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INVASIVE SPECIES - SHORT NOTE

Do native subtidal grazers eat the invasive kelp *Undaria pinnatifida*?

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Abstract Key to understanding the impacts of invasive macroalgae on local food webs is determining the extent to which native herbivores consume the invasive macroalga. We used multiple-choice feeding assays to ascertain the relative feeding preferences of four subtidal grazers (the amphipod *Aora typica*, the isopod *Batedotea elongata* and the gastropods *Cookia sulcata* and *Haliotis iris*) for the invasive macroalga *Undaria pinnatifida* and six native macroalgae (*Macrocystis pyrifera, Durvillaea antarctica, Carpophyllum flexuosum, Cystophora scalaris, Marginariella boryana* and *Ulva* spp.) that are all abundant along the Otago coast of southern New Zealand. Multiple-choice feeding assays were run under laboratory conditions during the austral autumn (April and June) of 2013. The relative abundances of the macroalgae in the field were also determined. All of the grazers ate *U. pinnatifida* at rates comparable to most of the native macroalgae, except for *B. elongata*, which barely consumed it. This indicates that *U. pinnatifida*, which was shown to be more abundant than native macroalgae in subtidal habitats, has the potential to contribute organic matter to the local food web and may be an undesirable food for some group of grazers. We suggest that *U. pinnatifida* could potentially alter existing trophic relationships.

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Introduction

Interactions between invasive macroalgae and native grazers can potentially alter consumer populations and modify existing trophic relationships, and food web structure (e.g. Deudero et al. 2011; Salvaterra et al. 2013). Invasion dynamics can in turn be affected, as native grazers could either control the abundance of the invader by actively grazing on it ('biotic resistance' hypothesis; Elton 1958) or the distribution and abundance of invaders could increase in the absence of regulation by native grazers in the new region ('enemy release' hypothesis, Keane and Crawley 2002). Therefore, understanding how native grazers interact with invasive macroalgae is necessary to comprehend the potential effects of invasive macroalgae on the food web and ecosystem structure in invaded ecosystems.

In contrast to what has been observed in terrestrial and freshwater ecosystems (Parker and Hay 2005), numerous studies have shown that many native marine grazers preferentially consume native species over invasive macroalgae (e.g. Sumi and Scheibling 2005; Monteiro et al. 2009; Tomas et al. 2011). This suggests that invasive macroalgae may not necessarily represent a suitable food source (or are

not recognised as one), indicating that native grazers may not control the establishment and spread of invasive macroalgae (Parker and Hay 2005; Parker et al. 2006).

The Asian kelp *Undaria pinnatifida* is considered one of the world's 100 most invasive species (Lowe et al. 2000). Native to China, Korea and Japan, *U. pinnatifida* is now present on most temperate coasts worldwide (e.g. Floc'h et al. 1991; Piriz and Casas 1994; Silva et al. 2002). Despite this, *U. pinnatifida* is one of the least studied invasive macroalgae (Schaffelke and Hewitt 2007; Williams and Smith 2007) and very little is known about its importance as a food source for native grazers in invaded regions.

We investigated the feeding preferences of four common subtidal grazers for *U. pinnatifida* versus six species of common native macroalgae found in the Otago coast region of southern New Zealand, where *U. pinnatifida* was first detected more than 25 years ago (Hay and Luckens 1987) and has become well established in the region (Russell et al. 2008; Suárez et al. 2015). Based on the literature, we hypothesised that the native grazers would prefer consuming native macroalgae over *U. pinnatifida*. To examine the potential implications of their grazing preferences, we have quantified the contribution of *U. pinnatifida* relative to native macroalgal species.

