	0.1	0.2	0.3	0	0	0.15	0	0	0
	18 Rotifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.35	0	0.1	0.1
	19 Cyanobacteria	0	0	0	0	0.05	0.05	0	0	0	0	0	0	0.2	0	0	0.1	0	0.3
	20 Phytoplankton (large)	0	0	0	0	0.1	0.1	0	0.1	0.1	0	0	0.1	0.3	0.5	0	0.3	0.2	0.4
	21 Phytoplankton (small)	0	0	0	0	0.1	0.1	0	0.1	0.1	0	0	0.1	0.3	0	0	0.6	0.7	0.2
	22 Detritus	0	0	0	0	0	0	0	0	0	0	0	0.3	0.1	0.5	0	0	0	0

In particular, diet composition of *Salmo carpio* was obtained from [Melotto and Alessio \(1990\)](#), who carried out samplings between 1987 and 1988 and reported several biological and ecological aspects of Lake Garda carpio, including an assessment of fishes' gastric content. This analysis found that the planktonic crustacean *B. longimanus* constitutes the primary dietary component from July to September, whereas the benthic crustaceans *Asellus aquaticus* and *Echinogammarus cf. stammeri* are the most important component from October to June.

The diet content of *Alburnus arborella* was obtained from [Biro and Muskó \(1995\)](#), who analysed the gut contents of 224 individuals of the *Alburnus alburnus* population in Lake Balaton (Hungary), and adapted with information from [Arlati \(1984\)](#), who reported more specific information from Lake Garda. According to [Arlati \(1984\)](#), in Lake Garda the alborella, in addition to herbivorous cladocerans (*Daphnia* and Diptomidae), assumes a discrete amount of non-zooplanktonic components, particularly insects, and several filamentous and unicellular algae. This food spectrum is quite consistent with the quantitative analysis performed by [Biro and Muskó \(1995\)](#) in Lake Balaton. Similarly, for the diet composition of *Coregonus lavaretus*, the quantitative analyses carried out by [Eckmann et al. \(2002\)](#), [Gerdeaux et al. \(2002\)](#), [Volta \(2010\)](#), respectively in Lake Constance, Lake Annecy and Lake Maggiore, were considered and compared with the discussion in [Arlati \(1984\)](#) referring to Lake Garda. In general, all the analyses conclude that *C. lavaretus* consumes cladocerans (*D. galeata*, *D. hyalina*, *L. kindtii*, and *B. longimanus*) and cyclopoid copepods, with *B. longimanus* representing the most important food component, in particular from June to October.

Regarding *Alosa agone*, a detailed quantitative analysis of the stomach contents was performed in Lake Garda ([IRSA, 1974](#)). The results of this analysis are reported in terms of number of individuals. Therefore, after considering the different mass of planktonic species, it was found an average diet composition of 60% carnivorous cladocerans, 20% herbivorous cladocerans and 20% copepods.

Scardinius erythrophthalmus is an omnivorous species and the diet composition varies between different locations ([Ravera and Jamet, 1991](#); [García-Berthou and Moreno-Amich, 2000](#); [Tomec et al., 2003](#)). Observations carried out in Lake Trasimeno ([Zerunian, 2004](#)) highlighted that its diet is composed in part by algae and in part by zooplankton, benthic crustaceans and insect larvae. According to [Ravera and Jamet \(1991\)](#), in the lakes Maggiore, Varese and Comabbio (Northern Italy), among zooplankton, *S. erythrophthalmus* feeds mainly on herbivorous cladocerans of the genus *Daphnia* and *Bosmina*.

[Lorenzoni et al. \(2007\)](#) analysed a total of 275 stomachs of *P. fluviatilis* in Lake Piediluco (Central Italy), and found that the largest component of the its diet is clearly constituted by insects, in particular *Chironominae* larvae and pupae. The diet of *P. fluviatilis* also includes gammarids and small fish of diverse species. As piscivory is mainly observed in older specimens, only adult stanza was assumed to prey on fish.

Based on [Kangur and Kangur \(1998\)](#), [Zerunian et al. \(2004\)](#), [Alp et al. \(2008\)](#) and [Yazicioglu et al. \(2018\)](#), the juvenile *E. lucius* was assumed to prey on invertebrate groups and juvenile fish species, whereas adult stanza was assumed to prey mainly on fish, including adults.

The remaining diet information were obtained from: [Moore \(1975\)](#), [Kelly et al. \(2002\)](#), [Ingvason et al. \(2004\)](#), [Mirzajani et al. \(2011\)](#) and [Paganelli et al. \(2016\)](#), for crustaceans and chironomids; [DeMott \(1982\)](#), [Bleiwias and Stokes \(1985\)](#), [Sarnelle \(1986\)](#), [Herzig and Auer \(1990\)](#), [Branstrator and Lehman \(1991\)](#), [Branstrator \(1995, 2005\)](#), [Manca et al. \(1995, 1997\)](#) and [Adamczuk \(2016\)](#), for cladocerans; [Papinska \(1985\)](#), [Hansen and Santer \(1995\)](#) and [Błądzki and Rybak \(2016\)](#), for copepods; [Starkweather \(1980\)](#) and [Wallace et al. \(2006\)](#), for rotifers.

2.5 Dynamic simulations

In order to perform dynamic simulations based on climate change scenarios, the effects of water temperature increase were introduced in the Ecosim base equations. In particular, a forcing function was applied to manipulate the predator search rate ($f(T) \cdot a_{ij}$ in Eq. 14), so that predator could consume different amount of prey per unit energy spent searching. In this way, production rates of functional groups change accordingly with the temperature trend. In the case of primary producers, the forcing function directly modify primary production. For consumer groups, the forcing function used to modify the search rates was the one initially proposed by [Lassiter and Kearns \(1974\)](#) to relate the growth rate of a population to temperature:

$$f(T) = \begin{cases} \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^{c(T_{max} - T_{opt})} \cdot e^{c(T - T_{opt})} & \text{if } T < T_{max} \\ 0 & \text{if } T \geq T_{max} \end{cases} \quad (\text{Eq. 24})$$

where T is the water temperature, T_{opt} is the optimum temperature for a given species, at which, with other factors constant, the consumption and growth is maximum; T_{max} is the maximum tolerated temperature, above which the consumption and growth is null, and c is a parameter accounting for the sensitivity of a species to temperature variations.

For primary producers, the exponential forcing function proposed by [Eppley \(1972\)](#), relating productivity to temperature, was considered:

$$f(T) = 10^{0.0275 \cdot T - 0.07} \quad (\text{Eq. 25})$$

The parameters T_{opt} and T_{max} in Eq. 24 were estimated for each fish group based on the work by [Hasnain et al. \(2010\)](#), who compiled a comprehensive database summarizing the available data on temperature metrics for growth, reproduction, and survival of different freshwater fish species. Regarding *S. carpio*, endemic species of Lake Garda, T_{opt} was assumed as the current mean water temperature of the 80-200 m layer, where this species is known to feed and reproduce ([Regione Lombardia, 2013](#)).

Since the aim was to obtain a future representation of the Lake Garda system referring to the end of 21st century, the forcing functions were applied for 75 years, and the results were taken after 40 years to allow the system to stabilize.

