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Seaweed nutrient physiology: application of concepts to aquaculture and bioremediation

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ABSTRACT

Inorganic carbon, nitrogen and phosphorus are the main elements required by seaweeds for photosynthesis and growth. This review focusses mainly on nitrogen, but the roles of carbon and phosphorus, which may interactively affect seaweed physiological processes, are also explored. Fundamental concepts such as limiting nutrients, sources, and ratios, mechanisms of nutrient uptake, nutrient assimilation and storage, patterns of uptake and preferences for different nitrogen sources are discussed. The roles of abiotic (water motion, light, temperature, salinity and desiccation) and biotic (life stages and age class) factors in nutrient (nitrogen, phosphorous, carbon) uptake are also reviewed. Understanding species-specific nitrogen physiologies and nitrogen source preferences will enable polyculture of different seaweed species and the use of seaweeds as biofilters in integrated multitrophic aquaculture systems.

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INTRODUCTION

Inorganic carbon, light and nutrients are required for seaweed photosynthesis and growth, and interactively regulate rates of seaweed production. Nitrogen is the element most frequently observed to limit growth, although in some cases phosphorus may be limiting. Moreover, because inorganic carbon (C_i) in seawater occurs primarily as bicarbonate (HCO_3^-), the inability of some species to use HCO_3^- as a C_i source may lead to carbon limitation, especially among subtidal and tide pool species. This review will focus on nitrogen nutrition of seaweeds and will also consider phosphorus and carbon physiology which may interactively affect nitrogen uptake and assimilation, and consequently, seaweed photosynthesis and growth. This review is not intended for be comprehensive but to build on the earlier reviews of Harrison & Hurd (2001) and Hurd *et al.* (2014, ch. 6). Here, we outline fundamental concepts of natural nutrient sources to seaweeds, the mechanisms by which seaweeds take up and assimilate nutrients, and the utility of 'kinetic curves' in understanding mechanisms and rates of nutrient uptake. Next, we discuss how nutrient uptake and growth are regulated by abiotic and biotic factors using both classical and contemporary literature examples; the context is that seaweed growth can be enhanced by providing optimal environmental factors such as light, water motion, and nutrient supply. We then explain how concepts might be applied to seaweed polyculture and integrated multitrophic aquaculture (IMTA).

LIMITING NUTRIENTS, SOURCES, AND RATIOS

A fundamental understanding of the sources of nutrients (nitrogen, phosphorus, carbon) available to seaweeds and the seaweed's nutrient requirements for optimal growth is essential

to enhance the growth conditions in any production system (Hurd *et al.* 2014). When a seaweed's demand for a nutrient is greater than its supply, the nutrient becomes 'limiting'; that is, it limits growth (Harrison & Hurd 2001). Liebig's law of the minimum states that 'the nutrient available in the smallest quantity with respect to the requirements of the plant will limit its rate of growth' (see Hurd *et al.* 2014, ch. 6, p. 240): if the limitation by a particular nutrient (e.g. nitrogen) is overcome by increasing the supply, then a different nutrient may become limiting (e.g. phosphorous). There are also interactions among nutrients; for balanced growth, they are required in certain ratios (see below). For example, alleviating nitrogen limitation in *Fucus vesiculosus* Linnaeus triggered an increase in the uptake of phosphate (PO_4^{3-} ; Perini & Bracken 2014).

In natural systems, nitrogen is the nutrient that most commonly limits seaweed growth, with phosphorous being the second most common limiting nutrient. Nitrogen is available in the inorganic forms nitrate (NO_3^-) and ammonium (NH_4^+) and the organic form urea. Nitrate-based growth is termed 'new production' because NO_3^- is externally supplied; for example, from below the thermocline or from upwelling (Boyd & Hurd 2009). Primary production based on NH_4^+ and urea is termed 'recycled production' because it is internally regenerated within the system by invertebrates and fish associated with the seaweeds (Boyd & Hurd 2009; Taylor & Rees 1998). The relative preference index can be used to determine the preference of a seaweed for NO_3^- vs NH_4^+ vs urea, for example, between different seasons (Phillips & Hurd 2003).

Seawater nutrients have different seasonal cycles depending on geographic location, and it is important to have baseline data to understand when a particular nutrient might become limiting for seaweed growth. In many temperate

