



Herbivory and functional traits suggest that enemy release is not an important mechanism driving invasion success of brown seaweeds

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Abstract Invasive species are a global threat to biodiversity and there is a pressing need to better understand why some species become invasive outside of their native range, and others do not. One explanation for invasive species success is their release from concurrent natural enemies upon introduction to the non-native range. The so-called enemy release hypothesis (ERH) has conflicting support, depending upon the ecosystem and species investigated. To date, most studies testing the generality of the ERH have focused on terrestrial ecosystems. Here, we tested whether enemy release might contribute to the success of the invasive non-native brown seaweeds *Undaria*

pinnatifida and *Sargassum muticum* in the United Kingdom. We conducted choice and no choice experiments to determine herbivore preference on these invaders relative to six functionally-similar native species. We also measured and compared species traits associated with defence against herbivory (carbon to nitrogen ratio, polyphenolic concentration, tensile strength, and compensatory growth). There were no differences in the biomass consumed between invasive and native species for either choice or no choice tests. The carbon to nitrogen ratio (a measure of nutritional quality) was significantly lower for *S. muticum* compared to the three native furoid species, but measures of the other three defence traits were similar or even greater for invasive species compared with native species. Taken together, it is unlikely that

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the ERH applies to invasive seaweeds in the northeast Atlantic, suggesting that other factors may contribute to the success of invasive species in this system.

Keywords Macroalgae · Non-native species · Functional traits · Defence · Non-indigenous species · Herbivory

Introduction

A major challenge for ecologists is to understand why some species are successful and can become invasive outside their native range, and why some do not. There have been many proposed explanations for why some species become invasive (Catford et al. 2009), which ultimately stem from the characteristics of the recipient ecosystems and communities, characteristics of the invaders themselves, and the amount and type of propagule pressure (MacArthur and Levins 1967; Eschtruth and Battles 2011; Ricciardi et al. 2013; Kimbro et al. 2013; McKnight et al. 2017; Vedder et al. 2021). One leading explanation is the release from coevolved natural enemies in their introduced range, known as the enemy release hypothesis (ERH) (Keane and Crawley 2002). The enemy release hypothesis is based upon the premise that invasive species can benefit through a direct reduction in consumption from native herbivores and attack from pathogens and parasites (Mitchell and Power 2003; Liu et al. 2007), partially through changing the allocation of resources from defence mechanisms to growth and reproduction, thereby increasing competitiveness as well as direct benefits such as increased lifespan (Herms and Mattson 1992; Blossey and Nötzold 1995; Schwartz et al. 2016).

In the marine realm, herbivory by benthic invertebrates can strongly influence intertidal and shallow subtidal ecosystems, affecting recruitment, growth, diversity and abundance of seaweed species in particular (Aguilera 2011; Poore et al. 2012; Williams et al. 2013; Aguilera et al. 2015). Reducing herbivory can be achieved through traits that reduce attractiveness of the seaweed to herbivores, such as chemical and mechanical defences, and lowering of nutritional quality (Duffy and Hay 1990). For example, chemical defences in brown algae include phlorotannins which have multiple transient secondary roles, including herbivore defence, before transitioning to unreactive

components of the cell wall, allowing brown seaweeds to invest in both growth and defence (Arnold and Targett 2003). Seaweeds can also limit the effect of herbivory on their fitness by increasing growth to offset biomass lost to consumers (Duffy and Hay 1990). These traits can be costly, reducing overall fitness of an individual or species relative to its competitors (Dworjanyn et al. 2006; Haavisto et al. 2017). If invasive species experience release from herbivory, redirecting resources to growth and reproduction instead of costly defence traits could confer an advantage relative to native competitors (Blossey and Nötzold 1995; Schwartz et al. 2016).

Numerous studies have tested the ERH, but support for this hypothesis is inconsistent, with results varying by the type of invader, the experimental approach, and the recipient native community (Colautti et al. 2004; Heger and Jeschke 2014). The majority of investigations into the ERH, however, have focused on plants in terrestrial ecosystems. Heger and Jeschke (2014) reviewed 176 empirical tests of the ERH, of which 147 (83.5%) focussed on terrestrial systems, and just 15 (8.5%) on marine systems, with only five papers focussed on algae. Interestingly, studies that tested the ERH in marine ecosystems and those that focussed on algae had higher levels of empirical support than other habitat types and taxonomic groups, suggesting that research in both terrestrial and marine ecosystems is needed to more fully understand the generality of the ERH.

Even amongst seaweed species, differences in herbivore preference between invasive and native species may vary between taxonomic or functional groups. Enge et al. (2017) conducted a meta-analysis of 35 papers that examined feeding preferences of native herbivores for non-native compared to native seaweeds. Whilst non-native species were preferred less than native species, suggesting non-native species escaped herbivory, when grouped taxonomically this trend was only observed in filamentous species. Palatability of native and non-native brown seaweeds was similar (Enge et al. 2017). There has been a clear research bias towards only a few invasive seaweeds (e.g. *Caulerpa* spp., *Codium fragile* spp., *Sargassum muticum*), which have provided both strong support (Gollan and Wright 2006; Bulleri and Malquori 2015) and limited evidence for the ERH (Pedersen et al. 2016). Given that release from herbivory may vary temporally and spatially (Britton-Simmons et al.

2011), further investigations are required to determine whether the ERH describes an important mechanism influencing the spread of invasive seaweeds in marine ecosystems. In particular, understanding the specific mechanisms and traits that may influence herbivore preference will help to clarify the importance of ERH in these ecosystems.

