Functional diversity among herbivorous sea urchins on a coral reef: grazing rate, dietary preference, and metabolism

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ABSTRACT: Herbivores influence the structure and function of ecosystems, especially in the marine environment where ecosystems can be rapidly transformed due to the presence or absence of a single important grazer or grazing community. Intra-guild variation in the ecological functions of herbivores, however, likely determines their ultimate effects on benthic dynamics. For example, echinoids (sea urchins) can facilitate the growth of stony corals by consuming fleshy algal competitors, yet our understanding of taxonomic variation in their grazing behaviors remains limited. Here, we examined the trophic functions of 5 herbivorous echinoids on a coral reef in Maui, Hawaii. We conducted field-based assays to compare grazing rates and consumption profiles using several key algal functional groups and contrasted the results with reported differences in echinoid metabolism. Grazing rates varied among species by up to 10-fold, with taxonomic differences explaining 77–85 % of the variation among individual urchins and metabolic rate explaining 81–98 % of the taxonomic variation in mean biomass and energy ingestion rates. Though all species consumed several algae, they also exhibited distinct grazing behaviors. Species with lower metabolic rates exhibited the largest intraspecific variation in diets and showed no clear algal preferences. In contrast, species with higher metabolic rates consistently consumed or avoided specific macroalgae, indicating a positive relationship between metabolic rate and diet specificity. This phylogenetic variation in grazing and metabolism aligns with classic metabolic and foraging theory and suggests that species identity, community structure, and complementarity are likely key to understanding the functional roles of herbivorous echinoid communities on coral reefs.

KEY WORDS: Biodiversity · Metabolic theory · *In situ* · Field experiment · Hawaii · Macroalgae · Turf · CCA · Preference · Echinoid

1. INTRODUCTION

The ability of similar species to coexist has long fascinated ecologists (Hutchinson 1961, Sale 1977, Connell 1978). Equally intriguing is the effect of biodiversity on ecological processes (Elton 1958, Tilman et al. 2012) and how species losses or invasions affect ecosystem dynamics and responses to disturbance and environmental change (Williams & Smith 2007, Cardinale et al. 2012, Hooper et al. 2012, Reich et al. 2012, Dirzo et al. 2014). Biodiversity often enhances primary production (Tilman et al. 1997), resource utilization (Duffy et al. 2001), and stability (Naeem & Li 1997) of ecological communities; a pattern that persists across many ecosystems (Cardinale et al. 2006). Similar patterns have been observed in subtidal marine ecosystems (Covich et al. 2004, Stachowicz et al. 2007) and are critical to understanding the effects of wide-spread defaunation that has greatly altered the structure of marine communities across the globe (Jackson et al. 2001, Myers & Worm 2003, Munday 2004).

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Top-down (consumer) effects appear particularly strong in benthic marine habitats, thus simple changes in trophic structure can result in complex in-direct impacts on habitat-forming species and the communities and processes that depend upon them (Shurin et al. 2006, Heck & Valentine 2007, Lewis & Anderson 2012). The ecological effects of consumers, however, can vary greatly among ecosystems. In temperate rocky reefs, where fleshy algae (e.g. kelps) are the dominant habitat-forming species, herbivorous sea urchins may reduce the growth and extent of habitat-forming kelps, thus negatively im-pacting the system's structure and function (Estes & Palmisano 1974, Dayton et al. 1998, Steneck 2013). In contrast to kelp forests, herbivorous sea urchins on coral reefs can facilitate the dominance of habitat-forming corals by limiting the cover of fleshy algae, thus enhancing the structure and function of coral reef ecosystems (McCook et al. 2001, Hughes et al. 2007, Smith et al. 2010). On coral reefs, changes in the abundance of grazer communities (e.g. through fishing, predation, or disease) have had strong cas-cading ecological impacts resulting in coral-to-macroalgal phase shifts and subsequent degradation of reef habitats (Hughes 1994, Smith et al. 2001, Pan-dolfi et al. 2005, Mumby et al. 2006).

In addition to variation in abundance, changes in the structure of herbivore communities can also greatly influence their ecological function (Duffy et al. 2003, Farlin et al. 2010, Brandt et al. 2012). As a result, herbivorous fishes on coral reefs are often grouped into discrete functional groups (Sandin et al. 2008, Williams et al. 2011) and intra-guild diversity has been examined in observational (Cheal et al. 2010, Edwards et al. 2014, Kelly et al. 2016) and manipulative (Burkepile & Hay 2008, 2010, 2011) studies. Similar studies are needed for echinoids that dominate herbivore communities on many shallow coral reefs across the globe (Ebert 1971, Lessios 1988, McClanahan & Muthiga 2016), including compara-tive studies of feeding behaviors and ecological im-pacts (Ogden & Lobel 1978, McClanahan 1988, Car-reiro-Silva & McClanahan 2001, Brandt et al. 2012).

Though urchins are often regarded as generalists, functional differences among herbivorous echinoids have been described (Vadas 1977, Birkeland 1989). For example, while some echinoids appear to benefit coral reefs by controlling fleshy algae and enhancing coral growth (Hughes et al. 1987, Idjadi et al. 2010, Sandin & McNamara 2012), others might function primarily as reef bioeroders, excavating carbonate and consuming calcifiers, reducing the accretion and complexity of coral ecosystems (Glynn et al. 1979,

O'Leary & McClanahan 2010). Furthermore, echino-id species may avoid or prefer different types of algae and exhibit unique grazing behaviors (Lawrence 2013). For example, *Diadema* spp. appear to avoid algae in the order Fucales (e.g. *Sargassum* sp.) (Cop-pard & Campbell 2007) whereas *Tripneustes gratilla* may prefer them (Steinberg & van Altena 1992).

Previous studies of echinoid trophic ecology on coral reefs have yielded mixed results with respect to functional diversity and redundancy. Much of what we know stems from relatively few laboratory grazing assays (Coppard & Campbell 2007, Stimson et al. 2007) or field observations (McClanahan 1988, Ogden et al. 1989, Furman & Heck 2009). Inferences from laboratory assays should be interpreted cautiously because feeding behaviors can be altered due to star-vation, pre-conditioning (feeding), or stress associ-ated with transport and the laboratory environment (Cronin & Hay 1996, Lyons & Scheibling 2007, Stim-son et al. 2007). Furthermore, previous studies have examined a limited variety of echinoid and algal taxa, often omitting key species or algal functional groups (e.g. crustose coralline algae and fleshy turfs). Simi-larly, inferences from field observations should also be interpreted cautiously, as stomach contents also reflect prey availability, with preferred prey items often the most rare in nature (Chesson 1983). A hybrid approach (e.g. field assays), however, might be able to capitalize on the strengths and reduce the weak-nesses of laboratory and observational approaches.

Comparative assessments of functional diversity among sympatric echinoids remains an important gap in our understanding of the ecological roles of this important guild on coral reefs (Hughes 1994, Sandin & McNamara 2012, Steneck 2013). Differ-ences between field- and lab- based estimates of grazing and behavior also remain to be reconciled and contrasted with metabolic theory. For example, grazing rates of several echinoid species measured in laboratory settings (Coppard & Campbell 2007, Stim-son et al. 2007) appeared consistently higher than those measured *in situ* (Carreiro-Silva & McClana-han 2001). Contrasts between grazing behaviors and metabolic rates can provide further insights into the phylogenetic and ecological foundations of any ob-served variation in diets and behaviors. For example, variation in individual, mass-specific, and commu-nity metabolism may determine differences in eco-logical rates (e.g. grazing, predation, and turnover) and species behaviors (e.g. diet, reproduction, and migration) (Brown et al. 2004, Sibly et al. 2012).

