

Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake

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SUMMARY

1. We performed two field experiments using different cage sizes to determine the direct and indirect effects of carp on macrophytes and invertebrate community composition in a shallow lake.
2. The presence of carp produced a significant decrease in macrophyte abundance, changes in species composition and decreased abundance and diversity of invertebrates in small (2.5 × 2.5 × 2.0 m) cages. In large enclosures (15 × 5 m), only macrophyte stem length was significantly affected by carp.
3. There was considerable variation in the macrophyte and invertebrate responses to carp on different sides of the lake in the large enclosures, suggesting that wind and wave action are also important variables affecting macrophyte growth and persistence.
4. The data suggest that carp can significantly affect species abundance and diversity of macrophytes and some macroinvertebrates.

Keywords: common carp, eutrophication, lake ecology, pondweed, *Potamogeton pectinatus*

Introduction

Primary production and community composition in freshwater ecosystems have been affected by the introduction of exotic fish (Allan & Flecker, 1993; Zambrano, Scheffer & Martínez-Ramos, 2001; Tapia & Zambrano, 2003). Although many species were deliberately introduced for sport and as a food source, the economic benefit that these fish provide is outweighed by the very high annual economic loss because of the negative effect on native fish and aquatic communities (Pimentel *et al.*, 2000). The common carp (*Cyprinus carpio* L.), was probably the earliest fish to be introduced on a wide scale, and is the most frequently reported nuisance fish in the United States (Kohler & Stanley, 1984). Control and eradication measures have cost millions of dollars and have yielded only limited success (Pimentel *et al.*, 2000). The introduction of

common carp evidently causes dramatic ecological disruptions at both the community and ecosystem levels (Roberts *et al.*, 1995; Titus *et al.*, 2004).

Common carp can significantly impact wetlands and littoral zones (Robel, 1962) but the extent of damage depends on the density of carp and the types of macrophytes present (Pipalova, 2002). Common carp can significantly affect plant and animal communities in shallow freshwater environments both directly and indirectly (Robel, 1962; King & Hunt, 1967; Lamarra, 1976; Parkos, Santucci & Wahl, 2003; Loughheed *et al.*, 2004). Carp directly consume macrophytes, such as *Chara aspera* L., and indirectly uproot or break macrophytes by mechanically damaging plants while foraging (Robel, 1962; King & Hunt, 1967; Kerfoot & Sih, 1987; Loughheed, Crosbie & Chow-Fraser, 1998; Hinojosa-Garro & Zambrano, 2004). Carp feeding behaviour increases turbidity through resuspension of sediments (Robel, 1962; King & Hunt, 1967; Lamarra, 1976; Hamilton & Mitchell, 1997). Additionally, when macrophytes are lost, wind increases sediment resuspension that in turn reduces light availability for phytoplankton and submergent

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macrophytes (Lougheed *et al.*, 1998). Resuspended sediments increase nutrients in the water column that would otherwise remain in the benthos. Inadequate light caused by increased turbidity and continuous physical disturbance through carp activity decreases macrophyte reestablishment (Hootsman *et al.*, 1996; Hootsman, 1999). Thus, the presence of common carp can potentially cause changes in water quality, macrophyte abundance and composition, and richness and diversity of invertebrates (Zambrano *et al.*, 2001).

We performed two experiments in a large, shallow, eutrophic lake (Utah Lake), at two different spatial scales, to determine how carp directly and indirectly affect the shallow lake community. We used small ($2.5 \times 2.5 \times 2.0$ m) cages to determine whether common carp directly affect species composition and abundance of macrophytes and benthic invertebrates. We used larger enclosures ($15 \times 5 \times 1.5$ m) to determine the rate and extent of responses of macrophyte and the associated invertebrate community when carp are locally eliminated. We also quantified the abundance and diversity of invertebrates while retaining the complexity of natural assemblages of macrophyte and invertebrate communities under controlled conditions. Understanding the *in situ* effects of common carp on composition and abundance of macrophytes and invertebrates is an important step in remediation and restoration of shallow lakes.

