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Driving factors of biogeographical variation in seagrass herbivory

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Abstract

Despite the crucial role of herbivory in shaping community assembly, our understanding on biogeographical patterns of herbivory on seagrasses is limited compared to that on terrestrial plants. In particular, the drivers of such patterns remain largely unexplored. Here, we used a comparative-experimental approach in *Cymodocea nodosa* meadows, across all possible climate types within the seagrass distribution, 2000 km and 13° of latitude in two ocean basins, to investigate biogeographical variation in seagrass herbivory intensity and their drivers during July 2014. Particularly, the density and richness of herbivores and their food resources, seagrass size, carbon and nitrogen content, as well as latitude, sea surface temperature, salinity, chlorophyll, and sediment grain size, were tested as potential drivers. We found that shallow meadows can be subjected to intense herbivory, with variation in herbivory largely explained by fish density, seagrass size, and annual sea temperature range. The herbivorous fish density was the most important determinant of such variation, with the dominant seagrass consumer, the fish *Sarpa salpa,* absent at meadows from regions with low herbivory. In temperate regions where herbivorous fish are present, annual temperature ranges drive an intense summer herbivory, which is likely mediated not only by increased herbivore metabolic demands at higher temperatures, but also by higher fish densities. Invertebrate grazing (mainly by sea urchins, isopods, amphipods, and/or gastropods) was the dominant leaf herbivory in some temperate meadows, with grazing variation mainly influenced by seagrass shoot size. At the subtropical region (under reduced annual temperature range), lower shoot densities and seagrass nitrogen contents contributed to explain the almost null herbivory. We evidenced the combined influence of drivers acting at geographic (region) and local (meadow) scales, the understanding of which is critical for a clear prediction of variation in seagrass herbivory intensity across biogeographical regions.

Keywords: biogeography; *Cymodocea nodosa*; herbivorous fish; invertebrate grazer; plant-herbivore interactions; seagrass; temperature range.

1. Introduction

Whilst biogeography classically deals with the factors determining the geographic distribution of species or diversity, a more recent focus on species interactions is of paramount interest for understanding how biotic and abiotic conditions co-shape the variation of ecological functions (Reichstein et al., 2014). Among species interactions, herbivory can be an important modulator of community assembly and evolutionary adaptation (Ehrlich and Raven, 1964; Hulme, 1996; Wood et al., 2017). By playing a central role in the distribution of energy and biomass among producers and consumers, herbivory has the potential to mediate effects that cascade up and down through food webs (Schmitz, 2008; Estes et al., 2011; Ripple et al., 2016).

Strength variation in plant-herbivore interactions has been the focus of intense research in recent years, with particular attention on latitudinal gradients (Schemske et al., 2009; Moles et al., 2011; Baskett and Schemske, 2018; Gao et al., 2019). These studies provide controversial evidence regarding the biogeographical theory commonly known as the “Latitudinal Herbivory Hypothesis” (LHH), which dated from the 1990s, and predicts that herbivory is more intense, and plant defences better developed, at lower than higher latitudes (Coley and Aide, 1991; Coley and Barone, 1996). While some studies indicate either a decline or increase in herbivory at higher latitudes, others report no latitudinal patterns at all (reviewed by Anstett et al., 2016).

Biogeographical regions share similar natural conditions that entail climatic, environmental, ecological and evolutionary settings delineated across millennia, which may co-vary or not with latitude, affecting interaction strengths (Harley, 2003; Pennings et al., 2003; Hemingson and Bellwood, 2018). Thus, it can be difficult to infer the underlying causes of ecological variation in the strength of interactions between herbivores and plants based solely on latitude. The herbivory pressure may vary across biogeographical regions as a function of abiotic conditions, plant and herbivore (species) richness, herbivore densities, and/or intra- or inter-specific variation in *per capita* interaction strengths (Pennings and Silliman, 2005; Wood et al., 2012). Identifying the drivers of herbivory across biogeographical regions remains an important challenge for understanding variability in the strength of this relevant biotic interaction.

In the marine realm, herbivory can be remarkably intense (Poore et al., 2012), and top-down effects on plant production mediated by herbivores via trophic cascades are also stronger than in terrestrial systems (Shurin et al., 2002; Bakker et al., 2016). In seagrass meadows, for instance, extremely high consumption by sea urchins may cause phase shifts in ecosystem state towards unvegetated habitats (Eklöf et al., 2008). Thus, identifying the main drivers of variation in herbivory strength across biogeographical regions may have strong implications for seagrass ecology and conservation. This is of major concern, since seagrasses are fundamental habitat-forming species on coastal soft bottoms worldwide, which perform key ecological functions (e.g. provision of habitat and food, nutrient cycling) and provide ecosystem services contributing to human welfare (e.g. global carbon sequestration, shoreline protection, enhanced fisheries; see Orth et al., 2006, Fourqurean et al., 2012; O'Hare et al., 2018).

The seagrass *Cymodocea nodosa* (Ucria) Ascherson is widely distributed in the Mediterranean Sea and the adjoining coasts of the eastern Atlantic Ocean, including the Macaronesian archipelagos of Madeira and the Canaries, as well as the Mauritania and Senegal coasts (Green and Short, 2003, Cunha and Araujo, 2009). In this study, we investigated biogeographical variation in herbivory intensity on this wide-ranging seagrass, with a particular focus on fish and invertebrate herbivory. We used a comparative-experimental approach in seagrass meadows, across 13° of latitude within the species' distribution range, to relate observed patterns in herbivory to the density and richness of herbivores and their food resources, seagrass size, carbon and nitrogen content, as well as geographical and environmental conditions (latitude, sea surface temperature, salinity, chlorophyll, and sediment grain size). In brief, we aimed to determine which of these factors are the most relevant drivers of seagrass herbivory across biogeographical scales.

2. Methods

2.1 Study regions and sampling design

The study was simultaneously conducted in four biogeographical regions across a temperate-subtropical latitudinal gradient (ca. 2000 km, 13° of latitude; Fig. 1), extending from the Western Mediterranean (Ebro Delta, 41º N; Alicante, 38º N) to the South-Iberian (Ria Formosa, 37º N) and Macaronesian (Gran Canaria, 28º N) coasts in the North-eastern Atlantic Ocean. In order to focus on widely distributed herbivorous fishes and invertebrates, we specifically avoided the Southern and Eastern limits of *C. nodosa* distribution, where the green sea turtle (*Chelonia mydas*) can be intense seagrass consumers (Cardona et al., 2009; Casale et al., 2018). The study regions covered the full range of climate types within the *C. nodosa* geographic distribution according to the Köppen-Geiger classification (Kottek et al., 2006), which are as follows: Gran Canaria (BWh: hot desert climate) with mild temperatures year-round; Alicante (BSh: hot semi-arid climate) having mild winters and hottest summers with little rain; and the Ebro Delta and Ria Formosa with hot, dry summers and cool, relatively wet winters (Csa: warm temperate climate).

At each region, we sampled three shallow (< 10 m depth) *C. nodosa* meadows separated by 3-15 km, which were chosen arbitrarily to represent the variety of meadows within each region. Sampling took place in summer (July 2014), when herbivory is often higher (Prado et al., 2007, 2010) and plant growth is relative stable after the late-spring peak (Terrados and Ros, 1992).

2.2 Seagrass herbivory

Rates of seagrass herbivory by the sparid fish *Sarpa salpa* and/or the warm-temperate parrotfish *Sparisoma cretense,* as well as by invertebrates (the sea urchin *Paracentrotus lividus* and/or small crustaceans and gastropods, hereafter referred as mesograzers), were quantified in 20-22 undamaged shoots of *C. nodosa* at each meadow, following a tethering method (Figures A1-A3) modified from Kirsh et al. (2002). Each leaf within the shoot was measured, annotating the size and position of any previous scar. The bundle of leaves of each seagrass shoot was punched with a hypodermic needle just above the ligule of the outermost leaf. Each shoot was attached to a labelled tent peg separated by 1 meter from the next along a fishing line and fixed to the sediment at the level of the average height of the leaf canopy. After ca. 10 days, tethered shoots were retrieved and the leaf area loss due to new grazing scars was calculated for each leaf, using a 1 mm^2 grid. In those instances where the leaf apex was grazed, leaf loss was calculated by subtracting the remaining leaf area above the punching mark (i.e. excluding leaf tissue grown during the experiment) to the area measured at the start of the experiment. Conservatively, we ignored any scratch mark that was not confidently attributed to herbivory, as well as we did not consider unrecovered tethered shoots as potential losses due to herbivory. We differentiated between fish herbivory (which left crescent moon-shaped bites) and invertebrate grazing (which results in serrated edges or in holes irregularly slashed or round; see Boudouresque and Meisnez, 1982; Kirsch et al., 2002). Consumption rates by fish and invertebrates were separately quantified at the scale of individual shoots as leaf area consumed per day.

We also measured seagrass production rates at each meadow in 10-22 randomly selected shoots. Following the methods described by Zieman (1974), we estimated leaf production in shoots tagged in the field by punching the bundle of leaves with a hypodermic needle at 2 mm above the ligule of the outermost leaf. After ca. 10 days, tagged shoots were collected and new leaf material produced (i.e. leaf areas below the punching mark plus any new unmarked leaves) was measured. In those instances where the oldest leaf within the shoot was lost, its growth was set as zero according to the values measured in the oldest leaves of other collected shoots. Production was expressed as new leaf area produced per day and shoot. Meadow-specific mean production rates were used to convert losses due to herbivory into the proportion of daily shoot production consumed by herbivores, with proportions higher than 1 indicating that consumption exceeds production.

Rates of consumption and production were converted to biomass consumed (or produced) at the m^2 scale using site-specific leaf area to dry mass regressions obtained from four to 19 randomly collected shoots, as well as shoot density per meadow quantified as described below (Table B1).

