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# Feeding preference of the native sea urchin *Arbacia dufresnii* in an environment invaded by the kelp *Undaria pinnatifida*

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**Abstract:** In Argentina, the invasive kelp *Undaria pinnatifida* has modified the benthic community of Nuevo Gulf, northern Patagonia, where it was first recorded and is currently showing advanced invasion. *Arbacia dufresnii*, an abundant generalist omnivore sea urchin, has fully incorporated *U. pinnatifida* into its diet. Since sea urchins can influence the structure and dynamics of benthic macroalgal assemblages, determining the importance of *U. pinnatifida* in the feeding preferences of *A. dufresnii* complements the evaluation of the modifications caused by this species. Thus, this study aimed to assess the feeding preference of *A. dufresnii* in an environment invaded by *U. pinnatifida*. We conducted feeding experiments to determine whether *A. dufresnii* feeds on different developmental stages of *U. pinnatifida*, and preference experiments of this invasive species against six macroalgal species abundant in the environment. *Arbacia dufresnii* consumed both blades and sporophylls of *U. pinnatifida* at all the developmental stages evaluated, showing a preference for blades over sporophylls. *Arbacia dufresnii* showed preference for *U. pinnatifida* only when it was offered together with species that possess defense mechanisms against herbivory. The lack of preference for other macroalgae species over *U. pinnatifida* suggests that this invasive species may alter resource use and thereby affect the trophic structure of native communities. These findings complement previous diet studies, corroborating the feeding plasticity of *A. dufresnii*, as well as its ability to adapt to newly available resources. This research enhances the understanding of the impacts caused by invasive macroalgal species through feeding ecology studies of native grazers.

**Key words:** Food preference, echinoid, invasive kelp, Patagonia

**Resumen: Preferencia alimentaria del erizo de mar *Arbacia dufresnii* en presencia del alga invasora *Undaria pinnatifida*.** En Patagonia Argentina, el alga invasora *Undaria pinnatifida* fue registrada por primera vez en el Golfo Nuevo, donde ha modificado la comunidad bentónica, presentando actualmente un grado de invasión avanzada. El equinoideo *Arbacia dufresnii* es un omnívoro generalista que ha incorporado completamente el alga invasora a su dieta. Dado que los equinoideos pueden influir en la estructura y dinámica de los ensambles de macroalgas bentónicas, determinar la importancia de *U. pinnatifida* en las preferencias alimentarias del equinoideo complementa la evaluación de las modificaciones causadas por esta especie. Con este fin se realizaron experimentos de única opción para determinar si *A. dufresnii* se alimenta de diferentes estadios de *U. pinnatifida*, y experimentos de preferencia de esta especie invasora frente a seis especies de macroalgas. El equinoideo consumió los diferentes estadios de *U. pinnatifida*, tanto el esporofilo como de la fronde, mostrando preferencia por esta última. *Arbacia dufresnii* mostró preferencia por *U. pinnatifida* únicamente cuando fue ofrecida junto a especies que poseen defensas contra la herbivoría. La falta de preferencia por las otras especies de macroalgas sugiere que *U. pinnatifida* alteraría el uso de los recursos afectando la estructura trófica de las comunidades nativas. Estos hallazgos complementan los estudios existentes de la relación *U. pinnatifida* – *A. dufresnii*, corroborando la plasticidad alimentaria del equinoideo así como su capacidad para adaptarse a los nuevos recursos disponibles. Esta investigación aporta comprensión a los impactos causados por *U. pinnatifida* mediante estudios de ecología alimentaria de los herbívoros nativos

