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Global patterns in seagrass herbivory: Why, despite existing evidence, there are solid arguments in favor of latitudinal gradients in seagrass herbivory

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23 assessment of the relative amounts of production that could enter the seagrass grazing food web
24 among latitudes and climatic regimes. Consistent with recent meta-analyses, we found little
25 latitudinal effect on grazing rates. However, we argue that the following factors are likely to
26 confound these findings and potentially mask latitudinal trends in seagrass herbivory: 1) the
27 paucity of data available to test latitudinal trends in grazing rates at high latitudes; 2) the
28 mismatch between the geographic distribution of important grazers and studies on seagrass
29 herbivory; 3) the paucity of experimental studies from areas with little or no herbivory because
30 few researchers would initiate a study on something not observed to be occurring; 4) the high
31 level of seasonality in seagrass production in high latitudes, where seagrass production is very
32 low or nonexistent in winter months; 5) the fact that temperate areas with Mediterranean climates
33 behave very differently than temperate areas at similar latitudes with much greater seasonality,
34 thereby making latitude a much less informative independent variable than annual range in
35 temperature; and 6) anthropogenic disturbances, including the overharvesting to functional
36 extinction of large seagrass herbivores in both temperate and tropical regions. Thus, while we
37 currently cannot discount the lack of a latitudinal gradient in grazing intensity, we argue that the
38 intensity of grazing is likely to be greater in the tropics than high latitude regions where the
39 carrying capacity of seagrass meadows is far less stable. Either way, there are clear gaps in our
40 knowledge and ability to evaluate the role of grazing in seagrass ecosystems and inform future
41 efforts to conserve and restore these extraordinarily valuable ecosystems.

42

43

44 **Introduction**

45 A long-standing principle of community ecology, that the intensity of biological interactions is
46 much greater in the tropics than in temperate or polar regions, has been supported by a variety of
47 observational and experimental studies of terrestrial and aquatic taxa as far back as the mid 20th
48 century (Dobzhansky 1950) and continued to be represented in textbooks throughout the second
49 half of the last century (MacArthur 1972; Vermeij 1987). The logic underpinning this principle is
50 that the relatively mild seasonal fluctuations in the tropics allow more populations to approach
51 carrying capacity and this in turn increases the intensity and importance of biological interactions
52 such as competition and predation (including parasitism) among the highly diverse tropical flora
53 and fauna. In contrast, the greatly fluctuating environments of temperate and polar areas have
54 been suggested to, on average, experience more density-independent mortality that would often
55 keep populations below their carrying capacities and less frequently be regulated by biological
56 interactions.

57 In shallow water marine communities, this conventional wisdom about the manner by which
58 ecosystems are thought to be organized has been supported by observational and experimental
59 studies that have found greater rates of predation and herbivory at low latitudes (Bertness et al.
60 1981; Heck & Thoman 1981; Longo et al. 2019; Pennings et al. 2001; Pennings et al. 2009).
61 Consistent with this hypothesis, a review by Floeter et al. (2005) demonstrated higher
62 abundances and species richness of fish herbivores at lower latitudes. Further support for the
63 intensity of biological interactions at low latitudes is provided by the dramatic changes occurring
64 where the poleward expansion of tropical herbivores into warming temperate waters has led to
65 the runaway consumption of highly productive kelp forests and their transition to simple turf or
66 barren substrates (Vergés et al. 2014 and references therein) through a process known as
67 tropicalisation (Wernberg et al. 2013). This phenomenon has been documented in the southern

68 Mediterranean Sea, and in Japan and Australia (Vergés et al. 2014), with widespread loss of
69 extremely productive kelp forests through either direct overgrazing by tropical fishes or heat
70 stress followed by intense grazing by tropical herbivores (Wernberg et al. 2016).

71 In contradiction, the results of the meta-analyses published by Moles et al. (2011), Poore et al.
72 (2012), Bakker et al. (2016), and Verges et al. (2018) provide scant evidence for latitudinal
73 gradients in the intensity of herbivory, including consumption rates of habitat-forming plants in
74 shallow coastal waters. These reviews have generally relied on meta-analyses across broad suites
75 of studies on algae and vascular plants and have included a variety of measures of the intensity
76 of herbivory. The contradictory evidence for the existence of latitudinal gradients in herbivory,
77 despite the known and predicted increase in herbivory in temperate regions undergoing
78 tropicalization (Verges et al. 2014; Hyndes et al. 2016), led us to re-evaluate the arguments
79 around the presence or absence of latitudinal gradients in herbivory in coastal systems, focusing
80 on seagrass herbivory. To achieve this, we initially: (1) determine whether or not there is
81 evidence of a latitudinal gradient in seagrass consumption, and the proportion of NPP consumed,
82 by including a suite of additional studies that contain both experimental and observational
83 evidence of seagrass herbivory not included in prior meta-analyses; (2) compare the latitudinal
84 range of seagrass occurrence with the latitudes in which seagrass herbivory has been studied, to
85 establish whether studies of seagrass herbivory are representative of the full latitudinal range of
86 seagrasses; (3) contrast the latitudinal range of herbivores known to strongly impact seagrass
87 biomass with the latitudes at which seagrass herbivory has been studied; (4) assess the relative
88 amounts of production that can potentially enter seagrass grazing food webs across latitude by
89 analyzing a subset of studies that have provided temporal measures of primary production and
90 standing stock of seagrasses. Using our findings, we discuss how confounding factors, including

91 gaps and biases in available data and the effects of human activities, can influence conclusions
92 about the presence or absence of latitudinal trends in seagrass herbivory.

