Vol. 8: 9–14, 1982 | MARINE ECOLOGY - PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published April 9

Phytoplankton Biomass and Production in a Southern Benguela Kelp Bed System

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ABSTRACT: Seasonal variation in phytoplankton biomass and production in the vicinity of a Southern Benguela kelp bed is studied in relation to the upwelling cycle. Mean phytoplankton biomass was estimated as 56 mg chl *a* m^{-2} and phytoplankton production as 1.13 kg C m^{-2} yr^{-1} The top 10 m of the 20 m deep water column monitored contained 83 % of the biomass and 76.5 % of the production. Daily and seasonal variations in phytoplankton are described.

INTRODUCTION

In a trophic dynamic study of South African west coast kelp beds attention has been centered on the detritus pathway from macrophytes through filter and suspension feeders to carnivores (Field et al., 1977; Griffiths and King, 1979a, b; Griffiths and Seiderer, 1980; Pollock, 1982). Frond production, the major source of particulate detritus (Mann, 1972), by the 2 dominant kelps in the system, *Ecklonia maxima* Osbeck and *Laminaria pallida* (Grev.) J. Ag., is estimated at 1.17 kg C m^{-2} yr^{-1} (Jarman and Carter, 1982). Phytoplankton production estimates for water offshore of the kelp bed in the Southern Benguela upwelling plume range from 0.8 to 1.4 kg C m^{-2} yr^{-1} (Brown, 1980, 1982).

The Southern Benguela is characterised by 'pulses' of upwelling in response to south easterly wind stress (Bang, 1973; Andrews and Hutchings, 1980). Thus nutrients necessary for primary production rarely reach limiting levels and primary production is maintained over the spring/summer/autumn period when south easterly winds prevail. Another consequence of the 'pulsing' upwelling system is that the nearshore region is subjected to bouts of cold, nutrient rich, phytoplankton-poor water and warmer, lower nutrient, phytoplankton-rich water in active and relaxation phases of the upwelling cycle, respectively (Field et al., 1980).

The high phytoplankton production rates offshore plus cyclical importation of phytoplankton-rich water into the nearshore zone during the phases of the upwelling cycle led to the following questions being posed: (1) Does phytoplankton contribute significantly in terms of biomass and production to the nearshore zone dominated by kelp beds? (2) If so, is the depth distribution of the phytoplankton such that it is available to benthic filter and suspension feeders in the system? This report deals with the results of an investigation designed to answer these 2 questions.

RESEARCH AREA AND METHODS

Four seasonally spaced intensive surveys, each of 8 to 10 days duration, on phytoplankton biomass and production, water temperatures and surface winds were carried out at Oudekraal on the Cape Peninsula in 1979. The study site together with macrophyte and faunal distribution has been described by Velimirov et al. (1977). Field et al. (1980) showed that the kelp beds at this site were relatively well flushed and thus for the purposes of this investigation a single fixed sampling station was selected in 20 m water depth immediately offshore of extensive *Laminaria* beds (Fig. 1).

Water samples for phytoplankton biomass estimates (as chlorophyll *a*) were obtained by diver operated 5 l NIO bottles at 5 m depth intervals 4 h before and 4 h after local noon on each day of each survey. Concurrently water temperatures were measured, again at 5 m depth intervals, by hand-held thermometers. *In situ* incubations for primary production estimates, using the light/dark bottle technique, were carried out

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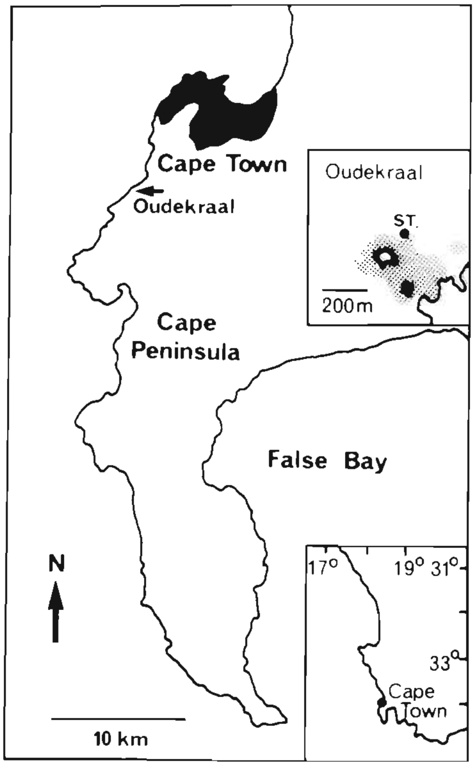