Methods

Study organisms

We assayed the feeding preferences of two species of mesograzer (small mobile invertebrate grazers), the amphipod *Aora typica* and the isopod *Batedotea elongata*, and two species of macrograzer (large grazers), the gastropods *Cookia sulcata* and *Haliotis iris* for the invasive macroalga *U. pinnatifida* and six native species: the brown macroalgae *Macrocystis pyrifera*, *Durvillaea antarctica*, *Carpophyllum flexuosum*, *Cystophora scalaris*, and *Marginariella boryana* and the green macroalga *Ulva* spp. All grazers are abundant in the coastal waters of Otago, New Zealand, where this study was undertaken: *A. typica* (20.25 ± 8.87 individuals per 100 g blotted algae), *B. elongata* (1.22 ± 0.61 individuals per 100 g blotted algae) (Suárez 2015), *C. sulcata* (6–10 individuals m^{-2}) and *H. iris* (0–4 individuals m^{-2}) (Richards 2009). In addition, we estimated the abundances on the Otago coast of the different macroalgal species used in the feeding assays.

Blades of living mature macroalgae and *C. sulcata* (80.4 ± 2.9 SE g, $n = 18$) were collected from Katiki Beach (45°27′S, 170°48′E) and transferred to an insulated bin containing seawater from the sampling site, in the dark. A set of captive *H. iris* animals at the University of Otago's Portobello Marine Laboratory, previously fed with fresh

macroalgae, were used for the feeding assays (100.4 ± 2.9 SE g, $n = 18$). The mesograzers *A. typica* (3.5 mm long, $n = 324$) and *B. elongata* (25 mm long, $n = 24$) were obtained from the macroalgae *C. flexuosum* and *C. scalaris* collected at Katiki Beach and Dowling Bay (45°47′S, 170°39′E), following methods from Taylor and Cole (1994), except that macroalgae were shaken in buckets containing seawater instead of formalin to obtain the associated animals. *C. sulcata* and *H. iris* were acclimatised to assay conditions for 3–4 days prior to the assays. *A. typica* and *B. elongata* were not acclimatised in order to minimise mortality during the assay. Only 6 out of 324 amphipods (1.85 %) and 1 out of 24 isopods (4.17 %) were found dead at the end of the assays. Preliminary observations revealed consumption of macroalgal tissue occurred in the first 2–3 days.

Macroalgae used for assays were collected 1–4 days prior to the assays and maintained inside plastic buckets (30–100 L) containing filtered (5 µm), UV-sterilised seawater and bubbled with air using an aquarium pump, in a room at 11 °C and natural light/dark cycle (9/15 h), 37 µmol photons m^{-2} s^{-1} (LI-COR Light Meter, LI-250).

Feeding assays

Multiple-choice assays, where all macroalgal species were simultaneously offered to the animals, were used to determine the feeding preferences of the grazers for the seven macroalgal species, including *U. pinnatifida*. Mesograzer assays were run in 500-mL glass jars containing 400 mL of seawater at the Department of Botany, University of Otago, while macrograzer assays were run in 10-L plastic buckets receiving continuously flowing seawater at Portobello Marine Laboratory. Assays were conducted between April and June 2013 under a natural light/dark cycle (9/15 h), with light maintained at 37 µmol photons m^{-2} s^{-1} (LI-COR Light Meter, LI-250) in the light cycle. Seawater used in all assays was at 11 °C, filtered to 5 µm and UV-sterilised. The assay for each grazing species consisted of containers with a sample of each macroalga and a grazer, and paired with containers comprising macroalgae but not animals, which acted as controls for autogenic change ($n = 18$).

In each assay, grazers were offered pieces of each macroalga with similar surface areas (approximately 15 × 15 mm for mesograzers and 45 × 45 mm for macrograzers) in order to equalise the probability that they would be encountered. In the mesograzer assays, these pieces weighed ~200 mg for *D. antarctica* and 20–80 mg for the other species, and in the macrograzer assays, the pieces weighed ~3 g for *D. antarctica* and 600–900 mg for the other species. All macroalgal pieces were cleaned by hand to remove macroscopic fouling organisms just before they were weighed and used for the assays. Treatments had

either 18 *A. typica*, one or two *B. elongata* (if individuals were >25 mm or <25 mm long, respectively), one *C. sulcata* or one *H. iris*. For the macrograzers, macroalgae were suspended on separate stainless steel hooks attached to the walls of the 10-L bucket, near to the base to ensure that macroalgae were accessible to grazers, whereas for the mesograzers the pieces were free at the bottom of the jars.