93 **Methods**

94 We restricted our data collection to studies that provided estimates of grazing rates obtained by
95 direct approaches in the field, including: (1) exclusion and inclusion experiments, which
96 compared the relative effects of herbivory on caged versus uncaged seagrasses; and (2) either
97 direct measurements and tethering experiments where grazing rates, and where available,
98 seagrass productivity data were provided. We initially sourced papers from the supporting
99 material for the meta-analyses by Poore et al. (2012), Wood et al. (2016) and Verges et al. (2018)
100 and restricted papers to only those that provided data on grazing on seagrasses, rather than on
101 epiphytes and other macrophytes. We restricted our analyses to those studies from which we
102 could extract or calculate grazing rate data in the unit $\text{g DW}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and where possible, seagrass
103 net primary production (NPP) in the same unit.

104 The above process provided 10 of the 20 studies used in Poore et al. (2012) and an additional 7
105 studies from Wood et al. (2016) and Verges et al. (2018). An additional 14 studies were provided
106 through our extended search in ISI Web of Science database (up to 2018) using a systematic
107 search based on the criteria “herbivor* OR grazing rate* AND seagrass*”, including studies that
108 have determined grazing rates through direct measurements and tethering approaches. The
109 results of this search were supplemented by studies included in published reviews on marine
110 herbivory and by our own personal libraries. This resulted in a larger group of 31 studies meeting
111 our criteria (see Supporting Material S1 for details).

112 For studies using enclosure experiments, we focused on those studies that allowed and excluded
113 grazers into plots, as these were considered to better represent natural grazing rates. Inclosure
114 experiments were only considered when the densities of grazers were stocked at natural levels.
115 For these cage experiments, we then calculated the grazing rates based on differences between
116 grazed and ungrazed plots, and the percentage of NPP grazed was either extracted or calculated
117 from data provided. For tethering studies, the percentage of NPP grazed was calculated when
118 both grazing and NPP data were provided. If the grazing rate was greater than the productivity
119 rate, the percent grazed was set at 100%. Grazing rate and NPP were extracted from each paper
120 using WebPlotDigitizer. Latitude and longitude, and seagrass and herbivore species were also
121 extracted from each study. Estimates of grazing rates and percentage of NPP consumed by
122 grazers were plotted against latitude, and grazing rates were plotted against NPP.

123 We also carried out a search for papers that provided at least four monthly averages for daily
124 above-ground NPP in the unit $\text{g DW}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ using the leaf punch or hole method, and above-
125 ground biomass (g DW m^{-2}) for different seagrass species, to examine latitudinal trends in the
126 daily production and standing biomass (standing stock) across the year at different latitudes. Data
127 for each study needed to include four or more data points, with at least one point representing
128 each season, including winter. Each species used in the analysis needed to be represented by both
129 above-ground NPP and standing stock, although these did not have to be from the same study.

130 We initially sourced papers from Olesen et al. (2015) and Beca-Carretero et al. (2019). We then
131 extended our search in ISI Web of Science database (up to 2018) using the terms “product* AND
132 eelgrass* OR seagrass genus, e.g. “*Zostera*” OR “*Thalassia*”. This yielded 49 papers for species
133 of *Zostera*, *Cymodocea*, *Halophila*, *Posidonia*, and *Thalassia* that satisfied the above criteria
134 (Supplementary Table S2).

135 Mean daily NPP and standing stock data were extracted from each paper using
136 WebPlotDigitizer. Coefficients of Variation (CV) were determined across months for each
137 location. Minimum, maximum and CV for NPP and standing stock were plotted against latitude.
138 Minimum and maximum values represent winter and summer levels of NPP and standing stock,
139 respectively, while CV represents the temporal variability at each location.

140 Consumption rate ($\text{g DW m}^{-2} \cdot \text{d}^{-1}$) and the percentage of production consumed were each
141 contrasted with latitude (i.e., degrees from the equator) using linear mixed models with location
142 as a random factor to account for the non-independence of multiple measures from a single
143 location within each published study. Analyses were run with the R package *lme4* (Bates et al.
144 2015), with the statistical test of the fixed factor (latitude) derived from a likelihood ratio test.
145 The relationship between consumption and production was analyzed with quantile regression
146 using the R package *quantreg*, with statistical inference for the 0.1, 0.5 and 0.9 quantiles derived
147 from bootstrapping. The relationships between seagrass variables (minimum, maximum and CV
148 for NPP and standing stock) and latitude were examined with linear regressions using SPSS
149 Version 25.

150 In addition, we overlaid the locations of studies that have measured grazing rates in seagrass
151 meadows over a map of the distributional range of the entire assemblage of known seagrass
152 species (UNEP-WCMC, Short 2017). Also, we determined the latitudinal ranges of all seagrass
153 genera based on the distribution maps provided in Green and Short (2003), except for *Ruppia*,
154 whose latitudinal range was based on distribution maps provided in the Global Biodiversity
155 Information Facility (GBIF, www.gbif.org). In a separate literature search, we determined the
156 species known to graze on seagrass (see SOM Table S3), and used the distribution of the records

157 contained in FishBase (www.fishbase.se) for fish species and GBIF (www.gbif.org) for other
158 herbivorous species to construct plots of their latitudinal ranges.

159

160 **Results**

161 Seagrass is distributed across a large latitudinal range along all continents except Antarctica, and
162 extends from the tropics to approximately 70° in the northern hemisphere (Figure 1A). The
163 genera *Zostera* and *Ruppia* have the widest distribution across both hemispheres, extending from
164 the equator to about 70°N and 50°S (Figure 1B). In comparison, the majority of genera,
165 including *Halophila*, *Halodule* and *Thalassia*, are restricted to tropical to warm temperate
166 regions (latitudes <~40° in both Hemispheres). The studies for which grazing rates were
167 measured have generally been restricted to tropical, subtropical or warm temperate regions in the
168 Caribbean Sea, Australia, Korea or Europe at latitudes <45°N. Only two studies have measured
169 grazing rates at higher latitudes, and even these did not extend higher than 55°N (Figure 1A).
170 While grazing studies have been measured on most seagrass genera (except *Thalassodendron*
171 and *Phyllospadix*), the latitudinal range has been restricted for each genus (Figure 1B). Far more
172 grazing studies have been based on *Thalassia* than any other genus (16), followed by *Posidonia*
173 (5).

