

Limnological research in the deep southern subalpine lakes: synthesis, directions and perspectives

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Based on a selection of 230 papers published during the last 15 years in international journals, the present work aims at evaluating the state of the art of limnological research in the deep southern subalpine lakes (DSL: Garda, Iseo, Como, Lugano and Maggiore). Historically, most of the limnological research was fostered by the need to find solutions to the problems connected with eutrophication and pollution. Many data are available on the thermal structure, algal nutrient concentrations and phytoplankton of the DSL, while other topics still remain more or less constrained to single lakes. Apart from this geographical bias, a number of aspects emerged from this synoptic view. Limnological research is still linked to the concept of scientific monitoring, while experimental studies and modelling are confined to specific niches; the integration of different disciplines is held back by the division of studies on different compartments; integration of studies and synoptic analyses at a macro regional scale have been carried out only for specific research areas. The DSL are increasingly threatened by new pressures (climatic change, excessive proliferation of toxic cyanobacteria, introduction of new species and new micropollutants) and by the interactions among these new and old stressors. In this rapidly changing situation, the paper emphasises the need to define criteria to be used to distinguish research able to produce relevant results and predictive models, which are essential elements for an efficient management of water resources.

Keywords: Italian deep lakes; state of the art; bibliometrics; limnological research; environmental stressors

1. Introduction

The geographical distribution of lakes in Italy is strongly biased in favour of the Alpine and subalpine regions. The number of lakes characterised by a surface greater than 0.2 km^2 is over 500, with an overall volume of water of more than $150 \times 10^9 \text{ m}^3$. Of these, around 80% of the water is concentrated in five lakes located along the southern border of the Alpine chain, namely the lakes Garda, Iseo, Como, Lugano and Maggiore (deep southern subalpine lakes, DSL; Figure 1; Table 1). In the catchment areas of these lakes, water is extensively used for the production of hydroelectric power, whereas south of the DSL, in the

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Figure 1. Geographical location of the deep southern subalpine lakes (DSL) in northern Italy.

Table 1. Morphometric and hydrological characteristics of the deep southern subalpine lakes (DSL) in Northern Italy.

	Garda	Iseo	Como	Lugano ¹	Maggiore
Altitude (m a.s.l.)	65	186	198	271	193
Area (km ²)	368	62	146	28	213
Maximum depth (m)	350	251	410	288	370
Mean depth (m)	133	123	154	171	178
Volume (km ³)	49.03	7.57	22.5	4.69	37.5
Catchment area (km ²)	2290	1842	4508	297	6599
Mean outflow discharge $(m^3 s^{-1})$	58.4	58.7	158.0	12.0	291.3
Renewal time (years)	26.6	4.1	4.5	12.4	4.1
Cryptodepression (m)	285	65	212	17	177

¹Northern basin.

plain of the River Po, water is intensively used in agriculture and industry, becoming a life-sustaining element for the economy of the most densely populated and productive area in Italy. In addition, these water bodies are one of the key elements for the tourist economy of the Alpine region. Since limnological studies began, the DSL have attracted a large

	Garda	Iseo	Como	Lugano	Maggiore	DSL
MorGeo		[1]	[2]			
Hydrol	[3,4]	[-]	[5-8]	[9]	[10-12]	[13]
Physic	[14–16]	[17]	[18,19]	[20-22]	23-28	[29-35]
Geoche	[36,37]		[38]	39–57	58-61	[62]
Eutrop	[63–66]	[67–69]		[70]	71–74	[75-79]
Phytop	80-86	[87]	[88–91]	[92]	[93-102]	[103,104]
Zoopla	[105,106]				[107 - 124]	
MicEco				[125]	[126–140]	[141,142]
Bentho	[143–146]	[147]	[148–150]		[151,152]	
Fishes	[153]				[154–160]	[161]
Birds			[162–164]	[165,166]		
Parasi	[167,168]		[169,170]			[171,172]
Ecotox		[173–175]	[176–179]	[180]	[181-210]	[211-218]
Paleol					[219]	[220,221]
RemSen	[222–227]	[228,229]				[230]

Table 2. Principal limnological studies carried out since 1995 in the deep southern subalpine lakes (DSL). Studies carried out on two or more lakes are reported under 'DSL'.

For every group (in square brackets), papers have been listed by year of publication. MorGeo, morphometric and geological studies; Hydrol, hydrology; Physic, physical limnology; Geoche, geochemistry; Eutrop, algal nutrients and eutrophication; Phytop, phytoplankton; Zoopla, zooplankton; MicEco, microbial ecology; Bentho, benthos; Fishes, fishes; Birds, birds; Parasi, micro- and macroparasites; Ecotox, ecotoxicology; Paleol, paleolimnology; RemSen, remote sensing.

number of scientists, fostering a large number of investigations in different fields (see Table 2 [1–230] and [231]).

The largest lakes south of the Alps share many common characteristics [32,232]. They are narrow, elongated and delimited laterally by steep sides. Their bottom is generally flat and the thalwegs are roughly north-south oriented, with the exception of the north basin of Lake Lugano, which is oriented east-west. Lake Garda is the largest Italian lake, followed by Lake Maggiore, Lake Como and Lake Iseo (Table 1). Lake Lugano stands out for its subdivision into three basins [233]. The northern basin is the largest of the three, accounting for around 80% of the total water volume. The maximum depths of the DSL range from 251 m (Lake Iseo) to 410 m (Lake Como). The DSL contribute about 40% to the discharge of the River Po, the largest Italian river. Their theoretical renewal times are around 4–5 years (lakes Maggiore, Como and Iseo), 12 years (Lake Lugano, N-basin) and 27 years (Lake Garda). Compared with the other deep subalpine lakes, Lake Garda has a longer theoretical water renewal time (27 years), due to its low catchments area to lake volume ratio and lower annual rainfall.

Large and deep lakes present peculiar ecological characteristics, which justify their inclusion in a separate typology [234]. The size and form of lakes regulate many transport processes – such as sedimentation and re-suspension, diffusion, mixing, and the burial of organic and inorganic matter – which regulate many abiotic factors, including phosphorus availability, water chemistry and water clarity [235]. In turn, variations in these fundamental ecosystem characteristics strongly regulate primary and secondary production [236]. The formation of a strong thermocline during the warmest period contributes to isolating large portions of the upper pelagic zone for many months, suppressing vertical mixing and inhibiting the transport of nutrients towards the trophogenic layers. In contrast to the shallower lakes of the temperate latitudes, which are strictly dimictic or

monomictic [237], complete vertical mixing of deep lakes can be prevented by warmer winter temperatures or low wind conditions. Therefore the deep hypolimnion may be characterised by several years of gradual warming caused by a downward transport of heat by turbulent diffusion during stratification, terminated by sudden cooling during harsh winters [238], with strong implications for the spring vertical replenishment of nutrients from the deeper layers and for primary production [15]. In this regard, the deep lakes south of the Alps could be classified as warm monomictic lakes. In this category, lakes circulate completely once a year in the winter at or above 4° C, showing stable stratification for the remainder of the year. Nevertheless, owing to their great depth, complete mixing can occur only during cold winters with complete cooling of the water column. This condition – known as oligomixis – is different from that of lakes which circulate freely every year (holomictic lakes) or show a constant stratification (meromictic lakes).

From a biogeochemical perspective, nutrient cycling in large lakes becomes more and more important compared with inputs from the watershed or interactions with the littoral or lake bottom, even though important differences exist due to hydrology and watershed size in relation to lake volume. An important pathway by which nutrients are recycled in the pelagic zone is through the microbial loop, whereas severe limitation of epilimnetic nutrients in summer can be detected in less enriched environments due to settling fluxes of plankton [239].

From a synecological perspective, large water bodies tend to operate as large inertial systems, minimizing the effects of external disturbances. Chronological sequences of phytoplankton assemblages generally show ordered cyclical patterns, in contrast with the unpredictable and disorderly development observed in smaller lakes, which are more susceptible to meteorological and hydrological events [84]. In turn, these properties allow a major degree of predictability and definition of management tools, e.g. [103,104].

In large and deep lakes, the contribution of the fauna and flora of the shores in shaping plankton composition and biotic interactions may become less important, even if only apparently for a few species (e.g. see section 3.7). Nevertheless, the naturalness of riparian zones is essential for the proper functionality, sustainability and recreational attractiveness of lake shores. Moreover, from a biodiversity perspective, many large lakes are known for hosting a large number of endemic species; see, e.g. [240,241]. A part from well known cases (e.g. *Salmo trutta carpio* in Lake Garda [242]), the biocenosis of the DSL present many common traits. Many changes due to anthropic pressure occurred, however, during the last decades.

