Trophic–salinity gradients and environmental redundancy resolve mesozooplankton dynamics in a large tropical coastal lagoon

ARTICLE · MARCH 2015

DOI: 10.1016/j.rsma.2015.04.003

10 AUTHORS, INCLUDING:

Rakhesh Madhusoodhanan

Kuwait Institute for Scientific Research

26 PUBLICATIONS **243** CITATIONS

SEE PROFILE

Akkur Raman

Andhra University

63 PUBLICATIONS **646** CITATIONS

SEE PROFILE

Kalavati Chaganti

Andhra University

53 PUBLICATIONS **259** CITATIONS

SEE PROFILE

G.V.M. Gupta

Ministry of Earth Sciences

24 PUBLICATIONS **289** CITATIONS

SEE PROFILE

Regional Studies in Marine Science 1 (2015) 72–84

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Trophic–salinity gradients and environmental redundancy resolve mesozooplankton dynamics in a large tropical coastal lagoon

M. Rakhesh [a,b], K.S.V.K.S. Madhavirani [a], B. Charan Kumar [a], A.V. Raman [a,*], C. Kalavati [a], Y. Prabhakara Rao [a], S. Rosamma [c], V. Ranga Rao [d], G.V.M. Gupta [d,e], B.R. Subramanian [d]

[a] Marine Biological Laboratory, Department of Zoology, Andhra University, Visakhapatnam 530 003, India
[b] Department of Biology, University of Bergen, Bergen-5020, Norway
[c] National Institute of Oceanography RC Kochi, 682018, India
[d] ICMAM Project Directorate, Ministry of Earth Sciences, NIOT Campus, Chennai 600 100, India
[e] CMLRE, Ministry of Earth Sciences, Kakkanad, Kochi, 682037, India

ARTICLE INFO

Article history:
Received 23 December 2014
Received in revised form
28 April 2015
Accepted 28 April 2015
Available online 5 May 2015

Keywords:
Tropical coastal lagoon
Zooplankton
Small copepods
Multivariate analysis
Eutrophication
Plankton dynamics

ABSTRACT

Coastal lagoons around the world have become increasingly vulnerable to eutrophication and often the impingement is severe with regard to plankton. In this study, we measured how environmental heterogeneity persuades mesozooplankton (MSP) community dynamics in a large tropical coastal lagoon wrought by human impingement, including the creation of a new mouth. Here, we hypothesised that trophic gradients and environmental redundancy resulting from the pooled effect of trophic and salinity–light gradients majorly influence MSP structure in one of Asia's largest brackish water lagoons in India. Multivariate analysis of environmental variables (May 2004–September 2006; n = 1008) and MSP examined (May 2004 to October 2005; n = 522) at monthly intervals revealed discrete hydrographical and MSP regimes. Beta diversity measures revealed ~50% community turn-over between assemblages. Residual analysis on salinity-corrected fractionated chlorophyll *a* and size-specific copepod functional groups revealed pico-nanoplankton (<20 μm) supporting spatial patterns of small omnivorous copepods lagoon wide (r^2:0.487). A lower than expected MSP grazing pressure on phytoplankton, revealed through MSP:phytoplankton biomass ratio, however, suggested the importance of alternative food sources and foraging effects, the significance of which varied spatially. MSP–environmental interactions through gradient analysis techniques revealed unimodal functionality of MSP to contrasting horizontal explanatory gradients offered by salinity–water column transparency and nutrients–chlorophyll *a*. Variance partitioning revealed the importance of measured (environmental redundancy 28%; trophic gradient 32%, salinity–light gradient, 6%) and unmeasured (residual, 34%) explanatory variables contributing to the total variation in MSP within the lagoon. Overall, the superseding effects of eutrophicants on MSP dynamics coupled with cyanophycean dominance in the system suggest that this tropical lagoon is on the verge of transformation into a eutrophic/hypereutrophic system, wherein the ecological benefits achieved through the opening of a new mouth in the year 2000 appear short lived. Such changes could result in large-scale implications through trophic cascades, altering MSP dynamics and ecosystem functioning.

1. Introduction

Coastal lagoons are naturally stressed systems that experience frequent environmental disturbances (Gamito et al., 2005). Located between land and sea, they act as filters, retaining inorganic and organic nutrients and materials (Kozlowsky-Suzuki and Bozelli, 2004). Many of them – notably those with shallow depths, restricted circulation, large freshwater inflow, low flushing rates, relatively longer water residence time, high light penetration and frequent water column mixing – are particularly vulnerable to nutrient enrichment from surface runoff, groundwater and atmospheric inputs (Kennish and Paerl, 2010). The resulting hydrological changes create environmental gradients that alter the chemical and biological properties of lagoons directly or indirectly. This results in high biomass accumulation and drastic changes in plankton food-web structure and ecosystem functioning (Setubal et al., 2013). Among these, salinity and nutrient availability are

* Corresponding author. Tel.: +91 891 2501098; fax: +91 891 2501098.
E-mail address: akkur.v.raman@gmail.com (A.V. Raman).

http://dx.doi.org/10.1016/j.rsma.2015.04.003
2352-4855/

considered the most important factors determining the composition and size-structure of phytoplankton (Comín and Valiela, 1993; Romo and Miracle, 1995; Lopez-Flores et al., 2006a; Specchiulli et al., 2008), often influencing mesozooplankton (MSP) community dynamics as well. Apart, salinity represents a major structuring factor that directly affects MSP diversity attributes (Horváth et al., 2014). Thus, at a given time, the composition and spatial distribution of MSP in an enclosed coastal system is determined by the extent and nature of environmental gradients and their interplay. However, there is a dearth of knowledge for such systems from tropical seas including the Indian sub-continent where monsoons play a key role.

Chilka lagoon, Asia's largest brackish water lagoon on the east coast of India, is one such tropical lagoon undergoing severe ecological transformations due to eutrophication. The lagoon undergoes wide seasonal and annual changes in salinity (range 0–35), light availability and nutrient regimes following heavy inflows from the surrounding rivers. Littoral drift and frequent migration and closure of inlet mouth (Chandramohan and Nayak, 1994) severely limit neritic incursion and thereby tidal mixing within the lagoon. Similar to reports from other tropical lagoons (Röderstein et al., 2014; Yáñez-Arancibia et al., 2014), the frequent occlusion of Lake mouth contributed to high residence time of nutrient laden freshwater inside favouring intense growth of invasive macrophytes especially freshwater weeds (e.g. *Eichornia, Hydrilla, Chara*) in the interior areas (Raman et al., 2007). In a span of 30 years, the cumulative effect has resulted in a shrinkage of the lagoon proper by >30 times. At a rate 15 km^2 per year (Pattnaik, 2002; Ghosh, 2002), the weeded area increased from 20 km^2 in 1972 to 685 km^2 by 2000 (CDA, 2005). Thus the unremitting deterioration of lagoon environment for many years in a row placed it under Montreux record of threatened wetland ecosystems (1993). Subsequently, remedial measures taken by the local authority through opening of a new mouth (100 m wide) in September 2000, augmented mixing with the sea and improved salinity conditions within the lagoon substantially (Ghosh et al., 2006). The hydrological intervention, considered historical and most successful at that time, also created large-scale changes in lagoon ecology such as dominance of bacillariophyceae (up to 72%) over cyanophyceae (Rath and Adhikary, 2006; Panigrahi et al., 2009), a reduction in weeded areas, and improved seagrass cover. However, water quality and plankton data collected in the subsequent years revealed that the lagoon is reverting to its pre-intervention status with consistently decreasing salinity and frequent outbursts of cyanophyceae blooms (Raman et al., 2007) with concomitant effects on MSP community in the Lake.

The present study describes spatial MSP dynamics as a function of hydrological variability created by environmental gradients within Chilka lagoon. Here, using an exploratory indirect gradient analysis, we hypothesised that trophic gradients and, environmental redundancy resulting from a combined effect of contrasting trophic and salinity–light gradients, influence MSP community dynamics in this large freshwater dominated coastal system. We believe that our study is the first ever attempt aimed at delineating the individual role of each of these counter environmental gradients on MSP composition and abundance in a tropical coastal system. By comparing present results with published information on MSP structural attributes post intervention (Naik et al., 2008), we have explored how such changes transformed the MSP community in Chilka Lake.

2. Materials and methods

2.1. Study area

Chilka Lake (av. depth ~1.4 m), the world's second largest brackish water lagoon, is located on the east coast of India (19°28′–19°54′N and 85°05′–85°42′E) (Fig. 1). The Lake is pear-shaped and covers a total area of approximately 1100 km^2 during monsoon season (August–October), a value that is reduced considerably during pre-monsoon season (April–May). Topographically, Chilka Lake can be divided into a south sector, a central and a north sector. The connection to the sea (Bay of Bengal) is through a long (6–8 km) narrow outer channel that runs parallel to the lagoon proper. The Lake has huge catchments, nearly four times its surface area (~4146 km^2) drain enormous quantities of freshwater, nutrients and suspended matter into the lake, resulting in significant spatial variability in hydrological conditions (Patro, 2001; Gupta et al., 2008).

Three hydrological subsystems mainly control the spatial and seasonal variability in hydrographical conditions within Chilka Lake (Kar, 2013). This includes (a) the land-based system comprising distributaries of the Mahanadi River on the northern side, (b) 52 river channels from the western side and (c) the Bay of Bengal on the eastern side. Two of the three southern branches of the Mahanadi River feed the Lake and nearly 61% of the total freshwater inflow into the Lake is contributed by these two branches. Coastal processes also play an important role in determining the ecological character of Chilka Lake. However, maintaining the Lake–Sea connectivity poses a tremendous challenge due to high annual littoral sediment drift and the Bay of Bengal being a net contributor of sediments into Chilka. In 2007, the Bay deposited 0.81 million tonnes of sediments within the Lake (Kumar and Pattnaik, 2010). High annual littoral sediment drift (1×10^6 m^3) causes the sea inlet to continually shift northwards leading to development of a long narrow channel running parallel to the coast (Chandramohan et al., 1993). The inlet condition is rendered unstable due to reduction in tidal prism with increasing length of the channel. This northward migration of the channel has been irregularly interrupted by major monsoon outflows or cyclones that re-opened the mouth closer to the entrance channel, for example the opening of a natural mouth at Gabakunda due to strong tidal action in August 2008. An assessment of outflow velocities indicate that the Lake outflows would never be sufficient enough to combat the littoral drift. Thus the Lake Management would have to factor in solutions for maintenance of the Lake–Sea connectivity through a mix of approaches including management of catchments and engineering solutions for mouth stabilisation and even periodic opening of new mouths. While available information does not permit determining the trends in nutrient loading within the wetland, the high intensity of chemical fertiliser and pesticide use within agriculture in the Lake catchments needs to be monitored and assessed in terms of carrying capacity of the system. Similarly, the implication of other non-point sources of pollution from the extensive habitation surrounding the Lake and connected to various river and tributary systems needs to be assessed (Kumar and Pattnaik, 2010).

