Responses of zooplankton assemblages to spatio-temporal variability in environmental conditions of brackish coastal ponds, Auckland, New Zealand

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Abstract

Brackish waters, including estuaries, lagoons and coastal ponds, all experience fluctuations in their physicochemical properties, particularly their salt concentrations, due to the mixing of marine and freshwater inflows. Brackish water ecosystems are particularly vulnerable to a number of threats, including sea-level rise projections, salinization and biological invasions. Most of the research pertaining to brackish waters is skewed towards lagoons and estuaries, while relatively little information exists on coastal ponds. Based on their intermediate trophic position and sensitivity to the environment, zooplankton are widely accepted as the ideal model group for aquatic research. Consequently, the aim of this study was to examine changes in zooplankton community composition and species richness relative to environmental conditions in brackish coastal ponds, Auckland, New Zealand. To achieve this, eight coastal stormwater ponds, four freshwater ponds, and four marine sites, all with varying salt concentrations, were selected to represent a wide salinity gradient. Zooplankton and environmental variables, including salinity, chlorophyll-*a*, temperature, dissolved oxygen, pH and seasonal change in salinity, were sampled in winter (22 July 2021) and summer (14 January 2022).

The coastal ponds displayed marked spatio-temporal variability in environmental conditions. Species richness was generally lower in brackish coastal ponds than in the freshwater and marine sites, providing some support for the predictions of Remane (1934). A canonical correspondence analysis (CCA) indicated that salinity explained the greatest proportion of variation in zooplankton community composition in summer (18.8 %, $p = 0.002$) and in winter 18.6 %, $p = 0.002$). In the winter ordination, seasonal change in salinity explained a large proportion of variation in zooplankton community composition (11.5 %, $p = 0.024$), independent of the variation explained by salinity. Temperature also explained a small proportion of variation in the winter ordination (10.4 %, p = 0.040). A community shift in dominance was recorded along the sampled salinity gradient. At the lower extreme of the gradient, the zooplankton assemblages of the freshwater sites were dominated by freshwater cladocerans, such as *Chydorus* sp. and *Alona* sp., and small rotifer species, including *Lecane closterocerca*, *Lecane luna*, *Trichocerca stylata* and *Trichocerca porcellus*. In sites characterised by intermediate salinities, euryhaline copepods, such as *Sulcanus conflictus* and *Gladioferens pectinatus*, and bdelloid rotifers dominated the assemblages. The zooplankton assemblages of marine sites and highly saline ponds were dominated by marine copepods, including *Paracalnus parvus* and *Oithona similis*, and the marine cladoceran *Penilia avirostris*, and crustacean larvae. Four non-indigenous zooplankton species were identified in this study, with only two species (*Daphnia galaeta* and *Sulcanus conflictus*) present in brackish coastal ponds. One cryptogenic species (*Notholca* cf. *salina*) was recorded in two brackish coastal ponds.

This study demonstrates that coastal ponds display high levels of spatio-temporal environmental variability and low species richness. Further, my findings suggest that salinity is the most important factor driving zooplankton community composition in coastal ponds, as widely reported in estuaries and lagoons. Changes in salinity may lead to the disappearance of species that are less tolerant to such changes and the appearance of euryhaline species. Overall, my study has provided insights into these overlooked ecosystems and their unique characteristics. I recommend that this study should be expanded to brackish coastal ponds outside of the Auckland region with the inclusion of further potential explanatory variables, such as fish and macroinvertebrate sampling. Future research should also be conducted to understand the effects of salinity on cryptic speciation in brackish waters.

Acknowledgements

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Chapter 1
Introduction

1.1 Brackish coastal waters

Brackish waters such as estuaries and coastal lagoons are recognised as transitional interfaces between terrestrial ecosystems, freshwater environments and the sea (Basset *et al.,* 2013a). The mixing of saline water and freshwater inflows in these ecosystems gives rise to unique properties shared by all brackish waters, such as the presence of strong gradients and fluctuations of their physicochemical properties, particularly their salt concentrations (Cognetti & Maltagliati, 2000; Paturej & Gutkowska, 2015; Gutkowksa *et al.,* 2019). Generally, high environmental variability, as seen in these ecosystems, translates to low overall biodiversity, but high abundances of adapted organisms that are tolerant of changing conditions (e.g., euryhaline species; Laprise & Dodson, 1994; Helenius *et al.,* 2017). Despite all belonging to the same conceptual class, a variety of brackish water ecosystems can be differentiated from one another by: (1) the degree of connection to adjacent freshwater and marine systems; (2) the extent of dilution of seawater by land run-off, and (3) their degree of enclosure (Tagliapietra *et al.,* 2009). For example, an estuary is a semi-enclosed water body that has a permanent or periodic connection to the sea and is also measurably diluted with freshwater from a river or rivers (McLusky, 1981; Potter *et al.,* 2010; Basset *et al.,* 2013b). Lagoons, on the other hand, are shallow areas of brackish water that are isolated from the sea, usually as a result of coastal terrestrial barriers (Barnes, 1980; Pérez-Ruzafa *et al.,* 2019), which have been coined by some authors as ‘coastal lakes’ (Tagliapietra *et al.,* 2009). As definitions of these systems can be interchangeable, the main difference is found in the flow dynamics. In estuaries, water typically flows fast and with force towards the ocean, while in lagoons, the water is shallower and flows comparatively slowly (Schubert & Telesh, 2017).

Relative to lagoons and estuaries, coastal ponds have been little studied. The distinction between coastal lagoons and ponds is difficult to establish as both are shallow bodies of water with restricted access to the sea. However, in freshwater ecosystems, ponds have been defined by the combination of their comparatively small size, being either less than 2 ha (Williams *et al.,* 2010) or less than 5 ha in area (De Meester *et al.,* 2005), and shallow depth, less than approximately 5 m (Richardson *et al.,* 2022). Generally, ponds display higher spatio-temporal environmental variability than larger water bodies due to their relatively small volumes and catchment sizes, which can be both beneficial and disadvantageous when it comes to their health (Biggs *et al.,* 2005). When exposed to pollutants, their small catchments provide little buffering capacity compared to larger water bodies (e.g., rivers and estuaries). On the other hand, some ponds can have exceptionally high water quality, as they are exposed to fewer sources of pollution than water bodies with larger catchments (Biggs *et al.,* 2005). Furthermore, smaller catchments are generally easier and less expensive to manage or mitigate anthropogenic practices that affect biodiversity (Declerck *et al.,* 2006). As such, for the sake of the present study, coastal ponds will represent a separate category of brackish ecosystem from estuaries or lagoons.

1.2 Vulnerability of brackish water ecosystems

Brackish waters are valuable from both an ecological and economic standpoint, as they are characterised by high biological productivity (Newton *et al.,* 2014), and contribute a range of goods and services, such as fisheries (Lamberth & Turpie, 2003) and tourism (Pérez-Ruzafa *et al.,* 2011). Despite their recognised value, extensive anthropogenic utilisation and activity, coupled with their geomorphology, have rendered brackish waters vulnerable to a large variety of threats, including climate change and biological invasions (Newton *et al.,* 2014).

It is now widely accepted that anthropogenic climate change is responsible for the recently observed changes in global temperature and precipitation patterns (Jeppesen *et al.,* 2015; Anton-Pardo & Armengol, 2011). The Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) has projected global mean sea level to rise between 0.09 m to 0.88 m and the global-mean temperature increase range to be from 1.4 °C to 5.8 °C by 2100 (IPCC, 2001a). Coastal aquatic environments, including estuaries, lagoons and coastal ponds, are particularly threatened by these projected changes, as they are vulnerable to an increase in saline intrusions from rising sea levels (IPCC, 2001b; Schallenberg *et al.,* 2003; Jeppesen *et al.,* 2015; Pereira *et al.,* 2018). For example, Robins *et al.* (2014) modelled the interaction of projected sea-level rise with maximal changes in river flow in the Conwy Estuary, United Kingdom. Their model predicted a prospective increase in the saline intrusion length and alteration of the longitudinal salinity gradient that would have far-reaching consequences for nutrient transport, water quality and ecosystem resilience (Robins *et al.,* 2014). Enclosed coastal lagoons are also extremely vulnerable to being overwhelmed by sea-level rise, which was modelled by Snoussi *et al.* (2008) along a 21 km coastline in Morocco. These authors predicted that between 24 % and 59 % of the coastline would be lost by flooding, including the lagoons and salt marshes, as they are unable to maintain elevation above sea level or migrate landwards (Snoussi *et al.,* 2008). In New Zealand, our long and highly variable coastline is punctuated by an average of 7.4 lakes, wetlands and lagoons (comprising an average of 260.5 ha) per 100 km (Schallenberg *et al.,* 2003), all of which are likely to be impacted by climate change. Due to the predicted salinisation of coastal aquatic environments associated with sea-level rise and climate change, it is becoming increasingly important to understand the effects of salinity on coastal brackish water communities.

Biological invasions are considered to be another of the major threats to biodiversity and the integrity of most ecosystems on Earth (Simberloff *et al.,* 2013). Aquatic ecosystems are in the midst of this crisis, as once an invader establishes itself in a water body, eradication is typically impossible and any control measures required may be ongoing and expensive (Parkes & Duggan, 2012). Brackish waters are particularly susceptible to biological invasions due to the combination of three essential elements: 1) high propagule pressure, 2) invasiveness of the non-native species and 3) high invasibility of the habitats themselves (Elton, 1958; Davis *et al.,* 2000). Propagule pressure, also known as 'introduction effort' (Blackburn & Duncan, 2001), has been defined as a measure of the frequency and/or the number of individuals released into a region to which they are not native (Carlton, 1996). Coastal brackish waters can be subjected to high propagule pressure because they are often located near anthropogenic vectors of aquatic introductions, such as shipping ports, aquaculture facilities and population centres that can lead to aquarium trade releases (Williams & Grosholz. 2008; Tang, 2020). Invasiveness, the second element of successful invasion, falls in the hands of the invaders themselves and is determined by their ability to adapt to their newly-inhabited conditions and outcompete previous occupants (Lee, 1999). The final element required for successful establishment of invaders to occur is invasibility, or the vulnerability of the ecosystem to invaders (Lonsdale, 1999; Davis *et al.,* 2000), which is largely controlled by environmental variability, disturbance regimes, and a reduced degree of biotic resistance by native species (Elton, 1958; Banks & Duggan, 2009). Generally, brackish waters meet all of these criteria, as they are characterised by fluctuating physicochemical properties, can have comparatively low levels of biodiversity (Remane, 1934; Wolff, 1999), and are among the most modified aquatic ecosystems globally (Nehring, 2006). These characteristics translate to low overall biotic resistance and the creation of 'empty niches' that can be readily occupied by non-native species with high environmental tolerances (Tang, 2020).

1.3 Constructed brackish waters

Urbanisation and the expansion of agriculture and commercial mining activities have promoted the engineering of artificial water bodies (e.g., dammed reservoirs, ornamental urban ponds, retired quarries) in many parts of the globe (Grinham *et al.,* 2018). Amongst these artificial ecosystems, there is a growing number of constructed brackish waters occurring alongside the development of coastal communities. For example, stormwater ponds are commonly used near residential and industrial areas to receive runoff, control flooding, and, ultimately, improve the water quality of adjacent natural aquatic ecosystems (Serrano & DeLorenzo, 2008; Greenfield *et al.,* 2019). Stormwater ponds are susceptible to stagnation in warmer months and have other water quality issues due to the combination of high pollutant loading and reduced flushing capacities (Novotny, 1995; DeLorenzo *et al.,* 2012). Furthermore, these unique systems span a wide range of salinities depending on the degree of direct or subsurface connectivity with tidal estuaries or the sea (Greenfield *et al.,* 2019). An emerging trend in the literature is that constructed waters are more susceptible than natural waters to the invasion of non-indigenous organisms (Johnson *et al.,* 2008; Banks & Duggan, 2009; Parkes & Duggan, 2012; Taylor & Duggan, 2012). Generally, constructed waters are significantly younger in age, experience higher levels of disturbance and have greater environmental variability than natural waters (Havel *et al.,* 2005; Taylor & Duggan, 2012). All of these attributes suggest that constructed waters have lower biotic resistance, which is likely to facilitate the successful establishment of non-indigenous species. Much of the literature pertaining to this trend has focused on constructed freshwater ecosystems, such as reservoirs (Havel *et al.,* 2005; Johnson *et al.,* 2008), retired quarries, open-cast mines and ornamental ponds (Banks & Duggan, 2009) and farm ponds (Le Quesne *et al.,* 2021). The invasibility of constructed brackish waters has received relatively little attention in comparison (e.g., Frisch *et al.,* 2005; Glasby *et al.,* 2007), which is unfortunate as constructed brackish waters may be just as, if not more, vulnerable to invasion than constructed freshwater ecosystems. Given the potential impacts of non-indigenous organisms on native aquatic biodiversity, it is important that we develop our understanding of constructed brackish waters, such as coastal stormwater ponds, to the same level that we have of constructed freshwater ecosystems.

1.4 Relationship between zooplankton and salinity

Zooplankton are an ideal model group for ecological research of aquatic ecosystems, as although typically small in size, they dominate the animal diversity found in standing freshwaters (Brönmark & Hansson, 2002), and can also be highly abundant and diverse in brackish and marine environments (Fossi *et al.,* 2001; Richardson, 2008; Belkahia *et al.,* 2021). Zooplankton are essential for supporting and maintaining ecosystem functioning due to their intermediary role in transferring nutrients and energy from primary producers to higher trophic levels in food chains (Gutierrez *et al.,* 2018). Additionally, their small size and short lifespans (<1 year) make them highly sensitive to changes in physical, chemical and biological conditions (Richardson, 2008; Duggan & White, 2010; Chiba *et al.,* 2018). As such, they are particularly susceptible to the environmental variability of brackish water habitats.

Salinity is an important determinant of life and often represents a major structuring gradient in aquatic systems, including near-sea, brackish waters (Schallenberg *et al.,* 2003; Jeppesen *et al.,* 2007; Dube *et al.,* 2010; Horváth *et al.,* 2013; Gutkowska *et al.,* 2019). Recent global studies have described how zooplankton communities are influenced by salinity gradients in brackish waters, including lagoons (e.g., Kozlowksy-Suzuki & Bozelli, 2003), estuaries (e.g., Froneman, 2004) and coastal ponds (e.g., Anton-Pardo & Armengol, 2011; Sgarzi *et al.,* 2019). The general agreement of prior research is that salinity has a pronounced effect on zooplankton community composition and that even moderate salinity increases can lead to significant structural changes (e.g. Schallenberg *et al.,* 2003; Froneman, 2004; Anton-Pardo & Armengol, 2011). A common pattern found is that as salinity increases from freshwater conditions (<0.05 PSU), to brackish conditions (between 0.05 PSU to 30 PSU) (Gutkowska *et al.,* 2018), to fully marine concentrations (>30 PSU), zooplankton composition shifts from smaller, less tolerant species, to larger, euryhaline species, and finally to fully marine species (Kozlowsky-Suzuki & Bozelli, 2004; Duggan & White, 2010). A further recurring phenomenon described across this gradient is referred to by 'Remane's curve' (Remane, 1934), whereby zooplankton species richness is expected to be highest at low salinities (i.e., freshwater systems) and high salinities, (i.e., fully marine systems), and is generally lowest between salinities of 5 and 8 PSU (Remane, 1934; Remane & Schlieper, 1971; Cognetti & Maltagliati, 2000; Jensen *et al.,* 2010).

