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Growth of *Capitella capitata* cultured on various levels of detritus derived from different sources¹

Abstract—*Capitella capitata* was cultured on three levels of five organic sources of detritus (*Spartina alterniflora*, *Zostera marina*, mixed cereal, *Fucus*, and *Gracilaria* sp.). Standing crops increased with increasing food levels of all types of detritus, with a general gradation in the nutritional value of marsh grass < eelgrass < mixed cereal < rockweed < *Gracilaria*.

The best index of nutritional value was the amount of nitrogen supplied to the polychaetes. The biomass obtained at the highest feeding level of nitrogen-poor eelgrass was about the same as that at the medium feeding level of rockweed. Once a given level of nitrogen (50 mg m⁻² d⁻¹) was available, caloric value apparently affected the nutritive quality of the detritus: the high feeding levels of rockweed resulted in greater standing crop of the polychaete than diets of *Gracilaria* containing similar levels of nitrogen but fewer calories.

The importance of detritus-based food chains in marine environments has long been recognized (see Darnell 1967; Mann 1972; Tenore 1976). But while it is tempting to equate nutritional importance with the total quantity of detritus present in a system, it is misleading because of the heterogenous nature of the detrital pool. Detritus, depending on its source, has different caloric and biochemical characteristics that affect its decomposition (de la Cruz and Poe 1975; Gunnison and Alexander 1975) and nutritive value to detritivores. In fact many seeming contradictions in the literature dealing with the significance of detritus as a food resource are probably related to differences in detrital age and in the development of an associated microbenthic community. For example, both initial particle size and aging significantly affected the incorporation of ¹⁴C-labeled eelgrass detritus (probably actually

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the associated microbes) by the polychaete *Capitella capitata* (Tenore 1975). It could be misleading to infer the nutritional value of detritus from short term tracer experiments that do not take into account decompositional changes.

Although long term growth experiments would provide information about the relative nutritive value of different detritus, few such data are available. Seki (1972) grew the brine shrimp *Artemia salina* on the microorganisms associated with sedimented organic materials. Tenore and Gopalan (1974) found differences in the feeding rate and growth efficiency of the polychaete *Nereis virens* cultured on different sources of detritus. The addition of marsh detritus to fish food did not increase the growth of the killifish *Fundulus heteroclitus* (Prinslow et al. 1974). However, there are no extensive comparisons of the nutritive value of different sources of detritus.

The experiments reported here were conducted to determine possible differences in the growth of *C. capitata* when fed different levels of detritus derived from macrophytes. I thank D. Wachter for his assistance in conducting these experiments and D. Menzel for reviewing the manuscript.

Growth experiments were done in plastic trays (0.1 m²) that each received 100 ml min⁻¹ of 1- μ m-filtered, temperature-regulated seawater (Tenore and Huguenin (1973)). Each tray was aerated. The trays were layered with clean fine grain (<0.3 mm) sand and four replicate trays at 10° and 20°C received three food levels (50, 150, and 250 mg dry wt d⁻¹) of marsh grass *Spartina alterniflora*, eelgrass *Zostera marina*, rockweed *Fucus*, the red algae *Gracilaria*, or Gerber's mixed cereal. The marsh grass was collected on Skidaway Island, Georgia; rockweed in Plymouth Harbor, eelgrass in West Falmouth Harbor, Massachusetts; the *Gracilaria* was provided by ESL at Woods Hole Oceanographic Laboratory. All plant material was rinsed with freshwater, freeze-dried, ground to 120 μ m with a Wiley mill, and kept frozen

until used. Caloric values were determined with a Parr microbomb and carbon-nitrogen with a Perkin-Elmer elemental analyzer (model 240).

After several additions of the daily food levels, each tray received 30 *Capitella* from a stock culture. The worms were cultured for 3 months at the appropriate temperature and food level, a period adequate for several generations (Grassle and Grassle 1974) and for obtaining maximum saturation density (*K*). At the end of this time all the sediment in each tray was sieved (0.297-mm mesh). The worms were allowed to free themselves of debris, collected, counted, and their biomass determined by drying (90°C for 24 h) and ashing (500°C for 12 h). The various treatments were completed over a period of 1 year. No effect of season was detected.

There was a wide range in caloric value and nitrogen content of the different types of detritus, but these were not correlated (Table 1).

There were no significant differences (*F*-test in ANOVA) in the biomass of *Capitella* due to temperature at given food levels of a particular detritus, so data at 10° and 20°C were combined for comparison of a particular detritus and food level.