The natural functionality of trophic webs in the DSL underwent alterations due to the introduction of allochtonous species, both in historical time – e.g. fishes, macrophytes, molluscs [242] – and more recently, e.g. with the introduction of new zooplankton, shrimps, molluscs and fishes (section 3). On the other hand, the principal alterations of the pristine ecological conditions were due to significant changes in the algal nutrient loads, and to the progression of eutrophication since the 1970s. Climate change, occurring on top of all other anthropogenic pressures, is considered a worsening factor for the ecological status of lake ecosystems [234], but the quantification of its exact role is still problematic due to the exceeding importance of nutrients compared with the slow changes occurring in the physical properties of the water columns. A further element of degradation was due to the discharge and deposition of toxic contaminants. A substantial pollution from specific contaminants is still present in a few lakes due to historical pollution (e.g. DDT in Lake Maggiore) or to release of paleo-contaminants from the melting of glaciers (e.g. lakes Como and Iseo, DDT).

Trying to go through these topics, this review has two specific objectives: (i) to synthesize the whole set of information published on the limnology of the DSL in peerreviewed journals since 1995, in order to identify the more recent important topics and research directions in the last 15 years and (ii) to highlight gaps in the research topics, identifying future research directions in relation to the present and future multi-stressor scenarios.

The review of limnological literature was based on a search made on international journals from 1995 to January 2010. Besides consulting the ISI Web of Science (ISI-WoS, Thomson Scientific's Institute for Scientific Information), other limnology serials were consulted, including Memorie dell'Istituto Italiano di Idrobiologia (1995-1998) and its successor, the Journal of Limnology, volumes 58(1)-69(1); Documenta Istituto Italiano di Idrobiologia (1995–1997); Proceedings of the International Society of Limnology (Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie), volumes 26(1)-30(9). Other papers with impact factor not yet included in ISI-WoS but with DOI (Digital Object Identifier) were considered whenever possible. The use of international sources constrains the selection to peer reviewed papers, allowing easy accessibility to the literature by interested readers. However, besides these sources, a lot of information is also included in grey literature, which is often difficult to obtain. Bibliographical information about papers published in local journals or in many national proceedings have been partly summarised in Tartari et al. [243], www.limno.eu and www.iii.to.cnr.it. The papers published on the limnology of the DSL were analysed by Correspondence Analysis [244], taking into consideration the mutual relationships between lakes and topics (see section 3). Before CA computation, the data were subjected to a square root transformation $(Y_i = X_i^{0.5})$ to reduce the weight of the topics with the highest number of papers.

Besides a critical description based on published literature, this work will also provide an update of the long-term series of temperature, TP and hypolimnetic dissolved oxygen recorded until 2008. Since serial correlation in the climate time series can influence the estimate of trend, besides the usual Mann–Kendall (MK) test [245], the significance of the temperature trends were computed utilizing the trend-free pre-whitening (TFPW) procedure proposed by Yue et al. [246]. Moreover, the significance of the MK analyses was confirmed with the application of bootstrap tests for trend detection [245]. The degree of temperature change (slopes) was estimated with the non-parametric Theil-Sen Approach [245]. Statistical analyses were carried out with the R package [247].

2. A brief overview of the studies carried out in the DSL in the 1900s

Deep lakes were considered of primary interest from the earliest limnological studies, in spite of the practical difficulties deriving from their dimensions. The model of scientific study of lakes remained for decades the fundamental work of F.A. Forel and of the staff of scientists he coordinated, resulting in the impressive monograph on Lake Geneva [248]. Following these activities, Pietro Pavesi started his observations on Lake Maggiore, looking for the pelagic forms of life highlighted in Lake Geneva. In a synthesis of his work, Pavesi [249] compared the numerous species he found with those observed in Lake Geneva, and discussed the presence of plankton in lakes in the light of the theory accepted at the time. Two of Pavesi's collaborators developed the hydrobiological studies. Marco De Marchi, from the laboratory he installed in his villa in Pallanza, on the shore of Lake

Maggiore, continued with greater regularity the sampling of plankton species, trying to individuate the relationships among the different organisms and the main physical variables (light, water temperature) influencing their distribution in the water column [250]. More regular and organised was the activity of Rina Monti, who progressively considered waters of subalpine and high altitude lakes. She organised a group of specialists in different types of aquatic organisms, carrying out regular sampling of plankton in many of the lakes of northern Italy. Among her most important results is a monograph on Lake Como [251] and the first synoptic work on the DSL [252].

With the foundation of the Istituto Italiano di Idrobiologia, studies on the DSL were enhanced, with special attention being paid to Lake Maggiore. Following Monti's tradition, Edgardo Baldi produced a second important synoptic paper on the DSL [253]. Between the 1950s and the 1970s, further scholars of Monti's, Livia Pirocchi Tonolli and Vittorio Tonolli, coordinated activities dealing with different physical, chemical and biological aspects of Lake Maggiore (for a review see [231]). Special attention was directed towards the mixing dynamics of the lake and the effects on the biology, the progressive deterioration of lake water because of eutrophication, and the long-term variation of biota as an effect of the modified trophic conditions [76,232,254]. Richard Vollenweider [255,256] made important comparisons between lakes Maggiore, Lugano and Como, considering in detail the mixing processes and their effects on water-column chemistry, with special attention given to the redistribution of nutrients from deep to productive waters.

A comparative study of the deep southern alpine lakes was also made from 1973 to 1982 within the framework of the C.N.R. National Project for the Improvement of Environmental Quality [257]. This study started a regular monitoring of the chemistry of the DSL, performed in spring, mainly aimed to follow the trophic evolution and the extent of the vertical mixing of waters. Furthermore, the growing interest in eutrophication led to the setting up of a scientific committee within the International Commission for the protection of Italian Swiss Common Waters (CIPAIS), with the specific aim of controlling the eutrophication of lakes Maggiore and Lugano. The first results highlighted the need for homogeneous sampling and analysis techniques, as well as long-term observations to obtain comparable results and reliable information on the temporal trophic development.

Since the 1980s and 1990s, further studies were promoted in the whole group of the DSL by a larger number of research institutions. The collaboration between scientists operating in the different limnological centres has been organised in an informal working group on the limnology of the DSL, which synthesised the chemical and biological analyses recorded in the different institutes and promoted a harmonization of field and laboratory methods, improving the comparability of results [258]. The studies were also aimed at evaluating the effects of the remedial measures adopted in the 1980s and 1990s on the different lakes, which were intended to reduce the impact of the discharge of pollutants, with special attention to phosphorus, on biotic communities [259]. Besides these basic limnological studies, further investigations focused on other specialised topics related to urgent environmental concerns (e.g. ecotoxicology) and other emerging environmental and scientific issues (e.g. global warming, microbial ecology).

3. Limnological research at the turn of the twenty-first century

A total of 230 papers were obtained from the exploration of the available literature published in international peer reviewed journals (Table 2). A selection of these papers will



Figure 2. Ordination of the DSL and research topics in the correspondence analysis plane defined by the first two axes. Research topics have been coded as in Table 2. Gar, Garda; Ise, Iseo; Com, Como; Lug, Lugano, Mag, Maggiore; DSL, deep southern subalpine lakes.

be commented in the sections 3.1–3.12. The references have been listed for studies carried out in individual lakes or in groups of lakes. Further, the papers were classified into different topics. In a few circumscribed cases, such an attempt met difficulties due to the multidisciplinary nature of investigations, so specific choices may not be considered satisfactory for everybody. Nevertheless, even in these few cases, the choices were based on the prevalent activities, so the proposed classification can be considered representative of the current status of the research in the DSL. The archive obtained this way can be analysed with different bibliometric approaches. However, in this context, we will limit our goal to an analysis of the scientific topics.

