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Relation of food preference to fitness for the green sea urchin, *Strongylocentrotus droebachiensis*

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Abstract We maintained 30 to 35 mm sea urchins (*Strongylocentrotus droebachiensis*) on 17 different macroalgal diets in the field over a 130-d period and correlated the resulting changes in somatic and gonadal tissues with measures of food preferences. The various algae fell into three distinct categories according to their ability to support growth. The most striking effect of diet was on gonadal mass, there being a 14-fold increase for the best algal diet, compared to initial gonadal mass, and nearly a threefold decrease for the worst diet. The relation of food preference to somatic growth was nonlinear. A sharp increase in the growth of test diameter, total mass and test mass occurred between the nonpreferred and intermediately preferred algae, but growth rates were similar for intermediate and preferred algae. Gonadal growth tended to increase exponentially with an important measure of food preference, feeding rate (g ingested d^{-1}). These observations suggested that urchins only channel food resources into somatic growth up to a given point, additional reserves being used for producing gametes. The positive relationship of food preference to growth, and especially the strong correlation with gonadal production, indicates that the highly selective feeding of the urchin contributes to its fitness.

Introduction

Foraging models are based on the premise that strategies used in exploiting prey have evolved to maximize fitness (Schoener 1971; Pyke et al. 1977). Thus, feeding

behaviours represent long term (evolutionary) adaptations to optimize growth and reproduction and ultimately the production of offspring. Several factors influence the fitness a predator derives from exploiting a given prey resource (Sih 1987). The most obvious is the nutritional value of the prey resource relative to the needs of the predator. Most studies equate the nutritional value of a prey resource to its energetic content, but specific nutrient composition may also be important (Lowe and Lawrence 1976). A second factor affecting fitness is the time required for handling prey. Often plant prey have evolved structural and chemical defenses, which increase the handling costs for the predator (Hay and Fenical 1988). Finally, fitness may be affected by the time and costs involved in searching for prey. Here critical factors are prey abundance and distribution (patchiness), and in the case of animal prey, prey behaviours are often important (Lima and Dill 1990). Whereas models of optimal foraging have developed rapidly, testing of predictions, which are required to improve models, has lagged (Schoener 1971; Pyke et al. 1977; Vadas 1977; Sih 1987).

In the present study, we first quantify two instantaneous components of fitness, somatic and gonadal growth, for the green sea urchin, *Strongylocentrotus droebachiensis* O.F. Müller, when it is maintained on 17 different macroalgal diets. Then, we relate these correlates of fitness to two measures of the urchin's preference for the same macroalgae, as quantified by Himmelman and Nédélec (1990). The first was "attraction", the degree to which urchins detect and locate different algae under field conditions. Water-borne substances are important in determining attraction (Himmelman and Nédélec 1990). The second measure of preference was the urchin's feeding rate (g ingested d^{-1}), when supplied with each alga in laboratory experiments. The latter involves tactile responses of the urchin and its ability to manipulate the food (Himmelman and Nédélec 1990) and represents a robust measure of preference (Vadas 1977). The determination

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of both indices of preferences were made in early summer, when the urchins had likely finished spawning and when feeding rates were high (Larson et al. 1980; Himmelman 1984).

Strongylocentrotus droebachiensis is an abundant herbivore in subtidal systems in northern temperate waters and frequently depletes macroalgal resources causing urchin barrens, areas nearly devoid of fleshy macroalgae and associated fauna (Himmelman 1969, 1984, 1986; Foreman 1977; Propp 1977; Hagan 1983; Himmelman et al. 1983; Scheibling and Stephenson 1984; Keats et al. 1990). Previous studies in both the eastern North Pacific (Vadas 1968, 1977) and western North Atlantic (Himmelman 1969, 1984; Larson et al. 1980; Keats et al. 1983; Himmelman and Nédélec 1990) demonstrate it is a highly selective feeder. For example, attraction can vary by a factor of 7 and feeding rate by a factor of 20 for different algae (Himmelman and Nédélec 1990). Previous studies analyzing the relation of food selection to fitness (somatic and gonadal growth) considered only a small number of the macroalgal species available to the urchin. Vadas (1977) evaluated four algae from the eastern North Pacific (Washington State) and Larson et al. (1980) five algae from the western North Atlantic (Maine). Himmelman and Nédélec (1990) quantified preference of urchins for 18 algae, representing most of the common macrophytes in the northern Gulf of St. Lawrence. However, they did not quantify the ability of these algae to enhance fitness. Therefore, they could only compare preference to growth rates for some of the species studied, using growth estimates reported for urchins in other geographical areas. Limited sets of data have similarly limited rigorous examination of the relation of preference to fitness for other predators (Carefoot 1967; Sierszen 1990). Our study represents the first analysis for a marine invertebrate predator of the relation of preference to fitness considering most of the prey types available to the predator.

