Research Article

Skistodiaptomus pallidus (Copepoda: Diaptomidae) establishment in New Zealand natural lakes, and its effects on zooplankton community composition

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Abstract

The North American calanoid copepod *Skistodiaptomus pallidus* is an emerging invader globally, with non-indigenous populations recorded from constructed waters in New Zealand, Germany and Mexico since 2000. We examined the effects of *S. pallidus* establishment on the zooplankton community of a natural lake, Lake Kereta, where it was first recorded in late-2008, coincident with releases of domestically cultured grass carp (*Ctenopharyngodon idella*). Although not present in any of our samples prior to August 2008, *S. pallidus* was found in all samples collected in the subsequent five years. ANOSIM indicated zooplankton community composition significantly differed between samples collected before and after *S. pallidus* invasion, whether the invader was included in the analysis or not. Zooplankton species affected most greatly were the copepods *Calamoecia lucasi* and *Mesocyclops* sp., which decreased in their relative importance, and the cladocerans *Bosmina meridionalis* and *Daphnia galeata*, which increased. Rotifer species were relatively unaffected. As the length of grass carp released were >6.5 cm, direct predatory effects by this species on the zooplankton community are unlikely. Associated reductions in macrophyte biomass could explain increases in the relative abundances of planktonic cladocerans (*B. meridionalis* and *D. galeata*). However, the effect of macrophyte reduction by grass carp on zooplankton communities is considered to be limited elsewhere, while the reduced macrophyte biomass cannot explain the decrease in relative abundance of the native planktonic calanoid copepod *C. lucasi*. Competition between *C. lucasi* and *S. pallidus* is the most compelling explanation for the reduction in importance of the native calanoid copepod species. *Skistodiaptomus pallidus* appears to have undergone a "boom-and-bust" cycle in Lake Kereta, increasing in relative abundance in the first three years following establishment, before declining in importance.

Key words: boom-and-bust, *Ctenopharyngodon idella,* exotic species, calanoid copepods, constructed waters

Introduction

A common pattern observed in aquatic invasions is the relative ease of establishment in constructed waters (e.g., retired quarry and mine pits, dams constructed for water supply or electricity generation, and ornamental ponds) compared with natural waters. New water bodies have increased the number, area and spatial distribution of lakes and ponds in many areas globally, and have seemingly aided in the establishment and spread of non-indigenous species (Havel et al. 2005; Johnson et al. 2008; Banks and Duggan 2009; Parkes and Duggan 2012). The African cladoceran *Daphnia lumholtzi* G.O. Sars, 1885, for example,

spread through the United States after first establishing in a Texan reservoir, primarily with dams at the invasion front (Havel et al. 2005). Johnson et al. (2008), similarly, found five other widespread, high profile, invaders in Wisconsin and Michigan, USA (Eurasian watermilfoil, zebra mussel, rusty crayfish, spiny waterflea and rainbow smelt) to have higher rates of occurrence in dams than natural waters. New Zealand has similar examples, with four calanoid copepod species recorded exclusively in constructed water bodies (Banks and Duggan 2009). Parkes and Duggan (2012) found zooplankton community composition to vary between natural and constructed waters in New Zealand; natural waters housed species

better adapted to pelagic conditions, with composition largely governed by trophic state, while constructed waters had more varied assemblages and composition related to opportunity for colonisation (i.e., closeness to other lakes and number of water bodies nearby were an important determinant). Reduced biotic resistance from poorly adapted species in newer water bodies may allow for easier establishment of non-indigenous species. Once established in constructed waters, however, these water bodies can provide sites of high propagule supply to other water bodies, allowing greater opportunities for invasion of natural waters through large release sizes and frequencies. As such, species can commonly spread to natural water bodies following invasion of constructed water bodies. For example, *D. lumholtzi* spread from dams to natural waters in North America, while the calanoid copepod *Boeckella triarticulata* (Thomson, 1883) first invaded constructed ponds in northern Italy before spreading to other Italian constructed and natural waters (Ferrari 1991; Ferrari and Rossetti 2006; Alfonso and Belmonte 2008).

