

Research



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Invasion-mediated effects on marine trophic interactions in a changing climate: positive feedbacks favour kelp persistence

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The interactive effects of ocean warming and invasive species are complex and remain a source of uncertainty for projecting future ecological change. Climate-mediated change to trophic interactions can have pervasive ecological consequences, but the role of invasion in mediating trophic effects is largely unstudied. Using manipulative experiments in replicated outdoor mesocosms, we reveal how near-future ocean warming and macrophyte invasion scenarios interactively impact gastropod grazing intensity and preference for consumption of foundation macroalgae (*Ecklonia radiata* and *Sargassum vestitum*). Elevated water temperature increased the consumption of both macroalgae through greater grazing intensity. Given the documented decline of kelp (*E. radiata*) growth at higher water temperatures, enhanced grazing could contribute to the shift from kelp-dominated to *Sargassum*-dominated reefs that is occurring at the low-latitude margins of kelp distribution. However, the presence of a native invader (*Caulerpa filiformis*) was related to low consumption by the herbivores on dominant kelp at warmer temperatures. Thus, antagonistic effects between climate change and a range expanding species can favour kelp persistence in a warmer future. Introduction of species should, therefore, not automatically be considered unfavourable under climate change scenarios. Climatic changes are increasing the need for effective management actions to address the interactive effects of multiple stressors and their ecological consequences, rather than single threats in isolation.

1. Introduction

Climate change is a global environmental threat with consequences for ecological community structure and ecosystem function [1–3]. Community-level effects associated with climate change stem from combinations of direct effects (i.e. phenology, biology, physiology, distribution) [4–6] and indirect effects such as changes in biological interactions (e.g. trophic structures, competition) [7–9]. The predictability of such community-level responses to climate change is challenged by shifts in species' range and expansions of introduced species or 'invasions', which can facilitate alternations in species interactions and ecosystem properties [10–13]. Both introduced (i.e. non-native) and native species can shift distribution in response to climate change, but the interactive effects of such changes for community structure and function are still not well understood [14–18].

Marine invasions are predicted to increase with climate change [19,20], but only a limited body of literature has empirically evaluated how invasive species will alter ecosystem dynamics under such scenarios [21–23]. While the effects of invasion and different aspects of climate change have often been evaluated

separately, these stressors can interact in complex ways [24–27]. Theoretical models forecast that the interactive effects between global warming and invasive species will most often be additive or synergistic [24,25]. In aquatic systems, for example, warming temperatures may reduce survival of native cold-adapted species and facilitate the establishment and reproductive success of non-native warm-adapted species [21]. This could lead to invasive species dominating over native species (i.e. owing to efficiency to compete or avoid predation), altering the structure and function of communities and intensifying impacts of climate change on ecosystem properties.

The influence of ocean warming on ecosystem dynamics often depends on the extent that such environmental change alters species interactions [8]. For example, plant–herbivore interactions may be altered at elevated ocean temperatures, as a result of a mismatch between production and herbivore consumption [28–30]. Increasing ocean temperatures enhance respiration, metabolism and grazing activity of herbivores up to their thermal maxima. However, photosynthetic production in many primary producers does not vary as temperature increases [31–34].

Climate-mediated change to trophic interactions can have substantial consequences for marine systems [35–36]. In particular, ocean warming is predicted to increase the metabolism of herbivores [8,34,37], intensifying the pressure on key native macrophytes in temperate rocky reef systems, as tropical herbivores expand into temperate latitudes [2,36]. Concurrently, native tropical algae are expanding their distribution into temperate habitats prompting novel shifts in competitive and trophic interactions [38–40]. While we have an emerging understanding of climate-mediated impacts of range expanding consumers on native algae [2,36], the impacts and consequences of range expanding algae on competitive and trophic interactions are poorly known.

