11 Ecological Aspects of Harmful Algal In Situ Population Growth Rates

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11.1 Introduction

The in situ growth of phytoplankton populations, although apparently a simple process, is not consequently dealt with in phytoplankton population ecology. In experimental phytoplankton research, population density is often expressed as cell concentration, and growth is therefore expressed as the cell division rate. In biological oceanography, chemical indicators like chlorophyll-*a* or other pigments are used to describe the phytoplankton population density, and growth rates are consequently expressed as the rate of change of these indicators. Since single phytoplankton cells double in biomass between two subsequent divisions, and may vary in cellular composition, especially pigment content, these measures of growth rate are not necessarily the same. To measure in situ growth rate of individual harmful algal bloom (HAB) species, bulk biomass parameters are usually not suitable, as other phytoplankton may also be present. Moreover, different methods have been applied to assess the in situ growth rate of phytoplankton populations giving different type of results. Therefore, a definition of terms is justified.

Assuming a homogeneous population with density N, the population growth rate dN/dt is proportional to the population density, and the specific or per-capita growth rate μ (in d^{-1}) is used to characterize the population growth.

$$\frac{dN}{dt} = \mu N \,, \qquad \text{Eq. (11.1)}$$

In case the per-capita growth rate μ is constant over time, the population density will change exponentially according to:

$$N_t = N_0 e^{\mu t} \,, \qquad \text{Eq. (11.2)}$$

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where N_t and N_0 are the population densities at time t and time 0, respectively. At optimal availability of resources (light, nutrients) and at given physical circumstances (temperature, salinity) the per-capita growth rate is defined as the maximum per-capita growth rate $\mu_{m(T,S)}$. Typically, this value is determined from the washout rate in chemostat (Pirt 1975).

In this chapter, reported growth rates of HAB and non-HAB species measured in the field are analysed to better understand the ecology of certain HAB groups.

11.2 Ecological Interpretation of In Situ Growth Rate Measurements

Phytoplankton populations need to grow in order to compensate for loss factors such as sedimentation, grazing and lysis. The net per-capita changes in population density (μ_{net}) can be expressed as

$$\mu_{\text{net}} = \mu_{\text{gross}} - l - g - e + i \qquad \text{Eq. (11.3)}$$

where μ_{gross} is the per-capita population gross growth rate, l is the lysis rate (due to viruses, parasites, or autolysis), g is the per-capita grazing rate, e and i are the per-capita export and import rates.

Phytoplankton show different strategies in order to minimize losses and maximize resource utilization. Populations can be classified as either *r*- or *K*-selected with respect to their growth strategy (MacArthur and Wilson 1967). This theory has its base in the logistic growth equation, which predicts that net growth approaches zero when population density approaches K or the *carrying capacity* of the environment for that particular species

$$\frac{dN}{Ndt} = \mu_{net} = r\left(1 - \frac{N}{K}\right), \qquad \text{Eq. (11.4)}$$

where r is the value of μ at infinitely low population density and can be interpreted as the maximum per-capita growth rate of the species at the prevailing conditions (compare to $\mu_{\max(T,S)}$). The cause of this negative correlation (Fig. 11.1) is not specified by the logistic model, but may result from intraspecific competition, grazing, etc. Although simple, the theory has been applied successfully as a framework for better understanding of ecological processes. For phytoplankton populations, succession during a growth season is from *r*-selected phytoplankton species, which have optimized their fitness for conditions with ample resources and low mortality rates, to more *K*-selected species, which have optimized their fitness for conditions with low resource availability and high risk of mortality (Margalef 1958; Sommer 1981). Typi-

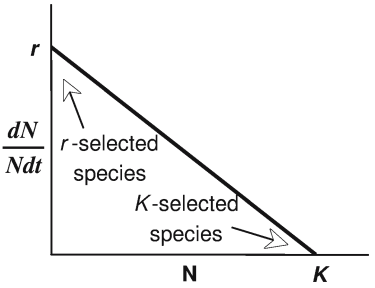

Fig. 11.1. Schematic representation of Eq. (11.4); *r*-selected species have optimized their fitness for conditions that allow for high net per capita growth rates, *K*-selected species for conditions that do not allow for high net per capita growth rates