2.3 Biotic and environmental context

In conjunction with the herbivory experiments, we also quantified biotic and abiotic characteristics of the plant and the meadow. Plant size was measured in those shoots used to estimate consumption rates prior to the experiments (n = 20-22) and expressed as leaf area (excluding sheaths) in cm^2 per shoot. We also analysed carbon and nitrogen content in powdered dry samples of seagrass leaves without epiphytes (five replicates of pooled material from three shoots each) using a Carlo-Erba elemental analyser (Instruments EA 1108), which were expressed as % of dry weight on a molar basis.

To quantify the richness and abundance of potential food resources for herbivores at each meadow, immediately before the experiments, we collected four to five replicate samples of vegetation separated by ca. 5 m, by placing a fine mesh bag (<1 mm) affixed to a flexible 25 cm diameter hoop over the seagrass canopy, which was then cut at the sediment surface level (Best and Stachowicz, 2012; see Figure A4). Sample bags were transported to the laboratory, where we counted the number of *C. nodosa* shoots and expressed shoot density per m^2. We also quantified the richness of the seagrass-associated macroalgae (i.e. number of species) and their total abundance (i.e. expressed as the area covered after spreading all algal species on a horizontal surface in cm^2 per m^2). Leaf epiphytes were scraped from each of four to 18 of those seagrass shoots collected in the mesh bags, and epiphyte biomass was expressed as mg of dry weight per g of seagrass leaf dry mass. Logistical constraints prevented us from obtaining epiphyte samples in the Ebro Delta region.

We also quantified the density of invertebrates and herbivorous fishes at each meadow. Among invertebrate grazers, we differentiated between large-size (sea urchins) and small-size invertebrates or mesograzers (mostly amphipods, isopods, gastropods, and shrimps). Sea urchins at each meadow were counted along five transects (10 m length x 1 m width), where *Paracentrotus lividus* was the only sea urchin found. Mesograzers were collected simultaneously to vegetation using the same mesh bags, and then sorted, identified and counted under a stereomicroscope

(Figure A4). They comprised small-size invertebrates that may potentially consume algae or seagrass leaves, including omnivorous species (58 taxa; see Table C1). Most of the mesograzers that we identified are generalist feeders that mainly consume algae, microalgae, epiphytes, detritus, and small animals, while only nine species are reported to actually feed on living seagrass (see species identity and supporting references in Table C1). For each sample, we determined the density and species richness of all mesograzers and of those mesograzers that are seagrass-consumers. Herbivorous fishes were identified and counted along six transects (25 m length x 2 m width) at each meadow, performed around noon (10:00 to 15:00 h) before the experiments or at different days. In Gran Canaria, only three transects were done, but fish counts in this region were consistent to several divers´ observations at different days. All herbivore densities were expressed as number of individuals per m^2.

Sediment grain size, as well as the proportion of fine and coarse fractions, were quantified in five sediment samples collected from each meadow with a 5 cm diameter core inserted 5 cm into the sediment, after organic matter removal with H_2O_2 6% and drying at 60 °C for 48 h. The grain size was expressed in phi units defined as: $\varphi = -\log_2 d$ (mm), where d is the particle diameter in mm. Coarse (sand and gravel) and fine (clay and silt) fractions were wet sieved through a 0.062 mm mesh. The coarse fraction was mechanically sieved at 1 φ intervals from -4.00 φ (16 mm) to 4.00 φ (0.062 mm). Pipette analysis was performed at 1 φ intervals in the fine fraction, after the addition of 0.5% sodium hexametaphosphate solution as dispersant.

Lastly, we retrieved for each meadow estimates of monthly sea surface temperature (Reynolds Optimum Interpolation Sea Surface Temperature provided by NOAA), chlorophyll (multiple-satellite cross-calibrated chlorophyll product provided by NASA), and salinity (Hadley EN4 subsurface salinity), made available using the

NAUPLIUS Spatiotemporal Data Toolkit (https://www.st.nmfs.noaa.gov/copepod/about/about-nauplius.html). We used the retrieved time series to average, for the period 2000-2014, the annual sea surface temperature mean and range, as well as the annual mean salinity and chlorophyll. Such environmental variables were chosen as geographical predictors since they mostly vary among regions.

2.4 Statistical analyses

2.4.1 Biogeographical variation in seagrass herbivory

We examined differences in seagrass herbivory among biogeographical regions using a series of generalized linear mixed models (GLMMs), with `region´ as a fixed factor (four levels) and `meadow´ as a random factor nested within `region´ (three levels). We tested separately the consumption by fish and invertebrates as response variables, as well as the total consumption and the proportion of the leaf production consumed by herbivores. We used a negative binomial error distribution with a squared root link function, since we were dealing with overdispersed count data (Buckley, 2014). We fitted a random intercept model, allowing intercepts to vary among meadows within each region, but with the same slope for each region (Bates et al., 2015). For each response variable, we used a null-hypothesis significance approach, in which the full mixed model was compared, using a χ^2 likelihood ratio test, against the corresponding `null´ model lacking the fixed term, i.e. only the random effect `meadow´ is included (Harrison et al., 2018). In this approach, significant p-values denoted a significant effect of the fixed factor `region´, since models significantly differ in their likelihood.

2.4.2 Predictor variables that regulate seagrass herbivory

We implemented generalized linear models (GLMs) to explore the relative contribution to seagrass herbivory of the measured predictor variables. Separate models were fitted for fish and invertebrate consumption, as well as for total consumption and for the proportion of leaf production consumed. In order to focus on comparisons among biogeographical regions, we used the mean value of each meadow (per region) as replicate. To prevent collinearity among predictors, we selected those with a larger biological significance among predictors that were significantly correlated (Spearman correlation coefficients; Table C2). Specifically, we tested seagrass nitrogen, shoot-specific plant size, and temperature range as predictor variables; in addition to fish density for fish consumption or mesograzers density for invertebrate consumption. Since algal cover and richness were highly correlated to each other and to mesograzer density, algal cover was only included to model fish consumption (see unselected predictors variables in Figs C1-C2). To estimate collinearity among predictors, variance inflation factors (VIF) were calculated using the ‘car’ package (Fox and Weisberg, 2019). We excluded variables with a VIF higher than 10, according to Quinn and Keough (2002). Then, fine sediment was excluded from all models, as well as production was only included to model invertebrate consumption due to high collinearity when modelling other response variables. To model total seagrass consumption and the proportion of the leaf production consumed, we considered both, mesograzer and fish densities, as predictor variables. After checking model assumptions of homogeneous variances and normality of errors through visual inspection of residuals and quantile-quantile (QQ) plots (Harrison et al., 2018), as well as the Breush-Pagan heteroscedasticity test, we used a linear model (i.e. Gaussian error distribution with an identity link function) to fit each dataset.

For model selection, we firstly performed a backward stepwise approach by iteratively dropping from the full model the predictor variable with a lowest contribution, until getting the most parsimonious model according to the Akaike Information Criterion (AIC). To this aim, we used the ` MASS´ package (Venables and Ripley, 2002). Lastly, we used the ` MuMIn´ package (Bartoń, 2019) with a double aim: (i) to validate the previous model (stepwise) selection, by performing a multimodel averaging that incorporate model selection uncertainty and rank candidate models by the AIC corrected for small samples (AICc); and (ii) to estimate the relative importance of each predictor variable, as the sum of Akaike weights over all possible models. Visual inspection of model assumptions was performed on selected models. When more than one predictor variable was selected, low collinearity among them (VIF < 5) was also checked. All modelling was performed using the `lme4´ package (Bates et al., 2015). All packages were implemented in the open source software R3.6.1 (www.r-project.org).

3. Results

3.1 Biogeographical variation in seagrass herbivory

Total herbivory on seagrass leaves significantly differed among regions, with plants in Alicante and Ria Formosa subjected on average to 15 times greater consumption than those in Gran Canaria and Ebro Delta (Table 1, Figs 1, 2a). Gran Canaria plants were almost not consumed (with only few marginal fish bites recorded in two meadows), whilst those in the Ebro Delta experienced significantly lower herbivory, which was almost exclusively due to invertebrate grazing (only marginal fish bites occurred in one meadow).

Fish herbivory significantly differed among regions following the same global pattern, while this pattern was slightly non-significant (p=0.051) for invertebrate grazing (Table 1, Fig. 2a). Intra-regional variability in consumption by both, fish and invertebrates, was also particularly large in Alicante and Ria Formosa regions (Table B1, Fig. 2a). Fish herbivory was dominant at two meadows in Alicante and one in Ria Formosa (where it was exclusive), while invertebrate grazing was dominant in the two other Ria meadows. The other Alicante meadow suffered an intense herbivory, which was equally due to fish and invertebrates.

We also found a significant biogeographical variation in herbivory impact, with herbivory levels exceeding seagrass production in Alicante and Ria Formosa, but not in the Ebro Delta or Gran Canaria (Table 1, Fig. 2b). On average, herbivore consumption was 4- and 2-fold greater than seagrass production in Alicante and Ria Formosa, respectively. Specifically, herbivory exceeded seagrass production in five out of the six meadows from Alicante and Ria Formosa, reaching herbivore consumption 8.5 times seagrass production at the Alicante meadow where both, fish and invertebrate consumptions were high.

3.2 Predictor variables that regulate seagrass herbivory

Fish density was the only relevant predictor of seagrass consumption by fish, accounting for ca. 71% of the total variance, and with consumption increasing with fish density (Table 2). Two predictors, seagrass nitrogen and sea temperature range, separately increased the amount of explained variance (i.e. higher adjusted R^2), although the model improvement was not large enough for the selection of both variables in a more parsimonious model (Table S5).

From the three predictors determining invertebrate consumption that were initially selected by the stepwise procedure, seagrass size was the most important despite a lack of significance due to a high intra-regional variability (Tables 2-3). The two other predictors, seagrass production and temperature range, were not selected in the MuMIn averaging due to a low importance (Table 3).

