

# Predicting marine eutrophication: the yield of chlorophyll from nitrogen in Scottish coastal waters

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**ABSTRACT:** There is perceived to be a problem of eutrophication in European marine coastal waters and hence a need to predict the response in terms of enhanced biomass of phytoplankton resulting from the input of anthropogenic nitrogen. This response was investigated indirectly by studying the relationship between nitrate and phytoplankton chlorophyll concentrations in waters of the Scottish west coast. Two-thirds of the 60 data sets analysed gave significant inverse regressions of chlorophyll on nitrate concentration. This result is explained by interpreting synoptic data as representing variation in time, with nitrate decreasing as a result of its assimilation by phytoplankton and conversion into chlorophyll-containing biomass. Thus the absolute value of the slope of each significant regression estimates the yield ( $q$ ) of chlorophyll from nitrate and, indeed, from any form of nitrogen assimilable by microalgae. The median value for  $q$  was  $1.05 \text{ mg chl (mmol N)}^{-1}$ ; the range from 0.25 to 4.4 encompassed 95 % of values. Some, but not all, of the variation in  $q$  could be explained by error in individual estimates due to chemical-analytical and sampling errors or to inhomogeneities in each sampled phytoplankton population. The remaining variation in  $q$  included a seasonal trend, which might have resulted from changes in phytoplankton species composition, nutrient limitation status, or the balance between autotrophic and heterotrophic partitioning of nitrogen. It is suggested that an appropriate value of  $q$  can be used to predict the potential maximum increase in phytoplankton which would result from a given anthropogenic nitrogen discharge. The sensitivity of such predictions to error in determination of  $q$  is discussed, and the values obtained for  $q$  compared with observations in algal culture and mesocosms.

## INTRODUCTION

There is perceived to be a problem of eutrophication in European coastal waters and hence a need to predict the potential enhancement of phytoplankton as a result of anthropogenic nutrient discharge. Complex numerical models of phytoplankton growth in relation to physical processes (e.g. Radach & Maier-Reimer 1975, and others reviewed by Tett 1987a) seem inappropriate predictive tools at this stage in their development. In the case of freshwaters, an empirical approach (Vollenweider 1968, 1976) has provided a successful basis for managing eutrophication. It and similar methods (Reynolds 1984, p. 186–191) relate

typical phytoplankton biomasses to the phosphorus loading of lakes. An analogous method might allow estimation of the potential effects of nutrient discharge in coastal seas. As discussed here, the method differs from Vollenweider's in 2 main respects. Firstly, it stresses the dynamical (ratio of relative changes) rather than the static (ratio of concentrations) aspect of the relationship between phytoplankton and nutrients. One reason for this is the relative intensity, compared with lakes, of horizontal exchange in coastal seas (e.g. Prandle 1984, Tett 1986). Hypernutrient waters thus often exchange rather rapidly with their surroundings. Secondly, nitrogen is seen as the nutrient most likely to limit marine algal production. This follows from Ryther & Dunstan (1971), supported by cell-quota arguments (e.g. Tett 1987b, Tett & Droop 1988, but see also Hecky & Kilham 1988). We recognise, however, that in low-salinity environments phosphorus can be the limiting

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nutrient and that hypereutrophication can result in a change in the limiting nutrient, such as silicate in the case of diatoms (Officer & Ryther 1980).

The proposed method uses the following equation to estimate potential maximum phytoplankton biomass ( $\text{mg chl m}^{-3}$ );

$$X_{\max} = X_0 + q \left( S_0 + \frac{\langle S \rangle}{DV} \right) \quad (1)$$

In this equation,  $X_{\max}$  is the maximum chlorophyll concentration that could occur under nitrogen limitation, all other factors being in excess, in a well-mixed water body of volume  $V \text{ m}^{-3}$ , exchanging at relative dilution rate  $D \text{ d}^{-1}$  with surrounding water in which the concentrations of chlorophyll and algal-assimilable dissolved nitrogen are, respectively,  $X_0 \text{ mg chl m}^{-3}$  and  $S_0 \text{ mmol N m}^{-3}$ .  $\langle S \rangle$  is the daily molar flux of assimilable nitrogen received by the water body from local, natural and anthropogenic, sources. The yield of planktonic chlorophyll from assimilated nitrogen is  $q$  and is the subject of this paper. Eq. (1) estimates the chlorophyll resulting from the conversion of all available nitrogen at yield  $q$ , although the biological results of hypereutrophication might be less than this if phytoplankton growth rate cannot sustain the maximum biomass against dilution or other losses such as grazing.

