

## Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure

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### Abstract

We characterized the seasonal and interannual variation in macrophytes, epiphytes, invertebrate herbivores, small demersal predators, and physicochemical characteristics of an eelgrass (*Zostera marina*) bed in Chesapeake Bay, Virginia, over 10 yr, to explore the relative importance of abiotic and biotic forcing on community composition and abundance. Our hypotheses were (1) physicochemical drivers affect community structure directly, (2) bottom-up trophic control is evidenced by positive covariance among trophic levels, (3) top-down control generates inverse patterns of abundance at adjacent trophic levels, and (4) species diversity among herbivores contributes to temporal stability. Composition and abundance of eelgrass-associated species varied strongly among seasons and years. Much of this variation correlated with temperature and salinity anomalies, and multivariate analysis grouped communities roughly by season, supporting our first hypothesis. Severe seagrass loss during the hot summer of 2005 shifted the community toward a novel composition, but community structure rebounded within a year. Evidence for trophic control was mixed: selected taxa showed patterns consistent with top-down or bottom-up control, but these patterns generally disappeared at the level of whole years and entire trophic levels. Our ability to detect trophic effects may have been limited, however, by consumer movement or changing behavioral responses to resource availability and predation. There was also little evidence that diversity stabilized total herbivore abundance. Although consumer effects on lower levels were inconsistent, the strong physicochemical forcing of community structure supports suggestions that eelgrass communities are highly vulnerable to natural and anthropogenic changes in climate and hydrography.

Productivity, the distribution of biomass, and other aspects of ecosystem structure can be determined by “bottom-up” effects, which propagate from basal resources or prey to successively higher consumers, or by “top-down” effects, which propagate from consumers down to prey or basal resources. While the relative importance and generality of top-down vs. bottom-up control has been the subject of vigorous debate (Polis and Strong 1996), there is a growing consensus that both top-down and bottom-up processes, and their interactions, affect most ecosystems (Worm et al. 2002). Consequently, some ecosystems previously studied from a predominantly top-down or bottom-up perspective are now being evaluated from the alternative, or an integrated, view (Frank et al. 2007; Eriksson et al. 2009). For example, ecological studies of seagrass ecosystems, which have focused largely on physicochemical influences and bottom-up effects of plants on consumers, are increasingly considering the potential importance of top-down control (Hughes et al. 2004; Heck and Valentine 2007).

Seagrasses form productive and species-rich habitats in coastal areas throughout the world (Hemminga and Duarte 2000), where they contribute to human well-being by stabilizing sediments, improving water quality, and enhancing fisheries resources (Worm et al. 2006). Unfortunately, seagrasses have declined dramatically in many regions (Orth et al. 2006). Effects of human activities on habitat quality have been implicated in most of these

declines; increased sediment and nutrient inputs lead to high turbidity and eutrophic overgrowth of seagrass by epiphytes (Kemp et al. 2004; Orth et al. 2006), and anthropogenic changes in climate and hydrography can exceed the physiological tolerances of seagrasses (Moore and Jarvis 2008). Yet the abundance and species composition of herbivores (Hughes et al. 2004, Valentine and Duffy 2006) and predators (Heck and Orth 2006) also affect seagrass. These top-down factors may be changing as a result of fishing and other effects on marine animals, potentially contributing to seagrass declines (Jackson et al. 2001; Heck and Valentine 2007).

Seagrass herbivory can be divided into two broad classes: direct grazing, which removes seagrass biomass, and epiphyte grazing, which removes algal competitors and can indirectly benefit seagrass (Valentine and Duffy 2006). Metaanalyses of mesocosm and field experiments show that the effects of both types of grazing on seagrass growth and biomass tend to be equal to or greater in magnitude than nutrient enrichment effects (Hughes et al. 2004) and that epiphyte grazing in particular can counteract some negative effects of nutrients (Neckles et al. 1993). This has led some to hypothesize that eutrophic overgrowth of seagrass by epiphytes can only occur when healthy grazer communities have been disturbed by outside factors, such as trophic cascades stemming from overharvesting of top predators by humans (Heck and Valentine 2007). Overfishing of predatory species could either increase or decrease grazing intensity, depending on the structure of the seagrass-associated food web and the trophic position of the

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predators harvested (Valentine and Duffy 2006; Heck and Valentine 2007). To effectively conserve and restore seagrass beds, we need a better understanding of seagrass community interaction webs: how top-down and bottom-up effects interact with physicochemical factors to determine seagrass survival and persistence. One approach toward this understanding involves connecting the results of small-scale, manipulative experiments to our interpretations of seagrass dynamics at landscape scales.

Controlled experiments have been useful in evaluating the relative importance of top-down and bottom-up factors affecting seagrasses at local scales (Hughes et al. 2004), including the important roles of consumer species composition and diversity in determining ecosystem properties and buffering against disturbance (reviewed by Duffy 2006). These experimental studies have generally found strong effects of consumers on primary producers (Hughes et al. 2004), but artifacts of small-scale experiments, including short duration, simplified food webs, and lack of dispersal and recruitment, raise questions as to how well their interpretations can be extrapolated to the scale of real seagrass beds, as in ecosystems generally (Carpenter 1996). Although field survey data have their own limitations, notably the ambiguous covariation of multiple interacting species and environmental factors (Bender et al. 1984), they can help to assess the relevance of experimental findings to large-scale community dynamics and to identify differences that may reveal other, important processes occurring at natural scales. For instance, comparison of the temporal variation in total mesograzer abundance to that of individual mesograzer species could test the “insurance hypothesis,” which states that diversity helps to maintain consistent biomass or function through changing conditions (Naem and Li 1997). Unfortunately, mobile epifauna have seldom been included in observational studies designed to relate seagrass performance to physicochemical conditions (Kemp et al. 2004), making it difficult evaluate the contributions of consumers to seagrass ecosystem properties. Likewise, observations of consumer abundance and distribution in seagrass beds (Marsh 1973; Nelson et al. 1982; Edgar 1990b) have rarely assessed their top-down effects on seagrass health, with the notable exception of Jørgensen et al. (2007). Analysis of long-term monitoring data with both physical and biological components is one approach to more fully understanding how top-down and bottom-up processes interact to affect seagrass beds in natural settings.

The dominant forcing in temperate seagrass beds is likely to be seasonality, because seasonal changes in the physicochemical environment directly affect many plants and animals, and top-down or bottom-up processes stemming from the affected organisms can lead to further community changes (Edgar and Barrett 2002). Where top-down control occurs it is probably superposed on seasonal patterns set by physicochemical and bottom-up forces, and it might reveal itself in either of two ways. One indication would be inverse correlations in the abundance of adjacent trophic levels across spatial and/or interannual temporal scales. A second indication would be asynchronous peaks in abundance of adjacent trophic levels within years, as Stoner (1980) and

Nelson et al. (1982) observed for small fish and mesograzers in Florida seagrass beds. These two types of patterns have often been hypothesized and suggested experimentally (Duffy et al. 2005), but field data supporting the patterns remain rare and mostly limited to just two adjacent trophic levels (but see Jørgensen et al. 2007).

In the Chesapeake Bay estuary (Virginia), submerged aquatic vegetation including eelgrass (*Zostera marina* L.) has been monitored extensively since the 1970s (Moore et al. 2000; Kemp et al. 2004). While this monitoring has included both seagrass areal coverage and water quality parameters to address the bottom-up relationship between physicochemical conditions and seagrass, surveys of seagrass-associated fauna and epiphytes are rare and inconsistent prior to 1998, precluding analysis of trophic dynamics. Since 1998, however, we have maintained an approximately monthly monitoring program, keeping track of lower levels of the food web, including seagrass, epiphytic algae, mesograzers, and small demersal predators, in an eelgrass bed in the polyhaline region of the lower Chesapeake Bay. Here we have assembled these data, together with climate and water quality information, to assess and compare the variation in both biotic and abiotic aspects of an eelgrass community. We sought to test the following hypotheses: (1) physicochemical drivers, including temperature, salinity, and turbidity, control community structure via direct effects on organisms; (2) eelgrass communities are structured via bottom-up trophic control, as evidenced by positive covariance among trophic levels; (3) top-down control generates inverse patterns of abundance at algal, herbivore, and predator trophic levels; and (4) diversity of herbivores contributes to stability through time of the important intermediate trophic level that links primary producers to harvested fish and crustaceans.

## Methods

*Study location*—Our data were collected at the Goodwin Islands National Estuarine Research Reserve, located at the mouth of the York River in Chesapeake Bay (Virginia, 37°13'N, 76°23'W). Goodwin Islands is a 3.15 km<sup>2</sup> hectare archipelago of salt-marsh islands surrounded by intertidal flats and subtidal seagrass beds (*Z. marina* and *Ruppia maritima*) extending to a maximum of about 1 m mean-low-water depth. The area is closed to development and destructive use but remains open to commercial and recreational fishing. Surveys were performed in an area of seasonally dense *Z. marina* (hereafter “eelgrass”) on the southeast side of the islands.

*Data collection overview*—Water quality and meteorological data have been monitored semicontinuously at Goodwin Islands since October 1997 by the Chesapeake Bay National Estuarine Research Reserve System (NERRS). Water temperature, salinity, dissolved oxygen, pH, and turbidity are recorded at 15-min intervals from a permanent monitoring station in the eelgrass bed by a Yellow Springs Instruments (YSI) 6600 extended deployment system data sonde, following standard YSI and NERRS System-wide Monitoring Program protocols



ed from roots and rhizomes, and all flora and sessile epifauna were identified to the lowest taxonomic level possible, usually species. Sessile organisms including eelgrass were dried at 60°C, weighed, and combusted to determine ash-free dry weight (AF dry wt). Mobile epifauna were sorted by size class with a nested series of sieves (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, and 0.50-mm screens), then identified to species and counted. Counts of individuals within each size class were multiplied by empirically derived coefficients to convert them to biomass (mg AF dry wt) and production ( $\mu\text{g AF dry wt d}^{-1}$ ) (Edgar 1990a). Figures and statistical analyses of mesograzers abundance all use biomass unless otherwise noted.

*Epiphyte sampling*—A single eelgrass shoot (approximately five blades) was collected from each of the five sampling spots along a transect. Fouling material was scraped from the blades and collected on Whatman glass fiber filters, and blade surface area was determined with a Li-Cor 3100 area meter (Li-Cor). We measured Chl *a* as a proxy for the biomass of photosynthesizing algae on the blades. Filters with algae were extracted in 20 mL 90% acetone at  $-20^{\circ}\text{C}$  for 24 h. The extract was passed through a 0.45- $\mu\text{m}$  polytetrafluoroethylene membrane filter (Millipore Corporation), and absorbance was monitored at 480, 510, 630, 647, and 750 nm using a Shimadzu UV-1601 spectrophotometer (Shimadzu Scientific Instruments). Chl *a* concentration was calculated with the trichromatic equation (Lorenzen 1967), and Chl *a* mass was calculated and normalized to blade area to serve as a proxy for epiphyte density.

*Eelgrass biomass sampling*—At each of the five sampling spots along a transect, a core of eelgrass and rhizomes approximately 15-cm deep was collected with a 15-cm diameter tube. Cores were taken even if no aboveground eelgrass biomass was apparent. Blades and rhizomes from the core were separated, dried, and combusted to determine aboveground and belowground biomass (AF dry wt) for the core.

*Eelgrass cover and small predator sampling*—At each sampling spot, a 5-m rope was stretched perpendicular to the transect line. A 52-cm wide dip net was swept once along the rope to collect small, demersal predators such as shrimp and juvenile fish. Numbers of each predator species in the net were recorded, and fish and crabs were measured to the nearest millimeter. Concurrent with the predator sweep, eelgrass presence or absence was recorded as 1 or 0 for each 1-m interval along the 5-m rope. A 0 was recorded if less than 10% of the sediment along the 1-m stretch of rope was occluded by eelgrass. Binary data were later converted to proportional cover (0, 0.2, 0.4, 0.6, 0.8, or 1.0) by adding up the ones and dividing by five. This measure was intended to capture mesoscale patchiness of the bed that was not detected by aerial surveys.

*Data analysis*—Time series of biological data were generated from the mean and standard error of replicate samples within each monthly sample date. Time series for temperature, salinity, and turbidity were based on averages

of the continuously monitored data from the 30 d leading up to each focal date. Average annual cycles were derived by taking mean values for each day of the year across all years of the data set. For chemical and biological data, which were recorded less often than daily, we used linear interpolation to estimate daily values within years before deriving annual cycles as described above.