In order to test changes in the food web induced by different combinations of temperature increase effects on consumer groups and changes in primary productivity, a set of 4 scenarios were performed:

- a) temperature-based forcing functions to search rates, with constant primary production, considering the emission scenario RCP 4.5;
- b) temperature-based forcing functions to search rates, with exponential increase in primary production, considering the emission scenario RCP 4.5;
- c) temperature-based forcing functions to search rates, with constant primary production, considering the emission scenario RCP 8.5;
- d) temperature-based forcing functions to search rates, with exponential increase in primary production, considering the emission scenario RCP 8.5.

The two climate scenarios are based on the EUROCORDEX project (<http://www.euro-cordex.net/>), a high-resolution regional climate change ensemble established for Europe within the World Climate Research Program Coordinated Regional Downscaling Experiment (CORDEX), which provides an internationally coordinated framework for regional climate scenarios. The EUROCORDEX initiative provides regional climate projections for Europe at 50 km (EUR-44) and 12.5 km (EUR-11) resolution, downscaling the CMIP5 global climate projections and the representative concentration pathways (RCPs) (Jacob et al., 2014).

Climate projections of the Lake Garda region have been then used as input to generate temporal water temperature profiles, using the General Lake Model (GLM; Hipsey et al., 2013). GLM is a one-dimensional (1D) hydrodynamics model which combines fluxes of mass and energy with a Lagrangian layer structure that adapts to changes in vertical gradients. Time-series input variables to GLM include air temperature, wind speed, relative humidity, precipitation, and downwelling long and shortwave radiation. At each time step, GLM accounts for energy fluxes into and out of the lake, and propagates the resultant temperature changes to various layers according to heat transfer and vertical mixing algorithms. Detailed formulation of the GLM can be found in Hipsey et al., 2019.

From the vertical water temperature profiles thus obtained, four different time-series have been extracted, according to the depth ranges of the different functional groups:

- 0-30 m (phytoplankton and *P. fluviatilis*)
- 0-50 m (*A. arborella*, *S. erythrophthalmus* and *E. lucius*)
- 0-100 m (*A. agone* and *C. lavaretus*)
- 20-200 m (*S. carpio*)

The four time-series represent mean temperature values in each depth range, and have been used as water temperature parameter (T) in Eq. 24 and Eq. 25.

3. Results

3.1 Current status

The basic input values and the computed parameters estimated by the balanced Ecopath model for Lake Garda at the current status are shown in **Table 4**, whereas **Fig. 35** represents flow and biomass for the Lake Garda ecosystem, with fractionated trophic levels.

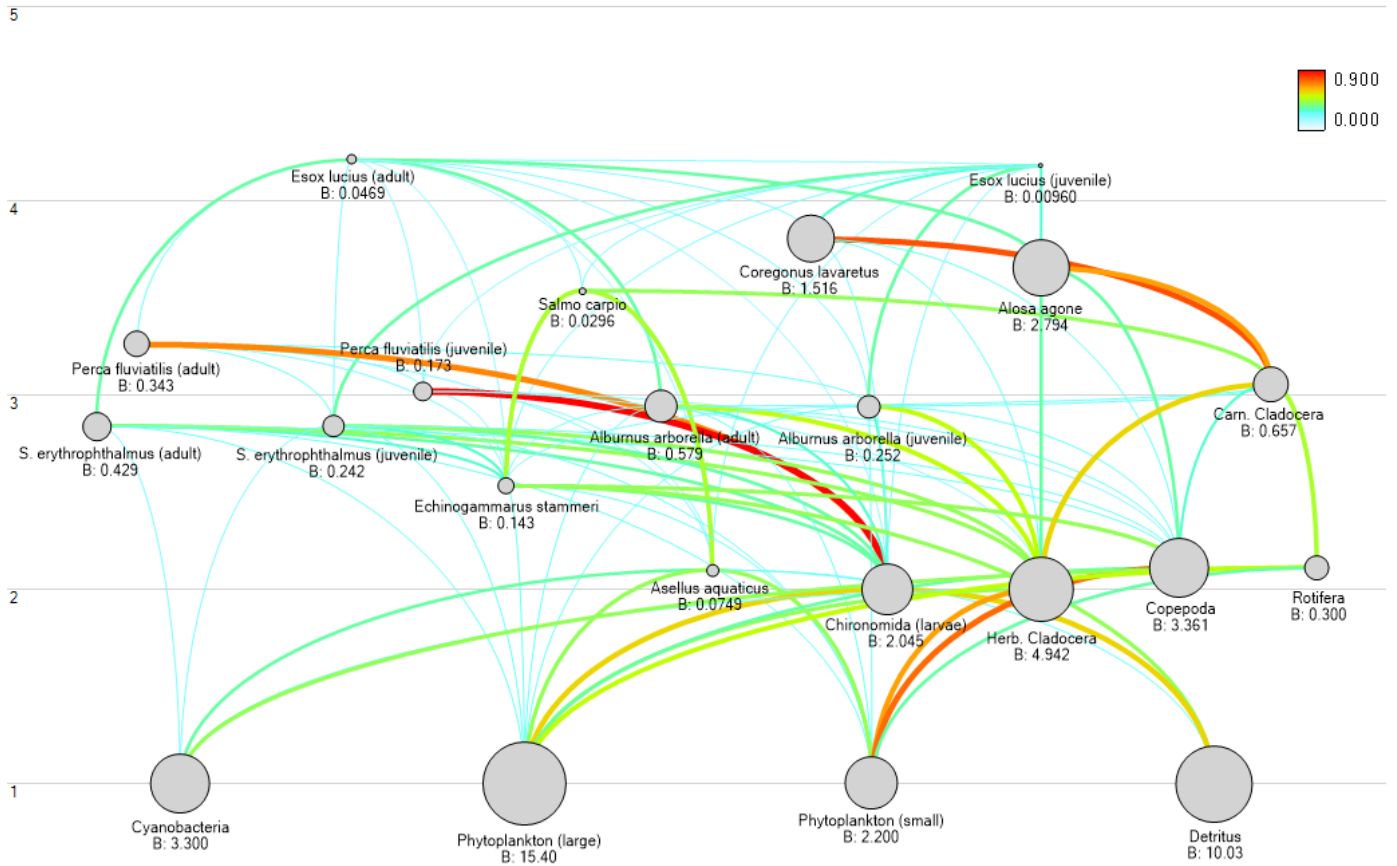


Fig. 35 Flow diagram showing trophic flows in Lake Garda. The modelled groups are placed on the Y-axis according to trophic level and the size of each circle is proportional to biomass (the values in t/km² are also displayed). Thickness and colour of the lines illustrate the magnitude of the flow rates.

Except for *S. erythroththalmus* and *A. arborella*, feeding mainly on phytoplankton and herbivorous zooplankton, all fish species have an estimated trophic level (TL) higher than 3. *E. lucius* was the only species with TL higher than 4 (4.211 for adult stanza and 4.179 for juvenile stanza), as it preys on the highest trophic levels. Carnivorous cladocerans were the only non-fish consumer group with TL higher than 3 (3.056). The other non-fish groups were classified to TLs between 2.000 and 2.533, with the lowest TLs among the consumers occupied by herbivorous cladocerans and chironimida larvae.

