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Developmental and spatial variations in the diet signatures of hyperbenthic shrimp *Nauticaris marionis* at the Prince Edward Islands based on stable isotope ratios and fatty acid profiles

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ABSTRACT

The caridean shrimp *Nauticaris marionis* is an ecologically important species in the benthic community around the sub-Antarctic Prince Edward Islands (PEI) as it represents a key prey item for a variety of top predators breeding on the islands. We hypothesized that the diet of *N. marionis* shifts during its development, and that spatial variability in food availability results in differentiation in the diet signatures of specimens collected from various locations of the shelf waters around the PEI. Specimens were collected from nine stations (depth range 70 to 240 m) around the PEI at inter-island shelf (from west to east: upstream, between and downstream) and nearshore regions during austral autumn 2009. Stable isotope and fatty acid data both revealed spatial and developmental variations in the shrimp diet. Nearshore shrimp were more ^{13}C-enriched than those from the inter-island region, suggesting increased kelp detritus entered the food web in the nearshore regions. The shrimp showed increases in $\delta^{13}C$ and $\delta^{15}N$ signatures (and trophic position) with an increase in body size, resulting in distinctions between size classes that reflected shifts in their trophic niche through development. The fatty acid profiles similarly indicated distinctions in diet with increased shrimp size (in the deep regions), and spatial variability was evident in relation to region and depth. All shrimp contained large proportions of polyunsaturated and essential fatty acids, indicating that the quality of food consumed was similar between regions despite the diet variability. Our results provide new dietary information about a key species operating near the base of the food web at the highly productive PEI, and show that there were no areas of enhanced nutrition available to the shrimp. As such, there was no nutritional advantage to shrimp inhabiting any specific region around the PEI.

1. Introduction

The Prince Edward Islands (PEI) are located in the Indian sector of the Southern Ocean and comprise Marion Island and Prince Edward Island, which are separated by an inter-island shelf (mean depth ~ 180 m) that deepens sharply to 3000 m within a 20 km radius of the archipelago (Allanson et al., 1985). The islands are situated in the path of the easterly flowing Antarctic Circumpolar Current in the transitional Polar Frontal Zone (Lutjeharms and Valentine, 1984). Despite their location in a region of low productivity (Laubscher et al., 1993), the islands support a diverse and biomass-rich inter-island benthic community (Branch et al., 1993) and up to five million land-based predators, including seals and seabirds (penguins in particular), during the summer breeding season (Ryan and Bester, 2008). The elevated biomass of the benthic community in the shelf waters around the islands is sustained by enhanced phytoplankton production in the immediate vicinity of the islands, a phenomenon termed the Island Mass Effect (Allanson et al., 1985). The enhanced production and elevated phytoplankton biomass around the islands originate from land-based nutrient inputs, the vertical stability of the water column, and the occurrence of anti-cyclonic eddies that retain water above the island shelf (Allanson et al., 1985; Perissinotto and Duncombe Rae, 1990).

Nauticaris marionis (Bate, 1888) is a sub-Antarctic hyperbenthic shrimp (family Nauticaridae) inhabiting the shelf around the PEI. Although it ranges from 5 to 697 m in depth, this shrimp is most abundant between 50 and 100 m (Branch et al., 1993) and it represents a major component of the benthic community, comprising the second highest biomass after bryozoans (Beckley and Branch, 1992; Branch et al., 1993). Gut content and pigment techniques indicated that the diet of *N. marionis* can change inter-annually, but generally the megalope larvae [carapace length (CL) < 4.0 mm] consume phytoplankton, while the juveniles to

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adults (CL > 4.0 mm) feed on benthic suspension- and deposit-feeders (bryozoans, hydrozoans, polychaetes and foraminifera), detritus and pelagic organisms (euphausiids and copepods; Perissinotto and McQuaid, 1990; Pakhomov et al., 1999). *Nauticaris marionis*, in turn, contributes substantially to the diets of seabirds such as Gentoo penguins, Imperial shags (Espitalier-Noël et al., 1988; Adams and Klages, 1989) and Macaroni and Rockhopper penguins (Brown and Klages, 1987), thus linking the pelagic production to land-based predators. As such, this shrimp fills an exceptionally important ecological role within the inter-island ecosystem of the PEI.

Nauticaris marionis at the PEI has experienced an overall decrease in $\delta^{13}C$ signatures between 1984 and 2009, likely reflecting changes in the overall productivity of the PEI ecosystem (Pakhomov et al., 2004; Allan et al., 2013). Decreases in primary productivity in the vicinity of the islands arising from shifts in global climate have culminated in the decreased frequency of occurrence of the Island Mass Effect (Pakhomov et al., 2004), which in turn probably affects the population dynamics of *N. marionis*. Unfortunately, there are no quantitative biomass and abundance data for *N. marionis* in the PEI region since the photographic assessments of the benthos conducted between 1984 and 1989 (Branch et al., 1993). As a consequence, any potential long-term changes in the ecology of *N. marionis* at the PEI remain speculative. Over the last decade, there have been measurable decreases in the population sizes of inshore pursuit feeders such as Gentoo penguins, Imperial shags and Rockhopper penguins at the PEI (Ryan and Bester, 2008), possibly owing to decreased availability of *N. marionis*. As *N. marionis* forms a crucial link between plankton and top predators, it is important to ascertain the spatial, temporal and developmental variations in its diet to enable predictive modelling of climate change effects on the greater food web.

