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Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California

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Synopsis

Herbivory by wide-ranging fishes is common over tropical reefs, but rare in temperate latitudes where the effects of herbivorous fishes are thought to be minimal. Along the west coast of North America, herbivory by fishes on nearshore reefs is largely restricted to a few members of the Kyphosidae, distributed south of Pt. Conception. This paper presents information on natural diets and results from feeding choice experiments for two abundant kyphosids from intertidal habitats in San Diego, California – *Girella nigricans* and *Hermosilla azurea,* and similar data for the lined shore crab, *Pachygrapsus crassipes,* which also forages over intertidal reefs. These results are compared with the availability of algae in intertidal habitats measured during summer and winter, on both disturbed and undisturbed habitats. The diets of juveniles of *G. nigricans* and *H. azurea* collected from nearshore habitats were dominated by animal prey (mainly amphipods), but adults of these fishes, and *P. crassipes,* consumed algae nearly exclusively, with 26, 10, and 14 taxa of algae identified from *G. nigricans, H. azurea,* and *P. crassipes,* respectively. Algae with sheet-like morphologies (e.g. *Ulva* sp., *Enteromorpha* sp., members of the Delesseriaceae) were the principal algae in the diets of the fishes, and calcareous algae (e.g. *Corallina* sp., *Lithothrix aspergillum*) and sheet-like algae (*Enteromorpha* sp.) comprised the greatest identifiable portion of the shore crab's diet. Feeding choice experiments indicated that the fishes preferred filamentous algae (e.g. *Centroceras clavulatum, Polysiphonia* sp., *Chondria californica*) and sheet-like algae (e.g. *Enteromorpha* sp., *Ulva* sp., *Cryptopleura crispa*) over other algal morphologies, whereas the shore crab chose jointed calcareous algae (e.g. *Lithothrix aspergillum, Corallina vancouveriensis, Jania* sp.) most frequently. The diets and preferences for algae by the fishes were generally most similar to the assemblage of algae available in early successional (disturbed) habitats during summer when sheet-like and filamentous algae are abundant. The shore crab exhibited the opposite trend with a diet more similar to late successional (undisturbed) habitats.

Introduction

Compared to tropical reefs where grazing by fishes limits the distribution of algae (Randall 1961, 1965, Ogden & Lobel 1978, Gaines & Lubchenco 1982, Carpenter 1986, Horn 1989), herbivory by highly mobile fishes and decapods is apparently ineffective in controlling the distribution of algae on intertidal and shallow subtidal reefs in temperate latitudes. The presence of extensive turfs of macroalgae in low intertidal and shallow subtidal zones, low diversity and abundance of highly mobile herbivores, and assumed indigestibility of algae by temperate fishes has led to the consensus that herbivory by fishes does not control the structure of algal communities in shallow marine habitats of temperate latitudes. However, the effects of herbivory by fishes and decapod crustaceans on the structure of algal communities, as well as diet, digestive physiology, and feeding preference for various macroalgae, have received little attention and are poorly documented in temperate latitudes (Dayton 1975, Horn 1989, but see Sousa 1979).

The diverse families of herbivorous and omnivorous fishes that forage actively in groups over tropical reefs (e.g. Acanthuridae, Siganidae, Sparidae, Kyphosidae; Hiatt & Strasburg 1960, Randall 1967) are largely absent in temperate latitudes where wide ranging herbivorous fishes are relatively rare (Horn 1989). In contrast to the effects of fishes in tropical latitudes, echinoderms and molluscs have been implicated as the major herbivores in temperate habitats (Gaines & Lubchenco 1982, Schiel & Foster 1986, see review by Horn 1989). North of Pt. Conception along the western coast of North America the most abundant herbivorous fishes belonging to the reclusive Stichaeidae (Eschmeyer et al. 1983) and the majority of roving fishes are carnivores and omnivores (e.g. Embiotocidae) that forage over beds of macroalgal turf and consume mainly small crustaceans and polychaetes (Quast 1968, Bray & Ebeling 1975, Hobson & Chess 1976, Laur & Ebeling 1983). The southern California bight, however, includes a transitional fish fauna derived from both tropical and temperate zones (Eschmeyer et al. 1983), and it is here that the effects of herbivory by fishes on the structure of temperate algal communities should be evident.

This transition zone includes three predominantly herbivorous species of fish from three subfamilies of the Kyphosidae (Eschmeyer 1990). Because they are common in inshore habitats, zebraperch (*Hermosilla azurea,* Kyphosinae), opaleye (*Girella nigricans,* Girellinae), and halfmoon (*Medialuna californiensis,* Scorpidinae) potentially affect algal communities on shallow reefs. *Girella nigricans* recruit to intertidal pools as small juveniles, and move to subtidal nearshore habitats as adults (Norris 1963, Feder et al. 1974). *Hermosilla azurea* are also abundant in intertidal pools as juveniles (Barry personal observation) and are restricted to shallow inshore waters (Feder et al. 1974). Both species, and to a lesser extent *Medialuna californiensis,* forage in monospecific or mixed schools over the intertidal reefs (DeMartini 1981, Barry 1988, personal observation).

Detailed studies of diets and prey preferences of these herbivores in southern California should indicate the potential for control of algal community structure by herbivory. Kyphosids are omnivorous, with varying degrees of herbivory (Quast 1968, Feder et al. 1974, Bray & Ebeling 1975, Hobson & Chess 1976, Laur & Ebeling 1983). However, even though algae were the dominant component of some species' diets, Quast (1968) and others (Mitchell 1953, Burge & Schultz 1973, Wheeler 1980) assumed that algae were consumed incidentally and were unimportant, relative to animal prey due to the apparent lack of cellulolytic enzymes or gut symbionts for cellulose digestion (Stickney & Shumway 1974). More recent studies have shown that two members of the Kyphosidae in the southern hemisphere (*Kyphosus cornelii* and *K. sydneyanus*) are capable of fermentive digestion of marine algae (Rimmer & Wiebe 1987). A third kyphosid from Australia *Girella tricuspidata,* is known to assimilate radioactive carbon from ^{14}C labelled protoplasts and cell walls of the green alga, *Enteromorpha* sp. (Anderson 1987). Owing to its taxonomic affinity and similar feeding modes, *G. nigricans* is likely to have similar physiological capabilities.

Several species of crabs also occur in intertidal and shallow subtidal habitats of California. The lined shore crab, *Pachygrapsus crassipes,* has important effects on the structure of high intertidal communities (Robles & Cubit 1981, Robles 1982, Shanks & Wright 1986), and potentially affects lower zones as well. The shore crab is common throughout temperate latitudes of the north Pacific and is most abundant near refuge crevices from the middle to upper intertidal (Morris et al. 1980). It is largely herbivorous (Bovbjerg 1946, Hiatt 1948, Sousa 1979), but will also take animal prey when available.

Preferences for particular species of macroalgae are little known for temperate herbivores, but are important in identifying the effects of herbivory on the structure of the algal communities. Opaleye are thought to graze preferentially the red alga, *Gigartina canaliculata,* in subtidal kelp beds near Santa Barbara, California, such that cover of *G. canaliculata* increases within fish exclusion cages (Foster 1975). *Pachygrapsus crassipes* has been shown to consume the chlorophyte, *Ulva,* preferentially over several other species of red and brown algae, and to increase the rate of succession in the algal community on intertidal boulders (Sousa 1979).

In this paper, we describe diets of two, dominant herbivorous fishes (*G. nigricans* and *Hermosilla azurea*) and the lined shore crab (*P. crassipes*) from intertidal habitats, and measure algal feeding preferences of these herbivores in multi-species algal choice experiments in the laboratory. Diet and algal preference of these species are compared to the cover of algae on intertidal reefs during winter and summer, as well as in early and late successional (disturbed and undisturbed, respectively) habitats.

Materials and methods

Study sites

Collections of fishes, shore crabs, and marine plants were made at three sites (Casa Pool, Bench Reef, and North Bird Rock) located on the moderate to highly exposed outer coast in La Jolla, California. The sites were characterized by friable sandstone headlands contiguous with gently sloping platform reefs from the mid-shore to the subtidal.