Three uncorrelated (VIF < 1.5) predictor variables were key determinants of both, total seagrass consumption and the proportion of leaf production consumed by herbivores, explaining 88% and 92% of the total variance, respectively (Tables 2 and 3). Fish density was the most important predictor for both responses, while the second most important predictor was seagrass size for the total consumption and temperature range for the proportion of leaf production consumed (Table 3, Fig. 3).

Fish density showed a high intra-regional variation in Alicante and Ria Formosa, whereas no fish was found in the Ebro Delta, and low densities were consistently found in Gran Canaria (Fig. 3a). Fish density was highest in meadows where fish herbivory was high (Figs 2a, 3a). The only herbivorous fish found at temperate meadows was *S. salpa*, whilst at subtropical meadows it was *S. cretense*. Fish density only negatively correlated with salinity (Table C2, Fig. 3h).

A high inter- and intra-regional variation was observed for seagrass size. A much higher size was found in Ria Formosa than in the other regions (Fig. 3b); however, the lowest plant size was also found in a meadow from this region, as a result of intense fish herbivory. Seagrass size did not significantly correlate with other predictors (Table C2).

Sea temperature range increased monotonically with latitude, from 13.1ºC in the northernmost region to 4.9ºC in the subtropical region. Indeed, temperature range largely correlated with latitude (Spearman r=0.96; Table C2, Fig. 3g), and both biogeographic variables positively correlated with seagrass nitrogen, shoot density, salinity, and chlorophyll, and negatively correlated with seagrass C:N (Table C2; Fig. 3c-i). Seagrass nitrogen and shoot density increased with temperature range (and latitude), with Alicante and Ria Formosa (middle-latitude regions) having similar intermediate values on average (Fig. 3d-f). Salinity variation was marked by differences in ocean basins, with Mediterranean regions having larger values than Atlantic regions (Fig. 3h). Chlorophyll product was greater in the Ebro Delta and Ria Formosa, both more enclosed and productive systems than Alicante and Gran Canaria (Fig. 3i).

4. Discussion

We found that herbivore consumption on seagrass was, on average, 15 times higher and more variable in two biogeographical regions: Alicante and Ria Formosa. On such regions, herbivory greatly exceed seagrass production, removing on average ca. 3 times leaf production. A low herbivory impact was observed in the two other regions, with leaf production consumed averaging 28% in the Ebro Delta and almost zero in Gran Canaria. Biogeographical variation in herbivory was mainly driven by contrasting fish density, seagrass size, and sea temperature range across meadows or regions. The highest leaf herbivory at higher temperature ranges (mid latitudes) that we found, contrasts with the typically greater herbivory at lower latitudes predicted by the LHH, as previously found in terrestrial systems (Adams and Zhang, 2009) and intertidal mangrove forests (Feller et al., 2013). Our findings also contrast with a previous study reporting higher herbivory at lower latitudes for a seagrass species (*Amphibolis antarctica*) of austral distribution (Vergés et al., 2018).

The herbivorous fish density was the most important determinant of both, total seagrass consumption and the proportion of leaf production consumed by herbivores. Fish density was, as well, the only significant driver of fish consumption alone, thus indicating a prevalence of the influence of fish impact in the overall herbivory pattern. The herbivory variation narrowly related to the density of the dominant herbivore is consistent with the pattern globally reported for aquatic ecosystems (Bakker et al., 2016; Wood et al., 2017). On average, the density of herbivorous fish was higher in Alicante and lower in Gran Canaria meadows, with no occurrence in meadows from the Delta Ebro. This trend was unforeseen, since higher densities would be expected in the subtropical Canaries, where herbivorous fish are more diverse compared to temperate regions following the typical herbivorous fish diversity pattern (Floeter et al., 2005). However, we found parrotfish (*S. cretense*) but not sparid fish (*S. salpa*) in Gran Canaria meadows, which is consistent with previous observations at subtropical meadows from the Canary Islands (Espino et al., 2011, 2016). Parrotfish populations are abundant in the Canaries, where they use meadows as nursery grounds (Tuya et al., 2006; Espino et al., 2016), although juveniles are not able to feed on *C. nodosa* likely because their jaws are not powerful enough to bite seagrass leaves (Del Río et al., 2016). Parrotfish adults are reported to inhabit shallow rocky bottoms in the Canary Islands, and only perform occasional incursions into *C. nodosa* meadows adjacent to rocky reefs (Tuya et al., 2006; Espino et al., 2015). This highlights that fish abundance depends on habitat use or preference, which is consistent with previous studies reporting that rocky and coral reefs often hold higher herbivorous fish densities than seagrass habitats (Eggertsen et al., 2019).

The only fish with a relevant herbivory impact on seagrass in our study was *S. salpa*, a motile fish that commonly occurs in schools up to 50-60 individuals (Peirano et al., 2001; Raventos et al., 2009). The density of *S. salpa* showed a high local variation within the two regions that averaged the higher herbivory intensity (i.e. Alicante and Ria Formosa). Both, regional and local variation in fish density, were in accordance with the pattern in herbivory impact. Particularly, the values of *S. salpa* density that we found in our study regions agree previous studies. High densities of *S. salpa* have been reported in Alicante, which in summer preferentially feed on *C. nodosa* patches surrounded by mixed meadows of *Posidonia oceanica* and *Caulerpa prolifera*, likely attracted by habitat heterogeneity and complexity (Marco-Méndez et al., 2017). In Ria Formosa, *S. salpa* populations preferentially inhabit areas close to hard substrates (Isidoro Costa, personal communication); they are also common in seagrass meadows and rare in unvegetated bottoms (Ribeiro et al., 2006 and 2008). We found no *S. salpa* at meadows in Gran Canaria, where they commonly inhabit rocky bottoms (Tuya et al., 2019). Similarly, no *S. salpa* was found in the Ebro Delta, in spite of the similar temperature range, shoot size, and even higher seagrass density and nitrogen content relative to values observed in Alicante and/or Ria Formosa. *Sarpa salpa* absence inside the Ebro Delta is consistent with a previous study (Costa et al., 2002). This enclosed environment is characterized by low water depths, reduced tidal influence and large freshwater inputs, coupled with a lack of hard-bottom habitats, in which *S. salpa* is known to recruit (Harmelin-Vivien et al., 1995). Proximity to other habitats, among other factors, are reported to largely influence the density of herbivorous fish and subsequent herbivory intensity (Downie et al., 2013; Unsworth et al., 2008). Such habitat interconnectivity is particularly relevant within fish home ranges, which in the case of *S. salpa* may extend to few km^2 in Mediterranean areas (averaging 1.3 and 5 km^2 in Pagès et al., 2013 and Jadot et al., 2006, respectively) to broader ranges (43 km^2) at the Ria Formosa lagoon (Abecasis et al., 2012).

Interestingly, we found that mean annual temperature did not co-vary with latitude, but followed the Köppen-Geiger climate types (Kottek et al., 2006); that is, the hot desert climate region (Gran Canaria) showing the highest mean sea surface temperature, and the warm temperate regions (Ebro Delta and Ria Formosa) having the lowest temperatures. In our study, annual temperature ranges monotonically vary with latitude, mediating a greater (and more variable) herbivory in two out of the three temperate regions, which are characterized by dry, hot summers and cool winters with different rain levels. The behaviour of temperate herbivores is commonly adjusted to seasonal variation in environmental conditions (e.g. temperature, photoperiod), food resources (e.g. plant quality and biomass) and energetic requirements (Silva et al., 2017; Abarca, 2019; Huang et al., 2020). For instance, this variation largely drives changes in herbivore movement patterns and home range sizes (Morellet et al., 2013). Specifically, massive schools of *S. salpa* are known to actively feed on shallow temperate Mediterranean seagrass meadows from June to September. They accumulate reserves for the winter, when adult individuals migrate to deeper waters (> 40 m) during a period of less feeding and preparation for reproduction (Francour, 1997; Peirano et al., 2001). In the autumn-winter period, adult individuals are also reported to leave the Atlantic lagoon, Ria Formosa, towards open coastal waters (Ribeiro et al., 2006). Our study was conducted in summer, when *per capita* consumption rates that match, or even exceed, rates of primary production are common, since increased herbivore metabolic demands are generally more sensitive to higher temperatures than rates of photosynthesis (O´Connor, 2009). Thus, we evidenced that some shallow temperate seagrass meadows can endure substantial summer herbivory, which is underpinned by large annual temperature ranges that mediated seasonal patterns of variation not only in herbivore (fish and invertebrates) metabolic demands, but also in fish densities. Previous studies conducted in shallow temperate meadows of the Mediterranean endemic *P. oceanica* suggest that the spatially variable and intense fish herbivory that we observed in summer is consistent across seagrass species and over the years (Prado et al., 2007 and 2010; Planes et al., 2011).

In the subtropical region, under reduced annual temperature range, a lower shoot density and seagrass nitrogen content contributed to explain the almost null herbivory that we found. Such explanation would agree with previous studies showing reduced densities of *S. salpa* at meadows featuring lower seagrass shoot densities (Guidetti and Bussotti, 2000). In contrast, reports on the effects of seagrass nitrogen content on *S. salpa* consumption are not uniform, indicating either an increase (Prado et al., 2010) or no effect (Peirano et al., 2001; Marco-Méndez et al., 2016). We detected, however, no link between these biotic predictors and herbivory across the other (temperate) regions. The observed increase in plant nitrogen content with latitude is consistent with previous studies in terrestrial, freshwater and marine plants (Borer et al., 2013; Reich and Oleksyn, 2004).

We found that *C. nodosa* shoot size was the second most important predictor of total consumption, and the third in determining the proportion of leaf production that was consumed by herbivores. Seagrass size is likely associated with invertebrate grazing, which followed the same biogeographical pattern than fish herbivory (albeit slightly not significant, $p=0.051$). Both, seagrass size and invertebrate grazing on seagrass showed markedly high intra-regional variability, which may surpass inter-regional variation according to previous studies (Mascaró et al., 2009; Vergés et al.