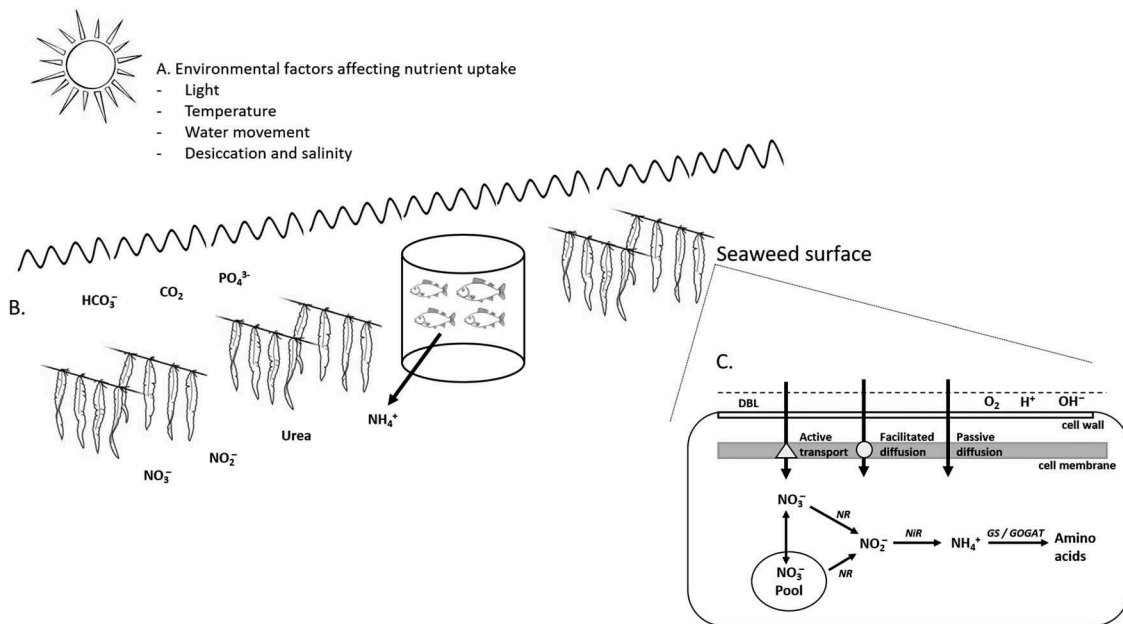


Fig. 1. Schematic of (A) environmental factors regulating uptake nutrient by seaweeds; (B) inorganic carbon, phosphorous and nitrogen sources available in seawater for seaweeds, including the organic form of nitrogen, urea. Ammonium is naturally available in seawater at relatively low concentrations, but levels can be enhanced via excretion from marine animals, including in an IMTA situation (e.g. salmon); (C) for seaweeds to take up nutrients, they must first cross the diffusion boundary layer (DBL) and cell wall. Within the DLB, products released via photosynthesis, respiration and nutrient uptake may accumulate (e.g. O_2 , H^+ and OH^-). Once they have crossed the cell wall, nutrients are taken into the cell via active transport, and/or facilitated transport, and/or passive diffusion across the cell membrane. Within the cell, nutrients may be stored in various pools or are assimilated. The example given is for nitrate uptake and assimilation; nitrate may be stored in an inorganic pool or converted to ammonium via the enzymes NR and nitrite reductase (NIR). Unlike nitrate, ammonium storage is limited in seaweeds and it is rapidly converted to amino acids via glutamine synthetase (GS) and glutamate synthase (GOGAT).

regions, seawater NO_3^- concentrations in surface waters have a strong seasonal cycle due to seasonal thermoclines. In winter, NO_3^- concentrations are maximal, ranging from 5 to 20 μM depending on geographic location. With increased light in spring, temperature rises and the thermocline forms, separating the surface mixed layer from the cooler, NO_3^- -rich waters below. Biological activity – mostly phytoplankton – removes NO_3^- from surface waters which become NO_3^- deplete (Boyd & Hurd 2009). However, in other systems, nitrate supply is driven by seasonal upwelling events; for example, the California current (Jacox *et al.* 2015). PO_4^{3-} follows a seasonal pattern similar to NO_3^- , but concentrations rarely reach ‘zero’; that is, below the detection limit. In summer, recycled production predominates, with seaweeds using NH_4^+ excreted by zooplankton, invertebrates and fish. In tropical waters, concentrations of seawater NO_3^- are comparatively low year-round, and the systems are based largely on regenerated NH_4^+ . Tropical systems tend to be dominated by symbiotic corals, and seaweed biomass is naturally low due to higher levels of herbivory (Briggs *et al.* 2018; Lewis 1985). However, under eutrophic conditions, seaweed biomass can increase at the expense of corals (Schaffelke 1999).

In natural systems, seaweeds can take up a substantial proportion of their nitrogen from invertebrates and fish with which they are associated (Taylor & Rees 1998). For example, the relationship between *Macrocystis pyrifera* (Linnaeus) C. Agardh and hydrozoans is mutualistic: growth rates of *M. pyrifera* are enhanced by hydrozoans which excrete NH_4^+ that is taken up by the underlying seaweed (Hepburn & Hurd 2005; Hepburn *et al.* 2012). From an aquaculture perspective, however, such ‘fouling’

by invertebrates can be detrimental to offshore production (Buck *et al.* 2017; Stévant *et al.* 2017). Urea is also an important source of nitrogen for seaweeds: in southern New Zealand urea provided *c.* 30% of nitrogen to four species of intertidal seaweed in summer (Phillips & Hurd 2003), and in California, USA, urea represents an important year-round supply of nitrogen to *M. pyrifera* (Smith *et al.* 2018). Seaweeds can utilise organic phosphorous via the external enzyme alkaline phosphatase, which breaks down organic matter on the seaweed’s surface into PO_4^{3-} , which is then taken up (Schaffelke 2001).

Dissolved inorganic carbon (DIC, such as CO_2 and HCO_3^-) is usually considered in terms of photosynthesis, rather than as a nutrient *per se*. Because the concentration of HCO_3^- in seawater is high (2000 μM) relative to dissolved CO_2 (14 μM), seaweeds that use HCO_3^- are unlikely to be limited by C_i supply (Raven *et al.* 2011). However, around 35% of seaweeds cannot utilise HCO_3^- (Kübler & Dudgeon 2015) and they may be carbon limited under certain conditions, such as high light levels which may cause an increase in carbon requirement (Cornwall *et al.* 2015). In addition, seaweed photosynthesis removes DIC from the surrounding seawater, which modifies the seawater carbonate system such that pH increases and the supply of both CO_2 and HCO_3^- decreases: at pH 9.0 most DIC is available as carbonate which cannot be used in photosynthesis (Björk *et al.* 2004). Therefore, in highly productive systems, carbon may limit growth of some seaweeds, although this will depend on the mechanisms of DIC uptake and their carbon requirements for growth (van der Loos *et al.* 2019).

For balanced growth, seaweeds require essential nutrients (C, N, P) in species-specific ratios (Duarte 1992). Using literature values from 46 seaweeds, Duarte (1992) found that the percentage tissue carbon (per unit tissue dry weight) is 10%–50% with a median value of 25%; tissue nitrogen range is 0.2%–4.2% with a median range of 0.6%–2.2%, and phosphorous from 0.1% to 0.5% with a median of 0.1%. The ratios of these elements (C:N:P) are often used to infer nutrient limitation. For example, for the giant kelp *M. pyrifera*, a C:N of < 20 indicates nitrogen sufficiency; whereas, > 25 indicates nitrogen-limited growth (Hurd *et al.* 1996). However, to confirm whether or not a particular nutrient is limiting requires experimental testing, in which seaweeds are grown at a range of nutrient concentrations and the relationship between percentage N (or percentage P) and growth is determined (i.e. growth kinetics; cf. Hanisak 1979; reviewed in Hurd *et al.* 2014).