174 The most well-known consumers of seagrasses occur primarily in tropical to warm temperate
175 regions, extending from 0-10° to 30-40° (Figure 2). These include the dugong (*Dugong dugon*),
176 manatee (*Trichechus manatus*), green turtle (*Chelonia mydas*), sea urchins (*Tripneustes*
177 *ventricosus*, *Lytechinus variegatus* and *Diadema antillarum*), the sea bream (*Archosargus*
178 *rhomboidalis*) and the bucktooth parrotfish (*Sparisoma radians*). Similarly, the distribution of

179 the pinfish *Lagodon rhomboides* extends from 20° to 40°, while the sea urchin (*T. gratilla*) and
180 black rabbitfish (*Siganus fuscescens*) extended to 45°N. In comparison, only a few seagrass
181 grazers, including the purple sea urchin (*Paracentrotus lividus*) and the salema (*Sarpa salpa*) are
182 distributed solely in temperate regions from 30-35° to 45-65°. With the exception of the black
183 swan (*Cygnus atratus*), whose distribution extends across the entire latitudinal range of
184 Australia, waterfowl (e.g., the widgeon *Anas americana*, the redhead duck *Aythya americana*
185 and the brant *Branta bernicla*) are the only species that graze seagrass and occur at latitudes
186 >50°N (Figure 2). Among the seagrass-consuming fish and urchin species found in temperate
187 waters, the majority occur in Mediterranean climates, such as those along the eastern and western
188 coasts of Australia and in the Mediterranean itself, where annual fluctuations in water
189 temperature are much less than those at similar latitudes in temperate locations in, for example,
190 the Western Atlantic Ocean. The latitudinal range of many grazers, particularly birds and
191 invertebrates, extended poleward by 10-30° compared to the majority of grazing studies in both
192 Hemispheres (Figure 2).

193 There was no relationship between either consumption rate ($\chi^2 = 0.14$, $P = 0.71$) or percent of
194 production consumed ($\chi^2 = 0.17$, $P = 0.68$) with latitude. The geographical pattern of
195 consumption rates and the percent of production consumed show a great deal of variation, with
196 many high values occurring in the 5-15° latitudinal band and the 30-40° latitudinal band that
197 includes Mediterranean climates (Fig. 3A and B). There, rates of seagrass herbivory are much
198 greater than those at similar latitudes in more seasonal locations such as the Western North
199 Atlantic. Overall, even given the influence of Mediterranean climatic areas, the relationship
200 between seagrass production and consumption shows a significant positive slope (Fig. 3C;

201 p<0.001 for 10, 50 and 90 quantiles), indicating that seagrass consumption rates increase with
202 production.

203 Seasonality in standing stock of seagrass has been measured at only seven locations at latitudes
204 >50°, while net primary production (NPP) has been measured at one location (Figure 4, SOM
205 Table S2). When the maximum and minimum monthly NPP are plotted by latitude (Figure 4A
206 and B), it is clear that there is great variation across latitudes, although the relationships are not
207 always linear. There was a negative linear relationship between minimum NPP (P=0.021) and
208 latitude but not for maximum NPP (P=0.64). Maximum NPP was high and variable at mid
209 latitudes and low with small variability at ~60°. Similar to NPP, there was a negative linear
210 relationship between minimum standing stock (P=0.000) and latitude, but not maximum standing
211 stock (P>0.11). Minimum standing stock was generally <200 g DW m⁻² across all latitudes, but a
212 decrease in the variability at high latitudes. Maximum standing stock was generally <800 g DW
213 m⁻² with greater values and variability generally at mid latitudes. The coefficients of variation
214 (CV) for both NPP and standing stock showed a positive linear relationship with latitude (Fig.
215 4C and F; P<0.05). The CV in NPP and standing stock clearly show maxima around the 40-50°
216 range, with small values at tropical locations, indicating large differences in production rates and
217 standing stock between warm and cold months at higher latitudes, with the exception of studies
218 done in Mediterranean climates.

219 **Discussion**

220 Similar to previous meta-analyses on seagrasses (Verges et al. 2018), and plants more generally
221 (Poore et al. 2012, Wood et al. 2016), we found no latitudinal gradient in consumption rates on
222 seagrasses by herbivores, even after data from an additional 14 studies were included. These

223 results contrast with many older and recent comparisons of the intensity of biological
224 interactions in temperate and tropical locations (Bertness et al.1981; Heck and Thoman 1981;
225 Pennings et al. 2001; Pennings et al. 2009; Bennet and Bellwood 2011; Freestone et al. 2011;
226 Longo et al. 2018). But, how confident can we be that the results of these meta-analyses truly
227 reflect global patterns in grazing rates? In light of the recent arguments that grazing intensity is
228 not altered by latitude, based on meta-analyses, there is a need for debate over this emerging
229 paradigm on the role of grazing in seagrass ecosystems. Below, we discuss the factors that could
230 confound conclusions on the presence or absence of latitudinal gradients in the intensity of
231 grazing on seagrasses. We base these discussions on the following potentially confounding
232 effects: (1) a bias in the available data on seagrass herbivory that primarily comes from lower
233 latitudes and seasons when seagrass productivity is greatest; (2) seasonality in the carrying
234 capacity of seagrass meadows; (3) variation in the annual range of sea temperatures at similar
235 latitudes in temperate areas across the globe; (4) the greater diversity of herbivores in lower
236 latitudes; and (5) human activities such as harvesting and eutrophication that can alter the
237 grazing intensity on, or carrying capacity of, seagrass habitats.