Our approach has been to make observations on natural phytoplankton populations under conditions approximating those in which biomass might be stimulated by nutrient enrichment. Using linear regression analysis, changes ( $\Delta X$ ) in chlorophyll concentration have been related to changes ( $\Delta S$ ) in nitrate concentration, and the regression slope treated as an estimate of  $-q = \Delta X / \Delta S$ . In the present case the conditions are those of Scottish west coastal waters, which can be subject to input of ammonium and other forms of assimilable nitrogen from fish farms (Gowen & Ezzi 1992). However, an assumption about the equivalence of all forms of assimilated nitrogen allows us to study cases involving dominant nitrate.

The aims of the paper are thus (1) to test the hypothesis about the chlorophyll-nitrate relationship, and (2) estimate values of  $q$  for our waters. Because most of these waters are naturally low in nutrients and phytoplankton biomass, our observations were necessarily made under oligotrophic conditions.

## METHODS

Data were obtained from quasi-synoptic surveys of Scottish coastal waters (sea-lochs, firths and sounds; Fig. 1) carried out over a period of 15 yr. Each data set was derived from a survey which did not take more than 2 d to complete. Descriptions of some of these

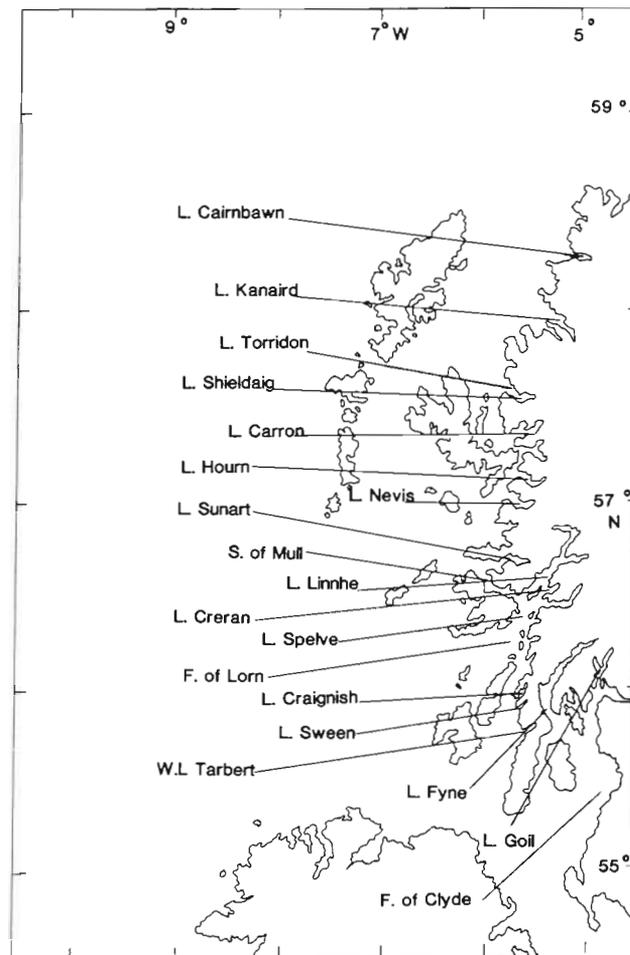


Fig. 1. The Scottish west coast showing locations of the sea-lochs surveyed

regions are given in Tett & Wallis (1978), Grantham (1981), Gowen et al. (1983) and Jones et al. (1984).

The introduction of nitrate or ammonia into these surface waters during the period November to February is unlikely to result in phytoplankton growth because of light limitation at this time. For this reason only chlorophyll and nitrate data which had been collected from the euphotic zone during March to October were used in the analysis. On those occasions when the attenuation coefficient of downwelling irradiance had been measured, this was used to determine the bottom of the euphotic zone taken as being 1 % of surface irradiance. Where no irradiance data were available, 25 m was taken as the depth of the euphotic zone. Data sets were further screened and data collected from water of less than 30 ppt salinity were rejected on the grounds that significant dilution of chlorophyll or enrichment of nitrate or ammonia by freshwater may have occurred. For statistical reasons only data sets with 4 or more data pairs were analysed.