The total zooplankton biomass computed by the model was 9.26 t/km², whereas the total biomass for crustaceans and insects resulted 2.263 t/km², compared to 20.9 t/km² for primary producers and 6.415 t/km² for fish groups.

Table 4 Basic input and estimated parameters by Ecopath (in bold) for the food web model of Lake Garda. P/B stands for production/biomass ratio, Q/B is consumption/biomass ratio, EE is ecotrophic efficiency, P/Q is production/consumption ratio, R/A is respiration/assimilation ratio, P/R is production/respiration ratio, FD is the flow to detritus (t/km²/year), NE is net efficiency (i.e. production divided by the assimilated part of the food) and OI is the omnivory index.

	Group name	Trophic level	Biomass (t/km²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q	R/A	P/R	FD (t/km²/year)	NE	OI
1	<i>Esox lucius</i> (adult)	4.211	0.047	0.379	1.781	0.940	0.213	0.734	0.362	0.018	0.266	0.203
2	<i>Esox lucius</i> (juvenile)	4.179	0.010	0.400	3.302	0.878	0.121	0.849	0.178	0.007	0.151	0.362
3	<i>Perca fluviatilis</i> (adult)	3.261	0.343	0.596	3.919	0.362	0.152	0.810	0.235	0.399	0.190	0.158
4	<i>Perca fluviatilis</i> (juvenile)	3.019	0.173	0.700	7.200	0.572	0.097	0.878	0.138	0.302	0.122	0.007
5	<i>Scardinius erythrophthalmus</i> (adult)	2.841	0.429	0.600	3.155	0.158	0.190	0.762	0.312	0.488	0.238	0.269
6	<i>Scardinius erythrophthalmus</i> (juvenile)	2.841	0.242	0.800	5.913	0.749	0.135	0.831	0.204	0.335	0.169	0.269
7	<i>Salmo carpio</i>	3.538	0.030	0.537	4.002	0.626	0.134	0.832	0.202	0.029	0.168	0.148
8	<i>Alburnus arborella</i> (adult)	2.943	0.579	1.000	7.196	0.178	0.139	0.826	0.210	1.310	0.174	0.324
9	<i>Alburnus arborella</i> (juvenile)	2.943	0.252	1.100	14.552	0.523	0.076	0.906	0.104	0.865	0.094	0.324
10	<i>Coregonus lavaretus</i>	3.803	1.516	0.507	2.889	0.353	0.175	0.781	0.281	1.374	0.219	0.192
11	<i>Alosa agone</i>	3.656	2.794	0.539	2.761	0.328	0.195	0.756	0.323	2.555	0.244	0.241
12	<i>Echinogammarus stammeri</i>	2.533	0.143	7.000	10.000	0.950	0.700	0.125	7.000	0.336	0.875	0.286
13	<i>Asellus aquaticus</i>	2.100	0.075	2.000	5.000	0.950	0.400	0.500	1.000	0.082	0.500	0.090
14	Chironomida (larvae)	2.000	2.045	2.200	49.000	0.950	0.045	0.944	0.059	20.270	0.056	0.000
15	Carn. Cladocera	3.056	0.657	14.000	18.000	0.950	0.778	0.028	35.000	2.823	0.972	0.003
16	Herb. Cladocera	2.000	4.942	18.000	25.000	0.134	0.720	0.100	9.000	101.782	0.900	0.000
17	Copepoda	2.111	3.361	11.000	20.000	0.143	0.550	0.313	2.200	45.133	0.688	0.111
18	Rotifera	2.111	0.300	45.000	65.000	0.950	0.692	0.135	6.429	4.568	0.865	0.111
19	Cyanobacteria	1.000	3.300	100.000		0.056				311.590		0.000
20	Phytoplankton (large)	1.000	15.400	100.000		0.071				1430.273		0.000
21	Phytoplankton (small)	1.000	2.200	100.000		0.575				93.605		0.000
22	Detritus	1.000	10.030			0.025						0.109

The estimated values of ecotrophic efficiency (EE), the proportion of the production used in the system, were generally higher for fish groups and lower for zooplankton and primary producers, ranging between 0.025 (detritus) and 0.940 (adult *E. lucius*). EE of large phytoplankton (0.071) and cyanobacteria (0.056) were very low, indicating that only a small fraction of their production is consumed, and most of it goes to detritus, whereas EE of small phytoplankton is higher (0.575). EE were relatively low (<0.500) for all adult stanzas of fish species, except for *S. carpio* and *E. lucius*, which is likely due to the low biomass value relative to the fishing pressure. For the juvenile stanzas, on the contrary, EE resulted relatively high (>0.500) in all species.

The production/consumption ratio (P/Q), or gross food-conversion efficiency (defined by $GE = Z/(Q/B)$), were lower than 0.300 for all fish species, and higher than 0.400 for lower trophic levels groups, excluding chironomids larvae. Within the very high range of P/Q values, the lowest were found for chironomids larvae (0.045) and the juvenile *A. arborella* (0.076) and *P. fluviatilis* (0.097). The highest values were obtained for carnivorous (0.778) and herbivorous cladocerans (0.720).

According to the model outputs, the highest flow to detritus (representing the rate at which the detritus pool is replenished by the egested food, the fecal material or the non-living particulate matter) comes mainly from large phytoplankton (1430.273 t/km²/year), followed by cyanobacteria (311.590 t/km²/year) and herbivorous Cladocera (101.782 t/km²/year). The values of the respiration/assimilation ratios (R/A) were less than 1 for all groups, which was one of the criteria used to accept the Ecopath solution, whereas the production/ respiration ratios (P/R) exceeded unity for most non-fish groups. The Omnivory index (OI) values indicate a high specialization for the juvenile *P. fluviatilis* (0.007), *A. aquaticus* (0.090) and carnivorous cladocerans (0.003), whereas the feeding patterns of the juvenile *E. lucius* (0.362) and *A. arborella* (0.324) appear to be more flexible.

