Studies of Food Preference in Algivorous Invertebrates of Southern California Kelp Beds[1]

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ABSTRACT: Stands of the giant kelp, *Macrocystis pyrifera,* frequently suffer attack by grazing organisms and in some cases complete destruction has been observed. The present investigation of the feeding habits of grazing organisms is primarily concerned with food preferences. Discrimination in choice of plant foods was examined in 11 common invertebrate species of the sublittoral rock bottom fauna of southern California by measuring the differential consumption of seven common algal species in the laboratory. The algae were selected as representing the major floral elements of the kelp bed (*Macrocystis pyrifera*) community. All of the grazers exhibited high degrees of preference for *Macrocystis.* Shallow water grazers revealed stronger preferences for *Egregia* than for *Macrocystis.* Herbivores found at greater depths indicated strongest preferences for *Macrocystis, Laminaria,* and *Pterygophora,* plants that are generally common at these depths. The deepest-living herbivore, *Lytechinus,* showed greatest preference for a red alga, *Gigartina;* red algae generally supplant brown algae in dominance at greater depths. Some of the invertebrates refused certain of the marine plants. A specific distaste factor may exist in these cases.

THE LARGE LAMINARIAN BROWN ALGA, *Macrocystis pyrifera,* has attracted interest during the past decade since it became apparent that the once extensive beds of this plant were on the decline in southern California and northern Baja California (North, 1962, 1963:7). A five-year study of the kelp beds was undertaken at the Scripps Institution of Oceanography (Institute of Marine Resources) to seek causes of the kelp regression. (The final report is in preparation.) Physical and chemical factors possibly detrimental to kelp, e.g., elevated temperature and high turbidity of nearshore water and toxicity associated with industrial wastes discharged into the sea, are discussed elsewhere (North, 1963). Studies of food habits and behavior of kelp-associated fauna were prompted when it was found that grazing by organisms normally a part of the kelp community was frequently a cause of kelp destruction (Leighton, 1960; North, 1963). Because gut contents provide unreliable clues to food habits in algivorous animals, studies were carried out in marine laboratory aquaria where food selection could be observed.

Studies of algal preferences in the marine snail, *Littorina obtusata,* considered chiefly scent perception and orientation to algae which were variously distributed within large tanks in which slow unidirectional water flow was usually maintained (Barkman, 1955; Van Dongen, 1956; Bakker, 1959). The present study and an earlier one (Leighton and Boolootian, 1963) report gustatory preference and quantitative measurement of the amounts of algal foods ingested. The method reflects more certainly the animals' genuine food preference in contrast to selection of algae through other motivation (e.g., for spawning substrate, specific plant shelter, etc.). Barkman (1955:50) states that *L. obtusata* deposits its eggs on fronds of Fucaceae, particularly on *Fucus serratus.*

MATERIALS AND METHODS

The procedure employed was simple. Groups of a grazing species, held either in large concrete tanks or in glass aquaria, were provided equal weights of each of several common algae occurring in or near kelp beds. Amounts ingested

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were determined by measuring loss in weight of algae after a feeding period. Data were tested statistically for consistency of ranks and for significant differences in means of consumption values. The method and its analysis are considered to be an improvement over that reported earlier (Leighton and Boolootian, 1963).

The following 11 common benthic invertebrates, known to be exclusively or predominantly macro-herbivores, were studied:

Echinoids
- *Lytechinus anamesus* Agassiz and Clark
- *Strongylocentrotus franciscanus* Agassiz
- *Strongylocentrotus purpuratus* (Stimpson)

Gastropods
- *Aplysia californica* Cooper
- *Astraea undosa* (Wood)
- *Haliotis corrugata* Gray
- *Haliotis fulgens* Philippi
- *Haliotis rufescens* Swainson
- *Norrisia norrisii* (Sowerby)

Crustacea
- *Pugettia producta* (Randall)
- *Taliepus nuttallii* (Randall)

The animals were collected from a variety of habitats and depths to insure that the results obtained would not reflect conditions imposed by the environment in any single habitat. Individuals employed varied about an average adult size found in the field. During the years 1960 and 1961 at least 10 experiments were run with each grazing species. Numbers of animals in experiments ranged from 2 to 10 depending on the size of the particular species.

