



Does biodiversity of estuarine phytoplankton depend on hydrology?

J.G. Ferreira^{a,*}, W.J. Wolff^b, T.C. Simas^a, S.B. Bricker^c

^a *IMAR-Institute of Marine Research, Centre for Ecological Modelling, DCEA-FCT, Qta. Torre, 2829-516 Monte de Caparica, Portugal*

^b *University of Groningen, Biological Center, Department of Marine Biology, Kerklaan 30, P.O. Box 14, 9750 AA Haren (Gn), The Netherlands*

^c *NOAA-National Ocean Service, National Centers for Coastal Ocean Science, 1305 East West Highway, Silver Spring, MD 20910, USA*

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Abstract

Phytoplankton growth in estuaries is controlled by factors such as flushing, salinity tolerance, light, nutrients and grazing. Here, we show that biodiversity of estuarine phytoplankton is related to flushing, and illustrate this for some European estuaries.

The implications for the definition of reference conditions for quality elements in estuaries of different types are examined, leading to the conclusion that constraints on the number of estuarine and coastal types that may be defined for management purposes require that quality classes take into account natural variability within types, in order to be ecologically meaningful. We develop a screening model to predict the growth rate required for a phytoplankton species to be present under different flushing conditions and apply it to estuaries in the EU and US to show how changes in physical forcing may alter biodiversity. Additional results are presented on the consequences for eutrophication, showing that changes in residence time may interact with species-specific nutrient uptake rates to cause shifts in species composition, potentially leading to effects such as harmful algal blooms.

We discuss applications for integrated coastal zone management, and propose an approach to normalization of estuarine phytoplankton composition as regards species numbers.

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1. Introduction

Increased nutrient loading to the coastal zone has resulted in eutrophication problems in estuarine systems throughout the world (e.g. Chiaudani et al., 1980;

* Corresponding author. Tel.: +351 21 2948300x10117; fax: +351 21 2948554.

E-mail address: joao@hoomi.com (J.G. Ferreira).

Gillbricht, 1988; Hodgkin and Hamilton, 1993; Joint et al., 1997; Okaichi, 1997). Assessment of eutrophication in coastal systems, and particularly in estuaries, is highly complex; some reasons for this are outlined below:

1. The symptoms are diverse (Bricker et al., 1999; OSPAR, 2001), may potentially be due to a range of causes, and vary greatly in severity (e.g. Gerlach, 1990; Rabalais et al., 1996; Burkholder et al., 1999).
2. Although there is an association between pressure and state, the relationship between them is strongly influenced by estuarine geomorphology and hydrodynamics: estuaries subject to similar nutrient-related pressure often exhibit totally different eutrophication symptoms, and in some cases no symptoms at all. Factors such as water residence time (e.g. Ketchum, 1954; Lucas et al., 1999a; Tett et al., 2003), tidal range (Alvera-Azcarate et al., 2003) and turbidity (May et al., 2003) play a major role in determining the nature and magnitude of symptom expression.
3. Biological interactions, particularly due to grazing (e.g. Cloern, 1982; Lucas et al., 1999b), may provide a top-down control of eutrophication symptoms. These may occur in similar types of estuaries, due to natural variability, but also due to human activities such as shellfish aquaculture (Nunes et al., 2003). In the latter case, selective filtration by bivalves may additionally affect biodiversity by altering the phytoplankton species composition (Shumway et al., 1985; Bougrier et al., 1997).
4. Changes in biodiversity may be natural, related to eutrophication (e.g. Marques et al., 1997; Fonseca et al., 2000) or xenobiotic pollution or linked to phenomena such as climate change (Simas et al., 2001).

An improved understanding of these issues is currently driven by regulatory requirements, in order to support water quality management in estuarine and coastal systems. In the EU, Directive 2000/60/EC (Water Framework Directive, WFD) establishes the division of transitional¹ and coastal systems into different types. For each type, reference conditions must be defined for biological, physico-chemical and hydro-morphological quality elements, in order to determine ecological quality ratios (see e.g. Vincent et al., 2003).

In the US, the legislative context at the federal level is based on the Environmental Protection Agency (EPA) Clean Water Act (1977; see for example, Gibson et al., 2000), and there is widespread recognition that type-specific reference conditions for eutrophication symptoms are a prerequisite for appropriate assessment and management (e.g. Bricker et al., 2004; Smith et al., 2004). In other words, identical water quality status categories will correspond to different type-specific ranges for assessment parameters, due to the recognition that reference conditions are subject to natural variability.

Phytoplankton is listed in the WFD as a biological quality element (BQE) for both transitional and coastal waters, and phytoplankton indicators form an integral part of the National Estuarine Eutrophication Assessment (NEEA) (Bricker et al., 1999), OSPAR Comprehensive Procedure (OSPAR, 2001), ASSETS (Bricker et al., 2003) and ICES (ICES, 2004) eutrophication assessment methods, with biomass, abundance and composition defined as the key parameters.

The definition of reference conditions for these is considered to be type-specific, and therefore requires an analysis of natural variability, particularly as a function of the factors outlined in (2) above. These factors are a major component of the physical variables for WFD typology, and have been used for estuarine typology by NOAA in the US, through the application of the land-ocean interactions in the coastal zone (LOICZ) approach named Deluxe Integrated System for Clustering Operations (DISCO; Smith and Maxwell, 2002; Smith et al., 2004).

Ketchum (1954) demonstrated how the rate of estuarine flushing determines the presence of phytoplankton populations in estuaries, using a simple steady-state model applied to estuarine segments. The effect of flushing rate on the biomass of estuarine phytoplankton has been widely reported (e.g. Lucas et al., 1999a; May et al., 2003; Tett et al., 2003), however until now the consequences of Ketchum's conclusions for estuarine biodiversity do not seem to have been understood.

