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Abstract – Invasive macrophytes are usually associated with negative impacts on habitat quality and a threat to native biodiversity. However, they might provide the same beneficial functions of native macrophytes, i.e., the provision of food and shelter for fish, in the absence of native macrophytes. To assess the value of the invasive macrophyte *Lagarosiphon major* as a fish habitat, we investigated the spatio-temporal variation in the distribution of a small littoral fish species (common bully) in the littoral of Lake Dunstan, a New Zealand hydro lake. Large- and fine-scale common bully distribution could partly be explained by the occurrence of dense *L. major* stands. Additionally, variability in catch per unit effort was partly explained by season and recruitment. Diet analysis indicated that common bullies in the *Lagarosiphon*-dominated littoral fed on invertebrates (Mollusca, Trichoptera, Chironomidae) found on exotic *L. major*, therefore suggesting its role as a food provider in the system. These results indicated that invasive macrophytes can provide important ecosystem functions in disturbed habitats that are otherwise devoid of native macrophytes. Any macrophyte management strategy should therefore carefully consider the costs and benefits associated with macrophyte control.

T. O. Bickel, G. P. Closs

Department of Zoology, University of Otago,
Dunedin, New Zealand

Key words: invasive macrophyte; *Lagarosiphon major*; common bully; diet; fish distribution

Tobias O. Bickel, Department of Zoology,
University of Otago, P.O. Box 56, Dunedin,
New Zealand; e-mail: tobias-bickel@web.de

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Introduction

The effects of invasive species on ecosystem processes (Walker 1989; Ehrenfeld 2003) and biodiversity have been of special interest in recent years (Callaway & Maron 2006). Exotic species are often regarded as a major threat to natural systems and an economic burden (Vitousek et al. 1997; Keane & Crawley 2002). The invasion of habitats with exotic species is quite often directly linked to human disturbance and land-use change (Mack et al. 2000), as intact ecosystems can resist invasion to a certain degree (Seabloom 2003). Habitats that are profoundly altered by humans may be dominated by invasive species that are generalists with effective means of dispersal.

Lagarosiphon major (Ridley) Moss (hereafter *Lagarosiphon*) is an exotic macrophyte species that

quickly established throughout New Zealand after introduction in the 1950s. It is a threat to native biodiversity because of its ability to outcompete and replace native macrophyte species (Howard-Williams & Davies 1988; Rattray et al. 1994). Besides the impact on the biodiversity of native macrophytes (and associated invertebrates), *Lagarosiphon* may also have far reaching impacts on local physico-chemical water properties as the tall stands might interfere with effective exchange of water. Gradients, as a result of oxygen depletion during night, and an increase in pH during photosynthetic activity might be detrimental to fishes and invertebrates. Similar effects have been demonstrated in other dense-growing macrophytes (Cheruvilil et al. 2001).

Because of the high density and biomass of *Lagarosiphon*, management becomes necessary to

prevent further spread, restore native macrophytes and improve recreational values of waterways (Johnstone 1986; Van Nes et al. 2002). However, despite the negative impacts of this invading species, it is likely to perform the multiple beneficial functions of macrophytes in lake ecosystems (Carpenter & Lodge 1986), including the support of a high density of invertebrates (Biggs & Malthus 1982; Kelly & Hawes 2005) as food, and presumably shelter for fish.

Lagarosiphon is a structurally complex plant across several spatial scales: (i) it has a high number of small leaves that are curled back towards the stem, effectively creating a sheltered habitat; (ii) the stems display a high degree of ramification and (iii) the stands are very tall creating a complex three-dimensional structure. Generally, more complex macrophytes are known to support a higher invertebrate diversity and/or biomass. Very dense macrophyte stands can create shelter from predation for both fish and invertebrates (Chick & McIvor 1994; Diehl & Kornijow 1997; Grenouillet et al. 2000). Based on this, we would expect *Lagarosiphon* to be a good habitat provider for invertebrates and fish, as has already been demonstrated in other systems including Lake Wanaka and the Clutha River (Biggs & Malthus 1982; Kelly & Hawes 2005). However, the *Lagarosiphon* infestations in these systems are of much smaller scale and intermixed with native macrophyte species, when compared with Lake Dunstan that features monospecific and massive *Lagarosiphon* beds. Hence, there is a degree of uncertainty in the prediction of the habitat value of *Lagarosiphon* in the case of Lake Dunstan.

