

Safety factors and nutrient uptake by seaweeds

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ABSTRACT: The differences in the kinetic characteristics of nutrient (nitrate, ammonium and phosphate) uptake by seaweeds are evaluated using published half-saturation constants (K_m), maximum rates of uptake (V_{max}) and calculated safety factors for nitrate, ammonium and phosphate uptake. The safety factor is the ratio of maximum nutrient uptake rate to uptake rate at maximum ambient concentration of nutrient and provides a simple estimate of the amount of surplus capacity of a nutrient uptake system. Frequency distributions of K_m values for nitrate, ammonium and phosphate uptake show similar patterns, though values tend to be lower for phosphate uptake and greater for ammonium uptake. There is no relationship between the K_m values for nitrate or ammonium uptake and seaweed surface area:volume ratio (SA:V). Frequency distributions of $V_{max}:K_m$ values for nitrate, ammonium and phosphate uptake show similar patterns, but $V_{max}:K_m$ values tend to be lower for phosphate uptake and greater for ammonium uptake. Moreover, rates of nitrate uptake (at 5 μM nitrate) are comparable to rates of ammonium uptake (at 1.5 μM ammonium) at any value of seaweed SA:V ratio, i.e. the efficiency of ammonium uptake is greater. For nitrate and phosphate uptake by seaweeds and ammonium uptake by phytoplankton values for safety factors are low. In contrast, values for ammonium uptake by seaweeds are high. It is suggested that the reason for the high surplus capacity for ammonium uptake in seaweeds is a combination of the size of the plant and the spatially and temporally variable concentration of ammonium in the seawater that surrounds these plants.

KEY WORDS: Seaweed · Nutrient uptake · Safety factor · Scaling · Surface area:volume ratio

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INTRODUCTION

Seaweeds are important primary producers in shallow coastal and estuarine ecosystems. One indication of this importance is that seaweed biomass per unit area is about 400 times greater than that of phytoplankton in these ecosystems (Smith 1981). Moreover, intertidal seaweeds can be extremely productive, with annual production of dry matter per unit area on exposed shores in excess of rain forests or grasslands (Leigh et al. 1987). The relative amount of net primary production attributable to seaweeds or phytoplankton varies with location and may be almost exclusively pelagic or benthic (Borum & Sand-Jensen 1996). In general, areal rates of net primary production are greater for seaweeds than phytoplankton, but globally, seaweeds are responsible for about 5% (Smith 1981) to 10% (Charpy-Roubaud & Sournia 1990) of marine primary production. This value increases to 37% for continental shelf

waters (Charpy-Roubaud & Sournia 1990) and, often, an even greater percentage in shallow coastal waters and estuaries (Borum & Sand-Jensen 1996).

Clearly, seaweed-based ecosystems are potentially very productive. However, this productivity can only be sustained through the acquisition and utilization of nutrients, particularly nitrogen. In pristine coastal and estuarine waters the most abundant source of nitrogen is nitrate (Sharp 1983), but for many estuaries and coastal areas adjacent to human population centres there is evidence that nitrogen loading is increasing. About 37% of the world's population lives within 100 km of the coastline (Cohen et al. 1997). Consequently, it is hardly surprising that the input of anthropogenic nutrients into coastal waters has increased in recent times (Morand & Briand 1996, Valiela et al. 1997, Schramm 1999). There are many instances of increased levels of nitrate (Cloern 2001) and ammonium (Campbell 2001, Barr & Rees 2003).

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The rate of uptake of a given nutrient should be a function of the surface area presented by the seaweed per unit of its biomass, i.e. its surface area:volume (SA:V) ratio. In general, this scaling relationship has been observed (Rosenberg & Ramus 1984, Hein et al. 1995), with increased rates of uptake per unit biomass for increasing SA:V ratios. However, the relationships for ammonium uptake by seaweeds differ depending on the geographical region (Taylor et al. 1998). In addition, it has been suggested that for algae in general (phytoplankton and seaweeds) there is a negative relationship between K_m (the concentration of substrate that gives half the maximum rate of uptake) for nutrient uptake and SA:V ratio (Hein et al. 1995).

A major difference between phytoplankton and seaweeds is their protein content. Phytoplankton have a high protein content (about 50% dry weight) and a low C:N ratio (Redfield ratio = 6.6), whereas seaweeds generally have a lower (about 15% dry weight) protein content and a higher C:N ratio (about 20) (Atkinson & Smith 1983, Duarte 1992). However, there are exceptions. For example, red algae may have a high protein content (up to 30% dry weight) (Rico & Fernandez 1996) and a low C:N ratio (<9), particularly if their growth is light limited (Bird et al. 1981, Lapointe & Duke 1984). In general, the mass-specific nitrogen demand of a seaweed will be lower than that for a phytoplankton cell. In addition to a lower protein content, the maximum growth rate of seaweeds is considerably lower than that of phytoplankton (Nielsen & Sand-Jensen 1990). This translates into a lower demand for nitrogen per unit biomass. However, at an ecosystem level, there can be considerably more biomass of seaweed (Smith 1981) and the ecosystem nitrogen demand may be as great or greater for seaweeds than phytoplankton.

This demand for nutrients by seaweeds, together with the enhanced (largely anthropogenic) input of nutrients into coastal and estuarine waters suggest that an improved understanding of the characteristics of nutrient uptake by seaweeds is of central importance in understanding their contribution to nutrient utilization. Given that the major sources of nitrogen and phosphorus for seaweeds are nitrate, ammonium and phosphate, how much of their capacity to take up these nutrients is utilized by seaweeds in nature? Safety factors (Diamond 1998, 2002) provide a measure of the amount of surplus capacity that exists when a transporter or enzyme is utilizing the maximum ambient concentration of the substrate. It should be emphasized that this represents surplus capacity relative to the maximum concentration of the nutrient that a given seaweed is likely to encounter in nature. This is not the same as the extent to which a rate of uptake is surplus to the maximum growth rate (McCarthy & Goldman

1979). Here, I review the available data on the kinetic characteristics of nutrient (nitrate, ammonium and phosphate) uptake by seaweeds and suggest that safety factors (the ratio of maximum nutrient uptake rate to uptake rate at maximum ambient concentration of nutrient) provide a simple estimate of the surplus capacity of nutrient uptake, which is markedly greater for ammonium uptake than either nitrate or phosphate uptake in seaweeds.

METHODS

I searched the literature for kinetic parameters for nitrate, ammonium and phosphate uptake and SA:V ratios for seaweeds. The 2 kinetic parameters derived from the hyperbolic relationship between nutrient concentration and rates of nutrient uptake are K_m , which is the concentration of nutrient that gives half the maximum rate of uptake, and V_{max} , which is the maximum rate of uptake achieved at saturating concentrations of the nutrient. It should be noted that values for SA:V ratios were usually obtained from different published sources to kinetic parameters. The data include both fast-growing, ephemeral species, with high SA:V ratios (e.g. *Enteromorpha intestinalis*, *Ulva lactuca*), and slow-growing perennial species, with low SA:V ratios (e.g. *Fucus vesiculosus*, *Xiphophora gladiata*). When more than 1 value for K_m and V_{max} are given for a species from the same location, mean values were used. If the relationship between rate of uptake and concentration was linear, values for K_m were recorded as >25 μ M. In most instances each recorded value was for a single species or subspecies. However, data for the same species from different geographical regions were kept as separate values. These species (with the number of regions in parentheses) were for ammonium uptake *Chaetomorpha linum* (2), *Ulva lactuca* (3), *Ceramium rubrum* (2) and *Fucus distichus* (2); for nitrate uptake *Chaetomorpha linum* (2); and for phosphate uptake *Fucus vesiculosus* (2).