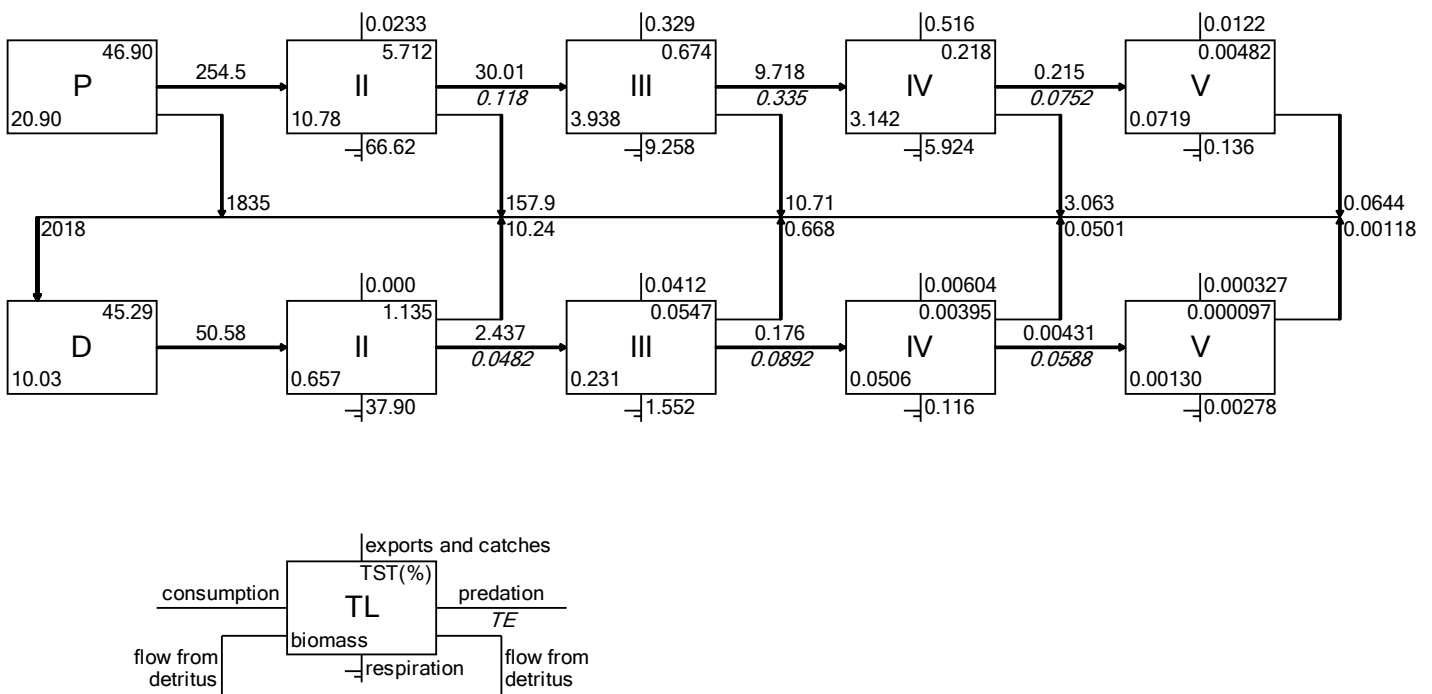


Fig. 36 Biomasses and trophic flows of Lake Garda ecosystem organized by integer trophic levels (TL) in the form of Lindeman spine. TL I is split into primary producers (P) and detritus (D). The upper part represents the grazing food chain and the lower part the detritus-based food chain. TE stands for transfer efficiency and TST for total system throughput. All flows and biomasses are expressed in t/km²/year.

Fig. 36 shows the Lindeman spine for the model, where biomass and flow were aggregated into integer TLs, excluding TLs higher than V. Generally, biomass was found to decline with increasing TL and the main flows occurred within TL I and TL II. The Lindeman spine demonstrated that flows at lower TLs in the grazing food chain (from I to II = 254.5 t/km²/year and from II to III = 30.01 t/km²/year) were much larger than the detritus food chain (50.58 and 2.437 t/km²/year, respectively). Excluding TL III, transfer efficiencies (TEs) show a clear decreasing trend as one ascends the trophic pyramid (10.64% for TL II, 31.63% for TL III, 7.49% for TL IV and 6.68% for TL V), resulting into a mean TE of 13.61% that deviated from the 10% Lindeman rule of trophic transfer efficiency.

Table 5 presents the summary statistics of energy flows and biomasses and network flow indices in Lake Garda. The sum of all consumption and all respiratory flows in the system were estimated to be 349.6 and 121.5 t/km²/year, respectively. Primary production in the lake reached up to 2090 t/km²/year. A total of 2018 t/km²/year of detritus was recycled into the system, which represent 45.27% of total system throughput (4457 t/km²/year). In comparison, consumption and respiration represent, respectively, only 7.84% and 2.72% of total throughput. As showed in the Lindeman spine (**Fig. 36**), flow to detritus was almost entirely (90.9%) from TL I, i.e. phytoplankton groups.

The total primary production/total biomass ratio of the system was found to be 53.81. This relatively high value, indicating accumulation of biomass over time, and the low total biomass/total throughput ratio of 0.009, indicating that low available energy flow is used to support the total system biomass, suggest that the system is undergoing an early developmental stage. This is also in accordance with the estimated total primary production/total respiration ratio of 17.20, since production normally exceeds respiration in early phases of development and the ratio approaches unity in matured ecosystems as energy fixed tends to be balanced by the energy cost of maintenance (Christensen and Pauly, 1993). The mean TL of the fish catch was 3.58, with the 39.87% confined to TL III and 56.25% to TL IV. The total catch resulted to be 0.928 t/km²/year, with a gross efficiency (catch/net primary production) of 0.0004, due to the fact that the fishery in Lake Garda is mainly concentrated on highest TLs. Primary production required for total catch in the lake is 88.43 t/km², which corresponds to 4.23% of total primary production, with the highest requirements for *A. agone* (1.26%) and *P. fluviatilis* (1.02%).

Table 5 Summary statistics describing the Lake Garda ecosystem structure.

Parameter	Value	Unit
Sum of all consumption	349.6289	t/km ² /year
Sum of all exports	1968.577	t/km ² /year
Sum of all respiratory flows	121.5075	t/km ² /year
Sum of all flows into detritus	2018.228	t/km ² /year
Total system throughput	4457.941	t/km ² /year
Sum of all production	2248.196	t/km ² /year
Mean trophic level of the catch	3.588887	
Gross efficiency (catch/net p.p.)	0.000444	
Calculated total net primary production	2090	t/km ² /year
Total primary production/total respiration	17.20058	
Net system production	1968.493	t/km ² /year
Total primary production/total biomass	53.81395	
Total biomass/total throughput	0.008711	/year
Total biomass (excluding detritus)	38.83752	t/km ²
Total catch	0.92818	t/km ² /year
Connectance Index	0.222222	
System Omnivory Index	0.141720	
Shannon diversity index	2.081606	

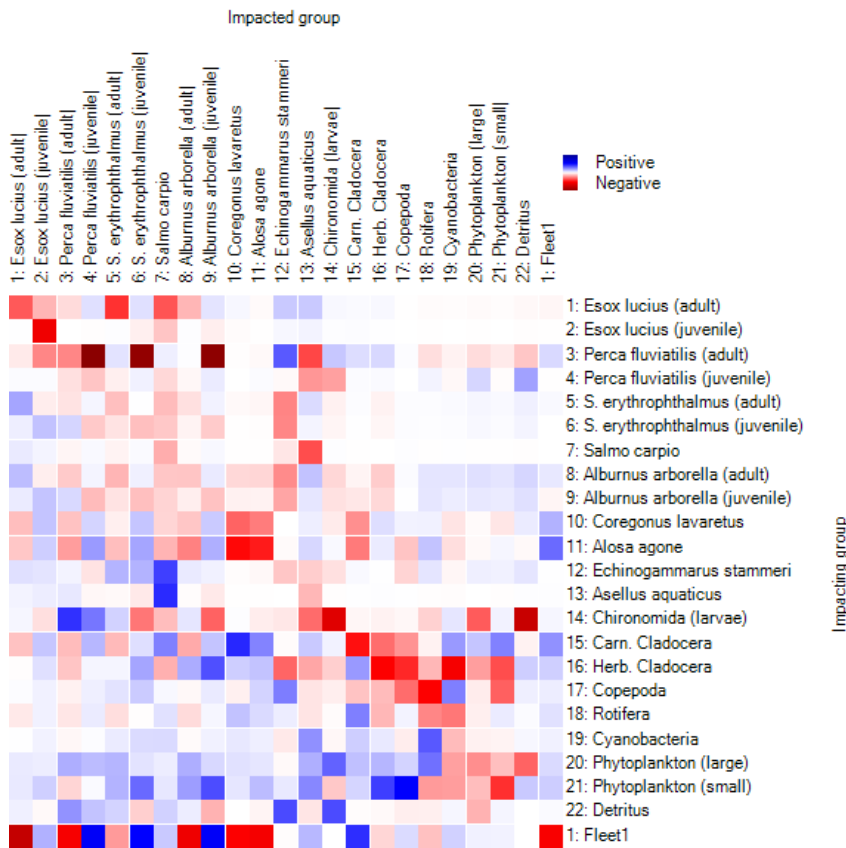


Fig. 37 Mixed trophic impacts (MTI) in Lake Garda food web showing the combined direct and indirect trophic impacts that the groups on the right have on those on the top. Blue values represent a positive impact, whereas red values represent a negative impact, and the intensity of colours is proportionate to the magnitude of the impact. The impacts should not be interpreted in an absolute sense, but they are relative and comparable between groups.