These reefs are nearly covered by many species of algae, the surf grasses *Phyllospadix* sp., and low densities of invertebrates. Upright coralline algae (mainly *Corallina pinnatifolia, C. vancouveriensis,* and *Lithothrix aspergillum*), *Gigartina canaliculata,* and *Pterocladia capillacea* are usually the dominant species on rocky substrata. This assemblage of epilithic algae, and particularly members of the Corallinaceae, provide a substratum (anchor species, sensu Stewart 1982) occupied by several common epiphytic species of seasonal or perennial algae. *Ulva* sp., *Enteromorpha* sp., *Binghamia forkii,* and other rapidly recruiting species are common on newly created bare space, particularly during spring and summer. The surfgrasses, *Phyllospadix* sp. are conspicuously dominant in the lower intertidal, but are restricted from shallower portions of intertidal reefs by desiccation (Stewart 1988, 1989, Barry 1988, unpublished data). Anchor species and epiphytes also are damaged by desiccation events when dry desert winds and warm temperatures coincide with extreme low tides that occur during afternoon hours from fall to spring (Emerson & Zedler 1978, Littler 1980, Gunnill 1985, Barry 1988).

Several carnivorous species of Embiotocidae, as well as the opaleye, zebraperch, and halfmoon, forage individually or in groups over intertidal reefs during high tide, and return to tidal pools or subtidal channels as the tide recedes. Juveniles of opaleye, zebraperch, and dwarf perch, *Micrometris minimus,* were the most abundant tide pool perciforms and adults were generally found in the subtidal (Barry 1988). *Medialuna,* though present in southern California, is less abundant in nearshore habitats than *Girella,* and was low in abundance or absent during surveys over these intertidal reefs (Barry 1988).

Food habit studies

We evaluated the relative importance of animal and plant material in the diets of three species of dominant fishes on intertidal reefs (*G. nigricans,* N = 86, *H. azurea,* N = 23, *M. minimus,* N = 5) and the shore crab (*P. crassipes,* N = 12). Intertidal fishes were collected by hand, dip net, and traps during low tides from pools treated with an anesthetic (quinaldine). Fifteen collections were made between January and August from 1984 to 1986. The lined shore crab was collected by hand during the same period. Specimens were placed in a 10% to 20% formalin solution immediately upon collection (within 1 minute), stored for 2 to 3 days, then rinsed in fresh water and transferred to 70% isopropyl alcohol until analyzed. A few individuals regurgitated part of their stomach contents when preserved. The bias, if any, resulting from regurgitation was not evaluated. However, because the parameter of interest was dietary breadth, rather than quantity or rate of food intake, partial regurgitation by a small portion of the fishes sampled should have little effect on the results of the study.

Handling of specimens

Individual fish were measured (standard length to 1 mm), weighed (to 0.1 g), and dissected. The total length of the digestive tract was measured (to 0.1 mm), and the contents of the cardiac and pyloric stomachs were identified to the lowest possible taxon. The percentage contribution of each prey type to the total volume content of the gut contents was estimated visually, with all items totalling 100%. For the shore crab, the carapace was measured (maximum width to 1 mm) and removed, and the contents of the cardiac stomach were treated as above.

Comparison of diets among herbivores

Food habits were summarized by calculating a mean percentage volume (± 1 SD) for each prey species (or lowest taxon possible) and for taxa lumped into higher groups (e.g. plant functional groups) over all individuals of each herbivore species. Plant functional groups (sheet-like, filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose) were defined by the morphology of plant thalli according to Littler & Littler (1980). Similarity between the diets of pairs of herbivore species were calculated using a percentage similarity index, PSI (Saunders 1960):

$$\mathrm{PSI} = \sum \min (A_i, B_i),$$

where A_i and B_i are the mean percentage contribution to each herbivore's diet by each alga i or functional group i for herbivore A and B, respectively. PSI ranges from 0.0 (no overlap in diet) to 1.0 (identical diets).

Feeding preference studies

Preferences by herbivores for marine plants were evaluated in laboratory aquaria using multi-species choice experiments. These tests were replicated for *G. nigricans* (n = 16) and *P. crassipes* (n = 14), using methods similar to Leighton (1966) and Horn et al. (1982). Preference tests were completed only once for *H. azurea*, for comparison of its algal preferences to *G. nigricans*. Animals were collected as above, transferred to large holding tanks (ca. 1.5 × 1.5 × 1 m), and held for 2 to 3 weeks. These fishes and crabs were fed a wide variety of marine algae and *Phyllospadix* sp. collected from intertidal habitats. Prior to laboratory feeding trials, animals were maintained in aquaria without food for 5 to 7 days. Pre-weighed, similar-sized portions (ca. 3 g) of many (20–55) species of algae (and *Phyllospadix* sp.) were placed in a polyethylene tub (25 × 33 × 15 cm, 12.3 l) filled with fresh, filtered sea water at ambient temperature (10–13° C). The initial weight (to 0.01 g) of each alga was obtained after it was spun for approximately 15 seconds in a salad spinner to remove excess water. This procedure was repeated until the difference between sequential weights was less than or equal to 0.05 g. Two large fish (> 100 mm standard length) or 4 to 6 smaller fish or crabs were placed in a mesh-covered tub with an air stone to circulate and aerate the water. One to three tubs with fish or crabs, and a control tub with algae, but no herbivores, were placed in an undisturbed room with a 12 : 12 h light : dark schedule. Room temperature was maintained between 10 to 13° C. After 24 hours the herbivores were removed and the algae were sorted and reweighed. Owing to changes in availability of algae at the study sites, the number of algal species used varied between experimental trials.

For each trial, a corrected daily ingestion rate for each species of algae was calculated as its average percentage weight loss in tubs with herbivores minus its average percentage weight loss in control aquaria (presumed to be respiratory losses). Corrected ingestion rates for each algal species were summed in groups by plant functional morphology, and divided by the number of species within the group during the run as an index of the average percentage ingestion rate for species within each functional group. Thus, differences between the ingestion rates among functional groups of algae were not biased by differences in the number of plant species within a functional group, and represented the mean percentage ingested per day per species within the group. Corrected ingestion rates for each species within the group and the functional group as a whole were averaged over all experimental trials for each species of herbivore. Because the abundance of marine plants were nearly equal (by weight) during each trial, comparison of ingestion rates among species or functional groups of algae were indicative of relative preferences for algae by herbivores.

Selection or avoidance of algal functional groups by herbivores was also measured using an index of electivity, E (Ivlev 1961):

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i is the ingestion rate of functional group i, as a percentage of the total of all algae ingested during each feeding choice trial, and p_i is the percentage of the total algae presented belonging to functional group i. Electivity indices for each functional group were averaged over all feeding trials for each herbivore. E ranges from $+1.0$ to -1.0. If $E > 0.0$, the food item was consumed in greater proportion than its availability (positively selected) during experimental trials. If $E < 0.0$, the food item was avoided relative to its availability.

Algal cover in intertidal plots

To assess selection by herbivores for particular species or groups of macroalgae in the field, the cover of algae on intertidal reefs was estimated in permanently marked 0.15×0.15 m plots in the low intertidal near the sites where herbivores were collected. The cover of each species of algae was assumed to represent its availability to herbivores. Because herbivores may select foraging areas by general characteristics (e.g. algal assemblage), we assessed the availability of algae within patch types of early or late successional stages. Algal cover was measured during winter (January – March 1985) and summer (June – July 1986) in 'undisturbed' control plots with a late successional algal assemblage ($N = 17$ plots in winter, $N = 13$ plots in summer), and in 'disturbed' plots containing early successional algae ($N = 9$ plots in winter and summer). Disturbed plots sampled during winter 1985 had been scraped to bare rock in June 1984. Plots sampled in summer 1986 had been scraped during January 1986.

Cover of each species of algae in intertidal plots was calculated as the percentage of 100 points uniformly distributed in each plot under which the species was present. These measurements were made directly from field observations (winter data) or from photographs supplemented by field notes (summer data). Data for percentage cover were compiled by species and by algal functional group as in the food habits studies.

Overlap between the cover of algae in intertidal habitats and the diets or preferences for algae of herbivores was measured using the percentage similarity index (described above). Chi-square tests were used to assess whether feeding patterns (diets and preferences for algae) of herbivores were more similar to algal cover during winter versus summer, and in disturbed versus undisturbed plots.

Positive and negative selection for particular functional groups of algae was evaluated using Ivlev's (1961) electivity index (above), by comparing diets and preferences for algae of herbivores to the percentage cover of algae in intertidal plots.

Results

Food habit analyses

Algae were the major food group for field-collected opaleye, *G. nigricans*, zebraperch, *H. azurea*, and lined shore crab, *Pachygrapsus crassipes* (Ta-

Table 1. Summary of diet analyses for 3 intertidal herbivores. Values are means and standard deviations over all samples for *Girella nigricans* (N = 86), *Hermosilla azurea* (N = 23), and *Pachygrapsus crassipes* (N = 12).