The kelp *Undaria pinnatifida* and the fucoid *Sargassum muticum* are invasive seaweeds which are both native to Asia (Epstein and Smale 2017; Le Cam et al. 2020), and were first recorded in the United Kingdom (UK) in 1991 (Farrell and Fletcher 2000) and 1973 (Jones and Farnham 1973) respectively. These species were accidentally introduced into the UK attached to oysters used in aquaculture or attached to vessel hulls (MacLeod et al. 2016). Since introduction to the UK, these global invaders have proliferated and have spread rapidly along the UK coastline (Harries et al. 2007; Epstein and Smale 2017), often becoming abundant (Harries et al. 2007; Heiser et al. 2014), and in some cases causing detectable ecological change in native ecosystems (Salvaterra et al. 2013; McLaughlan et al. 2014; Epstein et al. 2019). These factors of spread rate, abundance, and impact all contribute to their classification as invasive species. Despite their relative success in occupying new habitats in their invaded ranges, the importance of enemy release as a mechanism facilitating the invasion of *U. pinnatifida* and *S. muticum* remains unclear. Previous investigations have found conflicting results, concluding that *S. muticum* is both readily consumed by native herbivores (Kurr and Davies 2018; Strong et al. 2009), and grazed less than native species (Monteiro et al. 2009; Pedersen et al. 2016). Fewer investigations have examined the role of the ERH in mediating the spread of *U. pinnatifida*, but where it has been investigated *U. pinnatifida* was consumed at equal rates to native species (Thornber et al. 2004; Jiménez et al. 2015; Cardoso et al. 2020).

This study aims to contribute to our understanding of the importance of the ERH in marine ecosystems by examining herbivore choice alongside the role of traits that may offer defence against herbivory in native and invasive brown seaweeds. We addressed two specific questions: (1) Are these invasive species more readily consumed by native generalist herbivores than native seaweed species of similar functional groups? (2) Do invasive and native seaweed species differ in their traits related to defence against

herbivory? We predicted that the ERH would be an important mechanism in explaining the success of both *U. pinnatifida* and *S. muticum*, and therefore these species would be consumed less readily than native species. The traits investigated (carbon to nitrogen ratio, polyphenolic concentration, tensile strength and compensatory growth) are expected to explain the patterns shown in the herbivore experiments, to determine whether any observed enemy release is due to characteristics of the invasive seaweeds, or whether they are not differentiated among by herbivores.

Methodology

Study species

Four kelp species and four fucoid species were used for this study. Kelp species included the invasive *Undaria pinnatifida* and the natives *Saccharina latisima*, *Laminaria digitata*, and *Saccorhiza polyschides* (n.b. although *S. polyschides* is taxonomically-speaking not a true kelp belonging to the order Laminariales, it is included here due to its functional similarity with kelps (Norton 1977; Teagle et al. 2017)). The fucoid species were the invasive *Sargassum muticum* and the natives *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*. The native species were chosen due to their general ecological similarity to the two invasive species, to reduce the variability regarding herbivore choice and allow for meaningful comparisons (Cacabelos et al. 2010). All species were sampled in June 2019 from the rocky shores in and around Plymouth Sound on the southwest coast of the UK (Fig. S1; Table S1). All species were sampled by collecting the whole individual (excluding the hold-fast) from one population for each species. Following collection, samples were immediately returned to the laboratory in cool boxes where they were stored in an aerated seawater tank for no more than a week before the experiments began.

The seaweed species used in these experiments are consumed by a range of herbivores, including sea urchins (Cacabelos et al. 2010; Cardoso et al. 2020), gastropods (Hagerman 1966; Cacabelos et al. 2010; Jiménez et al. 2015), amphipods, and isopods (Hagerman 1966; Jiménez et al. 2015). In this study, the native generalist herbivores *Steromphala cineraria* and *Littorina littorea* (Bakker 1960; Norton

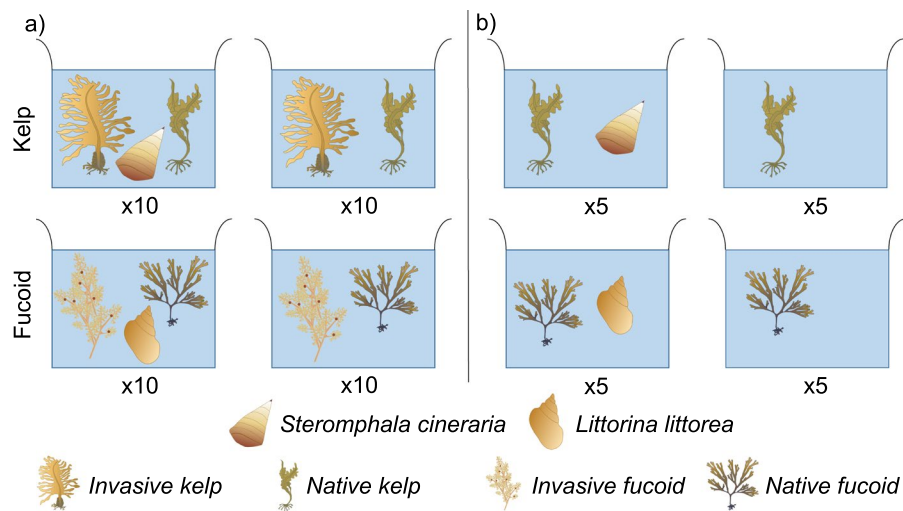


Fig. 1 Experimental design of **a** choice tests between invasive and native species and **b** no choice tests of invasive and native species with native herbivores present in the treatment tanks and absent in the control tanks. Kelp species included were *Undaria pinnatifida* (invasive), *Saccharina latissima*, *Laminaria digitata*, and *Saccorhiza polyschides* (native). The

furoid species included were *Sargassum muticum* (invasive), *Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum* (native). The number of replicates is shown under each tank type. Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/)

et al. 1988) were selected to graze on kelp and furoid species respectively. A significant part of the diet of *Steromphala* species can come from kelp, as they can consume both the kelp tissue directly, and the associated biofilm and epiphytes (Leclerc et al. 2013; Pessarrodona et al. 2019). *Littorina littorea* consumes a wide range of both micro and macroalgae (Menge 1975; Watson and Norton 1985). These generalist herbivores are used in this study because they have been found to exert top-down pressure and influence algal assemblage diversity and composition in intertidal ecosystems (Lubchenco 1978; Turner and Todd 1991), and are therefore an important part of the trophic structure. Given that specialist herbivores are rare in marine ecosystems (Lubchenco and Gaines 1981; Poore and Hill 2006; Cacabelos et al. 2010), and that generalist herbivores have shown stronger impacts on seaweed community structure (Hay and Steinberg 1992), our focus on generalist herbivores to investigate the enemy release hypothesis is both valid and representative of herbivore-seaweed interactions in this ecosystem. Sixty individuals of each species were collected from the Plymouth sound area during June 2019; herbivores were immediately returned to the laboratory where they were kept in a 34 L tank of aerated seawater for four days without food to

acclimatise to experimental conditions and standardise time since feeding.

