

Feeding and Nutritional Ecology of the Sea Urchin *Strongylocentrotus drobachiensis* in Maine, USA

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Abstract

The sea urchin *Strongylocentrotus drobachiensis* exhibited a high degree of food selectivity, whether foods were presented singly or in combination. Foods ranked from most to least preferred were, in summer, *Laminaria longicruris*, *Chondrus crispus*, *Corallina officinalis*, *Ascophyllum nodosum*, and *Agarum cribrosum*, whereas in winter *A. nodosum* and *A. cribrosum* exchanged ranks. Food preference was not correlated with caloric content but, because of higher feeding rates on preferred foods, caloric intake was positively correlated with preference. Similarly, food absorption rankings were not correlated with food preference, with the exception of gravimetric efficiencies in winter. However, the absorption of *L. longicruris*, the most preferred alga, was highest in all measurements. Growth and reproductive development of *S. drobachiensis* on single species diets were positively correlated with food preference. Highest values occurred with animals fed *L. longicruris*. Urchins transferred from non-preferred to preferred diets showed increased somatic and reproductive growth compared to control animals on the original, non-preferred diets. Conversely, when transferred from preferred to non-preferred diets, urchins showed reduced growth compared to controls. No combination diet tested supported significantly better gonadal growth than *L. longicruris* alone. However, the combination of 75% *L. longicruris*: 25% *C. crispus* supported slightly better somatic growth than *L. longicruris* alone. These data support the view that *S. drobachiensis* has evolved a feeding strategy resulting in the maximization of growth and reproduction.

Introduction

Evaluation of the cause for preferential selection of foods is rooted in the assumption that animals are under strong selective pressure to choose that food or combination of foods from which they may derive the most "value" (Emlen, 1973). In a temporal sense "food value" may be expressed in terms of nutrient content or availability (Lawrence, 1975; Paine and Vadas, 1969; Vadas, 1977) but in an evolutionary context "value" must be considered in terms of differential reproductive success such that species persist in the "evolutionary game" (Slobodkin, 1964; Rapport, 1971). Animals capable of locating superior prey items efficiently have considerable selective advantage and a higher probability of leaving offspring with similar behavioral traits (Rapport, 1971; Emlen, 1973; Himmelman and Carefoot, 1975). Through differential survival and reproduction, this strategy (food preference) becomes an adaptive feature of the species.

Since the late 1960's a number of investigators have presented empirical data on the relationship of feeding strategies to various fitness parameters. Animals eating preferred foods in the field and laboratory grew most rapidly and had the highest food and energy absorption, growth efficiency and reproductive potential (Carefoot, 1967a, b, 1970; Vadas, 1977). However, none of these studies examined somatic and reproductive growth on combination diets of preferred or non-preferred foods in differing abundance ratios. In addition, combination diets simulate more realistic field situations and more accurately depict feeding behavior in heterogeneous marine environments. Such laboratory studies, therefore, would provide an assessment of the relative degree of food specialization in nature.

This study examines the feeding ecology of the sea urchin *Strongylocentrotus drobachiensis* Muller, the dominant subtidal herbivore in the Gulf of Maine, USA. Although several aspects of the ecology of *S. drobachiensis* have been investigated in the Northwestern Atlantic (Himmelman, 1969; Himmelman and Steele,

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1971; Miller and Mann, 1973; Vadas and Grant, 1973; Breen and Mann, 1976a, b; Vadas *et al.*, in preparation) and the Northeastern Pacific (Vadas, 1968, 1977), the relationship between the feeding behavior of *S. drobachiensis* and its growth and reproduction has not been closely examined in the Atlantic. Our intent was to determine the potential adaptive significance of selective feeding through an analysis of food value, absorption of food components and growth and reproductive development on single and combination diets.

Materials and Methods

Collection and Maintenance of Sea Urchins and Algae

Sea urchins, 20 ± 5 mm horizontal diameter, were collected in early March, 1975 at low tide at Moose Point State Park, Searsport, Maine and transported to the aquaculture laboratory of the University of Maine Ira C. Darling Center (Walpole, Maine). Subsequent collections were made at Pemaquid Point, Maine (June, 1976) and Salt Pond near Blue Hill, Maine (August, 1976).

Algae used in this study were selected on the basis of potential importance in the field diet of *Strongylocentrotus drobachiensis*, and their present or potential economic value (Himmelman and Steele, 1971; Miller and Mann, 1973; Vadas and Grant, 1973). The 5 species were: *Agarum cribrosum*, *Ascophyllum nodosum*, *Chondrus crispus*, *Corallina officinalis* and *Laminaria longicuris*.

Food Preference

Preference tests were performed in winter (January–March, 1976, 1.5° – 3.5° °C) and summer (June–September, 1976, 15° – 18° °C) to detect possible seasonal differences. Urchins were starved for 2 wk prior to the experiments to obtain uniformity of response and minimize dietary preconditioning (Lasker and Giese, 1954; Boottian and Lasker, 1964; Leighton, 1966; Vadas, 1968). Individuals with test diameters of 25 to 30 mm were used to 1) facilitate comparisons with growth data, and 2) minimize size-specific differences in preference. The food preferences of *Strongylocentrotus drobachiensis* were determined in 4 experiments.

Chemoreceptive responses of *Strongylocentrotus drobachiensis* to algae (Preference Experiment 1, PE1) were tested in a 1 m, Y-shaped Plexiglas tank. A similar apparatus used by Vadas (1977) for sea urchins was modified according to Castilla and Crisp (1970). At the beginning of each experiment, 20 individuals were released in the starting area (drain end) and observations made at 15, 30, 45 and 60 min intervals. The number of individuals entering the arms were recorded and removed. Foods were tested in pairs, the data pooled and tested with chi-square.

Algal preferences were determined in Preference Experiment 2 (PE2) by randomly placing equal quantities

(by fresh wt.) of the 5 algae and 30 urchins in a square tank (0.6 m \times 0.6 m \times 0.2 m) with a centrally located drain. The quantity of each alga consumed was determined at 24, 48 or 72 h intervals and preference rankings were established on the basis of relative amounts consumed (Leighton, 1966; Vadas, 1968, 1977).

In Preference Experiment 3 (PE3), individual sea urchins were isolated in small tanks (ca 5 l) and fed known quantities of a single alga. At the conclusion of each experiment the amount of algae consumed was determined and preference rankings were established on the basis of feeding rate. These experiments were run concurrently with gravimetric absorption efficiencies.

Feeding rates were calculated monthly in Preference Experiment 4 (PE4) from the quantities of each alga consumed in growth experiments (see below). For single species diets (Growth Experiment A) and reciprocal diet transfers (Growth Experiment B), feeding rates were expressed in percent of body weight consumed per day since rates were measured with sea urchins of different sizes and growth. For urchins raised on combination diets (Growth Experiment C) feeding rates were compared with respect to the ratios between the quantities of each food consumed. Preference was determined on the basis of whether observed feeding ratios differed from expected ratios. In the absence of preferences the expected feeding ratios for the combinations 25:75, 50:50, and 75:25% of Algae 1 and 2 would be 0.33, 1.0 and 3.0, respectively. Observed values higher than the expected ratios reflected a preference for *Laminaria longicuris*, whereas lower values reflected a preference for the alternative alga (*Ascophyllum nodosum* or *Chondrus crispus*). Values corresponding to expected ratios were interpreted as feeding on the basis of availability.

Calorimetry and Ashing

The calorific value of foods and urchin feces were determined by combustion in a Parr adiabatic macrobomb calorimeter. Due to the high ash content and difficulty in forming suitable pellets, several drops of mineral oil (Paine, 1966) were added to the samples. The excess calories produced by the oil (9.39 Kcal g^{-1}) were treated as an additional correction factor and subtracted from the calculated calorific value. Percentage ash was determined by heating the samples to 550° °C for 4 h in a muffle furnace. These data were used to compare samples on the basis of ash-free caloric content and to calculate absorption of total organic matter.

Absorption Efficiencies

Absorption efficiencies of *Strongylocentrotus drobachiensis* on the 5 test algae were determined by 3 methods. In the gravimetric analysis (performed in winter and summer), individual sea urchins were fed a meal of marker algae, *Palmaria palmata* (*Rhodymenia palmata*)

died blue with Perfection Dyes (W. Cushing and Co., Dover-Foxcroft, ME) prior to and following the test alga. Fecal pellets were collected daily (Fuji, 1962; Boolootian and Lasker, 1964; Vadas, 1968; Miller and Mann, 1973), rinsed with distilled water over suction, dried to a constant weight at 50 °C, and held in a desiccator over CaCl₂ for at least 48 h before weighing. Absorption of organic matter was determined by the method of Conover (1966). Feces were collected daily from groups of 10 sea urchins, dried, and along with samples of algae, ashed in a muffle furnace. Efficiency of caloric absorption was determined by measuring the caloric content of the feces and foods collected for ash analyses.

