

## Rocky intertidal benthic systems in temperate seas: A synthesis of their functional performances

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**ABSTRACT:** Species composition and values of diversity, biomass, quantities of chlorophyll *a* and carotenes of 5 algal communities, located at different intertidal levels in northwestern Spain, were studied at monthly intervals. Productivity and loss of matter, as well as the production/biomass ratio in the same communities, are related to environmental stress (e.g. emersion, high temperature) and used to explain the dynamics of the system. Dynamic performances are also related to seasonal changes of patterns of zonation and special micro-patchiness. High productivity values (computed values between 0.50 and 2.71 g C m<sup>-2</sup> day<sup>-1</sup>) are ascribed to extra-energy inputs (not due to illumination) in terms of waves, tides and other water movements. The importance of such extra energy for productivity is discussed. Extra-energy is more important at low levels; at high levels its role is substituted by the ability of plants to photosynthesize during emersion periods. High intertidal communities are resistant to stress and hence, "physically controlled"; in contrast, low-level communities are "biologically controlled". The former are more conservative, the latter less efficient. Based on all data obtained, a hypothesis is presented, regarding the general functioning of intertidal communities.

### INTRODUCTION

In a recent paper (Niell, in press a) some data on quantitative species composition, biomass (*B*), species diversity (*H'*), amount of liposoluble assimilative pigments, and production (*P*) values of intertidal communities studied in northwestern Spain have been presented. Indexes such as *P/B* or *D*<sub>430</sub>/*D*<sub>665</sub> have been obtained from these figures and related to environmental factors which act as stress.

The aim of this work is the inclusion of some features of intertidal-system dynamics in larger the and more general principles of the ecological theory (Margalef, 1974).

### MATERIAL AND METHODS

The data mentioned above were obtained from monthly samples in 5 intertidal communities of the Ria of Vigo (NW Spain). Particulars of location and environment are presented in Table 1.

Sampling method and determination of sample size were described in two previous papers (Niell, 1974; Niell, in press a). All calculations were made from biomass units, because the concept of an individual is frequently not clearly applicable to algal populations. Laboratory procedures for obtaining dry weight were standardized as mentioned by Niell (1974); they are in agreement with Vollenweider (1969) and Holme & McIntyre (1971).

Diversity values were obtained as described by Niell (1974 and in press a) and Niell & Rucabado (in press): dry weight values were taken as units and calculations were made using Shannon's formula (Wilhm, 1968).

Table 1  
Sampling conditions

Code	Horizon*	Level** (m)	Exposition	Substratum	Observations
I	<i>Pelvetia canaliculata</i>	2.85–2.90	not exposed	rocks	—
II	<i>Fucus spiralis</i>	2.45–2.60	not exposed	rocks	—
III	<i>Himantalia elongata</i>	0.60–0.90	semi-exposed***	sandy-rock	abundance of <i>Bifurcaria bifurcata</i>
IV	<i>Himantalia elongata</i>	0.40–0.60	exposed***	rocks	—
V	<i>Himantalia elongata</i>	0.30–0.60	more exposed than IV***	rock	high abundance of red algae

\* From Niell (in press).  
 \*\* Measured above lower spring tidal level (L. S. T. L.).  
 \*\*\* Relative units based on Lewis (1964).

Values of liposoluble pigment concentration per surface unit were calculated from spectrophotometric measurements of metabolic extracts, following Talling & Driver (1963) for chlorophyll *a* and a UNESCO report (Anonymous, 1966) for carotenes.

Production and P/B ratios were calculated from the difference between biomass values obtained at two consecutive sampling times. Carbon equivalence of dry matter was obtained by means of an elemental analysis using a Perkin Elmer autoanalyzer (Niell, in press b).

## RESULTS

### Species composition

Macroalgae are codified in Table 2; their abundance in grams of dry matter  $m^{-2}$  at different intertidal levels is listed in Tables 3, 4, 5, 6 and 7.

