

## ORIGINAL PAPER

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## Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass

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**Abstract** The structure of rocky intertidal communities may be influenced by large-scale patterns of productivity. In this study we examine the in situ rates of production by intertidal epilithic microalgae (chlorophyll *a* production per unit area per month), intertidal nutrient concentrations (nitrates, nitrites, phosphates and silicates), and standing stocks of different functional-form groups of macroalgae around the South African coast, and their relationships to consumer biomass. Clear gradients of in situ intertidal primary production and nutrient concentrations were recorded around the South African coast, values being highest on the west coast, intermediate on the south and lowest on the east coast. Primary production by intertidal epilithic microalgae was correlated with nutrient availability and could also be related

to nearshore phytoplankton production. The dominance patterns of different functional forms of macroalgae changed around the coast, with foliose algae prevalent on the west coast and coralline algae on the east coast. However, overall macroalgal standing stocks did not reflect the productivity gradient, being equally high on the east and west coasts, and low in the south. Positive relationships existed between the average biomass of intertidal invertebrate consumers (grazers and filter-feeders) and intertidal productivity, although only the grazers were directly “connected” to in situ production by epilithic intertidal microalgae. The maximum body size of a widely distributed limpet, *Patella granularis*, was also positively correlated with level of in situ primary production. The maximal values of biomass attained by intertidal filter-feeders were not related to intertidal primary production, and were relatively constant around the coast. At a local scale, filter-feeder biomass is known to be strongly influenced by wave action. This implies that the local-scale water movements over-ride any effects that large-scale gradients of primary production may have on filter-feeders. The large-scale gradient in intertidal productivity around the coast is thus strongly linked with grazer biomass and individual body size, but any effect it has on filter-feeder biomass seems subsidiary to the local effects of wave action.

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 Community · Consumers

### Introduction

The role of variation in primary productivity has been a neglected factor in many past studies of community organization on intertidal rocky shores (Menge and Olson 1990; Menge 1992). In freshwater ecosystems, by contrast, the influences of variation in primary production and nutrient concentration on trophic food webs have been extensively investigated and integrated into studies of ecosystem functioning (e.g. Carpenter and Kitchell

1984, 1987; Stanley et al. 1990; Hill et al. 1992; Power 1992; Wootton and Power 1993). Only in the past 10 years has the role of primary productivity been incorporated, at least in a nominal form, into models explaining the structure and functioning of marine benthic communities (e.g. Menge and Sutherland 1987; Hatcher 1990; Menge and Olson 1990; Menge 1992).

In those few studies where rates of primary production have been measured on intertidal rocky shores, the aim was to use it as an index of food availability for competing consumers, succession and diversity of microflora assemblages, and small-scale distribution patterns (e.g. Castenholz 1963; Nicotri 1977; Branch and Branch 1980; McQuaid 1981; Underwood 1984c; MacLulich 1986a, b, 1987; Hill and Hawkins 1990, 1991). However, large-scale variation in intertidal productivity and its relationship with different components of rocky shore communities have largely been ignored. Several studies of South African rocky shores have focused on the nutrients and primary productivity, but have been restricted to a local geographical scale and to interactions with particular species (e.g. Bosman 1988; Bosman and Hockey 1988; Dye and White 1991; Lasiak and White 1993).

A well-documented productivity gradient exists in the pelagic ecosystem around southern Africa, due to the existence of strong upwelling on the west coast and its virtual absence on the east coast (e.g. Shannon 1985; Brown and Cochrane 1991; Brown et al. 1991; Moloney 1992). In a review of most of the published productivity data for the Benguela and Agulhas ecosystems, Brown (1992) demonstrated this productivity gradient for waters lying inshore of the 200-m isobath. The north-west coast is highly productive, supporting chlorophyll biomass up to 16.5 mg chlorophyll *a* (Chl-*a*) m<sup>-3</sup>, whereas intermediate concentrations (about 5.0 mg Chl-*a* m<sup>-3</sup>) occur in the south-west or southern Benguela. Off the south-east coast, chlorophyll concentrations are an order of magnitude lower than the north-west coast (<2.0 mg Chl-*a* m<sup>-3</sup>). However, this pattern disappears offshore (i.e. beyond the 200-m isobath), where the overall chlorophyll concentrations are considerably lower, lying between 0.5 and 3.0 mg Chl-*a* m<sup>-3</sup> (Brown 1992).

In a small-scale study in False Bay (Fig. 1), Cliff (1982a, b) analysed chlorophyll, nutrients, bacteria, and organic detritus concentrations from the intertidal zone to about 150 m offshore. He found that intertidal waters exhibited low values and no seasonal pattern in most nutrient concentrations, and were consistently depleted of chlorophyll relative to water samples from the deeper waters (Cliff 1982a). These results are in line with those reported by Demers et al. (1989), who found consistently low concentrations of nutrients, and also lower values of phytoplankton biomass, in the nearshore compared with offshore waters. Several hypotheses based on biogenic explanations have been proposed in order to account for these patterns, among them the activity of benthic filter-feeders which may reduce phytoplankton biomass in the littoral zone (Demers et al. 1989). Similarly, low inshore nutrient concentrations (principally nitrogen) have been

explained by the effect of shallow-water and intertidal macrophyte communities acting as a nitrogen sink (Raine and Patching 1980).

Bustamante (1994) have described several patterns of community structure for rocky shores around southern Africa. Among them, a gradient of consumer biomass emerged as a conspicuous feature. In particular, there is a markedly higher grazer biomass on the west coast, declining towards the east coast. A similar pattern emerged for filter-feeders.

In this work we use monthly chlorophyll *a* accumulation per unit area as an index of intertidal in situ primary production, to explore large-scale patterns in epilithic micro- and macroalgal production around the South African coast. We also correlate this productivity index with nutrient concentrations in intertidal waters. In a less intense sampling procedure, we document macroalgal standing stocks and their geographical variation for three different functional groups of algae. We then draw on data presented in Bustamante (1994) to correlate patterns of community structure with the primary production recorded for rocky shores. In particular, the local abundance (i.e. average and maximum biomass) of the filter-fed guild was correlated with both intertidal productivity (empirically determined) and nearshore primary productivity patterns (obtained from published data). Similarly, the local abundance of the grazer guild was related to intertidal primary production. Using the widely distributed patellid limpet *Patella granularis* as an indicator species, a correlation between epilithic microalgal production and the maximum size attained by this limpet was also sought.

The overall aim was thus to determine if there is a large-scale geographic pattern (gradient) of intertidal primary production around the coast of southern Africa and then to seek correlations which may suggest the degree to which this production influences intertidal primary consumers, i.e. filter-feeders and grazers.

