



## Consumption of submerged aquatic macrophytes by rudd (*Scardinius erythrophthalmus* L.) in New Zealand

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### Abstract

In experiments in New Zealand, rudd (*Scardinius erythrophthalmus* L.) of 108–277 mm fork length (FL) ate a wide range of native and introduced submerged aquatic macrophytes in captivity and in the field. Rudd consumed the native charophytes *Chara globularis* Thuill., *Chara fibrosa* Ag. ex Bruz., and *Nitella* spp., the native macrophytes *Potamogeton ochreatus* Raoul. and *Myriophyllum propinquum* A. Cunn., and the introduced macrophytes *Elodea canadensis* Michx., *Egeria densa* Planch., *Lagarosiphon major* L., and *Ceratophyllum demersum* L. Rudd consistently consumed the *Nitella* spp. and *Potamogeton ochreatus* before *Ceratophyllum demersum*. From the results of experiments in tanks and in the field, we found the order of highest to lowest palatability was: *Nitella* spp. > *Potamogeton ochreatus* > *Elodea canadensis* > *Chara globularis* = *Chara fibrosa* > *Egeria densa* = *Lagarosiphon major* > *Myriophyllum propinquum* > *Ceratophyllum demersum*. The order of consumption was subject to some variation with season, especially for *Egeria densa*, *Lagarosiphon major*, and *Myriophyllum propinquum*. Rudd consumed up to 20% of their body weight per day of *Egeria densa* in spring, and 22% of their body weight per day of *Nitella* spp. in summer. Consumption rates were considerably lower in winter than in summer. The results of our field trial suggested that the order of consumption also applies in the field and that rudd are having a profound impact on vulnerable native aquatic plant communities in New Zealand. *Nitella* spp. and *Potamogeton ochreatus* are likely to be selectively eaten, and herbivory by rudd might prevent the re-establishment of these species in restoration efforts.

### Introduction

Rudd (*Scardinius erythrophthalmus* L.: Cyprinidae) are native to the temperate parts of Europe, and were illegally introduced into New Zealand in 1967. Subsequent illegal releases into a large number of ponds, lakes, and river systems has established rudd widely north of about latitude 39 ° S. Rudd are now the only large, naturalised herbivorous freshwater fish in New Zealand, and biologists, conservationists, and trout anglers have become concerned that rudd, like many other introduced species, might have a detrimental effect on the New Zealand environment.

Despite being in the country for over 30 years, very little research has been carried out on rudd. Ten years after their introduction, Cadwallader (1977) reviewed the overseas literature on the species and speculated on some of the possible implications of its presence in New Zealand. Since then only a few studies have been done, all but one (Cadwallader, 1978) dealing with the autecology of rudd (Coates & Turner, 1977; Lane, 1983; Wise, 1990; Kane, 1995).

Lentic habitats dominated by aquatic macrophytes are preferred by rudd, which rely on aquatic vegetation for shelter, food, and sometimes spawning substrate (Giles, 1994). In their first year, small rudd consume a

wide range of organisms including terrestrial invertebrates, aquatic insects, crustaceans, and algae (Kennedy & Fitzmaurice, 1974). As rudd grow, aquatic macrophytes become increasingly important in their diet (Prejs, 1984; Giles, 1994). In New Zealand, rudd undergo an ontogenetic dietary shift from benthic invertebrates to aquatic macrophytes at about 150 mm in length (Lane, 1983; Wise, 1990; Kane, 1995). For rudd >200 mm, aquatic macrophytes form >80% of their diet (Wise 1990; Kane 1995).

In Europe, rudd are considered more desirable members of a fish community than carp (*Cyprinus carpio* L.) or bream (*Abramis brama* L.), as rudd are not zooplanktivorous for long periods of their lives, and are not especially destructive at normal densities (Moss et al., 1996). However, in New Zealand, without their natural predators, rudd have the potential to form significant populations and to influence the abundance of macrophyte communities through their herbivory. Changes in macrophyte species dominance caused by rudd have been recorded in the Netherlands (Van Donk & Otte, 1996), and in New Zealand rudd have been proposed as a causal factor in the widespread decline of aquatic macrophytes in the Waikato (Clayton & De Winton, 1994) and Auckland regions. The macrophyte community in Lake Rotoroa (Hamilton Lake), in which *Egeria densa* Planch. was dominant, collapsed in about 1989, with an accompanying decrease in water clarity. Rudd were introduced into Lake Rotoroa in about 1977 (Hicks, 1994), and the lake is currently the subject of a restoration plan that involves re-establishing submerged macrophytes over much of the lake bed. Rudd have been suggested as both a cause of the initial decline and a potential barrier to the re-establishment of plant communities in the lake (Clayton & De Winton, 1994).

The objective of this work was to evaluate the potential impact of herbivory by rudd in New Zealand. To do this, we determined the selectivity of plants by rudd both in captivity and in the field, and the consumption rates of a range of submerged aquatic macrophytes by rudd of different sizes.

## Methods

### *Fish capture and care*

Adult rudd were collected from Lakes Karapiro and Ngaroto between September and October 1997, and from Lake Karapiro in December 1998. All of the fish

were caught using fyke nets or gill nets set overnight near submerged macrophyte beds. The fish were released into large, well-oxygenated concrete tanks that were 5.3–5.8 m long, 1.3 m wide and 0.8 m deep (volume 5.5–6.0 m<sup>3</sup>). The rudd were held in these tanks over the course of the trials. The tanks were covered with black cloth that shaded out 95% of the light to limit algal growth and to prevent the entry of terrestrial invertebrates and plant material. Water quality was maintained by a combination of flushing through with dechlorinated water and siphoning out solid wastes. In the 1999 tank trials, the walls and floors of the tanks were regularly scrubbed to remove biofilms. Rudd were fed trout pellets at a rate of approximately 3% of their body weight per day when not being offered macrophytes during the trials. The exponential relationship of weight ( $Y$ ) to length ( $X$ ) for the rudd, determined from the linear regression of log-transformed data, was  $Y = 0.00000365 X^{3.301}$ . For this regression,  $r^2 = 0.996$ ,  $N = 62$ , and  $P < 0.001$ .

