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Zooplankton seasonal dynamics in a recently filled mine pit lake: the effect of non-indigenous *Daphnia* establishment

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Abstract We examined the temporal and vertical dynamics of zooplankton in Weavers Lake, New Zealand, between October 2004 and October 2005, at a time when it was colonised by a non-indigenous *Daphnia* species. Zooplankton community composition changed during the study from one of rotifer dominance (e.g. *Asplanchna*, *Polyarthra*, *Brachionus* and *Keratella* species) to cladoceran (*Daphnia dentifera*) dominance. Temporal changes in zooplankton community composition were strongly associated with a gradual increase in lake water clarity, and were attributable to the highly efficient filter feeding of *D. dentifera*. The corresponding reduction in rotifer densities may have resulted from the superior competitive abilities of the newly established *Daphnia*. As *Daphnia* were rare inhabitants of New Zealand lakes before 1990, the arrival and rapid spread of the non-indigenous *D. dentifera* has lead to widespread changes in both water clarity and zooplankton community composition. An apparent lack of mixing in the lake was facilitated by the lake's extremely small surface area:depth ratio. However, we conclude that physical features of the lake had minimal influence on water clarity relative to the invasion of *D. dentifera*.

Keywords *Daphnia dentifera* invasion · Succession · Lake morphology · Rotifera

Introduction

New Zealand lakes have fairly predictable zooplankton assemblages. For rotifers, compositional variation among lakes is largely determined by trophic state, while calanoid copepod distributions are determined by geological history (Jamieson 1998; Duggan et al. 2001). Cladoceran and cyclopoid copepod species, in contrast, are seemingly ubiquitous, with *Bosmina* and *Ceriodaphnia* the typical cladoceran inhabitants of any lake (Chapman and Green 1987). *Daphnia* have traditionally been an uncommon component in New Zealand lakes (Chapman and Green 1987), although the North American *Daphnia dentifera* has recently become widespread and abundant throughout North Island lakes (Duggan et al. 2006). A high efficiency of filter feeding has been observed for daphnids relative to other zooplankton species, and these species are generally considered responsible for initiating the spring "clear water phase" in many lakes elsewhere (e.g. Lampert et al. 1986; Leibold 1989). Additionally, *Daphnia* species are commonly found to have superior competitive abilities relative to other zooplankton, and their presence can have profound effects on zooplankton community composition (e.g. Gilbert 1988; MacIsaac and Gilbert 1989).

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The establishment and spread of this species in New Zealand may thus have profound effects on water quality, at least seasonally, and on the seasonal dynamics and composition of New Zealand zooplankton communities.

Weavers Lake (max. depth 64 m; surface area 54 ha) is a former open-cast coal mine in the Waikato region of New Zealand, which gradually filled with water following the mine's closure in 1993, reaching full capacity in 2004. It represents the first large coal pit to be rehabilitated into a lake in New Zealand, but such lakes will become more common as further mines are retired. "Pit" lakes are unusual in having relatively small surface area:depth ratios. Weavers Lake, for example, is highly unusual in having the smallest surface area:depth ratio for any New Zealand lake greater than 20 ha in size (Fig. 1; cf. Viner 1987), and is situated in an area dominated by shallow lakes (i.e. with maximum depths typically <5 m; Viner 1987). The unusual morphology of pit lakes will have implications for lake physical processes, such as stratification and deoxygenation patterns that may affect zooplankton dynamics. In this study, we present the results of a one-year study of Weavers Lake. During this study *Daphnia dentifera* invaded the lake. Accordingly, our aims were to examine the temporal and vertical dynamics of zooplankton and environmental variables in a recently filled lake, and to examine the influence of the *Daphnia dentifera* invasion on zooplankton dynamics and water quality.

Materials and methods

Physico-chemical variables

A single site was selected at the deepest point in Weavers Lake (64 m; Fig. 1). Sampling was undertaken twice monthly for one year between 6 October 2004 and 12 October 2005, and was conducted on each occasion around 10 am. A conductivity–temperature

