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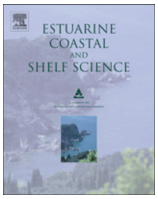

Contrasting effects of managed opening regimes on water quality in two intermittently closed and open coastal lakes

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ABSTRACT

Intermittently closed and open lakes and lagoons (ICOLLs) are shallow barrier lakes which are intermittently connected to the sea and experience saline intrusions. Many ICOLLs are mechanically opened to prevent flooding of surrounding agricultural and urban land and to flush water of poor quality. In this study, the effects of modified opening regimes (frequency and duration of barrier openings and closures) on water quality and phytoplankton in two New Zealand ICOLLs were investigated over a number of opening/closure cycles. Water quality in Lake Ellesmere (Te Waihora) responded weakly to both opening and closing events, indicating that sea–ICOLL exchange did not markedly improve water quality. Conversely, water quality in Waituna Lagoon responded rapidly to barrier openings; water level decreased to near sea level within days of opening and subsequent seawater exchange resulted in rapid decreases in nitrate and chlorophyll *a* concentrations. The closure of Waituna Lagoon resulted in rapid rise in water level and a pulse of nitrate and phosphorus in the water column and phytoplankton chlorophyll *a* concentrations increased with increasing closed-period duration. Based on data on the underwater light climate and nutrient dynamics, phytoplankton in Lake Ellesmere was probably light-limited, whereas phytoplankton in Waituna Lagoon was rarely light-limited, and appeared to be predominately P-limited. The marked differences in responses of Lake Ellesmere and Waituna Lagoon to barrier openings and closures reflected differences in ICOLL water levels and morphological characteristics, which dictated the degree of tidal flushing when the barriers were open. The inter-ICOLL differences observed in this study indicate that unless the effects of ICOLL openings/closures on phytoplankton and nutrient dynamics are understood, changes to ICOLL opening regimes may have unintended consequences for the water quality and ecology of these systems.

1. Introduction

The biology and biogeochemistry of estuaries with permanent openings to the sea have been investigated for nearly two centuries (McLusky and Elliott, 2004), yet far less research effort has been devoted to estuaries with intermittent connections to the ocean like those common to arid, semi-arid and sub-humid coastlines. Many of these estuaries (sometimes termed intermittently closed and open lakes and lagoons or ICOLLs; Roy et al., 2001), have been degraded by eutrophication and declining river inflows (Doody, 2001). ICOLLs are characterized as barrier estuaries with shallow embayments, moderate to low river inflows relative to volume, and high rates of long-shore and/or on-shore sediment transport (Ranasinghe et al., 1999; Kirk and Lauder, 2000; Roy et al., 2001; Haines et al., 2006). River inflow to ICOLLs is insufficient to maintain permanent openings resulting in the closure of seaward margins for months to years. During closed periods, freshwater inputs from rivers, groundwater and rainfall create brackish or freshwater lakes, with natural openings resulting either from rising lake levels overtopping and subsequently eroding barriers or through erosion by ocean waves (Stretch and Parkinson, 2006). Openings facilitate lake water outflow and tidal sea–ICOLL exchange until re-closure by sediment deposition into the openings.

Under natural conditions, alternating inundation and exposure of large areas of fringing wetland occurs as a result of the opening

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regime. In many ICOLLs, artificial opening regimes are employed to facilitate agriculture by maintaining low water levels (Gale et al., 2006; Haines et al., 2006). As a result, agricultural land has claimed the wetland margins of many ICOLLs (Kirk and Lauder, 2000; Haines et al., 2006). Such agricultural development around ICOLLs increases nutrient loading (Gerbeaux, 1993; Twomey and Thompson, 2001; Qu et al., 2003), leading to eutrophication, the loss or reduction of macrophyte beds, and the destabilization of lake bed sediments (Nienhuis, 1992; Gerbeaux, 1993; Qu et al., 2003). Artificially increasing the frequency and/or duration of barrier openings has been carried out in some ICOLLs to attempt to alleviate eutrophication by facilitating flushing and sea–ICOLL exchange (e.g. Suzuki et al., 1998; Roy et al., 2001). However, in some ICOLLs increasing the frequency of opening led to unintended ecological consequences such as nutrient enrichment (dos Santos et al., 2006), macrophyte die-offs, (dos Santos and Esteves, 2002) and increased chlorophyll *a* concentrations (Twomey and Thompson, 2001; Gobler et al., 2005). Therefore, while agricultural encroachment and intensification within the catchment encourages more frequent artificial ICOLL openings, the relationship between opening regimes and eutrophication may depend on multiple factors specific to each ICOLL. ICOLLs embody a variety of intrinsic values and ecosystems services and an understanding of how opening regimes affect these is important for ICOLL conservation, management and restoration.

In this study, we compared the timing and duration of barrier openings and closures of two New Zealand ICOLLs, Lake Ellesmere (Te Waihora) and Waituna Lagoon. While hydrological and water quality data are available for both, relationships between opening regimes, inflows, turbidity, nutrient levels and phytoplankton is rudimentary. We compared the degrees of flushing and sea–ICOLL exchange facilitated by openings and examined the effects of opening regimes on light and nutrient availability, factors that may limit phytoplankton and macrophyte growth. Finally, we compare the water quality responses of barrier openings/closures in our study with those from South America, Australia and the USA.

2. Materials and methods

2.1. Study sites

Lake Ellesmere and Waituna Lagoon occupy depressions between alluvial fans on the east and south coasts of New Zealand's South Island (Fig. 1; Table 1). These microtidal coasts (<2 m amplitude) are characterized by substantial long-shore drift associated with the north-flowing Canterbury and Southland Currents, moderate wave energy and high rates of gravel supply to the coast from rivers draining the Southern Alps and foothills (Kirk and Lauder, 2000). These conditions result in the rapid formation of coastal berms above the high tide level.

The current opening prescriptions at Lake Ellesmere and Waituna Lagoon are based on water surface elevations: Lake Ellesmere is opened when the water level near the barrier reaches 1.05 m above mean sea level (a.s.l.) (August–March), or 1.13 m a.s.l. (March–August), while Waituna Lagoon is opened when the water level reaches 1.69 m a.s.l. in the eastern arm of the lagoon (Table 1). Mean sea level at Waituna Lagoon was calculated as the mean water level during open periods excluding data from the first 7 days after opening the ICOLL (Schallenberg and Tyrrell, 2006). Waituna Lagoon was recently re-surveyed and the trigger level was revised to 2.008 m a.s.l. (C. Jenkins, Environment Southland, unpubl. data), a difference of +318 mm relative to the earlier trigger level estimate used in this study.

Lake Ellesmere and Waituna Lagoon are windswept polymictic ICOLLs in which temporary horizontal and vertical density stratification occur near barrier openings due to saline intrusions. Based on the trophic classification of Burns et al. (1999, 2000), Lake Ellesmere is hyper-eutrophic, while Waituna Lagoon is meso-eutrophic. Water quality in Lake Ellesmere has been monitored by the Canterbury environmental management authority (Environment Canterbury) monthly since 1992, while water quality in Waituna Lagoon has been monitored by Environment Southland monthly since 2001.