Table 2

Algal species important in terms of their biomass (and code numbers)

1	<i>Himantalia elongata</i> (L.) S. F. Gray	41	<i>Calliblepharis ciliata</i> (Hudson) Kützing
2	<i>Bifurcaria rotunda</i> (Hudson) Papenfuss	42	<i>Callithamnion corymbosum</i> (Smith) Lyngbye
3	<i>Gigartina teedii</i> (Roth) Lamouroux	43	<i>Laurencia obtusa</i> (Hudson) Lamouroux
4	<i>Ceramium echionotum</i> J. Agardh	44	<i>Gelidium pulchellum</i> (Turner) Kütz.
5	<i>Laurencia pinnatifida</i> (Hudson) Lamouroux	45	<i>Callithamnion tetragonum</i> (Withering) C. Agardh
6	<i>Enteromorpha ramulosa</i> (Hudson) Kylin	46	<i>Acrosorium reptans</i> (Crouan) Kylin
7	<i>Cryptopleura ramosa</i> (Hudson) Kylin	47	<i>Caulacanthus ustulatus</i> (Mertens) Kütz.
8	<i>Gymnogongrus norvergicus</i> (Gunner) C. Agardh	48	<i>Ceramium shuttleworthianum</i> (Kütz.) Silva
9	<i>Hypoglossum woodwardii</i> Kützing	49	<i>Laminaria ochroleuca</i> de la Pylaie
10	<i>Gigartina acicularis</i> (Wulfen) Lamouroux	50	<i>Fucus vesiculosus</i> (L.)
11	<i>Chondria dasyphylla</i> (Wood.) C. Agardh	51	<i>Polisiphonia macrocarpa</i> Harvey
12	<i>Saccorbiza polyschides</i> (Light.) Batters	52	<i>Lithophyllum incrustans</i> Philippi
13	<i>Lomentaria articulata</i> (Hudson) Lyngbye	53	<i>Chaetomorpha aerea</i> (Dillwyn) Kütz.
14	<i>Halopteris scoparia</i> (L.) Sauvageau	54	<i>Rhodymenia pseudopalmata</i> (Lam.) Silva
15	<i>Ulva gigantea</i> (Kützing) Bliding = <i>Ulva lactuca</i> L.	55	<i>Cystoseira nodicaulis</i> (Withe) Roberts
16	<i>Chondrus crispus</i> (L.) Lyngbye	56	<i>Gelidium sesquipedale</i> (Turner) Thuret
17	<i>Gigartina pistillata</i> (Gmelin) Stackhouse	57	<i>Aglothamnion scopulorum</i> (C. Agardh) G. Feldmann
18	<i>Boergensiella thuyoides</i> (Harvey) Kylin	58	<i>Pterocladia capillacea</i> (Gmelin) Bormet et Thuret
19	<i>Corallina mediterranea</i> Areschoug	59	<i>Pterosiphonia complanata</i> (Clemente) Falk.
20	<i>Enteromorpha linza</i> (L.) J. Agardh	60	<i>Cystoseira tamariscifolia</i> (Hudson) Papenfuss
21	<i>Pylaiella littoralis</i> (L.) Kjellman	61	<i>Gracilaria folifera</i> (Forsk.) Boergesen
22	<i>Boergensiella martensiana</i> (Kütz.) Ardre	62	<i>Champia parvula</i> (C. Agardh) Harvey
23	<i>Ceramium rubrum</i> (Hudson) C. Agardh	63	<i>Ceramium ciliatum</i> (Ellis) Ducl.
24	<i>Gastroclonium ovatum</i> (Hudson) Papenfuss	64	<i>Enteromorpha clathrata</i> (Roth) Greville (1)
25	<i>Sciniaia furcellata</i> (Turner) Bivona	65	<i>Corallina squamata</i> Ellis et Solander
26	<i>Dictyota dichotoma</i> (Hudson) Lamouroux	66	<i>Gelidiella pannosa</i> (Bormet) Feldmann et Hamel
27	<i>Sphacelaria cirrosa</i> (Roth.) C. Agardh	67	<i>Halurus equisetifolius</i> (Light.) Kütz.
28	<i>Cladophora sericea</i> (Hudson) Kützing	68	<i>Goniotrichum elegans</i> (Chauvin) Le Jolis
29	<i>Chondria coerulescens</i> (J. Agardh) Falk	69	<i>Enteromorpha intestinalis</i> (L.) Lmk.
30	<i>Jania rubens</i> (L.) Lamouroux	70	<i>Codium tomentosum</i> (Hudson) S. F. Gray
31	<i>Cladostephus verticillatus</i> (Lightfoot) Lyngbye	71	<i>Goniotrichum cornu-cervi</i> (Reinsch) Hanck.
32	<i>Mesophyllum lichenoides</i> (Ellis) Lemoine	72	<i>Gelidium attenuatum</i> (Turner) Thuret in Bormet
33	<i>Dermatolithon pustulatum</i> (Lamouroux) Foslie	73	<i>Corallina officinalis</i> (L.)
34	<i>Gigartina stellata</i> (Stack) Batters	74	<i>Myriogramme versicolor</i> Kylin
35	<i>Porphyra umbilicalis</i> (L.) Kütz.	75	<i>Nitophyllum punctatum</i> (Stack) Greville
36	<i>Chylocladia verticillata</i> (Lightfoot) Blinding	76	<i>Pelvetia canaliculata</i> (L.) Decaisne et Thuret
37	<i>Plocamium coccineum</i> (Hudson) Lyngbye	77	<i>Lichina pygmaea</i> (Lightfoot) C. Agardh
38	<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	78	<i>Fucus spiralis</i> (L.)
39	<i>Schizymenia dubyii</i> (Chauvin) J. Agardh	79	<i>Lophosiphonia obscura</i> Falk.
40	<i>Callophyllis laciniata</i> (Hudson) Kützing		