Methods

We quantified growth for 18 groups of sea urchins maintained in cages from late June to the end of October 1991 at Île du Havre, Mingan Islands, northern Gulf of St. Lawrence (50°14'N; 63°36'W). The cages measured 60 × 60 × 30 cm and permitted elimination of faeces and ample water circulation, the sides and bottoms being constructed with 6-mm galvanized mesh screening. They were installed at 18 m depth, on a pebble bottom, 100 m from shore, which was relatively free of macroalgal debris. Also, colonization by macroalgae and diatoms was slow because of the low irradiance at the experimental depth.

One day prior to the experiment, we collected urchins measuring 30 to 35 mm in diameter from a dense population on rocky substratum at 4 to 8 m in depth on the east side of Île du Havre (Cap du Corbeau), and randomly formed 19 groups of 30 individuals. Urchins of this size still have a strong potential for somatic growth

(Larson et al. 1980) and at the same time are capable of producing maximum-sized gonads (gonadal mass relative to total mass, Himmelman unpublished). One group was sacrificed to obtain a measure of the wet mass of the gonads and test (including spines, musculature and hydrovascular system) at the beginning of the experiment. Mass determinations were recorded after draining for 10 min on paper towels to remove excess water. ANOVAs indicated that initial test diameter ($F_{1,7} = 0.058$, $P = 1.000$) and wet mass ($F_{1,7} = 0.381$, $P = 0.991$) of the urchins were homogeneous among groups.

The other 18 groups of urchins were placed in separate cages in the field. Single macroalgal diets, freshly collected by diving in the subtidal zone, were supplied to 17 of the groups. The 18th group was not provided with food (unfed), and acted as a control for possible gains from algal debris in the area and nutrients in the water column. The macroalgal diets studied were the phaeophytes, *Alaria esculenta*, *Laminaria digitata*, *Saccorhiza dermatodea*, *Fucus edentatus*, *Ascophyllum nodosum*, *Scytosiphon lomentaria*, *Chordaria flagelliformis* and *Agarum cribrosum*; the rhodophytes, *Devaleraea ramentacea*, *Palmaria palmata*, *Porphyra miniata*, *Ptilota serrata*, *Phycodrys rubens*, *Turnerella pennyi* and *Lithothamnium* spp. (encrusted pebbles); and the chlorophytes, *Spongomorpha arcta* and *Ulvaria obscura*. Each alga was supplied in excess (≈ 1 kg) at 14-d intervals to ensure uninterrupted food access and to limit the effects of competition. After 130 d (25 June to 31 October 1991) the urchins were brought to the laboratory for determinations of growth parameters (final diameter, total mass, test mass and gonadal mass).

The measures of urchin preference (attraction and feeding rate) used in this study were determined for urchins from the same location (Cap du Corbeau) by Himmelman and Nédélec (1990). To measure the relative levels of attraction, Himmelman and Nédélec (1990) used 60 g monospecific bundles of different algae which were attached at random to steel spikes placed at equidistant points (3 m spacing) on a homogeneous 10-m deep flat, covered with *Lithothamnium*-encrusted pebbles. The site initially had an homogeneous distribution of urchins and was devoid of fleshy macroalgae. After 24 h, the number of urchins observed within a 0.25 m² quadrat around each algal bundle was counted. As a control, points where no fleshy macrophytes were anchored to the bottom were sampled. We considered that their control provided an approximation of the attraction of urchins for *Lithothamnium* spp. (although it was not equivalent to the values for the other algae since *Lithothamnium* spp. was not distributed at distinct points on the bottom). Further, feeding rates in 4 litre containers (20 cm in diameter) were determined by measuring the wet algal mass consumed per day by groups of 4 urchins (10 replicates per algal diet) fed with single algal diets.