### *Plant collection*

A range of native and introduced submerged macrophytes were collected from water bodies in the Waikato and Bay of Plenty regions. The species were chosen because of their common occurrence in North Island lakes within the present range of rudd, and because some, especially charophytes, are important in the restoration of devegetated lakes. Prior to each set of trials, fresh plant material was collected to allow for seasonal changes in nutritional content.

The native charophytes used in plant selectivity tests were *Chara globularis* Thuill., *Chara fibrosa* Ag. ex Bruz., and *Nitella* spp. The *Nitella* material used in this study included *N. hookeri* A.Br. and *N. cristata* A.Br., em. R.D.W., but differentiation between these two species was generally not possible without fruiting bodies (Wood & Mason, 1977; Clayton & Wells). The native macrophytes *Potamogeton ochreatus* Raoul. and *Myriophyllum propinquum* A. Cunn., and the introduced macrophytes *Elodea canadensis* Michx., *Egeria densa* Planch., *Lagarosiphon major* L., and *Ceratophyllum demersum* L. were also used.

### *Plant selectivity*

#### *Experiment 1: Vascular species*

To test the seasonal variation in palatability of macrophytes to rudd in captivity, three fish were introduced into each of four tanks in October 1997. The rudd used

in the experiment were 201–246 mm FL (fork length) at capture because fish of this size were considered to be herbivorous (e.g. Kane, 1995). The rudd grew over the course of the trials so this size class increased slightly with each successive experiment. One 100 g FW (fresh weight) bunch of each of the macrophytes *Potamogeton ochreatus*, *Myriophyllum propinquum*, *Elodea canadensis*, *Egeria densa*, *Lagarosiphon major*, and *Ceratophyllum demersum* was tied at the base and secured to the bottom of each tank. The plants were removed, blotted dry, weighed, and then replaced at 24 h intervals for the first 5 days then every 48 h for a further 16 days.

Experiments using these rudd were repeated seasonally in 1997 in October and November (spring), and in 1998 in January and February (summer), April (autumn), and late July to mid August (winter). Prior to each trial, the tanks were cleaned and the fish were weighed and measured. To increase their appetite, the rudd used in each trial were not fed their usual maintenance diet of trout pellets for 48 h prior to the start of the trials. Mean temperatures during each of the trials were recorded by temperature loggers.

#### *Experiment 2: Charophyte selection by small rudd*

To compare their palatability to small rudd (158–169 mm FL) in captivity, *Nitella* spp., *Potamogeton ochreatus*, and *Elodea canadensis* were offered to rudd in indoor tanks between 17 April and 8 May 1998. One 17 g bunch of each of the macrophytes was anchored to the bottom of each of four glass tanks 0.81 m × 0.72 m × 0.45 m, and one rudd was put into each tank. The plant bunches were removed, blotted dry, and weighed daily. Fluorescent lighting was used to give a 12 h light, 12 h dark cycle. Low levels of daylight also entered through laboratory windows.

#### *Experiment 3: Charophyte selection by large rudd*

To compare the palatability of charophytes to larger rudd in captivity, groups of three fish (209–227 mm, mean weight 199 g) were introduced into each of the four tanks and held for 14 days in January 1999. One 100 g FW bunch of each of the macrophytes *Chara globularis*, *Chara fibrosa*, *Nitella* spp., *Potamogeton ochreatus*, *Elodea canadensis*, and *Ceratophyllum demersum* was tied at the base and secured to the bottom of each tank. At 24 h intervals, the plants were removed, weighed, and then replaced.

#### *Experiment 4: Selectivity in the field*

To compare the palatability of macrophytes to rudd in the field, the macrophytes *Nitella* spp., *Chara globularis*, *Elodea canadensis*, *Egeria densa*, and *Ceratophyllum demersum* were attached in 70 g bunches that were evenly spaced along 2 m long buoyant, PVC pipes. These pipes were anchored in 3–4 m depth of water in Lake Karapiro so that each pipe floated horizontally 1.5 m below the water surface, positioned close to naturally growing *Ceratophyllum demersum* weed beds known to be frequented by rudd. Controls to exclude rudd grazing were established by enclosing plants similarly attached to PVC pipes within 10 mm plastic mesh cages. Field trials were run for 72 h in March ( $N = 4$  structures), April ( $N = 3$ ), and June ( $N = 3$ ) 1999. At the end of the trials, the plants were recovered and weighed. On two further occasions in December the same experiment was set up but filmed by a remote video camera recording for a 10 s period every 5 min for 12 h.

#### *Consumption rate*

#### *Experiment 5: Effect of fish size*

Four size classes of rudd (initially 111–135 mm, 178–181 mm, 226–236 mm, and 266–277 mm FL) were used to examine the effect of fish size and season on consumption rates. In October 1997, four rudd of each size class were introduced into each of four tanks. Stems of *Egeria densa* 300 mm long were tied in bunches of about 140 g FW and weighted to the tank bottom. After 24 h, the bunches were blotted free of excess water and weighed. The procedure was repeated five times in spring between 30 October and 5 November 1997, five times in summer between 27 January and 2 February 1998, and five times in autumn between 25 and 29 April 1998, using the same fish. The rudd grew over the course of the trials, so the size classes increased slightly between successive seasons.

