

# Herbivory on freshwater macrophytes

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## ABSTRACT

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Conventional wisdom holds that live macrophytes are rarely consumed and are functionally unimportant in aquatic food webs. With a review of the literature, I first demonstrate that macrophyte biomass, productivity, and species composition is often influenced by a variety of vertebrate and invertebrate grazers. Many grazers destroy much more macrophyte tissue than they eat. Contrary to conventional wisdom, live macrophytes are engaged in aquatic food webs, but the functional importance of grazing remains largely untested. Second, I evaluate the hypothesis that macrophytes are a poor quality food (low in protein). Nitrogen content (as a percentage of dry weight), as summarized from published literature, differs little among algae, emergent macrophytes, floating macrophytes, submersed macrophytes, trees, terrestrial forbs, and terrestrial grasses. Thus, nitrogen content could not be a reason to expect low herbivory on macrophytes. Third, I present previously unpublished data on the selectivity of crayfish grazing. A correlational analysis of the grazing hierarchy of crayfish and published hierarchies of other grazers (moose, carp, snails, and crayfish) suggest that herbivores have apparently similar selectivities among macrophyte species. Previously unpublished (for crayfish) and published proximate and mineral analyses of macrophytes eaten by grazers suggest no basis for selectivity by crayfish and other grazers, with the exception of a preference for moose for high sodium and protein. However, a correlational analysis of independently published grazer preferences and plant tissue phenolic and alkaloid concentrations suggests that phenolic, but not alkaloid, content is negatively related to grazing preference. Finally, I point out the need for unifying approaches in the study of freshwater herbivory. To understand the influence of herbivory (relative to other biotic and abiotic factors) on macrophyte populations and assemblages, extensive comparisons of grazing damage across environmental gradients and across macrophyte and grazer species must be made. Susceptibility to grazers must be evaluated in light of the contrasting life history strategies evident in different macrophytes. Reasonable starting points for general approaches to macrophyte–herbivore interactions may include the apparency and resource availability models developed for terrestrial plant–herbivore interactions. Given the apparently negative relationship between grazing preference and phenolic content of macrophytes, more investigation of the role of secondary compounds is necessary.

## INTRODUCTION

Shelford (1918) got 20th century aquatic ecologists off to a bad start regarding freshwater macrophytes when he wrote: “One could probably remove all the larger plants and substitute glass structures of the same form and sur-

face texture without greatly affecting the immediate food relations". Unfortunately, this opinion was published in a reference volume (Ward and Whipple, 1918) that was widely consulted until mid-century. A contemporaneous volume on aquatic plants (Arber, 1920) included only one tangential mention of grazing (p. 287), and did little to dispel the notion that live macrophytes were not engaged in food webs.

There was a countervailing tradition, however, exemplified by Welch in his first (1935) and second (1952) editions of 'Limnology'. Welch's opinion, seconded by Frohne (1956), was that "... studies made during recent years have shown conclusively that they [macrophytes] are a very significant element in the food chain; that a great variety of animals feed directly upon them; and that large quantities of these plants are often consumed (Welch, 1952, p. 305)." Fassett's (1940, pp. 343–358) 'A Manual of Aquatic Plants' included a richly referenced, 15 page appendix listing the use of many macrophyte species by many birds, mammals, and fish. In the same vein, Sculthorpe (1967) devoted a four page section (pp. 452–455) of his monograph on aquatic plants to grazing, including a table listing the importance of various macrophyte taxa to fish, birds, and mammals. The stupefyingly comprehensive review by Gaevskaya (1969) listed 620 species (259 genera, 85 families) of animals that eat live macrophytes (p. 236). The importance of live macrophyte consumption in the nutrition of many of these grazers was amply demonstrated through laboratory and field observations (Gaevskaya, 1969, Chap. VII). While many of the studies reviewed by Gaevskaya (1969) also suggested that grazing had a significant impact on macrophytes, the evidence on this point was largely qualitative and anecdotal (Gaevskaya, 1969, Chap. VIII).

Subsequently leading references supported the Shelfordian idea that few grazers eat live macrophytes and that herbivory results in an insignificant loss of biomass for macrophytes. Hutchinson (1975, pp. 545–546) argued that "the majority of the herbivorous invertebrates of freshwaters do not feed on higher plants but rather on ... algae, bacteria, and associated detritus". According to Wetzel (1975, p. 380; 1983, p. 543), "values of grazing loss ... usually range from about 0.5 to 8 per cent of the total [annual macrophyte production]", values to which Wetzel attributed no functional importance. The most recent reviews have continued this tradition: "living aquatic vascular macrophytes generally are not a major component of the diet of herbivores in lotic systems" (Gregory, 1983, p. 161). A recurrent theme in Polunin (1984) is that emergent macrophytes enter the food web only as detritus. Several authors (Hutchinson, 1975; Gregory, 1983; Lamberti and Moore, 1984) have even provided explanations for the supposed lack of herbivory on macrophytes (see Section "Should herbivores eat macrophytes?").

This Shelfordian conventional wisdom, however, ignores the contradictory evidence presented by Welch (1935, 1952), Gaevskaya (1969) and others.

Furthermore, it is based largely on a lack of investigation, not on a critical body of evidence that establishes the rarity or unimportance of grazing. While it may be true that a majority of herbivorous invertebrates eat periphyton (Hutchinson, 1975), many do eat macrophytes. More importantly, the supposed minority of grazers that eat macrophytes may be functionally important in food webs and nutrient fluxes, and they may have an appreciable impact on macrophytes (Carpenter and Lodge, 1986). Even if it is usually true that less than 10% of macrophyte production is consumed live (Wetzel, 1983), such a trophic link could be a significant one in community and ecosystem function (see Crawley, 1983, pp. 9–17).

I argue in this chapter that much recent work on macrophyte herbivory continues to cast doubt on the Shelfordian perspective, but that the state of our understanding regarding herbivory is still dismal. We need to redress the imbalance in recent ecological field experiments noted by Sih et al. (1985, p. 281): "... perhaps the most glaring gaps are the almost total lack of manipulations of herbivores in freshwater ...".

The macrophyte–grazer relationship is far too complex (Lodge et al., 1988) to be covered completely in this review. Therefore, I restrict my focus largely to direct interactions between grazer and macrophyte, and ignore the potentially important indirect links via epiphyton (see Brönmark, 1989; Sand-Jensen and Borum, 1991). I focus on naturally occurring macrophyte–grazer interactions, and therefore draw only tangentially on the extensive literature of applied biotic control of nuisance macrophytes (see Nichols, 1991). Some of the studies I review do focus on exotic plants and grazers, but not in contexts of deliberate human management. While estuarine and salt marsh vegetations are included, seagrasses are not (see review by Thayer et al., 1984).

I have four major goals. First, in Section "Do herbivores have an impact on macrophytes?", I review recent, mostly experimental, studies testing the impact of grazers on macrophyte biomass, productivity, and community structure to determine if grazing is inconsequential. Second, in Section "Should herbivores eat macrophytes?" I evaluate previously published hypotheses explaining the assumed lack of grazing on macrophytes. Third, in Section "Selective grazing on macrophytes", I report previously unpublished data on selective grazing by crayfish, compare grazing selectivity by different grazers, evaluate the basis for selectivity, and relate aquatic macrophyte–herbivore interactions to models of terrestrial herbivory. Finally, in Section "Conclusions and future research", I make suggestions for future research.