1.5 Zooplankton in New Zealand brackish waters

While these international studies provide a useful overview for understanding broad-scale influences of brackish waters on zooplankton communities, there have been few studies conducted in New Zealand. Roper *et al.* (1983) sampled a wide spatial salinity gradient (2.0 to 33.5 PSU) within the Avon-Heathcote Estuary, a bar-built estuary situated on the east coast of the South Island. They collected zooplankton from five stations along the estuary over a six-month period and observed longitudinal changes in community composition, with marine zooplankton species generally most abundant in stations closer to the estuary mouth, while estuarine and freshwater species were most abundant in stations up river. Duggan & White (2010) found similar zooplankton variability to Roper *et al.* (1983) in Waituna Lagoon, a large (surface area 3556 ha), temperate lagoon located in the South Island of New Zealand. Waituna Lagoon is subjected to occasional 'artificial' breaches of the sandbar that separates it from the ocean. These authors noted considerable variability in salinity over the two-year study period, with the lagoon displaying initial high salinities (>30 PSU) while the barrier bar was open, which gradually returned to low salinities following the natural closure of the barrier bar (<5 PSU). Following a barrier breach, the zooplankton community shifted from dominance of freshwater species to either mesohaline or fully marine species, in association with the rapid, extreme increases in salinity. They attributed this shift to the removal of freshwater species that were either killed by osmotic shock or flushed out to the ocean, and correspondingly, the immigration of marine taxa entering the lagoon via marine inflows. Following the reclosure of the barrier bar, freshwater species were able to gradually re-establish as salinity concentrations declined. Hall & Burns (2003) examined the influence of salinity and tidal currents on the crustacean zooplankton community in Lake Waihola, a large (surface area 544 ha), coastal lake in the South Island. The salinity gradient observed within Lake Waihola (<1 to 4.8 PSU) is created by the combination of brackish water intrusions from regular tidal cycles and freshwater inflows from several small connections to the Waipori River. In accordance with international studies, they found that salinity was the strongest driver of the variation in the abundance and species composition of the zooplankton assemblage. Furthermore, they proposed that increases in salinity at Lake Waihola during high salinity periods (i.e., summer) promoted a seasonal transition from a community dominated by freshwater cladocerans to one dominated by euryhaline copepods. Schallenberg *et al.* (2003) also examined Lake Waihola and reiterated the importance of salinity as the dominant environmental variable influencing zooplankton taxonomic richness, abundance and community composition. Schallenberg *et al.* (2003) concluded that if their results can be generalised, then climate-induced salinity increases will have a negative impact on the freshwater zooplankton communities in other similar freshwater-to-brackish ecosystems. The above studies all examined single ecosystems. To date, few published studies have examined salinity gradients among ecosystems at a landscape scale, internationally or in New Zealand (e.g., Anton-Pardo & Armengol, 2011; Lucena-Moya &

Duggan, 2017). Lucena-Moya & Duggan (2017) selected multiple sites in the North Island, New Zealand, which included representatives of different estuary types as designated by the 'Estuary Environment Classification' (EEC), proposed by Hume *et al.* (2007). These authors concluded that abiotic variability, such as salinity gradients, is a major factor influencing zooplankton distribution and diversity among distinct estuarine systems. Furthermore, they found that zooplankton diversity met the expectations of Remane's curve, with the lowest zooplankton richness observed in estuarine systems with intermediate salinities. That study is the only New Zealand research that has focused on a salinity gradient represented among ecosystems across a broad geographical area.

1.6 Zooplankton in brackish coastal ponds

New Zealand-based research of zooplankton on brackish waters has to date been confined to examining assemblages in larger habitats, such as estuaries or lagoons, and within single ecosystems, from which it can be difficult to assess spatial trends and make wider generalisations. Although these studies have reached similar conclusions, there is a clear research deficit in research on smaller brackish water bodies (i.e., coastal ponds). Internationally, also, research on zooplankton in brackish coastal ponds is limited. Those that have been were conducted in a geographically confined area, in the Mediterranean region, as models have indicated that coastal wetland areas there, comprised of temporary and permanent ponds, lagoons and marshes, are at high risk of climate change and sea-level rise (Sala *et al.,* 2000). For example, Anton-Pardo & Armengol (2011) investigated zooplankton in several shallow coastal ponds with different conductivities (1.1 to 18.6 mS cm^{-1}) and water permeance times along the east coast of Spain. Overall, they found that salinity was the main environmental variable structuring zooplankton communities and that increases in this variable led to reductions in cladoceran density and richness. By sampling from a range of pond sites, these authors were able to assess the possible consequences of climate change on Mediterranean pond ecosystems with a broader perspective than would be possible by focusing on a single system alone. Sgarzi *et al.* (2019) investigated the effects of abiotic (i.e., conductivity, pond morphology, etc.) and biotic (i.e., fish predation, food resource availability, etc.) factors on the size and taxonomic structure of phytoplankton and zooplankton assemblages in 13 permanent brackish ponds in Catalonia, Spain. These authors concluded that while phytoplankton size diversity was influenced by food resource availability, zooplankton size diversity was not influenced by any of the tested factors. Interestingly, they did not find a significant effect of conductivity (i.e., a proxy for salinity) on phyto- and zooplankton taxonomic diversity, but that pond morphology was a key predictor - a result that differs from what has been reported in larger brackish waters (e.g., Schallenberg *et al.,* 2003; Brucet *et al.,* 2009; Paturej & Gutkowska, 2015; Yuan *et al.,* 2020). It is important to consider the biotic and abiotic components of small coastal ponds to the same degree as we have of larger water bodies, as small ponds may support higher diversities of aquatic species than larger adjacent ecosystems due to environmental heterogeneity (Scheffer *et al.,* 2006; Davies *et al.,* 2008; Le Quesne *et al.,* 2021). Furthermore, the above studies have focused on naturally occurring coastal ponds. Therefore, a large research gap exists when it comes to understanding how zooplankton communities are affected by environmental variables in constructed coastal ponds, such as stormwater ponds.

1.7 Aims and hypotheses

The purpose of the present study was to determine the effects of environmental factors on zooplankton communities within eight New Zealand constructed coastal ponds, relative to four marine and four freshwater control sites. The coastal ponds have different degrees of connection to the ocean and thus varying salinity conditions, covering a wide salinity gradient.

My research will, locally and globally, develop knowledge of how zooplankton communities respond to environmental fluctuations in constructed coastal ponds, which, given their trophic level and sensitivity, will be useful for understanding brackish water ecosystem health and functioning.

My study is the first to focus on zooplankton assemblages in brackish coastal ponds in New Zealand, rather than in larger brackish standing water bodies or estuaries, and one of only a limited number globally. Furthermore, to better determine trends among coastal ponds, the present study will focus on a salinity gradient across multiple sites, rather than taking a single system approach.

My hypotheses are as follows:

1. Salinity will have the greatest influence on zooplankton community composition among coastal brackish ponds, as reported in estuaries and lagoons.
2. Zooplankton community composition will not only vary spatially, among sites along the salinity gradient, but temporally, between seasons.
3. Zooplankton community composition will be similar to larger systems that have been previously examined in New Zealand and around the world.
4. Species richness will be low among the coastal ponds and high in the freshwater and marine sites, matching the predictions of Remane's curve.
5. Non-native zooplankton species will be found in the coastal pond sites as they are recently constructed, have low biotic resistance and experience high levels of anthropogenic activity and disturbance.

Chapter 2
Methods

2.1 Site selection

A list of 23 coastal ponds in Auckland, New Zealand, was compiled using satellite imagery on Google Maps, New Zealand Landcover Explorer Maps and through conversations with colleagues. These preliminary ponds were selected as they appeared to be constructed and potentially marine-influenced due to their proximity to the ocean (i.e., within ~400 m of the coastline). Initial assessment of accessibility of all sites was conducted in May 2021. Upon initial site visitation, some pond sites were removed from consideration as they were inaccessible (e.g., within fenced industrial areas) or the influence of the ocean on them was limited (e.g., due to being at a significantly higher elevation than sea level), and thus were not saline enough to be considered brackish. Salinity was measured *in situ* using a Yellow Springs Instruments Model ODO/CT Prosolo hand-held meter (YSI; Yellow Springs, OH, USA) at a depth where the probe was entirely submerged below the surface (~10 cm).

From this assessment, a subset of eight constructed pond sites were selected that represented a range of salinities; above the average salinity of normal freshwaters (0.0 to 0.5 PSU), but lower than the average salinity of seawater (34 to 36 PSU) (Table 1). All of these sites were constructed or highly modified stormwater ponds. Two coastal pond sites also have secondary purposes. Onepoto Lagoon (Site 7) was initially designed as a stormwater pond but is used for the recreational sailing of model boats. Wattle Farm 1 (Site 11) was a sewage treatment pond that was decommissioned and modified to be a stormwater pond (Auckland Council, 2018). Site 11 is also frequently used for model boat sailing and waka ama racing. Information regarding the construction of the pond at Savill Drive (Site 12) was unavailable, though it is most likely a stormwater pond as it is located near a residential area and large industrial buildings. Four marine and four freshwater sites were also selected for comparison with the brackish pond sites and to extend the examined salinity gradient. These control sites were chosen due to their close proximity to the eight coastal ponds, while also being geographically isolated from one another. In total, 16 sites were chosen for this study (Figure 1, Table 1). The total surface areas (m^2) for each of the freshwater and coastal ponds were estimated by outlining the boundary of each pond using the 'measure distance' tool on Google Maps (Table 1).

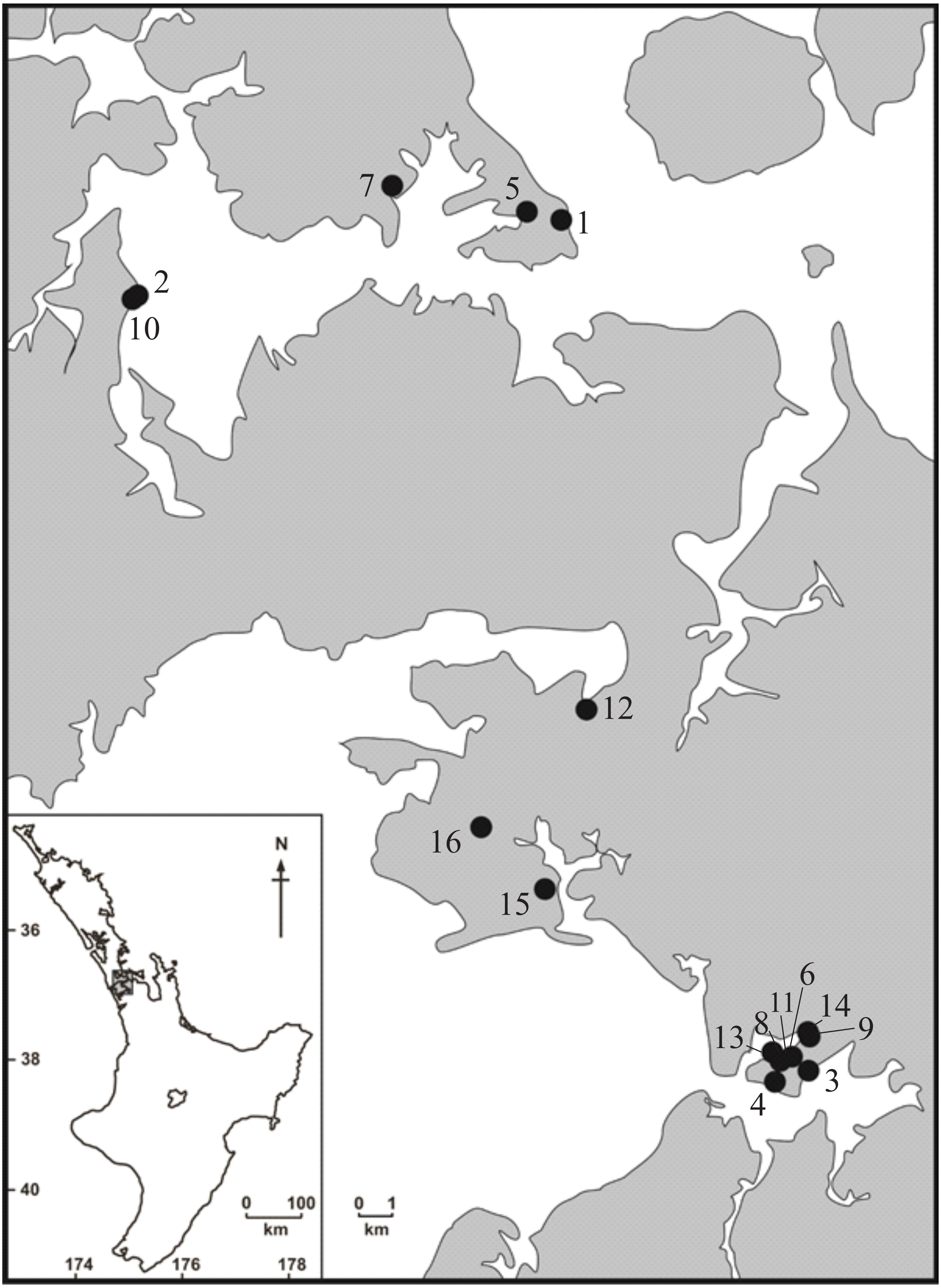

Figure 1. Map of the coastal pond, freshwater and marine site locations for sampling within Auckland, New Zealand.

Table 1 The location and site type of the 16 sites that were sampled in this study. Includes estimated total area (m^2) of the coastal pond and freshwater sites.

Site	Name	Site type	Latitude	Longitude	Estimated total area (m^2)
1	Cheltenham Beach	Marine	36°49'11.0"S	174°48'30.8"E	N/A
2	Te Atatū Peninsula	Marine	36°50'29.4"S	174°39'37.9"E	N/A
3	Carnouistie Drive	Marine	37°03'02.2"S	174°53'33.4"E	N/A
4	Saint Annes	Marine	37°03'15.2"S	174°52'46.8"E	N/A
5	Waitemata Golf	Coastal pond	36°49'02.9"S	174°47'43.6"E	387.29
6	Fergy Crescent 1	Coastal pond	37°02'50.0"S	174°53'07.2"E	3,653.55
7	Onepoto Lagoon	Coastal pond	36°48'33.7"S	174°45'02.3"E	10,295.93
8	Esplanade Reserve	Coastal pond	37°02'55.2"S	174°52'55.5"E	3,677.57
9	Wattle Farm 1	Coastal pond	37°02'29.7"S	174°53'29.1"E	20,349.83
10	Harbour View Beach Reserve	Coastal pond	36°50'25.7"S	174°39'40.3"E	675.11
11	Fergy Crescent 2	Coastal pond	37°02'51.1"S	174°53'08.0"E	220.68
12	Savill Drive	Coastal pond	36°57'10.7"S	174°48'57.9"E	453.89
13	Stranraer Crescent	Freshwater	37°02'47.9"S	174°52'43.6"E	1870.00
14	Wattle Farm 2	Freshwater	37°02'25.4"S	174°53'28.6"E	19015.00
15	Auckland Airport	Freshwater	37°00'04.4"S	174°48'04.4"E	3269.77
16	Montgomerie Road Reserve	Freshwater	36°59'06.0"S	174°46'46.3"E	2427.23

2.2 Fieldwork sampling

2.2.1 Environmental variable sampling

Environmental variable sampling was conducted on 22 July 2021 (austral winter) and 14 January 2022 (austral summer). For determination of chlorophyll-*a*, a known volume of water was collected at approximately 5 cm beneath the surface of each site using a 60 mL syringe. Each sample was immediately filtered through a Whatman GF/C glass microfibre filter (nominal pore size 1.2 µm) under low pressure. Each filter was then folded in half (sample side inwards), wrapped in aluminium foil to prevent light exposure and stored in a plastic container on ice until return to the laboratory. The filters were then stored in a freezer (~-20 °C) for up to three weeks until further analysis.