Mean daily consumption rates for rudd feeding on *Egeria densa* were calculated as a proportion of fish body weight, and as dry weight consumed relative to fresh weight of fish. Dry weight of *Egeria densa* consumed was calculated from the predetermined ratios of dry weight to fresh weight. To calculate the ratio of fresh weight–dry weight, five plant bunches of 100 g FW were weighed and dried at 80 °C to a constant weight. Consumption rates for each size class and season were compared with ANOVA and Bonferroni tests carried out using SYSTAT<sup>®</sup> version 7 for Windows<sup>®</sup>.

### Experiment 6: Consumption rate of charophytes

To compare the consumption of charophytes by rudd compared with other macrophytes, groups of three rudd (192–236 mm FL, mean weight 213 g) were transferred to each of six tanks. Macrophytes were introduced into the tanks in bunches of approximately 100 g FW that were secured to the bottom. Two tanks each had three bunches of *Elodea canadensis*, a further two tanks had three bunches of *Chara globularis*, and the other two tanks each had five bunches of *Nitella* spp. After 48 h, the bunches were removed and re-weighed. This procedure was repeated but the macrophyte species were rotated so that no fish received the same species the second time. The experiments were carried out in both summer (8–10 February and 11–13 February 1999) and winter (23–25 June and 29 June–1 July 1999). For each collection of macrophytes (summer and winter), the dry weight–fresh weight ratios were determined for *Nitella* spp., *Chara globularis*, and *Elodea canadensis* by making bunches of 20 g FW and then drying the bunches to a constant weight at 80 °C. Temperatures in the tanks were logged at 15 min intervals.

## Results

### Plant selectivity

#### Experiment 1: Vascular species

There were marked seasonal differences in the time taken for captive rudd to consume the different macrophytes, and the order of consumption was also affected by season. In spring and autumn, the macrophytes were consumed in the order *Potamogeton ochreatus* > *Elodea canadensis* > *Egeria densa* > *Lagarosiphon major* > *Myriophyllum propinquum* > *Ceratophyllum demersum* (Fig. 1). The order of *Egeria densa* and *Lagarosiphon major* appears to be labile, as in summer there was no difference in their rates of disappearance, and in winter *Lagarosiphon major* was consumed before *Egeria densa*. Though *Myriophyllum propinquum* was usually consumed after *Lagarosiphon major*, in summer there was little difference between the order of consumption. *Ceratophyllum demersum* was always the last plant to be consumed, and in autumn and winter it was barely eaten. All macrophytes were generally eaten more slowly in autumn and winter than in spring and summer. The mean tank temperature in summer was 22 °C (range 21–24 °C), and in winter was 10 °C (range 9–11 °C).

The palatability of *Egeria densa* and *Lagarosiphon major* to rudd appeared to be very similar, but overall *Lagarosiphon major* seemed to be slightly more preferred. In six out of 16 trials *Lagarosiphon major* was completely consumed before *Egeria densa*. In three trials, *Egeria densa* was consumed before *Lagarosiphon major*. For the other seven trials, the palatability of the two taxa could not be separated, either because both were completely consumed during the same time period or because neither was fully consumed within the 21 days of the trial.

#### Experiment 2: Charophyte selection by small rudd

At constant temperature (mean 20.1±0.2 °C), the charophyte *Nitella* spp. was eaten by small rudd (158–169 mm FL) much faster than *Potamogeton ochreatus*, which was eaten before *Elodea canadensis* (Fig. 2). The time for 50% of the *Nitella* spp. to be consumed was 1.3 days, compared to 7.8 days for *Potamogeton ochreatus* and 14.0 days for *Elodea canadensis*.

#### Experiment 3: Charophyte selection by large rudd

When charophytes were offered to larger rudd (209–227 mm FL) in January 1999, the order of consumption was *Nitella* spp. > *Potamogeton ochreatus* > *Elodea canadensis* > *Chara globularis* = *Chara fibrosa* > *Ceratophyllum demersum*. *Ceratophyllum demersum* remained largely uneaten (Fig. 3). Mean temperature during the experiment was 23.8 °C (range 21.8–27.3 °C).

#### Experiment 4: Selectivity in the field

In the field, *Nitella* spp. was always consumed completely, and *Egeria densa* and *Ceratophyllum demersum* were eaten the least (Fig. 4). In March and April, the order of consumption was generally *Nitella* spp. > *Elodea canadensis* > *Chara globularis* > *Egeria densa* = *Ceratophyllum demersum*. *Egeria densa* exhibited loss of entire stems, and *Ceratophyllum demersum* was least eaten. In June, *Nitella* spp. was completely consumed, and *Chara globularis* had greater biomass reduction than *Elodea canadensis*. Mean water temperatures were lower in June (13.0 °C) than in March (20.7 °C) or April (18.4 °C), but direct comparisons of consumption between dates is not valid because the number of grazing fish was unknown and probably variable. Rudd were observed by video camera to tug roughly on the tethered plant bunches. During the 72 h that the plants were left in the lake, control plants inside their mesh enclosures showed no signs of plant leaf loss or fragmentation (Fig. 4). Rudd