The blotted wet weights of macroalgal pieces offered were recorded (±0.1 mg) at the start and at the end of the assay. The amount of consumption of each macroalgal piece was checked every 4–6 h and recorded after 48 h or when at least one of the pieces was half consumed, whichever occurred first (Taylor et al. 2002).

Macroalgal abundance

Three reefs with populations of *U. pinnatifida* (Russell et al. 2008; Suárez et al. 2015) were chosen: Harrington Point (45°47′S, 170°43′E), Aramoana (45°46′S, 170°43′E) and Mapoutahi (45°44′S, 170°37′E). Subtidal algal communities were examined during the early austral summer (December 2011 and 2012), following *U. pinnatifida*'s recruitment period, and early winter (April 2012 and 2013), after *U. pinnatifida*'s senescence period. A 30-m transect line was laid on each of the reefs along the 2–3 m depth contour below mean low water, where *U. pinnatifida* is most abundant (Richards 2009), using SCUBA. Twenty 1 m^2 quadrats were used to determine the percent cover of canopy-forming algal species using a digital camera (Canon G10, 14.7 MPs). All quadrats were randomly deployed along each transect.

Data analyses

Macroalgal consumption was calculated as: $(H_i \times C_f/C_i) - H_f$, where H_i and H_f were initial and final blotted wet weights, respectively, of tissue exposed to the animals, and C_i and C_f were blotted weights of paired controls for pre-assay and post-assay, respectively (Taylor and Brown 2006). Replicates in which total consumption was zero (one replicate for *B. elongata*) or the animals died (one replicate for *B. elongata*) were discarded as they did not inform feeding preferences (removal of replicates where total consumption was zero did not affect the results).

Underwater photographs were analysed using the software CPCe 4.1 (Coral Point Count with Excel extensions; National Coral Reef Institute). First, a code file was created to identify different algal species. Fifty random points (10 rows × 5 columns) were overlaid on each of the underwater photographs. Each random point was then identified with the appropriate code, from which the percent cover was estimated. For the presentation and analysis of the macroalgal abundance data, we treated the 12 site–time
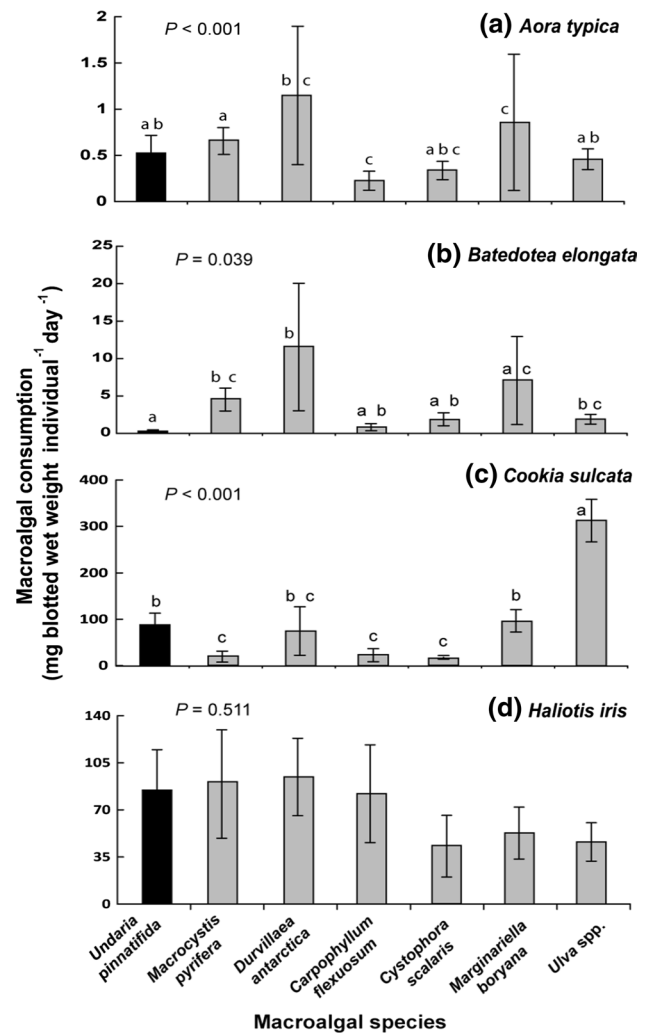

