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Phytoplankton carrying capacity: Is this a viable concept for coastal seas?

Subrata Sarker*, Karen H. Wiltshire

Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Germany

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ABSTRACT

Carrying capacity estimations for any population of organisms is made in order to determine the maximum population densities that could result under set environmental conditions. Carrying capacity (K) is often used in terrestrial ecosystems to estimate potential plant densities (yields) related to the availability of resources. Here we wanted to see whether a similar concept could be applied to the plants of the ocean: Phytoplankton. Using the Helgoland Roads Time Series data sets, the main focus was on those which control phytoplankton growth in the ocean. We aimed to estimate K and determine whether K is static or variable, evaluated the relationship of phytoplankton K with higher trophic levels. We also provided a guideline to use K as ecosystem management tool. Algorithms were developed to estimate the K based on each controlling factor. A pair-wise comparison matrix was used for weighting the controlling factors and then to integrate the estimated K based on controlling factors to obtain an overall K. Long-term intra-annual and inter-annual mean K were estimated 10.13×10^7 cells m^{-3} and 1.30×10^8 cells m^{-3}, respectively. Our analyses suggest that K should not be considered as a static permanent value. This is because it is driven by overall environmental conditions and is subject to change when overall environment change. We linked the estimated K to pelagic fisheries data of the North Sea and found that phytoplankton K is correlated with the pelagic fisheries of this area. Our overall conclusion is that phytoplankton K is a viable concept and could be utilized as a valuable management tool.

1. Introduction

Phytoplankton represents a diverse group of primary producers and although it makes up less than 1% of the plant biomass on the earth, it accounts for 50% of global primary production (Field et al., 1998). Being the dominant primary producers in the sea, phytoplankton act at the base of the marine trophic webs (Sterner and Elser, 2002). Phytoplankton abundance as the main food source, governs the abundance of herbivorous zooplankton, which in turn regulates the level of planktivorous. Thus, changes in the abundance of phytoplankton affect both the herbivorous zooplankton and planktivorous fish.

In the oceanic ecosystem phytoplankton dynamics are regulated by both “bottom-up” factors (e.g. light and nutrients) and “top-down” mechanisms (e.g. zooplankton) (Wiltshire et al., 2008). The maximum densities of phytoplankton that can be supported by a given environment could be, as in plant terrestrial systems (Hobbs et al., 1982; Hobbs and Swift, 1985), considered to be a type of phytoplankton carrying capacity (K). It is this potential which we wish to consider in this study.

Carrying capacity estimations for any population of organisms is traditionally made in order to determine the maximum population densities that could result under set environmental conditions. This is often used in terrestrial ecosystems to estimate potential plant species densities (yields) related to the availability of resources. The K of a population is generally dependent on food, shelter, predation and exploitation (Kashiwai, 1995), and similarly a considered phytoplankton K in a marine system could be considered to be directly dependent on the resources important for phytoplankton. In a shallow coastal sea, phytoplankton dynamics are controlled by light availability, temperature, nutrients and zooplankton (Mitchell et al., 1991; Wiltshire et al., 2015) and thus these factors can be used to estimate the phytoplankton K in the coastal seas.

Generally marine food web studies focus on the links between resources (e.g. nutrients) to phytoplankton through zooplankton and to fisheries. Changes at any of these levels will affect any

* Corresponding author.
E-mail address: subrata.sarker@awi.de (S. Sarker).

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trophic level dependent upon them. Such changes can be anything from pollution mitigation with a reduction in nutrients through to the introduction of a new species into a system. Any change in phytoplankton *K* might affect the phytoplankton densities which will affect the following tropic levels (i.e. zooplankton and fisheries). The "classical" *K* concept is based on the idea that once the population of a system has exceeded the *K*, the population will suffer a crash (Abel and McConnell, 2001). Applying this concept to our study system one can hypothesize that once phytoplankton density exceeds its *K*, the phytoplankton stock in the system will crash, and in terms of higher trophic levels, this could mean a decrease in zooplankton and fish abundance. Considering the importance of phytoplankton to the marine ecosystem and fisheries, we consider *K* for phytoplankton can be an interesting management tool for marine systems.

Algorithms for *K* estimation have been developed (Moen, 1973; Robbins, 1973) and used to evaluate the quality of ungulate habitat (Bobek, 1977; Wallmo et al., 1977). Some work has been carried out for fisheries (e.g. (Byron et al., 2011; Cross et al., 2011; Dame and Prins, 1997; Perry and Schweigert, 2008; Vasconcellos and Gasalla, 2001).) and environment (Mazaris et al., 2009; Wang et al., 2017). But studies for plankton *K* are very rare i.e. Hopkinson et al. (2013) performed an experimental study. In theoretical studies of phytoplankton, *K* is considered as a constant, which is not often realistic (Safuan et al., 2012). Carrying capacities in nature are variable and many studies have discussed about the importance of time dependent *K* (Banks, 1993). Carrying capacity of a population depends on the physical and biotic environment (Arrow et al., 1995) and thus phytoplankton *K* should not be constant. In our extensive literature search, no studies were found for plankton *K* estimation using real data on the long-term taking the phytoplankton requirements of resources into account.