Functional group	Division	Prey species	*Girella nigricans*		*Hermosilla azurea*		*Pachygrapsus crassipes*	
			Mean	STD	Mean	STD	Mean	STD
f	r	*Acrochaetium* sp.	0.02	0.17				
b	r	*Binghamia forkii*	3.65	5.91	19.97	19.75	2.30	4.13
b	g	*Bryopsis* sp.	0.04	0.30				
f	r	*Centroceras* sp.	2.34	7.18	0.61	2.66	3.40	4.04
f	g	*Chaetomorpha* sp.	2.08	4.48	0.61	2.66	0.47	1.56
f	c	*Cladophora* sp.					0.41	0.96
s	b	*Colpomenia sinuosa*	0.17	1.61				
j	r	*Corallina* sp.	2.18	6.64			23.07	12.48
s	r	Delesseriaceae	17.24	22.95	0.10	0.44		
s	g	*Enteromorpha* sp.	6.12	14.55	52.52	34.69	21.70	18.81
f	r	*Erythrotrichia* sp.	0.04	0.28				
b	r	Gelidaceae	1.13	7.59				
b	r	*Gigartina canaliculata*	1.44	5.74			16.45	14.61
s	r	*Helminthora stricta*	0.04	0.26				
f	r	*Herposiphonia* sp.	0.43	1.90				
f	r	*Heterosiphonia* sp.	3.82	12.78				
b	r	*Hypnea johnstonii*	0.02	0.21			2.26	5.62
b	r	*Hypnea valentiae*	0.46	3.63				
j	r	*Jania crassa*					1.10	1.70
b	r	*Laurencia* sp.	0.31	1.77	0.10	0.44		
j	r	*Lithothrix aspergillum*					15.07	11.40
s	r	*Myriogramme* sp.			3.71	5.76		
s	r	*Nienburgia andersoniana*	1.22	10.72				
l	s	*Phyllospadix* sp.	0.88	4.15	0.15	0.48		
b	r	*Plocamium cartilagineum*	0.49	3.58				
f	r	*Polysiphonia* sp.	17.35	24.85	0.99	2.90	3.46	4.31
b	r	*Pterocladia capillacaea*					1.32	5.31
s	r	*Rhodymenia* sp.	0.41	3.20				
l	b	*Sargussum* sp.	0.26	2.41				
f	b	*Scytosiphon* sp.					1.07	1.86
f	r	*Tiffaniella snyderiae*	0.57	2.74				
s	g	*Ulva* sp.	24.04	24.91	18.61	18.20	1.27	2.43
		Hydroida	0.75	2.75				
		Ectoprocta	0.02	0.21				
		Cirripedia	0.09	0.81				
		Polychaeta	0.01	0.12			1.92	4.29
		Gammaridea	11.79	25.20	0.25	1.09	1.62	3.31
		Isopoda			1.00	3.00		
		Mollusca	0.39	2.26	0.05	0.22		
		Plant division						
		Chlorophyta (g)	32.28	33.35	72.70	22.04	26.24	21.29
		Phaeophyta (b)	0.17	1.61	0.00	0.00	1.12	1.94
		Rhodophyta (r)	53.17	34.45	27.14	22.03	72.64	22.24
		Spermatophyta (s)	1.15	4.75	0.16	0.50	0.00	0.00
		Chrysophyta (d)	0.00	0.00	0.00	0.00	0.00	0.00
		Plant functional group						
		Sheet-like (s)	49.25	33.80	75.95	20.99	25.25	19.95
		Filamentous (f)	26.65	27.67	2.21	8.00	9.47	8.92
		Coarsely Branched (b)	8.43	13.65	21.83	19.30	22.87	14.60
		Thick Leathery (l)	0.26	2.41	0.00	0.00	0.00	0.00
		Jointed Calcareous (j)	2.18	6.64	0.00	0.00	42.41	17.13
		Crustose (c)	0.00	0.00	0.00	0.00	0.00	0.00

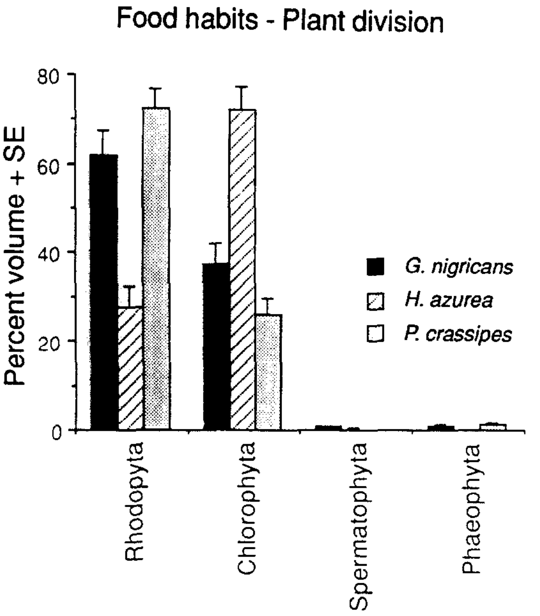

Fig. 1. Mean percentage contribution by plant division to the total plant content of the diet for three intertidal herbivores, *Girella nigricans, Hermosilla azurea,* and *Pachygrapsus crassipes.* SE = standard error.

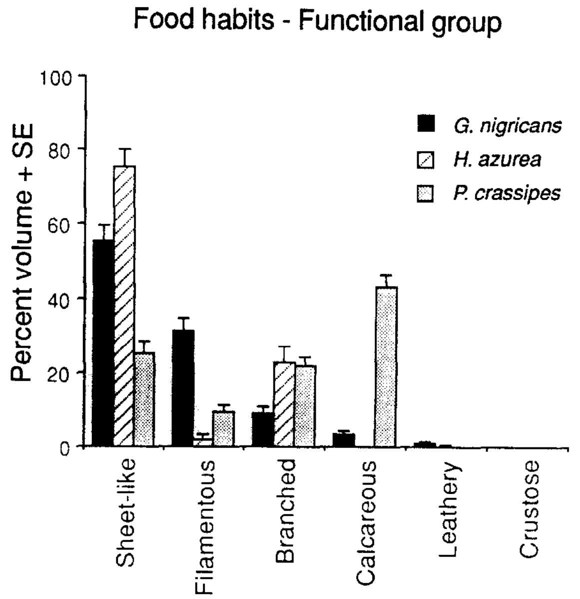

Fig. 2. Mean percentage contribution by plant functional morphological group to the total plant content of the diet for three intertidal herbivores. Note the high importance of jointed calcareous algae to the diet of *Pachygrapsus crassipes,* relative to the fishes. Branched = coarsely branched, calcareous = jointed calcareous. SE = standard error.

ble 1). Animal prey, except for amphipods in the diet of small *G. nigricans* and *H. azurea,* were minor elements of the diets. In contrast, all *M. minimus* examined fed exclusively on small gammarid amphipods.

Girella nigricans (N = 86) had the most diverse diet, which included more than 30 taxa (26 + species of algae). Plant material comprised more than 85% of its diet by volume. Gammarid amphipods were second in volumetric importance to plants, with a mean volume of 14%. The diets of *H. azurea* (N = 23) and *P. crassipes* (N = 12) were somewhat less diverse, perhaps related to smaller sample size. Comparisons of the change in either the diversity of the diet or the mean percentage contribution by prey types (evenness) with increasing sample size showed that prey diversity stabilized after examining ca. 35 individuals, whereas evenness stabilized after only 15 to 20 individuals. Thus, the sample size for all herbivore species was adequate to identify the major food types and indicate the relative importance of plant versus animal material in the diets of *H. azurea* and *P. crassipes,* but were marginal or inadequate to identify the total dietary breadth of these herbivores. Thirteen taxa, including 10 plant species, were identified from the stomachs of *H. azurea.* Animal material, consisting mainly of isopods and gammarid amphipods, comprised only 1.5% of the diet. *P. crassipes* also fed primarily on plant material, with 14 species of algae accounting for 96% of the volume of the identifiable contents of the gut. The remaining 4% was polychaeta and small crustacea. For most *P. crassipes,* however, a large percentage of the gut contents was unidentifiable (mean = 43.5%).

A few species of algae were important to all three herbivores, including *Enteromorpha* sp., polysiphonous members of the Ceramiales (e.g. *Polysiphonia* sp.), *Ulva* sp., and *Binghamia forkii.* On a higher taxonomic level, Rhodophyta and Chlorophyta accounted for the greatest percentage volume among algal divisions for all three species (Fig. 1). Phaeophyta and the spermatophytes, *Phyllospadix* sp., were rare and relatively unimportant.