Fig. 1 Mean consumption ($X \pm$ SE, $n = 18$) of *Undaria pinnatifida* (*black bars*) and native macroalgae (*grey bars*) by the mesograzers (**a**) *Aora typica* and (**b**) *Batedotea elongata* and the macrograzers (**c**) *Cookia sulcata* and (**d**) *Haliotis iris* during a multiple-choice feeding assay. Statistics are for Friedman nonparametric test of ranks (Conover 1980). *Bars* labelled with *same letter* do not differ significantly (post hoc, Wilcoxon signed-rank test, $P < 0.02$)

combinations as replicates (i.e. after averaging percent covers for the 20 quadrats surveyed at each site–time combination).

Since treatments in multiple-choice assays and estimations of percent cover lack independence (see Peterson and Renaud 1989), Friedman nonparametric test of ranks (Conover 1980; Taylor and Brown 2006) followed by a post hoc Wilcoxon signed-rank test was run (IBM SPSS Statistics 20). To minimise Type I errors in multiple pairwise comparisons, a more stringent *p* value of 0.02 was used. Bonferroni adjustments were avoided as they can increase Type II error (Cabin and Mitchell 2000).

Results

All of the grazers consumed the invasive *U. pinnatifida* at variable but comparable rates to most of the native macroalgae, except for the isopod *B. elongata*, which barely consumed the invasive macroalga (Fig. 1). The amphipod *A. typica* consumed *U. pinnatifida* at similar rates to native macroalgae, except compared to *C. flexuosum* and *M. boryana*, which were consumed at relatively lower and higher rates, respectively (Fig. 1a). The isopod *B. elongata* consumed significantly more (at least 85 %) *Durvillaea antarctica*, *M. pyrifera* and *Ulva* spp. than *U. pinnatifida* (Fig. 1b). The gastropod *C. sulcata* consumed at least 69 % more *Ulva* spp. than any other macroalgae, and consumed at least 73 % more *U. pinnatifida* than *M. pyrifera*, *C. flexuosum* and *C. scalaris* (Fig. 1c). The gastropod *H. iris* did not prefer any particular macroalga, although average macroalgal consumption ranged from 94.5 ± 28.1 SE mg ($n = 18$) of blotted *D. antarctica* individual^{-1} day^{-1} to 43.3 ± 22.9 SE mg ($n = 18$) of blotted *C. scalaris* individual^{-1} day^{-1} (Fig. 1d).

U. pinnatifida showed the highest mean cover values, comprising 25 % of the total canopy cover (Fig. 2). The natives *Marginariella* spp., *C. flexuosum* and *M. pyrifera* were the next most abundant macroalgae occupying 21, 16 and 8 % of the canopy, respectively (Fig. 2). The species *D. antarctica, C. scalaris* and *Ulva* spp. were the least abundant species used in the feeding assays (0.9–2.5 % of the canopy) (Fig. 2). Mean cover values of coralline and miscellaneous red algae were 4.9 and 2.8 %, and substrate (sand, rock, sediment) comprised 11.3 % of the total percent cover of the reefs.