**Palabras clave:** Preferencia alimenticia, equinoideo, algas invasoras, Patagonia

## INTRODUCTION

Invasive species are globally recognized as one of the five major direct drivers of environmental change, alongside land and sea use change, direct exploitation of organisms, climate change, and pollution (Roy *et al.*, 2023). The magnitude and types of impacts of the invasion vary among different invasive species and across ecosystems and regions. In the marine environment, the predominant ecological impacts of invasive macroalgae are space monopolization and altered community composition (Davidson *et al.*, 2015). Specifically, the macroalga *Undaria pinnatifida* (hereafter referred to as *Undaria*), native to northeast Asia (Akiyama & Kurogi, 1982), is in the top 10 most widespread invasive algae species worldwide (Kulhanek *et al.*, 2011; Seebens *et al.*, 2023). In Argentina, this species was first recorded in Nuevo Gulf, northern Patagonia, in 1992 (Casas & Piriz, 1996). Since its introduction, it has spread over most of the Argentine coast, with the densest kelp beds in northern Patagonia, with densities occasionally higher than 4 kg·m$^{-2}$ (Dellatorre *et al.*, 2014). *Undaria* is an annual species with a heteromorphic life cycle typical of the Laminariales, with alternating gametophytic (microscopic) and sporophytic (macroscopic) generations (Choi *et al.*, 2007). Prior to the *Undaria* invasion, macroalgal communities in Nuevo gulf were characterized by small species (*Ulva* sp., *Codium* sp., *Dictyota dichotoma*, among others), which did not exceed 50 cm in height (Boraso & Zaixso, 2008). Because of its invasive features, the presence of *Undaria* has modified the benthic community of Nuevo Gulf (Orensanz *et al.*, 2002; Raffo, 2014), causing a decrease in the populations of native macroalgae (Casas *et al.*, 2004), an increase of 800% in biomass availability for herbivores (Casas *et al.*, 2008; Raffo *et al.*, 2015), and an increase in the populations of some invertebrates. For example, in the presence of *Undaria*, the abundance of the sea urchin *Arbacia dufresnii* has increased three times (Irigoyen *et al.*, 2011).

*Arbacia dufresnii* is the most common sea urchin in the northern Patagonian coast of Argentina (Zaixso & Lizarralde, 2000; Brogger *et al.*, 2013). Depending on the availability of food in the environment, this species can be considered as a herbivore, carnivore, or generalist omnivore (Vásquez *et al.*, 1984; Penchaszadeh & Lawrence, 1999; Newcombe *et al.*, 2012; Zárate, 2014; Castro *et al.*, 2022). Particularly, in Nuevo Gulf, *Undaria* is consumed and assimilated in the tissues of *A. dufresnii*, suggesting a complete incorporation of the invasive kelp into the sea urchin diet (Castro *et al.*, 2022). However, questions such as whether the sea urchin prefers to feed on *Undaria* or other macroalgae available in the environment have not yet been resolved. Considering that sea urchins can impact the structure and dynamics of benthic macroalgal assemblages in coastal habitats (Scheibling & Anthony, 2001; Valentine & Johnson, 2003), determining the relevance of *Undaria* in their feeding preferences may contribute to evaluating the magnitude of the impacts caused by the invasive species.

Feeding preference occurs when a consumer actively selects prey based on specific behaviors (Singer, 2000). This behavior is typically assessed by comparing the consumption of a prey item when presented alone versus when presented alongside another prey item (Underwood & Clarke, 2005). These studies are often useful to evaluate the role of grazers such as sea urchins in structuring benthic communities, but also to understand the interactions between consumers and prey (Jackson & Underwood, 2007; Aguilera, 2011). However, feeding preference studies performed in the field are challenging due to multiple variables acting simultaneously, making any interpretation uncertain. The aim of this study was to assess the feeding preference of the native sea urchin *Arbacia dufresnii* from an environment invaded by *Undaria pinnatifida*. To achieve this, we performed feeding experiments at controlled aquarium conditions, using *Undaria* at different developmental stages to determine whether the sea urchin can graze on the invasive kelp throughout the year. Additionally, we evaluated the feeding preferences of *A. dufresnii* comparing *Undaria* with the six most abundant macroalgae species available in the environment.

## METHODOLOGY

Adults of *A. dufresnii* (N =112 in all experiments) were randomly collected by scuba diving from Punta Cuevas, Nuevo Gulf (42°46´44´´S; 64°59´52´´W) in different seasons, according to the developmental stages of the *Undaria* life cycle reported by Casas *et al.* (2008) for the study area: i) winter (August 2014), when the sporophytes were starting to grow, *Undaria* formed dense stands and the mean densities were maximum (***growth stage***); ii) spring (November 2014), when sporophylls were mature, showing the highest average of biomass (***maturity stage***); and iii) summer (January 2015), when the kelp was senescent (***senescence stage***). In winter, we also collected entire *Undaria* individuals and the most frequent and abundant macroalgal species, such as *Dictyota dichotoma*, *Lomentaria clavellosa*, *Codium vermilara*, *Ceramium* sp., *Ulva* spp., and a Corallinales (rhodolith) species. After collection, sea urchins were transported to the Experimental Aquarium of the Centro Nacional Patagónico (CCT CONICET CENPAT), Puerto Madryn, Chubut, Argentina, where they were maintained on a 12 h light:12 h dark photoperiod with a salinity constant with a mean value of 34 and temperature between 14 and 16 °C. Water quality was maintained within optimal parameters. *Undaria* and the other macroalgae were manually cleaned to remove visible epiphytes or animals and separately preserved in containers with flowing seawater.

