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Estimates of nutrient loading, water residence time, light attenuation coefficients, phytoplankton abundance, and colonisation depth and abundance of benthic macrophytes in European coastal areas of different nutrient regime

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Executive Summary

The objective of this deliverable is to compile data from the literature and available data-bases on nutrient loading and concentrations in the water column, water residence time, light attenuation in the water column, phytoplankton abundance, and the colonization depth and abundance of the dominant benthic vegetation, to analyse relationships and define thresholds between drivers and indicators of ecosystem structure. We do so, by compiling and analysing two data sets:

- data set on nutrient loading and concentrations in coastal European waters, in order to develop thresholds and shifts of planktonic biomass development driven by nutrient inputs and concentrations in coastal waters
- data set on seagrass colonisation depths and light attenuation coefficient to set the threshold of minimum light requirements for a shift from sediments colonised by seagrasses to sediments without them.

The results obtained indicate that moderately eutrophic European coastal waters are characterized by an excess N relative to P in its waters, identifies total nitrogen concentration and loading as drivers for phytoplankton biomass and production, and shows that light attenuation in coastal waters is the primary driver for benthic communities to shift from seagrass to sediment dominated ones. Relationships between drivers and phytoplankton and seagrass responses are provided.

1. Introduction

Nutrient loading to the coastal zone alters species hierarchies in the communities of primary producers favouring those species with fast growth and fast nutrient uptake rates (Duarte 1995). Proliferation of fast growing primary producers reduces light availability for benthic vegetation, often resulting in losses of benthic plant populations. The decline of benthic macrophytes, reduces the amount of oxygen pumped into the sediments and, simultaneously with the accumulation on the sediment surface of part of the organic matter produced by fast-growing primary producers, increases sediment oxygen demand. The risk of sediment anoxia thereby increases and may further threaten the benthic vegetation. In addition, the loss of benthic vegetation enhances sediment resuspension, and, thus, deterioration of light conditions, accelerating the decline of benthic plant populations. As a result slow-growing macrophytes (mainly seagrasses) are replaced by fast-growing macrophytes (chlorophytes, epiphytes) and phytoplankton (Duarte 1995). Effect of nutrient loadings and altered patterns of abundance of the different groups of primary producers are, in turn, controlled by the turnover rate of the water mass in the coastal zone.

The objective of this deliverable is to compile data from the literature and available data-bases (including monitoring data) on nutrient loading and concentrations in the water column, water residence time, light attenuation in the water column, phytoplankton abundance, and the colonization depth and abundance of the dominant benthic vegetation, to analyse relationships and define thresholds between drivers and indicators of ecosystem structure. We do so, by compiling and analysing two data sets:

- data set on nutrient loading and concentrations in coastal European waters, in order to develop thresholds and shifts of planktonic biomass development driven by nutrient inputs and concentrations in coastal waters
- data set on seagrass colonisation depths and light attenuation coefficient to set the threshold of minimum light requirements for a shift from sediments colonised by seagrasses to sediments without them.

2. Planktonic biomass and nutrient inputs and concentrations in coastal waters

2.1. Data base and statistical analyses.

The data base produced contains data for 1213 marine systems in total. The data base, containing scattered values for ecosystem properties has been assimilated into a relational data set, whereby all values available for an individual system in a given year have been averaged, thereby avoiding, whenever possible, over-representing individual samples, which may introduce great uninformative variation in the analysis. Whenever data from multiple years were available, these were used as independent observations in the analysis. See sample size in Table 1. The data pertains to coastal areas throughout Europe, although it is heavily biased towards Atlantic coastal waters. Hence, the mean values reported do not represent unbiased estimates of mean values for European coastal waters as a whole. In order to avoid this bias, we chose to analyze the data using linear regression analysis, following logarithmic transformation, which was found to be necessary in order to comply with the requirements of the analysis. We have also provided additional information on nutrient loading data using published reports of total nutrient concentrations and nutrient inputs in coastal areas around the world (Nixon 1995, Borum 1996, Downing 1997).

2.2. Relationships between nutrient concentrations, and nutrient ratios

Nutrient concentrations in European coastal waters ranged greatly, typically spanning over three orders of magnitude (Table 1). Nutrient concentrations were highly correlated to one another, with nitrate and ammonium concentrations being closely correlated ($r = 0.85$, $P < 0.0001$; Fig. 2.1).

The relationship between the concentrations of ammonium and nitrate was best described by the regression equation:

$$\log \text{NH}_4 (\mu\text{M}) = -0.078 + 0.607 (0.03) \log \text{NO}_3 (\mu\text{M})$$

($N = 13$, $R^2 = 0.713$, $F = 323.45$, $P < 0.00001$)

which indicates that the concentration of ammonium increases as the $2/3$ power of that of nitrate. Hence, the concentration of ammonium increases slower than that of nitrate, so that the ratio of ammonium to nitrate concentration should decrease with increasing nutrient concentration (Fig. 2.2). The shift from a dominance of ammonium to a dominance of nitrate in the dissolved inorganic nitrogen pool occurs when the average nitrate concentration exceeds $1 \mu\text{M}$. The relationships between the concentrations of dissolved inorganic nitrogen forms and phosphorus were also strong (ammonium vs. phosphate, $r = 0.85$, $P < 0.0001$; nitrate vs. phosphate, $r = 0.83$, $P < 0.0001$; Fig. 2.3). These relationships were described by the equations:

$$\log \text{PO}_4 (\mu\text{M}) = -0.76 + 0.81 (0.03) \log \text{NO}_3 (\mu\text{M})$$

(R2 = 0.68, N = 322, F = 684, P < 0.00001)

and,

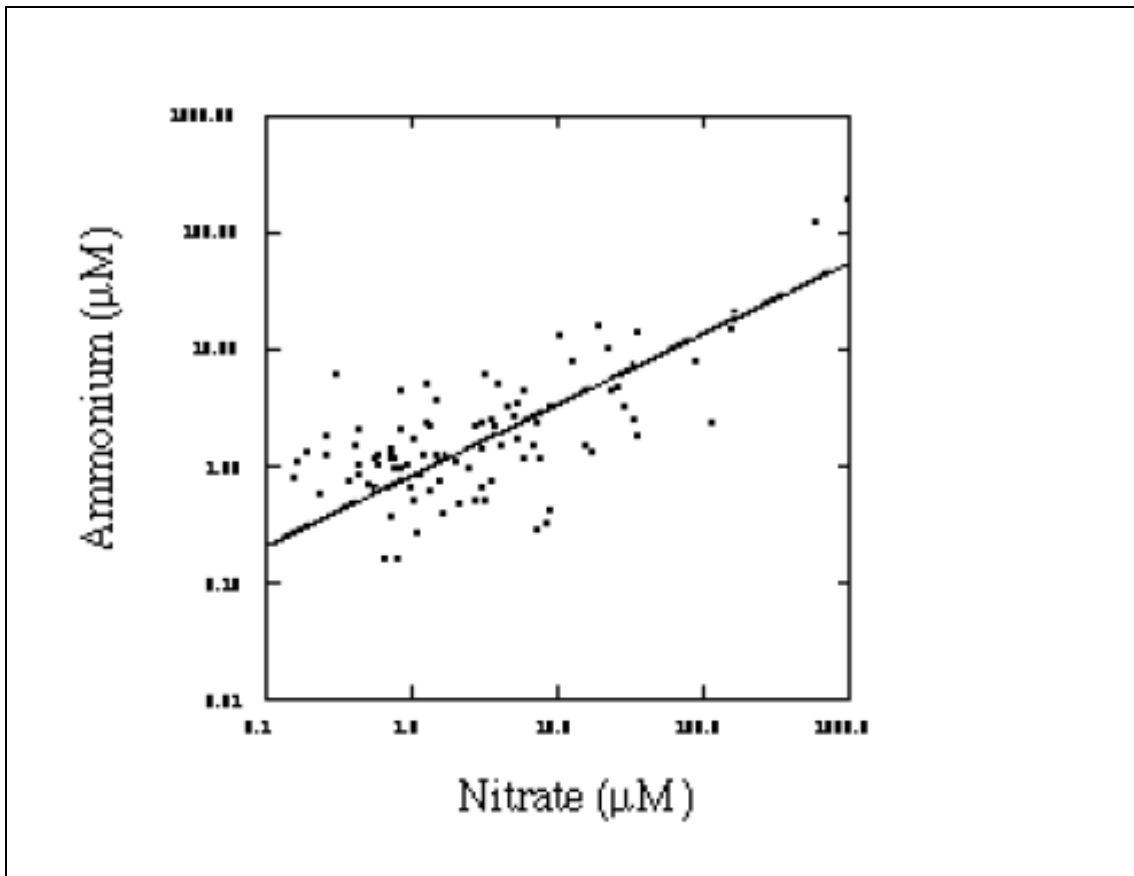
$\log \text{PO}_4 (\mu\text{M}) = -0.51 + 1.18 (0.06) \log \text{NH}_4 (\mu\text{M})$
 (R2 = 0.71, N = 140, F = 347, P < 0.00001)

Table 2.1 Sample sizes on annual values of nutrient concentrations and loading and resulting phytoplankton biomass (as Chl *a* concentration) and primary production in European coastal waters