Here we report on the invasion of the North American diaptomid copepod *Skistodiaptomus pallidus* (Herrick, 1879) into two natural North Island, New Zealand, lakes, a species previously only recorded there from constructed waters. We also provide the first record for this species in the South Island, from a constructed lake. All of the new distribution records are in lakes where domestically produced grass carp (*Ctenopharyngodon idella* (Valenciennes, 1844)) have been introduced for aquatic macrophyte control. *Skistodiaptomus pallidus* is an invader of emerging importance globally, having expanded its geographical distribution in North America (Byron and Saunders 1981), and recently establishing populations in constructed waters in Germany and Mexico (Brandorff 2011; Suárez-Morales and Arroyo-Bustos 2012). In New Zealand, *S. pallidus* was first recorded in 2000 in ponds at the Auckland Regional Botanic Gardens, but may have been present for some time prior to this (Duggan et al. 2006). Banks and Duggan (2009) expanded these records, finding the species in other New Zealand localities (again, all constructed). As there are few studies documenting the effects of non-indigenous freshwater zooplankton globally, including *S. pallidus,* we examined the consequences of establishment of this species over a six year period following invasion on the zooplankton community in one natural lake, Lake Kereta.

Methods

Skistodiaptomus pallidus was recorded from a series of samples from Lake Kereta, North Island (36°35'34.66"S, 174°16'50.26"E) from late 2008, from a one-off sample from Lake Omapere, North Island (35°20'40.58"S, 173°47'21.76"E) from mid-June 2012, and a one-off sample from Lake Hood, South Island (43°58'00.3"S, 171°46'16.4"E) on 18 January 2014. Lake Kereta is a eutrophic lake, with a maximum depth of 1.5 m. Zooplankton samples were collected from Lake Kereta briefly in 1997, and then quarterly from September 2001, using vertical hauls from a central lake station with a 40 μm plankton net. Samples were preserved in ethanol (>50% final concentration). While samples have been lost in the intervening period, 13 samples from Lake Kereta were available prior to the first record of *S. pallidus* on 13 August 2008, with 20 samples available to 20 May 2013. Where possible, samples were enumerated in aliquots until at least 300 zooplankton individuals were counted. Because net hauls provide only semi-quantitative results, we calculated the relative abundances of zooplankton in each sample for all analyses. Non-metric multi-dimensional scaling (MDS) and analysis of similarities (ANOSIM) were used to infer whether changes have occurred in the Lake Kereta zooplankton community composition before and after the invasion of *S. pallidus* (Primer v.6.1.13; Primer-E Ltd 2009). MDS is a multivariate ordination technique that builds a 2-D 'map' of samples based on their similarity to each other as defined by a distance metric; a stress value measures the goodness of fit of the map, showing how well correlated the distances on the map are to those of the underlying similarity matrix. We performed MDS on the Bray-Curtis similarity matrix. Zooplankton data were $\log(x+1)$ transformed to down weigh the influence of dominant species in the analyses. Only zooplankton species found in two or more samples were included in our analyses, to reduce the influence of rare species potentially sampled by chance. ANOSIM was applied to the similarity matrix to test whether differences in zooplankton community composition between samples collected before and after the first detection of *S. pallidus* were statistically significant. For all tests, 999 permutations were executed. SIMPER analysis was used to explore the contribution of individual species to the average dissimilarity of samples collected before and after

Table 1. Zooplankton species observed in Lake Kereta during the study period.


Rotifera

Ascomorpha ovalis (Bergendal, 1892)	*Keratella tropica* (Apstein, 1907)
Ascomorphella volvocicola (Plate, 1886)	*Lecane bulla* (Gosse, 1851)
Asplanchna brightwelli Gosse, 1850	*Lecane closterocerca* (Schmarda, 1859)
Asplanchna priodonta Gosse, 1850	*Lecane flexilis* (Gosse, 1886)
Bdelloids	*Lecane luna* (Müller, 1776)
Brachionus caudatus Barrois & Daday, 1894	*Lecane lunaris* (Ehrenberg, 1832)
Brachionus quadridentatus Hermann, 1783	*Lepadella acuminata* (Ehrenberg, 1834)
Cephalodella gibba (Ehrenberg, 1832)	*Macrochaetus collinsi* (Gosse, 1867)
Collotheca sp.	*Mytilina ventralis* (Ehrenberg, 1832)
Cupelopagis vorax (Leidy, 1857)	*Polyarthra dolichoptera* Idelson, 1925
Dicranophorus epicharis Harring & Myers, 1928	*Pompholyx complanata* Gosse, 1851
Dicranophorus grandis (Ehrenberg, 1832)	*Proales* cf. *alba* (Wulfert, 1938)
Euchlanis calpidia (Myers, 1930)	*Synchaeta oblonga* Ehrenberg, 1832
Euchlanis dilatata Ehrenberg, 1832	*Synchaeta pectinata* Ehrenberg, 1832
Euchlanis meneta Myers, 1930	*Testudinella mucronata* (Gosse, 1886)
Filinia longiseta (Ehrenberg, 1834)	*Testudinella patina* (Hermann, 1783)
Filinia terminalis (Plate, 1886)	*Trichocerca brachyura* (Gosse, 1851)
Hexarthra intermedia (Wiszniewski, 1929)	*Trichocerca pusilla* (Jennings, 1903)
Keratella cochlearis (Gosse, 1851)	*Trichocerca similis* (Wierzejski, 1893)
Keratella procurva Thorpe, 1891	*Trichocerca tenuior* (Gosse, 1886)
Keratella tecta (Gosse, 1851)	