Seawater samples at Waterfall Reef, northeastern New Zealand (36° 55' S, 175° 7' E), have been collected at weekly intervals since January 1995. These data allow safety factors to be calculated for nutrient uptake by seaweeds collected from the same site. Samples were frozen (–18°C) unfiltered in acid-washed polycarbonate bottles. There was no significant difference in nutrient concentrations in filtered and unfiltered seawater (Barr & Rees 2003). Nutrient (nitrate, ammonium and phosphate) concentrations were determined in triplicate. Nitrate was determined as described by Parsons et al. (1984), ammonium as described by Koroleff (1983b), and phosphate as described by Koroleff (1983a).

Safety factors (Diamond 1998, 2002) provide a measure of the amount of surplus capacity that exists when a transporter or enzyme is utilizing the maximum available concentration of the substrate. For seaweed nutrient uptake, safety factors were calculated as:

$$\frac{V_{\max} \text{ for nutrient}}{\text{rate of nutrient uptake at maximum ambient concentration of nutrient}}$$

Rates of nutrient uptake ($\mu\text{mol g}^{-1}$ dry weight h^{-1}) at defined concentrations (Table 1) were calculated from the Michaelis-Menten formula:

$$\frac{V_{\max} \times \text{maximum ambient concentration}}{K_m + \text{maximum ambient concentration}}$$

If V_{\max} values were not available, safety factors were calculated from the K_m value as:

$$\frac{K_m + \text{maximum ambient concentration}}{\text{maximum ambient concentration}}$$

For phytoplankton, only kinetic data for cultured, coastal clones were used. If both K_m and V_{\max} values are available, the 2 formulae give identical values for the safety factor. If the relationship between rate of uptake and concentration was linear the safety factor is infinite and, for convenience, such values for safety factor were recorded as >10 . Ideally, the safety factor for the uptake of a nutrient by any given seaweed should be calculated for the maximum concentrations of the nutrient that it normally encounters. Safety factors were calculated for seaweeds from the Baltic Sea and New Zealand based on maximum measured concentrations of these nutrients at the same sites that the seaweeds were collected (Table 1). In the absence of these data, I calculated safety factors based on maximum nitrate, ammonium and phosphate concentrations in coastal seawater of 5, 1.5 and 1 μM , respectively. These values were chosen based on measured maximum concentrations of these nutrients from 3 geographical regions (Baltic Sea, New Zealand and Nova Scotia) (Table 1). Data for seaweeds from these

Table 1. Maximum concentrations (μM) of nitrate, ammonium and phosphate in seawater from the Baltic Sea (Wallentinus 1984), Nova Scotia (Chapman & Craigie 1977, Gagne et al. 1982, Probyn & Chapman 1983), Brighton Beach, South Island, New Zealand (Brown et al. 1997, Phillips 2001), and Waterfall Reef, North Island, New Zealand. Only data for entire annual cycles are included. Where given, values are means \pm SE

	Nitrate	Ammonium	Phosphate
Baltic Sea	5.43	0.83	0.78
Nova Scotia	5.50 \pm 0.99	1.09 \pm 0.30	0.77 \pm 0.09
Brighton Beach	4.98	1.67	0.63
Waterfall Reef	4.69 \pm 0.59	2.44 \pm 0.67	2.19 \pm 0.87

regions provide 40, 50 and 57 % of the K_m and safety factor data for ammonium, nitrate and phosphate uptake that are used here.

The entire data set is given in Appendices 1 to 5 (available at www.int-res.com/journals/suppl/rees_appendices.pdf). Reduced major axis (RMA) regression (Sokal & Rohlf 1995) was used to describe relationships between SA:V ratio and uptake rates.

RESULTS

For nitrate uptake by seaweeds, most (70%) of the K_m values were less than 10 μM (Fig. 1). Similarly, K_m values for phosphate uptake were also low; 80% were

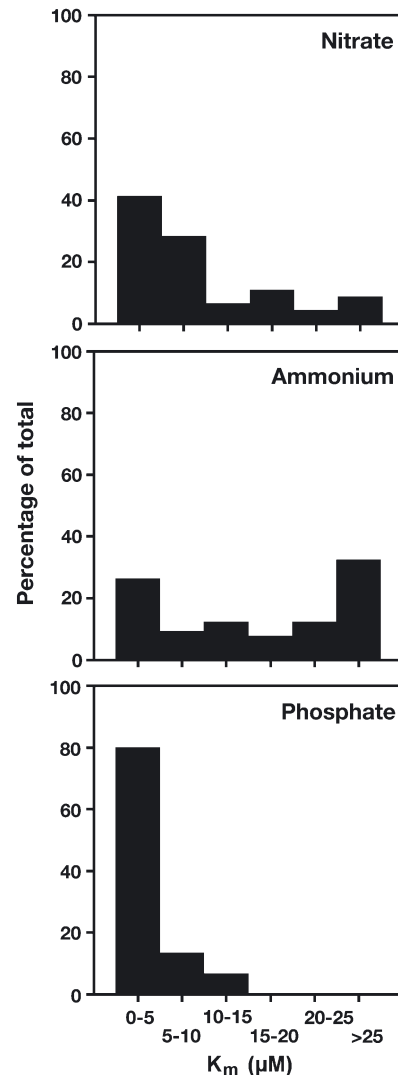


Fig. 1. Frequency distribution of K_m values for nitrate ($n = 46$), ammonium ($n = 65$) and phosphate ($n = 30$) uptake by seaweeds

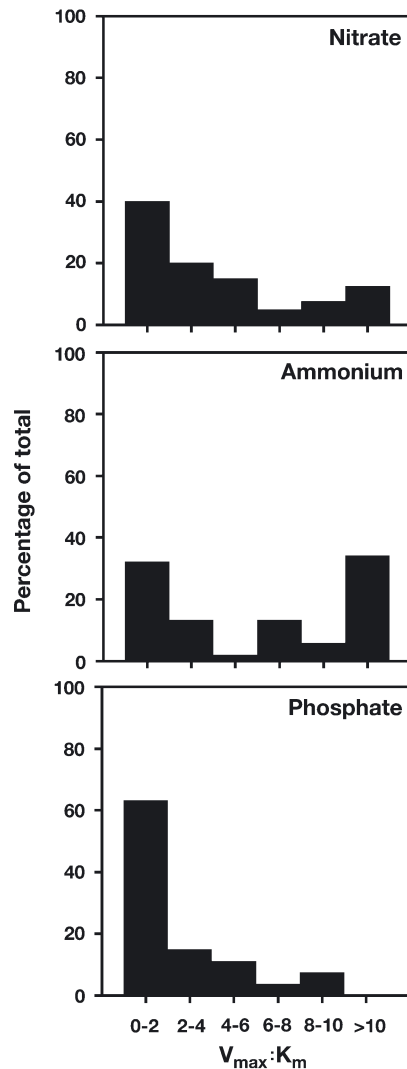


Fig. 2. Frequency distribution of $V_{\max}:K_m$ for nitrate ($n = 40$), ammonium ($n = 53$) and phosphate ($n = 27$) uptake by seaweeds