Fig. 1. Cape Peninsula showing location of study area at Oudekraal. Inserts: location on south west coast of South Africa and detail of study site; stippled area represents the extent of the kelp bed at Oudekraal; ST: station location

once per day at the surface, 10 m and 20 m depths. Incubations were generally initiated between 09:00 h and 10:00 h local time and the duration was typically 4 h. Chlorophyll *a* was determined according to the spectrophotometric method of Strickland and Parsons (1972), 1 l of water being processed from each depth sampled. Phaeophytin was not estimated separately and thus the chlorophyll *a* results include phaeophytin *a*. Production was estimated by the oxygen evolution method (Strickland and Parsons, 1972) using a conversion factor of 1 ml O_2 = 0.536 g C (Henry et al., 1977).

Surface winds were estimated ashore, approximately 600 m from the sampling site, immediately prior to each sampling session.

RESULTS

Phytoplankton and Upwelling Cycle

Time series for each of the parameters measured during each of the study periods are presented in Figs. 2 to 5. Phytoplankton biomass and production are expressed per square metre surface area, these values being obtained by hand integrating the water column values. For purposes of elucidating hydrographic events of the scale of active and relaxation phases in the upwelling cycle only surface temperature is displayed. Surface winds are displayed as vectors.

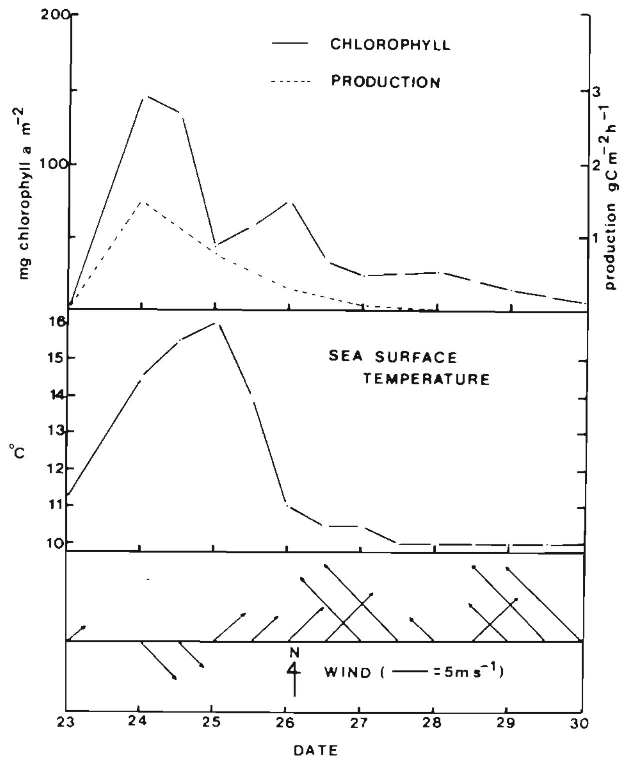

Fig. 2. Time series of phytoplankton biomass, production, surface temperatures and winds for a 20 m deep station at Oudekraal; 23 to 30 January, 1979 (summer)

Figs. 2, 3 and 4 all show similar trends. These correspond to the summer (January), autumn (May) and spring (October/November) seasons.

The variations in phytoplankton biomass and production can be explained in terms of the upwelling cycle. Selecting Fig. 2 as an example, it can be seen that high phytoplankton values occurred in conjunction with light south westerly (23rd Jan.) and moderate north westerly (25th) winds. High water temperatures indicate that these high phytoplankton biomass and production levels occurred in the relaxation phase of upwelling. From the 25th through the afternoon of 26th the wind blew from the south west increasing gradually in strength. Water temperatures declined from a peak of 16° to 10.5 °C during this period.

