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Algal seasonality on an exposed rocky shore in Hong Kong and the dietary implications for the herbivorous crab *Grapsus albolineatus*

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Abstract Patterns of algal seasonality, and their effect on the diet and feeding preferences of the herbivorous crab *Grapsus albolineatus*, were investigated over an 18-mo period from March 1993 to August 1994 on an exposed tropical rocky shore (Hok Tsui Peninsula at Cape d' Aguilar, Hong Kong). Algal cover was greatest in the winter months, and lowest in the summer. Foliose algae such as *Ulva fasciata*, *Porphyra suborbiculata*, and *Dermonema frappieri* were dominant in the winter, but died off in the summer. During the hot summer months, perennial encrusting algae e.g., *Ralfsia expansa*, *Hildenbrandia rubra*, *H. occidentalis*, coralline crusts and the encrusting cyanobacteria *Kyrtuthrix maculans*, were the dominant algal species. Seasonal variation in algal abundance influenced the dietary selectivity of the herbivorous crab *G. albolineatus*. In the winter, the crab fed selectively on filamentous algae (e.g. *Hincksia* spp., *Cladophora* spp., *Enteromorpha* spp., and the cyanobacteria *Lyngbya* sp.). Foliose algae (e.g. *U. fasciata*, *P. suborbiculata*, *Pterocladia tenuis*) formed a small part of the diet, despite being the dominant species on the shore. Foliose and filamentous algae were virtually absent from the shore in the summer, and the crabs switched to feeding solely on encrusting algae. Electivity indices revealed preferences for green and brown turf species, and avoidance of foliose algae. Faecal analysis revealed that a greater proportion of the food is digested in the winter, suggesting that *G. albolineatus* is able to digest filamentous algae more efficiently than encrusting algae. Feeding preferences of *G. albolineatus* appear to be influenced by a number of factors, including the availability, digestibility and morphology of algae. The foraging behaviour and cheliped morphology of the crab also affect food choice. The monsoonal nature of Hong Kong's climate controls the diversity and abundance of intertidal algae and, therefore, indirectly influences the diet and subsequent growth and reproductive success of the herbivorous crab *G. albolineatus*.

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Introduction

Intertidal macroalgae exhibit seasonal changes in their abundance and diversity on temperate (Underwood 1981; Cubit 1984) and tropical shores (for review see Brosnan 1992). Workers have documented the physical and biological factors affecting the seasonal abundance of algae and the role herbivores play in structuring rocky intertidal communities.

Fewer studies have, however, examined how this seasonal change in food supply affects the ecology of herbivores present on these shores. A seasonally changing food supply has been shown to affect the food selection of terrestrial herbivorous lizards (van Marken Lichtenbelt 1993) and herbivorous fishes on rocky intertidal shores (Horn 1989; Clements and Choat 1993). Herbivores in these predictably changing environments have periods of growth and reproduction synchronised to when food is most abundant (van Marken Lichtenbelt et al. 1993).

The rocky shores of Hong Kong (22°N; 114°E) have very diverse fauna and flora (Morton and Morton 1983) and, being in a monsoonal system, experience marked differences in physical conditions through the year. The summer months (June to August) are characterised by high air temperatures (mean = 30 °C, max. 36 °C) and heavy rainfall, whereas the winter months (December to February) are cool and dry (mean = 17 °C). The shores display clear seasonal patterns of macroalgal abundance. In the summer months the shores appear bare, but in fact support encrusting algal species, with mobile fauna being restricted to cracks and crevices (Williams 1993a). In the winter months the shores support large patches of erect macroalgae (Hodgkiss 1984; Ho 1986; Williams 1993a).

In Hong Kong, the herbivorous grapsid crab *Grapsus albolineatus* Lamarck is one of the dominant herbivores (Williams 1993b), and can be found throughout the intertidal zone on exposed rocky shores. The crab feeds at low tide (Kennish unpublished data), and it rarely enters the sea, spending most of the time foraging across the rock surface or in rockpools. The crab feeds using its chelipeds which have fine sharp points and appear to be efficient at removing microalgae and sporelings off the rock surface, in a similar method suggested for *G. grapsus* (Schäfer 1954).

Many studies have examined the feeding ecology of predatory crabs in the intertidal (e.g. Elner 1981; Vannini et al. 1989) and subtidal (e.g. Haddon and Wear 1987; Cerda and Wolff 1993). Relatively few studies however have examined the feeding ecology of herbivorous crabs, especially those occurring on rocky shores (reviewed in Wolcott and O'Connor 1992), although for temperate species see Birch (1979) and Hines (1982) and for tropical species Coen (1988). This paper examines how the diet and feeding preferences of the herbivorous crab *Grapsus albolineatus* change through the year in response to seasonal patterns of algal availability, and examines the possible causes of these preferences.

Materials and methods

Study sites

The macroalgal survey and the crab collections were made at two similar south east facing exposed rocky shores on Hok Tsui peninsula at Cape d'Aguilar, Hong Kong. Both sites were of similar faunal and floral composition. The lower shore was dominated by a band of mussels (*Septifer virgatus*), in the midshore the barnacle *Tetraclita squamosa* dominates, with mobile gastropods restricted to cracks and crevices. The higher shore was bare of sessile species, but supported *Nodilittorina* species [see Morton and Morton (1983) for general description of Hong Kong shores and see Williams (1993 b) for a map of Cape d'Aguilar].