Just a brief glance at Table 2 allows differences in the quantity of works published in the different lakes to be recognised. The largest number of papers reported studies on the limnology of Lake Maggiore (100 contributions), followed by studies concerning lakes Garda and Lugano, as well as the entire group or different group of lakes (DSL, around 30 papers); lakes Como and Iseo had the least number of contributions. Further differences emerge when the analyses take into consideration the main topics covered in the different studies. The results of the Correspondence Analysis (CA) based on Table 2 clearly indicated the existence of clusters of topics strongly associated with single lakes, or groups of lakes (Figure 2). The CA did not include topics with less than three cases (MorGeo). The eigenvalues associated with the first two CA axes were 0.23 and 0.19, with explained proportions of 35 and 30%, respectively. The most striking differences in Figure 2 include the association of the studies on microbial ecology, zooplankton, paleolimnology, fishes and ecotoxicology with Lake Maggiore; geochemistry with Lake Lugano; birds with lakes Como and Lugano; and remote sensing with lakes Iseo and Garda. The remaining topics (physical limnology, hydrology, eutrophication, phytoplankton, benthos, aquatic parasites) contributed less to the observed differences among lakes. A striking element which

emerges from the analysis is the absence of international studies on the littoral macro- and micro-vegetation (macrophytes and periphytic communities).

A few differences emerged from a comparison of the works published in the first and second half of the considered period (1995–2002 and 2003–2010). The most significant changes included a decrease of papers dealing with eutrophication, microbial ecology, zooplankton and fish, and an increase of studies regarding phytoplankton and ecotoxicology.

3.1. Physical limnology

Before the 1990s, physical limnology in the DSL was mainly directed towards climatology and hydrology, thermal characteristics and heat exchanges, mechanical energy exchanges and thermal hydrodynamics [232]. While many of these aspects were still under study during the last 15 years, a major focus was on the effects of global climate change on the physical structure of the water column and, owing to its impact on the biotic communities, deep mixing dynamics [25].

The existence of an increasing and temporally coherent overall trend in the temperature of the DSL was clearly recognised for the first time by Ambrosetti and Barbanti [33]. They found that the heat content of hypolimnetic waters at the end of the winter months strictly depended on winter climatic conditions (air temperature, solar radiation, wind) and on the quantity of heat reaching the deep layers before and after the onset of thermal stratification. In Lake Maggiore this quantity was around 2–4% of the total heat budget of the lake, which was sufficient to cause a progressive increase in the heat content of deep waters. Similar percentages in the heat transfer were found in the other DSL. It was further noted that the warming of the deep layers of Lake Maggiore occurred in parallel with an increase in temperature of about 1.5°C in its inflows during the 1990s. The conclusion was that the hydrodynamic processes and water temperatures depended on large-scale climatic fluctuations controlled by an ongoing process of climate change. In the Alpine region, temperature changes appear of greater magnitude than the global temperature changes, reflecting an amplification of the global signal in this region [260]. The increase in temperature in the deep lakes south of the Alps was successively confirmed in a more general study on the trophic development of DSL (see section 3.3; [79]). The analysis of a long-term data series recorded from the 1970s to 2005 at the time of maximum spring overturn allowed the increase in water temperature to be estimated at around 0.012-0.028°C year⁻¹, which was very close to the warming rate found in other large lakes in Europe and North America, i.e. 0.015–0.030°C year⁻¹ [261]. An update of these results for lakes Garda, Iseo, Como and Maggiore is reported in Figure 3. Even considering the occurrence of sharp temperature reductions following full overturn events (e.g. in 1981-1982, 2005–2006), the overall upward trend was still manifest, confirming previous results and temperature slopes (0.011–0.021°C year⁻¹). In the case of Lake Como, however, the overall temperature increase based on the MK, BS-MK and TFPW-MK tests (Figure 3) was at the limit of significance (P < 0.10). Nevertheless, besides the long-term trend, the data were clearly characterised by short-term structures with a periodicity greater than 10 years, highlighting that information relevant to climate change in these types of water bodies need to be based on sufficiently long time series. In this regard, after removing the effect of serial correlation, the upward trend decreased in significance, especially in Lake Garda (*P* < 0.10).



Figure 3. Volume-weighted mean lake temperature from the beginning of the 1970s to 2009 (updated from [79]). (a) Garda; (b) Iseo; (c) Como; (d) Maggiore. Measurements were made during spring, at the time of maximum overturn. Data are smoothed using the LOWESS procedure. Dashed lines show the Theil-Sen slopes of the linear trends. For every temperature series, various statistics have been computed: MK, Mann–Kendall test [245]; BS-MK, Bootstrap-based MK test with 10000 replications [245]; TFPW-MK, trend-free pre-whitening procedure (TFPW) and MK test [246]; TS-slope, Theil-Sen's slope estimates (°C year⁻¹) [245].

Numerous studies in this period addressed the problem of the factors controlling mixing and deep-water dynamics. A first line of research studied the meromixis of lakes Iseo and Lugano. The decrease in the intensity of deep mixing in Lake Iseo was observed since the mid 1980s, whereas meromixis took place in the mid 1990s. Studying the evolution in time of stability in relation to water temperature, solute and dissolved oxygen concentrations, Ambrosetti and Barbanti [17] showed that the increase in total water stability (thermal and chemical) was determined by an increase in the thickness of the surface water layer involved in the annual heat exchange and by an increase of solutes present in the deep layers. The solutes were partially related to the sinking of calcite produced in the photic zone and to their dissolution in the tropholitic layers. A partial deep-water renewal of the lake was documented in 2005 [79] and 2006, during severe winters. The absence of complete overturn was even more marked in the northern basin of Lake Lugano, which showed a permanent stratification over the last 40 years because of an increased dissolution of mineral particles and increased water stability in response to strong eutrophication [22]. After the 1960s, the meromixis determined the complete disappearance of oxygen in the deeper layers, and an increase in the concentrations of reducing chemical compounds such as ammonium, hydrogen sulphide and methane [70]. During this period, the regular increase in the deep water temperature approached a

threshold above which the cooling of the surface water could force overturn, which, nevertheless, was prevented by mild winter temperatures [21]. The use of environmental tracers allowed detailed documentation of the interruption of meromixis after two consecutive cold and windy winters (2004–2005 and 2005–2006), which destabilised the water column, leading to two strong mixing events [22]. However, the process was associated with a significant reduction in the trophic level of the lake, due to treatment of sewage in the watershed. In this regard, the meromixis should be considered as favoured by eutrophication, which regulates the fluxes of calcite from the productive layer to the hypolimnion and the CO_2 concentrations in the whole water column.

A second line of research in deep-water dynamics considered the transport mechanisms determining the extent of the overturn of hypolimnetic waters. Analysing a long-term data set of physical and chemical data measured in Lake Maggiore from 1951 to 2008, Ambrosetti et al. [27] showed that - besides convective mixing - at least other three mechanisms favoured the mixing and oxygenation of deeper waters: i.e. conveyor belt currents, the inflow of colder and denser fluvial water that consequently slide down to the lake bottom, and differential cooling of littoral waters sinking down the lake flanks. While the water mass undergoing convective motion increases in thickness during the winter months, these three mechanisms can contribute significantly to the penetration and mixing of surface waters at depth. As for the inflows, the role played by flood-induced turbidity currents in favouring the circulation of Lake Lugano was studied by De Cesare et al. [20]. The overall conclusion reached by Ambrosetti et al. [27] was that deep water dynamics in the DSL can be driven by a variety of mechanisms depending on the dynamics of atmospheric forcing. From a slight different point of view, Salmaso [15] analysed the impact of the winter climatic fluctuations on the extent of the spring vertical water mixing and phosphorus fertilization in Lake Garda. A strong causal relationship was found between the severity of winter and the spring temperature of the upper hypolimnion. In turn, the cooling of the water column strongly controlled the vertical extent of spring overturn and the degree of phosphorus fertilization and phytoplankton growth of the trophogenic layers [65,66,86]. An attempt was also made to relate the winter climate and mixing dynamics to large scale climatic phenomena [15]. Nevertheless, the relationship between the winter climate and the North Atlantic Oscillation (NAO) was uncertain. probably because of the location of the lake between different centres of action of the NAO (the Mediterranean region and central and northern Europe).

Apart from a contribution by Buzzi et al. [18], who analysed the oscillation periods of surface seiches in Lake Como, only a few numerical applications analysing the thermal regime and water movements in the DSL have appeared very recently. Castellano et al. [28] described a numerical study for estimating the spatial distribution of the hydraulic residence time in Lake Maggiore. The model was used to simulate the velocity distributions, the paths of different massless markers and their residence times within the lake. The estimated residence times were in accordance with the mechanisms of mixing and deep-water oxygenation described by Ambrosetti et al. [27]. A different logic animated the work of Morillo et al. [19], which originated within the framework of a pilot experiment aimed at removing polluted waters from a coastal margin of Lake Como by using a downward-pointing impeller. A field study conducted using rhodamine dye introduced into the impeller was used to validate a three-dimensional numerical hydrodynamic model. Successive simulations showed that a reduction in the amount of pollutants adjacent to the City of Como by half could be reached within 2 weeks with the use of six impellers.

