Journal of Experimental Marine Biology and Ecology 500 (2018) 1–11

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Composition of phytodetrital food resources affects reproductive success in the deposit-feeding sea cucumber, *Parastichopus californicus* (Stimpson 1857)

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ARTICLE INFO

Keywords:
Food quality
Maternal investment
Reproductive success
Larval development
Fatty acids

ABSTRACT

Phytoplankton are important sources of dietary fatty acids (FAs) for higher trophic levels, yet FA composition varies among phytoplankton taxa, and under different growth conditions. Changes in the environment that lead to shifts in the composition of phytoplankton communities may thus alter FA supply in marine food chains. Reproductive processes in free-spawning marine invertebrates, which provision eggs with lipid to fuel early embryonic development, are particularly impacted by FA composition of the diet. In order to explore the effects of taxonomic changes in the source of phytodetrital food resources on invertebrate consumers, we conducted captive feeding experiments to examine differences in reproductive fitness of deposit-feeding sea cucumbers (*Parastichopus californicus*) fed two different algal diets. Body- and egg-condition variables were measured in females that were fed detritus of either the green alga *Tetraselmis* sp. or the diatom *Thalassiosira* sp., which differ in nutritional and FA composition. Subsequent timing of development and survival were recorded for pre- and post-feeding larval stages. FA analyses were conducted on feeds, spawned gonads, and eggs to identify specific FAs allocated to reproduction. Females that were fed *Tetraselmis* sp. had higher fecundity, but showed reduced larval survival relative to females that were fed the diatom *Thalassiosira* sp. Similar rates of larval development were recorded in both treatments. Significant differences were observed in the abundance of 20:5ω3 (EPA), 20:4ω4 (ARA), 22:3ω6 (DHA), 12:0, 16:0, and 18:0 FAs in eggs and gonads from females fed the two diets. Diet-related variation in fecundity and egg quality could directly affect recruitment success in *P. californicus*, and suggests that reproductive strategies may be altered under different environmental conditions. If feeding conditions are favorable to planktotrophic larvae, then producing a larger number of eggs with lower energy density (such as under *Tetraselmis*-fed treatments) may be acceptable, whereas different conditions may favor maternal investment in a smaller number of better-provisioned eggs (such as in *Thalassiosira*-fed treatments).

1. Introduction

Regional climate variability is causing large-scale changes in patterns of primary production and species composition of marine phytoplankton (e.g., Chavez et al., 2011), and these changes may have important nutritional consequences for marine consumers (Parrish, 2009; Kelly and Scheibling, 2012). Phytoplankton community composition is influenced by oceanographic conditions, including nutrient and freshwater inputs and sea surface temperatures (Behrenfeld et al., 2006). For example, while the green alga *Tetraselmis* has not been abundant in the North Pacific over the last few decades (Hori et al., 1982; Balzano et al., 2012), large blooms have occurred since the early 2000s at temperate Pacific latitudes, where mean sea surface temperatures have warmed roughly 2–5 °C (Pizarro et al., 2012, Southern California Coastal Ocean Observing System, 2013). Warming and freshening of surface waters favors smaller green algae and flagellates, and may stimulate future such blooms at higher latitudes in the Northwest Pacific in areas where diatoms are now seasonally dominant (Laws et al., 1988; Morán et al., 2010; Chavez et al., 2011).

The biochemical composition of phytoplankton is variable; thus, changes in phytoplankton community structure will likely impact the nutritional quality of phytodetrital food resources available to consumers, with potential consequences for benthic community structure and ecosystem function (cf. Campanyà-Llovet et al., 2017). In particular, fatty acid (FA) composition of phytoplankton is well-known to reflect differences in taxonomic composition (Brown et al., 1997; Kelly and Scheibling, 2012), growth conditions (e.g., irradiance and temperature; Guschina and Harwood, 2009, Leu et al., 2010), and changes in assemblage structure over the course of a bloom event (Wang et al., 2014). Dietary fatty acids are transferred directly from marine primary producers into consumer tissues without transformation (e.g., Parrish, 2013). Thus, FAs provide a useful metric for examining effects of

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https://doi.org/10.1016/j.jembe.2017.12.004
Received 14 May 2017; Received in revised form 6 November 2017; Accepted 1 December 2017

changing patterns of primary production on marine food chains.

