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Consequences of human-mediated marine intrusions on the zooplankton community of a temperate coastal lagoon

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Barrier bars separating lagoons from oceans are frequently breached as a management tool to prevent flooding of terrestrial ecosystems. The effects of such human-mediated openings on zooplankton have been investigated only in one tropical system. We investigated the temperate Waituna Lagoon, New Zealand, over a 2-year period when the barrier bar was ‘artificially’ breached on three occasions. Increases in salinity associated with opening of the barrier bars greatly influenced zooplankton community composition, and recovery of communities was dependent on the rate at which salinity returned to pre-disturbance conditions. As such, resilience of zooplankton in coastal lagoons is a function of the lagoon conditions returning to those experienced prior to barrier breach, rather than being a result of the zooplankton community simply recovering from a single defined disturbance event. In contrast to the tropical lagoon studies, temperature in Waituna Lagoon was inferred to explain a significant proportion of the variability in zooplankton community composition, independent of salinity. Appropriate timing for the opening of barrier bars by management authorities in temperate lagoons, which would allow the greatest opportunity for freshwater zooplankton communities to recover rapidly, will rely on determining the best time for rapid barrier bar reformation and high freshwater inflow rates (i.e. the recovery of zooplankton relies on return to initial conditions). However, such an approach is in direct conflict with the opening of barrier bars for management of water levels.

Keywords: sandbar opening; Waituna Lagoon; community resilience; New Zealand

Introduction

Lagoons have restricted connections to the ocean, being typically completely isolated by a barrier that periodically breaches to the ocean (Kjerfve 1994). The natural opening and closing of connections between lagoon and ocean are dependent on the inflow of freshwater into the lagoon (i.e. rainfall, streamflow) and longshore processes, respectively (Kjerfve 1994). The timing of seawater influence on lagoons should thus be fairly predictable (Elwany et al. 1998). Lagoons are strongly impacted by anthropogenic effects, such as by increased nutrient inputs from their

catchments and high siltation rates, with the effects exacerbated by the lagoons typically shallow depth (Suzuki et al. 1998; Santos et al. 2006). Additionally, lagoons can conflict with urban and rural land usage. Potential or actual flooding of these areas has led to barrier bars being unnaturally opened to increase flushing and to reduce the threat of flooding (e.g. Dye 2006). Opening of barrier bars leads to rapid rises in salinity into a typically low salinity environment, and occurs at a considerably greater frequency than would happen naturally (e.g. Kozłowski-Suzuki & Bozelli 2004; Santangelo et al. 2007).

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Zooplankton are generally small, and therefore highly sensitive to changes in physical, chemical and biological conditions. Several recent studies have shown that even relatively moderate saline intrusions into inland waters can have a large influence on zooplankton community composition (e.g. Froneman 2004; Schallenberg et al. 2003; Kozłowski-Suzuki & Bozelli 2004). Few studies exist, however, of zooplankton dynamics in lagoon environments with intermittent artificial opening of barrier bars (e.g. the tropical Imboassica Lagoon, Brazil; Kozłowski-Suzuki & Bozelli 2004; Santangelo et al. 2007). In those studies, dramatic changes in environmental and biotic conditions were observed when barrier bars were opened, including sharp increases in salinity, and changes in nutrient levels, algal biomass and pH. Zooplankton in these studies were found to be greatly affected by changes in salinity and trophic state associated with barrier bar opening. Additionally, the community responses to barrier reformation in the Kozłowski-Suzuki and Bozelli (2004) study indicated community recovery (i.e. the time taken for assemblages to return to that observed before disturbance) was rapid, while Santangelo et al. (2007) conversely suggested zooplankton recovery was a slow process. Return of zooplankton communities to, or towards, pre-disturbance composition relies on a supply of individuals immigrating into the waterbody or for species to survive adverse periods using diapausing eggs (e.g. Brock et al. 2003). Despite the anthropogenic induced opening of lagoons being common globally (e.g. Elwany et al. 1998: USA; Dye 2006: Australia), no data exist for the effects of artificial openings on zooplankton in temperate lagoons. We examined four sites in Waituna Lagoon, New Zealand, with the aim of assessing the importance of barrier bar openings as a driver of zooplankton community dynamics in temperate lagoons and consider the recovery time of these assemblages.