## Biomass

Figure 1 shows the seasonal expression of biomass changes for high-level communities and Figure 2 for communities growing at low levels on the *Himantalia elongata* horizon.

In Communities I and II (Table 1), growth ceases as a function of reproductive maturation during winter and spring before maximum biomasses are attained in July (Fig. 1). This growth pause was described by Subrahmayan (1960, 1961) in Manx populations of *Pelvetia canaliculata* and *Fucus spiralis*, and in Portuguese populations of *Pelvetia canaliculata* by Ardré (1971).

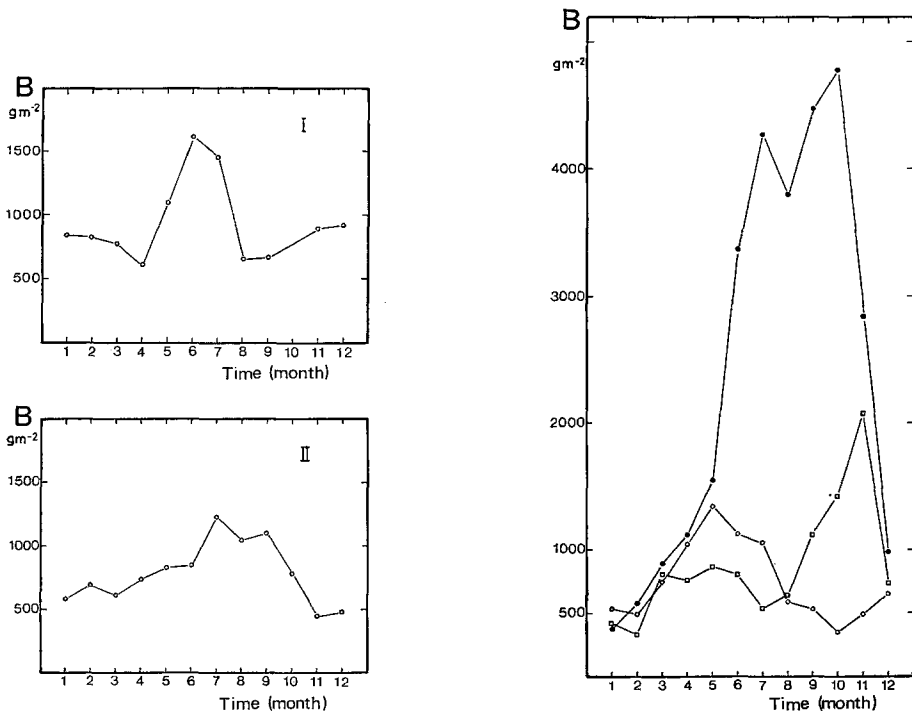


Fig. 1: Biomass values (g dry matter m<sup>-2</sup>) in high intertidal horizons. (I) *Pelvetia canaliculata*, Horizon I. (II) *Fucus spiralis*, Horizon II

Fig. 2: Values of biomass (g dry matter m<sup>-2</sup>) in low-level communities in the *Himantalia elongata* horizon. Circles: *Bifurcaria bifurcata*. Dots: *Himantalia elongata*, Community IV. Squares: Red algae, Community V

In low-level communities, maximum biomass (Fig. 2) depends, as other extrinsic parameters, on the *Himantalia elongata* cycle. In this species biomass attains maximum values, delayed in depth with time (see Species 1, Tables 5, 6, 7), followed by a reduction in the whole population after reproduction.

Communities IV and V (Table 1) attain two maximum values of biomass, in accordance with alterations of two kinds of red algae (Fig. 2).