This is the first review of the freshwater macrophyte–grazer interaction since Gaevskaya (1969), with the exception of several recent, more limited or tangential reviews: Brinson et al. (1981) on freshwater wetlands; Gregory (1983) on grazing on stream algae; Lamberti and Moore (1984) on insect grazing on algae; Odum (1988) on marshes; Carpenter and Lodge (1986) on submersed

macrophytes and ecosystem processes; Stevenson (1988) on freshwater, estuarine, marine grass beds.

#### DO HERBIVORES HAVE AN IMPACT ON MACROPHYTES?

Submersed, emergent, and floating-leaved macrophytes are all subject to substantial grazing losses, which often alter relative abundance of macrophyte species, and sometimes affect plant productivity (Table 1). It is impossible to generalize from the published literature on the importance of grazing to macrophytes or on the relative importance of different grazers because negative results are rarely published. However, the studies cited (Table 1) indicate that it is probably not a rare occurrence for grazers to have substantial effects on macrophytes. The prominence in the literature of large, easily observed grazers (crayfish, waterfowl, and mammals) may reflect a disproportionate impact by those groups or it might reflect the difficulty in testing the impact of small, often inconspicuous, organisms like insect larvae (e.g. Soszka, 1975; Urban, 1975). Several mostly qualitative studies suggest that many large and small grazers may affect macrophytes: manatees (Campbell and Irvine, 1977), waterfowl (T.J. Smith, 1982), fish (Prejs, 1978, 1984; Prejs and Jackowska, 1978; Brabrand, 1985; Araujo-Lima et al., 1986), isopods (Marcus et al., 1978), and insects (Berg, 1949; McGaha, 1952; Frohne, 1956; Fiance and Moeller, 1977). Below, I consider in detail the available quantitative studies of grazer impact on macrophyte biomass, productivity, and relative species abundance.

#### *Grazer impact on macrophyte biomass*

Reductions of macrophyte root or shoot biomass by grazers range up to 100%, with reductions exceeding 50% reported for crayfish (Abrahamsson, 1966; Dean, 1969; Lodge and Lorman, 1987; Feminella and Resh, 1989), insect larvae (Painter and McCabe, 1988), snails (Bertness, 1984), fish (Hansson et al., 1987), and waterfowl (Kiørboe, 1980; T.J. Smith and Odum, 1981; T.J. Smith, 1982; Carter and Rybicki, 1985; Bazely and Jeffries, 1986) (Table 1). Submersed, emergent, and floating-leaved species sustain substantial damage, but emergent macrophytes appear to be less susceptible to damage by invertebrates than are submersed and floating-leaved forms (Table 1; see later section on relative abundance of macrophytes).

Waterfowl influence submersed and emergent plants locally and seasonally; snow geese substantially reduce macrophyte biomass on their summer breeding grounds (Bazely and Jeffries, 1986), at migration stop-over sites (Giroux and Bédard, 1987), and on their wintering grounds (T.J. Smith and Odum, 1981; T.J. Smith, 1982). Less gregarious waterfowl, e.g. breeding ducks and swans during the macrophyte growing season, also substantially reduce plants,

perhaps over larger areas than colonially nesting geese (Anderson and Low, 1976; Jupp and Spence, 1977; Smith and Kadlec, 1985) (Table 1).

For many grazers (Table 1), reductions in plant biomass result from non-consumptive destruction, as well as from consumption. For example, shoots of submersed macrophytes clipped near the sediments by crayfish may float away (Lodge and Lorman, 1987). In laboratory experiments, non-consumptive destruction by *Orconectes rusticus* (Girard) comprised 30–95% of cut macrophyte biomass (with the percentage differing among macrophyte species) (D.M. Lodge, unpublished data, 1990). An unknown fraction of the biomass destruction by muskrats, coypu, and some waterfowl goes into nest building or becomes waste (Anderson and Low, 1976; L.M. Smith and Kadlec, 1985). Similar, non-consumptive destruction constitutes the 'greenfall' of terrestrial forests (Crawley, 1983, p. 47; Schowalter et al., 1986, pp. 184–185; Risley and Crossley, 1988).

Other, more subtle, effects may lead to even greater losses of macrophyte biomass than are indicated by the data (Table 1). A large part of the impact of *Littorina* on *Spartina* is attributable to reduced sediment accumulation as a result of snail grazing (Bertness, 1984). Even a small amount of tissue consumption may result in considerably greater plant tissue death from disease (Rogers and Breen, 1983) and fragmentation (van der Velde et al., 1982; Pieczynska, 1986). If young tissue is preferentially grazed, as is the case for many terrestrial herbivores (Coley, 1983), grazing could result in a large negative impact on the plant even if only a small amount of tissue is removed. Thus, through a variety of mechanisms, small amounts of grazing (such as found in some of the studies listed in Table 1) may produce large decreases in future plant biomass.

On the other hand, consumption of macrophyte seeds by fish and duck grazers can have positive as well as negative effects. Many seeds are digested, but those that are not have improved germination (Agami and Waisel, 1986a, 1988). The population impact of such consumption of seeds and other overwintering bodies like *Vallisneria* turions by waterfowl (Donnermeyer and Smart, 1985) is unknown.

In summary, the quantitative literature (Table 1) demonstrates that at least some populations of all growth forms of macrophytes are subject to heavy losses from a variety of grazers. Even when direct losses are small, additional macrophyte biomass may be lost via tissue fragmentation, disease, and through reduction in future growth via destruction of young tissue.

#### *Grazer impact on primary production*

In three of six studies (Table 1), grazers reduced production of emergent plant shoots (L.M. Smith and Kadlec, 1985; Giroux and Bédard, 1987) and roots (T.J. Smith and Odum, 1981; Giroux and Bédard, 1987), whereas in

TABLE 1

Results of selected studies on grazer-induced changes of biomass (B), community primary production (PP), and relative species abundance (RA) of submersed, emergent and floating-leaved macrophytes. Types of studies were natural field experiments (NFE, in which a macrophyte response to a natural change in grazer abundance was observed), deliberate field experiments (DFE, in which grazer abundance was manipulated by the author), laboratory experiments (LE), and non-experimental field observations (FO). Grazer impact was calculated as:  $I = \frac{\text{parameter in the absence of grazer} - \text{parameter in the presence of grazer}}{\text{parameter in the absence of grazer}}$  [parameter in the absence of grazer = parameter in the presence of grazer] / (parameter in the absence of grazer)  $\times 100$ . Thus, an impact in excess of 0 indicates a reduction in the presence of the grazer, while an impact of less than 0 indicates enhancement by the grazer. Grazer impact refers to above-ground parameters, except where \* indicates below-ground parameters were measured. ? indicates response not reported; Y indicates grazer changed RA; N/A indicates response not applicable. Except for the experiment of Flint and Goldman (1975), in which all treatment densities of crayfish were artificially high (cf. Flint and Goldman, 1977), abundance of grazers in all studies was within the natural range of abundance

Grazers	Macrophyte community	Type of study	Grazer impact		Ref.
			B (%)	PP (%)	
Submersed macrophytes, invertebrate grazers					
<i>Astiacus</i> (Decapoda)	$\geq 6$ spp.	NFE	~100	?	Y Abrahamsson, 1966
<i>Orconectes</i> (Decapoda)	~14 spp.	NFE	50-90	?	Y Dean, 1969
<i>Pacifastacus</i> (Decapoda)	<i>Myriophyllum</i>	DFE	?	-/+	N/A Flint and Goldman, 1975
<i>Orconectes</i>	1-7 spp.	DFE	0-100	?	Y Lodge and Lorman, 1987
<i>Procambarus</i> (Decapoda)	<i>Potamogeton</i>	NFE,DFE	100	?	Y Feminella and Resh, 1989
Lepidoptera, etc.	4 spp.	FO	3-100 <sup>1</sup>	?	? Sozka, 1975
Insect larvae	3 spp.	FO	0-16 <sup>2</sup>	?	? Urban, 1975
Lepidoptera, Coleoptera	<i>Myriophyllum</i>	LE,NFE	95	?	N/A Painter and McCabe, 1988
Gastropoda <sup>3</sup>	9 spp.	LE,FO,DFE	33	?	Y Sheldon, 1987