2.2. Sampling and analysis

2.2.1. Environmental variables

Water quality estimations (June 2004–September 2006, $n = 1008$) included a suite of physico-chemical variables namely, depth, temperature, secchi-disk transparency, pH, suspended particulate matter, salinity, dissolved oxygen, turbidity, dissolved inorganic nitrogen (DIN = NH_4–N + NO_2–N + NO_3–N), soluble reactive phosphorus (PO_4–P), dissolved reactive silicate (SiO_4–Si), total nitrogen (TN), total phosphorus (TP), dissolved organic nitrogen (DON = TN–DIN) and dissolved organic phosphorus (DOP = TN–DIP). Surface water samples were collected using a 5 L Niskin sampler (Hydrobios. Germany). Except for in-situ estimations, such as depth (sounding lead), temperature (hand-held

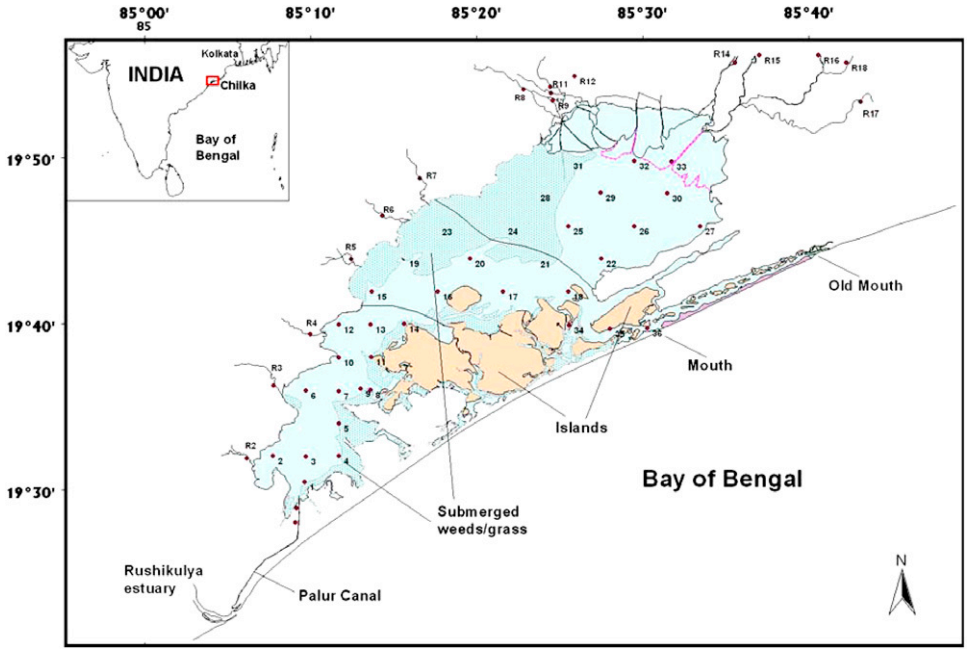


Fig. 1. Chilka lagoon with sampling locations (1–36).

thermometer, 1–51°C range within ±0.1 °C, Brannan) and secchi-disk transparency, all other analyses were carried out in the shore laboratory based at INS Chilka. pH and turbidity were estimated using a WTW GmbH Multi-parameter water quality analyser (Germany). Salinity was estimated by Knudsen's method and dissolved oxygen by Winkler method. Samples meant for nutrient analyses were transported to the shore laboratory, (Millipore) filtered (GF/F; pore size 0.7 μM) and analysed according to standard procedures (Grasshoff et al., 1999). SPM was estimated gravimetrically after filtration (pore size 0.45 μM).

2.2.2. Mesozooplankton and size-fractionated phytoplankton biomass

Between May 2004 and October 2005, a total of 522 MSP samples were collected at periodic monthly intervals from 36 GPS fixed locations. A bongo net (mouth area 0.08 m^2, 200 μm nitex) equipped with a digital flow meter (HYDROBIOS) was towed horizontally behind a boat for 10–15 min to collect the samples. Samples from both nets were mixed and then preserved on ice after removing any extraneous materials. In the laboratory, using a Folsom plankton splitter, each sample was divided into two halves. All large-sized organisms were sorted out separately prior to subsampling. While one-half of the sample, meant for species composition and numerical abundance, was preserved in 5% buffered formaldehyde, the remaining half for biomass estimation was kept in cold conditions until analysis at the shore laboratory. The samples were oven dried at 60 °C for 24 h or until constant weight gain (depending on the composition of plankton) and weight (dry mass, mg DM) determined (Afcoset electronic balance, model ER 200 A; ±0.1 mg accuracy). Each time, 1–3 aliquots (1/2 to 1/100 of the sample depending upon the concentration of samples and taxonomic sufficiency) were used for taxonomic identification and enumeration following standard taxonomic references: ICES (2000), Kasturirangan (1963), Smith (1977), Newell and Newell (1977), Zhong (1989), Yamani and Prusova (2003) and Conway et al. (2003). In each sample, a minimum of 150 individuals were counted/identified at the group level and, in the case of copepods, to their specific or generic levels. All large-sized organisms sorted out earlier were accounted for before making the final quantification. Subsequently, final calculations on MSP abundance (ind.100 m^{-3}) and biomass (mg DM m^{-3}) were made taking into account the amount of water filtered through the nets (ICES, 2000).

Samples (0.5–1 l volume depending on filtration efficiency) meant for size-fractionated phytoplankton biomass (i.e., chlorophyll *a*) estimates were first filtered through a 0.7 μm filter (GF/F) to determine total Chl *a* concentrations. For small size-fractions (0.7–20 μm), samples first passed through 20 μm plankton gauze were filtered on 0.7 μm (GF/F) filter. After filtration, pigments were extracted with 90% acetone at 4 °C overnight and analysed spectrophotometrically (Strickland and Parsons, 1972) without an acid correction factor. Chl *a* estimates from the second filter (0.7–20 μm) were designated as small fraction (pico- and nanoplankton). Large fractions (>20 μm, microplankton) were determined from the difference between total Chl *a* (>0.7 μm) and small fractions (0.7–20 μm).

Calculation of zooplankton: phytoplankton biomass ratios were based on carbon converted values of zooplankton dry mass (particulate carbon = 30% of DM, data unpublished), and chlorophyll estimates (C:Chl a conversion factor 50), according to Riemann et al. (1989).

2.3. Analysis of community structure and environmental interactions

Data on environmental variables (station-wise average values for the period June 2004–September 2006) were tested for co-linearity using Spearman rank correlation based draftsman plot test. Only one among a pair of variables that shows correlation value >0.95 (or −0.95) was selected and included with other variables. The data set was subsequently normalised and standardised before calculating Euclidean distance based ratio matrix. Further analysis using non-metric multi-dimensional scaling, NMDS (Kruskal and Wish, 1978) revealed discrete hydrographical assemblages. MSP abundance data were subjected to normality test using D'Agostino and Pearson Omnibus normality test. As the analysis revealed a non-normal MSP distribution pattern, we used non-parametric measures to probe MSP community characteristics in the lagoon. NMDS analysis followed by SIMPROF (Similarity Profile) on square-root transformed MSP species/stations data matrix, based on Bray–Curtis similarity and group-average linking, classified the MSP assemblages according to standard

protocols (Clarke and Green, 1988; Clarke and Warwick, 2001; Clarke and Gorley, 2006). Subsequently, BVSTEP analysis identified the best subset of MSP species from the complete data set. Briefly, the procedure involves a step wise search, through both forward selection and backward elimination steps, for a sub-set of taxa that best matches the multivariate patterns exhibited by a full set of taxa in the data table. Relatedness of the NMDS ordinations was determined by Spearman rank correlation (ρ) from the underlying Bray–Curtis similarity matrices (PRIMER version 6.1.13). Taxa responsible for community level differences between the assemblages (i.e. discriminating zooplankton taxa) were identified using the SIMPER routine described earlier Rakhesh et al. (2013).

Patterns of MSP diversity across the assemblages and species-turnover were measured using different alpha (Number of species, *SRp*; Shannon–Wiener index, H', and Pielou's evenness index, J'), and beta diversity measures (beta diversity index, β, beta dissimilarity based on Bray–Curtis and, index of multivariate dispersion, IMD), respectively. We used Venn-diagram to represent total mesozooplankton and or copepod species turnover across different mesozooplankton assemblages. Inputs to these analyses are the number of species (SRp) that are present either in a single sector or in many sectors. Numerical letters at the centre of Venn-diagram represents the number of species that are present commonly across the assemblages. (for details on beta diversity measures, see also Rakhesh et al., 2013). There was a close similarity between 'endemic species' identified through this method with 'characterising species' found using the multivariate Similarity Percentage procedure (SIMPER). Therefore only SIMPER results (for species identity) were considered for the analysis. Kruskal–Wallis followed by Dunn's multiple comparison (for abundance) or one-way ANOVA followed by Bonferroni multiple comparison post hoc tests (for biomass, and diversity indices) were used to check if MSP structural properties differ significantly between assemblages/regions.

To decide the appropriateness of ordination analysis on MSP–environmental data, we checked the nature of the environmental gradient (whether it was homogeneous/heterogeneous) using Detrended correspondence analysis (DCA). Generally, lengths of the DCA axis-I less than 1.5 SD or more than 4 SD suggest linear or unimodal analysis, respectively, while a moderate gradient length allows usage of either method (ter Braak and Prentice, 1988). As the length of the environmental gradient in the first DCA axis was greater than 1.5, we used the unimodal canonical correspondence analysis (CCA) to explain variations in zooplankton composition as described by measured environmental variables detailed by ter Braak (1986). Our Raison d'être on the choice of analysis is CCA's amenability to both linear and unimodal models. The difference between 'total inertia' (DCA) and 'explained inertia' (CCA) revealed the residual or unexplained variation. The Monte Carlo randomisation test (499 permutations under the reduced model) was carried out to assess the probability of the observed pattern being due to chance. By co-varying out the counter environmental variables on lines suggested by Økland and Eilertsen (1994), we used variation partitioning to probe importance of each environmental gradient on MSP distribution.

Since the variance partitioning in CCA is not really a true variance, but rather an inertia, as opposed to the true variance explained in Redundancy Analysis (RDA), results from both CCA and RDA are provided. While CCA explains variance in MSP composition, RDA explains variance in MSP abundance.

Variation inflation factor (VIF) provided the first-hand information on environmental redundancy in the study area (CANOCO version 4.53) of ter Braak and Smilauer (2002). Regression analyses to evaluate relationships between environmental parameters and biological measures were carried out using Microcal Origin 7.5 and STATISTICA vs.8.

3. Results

3.1. Environmental variables

The climate of Chilka lagoon is governed by its location in tropics. During the study period (based on India Meteorological Department), mean daily temperature ranged from a minimum of 21.5 (December, 2005) to a maximum of 30.3 °C (June, 2005), and the wind speed (mean of observations recorded at 11:30 and 14:30 h IST) marked a minimum of 5.2 m s^{-1} (November '04) and a maximum of 16.84 m s^{-1} (May '05), with an overall mean of 10 m s^{-1}. Between 2004 and 2006, the total rainfall amounted to 3380 mm, the bulk of which (72.2%) was recorded during the July–September period, corresponding to the southwest monsoon when the rivers are in floods. The catchment area of Chilka lagoon experiences high inter-annual variability in precipitation and receives an annual average rainfall of ∼1238 mm during the wet season (July–December). The huge difference in precipitation between the wet and dry (March–June) seasons affects the volume of freshwater discharge into the lagoon. Contemporary current meter observations show that the freshwater influx during wet season could be as high as fifty times that of dry season (i.e., 166.8 and 3.1 × 10^6 m^3 d^{-1} respectively). Such huge spatio-temporal differences in freshwater discharges create strong horizontal gradients in salinity ranging between limnetic to mesohaline conditions during wet period and mesohaline to polyhaline conditions during dry period.