Phytoplankton *K* indicates the highest potentiality for phytoplankton growth of the ecosystem. Fisheries recruitment is highly related with this highest potentiality and phytoplankton densities in the ecosystem, for example cod recruitment in the North Sea (Beaugrand et al., 2003). Another example is monitoring of ecosystem potentiality using phytoplankton *K* could help farmers to decide when to sow, maintains, and harvest their marine aquaculture items (for example oyster). Maximum numbers of marine aquaculture farms are also dependent on phytoplankton *K*. Thus considering the importance of phytoplankton *K* as a management tool, it is important to estimate phytoplankton *K*. In addition as theoretical studies consider *K* as a static permanent value; it is also an exciting scientific question to see if a change in ecosystem variables also changes the phytoplankton *K*.

Therefore, our aims for this study are to:

(i) Estimate phytoplankton *K* in the North Sea using the Helgoland Roads Time Series data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004).
(ii) Work out if *K* can remain constant over the time or changes with a change in environmental variables.
(iii) Relate phytoplankton *K* with the higher trophic levels (e.g. with fisheries) and provide information on how to use *K* as an ecosystem management tool.

2. Materials and methods

2.1. Pelagic data collection

Phytoplankton *K* for the German Bight was estimated by using the Helgoland Roads long-term data sets. The Helgoland Roads Time Series station (54°11.3′ N, 7°54.0′ E) is located between two islands, i.e. Helgoland and Düne (Fig. 1), in the North Sea. Long-term monitoring of biological, chemical and physical parameters has been carried out continuously at Helgoland Roads on a work daily basis since 1962 by Biologische Anstalt Helgoland (BAH) of the Alfred Wegener Institute, Germany and is one of the longest and most species rich aquatic data sets available (Wiltshire and Dürselen, 2004).

The water samples are taken from the surface (1 m depth) as representative of the entire water column, which is generally well-mixed as a result of strong tidal currents (Hickel, 1998).

Secchi depth as a measure of water transparency and temperature are measured directly on station. The bucket sample is mixed and sub-sampled into a glass bottle for future analyses of nutrients, salinity and phytoplankton (Wiltshire et al., 2010). This long-term dataset is quality controlled through a careful comparison with data sets from the same water bodies and reference data sets [e.g., BSH (Hamburg), ICES (Copenhagen) and MUDAB (Hamburg)] for the North Sea (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). The pelagic biotic and abiotic data sets are now sufficiently understood with problems, errors and corrections documented, and can be used as reference data to assess long-term changes in the North Sea (Wiltshire et al., 2010). The nutrients (silicate, phosphate, ammonium, nitrate and nitrite) are measured

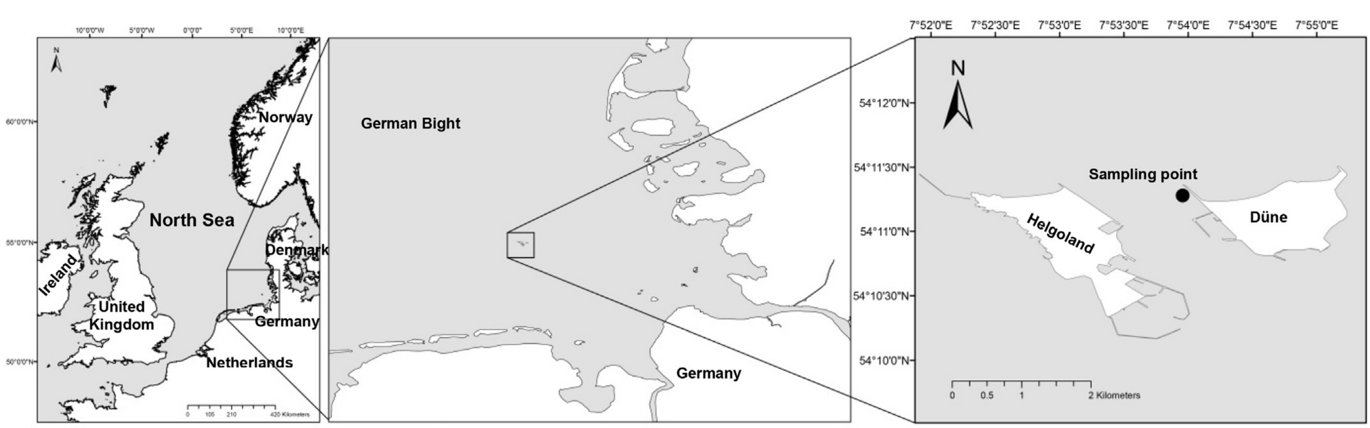

Fig. 1. Geographical location of the study area. Left panel shows the map of northern Europe with a black rectangular box indicating the location of the German Bight. Middle panel map shows a close up of the German Bight. Black rectangular box indicates the position of Helgoland. Right panel map shows the location of Helgoland Roads Times Series station (sampling point marked as filled black circle) located between two islands i.e. Helgoland and Düne.