The objective of this paper is to present a holistic screening model, in order to derive some general features relating phytoplankton species composition to estuarine hydrology, developing principles first outlined by Ketchum (1954). The scope of the work reported herein is not a detailed analysis of specific processes for a particular estuary, but an overview

¹ Estuaries are defined in WFD Article 2(6) as Transitional Waters.

of the general behavior of a number of systems, in order to explore relationships which may (a) assist in a coherent definition of reference conditions and (b) contribute to informing eutrophication management in estuaries and coastal waters.

2. Data acquisition

A 1-year project aimed at collecting and interpreting data for the application of the European Union Water Framework Directive to estuarine and coastal waters in Portugal (Bettencourt et al., 2004) has been the framework for this study. About 10^6 records of physical, chemical and biological data on coastal and estuarine systems were collected and organized in relational databases and GIS. The water bodies studied were categorized into types based on physical characteristics, following Vincent et al. (2003). In parallel, ongoing work led by NOAA, aiming to update the US National Estuarine Eutrophication Assessment and to develop a type-specific approach (Bricker et al., 2004; Smith et al., 2004) was incorporated in this analysis, particularly as regards the possible relationship between estuarine residence time and harmful algal blooms (HAB).

3. Typology

Portuguese estuaries and lagoons were divided heuristically into four types (Table 1). This top-down approach was complemented by the application of the LOICZ DISCO bottom-up approach (Smith and Maxwell, 2002). This provided similar broad categories, separating estuaries from lagoon systems, and, stratified estuaries with high discharge and low residence time from “Mediterranean” estuaries with a high residence time and subject to highly variable freshwater discharge. The phytoplankton biomass and species number were then related to typology.

4. Phytoplankton species composition

We used an extensive historical data set consisting of phytoplankton species lists compiled over multiyear periods since the 1930s for a number of estuarine and

Table 1

Summary statistics for phytoplankton species composition in estuaries and lagoons along the Portuguese coast

Type	System	Number of species	% of total species
A1	Minho	99	8.0
A2	Mondego	174	14.0
A2	Ria de Aveiro	293	23.6
A2	Tagus	342	27.5
A2	Sado	416	33.5
A2	Guadiana	135	10.9
A3	Lagoa de Albufeira	200	16.1
A3	Lagoa de Óbidos	403	32.4
A3	S. Martinho do Porto	264	21.3
A4	Ria Formosa	213	17.1
Total number of species		1242	

A1: high discharge, stratified, mesotidal NE Atlantic estuary; A2: irregular discharge, well-mixed, mesotidal, “Mediterranean” estuary; A3: coastal lagoon; A4: barrier island lagoon.

coastal systems in Portugal (Moita and Vilarinho, 1999; Chícharo et al., 2000) (Table 1).

With the possible exception of the Guadiana estuary, where the species list is more recent, the species lists used encompass a large period (range: 9–31 years) when all these estuaries may be considered to have been in pristine conditions. This reduces the probability that the relationships shown are influenced by anthropogenic factors such as pollution.

A principal components analysis (PCA) carried out on the dataset showed that the distribution of phytoplankton families in general supports the physical typology division. This was then developed by means of a PCA using only the six estuaries, belonging to types A1 and A2, which shows (Fig. 1) that the species distribution for the various families may be further discriminated, with the systems on the left side being characterised by a low water residence time (<5 days), and those on the right having a water residence time of 10 days or more. The PCA indicates that despite their classification into different physical types based on the freshwater discharge regime, estuaries may group together on some biological features due to other physical factors.

The implication is either that typology needs to be further refined or that type-specific reference conditions must be modulated by accounting for intra-type

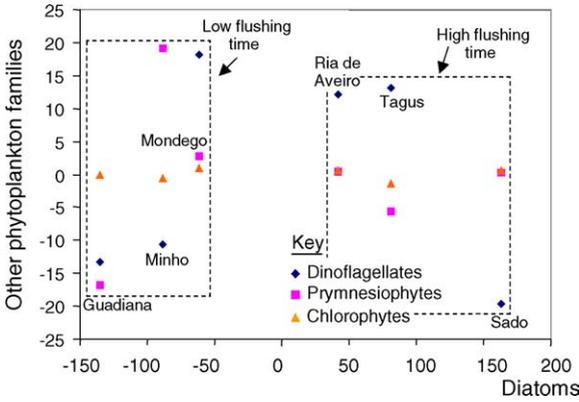


Fig. 1. Principal components analysis for phytoplankton families in six estuaries, using diatoms (x -axis), dinoflagellates, prymnesiophytes and chlorophytes (y -axis).

variability. The former approach potentially leads to a large increase in the number of types, which is a major management concern for the WFD, where the total number of types is envisaged to be no greater than 50–60 for all EU transitional and coastal waters. Similarly, in the US, EPA guidance states that “The intent of classification is to identify the smallest number of groups of estuarine or coastal marine categories that under ideal conditions would have comparable biological communities for that region” (Gibson et al., 2000), and NOAA recommends a maximum of 10 estuarine types (Bricker et al., 2004).

The physical limitation to the maintenance of phytoplankton populations in estuaries due to flushing thus appears to be a possible mechanism regulating species composition. This may be explored by examining the conditions under which a phytoplanktoner may exist and potentially grow in an estuary, which depend in the first instance on the species-specific physiological parameters of the photosynthesis–irradiance (P – I) curve.