cally, *r*-selected species have high maximum per-capita growth rates, poor competitive abilities, and/or lack mechanisms to avoid grazing or sedimentation. Typical *K*-selected species have comparatively low maximum per-capita growth rates, are good competitors, and have developed mechanisms to avoid losses due to grazing and sedimentation. Moreover, differences in life-history may play an important role. Unfortunately, data to evaluate the whole suite of characteristics for phytoplankton are scarce or lacking. Besides, there are no objective criteria to judge the "*r*-ness" or "*K*-ness" of a certain characteristic. Alternatively, the observed in situ growth rates (μ_{net}) for individual species should reflect the strategy of a species. "*r*-Strategists" should occur relatively often at conditions that allow for high per-capita growth rates. Contrastingly, *K*-strategists should occur relatively often under conditions that do not allow for high growth rates (Fig. 11.1).

In this chapter, we aim to integrate the current knowledge on phytoplankton in situ growth rates in order to find patterns that may classify different harmful phytoplankton groups as relative *r*- or *K*-strategists. This should lead to simple, testable hypotheses concerning the occurrence and timing of HABs.

Data on field measurements of phytoplankton population growth rates are relatively rare, especially from HAB species. Moreover, different growth and loss-processes are determined depending on the used method (Table 11.1). Traditional methods that require incubation of whole samples and microscope counting of individual species (Methods 1 and 2, Table 11.1) may include the effects of phytoplankton lysis and losses due to grazers present in the incubation bottle. Incubation methods with chemical detection may have the same drawback (Methods 3, 4, 5, 6, Table 11.1). Isolation of individual cells by hand-picking in combination with ^{14}C uptake measurements have been applied to measure specific carbon uptake and growth rate independent of lysis and/or grazing (Method 3, Table 11.1; Granéli et al. 1997). Recently, more advanced methods have been applied to identify the growth rate of individual species in the field, such as cell cycle methods (Method 8, Table 11.1) that do not require incubation at all. This method relies on the fact that representative samples are taken from the same field population under a period of 1–2 days.

Table 11.1. Overview of the ecological interpretation of different in situ growth rate methods. *Numbers* in first column are referred to in Table 11.2

	Method description	Ecological interpretation (see Eq. 11.3)	References
1	Dialysis incubation (by measuring change in cell, particle or chlorophyll concentration or alternative biomass index)	μ_{gross} - l - g^a	Prakash et al. 1973; Maestrini and Kossut 1981
2	Diffusion incubation (by measuring change in cell, particle or chlorophyll concentration or alternative biomass index)	μ_{gross} - l - g^a	Furnas 1982a; Vargo 1984; Ferrier-Pagès 2001; Tang 2003
3	^{14}C-carbon uptake = rates of carbon and/or chlorophyll accumulation	μ_{gross}(- l - g^a)	Eppley et al. 1970; Granéli et al. 1997
4	Nutrient assimilation	μ_{gross} - l - g^a	Furnas 1982b; Nelson and Smith 1986
5	ATP synthesis	μ_{gross} - l - g^a	Sheldon and Sutcliffe 1978
6	Protein synthesis and turnover	μ_{gross} - l - g^a	DiTullio and Laws 1983
7	Pigment specific activity = Pigment labelling	μ_{gross} – l	Redalje and Laws 1981; Goericke and Welschmeyer 1993
8	Cell cycle method or cytological index or mitotic index or biochemical cell cycle markers	μ_{gross} or PGR^b	Swift and Durbin 1972; Smayda 1975; Carpenter and Chang 1988; Chang and Carpenter 1991; Garcés et al. 1998a; 1999; Garcés and Masó 2001, and references therein
9	In vivo fluorescence ratios	μ_{gross} or PGR^b	Heath 1988
10	Thymidine or germanium	μ_{gross} or PGR^b	Rivkin and Voytek 1986
11	Dilution technique	μ_{gross} – l and g^a	Landry et al. 1995; Garcés et al. 2005, and refs therein [a]grazing is taken into account only from grazers that are included in the incubation bottle (often only microzooplankton)

[a] Grazing is taken into account only from grazers that are include in the incubation bottle (ofen only microzooplankton)

[b] PGR = potential growth rate

The application of flow-cytometric DNA-cycle detection for individual species is an especially powerful method to measure gross growth rates in the field. However, in this case it is assumed that populations can be recognized by flow-cytometric detection methods.