Water samples for chlorophyll estimation were filtered and either extracted immediately or the phytoplankton and filters frozen for later extraction. A standard fluorometric method (Tett & Wallis 1978) was used to estimate chlorophyll. This method discriminates between chlorophyll and pheopigments but does not distinguish between chlorophyll and chlorophyllide (Gowen et al. 1982). Water samples collected for the determination of dissolved inorganic nitrate (and nitrite) were either analysed immediately or filtered and frozen for later analysis. The methods of Strickland & Parsons (1972) and Folkard (1979) for manual and automated methods respectively were followed.

The yield  $q$  was estimated from each data set by plotting chlorophyll against nitrate concentration with the expectation that the formation of phytoplankton chlorophyll would be linearly proportional to the disappearance of nitrate from packets of seawater moving into a loch. Linear regression analysis and an  $F$ -test was used to determine the significance of the slope. The analysis was based on 40 surveys carried out during the period 1974 to 1989.

## RESULTS

Of the 60 data sets analysed 38 gave significant negative regressions, 1 gave a significant positive regression and 21 were not significant. Examples of the relationship between chlorophyll and nitrate are presented in Fig. 2 and the results of the analysis are presented in Table 1.

## DISCUSSION

Our use of  $q$  makes 2 fundamental assumptions. The first, resting on cell-quota nutrient-limitation theory (Droop 1983, Tett & Droop 1988), is that all forms of assimilable nitrogen are similar in terms of their growth-controlling effects once inside algal cells, notwithstanding known differences in assimilability of ammonium, nitrate or dissolved organic nitrogen. We extend this argument to include the link between assimilated nitrogen and chlorophyll synthesis. This assumption allows cellular nutrient content, and even  $q$ , to vary as a function of cell nutrient quota or illumination (e.g. Laws & Bannister 1980); it states only that chlorophyll synthesis is independent of the chemical form in which nitrogen is taken up by algae. The data in Table 2 (from Caperon & Meyer 1972) provide some support for this, partly by suggesting that, at least under N-limited conditions, most variation in  $q$  relates to growth rate or species.

The second basic assumption is that, despite the likely dependence of the chlorophyll yield on algal physiology and species,  $q$  does not vary much during, for example, an algal bloom or the growth of a population of phytoplankton as a packet of coastal sea water enters a sea-loch or estuary. Since  $q$  as used in Eq. (1) is in fact an ecosystem rather than a purely algal property, this assumption also requires a constant partitioning of algal-assimilated nitrogen between algae, grazers, and detritus. The preceding statement makes it clear that data from algal culture cannot be used directly to estimate  $q$ , although they are of use in indicating an upper limit to expected values of  $q$ .

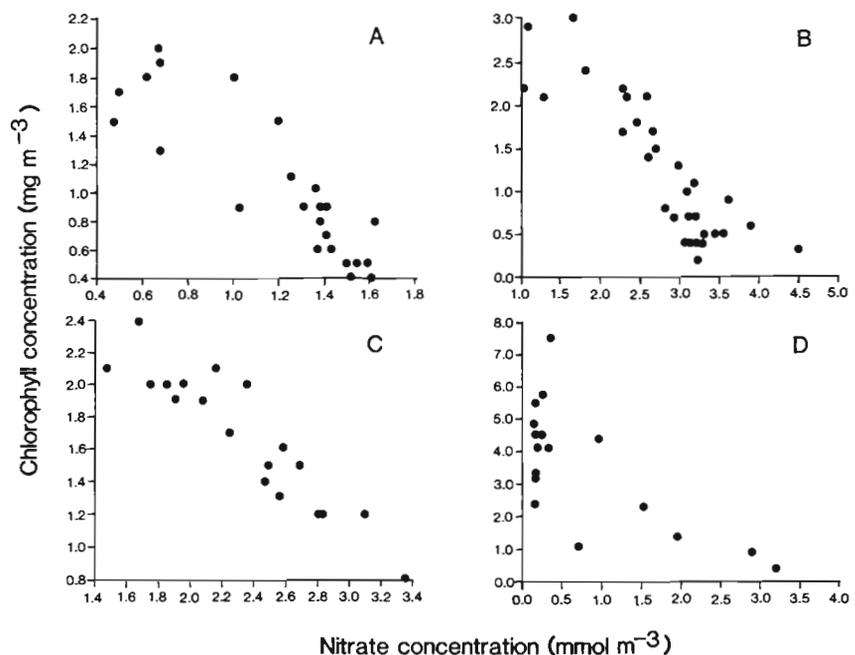


Fig. 2. Examples of the relationship between phytoplankton chlorophyll and nitrate from 4 locations on the Scottish west coast. (A) Loch Cairnbawn, (B) Loch Sunart, (C) Loch Sween, (D) Loch Torridon

