

Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success

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Abstract The effect of herbivory and nutrient enrichment on the growth of invasive and native macroalgal species was simultaneously studied in two biogeographic regions: the Caribbean and Hawaii. Herbivores suppressed growth of invasive algae in their native (Caribbean) and invaded range (Hawaii), but despite similar levels of herbivore biomass, the intensity of herbivory was lower in Hawaii. Algal species with a circumtropical distribution did not show a similar effect of herbivores on their growth. Nutrient enrichment did not enhance growth of any algal species in either region. The reduction in herbivore intensity experienced by invasive algae in

Hawaii rather than an escape from (native) herbivores provided invasive macroalgae with “enemy release” sensu the Enemy Release Hypothesis (ERH). Since native, Hawaiian herbivores still feed and even prefer invasive algae over native species, invasion scenarios that involve predation (e.g. the ERH) could be falsely dismissed when invasive species are only studied in their invasive range. We therefore argue that escape from herbivores (i.e. enemy release) can only effectively be determined with additional information on the intensity of predation experienced by an invasive species in its native range.

Keywords Herbivory · Macroalgae · Invasive species · Enemy Release Hypothesis · Resource Hypothesis · Hawaii · Caribbean · Invasive algae · Nutrient enrichment

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Introduction

Human-mediated introductions of non-native marine species have broken down the historic biogeographical separation between floras and faunas in various parts of the world. An interconnected global economy now allows for unnatural long-distance transport of marine organisms beyond their natural dispersal boundaries. The intake and release of ballast water by ships, “hitchhiking” on floating debris and ships, the aquarium trade and intentional introductions for aquaculture and fisheries enhancement represent the

most common routes by which such transport takes place (Carlton 1989; Inderjit et al. 2006; Williams and Smith 2007). While many introductions are unsuccessful, some introduced organisms become extremely abundant which can negatively impact native flora and fauna. Such introduced species are often referred to as “invasive species”. Because invasive species presently cause major economic losses (Pimentel et al. 2005) and local and global reductions in biodiversity (World Conservation Monitoring Centre 1992; Vitousek et al. 1997; Mooney and Hobbs 2000), understanding the factors that allow species to become abundant after they are introduced, is a critical step towards future prevention and management of marine invasions (Hiero et al. 2005).

Macroalgae represent roughly 20% of the world’s marine invasive species (Schaffelke et al. 2006) that cause significant local ecological and economic damage by altering the structure and functioning of ecosystems they invade (Schaffelke et al. 2006; Williams and Smith 2007). For invasive macroalgae and invasive species in general, regulatory processes that control their abundance in their native range often no longer exist or have changed at their new location. A commonly proposed mechanism that builds on this premise is the Enemy Release Hypothesis (ERH; Keane and Crawley 2002; Torchin et al. 2003), also named “herbivore escape”, “predator escape” or “ecological release hypothesis” (Keane and Crawley 2002). The ERH states that introduced plant species increase in distribution and abundance because co-evolved herbivores or other natural enemies are generally not transported with them to the invaded location. The effects of the ERH become enhanced when introduced plants face ample supply of resources at their new location that can be allocated to growth and reproduction (Davis et al. 2000; Blumenthal 2006). This stimulating effect of higher resource availability on a species’ invasive success is commonly known as the Resource Hypothesis (RH; Davis et al. 2000; Daehler 2003). Resource availability does not necessarily affect invasive plant species differently than native plants, but merely provides a pathway that can intensify the effects of initial “enemy release”. Both the ERH and RH thus assume that that invasive species are successful in their invaded range because controlling or limiting factors in their

native range are no longer present (see Inderjit et al. 2006 for further details on the ecological attributes of marine algal invasions).

Parker et al. (2006) showed that across a wide range of systems and types of organisms, generalist herbivores often consume introduced species, presumably because these are not adapted to deter their new enemies. Introduced species therefore do not escape predation if generalist herbivores functionally replace a plant’s native enemies (Keane and Crawley 2002). Following the predictions of Parker et al. (2006) newly arrived (i.e. invaded) algae would simply face a community of generalist herbivores capable of controlling their subsequent proliferation. Because marine herbivores are often generalists with a low degree of host specialization (Hay 1991; Hay and Steinberg 1992), the Enemy Release Hypothesis might be of limited use to explain invasions of marine algae.