Materials and methods

Study area

Waituna Lagoon (Fig. 1) is a moderately sized (3556 ha), shallow (maximum depth 2 m under

modified regime, up to 4 m under natural regime), temperate coastal lagoon, located on the south coast of New Zealand's South Island, separated from the sea by a narrow gravel bar (Thompson & Ryder 2003). The management history of Waituna Lagoon was reviewed by Thompson and Ryder (2003), which we summarise here. The lagoon is periodically opened to the sea for management of water levels, enhancing drainage on bordering farmland. Historically, Waituna Lagoon increased in depth because of rainfall and creek inflows until it naturally overtopped the gravel barrier bar, emptying the lagoon. The first human-induced barrier breach was made in 1908 to improve fishing, and the lagoon was periodically opened for this purpose following this time. Since the late 1960s, openings have been made to allow free drainage of the surrounding farmland. Throughout the 1970s and 1980s, it was opened approximately annually, maintaining the water level between 2.0 and 2.5 m. The amount of time for the barrier bar to close has gradually increased through time; for example, in the 1970s the opening time was typically less than 50 days, whereas in 1997 the bar opened and remained open for 2.5 years. No natural breaches have occurred since 1972, although regular artificial breaching continues (Thompson & Ryder 2003).

The lagoon was opened to the ocean on three occasions during this study: in June 2004 (austral winter), January 2005 (summer) and July 2005 (winter). The first and second openings of the barrier bar were closed after short time periods (<2 months), while the third opening was prolonged (remaining open >8 months, and was not closed by the end of the study).

Sampling and analyses

Four sites (west, centre, east, south), chosen to capture any horizontal variability of the lagoon brought about by inflows, were monitored approximately monthly by Environment Southland (the regulatory authority managing Waituna Lagoon) for zooplankton and environmental data, from 22 April 2004 to 9 April 2006 (Fig. 1). In total, sampling was undertaken on 23 occasions. Zooplankton were

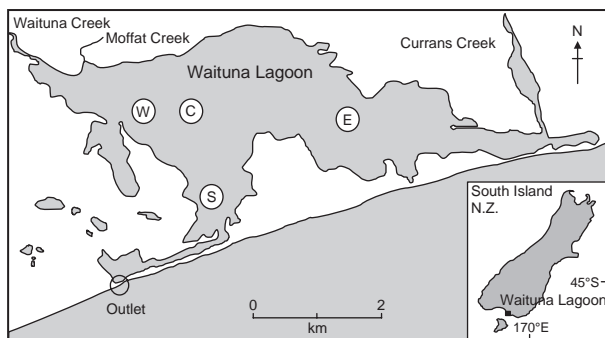


Fig. 1 Location map of Waituna Lagoon, New Zealand, showing sample sites in proximity to inflows, barrier bar and breach point (W, west; C, centre; E, east; S, south).

sampled quantitatively using at least four surface water samples at each site with a volumetric jug to a final volume of 20 l (i.e. multiple subsamples combined into one sample per site per month). Samples were concentrated using a 40- μ m mesh net, and preserved in 70% ethanol. Owing to the shallow nature of the lagoon, it was assumed to be well mixed during each sampling period. Surface temperature and dissolved oxygen (DO) were measured using a YSI model 95 DO and temperature meter. Total nitrogen (TN), total phosphorus (TP), pH, chlorophyll *a*, conductivity, salinity (PSU) and turbidity were determined from surface water samples using standard APHA methods for each occasion and site (APHA 2005). Occasionally, some sites were not accessible owing to low water levels (seven occasions at the eastern site and twice at the central site), giving a total of 83 sample points.

Zooplankton samples were examined until at least 300 individuals, or the whole sample, were counted. Identification was performed using standard taxonomic guides (e.g. Lang 1948; Bradford 1972; Chapman & Lewis 1976; Shiel 1995). An exploratory Detrended Correspondence Analysis (ter Braak & Smilauer 1998) indicated that the zooplankton community responded to underlying environmental gradients in a unimodal manner (length of gradient = 3.5). Canonical Correspondence Analysis (CCA) was therefore used to determine important physical or chemical variables determining zooplankton community structure (CANOCO v. 4.51, Biometris, Wageningen).