Variable	units	minimum	maximum	mean	n
<u>Coastal Seas</u>					
Nitrate	$\mu\text{M N}$	0.15	980.46	6.29	357
Nitrite	$\mu\text{M N}$	0.07	9.43	0.30	54
Ammonium	$\mu\text{M N}$	0.07	400.00	2.21	144
Phosphate	$\mu\text{M P}$	0.01	376.91	0.71	439
Silicate	$\mu\text{M Si}$	0.00	7732.68	12.35	169
Total Nitrogen	$\mu\text{M N}$	1.00	4360.04	93.76	123
Total Phosphorus	$\mu\text{M P}$	0.03	538.60	3.66	130
Chlorophyll a	$\mu\text{g/L}$	0.09	110.60	5.52	161
Primary Production	$\text{mol C/ m}^2 / \text{year}$	1.57	425.00	25.46	129
Particulate matter	mg/L	5.00	40.89	17.43	26
Particulate C	$\mu\text{M C}$	2.00	242.67	30.01	17
Particulate N	$\mu\text{M N}$	1.62	29.30	6.86	8
Particulate P	$\mu\text{M P}$	0.26	1.42	0.42	4
Residence time	month	0.15	180.00	2.34	15
Depth	m	2.00	210.00	19.25	40
<u>Inputs¹</u>					
Nitrate	$\mu\text{M N}$	0.13	541.00	71.88	49
Ammonium	$\mu\text{M N}$	0.47	25.33	3.50	4
Phosphate	$\mu\text{M P}$	0.02	20.00	2.21	56
Total Nitrogen	$\mu\text{M N}$	0.00	14269.54	74.55	183
Total Phosphorus	$\mu\text{M P}$	0.00	1309.00	5.34	177
inflow	m^3/s	1.85	17000.04	309.91	87

1. Nutrient concentration in inflowing waters.

Figure 2.1 The relationship between the concentrations of ammonium and that of nitrate in european coastal waters



which indicate that phosphate concentrations increases somewhat faster than ammonium concentrations does, but somewhat slower than nitrate concentration does. Because both nitrate and ammonium concentrations were highly correlated to that of phosphate, this was also closely related to the dissolved inorganic nitrogen concentration (ammonium + nitrite + nitrate, Fig. 2.4), as described by the equation:

$$\log \text{PO}_4 (\mu\text{M}) = -0.88 + 0.86 (0.03) \log \text{DIN} (\mu\text{M})$$

($R^2 = 0.68$, $N = 140$, $F = 367$, $P < 0.00001$)

This equation indicates that the relationship between phosphate and dissolved inorganic nitrogen concentration is not linear in European coastal waters, though the geometric mean ratio of phosphate to dissolved inorganic nitrogen is close to Redfield (Fig. 2.5).

Total nitrogen and total phosphorous were strongly correlated (Fig. 2.6), but their relationship was not linear, such that total nitrogen concentrations far exceed the values expected from Redfield stoichiometry at low total phosphorus concentrations (total phosphorus $< 1 \mu\text{M}$, Fig. 2.7). Hence, moderately eutrophic European coastal waters are characterized by an excess N relative to P in its waters, evident both in the dissolved and the total nutrient pools (Fig. 2.4, Fig. 2.6).

Figure 2.2 The relationship between the concentrations of ammonium and nitrate in European coastal waters. The solid line represents the fitted regression equation

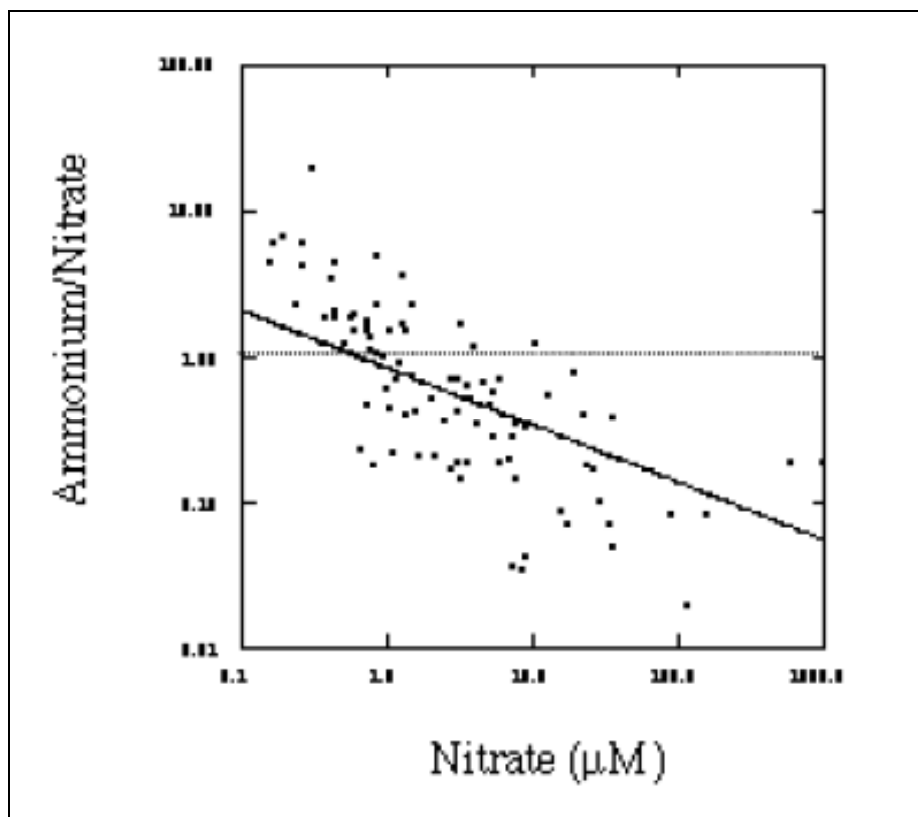


Figure 2.3 The relationship between the concentrations of phosphate and those of ammonium and nitrate in European coastal waters

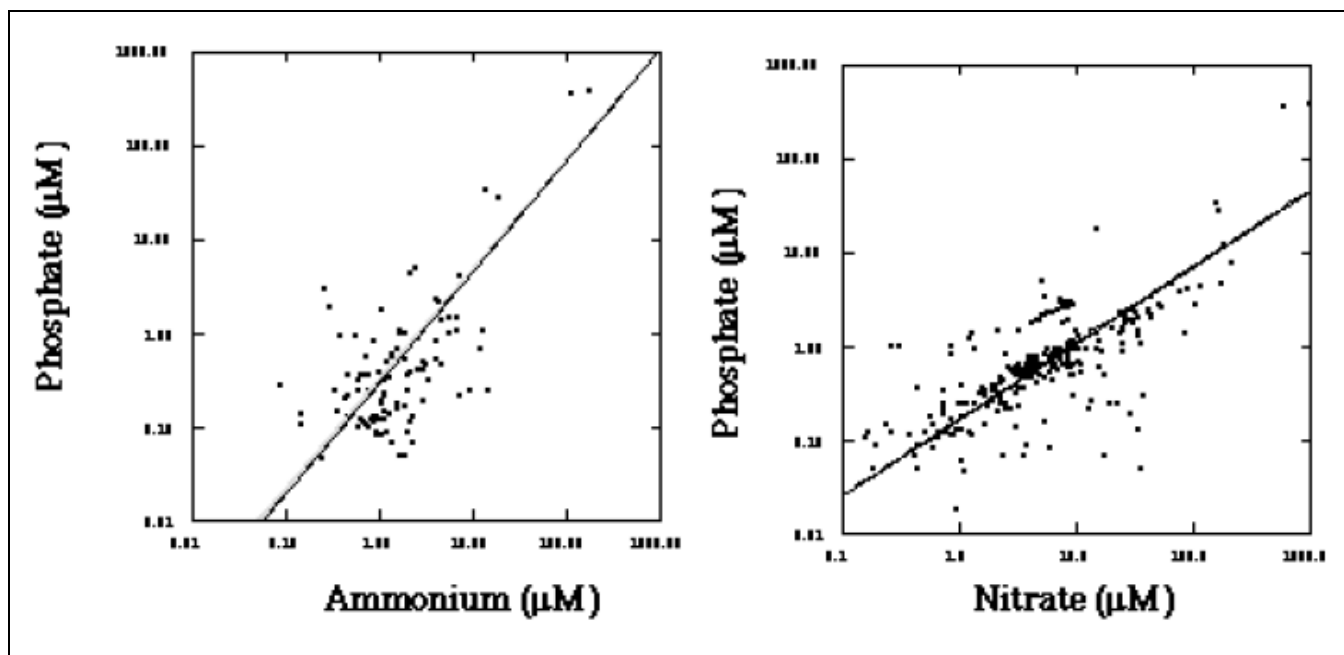


Figure 2.4 The relationship between the concentrations of phosphate and dissolved inorganic nitrogen European coastal waters. Dotted and solid lines indicate the fitted regression line and the Redfield stoichiometry, respectively