Growth Experiments

Growth was monitored monthly by measuring test diameters from the ambulacral groove to the interambulacral groove of the opposite side (nearest 0.05 mm) with vernier calipers. In addition, blotted wet weights (nearest 0.1 g) were recorded monthly. Urchins were reared in tanks supplied with fresh running seawater. Tanks were cleaned weekly and replenished with freshly collected algae.

The effect of diet on growth was measured in 3 experiments. In Experiment A growth was monitored from March, 1975 to March, 1976 on single species diets of the 5 algae. Each diet was replicated 3 times, each replicate having 11 individuals.

At the end Experiment A one of the 3 replicates was used for gonadal analysis. Experiment B was initiated with the remaining 2 replicates. Sea urchins from one of these 2 replicates were reciprocally transferred from a preferred to a non-preferred diet and *vice versa*. The other replicate was maintained on the original diet (Experiment A) as a control. Experiment B was terminated after 6 months in September, 1976.

Experiment C monitored the growth of sea urchins from March, 1975 to September, 1976 on combination diets of (a) *Ascophyllum nodosum* and *Laminaria longicruris*, (b) *A. nodosum* and *Chondrus crispus* and (c) *C. crispus* and *L. longicruris*. Algae in the above combinations were presented in ratios of 75:25, 50:50, and 25:75% (by fresh wt.).

Determination of Gonad Development

The replicate sacrificed for gonad analysis at the termination of Experiment A (March, 1976) was selected at random. In addition, 5 urchins feeding on each combination diet (Experiment C) were also sacrificed at this time. Urchins in Experiment B and the remaining individuals from Experiment C were sacrificed in September, 1976. Urchins were opened on the oral side, the gonads removed, weighed and the gonad index calculated (Lasker and Giese, 1954).

Table 1. *Strongylocentrotus drobachiensis*. Responses to algal foods in a Y-maze. Algae were tested in pairs

Pairs tested	Summer				Winter			
	N	No. of urchins choosing	χ^2	Significance	N ^a	No. of urchins choosing	χ^2	Significance
<i>Laminaria longicruris</i> <i>Chondrus crispus</i>	7	63 33	4.69	P ≤ 0.05	3	19 21	0.05	ns
<i>Laminaria longicruris</i> <i>Chondrus crispus</i>	7	50 34	1.52	ns	4	21 19	0.05	ns
<i>Laminaria longicruris</i> <i>Ascophyllum nodosum</i>	7	62 27	6.88	P ≤ 0.01	3	24 9	3.46	ns
<i>Laminaria longicruris</i> <i>Agarum cribrosum</i>	6	50 18	7.53	P ≤ 0.01	9	70 42	3.50	ns
<i>Chondrus crispus</i> <i>Corallina officinalis</i>	4	20 19	0.01	ns	3	21 14	0.70	ns
<i>Chondrus crispus</i> <i>Ascophyllum nodosum</i>	3	23 20	0.11	ns	—	—	—	—
<i>Chondrus crispus</i> <i>Agarum cribrosum</i>	3	23 18	0.31	ns	3	24 13	1.64	ns
<i>Corallina officinalis</i> <i>Ascophyllum nodosum</i>	3	19 18	0.01	ns	—	—	—	—
<i>Corallina officinalis</i> <i>Agarum cribrosum</i>	3	29 13	3.05	ns	2	10 8	0.11	ns
<i>Ascophyllum nodosum</i> <i>Agarum cribrosum</i>	3	27 16	1.41	ns	2	6 11	0.74	ns

^a N = Number of experiments using 20 animals each. ns = not significant

Table 2. *Strongylocentrotus drobachiensis*. Responses to single algal species placed in one arm of a Y-maze. Nothing was placed in the other arm. Experiments were performed during the summer (1976)

Species	No. of urchins choosing				Significance
	N ^a	Alga	Empty arm	χ^2	
<i>Laminaria longicruris</i>	3	39	6	24.20	$P \leq 0.01$
<i>Chondrus crispus</i>	2	22	10	4.50	$P \leq 0.05$
<i>Corallina officinalis</i>	2	29	8	11.92	$P \leq 0.01$
<i>Ascophyllum nodosum</i>	2	24	12	4.00	$P \leq 0.05$
<i>Agarum cribrosum</i>	2	26	10	7.11	$P \leq 0.01$

^a N = the number of experiments using 20 animals each

Results

Food Preference

In PE1, *Strongylocentrotus drobachiensis* consistently selected *Laminaria longicruris* over *Ascophyllum nodosum*, and *Agarum cribrosum*, but responses to either species in these 2 or any other pairs of algae tested in winter were not significant (Table 1). However, in summer *L. longicruris* was preferred significantly over all other algae except *Corallina officinalis*. There were no significant ($P \geq 0.5$) differences between the other pairs

of foods. This behavior exhibits a true "choice" since urchins showed a positive response to all algae during summer when given a choice between an alga and seawater (Table 2).

In both winter and summer experiments, foods ranked from most to least preferred, based on feeding rates on multiple prey (PE2), were *Laminaria longicruris*, *Chondrus crispus*, *Corallina officinalis*, *Ascophyllum nodosum* and *Agarum cribrosum* (Table 3). Correlation coefficients (Kendall's Coefficient of Concordance: W. Siegel, 1956) between the rankings of individual experiments were significant (0.886 and 0.857 for winter and summer, respectively). The consumption of *L. longicruris* was significantly higher ($P \leq 0.05$) than all other algae during both seasons (14.88 and 19.00 mg urchin⁻¹ h⁻¹ for winter and summer). The consumption rates of *A. nodosum* (1.75 and 2.11 mg urchin⁻¹ h⁻¹ for winter and summer) and *A. cribrosum* (1.60 mg urchin⁻¹ h⁻¹ for both seasons) were significantly lower. Feeding rates of sea urchins on *L. longicruris* and *C. crispus* were significantly lower in winter than in summer. No significant seasonal differences were noted with the other species.

Based on feeding rates of individual *Strongylocentrotus drobachiensis* fed a single alga (PE3), *Laminaria longicruris* and *Corallina officinalis* were significantly preferred over other species in both seasons (Table 3). Feeding rates on *L. longicruris* and *C. officinalis* were 26 and 32 mg urchin⁻¹ h⁻¹, respectively, in winter and 53 mg urchin⁻¹ h⁻¹ for both species in summer. *Ascophyllum nodosum* and *Agarum cribrosum* consistently were least preferred with both being consumed at a rate of 10 mg urchin⁻¹ h⁻¹ in winter and 22 and 16 mg urchin⁻¹ h⁻¹, respectively, in summer. The ingestion rate of *Chondrus crispus* was not significantly different

Table 3. *Strongylocentrotus drobachiensis*. Seasonal feeding rates given the choice between equal quantities of 5 algal species (Food Preference Experiment 2) and the feeding rates of individual *S. drobachiensis* on algae presented singly (Food Preference Experiment 3)

Food Preference Experiment 2 (based on multiple prey)						
Food	Summer			Winter		
	mg urchin ⁻¹ h ⁻¹	P < 0.05	Preference rank	mg urchin ⁻¹ h ⁻¹	P < 0.05	Preference rank
<i>Laminaria longicruris</i>	19.0	a	1	14.9	a	1
<i>Chondrus crispus</i>	11.8	b	2	4.7	b	2
<i>Corallina officinalis</i>	6.0	c	3	3.9	b	3
<i>Ascophyllum nodosum</i>	2.1	d	4	1.8	b	4
<i>Agarum cribrosum</i>	1.6	d	5	1.6	c	5

Food Preference Experiment 3 (based on single prey)						
Food	Summer			Winter		
	mg urchin ⁻¹ h ⁻¹	P < 0.05	Preference rank	mg urchin ⁻¹ h ⁻¹	P < 0.05	Preference rank
<i>Laminaria longicruris</i>	52.9	a	1.5	25.9	a	2
<i>Chondrus crispus</i>	39.7	b	3	12.2	b	3
<i>Corallina officinalis</i>	52.6	a	1.5	32.4	a	1
<i>Ascophyllum nodosum</i>	21.6	c	4	9.9	b	4.5
<i>Agarum cribrosum</i>	16.3	c	5	9.9	b	4.5