Macroalgal survey

Macroalgal abundance (% cover) was determined on a monthly basis from March 1993 to August 1994. A stratified random sampling method was employed at both sites. Vertical heights at 0.5 m intervals were marked on the shore from 2.0 to 4.0 m above Chart Datum, which covered the foraging range of the crabs. A total of 15 quadrats (50 × 50 cm double strung with 81 intersection points) were randomly located along a 20 m belt transect at each of the five heights, with all substrate types sampled (including pools and crevices). The alga under each point was recorded and abundance (% cover) calculated.

Diet composition

The fore-gut and faecal pellet contents of *Grapsus albolineatus* were analysed each month from December 1992 to June 1994. Ten crabs (five males and five females, carapace width 30 to 56 mm) were caught from each site. Sampling was conducted at, or around, low tide at night, since the majority of crabs feed during this period (Kennish unpublished data). Once caught the stomach contents were preserved immediately by injecting 5% buffered saline formalin into the mouth of the crabs. In the laboratory the crabs were dissected to remove the fore-gut and the faecal pellets from the hind-gut and mid-gut. The fore-gut contents and faecal pellets were stored in 5% buffered saline formalin prior to analysis.

Table 1 Algal species found at Cape d'Aguilar, with accompanying morphological groups and the abbreviations used in Fig. 6

Species	Group	Abbrev.
Hincksia mitchelliae (Harvey) Silva	Filamentous, Brown turf	Btf
Hincksia sp.	Filamentous, Brown turf	Btf
Sphacelaria tribuloides Meneghini	Filamentous, Brown turf	Btf
Enteromorpha spp.	Filamentous, Green turf	Gtf
Cladophora spp.	Filamentous, Green turf	Gtf
Lyngbya sp. (Cyanobacteria)	Filamentous, Green turf	Gtf
Chaetomorpha antennina (Bory) Kützing	Filamentous, Green	Cha
Gelidium pusillum (Stackhouse) Le Jolis	Filamentous, Red turf	Rtf
Polysiphonia spp.	Filamentous, Red turf	Rtf
Ceramium byssoideum Harvey	Filamentous, Red turf	Rtf
Porphyra suborbiculata Kjellman	Foliose, Red	Por
Pterocladia tenuis Okamura	Foliose, Red	Pte
Dermonema frappieri (Mont. & Mill.) Børgesen	Foliose, Red	Dne
Endarachne binghamiae J. Agardh	Foliose, Brown	End
Ulva fasciata Delile	Foliose, Green	Ulv
Kyrtuthrix maculans (Gomont) Umezaki	Encrusting, Blue-Green	Kyr
Dermocarpa sp.	Encrusting, Blue-Green	Dca
Ralfsia expansa (J. Agardh) J. Agardh	Encrusting, Brown	Ral
Hapalospongidion gelatinosum Saunders	Encrusting, Brown	Ral
Endoplura aurea Hollenberg	Encrusting, Brown	Ral
Hildenbrandia rubra (Sommerfelt) Meneghini	Encrusting, Red	Enc
Hildenbrandia occidentalis Setchell	Encrusting, Red	Enc
Corallina sessilis Yendo	Coralline, (Erect) Red	Cor
Corallina pilulifera Postels & Ruprecht	Coralline, (Erect) Red	Cor
Crustose corallines	Coralline, (Crust) Red	Cor

The fore-gut and faecal pellet contents were identified and scored using an adaptation of a method used by Jones (1968) and Tsuda and Randall (1971) for quantifying algal material in fish stomachs. Homogeneous preparations of the contents were made, and then three sub-samples were mounted on slides. Contents were viewed at low power × 100 (Zeiss binocular light microscope), and the occurrence of each item was recorded under an ocular grid marked with 25 intersection points. Contents were also scanned at × 200 and × 500 to aid algal identification and to ensure that no microalgae were missed. Five fields of view were examined from each of the three slides giving a total number of 375 intersection points. The relative abundance of each food item was determined by the following equation:

$$RA\% = (i_a/\Sigma i) \times 100,$$

where i_a = number of intersection points for Species a; Σi = total number of intersection points for all species. Algal fragments were identified to the lowest possible taxonomic level (using standard regional texts). For the faecal analysis an item was regarded as digested if identification was impossible due to the disruption of cell structure, and also if the plant material lacked cell contents.

Dietary selectivity

Dietary selectivity for the crab was determined each month for 14 groups of macroalgae (listed in Table 1). Both Ivlev's electivity index (Ivlev 1961) and Vanderploeg and Scavia's selectivity coefficient (Vanderploeg and Scavia 1979) were used to analyse any patterns of diet selection, as it has been suggested that the use of more than one index is preferable since no single index satisfies all the criteria considered essential for an unbiased assessment of diet selection (Lechowicz 1982).

Results

Seasonality and zonation patterns of the algal assemblage

Total algal cover varied throughout the year (Fig. 1a). The maximum shore cover was in February, 61.4% (±2.8 SE), compared to a minimum of 13.6% (±1.7 SE) in July. Algal cover was greatest throughout the year at the 2.0 m station (the lowest), ranging from 93% in March to 39% in July. At the highest station sampled (4.0 m), algal cover ranged from 53% in March to 0.6% in July. No algae occurred above the 4.0 m station at any time during the year.