To reconcile the seemingly contradictory predictions for marine algae from the ERH (Keane and Crawley 2002) and those of Parker et al. (2006), explicit experimental comparisons of the strength rather than the existence of an herbivore-prey interaction are required between a species’ native and invaded range (Hiero et al. 2005). Only then can the potentially variable impact that local herbivores exert on a plant species in its native and invaded range be determined and assessed to see whether “enemy escape” occurs. Biogeographic comparisons of invasive plants in their native and invaded range are extremely rare and generally focus on differences in density, fecundity and plant size (see review by Hiero et al. 2005 for examples). Such approaches inherently assume that an invader behaves “differently”, but neglect that increased plant performance can also result from the fact that their native strategy is simply more successful in its invaded range. High abundance at the invaded location thus stems from a relaxation of external regulatory and limiting processes in the wider community that normally control the species’ abundance in its native range. Studies focusing on biogeographic differences in community level processes are rare and generally focus on impact of variable soil microbes on plant performance (e.g. Reinhart et al. 2003, Callaway et al. 2004). In a recent review (Hiero et al. 2005), only two studies are listed that specifically addresses biogeographical differences in herbivore pressure experienced by an

invasive species in its native and invasive range (Wolfe 2002; DeWalt et al. 2004).

In this study we aim to quantify the difference in herbivore pressure experienced by two native and two invasive macroalgal species in their native (Caribbean) and invasive range (Hawaii). Secondly, we provided the same species with additional nutrients to see whether invasive species respond differently to higher resource availability than their native congeners. This information will aid in determining if (1) the negative impact of local herbivores on plant growth differs between a species' native and invasive range, thus providing a species with "enemy release" sensu the ERH, and if (2) invasive species respond differently to increased nutrient availability compared to native species, suggesting that biogeographic differences in nutrient availability could drive invasive success.

Methods

General design

We used a combination of herbivore exclusion and nutrient addition to determine their single and interactive effects on the growth of four algal species that occur on coral reefs in two widely separated biogeographical regions: Hawaii and the Caribbean. Two of the four algal species are native to the Caribbean but were introduced to Hawaii. For these species the effects of the treatments mentioned above could hence be compared among their native and invasive range and to the two circumtropical species that were considered as native species in both regions.

Study species

The red algae *Acanthophora spicifera* (Vahl) Borgesen 1910 and *Hypnea musciformis* are native to the Caribbean and were introduced to Hawaii (Russell 1992; Smith et al. 2002). *Acanthophora spicifera* is the most widespread and successful invasive alga in Hawaii and was introduced around 1950. This species invades reefs and intertidal habitats where it is frequently observed smothering reef organisms such as corals and native algae. Its fragile morphology results in frequent fragmentation, likely enabling this

species to spread within and between islands (Smith et al. 2002). *Hypnea musciformis* (Wulfen) J.V. Lamouroux (1813) was introduced to Oahu in 1974 from Florida to investigate its potential for commercial κ -carrageenan production (Russell 1992). *Hypnea musciformis* now forms dense thickets from the intertidal zone to depths of 6 m where it, like *A. spicifera*, smothers native coral and algal communities (Smith et al. 2002). It is most commonly found as an epiphyte on other algae, as well as on itself, attached by small hooks on the tips of its branches. *Hypnea musciformis* lacks the ability to sexually reproduce in Hawaii (Smith et al. 2002) and frequent generation of asexual fragments most likely drives the dispersal of this species between and within islands (Smith et al. 2002; Russell and Balazs 1994). Two species with a global distribution were also included: the green alga *Ulva fasciata* (Delile 1813) and the brown algal species complex *Sargassum* spp. that are considered native to both the Caribbean and Hawaii. *Ulva fasciata* is commonly found in areas of high nutrient input, low wave forces and reduced herbivory. Blooms of *Ulva* often occur in coastal waters near harbors, industrial complexes and residential areas with nutrient-rich and/or fresh water input (Harlin 1993). Taxonomic classification of *Sargassum* species in our study was not straightforward as species descriptions in the literature are not complete or are based on variable characteristics. The species used in Hawaii is most likely *S. polyphyllum*, whereas that in the Caribbean is mostly *S. polyceratum*. Both species have similar gross morphologies and are often found in communities on wave swept benches with high energy and subtidally on reef flats. Closely related algal species often show similar resistance to resident herbivores despite differences in geographical occurrence (Ricciardi and Ward 2006). We thus assume that the different species of *Sargassum* used in the Caribbean and Hawaii did not affect the outcome of our experiments.