Prior to 1968, macrophyte beds consisting of *Ruppia megacarpa*, *Potamogeton pectinatus* and *Lepiliana bilocularis* were reported on the margins of Lake Ellesmere, where water clarity was noticeably greater than in the middle of the lake. The extent of macrophyte beds fluctuated until 1968, when they were nearly eliminated, coincident with a severe storm (Hughes et al., 1974; Gerbeaux, 1993). The macrophyte beds have not recovered since that time and now only isolated plants are found in some sheltered bays. Since the loss of substantial macrophyte beds 41 years ago, turbidity and phytoplankton biomass in Lake Ellesmere have remained high (Taylor, 1996), conditions which have been attributed to the loss of macrophyte beds and to increasing nutrient loading from the surrounding catchment (Gerbeaux, 1993; Taylor, 1996).

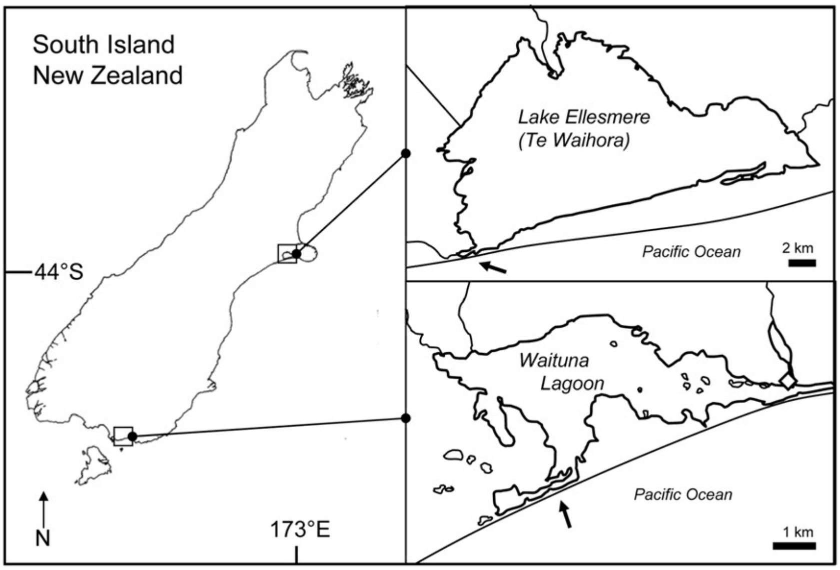

Fig. 1. Map showing locations of Waituna Lagoon and Lake Ellesmere. Arrows show current locations of barrier breaches.

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Table 1
Physical and hydrological characteristic of Lake Ellesmere and Waituna Lagoon. m a.s.l. indicates water levels in metre above mean sea level. Mean sea level at Waituna Lagoon was calculated as the mean water level during open periods excluding data from the first 7 days after opening the ICOLL (Schallenberg and Tyrrell, 2006).

	Lake Ellesmere	Waituna Lagoon
Latitude/Longitude	43° 47′ S/172° 28′ E	46° 33′ S/168° 35′ E
Trigger level (m a.s.l.)	1.05 (1 Aug–31 Mar) 1.13 (1 April–31 July)	1.69[a]
Maximum (mean) depth when open (m a.s.l.)	1.9 (0.77)	1.6 (0.66)
Maximum (mean) depth at trigger level (m)	2.95 or 3.03 (1.41 or 0.77)	3.29 (1.59)
Area when open (km^2)	144.6	7.21
Area at trigger level (km^2)	213 (at 1.13 m a.s.l.)	16.34
Volume when open (m^3)	111.1×10^6	4.77×10^6
Volume at trigger level (m^3)	301.4×10^6	26.06×10^6
Mean annual water input from catchment (m^3)	3.9×10^8	1.2×10^8
Catchment land area (km^2)	2500	210
Water residence time based on freshwater inflows (d)	104	14.5
Entrance closure index	0.82 (1983–2007)	0.46 (1983–2007[b])

[a] Re-surveyed by Environment Southland in 2006: new trigger level is 2.008 m above mean sea level.
[b] Data from 10 October 2000 to 10 June 2002 were not available.

In contrast to Lake Ellesmere, macrophyte beds dominated by *Ruppia megacarpa*, *Ruppia polycarpa* and *Myriophyllum triphyllum* often develop in Waituna Lagoon during periods when the ICOLL is closed and salinity, temperature and irradiance are favourable for growth (Johnson and Partridge, 1998; Schallenberg and Tyrrell, 2006). Increasing nutrient runoff from agricultural intensification in the Waituna Lagoon catchment has been linked to increases in phytoplankton biomass and turbidity in the ICOLL, which may pose a threat to the macrophyte beds (Schallenberg and Tyrrell, 2006).

2.2. *Data compilation and analysis*

A hypsographic curve for Lake Ellesmere was constructed using lagoon areas and water level data from Environment Canterbury for elevations >0.3 m a.s.l. (D. Ayres, Environment Canterbury, unpubl. data collected in 1998), and the bathymetric chart of Irwin and Main (1989). A hypsographic curve for Waituna Lagoon was constructed using bathymetric data provided by Environment Southland, corrected to mean sea level datum (C. Jenkins, Environment Southland, unpubl. data collected in 2001).

Water quality, phytoplankton data and dates of barrier openings and closures were obtained from Environment Canterbury and Environment Southland (Table 2). Water quality and phytoplankton data were from samples collected at mid-basin stations for both ICOLLs. Solute and phytoplankton chlorophyll *a* concentrations that were below analytical detection limits were replaced with values of 0.5 × detection limit. Water quality data were available for periods comprising 76 and 4 opening/closure cycles for Lake Ellesmere and Waituna Lagoon, respectively. All barrier breaches at Lake Ellesmere and Waituna Lagoon during the study periods were human induced (artificially breached using heavy machinery). All data were screened for accuracy and consistency before analysis.

Rates of nutrient loading from ICOLL tributaries were estimated as the products of nutrient concentrations and tributary flow rates measured on each sampling date. Although Lake Ellesmere has 14 main tributaries, nutrient and flow rate data were available for eight of the tributaries at monthly intervals since 1996 (≥145 sampling dates for each tributary), accounting for around 85% of the tributary N and P inputs (S. Larned, unpubl. data). Similarly, while Waituna Lagoon has 11 tributaries, nutrient and flow rate data were available for the three largest tributaries at monthly intervals since 2001 (≥75 sampling dates for each tributary); however the hydrology of Waituna Lagoon is less well understood and the proportion of the total hydrological input accounted for is unknown. For both systems, the nutrient data consist of total N (TN), total P (TP), dissolved reactive P (DRP), ammonium, nitrate + nitrite (hereafter referred to as nitrate) and dissolved inorganic N (DIN) concentrations. To assess relationships between nutrient loading vs. ICOLL phytoplankton dynamics, average loading rates ($mg\,N\,s^{-1}$ or $mg\,P\,s^{-1}$) and phytoplankton chlorophyll *a* concentrations ($\mu g\,L^{-1}$) were calculated for each season in each year of record. Seasonal averaging was used in lieu of a fixed lag time between nutrient input and phytoplankton response. Average loading rates were summed across tributaries to minimize spatial variability and provide an index of whole-lake nutrient loading. Nevertheless, these indices underestimated whole-lake nutrient loads because they did not include inputs from small unmonitored tributaries, groundwater seepage, direct atmospheric deposition, cyanobacterial N fixation, or bird feces. Nutrient input stoichiometries (DIN:DRP, TN:TP, and DIN:TP ratios) were derived from loading rates.

Table 2
Data sources and periods of record.