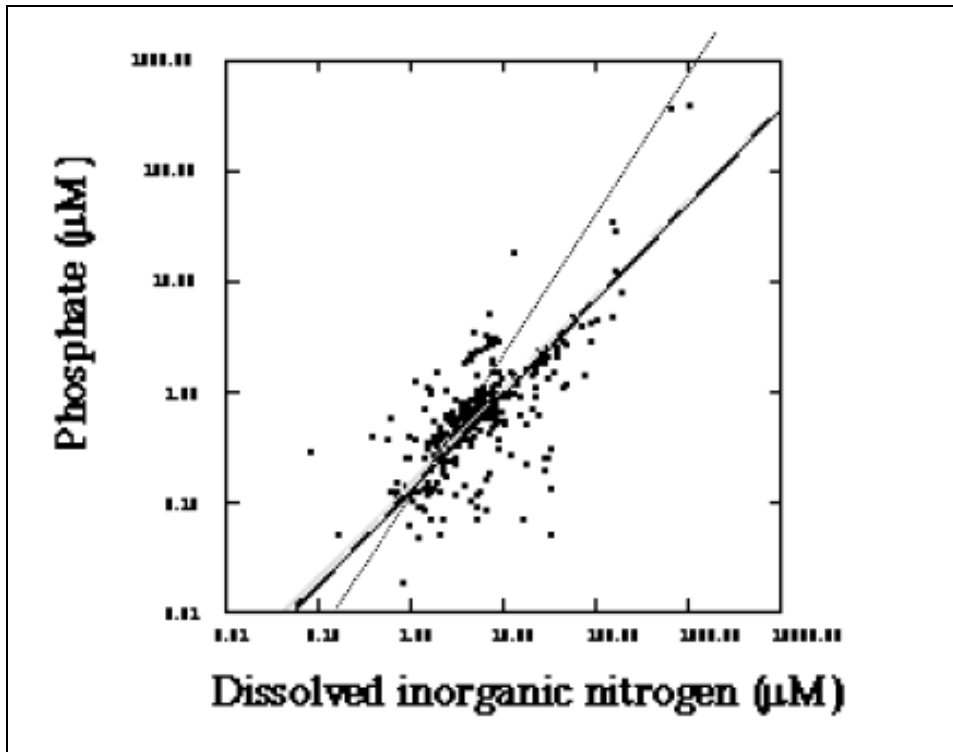


Figure 2.5 The frequency distribution of phosphate to dissolved inorganic nitrogen in European coastal waters. The arrow indicates the Redfield ratio

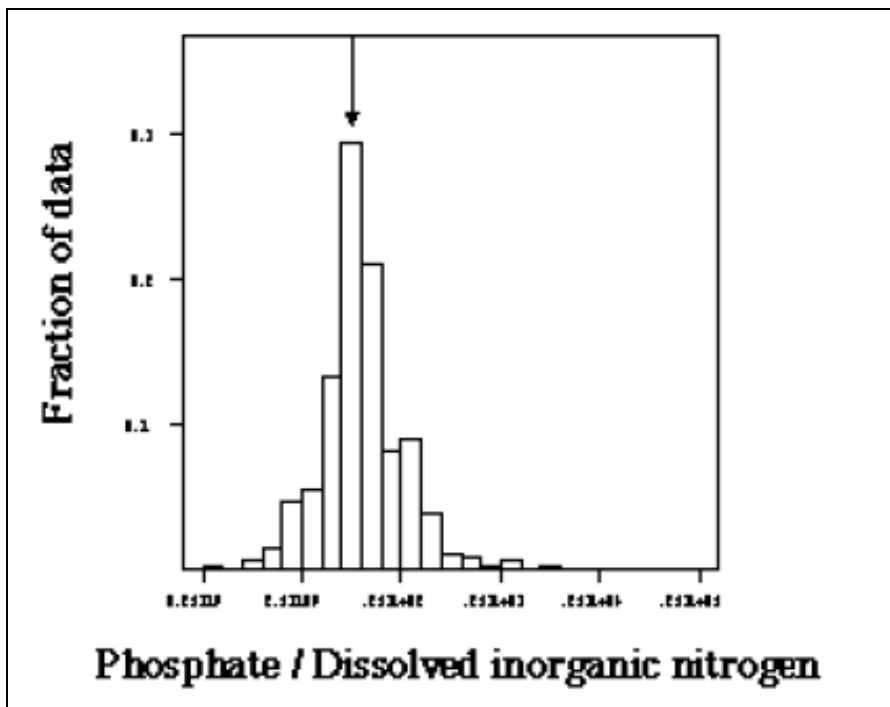


Figure 2.6 The relationship between total nitrogen and total phosphorus concentrations in European coastal waters. The solid lines represents the fitted regression line, and the dotted line represents the Redfield ratio

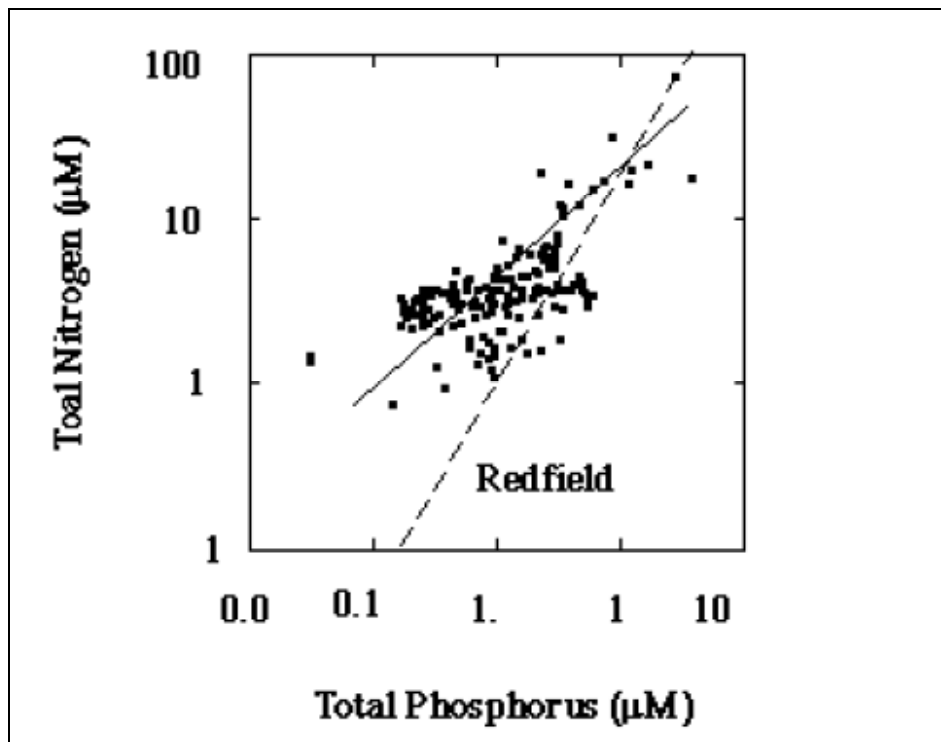
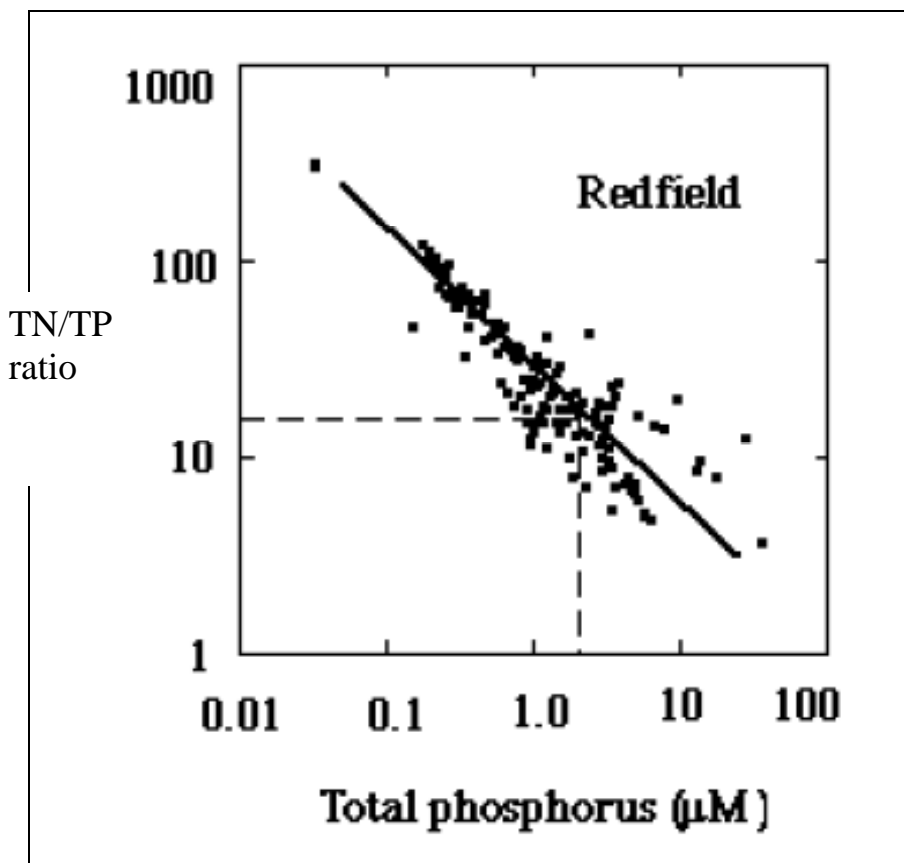


Figure 2.7 The relationship between the ratio of total nitrogen to total phosphorus and the total phosphorus concentration in European marine waters. The dotted line indicates the total phosphorus concentration at which the TN/TP ratio corresponds to the Redfield ratio