Site selection

In the Caribbean, two sites were selected on St. Thomas (United States Virgin Islands) and four on Curacao (Netherlands Antilles) respectively. In Hawaii, one site was used on the island of Maui and one on the island of Oahu. The limited number of sites per island in Hawaii results from the limited

number of sites that met our site selection criteria (see below) and harbored existing populations of *A. spicifera* and *H. musciformis*. Based on ethical concerns, we did not want to introduce these species to areas where they are still absent. Site selection was accomplished by firstly determining the biomass of herbivorous fishes following the methods described in Sandin et al. (in press). Sites were only chosen so that herbivorous biomass ranged between 110 and 190 kg/h to ensure relatively high (Newman et al. 2006) and similar biomass of herbivores at each site. Besides similar herbivorous fish biomass, additional selection criteria were: (1) low abundance of macroalgae (<2% bottom cover) that fish could target instead of those in our experiments; (2) a fore reef environment that allowed experiments between 6 and 8 m water depth; (3) sufficiently large area to space the algae used in our experiments (± 5 m) in order to maximize the independent behavior of each sample; (4) sufficient space to keep experimental plots away from damselfish territories that are actively protected against herbivorous fish; and (5) absence of other macroscopic herbivores such as sea urchins. Only sites meeting these selection criteria were used in this

study and are shown in Fig. 1. All experiments were conducted in January 2007. Background levels of nutrients in the reef water in Hawaii and the Caribbean show similar ranges at the selected sites (Phosphate 0.1–0.3 μM ; Nitrate + Nitrite 0.3–0.5 μM and Ammonium 0.5–1.5 μM ; Smith et al. 2005; Department of Nature and Environment of the Netherlands Antilles (MINA), unpublished data; Herzfeld, unpublished data) thus minimizing the possibility that differences in background nutrient concentrations influenced the outcome of our study. Water temperatures for all sites ranged between 24.4 and 26.7°C during the experiments.

Experimental treatments

At each site forty individuals of each algal species were collected, dry-spun to constant weight in a salad spinner and selected to weigh between 1.0 and 1.2 g. Then, ten individuals were randomly assigned to each of the following four treatments: herbivore exclusion (–H–N), nutrient addition (+H+N), herbivore exclusion and nutrient addition (–H+N) and a control (+H–N). Herbivores (mainly large and medium sized

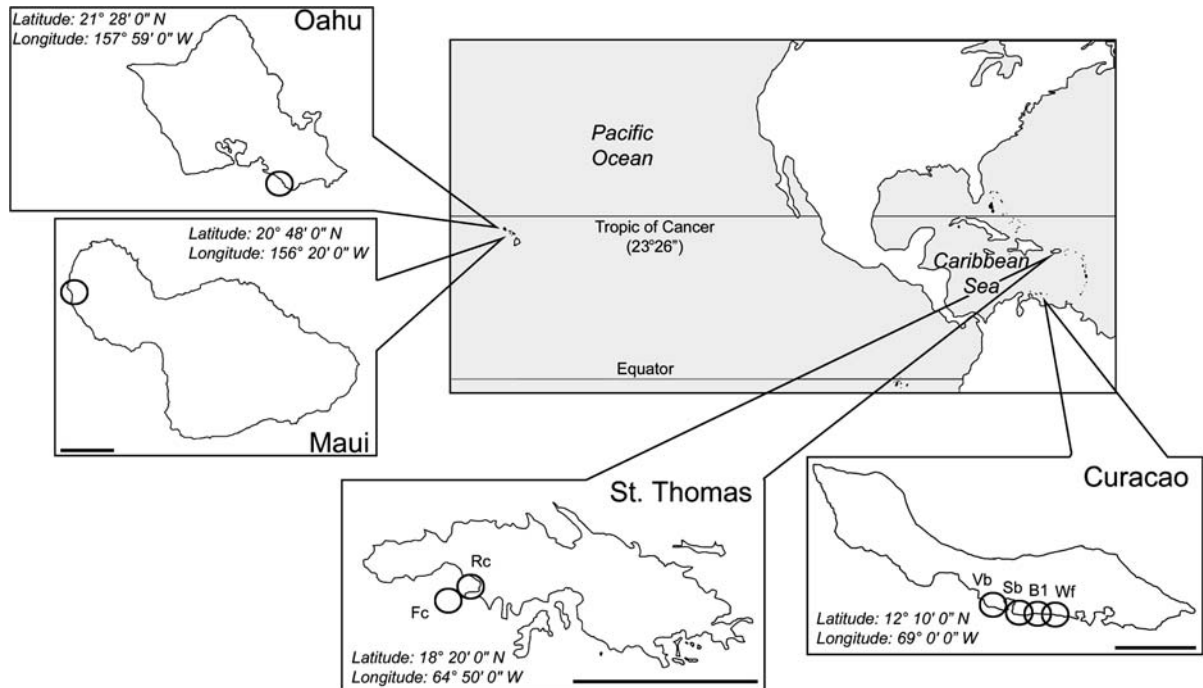


Fig. 1 Overview of sites that were selected in this study. Coordinates indicate the location of each island whereas study sites are indicated by open circles. Rc = Range Cay, Fc = Flat

Cay, Vb = Vaersenbaai, Sb = Slangenbaai, B1 = Buoy 1, Wf = Waterfactory. Scalebars indicate 10 km