238 **Bias in data sets on seagrass herbivory**

239 We do not dispute the finding that there is a lack of a latitudinal gradient in the intensity of
240 seagrass herbivory based on the available data in published meta-analyses (cf, Poore et al. 2012;
241 Wood et al. 2016; Verges et al. 2018), and, indeed, in our own analyses. However, the data sets
242 used for these analyses are incomplete, owing to the lack of data gathered from high latitudes. As
243 is well understood, meta-analysis is a powerful tool for synthesizing the results of multiple
244 independent studies. It is also true that meta-analyses only include data from subsets of
245 publications that meet pre-selected criteria and are homogeneous in the way outcomes are

246 measured. In addition, meta-analyses are usually restricted to studies that randomly allocate
247 treatments in experimental trials. This will result in the elimination of studies not meeting the
248 selection criteria and exclude observational studies and less common types of experiments. This
249 was the case in the Poore et al. (2012) meta-analysis, which only included 11 studies of seagrass
250 herbivory, all derived from herbivore exclusion experiments, once the selected criteria were
251 applied, and the meta-analysis by Verges et al. (2018), which included those studies analyzed by
252 Poore et al. (2012) plus 10 more. Even in our analysis, with the expansion of selection criteria to
253 include studies measuring seagrass grazing rates from direct measurements and tethers in concert
254 with net primary production measures, there was no clear, strong latitudinal effect of grazing
255 rates on seagrasses. However, we note that our data set was expanded by only an additional 10
256 studies.

257 We argue that the lack of evidence for a broad latitudinal effect on seagrass grazing is likely due,
258 in large part, to the fact that experimental studies of herbivory have not been done where there is
259 little or no observational evidence it is occurring. In other words, studies of herbivory are most
260 likely to take place when there is a high chance of finding a significant grazing effect. This
261 explains why there are few studies of seagrass herbivory in higher latitudes, where populations
262 of the only potential herbivores - ducks, geese and swans - have been hunted to functional
263 extinction in many locations (Bakker et al. 2016). In support of this argument, the latitudinal
264 distribution of studies on the seagrasses themselves, along with the latitudinal distribution of
265 studies of seagrass herbivory, shows several studies of seagrass standing stock and productivity
266 at latitudes as far as 55-61°N, whereas all but two studies on seagrass herbivory were at latitudes
267 <43° (only two studies located at 55°N, Figure 1). This suggests that herbivory is unlikely and
268 very limited at those higher latitudes; otherwise, grazing studies of eelgrass would have been

269 done at cold temperate or boreal locations on the coasts of Alaska, Canada, Sweden and Norway.
270 It would, therefore, be most informative if data on production and consumption rates were
271 gathered year round in locations with strong seasonality in water temperatures.

272

273 **Effects of Seasonality**

274 Most studies of seagrasses in cold temperate regions are carried out in the summer months
275 during the main part of the growing season, when biological activity including feeding would be
276 highest. Not surprisingly, few studies of seagrass productivity or herbivory have been done
277 during the colder months when there is little seagrass growth and/or feeding activity. Indeed, in
278 our search of the literature, only Portig et al. (1994) and Nacken and Reise (2000) measured
279 consumption rates in winter at latitudes $>42^{\circ}$ (see SOM Table S2). As a food resource for
280 herbivores, seagrass exhibits far greater seasonal variability at higher latitudes, as supported by
281 the increase in variability in both production rates and standing stock of seagrass with increasing
282 latitude in our analysis of seagrass NPP and standing stock (Figure 4). The lower minimum NPP
283 and standing stock (reflecting winter NPP and standing stock) in higher latitudes, shown in our
284 analysis, and reduced leaf formation (Olesen et al. 2015, Beca-Carretero et al. 2019), indicate a
285 far reduced food resource during winter months. Indeed, seagrasses at higher latitudes can be
286 covered in ice during the winter when no above-ground biomass is present (e.g., at 45.7°N in
287 Nova Scotia; Robertson & Mann 1984), which would severely limit or prohibit herbivory.
288 Alternatively, NPP and standing stock of seagrass meadows can be high in summer at these
289 latitudes and provide an abundant food resource to herbivores, but only during those warmer
290 months. It is therefore not possible to compare annual amounts of seagrass production consumed
291 by herbivores in areas where water temperature varies greatly from summer to winter, since few

292 data exist from the months of low growth or herbivory. Typically, published estimates of
293 herbivory for higher latitudes are from warmer months (SOM Table S1), which are likely to be
294 the highest values of the year and not representative of annual values. A similar point was made
295 by Cheng et al. (2019), who found little evidence for variation in predation risk with latitude, and
296 suggested that this may have been because data in temperate areas were only gathered during
297 warmer months when biological activity is greatest, and not during colder months when
298 biological activity is much less. Consistent with this, the meta-analysis of exclusion experiments
299 by Poore et al. (2012) found that temperature had little effect of herbivore impacts on marine
300 primary producers when experiments were run in the warmer months, with temperature only
301 affecting impacts in the cooler months.

302 Among the herbivorous fish and urchin species that actively consume seagrass in temperate
303 waters, the majority occur in locations with Mediterranean climates, such as those along the east
304 and west coasts of Australia (MacArthur & Hyndes 2007; Wressnig & Booth 2008; White et al.
305 2011) and in the Mediterranean Sea itself (Tomas et al. 2005; Verges et al. 2007; Prado et al.
306 2007; Marco-Mendez et al. 2015), where annual fluctuations in water temperature are much less
307 than those at similar latitudes in temperate locations. For example, in the Spanish region of the
308 Mediterranean Sea, the salema *Sarpa salpa* and the urchin *Paracentrotus lividus* are major
309 consumers of the seagrasses *Posidonia oceanica* and *Cymodocea nodosa* (Prado et al 2007,
310 Prado et al 2010 for *S. salpa*; Tomas et al. 2005, Pinna et al. 2009, Farina et al. 2009 for *P.*
311 *lividus*). In contrast, at similar latitudes in the North Atlantic, there is no study of seagrass
312 herbivory reported (cf. Figure 1). To understand why these differences exist, consider mean
313 monthly minimum temperatures in Boston (USA), located at 42.3°N, where temperatures range
314 from an average low of only 4.0°C in January to 20.0°C in August, for an annual difference of

315 16.0°C (weather-and-climate.com). In comparison, those in Barcelona (Spain), at 41.4°N, range
316 from 13.5°C in March to 24°C in August, for a winter-summer difference of 10.5°C (weather-
317 and-climate.com). These differences in minimum winter temperatures and between winter and
318 summer minima would explain the discrepancies in the numbers of studies on seagrass herbivory
319 between the two regions, and the likely dissimilarities in herbivory.

