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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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Abstract

The ecological paradigm that biological interactions are more intense in the tropics than in temperate or polar regions has existed since the mid-20th century, but several recent meta-analyses have provided scant evidence for latitudinal gradients in the intensity of herbivory. This contradictory evidence led us to carefully review the data and results of several of those papers that failed to find latitudinal gradients in rates of seagrass herbivory. To re-evaluate the arguments around the presence or absence of latitudinal gradients in herbivory in seagrass, we began by expanding the selection criteria to include more studies to compare the published latitudinal range of seagrass occurrences with the latitudes in which seagrass herbivory has been studied. We also compared the latitudinal range of known seagrass herbivores with the distribution of studies on seagrass herbivory. Finally, we investigated a studies that provided seasonal data on net primary production and standing stock of seagrasses, which allowed an assessment of the relative amounts of production that could enter the seagrass grazing food web among latitudes and climatic regimes. Consistent with recent meta-analyses, we found little latitudinal effect on grazing rates. However, we argue that the following factors are likely to confound these findings and potentially mask latitudinal trends in seagrass herbivory: 1) the paucity of data available to test latitudinal trends in grazing rates at high latitudes; 2) the mismatch between the geographic distribution of important grazers and studies on seagrass herbivory; 3) the paucity of experimental studies from areas with little or no herbivory because few researchers would initiate a study on something not observed to be occurring; 4) the high level of seasonality in seagrass production in high latitudes, where seagrass production is very low or nonexistent in winter months; 5) the fact that temperate areas with Mediterranean climates behave very differently than temperate areas at similar latitudes with much greater seasonality, thereby making latitude a much less informative independent variable than annual range in temperature; and 6) anthropogenic disturbances, including the overharvesting to functional extinction of large seagrass herbivores in both temperate and tropical regions. Thus, while we currently cannot discount the lack of a latitudinal gradient in grazing intensity, we argue that the intensity of grazing is likely to be greater in the tropics than high latitude regions where the carrying capacity of seagrass meadows is far less stable. Either way, there are clear gaps in our knowledge and ability to evaluate the role of grazing in seagrass ecosystems and inform future efforts to conserve and restore these extraordinarily valuable ecosystems.

Introduction

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

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

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

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

Methods

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

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

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

We also carried out a search for papers that provided at least four monthly averages for daily above-ground NPP in the unit g DW.m^{-2}.d^{-1} using the leaf punch or hole method, and above-ground biomass (g DW m^{-2}) for different seagrass species, to examine latitudinal trends in the daily production and standing biomass (standing stock) across the year at different latitudes. Data for each study needed to include four or more data points, with at least one point representing each season, including winter. Each species used in the analysis needed to be represented by both above-ground NPP and standing stock, although these did not have to be from the same study. We initially sourced papers from Olesen et al. (2015) and Beca-Carretero et al. (2019). We then extended our search in ISI Web of Science database (up to 2018) using the terms “product* AND eelgrass* OR seagrass genus, e.g. “*Zostera”* OR “*Thalassia*”. This yielded 49 papers for species of *Zostera, Cymodocea, Halophila, Posidonia, and Thalassia* that satisfied the above criteria (Supplementary Table S2).

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

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

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

Results

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

The most well-known consumers of seagrasses occur primarily in tropical to warm temperate regions, extending from 0-10° to 30-40° (Figure 2). These include the dugong (*Dugong dugon),* manatee (*Trichechus manatus)*, green turtle *(Chelonia mydas)*, sea urchins *(Tripneustes ventricosus*, *Lytechinus variegatus* and *Diadema antillarum*), the sea bream (*Archosargus rhomboidalis)* and the bucktooth parrotfish *(Sparisoma radians*). Similarly, the distribution of the pinfish *Lagodon rhomboides* extends from 20° to 40°, while the sea urchin (*T. gratilla*) and black rabbitfish *(Siganus fuscescens)* extended to 45°N. In comparison, only a few seagrass grazers, including the purple sea urchin (*Paracentrotus lividus)* and the salema (*Sarpa salpa*) are distributed solely in temperate regions from 30-35° to 45-65°. With the exception of the black swan (*Cygnus atratus)*, whose distribution extends across the entire latitudinal range of Australia, waterfowl (e.g., the widgeon *Anas americana*, the redhead duck *Aythya americana* and the brant *Branta bernicla*) are the only species that graze seagrass and occur at latitudes >50°N (Figure 2). Among the seagrass-consuming fish and urchin species found in temperate waters, the majority occur in Mediterranean climates, such as those along the eastern and western coasts of Australia and in the Mediterranean itself, where annual fluctuations in water temperature are much less than those at similar latitudes in temperate locations in, for example, the Western Atlantic Ocean. The latitudinal range of many grazers, particularly birds and invertebrates, extended poleward by 10-30° compared to the majority of grazing studies in both Hemispheres (Figure 2).