2018). Interestingly, invertebrate grazing was almost the exclusive leaf herbivory in the Ebro Delta, while dominated at one and two meadows in Alicante and Ria Formosa, respectively. Whilst sea urchins are often important seagrass consumers (e.g. Prado et al., 2007; Heck and Valentine, 2006), we found that they were absent or scarce in most *C. nodosa* meadows. In our study meadows, sea urchins were associated with larger shoots in Ria Formosa, as well as with the large bivalve *Pinna nobilis* in the Ebro Delta (see also Camps- Castellà et al., 2020). We found no sea urchin at Gran Canaria and Alicante meadows, although they are relevant *C. nodosa* consumers in seagrass meadows interspersed with rocky reefs in Alicante (Marco-Méndez et al., 2015). This would indicate that homogeneous *C. nodosa* is not a suitable habitat for sea urchins in terms of refuge provision.

5. Conclusions

In summary, we found that shallow seagrass meadows in temperate regions (i.e. with a marked annual temperature range) can be subjected to intense herbivory during summer, but only in environments where meadows are accessible within herbivorous fish home ranges. We evidenced an interplay of drivers acting at geographic (region) and local (meadow) scales, which understanding is critical for a clear prediction of variation in herbivory intensity across biogeographical regions. As ocean temperatures continue to rise under near-future climate change, wider annual temperature ranges are expected to promote biogeographical variation in seagrass herbivory via enhanced summer metabolic requirements, and thus, increased consumption at temperate meadows supporting high densities of herbivorous fish. This is a matter of major concern under current climate change, with associated marine heat waves and expanding distribution ranges of warm-water herbivorous fishes.

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Table 1. Results of GLMMs examining variation in seagrass herbivory among biogeographical regions. Significant effect of the fixed factor \`region´, based on χ^2 likelihood ratio tests, is highlighted in bold.

Response variable	**Fixed factor**	χ^2	**df**	**p-value**
Total consumption	Region	12.5	3	**< 0.01**
Fish consumption	Region	11.3	3	**0.01**
Invertebrate consumption	Region	7.8	3	0.051
Leaf production consumed	Region	12.2	3	**< 0.01**

Table 2. Predictor variables regulating seagrass herbivory, according to results of model selection from stepwise approach and multimodel averaging. For each selected model, the Breush-Pagan heteroskedasticity test and collinearity (via the VIF) among predictors (when more than one was selected), are shown. See full results in Tables C3-C4.

	Stepwise selection	**Multimodel averaging selection**					
Response variable	**Significant predictors (p-value)**	**Model predictors (VIF)**	**df**	**AICc**	**weight (wi)**	**Adjusted R2**	**Breush-Pagan test (p-value)**
Fish consumption	Fish density (p< 0.001)	Fish density	3	-1.5	0.48	0.71	BP = 0.72 (p = 0.40)
Invertebrate consumption	Seagrass size (p<0.01), production (p=0.03), temperature range (p=0.04)	Seagrass size	3	7.5	0.55	0.42	BP = 6.8 (p = 0.01)
Total consumption	Fish density (p<0.0001), seagrass size (p<0.001), Temperature range (p<0.01)	Fish density (1.1), seagrass size (1.2), temperature range (1.1)	5	9.4	0.91	0.88	BP = 0.05 (p = 0.82)
Leaf production consumed	Fish density (p<0.00001), temperature range (p=0.003), seagrass size (p=0.006)	Fish density (1.1), seagrass size (1.2), temperature range (1.1)	5	40.2	0.84	0.92	BP = 0.03 (p = 0.87)

Table 3. Relative importance of the predictor variables regulating seagrass herbivory from multimodel averaging of GLMs (full method: sum of Akaike weights over all possible models). Significant predictors are highlighted in bold.

Response variable	Predictor	Estimate	Adjusted SE	z statistic	p-value	Relative importance
Fish consumption	**Fish density**	5.81	1.23	4.73	**0.000002**	1.00
	Seagrass nitrogen	0.03	0.07	0.45	0.66	0.24
	Temperature range	0.004	0.01	0.36	0.72	0.18
	Seagrass size	0.0001	0.00	0.06	0.96	0.05
	Algal cover	0.000000004	0.000001	0.00	0.998	0.05
Invertebrate consumption	Seagrass shoot size	0.02	0.01	1.64	0.10	0.91
	Temperature range	0.01	0.03	0.51	0.61	0.33
	Seagrass production	-0.05	0.39	0.13	0.90	0.23
	Mesograzer density	-0.000001	0.00002	0.07	0.95	< 0.01
	Seagrass nitrogen	0.0001	0.01	0.01	0.99	< 0.01
Total consumption	**Fish density**	10.13	1.57	6.47	**< 2e-16**	1.00
	Seagrass size	0.03	0.01	4.13	**0.00004**	0.99
	Temperature range	0.06	0.02	2.42	**0.02**	0.94
	Algal cover	-0.0000002	0.000002	0.09	0.92	0.02
	Seagrass nitrogen	-0.0000610	0.02	0.00	1.00	0.01
Leaf production consumed	**Fish density**	49.13	5.98	8.22	**<2e-16**	1.00
	Temperature range	0.23	0.10	2.31	**0.02**	0.92
	Seagrass size	0.06	0.03	2.03	**0.04**	0.89
	Seagrass nitrogen	-0.008	0.10	0.08	0.93	0.02
	Algal cover	-0.0000001	0.000004	0.02	0.98	0.01

Figure 1. Map of the four biogeographical regions in the NW Mediterranean and the NE Atlantic Ocean, where seagrass herbivory and potential predictors were studied. Circles represent *Cymodocea nodosa* meadows within each region, with more intense circle colour indicating greater herbivory intensity (as total consumption). Pictures show a meadow from each region ordered from north (left) to south (right). The map was created with QGIS 3.8.1 using Natural Earth Data.

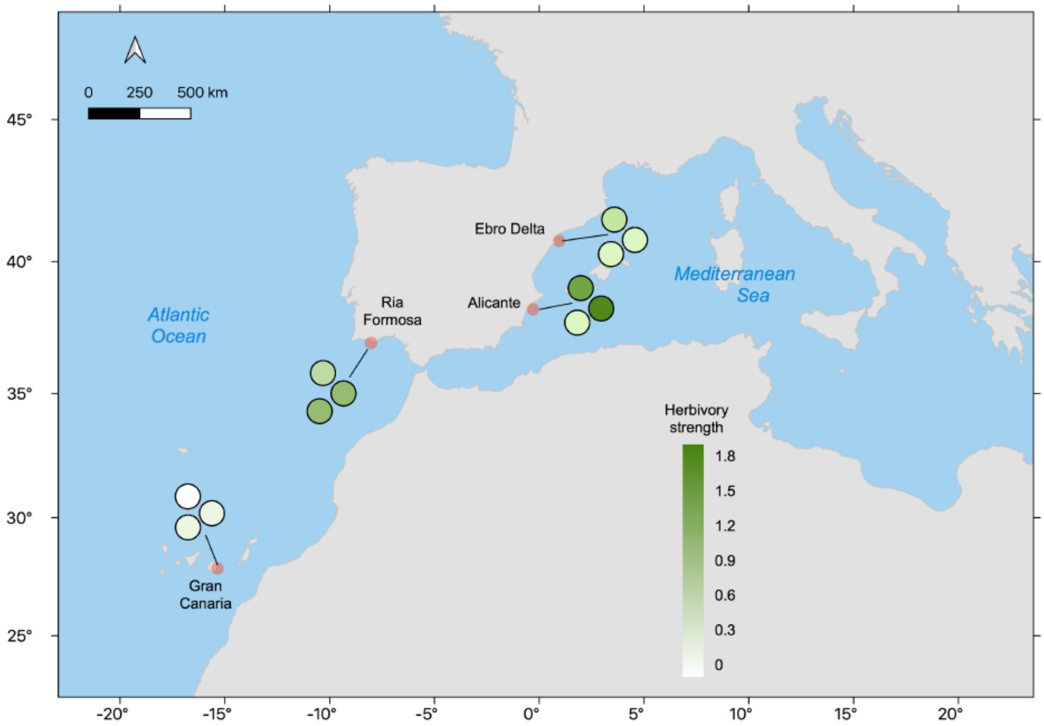


Figure 2. Seagrass herbivory at each meadow within the four biogeographical regions, from north to south (mean ± SE). (a) Seagrass consumption by fish (solid fill) and invertebrates (hatched lines), and (b) proportion of the site-specific leaf production consumed by herbivores, with values higher than 1 (red dashed line) indicating that consumption exceeds production. Useful replicates (retrieved shoots) are shown in parentheses.

