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Examination of small- and large-scale influences on the diet of an omnivorous polychaete indicates weak effects of upwelling

Victoria J. Cole *, Kirsty A. McQuaid, Christopher D. McQuaid

Coastal Research Group, Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

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ABSTRACT

The relationship between the distributions of predators and their prey is particularly strong for predators with specialised diets. Predicting the diet of omnivores is, however, more complex. We investigated the diet of the omnivorous nereidid polychaete, *Pseudonereis variegata* with respect to spatial scale, upwelling and small-scale behaviour. To investigate the diet of *P. variegata* across a range of spatial scales, shores in the Eastern and Western Regions, within the Warm Temperate South Coast (Agulhas) biogeographic province of South Africa were sampled. Two shores, kilometres apart within an area of upwelling and two within a non-upwelling area were sampled within each region. Gut-contents were composed of plants and animals. Neither region nor upwelling was found to affect the overall diet of *P. variegata*, with significant differences occurring only between shores in the Eastern Region. When the species were separated into plants and animals, in the Eastern Region, significantly more animals were consumed by *P. variegata* in the upwelling area compared to the non-upwelling area. Carefully designed laboratory experiments for preference showed that *P. variegata* consumed amphipods (various species of Gammaridae) and macroalgae (*Hypnea spicifera*), but rarely ate gastropods (*Afrolittorina knysnaensis*). It was clear that *P. variegata* rarely chose to eat gastropods, but there was no experimental evidence to support that they preferred amphipods and macroalgae over gastropods. Findings from the experiment based on gut-contents required knowledge of whether *P. variegata* were making active choices among the range prey that were available in the field. Similarly, the laboratory experiments in which individuals were offered different types of food required background knowledge of the entire suite of prey consumed and also an understanding of the broader-scale environmental factors influencing the diet of *P. variegata*. This study, therefore, highlights the usefulness of combining large-scale studies with carefully planned laboratory experiments that consider preferences for specific types of food.

1. Introduction

The role of environmental conditions and interactions among species in determining the distribution and abundance of populations is a central problem in ecology (Andrewartha and Birch, 1984). Top-down effects of consumers have been shown to structure populations of prey in freshwater (Cooper et al., 1990; Peckarsky, 1980), terrestrial (McLaren and Peterson, 1994; Spiller and Schoener, 1994), and marine systems (Fairweather, 1988; Paine, 1966). Relationships between the distributions of predators and their prey are particularly strong for predators with specialised diets (Heinemann et al., 1989; Veit et al., 1993). Predicting the diet of animals that feed on both animals and plants (i.e. animals that are omnivores) is, however, more complex. Although many omnivores are opportunistic and are able to switch prey depending on availability, it is expected that they will balance their diet as a result of nutritional needs, food quality and availability of alternate foods (Agrawal and Klein, 2000). For example, the Asian shore crab, *Hemigrapsus sanguineus*, is an opportunistic omnivore that, in experiments, has been shown to consume mussels and barnacles over less nutritional macroalgae, except under intense intraspecific competition, when they eat both types of food (Brousseau and Baglivo, 2005).

Many biotic and abiotic factors influence the availability and quality of food for omnivores across a wide range of spatial scales (Agrawal and Klein, 2000). Over tens to hundreds of kilometres, the distributions of species generally result from processes influencing recruitment, particularly for species with planktonic larvae (Underwood and Chapman, 1996). Distinct patterns of distribution and abundance of intertidal organisms over such scales have been shown to be correlated with environmental gradients (Benedetti-Cecchi, 2001; McQuaid et al., 2000), including oceanographic processes such as upwelling (Menge, 2000). Upwelling has been shown to influence the diet of a range of

* Corresponding author. Tel.: +27 76 686 7484; fax: +27 46 622 8959.
E-mail address: victoriajcole@gmail.com (V.J. Cole).

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marine taxa, with some predators eating large and energetically superior items of prey during times of upwelling (Ainley et al., 1996). For example, Brodeur and Pearcy (1992) found the dietary composition of 18 species of small fish changed depending on the intensity of upwelling. Sanford (2002) did a series of laboratory experiments observing predation by the sea star *Pisaster ochraceus* and the whelk *Nucella canaliculata* under conditions mimicking sea temperatures on the Oregon coast during upwelling, and found that at cooler temperatures the predators ate fewer prey, but achieved the same final size by having reduced metabolic costs. Conversely, warmer temperatures favouring growth of individuals may override the effects of increased availability of food and cooler temperatures associated with upwelling (Menge et al., 2008).

Before it is possible to make quantitative comparisons of the importance of a process (e.g. upwelling) from one region to another, local spatial variation must also be taken into account (Underwood and Petraitis, 1993). Because multiple upwelling centres occur within more than one biogeographic region in South Africa, this coastline provides an ideal opportunity to investigate effects of upwelling and local variation without confounding regional influences (Cole and McQuaid, 2010). Previous studies of the fauna associated with mussel beds in this system found effects of biogeographic, regional and local-scale processes, but little evidence of the role of upwelling (Cole and McQuaid, 2010, 2011). As the diet of species is often determined by the distribution of their prey (Arnold, 1972), the diet of an omnivorous predator may also be influenced by such effects.