Analyses reveal low Secchi-disk transparency, low and fluctuating salinity, dissolved oxygen that pulses between near zero conditions and super saturation, alkaline pH, high levels of turbidity, suspended particulate matter, total nitrogen, total phosphorus, and silicate within the lagoon, suggestive of high allochthonous nutrient inputs typical of most tropical coastal lagoons (Table 1). The findings were suggestive of north–south gradients in nutrients and salinity within the lagoon. As Spearman rank correlation revealed strong co-linearity between suspended particulate matter (SPM) and turbidity ($\rho > 0.95$), we removed SPM from further analyses. Subsequently, NMDS analysis categorised the lagoon into 3 different regions: the southern side of the lagoon representing the south Bay, the northern part representing the north sector, and a transitional body of water in between that extends up to the Lake mouth named the trans/central/channel sector (ANOSIM, Global R: 0.815, $P = 0.1\%$). St.33 (closest to the river mouth) remained as an outlier (Fig. 2(A)). The northern sector, where major rivers open, is characterised by high turbidity, nutrient levels, and chlorophyll *a* compared to the relatively saline and transparent waters in the south or the central–channel sectors. One-way ANOVA followed by Bonferroni post hoc multiple comparison test revealed their spatial differences within the lagoon (supplement Fig. 1).

3.2. Mesozooplankton community structure

3.2.1. Abundance and distribution

Altogether, 63 taxa of MSP representing diverse holoplankton and meroplanktonic forms composed the MSP community. Copepods (62%) represented by 41 species were the most diverse and numerically abundant forms (Fig. 3). Among them, *Acartia chilkaensis* (33%), *Acartiella major* (13%) and *Pseudodiaptomus annandalei* (12%) were the most dominant species. Together with mysids (13%), *Lucifer* sp. (10%) and amphipods (4%) they contributed 85% of the total MSP abundance in the lagoon. The larval plankton consisted mostly of mysis stages of crustacea (4.32%). Copepods, such as *Pseudodiaptomus annandalei, Labidocera pavo, Acartia chilkaensis, Acartiella major*, and *Oithona hebes*, chaetognaths (*Sagitta* sp.), amphipods, mysids, and sergestiids (*Lucifer* sp.) were the most frequently met taxa at the majority of locations.

Table 1
Sector-wise surface water quality characteristics in Chilka lagoon (May 2004–September 2006).

Characteristic	South sector		Trans/central/channel		North sector	
	Min–Max	(Mean ± SE)	Min–Max	(Mean ± SE)	Min–Max	(Mean ± SE)
Depth (m)	0.1–4.25	(1.89 ± 0.04)	0.2–4.5	(1.72 ± 0.06)	0.25–3.75	(1.37 ± 0.05)
Secchi-disk transparency (m)	0–3	(0.8 ± 0.03)	0–3.75	(0.49 ± 0.04)	0–1.25	(0.18 ± 0.02)
Water temperature (°C)	21.1–34.6	(29.2 ± 0.1)	20.1–36.2	(28.6 ± 0.2)	23.2–36.0	(29.4 ± 0.1)
Salinity	0.03–32	(14.67 ± 0.29)	0.02–35.30	(15.33 ± 0.86)	0–34.50	(5.37 ± 0.48)
Turbidity (NTU)	0.04–408	(18.11 ± 1.66)	0.06–996	(75.23 ± 10.45)	0.09–870	(127.5 ± 10.12)
Dissolved Oxygen, D.O. (mg l^{-1})	1.11–13.05	(7.1 ± 0.08)	2.17–15.95	(7.09 ± 0.12)	1.49–13.45	(7.51 ± 0.11)
pH	7.28–9.73	(8.39 ± 0.02)	6.76–9.85	(8.28 ± 0.04)	7.03–10.05	(8.18 ± 0.04)
Suspended Particulate Matter, SPM (mg l^{-1})	1.20–400.40	(38.52 ± 2.03)	0.80–858	(89.76 ± 8.61)	2.40–2656	(152.2 ± 16.13)
Ammonium-N (μM)	0–21.22	(3.04 ± 0.13)	0–22.12	(3.81 ± 0.23)	0–14.36	(2.84 ± 0.16)
Nitrite-N (μM)	0–2.66	(0.19 ± 0.02)	0.02–2.55	(0.35 ± 0.03)	0.02–5.75	(0.42 ± 0.04)
Nitrate-N (μM)	0.02–20.51	(1.76 ± 0.12)	0.02–22.79	(2.84 ± 0.30)	0.01–22.24	(3.18 ± 0.27)
Phosphate-P (μM)	0–9.30	(0.27 ± 0.03)	0.01–6.90	(0.30 ± 0.05)	0.01–3.70	(0.34 ± 0.04)
Silicate-Si (μ mol l^{-1})	0.87–142.6	(37.19 ± 1.04)	0.37–194	(38.67 ± 2.55)	0.46–194	(52.16 ± 2.22)
Total Nitrogen, TN (μM)	1–104	(26.96 ± 0.60)	2.50–125.70	(32.45 ± 1.44)	4.80–138.80	(35.43 ± 1.27)
Total Phosphorus, TP (μM)	0.07–17.40	(0.69 ± 0.06)	0.11–11.40	(0.86 ± 0.09)	0.11–13.44	(1.01 ± 0.09)

Table 2
Mesozooplankton structural properties in Chilka Lake. For diversity and biomass, values are presented as min–max. Values inside parenthesis indicate mean and coefficient of variation, CV for each individual measure. Values in bold indicate percent contribution of major zooplankton taxa and species to the average similarity within each assemblage.

Assemblage characteristics	South sector (Group-I)	Trans/central/channel (Group-II)	North sector (Group-III)
Total zooplankton			
No. species (*SRp*)	18–33 (25; 0.16)	17–50 (33; 0.34)	18–29 (23; 0.12)
Abundance (N) Ind.100 m^{-3}	1527–24 877 (6760; 0.87)	8500–39 838 (19 344; 0.49)	18 100–226 681 (66 394; 0.90)
Evenness index (J')	0.33–0.76 (0.57; 0.21)	0.38–0.74 (0.59; 0.20)	0.35–0.62 (0.49; 0.18)
Rarefaction ($ES_{(100)}$)	7.72–17.09 (12.49; 0.23)	8.14–22.30 (14.21; 0.34)	6.63–10.94 (8.81; 0.18)
Shannon–Wiener (H' $\log_2$)	1.49–3.46 (2.63; 0.22)	1.83–4.15 (2.94; 0.28)	1.60–2.83 (2.24; 0.18)
Copepods			
No. species (*SRp*)	6–14 (10; 0.23)	6–29 (16; 0.47)	8–14 (10; 0.17)
Abundance (N) Ind.100 m^{-3}	315–6120 (2242; 0.79)	4264–16 354 (10 301; 0.41)	7843–182 259 (47 197; 1.14)
Evenness index (J')	0.23–0.73 (0.52; 0.30)	0.41–0.73 (0.57; 0.20)	0.36–0.68 (0.51; 0.25)
Rarefaction ($ES_{(100)}$)	4.85–9.94 (6.82; 0.24)	4.94–14.36 (8.48; 0.37)	3.64–7.17 (5.55; 0.25)
Shannon–Wiener (H' $\log_2$)	0.73–2.51 (1.70; 0.34)	1.66–3.47 (2.20; 0.30)	1.15–2.19 (1.69; 0.24)
MSP biomass (mg DM m^{-3})	1.33–14.24 (5.61; 0.64)	4.34–15.99 (9.87; 0.35)	3.46–26.97 (16.85; 0.41)
Average similarity	59.47%	55.46%	60.59%
Major groups (mean %)	Lucifer (42,7%); copepods(33.9%); larval plankton (16.3%)	Copepods (53.7%), Lucifer (21.1%), amphipods (10.8%); larval plankton (10.1%)	Copepods (71.1%), Mysids (17.4%), larval plankton (6.6%)
Major contributors to similarity within each assemblage	Lucifer, **10.33**%; *Acartia chilkaensis***10.26**%; Protozoea of Lucifer, **6.75**%; *Acartiella major*, **3.97**%; *Labidocera pavo*,**3.82**%; Amphipods, **3.55**%; *Sagitta*, **3.26**%.	*Acartia chilkaensis*, **11.7**%; *Acartiella major*, **6.4**%; Lucifer, **5.01**%; *Pseudodiaptomus annandalei*, **4.09**%; *Oithona hebes*, **3.59**%; Amphipods, **3.38**%; *Labidocera pavo*, **2.68**%; Mysids, **2.62**%	*Acartia chilkaensis*, **15.2**%; Mysids, **10.38**%; *Acartiella major*, **9**%; *Pseudodiaptomus annandalei*, **7.75**%; Mysis Larvae, **3.88**%; Amphipods, **3.64**%; *Oithona hebes*, **2.54**%; Lucifer, **1.53**%

3.2.2. Assemblage patterns and species contribution

Bray–Curtis similarities were calculated on square root-transformed zooplankton abundance data. Subsequent cluster analysis and NMDS (powered with SIMPROF analysis) provided a sequence of fairly convincing groups of stations at 49% similarity. Group-I consisted of the south sector, i.e., south Bay, Group-II the trans/central/channel locations, and Group-III the north sector (Fig. 2(B)). An auxiliary effort using the BVSTEP routine identified a subset of 10 taxa (*Influential species*) as with Clarke and Warwick (2001), consisting of amphipods, mysids, *Lucifer* sp., protozoea of *Lucifer* and, copepods such as *Bestiolina similis, P. annandalei, Temora turbinata, Acartia chilkaensis, Acartiella major and Oncaea venusta* precisely matching the assemblage structure generated from the full set of 63 taxa. These species were capable of adequately reproducing similarity relationships between the ordinations (Rho = 1.00, $p = 0.01\%$). ANOSIM (Global R: 0.763 at $p = 0.1\%$) revealed the difference in zooplankton communities between the groups/regions identified. The patterns were in agreement with environmental ordination.

Following the environmental patterns, MSP stock exhibited a north–south gradient in the lagoon. The north sector with high nutrients supported maximum MSP abundance and biomass in contrast to comparatively low abundance and biomass in the high saline central–channel and south sector locations (Table 2). While copepods *Acartia chilkaensis* (36.7%), *P. annandalei* (14.7%), *Acartiella major* (13.8%) and mysids (17.9%) were the principal inhabitants (83%) in the north sector, non-copepod crustaceans *Lucifer* sp. (44.1%), Amphipods (3.4%) and *Sagitta* sp. (3.4%) and the calanoid *Acartia chilkaensis* (20.2%) were the predominant taxa in the south sector. In the central–channel sector, *Lucifer* sp. (22.1%), *Acartia chilkaensis* (21.7%), *Acartiella major* (11.9%), Amphipods (11.8%) and *P. annandalei* (5.1%) were numerically important. Meroplanktonic forms recorded high abundance in the south sector (16.5%), relative to either central–channel (7%) or north (5.8%) locations. Among them, the brachyuran protozoea, zoaea and fish larvae were ubiquitous, being found through most of the lagoon. Alima larvae, protozoea and mysis stages of *Lucifer*, and bivalve veligers remained restricted to south sector and central–channel locations.