Fourteen species of echinoids are found in Hawaii, occurring at densities >70 ind. m^{-2} (Ogden et al. 1989)

and biomass >900 g m^{-2} (Ebert 1971) on shallow fringing coral reefs. Thus urchins are often the dominant herbivores on many of Hawaii's coral reefs, as is often the case on heavily-fished coral reefs around the world (Hay 1984, McClanahan 1997). As a result, the conservation of herbivorous echinoids has become an important strategy for managers of Hawaii's coral reefs, with population enhancement (Stimson et al. 2007, Neilson et al. 2018) and herbivore-specific refuges currently being tested (Williams et al. 2016, Kelly et al. 2017). The degree of dietary overlap and potential for complementary grazing functions among herbivorous echinoids, however, remain important questions in coral reef ecology and conservation.

Here, we conducted field-based grazing assays to explore variation in trophic function among 5 common coexisting herbivorous echinoids on a fringing coral reef in Maui, Hawaii. Field-based grazing assays, though logistically challenging, allowed us to maximize the strengths and minimize the weaknesses of experimental and mensurative approaches. Assays allowed us to contrast differences in grazing rates and relative consumption of 6 important algal functional groups. Furthermore, mean grazing rates and behaviors were contrasted with mean metabolic rates for each species, thus providing inferences regarding relationships between feeding behaviors and metabolism. Results of this work provide new insights regarding intra-guild functional diversity among herbivorous echinoid species and communities that are common on coral reefs around the globe.

2. MATERIALS AND METHODS

2.1. Study site and echinoid taxa

Field work was conducted at 5–7 m depth on fringing coral reefs along West Maui, Hawaii (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m625p071_supp.pdf; all Supplements are available at this URL). Coral reefs in Hawaii were once dominated by corals in the genera *Porites*, *Montipora*, and *Pocillopora*; however, live coral cover has declined rapidly over the last several decades (Pandolfi et al. 2005, Walsh et al. 2013). Wide-spread declines in coral cover have been associated with an increase in fleshy algae known to directly and indirectly harm corals (McCook et al. 2001, Smith et al. 2001, Vermeij et al. 2010). Herbivorous echinoids are considered critical to restoring Hawaii's degraded coral reefs, especially since overfishing of herbivorous fishes (Friedlander & DeMartini 2002, Friedlander et al. 2007) and waste-

water-induced eutrophication (S. Smith et al. 1981, J. Smith et al. 2005, Dailer et al. 2010) appear to have enhanced algal production and abundance.

Several herbivorous echinoid species in the genera *Echinometra*, *Heterocentrotus*, *Echinothrix*, and *Tripneustes* exist in sympatry on Maui's fringing coral reefs (Ogden et al. 1989) (Fig. 1). *Echinometra matthaei* (EM, rock boring) and *Heterocentrotus mamillatus* (HM, slate pencil), in the Family Echinometridae, are commonly found in cryptic habitats, with EM highly abundant (densities up to 128 m^{-2}) and HM less common (densities up to 1 m^{-2}). *Echinothrix calamaris* (EC, black banded) and *Echinothrix diadema* (ED, blue banded), in Family Diadematidae, are long-spined urchins commonly found grazing on exposed coral reef habitats. EC is generally more active and abundant (up to 4 m^{-2}) than ED (up to 0.14 m^{-2}). *Tripneustes gratilla* (TG, collector), Family Toxopneustidae, is a short-spined browsing species that is commonly found on exposed reef habitats at densities up to 3.7 m^{-2}. Though these echinoid densities on Maui are informative, local densities of each species can vary greatly on coral reefs throughout the Hawaiian Islands (Ebert 1971, Walsh et al. 2013).

2.2. Grazing assays

Our specific goal was to examine ecologically relevant variation in the grazing behaviors of echinoids on a coral reef, incorporating (vs. excluding) their recent ecological history. Though lab-based studies facilitate greater control and observation during assays, *in situ* grazing assays (e.g. conducted in habitats where organisms naturally occur) can provide more ecologically relevant grazing rates and behaviors. For example, though all standardized assays require enclosure and manipulation of prey items, *in situ* assays are not influenced by intensive handling, transport, and long-term storage of grazers in laboratory conditions; or by pre-treatments such as starvation or diet pre-conditioning. Echinoids are known to exhibit unnatural grazing behaviors due to starvation (Cronin & Hay 1996, Siikavuopio et al. 2008), and pre-conditioning in the laboratory can result in unnatural selection or avoidance of supplied diet items in subsequent grazing assays (Lyons & Scheibling 2007, Stimson et al. 2007).

Given the ecological nature of the study, we developed an *in situ* grazing assay approach to quantify grazing rates and algal consumption profiles for the 5 common co-existing species of herbivorous echinoids on Hawaiian coral reefs mentioned above: EC, ED,
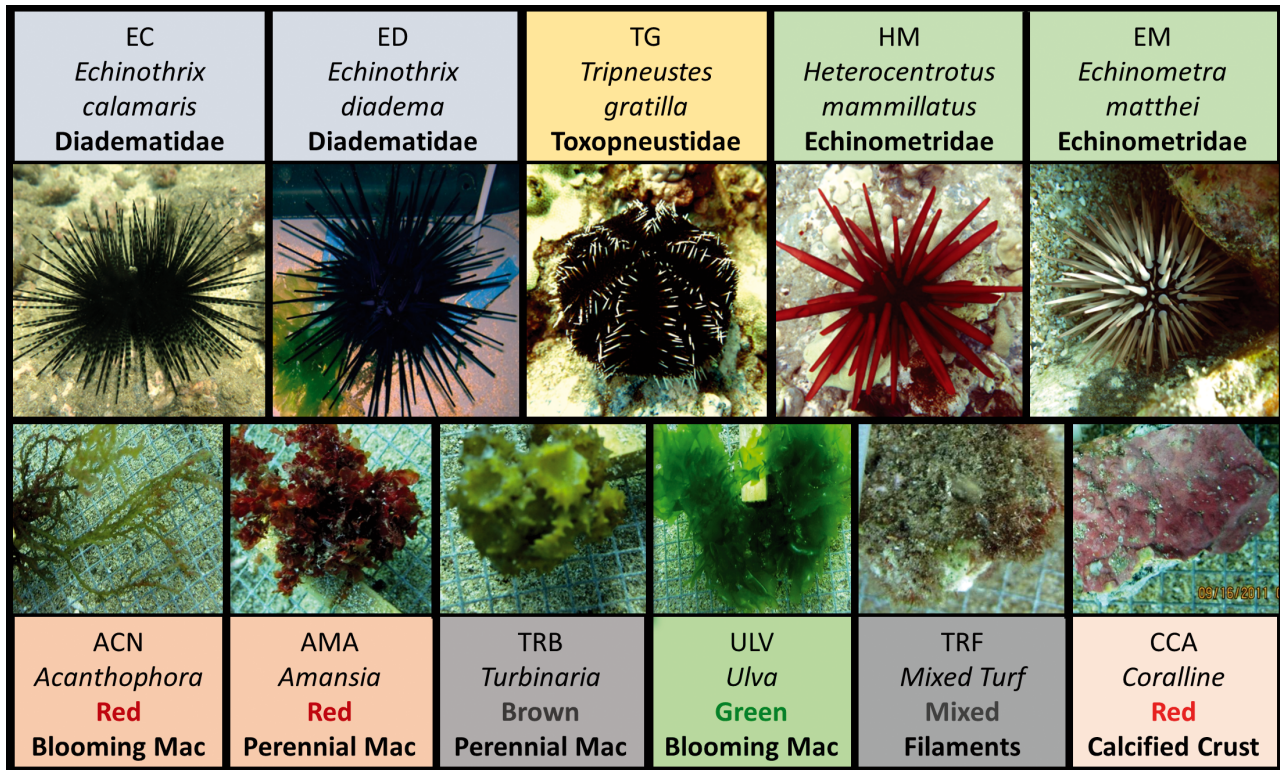
Fig. 1. Echinoids (top) and algae (bottom) included in grazing assays