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

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

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

Discussion

Similar to previous meta-analyses on seagrasses (Verges et al. 2018), and plants more generally (Poore et al. 2012, Wood et al. 2016), we found no latitudinal gradient in consumption rates on seagrasses by herbivores, even after data from an additional 14 studies were included. These results contrast with many older and recent comparisons of the intensity of biological interactions in temperate and tropical locations (Bertness et al.1981; Heck and Thoman 1981; Pennings et al. 2001; Pennings et al. 2009; Bennet and Bellwood 2011; Freestone et al. 2011; Longo et al. 2018). But, how confident can we be that the results of these meta-analyses truly reflect global patterns in grazing rates? In light of the recent arguments that grazing intensity is not altered by latitude, based on meta-analyses, there is a need for debate over this emerging paradigm on the role of grazing in seagrass ecosystems. Below, we discuss the factors that could confound conclusions on the presence or absence of latitudinal gradients in the intensity of grazing on seagrasses. We base these discussions on the following potentially confounding effects: (1) a bias in the available data on seagrass herbivory that primarily comes from lower latitudes and seasons when seagrass productivity is greatest; (2) seasonality in the carrying capacity of seagrass meadows; (3) variation in the annual range of sea temperatures at similar latitudes in temperate areas across the globe; (4) the greater diversity of herbivores in lower latitudes; and (5) human activities such as harvesting and eutrophication that can alter the grazing intensity on, or carrying capacity of, seagrass habitats.

Bias in data sets on seagrass herbivory

We do not dispute the finding that there is a lack of a latitudinal gradient in the intensity of seagrass herbivory based on the available data in published meta-analyses (cf, Poore et al. 2012; Wood et al. 2016; Verges et al. 2018), and, indeed, in our own analyses. However, the data sets used for these analyses are incomplete, owing to the lack of data gathered from high latitudes. As is well understood, meta-analysis is a powerful tool for synthesizing the results of multiple independent studies. It is also true that meta-analyses only include data from subsets of publications that meet pre-selected criteria and are homogeneous in the way outcomes are measured. In addition, meta-analyses are usually restricted to studies that randomly allocate treatments in experimental trials. This will result in the elimination of studies not meeting the selection criteria and exclude observational studies and less common types of experiments. This was the case in the Poore et al. (2012) meta-analysis, which only included 11 studies of seagrass herbivory, all derived from herbivore exclusion experiments, once the selected criteria were applied, and the meta-analysis by Verges et al. (2018), which included those studies analyzed by Poore et al. (2012) plus 10 more. Even in our analysis, with the expansion of selection criteria to include studies measuring seagrass grazing rates from direct measurements and tethers in concert with net primary production measures, there was no clear, strong latitudinal effect of grazing rates on seagrasses. However, we note that our data set was expanded by only an additional 10 studies.

We argue that the lack of evidence for a broad latitudinal effect on seagrass grazing is likely due, in large part, to the fact that experimental studies of herbivory have not been done where there is little or no observational evidence it is occurring. In other words, studies of herbivory are most likely to take place when there is a high chance of finding a significant grazing effect. This explains why there are few studies of seagrass herbivory in higher latitudes, where populations of the only potential herbivores - ducks, geese and swans - have been hunted to functional extinction in many locations (Bakker et al. 2016). In support of this argument, the latitudinal distribution of studies on the seagrasses themselves, along with the latitudinal distribution of studies of seagrass herbivory, shows several studies of seagrass standing stock and productivity at latitudes as far as 55-61°N, whereas all but two studies on seagrass herbivory were at latitudes <43° (only two studies located at 55°N, Figure 1). This suggests that herbivory is unlikely and very limited at those higher latitudes; otherwise, grazing studies of eelgrass would have been done at cold temperate or boreal locations on the coasts of Alaska, Canada, Sweden and Norway. It would, therefore, be most informative if data on production and consumption rates were gathered year round in locations with strong seasonality in water temperatures.