Depending on the method, a value between net and gross growth rate is determined (summarized in Table 11.1). Since the effect of cell lysis and grazing can be large, often in the same order of magnitude as growth, gross and net growth rates may differ substantially. However, differences in growth rates between methods in our analysis were not significant (Kruskal-Wallis test).

The measurement of an individual population's growth rate in the field is only possible when individual species can be analysed. Usually, microscopic or flow-cytometric techniques are used for quantification (Methods 1, 2, 8 and 11, Table 11.1) or physical separation of cells before analysis (e.g. Method 3, but in principle applicable for other methods too). Detection of biochemical markers such as pigments (e.g. Method 7, but also applicable with Methods 1, 2 and 11) are taxon-specific rather than species-specific (Mackey et al. 1996), and are influenced by the variability of cellular pigment content (Stolte et al. 2000). In our analysis, we have only used data obtained from individual populations.

11.3 In Situ Growth Rates; Variation Among Taxonomic Groups

In total, 178 entries from six taxonomical classes are listed in Table 11.2, including harmful and non-harmful species. Due to the different methods that were applied to measure the in situ growth rates, values vary between net- and gross-values (compare Table 11.1). Because the different methods represent different concepts (Table 11.1), no statistical significance-tests were applied. Still, there are some interesting trends worth further investigation. When ranking phytoplankton after their observed in situ growth rates, the highest values were recorded for cryptophytes, chrysophytes and diatoms (Fig. 11.2), groups that are rarely involved in harmful events. However, prymnesiophytes, which frequently cause harmful blooms, also show high in situ growth rates. Conversely, cyanobacteria and dinoflagellate in situ growth rates are clearly lower (Fig. 11.2). It may therefore be hypothesized that among HAB-forming classes, prymnesiophytes are more *r*-selected, and dinoflagellates are more *K*-selected species. For cyanobacteria, only non-HAB coccoid species are represented, and no filamentous forms, which are responsible for HABs in brackish and fresh water.

Table 11.2. Reported in situ per-capita growth rates (μ) for different taxonomic groups, and possible harmful effects

Species	μ	Harmful effect*	Reference
Cyanobacteria			
Prochlorococcus sp.[8]	1.21, 0.50, 0.50, 0.67, 0.54, 0.58, 0.72	–	a
Prochlorococcus sp.[2]	0.75, 0.54, 0.80, 0.70, 0.64, 0.56, 0.84	–	a
Synechococcus sp.[2]	0.42	–	b
Bacillariophyceae (centrales)			
Bacteriastrum spp.[2]	1.52	–	b
Cerataulina pelagica[2]	1.32, 0.42	–	b
Cerataulina pelagica[3]	0.20	–	c
Cerataulina pelagica[11]	0.70	–	c
Chaetoceros curvisetum[2]	2.22	–	b
Chaetoceros peruvianum[2]	0.76	–	b
Chaetoceros subtilis[2]	0.28	–	b
Chaetoceros sp. solitary[2]	0.35	–	b
Chaetoceros sp. chained[2]	0.42	–	b
Chaetoceros spp.[2]	2.08	–	b
Chaetoceros sp.[3]	0.30, 0.30	–	c
Chaetoceros sp.[11]	0.30, 0.10	–	c
Cyclotella caspia[3]	2.90	–	c
Cyclotella caspia[11]	2.50	–	c
Cyclotella striata[3]	0.60	–	c
Cyclotella striata[11]	1.70	–	c
Hemiaulus spp.[2]	0.55	–	b
Leptocylindrus danicus[2]	1.11, 0.97	–	b
Leptocylindrus minimus[2]	1.04	–	b
Rhizosolenia alata[2]	0.14	–	b
Rhizosolenia delicatula[2]	0.69	–	b
Rhizosolenia fragilissima[2]	0.83, 0.28	–	b
Rhizosolenia setigera[2]	0.35	–	b
Rhizosolenia stolterfothii[2]	0.35	–	b
Rhizosolenia styliformis[2]	0.14	–	b
Skeletonema costatum[2]	1.94, 0.49	–	b
Skeletonema costatum[3]	1.00, 0.50, 0.30	–	c
Skeletonema costatum[11]	1.60, 1.00, 0.50	–	c
Thalassiosira rotula[3]	0.40, 0.20	–	c
Thalassiosira rotula[11]	0.50, 0.20	–	c
Thalassiosira sp.[2]	1.11	–	b
Thalassiosira sp. „small“[2]	0.97	–	b
Bacillariophyceae (pennates)			
Asterionella glacialis[2]	0.90	–	b
Nitzschia closterium[2]	1.04	–	b
Nitzschia closterium „medium“[2]	1.52	–	b
Nitzschia closterium „medium“[3]	0.35	–	b