TG, HM, and EM (Fig. 1). Two replicate assays of 10 individuals and 3 controls (20 ind. and 6 controls in total) were conducted for each of the 5 echinoid species (total of 10 assays). Echinoids were provided 6 algal taxa representing key functional groups (Steneck & Dethier 1994): *Ulva lactuca* (ULV, green bloom-forming macroalga), *Turbinaria ornata* (TRB, brown perennial macroalga), *Amansia glomerata* (AMA, red perennial macroalga), *Acanthophora spicifera* (ACN, red bloom-forming invasive macroalga), mixed crustose coralline algae (CCA, calcified encrusting algae), and mixed turf algae (TRF, fine filamentous algae) (Fig. 1). Algal specimens consisted of individual thalli for macroalgae and pieces of carbonate rubble with attached CCA or TRF (Fig. 1). One day before each assay began, macroalgae were collected from the reef, cleaned of sediments and epiphytes, and trimmed to similar sizes (approximately 2–3 g; Supplement 2). Macroalgae were spun and blotted to remove excess water and weighed (to 0.001 g) before and after the grazing period. TRF and CCA were collected and a thin nylon cable tie used to attach samples to clips in the assay enclosure (Fig. 2b). CCA and TRF were tightly adherent on calcium carbonate rubble substrate which overwhelmed algal biomass. Therefore, these were photographed

before and after the grazing period, and the change in area (cm^2) was measured using Image J v.1.45s (National Institutes of Health). Mass consumption was then estimated using empirical mass/area relationships (Supplement 2).

Enclosures were constructed of inverted plastic 28 × 20 × 10 cm coverings attached to 32 × 25 × 0.63 cm flat PVC bases. Base corners were each attached to a 50 cm long piece of 1 cm diameter rebar suspended 15 cm above the reef (to limit sediment accumulation in enclosures). Each enclosure was covered with 6 mm perforations which allowed for water exchange (Fig. 2a). Pilot assays indicated this shielded design (de Souza & Kuribara 2006) minimized stress due to exposure, especially for cryptic, light-sensitive taxa (e.g. EM and HM). Though this design could have enhanced diurnal grazing by light-sensitive taxa, grazing rates for these taxa remained quite low and matched predictions based on both metabolic rates and grazing rates reported in the literature. Shielding likely had little effect on other taxa as they are known to feed in all light conditions (Ogden et al. 1989).

Echinoids were collected by SCUBA divers from the nearby reef and placed directly into assay enclosures already containing algae. Test diameter of each
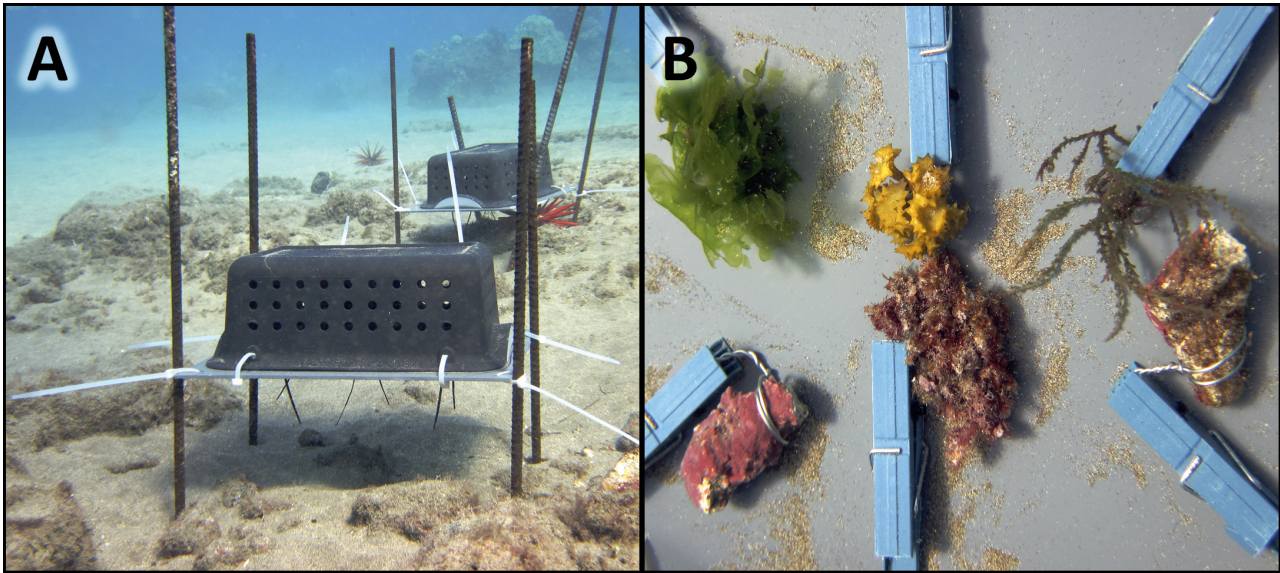
Fig. 2. (A) Grazing assay chamber and (B) an enclosed algal array

individual was measured with calipers at the end of each assay (to 0.1 cm) and used to estimate echinoid biomass (Supplement 3) and mass-specific grazing rates. Control cages contained algae without echinoids to account for autogenic (ungrazed) tissue loss, and placement of controls was random for each grazing assay. Pilot studies indicated that a single duration (e.g. 48 h) could result in over-consumption by fast grazers (e.g. EC) or immeasurable consumption by slow grazers (e.g. HM). Therefore, assays were checked every 24 h and terminated after 1−6 d, depending on grazing rate (Paul & Hay 1986), to ensure sufficient time for measurable consumption without over-consumption (e.g. minimum of 1 alga fully grazed or 2 partially grazed).

All assays were conducted in the same season (May−July) and during similar field conditions. Stable conditions allowed for all 5 echinoid species to be assayed using the same 6 algal prey (30 unique urchin–algal pairs) throughout the course of the study. However, not all assays could be conducted in the same year due to method development and logistical constraints of working at a remote field site. Thus EM, HM, and ED were assayed in 2012 whereas EC and TG were assayed in 2014. Oceanographic conditions were similar among years, with equal wave intensity and salinity across years, and slightly higher temperatures ($+1.4°C$) and pCO_2 ($+20$ μatm) in 2014 (Supplement 4). To further assess the potential for temporal influence, we contrasted measured grazing rates with independent estimates of grazing and metabolic rates reported in the literature. For example, taxon-specific grazing rates matched previous *in situ* estimates in the literature and were strongly and linearly correlated with phylogenetic variation in metabolism (see Sections 3 and 4). Furthermore, algal consumption patterns corresponded with phylogeny, even for congeners assayed in different years (e.g. EC and ED). Thus, oceanographic conditions, algal prey, and grazing behaviors appeared stable among assays and studies.

2.3. Grazing calculations

Consumption (wet mass grazed, M_g) of each algal specimen was calculated as the additive inverse of its change in wet mass (Δ_M) and constrained to values between initial mass and zero:

$$\Delta_M = M_f - M_i \tag{1}$$

$$M_g = -\Delta_M, \; 0 \le M_g \le M_i \tag{2}$$

where M_i and M_f are the initial and final algal mass, respectively (in grams).

To account for autogenic loss of mass (e.g. due to breakage or senescence), control factors (CF) were calculated as for M_g using urchin-free 'control' enclosures (3 assay^{-1}), thus providing assay-specific corrections for each alga $CF_{t,a}$ that were used to provide corrected mass grazed values (M_{gC}) (Fig. S5c in Supplement 5):

$$CF_{t,a} = \left[\left(\sum_{c=1}^{n} M_{g,c} \right) / n \right]_{t,a}, 0 \le CF_{t,a} \tag{3}$$

$$M_{gC,t,u,a} = M_{g,t,u,a} - CF_{t,a}, 0 \le M_{gC,t,u,a} \le M_{gC,t,u,a} \quad (4)$$

where $t = t^{th}$ assay of the experiment (2 per urchin species = 10 total), $a = a^{th}$ algal taxon (of 6 algal taxa), $c = c^{th}$ control (3 assay^{-1}) in assay t, and $u = u^{th}$ urchin replicate of assay t (10 assay^{-1}).