SIMPER analysis determined the percent contribution of species to within-group similarity (*characterising species*) as well as between group dissimilarity (*discriminating species*, i.e. species responsible for β-dissimilarity). Intra-group similarities varied from 55.5% to 60.6%, and the highest average similarity was observed

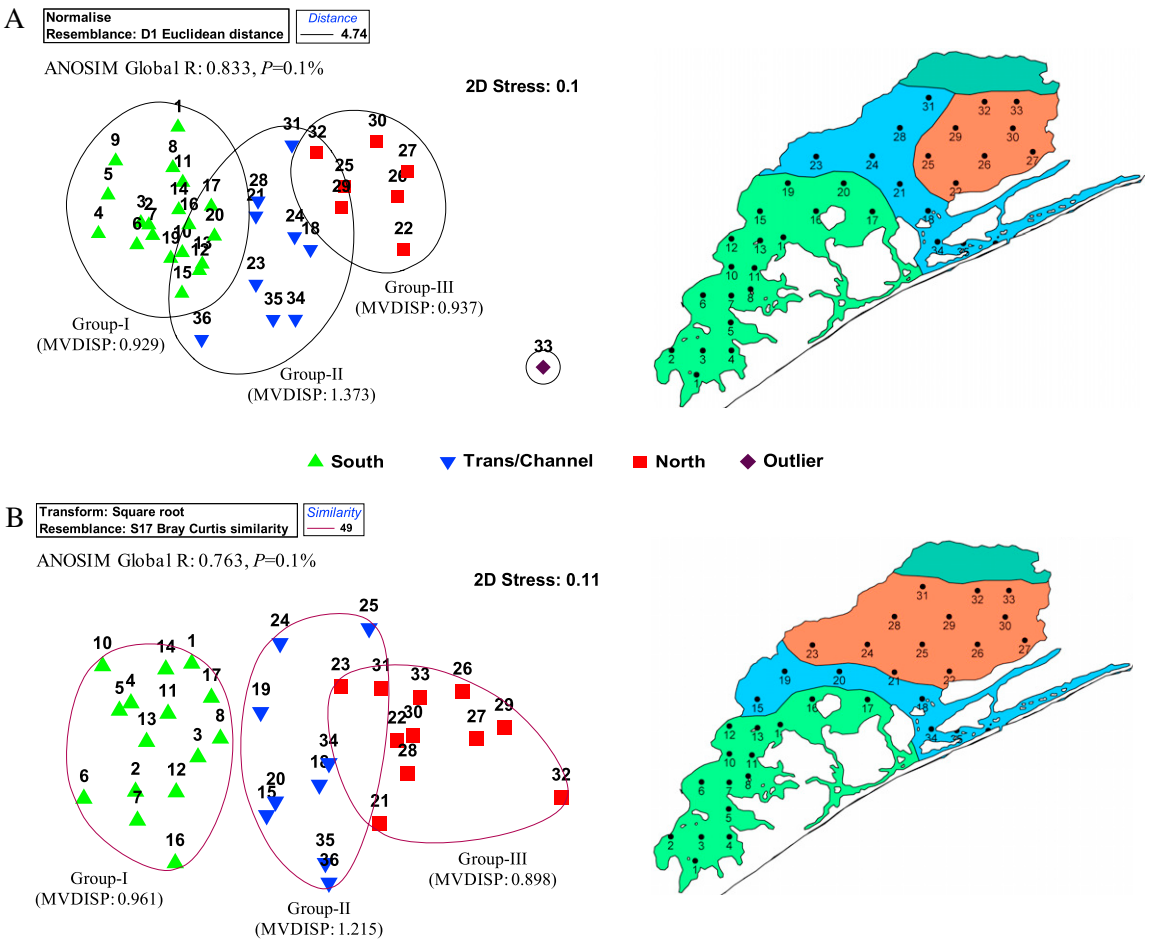


Fig. 2. (A) Euclidean distance based environmental classification showing spatial segregation of sampling locations named after south, Trans/channel and north areas in the lagoon. (B) NMDS (powered with SIMPROF analysis) on Bray–Curtis similarities based square root-transformed MSP data showing. Discrete MSP assemblages at 49% similarity. Hydrographical and biotic patterns that showed close similarity superimposed on geographical locations.

among stations of the north sector. Table 2 summarises information on characterising species that contributed foremost to the average similarity, along with their percent contribution to the total MSP abundance, within each sector. Bray–Curtis dissimilarity, however, revealed that, while the north sector (Group III) sustained a population of Mysids and *A. chilkaensis*, the central–channel locations (Group II) consisted predominantly of *Acartiella major* and *O. hebes* and the south sector large populations of *Lucifer* sp. and Protozoea of *Lucifer* sp. Their variability in distribution between these regions conferred them the status of being '*discriminating species*'.

3.2.3. Diversity

Alpha diversity: MSP species richness and diversity varied significantly among the assemblages. Comparatively, MSP diversity (Species richness, SRp; Shannon–Wiener Index, H', and Evenness index, J') was higher in the central sector and channel locations. One-way ANOVA followed by Dunn's multiple comparison test revealed significant differences between the assemblages (Table 3). In the north sector located close to the river mouths, H' recorded lower values. The low diversity in this region is attributable to the overwhelming dominance of *Acartiella major* and *Acartia chilkaensis* that together constituted 42% of total MSP community. Alternatively, relatively high values were recorded in the central–channel locations and south sector. Overall, species richness and other conventional diversity measures for copepods exhibited a pattern analogous to total MSP (Table 2).

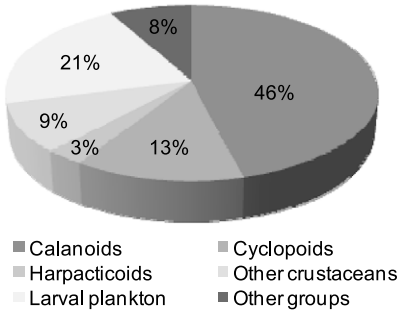


Fig. 3. Mesozooplankton community composition based on copepods.

Beta diversity: MSP species turnover rate or difference in diversity within and between the assemblages (i.e., differentiation diversity) was investigated using two different approaches, beta dissimilarity index (based on Bray–Curtis dissimilarity and beta diversity index, β) and within area heterogeneity (using index of multivariate dispersion, MVDISP). The β-dissimilarity index calculated using Bray–Curtis dissimilarity revealed significant intergroup differences. The maximum β-dissimilarity was observed between the south and north sectors, and minimum between central/channel and north sectors. ANOSIM further substantiated the differences noticed between these assemblages (Fig. 4(A) and (B)). The relative variability within each MSP assemblage (MVDISP)

Table 3
Kruskal–Wallis and one-way ANOVA measures followed by post hoc multiple comparison tests showing differences in MSP and copepod structural properties between different biotic assemblages in the lagoon.

	Kruskal–Wallis	One-way ANOVA				
Total MSP	*N*	Dry mass	SRp	J'	H'	$ES_{(100)}$
Kruskal–Wallis statistics/F-ratio and *P* value	23.77; $P < 0.001$	17.15; $P < 0.001$	7.04; $P < 0.05$	2.08; $P > 0.05$	3.44; $P < 0.05$	7.77; $P < 0.05$
Post hoc tests						
South sector vs. central sector	*	ns	*	ns	ns	ns
South sector vs. north sector	***	***	ns	ns	ns	*
Central sector vs. north sector	ns	**	**	ns	*	**
Copepods alone	*N*		SRp	J'	H'	$ES_{(100)}$
Kruskal–Wallis statistics/F-ratio and *P* value	27.06; $P < 0.001$		7.04; $P < 0.05$	0.60; $P > 0.05$	2.86; $P > 0.05$	5.15; $P < 0.05$
Post hoc tests						
South sector vs. central sector	**		*	ns	ns	ns
South sector vs. north sector	***		ns	ns	ns	ns
Central sector vs. north sector	ns		**	ns	ns	**

ns—Not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

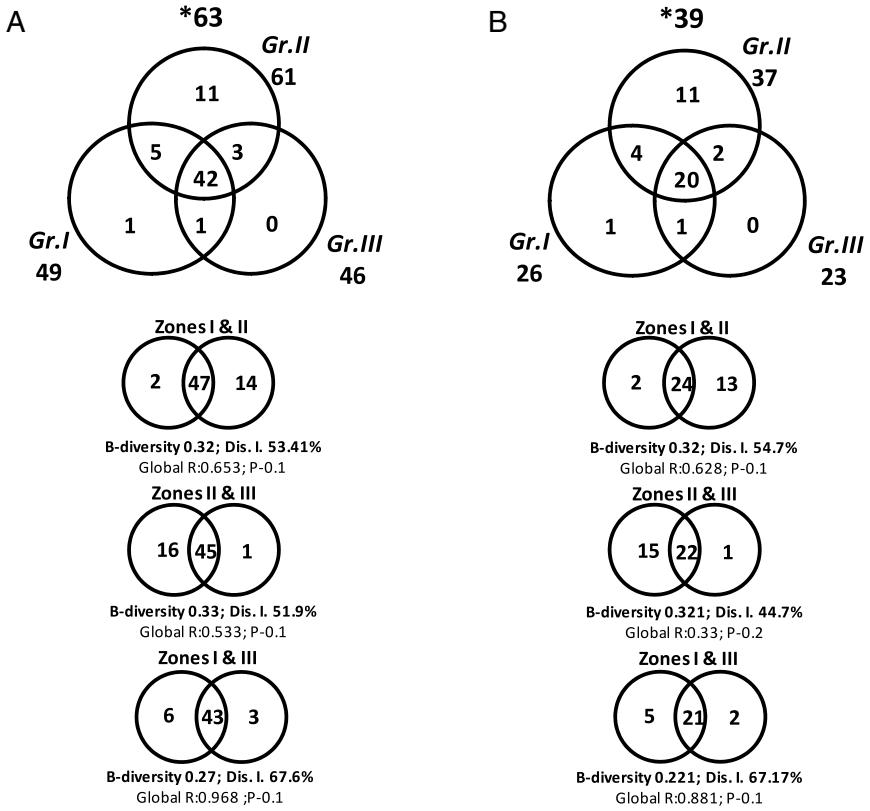


Fig. 4. Venn diagram showing both alpha and beta diversity measures for (A) total MSP and (B) copepods in the lagoon.

points to the high biotic heterogeneity within the central–channel area.

3.2.4. Small-sized copepods and mysids

The present study revealed the importance of small copepods (<1 mm) and mysids in shaping zooplankton community attributes in Chilka lagoon. Copepods belonging to the families Paracalanidae, Acartiidae, Pseudodiaptomidae, Oithonidae, Corycaeidae, Oncaeidae, Centropagidae and Tachidiidae dominated the size spectrum, increasing from 74% of total copepods in the south sector (Assemblage I) to 99% in the north sector (Assemblage III) (Fig. 5). As with large copepods, calanoids constituted the dominant taxa. The regression analysis between small copepod abundance and species richness (SRp) with total MSP (R^2:0.922 and 0.884 respectively) and total copepod abundance (R^2:0.999 and 0.951 respectively), revealed the significant ecological role of small copepods within the lagoon. However, distribution of mysids in the lake appeared greatly favoured by generous and diverse food sources in the north sector. Dominance of pico-nanoplankton, steady availability of prey-species (small-sized copepods, especially in the north), and seasonally driven putrefaction of aquatic weeds appeared important in the distribution of mysids in general and their overwhelming abundance in the north sector in particular.

3.2.5. Zooplankton: phytoplankton biomass ratio

The total mesozooplankton: phytoplankton biomass ratio showed low values throughout the lake, suggesting modest grazing by MSP on the resident phytoplankton population. However,

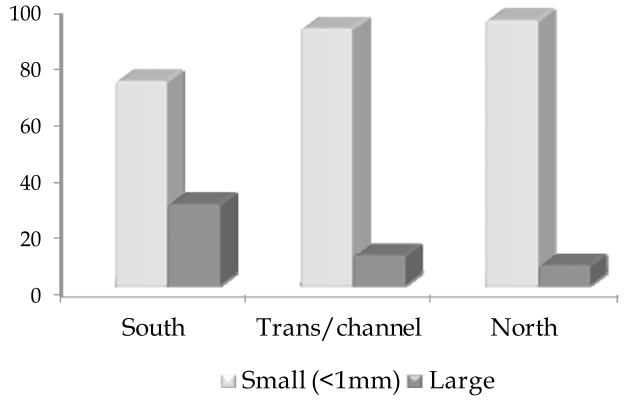


Fig. 5. Copepod size-structure inside the lagoon. Small copepods (<1 mm) increased their abundance from 74% in the Rambha Bay to 99% in the North Bay.

the abundance (%) of copepods plotted against chlorophyll *a* values suggested significant grazing of phytoplankton stock by small copepods. This was in contrast to the patterns exhibited by other crustaceans (Fig. 6). Such a tendency and the absence of any spatial patterns in total biomass ratios, along with the shallow nature of the lake, point to the importance of food sources other than phytoplankton (such as micro zooplankton, microphytobenthos and detritus). In the lagoon, dominance of pico and nanoplankton (high Chl *a* levels, <20 μm), high micro zooplankton standing stock, high amount of macrophyte derived detritus (during summer and recovery period), and high regional abundance of detritivorous zooplankton (mysids) provide support to this hypothesis. In this context, it is noteworthy that zooplankton registered significantly high biomass during summer and recovery periods (with a possible shift to detritivory) compared to monsoon season.