Lake Dunstan is a large hydro lake (approximately 30 km²) in Central Otago, New Zealand, heavily infested with *Lagarosiphon*. Currently, *Lagarosiphon* is forming surface reaching stands from the lake margin down to its physiological limit of 6 m depth (Coffey & Wah 1988), where it occupies virtually 100% of the available littoral area and forms a continuous monospecific macrophyte belt along the entire lake shoreline (Strickland et al. 2000). Because of its enormous biomass and the large area covered by *Lagarosiphon*, it is believed to influence the Lake Dunstan ecosystem significantly. Therefore, large-scale eradication of *Lagarosiphon* from Lake Dunstan may have negative impacts on the abundance of native fish species (common bully) in this lake. Generally, reduction of macrophyte biomass and diversity can result in changes in community composition, a reduction in fish abundance in the littoral and a shift towards pelagic species (Maceina et al. 1991; Bettoli et al. 1993), and modification of foraging behaviour (Sammons et al. 2003). However, excessive densities of macrophytes, which are often the case with invasive species, are thought to interfere with prey capture and

the foraging success of fish, but this clearly depends on plant type and architecture, fish size and species (Diehl 1993; Brown & Maceina 2002; Warfe & Barmuta 2004). Small fish species like common bully (*Gobiomorphus cotidianus*: Eleotridae; McDowall 1975) that are present in Lake Dunstan might be less disadvantaged from this perspective.

To assist with macrophyte management strategies in Lake Dunstan, we investigated the value of *Lagarosiphon* as a fish habitat. Specifically, we tested the following hypotheses: (i) Common bullies are closely associated with *Lagarosiphon* on a small-scale; (ii) large-scale common bully distribution is related to environmental factors including *Lagarosiphon* density and (iii) bully diet contains invertebrates that are common on *Lagarosiphon* (e.g., Mollusca and Trichoptera) as this macrophyte is an important feeding area in the Lake Dunstan littoral.

Materials and methods

Study area

This study was completed within the littoral of Lake Dunstan, Central Otago, New Zealand (45°02'S, 169°12'E). Lake Dunstan is a large oligotrophic hydroelectric lake (approximately 30.55 km², vol. 0.370 km³, max depth 60 m, mean depth 12.1 m, hydraulic residence time 6.4 days), the result of the impoundment of the Clutha and Kawarau Rivers (Schallenberg & Burns 1997). Lake Dunstan is a comparatively new system, only reaching its full operational level in 1993. Source water for the Clutha (mean flow rate 387 m³·s⁻¹, min 199 m³·s⁻¹, max 909 m³·s⁻¹) and Kawarau Rivers (mean 240 m³·s⁻¹, min 102 m³·s⁻¹, max 630 m³·s⁻¹) comes from Lakes Wanaka/Hawea and Lake Wakatipu, respectively (Fig. 1). The enormous size of the source systems for the Kawarau and Clutha Rivers result in a very stable physical and chemical environment in the lake year round [mean surface temperature 11 °C (min 7 °C max 17 °C), mean oxygen 11.29 mg·l⁻¹ (±1.09 SD)] (Leach 1997). Lake Dunstan has a sparse zooplankton community, presumably because of the short hydraulic retention time of the Lake.

Although Lake Dunstan is an artificial lake used to generate electricity, daily water level fluctuation is restricted to 1 m (i.e., operational levels range between 193.5 and 194.5 msl) to adjust power generation to daily fluctuations in energy demand. The study was restricted to the Clutha Arm of Lake Dunstan as it is the largest part of the lake (approximately 19.06 km², vol. 0.177 km³, max depth 23 m, mean depth 9.3 m, hydraulic residence time 7.7 days) (Schallenberg & Burns 1997) with extensive shallow areas providing a suitable habitat for macrophyte growth. The eastern

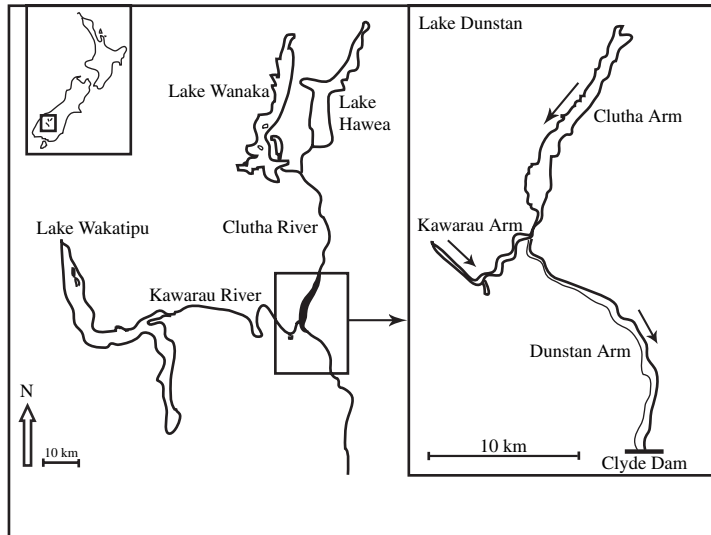


Fig. 1. The Clutha system (left) is situated on the South Island of New Zealand (top left inlay). Lake Dunstan, downstream of Lakes Wakatipu, Wanaka and Hawea, consists of three arms (right). This study was restricted to the Clutha Arm. Arrows indicate the direction of flow. Bullies and invertebrates were sampled within 30 random sites scattered throughout the Clutha Arm of Lake Dunstan.