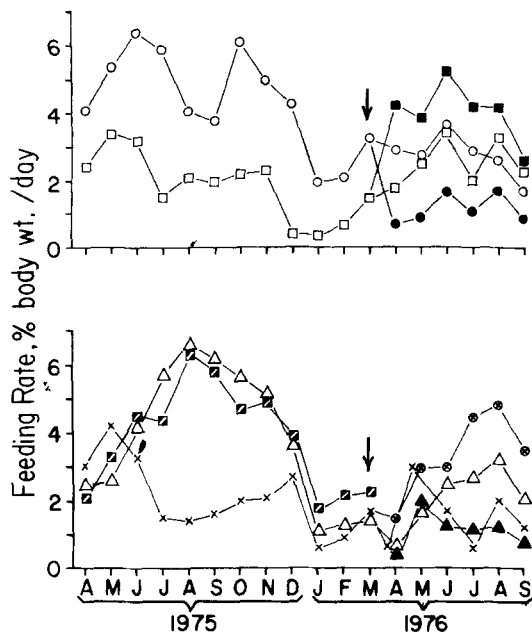


Fig. 1. *Strongylocentrotus drobachiensis*. Feeding rates on 5 species of algae. Rates were calculated from quantities of food consumed in single species diets and in reciprocal diet transfers. Arrows indicate time of diet reversals. Key: Urchins fed continuously: unfilled circles \circ *Laminaria longicruris*; unfilled triangles \triangle *Chondrus crispus*; squares with diagonal corners darkened \square *Corallina officinalis*; crosses \times *Ascophyllum nodosum*; unfilled squares \square *Agarum cribrosum*; Urchins transferred from: filled circles \bullet *L. longicruris* to *A. cribrosum*; filled triangles \blacktriangle *C. crispus* to *A. nodosum*; crossed circles \otimes *A. nodosum* to *C. crispus*; filled squares \blacksquare *A. cribrosum* to *L. longicruris*

from the latter two species in winter but was higher in the summer. Respective consumption rates of each by *S. drobachiensis* were significantly higher ($P \leq 0.5$) in summer than in winter.

In PE4, the percentage of body weight ingested per day (Fig. 1) in the single species diets was variable from month to month, but paralleled the preference rank established in PE2. Consumption of *Laminaria longicruris*, the most preferred alga, ranged from 2.0 to 6.4% of body weight per day. In contrast, the consumption of *Agarum cribrosum*, the least preferred alga, ranged from 0.4 to 3.4% of body weight per day. Feeding rates on all algae varied seasonally with the lowest values occurring in January and February. The analysis of feeding rates observed during the latter part of the first year and during the subsequent 6 months was complicated by the size differential of the individuals raised on different algae (see below). When the feeding rates of urchins switched to alternate diets and their respective controls are compared, the following generalizations can be made. Urchins switched to preferred foods showed increased feeding rates compared to control individuals maintained on the original non-preferred diet. Conversely, when

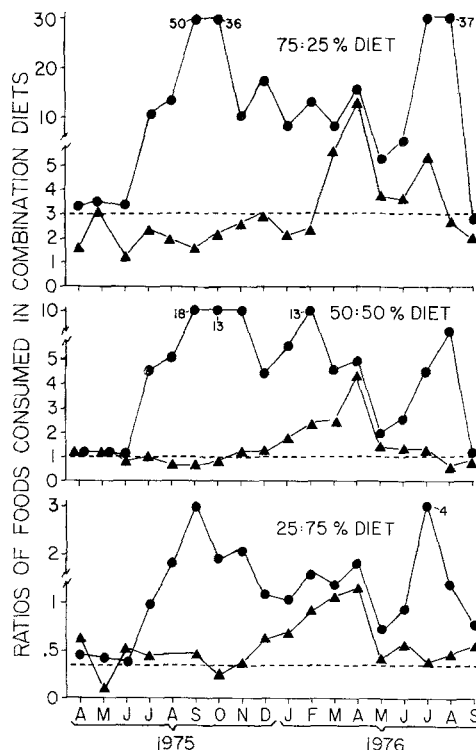


Fig. 2. *Strongylocentrotus drobachiensis*. Monthly ratios of foods consumed in 2 species combination diets. A ratio above the expected line (non-preference) (dashed line - - -) in each diet combination reflects a preference for *Laminaria longicruris*, whereas below the expected line shows a preference for *Ascophyllum nodosum* or *Chondrus crispus*. *L. longicruris*:*C. crispus* combination filled triangles \blacktriangle ; *L. longicruris*:*A. nodosum* combination filled circles \bullet

urchins originally fed preferred foods were switched to non-preferred foods, consumption rates declined sharply (Fig. 1).

The ratios of amounts consumed in the *Laminaria longicruris*:*Ascophyllum nodosum* combination diets were consistently above the availability line indicating a strong preference for *L. longicruris* (Fig. 2). Urchins consumed from 0.4 to 4.0 times more *L. longicruris* than *A. nodosum* in the ratio containing only 25% *L. longicruris*. Similarly, in the 50:50 and 75:25 diets, *Strongylocentrotus drobachiensis* consumed respectively from 1.1 to 17.7 and 2.8 to 50.0 times more *L. longicruris*. Although the ratios were not as pronounced in the *L. longicruris*:*Chondrus crispus* combinations, *L. longicruris* was eaten preferentially. The consumption of *L. longicruris* ranged from 0.1 to 1.3 times more than that of *C. crispus* in the 25:75 combination despite the low concentration (25%) of the former in the diet. As the proportion of *C. crispus* in the diet increased the preference for *L. longicruris* was less distinct (Fig. 2). However, the consumption of *L. longicruris* averaged better than 1.4 and 3.4 times more than *C. crispus* in the 50:50 and 75:25% diets, respectively.

Table 4. *Strongylocentrotus drobachiensis*. Absorption efficiency on selected algae

Food	Season	Gravimetric ^a		Organic matter ^b		Food energy ^c	
		%	P ≤ 0.05 ^d	%	P ≤ 0.05	%	P ≤ 0.05
<i>Laminaria longicurris</i>	Summer	65	ab	77	a	79	a
	Winter	67	a	—	—	—	—
<i>Chondrus crispus</i>	Summer	41	e	28	b	55	c
	Winter	62	abc	—	—	—	—
<i>Corallina officinalis</i>	Summer	34	e	26	b	49	d
	Winter	59	c	—	—	—	—
<i>Ascophyllum nodosum</i>	Summer	45	de	67	c	70	ab
	Winter	46	de	—	—	—	—
<i>Agarum cribrosum</i>	Summer	56	bcd	47	d	68	b
	Winter	47	de	—	—	—	—

$$^a \text{ Gravimetric absorption (\%)} = \frac{\text{Dry wt. eaten} - \text{dry wt. feces}}{\text{dry wt. eaten}} \times 100$$

$$^b \text{ Organic matter absorption (\%)} = \frac{\text{Fraction of organic matter in food} - \text{Fraction of organic matter in feces}}{(1 - \text{fraction organic matter in feces}) (\text{Fraction of organic matter in food})} \times 100$$

$$^c \text{ Food energy absorption (\%)} = \frac{\text{Calories in food eaten} - \text{calories in feces egested}}{\text{Calories in food eaten}} \times 100$$

^d The analysis is based on an Arcsin transformation of original data. Means followed by the same letter are not significantly different (ANOVA, DMRT)

^e Means not significantly different statistically

Table 5. Seasonal calorific values, percentage dry and ash weights of foods used in growth and preference experiments: N is the number or combustions used for determination of Kcal g⁻¹ values; percentage ash is the mean of 5 ashings for each species and season; percentage water is based on the mean of at least 9 samples

Food	Season	N	Kcal g dry weight ⁻¹	P ≤ 0.05 ^a	Ash (% of dry weight)	P ≤ 0.05	Kcal ash free g weight ⁻¹	P ≤ 0.05	% H ₂ O	Kcal g fresh weight ⁻¹
<i>Laminaria longicurris</i>	Summer	5	3.17	ab	19.4	d	3.93	bc	81.9	0.57
	Winter	5	3.10	a	39.2	b	5.09	a	88.2	0.37
<i>Chondrus crispus</i>	Summer	5	3.13	ab	24.3	c	4.13	b	75.4	0.77
	Winter	6	3.16	ab	22.6	cd	4.08	b	73.3	0.84
<i>Corallina officinalis</i> ^b	Summer	5	0.68	d	71.7	a	2.42	d	40.4	0.41
	Winter	5	0.89	e	74.5	a	3.52	c	32.6	0.60
<i>Ascophyllum nodosum</i>	Summer	5	3.40	c	20.4	cd	4.27	b	71.4	0.97
	Winter	9	3.44	c	21.7	cd	4.40	b	69.9	1.04
<i>Agarum cribrosum</i>	Summer	5	3.14	ab	24.6	c	4.17	b	80.1	0.63
	Winter	5	3.20	b	39.4	b	5.28	a	82.3	0.60

^a Means followed by the same letter are not significantly different (ANOVA, DMRT)

^b Endothermy correction applied (Paine, 1966)

Absorption Efficiency

Gravimetric absorption efficiencies generally were highest in winter, with values of 67, 62, 59, 47 and 46% for urchins fed *Laminaria longicurris*, *Chondrus crispus*, *Corallina officinalis*, *Agarum cribrosum* and *Ascophyllum nodosum*, respectively (Table 4). In summer the absorption of *L. longicurris* (65%) was significantly higher (P ≤ 0.5) than *A. cribrosum* (56%). There were no significant differences between the absorption efficiencies of *A. cribrosum* and *A. nodosum* (45%) at this time. Significant seasonal variation in dry matter absorption by *Strongylocentrotus drobachiensis* was noted with *C.*

officinalis, 34% and 59%, and *C. crispus*, 41% and 62% for summer and winter, respectively.