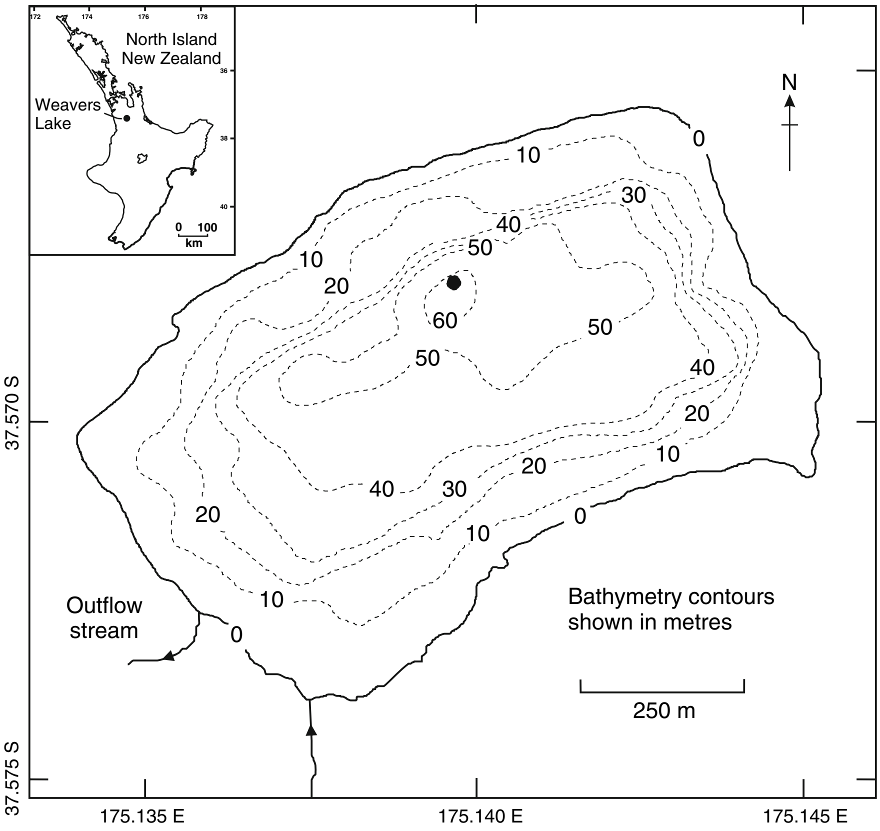


Fig. 1 Map showing bathymetry of Weavers Lake and study site. Inset shows location of Weavers Lake, North Island, New Zealand

–depth (CTD) meter (Seabird Electronics), with additional mounted sensors for dissolved oxygen (DO) and chlorophyll *a*, was used to measure continuous vertical profiles of these variables to a depth of 60 m. Water samples were collected at 10 depths (0, 5, 10, 15, 20, 25, 30, 40, 50, 60 m) with a 10 l modified Schindler-Patalas trap; from these, pH was measured using a Jenco vision plus pH618 meter. Water transparency was measured using a 25 cm Secchi disc. Samples for total phosphorus determination were taken from the surface waters and analysed by ascorbic acid colorimetry. Schmidt Stability was calculated from temperature profiles (Wetzel and Likens 2000).

Zooplankton composition and dynamics

Duplicate zooplankton samples were collected using the 10 l Schindler-Patalas trap at each of the 10 depths used for the physico-chemical measurements. Samples were sieved through a 37 µm mesh filter to capture zooplankton, which were immediately preserved in 70% ethanol. Samples were collected twice monthly over spring, summer and autumn, and monthly over winter, as zooplankton abundance is generally low and compositional changes are minimal during this time (Forsyth and McCallum 1980). Zooplankton were counted and identified in the laboratory. Subsamples were examined until at least 300 individuals, or the whole sample, were counted. Data were averaged for replicate samples at each depth. Identification was performed using standard taxonomic guides (e.g. Chapman and Lewis 1976; Shiel 1995).

Temporal and spatial distributions of dominant zooplankton species were plotted using NOeSYS Transform (v.3.4, Fortner Software, Virginia). This produces greyscale and contour plots from a three dimensional array of numbers (i.e. time, depth, abundance). Dominant species were considered as any species achieving greater than 4% of the composition at any one depth on any day. Multivariate statistical analyses were then used to elucidate patterns in zooplankton community composition, and to infer environmental variables important in determining zooplankton distribution. Preliminary cluster and Redundancy analysis (RDA) analyses showed variation in community composition with depth was minimal relative to temporal variability. For clarity, we only present results here from two depth groupings on each date; 0–15 m (above thermocline) and 20–60 m (below thermocline). RDA was used to infer important physical or chemical variables that lead to the dynamics of zooplankton assemblages (CANOCO v. 4.51, Biometris, Wageningen, Netherlands). Species data were transformed (fourth root) to down-weight abundant taxa.