Methods

Study sites

Utah Lake ($40^{\circ}10'58''\text{N}$, $111^{\circ}43'46''\text{W}$) is located in north-central Utah. The lake is large and shallow with a surface area of approximately 388 km^2 , a mean depth of 2.9 m and a maximum depth of 4.2 m at maximum lake elevation. Utah Lake is highly eutrophic, turbid (average Secchi depth 12 cm), and slightly saline (average salinity 1.5 g L^{-1}). Utah Lake is dominated by mud substrate with some sand and gravel in littoral areas. Algal blooms occur in several areas of the lake during the summer. Non-native carp (*C. carpio* L.), white bass (*Morone chrysops* L.) and walleye (*Stizostedion vitreum* L.) are the predominant fish species. Utah Lake's main tributaries are the Provo and Spanish Fork rivers, with other smaller tributaries dominated by nutrient-rich irrigation return flows.

Common carp were first introduced into Utah Lake in 1886 as a commercial food source. Since then, carp have caused extensive damage to macrophyte communities and the endemic fish. Maps and species lists from the early 1800s confirm the lake was once covered widely with many different emergent and submergent macrophyte taxa [Brotherson, 1981; National Archives Microfilm Publications (RG48: Utah, 1850–1902 'M 428, six rolls')]. Today, aquatic macrophytes are sparse. Only three macrophyte taxa remain in Utah Lake: one submergent, *Potamogeton pectinatus* L., and two emergents, *Typha latifolia* L. and *Scirpus validus* L., which are fairly rare and have an inconsistent distribution. Despite being named the most plentiful macrophytes by missionaries in the late 1700s, macrophytes such as *C. aspera* L. and *Ceratophyllum demersum* L. have been extirpated (Brotherson, 1981).

Small cage experiment

During the summer of 2002, we placed six cages ($2.5 \times 2.5 \times 2.0$ m high) at a depth of 0.5 m in a shallow, near-shore area of Utah Lake with homogeneous mud/clay substrate. Cages were enclosed on all sides and bottom by 5 mm nylon mesh that enabled movement of both nutrients and small invertebrates while controlling movement of fish and larger macroinvertebrates. Cages were left open on the top to allow adequate light for macrophyte growth. No birds were observed on or near any cages during this experiment. All six cages were clustered tightly together to avoid environmental differences and help protect against intense the wave action on Utah Lake. In addition, a large mesh barrier was set up on the windward side of the cages to decrease disturbance associated with wave and wind action.

Prior to carp introductions, macrophytes were planted in plastic boxes ($32 \times 19.5 \times 9.5$ cm high) containing sediment obtained from Utah Lake. Four macrophyte species (*P. pectinatus*, *C. demersum*, *S. validus*, and *C. aspera*) were used in this experiment. *Potamogeton pectinatus* and *S. validus* were obtained from Utah Lake, *C. aspera* was collected from a nearby pond and *C. demersum* was collected from Mona Reservoir, just south of Utah Lake. In July 2002, eight boxes of each macrophyte species were placed in each cage giving a total of 32 boxes per cage. Three weeks after macrophytes were added, two carp from Utah

Lake were randomly added to three of the six cages. Carp ranged in size from 150 to 193 mm and averaged 51 g. The experiment was maintained for 6 weeks.

Plants were harvested on 19 and 20 September 2002. All boxes, including sediments and plants, were removed from the cages, bagged, placed in coolers containing ice and transported to the laboratory for plant and invertebrate analysis. Plants, sediment and root mass from each box were washed over a 500 µm sieve to remove invertebrates. Invertebrates were stored in 95% ethanol. All plants were cut at soil level in order to quantify stem length and root mass of each species. As no *C. aspera* remained in either treatment these samples were excluded from analyses. Stems of each macrophyte species were counted and their length measured. Individual stems were dried for a minimum of 24 h at 60 °C to obtain a dry weight. Each stem was ashed for 1 h at 550 °C and ash-free-dry-weight (AFDW) was calculated for each stem.