Effects of Seasonality

Most studies of seagrasses in cold temperate regions are carried out in the summer months during the main part of the growing season, when biological activity including feeding would be highest. Not surprisingly, few studies of seagrass productivity or herbivory have been done during the colder months when there is little seagrass growth and/or feeding activity. Indeed, in our search of the literature, only Portig et al. (1994) and Nacken and Reise (2000) measured consumption rates in winter at latitudes >42° (see SOM Table S2). As a food resource for herbivores, seagrass exhibits far greater seasonal variability at higher latitudes, as supported by the increase in variability in both production rates and standing stock of seagrass with increasing latitude in our analysis of seagrass NPP and standing stock (Figure 4). The lower minimum NPP and standing stock (reflecting winter NPP and standing stock) in higher latitudes, shown in our analysis, and reduced leaf formation (Olesen et al. 2015, Beca-Carretero et al. 2019), indicate a far reduced food resource during winter months. Indeed, seagrasses at higher latitudes can be covered in ice during the winter when no above-ground biomass is present (e.g., at 45.7°N in Nova Scotia; Robertson & Mann 1984), which would severely limit or prohibit herbivory. Alternatively, NPP and standing stock of seagrass meadows can be high in summer at these latitudes and provide an abundant food resource to herbivores, but only during those warmer months. It is therefore not possible to compare annual amounts of seagrass production consumed by herbivores in areas where water temperature varies greatly from summer to winter, since few data exist from the months of low growth or herbivory. Typically, published estimates of herbivory for higher latitudes are from warmer months (SOM Table S1), which are likely to be the highest values of the year and not representative of annual values. A similar point was made by Cheng et al. (2019), who found little evidence for variation in predation risk with latitude, and suggested that this may have been because data in temperate areas were only gathered during warmer months when biological activity is greatest, and not during colder months when biological activity is much less. Consistent with this, the meta-analysis of exclusion experiments by Poore et al. (2012) found that temperature had little effect of herbivore impacts on marine primary producers when experiments were run in the warmer months, with temperature only affecting impacts in the cooler months.

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

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

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

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

Our results show that seagrass production can be high in the higher latitudes, which reflects production in the warmer months of Europe and North America, where the primary seagrass herbivores are waterfowl (Valentine & Duffy 2006). As is well-established, many species of waterfowl, including seagrass-consuming ducks, geese and swans, were heavily hunted and their populations dramatically reduced in the 1960s (Bakker et al. 2016). While conservation programs have led to increasing waterfowl populations in the past several decades (Madsen 1998; Fox et al. 2010), numbers still remain well below pre-harvesting, historical levels. Therefore, from the 1970s onwards, when most studies of seagrasses have taken place, but focused mainly in temperate regions in Europe, North America and Australia (Waycott et al. 2009), the lack of waterfowl grazers is the main reason that grazing was not thought to be consequential in the vast majority of temperate seagrass meadows, leading to the perception that seagrass food webs were detrital based (Valentine & Duffy 2006). Thus, historically, these grazers would have fed on seagrasses at considerable rates, but only in the warmer months when seagrass was productive and the carrying capacity of seagrass meadows was high. With limited data on the grazing rates of waterfowl (except Potig et al. 1994, Nacken & Reise 2000), we can only speculate on the relative grazing intensity in those Boreal regions prior to harvesting and as waterfowl abundances return to their pre-harvesting levels. However, with grazing intensity reduced to warmer months and fewer grazing species relative to tropical regions (Figure 2), annual grazing rates are likely to be lower in these high latitude regions compared to the tropics.

Similar to waterfowl in Boreal regions, mega-herbivores such as green turtles, dugongs and manatees have been hunted to functional extinction in many tropical regions (Jackson 1997; Jackson et al. 2001). Nevertheless, a variety of common fishes and sea urchins feed on seagrasses in sub-tropical and tropical seagrass meadows (Figure 2) of Africa, the Indo-West

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

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

Conclusions

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

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Literature Cited

Bakker, E.S., Wood, K.A., Pages, J.F., Veen, G.F. Christianen, M.J.A., Santamarina, L., Nolet, B.A., & Hilt, S. (2016). Herbivory on freshwater and marine macrophytes: a review and perspective. *Aquatic Botany 135*: 18-36.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software 67(1)*: 1-48.