immediately using the standard colorimetric methods after Grasshoff (1976) on a filtered sub-sample of the water sample (Wiltshire et al., 2010). The phytoplankton sub-sampled from the Helgoland Roads sample is preserved in brown glass bottles using Lugols' solution and counted daily under an inverted microscope to species level, when possible, or otherwise differentiated into defined size classes, using Utermöhl settling chambers to the species level (Hoppenrath et al., 2007; Wiltshire and Dürselen, 2004; Wiltshire et al., 2010). The dominant microalgae in the North Sea are the diatoms. These are also the most reliable in the data set in-terms of data quality control (Wiltshire and Dürselen, 2004) and thus, used here. The corresponding zooplankton time series started in 1974 (Greve et al., 2004; Wiltshire et al., 2015). Two nets have been deployed three times a week with a 150-µm Nansen net and a 500-µm CalCOFI (Wiltshire et al., 2010). Oblique hauls are made with a Nansen net, whereas the CalCOFI net is towed behind the research vessel (Greve et al., 2004).

2.2. Phytoplankton carrying capacity assessment

In this study we defined phytoplankton K as the maximum diatom cell densities which can be supported by a given environmental condition at a given time. This K is derived from the number sunshine hours, SiO_2 concentration (µmol/L), PO_4 concentration (µmol/L), NO_3 concentration (µmol/L), and the grazing potential of herbivore zooplankton, using the data of the Helgoland Roads Time Series station. However, a number of other factors i.e. wind speed, current velocity etc. also drive the phytoplankton dynamics which are not considered in our study. This is one of the limitations of our study.

As the first stage of analysis, also mostly done for plant K in terrestrial ecosystems, we estimated diatom K in-terms of sunshine hours, SiO_2, PO_4 and NO_3 (i.e. maximum diatom densities supported by the amount of these resources found in the system) using the following formula:

$$K_m = \frac{N}{M_m} \times S_{mt} \tag{1}$$

In Eq. (1), K_m denotes the K in-terms of resource m, where m = sunshine hours or SiO_2 or PO_4 or NO_3. $\frac{N}{M_m}$ is a constant which represents the ratio of diatom cell densities (N) and amount of resource m (M_m) when the molar ratio of nutrients maintain the “Redfield Ratio” (Redfield, 1934) in the ecosystem. This is based on the fact that Redfield (1934) discovered that when nutrients are not limited at the ecosystem, the molar elemental ratio N: P in most phytoplankton and sea water is 16:1. Diatoms, being silicified organisms, require silicate on top of the other plant nutrients. Brzezinski (1985) sets the “Redfield Ratio” for diatoms as: Si: N: P = 15:16:1. We used this version here. We considered the maximum diatom densities to be the standard K when the molar ratio of nutrients in the system reached the “Redfield Ratio”. Thus: S_{mt} represents the observed values of resource m at time t.

The concept we devised for the K assessment of phytoplankton for the German Bight is shown in Fig. 2. This came into play for the second step of our analysis. The sunshine hours, SiO_2, PO_4 and NO_3 were weighted relative to each other, by applying a pair-wise comparison matrix in the context of a decision making process known as the “Analytical Hierarchy Process (AHP)” (Saaty, 1990). Details on AHP method are given as supplementary information of this article (S1). This pair-wise comparison allowed us to determine the relative weight of resources considered for K estimation. This weighting of resources also reflects their relative importance for diatom growth. The pair-wise comparison matrix developed for diatom K estimation is shown in Table 1.

In the third step we combined estimated diatom K in-terms of sunshine hours, SiO_2, PO_4 and NO_3. In order to do this the K for each resource (Eq. (1)) as estimated in the first step, was multiplied by their respective weight calculated in a pair-wise comparison matrix (Table 1) in second step of analysis. The product of K for each resource and respective weight is then added: $K_{Diatom} = \sum(K_m \times Weight_m)$.

The four resources for diatom K were calculated by Eq. (2).

$$K_{Diatom} = (K_{Sunshine\ hours} \times 0.07) + (K_{SiO_2} \times 0.24) + (K_{PO_4} \times 0.34) + (K_{NO_3} \times 0.35) \tag{2}$$

As herbivore zooplankton density cannot be ignored because it also affects diatom densities through grazing (Griffin and Rippingale, 2001) we included it in our analyses in the final step. Thus, Eq. (2) is extended to Eq. (3) with herbivore zooplankton effect. This was the product of herbivore zooplankton densities at the time t and, the ratio between average diatoms K (estimated by using equation (2)) and average herbivore zooplankton densities.

$$K_{Diatom} = (K_{Sunshine\ hours} \times 0.07) + (K_{SiO_2} \times 0.24) + (K_{PO_4} \times 0.34) + (K_{NO_3} \times 0.35) + \textit{Zooplankton effect} \tag{3}$$