To permit consideration of most of the algal prey types available to urchins (17 species) in our examination of the relation between food preference and fitness, we did not make replicate measures of the growth parameters associated with each alga. It would have been logistically infeasible to maintain twice as many cages in the field for a prolonged period. Since we did not have replicate cages for each alga, and the urchins within each cage were not independent (Hurlbert 1984), we did not apply ANOVAs to compare the ability of the various algae to support growth. Rather, we used the mean growth parameters obtained for each algal diet to examine the relation of food preference to fitness. This was done using Spearman rank correlation analyses. We considered three measures of food preference: attraction, feeding rate and calories ingested. Calories ingested was calculated for each alga from the feeding rates and energetic values reported by Himmelman and Nédélec (1990).

A hierarchical cluster analysis, applying the complete linkage method, was performed using the calculated growth parameters (test diameter, total mass, test mass and gonadal mass) to classify the different algae according to their ability to support growth (Hair et al. 1992). We employed a step-by-step procedure where each object (algal diet) starts out as its own cluster. The primary purpose of cluster analyses is to identify similar entities from the characteristics they possess (Hair et al. 1992).

Results

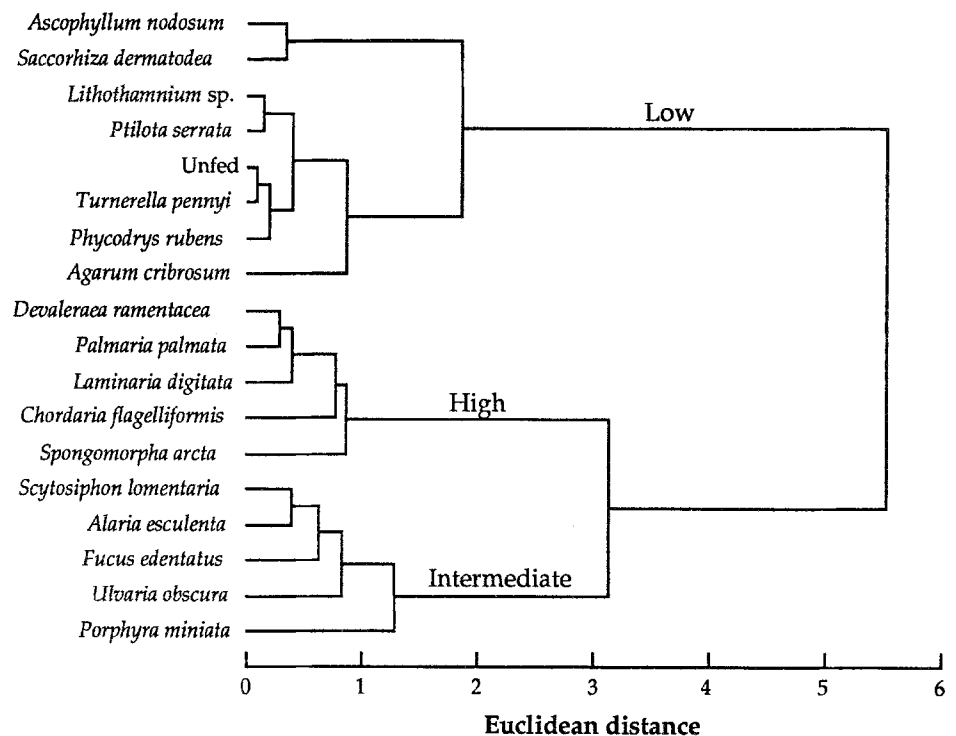
Growth of urchins varied markedly with algal diet (Table 1). The cluster analysis (Fig. 1) based on the four parameters (test diameter, total mass, test mass and gonadal mass) separated the algae into three groups of similar growth: (1) *Chordaria flagelliformis*, *Devaleraea ramentacea*, *Laminaria digitata*, *Palmaria palmata*, and *Spongomorpha arcta* which supported the highest rate

of growth; (2) *Alaria esculenta*, *Fucus edentatus*, *Scytosiphon lomentaria*, *Porphyra miniata* and *Ulvaria obscura* which permitted an intermediate rate of growth; and (3) *Agarum cribrosum*, *Ascophyllum nodosum*, *Lithothamnium* spp., *Ptilota serrata*, *Phycodrys rubens*, *Saccorhiza dermatodea* and *Turnerella pennyi* which permitted little or no growth. The diameter and tissue mass measurements of unfed urchins were equivalent to those for urchins maintained on algae of the third group (Fig. 1).