side of the Clutha Arm is characterised by a steep topography and rocky shores; the western site features gravely beaches with a variety of slopes and small inlets and bays. Lagarosiphon density is highest in the northern end of the Lake (Clutha River inflow). There are records of other macrophyte species beyond the Lagarosiphon belt in deeper water, consisting mainly of *Elodea canadensis*, *Potamogeton cheesemanii*, *P. ochreatus* and Charophytes (own observation and Strickland & Asher 1998) but these communities have never been quantified. However, because of the low average depth of 9.3 m of the Clutha Arm, the temporal high inflow of glacial silts and the distribution of Lagarosiphon down to about 6.5 m (Strickland et al. 2000), it is assumed that this tall vascular community beyond the Lagarosiphon belt is not comparable to the Lagarosiphon stands in either total biomass or aerial cover. Environmental factors (turbidity, steep shoreline and rocky substrate) are less favourable for macrophyte growth in the other arms of the lake.

Fish sampling

Lake Dunstan has a species-poor fish community typical for New Zealand high country lakes that are generally numerically dominated by only three species: the native species common bully (*Gobiomorphus cotidianus*: Eleotridae), and the introduced rainbow and brown trout (*Salmo trutta*, *Oncorhynchus mykiss*: Salmonidae). Because of the high mobility of trout, only common bully distribution was studied here.

To investigate the spatial and temporal variability in small littoral fish (common bully) biomass, bullies were caught within 30 randomly chosen sites within the littoral of the Clutha Arm of Lake Dunstan between March 2004 and April 2005. Sampling

periods covered three seasons (summer: December–February; autumn: March–May and winter: June).

To study the fine-scale distribution of common bullies in relation to the Lagarosiphon stands, we placed multiple fish traps vertically and horizontally within the Lagarosiphon belt in each site. Within each site, the Lagarosiphon belt was divided into the three zones: 'in' (inside the belt), 'edge' (on the inshore margin of the Lagarosiphon belt) and 'out' (in the Lagarosiphon free area between lake shore and the continuous Lagarosiphon belt). As Lagarosiphon stands were between 1 m and 3 m tall in the 'in' and 'edge' zones, trap positions were further divided into two vertical levels: top (on top of the macrophytes) and bottom (bottom of the macrophyte beds). However, we found no difference in top versus bottom (Kruskal–Wallis test: $\chi^2 = 2.459$, $d = 4$, $P = 0.652$) and pooled the data for subsequent analysis. In each site, 15 unbaited 'minnow traps' (Gansell, Milperra, Australia) with 1 mm mesh and a 7-cm diameter opening at each end were randomly set overnight (mean trap time $20.9 \text{ h} \pm 1.6 \text{ h SD}$). Average trap depth was comparable between sites with the following average trap depths in the plots: $0.9 \pm 0.5 \text{ m SD}$ 'out', $1.5 \pm 0.6 \text{ m SD}$ 'edge', and $2.2 \pm 0.7 \text{ m SD}$ 'in'.

Next morning, all traps were retrieved and all bullies counted and measured (total length in mm), after which the fish were released immediately. A diver recorded several environmental variables at each site: slope (shore gradient), Lagarosiphon canopy height (cm), aerial biomass ($\text{g dry mass}\cdot\text{m}^{-2}$), Lagarosiphon stem density ($\text{N}\cdot\text{m}^{-2}$), and water temperature ($^{\circ}\text{C}$). Water temperature, canopy height, aerial biomass and stem density was recorded at three random locations in the 'in', 'edge' and 'out' areas. Values were averaged by sites for later statistical

analysis. Slope was measured along two transects running perpendicular to the shoreline and averaged for sites.

Diet analysis

To investigate common bully diet, random individuals were retained from the spatial analysis (up to nine fish per site). Bullies from a range of sizes (18 mm–125 mm) were euthanized and frozen at -20°C for later processing. In the laboratory, retained bullies were weighed to the nearest 0.1 g and measured to the nearest 1 mm (total length). A regression analysis ($R^2 = 0.97$) was performed ($N = 293$ bullies, fish from all seasons included) to establish a length–mass model, so the weight of bullies could be estimated from the length measurements recorded in the field.

$$M_F = L_T^{3.5} \times 1.43 \times 10^{-06}$$

where M_F = Fresh mass in g and L_T = total length in mm.

For diet analyses of bullies, the entire digestive track was removed from the fish and all invertebrates were identified under a dissecting microscope to the lowest practical taxonomic unit (species or family) after Winterbourn et al. (2000). Results of fish diet are presented in two ways, as an ordination plot derived from the average abundance of each food item in the fish diet and as a plot showing % biomass contribution of diet groups. Biomass of invertebrates in the diet was estimated using previously established mean mass values for the most common species (data not published) and from published values of rarer species (Stoffels et al. 2003b). To account for the high proportion of inorganic components in Mollusca, ash free dry mass was estimated instead of dry mass as for the other organisms.