Declines in diatom abundance decrease the availability of some essential FAs to marine consumers (Litzow et al., 2006; Kelly and Scheibling, 2012). For example, diatoms are particularly high in the essential polyunsaturated fatty acid (PUFA) 20:5ω3 (eicosapentaenoic acid, EPA), although they are low in the PUFA 22:6ω3 (docosahexaenoic acid, DHA; Parrish, 2013). In contrast, green algae are generally high in both EPA and DHA (Dunstan et al., 1993; Dalsgaard et al., 2003; Kelly and Scheibling, 2012). Decreased abundance of commercial fish and shellfish species such as salmon and Dungeness crabs (Hare et al., 1999; Zheng and Kruse, 2006) has already been linked to declines in diatom biomass in the Northeast Pacific (Chappell et al., 2013). The Essential FA Hypothesis proposed for North Pacific fisheries suggests that recent climate change is driving shifts in the relative population size of different forage fish species as a result of differences among taxa in susceptibility to FA limitation (Litzow et al., 2006; Litz et al., 2010).

Although there is evidence that some species of marine fish can synthesize PUFAs *de-novo*, most marine invertebrates have a limited ability to elongate precursors into long-chain PUFAs such as EPA and DHA (Brett and Muller-Navarra, 1997; Litzow et al., 2006; Parrish, 2013). Thus, many FA that are particularly important to animal health must be acquired through direct consumption of primary producers or through trophic transfer (Bergé and Barnathan, 2005; Reppond et al., 2008). In marine invertebrates, levels of essential FAs (e.g., EPA, DHA, and 20:4ω4 [arachidonic acid, ARA]) in the diet affect reproductive output, lipid density of eggs, and larval survival (e.g., Xu et al., 1994; Hendriks et al., 2003; Ehteshami et al., 2011). FAs provisioned to eggs are utilized as energy reserves (triglycerides, TAG), and as structural components of cell membranes in developing embryos and larvae (phospholipids, PL; George, 1994). In shrimp and oysters, high levels of EPA and DHA in adult diets result in the production of larger, faster-growing larvae with better survival rates (Xu et al., 1994; Hendriks et al., 2003). The percent composition of saturated fatty acids (SFA; specifically 14:0, 16:0, and 18:0) in phytoplankton supplied as larval feed has also been correlated with larval growth and survival rate (Goedkoop et al., 2007). SFAs may enhance larval growth because energy stored in SFAs is released more quickly and efficiently than in more complex, unsaturated FA. Thus, changes in the relative abundance of FAs in the diet of marine invertebrates due to shifts in the primary productivity regime may have consequences for reproduction and recruitment success.

We tested the effects of changes in species composition of the algal food source on reproduction in the commercially-harvested sea cucumber, *Parastichopus californicus*. This species has one of the widest distributions of any benthic invertebrate in the Northeast Pacific, ranging from Baja California, Mexico to the Aleutian Islands, Alaska, USA (Zhou and Shirley, 1996). Deposit feeders such as *P. californicus* are bioturbators that influence carbon cycling of the sea floor (Yingst, 1982). *P. californicus* is also a food resource for sea otters and bearded seals (Kvitek et al., 1992; Clark et al., 2009), and supports profitable commercial fisheries in the Northeast Pacific. Recent reports suggest that some populations of *P. californicus* are declining in abundance and average body size (Clark et al., 2009; Anderson et al., 2011). Changes in food supply have been linked to such declines in other taxa, as outlined above, and may be a factor here due to regional changes in oceanographic conditions (Strom et al., 2015).