Table 1 Mean values ($n = 30$) and standard deviations (in parentheses) of final body measures for groups of urchins maintained on monospecific macroalgal diets from 25 June to 31 October 1991. Initial test diameter and total mass were calculated from measures of all urchins ($n = 570$) prior to the experiment, whereas initial mass of the test and gonads were based on a sample of 30 urchins which were dissected

Algae	Diameter (mm)	Total mass (g)	Test mass (g)	Gonadal mass (g)
<i>Spongomorpha arcta</i>	38.41 (1.90)	24.21 (3.18)	11.96 (1.58)	2.77 (0.70)
<i>Palmaria palmata</i>	37.52 (1.99)	23.40 (3.10)	11.36 (1.45)	2.64 (0.68)
<i>Laminaria digitata</i>	37.02 (1.76)	22.91 (3.15)	11.52 (1.52)	2.47 (0.87)
<i>Devaleraea ramentacea</i>	37.72 (1.93)	22.95 (2.97)	11.21 (1.32)	2.41 (0.80)
<i>Chordaria flagelliformis</i>	38.41 (1.77)	23.23 (5.19)	11.54 (1.31)	2.09 (0.56)
<i>Porphyra miniata</i>	37.08 (1.67)	21.42 (2.67)	10.82 (1.40)	1.43 (0.51)
<i>Alaria esculenta</i>	36.80 (1.76)	20.84 (2.60)	10.13 (1.26)	1.14 (0.56)
<i>Scytosiphon lomentaria</i>	36.26 (1.64)	20.34 (2.66)	9.72 (1.15)	1.04 (0.29)
<i>Fucus edentatus</i>	36.04 (1.78)	20.98 (2.61)	10.65 (1.33)	0.92 (0.34)
<i>Ulvaria obscura</i>	35.53 (1.72)	19.98 (2.71)	9.99 (1.35)	0.63 (0.33)
<i>Ascophyllum nodosum</i>	34.13 (1.41)	17.67 (2.50)	9.28 (1.23)	0.50 (0.20)
<i>Saccorhiza dermatodea</i>	34.50 (1.96)	18.46 (2.75)	9.53 (1.27)	0.44 (0.23)
<i>Agarum cribrosum</i>	33.65 (1.72)	16.46 (2.34)	5.54 (1.30)	0.19 (0.18)
<i>Ptilota serrata</i>	32.82 (1.61)	15.57 (1.78)	7.94 (0.98)	0.14 (0.12)
<i>Phycodrys rubens</i>	32.97 (1.53)	15.53 (2.02)	7.62 (1.20)	0.13 (0.14)
<i>Lithothamnium</i> spp.	33.08 (2.26)	15.35 (3.16)	7.86 (1.96)	0.12 (0.17)
<i>Turnerella pennyi</i>	33.08 (2.15)	15.06 (1.83)	7.57 (0.94)	0.07 (0.06)
Control (unfed)	33.10 (1.69)	15.08 (2.10)	7.41 (0.88)	0.08 (0.06)
Initial value	32.48 (1.49)	14.51 (2.02)	7.55 (0.96)	0.27 (0.26)

Fig. 1 *Strongylocentrotus droebachiensis*. Tree diagram resulting from a cluster analysis on mean values for each four correlates of fitness (growth in test diameter, total mass, test mass and gonadal mass) for urchins maintained on different macroalgal diets and one unfed group