Multiple linear regressions were used to assess correlation among deviations from the average seasonal patterns of biological and physicochemical variables. Each “deviation” was calculated as the difference between the sample datum for a given date and the multiyear average estimated for the same day of year. This transformation reduced the severity of serial correlation and helped the data meet the normality and homoscedasticity assumptions of linear regression, so no further data transformations were applied. The regression models used were a small subset of all possible variable combinations; we only tested for correlations that were predicted by knowledge of the natural history of the system and that could be interpreted in light of our hypotheses (Burnham and Anderson 2002). Decisions about what factors to include in models were also dictated by the temporal extent of the data (Table 1); we opted to include epiphytic Chl *a* in most models, limiting the usable data to the years 2001–2006. We excluded eelgrass shoot biomass from most models because it was only monitored after 2004, but we included it in some models of predator abundance to examine the influence of habitat on predators (Orth and Heck 1980). We ran separate models using data from the whole year, only spring data (days 70–150), and only summer data (days 180–260), under the assumption that deviations in certain factors (i.e., temperature) might have different effects during the early vs. late season. In addition to the regressions described above, we evaluated models predicting spring eelgrass extent at Goodwin Islands, for which we had only one datum per year. The predictor variables for these regressions were not deviations from multiyear averages, but rather averages of daily values from each of two periods we hypothesized to be relevant to spring eelgrass abundance: spring days 70–120, when much growth occurs (Orth and Moore 1986), and summer days 200–250 of the preceding year, when much senescence occurs (Moore and Jarvis 2008).  $R^2$  values were calculated for all models, and the relative likelihood of models was compared using Akaike’s Information Criterion (AIC). We considered “good” models to be those that explained a sizeable portion of the variance in a response and that were weighted favorably relative to the other models by AIC (Burnham and Anderson 2002). Only results for models in which both  $R^2$  and weighted model probability ( $w_i$ ) were  $> 0.1$  are presented here, but full model results are presented in the supplemental material.

The potential contribution of mesograzers species richness to the stability of total mesograzers abundance over time was assessed by comparing the temporal variance of total mesograzers abundance to the temporal variances of the abundances of individual species (Frost et al. 1995; Downing et al. 2008). The following ratio

was used for this comparison:  $(S_{\text{total mesograzer abundance}}^2) \times (\sum S_{\text{individual species abundance}}^2)^{-1}$ . A ratio value  $> 1$  would indicate that mesograzers of different species tended to vary synchronously, increasing the temporal variance of total mesograzer abundance, whereas a ratio  $< 1$  would indicate that mesograzers tended to vary in an asynchronous, compensatory manner, reducing the variance of total mesograzers. Temporal variances were assessed over four, alternate timescales: (1) all sample dates ( $n = 58$ ), (2) annual averages ( $n = 9$ ), (3) monthly averages calculated from across all years ( $n = 9$ , March, April, May, June, July, August, September, October, November), and (4) all sample dates, but with the ratio of variances calculated separately for each year and then averaged across years ( $n = 58$ ). The statistical significance of variance ratios was tested with resampling, over 10,000 iterations. Univariate statistical analyses were done using Minitab, Resampling Stats for Microsoft Excel, and our own calculations in MS Excel.

Although we used univariate statistics to examine our hypothesized relationships among eelgrass community components, we also assessed the multivariate community structure in a subset of the data using the nonmetric multidimensional scaling (MDS) and hierarchical clustering analysis routines in the Primer v6 software package (Clarke and Gorley 2006). The subset of data used was limited to dates between 2001 and 2006 in order to include the following variables: epiphytic Chl *a*, the biomass of each species of mesograzer per unit plant biomass, and the abundance of several categories of small predator: pipefish (*Syngnathus* spp.), other fish, blue crabs (*Callinectes sapidus*), and *Palaemonetes* spp. and *Crangon* spp. shrimp. Before analysis these data were rescaled to the maximum within each class of variables—epiphytic Chl *a*, caprellid amphipods, mesograzers, fish, blue crabs, and decapod shrimp—and were square-root transformed. (Caprellids were rescaled separately from the other mesograzers to allow for the possibility that their filter feeding habits diminish their per-biomass grazing effects.) The MDS results were plotted in two dimensions and labeled according to month and year. The cluster analysis routine was run with a similarity profile test (Clarke and Gorley 2006), which identified the multivariate groupings of the data that were statistically supported at the  $p < 0.05$  level. A similarity percentage test, which identified the contributions of each variable to the differentiation at each branch in the cluster dendrogram, was also run.

## Results

*Physicochemical conditions*—Thirty-day average water temperature at Goodwin Islands exhibited strong, unimodal, annual cycles, ranging from 0°C to 30°C (Figs. 1, 2). Interannual variation was apparent both in minimum winter temperatures and in maximum summer temperatures, with the warmest summer occurring in 2005 (Fig. 1). Thirty-day average salinity ranged from 13 to 26 g L<sup>-1</sup> with a weak seasonal cycle and high variability on an interannual scale (Figs. 1, 2). Notably, there was some indication of multiyear salinity regimes with the period

between 1999 and 2003 averaging  $\sim 22$  g L<sup>-1</sup>, while before and after that period the salinity averaged about 18 g L<sup>-1</sup>. Daily averages for turbidity ranged from near 0 to over 200 nephelometric turbidity units (NTU) after storm events. This stochastic variability remained apparent in 30-d averages, which ranged from 3 to 30 NTU (Fig. 1). Despite this high variation, turbidity exhibited a distinct seasonal trend, with higher values usually occurring in the late summer or fall (Fig. 2).

*Eelgrass and epiphytes*—Density adjusted eelgrass coverage on the southeast side of Goodwin Islands increased from 36 to 56 ha from 1998 to 2002, then declined to 23 ha by 2006 (Fig. 1). These data came from aerial photographs taken only in the spring of each year when eelgrass was usually dense, but our ground-based eelgrass biomass monitoring from March 2004 through October 2007 captured seasonal as well as interannual variation (Fig. 3). In 2004 and 2005, eelgrass biomass and cover peaked in the spring and early summer and declined in late summer: a cycle previously documented for the Chesapeake Bay (Orth and Moore 1986). The late summer decline was severe in 2005, however, and the seasonal cycle appeared disrupted in 2006 (Moore and Jarvis 2008). Interestingly, in 2006, shoot biomass reached its highest level quite late in the year. Seasonal cycles were clear in the time series of epiphyte density (Fig. 3), but epiphytes peaked much later in the year than eelgrass (Fig. 4). The 2005 eelgrass dieback was followed by a surge in epiphyte density; the sparse eelgrass remaining after the event was heavily epiphytized.

*Mobile epifauna*—From 1998 to 2006 we collected and sorted 52,511 mobile epifauna individuals from core and grab samples, representing 29 species or lowest taxonomic level categories (Table 2). Incidentally collected sessile and/or infaunal species and larger fish and decapod predators were not included in this count. The average species richness of mobile epifauna for a single sample date was 11.5 (range 3–17).

The most abundant species in terms of both numbers and estimated biomass was the caprellid amphipod *Caprella penantis*, comprising 32% of total individuals by number and 34% by biomass (Table 2; Figs. 4, 5). Though *C. penantis* is capable of suspension feeding, we categorized it along with 16 other epifaunal species as a mesograzer (Table 2), based on experimental and observational evidence that it grazes extensively on epiphytes and can reduce epiphyte abundance in mesocosms (Caine 1974; Duffy 1990; Guerra-Garcia et al. 2004). We later repeated our statistical analyses with the exclusion of *C. penantis* from the mesograzer grouping but found no significant changes, and therefore we present only the original results here. The second most abundant mesograzer in terms of biomass was the gammaridean amphipod *Gammarus mucronatus*, with 16% of the total, followed by the isopod *Erichsonella attenuata* with 14% (Table 2; Figs. 4, 5). In total, mesograzers comprised 96% of mobile epifauna, with the remainder consisting of filter feeders, micropredators, and omnivores. Numeric density of total mesograzers averaged 205 individuals g<sup>-1</sup> plant dry wt (Fig. 5), but ranged from

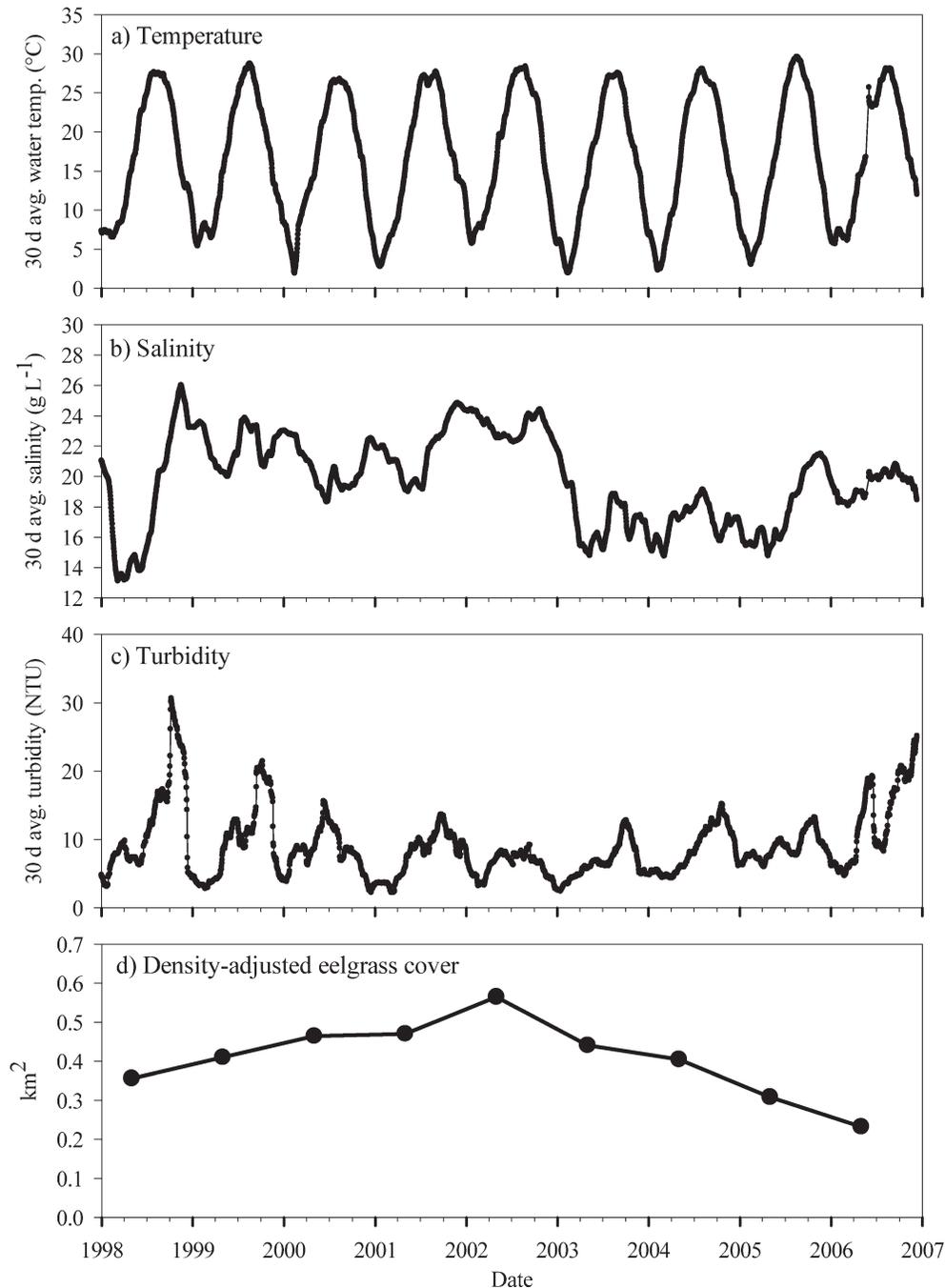


Fig. 1. Time series of (a) 30-d average water temperature, (b) salinity, and (c) turbidity at the Goodwin Islands eelgrass study site from January 1998 to January 2007. (d) Time series of aerial-photo-based springtime eelgrass bed area on the southeast side of Goodwin Islands, corrected for vegetation density (see text).

near absence to more than 1000 individuals  $g^{-1}$  (Fig. 6). These figures were similar to the epifaunal densities reported by Marsh (1973) for another *Zostera* bed, now extinct, in the York estuary. The average annual densities of Marsh (1973) were 100–170 individuals  $g^{-1}$  plant dry wt, with maximum densities near 500 individuals  $g^{-1}$ . Our values for total mesograzer biomass and production averaged 61 mg AF dry wt  $\times$  g plant dry wt $^{-1}$  and 1.4 mg AF dry wt  $\times$  g plant dry wt $^{-1} \times$  d $^{-1}$ , respectively.

These mesograzer biomass and production averages per plant weight are up to about one order of magnitude higher than those reported for epifauna in *Sargassum* spp. algae by Edgar and Klump (2003).

