Seaweed factsheet:

Nutrient uptake and requirements

Carrying capacity in seaweed cultivation

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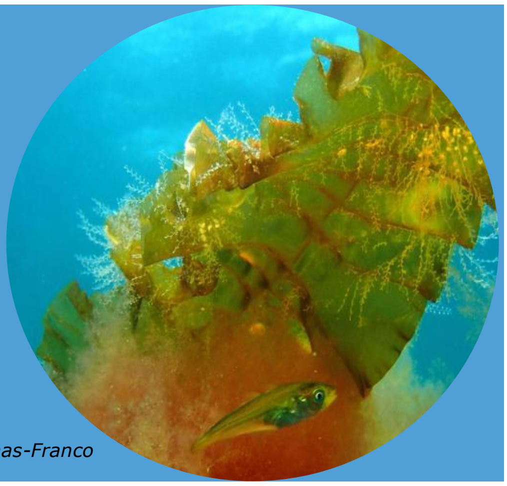

Nutrient requirements in seaweeds

The requirements for carbon (C), nitrogen (N), and phosphorus (P) in seaweeds are highly dynamic. Each seaweed species has its own growth characteristics and internal composition, consequently the mean requirements for C, N, and P differ from species to species. The macronutrients that seaweeds need to grow, are usually relatively abundant in temperate waters. The nutrients are concentrated in the cell tissues of the seaweeds in about 100.000 times for N and P and 10.000 for carbon compared to their ambient seawater concentrations.
In all seaweeds, the general demand of CNP is:

C > N > P

The limiting elements for seaweed growth are N and P, while C is generally not limiting, due to a profound exchange between water surface and atmosphere, as well as input by biological and geothermal activity in the aquatic milieu and its release of CO_2 and CH_4. However, a C limitation may occur spatially and temporarily, especially in artificially introduced industrial-sized seaweed operations. In addition, different forms of N and P require an active transport to enter the cell, while C in form of a bicarbonate ion (HCO_3^-) enters the cell via diffusion pathways.

Phytoplankton vs seaweeds

In phytoplankton the atomic ratio of C:N:P is the classic Redfield ratio of 106C:16N:1P. However, most macroalgae have a higher nutrient ratio, which is species specific but a mean of 92 species showed a ratio of 550C:30N:1P. Which means that seaweeds are more carbon rich and require a lower concentration of P then of N, compared to phytoplankton. Therefore macroalgae become sooner N limited than. However in recent years the amount of anthropogenic riverine water entering the north sea has changed. Due to a change in agriculture policy and stricter pollution regulations, the amount of phosphorus has decreased significantly in the coastal regions.

Nitrogen has also decreased however not in the same amount as P. In the past nitrogen used to be the limiting macro nutrient for most primary productivity at sea. However due to the cleaner riverine input in the North sea, phosphorous has now become the limiting factor. This change in the traditional balance of nutrients in het North Sea could lead to a change in the phytoplankton community composition which can lead to changes further in the food chain.

Nutrient balance in the North sea

When cultivating seaweeds in the marine environment the balance of the natural system should always be kept in mind. Due to the anthropogenic influence of first increasing the nutrient load due to riverine pollution in the north sea and now in more recent years taking selective mitigation efforts the N:P ratio has increased and had become unbalanced. According to a study of Burson et al, the highest N:P ratio's in the north sea are found in march, ~30 µmol L^{-1} and ~0.63 µmol L^{-1} respectively. This is also the time the spring bloom is at its peak as well as the growth season of many seaweed species. The ratio of N:P has a gradient from 54:1 in the nearshore region to 4:1 in the off shore region. The Redfield ratio is found around ~130 km offshore in March. However, this gradient also changes with the seasons and in April just after the peak of the spring bloom the nutrients are becoming depleted in the near shore areas, the most extreme N:P measurements had ratios of 357:1 in the nearshore region to 1:1 in the off shore area. However this study was conducted with a transact from Texel up through the north of the North sea. Most seaweed studies for cultivation in the Dutch part of the North sea are more focused on the southern area near the border with Belgium. However here the seaweed cultivation might lead to a competition of nutrients with the shellfish sector which also extract the excess nutrients in the coastal areas see figure 1.