Cladocera

Alona sp.	*Daphnia galeata* G.O. Sars, 1864
Bosmina meridionalis G.O. Sars, 1904	*Ilyocryptus sordidus* (Liévin, 1894)
Ceriodaphnia dubia Richard, 1894	*Simocephalus vetulus* (Müller, 1776)
Chydorus sp.	*Graptoleberis testudinaria* (Fischer, 1851)

Copepoda

Calamoecia lucasi Brady, 1906	*Mesocyclops* sp.
Eucyclops serrulatus (Fischer, 1851)	*Skistodiaptomus pallidus* (Herrick, 1879)
Macrocyclops albidus (Jurine, 1820)	

Ostracods

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invasion of *S. pallidus*. Analyses were undertaken using *S. pallidus* included (a combined total of copepodites and adults), to determine whether the presence of this species significantly influenced community composition. The analyses were repeated with *S. pallidus* excluded, to infer whether the invasion of this species has altered the community composition of other zooplankton present. Copepod nauplii were excluded from all analyses as these could not be confidently ascribed to species.

Results

The last samples collected without *S. pallidus* in Lake Kereta were on 2 April 2008, with its first detection on 13 August 2008. *Skistodiaptomus pallidus* was present in all samples collected following this date. Fifty-five taxa were observed in the lake during the study period, comprising 41 rotifers, 8 cladocerans and 5 copepod species (Table 1). Prior to the invasion of *S. pallidus*, the native calanoid copepod *Calamoecia lucasi* Brady, 1906 was typically present, and occasionally dominated the community (e.g., March 2003, January 2005; Figure 1). At various times, rotifers, cyclopoid copepods or cladocerans dominated the community. Following invasion, *S. pallidus* generally increased in relative abundance through time, commonly dominating the community (>25% of numbers), and particularly so in August 2010 (94.1%) and June 2011 (91.8% of individuals counted). Following this time, the relative abundance of *S. pallidus* decreased (always <25% of total numbers over the last 13 months). Excluding *S. pallidus*, cladocerans and rotifers (as a group) became relatively more important post-invasion, and other copepods (including *C. lucasi*) decreased in their relative importance, compared to before the invasion.
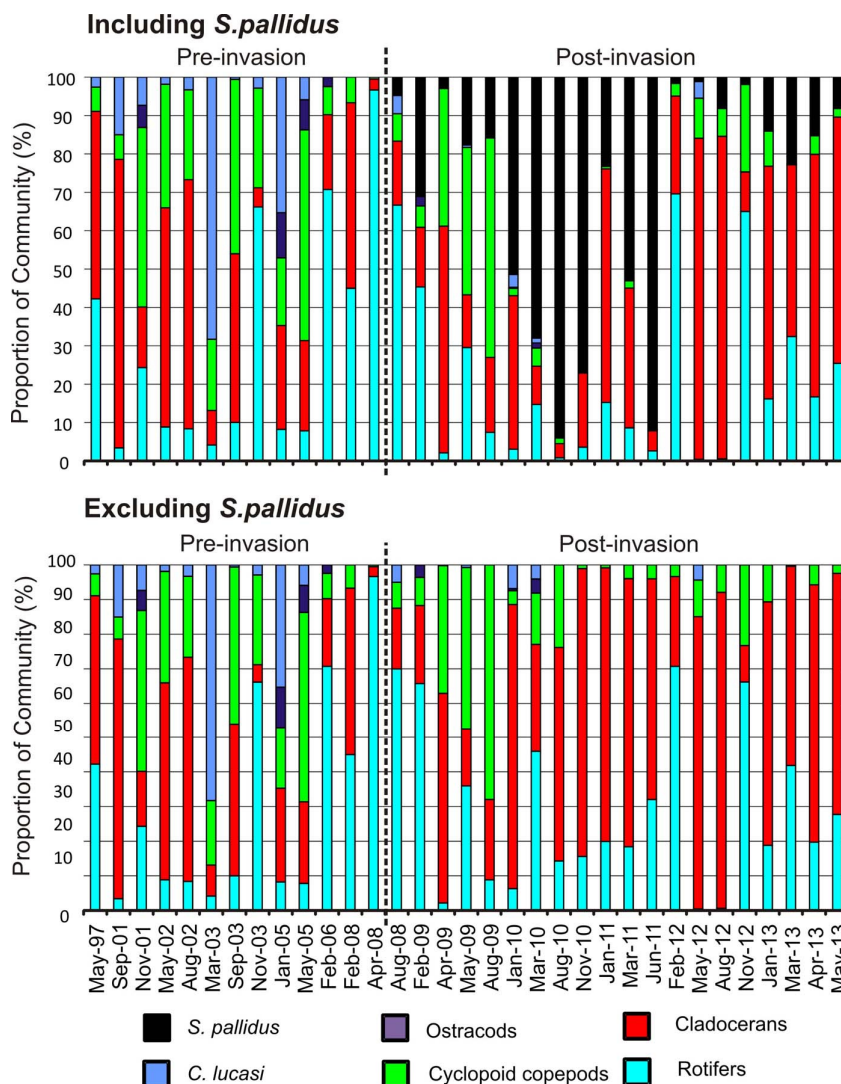
Figure 1. Relative abundances of the major zooplankton groups in Lake Kereta between 1997 and 2013, with *S. pallidus* included (top) and excluded (bottom).

