

Feeding behavior of *Tigriopus californicus* fed urchin feces vs fresh algae

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Abstract

Primary productivity does not occur in deeper waters due to limiting light availability, and thus deep subtidal organisms receive energy in the form of detritus. Urchins in the San Juan Archipelago catch and consume large quantities of kelp detritus, and due to inefficient digestive systems their feces have high caloric value and are readily available to benthic organisms. The nutritional value of fresh *Nereocystis luetkeana* and *Saccharina latissima* were compared to that of feces from urchins fed the same algal species in a set of population growth and dietary preference experiments using the copepod species *Tigriopus californicus*. Population growth rates were not recorded due to massive mortalities; however, significant copepod preference for urchin feces over both algal species was observed. This suggests urchins may provide a substantial link between shallow habitats of high algal productivity and deeper subtidal environments of low productivity by providing detritus in the form of high nutrient fecal matter.

Introduction

The movement and exchange of energy between marine habitats is a complex phenomenon that is not fully understood. Due to the limitations of light availability, the majority of primary productivity in the ocean occurs in the shallow photic zone (Connell and Orias 1964). Despite the decrease in primary productivity in deeper waters, secondary producers and consumers are able to thrive in subtidal and deep benthic environments (Vetter 1995; Vetter and Dayton 1999). This is due to the availability of detritus originating from photic zones that is transported by hydrodynamic forces into subtidal and pelagic ecosystems, providing deep subtidal organisms with otherwise unavailable energy (Newell 1965; Polis et al. 1997; Britton-Simmons et al. 2009;

Krumhansl and Scheibling 2012). Detritus is composed of a size range of particles from full kelp plants to particulate matter and feces (Newell 1965). In the San Juan Archipelago (SJA) detritus in the form of drift kelp is abundant at depths down to 120 m (Britton-Simmons et al. 2012).

The method and speed of movement of detritus among habitats is relatively unknown. One proposed pathway for detritus distribution is the activity of sea urchins. Urchins are common herbivores that dramatically affect ecosystems by consuming entire kelp forests (Paine and Vadas, 1969; Breen and Mann 1976). In the SJA, local deep dwelling urchin species are common to depths of 100 m and predominantly consume readily available drift algae (Britton-Simmons et al. 2009); average consumption rates of 21.2 g of drift algae per day has been observed in individual urchins (Lowe et al. 2014). Interestingly, despite the large amount of algae urchins consume, they are inefficient digesters with a low assimilation efficiency (Vadas 1977). Algae can even survive passage through the digestive tract (de Oliveira 1991), and on average 50-75% of ingested algal biomass is released in the feces (Mamelona and Pelletier 2005). These feces are then transported by hydrodynamic forces and deposited in deeper sedimentary habitats (Sauchyn and Scheibling 2009a). This suggests that urchin fecal matter is readily available to subtidal organisms and may provide them with otherwise lacking nutrients.

The carbon content of fresh urchin feces was found to be similar to that of dead algae, while also containing high levels of nitrogen and phosphorous (Koike et al. 1987). The caloric value, particularly that of aged feces, was higher than that of fresh algae (Kimber 2012; Hoins 2014). This is likely a product of increased microbe settlement and growth, which increases the nutritional value of feces (Fabiano et al. 1994; Thor et al. 2003) and

suggests that organisms would gain more energy from consuming urchin feces over drift kelp. However there has been no research done on secondary consumer preferences of urchin feces and their effect on growth. While previous research has shown no significant difference in *Tigriopus californicus* growth when they eat fresh vs. aged algae (Brown 2013), the process of algal digestion by urchins may lead to variation in growth between copepod populations fed urchin feces vs. undigested algae.

T. californicus is an abundant harpacticoid copepod species with a short generation time that is common in the SJA (Harris 1973; Powlik 1998) and predominantly consumes algae and detritus (Morris et al. 1980). In this study, I investigated the nutritional value of urchin feces by comparing growth of populations of *T. californicus* fed controlled diets of *Nereocystis luetkeana*, *Saccharina latissima*, and feces from urchins fed the same algal species. Population growth was predicted to differ between the diets of algae and feces, with greater growth in populations consuming feces.