All response variables were log₁₀ transformed to normalise the data and stabilise variance. Final stem length (mm), total plant abundance (g AFDW) and plant diversity (Simpson's *D*) were compared between treatments using a one-way ANOVA with carp presence/absence as the main factor. In addition, the response of individual invertebrate taxa abundances and invertebrate diversity, calculated using Simpson's diversity, were analysed using a one-way ANOVA with carp presence/absence as the main effect. All ANOVAs were performed using the PROC GLM procedure of SAS statistical software (SAS Institute Inc., 2002). When multiple ANOVAs were performed, we used a Bonferroni correction factor to control for experiment-wise error rates. All analyses were interpreted using a Bonferroni corrected $P < 0.05$ for significance.

Large enclosure experiment

In June 2003, we installed large (15 × 5 × 1.5 m) enclosures in two different sides of Utah Lake around existing *P. pectinatus* beds. Existing beds were at depths of 1.0–1.25 m and all enclosures were installed to cover plant beds at an additional 0.5 m. We installed a total of seven enclosures and seven open controls on two different sides of the lake: three enclosures and three controls on the east side of the lake (Provo) and four enclosures and four controls on the west side (Saratoga). Every enclosure and open control was

constructed with metal T-posts and large plastic fencing (2.5 × 2 cm mesh). We folded at least 0.25 m of mesh towards the outside of the enclosure at the substrate and placed sandbags on the mesh to secure the bottom. Enclosures had mesh fencing, to completely exclude carp whereas open controls consisted of three sides of fencing only, with the side facing the open lake being unfenced to allow carp access to macrophytes. This design excluded large carp from the macrophyte bed which was used to estimate macrophyte growth and survivorship without carp, while allowing carp to enter in the open controls. Although other fish species are found in Utah Lake, carp is the dominant fish reaching in excess of 90% of the lake biomass (R. Valdez, pers. comm.); no other fish species are herbivorous or use macrophyte beds as adults. We assume minimal damage occurred to macrophytes by herbivorous birds as none were observed on or near any enclosure during the length of the experiment. In addition, staggered wave breaks were constructed 5 m from each enclosure and open control, on the lakeside, allowing carp to enter open controls but reducing the action of the waves and high winds that frequently occur on Utah Lake.

To monitor the physical-chemical variable conditions we measured total depth (m), temperature (°C), Secchi depth (cm), conductivity (µs), turbidity (ntu), chlorophyll *a* (µg L⁻¹), and zooplankton (individuals L⁻¹). Each parameter was measured on days 0, 15 and 30, in both open controls and enclosures.

Conductivity and turbidity samples were taken *in situ* and measured using a Hanna model HI 8734 and HI 93703, respectively. Chlorophyll *a* samples were collected and immediately put on ice. We then filtered samples using Whatman GF/C 47 mm filters (cat. no. 1822 055) and a hand-held vacuum pump (Mityvac model 79301-20; Lincoln Industrial, St Louis, MO, U.S.A.) suctioning at 10 psi. Samples were processed at the laboratory using methods as described by Welschmeyer (1994). We extracted samples for 24 h in 15 mL of ethanol and measured extracts with a Turner 10 AU fluorometer (Arar & Collins, 1997). Zooplankton samples were collected using a vertical tow net from 0.25 m deep to the surface and filtered through an 80 µm mesh net. Zooplankton samples were preserved in 95% ethanol in the field. Three 2-ml aliquot subsamples were taken from a 100-mL sample. Zooplankton were then counted and identified to family level.

To monitor whether changes occurred in zooplankton abundance and species composition over the three sampling dates, we analysed densities using a randomised block design with repeated measures. For simplicity, all individual taxa were summed according to their respective orders: Copepoda, Cladocera, Rotifera and total zooplankton for each sample date. We \log_{10} transformed zooplankton taxa densities to normalise the data.