Experimental design and set up

The midsection of the thallus of each seaweed sample was blotted dry and cut to a standardised wet weight ($2 \pm (0.5)$ g for kelp species, and $3 \pm (0.5)$ g for furoid species) and epiphytes were removed. Choice and no choice experiments were carried out in a temperature-controlled room held at 15–17 °C on a light: dark cycle of 8: 16 h. During the experiments, 800 ml tanks were filled with 450 ml of untreated seawater, which was changed every other day. Choice and no choice experiments consisted of paired tanks (Fig. 1): the treatment tank contained one herbivore, and the control tank did not contain a herbivore. One herbivore was used per treatment tank because this stocking density was proportional to the size of the seaweed sample. It also facilitated the measurement of individual grazing rates and standardisation by herbivore wet weight. For choice experiments, ten replicates were included for each combination of invasive and native species, and for the no choice experiments five replicates were used for each seaweed species. Fewer replicates were used during the no choice tests

as less variability was expected given the herbivores only had one choice available. During the choice tests, native seaweed species were compared against the invasive species of the corresponding coarse taxonomic group (i.e., kelp or furoid). The experiments ran for seven days to ensure sufficient time for the herbivores to consume the seaweed samples. The seaweed samples were blotted dry and weighed at the beginning and end of the experiment.

The amount of biomass consumed was scaled to account for autogenic mass changes in the control samples using the formula $[(T_B * C_E/C_B) - T_E]$, where T and C are the treatment and control wet weights respectively at the beginning (B) and end (E) of the experiments (Sotka et al. 2002), which corrects for autogenic growth. The amount of biomass consumed was then divided by the wet weight of the herbivore (including the shell) in grams at the start of the experiment to control for herbivore weight.

Tissue carbon to nitrogen ratio

Tissue carbon to nitrogen ratio (hereafter C:N) of the midsection of the thallus was measured to determine food quality (Ebeling et al. 2014; Krumins et al. 2015). Additional samples not used in herbivory experiments were frozen then freeze-dried. The freeze-dried samples were ground to a powder using a pestle and mortar. Approximately 1 mg of the samples were weighed into tin capsules and were analysed using an Elemental PYRO Cube Elemental Analyser running in CNS mode and equipped with a thermal conductivity detector. C:N was calculated for each sample. C:N of ten samples were measured and calculated for each species, except for *A. nodosum* where only nine samples could be measured and therefore C:N calculated.

Total polyphenolic concentration

Total polyphenolic concentration is a measure of chemical defence, which deters herbivores from consuming plant and algal tissue (Steinberg 1988; Van Alstyne 1988). Polyphenolic concentration was measured from six of the same samples which were also measured for C:N, and was also measured from three of the no choice replicates to see whether polyphenolic concentrations varied in the presence or absence of herbivory in furoid species (there was not enough

sample remaining to perform these analyses on kelp samples from no choice analysis). All samples came from the mid-section of the thallus. Polyphenolic concentration was determined by applying an adapted version of the Hargrave et al. (2017) method. 100 mg of powdered freeze-dried material from the midsection of the thallus was weighed and added to 1 ml of methanol (50%, diluted with distilled water) in a 1.5 ml Eppendorf tube. The samples were vortexed and refrigerated for 24 h. The samples were vortexed again and centrifuged for 5 min at $17,000 \times g$. 100 μ l of the supernatant was decanted into another 1.5 ml Eppendorf tube, and was diluted with 900 μ l of distilled water. The samples were vortexed, and 160 μ l was pipetted into a 96-well plate with 20 μ l Folin-Ciocalteu reagent (50%, diluted with water). After 5 min incubation at room temperature, 10 μ l 1.5 M Na_2CO_3 was added. Absorbance was read at 765 nm (FLUOstar OPTIMA microplate reader, BMG Labtech) with a solvent blank. Absorbance was converted to percentage total of dry mass using a phloroglucinol standard curve.

Tensile strength

Tensile strength was measured to examine how physical characteristics (i.e., robustness) influence susceptibility to herbivory. For kelp species, samples from the mid-section of the blade were cut to approximately 20 mm by 70 mm. For furoid species, a mid-section of the thallus was cut to an approximate length of 85 mm. *Fucus* samples were also cut to an approximate width of 10–25 mm, depending on the width of the thallus. For *S. muticum* samples, an approximately 90 mm section of the primary axis was used, and the width of the axis was measured twice to allow the cross-sectional area to be calculated. None of the samples used to measure tensile strength had been exposed to herbivory. For each sample, the width and length of the samples were measured to 1 mm, and the thickness of the samples were measured to 0.1 mm. Where the thickness was not uniform across the sample (such as for *Fucus* species) the average thickness was calculated from the maximum and minimum thickness. Each sample was secured in place with clamps (Fig. S2), leaving a 30 mm (± 2 mm) gap in the centre. The clamps were pulled apart at a constant speed, and the distance between the clamps was measured every 0.05 kg for fragile

seaweeds, and every 0.1 kg for stronger seaweeds. This continued until the seaweed sample ruptured. The number of samples measured for each species varied depending upon the amount of thallus available: seven samples were measured for *U. pinnatifida*, eight samples for *F. serratus*, nine samples each for *S. latissima*, *L. digitata*, and *F. vesiculosus*, ten samples each for *S. muticum* and *A. nodosum*, and 12 samples were measured for *S. polyschides*. Force to tear (F_t) was calculated using the methods in (Pérez-Harguindeguy et al. 2013). The force at breaking (N) was divided by the cross-sectional area (mm^2) (which was calculated by multiplying the width by the thickness).