3.3. Zooplankton–environmental relationships

MSP composition and abundance appeared largely governed by a variety of abiotic factors. This could be explained by superimposing the values, variable-wise, on the MSP assemblage patterns. Supplement Fig. 2 represents turbidity, water column transparency, salinity, nitrate-N, silicate-Si, and small chlorophyll *a* (<20 μm) by circles of differing diameter placed at the corresponding site locations on the biotic NMDS. A general examination would reveal that, in group I stations (South), water column transparency and salinity were high, but turbidity, silicate, nitrate and (small) chlorophyll *a* levels were relatively low. The opposite was the case (least salinity and transparency, highest turbidity, nutrient levels and chlorophyll *a*) in group III (North), whereas intermediate conditions prevailed in group II locations (central–channel).

Though differences in zooplankton community structure in the lagoon were in clear agreement with varying hydrological conditions, inferences based on the correlation of biotic patterns with a single environmental variable at a time could lead to erroneous results. To overcome this difficulty, we examined the biotic–abiotic relations using the BIOENV protocol based on weighted Spearman rank correlation Pw implemented in PRIMER (see Clarke and Warwick, 2001). The single most abiotic variable that best differentiated the sites, in a manner consistent with zooplankton distribution patterns, was the salinity ($Pw = 0.513$). However, the best combination was offered by turbidity, silicate, secchi-disk transparency, nitrite, nitrate, and small Chl. *a* fraction ($Pw = 0.665$). Furthermore, using residual analysis, we investigated the influence of size-structure of phytoplankton (<20 μm Chl. *a*) on resident MSP, after removing the effect of salinity on biotic distribution patterns (which is analogous to co-varying out the effect of salinity on MSP composition and Chl *a* in constrained gradient analyses). Analysis revealed that availability of small phytoplankton contributes up to 50% of variation in the abundances and 16% variation in the species richness of total zooplankton, small copepods and total copepods (supplement Fig. 3).

The comparison of unconstrained (DCA) and constrained (CCA) gradient analyses revealed that residual variables are responsible for up to 34% of the variability in MSP composition in the lagoon. Correlations between 'discriminating' MSP taxa and measured explanatory variables revealed that canonical axis-I with maximum correlations for all variables (except NH_4–N) represents the main environmental gradient (i.e., it has the highest Eigenvalue) in the study area. On this axis, divergent environmental gradients offered by high water column transparency–salinity (positively correlated) separated the south Bay MSP from their counterparts in the turbid, nutrient, phytoplankton-rich low-saline waters (negatively correlated) of the north sector. MSP in the transition waters were typified by intermediate conditions offered by combative salinity–trophic gradients. Unlike the south and north sectors, high NH_4–N levels typified north stations of central–channel locations as seen in canonical axis-II. The spatial distributions of MSP in central–channel locations were further influenced by proximity of sampling locations to the sea. Overall, the first two axes taken together explained more than two-thirds of spatial variation in MSP that could be explained by the measured variables (i.e. 68% of the total 66% constrained variability, Fig. 7(A); Table 4). The Monte Carlo permutation test (499 permutations under the reduced model) revealed that the influence of canonical axis-1 on MSP distribution was stronger than expected. The trace statistic (the sum of all canonical axes) revealed a significant overall relationship ($P = 0.002$) between MSP taxa and all environmental variables measured. Overall, the results show the presence of two dominant environmental gradients (related to the variables we measured) controlling MSP distribution in Chilka lagoon: one is related to trophic conditions, and the other one to salinity and water column transparency. It would appear that these two gradients are somewhat related to each other, as they proceed in opposite directions. To test whether variables in these gradients exhibit any redundancy or whether each explains unique aspects of MSP composition (CCA) and or abundance (RDA), we performed a partitioning of the total variance explained. Variance partitioning revealed that, while trophic gradients quash the salinity effects, the interrelationship or cumulative effect of these gradients generated more than a quarter of the total variation in MSP distribution in the lagoon (Fig. 7(B)). Generally, an environmental variable with a variation inflation factor (VIF) of 1.00 is highly uncorrelated with other variables and shows unique information. Conversely, VIF ranging from 1.8 to 11.9, in the present study, supports the extent of environmental redundancy or interrelationship of measured environmental variables in explaining MSP distribution in Chilka lagoon.

4. Discussion

4.1. Environmental characteristics

Coastal lagoons are adversely affected by human impingement, and eutrophication is one of the several processes that degrade water quality and alter plankton dynamics. Nutrient rich freshwater influx brings about major changes in lagoon systems, affecting the plankton dynamics (Borja, 2005). This is particularly true in the case of Chilka lagoon where hydrobiological conditions are governed by seasonally driven freshwater inflow from numerous rivers/rivulets lake-wide. Findings revealed that the volume of annual freshwater discharge, especially during active flow conditions (July–December), brings substantial quantities of nutrients and suspended matter into the Lake within the north sector severely infested with macrophytes (Raman et al., 2007). The limited neritic

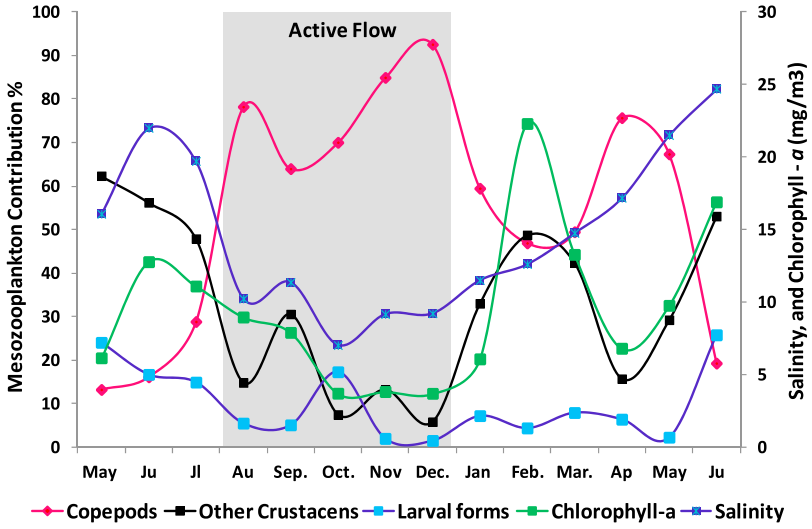
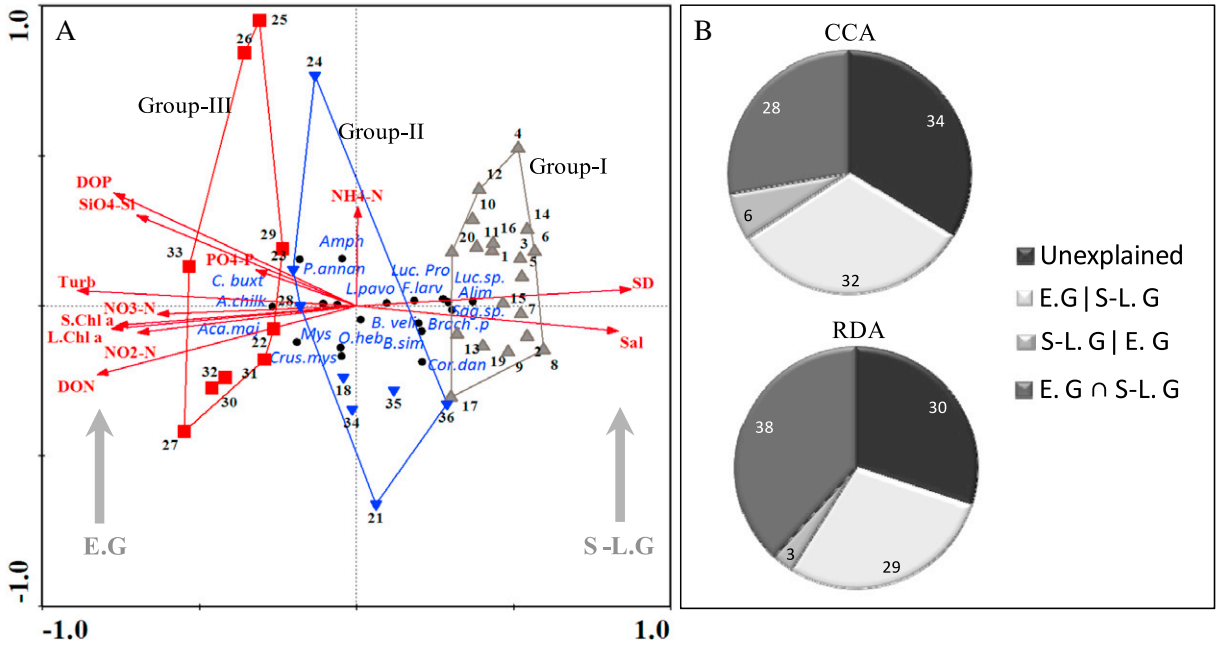


Fig. 6. Seasonal variation in copepods, larval forms and other crustaceans in relation to salinity and total chlorophyll-a. Distribution patterns show a copepod regulated phytoplankton population, especially during low saline active flow conditions. Values represent mean observations for each month.

Table 4
Detrended correspondence analysis (DCA) and Canonical correspondence analysis (CCA) showing the extent of environmental regulation of MSP community in Chilka lagoon.

DCA	1	2	3	4	*Total inertia*
Eigenvalues	0.252	0.049	0.030	0.017	0.598
Lengths of gradients	1.741	1.044	1.075	0.760	
Cumulative percentage variance of species data	42.1	50.3	55.3	58.2	
Sum of all eigenvalues					0.598
CCA					
Eigenvalues	0.214	0.057	0.043	0.03	0.598
Species–environment correlations	0.924	0.911	0.794	0.801	
Cumulative percentage variance of species data	35.7	45.3	52.5	57.4	
of species–environment relation	53.9	68.4	79.2	86.7	
Sum of all eigenvalues					0.598
Sum of all canonical eigenvalues					0.396
Total percentage variability in species data explained by measured environmental variables together					**66.2**%
Environmental variables					
Secchi disc transparency (m)	0.808	0.051	0.077	0.033	
Salinity	0.771	−0.077	−0.028	0.403	
Turbidity (NTU)	−0.821	0.047	−0.066	0.157	
Ammonia-N (μM)	0.004	0.302	0.012	0.392	
Nitrite-N (μM)	−0.643	−0.081	−0.194	0.196	
Nitrate-N (μM)	−0.585	−0.024	0.036	0.165	
Phosphate-P (μM)	−0.296	0.109	−0.021	0.140	
Silicate-Si (μM)	−0.646	0.275	−0.190	−0.283	
Dissolved Organic Nitrogen (μM)	−0.764	−0.209	−0.131	−0.192	
Dissolved Organic Phosphorous (μM)	−0.714	0.343	−0.042	0.113	
Large Chlorophyll-*a* (mg m^{-3})	−0.721	−0.069	−0.065	−0.199	
Small Chlorophyll-*a* (mg m^{-3})	−0.706	−0.060	−0.161	−0.227	
Summary of Monte Carlo test (499 permutations under reduced model)					
Test of significance of first canonical axis: eigenvalue	= 0.214				
F-ratio	= 12.77				
P-value	= 0.002				
Test of significance of all canonical axes: Trace	= 0.396				
F-ratio	= 3.761				
P-value	= 0.002				

incursion does not allow adequate mixing responsible for the spatial gradients noticed in the water body that supports distinct biotic assemblages. According to the definition proposed by Nixon (1995) and the trophic state index (TRIX) proposed by Vollenweider et al. (1998) for coastal zones, Chilka Lake exhibits moderate/poor water quality, characteristic of mesoeutrophic (south sector) to eutrophic (central/channel and north sector) conditions (TRIX: 5–7) described earlier by Raman et al. (2007). Simultaneous observations on frequent outbursts of cyanophyceae blooms and high Chl *a* build-up support our view that Chilka Lake is already transformed into a freshwater dominated eutrophic–hypereutrophic system. Similar to the observations by Carpenter et al. (2010), such changes could result in wide implications through trophic cascades, altering zooplankton community dynamics as well.