Table 1. Results of linear regression analysis of the relationship between phytoplankton chlorophyll and nitrate, based on data sets collected from the Scottish west coast 1974 to 1989. (Only results from significant regressions are presented.) *F*: ratio of the explained and unexplained error; *df*: degrees of freedom; *q*: yield of chlorophyll from nitrate [ $\text{mg chl} (\text{mmol nitrate})^{-1}$ ]

Location	Year	Julian day	<i>F</i>	<i>df</i>	<i>q</i>
Loch Cairnbawn	1981	218	63.40	1, 21	1.16
Loch Carron	1987	84	8.69	1, 10	0.25
Loch Craignish	1985	281	382.70	1, 5	1.28
Loch Creran	1974	252	21.23	1, 4	2.78
	1979	138	11.76	1, 3	4.40
		227	19.03	1, 3	3.99
Loch Duich	1988	263	11.22	1, 12	0.75
Loch Fyne	1986	164	14.73	1, 31	0.76
Loch Goil	1986	140	20.18	1, 23	1.13
Loch Hourn	1988	194	9.88	1, 9	1.80
		263	19.57	1, 15	0.75
	1989	75	32.52	1, 35	1.40
		94	4.46	1, 19	0.52
		164	18.31	1, 19	3.87
		185	19.57	1, 14	3.24
		212	22.89	1, 23	1.01
		231	5.95	1, 10	0.25
		239	25.07	1, 28	0.58
		260	51.69	1, 36	1.58
Loch Kanaid	1981	218	7.99	1, 32	0.79
Loch Linnhe	1981	225	16.69	1, 4	1.02
	1982	202	11.49	1, 27	1.34
Loch Nevis	1982	193	4.99	1, 19	1.05
Loch Sheldaig	1982	118	12.27	1, 5	1.04
Loch Spelve	1985	67	4.66	1, 23	0.26
		204	7.67	1, 37	1.79
		242	12.15	1, 33	1.85
		268	50.54	1, 27	2.74
Loch Sunart	1982	264	87.55	1, 29	0.89
Loch Sween	1985	281	93.92	1, 17	0.77
Loch Torridon	1982	197	15.05	1, 15	1.37
West Loch Tarbert	1985	282	18.61	1, 14	5.35
Firth of Clyde	1986	141	41.15	1, 61	0.76
		162	17.57	1, 52	0.98
Firth of Lorne	1986	165	14.73	1, 31	0.76
Sound of Mull	1982	265	8.45	1, 15	0.32
Sound of Sleet	1986	163	29.10	1, 5	0.12
	1986	166	11.81	1, 9	1.05

Simple enrichment experiments can be ruled out on the grounds of 'bottle effects', such as disturbance to species balance, when carried out over the several days necessary to determine the yield of chlorophyll from added nitrogen.

Our approach has been to use observational data collected from quasi-synoptic surveys. In principle, however, such studies should concern changes with time, as in the case of observations during a spring phytoplankton bloom (Tett et al. 1975, 1985), and the mesocosm study of Jones et al. (1978a, b) used in Table 3. Furthermore, there is a choice of methods: (1) *q* could be estimated statically, from the ratio of chlorophyll concentration to observed particulate nitrogen, as in Table 2. In fact the data in Table 2 derive from chemostat steady states, in which nutrient uptake is in equilibrium with growth; under these

conditions static and dynamical estimation is equivalent. (2) *q* is better estimated dynamically, from the relative rate of change of chlorophyll and nitrogen: (a) directly, from  $\Delta X/\Delta[\text{PON}]$ , where [PON] is the concentration of particulate organic nitrogen; or (b) indirectly, from  $-\Delta X/\Delta S$ . The dynamical method is better because it relates more closely to the coupling of nitrogen assimilation and chlorophyll synthesis, whereas the static method embodies only the coincidence of values measured at the same time. In addition, a dynamical estimate of *q* should be more appropriate to assessing eutrophication potential in freely exchanging waters.

