



Incidence of herbivory of the invasive crab *Percnon gibbesi* on the endemic Mediterranean seagrass *Posidonia oceanica*

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Abstract Seagrasses are one of the most productive marine ecosystems in the world. *Posidonia oceanica*, an endemic Mediterranean seagrass, is under high and constant anthropogenic and natural pressures, including climate change and the introduction of invasive species. *Percnon gibbesi*, a small crab with a tropical and subtropical distribution, was first reported in the Mediterranean Sea in 1999, and today is established across the entire Mediterranean Basin, inhabiting the shallow rocky infra-littoral zone. Given that *P. gibbesi* and *P. oceanica* can co-occur in the same environments, an experiment was set up to study their plant–herbivore interaction. Using two experiments at two different temperatures (19 °C and 25 °C), the incidence of herbivory on the seagrass tissues (fruits, leaves, rhizome, and whole shoot) by the invasive crab was assessed. The fruits along with the rhizome were the most consumed tissues, and the leaves of *P. oceanica* were the least consumed, which could be a consequence of tissue structure characteristics and/or nutrient quality. The incidence of herbivory on the leaves of *P. oceanica* was not affected by temperature. The herbivory pressure of the exotic crab *P. gibbesi* on native seagrass *P. oceanica* will likely be limited to a shallow bathymetric range; however, given the

large scale of the invasion, the consumption of *P. oceanica* could become a relevant ecological issue in the Mediterranean Sea.

Keywords Herbivory · Invasive species · Mediterranean sea · Non-native species · *Percnon gibbesi* · *Posidonia oceanica*

Introduction

Seagrasses are productive marine ecosystems (Murphy et al. 2021; Anton et al. 2020a) that provide important ecological and economic services (Anton et al. 2011; Boudouresque et al. 2006; Giomi et al. 2019; Bidak et al. 2021). They form habitat for hundreds of species of fish and invertebrates (Anton et al. 2009; McHenry et al. 2021), some with high economic value (Barbier et al. 2011; Besson et al. 2016). They also play a key role in mitigating the effects of global warming through carbon accumulation and sequestration in their sediments (Serrano et al. 2012; Monnier et al. 2021). *Posidonia oceanica* is an endemic long-lived Mediterranean seagrass that forms extensive meadows on both soft and hard substrates (Gaglianone et al. 2017; Badalamenti et al. 2015) near the coast at depths between 0 and 45 m (Marbà et al. 2014a). *Posidonia oceanica* is under constant high anthropogenic and natural pressures. Increased anthropogenic activities include destructive fishing methods such as bottom trawling

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(Boudouresque et al. 2009), nutrient enrichment (Burkholder et al. 2007), anchoring methods, and land-use change involving construction or recreational activities (Merino et al. 2017). Natural pressure includes the competition for space and light with other plants and algae (Ralph et al. 2007) and ocean warming (Marbà et al. 2009).

In the last century, global sea surface temperatures have increased on average by just over 1 °C (Poloczanska et al. 2013). Over the past three decades, the mean rate of increase has been 0.15 ± 0.01 °C per decade, which is lower than the rate observed in the Mediterranean Sea in the same period, where the mean increase has been 0.37 ± 0.03 °C, making it a hot spot for climate change (Giorgi 2006; Garcia-Soto et al. 2021). This increase in temperature is boosting the grazing rates of many herbivores, such as sea urchins (Brown et al. 2014), sea stars (Sanford 2002), and gastropods (Petraitis 1992), due to an increase of their metabolic rates (Brown et al. 2004). Rising sea surface temperatures also allow non-indigenous species from warmer thermal regimes to settle in new areas (Katsanevakis et al. 2011; Wesselmann et al. 2020, 2024). Such invasive species are often, but not always (Geraldi et al. 2014), a serious threat to ecosystems with the potential to reduce the abundance and presence of native species through predation or competition (Anton et al. 2019, 2020b) and to affect food webs, ecosystem functioning, and human health (Mainka and Howard 2010; Marbà et al. 2014b; Tiralongo et al. 2021). Invasions by marine herbivores can be particularly damaging since marine systems tend to be strongly regulated by top-down forces (Shurin et al. 2006). A global study showed that marine herbivores strongly reduce producer abundance by an average of 68% (Poore et al. 2012). The introduction of herbivorous species, such as rabbit fish species (*Siganus rivulatus* and *Siganus luridus*) in the western Mediterranean, can drive shifts in grazing patterns that increase the vulnerability of native macrophytes (Santana-Garcon et al. 2023). Also, the invasion of grazers like the sea urchin *Centrostephanus rodgersii* in eastern Tasmania can decrease macroalgae abundance and led to the creation of barrens (Strain and Johnson 2009, 2013). A recent meta-analysis showed that more than 70% of marine invasive herbivores—the majority of which are filter-feeders

such as bivalves and gastropods feeding on pelagic microalgae—have sizeable impacts on primary producers (Anton et al. 2019). However, the effects of invasive herbivore species that feed on benthic macroalgae are barely quantified (Anton et al. 2019, Santana-Garcon et al. 2023).