Researchers studying the feeding dynamics of *N. marionis* and other organisms at the PEI have utilized gut content and pigment analyses (Perissinotto and McQuaid, 1990; Pakhomov et al., 1999), and more recently, stable isotope ratios (Pakhomov et al., 2004). The more traditional methods have provided valuable information on recent feeding activities of the shrimp, and in the case of gut fluorescence techniques, specifically on herbivorous feeding. Unfortunately, it is extremely difficult to identify detritus and soft-bodied or partially-digested prey in gut contents, and characterization of food assimilated by the consumers is not possible. Methods such as fatty acid and stable isotope ratio analyses provide time-averaged information about a consumer's feeding history over medium- to long-terms (weeks to months) and have become more frequently used to study trophic pathways in polar and sub-polar aquatic systems (Budge et al., 2007; Richoux and Froneman, 2009; Richoux, 2011). Ratios of stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) can fractionate predictably through a food chain due to respiration and excretion of lighter isotopes by consumers (Peterson and Fry, 1987). Thus, measurements of these ratios in baseline food and animals can be used to trace the original sources of carbon utilized by, and the trophic level of, a consumer (Peterson and Fry, 1987). Fatty acids are important in maintaining the structure and function of cell membranes and are therefore vital for growth and reproduction (Arts et al., 2001). Different primary producers and heterotrophs exhibit distinctions in their fatty acid profiles that are at least partially retained in consumers, thus these profiles can illustrate feeding interactions (Graeve et al., 1997, Budge et al., 2007). Stable isotope and fatty acid methods thus serve as ideal complementary approaches for investigating food web dynamics.

Differences in the quantity [concentrations of chlorophyll-*a* and suspended particulates; Kaehler et al., 2006] and quality [concentrations of total fatty acids (TFAs); Allan, 2011] of seston between the PEI vs. the upstream region reflect the importance of the Island Mass Effect. As spatial differences were detected in the fatty acid profiles and stable isotope signatures of the benthic invertebrates at the PEI (Allan, 2011), and as these organisms represent important dietary components of *N. marionis* (Pakhomov et al., 1999), regional differences in the seston consumed by the benthos may also be reflected in the shrimp. In turn, changes in the nutritional condition of the shrimp can affect top predators, particularly those that feed predominantly inshore. Thus, the aim of our study was to assess the spatial and developmental variations in the diet signatures of *N. marionis* collected from different locations around the PEI. We hypothesized that the diet of the shrimp changes with development (following published gut content and stable isotope data), and that spatially changing food quality results in distinctions of trophic tracers in shrimp tissues.

2. Materials and methods

2.1. Study area and sample collections

The study was conducted in the vicinity of the sub-Antarctic PEI (46.77°S, 37.85°E) aboard the MV SA Agulhas during Voyage 145 in April 2009. To determine developmental and spatial variations in the diet signatures of *Nauticaris marionis*, ten stations at depths ranging from 70 to 295 m were sampled (seven stations in the inter-island shelf region and three stations in the nearshore regions of Marion Island and Prince Edward Island; Fig. 1). The inter-island stations were differentiated into regions: upstream [west of the islands; Stations 1 (depth 130 m), 2 (295 m) and 3 (100 m)], between the islands [Stations 4 (140 m), 5 (70 m) and 6 (150 m)] and downstream [east of the islands; Station 7 (240 m)]; and Stations 8 (70 m), 9 (158 m) and 10 (111 m) represented the nearshore locations. Collections of *N. marionis* were completed at each of the ten stations using a benthic trawl (mouth size: 100 × 30 cm), and shrimp were found at every location except Station 2. Permission for collections and ethical clearance were granted by the Department of Environmental Affairs and Tourism, South Africa.

2.2. Sample treatment

Following collection, the shrimp were maintained at low densities in filtered seawater for at least 12 h to facilitate gut evacuation. The containers were repeatedly checked for dead individuals, which were immediately removed to prevent cannibalism. All *N. marionis* samples were frozen at −20 °C for the duration of the cruise, and then transferred to −80 °C in the laboratory. Frozen shrimps were dissected and muscle tissue from the abdomen removed for analyses. Carapace length (CL) of each individual was measured from the posterior margin of the orbit to the dorsal midline of the posterior carapace margin (Pakhomov et al., 1999, 2000). The shrimps were divided into size classes based on previous studies (Pakhomov et al., 1999): (I) 4.0–5.4 mm, (II) 5.5–6.9 mm, (III) 7.0–8.4 mm, (IV) 8.5–9.9 mm and (V) 10.0–11.5 mm. The majority of the specimens collected were between 7.0 and 9.9 mm (size classes III and IV), with very few large (10.0–11.5 mm) or small (4.0–5.4 mm) individuals. As megalope larvae generally have a CL < 4.0 mm (Pakhomov et al., 2000), it is likely that only subadults and adults (and the occasional juvenile) were collected during this investigation. All samples were lyophilized at −60 °C for 24 h, and then individually homogenised using a mortar and pestle.

2.3. Stable isotope analysis

Shrimp were treated with 1 M hydrochloric acid to remove carbonates, rinsed in distilled water and dried for 24 h at 60 °C