A large number of papers addressed the question of relating heat content, thermal structures and the depth of the thermocline of a large number of Italian lakes (including the DSL) to their morphometric characteristics [29–31,34,35]. Lake flood episodes and the climate of Lake Maggiore watershed were analysed in other specific papers [23,24,26].

3.2. Geochemistry

Geochemistry was the object of many investigations, particularly in Lake Lugano. An important research line regarded isotopic geochemistry, with the quantification of different isotopes (Cesium, Boron, Berillium, and Uranium) in the pelagic zone and sediments [37,42,46,47,50,61,62]. In this field, specific studies were made to assess the risk of radioactivity on human health. Rusconi et al. [37] evaluated the possible impact of some unused conventional bombs which had been dropped into Lake Garda in 1999, during the Kosovo conflict. They found ²³⁸U concentrations typical of natural samples, ranging from 10 to 20 mBq l⁻¹. Moreover, ²³⁴U/²³⁸U ratios were never significantly less than 1, as would have been the case in samples heavily contaminated by depleted uranium.

In the fields of biogeochemistry and organic geochemistry, many studies analyzed the processes involved in the mineralization and isotopic composition of carbon, nitrogen and oxygen in settling organic matter [41,51–56]. In particular, analysing the evolution of δ^{13} C and δ^{15} N of sedimenting particulate organic matter (SPOM) of Lake Lugano from 1985 to 1998, Lehmann et al. [55] demonstrated a parallel decrease of δ^{13} C and phosphorus loading, suggesting that δ^{13} C in SPOM was a good indicator of P availability. This was explained considering the control of available PO₄^{3–} on algal biomass, and thus on CO₂ reduction, and with the relationship existing between the intensity of aqueous CO₂ depletion and δ^{13} C values of autochthonous organic matter. Conversely, changes in total phytoplankton biomass did not seem to affect δ^{15} N values.

Due to their importance in the co-precipitation processes involving phosphorus and in the determination of density profiles, a few studies analyzed the processes controlling the formation and dissolution of calcite particles in the epilimnion and hypolimnion [36,45]. In Lake Garda, Salmaso and Decet [36] found that the reduction of Ca^{2+} in the whole lake could be estimated as between 23,800 and 17,500 t year⁻¹, which corresponds to a precipitation rate between 50 and 65 g $Ca^{2+} m^{-2} year^{-1}$. These values are lower than those found in other two deep eutrophic lakes (Lake Lugano and Sempachersee; about 170 g $Ca^{2+} m^{-2} year^{-1}$ [45]), confirming the dependence of Ca precipitation on phytoplankton productivity (see section 3.1).

In Lake Lugano, other studies considered the chemistry and distribution of reducing compounds [40,57], the transport of suspended matter in the hypolimnion [39,43], and the dissolved silica budget in the North basin [49].

3.3. Chemistry and eutrophication: different responses due to different management strategies

The studies on water chemistry carried out on the DSL were directed mainly at evaluating lake trophic status, as eutrophication has always been the main cause of deterioration for these water bodies. Nevertheless, other important uses of the chemical data are in evaluating the extent of the spring vertical mixing of the waters, and in investigating the interactions between biological processes and effects on water chemistry, such as the

formation of calcite in the productive layers and its subsequent partial dissolution during sedimentation (see section 3.2). As biological production in the DSL is essentially P limited, P concentrations are a reliable indicator of lake trophic status. Therefore all the processes related to P (input from the watershed, consumption in the epilimnion, sedimentation, release in the hypolimnion and storage in the sediments) have been of major interest. The concentrations of P in water, both in the reactive and total forms (SRP and TP), are a reliable indicator of the excess of P loading from the watershed reaching the lake; on the other hand, the increase or decrease of P concentrations indicate the effects of remedial measures. The long-term series of P concentrations documented an increase in the trophic level of Lake Lugano and of the remaining lakes since the 1960s and 1970s, respectively [76]. At the end of the 1980s eutrophication ranged between the oligomesotrophy of Lake Garda to the eutrophy-hypereutrophy of Lake Lugano, whereas Lake Maggiore and lakes Como and Iseo showed meso-eutrophic and eutrophic conditions. respectively (Figure 4a). The remedial measures produced positive effects for lakes Maggiore, Como and Lugano since the early 1990s, but not for lakes Iseo and Garda. These modifications were documented and commented upon in several papers, e.g. [63,64,68,71,75–79].

Among the other chemical variables, of particular interest were nitrate and dissolved oxygen. Nitrate is the most important N species present in lake waters and for several years it was associated with P as a cause of eutrophication. Nitrate showed a relevant increase since the 1960s in lakes Maggiore, Como and Iseo, while remained almost stable in Lake Garda. In Lake Lugano nitrate showed a more complex dynamic in relation to the anoxic conditions of deep waters [70,79]. Other specific studies, based on a multiyear analysis of the sources of nitrogen to the lakes, clearly showed the importance of the atmospheric loads reaching the lake and watershed surface in precipitation, in addition to the N load produced by human activities in the watershed [73]. The relative contribution to the total N load was estimated as being between 65 and 75%, depending on the interannual variability of the amount of precipitation [74]. The increase in nitrate in the DSL could be related to the atmospheric cycle of ammonium, deriving from zootechnical activities and manure, and nitrogen oxides, resulting from car exhaust emissions and, more generally, from high temperature combustion [262]. The absence of a positive trend in Lake Garda can be related to the lower atmospheric load and to the higher water retention time, which could allow a relatively higher incidence of biological processes consuming nitrogen. On the other hand, due to reduction processes, nitrate concentrations strongly depend on the oxygen concentrations in the deeper waters, as clearly shown in Lake Lugano [70] and, less manifestly, Lake Iseo [67].

As for nitrates, it is interesting to observe that in lakes Garda and Lugano, the epilimnetic nitrate concentrations during the summer months could reach far lower values than in the other lakes ($< 30 \,\mu g \, N \, l^{-1}$), suggesting that a limitation of phytoplankton growth in the top few metres of the water column in these two lakes during the periods of maximum nutrient consumption may be determined by N as well as P [82,103].

The oxygen profiles over the water column were always used, together with temperature and a few other variables (e.g. pH, conductivity, nitrates, silica), as an indicator of mixing depth at the time of maximum late winter and early spring overturn, see, e.g. [15,17,36,72,76,79]. An update of the long-term concentrations of O_2 considered in previous works is reported in Figure 4b. The use of this variable still represents a useful and synthetic way to follow the mixing dynamics in deep lakes. In particular, the long-term



Figure 4. Volume-weighted average concentrations of (a) total phosphorus in the whole lake and (b) dissolved oxygen in the layer below 200 m from the beginning of the 1970s to 2008. The series are based on measurements carried out at the time of maximum overturn during spring (updated from Refs [75,76,79]).

trends clearly showed the partial and almost complete oxygenation of the deeper layers of lakes Lugano and Iseo in 2005–2006.

Other aspects related to the chemical studies of the DSL are the chemical budget of nutrients and main ions originating from the watershed, and atmospheric concentrations, mainly focusing on P loads as the main cause of eutrophication. Continuing studies of these budgets are available since 1978 for Lake Maggiore and Lake Lugano. Studies lasting 1 or 2 years were performed on lakes Como and Iseo, while no definite budget studies are available in the case of Lake Garda. Results showed a regular decrease in the P load in lakes Maggiore and Lugano, in agreement with the decrease in P in lake water and the decrease in lake water production [75]. As for lakes Iseo [69] and Como, the short period of measurement only allowed evaluation of the agreement of the relationship

between annual P load and lake P concentrations, and of its agreement with the OECD [263] models.

3.4. Phytoplankton

Besides physical and chemical limnology, phytoplankton and zooplankton (see section 3.5) represent another two important topics in historical development of limnology in Italy. A review of the main studies on planktonic communities before the 1990s was carried out by Manca et al. [254] and Ambrosetti et al. [264]. During the last 15 years, the main studies on phytoplankton were directed toward understanding the effects of eutrophication and oligotrophication processes on the composition, structure and dynamics of algal assemblages, and on the temporal dynamics of algal communities. Only in very recent years have studies also been directed towards understanding the role of climatic fluctuations and global change in shaping phytoplankton assemblages.