The average seasonal cycle in total mesograzer density was variable and showed little pattern (Fig. 5). Trends in numbers and biomass were qualitatively similar, with no consistent seasonal peak (Fig. 5a,b), whereas estimated secondary production, which is related to water tempera-

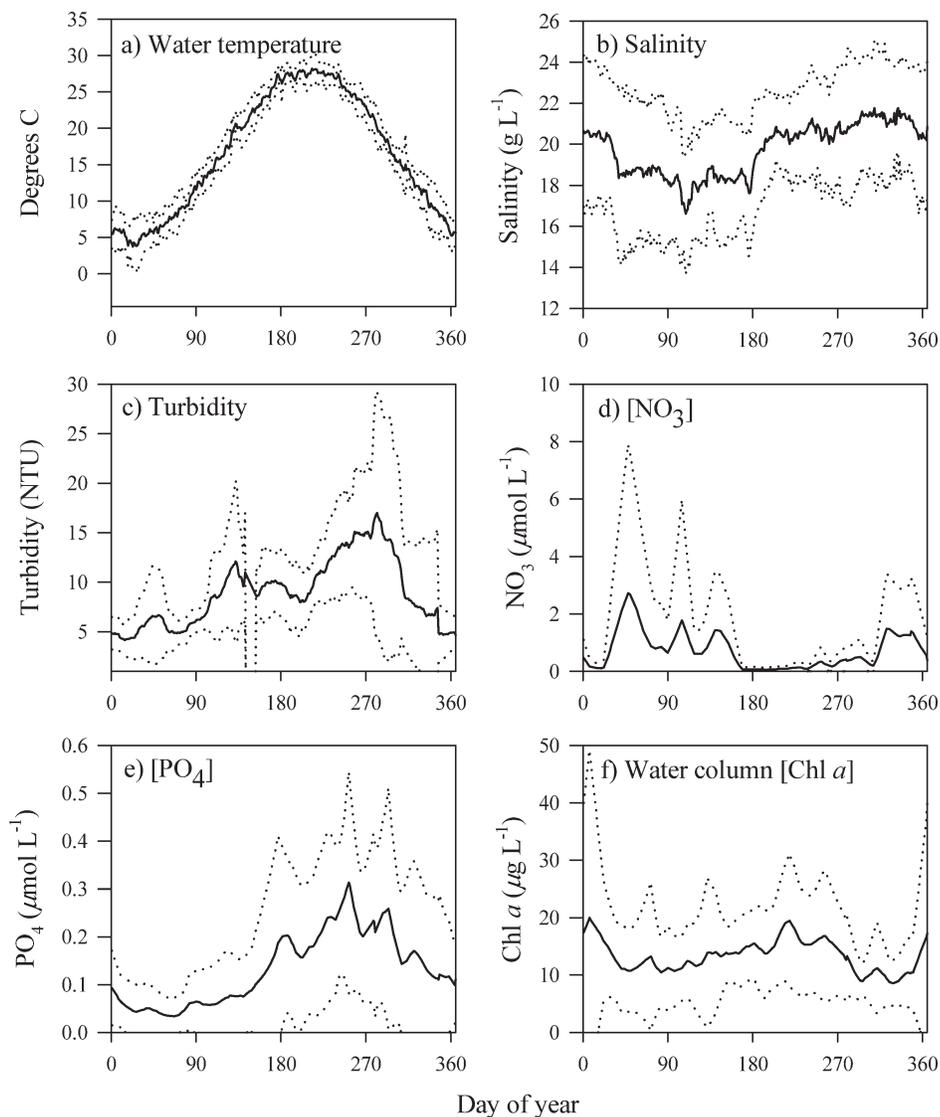


Fig. 2. Average annual cycles of water column conditions in the Goodwin Islands eelgrass bed, calculated as averages for each day of the year over 8 yr from 1998 through 2006. Solid lines are mean values. Dotted lines are mean  $\pm$  1 standard deviation (SD).

ture, was greatest during the summer (Fig. 5c). The seasonal trends varied among different mesograzer species (Fig. 4). *C. penantis* was most abundant during the winter, *G. mucronatus* in the spring, and most other mesograzers during the summer and into the fall (Figs. 4, 6).

There was strong interannual variation in the species composition and abundance of mesograzers (Fig. 6). For instance, *G. mucronatus* was most abundant in spring, and in the low-salinity years beginning in 2003, whereas *Elasmopus levis* was abundant only in the high-salinity years between 1999 and 2003. The large isopod *Idotea balthica* was rare before 2002, seasonally dominant between 2002 and 2005, and virtually absent from collections after the 2005 eelgrass die-off (Fig. 6).

The variance of total mesograzer biomass was significantly greater than the summed variances of individual mesograzer species when calculated over the entire record of sample dates (ratio = 1.94,  $p = 0.0001$ ), indicating that

populations of different mesograzer species tended to vary in synchrony more so than in an asynchronous, compensatory manner. This was also the case for annual averages of mesograzer abundance (ratio = 2.81,  $p = 0.0001$ ), and, typically, for months within a year (average ratio = 1.47,  $p = 0.0004$ ). However, in monthly averages taken across all years (akin to the seasonal cycles of abundance in Fig. 4), mesograzers tended to vary in an asynchronous manner, and the variance of total mesograzers tended to be less than the summed variances of the individual species, but not significantly so (ratio = 0.65,  $p = 0.1114$ ). These patterns suggest that underlying seasonal dynamics vary among mesograzer species but that they tend to respond similarly and synchronously to the major interannual variance in environmental forcing.

*Predators*—From 1998 to 2006, we collected 14,624 small predators from dip-net sweeps, representing 19

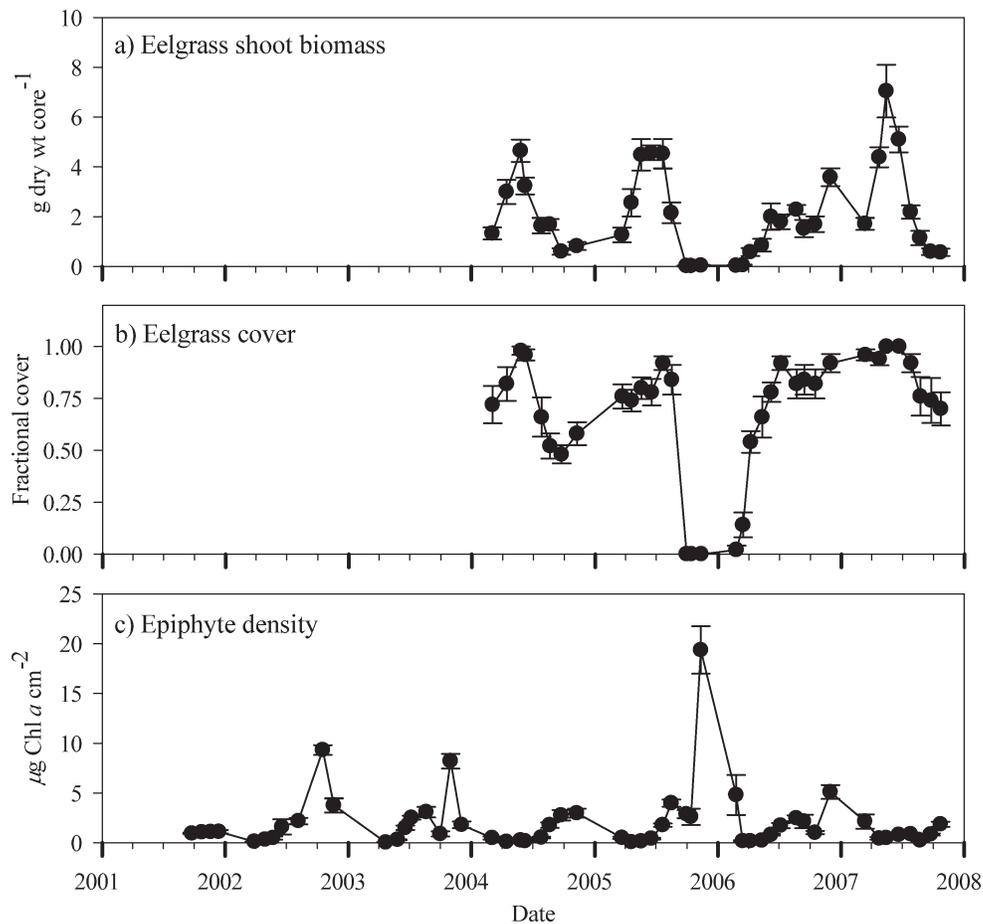


Fig. 3. (a) Mean eelgrass shoot dry mass per 314-cm<sup>2</sup> core, (b) proportional cover, and (c) epiphyte density ( $\mu\text{g Chl } a \times \text{cm}^{-2}$ ), from monthly samples taken at the Goodwin Islands eelgrass bed. Error bars show  $\pm 1$  standard error of the mean (SEM).

species or lowest taxa determinations (Table 3). Grass shrimp, *Palaemonetes* spp. (mostly *Palaemonetes vulgaris* but also including some *Palaemonetes pugio* and *Palaemonetes intermedius*), were the most abundant predators collected, followed by sand shrimp (*Crangon* spp.), blue crabs (*C. sapidus*), pipefish (*Syngnathus* spp., mostly *Syngnathus fuscus* with some *Syngnathus floridae*), and gobies (*Gobiosoma boscii*). Other small fishes comprised about 3% of total predator individuals. Predator abundance varied strongly on both seasonal (Fig. 4) and interannual (Fig. 7) scales. Fish abundance exhibited the most consistent patterns, with unimodal peaks occurring in midsummer (pipefish) and late summer (other fish). The abundance of shrimp and blue crabs was more variable within years, often peaking in both spring and fall, but shrimp exhibited relatively consistent spring peaks after 2002. The apparent decline in shrimp after 2001 (Fig. 7) is probably an artifact of a procedural change, because shrimp < 2 cm total length were not counted in predator surveys after 2001. The concurrent decline in blue crabs, however, reflects a real drop in density at Goodwin Islands, because blue crabs of all sizes were counted throughout the survey period.

*Regression analyses of eelgrass community control*—The spring eelgrass index at Goodwin Islands, a landscape-scale measure based on aerial photographs taken once per year, was best predicted by the regression model based solely on spring turbidity, which was negatively related to the index ( $R^2 = 0.27$ ; Table 4a). However, several other models also explained a fair portion of the eelgrass index and had similar weighted probability based on AIC. The spring eelgrass index was positively related to spring mesograzer density and salinity, but negatively related to summer temperature (Table 4a; see Web Appendix, [www.aslo.org/lo/toc/vol\\_55/issue\\_4/1499a.html](http://www.aslo.org/lo/toc/vol_55/issue_4/1499a.html), Table A1a). Eelgrass shoot biomass, a small-scale measure of bed density based on monthly samples taken only between 2004 and 2007, had largely different model relationships than did the spring eelgrass index (Table 4b; see Web Appendix, Table A1b). While deviations in shoot biomass were positively related to mesograzer density (see Web Appendix, Table A1b), their strongest association was a negative relationship with salinity, in contrast to the positive association with salinity for the landscape-scale spring eelgrass index (Table 4b). Deviations in monthly epiphytic chlorophyll density (the proxy for epiphyte density) were not predicted

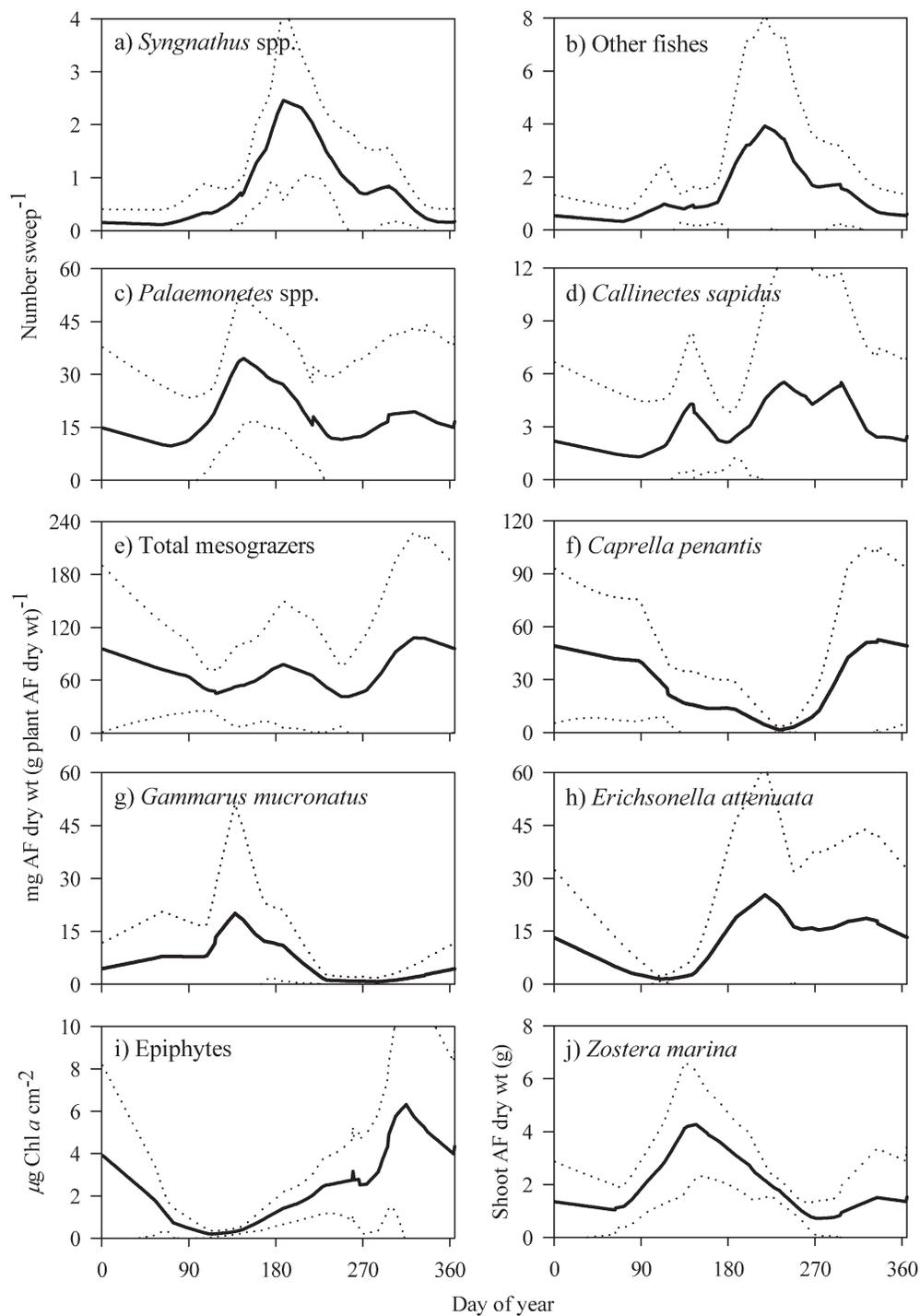


Fig. 4. Average annual cycles of major primary producers, mesograzers, and predators at the Goodwin Islands eelgrass bed, calculated as averages for each day of the year. Predator averages are based on sampling from 1998 to 2007; mesograzer averages are from 1998 to 2006; epiphyte averages are from 2001 to 2007; eelgrass averages are from 2004 to 2007. Dotted lines are mean  $\pm$  1 SD. Total mesograzers includes 17 species (see Table 1). (a) *Syngnathus* spp. pipefish; (b) all other fish; (c) *Palaemonetes* sp. shrimp; (d) blue crabs, *C. sapidus*; (e) total mesograzer biomass; (f) *C. penantis* biomass; (g) *G. mucronatus* biomass; (h) *E. attenuata* biomass; (i) epiphytic algae density ( $\mu\text{g Chl } a \times \text{cm}^{-2}$ ); (j) eelgrass, *Z. marina*, shoot biomass.