less than $5 \mu\text{M}$ and 40% were $1 \mu\text{M}$ or less. K_m values for ammonium uptake were, in general, higher than those for nitrate or phosphate, with 65% greater than $10 \mu\text{M}$ (Fig. 1). There was no relationship between seaweed SA:V and K_m for ammonium or nitrate uptake (nitrate $r^2 = 0.035$; ammonium $r^2 = 0.001$) (data not shown). The ratio $V_{\max}:K_m$ has been used as a measure of uptake capacities at low concentrations (Healey 1980, Duke et al. 1989). There was relatively little difference in the distribution of values for $V_{\max}:K_m$ for nitrate, ammonium and phosphate uptake (Fig. 2), because nitrate and phosphate uptake had low K_m and V_{\max} values and ammonium uptake had high K_m and V_{\max} values. However, $V_{\max}:K_m$ for ammonium uptake (median = 6.28) were greater than for nitrate (median =

3.10) and phosphate (median = 1.56) uptake. Though there was a trend for higher values of $V_{\max}:K_m$ with increasing SA:V (data not shown), this was due to increased V_{\max} with increasing SA:V and the invariant relationship between K_m and SA:V. However, of the 5 species of seaweeds (*Chaetomorpha linum*, *Cladophora glomerata*, *Dictyosiphon foeniculaceus*, *Enteromorpha ahlnieriana* and *E. prolifera*) that exhibited high (>10) $V_{\max}:K_m$ values for nitrate and ammonium uptake, 4 are species that belong to genera that form nuisance blooms (*Chaetomorpha*, *Cladophora*, *Enteromorpha*) (Morand & Briand 1996). The relationships between seaweed SA:V and rates of uptake of nitrate at $5 \mu\text{M}$ and ammonium uptake at $1.5 \mu\text{M}$ were almost identical (Fig. 3).

Most safety factors for nitrate and phosphate were 4 or less (78 and 73% respectively) assuming maximum concentrations of 5 and $1 \mu\text{M}$, respectively (Fig. 4). In contrast, only 18% of safety factors for ammonium uptake (assuming a maximum concentration of $1.5 \mu\text{M}$) were this low and most (55%) were in excess of 10. There was no relationship between seaweed SA:V and safety factors for ammonium or nitrate uptake (nitrate $r^2 = 0.044$; ammonium $r^2 = 0.0015$) (data

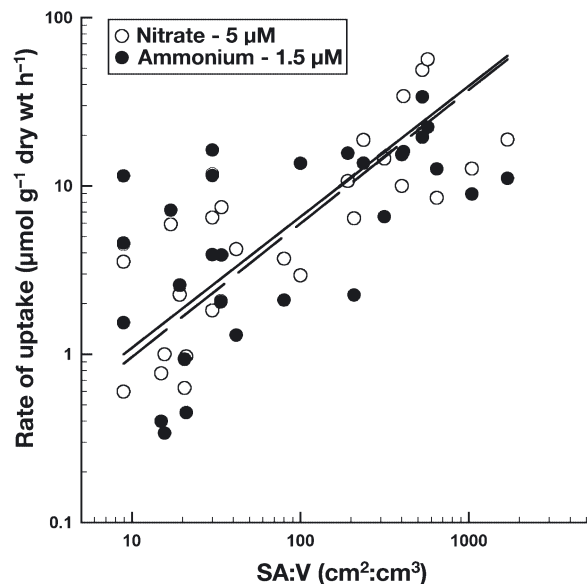


Fig. 3. Biomass-specific rates of nitrate (solid line) and ammonium (dashed line) uptake vs SA:V ratio for seaweeds. Rates of nitrate uptake were calculated for $5 \mu\text{M}$ nitrate and ammonium uptake for $1.5 \mu\text{M}$ ammonium. Each data point corresponds to a single species or subspecies and only data where kinetics of both nitrate and ammonium uptake were available for the same species or subspecies at the same location were included. Reduced major axis regression equations and coefficients of determination are $y = 0.18x^{0.78}$, $r^2 = 0.61$, p (slope = 0) < 0.0001 for nitrate uptake and $y = 0.16x^{0.79}$, $r^2 = 0.38$, p (slope = 0) = 0.0004 for ammonium uptake

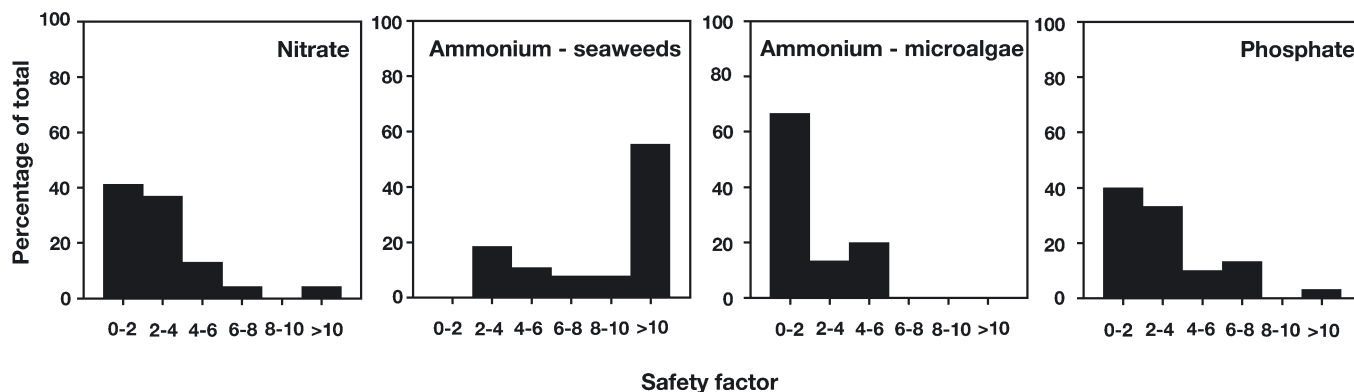


Fig. 4. Frequency distribution of safety factors for nitrate ($n = 46$), ammonium ($n = 65$) and phosphate ($n = 30$) uptake by seaweeds and ammonium uptake by coastal species of phytoplankton ($n = 15$). Safety factors were calculated assuming maximum concentrations for nitrate, ammonium and phosphate of 5, 1.5 and 1 μM , respectively

not shown). Moreover, safety factors for ammonium uptake by coastal species of phytoplankton were similar to those for nitrate uptake by seaweeds (Fig. 4). A similar pattern was found when safety factors for seaweeds were calculated using maximum measured concentrations of nutrients. Safety factors for seaweeds from both the Baltic Sea and New Zealand had low values for nitrate uptake and high values for ammonium uptake (Fig. 5); Baltic seaweeds also had low safety factors for phosphate uptake (Fig. 5).