Percnon gibbesi (H. Milne Edwards, 1853) is a small herbivorous crab with a subtropical and tropical distribution. It is naturally found on the Pacific coast from Chile to California, in the western Atlantic Ocean from Brazil to Florida, and from the Azores to Angola in the eastern Atlantic Ocean (Manning and Holthuis 1981; Sciberras and Schembri 2008; Azzurro et al. 2010), inhabiting the infralittoral rocky zone from 0 to 4 m deep (Deudero et al. 2005) although has been observed in the Balearic Islands at depths of up to 8 m of depth (Anton, personal communication). *Percnon gibbesi* was first recorded in the Mediterranean Sea in 1999 in Linosa (Sicily Strait, Italy) and in Mallorca (Balearic Islands, Spain) (Garcia and Reviriego 2000; Relini et al. 2000). *Percnon gibbesi* feeds primarily on algae, including almost 50 species of macroalgae (Puccio et al. 2006; Katsanevakis et al. 2011; Puentes and Anton, unpublished results). A recent study showed the presence of fragments of leaf detritus of the endangered *P. oceanica* in the stomachs of *P. gibbesi* on the rocky coast of Algeria (Bada et al. 2022). In addition, juveniles of *P. gibbesi* were collected in a *P. oceanica* meadow nearby the Castello d'Ischia (Italy) in 2011 (Gambi et al. 2016). Therefore, there is a co-occurrence of the two species within the same habitat: *Percnon gibbesi* has been observed in shallow areas where *P. oceanica* thrives both in sandy patches between and near shallow rocky environments. Apart from the recent publication by Bada et al. (2022), our understanding of the plant–herbivore interaction between the seagrass *Posidonia oceanica* and the invasive crab *Percnon gibbesi* remains unknown.

To address this gap, our objective is to investigate the herbivory incidence of *P. gibbesi* on the vegetative (leaves and rhizomes) and reproductive tissues (fruits) of the seagrass *P. oceanica*. Additionally, we want to evaluate the potential effect of temperature on the grazing intensity of *P. gibbesi* on *P. oceanica* tissues by conducting experiments at two different temperatures (19 °C and 25 °C). We hypothesize that consumption rates would be higher, if present, on tissues with greater nutritional value (fruits and young

leaves; Castejón-Silvo et al. 2019), and that herbivory would increase at higher temperatures, as observed in other herbivores (Petraitis 1992; Brown et al. 2014).

Methods

Specimens of *P. gibbesi* were collected in the Mediterranean Sea at Cala d'Estellencs (39.656944° N, 2.472811° E) located on the island of Mallorca, Spain (Fig. 1). The sampling was performed twice during daytime (in April and May 2023), with the aid of hand fishing nets in a rocky area at a depth of 0–2 m. The collected organisms were carefully transferred into aerated coolers and transported to the Mediterranean Institute for Advance Studies (IMEDEA) facilities in Esporles within 1–2 h from collection, where 16 crabs were put individually into glass aquariums (25 cm × 25 cm × 30 cm) of 16 L equipped with a recirculating water filter (Eheim). Before the experiment, we conducted preliminary trials with *P. gibbesi* in these aquariums to assess their suitability. The tanks offered enough space for the crab to move and the crabs appeared to be in excellent health and well-being. In this study, we achieved 100% survival of *P. gibbesi* using the 16-L aquariums, confirming them as a suitable option for this type of experiment, although

the suitability of larger tanks was not evaluated. *Posidonia oceanica* healthy shoots that were drifting near the shore in Estellencs were collected by hand and brought to IMEDEA.

The collected *P. gibbesi* were kept in tanks to acclimatize for a period of 7 days, during which they were provided with *P. oceanica* as a food source. To aid the survival of each specimen during the whole experiment, salinity of 37–38 ppt, and oxygen at 100% saturation were maintained during both acclimatization and experiment period. After acclimatization, the 16 crabs were put into four different food treatments (4 crabs per treatment; $n=4$): (1) six *P. oceanica* leaves (including the first two youngest leaves, two adult leaves, and two brown leaves); (2) three *P. oceanica* fruits; (3) one *P. oceanica* aerial rhizome; and (4) one seagrass shoot (Fig. 2).

For each replicate, the plant tissue was taken out of the water and stirred for twenty rounds in a salad spinner (Prince and LeBlanc 1992) and then weighed on a scientific scale accurate to three decimal places in grams. Tissues were also photographed to assess the surface area using the program ImageJ (Java). These measurements were taken both at the beginning and at the end of each experiment (subtracting final wet weight/area to the initial wet weight/area) to assess the change in plant biomass (wet weight loss)