In the winter the 2.0 m station was dominated by Rhodophyta (encrusting coralline algae, the erect coralline algae *Corallina sessilis* and *C. pilulifera*, other non-coralline red crusts e.g. *Hildenbrandia rubra* and *H. occidentalis*, the foliose red *Pterocladia tenuis*, and a bed of red turf algae, Table 2). The corallines, both erect and encrusting, dominated this station in the summer (Table 2) when the abundance of the other species decreased. The stations at 2.5 and 3.0 m (Table 2) were characterised in the winter months by patches of the brown crust *Ralfsia expansa*, green turf and brown turf species, *Chaetomorpha antennina* and by the red alga *Dermonema frappieri*. In the summer months only *R. expansa* and *C. antennina* remained. The highest stations (3.5 and 4.0 m) (Table 2) also had fewer species present in the summer, than the winter months, when *Porphyra suborbiculata* and *Ulva fasciata*

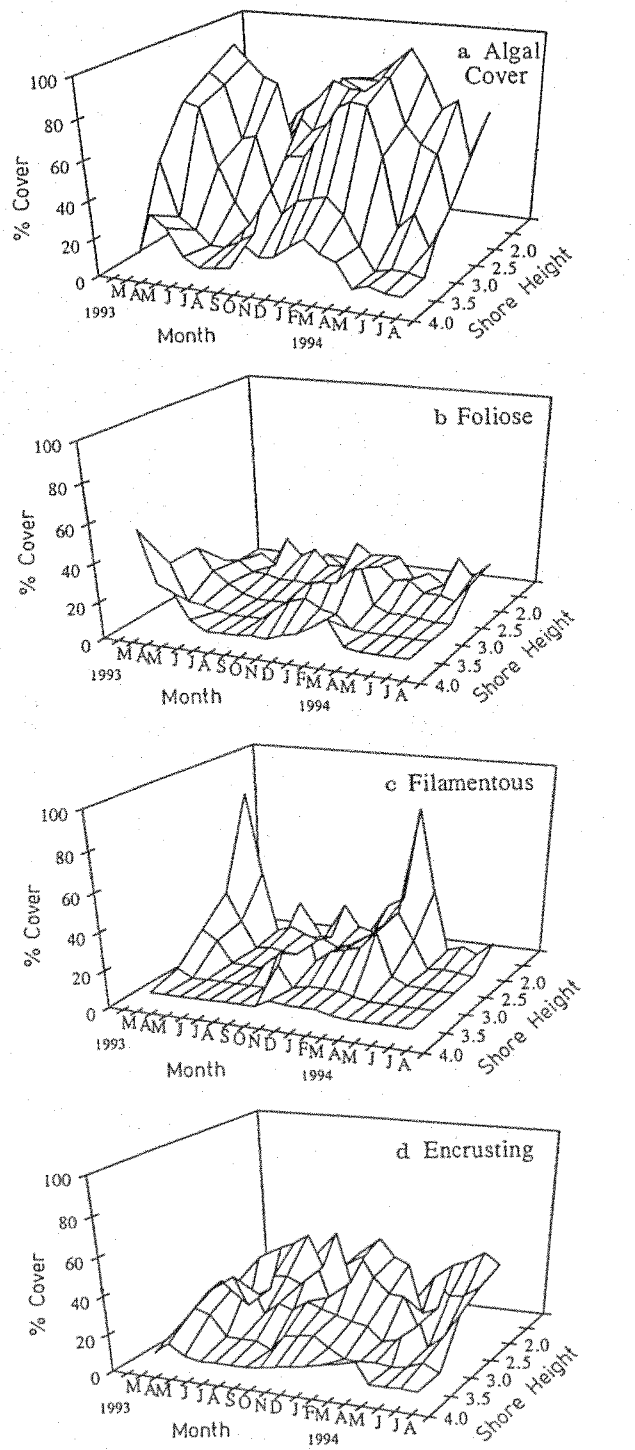

Fig. 1 Seasonal variation in zonation and abundance of algal groups on an exposed rocky shore at Cape d'Aguilar, Hong Kong. **a** Total algal cover. **b** Foliose algae. **c** Filamentous algae. **d** Encrusting algae

Table 2 Monthly mean percentage cover of algae at different tidal heights on an exposed rocky shore at Cape d'Aguilar, Hong Kong. See Table 1 for species' full names