Total grazing rate (TGR; in g d^{-1}) for each urchin was calculated as the sum of control-corrected mass grazed across all 6 algal taxa divided by the assay duration (in d):

$$TGR_{t,u} = \left(\sum_{a=1}^{6} M_{gC,t,u,a} \right) / d_t \quad (5)$$

TGRs could vary due to both variation in intrinsic consumption rates and variation in echinoid size; therefore, mass-specific grazing rate (MSGR; in mg g^{-1} d^{-1}) was also calculated as TGR divided by echinoid mass (M_e):

$$MSGR_{t,u} = TGR_{t,u} / M_{e,t,u} \quad (6)$$

The percentage grazed (P_g) of each algal specimen was calculated using the ratio of the corrected grazed mass (M_{gC}) and initial mass (M_{iC}, calculated as for M_{gC}):

$$P_{g,t,u,a} = 100 \times M_{gC,t,u,a} / M_{iC,t,u,a} \quad (7)$$

Relative consumption (RC) for each alga by each urchin was calculated as the ratio of the percentage consumed of alga a relative to the value for the most consumed alga (*max*), thus ranging from 0 (least consumed) to 1 (most consumed):

$$RC_{t,u,a} = P_{g,t,u,a} / P_{g,t,u,max}, 0 \le RC_{t,u,a} \le 1 \quad (8)$$

Variation in echinoid RC profiles was visualized as a heat map and used to infer taxonomic differences in algal preferences. The RC heat map could represent a variety of grazing behaviors: non-selective uniform, non-selective variable, highly selective, and all other intermediate degrees of selective consumption (Fig. S6 in Supplement 6).

2.4. Echinoid metabolism

Metabolic rates vary significantly among echinoid taxa and differences appear to correspond to variation in ecological function (Lewis 1968, Lewis et al. 2018). We therefore assessed metabolism–grazing relationships by contrasting taxonomic differences in feeding behaviors (observed in the present study) with variation in metabolic rates reported in the literature (Lewis et al. 2018). Specifically, we examined how well species' mean grazing rates (TGR and MSGR) could be predicted from their respective mean total and mass-specific routine metabolic rates (TMR in

mg O$_2$ h^{-1} and MSMR in mg O$_2$ g^{-1} h^{-1}, respectively). Total grazing and metabolic rates reflect per capita differences among species whereas mass-specific rates reflect physiological differences independent of variation in size. The relationship between dietary breadth (i.e. multivariate dispersion and echinoid metabolism) was also examined (see Section 2.6).

2.5. Energy equivalents of ingestion and metabolism

Algae vary greatly with respect to moisture and energy content, thus mass-based grazing rates may obscure relationships between energy ingestion and demand. In order to directly compare energy ingestion rates with routine metabolic demand, we converted both routine metabolic and algal ingestion rates into hourly energy equivalents (J h^{-1}). First, routine metabolic rates (mg O$_2$ h^{-1}) were converted to energy equivalents assuming 3.38 cal mg O$_2$$^{-1}$ (Elliott & Davison 1975) and 4.184 J cal^{-1}. Second, water content for each of the 6 algal taxa was empirically assessed by measuring the dry masses (dried for 48 h at 60°C) of frozen algal specimens collected from ungrazed control assays and contrasting these with respective prior measurements of their wet masses (n = 15 for each macroalga and n = 11 for CCA and TRF) (Fig. S7a, Table S2 in Supplement 7). Next, we conducted a literature search to collate estimates of dry algal energy content (kcal g^{-1} dry mass) of congeneric or closely related algal taxa from the literature (Fig. S7b, Table S3). Last, using moisture content, alga-specific estimates of energy content per gram dry mass were converted into equivalents per gram wet mass (Table S2) and these were used to convert alga-specific daily mass consumption rates (g d^{-1}) into alga-specific energy ingestion rates (J d^{-1}) assuming 4184 J kcal^{-1}. Daily energy ingestion rates for all algae consumed by each echinoid were then summed and divided by 24 h d^{-1} to provide a total hourly energy ingestion rate (J h^{-1}) for each individual.

2.6. Statistical analyses

Differences in total and mass-specific rates of grazing and oxygen consumption were compared among echinoid species with 1-way ANOVA. First, intraspecific heterogeneity among replicate rounds of grazing and metabolic assays was examined by ANOVA and found to be non-significant (Supplements 8 & 9), thus assays were pooled for each species (Under-

wood 1997). Relationships between mean grazing and metabolic rates, and energy ingestion versus demand were assessed by linear regression. Parametric assumptions were evaluated for each test using Q–Q plots, Levene's tests, and residual plots. Where appropriate, data were square-root transformed to meet model assumptions (see Table 1) (Underwood 1997). Differences in dietary preference profiles were visualized using non-metric multidimensional scaling (nMDS) ordination based on untransformed Bray-Curtis (BC) distances. Significance of observed differences in preference profiles was evaluated using permutation-based multivariate analysis of variance (PERMANOVA; species fixed, 999 permutations) and differences in multivariate dispersion (dietary breadth) evaluated using PERMDISP (Anderson 2001, Anderson & Walsh 2013). Parametric statistics were conducted using R Studio v.0.95.263 (RStudio) and non-parametric analyses and ordination conducted using PrimerE v.6.

3. RESULTS

3.1. Grazing assays

A total of 20 grazing assays were completed for each echinoid species except TG, where only 18 were completed (due to sample loss upon retrieval). Mean (±SE) test diameters were 4.0 ± 0.1 (EM) to 7.0 ± 0.1 (TG) cm and wet masses were 32.3 ± 2.7 (EM) to 149.7 ± 12.3 (TG) g total mass (Fig. S5a in Supplement 5). Mean proportional autogenic loss of algae in control assays ranged from 0 (CCA and TRF) to 0.25 (ACN) (Fig. S5c in Supplement 5). Grazing rates ranged from 0.26–4.93 g d^{-1} (TGR) and 3.20–46.70 mg g^{-1} d^{-1} (MSGR), with significant differences among species explaining 85 and 77% of the variation in TGR and MSGR, respectively (Table 1, Fig. 3a,b). TG and EC exhibited similar TGRs that were 10-fold greater than

EM and HM and 3-fold greater than ED (Fig. 3a). Similar patterns were observed for MSGRs, though TG exhibited significantly lower MSGRs than EC (Fig. 3b).

3.2. Metabolic assays

Routine metabolic rates for 9 individuals of each echinoid species were provided in Lewis et al. (2018). Test diameters ranged from 4.1 ± 1 (EM) to 7.0 ± 0.1 (TG) cm and masses from 32.1 ± 1.6 (EM) to 154.3 ± 8.3 (HM) g (Fig. S5b in Supplement 5). Routine metabolic rates ranged from 0.46–4.67 mg O_2 h^{-1} (TMR) and 0.006–0.034 mg O_2 g^{-1} h^{-1} (MSMR), with significant differences among species explaining 90.0 and 80.3% of the variation in TMR and MSMR, respectively (Table 1, Fig. 3c,d). Echinoid species differed significantly in both total and mass-specific metabolic rates, with EC and TG exhibiting approximately 3-, 4-, and 8-fold greater total metabolic rates than ED, HM, and ED, respectively. In contrast to total rates, ED exhibited a significantly higher mass-specific metabolic rate than TG, and EM was 2-fold greater than HM.