For a better understanding of K, we divided the estimated K into two components i.e. “actual carrying capacity” (AK) and “theoretical maximum carrying capacity” (TMK). In addition, we estimated

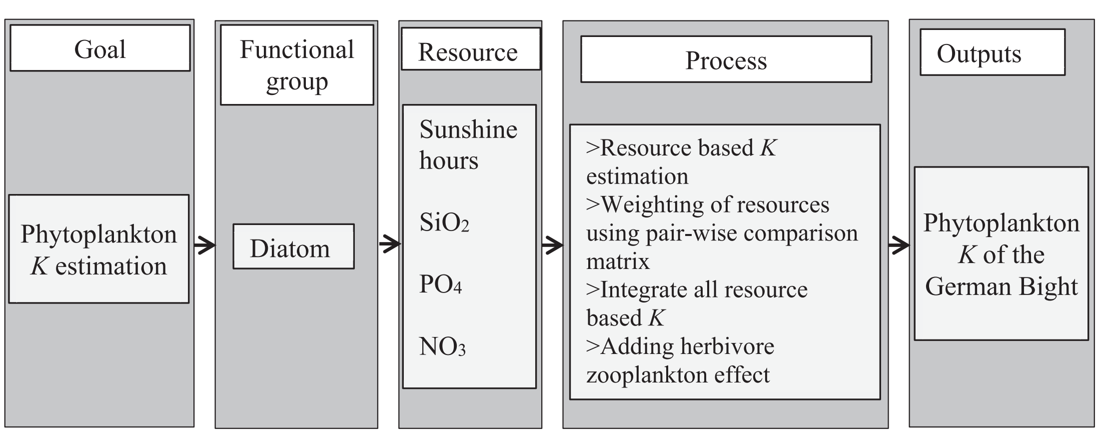

Fig. 2. Analytical hierarchy schemes for diatom K estimation in the German Bight using the Helgoland Roads Time Series data sets.

Table 1
Pair-wise comparison matrix to assess the relative importance of selected resources for diatom *K* estimation. “Values” represents the pair-wise comparison between each pair of resources (SH=Sunshine hours, Si=SiO_2, P=PO_4, N=NO_3), “Decimal” represents the fractional values of respective paired comparison and “Normalization” represents normalized value of “Decimal”. Weight (Wt) of each resource, consistency index (CI), random consistency index (RI) and consistency ratio (CR) were calculated following Saaty (1990).

	Values				Decimal				Normalization				Wt	λ_{max}	CI	RI	CR
	SH	Si	P	N	SH	Si	P	N	SH	Si	P	N					
SH	1	1/3	1/5	1/5	1	0.33	0.2	0.2	0.71	0.07	0.07	0.07	0.07	4.10	0.03	0.9	0.04
Si	3	1	3/4	3/4	3	1	0.75	0.75	0.21	0.22	0.25	0.25	0.24				
P	5	3/2	1	1	5	1.5	1	1	0.36	0.34	0.34	0.34	0.34				
N	5	7/4	1	1	5	1.75	1	1	0.36	0.38	0.34	0.34	0.35				
Column sum					14	4.58	2.95	2.95									

“ecosystem potential” by subtracting *AK* from *TMK*. We defined these terminologies (i.e. *AK*, *TMK* and ecosystem potential) in Table 2.

3. Results

Long-term intra-annual mean diatom A*K* (Fig. 3A) was found to be 10.13 × 10^7 cells m^{-3} with a maximum during week 29 (33.25 × 10^7 cells m^{-3}). This maximum A*K* is the “theoretical maximum *K*” (TM*K*) for intra-annual case. Minimum intra-annual A*K* was found to be 0.01 × 10^7 cells m^{-3} during week 51. Mean inter-annual A*K* was found to be 1.30 × 10^8 cells m^{-3} (Fig. 3B) with a maximum (i.e. TM*K* for inter-annual case) of 2.004 × 10^8 cells m^{-3} in 1994 and a minimum 0.70 × 10^8 cells m^{-3} in 2011.

Both intra-annual and inter-annual diatom *AK* at Helgoland Roads showed variability over the time (Fig. 3). Estimated intra-annual A*K* increased from week 1–22 and then fluctuated during summer (week 23–34) and followed a decreasing trend at the end of summer. Overall inter-annual diatom A*K* has an increasing trend ($R^2 = 0.13$, $p = 0.03$). These temporal variations in estimated intra-annual and inter-annual A*K* indicate that phytoplankton *K* is not constant and changes over time, depending on the environmental conditions. By taking the maximum value of *K* as a reference (i.e. TM*K*), we calculated the deviation of A*K* from this TM*K* (i.e. ecosystem potential) for both intra-annual and inter-annual cases (Fig. 4). We found that at low deviation the observed diatom densities are higher and at high deviation, diatom densities are low for both intra-annual (Fig. 4B; $R^2 = 0.50$, $p < 0.0001$) and inter-annual data (Fig. 4D; $R^2 = 0.12$, $p = 0.03$). Interestingly, inter-annual diatom densities have a significant positive trend ($R^2 = 0.27$, $p < 0.001$) while deviations have significant negative trend ($R^2 = 0.13$, $p = 0.03$). This indicates that the ecosystem potentiality for phytoplankton growth has increased on the long-term and thus the diatom densities have also increased.