Table 11.2. (*Continued*)

Species	μ	Harmful effect*	Reference
Nitzschia closterium „large“[2]	0.90	–	b
Nitzschia curta[3]	0.21	–	b
Nitzschia fraudulenta[2]	0.49	ASP	b
Nitzschia lineola[2]	1.25	–	b
Nitzschia pungens[2]	0.55	ASP	b
Nitzschia pungens[3]	0.20, 0.50	ASP	c
Nitzschia pungens[11]	0.70	ASP	c
Thalassionema (Thalassiosira) nitzschioides[2]	0.90	–	b
Thalassionema (Thalassiosira) frauenfeldii[2]	0.97	–	b
Thalassiothrix spp.[2]	0.62	–	b
Unknown pennate species[2]	0.90	–	b
Cryptophyceae			
Rhodomonas lacustris[3]	3.00, 0.70, 0.40, 0.30	–	c
Rhodomonas lacustris[11]	2.70, 1.60, 0.20, 0.30	–	c
Rhodomonas sp[3]	1.80, 0.60, 0.40	–	c
Rhodomonas sp[11]	1.20, 0.30, 0.60	–	c
Dinophyceae			
Alexandrium catenella[11]	0.22, 0.24	PSP	d
Alexandrium minutum[2]	0.76, 0.97	PSP	e
Alexandrium tamarense[2]	0.23	PSP	f
Alexandrium taylori[11]	0.67, 0.24, 0.30, 0.04, 0.64, 0.17	HBNT	d
Ceratium arietinum[8]	0.09	–	b
Ceratium candelabrum[8]	0.09	–	b
Ceratium contrarium[8]	0.15	–	b
Ceratium declinatum[8]	0.12	–	b
Ceratium furca[3]	0.28, 0.60	HBNT	g
Ceratium horridum[8]	0.08	–	b
Ceratium lineatum[3]	0.48, 0.81	HBNT	g
Ceratium macroceros[8]	0.08	–	b
Ceratium massilience[8]	0.15	–	b
Ceratium pulchellum[8]	0.19	–	b
Ceratium symmetricum (summetricum)[8]	0.14	–	b
Ceratium tripos[3]	0.17	HBNT	g
Dinophysis acuminata[8]	0.22, 0.12	DSP	h
Dinophysis acuminata[3]	0.59, 0.49	DSP	g
Dinophysis acuta[8]	0.11	DSP	h
Dinophysis acuta[3]	0.41, 0.35	DSP	g
Dinophysis caudata[8]	0.19	DSP	h
Dinophysis norvegica[3]	0.63, 0.29, 0.18	DSP	g
Dinophysis norvegica[8]	0.17, 0.13, 0.21, 0.40	DSP	i
Dinophysis tripos[8]	0.21	DSP	h

Table 11.2. (*Continued*)

Species	μ	Harmful effect*	Reference
Gymnodinium spp.[3]	0.30, 0.30	–	c
Gymnodinium spp.[11]	0.10, 0.10	–	c
Gymnodiniacea „medium“[2]	0.07	–	b
Gymnodiniacea „small“[2]	0.21	–	b
Heterocapsa triquetra[8]	0.10, 0.21, 0.17, 0.05, 0.03, 0.02, 0.03, 0.04, 0.05, 0.04, 0.11, 0.06, 0.02, 0.02	–	j
Karlodinium sp.[8]	0.94, 0.60, 0.59, 0.50, 0.39,	FK	k
Katodinium rotundatum[3]	2.60, 1.00, 0.80	–	c
Katodinium rotundatum[11]	2.40, 0.50, 0.10	–	c
Prorocentrum minimum[2]	0.21	UNK	b
Prorocentrum triestinum[2]	0.14	–	b
Chrysophyceae			
Ochromonas minima[3]	1.00, 1.20, 1.10	–	c
Ochromonas minima[11]	0.90, 0.20, 0.60	–	c
Prymnesiophyceae			
Chrysochromulina spp.[3]	0.90, 0.80	FK	c
Chrysochromulina spp.[11]	1.00, 1.00	FK	c
Phaeocystis globosa single[8]	0.68, 0.49	HBNT	l
Phaeocystis globosa colony[8]	0.73, 0.76, 0.93	HBNT	l