Baum, J.O., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., & Doherty, P.A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science 299*: 389-391.

Beca-Carretero, P., Stanschewski, C.S., Julia-Miralles, M., Sanchez-Gallego, A., & Stengel, D.B. (2019). Temporal and depth-associated changes in the structure, morphometry and production of near-pristine *Zostera marina* meadows in western Ireland. *Aquatic Botany 155*: 5-17.

Bennett, S., & Bellwood, D.R. (2011). Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series 426*: 241-252.

Bertness, M.W., Gaines, S.D., & Levings, S.C. (1981). Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution 35*: 995-1007.

Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., et al. (2013). Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability in single species population models. *Fish Fish 14*, 89–109.

Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci. 38*: 209-221.

Domning, D. P.(2001). Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. Paleogeography, Paleoclimatology and Paleoecology 166:27-50.

Eklof, J.S., de la Torre-Castro, M., Gullstrom, M.,Uke, J., Muthiga, N., Lyimos, T., & Bandeira, O. (2008). Sea urchin overgrazing of seagrasses: A review of current knowledge on causes, consequences, and management. *Estuarine Coastal and Shelf Science 79*: 569-580.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., et al. (2011). Trophic downgrading of planet earth. *Science 333*: 301-306.

Farina, S., Tomas, F., Prado, P., Romero, J., & Alcoverro, T. (2009). Seagrass meadow structure alters interactions between the sea urchin *Paracentrotus lividus* and its predators. *Marine Ecology Progress Series 377*: 131–137.

Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddack, M.J., & Horn, M.H. (2005). Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology 147*: 1435-1447.

Fox, A.D., Ebbinge, B.S., Mitchell, C., Heinicke, T., Aarvark, T., Colhoun, K., Clausen,P., Dereliev, S., Farago, S., Koffijberg, K., Kruckenberg, H., Loonen, M.J.J.E., Madsen, J., Mooij, J., Musil, P., Nilsson, L., Pihl, S., & van der Jeugd, H. (2010). Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. *OrnisSvec 20*: 115–127.

Freestone, A.L., Osman, R.W., Ruiz, G., & Torchin, M.E. (2011). Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology 92*: 983-993.

Green, E.P., & Short, F.T. (2003). World atlas of seagrasses. University of California Press, Berkeley, AA, USA. 298 pp.

Heck, K.L.Jr., & Thoman, T.A. (1981). Experiments on predator prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol. 53*: 124-134.

Hyndes, G.A., Heck, K.L., Verges, A., Harvey, E.S., Kendrick, G.A., Lavery, P.S., et al. (2016). Accelerating tropicalization and the transformation of temperate seagrass meadows. *Bioscience 66*: 938-948.

Jackson, J. (1997). Reefs since Columbus. *Coral Reefs* 16, Supplement: S23-S32.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science 293*: 629-637.

Longo, G.O., Hay, M.E., Ferreirra, C.E.L., & Floeter, S.R. (2019). Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Global Ecology and Biogeography 2018*: 1-11.

MacArthur, R.H. (1972). Geographical ecology. Harper and Row, NY.

MacArthur, L.D., & Hyndes, G.A. (2007). Varying foraging strategies of Labridae in seagrass habitats: herbivory in temperate seagrass meadows? *Journal of Experimental Marine Biology and Ecology 340*: 247-258

Madsen, L. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. *Journal of Applied Ecology* 35: 386-397.

Marco-Méndez, C., Ferrero-Vicente, L.M., Prado, P., Heck, K.L., Cebrián, J., & Sánchez-Lizaso, J.L. (2015). Epiphyte presence and seagrass species identity influence rates of herbivory in Mediterranean seagrass meadows. *Estuarine, Coastal and Shelf Science 154*: 94–101.

Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R., & Foley, W.J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology 25*: 380-388.

Olesen, B., Krause-Jensen, D. Marba, N. & Christensen, P.B. (2015). Eelgrass *Zostera marina* in subarctic Greenland: dense meadows with slow biomass turnover in cold waters. *Marine Ecology Progress Series 518*: 107-121.