Results

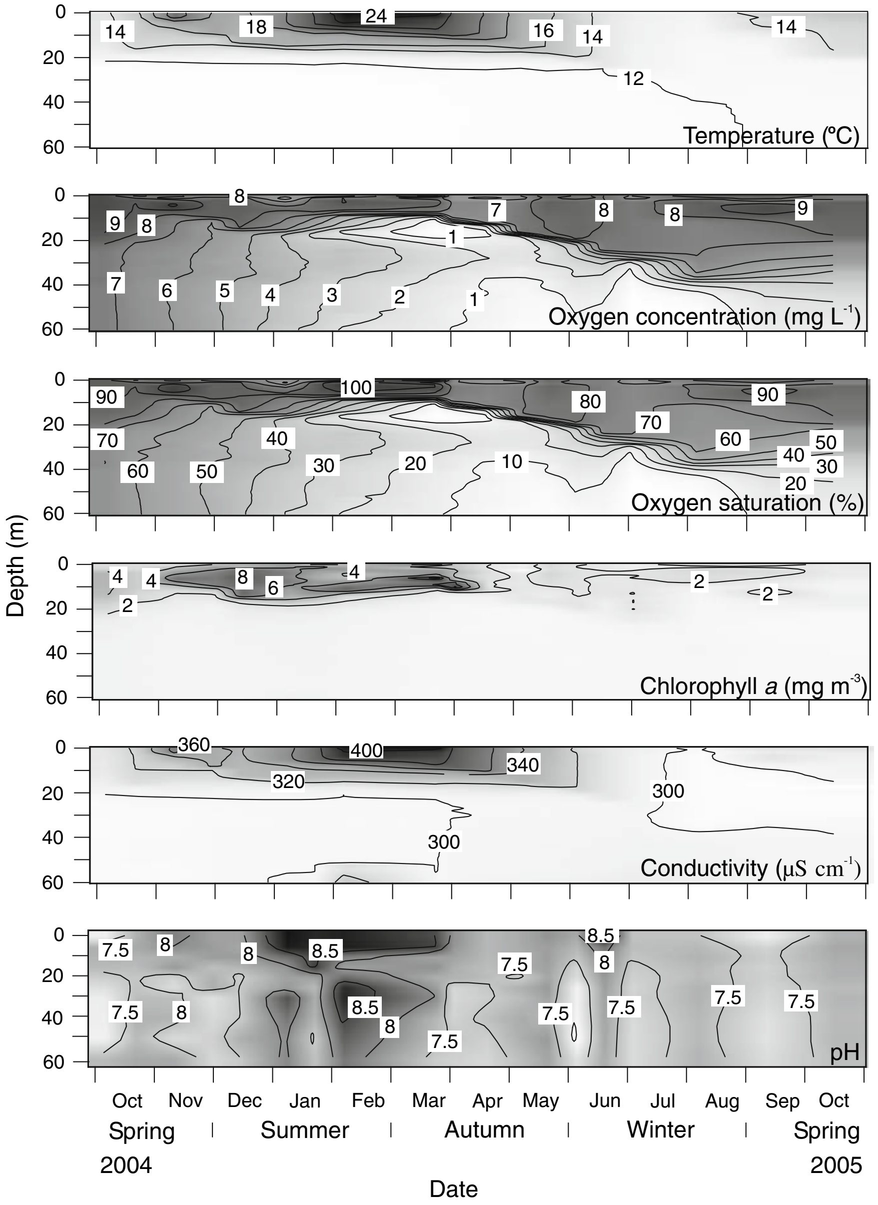
Physico-chemical variables

Weavers Lake surface water temperatures had a seasonal range of 12.9°C, with a maximum of 25.6°C on 4 February 2005 (summer) and a minimum of 12.7°C on 4 August 2005 (winter). The lake was thermally stratified from the start of monitoring (6 October 2004; spring) and remained strongly stratified until June 2006 (early winter; Fig. 2). The hypolimnion was deficient in oxygen throughout the study (Fig. 2), gradually decreasing from the start of the study until becoming depleted (<10% saturation) in April 2005. The hypolimnion was not fully recharged with oxygen during winter (June, July, August), indicating that the lake did not become holomictic. The epilimnion remained at or near saturation for the duration of the study. A metalimnetic oxygen minimum was observed during March and April 2005, with a minimum oxygen concentration of 0.19 mg l^{-1} at 16 m on March 23 2005.

Maximum chlorophyll *a* concentrations were recorded during late spring and summer (November 2004–March 2005; Fig. 2). Concentrations were highest in the surface waters and decreased dramatically below the thermocline. Chlorophyll *a* concentrations were far lower at the end of the study (October 2005) than they were at the beginning (October 2004).

The hypolimnion had the lowest conductivity with little temporal variation (300 µS cm^{-1}). pH in Weavers Lake was neutral to slightly basic throughout the study period and at all depths (Fig. 2), ranging from 7.00 to 8.94. The highest pH values were recorded during and just after the chlorophyll *a* peak (December 2004–March 2005). Secchi depth (Fig. 3) generally increased throughout the study period,

Fig. 2 Spatial and temporal distribution of physical and chemical variables in Weavers Lake; temperature, oxygen concentration, oxygen saturation, chlorophyll *a*, conductivity and pH



ranging from 1.6 m (October 2004) to 10.9 m (September 2005). Lowest Secchi transparencies coincided with peak chlorophyll *a* concentrations. The average yearly phosphorus concentration was 11.6 mg m^{-3}, and generally decreased from a maximum in February 2005 (16 mg m^{-3}) to a minimum in August 2005 (8 mg m^{-3}; Fig. 3). Stability peaked in March 2005 (early autumn; 2471.4 g-cm cm^2), and declined to a minimum in early August (late winter; 58.5 g-cm cm^2), indicating the lake was unlikely to have fully mixed during the study (Fig. 3).