Compensatory growth

Compensatory growth was measured as a potential mechanism to mitigate damage from herbivory (Cerdeira et al. 2009). The experiment to test for compensatory growth consisted of three replicates per species, which included a treatment and a control in separate tanks (two tanks per replicate). For the treatment samples, an emery board was used to mimic the rasping motion of the snail radula (Borell et al. 2004). The emery board was used to make 20 scrapes on the same point of the sample. The seaweed was blotted dry and weighed before and after the treatment to quantify how much mass had been lost. This was done daily for seven days, except on day 3 and day 6, when no treatment was applied to allow the samples to grow without artificial herbivory. The samples were still blotted dry and weighed on these days. The control plants were not treated but still weighed daily after being blotted dry. For each species, three samples were included as a control, and three underwent treatment, resulting in six samples per species. Where sample weight could not be accurately determined at the end of the experiment, samples were excluded from analysis. This experiment ran for seven days, in the same room and conditions as the choice and no choice tests.

Percentage change in mass was calculated for the control samples using the equation $[(M_n - M_{n-1}) / M_n] \times 100$ where M_n is the mass on day n , and M_{n-1} is the mass on the previous day. The same equation was used to calculate percentage change in mass for treated samples, but to account for the loss in mass from the treatment, M_n was the weight before the treatment, and M_{n-1} was the weight after the treatment was applied.

The percentage change in mass was calculated for each sample on each day of the experiment, and then this was used to calculate the average percentage change in mass of each sample over seven days (the length of the experiment) for ease of statistical analysis.

Statistical analysis

All analysis was completed in RStudio using R 4.1.2. One-way ANOVA tests were used to test for differences among species for no choice tests, C:N, polyphenolic concentration, and tensile strength with kelp and fucoid species being analysed separately using the R package 'stats' (R Core Team 2021). Assumptions of equal variance and normality were tested using Levene's test and Shapiro-Wilks test respectively, using the R packages 'car' (Fox and Weisberg 2019) and 'stats' (R Core Team 2021). Where these assumptions were not met, the dependent variable was log transformed (which was required for all of the C:N data, the polyphenolic concentration data for kelp species, and the tensile strength data for kelp species). Where the assumptions were met, Tukey post hoc pair-wise tests were implemented using the R package 'stats' (R Core Team 2021). Even after log transformation, the assumption of normality was not met for the tensile strength kelp data, so a Kruskal Wallis test was applied using R package 'stats' (R Core Team 2021), with a Dunn test for post hoc analysis using R package 'FSA' (Ogle et al. 2021).

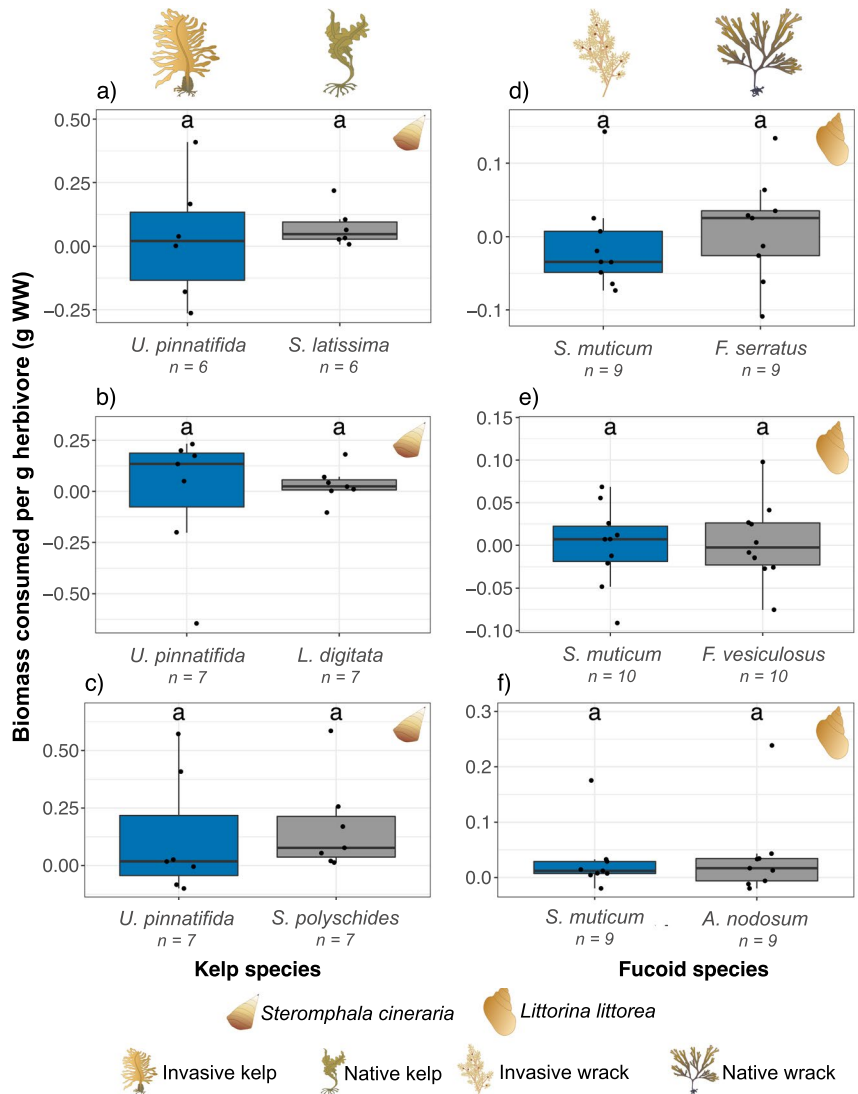
Paired Wilcoxon tests were used to analyse the difference of biomass consumed between invasive and native species in the choice tests, and unpaired Wilcoxon tests were used to analyse the difference between treatment and control groups for the polyphenolic concentration in the no choice tests for fucoid species, and to analyse the difference between the percentage change in mass (averaged over seven days) for treatment and control groups for compensatory growth. Wilcoxon tests were used as they are non-parametric, and all tests were two-sided. All Wilcoxon tests used the R package 'stats' (R Core Team 2021).

