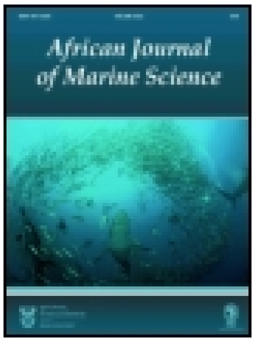

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Short Communication

Primary production in the Benguela ecosystem, 1999–2002

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Phytoplankton production was investigated throughout the whole Benguela ecosystem in winter 1999 and in summer 2002 during two four-week research cruises from Cape Town, South Africa, through Namibian waters to Namibe in southern Angola. Primary production ranged from 0.14–2.26 g C m^{-2} d^{-1} during June–July 1999 and from 0.39–8.83 g C m^{-2} d^{-1} during February–March 2002. Mean productivity values indicated that the Benguela ecosystem was twice as productive in summer than in winter. In 1999, most of the productivity occurred within a temperature range of 13.5–18 °C, whereas in 2002 elevated production was associated with temperatures of 14–22 °C. The relationship between primary production and chlorophyll *a* was good for winter 1999 but poor for summer 2002, suggesting that predicting primary production from chlorophyll *a* is not straightforward for the Benguela ecosystem.

Keywords: chlorophyll *a*, primary production, temperature

Introduction

The oceanography of the Benguela ecosystem is dominated by coastal upwelling and is unique in that the northern and southern boundaries are formed by warm-water regimes (Shannon 1985, Shannon and Nelson 1996). As a consequence of upwelling, primary production is highly variable. Brown et al. (1991) estimated average primary production of 1.2 g C m^{-2} d^{-1} for the northern Benguela and 2.0 g C m^{-2} d^{-1} for the southern Benguela, but nearshore studies around the Cape Peninsula have shown that primary production can average 4.05 g C m^{-2} d^{-1} in summer and 2.23 g C m^{-2} d^{-1} in winter (Brown 1984). Other investigations estimated productivity in newly upwelled water off the Cape Peninsula at 1.02 g C m^{-2} d^{-1}, whereas in mature upwelled water the range in production was 1.48–10.07 g C m^{-2} d^{-1} (Brown and Field 1986). St Helena Bay on the West Coast is another area of elevated productivity, and an anchor station time-series study there revealed that daily production varied between 0.99 g C m^{-2} d^{-1} and 7.85 g C m^{-2} d^{-1} (Mitchell-Innes and Walker 1991), whereas Mitchell-Innes et al. (2000) reported rates of 2.4–5.6 g C m^{-2} d^{-1} along a transect off Lambert's Bay. For the northern Benguela, Estrada and Marrasé (1987) estimated production to be 0.4–1.1 g C m^{-2} d^{-1} in spring and 0.5–3.6 g C m^{-2} d^{-1} in autumn. A more recent study revealed productivity rates of 0.52–4.1 g C m^{-2} d^{-1} in the vicinity of the Angola–Benguela front and the Cape Frio upwelling cell in northern Namibia (Wasmund et al. 2005).

Benguela phytoplankton communities are generally dominated by diatoms and dinoflagellates, although some studies have highlighted the importance of nanoflagellates (Mitchell-Innes and Winter 1987, Pitcher et al. 1992). Diatoms tend to dominate inshore in nutrient-rich water, whereas nanoflagellates are more important offshore on the seaward side of the fronts. Red tide blooms occur throughout the region, particularly during quiescent periods in aged upwelled water as stratification increases (Pitcher et al. 1998), and primary production can reach 12 g C m^{-2} d^{-1} in these blooms (Mitchell-Innes et al. 2000). Phytoplankton abundance is also highly variable and in the southern Benguela maximum biomass tends to occur inshore, although significant levels can extend to 100 km offshore following periods of active upwelling (Brown et al. 1991). Chlorophyll *a* is a convenient indicator of phytoplankton biomass and concentrations in recently upwelled water, maturing upwelled water and aged water are reported to be <1 mg m^{-3}, 1–20 mg m^{-3} and 5–30 mg m^{-3} respectively (Barlow 1982).