Lake Ellesmere	Time period	Source
Hypsographic data	1988	Irwin and Main (1989)
Opening/closing dates and durations	June 1983–August 2005	Environment Canterbury
Physico-chemical data	November 1983–May 2005	Environment Canterbury
Tributary flow and chemical data	February 1996–October 2006	Environment Canterbury
Waituna Lagoon		
Hypsographic data	Aug. 2001 and Oct. 2001	Environment Southland
Opening/closing dates and durations	May 1975–June 2006 (missing data: 14 October 2000–10 Jun 2002)	Environment Southland
Physico-chemical data	August 2003–August 2007	Environment Southland
Tributary flow and chemical data	August 2001–September 2007	Environment Southland

The potential effects of nutrient availability on phytoplankton growth were estimated using nutrient concentrations from mid-lake stations in Lake Ellesmere and Waituna Lagoon, and nutrient loading rates from their tributaries. We used Ln(DIN:TP) as an indicator of the form and severity of nutrient limitation as this index appears to be a more accurate predictor of nutrient limitation than the more commonly applied DIN:DRP and TN:TP ratios (Morris and Lewis, 1988; Schallenberg, unpubl. data). Nutrient limitation assays from lakes representing a broad range of trophic levels indicate that states of N- and P-limitation can be accurately distinguished by the threshold: Ln(DIN:TP) ≈ 0, or DIN:TP ≈ 1 (Morris and Lewis, 1988; Downs et al., 2008; Schallenberg and Lill, submitted for publication). We used a threshold Ln(DIN:TP) value of zero and 95% confidence intervals (Schallenberg, unpubl. data) for our inference of nutrient limitation status.

Depth profiles of photosynthetically active radiation (PAR) were obtained using a LI-COR LI-1000 underwater light meter and a LI-192SA 2π underwater PAR sensor.

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2.3. Statistical analyses

Data were ln-transformed as necessary to meet assumptions of ANOVA, correlations, regression, and principle components analysis (PCA). Pearson correlation and least-squares linear regression was used to test the significance of univariate relationships between water quality, salinity and durations of open and closed periods. Where trends in means, minima or maxima were evident, curves were fitted to the graphs by eye for the purpose of trend illustration. PCA, based on the correlation matrix, was used to identify multivariate relationships between water quality variables and environmental variables, including ICOLL barrier state (open or closed). One-way ANOVAs were used to compare water quality variables during open or closed periods. Within-group homogeneity of variance was tested with Bartlett's tests. ANOVAs, Bartlett's tests and linear regressions were run using SYSTAT (Wilkinson, 1991) and PCAs were run using CANOCO Version 4 (ter Braak and Smilauer, 1998).

3. Results

3.1. Description and comparison of opening regimes

For the period 1983–2007, Lake Ellesmere and Waituna Lagoon were closed to the sea 82% and 46% of the time, respectively (Table 1). Openings at Lake Ellesmere were generally shorter than 40 days and never exceeded 120 days, whereas durations of openings at Waituna Lagoon were more variable, with most exceeding >120 days (Fig. 2A, B). The higher frequency of short openings at Lake Ellesmere suggests faster gravel accretion in the barrier opening at Lake Ellesmere than at Waituna Lagoon, necessitating more frequent re-openings. Most openings of both ICOLLs occurred in winter and spring, when runoff tends to be greater.

3.2. Sea–ICOLL exchange and flushing

The salinity range in Lake Ellesmere was moderate (2.3–14.2) in comparison to Waituna Lagoon (0.7–33.6; Table 3). Bivariate mixing diagrams, based on relationships between water quality variables and salinity, indicated that none of the water quality variables tested was clearly related to salinity in Lake Ellesmere (Fig. 3). In contrast, chlorophyll *a* concentrations in Waituna Lagoon decreased non-linearly with increasing salinity, and DIN concentrations peaked at salinities of 5–10, and decreased markedly at higher salinities (Fig. 3B, F). The mixing diagrams indicate that sea–ICOLL exchange reduced DIN and chlorophyll *a* levels in Waituna Lagoon, however, the non-linear relationships suggest complex dilution dynamics.

3.3. Effects of open and closed states on water quality

PCAs were used to examine relationships between opening regimes and water quality in Lake Ellesmere and Waituna Lagoon. For Lake Ellesmere, the primary PCA axis explained 27% of the variance and represented a gradient related to total suspended solids, chlorophyll *a*, TN, and TP concentrations (Fig. 4A). Coding samples by open

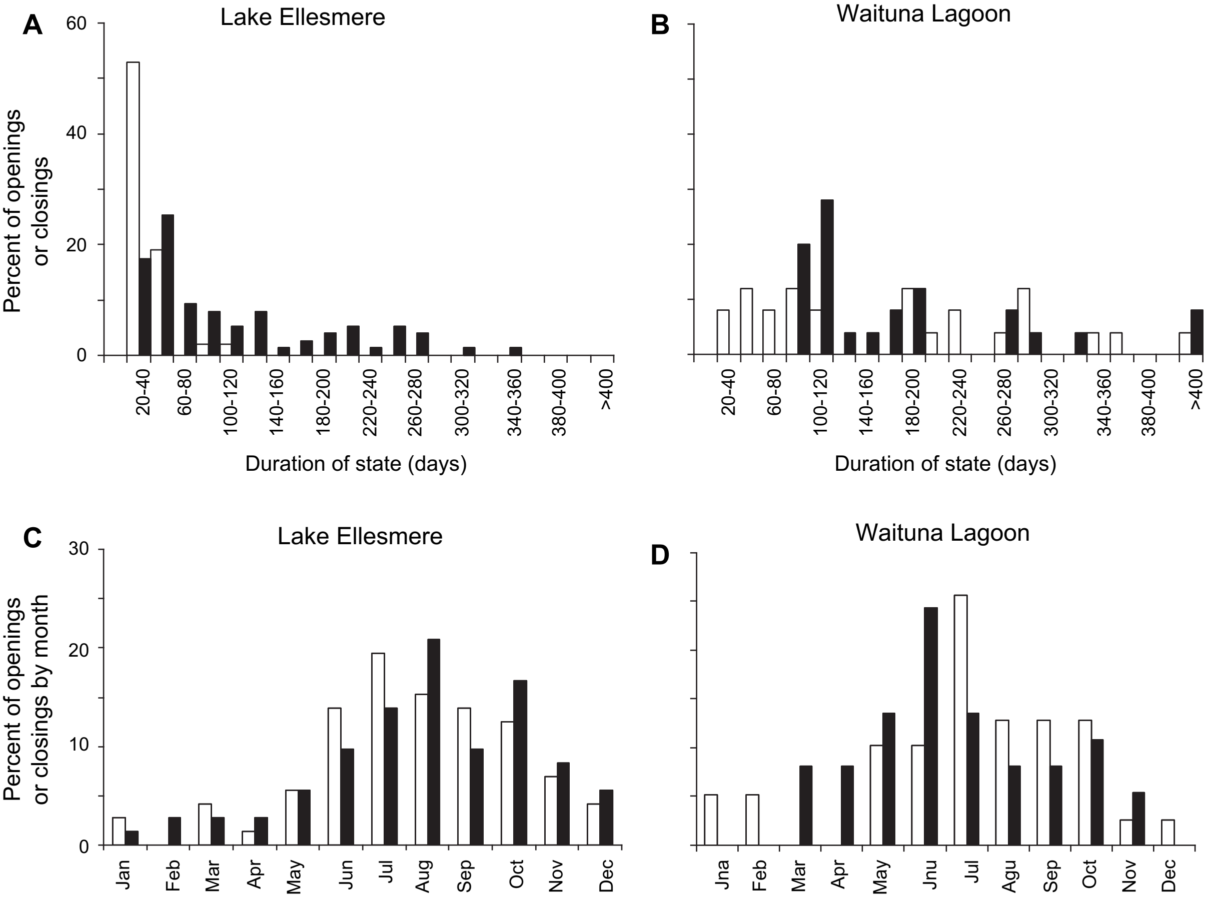

Fig. 2. Data showing the opening regimes of Lake Ellesmere (A, C) and Waituna Lagoon (B, D). Panels A and B: percentages of open (white bars) and closed (black bars) periods versus duration. Panels C and D: percentages of opening (white bars) and closure (black bars) events by month.