3.3. Grazing rate versus routine metabolism

Interspecific variation in mean total and mass-specific metabolic rates explained 97.9 and 81.3% of the interspecific variation in mean TGRs and MSGRs, respectively, confirming that echinoid grazing rates were strongly correlated with taxon-specific differences in metabolism (Fig. 3e,f). Conversion of algal ingestion rates (g wet mass d^{-1}) and oxygen consumption rates (mg O_2 h^{-1}) into energy equivalents (J h^{-1}) indicated that 97.1% of the interspecific variation in energy ingestion rates could be predicted from differences in routine metabolic demand (p < 0.001) (Fig. 4a). Energy ingestion was 3- to 8-fold greater than routine demand (Fig. 4b), similar to values reported in previous consumption–metabolism studies of echinoids (Siikavuopio et al. 2008, Carr & Bruno 2013), with relative energy ingestion rates greatest for the more metabolically active species (e.g. EC and TG).

3.4. RC and diet specificity

Mean percent consumption of algal taxa ranged from 0–80%, with echinoids exhibiting consistent patterns across replicate assays

Table 1. Results of 1-way ANOVA examining differences among urchin taxa in total and mass-specific grazing and metabolic rates. **Bold** indicates statistical significance (p < 0.05)

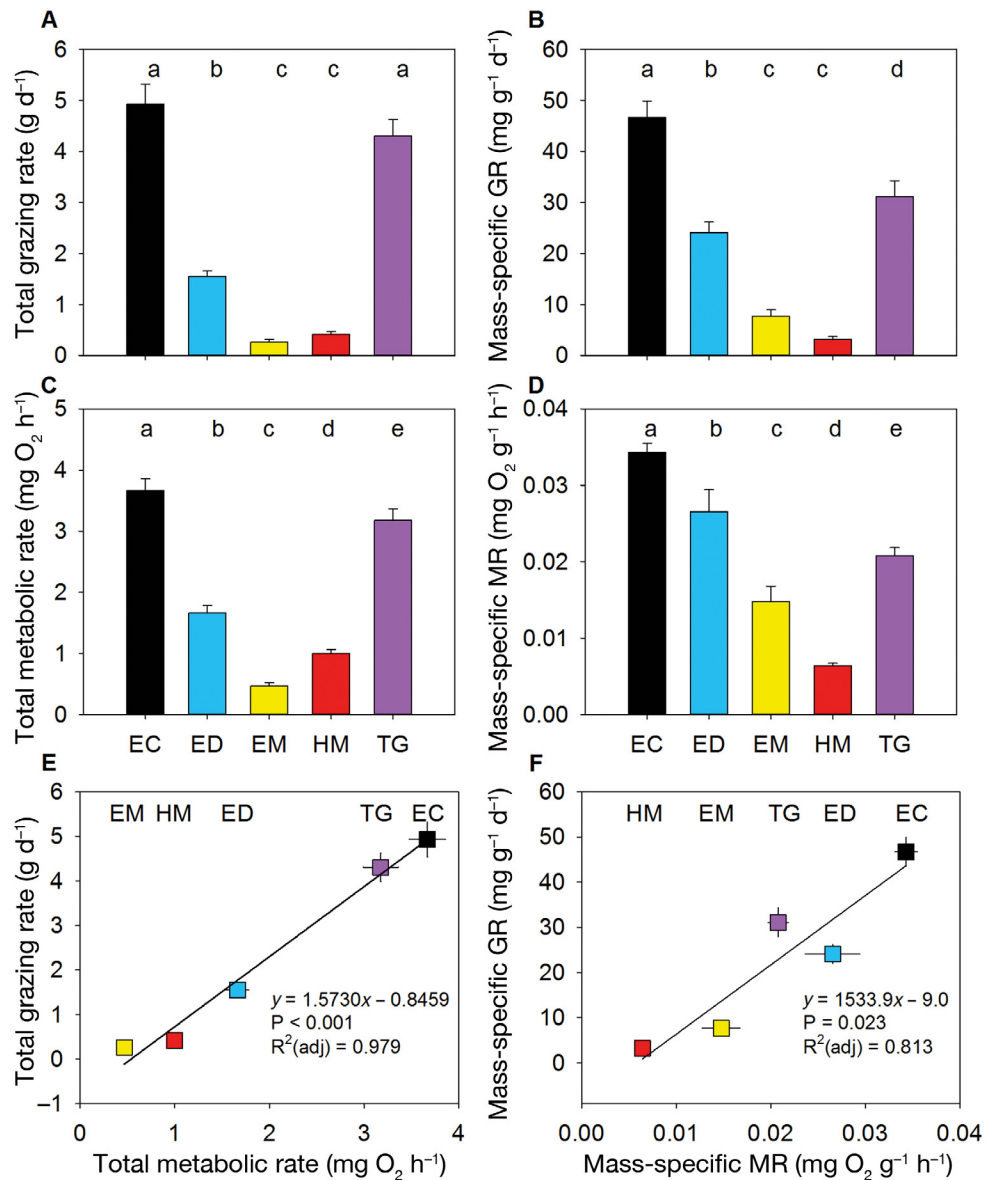| Type	Metric	MS	df	*F*	p	R^2 (adj)
Grazing rate	Total[a]	12.4	4,93	138.1	**<0.001**	0.850
	Mass-specific[a]	86.0	4,93	78.4	**<0.001**	0.771
Metabolic rate	Total	17.2	4,40	101.1	**<0.001**	0.900
	Mass-specific[a]	0.058	4,40	45.8	**<0.001**	0.803

[a]Data square-root transformed

Fig. 3. (A–B) Total and mass-specific grazing and (C–D) metabolic rates, and relationships between (E) total and (F) mass-specific grazing vs. metabolic rates. Values are means (±SE) of 20 and 9 replicate assays for grazing and metabolism, respectively. Metabolic rates from Lewis et al. (2018). Different letters indicate groups separated by Fishers LSD test (p < 0.05). Urchin codes as in Fig. 1

(Fig. 5a). Differences among echinoid species in algal consumption profiles (Fig. 5b) were highly significant (PERMANOVA, 999 permutations, $F_{4,93}$ = 7.01, p < 0.001; Table 2). TG was the only echinoid to exhibit high consumption of the brown leathery macrophyte TRB. Both diadematids (ED and EC) exhibited similar consumption profiles, consistently consuming the invasive, exotic red ACN and native green ULV over other algal taxa. Nearly all echinoids avoided the calcified CCA, except for HM which consumed slightly more CCA and TRF than any macroalga (Fig. 5a,b). Both echinometrids (HM and EM) exhibited low

mean RC values for all algae (Fig. 5b), indicative of high variability among individuals and limited algal selectivity. Ordinal comparisons (i.e. nMDS) of individual consumption profiles indicated interspecific differences in algal consumption profiles and multivariate dispersion (intraspecific variation) (Fig. 5c). Algal consumption profiles differed significantly among TG and the diadematid species (EC and ED), but not between the 2 diadematids (Table 2). Multivariate dispersion in algal consumption (Fig. 5c) was 200% greater for echinoids with lower (EM and HM) versus higher (EC, ED, and TG) metabolic rates
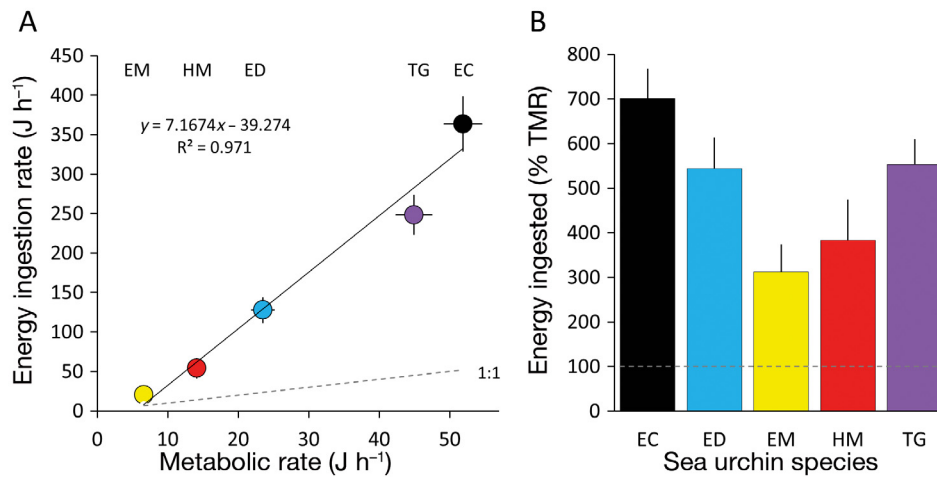
Fig. 4. Energy equivalents of total grazing and metabolic rates (TGR and TMR, respectively). (A) Hourly energy ingestion rate versus demand due to routine metabolism for each echinoid species. (B) Energy ingested relative to routine metabolic demand for each echinoid species. Dashed lines: ingestion = demand. Error bars: 1 SE

(PERMDISP, 999 permutations, $F_{4,93} = 39.4$, p < 0.001), indicating that intraspecific diet specificity was positively correlated with routine metabolic rate.