Zooplankton composition and dynamics

Rotifers were the most numerically dominant as well as the most speciose group of zooplankton, accounting for 34 of the total 40 species identified during the study (Table 1). Four cladoceran species and two calanoid copepod species were also identified. Fifteen species comprised greater than 4% of any one sample and thus were included in statistical analyses (Fig. 4). *Keratella cochlearis* was the most abundant rotifer, dominating during the first

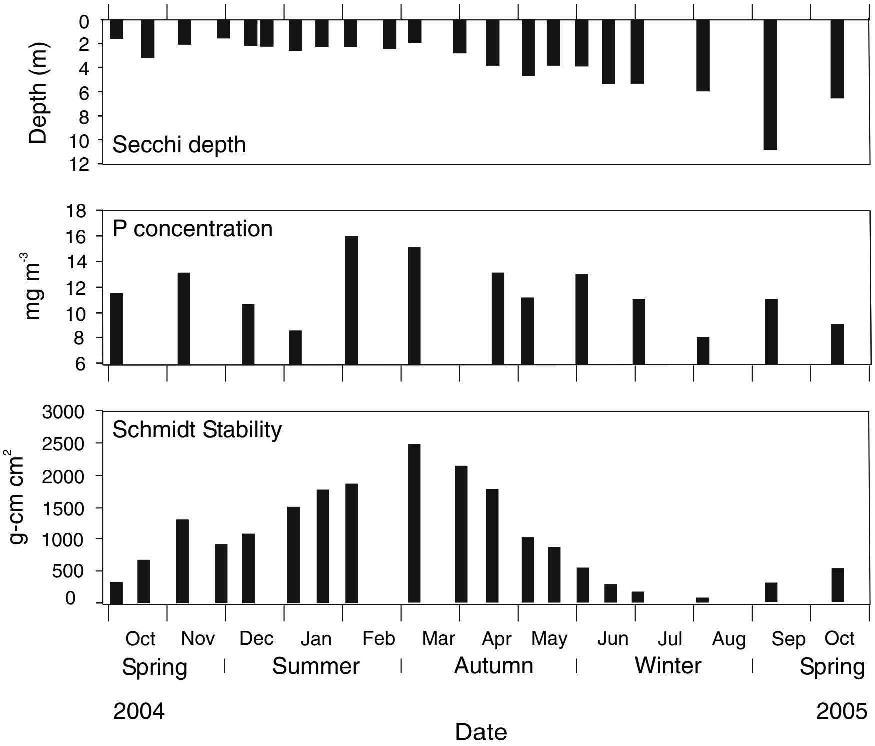


Fig. 3 Spatial and temporal distribution of physical and chemical variables in Weavers Lake; Secchi depth, Phosphorus concentration and Schmidt Stability

six months of sampling (to April 2005), with a peak of 1145 ind. l^{-1} recorded on 30 November 2004 at 5 m. All other numerically dominant species were found for shorter periods of two to six months. Species composition shifted over time from one of rotifer dominance (mid-October–mid-May) to crustacean dominance (June–October). The rotifers *Ascomorpha ovalis, Keratella cochlearis, Polyarthra dolichoptera, Synchaeta longipes* and *Filinia longiseta* were abundant from spring 2004 to autumn 2005, but did not reappear in spring 2005.

Daphnia dentifera was the dominant cladoceran, occurring in high numbers from August to October 2005 (end of study). *Daphnia* were first recorded in the lake in late April 2005 (a single occurrence), and were not recorded again until July 2005 when they became common. *Daphnia dentifera* was not found in Weavers Lake from net samples collected on 4 June 2004 and 26 July 2004, prior to this study, indicating that they may have been absent from the lake prior to April 2005. Calanoid copepods, copepod nauplii and *Asplanchna priodonta* were found throughout the year, although the copepods were most abundant at the start and end of the study (spring). No species were associated with, or restricted to, any specific depths, although most had higher numbers in the surface waters (Fig. 4).

RDA was used to infer relationships between sample groupings based on species data and observed environmental variables (Fig. 5, Table 2). RDA was used because a preliminary detrended correspondence analysis (DCA) indicated species were responding to underlying environmental gradients in a linear, not unimodal, manner (ter Braak and Smilauer 1998). The eigenvalues of Axes 1 and 2 were 0.350 and 0.115, respectively (Table 3), together accounting for 46.5% of the variation in zooplankton species abundances. The high eigenvalue of Axis 1 relative to Axis 2 indicates that Axis 2 explains relatively little of the variation. Samples from early in the study were predominantly negatively associated with Axis 1 (located on the left of the plot), samples from autumn and winter group (middle of study) were in the centre of the plot, and samples from spring 2005 were predominantly positively associated with Axis 1 (located on right of the plot; Fig. 5). The rotifers *Keratella cochlearis*, *Brachionus lyratus*, *Keratella tecta*, *Filinia*