DISCUSSION

K_m values for nitrate and phosphate uptake by seaweeds are similar to the maximum concentrations of these nutrients encountered in coastal waters. The seasonal pattern of nitrate concentration in seawater is reasonably predictable, with high concentrations from late autumn to early spring, which decrease to nearly zero in late spring to early autumn. Moreover, at any given location, the maximum concentration of nitrate is

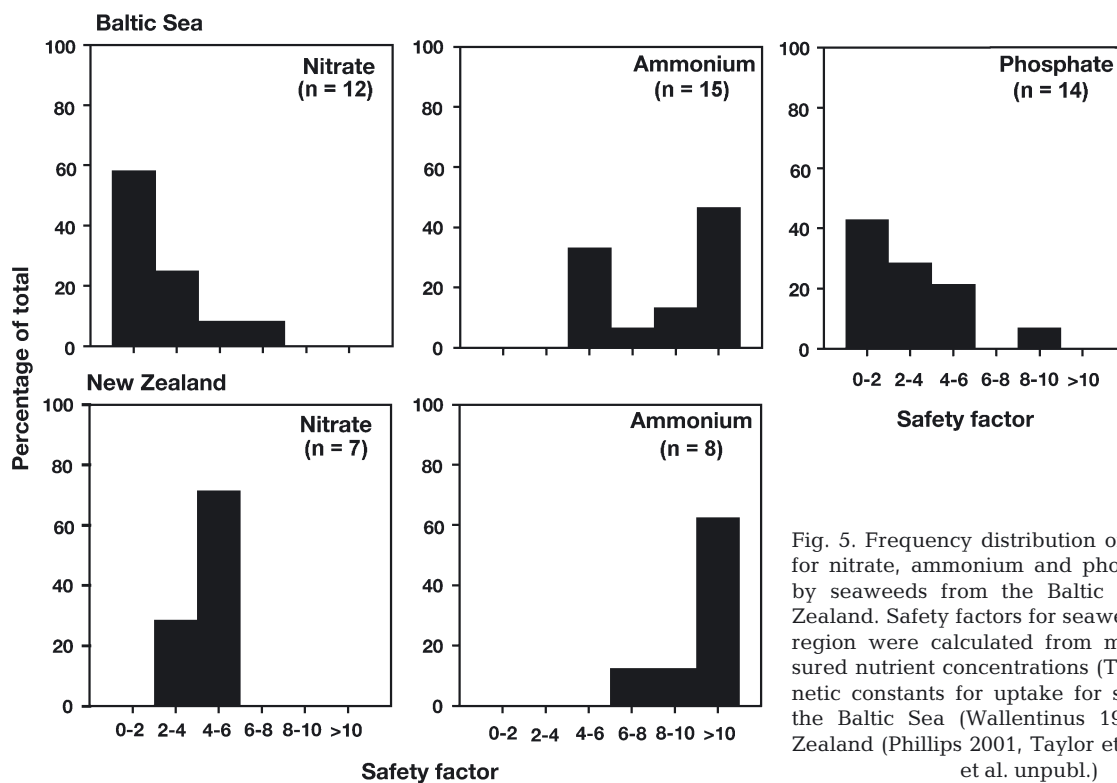


Fig. 5. Frequency distribution of safety factors for nitrate, ammonium and phosphate uptake by seaweeds from the Baltic Sea and New Zealand. Safety factors for seaweeds from each region were calculated from maximum measured nutrient concentrations (Table 1) and kinetic constants for uptake for seaweeds from the Baltic Sea (Wallentinus 1984) and New Zealand (Phillips 2001, Taylor et al. 1998, Rees et al. unpubl.)

also reasonably predictable. The measured concentrations of nitrate in seawater are bulk concentrations, but it is unlikely that they vary greatly over the spatial scales that are likely to be of any consequence to a seaweed. This predictability and uniformity allows a low safety factor (i.e. uptake system operating close to the maximum rate). Phosphate is derived from mixing, sediments and excretion by animals and microorganisms, and, in general, is unlikely to limit growth of seaweeds in temperate silicalastic waters (Lapointe et al. 1992, Lobban & Harrison 1994). Consequently, relative to the seaweed demand for phosphate to sustain growth, the ambient concentration of phosphate is stable and predictable. Moreover, in contrast to ammonium uptake, K_m values for phosphate uptake by coastal clones of marine phytoplankton (Cembella et al. 1984) are similar to those for seaweeds. However it should be noted that the availability of phosphate may limit seaweed growth at certain times of the year (e.g. O'Brien & Wheeler 1987), and it is uncertain to what extent anthropogenic inputs into coastal waters have resulted in increased seawater phosphate concentrations. The latter would have caused a decrease in the safety factor for phosphate uptake (assuming no changes in the K_m for uptake) and the incidence of phosphate limitation of seaweed growth. If, in the past, concentrations of phosphate in coastal seawater were substantially lower than current levels, the supply of phosphate would presumably have been more unpredictable and seaweeds would have been at a selective advantage if they possessed high safety factors for phosphate uptake. Seaweeds from carbonate-rich tropical waters are limited by the availability of phosphate (Lapointe et al. 1992). The only available data for such seaweeds is for *Sargassum baccularia* and the K_m for phosphate uptake is very low compared to other seaweeds (Schaffelke & Klumpp 1998). However, measured concentrations of phosphate in the coastal waters (Great Barrier Reef) where this seaweed occurs are generally at or below the detection limit (Schaffelke & Klumpp 1998). Assuming a detection limit of 30 nM, the safety factor for phosphate uptake by *S. baccularia* would be a high value of 9.7. With a safety factor of about 2 or less, the relationship between the rate of uptake and nutrient concentration is approaching zero-order. The effect of this on nitrate uptake is that increasing the ambient nitrate concentration from 5 to 10 μM results in only a median 37% (range = 6 to 100%) increase in the rate of uptake. For phosphate uptake, increasing the ambient phosphate from 1 to 2 μM results in a median 38% (range = 12 to 84%) increase in the rate of uptake.

The most likely explanation for the relatively high K_m values and safety factors for ammonium uptake by seaweeds is that uptake is dominated by a trans-

porter(s) with a low affinity and high capacity. However, despite relatively high K_m values for ammonium uptake, the high uptake capacity allows seaweeds to take up the nutrient at about the same rate as nitrate, even when the latter is present at a 3.3-fold higher concentration. Moreover, this ignores the sometimes greater effect of darkness on nitrate uptake (e.g. Hanisak & Harlin 1978, Korb & Gerard 2000). Consequently, the central issue with high safety factors for ammonium uptake is not the rate of uptake *per se*, but the reason for the surplus capacity. What are the ecological benefits to seaweeds of possessing a high surplus capacity for ammonium uptake?

In contrast to nitrate uptake, high safety factors for ammonium uptake suggest that the concentration of ammonium in the vicinity of a seaweed is unpredictable and that measured concentrations of ammonium in seawater do not account for spatial and temporal heterogeneity. A similar relationship between variable loads and high safety factors has been advanced for animal systems (Alexander 1981, Diamond 2002). With a high value for the safety factor, the relationship between the rate of uptake and nutrient concentration is closer to first-order. For ammonium uptake, increasing the ambient ammonium concentration from 1.5 to 3 μM gives a median 84% (range = 34 to 100%) increase in the rate of uptake for seaweeds. Moreover, the limited amount of data suggests that ammonium assimilation will also have a high safety factor. Values (assuming a maximum external ammonium concentration of 1.5 μM) for *Enteromorpha* sp. and *Osmundaria colensoi* are 13 and 28, respectively (Taylor & Rees 1999). One instance where unpredictable increases in ammonium concentration are likely to occur is excretion by animals associated with seaweeds.