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Table 3
Mean physico-chemical conditions in Lake Ellesmere (June 1993–May 2005) and Waituna Lagoon (August 2003–August 2007). Ranges are in parentheses. N/A: not available.

	Lake Ellesmere	Waituna Lagoon
Ammonium N ($mg\,l^{-1}$)	0.029 (0.003–0.220)	0.021 (0.005–0.090)
Nitrate N ($mg\,l^{-1}$)	0.062 (0.005–1.000)	0.29 (0.005–1.500)
Dissolved inorganic N ($mg\,l^{-1}$)	0.092 (0.008–1.012)	0.301 (0.005–1.512)
Total N ($mg\,l^{-1}$)	2.296 (0.200–7.500)	0.77 (0.100–2.300)
Dissolved reactive P ($mg\,l^{-1}$)	0.007 (0.002–0.058)	0.017 (0.003–0.150)
Total P ($mg\,l^{-1}$)	0.277 (0.013–0.900)	0.040 (0.005–0.190)
Ln(DIN:TP)	−1.5 (−3.5 to 2.7)	1.3 (−1.4 to 3.6)
Chlorophyll *a* ($\mu g\,l^{-1}$)	88.4 (6.0–221.0)	5.2 (0.5–37)
Salinity	7.0 (2.3–14.2)	16.8 (0.7–33.6)
pH	8.29 (7.90–8.70)[a]	7.74 (6.8–8.3)
Turbidity (NTU)	N/A	6.7 (2.4–27)
Total suspended solids ($mg\,l^{-1}$)	229.7 (44.0–700.0)	N/A
Temperature (°C)	12.5 (4.3–22.1)	11.1 (4.9–20.5)
Euphotic depth (m)	0.31[b]	1.74[b]

[a] 1983–1992.

[b] Measured on 8 April 2004 at Lake Ellesmere, and 25 June 2006 at Waituna Lagoon.

vs. closed state indicated that, while open periods were characterized by slightly reduced total suspended solids and nutrient concentrations, there was substantial overlap between open and closed states along the first PCA axis. Mean DRP, TN and total suspended solids concentrations were significantly higher when the ICOLL was closed (ANOVA; $P = 0.006$ for DRP, $P = 0.05$ for TN, and $P = 0.021$ for total suspended solids). DIN concentration loaded strongly on PCA axis 2 but was not significantly related to ICOLL openings/closures ($P > 0.05$).

In contrast to the ordination for Lake Ellesmere, open and closed periods in Waituna Lagoon were clearly separated by the first PCA axis, which explained 45% of the total variation in the variables and represented a gradient related to water level, salinity, pH, and concentrations of DIN and TN (Fig. 4B). Mean chlorophyll *a*, DIN, nitrate and TN concentrations were significantly higher during closed periods (ANOVA; $P = 0.001$ for chlorophyll *a*, $P < 0.0001$, for DIN, $P = 0.001$ for nitrate and $P < 0.0001$ for TN), and mean salinity and pH were significantly higher during open periods ($P < 0.0001$ for both salinity and pH).

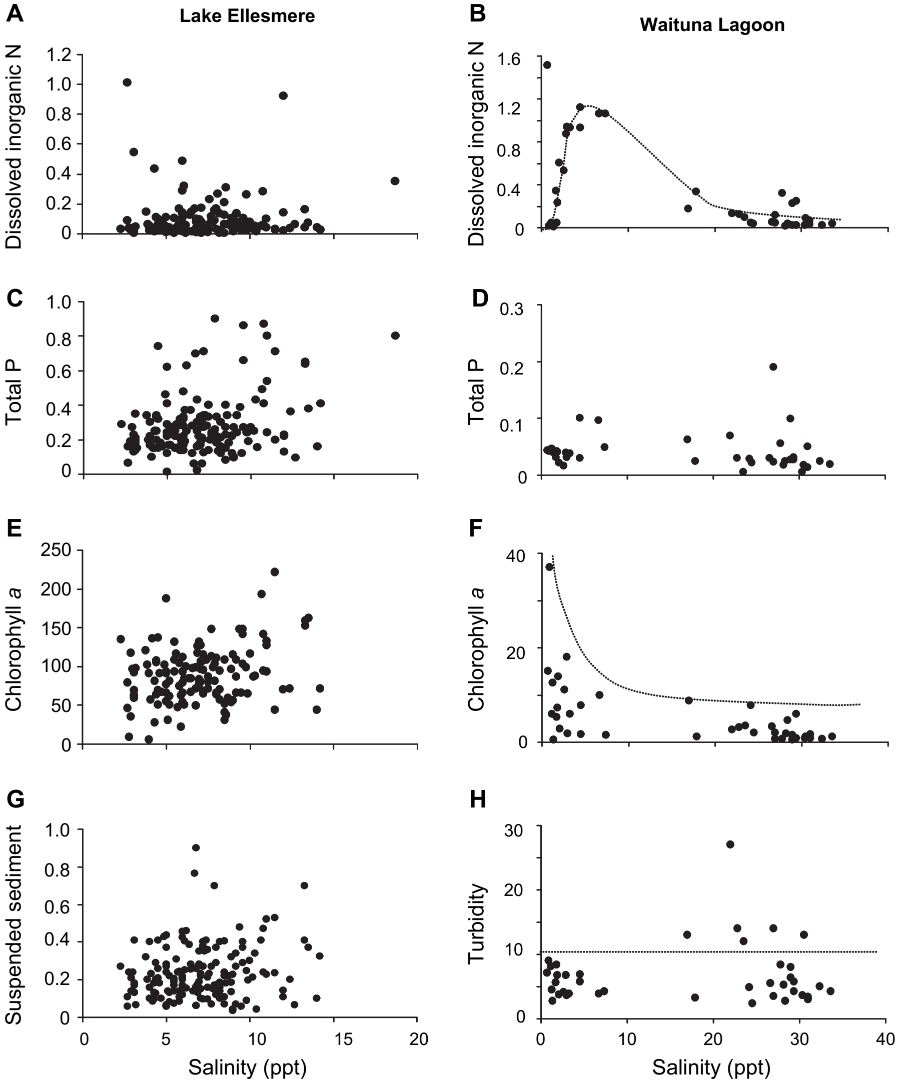

Fig. 3. Mixing diagrams for selected water variables. Lines fitted by eye are indicative of relationships, constraining functions, or thresholds. Units: nutrients – $mg\,l^{-1}$, suspended sediment – $g\,l^{-1}$, turbidity – nephelometric turbidity units, chlorophyll *a* – $\mu g\,l^{-1}$.

