Effects of food-level acclimation on digestive enzyme activities and feeding behavior of *Calanus pacificus*

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Abstract

A recent hypothesis in the zooplankton literature states that zooplankton acclimate to ambient food concentrations such that higher digestive enzyme activities and, consequently, higher maximum ingestion rates are achieved at higher food levels. To test this hypothesis, adult female *Calanus pacificus*, collected from the main basin of Puget Sound, Washington, USA, in August 1979 and May 1982, were conditioned for 2 wk at different concentrations of the diatom *Thalassiosira weissflogii* (=*fluviatilis*). Ingestion rates and the activity of the digestive enzymes laminarinase, maltase, and cellobiase were measured periodically during acclimation and in a block-designed feeding experiment at the end of acclimation. Consistent with the hypothesis, maximum ingestion rate and digestive enzyme activity were positively correlated. However, in contrast to the hypothesized mechanism, this result arose because both maximum ingestion rate and digestive enzyme activity were negatively correlated with food concentration during acclimation. The enhanced ingestion of copepods following long-term (12 to 14 d) acclimation to low food is similar to that previously described for short-term (e.g. 1 d) starvation. It might be energetically optimal for copepods experiencing a patchy food environment to maintain higher levels of digestive enzymes at low food concentrations in order to exploit high concentrations of food when encountered.

Introduction

Although the feeding of marine copepods has been a focus of considerable research for the past two decades, feeding rates, relationships, and behavior under natural conditions are, even for the best-studied species, largely speculative. As a case in point, there is a remarkable diversity of opinion regarding the most basic of feeding interactions: namely, response to food concentration. Various investigators have implied that copepods are either never (e.g. McLaren, 1978), sometimes (e.g. Frost, 1974), or always (e.g. Poulet, 1974; Huntley, 1981) food-limited in nature. In the present paper, we examine one of the hypotheses generated by these divergent viewpoints – that copepods acclimate behaviorally and biochemically to food concentration.

Evidence from laboratory studies generally supports a relationship between copepod ingestion rate (biomass consumed copepod~1 d~1~) and food concentration characterized by a critical or incipient food concentration above which ingestion rate is constant and maximum (e.g. Mullin, 1963; Frost, 1972, 1977): this is termed a saturation response. Below the critical concentration, there is a range of food concentration over which ingestion rate increases approximately linearly with increasing food, i.e., where volume clearance rate per individual is constant. Above the critical concentration, the food handling or processing capabilities of the copepod appear to be saturated, as clearance rate (volume cleared copepod~1 d~1~) decreases monotonically with increasing food.

A saturation response for copepods in nature was brought into question by the results of studies of the seasonal feeding and biochemistry of field populations. Poulet (1974), for instance, observed that ingestion rate was linearly related to food abundance when copepods were fed natural particulates at ambient concentrations (see also Huntley, 1981). The range of ambient particulate carbon concentrations covered the range of phytoplankton carbon used in the laboratory studies. In addition, Mayzaud and Conover (1976) found that seasonal changes in the activities of digestive enzymes of mixed zooplankton were positively correlated with changes in the abundance of particulate matter. These observations form the basis for an acclimation hypothesis of copepod feeding behavior.
that digestive enzymes of copepods acclimate to the level of available food such that ingestion is directly proportional to the ambient concentration of food (Mayzaud and Conover, 1976). According to the acclimation hypothesis, the saturation response observed in the laboratory can be an artifact of short-term experiments when copepods acclimated to relatively low food concentrations in nature are exposed to high food levels exceeding their digestive capability (Conover, 1978; Mayzaud and Poulet, 1978).

More significantly, the acclimation hypothesis implies that the recent food environment of a copepod will be reflected in the activity of the copepod’s digestive enzymes and, thus, that enzyme analyses of field-collected individuals might provide useful insights into the quantity and quality of food in the marine environment and the temporal and spatial scales of feeding interactions (e.g. Cox, 1981).

The acclimation hypothesis yields three predictions regarding the behavior or biochemistry of copepods acclimated to different food levels. The first prediction is that the feeding capacity (i.e., maximum ingestion rate at high food concentration) should be positively related to food concentration during acclimation (Fig. 1). The second prediction is that digestive enzyme activities of copepods should be positively correlated with food abundance during acclimation. The third prediction is that, at a given high concentration of food, ingestion rates should be positively correlated with digestive enzyme activity. In this paper, we describe results of experiments designed to test the predictions of the acclimation hypothesis for the copepod Calanus pacificus.

Materials and methods

Adult female specimens of Calanus pacificus were collected from the main basin of Puget Sound, Washington, USA, in late August, 1979, and subjected to an acclimation experiment in two phases. In the first phase, groups of copepods were acclimated to different food concentrations for 12 d. This was followed by a short-term, block-designed grazing experiment. Both phases of the experiment were conducted at 12 °C and in constant dim light. Cultures of the diatom Thalassiosira weissflogii (=fluvialis) were used as food.

During the acclimation phase of the experiment, groups of 160 copepods were maintained at 4 concentrations of food particles. Initially, cell densities of 500, 1 000, 2 000, and 4 000 Thalassiosira weissflogii ml⁻¹ were selected (1 000 cells ml⁻¹ = approximately 100 μg C l⁻¹), but the food levels were increased to 1 000, 2 000, 4 200, and 6 600 cells ml⁻¹ when Calanus pacificus showed much reduced clearance rates at 500 cells ml⁻¹ (see Frost, 1975). The culture containers, 26-liter glass jars, were continuously stirred with a rotating plunger (as in Frost, 1972; Vidal, 1980) to keep cells in suspension. Settled material, fecal pellets and copepod eggs were siphoned from the bottom of the containers once a day. The discarded water, about 15% of container volume, was replaced with filtered sea water and fresh food.

Concentrations of algal cells were maintained within about ±15% of desired levels by monitoring particle densities twice daily using a Coulter Counter (Model TAI1). Copepod feeding rates were calculated from changes in cell densities between sampling times. Algal growth rates (i.e., grazing controls) were determined from changes in cell densities in samples of water (without copepods) drawn from the acclimation containers and incubated in replicated 1 000 ml beakers under similar conditions. Calculations were according to the equations of Frost (1972).

Subsamples of the copepod populations in the acclimation containers were taken on Days 0, 5, 8, and 12 for determination of dry weights and digestive enzyme activities. The copepods were quick-frozen in liquid nitrogen, freeze-dried, and stored at −40 °C for later analysis.

The second phase of the experiment, performed on Day 13, involved constructing a functional response relationship for each acclimation condition by exposing copepods acclimated to given food levels to all four concentrations of food used during acclimation. Fifteen 500 ml jars were prepared for each food concentration (1 000, 2 000, 4 200, 6 600 cells of Thalassiosira weissflogii ml⁻¹). Six copepods from each acclimation condition were added to each of 3 jars, and the remaining 3 jars served as grazing controls. The jars were attached to a rotating wheel and the copepods were allowed to feed for 10 h. Ingestion and clearance rates were determined from the difference in initial and final particle counts corrected for algal growth rates (Frost, 1972). The copepods in each jar were killed in liquid nitrogen and saved for later analyses as described above.

A second acclimation experiment with some modifications was conducted with Calanus pacificus females collected in May, 1982. Groups of copepods were acclimated to concentrations of 500, 1 000, 2 000, 4 000, and 8 000 cells...