Plant abundance was quantified at the beginning and end of the experiment by complete census of total stem length in both the open controls and in each enclosure. We measured plants from lake-bottom to plant tip using a meter stick. To avoid disturbing plants and the sediments, the initial census was performed by measuring each individual plant from a raft; no fish were observed in enclosures during this census. At the final census we stood inside the enclosures and measured individual plants, which concurrently insured that no adult fish were present in enclosures. We determined the total initial and final stem lengths and calculated a ratio from final : initial stem length within treatments.

After the initial plant census, two Hester-Dendy invertebrate samplers (EPA 600-4-90-030, 2001) were randomly placed in the open control and two in each enclosure. The Hester-Dendy samplers were removed at the same time the final plant census was performed, preserved in 95% ethanol in the field, then scrubbed and sieved (250 μm) to remove all invertebrates. The Hester-Dendy samples were put in a 73 cm^2 plastic dish. A 19% subsample was taken by vacuum suctioning a 14 cm^2 section through a plastic tube. Invertebrates were identified to at least order and to family when possible. Simpson's diversity estimates were calculated for invertebrate samples obtained from the Hester-Dendy samplers.

To determine how *P. pectinatus* and the associated invertebrate community responded to the effect of excluding carp, we used a completely randomised block design ANOVA with carp presence (open)/absence (excluded) as the main fixed effect and Provo and Saratoga (block) as a random factor. We then calculated the final : initial stem length and the densities of invertebrates and \log_{10} transformed these results to normalise the data. Statistical analyses were conducted using the PROC MIXED procedure of SAS version 9.0 (SAS Institute Inc., 2002). *Post hoc* analysis using the SLICE option in SAS 9.0 allowed us to

analyse the simple fixed effects of open controls and enclosures within each block. *Post hoc* analysis using the Ryan-Einot-Gabriel-Welsh Quotient (REGWQ) option in SAS 9.0 allowed us to compare the two groups setting significance to $P > 0.05$.

Results

Small cage experiment

Carp significantly affected species composition, abundance and diversity of macrophytes relative to the controls in the small cages. Both total macrophyte AFDW biomass ($F = 16.10$, $P = 0.016$) and species diversity ($F = 7.30$, $P = 0.050$) were significantly lower when carp were present. When individual plant species were compared using *post hoc* REGWQ comparisons, both *C. demersum* and *S. validus* had significantly decreased whereas, *P. pectinatus* was unaffected by carp (Fig. 1). Total benthic macroinvertebrate diversity decreased by 67% ($P < 0.001$) in the presence of carp relative to controls. *Post hoc* comparisons of individual taxa showed that abundance of chironomids and oligochaetes significantly increased with carp. Amphipods, tabanids and hirudinids significantly decreased in the presence of carp (Fig. 2a,b) relative to controls.

Large enclosure experiment

Exclusion of carp significantly affected *P. pectinatus* in the large enclosures (Table 1). Open controls, which allowed entry of carp, showed significantly (90%)

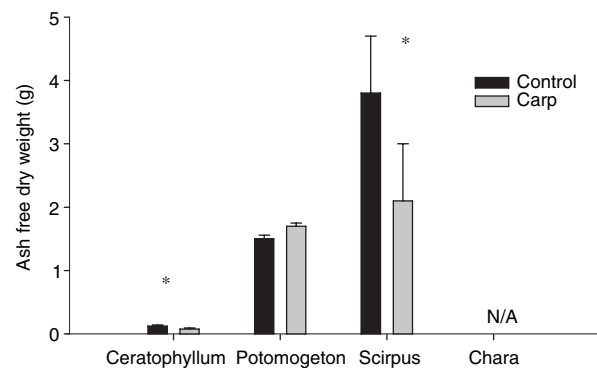


Fig. 1 Mean macrophyte abundance in small cages with and without carp. Error bars represent +1 SE ($n = 8$). No *Chara aspera* remained at the conclusion of the experiment in either treatment. Asterisks represent significant treatment differences ($P < 0.05$).