The direct and indirect dynamical methods are exemplified by the results presented in Table 3. During the spring increase in Loch Creran there was no significant difference between values of *q* estimated

Table 2. Estimates of  $q$  derived from steady state, nitrogen-limited unialgal cultures. Data from Caperon & Meyer (1972) who are amongst authors defining  $q$  as a 'variable yield coefficient'. We have followed Droop (1968, 1983) in using  $Q$  for the cellular ratio of growth-controlling nutrient to biomass, in order to use  $q$  for the yield of chlorophyll from nitrogen. We have used values given by Caperon & Meyer (1972) for algal N:C ratios and calculated  $q$  from their Table 1 data.  $\mu$ : specific growth rate; NO, NH: nitrogen in medium supplied as nitrate or ammonium respectively

Alga	$\mu$ d <sup>-1</sup>	$Q$ mmol N (mmol C) <sup>-1</sup>	$q$ mg chl (mmol N) <sup>-1</sup>
<i>Dunaliella</i> <sup>a</sup> (NO)	0.51	0.062	1.8
<i>Dunaliella</i> (NH)	0.42	0.062	1.3
	1.28	0.127	3.2
<i>Monochrysis</i> <sup>b</sup> (NH)	0.19	0.051	0.7
	1.20	0.092	1.9
<i>Cyclotella</i> <sup>c</sup> (NO)	0.21	0.050	0.5
	1.70	0.158	1.4

<sup>a</sup>*Dunaliella* is *D. tertiolecta*; <sup>b</sup>*Monochrysis* is now *Pavlova lutheri*; <sup>c</sup>*Cyclotella pseudonana* is now *Thalassiosira nana*

by  $\Delta X/\Delta[\text{PON}]$  and by  $-\Delta X/\Delta S$ ; correction of PON for detrital nitrogen did not make any significant difference. This may have been because of the additional error introduced by the detrital correction, since the value of  $q$  estimated from the results of the mesocosm experiment (with low detrital content and nitrogen-controlled phytoplankton) was significantly higher than the spring value. Interestingly, the value of  $q$  estimated for the phosphorus-controlled phase of the mesocosm experiment was significantly and substantially higher than the nitrogen-controlled value.

Since data were acquired during rapid surveys of sea-lochs or inner coastal waters rather than from time-series, a further assumption is required: that synoptic sampling of a loch is equivalent to following the evolution of phytoplankton biomass at the expense of nitrate in a packet of water entering the loch and originally of low chlorophyll and high nitrate concentration. The cause of algal growth in the packet may be a greater mean illumination in the shallower surface layer of a salinity-stratified loch. Although the formal model of Eq. (1) views the process from an Eulerian (fixed) rather than a Lagrangian (particle-tracking) perspective,  $X_0$  and  $S_0$  can nevertheless be identified with the initial chlorophyll and nutrient content in each packet, and  $DV$  totals the volume exchange resulting from all packets moving into and out of the loch during a day. The model, and the procedure for estimating  $q$ , assumes a steady state (at least on a timescale of  $1/D$ ); in the Lagrangian perspective this merely requires each packet of water to evolve in the same way in respect of chlorophyll and nitrate, or at least to depart only randomly and linearly from such behaviour.

Table 3. Estimates of  $q$  derived from data collected during the spring increase of phytoplankton in Loch Creran and mesocosm experiments using Loch Creran water. In both cases regression slopes are taken as estimates of  $q$ . Data have been analysed according to the algal nutrient deemed to be growth-controlling on the basis of C:N:P ratios

Regression of chlorophyll on:	Intercept (SE) mg chl m <sup>-3</sup>	Slope (SE) mg chl (mmol N) <sup>-1</sup>	r <sup>2</sup> (n)
<b>Spring increase in Loch Creran<sup>a</sup></b>			
DIN	+8.36 (1.58)	-1.54 (0.38)	0.81 (6)
PON	-1.28 (0.62)	+1.56 (0.21)	0.88 (10)
PPN	+0.25 (0.94)	+1.96 (0.53)	0.66 (9)
<b>Mesocosm measurements using Loch Creran water<sup>b</sup></b>			
PON under N-control	-4.4 (3.2)	+2.16 (0.25)	- (15)
PON under P-control	-12.9 (5.6)	+3.04 (0.26)	- (10)