MECHANISMS OF NUTRIENT UPTAKE

Nutrient uptake kinetics is a useful method to infer the mechanisms of uptake, to determine the uptake rate at a range of concentrations (Hurd *et al.* 2014), and to examine the potential of a seaweed for IMTA (Kang *et al.* 2013). Inorganic nutrients move across the cell membrane via three general mechanisms: (1) passive transport in which nutrients move via passive diffusion down a concentration gradient; (2) facilitated diffusion which is also by transport down an electrochemical gradient but carrier or channel proteins are involved; and (3) active transport against a concentration gradient, which, unlike 1 and 2, requires energy to fuel membrane transport systems; for example, carrier proteins (see Harrison & Hurd 2001; Hurd *et al.* 2014). To obtain a ‘kinetic curve’ for a seaweed, uptake rate is measured at a range of nutrient concentrations using either a time course of depletion or multiple flask method: the relative utility of each method is discussed in Harrison & Druehl (1982), Hurd & Dring (1990), and Pedersen (1994).

A plot of nutrient uptake rate against concentration yields various patterns, which can be used to infer the mechanism of uptake. If a linear regression is observed, then uptake is most likely via passive diffusion. If uptake rate follows a hyperbolic curve whereby the rate is linear at low concentrations and then reaches a plateau (termed saturated uptake), then the mechanism is either active transport or facilitated diffusion: it is not possible to categorically determine which of these mechanisms is operating without further mechanistic experiments using inhibitors (e.g. Barr *et al.* 2004). A hyperbolic curve is often called a ‘Michaelis-Menten’ curve from which two ‘kinetic parameters’ are derived: maximum uptake rate (V_{\max}) and half-saturation constant (K_s). A low K_s value indicates a high affinity for the nutrient at low concentrations, but because its value is dependent on V_{\max} , other parameters are used to determine uptake abilities at low concentrations: (1) ‘uptake efficiency’, the ratio V_{\max}/K_s (Perini & Bracken 2016; Smit 2002), and (2) ‘initial slope’ (I_s , also termed alpha) of a rectangular hyperbola which can be determined directly by plotting a linear regression to the linear part of the Michaelis-Menten curve (Nishihara *et al.* 2005; Smit 2002). The advantage of the latter method is that it allows a direct

comparison with seaweeds that exhibit linear (i.e. diffusive) uptake. Finally, both passive and saturated uptake systems can occur simultaneously, which is termed ‘biphasic’ or ‘multiphasic’ uptake, and indicates that two or more uptake systems are operating (Rees 2014; Taylor *et al.* 1998).

NO_3^- uptake by macroalgae is thought to be via active transport, although this has been confirmed (using inhibitors) for very few species. NH_4^+ uptake tends to be via passive diffusion, although for *Scytothamnus australis* (J.Agardh) J.D.Hooker & Harvey, uptake was linear in summer but showed saturating kinetics in winter. In addition, when very high concentrations of NH_4^+ were supplied (700 μM) in a time course experiment, saturating uptake kinetics were observed for *Undaria pinnatifida* (Harvey) Suringar, *Ecklonia cava* Kjellman, *Gracilaria incurvata* Okamura, *Porphyra yezoensis* [= *Pyropia yezoensis* (Ueda) M.S. Hwang & H.G.Choi] and *Ulva compressa* Linnaeus (Kang *et al.* 2013): this study illustrates that if concentrations are sufficiently high, NH_4^+ uptake will become saturated; that is, the supply is greater than the metabolic demand.

For DIC acquisition, CO_2 is taken up via passive diffusion which is energetically ‘inexpensive’ compared to HCO_3^- uptake which is via active transport and requires energy (Raven *et al.* 2011). Mechanisms of HCO_3^- uptake have been investigated for relatively few species and can include proton pumps, H^+ -ATPase, direct HCO_3^- uptake via an anion exchange (AE) protein and external HCO_3^- dehydration mediated by CA_{ext} (Fernández *et al.* 2014). Seaweeds growing in light-limited habitats can increase uptake of CO_2 relative to HCO_3^- as a mechanism of reducing energetic costs (Cornwall *et al.* 2015; Hepburn *et al.* 2011).

NUTRIENT ASSIMILATION AND STORAGE

NO_3^- uptake and assimilation require energy from the light reactions of photosynthesis (Pritchard *et al.* 2015; Raven *et al.* 1992). NO_3^- is assimilated to NH_4^+ , which requires the synthesis and maintenance of two enzymes (nitrate and nitrite reductase) and energy from eight electrons (Boyd & Hurd 2009). However, NO_3^- can be stored in its inorganic form in cellular vacuoles. In temperate regions, NO_3^- storage may occur during winter when both temperature and light levels are low, and the stores are used in spring when light and temperature increase (e.g. Hurd *et al.* 1996). Urea is broken down into NH_4^+ and CO_2 via the enzyme urease (Phillips & Hurd 2004). NH_4^+ is not typically stored in large concentrations within the cell and is rapidly metabolised to amino acids via glutamine and glutamate synthetase (Taylor & Rees 1999).

PATTERNS OF UPTAKE AND PREFERENCES FOR DIFFERENT NITROGEN SOURCES

Understanding patterns of uptake and preferences of seaweeds for particular sources of a nutrient are key in optimising growth in aquaculture systems: some species prefer NH_4^+ over NO_3^- ; whereas, others show no preference and grow equally well on both. Seaweeds may show ‘surge uptake’, a term used to describe a rapid uptake of a nutrient over a relatively short period of time (10–60 min), often following a period of reduced nutrient supply. Surge uptake of N_i has been reported for several species.