Salinity, temperature and dissolved oxygen saturation were measured at each site *in situ* using a Yellow Springs Instruments Model ODO/CT Prosolo hand-held meter (YSI; Yellow Springs, OH, USA). A hand-held calibrated pHTestr 30 meter was used to measure pH at each site *in* *situ*. All measurements were taken at a depth where the probe of each meter was entirely submerged below the surface (~10 cm). All environmental variables were measured twice, approximately 5 m apart from one another, at each site to produce two individual replicate measurements. An estimate of the relative degrees of seasonal change in salinity for each site was calculated as the difference between their average summer and winter salinity values.

Rainfall data were obtained from the National Institute of Water and Atmospheric Research (NIWA) CliFlo database (cliflo.niwa.co.nz, accessed March 2022). Monthly and daily rainfall (mm) data were extracted from the climate station report that was most central to the 16 sites, which was at Mangere, Auckland (36°57'53.3"S, 174°46'49.9"E). Data were extracted for monthly rainfall so as to summarise the overall precipitation patterns of the two sampling months (July 2021 and January 2022); that is, the total rainfall (mm) in each month. Daily rainfall data (mm) was also extracted for precipitation in the seven days prior to the sampling dates.

2.2.2 Zooplankton sampling

Samples for biological analyses were collected via wading on 22 July 2021 (austral winter) and 14 January 2022 (austral summer). Quantitative zooplankton samples were collected using five replicated fillings of a 2-L semi-transparent measuring jug, at a depth of ~0.25 m, and subsequent filtering using a plankton net with a mesh size of 40 µm, resulting in a total volume filtered of 10 L per sample. This was repeated twice so that two quantitative zooplankton replicates were collected for each of the 16 sites in each season. Immediately following collection, each sample was washed from the plankton net into a 250 mL container with water, and the filtrate preserved with ethanol (final concentration ~70 %).

2.3 Laboratory analyses

2.3.1 Chlorophyll-*a* extraction and analysis

For chlorophyll-*a* extraction, a solution of buffered acetone was produced. To do so, a saturated magnesium carbonate ($MgCO_3$) solution was made by adding 10 g of magnesium carbonate to 1000 mL of Ultrapure water and then mixed. This solution was settled for approximately 48 hours and then decanted into a clean container for the use in preparation of buffered acetone. To produce 90% (v/v) buffered acetone, 100 mL of the saturated $MgCO_3$ solution was added to 900 mL of analytical-grade acetone. To produce a 0.1 N HCl solution, in a fume hood wearing nitrile gloves, 0.85 mL of concentrated HCl was added to 50 mL of Ultrapure water, then made up to 100 mL. For homogenisation of the chlorophyll-*a* samples, clean 50 mL screw-cap Falcon tubes (rinsed with Ultrapure water) corresponding to one tube for each of the 64 chlorophyll-*a* samples were used. Each tube and lid were numbered accordingly with the site identification and replicate number. The stored filters were removed from the freezer and placed in the fume hood away from direct sunlight. Each filter was placed into a prelabelled 50 mL Falcon centrifuge tube with 20 mL of buffered acetone and was then ground to a slurry using an electric tissue grinder (DLAB D-160). The grinder was rinsed in buffered acetone before continuing to the next sample to prevent cross-contamination. Each homogenised Falcon tube was capped and stored in darkness under aluminium foil while working through the remainder of the samples. All samples were then steeped for 24 hours in the dark at 4 °C, shaken once over the 24-hour period. After the steeping period, the tubes were shaken vigorously and centrifuged for 10 minutes at 1583 *g* with a high brake at room temperature using a centrifuge (Universal 320 R).

Following acetone extraction, a standard protocol for fluorometric determination of chlorophyll-*a* pigments was performed using a Turner Designs 10-AU fluorometer (Paul, 2010). An initial blank reading was taken using a clean glass cuvette and 5 mL of 90 % buffered acetone solution. For the chlorophyll-*a* analysis, the fluorescence of 5 mL of supernatant of each replicate was measured. Following the first measurement, 50 µL of 0.1 N HCl was added to the solution to account for phaeophytin degradation and returned to the fluorometer. Each new glass cuvette was wiped with a clean tissue between use to ensure no fingerprints or smudges affected the measurements. Total chlorophyll-*a* concentrations were calculated from calibration curves based on known chlorophyll-*a* concentrations.

2.3.2 Zooplankton counts and taxonomic identification

In the laboratory, each 10 L zooplankton sample was filtered through a clean 40 µm mesh to remove ethanol. The sample was then transferred into a clean 250 mL measuring cylinder using distilled water and the final total volume of liquid (mL) was recorded for each sample. For zooplankton counts and identification, the sample was separated into 5 mL aliquots using an autopipette in a gridded Perpsex tray. The autopipette was moved in a figure eight-like motion within the 250 mL container to ensure that each aliquot was representative of the sample. The taxa within each sample were enumerated in 5 mL aliquots until a minimum of 300 individuals, or the entire sample, was counted (Branford & Duggan, 2017). For identification, individuals were examined using a stereomicroscope (Nikon, SMZ645, Japan) and compound microscope (Olympus, BH-2, Japan), at up to 400x magnification. Zooplankton were identified to species level where possible, using relevant taxonomic guides (e.g., Bradford-Grieve, 1994, 1999; Shiel, 1995; Chapman *et al.,* 2011). Data from the replicate samples from each site were combined and expressed as numbers per litre for analysis.

2.4 Statistical analyses

2.4.1 Environmental variables

The relationships among environmental variables from summer and winter were examined individually using Pearson's correlation analysis in STATISTICA version 13.5.0.17 (Statsoft, Inc., Tulsa, OK, USA). Environmental data that were not normally distributed were log(x+1) or $\log_{10}$ transformed prior to analysis.

2.4.2 Species richness

It is considered to be an almost unattainable goal in biological studies to produce a complete species inventory at any site, and one that would require extraordinary sampling effort (Chao & Chiu, 2016). Consequently, the simple method of counting species often underestimates the true species richness of a sample. The Chao-1 estimator (Harris, 1959; Chao, 1984) was developed to approximate species richness when there are many undetectable or 'invisible' species in a diverse assemblage. This method focuses on finding the true number of species based on the number of rarer species rather than the number of dominant species in an assemblage (Colwell & Coddington, 1994). In the present study, the Chao-1 estimator (classic and bias-corrected form) was used to estimate species richness for all sites in both summer and winter (Coddington *et al.,* 1996; Chao & Chiu, 2016) (Figure 6). Copepod nauplii were removed from calculations as they could not be confidently designated to a species and were likely already represented among identified adults at any site.

Equation 1: $S_{Chao1} = S_{obs} + f_1^2/(2f_2)$

Equation 2: $S_{Chao1} = S_{obs} + f_1(f_1 - 1) / 2(f_2 + 1)$

Where 'S_{Chao1}' is estimated species richness, 'S_{obs}' is the total number of species observed in a sample, 'f_1' is the number of species represented by a single individual (number of singletons) and 'f_2' is the number of species represented by two individuals (number of doubleton species).

The classic form of the Chao-1 estimator (Equation 1) was used for all calculations except when the number of doubletons was zero ($f_2 = 0$), in which case, the bias-corrected form (Equation 2) was used. Chao-1 estimated species richness and salinity were averaged for each of the three site categories (i.e., marine, freshwater and coastal ponds) for both seasons, to produce a simplified visual depiction of the relationship between the two variables. Statistical differences were tested using one-way ANOVA.

2.4.3 Zooplankton community composition

An exploratory Detrended Correspondence Analysis determined that the zooplankton communities were responding to underlying environmental gradients in a strongly unimodal rather than linear manner (ter Braak & Smilauer 1998). Canonical Correspondence Analysis (CCA) was thus performed separately on datasets from winter and summer, using CANOCO version 5.12 (Biometris, Wageningen, Netherlands) to investigate the influence of the measured environmental variables on zooplankton community composition among all of the sites. The datasets from winter and summer were analysed individually due to the high variability in salinity observed within several sites between seasons. For each analysis, zooplankton taxa were included in multivariate analyses only if they were present in at least two sites, so as to reduce the influence of species sampled by chance. Copepod nauplii were removed from this analysis as their inclusion could have skewed results due to; 1) their presence in proportionately high abundances across the entire salinity gradient, and 2) as they cannot be confidently designated to particular species. Following removal of taxa that did not meet these criteria, species abundance data for summer and winter were log(x+1) transformed to down weight the contribution of highly abundant species in the analysis. Where appropriate, environmental variables were transformed for normality and then all variables were standardized to zero mean and unit variance to eliminate the influence of differing scales of measurement (ter Braak & Smilauer, 1998).

Chapter 3

Results

3.1 Environmental variables

In summer, salinity ranged from 0.04 PSU to 40.13 PSU. Salinity was found to be greater in summer than in winter at most sites, with some exceptions (Figure 2). The four marine sites (Sites 1-4) generally had higher average salinities (>35 PSU) compared to those found in the brackish (Sites 5-12) and freshwater (Sites 13-16) sites. One coastal pond (Site 5) experienced an unusually high average salinity (37.34 PSU) in summer, which was greater than one of the marine sites (Figure 2). Results from the summer correlation matrix indicated that salinity was strongly negatively correlated with pH (R = -0.87, p = <0.001) and moderately negatively correlated with chlorophyll-*a* (R = -0.69, p = 0.002) (Table 3). That is, as salinity values increased, pH and chlorophyll-*a* generally decreased. Salinity was also moderately positively correlated with seasonal change in salinity (R = 0.66, p = 0.005) (Table 3). On average, the salinity of the freshwater sites increased by 0.03 PSU from winter to summer. Salinity increased on average by 10.67 PSU in the coastal pond sites between winter and summer, and by 7.44 PSU on average in the marine sites.

In winter, salinity ranged from 0.06 PSU to 37.60 PSU and was negatively correlated with pH (R = -0.55, p = 0.027) (Table 4). Despite the general trend that salinity was greater in all sites during the summer sampling period, there were three sites (Site 10, Site 15 and Site 16) where the salinity was higher in winter (Figure 2). Of these three sites, two were freshwater control sites (sites 15 and 16) that both showed an increase of less than 0.10 PSU from summer to winter. The other was a coastal pond site (Site 10) which increased by 8.32 PSU from summer to winter.

Chlorophyll-*a* concentrations ranged from 6.38 μg/L to 225.12 μg/L in summer and from 0.38 μg/L to 346.23 μg/L in winter. The lowest chlorophyll-*a* concentrations were found in the marine sites, ranging from 1.00 μg/L to 13.92 μg/L in winter and 6.38 μg/L to 13.65 μg/L in summer. The coastal pond sites showed extreme variation, with chlorophyll-*a* concentrations ranging from 8.50 μg/L to 225.12 μg/L in summer (average = 60.36 μg/L) and from 0.38 μg/L to 346.23 μg/L in winter (average = 73.59 μg/L). Chlorophyll-*a* was not correlated with salinity in winter, but was in summer (as described above). The chlorophyll-*a* concentration of Harbour View Beach Reserve (Site 10) notably decreased from 346.23 μg/L in winter to 52.92 μg/L in summer (Figure 2). Esplanade Reserve (Site 8) also notably decreased from 205.14 μg/L in winter to 26.38 μg/L in summer (Figure 2).

Temperature was relatively similar amongst the sites within each season, but showed typical seasonal variation. In summer, temperature ranged from 21.0 °C to 30.9 °C (average = 26.1 °C). In winter, temperature ranged from 12.3 °C to 15.4 °C (average = 14.0 °C).

Dissolved oxygen saturation ranged from 23.35 % to 175.85 % during summer and from 68.80 % to 139.60 % during winter. The Auckland Airport site (Site 15), a freshwater site, had higher dissolved oxygen saturation values in both seasons compared to the other sites. The dissolved oxygen concentration of the Waitemata Golf pond (Site 5) notably decreased from 83.55 % in winter to 23.35 % in summer (Figure 2).

Most sites had greater pH values in summer than in winter (Figure 2). In summer, pH ranged from 7.46 to 9.76 and from 6.75 to 11.15 in winter. Generally, the freshwater sites had the highest pH values, ranging from 8.10 to 11.15 in winter (average = 9.33) and 9.25 to 9.76 in summer (average = 9.42) (i.e., were more alkaline). The coastal pond and marine sites were relatively similar in pH. In winter, the Stranraer Crescent pond (Site 13) had an average pH of 11.15, which was noticeably greater and more alkaline than any other site across both seasons (Figure 2).

The extracted rainfall data showed that there was significantly greater total rainfall (mm) in the entire month of July 2021 (Austral winter: 88.4 mm) than there was during the month of January 2022 (Austral summer: 5.4 mm). There was 24.4 mm of rain in the week leading up to the winter sampling date (Table 2). In the week leading up to the summer sampling date, 0.0 mm of rain was recorded.

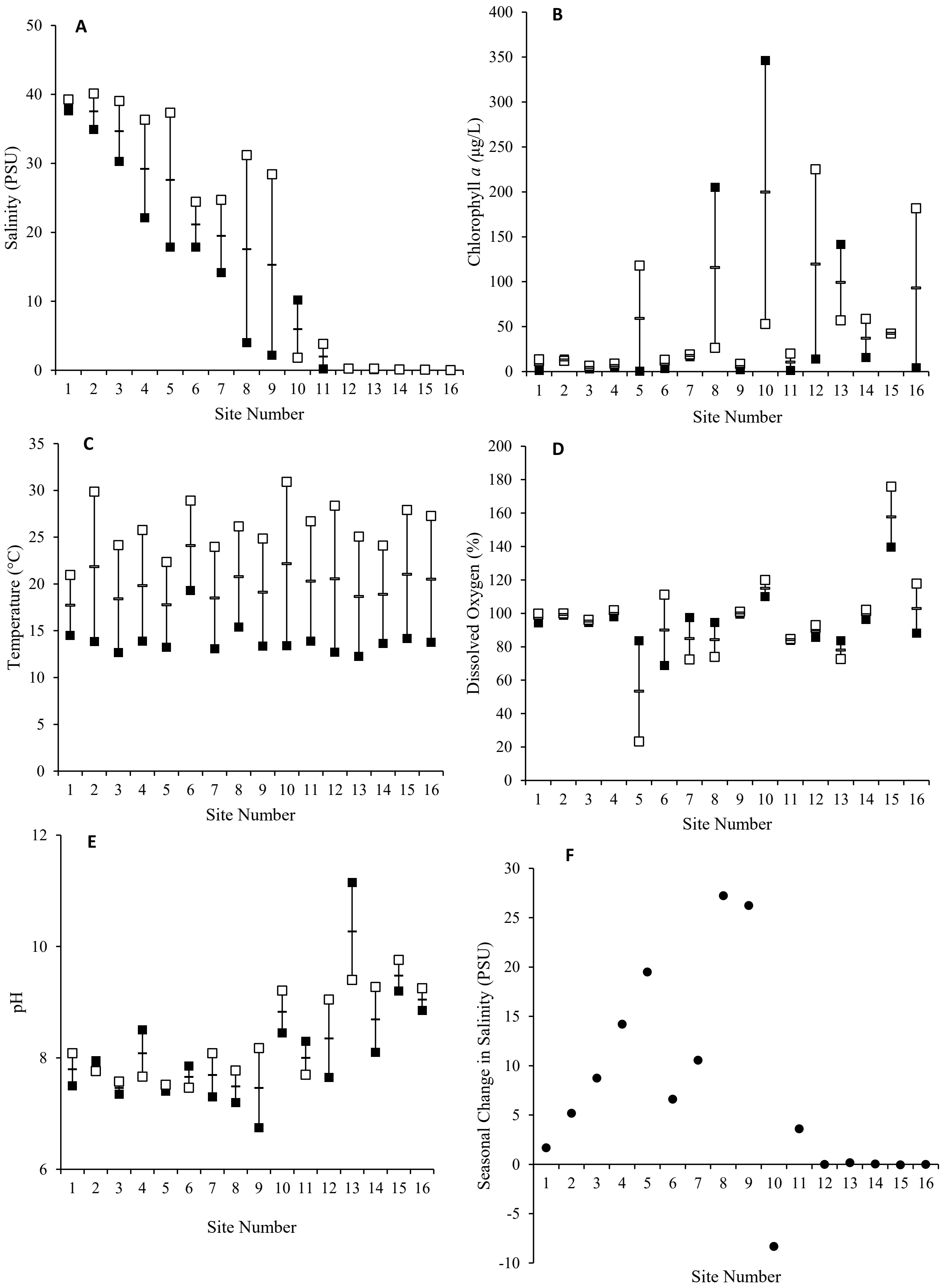

Figure 2. Averages of environmental variables (A: salinity, B: chlorophyll-*a*, C: temperature, D: dissolved oxygen saturation, E: pH, and F: seasonal change in salinity) for 16 sites. Sites are ordered from highest average salinity to lowest average salinity. Mean values for summer are represented by open squares, and mean values for winter are represented by closed squares. Average between the two seasons are represented by horizontal lines.