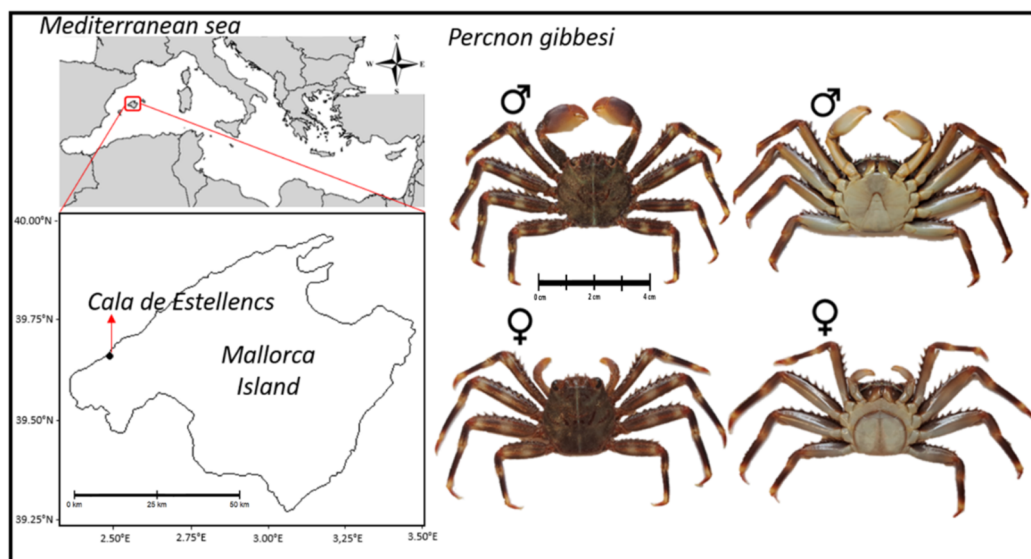


Fig. 1 Collection area at Cala d'Estellencs on the island of Mallorca in the Mediterranean Sea on the left. *Percnon gibbesi* male and female top and bottom view on the right

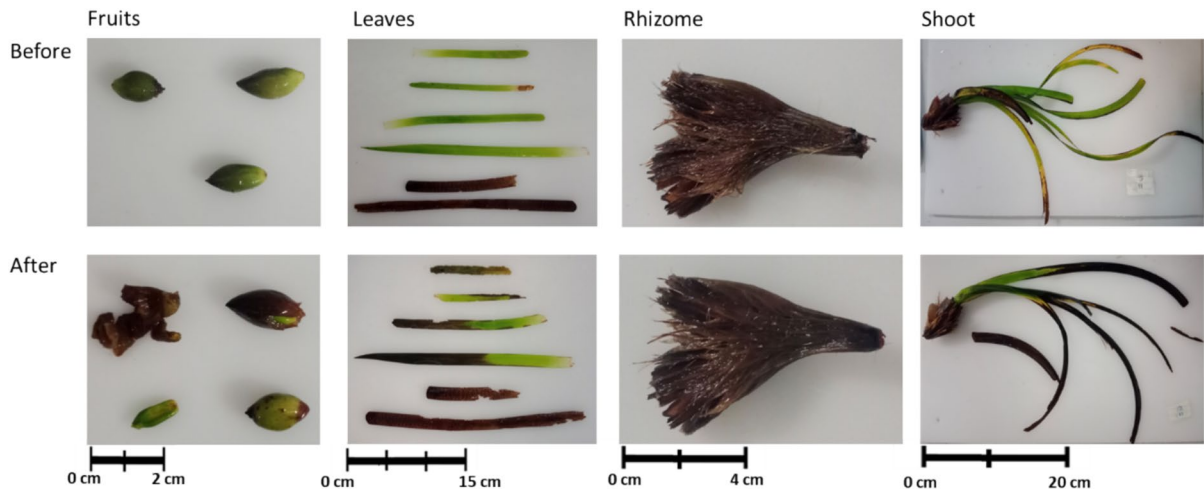


Fig. 2 Example of *Posidonia oceanica* tissues used as treatments in the experiments: fruits, leaves with the youngest green leaves, adult green leaves and the older brownish leaves,

rhizome, and shoot. Example tissue is represented “before” and “after” the experiment

and surface area loss for each treatment. For leaves, we also measured the number of bite marks. To account for the effect of crab gender and size of the crabs in each experiment, their wet weight, width, and sex were quantified before and after the experiment. Epiphytes were gently removed from the leaves with a blade prior to the beginning of each experiment. Each experimental aquarium contained two mesh cages, one placed above the other, as shown in Fig. 3. One specimen of *P. gibbesi* was randomly placed in one of the two cages together with the *P. oceanica* tissue treatment. The other cage only contained the *P. oceanica* tissue as a control treatment without herbivore.

Two analogous experiments were performed at two different targeted temperatures, 19 °C and 25 °C. The former corresponds to the temperature found in

late spring, when fewer specimens are seen in the field, while the latter corresponds to the average summer sea surface temperature in Mallorca, when *P. gibbesi* is usually more abundant (Anton, *unpublished results*).