When NH_4^+ was the sole nitrogen source for *Kappaphycus alvarezii* (Doty) Doty ex P.C.Silva, increasing concentrations resulted in surge uptake for the first 30 min: the rate of surge uptake was greater with a higher initial NH_4^+ concentration (Dy & Yap 2001). Similarly, surge NH_4^+ uptake was reported for *Stictosiphonia arbuscula* (= *Bostrychia arbuscula* W.H.Harvey) and *Scytothamnus australis* (Phillips & Hurd 2003). Interestingly, surge NH_4^+ uptake also occurs when both NO_3^- and NH_4^+ are supplied together: NO_3^- uptake by *Laminaria groenlandica* [= *Saccharina latissima* (Linnaeus) C.E.Lane, C. Mayes, Druehl & G.W.Saunders] was completely suppressed in the first 30 min while surge NH_4^+ uptake occurred (Harrison et al. 1986). Thereafter, *S. latissima* took up both nitrogen sources simultaneously, at similar rates that were also equal to the rates when only NO_3^- or NH_4^+ was present in the medium (Harrison et al. 1986).

Seaweeds often take up NO_3^- and NH_4^+ simultaneously, but rates may be different for each nitrogen source. For example, NH_4^+ was taken up more rapidly than NO_3^- in both *Hypnea musciformis* (Wulfen) J.V.Lamouroux and *Macrocystis pyrifera*, but at high NH_4^+ concentrations NO_3^- uptake was partially inhibited for *Hypnea* but not by *Macrocystis* (Haines & Wheeler 1978). In contrast, when NO_3^- , NH_4^+ and urea were provided simultaneously, four intertidal seaweed species (*Bostrychia arbuscula*, *Apophlaea lyallii* J.D.Hooker & Harvey, *Scytothamnus australis*, and *Xiphophora gladiata* (Labillardière) Montagne ex Kjellman) were capable of simultaneous uptake of all N forms at different rates (Phillips & Hurd 2003).

In phytoplankton and higher plants, NH_4^+ has a range of interactive effects with other aspects of cellular metabolism; it can inhibit NO_3^- uptake, stimulate or depress primary production and growth, and, at high concentrations or when supplied as an exclusive source of N, cause toxicity (Britto & Kronzucker 2002; Collos & Harrison 2014). In seaweeds, such interactions are not well understood. For *Codium fragile* (Suringar) Hariot, the ability of NH_4^+ to inhibit NO_3^- uptake depends on the NH_4^+ concentration: NH_4^+ concentrations of 1 μM can reduce the uptake of both NO_3^- and NO_2^- by 26% and 31%, respectively; whereas, at higher concentrations (10 μM), NH_4^+ completely inhibited NO_3^- and NO_2^- uptake (Hanisak & Harlin 1978). For *Gracilaria vermiculophylla* [= *Agarophyton vermiculophyllum* (Ohmi) Gurgel, J.N.Norris et Fredericq], in the presence of high concentrations of both NH_4^+ (150 μM) and NO_3^- (450 μM), a higher NO_3^- uptake rate was observed than for NH_4^+ (Abreu et al. 2011a). However, following a single addition of each N_i source at a lower concentration (50 μM), the NH_4^+ uptake rate was higher than that of NO_3^- . It is unclear whether the NH_4^+ supplied at a high concentration facilitated NO_3^- uptake or caused a reduction in its own uptake as a control mechanism against toxicity (Abreu et al. 2011a). Furthermore, the ability of NH_4^+ to inhibit NO_3^- uptake appears to be life-stage dependent: the presence of NH_4^+ inhibited NO_3^- uptake in mature plants but not in germlings of *Fucus distichus* Linnaeus (Thomas et al. 1985).

Algal growth and biomass production under different N_i forms can be used as a proxy for nitrogen uptake and use efficiency. For example, *Fucus spiralis* Linnaeus grew similarly

on either NH_4^+ or NO_3^- (Topinka & Robbins 1976); whereas, *Gracilaria foliifera* (Forsskål) Borgesen and *Neogardhiella baileyi* [= *Agardhiella subulata* (C.Agardh) Kraft & M.J. Wynne] grew faster in NH_4^+ -enriched cultures than in NO_3^- - or sewage-enriched cultures (DeBoer et al. 1978). Higher growth rate and consistently higher biomass yield was also reported in *Ulva lactuca* Linnaeus fertilised with NH_4^+ than with NO_3^- (Ale et al. 2011). These examples show species-specific differences in the preference of NH_4^+ and NO_3^- and corresponding growth responses.

Research on nitrogen nutrition in seaweeds has focused on inorganic sources NO_3^- and NH_4^+ , the mechanisms and rates of uptake, and the relative preference of one source over the other. However, some species are able to take up a third inorganic source, nitrite (NO_2^-); for example, *Codium fragile* subsp. *tomentosoides* [= *Codium fragile* subsp. *fragile* (Suringar) Hariot], which may be responsible for its competitive advantage over other algae (Hanisak & Harlin 1978) and its invasive success. However, NO_2^- uptake and assimilation by seaweeds has rarely been studied because NO_2^- is not considered a major form in natural seawater: this view may have hampered our understanding of the relative importance of NO_2^- as an inorganic source for seaweeds. Moreover, NO_2^- can be an important component of discharge from some marine animal hatcheries; for example, concentrations of 8 mM were observed in effluent from a shrimp farm in Malaysia (Rabiei et al. 2016). Therefore, knowledge of the rates and mechanisms of NO_2^- uptake are needed for further development of some IMTA systems.

ABIOTIC FACTORS AFFECTING NUTRIENT UPTAKE

Knowledge of seaweed nutrient physiology and the environmental factors affecting nutrient uptake and metabolism is important to evaluate for the enhancement of commercial biomass production. Here, we explore the effects of the key abiotic factors on seaweed nutrient uptake.