Table 3  
Species abundance in the *Pelvetia canaliculata* horizon throughout the year  
(g dry matter m<sup>-2</sup>)

Code number	I 37	II 38	III 39	IV 40	V 41	VI 42	VII 43	VIII 44	IX 45	X 46	XI 47	XII 48
76	862.40	780.90	795.50	783.42	623.49	1212.75	1648.75	1472.88	662.68	669.92	870.28	933.02
77	4.16	10.00	30.75								107.56	
78	93.70	34.78									89.60	
6	1.92	0.22										

Table 4  
Species abundance in the *Fucus spiralis* horizon throughout the year  
(g dry matter m<sup>-2</sup>)

Code number	I 49	II 50	III 51	IV 52	V 53	VI 54	VII 55	VIII 56	IX 57	X 58	XII 59
78	539.02	707.38	620.06	751.08	850.89	868.10	1262.64	1080.90	1121.12	467.38	497.45
79			0.03								
6									0.05		

Table 5  
 Species abundance in the *Himantalia elongata* horizon.  
 (Community III in Table 1; g dry matter m<sup>-2</sup>)

Code number	I 1	II 2	III 3	IV 4	V 5	VI 6	VII 7	VIII 8	IX 9	X 10	XI 11	XII 12
1	27.81	58.44	316.39	467.25	1025.95	860.67	551.24	195.11	158.65	42.12	59.96	23.25
2	425.56	201.36	244.97	279.55	178.20	179.33	334.47	258.00	246.51	152.62	230.56	546.20
3			3.03							5.62	0.84	
4	3.11	3.49	1.74	11.90	2.20	2.22	0.98	0.06	0.35	0.06	5.63	12.98
5							0.01	0.01	4.96	2.18	0.02	
6			0.17	3.52	0.20		0.45			3.00		
7				7.09	3.50	2.09	0.08	1.26	1.83	0.12	1.51	1.12
8							0.01	0.06	0.01	9.25		3.72
9							0.77	27.42	8.34	0.18		0.42
10	0.05	8.34	5.59	100.17	21.80	13.44	0.77	27.42	8.34	32.56	53.84	38.61
11				0.11		2.01				1.50	0.42	6.28
12			0.87	0.78	0.60	4.77	0.08	0.51				7.30
13										1.93		
14										16.25	20.01	1.05
15	1.09	1.59	5.24	7.15	8.30	6.41	6.88	6.25	17.19	65.93	48.10	4.07
16	34.89	27.18	33.98	22.08	13.60					0.56		
17						0.37						
18										1.50	0.01	0.40
19	32.28	206.52	129.77	103.97	89.35	60.58	179.42	113.40	75.76	32.81	67.42	56.79
20										1.25		
21		0.22	1.80								21.05	
22	0.38	0.30	0.87		0.25		2.54		0.67		11.68	
23			6.70	21.80	0.40	0.83	0.36	0.03	1.94		1.34	
24											0.16	0.20
25											1.59	
26	0.07	0.07	0.17	0.27			0.04	0.06			0.42	



Table 6  
 Species abundance in the *Himantalia elongata* horizon.  
 (Community IV in Table 1; g dry matter m<sup>-2</sup>)

Code number	I 13	II 14	III 15	IV 16	V 17	VI 18	VII 19	VIII 20	IX 21	X 22	XI 23	XII 24
1	63.00	206.82	611.64	827.40	1279.84	2946.81	3975.16	3567.12	3986.17	4442.15	2636.87	533.62
2	59.96	9.83	22.30	20.93	21.85		10.54	6.72	92.37		18.60	29.12
3												4.25
5		1.57		21.64		14.64		2.10	7.31	0.55	0.57	12.87
6											0.33	0.65
7			4.35	3.78	20.24			0.98			0.09	
8	0.13	7.67	4.61	8.22					8.75	15.76	3.56	0.70
9		0.42	1.92	3.30							0.18	
10	61.44	62.17		1.46	2.74	77.17	92.10	107.19	308.25	250.31	102.71	96.00
11						0.41						
12						0.63		0.75				
13	1.76	0.89	1.21			8.32	11.59	18.70	29.56	3.60	5.49	2.31
14		0.10	0.12						3.06			
15	1.36	8.36	2.11	8.27	13.23	23.45	6.32	4.12	19.43	2.10	2.31	1.68
16	5.68	20.35		0.48	1.13	1.80	204.37	95.12	28.75	56.34		24.75
18								0.02				
19	189.18	259.42	201.20	213.96	175.62	125.40	29.19	27.65	39.12	47.75	112.20	302.56
21							0.01					
22					1.05							
23			0.19		5.29	4.23		4.12				
24				9.35				0.22				
26								0.01				
30		0.82	2.41	0.09	0.12	0.02						0.85
31					0.06							
34										13.01		