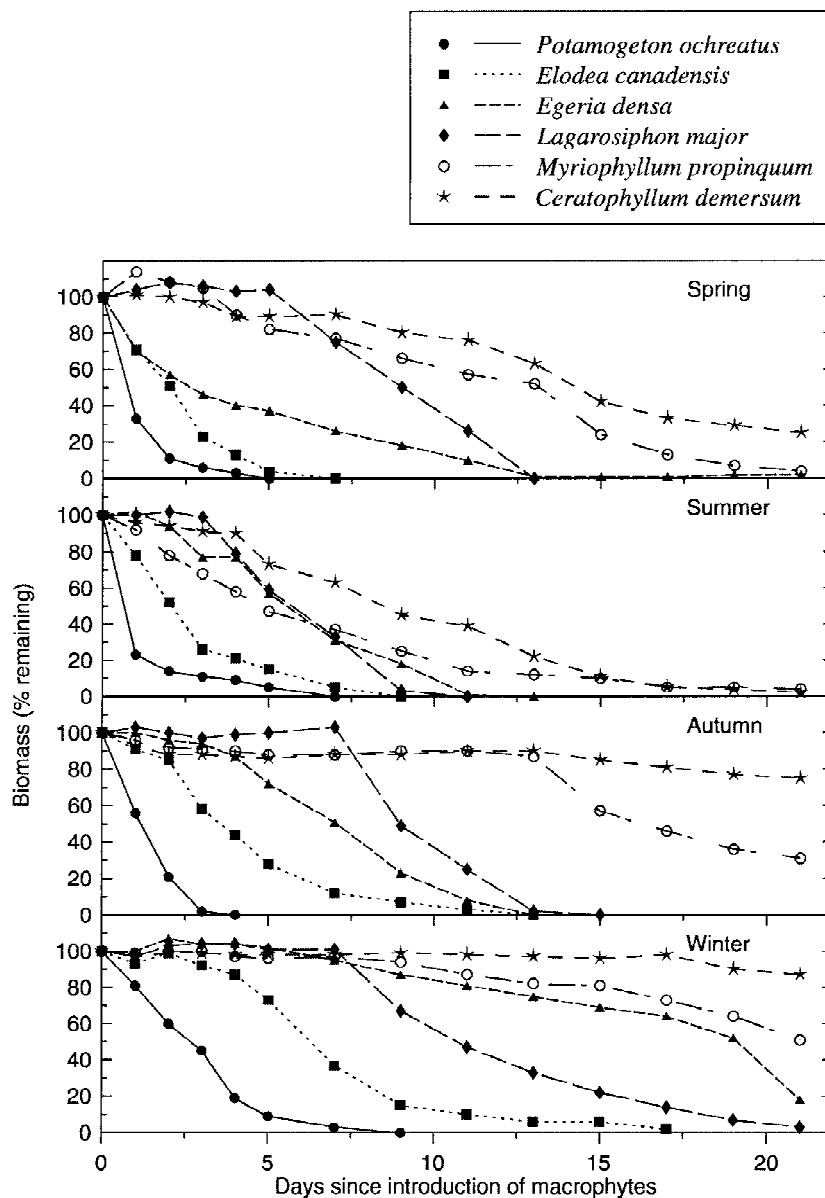


Figure 1. Mean biomass remaining of four 100 g fresh weight bunches of submerged aquatic macrophytes exposed to grazing by 201–246 mm fork length rudd in captivity in outdoor tanks at ambient temperatures. Four rudd were placed in each tank.

ate mostly *Nitella* spp., and were not observed eating the *Ceratophyllum demersum*.

#### Consumption rate

##### Experiment 5: Effect of fish size

The mean daily consumption rate of *Egeria densa* in spring 1997 was less for small fish (1.3 mg DW plant  $g^{-1}$  FW fish  $d^{-1}$ ) than for the largest fish (16.5 mg DW plant  $g^{-1}$  FW fish  $d^{-1}$ ; ANOVA,  $P <$

0.001; Table 1). Mean water temperatures in the tanks were 18.3 °C in spring, 25.0 °C in summer, and 18.2 °C in autumn. Dry weight was 8.14% of fresh weight in spring and summer, and 7.39% of fresh weight in autumn. Consumption rates for the three larger size classes were not different (Bonferroni  $P \geq 0.387$ ). In summer, consumption rates for the smallest fish were greater than in spring, whereas for all larger size classes, summer rates were lower than spring rates.

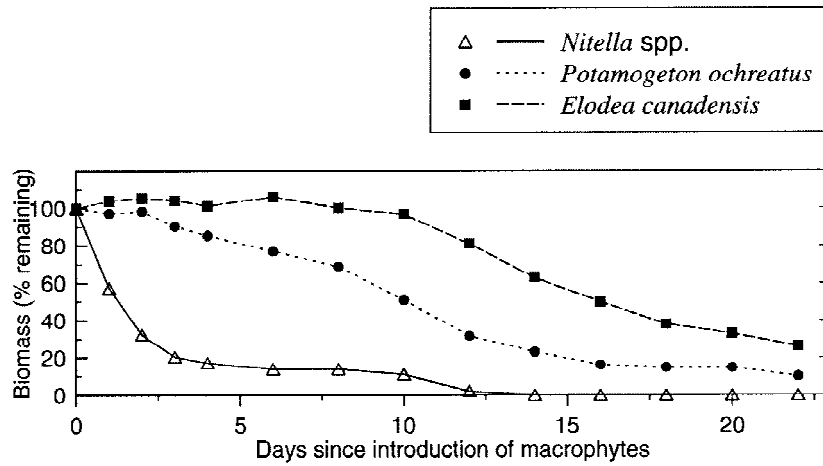


Figure 2. Mean biomass remaining of four 17 g fresh weight bunches of submerged macrophytes exposed to grazing by 158–169 mm fork length rudd in captivity at constant temperature (20 °C) in autumn (16 April–8 May 1998). One bunch of each species was placed in a tank with one fish.