Table 1 Zooplankton species collected during study

Rotifera	
Ascomorpha ovalis	*Lecane bulla*
Ascomorpha saltans	*Lecane closterocerca**
Asplanchna priodonta	*Lecane flexilis**
Brachionus caliciforus	*Lecane hornemanni*
Brachionus lyratus	*Lecane luna*
Brachionus quadridentatus	*Lecane lunaris*
*Brachionus urceolaris**	*Lepadella acuminata**
Collotheca sp.	*Platyias quadricornis**
Filinia longiseta	*Pleurotrocha petromyzon**
Filinia pejleri	*Polyarthra dolichoptera*
Hexarthra intermedia	*Pompholyx complanata*
Keratella cochlearis	*Proales* sp.
*Keratella procurva**	*Synchaeta longipes*
*Keratella slacki**	*Trichocerca longiseta**
Keratella tecta	*Trichocerca similis*
Keratella tropica	*Trichocerca* cf. *stylata*
*Keratella valga**	Bdelloids
Cladocera	
Alona guttata	*Ceriodaphnia dubia*
Bosmina meridionalis	*Daphnia dentifera*
Copepoda	
Boeckella delicata	indeterminate nauplii
Calamoecia lucasi	indeterminate cyclopoids

Species with only one individual found during study marked with *

pejleri, *Synchaeta longipes*, *Ascomorpha ovalis*, *Polyarthra dolichoptera* and *Filinia longiseta* have a strong to moderate negative association with Axis 1, and are therefore associated with early samples. *Bosmina meridionalis* is moderately positively associated with Axes 1 and 2, and with the intermediate samples. *Daphnia dentifera* and calanoid copepods are strongly positively associated with Axis 1, and their distributions were associated with the spring 2005 (late study) samples.

Secchi depth is strongly positively associated with Axis 1, and explained most (33%) of the total variation in zooplankton distribution; no other variable explained greater than 10% of the total variation when considered alone (Table 3). Conductivity, pH and temperature are moderately negatively associated with this axis. The species associated with early samples (i.e. rotifers) were therefore associated primarily with low water clarity, and also high conductivity, high pH and high temperature. Late samples and associated species (i.e. crustaceans, and particularly *Daphnia dentifera*) were associated primarily with high water clarity, and also low temperature, low conductivity and low pH. *Bosmina meridionalis* dominated at a time of intermediate water clarity. There are temporal changes in the community from left to right on the ordination, and therefore the community changed in concert with a general increase in clarity.