The MDS undertaken with *S. pallidus* included revealed a clear separation between samples before and after *S. pallidus* invasion (Figure 2). ANOSIM indicated community composition significantly differed before and after the invasion (Global R=0.501; P=0.001). SIMPER analysis indicated that species contributing most greatly (>5%) to the average dissimilarity calculated between sample groups before and after invasion were crustaceans: *S. pallidus* (responsible for 13.5% of the dissimilarity between sample groups before and after invasion), *Mesocyclops* sp. (7.3%; decreased post-invasion), *Bosmina meridionalis* G.O. Sars, 1904 (7.2%;

increase), *Daphnia galeata* G.O. Sars, 1864 (6.9%; increase) and *C. lucasi* (6.8%; decrease). This indicates the dominance of *S. pallidus* in many samples following its invasion was the most important species differentiating the sample groups before and after the invasion.

The MDS excluding *S. pallidus* showed a separation in samples before and after the *S. pallidus* invasion, with 'before' samples distributed primarily on the left of the ordination, and 'after' samples on the right. However, the separation of 'before' and 'after' samples was not as clearly defined as in the ordination where *S. pallidus* was included (Figure 2). Nevertheless, ANOSIM
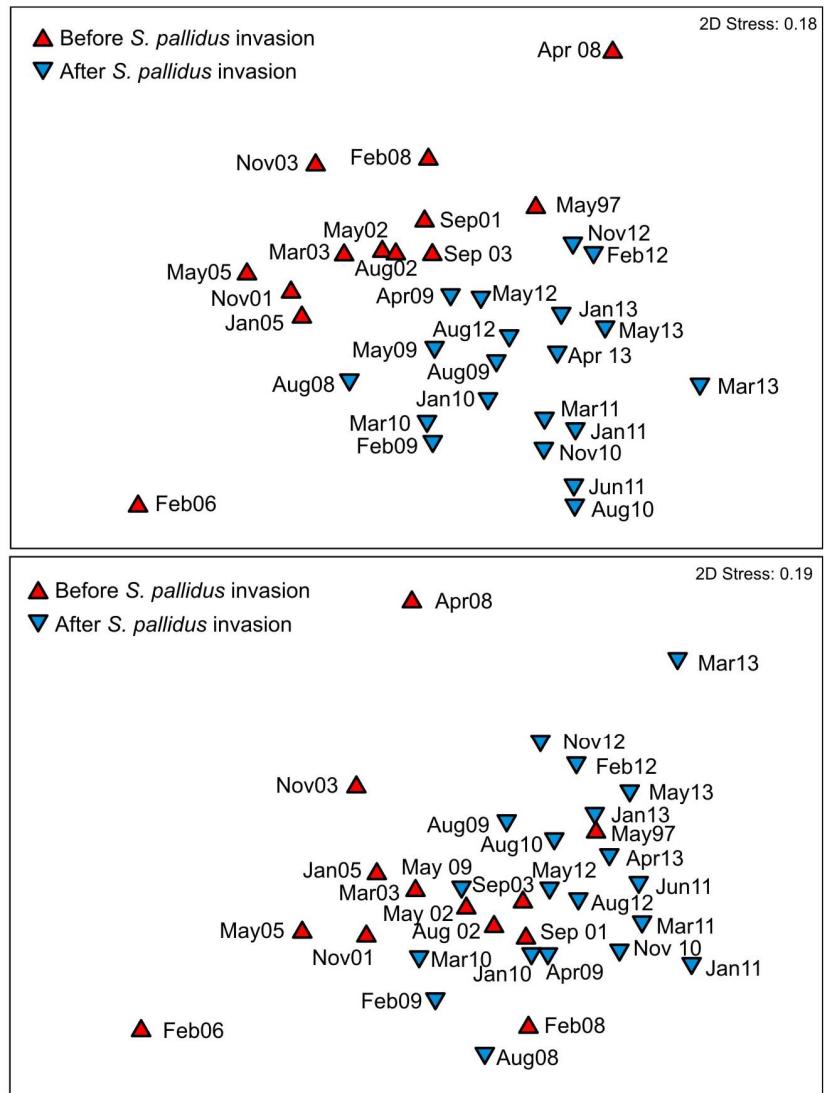
Figure 2. Multidimensional scaling plots showing change in species composition before and after invasion of *Skistodiaptomus pallidus* into Lake Kereta. Analyses were undertaken with *S. pallidus* included (above) and excluded (below) from the dataset.