## Materials and methods

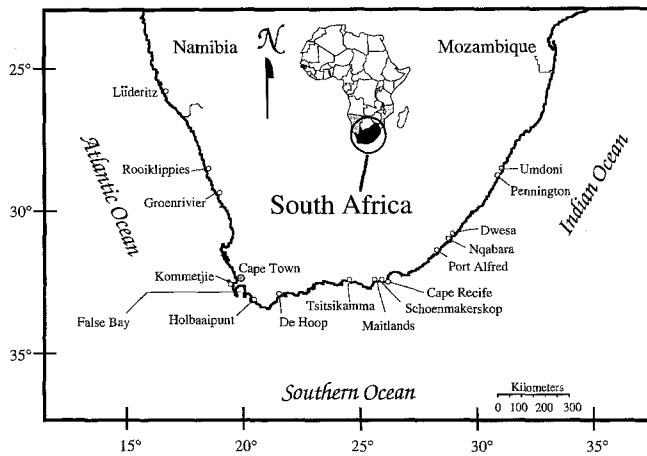
### Study sites and data analyses

Data were collected at 15 different localities around the southern African rocky shores (Fig. 1). A summary of all samples taken at each locality is given in Table 1. All localities had similar coastal morphology, i.e. moderately exposed rocky platforms of no more than 15° of slope, facing directly into the waves, and the layout of the monitoring experiments was exactly the same.

Statistical analyses, including analysis of variance (ANOVA), *a posteriori* tests, regression and correlations were all performed with SAS software, version 5.0 (SAS 1986). Quantitative response variables (e.g. chlorophyll and nutrient concentrations) were square root transformed (Zar 1984) before analysis to conform with assumptions of parametric statistics. Qualitative variables (e.g. sites, seasons, dates, geographical regions) were coded as indicators and were not transformed.

### Chlorophyll *a* determination

The monthly in situ production by epilithic micro- and macroalgae was determined at 12 different rocky intertidal localities from March 1991 to June 1992 (Table 1). In addition, less complete da-



**Fig. 1** Outline of the southern African shoreline south of 25° S. Names indicate localities mentioned in the text and circles show the study sites

ta sets were obtained for Tsitsikamma and Lüderitz, which were insufficient for analysis of seasonality, but allowed comparisons with other localities.

At each site, midway between mid-tide and low spring tide, four randomly selected plots of about 0.5 m<sup>2</sup> each were cleared of all biological growth and their perimeters painted with antifouling paint to stop invasion by vagrant grazers. Every month, for a period of 16 months, eight sterile clear acrylic plates of 25 cm<sup>2</sup> each, sand-blasted to roughen their surfaces, were glued down within each plot simultaneously at all localities. After the plates had been in position for a month, they were lifted from the substratum, washed to remove all sand and loose inorganic material, wrapped in aluminium foil and stored at -20° C. Monthly measurements of the total chlorophyll *a* extracted from the algae growing on each acrylic plate were undertaken by spectrophotometric techniques, using hot methanol as the extraction solvent for plant pigments (HMSO 1986). For each month, four plates were taken randomly from each individual plot at each locality, all plant material was scraped off the surface, placed in a pre-weighed foil dish and wet weighed. Measures of the absorbance of the chlorophyll *a* extract at wavelengths of 665 nm (maximum absorbance of chlorophyll *a*) and 750 nm (compensation for 'background turbidity') were taken

**Table 1** Summary of sampling sites (+ samples taken, - not sampled). Responsibility indicates the research group responsible for the collection of samples. (UCT R.H. Bustamante, S. Eekhout and G.M. Branch, University of Cape Town, UWC D. Keats and M. Jurd, University of Western Cape, EMATEK P. Zoutendyk, Earth

	Sites	Chlorophyll <i>a</i>	Algal standing-stock	Nutrients	Responsibility
West coast	Rooiklippias	+	+	+	UCT
	Groenrivier	+	+	+	UCT
	Kommetjie	+	+	+	UCT
	Holbaaipunt	+	-	-	UWC
South coast	De Hoop	+	+	+	EMATEK
	Tsitsikamma	-	+	-	NPB
	Maitlands	+	+	-	UPE
	Cape Recife	+	+	+	UPE
	Schoenmakerskop	+	-	+	UPE
	Port Alfred	+	-	-	RU
East coast	Dwsa	-	+	-	UNITRA
	Nqabara	+	-	-	UNITRA
	Pennington	+	+	+	ORI
	Umdoni	+	+	+	ORI

using a spectrophotometer, and chlorophyll-*a* concentration (in µg cm<sup>-2</sup>) was calculated using the equation

$$[\text{Chl} - a] = \frac{A \cdot V \cdot 13.9}{a \cdot 1.0}$$

where A=absorbance at 665 nm - absorbance at 750 nm, V=volume of solvent, 13.9=spectrophotometric constant (Jeffrey and Humphrey 1975), a=area of acrylic plate (cm<sup>2</sup>), and 1.0=cell path-length (cm).

#### Nutrients

Every month, six to twelve 50-ml water samples were taken intertidally at eight localities during spring low-tide for the determination of micronutrients (Table 1). The water samples were prefiltered using Whatman glass-microfibre filters (GF/F), poured into high-density polyethylene tubes and then wrapped in aluminium foil, stored vertically, and frozen at -20° C.

The concentrations of nitrite- and nitrate-bound nitrogen (NO<sub>2</sub>-N, NO<sub>3</sub>-N), phosphate-bound phosphorus (PO<sub>4</sub>-P) and silicate-bound silica (SiO<sub>3</sub>-Si) were automatically determined using a TA II autoanalyser following the procedures of Mostert (1983, 1988). Nutrient concentrations were expressed in micromoles per litre (µmol l<sup>-1</sup>).

#### Macroalgal standing stock

The standing stock of macroalgae was measured at ten different rocky intertidal localities around the South African coast from March 1991 to June 1992 (Table 1). Four randomly selected transects, set perpendicularly to the coast from MLWS to MHWS, were permanently marked, and between nine and twelve 0.25 m<sup>2</sup> quadrats were randomly placed along them, covering the full intertidal zonation. Every 3 months, for a period of 12 months, all macroalgal material in each quadrat was scraped off, washed to remove all sand and inorganic material, sorted by algal groups, and their wet weight measured. Subsequently, all algal mass was expressed as grams dry mass per square metre (g m<sup>-2</sup> DM). The relationship between the algal wet mass (WM) and its dry mass (DM) was described by the significant linear function DM=0.2535\* WM (n=470, r<sup>2</sup>=0.86, P<0.0001), with the intercept forced through zero (a=0). The algal species were classified into three functional groups according to their respective form: (a) filamentous or foliose and corticated forms (referred to hereafter as "foliose algae"); (b) articulated and crustose coralline forms ("corallines"); and (c) non-coralline turfs ("turfs").

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Patterns of community structure

Data for two main functional groups of consumers, filter-feeders and grazers were extracted from the biomass community patterns described in Bustamante (1994), to relate abundance of these functional groups to intertidal productivity. Specifically, both mean and maximum values of ash free dry mass per unit area (g AFDW m<sup>-2</sup>), are expressed relative to the distance around the coast of each surveyed locality from Lüderitz (Namibia, Fig. 1). All distances were measured linearly on a 1:2,500,000 scale map. The sampling procedures to obtain biomass have already been described fully by Bustamante (1994). In brief, four transects were surveyed at each site, running between high and low water spring tide levels. Eight to ten 0.5 m<sup>2</sup> quadrats were sampled on each transect, using point intercepts to quantify percentage cover. Sub-samples of all species were taken to allow conversions from either cover or wet biomass to ash free dry biomass. Maximal body size achieved by the limpet *Patella granularis*, was also determined at

each surveyed site. All individual *P. granularis* present in quadrats on each transect were measured with a vernier micrometer to a precision of 0.5 mm. Mean maximal size was determined by averaging the 100 biggest animals recorded for each site.