The absorption of food energy (calories) during summer by *Strongylocentrotus drobachiensis* (Table 4) was highest for *Laminaria longicurris* (79%) though not significantly higher than *Ascophyllum nodosum* (70%). Energy absorption was significantly lower for the remaining species ranging from 49% for *Corallina officinalis* to 68% for *Agarum cribrosum*. Similarly, the absorption of the organic fraction of each food in summer was greatest for the brown algae *L. longicurris*, *A. nodosum* and *A. cribrosum* (77, 67 and 47%, respectively Table 4). Red algae *Chondrus crispus* and *C. officinalis* were absorbed

Table 6 *Strongylocentrotus drobachiensis*. Caloric intake and absorption on 5 algal diets. Intake is based on feeding rates observed in Food Preference Experiments 2 and 3. Absorption is based on values observed in absorption efficiency experiments

	Food Preference Experiment 2 (based on multiple prey)				Food Preference Experiment 3 (based on single prey)			
	Summer		Winter		Summer		Winter	
	Intake ^a	Absorption ^a	Intake	Absorption	Intake	Absorption	Intake	Absorption
<i>Laminaria longicuris</i>	0.260	0.206	0.132	0.105	0.723	0.573	0.230	0.182
<i>Chondrus crispus</i>	0.219	0.120	0.094	0.052	0.733	0.402	0.245	0.135
<i>Corallina officinalis</i>	0.059	0.029	0.056	0.027	0.518	0.253	0.466	0.227
<i>Ascophyllum nodosum</i>	0.049	0.034	0.043	0.030	0.504	0.353	0.246	0.172
<i>Agarum cribrosum</i>	0.024	0.016	0.023	0.016	0.246	0.167	0.143	0.097

^a Kcal urchin⁻¹ d⁻¹

at efficiencies (28 and 26%, respectively) significantly lower ($P \leq 0.05$) than the other species.

Calorimetry

Calorific values and percentage ash and water content of the foods used in all experiments are shown in Table 5. The Kcal g⁻¹ of dry wt. values were converted to Kcal ash-free g⁻¹ and Kcal fresh-wt g⁻¹ with appropriate ash and water content values. Average caloric values ranged from 0.79 Kcal g dry wt.⁻¹ for *Corallina officinalis* to 3.42 Kcal g dry wt.⁻¹ for *Ascophyllum nodosum*. Only *C. officinalis* showed significant seasonal variation in Kcal g dry wt.⁻¹ (0.68 and 0.89 for summer and winter, respectively). Average values for Kcal ash-free g⁻¹ ranged from 2.97 to 4.73 for *C. officinalis* and *Agarum cribrosum*, respectively. All species except *A. nodosum* and *Chondrus crispus* exhibited significant seasonal differences in ash content. On a fresh weight basis, which is probably the most important ecologically to the urchin (Paine and Vadas, 1969), *Laminaria longicuris*, *C. crispus* and *C. officinalis* exhibited seasonality in caloric content. Average values ranged from 0.50 to 1.00 Kcal fresh-wt g⁻¹ for *C. officinalis* and *A. nodosum*, respectively.

Caloric Intake and Absorption

Caloric intake and absorption by *Strongylocentrotus drobachiensis* was highest for *Laminaria longicuris* followed in decreasing order by *Chondrus crispus*, *Corallina officinalis*, *Ascophyllum nodosum* and *Agarum cribrosum* when urchins had 5 foods to choose from (PE2) or in summer when they were fed a single species (PE3) (Table 6). In PE2, there was a perfect correlation (r_s , Spearman's Rank Correlation Coefficient = 1.0) between preference ranking and caloric intake in both seasons. Correlation coefficients between algal preference (PE2) and absorption were 0.90 in summer and 0.90 in winter. In winter measurements (PE3), caloric intake was greatest for urchins fed *C. officinalis*. *C. crispus*, *A. nodosum*, *L. longicuris* and *A. cribrosum* were ranked second to fifth,

respectively. Caloric absorption in summer was also highest for *C. officinalis*, but *L. longicuris* and *C. crispus* exchanged ranks. Correlations between food preference (PE3) and caloric intake were 0.70 for winter and 0.30 for summer, whereas correlations between food preference and absorption were 0.58 in winter and 0.83 in summer.

Growth Experiments

In Experiment A (single species diets), the increases in test diameter were greatest for *Strongylocentrotus drobachiensis* feeding on *Laminaria longicuris*, *Chondrus crispus* and *Corallina officinalis* (Fig. 3a). Differences in test diameter at the end of the experiment between urchins fed these diets were not significant ($P \geq 0.05$), but differences between mean monthly increases in diameter were significant. Increases were 1.40, 1.29 and 1.19 mm month⁻¹ for *L. longicuris*, *C. crispus* and *C. officinalis*, respectively. Increases in test diameter on *Ascophyllum nodosum* and *Agarum cribrosum* were significantly lower; 0.55 and 0.33 mm month⁻¹, respectively. Similarly, increases in weight were highest for *S. drobachiensis* fed *L. longicuris* (1.64 g month⁻¹) (Fig. 3b) and lowest for *A. cribrosum* (0.28 g month⁻¹). The weight gain of urchins fed *A. nodosum* was also low (0.47 g month⁻¹), whereas gains on *C. crispus* and *C. officinalis* diets were intermediate (1.27 and 1.29 g month⁻¹, respectively).

Increases in test diameter of urchins involved in reciprocal diet transfers (Experiment B) were greatest for urchins switched from *Agarum cribrosum* to *Laminaria longicuris* (8.01 mm) (Fig. 3a). These increases were significantly greater ($P \leq 0.05$) than control individuals fed either *L. longicuris* (5.52 mm) or *A. cribrosum* (3.36 mm). When urchins originally fed *L. longicuris* were switched to *A. cribrosum* the increases in test diameter were not significantly different ($P \geq 0.05$) from control urchins continuously fed *A. cribrosum* (3.36 mm for those switched from *L. longicuris* and 3.34 mm for the *A. cribrosum* controls). The increase in diameter of individuals transferred from *L. longicuris* was signifi-