The *Caulerpa* genus is one of the most successful groups of invasive algae around the world. *Caulerpa filiformis* is a green alga found in South Africa, Mozambique, Peru and Australia [38–41]. On the east coast of Australia, *C. filiformis* has become locally abundant on temperate shallow rocky reefs well outside its historic distribution [40–42]. These range expansions have negative effects on co-occurring macrophytes [43] representing a similar invasive behaviour as *Caulerpa taxifolia* and *Caulerpa racemosa* in southeastern Australia, the Mediterranean and United States [44,45]. Although *C. filiformis* has been considered ‘native’ in southeastern Australia by some authors [40,46], and ‘invasive’ by others [47,48], some impacts have been described [43] and their origin is still unsolved [47,48]. Hence, this species has been carefully termed here as a ‘native invader’ [43,49,50], based on biological invasion definitions by [51]. *Caulerpa filiformis* is structurally simpler than common co-occurring macroalgal species (e.g. *Sargassum* spp. and *Ecklonia radiata*) and, once established, can form large and persistent mono-specific stands that can spread via vegetative reproduction. The cover of *C. filiformis* is greater at subtidal than intertidal sites and mean percentage cover varies between 1 and 62% [40]. *Caulerpa filiformis* is heavily chemically defended with active secondary metabolites (e.g. caulerpenyne) which putatively leach into the surrounding water, impacting nearby macrophytes and potentially altering diversity of epibiotic assemblages [46]. *Caulerpa filiformis* is unpalatable to several key herbivores [48], which contributes to the dominance of this taxon once established.

Turbinid gastropods are common and abundant generalist herbivores in shallow subtidal reefs of eastern Australia [52,53]. Density of turbinid gastropods, such as *Turbo militaris* varies from 1 to 30 individuals per 4 m² depending on protected or non-protected areas [54]. This species co-occurs and preferentially consumes brown algae *E. radiata* and *Sargassum* spp. rather than the chemically defended *C. filiformis* [47,55]. What is unknown, however, is how future ocean conditions, particularly warming, might directly alter the condition and palatability of these macrophytes, as well as the preferences and grazing rates of herbivores. Understanding interactions among these key ecological processes is necessary to predict likely future ecological consequences of climate-mediated invasions.

Here, we investigated the interactive effects of ocean warming and invasion (using the ‘native invader’ *C. filiformis*) on herbivory of native macroalgae. Using a series of manipulative experiments, we evaluate how gastropod grazing intensity and preference impacted consumption of native algae under combinations of near-future ocean warming and invasion scenarios. We hypothesized that temperature will increase gastropod grazing activity and intensify consumption of preferred native macrophytes, but this impact will be ameliorated in the presence of the chemically defended invasive macrophyte, *C. filiformis*.

2. Material and methods

(a) Experimental system

To test hypotheses about the influence of ocean warming and biological invasions on trophic interactions, three experiments were conducted in an outdoor mesocosm system at the National Marine Science Centre (NMSC) in Coffs Harbour, Australia (30.3022° S, 153.1189° E). The system was composed of 20, 230 l round, fibreglass, outdoor mesocosms (80 cm diameter × 45 cm high), 20 aquariums (30 cm length × 19.5 cm width × 20.5 cm high) and 20 trays (81 cm length × 61 cm width × 9 cm high). Each tray contained one aquarium (30 cm length × 19.5 cm width × 20.5 cm high) that received water from the respective mesocosm connected by a pipe at a rate of 2 l min⁻¹. Mesocosms were set up in orthogonal combinations of ocean warming (temperature level: current (23°C), and future (26°C)) and invasion (*C. filiformis* present and absent, hereafter: invaded and non-invaded, respectively). An increase in ocean temperature of 3°C approximates near-future changes predicted by the Representative Concentration Pathway (RCP) 8.5 climate model for 2081–2100 [56,57]. Each mesocosm and aquarium was supplied with 50 µm filtered seawater (at a flow rate of 2 l min⁻¹) continuously sourced from an adjacent beach (30.2670° S, 153.1407° E). Water temperature was controlled using heater/chiller units (AquaHort Ltd, Omana Beach, New Zealand), and oxygen levels and water movement were maintained by bubbling ambient air into each mesocosm. The outdoor mesocosms were situated under shade cloth and exhibited diurnal cycles where water temperatures varied by less than 1°C. Water temperature and salinity were measured daily with a Hach HQ40d multiprobe calibrated with high precision buffers. The average (s.e.) measured and calculated seawater conditions for each treatment are presented in the electronic supplementary material, table S1.