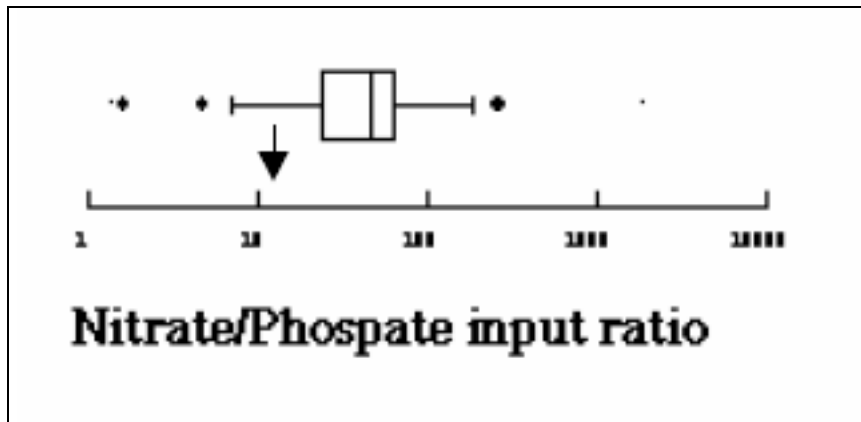


2.2.1. Stoichiometry in nutrient inputs

The results presented above indicate that most coastal waters deviate from the Redfield scaling between nitrogen and phosphorus concentrations. These differences clearly suggest differences in the stoichiometry of nitrogen and phosphorus between terrestrial nutrient sources and the marine end member. Indeed the ratio between nitrate and phosphate concentrations in terrestrial inputs deviate strongly from the Redfield ration (Fig. 2.8), with a median ratio of 32 N : 1 P, twice the Redfield ratio. This deviation tended to be greater in areas receiving freshwater inputs with high nutrient loads (nitrate > 100 μM), where the nitrate to phosphate ratio far exceeded a ratio of 50, and often exceeded 100.

Hence, the high N/P ratio of moderate eutrophic European waters derives from an excess nitrogen input relative to that of P, instead of a differential uptake of P compared to N from the dissolved inorganic pool. Recent experimental evidence (Duarte et al. unpubl. data) conclusively showed that the biomass yield of Mediterranean coastal phytoplankton was greatest under high N/P loading ratios, consistent with the development of eutrophication problems in European areas receiving nutrient inputs with high N/P ratios.

Figure 2.8 Box plot showing the distribution of the nitrate to phosphate ratio in freshwater inputs to coastal European ecosystems. The arrow indicates the Redfield ratio



2.3. Relationship between nutrient concentrations and phytoplankton biomass and production

The data set spanned broad ranges of both phytoplankton biomass and production, as well as broad ranges in nutrient concentrations, providing a unique opportunity to investigate the relationship between these properties implicit in simple statistical eutrophication models. The analysis revealed a strong correlation between the total nitrogen concentration, corrected to remove the nitrogen contained within phytoplankton, and chlorophyll a concentration (Fig. 2.9). The relationship between total phosphorus and chlorophyll a concentration was, in contrast, not statistically significant ($r = 0.45$, $P > 0.05$). This is probably so because much of the phosphorus present in coastal waters is either in dissolved organic form, that is less reactive/available, or contained within heterotrophic bacteria, which may exceed the biomass of phytoplankton (Gasol et al. 1997). The relationships between chlorophyll a concentration and dissolved inorganic nutrient concentrations were relatively weak (Fig. 2.10), and were only statistically significant for that between chlorophyll a concentration and ammonium ($r = 0.64$, $P = 0.00013$) and that with phosphate concentration, which was weaker ($r = 0.47$, $P = 0.00008$). The relationship between chlorophyll a concentration and nitrate concentration was not statistically significant ($r = 0.18$, $P = 0.172$).

Figure 2.9 The relationship between total nitrogen concentration, excluding the nitrogen contained in phytoplankton, and chlorophyll a concentration of European coastal waters.

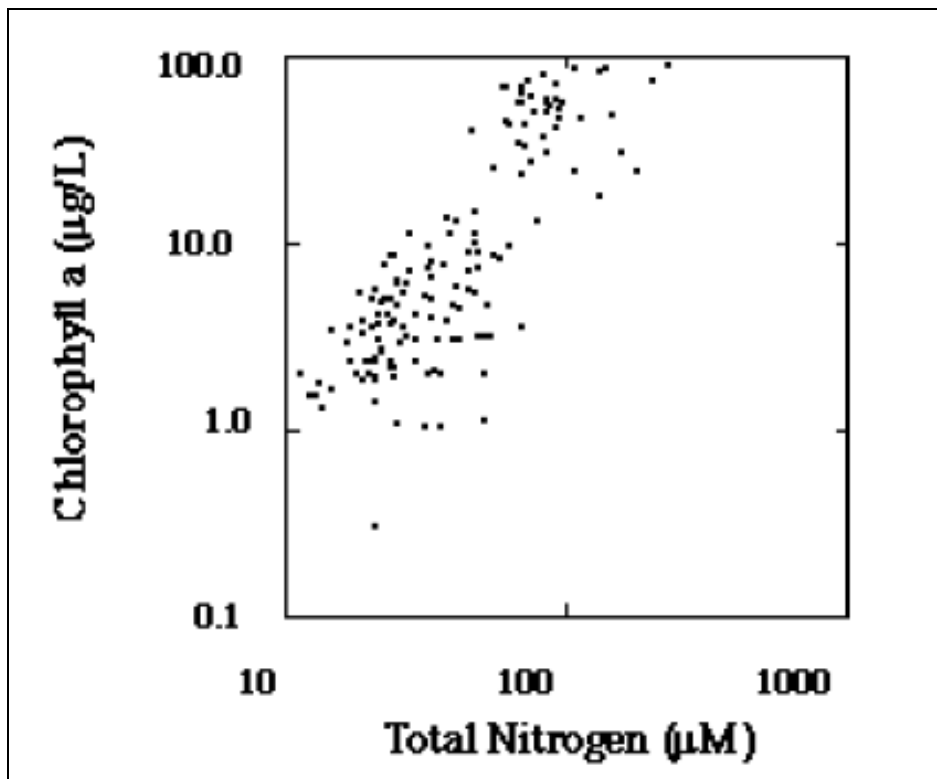
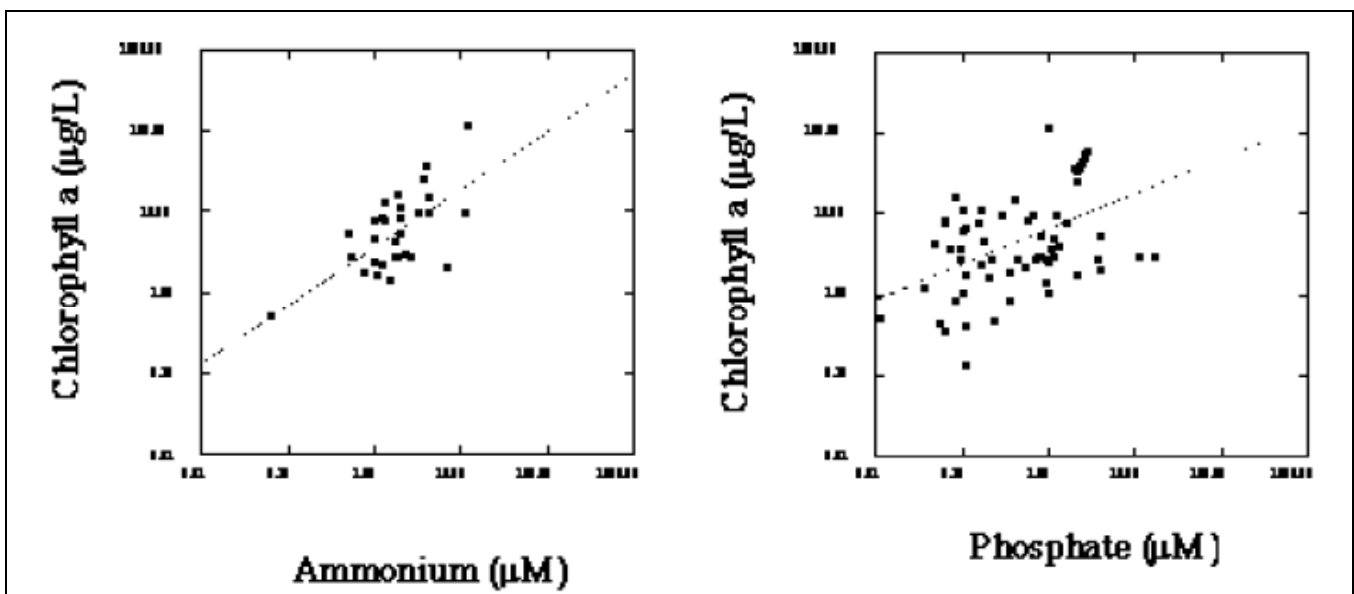
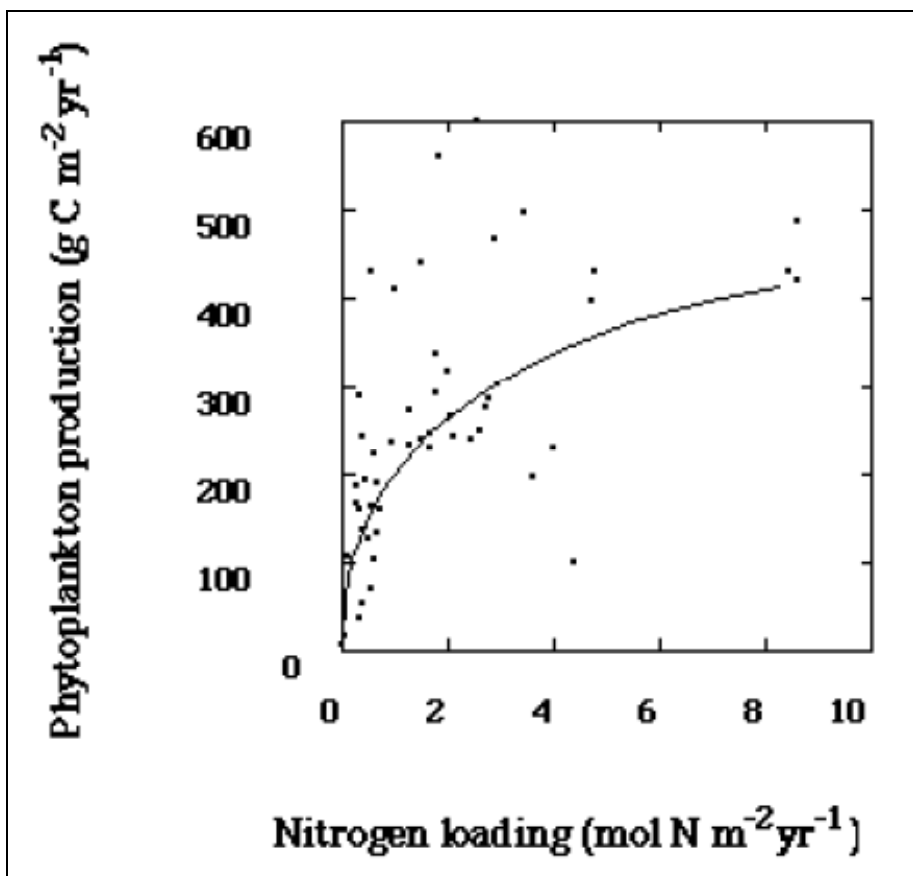