To compare fish diet composition and the available invertebrate community in the littoral, invertebrate samples were collected in *Lagarosiphon* stands. *Lagarosiphon* samples were collected by SCUBA diving (using 250 μm mesh bags) in the same ‘bully collection’ sites following the same site layout [20 samples in each site (five samples in the four areas with *Lagarosiphon* stands), 600 in total]. The mesh bags were carefully lowered over several stems of *Lagarosiphon* and closed with a drawstring to prevent the loss of invertebrates. Additionally, random benthic samples were collected both from the bottom of the *Lagarosiphon* beds (in) and in the cobbly/rocky near shore ‘out’ area that lacked *Lagarosiphon* growth. Benthic invertebrates were sampled using a surber sampler modified for underwater sampling (Stoffels et al. 2003a). Invertebrate samples from macrophyte beds and benthic samples were processed as described for the fish gut samples.

Statistical analyses

To account for differences in trapping time between sites, bully biomass was adjusted for trapping time and is expressed as catch per unit effort (CPUE) biomass and abundance per trap and hour. To analyse large-scale temporal and spatial variation in the littoral of Lake Dunstan (between sites) total CPUE biomass and abundance was calculated for each site; i.e., the summed biomass/abundance for each site. A multiple stepwise regression was used to investigate the relationship between measured environmental variables and bully CPUE biomass and abundance. To investigate fine-scale distribution of bullies within sites, total CPUE biomass was calculated for zones in each site. SPSS 10 for Windows was used for all statistical analyses. Data were square root transformed to meet requirements (normality and homoscedasticity) for ANOVA and regression. Nonparametric tests (Kruskal–Wallis test, Mann–Whitney U -test) were applied if the requirements for parametric ANOVA were not met.

Similarity in diet between common bully and the invertebrate community in *Lagarosiphon* and the benthos was investigated using an ordination (Multi-Dimensional Scaling: MDS; PC-ORD 4.0 for Windows) using the Bray–Curtis distance with procedures following the recommendations of the software package (McCune & Mefford 1999). The MDS is presented as a biplot including calculated scores for invertebrate taxa that had more than 25% correlation with one of the ordination axes (Pearson and Kendall Correlations >0.25). Following ordination, we performed Multi-Response Permutation Procedures (MRPP) to test for differences between groups (McCune & Mefford 1999).

Results

Large-scale temporal and spatial variation

The distribution of average CPUE bully biomass was patchy over the sites and fluctuated widely between a minimum of $<1 \text{ g}\cdot\text{trap}^{-1}\cdot\text{h}^{-1}$ and a maximum of approximately $12 \text{ g}\cdot\text{trap}^{-1}\cdot\text{h}^{-1}$ (Fig. 2a). There was no significant difference in bully biomass between the sampled seasons, summer, autumn, and winter (one-way ANOVA: $F = 2.966$, d.f. = 2; $P = 0.068$). Variation in average CPUE abundance between sites was similar to variation in biomass (Fig. 2b). CPUE generally varied between $<1 \text{ bully}\cdot\text{trap}^{-1}\cdot\text{h}^{-1}$ and $<2 \text{ bullies}\cdot\text{trap}^{-1}\cdot\text{h}^{-1}$. There was a roughly three times higher total CPUE abundance in one of the sites (Site 19, summer) when compared with the other sites. Mean CPUE was significantly different between the sampled seasons (one-way ANOVA: $F = 1.625$,