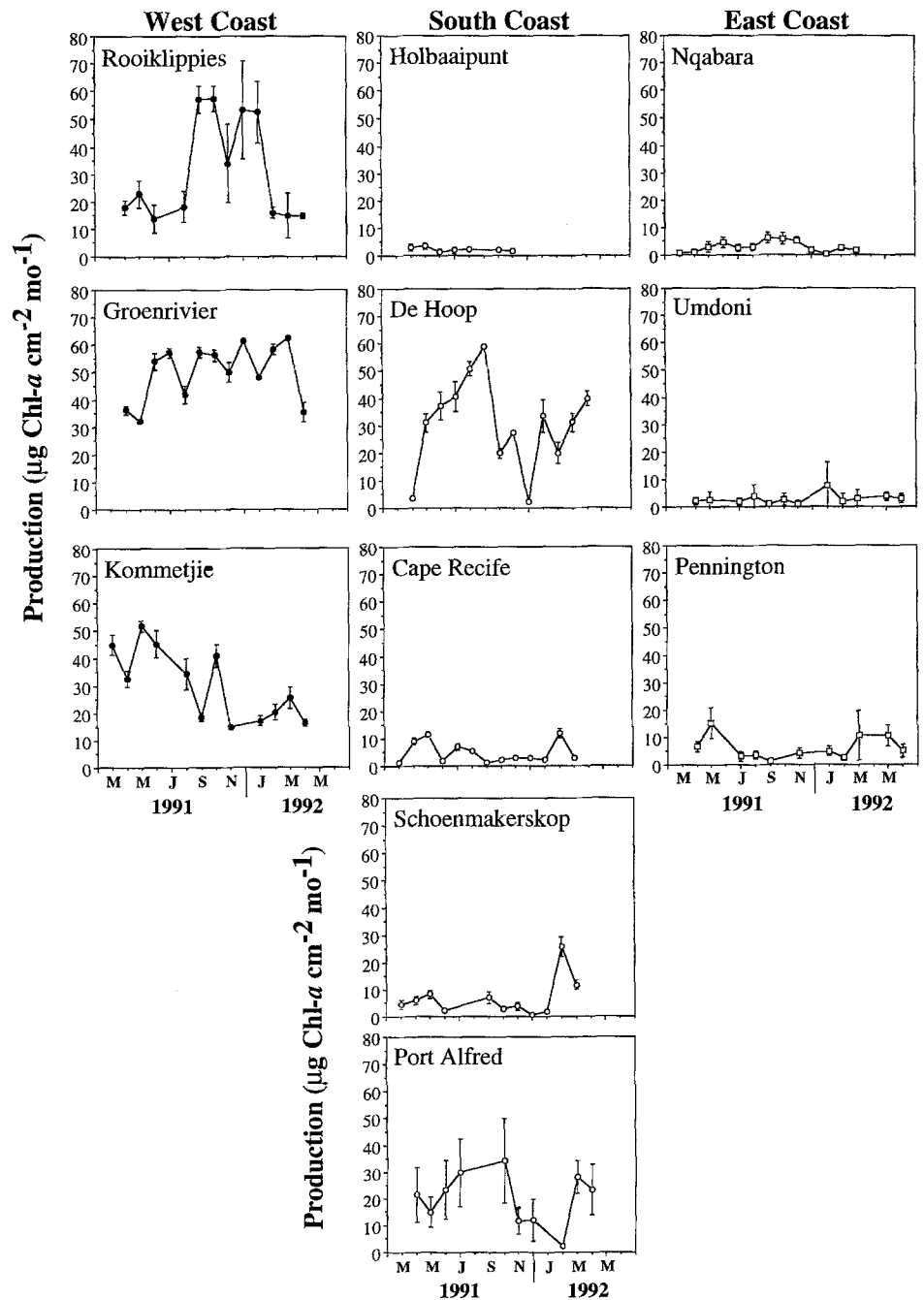
Results

Intertidal productivity

*Chlorophyll a* as productivity index

The monthly production ( $\pm 1$  SD) at each locality (grouped into the three coastal zones) is shown in Fig. 2. Considerable monthly and seasonal variations in the mi-

Fig. 2 Monthly average ( $\pm 1$  SD) of epilithic intertidal production at 11 sites around the South African rocky shores



**Table 2** ANOVA for monthly values of chlorophyll *a* ( $\mu\text{g cm}^{-2}$ )

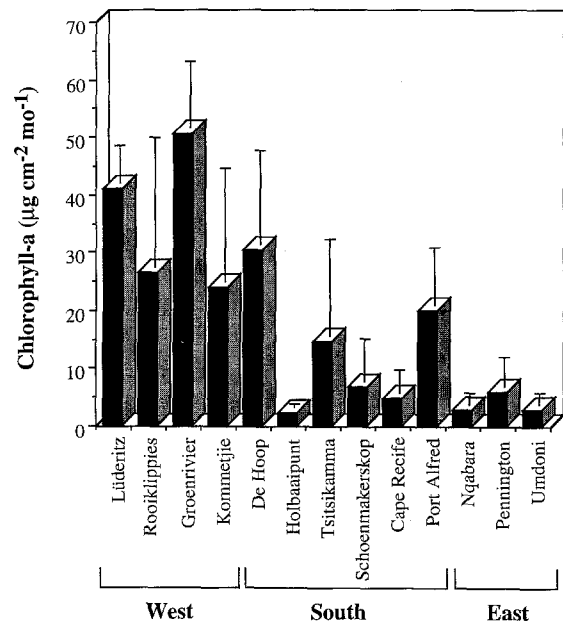
Source of variation	$r^2$	CV 43.94%			
	$df$	SS	MS	$F$	$P$
Seasons	3	14,347,605.65	4,782,535.22	20.40	0.0001
Provinces	2	219,691,256.77	109,845,628.39	468.53	0.0001
Sites (provinces)	9	142,708,744.77	15,856,527.20	67.63	0.0001
Plots (sites)	39	10,396,281.83	266,571.33	1.14	0.259
Error	2149	503,823,818.98	234,445.70		

croalgal production occurred at most localities. Although the west coast localities showed great variation, the average production was high. Even the minimum achieved never dropped below  $10 \text{ gm Chl-}a \text{ m}^{-2} \text{ month}^{-1}$ , whereas at the south and more obviously at the east coast localities, the majority of the monthly average values were below  $10 \mu\text{g Chl-}a \text{ m}^{-2} \text{ month}^{-1}$  (Fig. 2).