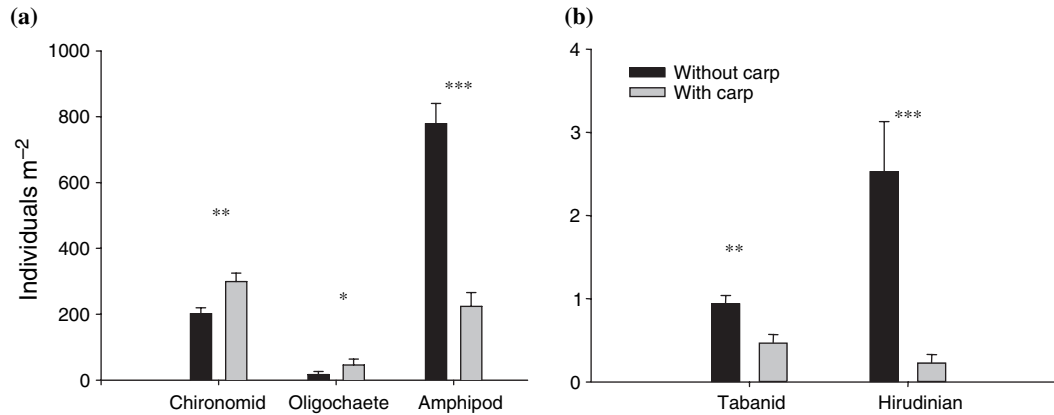


Fig. 2 Mean abundances of invertebrate taxa in small cages with and without carp. Error bars represent +1 SE ($n = 8$). (a) Chironomids, Oligochaetes and Amphipods, (b) Tabanids and Hirudinians. Asterisks denote variables that are significantly different ($P < 0.05$, $**P < 0.01$, and $***P < 0.001$).

Table 1 (a) Randomised block design ANOVA results for final : initial stem length in large enclosures comparing closed treatment and open control and lakesides (Provo and Saratoga). (b) *Post hoc* results partitioning closed treatment and open control final : initial stem length between lake sides using the SLICE option in SAS.

Response variable	<i>df.</i>	<i>F</i> -value	<i>P</i> -value
(a)			
Lake side	1.5	15.48	0.0110
Treatment	1.5	11.5	0.0194
Lake side × treatment	1.5	2.43	0.1794
(b)			
Provo × treatment	1.5	10.72	0.0221
Saratoga × treatment	1.5	1.95	0.2210

decreased *P. pectinatus* total stem length in both Provo and Saratoga. Enclosures, at the end of the experiment, had 58% more *P. pectinatus* than open controls. Although an overall significant effect was found in our final model (Table 1a), more of the variance is explained by differences between lakeside by treatments (Table 1b). In closed treatments, total stem length increased (final : initial stem length >1) in Saratoga, but decreased by 31% in Provo. In Saratoga, the final : initial ratio of total stem length of *P. pectinatus* was significantly lower in open treatments than in enclosures (Fig. 3). Overall, Saratoga open controls decreased in *P. pectinatus* stem length by 10%, while total stem length in enclosures increased by 110%. Provo open controls lost 100% of the plants, while the enclosures had a 30% decrease in plant stem length (Fig. 3). Excluding carp from *P. pectinatus* beds

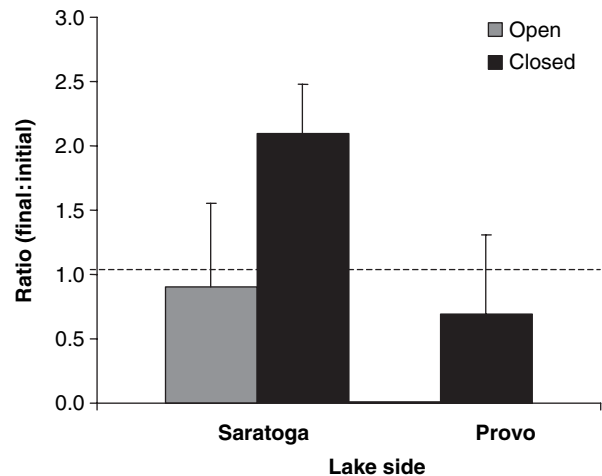


Fig. 3 Mean final : initial total stem length of *P. pectinatus* in open (carp access) and closed enclosures at each lakeside (Provo and Saratoga). The dashed line represents a ratio of 1, which means no change occurred.

increased the total stem length of plants in Saratoga and reduced the decrease in Provo.