The first experiment tested the interactive effects of ocean warming and invasion (presence of *C. filiformis*, hereafter *Caulerpa*) on the consumption rate of native macrophytes (*E. radiata* and *Sargassum vestitum*, hereafter *Ecklonia* and *Sargassum*, respectively) by a large turbinid gastropod (*T. militaris*). *Ecklonia* and *Sargassum* are two of the most common and ubiquitous taxa

characterizing Australia's temperate reefs and play a key role in underpinning temperate biodiversity and ecosystem services [58,59]. This experiment ran in the tanks for 15 days for *Ecklonia* and 35 days for *Sargassum* from December 2017 to January 2018. The duration of the experiments was determined by the time required for the gastropod to eat close to 100% of any macrophyte individual in at least one mesocosm. Each tank contained four cages (enclosed plastic mesh baskets 26.5 cm length \times 18.5 cm width \times 10.5 cm high) with a mesh on top. Inside each of two cages, we placed native macrophytes ($n = 3$) without gastropods (autogenic control, one cage for each algal species); whereas the other two cages contained macrophyte plants ($n = 3$; one cage for each algal species) exposed to gastropod grazing (one *T. militaris* for each cage). These individual numbers were used to simulate natural densities considering the dimensions of the cages. Ten *Caulerpa* plants were placed outside of the cages in each mesocosm, to simulate (i) dominance condition in the tanks that correspond approximately 30% (mean percentage cover) of the substrate considering similar abundances found in nature (between 1 and 62%, see [43]), and (ii) to simulate chemical effect in the mesocosm water, but avoiding physical influence of gastropod grazing on the invasive alga. Individual *Caulerpa* plants were replaced if their fronds began to bleach or necrose throughout the experiment.

Ecklonia (17.8 ± 0.3 cm length and 4.3 ± 0.1 g weight, mean \pm s.e.), *Sargassum* (20.9 ± 0.3 cm length and 17.7 ± 0.2 g weight) and gastropods (*T. militaris* 7.9 ± 0.1 cm length and 141.8 ± 3.9 g weight) were collected from nearby rocky reefs and *Caulerpa* plants (28.3 ± 0.6 cm length and 33.4 ± 0.8 g weight) were collected from the closest accessible location at Anna Bay (32.7898° S, 152.1157° E). Collected *Ecklonia* plants were in their second stage of growth, which is in between juveniles and adults [60], *Sargassum* were small adults and *Caulerpa* adult plants. Algae were attached to a plastic grid weighted with two rocks and enclosed in permeable cloth to facilitate their natural erect position in the tanks. The gastropods were acclimatized in aquarium conditions with the same mesocosm temperature for three weeks prior being included in any experiment. The wet weight of *Ecklonia*, *Sargassum* and *Caulerpa* was determined prior being placed into the mesocosms, and again when removed at the end of the experiment, by patting dry with paper towel and weighing without the mesh or weights. The weight and length of the gastropods were also measured at the start and end of the experiment.

The photosynthetic health of macrophytes was measured as effective quantum yield ($\Delta F/F'_m$) on day 1, 7 and 15 for *Ecklonia*, or on day 1 and 35 of the experiment for *Sargassum*, respectively. Effective quantum yield was determined using a pulse amplitude modulation (PAM) fluorometer (Diving-PAM, Walz, Effeltrich, Germany); where $\Delta F = F'_m - F_t$, with F'_m being the maximal fluorescence, and F_t the steady-state fluorescence under illumination at time t [61,62]. Plants were dark acclimated for at least 15 min prior to measurements using leaf clips. Fluorescence was measured by holding the fibreoptic of the PAM fluorometer 1 mm from the algae frond using a clip *in situ* in the mesocosm. The algae surface was then exposed to a pulsed measuring beam of weak red light ($0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$, 650 nm) to measure F_t . Once the signal was stabilized (5 s), a pulse of saturating light ($6000 \mu\text{mol m}^{-2} \text{s}^{-1}$) was applied and F'_m was recorded. Measurements commenced in the morning, at the same time each day around 08.00, after plants had been exposed to approximately 2 h of natural daylight and were completed in less than 2 h. One reading per individual plant was recorded on haphazardly selected areas of the algal frond. To ensure independence in analyses, individual readings were averaged to provide a mean value of $\Delta F/F'_m$ for each mesocosm.