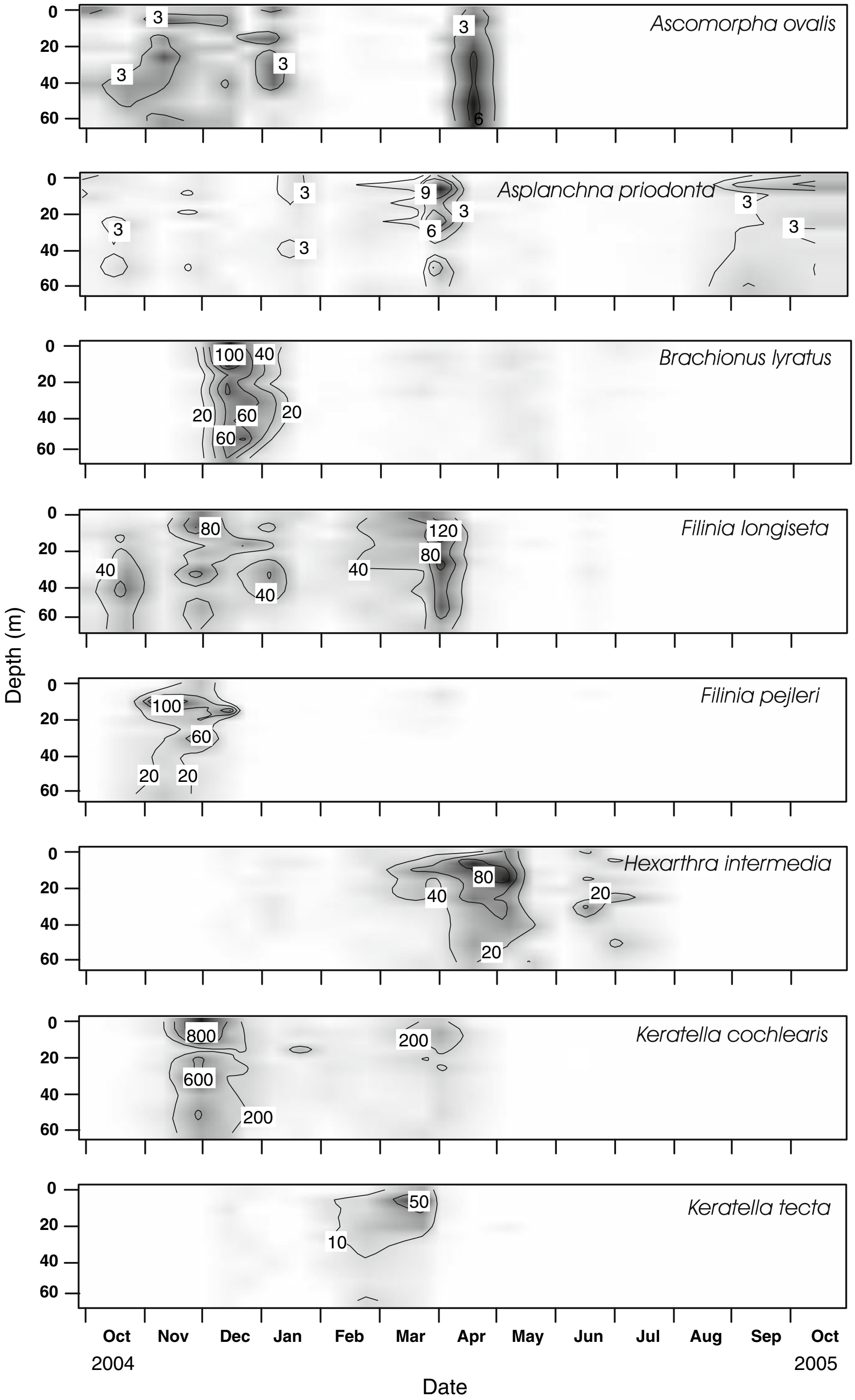
Discussion

Zooplankton dynamics and water clarity

The Weavers Lake zooplankton community showed considerable temporal variation through the study. However, the community did not follow predictable seasonal changes, as the composition at the beginning of the study (spring 2004; dominated by rotifers, e.g. *Asplanchna*, *Polyarthra*, *Brachionus* and *Keratella* species) differed from that found at the end of the study (spring 2005; dominated by *Daphnia*). This finding is likely due to continued colonisation of zooplankton in this young lake. *Daphnia dentifera* were not recorded during this study until late April 2005 (a single occurrence), and were not recorded again until July 2005, when they became abundant. We cannot be certain that these were the first appearances in this lake of this non-indigenous North American species, which first appeared in New Zealand around 1990 (Duggan et al. 2006). However, we did not record this species in preliminary samples from this lake on 4 June and 26 July 2004, suggesting that it established during this study and was absent beforehand.

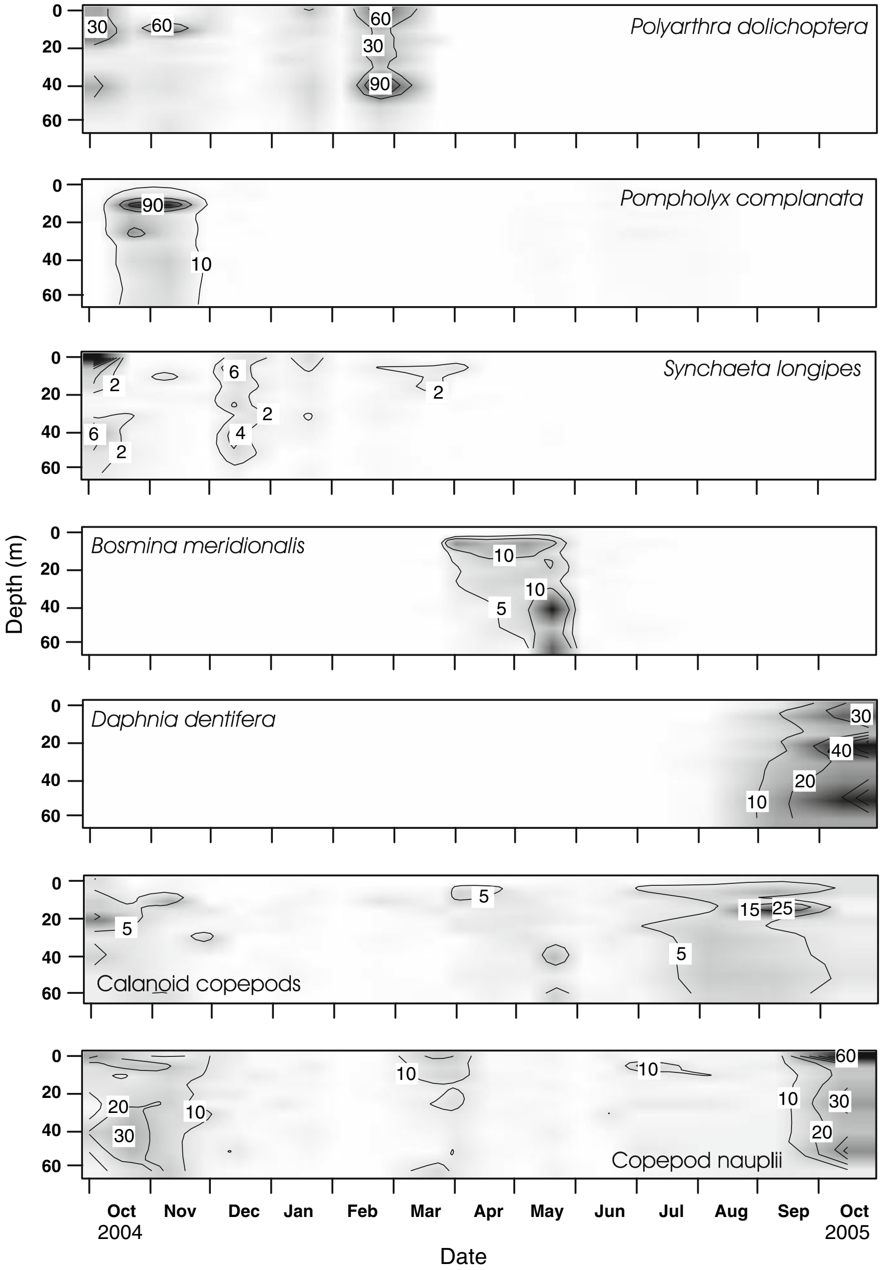
RDA analysis inferred that changes in Weavers Lake zooplankton composition were primarily associated with a gradual improvement in water clarity (Secchi depth) through time. This increase in water clarity was the result of a general decrease in phytoplankton biomass observed during the study, which in turn was likely due to the colonisation of the non-indigenous *Daphnia dentifera*. *Daphnia* species have a large impact on phytoplankton standing crop as they exert intense grazing pressure and have a