For macroinvertebrates, Simpson's diversity index (ANOVA *d.f.* = 2,11, $F = 0.02$, $P = 0.98$), abundance (ANOVA, *d.f.* = 2,11, $F = 0.47$, $P = 0.6361$) and taxon richness (ANOVA, *d.f.* = 2,11, $F = 0.87$, $P = 0.4476$) did not vary between open controls and enclosures, but did vary by lake side (Table 2).

During the summer, lake conditions at each side of the lake (Provo and Saratoga) were essentially the same. The highest water temperatures were on day 15 at Provo (29.2 °C) and Saratoga (29.3 °C). The lowest

water temperatures were recorded on the final day of the experiment at both Provo (21.3 °C) and Saratoga (23.4 °C). Conductivity ranged from 1812 to 2370 μs at Provo and 2143 to 2430 μs at Saratoga. There was virtually no difference in physical-chemical parameters between treatments. Turbidity and Secchi disk readings varied slightly between Provo and Saratoga. The water level in Utah Lake decreased 0.5 m during the experiment.

We found similar trends in mean chlorophyll *a* concentrations comparing open controls versus enclosures but slight differences occurred between lake sides (Fig. 4). At both Provo and Saratoga, chlorophyll *a* levels between treatments were similar on days 0

and 30, but differed greatly on day 15. Saratoga open controls and Provo enclosures peaked on day 15 and with an 80% increase in chlorophyll *a* at Saratoga.

Overall densities (individuals L^{-1}) of cladocerans (closed 308.8 \pm 0.10; open 371.0 \pm 0.08), rotifers (closed 82.8 \pm 0.09; open 93.9 \pm 0.09), and copepods (closed 21.1 \pm 0.05; open 28.7 \pm 0.05) were not significantly different between treatments or blocks. All orders, with the exception of copepods, had decreased on the second sampling date and increased on the last date.

Discussion

Our small-scale cage experiment showed that continuous presence of carp directly affected plant species composition and abundance and indirectly affected macroinvertebrate community composition. Carp do not consume enough macroinvertebrates to produce the changes observed in our experiment (Bronmark & Miner, 1992). The decreases of certain taxa (e.g. amphipods, hirudinians and tabanids) likely occurred because of the decrease in two of the three macrophyte species in cages that contained carp (indirect effect of carp). Similarly, the increase in chironomids and oligochaetes, which almost entirely inhabit the soft sediments, was most probably because of increased carbon resources from exposed detritus present after carp uprooted macrophytes during foraging (Bremigan *et al.*, 1997). Therefore, several invertebrate groups may be reduced in abundance and invertebrate community composition altered if macrophytes are reduced by carp, because

Table 2 Total mean invertebrate densities (individuals m^{-2} and standard errors (SE) across all large-scale experimental units for each lake side (Provo and Saratoga)

Taxa	Individuals m^{-2}			
	Provo (<i>n</i> = 6)	SE	Saratoga (<i>n</i> = 8)	SE
Amphipoda	6321	498	7401	3406
Bryozoa	445	164	0	0
Ostracoda	438	95	866	343
Oligochaete	296	160	230	100
Chironomidae	761	217	1474	585
Nematoda	1523	514	498	157
Gastropoda	0	0	105	98
Coelenterata	0	0	39	33
Ceratopogonidae	40	40	62	35
Trichoptera	0	0	90	87
Hirundinea	0	0	11	11
Hydracarina	674	343	104	51
Ephemeroptera	27	17	20	13