Variations in the number of worms were too high for consistent detection of significant differences (by *t*-test analysis) due to feeding effects, but the biomass showed increasing standing crops with increased food levels for all types of detritus. There was a gradation in the nutritional value of the different kinds of detritus, as indicated by the worm biomass attained in the trays, from marsh and eelgrass (the lowest) to *Gracilaria* and rockweed detritus (the highest).

Differences in the slopes between marsh and eelgrass versus rockweed and *Gracilaria* detritus suggested differences in absolute amount of some limiting constituent (Fig. 1). No relation was found between food value and caloric content of the detritus. For example, although marsh grass had the highest caloric content, it yielded the least *Capitella*, while *Gracilaria*, with the

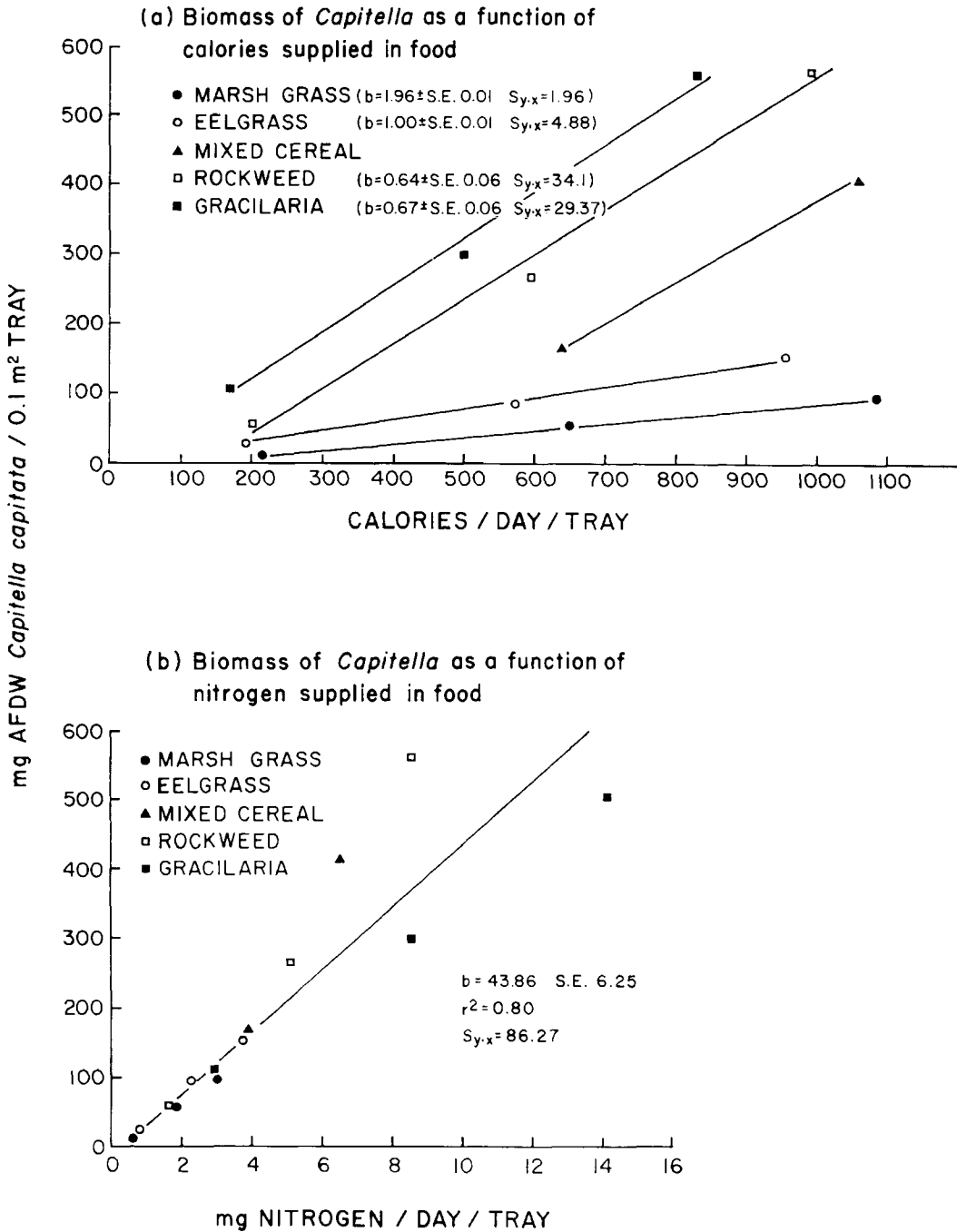


Fig. 2. Biomass of *Capitella capitata* at three food levels of five different types of detritus: a—based on calories; b—based on amount of nitrogen. Each value is based on eight replicates (four each at 10° and 20°C).