320 Over half the studies in our analyses of seagrass grazing rates were located in tropical and warm
321 temperate areas at latitudes <30°N and S, where NPP and standing stock of seagrasses are
322 generally less variable, thereby providing a more consistent food resource than seagrasses in cold
323 temperate and boreal regions. Temperature strongly influences leaf formation rates (Olesen et al.
324 2015; Beca-Carretero et al. 2019), and also influences minimum NPP and standing stock of
325 seagrass (this study). This indicates that the replacement rate of seagrass food resources, and
326 therefore the year-round carrying capacity for herbivores, will be greater in warmer regions. The
327 relatively constant availability of food resources may have provided the opportunity for the
328 evolution of a greater number of herbivorous species that feed on seagrass, such as dugongs and
329 parrotfishes, in these less variable regions (Figure 2) and is consistent with the conclusions by
330 Floeter et al. (2005) that species richness (and higher abundances) of fish herbivores occur at
331 lower latitudes. Based on this logic, seagrass meadows in low latitude, warm regions will
332 experience higher rates of seagrass consumption.

333

334 **The shifted baseline of seagrass-dominated ecosystems and its effects on studies of seagrass**
335 **herbivory**

336 Our results show that seagrass production can be high in the higher latitudes, which reflects
337 production in the warmer months of Europe and North America, where the primary seagrass
338 herbivores are waterfowl (Valentine & Duffy 2006). As is well-established, many species of
339 waterfowl, including seagrass-consuming ducks, geese and swans, were heavily hunted and their
340 populations dramatically reduced in the 1960s (Bakker et al. 2016). While conservation
341 programs have led to increasing waterfowl populations in the past several decades (Madsen
342 1998; Fox et al. 2010), numbers still remain well below pre-harvesting, historical levels.
343 Therefore, from the 1970s onwards, when most studies of seagrasses have taken place, but
344 focused mainly in temperate regions in Europe, North America and Australia (Waycott et al.
345 2009), the lack of waterfowl grazers is the main reason that grazing was not thought to be
346 consequential in the vast majority of temperate seagrass meadows, leading to the perception that
347 seagrass food webs were detrital based (Valentine & Duffy 2006). Thus, historically, these
348 grazers would have fed on seagrasses at considerable rates, but only in the warmer months when
349 seagrass was productive and the carrying capacity of seagrass meadows was high. With limited
350 data on the grazing rates of waterfowl (except Potig et al. 1994, Nacken & Reise 2000), we can
351 only speculate on the relative grazing intensity in those Boreal regions prior to harvesting and as
352 waterfowl abundances return to their pre-harvesting levels. However, with grazing intensity
353 reduced to warmer months and fewer grazing species relative to tropical regions (Figure 2),
354 annual grazing rates are likely to be lower in these high latitude regions compared to the tropics.
355 Similar to waterfowl in Boreal regions, mega-herbivores such as green turtles, dugongs and
356 manatees have been hunted to functional extinction in many tropical regions (Jackson 1997;
357 Jackson et al. 2001). Nevertheless, a variety of common fishes and sea urchins feed on
358 seagrasses in sub-tropical and tropical seagrass meadows (Figure 2) of Africa, the Indo-West

359 Pacific and Central America (see reviews by Heck & Valentine 2006; Valentine & Duffy 2006;
360 Eklof et al. 2008). Thus, even though mega-herbivores are missing from most tropical seagrass
361 meadows, herbivory by fishes and urchins remains common and significant (Valentine & Heck
362 1999). Today, it is widely understood that significant amounts of production in many tropical
363 and some temperate seagrass meadows enter the direct grazing pathway, but that much more
364 energy must have flowed through the direct grazing channel in the past when mega-herbivores
365 were abundant (Heck & Valentine 2006; Valentine & Duffy 2006). Thus, even though both
366 temperate and tropical mega-herbivores have been greatly overharvested, there are far more
367 herbivorous fish and urchin species in the tropics that are capable of consuming large amounts of
368 seagrass production compared to most temperate regions (Figure 2). Again, grazing intensity is
369 likely to increase substantially as the abundances of mega-herbivores return to pre-harvest levels.
370 For example, manatees and their relatives have inhabited seagrass meadows in the Western
371 Atlantic-Caribbean throughout the Cenozoic, and it is likely that the majority of seagrass
372 production was once consumed by these marine mammals (Domning 2001; Velez-Juarbe et al.
373 (2013). In addition, dugongs are known to feed in herds comprising 100s of animals and can
374 remove 30–67% of above- and below-ground biomass of seagrass (Marsh et al. 2011). However,
375 in contrast to meadows in boreal regions, above-ground biomass is available as a food resource
376 throughout the year. Thus, grazing intensity in the tropics is likely to be far more consistent
377 across the year, leading to higher annual grazing rates.