Plant morphology was also clearly important. The fishes fed primarily on sheet-like algae and to a

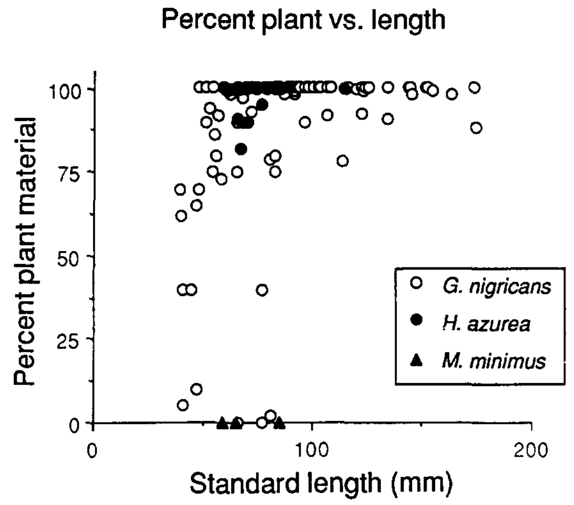

Fig. 3. Percentage plant material of the total stomach contents versus standard length. Each point represents one individual. For *Girella nigricans* and *Hermosilla azurea*, animal material is more important in the diets of small individuals. *Micrometris minimus* did not feed on plant material.

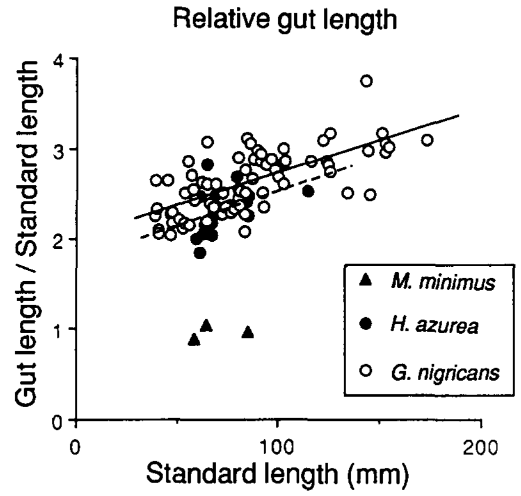

Fig. 4. Relative gut length versus standard length. Relative gut length is the ratio of total gut length (mm) over the standard length (mm) of the fish. Solid line indicates linear regression line for *Girella nigricans* ($r = 0.68$, $p < 0.01$). Dashed line is the regression line for *Hermosilla azurea* ($r = 0.41$, $p < 0.05$). Note the high ratio for *G. nigricans* and *H. azurea* compared to *Micrometris minimus*, and the increase in the ratio with increased length.

lesser extent on filamentous and coarsely branched fleshy algae (Fig. 2). In contrast, the lined shore crab, in addition to consuming sheet-like and branched algae, fed heavily on jointed calcareous algae, mainly the genera *Lithothrix* and *Corallina* (Table 1, Fig. 2). However, even though upright coralline algae accounted for the greatest volume of the identifiable prey items in the diet of *P. crassipes*, the actual importance of other algal and animal prey may be underrepresented in our analyses, owing to several factors, including the high proportional volume of unidentifiable material in the guts (mean = 43.5%), and relative ease of identification of coralline algae, compared to other species.

Greater size and proportional length of gut were accompanied by an increase in percentage volume of plant material in the diet of *G. nigricans* and to some extent of *H. azurea* (Fig. 3, 4), and may be related to ontogenetic changes in these species' ability to digest plant material (Montgomery 1977). Small opaleye and zebraperch with relatively shorter guts fed partially or primarily on animal prey (60–95% by volume for the smallest juveniles), whereas most individuals greater than 80 mm fed exclusively on plant material.

Herbivore morphology

The length of the digestive tract varied between fish species and between size classes within a species, and was related to changes in the percentage contribution of plant material in the diet. Gut length was greatest in herbivorous species and similar to values for other kyphosids that digest algae (Horn 1989). The ratio of digestive tract length to standard length (relative gut length) was 2 to 4 for *H. azurea* and *G. nigricans*, compared to near 1.0 for the dwarf perch (Fig. 4). Relative gut length increased with standard length for opaleye ($r = 0.68$, $p < 0.01$) and zebraperch ($r = 0.41$, $p < 0.05$).

Comparison of diets among herbivores

Similarity indices (PSI) comparing overlap between pairs of the three herbivores' diets, were greater between *G. nigricans* and *H. azurea* (0.38) than between either fish species and the shore crab (mean = 0.28). PSI indices based on dietary species were lower than those calculated for plant functional groups (Table 2). The importance of jointed calcareous algae in the diet of *P. crassipes* is reflected in the lower overlap between the crab and fishes (mean = 0.48), compared to the dietary overlap between fish species (0.67), which consumed primarily sheet-like green algae.

Feeding preference studies

Feeding experiments in laboratory aquaria using *G. nigricans* (N = 16), *P. crassipes* (N = 14), and *H. azurea* (N = 1) indicated that each species strongly preferred (or avoided) particular species or groups of marine plants. Several species of algae (*Enteromorpha* sp., *Binghamia forkii, Ulva* sp., *Scytosiphon* sp., and others) were preferred by these herbivores (Table 3). Six of the top 10 species ingested by *G. nigricans* during experiments also were in the top 10 ranking species in the fishes' natural diets. Three and 4 of the most highly selected algae in feeding experiments also ranked high in the diets of *H. azurea* and *P. crassipes,* respectively. The most striking difference between the fish species and *P. crassipes* was the markedly higher ingestion rate of Corallinaceae (*Lithothrix* and *Corallina*) by *P. crassipes.* Coralline algae were avoided by the fishes.

Comparisons of ingestion rates of algae by functional group indicated that filamentous Rhodophyta and sheet-like Chlorophyta were positively selected by *G. nigricans,* and *H. azurea* (Table 3, Fig. 5). Branched algae, primarily from the Rhodophyta, were slightly less preferred by the two fish species and jointed calcareous or thick leathery algae were the lowest ranked. Although *P. crassipes* also favored sheet-like algae (mainly *Enteromorpha* and *Ulva*), it exhibited a high selectivity for jointed calcareous algae (e.g. *Lithothrix aspergillum* and others and, unlike *G. nigricans, P. crassipes* tended to prefer Phaeophyta (*Scytosiphon* sp., *Petalonia*/*Endarachne*) over Rhodophyta. *Phyllospadix* sp., the only intertidal spermatophytes available at the study sites, were the least ingested species during laboratory experiments.

Most algae in control trials with no herbivores lost little or no weight during the 24 hour experimental period (mean weight loss = 2.3%, SD = 3.2, N = 13 control trials). Two species that ranked high by ingestion rates among herbivores, however, lost a large percentage of their initial weights, even in the absence of herbivores. *Chondria californica* and *Binghamia forkii* lost an average of 14.6% (SD = 10.9, N = 3) and 9.5%, SD = 10.3, N = 7), per trial.

Overlap, measured as PSI, between the average ingestion rates of algae exhibited by these herbivores in laboratory experiments, was generally greater than the overlap among their diets determined from field-collected animals (compare Table 4 and 2, respectively). Because all three herbivores favored green algae (Fig. 5), mainly the sheet-like *Enteromorpha* and *Ulva,* and filamentous polysiphonous Ceramiales such as *Polysiphonia* sp., *Centroceras* sp., and *Ceramium* sp., overlap among algal preferences was fairly high. At the level of algal species, mean overlap for preference values among the herbivores was 0.49. In comparison, the mean overlap among the herbivores' natural diets was 0.31. This lower overlap may be related to different availability of algae to herbivores in experimental trials and in intertidal habitats; if all herbivores prefer similar algae and the most preferred algae are abundant, as in laboratory trials, the diets would be expected to converge. Conversely, diets should become more diverse when preferred foods are scarce. The average PSI for algal preference by functional group (mean = 0.61) was also slightly higher than that for comparisons of herbivore diets (mean = 0.54). Even though the sample size was one for *H. azurea,* the

Table 2. Summary of dietary overlap between herbivores in the field. Comparisons are based on the percent similarity index (PSI). Species comparisons are the PSI calculated from the dietary mean percent volume for each species. Functional group comparisons were calculated from the mean percent volume from within each of those categories, respectively.

Comparison	Species	Functional group
G. nigricans × *H. azurea*	0.38	0.67
G. nigricans × *P. crassipes*	0.24	0.47
H. azurea × *P. crassipes*	0.33	0.49

Table 3. Summary of plant feeding preferences for *H. azurea*, *G. nigricans*, and *P. crassipes*. Species data are mean percent weight lost per experiment per day. Functional group and plant division data represent the mean percent weight lost per run per species presented to the herbivore. Functional group refers to plant morphology; f = filamentous, b = coarsely branched, s = sheet-like, j = jointed calcareous, l = thick leathery. Division refers to plant division; r = Rhodophyta, g = Chlorophyta, b = Phaeophyta, s = Spermatophyta.