4. DISCUSSION

4.1. Functional diversity among herbivorous echinoids

Sea urchins exhibited significant taxon-specific differences in grazing rates and behaviors, with differences matching predictions based on phylogenetic variation in metabolism. Per capita algal consumption rates varied by greater than an order of magnitude and significant differences in MSGRs indicated intrinsic differences independent of size. Strong correlations between independently measured grazing and metabolic rates confirmed that differences in grazing rates were taxon-specific and physiologically driven, and energy ingestion rates were also strongly correlated with routine metabolic demand. Significant differences in algal consumption profiles indicated that echinoid taxa exhibit unique grazing preferences that may be complementary in nature. Species with higher metabolic rates grazed faster and focused on specific fleshy macroalgae, possibly indicating a trade-off between metabolic activity and diet specificity. In contrast, species with lower metabolic rates grazed slower and exhibited little or no discrimination among algal taxa. This phylogenetic variation in diet and metabolism is supported by previous observations and aligns with classic optimal foraging theories. Therefore, efforts to assess benthic dynamics on coral reefs can, and likely should, account for variation in the structure and function of herbivorous echinoid communities.

4.2. Variation in echinoid grazing rates

Grazing rates from our *in situ* assays (0.26–4.93 g wet mass ind.$^{-1}$ d^{-1}) were comparable to previous estimates of *in situ* consumption rates. Bronstein & Loya (2014) quantified *in situ* grazing rates of echinoids around Zanzibar, Tanzania, using gut fullness and evacuation rates. Total (dry) algal consumption rates of 0.13 and 3.87 g dry mass ind.$^{-1}$ d^{-1} were estimated for EM and ED, respectively. For comparison, if we conservatively assume that water makes up approximately 60 ± 5% of mixed algal wet mass (Hughes et al. 1987), estimated wet consumption rates were 0.33 and 9.68 g wet mass ind.$^{-1}$ d^{-1}, respectively; similar to the rates reported in our study, accounting for differences in ED size. *In situ* echinoid grazing rates were also similar in Kenya, where all 3 species of diadematids examined grazed at approximately 1–2 g dry mass ind.$^{-1}$ d^{-1} (or approximately 2.5–5.0 g wet mass) and EM grazed at 0.14 g dry mass ind.$^{-1}$ d^{-1} (or approximately 0.35 g wet mass) (Carreiro-Silva & McClanahan 2001); also comparable to our measurements. In Hawaii, field observations of gut fullness supported these modeled rates, with HM and EM often exhibiting empty stomachs, whereas EC and TG were always actively grazing (Ogden et al. 1989).

In contrast, laboratory-based assays for TG, EC, and ED have yielded grazing rates much higher than those measured *in situ*. For example, lab-based as-
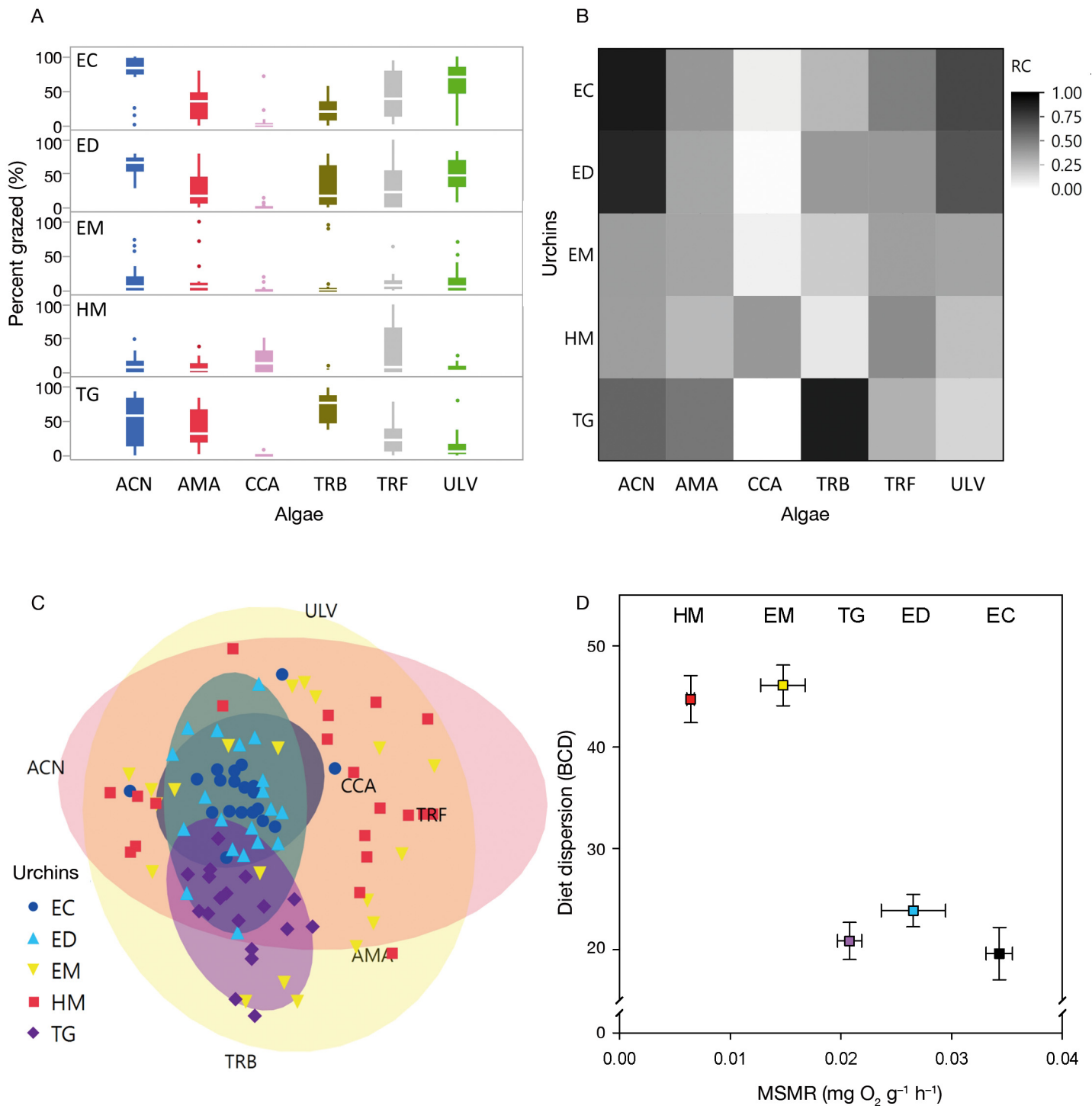
Fig. 5. Echinoid algal consumption profiles. (A) Percent consumption for each of 6 algal taxa based on 20 replicate assays per echinoid species. (B) Relative consumption (RC) heatmap with darker shading indicating consistently high consumption of the respective alga relative to other algae. RC profiles may indicate non-selective uniform grazing (all black cells), non-selective variable grazing (all grey cells), highly selective grazing (single black cell), and all other degrees of selective consumption (Supplement 7). (C) Non-metric multidimensional scaling biplot representing dissimilarity (distance) in RC profiles among echinoid species. Points: individual urchins; shaded areas: 90% confidence ellipses; algal annotations represent expanded Spearman correlations for each alga (stress = 0.22). (D) Diet dispersion, as the mean (± SE) Bray-Curtis distances from group centroids, versus mass-specific metabolic rate (MSMR). HM and EM exhibited significantly higher diet dispersion and lower MSMR than EC, ED, and TG. Echinoid and algae codes as in Fig. 1