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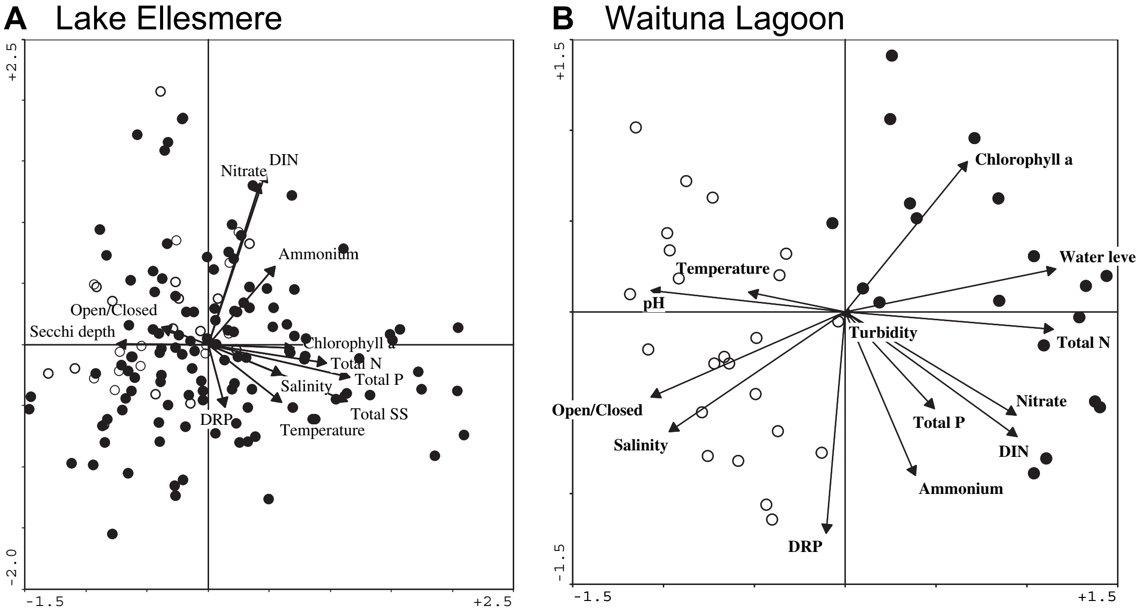

Fig. 4. PCA of water quality variables for Lake Ellesmere (A) and Waituna Lagoon (B). In A, Axes 1 and 2 explained 27% and 17% of the total variance, respectively. In B, Axes 1 and 2 explained 45% and 14% of the total variance, respectively. Open circles: samples collected during open periods. Solid circles: samples collected during closed periods.

3.4. *Effects of duration of closures and openings on water quality*

Long-term closures reduced the maximum salinity, nitrate and TP concentrations in both ICOLLs, while chlorophyll *a* concentrations increased in Waituna Lagoon but became more variable in Lake Ellesmere (Fig. 5). In Waituna Lagoon, nitrate and TP concentrations increased sharply in the first 50 days after closure, declining only during longer closed periods (Fig. 5F, H). The decrease in water level in Waituna Lagoon after closed periods of >50 days suggests that there was substantial outward seepage of ICOLL water through the barrier when water levels exceeded 0.8 m a.s.l. (Fig. 5B). While a seepage loss of 18% has been calculated for Lake Ellesmere (G.A. Horrell, Environment Canterbury, unpublished data), this was not apparent from the water level data in our study (Fig. 5A).

During open periods in Lake Ellesmere, salinity increased at an average rate of 1.6 d^{-1} ($R^2 = 0.64$, $P < 0.001$; Fig. 6C), while maximum chlorophyll *a* concentrations appeared to decrease after long open periods (Fig. 6I). No other effects of open-period duration on water quality were apparent. Both flushing and subsequent sea–ICOLL exchange were greater in Waituna Lagoon. During open periods, the water level dropped to near sea level within 11 days (first post-opening sampling) of opening (Fig. 6B) and tidal flushing caused salinity to increase and nitrate and chlorophyll *a* concentrations to decrease rapidly; thereafter, their concentrations remained relatively stable until the ICOLL closed (Fig. 6D, F, J).

3.5. *Controls on phytoplankton growth*

Chlorophyll *a* concentrations in Lake Ellesmere were positively correlated with TN ($r = 0.44$, $P < 0.0001$) and TP ($r = 0.37$, $P < 0.0001$) concentrations, suggesting that phytoplankton comprised a relatively constant proportion of the TN and TP pools. In Waituna Lagoon, chlorophyll *a* concentrations were positively correlated with TN concentration ($r = 0.52$, $P < 0.0001$) and negatively correlated with DRP concentrations ($r = -0.32$, $P = 0.037$). Mean Ln(DIN:TP) values at mid-lake stations were −1.5 in Lake Ellesmere and 1.3 in Waituna Lagoon, indicating that, in the absence of other growth limiting factors, Lake Ellesmere phytoplankton would have been N-limited, and Waituna Lagoon phytoplankton would have been P-limited (Table 3).

Mean tributary Ln(DIN:TP) values in Waituna Lagoon were 1.6 when based on concentrations and 3.1 when based on loading rates (Table 4). In contrast, mean Ln(DIN:TP) values for Lake Ellesmere tributaries were 4.2 based on concentrations and 4.3 based on loading rates, indicating extremely high loadings of available N in relation to P. For both ICOLLs, DIN:DRP, TN:TP, and Ln(DIN:TP) ratios in tributary loadings were higher than in the ICOLL water column, suggesting that N inputs were lost from the water column at a faster rate than P inputs. The very large decrease in Ln(DIN:TP) from 3.8 in Lake Ellesmere tributaries to −1.5 mid-lake site was due to a 30-fold reduction in DIN concentrations and a 5-fold increase in TP concentration in the ICOLL, compared to the tributary loadings (Tables 3, 4).

Phytoplankton chlorophyll *a* concentrations in Lake Ellesmere increased linearly with tributary DRP loading, based on annual averages from 1996 to 2007 ($R^2 = 0.34$, $P = 0.04$), but no other relationships between seasonal or average annual chlorophyll *a* concentrations and nutrient loading rates or stoichiometry were significant. Similarly, no statistical relationships between ICOLL chlorophyll *a* concentration and nutrient loadings were detected in the shorter Waituna Lagoon dataset (2001–2007).

In both ICOLLs, turbidity peaks occurred during high wind events. Secchi depth in Lake Ellesmere was <0.5 m, except during extended periods of calm weather. Waituna Lagoon generally had higher Secchi depths (>1.0 m) and lower inorganic suspended sediment concentrations than Lake Ellesmere. Assuming that the light profile obtained from each ICOLL was indicative of general water clarity in the ICOLL, the ratio of maximum depth:euphotic depth (Z_{mix}:Z_{eu}) was 6.2–9.7 in Lake Ellesmere compared to 0.9–1.9 in Waituna Lagoon (ranges account for water level variation).