Table 2
Descriptions of terminologies used in this study.

Terminology	Description
Actual carrying capacity (A*K*)	Maximum number of diatom cells that can be supported by a given environment in a particular time. For intra-annual and inter-annual cases, each week and year have a value of A*K* respectively which is calculated based on the environmental conditions of respective week and year.
Theoretical maximum carrying capacity (TM*K*)	The maximum value of A*K* calculated from intra-annual and inter-annual cases. Lon-term intra-annual cycle has one value of TM*K* and similarly long-term inter-annual case also has one value of TM*K*.
Ecosystem potential	The deviation of A*K* from TM*K*. This deviation provides information on the overall conditions of the system. High deviation of the A*K* from the TM*K* means the system has less potentiality for phytoplankton growth and low deviation means the system has high potentiality. The 0 difference between TM*K* and A*K* indicates no deviation and this means that A*K* reached at the TM*K* of ecosystem.

4. Discussion

Carrying capacity is assumed to be constant in population growth models, but the need to treat the *K* as a function of time has long been recognized in order to model population dynamics in an environment that undergoes change. In this study we showed that it is possible to estimate the *K* values also for phytoplankton and, found that as the biotic and abiotic factors in the ecosystem change intra and inter-annual phytoplankton *K* also changes (Fig. 3). This underpins our expectation that the phytoplankton A*K* is variable and dependent on environmental conditions.

We found that estimated diatom *K* is low during winter season and that is related with the low light availability in the system. During winter light is the limiting factor for phytoplankton rather than nutrients in the shallow North Sea (Wiltshire and Manly, 2004) though during this time nutrients reach at maxima (Hernández-Fariñas et al., 2014). The role of nutrients as determinant of phytoplankton *K* during winter is less as the system is driven by light during this period. Thus, during winter this light-driven system has low *K*.

During spring observed diatom densities are high due to spring bloom. At the beginning of spring diatom densities increased and nutrients levels become reduced. At the same time zooplankton grazing on microalgae is less. The spring bloom starts with the increasing light conditions (Richardson, 1989) and ends when conditions of nutrients concentrations in the water column are low (Loebl et al., 2009; Sharples et al., 2006). As spring goes on, nutrients decrease rapidly in the system due to uptake by phytoplankton and winter stock of nutrient is depleted. Even when during spring grazing is low and light is on the increase trend but continuous uptake of nutrients by phytoplankton causes a difference between estimated *K* and observed diatom densities.

At the beginning of the summer, nutrient levels go up (Hernández-Fariñas et al., 2014; Wiltshire et al., 2015) due to depletion of the water and local remineralization process (Wiltshire et al., 2015). At the same time, less turbulent conditions result higher light penetration depth (Richardson, 1989; Wiltshire et al., 2015) and thus create better conditions for the system to support higher densities of phytoplankton. During autumn, both nutrient levels and light start to decrease and concurrently, diatom *K* also starts to decrease. During this period observed densities exceed the *K* and therefore, suffer a crash.

During the early years of this analysis (from 1975 to 1990), diatom *K* and observed diatom densities were concomitant. But

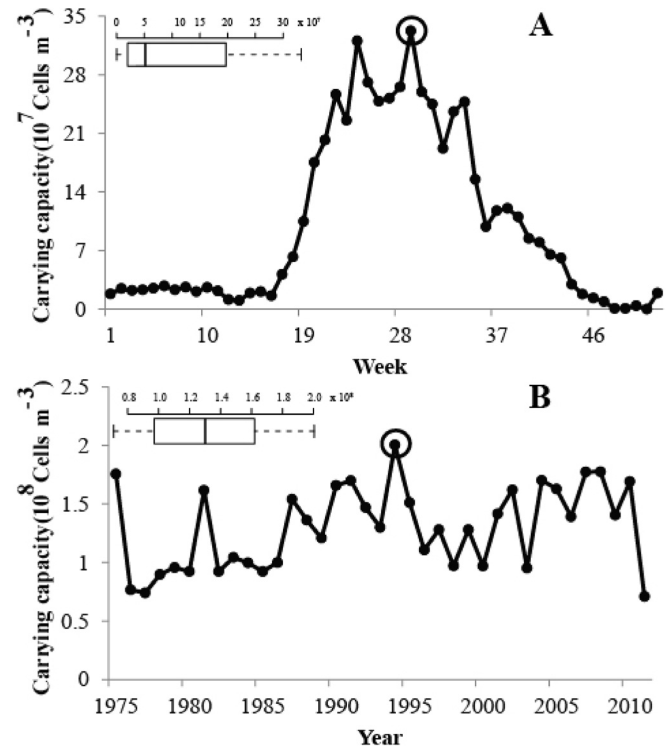

Fig. 3. Intra-annual (A) and inter-annual (B) variation of A*K* at the Helgoland Roads time Series station. Hollow black circles in both A and B graphs indicate the TM*K* for intra-annual and inter-annual respectively. Box plots represent the mean of intra-annual (A) and inter-annual (B) A*K*.