The result of the Mixed trophic impact (MTI) analysis shows both positive and negative effect among the different groups (**Fig. 37**). In fact, only detritus and phytoplankton groups have positive impacts on most other groups, whereas all the other compartments show a combination of different effects, related to direct predator-prey interactions, cascading effects or competition. Piscivorous fish, namely *E. lucius* and *P. fluviatilis*, generally have negative effects on other fish groups and phytoplankton, and positive effects on crustaceans and zooplankton. This analysis particularly highlighted the central role of the adult *P. fluviatilis* in Lake Garda, which demonstrated a wide range of strong impacts on several groups at both higher and lower TLs. For instance, *P. fluviatilis* has a very high negative effect on the juvenile *P. fluviatilis*, *S. erythrophthalmus* and *A. arborella*, which represent the main fish component of its food spectrum. It can be noted that, differently from *E. lucius*, among crustaceans, only *E. stammeri* is positively impacted by *P. fluviatilis*, whereas *A. aquaticus* is negatively impacted. Moreover, the effect on chironomids larvae is positive, despite they represent the main diet component of the adult *P. fluviatilis*. The cascading effect on zooplankton (positive) and phytoplankton (negative) groups is also stronger respect to that of *E. lucius*. Among planktivorous fish, *S. erythrophthalmus* and *A. arborella* have a slight effect on the food web, negative on most fish groups, chironomids larvae and cladocerans, and positive on other zooplankton groups and phytoplankton. *C. lavaretus* and *A. agone* show a different and mixed type of impacts, with positive effects on juvenile stanzas of fish groups and negative effects on adult stanzas and carnivorous cladocerans. The MTI analysis also emphasized the tight coupling between phytoplankton and zooplankton, suggesting a critical importance for the Lake Garda food web. In fact, phytoplankton have a strong positive impact on most herbivorous zooplankton groups, which have, in turn, a strong negative effect on phytoplankton. Phytoplankton also provide a benefit for most fish groups, in particular *S. erythrophthalmus* and *A. arborella*, which directly feed on them. Carnivorous cladocerans have a relatively positive impact on fish groups, in particular *C. lavaretus*, whereas they have a substantial negative impact on lower TL consumers, in

particular herbivorous cladocerans and copepods. Fishery has very strong negative impacts on all adult fish groups, except *S. carpio*, and positive impacts on juvenile stanzas.

3.2 Dynamic simulations

Fig. 38 shows the results of the simulations, in terms of relative biomass, based on the temperature increase scenarios, RCP 4.5 and RCP 8.5, for the different groups. With constant primary production, the effects are mixed, mainly reflecting the different temperature requirements and tolerance of the various species, as well as food web interactions in the system. In the two temperature scenarios, the effects are similar, but with higher magnitudes in RCP 8.5 respect to RCP 4.5. Among fish groups, *C. lavaretus*, *S. carpio* and *P. fluviatilis* are the only species to be negatively affected by the raise of temperatures. In particular, in the RCP 8.5 scenario, *S. carpio* showed a marked decline in biomass of about 36%, whereas *P. fluviatilis* and *C. lavaretus* showed a decrease of 8% and 6%, respectively. In the RCP 4.5 scenario, biomass declines are, instead, less pronounced (13% for *S. carpio*, 3% for *P. fluviatilis* and 2% for *C. lavaretus*). Conversely, *A. arborella* particularly benefited from the temperature increase, with a biomass increase of 17% in the RCP 8.5 scenario. *E. lucius* and *S. erythrophthalmus* also increased in biomass (up to 5% in RCP 8.5), whereas the biomass of *A. agone* resulted substantially unchanged in both scenarios. Among invertebrates, in the RCP 8.5 scenario, *Echinogammarus stammeri* showed the strongest decline (26%), followed by chironomids larvae (11%) and carnivorous cladocerans (7%), whereas rotifers showed an increase of 5%. Regarding simulations including primary production, the effects of temperature rise are positive for most groups, except for *S. carpio* and *Echinogammarus stammeri*. In this case, the increase in biomass is particularly marked in the RCP 8.5 scenario, up to 50% for *A. arborella*, 45% for *E. lucius*, 37% for *S. erythrophthalmus*, 30% for *A. agone*, 21% for *C. lavaretus* and 19% for *P. fluviatilis*. Lower TL groups showed an increase in biomass of around 20%. In the RCP 4.5 scenario, the increase was lower than 20% for all fish groups and lower than 10% for phytoplankton, zooplankton and benthic crustaceans. *S. carpio* resulted the only fish species with decreasing biomass in all the scenarios examined. In the RCP 8.5 scenario with raise in primary production, the flow to detritus from large phytoplankton, cyanobacteria and herbivorous cladocerans, representing the largest part of the flow, resulted to increase of 19%, 18% and 21%, respectively. However, the largest relative increases occurred in the highest TLs, particularly in *E. lucius* (41%) and *A. arborella* (47%). In general, flows at the lower TLs in the grazing food chain continue to dominate respect to the grazing food chain. The model predicted a slight increase in the TE for TL II (11.58 %) and a slight decrease for TL III (29.53%), with a mean TE of 13.76%.

Comparing summary statistics of energy flows and network flow indices between the current status and the RCP 8.5 scenario, it was found that the sum of all consumption and all respiratory flows in the system decreased by 3% and 6%, respectively, without raise of primary production, and increased by 20% and 17% with raise of primary production. In the latter scenario, total net primary production reached 2482 t/km²/year, with an 18% increase. The total flow into detritus also increased by 18%. However, the ratio to the total system throughput (5299 t/km²/year) remained unchanged, as well as the total primary production/total biomass ratio. Regarding total primary production/total respiration ratio, it was found a slight increase, from 17.20 to 18.46, in the scenario without raise in primary production. The mean TL of the catch, with the increase in primary production, remained stable (3.54), while the total catch resulted to increase by 29% (1.201 t/km²/year), with gross efficiency