4. Discussion

4.1. *Effect of opening regime on tidal flushing*

Eutrophication has affected ICOLLs, estuaries and coastal lakes, world-wide (Cloern, 2001; Boesch, 2002). A survey of ICOLL case

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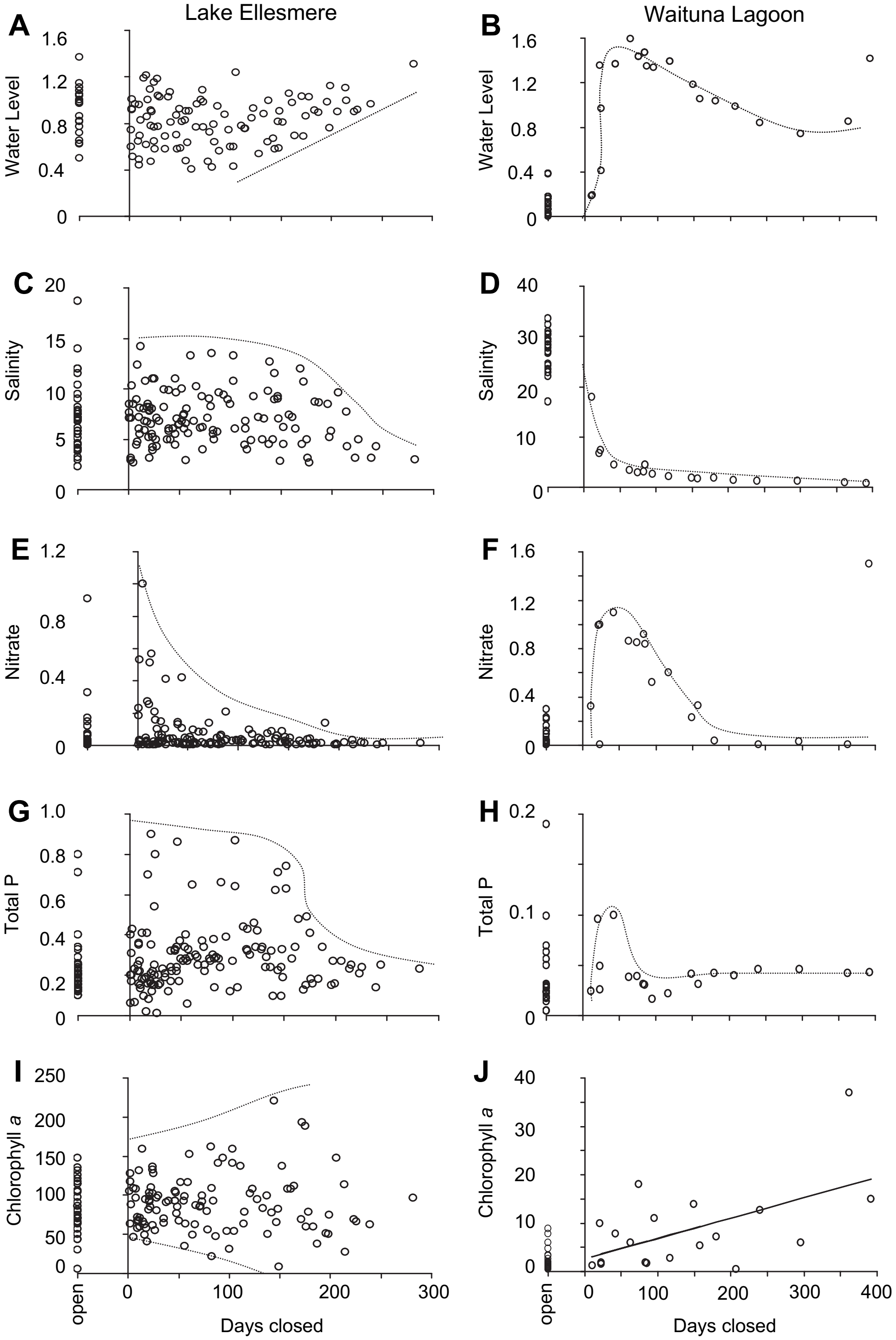

Fig. 5. Relationships between physical and chemical variables and duration of closed periods. Points to the left of the *y*-axes indicate samples collected during open periods. The line in J was fitted by least-squares linear regression ($R^2 = 0.32$; $P = 0.012$). Other lines were fitted by eye and are indicative of relationships, constraining functions, and thresholds. Samples on Day 362 in Waituna Lagoon were collected after a large flood on 29 June 2007, which triggered a barrier opening. Data for Lake Ellesmere and Waituna Lagoon represent 76 and 4 closed periods, respectively. Units: water level – m a.s.l., salinity – no units, nutrients – mg l^{-1}, suspended sediment – g l^{-1}, turbidity – nephelometric turbidity units, chlorophyll *a* – μg l^{-1}.

studies indicated that attempts to alleviate eutrophication by artificial openings often resulted in either minor improvements or deteriorations in water quality, but rarely in substantial improvements. For example, artificial openings of Brazilian ICOLLs resulted in substantial nutrient enrichment of the water column due to the exposure, mortality and decomposition of previously submerged vegetation (e.g., dos Santos and Esteves, 2002; dos Santos et al., 2006). The artificial opening of an ICOLL in the USA resulted in increased chlorophyll *a* concentrations which then peaked within weeks of ICOLL re-closure, while chlorophyll *a* concentrations in the adjacent coastal ocean were consistently lower than those in the ICOLL (Gobler et al., 2005). This dynamic was attributed to an influx of seawater with elevated DRP and DIN concentrations. Chlorophyll *a* concentrations also increased during open periods in

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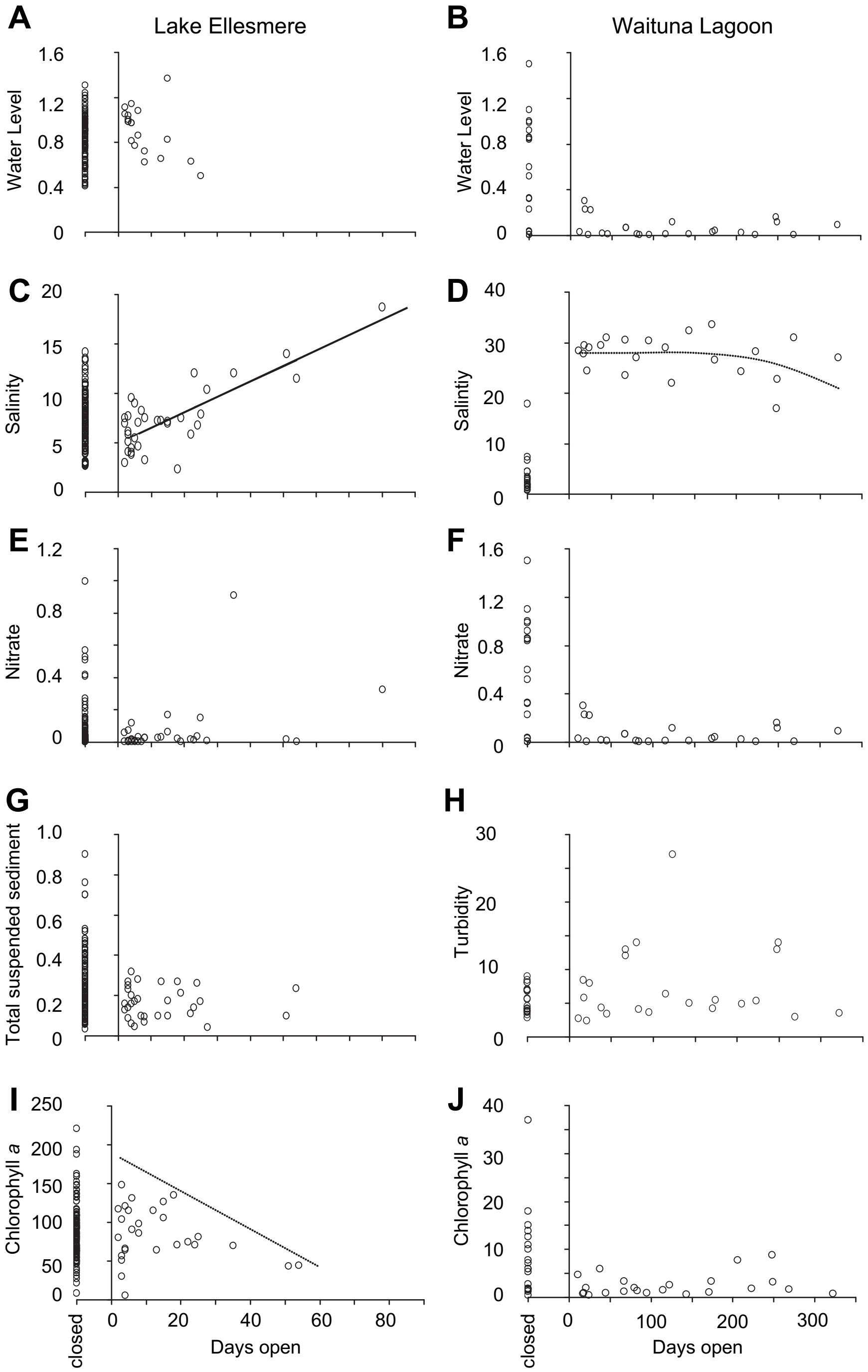