Results

Choice experiments

There was no evidence that either herbivore consumed invasive seaweeds more or less than native

Fig. 2 Proportion of biomass consumed per g herbivore (wet weight) during choice tests between an invasive species (blue) and a native species (grey). Each graph represents a different comparison between an invasive seaweed and a functionally similar native species. Kelp species are shown in the left column, and fucoids are shown in the right column. Different herbivores were used for comparisons between kelp species (a–c) and fucoid species (d–f). Sample sizes are shown under species names. Different letters indicate significant differences (paired Wilcoxon test, $p < 0.05$). Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/)



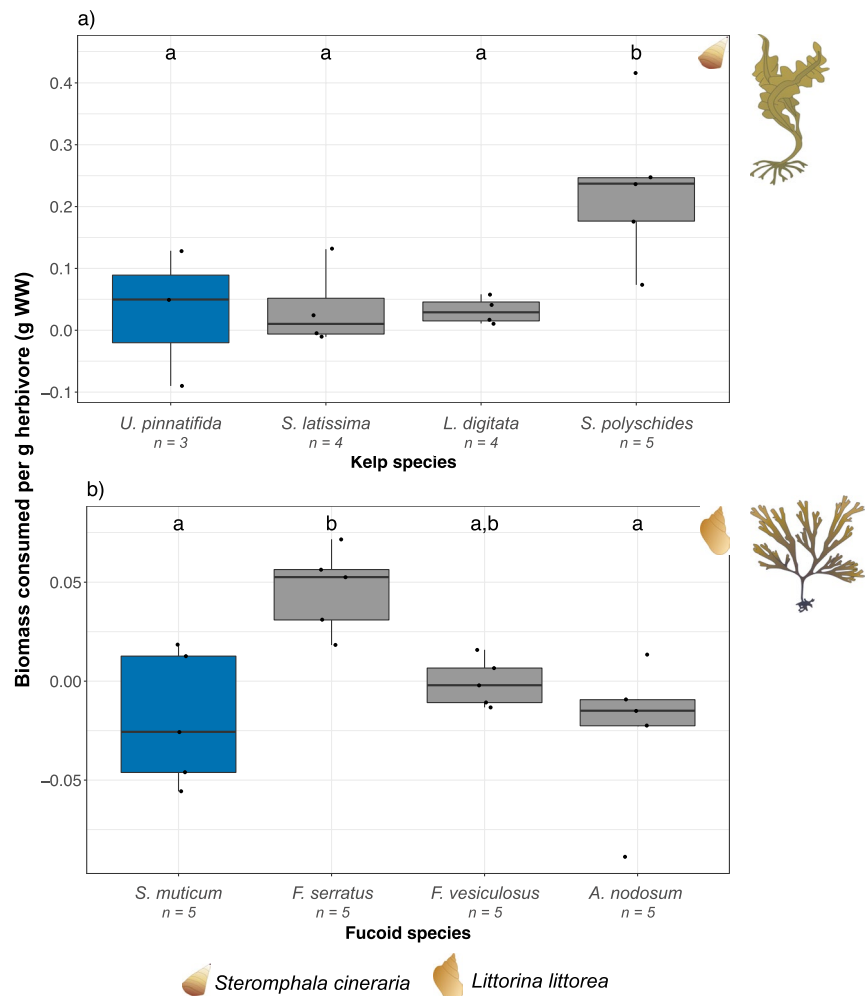
species for either kelp or fucoid species (Fig. 2, Table S3).

No choice experiments

There was moderate evidence to suggest that there were differences in the amount of biomass consumed per unit herbivore amongst kelp species [$F_{3,12} = 5.297$, $p = 0.015$] (Fig. 3). These differences were driven by *S. polyschides* for which there was moderate evidence that this species was consumed more than *U. pinnatifida* ($p = 0.048$), *S. latissima* ($p = 0.036$), or *L. digitata* ($p = 0.033$) (Table S4). Amongst fucoid species, there was strong evidence to suggest there were

differences in the amount of biomass consumed per unit herbivore [$F_{3,16} = 6.4$, $p = 0.005$] (Fig. 3). This was explained by moderate evidence that *F. serratus* was consumed more than *S. muticum* ($p = 0.011$), and strong evidence that *F. serratus* was consumed more than *A. nodosum* ($p = 0.006$) (Table S4). For both kelp and fucoid species, there was no evidence that the invasive species *U. pinnatifida* and *S. muticum* were consumed differently to the majority of native species used in this comparison.

Fig. 3 Biomass consumed per g herbivore (wet weight) during no choice tests of invasive (blue) and native (grey) species. Different herbivores were used for **a** kelp and **b** furoid species. Different letters indicate significant differences (Tukey post hoc, $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby, Diana Kleine, and the Integration and Application Network (ian.umces.edu/symbols/)