Tidal height	1993										1994						
Taxon	M	A	M	J	J	A	S	O	N	D	F	M	A	M	J	J	A
2.0 m																	
Coralline crust	12	6	19	16	10	10	22	18	19	25	13	11	15	18	12	10	12
Corallina	1		2	7	3	2	4	2	2	2	1	1	1	1			1
Hildenbrandia	6	5	1	1	3	3	4	4	4	6	7	5	5	1	1	2	2
Ralfsia	6	2	5	8	8	3	9	6	7	9	7	6	5	4	4	2	2
Gelidium	12	13	1	6	3	1	6	16	6	3	6	7	8	5	3	1	1
Pterocladia	2	2	15	16	10	13	4	6	16	10	5	8	10	12	10	10	14
Chaetomorpha	10	12	10	6	1	7	10	19	10	6	10	10	12	12	8	9	7
Dermocarpa	1	15	8	7	1	14	2	2						5	6	8	8
Ulva	3	6	1	1					1	1	5	8	6				
Ceramium	10	2							4	4	14	15	6				
Dermonema	1	1							2	3	5	1	1				
Endarachne	1	1									2	1	1	1			
Green turf	22	15									4	18	20	6			
Polysiphonia	2										2	8					
Hincksia	4								1	2	6	5					
2.5 m																	
Coralline crust	15	4	7	7	2	8	13	12	10	17	14	12	8	3	6	5	4
Corallina			5	2	1						1			1		2	
Hildenbrandia	6	4	4	2	5	5	12	10	8	8	3	4	4	6	5	4	6
Ralfsia	3	3	7	7	4	6	10	8	14	14	3	4	4	7	5	5	4
Gelidium			1	2	1			3	2	1	1	1	1	2			
Pterocladia	1	1	4	3	2	3	2	6			1	1	1	4	5		
Chaetomorpha	17	20	13	9	1	9	9	8	13	18	14	15	15	16	10	6	6
Dermocarpa	2	15	10	11	4	9	4	3	1	1	7	8	10	16	10	8	5
Ulva	6	10	1	2				1	1	1	5	6	12				
Ceramium	11								1	4	8	13					
Dermonema	2							1	3	10	4	2					
Endarachne	7	1									7	10	2				
Green turf	3	1					8	8	3	3	2	3	5				
Hincksia	11	2					2	2	2	4	14	12	1				
3.0 m																	
Coralline crust	12	13	9	6	1	7	7	11	13	10	10	10	11	11	11	10	10
Corallina	1	1	1														
Hildenbrandia	1	1	3	4	1	9	7	5	1	1		1	2		4		3
Ralfsia	4	5	3	4				4	4	4		3	2	1	1	1	
Gelidium	3	4	1								1	1	1	2			
Pterocladia	7	1	3	1				1	1								
Chaetomorpha	2	3	2					2	3	4	7	5	4	2			
Dermocarpa	7	18	18	6	1	1	8	4	1	1	14	16	18	19	10		
Ulva	10	12	3	1					1	3	15	13	12	5			
Ceramium	1	1							3	5	10	6	5				
Dermonema	3								16	21	10	2					
Endarachne	5	1									2	6	1	1			
Green turf	1	2				9	15	5			7	1					
Polysiphonia											1	1	2				
Hincksia	13	5						2	5	9	1	1	1				
Porphyra									2	6	1						
3.5 m																	
Coralline crust	6	2	1		1	1	1	4	8	11	1	4	2	1			
Hildenbrandia		1		1	1	2			1	1		1		1		1	
Ralfsia		1	1						1	1					1		
Dermocarpa	10	9	5	1		2	2	2	3	1	15	10	11	2	1	1	1
Ulva	5	3	1						1	1							
Ceramium	1								1	2	3	1					
Dermonema	2	1						1	3	3	3	2	1				
Endarachne	1	1									1	1	1				
Hincksia	2								1	1							
Porphyra	17	2							8	10	5	3	2	1			
Kyrtuthrix	1	1		1	1	2	7		1	1	1	1	1	1	1	1	1

(continued overleaf)

Table 2 (continued)

Tidal height	1993										1994						
Taxon	M	A	M	J	J	A	S	O	N	D	F	M	A	M	J	J	A
4.0 m																	
Coralline crust	1	1						1	1	4	6	3	1				
Hildenbrandia		1						1	1		1			1	1		
Dermocarpa		1	1								1		1				
Ulva	8	3									5	3	2	1			
Green turf								3	4	3	3	2	1				
Porphyra	42	20	19	5						3	4	18	35	12	6		
Kyrtuthrix	1	1			1	1	2	3	4	1	3	3	4	3	2	4	3

were abundant (March shore covers of 42 and 8.3%, respectively).

In the winter the dominant algae were the foliose and filamentous groups, whereas the encrusting algae were dominant in the summer (Fig. 2). The algal groups exhibited differing seasonal and spatial zonation patterns. Foliose algae reached peak abundance in February and March (Fig. 1b). *Pterocladia tenuis* was the only species found at 2.0 m, the other foliose species generally occurred higher on the shore. Filamentous algae were most abundant in the low shore during March (Fig. 1c), with lowest abundance in July and August. The encrusting algae displayed a general pattern of being more abundant on the low shore than the high shore (Fig. 1d), although there was little apparent change in abundance throughout the year. The crusts do however show a partitioning of vertical zonation between the species (Table 2). Corallines were most abundant at the 2.0 m station, *Hildenbrandia* spp. at the 2.5 m station, with *Ralfsia expansa* at the 3.0 m station. The only crust present throughout the year at the higher levels was the cyanobacteria *Kyrtuthrix maculans*.

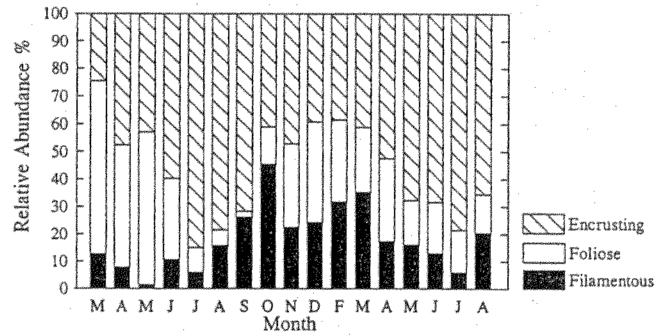

Fig. 2 Seasonal variation in the relative abundance of the different algal groups found at Cape d'Aguilar, Hong Kong

Diet and faecal composition

Examination of the stomach contents of *Grapsus albolineatus* revealed clear differences in the consumption of algal species throughout the year (Fig. 3a). The summer diet was almost entirely encrusting algae, (mainly *Corallina* spp., *Ralfsia expansa* and *Hildenbrandia* spp.). These algae were, however, only a minor component of the diet in the winter when filamentous algae were the major food item. Different species of filamentous algae were consumed through the year. In the winter the main species were the green and brown turfs (listed in Table 1), whereas in the summer *Gelidium pusillum* was the most common filamentous alga ingested.