A second observational experiment of *T. californicus* feeding behavior was also performed to test the hypothesis that secondary producers prefer urchin feces over fresh algae. Groups of copepods were allowed equal access to either *N. luetkeana* and *N. luetkeana* urchin feces or *S. latissima* and *S. latissima* urchin feces. Individuals were expected to consume feces over fresh algae.

Methods

T. californicus were collected from splash pools in front of Lab 12 at Friday Harbor Laboratories (FHL). *N. luetkeana* and *S. latissima* were collected off the FHL dock shortly before each treatment.

Fresh urchin feces were taken from *Strongylocentrotus franciscanus* kept in individual containers at FHL and fed controlled diets of either *N. luetkeana* and *S. latissima* (further explained in Hoins 2014). The feces were kept frozen until each treatment.

Population growth rate experiment – Groups of 30 gravid females were distributed into 12 jars and housed in a temperature controlled room at 14°C for 22 days. During the last week the temperature increased to 24°C. Jars were randomly assigned to experimental diets and numbered as follows:

- Jars 1 - 3 received *N. luetkeana* blade.
- Jars 4 - 6 received *N. luetkeana* urchin feces.
- Jars 7 - 9 received *S. latissima* blade.
- Jars 10 - 12 received *S. latissima* urchin feces.

Diets were kept at a constant volume in all jars to control for difference in sample weights.

At the end of three weeks, it was observed that the majority of the copepods had died and that a population of ciliates, identified as subclass Stichotrichia, were growing in the jars. Surviving copepods were counted and recorded. Ciliate density was determined by counting individuals in 0.5 mL of seawater taken from each jar.

Feeding behavior experiment – Groups of 20 *T. californicus* of similar life stages were distributed into ten Petri dishes. The dishes were randomly split between two treatments: five dishes received one square of *N. luetkeana* and an equal volume of *N. luetkeana* urchin feces each, while the additional five received *S. latissima* and *S. latissima* urchin feces.

The copepods were allowed equal access to both food samples and given fifteen minutes to settle. At 15 min, 45 min, and 75 min, counts were recorded of individuals

settled on algae, feces, or free swimming (defined as not within 3mm of either food source). The experiment was repeated five times, with new copepods and food samples for each new trial.

Results

Population growth rate – The number of surviving copepods per jar was highly variable.

The highest numbers of survivors were in *S. latissima* blade treatment jars, while *N.*

luetkeana blade jars had the smallest numbers (Figure 1). There was a positive correlation

between the number of copepod survivors and the density of ciliates (Figure 2, $R^2 = 0.43$).