5. Physical requirements for phytoplankton development

Ketchum (1954) showed how flushing physically controls the maintenance of estuarine planktonic populations, with examples for phytoplankton, planktonic larvae and coliform bacteria. Although growth rates for mixed estuarine phytoplankton populations were reported by that author, the implications for estuarine

biodiversity were not addressed. The equations below extend this analysis, by relating the development of one phytoplankton species to its growth rate and to the combination of advective flow and turbulent mixing, driven by freshwater inflow and tidal exchange. The present approach is applied to the estuary as a whole, with the caveat that our objective is not to examine differences in phytoplankton biomass, productivity and species distribution within sections of a particular estuary, and that other factors such as cell death, planktonic and benthic grazing or cell sinking are not taken into account. Neither do we address the within-estuary variability of flushing time or residence time (for reviews, see e.g. Monsen et al., 2002; Sheldon and Alber, 2002):

$$\frac{dB_e}{dt} = PB_e + Qb_r - Qb_e + k_{e,s}(b_s - b_e) \quad (1)$$

where B_e is mass of a phytoplankton species A in estuary (kg), t the time (days), P the phytoplankton growth rate (day^{-1}), Q the river flow ($\text{m}^3 \text{day}^{-1}$), $k_{e,s}$ the bulk dispersion coefficient ($\text{m}^3 \text{day}^{-1}$), b_r the concentration of phytoplankton species A in river (kg m^{-3}), b_e the concentration of phytoplankton species A in estuary (kg m^{-3}) and b_s is the concentration of phytoplankton species A in offshore waters (kg m^{-3}).

Eq. (1) may be simplified by considering that freshwater phytoplankton will not survive in the estuary, and neither will stenohaline offshore phytoplankton, i.e. by classifying species A as autochthonous to the estuary:

$$\frac{dB_e}{dt} = PB_e - Qb_e - k_{e,s}b_e \quad (2)$$

which divided by the estuary volume V , becomes:

$$\frac{db_e}{dt} = Pb_e - \frac{Q}{V}b_e - \frac{k_{e,s}}{V}b_e \quad (3)$$

but (e.g. Chapra, 1997):

$$k_{e,s} = \frac{QS_e}{\Delta S} \quad (3a)$$

where S_e is median estuary salinity and ΔS is difference between offshore and estuary salinity.

Therefore,

$$\frac{db_e}{dt} = b_e \left[P - \frac{Q}{V} \left(1 + \frac{S_e}{\Delta S} \right) \right] \quad (4)$$

Thus, the lower bound for species A to be present in an estuary is when $\frac{db_e}{dt} = 0$:

$$P = \frac{Q}{V} \left(1 + \frac{S_e}{\Delta S} \right) \quad (5)$$

where the right hand term corresponds to the estuary freshwater flushing rate ρ (day^{-1}). As regards estuarine flushing and specific growth rate, the necessary condition for species A to exist, and to potentially develop in the estuary may be thus defined by rearranging Eq. (4) as:

$$\frac{db_e}{b_e} = \left[P - \frac{Q}{V} \left(1 + \frac{S_e}{\Delta S} \right) \right] dt \quad (6)$$

which may be integrated for species A between the limits of maximum biomass b_{\max} and initial biomass b_{ini} over the development period t to yield:

$$\ln \left(\frac{b_{\max}}{b_{\text{ini}}} \right) = \left[P - \frac{Q}{V} \left(1 + \frac{S_e}{\Delta S} \right) \right] t \quad (7)$$

If we consider only the maintenance of species A in an estuary, Eq. (7) simplifies to become Eq. (5). Additionally, by defining the ratio k_b of maximum biomass to initial biomass, and specifying a typical time scale t , the physical descriptors of an estuary may be used to calculate the growth rate P necessary to allow species A to develop in the estuary.

Eqs. (5) and (7) may then be related to the physiology of estuarine phytoplankton, to assess which species may be present and potentially develop under these physical constraints.

The number of phytoplankton species present in the six estuaries from Fig. 1 has been plotted as a function of the flushing time $1/\rho$ from Eq. (5), which reflects both the advective exchange due to freshwater inflow and the tidally driven turbulent mixing (Fig. 2).

The highly significant ($p < 0.01$) linear relationship obtained may be interpreted from the equation set above as the composite capacity of individual phytoplankton species to remain within an estuary, i.e. to the phytoplankton biodiversity within the system. Estuaries with a very high water turnover might be expected to have about 120 species under pristine conditions, although these would only be autochthonous in special cases, e.g. where the existence of flow refugia (Reynolds et al., 1991) or specific dispersion patterns (Speirs and Gurney, 2001) makes this possible. Under

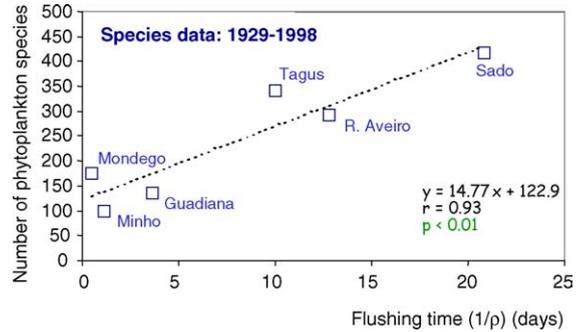


Fig. 2. Number of phytoplankton species as a function of flushing time, for six Portuguese estuaries from two different types (A1–1 estuary and A2–5 estuaries).

other conditions, these species must be either dying freshwater species or dying stenohaline species or both. This leads to the conclusion that using a worst-case approach, each system probably has about 120 species (combined riverine and oceanic) which have to be subtracted from the number recorded for each estuary in Table 1 to obtain the number of real estuarine species. At the opposite extreme the linear relationship will tail off at between 450 and 550 species, which is the number present in open coastal water off Portugal. Systems (such as the Sado) falling into this category behave like large, slow-turnover coastal lagoons.