Throughout the study, nearly all crabs contained some filamentous algae (Fig. 4a), with 100% of crabs containing filamentous algae for 8 mo of the survey. The occurrence of encrusting algae (Fig. 4b)

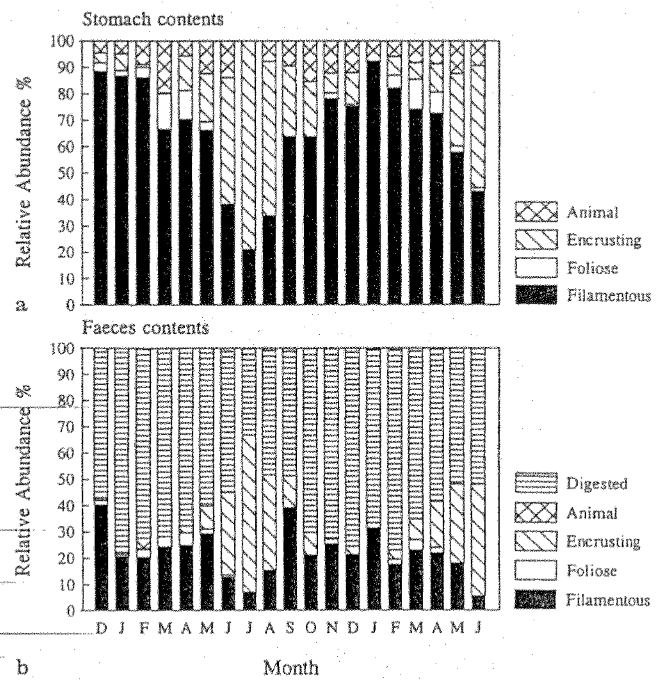

Fig. 3 *Grapsus albolineatus*. Seasonal patterns of relative abundance of **a** different food groups in the stomach contents and **b** algal species found in the faeces

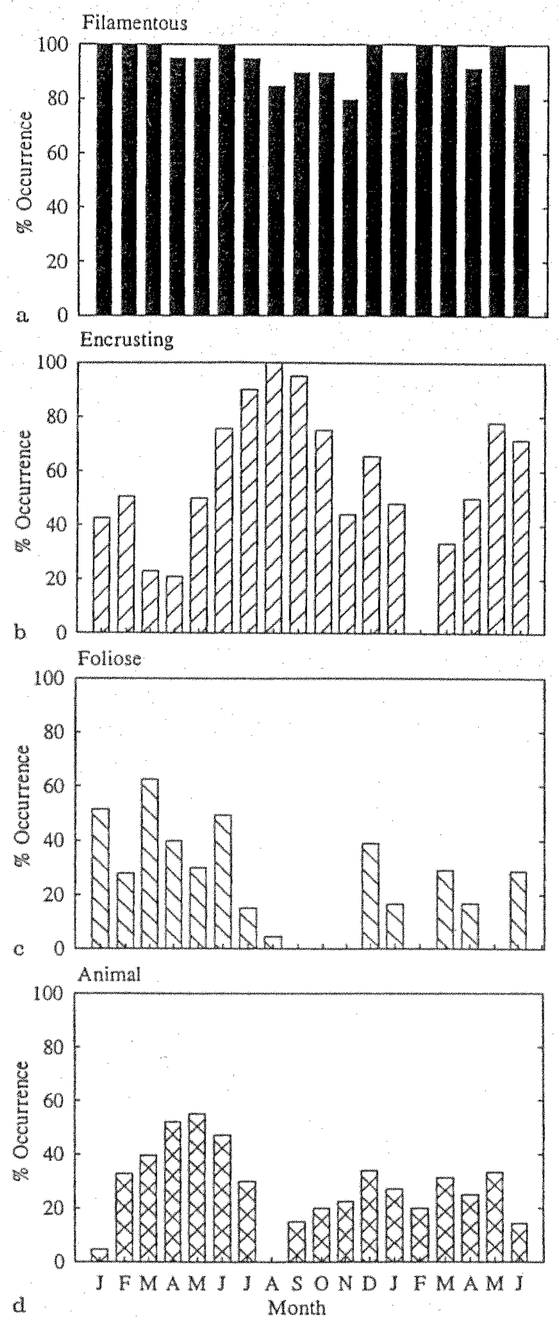

Fig. 4 *Grapsus albolineatus.* Seasonal variation in the percentage of crabs containing the different food groups in the stomach contents. **a** Filamentous algae. **b** Encrusting algae. **c** Foliose algae. **d** Animal material

had a distinct seasonal pattern, with 100% of crabs containing encrusting algae in July as compared to 0% in February. The pattern for foliose algae was in direct contrast to this (Fig. 4c), since more crabs contained foliose algae in their guts during the winter (~50%) than in the summer (0%). The number of crabs that consumed animal matter (Fig. 4d) showed little change through the year (~30%).

The proportion of digested matter in the faeces varied throughout the year in relation to the algae consumed, indicating that the crabs digest some algae more efficiently than others (Fig. 3b). In January the digested portion was 78%, as compared to a low of 33% in July. The abundance of filamentous algae in the faeces was never more than 40%, whereas the encrusting algae composed 60% of the faeces in July.

Data for male and female crabs were pooled as there was no significant difference in consumption of filamentous algae between males and females (Mann–Whitney test, $P = 0.133$). There was however a significant difference in the abundance of filamentous algae between the months of the year (Table 3), with the month of July having less filamentous algae than all other months. The multiple comparison test revealed clear monthly groupings (Table 3), with increasing amounts of filamentous algae being eaten in the colder, winter months.

There was also no significant difference in the consumption of encrusting algae between the sexes (Mann–Whitney test, $P = 0.594$), but the amount eaten varied between the months. Groupings were again based on seasons with a "spring–autumn" group, a "winter" group, and an "early winter–early summer" group followed by the summer months. In contrast to the pattern for filamentous algae, however, the abundance of encrusting algae increased from the cooler months to the summer months (Table 3). The abundance of foliose algae (Fig. 3a) was never greater than 14% of the diet. The animal component of the diet remained constant throughout the year (mean = 9.36 ± 1.0% SE), and displayed no seasonal pattern (Fig. 3a).