Water motion

Water motion is a fundamental driver of nutrient uptake and seaweed productivity because it regulates both the larger scale supply of nutrients and DIC via advection to the seaweed surface and the thickness of the velocity and diffusion boundary layers (DBLs) that form at the seaweed surface (Hurd 2017). Nutrients move across the DBL via molecular diffusion; therefore, in slow flows, where thicker boundary layers form, the supply of nutrients may be reduced compared to fast flows, termed 'mass transfer limitation' of growth (Hurd 2000). Many laboratory studies illustrate how NO_3^- and NH_4^+ uptake rates increase with seawater velocity, until a maximum rate is reached (see review by Hurd 2017). Simulating wave action can also cause increased growth rates (Barr et al. 2008). The velocity at which the uptake rate saturates will depend on the species' requirement for a nutrient and also on the seaweed's morphology and growth form. Seaweeds growing in dense beds create a 'canopy boundary layer', an additional layer across which nutrients must travel in order to reach the seaweed surface (Hurd 2017).

Increasing velocities do not always cause an increase in uptake rate. For the red seaweed *Adamsiella chauvinii* (Harvey) L.E. Phillips & W.A. Nelson, increasing water motion caused an increase in NH_4^+ uptake but not NO_3^- (Kregting *et al.* 2008). In addition, if the concentration of nutrients within the water column is low (e.g. in summer in temperate systems), water velocity may have no effect on growth rate. For example, growth rates of the giant kelp *M. pyrifera* were enhanced by water velocity in autumn, at which time the seaweeds were nitrogen limited and the supply of nitrogen in the water column was relatively high. However, water motion had no effect on growth in the other seasons. In winter, light was the factor limiting growth; in spring the seaweeds were nitrogen sufficient, and thus, increasing N supply had no effect on growth, and in summer there was no N_i in the seawater (Hepburn *et al.* 2007; Hurd 2017).

In general, in both onshore and offshore seaweed cultivation systems, optimal seawater flow is beneficial for maximal nutrient and DIC supply; that is, DBLs are as thin as possible. For example, line cultivation of *Undaria pinnatifida* in Galicia, northwest Spain, yielded higher biomass when grown in a moderately exposed compared to a wave-sheltered site (Peteiro & Freire 2011). Water motion also generates drag forces on seaweed thalli, which may enhance productivity via increased DIC uptake (Kraemer & Chapman 1991), but too much water motion damages thalli and can rip seaweeds off the substratum (Kawamata 2001).

Light

Seaweeds are exposed to a diurnally variable and dynamic light regime which drives photosynthesis and growth; likewise, light intensity affects nutrient uptake. Consequently, under suboptimal light levels, addition of nutrients will have minimal effect on growth rate. Diurnal regulation in N_i uptake by phototrophs has significance in terms of the overall energy budget, for example, the amount of energy that can be allocated to growth. It is generally considered that nitrogen incorporation during the day is energetically less expensive than at night. This is because during daylight, the energy and carbon necessary for the assimilation process are provided directly by photosynthesis; whereas, in the dark, accumulated carbohydrates are the energy source (Huppe & Turpin 1994; Turpin 1991). Several studies have revealed higher daytime uptake rates of NH_4^+ and NO_3^- compared to nighttime. For example, in *Laminaria longicuris* [= *Saccharina longicuris* (Bachelot de la Pylaie) Kuntze], NO_3^- uptake in the dark is 20%–40% lower than that in light (Harlin & Craigie 1978). In *Hypnea musciformis*, nighttime uptake of NO_3^- and NH_4^+ is also reduced by 41% and 64%, respectively, than under light (Haines & Wheeler 1978). The same light response has been reported in other brown and red seaweeds (e.g. Gordillo *et al.* 2002; Harrison *et al.* 1986; Pereira *et al.* 2008). Moreover, NO_3^- (and PO_4^{3-}) uptake rates increase with increasing daylength (Gordillo *et al.* 2002). Conversely, in *F. spiralis*, light has no effect on uptake of either NH_4^+ or NO_3^- , but it did stimulate NO_2^- uptake (Topinka 1978). The effect of light on N_i transport is likely related to active transport which is an energy-

related process, as opposed to passive diffusion, which does not require a light-dependent energy source.

It is more energetically expensive to incorporate NO_3^- than NH_4^+ because NO_3^- must be reduced to NH_4^+ (see above; Gordillo 2012). The strong preference for NH_4^+ and restricted use of NO_3^- in the slow-growing red macroalga *Anotrichium crinitum* (Kützting) Baldock inhabiting low-light habitats indicates the direct contribution of photosynthesis in providing energy for nutrient assimilation (Pritchard *et al.* 2015). Similarly, diffusive uptake of CO_2 by seaweeds increases relative to active uptake of HCO_3^- in low-light environments, and this, too, is considered a mechanism for reducing energetic costs when light is a limiting factor (Cornwall *et al.* 2015; Hepburn *et al.* 2011).

Temperature

Temperature affects all aspects of seaweed physiology through its regulation of enzyme activity, rate constants of chemical reactions, and the rate of diffusion of nutrients across boundary layers. For nutrients that are taken up by active transport, temperature is likely to affect rates because it will affect the activity of membrane transporters; whereas, there may be less effect on uptake via passive diffusion. For example, NO_3^- uptake by *Laurencia brongniartii* J. Agardh was higher at higher temperatures; whereas, NH_4^+ uptake was unaffected by temperature, probably because uptake is by passive diffusion (Nishihara *et al.* 2005). In temperate regions, seasonal patterns are also observed in uptake rates likely to be driven by monthly temperature changes. For summer-adapted *S. longicuris*, maximum NO_3^- uptake was observed at 15 °C, and at lower temperatures – 10, 5 and 0 °C – uptake was 13%, 34%, and 70% lower, respectively, than at 15 °C (Harlin & Craigie 1978). Seasonal variation in nutrient uptake is tightly coupled to temperature acclimation. For example, nutrient uptake of winter-adapted (10 °C) *S. longicuris* was 27% lower than that of summer adapted (15 °C) tissue; however, uptake at 10 °C was 32% higher in winter-adapted sporophytes than summer-adapted sporophytes exposed to winter temperature; that is, 10 °C (Harlin & Craigie 1976). An exception is the red seaweed *A. chauvinii*, for which uptake rates of NO_3^- and NH_4^+ were lower in summer than in winter (Kregting *et al.* 2008).