Table 2. Total biomass and proportional abundance of mobile epifaunal taxa collected from eelgrass core and grab samples in the Goodwin Islands eelgrass bed from 1998 to 2006. Incidentally collected infaunal taxa are not included, nor are larger predatory epifauna that were sampled with dip-net sweeps; however the latter are presented in Table 3.

| Taxon                            | Category             | Feeding mode             | References   | Biomass<br>(mg AF<br>dry wt) | % total |
|----------------------------------|----------------------|--------------------------|--|------------------------------|---------|
| <i>Caprella penantis</i>         | Caprellid amphipod   | Mesograzer and filter    | Caine (1974); Guerra-Garcia et al. (2004)                          | 5613.10                      | 34.16   |
| <i>Gammarus mucronatus</i>       | Gammaridean amphipod | Mesograzer               | Zimmerman et al. (1979); Neckles et al. (1993)                     | 2644.49                      | 16.09   |
| <i>Erichsonella attenuata</i>    | Isopod               | Mesograzer               | Marsh (1973); van Montfrans et al. (1984); Howard and Short (1986) | 2271.94                      | 13.82   |
| <i>Idotea balthica</i>           | Isopod               | Mesograzer and omnivore  | van Montfrans et al. (1984); Borum (1987)                          | 1579.49                      | 9.61    |
| <i>Ampithoe longimana</i>        | Gammaridean amphipod | Mesograzer               | Bousfield (1973); Duffy and Hay (2000); Nelson (1979)              | 1525.10                      | 9.28    |
| <i>Elasmopus levis</i>           | Gammaridean amphipod | Mesograzer               | Nelson (1979); Duffy and Hay (2000)                                | 584.09                       | 3.55    |
| <i>Edotea triloba</i>            | Isopod               | Mesograzer and scavenger | Orth (1973)  | 487.47                       | 2.97    |
| <i>Cymadusa compta</i>           | Gammaridean amphipod | Mesograzer               | Zimmerman et al. (1979)  | 482.55                       | 2.94    |
| <i>Bittium varium</i>            | Gastropod            | Mesograzer               | Marsh (1973, 1976); van Montfrans et al. (1982)                    | 244.08                       | 1.49    |
| <i>Ampithoe valida</i>           | Gammaridean amphipod | Mesograzer               | J. G. Douglass unpubl. data  | 191.72                       | 1.17    |
| <i>Paracaprella tenuis</i>       | Caprellid amphipod   | Filter                   | Caine (1974)   | 153.18                       | 0.93    |
| <i>Nassarius vibex</i>           | Gastropod            | Omnivore                 | Hurst (1965)   | 153.08                       | 0.93    |
| <i>Microtopos raneyi</i>         | Gammaridean amphipod | Mesograzer               | J. G. Douglass unpubl. data  | 139.13                       | 0.85    |
| <i>Hippolyte pleuracanthus</i>   | Decapod shrimp       | Mesograzer               | Howard and Short (1986)  | 135.50                       | 0.82    |
| <i>Caprella equilibria</i>       | Caprellid amphipod   | Filter                   | Guerra-Garcia et al. (2004)  | 72.58                        | 0.44    |
| Nudibranchs                      | Gastropod            | Various                  |  | 39.47                        | 0.24    |
| <i>Dulichella appendiculata</i>  | Gammaridean amphipod | Mesograzer               | Duffy and Hay (2000)   | 26.10                        | 0.16    |
| <i>Odostomia bisuturalis</i>     | Gastropod            | Predator                 | Marsh (1976)   | 23.93                        | 0.15    |
| <i>Nassarius obsoletus</i>       | Gastropod            | Omnivore                 | Scheltema (1964)   | 23.60                        | 0.14    |
| <i>Eupleura caudata</i>          | Gastropod            | Predator                 | Manzi (1970)   | 11.80                        | 0.07    |
| <i>Erichthonius brasiliensis</i> | Gammaridean amphipod | Mesograzer               | Duffy (1990)   | 8.38                         | 0.05    |
| <i>Mitrella lunata</i>           | Gastropod            | Predator                 | Osman et al. (1992)  | 6.61                         | 0.04    |
| <i>Haminoea solitaria</i>        | Gastropod            | ?                        |  | 5.71                         | 0.03    |
| <i>Epitonium rupicolum</i>       | Gastropod            | ?                        |  | 5.00                         | 0.03    |
| <i>Triphora nigrocincta</i>      | Gastropod            | ?                        |  | 2.44                         | 0.01    |
| <i>Paracerceis caudata</i>       | Isopod               | Mesograzer               | Marsh (1973); Duffy and Hay (2000)                                 | 1.86                         | 0.01    |
| <i>Melita nitida</i>             | Gammaridean amphipod | Mesograzer               | Zimmerman et al. (1979)  | 1.48                         | 0.01    |
| <i>Odostomia impressa</i>        | Gastropod            | Predator                 | Marsh (1976)   | 0.17                         | 0.00    |
| <i>Hydrobia</i> sp.              | Gastropod            | Mesograzer               | Borum (1987)   | 0.03                         | 0.00    |

well by the regression models in spring, but in summertime there was a strong negative effect of turbidity on epiphytic chlorophyll (Table 5; see Web Appendix, Table A2).

Deviations in total mesograzer density were negatively related to turbidity, both in the spring and throughout the year (Table 5; see Web Appendix, Table A3). Mesograzer density was also correlated with total fish abundance, but the relationship was positive, in contrast with the negative effect predicted by our top-down control hypothesis (Table 5). In summer, the best model for mesograzer density included *Palaemonetes* spp. shrimp and blue crabs, as well as fish, with the crustacean predators having a modest negative correlation with mesograzers in the regression (Table 5).

Deviations in the density of the most abundant mesograzer, *C. penantis*, were not explained well by the models tested, except during the summer when higher than normal temperatures were associated with lower than normal density of this cold-weather amphipod (Table 5;

see Web Appendix, Table A4). *G. mucronatus*, the most abundant gammaridean amphipod, was negatively associated with salinity and water temperature when the whole year was considered and was negatively associated with blue crabs in spring (Table 5; see Web Appendix, Table A5). As with total mesograzer density, *E. attenuata* density was positively associated with total fish abundance, suggesting bottom-up control, but was sometimes negatively associated with predatory crustaceans (Table 5; see Web Appendix, Table A6). *I. balthica* had a positive association with total fishes and other predators in spring, although in the summer, a negative association with salinity was a stronger predictor of *I. balthica* (Table 5; see Web Appendix, Table A7). *Ampithoe longimana* abundance was predicted well by epiphyte abundance in spring (Table 5; see Web Appendix, Table A8), but on a whole-year basis, most of the variation in *A. longimana* density was unexplained by the regression models. *E. levis* abundance was positively associated with salinity overall and during

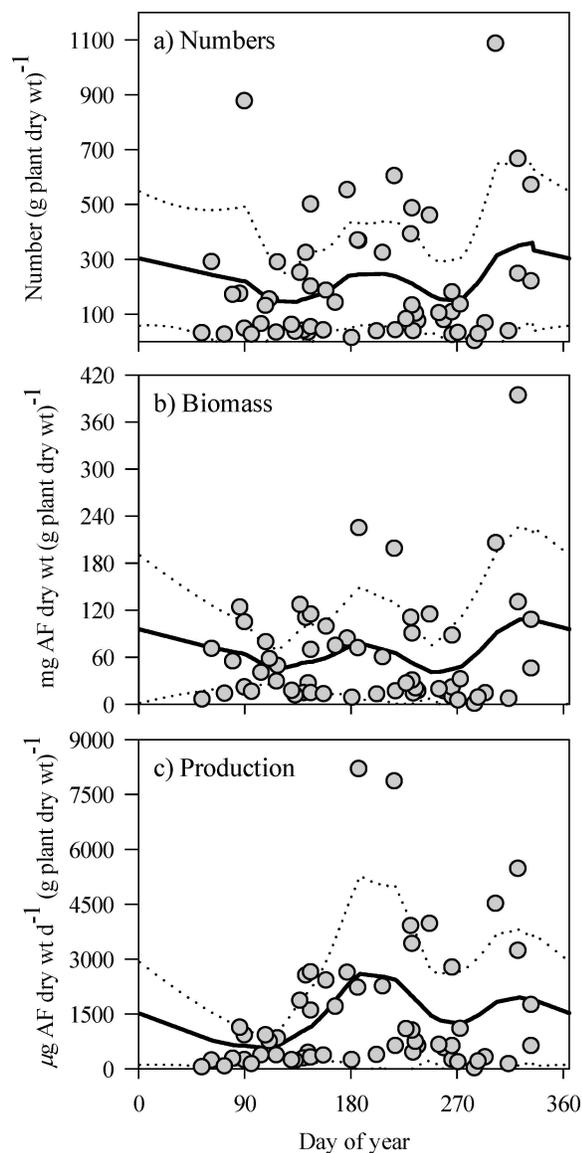


Fig. 5. Mesograzer abundance per gram eelgrass shoot dry weight, vs. day of year. Solid black lines are averages for the day of year, and dotted black lines are mean  $\pm$  1 SD. Gray dots are observed values for particular sample dates. (a) Raw counts of individuals. (b) Mesograzer biomass estimated from size fractionated counts (Edgar 1990a). (c) Mesograzer daily secondary production estimated from size fractionated counts and water temperature (Edgar 1990a).

summer, but in spring *E. levis* abundance was best predicted by a multipredator model with positive relationships to fish and crabs and a negative relationship with shrimp (Table 5; see Web Appendix, Table A9). Epifaunal species richness was best modeled by salinity in summer and by epiphytic chlorophyll in spring, while on a whole-year basis it was best predicted by a heavily parameterized model including all physical factors, epiphytes, mesograzer density, and total fish abundance (Table 5; see Web Appendix, Table A10). The positive relationship between epifaunal species richness and salinity was the most consistent result. In summary, a mix of positive and

negative correlations between mesograzers and adjacent trophic levels suggested that both bottom-up and top-down forces had some influence on the mesograzer community. However, the most common and strongest correlations indicated direct connections between mesograzers and abiotic drivers.

Total fish abundance was positively associated with total mesograzer density in all seasons, although turbidity was a stronger (negative) predictor in spring (Table 6; see Web Appendix, Table A11). Pipefish were also positively associated with total mesograzer density, although only in summer, which is the season when they were most abundant (Table 6; see Web Appendix, Table A12). Blue crabs were positively associated with salinity in spring, but otherwise poorly predicted (Table 6; see Web Appendix, Table A13), perhaps because their sharp decline in the first years of monitoring was related to reduced recruitment and not to ecological factors within the eelgrass bed. Grass shrimp were strongly positively associated with eelgrass shoot biomass and negatively associated with turbidity in the post-2004 data and were negatively related to spring turbidity in the full data set, as well (Table 6; see Web Appendix, Table A14). The omnivorous shrimp were also positively associated with epiphytes, one of their food sources, in summer. These correlations suggest that the availability of prey and habitat each had some influence on predator and omnivore abundance, and, as with mesograzers, physicochemical factors also played a strong role.

Nonmetric multidimensional scaling of biological community data yielded a two-dimensional plot of differences among sample dates with a stress of 0.17 (Fig. 8). The relatively high stress statistic indicated that the two-dimensional representation was moderately distorted from the true multivariate differentiation of the data. Nevertheless, the plot suggested that community structure varied more or less consistently by season, with the same months of different years tending to cluster together. The analysis also showed outlying samples following the 2005 summer eelgrass die-off, which differed from either summer or winter samples from the other years. Later samples had reintegrated with the main body of samples by late spring 2006.