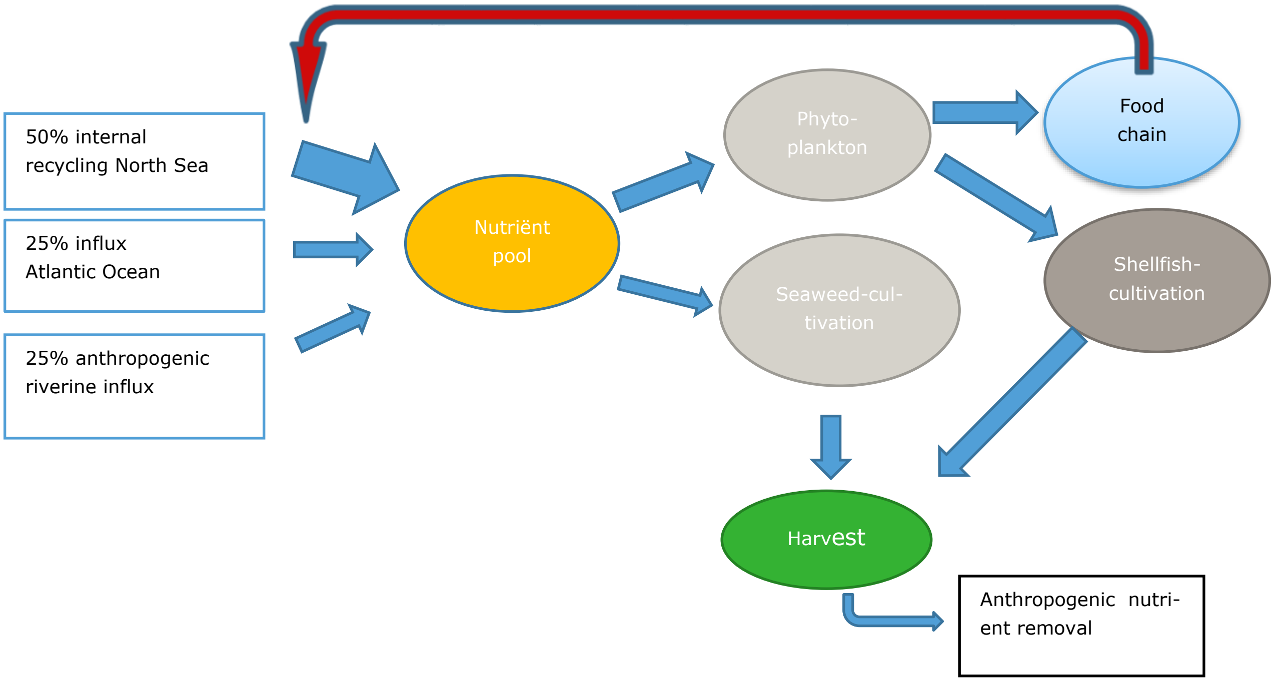

Figure 1. Nutrient cycle in the north sea Dutch coastal region, which shows the pathway of the nutrients and the extraction of anthropogenic inputs.

Seaweed metabolism

Depending on the nutritional background of the cell, respectively internal level of C, N, and P storages, uptake rates for N and P can vary. Hence, the nutrient uptake by seaweed can be split into three distinct phases, referred to as **surge uptake (V_S)**, internally controlled or **metabolic uptake (V_M)**, and externally controlled uptake (V_e), which describes an uptake limited by nutrient availability and environmental factors that influence the physiology of the seaweed. V_S refers to the filling of internal nutrient pools, uncoupled from growth. The uptake rates gradually decrease as internal nutrient pools in cytoplasm and vacuoles are filled. When internal nutrient concentrations are constant and relative uptake rates of nutrients remain relatively stable over time, V_M, which is considered equal to the rate of assimilation, is attained (Fig. 2). The uptake rate under V_M can be up to 80-90% smaller than under V_S. The previously filled internal nutrient storage (ISC) can be utilized at times of low external nutrient availability.