Functional group	Division	Plant species	*H. azurea* Percent loss	*G. nigricans*			*P. crassipes*		
				N	Mean % loss	STD	N	Mean % loss	STD
s	r	*Acrosorium uncinatum*		8	28.87	35.14			
b	r	*Binghamia forkii*	76.70	10	28.70	29.36	10	16.25	18.50
f	r	*Centroceras clavulatum*	22.12	12	33.42	27.17	11	10.07	15.38
f	g	*Chaetomorpha spiralis*		4	0.99	2.38	3	24.59	20.86
b	r	*Champia parvula*		2	52.35	15.06			
f	r	*Chondria californica*	21.87	12	20.08	26.48	9	19.82	23.32
l	g	*Codium fragile*	3.66	9	3.60	5.81	14	8.23	16.33
b	r	*Coelosiera compressa*		2	15.90	9.05			
s	b	*Colpomenia sinuosa*	8.90	14	13.05	11.01	10	3.18	5.39
j	r	*Corallina pinnatifolia*	3.17	3	3.92	5.25			
j	r	*Corallina vancouveriensis*	– 1.14	15	1.01	4.31	14	40.24	19.91
s	r	*Cryptopleura crispa*	16.34	11	38.92	36.30	8	3.88	4.54
s	b	*Dictyopteris undulata*	14.15	11	8.80	12.31	13	9.55	14.14
s	b	*Egregia menziesii*	2.80	8	11.33	6.93	10	9.52	10.07
b	r	*Endocladia muricata*	6.10	9	3.16	4.06	8	3.44	5.55
s	g	*Enteromorpha* sp.	68.80	15	79.73	25.92	8	62.28	10.41
b	r	*Gastroclonium coulteri*	19.70	11	10.02	24.54	10	2.02	2.41
b	r	*Gelidium coulteri*	0.80	13	9.55	19.11	10	5.97	15.65
b	r	*Gelidium purpurascens*		8	1.51	4.48	10	– 0.03	1.49
b	r	*Gigartina canaliculata*	17.21	13	6.00	5.91	14	0.89	5.76
b	r	*Gymnogongrus leptophyllus*		3	5.78	9.1			
b	r	*Haplogloia andersonii*		3	10.40	7.73			
b	r	*Hypnea johnstonii*	15.80	8	13.10	16.62	10	1.08	2.99
b	r	*Hypnea valentiae*	38.60	11	31.60	29.07	10	10.85	3.45
j	r	*Jania crassa*	0.51	3	4.21	17.85	13	20.50	19.60
j	r	*Jania tenella*	– 5.80	8	17.38	18.60	1	36.03	
b	r	*Laurencia lajolla*	3.60	10	0.93	2.83	14	4.89	5.59
b	r	*Laurencia pacifica*	1.85	13	8.66	13.83	10	– 0.90	2.68
b	r	*Laurencia spectabilis*	4.30	8	– 0.61	2.18	6	– 0.33	1.16
b	r	*Laurencia subopposita*	7.10	5	– 0.17	0.85	5	4.88	3.86
j	r	*Lithothrix aspergillum*	– 1.65	9	2.10	12.75	12	72.00	25.11
b	b	*Nemalion helminthoides*		4	– 1.24	0.93	3	4.23	1.44
s	r	*Nienburgia andersoniana*	25.30	5	9.78	8.75	4	4.01	5.05
s	b	*Pachydictyon coriaceum*	6.25	14	9.97	11.51	14	8.32	10.20
l	b	*Pelvetiopsis limitata*	2.40	12	5.10	7.22	10	9.21	7.07
s	b	*Petalonia/Endarachne*	12.50	13	8.32	10.11	14	36.53	28.84
l	s	*Phyllospadix* sp.	– 1.35	13	3.20	6.96	13	4.42	5.77
b	r	*Plocamium cartilagineum*	2.60	16	2.49	10.74	13	4.16	10.92
f	r	Polysiphonous Filamentous Turf		15	34.23	24.78	7	16.60	11.25
b	r	*Prionitis* sp.		4	4.91	8.36			
b	r	*Pterocladia capillacea*	– 3.86	14	3.44	14.88	13	2.96	8.64
s	b	*Rhodoglossum affine*		6	2.05	2.35	11	2.46	8.11
s	r	*Rhodymenia californica*	20.86	8	8.28	7.85	9	5.10	7.13
s	r	*Rhodymenia* sp.	2.96	4	0.54	1.29	5	2.09	7.80
l	b	*Sargassum agardhianum*		5	4.01	1.44	9	2.62	2.76

Table 3. Continued

Functional group	Division	Plant species	*H. azurea* Percent loss	*G. nigricans* N	Mean % loss	STD	*P. crassipes* N	Mean % loss	STD
l	b	*Sargussum muticum*	3.75	13	7.07	10.12	10	4.14	3.95
f	b	*Scytosiphon dotyi*	22.74	13	16.81	28.23	3	55.08	21.70
s	b	*Scytosiphon lomentaria*	16.84	7	27.64	34.66	14	38.23	26.41
l	g	*Ulva* sp.	− 3.24	13	29.02	28.13	14	29.89	12.84
l	b	*Zonaria farlowii*		5	6.43	7.37			
		Plant division							
		Chlorophyta	22.81	16	46.29	30.31	14	19.31	19.90
		Phaeophyta	10.00	16	10.47	9.25	14	10.82	12.51
		Rhodophyta	12.55	16	13.53	10.55	14	6.85	9.36
		Spermatophyta	− 1.35	13	2.57	6.42	14	4.42	4.58
		Plant functional group							
		Sheet-like	16.16	16	24.14	11.35	14	11.86	13.80
		Filamentous	19.25	16	29.31	20.27	14	11.13	14.83
		Coarsely branched	15.34	16	10.57	7.95	14	2.53	5.24
		Thick leathery	2.02	16	5.66	7.20	14	4.22	4.00
		Jointed calcareous	− 0.95	16	4.13	8.19	14	30.48	31.39

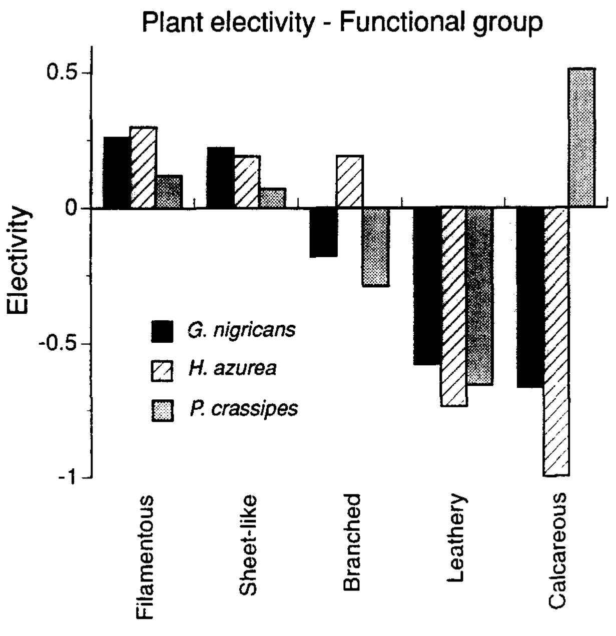

Fig. 5. Summary of herbivore electivity indices by algal functional group. Bars represent the mean (1 standard error) percentage weight loss of each algal group over all experimental runs in which the group was included, corrected by the mean percentage weight loss (or gain) of control algae. The total number of preference runs were 16, 1, and 14, for *G. nigricans*, *H. azurea*, and *Pachygrapsus crassipes*, respectively.

two fishes had quite similar preferences (0.54 by species, 0.85 by functional group). Overlap values for laboratory ingestion rates between the fishes and *P. crassipes* were lower (mean = 0.46 by species, 0.50 by functional group), than among the fishes, again due primarily to the crab's preference for jointed calcareous algae.

Algal availability

The cover of marine plants in intertidal plots varied

Table 4. Summary of algal preference overlap between herbivores in the laboratory. Comparisons are based on the percent similarity index (PSI). Species comparisons are the PSI calculated from the percent weight lost per species per day (adjusted to 100 percent total for all species) from the algal preference experiments. Functional group comparisons were calculated from the mean percent weight lost (adjusted to total 100%) from within each of those categories, respectively.