Scarids and Acanthurids, but not their juveniles or other microherbivores) were excluded by placing algae in a cage made out of stainless galvanized mesh wire with a 1.2×1.2 cm mesh size. Light levels inside the cage were similar to ambient light levels at the same depth and determined with a diving PAM (Heinz Walz GmbH, Germany). To control for the presence of metal, all algae subjected to predation by herbivores were kept in a similar cage but without the top cover. Nutrient additions consisted of placing a mesh bag filled with 60 g of slow releasing garden fertilizer (Osmocote™, Sierra Chemical Company, Milpitas, CA, USA) within 30 cm of the targeted algae. Similar fertilizer additions have increased local N levels by 50–130% and P levels by 50–70% relative to background levels (Carreiro-Silva et al. 2005) and are commonly used in macroalgal enrichment experiments (Littler et al. 2006). Non enriched samples were placed at least 5 m away from the enriched samples to prevent cross contamination. All algae were attached to the same mesh wire that the cages were made of using standard wooden cloth pins that were padded with flagging tape (Empire Level Mfg. Corp., Mukwonago, WI, USA) to minimize abrasion. Algae were left for six days on the reef, collected, spun to constant weight in a salad spinner and weighed again. Growth rates were calculated as relative changes in algal biomass to correct for small variations in the starting weight of algae samples. The dimensionless relative growth rate was then calculated as:

$$\text{Relative growth} = \frac{\text{Weight}(\text{day}6) - \text{weight}(\text{day}0)}{\text{Weight}(\text{day}0)}$$

and analyzed as a response to the varying treatments.

Statistical analyses

Growth data were log-transformed ($\log[x + 1]$) to ensure normally distributed data and homogeneity of variances. Firstly, data for Curacao and St. Thomas were used in a three-way ANOVA to test for within island variation in the effect of similar levels of herbivore biomass on algal growth with adjusted *P* values using the Bonferroni procedure. Island, site and treatment were all used as fixed factors and significant factors (or their interaction) were analyzed using Scheffé's test for post-hoc pairwise comparisons. Comparisons between +H+N and -H-N treatments are not considered in post-hoc analyses.

Because there were no within-island differences in the effects of herbivores and nutrient additions (see "Results"), all data were subsequently subsampled per island to generate equal sample sizes for all islands. Data were transformed as described above and data were analyzed in a mixed nested/factorial ANOVA in which "region" and "treatment" were used as fixed factors and "island" was nested within "region". All analyses were carried out for each individual algal species and differences between algal species were not considered here.

To generalize between invasive and native species in the two regions, we analyzed the overall effects of herbivore presence and nutrient enrichment on invasive species (*A. spicifera* and *H. musciformis*) in their native (Caribbean) and invasive range (Hawaii) and on the species with a global distribution (*U. fasciata* and *Sargassum* spp.) in both regions. To assess the overall effect of herbivores on algal growth data from the +N and -N treatments were combined for each combination of two species (i.e. invasives and natives) and standardized using the unweighted log response ratio $RR_u = \ln(X^{+h})/(X^{-h})$. Vice versa, herbivore treatments (+H and -H) were pooled to determine the effect of nutrient enrichment. Log response ratio's can be calculated without further reference to sample size or error (Hedges et al. 1999) which allows data from different islands and treatments to be pooled. X^{+y} indicates the average weight of algae after 6 days in the presence of factor *y* (i.e. herbivores or nutrients), whereas X^{-y} indicates such weight in absence of this factor. The weight of algae after 6 days was used instead of the relative growth rate to calculate RR_u 's because relative growth rates can result in negative values that cannot be log-transformed. Positive RR_u values indicate a positive effect of herbivores on algal growth whereas negative values indicate that herbivores negatively impacted algal growth. Differences between RR_u were analyzed using a non-parametric Kruskal-Wallis ANOVA. All analyses were performed in STATISTICA 6.0 (Stat Soft Inc. Tulsa, OK, USA).

Results

Within island variation in herbivore biomass

Mean herbivorous fish biomass per site averaged 14.3 g m^{-2} (SD 5.1; $n = 6$) for the Caribbean and

18.9 g m⁻² (SD 0.4; $n = 2$) on Hawaii. When sites were chosen according to our selection criteria (see “Site selection”), between-site variation in herbivore biomass did not significantly alter the outcome of the experimental treatments (Tables 1, 2), despite one site with lower than intended herbivore biomass on St. Thomas (Flat Cay). Across the range of biomass present at the sites in the Caribbean (5.9–18.7 g m⁻²) no correlation existed between herbivore biomass and (negative) algal growth for any of the species considered ($r > 0.35$; $P > 0.07$). We assumed that a similar pattern can be expected for Hawaii, where we were unable to conduct similar tests because sites were either unsuitable according to the selection criteria or because of ethical issues regarding the active relocation of invasive algae outside their current range.