Abbreviations: (A) Sag.sp – *Sagitta* sp.; F.larv – Fish larvae; B.veli- Bivalve veligers; Amph- Amphipods; Brach.prot- Brachyuran protozoea stages; Mys- Mysids; Crus.mys- Crustacean mysis stages; Luc. sp- *Lucifer* sp.; Luc. Prot- Lucifer protozoea stages; Alim- Alima larvae; B.sim- *Bestiolina similis*; P. annan- *Pseudodiaptomus annandeli*; L.pavo- *Labidocera pavo*; A.chilk- *Acartia chilkaensis*; Aca.maj- *Acartiella major*; C.buxt- *Cyclops buxtoni*; O.heb- *Oithona hebes*; Cor.dan- *Corycaeus danae*.
(B) E.G – Eutrophic gradient; S-L.G – Salinity-light gradient

Fig. 7. (A) Canonical correspondence Analysis (CCA) shows how various abiotic and biotic factors persuade MSP assemblage patterns in Chilka lagoon. (B) Variance partitioning showing the influence of discrete environmental gradients on MSP species composition. E.G □ S–L.G shows the variance distinctively described by trophic gradient; S–L.G □ E.G, the variance uniquely described by salinity–light gradient; E.G ∩ S–L.G the variance jointly described by both trophic–salinity gradients (i.e. redundant variation) and unexplained variance represents the variation explained by residual explanatory variables.

4.2. Mesozooplankton characteristics, species turn-over and environmental heterogeneity

There was a close semblance between hydrographical patterns and MSP assemblages in Chilka lagoon. Distribution of small copepods, mysids, sergestiids, and amphipods was mainly accountable to observed assemblage patterns and differences in MSP structural properties between the assemblages. Small copepods and mysids are benefited mostly from the low saline-high turbid-high nutrient-high chlorophyll situations in the north sector. In the presence of surplus food, copepod-mysid populations seemed to have followed a prey–predator relationship (more in Section 4.3). The south sector in contrast supported a MSP community dominated by sergestiids, small copepods, amphipods, and chaetognaths in their order of abundance. Trans/channel locations as the name indicates are inhabited by a mix of populations from both south and north sectors. However, plankton and background variables examined in later years suggest that the spatial extends of these assemblages may change seasonally and or annually depends upon allochthonous freshwater influx. High river inflow coupled with limited tidal exchange expanded oligohaline conditions in the north sector to central–channel locations. Thus, contrasting environmental gradients offered by nutrients–light availability and salinity and their spatial and seasonal interactions would seem governing the environmental ranges of brackish MSP populations in Chilka lagoon.

MSP abundance and percent contribution of copepods relative to situations immediately after the hydrological intervention in September 2000 revealed changes in MSP standing stock. Copepod densities in the north sector (current study) reduced to 34% of values recorded by Naik et al. (see Naik et al., 2008). In the central–channel locations and south sector, copepod abundance reduced to 1%–2% of populations found earlier. Creation of a new lagoon mouth accentuated tidal mixing ensuring high abundance (up to 83%) of neritic (copepod) species in the south and central sectors in the Lake. However, the following years witnessed changes in MSP community and (neritic) species which dominated in 2001 were replaced by brackish water taxa by 2004–2005. Within the same period, there was a diminution in the relative contribution of copepods to total MSP in the south and trans/channel locations (33%–53%) suggestive of deteriorating water quality over the years Shannon–Weiner diversity for total MSP or copepods was low compared to other tropical lagoons (Pliŭraitë, 2003) attributable to stressful conditions in the Lake. Contemporary studies on phytoplankton community changes in the Chilka Lake appeared to lend support to this contention.

Beta dissimilarity measures revealed varying degrees of species turn-over between the assemblages representing a north–south gradient. In general, high community turn-over was reported between assemblages with maximum transparency, nutrients and chlorophyll turn over. The observed Bray–Curtis dissimilarity across the assemblages suggest that total MSP and copepod communities in Trans/channel locations were 45%–55% similar to both south and north sectors. As beta diversity can be measured at different levels, within group-heterogeneity using MVDISP revealed high beta diversity within Trans/channel locations indicating high species variability and low predictability characteristic of transitional waters compared to the other two sectors. Several authors have related elevated beta diversity to high environmental

heterogeneity (Nabout et al., 2007; Verleyen et al., 2009) and disturbance regime (Vanschoenwinkel et al., 2010) which in turn influences ecological patterns and processes, affecting species distributions (Zajac et al., 2003) and community composition (Ellingsen and Gray, 2002). In Chilka lagoon, MSP within-group variability (i.e., intra-group heterogeneity) positively related to environmental heterogeneity. Interactions of trophic and salinity–light gradients inflicting stress (hydrographical MVDISP value highest at Trans/channel locations) on resident MSP community are higher in the transitional waters between south and north sectors. Considering the hydrographical assemblage patterns and north–south environmental gradients, we believe that environmental redundancy played a comparatively higher role regulating MSP community in the Trans/channel locations. In the north and south sectors, MSP patterns are controlled by salinity–light and nutrient–phytoplankton availability, respectively.

4.3. Importance of small copepods and mysids

The present study has revealed a close correlation between copepods and total MSP abundance, suggesting that the MSP community dynamics in Chilka lagoon are chiefly governed by copepods, especially the small-sized forms. Among these, the calanoids Acartiidae are known for their wide distribution in estuary and coastal waters throughout the world because of their broad environmental adaptability (Hsu et al., 2008). In mixed estuaries, they are often abundant in turbidity maximum zones, where they use accumulated particulate organic matter, mainly phytoplankton and detritus (Suzuki et al., 2008; Botto et al., 2011; Watanabe et al., 2014). In such environments, they are often the most quantitatively important components to MSP standing stock (Day et al., 1989). In the turbid north sector of Chilka lagoon, under heavy freshwater inflow and high nutrient levels that support a rich population of pico-plankton and ciliates (Raman et al., 2007), distinct populations of *Acartia chilkaensis* and *Acartiella major* often contribute up to 99% of the total copepod population. High abundances of these small calanoids suggest their potential in harvesting energy available with both classical and microbial pathways alike (Turner and Roff, 1993; Kiørboe and Nielsen, 1994). Similar to the present findings, we have shown earlier the importance of small calanoid copepods structuring MSP communities in the estuarine waters of the east coast of India (Rakhesh et al., 2013, 2008) that could go as well with Cochin backwaters (Madhupratap et al., 1979; Madhu et al., 2007) and the Mandovi–Zuari estuarine systems (Padmavati and Goswami, 1996) along the west coast of India.

Mysids are equally important in structuring plankton communities in coastal and estuarine systems (Mauchline, 1980; Mees and Jones, 1997). They are opportunistic omnivores and make use of the most abundant food sources with seasonal and ontogenetic diet changes (Fockedey and Mees, 1999; Branstrator et al., 2000). Recent studies based on Δ^{15}N stable isotope analysis of the pelagic food web suggest that, during summer, other MSP (mainly copepods) form the main component of the mysid diet and that, during post summer, they shift their diet to phytoplankton or plant detritus (Lesutien et al., 2007). Thus, their selective feeding can modify the structure of estuarine zooplankton (Kouassi et al., 2006) and phytoplankton (Siegfried and Kopache, 1980). In Chilka lagoon, supported by a wealth of different food sources, mysids form a crucial component of MSP in the north sector. Their ecological relevance has also been reported from many other estuaries, where they constitute the key prey for many young stages of fishes and crustaceans (Elliott et al., 2002). Chong and Sasekumar (1981), while describing the food and feeding habits of the white shrimp *Penaeus* sp., maintained that, while pelagic post larvae feed on copepods, epibenthic late post larval stages and juvenile forms mainly feed on copepods and detritus. In contrast, sub-adult and adult forms graze mainly on mysids and copepods, and less on detritus. In Chilka Lake, increased farming of *Penaeus* sp. and high fish production in the north sector appeared largely supported by the customary availability of detritus along with high abundance of small copepods and mysids that support various life stages of *Penaeus* sp. through different seasons. These relationships show the foraging effect of large crustaceans and fish community on MSP in Chilka lagoon.

4.4. Zooplankton: phytoplankton biomass ratio

The lower than expected zooplankton: phytoplankton biomass ratio in Chilka Lake is suggestive of the importance of other food sources. According to McCauley and Kalff (1981), the greater importance of the "detritus food chain", along with the reduction in the proportion of nanoplankton in eutrophic waters, would reduce zooplankton grazing on phytoplankton and thereby cause a reduction in the zooplankton: phytoplankton biomass ratio. Another reason could be that, with increasing trophy, many shallow lakes switch over to a more turbid state, with a high concentration of small sized (pico) phytoplankton (Timms and Moss, 1984; Scheffer, 1998) even at high macrophyte abundance (Jeppesen et al., 1994). Under such circumstances, zooplankton grazing would also suffer from low visibility and higher than optimal food concentration, as observed in the north sector of Chilka lagoon. Another possible factor for such a low zooplankton: phytoplankton biomass ratio could be the high fish and invertebrate (such as *Penaeus* sp. and mysids) predation on copepods, as observed in Lake Kogleaks (Jeppesen et al., 2007).