Figure 2.10 The relationship between inorganic nutrient concentration and chlorophyll a concentration in European coastal waters. Solid lines represent the fitted regression equation



Estimates of the areal loading of phosphorus available to date were few and did not suffice to attempt and statistical analysis of its relationship to phytoplankton biomass. Indeed a major bottleneck for the examination of the relationship between nutrient loading and phytoplankton production was the difficulties in calculating the area affected by the loading. This was possible only in estuaries and semienclosed bays, whereas it could not be determined in open coastal areas, where the area where the loading is distributed varies with currents, wind, mixing, etc. However, the data collected were sufficient to explore the relationship between the primary production of phytoplankton and nitrogen loading (Fig. 2.11).

Figure 2.11 The relationship between the primary production of phytoplankton and nitrogen loading in European coastal waters. Solid line represents the fitted regression equation



The relationship was statistically significant, accounting for 36 % of the variance in phytoplankton production in European coastal areas where nitrogen loading rates were available. The relationship was best described by the regression equation:

$$\log \text{ Primary production (g C m}^{-2} \text{ yr}^{-1}) = 1.83 + 0.82 \log \text{ N loading (g N m}^{-2} \text{ yr}^{-1})$$

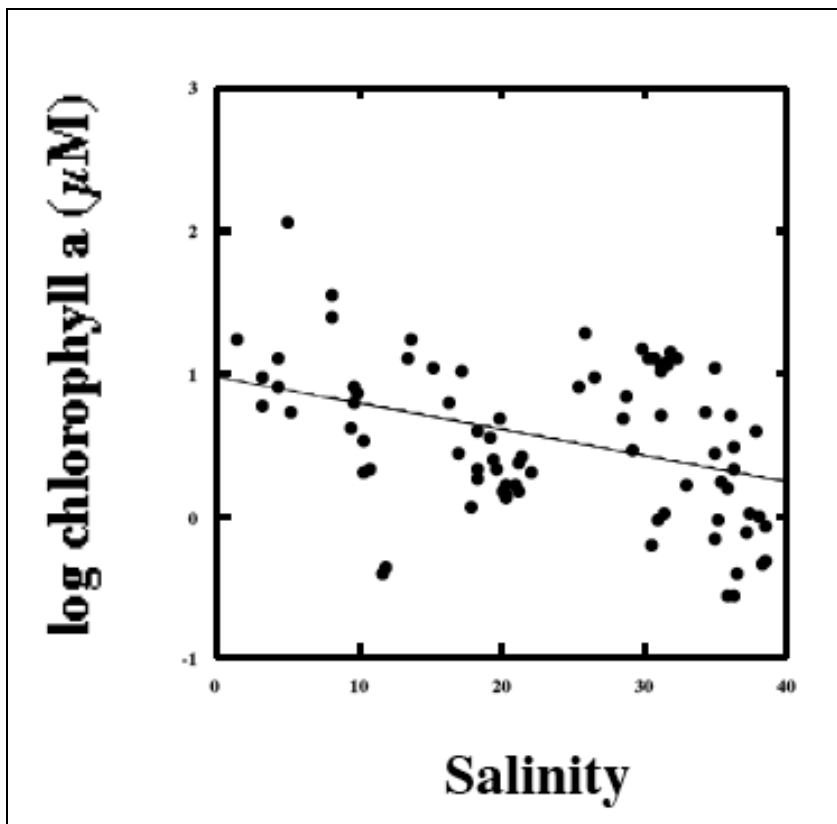
($R^2 = 0.36$, $N = 51$, $P < 0.00001$, $F = 29.8$, $P < 0.00001$)

Examination of the data suggested the relationship to be non linear (Fig. 2.11), suggesting that primary production levels off at high nitrogen loading. In contrast, however, phytoplankton biomass increases

proportionally to total nitrogen concentration (Fig. 2.9), clearly suggesting that the turnover of phytoplankton biomass is reduced at high nitrogen loading. This likely results from reduced losses, probably associated to the development of communities including forms able of chemical defence. The net result is that phytoplankton biomass accumulates in nitrogen-rich waters, whereas it is rapidly removed in nitrogen-poor to moderate waters.

There was a significant tendency for the chlorophyll a concentration of European coastal waters to increase towards increasingly brackish waters (Fig. 2.12), indicative that high phytoplankton development is more frequent in estuarine waters, where nutrient inputs are less diluted than in open coastal waters.

Figure 2.12 The relationship between the chlorophyll a concentration and the salinity of European coastal waters. The line represents the fitted regression equation



Source: jfdksjfv

2.4. Regional patterns in nutrient concentration and loading, and phytoplankton biomass in European coastal waters.

We tested for the existence of differences in the chlorophyll a concentration, nutrient concentration, N/P ratio, and nutrient inputs among different European regions. Chlorophyll a concentrations in nutrient-impacted European coastal areas were highest in the Baltic Sea and the Adriatic Sea, whereas they were lowest in the NW Mediterranean (Table 2). Baltic and Adriatic coastal waters had indeed the

highest dissolved inorganic nutrient, particularly nitrogen concentrations (Table 2). The distribution of the data were skewed by the presence of a few, highly nutrient and chlorophyll a rich coastal areas in the data set, so that the mean values do not necessarily represent the central tendency for the coastal regions in different European waters. This is best represented by the median values (Table 2). The median dissolved inorganic N/P ratios were low, indicative of a general nitrogen deficiency in all regions, except the Adriatic Sea, where dissolved inorganic nitrogen is in excess.

Table 2.2 Mean, median and range of chlorophyll and dissolved inorganic nutrient concentration in the different regions comprised within the data set. Data base statistics include non-European coastal waters.