Two experiments were carried out. One experiment was aimed to evaluate the consumption of the different structures of *Undaria* (blades and sporophylls) at the different developmental stages (growth, maturity and senescence) (***Undaria* experiment).** The other experiment was aimed to determine the feeding preference of sea urchins between *Undaria* and the other macroalgae species available in the environment (**feeding preference experiment**). Experiments were carried out in 90-L containers with water recirculation, biofilter and air pump to ensure good water oxygenation, for three days. Each container was subdivided into eight equal compartments (15x15x15 cm) using a plastic screen of 1 mm of mesh for water circulation. Prior to the start of the experiments, sea urchins were starved for three days to promote uniform nutritional state. Each individual was measured (test diameter, caliper accuracy of 0.1 mm), and a one-way ANOVA ($\alpha=0.05$) was performed to corroborate the homogeneity of individual sizes across treatments and trials. The mean (± SD) diameter of the sea urchin was 28.35 mm (± 3.8 mm).

### ***Undaria*** **experiment**

To evaluate the consumption of the different structures of *Undaria* (blade and sporophyll) at the different developmental stages (growth, maturity, and senescence), six trials were conducted (two structures × three developmental stages), using two containers per trial. Sea urchins were randomly assigned to one part of each container (n=7 per container) and fed with a monospecific diet of blade or sporophyll (~2 g). The excess of water on the kelp surface was first dried using a salad spinner (high speed centrifugal force, 20 turns), following a modification of the method used by Hay *et al.* (1986). Blades and sporophylls were weighed at the beginning and at the end of the three-day experiment.

The remaining part of the container was used to evaluate the autogenic change of the kelp (i.e. *Undaria* structure in the absence of the sea urchin). To consider the potential variability in kelp weight attributable to autogenetic changes (Manly, 1993, Trowbridge, 1995), the consumption of *Undaria* was calculated considering the *Undaria* weight lost in the absence of the sea urchin (control) (Cacabelos *et al.*, 2010). The consumption of *Undaria* was calculated using the following formula (1): *Weight consumed (WC) = (Wi - Wf) - (WCi-WCf)*, where *Wi* is the initial blade or sporophyll wet weight and *Wf* is the final wet weight (after consumption). *WCi* is the initial wet weight of the control and *WCf* is the final wet weight of the control. In the cases where consumption had a negative value close to zero, this value was corrected to zero because it may be attributed to a scale error.

Differences in consumption between the different *Undaria* developmental stages were tested by using a nested ANOVA, using the container (1 and 2) factor nested within the developmental stage factor (growth, maturity and senescence) for each structure (blade or sporophyll).

### **Feeding preference experiment**

To determine whether *A. dufresnii* chose *Undaria* blades over sporophylls or other macroalgae available in the environment, a feeding preference experiment was conducted following the methodology proposed by Underwood & Clarke (2005). The experiment consisted of two treatments: i) a **no-choice treatment**, aimed to estimate the quantity of each macroalgae species consumed when it was offered individually to the sea urchin, and ii) a **choice treatment**, aimed to estimate the consumption when two species were offered. Thus, **preference** was defined when the consumption of one item in the **no-choice treatment** was lower than that in the **choice treatment**, while the consumption of the other item remained unchanged.

For the no-choice treatment, all macroalgae collected in winter were dried with a salad spinner (20 turns for laminar species and 40 turns for filamentous species). Two containers subdivided into eight compartments were used for each trial, as previously described for the *Undaria* experiment. Two grams (initial wet weight) of the same sections of each macroalgal species was always offered to avoid variation. After three days, the remains of macroalgae were removed, dried with the salad spinner, and weighed to obtain the final wet weight. The consumption of *Undaria* blades and sporophylls and each macroalgal species was calculated with the formula described above (1).