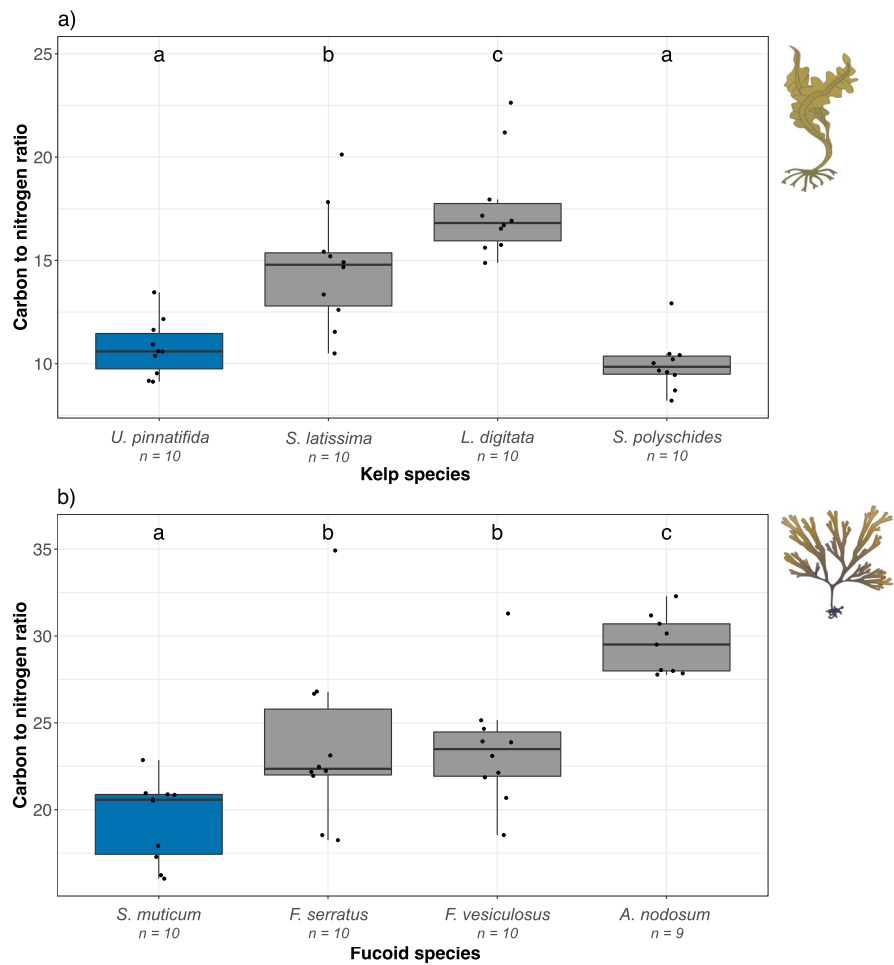
Tissue carbon to nitrogen ratio

There was very strong evidence that carbon to nitrogen ratio of the midsection of the thallus differed amongst species for both kelp [$F_{3,36}=32$, $p < 0.001$] and furoid species [$F_{3,35}=15.12$, $p < 0.001$] (Fig. 4). There was very strong evidence that the invasive *U. pinnatifida* had lower C:N than *S. latissima* ($p < 0.001$) and *L. digitata* ($p < 0.001$), but no evidence that C:N differed between *U. pinnatifida* and *S. polyschides* ($p=0.656$) (Table S5). There was moderate evidence that *U. pinnatifida* had lower C:N than *F. serratus* ($p=0.019$) and *F. vesiculosus* ($p=0.019$), and very strong evidence that *U. pinnatifida* had lower C:N than *A. nodosum* ($p < 0.001$) (Table S5).

Total polyphenolic concentration

There was very strong evidence that polyphenolic concentrations differed amongst species for both kelp [$F_{3,18}=48.42$, $p < 0.001$] and furoid species [$F_{3,20}=9.373$, $p < 0.001$] from samples which were not exposed to herbivory (Fig. 5). There was very strong evidence that the invasive *U. pinnatifida* had higher percentage dry weight of polyphenolic concentrations than the three native species ($p < 0.001$ for all comparisons) (Table S6). Polyphenolic concentrations of *S. muticum* were similar to *F. vesiculosus* ($p=0.877$) and *A. nodosum* ($p=0.484$), although there was strong evidence that polyphenolic concentrations of *S. muticum* were higher than *F. serratus* ($p=0.003$) (Table S6). There was no discernible difference between polyphenolic concentrations in the

Fig. 4 Carbon to nitrogen ratio of invasive (blue) and native (grey) seaweed samples of **a** kelp and **b** furoid species. Different letters indicate significant differences (Tukey post hoc, $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/)



control and treatment samples taken from no choice experiments for all species (Fig. S3, Table S7).

Tensile strength

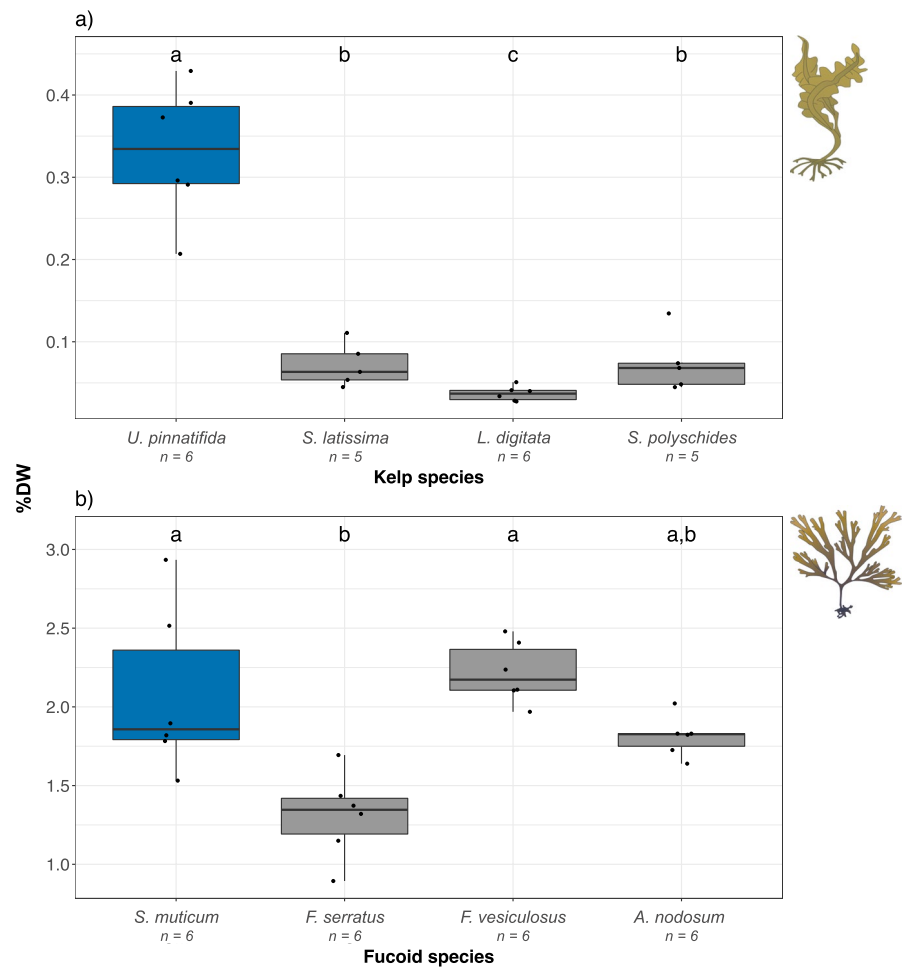
There was very strong evidence that tensile strength of the midsection of the thallus differed amongst species for both kelp [$H_3 = 25.58$, $P < 0.001$] and furoid species [$F_{3,33} = 8.556$, $p < 0.001$] (Fig. 6). Amongst kelp species, there was strong evidence that *U. pinnatifida* was weaker than *S. latissima* ($p = 0.003$) and *L. digitata* ($p < 0.001$), but there was no discernible difference in tensile strength between *U. pinnatifida* and *S. polyschides* ($p = 0.135$) (Table S8). There was very strong evidence that *S. muticum* was weaker than *F. vesiculosus* ($p < 0.001$), and weak evidence that *S. muticum* was weaker than

A. nodosum ($p = 0.075$) (Table S8). There was no discernible difference in tensile strength between *S. muticum* and *F. serratus* ($p = 0.969$) (Table S8).