Pennings, S.C, Siska, E.L., & Bertness, M.D. (2001). Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology 82*: 1344-1359

Pennings, S.C., Ho, C.K., Salgado, C.S., Wieski, K., Dave, N., Kunza, A.E., & Wason, E.L. (2009). Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology 90*: 183-195.

Pinna, S., Pais, A., Chessa, L., Sechi, N., & Ceccherelli, G. (2009). Leaf partitioning of the seagrass *Posidonia oceanica* between two herbivores: is *Sarpa salpa* herbivory underestimated because of *Paracentrotus lividus* grazing? *Estuarine, Coastal and Shelf Science 84*: 21–27.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.A., et al. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters 15*: 912-922.

Portig, A.A., Mathers, R.G., Montgomery, W.I., & Govier, R.N. (1994). The distribution and utilisation of *Zostera* species in Strangford Lough, Northern Ireland. *Aquatic Botany 47*: 317–328.

Prado, P., Tomas, F., Alcoverro, T., & Romero, J. (2007). Extensive direct measurements of *Posidonia oceania* defoliation confirm the importance of herbivory in temperate seagrass meadows. *Marine Ecology Progress Series 340*: 63-71.

Prado, P., Romero, J., & Alcoverro, T. (2010). Nutrient status: plant availability and seasonal forcing mediate fish herbivory in temperate seagrass beds. *Marine Ecology Progress Series 409*: 229-239.

Robertson, A.I., & Mann, K.H. (1984). Disturbance by ice and life-history adaptations of the seagrass *Zostera marina. Marine Biology 80*: 131-141.

Tomas, F., Turon, X., & Romero, J. (2005). Seasonal and small-scale spatial variability of herbivory pressure on the temperate seagrass *Posidonia oceanica*. *Marine Ecology Progress Series 301*: 95-107.

UNEP-WCMC, Short, F.T. (2017). Global distribution of seagrasses (version 6.0). Sixth update to the data layer used in Green and Short (2003). Cambridge (UK): UN Environment World Conservation Monitoring Centre. URL: http://data.unepwcmc.org/datasets/7.

Valentine, J.F., & Duffy, J.E. (2006). The central role of grazing in seagrass ecology. In: Larkum, A.W.D., Orth, R.J. and Duarte, C.M. (eds). Seagrasses: Biology, Ecology and Conservation. Springer, NY. Pp. 463-501.

Vasilakopoulos, P., Maravelias, C.D., & Tserpes, G. (2014). The alarming decline of Mediterranean fish stocks. *Curr. Biol. 24*: 14.

Velez-Juarbe, J. D.P. Domning & A.D. Pyenson. (2013). Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past ,26 Million years. PLOS ONE 7: e31294

Vergés, A., Becerro, M.A., Alcoverro, T., & Romero, J. (2007). Variation in multiple traits of vegetative and reproductive seagrass tissues influences plant-herbivore interactions. *Oecologia 151*: 675-686.

Verges, A., Steinberg, P.D., Hay, N.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., et al. (2014). The tropicalizationof temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B. 281*: 20140846.

Verges, A., Doroupoulos, C. Czarnik, R., McMahon, K., Llonch, N., & Poore, A.G.B. (2018). Latitudinal variation in seagrass herbivory: global pattern and explanatory mechanisms. *Global Ecology and Biogeography* 27: 1068-1079.

Vermeig, G.J. (1987). Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, NJ. 527 pp.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., & Rousseaux, C.S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change 3*: 78-82.

Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., et al. (2016). Climate driven regime shift of a temperate marine ecosystem. *Science 353*: 68-72.

White, K.S., Westera, M.B., & Kendrick, G.A. (2011). Spatial patterns in fish herbivory in a temperate Australian seagrass meadow. *Estuarine, Coastal and Shelf Science 93*: 366-374.

Waycott, M., Duarte, C.M., Carruthers, T.J. B., Orth, R.J., Dennison, W.C., Olyarnik, S., et al. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences 106*: 12377-12381.

Wood, K.A., O'Hare, M.T., McDonald, C., Searle, K.R., Daunt, F., & Stillman, R.T. (2016). Herbivore regulation of plant abundance in aquatic ecosystems. *Biological Reviews 92*: 1128-1141.