Cluster analysis of the same data found several significant divisions between related groups of samples, which are indicated by black circles on nodes in the dendrogram (Fig. 8b). The strongest division (between the most dissimilar groups) was between samples taken shortly after the eelgrass die-off and non-die-off samples. The other divisions were roughly related to season. Early spring and October 2003 samples formed a separate group, and the remaining samples were split between late season (August–December) and midseason (April–July) samples, although those from November–December 2001 were included with the midseason group. Similarity percentage tests within the cluster analysis, intended to identify which variables accounted for the differentiation between groups of similar samples, showed that no single variable accounted for more than 13% of the total dissimilarity at any of the significant divisions but that *Palaemonetes* spp. shrimp and *C. penantis* amphipods were always among the

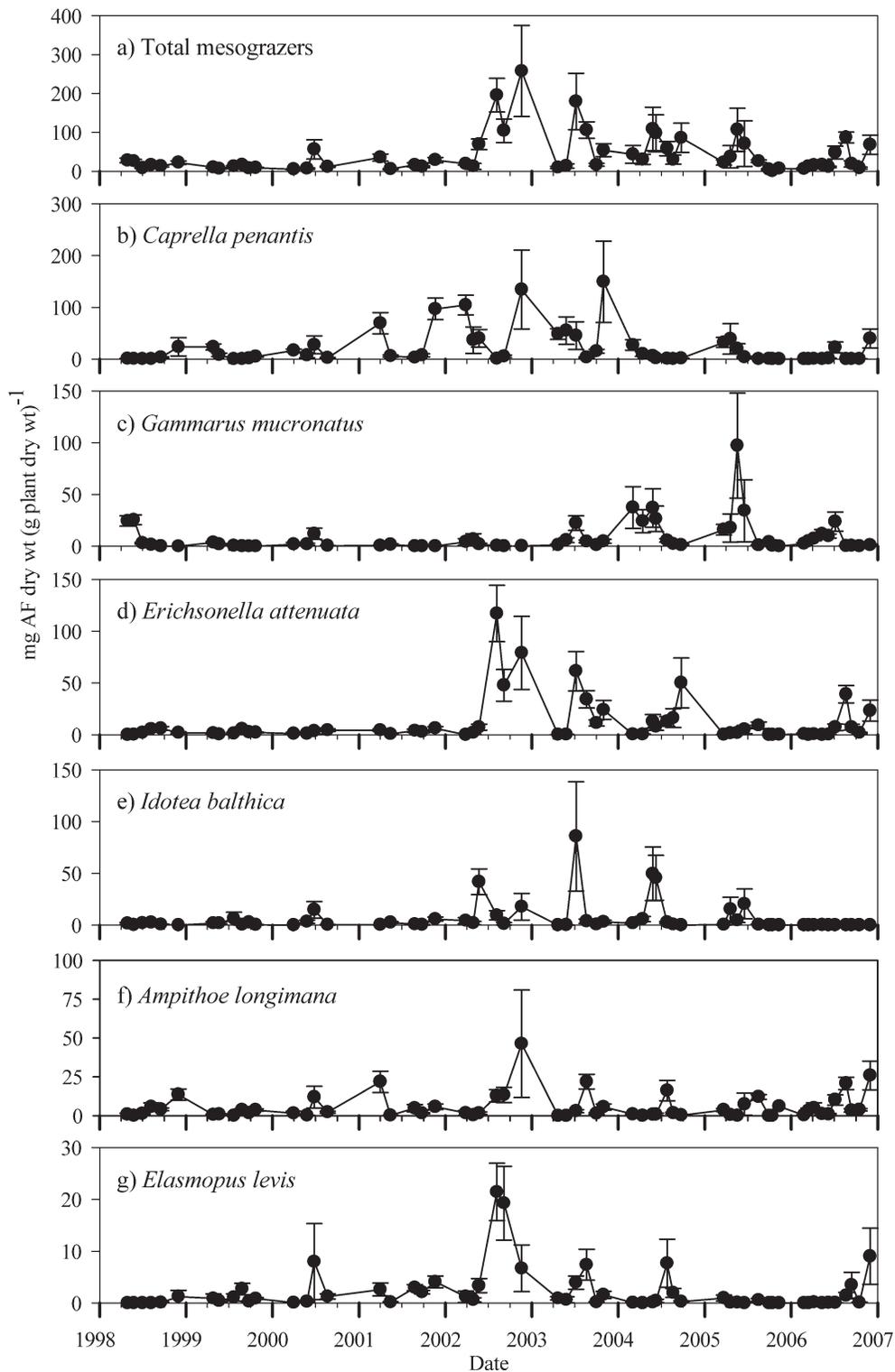


Fig. 6. Mean ( $\pm$  SEM) biomass (mg AF dry wt  $\times$  g plant dry wt<sup>-1</sup>) for the most abundant mesograzers species at Goodwin Islands.

Table 3. Total numbers and proportional abundance of small predators collected in dip-net sweeps at the Goodwin Islands eelgrass bed from 1998 to 2006.

| Taxon                          | Common name          | Total No. | % total | Length (mm) mean±SD |
|--------------------------------|----------------------|-----------|---------|---------------------|
| <i>Palaemonetes</i> spp.       | Grass shrimp         | 9363      | 63.16   |                     |
| <i>Crangon septemspinosa</i>   | Sand shrimp          | 2904      | 19.59   |                     |
| <i>Callinectes sapidus</i>     | Blue crab            | 1191      | 8.03    | 22±19               |
| <i>Syngnathus</i> spp.         | Pipefish             | 558       | 3.76    | 101±39              |
| <i>Gobiosoma boscii</i>        | Naked goby           | 378       | 2.55    | 25±8                |
| Unidentified juvenile fishes   | Fish                 | 105       | 0.71    | 23±9                |
| <i>Fundulus</i> spp.           | Killifish            | 88        | 0.59    | 27±9                |
| <i>Gobiosox strumosus</i>      | Skilletfish          | 54        | 0.36    | 28±16               |
| Gasterosteidae                 | Stickleback          | 49        | 0.33    | 33±12               |
| <i>Anguilla rostrata</i>       | American eel         | 29        | 0.20    | 55±14               |
| <i>Symphurus plagiusa</i>      | Tonguefish           | 25        | 0.17    | 32±11               |
| <i>Micropogonias undulatus</i> | Croaker              | 21        | 0.14    | 30±16               |
| <i>Menida menida</i>           | Atlantic silversides | 19        | 0.13    | 44±22               |
| Pleuronectiformes              | Flounder             | 13        | 0.09    | 48±29               |
| <i>Bairdiella chrysura</i>     | Silver perch         | 9         | 0.06    | 39±20               |
| Blennidae                      | Blenny               | 8         | 0.05    | 21±4                |
| <i>Anchoa mitchilli</i>        | Bay anchovy          | 5         | 0.03    | 31±7                |
| <i>Pomatomus saltatrix</i>     | Bluefish             | 4         | 0.03    | 30±9                |
| <i>Leiostomus xanthurus</i>    | Spot                 | 1         | 0.01    | 40                  |

top two discriminators. *C. sapidus* crabs and *E. attenuata* isopods were also always in the top five discriminating variables. Epiphytic *Chl a* was the number four discriminator in the die-off vs. non-die-off division; there tended to be more epiphytes in the post-die-off samples.

## Discussion

Our analyses revealed a dynamic seagrass community in which strong seasonal cycles in species composition and abundance were overlain by equally strong interannual variability. The most obvious drivers of this biological variation were temperature, salinity, and turbidity. In contrast, evidence for bottom-up and top-down trophic control was inconsistent; there were some significant positive and negative correlations between individual taxa and their putative predators and prey, but few consistent relationships among broader trophic groupings. These results differ strongly from the results of several experimental manipulations in mesocosms (Duffy et al. 2005) and field cages (Heck et al. 2006; Douglass et al. 2007; Moksnes et al. 2008), where covarying environmental factors have been controlled. These experiments have consistently found strong top-down effects of grazing and predation on seagrass communities, often including negative correlations of abundance at adjacent trophic levels. Our results also differ from temporal patterns of mesograzers documented on the Gulf and Atlantic Coasts of Florida (Stoner 1980; Nelson et al. 1982), where summer minima in mesograzers have been associated with strong top-down control by predatory fish. Predators were most abundant at our field site in summer, as well, but perhaps not abundant enough, long enough to noticeably depress mesograzers abundance. Our field site, at 37°N, is at a higher latitude than the sites surveyed by Stoner (1980) and Nelson et al. (1982), which were at 30°N and 28°N, respectively, so our differing results support the suggestion by Nelson (1980)

that the intensity of predation on mesograzers decreases with increasing latitude.

Of course, geographic differences cannot explain the discrepancy between the results of our observational study and the results of experimental studies in the same system (Duffy et al. 2005; Douglass et al. 2007). Several caveats make it difficult to compare the quite different approaches of controlled experiments and correlational analyses of time series data. For example, top-down control can be strengthened by spatial confinement of consumers (Christie and Kraufvelin 2004; France and Duffy 2006) and by low prey diversity (Duffy et al. 2005), both of which are characteristic of many experiments. These factors may exaggerate the apparent importance of top-down control in experiments. Conversely, coarse-scale correlative comparisons of field patterns can obscure strong trophic controls evident on closer examination (Frank et al. 2007). Another limitation of the field data is that, whereas the entire consumer community is known in an experiment, we could only quantify the abundance of those organisms that were captured in our sampling gear. Larger and/or faster fishes than those caught in our dip-net sweeps could potentially exert strong top-down controls on mesograzers that went undetected in our study; it would be useful to quantify those predators with additional surveys.

It should also be noted that the infrequency of negative correlation between consumers (predators or mesograzers) and prey (mesograzers or epiphytes) at the scale of our sampling does not necessarily imply the absence of top-down control, since it is quite conceivable that mobile consumers congregate where their prey are abundant and quickly disperse to other habitat patches after depleting that prey (McCann et al. 2005; France and Duffy 2006). The abundance of mesograzers in the gut contents of demersal fishes in seagrass beds (Edgar and Shaw 1995; J. G. Douglass et al. unpubl. data) and the negative effects of fish and decapod predation on mesograzers in experiments

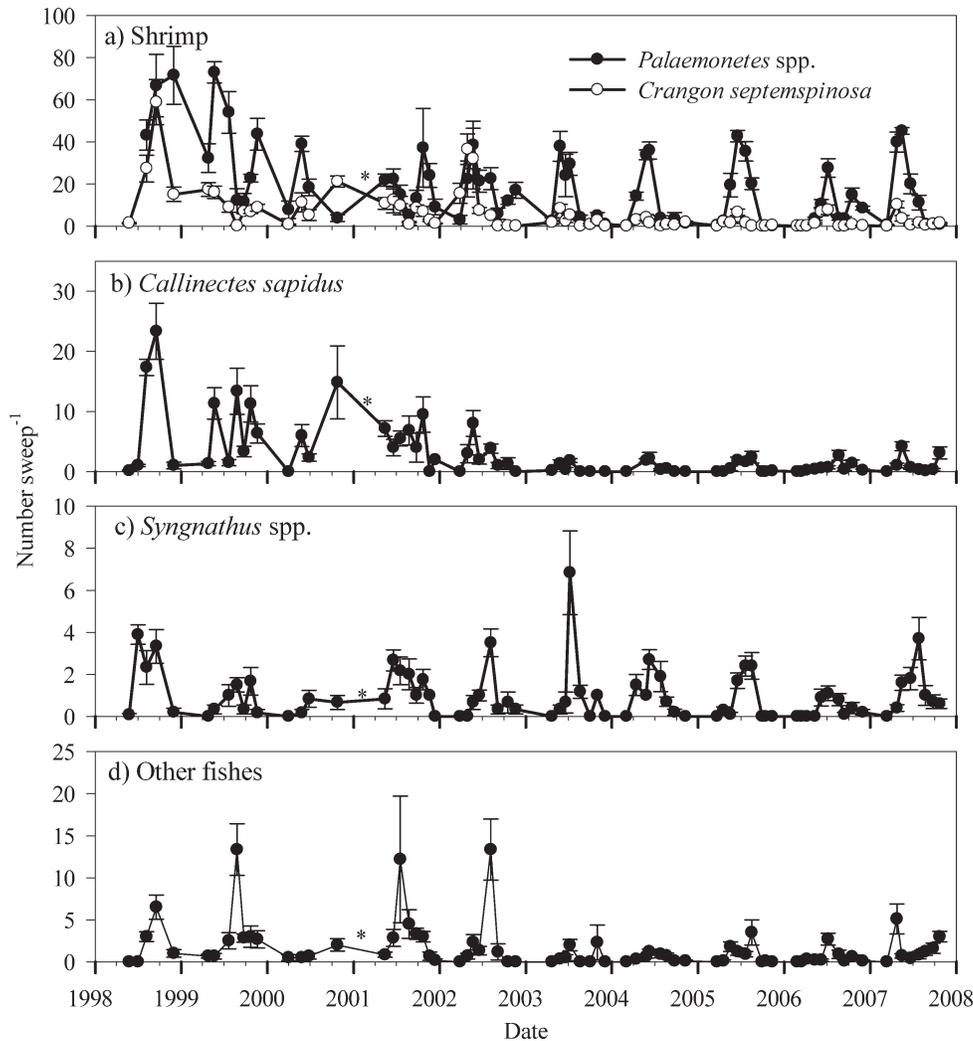


Fig. 7. Mean ( $\pm$  SEM) abundance of small predators from 2.65 m<sup>2</sup> dip-net sweeps. (a) Grass shrimp (*Palaemonetes* spp.) and sand shrimp (*Crangon septemspinosa*); (b) blue crab (*C. sapidus*); (c) pipefish (*Syngnathus* spp.); (d) all other fishes. Asterisks indicate a long gap in the data set between 26 June and 24 October 2000.

(Duffy et al. 2005; Douglass et al. 2007, 2008) at least demonstrate the potential of predation to influence mesograzers, and grazer consumption of epiphytes is well known from studies both in the lab and in the field (Hughes et al. 2004; Valentine and Duffy 2006). Overfishing can certainly change the abundances of some of the demersal predators of mesograzers, as exemplified in our own data by the decline in juvenile blue crab abundance coincident with overharvesting of adult blue crabs (Lipcius and Stockhausen 2002). Therefore, despite the fact that abiotic effects appeared predominant in this first analysis of the field data, it would be premature to dismiss the potential of trophically mediated processes to affect eelgrass growth and survival in this system.