6. Eutrophication symptoms and biodiversity

The modelling approach described below was used to determine the relationship between P , the average production required for the presence of phytoplankton species A, and the maximum potential production P_{\max} . There is an abundance of P_{\max} data available for numerous phytoplankton species, which may be used to predict which species could, under pristine conditions, be present in an estuary, i.e. give an indication of potential phytoplankton biodiversity in a particular system.

A value for P_{\max} was determined by running a dynamic model that determines the potential production based on the light energy available in the water column. This was carried out using the visual modelling software Powersim™, by running a simulation over a period of 10 days starting at Julian day 150, modelling the cumulative production and deriving an average value for P .

The diel surface light was simulated after Brock (1981) for latitudes at 10° intervals from 30° to 60°N, using three different light extinction coefficients corresponding to Secchi depths of 1, 3 and 5 m. P was simulated considering photosaturation after Platt et al. (1980), with a light half saturation constant I_k of 120 $\mu\text{E m}^{-2} \text{s}^{-1}$, and photoinhibition after Steele (1962), with optimal light intensity I_{opt} of 150 $\mu\text{E m}^{-2} \text{s}^{-1}$. The values for I_k and I_{opt} were determined as an average for dinoflagellates, diatoms and chlorophytes (Raven and Richardson, 1986).

In order to cover the main light uptake situations of different phytoplankton species, two cases were considered, one for a phytoplankton cell at a fixed depth of 3 m and one for a cell moving vertically in the water column between 0.5 and 5 m with a period of 2 h, thus addressing the potential sensitivity of the dynamic model to photoinhibition effects.

A two-way ANOVA performed on the results showed that P differed significantly with turbidity ($p < 0.01$) but that there was no significant difference among latitudes. A ratio of 5.6 between P_{max} and P was determined using Steele's model (Steele, 1962) (C.V.

39%), averaged over all latitudes and light extinction coefficients.

Table 2 shows the abridged results of the application of Eq. (7) to a number of EU and US estuaries, considering both the minimum requirements for the presence of a species and an arbitrary example for a bloom, with t of 10 days and k_b of 5. Higher values of P limit biodiversity by allowing only a few species to grow in a system. The term P is related to the P – I curve parameters of a phytoplankter, to its response to nutrients and to the light climate and nutrient availability in an estuary, and is therefore verifiable only through the application of a model.

From Fig. 2 and Table 2 it can be seen that systems with a flushing time $1/\rho$ greater than about a week would be able to accommodate phytoplankton species with a P_{max} of about 1 day^{-1} or lower, whereas in the shorter residence time estuaries only phytoplankters with a higher P_{max} could exist. The gap between the P_{max} required for maintenance and for bloom development also widens (Table 2) as $1/\rho$ decreases. P_{max} data are available for numerous phytoplankton species, and may in principle be used to predict which

Table 2
Application of a simple estuarine phytoplankton model

Estuary	Q ($\text{m}^3 \text{s}^{-1}$)	V (10^6m^3)	S_e	S_s	ρ^a (day^{-1})	P (day^{-1})	P_{max}^b (day^{-1})
Mira (P)	10	16.5	36.0	36.5	4.15	4.32	24.29 (23.39)
Douro (P)	541	39	17.5	36.5	2.30	2.46	13.86 (12.96)
<i>Mondego (P)</i>	<i>80</i>	<i>10.7</i>	<i>25.0</i>	<i>36.5</i>	<i>2.05</i>	<i>2.21</i>	<i>12.44 (11.54)</i>
<i>Minho (P)</i>	<i>400</i>	<i>76</i>	<i>17.5</i>	<i>36.5</i>	<i>0.87</i>	<i>1.03</i>	<i>5.82 (4.92)</i>
Connecticut River (US)	512	93	7.0	32.5	0.60	0.76	4.30 (3.40)
<i>Guadiana (P)</i>	<i>82</i>	<i>96</i>	<i>26.8</i>	<i>36.5</i>	<i>0.28</i>	<i>0.44</i>	<i>2.47 (1.56)</i>
Savannah River (US)	344	373	22.0	35.2	0.21	0.37	2.10 (1.20)
Mobile Bay (US)	1812	2057	15.0	33.5	0.14	0.30	1.68 (0.78)
<i>Tagus (P)</i>	<i>400</i>	<i>2179</i>	<i>30.7</i>	<i>36.5</i>	<i>0.10</i>	<i>0.26</i>	<i>1.47 (0.56)</i>
<i>Aveiro (P)</i>	<i>25</i>	<i>84</i>	<i>24.5</i>	<i>36.5</i>	<i>0.08</i>	<i>0.24</i>	<i>1.35 (0.44)</i>
Newport Bay (US)	2	12.9	28.0	33.5	0.07	0.23	1.30 (0.40)
<i>Sado (P)</i>	<i>40</i>	<i>847</i>	<i>33.4</i>	<i>36.5</i>	<i>0.05</i>	<i>0.21</i>	<i>1.18 (0.27)</i>
S. Francisco Bay (US)	837	5621	18.0	33.2	0.03	0.19	1.06 (0.16)
Oosterschelde ^c (NL)	70	3050	29.2	33.4	0.02	0.18	0.99 (0.09)
Oosterschelde ^d (NL)	25	2750	30.6	33.4	0.01	0.17	0.96 (0.05)
Westerschelde (NL)	105	2750	23.0	33.4	0.01	0.17	0.97 (0.06)
Long Island Sound (US)	179	63452	28.0	32.5	0.002	0.16	0.92 (0.01)

Values are ranked according to the required P , and match the order shown in Fig. 2 (systems in italics). The results shown are abridged from a dataset of 11 EU and 138 US systems.

^a US estimates from NOAA (1999).

^b P_{max} for a hypothetical bloom scenario shown first, P_{max} required for a species to be present shown in brackets.