For the choice treatment, two containers were used for each trial (algae-*Undaria* pair). Four parts of each container were used for individual feeding of four sea urchins with 1 g of the macroalgae (*Undaria* sporophylls, Corallinales species, *D. dichotoma*, *L. clavellosa*, *C. vermilara*, *Ceramium* sp., or *Ulva* spp.) and 1 g of *Undaria* blades (growth stage). The remaining four parts were used as control (same amount of feed but in the absence of sea urchins). The total weight of feed offered during the no-choice treatment was equal to that offered at the choice treatment to avoid effects due to different encounter rates (Underwood & Clarke 2005). After three days of trials, macroalgae were dried, weighed and the consumption was calculated with the formula described above (1).

Preference was analyzed with a nested ANOVA, using the container (1 and 2) as a factor nested within the treatment (no-choice or choice) factor for each trial (Martins *et al.*, 2014). All analyses were performed in INFOSTAT (Di Rienzo *et al.*, 2019).

## RESULTS

### *Undaria* experiment

*Arbacia dufresnii* consumed both the blades and sporophylls of *Undaria* at all the developmental stages (Fig. 1). The consumption of blades did not differ significantly between developmental stages ($F=0.74$, $p>0.05$), whereas that of sporophylls was greater during the maturity stage than during the senescence stage ($F=3.93$, $p<0.05$).

### Feeding preference experiment

The feeding preference experiment showed that, when *Undaria* was at the growth stage, *A. dufresnii* individuals preferred to feed on blades rather than on sporophylls. The weight of *Undaria* blades consumed was higher during the choice treatment than during the no-choice treatment (weight consumed: $F=39.35$, $p<0.0001$). Only 25% of sea urchins consumed sporophylls during the choice treatment (Fig. 2a).

Concerning the preference between *Undaria* blades and the other macroalgae available in the environment in winter, *A. dufresnii* selected *Undaria* blades over the Corallinales macroalgae and *D. dichotoma*. For the Corallinales species, the wet weight consumed was lower during the choice treatment ($F=5.01$, $p<0.05$, Fig. 2b), while *D. dichotoma* was not consumed during this treatment (Fig. 2c). In both cases, the *Undaria* wet weight consumed did not vary between treatments (*Undaria*- Corallinales: $F=0.44$, $p>0.05$; *Undaria-D. dichotoma*: $F=1.40$, $p>0.05$; Fig. 2 b,c).

*Arbacia dufresnii* did not show preference for either *Undaria* or *Lomentaria clavellosa* (Fig. 2d). The *Undaria* wet weight consumed showed no differences between treatments ($F=0.41$, $p>0.05$); however, there was a significant difference in the consumption of *L. clavellosa* ($F=109.12$, $p<0.0001$), but it was almost 100% consumed during both treatments. Regarding the consumption of *Codium vermilara*, *A. dufresnii* fed higher amounts during the choice treatment than during the no-choice treatment ($F=7.87$, $p=0.01$), while the consumption of *Undaria* did not vary between treatments ($F=0.004$, $p>0.05$) (Fig. 2e). In addition, in the *Undaria-Ceramium* sp. trial, no differences in the weight consumed were observed between treatments (*Undaria*: $F= 0.78$, $p>0.05$, *Ceramium* sp: $F=3.31$, $p>0.05$, Fig. 2f). Similarly, no preference in consumption was observed between *Undaria* and *Ulva* spp. and no differences between treatments were recorded (*Undaria* weight consumed $F=0.73$, $p>0.05$ and *Ulva* spp. weight consumed $F=1.57$, $p>0.05$, Fig. 2g).

## DISCUSSION

*Arbacia dufresnii* consumed both blades and sporophylls of *Undaria* at all developmental stages. These results complement previous diet studies evaluating stomach contents and stable isotopes, which determined that the sea urchin consumes and assimilates the kelp in both spring and summer, when the sporophytes are mostly mature and senescent, respectively (Castro *et al.*, 2022). Although sporophylls were consumed in all trials, preference experiments indicated that *A. dufresnii* preferred feeding on *Undaria* blades rather than on sporophylls at the growth stage. Similar results have been found in the native crab *Pugettia producta*, which also prefers blades over sporophylls in California, USA (Thornber *et al.*, 2004). Previous studies have demonstrated that