Comparison	Species	Functional group
G. nigricans × *H. azurea*	0.54	0.85
G. nigricans × *P. crassipes*	0.52	0.55
H. azurea × *P. crassipes*	0.40	0.44

Table 5. Algal abundance on disturbed and undisturbed intertidal plots during winter and summer. These data represent the mean percentage cover of each species in 15 by 15 cm square plots. Disturbed plots were scraped to bare rock 6 to 9 months prior to sampling. Symbols as per Table 3, d = Chrysophyta, c = Crustose algae.

Functional group	Division	Species	Winter		Summer	
			Disturbed	Undisturbed	Disturbed	Undisturbed
s	r	*Acrosorium uncinatum*		0.09		
f	d	*Berkeleya palmiformis*				0.18
b	r	*Binghamia forkii*	11.04	2.26	3.44	9.94
j	r	*Calliarthron cheilosporioides*				0.09
f	r	*Centroceras clavulatum*		6.79	14.54	23.67
b	r	*Champia parvula*			0.88	0.81
f	r	*Chondria californica*	0.42	0.09		
s	b	*Colpomenia sinuosa*	1.67	1.72	25.34	5.60
j	r	*Corallina pinnatifolia*	5.00	23.17	7.17	24.93
j	r	*Corallina vancouveriensis*	1.67	10.50		0.54
c	r	Crustose Corallinaeceae			2.26	0.18
s	r	*Cryptopleura crispa*				0.18
s	g	*Enteromorpha* sp.	0.83	2.35	5.70	0.72
b	r	*Gelidium coulteri*	0.21	1.36		
b	r	*Gigartina canaliculata*		1.90	1.38	1.26
b	r	*Hypnea johnstonii*		0.63		
b	r	*Hypnea valentiae*			2.85	2.62
j	r	*Jania crassa*	0.21	5.34		0.18
j	r	*Jania tenella*	3.33	3.35		0.18
b	r	*Laurencia lajolla*	6.88	7.06	10.61	15.00
b	r	*Laurencia pacifica*	0.83	0.18		0.18
j	r	*Lithothrix aspergillum*	8.96	8.87	4.62	4.34
l	s	*Phyllospadix* sp.		1.09		
f	r	Polysiphonous filamentous turf	26.00	10.90	4.91	0.18
b	r	*Pterocladia capillacea*		6.52		5.78
l	b	*Sargussum muticum*	16.04	0.54		
b	b	*Scytosiphon dotyi*	2.50	0.09		
f	b	*Scytosiphon lomentaria*			0.79	
s	g	*Ulva* spp.	0.83	2.90	15.52	3.43
		Plant division				
		Chlorophyta	1.67	5.25	21.22	4.16
		Phaeophyta	21.04	2.44	26.13	5.60
		Rhodophyta	71.88	90.95	52.65	90.06
		Spermatophyta	0.00	1.09	0.00	0.00
		Chrysophyta	0.00	0.00	0.00	0.18
		Plant functional group				
		Coarsely branched	19.71	21.78	19.16	35.59
		Filamentous	34.59	17.97	20.24	24.00
		Jointed calcareous	22.64	52.18	11.79	30.26
		Thick leathery	16.14	0.54	0.00	0.00
		Sheet-like	3.35	7.08	46.56	9.94
		Crustose	0.00	0.00	2.26	0.18
		Number of plots sampled	9	17	7	17

between seasons (winter, summer) and between plots with early and late successional status (disturbed and undisturbed plots, respectively; Table 5). Red algae were consistently the dominant plant division in plots. Jointed calcareous algae, mainly *Corallina* sp., had the greatest cover in late successional plots (52.6% cover) with significantly greater cover than in early successional plots (19.2%, MANOVA, $F = 21.7$, $p < 0.001$). Jointed calcareous algae were also more abundant during winter (52.5%) than summer (25.3%, MANOVA, $F = 11.1$, $p < 0.01$), perhaps related to the decrease in other more seasonal algae. Several ephemeral species of algae, such as the sheet-like green algae *Enteromorpha* sp. and *Ulva* sp., the brown alga *Colpomenia sinuosa,* and the filamentous red alga *Centroceras* sp., increased significantly from winter (7.2%) to summer (24.1%, MANOVA, $F = 27.8$, $p < 0.001$). These species were also more abundant in disturbed (24.7%) than undisturbed (9.1%) plots (MANOVA, $F = 15.3$, $p < 0.001$).

Variation in abundance of algae between seasons and the successional status of the algal assemblage may each influence foraging patterns of local herbivores. Gut contents and experimentally-determined preferences for algae of opaleye and zebraperch generally were most similar to the algal assemblage present during summer, and still more similar when compared to disturbed plots (Table 6, 7). Comparisons between the similarity of gut contents or algal preferences of fishes and the cover of algae in intertidal plots suggested greater similarity to the algal assemblage on disturbed plots more frequently than to undisturbed plots ($\chi^2 = 4.66$, $p < 0.05$). Similar comparisons indicated that diets and preferences for algae by fishes were more like the algal assemblage during summer than winter ($\chi^2 = 4.66$, $p < 0.05$). Thus, even though the majority of fish used for food habit studies were collected during winter, their diets and feeding rates on algae in the laboratory were more similar to the algal assemblage present in the intertidal during summer, owing to selective feeding on seasonal algae.

Pachygrapsus crassipes' diet differed from this pattern and showed only slight differences in similarity between either disturbed and undisturbed plots or summer versus winter comparisons (Table 6, 7). *Pachygrapsus crassipes'* algal preferences and its diet were somewhat more similar to the late successional algal assemblage (undisturbed plots) found in winter where upright Corallinaceae were most abundant. *Ulva* sp. and other sheet-like ephemeral algae, which increase in early successional intertidal plots during summer, also were

Table 6. Similarity between herbivore gut contents and the abundance of algae in disturbed and undisturbed plots during winter and summer. Values are PSI indices for comparisons within species or functional group. Higher indices indicate a greater similarity between herbivore gut contents and algal abundance. Sp. and FG. indicate species and functional group comparisons.

Comparison	Disturbed		Undisturbed	
	Sp.	FG.	Sp.	FG.
Winter				
Girella nigricans	0.34	0.48	0.20	0.30
Hermosilla azurea	0.15	0.28	0.13	0.32
Pachygrapsus crassipes	0.25	0.55	0.52	0.82
Summer				
Girella nigricans	0.29	0.76	0.17	0.44
Hermosilla azurea	0.28	0.71	0.41	0.34
Pachygrapsus crassipes	0.39	0.69	0.43	0.70

Table 7. Similarity between algal preferences of herbivores and the abundance of algae in disturbed and undisturbed plots during winter and summer. Values are PSI indices for comparisons within species or functional group. Higher indices indicate a greater similarity between herbivore algal preferences and algal abundance. Sp. and FG. indicate species and functional group comparisons.

Comparison	Disturbed		Undisturbed	
	Sp.	FG.	Sp.	FG.
Winter				
Girella nigricans	0.18	0.65	0.27	0.39
Hermosilla azurea	0.19	0.62	0.15	0.40
Pachygrapsus crassipes	0.28	0.53	0.39	0.74
Summer				
Girella nigricans	0.32	0.65	0.23	0.51
Hermosilla azurea	0.23	0.59	0.39	0.58
Pachygrapsus crassipes	0.33	0.53	0.24	0.62

Table 8. Algal electivity summary. This is a summary table of electivity indices (E) for comparisons of algal dietary percent volume versus algal cover in disturbed and undisturbed plots during winter and summer. Positive electivity indicates a high selection for that group. Negative electivity indicates avoidance, or utilization of the group (dietary percent) less than its natural abundance. GN = *G. nigricans*, HA = *H. azurea*, PC = *P. crassipes*.

Comparison	Winter						Summer					
	Disturbed			Undisturbed			Disturbed			Undisturbed		
	GN	HA	PC	GN	HA	PC	GN	HA	PC	GN	HA	PC
Functional group												
Sheet-like	0.88	0.91	0.75	0.75	0.81	0.52	0.04	-0.19	-0.35	0.72	0.78	0.47
Filamentous	-0.04	-0.90	-0.55	0.55	-0.66	0.04	0.43	-0.75	-0.13	0.17	-0.85	-0.40
Coarsely branched	-0.43	0.01	0.02	-0.44	-0.02	-0.03	-0.32	0.12	0.11	-0.62	-0.26	-0.27
Jointed calcareous	-0.73	-1	0.37	-0.90	-1	-0.14	-0.68	-1	0.46	-0.81	-1	0.19
Thick leathery	-0.89	-0.98	-1	-0.30	-0.84	-1	1	1	-	0.68	-0.07	-1
Crustose	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1

preferred by *P. crassipes* and resulted in higher overlap of gut contents and algal preference with the cover of algae in disturbed plots during summer.