The main changes in phytoplankton assemblages during the eutrophication and oligotrophication phases of Lake Maggiore during the last 30 years were the object of many studies (see [96]), the first of which was conducted by Ruggiu et al. [93]. A number of synthetic variables expressing variations in abundance and morphological phytoplankton features allowed two phases in the long-term process of oligotrophication to be identified. Despite the reduction of lake phosphorus concentrations (see 3.3; [99]) between 1978 and 1987, the phytoplankton structure showed no significant changes. In the following years, between 1988 and 1995, the phytoplankton underwent noteworthy changes, including an increase in biodiversity, a reduction in biovolume and a decrease in average community cell size. The decrease in average cell volume and its close association with the oligotrophication of the lake was further confirmed by successive analyses [102]. Modifications in these synthetic features were followed by a strong reorganization of the community [93,102]. Many persistent large taxa tolerating a wide spectrum of trophic conditions showed a consistent biovolume reduction (e.g. Asterionella, Fragilaria, Aulacoseira, Cyclotella, Planktothrix, and Ceratium). Other alterations were observed in species more closely related to the trophic changes. Synedra, Melosira, Stephanodiscus and Microcystis – all important during the first phase – were followed by the gradual development of Aphanothece, Chrysochromulina, Snowella and thin Oscillatoriales.

Similarly, the slow process of eutrophication in Lake Garda was paralleled by many qualitative and quantitative changes [83]. Compared with the pristine oligotrophic conditions, other new, important species appeared in the lake during the 1970s, such as *Planktothrix* and *Mougeotia*, which are now among the dominant taxa in the community. During the 1980s, new cyanobacteria (*Planktolyngbya* and *Anabaena*) also appeared. Changes in the phytoplankton on a smaller temporal scale (1993–2007) were analysed by Salmaso [86]. Following the slight and continuous increase in phosphorus concentrations, after a first long period of dominance by conjugatophytes (*Mougeotia*) and diatoms (*Fragilaria*), the recent phytoplankton biomass in Lake Garda was mainly sustained by cyanobacteria (*Planktothrix*). Superimposed over this pattern, other modifications were directly or indirectly induced by fluctuations in the winter climate, mediated by the deep mixing dynamics at spring overturn (see also section 3.1) and by the thermal structure of the water column during the growing season.

A further line of research concentrated on understanding the processes and mechanisms controlling the selection of phytoplankton assemblages along temporal gradients. In particular, a number of studies highlighted the higher regularity and predictability that characterise the annual cycles of phytoplankton development in the largest DSL compared with smaller and shallower ecosystems, e.g. [80,82,84,86,88,97,100]. The regular annual cycles in the DSL are favoured by a complex of causes which include the seasonal variability of the climate, the vertical mixing of the water column from late autumn to early spring, the formation of extended and stable epilimnetic layers, and the high inertial characteristics of large lakes, which minimise the effects of local and stochastic perturbations (meteorological events, hydrological inputs) [84].

An important aspect investigated in Lake Maggiore was primary production (PP). In line with the decrease in algal biomass after the recovery of the lake, the mean annual PP showed a clear decrease from $300 \text{ g C m}^{-2} \text{ year}^{-1}$ during the 1970s to $190 \text{ g C m}^{-2} \text{ year}^{-1}$ in the period 1994–1995 [94]. More recent measurements made in 2002 confirmed the recent oligotrophic state of the lake (150 g C m⁻² year⁻¹; [101]).

Other studies in individual lakes addressed specific ecological topics, which included the definition and use of morpho-functional phytoplankton groups in the comparison of communities across lakes [85]; autoecological studies of diatoms [90,91,95]; and the assessment of carbon assimilation and phytoplankton growth rates in Lake Maggiore and other water bodies of contrasting trophic status [98].

In recent years, the phytoplankton composition and structure across the deep southern subalpine lakes were the object of two synoptic studies [103,104] based on a group of concurrent investigations made on the individual water bodies by Buzzi [89], Morabito et al. [96], Salmaso [83]; Garibaldi et al. [87] and Simona [92]. With a few exceptions, the lists of the more abundant species were highly comparable. The major differences were between the eastern lakes (Garda and Iseo) and the western ones (Lugano and, partly, Maggiore), with intermediate characteristics in Lake Como. Nevertheless, the most apparent differences were due to quantitative changes in the dominance relationships among the constituent taxa and only secondarily to compositional changes. At the community level, it was possible to recognize common patterns in the replacement of the seasonal assemblages, which were mainly represented by the development of large diatoms during spring, a more diversified community in summer (mostly Zygnemales, Peridiniales and Ochromonadales), and cyanobacteria and Chlorococcales in summer and autumn. Of the cyanobacteria, the most representative species was *Planktothrix rubescens*, which was present with the highest biovolumes in lakes Iseo and Como. Of the remaining cyanobacteria, it was stressed that a consolidated difference was the strong development of Aphanizomenon flos-aquae in Lake Lugano and its presence in Lake Maggiore, and the occurrence of oligotrophic blooms of Anabaena lemmermannii in lakes Garda and Iseo [82,103]. It is interesting to observe that in very recent years the blooms of *Anabaena* have rapidly extended also to lakes Maggiore (2005) and Como (2006). At the same time, a spreading of blooms of *Microcystis aeruginosa* was observed in lakes Como, Iseo and Lugano. The results obtained within the framework of these investigations were used to define new ecological indices based on phytoplankton (PTIs indices) as suggested by the European Union Water Framework Directive [104].

3.5. Zooplankton

Excluding two sporadic contributions on Lake Garda, in the last 15 years zooplankton was the object of intensive studies exclusively in Lake Maggiore. Paralleling what was

extensively done for phytoplankton, a few studies analysed the consequences of the longterm lake oligotrophication process on the zooplankton community [107,112,116], de Bernardi and Canale [107] described in detail the modifications of the zooplanktonic biocenosis from 1948 to the beginning of the 1990s, demonstrating important differences due to a dominance of cladocerans and rotifers in the period of maximum eutrophication, and a returning of the community to conditions typical of the 1950s - with a dominance of copepods - after the first phases of the oligotrophication process. As for the possible impact of allochtonous species on the aquatic ecosystems, it is worth observing that the disappearance of Sida cristallina and Heterocope saliens at the beginning of the 1960s was correlated with a significant development of an allochtonous coregonid introduced into Lake Maggiore in the middle of the 1950s. By contrast, new species of Daphnia (D. galeata and D. cucullata) made their appearance in the lake since the end of the 1980s. These changes were followed by modifications in the food webs. Manca and Ruggiu [112] and Manca et al. [116] showed that *Daphnia* population dynamics in Lake Maggiore in the middle of the 1990s appeared to be mainly controlled by *Bythotrephes* predation in June, which constituted a quite different situation from that documented at the beginning of the 1970s, when *Leptodora* was the prevalent predatory cladoceran. In two subsequent works, Manca et al. [120] and Manca and DeMott [124] related the 10-fold increase in the abundance of Bythotrephes from the middle of the 1980s to the beginning of the 1990s to a rise in lake temperature, which could have affected Bythotrephes reproduction and population growth. In the following years, Bythotrephes further increased as water temperature continued to increase. The alteration of the thermal stratification regime of the lake could also have caused an increase in the depth and duration of a dark refuge of relatively warm water, which might be able to support growth and development while minimizing the risk of predation by visually orienting fish predators. The results provided evidence of the complex modifications in the population density and phenology of key planktonic species and functioning of the pelagic food webs triggered by climatic changes.

Testing the hypothesis of an overall eutrophication-like effect of climate warming on zooplankton, Visconti et al. [123] compared the structure of the zooplankton community in the warmest years of the recent oligotrophic phase with that observed during the non-warm years of oligotrophy, and during years of the mesotrophic phase. They observed an abrupt increase in zooplankton abundance during 2003, one of the warmest years, particularly due to a larger development of *Daphnia*, which reached values typical of the mesotrophic phase. These abundances strongly differed from those observed during cooler years since re-oligotrophication. The results supported the hypothesis that warming may result in an eutrophication-like signal.