Submersed macrophytes, vertebrate grazers								
Waterfowl (Aves)	<i>Potamogeton</i>	DFE	40	?	?	Anderson and Low, 1976		
Waterfowl	<i>Potamogeton</i>	DFE	20-30	?	?	Jupp and Spence, 1977		
Waterfowl	4 spp.	FO,DFE	50	?	?	Kjørboe, 1980		
Waterfowl, etc.	<i>Vallisneria</i>	DFE	0-100	?	N/A	Carter and Rybicki, 1985		
<i>Rutilus</i> , <i>Scardinius</i> (Osteichthyes)	6 spp.	LE,FO	0-34	?	?	Prejs, 1984		
<i>Scardinius</i>	<i>Elodea</i> , <i>Chara</i>	LE,DFE	72	?	?	Hansson et al., 1987		
Emergent macrophytes, invertebrate grazers								
<i>Altica</i> (Coleoptera)	<i>Ludwigia</i>	FO	5-9	?	?	Scott and Haskins, 1987		
<i>Liitorina</i> (Gastropoda)	<i>Spartina</i>	DFE	75	?	N/A	Bertness, 1984		
Emergent macrophytes, vertebrate grazers								
<i>Ondatra</i> (Mammalia)	<i>Typha</i> , <i>Phragmites</i>	FO	5-10	?	?	Pelikán et al., 1971		
<i>Myocaster</i> (Mammalia)	<i>Scirpus</i> , <i>Phragmites</i>	DFE	?	?	Y	Bassett, 1980		
Waterfowl, <i>Ondatra</i>	<i>Scirpus</i> , <i>Typha</i>	DFE	14-36	15-55	?	L.M. Smith and Kadlec, 1985		
<i>Anser</i> (Aves)	3 spp.	DFE	58*	60-100*	Y	T.J. Smith and Odum, 1981; T.J. Smith, 1982		
<i>Anser</i>	> 18 spp.	DFE	67-83	-35 to -77	Y	Bazely and Jeffries, 1986; Cargill and Jeffries, 1984		
<i>Anser</i>	> 5 spp.	DFE	?	28	Y	Giroux and Bédard, 1987		
Floating-leaved macrophytes, invertebrate and vertebrate grazers								
<i>Pyrithalia</i> (Coleoptera)	<i>Nuphar</i>	FO,DFE	7-27 <sup>1</sup>	+	N/A	Wallace and O'Hop, 1985		
Invertebrates, waterfowl	<i>Nymphoides</i>	FO	10-22 <sup>1</sup>	?	N/A	Van der Velde et al., 1982		

<sup>1</sup>Leaf area.<sup>2</sup>Stem biomass.<sup>3</sup>See text.

two studies production of emergent shoots (Cargill and Jeffries, 1984) and floating leaves (Wallace and O'Hop, 1985) was enhanced. Where above-ground production was enhanced, underground biomass of the floating-leaved plants was not measured (Wallace and O'Hop, 1985), but was unaffected in the emergent plants (Cargill and Jeffries, 1984). In the one study in which multiple grazer densities were used, production of a submersed macrophyte was apparently enhanced at low grazer density and reduced at high grazer density (Flint and Goldman, 1975).

However, the density-dependent response of productivity reported by Flint and Goldman (1975) is particularly difficult to evaluate. For the caging experiment with *Pacifastacus* in a *Myriophyllum* bed in Lake Tahoe, Flint and Goldman (1975) did not report the timing or duration of the apparently unreplicated experiment, and analyzed the experiment in a way that ignored the pairing of inclusion and exclusion cages (which presumably was designed to control for the patchiness of macrophyte biomass). Apparently on the basis of one low crayfish density cage that had substantially higher final plant biomass than the mean final biomass of all exclusion cages (fig. 5 in Flint and Goldman, 1975), the authors concluded: "these results imply that the lower biomasses of crayfish actually enhanced the growth of the aquatic plants ..." (p. 939). This interpretation has been widely cited, but is not strongly supported by the data. In addition, the mechanism of enhanced productivity proposed by Flint and Goldman (1975) — nutrient regeneration by crayfish — is unlikely to work for rooted submersed macrophytes (see below).

#### *Mechanisms of productivity enhancement by grazers*

Compensatory growth commonly occurs in terrestrial plants attacked by herbivores, but is strongly dependent on a number of biotic and abiotic factors (Crawley, 1983, pp. 86–110; McNaughton, 1986 and papers cited therein). In at least one terrestrial case, productivity of both shoots and roots of individual plants is enhanced by mammalian grazing (Paige and Whitham, 1987). More careful study of the macrophyte–grazer interaction is necessary to see under what circumstances compensatory production occurs.

Potential mechanisms of grazer enhancement of whole-plant primary productivity include five mechanisms ((i)–(v)) operating for individual plant species and one (vi) operating at the community level: (i) nutrient regeneration by grazers of phytoplankton (Sterner, 1986; Bergquist and Carpenter, 1986), periphyton (Flint and Goldman, 1975; Lamberti and Moore, 1984), and terrestrial vegetation (McNaughton, 1979; Crawley, 1983); (ii) reduction in self-shading through biomass removal by grazers of periphyton (Lamberti and Moore, 1984) and terrestrial vegetation (Crawley, 1983; McNaughton, 1985); (iii) removal of older, less productive tissue by grazers of periphyton (Lamberti and Moore, 1984) and terrestrial vegetation (Crawley, 1983; McNaughton, 1985); (iv) stimulation of terrestrial plant growth

by grazer saliva (see references in McNaughton, 1986); (v) increased efficiency of water use by grazed (low biomass) terrestrial plant stands (McNaughton, 1985); (vi) at the plant community level, grazing may alter competitive interactions, and allow a more productive species to replace a less productive one (Crawley, 1983; McNaughton, 1986). This last mechanism operates among grazed phytoplankton (Bergquist and Carpenter, 1986; Carpenter et al., 1987).

Of these mechanisms, increased efficiency of water use (v) is unlikely to be important for any macrophyte, and certainly not for submersed macrophytes. Stimulation via grazer hormones (iv) could operate for above-water grazing, but, because of rapid diffusion in water, probably not for any submersed macrophyte. Decreased shading (ii) and removal of senescent tissue (iii) could operate for any macrophyte growth form, but neither has been documented for any macrophyte.

The two mechanisms of productivity enhancement that have been documented for aquatic macrophytes are nutrient regeneration (i) via goose feces for emergent macrophytes (Bazely and Jeffries, 1985), and species replacements (vi) (Bazely and Jeffries, 1985) that in one case (Giroux and Bédard, 1987) led to increased production of some species while community production declined with grazing. Species replacements and concomitant changes in productivity may occur for submersed species (see Agami and Waisel, 1986b), but nutrient regeneration is unlikely to operate for submersed species. Fecal nutrients are likely to be rapidly dissolved and transported by water. Even if nutrients from feces or liquid waste remained close to the grazed plant, they would probably be lost to the macrophyte. Because the vast majority of macrophytes have limited capability of nutrient uptake through shoots (Barko and Smart, 1981; C.S. Smith and Adams, 1986; Chambers et al., 1989), excreta would likely be taken up by algae instead of macrophytes (cf. Miura et al., 1978).