Dietary selectivity

Crabs appeared to preferentially consume certain species of algae when compared to algal abundance on the

Table 3 *Grapsus albolineatus.* Kruskal–Wallis non-parametric equivalent to a one-way ANOVA to compare monthly differences in the abundance of filamentous and encrusting algae in the stomach contents. A non-parametric multiple comparison procedure was used to investigate differences between months. Months *underlined* are not significantly different from each other

Dietary item	*H*	*df*	*P*	Months											
Filamentous algae	80.857	11	< 0.001	Jul	Aug	Jun	May	Mar	Apr	Sep	Oct	Nov	Dec	Jan	Feb
Encrusting algae	128.8	11	< 0.001	Feb	Mar	Oct	Jan	Nov	Apr	Dec	Sep	May	Jun	Aug	Jul

shore (Fig. 5a–d), this was especially true for the green and brown turfs. The relative abundance of green turf on the shore (Fig. 5a) never exceeded 25% at any time during the year, yet the relative abundance in the gut regularly (especially in the winter months) exceeded this amount, peaking at ~60% in September and October. A similar pattern of low abundance on the shore and high abundance in the gut was revealed for the brown turf species (Fig. 5b). In contrast, the foliose alga *Porphyra suborbiculata*, had a seasonally high abundance on the shore, reaching a maximum of ~50% in May (Fig. 5d), and yet in the stomach the abundance was never more than 15%. The proportion eaten of the encrusting brown alga *Ralfsia expansa*, was similar to its abundance on the shore, showing a distinct seasonal pattern, with the highest values in the gut and on the shore in July, and lowest values in March.

Electivity indices revealed that the crabs displayed a clear and seasonally constant preference (+0.1 → +1.0) for green and brown turf species (Figs. 6, 7). Preference for *Ralfsia expansa* and the coralline algae varied seasonally, as in the summer these algae were preferred, whilst in the winter they were avoided (−0.1 → −1.0). Foliose algae, however, were avoided throughout the year (Fig. 6a, b). Although the overall electivity rankings for the species

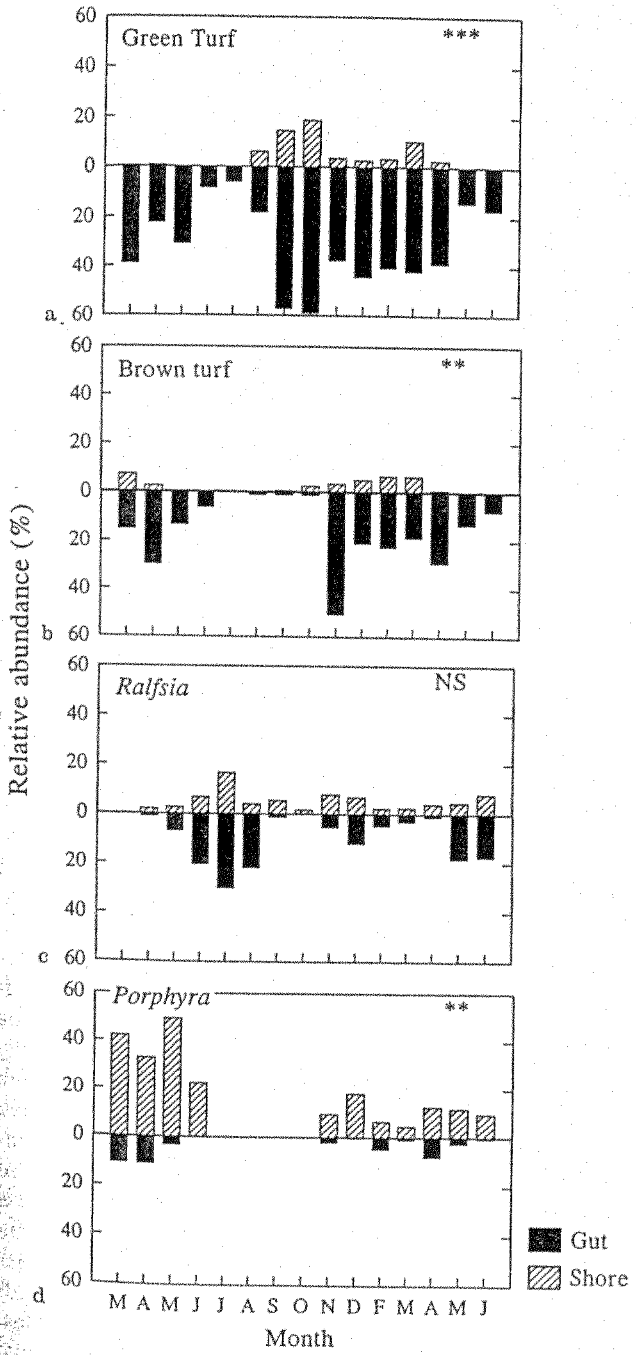

Fig. 5 *Grapsus albolineatus*. Relative abundance of different algal species in the stomach contents (*filled bars*) and on the shore (*hatched bars*). (*** $P < 0.001$; ** $P < 0.05$; *NS* Not significant, Mann-Whitney test)