378

379 Other human activities are likely to have impacted seagrass-herbivore interactions, and possibly
380 global patterns in grazing intensity. To date, an unaccounted for factor influencing estimates of
381 herbivory in temperate seagrass meadows is a likely result of the massive removal of top

382 predators from the world's oceans. Overharvesting of large predatory fishes is a global
383 phenomenon that has produced many direct and indirect effects on marine ecosystems (Jackson
384 et al. 2001; Myers & Baum 2003; Estes et al. 2011). In temperate waters with relatively simple
385 food webs, it is common to have three trophic levels. In these regions, removal of large predatory
386 fish will lead to the increase in small fishes, including herbivorous species. For example, under
387 current conditions, salema (*Sarpa salpa*) feeds heavily on *Posidonia oceanica* in the
388 Mediterranean Sea (Tomas et al. 2005; Prado et al. 2007), but historical overfishing of its
389 predators may have elevated this grazer's influence on seagrass ecosystems in the region
390 (Colloca et al. 2013; Vasilikoupoulos et al. 2014). We also note that there are other
391 anthropogenic disturbances that can influence the production and consumption of seagrasses.
392 Seagrass meadows have been impacted by a range of human-induced disturbances such as
393 nutrient enrichment and other chemical pollution, as well as physical disturbance from boats and
394 fishing gear (Waycott et al. 2009). Also, global changes in sea temperature are leading to range
395 extensions of tropical herbivores into temperate seagrass systems (Hyndes et al. 2016).
396 Individually and cumulatively, these pressures have almost certainly influenced the presence,
397 densities, and species composition of seagrass meadows and their interactions with consumers.
398 Thus, these pressures are likely to have influenced our results, as well as those of others, and
399 contribute to variance in the existing data. For the most part, these factors are not presently able
400 to be properly taken into account.

401

402 **Conclusions**

403 Based on our analyses of existing published data on grazing rates, the meta-analyses of Verges et
404 al. (2018) and Poore et al. (2012), there is little support for the existence of latitudinal gradients
405 in grazing intensity on seagrasses. These studies all provide data that contradicts the conclusions
406 of many older and recent comparisons of the intensity of biological interactions in temperate vs
407 tropical locations (Bertness 1981; Heck & Thoman 1981; Pennings et al. 2001; Pennings et al.
408 2009; Bennet & Bellwood 2011; Freestone et al. 2011; Longo et al. 2018). However, we contend
409 that caution is advised in accepting this finding for the following reasons: 1) the paucity of data
410 available to test latitudinal trends in grazing rates at high latitudes; 2) the mismatch between the
411 geographic distribution of important grazers and studies on seagrass herbivory; 3) the paucity of
412 experimental studies from areas with little or no herbivory because few researchers would
413 initiate a study on something not observed to be occurring; 4) the high level of seasonality in
414 seagrass production in high latitudes, where seagrass production is very low or nonexistent in
415 winter months; 5) the fact that temperate areas with Mediterranean climates behave very
416 differently than temperate areas at similar latitudes with much greater seasonality, thereby
417 making latitude a much less informative independent variable than annual range in temperature;
418 and 6) anthropogenic disturbances, including the overharvesting to functional extinction of large
419 seagrass herbivores in both temperate and tropical regions. While we currently cannot discount
420 the lack of a latitudinal gradient in grazing intensity, we argue that the intensity of grazing is
421 likely to be greater in the tropics than high latitude regions where the carrying capacity of
422 seagrass meadows is far less stable. Indeed, a weak gradient in grazing rates has been
423 demonstrated in the only published study that has measured grazing rates in a field study over a
424 reasonable latitudinal range (12°) a Either way, there are clear gaps in our knowledge and ability

425 to evaluate global patterns in grazing rates in seagrass ecosystems and inform future efforts to
426 conserve and restore these extraordinarily valuable ecosystems.