The following seven species of algae were employed, representing the major noncalcareous plants available to grazers in southern California kelp beds in terms of biomass (Dawson et al., 1960):

Phaeophyta
- *Cystoseira osmundacea*[2] (Turner) Agardh
- *Egregia laevigata* Setchell
- *Eisenia arborea* Areschoug
- *Laminaria farlowii* Setchell
- *Macrocystis pyrifera* (L.) Agardh
- *Pterygophora californica* Ruprecht

Rhodophyta
- *Gigartina armata* Agardh

Blotted fresh blades or fleshy thalli were cut either into pieces about 4 cm square or into 2.5 cm discs. Equal weights of the seven algae were then thoroughly mixed and placed in experimental and control containers alike. In most cases the quantity of food provided aggregated 70 g, comprising 10 g of each species. Larger grazers were offered twice this amount. The controls, containing algal pieces prepared in the same manner, but no grazers, provided a measure of any weight changes due to decomposition and/or imbibition. Experiments were of 24 hr duration. All algal pieces sank and remained on the bottom within easy reach of all the animals; pneumatocysts were excluded.

A number of precautions were taken to assure uniformity in responses and to maximize random contacts between animals and seaweed fragments:

1. Freshly collected algae were always used.
2. A free flow of water was maintained continuously in the containers.
3. The algal pieces were thoroughly mixed several times during each experiment.
4. Numbers of grazers and sizes of containers were selected so that each food species should be equally within reach of each individual.
5. After one to three experiments, grazers were replaced by newly collected individuals.
6. Between experiments animals were allowed to feed on a variety of algae but were subjected to approximately two days' starvation immediately prior to each experiment.
7. Feeding experiments were suspended during times of unusually high ambient water temperatures. (Algal deterioration was most evident at temperatures above 20 C.)

At the end of a feeding period all remaining algal fragments were removed from each tank, segregated as to species, blotted free of adhering water, and weighed to the closest decigram. Weight losses, corrected for changes in the con-

[2] *Halidrys dioica* Gardner is indistinguishable from *Cystoseira osmundacea* when fruiting organs are not present (Dawson et al., 1960) and both forms have undoubtedly entered the experiments. The low preference values observed for *Cystoseira-Halidrys*, in most cases, suggests there is no serious objection to the chance mixing of the two forms as one. Most experiments were performed in late winter, spring, and summer when fruiting organs permitted distinction of these two species.

trols, were taken as the seaweed consumed by grazers. Weight changes in the controls were usually very small.

RESULTS

The allowance method of Tukey (1953:90) was used to test for differences in consumption. Differences between the means of algal consumption values, significant at a 5% error rate, are indicated by separate boxes in Figure 1. Plant species falling in intermediate positions and not significantly different from adjacent groups are not enclosed. In most cases three distinct levels of consumption are evident. The results show that in many cases *Macrocystis* was consumed in relatively large amounts, appearing at or near the highest level; *Cystoseira, Gigartina,* or *Pterygophora* were frequently, but not always, at the lowest level; and the other algal species were at intermediate levels.

Means and ranges of quantitative data for all grazers are provided in Figure 2. The ranges are, in some instances, rather great. Variations in ambient temperature between 13 and 19 C caused fluctuation in feeding rate. Sizes of animals, while similar, did vary. Other factors doubtless affected feeding rate and selection. Despite the variability, a considerable degree of correspondence was found between experiments. To test the agreement of results, a ranking method described by Kendall (1955:95) was employed. In each trial, the algae were assigned ranks from 1 to 7 in order of decreasing quantities consumed. Values of W, the coefficient of concordance, ranged from 0.41 to 0.79 (Table 1); all were significant beyond the .001 level. The order of preference of each grazing species, therefore, may be regarded as consistent and the mean values for consumption (Fig. 2) afford the best estimate of the relative degree of attractiveness of the algae to the grazing animals.