Forward selection and Monte Carlo permutation tests (using 99 unrestricted permutations) were performed to identify the environmental variables that were statistically significant in determining the variations in zooplankton species. Species were included in the analysis only if they comprised >4% of the abundance of any one sample, and were found in at least four samples over at least two sampling occasions. Nine samples were removed that had fewer than 1.5 individuals/l (i.e. 30 individuals total) and fewer than 5 species present. In these instances, rare species may have been collected by chance rather than reflecting environmental conditions. Seventy-four samples were therefore used in the analysis. Species data were $\log(x+1)$ transformed to reduce the potential effects of dominant taxa on the analysis (ter Braak & Smilauer 1998). Where appropriate, environmental data was $\log(x+1)$ transformed to improve normality, and all variables were standardised to zero mean and unit variance in order to remove the influence of different scales of measurement (ter Braak & Smilauer 1998). Some environmental data were missing owing to equipment malfunction, and were interpolated for the CCA analysis using relationships with other variables (e.g. two salinity values were interpolated from conductivity values) or seasonal cycles (e.g. 12 water temperature values were interpolated based on having predictable seasonal variability).

Results

Environmental variables

The lagoon was open to the ocean immediately prior to the beginning of this study (i.e. the salinity was >30 PSU in all sites in March 2004). Openings of the barrier bar profoundly affected the environmental conditions measured at each site. Salinity showed clear signals of barrier bar opening and closing, being markedly higher (>30 PSU) when the bar was open than when it was closed (returning to <5 PSU; Fig. 2). The eastern site, furthest from the opening to the sea, commonly had lower salinity values than the other three sites (average 13.1 ± 9.2 PSU at the eastern site, >18.5 PSU at all other sites). As barrier bar openings occurred in both summer and winter, salinity was not observed to vary in a seasonally predictable manner. Temperature showed typical seasonal variability, being lowest in June–August (winter; minimum 4.9°C) and

highest in December–January (summer; maximum 21.0°C). TN, chlorophyll *a* and pH were all influenced by barrier openings. TN and chlorophyll *a* decreased to relatively low values after barrier bar opening, and generally increased gradually after barrier bar closing (e.g. sites typically had <1 mg/l TN and <1 $\mu\text{g/l}$ chlorophyll *a* when salinity was >20 PSU, but >1 mg/l TN and >5 $\mu\text{g/l}$ chlorophyll *a* when salinity was <10 PSU). TP was not consistently affected by the barrier openings. Measured TP and chlorophyll *a* concentrations indicated that the lagoon was eutrophic during periods of low salinity conditions (bar closed), although chlorophyll *a* concentrations were more indicative of oligotrophic conditions when salinity values were high (bar open). Lagoon pH was typically higher (pH 8.0–8.5) when the barrier bar was open, and circumneutral when the lagoon was closed. Turbidity was seemingly not affected by barrier bar

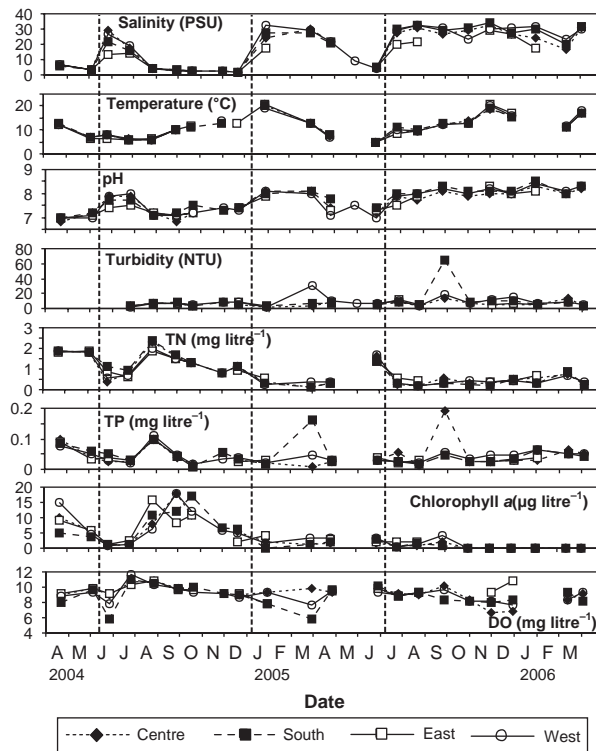


Fig. 2 Temporal dynamics of environmental conditions in Waituna Lagoon (South Island, New Zealand) at the four sampling stations, showing timings of barrier breaching (vertical broken lines).

opening, being high on two occasions (25 March 2005 and 25 September 2005; maximum 2.4 NTU). DO generally decreased after opening of the barrier bar, but commonly returned to typical readings of 8–10 mg/l by the next sampling occasion (Fig. 2).