Table 7  
 Species abundance in the *Himantalia elongata* horizon.  
 (Community V in Table 1; g dry matter m<sup>-2</sup>)

Code number	I 25	II 26	III 27	IV 28	V 29	VI 30	VII 31	VIII 32	IX 33	X 34	XI 35	XII 36
1	9.36	6.72	50.73	166.14	364.97	328.10	276.34	262.77	416.66	618.13	1195.64	130.28
2	13.00		14.18	36.59	0.49	18.12	34.76	29.76	30.12	112.07	155.76	4.60
5	0.12	12.95	53.14	24.56	29.09	15.07	10.39	42.03	118.34	32.01	16.89	8.02
6							11.12					
7		3.03	32.00	2.80	8.78	3.76	2.44					
8			5.31	3.01	4.83			6.82	0.68	0.92	1.40	
9			7.79		1.08							
10	22.36	1.49	10.61	50.00	28.00	23.12	14.44	28.19	39.92	42.12	103.92	22.36
11					0.25		0.69					
12			11.19									
13	0.12	12.95	53.14	24.56	28.09	32.06	10.39	42.03	118.34	37.20	16.89	0.85
14												
15			5.21	3.01	4.83			6.82	0.68	0.72	1.40	
16	125.73	219.68	210.07	127.16	193.21	109.17	52.33	66.59	306.03	278.03	300.10	178.13
17												120.00
18							0.69					
19	189.79	69.70	135.96	229.35	194.64	160.17	130.49	160.22	86.01	105.09	284.49	145.06
21				0.16								
22						0.12					2.44	



## Diversity

Values of diversity obtained at high levels were near zero. *Pelvetia canaliculata* and *Fucus spiralis* communities were composed of unispecific populations of these species; sometimes ephemerophyceae (Feldmann, 1966) appear, but do not attain large amounts of biomass.

At low levels, the community "richness" is greater than at high levels. Species equitability changes considerably over the year with changes in dominance of *Himantalia elongata* (Fig. 3).

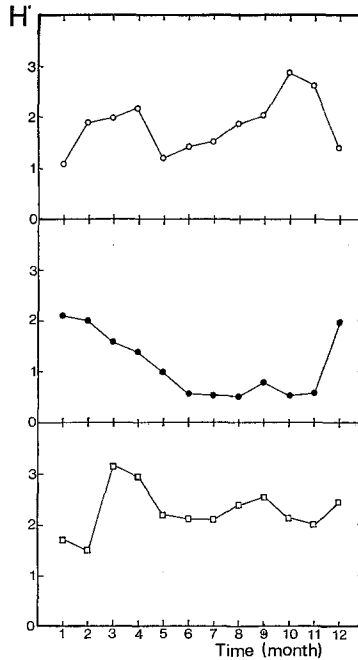


Fig. 3: Values of diversity ( $H'$ ) in the *Himantalia elongata* horizon. Circles: *Bifurcaria bifurcata*, Community III. Dots: *Himantalia elongata*, Community IV. Squares: Red algae, Community II

Communities situated at the periphery of the *Himantalia elongata* horizon reveal two diversity maxima, coinciding with maximal "equitability" between this species and the others of the system; obviously, maximum diversity values are inverse to the dominance of *Himantalia elongata*.

Chlorophyll *a* and carotenes

The quantity of chlorophyll *a* expressed per surface unit ( $\text{mg chlorophyll } a \text{ m}^{-2}$ ) in intertidal communities is very high; the values obtained (Fig. 4) are sometimes

higher than those measured in other (aquatic and terrestrial) communities (Margalef, 1974). The same values of chlorophyll *a* content, related to biomass units (mg of chl. *a* g<sup>-1</sup> dry matter) are also expressed in Figure 4. Both values are of interest for the analysis of seasonal changes. The quantity of chlorophyll *a* per surface unit increases along the succession; in contrast, its concentration per unit of biomass decreases. During high productivity periods, the relative amount of chlorophyll *a* is greater than during non-productive periods.