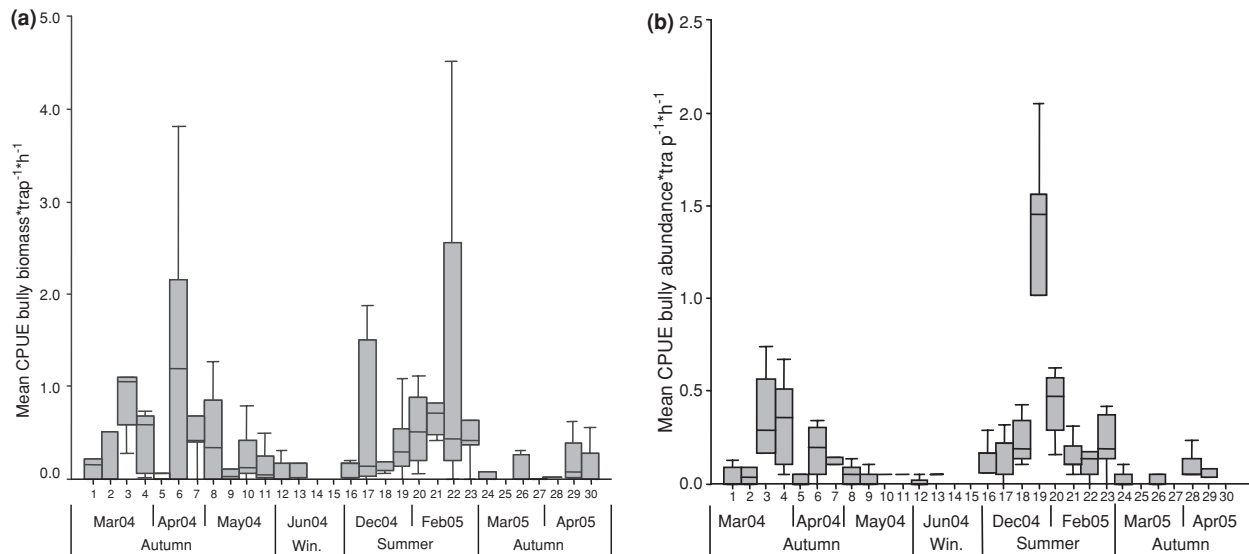


Fig. 2. Box-Whisker plot showing average bully CPUE biomass and abundance over the sites. Shaded boxes represent quartiles around the median (bar) and whiskers indicate the spread of the data (95%).

d.f. = 2, $P = 0.0003$). Multiple comparisons indicated that abundance was significantly higher in summer than in autumn (LSD: $P = 0.001$), higher in summer compared with winter (LSD: $P = 0.0002$) but did not differ between autumn and winter (LSD: $P = 0.080$).

Multiple stepwise regression between total bully CPUE biomass or abundance in sites and environmental variables (Lagarosiphon aerial density, canopy height, slope, temperature and the distance of sites from the Clutha River inflow) showed that the measured variables were poor predictors of bully CPUE biomass. Of these variables, only Lagarosiphon density explained a certain amount in the variability of bully CPUE biomass distribution over the sites (Model 1 density: $R^2 = 0.302$, $P = 0.009$, all other variables excluded: Fig. 3a.). Average Lagarosiphon stem density in the sites was similar over all seasons (one-way ANOVA: $F = 0.019$, d.f. = 2, $P = 0.981$). Multiple stepwise regression between the environmental variables and the total bully abundance in the sites was partly explained by either the distance from the Clutha River inflow (Model 1 Clutha River inflow: $R^2 = 0.275$, $P = 0.006$) or a combination of temperature and the Clutha River distance (Model 2 temperature + Clutha River distance: $R^2 = 0.416$, $P = 0.027$). All other environmental variables were excluded from both models. The linear regression between bully abundance and water temperature (Fig. 3b) and the Clutha River inflow (Fig. 3c) are presented above.

Fine-scale distribution

There was a significant difference in CPUE bully biomass between the zones (out, edge, in) of the

Lagarosiphon belt (ANOVA: $F = 3.245$, d.f. = 2, $P = 0.04$; Fig. 4) and between seasons (ANOVA: $F = 4.585$, d.f. = 3, $P = 0.005$). Interaction between zones and seasons was not significant (ANOVA: $F = 1.466$, d.f. = 6, $P = 0.201$). Bully biomass was significantly lower outside the Lagarosiphon belt (out) compared with the margin of the macrophyte beds (edge) (LSD: $P = 0.015$) or inside the stands (LSD: $P = 0.002$). There was no difference in CPUE biomass between the 'edge' and the 'in' zones (LSD: $P = 0.431$). These biomass differences between zones were not influenced by variations in fish size classes as common bully size (total length) was similar in zones (Kruskal-Wallis test: $\chi^2 = 1.403$, d.f. = 2, $P = 0.496$). There was no linear relationship between trap depth and CPUE biomass (linear regression: $r^2 = 0.03$, $F = 0.216$, $P = 0.643$).

Fish diet

Analysis of gut samples indicated that the diet of common bully sampled in the littoral of Lake Dunstan consisted mainly of invertebrates. We identified 33 prey taxa in common bully (27 excluding Chironomidae taxa). This prey community consisted mainly of Mollusca (5 taxa), Trichoptera (7 taxa), Odonata (2 taxa) and Chironomidae (6 taxa). The invertebrate community on Lagarosiphon comprised 41 species (31 excluding Chironomidae) and consisted primarily of Mollusca species (5 taxa; approximately 95% of biomass), Trichoptera (7 Taxa) and Chironomidae (10 taxa) (Fig. 5). The benthic samples from the bottom of the Lagarosiphon beds and the rocky shore area had a total of 30 taxa (24 excluding Chironom-