Experiment 1 started on April 12th 2024 and finished on April 21st 2024. The temperature was held at 25 °C in the aquariums, with 4 replicates on each of the four treatments (leaves, fruits, rhizome, and whole shoot; $n=4$). Seven aquariums contained a female crab and nine contained a male crab. Experiment 2 started on May 9th and finished on May 18th 2024, where the temperature was kept at 19 °C for three treatments (leaves, fruits, and rhizome; $n=4$). An additional treatment was conducted at 25 °C with 4 replicates that contained the leaves of *P. oceanica* to

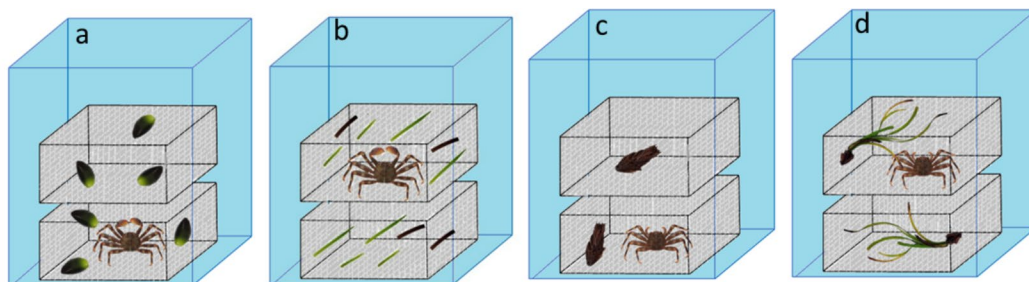


Fig. 3 Illustrations of the experiment setup displaying the two mesh cages in the aquariums, with the respective treatment and crab. **a** *P. oceanica* fruit treatment. **b** *P. oceanica* leaf treatment. **c** *P. oceanica* rhizome treatment. **d** *P. oceanica* shoot treatment

allow a comparison of the effects of temperature (19 vs 25 °C) within the same experiment. Nine aquariums contained a female crab and seven contained a male crab. The number of experimental days was not selected a priori, as we were not sure about the rate (if any) of consumption of seagrass tissues by *P. gibbesi*. Therefore, the seagrass tissues within the experimental cages were observed throughout the experiments to ensure the food source was not depleted (Vergés et al. 2007; Castejón-Silvo et al. 2019), and both experiments lasted 10 days.

Data analysis

The seagrass biomass consumption by *P. gibbesi* per day per crab, independently for each of the tissues (fruits, leaves, rhizomes and shoots), was calculated using this formula:

Seagrass biomass consumption

$$(g \text{ WW tissue day}^{-1}) = (W_{fe} - W_{ie}) - (W_{fc} - W_{ic})/d$$

where W_{fe} is the final seagrass wet weight (WW) in the cage where the crab is present, W_{ie} the initial seagrass WW in the cage where the crab is present, W_{fc} the final seagrass WW in the cage where no crab is present, W_{ic} the initial seagrass WW weight in the cage where no crab is present and d in the number of days of experiment. We subtracted the changes in biomass in the control cages (no crab present) from the experimental ones (one crab present) to account for any autogenic effects of the aquarium or the mesh cages on biomass gain/loss.

The area of leaf consumed by *P. gibbesi* per day per crab was calculated as follows:

Seagrass leaf area consumption

$$(cm^2 \text{ seagrass leaf day}^{-1}) = (A_{fe} - A_{ie}) - (A_{fc} - A_{ic})/d$$

where A_{fe} is the final seagrass area in the cage where the crab is present, A_{ie} the initial seagrass area in the cage where the crab is present, A_{fc} is the final seagrass area in the cage where no crab is present, A_{ic} the initial seagrass area in the cage where no crab is present, and d in the number of days of experiment. We subtracted the changes in area in the control cages (no crab present) from the experimental ones (one crab

present) to account for any autogenic effects of the aquarium or the mesh cages on area gain/loss.

The number of bites by *P. gibbesi* per leaf per day per crab was calculated as follows:

$$\text{Number of bites (number of bites leaf}^{-1}\text{day}^{-1}) = N_{fe}/d$$

where N_{fe} is the number of bites per leaf at the end of the experiment in the cage where the crab is present and d in the number of days of experiment.

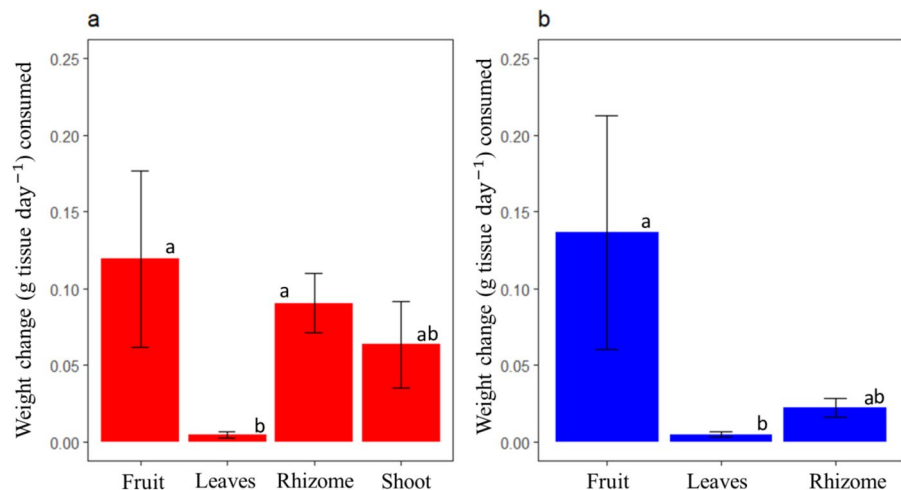
Normality and homoscedasticity assumptions were tested, and non-parametric tests were employed because these assumptions were not satisfied. A Kruskal–Wallis H Test, an equivalent to the One-way ANOVA for non-parametric data, was performed to test if there were significant differences among the different tissues for Experiments 1 and 2 (Fig. 4). In addition, in Experiment 1 and for the leaf treatment only, the change in biomass, the loss of surface area and the number of bite marks were also assessed with a non-parametric Kruskal–Wallis H Test to assess differences between the three types of leaves (Fig. 5a, b and c). In Experiment 2, the same non-parametric test was performed to assess the effect of temperature and type of leaf on change in biomass, the loss of surface area and the number of bite marks (Fig. 5d, e and f). If the result from any of the Kruskal–Wallis H Test was significative, a Dunn's post-hoc test was performed to estimate differences among treatments (Fig. 4). The significance level for the Kruskal–Wallis H and the Dunn's post-hoc tests was set at $\alpha=0.05$. All data was analyzed using R statistical program.