#### *Grazer impact on relative abundance of macrophyte species*

Grazing altered the relative abundance of macrophyte species in every study in which this response was monitored (Table 1). In some cases, responses in assemblage structure were not monitored, but changes were so striking that authors reported qualitative results in text. For example, crayfish reduced submersed macrophytes, but did not have any noticeable impact on several species of emergent plants (Abrahamsson, 1966; Dean, 1969; Magnuson et al., 1975; Feminella and Resh, 1989). However, emergent species are readily consumed by other invertebrates, mammals, and geese (see references in Table 1). Mechanical attributes and other macrophyte characteristics that may effect grazer preference have, in general, not been tested (see Section "Selective grazing on macrophytes").

In the two studies designed to quantify changes in relative abundance among submersed macrophyte species (Table 1), assemblage structure changed dramatically (Sheldon, 1987; Lodge and Lorman, 1987). For snail grazers, Sheldon (1987) found that in a field experiment and across nine Minnesota lakes, plant species composition was related to total snail abundance. Furthermore, the most abundant plant occurring with high snail densities (*Ceratophyllum* sp.) was the species that the snail *Physa* most preferred to inhabit in laboratory experiments. However, as pointed out by Brönmark (1990) and acknowledged by Sheldon (1990), this study did not document the occurrence of other macrophyte grazers. Given that freshwater snails primarily graze algae (Lodge, 1985, 1986), the patterns of macrophyte occurrence documented by Sheldon (1987) may have resulted from non-molluscan grazers.

Lodge and Lorman (1987) suggested that changes in assemblage structure of macrophytes resulted not only from selective consumption by crayfish, but also from non-consumptive destruction that is partly a function of plant architecture. Their results suggested, for example, that single-stemmed species were more vulnerable than rosulate growth forms because an entire single-stemmed plant can be destroyed with one bite from a benthic grazer. In contrast, a single bite of a rosulate macrophyte destroys only a small fraction of the plant and the basal meristem remains intact (Lodge and Lorman, 1987).

A similar mechanism was proposed by Bazely and Jeffries (1986) to explain the different impact goose grazing has on different emergent plant species. In the presence of geese, dicotyledonous species declined relative to graminoid species because destruction of the dicot's apical meristems resulted in little regrowth. In contrast, the basal meristems of graminoid species produced new growth after grazing (Bazely and Jeffries, 1986). Additional mechanisms of grazer impact on macrophyte species composition, including determinants of consumption preferences require much greater investigation (see Section "Selective grazing on macrophytes").

#### SHOULD HERBIVORES EAT MACROPHYTES?

In spite of the mounting evidence (reviewed above) that herbivores have large effects on macrophyte biomass, productivity, and species composition, many recent authors have continued the Shelfordian tradition. Some who have assumed that grazing on macrophytes is unimportant have offered explanations for the lack of grazing. The argument given the most credence (Hutchinson, 1975, p. 547–548) is that of the foods available to aquatic herbivores (periphyton and macrophytes), periphyton is a higher quality food and is therefore preferred.

McMahon et al. (1974) measured food quality as the ratio of carbon to nitrogen, and argued that a ratio of less than 17 is required by herbivores. Gregory (1983, pp. 161–162) adopted this argument, but added that "tough

cell walls” and “lignified structures” may also decrease the usefulness of macrophytes (relative to algae) as food. Using a small number of literature values, Lamberti and Moore (1984, table 7.3) compared the tissue content (protein, lipid, carbohydrate, cellulose and lignin, and ash) of bacteria, algae, vascular plants, and detritus. They concluded that aquatic grazers prefer bacteria and microscopic algae because in general these groups have higher protein and lower cellulose and lignin and ash contents. However, the small number of data used in the analysis makes those conclusions tentative.

While algae may have higher ‘food quality’ than macrophytes, the framing of the food quality argument is too limited from an evolutionary point of view. Many species (terrestrial and aquatic), especially many well known terrestrial grazers, are adapted to feed on low quality plants. Evolution has constraints (Gould and Lewontin, 1979), but it is unlikely that a feeding niche as large as vascular macrophytes remains open. For the food quality argument to be plausible then, vascular macrophytes should have tissue quality much lower than any other group of plants. I reviewed the literature to test this possibility with regard to protein content.

### *Nitrogen content of terrestrial and aquatic plants*

Because few measurements of macrophyte carbon content are available, I could not compare plant groups on the basis of the carbon to nitrogen ratio. For most authors, though, the crux of the food quality argument is that nitrogen (protein) is limiting for herbivores (Mattson, 1980). Because nitrogen content is often measured, I could compare nitrogen content across aquatic and terrestrial plants (Fig. 1).

Contrary to earlier statements, little difference exists in nitrogen content between algae (Fig. 1A) and vascular macrophytes (Fig. 1B–1D). Among aquatic plants, floating plants (Fig. 1C) appear to have higher nitrogen content than other aquatic groups (Fig. 1A, 1B and 1D). These patterns must be interpreted with caution, however, because tissue content depends on plant parts and on season (e.g. Boyd, 1968, 1971; Riemer and Toth, 1969, 1970; Mochacka-Lawacz, 1974; Best, 1977; Carpenter and Adams, 1977; Moeller, 1978; Brock et al., 1983; Donnermeyer and Smart, 1985; Twilley et al., 1985; Melzer and Kaiser, 1986; Boston and Adams, 1987), on intensity of grazing (Cargill and Jeffries, 1984), and on available nutrients (Gerloff and Kromholz, 1966; Barko and Smart, 1986). For example, the ranges of nitrogen content reported for the three most often analyzed submersed species (*Vallisneria americana* Michx., 1.6–4.1%; *Elodea canadensis* Michx., 1.4–5.0%; *Ceratophyllum demersum* L., 1.3–2.7%) encompass most of the range of mean values plotted for all plant types (Fig. 1). If the plotted values (on Fig. 1) are