Zooplankton composition and dynamics

Forty-four zooplankton taxa were identified, including three calanoid copepod, seven harpacticoid copepod, two cyclopoid copepod, two cladoceran and 15 rotifer species (Appendix 1). The calanoid copepod *Gladioferens pectinatus* attained the highest abundances of any species during the study, generally peaking (>60 individuals/l) when salinity was at intermediate levels (salinity 2.5–27.0 PSU), but was usually at low abundances (<15 individuals/l) when the barrier bar was open (salinity >30 PSU; Fig. 3). *Amphascioides* sp., Canuellidae, *Paradactylopodia* sp., *Tisbe* sp., ostracods, copepod nauplii and polychaete larvae typically dominated in the month or two after barrier bar opening at times of moderately high salinity levels (>20PSU). The rotifer *Synchaeta oblonga* dominated in October–November 2004 (spring) during ‘freshwater’ conditions (salinity <3 PSU). *Acartia ensifera*, *Ectinosoma* sp., *Euterpina acutifrons*, *Mesochra parva*, *Halicyclops* sp., *Synchaeta vorax* and gastropod larvae dominated mostly late in the study, during the long-term opening of the barrier bar (salinity >30 PSU; Fig. 3).

CCA was used to explore the environmental variables associated with observed patterns in community composition (Fig. 4). Results of forward selection and Monte Carlo permutation tests from CCA indicated that salinity explained the largest proportion of the variability in zooplankton community composition (lambda A = 0.28, $P = 0.002$; Table 1). Salinity therefore was most strongly associated with Axis 1, the axis that explained most of the variability in species composition (Fig. 4). Samples associated with low salinity periods were distributed on the left of the ordination, and those when the barrier bar was open were distributed on the right of the ordination. *S. oblonga* was most strongly associated with lower salinity samples, with a gradient of

species occurring with *G. pectinatus*, *Encentrum marinum*, copepod nauplii and *Paradactylopodia* sp. most strongly associated with intermediate salinity, through to *A. ensifera* and *E. acutifrons* most strongly associated with high salinity conditions. Salinity was strongly associated with pH, and negatively associated with chlorophyll *a*, DO and TN (Fig. 4). Thus, species and samples associated with low salinity conditions also occurred at higher chlorophyll *a*, DO and TN concentrations, and lower pH. Species and samples associated with high salinity conditions were related to these variables in an opposite manner. Temperature explained the greatest proportion of additional variation in species data after salinity was added to the model (i.e. temperature explained a significant amount of variation not explained by salinity; Monte Carlo test, lambda A = 0.09, $P < 0.002$; Table 1). Temperature was positively associated with Axis 1, indicating some relationship between salinity and temperature (i.e. open barrier bar [high salinity] conditions most commonly coincided with warmer conditions). However, the mildly negative association of temperature with Axis 2 (as opposed to positive association of salinity), combined with the Monte Carlo permutation test results, indicated an independence of the two factors, and that a seasonal influence on zooplankton composition existed when the barrier bar was opened or closed (e.g. *S. vorax*, *A. ensifera* and *E. acutifrons* were found at higher temperatures and moderate salinity, whereas *M. parva* and *Halicyclops* sp. were found at similar salinity levels but during periods of lower temperatures). Samples from cooler periods were generally distributed on the top left of the ordination, and warmer periods on the bottom right. Turbidity was most strongly positively associated with Axis 2 and with three samples from 29 March 2005 and 25 September 2005, at periods when *Tisbe* (and to a lesser extent ostracods) were abundant (both benthic groups). However, Axis 2 explained comparatively little of the variation relative to Axis 1 (eigenvalue Axis 1 = 0.330 vs Axis 2 = 0.117), indicating the over-riding importance of salinity (and barrier opening) on zooplankton dynamics in the lagoon (Fig. 4).