Results

The control treatments (mesh cages without crabs) presented very small changes in both weight (for the four treatments; fruit, rhizome, leaves, and shoot) and area/number of bites in the leaves; and this data was therefore not included in the subsequent analyses. The sex of each crab as well as their individual weight did not show to have a significant effect in the response of the dependent variables.

Comparing biomass loss between the four treatments allows for the identification of which part of the plant was more heavily consumed by the crabs. For Experiment 1 (at 25 °C), significant differences were found when testing the weight

Fig. 4 Wet weight change of the *Posidonia oceanica* by treatment, which included three fruits, six leaves, one rhizome and one shoot, for Experiment 1 at 25 °C (a) and Experiment 2 at 19 °C (b) attributed to one *Percnon gibbesi*. Error bars indicate standard error. Both experiments lasted 10 days



difference with the four treatments ($\chi^2 = 11.087$, $p = 0.0112$; Fig. 4a). Dunn's post-hoc pairwise test detected significant differences between fruits and leaves ($p = 0.005$) and between rhizome and leaves ($p = 0.039$; Fig. 4a). The highest average weight loss was found in the fruit treatment (mean $\pm$ SE; 1.19 ± 0.57 g or 0.12 ± 0.05 g WW day⁻¹), followed by the rhizome treatment (mean $\pm$ SE; 0.90 ± 0.19 g WW or 0.09 ± 0.02 g WW day⁻¹), then the shoot treatment (mean $\pm$ SE; 0.63 ± 0.28 g WW or 0.06 ± 0.02 g WW day⁻¹), and finally the leaf treatment (mean $\pm$ SE; 0.04 ± 0.02 g WW or 0.004 ± 0.002 g WW day⁻¹; Fig. 4a).

For Experiment 2, significant differences were found among the treatments conducted at 19 °C when testing for the weight difference ($\chi^2 = 6.4857$, $p = 0.0395$; Fig. 4b). Post-hoc pairwise analysis detected significant differences between fruits and leaves ($p = 0.006$). The largest average weight loss was found in the fruit (mean $\pm$ SE; 1.36 ± 0.76 g WW or 0.14 ± 0.08 g WW day⁻¹), and rhizome treatments (mean $\pm$ SE; 0.22 ± 0.06 g WW or 0.02 ± 0.006 g WW day⁻¹), followed by leaf treatment (mean $\pm$ SE; 0.04 ± 0.01 g or 0.004 ± 0.001 g day⁻¹; Fig. 4b).

Given the leaf treatments had three different types of leaves, additional analyses were performed to assess which set of leaves lost more biomass using weight, area, and number of bites.

For Experiment 1, there were no significant differences between the three different types of leaves for weight loss ($\chi^2 = 2.9231$, $p = 0.2319$; Fig. 5a)

(mean $\pm$ SE; 0.04 ± 0.02 g or 0.004 ± 0.002 g day⁻¹), area loss ($\chi^2 = 1.0769$, $p = 0.5836$; Fig. 5b), (mean $\pm$ SE; 3.11 ± 0.98 g or 0.311 ± 0.09 cm² day⁻¹), or number of bites ($\chi^2 = 1.2049$, $p = 0.5475$; Fig. 5c).

In Experiment 2, the effect of temperature (19 vs 25 °C) was included in the analyses comparing the three types of leaves. There was no significant effect of temperature ($\chi^2 = 0.3333$, $p = 0.5637$; Fig. 5d) and leaf type for weight loss ($\chi^2 = 1.28$, $p = 0.5273$; Fig. 5d). There was no significant effect of temperature ($\chi^2 = 0.7533$, $p = 0.3861$; Fig. 5e) and leaf type for area loss ($\chi^2 = 0.105$, $p = 0.9489$; Fig. 5e). Finally, there was no significant effect of temperature ($\chi^2 = 0.0204$, $p = 0.886$; Fig. 5f) and leaf type for the number of bites ($\chi^2 = 0.8043$, $p = 0.3698$; Fig. 5f).

Discussion

This study provides experimental evidence for the incidence of grazing of the invasive crab *Percnon gibbesi* on several tissues (fruits, rhizome, leaves, and the whole shoot) of the endemic seagrass *Posidonia oceanica*, indicating a novel ecological hazard for this already threatened species (IUCN 2018) in the Mediterranean Sea.