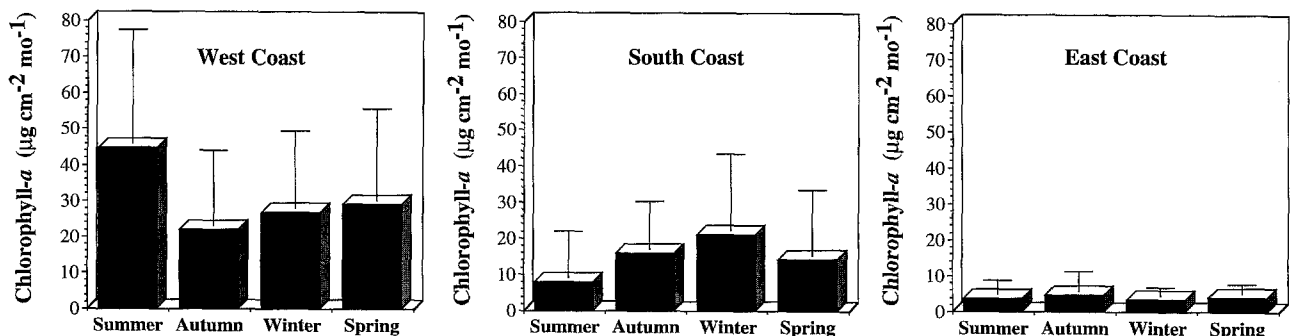
Significant variation in microalgal productivity could be attributed to differences between biogeographic provinces (i.e. west, south and east coasts), as well as between seasons and sites within provinces (ANOVA,  $P < 0.0001$ , Table 2). Conversely, within each locality little variation existed among the replicated production plots (ANOVA,  $p = 0.259$ , Table 2).

The average monthly production at each site is expressed in Fig. 3. The average production of the west coast localities, i.e.  $28.8 \pm 23.0 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ month}^{-1}$ , was significantly higher (Tukey *t*-test  $P < 0.05$ ) than that of south and east coasts. Similarly, the monthly average at the south coast localities ( $15.2 \pm 18.0 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ month}^{-1}$ ) was significantly higher (Tukey *t*-test,  $P < 0.05$ ) than the east coast ( $3.9 \pm 3.9 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ month}^{-1}$ ). The localities of De Hoop and Port Alfred had production rates only slightly lower than those of the west coast, exhibiting mean values of about 30 and  $20 \mu\text{g Chl-}a \text{ cm}^{-2} \text{ month}^{-1}$  respectively, but their combined monthly average was still significantly lower (Tukey *t*-test,  $P < 0.05$ ) than that of the west coast.

Notwithstanding the apparently random monthly variations in the chlorophyll *a* production at each of the monitored localities (Fig. 2), there was a seasonal trend when the monthly values were pooled into seasons and into the three coastal biogeographic provinces (Fig. 4). The localities on the west coast exhibited a peak of production in the spring-summer (September–February) and a decline in autumn-winter (March–October), whereas the reverse pattern was found on the south coast. Values were consistent-

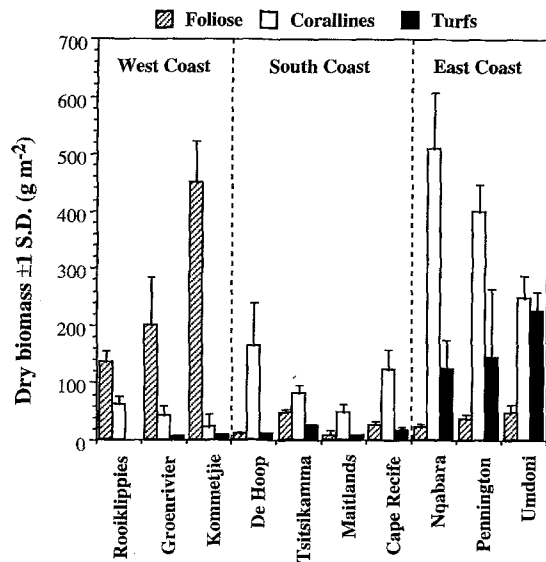
**Fig. 3** Average monthly production of chlorophyll *a* ( $\pm 1$  SD) at 13 localities around southern Africa. The value for Lüderitz represents the average of a single month (March 1991) which is not included in the statistical and seasonal analyses

ly low in the east coast province (Fig. 4). When the variability of the monthly production of chlorophyll *a* was analysed per biogeographic province (Table 3), it was found that these seasonal trends were significant for the west (ANOVA,  $P < 0.0009$ ) and the south coasts (ANOVA,  $P < 0.0001$ ), whereas no significant (ANOVA,  $P > 0.18$ ) trend was found on the east coast (Table 3). Differences between localities and seasons, and the interaction be-

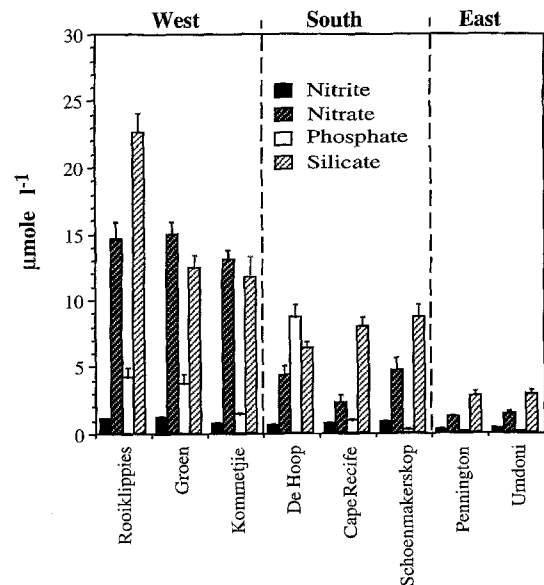
**Fig. 4** Seasonal epilithic chlorophyll *a* production per month in three biogeographic provinces around southern Africa

**Table 3** ANOVA for monthly chlorophyll production per biogeographic province. Chlorophyll values were log transformed

Source of variation	Dependent variable: chlorophyll <i>a</i> ( $\mu\text{g cm}^{-2}$ )																												
	<i>r</i> <sup>2</sup> 0.64					CV 31.29%					<i>r</i> <sup>2</sup> 0.57					CV 42.54%					<i>r</i> <sup>2</sup> 0.43					CV 0.89%			
	West province					South province					East province																		
	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>														
Seasons	3	12.27	4.09	5.59	0.0009	3	157.37	52.46	69.89	0.0001	3	3.10	1.03	1.63	0.1820														
Sites	4	129.54	32.39	44.24	0.0001	4	474.17	118.54	157.94	0.0001	2	64.78	32.39	51.05	0.0001														
Sites* seasons	6	387.40	64.57	88.20	0.0001	10	120.02	12.00	15.99	0.0001	6	219.40	36.57	57.63	0.0001														
Plot (sites)	1	9.42	0.86	1.17	0.3043	16	30.27	1.89	2.52	0.0009	8	2.80	0.35	0.55	0.8181														
Plates (plot)	39	18.79	0.48	0.66	0.9470	28	12.58	0.45	0.60	0.9513	21	4.86	0.23	0.36	0.9962														
Error	626	458.25	0.73			787	590.68	0.75			656	416.22	0.64																



**Fig. 5** Macroalgal standing stock around the South African shores. Bars represent the mean ( $\pm 1$  SD) dry biomass for each of three functional-form groups of algae



**Fig. 6** Annual averages ( $\pm 1$  SD) of nutrient concentrations in intertidal water

tween these two factors, explained more than 50% of the variance in the west and south provinces, while in the east province differences between sites and the interaction with seasonal variation explained more than 40% of the total variance (Table 3). Variations within localities were not significant on the west or east coasts ( $P > 0.1$ , Table 3) but were significant in the south (ANOVA,  $P < 0.0001$ , Table 3). Variations between plates (within plots) were never significant for any of the coasts (Table 3).