The data for the entire experimental series are included for two species, *Strongylocentrotus purpuratus* (Table 2) and *Lytechinus anamesus* (Table 3), in order to provide an indication of the intraspecific variability of results. *S. purpuratus,* collected from a variety of habitats, showed limited variation in preference behavior. Mean values for *L. anamesus* from the La Jolla Canyon and from the Mission Bay entrance show general agreement. The same tendency toward a specific pattern of preferential response to the algae tested here was found in other grazing organisms collected from a variety of plant environments. (A recent extension of these studies has shown similarities in response by *Haliotis* and *Strongylocentrotus* collected at latitudes well beyond the range of certain of the algae used here. Hence a species-specific pattern of selection appears to exist, some species being characteristically attractive while others are not.)

Macrocystis was most highly preferred in 7 of 11 cases; typical kelp bed inhabitants fall within this group. *Egregia,* a shallow water kelp (0–8 m) was most preferred by *Norrisia, H. fulgens,* and *Aplysia,* all most common at lesser depths. *Lytechinus,* normally a relatively deep water dweller, preferred red algae (represented in these experiments by *Gigartina armata*). Red algae generally supplant brown algae in dominance at depths exceeding 35 m.

Several species of brown algae were consistently consumed in greatest relative quantities by all grazers. *Egregia* and *Laminaria,* in addition to *Macrocystis,* were generally favored. *Cystoseira,* on the other hand, was seldom ingested by grazers other than *Pugettia, Taliepus,* and *H. corrugata. Gigartina* was readily eaten by *Lytechinus, Aplysia, Astraea,* and *Strongylocentrotus,* but was hardly touched by *Pugettia, Taliepus, Norrisia,* and *H. corrugata.*

The coefficient of concordance (W_t) was determined for a summation of the rankings of preference for all 11 grazing species (Table 4) and is significant at better than the 0.1% level. The order of preference is, therefore, generally consistent throughout the group of species, with *Macrocystis* as the most commonly preferred item and *Cystoseira* as the least acceptable.

Since some closely allied species equipped with similar chewing, biting, or rasping organs exhibited divergent preference behavior, the results are not considered to be a consequence of relative mechanical ability to cope with a particular food. Toughness of foods might be suggested as influencing choice when measured by the techniques employed; the resilient, denser algae being consumed at a slower rate than the tenderer tissues. If this were true, one would ex-