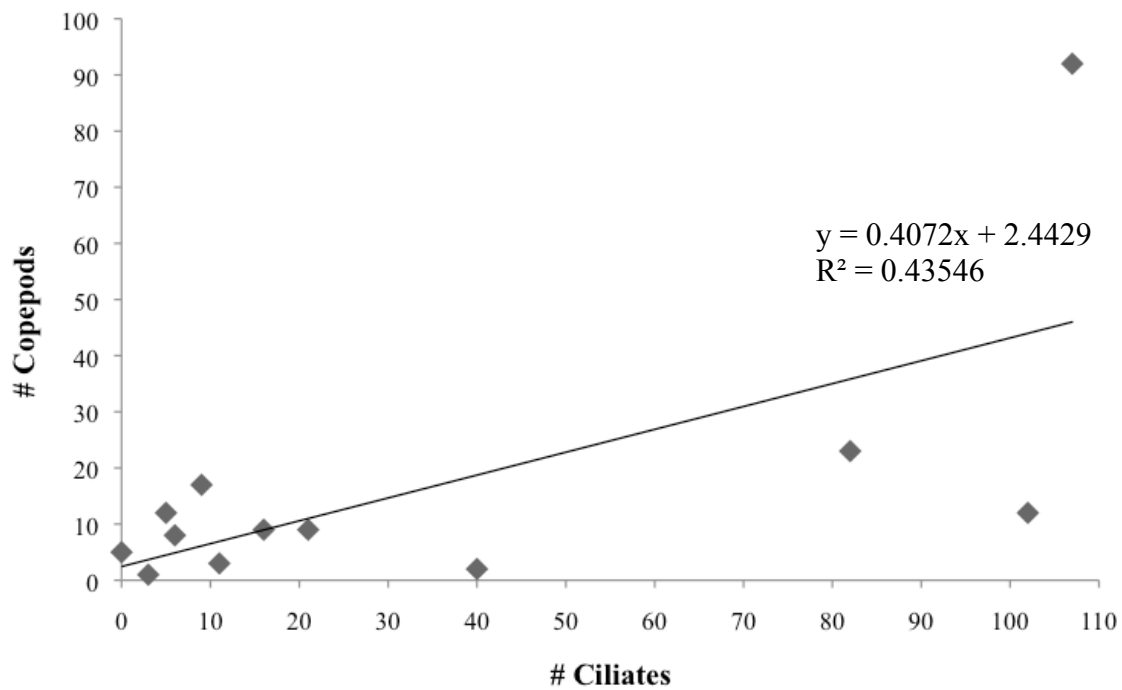


Fig. 1 Correlation between ciliate populations in 0.5 ml of jar water and surviving copepod numbers in corresponding jars.

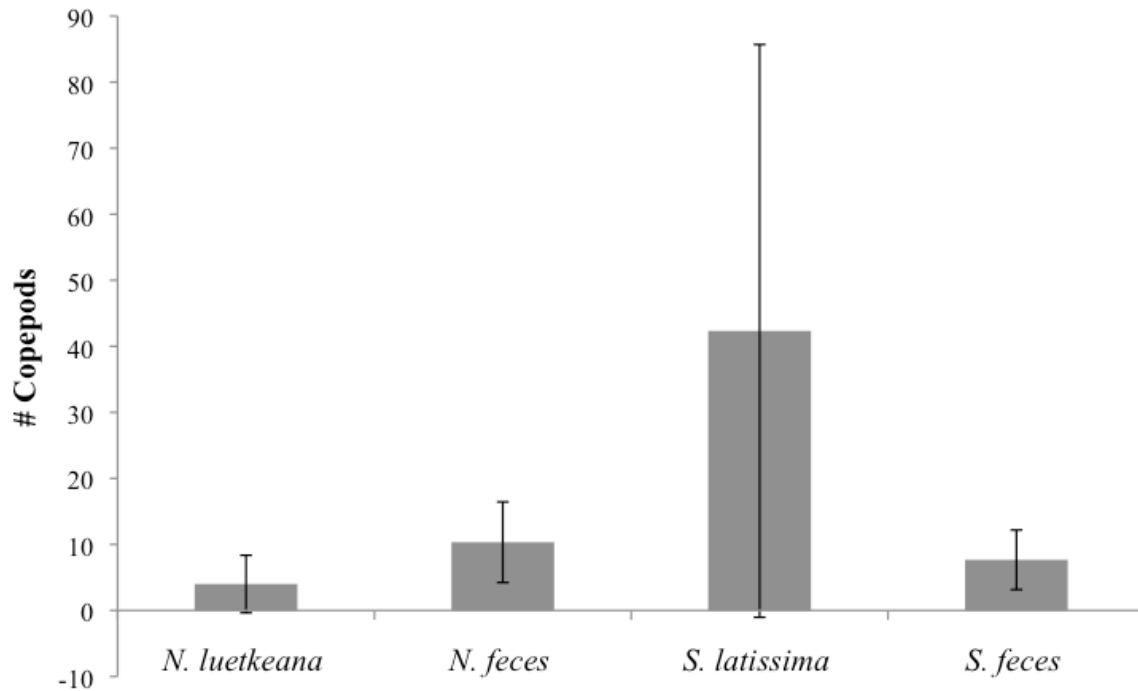


Fig. 2 Surviving copepod count by diet treatments: *N. luetkeana* blade, *N. luetkeana* urchin feces, *S. latissima* blade, and *S. latissima* urchin feces.