Table 2 Daily rainfall data obtained from National Institute of Water and Atmospheric Research (NIWA) CliFlo database. Data was originally recorded at the Mangere, Auckland climate station (36°57'53.3"S, 174°46'49.9"E). Daily rainfall is the amount of rainfall per day (mm), seven days prior to both sampling dates.

Date	Daily rainfall (mm)	Date	Daily rainfall (mm)
14 July 2021	0.0	6 January 2022	0.0
15 July 2021	0.0	7 January 2022	0.0
16 July 2021	0.0	8 January 2022	0.0
17 July 2021	0.8	9 January 2022	0.0
18 July 2021	11.0	10 January 2022	0.0
19 July 2021	10.2	11 January 2022	0.0
20 July 2021	2.4	12 January 2022	0.0
21 July 2021	0.0	13 January 2022	0.0

Table 3 Correlations between the environmental variables (*R* values in italic) sampled during summer. Bold values indicate a significant correlation ($p < 0.05$).

	Salinity		Temperature		pH		Dissolved oxygen		Chlorophyll-*a*		Seasonal change in salinity	
	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value
Salinity	*1.00*	1.00										
Temperature	*-0.36*	0.17	*1.00*	1.00								
pH	*-0.88*	**< 0.01**	*0.25*	0.35	*1.00*	1.00						
Dissolved oxygen	*-0.41*	0.12	*0.50*	0.05	*0.51*	**0.04**	*1.00*	1.00				
Chlorophyll-*a*	*-0.70*	**< 0.01**	*0.15*	0.57	*0.62*	**0.01**	*-0.10*	0.72	*1.00*	1.00		
Seasonal change in salinity	*0.66*	**0.01**	*-0.38*	0.15	*-0.62*	**0.01**	*-0.47*	0.06	*-0.37*	0.16	*1.00*	1.00

Table 4 Correlations between the environmental variables (*R* values in italic) sampled during winter. Bold values indicate a significant correlation ($p < 0.05$).

	Salinity		Temperature		pH		Dissolved oxygen		Chlorophyll-*a*		Seasonal change in salinity	
	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value	R	*p*-value
Salinity	*1.00*	1.00										
Temperature	*0.25*	0.35	*1.00*	1.00								
pH	*-0.55*	**0.03**	*-0.19*	0.49	*1.00*	1.00						
Dissolved oxygen	*-0.09*	0.73	*-0.28*	0.29	*0.10*	0.70	*1.00*	1.00				
Chlorophyll-*a*	*-0.24*	0.37	*-0.10*	0.71	*0.42*	0.11	*0.39*	0.13	*1.00*	1.00		
Seasonal change in salinity	*0.35*	0.18	*-0.12*	0.66	*-0.55*	**0.03**	*-0.15*	0.57	*-0.26*	0.34	*1.00*	1.00

3.2 Zooplankton composition and dynamics

A total of 45 zooplankton taxa were recorded throughout the study, including 5 calanoid copepods, 4 cyclopoid copepods, 2 harpacticoid copepods, 6 cladocerans, 19 rotifers and 9 other taxa (Table 5). All taxa have been previously identified in New Zealand, except for a possibly undescribed rotifer, *Notholca* cf. *salina*, which was found in two coastal pond sites within the Wattle Downs area (sites 6 and 11).

More zooplankton taxa were identified in summer (40) than in winter (31). Species richness, estimated using the Chao-1 estimator, varied seasonally and among sites (Figure 4). Although not statistically significant ($p = 0.07$), the coastal pond sites had comparatively low estimated species richness values (Figure 4). Estimated species richness was averaged according to site type (freshwater, coastal pond and marine) for both seasons (Figure 5). The marine sites had an average estimated species richness' of 8.4 in summer and 10.9 in winter. The coastal pond sites had an average estimated species richness' of 5.6 in summer and 5.8 in winter. The freshwater pond sites had an average estimated species richness' of 9.7 in summer and 9.3 in winter. Overall, the marine sites had the highest average taxon richness', followed closely by the freshwater sites. The coastal pond sites had the lowest average taxon richness'.

Table 5 List of zooplankton taxa according to the season and site category each was identified in. Summer: S, winter: W, freshwater: F, brackish: B, and marine: M.

Species	Season	Site category
Corycaeus aucklandicus (cop)	S, W	M
Euterpina acutifrons (cop)	S, W	M
Gladioferens pectinatus (cop)	S, W	B, M
Macrocylcops albidus (cop)	S	F
Mesochra parva (cop)	S, W	B
Mesocyclops australienses (cop)	S, W	F
Oithona similis (cop)	S, W	M
Paracalanus parvus (cop)	S, W	M
Skistodiaptomus pallidus (cop)	S	F
Sulcanus conflictus (cop)	S, W	F, B
Temora turbinata (cop)	S, W	M
Aslpanchna brightwellii (rot)	S	F
Asplanchna priodonta (rot)	S	F
Bdelloid spp. (rot)	S, W	F, B
Filinia sp. (rot)	S	F
Brachionus angularis (rot)	S	F
Brachionus quadridentatus (rot)	S	F, B
Keratella spp. (rot)	S, W	F, B, M
Lecane closterocerca (rot)	S	F, B
Lecane luna (rot)	S	F, B
Lepadella ovalis (rot)	S	F
Notholca cf. *salina* (rot)	S, W	B
Polyarthra dolichoptera (rot)	S	F
Rotaria neptuna (rot)	W	F
Synchaeta oblonga (rot)	S, W	F, B
Synchaeta pectinata (rot)	W	F
Synchaeta vorax (rot)	S	M
Trichocerca porcellus (rot)	S, W	F, B
Trichocerca stilata (rot)	S	F
Trichocerca tenuior (rot)	S, W	F
Alona sp. (cla)	S, W	F, B
Chydorus sp. (cla)	S, W	F, B
Daphnia galeata (cla)	S, W	F, B
Daphnia pulex (cla)	S, W	F
Ilycryptus sordidus (cla)	W	F
Penilia avirostris (cla)	S, W	M
Barnacle cyprid (cir)	W	M
Barnacle nauplii (cir)	S, W	B, M
Crab zoea (dec)	S, W	B, M
Sundry decapod larvae (dec)	S	M
Oikopleura spp. (lar)	S, W	M
Amphipod (amp)	W	M
Bivalve larvae	S, W	B
Ostrocod spp.	S, W	B, M
Polychaete larvae	S, W	B, M

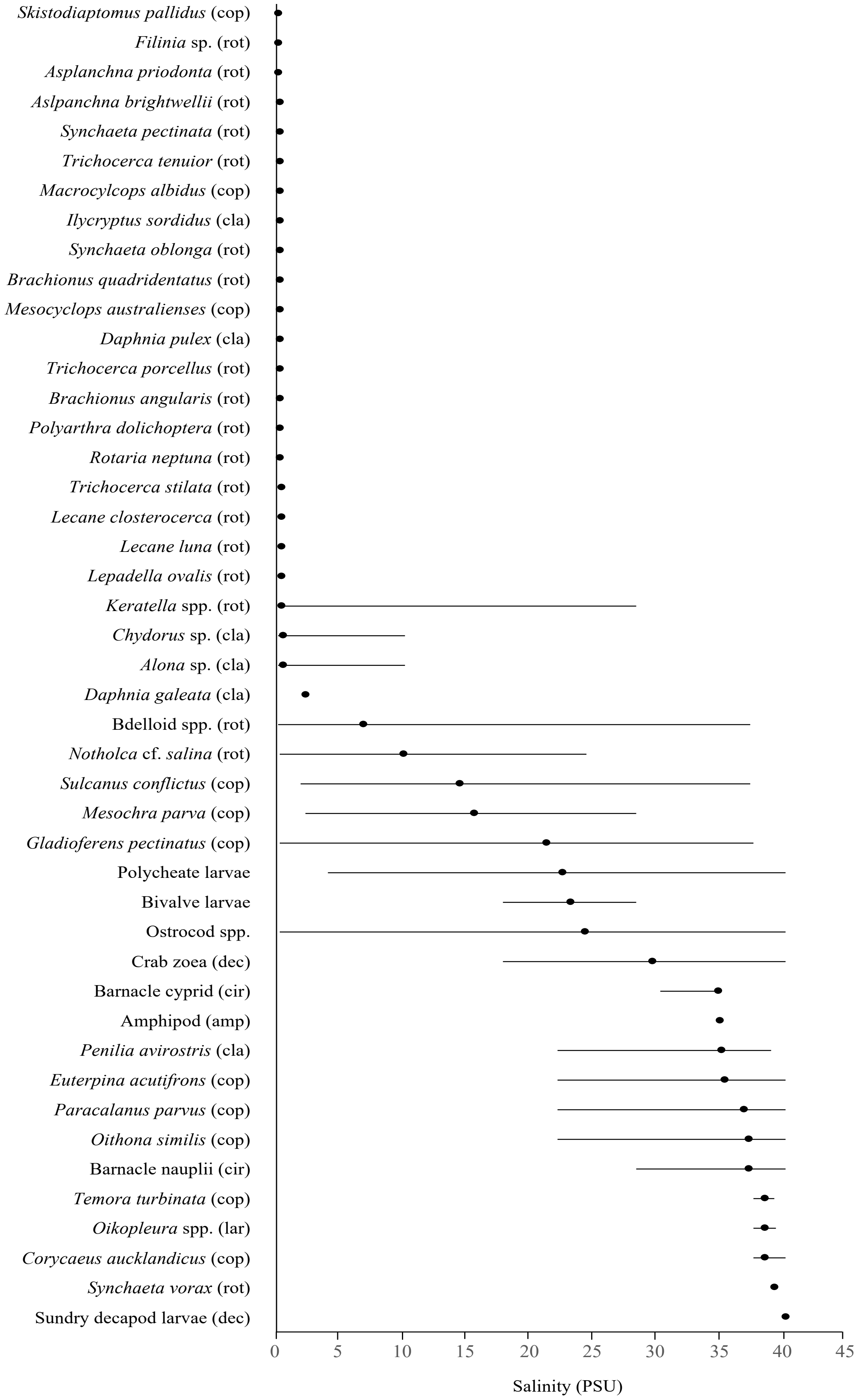

Figure 3. Distribution of the identified zooplankton taxa across a salinity gradient (black point is the weighted average, lower tail is the minimum salinity and upper tail is the maximum salinity of each taxon). The x-axis shows a salinity gradient, and the y-axis lists the zooplankton taxa identified. Taxonomic groups in brackets (rot: rotifers, cla: cladocerans, cop: copepods, dec: decapods, amp: amphipods, cir: cirripods, lar: larvaceans).

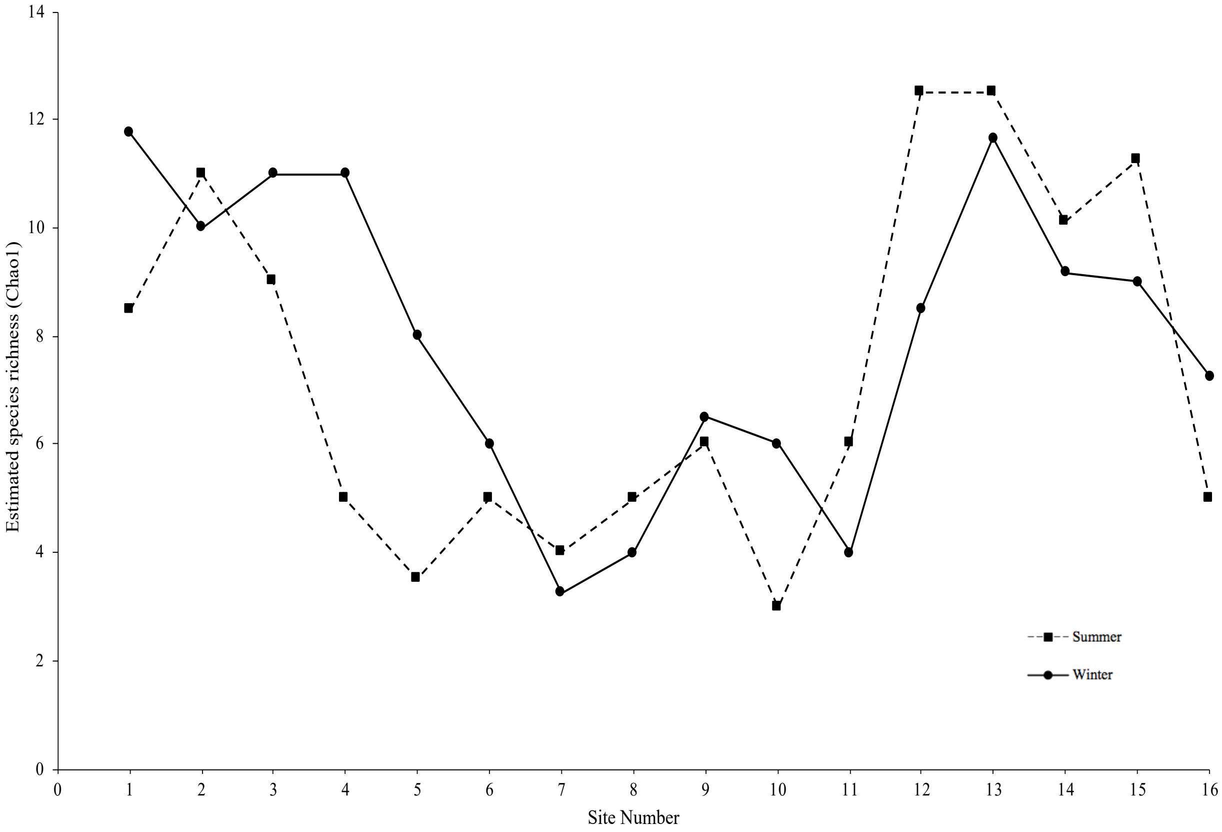

Figure 4. Average Chao-1 estimated zooplankton species richness from 16 sites that were sampled in this study across both seasons.