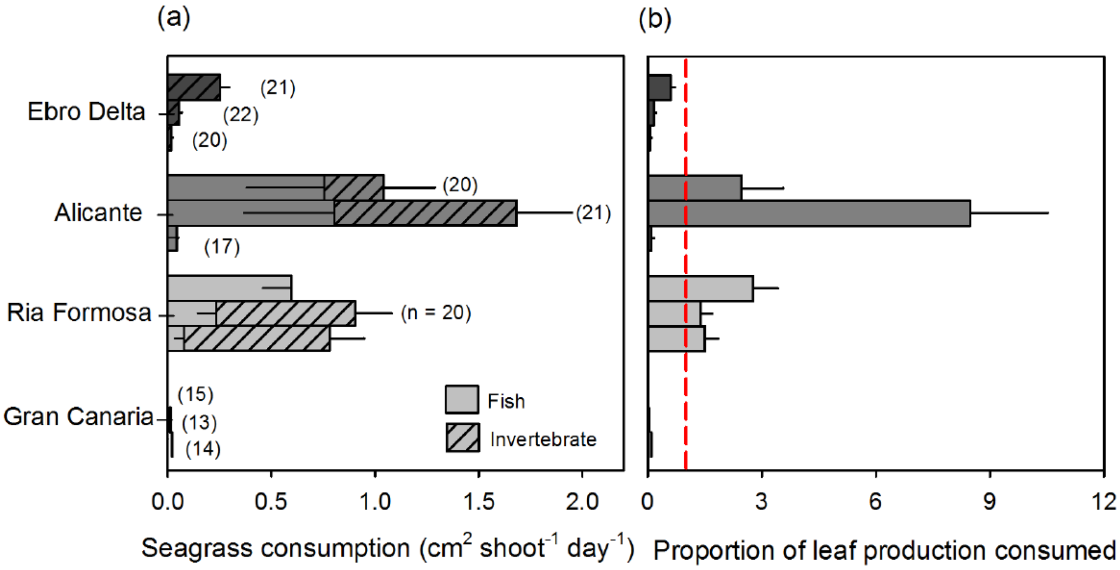
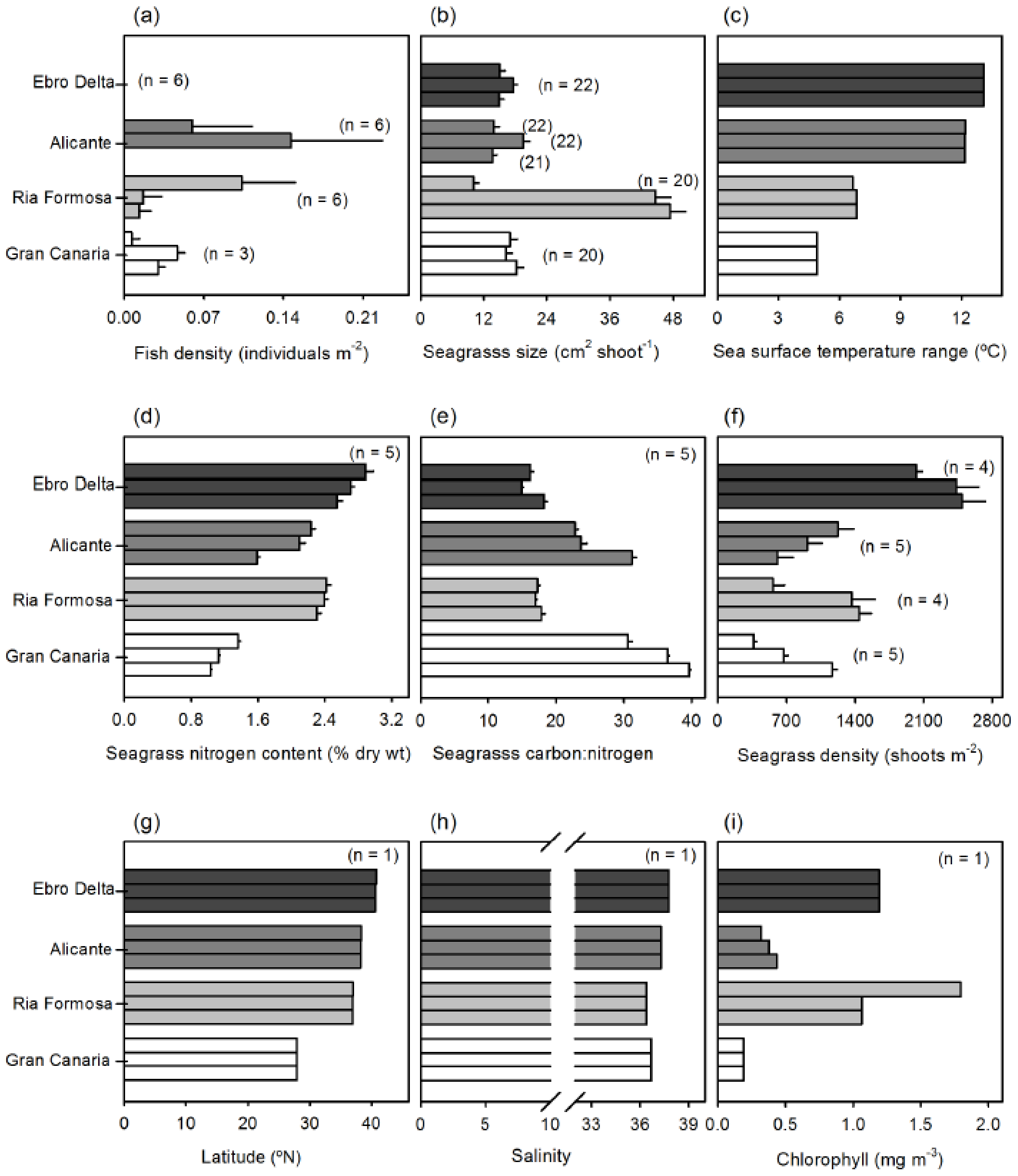


Figure 3. Key predictor variables that regulate seagrass herbivory at each meadow within the four biogeographical regions, from north to south (mean ± SE). Useful replicates are shown in parentheses. Data on herbivorous fish density refers to *Sarpa salpa* at temperate meadows and to *Sparisoma cretense* at subtropical meadows.



Supplementary Information for

Driving factors of biogeographical variation in seagrass herbivory

Begoña Martínez-Crego, Patricia Prado, Candela Marco-Méndez, Yolanda Fernández-Torquemada, Fernando Espino, Jose Luis Sánchez-Lizaso, Jose Antonio de la Ossa, David Mateu Vilella, Margarida Machado, Fernando Tuya

APPENDIX A. METHODS

Figure A1. Tethering method used to quantify rates of seagrass herbivory by fish and invertebrates. Each shoot was attached to a labelled tent peg separated by 1 meter from the next along a fishing line and fixed to the sediment at the level of the average height of the leaf canopy.

Figure A2. Tethering method used to quantify rates of seagrass herbivory by fish and invertebrates. After ca. 10 days of experiment, tethered shoots were retrieved and leaf area loss due to herbivory was calculated. Lateral grazing scars were measured using a 1 mm^2 grid. In those instances where the leaf apex was grazed, leaf loss to herbivory was calculated by subtracting the remaining leaf area above the punching mark (i.e. excluding leaf tissue grown during the experiment) to the area measured at the start of the experiment. We differentiated between fish herbivory (which left crescent moon-shaped bites) and invertebrate grazing (which results in serrated edges or holes). Animal images were courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

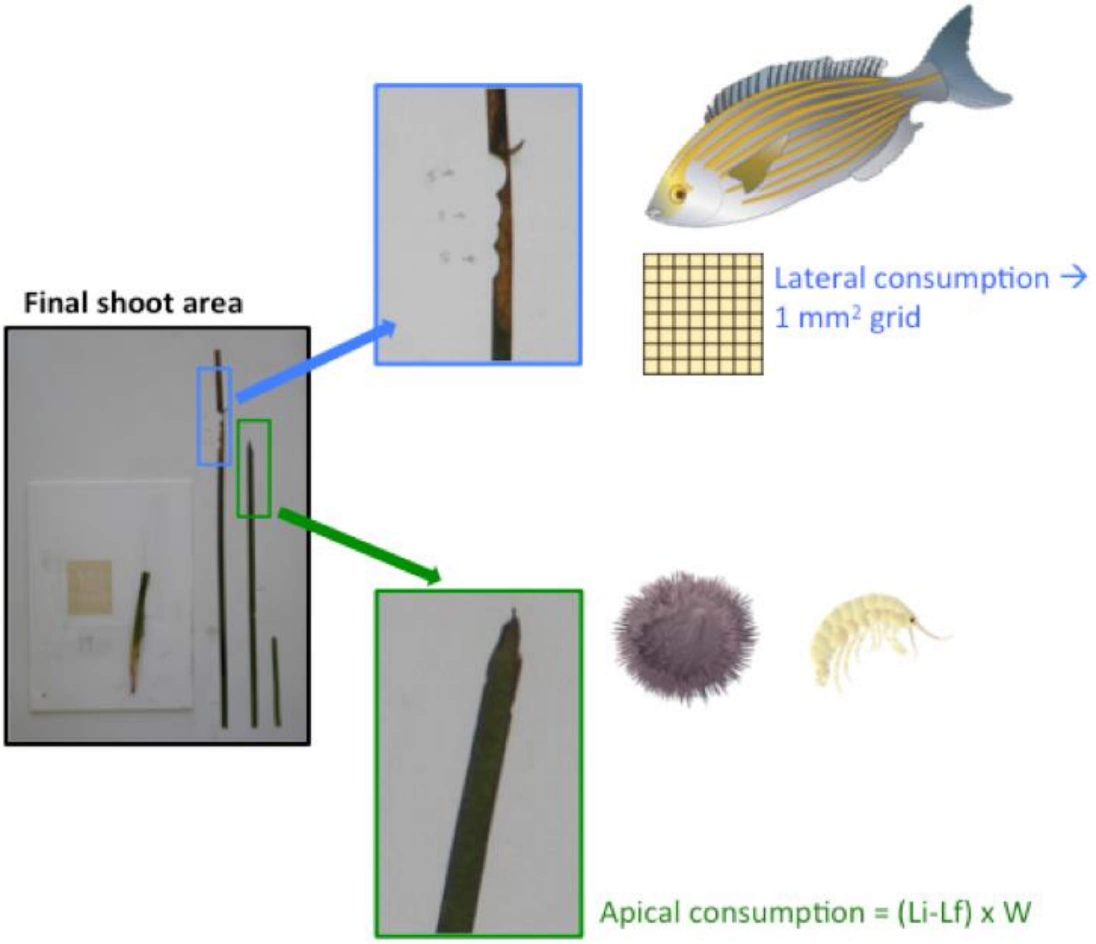


Figure A3. Tethering method used to quantify rates of seagrass herbivory by fish and invertebrates. Details of the punching mark used to exclude leaf tissue grown during the experiment from the herbivory loss, as well as of the leaf width (W), initial (Li) and final lengths (Lf), used to calculate apical consumption. The new leaf represents material entirely grown during the experiment.