Region	Chlorophyll a ($\mu\text{g/L}$)			Nitrate (μM)			DIN (μM)		
	Mean \pm SE	Median	Range	Mean \pm SE	Median	Range	Mean \pm SE	Median	Range
Baltic	26.2 \pm 2.5	31.7	1.47 - 110.6	55.8 \pm 13.5	4.3	0.4 - 980	61.9 \pm 15.2	4.4	0.47 - 1159
North Sea	4.24 \pm 0.68	4.93	0.65 - 9.6	26.1 \pm 4.72	10.1	0.56 - 214	23.7 \pm 4	9.5	0.09 - 214
Kattegat/Skagerak	2.3 \pm 0.21	2.49	1.61 - 2.79	10.4 \pm 1.19	3.9	0.16 - 35.35	10.8 \pm 1.0	7.3	0.81 - 37
North Atlantic	6.55 \pm 1.63	2.78	0.3 - 33.1	14.51 \pm 4.09	8.4	0.3 - 96	15.8 \pm 4.4	8.9	0.8 - 103
NW Mediterranean	2.18 \pm 0.5	1.06	0.09 - 10.5	11.32 \pm 4.3	4.7	0.067 - 113	17.0 \pm 4.0	7.8	0.07 - 115
Adriatic Sea	9.31 \pm 1.04	9.2	0.12 - 50.25	58.7 \pm 9.7	24.7	0.29 - 184	54.5 \pm 9.1	13.8	0.95 - 184.5
Aegean Sea	3.99 \pm 1.7	3.12	0.36 - 12	0.87 \pm 0.14	0.7	0.17 - 3.28	2.04 \pm 0.34	1.7	0.67 - 8.8
Black Sea	3.33 \pm 0.67	3.62	0.24 - 6.57	5.98 \pm 1.6	4.7	0.15 - 12.8	6.0 \pm 1.6	4.7	0.15 - 12.9
Data base	15.4 \pm 0.99	8.85	0.09 - 140	34.0 \pm 5.5	5	0.02 - 980	35.2 \pm 5.7	5.6	0.02 - 1159

	Phosphate (μM)			N/P ratio (DIN)		
	Mean \pm SE	Median	Range	Mean \pm SE	Median	Range
Baltic	15.5 \pm 4.1	0.58	0.05 - 376	10.8 \pm 0.9	6.9	2.05 - 102
North Sea	1.5 \pm 0.18	0.94	0.07 - 11.7	20.6 \pm 4.1	12.3	0.32 - 252
Kattegat/Skagerak	0.8 \pm 0.13	0.6	0.04 - 17.7	28.2 \pm 9.2	11.8	0.8 - 740
North Atlantic	3.2 \pm 1.0	1.25	0.12 - 14.8	14.1 \pm 3.3	9.8	0.98 - 60.5
NW Mediterranean	15.6 \pm 5.1	0.85	0.01 - 97.3	18.9 \pm 5.5	9.6	1.08 - 163
Adriatic Sea	1.17 \pm 0.2	0.19	0.02 - 5.23	44.8 \pm 3.1	39.1	5 - 114
Aegean Sea	0.44 - 0.1	0.14	0.08 - 2.07	19.4 \pm 9.7	9.6	1.4 - 19.4
Black Sea		0.05	-		3.6	-
Data base	8.2 \pm 1.8	0.62	0.01 - 377	19.3 \pm 2	9.5	0.03 - 740

3. Seagrass colonisation depths and light attenuation coefficient: thresholds for a shift from seagrass to sediment dominated communities

3.1. Introduction

Eutrophication ranks amongst the highest pressure (Duarte 2002) enhancing seagrass decline, and reduced underwater light penetration appears to be a primary driver (Duarte 1995). Seagrass depth limits are strongly related to the underwater light penetration and the light attenuation coefficient (Dennison 1987, Duarte 1991, Nielsen et al. 2002). Relationships between underwater light attenuation and seagrass depth limits have been developed for individual species (*Zostera marina*, cf. Dennison 1987, Nielsen et al. 2002, Greve and Krause-Jensen 2005) and across the seagrass flora (Duarte 1991). These relationships are sufficiently general and robust as to potentially predict the threshold of light attenuation above which benthic communities (I think benthos refer to fauna) would shift from seagrass to sediment dominated ones. The assessment of the predictive capacity of the relationship between underwater light attenuation and seagrass depth limits has not yet been tested across a broad range of species and light attenuation, and, hence, to establish this critical threshold.

Here we assess the predictive power of the relationships between underwater light attenuation (K , m^{-1}) and seagrass depth limits or colonization depth (Z_c , m). We do so using a compilation of reports of seagrass depth limits produced after the relationship of Duarte (1991) was published. We compare the reported depth limits with that predicted using the equation by Duarte (1991): $\log Z_c = 0.26 + 1.07 K$, as other equations available are specific of *Zostera marina* (Dennison 1987, Nielsen et al. 2002, Greve and Krause-Jensen 2005).

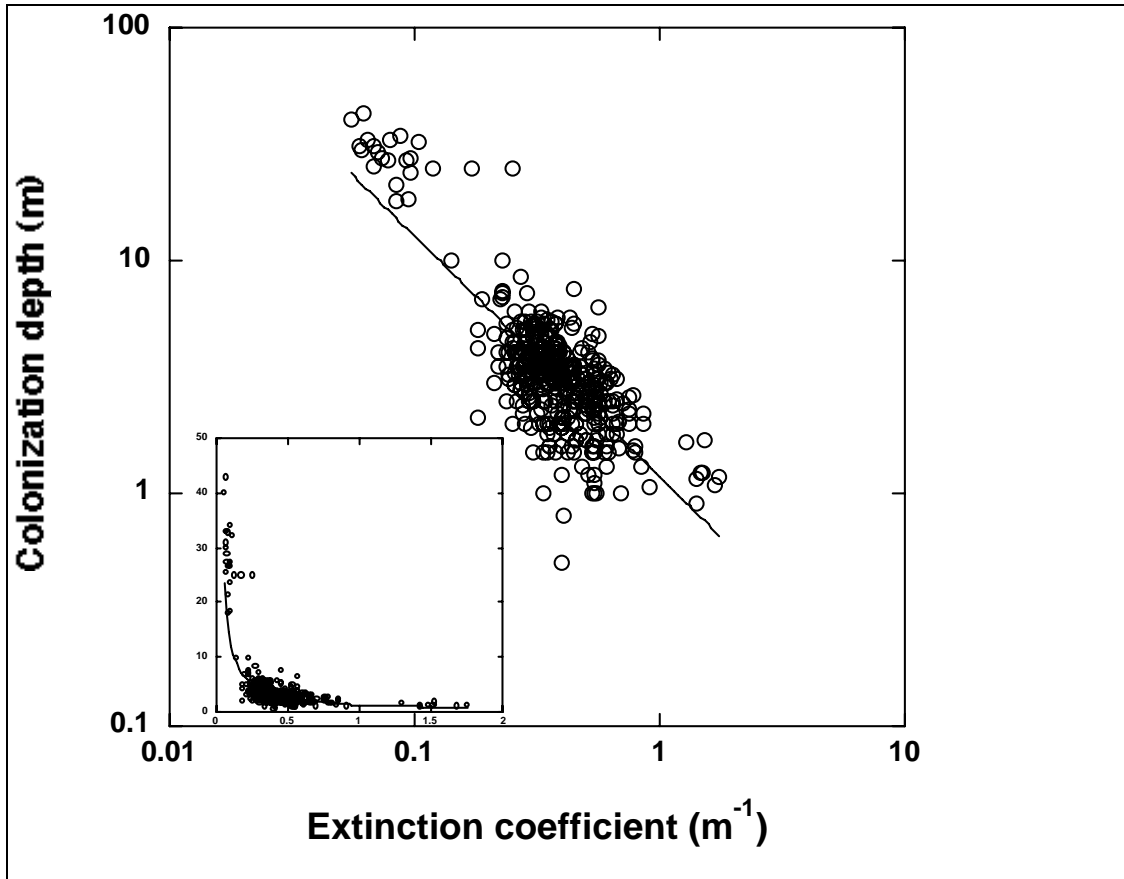
3.2. Results and discussion

The data set encompassed 424 reports of seagrass colonization depth and water transparency, which represents a larger data set than that used ($N = 72$ observations) to derive the original relationship by Duarte (1991). However, the present data set includes data for 10 seagrass species, whereas the analysis by Duarte (1991) included data for 16 species. Most (86 %) of the reports in the validation set assembled pertained to observations of colonization depth of *Zostera marina* in Danish waters. Seagrass colonization depths ranged 50 fold, from 0.5 to 43 m, and the depth of the Secchi disc and the corresponding light extinction coefficient (K) ranged from 1.2 to 28.7 m and 0.055 and 1.75 m^{-1} , respectively. These ranges are comparable to those used to derive the relationship by Duarte (1991), which included data for even more turbid waters (maximum $K = 3.57 m^{-1}$).

As expected, there was a strong negative relationship between the seagrass colonization depth (Z_c) and K (Fig. 3.1), as described by the fitted regression equation,

$$\text{Log } Z_c \text{ (m)} = 0.07 (\pm 0.019) - 1.03 (\pm 0.04) K \text{ (m}^{-1}\text{)} \\ (R^2 = 0.61, P < 0.001)$$