Chesapeake Bay is one of the most variable aquatic environments in the world in terms of physicochemical conditions, so it comes as no surprise that the biotic components of the Goodwin Islands eelgrass bed exhibited such high variation on annual and interannual scales.

Eelgrass growth, biomass, and density, which respond to changing temperature and light (Orth and Moore 1986), are clearly primary drivers of many of the annual patterns in eelgrass-associated species, which have been shown to respond strongly to habitat availability (Orth and Heck 1980). The seasonal cycles of abundance and density of eelgrass that we observed between 2004 and 2007 are similar to patterns described previously for the lower Chesapeake Bay (Orth and Moore 1986; Moore and Jarvis 2008): sparse eelgrass in the winter, increasing in density through the late spring, and senescing through midsummer into the fall (Figs. 3a,b, 4j). The annual cycle of epiphyte density on eelgrass was nearly the inverse of the pattern of eelgrass density (Figs. 3c, 4i). Epiphytes increased throughout the summer and into the fall and winter but were scarce during the spring, a pattern similar to that seen in a previous study of eelgrass and epiphyte growth in the York River (Moore et al. 1996). A simple explanation for the inverse pattern of eelgrass and epiphytes is that epiphyte

Table 4. Comparison of selected linear regression models of eelgrass abundance. Predictor variables in models are indicated by their  $T$  values (regression coefficient  $\times$  SE of coefficient<sup>-1</sup>) in columns 4-11. Blanks cells indicate that the predictor variable denoted by that column was not included in the model presented in that row. Model fit statistics indicate the explanatory power and parsimony of a model.  $n$  is the sample size,  $K$  is the number of parameters in the model, and  $RSS$  is the residual sum of squares for the regression. The model with the lowest Corrected AIC value is considered the "best" model of those evaluated, and  $w_i$  gives the proportional weight or confidence that model is given among the set of models.  $R^2$ , which is adjusted for sample size in this formulation, gives the proportion of the data's variance explained by a given model. Only models that yielded  $w_i > 0.1$  and  $R^2 > 0.1$  are shown here; other models are in the appendix tables (see Web Appendix). (a) Models for density adjusted eelgrass area at Goodwin Islands, as determined by aerial photos taken in the late spring of 1998 through 2006. The predictor variables used in these models—water temperature, "temp."; salinity, "salin."; turbidity, "turb."; and mesograzed density, "meso."—are average values from summer days 200–250 of the preceding year, "Prev. sum.", or spring days 70–120 of the focal year, "Sprn." The constant term is indicated by "Cnst." (b) Models for deviation from the mean value of eelgrass shoot biomass for monthly samples taken between 2004 and 2007. Predictor variables are themselves deviations from the mean value of the selected variable for the day of the year on which the sample was taken. Additionally, temperature, salinity, and turbidity are based on average values from 30 d prior to the sample date. Epiphytic Chl  $a$  is abbreviated "Epi. Chl  $a$ ."

| Response                | Model No. | Predictor variables with $T$ values |              |             |             |              |                  |                   |                  |                  |       | Model fit statistics |         |         |       |       |
|-------------------------|-----------|-------------------------------------|--------------|-------------|-------------|--------------|------------------|-------------------|------------------|------------------|-------|----------------------|---------|---------|-------|-------|
|                         |           | Sprn. temp.                         | Sprn. salin. | Sprn. turb. | Sprn. meso. | Temp.        | Prev. sum. temp. | Prev. sum. salin. | Prev. sum. turb. | Prev. sum. meso. | $n$   | $K$                  | $RSS$   | $AIC_c$ | $w_i$ | $R^2$ |
| Spring eelgrass index   | 4         | 0.13                                | 1.54         |             |             |              |                  |                   |                  |                  | 8     | 3                    | 527.7   | 45.51   | 0.13  | 0.16  |
|                         | 5         | 6.11                                |              | -1.88       |             |              |                  |                   |                  | 8                | 3     | 463.4                | 44.47   | 0.22    | 0.27  |       |
|                         | 6         | 4.48                                |              |             | 1.70        |              |                  |                   |                  | 8                | 3     | 496.0                | 45.02   | 0.17    | 0.21  |       |
|                         | 9         | 2.04                                |              |             |             | -1.71        |                  |                   |                  | 8                | 3     | 494.1                | 44.99   | 0.17    | 0.22  |       |
| 10                      | -0.49     |                                     |              |             |             | 1.73         |                  |                   | 8                | 3                | 491.0 | 44.94                | 0.18    | 0.22    |       |       |
| Response                | Model No. | Cnst.                               | Temp.        | Salin.      | Turb.       | Epi. Chl $a$ | Meso.            |                   |                  | $n$              | $K$   | $RSS$                | $AIC_c$ | $w_i$   | $R^2$ |       |
| Post-2004 shoot biomass | 6         | -2.74                               |              | -2.90       |             |              |                  |                   |                  | 26               | 3     | 23.3                 | 4.29    | 0.71    | 0.23  |       |

Table 5. Comparison of selected linear regression models of epiphyte density ( $\mu\text{g Chl } a \times \text{cm}^{-2}$  eelgrass blade), mesograzer biomass (mesograzer AF dry wt [mg] per plant dry wt [g]), biomass of individual mesograzer species, and species richness of mobile epifauna. Predictor variables in models are indicated by their  $T$  values (regression coefficient  $\times$  SE of coefficient<sup>-1</sup>). Variable abbreviations and model fit statistics are as in Table 4, with the addition that “*Pala.*,” “Blue crabs,” and “Tot. fish” indicate *Palaemonetes* spp. shrimp, *C. sapidus* crab, and total predatory fish abundance, respectively. The three sets of models for each response (all dates, spring, summer) incorporate all dates in which mesograzers, epiphytic chlorophyll, and predators were sampled, only those dates between days 70 and 150 of a year, and only those dates between 180 and 260 of year, respectively. Several models for each response were tested, but only results from models that yielded  $w_i > 0.1$  and  $R^2 > 0.1$  are shown here, which is why some responses are followed by blank cells. The full sets of models are shown in the supplemental material (see Web Appendix).

| Response                            | Predictor variables with $T$ -values |       |       |        |       |              |       |              |             |           | Model fit statistics |     |         |         |       |       |
|-------------------------------------|--------------------------------------|-------|-------|--------|-------|--------------|-------|--------------|-------------|-----------|----------------------|-----|---------|---------|-------|-------|
|                                     | Model No.                            | Cnst. | Temp. | Salin. | Turb. | Epi. Chl $a$ | Meso. | <i>Pala.</i> | Blue crabs. | Tot. fish | $n$                  | $K$ | $RSS$   | $AIC_c$ | $w_i$ | $R^2$ |
| Epiphytic Chl $a$ , all dates       |                                      |       |       |        |       |              |       |              |             |           |                      |     |         |         |       |       |
| Epiphytic Chl $a$ , spring          |                                      |       |       |        |       |              |       |              |             |           |                      |     |         |         |       |       |
| Epiphytic Chl $a$ , summer          | 6                                    | 2.20  |       |        | -2.78 |              |       |              |             |           | 12                   | 3   | 8.87    | 5.37    | 0.81  | 0.38  |
| <i>C. penantis</i> , all dates      |                                      |       |       |        |       |              |       |              |             |           |                      |     |         |         |       |       |
| <i>C. penantis</i> , spring         | 4                                    | 0.38  | -1.78 |        |       |              |       |              |             |           | 12                   | 3   | 951.08  | 61.47   | 0.36  | 0.17  |
| <i>C. penantis</i> , summer         | 6                                    | 1.99  |       |        | -2.53 |              |       |              |             |           | 48                   | 3   | 204,763 | 407.7   | 0.35  | 0.10  |
| Mesograzers, all dates              | 8                                    | 2.07  |       |        |       |              | 1.05  | -2.06        |             | 2.65      | 48                   | 5   | 188,490 | 408.7   | 0.23  | 0.14  |
| Mesograzers, spring                 | 6                                    | 0.98  |       |        | -1.53 |              |       |              |             |           | 13                   | 3   | 17,475  | 102.3   | 0.15  | 0.10  |
| Mesograzers, summer                 | 11                                   | 2.52  |       |        |       |              |       |              |             | 2.29      | 13                   | 3   | 14,352  | 99.8    | 0.53  | 0.26  |
|                                     | 8                                    | 2.21  |       |        |       |              | -1.07 | -0.12        |             | 4.06      | 12                   | 5   | 13,860  | 104.6   | 0.18  | 0.56  |
|                                     | 11                                   | 1.81  |       |        |       |              |       |              |             | 2.16      | 12                   | 3   | 29,581  | 102.7   | 0.47  | 0.25  |
| <i>G. mucronatus</i> , all dates    | 3                                    | 1.72  | -1.30 | -2.15  | -0.71 |              |       |              |             |           | 48                   | 5   | 6672    | 248.3   | 0.19  | 0.16  |
|                                     | 4                                    | 2.15  | -2.56 |        |       |              |       |              |             |           | 48                   | 3   | 7398    | 248.4   | 0.18  | 0.11  |
| <i>G. mucronatus</i> , spring       | 5                                    | 1.48  |       | -2.98  |       |              |       |              |             |           | 48                   | 3   | 7084    | 246.3   | 0.51  | 0.14  |
| <i>G. mucronatus</i> , summer       | 10                                   | -0.33 |       |        |       |              |       |              | -1.86       |           | 13                   | 3   | 4744    | 85.36   | 0.35  | 0.17  |
| <i>A. longimana</i> , all dates     | 4                                    | 1.75  | -1.62 |        |       |              |       |              |             |           | 12                   | 3   | 228.8   | 44.38   | 0.32  | 0.13  |
| <i>A. longimana</i> , spring        | 7                                    | -1.11 |       |        |       | 2.46         |       |              |             |           | 13                   | 3   | 17.16   | 12.27   | 0.66  | 0.30  |
| <i>A. longimana</i> , summer        |                                      |       |       |        |       |              |       |              |             |           |                      |     |         |         |       |       |
| <i>Erich. attenuata</i> , all dates | 8                                    | 1.63  |       |        |       |              |       |              |             |           | 48                   | 5   | 17,268  | 293.9   | 0.56  | 0.18  |
|                                     | 11                                   | 2.37  |       |        |       |              |       |              |             |           | 48                   | 3   | 19,497  | 294.9   | 0.35  | 0.12  |
| <i>Erich. attenuata</i> , spring    | 9                                    | 0.76  |       |        |       |              | 1.52  |              |             | 2.70      | 13                   | 3   | 129.7   | 38.57   | 0.15  | 0.10  |
|                                     | 11                                   | 1.56  |       |        |       |              |       |              |             | 2.01      | 13                   | 3   | 114.8   | 36.99   | 0.33  | 0.20  |
| <i>Erich. attenuata</i> , summer    | 8                                    | 2.35  |       |        |       |              | -1.13 | -0.35        |             | 5.57      | 12                   | 5   | 2245    | 82.78   | 0.58  | 0.72  |
|                                     | 11                                   | 1.75  |       |        |       |              |       |              |             | 2.86      | 12                   | 3   | 6131    | 83.83   | 0.35  | 0.40  |
| <i>Elasmopus levis</i> , all dates  | 5                                    | 1.25  |       | 3.25   |       |              |       |              |             |           | 48                   | 3   | 702     | 135.3   | 0.71  | 0.17  |
| <i>Elasmopus levis</i> , spring     | 8                                    | 3.05  |       |        |       |              |       |              | 4.09        | 2.29      | 13                   | 5   | 2.55    | -2.62   | 0.12  | 0.68  |
|                                     | 10                                   | 2.10  |       |        |       |              |       |              | 4.26        |           | 13                   | 3   | 4.05    | -6.48   | 0.83  | 0.59  |
| <i>Elasmopus levis</i> , summer     | 5                                    | 1.45  |       | 2.61   |       |              |       |              |             |           | 12                   | 3   | 342.2   | 49.21   | 0.71  | 0.35  |
| <i>Idotea balthica</i> , all dates  | 9                                    | 1.74  |       |        |       |              |       |              |             |           | 13                   | 3   | 2097    | 74.75   | 0.15  | 0.10  |
| <i>Idotea balthica</i> , spring     | 10                                   | 1.88  |       |        |       |              |       | 1.83         |             |           | 13                   | 3   | 1940    | 73.74   | 0.24  | 0.16  |
|                                     | 11                                   | 2.14  |       |        |       |              |       |              |             | 1.88      | 13                   | 3   | 1918    | 73.59   | 0.26  | 0.17  |
| <i>Idotea balthica</i> , summer     | 5                                    | 0.19  |       | -1.81  |       |              |       |              |             |           | 12                   | 3   | 3658    | 77.64   | 0.38  | 0.17  |
| Epifaunal SR, all dates             | 1                                    | 1.97  | -0.33 | 3.12   | 1.98  | -1.12        | 2.44  |              |             |           | 48                   | 8   | 103     | 56.19   | 0.70  | 0.34  |
|                                     | 5                                    | 2.02  |       | 3.32   |       |              |       |              |             |           | 48                   | 3   | 144     | 59.14   | 0.16  | 0.18  |
| Epifaunal SR, spring                | 5                                    | 0.29  |       | 2.52   |       |              |       |              |             |           | 13                   | 3   | 24.78   | 17.05   | 0.13  | 0.31  |
|                                     | 7                                    | 2.57  |       |        |       | 3.39         |       |              |             |           | 13                   | 3   | 19.13   | 13.69   | 0.72  | 0.47  |
| Epifaunal SR, summer                | 5                                    | 0.78  |       | 1.53   |       |              |       |              |             |           | 12                   | 3   | 26.24   | 18.39   | 0.22  | 0.11  |