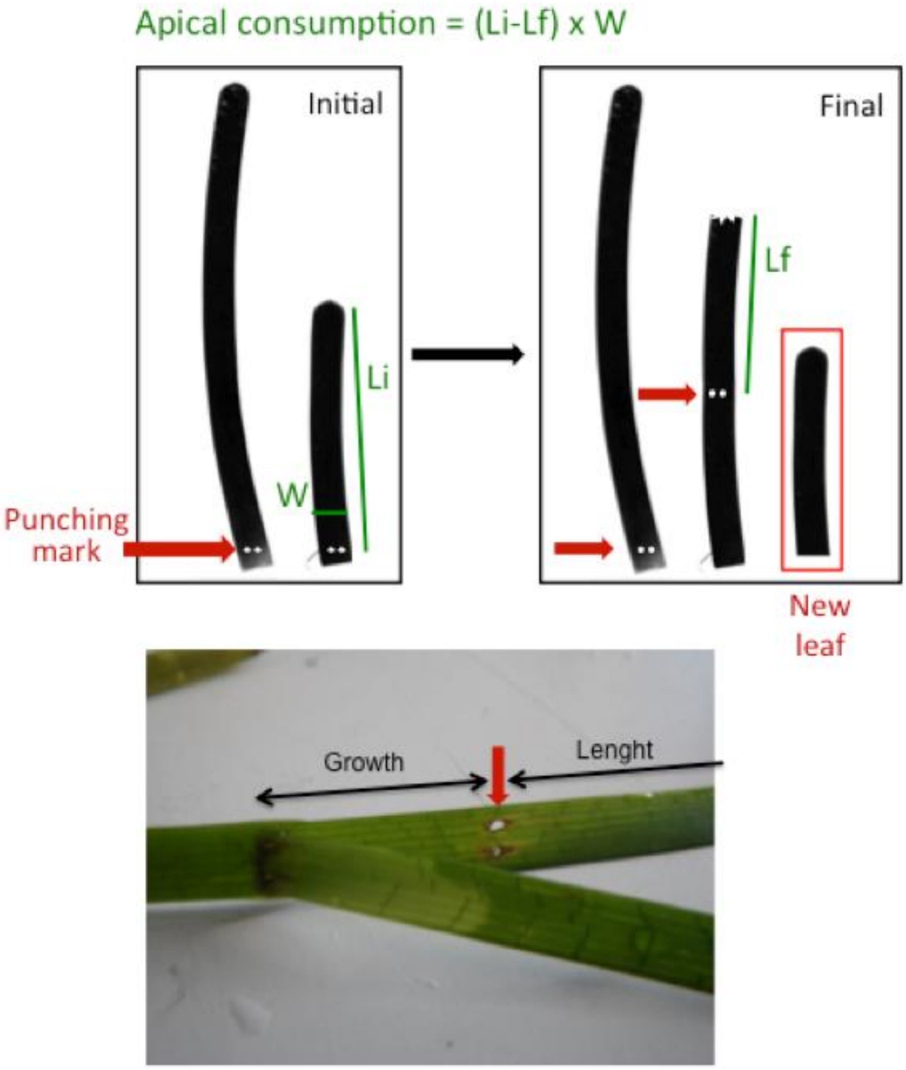


Figure A4. General view of the fine mesh bag affixed to a flexible 25 cm diameter hoop used to quantify the richness and abundance of mesograzers and vegetation (potential food resources for herbivores) at each meadow. Mesh bags were placed separated by ca. 5 m over the seagrass canopy, which was then cut at the sediment surface level.

APPENDIX B. BIOGEOGRAPHIC VARIATION IN SEAGRASS HERBIVORY

Table B1. Rates of seagrass consumption and production converted to biomass consumed/produced at the m^2 scale using site-specific surface area to weight regressions and shoot density values.

			g dry wt m^{-2} day^{-1}	
Region	**Meadow**	**Fish consumption**	**Invertebrate consumption**	**Production**
Ebro Delta (41ºN)	Fangar	0.03	2.52	8.33
	Trabucador	0	0.68	8.04
	Banya	0	0.20	6.07
Alicante (38ºN)	Albufereta	2.04	2.24	0.77
	CIMAR	0.10	0.01	1.38
	Vatasa	2.80	1.05	1.98
Ria Formosa (37ºN)	Praia	1.41	0	0.51
	Ramalhete	1.58	4.50	7.60
	Culatra	0.46	4.06	5.70
Gran Canaria (28ºN)	Caballo	0.002	0	0.52
	Gando	0.002	0	0.44
	Burrero	0	0	0.10

APPENDIX C. PREDICTOR VARIABLES THAT REGULATE SEAGRASS HERBIVORY

Table C1. Taxonomic list of small invertebrates identified as mesograzers. Those 9 species reported as seagrass consumers are detailed (`Yes´ in last column), including the supporting references. * Selected as mesograzed based on the trophic position or diet of species of the same genus.

Phylum	Class	Order	Family	Species	Seagrass consumer
Mollusca	Polyplacophora	-	-	*Polyplacophora* spp.	-
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae	*Bittium reticulatum*	-
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae	*Cerithium renovatum*	-
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae	*Cerithium vulgatum*	-
Mollusca	Gastropoda	Neogastropoda	Columbellidae	*Columbella rustica*	-
Mollusca	Gastropoda	Cephalaspidea	Haminoeidae	*Haminoea* spp.	-
Mollusca	Gastropoda	Cycloneritida	Neritidae	*Smaragdia viridis*	Yes[1,2]
Mollusca	Gastropoda	Trochida	Phasianellidae	*Tricolia pullus*	-
Mollusca	Gastropoda	Trochida	Phasianellidae	*Tricolia tenuis*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Pusillina radiata*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa auriscalpium*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa membranacea*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa monodonta*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa parva*	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa similis**	-
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	*Rissoa ventricosa**	-
Mollusca	Gastropoda	Trochida	Trochidae	*Steromphala adriatica*	-
Mollusca	Gastropoda	Trochida	Trochidae	*Phorcus richardi*	-
Mollusca	Gastropoda	Trochida	Trochidae	*Steromphala umbilicaris*	-
Mollusca	Gastropoda	Trochida	Trochidae	*Jujubinus striatus*	-
Arthropoda	Malacostraca	Decapoda	Hippolytidae	*Hippolyte inermis*	-
Arthropoda	Malacostraca	Decapoda	Hippolytidae	*Hippolyte leptocerus**	-
Arthropoda	Malacostraca	Decapoda	Palaemonidae	*Palaemon adspersus*	-
Arthropoda	Malacostraca	Decapoda	Palaemonidae	*Palaemon elegans*	-
Arthropoda	Malacostraca	Decapoda	Palaemonidae	*Palaemon* sp.*	-
Arthropoda	Malacostraca	Amphipoda	Ampithoidae	*Ampithoe rubricata*	-
Arthropoda	Malacostraca	Amphipoda	Ampithoidae	*Ampithoe ramondi*	-
Arthropoda	Malacostraca	Amphipoda	Ampithoidae	*Sunamphitoe pelagica*	-
Arthropoda	Malacostraca	Amphipoda	Aoridae	*Aora gracilis**	-
Arthropoda	Malacostraca	Amphipoda	Aoridae	*Aoridae n.i.**	-
Arthropoda	Malacostraca	Amphipoda	Aoridae	*Lembos websteri*	-
Arthropoda	Malacostraca	Amphipoda	Aoridae	*Microdeutopus stationis**	-
Arthropoda	Malacostraca	Amphipoda	Aoridae	*Microdeutopus gryllotalpa*	-

Phylum	Class	Order	Family	Species	Seagrass consumer
Arthropoda	Malacostraca	Amphipoda	Calliopiidae	*Apherusa chiereghinii*	-
Arthropoda	Malacostraca	Amphipoda	Calliopiidae	*Apherusa ovalipes**	-
Arthropoda	Malacostraca	Amphipoda	Dexaminidae	*Dexamine spinosa*	-
Arthropoda	Malacostraca	Amphipoda	Gammaridae	*Gammarus insensibilis*	Yes[3,4]
Arthropoda	Malacostraca	Amphipoda	Gammaridae	*Gammarus* sp.*	Yes[3,4]
Arthropoda	Malacostraca	Amphipoda	Ischyroceridae	*Ischyroceridae* n.i.*	-
Arthropoda	Malacostraca	Amphipoda	Ischyroceridae	*Ericthonius punctatus*	-
Arthropoda	Malacostraca	Amphipoda	Lysianassidae	*Lysianassa costae*	-
Arthropoda	Malacostraca	Amphipoda	Maeridae	*Elasmopus rapax*	-
Arthropoda	Malacostraca	Amphipoda	Nuuanuidae	*Gammarella fucicola*	-
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Caprella acanthifera*	-
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Caprella caveidinae**	-
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Caprella equilibra*	-
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Caprella* sp.*	-
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Phtisica marina*	-
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Cymodoce truncata*	Yes[3]
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Lekanesphaera hookeri*	Yes[5]
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Sphaeroma sp.**	-
Arthropoda	Malacostraca	Isopoda	Holognathidae	*Cleantis prismatica*	-
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Idotea balthica*	Yes[6]
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Idotea chelipes*	Yes[3,4,5,7,8]
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Synischia hectica*	Yes[3,6,9]
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Stenosoma wetzerae**	-
Arthropoda	Malacostraca	Tanaidacea	Tanaididae	*Tanais dulongii*	-
Annelida	Polychaeta	Phyllodocida	Nereididae	*Platynereis dumerilii*	Yes[10]

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Table C2. Spearman correlation coefficients, and associated p-values, between the battery of potential predictor variables. Significant correlation coefficients (p<0.05) are highlighted in bold. Abbreviations are: Seagrass production (Prod); Seagrass (SG); Mesograzer (Mgrazer), Sea surface temperature (SST), Salinity (S), Sediment (sed), Chlorophyll (chl). Replicates were n= 12, except for epiphyte biomass n=9 since data from Ebro Delta were not available.