Discussion

To the best of our knowledge, this is the first attempt to identify the potential response of native invertebrate grazers to the invasive *U. pinnatifida*, through the investigation of the feeding preferences of a range of subtidal grazers for a range of native macroalgae and the invasive kelp. Although *U. pinnatifida* was the most abundant food source on the reefs in the Otago region, it was usually consumed by the grazers at similar or lower rates than native algal species. The relative preference of grazers for *U. pinnatifida* compared to native macroalgae, therefore, depended on the identity of both the grazer and the macroalga.

Our hypothesis that the grazers would prefer native macroalgae over the invasive *U. pinnatifida* was supported only for the isopod *B. elongata*, which grazed very little *U. pinnatifida* compared to native macroalgae (85 % less than any other macroalga). This could be due to chemical deterrents (secondary metabolites such as phenolics, galactolipids)
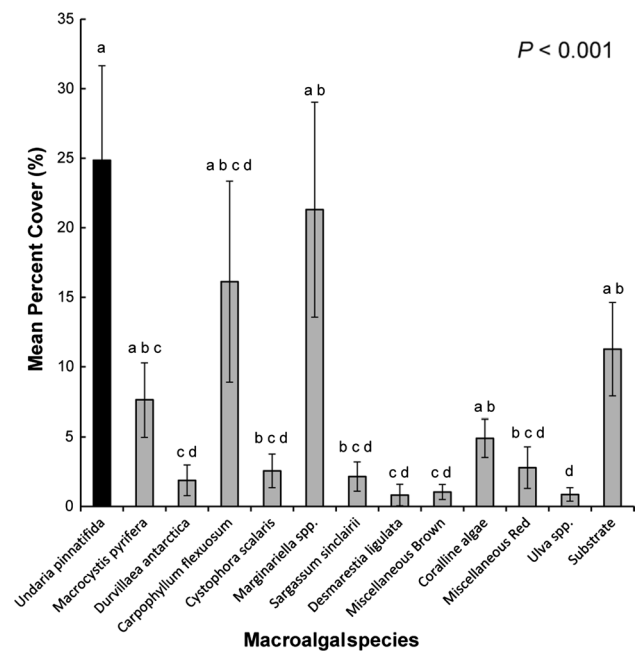

Fig. 2 Mean percent cover (%; $X \pm$ SE, $n = 12$) of *Undaria pinnatifida* (*black bars*) and native macroalgae (*grey bars*) recorded during spring–summer (2011 and 2012) and autumn–winter (2012 and 2013) at three sites within the Otago coast. *Marginariella* spp. includes *M. urvilliana* (from wave sheltered sites Harrington Point and Aramoana) and *M. boryana* (from the wave exposed site Mapoutahi). Statistics are for Friedman nonparametric test of ranks (Conover 1980). *Bars* labelled with *same letter* do not differ significantly (post hoc, Wilcoxon signed-rank test, $P < 0.02$)

that only affected this isopod species (Davis et al. 2005) or because consumption of *U. pinnatifida* may compromise the isopod's fitness (e.g. reduce growth, Nejrup et al. 2012). These results highlight the need to further investigate the invasive macroalga's chemical composition and potential detrimental effects on this grazer's fitness if forced to consume it (e.g. Boudouresque 1996; Scheibling and Anthony 2001).