Compensatory growth

There was no evidence that any of the species showed compensatory growth, as in all cases there was no evidence that the percentage change in biomass increased for samples which underwent artificial herbivory, relative to those samples that did not (Fig. S4-5, Table S9). In most cases, samples exposed to artificial herbivory decreased in mass more than control samples.

Fig. 5 Percentage dry weight of polyphenolic of invasive (blue) and native (grey) seaweed samples of **a** kelp and **b** fucoid species. Different letters indicate significant differences (Tukey post hoc, $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/)



Discussion

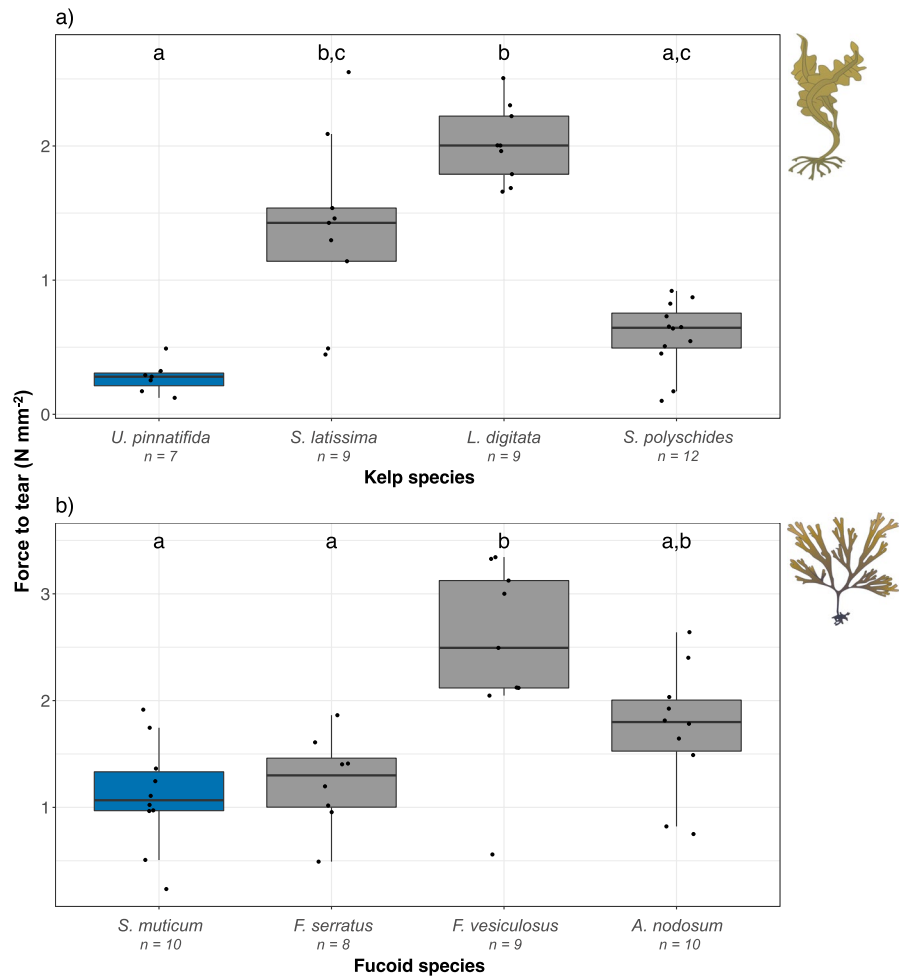
In this study, we found no evidence that these invasive seaweeds experienced a release from consumption by generalist gastropods, and limited evidence that either of these species exhibited different herbivore defence traits relative to native species. Therefore, it is unlikely that the ERH is an important mechanism in facilitating the success of the invasive *U. pinnatifida* and *S. muticum* in this system.

We initially predicted that the invasive species would experience less consumption by native generalist herbivores than comparable seaweed species from the same coarse functional group (i.e., kelps or fucoids). We found no evidence to support this hypothesis, as there was no discernible difference in the amount of biomass consumed between invasive and native species of similar functional groups.

Therefore, it is unlikely that these invasive species are escaping herbivory from the two generalist gastropod herbivores used in this study. Previous investigations have found that other herbivores, such as amphipods (Jiménez et al. 2015), sea urchins (Pedersen et al. 2016; Cardoso et al. 2020) and other gastropod species (Jiménez et al. 2015) also showed no difference in consumption of either *S. muticum* or *U. pinnatifida* compared to native species.

Our second prediction was that traits related to defence against herbivory, specifically tissue C:N, polyphenolic concentration, tensile strength and compensatory growth, would reflect and explain the patterns in consumption observed in the herbivory experiments. Given that in both choice and no choice experiments there was no evidence that invasive species were consumed more or less than native species, it is expected that there would also be no discernible

Fig. 6 Force required to tear invasive (blue) and native (grey) seaweed samples of **a** kelp and **b** furoid species. Different letters indicate significant differences (Dunn post hoc (kelp species), Tukey post hoc (furoid species), $p < 0.05$). Sample sizes are shown under species names. Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/)



difference amongst invasive and at least one native species for the majority of traits measured. This was true for all traits except for C:N of *S. muticum* for which there was strong evidence that it was lower than native species, and polyphenolic concentration of *U. pinnatifida* for which there was strong evidence that it was higher than native species. Overall, these patterns suggest that herbivore consumption is not primarily driven by traits against herbivory, but caveats are noted below.

C:N was measured to investigate the nutritional quality of the seaweeds, where species with lower C:N would have more nitrogen available per unit of food, therefore being more attractive to herbivores (Coviella et al. 2002). Given that herbivores are nitrogen limited, it is expected that they would have a preference for seaweeds with low C:N relative to similar species (Mattson 1980; Van Alstyne et al. 2001).