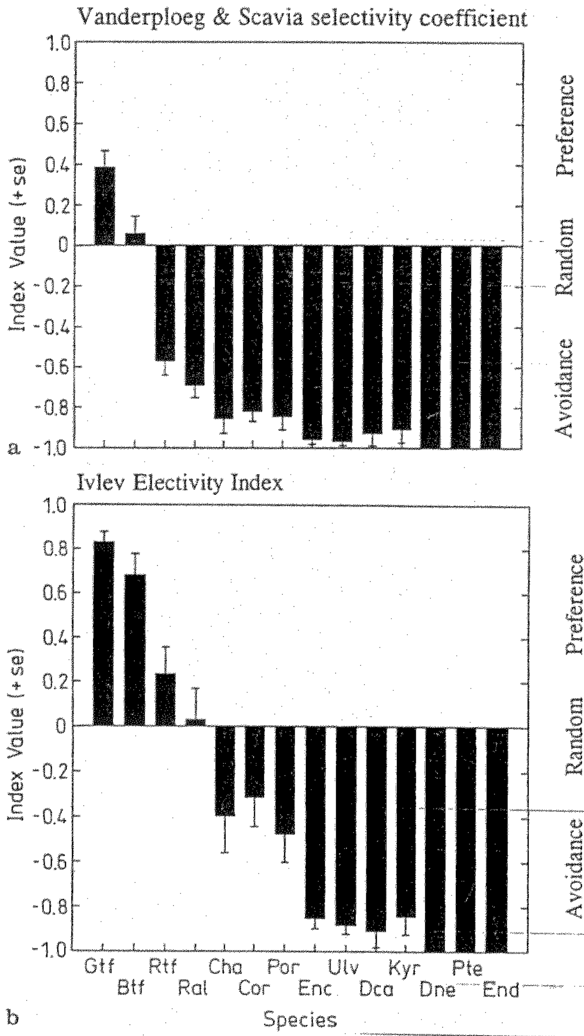

Fig. 6 *Grapsus albolineatus*. Electivity index values for dietary items (abbreviations in Table 1). Data are means ± SE, $n = 15$ mo. **a** Vanderploeg and Scavia's selectivity coefficient. **b** Ivlev's electivity index

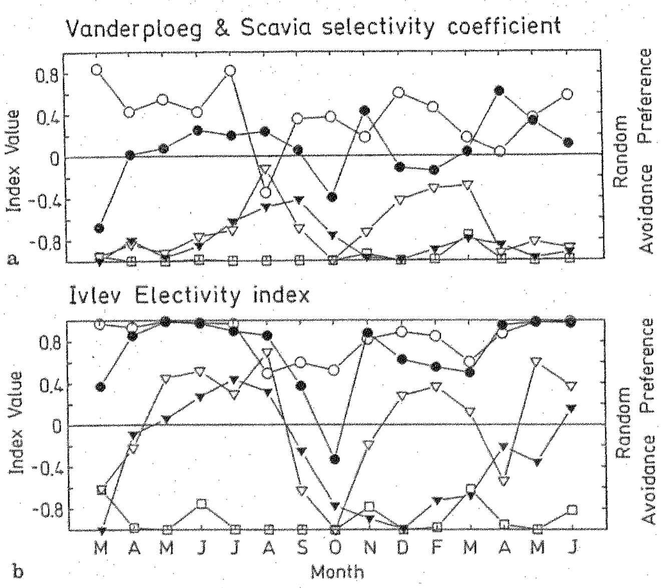

Fig. 7 *Grapsus albolineatus.* Seasonal variation in preference for five dietary items. **a** Vanderploeg and Scavia's selectivity coefficient. **b** Ivlev's electivity index. (○ Green turf; ● Brown turf; ▽ *Ralfsia*; ▼ Corallines; □ *Ulva*)

were similar, the mean values for the year varied between the two indices (Figs. 6, 7). Ivlev's index gave three preferred food items, green turf, brown turf, red turf, with *R. expansa* being randomly fed on (~ 0). Vanderploeg and Scavia's index, however, resulted in two preferred food items, green turf and brown turf, with the other items being avoided.

Discussion

Seasonal changes in abundance and species composition of algae at Cape d'Aguilar influenced the diet of the herbivorous crab *Grapsus albolineatus*. In the winter months the shores supported almost equal mixtures of foliose, filamentous, and encrusting algae, yet the crabs' diet consisted mainly of filamentous algae. In the summer, physical stresses and herbivore effects (Williams 1993a, b; Williams 1994) greatly reduce the abundance of filamentous and foliose algae, and the only algae which remained were perennial encrusting algae. In this hotter period the crabs' diet consisted primarily of encrusting algae (although filamentous algae were still eaten, accounting for ~25% of the diet). The electivity indices demonstrated that the crabs had a year-round preference for green and brown turf algae, and a seasonal (summer) preference for encrusting algae. Individual electivity indices can prove biased under certain conditions (Lechowicz 1982), so the use of two indices here allowed cross-comparison and confirmed ranking of the preferences.

Herbivore food choice/preference is influenced by a complex array of species specific factors. These include plant nutritional characteristics, morphology, chemical composition, the nutritional requirements of the herbivore, its digestive capabilities and its mode of feeding [for a full review of plant–herbivore interactions see Lubchenco and Gaines (1981)].

Algae have greater mass and predictable availability than animal prey, but they are an inadequate source of nutrients, especially nitrogen (Wolcott and O'Connor 1992). Nitrogen is often a limiting nutrient for many herbivorous animals (Mattson 1980), and this includes herbivorous crabs which sometimes supplement their diets with animal protein thereby enhancing growth (Wolcott and Wolcott 1984; O'Connor 1992). Growth of *Grapsus albolineatus* was enhanced when fed a mixed diet of algae and animal material as compared to a pure algal diet in the laboratory (Kennish 1995). If *G. albolineatus* is limited by nitrogen it should prefer the most nitrogen rich algae.