inferred community composition to significantly differ before and after the invasion (Global R=0.246; P=0.002). SIMPER analysis indicated that species contributing most greatly (>5%) to the dissimilarity calculated between samples before and after invasion were *D. galeata* (9.5%; increase), *B. meridionalis* (7.8%; increase), *C. lucasi* (7.3%; decrease), *Mesocyclops* sp. (6.8%; decrease), and *Chydorus* sp. (5.2%; decrease). Due to the clear statistical differences between community composition in samples collected before and after *S. pallidus* invasion, missing samples in the dataset were unlikely to have affected the statistical results.

Discussion

Skistodiaptomus pallidus was first recorded in Lake Kereta on 13 August 2008. Although not present in 13 samples prior to this date, it was present in all 20 samples collected in the following five years. First detection of *S. pallidus* in Lake Kereta coincided with releases of grass carp (*Ctenopharyngodon idella*) into the lake to aid in the control of hornwort (*Ceratophyllum demersum* L., 1753); hornwort had invaded the lake prior to 1999. Between March 2008 and April 2009, four grass carp releases were made into Lake Kereta, comprising almost 15000 fish (de Winton 2012).

Translocations in association with fish appears to be a common transportation vector for zooplankton invasions globally with, for example, *Daphnia lumholtzi* potentially having been released into North America with introductions of Nile Perch (Havel and Hebert 1993), while the first introduction of *Boeckella triarticulata* to northern Italy likely also occurred with introductions of fish (Ferrari 1991). Lake Omapere, where we also recorded *S. pallidus*, had over 40000 grass carp released as a method of controlling Brazilian waterweed *Egeria densa* Planch., 1849 in 2000 (Champion 2004; Ray et al. 2006), while Lake Hood had over 2000 grass carp released in 2005. Grass carp utilized in New Zealand are domestically produced, from stock originally derived from Hong Kong (McDowall 1990), and it may be that ponds for the stocking of carp are contaminated with *S. pallidus*. However, *S. pallidus* has also been recorded among live fish food (*Daphnia carinata* King, 1852) in aquarium stores (Duggan et al. 2006), and is present in several constructed Auckland lakes, leaving the possibility that it may have been spread by vectors other than grass carp. *Skistodiaptomus pallidus* has not yet been recorded from some lakes where grass carp have been released, for which we have zooplankton samples (Western Springs and Lake Wainamu; de Winton and Edwards 2012). However, the consistent timing of the first records of *S. pallidus* in Lake Kereta with grass carp releases appears compelling.