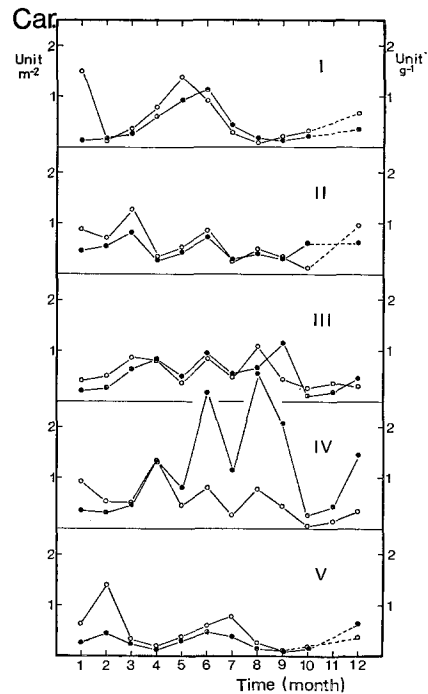
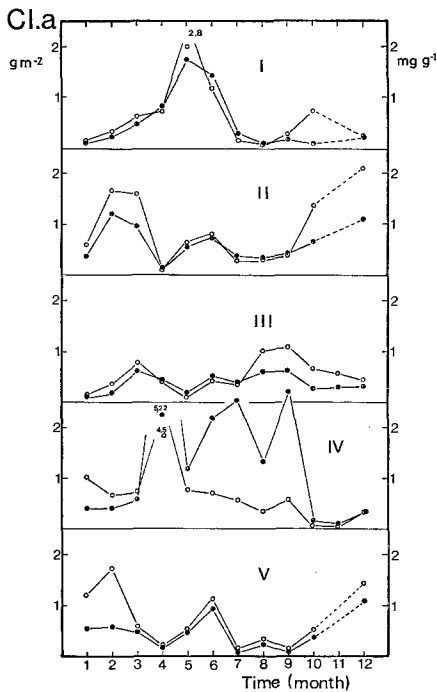


Fig. 4: Values of chlorophyll *a* per surface unit (dots) and per unit biomass (circles) in the communities studied (see Table 1)

Fig. 5: Annual variations in carotenes values. Dots: surface units (unit of carotene m<sup>-2</sup>). Circles: biomass units (unit of carotene g<sup>-1</sup> dry matter; all values multiplied by 10<sup>-6</sup>)

Absolute values per surface unit are indicative of an inefficient system in which great quantities of chlorophyll *a* are not used as assimilative pigment; chlorophyll *a*, on the other hand, is a potential productivity indicator. In general, there exists a relation between biomass and chlorophyll *a* curves: the latter seem to predict maximum values of the former. Also maximum carotene values are correlated with maximum biomass values. The curves of chlorophyll *a* exhibit less pronounced fluctuations than those of carotenes (Fig. 5).

In general, the relations were not so clear as to postulate regularities. A general quantitative aspect arises from the cycles: the high quantity of assimilative pigments stored in the plants cannot be used with maximum efficiency.

## Production and losses

Net production values were calculated by taking the difference of biomass values plotted in Figures 1 and 2.

Figure 6 presents monthly production results from Niell (1975). The negative values obtained are due to the amount of organic matter degraded during a given interval of time greater than production. Numerous assimilation values in the literature have been obtained by extrapolation from punctual measurements; these must be considered with care because of the different methods employed and different interpretations.

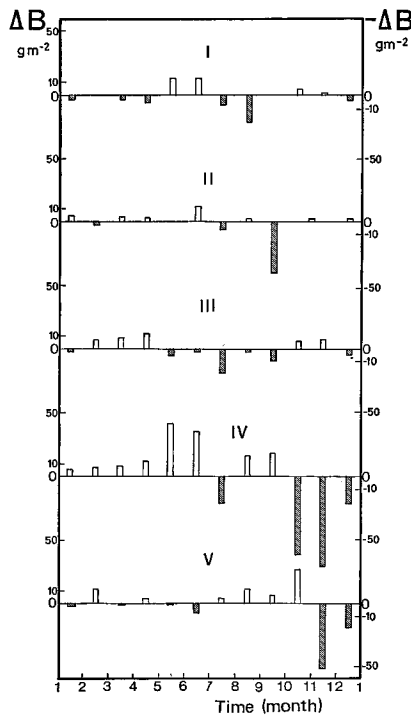


Fig. 6: Net production (white bars) and losses of organic matter (shaded bars)

Table 8 compares values of production obtained by other authors with those obtained in this study. Some values shown seem too high; possibly because they were obtained from short-term experiments and extrapolated to daily, weekly, monthly or even annual figures. Such procedure is not really permissible, as demonstrated graphically in Table 9 where our monthly production values reveal several considerable differences. The mean value of annual production obtained in our work was  $416.10 \text{ gC m}^{-2}$ ; this productivity is nearly twice as high as the value for plankton,  $260 \text{ g C m}^{-2}$ , obtained in the same zone by Fraga (1976).