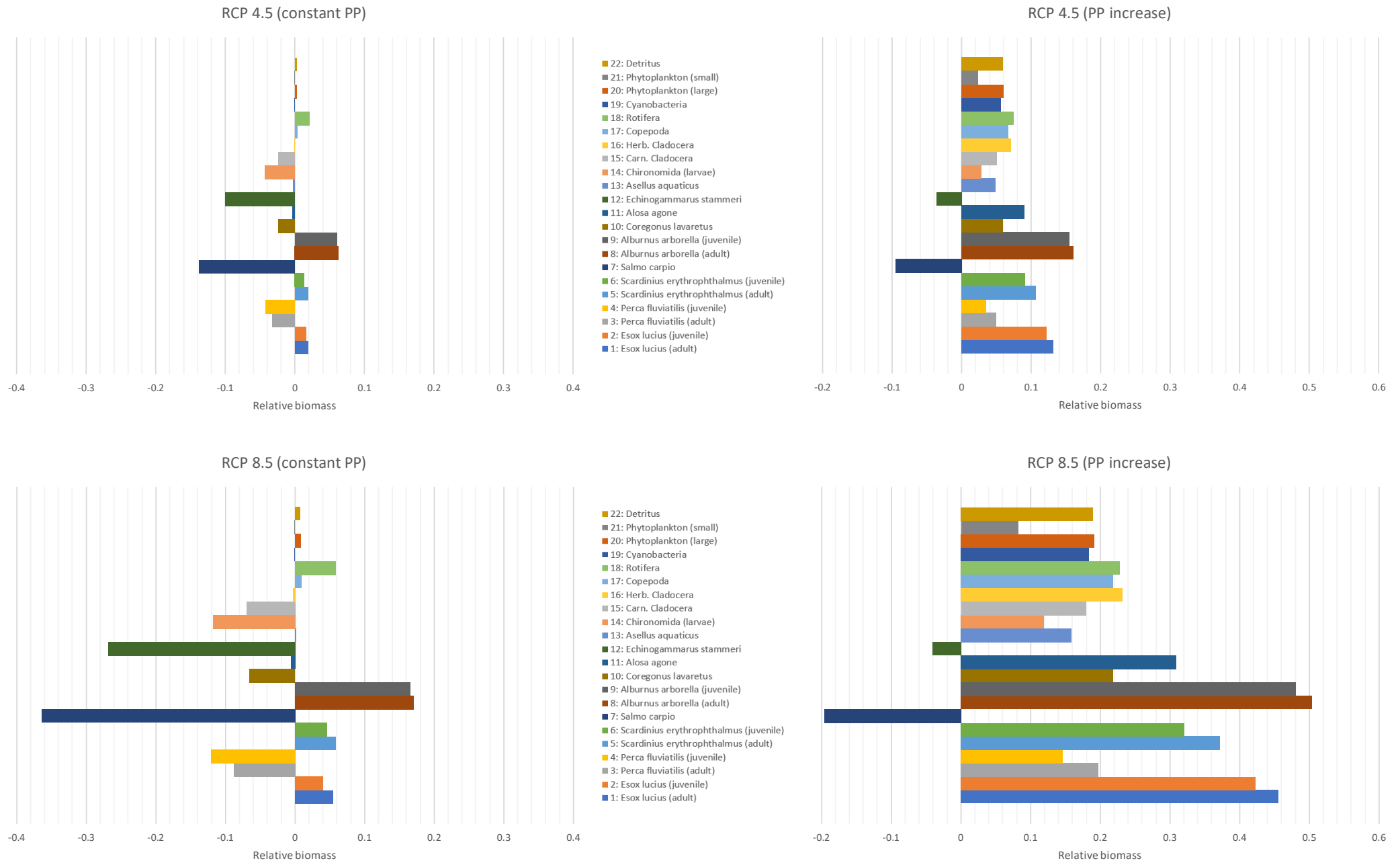


Fig. 38 Results of the simulations based on temperature increase scenarios, RCP 4.5 (upper panels) and RCP 8.5 (lower panels), in terms of relative biomass anomaly. Right panels show simulations including the temperature forcing on primary production, left panels show simulations with constant primary production.

reaching 0.0005. In the same scenario, primary production required for total catch increased to 110 t/km², corresponding to 4.43% of total primary production.

Table 6 Biomass-based ecological indicators calculated at the current status and in the four scenarios considered. Biomasses are expressed in t/km².

	Current status	RCP 4.5 (constant PP)	RCP 4.5 (PP increase)	RCP 8.5 (constant PP)	RCP 8.5 (PP increase)
Total B	48.8675	48.7833	51.8739	48.7657	58.7828
Commercial B	5.7382	5.6953	6.2374	5.7094	7.4675
Fish B	6.4150	6.3762	6.9828	6.4183	8.3722
Invertebrates B	11.5225	11.3985	12.2030	11.2307	13.8405
Invertebrates / Fish B	1.7962	1.7877	1.7476	1.7498	1.6532
Demersal B	2.3366	2.2517	2.4519	2.1400	2.7858
Pelagic B	4.9529	4.9660	5.4355	5.0690	6.5848
Demersal / Pelagic B	0.4718	0.4534	0.4511	0.4222	0.4231
Predatory B	0.0565	0.0577	0.0639	0.0595	0.0819
Kempton's Q	4.0900	4.0081	4.0833	3.8832	4.1111
Shannon diversity	2.0816	2.0755	2.0841	2.0702	2.0947

Analysing some biomass-based ecological indicators, listed in **Table 6**, it was found a significant increase in the total biomass of the system in both scenarios with raise in primary production, of 6% in RCP 4.5 and 20% in RCP 8.5. In particular, fish biomass resulted to increase by 9% and 30%, respectively. The increase of invertebrates' biomass is, instead, less pronounced (6% and 20%, respectively), resulting in a decrease in the invertebrates/fish biomass ratio of 2% and 8%. A decrease of 2% in this ratio was also found in the RCP 8.5 scenario with constant primary production, due entirely to the decrease of invertebrates' biomass. Moreover, a decrease of 5% the demersal/pelagic biomass ratio resulted in both RCP 8.5 scenarios: with raising primary production, however, this is due to the higher increase in pelagic biomass (32%) respect to the demersal biomass (19%), whereas, with constant primary production, this is due to the slight increase (2%) in the pelagic biomass respect to a decline (8%) in demersal biomass. A similar change occurred in RCP 4.5 scenarios, with a decrease in the demersal/pelagic biomass ratio of 2%.

4. Discussion

A food web model was implemented in Lake Garda to quantify the main energy flows in the ecosystem, the dominant food web dynamics, the direct impacts of predicted temperature increase on the different species through altered growth and consumption and the indirect effects via food web structure. This is the first EwE study performed on Lake Garda and one of the first on a European lake ecosystem, thus providing a useful tool also for other European freshwater systems.

The model analysis revealed that bottom-up control in Lake Garda was the most dominant pattern, whereas top-down control was limited. The importance of low trophic level groups to the higher ones is indicated by mass flows in the ecosystem. In fact, as showed in the trophic flow structure of Lake Garda, the greatest part of the biomass was represented by the low trophic level groups (zooplankton, phytoplankton and benthic invertebrates), with *C. lavaretus* and *A. agone* having the highest biomass among fish groups. Low trophic levels (TL I and TL II) also contributed the most to Total System Throughput (TST) values (by more than 99%), as reported in the Lindeman spine.

