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Light and nutrient limitation on phytoplankton production in the strait of an enclosed coastal sea (Bisan Strait, eastern Seto Inland Sea, Japan)

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ABSTRACT

The Bisan Strait is a vertically well-mixed, shallow area (mean depth 13.9 m) in the Seto Inland Sea. The strait has the lowest Secchi transparency (mean 4.5 m) within the Inland Sea because of active sediment re-suspension. Therefore, in comparison with adjacent areas, phytoplankton production in the strait may be strongly affected by light availability in addition to nutrient availability. In this study, we examined environmental variables, photosynthesis–irradiance (P–I) curves and phytoplankton production in the Bisan Strait over 1 year. There were temporal variations in the light-saturated photosynthesis rate ($P^B{}_m$) and initial slope of P–I curve (α^B), with maxima in autumn and minima in spring. Most of the variability in $P^B{}_m$ and α^B was explained by variations in nutrient concentrations (dissolved inorganic nitrogen) and water temperature. Meanwhile, phytoplankton production reached a peak in summer and a nadir in spring, but an autumn peak in production was not observed. Diagnostic analysis suggested that, for almost all of the year, nutrients were more important for phytoplankton growth than light limitation. However, light limitation became more important in autumn when underwater irradiance reached low levels. Therefore, the lack of an autumn peak in production is likely to be related to light limitation. We suggest that low light availability during the autumn depresses the annual rate of phytoplankton production in the Bisan Strait, in comparison with adjacent areas where seasonal stratification is established and phytoplankton blooms frequently occur in early autumn.

1. Introduction

Enclosed coastal seas, such as Chesapeake Bay, the Baltic Sea, the Black Sea, and the Seto Inland Sea, are surrounded by land and connected to other seas or the ocean through narrow waterways (International EMECS Center, 2003). Relatively large amounts of anthropogenic nitrogen and phosphorus tend to be delivered from adjacent terrestrial areas into enclosed coastal seas. These adjacent areas are often heavily used for human activities, including urbanization and industrialization, because they are usually sheltered coastlines with calm waters. Therefore, high rates of phytoplankton production, usually over 185 g C m^{-2} y^{-1} (median of 131 estuarine-coastal areas (Cloern et al., 2014)), are frequently observed in enclosed coastal seas. Conversely, phytoplankton production remains relatively low in some seas despite sufficient nutrient input (e.g. Northern San Francisco Bay, Cole and Cloern, 1984). The low production indicates that nutrients alone are insufficient to explain differences in phytoplankton production among enclosed coastal seas.

In addition to nutrients, other important factors for phytoplankton growth and production include light, water temperature, and herbivorous grazing. In particular, light availability seems to be critical when there is high turbidity in the seawater. Monbet (1992) analyzed the chlorophyll-*a* concentration in 40 estuaries, and reported that concentrations were significantly lower in macrotidal areas than in microtidal areas, when nitrogen concentration was similar in both estuaries. The study also emphasized that this pattern is partly due to differences in the inhibition of phytoplankton growth by re-suspended bottom sediments. It should be noted that turbidity levels are generally lower in enclosed coastal seas than in estuaries (e.g. Cloern, 1987). However, it is still important to examine the effects of light limitation on phytoplankton growth in enclosed coastal seas, where water clarity is frequently lower than in open coastal environments.

The Bisan Strait (Fig. 1) is part of the Seto Inland Sea, which is the largest enclosed sea in Japan. The Inland Sea has a mean depth of 37.3 m and has one of the highest fishery yields per unit area of all enclosed seas globally (Okaichi and Yanagi, 1997). The water column in this strait is vertically mixed through the year because of its strong tidal current (up to >1 m s^{-1}), shallow depth (mean 13.9 m), and archipelagic nature (Takahashi et al., 2012). This homogeneity is in

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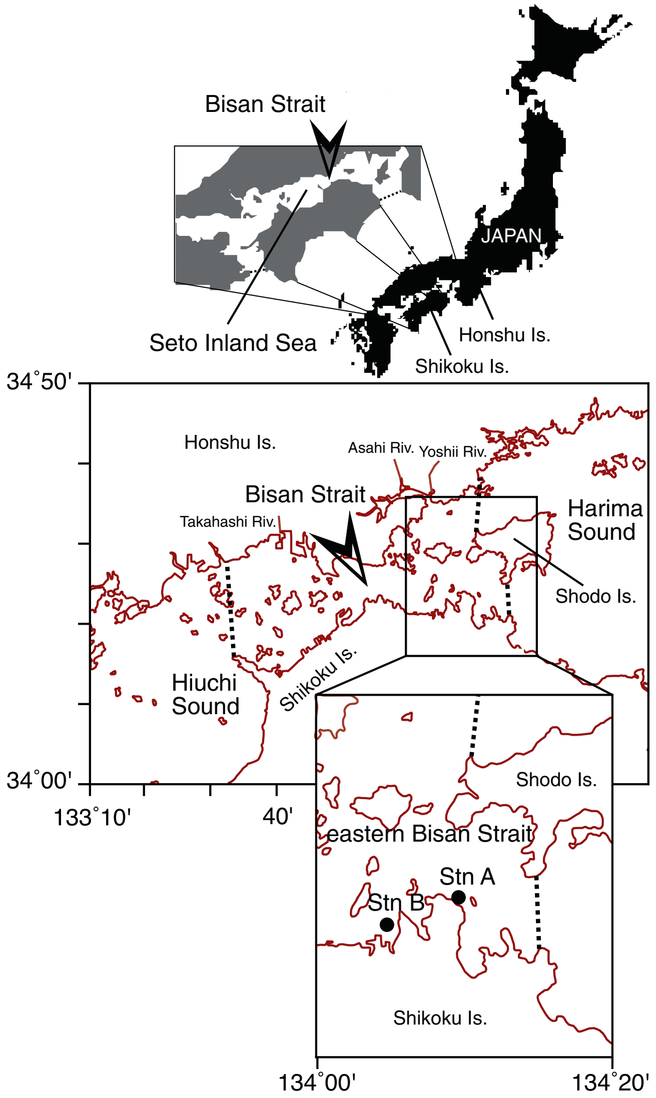

Fig. 1. Study area and location of sampling sites in the Bisan Strait, Seto Inland Sea, Japan.

contrast to adjacent areas in the Inland Sea, where density stratification appears from late spring to early autumn (Hashimoto et al., 1997).