Concurrently phytoplankton production declined and phytoplankton biomass followed this trend although not as closely. From the 27th onwards strong south easterly winds, which are almost directly offshore (Fig. 1), blew, apart from a south westerly wind on the afternoon of the 28th. In conjunction surface temperature decreased still further to 10 °C, phytoplankton production declined to below detection limits and reduced levels of phytoplankton biomass were found. From the surface temperatures it can be inferred that upwelling was initiated by the south westerly winds of the 25th and 26th this being reinforced by the south easterly winds for the remainder of the study period.

This situation is mirrored in the results obtained in May (autumn) where again the dramatic effects of the south easterly winds by driving active upwelling reduce surface temperatures as well as phytoplankton biomass and production levels (Fig. 3).

In October/November (spring) two bouts of south-easterlies, one on the 24th October and one on the 30th October led to active upwelling with the relaxation phase with its associated peaks in phytoplankton sandwiched in between (Fig. 4).

The results obtained for August (winter, Fig. 5), do not follow the trends displayed in the 3 time series discussed above. The upwelling effect is reduced in the Southern Benguela system in this season although south easterly winds do blow on occasion (Andrews and Hutchings, 1980). This is attributed to the Atlantic Central water body sinking down the shelf due to seasonal variations in the position and intensity of the

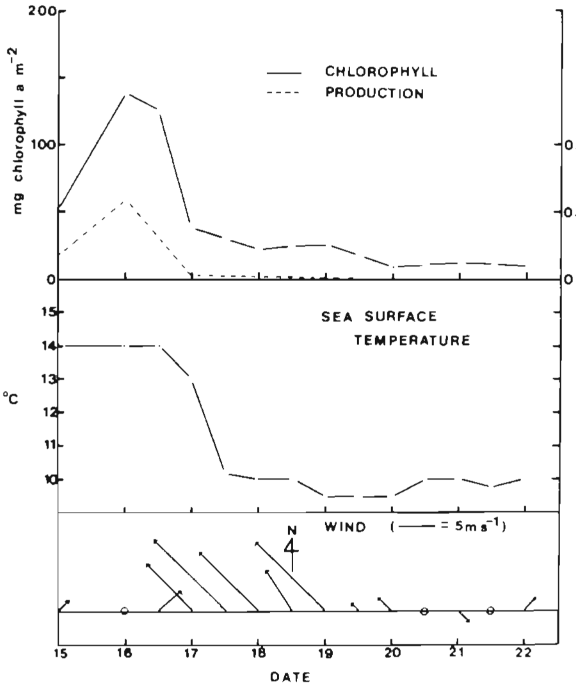

Fig. 3. Time series of phytoplankton biomass, production, surface temperatures and winds for a 20 m deep station at Oudekraal; 15 to 22 May, 1979 (autumn)

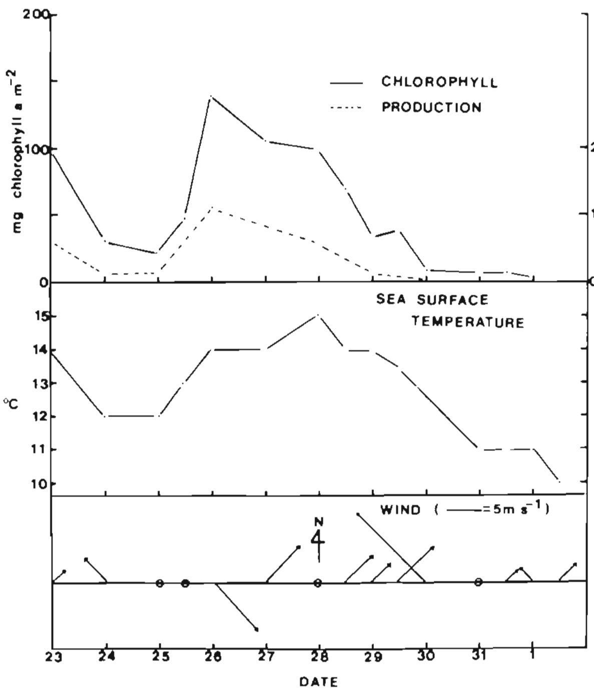

Fig. 4. Time series of phytoplankton biomass, production, surface temperatures and winds for a 20 m deep station at Oudekraal; 23 October to 1 November, 1979 (spring)