Table 2. Results of global PERMANOVA and pairwise tests (based on 999 permutations each) examining differences in algal preference profiles among 5 echinoid species and corresponding pairwise comparisons. **Bold** indicates statistical significance ($p < 0.05$). Significant pair-wise comparisons for *Echinometra matthaei* (EM) and *Heterocentrotus mamillatus* (HM) (vs. other species) likely reflect significant differences in dispersion (variability) rather than a lack of overlap. EC: *Echinothrix calamaris*; ED: *Echinothrix diadema*; TG: *Tripneustes gratilla*

Source	df	SS	Pseudo-F	p(perm)
PERMANOVA				
Species	4	35497	7.0157	**0.001**
Residual	93	1.18×10^5		
Total	97	1.53×10^5		
Groups			t	p(perm)
Pairwise comparisons				
EC,ED			1.0	0.400
EC,EM			1.7	**0.043**
EC,HM			2.5	**0.001**
EC,TG			5.1	**0.001**
ED,EM			1.8	**0.013**
ED,HM			2.8	**0.001**
ED,TG			4.4	**0.001**
EM,HM			1.6	0.052
EM,TG			2.6	**0.001**

says of TG in Hawaii (Stimson et al. 2007) yielded TGRs (mean = 22.3 g wet mass ind.$^{-1}$ d^{-1}) that were 5-fold greater than field measurements (present study) using similar-sized (7–8 cm) individuals. Lab-based assays of EC and ED in Fiji (Coppard & Campbell 2007) also yielded grazing estimates (mean = 32 and 34 g wet mass ind.$^{-1}$ d^{-1}, respectively) that were approximately 5- to 10-fold greater than *in situ* assays (present study) and field observations (Carreiro-Silva & McClanahan 2001, Bronstein & Loya 2014). The lower estimated grazing rates from *in situ* assays and field observations and consistently higher rates from lab-based assays support the hypothesis that *in situ* approaches may better reflect echinoid feeding in the wild. However, standardized comparisons of field versus laboratory approaches (that control or account for variation in echinoid sizes, environmental conditions, and algal prey properties) are needed to rigorously assess this hypothesis.

4.3. Variation in echinoid grazing behaviors

Echinoid species exhibited significantly different consumption profiles (indicative of unique preferences) for 6 algal taxa representing the most common algal functional forms on Maui's coral reefs (e.g. turf algae, crustose coralline algae, and perennial and blooming red, brown or green macroalgae) (Steneck & Dethier 1994, Dailer et al. 2012b). Though often treated as generalists in their feeding behaviors, previous studies have indicated that tropical echinoids may exhibit preferences for, and avoidances of, certain types of algae (Ogden et al. 1989, Coppard & Campbell 2007, Stimson et al. 2007, Lawrence 2013). Though recent studies of community-wide echinoid grazing have incorporated taxon-specific estimates of TGRs (Bronstein & Loya 2014), many studies still treat echinoids as generalists and do not account for taxon-specific variation in grazing rates and behaviors. Studies that have explicitly examined variation in grazing behaviors among echinoids are often limited with respect to the diversity of grazer and algal species examined, such that the ecological relevance *in situ* is difficult to infer or extrapolate. Experimental examination of differences among common sympatric echinoid species in their preference and avoidance patterns for a variety of dominant algal functional groups, and the consequent implications for benthic community dynamics, remains an important topic for future scientific inquiry on coral reefs.

Here, TG was the only echinoid to consistently exhibit preferential consumption of the brown alga *Turbinaria ornata* (Fig. 5b) while collecting and 'wearing', but not consuming, *Ulva*. Like other brown algae in the order Fucales, *Turbinaria* is difficult to consume and often avoided by grazers due to thick and leathery thalli, chemical defenses, and complex fibers that require specialized guts or microflora for digestion (Eppley & Lasker 1959, Clements et al. 2009, Bittick et al. 2010). These features have likely contributed to the invasion of *Turbinaria* on coral reefs throughout French Polynesia since the 1980s (Andréfouët et al. 2004, Bittick et al. 2010). Although TG is a generalist, consuming many types of algae (Stimson et al. 2007, Lawrence & Agatsuma 2013), this species appears unique in its preference for *Turbinaria*. Previous studies have shown TG to consume a variety of brown algae including species of *Sargassum*, *Padina*, *Dictyota*, as well as *Turbinaria* (Lawrence & Agatsuma 2013). Though phenolic compounds in brown algae are generally thought to serve as chemical deterrents to grazers (Targett & Arnold 1998), TG appears to prefer foods with higher phenolic concentrations and without any negative effects on growth (Steinberg & van Altena 1992). TG's apparent preference for *Turbinaria* in our study suggests this species is uniquely adapted to utilizing this food source and may be an important comple-

ment to echinoid communities that otherwise would likely target more palatable types of algae.

In contrast with TG, both diadematids (EC and ED) primarily consumed the simpler, bloom-forming macroalgae *Acanthophora* and *Ulva* over all other algal forms, including *Turbinaria*. A preference for the invasive red *Acanthophora* would suggest that these species, like many other herbivores, could be important for resisting and limiting invasions of this alga on coral reefs (Vermeij et al. 2009). These grazing behaviors are supported by previous laboratory grazing assays in Fiji, where 5 different species of diadematid echinoids (including EC and ED) preferred simpler algal forms (e.g. *Codium*, *Padina*, *Hydroclathrus*, and filamentous algae), and avoided leathery, chemically defended browns in the order Fucales (e.g. *Sargassum* and *Turbinaria*) (Coppard & Campbell 2007). The consumption profiles and dietary breadth of these 2 congeners differed significantly from other species, but were indistinguishable from each other despite being assayed in different years, thus indicating consistent phylogenetically determined similarities in grazing behaviors.

The echinometrid EM is described as exhibiting a generalist diet corresponding to its low metabolic rate and stationary lifestyle (Webster 1975, McClanahan & Muthiga 2013). In our study, both echinometrids HM and EM exhibited such patterns, with low grazing and metabolic rates and widely dispersed and overlapping grazing profiles. These 2 species, however, appeared to differ slightly in grazing behaviors. Though HM consumed most fleshy algae, it appeared to avoid the brown alga *Turbinaria* and was the only echinoid to exhibit significant consumption of heavily-calcified CCA, which it consumed greater than or equal to any of the fleshy macroalgae. These results are supported by field observations that suggest HM consumes significant quantities of calcified algal crusts (Ogden et al. 1989). In contrast, EM consumed little CCA while targeting all other fleshy algae equally. Though EM is known to consume CCA and function as a bioeroder (O'Leary & McClanahan 2010, McClanahan & Muthiga 2013), it appeared to prefer fleshy algae when available. This pattern may reflect EM's ability (and preference) to feed on benthic and drift algae when abundant, but also its plasticity and capacity to switch between feeding behaviors (McClanahan & Muthiga 2013). We did not evaluate erosion in this study; however, HM's proclivity for TRF and CCA over macroalgae and the deep scars it left on the underlying carbonate suggest it may be a more effective eroder than EM.

In contrast, EM's higher relative consumption of fleshy algae in this study suggests bioerosion by this species may be influenced by the availability (or lack thereof) of preferred fleshy algae (attached or drifting).