Primary production measurements have been conducted at infrequent intervals in the Benguela ecosystem, although more data are available for the southern Benguela compared with the northern Benguela (Wasmund et al. 2005). Opportunities to investigate productivity within the whole ecosystem were offered through the regional Benguela Environment, Fisheries Interaction and Training (BENEFIT) programme. Two research and training cruises were conducted during winter 1999 (June–July) and in summer 2002 (February–March) between Cape Town, South Africa, and Namibe in southern Angola. A suite of physical, chemical and biological data was collected during these

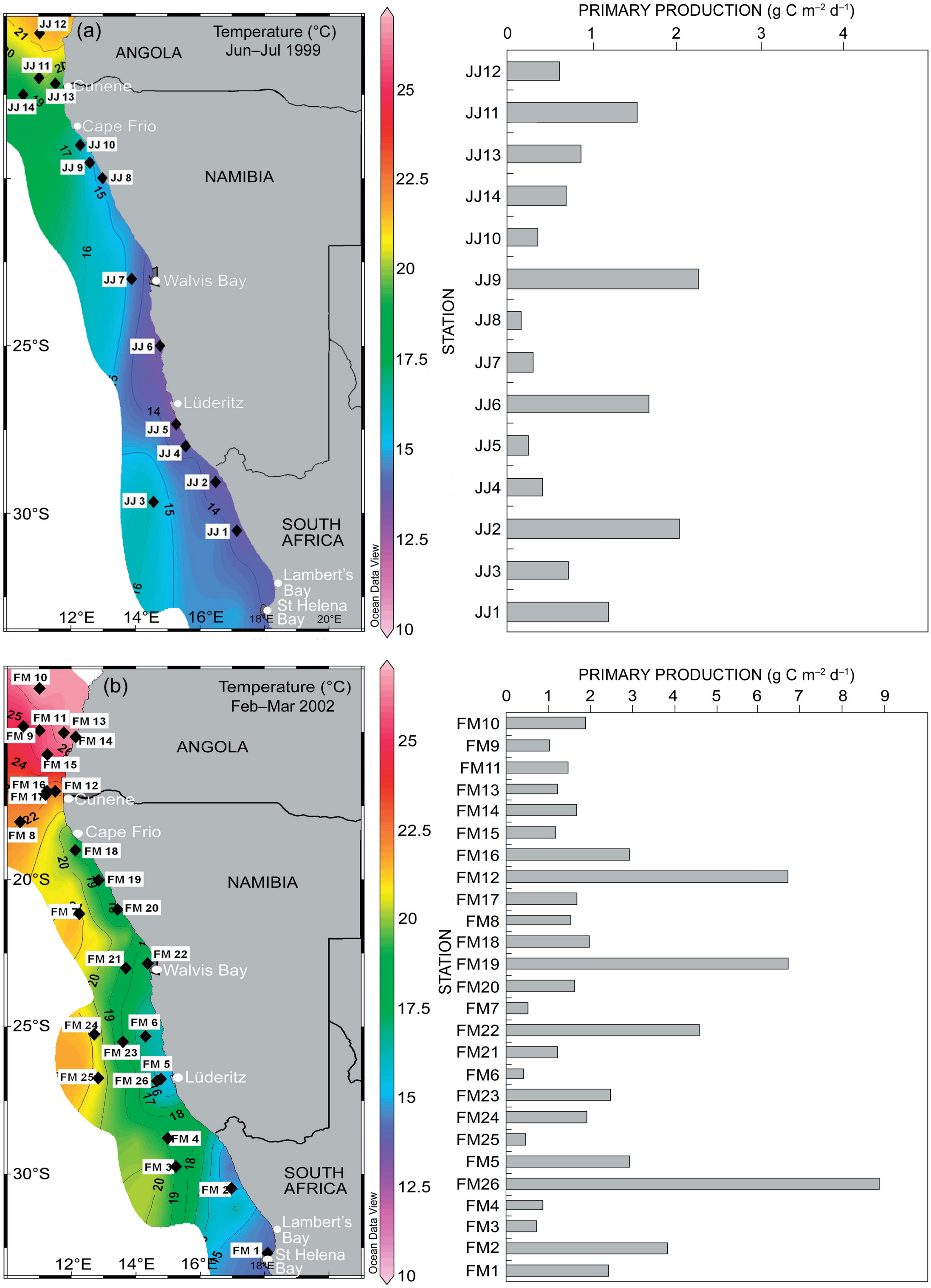

Figure 1: Primary production in the Benguela ecosystem during (a) June–July 1999 and (b) February–March 2002. Location of stations are displayed on surface temperature maps

cruises, including daily production measurements. This paper reports on the primary production studies conducted during these cruises and two key questions are addressed: (1) what is the spatial variability in primary production in the Benguela ecosystem and (2) are there significant seasonal differences in productivity?