Numbers behind species names refer to methods in Table 11.1

[a] (Liu et al. 1998);
[b] (Furnas 1990);
[c] (Fahnenstiel et al. 1995);
[d] (Garcés et al. 2005);
[e] (Garces et al. 1998b);
[f] (Ichimi et al. 2001);
[g] (Granéli et al. 1997);
[h] (Reguera et al. 1996);
[i] (Gisselson et al. 2002);
[j] (Litaker et al. 2002);
[k] (Garcés et al. 1999);
[l] (Veldhuis et al. 2005)

* *HBNT* high biomass but no toxins detected, *FK* fish killing bloom, *ASP* amnesic shellfish poisoning, *PSP* paralytic shellfish poisoning, *DSP* diarrhetic shellfish poisoning, *UNK* unknown toxin, “–” not known to be harmful

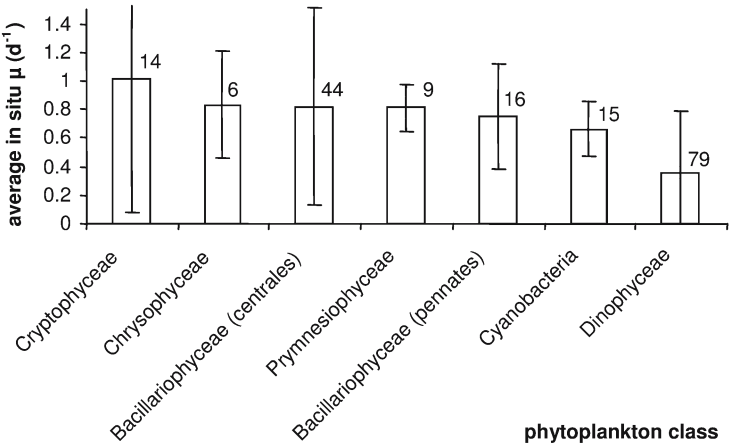

Fig. 11.2. Average in situ per capita growth rates (d^{-1}) with standard deviations for each phytoplankton class in descending order. The number of observations is stated above each column

11.4 Are Harmful Algal Species r- or K-Strategists?

Harmful algal species have on average lower reported in situ growth rates than non-HAB species (Fig. 11.3). This result is in agreement with the hypothesis that harmful algae are relatively *K*-adapted species, capable of reducing their losses due to grazing, either by being toxic or via other mechanisms. However, the diversity of HAB-species is great, hampering the possibility to draw conclusions on a possible general strategy for all HAB species.

It is unlikely that all phytoplankton that are harmful from a human perspective have a general growth strategy. However, it is likely that growth strategies correspond to the type of harmful effect, or more specifically, the mechanism or toxin that is responsible for the harmful effect. The data were therefore analysed according to the type of harmful effect that the particular species may cause.

The highest observed in situ growth rates are reported for high-biomass non-toxic (HBNT) species (Fig. 11.4), and fish-killing (FK) species (both on average 0.59 d^{-1}). Species that are not known for any harmful effect have similar growth rates to HBNT and FK species (Fig. 11.4). Dinoflagellates responsible for diarrhetic shellfish poisoning (DSP) have the lowest in situ growth rates (0.3 d^{-1}). Based on in situ growth rates, DSP-causing species *Dinophysis* spp. could be considered to be relatively *K*-selected species. Indeed, *Dinophysis* spp. are recognized for their relatively low growth rates (Smayda and Reynolds 2001) and poor edibility (Carlsson et al. 1995). Moreover, they often

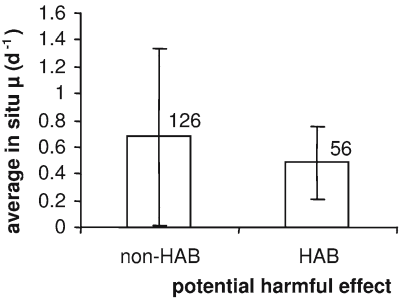

Fig. 11.3. Average in situ per capita growth rates (d^{-1}). Harmful species are any species with a harmful effect according to Table 11.1. The number of cases is reported above each bar