Table 8

Comparison of productivity values obtained in studies on benthic communities

Vegetation	g C m <sup>-2</sup> day <sup>-1</sup>	References
<i>Caulerpa beds</i> , Canary Islands	1.0	Johnston (1969)
Seaweed population	1.0-9.0	Blinks (1955)
Marine, macrophytic algae, Canary Islands	1.5-3.0	Johnston (1969)
Reef communities, Eniwetok Atoll	1.6-7.2	Smith (1973)
Seaweed littoral zone, St. Margareth	4.8	Mann (1972)
Crustose coralline algae, Hawaii	0.5-2.6	Littler (1973)
<i>Thalassia</i> and <i>Cymodocea</i> , Kavaratti Atoll	5.8	Qasim & Bhattathiri (1974)
Intertidal algal populations, S. Clemente (California)	0.4-3.1	Littler & Murray (1974)
<i>Cystoseira abies-marina</i> vegetation, Canary Islands	10.56	Johnston (1969)
<i>Laminaria hyperborea</i> , Argyll, Scotland	2.0	Jupp & Drew (1975)
<i>Pelvetia canaliculata</i> , Type I	0.67	This work
<i>Fucus spiralis</i> , Type II	0.50	This work
<i>Bifurcaria</i> , Type III	0.64	This work
<i>Himantbalia</i> , Type IV	2.71	This work
Red algae, Type V	1.8	This work

Table 9

Monthly production g C m<sup>-2</sup> day<sup>-1</sup> in intertidal vegetation

Interval of samples (months)	<i>Pelvetia canaliculata</i> Type I	<i>Fucus spiralis</i> Type II	<i>Bifurcaria</i> Type III	<i>Himantbalia</i> Type IV	Red algae Type V
I-II	-0.45	1.62	0.22	1.82	0.79
II-III	0.007	- 0.65	1.93	2.34	3.44
III-IV	-0.41	1.26	2.57	2.40	- 0.42
IV-V	1.59	0.99	3.12	4.14	1.18
V-VI	4.41	0.12	- 1.52	12.28	- 0.47
VI-VII	4.21	3.81	- 0.68	10.89	- 2.46
VII-VIII	- 2.28	- 2.37	- 6.19	- 6.44	1.39
VIII-IX	- 6.23	0.30	- 0.52	5.24	3.78
IX-X	0.11	- 12.25	- 2.97	6.74	1.82
X-XI	1.94	0.15	1.46	- 18.81	8.46
XI-XII	0.72	(X-XII)	2.07	- 21.44	- 15.90
XII-I	- 0.78	0.45	- 1.98	- 7.02	- 6.01

The losses of dry matter recorded indicate insignificant effects of consumers. The biomass of herbivorous animals in the system is not important, and practically all the biomass produced was degaged and mineralized "out of the system".

### P/B Ratio

P/B values are of special interest as a measure of energy flow. In immature communities, high productivity is supported by a low biomass; in contrast, mature systems exhibit low productivity values relative to those of biomass.

For algal communities, Mann (1972) pointed out that the P/B ratio is too small to be considered when measured over short periods of time in communities with biomass values exceeding 300 g dry matter  $m^{-2}$ . For this reason, values were computed over the whole year. Surprisingly, they were lower for high-level communities than for low-level ones (*Pelvetia canaliculata* community P/B = 1.98; *Fucus spiralis* community P/B = 1.97; *Bifurcaria bifurcata* community P/B = 3.02; *Himantalia elongata* community P/B = 12.25; *Red algae* community P/B = 6.25).

### Succession

Surface areas cleaned in experiments were occupied by different species. Within 2 years, all intertidal communities, except *Pelvetia canaliculata*, had returned to their original structure. The time for community regeneration depends on the season of clearance, because the settling of different species is strongly controlled by abiotic environmental factors. A recent paper (Niell, in press a) considers dynamics and speed of community regeneration. Three stages can be distinguished: (1) a "colonization" stage, composed of microalgae forming a layer or a thin carpet; (2) characterized by the dominance of different species of Ulvales; and (3) the substitution of green algae by red and brown algae (Niell, in press a).

### DISCUSSION

The most characteristic feature of the intertidal is the emersion period; intertidal species must be adapted to temporary atmospheric exposure and related environmental stresses.

The quantity of biomass employed in reproduction, is greater in low-level species, such as *Himantalia elongata*, than in high-level ones, related to the availability of nutrients which depends on the time of emersion and mixing processes (waves, tides, currents). Low-level systems are highly productive (Fig. 6).