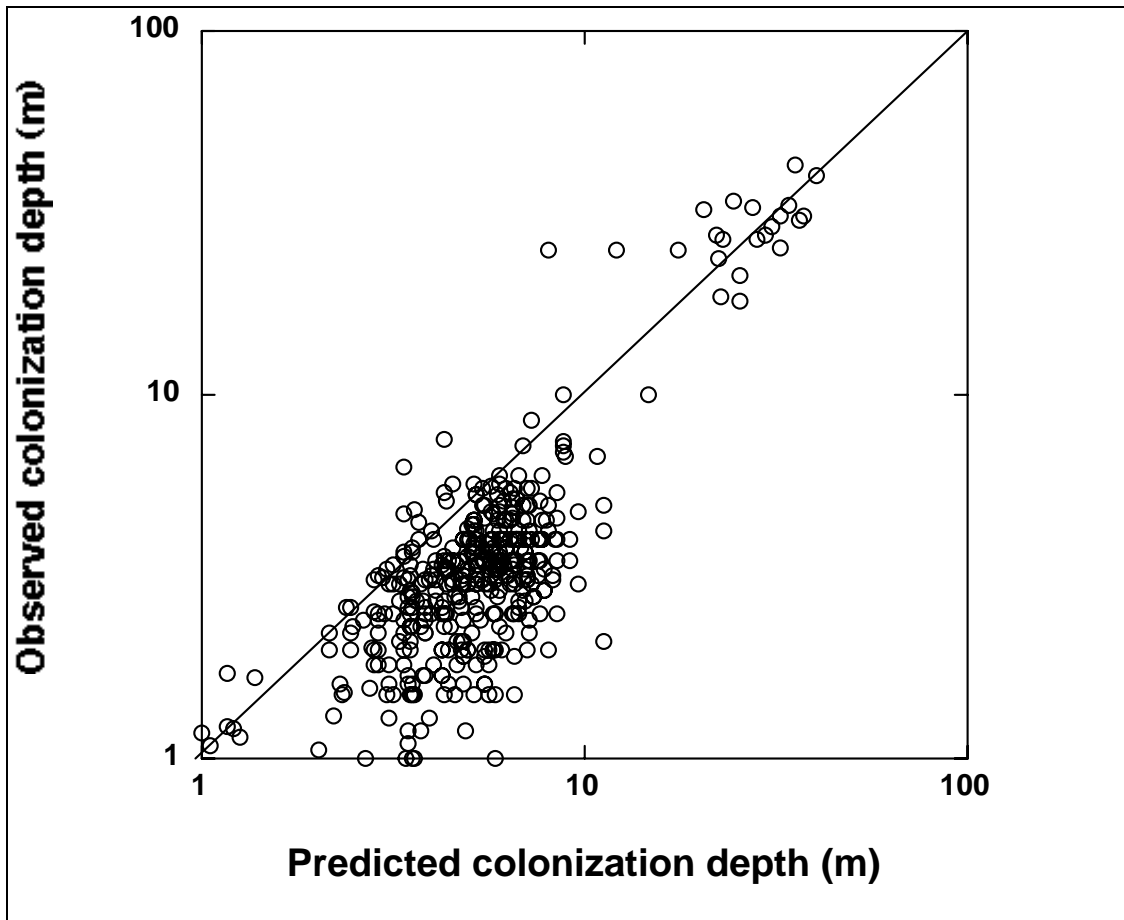
Figure 3.1 The relationship between seagrass colonization depth and the light extinction coefficient. The solid lines show the fitted regression equation, and the insert shows the data in arithmetic units.



Source: Duarte et al (submitted)

The slope of the equation reported by Duarte (1991) is rather similar and not significantly different from that of the regression equation fitted to the present validation set (1.07 ± 0.07 vs. 1.03 ± 0.04 , respectively, t-test, $P > 0.3$). However, the intercept is significantly lower (0.26 ± 0.04 vs. 0.07 ± 0.02 , respectively; t-test, $P < 0.05$). This indicates that a tendency for the values predicted using the regression equation in Duarte (1991) to overestimate realized seagrass colonization depths. Examination of the relationship between predicted (from Duarte, 1991) and observed colonization depth clearly shows that whereas observed and predicted colonization depths are strongly correlated ($r = 0.78$, $P < 0.001$), the regression equation by Duarte (1991) overestimated observed colonization depths (Fig. 3.2). A total of 89.2 % of the predictions over-estimated the observed colonization depth by, on average (\pm SE), 1.81 ± 0.11 m. Published equations for *Z. marina* [$Z_c = 1.62/K$, Dennison (1987); $Z_c = 1.53/K$, Nielsen et al. (2002)] also overestimated colonization depth for 77% and 71%, of the observations, respectively, although the prediction error was, on average, smaller (0.60 ± 0.13 and 0.31 ± 0.14 , respectively) than that predicted using the equation of Duarte (1991).

Figure 3.2 The relationship between predicted (from the equation in Duarte, 1991) and observed seagrass colonization depth. The solid line represents the 1:1 line.

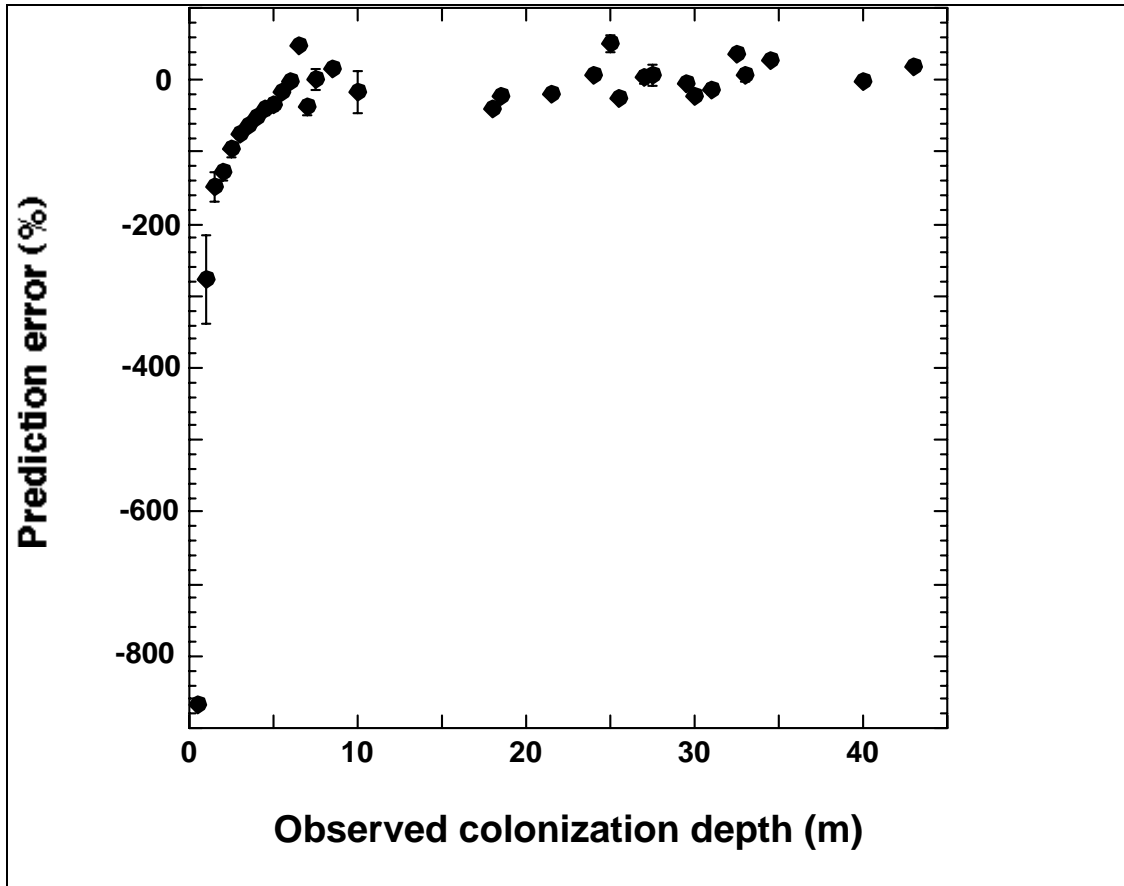


Source: Duarte et al submitted

The prediction error of the model by Duarte (1991) was not independent of the colonization rate, as the relative prediction error was greatest at low colonization depths and declined rapidly as the colonization depth increased (Fig. 3.3). This analysis revealed that the predictions were biased, overestimating the colonization depth at colonization depths < 5 m (Fig. 3), but that there was no prediction bias above this threshold, with the relative prediction error at colonization depths > 5m being negligible (mean \pm SE = 1.8 ± 5.1 %). The prediction error differed greatly among the species studied, with the average prediction error of the model by Duarte (1991) being small (< 10 %) for *Posidonia oceanica*, *Thalassia testudinum* and *Halophila* spp., and large (> 30% overestimation) prediction errors for *Zostera* spp., *Halodule wrightii*, *Syringodium filiforme* and *Cymodocea nodosa* (Fig. 3.4), all of which colonized shallow waters. The test data set included species not present in the data set used to develop the original model of Duarte (1991), for which the model performed reasonably well: *Halophila ovalis* (prediction error -9%) *Zostera japonica* (prediction error -39%). In contrast, the models specific of *Zostera marina* of Dennison (1987) and Nielsen et al. (2002) performed better at predicting the colonization depths for this species, as well as those of *Cymodocea nodosa*, than the multispecies model of Duarte (1991) did, but grossly underestimated the colonization depth of the deep-growing species in the data set (e.g. *Posidonia oceanica* and *Halophila stipulacea*, Fig. 4). Hence, the models tested tended to either overestimate the colonization depths of shallow-growing species