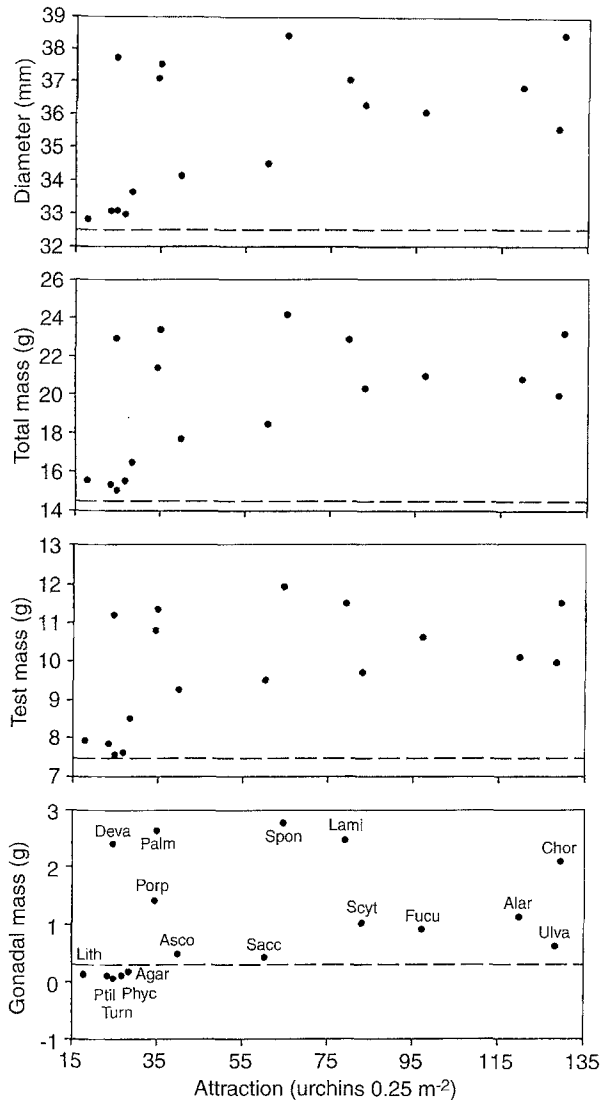


Fig. 2 *Strongylocentrotus droebachiensis*. Relation of fitness correlates (changes in test diameter, total mass, test mass and gonadal mass) to attraction for urchins maintained on different macroalgal diets from 25 June to 31 October 1991. "Attraction" was the mean number of urchins observed within 0.25 m² quadrats around 60-g bundles of the various algae. Macroalgae (listed in Table 1) are identified by the first four letters of the generic name on the bottom graph and are in the same position horizontally in the upper graphs. Dashed horizontal line indicates body measure at the beginning of the study

Positive relationships were found between attraction for the various algae (the degree to which urchins can detect and locate the algae in the field) and their ability to support growth in test diameter ($r_s = 0.53$, $P = 0.034$), total mass ($r_s = 0.50$, $P = 0.044$), test mass ($r_s = 0.56$, $P = 0.026$) and gonadal mass ($r_s = 0.48$, $P = 0.057$) (Fig. 2). Higher correlations were found between feeding rate (the rate at which urchins can ingest the algae) and the ability to support growth in test diameter ($r_s = 0.71$, $P = 0.006$), total mass ($r_s = 0.80$, $P = 0.002$), test mass ($r_s = 0.77$, $P = 0.003$) and gonadal mass ($r_s = 0.77$, $P = 0.003$) (Fig. 3). Positive correlations, but weaker than those previously cal-

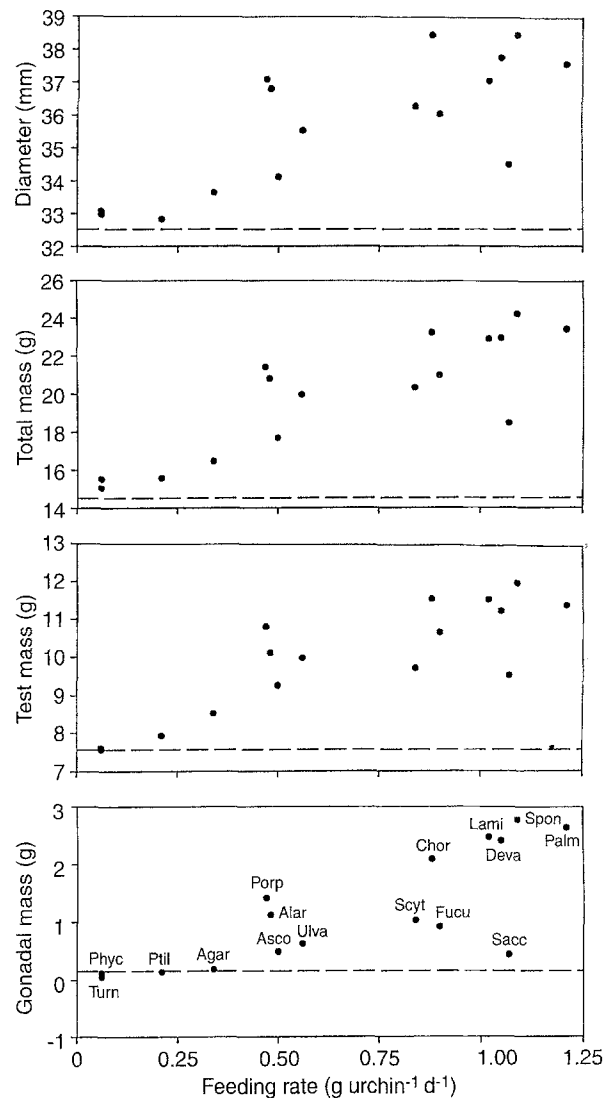


Fig. 3 *Strongylocentrotus droebachiensis*. Relation of fitness correlates (changes in test diameter, total mass, test mass and gonadal mass) to feeding rate for urchins maintained on different macroalgal diets from 25 June to 31 October 1991. Macroalgae (listed in Table 1) are identified by the first four letters of the generic name on the bottom graph and are in the same position horizontally in the upper graphs. Dashed horizontal line indicates body measure at the beginning of the study