From a community perspective, one research line was concerned with the impact of predation on zooplankton, with specific studies considering the trophic relationships between *Daphnia* and ciliates [119], the role played by zooplanktivorous fish and invertebrate predators on the population dynamics of *Daphnia* [122], and the relationship between the feeding basket of *Leptodora* and the size of the prey that can be captured [108]. Along the same line of research, studies were also carried out on the first (1992) identification of exotopic protrusions and ellobiopsid infection in copepods [118].

The recent colonization of Lake Maggiore by *Eudiaptomus gracilis* and its consequences for the indigenous and abundant *E. padanus* populations were discussed by Riccardi and Rossetti [121]. It was postulated that, provided *E. gracilis* were permanently established, Lake Maggiore could become an invasion hub, facilitating further spreading owing both to natural and human-mediated connections to other water bodies in the region.

In Lake Maggiore, other specific studies regarded the role of zooplankton in biogeochemical cycles and in the transport of potential energy and chemical elements [111,113,114,117], and population dynamics in rotifers [110].

As for Lake Garda, a comparison of the historical results obtained before and in the middle of the 1990s did not seem to demonstrate substantial shifts in the composition of the dominant zooplankters [105]. The only differences were due to the disappearance of *Sida cristallina* since the 1950s, and the appearance of new rotifers since the 1970s and 1980s. Of particular interest was the appearance of 'black spots' spreading throughout the lake between July and early September 2004 [106]. The phenomenon was due to a strong development of *Stentor amethystinus*, a ciliate, and its symbiotic alga, *Chlorella* sp.

3.6. Microbial ecology

Similarly to zooplankton, the study of the smaller constituents of the aquatic food webs was carried out almost exclusively in Lake Maggiore. The rationale of the studies carried out before the 1990s was synthesized by Bertoni and Callieri [265]. In line with the discoveries made during the previous 15 years [266], this research line started with the consideration that most of the organic carbon was present in the smaller planktonic particles and in the dissolved fraction [141].

A number of papers dealing with the constituents of the microbial loop focused on heterotrophic (HPP) and autotrophic (APP) picoplankton, e.g. [126,127,142]. Using a trophic gradient approach [133], it was possible to examine the influence of resource availability on picocyanobacteria growth and abundance. As for Lake Maggiore, the decrease of phytoplankton biomass in the recent oligotrophication phases (see section 3.4) was followed by an increase in the abundance and production of picocyanobacteria. More generally, it was argued that the success of picocyanobacteria in oligotrophic lakes could be achieved only if additional conditions different from low ambient concentrations of nutrients were met, including low grazing and competition, and favourable light climate. Therefore, the success of these organisms in oligotrophic lakes should not be considered as a certainty, but a potentiality.

Other studies considered the relationships between nutrient enrichment and bacterioplankton [140], as well as the size distribution of POC [131], the implications of the formation of aggregates and microcolonies in chroococcoid cyanobacteria [134], and the horizontal distribution of organic carbon and picoplankton [137].

A number of investigations considered the functional and physiological characteristics of picoplanktonic organisms. The study of the photosynthetic characteristics and genetic diversity of *Synechococcus* populations under various light and mixing conditions showed that samples from different depths and with different nutrient concentrations hosted different strains characterised by different genetic fingerprints and photosynthetic properties [139]. As for the production of organic matter accounted for by the smaller photosynthetic organisms, it was estimated that the annual average productions of autotrophic picoplankton in 1994 and 1998 were 16 and $41 \text{ g Cm}^{-2} \text{ year}^{-1}$, which represented a total phototrophic production of between 10 and 20%. However, in the seasonal periods of high P limitation, APP carbon fixation ($13 \text{ mg Cm}^{-3} \text{ h}^{-1}$) in the upper epilimnion (3 m) exceeded that due to larger photosynthetic fractions [135]. Furthermore, it was shown that, under natural UVB irradiance, the activity of picoplankton (both HPP and APP) and of the greater autotrophic fraction (>2 μ m) was not significantly inhibited [130].

With a more general approach, further studies carried out in Lake Maggiore [129] showed that the total amount of carbon fixed per unit of chlorophyll-a (Chl-a) increased from 1981 (meso-eutrophic phase) to 1994 (oligotrophication period). These changes were reflected in a change in the qualitative characteristics of the organic matter, with an increase in the POC/Chl-a ratio, suggesting a more efficient utilization of energy and nutrients during the oligotrophic phase of the lake.

A specific research line studied the implications of grazing on picoplankton [132]. In particular, the size of picocyanobacteria was inversely correlated with the clearance rate of heterotrophic micrograzers, indicating a less efficient cell uptake by protozoa when picocyanobacteria are composed of larger cells. A preliminary annual energy balance demonstrated that 80% of the carbon produced by picocyanobacteria could be taken up by protozoa [136].

3.7. Benthos

In the only available review of the macrobenthos of the deep lakes, Bonacina et al. [267] limited their analysis to a specific period (1963–1973), highlighting the fact that many other data collected sparsely after the 1970s were still unpublished. After the 1990s, the benthos was still among the more poorly studied communities in the DSL. At least two reasons may have favoured this negative bias. Many investigations were directed towards one of the most critical invasive species, *Dreissena polymorpha* (zebra mussel), which was detected in Lake Garda for the first time in the late 1960s. A second reason is that many efforts were directed towards the effects of micropollutants on specific target species (mainly *D. polymorpha*; see below, section 3.9). Overall, these applied issues contributed to shifting attention towards population ecology and ecotoxicology, at the expense of community ecology.

Investigations covering diverse autoecological characteristics of *Dreissena* have been carried out in different DSL [147–150]. More specifically, the role in nutrient cycling played by *Dreissena* was investigated in the western basin of Lake Como [148]. The entire population was able to filter epilimnetic waters 2.1 times per year, transferring 2.9×10^4 t year⁻¹ of pseudofaeces to the sediments. In a recent study aimed at tracking humanmediated dispersal pathways, the genetic structure of three populations from Lake Garda was compared with that of two populations from Lake Constance [145]. In order to define phylogeographic relationships, the results of the five populations were compared with all the available sequences available from GenBank (the National Institutes of Health genetic sequence database). All the Italian samples joined with both German and mid-European samples, suggesting a mixed origin of the Italian *Dreissena*. Further studies concerned other larger molluscs, such as the populations of *Unio pictorum mancus* and *Viviparus ater* in Lake Maggiore [151,152].

A few studies have focused on recent new introductions of shrimps and molluscs in Lake Garda (*Dikerogammarus villosus* [144]; *Corbicula fluminalis* and *C. fluminea* [146]), and on the identification of new species of Gastrotrichs (Lake Garda [143]).

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3.8. Fishes

Studies on fishes have been carried out almost exclusively in Lake Maggiore. A few investigations concerned the management of fish resources [156,157], ecology [155], physiology [158,161], the implications of the introduction or invasion of new species [159,160], and population genetics [153,154]. Implications of the contamination of fishes by persistent organic pollutants (POPs) will be considered in the next section. As for the contribution of genetic studies, evidence was proposed to support the hypothesis that *Salmo carpio* (a species endemic to Lake Garda) issued from a recent hybridization of *Salmo marmoratus* and *S. trutta fario* [153]. Further, significant differences were found between the natural populations of *Salmo* of the Po basin and three of the major Italian fish-farm strains, which were of Atlantic origin. The 'natural' populations showed introgression rates ranging from 0 to 70% due to contamination by stocking.