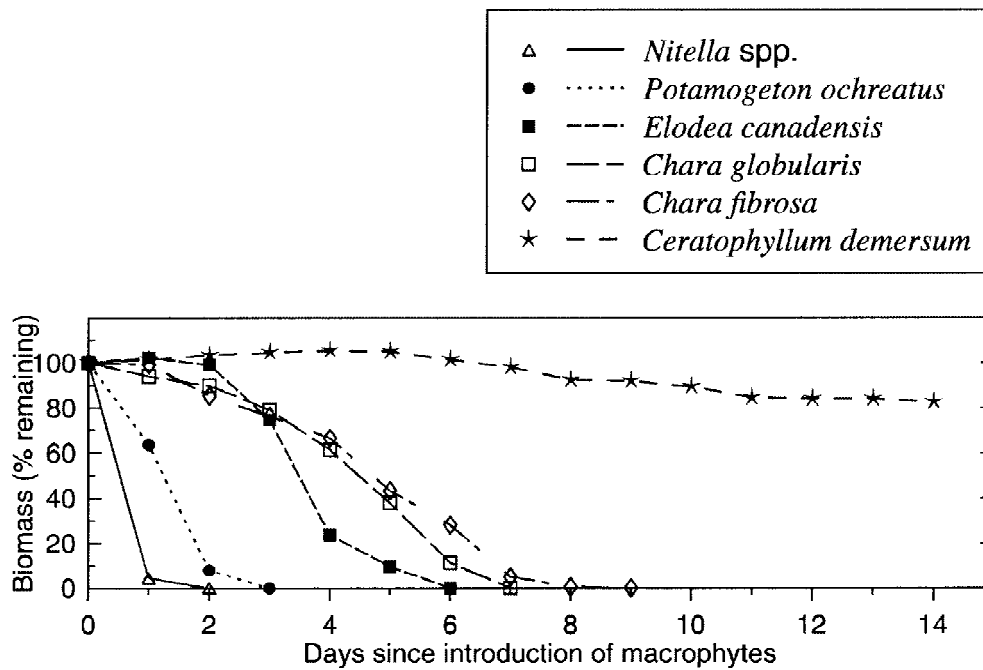


Figure 3. Mean biomass remaining of four 100 g fresh weight bunches of macrophytes by 209–227 mm fork length rudd in captivity in summer (January 1999). One bunch of each species was placed in a tank with three fish.

Consumption rates were lowest in autumn, and were not different among the size classes (Bonferroni  $P \geq 0.056$ ). Mean consumption rates across all size classes were greater in summer than in autumn (Bonferroni  $P = 0.022$ ).

Experiment 6: Consumption rate of charophytes

In both summer and winter, consumption rates were greater for *Nitella* spp. than for *Elodea canadensis* or *Chara globularis* (Bonferroni  $P \leq 0.001$ ), but were not significantly different between *Elodea canadensis* and *Chara globularis* (Bonferroni  $P = 0.233$ ; Table 2). In winter, consumption rates were 65–93% less than

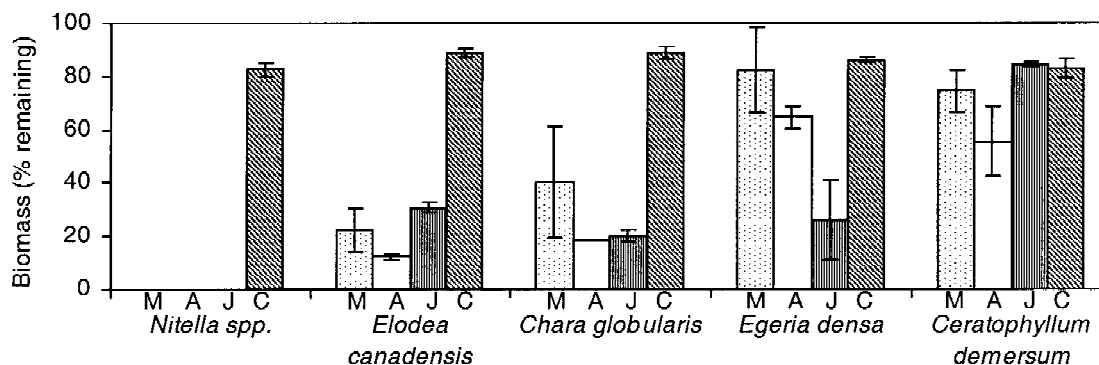


Figure 4. Mean percentage biomass of five macrophytes remaining after 72 h exposure to rudd grazing in Lake Karapiro in March (M), April (A) and June (J) 1999. One set of controls (with fish excluded) for June is shown (C). Error bars are one standard error of the mean.