We carried out a second experiment in the 20 aquariums to compare gastropod grazing activity (independent of macrophytes)

among treatments by investigating grazing scars on wax surfaces [63,64], over a 4 day period. One dental wax square (4.5×4.5 cm) glued onto a ceramic tile (15×15 cm) was placed in a separate aquarium with an individual gastropod (*T. militaris* 8.1 ± 0.1 cm length and 145.3 ± 4.7 g weight) acclimated as above. The duration of this experiment was determined by the time required for a gastropod to make notable radula scrapings on wax surfaces from grazing on fast-growing epilithic algae in at least one mesocosm.

A third experiment ran for 4 days in the tanks that were cleaned immediately following the first experiment. It was a multiple choice assay to evaluate whether ocean warming influences the grazing preferences of gastropods with respect to *Ecklonia*, *Sargassum* and *Caulerpa*. Elucidating preference hierarchies of gastropods is important to understand the magnitude of herbivory on preferred algal species relative to less preferred species [65,66]. The duration of this experiment was determined by the time required for a gastropod to eat close to 100% of any macrophyte individual in at least one mesocosm. For this experiment, 40 cages were cleaned of epiphytes and biofilms by placing them in freshwater for 2 days and then carefully scrubbing them with a brush and rinsing them with a jet of freshwater. Two of these cages were placed in each of the 20 mesocosms ($n = 10$ per temperature level: 23°C and 26°C). In each mesocosm, one cage had one plant of *Ecklonia*, *Sargassum* and *Caulerpa* as autogenic controls without gastropods. The other cage also had one plant of each species with one individual gastropod. The *Ecklonia*, *Sargassum* and *Caulerpa* plants ranged in size from 25.4 ± 0.7 cm length (6.4 ± 0.3 g weight), 13.7 ± 0.5 cm length (13.9 ± 0.3 g weight) and 25 ± 0.7 cm length (12.9 ± 0.3 g weight), respectively.

(b) Data analysis

Experiments 1 and 2 had two orthogonal fixed factors: warming (two levels, current 23°C and future 26°C) and invasion (two levels, invaded and non-invaded). Consumed biomass of native algae, yield and per cent cover of gastropod bites were analysed with general linear models (GLM) using a Gaussian distribution. The effects of treatments on the health of algae of autogenic control (weight and photosynthetic yield) were tested separately (see the electronic supplementary material, table S2). Experiment 3 had two orthogonal fixed factors: warming (two levels, current 23°C and future 26°C) and species (three levels, *Caulerpa*, *Ecklonia* and *Sargassum*). The amount of biomass consumed was calculated with the equation: Consumption ($S_i \times C_f/C_i$) $- S_f$, where S_i and S_f were the mass of the plants exposed to gastropods before (initial or i) and after (final or f) the assay, respectively; and C_i and C_f were the biomass of the paired autogenic control plants before and after the assay, respectively [67]. The consumption data were normally distributed and thus analysed using the Hotelling's T^2 test [68]. The *Caulerpa* weight loss differences between autogenic control and herbivory treatment were tested using Kruskal–Wallis. A *post hoc* Tukey test was used when significant differences were found. The GLMs and Kruskal–Wallis tests were performed using the R software [69] using the packages *lme4* and *MASS*. The Hotelling's T^2 test was performed using SPSS software.