	SG size	SG N	SG CN	SG density	Epiphyte biomass	Algal cover	Algal richness	Fish density	Urchin density	Mgrazer density	Mgrazer richness	SG-grazer density	SG-grazer richness	Fine sed	Latitude	SST mean	SST range	S	chl
Prod	0.38	0.43	-0.50	**0.68**	0.57	0.20	0.04	-0.51	**0.60**	0.48	0.47	0.33	0.53	0.15	0.31	-0.41	0.45	0.19	0.29
	0.22	0.15	0.09	0.01	0.10	0.51	0.90	0.08	0.04	0.11	0.12	0.28	0.07	0.62	0.32	0.18	0.13	0.54	0.35
Shoot size		-0.14	-0.07	0.27	0.47	0.13	0.57	0.08	0.42	0.36	0.45	0.18	0.32	0.29	-0.33	-0.02	-0.17	-0.23	-0.25
		0.65	0.82	0.38	0.19	0.68	0.051	0.78	0.17	0.23	0.14	0.56	0.30	0.34	0.28	0.94	0.57	0.46	0.43
SG N			**-0.94**	**0.66**	**0.77**	0.08	-0.02	-0.40	0.51	**0.63**	0.55	0.48	0.39	-0.25	**0.81**	**-0.79**	**0.77**	0.36	**0.91**
			<0.0001	0.02	0.01	0.80	0.94	0.18	0.08	0.03	0.06	0.11	0.20	0.42	0.0001	0.001	0.002	0.24	<0.0001
SG CN				**-0.58**	**-0.78**	-0.03	-0.07	0.30	-0.55	**-0.62**	**-0.64**	-0.53	-0.52	0.09	**-0.66**	**0.83**	**-0.62**	-0.15	**-0.83**
				0.04	0.01	0.92	0.80	0.34	0.06	0.03	0.02	0.07	0.07	0.77	0.02	<0.0001	0.03	0.64	<0.0001
SG density					**0.72**	0.06	-0.02	-0.47	**0.69**	**0.64**	0.44	0.55	0.54	-0.36	**0.58**	-0.43	**0.74**	0.51	0.48
					0.02	0.83	0.92	0.12	0.01	0.02	0.14	0.06	0.07	0.23	0.04	0.16	0.01	0.08	0.11
Epiphyte biomass						0.43	0.52	0.23	**0.73**	**0.87**	**0.88**	0.43	0.47	**0.92**	0.52	**-0.79**	0.66	-0.23	**0.72**
						0.22	0.14	0.52	0.02	<0.0001	<0.0001	0.22	0.19	<0.0001	0.14	0.01	0.050	0.52	0.02
Algal cover							**0.71**	-0.21	0.49	**0.64**	0.54	0.34	0.24	0.43	-0.15	-0.34	-0.06	-0.21	0.27
							0.01	0.48	0.10	0.02	0.07	0.26	0.44	0.15	0.62	0.27	0.83	0.50	0.38
Algal richness								0.19	0.37	**0.60**	**0.62**	0.21	0.24	0.54	-0.27	-0.24	-0.21	-0.37	0.04
								0.54	0.22	0.04	0.03	0.50	0.43	0.07	0.38	0.43	0.50	0.22	0.90
Fish density									-0.39	-0.15	0.03	-0.13	-0.09	0.50	-0.39	0.03	-0.45	**-0.60**	-0.32
									0.20	0.64	0.90	0.68	0.75	0.09	0.20	0.90	0.14	0.04	0.31
Urchin density										**0.78**	**0.63**	**0.70**	**0.66**	0.02	0.21	-0.56	0.36	0.05	0.46

SG size	SG N	SG CN	SG density	Epiphyte biomass	Algal cover	Algal richness	Fish density	Urchin density	Mgrazer density	Mgrazer richness	SG-grazer density	SG-grazer richness	Fine sed	Latitude	SST mean	SST range	S	chl
									0.001	0.03	0.01	0.02	0.96	0.50	0.055	0.24	0.87	0.13
									Mgrazer density	**0.92**	**0.68**	**0.58**	0.21	0.34	**-0.75**	0.45	0.01	**0.67**
										<0.0001	0.01	0.04	0.50	0.27	0.003	0.14	0.96	0.02
										Mgrazer richness	0.50	0.46	0.46	0.28	**-0.77**	0.35	-0.13	**0.62**
											0.09	0.12	0.13	0.36	0.002	0.25	0.67	0.03
											SG-grazer density	**0.88**	-0.12	0.06	**-0.64**	0.15	-0.22	0.51
												<0.0001	0.70	0.83	0.02	0.64	0.48	0.08
												SG-grazer.richness	0.02	0.03	-0.52	0.13	-0.23	0.29
													0.94	0.90	0.07	0.68	0.47	0.35
													Fine. sed	-0.36	-0.26	-0.33	**-0.64**	-0.12
														0.24	0.40	0.28	0.02	0.70
														Latitude	-0.41	**0.96**	**0.74**	**0.66**
															0.18	<0.0001	0.005	0.02
															SST mean	-0.39	0.22	**-0.86**
																0.20	0.48	<0.0001
																SST range	**0.78**	**0.60**
																	0.002	0.04
																	S	0.18
																		0.57

Figure C1. Battery of unselected biotic predictor variables at each meadow within the four biogeographical regions, ordered from north to south (mean ± SE). Useful replicates are shown in parentheses. NA: data not available.

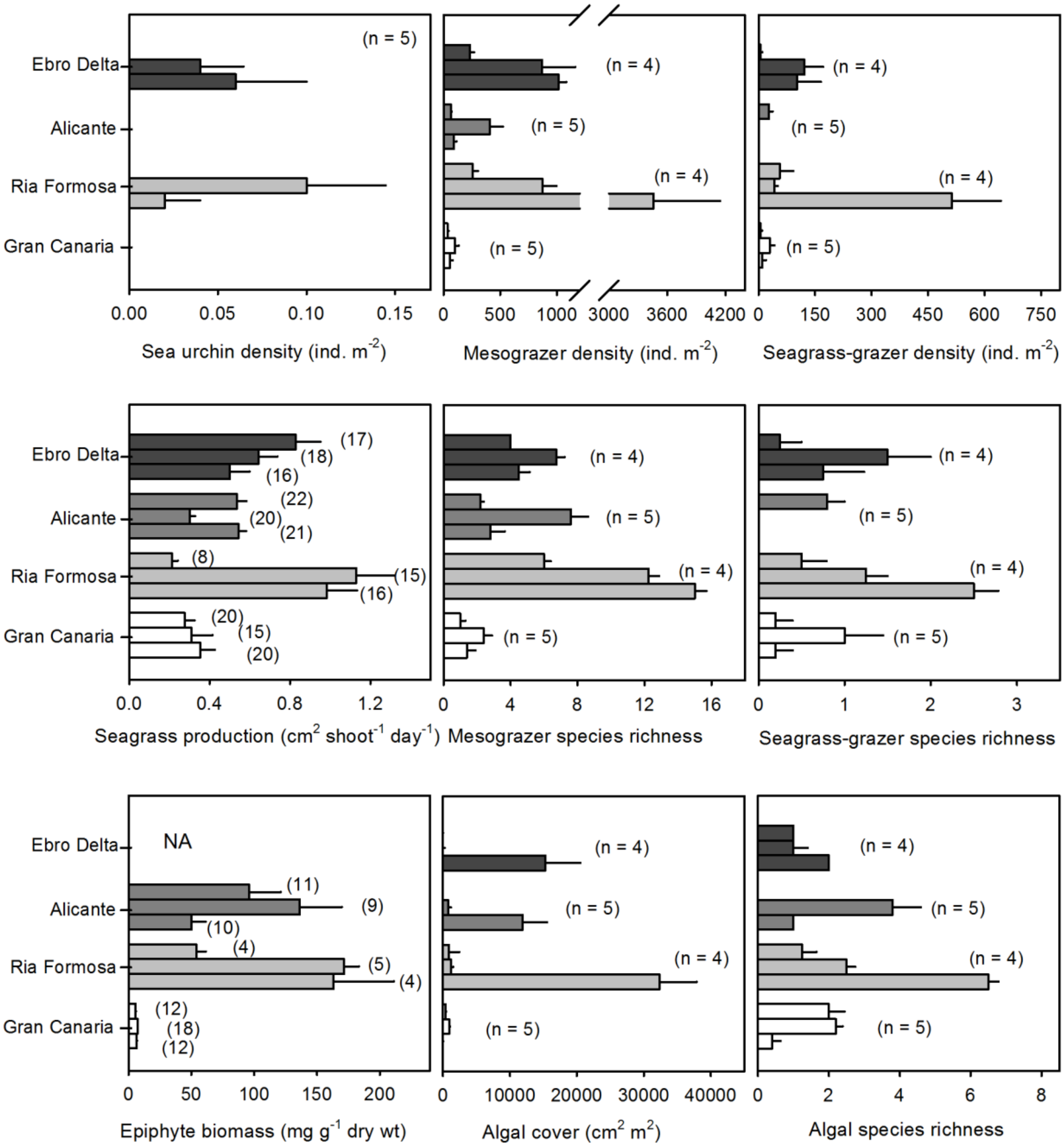

Figure C2. Unselected environmental predictor variables at each meadow within the four biogeographical regions, from north to south (mean ± SE). Useful replicates are shown in parentheses.