The first records of *S. pallidus* in the North Island of New Zealand were from constructed waters (Duggan et al. 2006; Banks et al. 2009). Here we present the first record from the South Island, in a lake constructed for water sports activities such as fishing, rowing and water skiing. Taylor and Duggan (2012) demonstrated that *S. pallidus* could readily establish populations in experimental tanks where native New Zealand calanoid copepods (primarily *C. lucasi*) were absent, while invasions were repelled where calanoid copepods were present. However, these authors noted that any community could be invaded if presented with adequate propagule supplies, ultimately overwhelming biotic resistance (see also von Holle and Simberloff 2005). Abundant propagule supplies of *S. pallidus* could have been provided to the natural lakes in this study in association with large releases of grass carp, if ponds used in the culture of this fish species contained *S. pallidus*. While recent invasions of *S. pallidus* in Germany (Brandorff 2011) and tropical Mexico (Suárez-Morales and Arroyo-Bustos 2012) are currently restricted to constructed water bodies, it is likely a matter of time before they spread to natural waters also (as has also been the case for *D. lumholtzi* in North America, and *B. triarticulata* in Italy). In New Zealand, the Japanese calanoid copepod *Sinodiaptomus valkanovi* Kiefer, 1938, and Australian species' *Boeckella minuta* G.O. Sars, 1896 and *B. symmetrica* G.O. Sars, 1908, are seemingly still confined to constructed waters (Banks and Duggan 2009; Makino et al. 2010), but may also establish in natural waters given time.

A significant change in zooplankton community composition coincided with the establishment of *S. pallidus* in Lake Kereta. When considering *S. pallidus* as part of the community, the assemblages before and after the invasion differed significantly, as *S. pallidus* commonly dominated. However, even when *S. pallidus* was removed from the analyses, the zooplankton assemblages were still found to be significantly different, primarily due to changes in the relative abundances of other crustacean species. Most notably, the native calanoid copepod *C. lucasi* decreased in relative abundance. Calanoid copepods of similar size, or with significant dietary overlap, cannot co-exist, such that in many lakes coexistence is rare unless they are of significantly different size (e.g., Hutchinson 1967; Maly and Maly 1997). Similar to the current study, the non-indigenous population of *S. pallidus* in the Tahoe Keys marina, southern Lake Tahoe, United States, was found to displace the native calanoid copepods *Leptodiaptomus tyrelli* (Poppe, 1888) and *Epischura nevadensis* Lilljeborg, 1889 (Byron and Saunders 1981). In the current study, the planktonic cladocerans *Bosmina meridionalis* and *Daphnia galeata* increased in relative abundance, and the cyclopoid copepod *Mesocyclops* sp. and the cladoceran *Chydorus* sp. decreased, while no rotifer species contributed greater than 5% to the average dissimilarity between zooplankton communities before and after *S. pallidus* invasion.

Complicating the identification of potential effects of *S. pallidus* on the zooplankton community was the concomitant release of grass carp and associated reduction in macrophyte biomass. However, studies of grass carp introductions have typically found limited effects on zooplankton communities. Grass carp introduced to Lake Kereta were all greater than 6 cm in length (de Winton 2012). Although grass carp fry utilize zooplankton as a primary food source, these were not released to the lake, and adults rarely eat anything except plant material (Richard et

al. 1985). Grass carp transition from a diet of zooplankton or benthos to aquatic macrophytes at approximately 5.5 cm (He et al. 2013). For example, fish >6.3 cm in a Florida pond were found to be strict herbivores (Colle et al. 1978). Indeed, Prowse (1971) noted that adult grass carp may starve in ponds lacking vegetation even if they have high abundances of zooplankton. As such, direct effects of grass carp are unlikely. Macrophyte biomass decreased markedly following grass carp introduction. Observations in 2008 showed hornwort to have >75% coverage in the lake, while >99.9% of biomass was removed when the lake was resurveyed in February 2012 (de Winton 2012). Conditions may have thus become more favourable for some species by providing more open water for planktonic species, while the reduced extent of weedbeds may have reduced the abundances of typically littoral species. This reduction in macrophytes could explain increases in the planktonic cladoceran species, *B. meridionalis* and *D. galeata*, and the associated decrease in the littoral *Chydorus* sp. However, the reduction in macrophytes cannot provide an explanation for the decreased importance of the planktonic *C. lucasi*. Most studies on the indirect effects of grass carp on zooplankton, through macrophyte removal, have found limited effects also. Fry and Osbourne (1980) found grass carp additions to have little direct or indirect effect upon the zooplankton in three experimental Florida ponds, while Pípalová et al. (2009) found no changes in zooplankton composition or abundance associated with increasing grass carp densities from 29 kg/ha to 92 kg/ha in a Czech Republic pond, despite a reduction in macrophyte density from 109 g/m^2 to 33 g/m^2. Kirkagac and Demir (2004) found increases in zooplankton abundance in ponds stocked with increasing densities of grass carp (>19.5 cm) in Turkey, largely as a result of a greater availability of nutrients for phytoplankton, providing food for zooplankton. Where effects on composition have been noted, it is usually related to subsequent increases in the abundances of planktivorous fishes following macrophyte reduction (e.g., Maceina et al. 1992; Richard et al. 2005). However, New Zealand zooplankton communities are likely to be under reduced pressure from zooplanktivorous fish relative to elsewhere (Chapman and Green 1987). Overall, competitive interactions with *S. pallidus* provide the most convincing explanation for the reduction in *C. lucasi*, rather than any direct or indirect effects of grass carp.