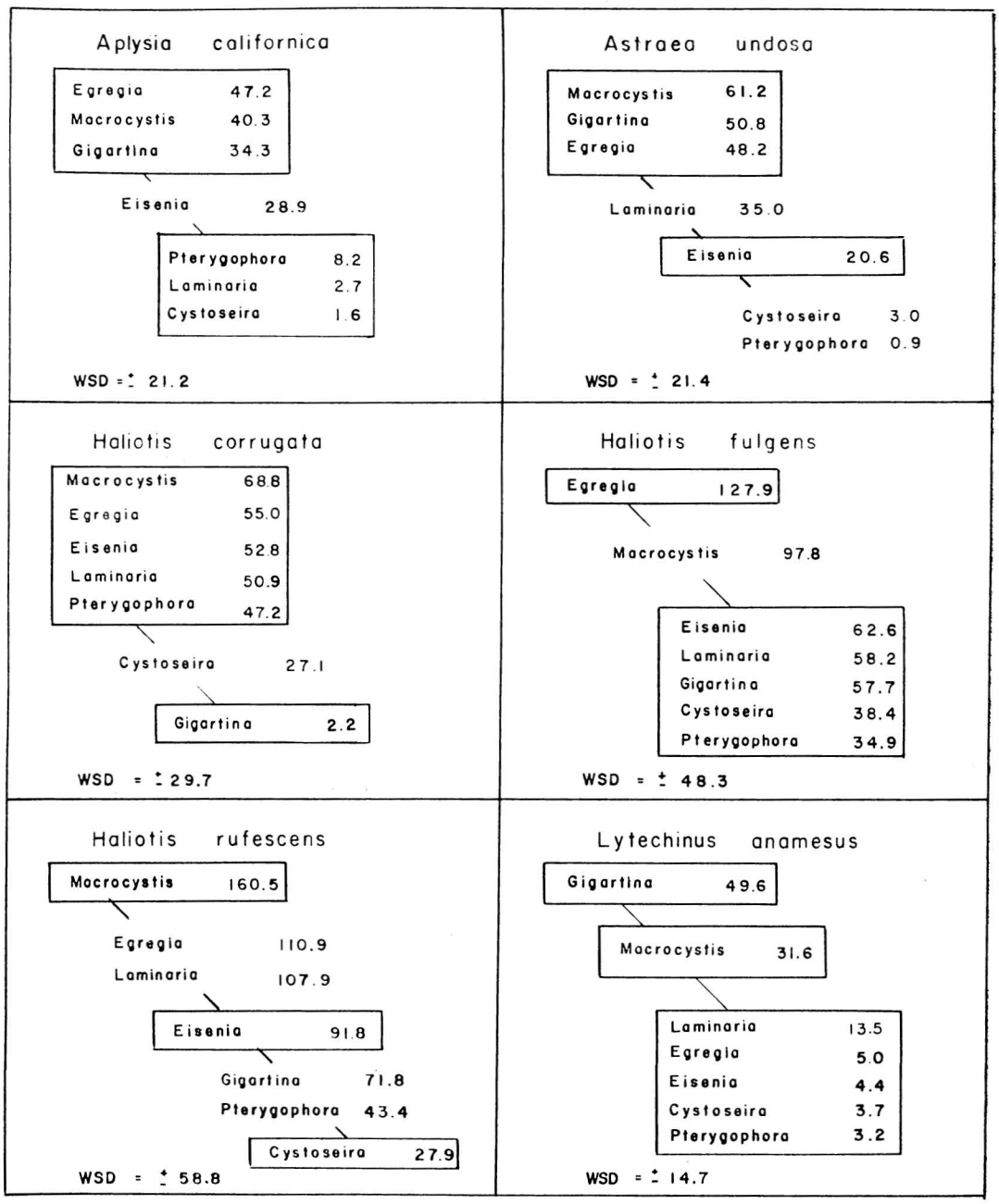

FIG. 1. Differences in amounts of various algae consumed by invertebrate grazers. Species in boxes are not significantly different (.05 level) from each other, but do differ from those in preceding or following boxes. Intermediates are not boxed. Algae are arranged from top to bottom in order of decreasing preference. WSD, the wholly significant difference, is the minimum difference between species which would be significant at the 5% level (see Tukey, 1953).

