Progress in Oceanography 155 (2017) 1–12

Contents lists available at ScienceDirect

Progress in Oceanography

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

Temporal variation in the biochemical ecology of lower trophic levels in the Northern California Current

J.A. Miller [a,*], W.T. Peterson [b], L.A. Copeman [c,d], X. Du [d], C.A. Morgan [d], M.N.C. Litz [a]

[a] Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Hatfield Marine Science Center, 2030 SE Marine Science Dr., Newport, OR 97365, USA
[b] NOAA-Fisheries, Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365, USA
[c] College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA
[d] Cooperative Institute for Marine Resources Studies, Hatfield Marine Science Center, Newport, OR 97365, USA

ARTICLE INFO

Article history:
Received 17 January 2017
Received in revised form 17 April 2017
Accepted 4 May 2017
Available online 6 May 2017

Keywords:
Biochemical ecology
Lower trophic levels
Lipids and fatty acids
Northern California Current, Oregon, USA

ABSTRACT

There is strong correlative evidence that variation in the growth and survival of secondary consumers is related to the copepod species composition within the Northern California Current. Potential mechanisms driving these correlations include: (1) enhanced growth and survival of secondary consumers when lipid-rich, boreal copepod species are abundant, with cascading effects on higher trophic levels; (2) the regulation of growth and condition of primary and secondary consumers by the relative proportion of certain essential fatty acids (FAs) in primary producers; or (3) a combination of these factors. Disentangling the relative importance of taxonomic composition, lipid quantity, and FA composition on the nutritional quality of copepods requires detailed information on both the consumer and primary producers. Therefore, we collected phytoplankton and copepods at an oceanographic station for 19 months and completed species community analyses and generated detailed lipid profiles, including lipid classes and FAs, for both groups. There was strong covariation between species and biochemistry within and across trophic levels and distinct seasonal differences. The amount of total lipid within both the phytoplankton and copepod communities was twice as high in spring and summer than in fall and winter, and certain FAs, such as diatom indicators 20:5ω3 and 16:1ω7, comprised a greater proportion of the FA pool in spring and summer. Indicators of bacterial production within the copepod community were proportionally twice as high during fall and winter than spring and summer. Seasonal transitions in copepod FA composition were consistently offset from transitions in copepod species composition by approximately two weeks. The timing of the seasonal transition in copepod FAs reflected seasonal shifts in the species composition and/or biochemistry of primary producers more than seasonal shifts in the copepod species composition. These results emphasize the importance of interactions between the copepod community and their available phytoplankton prey in regulating the nutritional quality of primary consumers.

1. Introduction

The influence of environmental variation on the productivity of marine species has long been recognized (Mantua et al., 1997; McGowan et al., 1998) although mechanistic linkages remain poorly understood (Botsford, 2001; Beamish and Noakes, 2002). Strong relationships between variation in primary production, which is largely regulated by light, nutrients, and temperature, and the abundance of zooplankton and fish are often cited as evidence for "bottom-up" regulation (Ware and Thomson, 2005; El-Sabaawi et al., 2012; Batten et al., 2016; Kvile et al., 2016). Seasonal and interannual variation in the species composition and abundance of primary consumers, such as copepods, can also be directly linked to environmental (Peterson and Miller, 1975) and climate variability, such as the Pacific Decadal Oscillation (Hooff and Peterson, 2006; Keister et al., 2011; Peterson et al., 2014) and El Niño-Southern Oscillation (Peterson et al., 2002; Fisher et al., 2015). There is also evidence that large-scale shifts in the composition and abundance of boreal marine fish communities are related to variation in the nutritional quality of their prey, i.e., the relative abundance of certain fatty acids (FAs), in addition to, and perhaps more than, the quantity of lower trophic level production (Litzow et al., 2006).

Variability in productivity and community structure of intermediate trophic levels, such as forage fish and other secondary con-

* Corresponding author.
E-mail address: Jessica.Miller@oregonstate.edu (J.A. Miller).

http://dx.doi.org/10.1016/j.pocean.2017.05.003
0079-6611/

sumers, has been related to lipid quantity and quality of primary producers (St. John and Lund, 1996; Brett and Muller-Navarra, 1997; Litzow et al., 2006). Potential mechanisms for relationships between enhanced productivity and growth in these intermediate trophic levels and the lipid quantity and composition within lower trophic levels include greater energy density or more efficient energy transfer associated with lipid-rich prey that contain high levels of polyunsaturated FAs. Litzow et al. (2006) posit that observed species community shifts in boreal oceans may be initiated by changes in the relative amounts of certain FAs, such as docosahexaenoic (DHA: 22:6ω3) and eicosapentaenoic (EPA: 20:5ω3) acids, in primary producers that differentially impact growth and survival of lipid-rich and lipid-poor consumers. Disentangling the relative importance of prey species composition, lipid quantity, and lipid composition on growth and productivity requires an understanding of the temporal variation in each of those factors across trophic levels (Budge et al., 2014). While there is a growing body of information on how species composition responds to seasonal and environmental variation (Mackas et al., 2001; Hooff and Peterson, 2006; Du and Peterson, 2014a, 2015; Fontana et al., 2016), less is known about the biochemical responses of those communities to environmental variability (El-Sabaawi et al., 2009a,b; Connelly et al., 2016).