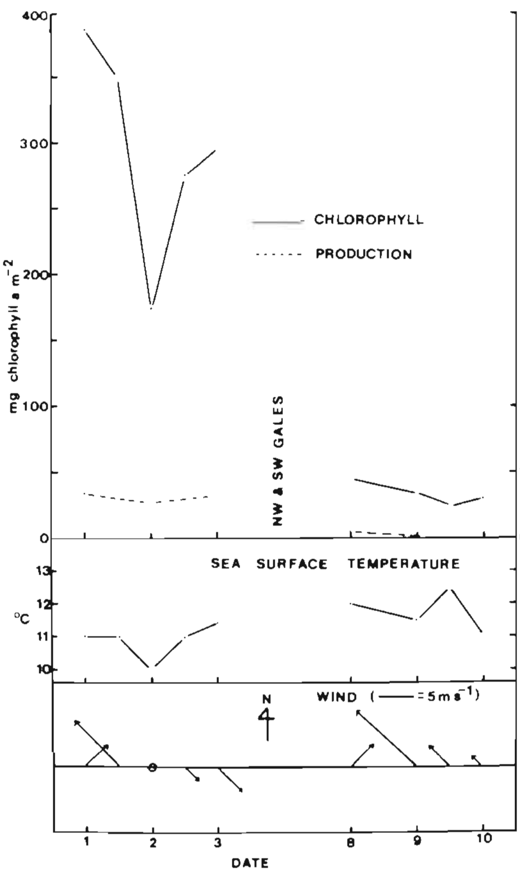

Fig. 5. Time series of phytoplankton biomass, production, surface temperatures and winds for a 20 m deep station at Oudekraal; 1 to 3 and 8 to 10 August, 1979 (winter)

South Atlantic gyre (Bang, 1973). Thus the supply of nutrients to the euphotic zone is reduced in winter and consequently so is phytoplankton development. However, Fig. 5 shows that very high phytoplankton biomass levels were found in the first half of this gale-interrupted time series. The reason for this particular phenomenon was probably the unseasonal calm weather that existed for the ten days prior to the commencement of study and thus water column stability would have been enhanced. Brown (1980) has shown in her comparison of a vigorous upwelling site 2 km offshore from Oudekraal with a non-upwelling site near Robben Island that water column stability is important in the development of dense phytoplankton blooms in the Southern Benguela system. Water column phytoplankton production levels during this winter time series were not high even though surface estimates for the 1st, 2nd and 3rd August were all above 100 mg C m^{-3} h^{-1}. This is due to the fact that subsurface rates were generally negative. Since nitrate-nitrogen levels, the limiting nutrient in the Southern Benguela (Andrews and Hutchings, 1980), ranged from 2.36 to 6.64 µg at l^{-1} (Carter, unpubl.) this is attributed to reduced winter incident light levels and self-shading by the phytoplankton. After 4 d of north westerly and south westerly gales both phytoplankton biomass and production levels were reduced, probably due to dispersion of the bloom, and values remained low until the end of the study period.

Seasonal Variations in Phytoplankton

Table 1 depicts seasonal variation in phytoplankton biomass, production and production/biomass ratios. The major feature is that although no clear trends are evident in either the biomass or production values the P/B ratios show peaks in spring and summer and troughs in autumn and winter. This accords with the findings of Andrews and Hutchings (1980) who attribute this feature to reduced light and nutrient levels.

Phytoplankton Depth Distribution

From the 52 measurements carried out in the seasonal time series plus 14 other measurements at the Oudekraal study site scattered throughout the year, 3 characteristic phytoplankton biomass depth distribution patterns have been identified. Representative examples are presented in Fig. 6 A, B and C.

Fig. 6 A depicts a vertically stratified water column with warm, phytoplankton-rich water above 10 m and colder, phytoplankton-poor water below 10 m. Of the total of 138 mg chl *a* m^{-2} measured in this example 85 % was distributed in the top 10 m.