*Macroalgal standing stock*

The monthly average standing stock of macroalgae found at the west coast localities showed an obvious biomass dominance by filamentous, foliose and corticated forms (“foliose algae”) over articulated and crustose corallines and non-coralline turfs, these three functional groups averaging about 300, 42 and  $< 5 \text{ g m}^{-2}$  DM respectively (Fig. 5). A different pattern was found at the south coast localities, where corallines were more abundant than foliose al-

gae, exhibiting averages about 62 and  $5 \text{ g m}^{-2}$  respectively, and there was an increase in turfs, with averages up to  $25 \text{ g m}^{-2}$  (Fig. 5). Similarly, at the east coast localities, corallines were much more abundant than foliose forms, with averages of about 384 and  $35 \text{ g m}^{-2}$  respectively, and a

**Table 4** ANOVA for the nutrient concentration ( $\mu\text{mol per litre}$ ) of intertidal water samples

Source of variation	$\text{NO}_2$				
	<i>r</i> <sup>2</sup> 0.59	CV 57.60%			
	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
Date	14	3.46	0.25	1.58	0.0958
Province	2	14.92	7.46	47.76	0.0001
Province* date	14	3.28	0.23	1.50	0.1234
Site (province)	5	1.27	0.25	1.62	0.1598
Samples (site)	18	1.03	0.06	0.37	0.9912
Error	107	16.71	0.16		

large proportion of the macroalgal biomass was attributable to turfs, with values up to 250 g m<sup>-2</sup> (Fig. 5). The overall average macroalgal standing stocks found in the west and east provinces were not significantly different (Tukey *t*-test, *P*>0.5), whereas that in the south province was significantly smaller than that of either the west or the east coast provinces (Tukey *t*-tests, *P*<0.005).

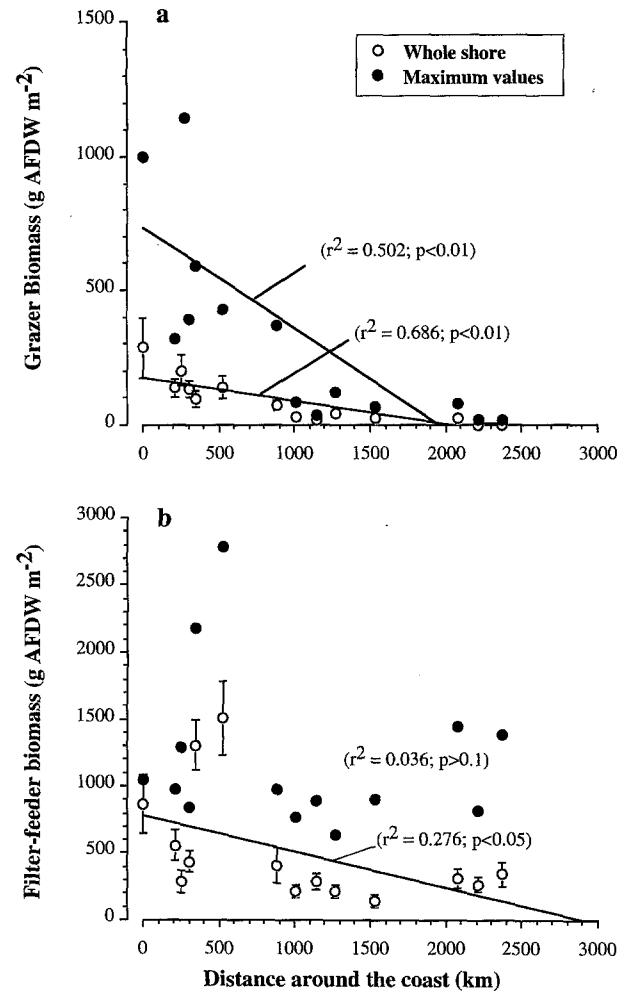
**Intertidal nutrients**

The average nutrient concentrations in water samples taken from the rocky intertidal zone are shown in Fig. 6. There was a strong gradient of total nutrient concentration around the South African coasts, with higher average values in the west, intermediate values in the south, and the lowest concentrations in the east coast province (Fig. 6). This trend is significant for all four nutrients, i.e. nitrite, nitrate, phosphate and silicate (ANOVA, *P*<0.0001, Table 4). One south coast site (De Hoop) had unusually high phosphate values that interrupted the trend. The major source of variation in the average nutrient concentrations was that produced by differences between biogeographic provinces (ANOVA, *P*<0.0001, Table 4). Differences between months, as well as the interaction between months and province, were significant in explaining the variation of the average concentration of nitrate, phosphate and silicate (ANOVA, *P*<0.0001). Variations between localities within a given biogeographic province were significant only for phosphate and silicate (*P*<0.0001, Table 4), while no significant differences were found between the different samples within localities (ANOVA, *P*>0.2, Table 4).

Significant positive linear relationships existed between all four nutrients and the intertidal production index (ANOVA, *P*<0.002, Table 5), indicating that the in situ microalgal production is significantly correlated with the concentration of nutrients in the intertidal water.

**Patterns of community structure**

Grazer biomass decreased significantly from west to east (Fig. 7a). Both the average biomass for the whole shore (*r*=-0.709, *P*<0.01) and the maximum grazer biomass recorded for a quadrat (*r*=-0.828, *P*<0.01) were correlated negatively with distance around the coast from west to



**Fig. 7** Relationships between biomass (mean ±1 SD and maximum values) and distance around the southern African coast, for a grazer, and **b** filter-feeder biomass. The zero distance corresponds to Lüderitz (Namibia). Trends are indicated by least squares fitted lines

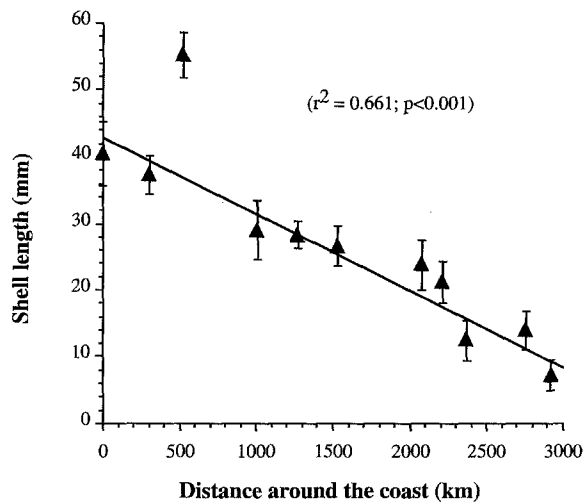
east (Fig. 7a). The maximal values of grazer biomass found on the west, south and east coasts were significantly different (one-way ANOVA, *P*<0.0001).