Skistodiaptomus pallidus appears to have undergone a "boom-and-bust" cycle in Lake Kereta. The species gradually increased in its numerical importance following establishment, peaked in relative abundance in late-2010 and mid-2011 when it comprised >90% of individuals counted, and thereafter declined dramatically in its importance, comprising <25% of the relative abundance over the last 13 months of study. Such boom-and-bust cycles are typically expected when food of the invader is previously under-utilised by the existing species, leading to a boom period for the invader, followed by a decline towards an equilibrium with available resources (bust) (Williamson 1996). Alternatively, but less likely, pathogens or predators may also have played a role in reducing the importance of this species. Further monitoring is required to determine whether *S. pallidus* remains integrated in the lake community at low densities, is extirpated, or if the species may continue to dominate in a cyclic or irregular manner (*sensu* Strayer and Malcom 2006). Such monitoring is also important to determine the long-term effects on the native calanoid copepod, *C. lucasi*, whose population had not attained their pre-invasion importance following the decline in *S. pallidus*.

Acknowledgements

References

Alfonso G, Belmonte G (2008) Expanding distribution of *Boeckella triarticulata* (Thomson, 1883) (Copepoda: Calanoida: Centropagidae) in Southern Italy. *Aquatic Invasions* 3: 247–251, http://dx.doi.org/10.3391/ai.2008.3.2.17

Banks CM, Duggan IC (2009) Lake construction has facilitated calanoid copepod invasions in New Zealand. *Diversity and Distributions* 15: 80–87, http://dx.doi.org/10.1111/j.1472-4642.2008.00524.x

Brandorff G-O (2011) The copepod invader *Skistodiaptomus pallidus* (Herrick, 1879) (Crustacea, Copepoda, Diaptomidae) from North America in water bodies of Bremen, northern Germany. *Aquatic Invasions* 6 (Suppl. 1): S1–S6, http://dx.doi.org/10.3391/ai.2011.6.S1.001

Byron ER, Saunders JF (1981) Colonization of Lake Tahoe and other western habitats by the copepod, *Skistodiaptomus pallidus* (Herrick) (Calanoida). *The Southwestern Naturalist* 26: 82–83, http://dx.doi.org/10.2307/3671345

Champion P (2004) Lake Omapere restoration and management project. NIWA Client Report HAM2004-061

Chapman MA, Green JD (1987) Zooplankton ecology. In: Viner AB (ed), Inland Waters of New Zealand. Department of Scientific and Industrial Research, Wellington, New Zealand, pp 225–263

Colle DE, Shireman JV, Rottmann RW (1978) Food Selection by Grass Carp Fingerlings in a Vegetated Pond. *Transactions of the American Fisheries Society* 107: 149–152, http://dx.doi.org/10.1577/1548-8659(1978)107<149:FSBGCF>2.0.CO;2

De Winton M (2012) Assessment of hornwort status in Lake Kereta. NIWA Client Report HAM2012-019, prepared for New Zealand Waterways Restoration Ltd

De Winton M, Edwards T (2012) Assessment of Auckland lakes using LakeSPI. Auckland Regional Council Technical Report 2012/034

Duggan IC, Green JD, Burger DF (2006) First New Zealand records of three non-indigenous zooplankton species: *Skistodiaptomus pallidus, Sinodiaptomus valkanovi,* and *Daphnia dentifera. New Zealand Journal of Marine and Freshwater Research* 40: 561–569, http://dx.doi.org/10.1080/00288330.2006.9517445

Ferrari I, Farabegoli A, Pugnetti A, Stella E (1991) The occurrence of a calanoid Australasian species, *Boeckella triarticulata* (Thomson), in fish ponds of Northern Italy. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 24: 2822–2827

Ferrari I, Rossetti G (2006) New records of the centropagid *Boeckella triarticulata* (Thomson, 1883) (Copepoda: Calanoida) in Northern Italy: evidence of a successful invasion? *Aquatic Invasions* 1: 219–222, http://dx.doi.org/10.3391/ai.2006.1.4.5