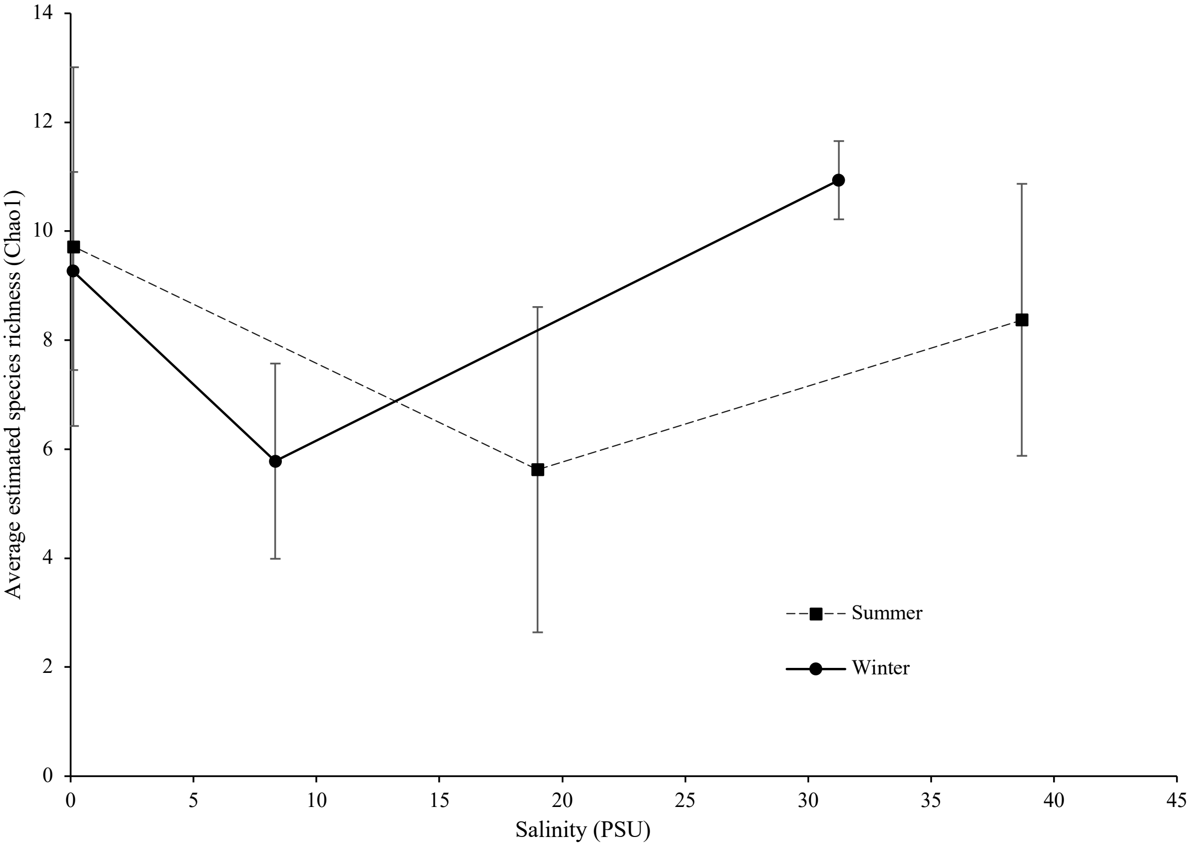

Figure 5. Relationships between average Chao-1 estimated species richness and average salinities for each site category (freshwater, coastal ponds and marine) in winter and summer.

3.3 Variation in zooplankton community composition

Canonical correspondence analysis, and associated forward selection and Monte Carlo permutation tests, were used to explore the environmental variables associated with patterns in zooplankton community composition in summer and winter. Environmental variables are represented by arrows. The direction of the arrows indicates the association of the sites and species with the environmental variables and the length of the arrows represents the strength of these associations.

The results of the forward selection and associated Monte Carlo permutation tests for summer indicated that the environmental variables collectively described 49.85 % of the variation in the data set (Table 6, Figure 6). The eigenvalues for axes 1 and 2 were 0.86 and 0.35 respectively, indicating variability along Axis 1 explains a high proportion of the variability in this season. Salinity was most strongly negatively associated with Axis 1 and explained the greatest proportion of variation in zooplankton community composition (18.8 %, P = 0.002; Table 6) when environmental variables were considered individually. No other variable explained any significant additional variation in zooplankton composition in summer. Marine sites (Sites 1-4) were all negatively associated with Axis 1 (Figure 6) and all had high average salinities (>35 PSU). Freshwater sites (Sites 13-16) were positively associated with Axis 1 (Figure 6) and all had low average salinities (<1 PSU). Zooplankton taxa that were strongly negatively associated with Axis 1 were the cladoceran *Penilia avirostris*, copepods *Oithona similis*, *Euterpina acutifrons*, *Coryceaus aucklandicus* and *Paracalanus parvus*, and barnacle nauplii, indicating that these taxa were generally found in sites with high salinities. The copepods *Gladioferens pectinatus, Sulcanus conflictus,* ostracods, and bdelloids rotifers were distributed in the centre of the summer ordination, indicating that these taxa were associated with intermediate salinities. The cladoceran *Chydorus* sp. and rotifers *Lecane luna*, *Brachionus* *quadridentatus*, *Trichocerca porcellus* and *Polyarthra dolichoptera* were positively associated with Axis 1, indicating that these species are associated with low salinity values (i.e., freshwater conditions).

The winter results indicated that the environmental variables collectively described 57.01% of the variation in the data set (Table 7, Figure 7). Eigenvalues of axes 1 and 2 were 0.78 and 0.52, respectively. Salinity, seasonal change in salinity, and temperature were all significant environmental variables explaining the variability in species composition at the time of their inclusion in the model. In accordance with the summer results, salinity was most strongly negatively associated with Axis 1 and explained the greatest amount of variation in zooplankton community composition during winter (18.6 %, P = 0.002, Table 7). Sites 1, 2, 3, 5 and 7 were all negatively associated with Axis 1 (Figure 7) and all had high salinities (>28 PSU). Sites 11, 13, 14, 15 and 16 were all positively associated with Axis 1 (Figure 7) and all had low salinities (<4 PSU). As observed in summer, the cladoceran *P. avirostris* was most strongly negatively associated with Axis 1, and was therefore found in sites with high salinities. The copepods *E. acutifrons* and *P. parvus*, barnacle cyprid larvae and crab zoea were also strongly negatively associated with Axis 1. From these salt-tolerant species, there was a gradient in composition, with copepod species such as *G. pectinatus* and *S. conflictus*, and the rotifer *Notholca* cf. *salina*, associated with intermediate salinities in the middle of the ordination, through to taxa that were strongly associated with low salinities (i.e., freshwater conditions) on the right, such as the cladoceran *Ilyocryptus sordidus*, bdelloid rotifers and *Keratella* species.

Seasonal change in salinity (PSU) explained a large proportion of variation in zooplankton community composition (11.5 %, P = 0.024, Table 7), independent of the variation explained by salinity, and this variable was positively associated with Axis 2 on the winter ordination. Two coastal ponds, sites 8 and 9, were most strongly positively associated with Axis 2, and were the sites that experienced the largest fluctuations in salinity between winter and summer (Figure 2; Figure 7). The copepods *S. conflictus* and *Mesochra parva* were positively associated with Axis 2, indicating that these species were abundant in sites that experienced the greatest seasonal change in salinity. Zooplankton taxa such as the copepods *P. parvus* and *O. similis* were negatively associated with Axis 2, indicating that they were not as common or abundant in sites that showed wide seasonal changes in salinity and had a preference for more stable sites (e.g., Cheltenham Beach (Site 1) and Te Atatū Peninsula (Site 2)). Although seasonal change in salinity did explain a significant proportion of variation, Axis 2 explained comparatively little variation relative to Axis 1 (eigenvalue Axis 1 = 0.78 vs Axis 2 = 0.53), indicating the dominant role that salinity concentration has on influencing zooplankton community composition among marine-influenced coastal pond sites. Temperature explained a smaller, but significant proportion of variation in the winter species composition (10.4 %, P = 0.040, Table 7), but was only weakly positively associated with Axis 2 of the winter CCA ordination.

Table 6 Forward selection and Monte Carlo permutation test results from Canonical Correspondence Analysis (CCA) of zooplankton taxa with respect to environmental variables sampled during summer in 16 selected sites. Bold values indicate a significant result ($p < 0.05$) at the time of their inclusion in the model.

Conditional Term Effects		
Variable	Explains %	*p*
Salinity	18.8	**0.002**
pH	7.8	0.162
Seasonal change in salinity	6.8	0.224
Chlorophyll-*a*	6.6	0.288
Dissolved oxygen	5.3	0.524
Temperature	4.5	0.600

Table 7 Forward selection and Monte Carlo permutation test results from Canonical Correspondence Analysis (CCA) of zooplankton taxa with respect to environmental variables sampled during winter in 16 selected sites. Bold values indicate a significant result ($p < 0.05$) at the time of their inclusion in the model.

Conditional Term Effects		
Variable	Explains %	*p*
Salinity	18.6	**0.002**
Seasonal change in salinity	11.5	**0.024**
Temperature	10.4	**0.040**
Chlorophyll-*a*	7.6	0.088
Dissolved oxygen	5.1	0.382
pH	3.9	0.640

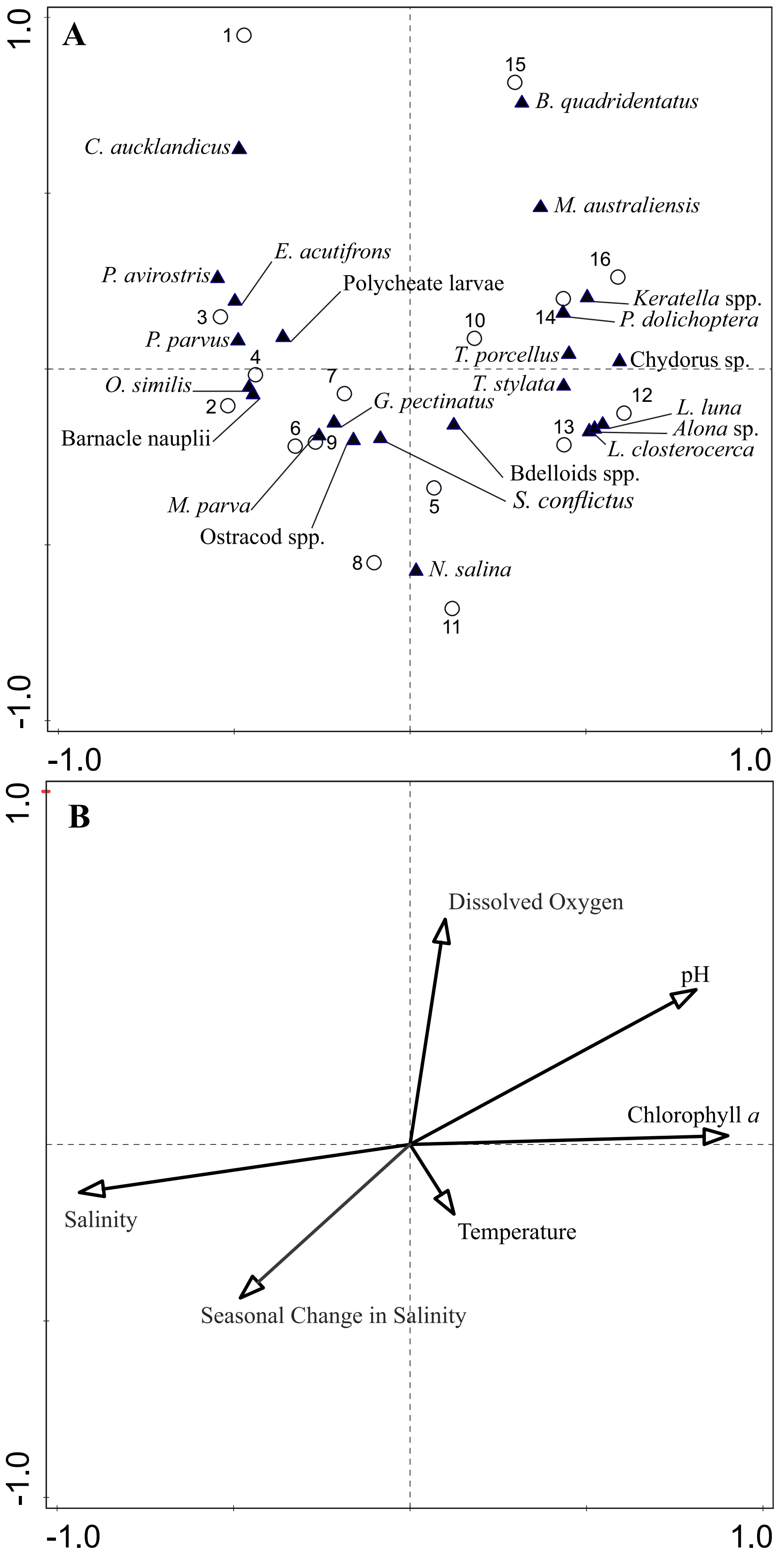

Figure 6. Ordination biplots generated from Canonical Correspondence Analysis (CCA) of zooplankton taxa with respect to environmental variables sampled during summer in 16 selected sites. A, site (numbers) and species (close triangles) biplot, and B, environmental variables (arrows). Numbers indicate site location in Auckland, New Zealand (Figure 1). Eigenvalues for Axis 1 and 2 = 0.87 and 0.35, respectively.