Table 6. Comparison of selected linear regression models of predator abundance, measured as the average number of individuals per net sweep per collection date, at Goodwin Islands. Predictor variables in models are indicated by their  $T$  values (regression coefficient  $\times$  SE of coefficient<sup>-1</sup>). Variable abbreviations and model fit statistics are as in Tables 4 and 5. The three sets of models for each response (all dates, spring, summer) incorporate all dates in which mesograzers, epiphytic chlorophyll, and predators were sampled, only those dates between days 70 and 150 of a year, and only those dates between 180 and 260 of year, respectively. Several models for each response were tested, but only results from models that yielded  $w_i > 0.1$  and  $R^2 > 0.1$  are shown here, which is why some responses are followed by blank cells. The full sets of models are shown in the supplemental material (see Web Appendix).

| Response                        | Model No. | Predictor variables with $T$ -values |       |        |       |             |              | Model fit statistics |     |     |       |         |       |       |
|---------------------------------|-----------|--------------------------------------|-------|--------|-------|-------------|--------------|----------------------|-----|-----|-------|---------|-------|-------|
|                                 |           | Cnst.                                | Temp. | Salin. | Turb. | Eelg. dens. | Epi. Chl $a$ | Meso.                | $n$ | $K$ | $RSS$ | $AIC_c$ | $w_i$ | $R^2$ |
| Pipefish, post-2004             |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Pipefish, all dates             |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Pipefish, spring                |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Pipefish, summer                | 6         |                                      |       |        |       |             |              | 1.96                 | 12  | 3   | 22.06 | 16.30   | 0.58  | 0.21  |
| <i>Palaemonetes</i> , post-2004 | 2         | -1.97                                | 0.15  | 1.43   | -2.97 | 4.71        |              |                      | 26  | 6   | 927.0 | 109.34  | 0.12  | 0.51  |
|                                 | 5         | -4.11                                |       |        | -2.80 | 4.56        |              |                      | 26  | 4   | 1032  | 105.60  | 0.76  | 0.50  |
| <i>Palaemonetes</i> , all dates |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| <i>Palaemonetes</i> , spring    | 3         | -5.70                                | -0.47 | 2.21   | -4.43 |             |              |                      | 13  | 5   | 196.3 | 53.86   | 0.20  | 0.69  |
|                                 | 6         | -4.79                                |       |        | -3.97 |             |              |                      | 13  | 3   | 341.3 | 51.15   | 0.78  | 0.55  |
| <i>Palaemonetes</i> , summer    | 7         | -0.36                                |       |        |       |             | 2.58         | -0.96                | 12  | 4   | 2172  | 76.10   | 0.36  | 0.31  |
| Blue crab, post-2004            |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Blue crab, all dates            |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Blue crab, spring               | 4         | -2.96                                |       | 2.73   |       |             |              |                      | 13  | 3   | 22.79 | 15.96   | 0.81  | 0.35  |
| Blue crab, summer               |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Total fish, post-2004           |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Total fish, all dates           |           |                                      |       |        |       |             |              |                      |     |     |       |         |       |       |
| Total fish, spring              | 5         | -7.80                                |       |        |       | -2.82       |              |                      | 13  | 3   | 3.84  | -7.18   | 0.69  | 0.37  |
|                                 | 6         | -7.58                                |       |        |       |             | 2.29         |                      | 13  | 3   | 4.48  | -5.19   | 0.25  | 0.26  |
| Total fish, summer              | 6         | -1.24                                |       |        |       |             | 2.16         |                      | 12  | 3   | 181.2 | 41.58   | 0.72  | 0.25  |

accumulation is reduced when eelgrass blades are growing and being replaced rapidly in the spring (Borum 1987) but that epiphyte growth continues to increase as eelgrass growth decreases due to temperature stress in summer. It is also possible that epiphytes are scarce in spring for reasons other than substrate turnover, such as strong herbivory by mesograzers in the absence of control by predatory fish, many of which do not migrate or recruit into Chesapeake Bay until later in the season (Fig. 4a,b; Lazzari and Able 1990). Our data did not seem to support this top-down hypothesis, however, because total mesograzers abundance was usually lower in the spring than in the summer and fall (Figs. 4e, 5), and correlations between deviations of mesograzers and epiphyte density tended to be minor and positive (see Web Appendix, Tables A3–A9). Thus, within the range of grazer densities found in this survey, variation in epiphyte density appears to be controlled largely by nontrophic processes, including light (turbidity) and stability of the substratum (eelgrass leaf growth rate).

The occurrence of high densities of mesograzers despite relatively abundant predators in the late summer may be attributable in part to the often low clarity of water at that time of year (Fig. 2c,f), which could reduce predation rates. It could also be due to increased cryptic or defensive behavior by mesograzers in the presence of predators. The high epiphyte densities in late summer and fall might result from mesograzers avoiding predators and thus reducing their grazing of epiphytes in a trait-mediated indirect interaction (TMII; Werner and Peacor 2003). Such a TMII was evident in a mesocosm experiment in this system, where the presence of predatory blue crabs strongly,

indirectly enhanced algae biomass without strongly depressing the numerical abundance of mesograzers (Duffy et al. 2005). A simpler, but not mutually exclusive, explanation of mesograzers abundance in spite of summer predators is that high secondary production overwhelms losses to predation. Water temperatures at Goodwin Islands often exceed 25°C for 3 months or more (Fig. 2), during which time mesograzers can grow and reproduce very rapidly (Fredette et al. 1990; Duffy et al. 2005).

Abundances of pipefish and other small fishes varied from year to year, but there was no clear trend in the variation across multiple years. With blue crabs and shrimp, however, abundance was distinctly higher before 2001 than after (Fig. 7). The decline in shrimp is probably an artifact of a change in survey methods, because very small (< 2 cm) shrimp were not counted after 2001. The decline in blue crabs is more likely to reflect real trends in abundance, though, because all sizes of crabs were counted throughout the survey period. The blue crab decline may be related more to poor recruitment at the landscape scale than to processes occurring within the eelgrass bed, since the bay-wide spawning stock of adult female blue crabs reached an historic low in 2000 (Lipcius and Stockhausen 2002) and has remained at low levels.

Of all taxa studied, mesograzers showed some of the greatest interannual variability, presumably because their populations can grow very rapidly under favorable conditions but are not buffered by pelagic larval recruitment from outside the study area. Two of the most abundant species, *G. mucronatus* and *E. levis*, had nearly inverse patterns of abundance among years (Fig. 6) and opposite correlations

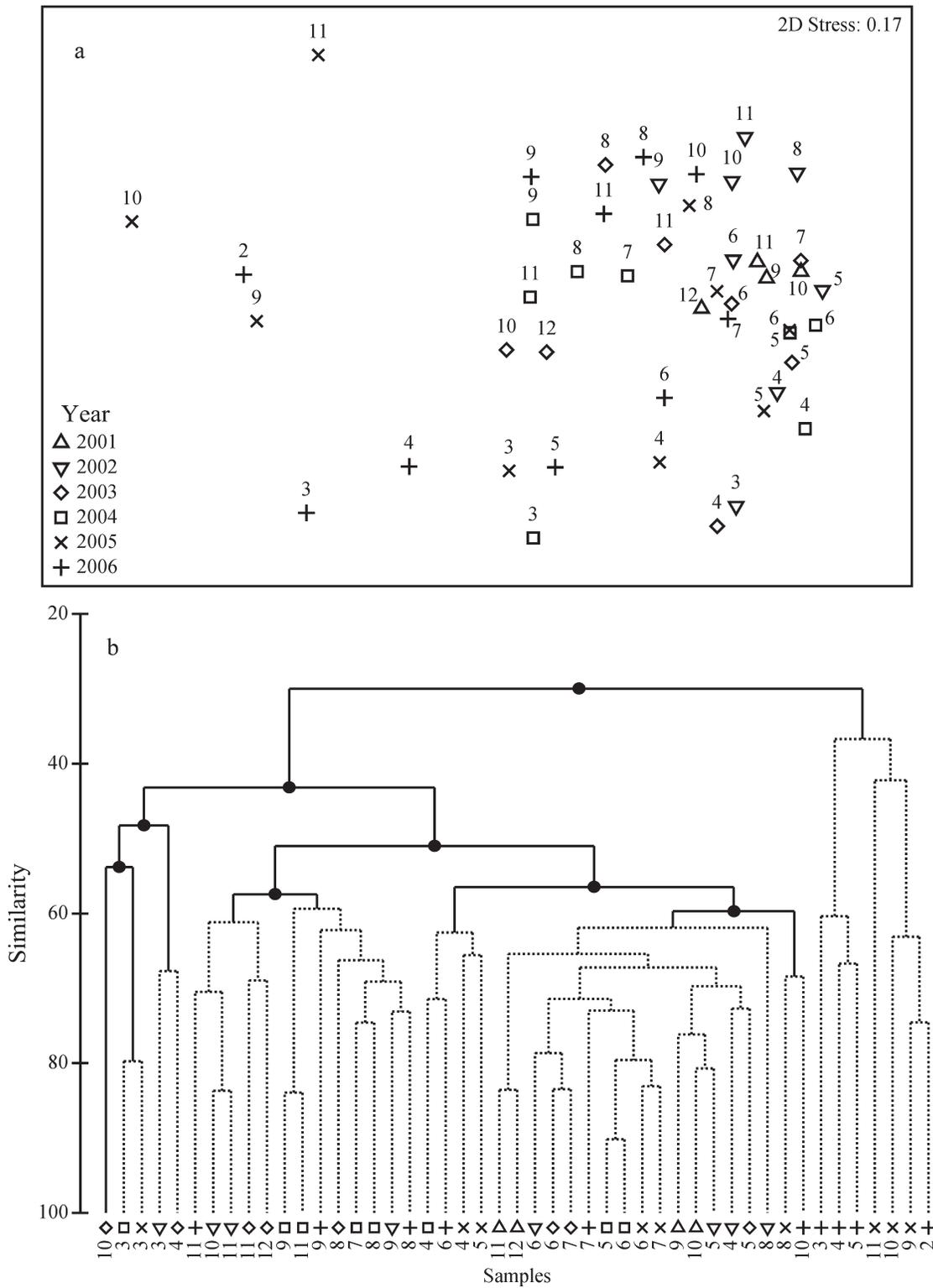


Fig. 8. (a) Nonmetric multidimensional scaling plot of eelgrass community data from samples taken at Goodwin Islands from 2001 through 2006. Community data include epiphyte density, biomass of 15 mesograzer taxa, and the abundance of six taxa of small, demersal predators. Years are indicated by symbol shape, and months by the numbers 1–12. (b) Cluster analysis dendrogram of the same data. Dark circles at nodes indicate divisions statistically supported at the  $p < 0.05$  level. Nondotted divisions are not supported at that level.

with salinity (Table 5; see Web Appendix, Tables A5, A9). *G. mucronatus* appears to capitalize on low salinity and cooler spring waters, while *E. levis* apparently requires high salinity to flourish. Mesocosm experiments (R. E. Blake and J. E. Duffy unpubl. data) also suggest that *E. levis* is less tolerant of freshwater shock than *G. mucronatus* and *E. attenuata*. The positive correlation of epifaunal species richness and salinity suggests that some of the rarer epifaunal species that we observed could similarly depend on high salinity, immigrating from more marine waters during high-salinity conditions (Table 5; see Web Appendix, Table A10). Negative responses of mesograzers to freshwater disturbance on landscape scales have been documented previously in this system. Prior to intense freshwater flooding associated with Hurricane Agnes in 1972, the isopod *Paracerceis caudata* was by far the most abundant crustacean mesograzer in an eelgrass bed of the York estuary (Marsh 1973) and presumably throughout Chesapeake Bay (Anderson et al. 1973). While the species is still common in the salty coastal bays of Virginia's Eastern Shore, it has apparently never returned to abundance within Chesapeake Bay; we have collected only 18 individuals of *P. caudata* in 9 yr of sampling. In contrast, other species that were relatively rare in earlier documented collections were abundant in ours, for instance, *I. balthica* was nearly absent from a survey done at Goodwin Islands in the late 1990s (Parker et al. 2001) but was a prominent component of the community in our samples, especially between 1999 and 2005. However, *I. balthica* has been virtually absent from our collections since the 2005 eelgrass dieback, further evidence that a large disturbance can have lasting changes on the epifaunal community even after the eelgrass itself recovers. The shrinking distribution and increasing patchiness of eelgrass beds in Chesapeake Bay may alter population dynamics within mesograzer communities, increasing their interannual variability and increasing the chance of species extirpation (France and Duffy 2006).