4.4. Metabolic foundations for variation in herbivore traits

Consumers feed, in part, to satisfy their energy requirements, with metabolic rates driving much of the ecological variation in consumption rates and patterns among species (Hillebrand et al. 2009, Sibly et al. 2012). Metabolic rates of echinoids vary greatly among species, with more mobile, active species (e.g. EC and TG) exhibiting more than 7-fold greater total metabolic rates than stationary, rock-boring species (e.g. EM and HM) (Lewis et al. 2018) (Fig. 3). According to metabolic theory, species that are more active should consume larger quantities of high-quality food, whereas less active taxa could likely subsist on smaller quantities of lesser-quality foods (MacArthur & Pianka 1966, Pulliam 1974). Our results supported these predictions. We found that echinoid species with higher metabolic rates (i.e. EC, ED, and TG) consumed up to 10-fold more total algal biomass than those with lower metabolic rates (i.e. EM and HM), and routine metabolism explained 98% of the interspecific variation in consumption rates. Conversion of metabolic rates and ingestion rates into energy equivalents (J h^{-1}) indicated a strong, linear relationship ($R^2 = 0.97$) between energetic demand and ingestion (Fig. 4a).

In addition to bulk rates, intraspecific variation in feeding behaviors (e.g. diet specificity and algal preference) corresponded with variation in metabolism. More metabolically active echinoids (i.e. EC, ED, and TG) exhibited higher diet specificity and consistently selected fleshy macroalgae over turfs or calcified crusts, indicative of a preference for thicker, fleshier prey items. In contrast, EM and HM exhibited little consistent preference for specific algal types, with HM even consuming calcified crusts and filamentous turf algae at rates greater than or equal to fleshy macroalgae. Given that echinoid growth can be maximized by a diet of preferred algae (Stimson et al. 2007), the preference for fleshy macroalgae exhibited by echinoid species with faster metabolisms is in agreement with predictions based on classic metabolic and optimal foraging theories (MacArthur & Pianka 1966, Pulliam 1974).

4.5. Field-based assays in ecological studies of grazing behaviors

The use of unstarved individuals in field-based grazing assays has both strengths and weaknesses. Pre-conditioning and starvation are common in laboratory studies, as they limit variation among subjects in recent feeding history, thus reducing the amount of unexplained variance in experimental results. However, starvation is known to significantly modify consumption rates and algal selectivity (Cronin & Hay 1996, Siikavuopio et al. 2008) and pre-conditioning in the laboratory (e.g. due to laboratory feeds) is known to alter grazing preferences (Lyons & Scheibling 2007, Stimson et al. 2007). Field-based assays eliminate such unnatural pre-treatments on grazing subjects while also providing more natural environmental conditions and limiting transport and holding stress. By not imposing artificial prior treatments such as starvation or pre-conditioning, the rates and behaviors described herein likely reflect more ecologically relevant and comparable values to field conditions.

Given that we neither starved nor sacrificed our study organisms, however, differences in grazing could have been influenced by unmeasured natural variation in ecological state (e.g. recent feeding) among individuals, assays, or years. Yet interspecific variation was much greater than intraspecific variation, indicating limited effects of variation in individuals' recent feeding histories. To further strengthen confidence in the interpretation of results, field-based grazing rates can be contrasted with known variation in metabolic rates and with modeled *in situ* grazing rates based on field observations of gut fullness and evacuation rates. Here, we demonstrated strong agreement with independently measured phylogenetic differences in metabolism and modeled *in situ* grazing rates. Given these observations, phylogenetic variation appeared to be the best explanation for the observed taxon-specific differences in grazing behaviors.

4.6. Sources of variation in herbivore community structure and function

To maximize our ability to contrast grazing among species, assays were conducted in the same season, location, and in the absence of predation (due to enclosures). In the field, however, movement, reproduction, and grazing behaviors of echinoids may be influenced by several factors including season, location, size, food availability, and predation (Lewis & Storey 1984, Ogden et al. 1989, Stimson et al. 2007, O'Leary & McClanahan 2010). Thus, herbivore function might vary in space or time as a result of environmental conditions (Tuya et al. 2005, Boada et al. 2017). Furthermore, coexistence of multiple species of herbivorous echinoids in the Hawaiian Archipelago may lead to enhanced niche partitioning according to the 'diversity breeds complementarity' hypothesis (Tilman & Snell-Rood 2014). For example, echinoid niches on reefs with lower herbivore diversity may overlap more due to reduced competition.

Resource availability can influence *in situ* diet overlap for a variety of species. For example, crabs with limited mobility exhibit the broadest diets (Stachowicz & Hay 1999) and fishes consume less preferred prey more often when overall prey abundance is low (Werner & Hall 1974). In this study, all echinoids fed on several algae but also exhibited unique grazing preferences. On healthy coral reefs, where fleshy algae are scarce, it is likely that echinoids consume any food that is available and exhibit increased dietary overlap; on degraded reefs with abundant fleshy algae, echinoids likely only consume preferred algae and exhibit more unique diets. Resource-starved reefs may thus favor species with lower metabolic demands and broader diets (e.g. EM and HM), whereas more productive reefs may support species with higher metabolic demands and diet specificity (e.g. EC, ED, and TG) (McClanahan & Muthiga 2013). The abundance of EC, ED, and TG on Maui's productive (eutrophied) reefs (Smith et al. 2005, Dailer et al. 2010, 2012a) may support this hypothesis. Such hypotheses remain important topics for future ecological studies.

Functional diversity within trophic guilds can be an important driver of benthic dynamics on coral reefs. While the importance of functional redundancy and complementarity has been demonstrated for herbivorous coral reef fishes (Burkepile & Hay 2008, Rasher et al. 2013), such relationships among echinoid taxa remain uncertain, but are likely important (Ogden & Lobel 1978). Though feeding and movement patterns theoretically give these 2 herbivore guilds different ecological functions (Sandin & McNamara 2012), studies indicate certain fishes and echinoids may be functionally redundant competitors for algal resources (Hay & Taylor 1985) or partition resources spatially (Carpenter 1986). Some studies suggest that fishes remove more algae while causing less harm to coral recruits than echinoids (Korzen et al. 2011, O'Leary et al. 2013); however, others suggest that grazing by fishes can also harm coral recruits (Penin

et al. 2011). Functional comparisons with other herbivores such as sea turtles (Goatley et al. 2012) and highly diverse communities of meso- and micro-grazers (Klumpp et al. 1988, Stachowicz & Hay 1999, Glynn & Enochs 2011, Kramer et al. 2012) remain to be addressed. Well-designed studies that examine relative contributions and functional relationships among herbivores are needed for coral reefs; our results help to facilitate such comparisons.

5. CONCLUSIONS

Tropical echinoids exhibit phylogenetic variation in grazing rates and behaviors, and likely exert species-specific ecological effects on benthic coral reef communities. These unique ecological functions may be complementary, especially on degraded reefs where algae are most abundant. Similar variation in the ecological functions among herbivorous fishes results in positive relationships between diversity, grazing intensity, and coral growth (Burkepile & Hay 2008, Rasher et al. 2013). Such experiments are needed for herbivorous echinoids, which may be the most important grazers with respect to algal consumption and coral growth on many shallow coral reefs around the globe (Hughes 1994, Sandin & McNamara 2012). Given that TG and EC regularly coexist, are the most rapid grazers of fleshy macroalgae, and exhibit unique algal preference profiles, coral reef management and restoration efforts may benefit from protecting and enhancing populations of both species. In contrast, given the low grazing rates and high contributions to erosion by echinometrids (i.e. EM and HM), coral reefs might benefit from protection and enhancement of predators (e.g. balistid fishes) that limit echinometrid populations (Birkeland 1989, O'Leary et al. 2012). Intra-guild variation in the ecological functions of herbivores remains an understudied, but likely important, driver of benthic dynamics on coral reefs; exploration of such diversity can inform ecological models and enhance the management and conservation of coral reef ecosystems.

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