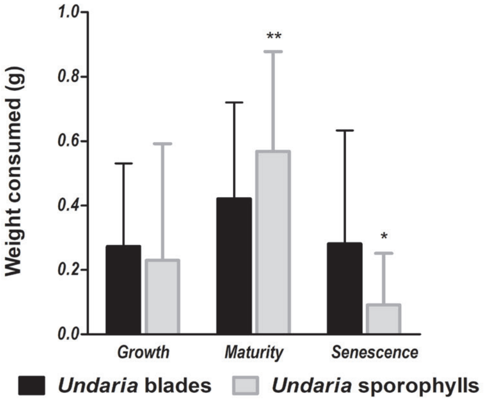

Fig. 1: Weight (g) of blades and sporophylls of *Undaria pinnatifida* consumed by *Arbacia dufresnii* in the feeding experiment at each developmental stage of the invasive macroalga (growth, maturity and senescence). * Lowest and ** Highest, statistically significant value.

the chemical composition of *Undaria* can change according to the tissue, developmental stage, and season, this latter related to abiotic factors, such as temperature or illumination (Skriptsova *et al.*, 2010; Ank *et al.*, 2014; Skriptsova, 2016; Arijon *et al.*, 2021; 2023; Solana, 2022). Among chemical compounds, phenolic compounds are known to act as chemical defenses under conditions of natural herbivory (Haavisto *et al.*, 2017) and have been found at higher amounts in *Undaria* sporophylls than in blades (Solana, 2022). Therefore, the preference of *A. dufresnii* for blades at the growth stage found in this study could be related to the higher concentration of chemical compounds in sporophylls, which may decrease their palatability and digestibility (Cronin & Hay, 1996, Van Alstyne *et al.*, 2001). Preferences of native species to incorporate an invasive species into their diet may vary according to its developmental stage (Thornber *et al.*, 2004). Future research involving preference experiments between blades and sporophylls of *Undaria* at different developmental stages could provide more information to understand consumption patterns of native sea urchins on the invasive kelp *Undaria*.

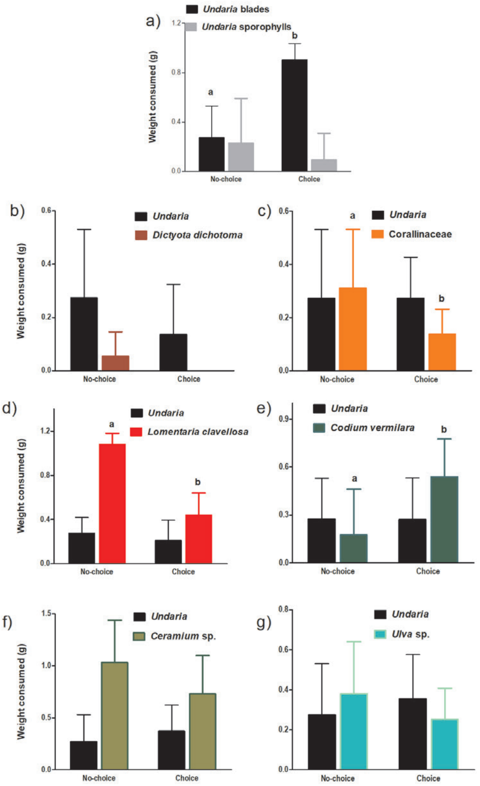

Fig. 2: Weight consumed (g) by *Arbacia dufresnii* during the no-choice and choice treatments of the feeding preference experiment. a) *Undaria* blades - sporophylls. b) *Undaria* - *Dictyota dichotoma*. c) *Undaria* - Corallinales. d) *Undaria* - *Lomentaria clavellosa*. e) *Undaria* - *Codium vermilara*. f) *Undaria* - *Ceramium* sp. g) *Undaria*-*Ulva* sp.

*Undaria* blades were also preferred over the brown seaweed *Dictyota dichotoma*. This result is in accordance with previous studies showing that although *D. dichotoma* is frequently present in the stomach contents of *A. dufresnii*, it is not assimilated into its tissues (Castro *et al.*, 2022). Previous studies have shown that many herbivores reject species of the genus *Dictyota*, presumably due to the presence of deterrent secondary metabolites (Hay *et al.*, 1986; Pereira *et al.*, 2000; Paul *et al.*, 2001; Souza *et al.*, 2008; Spiers *et al.*, 2021). *Dictyota dichotoma* is also an exotic species in the study area but, unlike *Undaria*, its introduction occurred much earlier (Orensanz *et al.*, 2002; Raffo, 2014). This suggests that the presence of specific compounds in *D. dichotoma* may explain why it is not a food source for *A. dufresnii*, despite the long- term availability of the macroalgae in the environment, and the known dietary plasticity of the sea urchin (Penchaszadeh & Lawrence, 1999; Castro *et al.*, 2022). The exclusive consumption of *D. dichotoma* in the no-choice treatment likely indicates that it was ingested solely because it was the only food source available. Regarding the Corallinales macroalgae, the sea urchin also showed preference for feeding on *Undaria*, probably because the calcification of coralline algae serves as a physical defense against herbivory (Litter *et al.*, 1983).