Filter-feeders, on the other hand, showed two different patterns when their biomass per unit area was related to distance around the coast (Fig. 7b). The whole shore average biomass exhibited a significant negative correlation with distance (*r*=-0.525, *P*<0.05), but the maximum

NO <sub>3</sub>					PO <sub>4</sub>					SiO				
<i>r</i> <sup>2</sup>	CV				<i>r</i> <sup>2</sup>	CV				<i>r</i> <sup>2</sup>	CV			
0.91	37.52%				0.89	65.16%				0.89	36.91%			
<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
14	1,376.86	98.35	17.13	0.0001	14	305.28	21.81	11.60	0.0001	14	2,277.42	162.67	16.68	0.0001
2	5,233.62	2,616.81	455.87	0.0001	2	510.18	255.09	135.65	0.0001	2	4,773.02	2,386.51	244.71	0.0001
15	647.34	43.16	7.52	0.0001	12	260.76	21.73	11.56	0.0001	14	1,065.99	76.14	7.81	0.0001
5	46.73	9.35	1.63	0.1576	5	554.52	110.90	58.98	0.0001	5	1,137.32	227.46	23.32	0.0001
18	35.93	2.00	0.35	0.9937	18	28.01	1.56	0.83	0.6646	18	208.37	11.58	1.19	0.2823
121	694.57	5.74			108	203.09	1.88			121	1,180.05	9.75		

**Table 5** Relationships between the monthly chlorophyll *a* and nutrient concentrations

	Chlorophyll <i>a</i>				
	<i>b</i>	<i>r</i> <sup>2</sup>	<i>df</i>	<i>F</i>	<i>P</i>
Nitrites	0.024	0.610	59	93.910	0.0001
Nitrates	0.251	0.550	59	74.575	0.0001
Phosphates	0.105	0.658	59	115.247	0.0001
Silicates	0.299	0.498	59	59.519	0.0020

**Fig. 8** Average ( $\pm 1$  SD) of the 100 biggest *Patella granularis* recorded at 11 localities around the southern African coast. Zero distance was set at Lüderitz (Namibia, see Fig. 1)

filter-feeder biomass recorded per square metre remained unchanged around the coast, there being no correlation with distance around the coast (Fig. 7b). As a consequence, the maximal biomass values for filter-feeders in the east, south and west were not significantly different (one-way ANOVA,  $P > 0.29$ ), despite two outlying high values on the west coast.

Maximal sizes attained by the limpet *P. granularis* decreased from west to east, and were also negatively correlated with distance around the coast ( $r = -0.778$ ,  $P < 0.001$ ) (Fig. 8).

## Discussion

The results presented in this study demonstrate quantitatively the existence of a strong gradient of intertidal primary productivity on rocky shores around the southern African coast, highest values being recorded on the west coast, decreasing progressively towards the south and east coast (Figs. 2, 3). This gradient had a clear seasonal component when the localities were "lumped" into the three biogeographic provinces proposed by Emanuel et al. (1992), even though seasonality was not consistently evident when individual localities were inspected (Figs. 2, 4). Different seasonal patterns existed between the

provinces, with summer-spring peaks on the west coast, winter-autumn peaks on the south coast, and a lack of seasonality on the east coast. These results are consistent with inshore seasonal productivity patterns reported for phytoplankton by Brown (1992). The rates of intertidal epilithic productivity (measured as monthly chlorophyll *a* accumulations), were significantly correlated with the nutrient status of intertidal waters (Table 5). Thus, the availability of nutrients is likely to be a major factor regulating the growth rates of intertidal epilithic algae. Although the data were insufficient to indicate a causal mechanism, it is well known that high nutrient concentrations enhance primary production (e.g. Hutchinson 1955; de Boer 1982; Bosman and Hockey 1986).

The west-to-east gradient of intertidal primary production (Figs. 2, 3) presented in this work is clearly related to oceanographic conditions. Along the west coast, there are nearshore upwelling cells, mainly induced by strong southerly and south-east winds, and these bring cold, nutrient-rich waters to the surface. This Benguela upwelling system supports a large biomass of primary and secondary consumers (including fish) due to the high productivity of the area (Payne and Crawford 1989). The present results confirm that upwelling events are also felt inshore, influencing the rates of intertidal primary production (Fig. 2). By contrast, the main oceanographic feature along the east coast is the warm Agulhas current. Waters of the Atlantic, Southern and Indian Oceans mix along the south coast (Fig. 1). The interaction between the fast flowing Agulhas current and the topography of the bottom generates very localized and ephemeral cells of dynamic upwelling on the south coast. In addition, easterly winds blowing over a number of the prominent south coast capes form focuses of localized upwelling (Schumann et al. (1982), including the De Hoop region (Coetzee and Zoutendyk 1994). This feature will enhance the primary production of particular shores (e.g. De Hoop and Port Alfred, Fig. 2). However, further north-east, the warm and nutrient-depleted waters of the Agulhas current maintain low average rates of offshore primary production (Schleyer 1981; Shannon 1989) and also low rates of primary production on the intertidal rocky shores (Figs. 2, 3).

In addition, the gradient of intertidal epilithic production recorded here was significantly and positively correlated ( $r = 0.896$ ;  $P < 0.001$ ) with the nearshore phytoplankton production reported by Brown (1992). Epilithic intertidal algae and nearshore phytoplankton are likely to be similarly influenced by nutrient levels, given that nearshore waters are well mixed by tidal and wind-driven water exchanges (Legendre et al. 1986). The concepts applied to phytoplankton dynamics are thus likely to be equally applicable to attached benthic plants (Mann and Lazier 1991).

The use of functional form groups for the analysis of macroalgal distribution patterns has long been established in the literature on benthic ecology (e.g. Littler and Littler 1980, 1984; Hay 1981; Littler and Arnold 1982; Steneck and Watling 1982). Vertical gradients of abundance and



spatial distribution have been described several times using functional aggregations of algal species with similar forms. Algal abundance generally decreases in a logarithmic fashion, from maximum levels in the lower intertidal and shallow subtidal zones towards a minimal level in the upper intertidal shore (e.g. Nicotri 1977; Raffaelli 1979; Hawkins and Hartnoll 1983; Underwood 1984a, b; Steneck et al. 1991). However, horizontal gradients of abundance at a larger geographical scale are seldom reported. Macroalgal standing stock has been used as a "productivity potential" index (*sensu* Steneck and Dethier 1994), indicating the upper limit of net primary productivity possible in a given environment. The data presented here demonstrate that the average standing stock of macroalgae per unit area in the west coast did not differ from that of the east coast, but the standing stock of the south coast was significantly lower than either west or east coast averages (Fig. 5). These findings stand in contrast to the gradient of intertidal primary production found around the southern African coast (Fig. 3). Clearly, in this case standing stock is a poor indicator of primary productivity potential. This is scarcely surprising: macroalgal standing stock represents the fraction of algae that accumulates after physical and biological disturbances (Littler and Littler 1980; Hay 1981; Bosman et al. 1987), and mere abundance per unit area need not necessarily relate directly to *in situ* primary productivity.