Wressnig, A., & Booth, D.J. (2007). Feeding preferences of two seagrass grazing monacanthid fishes. *Journal of Fish Biology 7*: 272–278.

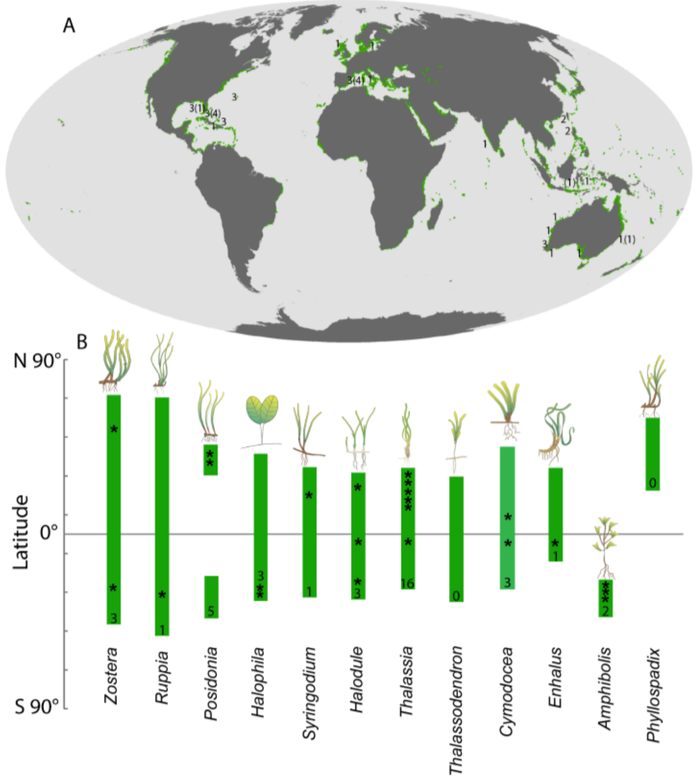

Figure 1 – (A) Global distribution of seagrass (green) based on UNEP-WCMC (Short 2017) with an overlay of the number of studies carried on grazing for which consumption and seagrass shoot production rates are available in g DW m^{-2}.d^{-1}. Numbers in parentheses indicate the number of additional studies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