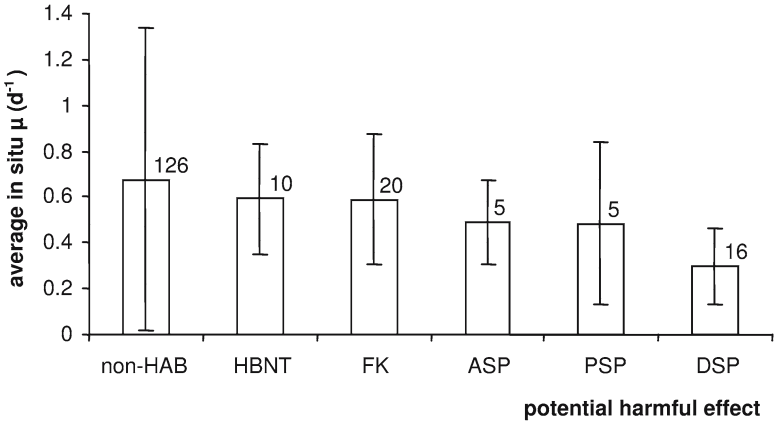

Fig. 11.4. Observed in situ per capita growth rates (d^{-1}) with standard deviations for harmful algae grouped per harmful effect

occur in high numbers at the pycnocline (Gisselson et al. 2002), an environment that is either stable in the case of tropical waters, or at least predictable in seasonally stratified temperate seas. In general, phytoplankton communities in stable and predictable environments would be growing close to their carrying capacity (MacArthur and Wilson 1967), and one would expect *K*-selective species to comprise an important part of those communities.

The dinoflagellates that cause paralytic shellfish poisoning (PSP), displaying intermediate values, do not seem to be clearly *r*- or *K*-selected based on in situ growth rates. This is not in conflict with the earlier classification of these types of dinoflagellates as species of intermediately nutrient-enriched waters (Smayda and Reynolds 2001).

11.5 Conclusions

With the current set of data, we provide support for the hypothesis that HBNT and FK blooms are *r*-selected, and will dominate in areas and during periods of ample nutrients and a low risk of losses due to grazing and sedimentation. These types of blooms can therefore be considered as indicators for eutrophication of the marine environment. Both types could also contribute to significant disturbances of marine coastal environments, either through hypoxia in bottom waters or through the effects of their toxins, contributing to an unstable environment even more suitable for *r*-selected species (MacArthur and Wilson 1967). This positive feedback mechanism might lead to shifts in ecosystem properties upon establishment of such HABs. This may be an additional explanation for recurring high-biomass and fish-killing blooms in eutrophicated areas.

We also provide support that DSP- and to a lesser extent PSP-causing species are more *K*-selected, and probably more resistant to grazing than other species (e.g. Teegarden 1999). Competition for nutrients by these groups is either avoided by using alternative nutrient sources, such as phagotrophy in case of *Dinophysis* spp., or is by choosing habitats with intermediate nutrient concentrations, such as coastal fronts in the case of some PSP-causing dinoflagellates (Smayda and Reynolds 2001). Life-history events that are hard to classify as either *r*- or *K*-selected traits such as cyst formation, swimming behaviour and sexual reproduction most probably contribute to the success of these species.

Compared to earlier efforts to classify phytoplankton, in particular harmful algal species, into a theoretical ecological framework (Margalef 1958; Smayda and Reynolds 2001), the current approach is simple. However, assuming that any growth strategy finally is reflected by the observed growth rate, some preliminary conclusions could be made with respect to different groups of HAB species. We provide additional support for a diversity of strategies within HAB-forming phytoplankton. An increasing problem of HAB occurrence in many coastal waters may therefore have different causes, and a variety of mitigation or prevention measurements must be applied if HAB prevalence is to be reduced.