In the "*Undaria - Lomentaria clavellosa*" trial, no preference for either macroalga was observed, but *L. clavellosa* was fully consumed during both the no-choice and choice treatments of the experiment. Previous studies have shown that *L. clavellosa* is found in high abundance in the stomach contents of *A. dufresnii* and is assimilated into the muscle (Castro *et al.*, 2022). This inconsistency may be attributed to the insufficient amount of food offered to the sea urchins. Therefore, future experiments providing sea urchins with a greater quantity of food are necessary to definitely confirm the absence of preference. Likewise, in the "*Undaria - Codium vermilara*" trial, it was not possible to determine preference. In the choice treatment, *A. dufresnii* consumed more *C. vermilara*, while *Undaria* consumption did not vary between treatments. Species of the genus *Codium* have been frequently observed in the stomach contents of the native sea urchin and are relevant assimilated items, contributing more than 50% to gonadal and muscle tissues according to isotopic values (Castro *et al.*, 2022). Various feeding experiments on different *Codium* species have shown that sea urchins consume cylindrical macroalgae more rapidly than flat-shaped macroalgae (Scheibling & Anthony, 2001; Lyons & Scheibling, 2007). However, despite the higher feeding rate, sea urchins obtain less energy from these cylindrical macroalgae (Lyons & Scheibling, 2007), suggesting the need to supplement with other items of higher nutritional quality.

When *Undaria* and *Ulva* sp. were offered together, we observed that *A. dufresnii* consumed both alternately, showing no preference between the two laminar macroalgae. Numerous reports have indicated that the green macroalgae *Ulva* sp. are often preferred by sea urchins (e.g. Navarrete *et al.*, 2008; Souza *et al.*, 2008; Cyrus *et al.*, 2015) and other herbivores such as gastropods (e.g. Van Alstyne *et al.*, 2009; Angell *et al.*, 2012). These preferences have been attributed to their high nutritional value (Lawrence, 1975; Van Alstyne *et al.*, 2009), and, in the case of *A. dufresnii*, it is significantly assimilated into muscle tissues (Castro *et al.*, 2022). The similarity in the consumption between *Undaria* and *Ulva* sp. could be considered in nutritional value tests under the hypothesis that the invasive kelp *Undaria* is nutritionally similar to native species of the genus *Ulva*.

In summary, the native sea urchin *Arbacia dufresnii* did not exhibit strong feeding preference behavior, supporting evidence that this species has significant dietary plasticity and can adapt to newly available resources in the environment (Castro *et al.*, 2022). The lack of preference for the most common macroalgae species over *Undaria*, even those with known high nutritional value, suggests that this invasive species may alter resource use and thereby affect the trophic structure of native communities. Similarly, this lack of preference has also been experimentally observed in other native herbivores (Thornber *et al.*, 2004; Jiménez *et al.*, 2015; Cardoso *et al.*, 2020; Mabey *et al.*, 2022). Therefore,our results also suggest that the successful distribution of *Undaria* is likely driven by factors other than herbivory escape (Cardoso *et al.*, 2020; Mabey *et al.*, 2022). On the other hand, our results differ from the experiments of Teso *et al.* (2009), where *A. dufresnii* did not feed on sporophylls, which could be due to the 10 years that have passed between studies. Santamaria *et al.* (2022) have recently suggested that native herbivores progressively learn to consume invaders. Hence, the differences associated with more than a decade of variation in the timing of macroalgal invasion also reinforce findings that *Undaria* contributes more significantly to the diet of *A. dufresnii* in sites with a longer history of invasion (Castro *et al.*, 2022). The present research contributes to better understanding the magnitude of impacts caused by invasive macroalgal species through feeding ecology studies of native grazers.

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