The low EE of detritus (0.025) suggested that this resource was not utilized adequately in the whole food web, similarly to phytoplankton. In fact, EE of cyanobacteria (0.056), large (0.071) and small phytoplankton (0.575) indicated that the supply of producers exceeded the demand of consumers and, therefore, the food web was mainly based on phytoplankton. Therefore, the low EE of phytoplankton and the high primary production/respiration ratio (PP/R) imply that this resource was a “sink” rather than a “link” to higher trophic levels, as normally expected in pelagic areas of oligotrophic lakes. This is also confirmed by the fact that most of biomass flow to detritus originated from TL I, which contributed approximately to 90% of the total biomass flow.

Despite an important part of the production of low trophic level groups was not utilized and was therefore lost, by being incorporated into the lake’s bottom sediments, the average TE of the lake’s ecosystem (13.61%) is higher than the value of 10% estimated by Lindeman and within the range (8-15%) described by [Christensen and Pauly \(1993\)](#), due to the significantly high TE of higher trophic levels (31.63% for TL III). Even though the transfer efficiency was good, this was not reflected in the gross efficiency of the fishery (catch/PP), estimated at 0.0004, which is lower than the oligotrophic Lake Annecy in France (0.00117, [Janjua and Gerdeaux, 2009](#)), but similar to the value of the eutrophic Lake Volvi in Greece (0.0002, [Moutopoulos et al., 2018](#)), indicating that primary production in Lake Garda is not well-utilized for fishery. The percentage of primary production required to sustain fisheries (4.2%) is also comparable with that found in Lake Volvi (4.5%).

Among fish groups, the EE of *E. lucius* (0.940) was quite high considering its status as top predator, but it is possible because of its high fishing mortality and low biomass. Minimum EE was found for adult *S. erythrophthalmus* (0.158) and *A. arborella* (0.178), probably due to a lower fishing and predation pressure. Except for *E. lucius*, EE of the juveniles were higher respect to adults, because of high predation pressure from *P. fluviatilis* and *E. Lucius*. EE of the two most commercially important fish species, *A. agone* and *C. lavaretus*, were less than 0.4, showing sustainable fisheries.

Mixed trophic impacts show the combined direct and indirect trophic effects, to evaluate the relative importance of the top-down and bottom-up control of the food web. For instance, it can be clearly observed that an increase in the abundance of detritus, phytoplankton and zooplankton, considered individually, would benefit most species’ groups, especially benthic invertebrates (for detritus), omnivorous fish species and herbivorous zooplankton (for phytoplankton). The positive and strong impact exhibited from detritus, phytoplankton and zooplankton to upper groups also supports the dominance of bottom-up control in the lake. On the other

hand, fisheries had negative effects mostly on the target species' groups, and to a lesser extent on some zooplankton groups (i.e. herbivorous cladocerans and rotifers). All the functional groups had a negative impact on themselves, except detritus, which had neither positive nor negative impact to itself.

The primary production/respiration ratio (PP/R) of Lake Garda was 17.20, which is higher than Lake Annecy in France (Janjua and Gerdeaux, 2009), Lake Volvi in Greece (Moutopoulos et al., 2018) and Lake Võrtsjärvi in Estonia (Cremona et al., 2018), indicating an early stage of ecosystem development, as the value approaches 1 with maturity, when energy fixed is balanced by maintenance (Christensen and Pauly, 1993). The Primary production/biomass ratio (PP/B) was 53.81, which is also rather high respect to values found in other European lakes (20.41 for Lake Annecy and 33.05 for Lake Volvi). Moreover, the ratio of total system biomass to the total system throughput (B/TST) was low (0.008) compared to Lake Annecy (0.018) and Lake Volvi (0.010). According to Christensen (1995), the estimated value of B/TST is directly proportional to system maturity, since it tends to be low during the ecosystem development phase and increases as a function of maturity. Therefore, all the above estimates show that the system is relatively in an immature state, even though it is not possible to clearly determine the direction of development. A possible explanation is that current changes in trophic status (from oligotrophy to mesotrophy) and circulation patterns are driving the system towards a new equilibrium. However, bacterial activity was not considered as a model functional group, possibly resulting in an underestimation of the community respiration of the system. In fact, a large fraction of the detritus assumed to be exported does not leave the system but is reutilized by bacteria and thus made available again to the systems. Therefore, EwE models from which bacterial activity is excluded can be expected to overestimate the PP/R ratios (Christensen and Pauly, 1993). Nevertheless, the low Connectance Index (CI) and System Omnivory Index (SOI) values, respectively 0.22 and 0.14, reveal that the lake did not display web-like features, which is a characteristic of younger systems (Christensen and Walters, 2004). Since it is generally believed that mature ecosystems demonstrate greater stability and therefore greater resilience, resistance, or persistence to overcome external disturbances (Christensen, 1995), the immature state of Lake Garda can result in a relatively high vulnerability to modifications due, for instance, to effects of climate change.

This analysis also represents the first attempt to predict the effects of climate change on freshwater food webs with the EwE modelling approach. A similar methodology, i.e. applying forcing functions related to temperature to manipulate predator search rates and primary production rates, however, has been previously applied in some marine systems, as in Northeast Pacific (Ainsworth et al., 2011) and Northern Adriatic Sea (Libralato et al. 2015).

Given the inherent uncertainty which characterize the EwE approach, and generally ecological simulation models, in assembling complex and fragmentary trophic data, due to difficulties in measuring some ecosystem components and processes (Christensen and Walters, 2004), the results of these dynamic simulations should be interpreted with caution. In particular, the lack of direct sampling data for some functional groups and different assumptions made in the estimation of parameters and diet compositions represent important sources of uncertainty. Moreover, in simulating effects of temperature increase, the model did not represent factors such adaptive capabilities of species and different other mechanisms by which changes in climate might affect the lake ecosystem, such as altering thermal stratification patterns or species behaviour. However, when considering strategic management questions, this kind of simulation can represent a useful tool in decision making, by providing a better understanding of climate change impacts under future scenarios and identifying research priorities.

In general, these simulation results in terms of biomass are consistent with the literature reporting observed or predicted effects of climate change on freshwater fish, according to which increased temperatures likely result in increases in trophic states and the replace of economically important species such as salmonids with smaller and less desirable species such as cyprinids (Ficke et al., 2007, Jeppesen et al., 2010). In this analysis, however, none of the considered scenarios induced extremely negative impacts to salmonids, to the point of extinction, even though *C. lavaretus* and, particularly, *S. carpio*, underwent a sharp relative decrease in biomass respect to *A. arborella* and *S. erythrophthalmus*. The decline in biomass of *S. carpio*, which occurred in all scenarios, differently to *C. lavaretus*, could be explained by the fact that food supply cannot sustain the increased metabolic demand. As pointed out by Ficke et al. (2007), this is expected for different cold-water species in temperate ecosystems. Generally, the response of cool-water species, such as percids, to increasing temperature could be variable (Comte et al., 2013). In this simulation, the response of *P. fluviatilis* depends, in fact, on the assumptions made on primary production. In the scenarios with constant primary production, the biomass response of *P. fluviatilis* is similar to that of salmonids, i.e. it decreases with increasing temperature (-4% in RCP 4.5, -12% in RCP 8.5), whereas, with raise in primary production, it increases with increasing temperature (4% in RCP 4.5, 14% in RCP 8.5). Differently to what expected in Jeppesen et al. (2010), however, in none of the scenarios *P. fluviatilis* is favoured at the expenses of *C. lavaretus*.