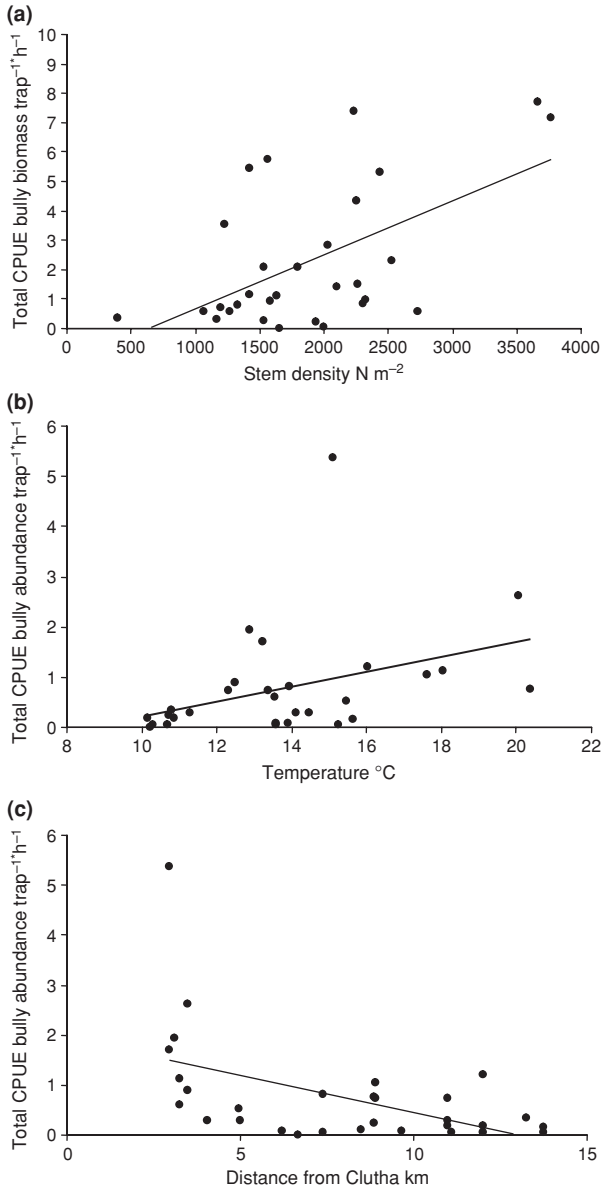


Fig. 3. (a) There was a linear relationship between Lagarosiphon stem density (stems per metre) and bully biomass over the sites. Each dot represents the average stem density and total bully biomass of each site. Variation in abundance was best explained by either water temperature (b) or the distance from the Clutha River inflow (c).

idae) and were dominated by the same Mollusca taxa (>85% of biomass) and to a lesser degree by Oligochaeta (approximately 11% of total biomass). Only a single taxon (water boatman) found in the bully diet that was not present in either Lagarosiphon or the benthic samples.

To further investigate differences among common bully diet and the invertebrate community on Lagarosiphon and the benthos over the sampled seasons we performed an ordination (MDS: final stress <8.2902, final instability = 0.00034, $P = 0.012$) (Fig. 6). MDS was based on the Bray–Curtis Distance between the

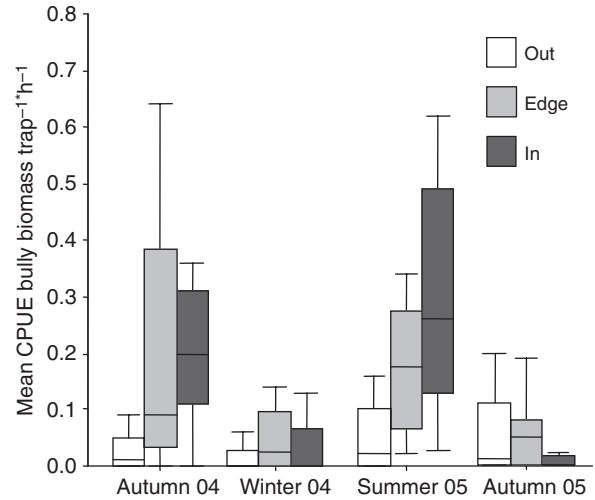


Fig. 4. Boxplot showing the average CPUE bully biomass in the 'edge' and 'in' and 'out' zones of the Lagarosiphon belt over the four sampled seasons. Shaded boxes represent quartiles around the median (bar); whiskers correspond to spread of the data (95%).

diet composition of fish (mean abundance of diet taxa) and the average invertebrate abundance in seasonal Lagarosiphon and benthos samples. The ordination explained 0.890 of the variation in the ordination space (Axis 1: 0.274, Axis 2: 0.615). There was little seasonal variability in Lagarosiphon and the benthic invertebrate communities. However, there was considerable seasonal variability in common bully diet composition. The benthic invertebrate communities from the rocky shore and the bottom of the Lagarosiphon were grouped closely together. The winter diet data of common bully appeared most similar to the benthic samples. Diet data from the remaining seasons were separated from the Lagarosiphon and benthic invertebrate samples along Axis 2. MRPP showed that the differences among groups in the ordination were all significant (common bully vs. Lagarosiphon: $T = -3.024$, $A = 0.189$, $P = 0.015$; common bully vs. benthic samples: $T = -3.019$, $A = 0.222$, $P = 0.017$; common bully vs. rocky shore benthic samples: $T = -2.412$, $A = 0.195$, $P = 0.032$).