Results from the experiments indicate that the reproductive tissue (fruits) and the rhizome were the most consumed tissues out of the four tested, with leaves being less consumed than the former two tissues. Neither *P. oceanica* fruits nor rhizome have been previously identified as food items for *P. gibbesi*.

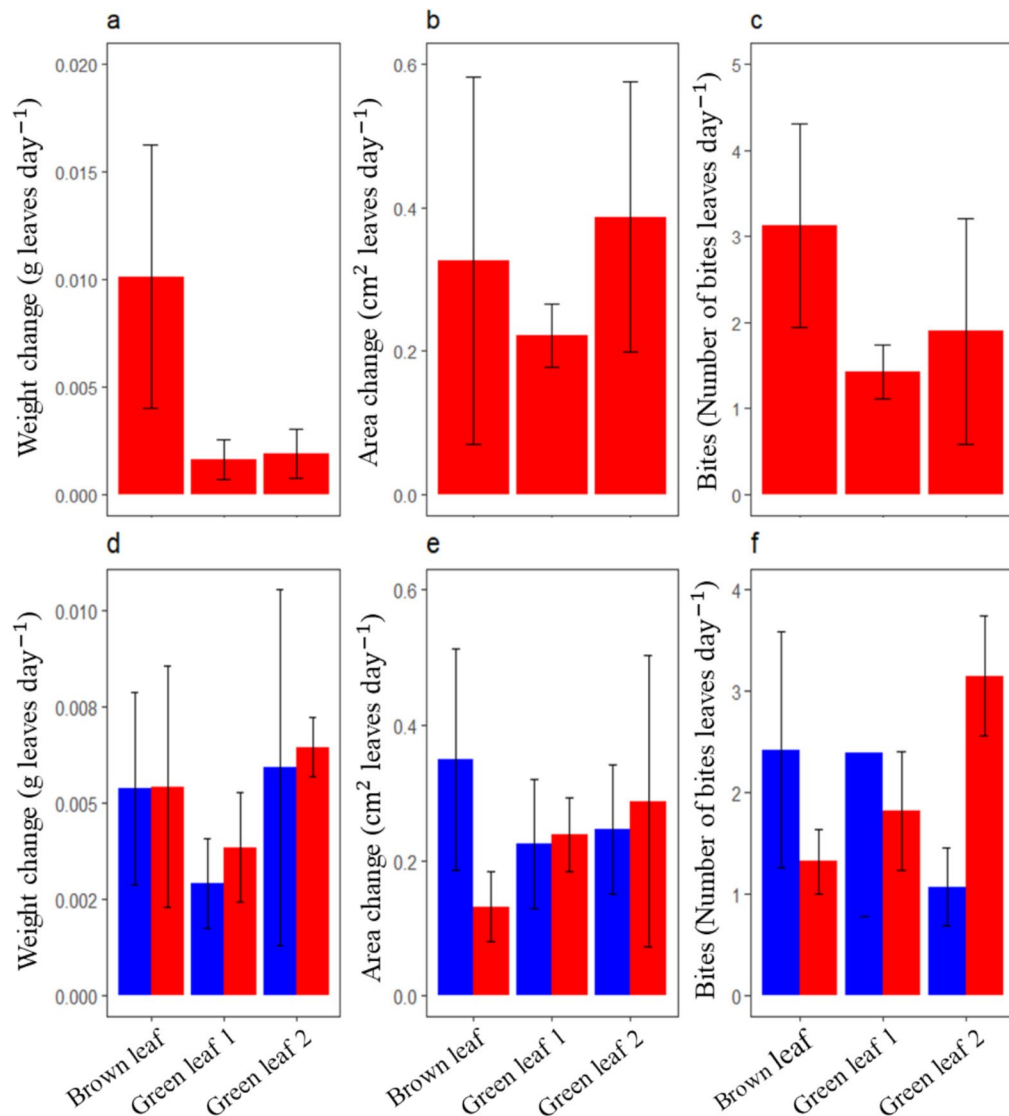


Fig. 5 The *Posidonia oceanica* wet weight change (a), area loss (b) and number of bites (c) for leaf type from Experiment 1 (25 °C) attributed to one *Percnon gibbesi*. Below are bar plots of the weight change (d), area loss (e) and number of

bites (f) for leaf type and the two temperatures from Experiment 2 (blue bars at 19 °C and red bars at 25 °C). Error bars indicate standard error. Both experiments lasted 10 days. Each bar represents changes in two leaves of each type

There is ample record of consumption on seagrass fruits by crustaceans. For instance, the fruits of *Zostera marina* are consumed by the American blue crab *Callinectes sapidus* in the York River (USA) and by *Zeuxo* sp. in Otsuchi Bay in Japan (Fishman and Orth 1996; Nakaoka 2002). The former species is also an invasive crab in the Mediterranean Sea (including Mallorca), typically occupying estuaries and brackish waters (Hines 2007; Schubart et al.