Electivity indices (E), calculated from comparisons of herbivore diets with algal abundance in intertidal plots, indicated a high electivity by all three herbivores for sheet-like green algae (Table 8). Positive and negative electivity values indicate that algae were present in the diet in greater and lesser proportions, respectively, than they were available in the intertidal. Jointed calcareous algae were strongly avoided by fishes, but were positively selected by *P. crassipes*. Filamentous algae, mainly *Polysiphonia* sp., were fed upon by *G. nigricans*, resulting in their higher electivity, but were not as large a component of *H. azurea*'s diet, causing a negative electivity. Crustose algae were not present in the diets of any of the herbivores, but were available in intertidal plots, producing the electivity indices of -1. A similar pattern of electivity was evident from calculations of electivity based upon herbivore algal preferences determined in laboratory trials and the cover of algae in intertidal plots (Table 9). All three herbivores generally selected sheet-like algae and filamentous algae, while

Table 9. Algal electivity summary. This is a summary table of electivity indices (E) for comparisons of herbivore's preferences for algae, based on laboratory trials, versus algal cover in disturbed and undisturbed plots during winter and summer. Positive electivity indicates a high selection for that group. Negative electivity indicates avoidance, or utilization of the group (dietary percent) less than its natural abundance. GN = *G. nigricans*, HA = *H. azurea*, PC = *P. crassipes*.

Comparison	Winter						Summer					
	Disturbed			Undisturbed			Disturbed			Undisturbed		
	GN	HA	PC	GN	HA	PC	GN	HA	PC	GN	HA	PC
Functional group												
Sheet-like	0.81	0.79	0.70	0.61	0.59	0.42	-0.22	-0.25	-0.45	0.56	0.54	0.37
Filamentous	0.08	0.04	-0.29	0.63	0.60	0.35	0.52	0.49	0.19	0.28	0.24	-0.09
Coarsely branched	-0.23	0.11	-0.69	-0.24	0.11	-0.69	-0.10	0.25	-0.62	-0.46	-0.14	-0.80
Jointed calcareous	-0.56	-1	0.43	-0.82	-1	-0.06	-0.49	-1	0.52	-0.68	-1	0.26
Thick leathery	-0.37	-0.63	-0.41	0.62	0.36	0.59	1	1	1	0.95	0.87	0.95
Crustose	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1

the fishes avoided calcareous or leathery algae. The shore crab preferentially selected jointed calcareous algae.

Discussion

Composition of herbivore diets

Our results corroborate other studies that describe *G. nigricans* and *H. azurea* as principally herbivorous, and does not support the hypothesis that algae are incidental or accidental components of their diets. Both species rely primarily, and often exclusively, on algae for food. Moreover, both have gut lengths and ontogenies typical of algivorous species (see Horn 1989). Even though Quast (1968) and others postulated that algae were taken incidentally with animal prey by kyphosids and girellids, his own data, as well as those from this study and others (Mitchell 1953, Williams & Williams 1955, Sousa 1979, DeMartini & Coyer 1981, Robles 1987) demonstrate the overwhelming importance of algae in the diets of *G. nigricans* and *H. azurea*. Similarly, congeners from other temperate areas (*G. elevata*, New South Wales, Bell et al. 1980, *G. punctata*, Japan, Saburomaru & Tsukahara 1984) also are primarily algivorous. Moreover, recent studies have demonstrated the physiological capabilities of closely related kyphosids to digest and assimilate algae (Anderson 1987, Rimmer & Wiebe 1987).

Herbivorous fishes often undergo ontogenetic changes in the morphology of the digestive tract (as do some carnivorous species), frequently with an increase in proportional length of the intestine with increasing body size or age (Barrington 1957, Montgomery 1977, Barton 1982, Gibson 1982). This increase in relative gut length is usually associated with a dietary shift from carnivory to herbivory (Mitchell 1953, Montgomery 1977, Christensen 1978, Bell et al. 1980, Grossman 1980, Barton 1982, Gibson 1982, Horn et al. 1982, Milton 1983), though it is not known whether the shorter absolute gut length of juveniles precludes digestion of algae (see review by Horn 1989). Barrington (1957) gives a typical range of 2 to 5 (up to 15) for the relative gut length of herbivores and less than 1 for carnivorous species. Opaleye and zebraperch, with ratios from 2 to 4, overlap the range in relative gut length typical for herbivorous fishes.

Low stomach pH, found in many tropical herbivorous fishes that do not have a pharyngeal grinding apparatus for crushing algal cell walls (Moriarty 1973, Lobel 1981), has also been found in temperate herbivorous fishes (Edwards & Horn 1982). Rough measurements of the pH (litmus paper) of the stomach and intestinal tract of one large *G. nigricans* (270 mm) used in this study were 3 for the cardiac and pyloric stomachs and near 7 in the intestine. Stomach pH was not particularly low compared to values reported by Lobel, but the gut was empty and these measurements are inconclusive. Nevertheless, the pyloric stomach wall of *G. nigricans* is very thin compared to the cardiac stomach, consistent with Lobel's (1981) observation that most fish using low pH for digestion have thin-walled guts. Rimmer & Wiebe (1987) also found that 2 other kyphosids (*Kyphosus cornelli, K. sydneyanus*) had acidic stomach pH (2.8 to 3.9), though this was not the primary mechanism of digestion.

The shore crab is also known to be predominantly herbivorous (Hiatt 1948, Bovbjerg 1946, Sousa 1979, Robles 1982), but can be an aggressive, opportunistic carnivore. It has attacked various species of intertidal mollusks (*Tegula* sp., *Littorina* sp., and others, Hiatt 1948; *Mytilus* sp., Okamura 1986) and crustaceans (*Chthamalus fissus*, Barry, personal observation, *Hemigrapsus* sp., Willason 1981), as well as intertidal fishes (Cottidae, Bovbjerg 1946, Barry personal observation). The few available food habit studies of *P. crassipes* indicate that it concentrates on fleshy algae and, in contrast to data presented here, avoids upright Corallinaceae. Hiatt (1948), in his monograph on *P. crassipes*, detailed the dominant algal food groups and ranked them by volumetric importance as follows: microscopic algae such as *Oscillatoria*, fleshy algae (*Ulva lactuca, Fucus, Enteromorpha, Grateloupia,* and *Endocladia*), a less important group of algae including several species of red, brown, and green coarsely branched algae, and the upright coralline *Corallina officinalis*. In the southern California bight, *P. crassipes* preferred *Ulva* sp. over all other species offered in preference tests (Sousa 1979), but no species of coralline algae were offered. *P. crassipes* probably consumes fleshy algae where available, but shifts its diet according to local floral availability.

Food availability and palatability of algae to herbivores

Plant morphology, successional status, secondary metabolites and other chemical or structural properties all contribute to food quality and availability to herbivores (Paine & Vadas 1969, Cates & Orians 1975, Fenical 1975, Atsatt & O'Dowd 1976, Hay 1978, Littler & Littler 1980, Lubchenco & Cubit 1980, Nicotri 1980, Lubchenco & Gaines 1981, Littler et al. 1983a, b, Horn 1989). The high selectivity for fleshy green algae by *G. nigricans* and *P. crassipes* likely is related to palatability, digestibility, food quality, and relative lack of chemical compounds or structural components that inhibit feeding. In their analysis of the quality of algal food for fishes, Montgomery & Gerking (1980) found that Chlorophyta were highest in quality, with a high caloric content and the greatest percentage protein and carbohydrate; Phaeophyta rank second and Rhodophyta are the poorest in food quality among fleshy macroalgae.

The role of secondary metabolites of algae

Although specific relationships between chemical deterrence and herbivory are still poorly known (Hay et al. 1987), secondary metabolites can affect the palatability, or acceptability, of several algal species to herbivores (Hay & Fenical 1988) and are likely to be important determinants of food habits and selectivity for the herbivores studied here. Several genera from this study are known to produce metabolites that are potential feeding deterrents.

Several brown algae contain phlorotannins (polyphenolics) which inhibit feeding by some invertebrates and fishes (Steinberg 1984, 1985, Hay & Fenical 1988). Phenolic or related compounds have been isolated from 3 species of Phaeophyta, *Zonaria farlowii* (Gerwick & Fenical 1982), *Dictyopteris undulata* (Welch & Prakasa Rao 1978, Gerwick et al. 1981), and *Pachydictyon coriaceum* (Hirschfeld et al. 1973, Ishitsuka et al. 1982), used in preferences studies, and were among the least preferred of all species tested. *Sargassum muticum,* recently introduced from Japan to this coast, ranked low in preference for all three herbivores, perhaps due to its known phenolic content (Glombitza et al. 1978, Steinberg 1986).