References

Carlsson P, Granéli E, Finenko G, Maestrini SY (1995) Copepod grazing on a phytoplankton community containing the toxic dinoflagellate *Dinophysis acuminata*. J Plankton Res 17:1925–1938

Carpenter EJ, Chang J (1988) Species specific phytoplankton growth rates via diel DNA synthesis cycles. I. Concept of the method. Mar Ecol Prog Ser 43:105–111

Chang J, Carpenter EJ (1991) Species specific phytoplankton growth rates via diel DNA synthesis cycles. V. Application to natural populations in Long Island Sound. Mar Ecol Prog Ser 78:115–122

DiTullio G, Laws EA (1983) Estimating of phytoplankton N uptake based on ^{14}C incorporation into protein. Limnol Oceanogr 28:177–185

Eppley RW, Reid FMH, Strickland JDH (1970) Estimates of phytoplankton crop size, growth rate and primary production. Bull Scripps Inst Oceanogr 17:33–42

Fahnenstiel GL, McCormick MJ, Lang GA, Redalje DG, Lohrenz SE, Markowitz M, Wagoner B, Carrick HJ (1995) Taxon-specific growth and loss rates for dominant phytoplankton populations from the northern Gulf of Mexico. Mar Ecol Prog Ser 117:229–239

Ferrier-Pagès C, Furla P (2001) Pico- and nanoplankton biomass and production in the two largest atoll lagoons of French Polynesia. Mar Ecol Prog Ser 211:63–76

Furnas MJ (1982a) An evaluation of two diffusion culture techniques for estimating phytoplankton growth rates in situ. Mar Biol 70:63–72

Furnas MJ (1982b) Growth rates of summer nanoplankton populations in lower Narragansett Bay, Rhode Island, USA. Mar Biol 70:105–115

Furnas MJ (1990) In situ growth-rates of marine-phytoplankton – approaches to measurement, community and species growth rates. J Plankton Res 12:1117–1151

Garcés E, Masó M (2001) Phytoplankton potential growth rate versus increase in cell numbers: estimation of cell lysis. Mar Ecol Prog Ser 212:297–300

Garcés E, Delgado M, Maso M, Camp J (1998a) Life history and in situ growth rates of *Alexandrium taylori* (Dinophyceae, Pyrrophyta). J Phycol 34:880–887

Garcés E, Delgado M, Vila M, Camp J (1998b) An *Alexandrium minutum* bloom: in situ growth or accumulation? In: Reguera B, Blanco J, Fernandez ML, Wyatt T (eds) Harmful algae. Xunta de Galicia and IOC- UNESCO, Vigo, pp 167–170

Garcés E, Delgado M, Masó M, Camp J (1999) In situ growth rate and distribution of the ichthyotoxic dinoflagellate *Gyrodinium corsicum* Paulmier in an estuarine embayment (Alfacs Bay, NW Mediterranean Sea). J Plankton Res 21:1977–1991

Garcés E, Vila M, Masó M, Sampedro N, Grazia Giacobbe M, Penna A (2005) Taxon-specific analysis of growth and mortality rates of harmful dinoflagellates during bloom conditions. Mar Ecol Prog Ser 301:67–79

Gisselson L-Å, Carlsson P, Granéli E, Pallon J (2002) *Dinophysis* blooms in the deep euphotic zone of the Baltic Sea: do they grow in the dark? Harmful Algae 1:401–418

Goericke R, Welschmeyer NA (1993) The carotenoid-labeling method: measuring specific rates of carotenoid synthesis in natural phytoplankton communities. Mar Ecol Prog Ser 98:157–171

Granéli E, Anderson DM, Carlsson P, Maestrini SY (1997) Light and dark carbon uptake by *Dinophysis* species in comparison to other photosynthetic and heterotrophic dinoflagellates. Aquat Microb Ecol 13:177–186

Heath MR (1988) Interpretation of in vivo fluorescence and cell division rates of natural phytoplankton using a cell cycle model. J Plankton Res 10:1251–1283

Ichimi K, Yamasaki M, Okumura Y, Suzuki T (2001) The growth and cyst formation of a toxic dinoflagellate, *Alexandrium tamarense*, at low water temperatures in northeastern Japan. J Exp Mar Biol Ecol 261:17–29

Landry MR, Kirshtein J, Constantinou J (1995) A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the Central Equatorial Pacific. Mar Ecol Prog Ser 120:53–63