<sup>a</sup> Data from Cottrell & Tett (1973) numerically analysed by Tett et al. (1975, 1985). DIN: dissolved inorganic nitrate plus nitrite; PON: particulate organic nitrogen. An attempt was made to correct PON for detrital nitrogen so as to estimate phytoplankton particulate nitrogen (PPN) free of contamination

<sup>b</sup> Data from Jones et al. (1978b) but see also Jones et al. (1978a) and Jones (1979)

The Lagrangian perspective identifies  $X_{\max}$  as the chlorophyll concentration that is reached within a packet when all original and any recycled or anthropogenic nutrient is used up. For  $X_{\max}$  to approximate an Eulerian mean over the loch – that is, if the whole loch is to be treated as the volume of interest to which Eq. (1) is applied – nutrient depletion must take place very soon after a water packet enters the loch. Formally, this requires algal specific growth rate to be high relative to  $D$ , and, in general terms, significant eutrophication will not take place unless this condition is satisfied. Finally, the proper estimation of  $q$ , from  $-\Delta X/\Delta S$ , required that we use data sets only from waters where local nutrient inputs [the flux  $\langle S \rangle$  in Eq. (1)] were such that  $\langle S \rangle / DV$  was small compared with  $S_0$ .

The results of regression analysis of the data sets provided a test of assumptions discussed above. Since two-thirds of the individual regressions were significant, and all but one of these showed the expected inverse relationship between nitrate and chlorophyll we conclude that there is, for these Scottish waters, a persistent inverse relationship between relative

changes in chlorophyll and nitrate analogous to the static relationship between chlorophyll concentration and phosphorus loading in freshwater. The median value of  $q$  was  $1.05 \text{ mg chl (mmol nitrate)}^{-1}$ , however, the range which encompassed 95 % of values was from 0.25 to 4.44. Furthermore, there was considerable scatter associated with most of the plots. This raises 2 questions. What was responsible for the scatter, and is the variation in  $q$  caused by the scatter? These questions need to be addressed before any conclusion can be drawn regarding the use of  $q$  as a predictor of coastal eutrophication.

The contribution of measurement error to the scatter is likely to be 11 % of observed concentrations for chlorophyll (Tett & Grantham 1980) and 2 to 5 % for nitrate (Jones 1979) at the concentrations reported here. In many cases (see Fig. 2) it is clear that methodological error alone does not explain all of the scatter. It is likely therefore, that much of the scatter is due to departures of individual chlorophyll and nitrate concentrations from those predicted by a ratio based on relative changes in those concentrations, perhaps as a result of short term uncoupling of nitrate assimilation from chlorophyll synthesis.

To investigate sources of variability in  $q$ , we assessed the frequency distribution of  $q$  in relation to the typical error of an estimate of  $q$ . The skewed frequency distribution (Fig. 3A) was approximately normalised (Fig. 3B) by logarithmic transformation of  $q$  values. The following procedure was used to obtain an approximate estimate of the variability in  $q$  to be expected according to the null hypothesis that such variability was due only to scatter within individual chlorophyll-nitrate plots. The standard error of each  $q$  estimate was converted to a coefficient of variation by dividing by that value of  $q$ , and weighted by multiplication by the square root of the degrees of freedom associated with that standard error. These weighted coefficients of variation were summed, and the total divided by the total of weights to give a weighted mean coefficient of variation of 0.28, corresponding to a symmetrical logarithmic deviation (LD) of approximately 0.125. Next we estimated approximate 95 % confidence limits for median  $q$  (given the null hypothesis) from  $\log_{10}(\text{median}) \pm 2\text{LD}$ , and these are shown in Fig. 3B. The expectation, on the null hypothesis, is that 5 % of values of  $q$ , or not more than 2 values, will lie outside these limits; in fact 14 values lay outside these limits. Despite the approximation used to estimate the limits, the probability of this excess is clearly very low. Hence it may be concluded that the scatter within individual plots of chlorophyll on nitrate was not the only cause of the variation in values of  $q$ . Such a conclusion is not unexpected. There is clearly a complex inter-relationship between algal growth and the ratios of carbon, chlorophyll and nitrogen which