3. Results

There were no direct effects of warming or invasion on the weight of *Ecklonia* and photosynthetic yield of *Sargassum* (autogenic controls) (electronic supplementary material, table S2a,d). All native algae in the autogenic controls remained in visibly good health during the experiment.

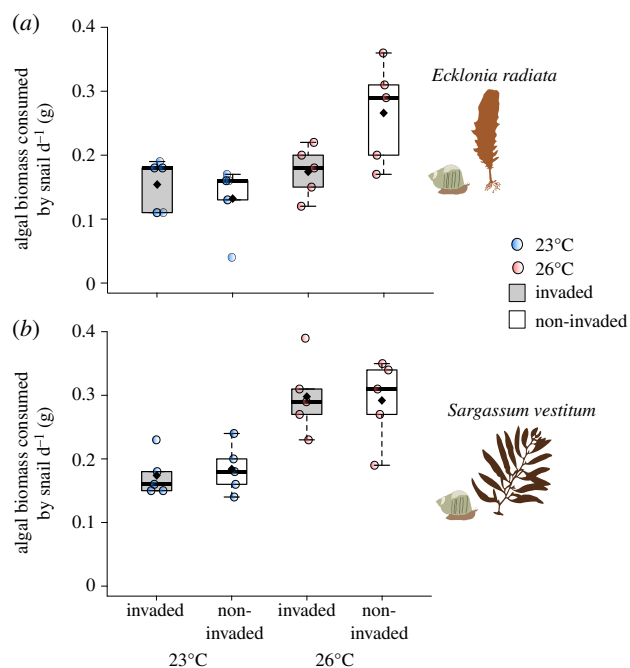


Figure 1. Algal biomass consumed by *Turbo militaris* under invaded and non-invaded conditions at 23°C and 26°C for *Ecklonia radiata* (a) and *Sargassum vestitum* (b). Box plot represents the median, Q_1 , Q_3 , minimum and maximum values, and outliers, black diamonds represent mean values; each circle represents a mesocosm.

There was an effect of warming on the weight of *Sargassum* with higher values in 26°C (electronic supplementary material, table S2c). Additionally, there was a significant effect of warming on the photosynthetic yield of *Ecklonia* with higher values in 23°C and the interaction with invasion was also significant with higher values without *Caulerpa* presence at 23°C (electronic supplementary material, table S2b).

(a) Macrophyte biomass consumed and photosynthetic yield

A significant effect of ocean warming on grazing of the kelp *Ecklonia* was observed, with greater biomass being consumed at 26°C than at 23°C (figure 1a; electronic supplementary material, table S3a). The interaction between ocean warming and invasion was also significant with less consumption of kelp under an invasion scenario (*Caulerpa* present) at 26°C (electronic supplementary material, table S3a). Temperature also had significant effects on grazing on *Sargassum*, with greater biomass consumed under warmer conditions (figure 1b; electronic supplementary material, table S3b). However, the interaction between warming and invasion had no significant effect on grazing on *Sargassum* (electronic supplementary material, table S3b). There were no direct effects of warming or invasion on the photosynthetic yield of native macrophytes (electronic supplementary material, table S4).

(b) Patterns of gastropod grazing intensity

The intensity of grazing on dental wax was significantly higher at 26°C in the absence of invasion (no *Caulerpa* presence) (figure 2; electronic supplementary material, table

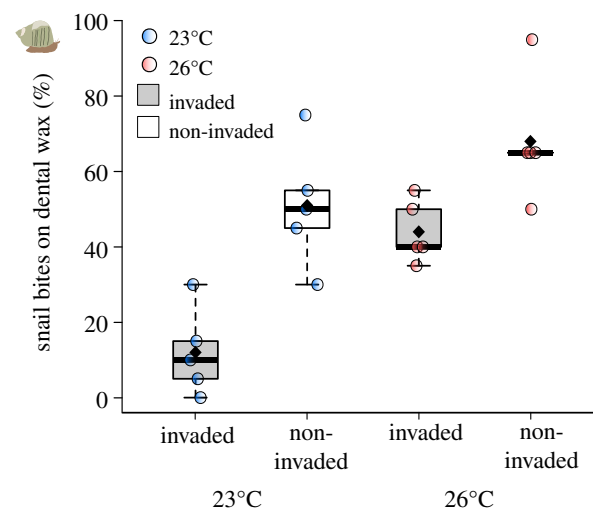


Figure 2. Grazing rates of *Turbo militaris* on experimental dental wax in invaded and non-invaded conditions at 23°C and 26°C. Box plot represents the median, Q_1 , Q_3 , minimum and maximum values, and outliers, black diamonds represent mean values; each circle represents a mesocosm.