The brown algae *Scytosiphon lomentaria, S. dotyi* and *Petalonia/Endarachne* were the only species of Phaeophyta consumed at relatively high rates by the herbivores tested, particularly *P. crassipes.* Both are heteromorphic algae with a perennial crustose stage and an upright stage that occurs seasonally, and were the only such species utilized in this study. Upright phases of heteromorphic algae are thought to be more susceptible to grazing pressure than crustose phases or isomorphic brown algae (Lubchenco & Cubit 1980, Slocum 1980, Dethier 1981). The life history 'refuge' of the crustose phase may allow heteromorphic algae to allocate more energy in a short-lived upright phase towards growth and reproduction, rather than to development of morphological or physiological defenses (Lubchenco & Cubit 1980).

Secondary metabolites from a few species of red algae have known qualities of chemical deterrence. Several species of *Laurencia,* including *L. pacifica* and *L. subopposita* utilized here, contain toxic brominated sesquiterpenes or other halogenated compounds (Hall et al. 1973). *Plocamium cartilagineum,* a member of the Gigartinales, contains cartilagineal, a terpene that is toxic to some fish (Crews & Kho-Wiseman 1977). These red algae ranked low in preference for fishes and the shore crab.

Some algae with complex secondary metabolites were preferred by herbivores. *Chondria californica,* which obtains its characteristic iridescent blue color from antibacterial cyclic polysulfides (Wratten & Faulkner 1976), ranked high in preference. Several genera from the Ceramiales (e.g. *Polysiphonia, Ceramium*) contain halogenated or sulfuric compounds that probably inhibit internal or epiphytic bacteria, rather than deter macroherbivores (Ikawa et al. 1973, Fenical 1975). Some calcified Cryptonemiales (*Corallina officinalis, Lithothrix aspergillus*) are apparently non-toxic to vertebrates (Habekost et al. 1955). *Ulva lactuca,* one of the most preferred algae, contains dimethyl sulfides that do not inhibit herbivory but function as antibacterial agents (Greene 1962).

Algal morphology and successional status

The functional form of algae affects their susceptibility to herbivores and also is related to food quality and successional status. Less protected sheet-like and filamentous forms are usually early successional species that grow rapidly and are most preferred and susceptible to herbivores, compared to coarsely branched, leathery, jointed calcareous, or crustose groups (Littler & Littler 1980, Gaines & Lubchenco 1982, Littler et al. 1983a, b). In temperate California, fish feeding habits and preferences generally conformed to these predictions and suggest that these considerations are important determinants of herbivore food choice. Patterns of selectivity for functional groups of algae by opaleye and zebraperch were generally consistent with Littler & Littler's (1980) hierarchy of algal susceptibility. Padilla (1989) showed, however, that patterns of susceptibility to grazing by docoglossan limpets, or 'thallus toughness', was nearly the reverse of that expected from the functional form model of Littler & Litter (1980), with uncalcified sheet-like algae and heavily calcified algae the most and least tough groups, respectively. These contrasting patterns imply that selection for defenses against herbivory, if functional morphology is related to herbivory, varies considerably depending upon the major herbivore group.

The diet and preferences for algae of the shore crab differed dramatically from the expected algal groups. *Pachygrapsus crassipes* ingested jointed calcareous algae (*Lithothrix aspergillum*) at higher rates than all other species in feeding preference studies and jointed calcareous algae comprised more than 42%, by volume, of the identifiable portion of its diet. This is puzzling considering the reported lower quality of upright calcareous algae (lower total calories, low percentage protein, lipid and carbohydrate, Montgomery & Gerking 1980). Because calcareous algae probably degrade more slowly in the stomach than fleshy species, it is likely that they remain identifiable within the stomach longer than fleshy species, particularly after processing by the gastric mill of crabs. Calcareous algae in the diet of shore crabs were easier to identify than other algal groups, and calcareous species were easily distinguished from the unidentifiable prey category (43.5% of the total diet volume), of which a large portion may be contributed by partially digested fleshy algae. This may have resulted in an overestimate of the importance of calcareous algae in the shore crab's diet.

Herbivore mobility and algal preference

The preferences of herbivores for particular groups of algae must have evolved in response to selective pressures based on several factors including food quality and palatability, the cost of search and handling time of prey, and exposure to predators (e.g. fishes, birds, octopuses). Surveys of the density of *P. crassipes* in intertidal habitats at the study sites (Barry 1988) indicate that shore crabs were more abundant near (within ca. 1.5 m) refuge habitats (crevices; density = 0.35 individuals per m^2, SD = 0.51, n = 8) than distant (ca. >5 m) from refuge habitats, where the abundance of shore crabs was zero (n = 8). Because of its more restricted mobility, leading to limited foraging range and presumably higher risk of predation (several birds and fishes, and mammals consume shore crabs, Morris et al. 1980), the shore crab may have had to survive on lower quality food available near refuge habitats; over evolutionary time food preferences may have shifted to balance caloric payoff with all associated costs. Consequently, *P. crassipes* may be better able to process calcified algae, compared to *G. nigricans* or *H. azurea,* which, because of their greater mobility, incur a much lower cost in searching for less abundant, but higher quality foods. Hay et al. (1988) indicates that a similar process may have been responsible for selection to overcome algal chemical defenses in mesoherbivore (amphipod) populations that also experience a restricted availability of food resources relative to mobile fish species.

Herbivory and the structure of temperate algal communities

Horn's (1989) review of herbivory by fishes discusses many aspects of herbivory, including the impact of fishes on algal communities in temperate zones. In general, herbivores are not effective in controlling the structure of algal communities in temperate latitudes, though some minor effects have been documented. *Girella nigricans*, in particular, has been implicated as a potentially important grazer of giant kelp (*Macrocystis pyrifera*) sporelings and *Gigartina* sp. (Foster 1975) in subtidal kelp beds off southern California. In both studies, opaleye and *Medialuna californiensis* were shown to decrease significantly the abundance of algae where it was accessible. The structure of algal and invertebrate communities on intertidal reefs in temperate latitudes may be affected directly by herbivorous fishes, but several other processes, including the direct and indirect effects of predation, competition, and physical disturbances, likely have an equal, or greater, role in regulating these communities. When the herbivores examined during this study were excluded from intertidal plots by cages mounted on the reef flat, there were slight to moderate increases in the cover of several algal taxa (*Gigartina canaliculata, Ulva* sp., *Centroceras clavulatum*) inside exclusion cages and decreases in the cover of other species (*Lithothrix aspergillum, Corallina* sp.), compared to control plots, suggesting that herbivores had a mild, but detectable effect on the structure of the algal community (Barry 1988). In contrast, predation on herbivores by fishes and crustaceans has been shown to have strong direct and indirect effects on temperate algal communities (e.g. Kennelly 1983, Robles 1987, Robles et al. 1990), and thus exert greater influence on the structure of temperate reef communities.

Several hypotheses have been proposed to explain the low diversity and abundance of herbivorous fishes in temperate latitudes (Choat 1982, Horn 1989), including, (1) adaptive radiation of herbivorous fishes has not yet occurred, (2) the digestive physiology of fishes is limited by cold water temperature, (3) suitable food for herbivorous fishes is seasonally unavailable in temperate latitudes and, (4) herbivory by fishes in temperate latitudes is restricted by greater algal toughness, chemical defenses, and lower nutritive quality. We propose that a combination of factors have contributed to the paucity of actively foraging (roving) herbivorous fishes in temperate systems. The greater seasonality and generally higher productivity of temperate, versus tropical, systems may have reduced the selective pressure for herbivory by fishes in two ways. First, seasonal shortages and surpluses of food occur on a time scale shorter than the generation time of roving fishes. Thus, excesses in algal food are available for mesoherbivore species (e.g. amphipods and worms) possessing short generation times that allow them to respond rapidly, via population growth, to elevated food levels. The excess invertebrate biomass would reduce selection for herbivorous fishes and select for generalist carnivores or omnivores that can forage over algal turf and subtidal reefs, supported by invertebrate grazer and detritivore species. Adaptive radiation in herbivorous fishes in temperate systems may be slower than in the tropics due to a modification of selection pressure related to these differences in patterns or productivity. Future studies on latitudinal variation in herbivory should consider fundamental differences in environmental variability and productivity. These factors ultimately control the evolution of biological systems.

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