4.5. Mesozooplankton–environmental relationship

Salinity as a factor regulating zooplankton structural properties (Santangelo et al., 2007) was reported from several tropical coastal lagoons, such as the eutrophic Massa lagoon, a Ramsar site in Southern Morocco (Badsi et al., 2010), the Grand-Lahou, a West African coastal lagoon (Etile et al., 2009), North African coastal lagoons of Merja Zerga, Ghar El Melh, and Lake Manzala (Ramdani et al., 2009), and the Bardwail Lagoon in Egypt (Mageed, 2006). Among other factors that influence lagoon plankton dynamics, suspended particulates and light penetration, along with nutrient properties, play a vital role. In this study, contrasting environmental gradients created by a multi-factorial combination of salinity, secchi-disk transparency, turbidity, nutrients and small Chl *a* ($<$20 μm) proved central for MSP distribution in the lagoon. While the abundance and dominance of small sized copepods were related to the availability of food (e.g., small chlorophyll *a*), species diversity was regulated by local hydrographical conditions. Similar observations are available from several shallow coastal lagoons (NE Iberian Peninsula) where zooplankton abundance and distribution was mainly related to biotic factors, such as food resources and availability, fish predation or inter/intra-specific competition and, taxonomic diversity to abiotic factors, such as nutrient concentration and speciation (Badosa et al., 2007). Variation partitioning analyses revealed that trophic gradient was the single most important factor responsible for variation in MSP distribution in the river dominated Chilka lagoon. We consider this as an indirect effect resulting from prey–predator relationships and interactions of member variables in trophic gradient such as nutrients and phytoplankton. Unlike several other tropical systems and our own observations from Godavari mangrove-estuarine system (data unpublished), salinity–light gradients alone played only a minor role regulating MSP composition (6%) or abundance (3%). Environmental redundancy, or the cumulative effect of background variables in these environmental gradients, was responsible for nearly one third of the total variation in MSP composition (28%) and or abundance (38%) within the lagoon. Equally important was the residual variation ($>$30%). We propose that foraging effects by shrimps and fishes, intra-guild predation, surplus availability

of detritus, dense ciliate and microphytobenthos populations, and hide-outs provided by submerged vegetation (data unpublished), could be the important variables, meeting most of the residual variation in MSP distribution within the lagoon. These evidences show that in river and macrophyte dominated choked systems like Chilka lagoon where high water residence time contributes to system eutrophy, plankton are frequently exposed to nutrient related changes than salinity related ones. This determines environmental ranges for brackish copepods such as *Acartia* sp., *Acartiella* sp. that dominate the MSP community as observed in this study. These observations are in agreement with other studies that revealed the cumulative or individual effect of these gradients on lagoon plankton dynamics, e.g., Messolonghi lagoon, Greece (Gotsis-Skretas and Satsmadjis, 1990); Indian River Lagoon, Florida (Phlips et al., 2002); Lake Alimini Grande, Italy (Vadrucci et al., 2004); Sontecomapan lagoon, southern Gulf of Mexico (Ake-Castillo and Vázquez, 2008) and Myall Lake, Australia (Ryan et al., 2008).

5. Conclusions

MSP community dynamics in this fresh water dominated tropical coastal lagoon is governed by varying hydrological conditions, resulting from limited neritic incursion on one hand and heavy freshwater-nutrient inflow on the other. Small copepods dominate the MSP community, and their swarming proportions lagoon-wide are suggestive of their potential in harvesting energy available with classical and microbial pathways alike. Lower than expected MSP grazing pressure suggests modest/varying zooplankton herbivory. This, along with the shallow nature of the lake, points to the importance of other food sources, such as micro zooplankton, microphytobenthos and detritus in the lagoon. The study also addresses factors that support rich populations of mysids, and increased farming of *Penaeus* sp. in the north sector of the Lake through different seasons.

Environmental redundancy resulting from the interplay of trophic-salinity-light gradients inflicts a great deal of variability in MSP distribution. The quashing effect of the trophic gradient over and above salinity–light gradients revealed the superseding role of eutrophicants on lagoon plankton dynamics and ecology five years post-intervention. Also, total MSP abundance and contribution of copepods within each lagoon sector was significantly lower than that reported immediately after the hydrological intervention. These evidences suggest that Chilka lagoon is on the verge of transformation into a eutrophic–hypereutrophic system, thereby counteracting any ecosystem benefits derived from the opening of a new lagoon mouth in the year 2000. From a conservation point of view, this shows a clear shift from a much-envisaged salinity-driven system to a least favoured eutrophicants-controlled coastal ecosystem. Such changes would result in large-scale implications via trophic cascades that would alter ecosystem functioning. Comparable findings from other coastal lagoons revealed the similarity in response of plankton communities to anthropogenic causes across the tropics.

Acknowledgements

This work was carried out with the financial assistance provided by the Ministry of Earth Sciences, Government of India, New Delhi (Sanction no DOD/ICMAM-PD/9/2001) for the Project on Ecosystem Modelling of Chilka lake through its Directorate at Chennai. We are grateful to Dr. Donald McLusky at the University of Stirling for his constructive criticism and helpful suggestions and to DRK Sastry who spent considerable time reading the manuscript. We are thankful to all those who helped in the field data collection. It is our privilege to place on record our grateful admiration to the Indian Navy and the successive Commandants of INS Chilka for their support and unfailing cooperation at the Field Station located at INS Chilka. This work was carried out at the Marine Biology Laboratory, Department of Zoology, Andhra University.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.rsma.2015.04.003.

References

Ake-Castillo, J.A., Vázquez, G., 2008. Phytoplankton variation and its relation to nutrients and allochthonous organic matter in a coastal lagoon on the Gulf of Mexico. Estuar. Coast. Shelf Sci. 78, 705–714.

Badosa, A., Boix, D., Brucet, S., Lopez-Flores, R., Gascon, S., Quintana Xavier, D., 2007. Zooplankton taxonomic and size diversity in Mediterranean coastal lagoons (NE Iberian Peninsula): Influence of hydrology, nutrient composition, food resource availability and predation. Estuar. Coast. Shelf Sci. 71, 335–346.

Badsi, H., Oulad Ali, H., Loudiki, M., El Hafa, M., Chakli, R., Aamiri, A., 2010. Ecological Diagnoses factors affecting the distribution of zooplankton community in the Massa Lagoon (Southern Morocco). Afr. J. Environ. Sci. Technol. 4, 751–762.

Borja, A., 2005. The European water frame work directive: a challenge for near shore, coastal and continental shelf research. Cont. Shelf Res. 25, 1768–1783.

Botto, F., Gaitan, E., Mianzan, H., Acha, M., Giberto, D., Schiariti, A., Iribarne, O., 2011. Origin of resources and trophic pathways in a large SW Atlantic estuary: an evaluation using stable isotopes. Estuar. Coast. Shelf Sci. 92, 70–77.

Branstrator, D.K., Cabana, G., Mazumder, A., Rasmussen, J.B., 2000. Measuring life history omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. Limnol. Oceanogr. 45, 463–467.

Carpenter, S.R., Cole, J.J., Kitchell, J.F., Pace, M.L., 2010. Trophic cascades in Lakes: Lessons and prospects. In: Terborgh, J., Estes, J.A. (Eds.), Trophic Cascades—Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, DC, pp. 55–70.

CDA, 2005. Chilika Development Authority, "Achievement Report 2005" Bhubaneswer, Orissa, India.

Chandramohan, P., Nayak, B.U., 1994. A study for the improvement of the Chilka lake tidal inlet, eastcoast of India. J. Coast. Res. 10, 909–918.

Chandramohan, P., Sanil Kumar, V., Nayak, B.U., 1993. Coastal processes along the shore front of Chilka Lake, east coast of India. Indian J. Mar. Sci. 22, 268–272.

Chong, V.C., Sasekumar, A., 1981. Food and feeding habits of the white prawn Penaeus mergulensis. Mar. Ecol. Prog. Ser. 5, 185–191.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual. PRIMER-E Ltd., Plymouth, United Kingdom.

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser. 46, 213–226.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities. An Approach to Statistical Analyses and Interpretation, second ed. Primer-E, Plumouth, p. 172.

Comín, F.A., Valiela, I., 1993. On the controls of phytoplankton abundance and production in coastal lagoons. J. Coast. Res. 9, 895–906.

Conway D.V.P., White R.G., Hugues-Dit-Ciles J., Gallienne C.P., Robins D.B., 2003. Guide to the coastal and surface zooplankton of the south-western Indian Ocean, Occasional Publication of the Marine Biological Association of the United Kingdom, No. 15, Plymouth, UK. (15) 354p.

Day, J.W., Hall, C.A.S., Kemp, W.M., Yanez-Arancibia, A., 1989. Estuarine Ecology. John Wiley and Sons, New York, p. 558.

Ellingsen, K.E., Gray, J.S., 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? J. Anim. Ecol. 71, 373–389.

Elliott, M., Hemingway, K.L., Costello, M.J., Duhamel, S., Hostens, K., Labrapoulou, M., Marchall, S., Winkler, H., 2002. Links between fish and other trophic levels. In: Elliott, M., Hemingway, K.L. (Eds.), Fishes in Estuaries. Blackwell Science, Oxford, pp. 124–216.

Etile, R.N., Kouassi, A.M., Aka, M.N., Pagano, Marc, Valentin, N., Kouassi, N.J., 2009. Spatio-temporal variations of the zooplankton abundance and composition in a West African tropical coastal lagoon (Grand–Lahou, Cote d'Ivoire). Hydrobiologia 624, 171–189.

Fockedey, N., Mees, J., 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. J. Mar. Syst. 22, 207–228.

Gamito, S., Gilabert, S., Marcos, C., Pérez-Ruzafa, A., 2005. Effects of changing environmental conditions on lagoon ecology. In: Gönenç, I.E., Wolflin, J.P. (Eds.), Coastal Lagoons: Ecosystem Processes and Modeling for Sustainable Use and Development. CRC Press, Boca Ratón, Florida, pp. 193–229.

Ghosh A.K., 2002. Integrated management strategy for Chilika. In: Chilika Development Authority and Department of Water Resources (Orissa) (Eds.). Proceedings of the International Workshop in Sustainable Development of Chilika Lagoon 12–14th December 1998, Bhubaneswar, 2002, pp. 274–280.

Ghosh, A.K., Pattnaik, A.K., Ballatore, T.J., 2006. Chilika lagoon: restoring ecological balance and livelihoods through re-salinization. Lakes Reserv. Res. Manag. 11, 239–255.

Gotsis-Skretas, O., Satsmadjis, J., 1990. Notes on the environmental response of phytoplankton in Greek lagoons. Obelia 14, 99–115.

Grasshoff K., Kremling K., Ehrhardt M., 1999. Method of sea water analysis. Third completely revised and extended edition-Weinheim, New york, Chiester.

Gupta, G.V.M., Sarma, V.V.S.S., Robin, R.S., Raman, A.V., Jai Kumar, M., Rakhesh, M., Subramanian, B.R., 2008. Influence of net ecosystem metabolism in transferring riverine organic carbon to atmospheric CO2 in a tropical coastal lagoon (Chilka Lake, India). Biogeochemistry 87, 265–285.