Effects of herbivores and nutrient additions on algal growth

Exclusion of herbivores corresponded to increased algal growth for *A. spicifera* and *H. musciformis* in both regions and for *U. fasciata* in the Caribbean (Fig. 2). In Hawaii, local herbivores negatively affected the growth of invasive species, but not of two native congeners (*Sargassum* spp. and *U. fasciata*), suggesting that Hawaiian herbivores preferably prey on invasive rather than native algal species. Hawaiian herbivores caused negative algal growth rates in *A. spicifera*, but not in *H. musciformis*. While herbivores preferably preyed on the invasive algae in Hawaii, the intensity of herbivory was two-times lower than that experienced by the same species in their native Caribbean range. We likely

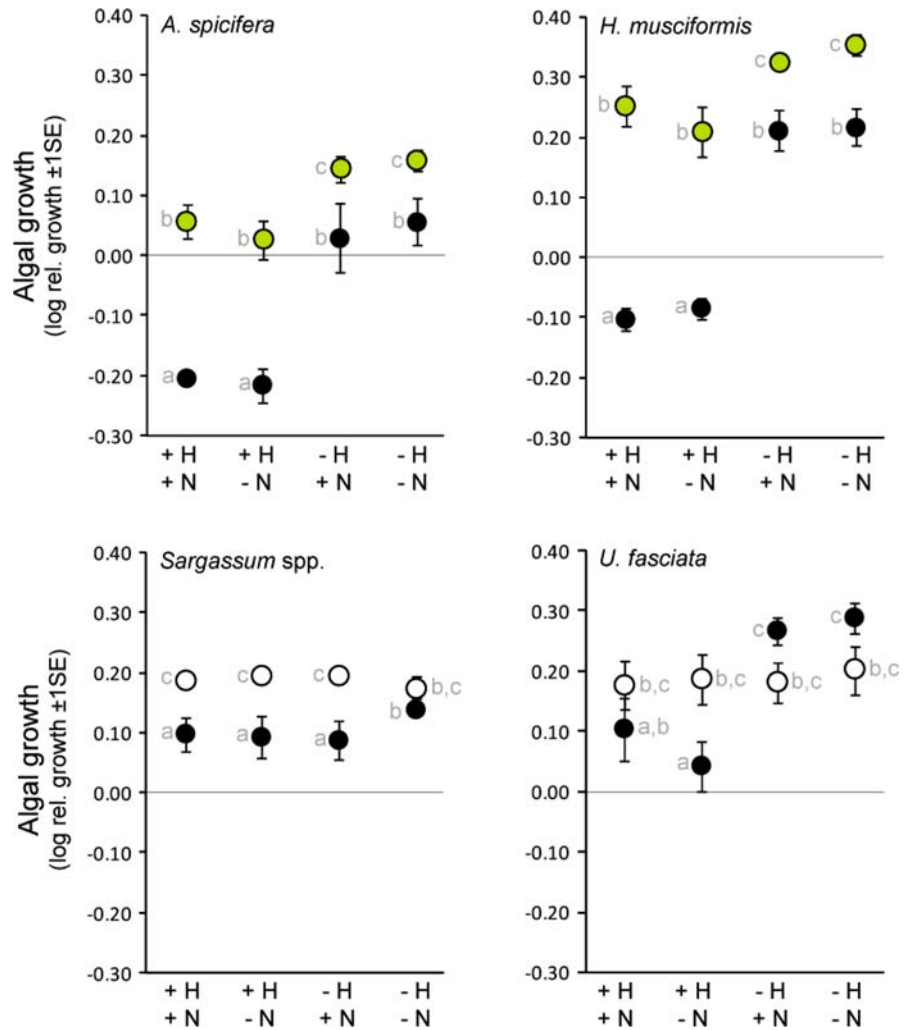
Table 1 Overview of sites and local biomass of herbivores

Island	Site	Coordinates		Herbivore biomass (g m ⁻²)	
				Mean	SD
Caribbean					
Curacao	Buoy 1	12°07'30.51" N	68°58'24.22" W	17.1	5.4
	Slangenbaai	12°08'20.06" N	68°59'49.84" W	18.6	8.2
	Waterfactory	12°06'38.49" N	68°57'27.73" W	18.7	7
	Vaersenbaai	12°09'40.23" N	69°00'21.11" W	14.3	6.2
St. Thomas	Flat Cay	18°19'06.97" N	64°59'21.87" W	5.9	1.8
	Range Cay	18°20'25.54" N	64°58'45.39" W	10.9	3.4
Hawaii					
Oahu	Kaimana	21°15'46.28" N	157°49'28.46" W	19.1	8.5
Maui	Kahekili	20°56'11.33" N	156°41'36.89" W	18.6	11.4