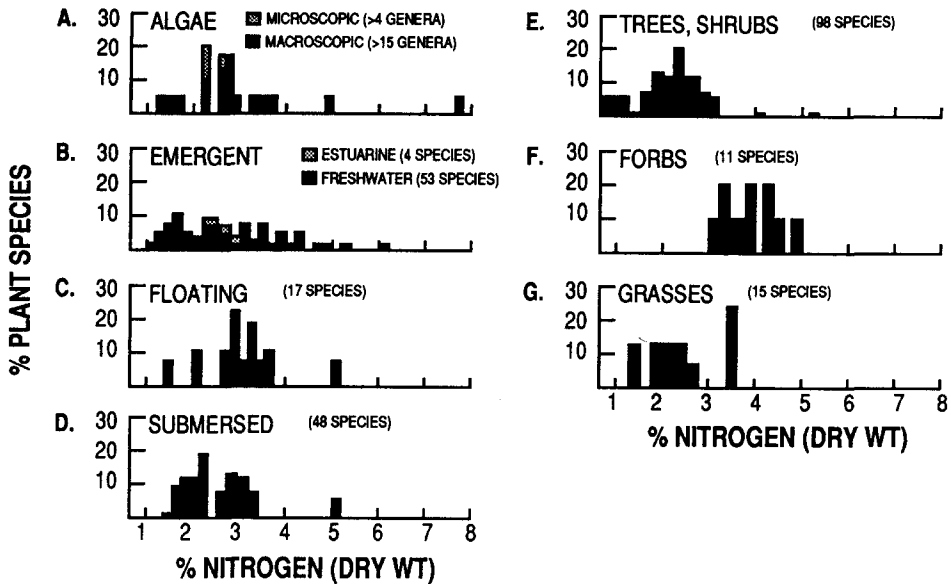


Fig. 1. Mean nitrogen content (as a percentage of plant dry weight) in: (A) freshwater algae, (B) freshwater and estuarine emergent macrophytes, (C) freshwater floating or floating-leaved macrophytes, (D) freshwater submersed macrophytes, and (E-G) non-cultivated terrestrial plants. One mean is plotted for each plant species. For studies reporting temporal patterns of  $N$ , the mean of the temporal data was used. For studies reporting on multiple sites, a mean across sites is plotted. Values for emergent plants, floating plants, and trees and shrubs are for leaves. Means for submersed aquatic plants include combinations of values for whole plants (roots and shoots), above-ground biomass, 'shoots', and leaves. Similarly, means for forbs and grasses include values for leaves and shoots. Data sources are indicated with the relevant letter (A-G) at the end of each source entry in the references.

meaningful, though, grazers could not prefer algae to macrophytes on the basis of nitrogen content.

The potential value of macrophytes as herbivore food is further emphasized in comparison with terrestrial vegetation (Figs. 1E-1G). The nitrogen content of tree and shrub leaves (Fig. 1E) and grasses (Fig. 1G), many of which are much consumed by grazers, is similar to or lower than that of macrophytes and algae (Fig. 1A-1D). In contrast, terrestrial forbs (Fig. 1F) appear to have the highest nitrogen content of any plant group, although sample numbers are low for forbs (and also for grasses). The lack of difference in nitrogen content between algae and macrophytes and the extensive consumption by grazers of tree and shrub leaves with lower nitrogen contents than many macrophytes (see e.g. Coley, 1983) refute the standard food quality argument for why grazers should not eat aquatic macrophytes.

In summary, Table 1 demonstrates that many grazers have substantial effects on many aquatic macrophytes. Figure 1 shows that this is not surprising, because macrophytes have as high or higher concentrations of nitrogen, the nutrient most limiting to herbivores, as algae and tree leaves. In general, then, evolution has produced grazers for most plants, even those with low tissue nitrogen. Within a group of food plants to which a grazer is adapted, however, grazers do graze preferentially, as suggested by the impacts of grazers on relative abundance of species (see Table 1). A grazer might, for example, choose plants with high nitrogen content. In the next section, I review the literature and present previously unpublished data on selective grazing, and explore the potential cues for grazer selectivity.

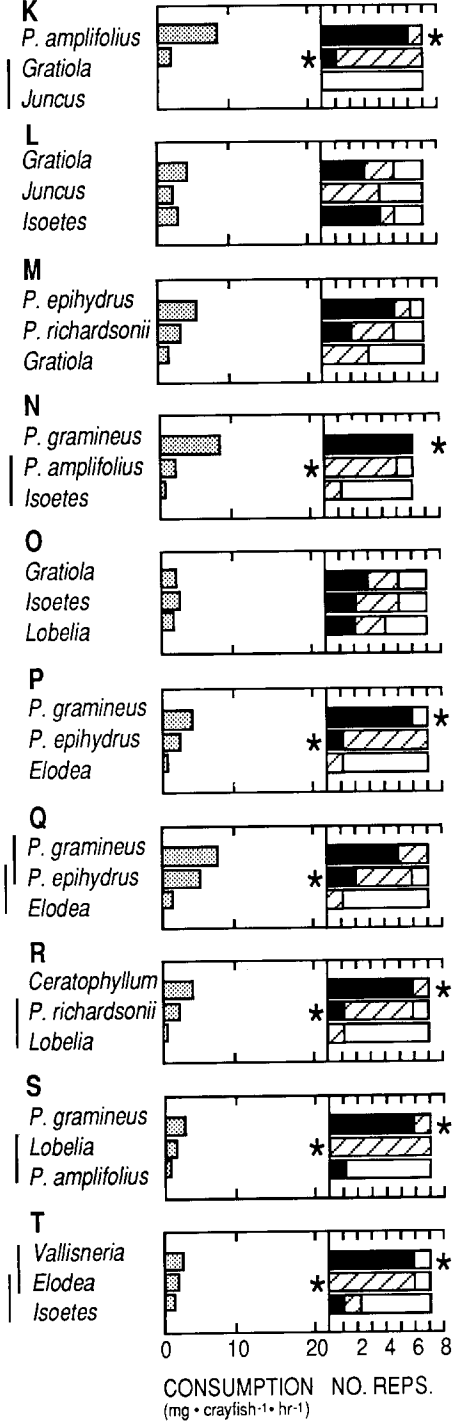
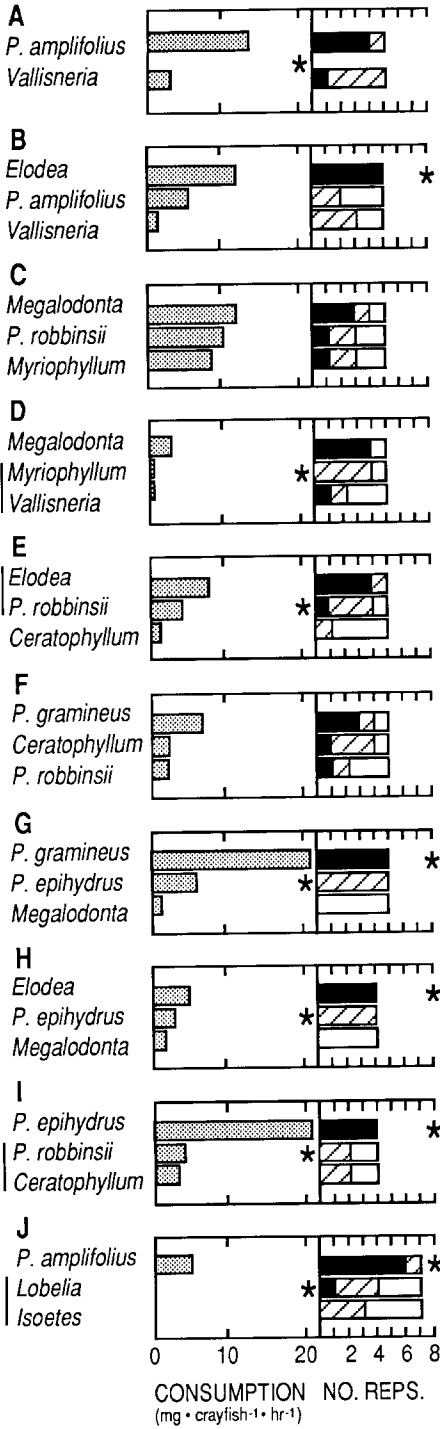
#### SELECTIVE GRAZING ON MACROPHYTES

The high frequency of grazer-induced changes in relative abundance of macrophyte species (see Table 1) suggests that many consumers graze selectively. In laboratory and field tests of feeding preferences, a variety of macrophyte grazers have exhibited strong selectivity: moose, among 19 submersed and emergent species (Fraser et al., 1984); grass carp, among nine submersed species (Wiley et al., 1986) and 12 floating and submersed species (Bowers et al., 1987); snails, among 14 submersed species (Sheldon, 1987; but see Brönmark, 1990 and Sheldon, 1990); crayfish, among three submersed species (Seroll and Coler, 1975).