Associations between seaweeds and animals involve both sessile and mobile animals. Ammonium is usually the major excretion product in these animals and evidence for uptake of this ammonium by seaweeds that are associated with the animal has been documented, together with the ecological role of this nutritional association (Carpenter 1990). Such nutritional associations with sessile animals include barnacles (Williamson & Rees 1994) and bryozoans (Hurd et al. 1994, 2000). Nutritional associations involving mobile animals include sea urchins (Williams & Carpenter 1988), small mobile invertebrates (Taylor & Rees 1998), limpets (Plagányi & Branch 2000) and fish (Meyer et al. 1983, Bray et al. 1986). These associations are likely to be of particular significance if they involve animals that feed on phytoplankton or other nitrogen-rich diets.

Another potential source of ammonium for seaweeds is sediments (Lavery & McComb 1991, Krause-Jensen

et al. 1996, Larned & Stimson 1996, Sundbäck et al. 2003). For example, *Caulerpa cupressoides* is capable of taking up ammonium from sediments through its rhizoids (Williams 1984), with both rhizoids (Williams 1984) and whole plants (Williams & Fisher 1985) having high K_m values for ammonium uptake. The high K_m values presumably reflect either the high (Williams & Fisher 1985) or variable (Williams et al. 1985) ammonium concentrations present in the sediments. Most temperate seaweeds are attached to rocky substrates and the benthic boundary layer may limit access to sediment ammonium (Raven 1981, Hanisak 1983, MacFarlane & Raven 1990). However, storms and animals may disturb sediments that are adjacent to seaweeds and cause temporally unpredictable, local increases in ammonium concentration that are accessible to seaweeds. With increased anthropogenic nitrogen loadings in estuaries and coastal waters (Morand & Briand 1996, Valiela et al. 1997, Schramm 1999), seaweeds with high safety factors for nutrient uptake have a greater potential to take advantage of these increased nutrient concentrations than seaweeds with low safety factors. The problem will potentially be far greater if ammonium is the major constituent of anthropogenic nitrogen loadings.

The ratio $V_{max}:K_m$ has been used as a measure of uptake capacities at low concentrations (Healey 1980, Duke et al. 1989). In essence it is a measure of the efficiency of uptake. The $V_{max}:K_m$ ratio tended to be greater for ammonium uptake than it was for either nitrate or phosphate uptake. Moreover, the relationships between nitrate and ammonium uptake at the maximum concentrations likely to be encountered in nature (5 and 1.5 μM , respectively) and the SA:V ratio were virtually identical. Both these lines of evidence suggest that uptake of ammonium is *more* efficient than that of nitrate. Though the $V_{max}:K_m$ ratio does not provide any indication of the marked surplus capacity associated with ammonium uptake in seaweeds, it should be emphasized that this surplus capacity does not compromise the high and efficient rates of ammonium uptake at low external concentrations.

Concentrations of ammonium may vary both temporally (Ramus & Venable 1987) and spatially (Eppley et al. 1979). For single-celled organisms such as phytoplankton, their small size means that the cell will be either entirely in or out of a patch of ammonium. In essence the probability is binary. If the cell is nitrogen deprived, covering the entire surface of the cell with high-affinity transporters would allow the cell to take maximum advantage of the elevated concentration of ammonium within the patch. However, most seaweeds are large plants relative to the size of most ammonium-excreting animals, and any patch of elevated ammonium would only cover a small proportion of the plant

surface area. In addition, it would be impossible for the plant to predict which part of its surface will be in contact with the patch. The most effective way of overcoming this problem is to ensure that a doubling in concentration at a given portion of the surface results in a close to doubling of the rate of uptake, i.e. to possess a high safety factor for uptake and assimilation.

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Appendix 1. Summary of kinetic constants (K_m and V_{max}) for ammonium uptake, calculated rates of uptake at 1.5 μM ammonium ($V_{1.5}$), calculated safety factors assuming a maximum ambient ammonium concentration of 1.5 μM [SF(1.5)] and $V_{max}:K_m$ for ammonium uptake by seaweeds, together with location of each species. inf.: infinity