since 1990, diatom *K* and observed diatom cell density have differed from each other significantly. This might be due to the long term changes in nutrient structures. The southern bight of the North Sea has been subject to nutrient enrichment since the 1960s and subsequent nutrient reduction mitigations since the late 1980s (Lenhart et al., 2010). Taking into account these changes in the ecosystem drivers, one key question is how these changes affect the *K* of the system as mentioned in Wiltshire et al. (2010). In this study we found that A*K* of the system has increased on the long-term. In addition, the deviation of A*K* from the TM*K* which shows a decreasing trend means the potentiality of the system for phytoplankton growth has increased. Years with high potentiality had the high diatom densities.

Here we estimated the *K* for diatoms and the effect of species composition on *K* is not evaluated. Therefore, it might be an interesting research question to see how the *K* is affected by species composition. Moreover, it will be also interesting to see how *K* varies in other aquatic ecosystems i.e. freshwater and estuary.

5. Potential application of *K* in relation to fisheries

The production of marine fisheries is limited and influenced by various factors, but phytoplankton is the most important and most fundamental necessity (Cushing, 1995; Hanson and Leggett, 1982; Pauly and Christensen, 1995). We evaluated the relationship between diatom A*K* and fish (Fig. 5) in the German Bight by using the mean fish trophic level (measure of the position of an organism in food web which starts from 1 which stands for primary producers, trophic level 2 stands for primary consumers that eat primary producers, 3 for secondary consumers, and so on). The pelagic fish catch data for the German Bight came from "The Sea Around Us" project (Pauly and Zeller, 2015). Detailed methods for trophic level calculation have been described in Kleisner et al. (2014). However, this is the first attempt to relate the *K* with fisheries and more detailed data at local level are needed for more insights.

According to data (Pauly and Zeller, 2015) the mean trophic level in the North Sea from 1975 to 2006 varied between 3.45 and 3.26 with a mean 3.34 (Fig. 5A). Pelagic fish catch values for the North

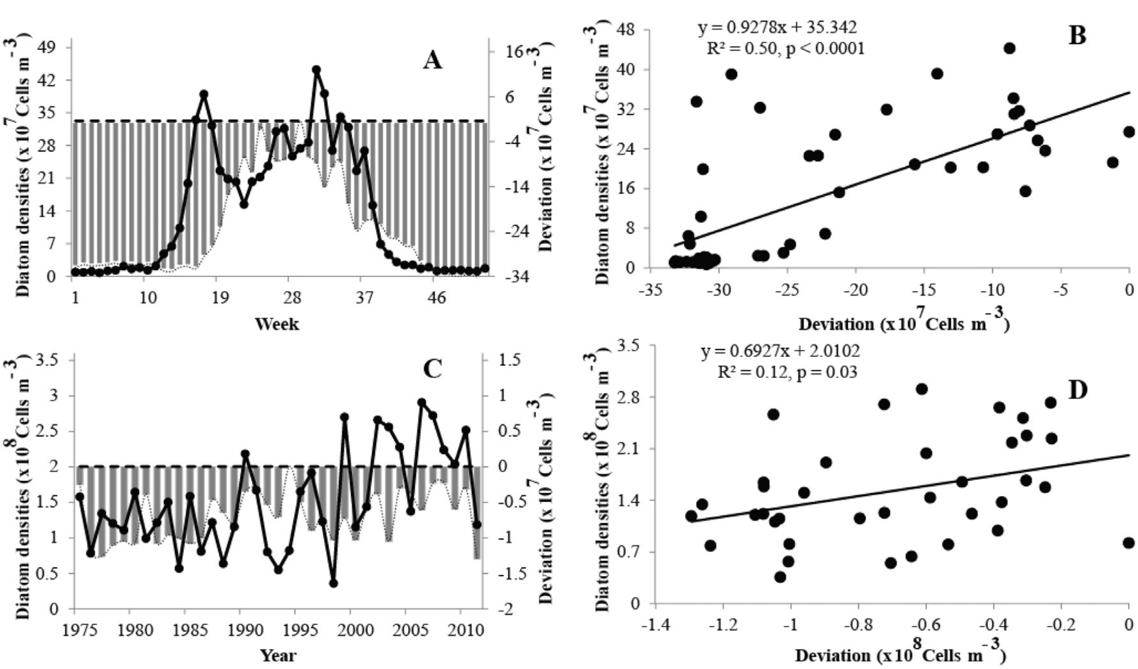

Fig. 4. Temporal variations of ecosystem potential (i.e. Deviation) and observed diatom densities (A and B), and relationship between ecosystem potential with observed diatom densities (B and D) at the Helgoland Roads Time Series station. Dashed black horizontal lines in A and C indicate the TM*K* for intra-annual and inter-annual cases respectively, dashed and solid black lines indicate the temporal variation in A*K* and observed diatom densities respectively, and grey colored bars (secondary axis) indicate the deviations of A*K* from the TM*K*.