Table 1. Mean consumption rates for captive rudd of different sizes feeding on *Egeria densa* in tanks in spring, summer, and autumn. Means of five trials using four fish in each of four tanks; FW = fresh weight, DW = dry weight. Standard errors given in parentheses

Fish fork length (mm)	Consumption rate relative to fish body weight					
	Percent of FW fish d <sup>-1</sup>			mg DW plant g <sup>-1</sup> FW fish d <sup>-1</sup>		
	Spring	Summer	Autumn	Spring	Summer	Autumn
108–167	1.6 (3.2)	5.4 (2.0)	0.5 (0.8)	1.3 (2.6)	4.4 (1.6)	0.4 (0.6)
178–221	16.7 (1.6)	8.5 (1.2)	-0.2 (0.1)	13.6 (1.3)	6.9 (1.0)	-0.2 (0.1)
226–253	14.1 (2.6)	1.0 (0.4)	1.8 (0.4)	11.5 (2.1)	0.8 (0.3)	1.3 (0.3)
266–293	20.2 (1.5)	3.3 (0.8)	1.5 (0.3)	16.5 (1.3)	2.7 (0.7)	1.1 (0.2)
Mean	13.1 (4.0)	4.6 (1.6)	0.9 (0.5)	10.7 (3.3)	3.7 (1.3)	0.7 (0.3)

in summer for all three macrophytes (ANOVA  $P \leq 0.002$ ). Dry weight for *Nitella* spp., *Chara* spp., and *Elodea canadensis*, respectively, was 11.14%, 12.28%, and 5.07% of fresh weight in February, and 7.61%, 11.14%, and 7.28% in June. Mean water temperatures were 22.0–23.2 °C in late summer (8–13 February 1999), and 9.3–10.2 °C in winter (23–25 June and 29 June–1 July 1999).

## Discussion

### Plant selectivity and consumption rates

European studies have established the palatability of *Elodea* spp. to rudd (Kennedy & Fitzmaurice, 1974; Prejs & Jackowski, 1978; Van Donk & Otte, 1996), and relative unpalatability of *Ceratophyllum demersum* (van Donk & Otte 1996). Similarly, from experiments 1, 2, and 3 we deduced the relative palatability, from the most to least palatable, to be: *Nitella*

spp. > *Potamogeton ochreatus* > *Elodea canadensis* > *Chara globularis* = *Chara fibrosa* > *Egeria densa* = *Lagarosiphon major* > *Myriophyllum propinquum* > *Ceratophyllum demersum*.

The order of consumption was subject to some variation with season, especially for *Egeria densa*, *Lagarosiphon major*, and *Myriophyllum propinquum*. The condition of *Egeria densa* and *Lagarosiphon major* varied considerably between seasons and this may have affected their palatability. However, the native taxa *Nitella* spp. and *Potamogeton ochreatus* were consistently preferred over other macrophytes. In the field, wide variation in loss of biomass at similar temperatures was probably attributable to variable numbers of fish feeding, as fish density was not controlled as it was in the tank experiments.

Some macrophytes seem palatable to a range of aquatic herbivores (Lodge, 1991), as *Nitella hookeri*, *Elodea canadensis*, and *Potamogeton* spp. are

Table 2. Mean consumption rates of three macrophytes by captive rudd 209–227 mm FL in summer (about 23 °C) and winter (about 10 °C). Means of four trials using three fish per tank for each macrophyte in each season; FW = fresh weight, DW = dry weight. Standard errors given in parentheses

Season	Consumption rate relative to fish body weight					
	Percent of FW fish d <sup>-1</sup>			mg DW plant g <sup>-1</sup> FW fish d <sup>-1</sup>		
Season	<i>Elodea</i>	<i>Chara globularis</i>	<i>Nitella</i> spp.	<i>Elodea</i>	<i>Chara globularis</i>	<i>Nitella</i> spp.
Summer	3.5 (0.6)	4.4 (0.6)	21.7 (1.8)	3.9 (0.7)	5.9 (0.8)	12.1 (1.0)
Winter	0.4 (0.2)	1.1 (0.2)	5.8 (0.6)	0.3 (0.2)	1.2 (0.2)	4.2 (0.5)

readily consumed by grass carp (*Ctenopharyngodon idella* Valenciennes; Edwards, 1974; Mitchell, 1980) and black swans (*Cygnus atratus* Latham; Mitchell & Wass, 1996). However, even *Ceratophyllum demersum*, the least preferred macrophyte in our study, is an important component in rudd diets where it is the dominant species (Prejs & Jackowski, 1978).

In the present study, a maximal consumption rate for rudd feeding on *Egeria densa* was 16.5 mg DW plant g<sup>-1</sup> FW fish d<sup>-1</sup> (20.2% of FW fish d<sup>-1</sup>) at a mean water temperature of 18.3 °C. A similar rate was estimated for the more preferred charophyte *Nitella* spp. (12 mg DW plant g<sup>-1</sup> FW fish d<sup>-1</sup>, or 22% of FW fish d<sup>-1</sup>) at a temperature of 22–23 °C. Variable consumption rates for rudd feeding on submerged macrophytes have been found, including 0.2–4% of FW fish d<sup>-1</sup> and 7.7–15.5% of FW fish d<sup>-1</sup> for *Elodea canadensis* (Prejs, 1978), and 20–43% of FW fish d<sup>-1</sup> at 16 and 20 °C, respectively, on *Chara* sp. (Hofer & Niederholzer, 1980).

Rudd of all sizes tested in captivity in our study were significant herbivores. Higher macrophyte consumption rates were recorded for larger fish, which is supported by the evidence of an ontogenetic shift in diet observed by Kane (1995). Kane found that the diet of rudd 100–149 mm FL in Lake Rotoroa was 62% chironomid larvae and pupae by volume, but only 27% macrophytes. The diet of rudd 150–199 mm FL was 23% chironomid larvae and pupae, and 54% macrophytes, whereas rudd 200–249 mm FL consumed 8% chironomid larvae and pupae, and 84% macrophytes. Thus rudd are herbivorous even at small sizes, but importance of plant material in their diet increases with size.