Species	K_m (μM)	V_{max}	$V_{1.5}$	SF(1.5)	$V_{max}:K_m$	Location	Source
Green							
<i>Acrosiphonia centralis</i>	19.07	115.21	8.40	13.71	6.04	Baltic	Wallentinus (1984)
<i>Caulerpa cupressoides</i>	48.00	8.70	0.26	33.00	0.18	Virgin Islands	Williams & Fisher (1985)
<i>Chaetomorpha linum</i>	inf.			inf.		W. Australia	Lavery & McComb (1991)
<i>Chaetomorpha linum</i>	13.00	132.00	13.66	9.67	10.15	Denmark	Pedersen & Borum (1997)
<i>Cladophora</i> sp.	20.70	130.00	8.78	14.80	6.28	W. Australia	Gordon et al. (1981)
<i>Cladophora glomerata</i>	32.68	327.83	22.35	14.67	16.36	Baltic	Wallentinus (1984)
<i>Cladophora serica</i>	13.00	122.00	12.62	9.67	9.38	Denmark	Pedersen & Borum (1997)
<i>Codium decorticatum</i>	12.00	13.43	1.49	9.00	1.12	N. Carolina	Rosenberg & Paerl (1981)
<i>Codium fragile</i> subsp. <i>tomentosoides</i>	1.61	23.66	11.49	2.06	15.02	Rhode Island	Hanisak & Harlin (1978)
<i>Codium fragile</i>	25.00	81.00	4.58	17.67	3.24	Denmark	Pedersen & Borum (1997)
<i>Enteromorpha</i> sp.	14.35	9.30	0.74	12.49	0.58	Massachusetts	Fujita (1985)
<i>Enteromorpha ahlneriana</i>	16.64	409.40	33.85	12.09	24.60	Baltic	Wallentinus (1984)
<i>Enteromorpha compressa</i>	24.00	36.79	2.16	17.00	1.53	Baltic	Kautsky (1982)
<i>Enteromorpha intestinalis</i>	inf.		6.57	inf.		New Zealand	Taylor et al. (1998)
<i>Enteromorpha prolifera</i>	8.53	138.40	19.47	7.11	15.92	Oregon	O'Brien & Wheeler (1987)
<i>Ulva</i> sp.	14.40	146.00	13.77	10.60	10.14	S. Australia	Campbell (1999)
<i>Ulva</i> sp.	inf.			inf.		New Zealand	Taylor et al. (1998)
<i>Ulva curvata</i>	13.80			10.20		Connecticut	Duke et al. (1989)
<i>Ulva lactuca</i>	20.50	225.50	15.36	14.68	10.99	Denmark	Pedersen & Borum (1997)
<i>Ulva lactuca</i>	27.70	2.35	0.15	15.46	0.11	Massachusetts	Fujita (1985)
<i>Ulva lactuca</i>	5.20	50.00	11.19	4.47	9.62	Israel	Cohen & Neori (1991)
<i>Ulva rigida</i>	inf.			inf.		W. Australia	Lavery & McComb (1991)
Red							
<i>Agardhiella subulata</i>	3.90	15.86	4.41	3.60	4.07	Massachusetts	D'Elia & DeBoer (1978)
<i>Apophlaea lyallii</i>	42.08	11.56	0.40	29.05	0.27	New Zealand	Phillips (2001)
<i>Ceramium rubrum</i>	29.00	271.00	13.33	20.33	9.34	Denmark	Pedersen & Borum (1997)
<i>Ceramium rubrum</i>	3.60	25.20	7.41	3.40	7.00	Massachusetts	DeBoer & Whoriskey (1983)
<i>Ceramium tenuicorne</i>	16.93	143.43	15.66	9.16	12.59	Baltic	Wallentinus (1984)
<i>Chondrus crispus</i>	35.50	61.71	2.50	24.67	1.74	France	Amat & Braud (1990)
<i>Furcellaria lumbricalis</i>	6.53	4.88	0.93	5.26	0.78	Baltic	Wallentinus (1984)
<i>Gracilaria foliifera</i>	1.60	23.82	11.53	2.07	14.89	Massachusetts	D'Elia & DeBoer (1978)
<i>Gracilaria gracilis</i>	76.45	216.70	4.17	51.97	2.83	South Africa	Smit (2002)
<i>Gracilaria pacifica</i>	10.00	30.00	3.91	7.67	3.00	British Columbia	Thomas et al. (1987)
<i>Gracilaria tikvahiae</i>	24.83	2.67	0.16	16.90	0.11	Massachusetts	Fujita (1985)
<i>Gracilariopsis lemaneiformis</i>	40.00	68.00	2.46	27.67	1.70	N. Carolina	Vergara et al. (1995)
<i>Hypnea musciformis</i>	16.64	115.00	9.51	12.09	6.91	Virgin Islands	Haines & Wheeler (1978)
<i>Phyllophora truncata</i>	7.93	9.71	1.54	6.29	1.22	Baltic	Wallentinus (1984)
<i>Polysiphonia decipiens</i>	2.60	57.40	21.00	2.73	22.08	Melbourne	Campbell (1999)
<i>Porphyra</i> sp.	inf.			inf.		New Zealand	Taylor et al. (1998)
<i>Pterocladia capillacea</i>	45.00	65.00	2.10	31.00	1.44	New Zealand	Taylor et al. (1998)
<i>Rhodomela confervoides</i>	23.86	38.07	2.25	16.91	1.60	Baltic	Wallentinus (1984)
<i>Stictosiphonia arbuscula</i>	inf.		1.30	inf.		New Zealand	Phillips (2001)

Appendix 1 (continued)

Species	K_m (μM)	V_{\max}	$V_{1.5}$	SF(1.5)	$V_{\max}:K_m$	Location	Source
Brown							
<i>Chorda filum</i>	3.44	23.64	7.18	3.29	6.87	Baltic	Wallentinus (1984)
<i>Chordaria flagelliformis</i>	4.35	61.95	13.63	4.54	18.48	Nova Scotia	Probyn & Chapman (1982), Rosenberg et al. (1984)
<i>Dictyosiphon foeniculaceus</i>	3.60	54.43	16.01	3.40	15.12	Baltic	Wallentinus (1984)
<i>Ecklonia radiata</i>	inf.			inf.		W. Australia	Paling (1991)
<i>Ectocarpus siliculosus</i>	3.46	39.79	12.03	3.31	11.50	Baltic	Wallentinus (1984)
<i>Elachista fucicola</i>	20.93	133.86	8.95	14.95	6.40	Baltic	Wallentinus (1984)
<i>Eudesme virescens</i>	4.78	38.14	9.11	4.19	7.98	Baltic	Wallentinus (1984)
<i>Fucus distichus</i>	4.00	60.00	16.36	3.67	15.00	British Columbia	Thomas et al. (1985)
<i>Fucus distichus</i>	3.61	13.90	4.08	3.41	3.85	Nova Scotia	Rosenberg et al. (1984)
<i>Fucus spiralis</i>	7.47	23.51	3.89	6.05	3.13	Massachusetts	Topinka (1978)
<i>Fucus vesiculosus</i>	14.93	24.62	2.05	12.01	1.60	Denmark	Wallentinus (1984), Pedersen & Borum (1997)
<i>Himantothallus grandifolius</i>	20.40			14.60		Antarctic	Korb & Gerard (2000)
<i>Hincksia sordida</i>	39.70	802.00	29.20	27.47	20.20	Melbourne	Campbell (1999)
<i>Laminaria abyssalis</i>	4.60	2.00	0.49	4.07	0.43	Brazil	Braga & Yoneshigue- Valentin (1996)
<i>Laminaria groenlandica</i>	inf.		0.27	inf.		British Columbia	Harrison et al. (1986)
<i>Laminaria solidungula</i>	12.70			9.47		Canadian Arctic	Korb & Gerard (2000)
<i>Macrocystis pyrifera</i>	4.85	20.00	4.41	4.54	3.77	S. California	Haines & Wheeler (1978), Wheeler (1979)
<i>Pilayella littoralis</i>	3.57	35.86	11.10	3.23	11.23	Baltic	Wallentinus (1984)
<i>Sargassum baccularia</i>	4.81	13.02	3.10	4.21	2.71	Great Barrier Reef	Schaffelke & Klumpp (1998)
<i>Scytosiphon lomentaria</i>	3.90	69.07	19.19	3.60	17.71	Baltic	Wallentinus (1984)
<i>Scytothamnus australis</i>	42.80	76.24	2.58	29.53	1.78	New Zealand	Phillips (2001)
<i>Undaria pinnatifida</i>	19.75	119.50	16.09	7.43	14.11	S. Australia	Campbell (1999)
<i>Xiphophora chondrophylla</i>	inf.		0.12	inf.		New Zealand	Taylor et al. (1998)
<i>Xiphophora gladiata</i>	36.69	8.72	0.34	25.46	0.24	New Zealand	Phillips (2001)

Appendix 2. Summary of kinetic constants (K_m and V_{\max}) for nitrate uptake, calculated rates of uptake at 5 μM nitrate (V_5), calculated safety factors assuming a maximum ambient nitrate concentration of 5 μM [SF(5)] and $V_{\max}:K_m$ for nitrate uptake by seaweeds, together with location of each species