^c Before 1986.

^d After 1987.

species could, under pristine conditions, be present in an estuary, i.e. give an indication of potential phytoplankton biodiversity in a particular system considered to be at the reference condition. However, if a species is also present in offshore waters then it may be present regardless of estuary residence time, although it will not necessarily be able to increase its biomass.

A comparison of P_{max} values obtained for the US estuaries was carried out with the results of the application of the NEEA/ASSETS eutrophication assessment (Bricker et al., 1999, 2003). This assessment showed that overall eutrophic conditions (based on a combination of measures of six indicators: (i) three primary symptoms—chlorophyll *a*, epiphytes and macroalgae and (ii) three secondary symptoms—dissolved oxygen, HAB and loss of submerged aquatic vegetation) are moderate in Savannah River, low in the Connecticut River and high in Long Island Sound. Thus, systems with high P_{max} requirements for phytoplankton growth (e.g. Connecticut River and Savannah River) generally have fewer eutrophication symptoms, in contrast with low P_{max} systems such as Long Island Sound.

This analysis has been extended to all 138 US estuaries considered in the original NEEA study (Bricker et al., 1999) for two eutrophication symptoms. A frequency distribution analysis for chlorophyll *a* (Fig. 3A) and HAB (Fig. 3B), classified according

to the calculated P_{max} necessary for phytoplankton development, indicates that systems with (a) P_{max} lower than 4 day^{-1} have worse scores for chlorophyll *a* and (b) P_{max} lower than 2 day^{-1} have worse scores for HAB. This suggests that problems regarding elevated phytoplankton biomass and the presence of nuisance or toxic algae are generally more prevalent in systems with lower flushing rates, even without accounting for human pressure (Ferreira et al., 2004).

The model used to determine P_{max} may also be applied to examine how an estuarine phytoplankton community may respond to physical changes. The model was extended to simulate biomass (Eq. (3)) for three different idealised species, over a period of 10 days in Spring, considering P_{max} values for each species of 1, 3 and 5 day^{-1} , respectively, using the same photosynthetic parameters as before and an initial biomass of 35 mgC m^{-3} . The hydrodynamic components of advection and dispersion were simulated according to Eq. (3). A nominal estuary volume of 10^6 m^3 was used and two different values for freshwater discharge were considered, simulating changes to the flow regime, either temporary due to climatic conditions or permanent due to damming or other watershed modifications. Exchange at the ocean boundary was implemented considering a simple one-dimensional dispersion coefficient approach (Eq. (3a)) (e.g. Chapra, 1997). The results are shown in

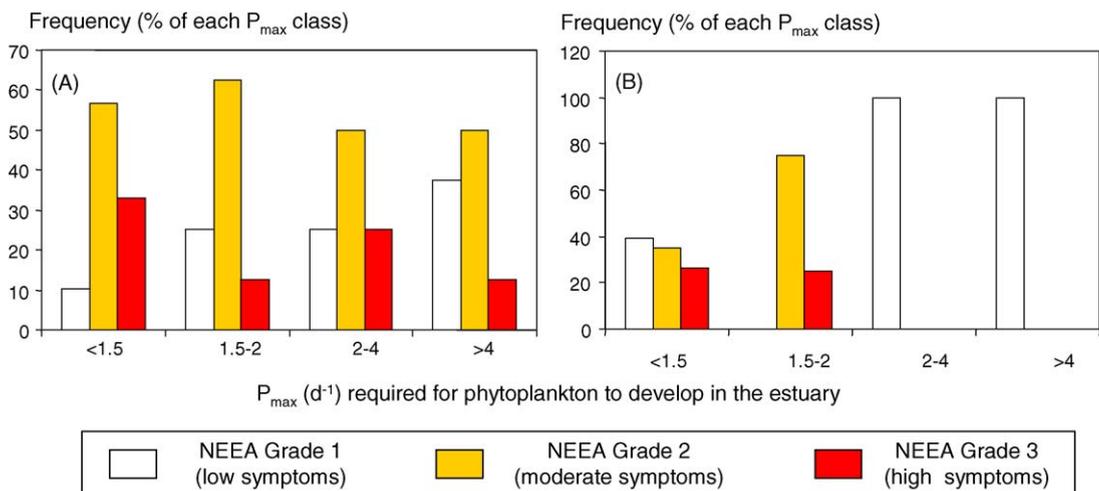


Fig. 3. Frequency distribution of NEEA scores for eutrophication symptoms (A) chlorophyll *a* and (B) nuisance and toxic blooms for 138 US estuaries.

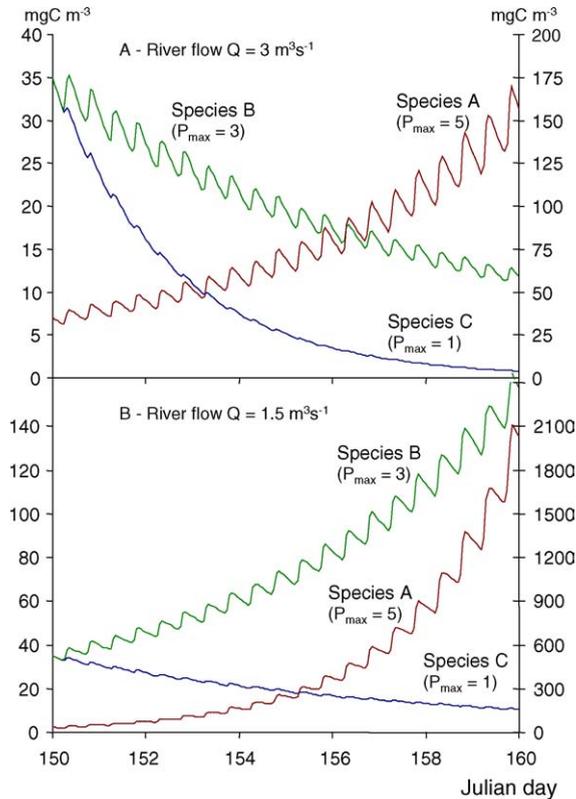


Fig. 4. Simulation of growth for three hypothetical phytoplankton species (species A shown on the right y-axis).