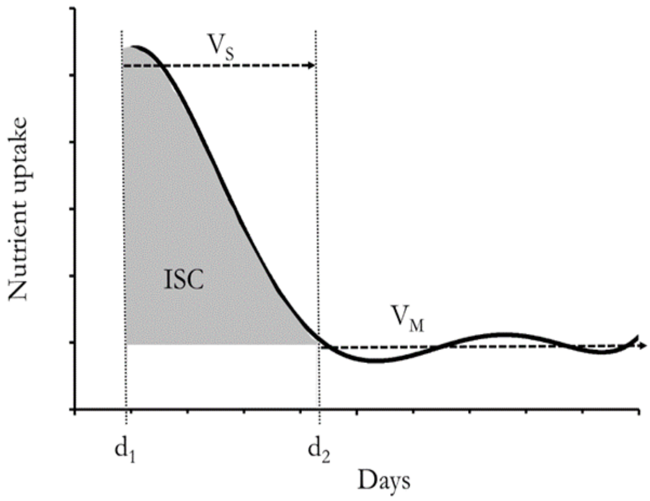

Figure 2. Example graph of nutrient uptake over time (days) illustrated with surge uptake (V_S), maintenance uptake (V_M), internal storage capacity (ISC), and d_1 and d_2 as difference operator between days, after a significant decrease in nutrient uptake occurs.

Coupled nutrients

Uptake rates for N and P in some seaweed species is **coupled**. For example, the red seaweed *Palmaria palamata* requires the availability of P in order to surge for N. In other species, for example the green seaweed *Ulva lactuca*, N and P uptake are **uncoupled**, i.e. independent of each other. Besides dynamic, coupled and un-coupled nutrient uptake rates, seaweed species developed different nutrient uptake strategies attributed to survival and competitive advantages. **Uptake rates under V_M may be rhythmic**, like in *P. palmata*, which shows a weekly oscillating uptake, **or almost linear** as observed for the brown seaweeds *Saccharina latissima* and *Laminaria digitata* and the green seaweed *U. lactuca*. Limitations are influencing metabolism, growth, and internal composition in seaweeds. N represents a key element in the protein production, respectively amino-acid synthesis and N-limitation directly affects the carbohydrate to protein ratio and therefore the nutritional value (Fig. 2). In addition, it has been shown that some forms of N increase growth rate in seaweed, whereas other forms increase tissue N, and therefore protein content (Grote 2016). Nitrate (NO_3) was found superior to ammonium (NH_4) as a source of N for growth and for example, *P. palmata* supplied with NH_4 accumulated more tissue nitrogen than plants supplied with NO_3 within the same time span

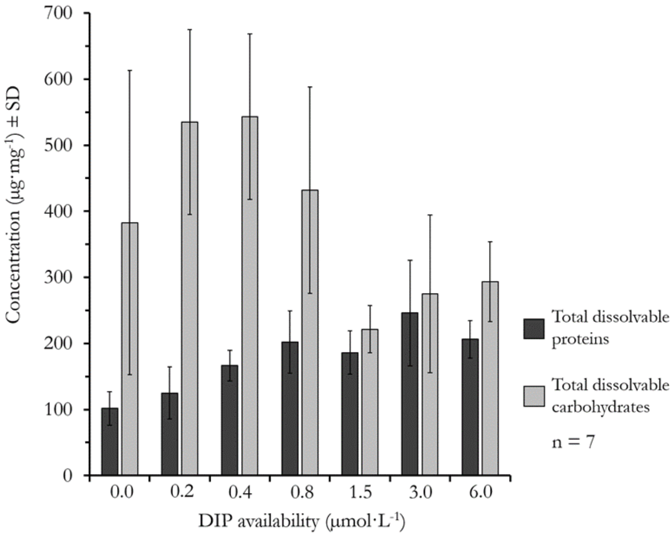

Figure 2. Mean total dissolvable protein and carbohydrate concentration (µg·mg^{-1} of dry weight) ± SD of young *Palmaria palmata* sporophytes (n=7), after cultivation in a range of dissolved inorganic phosphate (DIP) concentrations (0.0 – 0.2 – 0.4 – 0.8 – 1.5 – 3.0 – and 6.0 µmol·L^{-1}) and a dissolved inorganic nitrogen (DIN) concentration of 50 µmol·L^{-1} in a 'pulse-and-chase' assay for 5 weeks .

Table 1. Nutrient ratio's for some seaweeds species worth considering for cultivation in the Dutch North sea area, also shown is the carbohydrate and protein percentage if the seaweeds.