Material and methods

Temperature, salinity and oxygen were profiled during CTD casts on station and chlorophyll *a* was determined by fluorescence in 90% acetone using a calibrated Turner Designs fluorometer (Parsons et al. 1984). Productivity was measured using the ^{14}C-method (Parsons et al. 1984). Seawater samples (125 ml) were collected at depths corresponding to the 100%, 50%, 25%, 10%, 1% and 0.1% light levels and three light bottles and one dark bottle (all glass) for each depth were inoculated with 5 μCi $NaH^{14}CO_3$, and incubated in deck incubators for 24 h. At the end of the incubation period, the samples were filtered onto GF/F filters, and the filters were air-dried and fumed over concentrated HCl to remove remaining inorganic ^{14}C. Filters were placed in scintillation vials with scintillation cocktail and radioactivity was assayed using a Beckman LS 1800 scintillation counter. To calculate photosynthesis rates, 'light' ^{14}C uptake was corrected by subtracting the 'dark' uptake, which was generally <1% of the light uptake. Water column production was estimated by integrating the production for all depths over the euphotic zone to the 0.1% light depth.

Results and discussion

Primary production ranged from 0.14 g C m^{-2} d^{-1} to 2.26 g C m^{-2} d^{-1} during June–July 1999. Most of the stations were located near the coast and the highest productivity was at Station JJ2 (2.01 g C m^{-2} d^{-1}) in South African waters, just south of the Orange River, and at Stations JJ6 (1.65 g C m^{-2} d^{-1}) and JJ9 (2.26 g C m^{-2} d^{-1}) off Namibia in cool waters (13–15 °C) (Figure 1a). Angolan waters were warmer (18–22 °C) and highest production was recorded at Station JJ11 (1.52 g C m^{-2} d^{-1}). Production was greater and more variable during February–March 2002, with a range of 0.39–8.83 g C m^{-2} d^{-1} (Figure 1b). Stations were located both inshore and offshore and surface temperatures were cool off the west coast of South Africa (13–16 °C), warm in southern Angola (23–27 °C) and intermediate in Namibian waters (16–22 °C). High production was observed at four inshore stations: FM26 near Lüderitz (8.83 g C m^{-2} d^{-1}), FM22 near Walvis Bay (4.55 g C m^{-2} d^{-1}), FM19 (6.69 g C m^{-2} d^{-1}) and FM12 off the Cunene River (6.68 g C m^{-2} d^{-1}). Productivity was lower at offshore stations and in the warm Angolan waters production varied between 1 and 2 g C m^{-2} d^{-1} (Figure 1b). It is noteworthy that the highest productivity occurred near Lüderitz where strong wind forcing usually results in low productivity and biomass. During February–March 2002, however, the wind stress at Lüderitz was very low and downwelling conditions prevailed, allowing high photosynthetic rates and growth in nutrient-rich waters.