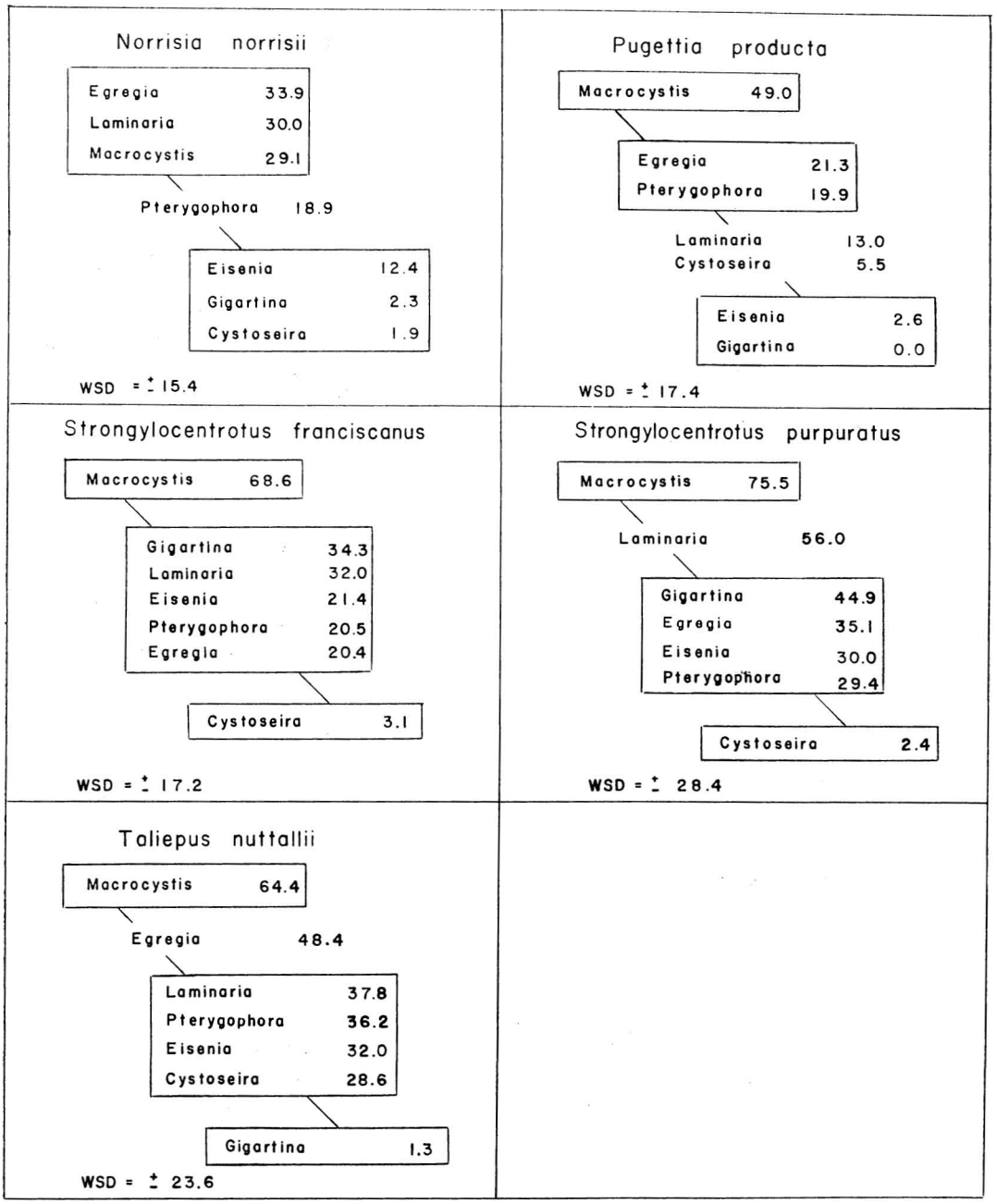

FIG. 1 (*cont.*). Differences in amounts of various algae consumed by invertebrate grazers.