Fig. 4, and are presented without smoothing, reflecting the diel variability in the light climate.

Fig. 4A shows that only species A is capable of growing in the estuary. Species B shows a slow decrease of biomass, and species C will be flushed out. When the flow is decreased by 50% (Fig. 4B) species A shows a dramatic increase, but more importantly, species B also increases and species C is still present after 10 days. Dinoflagellates, which account for 75% of all harmful algal bloom (HAB) species (Smayda, 1997) show maximum growth rates which are substantially lower than those of diatoms (Smayda, 1997; Furnas, 1990), and thus may only be able to grow in an estuary when the water residence time increases. Recurrent *Pfiesteria* blooms, which occurred in a Chesapeake Bay tributary due to dry summer conditions are an example of episodic eutrophication events which may potentially be explained in this way (Magnien, 2001).

The model described above only simulates potential production, but in practice nutrient limitation will control growth. An effect of this may be that a species with a lower half-saturation growth constant K_s for a particular nutrient, but which was previously unable to grow due to physical factors, will now out compete other species. This may be particularly important in the development of blooms by cyanophytes, due to their nitrogen fixing capacity.

Fig. 5 illustrates the effect of nutrient depletion on the relative growth of the three different species. The simulation develops the potential production model described earlier, but with a $10 \mu\text{mol L}^{-1}$ stock of nitrogen added to the system. Species A was assigned a high nutrient half-saturation constant k_s , whereas B and C were given low values for k_s . Under lower residence time conditions (Fig. 5A), only species A is able to grow, whereas in the higher residence time simulation in Fig. 5B, both species A and B are able to grow, but species B becomes dominant as the nutrient pool becomes limiting.

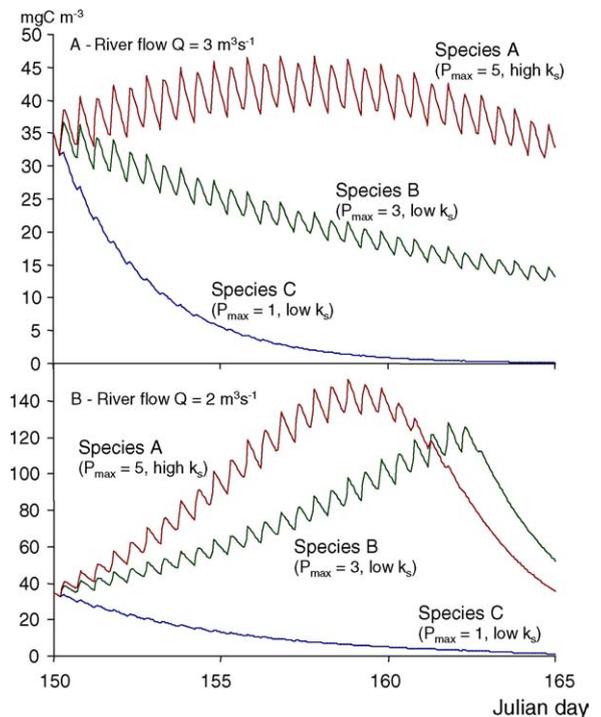


Fig. 5. Simulation of nutrient limited growth for three hypothetical phytoplankton species over a 15-day period.

7. Conclusions

In estuaries, there appears to be a clear relationship between phytoplankton biodiversity and water residence time. Since this is related to the capacity (or not) of algal species to grow faster than they are flushed, the species composition is at least partly determined by estuarine physics.

This has consequences for management, since regulatory instruments such as the EU Water Framework Directive require that type-specific reference conditions be defined for phytoplankton composition in transitional waters.

The general definition of reference conditions for phytoplankton composition may partly be accomplished by defining a set of typical species, which should (and/or should not) be observed in an estuarine type at high status (i.e. good quality), and partly by stipulating how many species might indicatively be present in a particular type. The material presented herein may potentially be used to address the latter point, by scaling ecological status classes for phytoplankton species composition within a type on the basis of estuarine flushing time. Fig. 6 shows a conceptual approach to the application of such a scheme to define five quality “bands”, scaling species number as a function of flushing time.

As a final note, the relationships explored in this paper are important in the design of river basin management plans, and particularly in the definition of the river flow required to maintain an acceptable level of ecological quality (i.e. the ecological flow). This must consider that a reduction in freshwater

supply is likely to affect estuarine phytoplankton species composition and biodiversity, and may result e.g. in an impairment or loss of shellfish resources due to increased occurrence of nuisance or toxic bloom events. This understanding may be used to develop improved models to support integrated (basin-scale) coastal zone management.

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References

Alvera-Azcarate, A., Ferreira, J.G., Nunes, J.P., 2003. Modelling eutrophication in mesotidal and macrotidal estuaries. The role of intertidal seaweeds. *Est. Coast. Shelf Sci.* 57 (4), 715–724.

Bettencourt, A., Bricker, S.B., Ferreira, J.G., Franco, A., Marques, J.C., Melo, J.J., Nobre, A., Ramos, L., Reis, C.S., Salas, F., Silva, M.C., Simas, T., Wolff, W., 2004. Typology and Reference Conditions for Portuguese Transitional and Coastal Waters. Development of Guidelines for the Application of the European Union Water Framework Directive, INAG/IMAR, 98 pp., <http://www.ecowin.org/TICOR/>.