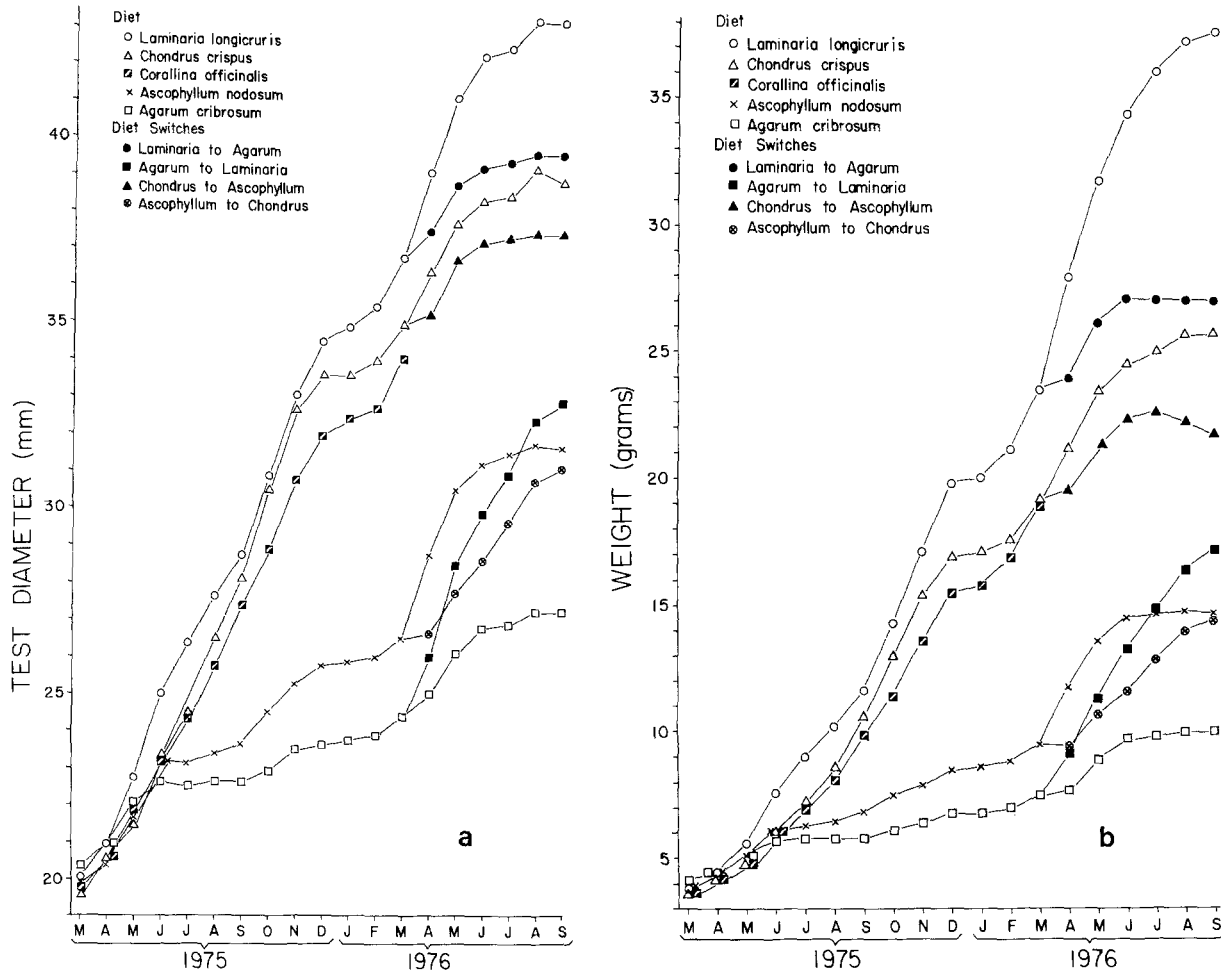


Fig. 3. *Strongylocentrotus drobachiensis*. Mean monthly increases in test diameter (a) and total body weight (b) on single species diets (Experiment A) and on reciprocal diet transfers (Experiment B)

cantly lower, however, than control urchins maintained on *L. longicuris*.

Similar patterns exist for increases in weight (Fig. 3b). Urchins switched from *Agarum cribrosum* to *Laminaria longicuris* more than doubled their weight during the experiment, whereas the average weight of control individuals on *A. cribrosum* increased by only one-third of their initial weight. The weight gain of *Strongylocentrotus drobachiensis* switched from *L. longicuris* to *A. cribrosum* was significantly lower ($P \leq 0.05$) than the controls on *L. longicuris*, and was not significantly greater than controls on *A. cribrosum*.

Growth of *Strongylocentrotus drobachiensis* involved in reciprocal transfers between *Chondrus crispus* and *Ascophyllum nodosum* reflected similar trends. The increases in test diameter and weight were significantly higher ($P \leq 0.05$) than control diet for urchins switched from *A. nodosum* to *C. crispus*. Conversely, urchins switched from *C. crispus* to *A. nodosum* showed no significant difference in test diameter or weight increase when compared to the *A. nodosum* controls.

The effect of the relative abundance of individual foods within each combination diet (Experiment C) on

the growth of *Strongylocentrotus drobachiensis* was consistent during the 18 months. In the combination diets of *Chondrus crispus*:*Laminaria longicuris* and *L. longicuris*:*Ascophyllum nodosum*, increases in test diameter and weight were greatest for the diets containing the highest ratio of *L. longicuris*, with the exception of the 50% *L. longicuris*:50% *C. crispus* combination. Similarly, differences in growth within the *C. crispus*:*A. nodosum* combination were directly related to the concentration of *C. crispus* in the diet (Fig. 4).

At the end of 1 yr, the growth (increases in test diameter and weight) of *Strongylocentrotus drobachiensis* ($N = 11$) was greatest on the combination of *Chondrus crispus* and *Laminaria longicuris*. Increases ranged from 1.33 to 1.49 mm month⁻¹ and from 1.58 to 1.82 g month⁻¹ respectively for test diameter and weight. Growth on *L. longicuris*:*Ascophyllum nodosum* and *A. nodosum*:*C. crispus* diets was lower than the above combination and ranged from 0.79 to 1.21 mm month⁻¹ for test diameter and from 0.96 to 1.27 g month⁻¹ for weight. During the following 6 months ($N = 6$), the increases in test diameter were greatest for the combinations of *L. longicuris* and *A. nodosum*. However, increases

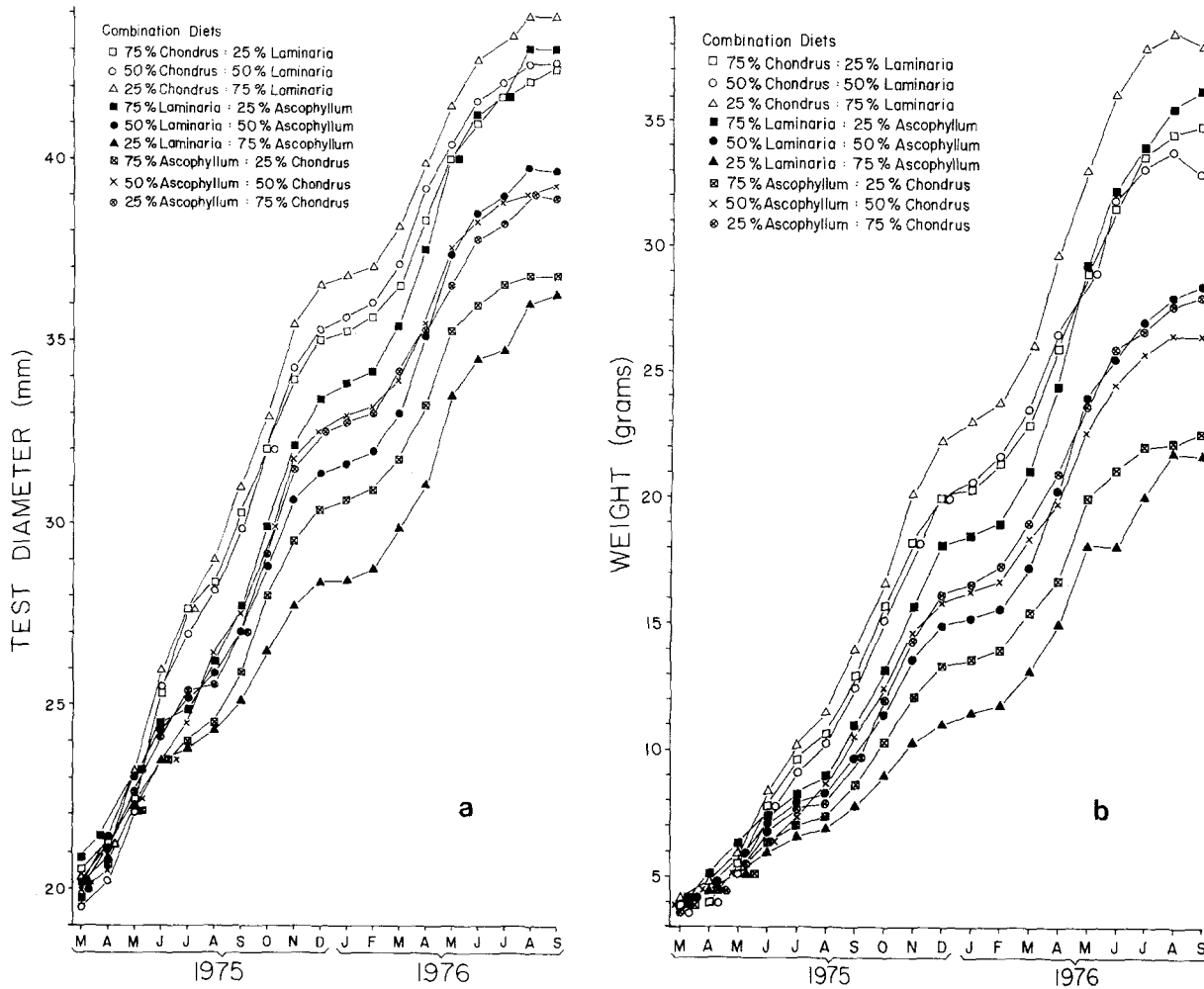


Fig. 4. *Strongylocentrotus drobachiensis*. Mean monthly increases in test diameter (a) and total body weight (b) on 2 species combination diets (Experiment C). Proportions of foods supplied are by fresh weight.

in weight were not different between the *C. crispus*:*L. longicruris* and *L. longicruris*:*A. nodosum* diets, but were significantly lower for combinations of *A. nodosum* and *C. crispus* (Fig. 4). The increase in weight on the 25% *C. crispus*:75% *L. longicruris* diet was greater than that for urchins fed only *L. longicruris*. Growth of urchins fed *C. crispus* was significantly lower ($P \leq 0.05$) than that for urchins fed any *L. longicruris*:*C. crispus* combination. Growth on the *L. longicruris*:*A. nodosum* combinations was higher than for individuals fed only *A. nodosum* but was significantly below that of growth on only *L. longicruris*. Similarly, growth on the combination of *C. crispus*:*A. nodosum* was not different from growth on *C. crispus* but was higher ($P \leq 0.05$) than that for urchins fed only *A. nodosum*.