These studies during the BENEFIT cruises were the first primary production measurements to be conducted throughout the whole Benguela ecosystem on one cruise. The datasets covered a distance of approximately 1 800 km and a latitudinal range of 20° (13°–33° S) over single four-week periods and are unique for the Benguela. The variation in primary production is within the range of previous observations made in the late 1970s, the 1980s and 1990s (Brown 1984, Brown and Field 1986, Estrada and Marrasé 1987, Brown et al. 1991, Mitchell-Innes and Walker 1991, Mitchell-Innes et al. 2000), suggesting that productivity in the Benguela has been consistent for at least two decades up to 2002. An analogous upwelling ecosystem with similar seasons and productivity rates is the Humboldt system along the coasts of Chile and Peru. Montecino et al. (2004) reported primary production rates of 0.7–7.5 g C m^{-2} d^{-1} inshore off central Chile during the summer upwelling season and rates of 0.2–1.9 g C m^{-2} d^{-1} during winter, whereas offshore production was <0.6 g C m^{-2} d^{-1}. Daneri et al. (2000) found productivity to vary from 0.5 g C m^{-2} d^{-1} to 9.3 g C m^{-2} d^{-1} along various sectors of the Chilean coast, with lower production in the winter and elevated production in summer when upwelling conditions prevailed. These rates are comparable to those estimated in this study and affirm the similarity between the Benguela and Humboldt ecosystems. Phytoplankton communities in the Benguela are composed of diatoms and small flagellates, with diatoms generally being dominant in the inshore zones and flagellates being more important offshore (Barlow et al. 2001, 2005, 2006). In this study, it is likely that the high productivity at inshore stations was on account of the dominance of diatoms and lower productivity offshore was associated with nanoflagellates.

Phytoplankton community structure in the ocean varies in a regular, predictable pattern with temperature. Microplankton such as diatoms usually dominate at low temperatures, small flagellates are prevalent at intermediate temperatures, whereas picoplankton are most abundant at high temperatures (Bouman et al. 2003, 2005). Figure 2 shows the variability of primary production as a function of temperature and indicates that in winter 1999 most of the productivity occurred within the range 13.5–18 °C. In summer 2002, the high production was associated with temperatures of 14–22 °C, although there was significant production up to 27 °C. However, inorganic nitrogen availability may be a

