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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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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

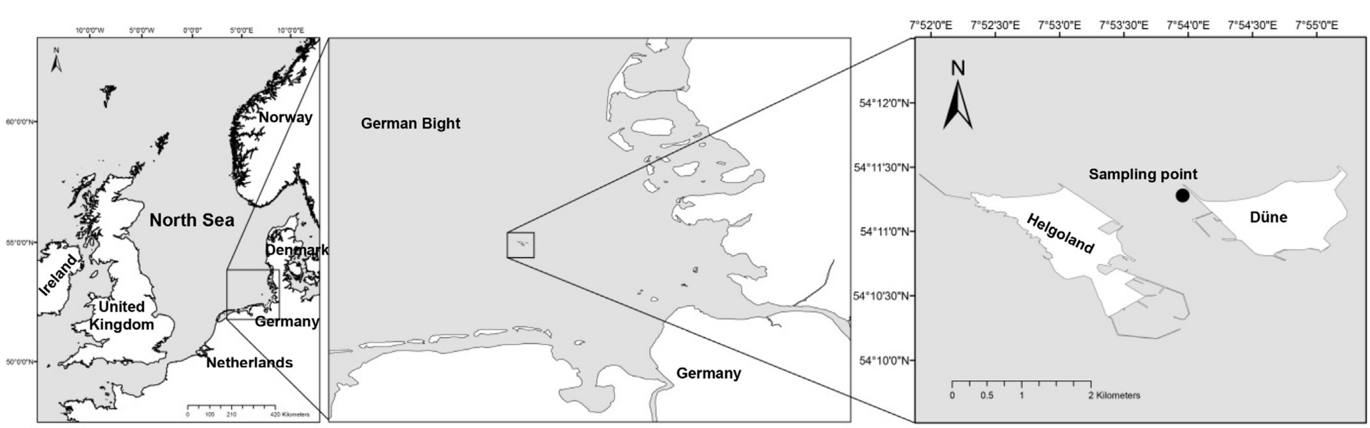

Fig. 1. Geographical location of the study area. Left panel shows the map of northern Europe with a black rectangular box indicating the location of the German Bight. Middle panel map shows a close up of the German Bight. Black rectangular box indicates the position of Helgoland. Right panel map shows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