Cellular metabolism is reduced at temperatures above and below the optimum range, which can affect nutrient uptake. Dose–response curves, whereby seaweeds are grown at a range of temperatures and their nutrient uptake rates measured, have rarely been studied for seaweeds. *C. fragilis* exposed to five different temperatures (6, 12, 18, 24 and 30 °C) showed different optimum temperature ranges for different N_i sources. An optimal temperature range for V_{max} for NO_3^- was 18–24 °C; whereas, the optimal temperature range for NO_2^- and NH_4^+ was 12–24 °C (Hanisak & Harlin 1978). At a lower temperature (15 °C), *Gracilaria gracilis* (Stackhouse) Steentoft, L.M. Irvine & Farnham also has a higher affinity for NH_4^+ than for NO_3^- than at 20 °C (Smit 2002). The efficient NH_4^+ uptake at lower temperatures may also be related to its relative importance as the primary N source in winter for some cold-temperate

seaweed species (Phillips & Hurd 2003). The seasonal preference for specific nutrient sources of four intertidal seaweeds from New Zealand was $\text{NH}_4^+ > \text{NO}_3^- > \text{urea}$ during winter and $\text{NH}_4^+ = \text{NO}_3^- > \text{urea}$ in summer (Phillips & Hurd 2003). The above examples support the theory that assimilating NO_3^- is energetically expensive; as such, its metabolism is favoured at seasonally higher temperatures and in a saturating light environment.

Carbon dioxide

Because both carbon and nitrogen are required for balanced growth, the concentration of DIC in seawater can affect seaweed nitrogen uptake. For example, in *Hizikia fusiformis* [= *Sargassum fusiforme* (Harvey) Setchell], NO_3^- uptake was higher in CO_2 -enriched culture than ambient CO_2 (Zou 2005). Moreover, the higher CO_2 concentration also enhanced nitrate reductase (NR) activity during the light period. Greater maximum NR activity, higher affinity for NO_3^- , and a higher V_{max}/K_m ratio were observed in high CO_2 -grown thalli than in ambient CO_2 -grown thalli, indicating efficient enzyme activity under high CO_2 (Zou 2005).

In *M. pyrifera*, uptake rates of both NO_3^- and NH_4^+ were higher under higher CO_2 concentrations when seawater was enriched with NH_4^+ compared to NO_3^- (Fernández *et al.* 2017a). Moreover, irrespective of the seaweed's initial N status, NO_3^- uptake rates and NR activity increased under higher CO_2 but there was no enhancement of photosynthesis rates and growth (Fernández *et al.* 2017b). This suggests that higher $[\text{H}^+]$ /reduced pH under higher CO_2 concentrations plays a role in regulating N metabolism. Similarly, enhanced NR activity was observed in *Ulva rigida* C.Agardh when it was grown under a combination of high CO_2 and NO_3^- concentrations; however, when grown under low NO_3^- , NR activity was reduced regardless of CO_2 concentration (Gordillo *et al.* 2001). This suggests that the effects of CO_2 on N metabolism of *U. rigida* are likely associated with *de novo* synthesis of NR rather than with changes in C metabolism. Together with higher CO_2 , optimum light and temperature may also play important roles in translating higher NO_3^- uptake and NR activity into higher growth rates.

Salinity

Freshwater input from rainfall and rivers to coastal areas can bring nutrients from agricultural activities, thereby increasing nutrient levels in the sea. Seasonal and/or recurrent exposure to nutrient-rich, low-salinity water can potentially affect seaweed farm sites and corresponding biomass production.

Very few studies have investigated the effect of salinity on nutrient uptake. In the tropical *Kappaphycus alvarezii*, NO_3^- uptake was not affected under different salinities (20, 25, 30, 35, 40) but temperature seems to have a synergistic effect on uptake rate: at lower salinities (20 and 25; nutrient uptake was highest at 20 °C; whereas, at higher salinities, uptake was higher at 30 °C; Mandal *et al.* 2015).

When cold-temperate *Saccharina latissima* and *Laminaria digitata* (Hudson) J.V.Lamouroux were cultivated in nutrient-enriched (NO_3^- and PO_4^{3-}) brackish water (salinity 18), total

tissue N (as a proxy for nutrient uptake) increased by 47% and 33%, respectively, compared to the same species that were grown in nutrient-sufficient seawater (salinity 34) from a deep fjord (Mortensen 2017). Although NO_3^- concentrations between brackish and full-salinity seawater were not comparable, the study showed that both species are able to survive for up to 13 days under lower salinity when nutrient concentrations are elevated. Reducing seawater salinity to 50% of ambient increased NO_3^- uptake in *Fucus serratus* Linnaeus by c. 40%, which resulted in a 20% higher growth rate than 100% seawater (Gordillo *et al.* 2002). Moreover, *Enteromorpha intestinalis* (= *Ulva intestinalis* Linnaeus), which thrives in nutrient-rich estuaries, rapidly takes up available nutrients under low salinity for growth and short-term osmoregulation (Cohen & Fong 2004). This mechanism is thought to be responsible for the outbreak of opportunistic algal blooms – for example, *Gracilaria tenuistipitata* [= *Agarophyton tenuistipitatum* (C.F. Chang et B.-M.Xia) Gurgel, J.N.Norris & Fredericq] – in brackish waters (Wang *et al.* 2014). The few studies available suggest that interactive effects of high nutrient concentrations in seawater and low salinity may compensate for any independent negative effects of low salinity. Further studies are required to test this hypothesis.