Seaweed Species	**Common name**	**C:N**	**N:P**	**C:N:P ratio in tissue**	**% carbohydrates**	**% protein**	**References**
Winter sp.							
Saccharina latissima	Sugar kelp	9:1 9:1	13:1 70:1 14:1	117:13:1 630:70:1 126:14:1	61	6-11	(Lubsch and Timmermans, 2019) (Bruhn *et al.*, 2016) (Morrissey, Kraan and Guiry, 2001)
Laminaria digitata	Oarweed	10:1 22:1	8:1 25:1	80:8:1 606:25:1	48	8-14	(Lubsch and Timmermans, 2019) (Schaal, Riera and Leroux, 2009) (Pedersen, Borum and Fotel, 2010)
Summer sp.							
Ulva lactuca	Sea lettuce	15:1 9:1	30:1 79:1	450:30:1 711:79:1	17-70	3-26	(Lubsch and Timmermans, 2019) (Tonk and Jansen, 2019) (Pedersen, Borum and Fotel, 2010)
Ulva rigida	Sea lettuce	11:1		110:10:1	42-64	15-25	(Faganeli *et al.*, 1988) (Morrissey, Kraan and Guiry, 2001)
Year round							
Fucus vesiculosus	Bladder wrack	23:1	34:1	782:34:1			(Pedersen, Borum and Fotel, 2010)
Ascophyllum nodosum	Knotted wrack	22:1	37:1	814:37:1			(Pedersen, Borum and Fotel, 2010)
Palmaria palmata	Dulse	10:1 15:1	10:1 12:1	100:10:1 180:12:1	22-54 46-50	10-25 12-21	(Lubsch and Timmermans, 2019) (Corey *et al.*, 2013) (Martinez and Rico, 2002)

Cultivation considerations for seaweed applications

In addition, it has been shown that some forms of N increase growth rate in seaweed, whereas other forms increase tissue N, and therefore protein content. Nitrate (NO_3) was found superior to ammonium (NH_4) as a source of N for growth and for example, *P. palmata* supplied with NH_4 accumulated more tissue nitrogen than plants supplied with NO_3 within the same time span. All these different CNP requirements, stoichiometry and uptake strategies should be paid attention to in operations of seaweed cultivation. For example when seaweed is used as bioremediation, especially when targeting crop-specific harvest for different applications, as in **feed (higher % protein desirable)** and/or **energy (higher % carbohydrate desirable)**. When nutrients are added to a cultivation site, a precise dosage is essential for optimal growth and to prevent eutrophication. On the other hand, large scale cultivation of seaweed in open systems can lead to spatial nutrient limitations and depletions, which can mitigate, shift, or change composition of phytoplankton blooms, thus affecting the whole food web. Ecosystem Knowledge on the CNP management and N:P stoichiometry of different seaweed species is therefore essential (see table 1). Whether it concerns **mono-cultures**, **layered cultures**, **integrated aquaculture systems**, or the integration of multiple approaches. In a similar context, seaweed cultures can conceivably be used for **bioremediation** purposes and, for example, minimize the impact of nutrients released by fish farms and areas of eutrophication, as well as in land-based **bio-filtration** facilities. Additionally knowing the nutrients requirements of the seaweeds can help estimate the caring capacity of the natural system you want to cultivate in. see table 2.

Table 2. Nutrient uptake of dissolved inorganic phosphate-and nitrate during a maintenance and starvation period of 4 seaweed species, also shown is the general storage capacity

Species	DIP uptake "maintenance" µmol.cm².day	DIP uptake "starvation" µmol.cm².day	DIN uptake "maintenance" µmol.cm².day	DIN uptake "starvation" µmol.cm².day	Storage of DIP and DIN µmol.cm²
Ulva lactuca	0.07± 0.04	0.66± 0.12	2.3± 0.9	12.5± 5.2	0.7 and 23
Saccharina latissima	0.30± 0.09	0.80± 0.03	3.9± 0.7	11.3± 0.6	14 and 49
Laminaria digitata	0.22± 0.01	0.38± 0.03	1.8± 0.4	3.9± 0.1	10 and 80
Palmaria palmata	0.57± 0.22	1.57± 0.29	5.6± 2.1	15.6± 4.3	22 and 222

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