Feeding behavior – The average number of copepods settling on to feces increased over time in both algal treatments. At 75 minutes, there was a significant difference in copepod distribution among the three location categories in both *N. luetkeana* and *S. latissima* treatments (ANOVA, $F_{2,72} = 139$, $p < 0.001$, and $F_{2,72} = 360$, $p < 0.001$, respectively), with the most copepods consistently found on the feces and the fewest on the fresh algae. The preference of individuals for feces over fresh algae was also significant (*post hoc*, $p < 0.001$ for both treatments).

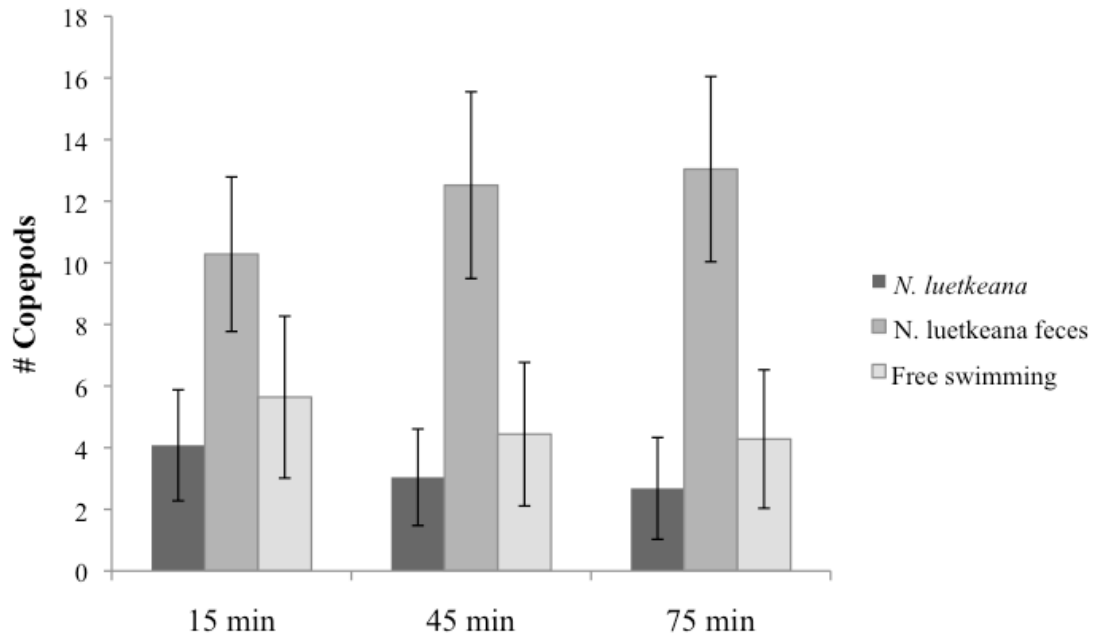


Fig. 3 Average *T. californicus* distribution among *N. luetkeana* and *N. luetkeana* urchin feces over time among five treatments with five replicates each. Bars represent standard deviation.