3.9. Ecotoxicology

The qualitative and quantitative determination of chemical pollutants and their impact on the DSL ecosystems have been the object of a large number of investigations, particularly in Lake Maggiore (Table 2). A lot of studies examined the presence and distribution of many POPs, such as dichlorodiphenvltrichloroethane (DDT), e.g. [186,192,196]; polychlorinated biphenyls (PCBs), e.g. [203,208,211]; polycyclic aromatic hydrocarbons (PAHs), e.g. [193,197,198]; polybrominated dyphenil ethers (PBDEs) [203,204,206,207]; polychlorinated dibenzodioxins (PCDDs, dioxins), e.g. [203,205]; perfluorooctanesulfonic acid (PFOS), perfluorooctanoic acid (PFOA) and nonylphenol [201]. Of particular concern is still the pollution by DDT in Lake Maggiore due to its production in a chemical plant located near the main influent of the Bayeno Bay until 1996. Even although the DDT pollution did not compromise the use of the lake water for drinking or bathing purposes, health authorities still prohibited fishing and the eating of many fish species [72,191]. After a heavy flood in autumn 2000, DDT concentrations increased due to the transport of insecticide from contaminated sediments still present in the area of the closed chemical plant. This was paralleled by a sharp increase in PCB pollution not due to the flood, but probably to improper release of contaminated sediments from numerous dams located in the watershed. The high concentrations of POPs represented a danger for the water community, and a possible risk to human health due to fish consumption [191]. In Lake Maggiore, the existence of high concentrations of DDT and its metabolites in fishes was proved in several studies. Bettinetti et al. [194] showed that concentrations of DDT were very close to, and sometimes exceeded, the Italian limit for human consumption (0.05 and 0.1 mg kg^{-1} w.w. of total DDT for fishes with lipid content of >5% and within the range of 5-20%, respectively). They concluded that the environmental quality standard of $0.2 \,\mathrm{ng}\,\mathrm{l}^{-1}$ in water could not guarantee the suitability of fish for human consumption. Volta et al. [210] showed that DDT and PCB concentrations in Coregonus macrophthalmus were dependent on season and fish age. They described a 2-fold increase in the lipidnormalised concentrations of DDTs and PCBs across season and also across age, resulting in an overall 4-fold increase. Seasonal variations in POPs content were related to the ecophysiological cycle of fishes, while the effect of the fish age was explained taking into account biomagnification mechanisms (see also [173]). At a higher trophic level, DDT and PCB monitoring of birds' eggs in Lake Maggiore revealed a situation of high

contamination in comparison with other aquatic environments [185]. Successive studies considered the birds' eggs contamination by these two POPs in lakes Maggiore and Garda [217], and carbofuran (another pesticide) poisoning in mallard ducks in Lake Lugano [180]. The evaluation of risk for human health of PCBs and PAHs due to fish from Lake Iseo was studied by Binelli and Provini [174].

The long-term risks posed by POPs were highlighted also by [216]. This study related the sharp increase of DDT and its metabolites observed in lakes Como and Iseo in 2005 to the meltwater rich in pollutants released by retreating glaciers. In particular, specimens of *Alosa fallax lacustris* collected from Lake Como showed DDT levels of 0.12 mg kg^{-1} (w.w.), which exceeded the Italian limit for human consumption.

The use of zebra mussel for lake biomonitoring was the object of different studies [199–200,214,218]. Based on the linkage between bioaccumulation and biomarker data, Binelli et al. [215] defined site-specific environmental quality indices for man-made chemicals. The application of these tools allowed three different degrees of xenobiotic contamination of the DSL to be distinguished. Lake Lugano had negligible pollutant levels and no effects on enzyme activities, while lakes Garda, Iseo and Como showed homogeneous poor water quality. The ecological status of Lake Maggiore was considered at risk due to the presence of some xenobiotic point-sources and the heavy DDT contamination revealed since 1996. The endocrine disrupting properties of DDT were confirmed in specific studies carried out on *Dreissena* populations in the lakes Maggiore [187,190] and Iseo [175]. In particular, histopathological analyses performed on mussels collected from Lake Iseo during the sharp increase of POPs (2005–2006) showed a disrupting action of DDT on the mechanisms involved in sperm release, as well as disturbances in the gametogenic phases of the ovary [175].

Further investigations were carried out on diverse ecotoxicological aspects. Among the others we can cite: metal and trace element concentrations in the environment and in aquatic biota, mainly molluscs: e.g. [181,188,189,202,209,213]; POPs in sediments [182]; the mutagenic activity of lake water used as drinking-water supply [212]; the use of advanced technologies for organic micropollutant removal from lake water [178]; and the development of models for the estimation of temporal emissions of DDT to Lake Maggiore [195].

3.10. Extending the temporal perspective: paleolimnology

The most complete paleolimnological studies were carried out in Lake Maggiore. In this lake, Marchetto et al. [221] demonstrated a good level of coherence between diatom assemblages in sediment cores and documentary data on phytoplankton and hydrochemistry. In particular, they clearly documented the displacement of 'small *Cyclotella* species', typical of the oligotrophic phase, by more meso-eutrophic species (e.g. *Tabellaria flocculosa*). Similarly good was the prediction of total algal biomass from the profile of a few paleopigments during a certain period of the lake's development. Interpretation of the results obtained with chironomids was less straightforward. Lake eutrophication did not appear to have a clear and immediate impact on the composition of this group. Most of the sharp changes in the littoral chironomid assemblages appeared to be linked to major fluctuations in lake level. In the same study [221], the results obtained in Lake Maggiore were compared with a preliminary investigation of fossil diatom assemblages recorded in short cores collected in lakes Garda, Iseo and Como at the beginning of the 1990s. During oligotrophic phases, *Cyclotella* spp., which were the dominant taxa in the oldest sediments, were successively replaced by more eutrophic and mesotrophic taxa, such as *Stephanodiscus* spp., *Aulacoseira* spp., *Fragilaria crotonensis, Asterionella formosa* and *T. flocculosa*. The authors concluded that the trophic histories of these lakes, as reconstructed from the diatom remains, were basically the same as in Lake Maggiore. Along the same line of research, sedimentary diatoms were used to reconstruct the long-term development of phosphorus [220].

More recently, Manca et al. [219] reconstructed the trophic dynamics of Lake Maggiore using subfossil cladoceran data from the beginning of the 1940s to 2002. The changes in the total abundance and the proportion of planktonic cladocerans clearly tracked the major changes that had occurred in the trophic characteristics of the lake, and the changes that had occurred in the composition and abundance of the fish populations due to the introduction of allochtonous species and to the ban on fishing because of the DDT pollution.

3.11. Extending the spatial perspective: remote sensing

The areal extension of the DSL may render difficult the evaluation of the representativeness of data collected in the pelagic zone or along the shoreline. Remote sensing has proved to be useful in large lakes research [268]. In the DSL, remote sensing was used to investigate selected water quality variables in lakes Garda and Iseo, and macrophytic vegetation in Lake Garda. A specific research line was directed at defining algorithms for the determination of optical properties, algal biomass concentrations and tripton using satellite data (Landsat, Earth Observing-1, Envisat) [222–224,226,228–230]. In the most recent study, Giardino et al. [226] compared the chlorophyll-*a* and tripton concentrations derived from Hyperion (hyperspectral sensor) records with concurrent *in-situ* data collected in Lake Garda both at fixed stations and by continuous flow-through systems. The correlation coefficient between the concentration was problematic due to resuspended material; however, if the sampling data from the resuspension zones were excluded, the correlation coefficient between the fixed stations and Hyperion-derived concentrations increased from 0.48 to 0.75.

A second line of research was concerned with the monitoring of macrophytes, i.e. submerged vegetation [225] and reeds [227]. A study of the distribution of submerged vegetation in the littoral zone of the Sirmione Peninsula (in the southern basin of Lake Garda) documented a marked decrease in macrophyte cover from 72% (1997) to 52% (2005), with a concomitant increase in sandy substrates [225].

3.12. Other topics

Other important limnological topics considered in these last 15 years have included lake morphometry and geology; hydrology and hydrochemistry in the watershed areas; and birds and aquatic parasites (for complete references, see Table 2).

Among the hydrological investigations, a study of the influence of the inflowing River Sarca in the northernmost section of Lake Garda by isotopic measurements in water samples showed no detectable effects and no vertical stratification of isotopes [4]. Strictly linked to ecological economics, a few studies [5,7,8] addressed the important problem of water availability and the allocation of water resources among competitors in the Adda River basin, especially during situations of water scarcity (such as in 2003, [5]). At the other extreme of the hydrological gradient, Luino et al. [12] presented the results of a model aimed at evaluating economic losses from the impact of floodwaters on exposed elements; the model was tested on a small watercourse flowing into Lake Maggiore, which was recently affected by a flash flood (the Boesio Stream).

From a purely ecological perspective, microparasites and macroparasites are considered crucial elements in the control of host populations [269]. However, the studies carried out in the DSL mostly addressed important problems linked to human health. These included the quantification of populations and the identification of mechanisms responsible for the persistence of *Enterococcus faecalis* in water bodies [167,168], and the study of *Diphyllobothrium latum*, associated with the reappearance of Human Diphyllobothriasis in localised areas of the DSL due to the increasing consumption of raw or undercooked fish because of the increasing influence of oriental cuisine [169–172].