Table 2 Factorial ANOVA results on within island variability on log transformed growth data for all Curacao and St. Thomas sites

	Curacao (4 sites)					St. Thomas (2 sites)				
	SS	df	MS	<i>F</i>	<i>P</i>	SS	df	MS	<i>F</i>	<i>P</i>
Site (Si)	0.001	3	0.000	0.7	ns	0.000	3	0.000	0.1	ns
Treatment (Tr)	0.619	3	0.206	446.7	<0.01	0.210	3	0.070	117.5	<0.01
Species (Sp)	0.322	3	0.107	232.6	<0.01	0.277	3	0.092	155	<0.01
Si × Tr	0.007	9	0.001	1.7	ns	0.003	9	0.001	1.7	ns
Si × Sp	0.004	9	0.000	0.9	ns	0.011	9	0.004	6.4	ns
Tr × Sp	0.691	9	0.077	166.2	<0.01	0.200	9	0.022	37.4	<0.01
Si × Tr × Sp	0.014	27	0.001	1.1	ns	0.013	9	0.001	2.4	ns
Error	0.257	556	0.000			0.117	197	0.001		

Fig. 2 Average growth rates of four algal species in response to four experimental treatments in the Caribbean (black markers) and Hawaii where invasive and native species are indicated by green and white markers respectively. Experimental treatments are indicated as follows: herbivore exclusion (-H-N), nutrient addition (+H+N), herbivore exclusion and nutrient addition (-H+N) and a control (+H-N). Letters next to the markers indicate significant groupings based on post-hoc analyses (Scheffé) on log-transformed growth data (see Table 3 for detailed statistical results)



underestimated grazing intensity in the Caribbean because *A. spicifera* and *H. musciformis* were completely grazed within two days, leaving only the tissue protected inside the cloth pins (Vermeij and T. B. Smith pers. obs.). In Hawaii, these species had not disappeared after three times the amount of time that it took Caribbean herbivores to completely eat them. *Acanthophora spicifera* and *H. musciformis* thus experienced higher predation by herbivores in their native range compared to that experienced in Hawaii and that observed for the two circumtropical species that we considered as native species in both regions (Fig. 3a). Invasive species in Hawaii thus experienced higher herbivore predation compared to native algal species, but less than they experienced in their native range (Kruskal-Wallis test: $H_{(1,16)} = 8.65$ $P < 0.01$). This reduction in the intensity of

herbivory relative to a species' native range provided invasive algae in Hawaii with "enemy release" sensu the ERH, despite the fact that they were preferred over native species by Hawaiian herbivores.

Effects of nutrient additions on algal growth

Algal growth rates were higher overall in Hawaii. When averaged over all experimental treatments, algal growth rates were 1.14 (*Sargassum* spp.) to 1.50 times (*H. musciformis*) higher in Hawaii. Only *U. fasciata* grew on average equally fast in both regions. For all other species, nutrient additions never resulted in higher growth rates for any species, in the presence (i.e. +H-N vs. +H+N) or absence (i.e. -H-N vs. -H+N) of herbivores (Scheffé's test; $P > 0.18$). When algal species were grouped as invasive and

Table 3 Factorial ANOVA results showing significant differences in growth rate for the four algal species considered in this study

	SS	df	MS	F	P	SS	df	MS	F	P
	<i>Acanthophora spicifera</i>					<i>Hypnea musciformis</i>				
Region (Re)	4.48	1	4.48	75.66	<0.001	21.94	1	21.94	215.84	<0.001
Island (Is) [Re]	6.04	2	3.02	51.00	<0.001	5.03	2	2.52	24.76	<0.001
Treatment (Tr)	9.05	3	3.02	50.93	<0.001	14.98	3	4.99	49.13	<0.001
Tr × Re	1.35	3	0.45	7.60	<0.001	2.27	3	0.76	7.46	<0.001
Tr × Is[Re]	7.44	6	1.24	20.95	<0.001	10.43	6	1.74	17.09	<0.001
Error	8.35	141	0.10			13.83	136	0.10		
	<i>Sargassum</i> spp.					<i>Ulva fasciata</i>				
Region (Re)	2.03	1	2.03	65.38	<0.001	0.02	1	0.02	0.09	ns
Island (Is) [Re]	4.57	2	2.29	73.50	<0.001	25.38	2	12.69	65.79	<0.001
Treatment (Tr)	0.02	3	0.01	0.17	ns	4.64	3	1.55	8.02	<0.001
Tr × Re	0.18	3	0.06	1.96	ns	4.17	3	1.39	7.21	<0.001
Tr × Is [Re]	0.60	6	0.10	3.24	<0.05	7.45	6	1.24	6.44	<0.001
Error	4.48	144	0.03			27.77	144	0.19		

Region and treatment are used as independent variables and Islands are nested within each region. Relative growth rates were $\log(x + 1)$ transformed before the analyses. Significant interactions are analyzed using Scheffé's post-hoc comparisons. Results of these analyses are given in Fig. 2 where significant differences between groupings are indicated by different letters

native in both regions (Fig. 3b), nutrient enrichment did not result in higher algal growth rates in any of the four grouping × region combinations (Kruskal–Wallis test: $H_{(3,32)} = 1.32$ $P = 0.72$).