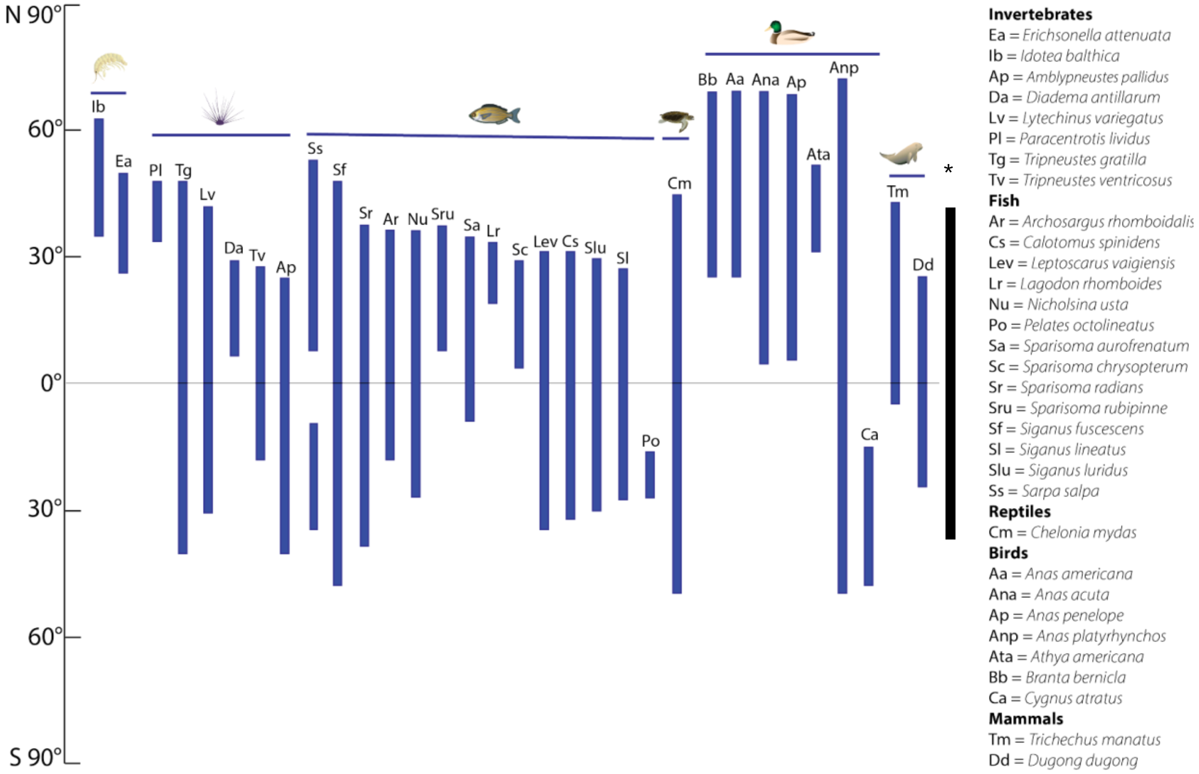

Figure 2 – The latitudinal range of grazers that have been shown to consume large proportions of seagrass material are represented by blue bars. Distributions of invertebrates, reptiles, birds and mammals are based on Global Biodiversity Information Facility (GBIF.org 2018), while distributions of fish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

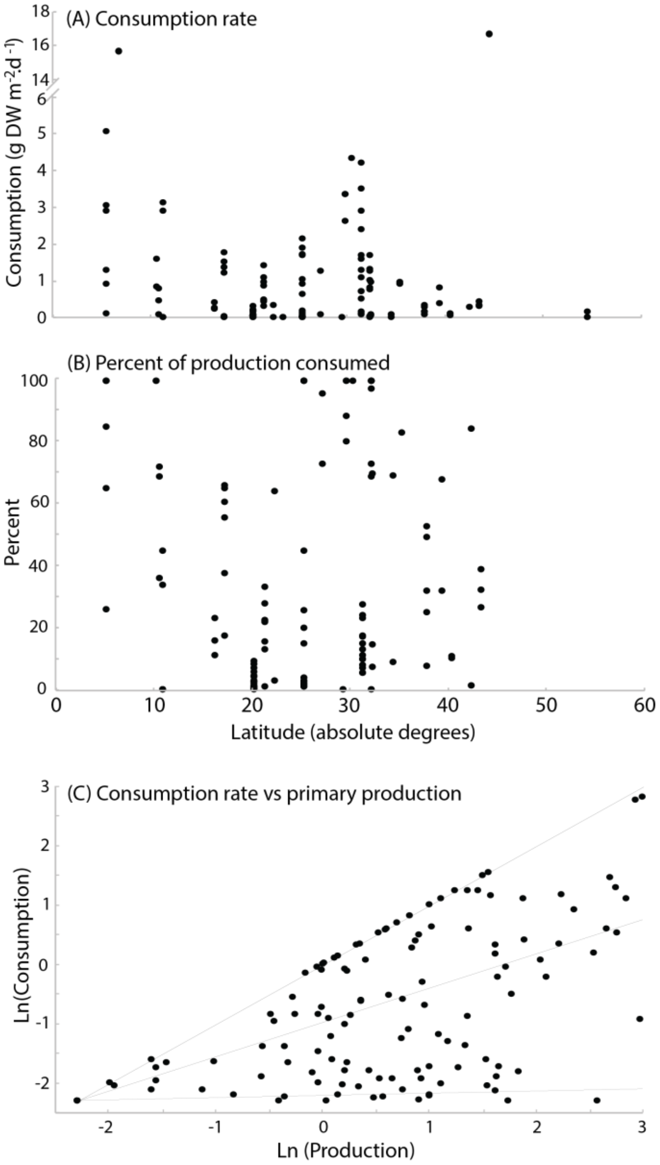

Figure 3 – Latitudinal trends in: (A) consumption rates (g DW $m^{-2}.d^{-1}$); (B) the percentage of seagrass production consumed across latitudes; and (C) the relationship between consumption rates and primary production rates (g DW $m^{-2}.d^{-1}$). Axes are ln(x+0.1). Estimate ± se for quantiles: 0.1 - 0.90 ± 0.11, $P < 0.001$; 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 Table S1. Where the reported consumption rate exceeded the production rate, it was set equal to the production rate and the proportion of production consumed was set at 100%.