4. Research gaps, new directions, perspectives

Synoptic analysis of the available peer-reviewed limnological literature has allowed us to acquire an overall picture of the most advanced research carried out during the last 15 years in the deep southern subalpine lakes. A few conclusions can be drawn. (i) Limnological research in the DSL is strongly linked to the concept of scientific monitoring, while experimental studies and modelling are still confined to specific niches; as a consequence, present limnological research is strongly biased towards specific research areas, while other research areas require urgent improvement. (ii) Integration of different disciplines is hampered by the fragmentation of studies on different compartments and by a general, reductionist approach. (iii) Integration of studies and synoptic analyses on a macro-regional scale have been carried out only for specific research areas. (iv) Huge differences exist both in the number and diversity of investigations carried out in the different DSL.

(i) There is no doubt that most of the limnological research conducted during the last 30 years has been fostered by an urgent need to find effective solutions to the problems connected with eutrophication and pollution, and by monitoring programmes. As in other countries, this more applied research has undoubtedly contributed a great deal to fundamental limnology [270]. In the case of long-term monitoring programmes, these activities have represented a triggering nucleus for the establishment of long-term ecological research projects. The legacy of this recent past has been responsible for promoting the investigations conducted on a few DSL (Garda, Maggiore) within the framework of the Long Term Ecological Research (LTER) network. The establishment of long-term monitoring programmes provides researchers with a more solid foundation for future environmental decisions [271]. The challenges of LTER are to achieve a predictive understanding of temporal and spatial patterns and variability [272,273]. Besides data collection, the scientific monitoring includes interpretation, modelling and experimental manipulation of an ample array of variables in order to identify the environmental stressors typical of different ecosystems on different temporal scales, and the degree and quality of interactions among these stressors. In this regard, the physical, chemical and biological (phytoplankton and, to a lesser extent, zooplankton) data collected in the DSL since the beginning of modern limnological analyses have allowed the effects of human impact and different eutrophication phases to be sufficiently determined.

Nutrient availability and climate change – along with organic pollutants – still represent the main ecosystem stressors linked to human activity in the DSL. The effects of the interactions, covariations and synergies between nutrients, climate and other stressors remain less well understood. An important role in remedying this lack of understanding may be played by lake models. Their use in the DSL began only very recently, and only on specific ecosystem compartments, essentially in the field of physical limnology. Both the integration of simple mechanistic models and the use of complex modelling represent a way to improve predictive ability and, at the same time, to formulate and test hypotheses.

Rapid adaptation of research is required in dealing with new environmental emergencies. The causes of the rapid proliferation of substantial cyanobacterial blooms in the whole group of large lakes south of the Alps are still poorly understood, and the fraction of toxic strains present in the populations as well as the diversity, quantity, distribution and seasonality of cyanotoxins remain largely unidentified. A thorough knowledge about the nature and quantity of algal toxins and their fate in the environment and trophic webs is a necessary prerequisite for effective risk assessment and management of water resources. Similarly, the impact of the appearance of new invasive species on the DSL has been overlooked. It is worth noting that, apart from a few studies, no experimental research has been conducted so far on the effects of successful invaders such as *D. polymorpha* and other smaller molluses, or new exotic shrimps (D. villosus). Besides the use of classical population and community ecology concepts, the adoption of recent rapid improvements in analytical methods in the field of genetics and metabolomics could add new insights and interpretative elements [274], allowing the study of organisms to include the intimate mechanisms controlling adaptation and – ultimately – the evolutionary features of populations and communities. These viewpoints, which encompass evolution, biogeography, phylogeography and systematics, are important for the study of biodiversity and the assessment of losses in biodiversity [237].

(ii) Twenty years ago, Peters [272] observed that the search for the components and the mechanisms of an ecosystem has fragmented limnology into expert, specialised fields, with limited interaction and negligible competition. It is difficult to disagree with this view, even if its judgment may be softened by taking into account the present greater specialization which is coupled - in many cases - with a necessary knowledge of advanced methodologies, both analytical and computational. The idea behind this view, i.e. that the different component properties may be put together to understand the whole system from them, has been largely disputed. Due to the result of interactions and feedback, ecosystem properties may differ appreciably from the sum of its elements, and therefore the properties of complex systems cannot be understood by looking solely at the single constituent parts [270,275]. It seems commonplace to bring up these observations yet again in this review, but it is worth underlining that, whereas a certain number of studies in the DSL have addressed the relationships between nutrients and planktonic communities, only a very few have considered the interactions between planktonic organisms, and between nekton, benthos and plankton. It seems that this situation arose not only from the idiosyncratic character of each individual discipline and the general consensus about the importance of resources availability, but also from an intrinsic weakness in defining quantitatively competition and predation processes from exclusive field observations. Therefore, the general view is that of a limnological science strongly biased towards the importance of bottom-up interactions rather than food-web interactions and top-down control. However, a less restricted vision should be adopted in studies of bottom-up regulation. The very low epilimnetic concentrations of nutrients documented during the

summer months in a few DSL must force research to adopt a different point of view, taking into account potential limitation by P and N (and by other potential limiting factors, e.g. Fe) over shorter, but still ecologically meaningful, time scales relevant for the control of biodiversity patterns [276]. When the microbial food web accounts for the main part of pelagic carbon flow and most nutrients are regenerated within the system [277], a better understanding of resource limitation at short time scales could be obtained by integrating purely chemical determinations with the knowledge of biological structures and activities at the microbial level. In addition, the implications of these aspects for the development of nitrogen-fixing cyanobacteria remain to be investigated. Even more intricate could appear the integration of other environmental stressors such as POPs in the classical bottom-up and top-down models. Nevertheless, taking into account the strong impact that POPs can have on the trophic webs, the impact of these pollutants should not be disregarded in the study of population interactions, community dynamics and risk assessment.

(iii) The difficulty of combining the different bricks to build the cathedral (sensu Peters [272]), is worsened by the difficulty of integrating the available observations on a supraregional level. One of the most important tasks of LTER (in different organisational systems, e.g. LTER networks, CIPAIS) is to compare the data obtained in various ecosystems at different temporal and spatial scales, favouring a greater level of integration and a better capacity to generalise and understand the mechanisms acting on continental scales. Nevertheless, the strong disequilibrium existing both in the number and diversity of investigations in the DSL does not allow a complete overall picture to be obtained. The only quantified generalities were defined considering physical, chemical and phytoplankton data collected - or re-calculated from seasonal data - on an annual scale, disregarding the intrinsic complexity existing at shorter time scales. Despite sufficient availability of data from the different lakes, the definition of general patterns in the development of phytoplankton communities on the seasonal scale begun only very recently. Similarly, a number of comparative studies have been made on the distribution of specific and selected POPs in the DSL. However, in this case, the adoption of a regionally integrated approach may be hindered by the large number of micropollutants, which are associated with specific analytical techniques.

(iv) The huge differences in the number of investigations carried out in the DSL has a number of historical reasons linked to the existence of limnological centres or research institutions working in specific lakes, and to the necessity to cope with environmental emergencies. The most common information available in the DSL is that collected within the framework of monitoring programs for the evaluation of the trophic status of water bodies, i.e. the basic limnological information (thermal structure, nutrients and phytoplankton). Complete series of these data exist since at least the 1970s and 1980s for lakes Maggiore and Lugano, and since the beginning of the 1990s for Lake Garda and - though with more scattered surveys -for lakes Iseo and Como. Similarly, the pollution of Lake Maggiore with DDT attracted a number of researchers, with the creation of schools dedicated to the study of different aspects of ecotoxicology, from the evaluation of the diversity and distribution of POPs and metals in the ecosystem compartments to the study of the magnification processes, fate and impact of specific pollutants. At the other extreme, other topics have been completely or insufficiently considered, such as macrophytes and benthonic communities, or have been completely disregarded in the majority of lakes, e.g. paleolimnology and microbial ecology. These topics should not be covered just for the sake of completeness, in the spirit of the multidisciplinary nature of limnology – quite the opposite in fact. Rather than fostering a more ample spectrum of field studies – just because information is lacking – we need to reflect seriously on the criteria that should be used to distinguish relevant scientific research from that lacking concrete aims. Inland waters are more and more threatened by new pressures – from climatic change to the excessive proliferation of toxic microalgae, from the introduction of new species and new micropollutants to the interactions among these new and old stressors. In this changing world, limnology has a great responsibility to produce high quality research and predictive models, which are essential elements for the efficient management of water resources.

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