Discussion

Acanthophora spicifera and *H. musciformis* are native to the Caribbean and were introduced to Hawaii approximately 30–50 years ago. Local herbivores in Hawaii prefer to feed on these species over native species (Fig. 3a) confirming earlier studies showing that invasive algae are a highly preferred food source of Hawaiian herbivorous fishes (Stimson et al. 2001; Conklin 2007) and marine turtles (Russell and Balazs 2000). Preference of local herbivores for invasive species is often interpreted as evidence against the Enemy Release Hypothesis, because introduced species appear “not released” from enemies when they arrive elsewhere (Torchin et al. 2003; Colautti et al. 2004). Because the majority of marine herbivores are generalists (Hay 1991; Hay and Steinberg 1992) invasive algal species that have escaped their native enemies, simply face new ones to which they have developed no defenses. This could explain why native herbivores prefer introduced algal species in Hawaii. However, our study shows how

studying invasive species in their invasive range only, could easily lead one to falsely conclude that the species have not escaped herbivory based on the observation that they have become a preferred food source of local generalist herbivores. While this problem has been recognized (Colautti et al. 2004; Hierro et al. 2005), we know of no studies that have previously addressed this problem for marine macroalgae.

This study showed that biogeographical comparisons of herbivore intensity are needed to determine if invasive species experience reduced predation in their invaded range and hence whether the ERH applies. First we showed that herbivorous fish negatively affected algal growth rates of invasive species in their native range (Fig. 2). This experimental test is necessary to ascertain that these mid and larger sizes herbivorous fish can indeed be regarded as “enemies” sensu the ERH. In Hawaii, *A. spicifera* and *H. musciformis* were both consumed by local herbivores, initially suggesting that the two algal species did not escape predation after they became introduced. Interestingly, herbivore predation in Hawaii did not cause negative algal growth rates that are required to remove such species from the community for one species (*H. musciformis*) or their impact was only half of that observed in the Caribbean (*A. spicifera*). Hence, the intensity of

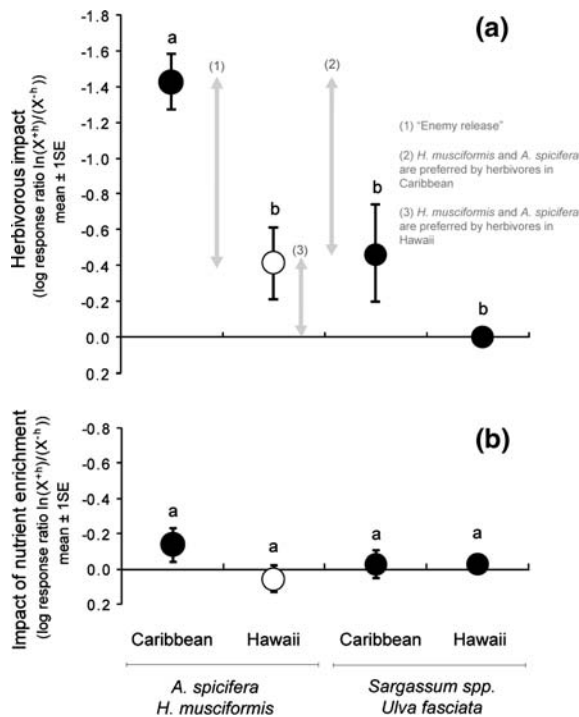


Fig. 3 (a: top) The effects of herbivores and (b: bottom) nutrients on the growth rate of *A. spicifera* and *H. musciformis* in their native (Caribbean) and invasive range (Hawaii) and of two species (*Sargassum* spp. & *Ulva fasciata*) that are native to both regions. White markers indicate invasive species. Note that because impact is calculated using unweighted log response ratios, greater impact of herbivores and nutrients is indicated by higher negative values. Statistically similar distributions are indicated in each graph by the letters above each data point. Grey arrows provide notional interpretations of the data that are discussed in more detail in the text

herbivorous pressure was lower for both invasive species in Hawaii compared to that observed in their native Caribbean range (Fig. 3a). This observation supports the Enemy Release Hypothesis as an explanation for the invasive success of two introduced algae in Hawaii. Based on these four algal species, we stress the value of experimental, biogeographic comparisons to determine whether the ERH is a candidate scenario to explain invasive success.