Fig. 6. Relationships between physical and chemical variables and duration of open periods. Points to the left of the *y*-axes indicate *y*-axis values when the ICOLLs were closed. The line in C, was fitted by least-squares linear regression ($R^2 = 0.64$; $P < 0.0001$). Other lines were fitted by eye and are indicative of relationships, constraining functions, and thresholds. Data for Lake Ellesmere and Waituna Lagoon represent 76 and 4 open periods, respectively. Units: water level – m a.s.l., salinity – no units, nutrients – mg l^{-1}, suspended sediment – g l^{-1}, turbidity – nephelometric turbidity units, chlorophyll *a* – μg l^{-1}.

an Australian ICOLL, despite lower concentrations in the adjacent coastal ocean (Twomey and Thompson, 2001). The stimulation of phytoplankton growth in this case was attributed to sediment nutrient release due to the development of anoxia as a result of a salt wedge which extended into the ICOLL. Together, these examples illustrate that ICOLL openings may not ameliorate eutrophication by flushing as well as the potential risks of artificially opening ICOLLs without prior understanding and consideration of the dynamics of specific ICOLL systems.

Lake Ellesmere is negatively affected by eutrophication, with high levels of phytoplankton biomass, high turbidity, and a failure of macrophyte beds to re-establish. The relatively slow increases in salinity observed in Lake Ellesmere during open periods (1.6 per day; Fig. 6C), together with the lack of a significant relationship between salinity and chlorophyll *a* (Fig. 3E), indicate that tidal flushing was not as effective in Lake Ellesmere as in Waituna Lagoon, where chlorophyll *a* levels were always below 10 μg l^{-1} when the ICOLL was open (Fig. 6J). However, the Lake Ellesmere

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Table 4
Tributary nutrient concentrations (mg L^{-1}), loading rates (mg s^{-1}), and stoichiometry of tributary nutrient input to Lake Ellesmere and Waituna Lagoon. Concentrations are means ± 1SD, and ranges in parentheses.

	Lake Ellesmere	Waituna Lagoon
DIN concentration	3.2 ± 1.7 (0.1–11.0)	0.3 ± 0.4 (0.01–1.5)
TN concentration	3.4 ± 1.8 (0.3–11.5)	0.8 ± 0.6 (0.1–2.3)
DRP concentration	0.03 ± 0.04 (<0.01–0.7)	0.02 ± 0.03 (<0.01–0.15)
TP concentration	0.05 ± 0.07 (0.01–0.92)	0.04 ± 0.03 (<0.01–0.19)
DIN loading	101,379	5011
DRP loading	720	119
TN loading	109093	7843
TP loading	1318	384
DIN:DRP	148:1	45:1
TN:TP	91:1	22:1
DIN:TP	85:1	15:1
Ln(DIN:TP) (based on loading rates)	4:3	3:1

data suggest that chlorophyll *a* concentrations may have been reduced somewhat during openings longer than 1 month (Fig. 6I). An extrapolation of the Lake Ellesmere data in Fig. 6C suggests that openings would have to be maintained for ~200 days for the salinity at the mid-lake site to approach that of seawater (near complete tidal flushing). However, artificially extending the opening periods could negatively affect: 1) fringing wetlands by de-watering (c.f. Johnson and Partridge, 1998), 2) remaining submerged macrophytes by increasing exposure to grazing waterfowl and wind-induced turbulence (Gerbeaux, 1993), and 3) other freshwater – mesohaline biota by increasing the salinity beyond their optima (c.f. Schallenberg et al., 2003).

Waituna Lagoon was more responsive to opening/closure than Lake Ellesmere, as indicated by rapid tidal flushing after openings (Fig. 6) and by rapid increases in water level, nitrate and TP concentrations after barrier closure (Fig. 5). This indicates that artificial barrier breaching ameliorated the effects of eutrophication in this system. However, as for Lake Ellesmere, increasing the frequency of opening could negatively affect fringing wetland vegetation (Johnson and Partridge, 1998), seagrass communities (Gerbeaux, 1993) and other biota sensitive to high salinities.

The large differences in apparent tidal flushing inferred from the water quality data can be explained by morphological differences in the ICOLLs. The ultimate size of a barrier breach scales to the 1/3 power of the outflow volume (Stretch and Parkinson, 2006) and is also proportional to the barrier's height (which determines the hydraulic head) and breadth (Stretch and Parkinson, 2006). The dynamics and rapidity of tidal flushing are also influenced by ICOLL size (Gale et al., 2007). For example, semidiurnal tides and wind mixing dominated tidal flushing in the smaller ICOLL (surface area = 0.6 km^2) whereas fortnightly spring/neap tide dynamics dominated tidal flushing of a larger one (surface area = 11 km^2). Consequently, Gale et al. (2007) showed that the timescale of flushing of the larger ICOLL was an order of magnitude greater than that for the smaller one. Such scale-dependent influences on tidal flushing are supported by our data (Fig. 6) and by typical tidal ranges reported for Waituna Lagoon (c. 120 mm; C. Jenkins, Environment Southland, unpublished data) and Lake Ellesmere (no clear semidiurnal tidal signal; G.A. Horrell, Environment Canterbury, unpublished data).

Flushing may also occur when an ICOLL is closed. For example, water level data for Waituna Lagoon indicated substantial seepage losses when the water level exceeded 0.8 m (Fig. 5B). In contrast, water level data did not suggest seepage losses from Lake Ellesmere.