Despite *S. muticum* having lower C:N relative to the three native furoid species included in this study, the invasive furoid was not consumed more, suggesting that C:N does not drive herbivore choice in this system. This is supported by Schwartz et al. (2016), who found that herbivores preferred the native species *F. vesiculosus* with high C:N, rather than the invasive *S. muticum* with low C:N in Germany. Amongst the kelp species, there was no discernible difference amongst the invasive *U. pinnatifida* and the native *S. polyschides*, indicating that the invasive species does not have more nitrogen per gram of food than the native species, and thus should not be more palatable.

The second trait investigated in this study was polyphenolic concentration, where high concentrations have been shown to deter herbivory in seaweeds (Steinberg 1984, 1988), and which can also be produced in response to other stressors, such as

increased temperatures (Hargrave et al. 2017; Mannino and Micheli 2020). *U. pinnatifida* had relatively higher concentrations of polyphenolics compared to the native kelp species. This relative difference was not reported in a study by Cardoso et al. (2020), who found *U. pinnatifida* to have similar levels of polyphenolics as *S. polyschides* in a Portuguese population. Given the relatively high levels of polyphenolics detected in *U. pinnatifida*, we could expect lower rates of herbivory on the invasive species, but this was not observed. The increased polyphenolic concentration may offset against the other traits that make *U. pinnatifida* more susceptible to herbivory, such as low C:N and low tensile strength which would be predicted to increase the likelihood of consumption (Duffy and Hay 1990; Van Alstyne et al. 2001). Higher polyphenolic concentrations could also be a result of increased growth as phlorotannins are incorporated into the cell wall (Arnold and Targett 2003), although this was not observed for *U. pinnatifida* in the compensatory growth tests. Amongst the fucoid species, there was no difference between the invasive *S. muticum* and the majority of the native species. The concentrations of polyphenolics reported in this study are lower than expected, and lower than have been reported for the same species elsewhere (Cacabelos et al. 2010; Schwartz et al. 2016; Cardoso et al. 2020). The reasons for this are unclear, but could be due to the inherent variability in polyphenolic concentrations, attributable to seasonality (Ragan and Jensen 1978; Steinberg 1995; Mannino and Micheli 2020), or environmental stressors such as UV radiation (Swanson and Druehl 2002).

The physical properties of seaweeds can also affect their attractiveness to herbivores (Duffy and Hay 1990). Here we used tensile strength to act as proxy for the toughness of seaweeds, with the expectation that seaweeds with lower tensile strength would be consumed more as they would be mechanically easier to consume. Both *U. pinnatifida* and *S. muticum* were in the lower range of tensile strength, but there was little to no evidence that tensile strength was associated with whether the species was invasive or native. The morphological structure of the whole seaweed has also been found to influence herbivory (Steneck and Watling 1982; Duffy and Hay 1990). However, given that the invasive and native species compared in this study were of the same functional groups (fucoid or kelp), it is

unlikely that the gross morphological differences would have affected the patterns in consumption found for these herbivores (Enge et al. 2017).

Whilst the native seaweed species used in this study were selected due to functional similarities to the invasive seaweeds, some of these native species were a closer match than others. Specifically, *U. pinnatifida* and *S. polyschides* are both short-lived annual species (Teagle et al. 2017) and *S. muticum* and *F. serratus* are abundant canopy forming species (Critchley et al. 1990; Ingólfsson 2008). Whilst there was still no difference in the amount of biomass consumed in the choice tests, both invasive species were consumed significantly less in the no choice tests than either *S. polyschides* or *F. serratus* respectively. This could be explained by higher polyphenolic concentrations conferring defence to both invasive species, relative to these two native species. However, *S. muticum* was still consumed less in the no choice tests despite being more palatable than *F. serratus* with a lower C:N ratio. Whilst this does not provide evidence to support the ERH, the difference in trait values between invasive species and functionally similar native species demonstrates the importance of selecting appropriate species for invasive and native comparisons.

A potential explanation for the lack of evidence for the ERH observed in this study is that time-since-invasion was not accounted for. Kurr and Davies (2018) found that grazing rates on *S. muticum* increased with time-since-invasion, suggesting that native marine herbivores may acquire an ability to feed on novel foods over time. The populations of *U. pinnatifida* and *S. muticum* sampled in this study were approximately 16 and 33 years old respectively (based upon the year each species was first recorded in the Plymouth area, which was 2003 (Heiser et al. 2014) and 1976 (Boalch and Potts 1977) respectively). Given that the introduced *U. pinnatifida* population is relatively young, we would expect to find evidence of enemy release even if there was a temporal effect, which we did not observe. It is possible that *S. muticum* experienced reduced herbivory when it was first introduced to the Plymouth area, but either way, we found no evidence that either invasive species is currently benefiting from enemy release, suggesting that any potential benefit of enemy release is relatively temporary.

In conclusion, we did not find evidence to support the ERH as an explanation for the invasion success and proliferation of either *U. pinnatifida* or *S. muticum* in the northeast Atlantic. We believe that the effect sizes and variabilities demonstrated in our data provide strong evidence that our robust experimental approaches provide genuine ‘evidence of absence’ of effects, and thus these are not merely experimental artefacts or ‘absence of evidence’. Whilst there were some exceptions, the traits of the invasive species were generally similar to or greater than those of native species, suggesting that there is no prolonged selection against these traits as we would expect to see if the invasive species were escaping herbivory. Combined with the lack of evidence for escape from herbivory from our choice and no choice experiments, as well as those from similar studies (Jiménez et al. 2015; Pedersen et al. 2016; Cardoso et al. 2020), this makes it unlikely that these invasive species are experiencing enemy release from herbivores. It is more likely that other traits such as fast growth (Norton 1977; Choi et al. 2007), thermotolerance (Henkel and Hofmann 2008) and high reproductive output (Casas et al. 2008) can better explain the spread of *U. pinnatifida* and *S. muticum* outside of their native ranges.

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Author contributions ALM, JAC, MR and DAS contributed to the study conception and design. Data collection was performed by ALM and AF. Data analysis was performed by ALM. The first draft of the manuscript was written by ALM and all authors commented on and contributed to previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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