2023). Future studies could evaluate the potential of *C. sapidus* to feed on *Posidonia oceanica* fruits if they become available, given that *Posidonia oceanica* cannot inhabit the low salinity areas where *C. sapidus* lives (Sánchez-Lizaso et al. 2008; Meinesz et al. 2009). Also, the crabs *Nectocarcinus integrifrons* and *Naxia aurita* feed on the fruits of *Posidonia australis* in Western Australia (Orth et al. 2006). In addition, two species of amphipod crustaceans,

Ampithoe ramondi and *Gammarella fucicola*, have been reported to heavily consume the fruits of *Posidonia oceanica* in the Balearic Islands in Spain (Castejon et al. 2019). The high nutritional value of seagrass fruits—mainly compound by starch and protein (Delefosse et al. 2016)—might have led to a higher consumption rate of *P. gibbesi* on *P. oceanica* fruits over other plant tissues, thereby potentially decreasing fruit survival and recruitment success rates.

The strong feeding incidence of *P. gibbesi* for the rhizome of *P. oceanica* was unexpected, given its lesser nutritional value, compared to the other plant tissues (Romero et al. 1998; Alcoverro et al. 2000). Despite its putative low nutritional value, some other herbivores, such as the sea urchin *Sphaerechinus granularis* (Velarque 1981; Martinez-Pita et al. 2008; Lourenco et al. 2022), and the young specimens (<2 cm diameter) of the sea urchin *Paracentrotus lividus* (Peirano et al. 2001), have been found to feed on the rhizome of *Posidonia oceanica*. The rhizome did not undergo prior cleaning before the commencement of the experiments, raising the possibility that the observed herbivory incidence could be influenced by organisms residing on or within the rhizome, such as epiphytes. Epiphyte cover serves as a significant feeding cue for some marine herbivores, guiding their grazing behaviors and dietary preference. This was demonstrated through an examination of the grazing behavior of two fish species on the *Posidonia australis*, where the leaves with epiphytes were favored over those without epiphytic cover, indicating a preference for the nutrient-rich organisms inhabiting the leaves (Wressnig and Booth 2007). In similar studies (Peirano et al. 2001; Tomas et al. 2005), two major herbivores of *Posidonia oceanica*, the sea urchin *Paracentrotus lividus* and the sparid fish *Sarpa salpa* showed a selective feeding preference for more epiphytized tissues. Future studies are needed to better understand the herbivory of *P. gibbesi* on the rhizomes of *P. oceanica* and to evaluate the factors contributing to biomass loss in this tissue. In addition, the significant herbivory observed on the rhizome at the basal level of the shoot in the shoot treatment could potentially lead to leaf detachment. This phenomenon occurred in one of our experimental trials with a whole shoot, therefore occurring approximately 25% of the time. This indirect negative effect may contribute to an

overall increase in *P. oceanica* leaf loss attributable to grazing of this exotic species.

A study performed by Bada et al. (2022), found leaf litter in the stomach of *P. gibbesi*, showcasing the potential herbivory incidence over this tissue. As confirmed in this study, *P. gibbesi* actively consumed *P. oceanica* leaves, although they were the least consumed tissue in the two experiments. Some characteristics of the leaves, such as their structural toughness and high content of carbon, could work as a defense to deter herbivores from feeding on them (Vergés et al. 2007; de los Santos et al. 2016). In this study (when offered six leaves), the biomass consumption per leaf per crab was 0.002 ± 0.001 g WW leaf⁻¹ day⁻¹ (mean $\pm$ SE) and 0.002 ± 0.0008 g WW leaf⁻¹ day⁻¹, the leaf surface area loss was 0.15 ± 0.04 cm² leaf⁻¹ day⁻¹ (mean $\pm$ SE) and 0.11 ± 0.04 cm² leaf⁻¹ day⁻¹ (mean $\pm$ SE), and the number of bites per leaf was 1.075 ± 0.29 and 0.98 ± 0.29 for the Experiment 1 at 25 °C and for the Experiment 2 at 19 °C, respectively. To our knowledge, there are no similar experimental per capita results published for native herbivores of *P. oceanica* in the Mediterranean. However, the two major grazers on the leaves of *P. oceanica*, the sea urchin *Paracentrotus lividus* and the fish *Sarpa salpa*, had respectively consumption rates (although not measured per capita) of 0.031 ± 0.04 cm² leaf⁻¹ d⁻¹ (mean $\pm$ SE) and 0.073 ± 0.08 – 1.06 ± 0.08 cm² leaf⁻¹ d⁻¹ (mean $\pm$ SE) calculated in field tethering experiments (Tomas et al. 2005; Prado et al. 2007). Therefore, further investigation on natural field consumption rates of invasive *P. gibbesi* is warranted to ascertain their ecological impact on the leaves of *P. oceanica*, as well as on the other tissues. The bite marks left on the *P. oceanica* leaves by *P. gibbesi* are identifiable as small and irregular cuts on the leaf (Fig. 6), similar to the ones left by the sea urchin *Paracentrotus lividus* (Prado et al. 2007), which could make it hard to distinguish between native and exotic herbivore species in the field.