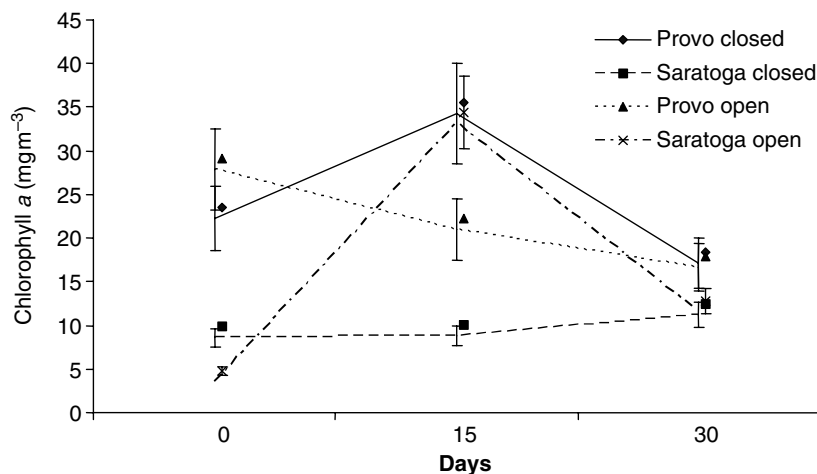


Fig. 4 Mean Chlorophyll *a* concentrations of open (carp access) and closed enclosures for each lake side (Provo and Saratoga). Error bars represent +1 SE (*n* = 8).

these areas provide refugia and food for invertebrates and larval fish (Pipalova, 2002; Williams & Moss, 2003).

The large enclosures surrounding existing macrophyte beds in Utah Lake allowed us to determine whether excluding common carp affected the abundance of *P. pectinatus* and associated invertebrate communities. We chose *P. pectinatus* because it is the only macrophyte that remains in abundance by the end of the summer decrease in water level. In this experiment, *P. pectinatus* abundance increased at Saratoga when carp were excluded relative to open controls. Abundance of *P. pectinatus* decreased in Provo enclosures, but the decrease was less severe in enclosures than in the open controls where all plants were completely removed.

Temperature, Secchi depth, chlorophyll *a*, zooplankton, conductivity, dissolved oxygen and turbidity showed slight variations between Provo and Saratoga but not between enclosures and open controls. Frequent high winds over Utah Lake cause severe wave action, mixing water layers, and lead to a high uniformity of lake water conditions, especially during the summer months when water levels decrease because of evaporation and reduced inflow from tributaries (Wetzel, 1983; Moss *et al.*, 1997). Differences in physical-chemical parameters between lakesides could be accounted for by differences in sediment, wind and wave activity, and carp densities (Zambrano *et al.*, 2001).

The different plant responses observed between Provo and Saratoga was most likely associated with plant protection from wind. During July and August 2003, average daily maximum wind speeds recorded at a Mesowest station adjacent to the Provo shoreline [Id: PVU (AWOS) NWS/FAA] approximated 29 km h^{-1} with wind direction predominantly from the north northwest (Olsen, 2004; Miller personal observation). Wind direction from the north would protect the north-western Saratoga side of the lake to a greater extent than eastern Provo side. Although windbreaks were constructed to reduce the effect of waves, Provo was more prone than Saratoga to detrimental effects caused by winds. However, wind direction is not consistent over years and certainly varies in daily and seasonal intensity. Nevertheless, when choosing locations of enclosures for possible reestablishment of plants in Utah Lake, consideration of wind effects will be critical.

Common carp did not affect macroinvertebrates in the large enclosures compared with open controls. This contrasts with findings from other studies (Barthelmes & Bramick, 2003; Parkos *et al.*, 2003) and with our small cage results. Experiments from 2002 showed macroinvertebrates had higher species richness and diversity and lower biomass when carp were excluded from potted macrophytes in Utah Lake. In the presence of carp, the benthic invertebrates were almost totally chironomids, which attained densities of $>100 \text{ m}^{-2}$. The large enclosures showed no clear trend in either abundance or diversity of benthic invertebrates, perhaps because the mesh size allowed small benthic invertebrates to move between treatments. In the small cages small mesh size prevented macroinvertebrate movement between treatments. Large enclosures during 2003, at both Provo and Saratoga, had slightly different orders of invertebrates (Table 2) suggesting that invertebrate distributions differ within the lake. These differences between lakesides may reflect greater abundance of macrophytes on Saratoga or differences in substrate; Saratoga is mostly mud with some large rocks and Provo is dominated by sand and small gravel.