Adult *P. californicus* spawn annually in early summer, and spawned eggs are fertilized in the water column where embryos develop into feeding planktonic larvae. After one to four months, larvae settle to the sea floor as 1 mm juveniles (Cameron and Fankboner, 1986). Larval mortality is likely high in species with long planktonic larval periods (e.g., Vaughn and Allen, 2010). In the Northeast Pacific portion of this species' range, the lengthy larval period combined with food-related depression of fecundity could impact recruitment success (e.g., Tayo et al., 2000; Becker et al., 2007). Moreover, the relatively late age of reproductive maturity (approximately four years) in this species leaves it vulnerable to overexploitation if reduced recruitment success prevents replacement of harvested adult animals. Therefore, identifying factors that affect reproductive output and recruitment success in a changing environment supports sustainabe management of *P. californicus* and other benthic marine invertebrates.

We conducted controlled feeding experiments with individuals collected in the Gulf of Alaska, USA, and examined the differences in body condition, reproductive output, and pre-feeding larval development in animals that were supplied with two different mono-specific algal feeds with different FA profiles: the green alga *Tetraselmis* sp., and the diatom *Thalassiosira* sp. We tested the hypotheses that taxonomic composition of the phytodetritus food source for adult females affects: 1) female body condition, 2)fecundity and egg size, 3) larval development and survival rates, and 4) total lipid content and FA signature of eggs and gonad tissues.

2. Materials and methods

2.1. Female collection and maintenance

Adult specimens of *P. californicus* ($n = 120$; total wet mass ≥ 95 g) were hand-collected by divers in Southeast Alaska (SEAK; 55° 20′ N, 131° 28′ W) in December 2012. Live animals were placed in groups of five in plastic bags filled with seawater (7–8 °C), and transported in coolers via air cargo to the University of Alaska, Fairbanks (UAF) Seward Marine Center (Seward, Alaska). Animals were transferred into experimental tanks within about 15 h of collection in the field. Evisceration (i.e., expelling of internal organs, sometimes including gonads) is common in holothurians when stressed, but eviscerations rates were low (8% of shipped animals). Although evisceration does not kill *P. californicus* (Fankboner and Cameron, 1985), all eviscerated animals were excluded because the gonad quality may be reduced if energy reserves are mobilized from gonads during regrowth of viscera.

Adults were maintained in twelve experimental tanks (six tanks for each of the two feeding treatments) for the duration of the 32-week feeding experiment (Fig. 1). Each 1 m × 1 m × 2.5 m tank was stocked with seven randomly selected animals, for a total of 84 animals. Live animals can not be sexed by visual inspection, but 1:1 sex ratios have been reported for this species (Cameron and Fankboner, 1986). Thus, each experimental tank was stocked with seven individuals in an effort to ensure multiple females were supplied to each tank. Stocking densities were within the range of abundance typically found in SEAK (2–12 animals m^{-2}; Clark et al., 2009). The tank bottoms were lined with a 5-cm layer of sterilized sand (grain size 2 mm) to facilitate deposit feeding, and filled with 20-μm filtered flow-through seawater (salinity 30). Seawater temperatures and light-dark cycles were adjusted bi-weekly to simulate the ambient conditions of SEAK based on National Oceanographic and Atmospheric Administration buoy data for Ketchikan, Alaska (ID 9450460; URL: http://pajk.arh.noaa.gov/).

2.2. Feed treatments

Tanks were randomly supplied with one of two feeds: the diatom *Thalassiosira* sp. (TW), or the green alga *Tetraselmis* sp. (TS; Fig. 1). Feeds were chosen to represent phytoplankton taxa that are favored under different oceanographic conditions in the Northeast Pacific (Jester et al., 2009; Balzano et al., 2012; Strom et al., 2015). These taxa contain significant differences in FA profiles that are representative of naturally occurring bloom-forming species typical of the Northeast Pacific and Alaska (Viso and Marty, 1993). Although natural diets would not consist of a single algal species, we used commercially available mono-specific algal cultures to ensure uniformity among batches of feeds supplied periodically throughout the experiments, and to minimize confounding effects of a mixed diet in our results. Algal feeds were purchased as whole-cell live concentrates from Reed Mariculture Inc.