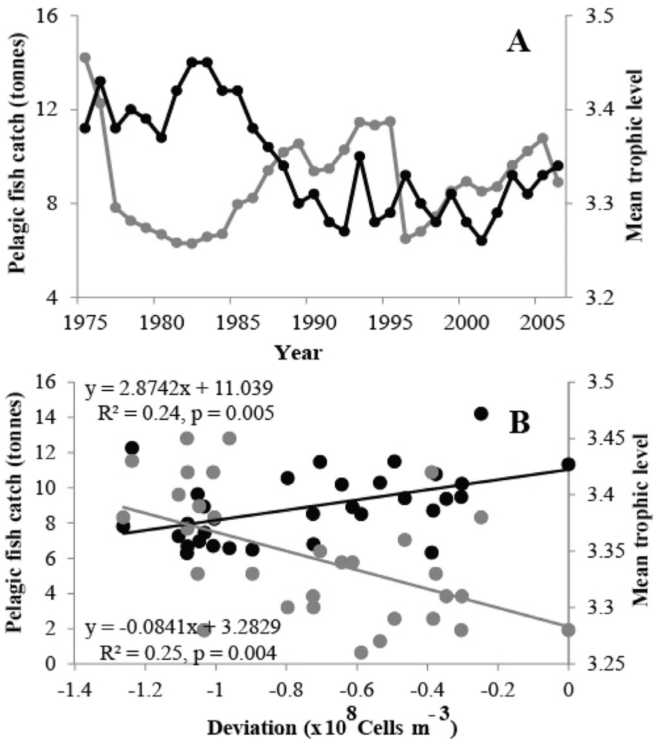

Fig. 5. Inter-annual variations in pelagic fish catch and mean trophic level (A) in the German Bight (Data source: SAUP, 2005), and relationship of ecosystem potential with pelagic fish catch and mean trophic level (B). Black and grey filled circles (B) represent the pelagic fish catch and mean trophic level of catch in the German Bight.

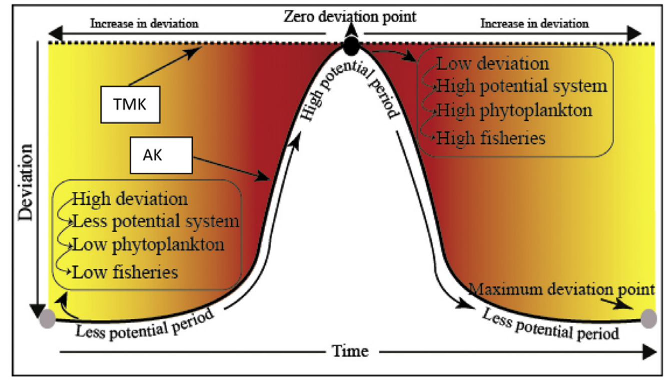

Fig. 6. Schematic presentation of the relationship of phytoplankton *AK* (Actual carrying capacity) and deviation from TM*K* (Theoretical maximum carrying capacity) with the fisheries. Depths of the filled area from the dashed black line indicate the deviation of *AK* from the TM*K*. The color gradient from yellow through red to yellow indicates low potentiality through high potential to low potential of the system. Black filled point indicates the point of no deviation (i.e. highly potential) and arrow lines from this point indicate the increase of deviation (i.e. decrease potentiality). Filled grey circles indicate the high deviation point with less potentiality of the ecosystem. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Sea varied between 14.21 × 10^5 to 6.29 × 10^5 tonnes with a mean 8.93 × 10^3 tonnes for that time period (Fig. 5A). The overall long term mean trophic level (1975–2006) showed a decreasing trend, while an increased trend was observed for both pelagic fish catch and diatom *AK*. Further comparison of deviation of *AK* from the TM*K* with pelagic fish catch data showed a significant positive relationship (Fig. 5B; $R^2 = 0.24$, $p = 0.005$) while a significant negative relationship was found with mean trophic level data (Fig. 5B; $R^2 = 0.25$, $p = 0.004$). These indicate that high potentiality for phytoplankton growth in the system supports high pelagic fisheries in the North Sea ecosystem. Thus we conclude that, high *AK* indicates high potential for growth and therefore higher densities of phytoplankton in the system, which in turn supports high pelagic fisheries. We summarized the relationship between fisheries and deviation of *AK* from the TM*K* in Fig. 6.