Consumption rates in captive rudd were lower in winter than in summer, and this was probably related to temperature, as rudd increase grazing rates with increased temperature, particularly above 16 °C (Hofer & Niederholzer 1980; Prejs, 1984). However,

the grazing that we observed at water temperatures as low as 10 °C suggests that rudd will continue to feed through winter throughout most if not all of their range in New Zealand. Different plant collection sites may also have contributed to the differences in selectivity (Chapman & Coffey, 1971; Bonar, et al. 1990). Though macrophytes in the two selectivity trials taken from different water bodies had the same order of selectivity, part of the decreased consumption in winter might have been caused by a reduction in palatability.

From a comparison of consumption rates of macrophytes by rudd and grass carp, we can speculate about the impact of rudd on submerged macrophytes. The high consumption rates by rudd in spring may be caused by the energy demands of gonad development, as rudd in New Zealand spawn in late spring. In contrast, consumption rates were not maximal in summer when temperatures were highest. Consumption rates recorded for rudd were generally lower than for grass carp; small grass carp (about 500 g) can consume over 100% of their body weight per day (Opusznski, 1972; Edwards, 1974; Venkatesh & Shetty, 1978), but as they grow, consumption rates decrease (Leslie et al. 1996) to about 25% at 6.5 kg (Osborne & Sassic, 1981).

In New Zealand, 4–6 year old grass carp, each weighing >2 kg, were stocked into the 1–92 ha Lake Parkinson at densities of 55 kg ha<sup>-1</sup>. These fish completely eliminated the aquatic vegetation, which included *Egeria densa* (Mitchell, 1980). Consumption rates up to about 20% of FW fish per d<sup>-1</sup> by rudd could feasibly have an impact on palatable species where rudd population densities are high enough.

#### Management implications

Clear guidance for managers is needed about the potential for harm from rudd to lake ecosystems. Rudd were illegally released in widespread areas of the northern half of the North Island of New Zealand



around 1975, and in almost every instance, persistent breeding populations became established. Frequently, rudd have been associated with macrophyte collapse and a switch from clear to turbid water. Not only do rudd find *Nitella* spp. and *Potamogeton ochreatus*, two key species in unmodified lake ecosystems, particularly palatable, but the ecological problems are likely to be compounded by the feeding habit of rudd. Typically rudd concentrate their grazing effort on the growing apices of *Egeria densa* (Lake, 1998), which are the meristems on which plant growth is dependent (Crawley, 1983). Therefore, the use of simple models incorporating the relative biomasses and growth of rudd and *Egeria densa* may not adequately quantify the impact of rudd grazing.

Though rudd have relatively low consumption rates of submerged aquatic macrophytes compared to grass carp, they may attain high densities without an efficient predator such as pike (*Esox lucius* L.). Rudd may prove to be a significant additive factor causing macrophyte decline in New Zealand once macrophytes become stressed through perturbations such as decreased water clarity caused by suspended sediment or algal blooms. Also, our study shows that rudd have the capacity to modify plant communities by selectively removing palatable charophytes such as *Nitella* spp. Charophytes were important early colonists of Lake Parkinson in New Zealand after removal of *Egeria densa* by grass carp (Tanner et al., 1990). Because their abundant oospores dominate the seed banks of most vegetated lakes, charophytes have been identified as a key component in the restoration of macrophyte communities attached to lake beds (De Winton et al., 2000). By direct suppression of plant regrowth, rudd in a devegetated lake are likely to inhibit or prevent re-establishment of charophyte vegetation from natural seed banks.

Selective feeding by rudd may also be significant in lakes that have been invaded by exotic oxygen weeds in New Zealand (e.g. *Egeria densa*, *Elodea canadensis*, and *Lagarosiphon major*) by facilitating their monospecific habit through suppression or exclusion of more desirable species. Van Donk & Otte (1996) observed a shift in macrophyte species composition in the Netherlands from *Elodea nuttallii* Planch. and *Potamogeton berchtholdii* (Fieb.) to *Ceratophyllum demersum*, which they attributed to the selective grazing of both rudd and coots (*Fulica atra* L.). A similar mechanism might be operating in Lake Karapiro and a number of other North Island lakes that have become dominated by *Ceratophyllum demersum*.

In addition to the direct consumption of aquatic macrophytes by larger rudd, the diet of small rudd (mean 56–65 mm FL) overlaps significantly with that of common smelt (*Retropinna retropinna* Richardson) in sympatry (Lake, 1998). Rudd populations go largely unchecked in New Zealand and form large populations of small fish that are of limited interest to anglers. Despite this, pressure still exists for further releases of rudd to new habitats that they currently do not occupy. Our study suggests that further releases of rudd should be resisted, and that where possible, rudd should be eradicated. The results of this work suggest that rudd are yet another threat to New Zealand's biodiversity of native species, and that expansion of their range threatens the survival of many of our aquatic communities.

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### References

- Bonar, S. A., H. S. Sehgal, G. B. Pauley & G. L. Thomas, 1990. Relationship between the chemical composition of aquatic macrophytes and their consumption by grass carp, *Ctenopharyngodon idella*. *J. Fish Biol.* 36: 149–157.
- Cadwallader, P. L., 1977. Review of the ecology of rudd and the implications of its introduction into New Zealand. In Cadwallader, P. L. (ed.), Introduction of Rudd, *Scardinius erythrophthalmus* into New Zealand. Fisheries Technical Report 147, N. Z. Ministry of Agriculture and Fisheries, Wellington: 1–18.
- Cadwallader, P. L., 1978. Acclimatisation of rudd *Scardinius erythrophthalmus* (Pisces: Cyprinidae), in the North Island of New Zealand. *N. Z. J. mar. Freshwat. Res.* 12: 81–82.
- Chapman, V. J. & B. T. Coffey, 1971. Experiments with grass carp in controlling exotic macrophytes in New Zealand. *Hydrobiologia* 12: 313–323.
- Clayton, J. S. & M. D. De Winton, 1994. Lake Rotoroa, a candidate for restoration or restraint? In Collier, K. J. (ed.), Restoration of Aquatic Habitats. Selected papers from the second day of the New Zealand Limnological Society 1993 Annual Conference. Department of Conservation, Wellington: 39–52.