Nutrient additions did not stimulate growth rates for any algal species in any of the treatments. This suggests that the success of Caribbean algae in Hawaii is unlikely to stem from faster growth in response to higher resource availability in Hawaii. Since we did not measure the nutrient concentrations in the water, one could theorize that the nutrients diffused too fast to stimulate algal growth. However,

this possibility seems unlikely as stronger than normal water movement was not observed at any of the sites during the experiment and the same technique has been tested and proven useful in a variety of other studies, including our study site on Maui (Carreiro-Silva et al. 2005; Smith et al. 2001; Littler et al. 2006). Hence, herbivores have greater effects on algal growth than nutrient enrichment, at least for the four species studied here (see Burkepille and Hay 2006 for a review). Algal growth rates were higher overall in Hawaii (factor 1.01–1.50, depending on species) and positive growth rates were recorded for all species except *A. spicifera* in the presence of herbivores. Regardless of what underlies this biogeographical difference in overall growth rates, it suggests that introduced species capitalize on resources unavailable in their native range in addition to a weakening (rather than the disappearance) of herbivore control. A combined scenario whereby plants first benefit from escape of natural enemies (i.e. the ERH) and then from greater resource availability in the invaded range has been named the Resource-Enemy Release Hypothesis (R-ERH; Blumenthal 2006). Our experiment is not useful to determine which cryptic resource allows algae to grow faster in Hawaii relative to the Caribbean, but potential candidates might include: (1) greater availability of a nutrient other than the ones considered here (e.g. iron) due to the different geological history of the regions; (2) absence of enemies other than the ones considered here such as micro- and mesoherbivores and pathogens (Carpenter 1986).

The majority of studies on introduced and invasive marine and terrestrial plants have been conducted solely within the introduced range (Hierro et al. 2005). Simultaneous studies, especially experimental ones, of herbivore-plants interactions in their native and invaded range are rare and to the best of our knowledge, ours is the first for tropical marine algae. Comparative biogeographic studies often focus on an inherent characteristic of a plant species in its invaded and native range, e.g. differences in biomass, maximum age or fecundity (see examples in Hierro et al. 2005). While species traits certainly differ across space and can explain invasive success for some species, the demographic consequences of these traits in native and invasive ranges are not often explicitly studied (but see: Hinz and Schwarzlaender (2004) and Mitchell et al. (2006) for recent overviews

of studies that did). While several invasive marine algal species have been well studied (see Inderjit et al. 2006 for a recent review), most of these studies focused on algal life-history characteristics in their non-native range only (Nyberg and Wallentinus 2005; Inderjit et al. 2006) and the facilitation of introductions by the new global economy (Coles and Eldredge 2002; Flagella et al. 2007; Mineur et al. 2007). It seems too early to synthesize the existing data as different species are successful for varying reasons (Williams and Smith 2007). Formulating general principles underlying macroalgal invasions seems therefore premature, especially for tropical species that lack data compared to temperate and subtropical algal species (Nyberg and Wallentinus 2005; Inderjit et al. 2006). Nevertheless, since algal abundance on reefs is supposed to be extremely low due to intense herbivory (Jackson et al. 2001; Sandin et al. 2008), herbivores likely represent an important ecological factor structuring the demographic success of macroalgal populations on reefs, and we propose that the lack of adequate herbivory deserves critical attention as a factor linked to the success of invasive algae in non-native coral reef environments.

Despite the general absence of experimental tests of the strength of herbivore impact in a species' native and invaded range, the few studies that have used such approach found similar results as those reported here. Terrestrial invasive plants experienced a 5–17-fold reduction in net herbivore pressure in their invaded range compared to their native range. (Wolfe 2002; DeWalt et al. 2004). The seemingly larger reduction in herbivore pressure of terrestrial relative to marine invasive plants (i.e. two-fold; this study) may reflect the fact that marine herbivores are typically generalists (Hay 1991; Hay and Steinberg 1992) whereas herbivores in the aforementioned studies were mostly specialist arthropods. The ERH predicts that invasive species that escape specialist herbivores benefit more after successful introduction than those escaping generalist herbivores that likely have functional equivalents in the invaded range (Keane and Crawley 2002; Blumenthal 2006). Hence, enemy release is expected to yield greater advantages for invasive terrestrial plants that generally face more specialized herbivores in comparison to tropical marine plants. To further explore the generality of such premature speculation, we recommend experimental manipulation of enemies or competitors in a

species' native and invaded range to study the demographic responses of both terrestrial and marine invasive plants to better understand which controlling factors break down when a species becomes introduced outside its natural range. For marine algae such studies are extremely timely since they are extremely difficult to exterminate once introduced and generally have severe negative impacts on native communities.

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