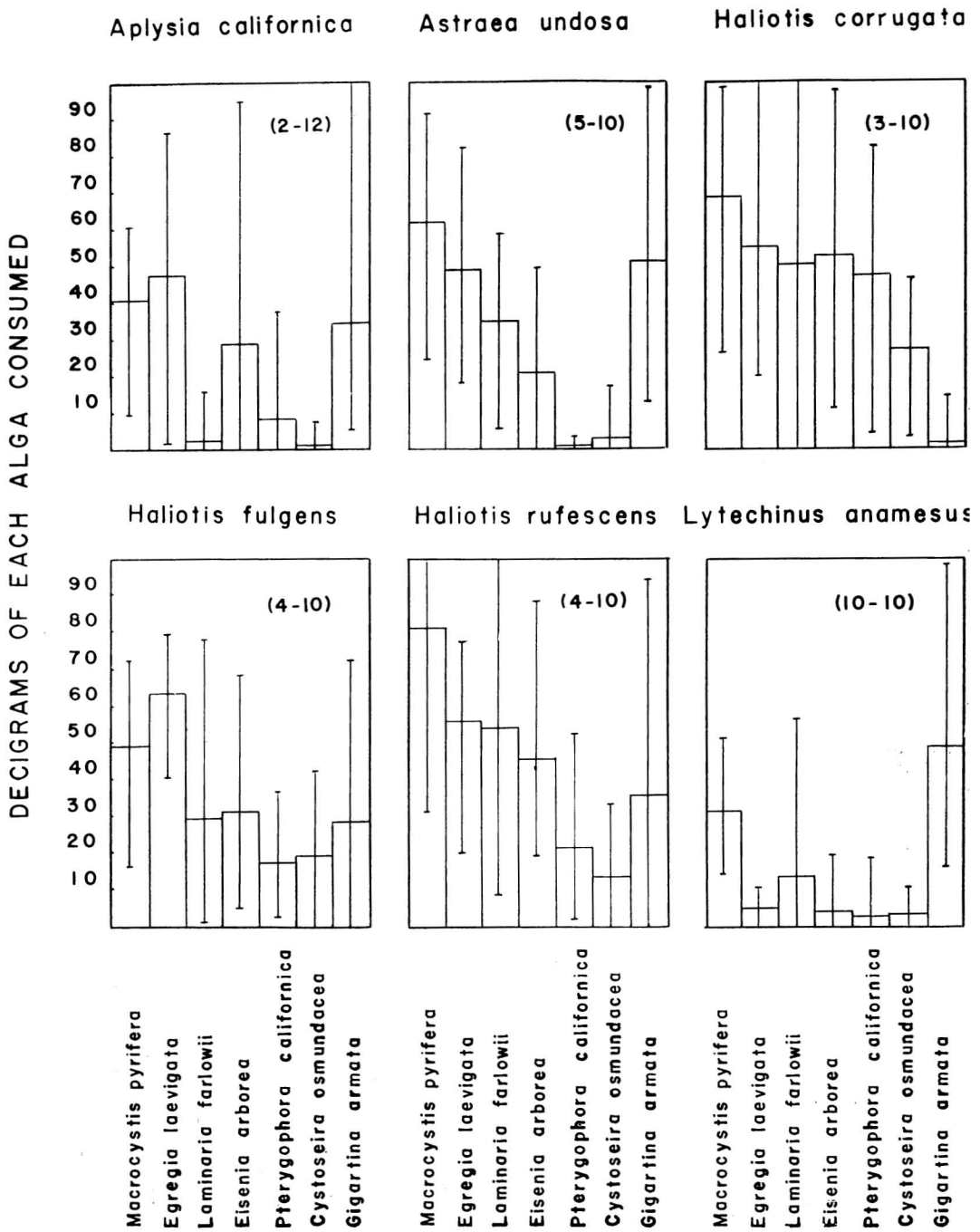

FIG. 2. Means of plant consumption values shown by histogram. Ranges are indicated by vertical lines. Consumption data for *Haliotis fulgens* and *H. rufescens* are reduced by one-half. Numbers of individuals employed and numbers of experiments are given in that order hyphenated in parentheses.