Several attempts have been made to relate the functional forms of algae to two basic regulating factors, i.e. herbivory and nutrient concentrations (e.g. Littler and Littler 1980, 1984, 1988). The basic model, originally proposed for a tropical environment, suggested that the relative dominance of four different functional groups of organisms (i.e. coral, coralline algae, fleshy macroalgae, and microfilamentous algae) compete vigorously for space and light, and each of these groups can predominate under specific conditions of nutrients and herbivory pressure. The macroalgal patterns presented here (Fig. 5) do not entirely agree with some of the predicted patterns that flow from this model. For example, one of the predictions refers to the dominance of foliose and late successional algal forms in areas of high productivity and low grazing pressure (Littler and Littler 1988). The west coast, an area of established high productivity, is indeed dominated by foliose forms of algae (Fig. 5). However, if invertebrate grazer biomass can be used as an index of potential herbivory, the west coast does not conform to the above prediction because grazer biomass is extremely high (Fig. 7). On the other hand, the shift from foliose algae to corallines and turfs, from west to east coasts (Fig. 5), does agree with the functional form model of Littler and Littler (1980) because on the south and east coast, nutrients are low (Fig. 6) and, although invertebrate grazer biomass is low, there is a high diversity and abundance of herbivorous fish that graze in the intertidal zone during high tide (van der Elst 1990; Burger 1990; Y. Lechanteur, personal communication).

In the above-mentioned functional model, the factors potentially controlling growth and dominance of intertidal

al primary producers are the concentrations of nutrients in the surrounding waters and rates of herbivory, although the relative importance of each factor is not clear. At the local scale, biotic interaction may determine the algal "landscape" and abundance (e.g. Underwood and Jernakoff 1981; Steneck and Watling 1982; Hawkins and Hartnoll 1983; Branch 1985; Vadas 1985; Hill and Hawkins 1991), while it appears that at large spatial scales, over hundreds or thousands of kilometres, nutrient concentrations may control primary productivity (Mann and Lazier 1991; DeAngelis 1992).

In principle, any one of the essential nutrient elements can limit the growth of aquatic plants. Nevertheless, in most aquatic systems, either nitrogen (N) or phosphorus (P) appears to be limiting (see Table 1 in Howarth 1988, and Table 3.2 in DeAngelis 1992). There are many case studies, mostly concerning pelagic and coastal lagoon ecosystems, which indicate that primary production can be limited by either N or P and very occasionally by silica (Si). However, several lines of evidence lead one to conclude that net primary production in most marine ecosystems is limited primarily by N, and only in particular cases by P or Si (Howarth 1988; Mann 1988).

The present results demonstrate a clear gradient of nutrient concentrations around the southern African coasts (Fig. 6). However, nutrient concentrations as such do not cast any light on the large-scale control of primary production. It is the rate of nutrient cycling which is important (DeAngelis 1992). One can explore evidence of potential nutrient limitation using the Redfield ratio between C, N and P (Redfield 1958). This is based on the uptake ratios for carbon, nitrogen and phosphorus (principally) by oceanic phytoplankton, which are 106 C:16 N:1 P (by atom). In this context, significant differences (ANOVA,  $P < 0.05$ ) between the average N:P ratios were found when the nutrient data were amalgamated in-

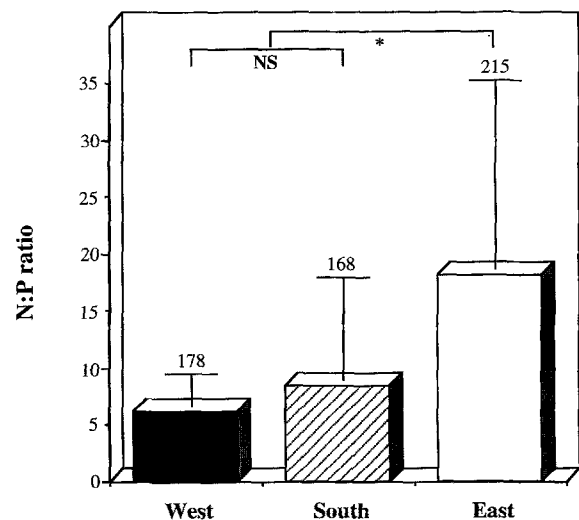


Fig. 9 Nitrogen to phosphate ratio (N:P) for samples of intertidal water. Error bars indicate 1 SD of the mean, and values above the bars show the number of samples. Statistics indicate \*  $P < 0.05$ , NS =  $P > 0.05$  in a posteriori comparison of means (Tukey *t*-test)

to the three biogeographic provinces (Fig. 9). The average N:P ratio for the west and south provinces were not significantly different (Tukey *t*-test,  $p > 0.05$ ) and were always below the expected 16:1 ratio proposed by Redfield (1958) (Fig. 9). Conversely, on the east coast the N:P ratio was significantly greater than that of the south and west provinces (Tukey *t*-test,  $p < 0.05$ ), and well above the expected 16:1, with an average of ca. 20:1 (Fig. 9). This result suggests that on the east coast phosphorus may limit intertidal productivity. Theoretically, the low Redfield ratio on the south and west coasts implies that nitrogen is more likely to be limiting. However, nutrient concentrations on the west coast are so high that it could be argued that nutrients are unlikely to be limiting. Certainly as far as phytoplankton is concerned, other factors such as shading and downwelling of water are more likely to limit productivity. The case of the intertidal system may, however, be different. Intertidal plants are unlikely to be limited by low light levels, and the issue of downwelling is irrelevant. Guano input from bird islands enhances algal growth on the west coast (Bosman and Hockey 1986). Coupled with evidence that algal productivity can be enhanced by experimental introduction of nutrients (Bosman et al. 1986), this provides powerful evidence that nutrients can limit the growth of intertidal algae.

The above large-scale variations in both rates of productivity and nutrients status are closely related to the structure and abundance of the intertidal biotic communities. The results presented here show that the average biomass of intertidal primary consumers (grazers and filter-feeders) declines from west to east in parallel with a decline in intertidal productivity and nutrient concentrations (Figs. 3, 6, 7). Indeed, there is a strong direct positive relationship between average grazer biomass and average rates of primary production (Fig. 10a), which are in turn related to nutrient concentrations (Table 5). The traditional notion of trophic functioning of biological communities is that the abundance of primary consumers in a given food chain should be positively correlated with in situ productivity (Leibold 1989; Menge and Olson 1990; Power 1992). Augmentation of the basal levels of a food chain (primary producers) should thus be reflected by corresponding increases in the abundance of the next trophic level (consumers; e.g. Power 1992, Fig. 3). This situation is, however, predicted only if the primary consumers are not held in check by secondary consumers (predators).