Litaker RW, Warner VE, Rhyne C, Duke CS, Kenney BE, Ramus J, Tester PA (2002) Effect of diel and interday variations in light on the cell division pattern and in situ growth rates of the bloom-forming dinoflagellate *Heterocapsa triquetra*. Mar Ecol Prog Ser 232:63–74

Liu H, Campbell L, Landry MR, Nolla HA, Brown SL, Constantinou J (1998) *Prochlorococcus* and *Synechococcus* growth rates and contributions to production in the Arabian Sea during the 1995 Southwest and Northeast Monsoons. Deep-Sea Res Part II-Topical studies in oceanography 45:2327–2352

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton Univ Press, Princeton, USA, 203 pp

Mackey MD, Mackey DJ, Higgins HW, Wright SW (1996) CHEMTAX - A program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. Mar Ecol Prog Ser 144:265–283

Maestrini SY, Kossut MG (1981) In situ cell depletion of some marine algae enclosed in dialysis sacs and their use for the determination of nutrient-limiting growth in Ligurian coastal waters (Mediterranean Sea). J Exp Mar Biol Ecol 50:1–19

Margalef R (1958) Temporal succession and spatial heterogeneity in phytoplankton. In: Buzzati-Traverso AA (ed) Perspectives of marine biology. Univ Calif Press, Berkeley, pp 323–349

Nelson DM, Smith WO (1986) Phytoplankton bloom dynamics of the western Ross Sea ice edge. II. Mesoscale cycling of nitrogen and silicon. Deep Sea Res 33:1389–1412

Pirt SJ (1975) Principles of microbe and cell cultivation. Blackwell Scientific Publications, Oxford, 274 pp

Prakash A, Skoglund L, Rysttad B, Jensen A (1973) Growth and cell size distribution of marine planktonic algae in batch and dialysis cultures. J Fish Res Board Canada 30:143–155

Redalje DG, Laws EA (1981) A new method for estimating phytoplankton growth rates and carbon biomass. Mar Biol 62:73–79

Reguera B, Bravo I, McCall H, Reyero MI (1996) Phased cell division and other biological observations in field populations of *Dinophysis* spp. during cell cycle studies. In: Yasumoto T, Oshima Y, Fukuyo Y (eds) Harmful and toxic algal blooms. IOC-UNESCO, Paris, pp 257–260

Rivkin R, Voytek M (1986) Cell division rates of eukaryotic algae measured by tritiated thymidine incorporation into DNA: coincident measurements of photosynthesis and cell division of individual species of phytoplankton isolated from natural populations. J Phycol 22:199–205

Sheldon RW, Sutcliffe WH Jr (1978) Generation time of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol Oceanogr 23:1051–1055

Smayda TJ (1975) Phased cell division in natural population of the marine diatom *Ditylum brightwelli* and the potential significance of diel phytoplankton behavior in the sea. Deep Sea Res 22:151–165

Smayda TJ, Reynolds CS (2001) Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. J Plankton Res 23:447–461

Sommer U (1981) The role of *r*- and *K*-selection in the succession of phytoplankton in Lake Constance. Acta Oecologica 2:327–342

Stolte W, Kraay GW, Noordeloos AAM, Riegman R (2000) Genetic and physiological variation in pigment composition of *Emiliania huxleyi* (Prymnesiophyceae) and the potential use of its pigment ratios as a quantitative physiological marker. J Phycol 36:529–539

Swift E, Durbin EG (1972) The phased division and cytological characteristics of *Pyrocystis* spp. can be used to estimate doubling times of their populations in the sea. Deep Sea Res 19:189–198

Tang KW (2003) Grazing and colony size development in *Phaeocystis globosa* (Prymnesiophyceae): the role of a chemical signal. J Plankton Res 25:831–842

Teegarden GJ (1999) Copepod grazing selection and particle discrimination on the basis of PSP toxin content. Mar Ecol Prog Ser 181:163–176

Vargo G (1984) Growth rates of natural populations of marine diatoms as determined in cage cultures. In: Holm-Hansen O, Bolis L, Gillus R (eds) Lecture notes in coastal and estuarine studies, vol 8. Springer, Berlin Heidelberg New York, pp 113–128

Veldhuis MJW, Brussaard CPD, Noordeloos AAM (2005) Living in a *Phaeocystis* colony: a way to be a successful algal species. Harmful Algae 4:841–858