Discussion

Bully biomass distribution

In the Lagarosiphon dominated part of the littoral, common bully biomass and abundance was closely linked to the dense Lagarosiphon beds across two spatial scales. Lagarosiphon stem density, temperature and the distance of sampling locations from the Clutha river inflow were the environmental variables that partly described CPUE bully biomass or abundance variations among sites. At the finer scale of within-sites, there was a clear pattern of higher fish

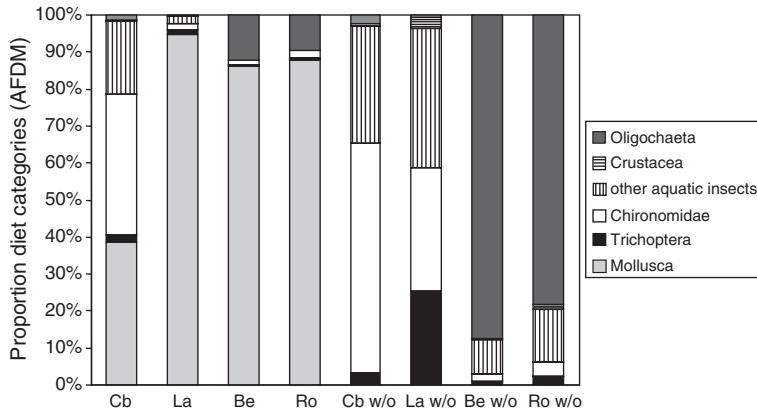


Fig. 5. The first four bars represent the categorical diet composition of common bully (Cb) when compared with the average invertebrate biomass in Lagarosiphon samples (La), benthic samples from the bottom of the Lagarosiphon beds (Be) and benthic samples collected from the rocky inshore area (Ro). The remaining four columns compare common bully diet with Lagarosiphon and benthic samples excluding molluscs (Cb, La, Be and Ro w/o).

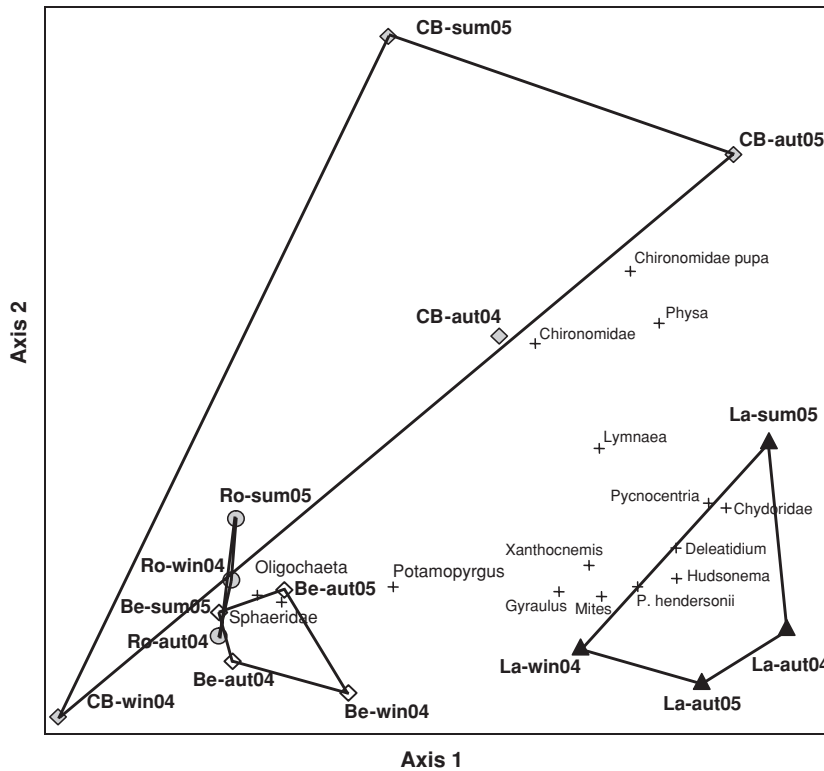


Fig. 6. MDS biplot of common bully diet (CB-season year) varied among seasons. The invertebrate communities found in Lagarosiphon (La-season year), and benthic samples from the bottom of the Lagarosiphon beds (Be-season year) and the rocky inshore area (Ro-season year) were less variable. Invertebrate scores that had more than 25% correlation with any of the axes are displayed for further information.

biomass and abundance in the interior and the edge area of the exotic macrophyte belt compared with the shallow inshore lake margin. This is not surprising as macrophytes are known to play an important role in the littoral as a refuge from predators for juvenile and prey fish (Damsgård & Ugedal 1997; Werner & Hall 1988). The high structural complexity of Lagarosiphon stands is likely to be a shelter from visually hunting predators present in the system, like trout or birds. Predators tend to have a lower foraging success rate in habitats with high structural complexity because of either a reduced prey encounter rate or a reduction in capture success (Diehl 1993; Warfe & Barmuta 2004). Moreover, small fish can be actively

attracted to areas with a high concentration of food (Petty & Grossman 1996), and macrophytes, in general, are areas of high invertebrate density (Diehl 1993; Crowder et al. 1998). It is not possible to say exactly why small fish actively seek the Lagarosiphon beds, although it is likely to be a mixture of all three contributing factors.