Desiccation

When intertidal seaweeds are exposed to air, they are removed from their sources of nitrogen and phosphorous (Hurd & Dring 1990; Thomas *et al.* 1987a) but they are still able to acquire DIC as CO_2 . Seaweeds growing higher in the intertidal zone – for example, *Porphyra*, *Ulva* and *Fucus* spp. – are adapted to desiccation. Upon resubmergence into seawater containing nutrients, an increase in nitrogen (NO_3^- and NH_4^+) uptake rates has been reported in several species, including *Gigartina papillata* [= *Mastocarpus papillatus* (C. Agardh) Kützing], *Gracilaria pacifica* I.A.Abbott, *Ulva intestinalis*, *Fucus distichus*, and *Pelvetiopsis limitata* (Setchell) N.L. Gardner (Thomas *et al.* 1987a, 1987b). Similar patterns have been observed for PO_4^{3-} uptake with high-shore *F. spiralis* showing a surge uptake of PO_4^{3-} (Hurd & Dring 1991). Relative to vertical distribution pattern and emersion duration, *Bostrychia arbuscula* inhabiting the upper intertidal zone is competitively superior in N uptake than the same species and other species inhabiting the mid- to lower intertidal zone (Phillips & Hurd 2003, 2004). Mild (< 30%) desiccation enhances photosynthesis, because fluxes of CO_2 in air are 10,000 times greater than those in seawater (Bell 1993; Dring & Brown 1982; Madsen & Maberly 1990; Oates 1985). However, greater levels of desiccation are typically detrimental to photosynthesis. Seaweeds that are desiccation tolerant have various cellular mechanisms for rapidly repairing cellular membranes and metabolic processes upon rehydration (Burritt *et al.* 2002; Im *et al.* 2017; Kim *et al.* 2009, 2013; Kumar *et al.* 2011).

Farming methods for commercially valuable intertidal seaweeds have taken advantage of their desiccation tolerance to reduce the incidence of disease and growth of competing algal species (Blouin *et al.* 2007; Food and Agriculture Organization 2005). For the cultivation of nori – that is, *Porphyra* and

Pyropia spp. – fixed net cultivation systems (also known as ‘pole systems’) in the intertidal are often preferred over floating or semifloating cultivation systems in deep water, because they ensure periodic exposure of the seaweed to air (Pereira & Yarish 2010; Tseng 1981).

BIOLOGICAL FACTORS AFFECTING NUTRIENT UPTAKE

Life stages and age class

Different age classes of perennial seaweeds exhibit different nitrogen uptake kinetics; however, there has been no systematic study on nutrient requirements, kinetics, and metabolism in early life history stages of seaweeds. Among the few available studies, NO_3^- and NH_4^+ uptake rates of germlings of *Fucus distichus* were higher than those of mature thalli (20 to 40 times for NO_3^- and 8 times for NH_4^+ ; Thomas *et al.* 1985). Germlings are physiologically similar to sectional meristematic tissue – for example, apical fronds of *Fucus* and basal lamina of *Saccharina* – and because they are actively growing they have correspondingly higher nutrient requirements. In contrast, older fronds/lamina and stipes of mature seaweeds have a lower nutrient uptake rate which reflects their relatively low physiological activity and low N demands for maintenance of non- or slow-growing parts (Topinka 1978).

Comparison between different age classes of kelp sporophytes showed that first-year *S. latissima* sporophytes are able to take up twice as much N_i than older age classes (Harrison *et al.* 1986). Moreover, first-year kelps showed diel periodicity – that is, light:dark response in NO_3^- and NH_4^+ uptake – whereas, second- and third-year sporophytes did not (Harrison *et al.* 1986). Consequently, sporophytes with higher nutrient uptake and higher tissue N can contain higher protein (e.g. Mortensen 2017). Changes in total protein content and amino acid composition have implications for industrial applications of wild and cultivated biomass. Furthermore, for bioremediation initiatives, young and physiologically active plants will be more efficient than adult plants in removing excess nutrients.

To date, no comparative study has looked into the nutrient physiology of different life history stages (e.g. spores, gametophytes, sporophytes) of kelps, which are cultivated primarily for food and other industrial applications. Despite this shortfall, a study showed that NO_3^- enrichment during indoor cultivation of rope-seeded *U. pinnatifida* gametophytes until juvenile sporophytes developed produced larger sporophytes after 2- to 3-month outgrowth in the field than the control group (Gao *et al.* 2013). This suggests that growth and biomass production in adult sporophytes are enhanced when the early life history stages are nitrogen replete.

APPLICATION TO SEAWEED CULTIVATION

The sections above describe fundamental information on seaweed nutrient uptake and its regulation by abiotic and biotic factors. Here, we apply this knowledge to the production of

commercial seaweed products other than biomass (e.g. polysaccharides) and in aquaculture systems.

Effect of tissue nitrogen status on commercial products

For agarophytes and carrageenophytes, the flow of photosynthate into various end products (e.g. carbohydrate and protein) is dependent on tissue nitrogen status (Bird 1988; Bird *et al.* 1981; Chopin *et al.* 1990, 1995; Macler 1986). Nitrogen fertilisation increases N-based tissue compounds (e.g. amino acids, phycobiliprotein and chlorophyll), thereby increasing photosynthetic activity and growth but reducing phycocolloid content (e.g. agar and carrageenan). Conversely, nitrogen limitation reduces photosynthesis and growth and induces an altered C allocation towards N-free macromolecules; for example, storage of carbohydrates and/or lipids (Bird *et al.* 1981; Li *et al.* 1990; Macler 1986; Roleda *et al.* 2013). The partitioning to different carbohydrates in *Gelidium coulteri* Harvey was also affected by tissue nitrogen status, where N-enriched algae had higher floridoside levels and significantly lower amounts of agar and starch than found in N-limited plants (Macler 1986). Therefore, optimising the yield of valuable products requires knowledge of the interactions between nitrogen, phosphorous and carbon metabolism.