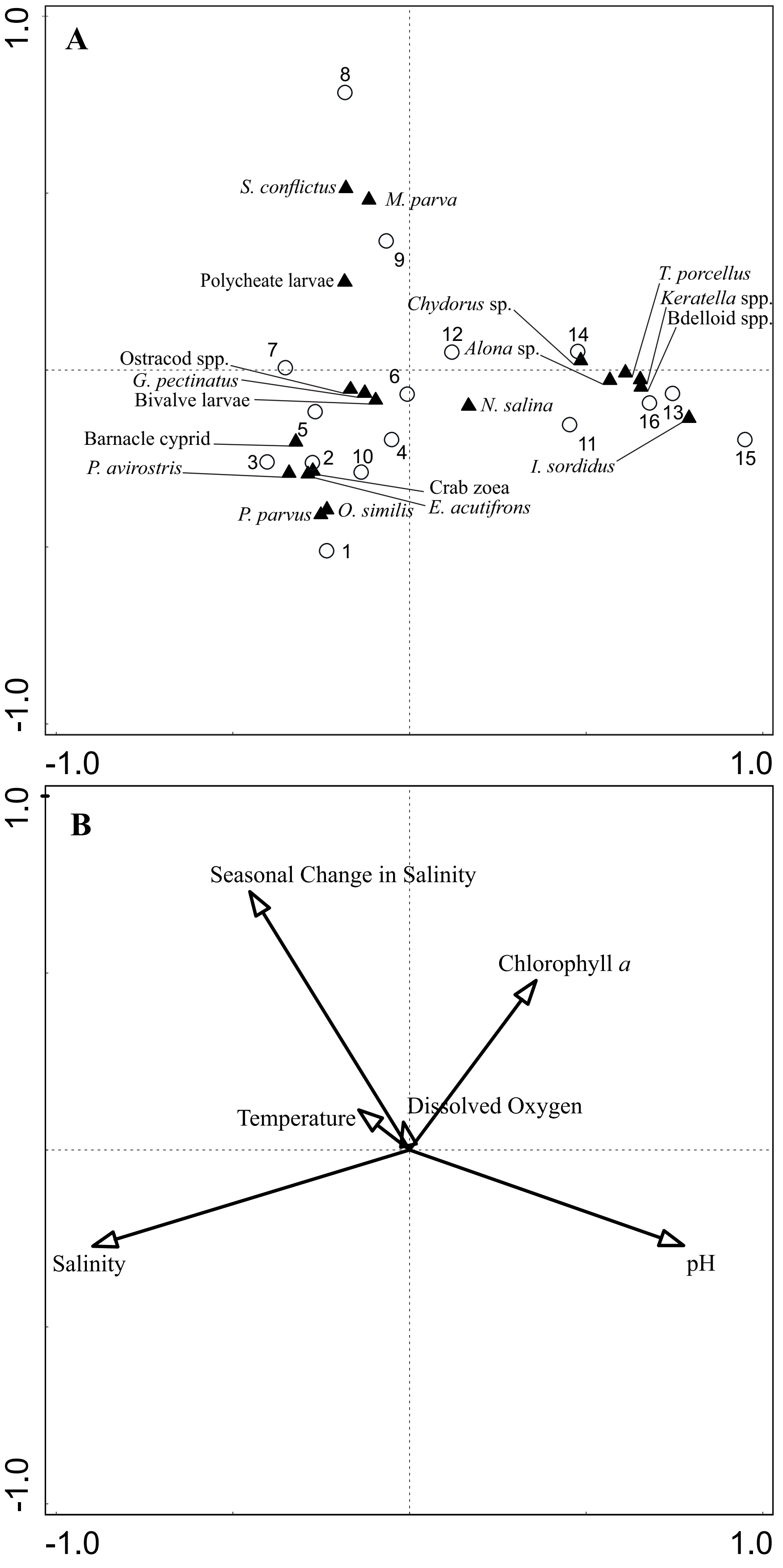

Figure 7. Ordination biplots generated from Canonical Correspondence Analysis (CCA) of zooplankton taxa with respect to environmental variables sampled during winter in 16 selected sites. A: site (numbers) and species (close triangles) biplot, and B: environmental variables (arrows). Numbers indicate site location in Auckland, New Zealand (Figure 1). Eigenvalues for Axis 1 and 2 = 0.78 and 0.53, respectively.

Chapter Four

Discussion

4.1 Spatial and temporal environmental variability of coastal ponds

Spatial environmental heterogeneity was observed across the coastal pond sites. It has been well documented that small, shallow water bodies often have greater physico-chemical variability than larger water bodies (Biggs *et al.,* 2005; Biggs *et al.,* 2017; Riley *et al.,* 2018; Kuczyńska-Kippen, 2019). This heterogeneity can be largely attributed to their small catchments, particularly compared to larger water bodies, and the exchange of matter, energy and nutrients across the aquatic-terrestrial zone from surrounding terrestrial environments (Biggs *et al.,* 2005; Riley *et al.,* 2018). Therefore, ponds and other small water bodies often reflect very local variations in climate (Biggs *et al.,* 2005; Riley *et al.,* 2018). Their small catchments and volumes make them particularly vulnerable to anthropogenic degradation from pollutants, as compared to larger water bodies, there is little possibility of successful dilution and buffering, further contributing to spatio-temporal changes in their physico-chemical properties (Biggs *et al.,* 2005). Despite freshwater ponds being the focus of most pond studies, the same attributes should be applicable to all small water bodies, including brackish coastal ponds. Indeed, small brackish waters may display greater internal heterogeneity through time, as well as spatial heterogeneity among ecosystems, as they are influenced not only by terrestrial environments, but by neighbouring freshwater and marine systems as well (Cognetti & Maltagliati, 2000; Basset *et al.,* 2006).

As expected, salinity varied considerably among the coastal ponds (Figure 2). This variation can be explained by two variables: 1) the degree of connection each pond has with the ocean (e.g., tidal or pipes), and 2) the volume of freshwater inflows received at each site (e.g., from neighbouring freshwater bodies or precipitation levels). These variables were not directly quantified in the current study. However, variation in salinity has been associated with the water exchange between brackish waters and their surrounding environments (Cui & Chui, 2017). In theory, as the coastal ponds have relatively small surface areas (<2 ha in area) and volumes, the dominant water type entering the system at any given time will dictate their overall salt concentrations. Therefore, if there is a higher volume of marine water entering a coastal pond than there is freshwater, they will have higher salinities, and vice versa. It is interesting to note that there were some unusually high average salinities recorded in summer. For example, two coastal pond sites, Waitemata Golf (Site 5) and Esplanade Reserve (Site 8) had average salinities greater than 31 PSU in summer, being close to that characteristic of sea water. Similar findings have been made with respect to spatial environmental variability in Mediterranean coastal ponds. For example, Anton-Pardo & Armengol (2011) examined 18 shallow, coastal ponds in Spain that were designated into categories according to salinity and water temporality: permanent freshwater ponds, temporary freshwater ponds, permanent brackish ponds and temporary brackish ponds. The greatest variations in salinity were found amongst the brackish ponds, while the salinities of the freshwater ponds were relatively similar.

Temporal fluctuations in salinity were also observed within the Auckland ponds. Generally, salinity was found to be higher in summer than in winter (Figure 2). The coastal pond sites experienced the greatest seasonal variation in salinity, whereas the freshwater control sites remained relatively stable between seasons (Figure 2). In the coastal pond sites, salinity ranged from 0.23 PSU to 37.34 PSU in summer and from 0.21 PSU to 17.85 PSU in winter. Two coastal ponds experienced the greatest changes in salinity from winter to summer. The average salinity of Esplanade Reserve (Site 8) was 3.98 PSU in winter and 31.20 PSU in summer, increasing by 27.22 PSU. The average salinity of Wattle Farm 1 (Site 9) was 2.18 PSU in winter and 28.41 PSU in summer, increasing by 26.23 PSU. Precipitation was likely a significant contributor to the seasonal variation in salinity observed in the present study. More rainfall was recorded during the month of the winter sampling date compared to the month of the summer sampling. Furthermore, the week leading up to the winter sampling date (i.e., seven days prior) can be characterised by relatively heavy rainfall, as 24.4 mm of rain was recorded in the Auckland area during that time. In contrast, no rain was recorded in the week leading up to the summer sampling date. These results suggest that the seasonal differences in salinity of the coastal ponds are likely explained by their freshwater-seawater mixing. In winter, there would have been an increase in freshwater inputs from rainfall and runoff into the coastal pond sites that could explain the lower salinities. Alternatively, in summer, the rainfall data illustrates that there would likely have been significantly lower freshwater inputs to counteract the influence of the nearby marine systems (e.g., tidal inputs), leading to significantly higher salinities in most coastal ponds. On average, the salinity of the freshwater sites increased by 0.03 PSU and the salinity of marine sites increased by 7.44 PSU from winter to summer. Ultimately, the moderate correlation between salinity and seasonal change in salinity in summer was due to the coastal pond sites and marine sites both having higher salinities across both seasons, especially in summer, and greater degrees of seasonal change in salinity, than the freshwater sites. My results are consistent with other international studies that have examined temporal variation in brackish waters (e.g., García & Niell, 1993; Gutkowska *et al.,* 2019). Gutkowska *et al.* (2019) investigated several environmental variables of Vistula Lagoon and Lake Łebsko, the two largest brackish waterbodies in Poland. In their study, the salinity of Vistula Lagoon was lower during winter and spring and higher during summer and autumn. They concluded that marine and riverine inflows, influenced by the changing seasons, were responsible for the seasonal variation in salinity at Vistula Lagoon (Paturej & Gutkowska, 2015; Gutkowska *et al.,* 2019). For example, the formation of ice cover over the Vistula Lagoon during winter hinders saline intrusions from the adjacent Baltic Sea and an increase in snowmelt and freshwater inflows from nearby rivers occurs during spring. In the warmer months, salinity values in the Vistula Lagoon increased as there were more intense and less restricted saline intrusions from the Baltic Sea (Gutkowska *et al.,* 2019). García & Niell (1993), investigating Fuente de Piedra, a temporary saline lake in Spain, found seasonal variation in salinity, with the lowest salinities occurring in February (i.e., winter) and highest salinities occurring in June (i.e., summer). They attributed this variation to the seasonal differences in precipitation and evaporation rates, as rainfall exceeded evaporation from October to February. Therefore, the salinity of Fuente de Piedra would have naturally decreased as more freshwater was added to the system via runoff and direct rainfall during this period.

It is important to note that not all of the coastal pond sites in the current study followed the trend of lower salinities in winter. For example, at Harbour View Beach Reserve (Site 10), salinity increased from 1.84 PSU in summer to 10.15 PSU in winter. This outlier may be explained by the tidal height of Te Atatū Peninsula at the time of both sampling days. The average high tide height of Te Atatū Peninsula was 3.3 m three days leading up to the winter sampling date (22 July 2021), based on data from the NIWA tide forecaster (NIWA 2019). In comparison, the average high tide height was 2.9 m in the three days prior to the summer sampling dates (14 January 2022) (NIWA 2019). It could be that a higher tide is required for sea water to enter Site 10 which, according to the 'measure distance' tool on Google Maps, is approximately 13.3 m away from the shoreline of Te Atatū Peninsula. If this is the case, the lower average high tide height in summer could mean that Site 10 was experiencing little to no tidal influence in the days leading up to the summer sampling date. As such, the freshwater inflows could have been exceeding the marine influence at this point. As the salinities of this site cannot be explained by differences in rainfall, it would also be useful to further investigate the type of connection the coastal pond sites have with nearby marine and freshwater systems. For example, a number of studies have described the effects of breaching or overtopping events on other larger brackish waters that are separated from the ocean, including open/closed estuaries (Froneman, 2004; Deale *et al.,* 2013) and lagoons (Santangelo *et al.,* 2007; Duggan & White, 2010).

Spatial and temporal variability in chlorophyll-*a* concentrations was observed. Chlorophyll-*a* concentrations varied more greatly amongst the coastal pond sites (Site 5-12) than the freshwater and marine sites. In the coastal pond sites, average chlorophyll-*a* concentrations ranged from 8.50 µg/L to 225.12 µg/L in summer and 0.38 µg/L to 346.00 µg/L in winter. Varying levels of anthropogenic nutrient inputs and nutrient-poor marine water are likely responsible for the spatial differences in chlorophyll-*a* concentrations observed across the coastal pond sites. Coastal stormwater ponds are highly susceptible to anthropogenic nutrient loading of nitrogen (N) and phosphorus (P) from the surrounding land, which can promote eutrophication, water quality degradation and harmful algal blooms (Paerl, 1997; National Research Council, 2000; Anderson, 2002, 2008). Although nutrients were not quantified in this study, the coastal pond sites likely varied in their levels of nitrogen and phosphorus, leading to differences in primary production and chlorophyll-*a* concentrations. Furthermore, ocean water can have relatively low concentrations of chlorophyll-*a* relative to inland waters, as it is depleted of nutrients required for primary production (e.g., nitrogen, phosphorus, silica and/or iron) (Bristow *et al.,* 2017). Chlorophyll-*a* was negatively correlated with salinity in summer. This correlation can be partially explained by the four marine sites having consistently low chlorophyll-*a* concentrations (i.e., between 1.00 µg/L and 13.92 µg/L) and high salinities (i.e., between 22.13 PSU and 40.13 PSU) across both sampling seasons. Furthermore, coastal pond sites with higher average salinities and low chlorophyll-*a* would likely have been influenced by more nutrient-poor marine water than coastal pond sites with lower average salinities. For example, Fergy Crescent 1 (Site 6) and Onepoto Lagoon (Site 7) were characterised by higher salinities (e.g., between 14.18 PSU and 24.73 PSU) and consistently low chlorophyll-*a* concentrations (e.g., between 3.20 µg/L and 18.96 µg/L) across both seasons. Generally, chlorophyll-*a* concentrations were lower in winter than in summer in the coastal ponds, with the exception of Esplanade Reserve (Site 8) and Harbour View Beach Reserve (Site 10), which had notably high chlorophyll-*a* concentrations in winter (Figure 2). Similar spatio-temporal variability of chlorophyll-*a* was reported by Anton-Pardo & Armengol (2014) in a more-extensive, 6-month examination of 16 shallow ponds and reservoirs from Mediterranean wetlands in Spain. These authors found that average chlorophyll-*a* ranged from 4.8 µg/L to 204.4 µg/L among their ponds and reservoirs, similar to the range found in the present study. Anton-Pardo & Armengol (2014) suggested that the greater concentrations of chlorophyll-*a* found in some of their water bodies highlighted their elevated trophic level. Despite the importance of this variable, Anton-Pardo & Armengol (2014) emphasised that discretion is needed when examining shallow systems, which can be macrophyte-dominated (Canfield *et al.,* 1983) and suggested that anthropogenic activity likely influenced the water quality of these small, shallow brackish ponds. Froneman (2004) examined the temporal dynamics of zooplankton community structure in the temporarily open/closed Kasouga estuary, southern Africa. Analogous to my study, Froneman (2004) reported the lowest chlorophyll-*a* concentrations during winter or during the periods where the estuary had been breached by the ocean and that chlorophyll-*a* was negatively correlated to salinity. Froneman (2004) attributed the elevated chlorophyll-*a* concentrations to a decrease in salinity in the estuary during summer, as freshwater inflow is a primary source of macronutrients required for the growth of phytoplankton (Allanson & Read, 1995; Adams *et al.,* 1999). Froneman (2004) also reported a significant positive correlation between temperature and chlorophyll-*a*, suggesting that elevated phytoplankton biomass can be partially attributed to the higher water temperatures in summer. However, as the Kasouga estuary was breached in winter, the low temperatures recorded align with the timing of nutrient-poor marine inflows entering the estuary. Therefore, the seasonal patterns of phytoplankton biomass were not necessarily directly influenced by temperature but instead by the interactive effects of the salinity and temperature combined. Temperature was not correlated with chlorophyll-*a* in the present study.

