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Note

Food selection of a generalist herbivore exposed to native and alien seaweeds

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ABSTRACT

Understanding which factors influence the invasion of alien seaweed has become a central concern in ecology. Increasing evidence suggests that the feeding preferences of native herbivores influence the success of alien seaweeds in the new community. We investigated food selection of a generalist native grazer *Paracentrotus lividus*, in the presence of two alien seaweeds (*Caulerpa cylindracea* and *Caulerpa taxifolia* var. *distichophylla*) and two native seaweeds (*Dictyopteris membranacea* and *Cystoseira compressa*). Sea urchins were fed with six experimental food items: *C. cylindracea*, *C. taxifolia* var. *distichophylla*, a mixture of *C. cylindracea* and *C. taxifolia* var. *distichophylla*, *D. membranacea*, *C. compressa* and a mixture of *D. membranacea* and *C. compressa*. *P. lividus* ingested all the combinations of food offered, though it preferentially consumed the alien mixture, *C. cylindracea* and *D. membranacea*. The alien *C. taxifolia* var. *distichophylla* was consumed significantly less than the other food items and, interestingly, it was ingested in a greater amount when mixed with *C. cylindracea* than when on its own. This finding suggests that *C. taxifolia* var. *distichophylla* may become vulnerable to sea urchin grazing when it grows intermingled with *C. cylindracea*, which does not gain immediate protection from the presence of the very low palatable congeneric seaweed. The present study highlights the potential role of native grazers to indirectly affect the interspecific competition between the two alien seaweeds in the Mediterranean Sea.

1. Introduction

The current rate of biological invasions by alien species in the marine realm is astonishing. Alien invasions have been widely recognized as severe threats to ecological integrity worldwide and can result in huge economic and societal impacts (Ruiz et al., 1997; Occhipinti-Ambrogi, 2007; Katsanevakis et al., 2014). Seaweeds make up a considerable proportion of alien invasions in coastal habitats, globally representing about 10 to 40% of the total marine alien species (Schaffelke et al., 2006; Williams and Smith, 2007). This may be due to a variety of factors such as their vegetative reproductive capacity (Gollan and Wright, 2006) and production of toxic metabolites (e.g. alkaloids and terpenoids) that act as chemical deterrents against competing species and local herbivores (Paul et al., 2007). In this regard, two prominent hypotheses have been proposed in the field of invasion ecology concerning the role of species interactions in affecting invasion processes. The enemy release hypothesis (ERH) predicts that alien species have a competitive advantage over native species because they are often introduced with few natural enemies and are not a preferred choice of generalist herbivores in their new habitat (Keane and Crawley, 2002; Hierro et al., 2005; Liu and Stiling, 2006). The biotic resistance hypothesis of Elton (1958) predicts that invasiveness of alien species can be restricted by the native species richness that is expected to decrease nutrient availability and increase competition, predation and natural enemies. Accordingly, generalist native grazers can potentially incorporate alien seaweeds in their diet, limiting their spread in recipient communities therefore contributing to invasion control (Gollan and Wright, 2006; Monteiro et al., 2009; Tomas et al., 2011).

Nevertheless, alien seaweeds may show considerable variation in their palatability to native herbivores, mainly because of their secondary metabolites that can function as deterrents against consumers (Paul and Fenical, 1986). These toxic compounds may influence native consumers by reducing their performance and fitness, enhancing the invasiveness of alien seaweeds (Tomas et al., 2011). Despite more than 50 years of research in the field of invasion ecology, the mechanisms behind the invasion success of introduced macrophytes are still highly

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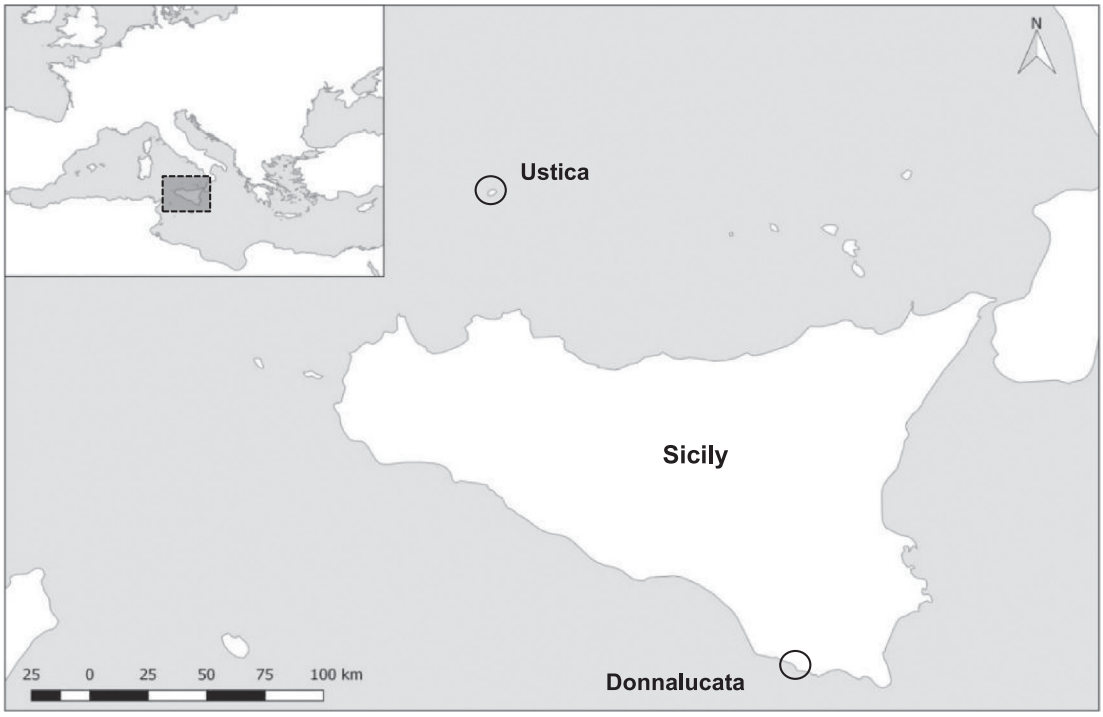