Common carp impact wetlands in a similar manner depending on the relative density of the carp population. Robel (1962) noted a strong negative linear correlation between vegetation yields and carp densities. More recent results suggest that these effects are not as linearly associated with carp biomass as once thought. Zambrano *et al.* (2001) suggested that changes in water chemistry associated with carp appear at a threshold of carp density, above which substantial impacts occur to the ecosystem, such as creating a highly eutrophic system. Waterbodies that receive more nutrients can become hypereutrophic and develop food webs dominated by producers. If these highly eutrophic systems lack top predators, the system can become highly stable and may become irreversible (Carpenter, Ludwig & Brock, 1999; Power, 2001). This large impact has been documented most frequently in eutrophic, shallow lakes and ponds similar to Utah Lake (Zambrano & Hinojosa-Garro, 1999; Zambrano *et al.*, 2001).

Carp likely did not cause differences between the two sides of the lake. Based on a 2004 inventory of Utah Lake, the fish community is dominated by common carp (73% based on number of individuals of each species caught), which are equally distributed

between shorelines (R. Valdez, pers. comm.). Tagging data suggested little movement of carp, and trap nets always contained carp. The current carp population of Utah Lake is estimated to be >100 million, with higher densities close to the shoreline (R. Valdez, pers. comm.).

Excluding carp from macrophyte beds, on average, increased the total stem length of *P. pectinatus* plants by as much as 90% with the greatest increases at Saratoga. However, the most dramatic effect of carp exclusion was at Provo, where treatments open to carp lost all vegetation by the end of the experiment. For remediation and restoration of *P. pectinatus* beds in Utah Lake, focusing on Saratoga may have greater potential for increasing structural refugia for larva based on possibly lower carp densities and/or greater protection from wind.

Carp densities may affect macrophytes through indirect changes in lake chemistry and turbidity, but direct effects because of carp within macrophyte beds may be a more important factor in macrophyte abundance. *Potamogeton pectinatus* may be able to withstand the indirect changes caused by carp but not physical carp disturbance (Hootsman, 1999; Engelhardt, 2000). Accurate assessment of each stressor caused by carp is an important step in remediation.

Carp significantly affected species composition, abundance and diversity of macrophytes as well as diversity of macroinvertebrates relative to the controls in small cages. In large enclosures, we found a significant difference in the ratio of initial and final stem length of *P. pectinatus* between Provo and Saratoga and between open controls and enclosures; however, we found no difference in macroinvertebrates. The results from both experiments demonstrated that carp negatively affect macrophyte species but whether because of direct or indirect effect of carp is uncertain.

The top-down effects of fish on aquatic food web structure have been well studied (Carpenter, Kitchell & Hodgson, 1985; Carpenter & Kitchell, 1992). However, many bottom-up effects also arise through the behaviour of benthivorous fish. Traditional methods that examine the impact of invasive fish have not included consideration of the important role some fish play in the incorporation of benthos-derived nutrients into primary and secondary production in shallow lakes (Lamarra, 1975, 1976; Bremigan *et al.*, 1997). Failing to understand the importance of these more subtle indirect effects and on the food web could

jeopardise effective restoration and biomanipulation of invaded waters (VanderZanden, Casselman & Rasmussen, 2002). Furthermore, the processes known to be important in shaping community structure and function differ across spatial scales (Stoffels, Clarke & Closs, 2005). To fully understand how top-level predators or exotic species affect communities, we must incorporate cross-scale approaches with experimental designs that incorporate both direct and indirect effects.

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