Mussels are important bioengineers on rocky shores around the world (Gutiérrez et al., 2003). In South Africa, on the East and South Coasts, the indigenous brown mussel, *Perna perna*, is often a dominant occupier of space on the low-mid shore (McQuaid et al., 2000). Their physical structure creates a complex habitat that supports a diverse assemblage of organisms (Lintas and Seed, 1994; Seed, 1996). Mussels provide refuge from thermal stress (Cole, 2010; Stephens and Bertness, 1991), trap fine-grained sediments and organic particles (Crooks and Khim, 1999; Tsuchiya and Nishihira, 1985), buffer competition among co-occurring species (Tokeshi et al., 1989), and provide protection from epibenthic predators (Gonzalez and Downing, 1999). Although mussel beds may provide protection from epibenthic predators, they can also support many species of infaunal consumers (Cole and McQuaid, 2010).

Polychaetes are one of the most ubiquitous and species-rich groups of benthic animals in the marine environment (Fauchald and Jumars, 1979), and form a major component of the infaunal assemblages associated with mussel beds (Cole, 2010). They play an important role in structuring benthic assemblages by regulating the density of infauna, such as amphipods, bivalves and other annelids, through predation and disturbance (Tita et al., 2000). The mussel worm, *Pseudonereis variegata* is a large, conspicuous polychaete living among mussels and other complex habitats on intertidal rocky shores in South Africa (Hammond and Griffiths, 2006; Hanekom, 2008). For example, at one site on the south-east coast of South Africa, it formed 74% of the biomass of infauna associated with *P. perna* (Hanekom, 2008). Previous studies have classified polychaete worms from the Family Nereididae as omnivores, consuming plant material, animal matter and detritus (Fauchald and Jumars, 1979), but no information is available about *P. variegata*. Nereidids may, however, show site to site variability in their diet, with different populations consuming different types of prey (Pardo and Dauer, 2003).

For the possibly omnivorous nereidid polychaete, *P. variegata*, we expected its diet to strongly reflect patterns of distribution of its prey. Specifically, we predicted no effect of upwelling on its diet, with the potential for strong regional and shore level differences as observed for infauna and algae (Cole and McQuaid, 2010; Cole and McQuaid, 2011; Mostert, 2010). Furthermore, we hypothesised that *P. variegata* would be opportunistic, with no preferences for specific items of prey.

2. Methods

2.1. Study sites

Within the Warm Temperate South Coast biogeographic province of South Africa there are several upwelling cells (Lutjeharms, 2006). To test whether upwelling affects the diet of *P. variegata* associated with *P. perna*, mussel beds in two regions within the Warm Temperate South Coast biogeographic province, South Africa, were sampled (Fig. 1). Sites were identified according to Cole and McQuaid (2010), with sampling kept within the same biogeographic pool of species to reduce variability. The two regions sampled within this province were separated by >350 km and each included a centre of upwelling. In each region, sampling was in an area of upwelling and an area of non-upwelling, and within each area two shores were sampled. Areas of upwelling and non-upwelling were separated by 10s to 100s of kilometres and shores within areas by kilometres. In the Eastern Region, sampling was focussed on the upwelling cell at Port Alfred (Fig. 1), where a relatively permanent upwelling cell exists (Lutjeharms, 2006). Shores influenced by upwelling were at Port Alfred and Kenton-on-Sea. The non-upwelling shores sampled were Kidd's Beach and Kayser's Beach near East London (Fig. 1). In the Western Region, the upwelling area sampled was at Robberg, where summer upwelling is driven by easterly summer winds (Lutjeharms, 2006). The upwelling shores were at Robberg and Brenton-on-Sea, while the non-upwelling shores were at Dana Bay and Glentana Bay (Fig. 1). All sampling sites were on the open coast in the lower intertidal zone where the mussels, *P. perna* dominated the low-shore.

2.2. Regional, mesoscale and local sampling

Sampling was done during the Austral late-Summer to early-Autumn, February/March 2011. On each shore, six replicate quadrats of 15 × 15 cm with >90% cover of *P. perna*, were sampled. A metal scraper was used to remove all mussels and associated infauna from within each quadrat and the samples were stored in 70% ethanol. All *P. variegata* were removed from each sample during collection and placed in a small jar in >70% ethanol to ensure that any defecated material was kept for analysis. In the laboratory, the entire gut contents of 48 *P. variegata* were removed and viewed individually in a petri-dish under a dissecting microscope following methods used by Pardo and Dauer (2003) and Caron et al. (2004). Six individuals

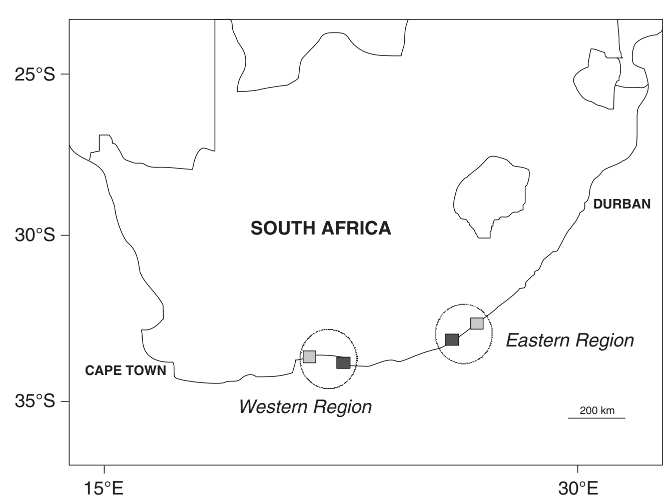

Fig. 1. Map of South Africa showing areas of upwelling (grey) and non-upwelling (black) that were sampled in the Eastern and Western Regions of the Warm Temperate South Coast Biogeographic Province. Two shores were sampled within each area of upwelling or non-upwelling, with $n = 6$ replicate quadrats at each shore.