4.2. *Factors related to phytoplankton productivity and biomass*

In ICOLLs, phytoplankton often responds positively to nutrient loading (e.g., Suzuki et al., 1998; Twomey and Thompson, 2001; Bonilla et al., 2005; Gobler et al., 2005), but light availability may also be growth limiting when the ratio of mixing depth to euphotic depth (Z_{mix}:Z_{eu}) exceeds 4–5 (Talling, 1971). In Lake Ellesmere, the average Z_{eu} range was 0.3–0.5 m (Gerbeaux and Ward, 1991; this study Table 3) and Z_{mix}:Z_{eu} was generally >5 when the water column was mixed. Thus, frequent light limitation may explain the absence of detectable relationships between chlorophyll *a* and either the duration of closure (Fig. 5I) or the concentrations of available nutrients in Lake Ellesmere (data not shown).

In contrast, the Z_{mix}:Z_{eu} ratio in Waituna Lagoon ranged from 0.9 to 1.9, suggesting that the phytoplankton community is rarely, if ever, light-limited. The positive correlation between chlorophyll *a* and ICOLL closure duration, the negative correlation between chlorophyll *a* and DRP concentrations, and the high DIN:TP stoichiometry in the ICOLL (Tables 3, 4) together suggest that phytoplankton growth was potentially controlled by P availability during closed periods, although this remains to be confirmed by bioassay experiments.

The loading rate of DRP was positively correlated with chlorophyll *a* in Lake Ellesmere, suggesting that a reduction in P-loading might facilitate reductions in phytoplankton biomass. While reductions in trophic status have been achieved by reducing the nutrient loading to some lakes (Anderson et al., 2005; Jeppesen et al., 2005; Kagalou et al., 2008), improvements in trophic state in shallow lakes often only become apparent after years of reduced external loading owing to internal nutrient loading, cycling and other ecological feedbacks (Jeppesen et al., 2007). The two ICOLLs in this study varied markedly in nutrient loading, availability and stoichiometry, which is consistent with different nutrient pathways and/or processing in the ICOLLs.

Our inferences concerning nutrient and light limitation of phytoplankton were based on correlations and limited light data. Salinity increases resulting from ICOLL openings may also limit phytoplankton biomass (Thomas et al., 2005) and alter community structure (Redden and Rukminasari, 2008) and our data from Waituna Lagoon (Fig. 3) were consistent with a potentially inhibitory effect of increased salinity on phytoplankton biomass. Experimental studies examining whether these factors control phytoplankton growth would improve understanding of how opening regimes can affect eutrophication in ICOLLs.

4.3. *Managed vs. natural opening regimes*

A common approach to restoring ecosystems impacted by human pressures is to attempt to revert them to their original condition by removing the pressures (Duarte et al., 2009). For example, the reinstatement of natural opening regimes of ICOLLs has been suggested to restore ailing coastal fisheries (Jones and West, 2005) and to protect and restore wetland plant communities surrounding Waituna Lagoon (Johnson and Partridge, 1998). As artificial openings occur before ICOLLs reach their natural overtopping levels, in most cases, the reinstatement of natural opening regimes would reduce the frequency of the openings (Haines et al., 2006) and would result in larger breaches because the ultimate size of a breach is related to the size of the hydraulic head or barrier height (Stretch and Parkinson, 2006). Therefore, under natural regimes, both openings and closures would be less frequent and of longer durations.

Where entrance closure indices are expected to increase under the natural opening regime, this would result in a greater mean water depth (with less light reaching the ICOLL bed) and a larger

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area of the ICOLL bed being intermittently dewatered. In Waituna Lagoon phytoplankton biomass increased linearly with increasing periods of closure (Fig. 5J) whereas tidal flushing reduced nitrate and chlorophyll *a* concentrations. However, at current trigger levels, the ICOLL maximum depth is around twice the euphotic depth (Tables 1, 3), indicating that at high water levels a substantial part of the ICOLL bed receives less than 1% surface irradiance and may not be suitable macrophyte habitat. Therefore, the reinstatement of the natural opening regime at current rates of nutrient loading would probably decrease water quality during closed periods and limit submerged macrophyte habitat availability compared to the artificially managed regime. Eutrophication would be expected to worsen and the risk of a shift in dominant primary producers from macrophytes to phytoplankton would increase.

The implications of adopting a natural opening regime for Lake Ellesmere are not as obvious because relationships between opening regime parameters and water quality variables were weaker than for Waituna Lagoon. However, chlorophyll *a* concentrations were relatively low on rare occasions when the duration of ICOLL opening exceeded 1 month (Fig. 6I). Prior to human intervention, natural openings at Lake Ellesmere occurred at c. 5 y intervals and the ICOLL level may have reached c. 4 m (G.A. Horrell, Environment Canterbury, unpubl. data). Although the data presented here suggest that variation in open-period duration had little effect on water quality, the putative natural hydraulic head of c. 4 m would enlarge barrier breaches, resulting in longer openings and greater tidal flushing, but at less frequent intervals.

It has been suggested that the restoration of macrophyte beds is a key to improving water quality in Lake Ellesmere as well as in other turbid lakes and ICOLLs that have lost macrophytes (Gerbeaux and Ward, 1991; Hamilton and Mitchell, 1996; Scheffer and van Nes, 2007). Restoring a natural opening regime to Lake Ellesmere would raise the mean water level and reduce turbulent shear stress on the lake bed, reducing sediment resuspension (c.f. Hamilton and Mitchell, 1997). However, reduced sediment resuspension could release phytoplankton from light limitation, ultimately resulting in increased phytoplankton biomass which might compensate for the reductions in turbidity from sediment resuspension. Conversely, if the ICOLL were maintained at a lower water level to enhance light penetration to the bed (Gerbeaux, 1993; Taylor, 1996), shear stress at the lake bed and turbidity due to sediment resuspension would increase, limiting the potential for the re-establishment of macrophytes. Thus, water level regulation alone may not restore macrophyte beds to Lake Ellesmere.

Our findings, together with other examples from the literature, highlight the need for careful consideration of ICOLL-specific factors such as the entrance closure index, tidal flushing, ICOLL size, morphology, phytoplankton growth limitation status, and the presence/absence of macrophytes when managing ICOLL openings because these factors mediate the ecological consequences of opening regimes (Haines et al., 2006; Ridden and Adams, 2008). For Lake Ellesmere, Waituna Lagoon and other ICOLLs subject to eutrophication, changing the opening regimes may achieve short-term improvements in water quality. However, long-term improvements are more likely to be achieved by strengthening phytoplankton nutrient limitation through reductions in nutrient loading from surrounding catchments (Webster and Harris, 2004), especially in large ICOLLs with poor tidal flushing.

The effectiveness of the opening regime as a tool to mitigate eutrophication in ICOLLs depends on a number of ICOLL-specific factors, many of which we have described in this study. For example, ICOLL openings were much more effective in flushing the smaller ICOLL than the larger one. In addition to size dependence, the effectiveness of tidal flushing was also dependent upon the entrance closure index. Phytoplankton growth and biomass appeared to be regulated by light and nutrient availability in Lake Ellesmere and Waituna Lagoon, respectively, but other factors including nutrient loading, flushing, the presence of macrophytes, and wind-induced sediment resuspension were also important. Apart from the strong scale dependence of tidal flushing, there appear to be few generalities to guide the ecological management of these complex systems. Thus, controls on nutrient loading from the catchment would appear to be the most direct and most promising way towards the long-term restoration of such systems. However, improvements may take time and the informed and prudent use of managed ICOLL openings may facilitate restoration in some cases.

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