Species	K_m (μM)	V_{\max}	V_5	SF(5)	$V_{\max}:K_m$	Location	Source
Green							
<i>Chaetomorpha linum</i>	inf.			inf.		W. Australia	Lavery & McComb (1991)
<i>Chaetomorpha linum</i>	3.00	30.00	18.75	1.60	10.00	Denmark	Pedersen & Borum (1997)
<i>Cladophora glomerata</i>	5.27	115.72	56.54	2.05	40.18	Baltic	Wallentinus (1984)
<i>Cladophora serica</i>	5.00	17.00	8.50	2.00	3.40	Denmark	Pedersen & Borum (1997)
<i>Codium fragile</i> subsp. <i>tomentosoides</i>	4.28	6.83	3.55	1.92	2.00	Rhode Island	Hanisak & Harlin (1978)
<i>Codium fragile</i>	5.00	9.00	4.50	2.00	1.80	Denmark	Pedersen & Borum (1997)
<i>Enteromorpha</i> sp.	16.60	129.40	29.95	4.32	7.80	Nova Scotia	Harlin (1978)
<i>Enteromorpha ahlnneriana</i>	1.73	27.80	20.65	1.35	16.07	Baltic	Wallentinus (1984)
<i>Enteromorpha intestinalis</i>	17.22	64.65	14.55	4.44	3.75	New Zealand	Rees et al. (unpubl.)
<i>Enteromorpha prolifera</i>	7.81	122.20	48.87	2.50	22.67	Oregon	O'Brien & Wheeler (1987)
<i>Ulva lactuca</i>	5.00	20.00	10.00	2.00	4.00	Denmark	Pedersen & Borum (1997)
<i>Ulva rigida</i>	25.68	71.89	11.72	6.14	2.80	W. Australia	Lavery & McComb (1991)
Red							
<i>Agardhiella subulata</i>	2.40	11.67	7.89	1.48	4.86	Massachusetts	D'Elia & DeBoer (1978)
<i>Apophlaea lyallii</i>	9.26	2.19	0.77	2.85	0.24	New Zealand	Phillips (2001)
<i>Ceramium rubrum</i>	7.57	5.99	2.38	2.51	0.79	Baltic	Wallentinus (1984)
<i>Ceramium tenuicorne</i>	3.91	18.67	10.69	1.75	5.56	Baltic	Wallentinus (1984)
<i>Furcellaria lumbicalis</i>	15.29	3.19	0.63	5.02	0.19	Baltic	Wallentinus (1984)
<i>Gracilaria foliifera</i>	2.48	9.71	6.49	1.50	3.92	Massachusetts	D'Elia & DeBoer (1978)
<i>Gracilaria gracilis</i>	5.80	26.28	12.16	2.16	4.53	South Africa	Smit (2002)
<i>Gracilaria pacifica</i>	6.00	4.00	1.82	2.20	0.67	Vancouver	Thomas et al. (1987)
<i>Hypnea musciformis</i>	4.90	28.50	14.39	1.98	5.82	Virgin Islands	Haines & Wheeler (1978)
<i>Phyllophora truncata</i>	9.21	1.69	0.60	2.84	0.18	Baltic	Wallentinus (1984)
<i>Pterocladia capillacea</i>	14.19	14.20	3.70	3.84	1.00	New Zealand	Rees et al. (unpubl.)
<i>Rhodomela confervoides</i>	4.46	12.14	6.42	1.89	2.72	Baltic	Wallentinus (1984)
<i>Stictosiphonia arbuscula</i>	18.68	16.21	4.21	3.85	1.43	New Zealand	Phillips (2001)

Appendix 2 (continued)

Species	K_m (μM)	V_{\max}	V_5	SF(5)	$V_{\max}:K_m$	Location	Source
Brown							
<i>Chorda filum</i>	0.60	6.63	5.92	1.12	11.05	Baltic	Wallentinus (1984)
<i>Chordaria flagelliformis</i>	5.10	5.93	2.94	2.02	1.16	Nova Scotia	Probyn (1984)
<i>Dictyosiphon foeniculaceus</i>	4.34	63.79	34.15	1.87	14.70	Baltic	Wallentinus (1984)
<i>Elachista fucicola</i>	1.94	17.57	12.66	1.39	9.06	Baltic	Wallentinus (1984)
<i>Eudesme virescens</i>	2.23	10.29	7.11	1.45	4.61	Baltic	Wallentinus (1984)
<i>Fucus distichus</i>	3.50	20.00	11.76	1.70	5.71	British Columbia	Thomas et al. (1985)
<i>Fucus spiralis</i>	6.70	17.56	7.47	2.35	2.62	Massachusetts	Topinka (1978)
<i>Fucus vesiculosus</i>	24.69	9.29	2.08	4.47	0.65	Denmark	Wallentinus (1984), Pedersen & Borum (1997)
<i>Himantothallus grandifolius</i>	12.80			3.56		Antarctic	Korb & Gerard (2000)
<i>Kjellmaniella crassifolia</i>	4.48			1.90		Japan	Ozaki et al. (2001)
<i>Laminaria abyssalis</i>	14.00	5.00	1.32	3.80	0.36	Brazil	Braga & Yoneshigue- Valentin (1996)
<i>Laminaria japonica</i>	2.56			1.51		Japan	Ozaki et al. (2001)
<i>Laminaria longicruris</i>	4.67	9.66	4.97	1.94	2.11	Nova Scotia	Harlin & Craigie (1978), Espinoza & Chapman (1983)
<i>Laminaria groenlandica</i>	inf.		0.85	inf.		British Columbia	Harrison et al. (1986)
<i>Laminaria solidungula</i>	35.00			8.00		Canadian Arctic	Korb & Gerard (2000)
<i>Macrocystis pyrifera</i>	6.82	13.79	5.14	2.69	1.64	S. California	Haines & Wheeler (1978)
<i>Pilayella littoralis</i>	8.64	51.32	18.82	2.73	7.05	Baltic	Wallentinus (1984)
<i>Scytosiphon lomentaria</i>	6.92	59.36	24.90	2.38	8.58	Baltic	Wallentinus (1984)
<i>Scytothamnus australis</i>	17.74	10.26	2.26	4.55	0.58	New Zealand	Phillips (2001)
<i>Xiphophora chondrophylla</i>	9.99	2.92	0.97	3.00	0.29	New Zealand	Rees et al. (unpubl.)
<i>Xiphophora gladiata</i>	20.97	5.19	1.00	5.19	0.25	New Zealand	Phillips (2001)

Appendix 3. Summary of kinetic constants (K_m and V_{\max}) for phosphate uptake, calculated rates of uptake at 1 μM phosphate (V_1), calculated safety factors assuming a maximum ambient phosphate concentration of 1 μM [SF(1)] and $V_{\max}:K_m$ for phosphate uptake by seaweeds, together with location of each species