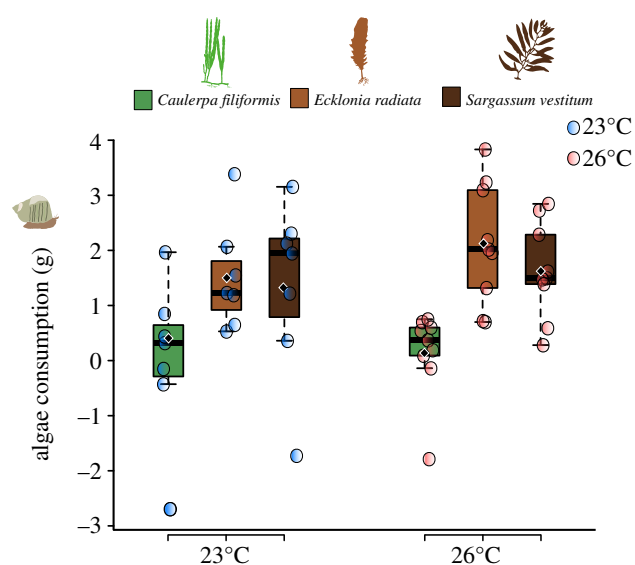


Figure 3. Preference of *Turbo militaris* for *Caulerpa filiformis*, *Ecklonia radiata* and *Sargassum vestitum* at 23°C and 26°C. Box plot represents the median, Q_1 , Q_3 , minimum and maximum values, and outliers, black diamonds represent mean values; each circle represents a mesocosm.

S5). Both main effects of warming and invasion increased grazing rates, but the interaction between these factors was not significant (electronic supplementary material, table S5). Grazing rates were higher at 26°C but lower under invasion conditions (figure 2; electronic supplementary material, table S5).

(c) Feeding preferences

Turbo militaris consumed significantly more *Ecklonia* and *Sargassum* than *Caulerpa* (*post hoc* tests following Hotelling's T^2 , $p < 0.05$; electronic supplementary material, table S6; figure 3). These clear preferences of *T. militaris* did not change with water temperature (Hotelling's T^2 , $p > 0.05$; electronic supplementary material, table S6; figure 3). The consumption of *Caulerpa* was very low and weight loss in

this species did not differ significantly from that in autogenic controls (electronic supplementary material, table S7).

4. Discussion

Climate change is modifying trophic interactions among range expanding native species [36,70], but the interactions with invasion in a changing climate are not yet fully understood. Here, we determined the interactive effects of ocean warming and invasion on consumption (grazing) of native algae and found that ocean warming increased consumption of two common native algal taxa through greater grazing intensity. However, for herbivory on the dominant habitat forming kelp (*Ecklonia*) at warmer temperatures, low consumption was related to the presence of *Caulerpa*. The interactive effects of ocean warming and invasion thus had a positive feedback for kelp, reducing biomass loss from gastropod grazing. In certain instances, therefore, invasion may contribute to the future persistence of kelp in warming oceans.