Turbidity is relatively high in the Bisan Strait because of sediment re-suspension. The Strait has one of the lowest levels of Secchi transparency (mean 4.5 m) in the Inland Sea (overall mean 6.9 m) (AECSIS, 2013). The last known record of production in the Bisan Strait comes from Tada et al. (1998), who examined phytoplankton production in the entire Inland Sea, including the Bisan Strait, during four cruises in 1993–1994. According to their simulated in situ method, the estimated production in the Bisan Strait was 122 g C m^{-2} y^{-1}. This value was much lower than the mean production of the Inland Sea (218 g C m^{-2} y^{-1}), despite nutrient levels in the strait being similar to other areas. Therefore, it can be hypothesized that light limitation inhibits phytoplankton growth more in the Bisan Strait than in surrounding areas, and that phytoplankton growth is strongly affected by both nutrient and light availability. In the Seto Inland Sea, the importance of nutrient limitation for phytoplankton growth is well recognized (e.g. Yamamoto, 2003). In contrast, the role of light availability has received less attention, although some studies have suggested its importance in parts of the Inland Sea (e.g. Hashimoto et al., 1997).

In this study, we examined environmental variables (e.g. nutrients and light-associated parameters) and photosynthesis–irradiance (P–I) curves of phytoplankton in the Bisan Strait over 1 year. Furthermore, we estimated phytoplankton production from the P–I curves, phytoplankton biomass and underwater irradiance. The aims of this study were to determine annual variations in phytoplankton production in the Bisan Strait, and to reveal how nutrient and, in particular, light availability affect production in this strait.

2. Materials and methods

2.1. Study area

The Bisan Strait covers an area of 920 km^2, which is 4.2% of the Seto Inland Sea, and connects the Harima Sound and Hiuchi Sound. We established two sampling stations, A and B, in the eastern Bisan Strait (Fig. 1). Station (Stn) A (mean depth *ca.* 8 m) was at the edge of a wharf, directly in front of the Aji Marine Station, Kagawa University, which is located on the northernmost end of Shikoku. Station B (mean depth 12.2 m) was 6 km away from Stn A. Although it was located offshore of a small river, the size of the river means that it had little effect on phytoplankton dynamics at Stn B (Asahi et al., 2014). Station B was an ideal sampling location, owing to its water depth, tidal flow, and the vessel traffic in the Strait. However, high frequency monitoring of Stn B was difficult because of shipping restrictions. Therefore, to compensate for monthly-based data from Stn B, we conducted high frequency monitoring at Stn A, which was easily accessible from the marine station.

2.2. Sampling and data collection

We conducted field sampling at both stations from April 2012 to March 2013. We visited Stn A 117 times during the year, each time during the morning, whereas Stn B was monitored 12 times (on a monthly basis) during the daytime.

During each visit to Stn A, sea surface temperature and conductivity were measured using an electrical conductivity meter (DKK TOA Corporation, CM-31P). The observed conductivity was converted to salinity using IAPSO standard seawater (Ocean Scientific International Ltd.) and the formulas described by the Japan Meteorological Agency (1999). A sample of surface seawater was also collected using a plastic bucket. The seawater sample was brought back to the marine station, and later analyzed for chlorophyll-*a* (Chl-*a*) and nutrient concentrations.

At Stn B, vertical profiles of water temperature, salinity, and downward photosynthetically available radiation (PAR) were measured by a CTD equipped with an underwater quantum sensor (JFE Advantec, AAQ-1183). From the vertical profile of downward PAR, we calculated the attenuation coefficient for PAR (K_d) using the Lambert–Beer Law:

$$I_z = I_0 e^{-K_d z} \qquad (1)$$

where z indicates depth (m), and I_0 and I_z denote PAR irradiance (μmol m^{-2} s^{-1}) just below the sea surface and at z, respectively. After CTD measurements, seawater samples were collected from four depths (0, 3, 6, and 9 m) using a Van Dorn water sampler. These samples were used for Chl-*a* analysis. Concentrations of nutrients, dissolved inorganic carbon (DIC), and particulate organic carbon (POC), and P–I curves were also examined in seawater samples from 3 m depth. Seawater for the P–I experiment was immediately passed through a 300-μm mesh on board to remove large zooplankton (e.g. Tada et al., 1998). These seawater samples were kept at in situ temperature, and immediately brought back to the marine station.

We obtained hourly measurements of global solar radiation, which were measured approximately 6 km away from Stn B by the Japan Meteorological Agency (http://www.jma.go.jp/jma/indexe.html). We multiplied the global solar radiation by 0.48 to obtain the PAR in the air (cf. Colijn and Cadée, 2003). The conversion of joules to moles was based on Ishikawa et al. (1988). To estimate the downward PAR just below the sea surface, we assumed that 15% of PAR in the air was lost