Gonad Development (Reproductive Potential)

At the termination of Experiment A (March, 1976) the gonad indices of urchins fed *Laminaria longicruris*, *Chondrus crispus*, and *Corallina officinalis* (22.2, 15.7,

and 19.7%, respectively) were twice those fed *Ascophyllum nodosum* (9.8) and three times those fed *Agarum cribrosum* (6.1) (Table 7). The average gonad weight was significantly highest ($P \leq 0.05$) for urchins fed *L. longicruris* (5.02 g) and lowest for urchins on the *A. nodosum* (0.92 g) and *A. cribrosum* (0.45 g) diets.

The gonad index of urchins from Experiment B originally fed *Agarum cribrosum* and switched to *Laminaria longicruris* (22.1) was not different ($P \geq 0.05$) from that of those continuously fed *L. longicruris* (22.5). However, the average gonad weight of control individuals on *L. longicruris* (8.33 g) was more than twice that of urchins transferred to the latter from *A. cribrosum* (3.99 g). This was caused by the size differential of the urchins when transferred and sacrificed. In contrast, urchins continuously fed *A. cribrosum* had a gonad index of 7.1% and an average gonad weight of 0.67 g (Table 8). Urchins switched from *L. longicruris* to *A. cribrosum* had a lower gonad index (6.8) than the *A. cribrosum* controls. This amounts to a substantial reduction in reproductive effort when compared to the *L. longicruris* controls and the urchins sacrificed previously (March, 1976) (Table 7).

Table 7. *Strongylocentrotus drobachiensis*. Reproductive potential of urchins feeding on preferred and non-preferred foods (Growth Experiment A, urchins sacrificed in March, 1976)

Food	Gonad index		Trans- formed ^a \bar{x}	$P \leq 0.05^b$	\bar{x} Gonad weight	$P \leq 0.05$	Preference rank
	\bar{X}	SD					
<i>Laminaria longicruris</i>	22.2	3.16	28	a	5.02	a	1
<i>Chondrus crispus</i>	15.7	4.36	23	b	3.20	b	2
<i>Corallina officinalis</i>	19.7	4.48	26	ab	3.35	b	3
<i>Ascophyllum nodosum</i>	9.8	2.50	18	c	0.92	c	4
<i>Agarum cribrosum</i>	6.1	2.47	14	d	0.45	c	5

^a Arcsin^b Means followed by the same letter are not significantly different (ANOVA, DMRT)**Table 8.** *Strongylocentrotus drobachiensis*. Reproductive potential of urchins feeding on preferred and non-preferred foods (Growth Experiment B)

Food	Original diet	Gonad index		Trans- formed ^a \bar{x}	$P \leq 0.05^b$	Gonad weight \bar{x}	$P \leq 0.05$
		\bar{x}	SD				
<i>Laminaria longicruris</i>	L.L.	22.5	3.99	28	a	8.33	a
<i>Laminaria longicruris</i>	A.C.	22.1	1.96	28	a	3.99	b
<i>Agarum cribrosum</i>	A.C.	7.1	1.84	15	d	0.67	e
<i>Agarum cribrosum</i>	L.L.	6.8	1.25	15	d	1.85	d
<i>Chondrus crispus</i>	C.C.	13.8	5.23	22	bc	3.51	bc
<i>Chondrus crispus</i>	A.N.	13.5	1.69	21	bc	1.95	d
<i>Ascophyllum nodosum</i>	A.N.	10.9	2.87	19	c	1.65	de
<i>Ascophyllum nodosum</i>	C.C.	11.6	5.71	24	b	2.44	cd

^a Arcsin^b Means followed by the same letter are not significantly different (ANOVA, DMRT)**Table 9.** *Strongylocentrotus drobachiensis*. Reproductive potential of urchins feeding on combination diets. Proportions of foods supplied are by fresh weight

Diet	Gonad index ^a				Gonad index ^b			
	\bar{x}	SD	Trans- formed ^c	$P \leq 0.05^d$	\bar{x}	SD	Trans- formed	$P \leq 0.05$
<i>Chondrus: Laminaria</i>								
75%:25%	16.6	3.93	24	bcd	18.7	3.75	26	abc
50%:50%	24.3	3.96	30	a	20.5	4.01	27	abc
25%:75%	24.7	4.04	30	a	15.9	3.64	24	cd
<i>Laminaria: Ascophyllum</i>								
75%:25%	22.9	2.59	29	b	23.9	3.14	29	a
50%:50%	18.4	2.12	25	bcd	22.0	3.25	28	ab
25%:75%	16.0	3.51	24	cd	16.4	2.76	24	bcd
<i>Ascophyllum: Chondrus</i>								
75%:25%	14.0	2.14	22	d	14.1	2.14	22	d
50%:50%	18.6	6.14	26	bcd	15.5	3.98	23	cd
25%:75%	17.3	3.72	25	cd	14.9	2.81	23	cd

^a March 1976, N = 5, one year's growth^b September 1976, N = 6, 18 months' growth^c Arcsin^d Means followed by the same letter are not significantly different (ANOVA, DMRT)

Differences in gonad indices of individuals in the *Ascophyllum nodosum* and *Chondrus crispus* switches were not as dramatic as those above. Urchins continuously fed *A. nodosum* had a gonad index significantly lower than urchins transferred from *C. crispus* to *A. nodosum*. However, the gonad indices of controls fed *A. nodosum*

or *C. crispus* were not significantly different ($P \geq 0.05$) from those urchins switched from *A. nodosum* to *C. crispus*.

In the combination diet of *Chondrus crispus* and *Laminaria longicruris* (Experiment C), gonad growth determined in March, 1976 was significantly higher

($P \leq 0.05$) for individuals fed the higher percentages of *L. longicuris* (gonad index = 24.3 and 24.7 for 50 and 75% *L. longicuris*, respectively) (Table 9). When determined again in September, 1976 there were no significant differences between gonad indices for urchins on the 3 ratios.

For the combination diets of *Laminaria longicuris* and *Ascophyllum nodosum*, gonad growth was also greatest for urchins with the highest percentage of *L. longicuris* (75%) in the diet. Although this value is not significantly higher than the 50% *L. longicuris*:50% *A. nodosum* diet, it was significantly higher than the diet containing only 25% *L. longicuris* (Table 9). The same pattern was apparent in the urchins sacrificed in September, 1976.

The gonad indices of urchins feeding on combination diets involving *Chondrus crispus* and *Ascophyllum nodosum* showed no significant differences between combinations, regardless of whether they were sacrificed in March or September, 1976. Despite the large percentage (75%) of *C. crispus* in one of the diets, gonad development was not significantly different from the diet with the lowest percentage (25%) of *C. crispus*.

A comparison of gonad indices of individuals feeding on combination diets, sacrificed in March, revealed that only the ratios of 50:50% and 25:75% *Chondrus crispus*:*Laminaria longicuris* produced significantly better gonad growth. However, this was not significantly different ($P \geq 0.05$) from urchins fed *Corallina officinalis* or *L. longicuris*, singly.

Discussion

The sea urchin *Strongylocentrotus drobachiensis* showed significant non-random feeding behavior in 4 preference experiments. Although the degree of preference varied with season, rankings did not change with the exception of *Corallina officinalis* and *Laminaria longicuris* in winter (PE3, Table 3). Preferences paralleled changes in the relative abundance of prey such that preferred algae were always consumed first in the combination diets. Switching to alternative prey when the relative abundance of the preferred prey was decreased (as observed with *Thais emarginata*, Murdoch, 1969) did not occur. Similarly, Landenberger (1968) found that the density of prey had little effect on the preferences of sea stars.