Whether the documented changes in mesograzer species diversity will influence the health and productivity of eelgrass beds is contingent upon the relationship between mesograzer diversity and the ecological functions of mesograzers, i.e., epiphyte grazing and secondary production. Does the presence of more species of mesograzers equate with higher or more consistent levels of grazing or production in the field? Two potential lines of evidence suggest that it could. First, mesocosm experiments have established that there is considerable variation in population growth rates and in the strength and selectivity of algal grazing among the mesograzer species of our system (Duffy and Harvilicz 2001) and that these differences lead to higher grazer biomass and lower algal biomass in treatments with diverse mesograzers, relative to the average of single species treatments (Duffy et al. 2005). Second, this study and field studies in other vegetated benthic systems (Stoner 1980; Edgar 1990b) demonstrate that seasonal and interannual patterns in abundance differ among mesograzer species at the same location. In theory, this could lead to complementary patterns of grazing and production when some species are at low and others are at high abundance, for example, in low-salinity periods when *E. levis* is rare but *G. mucronatus* is

flourishing. However, our quantitative tests of the variance in total mesograzer abundance vs. individual species abundance provide little evidence for such compensation. In fact, at most timescales the temporal variance in total mesograzer biomass was significantly higher, not lower, than the sum of the temporal variances in the biomass of individual species, indicating that populations of different mesograzer species tended to vary in synchrony rather than in an alternating manner. Only the generalized seasonal patterns, averages by month from across all years of sampling, provided some indication of complementarity in the seasonal timing of abundance of different species (Fig. 4e–h). It appears that the asynchronous seasonal timing among different mesograzer species is often overwhelmed by nonseasonal forcings that generate synchronous change across many species. For example, most of the abundant mesograzers, including *C. penantis*, *G. mucronatus*, *E. attenuata*, *I. balthica*, and *E. levis*, which all have different seasonal cycles, had similar, negative correlations with turbidity, presumably reflecting their shared dependence on algal production, which requires light. This highlights the importance of temporal scale and environmental variability in judging how diversity relates to stability and supports the notion that compensatory dynamics among species in a community may be rare, generally (Houlahan et al. 2007).

In our assessment of explanatory models of the Goodwin Islands eelgrass community, there was a surprising bias toward simple models based on a single, physicochemical factor (Tables 5, 6). The bias toward simplicity may be due to the small size of the data sets used in the models. Both the AIC and the adjusted- $R^2$  calculation introduce a penalty for larger numbers of explanatory variables, and this penalty is more severe for models with a small sample size. Thus, the best single factor models are likely to be favored in a small data set, even if models including several factors explain more of the variation in the data. Multicollinearity among predictive factors could also bias against multivariate models, although this seems unlikely among the physicochemical factors in our data set because correlations among temperature, salinity, and turbidity were all below 0.12. Continuation of the Goodwin Islands monitoring programs will allow more complex models to be evaluated fairly in the future as a larger data set is accumulated. In particular, it will be useful to include eelgrass density as a predictor in the models in order to evaluate the extensive theoretical and experimental work on the relationship of vegetation density to trophic interactions in seagrass (Heck and Orth 2006). Another benefit of an extended time series is the ability to capture community responses to unusual natural and anthropogenic events that strongly affect seagrass communities, such as the seagrass die-off we observed in late summer 2005.

Major eelgrass dieback events in Chesapeake Bay have been attributed to a variety of factors, such as the *Labyrinthula* sp. slime mold wasting disease in the 1930s (Muehlstein et al. 1988), turbidity and freshwater shock after Hurricane Agnes (Anderson et al. 1973), physical disturbance and burial in Hurricane Isabel (J. G. Douglass

pers. obs.), and abnormally high water temperatures in 2005 (Moore and Jarvis 2008). All these types of disturbance have the potential not only to affect eelgrass directly but also to affect it indirectly by altering composition of and interactions within faunal assemblages. For instance, freshwater inputs from a storm may simultaneously increase nutrients and sediments and decrease the abundance and diversity of mesograzers, reducing their capacity to control epiphytes. Thus, a single disturbance may generate both top-down and bottom-up effects, which act synergistically to compound the damage experienced by seagrass. An awareness of the synergy between top-down and bottom-up aspects of seagrass ecology will enhance the ability to diagnose and address the seagrass declines so apparent in observational data from around the world (Orth et al. 2006).

#### Acknowledgments

We thank John Parker, Jennifer Rhode, Kenneth Macdonald, Melanie Harris, Ruben Rios, Jessie Philpot, Mark Fitchett, Lana Lau, Molly Roggero, Amanda Spivak, Aaron Spivak, Susie Herbert, Kiara Smith, Laura Ladwig, Akwasi Cato, Breanna Korsman, Sara Grill, Timothy Montgomery, Lindsey Moore, Noah Yavit, William Tarantino, Martin Marquez, Phillip Mattich, Gabriella Blohm, Lindsey Albertson, Thomas Hill, Rachael Blake, Diana Chin, Matthew Whalen, and others for field and laboratory assistance. We also thank Kenneth Moore, Robert Orth, and the staff of the Chesapeake Bay National Estuarine Research Reserve Program for invaluable help and data sharing during the preparation of this manuscript. Finally, we thank Per-Olav Moksnes and an anonymous reviewer for help with the production of the final manuscript. This work was supported in part by grant numbers Office of the Chief Economist 95-21184, OCE-0099226, OCE 03-52343, and OCE-0623874 to J.E.D. This is Virginia Institute of Marine Science contribution 3070.

#### References

- ANDERSON, A. M., W. J. DAVIS, M. P. LYNCH, AND J. R. SCHUBEL. 1973. The effects of Hurricane Agnes on the environment and organisms of Chesapeake Bay. Early findings and recommendations. The Chesapeake Bay Research Council.
- BENDER, E. A., T. J. CASE, AND M. E. GILPIN. 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology* **65**: 1–13, doi:10.2307/1939452
- BORUM, J. 1987. Dynamics of epiphyton on eelgrass (*Zostera marina* L.) leaves: Relative roles of algal growth, herbivory, and substratum turnover. *Limnol. Oceanogr.* **32**: 986–992.
- BOUSFIELD, E. L. 1973. Shallow-water gammaridean Amphipoda of New England. Cornell Univ. Press.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer.
- CAINE, E. A. 1974. Comparative functional morphology of feeding in three species of caprellids (Crustacea, Amphipoda) from the northwestern Florida Gulf Coast. *J. Exp. Mar. Biol. Ecol.* **15**: 81–96, doi:10.1016/0022-0981(74)90065-3
- CARPENTER, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**: 677–680, doi:10.2307/2265490
- CHRISTIE, H., AND P. KRAUFVELIN. 2004. Mechanisms relating amphipod population density within macroalgal communities with low predator impact. *Sci. Mar.* **68**: 189–198, doi:10.3989/scimar.2004.68s1189
- CLARKE, K. R., AND R. N. GORLEY. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E.
- DOUGLASS, J. G., J. E. DUFFY, AND J. F. BRUNO. 2008. Herbivore and predator diversity interactively affect ecosystem properties in a marine community. *Ecol. Lett.* **11**: 598–608, doi:10.1111/j.1461-0248.2008.01175.x
- , ———, A. C. SPIVAK, AND J. P. RICHARDSON. 2007. Nutrient vs. consumer control of community structure in a Chesapeake Bay eelgrass habitat. *Mar. Ecol. Prog. Ser.* **348**: 71–83, doi:10.3354/meps07091
- DOWNING, A. L., B. L. BROWN, E. M. PERRIN, T. H. KEITT, AND M. A. LEIBOLD. 2008. Environmental fluctuations induce scale-dependent compensation and increase stability in plankton ecosystems. *Ecology* **89**: 3204–3214, doi:10.1890/07-1652.1
- DUFFY, J. E. 1990. Amphipods on seaweeds: Partners or pests? *Oecologia* **83**: 267–276, doi:10.1007/BF00317764
- . 2006. Biodiversity and the functioning of seagrass ecosystems. *Mar. Ecol. Prog. Ser.* **311**: 233–250, doi:10.3354/meps311233
- , AND A. M. HARVILICZ. 2001. Species-specific impacts of grazing amphipods in a seagrass community. *Mar. Ecol. Prog. Ser.* **223**: 201–211, doi:10.3354/meps223201
- , AND M. E. HAY. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol. Monogr.* **70**: 237–263, doi:10.1890/0012-9615(2000)070[0237:SIOGAO]2.0.CO;2
- , J. P. RICHARDSON, AND K. E. FRANCE. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol. Lett.* **8**: 301–309, doi:10.1111/j.1461-0248.2005.00725.x
- EDGAR, G. J. 1990a. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *J. Mar. Biol. Ecol.* **137**: 195–214, doi:10.1016/0022-0981(90)90185-F
- . 1990b. Population regulation, population-dynamics and competition amongst mobile epifauna associated with seagrass. *J. Exp. Mar. Biol. Ecol.* **144**: 205–234, doi:10.1016/0022-0981(90)90029-C
- , AND N. S. BARRETT. 2002. Benthic macrofauna in Tasmanian estuaries: Scales of distribution and relationships with environmental variables. *J. Exp. Mar. Biol. Ecol.* **270**: 1–24, doi:10.1016/S0022-0981(02)00014-X
- , AND D. W. KLUMPP. 2003. Consistency over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape. *Aquatic Botany* **75**: 275–291, doi:10.1016/S0304-3770(02)00194-8
- , AND C. SHAW. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *J. Exp. Mar. Biol. Ecol.* **194**: 83–106, doi:10.1016/0022-0981(95)00084-4
- ERIKSSON, B. K., L. LJUNGGREN, A. SANDSTRÖM, G. JOHANSSON, J. MATTILA, A. RUBACH, S. RÅBERG, AND M. SNICKARS. 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecol. Appl.* **19**: 1975–1988, doi:10.1890/08-0964.1
- FRANCE, K. E., AND J. E. DUFFY. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* **441**: 1139–1143, doi:10.1038/nature04729
- FRANK, K. T., B. PETRIE, AND N. L. SHACKELL. 2007. The ups and down of trophic control in continental shelf ecosystems. *Trends Ecol. Evol.* **22**: 236–242, doi:10.1016/j.tree.2007.03.002
- FREDETTE, T. J., R. J. DIAZ, J. VAN MONTFRANS, AND R. J. ORTH. 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in Lower Chesapeake Bay. *Estuaries* **13**: 431–440, doi:10.2307/1351787

- FROST, T. M., S. R. CARPENTER, A. R. IVES, AND T. K. KRATZ. 1995. Species compensation and complementarity in ecosystem function, p. 224–239. *In* C. G. Jones and J. H. Lawton [eds.], *Linking species and ecosystems*. Chapman and Hall.
- GUERRA-GARCIA, J. M., I. MARTINEZ-PITA, AND M. L. PITA. 2004. Fatty acid composition of the Caprellidea (Crustacea: Amphipoda) from the Strait of Gibraltar. *Sci. Mar.* **68**: 501–510.
- HECK, JR., K. L., AND R. J. ORTH. 2006. Predation in seagrass meadows, p. 537–550. *In* A. W. D. Larkum, R. J. Orth, and C. M. Duarte [eds.], *Seagrasses: Biology, ecology and conservation*. Springer.
- , AND J. F. VALENTINE. 2007. The primacy of top-down effects in shallow benthic ecosystems. *Estuar. Coasts* **30**: 371–381, doi:10.1007/BF02819384
- , ———, J. R. PENNOCK, G. CHAPLIN, AND P. M. SPITZER. 2006. Effects of nutrient enrichment and grazing on shoal-grass *Halodule wrightii* and its epiphytes: Results of a field experiment. *Mar. Ecol. Prog. Ser.* **326**: 145–156, doi:10.3354/meps326145
- HEMMINGA, M. A., AND C. M. DUARTE. 2000. *Seagrass ecology*. Cambridge Univ. Press.
- HOULAHAN, J. E., AND OTHERS. 2007. Compensatory dynamics are rare in natural ecological communities. *Proc. Natl. Acad. Sci. U.S.A.* **104**: 3273–3277, doi:10.1073/pnas.0603798104
- HOWARD, R. K., AND F. T. SHORT. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquatic Botany* **24**: 287–302.
- HUGHES, A. R., K. J. BANDO, L. F. RODRIGUEZ, AND S. L. WILLIAMS. 2004. Relative effects of grazers and nutrients on seagrasses: A meta-analysis approach. *Mar. Ecol. Prog. Ser.* **282**: 87–99, doi:10.3354/meps282087
- HURST, A. 1965. The feeding habits of *Nassarius vibex* (Say). *The Proceedings of the Malacological Society of London* **36**: 313–317.
- JACKSON, J. B. C., AND OTHERS. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629–638, doi:10.1126/science.1059199
- JØRGENSEN, P., S. E. IBARRA-OBANDO, AND J. D. CARRIQUIRY. 2007. Top-down and bottom-up stabilizing mechanisms in eelgrass meadows differentially affected by coastal upwelling. *Mar. Ecol. Prog. Ser.* **333**: 81–93, doi:10.3354/meps333081
- KEMP, W. M., AND OTHERS. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. *Estuaries* **27**: 363–377, doi:10.1007/BF02803529
- LAZZARI, M. A., AND K. W. ABLE. 1990. Northern pipefish, *Syngnathus fuscus*, occurrences over the Mid-Atlantic Bight continental shelf: Evidence of seasonal migration. *Env. Biol. Fishes* **72**: 177–185, doi:10.1007/BF00001671
- LIPCIUS, R. N., AND W. T. STOCKHAUSEN. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **226**: 45–61, doi:10.3354/meps226045
- LORENZEN, C. J. 1967. Determination of chlorophyll and phaeopigments: Spectrophotometric equations. *Limnol. Oceanogr.* **12**: 343–346, doi:10.4319/lo.1967.12.2.0343
- MANZI, J. J. 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Biol. