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Foraging decisions of a native whelk, *Trochia cingulata* Linnaeus, and the effects of invasive mussels on prey choice

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Biological invasions, which are occurring at an increasing rate, are recognised as major drivers of environmental change. Impacts from non-native species are particularly pertinent to species interactions, such as those between predators and prey. In this regard, impacts of invasive predators on their native prey have been widely examined, while the impacts of invasive prey on native predators have been largely overlooked. Here we investigate the impact of invasive mussel species on foraging decisions of a native predatory whelk, *Trochia cingulata*, on the West Coast of South Africa. This coastline has been subject to a number of mussel invasions, resulting in changes to intertidal communities and hence the foraging landscapes of mussel predators. We compared present day survey data with that from 30 years ago and found significant changes in the mussel assemblage available to the whelk. The native mussel *Choromytilus meridionalis* was no longer present on the shore, and there were reduced abundances of the native *Aulacomya atra*. On the other hand there were increases in the invasive *Mytilus galloprovincialis*, with the detection of a second invader *Semimytilus algosus*. We then examined predation by whelks on the different mussel species in laboratory feeding trials. When presented with single prey species, whelks consumed greater numbers of the invasive *M. galloprovincialis* and *S. algosus* compared to *A. atra*, which was previously their preferred prey. Similarly when these mussels were provided in combination, greater numbers of the invasive species were consumed. Chemical cue trials indicated that whelks did not select prey based on chemical recognition, indicating that tactile stimulation was an important driver of prey choice. Although there was no overall difference in shell thickness at drilling sites among mussel species, drill holes were concentrated at the centre of the invasive mussel shells, while this was not observed in the native shells. No differences in energy content were found between mussel species, suggesting that whelks drilled in locations that maximised energy gain. Overall we found that native predatory whelks that previously preferentially consumed the native mussel had shifted their selection of prey towards the invasive species. Notably, familiarity with one invasive mussel appears to have facilitated the assimilation of a second morphologically similar invasive mussel into the diet of whelks.

1. Introduction

The rate of biological invasions is increasing worldwide, and the introduction of non-native species to coastal marine systems is well documented (Levine and D'Antonio, 2003; Rilov and Crooks, 2009; Ruiz et al., 2000). Invasive species are recognised as major drivers in global marine biodiversity loss and this can have far-reaching environmental consequences (Molnar et al., 2008; Sala et al., 2000; Simberloff et al., 2013; Wonham and Carlton, 2005). Such impacts can have complex and varied outcomes, with invasive species outcompeting natives for resources (MacDonald et al., 2007), altering energy flows in food webs (Preston et al., 2012), and affecting the structure and functioning of the ecosystem itself (Baird et al., 2012).

Biological invasions can also affect predator–prey interactions. Much research has focused on the establishment of invasive predators (Carlsson et al., 2009; Lima, 2002; Sih et al., 2010), with studies demonstrating that native prey species may be especially vulnerable to local declines and extinctions (Cucherousset and Olden, 2011; Rindone and Eggleston, 2011; Salo et al., 2007). However, native predators may also affect the success of an invading prey species through predation driven biotic resistance (deRivera et al., 2005; MacNeil et al., 2013; Shinen et al., 2009). Indeed, some native predators may be able to incorporate new species into their diet without altering their foraging strategies (Rilov et al., 2002). However, an alien species that successfully displaces a native may also come to represent an abundant prey resource, resulting in potential changes to the foraging choices by native predators (Carroll et al., 2005; Phillips and Shine, 2006; Veiga et al., 2011).

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In South Africa there have been a number of prominent marine invasions (Mead et al., 2011), and the Mediterranean mussel *Mytilus galloprovincialis* is one such invasive species that has transformed wave-exposed coasts in the region (Robinson et al., 2007a). First detected in the late 1970s (Grant and Cherry, 1985), the species has now invaded more than 2000 km of coastline and has become the dominant intertidal organism on many rocky shores (McQuaid and Phillips, 2000; Robinson et al., 2005). The success of *M. galloprovincialis* has been attributed to its rapid growth rate and high reproductive output (Robinson et al., 2007a; Van Erkom Schurink and Griffiths, 1991) resulting in a superior competitive ability for primary rock space (Erlandsson et al., 2006; Steffani and Branch, 2005). This has subsequently resulted in the displacement of native mussel species such as *Aulacomya atra* and *Choromytilus meridionalis* along the west coast (Branch et al., 2008; Sadchatheeswaran et al., in press) although partial habitat segregation has resulted in this species co-existing with the native *Perna perna* on the south coast. More recently, South Africa is experiencing a second mussel invasion with the recent detection of *Semimytilus algosus*, a species native to Chile (de Greef et al., 2013). This species was first detected in 2009 and has subsequently shown rapid expansion along the west coast (de Greef et al., 2013).