A high-production system is characterized by low diversity; in contrast, systems with a high diversity (mature systems) have low values of biomass increase. Several values in this work do not agree with the empirical data obtained; systems with low diversity values average low values of production, while more diverse systems are more productive.

Energy flows faster through a low-structured system than through a high-structured one. Values of energy flow estimated by means of P/B ratio are higher in *Pelvetia canaliculata* and *Fucus spiralis* communities, than in the *Himantalia elongata* horizon; for this reason, high-level systems are more efficient than low-level ones despite values of diversity which are higher in the *Himantalia elongata* horizon.

*Pelvetia canaliculata* and *Fucus spiralis* are well adapted to temporary emersion; only few species are able to live under the forbidding conditions at high intertidal levels; hence upper intertidal communities are characterized by low species numbers.

The stress of emersion is characterized by regularity at high levels, but it attains



the characteristics of a catastrophe for low-level inhabiting species non-adapted to tolerate the prolonged exposure to air.

High-level systems are "physically controlled", where as low-level ones are "biologically controlled" (sensu Sanders, 1968). The spatial structure of intertidal systems (Niell & Rucabado, in press; Niell, in press a) agrees with Sanders' hypothesis: low-level communities exhibit patchy structures. The abundance of the different species changes gradually from one facet to another suggesting that the most important relation between the species is competition for space. More general than Sanders' concept, is the model of Brestky & Lorenz (1970) who expressed, in terms of genetic properties, the ability of communities to respond to stress. We use this model in Figure 7 to interpret the evolution of intertidal communities from initial colonization to maximum stability.

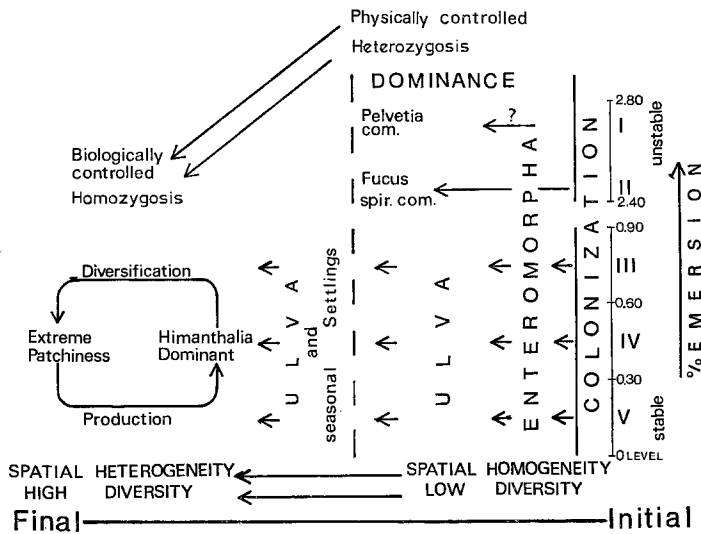


Fig. 7: Summary of succession and fluctuation in intertidal temperate systems. I to V: communities. Arrows mark the direction of change as succession advances

Brestky & Lorenz (1970) assume and demonstrate that physically controlled populations are a genetically heterocygote and the biological controlled ones feature genetical homocygosis; the latter ones suffer destruction under stress because of their low response capability related to low genetical variability. In Figure 7 genetic variability decreases from the right-top (PC) to the left-bottom (BC), and the succession proceeds from right to left, the spatial heterogeneity increasing in the same direction (expressed as diversity).

Other than structure, the data obtained facilitate analysis of the relation between production and intertidal position of different communities (Fig. 8).

Most investigators tend to neglect energy sources other than irradiation. Odum (1967) & Margalef (1974) pointed out the importance of extra-energy in nutrient intake processes. Extra-energy for intertidal communities is supplied by waves and

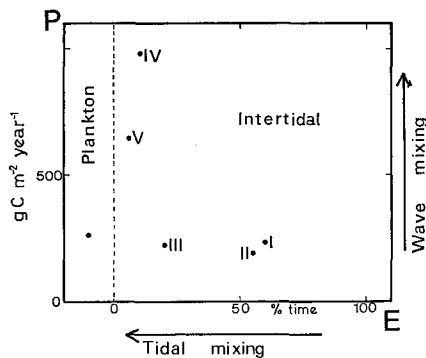


Fig. 8: Role of extra energy on production. Plankton-production values from Fraga (1976)

tidal water movements. Water movements, if strong enough, can be inhibitory but on semi-exposed coasts they have a positive effect due to mixing which renew the nutrient supply for algae.

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