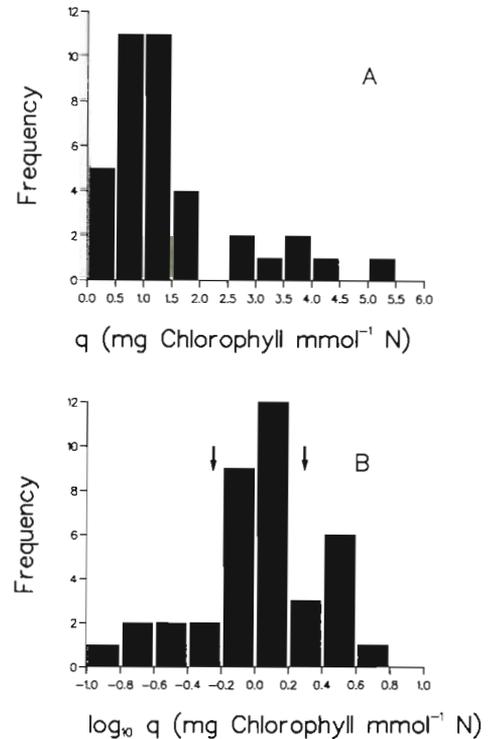


Fig. 3. Frequency distribution of  $q$ , the yield of chlorophyll from nitrate [ $\text{mg chl (mmol nitrate)}^{-1}$ ]. (A) Untransformed data, (B)  $\log_{10}$  transformed data. Arrows indicate approximate 95 % confidence limits of the median value of  $q$

may ultimately depend on whether the algae are light or nutrient limited (Laws & Bannister 1980).

In addition to the variation in  $q$ , 21 of the 60 data sets analysed did not give a significant regression. This suggests that, although the relationship between chlorophyll and nitrogen generally holds true for Scottish coastal waters, differences in coastal areas as environments for phytoplankton growth have a considerable influence on the potential for phytoplankton growth and the accumulation of biomass. Clearly, any process (other than the availability of nitrate) which limits growth or restricts the accumulation of biomass will result in a low yield. Thus it has been shown that despite a suitable light climate and available nutrients within a sea-loch, dilution can limit the accumulation of biomass (Gowen et al. 1983).

Zooplankton grazing will also reduce phytoplankton standing crop in relation to nitrate previously removed from seawater by algae. Local differences in grazing pressure might therefore be expected to contribute to variation in  $q$ . There is some evidence for differences in zooplankton biomass in adjacent sea-lochs (Gowen 1981) but there are no data on grazing levels in different coastal areas of the west of Scotland. However, an indication of zooplankton grazing pressure can be

derived from the amount of pheopigment and for phytoplankton in the euphotic zone the ratio of chlorophyll to pheopigment can be used as an index of grazing pressure. Loch Hourn was repeatedly surveyed during 1989 and a significant positive correlation ( $r = 0.69$ ) was found between mean chlorophyll pheopigment ratio and  $q$ . Thus it would appear that, for Loch Hourn at least, a low yield of chlorophyll from nitrate corresponded with high concentrations of pheopigment relative to chlorophyll. This suggests that some of the nitrate assimilated by algae had become associated with pheopigments as a result of grazing thus lowering the value of  $q$  obtained by regressing chlorophyll concentration on nitrate.

The value of  $q$  derived from sea-loch data may be further influenced by the effects of physical processes on the ecophysiology of phytoplankton in the source water with which lochs exchange. Droop et al. (1982) suggest that phytoplankton growth is controlled by the availability of light and nutrients in a threshold manner. When light controls growth, algae can take up nitrate in excess of their immediate needs. Such 'luxury' uptake would initially uncouple growth from an external supply of nitrate. It has been suggested (Jones & Gowen 1985) that phytoplankton advected into a sea-loch from mixed coastal water (where growth is light limited) would have a greater potential for growth compared to phytoplankton advected from stratified water (where growth is nutrient limited). In such cases the concentration of nitrate within the loch may be unimportant in controlling phytoplankton growth in the short term and high biomass could coincide with high concentrations of nitrate.