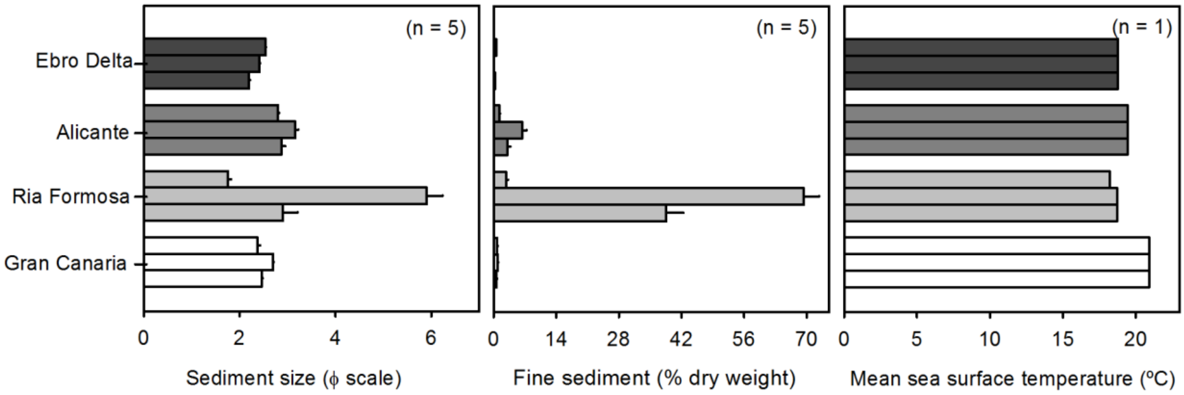

Table C3. Results from the stepwise model selection for seagrass herbivory, using the MASS package in R.

Response variable	Predictors (selected model)	Adjusted R^2	F	df	p-value	Significant predictors (p-value)
Fish consumption	Fish density, temperature range	0.74	16.9	2 and 9	0.001	Fish density (p=0.0003); SST range (n.s.)
Invertebrate consumption	Temperature range, mesograzer density, seagrass size, nitrogen and production	0.68	5.7	5 and 6	0.03	Seagrass size (p=0.006), production (p=0.03), SST range (p=0.04)
Total consumption	Fish density, seagrass size, temperature range	0.88	28.2	3 and 8	0.0001	Fish density (p=0.00004), seagrass size (p=0.0005), SST range (p=0.006)
Leaf production consumed	Fish density, seagrass size, temperature range	0.92	42.8	3 and 8	0.00003	Fish density (p=0.000004), SST range (p=0.003), seagrass size (p=0.006)

Table C4. Results of model selection for seagrass herbivory using the MuMIn package in R, including models ranked by the AICc. Adjusted R^2, p-values, and significant predictors for each model. For each selected model (the first one), the variance inflation factor (VIF) is shown when more than one predictor was selected. Breush-Pagan heteroskedasticity tests are also shown for the full and selected models. Abbreviations are: sea surface temperature (SST), non-significant (n.s.)

		MuMIn results					**Model summary**					
Variable	**Model predictors**	**df**	**logLik**	**AICc**	**delta AIC**	**weight (wi)**	**Adjusted R^2**	**F**	**p-value**	**Significant predictors (p-value)**	**VIF**	**Breush-Pagan test (p-value)**
Fish consumption	Fish density	3	5.3	-1.5	0	0.48	0.71	27.8	0.0004	0.0004		BP = 0.71 (p= 0.40)
	Fish density, seagrass nitrogen	4	6.9	-0.12	1.4	0.24	0.75	17.9	0.0007	Fish density (p < 0.001)		
	Fish density, SST range	4	6.6	0.5	2.0	0.18	0.74	16.9	0.001	Fish density (p < 0.001)		
	Fish density, seagrass size	4	5.3	3.1	4.6	0.05	0.68	12.7	0.002	Fish density (p < 0.001)		
	Fish density, algal cover	4	5.3	3.2	4.7	0.05	0.68	12.5	0.003	Fish density (p = 0.001)		
	All 5 (Seagrass nitrogen, seagrass size, fish density, algal cover, SST range)	7	7.6	27	28	0.0000003	0.67	5.4	0.031	Fish density (p=0.003)		BP = 1.73 (p = 0.19)
Invertebrate consumption	Seagrass size	3	0.8	7.5	0	0.55	0.42	9.1	0.01	Seagrass size (p= 0.01)		BP = 6.84 (p= 0.009)
	Seagrass size, SST range	4	2.2	9.4	1.9	0.21	0.49	6.3	0.02	Seagrass size (p< 0.01)		
	SST range, seagrass size and production	5	4.5	11.0	3.6	0.09	0.61	6.8	0.014	Seagrass size (p< 0.01); (SST range p = 0.03)		
	Seagrass production	3	-1.3	11.6	4.2	0.07	0.18	3.5	0.092	n.s.		
	Seagrass size and production	4	0.8	12.1	4.7	0.05	0.36	4.1	0.054	n.s.		
	SST range	3	-3.0	15.1	7.6	0.012	-0.09	0.1	0.75	n.s.		
	SST range, seagrass size and production, mesograzer density	6	6.3	16.2	8.7	0.007	0.67	6.6	0.02	Seagrass size (p< 0.01); SST range (p = 0.01); Production (p= 0.042)		
	Seagrass production, SST range	4	-1.3	16.3	8.9	0.006	0.09	1.6	0.26	n.s.		
	SST range, seagrass size, production and nitrogen	6	4.6	19.5	12.1	0.001	0.57	4.6	0.04	Seagrass size (p= 0.01)		
	All 5 (mesograzer density, SST range, seagrass size, nitrogen, and production)	7	7.4	27.2	19.7	0.00003	0.68	5.7	0.03	Seagrass size (p< 0.01); Production (p = 0.03); SST range (p= 0.04)		BP = 0.12 (p = 0.73)
Total consumption	Fish density, seagrass size, SST range	5	5.3	9.4	0	0.91	0.88	28.2	0.0001	Fish density (p < 0.0001); Seagrass size	Fish density:	BP = 0.05 (p = 0.82)

		MuMIn results					Model summary					
Variable	**Model predictors**	**df**	**logLik**	**AICc**	**delta AIC**	**weight (wi)**	**Adjusted R^2**	**F**	**p-value**	**Significant predictors (p-value)**	**VIF**	**Breush-Pagan test (p-value)**
										(p< 0.001); SST range (p< 0.01)	1.06, Seagrass size: 1.16, SST range: 1.12	
	Fish density, seagrass size	4	-0.7	15.2	5.8	0.05	0.71	14.6	0.002	Fish density (p< 0.001); Seagrass size p = 0.01		
	Fish density, SST range, seagrass size, algal cover	6	6.0	16.7	7.3	0.02	0.88	21.1	0.001	Fish density (p = 0.0001); Seagrass size (p = 0.001); SST range (p< 0.01)		
	Fish density, SST range, seagrass size and nitrogen	6	5.3	18.2	8.8	0.01	0.86	18.5	0.001	Fish density (p = 0.0001); Seagrass size (p = 0.002); SST range (p =0.047)		
	Fish density	3	-5.0	18.9	9.6	0.008	0.47	10.9	0.008	Fish density (p< 0.01)		
	Fish density, SST range	4	-4.4	22.5	13.1	0.001	0.47	5.8	0.02	Fish density (p< 0.01)		
	Seagrass size	3	-8.6	26.3	16.9	0.0002	0.03	1.3	0.28	n.s.		
	SST range	3	-9.2	27.4	18.0	0.0001	-0.07	0.3	0.60	n.s.		
	Seagrass size, SST range	4	-8.1	29.8	20.4	0.00003	0.02	1.1	0.37	n.s.		
	All 5 (fish density, algal cover, SST range, seagrass size and nitrogen)	7	6.1	29.9	20.5	0.00003	0.86	14.6	0.003	Fish density (p< 0.001); Seagrass size (p< 0.01); SST range (p = 0.046)		BP = 0.07 (p = 0.79)
Leaf production consumed	Fish density, seagrass size, SST range	5	-10.1	40.2	0	0.84	0.92	42.8	0.00003	Fish density (p< 0.00001); SST range (p= 0.003); Seagrass size (p= 0.006)	Fish density: 1.06, Seagrass size: 1.16, SST range: 1.12	BP = 0.025 (p = 0.87)
	Fish density	3	-18.3	45.6	5.4	0.06	0.75	33.6	0.0002	Fish density (p = 0.0002)		
	Fish density, SST range	4	-16.1	45.9	5.7	0.05	0.81	23.8	0.0003	Fish density (p< 0.0001)		
	Fish density, seagrass size	4	-17.0	47.7	7.4	0.02	0.78	20.0	0.0005	Fish density (p = 0.0001)		
	Fish density, SST range, seagrass size and nitrogen	6	-9.5	47.8	7.6	0.02	0.92	31.4	0.0001	Fish density (p = 0.00001); Seagrass size (p< 0.01); SST range (p = 0.01)		
	Fish density, SST range, seagrass size, algal cover	6	-10.0	48.9	8.7	0.01	0.91	28.4	0.0002	Fish density (p = 0.00002); SST range (p< 0.01); Seagrass size p = 0.02		

		MuMIn results			Model summary							
Variable	**Model predictors**	**df**	**logLik**	**AICc**	**delta AIC**	**weight (wi)**	**Adjusted R^2**	**F**	**p-value**	**Significant predictors (p-value)**	**VIF**	**Breush-Pagan test (p-value)**
	All 5 (fish density, algal cover, SST range, seagrass size and nitrogen)	7	-9.4	60.7	20	0.00003	0.91	22.04	0.0009	Fish density (p< 0.0001); SST range (p = 0.02); Seagrass size (p = 0.02)		BP = 0.37 (p = 0.54)
	SST range	3	-26.8	62.7	22	0.00001	-0.05	0.51	0.49	n.s.		
	Seagrass size	3	-27.1	63.2	23	0.00001	-0.10	0.01	0.91	n.s.		
	Seagrass size, SST range	4	-26.8	67.2	27	0.000001	-0.15	0.29	0.76	n.s.		