Prompted by earlier field work on crayfish grazing (see Table 1), I tested feeding preference among 14 submersed macrophyte species by the crayfish *Orconectes rusticus* (Fig. 2). These results defined a grazing preference hierarchy for the crayfish (Table 2). Thus, at least moose, carp, and crayfish feed selectively. The next two sections explore whether preferences are similar across grazers, and what the basis for preference may be.

#### *Do different grazers exhibit similar preferences?*

Olsen (1991) found experimentally that grazing preferences (among four macrophyte species) of two other *Orconectes* crayfish were the same as for *O. rusticus*. To test the similarity of preference hierarchies of moose, carp, and crayfish, I calculated rank correlations, comparing hierarchies two at a time (Table 3). The power of every comparison was low because the number of common species was low, and no correlation was significant. However, a disproportionate number of correlation coefficients was positive ( $P < 0.04$ ), suggesting that the preferences of these very different grazers were similar. One might, therefore, expect the basis for selection to be similar.



*Basis of grazer selection among macrophytes*

To find correlates of plant preferences exhibited by *O. rusticus*, I analyzed 19 tissue constituents of the 14 plant species in the crayfish grazing hierarchy (Table 4). My expectations included that preferred plants would have higher protein and digestible fractions than unpreferred plants, and that unpreferred plants would have higher cellulose and lignin concentrations.

Concentrations of all constituents were within previously reported ranges (Hutchinson, 1975), but the predicted patterns did not occur (Table 4). None of the mineral or nutritional variables differed significantly among preference categories, a result similar to that for European lake fishes such as roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.) (Prejs, 1984), grass carp (*Ctenopharyngodon idella* Val.) (Wiley et al., 1986), and marine macroalgae and their grazers (Lubchenco and Gaines, 1981). For moose, however, concentrations of sodium, phosphorus, and protein were higher in preferred than in unpreferred macrophyte species (Fraser et al., 1984). A sodium-based preference is expected for moose, but not for purely aquatic grazers, because of the low concentrations of sodium in terrestrial browse relative to aquatic plants (Hutchinson, 1975; Fraser et al., 1984). The biological

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Fig. 2. Results of 20 replicated laboratory trials (A–T) on consumption rate by the crayfish *Orconectes rusticus* of 14 species of submersed macrophytes (see Table 2 for full species names), presented two or three at a time. Crayfish were collected from Sparkling Lake (Vilas County, WI), held in flow-through aquaria, fed ad libitum, and used only once. Macrophyte shoots were collected from two Vilas County lakes, Sparkling Lake (*Potamogeton gramineus*, *Lobelia*, *Isaetes*, *Gratiola*, and *Juncus*) and Trout Lake (all other species), held in aquaria or refrigerated, and used within 1–3 weeks of collection. Each trial consisted of four to seven tanks in which crayfish were presented with thoroughly rinsed macrophytes and three to five control tanks in which only macrophytes were present. Each trial presented one to three starved (24 h) adult (carapace length range 20–51 mm) male or male and female crayfish with a superabundance (less than or equal to 33% consumed during trial; initial biomass, 2–10 g, with amounts of all species equal within a trial) of each macrophyte species in a rectangular fiber-glass tank (78 cm × 38 cm) filled to 4.5 cm depth with 18–22°C water. Photoperiod was natural, and each trial lasted 66–123 h. Because neither total consumption nor preference differed between crayfish genders, male and female results were pooled. Macrophyte mass (patted dry) was measured in each tank at the beginning and conclusion (including any fragments) of each experiment. Change in macrophyte biomass in tanks with crayfish was corrected for the mean change in macrophyte biomass in control tanks. Results were analyzed in two ways, and gave similar results: (i) on the left side of each figure, by ANOVA (\* =  $P < 0.05$ ) followed by Duncan's test (vertical bars to left of species names link species for which consumption rates did not differ); (ii) on the right side of each figure, by calculating the probability that by chance alone any plant would be consumed at the highest rate in a number of replicates greater than or equal to the number of replicates in which the plant was eaten the most. The latter calculation of probability was made for the top ranking macrophyte only in each trial (\* $P < 0.05$ ). On right-hand side of figures, the filled bar indicates the species consumed most, the hatched bar indicates the consumption ranked second, and the open bar indicates the consumption ranked third.

TABLE 2

Rank order of grazing preference by the crayfish *Orconectes rusticus* among 14 species of submersed macrophytes (nomenclature from Fassett, 1957) common in northern Wisconsin lakes, as determined by laboratory choice trials (see Fig. 2). Overall order was determined by transitivity of trial results (whether results were statistically significant or not). Where two or more trials gave inconsistent, non-significant ranking, species are listed in the same line in alphabetical order. In only two cases did trials give inconsistent, significant rankings: Trials H and P for *Potamogeton epihydrus* and *Elodea*, and Trials B and T for *Vallisneria* and *Elodea* (see Fig. 2). *Potamogeton epihydrus* and *Elodea* are therefore listed together. For *Vallisneria* and *Elodea*, the results of Trial B were given priority because other, unpublished experiments (D.M. Lodge, 1990) support a generally higher ranking for *Elodea*. As indicated by the superscripts, the Intermediate and Unpreferred groupings consist of species among which no statistical differences exist (neither statistical method employed detected a difference; see Fig. 2). The Preferred group is a more arbitrary grouping

## Preferred

*Potamogeton gramineus* L.

<sup>a</sup>*Elodea canadensis* Michx., *Potamogeton epihydrus* Raf.

<sup>a,b</sup>*Potamogeton amplifolius* Tuckerm.

<sup>b</sup>*Megalodonta beckii* (Torr.) Greene

## Intermediate

<sup>c</sup>*Potamogeton robbinsii* Oakes

<sup>c</sup>*Ceratophyllum demersum* L.

<sup>c</sup>*Myriophyllum exalbescens* Fern.

<sup>c</sup>*Vallisneria americana* Michx.

## Unpreferred

<sup>d</sup>*Potamogeton richardsonii* (A. Benn.) Rydb.

<sup>d</sup>*Gratiola lutea* Raf., *Isoetes* sp., *Lobelia dortmanna* L.

<sup>d</sup>*Juncus pelocarpus* E. Meyer forma *submersus* Fassett

TABLE 3

Comparison of grazing preference hierarchies for five grazers of aquatic macrophytes: two crayfish, *Orconectes rusticus* (O.r.) and *Orconectes immunis* (O.i.); one snail *Physa gyrina* (P.g.); grass carp *Ctenopharyngodon idella* (C.i.); moose, *Alces alces* (A.a.). Values in matrix are Spearman rank correlation coefficients, *N* is given in parentheses. For all comparisons, *N* is low (2–7), and none of the correlations are significant. However, 11 of the 14 correlations are positive. Based on the binomial distribution, with an equal chance of positive and negative correlation, this outcome has a probability of occurring by chance alone of 0.04

	O.i.	P.g.	C.i.	C.i.	A.a.	Ref.
O.r.	0.88(3)	-0.32(7)	0.50(3)	0.50(3)	0.90(5)	This paper
O.i.	-	0.13(3)	0.50(2)	0.13(3)	(0)	Seroll and Coler, 1975
P.g.	-	-	0.33(7)	0.73(6)	0.50(3)	Sheldon, 1987, but see Brönmark, 1990 and Sheldon, 1990
C.i.	-	-	-	0.68(5)	-1.00(2)	Wiley et al., 1986
C.i.	-	-	-	-	-0.50(3)	Bowers et al., 1987
A.a.	-	-	-	-	-	Fraser et al., 1984