Fig. 1. Map of Sicily (Italy) with indication of the two the sampling areas (○).

debated (Simberloff, 2000; Grosholz, 2002; Boudouresque and Verlaque, 2012). Patterns of alien seaweed invasiveness need to be investigated through examination of the complex interactions between native grazers and alien seaweeds, which become more intricate when multiple invasions co-occur. Therefore, an understanding of the feeding behaviour of generalist native grazers is necessary to predict their potential role in controlling the spread of algal invaders.

Among the world oceans, the Mediterranean Sea hosts more than 100 established species of alien seaweeds, including several taxa belonging to the algal genus *Caulerpa* (Zenetos et al., 2008). *Caulerpa cylindracea* (Sonders), original from southwestern Australia, is one of the most studied algal invaders to the Mediterranean Sea. It is a siphonous green alga, widely distributed in warm temperate and tropical seas, that has rapidly spread throughout the Mediterranean basin and the Canary Archipelago in the East Atlantic (Klein and Verlaque, 2008; Papini et al., 2013). After being invaded by the aquarium strain of *Caulerpa taxifolia* (Vahl) C. Agardh, (Klein and Verlaque, 2008; Papini et al., 2013), the Mediterranean Sea is now experiencing the invasion of a new morphologically slender variety of *C. taxifolia*, namely *C. taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman *et* Procaccini, arriving from southwestern Australia (Jongma et al., 2013). This new algal strain was first reported from Turkey in 2006 (Cevik et al., 2007) and recorded in the southernmost part of Sicily in 2007 (Meinesz et al., 2010) followed by a more recent spread northwards in the western and central basins of the Mediterranean Sea (Musco et al., 2014; Picciotto et al., 2016). Along the southeastern coast of Sicily, *C. taxifolia* var. *distichophylla* appears to be fully naturalized and it is often found intermingled with *C. cylindracea* on natural and artificial rocky bottoms (Musco et al., 2014).

The invasive success of *Caulerpa* species may be in part attributable to the synthesis of secondary metabolites that act as chemical defenses against herbivores (e.g. caulerpine). However, the ability of *Caulerpa* spp. to deter consumers is mainly attributed to the sesquiterpenoid caulerpenyne (hereafter CYN) that was found at relatively low concentrations in *C. cylindracea* compared to that of *Caulerpa taxifolia* (Dumay et al., 2002). Harmful effects of *C. cylindracea* ingestion on the health status of the white seabream *Diplodus sargus* (Terlizzi et al., 2011) and the performance of the sea urchin *Paracentrotus lividus* (Tomas et al., 2011) had been documented, suggesting that this alien species impairs the fitness of consumers. However, despite such detrimental effects, *C. cylindracea* is reported to be very palatable to herbivores (Ruitton et al., 2006) with particular reference to the sea urchin *P. lividus* that was found to highly consume this alien seaweed (Bulleri et al., 2009; Cebrian et al., 2011; Tomas et al., 2011). To date, nothing is known about trophic interactions between the new alien strain *C. taxifolia* var. *distichophylla* and native consumers, though CYN concentration level reported by Cevik et al. (2016) is higher than that recorded for *C. cylindracea* (Dumay et al., 2002). It is, therefore, presumable that native grazers may avoid the new alien strain and prefer the more palatable *C. cylindracea* due to lower CYN concentration. Moreover, the co-occurrence of the two alien seaweeds might impede native consumers from grazing on *C. cylindracea* by virtue of the presence of the presumed very low palatable *C. taxifolia* var. *distichophylla*.

We investigated the feeding behaviour of a generalist Mediterranean grazer, the sea urchin *P. lividus*, considering the presumed different palatability of the two alien seaweeds and how it might affect sea urchin feeding choice when the two invaders grow intermingled. In particular, we evaluated the food choice of *P. lividus*, when simultaneously provided with a suite of native and alien food sources, including a mixture of *C. cylindracea* and *C. taxifolia* var. *distichophylla* as one of the food items. Specifically, we predict that: (1) *P. lividus* would preferentially consume native seaweeds and *C. cylindracea* over *C. taxifolia* var. *distichophylla* and (2) when offered with a mix, the two alien seaweeds would be both avoided by *P. lividus* since the presence of *C. taxifolia* var. *distichophylla* would reduce herbivory on *C. cylindracea*.

2. Materials and methods

2.1. Collection of organisms

Sampling was carried out in Sicily in September 2016 (Fig. 1). Seaweeds were collected 3 days before starting the experiments. Alien (*C. cylindracea* and *C. taxifolia* var. *distichophylla*) and native (*Cystoseira compressa* and *Dictyopteris membranacea*) seaweeds were collected from