There was no correlation between the food preference of *Strongylocentrotus drobachiensis* and algal caloric content (Kcal g fres wt.⁻¹, dry wt.⁻¹, or ash-free⁻¹). Similar findings by others (Carefoot, 1967a, b; Paine and Vadas, 1969; Himmelman and Carefoot, 1975; Vadas 1977) suggest that caloric value is only one factor involved in the evolution of food preference, and that other nutritional components contributing to relative food value may be more important. Himmelman and Carefoot (1975) indicate that the sensory attractiveness of algae should correlate with the rate at which foods are eaten. Preferences therefore maximize caloric as well as nutrient intake. Although there is a positive correlation

between PE2 and caloric intake in our study ($r_s = 1.0$, $N = 5$ for winter and summer) (Table 6), we believe this correlation results from the proportionately higher feeding rates on preferred foods rather than being the sole basis for this feeding strategy (Vadas, 1977).

The effectiveness of feeding apparatus in handling specific foods has been considered the primary determinant of feeding rate (Himmelman and Carefoot, 1975). Our results do not support this idea. Feeding rates observed during the first 2 months of PE4 indicate that urchins of the same size were able to ingest the 5 foods equally well (Fig. 1). The percentage of body weight consumed of *Ascophyllum nodosum* and *Agarum cribrosum*, the 2 least preferred algae, was higher than the more preferred *Chondrus crispus* and *Corallina officinalis* for the first 2 months. The subsequent reduction in feeding rates is considered to be the result of palatability and not simply the ability to "chew". Urchins transferred to preferred algae showed increased feeding response, further supporting the importance of palatability. Feeding rate appears to be a valid measure of food preference since it requires an integration of sensory behavior (attractiveness and palatability) with the physical ability to ingest. Similarly, gustation was thought to provide the best assessment of preference because of the complex behavioral mechanisms involved and the significant positive correlation between the various measures of food preference (Vadas, 1977).

Finally, selective feeding behavior with these and perhaps other urchins may be related more to protein and nitrogen uptake than energy content. Guerinot *et al.* (1977) have shown that nitrogen fixation occurs in the gut of these urchins, and that N_2 fixation (C_2H_2 reduction) was highest in *Laminaria* spp. including *L. longicuris*, the most preferred alga in our studies. They suggested that 8 to 15% of the daily nitrogen requirements could be met by N_2 fixation. Interestingly, these *Laminaria* spp. had the lowest nitrogen content of the 4 taxa examined. A positive relationship between protein and feeding behavior is suggested by studies on *Lytechinus variegatus* (Lowe and Lawrence, 1976) in which growth and reproduction were thought to be more dependent on protein than energy.

The avoidance of *Agarum cribrosum* is intriguing because urchins are refusing to feed on a calorie rich food (3.14–3.20 Kcal g dry wt.⁻¹); one from which they can absorb 68% of the available energy. Similar behavior has been reported for *Strongylocentrotus drobachiensis*, *S. purpuratus* and *S. franciscanus* on the west coast of the USA (Vadas, 1968, 1977), for *S. intermedius* in Japan (Fuji, 1962, 1967) and for *S. drobachiensis* in eastern Canada (Himmelman, 1969). Vadas (1977) suggested that the low preference and growth promoting quality of *A. cribrosum* resulted from the presence of a chemical defensive mechanism evolved in response to persistent grazing. The results of the present study and the fact the *A. cribrosum* is usually the only macrophyte present in high urchin density, overgrazed areas (personal observation) lends additional support to this idea. Terrestrial plants are known to produce secondary plant substances

which act as repellants to most insects and herbivores, and as attractants to the animals that feed on the plants (Fraenkel, 1959; Ehrlich and Raven, 1965; Feeny, 1975). Compounds similar to secondary plant substances (acids, tannins, alkaloids, toxins and others) have been found in various species of algae and are thought to affect palatability (Sieburth, 1968; Vadas, 1968; Odgen, 1976; Odgen and Lobel, 1978).

There was no correlation between the summer rankings of food absorption and food preference of *Strongylocentrotus drobachiensis* ($r_s = 0.2$). The correlation between winter rankings, however, was significant ($r_s = 0.9$, $P \leq 0.05$). In both seasons *Laminaria longicruris*, the most preferred food, was absorbed with the greatest efficiency. Absorption efficiencies in *S. purpuratus* were highest on those algae usually eaten in the field (*Macrocystis pyrifera* 80%, and *Egregia laevigata* 62%) (Boolootian and Lasker, 1964). Similarly, positive correlations between preference ranks and food absorption occurred in *S. drobachiensis*. (Vadas, 1977).

Lowe and Lawrence (1976) argued that failure to consider the levels of nutrients in foods (in absorption efficiency estimates) led to inaccurate assessments of the true nutritional value of foods to sea urchins. However, the use of gravimetric, caloric and total organic matter efficiencies are justifiable for comparisons of relative food value when coupled with feeding and growth experiments, which yield indirect measures of net assimilation. This is especially relevant in the case of *Corallina officinalis*, where the sustained growth of *Strongylocentrotus drobachiensis* could not have been predicted on the basis of absorption efficiency, the comparatively high ash values (low organic matter) and the low caloric content of the alga. Feeding rate experiments indicated that on a per "mouthful" basis, urchins fed *C. officinalis* had an intake of 3 times the dry matter and twice the organic matter of urchins fed *Laminaria longicruris*. However, despite the greater intake of organic matter on *C. officinalis*, urchins fed *L. longicruris* actually absorbed twice as much organic matter per "mouthful". This leads to the possibility that the incorporation of specific nutrients into tissue (assimilation) was greater for urchins eating *C. officinalis*.

Preferential feeding contributed significantly to the growth (Fig. 2) and reproductive potential (Table 1) of *Strongylocentrotus drobachiensis*. Similarly, urchins showed the greatest growth on combination diets containing the greatest percentage of preferred foods (Fig. 3, Table 3). Urchins transferred from non-preferred to preferred foods showed increased gonad (Table 2) and somatic growth (Fig. 2), whereas urchins transferred from preferred diets to non-preferred diets showed decreased gonad and somatic growth.

Similar results were obtained in reciprocal diet transfers with *Strongylocentrotus drobachiensis* in the Pacific (Vadas, 1977). He observed that smaller urchins transferred from non-preferred to preferred foods exhibited higher growth rates than larger ones maintained on preferred diets. Since growth slows as urchins get larger (Fuji, 1967; Ebert, 1968; Vadas, 1977), Vadas sug-

gested that urchins originally fed preferred foods had a greater growth "inertia" to overcome and hence, had a lower growth potential. He also found that food quality altered the basic growth rates and sizes of urchins. It is evident in the present study that urchins originally fed preferred algae were encountering a similar "inertia". Nonetheless urchins fed *Laminaria longicruris* continued to grow despite their larger size.

Additionally, Experiment B allowed us to interpret the dynamics of gonad production following diet transfers, which Vadas (1977) was unable to determine due to lack of urchins for sacrifice. In the present study the reduction in the gonad index of individuals originally fed *Laminaria longicruris* and transferred to *Agarum cribrosum* (from 22.1 to 6.8%) is therefore the result of reabsorption of previously elaborated tissue, probably necessitated by low algal intake during this period (Fig. 1). This effect could not be attributed to spawning as evidenced by the lack of difference between urchins sacrificed in March and September. The increase in the gonad index of urchins transferred from *A. cribrosum* to *L. longicruris* thus represents a realistic measure of the food value of preferred algae.

Lang and Mann (1976) reproted that reproductive population of urchins can exist for many years in overgrazed areas devoid of macroalgae by feeding on encrusting coralline algae and detritus. Likewise, ephemeral algae and benthic diatoms contribute significantly to the maintenance of such populations (Vadas and Larson, in preparation). The early elaboration of gonad tissue especially on preferred foods (Table 1) and the earlier studies by Vadas (1968, 1977) and Lang and Mann (1976) showing that urchins feeding in kelp beds had greatly increased growth and gonad production substantiates the importance of food quality and prey selection to urchin growth and reproductive capacity. Attempts to assess the reproductive potential of sea urchins on the basis of size or age alone, e.g. Thompson (1979), can be misleading or erroneous.