Fry DL, Osborne JA (1980) Zooplankton abundance and diversity in central Florida grass carp ponds. *Hydrobiologia* 68: 145–155, http://dx.doi.org/10.1007/BF00019700

Havel JE, Hebert PDN (1993) *Daphnia lumholtzi* in North America: Another exotic zooplankter. *Limnology and Oceanography* 38: 1823–1827, http://dx.doi.org/10.4319/lo.1993.38.8.1823

Havel JE, Lee, CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *BioScience* 55: 518–525, http://dx.doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2

He S, Liang X, Li L, Sun J, Shen D (2013) Differential gut growth, gene expression and digestive enzyme activities in young grass carp (*Ctenopharyngodon idella*) fed with plant and animal diets. *Aquaculture* 410: 18–24, http://dx.doi.org/10.1016/j.aquaculture.2013.06.015

Hutchinson GE (1967) A treatise on limnology, vol 11. Wiley, New York

Johnson PTJ, Olden JD, vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 6: 359–365, http://dx.doi.org/10.1890/070156

Kirkagac M, Demir N (2004) The Effects of Grass Carp on Aquatic Plants, Plankton and Benthos in Ponds. *Journal of Aquatic Plant Management* 42: 32–39

Maceina MJ, Cichra MF, Betsill RK, Bettolic PW (1992) Limnological changes in a large reservoir following vegetation removal by grass carp. *Journal of Freshwater Ecology* 7: 81–95, http://dx.doi.org/10.1080/02705060.1992.9664673

Makino W, Knox MA, Duggan IC (2010) Invasion, genetic variation and species identity of the calanoid copepod *Sinodiaptomus valkanovi. Freshwater Biology* 55: 375–386, http://dx.doi.org/10.1111/j.1365-2427.2009.02287.x

Maly EJ, Maly MP (1997) Predation, competition, and co-occurrences of *Boeckella* and *Calamoecia* (Copepoda: Calanoida) in Western Australia. *Hydrobiologia* 354: 41–50, http://dx.doi.org/10.1023/A:1003042902584

McDowall R (1990) New Zealand Freshwater Fishes: A Natural History and Guide. Heinemann Reid, Auckland, New Zealand, 553 pp

Pípalová I, Květ J, Adámek Z (2009) Limnological changes in a pond ecosystem caused by grass carp (*Ctenopharyngodon idella* Val.) low stocking density. *Czech Journal of Animal Sciences* 54: 31–45

Parkes SM, Duggan IC (2012) Are zooplankton invasions in constructed waters facilitated by simple communities? *Diversity and Distributions* 18: 1199–1210, http://dx.doi.org/10.1111/j.1472-4642.2012.00913.x

Prowse GA (1971) Experimental criteria for studying grass carp feeding in relation to weed control. *Progressive Fish Culturist* 33: 128–121, http://dx.doi.org/10.1577/1548-8640(1971)33[128:ECFSGC]2.0.CO;2

Ray D, Champion P, Rowe D, Matheson F, Gibbs M (2006). Options to improve the water quality of the Utakura River. NIWA Client Report HAM2006-073

Richard D, Small JW Jr, Osborne JA (1985) Response of zooplankton to the reduction and elimination of submerged vegetation by grass carp and herbicide in four Florida lakes. *Hydrobiologia* 123: 97–108, http://dx.doi.org/10.1007/BF00018972

Strayer DL, Malcom HM (2006) Long term demography of a zebra mussel (*Dreissena polymorpha*) population. *Freshwater Biology* 51: 117–130, http://dx.doi.org/10.1111/j.1365-2427.2005.01482.x

Suárez-Morales E, Arroyo-Bustos G (2012) An intra-continental invasion of the temperate freshwater copepod *Skistodiaptomus pallidus* (Herrick 1879) (Calanoida, Diaptomidae) in tropical Mexico. *BioInvasions Records* 1: 255–262, http://dx.doi.org/10.3391/bir.2012.1.4.03

Taylor CM, Duggan IC (2012) Can biotic resistance be utilized to reduce establishment rates of non-indigenous species in constructed waters? *Biological Invasions* 14: 307–322, http://dx.doi.org/10.1007/s10530-011-0063-2

von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86: 3212–3218, http://dx.doi.org/10.1890/05-0427

Williamson M (1996) Biological Invasions. Chapman and Hall, London, 244 pp