One of the clear results of these dynamic simulations is that the indirect effect of primary production increase on higher TL groups is more marked respect to the direct effect of temperature increase. This is, however, an expected result, given that, as discussed before, Lake Garda is an oligo-mesotrophic system which is dominated by a bottom-up control. Moreover, scenarios with increasing primary production are particularly important because they are the most likely to happen, since a eutrophication trend, with increase in phytoplankton biovolume, has been already detected in Lake Garda in the last 25 years (Salmaso et al., 2018).

Even though the model includes three phytoplankton functional groups, mechanisms inducing shifts in phytoplankton composition, especially among those groups that are sensitive to temperature and mixing, such as cyanobacteria, diatoms, and flagellates, are not represented. In particular, longer periods of stratification create favourable conditions for cyanobacteria, which are inedible to most species of zooplankton and may produce compounds that are toxic to fish or their prey items (Ficke et al., 2007).

In fact, at higher temperatures and nutrient concentration, bloom-forming cyanobacteria have a competitive advantage over other phytoplankton groups, such as diatoms and green algae, with a higher maximum specific growth rate at temperatures above 23°C. Moreover, they can regulate their position in stable water columns through gas vacuoles, which makes them strong competitors with reduced vertical mixing and intensified stratification (Salmaso, 2010; Winder and Sommer, 2012). In Lake Garda, since 1995, cyanobacteria were characterized by an increase in their annual mean biovolumes and interannual variability, showing a strong dependence from both water temperature and TP (Salmaso et al., 2018). Even though the beginning of the recent meromictic period of the lake, with the corresponding decrease of TP in the mixolimnetic and trophogenic layers, induced a decline in biovolumes respect to peaks between 2005 and 2007, warmer water temperatures coupled with favourable hydrodynamic conditions will potentially further increase the relative contribution of cyanobacteria to the total phytoplankton biomass.

Reduction of oxygen levels in the hypolimnion in stratified lakes, favoured by eutrophication and prolonged stratification, may further stimulate a shift in fish community composition. Enhanced risk of oxygen depletion below the thermocline, triggering the shift from oxygenated to anoxic conditions in the bottom waters, will likely extremely affect cold-adapted species, such as salmonids (Jeppesen et al., 2010; Comte et al., 2013). In

fact, concentrations of dissolved oxygen below 2-3 mg/L can compromise the suitability of the hypolimnion as a refuge from high summer water temperatures for numerous cold-water stenothermal fishes. Currently, average O₂ concentrations in Lake Garda are always greater than 6 mg/l, even in the deep hypolimnion (200 m-bottom), indicating a satisfactory level of oxygenation. However, during periods characterized by incomplete vertical cooling and consequent partial overturn, the water column showed the presence of marked O₂ concentration gradients and a clear decreasing trend in deeper layers (Salmaso, 2005). This suggests that, with strengthen and prolonged stratification induced by a future temperature increase, which makes more difficult the mixing process, species such as *S. carpio* and *C. lavaretus* may increasingly face situations where the decreased oxygen supply cannot meet their increased demand due to higher water temperatures.

The significant increase of *A. arborella* in all scenarios considered, particularly in RCP 8.5, is an interesting result. *A. arborella* underwent a progressive decline in Lake Garda starting from 1990s, for reasons that are still unclear, and catches are currently prohibited (Regione Lombardia, 2013). The results of this analysis suggest that temperature increase is unlikely to represent one of the main reasons of the recent decline, which could be instead related to the decrease in water quality and habitat alteration of the littoral region of the lake, an important reproduction area for this species.

The general decrease in the invertebrates/fish biomass ratio found in all scenarios is possibly related to the decreasing proportion of piscivores and the higher dominance of zooplanktivorous and omnivorous fish, which implies increased predation on zooplankton and benthic crustaceans. This is particularly evident considering the marked decline of *E. stammeri*, which is entirely due to trophic interactions, since no forcing functions related to temperature have been applied to invertebrate groups. As pointed out by Jeppesen et al. (2009), this change in the trophic composition is expected with increasing temperatures.

Generally, relative changes in fish biomass among the four scenarios are also reflected in catches. Total catches remain substantially stable in both scenarios with constant primary production, whereas they increase with the raise in primary production, by 8% in RCP 4.5 and 30% in RCP 8.5. However, the composition of the catches is projected to change substantially, as catches of *A. arborella*, *S. erythrophthalmus* and *E. lucius* increase notably in all scenarios (up to 50% for *A. arborella* with raise in primary production), whereas catches of salmonids decrease or increase slightly.

The decline of *S. carpio*, both in biomass and catches, raises particular concerns. In fact, these simulation results confirm the drastic declining trend of this endemic species occurring in Lake Garda in the last decades, which currently results seriously threatened and classified as "Critically Endangered" according to the IUCN classification. As noted in previous studies (Regione Lombardia, 2013), the reason for this decline is mainly represented by the excessive fishing effort of the last decades, also on juvenile individuals and during reproductive periods. The anthropogenic alteration of reproductive areas and the rapid increase in the trophic status of the lake may have also contributed to the population reduction. According to these simulations, increasing water temperature will constitute an additional negative factor for this species in the next decades. Therefore, urgent conservation measures will be needed in order to preserve this species and reduce extinction risk, in particular through the application of highly restrictive regulations of fishing activity and restocking operations.

5. Conclusions

In this thesis, a first attempt to model the food web of a deep meso-oligotrophic sub-alpine lake with the EwE approach was made. In fact, it was possible to describe, for the first time, the structure and trophic interactions of Lake Garda ecosystem from a holistic point of view. The application of the Ecopath model demonstrated that, in terms of trophic flows, Lake Garda is currently an immature system which is characterized by a food web structure based on phytoplankton. Moreover, the relatively low number of energy pathways and low rates of matter cycling, can possibly result in a high vulnerability to external disturbances.

With this thesis it was also possible to provide a useful insight into the dynamics which can drive a shift in the food-web structure and functioning of Lake Garda under climate change, and the direction towards which the system can be expected to evolve. Results of simulations seem to show that the Lake Garda ecosystem may be directed towards an enrichment in terms of biomass, with a resulting increase in total catches, if the current increasing trend in primary production will continue. At the same time, however, results suggest that cyprinids may be favoured at the expenses of salmonids, therefore reducing the market value of the catch and enhancing extinction risk for *S. carpio*.

Considering that this kind of scenario, with an increase in primary production, is the most likely to happen, a consistent management effort will be required in the near future, with the main focus on vulnerable cold-water species, namely salmonids. In general, trends in primary production, more than trophic relations within the species' groups, seem to be the primary factor to take into account in the design of strategic plans for fisheries or conservation purposes.

In any case, given the significant uncertainty in some of the parameter estimates, even though the model appears overall balanced, these results are only preliminary. In particular, further studies are required in order to get more precise and specific data on productivity, biomass and feeding habitats of many of the groups. As this kind of information becomes more extensively available, it can be then incorporated into the model to improve estimates and reduce uncertainty. Analysis of temperature optima and tolerance limits may also be useful to verify the effects of temperature increase on single species and, concurrently with other natural and anthropogenic external disturbances, on food web structure of Lake Garda.

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