The estimates of  $q$  indicate that there may have been a trend of increasing  $q$  from spring to late summer (Fig. 4) suggesting the possibility of seasonal variation

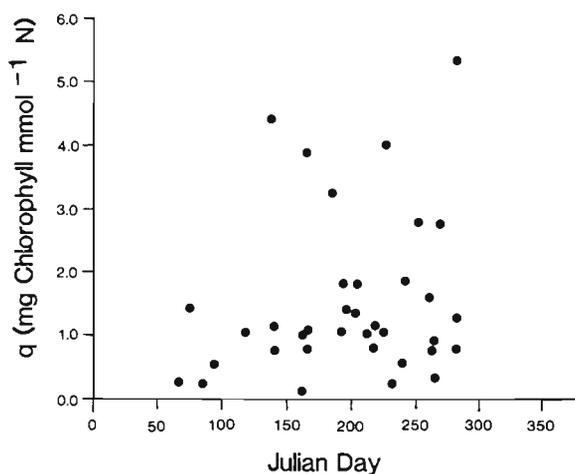


Fig. 4. Seasonal variation in  $q$ , the yield of chlorophyll from nitrate

in the value of  $q$ . Such a trend might reflect changes in the availability of nitrogen to phytoplankton, from early spring when there is an excess of nitrate (and presumably cellular nitrogen) but algal growth is limited by light (Tett et al. 1985) to conditions during the summer when growth is generally assumed to be controlled by the availability of nitrogen. The variation in  $q$  may also reflect changes in the species composition of phytoplankton, from diatom dominated populations in the spring to dinoflagellate and microflagellate dominated populations in the summer and autumn. No statistical test, however, showed a significant ( $p < 0.05$ ) seasonal component to the variability in the whole data set in Fig. 4. Seasonal data were collected from 2 sea-lochs, Spelve and Hourn. The Spelve data gave a significant correlation between the value of  $q$  and Julian day ( $r = 0.97$ ) but for the Loch Hourn data there was no significant correlation.

There were insufficient data from individual locations for a more detailed assessment of the variation in  $q$  and there is clearly a need for further work to investigate the cause of the variation. It follows, however, that since there are a number of factors which can influence the value of  $q$ , a single value may not be a good predictor of the yield of chlorophyll from nitrate. Furthermore, it is clear that variation in the topographic and hydrographic features of sea-lochs results in a range of physical conditions and hence environments for phytoplankton growth (Jones & Gowen 1985). As such it may be more appropriate to use loch specific values of  $q$  rather than a single value to predict eutrophication. In this respect  $q$  can be defined as the ecosystem response by phytoplankton to available nitrate. Therefore, in addition to providing a value for chlorophyll enhancement resulting from anthropogenic nitrogen,  $q$  could be used to provide an index of the sensitivity of individual sea-lochs to nutrient enrichment.

In conclusion, we obtained the theoretically-predicted result (a significant negative regression of chlorophyll on nitrate concentration) in 38 out of 60 cases. This convinces us of the reliability, in principle, of the method proposed in this paper for estimating the maximum increase in chlorophyll resulting from anthropogenic enrichment with algal-assimilable nitrogen. The 21 non-significant regressions can be explained as due either to inadequate data within surveys, or to a submergence of the expected relationship as a result of strong grazing, rapid dilution or severe light limitation. Under such circumstances, however, anthropogenic nitrogen enrichment would not give rise to increased algal biomass because nitrogen would not be the limiting factor.

A quantitative difficulty concerns the value of  $q$  to be used in Eq. (1). Of our estimates, 95 % lay between

0.25 and 4.44 mg chl (mmol N)<sup>-1</sup>, too great a range to be explained by within-survey variability. Furthermore, the median value of 1.05 mg chl (mmol N)<sup>-1</sup> is low compared with most of the values from cultured algae in Table 2 and the mesocosm data in Table 3. This suggests that grazing pressure, or slow intrinsic growth due to causes other than nitrogen shortage, effectively reduces the yield of algal biomass from assimilated nitrate in many of the coastal waters that we have studied. The median value of  $q$  therefore takes into account a range of ecosystem effects and would seem more appropriate for predicting the typical response of phytoplankton in western Scottish coastal waters to enrichment. Nevertheless, the potential effects of anthropogenic enrichment will be greatest when the influence of these factors which effect the yield are weakest. The 'precautionary principle' suggests, therefore, the desirability of using a value of  $q$  greater than the median in order to make a 'worst-case' estimate of the effects of enrichment. This approach may be particularly important with respect to short term events such as the occurrence of harmful algae. Our upper 95th percentile value of  $q$  is 4.4 mg chl (mmol N)<sup>-1</sup> and although this lies significantly above the range of values in Tables 2 & 3 we suggest that pending further studies the value of 4.4 mg chl (mmol N<sup>-1</sup>) may be used to predict the worst case, short-term, response to nitrogen enrichment.

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