In the present case, the herbivore grazer biomass appears to be directly influenced by the in situ microalgal production. On a large geographical scale, this pattern is comparable to local response's described by Bosman and Hockey (1986), who demonstrated that invertebrate grazer biomass and production can be enhanced by high algal productivity associated with guano input on west coast bird islands. The argument that primary productivity directly influences grazer dynamics is reinforced by the fact that the maximum size achieved by *P. granularis* is directly correlated with primary production (Fig. 10b).

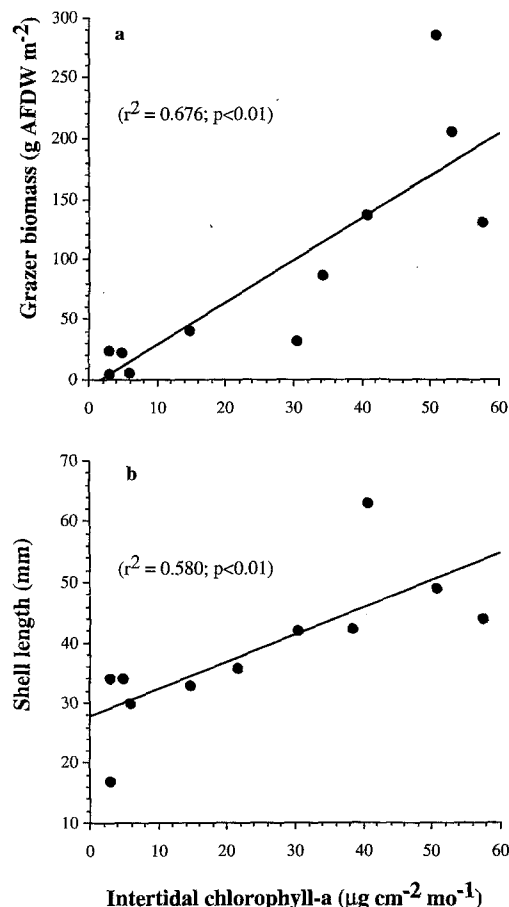
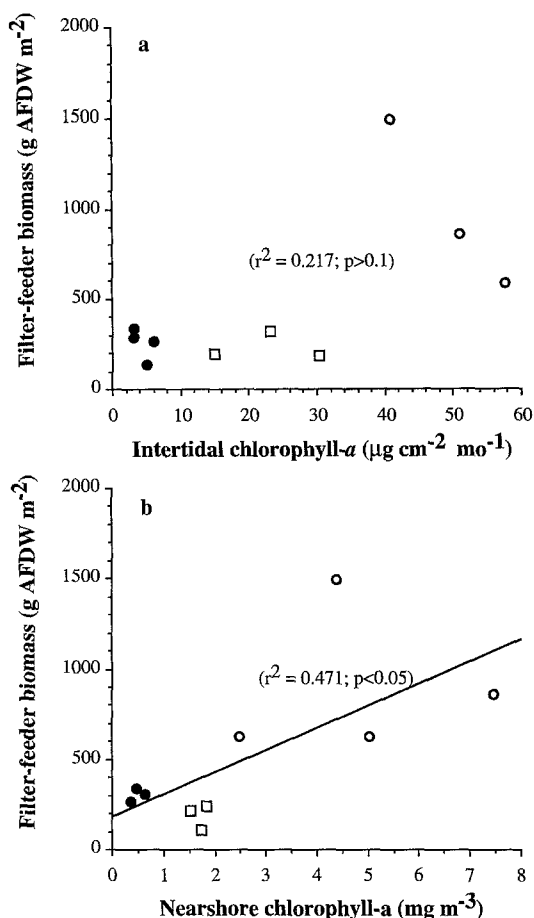


Fig. 10 Relationships between the intertidal productivity and a average grazer biomass, b maximum size of *P. granularis*

As maximum size is correlated with growth rate (Branch 1975), both size and growth are linked to primary productivity. Thus, enhanced primary production (due to coastal upwelling) may raise the upper limits of herbivore carrying capacity (Fig. 10a) and also have an influence on individual body size (Fig. 10b). Correlation is, of course, not proof. However, the mere existence of this broad geographic correlation between grazer biomass and intertidal productivity strongly suggests a bottom-up controlling effect (Menge 1992; Power 1992).

Although the average biomass of filter-feeders is also related to coastal productivity around the coast (Fig. 11b), this relationship is certainly indirect, due to the fact that filter-feeders depend on "imported" phytoplankton and suspended particulate organic matter (e.g. Stuart 1982; Stuart and Klumpp 1984). The data presented here show that filter-feeder biomass is indeed not related to in situ intertidal productivity (Fig. 11a), but positively related to the nearshore productivity (Fig. 11b). For this reason, their biomass is much more likely to be affected by local currents and wave action, which influence the rate of turnover of particulate matter in the intertidal zone, than by large-scale productivity gradients around the coast (Bustamante 1994). This argument is reinforced by the fact that biomass on exposed shores



**Fig. 11** Relationships between average filter-feeder biomass and **a** intertidal productivity, **b** nearshore productivity (data from Brown et al. 1991; Brown 1992). ○ West, □ south, and ● east coasts

is an order of magnitude higher than on sheltered shores (Bustamante 1994); the differences in filter-feeder biomass between wave-exposed and sheltered shores are far greater than any west-east gradient in their biomass that might be related to productivity (Bustamante and Branch, unpublished manuscript). This implies that local-scale water movement is of immense importance for filter-feeders. In addition, space is likely to set an upper limit to filter-feeder biomass. The maximum filter-feeders biomass (mainly mussels) does not show any predictable pattern around the coast (Fig. 7b), and a likely explanation is that there is a fixed ceiling set by spatial constraints rather than by the productivity or turnover of food supply.

These findings impinge on two important trophic considerations for rocky intertidal systems. The first is that the energy transfer in intertidal food webs, from the producer to primary consumer level, can be divided into two different compartments according to the main food source: the herbivore and filter- or suspension-feeder pathways. Intertidal herbivore species are directly supplied by the in situ intertidal primary production. The correlations presented in this work imply that inverte-

brate herbivore biomass is powerfully influenced by this production, but do not test whether in situ algal production is sufficient on its own to explain the high levels of herbivore biomass sustained on the west coast (Bustamante et al., 1994).

The second trophic consideration is that the energy used by filter- and suspension-feeders (the greatest biomass component within the intertidal rocky communities) is, to a large extent, “imported” as a subsidy from the adjacent pelagic and subtidal ecosystems (McQuaid and Branch 1985). As a consequence, maximal values achieved by filter-feeders are not related to intertidal productivity (Fig. 7), but are more likely to be limited by space availability (due to biotic interactions and the effects of wave action). Average (whole-shore) values for filter-feeder biomass are correlated with the gradient of offshore productivity around the coast (Fig. 11b), but appear to be even more powerfully influenced locally by wave action because of its effects on water turnover and, hence, the supply of food (Jørgensen 1990).

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