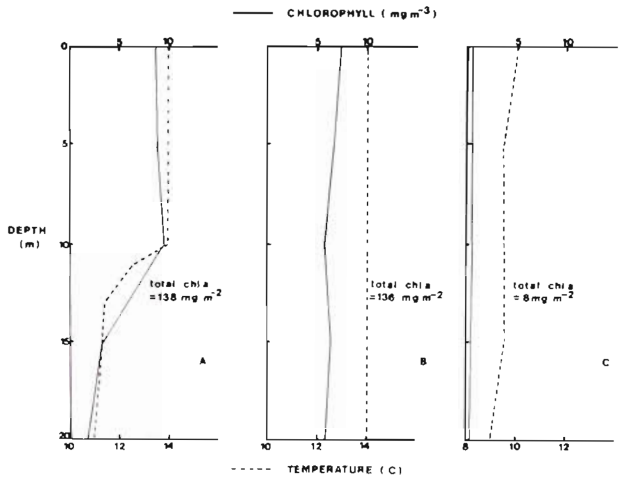

Fig. 6. Depth profiles of phytoplankton biomass and temperature. A: stratified, B: warm mixed, C: active upwelling type depth distributions

Fig. 6 B depicts a warm, totally mixed water column. Of the 136 mg chl *a* m^{-2} measured in this example 48 % was distributed in the top 10 m.

Fig. 6 C illustrates a uniformly cold water column typically found under active upwelling conditions. Phytoplankton biomass levels were low to undetectable in this example.

Table 1. Seasonal means of phytoplankton biomass, phytoplankton production and production/biomass ratios for a 20 m deep station at Oudekraal, Cape Peninsula, 1979. Daily production rates obtained by multiplying hourly rates by the number of daylight hours less 2 (After Brown, 1980)

Season	Biomass (mg chl *a* m^{-2})	(N)	Production (g C m^{-2} d^{-1})	(N)	Production (mg C m^{-2} h^{-1}) / Biomass (mg chl *a* m^{-2})	(N)
Summer	48	14	4.56	7	8.6	7
Autumn	35	14	0.72	8	2.5	8
Winter	96	10	2.84	6	3.5	6
Spring	45	14	4.28	8	8.6	8
$\overline{X}$	56		3.1			

Of the total of 66 vertical profiles measured during this study the upwelling situation (Fig. 6 C) comprises 52%, the thermally stratified (Fig. 6 A) 41% and the warm mixed (Fig. 6 B) less than 1%. Unclassifiable distributions form the remainder Since phytoplankton occurs in the region mainly associated with Fig. 6 A and 6 B type distributions it is evident from the data that 97.5% of the phytoplankton occurs in association with stratified water columns and thus 83% occurs in the top 10 m.

Table 2. Seasonal depth distribution of phytoplankton production in a 20 m deep water column at Oudekraal

	Depth range				
	0–10 m		11–20 m		
Season	$\bar{X}$ (g C m^{-2} d^{-1})	%	$\bar{X}$ (g C m^{-2} d^{-1})	%	N
Summer	3.01	66	1.55	34	7
Autumn	0.58	81	0.14	19	8
Winter	2.75	97	0.09	3	6
Spring	2.65	62	1.63	38	8
Mean	2.25	76.5	0.85	23.5	

A similar depth distribution pertains to phytoplankton production. A comparison of hand-integrated water column production values for the 0 to 10 and 11 to 20 m depth ranges for each of the seasonal time series studies presented in Table 2 reveals that 76.5% of the production estimate is derived from the 0 to 10 m depth range. This is probably an underestimate since a linear gradation in production between the surface, 10 m and 20 m sampling depths is assumed for the purposes of the calculation. This strategy overestimates the contribution of the 11 to 20 m depth range because the depth distribution of production follows that of biomass (c.f. Fig. 6 A).