Species	K_m (μM)	V_{\max}	V_1	SF(1)	$V_{\max}:K_m$	Location	Source
Green							
<i>Acrosiphonia centralis</i>	1.43	3.32	1.37	2.43	2.33	Baltic	Wallentinus (1984)
<i>Chaetomorpha linum</i>	10.35	21.52	1.90	11.35	2.08	W. Australia	Lavery & McComb (1991)
<i>Cladophora</i> sp.	0.48	3.61	2.43	1.48	7.47	W. Australia	Gordon et al. (1981)
<i>Cladophora glomerata</i>	0.33	3.06	2.30	1.33	9.29	Baltic	Wallentinus (1984)
<i>Enteromorpha ahlnneriana</i>	1.51	4.59	1.48	3.09	4.65	Baltic	Wallentinus (1984)
<i>Enteromorpha compressa</i>	1.00	1.90	0.95	2.00	1.90	Baltic	Kautsky (1982)
<i>Monostroma grevillei</i>	2.71	2.79	0.75	3.71	1.03	Baltic	Wallentinus (1984)
<i>Ulva rigida</i>	3.65	8.77	1.89	4.65	2.40	W. Australia	Lavery & McComb (1991)
Red							
<i>Agardhiella subulata</i>	0.40	0.47	0.34	1.40	1.18	Massachusetts	DeBoer (1981)
<i>Ceramium tenuicorne</i>	1.00	0.78	0.51	1.55	1.56	Baltic	Wallentinus (1984)
<i>Furcellaria lumbricalis</i>	2.97	0.13	0.03	4.00	0.64	Baltic	Wallentinus (1984)
<i>Phyllophora truncata</i>	0.37	0.12	0.08	1.37	0.32	Baltic	Wallentinus (1984)
<i>Rhodomela confervoides</i>	1.03	0.64	0.31	2.03	0.62	Baltic	Wallentinus (1984)
Brown							
<i>Ascophyllum nodosum</i>	1.22	0.07	0.03	2.20	0.07	Ireland	Hurd & Dring (1990)
<i>Chorda filum</i>	0.62	1.38	0.85	1.62	2.22	Baltic	Wallentinus (1984)
<i>Dictyosiphon foeniculaceus</i>	2.12	11.13	3.56	3.12	5.24	Baltic	Wallentinus (1984)
<i>Ectocarpus siliculosus</i>	1.22	0.75	0.34	2.22	0.61	Baltic	Wallentinus (1984)
<i>Eudesme virescens</i>	0.67	3.55	2.12	1.67	5.26	Baltic	Wallentinus (1984)
<i>Fucus serratus</i>	6.95	0.39	0.05	7.17	0.07	Ireland	Hurd & Dring (1990), Hurd et al. (1993)
<i>Fucus spiralis</i>	5.34	0.75	0.14	5.39	0.18	Ireland	Hurd & Dring (1990), Hurd et al. (1993)
<i>Fucus vesiculosus</i>	7.58	0.38	0.06	6.58	0.07	Ireland	Hurd & Dring (1990)
<i>Fucus vesiculosus</i>	11.17	1.05	0.15	6.95	0.21	Baltic	Wallentinus (1984)
<i>Kjellmaniella crassifolia</i>	0.31			1.31		Japan	Ozaki et al. (2001)
<i>Laminaria abyssalis</i>	2.21	0.83	0.26	3.21	0.38	Brazil	Braga & Yoneshigue- Valentin (1996)
<i>Laminaria japonica</i>	0.14			1.14		Japan	Ozaki et al. (2001)
<i>Macrocystis pyrifera</i>	3.51			4.51		California	Manley (1985)
<i>Pelvetia canaliculata</i>	5.96	0.36	0.05	6.94	0.06	Ireland	Hurd & Dring (1990)
<i>Pilayella littoralis</i>	3.07	4.89	1.22	3.99	1.71	Baltic	Wallentinus (1984)
<i>Sargassum baccularia</i>	0.26	0.43	0.34	1.26	1.65	Great Barrier Reef	Schaffelke & Klumpp (1998)
<i>Scytosiphon lomentaria</i>	0.77	6.58	3.71	1.77	8.50	Baltic	Wallentinus (1984)

Appendix 4. Summary of surface area:volume (SA:V) ratios for seaweeds

Species	SA:V	Source
Green		
<i>Codium fragile</i>	8.9	Rosenberg & Ramus (1984)
<i>Chaetomorpha linum</i>	237	Nielsen & Sand-Jensen (1990)
<i>Enteromorpha intestinalis</i>	315	Taylor et al. (1998)
<i>Ulva lactuca</i>	400	Odum et al. (1958)
<i>Enteromorpha ahlneriana</i>	529	Hein et al. (1995)
<i>Enteromorpha prolifera</i>	529	Hein et al. (1995)
<i>Cladophora glomerata</i>	569	Hein et al. (1995)
<i>Cladophora serica</i>	645	Nielsen & Sand-Jensen (1990)
Red		
<i>Phyllophora truncata</i>	8.9	Hein et al. (1995)
<i>Apophlaea lyallii</i>	14.9	Phillips (2001)
<i>Furcellaria lumbricalis</i>	20.5	Hein et al. (1995)
<i>Gracilaria foliifera</i>	30	Hein et al. (1995)
<i>Gracilaria pacifica</i>	30	Hein et al. (1995)
<i>Stictosiphonia arbuscula</i>	41.59	Phillips (2001)
<i>Pterocladia capillacea</i>	80	Taylor et al. (1998)
<i>Ceramium tenuicorne</i>	191	Hein et al. (1995)
<i>Rhodomela confervoides</i>	207.9	Hein et al. (1995)
Brown		
<i>Xiphophora gladiata</i>	15.6	Phillips (2001)
<i>Chorda filum</i>	17	Odum et al. (1958)
<i>Scytothamnus australis</i>	19.2	Phillips (2001)
<i>Xiphophora chondrophylla</i>	21	Taylor et al. (1998)
<i>Fucus distichus</i>	30	Hein et al. (1995)
<i>Fucus vesiculosus</i>	33.7	Odum et al. (1958), Nielsen & Sand-Jensen (1990)
<i>Fucus spiralis</i>	34	Nielsen & Sand-Jensen (1990)
<i>Chordaria flagelliformis</i>	100	Hein et al. (1995)
<i>Dictyosiphon foeniculaceus</i>	408.5	Hein et al. (1995)
<i>Elachista fucicola</i>	1042.3	Hein et al. (1995)
<i>Pilayella littoralis</i>	1694	Hein et al. (1995)

Appendix 5. Summary of K_m for ammonium uptake and calculated safety factors assuming a maximum ambient ammonium concentration of 1.5 μM [SF(1.5)] for coastal clones of phytoplankton

Species	K_m (μM)	SF(1.5)	Source
<i>Asterionella japonica</i>	1.05	1.70	Eppley et al. (1969)
<i>Chaetoceros debilis</i>	0.50	1.33	Conway & Harrison (1977)
<i>Coscinodiscus lineatus</i>	2.00	2.33	Eppley et al. (1969)
<i>Coscinodiscus wailesii</i>	4.90	4.27	Eppley et al. (1969)
<i>Ditylum brightwellii</i>	1.10	1.73	Eppley et al. (1969)
<i>Dunaliella tertiolecta</i>	0.10	1.07	Eppley et al. (1969)
<i>Gonyaulax polyedra</i>	5.50	4.67	Eppley et al. (1969)
<i>Gymnodinium splendens</i>	1.10	1.73	Eppley et al. (1969)
<i>Leptocylindricus danicus</i>	1.60	2.07	Eppley et al. (1969)
<i>Monochrysis lutheri</i>	0.50	1.33	Eppley et al. (1969)
<i>Phaeodactylum tricorutum</i>	1.47	1.98	Grant (2002)
<i>Rhizosolenia robusta</i>	7.45	5.97	Eppley et al. (1969)
<i>Rhizosolenia stolterfothii</i>	0.50	1.33	Eppley et al. (1969)
<i>Skeletonema costatum</i>	1.23	1.82	Conway et al. (1976), Conway & Harrison (1977)
<i>Thalassiosira gravida</i>	0.50	1.33	Conway & Harrison (1977)

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