Temperature did not vary greatly among the coastal ponds, as in each season all were sampled on the same day (Figure 2). Average water temperatures of the coastal ponds ranged from 22.4 °C to 30.9 °C in summer and from 12.7 °C to 19.3 °C in winter. The slight spatial differences in water temperature were likely due to some ponds being sampled during the early, colder hours of the morning and some sites being sampled around noon, when the air temperature was higher. As expected, temporal variation in temperature between the seasons was observed, as temperatures were much higher in summer than in winter at all sites. The average temperatures of the coastal ponds fluctuated more in summer than they did in winter. The main factors that affect the temperature of shallow waters are air temperature, wind speed, rainfall events and incoming short and long wave radiation (Jacobs *et al.,* 1997; Subehi *et al.,* 2010). Martin (1972) conducted continuous sampling of water temperatures in two ponds in Leicestershire, England over a period of two years. This author concluded that the water temperatures of the ponds and the variables involved differed between seasons. In winter, the temperatures of the ponds fluctuated slightly and were mainly influenced by surrounding air temperatures. Whereas, in summer, the temperatures of the ponds fluctuated considerably and were influenced by the amount of sunshine received (Martin, 1972). Continuous temperature sampling did not occur in the present study. However, it can be assumed that the spatial variability in temperature observed is due to the amount of solar radiation received, especially during summer. The sampling route taken in summer is likely to have influenced the amount of solar radiation received by the ponds. The first ponds sampled during summer were the coastal ponds in the North Shore area (i.e., sites 5 and 7) which had low average temperatures. The last pond sampled was Harbour View Beach Reserve (Site 10) in Te Atatū Peninsula which had the highest average temperature of 30.9 °C. The Te Atatū Peninsula marine site (Site 2) which was also sampled at the end of the day had a correspondingly high average temperature of 29.9 °C. This provides evidence that the sites exposed to more solar radiation in summer were likely to have higher water temperatures as well.

Oxygen saturation displayed spatial and temporal variability (Figure 2). Average oxygen saturation in the coastal ponds ranged from 23.35 % to 120.05 % in summer and from 68.8 % to 110 % in winter. Waitemata Golf (Site 5) was characterised by low average oxygen saturation in summer (23.35 %) and winter (83.55 %), relative to other sites. In contrast, Harbour View Beach Reserve (Site 10) was characterised by high average oxygen saturation in summer (120.05 %) and winter (110.00 %). Oxygen saturation was not correlated with any other environmental variables. Dissolved oxygen dynamics in aquatic ecosystems are affected by many processes, including oxygenation and de-oxygenation at the air-water interface, respiration, photosynthesis and mineralisation (Hull *et al.,* 2008; Prasad *et al.,* 2014). Therefore, a large range of oxygen saturation is indicative of the interactions of these processes that are likely occurring in coastal ponds. For example, high oxygen saturation has been attributed to high levels of photosynthesis of benthic algae, submerged aquatic vegetation and phytoplankton (Smith & Able, 2003). Site 10 was characterised by high chlorophyll-*a* concentrations (e.g., between 52.92 µg/L and 346.23 µg/L) suggesting that photosynthesis was an important process influencing oxygen saturation in the coastal ponds.

Spatial and temporal variability in pH was observed among the coastal ponds (Figure 2). The average pH values of the coastal ponds ranged from 7.52 to 9.21 in summer and from 6.75 to 8.45 in winter. Generally, pH was greater in summer than in winter. A negative correlation was reported between pH and salinity in summer ($p = <0.001$) and in winter ($p = 0.027$). Greenwald & Hulbert (1993) reported a similar negative correlation during a microcosm analysis on lagoon water from San Dieguito Lagoon, California. These authors concluded that the pH-salinity relationship is related to dissociation of the bicarbonate ion; as high salinities inhibit dissociation, resulting in lower concentrations of the hydroxide ion, and consequently, low pH values (Amit & Bentor, 1971). pH has also been related to the acidity of the bottom sediment, photosynthesis and stormwater run-off (Lawson, 2011).

4.2 Variation in zooplankton community composition along the salinity gradient

As expected, salinity was inferred to have the strongest influence on zooplankton community composition among the sampled sites, explaining the highest levels of variation in both the summer (18.8 %, $P = 0.002$) and winter (18.6 %, $P = 0.002$) analyses. The overriding importance of salinity corresponds to what has generally been observed both within (e.g., Schallenberg *et al.,* 2003; Duggan & White 2010) and among (e.g., Anton-Pardo & Armengol, 2011; Lucena-Moya & Duggan, 2017) brackish water systems elsewhere.

Several changes in community composition occurred along the sampled salinity gradient. In the freshwater sites (<1 PSU), zooplankton assemblages were characterised by small rotifer species, such as *Lecane closterocerca*, *Lecane luna*, *Trichocerca stylata* and *Trichocerca porcellus*. Freshwater cladocerans, including *Alona* sp. and *Chydorus* sp., were also present in the same freshwater sites and some coastal ponds with lower salinities (<10 PSU). Rotifers in the genus *Keratella* (such as *Keratella tropica*) were common among freshwater sites but were also present in ponds with higher salinities (i.e., up to 28.41 PSU) (Figure 3). In sites characterised with intermediate salinities (e.g., ~10 to 30 PSU), bdelloid rotifers and euryhaline copepods, such as *Sulcanus conflictus* and *Gladioferens pectinatus*, were present. At the upper extreme of the gradient, the zooplankton assemblages of the marine sites and the highly saline ponds (>30 PSU) were dominated by marine copepods, such as *Paracalanus parvus*, *Oithona similis*, *Euterpina acutifrons*, as well as the marine cladoceran *Penilia avirostris*. There were also several types of crustacean larval stages dominating this end of the gradient; barnacle nauplii, barnacle cyprid larvae and crab zoea. These crustacean larval stages were not found in sites that had salinities less than 17.85 PSU or in any freshwater sites. Across both seasons, no rotifer species were recorded in the most saline coastal ponds and the four marine sites, with the exception of the marine rotifer *Synchaeta vorax* which was found in Cheltenham Beach (Site 1). Similarly, Lucena-Moya & Duggan (2017) found three defined groupings of zooplankton (tidal-freshwater, true-estuarine and marine) along the salinity gradient represented by distinct New Zealand estuary types. The tidal-freshwater grouping was composed of bdelloid rotifers, cladocerans and the calanoid copepod *G. pectinatus*, which aligns with the communities found in intermediate salinities of the present study. The true-estuarine grouping of Lucena-Moya & Duggan (2017) was dominated by the copepods *E. acutifrons*, *Coryceaus* sp. and polychaete larvae, and were found in estuaries characterised by little river influence or freshwater inflows (Hume *et al.,* 2007). The marine and true-estuarine groupings identified by Lucena-Moya & Duggan (2017) complement the brackish sites with the highest salinities and marine sites of the present study. A key difference between the findings of Lucena-Moya & Duggan (2017) and the current study is that the cosmopolitan copepod *E. acutifrons*, was found across a variety of hydrodynamic categories of estuaries (Hume *et al.,* 2007) and marine sites. However, in the current study, *E. acutifrons* was only present in the four marine sites and not in any of the coastal pond sites. Anton-Pardo &

Armengol (2011) reported that most cladocerans were absent from permanent and temporary brackish ponds with higher conductivities but were often dominant in permanent and temporary freshwater ponds, similar to that found in the present study.

Similar changes in zooplankton community composition along salinity gradients have been observed in larger brackish water systems in New Zealand (e.g., Roper *et al.,* 1983; Halls & Burns, 2003; Duggan & White, 2010) and elsewhere (e.g., Kozlowsky-Suzuki & Bozelli, 2004; Yuan *et al.,* 2020). These studies focused on salinity gradients within single waterbodies, rather than a salinity gradient among multiple sites, as in the present study. For example, similar findings were reported by Roper *et al.* (1983) along a longitudinal salinity gradient in the Avon-Heathcote Estuary, Christchurch. The salinity gradient in that study ranged from 2.0 PSU to 33.5 PSU, almost as wide as that examined among sites in the present study, although without the lower, entirely freshwater end of the gradient. Roper *et al.* (1983) found two patterns in the abundances of zooplankton taxa along the estuary; either densities of zooplankton taxa were highest closest to the estuary mouth, and decreased up river, or vice versa. Zooplankton displaying the former distribution pattern were coastal species (e.g., the marine copepods *Acartia ensifera* or *Paracalanus indicus*). Estuarine species (e.g., *G. pectinatus*) and freshwater species that had entered the estuary via the river (e.g., *Daphnia carinata*) were found to display the second pattern and dominated sites at the lower end of the studied salinity gradient. Roper *et al.* (1983) found *E. acutifrons* individuals that tolerated salinities between 2.4 PSU to 17.6 PSU near the more riverine sites and at even higher salinities at the estuary mouth. As mentioned above, the *E. acutifrons* individuals identified in the present study had a comparatively narrow tolerance range, as they were not found below 22.1 PSU. Elsewhere, Yuan *et al.* (2020) conducted a 1-year investigation into the distribution and structure of the zooplankton community in the Pearl River Estuary, China, which had a temporal salinity gradient of 0.1 PSU to 25.0 PSU (Li *et al.,* 2006). This study found that salt-tolerant species dominated the high salinity sites, and that rotifer and cladoceran abundances had a negative relationship with salinity. As such, their study concluded that salinity was the most important factor affecting the structure of the Pearl River Estuary zooplankton community, which is consistent with the results of the present study.

4.3 Zooplankton composition and seasonal variation in salinity

The copepods *Sulcanus conflictus* and *Mesochra parva* were strongly positively associated with seasonal change in salinity in the winter CCA ordination, suggesting that these species can occur in habitats that vary widely in their salinities through time. These two copepods were associated with sites that experienced large increases in salinity from winter to summer (e.g., sites 7, 8 and 9). *Sulcanus conflictus* is a euryhaline calanoid copepod that was initially described from the mouth of the Georges River, Australia (Nicholls, 1945), and is now known to be more widespread in estuaries around southern Australia (Bayly, 1975). In New Zealand, the species has been recorded in Orakei Basin, Auckland (Bradford-Grieve, 1999), in Tauranga Harbour (Warr, 2001) and Onepoto Basin (Banks, 2007) (also Site 7 in the present study). Although there are varying reports of the exact tolerance range of *S. conflictus,* the general consensus is that they can tolerate salinities ranging from around 4 PSU to 25 PSU (Arnott & Hussainy, 1972; Ough & Bayly, 1989). In my study, *S. conflictus* was present in coastal pond sites with salinities ranging from 1.84 to 37.34 PSU in summer and 3.98 to 14.18 PSU in winter. These results suggest that the *S. conflictus* individuals in the present study had a wider range of tolerance to salinity than what has been previously recorded. *Mesochra parva* is a harpacticoid copepod that was initially described in the Swan River estuary, Australia (Thomson, 1946). In the present study, *M. parva* was present in coastal pond sites ranging from 24.44 PSU to 28.41 PSU in summer and 2.18 PSU to 17.85 PSU in winter. It is thought to be a euryhaline brackish-water species (Chapman & Lewis, 1976) and has been recorded in New Zealand brackish waters previously (e.g., Coull & Wells, 1981; Duggan & White, 2010). Bollmohr *et al.* (2009) examined the salinity adaptation of *M. parva* individuals during a 96 hr experiment, based on salinity conditions of the Lourens River estuary, South Africa. During their sampling of the estuary, these authors found *M. parva* populations across a wide range of salinities (between 1 PSU and 38 PSU). Furthermore, Duggan & White (2010) found *M. parva* individuals primarily late in their study, when the barrier bar was open and when salinities were > 30 PSU. The results of the present study align with the wide salinity tolerances of *M. parva* that have been previously reported (Bollmohr *et al.,* 2009; Duggan & White, 2010). In contrast, the marine copepods *Paracalanus parvus* and *Oithona similis* were strongly negatively associated with seasonal change in salinity in the winter CCA ordination, suggesting that these species are incapable of tolerating changing salinities through time. Instead, they could likely tolerate a narrow range of high salinities, but prefer salinities greater than 36 PSU. These marine species were strongly associated with Cheltenham Beach (Site 1).

Changes in salinity may lead to the disappearance of some species and the appearance of others. As previously mentioned, Esplanade Reserve (Site 8) and Wattle Farm 1 (Site 9) experienced the greatest increases in salinity from winter to summer. The loss of freshwater zooplankton taxa occurred alongside these significant seasonal increases. For example, *Alona* sp. and *Chydorus* sp. were present at both of these two sites during winter, when the ponds had low salinities (<4 PSU), but were absent during summer, when the ponds had high salinities (>28 PSU). This result is consistent with findings elsewhere, as cladocerans are typically present in freshwater ecosystems as most species cannot tolerate higher salt concentrations (Boix *et al.,* 2007; 2008; Brucet *et al.,* 2009; Anton-Pardo & Armengol, 2011). Brucet *et al.* (2009) examined 35 shallow coastal lagoons to determine how different environmental variables from two separate European regions affected crustacean zooplankton species composition. These authors found that most cladocerans were restricted to lower salinities in both regions (<10 PSU) and disappeared entirely at salinities greater than 18 PSU. Only three species, *Chydorus sphaericus*, *Bosmina coregoni* and *Daphnia magna*, were present at salinities greater than 10 PSU. This is similar to the present study as *Alona* sp. and *Chydorus* sp. were found in coastal ponds with salinities close to 10 PSU but then disappeared as the salinity of these ponds increased during the summer drought. Ultimately, the salinity-induced loss of freshwater zooplankton will further affect coastal pond ecosystems due to the intermediary position of zooplankton in aquatic food webs. For example, several studies have indicated that the loss of large-bodied grazing cladocerans may result in lower grazing capacity on phytoplankton which may compromise ecosystem services (e.g., enhancement of turbidity of shallow brackish ecosystems) (Jeppesen *et al.,* 2007; Jensen *et al.,* 2010; Moffett *et al.,* 2020).

4.4 Species richness in coastal ponds

Average estimated species richness (Chao1) was greater in the fully-marine sites and the freshwater sites than in the brackish coastal ponds (Figure 4, Figure 5). Despite the limitations of this study brought about by COVID-19 restrictions (e.g. the inability to sample all four seasons), this pattern in species richness matched the expectations predicted by Remane's curve (Remane, 1934). In summer, the coastal pond sites had an average estimated species richness' of 5.62 and an average salinity of 18.99 PSU, and in winter, an average estimated species richness' of 5.78 and an average salinity of 8.33 PSU. As such, although the salinity of the coastal ponds increased slightly during the summer drought, the average estimated species richness remained similar. The low estimated average species richness found across the coastal ponds in both seasons reflects the inability of many freshwater and marine species to tolerate intermediate salinities, while only a limited diversity of true brackish species are capable of surviving wide variations in salinity (Remane, 1934; Whitfield *et al.,* 2012). The average estimated species richness' of the freshwater sites was 9.72 in summer and 9.27 in winter, and the marine sites had an average estimated species richness' of 8.38 in summer and 10.94 in winter. These higher values reflect the presence of freshwater and euryhaline zooplankton in the freshwater sites, and similarly, the presence of marine and euryhaline zooplankton in the marine sites (Whitfield *et al.,* 2012). It is important to note that my results do not conform with the concept of the '*horohalinicum*', the area with the minimum species richness within the narrow salinity range of 5 PSU to 8 PSU, as posited by Kinne (1971). For example, in winter, the lowest estimated species richness, 3.25, was observed in Site 7 with a salinity of 14.18 PSU; this salinity concentration greatly exceeds the *horohalinicum* salinity range. The summer results also do not align with the *horohalinicum* concept, as the lowest estimated species richness was found in Site 10 with a salinity of 1.84 PSU. This dissonance is not unusual, as many studies have found limitations in applying Remane's curve to all brackish water ecosystems (Whitfield *et al.,* 2012; Telesh *et al.,* 2013) or have denied the existence of the *horohalinicum* altogether (Deaton & Green 1986). Furthermore, as mentioned previously, small water bodies are subject to rapid environmental change due to their small volumes and catchment sizes (Biggs *et al.,* 2005; Biggs *et al.,* 2017; Riley *et al.,* 2018; Kuczyńska-Kippen, 2019). Therefore, my results are likely to only represent a snapshot of the true species richness and environmental conditions of the pond sites due to the limited number of zooplankton samples and environmental measurements taken for this study.