Bougrier, S., Hawkins, A.J.S., Héral, M., 1997. Preingestive selection of different microalgal mixtures in *Crassostrea gigas* and *Mytilus edulis*, analysed by flow cytometry. *Aquaculture* 150, 123–134.

Bricker, S., Matlock, G., Snider, J., Mason, A., Alber, M., Boynton, W., Brock, D., Brush, G., Chestnut, D., Claussen, U., Denison, W., Dettmann, E., Dunn, D., Ferreira, J., Flemer, D., Fong, P., Fourqurean, J., Hameedi, J., Hernandez, D., Hoover, D., Johnston, D., Jones, S., Kamer, K., Kelty, R., Keeley, D., Langan, R., Latimer, J., Lipton, D., Magnien, R., Malone, T., Morrison, G., Newton, J., Pennock, J., Rabalais, N., Scheurer, D., Sharp, J., Smith, D., Smith, S., Tester, P., Thom, R., Trueblood, D., Van Dolah, R., 2004. National estuarine eutrophication assessment update: workshop summary and recommendations for development of a long-term monitoring and assessment program. In: Proceedings of a Workshop, September 4–5, 2002, Patuxent Wildlife Research Refuge, Laurel, Maryland. National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, Silver Spring.

Bricker, S.B., Clement, C.G., Pirhalla, D.E., Orlando, S.P., Farrow, D.R.G., 1999. National Estuarine Eutrophication Assessment. Effects of Nutrient Enrichment in the Nation’s Estuaries. NOAA—NOS Special Projects Office, Silver Spring.

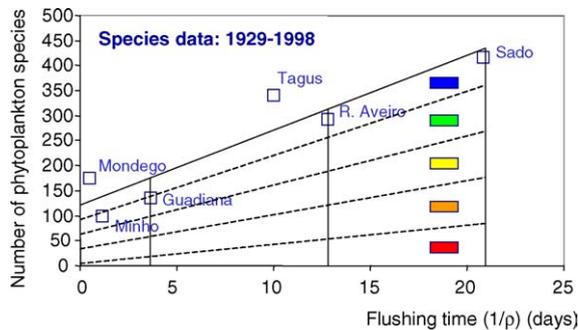


Fig. 6. Scaling of phytoplankton species composition into five quality classes (blue: better; red: worse). The divisions shown are conceptual.