Fig. 4 Spatial and temporal distribution of abundances (individuals L^{-1}) of dominant (>4% of any sample) Weavers Lake zooplankton species



generalist foraging strategy (Beisner 2001). High numbers of *Daphnia* commonly occur during, and lead to, the spring 'clear water phase' in many northern hemisphere temperate lakes, a period of phytoplankton minimum that results in increased light penetration and Secchi transparency (e.g. Sommer et al. 1986; Talling 2003). However, *Daphnia* have until recently been an uncommon component in

Fig. 4 continued



New Zealand lakes, being found more frequently in ponds rather than lakes, and more so in the South Island than in the North Island (Chapman and Green 1987). Instead, cladoceran populations in New Zealand have traditionally been dominated by relatively small sized *Ceriodaphnia* and *Bosmina* species, which are less efficient feeders than *Daphnia* (e.g. Mourelatos and Lacroix 1990). The invasion of *Daphnia dentifera*, evidenced by the differences in Secchi transparency at the start and end of the current study, may result in overall decreases in algal biomass' and an associated increased water clarity in New Zealand lakes—an effect similar to that observed after the establishment of the filter feeding zebra mussels in many North American lakes (e.g. Fahnenstiel et al. 1995; Idrisi et al. 2001). *Daphnia dentifera* has spread rapidly in New Zealand, and in recent years has dominated the zooplankton abundance and biomass of

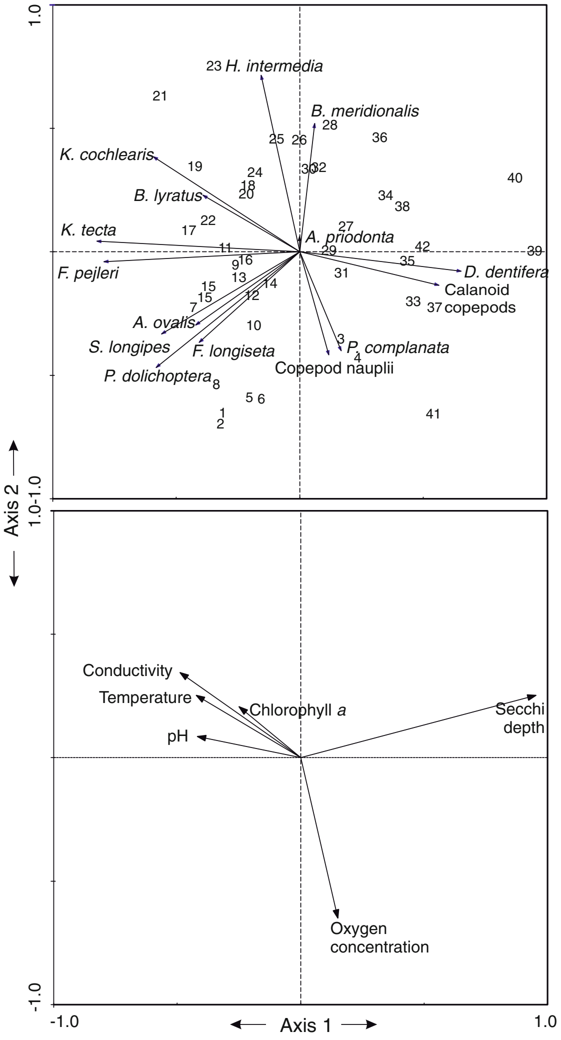


Fig. 5 Ordination diagram based on RDA of Weavers Lake zooplankton species with respect to environmental variables. Numbers correspond to sample numbers (Table 2)

many New Zealand rivers and lakes, and its effects are now likely to be widespread in New Zealand (Burger et al. 2002; Duggan et al. 2006). Regardless of whether or not *Daphnia* first invaded Weavers Lake during this study, their absence at the beginning of the study and presence at the equivalent time at the end of the study indicates the effects that this species can potentially have on phytoplankton biomass in New Zealand lakes.