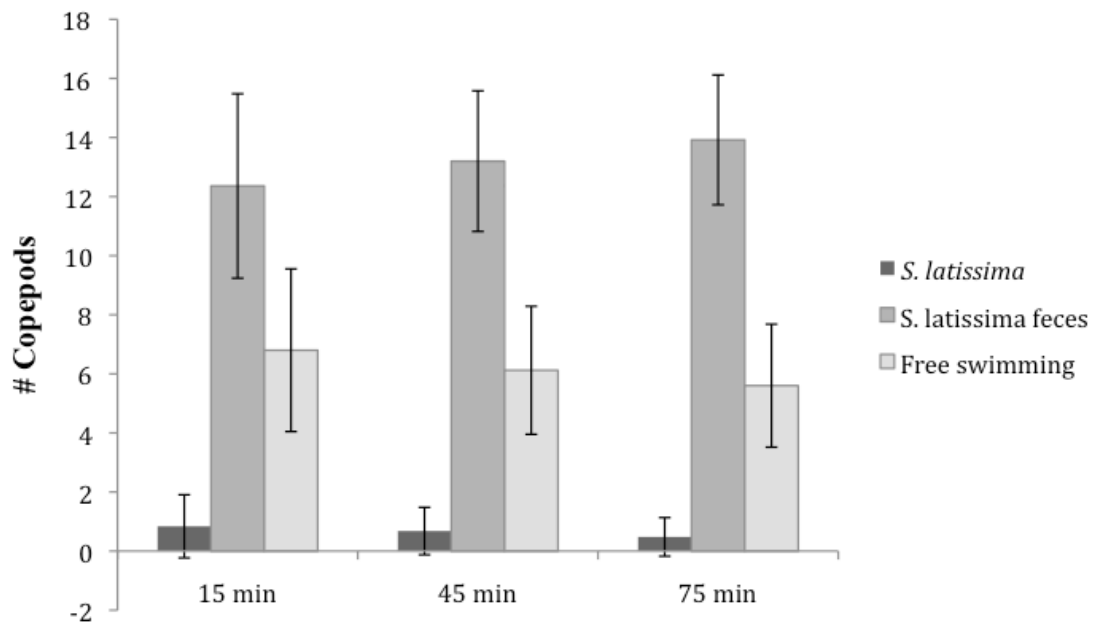


Fig. 4 Average *T. californicus* distribution among *S. latissima* and *S. latissima* urchin feces over time among five treatments with five replicates each. Bars represent standard deviation.

Discussion

Population growth rate – Stichotrichia is an abundant subclass of ciliates that feed on bacteria. It is unlikely that the ciliates found in the jars would have directly caused the death of the copepods, but their abundance may be a product of bacteria involvement and indicate that a bacterial bloom was responsible for copepod mortality. There were no noticeable bacteria populations observed when examining the water; however, the positive correlation between ciliate abundance and surviving copepods could relate to ciliates consuming harmful bacteria. The temperature spike, from 14°C to 24°C, may also have been a central factor in the copepod deaths, as it was the only consistent change between all 12 jars. *T. californicus* are continually subjected to large temperature variations in splash pools and it has been observed that 24°C is well within their tolerance levels (Ranade 1957; Vittor 1971). However, an abrupt change to a high temperature lasting over a week may have been highly stressful, resulting in mortality. Both the temperature spike and the presence of ciliates may be linked.

Feeding behavior – *T. californicus* clearly preferred eating feces over fresh algae of both species. While individuals consumed some fresh *N. luetkeana*, there were significantly higher numbers eating *N. luetkeana* urchin feces (Fig. 3). Very few copepods consumed fresh *S. latissima*, while feces were readily occupied (Fig. 4). *S. latissima* is rubbery and tough in composition and secretes a sticky mucus which may deter herbivory. *N. luetkeana* is softer and not chemically defended; this could explain these results.

Preference for feces over fresh algae may be explained a number of ways. Feces were partially decomposed and particulate, which may be easier for small copepods to eat compared to intact kelp blades. In addition, microbial settlement and the beginning of

decomposition of feces, which may occur both within an urchin's gut and after defecation, has been shown to increase the nutritional value of feces (Fabiano et al. 1994; Thor et al. 2003). Urchin feces have been shown to have a higher caloric value than fresh algae (Kimber 2012; Hoins 2014), and the caloric value of available food commonly influences organism diets (Emlen 1966). This is presumably because high nutrient foods result in increased growth and fitness.

Now that an obvious preference for feces has been observed, a successful recreation of the initial population growth rate experiment may yield significant results that support urchin importance in spatial subsidy between shallow regions of high productivity and deep subtidal environments. Urchins are common at depths below the photic zone in the SJA, where they consume the abundance of drift algae available in deeper waters (Britton-Simmons et al. 2012; Lowe et al. 2014). Increased densities of herbivore and detritivore communities have been observed under these urchins, presenting evidence that urchins provide appealing habitats to benthic organisms (Lowe et al. 2014). While this may in part be due to the shelter urchins offer with their spines, the feces urchins provide may also be an attractive and readily available food source organisms are taking advantage of. While *T. californicus* is not present in deep benthic communities, many harpacticoid copepod species are; they are an essential component of deep subtidal food webs as primary consumers. If they and other organisms are consuming urchin feces, this provides distinct evidence that urchins are a vital component in the movement and availability of energy in the deep subtidal.

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