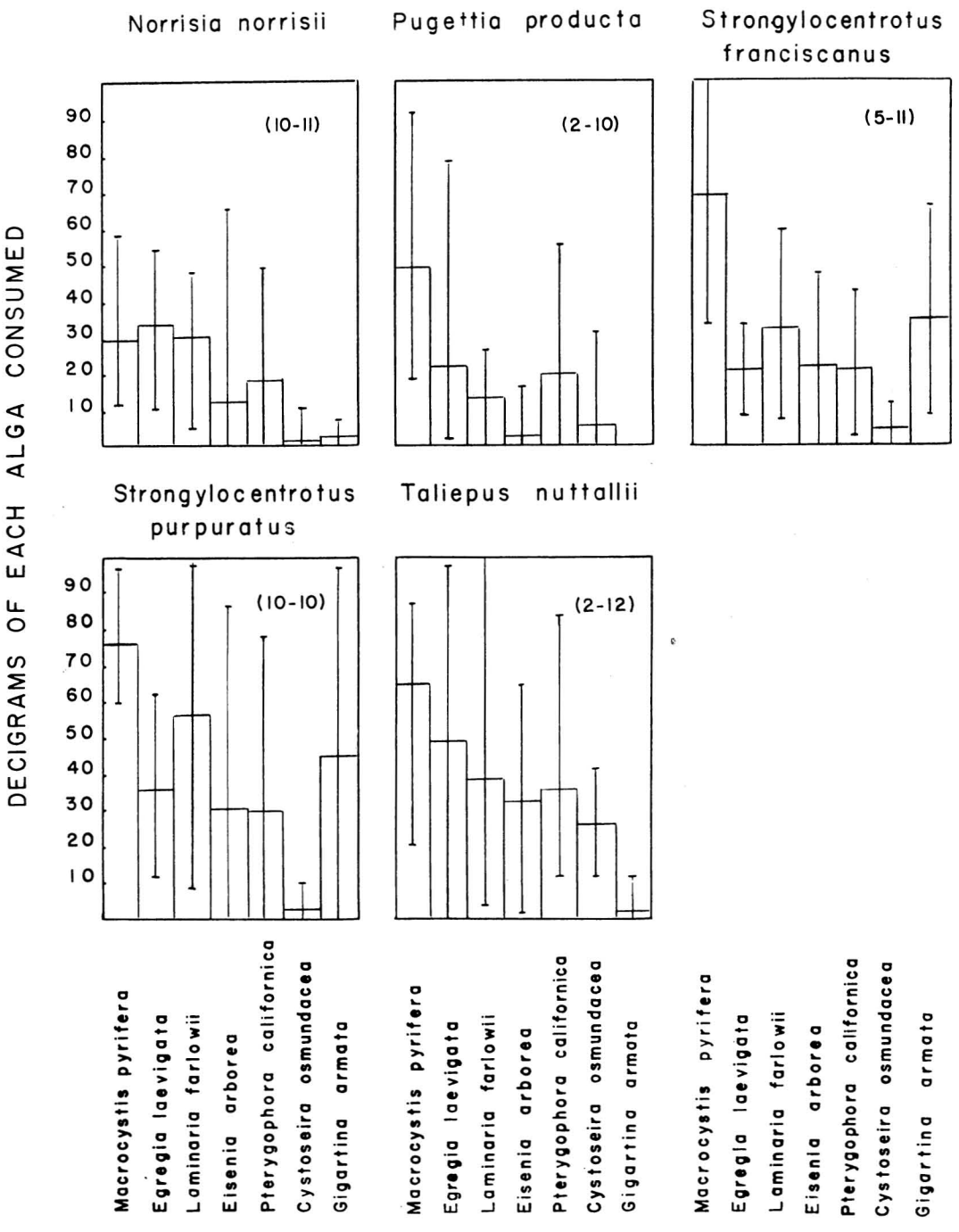

FIG. 2 (*cont.*). Means of plant consumption values. Ranges are indicated by vertical lines.

TABLE 1

CONSISTENCY IN RESULTS OF EXPERIMENTAL FEEDINGS OF SEVEN ALGAL FOODS TO INVERTEBRATES

INVERTEBRATE SPECIES	NUMBER OF EXPERIMENTS	NUMBER OF INDIVIDUALS EMPLOYED IN EACH EXPT.	TOTAL NUMBER OF DIFFERENT GROUPS EMPLOYED	COEFFICIENT OF CONCORDANCE* W =
Aplysia californica	12	2	6	0.59
Astraea undosa	10	5	5	0.79
Haliotis corrugata	10	3	3	0.51
Haliotis fulgens	10	4	6	0.47
Haliotis rufescens	10	4	5	0.58
Lytechinus anamesus	10	10	8	0.60
Norrisia norrisii	11	10	5	0.41
Pugettia producta	10	2	9	0.77
Strongylocentrotus franciscanus	11	5	8	0.58
Strongylocentrotus purpuratus	10	10	7	0.58
Taliepus nuttallii	12	2	5	0.51

* This coefficient is a measure of the degree of agreement between sets of repetitive experimental results (see text). Values may range from 0.0 to 1.0, the higher figures indicating a higher degree of agreement. All values in this table are significant at better than the 0.1% level.

TABLE 2

DECIGRAMS OF DIFFERENT ALGAE CONSUMED BY 10 ADULT *Strongylocentrotus purpuratus* IN 24-HOUR EXPERIMENTAL FEEDING PERIODS

EXPERIMENT	*Macrocystis*	*Egregia*	*Laminaria*	*Eisenia*	*Pterygophora*	*Cystoseira*	*Gigartina*
1	91	63	97	51	60	1	96
2	72	50	83	70	79	10	81
3	62	28	88	87	65	2	49
4	84	30	14	11	8	0	20
5	73	43	31	3	13	0	15
6	76	38	74	45	20	0	0
7	96	27	8	0	30	2	36
8	58	46	54	0	0	8	75
9	72	12	83	9	16	1	26
10	71	14	28	24	3	0	51
Mean	75.5	35.1	56.0	30.0	29.4	2.4	44.9

pect that preference orders would all tend to be similar among the grazing species examined. The consumption of some of the tougher algae (*Eisenia, Laminaria, Pterygophora, Gigartina, Cystoseira*) is greater than or equal to that of the relatively tender *Macrocystis* and *Egregia* in a sufficient number of cases to suggest that differential algal consumption could not be attributed solely to the degree of toughness of the algae. A more likely explanation of the observed results would involve selection of algal foods on the basis of chemical perception.