culated with feeding rate, were found between calories ingested and the various growth parameters, test diameter ($r_s = 0.69$, $P = 0.008$), total mass ($r_s = 0.70$, $P = 0.007$), test mass ($r_s = 0.66$, $P = 0.011$) and gonadal mass ($r_s = 0.66$, $P = 0.011$) (Fig. 4).

Discussion

Our examination of the food preferences of *Strongylocentrotus droebachiensis* was based on 17 macroalgae, a major portion of the algal types available to urchins in the Mingan Islands. We did not quantify preference and fitness for the coralline alga *Clathromor-*

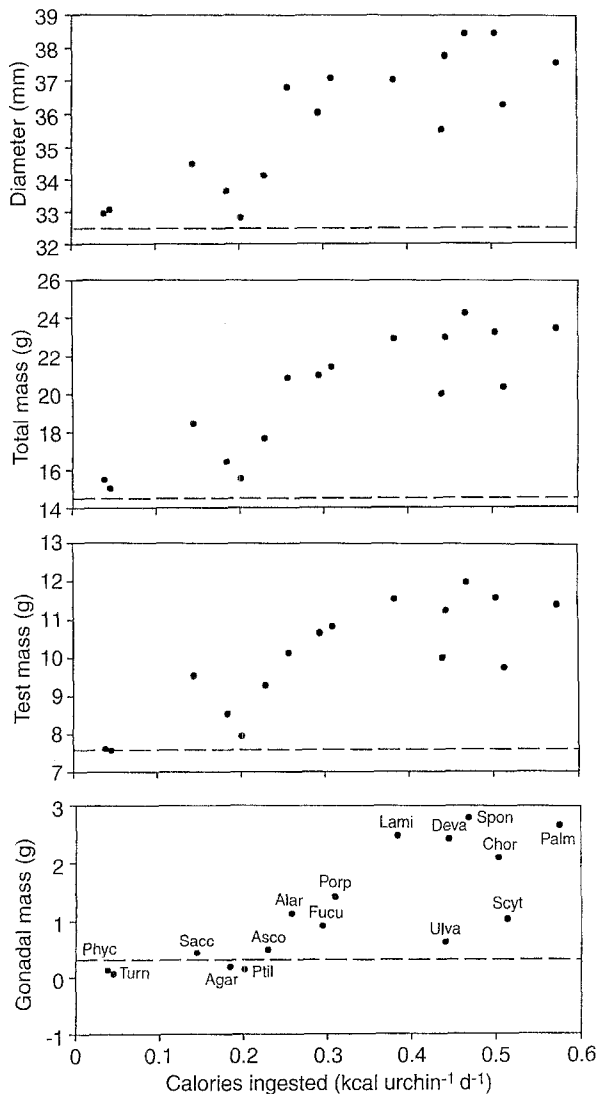


Fig. 4 *Strongylocentrotus droebachiensis*. Relation of fitness correlates (changes in test diameter, total mass, test mass and gonadal mass) to calories ingested, for urchins maintained on different macroalgal diets from 25 June to 31 October 1991. Macroalgae (listed in Table 1) are identified by the first four letters of the generic name on the bottom graph and are in the same position horizontally in the upper graphs. Dashed horizontal line indicates body measure at the beginning of the study

phum sp., for *Fucus vesiculosus*, for *Porphyra umbilicalis* or for *Laminaria longicruris* and *L. saccharina* but expect that values are roughly similar to those for the equivalent algae types which were studied, *Lithothamnium* spp., *F. edentatus*, *P. miniata* and *L. digitata*, respectively. Himmelman and Nédélec (1990) showed that the feeding rate on *L. longicruris* ($0.7 \text{ g ingested d}^{-1}$) is similar to that obtained for *L. digitata* (1.0 g d^{-1}), and Larson et al. (1980) and Keats et al. (1983) showed that *L. longicruris* supports rapid somatic and gonadal growth.