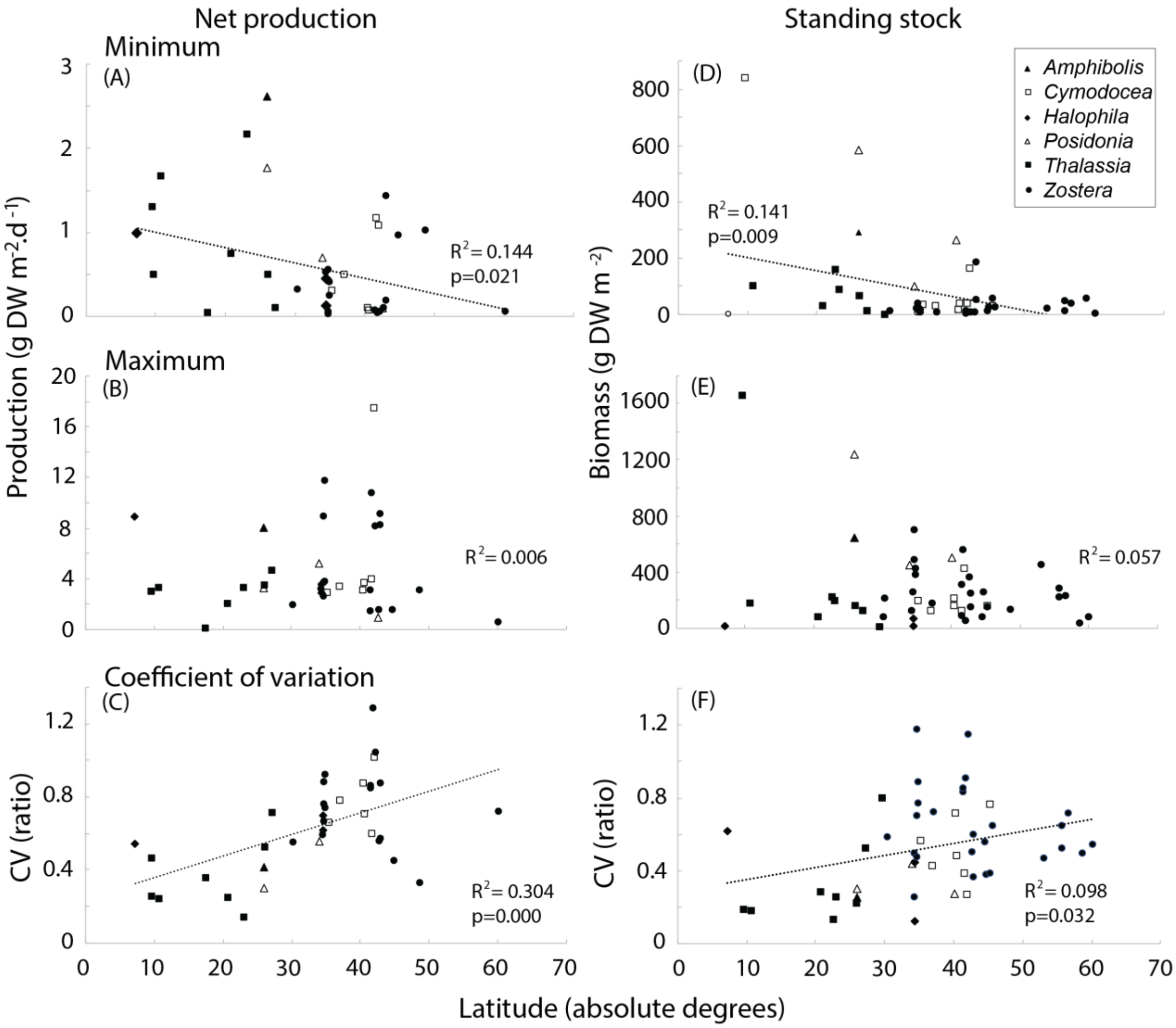

Figure 4 – Latitudinal trends in minimum and maximum primary production rates (A and B, respectively; g DW m^{-2}.d^{-1}) and biomass (D and E, respectively; g DW m^{-2}) of seagrass, along with the coefficient of variation (CV) of mean monthly (C) production rates and (F) standing biomass of different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