Lagarosiphon density explained large-scale common bully CPUE biomass distribution only to a certain degree, and the regression depends on the highest Lagarosiphon density measurements. Common bullies were distributed patchily on a large-scale and this patchiness could not be further explained by other measured environmental variables (slope, invertebrate

biomass, water temperature and season). The high patchiness of biomass distribution indicated that even the monospecific *Lagarosiphon* belt covering all available space in the littoral of Lake Dunstan is a heterogeneous environment from the perspective of a small fish species. Further research is needed to investigate this phenomenon.

There was a significant seasonal variation in large-scale bully CPUE abundance with higher numbers in the warmer summer and autumn months compared with winter, but this did not occur with bully CPUE biomass. Increased bully CPUE abundance in summer and autumn months can best be explained by the breeding behaviour of this species in spring (Stephens 1982; McDowall 1990), but also increased activity as a result of higher temperatures and therefore possibly a higher catch rate (bias). The linear relationship between water temperature and bully abundance corroborates this pattern. Additionally, the distance of sites from the Clutha River inflow had an impact on bully abundance, with a reduction in bully abundance with greater distance from the inflow. It is not entirely clear how this pattern can be explained, but it may be related to the recruitment of common bully. After hatching, common bully larvae enter a planktonic stage before they settle in the littoral (McDowall 1990). The short hydraulic residence time of Lake Dunstan (several days) might therefore impact on the recruitment of common bullies. Bully larvae likely drift downstream along the lake, thus limiting the number of recruits available at the top end of the lake.

Common bully diet

Gut content analysis is the most direct way to investigate diet of fish species. However, results must be interpreted with some caution as it only represents a point in time assessment of diet. Furthermore, results can be biased by the rapid digestion of soft-bodied invertebrates, resulting in over representation of hard-bodied invertebrates like snails and Trichoptera (case) and Chironomidae (head capsule). Based on gut analysis, the diets of common bully in Lake Dunstan were dominated by invertebrate species found commonly on macrophytes, including Mollusca, Trichoptera larvae (i.e., Hydroptilidae), Chironomidae and larval Odonata. All these invertebrates are found in high abundance on *Lagarosiphon* (Biggs & Malthus 1982; Kelly & Hawes 2005). The species community on *Lagarosiphon* in Lake Dunstan was similar to the common bully diet with identical species of Chironomidae, Mollusca and Trichoptera species. The benthic invertebrate community in the shallow littoral of Lake Dunstan, which was dominated by oligochaetes, appeared less similar to the diet of common bully, which contained very few oligochaetes.

Diet of common bully was also separated from the *Lagarosiphon* and benthic invertebrate communities in the ordination. Chironomidae larvae, Chironomidae pupae and *Physa* (Mollusca) appeared to be 'overrepresented' in the bully diet when compared with the *Potamopyrgus* (Mollusca) 'rich' *Lagarosiphon* samples. Nevertheless, Chironomidae are still highly abundant in *Lagarosiphon* considering the high standing crop of this macrophyte.

Conclusions

We have established that common bullies were associated with *Lagarosiphon* on a small-scale and that, on a large scale, *Lagarosiphon* density explained bully CPUE biomass to a certain degree. Furthermore, bully diet consisted of invertebrates found in *Lagarosiphon* beds.

As *L. major* is a nuisance species, the results presented here suggest that it can still play an important role as a feeding area for small fish species in the shallow littoral of Lake Dunstan. This macrophyte species essentially fulfils the same ecological role that native macrophyte species would provide were they present. Because of a scarcity of other macrophyte species, we could not compare the ecosystem functioning of *Lagarosiphon* with other macrophytes. In systems that have both, *Lagarosiphon* and native macrophyte species, *Lagarosiphon* still performs very well as invertebrate and fish habitat, i.e., supports a higher invertebrate and fish abundance than native macrophytes (Biggs & Malthus 1982; Kelly & Hawes 2005).

Because of the extremely high biomass of *Lagarosiphon* in Lake Dunstan, it supports a high biomass of invertebrates, and therefore will have a strong influence on littoral productivity. Restoration of a native macrophyte community in Lake Dunstan, even after complete removal of *Lagarosiphon*, is currently unrealistic, as the upstream presence of *Lagarosiphon* will ensure rapid reestablishment of this pest. Any macrophyte management strategy should therefore carefully weigh the costs and benefits associated with macrophyte removal. This means that it would be better to tolerate invasive macrophyte species to a certain degree than ending up with no macrophytes at all (Van Nes et al. 2002). For the weed management of Lake Dunstan, the importance of *Lagarosiphon* in the ecosystem has to be considered as large-scale rapid eradication of this macrophyte (currently not feasible) might have negative impacts on the lake fish community. At present, management should focus on small-scale local control in key areas to enhance recreational value of the lake and especially to prevent further spread of this invasive macrophyte to other waters by accidental transfer.

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