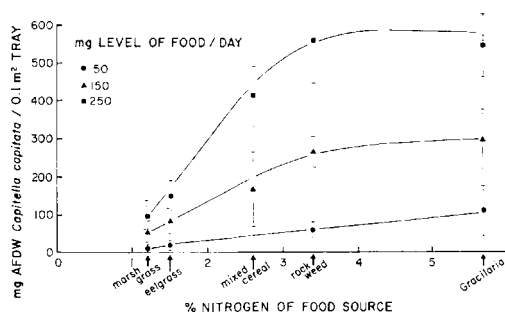


Fig. 3. Biomass of *Capitella capitata* at three food levels based on percentage of nitrogen of different types of detritus. Each value is based on eight replicates (four each at 10° and 20°C).

exploitation of a given environment by a particular species. However, biomass carrying capacity is a direct measure of the food chain transfers involved in secondary production. This is especially true for *Capitella* because individual sizes and weights vary considerably depending on the quality of food available. The numbers of individuals observed in the above experiments reflected differences in the stage of reproduction of the population when sampled.

The absence of consistent differences in the biomass produced at a given food level due to temperature is not surprising. Although initial growth rates at 10°C were probably lower than at 20°C, the population level obviously reached a carrying capacity (K) determined by the food level. The absence of predatory pressure probably enhanced this dominance of feeding effects. The temperature range between 10° and 20°C was optimum for the culture of *Capitella*, but temperatures above 20°C reduced reproductive rates.

The general approach of most food chain studies is centered on measurements of either energy or carbon as best representing intertrophic relations. In many "ecosystems approach" investigations caloric content has been used as the unit of measurement of trophic transfer. This is a valuable and appealing common denominator when we consider the broad problem of energy flow through different trophic levels. How-

ever, when the various uses and efficiency of transfer of energy at a given trophic level are considered, especially the food chain budget of a particular species, the sole use of the energetic component can be misleading. Even the use of carbon, the major structural component, does not adequately describe factors regulating trophic transfer. In most work in nutrition, fisheries, and aquaculture, the dominant role of nitrogen and of particular amino acids in secondary production has been recognized (see Natl. Res. Council 1975; Mann 1969).

The dietary calorie:protein ratio also affects transfer efficiencies and growth, and calculations of transfer efficiencies based only on calories miss this interaction. For example, fish fed diets with varying levels of energy and protein but with the same calorie:protein ratio have significantly different growth rates (Garling 1975). Though this point was emphasized early (Gerking 1955), many ecologists have not fully considered such data and have thus overlooked the regulatory role of nitrogen in secondary production.

The importance of the regulatory role of nitrogen can be seen especially in detrital food chains. The vast quantity of detritus entering coastal regions is generally quite low in nitrogen. The main sources of such detritus are species of marsh and seagrasses, poor nutritional sources for detritivores. Some ecologists have suggested that the reason for the poor food quality of these substances is that much of their caloric content is tied up in complex structural materials not readily available to the detritivores. But these plant materials also typically have an unfavorably high C:N ratio when they enter into the detrital pool. As the nitrogen content of the decaying plant material increases with aging, due to microbial activity, there is an increase in the nutritional value to the detritivores (Tenore 1975, 1977). In the study reported here, I added fresh detritus to the trays so that the oldest possible particle of detritus was 3-months old when the growing period ended.

Because organic nitrogen seems so im-

portant for the growth of *Capitella*, the possible use of alternate nitrogen sources should be considered further in investigations of the regulation of food chain dynamics. Certainly the role of nitrogen enrichment by the microbial community associated with detrital particles is of paramount importance in detrital food chains (Fenchel 1972). However, we should also consider the possible significance of nitrogen-rich particulate materials such as seaweeds and of dissolved organic nitrogen (DON) that occur in relatively low amounts in marine systems. Stephens (1972, 1975) demonstrated the uptake of naturally occurring primary amines by *Capitella* and suggested that the net influx could represent a significant supplement to the nutritional budget of animals. Although this idea has been criticized because of the concurrent levels of DON excretion (Johannes and Webb 1965), the DON pool might still function not so much as an energy source for detritivores but as a supplemental nitrogen source for organisms feeding on a nitrogen-limited food resource. Also, N_2 fixation by microorganisms in the guts of detritus feeders might supplement a nitrogen-poor detrital source.

Kenneth R. Tenore

Skidaway Institute of Oceanography
Savannah, Georgia 31406

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