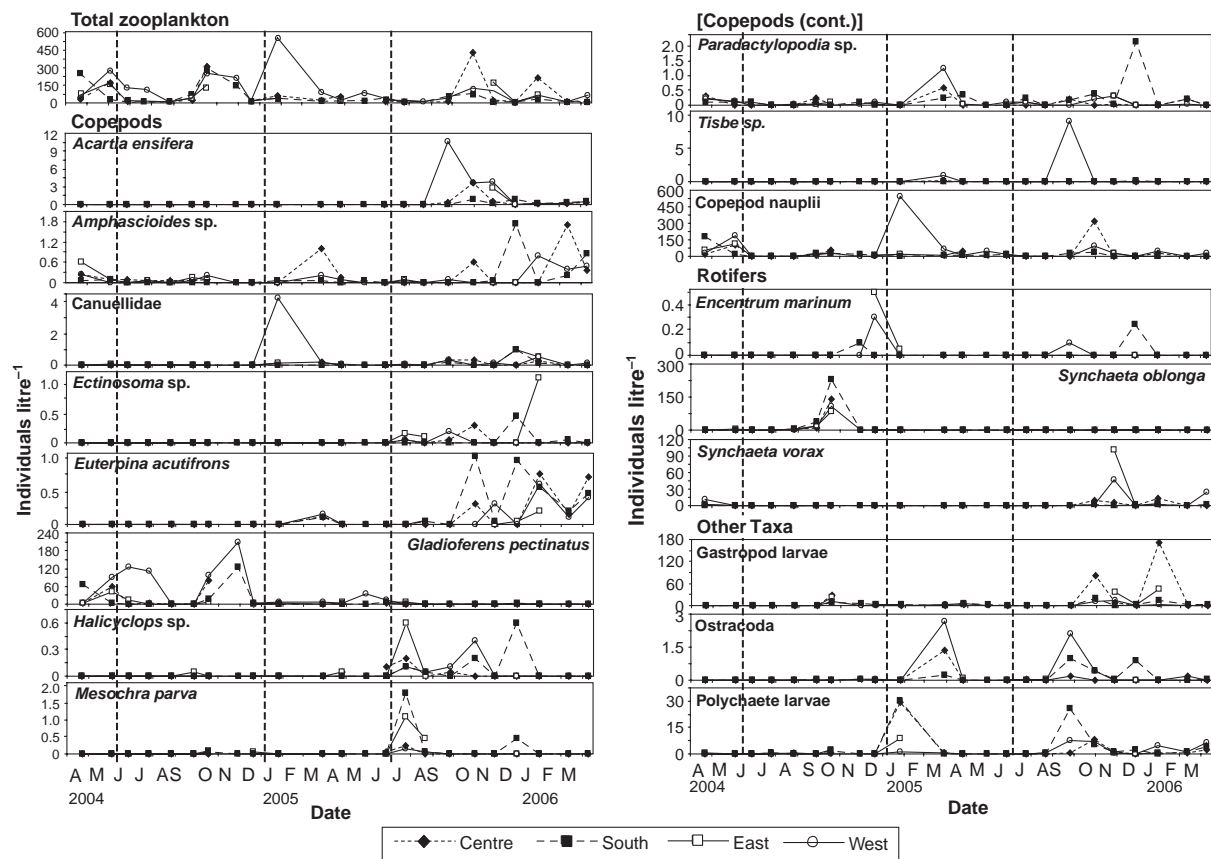


Fig. 3 Temporal dynamics of dominant zooplankton taxa in Waituna Lagoon (South Island, New Zealand) at the four sampling stations, showing timings of barrier breaching (vertical broken lines).