A worrying aspect regarding the invasion of *Daphnia dentifera* in New Zealand is that *Daphnia* species commonly have superior competitive abilities relative to other zooplankton (e.g. Gilbert 1988; MacIsaac and Gilbert 1989). Notably, many of the rotifer species present at the beginning of the study were absent at the end of the study, after the *Daphnia* invasion (e.g. *Ascomorpha ovalis*, *Filinia longiseta*, *Polyarthra dolichoptera*). The establishment of *Daphnia* may thus be having profound effects on native zooplankton communities. Predation by fish on *Daphnia* is commonly inferred to reduce the abundance, and therefore effects, of *Daphnia* in northern temperate lakes (e.g. Sommer et al. 1986). The fish fauna of Weavers Lake is currently unknown, but casual observations have included the introduced Koi Carp (*Cyprinus carpio*) and Mosquitofish (*Gambusia affinis*), particularly in the lake margins. However, due to less pronounced climatic variability in the North Island of New Zealand relative to the temperate northern hemisphere (which allows fish breeding to be less temporally concentrated), and due to native fish primarily being catadromous (with young plankton-feeding stages primarily being at sea), predation by native species is generally considered to have a muted impact in New Zealand (Chapman and Green 1987). This may allow *Daphnia dentifera* to have a prolonged impact on New Zealand lakes.

A possible alternative explanation for the gradual increase in water clarity in Weavers Lake over the study period was due to the loss of algal biomass by sedimentation and a lack of replenishment of nutrients due to the apparent absence of holomixis (e.g. Noges and Kangro 2005). An absence of holomixis was indicated both by the lack of oxygen replenishment to the hypolimnion and the high Schmidt Stability values during winter, indicating the significant amount of energy required to cause the lake to turn over (minimum Schmidt Stability recorded = 58.5 g-cm cm^2). This may be a result of the small surface area to depth ratio of the lake (both important components of stability calculations). Regardless, phosphorus was not depleted to a level where phytoplankton growth would likely be limited to the degree observed (see Lampert et al. 1986). Presence of strong herbivory by *Daphnia* has been observed to exert greater depletions in algal concentrations than by seasonal changes in nutrient levels elsewhere (e.g. Lathrop et al. 1996).

Analysis of zooplankton composition relative to environmental variables inferred that temperature change was unimportant. Interestingly, temperature is usually one of the main factors controlling the

Table 2 Key to sample numbers (date and site) for the RDA ordination

No.	Date	Depth (m)	no.	Date	Depth (m)	No.	Date	Depth (m)
1	10 Oct 04	≤20	14	20 Jan 05	≤20	29	19 May 05	≤20
2	10 Oct 04	>20	16	20 Jan 05	>20	30	19 May 05	>20
3	22 Oct 04	≤20	17	04 Feb 05	≤20	31	03 Jun 05	≤20
4	22 Oct 04	>20	18	04 Feb 05	>20	32	03 Jun 05	>20
5	10 Nov 04	≤20	19	24 Feb 05	≤20	33	17 Jun 05	≤20
6	10 Nov 04	>20	20	24 Feb 05	>20	34	17 Jun 05	>20
7	30 Nov 04	≤20	21	23 Mar 05	≤20	35	01 Jul 05	≤20
8	30 Nov 04	>20	22	23 Mar 05	>20	36	01 Jul 05	>20
9	14 Dec 04	≤20	23	01 Apr 05	≤20	37	04 Aug 05	≤20
10	14 Dec 04	>20	24	01 Apr 05	>20	38	04 Aug 05	>20
11	23 Dec 05	≤20	25	18 Apr 05	≤20	39	08 Sep 05	≤20
12	23 Dec 05	>20	26	18 Apr 05	>20	40	08 Sep 05	>20
13	06 Jan 05	≤20	27	06 May 05	≤20	41	12 Oct 05	≤20
14	06 Jan 05	>20	28	06 May 05	>20	42	12 Oct 05	>20

Table 3 Results of forward selection and Monte Carlo permutation tests from RDA of Weavers Lake zooplankton species

Variable	Lambda-1	Lambda-A	*P*-value
Secchi depth	0.33	0.33	0.002
Chlorophyll *a*	0.03	0.07	0.004
Oxygen concentration	0.06	0.05	0.002
Conductivity	0.10	0.03	0.032
Temperature	0.07	0.02	0.270
pH	0.07	0.02	0.196

The lambda-1 column lists the environmental variables and variance they explain singly. The lambda-A column indicates the environmental variables in order of their inclusion in the RDA model, the additional variance each explains at the time of inclusion, and its significance at that time (*P*-value). Environmental variables are listed in order of inclusion in the model

spatial and temporal dynamics of zooplankton species in temperate regions (e.g. Ruttner-Kolisko 1974; May 1983; Berzins and Pejler 1989). We suggest that our finding of water transparency, rather than temperature, as being the most important environmental variable influencing zooplankton dynamics in this study was due to continued development of the community, which in turn affected the water clarity in Weavers Lake. Accordingly, caution should be exercised when using multivariate statistics to examine developing or invaded communities versus assemblages simply reacting to changes in environmental conditions. Specifically, incoming organisms can act as the drivers of change for both species composition and the environment.

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