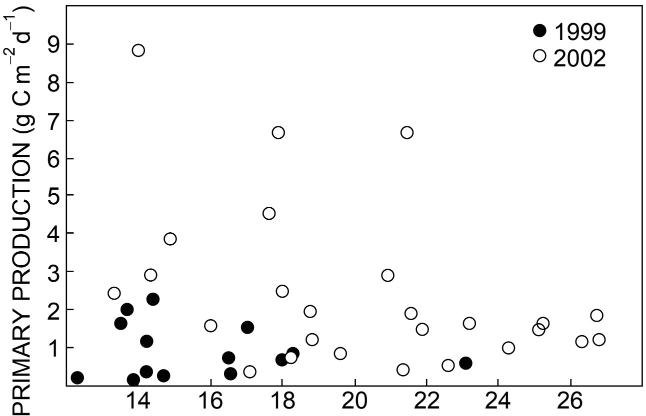

Figure 2: Variability of primary production as a function of temperature

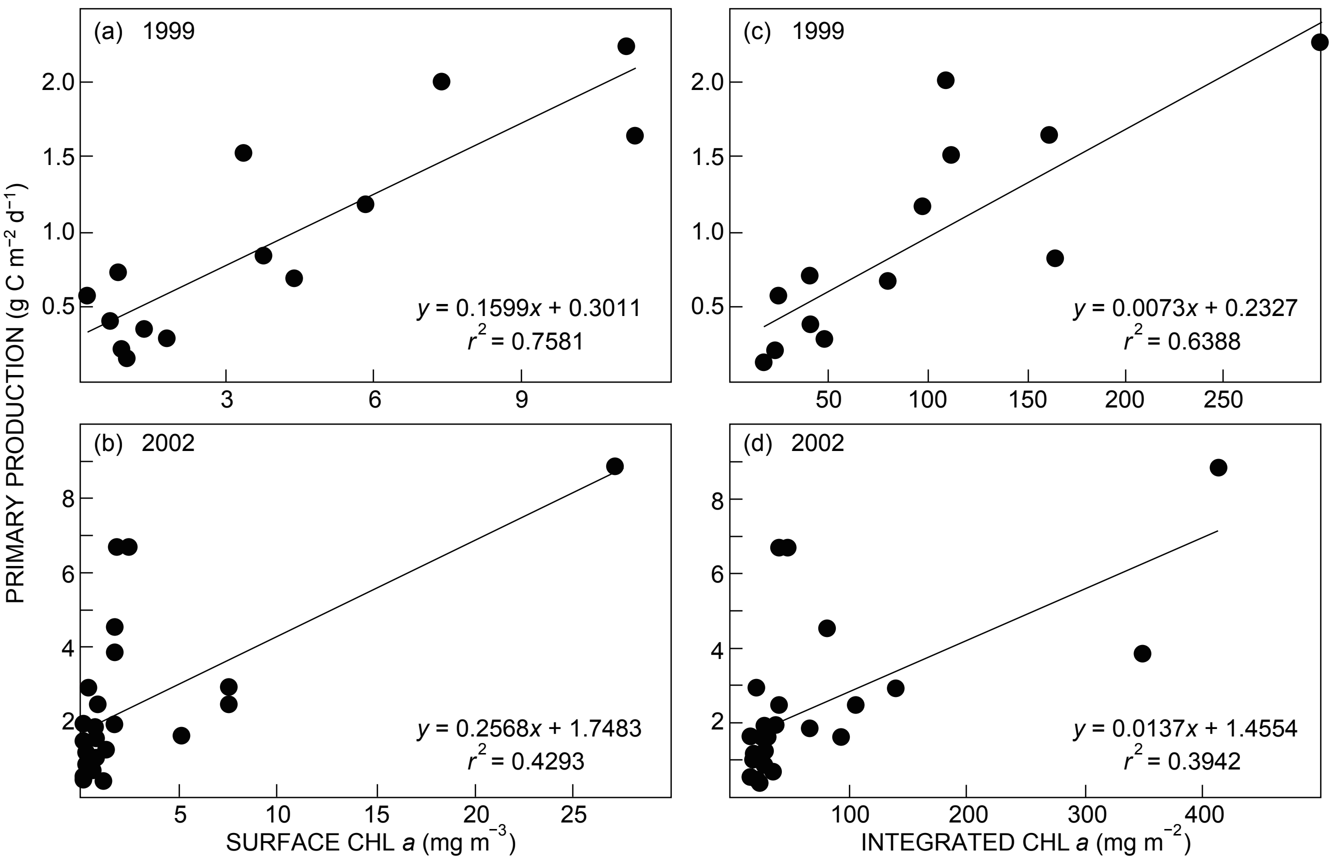

Figure 3: Relationship between primary production and (a, b) surface chlorophyll *a* and (c, d) integrated chlorophyll *a*

more important factor in governing primary production in the Benguela than temperature, as demonstrated by Probyn et al. (1990) and Probyn (1992).

Estrada and Marrasé (1987) and Montecino et al. (2004) found good correlations between primary production and surface and integrated chlorophyll *a*, and Eppley et al. (1985) suggested that such empirical models could be used to predict phytoplankton productivity from surface pigments. The relationship between primary production and chlorophyll levels was explored for the Benguela. Figure 3 (a, c) shows a good relationship for the winter 1999 dataset, in which surface chlorophyll explained 76% of the variance in primary production and integrated chlorophyll explained 64%. However, there was a poor relationship for the summer 2002 dataset in which only 39–43% of the variance is explained (Figure 3b, d). This inconsistency suggests that estimating primary production from chlorophyll *a* is not really feasible for the Benguela ecosystem. Predicting primary production for the Benguela has been attempted by Demarcq et al. (2008), in which self-organising maps to identify chlorophyll profiles and satellite chlorophyll data were used. Those authors estimated that productivity varied between 0.5 g C m^{-2} d^{-1} and 5 g C m^{-2} d^{-1} across the Benguela, but their upper estimate is lower than the 8.8 g C m^{-2} d^{-1} measured in this study and the 7.85 g C m^{-2} d^{-1} and 10.07 g C m^{-2} d^{-1} reported by Mitchell-Innes and Walker (1991) and Brown and Field (1986) respectively. These comparisons appear to confirm that predicting primary production from chlorophyll *a* is not straightforward for the Benguela ecosystem.

In summary, this study has demonstrated the considerable variability in primary production in the Benguela ecosystem, with the highest productivity of 8.8 g C m^{-2} d^{-1} measured in summer and 2.3 g C m^{-2} d^{-1} in winter. The mean summer productivity across the Benguela was estimated to be 2.4 g C m^{-2} d^{-1} and the mean winter value was 0.9 g C m^{-2} d^{-1}, indicating that the Benguela ecosystem appears to be twice as productive in summer than in winter.

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