- Bricker, S.B., Ferreira, J.G., Simas, T., 2003. An integrated methodology for assessment of estuarine trophic status. *Ecol. Model.* 169, 39–60.
- Brock, T.D., 1981. Calculating solar radiation for ecological studies. *Ecol. Model.* 14, 1–9.
- Burkholder, J.M., Mallin, M.A., Glasgow Jr., H.B., 1999. Fish kills, bottom water hypoxia and the toxic *Pfiesteria* complex in the Neuse River and Estuary. *Mar. Ecol. Prog. Ser.* 179, 301–310.
- Chapra, S.C., 1997. *Surface Water-Quality Modelling*. McGraw-Hill, NY, 844 pp.
- Chiaudani, G., Marchetti, R., Vighi, M., 1980. Eutrophication in Emilia-Romagna coastal waters (North Adriatic sea, Italy): a case history. *Prog. Water Technol.* 12, 185–192.
- Chícharo, M.A., Chícharo, L., Galvão, H., Barbosa, A., Reis, M., Marques, H., Barros, P., Miguel, C., Rocha, C., 2000. Caracterização Geral do Ecossistema do Estuário do Guadiana com base para Avaliação do Impacte de Alterações Ambientais. Final Report for Project INTERREG 15/REG II/6/96. Universidade do Algarve-UCTRA, Faro.
- Cloern, J.E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9, 191–202.
- Ferreira, J.G., Simas, T., Bricker, S.B., Wolff, W.J., Mason, A., Nobre, A., 2004. The use of ASSETS and phytoplankton species composition to define type-specific reference conditions for estuarine water quality management. In: ASLO/TOS 2004 Ocean Research Conference, Honolulu, Hawaii, 15–20 February, <http://www.aslo.org/meetings/honolulu2004/files/aslo-tos-2004-abstracts.pdf>.
- Fonseca, J.C., Marques, J.C., Paiva, A.A., Freitas, A.M., Madeira, V.M.C., Jørgensen, S.E., 2000. Nuclear DNA in the determination of weighing factors to estimate exergy from organisms biomass. *Ecol. Model.* 126, 179–189.
- Furnas, M.J., 1990. In situ growth rates of marine phytoplankton: approaches to measurement, community and species growth rates. *J. Plankton Res.* 12, 1117–1151.
- Gerlach, S.A., 1990. Nitrogen, phosphorus, plankton and oxygen deficiency in the German Bight and in Kiel Bay. *Kieler Meeresforschungen, Sonderheft* 7, 1–341.
- Gibson, G.R., Bowman, M.L., Gerritsen, J., Snyder, B.D., 2000. *Estuarine and Coastal Marine Waters: Bioassessment and Biocriteria Technical Guidance*. EPA 822-B-00-024. U.S. Environmental Protection Agency, Office of Water, Washington, DC.
- Gillbricht, M., 1988. Phytoplankton and nutrients in the Helgoland region. *Helgolander Meeresuntersuchungen* 42, 435–467.
- Hodgkin, E.P., Hamilton, B.H., 1993. Fertilizers and eutrophication in southwestern Australia: setting the scene. *Fertilizer Res.* 36, 95–103.
- ICES, 2004. Report of the Study Group to Review Ecological Quality Objectives for Eutrophication. ICES CM 2004/ACE:04.
- Joint, I., Lewis, J., Aiken, J., Proctor, R., Moore, G., Higman, W., Donald, M., 1997. Interannual variability of PSP (paralytic shellfish poisoning) outbreaks on the northeast UK coast. *J. Plankton Res.* 19, 937–956.
- Ketchum, B.H., 1954. Relation between circulation and planktonic populations in estuaries. *Ecology* 35, 191–200.
- Lucas, L.V., Koseff, J.R., Monismith, S.G., Cloern, J.E., Thompson, J.K., 1999a. Processes governing phytoplankton blooms in estuaries. II. The role of horizontal transport. *Mar. Ecol. Prog. Ser.* 187, 17–30.
- Lucas, L.V., Koseff, J.R., Cloern, J.E., Monismith, S.G., Thompson, J.K., 1999b. Processes governing phytoplankton blooms in estuaries. I. The local production-loss balance. *Mar. Ecol. Prog. Ser.* 187, 1–15.
- Magnien, R.E., 2001. The Dynamics of science, perception, and policy during the outbreak of *Pfiesteria* in the Chesapeake Bay. *BioScience* 51 (10), 843–852.
- Marques, J.C., Pardal, M.A., Nielsen, S.N., Jørgensen, S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. *Ecol. Model.* 102, 155–167.
- May, C.L., Koseff, J.R., Lucas, L.V., Cloern, J.E., Schoellhamer, D.H., 2003. Effects of spatial and temporal variability of turbidity on phytoplankton blooms. *Mar. Ecol. Prog. Ser.* 254, 111–128.
- Moita, M.T., Vilarinho, M.G., 1999. Checklist of phytoplankton species off Portugal: 70 years of studies. *Port. Acta Biol. Ser. B Sist.* 18, 5–50.
- Monsen, N.E., Cloern, J.E., Lucas, L.V., Monismith, S.G., 2002. A comment on the use of flushing time, residence time and age as transport time scales. *Limnol. Oceanogr.* 47 (5), 1545–1553.
- NOAA, 1999. Coastal Assessment and Data Synthesis System (CADS). NOAA, National Ocean Service, Special Projects Office, Silver Spring, <http://cads.nos.noaa.gov>.
- Nunes, J.P., Ferreira, J.G., Gazeau, F., Lencart-Silva, J., Zhang, X.L., Zhu, M.Y., Fang, J.G., 2003. A model for sustainable management of shellfish polyculture in coastal bays. *Aquaculture* 219 (1–4), 257–277.
- Okaichi, J.M., 1997. Red tides in the Seto Inland Sea. In: Okaichi, T., Tanagi, T. (Eds.), *Sustainable Development in the Seto Sea Inland Japan: from the Viewpoint of Fisheries*. Terra, Tokyo.
- OSPAR, 2001. Draft common assessment criteria and their application within the comprehensive procedure of the common procedure. Meeting of the Eutrophication Task Group (ETG), London, 9–11 October 2001 ed. OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic. OSPAR Commission, London.
- Platt, T., Gallegos, C.L., Harrison, W.G., 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* 38, 687–701.
- Rabalais, N.N., Turner, R.E., Justic, D., Dortch, Q., Wiseman Jr., W.J., Sen Gupta, B.K., 1996. Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* 19, 386–407.
- Raven, J.A., Richardson, K., 1986. Marine environments. In: Baker, N.R., Long, S.P. (Eds.), *Photosynthesis in Contrasting Environments*. Elsevier Sci. Pub., Amsterdam, pp. 337–396.
- Reynolds, C.S., Carling, P.A., Beven, K.J., 1991. Flow in river channels: new insights into hydraulic retention. *Archiv für Hydrobiologie* 121, 171–179.
- Sheldon, J.E., Alber, M., 2002. A Comparison of residence time calculations using simple compartment models of the Altamaha River Estuary, Georgia. *Estuaries* 25 (6B), 1304–1317.
- Shumway, S.E., Cucci, T.L., Newell, R.C., Yentch, T.M., 1985. Particle selection, ingestion and absorption in filter-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 91, 77–92.

- Simas, T., Nunes, J.P., Ferreira, J.G., 2001. Effects of global climate change on coastal salt marshes. *Ecol. Model.* 139 (1), 1–15.
- Smayda, T.J., 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* 42, 1137–1153.
- Smith, C.A., Maxwell, B.A., 2002. Deluxe Integrated System for Clustering Operations (DISCO), <http://www.narya.engin.swarthmore.edu/disco/>.
- Smith, S.V., Buddemeier, R.W., Bricker, S.B., Maxwell, B.A., Pacheco, P., Mason, A., 2004. Estuarine typology: perturbations and eutrophication responses. In: ASLO/TOS 2004 Ocean Research Conference, Honolulu, Hawaii, February 15–20, <http://www.aslo.org/meetings/honolulu2004/files/aslo-tos-2004-abstracts.pdf>.
- Speirs, D.C., Gurney, W.S.C., 2001. Population persistence in rivers and estuaries. *Ecology* 82, 1219–1237.
- Steele, J.H., 1962. Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.* 7, 137–150.
- Tett, P., Gilpin, L., Svendsen, H., Erlandsson, C.P., Larsson, U., Kratzer, S., Fouilland, E., Janzen, C., Lee, J., Grenz, C., Newton, A., Ferreira, J.G., Fernandes, T., Scory, S., 2003. Eutrophication and some European waters of restricted exchange. *Cont. Shelf Res.* 23, 1635–1671.
- Vincent, C., Heinrich, H., Edwards, A., Nygaard, K., Haythornthwaite, J., 2003. Guidance on Typology, Classification and Reference Conditions for Transitional and Coastal Waters. European Commission, Report of CIS WG2.4, European Commission, Brussels.