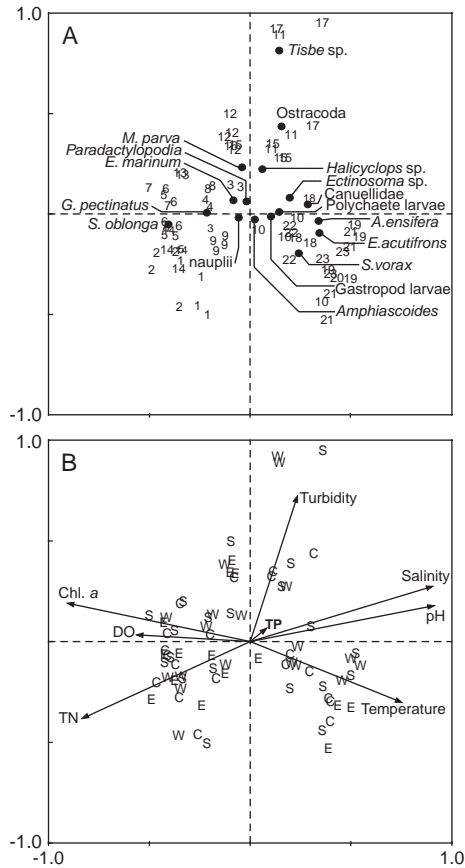


Fig. 4 Ordination biplots based on Canonical Correspondence Analysis of zooplankton taxa occurring in Waituna Lagoon (South Island, New Zealand). A, date (numbers) and species (closed circles) biplot, and B, site (letter) and environmental variables (arrows) biplot. Eigenvalues for Axis 1 and 2 = 0.330 and 0.177, respectively. Key to numbers: (1) 22 Apr 2004; (2) 03 Jun 2004; (3) 27 Jun 2004; (4) 25 Jul 2004; (5) 26 Aug 2004; (6) 27 Sep 2004; (7) 18 Oct 2004; (8) 29 Nov 2004; (9) 20 Dec 2004; (10) 26 Jan 2005; (11) 29 Mar 2005; (12) 24 Apr 2005; (13) 29 May 2005; (14) 26 Jun 2005; (15) 24 Jul 2005; (16) 21 Aug 2005; (17) 25 Sep 2005; (18) 30 Oct 2005; (19) 27 Nov 2005; (20) 28 Dec 2005; (21) 29 Jan 2006; (22) 12 Mar 2006; (23) 9 Apr 2006. C, Central; S, South; E, East; W, West.

Discussion

There are striking similarities among the effects of artificial barrier bar openings on zooplankton community dynamics in Waituna Lagoon and the tropical lagoon system (Imboassica Lagoon, Brazil) previously studied, indicating that generalisations may be made among such ecosystems. As expected, induced opening of barrier bars, regardless of location, leads to increases in salinity and dramatic associated changes in zooplankton community composition (cf. Kozłowski-Suzuki & Bozelli 2004;

Santangelo et al. 2007). However, secondary effects on zooplankton dynamics related to temperature regime were apparent in the current study, which were not important in the previous tropical studies.

In the current study, zooplankton composition shifted from freshwater species (e.g. the rotifer *S. oblonga*) to either mesohaline or fully marine species immediately following barrier breach (e.g. polychaete and gastropod larvae or marine copepods). These compositional changes with salinity are similar to

Table 1 Results of forward selection and Monte Carlo permutation tests from Canonical Correspondence Analysis of Waituna Lagoon (South Island, New Zealand) zooplankton taxa.

	$\lambda-1$	$\lambda-A$	<i>P</i>
Salinity	0.28	0.28	0.002
Temperature	0.21	0.09	0.002
Chlorophyll <i>a</i>	0.27	0.07	0.002
Total nitrogen	0.25	0.07	0.002
Turbidity	0.08	0.05	0.008
Dissolved oxygen	0.12	0.02	0.070
pH	0.28	0.02	0.174
Total phosphorus	0.02	0.02	0.574

Lambda-1 ($\lambda-1$) indicates the variance each environmental variable was inferred to explain when considered alone.

Lambda-A ($\lambda-A$) indicates the additional variance each variable explains after addition of that variable to the model, and its significance at that time (*P*). Environmental variables are listed by the order of their inclusion in the model ($\lambda-A$).

those observed elsewhere, with the dominant species observed during low salinity periods by Kozłowski-Suzuki and Bozelli (2004) and Santangelo et al. (2007) in Imboassica Lagoon, Brazil (over similar salinity ranges to the current study) being rotifers, with meroplankton (gastropod larvae, polychaete larvae) and copepods (including an *Acartia* species) most abundant during saline periods. Two processes could have led to the observed changes in the zooplankton community. First, many individuals of freshwater taxa were probably washed out to sea when the barrier bar was breached, and/or killed by osmotic shock, followed closely by the immigration of marine taxa as the lagoon filled with seawater. As Waituna Lagoon became saline, it is likely that the lagoon was almost entirely flushed with seawater following each opening (the exception possibly being the eastern arm, where salinities were generally slightly lower than in the main body). Following the initial barrier opening, salinity in the lagoon gradually decreased through time. Tolerances (or preferences) of individual zooplankton species to specific salinity ranges apparently determined the assemblages present as salinity progressively decreased. Species thus gradually changed in composition following barrier reformation and subsequent isolation from the ocean based on extant conditions.

Salinity is a key driving factor determining zooplankton community composition in estuarine environments, owing to osmotic considerations, with marine, mesohaline and freshwater species occurring along the resulting gradient. In New Zealand, Schallenberg et al. (2003), for example, found that even minor changes in salinity above 1.2 led to major changes in zooplankton species composition. However, despite salinity being an overriding factor determining zooplankton composition and dynamics in both lagoons and estuaries, the spatial and temporal scale of influence differs between these systems (Kjerfve 1994). While estuaries may experience fluxes of saline conditions over short time periods (i.e. tidal cycles), lagoon systems with barrier bars are influenced by high salinities relatively infrequently (seasonal or inter-annual), with subsequent return to freshwater conditions being a gradual process (i.e. taking weeks to years, depending on the time to barrier reformation and freshwater inputs; Kjerfve 1994; Kozłowski-Suzuki & Bozelli 2004). Additionally, zooplankton variability in association with salinity in estuaries occurs most strongly along a spatial gradient, from the river mouth to ocean (e.g. Roper et al. 1983; Marques et al. 2007). In contrast, lagoon systems tend to have little spatial variability relative to temporal variability, whether or not the barrier bars are open. However, zooplankton occurring along the respective salinity gradients, temporal in