Seaweed polyculture: Complementary use, competition and facilitation

Co-cultivation of different seaweed species with different nitrogen physiologies – that is, those preferring NH_4^+ and those preferring NO_3^- – may be beneficial because niche partitioning can reduce competition (Bracken & Stachowicz 2006). For example, when eight species of intertidal seaweeds [five reds: *Mastocarpus papillatus*, *Mazzaella flaccida* (Setchell & N.L.Gardner) Fredericq, *Microcladia borealis* Ruprecht, *Porphyra perforata* [= *Pyropia perforata* (J.Agardh) S.C. Lindstrom], and *Prionitis lanceolata* (Harvey) Harvey; one brown: *Fucus gardneri* (= *Fucus distichus* Linnaeus); and two greens: *Cladophora columbiana* Collins and *Ulva taeniata* (Setchell) Setchell & N.L.Gardner] were cultivated in mono- and polycultures in the presence of both NO_3^- and NH_4^+ , uptake by the diverse assemblages was 22% greater than that in the monoculture (Bracken & Stachowicz 2006).

The choice of seaweed species in a polyculture should consider their complementary use of different nitrogen forms because some species – for example, *Porphyra* and *Ulva* – may not be suitable for co-cultivation with other species because both have high N demand and, consequently, they perform best in monoculture (Bracken & Stachowicz 2006). *Ulva linza* Linnaeus was also observed to outcompete *Gracilaria lemaneiformis* [= *Gracilariopsis lemaneiformis* (Bory de Saint-Vincent) E.Y.Dawson, Acleto & Foldvik] when grown together due to its fast nutrient uptake and also through allelopathy (Gao *et al.* 2014). Co-cultivation of *Ulva* species with different morphologies – that is, sheet-like and tubular – may result in competitive exclusion. For example, *U. intestinalis* can outcompete *Ulva expansa* (Setchell) Setchell & N.L.Gardner for nutrients and negatively affect growth rate

of the latter (Fong *et al.* 1996). Moreover, the release or leaking of dissolved organic nitrogen (DON) from *U. expansa* was readily available for assimilation by *U. intestinalis*, which facilitated growth and dominance of the latter species (Fong *et al.* 1996).

Integrated multitrophic aquaculture: Seaweed as biofilters

Among the different environmental concerns related to intensive fish farming, such as the effects of farmed fish escapees on wild populations, heavy metal leaching from fish cages, and effects of unregulated use of antibiotics, coastal eutrophication is a primary concern. Decomposition of excessive fish feeds and animal excretion can increase dissolved nutrients, primarily nitrogen, into the water column, which can lead to harmful algal blooms and deterioration of coastal environments (e.g. Buschmann *et al.* 2008a; Chopin *et al.* 2001; Domingues *et al.* 2015). IMTA is a farming method that aims to mitigate the impact of eutrophication associated with fish farming and enhance the sustainability of aquaculture by driving ecological efficiency, environmental acceptability, product diversity, profitability and societal benefit (Kleitou *et al.* 2018). IMTA refers to the integrated farming of several organisms from different trophic levels, where one species complements another. For example, in an IMTA system where seaweed is cultivated in close proximity to fish, the seaweed serves as a biofilter, assimilating excess nutrients from the fish farm and converting them into valuable biomass (Fig. 1; Fernández *et al.* 2019).

IMTA can be established in land-based fish farms where nutrient-rich seawater from fish tanks is supplied to separate tanks where seaweed is either cultivated (e.g. Abreu *et al.* 2011b; Corey *et al.* 2014; Domingues *et al.* 2015) or seeded on longlines and deployed proximate to fish and mussel farms (e.g. Buschmann *et al.* 2008b; Marinho *et al.* 2015). Species with efficient nutrient uptake/removal capacity – for example, *Gracilaria* spp., *Macrocystis pyrifera* and *Saccharina latissima* – have proved suitable for reducing excess nitrogen in fish farms (Abreu *et al.* 2011b; Buschmann *et al.* 2008b; Marinho *et al.* 2015).

Light and temperature are the primary environmental factors that affect the capacity of seaweeds to remove nutrients, which, consequently, control seaweed growth and productivity. For example, in a land-based IMTA system, *Agarophyton vermiculophyllum* is more efficient in removing nitrogen from fish farms in northern Portugal from spring to summer (April–August) and less efficient during winter (Abreu *et al.* 2011b). Conversely, integration of *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr with Atlantic halibut in Nova Scotia for nitrogen removal is feasible below 10 °C, but not in summer due to the seasonal life cycle of *P. palmata*, when reproductive maturation leads to thallus disintegration (Corey *et al.* 2014). At higher temperatures (17–21 °C) in northern Portugal, both *P. palmata* and *Chondrus crispus* Stackhouse are able to remove approximately seven times more nitrogen in a cascade IMTA system (Matos *et al.* 2006) than that reported in Nova Scotia (Corey *et al.* 2014). The success of an IMTA system is dependent not



only on the biology of the seaweed species and its stocking density but also on several environmental factors controlling nutrient uptake and assimilation.

In summary, knowledge of a seaweed's nutritional requirements and the regulation of nutrient uptake and assimilation by abiotic and biotic factors are key to bringing new species into aquaculture. In addition to the economic value of seaweeds, seaweed farming can have positive environmental impacts because it makes use of nutrient emissions from fish farms and other anthropogenic nitrogen and phosphorus sources that enter the ocean. Seaweed aquaculture can also take up anthropogenic carbon dioxide emissions that cause ocean acidification. Therefore, sustainable seaweed farming is good not only for the economy but also for the health of the ocean.

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