The mechanisms behind the feeding patterns observed in this study are unknown. However, the feeding preferences by *B. elongata* do not appear to reflect the nutritional properties of the different macroalgae. Chemical analyses carried out for a different set of assays (Suárez 2015) show *U. pinnatifida* and *Ulva* spp. can contain almost 50 % more nitrogen than *M. pyrifera* or *D. antarctica,* which were the most consumed by this isopod species. In comparison, the calorific content of *U. pinnatifida* is similar to that of *D. antarctica*, but higher than that of *M. pyrifera* (Suárez 2015). Furthermore, the mechanical properties of algae, which can reduce their palatability to marine herbivores (e.g. Duffy and Hay 1991; Pennings and Paul 1992), did not correspond to the feeding preference shown by this grazing species. For example, *U. pinnatifida*, *M. pyrifera*

and *Ulva* spp. are at least 7–8 times less tough and elastic than *D. antarctica* (Suárez 2015), yet this last algal species was highly consumed. The mechanisms behind the food choice of *B. elongata* are, therefore, not clear and require further investigation. However, unlike the present study, the feeding preferences of the talitrid amphipod studied in Suárez (2015) did appear to reflect the relative abundances of the potential sources in the upper tidal zone of sandy beaches where it is most abundant.

All other grazers in this study consumed *U. pinnatifida* at similar or greater levels than several other native algal species. These results support previous findings that have indicated *U. pinnatifida* represents a potential food source for native grazers in invaded regions (Teso et al. 2009; Peteiro and Freire 2012). Our study also provides useful baseline information for better understanding the impacts of the invasive macroalga on food web and ecosystem structure and hypotheses for further research. For example, the amphipod *A. typica* and the gastropod *H. iris* seemed to prefer having a mixed diet, which may be the most nutritious option for them (e.g. Pennings et al. 1993; Cruz-Rivera and Hay 2000). As stated above, *U. pinnatifida* has similar or greater nutritional content and lower toughness than other species such as *D. antarctica* (Suárez 2015). In addition, we have shown that *U. pinnatifida* is relatively abundant compared to native algae in the region. The invasive *U. pinnatifida* therefore appears to provide a nutritious and accessible food source for several grazers in the region.

Both macro- and mesograzers strongly structure benthic macroalgal communities through grazing pressure (e.g. Duffy and Hay 2000; Vergés et al. 2009; Poore et al. 2012). However, the absence of a strong preference of local grazers for *U. pinnatifida*, and the high density of *U. pinnatifida* recorded across sites and seasons in our study region, indicates that native grazers in the Otago region are not controlling *U. pinnatifida*, as suggested for other invasive macroalgae (e.g. Gollan and Wright 2006; Cebrián et al. 2011; Hammann et al. 2013). In contrast, sea urchins reduce *U. pinnatifida*'s abundance in Tasmania (Valentine and Johnson 2005), and crabs have been shown to prevent individuals of *U. pinnatifida* attaining reproductive maturity in California (Thornber et al. 2004). Low densities of the New Zealand sea urchin *Evechinus chloroticus*, which are able to create urchin barrens and effectively control *U. pinnatifida* in other regions, may have contributed to its invasion success in the Otago region (Richards 2009).

Overall, *U. pinnatifida* has potential to contribute organic matter to the local food web, which may ultimately alter some natural trophic interactions (e.g. Deudero et al. 2011; Salvaterra et al. 2013). However, such potential is greatly dependent on its invasion dynamics and ability to alter native macroalgal communities (i.e. displacement, fugitive behaviour), but this potential remains unclear (e.g.

Valentine and Johnson 2003; Casas et al. 2004; Raffo et al. 2009). Importantly, this study also highlights that *U. pinnatifida*, despite being the most abundant food source in invaded reefs, may not always represent a potential food source. Given that the effects of a habitat-forming invasive species are biomass dependent (Gribben et al. 2013), *U. pinnatifida* has the potential to negatively impact some mesograzer populations (e.g. *B. elongata*) and ultimately affect secondary productivity and the flux of energy where they are key organisms (Edgar and Moore 1986; Taylor 1998; Newcombe and Taylor 2010). The impacts of invasive macroalgae on food webs and ecosystem structure are difficult to predict, but food-preference studies, in combination with macroalgal abundance data, are a useful first step in elucidating how consumers might be affected by a change in the identity and abundance of primary producers.

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