427

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432

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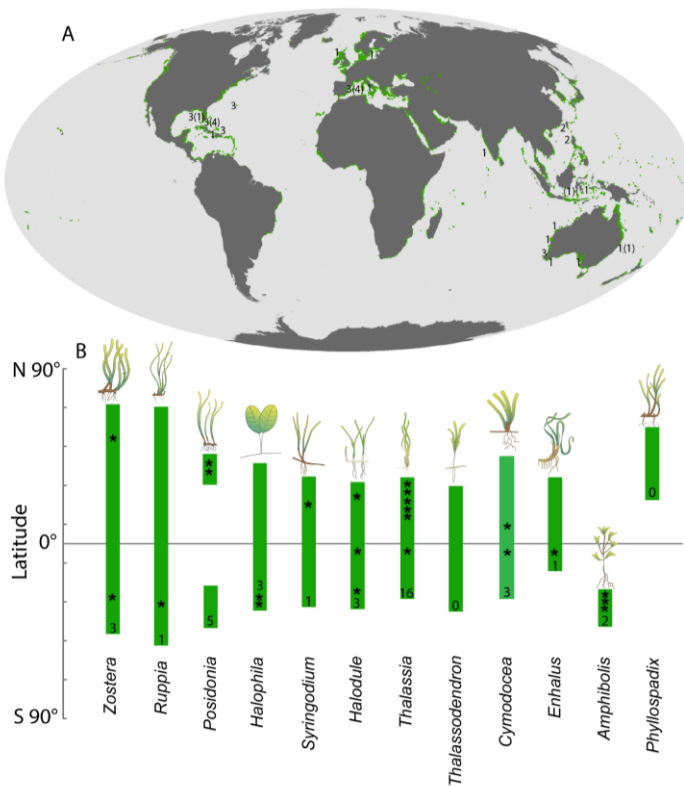
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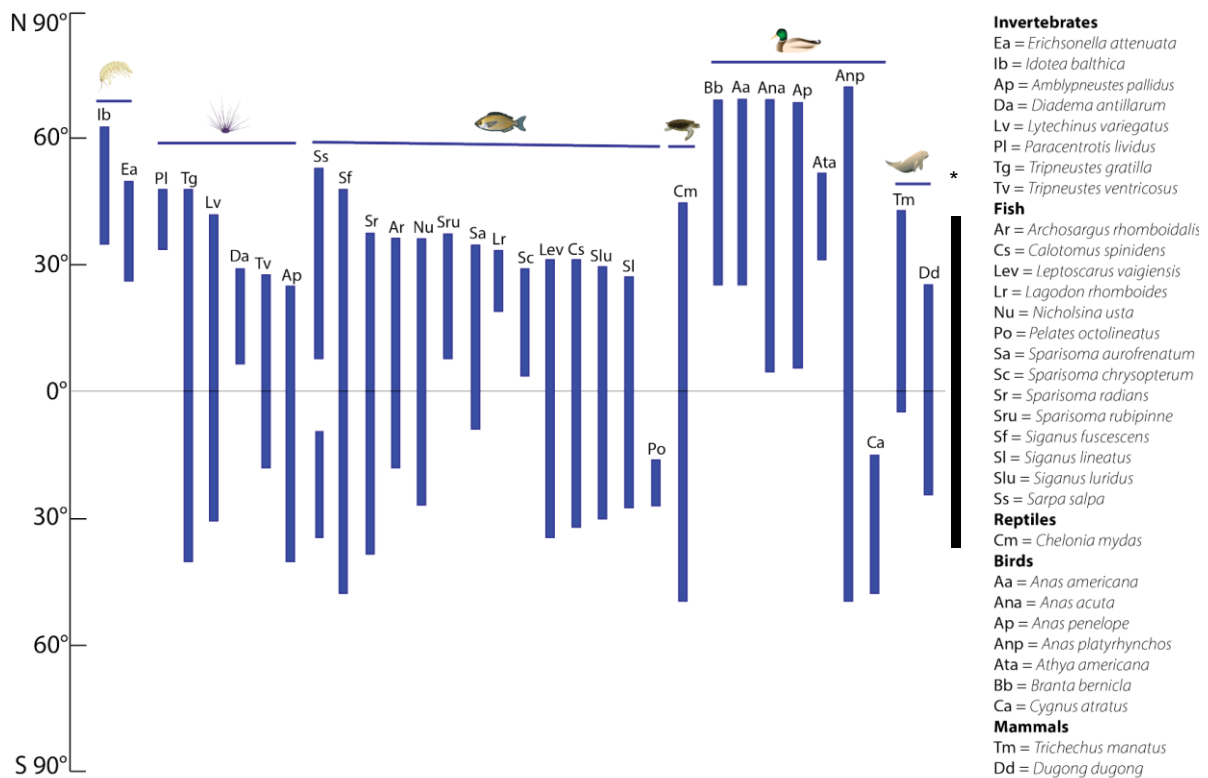
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577 **Figure 1** – (A) Global distribution of seagrass (green) based on UNEP-WCMC (Short 2017) with an overlay
 578 of the number of studies carried on grazing for which consumption and seagrass shoot production rates
 579 are available in $\text{g DW m}^{-2}.\text{d}^{-1}$. Numbers in parentheses indicate the number of additional studies that
 580 provide seagrass loss due to grazing that were not included in this study. (B) The latitudinal range of
 581 seagrass genera based on the distribution maps provided in Green and Short (2003). The distribution of
 582 *Ruppia* was based on distribution maps provided in the Global Biodiversity Information Facility
 583 (www.gbif.org). Asterisks indicate the location of grazing studies for each genus, while the number in
 584 each bar represents the number of studies (note: due to the overlap of locations, the number of
 585 asterisks do not represent the number of studies in each location). Seagrass images accessed through
 586 Integration and Application Network, University of Maryland Center for Environmental Science
 587 (ian.umces.edu/imagelibrary/).