The Northern California Current is a region of seasonal upwelling where coastal winds shift from predominantly northwesterly, upwelling favorable during spring and summer to southwesterly, downwelling favorable during fall and winter. The coastal copepod community within the Northern California Current consistently oscillates between one dominated by warmer water, sub-tropical, "southern" species transported from the south during fall and winter and one dominated by lipid-rich, boreal, "northern" species transported from the north during the spring and summer upwelling period (Morgan et al., 2003; Hooff and Peterson, 2006). This variation in copepod species composition is influenced by the strength of the poleward-flowing Davidson Current in winter and southward coastal flows in summer associated with coastal upwelling. There are also oscillations in copepod community composition on longer temporal scales that correlate with regional-scale oceanographic indices, such as the Pacific Decadal Oscillation and El Niño Southern Oscillation (Fisher et al., 2015), likely through variations in water transport within the coastal branch of the Northern California Current (Keister et al., 2011): a lipid-rich community dominates during negative (cold) phase of the PDO and a lipid-poor community during positive (warm) phase of the PDO.

There is strong correlative evidence that variation in the distribution, growth, and survival of higher trophic levels is related to the copepod species composition in Northern California Current coastal waters. For example, changes in the spatial distribution (Bi et al., 2011), growth and survival of juvenile Pacific salmon *Oncorhynchus* spp. (Peterson and Schwing, 2003; Burke et al., 2013; Miller et al., 2014), early growth and survival of northern anchovy *Engraulis mordax* (Litz et al., 2008; Takahashi et al., 2012), recruitment of sablefish *Anoplopoma fimbria* (MacFarlane and Beamish, 1992; Schirripa and Colbert, 2006), and seabird reproductive success (Sydeman et al., 2014) are correlated with copepod community composition. A potential mechanism responsible for these correlations (first proposed by Peterson and Hooff, 2005) is that a copepod community dominated by lipid-rich, boreal species supports greater growth and survival of early stages of forage fishes, such as northern anchovy, that directly feed on copepods and can have cascading effects on higher trophic levels (Bi et al., 2011; Takahashi et al., 2012). It is also likely that enhanced growth and survival of larval and juvenile fishes are due to greater availability of certain FAs, such as DHA and EPA, in their prey under certain environmental conditions (St. John and Lund, 1996; Copeman et al., 2002; Copeman and Laurel, 2010).

Lipid content can vary among copepod species, including contributions of neutral lipids, such as wax esters and triacylglycerols, and polar lipids, such as phospholipids and sterols (Lee et al., 2006; Kattner et al., 2007). Many boreal calanoid copepods store lipids as wax esters, which is hypothesized to be an adaptation to an herbivorous life history in regions with pulsed phytoplankton production such as coastal upwelling areas. However, there can be extensive variability in the proportion of wax esters within and among species, and some copepod species rely on triacylglycerols for storage, which appears to be more common in species that are active throughout the year (Kattner and Hagen, 2009). The proportion of phospholipids, which are the principal constituents of structural membranes, tends to vary less across species but phospholipids can contain high levels of the essential FAs EPA and DHA (Kattner and Hagen, 2009). A greater understanding of the seasonal and interannual variation in the lipid class quantity and composition of the coastal copepod community within the Northern California Current is needed to understand dietary effects on higher trophic levels.

There are at least three primary factors that can influence the lipid quantity and quality of the copepod community, including the copepod species composition and the species and lipid composition of their prey. The relative importance of each of these factors in regulating the nutritional quality of the copepod community is not yet well-understood. We hypothesized that the copepod species composition would account for more of the variation in copepod community lipid and FA composition than the species or lipid composition of primary producers. Our primary study objectives were to: 1) characterize the seasonal and interannual variation in the lipid quantity and quality (lipid class and FA composition) of the phytoplankton and copepod communities at a nearshore oceanographic station off central Oregon; and 2) evaluate the relative importance of species composition in regulating the lipid quantity and quality of those lower trophic levels. We also examined the relationships between coastal winds, salinity, and temperature and the observed variation in the species and lipid composition of the phytoplankton and copepod communities in order to evaluate the strength of those relationships within and between trophic levels. Finally, we estimated dates for the seasonal transitions within the Northern California Current using physical (coastal winds and upwelling), biological (phytoplankton and copepod species composition), and biochemical (particulate organic matter and copepod FA composition) data to evaluate the temporal consistency of these separate, yet related, indicators of seasonal change in oceanographic conditions.

2. Materials and methods

2.1. Sample collection

Samples were collected on the Newport Hydrographic Line at a station located 9 km off Newport, OR in 60 m water depth (44.6°N; 124.2°W), hereafter referred to as "NH05". Phytoplankton and zooplankton samples were collected approximately twice a month from June 2012 to December 2013. For phytoplankton, a 10 L water sample was collected from the surface using a bucket and 125 mL was preserved in Lugol's solution for species identification and enumeration. Additionally, 1000–4000 mL of surface waters were filtered onto ashed GF/F filters and stored at −80 °C for lipid extraction. These samples included biogenic detritus as well as phytoplankton and is hereafter referred to as "particulate organic matter". For zooplankton, samples were collected using a 50-cm diameter, 202-μm mesh ring net equipped with a TSK flow meter and towed vertically from 5 m above the sea floor to the surface at a rate of 30 m min^{-1}. During most sampling events, two plank-