TABLE 4

Mean concentration of tissue constituents in crayfish preference groups of submersed macrophytes (see Table 2). Analyses were conducted with standard van Soest (organic), Kjeldahl, and emission spectrophotometric (inorganic) methods on dried (60°C), ground samples (each sample consisting of several shoots) collected in Trout and Sparkling Lakes (Vilas County, WI) in late August 1984. *P*-values summarize the results of ANOVA (on log-transformed concentrations) comparing preference groups. Using  $\alpha=0.003$  ( $\alpha=0.05$  corrected for 19 comparisons), none of the tissue constituents differed significantly among preference groups

Tissue constituent (% dry matter)	Macrophyte preference categories			<i>P</i>
	Preferred ( <i>N</i> =5)	Intermed. ( <i>N</i> =4)	Unpreferred ( <i>N</i> =5)	
Crude protein	12.3	11.5	11.4	0.75
Digestible fraction	0.413	0.413	0.450	0.96
Cellulose	29.7	22.8	22.9	0.18
Hemicellulose	13.1	21.6	16.8	0.43
Lignin	14.0	12.6	9.1	0.41
Ash	0.84	0.88	3.08	0.17
P	0.22	0.28	0.19	0.32
K	2.87	2.52	2.12	0.46
Ca	2.31	1.46	0.89	0.07
Mg	0.26	0.41	0.31	0.33
S	0.35	0.25	0.33	0.49
B	0.0016	0.0016	0.0019	0.69
Zn	0.0047	0.0050	0.0048	0.92
Mn	0.047	0.088	0.089	0.40
Cu	0.00030	0.00029	0.00086	0.01
Fe	0.28	0.33	1.26	0.11
Al	0.013	0.007	0.037	0.08
Na	0.42	0.83	0.59	0.25
NO <sub>3</sub> -N	0.0024	0.0018	0.0134	0.03

significance of the differences in phosphorus concentration are unclear, whereas the apparent preference for high protein plant material is consistent with the general nitrogen limitation of grazers (Mattson, 1980).

With the rare exception of protein, commonly measured tissue characteristics and grazer preference are uncorrelated. Other plant characteristics, e.g. toughness and secondary compounds, must contribute strongly to grazer selectivity.

Several types of physical defenses against herbivory have been studied in terrestrial plants, including leaf toughness, hairs, and spines (Howe and Westley, 1988). Yet aquatic species do not exhibit the same range of these characters, and when they have been quantified in aquatic plants (e.g. leaf toughness in Prejs, 1984), they do not explain grazer preference.

Chemical defenses are widespread in terrestrial plants (Rosenthal and Janzen, 1979; Harborne, 1988; Howe and Westley, 1988), but authoritative re-

views of aquatic macrophyte ecology (McClure, 1970; Hutchinson, 1975, pp. 359–369) have held that most aquatic plants do not contain active concentrations of secondary compounds. Suggestions to the contrary (Otto and Svensson, 1981; Otto, 1983) are not supported by measurements of tissue chemistry.

Recent studies, however, do suggest that many aquatic macrophytes, like terrestrial plants, and marine macroalgae (Hay and Fenical, 1988), have secondary compounds that may reduce grazing: alkaloids (Su et al., 1973; Ostrofsky and Zettler, 1986); flavanoids, steroids, and saponins (Su et al., 1973); phenolics, including tannins (Su et al., 1973; Planas et al., 1981; Buchsbaum et al., 1984a,b; Kerfoot, 1988, 1989); glucosinolates (Newman et al., 1990). In some cases, the concentrations of these compounds have not been measured (Su et al., 1973) or have been low (Ostrofsky and Zettler, 1986). In other cases, the deterrent effect on grazers of natural concentrations of secondary compounds has been experimentally verified. For example, phenolic content contributes to plant selection by geese (Buchsbaum et al., 1984a,b) and water lily beetles (Kerfoot, 1988), and glucosinolates cause amphipods to prefer senescent over green water cress (Newman et al., 1990).

To determine whether concentrations of phenolics or alkaloids (the two groups for which quantitative surveys are available) are related to preference by grazers among species of submersed macrophytes, I compared the available preference ranks for grazers (reviewed above) with phenolic and alkaloid content measured by other authors (Table 5). Because such comparisons may clearly be confounded by macrophyte source and time of collection) both of which affect tissue chemistry), lack of correlations would not mean much. However, the high proportion of negative relationships between plant preference and phenolic content ( $P < 0.03$ ) suggests that phenolics do negatively affect plant choice by a diversity of grazers. The mix of positive and negative correlations between alkaloid content and preference may be meaningless, or, in contrast to the negative correlations of preference with phenolic content, may suggest that phenolics are more important than alkaloids in determining grazer preference. Other correlational and experimental studies with salt-

TABLE 5

Spearman rank correlation coefficients,  $r_s$  and ( $N$ ) for comparisons between grazing preference hierarchies for four different grazers and phenolic (from Kerfoot, 1989) and alkaloid (from Ostrofsky and Zettler, 1986) content of macrophytes. All  $r_s$  values are non-significant. The probability of obtaining the obtained number of negative coefficients was 0.03 for phenolics, and 0.30 for alkaloids

	Crayfish <sup>1</sup>	Snail <sup>2</sup>	Grass carp <sup>3</sup>	Grass carp <sup>4</sup>	Moose <sup>5</sup>
Phenolic	-0.50(3)	-0.35(4)	-1.00(3)	-1.00(4)	-0.14(7)
Alkaloid	-0.49(7)	0.20(9)	-0.20(5)	0.03(7)	-0.07(6)

<sup>1</sup>This paper; <sup>2</sup>Sheldon, 1987; <sup>3</sup>Wiley et al., 1986; <sup>4</sup>Bowers et al., 1987; <sup>5</sup>Fraser et al., 1984.

marsh (Buchsbaum et al., 1984a,b), freshwater (Kerfoot, 1988), and marine grazers (Hay and Fenical, 1988) support the importance of phenolics in deterring grazers. Any general conclusions are, however, tentative and beg for experimental tests of the impact of a variety of possible defenses against a variety of grazers.

*Need for general approaches to freshwater grazer–macrophyte interactions*

Unifying approaches are currently absent in the study of aquatic herbivory. As a first step, macrophyte researchers need to include measurements of herbivory with measurements of the diversity of other biotic and abiotic factors known to influence macrophyte distribution and abundance. For what macrophyte species, for what grazer species, and in what types of freshwater habitats is herbivory greatest? How common are specialist grazers on macrophytes? Is herbivory related to environmental gradients like lake trophic status? Only when such broad patterns are documented can we begin to test intelligently the responsible processes.

Crawley (1983, p. 334) emphasized that the minimum data set on life history parameters required to understand the population dynamics of even one terrestrial plant and one monophagous herbivore have not been acquired. The situation for freshwater macrophytes is even more dire. Until research on macrophyte life histories is designed to test explicitly the selective force of herbivory relative to other environmental factors, we will make little progress in understanding or managing macrophyte abundance.