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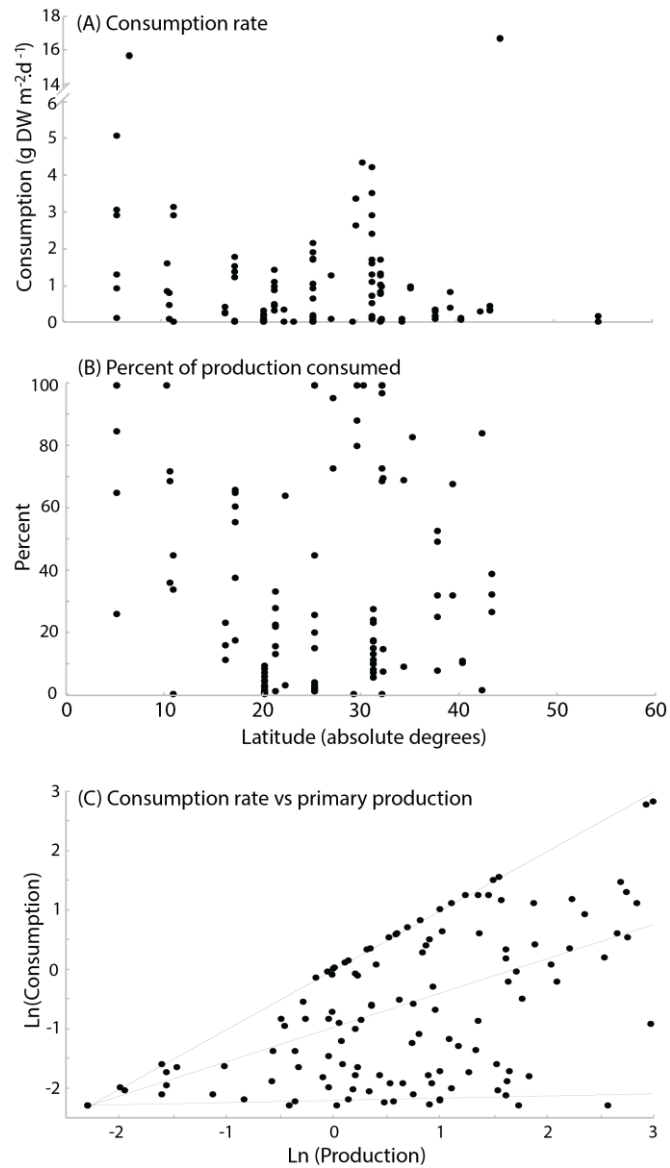
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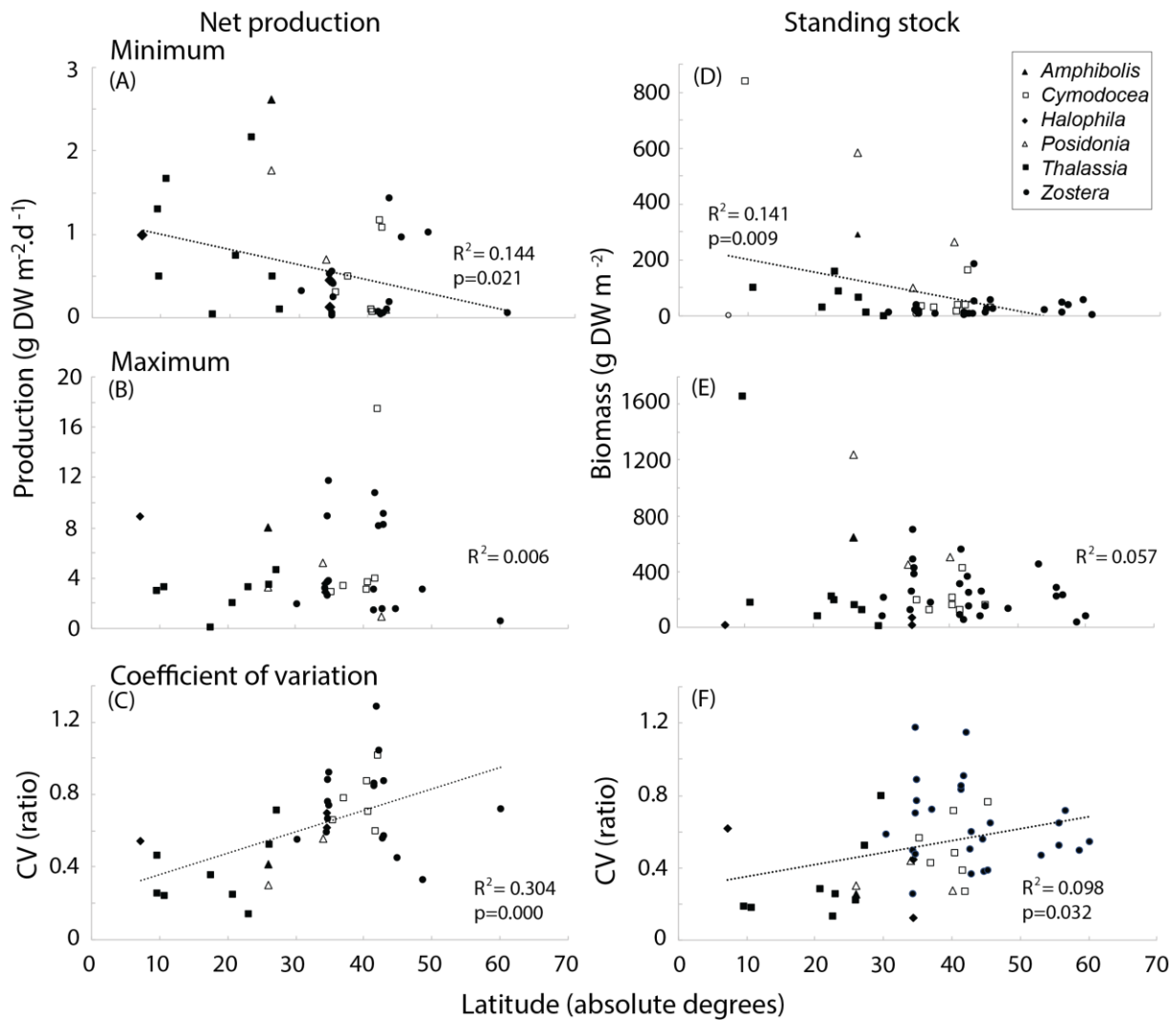
592 **Figure 2** – The latitudinal range of grazers that have been shown to consume large proportions of
 593 seagrass material are represented by blue bars. Distributions of invertebrates, reptiles, birds and
 594 mammals are based on Global Biodiversity Information Facility (GBIF.org 2018), while distributions of
 595 fish are based on FishBase (Froese & Pauly 2019). The latitudinal range of grazing studies is represented
 596 by the black bar, with an asterisk indicating the location of two outlier studies. Grazer images accessed
 597 through Integration and Application Network, University of Maryland Center for Environmental Science
 598 (ian.umces.edu/imagelibrary/).

599



600

601 **Figure 3** – Latitudinal trends in: (A) consumption rates (g DW m⁻².d⁻¹); (B) the percentage of seagrass
 602 production consumed across latitudes; and (C) the relationship between consumption rates and primary
 603 production rates (g DW m⁻².d⁻¹). Axes are ln(x+0.1). Estimate ± se for quantiles: 0.1 - 0.90 ± 0.11, P <
 604 0.001; 0.5 - 0.38 ± 0.09, P < 0.001; 0.9 - 0.33 ± 0.08, P < 0.001. Data based on the literature cited in SOM
 605 Table S1. Where the reported consumption rate exceeded the production rate, it was set equal to the
 606 production rate and the proportion of production consumed was set at 100%.



608

609 Figure 4 – Latitudinal trends in minimum and maximum primary production rates (A and B, respectively;
 610 g DW m⁻².d⁻¹) and biomass (D and E, respectively; g DW m⁻²) of seagrass, along with the coefficient of
 611 variation (CV) of mean monthly (C) production rates and (F) standing biomass of different seagrass
 612 genera. R² and p values are shown where linear regressions were significant (p<0.05). All data are based
 613 on the literature in SOM Table S2.

614