6. Carrying capacity as management tool

Our study represents the *K* for past and present time periods. Therefore, it is important to know how one can make *K* as an active part of future environmental management. Our analyses suggest that ecosystem potential (i.e. deviation of *AK* form the *TMK*) and observed phytoplankton in the ecosystem follow a positive linear relationship. Considering this relationship, we considered two scenarios i.e. A and B. Scenario A is a system where ecosystem potential increased at time 2 compared to time 1 and this also caused an increase in observed phytoplankton in the system.

On the other hand, scenario B is a system where ecosystem potential decreased at time 2 from time 1. This low *K* in current state than previous state indicates the basic requirements those drive the *K* are in short supply. For example, it might happen if the supply of specific nutrient is low. In addition, unbalanced supply of nutrients (i.e. high nitrogen and low phosphorus supply or vice versa) might change the *k* of the ecosystem. Decrease in potentiality means the system has differed from its real state and thus supports less phytoplankton. This will lead to a change in the structure of the entire ecosystem (i.e. change the primary production, fisheries production etc.). Therefore, scenario B demands some management practices.

For proper management, first attempt needed to identify the anticipated impact of *k* change on the ecosystem (i.e. less ecosystem potential will support less fisheries production which results in economical loss). Then it is essential to identify drivers those changed the *k* (i.e. change in nutrients supply might change the *K* of the phytoplankton). As next step, proper strategies need to formulate and implement (i.e. how to control suspended particulate matter loads/nutrient inputs). If the supply of a specific nutrient is less but is essential for the growth of phytoplankton then the supply needs to increase. As another option, we can also decide to decrease or stabilize the human population pressure.

In general, management means “able to influence the situation”. Therefore, for the open sea, how the concept of *K* can change the situation? Phytoplankton *K* is mainly dependent on light, nutrients and temperature and grazing. Among these nutrients are controllable at their input levels. We generally expect a gradient in nutrients distribution from coastal area to open sea (i.e. high concentration in the river and low in the open sea). Carrying capacity at the open sea can serve as an indicator of ecosystem health and changes in the nutrients distribution pattern from coast to open sea might change the *K*. Thus, current state of *K* can show if reduction of specific nutrients is required at the input level to reach at a balanced nutrients condition. It will then help to develop the guideline to formulate policy toward defining limits of input of ecological drivers from their sources to the ecosystem. Through a better policy formulation and then implementation would help the system to return in its *TMK* state. However, for these we need continuous monitoring.

Apart from management and policy, how this study can put the knowledge in the practice of the oyster and mussel farmers? Farmers can use this study as an indication of ecosystem state. As we did our study based on the one of the world largest and longest quality controlled data set, one can have an indication on long-term change in ecosystem potential in the German Bight. This indication might hold true for the coastal areas also (i.e. long-term trend might be similar). In addition, the seasonal cycle of carrying capacity may offer the information on when to sow and when to harvest the farmed species as both open sea and coastal area supposed to show the same seasonal pattern. However, to estimate the number of farms they can establish and stocking density of the species it is important to estimate the *K* at the local level. Though *K* can be utilized as an excellent management tool, however this approach needs regular monitoring of the ecosystem. This might requires some technical knowledge. As *K* is dependent on the environmental condition, this might vary at different geographical locations.

7. Conclusion

In conclusion, going back to our title: Is the phytoplankton carrying capacity a viable concept? The answer is “yes”. Phytoplankton *K* is driven by a set of environmental factors which are subjected to both temporal and spatial changes. There is really an A*K* which is also variable and possible to estimate. The TM*K* of an ecosystem can be considered an optimum goal and A*K* in the ecosystem always tends to achieve that goal, and this *K* concept plays an important role in the fields of population dynamics and resource management. Increase in A*K* reduces the deviation with TM*K*, increase the potentiality of the ecosystem and thus increase the phytoplankton densities. Fisheries resources strictly follow the timing and level of this potentiality for success of recruitment, peak of occurrence and decline of stock. As we already showed that high pelagic fish catch in the North Sea is related with the high potentiality of the ecosystem (Fig. 4). Changes in timing of this high potential of the system will shift the timing of fisheries recruitment and peak occurrence (match and mismatch can occur). Moreover to find a balance between ecosystem and aquaculture farms (i.e. oyster farms), this *K* can be also served as an important management tool. Thus, monitoring the phytoplankton *K* serve as an ecosystem based management tool (Box 1) by estimating A*K*, TM*K* and potential of the system, and then predicting the timing of fish recruitment, peak occurrence, decline of stock, sowing and harvesting of aquaculture species.

Box 1

Utilization of carrying capacity as fisheries management tool

Step 1: Calculate A*K* and TM*K* using environmental data.

Step 2: Calculate the deviation of A*K* from the TM*K*.

Step 3: # If deviation is less, the system has high potentiality for growth.

If deviation is high, the system has low potentiality for growth.

Step 4: # Determine the timing of fish recruitments, peak occurrences and stock decline.

Determine the timing of aquaculture species snowing and harvesting.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2017.07.015.

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