- Clayton, J. S. & R. Wells, 1980. Key to the common Characeae of New Zealand. *N. Z. J. Bot.* 18: 569–570.
- Coates, G. D. & A. S. Turner, 1977. First survey of a rudd population in New Zealand. In Cadwallader, P. L. (ed.), Introduction of Rudd, *Scardinius erythrophthalmus* into New Zealand. Fisheries Technical Report 147, N. Z. Ministry of Agriculture and Fisheries, Wellington: 19–24.
- Crawley, M. J., 1983. Herbivory: the Dynamics of Animal–Plant Interactions. Blackwell Scientific Publications, Oxford: 437 pp.
- De Winton, M. D., J. S. Clayton & P. D. Champion, 2000. Seedling emergence from seed banks of 15 New Zealand lakes with contrasting vegetation histories. *Aquat. Bot.* 66: 181–194.
- Edwards, D. J. 1974. Weed preference and growth of young grass carp in New Zealand. *N. Z. J. mar. Freshwater Res.* 8: 341–350.
- Giles, N., 1994. Freshwater Fish of the British Isles. Swan Hill Press, Shrewsbury: 192 pp.
- Hicks, B. J., 1994. The biology and feeding ecology of exotic fish. In Clayton, J. S. & M. D. De Winton (eds), Lake Rotoroa: Change in an Urban Lake: an Information Review and Bibliography. NIWA Ecosystems Publication 9, National Institute of Water and Atmospheric Research Limited, Hamilton: 71–79.
- Hofer, R. & R. Niederholzer, 1980. The feeding of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.), II. Feeding experiments in the laboratory. *Ekologia Polska* 28: 61–70.
- Kane, D. S., 1995. The status of freshwater fish in Hamilton Lake (Lake Rotoroa). Unpublished M.Sc. thesis, University of Waikato, Hamilton: 121 pp.
- Kennedy, M. & P. Fitzmaurice, 1974. Biology of the rudd *Scardinius erythrophthalmus* (L.) in Irish waters. *Proc. R Irish Acad.* 74: 245–303.
- Lake, M. D., 1998. The feeding ecology of rudd (*Scardinius erythrophthalmus*) in New Zealand. Unpublished M.Sc., University of Waikato, Hamilton: 63 pp.
- Lane, W. L., 1983. The population dynamics, food and reproductive habits of rudd (*Scardinius erythrophthalmus* L.) in New Zealand. Unpublished Ph.D. thesis, University of Auckland, Auckland, New Zealand: 119 pp.
- Leslie, A. J., J. R. Cassani & R. J. Wattendorf, 1996. An introduction to grass carp biology and history in the United States. In Cassani, J. R. (ed.), Managing Aquatic Vegetation with Grass Carp: a Guide for Water Resource Managers. American Fisheries Society, Introduced Fish Section, Bethesda, Maryland: 196 pp.
- Lodge, D. M., 1991. Herbivory of freshwater macrophytes. *Aquat. Bot.* 41: 195–224.
- Mitchell, C. P., 1980. Control of water weeds by grass carp in two small lakes. *N. Z. J. mar. Freshwat. Res.* 14: 381–390.
- Mitchell, S. F. & R. T. Wass, 1996. Grazing by black swans (*Cygnus atratus* Latham), physical factors, and the growth and loss of aquatic vegetation in a shallow lake. *Aquat. Bot.* 55: 205–215.
- Moss, B., J. Madgwick & G. Phillips, 1996. A guide to the restoration of nutrient-enriched shallow lakes. Broads Authority, Norwich: 180 pp.
- Opuszynski, K., 1972. Use of phytophagous fish to control plants. *Aquaculture* 5: 61–74.
- Osborne, J. A. & N. M. Sassic, 1981. The size of grass carp as a factor in the control of *Hydrilla*. *Aquat. Bot.* 11: 129–136.
- Prejs, A., 1978. Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.) II. Daily intake of macrophyte food in relation to body size of fish. *Ekologia Polska* 26: 537–553.
- Prejs, A., 1984. Herbivory of temperate freshwater fishes and its consequences. *Env. Biol. Fishes* 10: 281–296.
- Prejs, A. & H. Jackowski, 1978. Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.) I. Species composition and dominance relations in the lake and food. *Ekologia Polska* 26: 429–438.
- Tanner, C. C., R. D. S. Wells & C. P. Mitchell, 1990. Re-establishment of native macrophytes in Lake Parkinson following weed control by grass carp. *N. Z. J. mar. Freshwat. Res.* 24: 181–186.
- Van Donk, E. & A. Otte, 1996. Effects of grazing by fish and waterfowl on the biomass and species composition of submerged macrophytes. *Hydrobiologia* 340: 285–290.
- Venkatesh, B. & H. P. C. Shetty, 1978. Studies on the growth rate of grass carp *Ctenopharyngodon idella* (Valenciennes) fed two aquatic weeds and a terrestrial grass. *Aquaculture* 13: 45–53.
- Wise, R. G., 1990. The biology of three exotic freshwater fish species in Hamilton Lake. Unpublished M.Sc., University of Waikato, Hamilton: 104 pp.
- Wood, R. D. & R. Mason, 1977. Characeae of New Zealand. *N. Z. J. Bot.* 15: 87–180.