Changes to trophic interactions under ocean warming can influence community structure and marine ecosystem function [36,37], threatening key habitat forming species, such as kelp. Our experiments showed that gastropods intensified grazing rates at elevated temperatures, increasing consumption of preferred native macrophytes in response to ocean warming. The metabolic theory of ecology [71] predicts that the metabolic rates of organisms increase with temperature owing to biochemical reactions constrained by thermodynamics [32,34]. Enhanced metabolic performance in near-future climate change scenarios probably stimulated algal consumption by *Turbo militaris* and, therefore, might have consequences for *Ecklonia* and *Sargassum* populations in future oceans. Additionally, elevated temperatures could also intensify the strength of herbivory through changes to the susceptibility of plant tissues [8], such as changing nitrogen content [72], or plants could allocate reduced energy to grazing defence mechanisms. Therefore, when the effects of ocean warming are considered independently, our results reinforce the contention that herbivory will increase with temperature [34]. In turn, this could lead to overgrazing of native macrophytes and even complete regime shifts to more simple systems states [70,73].

Combined effects of warming and invasive species interacting in additive or synergetic ways have been demonstrated [74,75]. Mostly previous studies suggest that warming temperatures could favour invasive mechanisms leading to dominance over native species (i.e. owing to efficiency to compete or avoid predation) intensifying impacts of climate change on ecosystem properties. By contrast, we show that these combined effects can be antagonistic [26]. Indeed, our results demonstrated that consumption of *Ecklonia* was lower at elevated temperature under an invasion scenario (the presence of *Caulerpa*). Probably, the biologically active secondary metabolites (caulerpenynes) present in *Caulerpa* species act as a feeding deterrent that mediates grazing activity [47,48]. Presence of caulerpenyne in the water when *Caulerpa* is present probably inhibits the biological activity of gastropods, reducing feeding intensity on *Ecklonia*. Evidence that *Caulerpa* presence reduces gastropod grazing activity also comes through the fact that grazing was reduced even in the absence of native algae. Thus, our results show that invasion indirectly benefits *Ecklonia* by reducing herbivory and suggests that under certain

scenarios, antagonistic effects between climate change and invasive species can favour *Ecklonia* persistence as oceans warm in the future.

Although our findings show that effects between climate change and invasive species mediate positive feedbacks for *Ecklonia*, other studies have demonstrated both direct and indirect negative effects of *Caulerpa* on native macrophytes [46]. *Caulerpa*, once established, accumulates sediment favouring algal turfs which may then inhibit colonization by kelp [44]. Additionally, *Caulerpa* can affect the abundance of fauna associated with neighbouring macroalgal habitats [76]. Although theoretical evidence predicts that a warming climate will generally increase rates of invasion and negatively impact biodiversity [22,74,75], our results demonstrate that biotic interactions are more difficult to predict.

When considering direct and indirect effects of ocean warming, the future of kelp forests in many systems appears bleak independently of invasions [36,37,77–79]. Modelling projections suggest major climate-mediated changes to the suitable habitats for kelp forests, producing significant retreat of kelp forest around the Australian coast [78] and in many other parts of the world [80–82]. Elevated temperatures can directly reduce complex canopies [77] or decrease consumption at higher trophic levels, releasing pressure on consumers and indirectly increasing herbivory on kelp [37]. However, we demonstrate that the simple presence of an invasive macrophyte has the potential to alter existing relationships involving native herbivores and algae, possibly changing the predicted trajectories of kelp forests compared to scenarios where only ocean temperature is considered.

Overall, our results suggest that the current range expansions of *Caulerpa* may contribute to the persistence of kelp as oceans warm by reducing herbivory. However, such effects may not extend to other native macrophytes, as we demonstrate no effect of invasion on grazing on *Sargassum*. In a changing climate, it will be increasingly difficult to predict the impacts of invasive species on ecosystems. Nonetheless, understanding such complex ecological relationships will be key to predicting and managing marine environments under future ecological scenarios. It is clear that future management actions based on single-threat drivers will often be too simplistic and must be reconsidered in connection with interactive effects from climate change and other stressors.

Data accessibility. The datasets supporting this article are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.761js4b> [83].

Authors' contributions. R.J.M., B.P.K., M.A.C. and F.B. designed the study. R.J.M., A.T., M.S.R., L.T.M. performed the research. R.J.M. and B.P.K. analysed the data. All authors contributed to the writing of the manuscript.

Competing interests. The authors declare that they have no conflict of interests.

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