DISCUSSION

Table 3 has been compiled to facilitate comparison of phytoplankton biomass and production rates for the Southern Benguela as well as comparing these with kelp production estimates. Annual phytoplankton production estimates are given with some reservation since the assumption that daily and seasonal rates can be extrapolated to annual rates has pitfalls in systems as variable as the Southern Benguela. Table 3 shows close similarity between estimates derived from this study and those of Brown (1980, 1982). Brown's (1980) active upwelling site was situated 2 km offshore and slightly north of the time series station at Oudekraal. Her estimate for this site was 0.82 kg C m^{-2} yr^{-1} as opposed to 1.13 kg C m^{-2} yr^{-1} for this study. Brown's (1980) estimates were obtained in the period September, 1977 to March, 1979 as opposed to January to November, 1979 for this study and thus the 2 estimates appear to demonstrate the variability of the area.

Table 3. Annual primary production and biomass estimates for the Southern Benguela Current. Chlorophyll *a* values for this study converted to Carbon equivalents using seasonal conversion factors in Andrews and Hutchings (1980)

	Production (kg C m^{-2} yr^{-1})	Biomass (g C m^{-2})	Source
Phytoplankton	1.13	4.4	This study
Phytoplankton	0.82	–	(1) Brown (1980)*
Phytoplankton	1.43		(2)
Phytoplankton	1.13	–	Brown (1982)
Phytoplankton	3.70 (potential)	11.2	Andrew & Hutchings (1980)
Kelp frond	1.17	488	Jarman & Carter (1982)

* Brown's (1980) estimates were made at an active upwelling site (1) and a site characterised by water column stability (2)

The Andrews and Hutchings (1980) estimate is designated as potential production in Table 3 as their incubations were carried out at higher than *in situ* light levels. This probably accounts for the discrepancy between their estimates and those of Brown (1980, 1982) and this study.

The high phytoplankton biomass reported by Andrews and Hutchings (1980) as opposed to that derived from the time series measurements appears to be due to the fact that the former estimate was derived from values along the upwelling plume whereas the latter was derived from a fixed station near the base of the plume. Another factor that can apply here is the inherent variability of the system (c.f. production estimates).

Southern Benguela annual primary production rates are high when compared with the level cited by Ryther (1969) for upwelling areas (1.13 vs. 0.3 kg C m^{-2} yr^{-1}). However, daily estimates of production in the Southern Benguela and other upwelling sites do not differ all that much. For example, daily production rates range from 0.72 to 4.56 g C m^{-2} d^{-1} in the time-series measurements (Table 1) whereas Walsh (1976) quotes values of 5.6 g C m^{-2} d^{-1} for Peru, 7.1 for Baja California and 2.3 for North-west Africa. Platt (1971) reports 1.5 g C m^{-2} d^{-1} for St. Margaret's Bay, Nova Scotia. The difference in annual production estimates are ascribed to the high frequency of upwelling (Andrews and Hutchings, 1980; Jury, 1980), i.e. a pulsed nutrient supply (Parsons, 1979); as well as the long upwelling season in the Southern Benguela which extends on average from September to May (Andrews and Hutchings, 1980; this study).

The similarity between the kelp and phytoplankton production estimates is contrary to the findings of

Mann (1972) in Nova Scotia. It appears that in the Southern Benguela nearshore environment production by kelps and phytoplankton are at least of quantitatively equal significance even though biomass estimates differ by 2 orders of magnitude. This similarity in production levels is borne out by Newell et al. (in press).

83 % of the phytoplankton biomass and 76.5 % of the production was found to be distributed in the top 10 m during the time series measurements (Fig. 6; Table 2). In this depth range, 75 % of the filter feeding biomass at Oudekraal is also distributed (Velimirov et al., 1977). This correspondence suggests that quantitatively phytoplankton represents a significant food resource for the filter feeding community.

Acknowledgements. This study formed part of the Kelp Bed research programme carried out jointly by the University of Cape Town Zoology Department, South African Sea Fisheries Institute and the National Research Institute for Oceanology of the C.S.I.R. The National Research Institute for Oceanology funded the study.

I thank Messrs. Allen, Hutchinson and Gilman among others for valuable assistance during the field work; Prof. J. Field and Mr. K. Koop for valuable discussion, and Profs. Field and R. C. Newell for critically reading the manuscript. Thanks are also due to Mrs. S. Tolosana for typing the manuscript.

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