Horváth, Z., Vad, C.F., Tóth, A., Zsuga, K., Boros, E., Vörös, L., Ptacnik, R., 2014. Opposing patterns of zooplankton diversity and functioning along a natural stress gradient: when the going gets tough, the tough get going. Oikos 123 (4), 461–471.
Hsu, P.K., Lo, W.T., Shih, C.T., 2008. The coupling of copepod assemblages and hydrography in a eutrophic lagoon in Taiwan: seasonal and spatial variations. Zool. Stud. 47, 172–184.
ICES, 2000. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), Zooplankton Methodology Manual. Academic Press, California, USA, p. 684.
Jeppesen, E., Søndergaard, M., Kanstrup, E., Petersen, B., Henriksen, R.B., Hammershøj, M., Mortensen, E., Jensen, J.P., Have, A., 1994. Does the impact of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia 275–276, 15–30.
Jeppesen, E., Søndergaard, M., Pedersen, A.R., Jürgens, K., Strzelczak, A., Lauridsen, T.L., Johansson, L.S., 2007. Salinity induced regime shift in shallow brackish lagoons. Ecosystems 10, 47–57.
Kar, D., 2013. Wetlands and Lakes of the World. Springer, India, pp. 289–434.
Kasturirangan, L.R., 1963. A Key for the Identification of the More Common Plankonic Copepoda, of Indian Coastal Waters, Vol. 2. Publications of Council of Scientific Industrial Research, India, pp. 1–87.
Kennish, K.J., Paerl, H.W., 2010. Critical habitats of environmental change. In: Kennish, K.J., Paerl, H.W. (Eds.), Coastal Lagoons—Critical Habitats of Environmental Change. CRC Press, Taylor and Francis Group, pp. 1–16.
Kiørboe, T., Nielsen, T.G., 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. I. Copepods. Limnol. Oceanogr. 39, 493–507.
Kouassi, E., Pagano, M., Saint-Jean, L., Sorbe, J.C., 2006. Diel vertical migrations and feeding behavior of the mysid *Rhopalophthalmus africana* (Crustacea: Mysidacea) in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuar. Coast. Shelf Sci. 67, 355–368.
Kozlowsky-Suzuki, B., Bozelli, R.L., 2004. Resilience of a zooplankton community subjected to marine intrusion in a tropical coastal lagoon. Hydrobiologia 522, 165–177.
Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. In: Sage University Paper Series on Quantitative Applications in the Social Sciences, vol. 07–011. Sage Publications, Newbury Park.
Kumar, R., Pattnaik, A.K., 2010. Integrated planning management for Chilika Lake. Chilika Newslett. 5, 1–12.
Lesutien, E.J., Gorokhova, E., Gasi unaite, Z.R., Razinkovas, A., 2007. Isotopic evidence for zooplankton as an important food source for the mysid *Paramysis lacustris* in the Curonian lagon, the South-Eastern Baltic Sea. Estuar. Coast. Shelf Sci. 73, 73–80.
Lopez-Flores, R., Boix, D., Badosa, A., Brucet, S., Quintana, X.D., 2006a. Pigment composition and size distribution of phytoplankton in a confined Mediterranean salt marsh ecosystem. Mar. Biol. 149, 1313–1324.
Madhu, N.V., Jyothibabu, R., Balachandran, K.K., Honey, U.K., Martin, G.D., Vijay, J.G., Shiyas, C.A., Gupta, G.V.M., Achuthankutty, C.T., 2007. Monsoonal impact on planktonic standing stock and abundance in a tropical estuary (Cochin backwaters, India). Estuar. Coast. Shelf Sci. 73, 54–64.
Madhupratap, M., Venugopal, P., Haridas, P., 1979. Biochemical studies on some tropical estuarine zooplankton species. Indian J. Mar. Sci. 8, 155–158.
Mageed, A.A.A., 2006. Spatio–temporal variations of Zooplankton community in the hypersaline lagoon of Bardawil, North Sinai–Egypt. Egypt. J. Aquat. Res. 32, 168–183.
Mauchline, J., 1980. The biology of the euphausiids. Adv. Mar. Biol. 18, 373–623.
McCauley, E., Kalff, J., 1981. Empirical relationships between phytoplankton and zooplankton biomass in Lakes. Can. J. Fish. Aquat. Sci. 38, 458–463.
Mees, J., Jones, M.B., 1997. The hyperbenthos. Oceanogr. Mar. Biol. Ann. Rev. 35, 221–255.
Nabout, J.C., Nogueira, I.S., Oliveira, L.G., Morais, R.R., 2007. Phytoplankton diversity (alpha, beta and gamma) from the Araguaia River tropical floodplain lakes (central Brazil). Hydrobiologia 575, 455–461.
Naik, S., Panigrahy, R., Mohapatra, A., 2008. Spatio-temporal distribution of zooplankton in Chilka lake—A Ramsar site on the Indian east coast. Indian J. Sci. Technol. 1, 1–5.
Newell, G.E., Newell, R.C., 1977. Marine Plankton—A practical Guide. Hutchinson and Co. Publisher, p. 243.
Nixon, S.W., 1995. Coastal marine Eutrophication: A definition, social causes and future concerns. Ophelia 41, 199–219.
Økland, R.H., Eilertsen, O., 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. J. Veg. Sci. 5, 117–126.
Padmavati, G., Goswami, S.C., 1996. Zooplankton ecology in the Mandovi-Zuari estuarine systems of Goa, west coast of India. Indian J. Mar. Sci. 25, 268–273.
Panigrahi, S., Wikner, Johan, Panigrahy, R.C., Satapathy, K.K., Acharya, B.C., 2009. Variability of nutrients and phytoplankton biomass in a shallow brackish water ecosystem (Chilika Lagoon, India). Limnology 10, 73–85.
Patro, S.N., 2001. New challenges to Chilika. In: Proceedings of the 5th Asia Pacific NGOs Environmental Conference APNEC-5 22–25 September 2000 Agra, India, Ed. Indian Environmental Society, Delhi, pp. 229–234.
Pattnaik, A.K., 2002. Chilika Lake-an overview. In: Chilika Development Authority, (Ed.), Proceedings of the International Workshop on Sustainable Development of Chilika Lagoon. Chilika Development Authority, pp. 12–21.
Phlips, E.J., Badylak, S., Grosskopf, T., 2002. Factors affecting the abundance of phytoplankton in a restricted subtropical lagoon, the Indian River Lagoon, Florida, USA. Estuar. Coast. Shelf Sci. 55, 385–402.
Pliŭraitë, V., 2003. Species diversity of zooplankton in the Curonian Lagoon in 2001. Acta Zool. Litu. 13, 106–113.
Rakhesh, M., Raman, A.V., Ganesh, T., Chandramohan, P., Dehairs, F., 2013. Small copepods structuring mesozooplankton community dynamics in a tropical estuary-coastal system. Estuar. Coast. Shelf Sci. 126, 7–22.
Rakhesh, M., Raman, A.V., Kalavati, C., Subramanian, B.R., Sharma, V.S., Sunita Babu, E., Sateesh, N., 2008. Zooplankton community structure arocss an eddy-generated upwelling band close to a tropical bay-mangrove ecosystem. Mar. Biol. 154, 953–972.
Raman A.V., Kalavati C., Prabhakara Rao Y., Srinivasu P.D.N., 2007. Modelling Chilka Lake: An ecosystem approach. Final Report submitted to the Ministry of Earth Sciences, New Delhi. http://www.icmam.gov.in/CHIL pp. 1–150.
Ramdani, M., Elkhiati, N., Flower, R.J., Thompson, J.R., Chouba, L., Kraiem, M.M., Ayache, F., Ahmed, M.H., 2009. Environmental influences on the qualitative and quantitative composition of phytoplankton and zooplankton in North African Coastal Lagoons. Hydrobiologia 622, 113–131.
Rath, J., Adhikary, S.P., 2006. Seasonal variation of phytoplankton in Chilika Lake,east coast of India. Seaweed Res. Utln. 28, 43–48.
Riemann, B., Simonsen, P., Stensgaard, L., 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. J. Plankton Res. 11, 1037–1045.
Röderstein, M., Perdomo, L., Villamil, C., Hauffe, T., Schnetter, M.-L., 2014. Long-term vegetation changes in a tropical coastal lagoon system after interventions in the hydrological conditions. Aquat. Bot. 113, 19–31.
Romo, S., Miracle, M.R., 1995. Diversity of the phytoplankton assemblages of a polymictic hypertrophic lake. Arch. Hydrobiol. 132, 363–384.
Ryan, N.J., Mitrovic, S.M., Bowling, L.C., 2008. Temporal and spatial variability in the phytoplankton community of Myall Lakes, Australia, and influences of salinity. Hydrobiologia 608, 69–86.
Santangelo, J.M., Rocha, A.M., Bozelli, R.L., Carneiro, L.S., Esteves, F.A., 2007. Zooplankton responses to sandbar opening in a tropical eutrophic coastal lagoon. Estuar. Coast. Shelf Sci. 71, 657–668.
Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman and Hall Publishers, London, p. 346.
Setubal, R.B., Santangelo, J.M., de Melo, Rocha A., Bozelli, R.L., 2013. Effects of sandbar openings on the zooplankton community of coastal lagoons with different conservation status. Acta Limnol. Bras. 25, 246–256.
Siegfried, C.A., Kopache, M.E., 1980. Feeding of *Neomysis mercedis* (Holmes). Biol. Bull. 159, 193–205.
Smith, D.L., 1977. A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae. Kendall Hunt Publ. Comp., Dubuque, Iowa, p. 161.
Specchiulli, A., Focardi, S., Renzi, M., Scirocco, T., Cilenti, L., Breber, P., Bastianoni, S., 2008. Environmental heterogeneity patterns and assessment of trophic levels in two Mediterranean lagoons: Orbetello and Varano, Italy. Sci. Total. Environ. 402, 285–298.
Strickland, J.D.H., Parsons, T.R., 1972. A Practical Hand Book of Sea Water Analysis, second ed. In: Bull., vol. 167. Fisheries Research Board of Canada, Ottawa, p. 310.
Suzuki, K.W., Kasai, A., Isoda, T., Nakayama, K., Tanaka, M., 2008. Distinctive stable isotope ratios in important zooplankton species in relation to estuarine salinity gradients: potential tracer of fish migration. Estuar. Coast. Shelf Sci. 78, 541–550.
ter Braak, C.J.F., 1986. Canonical correspondence analysis: a neweigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.
ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. Adv. Ecol. Res. 18, 271–313.
ter Braak C.J.F., Smilauer P., 2002. CANOCO reference manual and Cano Draw for Windows user's guide: software for canonical community ordination (version 4.53). Micro computer Power, Ithaca, New York, USA.
Timms, R.M., Moss, B., 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceangr. 29, 472–486.
Turner, J.T., Roff, J.C., 1993. Trophic levels and trophospecies in marine plankton: lessons from the microbial food web. Mar. Microb. Food Webs 7, 225–248.
Vadrucci, M.R., Semeraro, A., Zaccarelli, N., Basset, N., 2004. Nutrient loading and spatial–temporal dynamics of phytoplankton guilds in a Southern Italian coastal lagoon (Lake Alimini Grande, Otranto, Italy). Chem. Ecol. 20 (Supplement 1), 285–S301.
Vanschoenwinkel, B., Waterkeyn, A., Jocque, M., Boven, L., Seaman, M., Brendonck, L., 2010. Species sorting in space and time-the impact of disturbance regime on community assembly in a temporary pool metacommunity. J. North Am. Benthol. Soc. 29, 1267–1278.
Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D.A., De Wever, A., Juggins, S., de Vijver, B.V., Jones, V.V., Vanormelingen, P., Roberts, D., Flower, R., Kilroy, C., Souffreau, C., Sabbe, K., 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. Oikos 118, 1239–1249.
Vollenweider, R.A., Giovanardi, F., Montanari, G., Rinaldi, A., 1998. Characterization of the trophic conditions of marine coastal waters with special reference to the NW Adriatic Sea: proposal for a trophic scale, turbidity and generalized water quality index. Environmetrics 9, 329–357.
Watanabe, K., Kasai, A., Antonio, E.S., Suzuki, K., Ueno, M., Yamashita, Y., 2014. Influence of salt-wedge intrusion on ecological processes at lower trophic levels in the Yura Estuary, Japan. Estuar. Coast. Shelf Sci. 139, 67–77.
Yamani, , Prusova, , 2003. Common Copepoda of the Northwestern Arabian Gulf: Identification Guide. Kuwait Institute for Scientific Research, pp. 1–162.
Yáñez-Arancibia, A., Day, J.W., Sánchez-Gil, P., Day, J.N., Laneb, R.R., Zárate-Lomelí, D., Vásquez, H.A., Rojas-Galaviz, J.L., Ramírez-Gordilloe, J., 2014. Ecosystem functioning: The basis for restoration and management of a tropical coastal lagoon, Pacific coast of Mexico. Ecol. Eng. 65, 88–100.
Zajac, R.N., Lewis, R.S., Poppe, L.J., Twichell, D.C., Vozarik, J., DiGiacomo-Cohen, M.L., 2003. Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. Limnol. Oceanogr. 48, 829–842.
Zhong, Zheng, 1989. Marine Planktonology. China Ocean Press Publications, p. 454.