The low algal diversity in the Mingan Islands permitted comparing preference and fitness for most of the algal types in the region. Both selection of prey by

predators and prey defences to predators may change in space and over time (Sih 1987; Lima and Dill 1990). One important aspect of our study is that preference and fitness were determined for urchins from the same location, Cap du Corbeau. Although preferences were quantified in 1985 and growth in 1991, we have worked intensively in this area from 1981 to 1995 and have observed only minor changes in the distribution and abundance of urchins and algae.

The algae exploited by an urchin greatly influence its somatic and gonadal growth, parameters likely to be strongly correlated with the ability to produce offspring. We demonstrate that somatic growth is accelerated on preferred compared to nonpreferred algae. However, the effect is even greater for gonadal growth. At the beginning of the study, in June, the gonads were small ($\bar{x} = 0.27 \text{ g}$, $\approx 1.9\%$ of total body mass), because the urchins were collected after spawning from a barrens where food resources were scarce. In these waters, spawning had probably taken place one to two months earlier (Himmelman 1984; Keats et al. 1984). Feeding on the least preferred algae over 130 d resulted in a decrease in gonadal size, whereas feeding on preferred algae permitted 7- to 14-fold increases. However, these values underestimate the potential effect of diet on annual gonadal production and fitness. The highest gonadal mass obtained was only 11.4% of total mass (for urchins fed *Spongomorpha arcta*; Table 1). Prior to spawning in the spring, mean percentage gonadal mass often exceeds 20% (Himmelman 1978; Keats et al. 1984), and individual values can attain 30 to 35% (Himmelman unpublished). The gonads were smaller in our study because the experiment was terminated on 31 October and thus only covered the beginning of the period when gonadal growth is favoured (autumn through winter; Miller and Mann 1973).

Our data demonstrate that food preference is positively related to fitness, but the relationship is nonlinear. Somatic growth increases sharply with a change in diet from nonpreferred to intermediately preferred algae, but little or no further increase occurs with a change in diet to highly preferred algae. In contrast, gonadal growth tends to increase exponentially with one of the measures of food preference, i.e. feeding rate. That somatic growth already attains the maximum for algae of intermediate preference, whereas gonadal growth tends to continue to increase with food preference, suggests that the urchin only channels food resources into somatic growth up to a given level. Additional resources are invested into gonadal production. The opposite is indicated when food is of undesirable quality. Somatic parameters tend to increase slightly when urchins are fed the least preferred algae, and gonadal size decreases. Thus, gonadal reserves appear to be channeled into somatic growth or maintenance.

Since we supplied urchins with an abundance of algae in our experiments, search time, which potentially affects fitness, was not taken into account. *Stron-*

glyocentrotus droebachiensis is a highly mobile urchin and frequently aggregates around preferred algae (Vadas 1977; Himmelman 1984; Himmelman and Nédélec 1990). The rate of attraction (Himmelman and Nédélec 1990) provides a measure of the efficiency of urchins in detecting and locating different algae when they are equally available. The low attraction values for some algae, especially the red algae, suggest that associated search costs would be greater. This would decrease their ability to promote urchin fitness.

Algal abundance and distribution patterns may also affect search costs. Fleshy macroalgae at Cap du Corbeau fall into two distinct categories (Himmelman and Nédélec 1990). One consists of the nonpreferred algae found mainly in the urchin dominated zone (*Agarum cribrosum*, *Ptilota serrata*, *Phycodryis rubens*, and *Turnerella pennyi*), and the second consists of algae found only in shallow water (intertidal species and those making up the subtidal algal fringe). Encrusting calcareous algae are most abundant in the urchin zone. That all of the medium to highly preferred algae are found only in shallow water may increase costs in exploiting them and in turn decrease their profitability. They can only be obtained when pieces are detached and carried to deeper water by currents, or through moving shoreward. The latter requires the production of stronger tests and increased maintenance costs because of the greater risk of damage from water turbulence (Ebert 1982), and further may increase vulnerability to predators such as gulls and crows (Himmelman and Steele 1971). In spite of the potential search costs associated with exploiting preferred algae, ours and previous studies (Vadas 1977; Larson et al. 1980) demonstrate that only urchins which feed on intermediately to highly preferred algae can produce gametes. Feeding on the nonpreferred algae permits, at most, survival through periods when preferred foods are scarce.

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