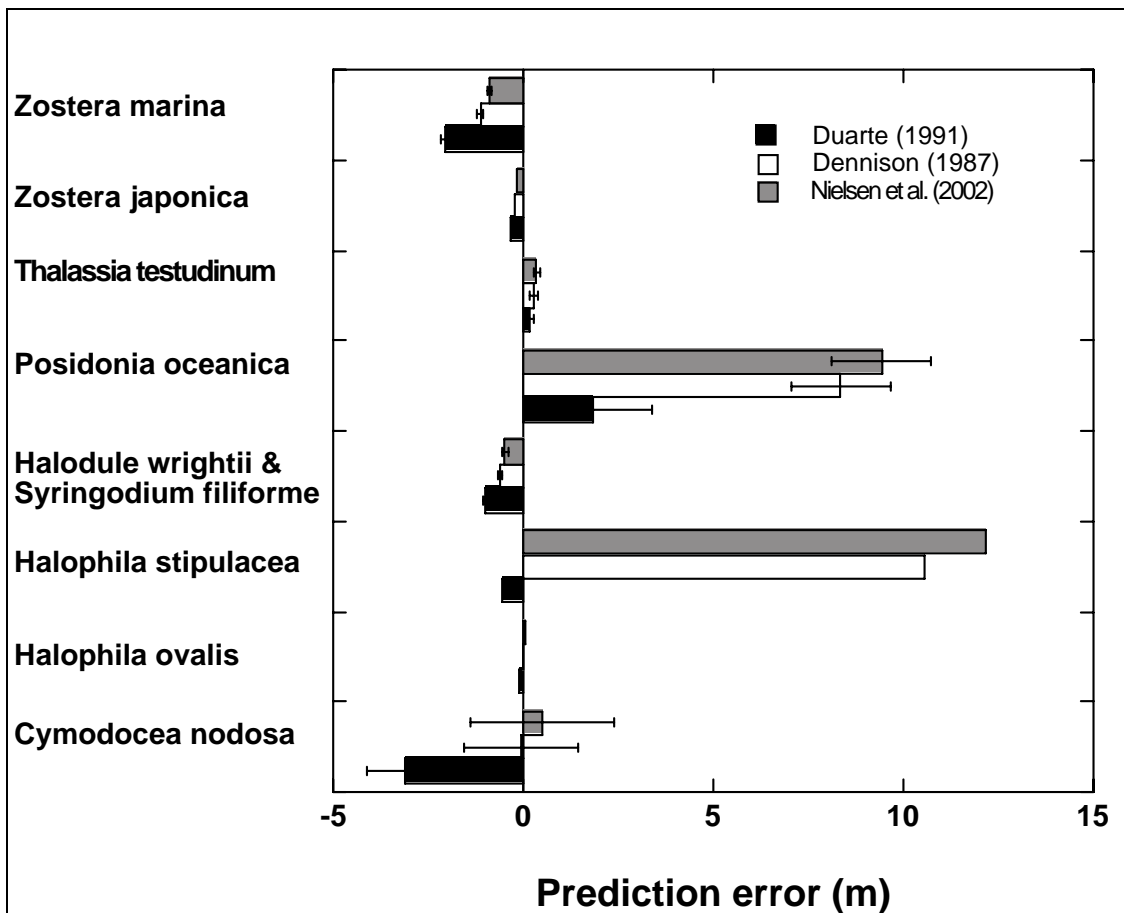
(Duarte 1991) or grossly underestimate that of deep-growing ones (i.e., Dennison 1987, and Nielsen et al. 2002)

Figure 3.3 The relationship between the average percent prediction error [$100 \cdot (\text{observed-predicted})/\text{observed}$] and seagrass colonization depth. Data points represent average (\pm SE) values for data binned by 1 m depth intervals.



Source: Duarte et al submitted

Figure 3.4 The average (\pm SE) prediction error for the colonization depths predicted for the different seagrass species represented in the test data set by the three models tested.



Source: Duarte et al submitted

Attempts to sort out the prediction bias by developing a new equation fitted to the present validation data set would not solve the problem, as the resulting regression equation still underestimates the colonization depth of seagrass growing deeper than 5 m (Fig. 3.1). The best avenue to avoid such bias maybe to use separate regression equations for predictions of seagrass colonization depth in turbid and clear waters, with the threshold K_z separating these waters being about 0.27 m^{-1} . The resulting equations are,

$$K_z < 0.27 \text{ m}^{-1}$$

$$\text{Log } Z_c \text{ (m)} = -0.34 (\pm 0.08) - 1.60 (\pm 0.10) K \text{ (m}^{-1}\text{)}$$

$$(R^2 = 0.79, P < 0.001)$$

and,

$$K_z > 0.27 \text{ m}^{-1}$$

$$\text{Log } Z_c \text{ (m)} = 0.10 (\pm 0.02) - 1.02 (\pm 0.04) K \text{ (m}^{-1}\text{)}$$

$$(R^2 = 0.63, P < 0.001)$$

where the intercept and slope for both these equations differ significantly (t-test, $P < 0.05$).

The difference in the relationship between colonization depth and light attenuation of deep and shallow-growing seagrasses implies that the light requirements vary greatly, in terms of the percent of the irradiance incident at the surface reaching to the depth limit, from shallow to deep-growing seagrasses. Indeed, the equations above imply that plants growing in turbid waters with their depth limit at 1 m reach down to the depth where 45.0 % of the incident irradiance reaches, in contrast to 33.3 % and 12.2% of the incident irradiance available to plants with maximum colonization depths of 5 and 30 m, respectively. The reasons for these differences may be multiple. The three-fold higher light requirements in turbid waters may reflect differences in the quality of the light available to the plants, as coastal waters with high attenuation coefficients are typically eutrophic, where chlorophyll a in phytoplankton would remove light at the same wavelengths as required by the plants (Kirk 1975). In contrast, clear waters allowing seagrass to grow down to 30 m or deeper (i.e. $K < 0.07 \text{ m}^{-1}$) are characterized by an important contribution of absorption of water itself, which filters out irradiance at red wavelengths while allowing high-energy blue light to penetrate and promote photosynthesis (Kirk 1975). Hence, for the same % irradiance at depth, the light field may be far more energetic and appropriate to support photosynthetic activity in clear compared to turbid waters.

The differences in the light requirements between plants growing in turbid and shallow waters may also be apparent and reflect other contrasting constraints that operate in shallow and turbid waters (Greve and Krause-Jesen 2005). For instance, turbid waters are likely to have higher nutrient concentrations, that may approach toxic levels for the plants, and also experience periods of hypoxia during the collapse of algal blooms, both of which will negatively impact the capacity of seagrasses to grow at low light (Greve and Krause-Jesen 2005). The percent irradiance at the colonization depth represents the compensation irradiance for growth ($I_{c \text{ growth}}$) of the plants, the irradiance at which gross primary production balances the carbon losses (respiration, herbivory, exudation of dissolved organic carbon, and reproduction) of the plants (Markager and Sand-Jensen, 1994). High $I_{c \text{ growth}}$ for plants growing in turbid waters may also reflect higher C losses, as C losses due to intense wave action and grazing, which may be higher in shallow than in deeper waters. Shallow waters may also be warmer in the summer, leading to higher respiratory losses than those for plants growing in deeper, colder waters.

In summary, the research presented showed that none of the currently available models are able to reliably predict seagrass colonization depths across the entire spectrum of water transparency, and that whereas the general model by Duarte (1991) predicts correctly colonization depths for seagrass species, even those not included in the original formulation of the equations, growing in relatively clear waters (i.e. $K_z < 0.27 \text{ m}^{-1}$), it does overestimate the colonization depth of seagrass growing in turbid waters. The converse applies to models developed for eelgrass growing in relatively turbid waters (Dennison 1987; Nielsen et al. 2002). The relationship between seagrass colonization depth and light attenuation shifts at a threshold of light attenuation of 0.27 m^{-1} , as seagrass growing in turbid waters apparently have higher light requirements than those in deeper waters. We, therefore, recommend that two different equations be used to predict colonization depths of plants growing in turbid and shallow waters, and to set targets for seagrass restoration and conservation efforts.

4. Conclusions

- Moderately eutrophic European coastal waters are characterized by an excess N relative to P in its waters.
- Phytoplankton biomass linearly couples total nitrogen concentration, corrected to remove the nitrogen contained within phytoplankton, in coastal waters.
- Phytoplankton primary production can be predicted from nitrogen loading. The resulting equation is,

$$\log \text{Primary production (g C m}^{-2} \text{ yr}^{-1}) = 1.83 + 0.82 \log \text{N loading (g N m}^{-2} \text{ yr}^{-1}) \\ (\text{R}^2 = 0.36, \text{N} = 51, \text{P} < 0.00001, \text{F} = 29.8, \text{P} < 0.00001)$$

- Because the relationship between phytoplankton production and nutrient loading is not linear, whereas the phytoplankton biomass responds linearly to nutrient loading, the turnover of phytoplankton biomass is reduced at high nitrogen loading. As a result, phytoplankton biomass accumulates in nitrogen-rich waters, whereas it is rapidly removed in nitrogen-poor to moderate waters.
- Light attenuation in coastal waters is the primary driver for benthic communities to shift from seagrass to sediment dominated ones. However, the relationship between seagrass colonization depth and light attenuation shifts at a threshold of light attenuation of 0.27 m^{-1} .
- Two different equations should be used to predict water depths where coastal areas shift from being seagrass to sediment dominated communities. These equations are,

$$\text{K}_z < 0.27 \text{ m}^{-1} \\ \text{Log Zc (m)} = -0.34 (\pm 0.08) - 1.60 (\pm 0.10) \text{K (m}^{-1}) \\ (\text{R}^2 = 0.79, \text{P} < 0.001)$$

and,

$$\text{K}_z > 0.27 \text{ m}^{-1} \\ \text{Log Zc (m)} = 0.10 (\pm 0.02) - 1.02 (\pm 0.04) \text{K (m}^{-1}) \\ (\text{R}^2 = 0.63, \text{P} < 0.001)$$

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