Lowe and Lawrence (1976) suggest that a mixed diet should be best for the tropical urchin *Lytechinus variegatus* because no one food supplied the greatest amount of all nutrients. This does not appear to be the case with *Strongylocentrotus drobachiensis* in Maine, nor with temperate-boreal urchins in general. The fact that the combination diet of 25% *Chondrus crispus*: 75% *Laminaria longicruris* produced greater weight increases than the pure *L. longicruris* diet should not be interpreted as an indication that combination diets are best for *S. drobachiensis* for several reasons. Test diameter increases on the 2 diets were not significantly different for the same period and more importantly, none of the combination diets resulted in significantly greater gonad production. In all cases growth and reproduction were directly related to the ratio of *L. longicruris* in the diet.

The field diet of *Strongylocentrotus drobachiensis* varies with both locality and season (Himmelman and Steele, 1971; Vadas, 1977; Vadas *et al.*, in preparation) with urchins feeding largely on the basis of availability (Lawrence, 1975). This "generalist" behavior might be

expected to evolve where food availability is unpredictable or where competition for food is especially keen (i.e. overgrazed areas). Ayling (1978) reported that laboratory food preferences of his urchins were not related to foods consumed in the field, supporting Lawrence's views and suggesting a generalist mode for those urchins as well. Although the good growth of *S. drobachiensis* on a number of single species diets and several combination diets (present study) tend to support the generalist view, strong non-random feeding, especially in the presence of foods that maximize growth and reproduction e.g. *Laminaria longicruris* in Maine and *Nerocystis luetkeana* in Washington, suggest that *S. drobachiensis* is a "facultative specialist". This dietary mode has adaptive significance. Preferential feeding results in a maximization of growth and reproduction and potential contribution to future generations in the shortest possible time, whereas the generalist behavior extends or assures survival even in overgrazed environments.

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Literature Cited

- Ayling, A. L.: The relation of food availability and food preferences to the field diet of an Echinoid *Evechinus chloroticus* (Valenciennes). *J. exp. Mar. Biol. Ecol.* **33**, 223–235 (1978)
- Booolootian, R. A. and R. Lasker: Digestion of brown algae and the distribution of nutrients in the purple sea urchin *Strongylocentrotus purpuratus*. *Comp. Biochem. Physiol.* **11**, 237–289 (1964)
- Breen, P. A. and K. H. Mann: Changing lobster abundance and the destruction of kelp beds by sea urchins. *Mar. Biol.* **34**, 137–142 (1976a)
- Breen, P. A. and K. H. Mann: Destructive grazing of kelp by sea urchins in eastern Canada. *J. Fish. Res. Bd Can.* **33**, 1278–1283 (1976b)
- Carefoot, T. H.: Growth and nutrition of three species of opisthobranch molluscs. *Comp. Biochem. Physiol.* **21**, 627–652 (1976a)
- Carefoot, T. H.: Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. mar. biol. Ass. U. K.* **47**, 565–590 (1967b)
- Carefoot, T. H.: A comparison of absorption and utilization of food energy in two species of tropical *Aplysia*. *J. exp. Mar. Biol. Ecol.* **5**, 47–62 (1970)
- Castilla, J. C. and D. J. Crisp: Responses of *Asterias rubens* to olfactory stimuli. *J. mar. biol. Ass. U. K.* **50**, 829–847 (1970)
- Conover, R. J.: Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* **11**, 338–345 (1966)
- Ebert, T. A.: Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* **49**, 1075–1091 (1968)
- Ehrlich, P. R. and P. H. Raven: Butterflies and plants: A study in coevolution. *Evolution* **18**, 586–608 (1965)
- Emlen, J. M.: *Ecology: An evolutionary approach*, 493 pp. Reading, Mass: Addison-Wesley 1973
- Feeny, P.: Biochemical coevolution between plants and their insect herbivores. pp 3–19. *In*: L. E. Gilbert and P. H. Raven (eds.) *Coevolution of animals and plants*. Austin, Texas: University of Texas Press 1975
- Fraenkel, G.: The raison d'être of secondary plant substances. *Science, N.Y.* **129**, 1466–1470 (1959)
- Fuji, A.: Studies on the biology of the sea urchin. V. Food Consumption of *Strongylocentrotus intermedius*. *Jap. J. Ecol.* **12**, 181–186 (1962)
- Fuji, A.: Ecological studies on the growth and food consumption of the Japanese common littoral sea urchin, *Strongylocentrotus intermedius* (A. Agassiz). *Mem. Fac. Fish. Hokkaido Univ.* **15**, 83–160 (1967)
- Guerinot, M. L., W. Fong, and D. G. Patriquin: Nitrogen fixation (acetylene reduction) associated with sea urchins feeding on seaweeds and eelgrass. *J. Fish. Res. Bd Can.* **34**, 416–420 (1977)
- Himmelman, J. H.: Some aspects of the ecology of *Strongylocentrotus drobachiensis* in eastern Newfoundland, 153 pp. M. Sc. Thesis: Newfoundland: Memorial University 1969
- Himmelman, J. H. and T. H. Carefoot: Seasonal changes in calorific values of three Pacific coast seaweeds, and their significance to some marine invertebrate herbivores. *J. exp. mar. Biol. Ecol.* **18**, 139–151 (1975)
- Himmelman, J. H. and D. H. Steele: Foods and predators of the green sea urchin *Strongylocentrotus drobachiensis* in Newfoundland waters. *Mar. Biol.* **9**, 315–322 (1971)
- Landenberger, D. E.: Studies on selective feeding in the Pacific starfish, *Pisaster*, in Southern California. *Ecology* **49**, 1062–1075 (1968)
- Lang, C. and K. H. Mann: Changes in sea urchin populations after the destruction of kelp beds. *Mar. Biol.* **36**, 321–326 (1976)
- Lasker, R. and A. C. Giese: Nutrition of the sea urchin, *Strongylocentrotus purpuratus*. *Biol. Bull.* **106**, 328–340 (1954)
- Lawrence, J. M.: On the relationship between marine plants and sea urchins. *Oceanogr. Mar. Biol. Ann. Rev.* **13**, 213–286 (1975)
- Leighton, D. L.: Studies of food preference in algivorous invertebrates of southern California kelp beds. *Pac. Sci.* **20**, 104–113 (1966)
- Lowe, E. F. and J. M. Lawrence: Absorption efficiencies of *Lytechinus variegatus* (Lamarck) (Echinodermata; Echinoidea) for selected marine plants. *J. exp. mar. Biol. Ecol.* **21**, 223–234 (1976)
- Miller, R. J. and K. H. Mann: Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. *Mar. Biol.* **18**, 99–114 (1973)
- Murdock, W. W.: Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* **39**, 335–354 (1969)
- Ogden, J. C.: Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquatic Bot.* **2**, 103–116 (1976)
- Ogden, J. C. and P. S. Lobel: The role of herbivorous fishes and urchins in coral reef communities. *Env. Biol. Fish.* **3**, 49–63 (1978)
- Paine, R. T.: Endothermy in bomb calorimetry. *Limnol. Oceanogr.* **11**, 126–129 (1966)
- Paine, R. T. and R. L. Vadas: Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar. Biol.* **4**, 79–86 (1969)
- Rapport, D. H.: An optimization model of food selection. *Am. Nat.* **105**, 575–587 (1971)

- Sieburth, J. M.: The influence of algal antibiosis on the ecology of marine microorganisms. pp. 63–94. *In*: M. R. Droop and E. J. F. Wood (eds.) *Advances in microbiology of the sea*, Vol. 1. New York: Academic Press 1968
- Siegel, S.: *Nonparametric statistics for the behavioral sciences*, 312 pp. New York: McGraw Hill 1956
- Slobodkin, L. B.: The strategy of evolution. *Am. Scient.* 52, 342–357 (1964)
- Thompson, R. J. Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*), the sea urchin (*Strongylocentrotus drobachiensis*), and the snow crab (*Chionoecetes opilio*) from populations in Nova Scotia and Newfoundland. *J. Fish. Res. Bd. Can.* 36, 955–964 (1979)
- Vadas, R. L.: The ecology of *Agarum* and the kelp bed community, 280 pp. Ph.D. Thesis, Washington: University of Washington 1968
- Vadas, R. L.: Preferential feeding: An optimization strategy in sea urchins. *Ecol. Monogr.* 47, 337–371 (1977)
- Vadas, R. L. and B. R. Larson: Significance of benthic diatoms in the diet of the sea urchin *Strongylocentrotus drobachiensis* in Maine, USA (in preparation)
- Vadas, R. L., B. R. Larson, K. Dunton and W. S. Grant: Diets, feeding and reproductive cycles of two estuarine populations of the green sea urchin *Strongylocentrotus drobachiensis* in Maine, USA (in preparation)
- Vadas, R. L. and W. S. Grant: Feeding and reproductive biology of an estuarine population of the sea urchin, *Strongylocentrotus drobachiensis*. *Bull. Ecol. Soc. AM.* 54, 34 (1973)

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