lagoons and spatial in estuaries, can be similar; for example, zooplankton composition in the current study was similar to that found in the Avon-Heathcote Estuary, New Zealand, by Roper et al. (1983). Factors that covaried with salinity in the current study, including chlorophyll *a*, TN and pH, may have played some role in determining zooplankton communities before and after barrier breaches. However, based on the taxa changing through a sequence of marine to mesohaline and freshwater taxa, the overriding variable responsible for these changes was clearly salinity.

Zooplankton communities were able to recover to some degree from the barrier breaches during the current study in the two events where the barrier reclosed, providing salinity was sufficiently reduced. For example, the freshwater rotifer *S. oblonga* was able to dominate when salinity became reduced following the first opening (<4 PSU), while cladocerans also appeared in low numbers when the lagoon returned to low salinities at this time. Thus, cladocerans and freshwater rotifers were able re-establish in Waituna Lagoon following return to near-freshwater conditions, despite regular induced openings to the ocean occurring regularly in Waituna Lagoon since 1908 (Thompson & Ryder 2003). Although no data exist of zooplankton communities from Waituna Lagoon under a natural regime, Branco et al. (2000) found freshwater zooplankton (e.g. rotifers and cladocerans) to dominate abundance and composition during a 3.5 year study of Lagoa Comprida, Brazil, where the barrier did not breach; Waituna Lagoon would likely have had similar communities under a natural regime. We were unable to test whether the Waituna Lagoon zooplankton community can recover to a point where a true freshwater community could return that may have existed under a natural regime, as truly freshwater conditions were not encountered during this study. Diapausing eggs of freshwater rotifer and cladoceran taxa have the ability to survive saltwater exposure, and to emerge once exposed to freshwater again, allowing recovery (e.g. Gray et al. 2005). Alternatively, re-establishment of these taxa may be through immigration from nearby streams or other waterbodies. Our results are similar to that found by Kozłowski-Suzuki & Bozelli (2004), who observed the effects

of repeated openings of a barrier bar on zooplankton communities. In their study, zooplankton composition shifted back to that observed at pre-disturbance relatively quickly, corresponding to the rapid return in salinity to pre-disturbance conditions. Santangelo et al. (2007), in contrast, examined the same lagoon over a period when it took 2 years for salinity to approach pre-opening conditions, owing to unusually dry weather, and for a freshwater community (albeit lacking cladocerans) to be re-established. As such, we propose that the recovery (or resilience) of freshwater (or pre-breach) taxa depends largely on the amount of time taken for pre-breach salinity conditions to be attained. Ultimately, zooplankton resilience in lagoons is therefore a function of the time taken for the sandbar to reform (i.e. barrier bar recovery owing to longshore processes) and the amount of precipitation in the lagoons' catchment (allowing freshwater to enter and pre-breach conditions to return to the lagoon), rather than being a recovery process to a defined disturbance effect (i.e. a salinity pulse). In contrast, during long-term opening, when salinities remain high, marine taxa were able to dominate in Waituna Lagoon (e.g. *Ectinosoma* sp., *E. acutifrons* and *S. vorax*). With lagoons increasingly being managed as open systems, domination of marine rather than meso- or oligohaline taxa through time will be widespread.

Unlike the studies on the tropical Imboassica Lagoon, Brazil, where temperature was not an important factor influencing species composition (Kozłowski-Suzuki & Bozelli 2004; Santangelo 2007), temperature was inferred to explain the highest proportion of variation in the zooplankton community independent of salinity in the Monte Carlo analysis here (i.e. temperature had the highest lambda-A value after the variability explained by salinity was accounted for by the model). Froneman (2004) found seasonal variation in zooplankton community composition independent of salinity change in the seasonally closed, moderately saline, temperate Kasouga Estuary, South Africa. Also, Roper et al. (1983) found seasonal variation for some of the species found in the current study in the Avon-Heathcote Estuary, New Zealand. Variation in faunal composition at times the barrier bar was open may also reflect the species that are available for entry

from the ocean at the time of opening. This variation in zooplankton composition is independent of lagoon temperature, but is likely to be related to ocean temperature in this temperate region. Nevertheless, the effect of temperature on zooplankton composition, directly or indirectly, is a major factor differentiating zooplankton dynamics between temperate and tropical lagoon systems.