Two models of terrestrial plant–herbivore interactions, which address a subset of the questions outlined above, may be helpful starting points in testing the differential susceptibility of macrophytes to grazers. Hay and Fenical (1988, p. 138) suggest that specialist marine herbivores are rare because most fish and invertebrate grazers have planktonic larvae whose ability to choose host plants is limited. However, freshwater grazers do not have planktonic larvae, and freshwater macrophytes and grazers share much evolutionary history with their terrestrial counterparts. Terrestrial models, then, may be a reasonable context in which to place macrophyte–grazer interactions. In the remainder of this paper, I only begin to evaluate the relevance to macrophytes of the two major models of terrestrial herbivory. More rigorous evaluation and broader conceptual approaches will require much more observational and experimental examination of the macrophyte–grazer interaction.

The apparency hypothesis (Feeny, 1976; Rhoades and Cates, 1976) suggests that apparent (long-lived) plants are inevitably subject to assault by a diversity of herbivores. These plants, therefore, defend themselves with expensive ‘quantitative’ defenses, i.e. secondary compounds whose effects are general and dose-dependent. Polyphenolics, including tannins, were thought to be such compounds. Unapparent (fast growing, short-lived, herbaceous,

early successional) plants, typically with distributions that are spotty in time and space, are unlikely to be found by many herbivores. These plants, therefore, defend themselves with inexpensive 'qualitative' defenses, i.e. secondary compounds that, in low concentrations, are effective against non-specialized grazers, e.g. alkaloids. Both the concept of apparency (see e.g. Crawley, 1983) and the relative expense to plants of quantitative and qualitative compounds (Fox, 1981) have been heavily criticized.

The resource availability hypothesis (Coley et al., 1985), like the apparency hypothesis, assumes that trade-offs exist between investments in defense and growth, and predicts many of the same correlations between defense and plant type, but for different reasons. Coley et al. (1985) interpret the patterns of amount of defense as a result of plant resource availability instead of plant apparency. They interpret patterns of defense type (e.g. polyphenolic vs. alkaloid) as a result of the interaction of tissue lifespan, cost per molecule and turnover rates of different types of defense, and relative availability of carbon and nitrogen. For plants adapted to low-nutrient habitats, and therefore with inherently low growth rates and low vegetative turnover, the cost of even high concentrations of defensive chemicals is offset by the high value of defended tissue. For inherently fast growing plants adapted to high nutrient habitats, tissue is cheap and therefore not worth much defense.

While the resource availability hypothesis seems more comprehensive and robust, the distinctions between the two hypotheses have not been clearly enough drawn, and the merits of each require much more testing (Howe and Westley, 1988, Chap. 4). Both hypotheses suffer from a lack of rigorous evaluation of the costs of different defenses and their effectiveness against different herbivores (Robbins et al., 1987; Hay and Fenical, 1988).

What few data are available for macrophytes are at least superficially consistent with both the apparency and resource availability hypotheses. Measurements of phenolic content across vegetation types (Boyd, 1968; Kerfoot, 1988, 1989) allow at least a partial test of the prediction from both hypotheses that defensive chemical content is positively associated with lifespan. While ranges for vascular plants overlap broadly, the rank order of mean phenolic content is: trees > floating-leaves > herbs = emergents > submersed  $\gg$  algae. As predicted, this rank order apparently correlates positively with plant (but not leaf) lifespan, but too little is known of both leaf and rootstock lifespan of macrophytes, especially of the perennial emergent and submersed macrophyte species. Such a comparison across macrophyte types is also partially confounded by phylogenetic relationships.

More restrictive comparisons, e.g. of grazer preferences among submersed macrophytes, also are consistent with both apparency and resource availability predictions. Four of five macrophyte species that are not preferred by crayfish (all except *Potamogeton richardsonii* (A. Benn.) Rydb.) are ever-

green, whereas all other species are usually perennial (see Table 2). Avoidance of evergreens by grazers is also a common pattern among terrestrial insect grazers (MacLean and Jensen, 1985). To the extent that this pattern results from secondary chemical defenses, it is consistent with both hypotheses. Evergreen macrophytes, and other isoetid species, grow slowly, and thrive in sandy, low-nutrient sediments (Boston, 1987). Therefore both hypotheses predict that these species should be more heavily defended than other submersed macrophytes. Unfortunately, none of the quantitative surveys of secondary compounds (Su et al., 1973; Ostrofsky and Zettler, 1986; Kerfoot, 1989) have included such species.

Thus, while both the apparency and resource availability hypotheses appear as plausible for aquatic macrophytes as for terrestrial plants, no solid test of either exists for macrophytes. Sheldon's (1987) results appear to offer preliminary support for the resource hypothesis and against the apparency hypothesis because snail preference for substrate is positively correlated with growth rate among submersed macrophyte species that are similar in apparency. However, Sheldon's (1987) measurements of growth rates in the laboratory were for small rootless pieces of macrophyte shoots, and probably did not provide an accurate index of natural growth rates (Brönmark, 1990). A rigorous test of the apparency and resource availability hypotheses would require comparative or experimental studies controlling apparency and plant relatedness, but contrasting growth rates and nutrient environments. Responses would include concentrations of immobile (quantitative) and mobile (qualitative) defenses.

#### CONCLUSIONS AND FUTURE RESEARCH

The Shelfordian perspective on the role of aquatic macrophytes is clearly mistaken. Live macrophytes are engaged in aquatic food webs, sometimes to the extent that macrophyte biomass, productivity, and relative species abundance is dramatically changed by grazing (see Table 1). The potential impact of grazing on aquatic ecosystems is large (Carpenter and Lodge, 1986), but our general understanding of the impact of grazing on macrophyte populations, communities, and material flow is currently dismal. To remedy the situation, we need surveys and experiments identifying plant grazers and documenting their impact along environmental gradients, and among plant species. Future work must include plants of all growth forms and life stages, and grazers of all sorts — birds, mammals, fish, crustaceans, and insects. Also required are better measurements of above- and below-ground macrophyte productivity, and experimental tests of mechanisms of productivity enhancement by grazers.

Any lack of grazing on macrophytes is not the result of low nutrient concentrations in macrophyte tissue. The nitrogen content of macrophytes is similar to that of algae and much terrestrial forage (Fig. 1).

Similar preferences among macrophytes are exhibited by diverse grazers (Table 3), and, in some cases, preference is a function of protein content. However, in many cases, preference is unrelated to commonly measured plant physical and chemical characteristics (Table 4). While far too few experimental tests of causes of preference are available, correlative evidence suggests that tissue phenolic content may be a general feeding deterrent (Table 5). Future tests of grazer selectivity need to include all growth forms of macrophytes, a diversity of grazers, and measurements of diverse physical, nutritional, and chemical characteristics of plants. More attention should be paid to the effect on grazer preference of variation in plant characteristics across time, space, and plant parts. Following the lead of terrestrial ecologists, special attention should be focused on secondary compounds.

If field experiments on grazer impact and laboratory experiments on selective grazing are to provide general predictions for effects of grazers on natural plant populations, they must include, at a minimum, measurements of non-consumptive destruction of macrophytes, and interactions among grazers. Some grazers, e.g. omnivorous crayfish, may reduce the abundance of other grazers (Lodge and Lorman, 1987). The interaction of grazing impact and interspecific competition among plants (see McCreary, 1991), together with a plethora of potential indirect trophic effects (Lodge et al., 1988), may also be crucial to understanding the structure of macrophyte communities. Only after much extensive work, will we understand the relative importance of grazing in determining macrophyte population and community characteristics.

Finally, future observations and experiments should be designed to test current and emerging models of plant–animal interactions, including the apparency hypothesis and the resource availability hypothesis.

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<sup>a</sup>See Fig. 1 caption.

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