Assuming that food preference, as demonstrated in the laboratory, must indeed contribute to the behavior of grazing populations in the field, one might expect *Macrocystis* to receive concentrated grazing and to provide support for a great number of animals of at least these 11 species. Grazing is selective under certain conditions in the field (Leighton, 1964, Kelp Investigation, Final Report, in preparation). Selectivity disappears when grazing pressures become extreme (Leighton, 1960:28). Although the food preference relationships found for the 11 benthic invertebrate species in the present study cannot be said to restrict any species to a given association of algae, as has been shown for the intertidal periwinkle, *Littorina obtusata* (Bakker, 1959), the preponderance of first choices falls under the headings *Macrocystis* and *Egregia.* In field studies some herbivores have appeared collectively oriented toward these plants and away from *Pterygophora* and *Cystoseira* (Leighton, 1964). A tendency may exist, therefore, for the grazing species to remain in *Macrocystis* and *Egregia* stands and, perhaps, to move into such stands from locations nearby which are less attractive with respect to food.[3] The attractiveness

[3] Experiments reported elsewhere (North, 1963), indicating the food value of *Macrocystis* as compared with other algae (*Egregia, Pterygophora,* and *Bossiella* sp.) based on conversion efficiencies, place the former in a leading position as a food plant for *Strongylocentrotus purpuratus* and *S. franciscanus.*

TABLE 3

DECIGRAMS OF DIFFERENT ALGAE CONSUMED BY 10 ADULT *Lytechinus anamesus* IN 24-HOUR EXPERIMENTAL PERIODS*

EXPERIMENT	*Macrocystis*	*Egregia*	*Laminaria*	*Eisenia*	*Pterygophora*	*Cystoseira*	*Gigartina*
Lytechinus from La Jolla Submarine Canyon; depth 20 m; bottom sand							
1	51	0	25	3	1	7	54
2	31	9	17	4	0	0	65
3	25	3	12	0	0	0	39
4	14	10	0	0	0	0	24
5	22	3	0	0	0	0	14
Mean	28.6	5.0	10.8	1.4	0.2	1.4	39.2
Lytechinus from channel of Mission Bay; depth 2–3 m; bottom sand							
6	39	0	8	0	0	0	39
7	50	9	9	12	6	10	35
8	50	2	55	7	6	6	99
9	15	8	9	18	18	3	64
10	19	6	0	0	1	11	63
Mean	34.6	5.0	16.2	7.4	6.2	6.0	60.0

* Results are given for groups collected from depths of 20 m and 2 m in different locations.

TABLE 4

SYNOPSIS OF PREFERENCE ORDER RANKINGS

GRAZING SPECIES	*Macrocystis*	*Egregia*	*Laminaria*	*Eisenia*	*Pterygophora*	*Cystoseira*	*Gigartina*
Aplysia	2	1	6	4	5	7	3
Astraea	1	3	4	5	7	6	2
H. corrugata	1	2	4	3	5	6	7
H. fulgens	2	1	3	4	6	7	5
H. rufescens	1	2	3	4	6	7	5
Lytechinus	2	4	3	5	7	6	1
Norrisia	3	1	2	5	4	7	6
Pugettia	1	2	4	6	3	5	7
S. franciscanus	1	6	3	4	5	7	2
S. purpuratus	1	4	2	5	6	7	3
Taliepus	1	2	3	5	4	6	7
Total (W_t* = 0.61)	16	28	37	50	58	71	48

* W_t = Coefficient of concordance for mean preference orders of all grazing species (see text); the value is significant at better than the 0.1% level.

of *Macrocystis* to its grazing species may help to explain why that alga in the field is often the center of grazing attack and why kelp beds hold the numbers and variety of grazers observed.

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