Taxon richness results from the present study were relatively limited compared to what has been found in larger brackish waters. For example, Lucena-Moya & Duggan (2017) used the Chao2 estimator to determine the average total number of taxa for all of their studied estuarine categories. These authors also found support for Remane's curve as the most freshwater and marine systems had significantly higher average species richness (Chao2) than the estuaries with intermediate salinities. More specifically, they found the lowest average species richness (18) among the Category D estuaries (*sensu* Hume *et al.,* 2007), shallow, circular basins with little river influence, and an average salinity of 27.50 PSU. Although significantly more taxa were identified by Lucena-Moya & Duggan (2017), the same overall pattern of higher species richness occurring in the fresh and marine categories of a salinity gradient was demonstrated. Another example supporting Remane's curve was a year-long study of zooplankton assemblages along a salinity gradient (freshwater to 25 PSU) in the Charente Estuary, France (Modéran *et al.,* 2010). Modéran *et al.* (2010) found the highest diversity in the freshwater and polyhaline (~25 PSU) zones and the lowest values in the oligohaline zone, defined as 0.5 to 5.0 PSU in this study. The oligohaline zone defined in their study does not align with the 5-8 PSU range either, but again, the overall pattern described by Remane (1934) was supported. As emphasised by other authors, although Remane's curve is the leading model that best describes the general pattern of diversity across salinity gradients in aquatic systems, it should be applied with caution (Whitfield *et al.,* 2012; Telesh *et al.,* 2013). Furthermore, although these examples are taken from estuaries, and not coastal ponds, they investigated wide salinity gradients similar to that of the present study and were the only relevant studies published. Overall, my results agree with the ideas of Remane (1934) and other brackish water studies, as a relatively low zooplankton taxon richness was found in the coastal ponds owing to the low tolerance of freshwater and marine species to brackish conditions (Virta *et al.,* 2020).

4.5 Non-indigenous zooplankton species

Constructed coastal ponds may be more susceptible to invaders than other aquatic systems as they match several criteria that influence invasion success; high propagule pressure, high environmental variability, and low biotic resistance (Elton, 1958; Davis *et al.,* 2000; Havel *et* *al.,* 2005). Four non-indigenous zooplankton species in total were identified in the current study (Table 5). Two non-native freshwater cladocerans, the Holarctic *Daphnia galeata* and North American *Daphnia pulex,* were recorded in this study and are well-documented invaders of New Zealand freshwater lakes and ponds (Duggan & Pullan, 2017; Ye *et al.,* 2021; Duggan *et al.,* 2021). *Daphnia pulex* was present in one freshwater pond (Site 14) during summer and winter. *Daphnia galeata* was present in one coastal pond (Site 9) during winter. The two sites these freshwater cladocerans were found in were both characterised by low salinities (i.e., <3 PSU). The North American copepod *Skistodiaptomus pallidus* was present in one freshwater pond (Site 16) and is also a known invader of constructed and natural waters in New Zealand (Duggan *et al.,* 2006; Duggan *et al.,* 2014). *Sulcanus conflictus* was present in five coastal ponds (sites 5, 7, 8, 9 and 10) and one freshwater pond (Site 13). *Sulcanus conflictus* was first recorded as a possible invader in New Zealand in Orakei Basin, Auckland (Bradford-Grieve, 1999). Bradford-Grieve (1999) concluded that the individuals found in Orakei Basin matched the original description of the species from Australia by Nicholls (1945) and suggested that this species may be non-indigenous to New Zealand. Orakei Basin is a lagoon that is isolated from Waitemata Harbour during the spring tide peaks of high water every one to two months, during which the salinity of the lagoon reduces if there are sufficient freshwater inflows (Bradford-Grieve, 1999). It has been speculated that *S. conflictus* is more widespread in New Zealand estuaries than is currently recognised, as our knowledge of saltwater zooplankton distributions has to date been largely based on deepwater (offshore) hauls (Banks, 2007). The spread of invasive euryhaline zooplankton across inland water bodies has been previously reported, a key example being the euryhaline copepod *Eurytemora affinis* (Lee, 1999). The ancestral habitats of *E. affinis* are thought to be estuaries, brackish seas and lakes across the globe (Lee, 1999). In the past 60 years, *E. affinis* has been recorded in many freshwater habitats in Europe, North America and Asia (Lee, 1999), prior to which, its known freshwater distribution was limited to only a few sites (Marsh, 1912; Willey, 1923). The remarkable spread of *E. affinis* has been attributed to; 1) an increase in human activities that offer transport into inland waters, and 2) an increase in altered or depauperate habitats (Lee, 1999), such as reservoirs and stormwater ponds. Another example is the estuarine copepod *Eurytemora velox* which is commonly found in weakly brackish estuaries and lagoons around the British Isles (Gurney, 1931). Duggan & Payne (2017) reported that *E. velox* has successfully invaded a range of inland constructed waters in the United Kingdom, developing upon the ideas of Elton (1927). These authors suggested that *E. velox* may have invaded freshwaters in the British Isles via constructed brackish environments, and that biotic resistance due to the presence of key species is important. The present study supports the speculation that *S. conflictus* is more widespread throughout New Zealand than originally thought (Banks, 2007) as it was present in five coastal pond sites in summer and four coastal pond sites in winter. Furthermore, New Zealand populations of *S. conflictus* are now known from more constructed waters (i.e., the highly-modified Orakei Basin and five coastal stormwater ponds) than natural waters (Waitemata and Tauranga harbours). In the present study, the constructed coastal pond sites experienced high temporal and spatial environmental variability (Figure 2), potentially providing opportunities for the establishment of non-native zooplankton that are more tolerant to change, such as the euryhaline copepod *S. conflictus*. Furthermore, the coastal pond sites are likely to experience human-facilitated propagule pressure, as they are located in heavily-populated coastal areas that are encompassed by Waitemata and Manukau harbours (Figure 1). For example, Wattle Farm 1 (Site 9) is frequently used for the recreational sailing of model boats (Northern Maritime Model Society 2019), which could introduce non-native species from other water bodies. Biotic resistance has been associated with species richness (Elton, 1958; Kennedy *et al.,* 2002; Ricciardi & MacIsaac, 2008) and the presence/absence of key species (Taylor & Duggan, 2012; Duggan & Payne, 2017). Low species richness generally translates to low biotic resistance, as species-poor communities are less able to utilise available resources in their environment compared to a species-rich community, providing opportunities for non-native species to outcompete them (Elton, 1958; Parkes & Duggan, 2012). In agreement with Remane (1934), species richness was generally lower in the coastal pond sites relative to the freshwater and marine sites, suggesting that these communities may not use resources in these habitats efficiently, or may lack key species capable of resisting newly introduced species. Ultimately, the high environmental variability and low species richness found among the coastal pond sites suggest that they may be the ideal ecosystems for non-native species to establish. It is important to note that the constructed coastal pond sites may not only act as the recipient ecosystems for marine invasions, but may also act as 'stepping stones' for the secondary spread of non-native species into inland freshwater ecosystems (Tang, 2020). The number of non-native zooplankton species identified in this study was low, and therefore, no statistical tests were performed to establish whether the coastal pond sites were more readily invaded than freshwater sites.

4.6 New species record for New Zealand

A species of note was *Notholca* cf. *salina*, a rotifer that was morphologically similar to *N. salina*, which is known to tolerate a wide range of salinities and temperatures (Focke, 1961; Björklund, 1972). *Notholca* cf. *salina* was found in two brackish ponds; Fergy Crescent 1 (Site 6) and Fergy Crescent 2 (Site 11). The salinity ranged from 17.9 PSU in winter to 24.4 PSU in summer at Site 6 and ranged from 0.21 PSU in winter to 3.8 PSU in summer at Site 11. Previously, there have been few recordings of *Notholca* species in New Zealand, with only three marine species recorded in the South Island; *N. salina*, *Notholca marina*, and *Notholca pacifica* , and a complete absence of the genus in freshwater bodies of the North Island (Duggan *et al.,* 2002a). *Notholca pacifica* is the only endemic taxon recognised in New Zealand.

Notholca salina has been previously recorded in Waituna Lagoon, New Zealand (Duggan & White, 2010). However, individuals in the current study could not be confidently designated to a described species; although they were morphologically similar to descriptions of *N. salina*, they had reduced occipital spination compared to previous depictions (Figure 8). Several studies have lamented that there is a significant level of intraspecific morphological variation found in the *Notholca* genus, which could explain the slight differences in spine length in my specimen (Björklund, 1972; Koste & Shiel, 1987; Luo *et al.,* 2012). However, in recent decades, the occurrence of complexes of cryptic species – groups of species that are morphologically indistinguishable – has become widely recognised and appear to be particularly abundant among brackish water organisms (Montero-Pau *et al.,* 2011; Mills *et al.,* 2016). High levels of cryptic diversity have been observed among the rotifers, primarily due to the paucity of taxonomically recognisable morphological features, their small size and the lack of rotifer taxonomists (Wallace *et al.,* 2006; Leasi *et al.,* 2013). The best-known example is the species complex *Brachionus plicatilis*, a cosmopolitan taxon that inhabits salt and brackish waters globally (Walker 1981), that was presumed to be a euryhaline taxon as it was found in salinities ranging from 1 PSU to 97 PSU (Epp & Winston, 1977; Walker, 1981). However, more than 20 cryptic species with differential adaptations to salinity have subsequently been elucidated using DNA taxonomy (e.g., Suatoni *et al.,* 2006; Fontaneto *et al.,* 2007). Field and laboratory studies have indicated that salinity differentially affects reproduction and life history traits among genetically identified taxa within the *B. plicatilis* complex, which confines cryptic taxa to different temporal and spatial distributions (Gómez *et al.,* 1997; Campillo *et al.,* 2011). There have been many other accounts of cryptic speciation of zooplankton inhabiting brackish waters (e.g., Ueda *et al.,* 2011; Karagianni *et al.,* 2018). For example, Karagianni *et al.* (2018) examined zooplankton community composition and biomass in seven temporary saline lakes, ranging between <2 and 300 PSU, in Cyprus. These authors found evidence to suggest the presence of cryptic species complexes (e.g., *Moina brachiata*), with different salinity preferences in the saline lakes. Genetic research has revealed that there might be four cryptic species constituting the *M. brachiata* complex (Nédli *et al.,* 2014), and that differences in these species are partially associated with variation in salinity. Karagianni *et al.* (2018) concluded that more attention needs to be paid to salinity as a major driver of zooplankton genetic diversity. In the current study, as *N.* cf. *salina* individuals identified are similar to previous depictions, but not identical, they may represent a new species to science (R.J. Shiel, University of Adelaide, personal communication).

Figure 8. An image of an *Notholca* cf. *salina* individual identified in two brackish coastal ponds, Auckland, New Zealand.

4.7 Limitations and future research

As is the case for most scientific research, there were some practical limitations to the present study. The first constraint was the limited number of samples that could be collected in only two months of the year, due to the time restrictions of a MSc degree, the 2021 COVID-19 lockdowns (including some that were Auckland-specific) and the 2022 COVID-19 household quarantines. Two quantitative zooplankton samples were collected from each site and two *in situ* measurements of the environmental variables were recorded in July 2021 (Austral winter), and then again, in January 2022 (Austral summer). In future, a higher number of zooplankton samples taken across all four seasons would be recommended to more fully comprehend how zooplankton community composition and species richness change temporally in coastal ponds. A greater frequency of *in situ* environmental measurements (e.g., monthly samples) would have produced a clearer picture of the heterogeneity experienced by small brackish waters (e.g., constructed coastal ponds) compared to larger brackish waters (e.g., estuaries and lagoons). Another potential option would be to implement continuous loggers to understand the rate of change in these ponds following rainfall events.

Another limitation of the present study was that several environment variables were unable to be assessed (e.g., pond age, nutrient concentrations, and the nature of connections to the ocean and freshwater sources). Total nitrogen (TN) and total phosphorus (TP) are important water quality indicators as these nutrients often limit and control macrophyte and algal growth rates, thereby impacting zooplankton and other organisms that are at higher trophic levels (Ryther & Dunstan, 1971). Nevertheless, chlorophyll-*a* was used as a direct indicator of phytoplankton abundance and biomass and was selected to represent the water quality of the sites as it is inexpensive to measure compared to nutrients, and more directly affects zooplankton than nutrients. Pond age would have been useful, as it has been associated with biological invasions of non-native species (Johnson *et al.,* 2008). Although it was assumed that the coastal stormwater ponds have been recently constructed, it was difficult to determine when they were all created as there is a lack of information available regarding small constructed ponds compared to larger waters. The degree and type of connection the coastal ponds had with the ocean and neighbouring freshwater sources were also not measured, but would be useful if the study was to be repeated. For example, this knowledge would better elucidate why some of the ponds displayed temporal variability in salinity.

The conclusions of the present study should be interpreted with some caution, as ultimately, a proportion of the variation in zooplankton community composition remained unexplained by the analyses that were conducted. While this is common in multivariate analyses, it is possible that other processes, variables or interactions were involved in influencing the zooplankton assemblages in these coastal pond sites that were not measured in the present study. For example, it has been well-documented that top-down effects, such as fish predation, can directly impact zooplankton communities (e.g., Carpenter *et al.,* 1987; Jakobsen *et al.,* 2003; Jensen *et al.,* 2010). As such, future research should include fish and macroinvertebrate sampling, as the lack of predator abundance data limits the potential to understand top-down effects on the zooplankton communities in coastal ponds.

As this is the first study in New Zealand to examine zooplankton communities in coastal ponds, a number of questions related to the ecology of these unique brackish ecosystems remain unanswered. The next step following on from this study would be to conduct a larger-scale experiment with the addition of further potential explanatory variables (e.g., fish composition and dynamics) and monthly sampling. It may also be valuable expanding this research to the constructed coastal ponds outside of the Auckland region to elucidate, for example, the effects of latitudinal gradients in temperature on zooplankton composition in brackish ponds. Finally, molecular genetic analysis would be valuable for elucidating the identity of *N.* cf. *salina*, and potentially other euryhaline species, observed in this study. The concept of cryptic species has become popular relatively recently and is poorly considered in current tests of evolutionary and ecological theory (Fišer *et al.,* 2018). Therefore, I recommend further research on cryptic speciation in New Zealand brackish waters, including focus on the effects of salinity due to projected sea-level rise and the associated salinisation of aquatic ecosystems.

4.8 Summary

In summary, marked spatial and temporal variability of environmental variables were observed among the coastal stormwater ponds, highlighting the distinctive nature of such ecosystems. As previously observed in larger brackish systems in New Zealand and around the world, zooplankton community composition varied spatially amongst the ponds. Salinity was found to have the greatest influence on zooplankton community composition in coastal ponds. A community shift occurred along the sampled salinity gradient. Temporal changes in community composition were observed as salinity increased in several coastal ponds in summer. Under these dynamic conditions, zooplankton taxa that were more tolerant to change dominated, while several freshwater species were lost entirely. Although there was a lack of statistical significance, species richness matched the predictions of Remane (1934), as species richness was generally lower in the brackish coastal ponds than in the freshwater and marine sites. The frequency of occurrence of non-indigenous zooplankton taxa was low in coastal ponds, with two non-indigenous species and one cryptogenic species present in the coastal ponds. The current study will be a useful reference for future research as constructed coastal ponds are particularly vulnerable to a number of threats, including sea-level rise projections, salinisation and biological invasions. Further research should be conducted to improve our knowledge and management strategies of such systems.

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