Samples from individual dates but different sites were generally closely associated with one another in the CCA ordination, indicating spatial variability in community composition was small relative to temporal variability. Dates that showed the greatest variability in species composition were when greatest variability was observed in turbidity and DO. In particular, ostracods and *Tisbe* sp., both benthic taxa, were highest when turbidity was greatest; their association with high turbidity probably indicates they have been suspended into the water column owing to wind action in shallow or exposed areas of the lagoon. However, such factors are of less importance relative to salinity and temperature.

One unexamined influence on zooplankton composition, which may have contributed to some seasonal and/or spatial variability, is fish composition and dynamics. As shown elsewhere (e.g. Yañez-Arancibia et al. 1994), seasonal and/or spatial variability in zooplankton abundance and assemblages may have been partially attributed to biological top-down controls. A variety of native freshwater and marine fishes are known to inhabit the lagoon, including longfin (*Anguilla dieffenbachii*) and shortfin (*Anguilla australis*) eel, yellow eyed mullet (*Aldrichetta forsteri*), cockabully (*Grahaminagrion*), kahawai (*Arripis trutta*), stargazer (*Leptoscopus macropygus*), parrotfish (*Pseudolabrus celidotus*) and various flounder species (*Rhombosolea* species) (Thompson & Ryder 2003). During this study, crustacean zooplankton were abundant almost throughout, despite the dominant species commonly changing, indicating that zooplankton may not become a limiting food resource for young fishes, regardless of lagoon salinity level. However, rotifers and cladocerans were absent during most of this study; these taxa likely dominated during freshwater conditions under a natural

regime, and generally comprise easier prey for zooplanktivorous larval stages of fish than do copepods (e.g. Morales-Ventura et al. 2004; Garcia et al. 2008). Longer periods of freshwater conditions may thus promote fish recruitment.

Conclusions

The opening and closing of lagoons to the ocean, as occurs in Waituna Lagoon, is a natural process. However, the opening of these lagoons for management of terrestrial environments leads to their timing and frequency being unusual. Zooplankton dynamics are affected predictably by lagoon openings, owing primarily to the associated salinity increases. As zooplankton responded to both salinity and temperature changes in the temperate Waituna Lagoon, the timing and duration of lagoon breaches has implications for zooplankton that may not be apparent under a natural regime. Ultimately, an appropriate timing for the opening of temperate lagoons that might allow a freshwater zooplankton fauna to return should rely on the best time for rapid barrier bar reformation and maximum freshwater input (i.e. the recovery of zooplankton relies on the rate of return to freshwater conditions). Rainfall will vary temporally depending on the climatic area in which the lagoon is situated (for example, in southern New Zealand, summer is one of the wettest seasons; Garr & Fitzharris 1991), precluding generalisations about this timing in temperate regions. However, lagoons are managed with terrestrial land use in mind, where it is preferable to maintain open systems with low water levels. A clear conflict therefore exists for the appropriate timing of barrier breaches between that which favours zooplankton recovery and that which favours terrestrial management.

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Appendix 1: Zooplankton taxa recorded from Waituna Lagoon, South Island, New Zealand, between 22 April 2004 and 9 April 2006

Cladocera
Chydorus sp.*Daphnia carinata***Calanoid copepods***Acartia ensifera**Gladioferens pectinatus**Centropages aucklandicus***Harpacticoid copepods***Amphiascoides* sp.*Mesochra parva*

Canuellidae

Paradactylopodia sp.*Ectinosoma* sp.*Tisbe* sp.*Euterpina acutifrons***Cyclopoid copepods***Diacyclops bicuspidatus**Halicyclops* sp.

indet. Copepod nauplii

Rotifers*Aspelta harringi**Notholca squamula*

Bdelloids

*Polyarthra dolichoptera**Cohurella adriatica**Synchaeta oblonga**Cohurella colurus**Synchaeta vorax**Encentrum marinum**Synchaeta* sp.*Keratella procurva**Trichocerca marina**Notholca marina/labis**Trichocerca rattus**Notholca salina***Other taxa**

Amphipoda

Gastropod larvae

Ascidian larvae

Isopoda

Barnacle larvae

Mites

Bivalve larvae

Mysidae

Chironomid larvae

Ostracoda

Cnidaria medusae

Polychaete larvae

Fish larvae

Tardigrada