The number of bites, leaf area and weight change did not show a significant difference when *P. gibbesi* was exposed to the two different temperatures (19 and 25 °C). A higher consumption of the leaves of *P. oceanica* was expected at the higher temperature (25 °C) due to a putative higher metabolic rate of the crab (Gillooly et al. 2001), as shown in the fish *Sarpa salpa*, which during summer feeds more

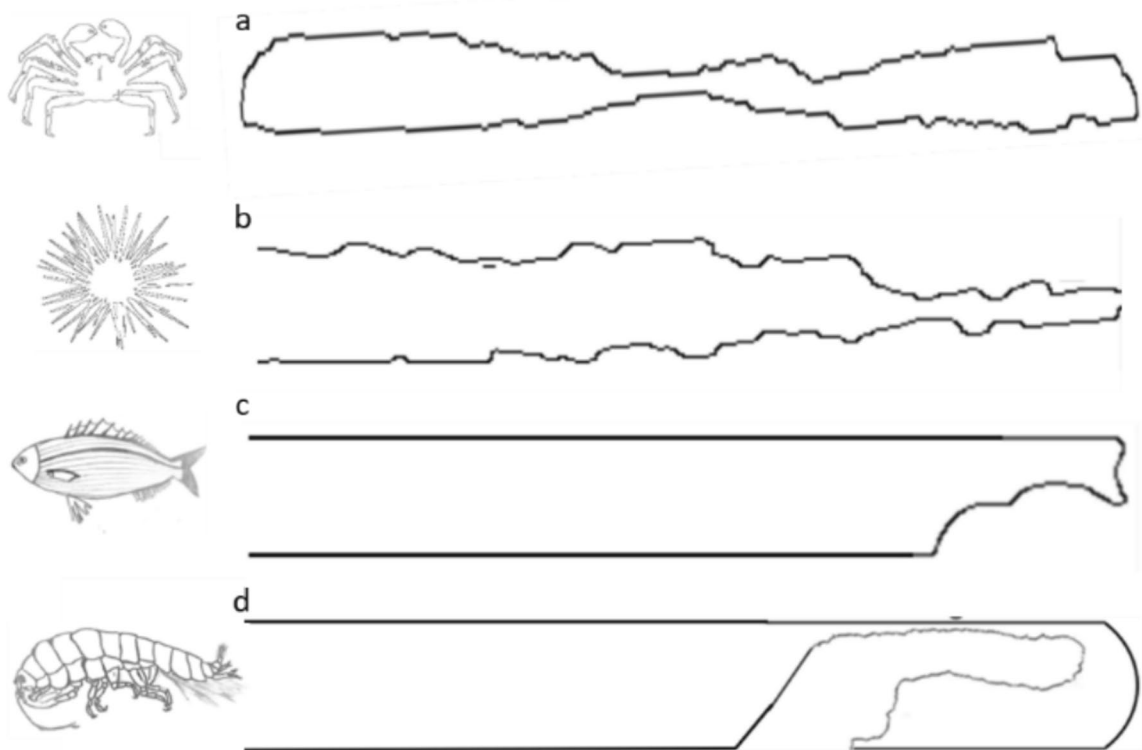


Fig. 6 *Posidonia oceanica* leaves displaying morphologically bite marks by: **a** *Percnon gibbesi*. **b** *Paracentrotus lividus*, **c** *Sarpa salpa* (Images based on the work of Prado et al. 2007). **d**

Gammarella fucicola and *Ampithoe ramondi* (Image based on the work of Castejon et al. 2019). Illustration created with R

intensively on the endemic seagrass in the Mediterranean (Ruíz et al. 2009). Similar results were reported for the pond snail *Lymnaea stagnalis*, whose feeding rates on the water weed *Elodea nuttallii* were shown to positively increase with temperature (Zhang et al. 2020). However, this study found a weak thermal-dependence of grazing incidence of *P. gibbesi* on the leaves of *P. oceanica*, suggesting that either *P. gibbesi* has a wide optimal feeding range with comparable rates from 19 to 25 °C or that we missed the thermal optimum by experimentally testing only two temperatures. To resolve this knowledge gap, future studies could investigate the thermal-dependence of grazing rates of *Percnon gibbesi* across a wider range of temperature.

Climate change opens suitable environments for species from warmer thermal regimes (Wessellmann et al. 2020), including herbivores (Verges et al.

2014; Santana-Garçon et al. 2023), thereby increasing the pressure on primary producers by non-indigenous species (O’Gorman et al. 2017), such as that of the invasive crab *P. gibbesi* on the seagrass *P. oceanica*. *Percnon gibbesi* has rapidly invaded the Mediterranean Basin in less than three decades. This is the first report of the exotic crab *P. gibbesi* feeding on multiple tissues of healthy *P. oceanica*, showing a high incidence of herbivory in the fruits and the basal rhizome. This rapid and large-scale marine invasion could become a great concern for the already threatened and important Mediterranean endemic seagrass species *P. oceanica*.

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Author contributions Anton A conceived the study and both authors contributed to the study design, data collection and data analysis. Puentes D. performed the experiment with help from Anton A. and Alex Morell. The first draft of the manuscript was written by Puentes D. with contributions from Anton A., and both authors edited subsequent versions of the manuscript. Both authors read and approved the final manuscript.

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Data availability Data will be made available on request.

Declarations

Conflict of interest The authors have no competing or financial interests to disclose.

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