The nutrient content of algae affects herbivore food preference. Ephemeral algae, because they are fast growing, are often energy rich. This is true for the green and brown turf species, but they are not significantly different in energy content to *Porphyra suborbiculata*, or *Pterocladia tenuis*. The more abundant crusts *Hildenbrandia* spp. and *Ralfsia expansa* do have higher protein and lipid contents and therefore are more rich in nitrogen and energy than the turfs. *R. expansa* does not contain polyphenolics, though *Hildenbrandia* spp. are thought to; these algae appear toughened which could deter feeding by *G. albolineatus*. Many algae on rocky shores have evolved a diverse array of chemical and physical defences to deter herbivores (Duffy and Hay 1990). The nitrogen gain in consuming these species may be offset by decreased digestibility or absorption efficiencies caused by these defences.

Many Phaeophyta and Chlorophyta contain polyphenolic compounds (Targett et al. 1992) and have been shown to deter feeding by herbivorous gastropods (Steinberg 1985; Steinberg 1988) and herbivorous fish (Van Alstyne and Paul 1990; Meyer and Paul 1992) and to affect herbivore dietary preferences (Irelan and Horn 1991; Meyer et al. 1994). Leaf litter preference of detritivorous mangrove crabs has been shown to be strongly influenced by leaf tannin content and nitrogen availability (Lee 1993). Algae can also be physically defended. Coralline algae have calcified thalli which interfere with digestion by increasing handling times and in herbivorous crabs cause wear of chelipeds, mandibles, and the teeth of the gastric mill (Coen 1987, cited in Wolcott and O'Connor 1992). Thalli calcification has been shown to influence the feeding preferences of herbivorous fish (Hay et al. 1988; Schupp and Paul 1994).

The filamentous algae that *Grapsus albolineatus* feeds on are mainly "ephemeral" species, and as such are fast growing, and are not thought to have chemical or physical defences (Littler et al. 1983). This may be a contributing factor to the food choice of *G. albolineatus*. Wylie and Paul (1988) reported that species of *Cladophora*, *Ectocarpus*, (closely related to *Hincksia*), *Polysiphonia*, *Enteromorpha* and *Chaetomorpha* have no secondary metabolites or calcification, and are thus highly preferred algae by the herbivorous fish *Zebrasoma flavescens*. These algae are also the major food items of *G. albolineatus*.

Algal abundance will also affect a herbivore's food choice, since it is not energetically worthwhile to search for rare food items even if they are very nutritious, as the energy and time spent in searching would not justify the gains obtained from eating the food. The filamentous algae, despite being the preferred food item, are not the most abundant algae on the shore at any time of the year.

The physical ability of the crab to eat certain algae appears to be the most important factor in determining food choice. The crab has sharp, fine pointed chelipeds which appear adapted to removing filaments off the rock surface. The crab does not use the chelipeds as suggested by Schäfer (1954) and Hawkins and Hartnoll (1983) to scrape the rock surface, but rather it feeds by picking algae off the rocks (Kennish personal observation). The foliose algal species may be simply too large for the crab to handle. Crab feeding is limited to periods of emersion and mainly at low tide, so it has to feed quickly in order to maximise its food intake. Feeding on difficult to handle foliose, or tough encrusting algae, would slow feeding rates down. In the summer at Cape d'Aguilar wave action is less and tides are more extreme (i.e. lower low tides) than in the winter (Apps and Chen 1973; Williams 1993a), resulting in extended feeding times for the crab. This allows the crab more time to search for the preferred but rare filamentous algae, and also more time to eat the tougher encrusting algae. This preference for filamentous forms of algae even extends to the different species of calcified coralline algae. *Grapsus albolineatus* feeds more on erect coralline algae than it does on encrusting forms, despite their similar nutrient contents (Kaehler and Kennish 1996).

The animal portion of the diet is constant throughout the year, and consists mainly of epiphytic amphipods, which have presumably been eaten incidentally with their host alga. *Cladophora* and *Hincksia* species support large numbers of amphipods which are certainly an important contributor of nitrogen to the crabs' diet, and as a result may influence the preference the crab shows for these algae. *Hincksia* spp. also supported an assemblage of diatoms which may supplement the crabs' diet. No other epiphytes were found on other algae or seen in the gut contents. *Corallina* spp. also support a rich epibiota, including many polychaetes and turf algae, which may account for their high consumption (over 30% of the diet in the summer), despite being nutritionally poor (ash content of ~75%, Kaehler and Kennish 1996).

The digestibility and assimilation efficiency of the crab will also influence food choice. Laboratory experiments on the assimilation efficiency of *Grapsus albolineatus* have shown crabs to assimilate nutrients three times more efficiently from *Enteromorpha* (one genus of the green turf species) than from coralline algae (Kennish 1995). The relatively small proportion of animal matter in the faeces indicates that this material is well digested by *G. albolineatus*. The total assimilation efficiency for animal material (fish) has been shown to be as high as 89% for laboratory maintained crabs (Kennish 1995).

The seasonal patterns of algal availability strongly affect the diet selection of *Grapsus albolineatus*, causing switching between food items through the year. The constant preference for filamentous algae and the avoidance of foliose algae appear to be influenced by a number of interacting factors. The most important factor determining food choice appears to be algal morphology in relation to the crab's cheliped structure. Other factors affecting food choice include algal abundance (and hence biomass) and distribution, algal nutrient content, physical and chemical defences and the digestive capabilities of the crab. The crab appears to invest energy in the digestive gland during periods of high algal abundance (in the winter) and utilise these reserves during the crab's reproductive season (March to September). This suggests that periods of growth and reproduction have been synchronised to make use of the plentiful food supply in the winter, and that patterns of algal seasonality have important consequences for the fitness of this crab.

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