The invasions by *M. galloprovincialis* and *S. algosus* have multiple implications for the native community. Driven primarily by changes in habitat complexity, changes in abundance and diversity of native biota have resulted in altered community composition (Sadchatheeswaran et al., in press). The presence of these non-native mussels also results in abundant new prey resources for local predators, such as the whelk *Trochia cingulata*. This predatory whelk commonly feeds on mussels (Wickens and Griffiths, 1985) and the presence of any new species has potential implications for behavioural decisions. Wickens and Griffiths (1985) found that in the rocky intertidal zone of Marcus Island, South Africa (33°02.59′ S, 17°58.26′ E), *T. cingulata* "appeared to preferentially consume *A. atra*" in comparison with the natives *C. meridionalis* and *P. perna*. However, it was later discovered that the species identified as *P. perna* in this study was in fact the invasive Mediterranean mussel *M. galloprovincialis* (Griffiths pers. comm.). Despite this misidentification, it remains that *T. cingulata* showed a preference towards the native *A. atra* in the field. Now, more than three decades on, this shore has changed considerably with the establishment of *M. galloprovincialis* as a dominant space occupier and the arrival of *S. algosus* (Sadchatheeswaran et al., in press). The current mixed mussel beds at this site thus differ markedly in composition to those studied by Wickens and Griffiths (1985), presenting a very different foraging landscape to *T. cingulata*.

Predatory boring whelks show complex foraging behaviours and some have been shown to recognise novel prey resources after a period of conditioning (Nakaoka, 2000; West, 1986). We were therefore interested in how prey selection by *T. cingulata* has changed over time, following sequential mussel invasions. First, through a repeat survey of the same area of shore studied by Wickens and Griffiths (1985), we established the current foraging landscape available to *T. cingulata*. Second, through laboratory feeding experiments we tested whether *T. cingulata* has incorporated the invasive mussels into its diet. Thirdly, trials investigating prey choice based on chemical and tactile cues were used to examine further elements of prey selection. Finally we studied whether aspects of the mussels' shell morphology and flesh energy content could explain our observations.

2. Materials and methods

2.1. Field surveys

A field survey was conducted during April 2014 on Marcus Island in Saldanha Bay (33°02.59′ S, 17°58.26′ E) on the West Coast of South Africa, sampling mussel beds at a tidal height corresponding to that examined by Wickens and Griffiths (1985). A total of 12 quadrats (10×10 cm^2) were sampled, and all mussels present identified, counted and measured (length in mm). Mussels less that 7 mm in length were considered to be recruits and were not included in these counts. This was done to quantify the availability of mussels within a size range that is readily consumed by *T. cingulata* (Wickens and Griffiths, 1985).

2.2. Laboratory experiments

2.2.1. Animal collection

Organisms used in experiments were collected from three locations along the West Coast of South Africa in November 2013 and March 2014. *T. cingulata* were collected from Elands Bay (32°20.11′ S, 18°18.51′ E), the native and invasive mussels, *A. atra* and *M. galloprovincialis* from Bloubergstrand (33°48.18′ S, 18°27.45′ E) and the invasive mussel *S. algosus* from Hout Bay (34°02.5211′ S, 18°21.38′ E). Each species was collected by hand at low tide, before being transported to Stellenbosch University. Here species were acclimated in separate tanks with aerated artificial seawater (28–32 ppt, approx. 15 °C) under a 12:12 h light:dark cycle for one week. During this time whelks were starved to standardise hunger levels. Mussels were maintained on a phytoplankton suspension of *Isochrysis* and *Pavlova* spp. For all experiments whelks ranged in size from 15 to 25 mm (from tip to base of shell) while mussel size (15–25 mm) was standardised across species. These ranges were selected as previous work indicated that this was the size of mussel most targeted by the size of whelk used here (Wickens and Griffiths, 1985).

2.2.2. Single prey-species presentations

We first investigated consumption of single prey species by whelks via functional response experiments. The functional response is defined as the relationship between predation rate and prey density and provides information on aspects of the predator–prey interaction across a range of resource densities (Holling, 1959; Solomon, 1949). To establish the functional response of whelks towards the mussel prey species, *T. cingulata* were selected from holding tanks and randomly allocated to experimental pots (10 cm diameter) filled with 500 ml seawater for 24 h prior to the addition of prey, to allow acclimatisation to the arena. Individual whelks were presented with one of the three mussel species (*M. galloprovincialis*, *S. algosus* or *A. atra*) at each of four prey densities (1, 2, 3, 6 per trial; $n = 5$ at each density). Trials were run for 40 days and were inspected daily, with mussels being replaced when consumed by whelks. Seawater was replaced every two days and mussels were fed the phytoplankton suspension. Controls were three replicates of each prey density per species in the absence of predators.

The numbers of the different mussel prey species consumed overall by *T. cingulata* were assessed using a generalised linear model (GLM) with quasipoisson distribution. We determined functional response type using logistic regression of the proportion of prey consumed against initial prey density (Juliano, 2001; Trexler et al., 1988) and modelled them using Holling's disc equation that accounts for replacement of prey as they are consumed (Holling, 1959). This allowed an estimation of a number of behaviour parameters, namely attack rate a, handling time h and maximum feeding rate $1/hT$. We did not, however, compare attack rates of whelks among the different prey species as we believe, given the slow rate of consumption by these predators, that this is not a very informative parameter. However, the functional response data were then bootstrapped ($n = 30$) and the parameters handling time h and maximum feeding rate $1/hT$ (T = experimental time) were compared using GLMs.

2.2.3. Simultaneous prey-species presentations

Simultaneous presentations tested prey choice by whelks when they were allowed physical access to mixed groups of mussels. Whelks were randomly selected from holding tanks and four individuals were allocated to each experimental pot. Each tub of whelks was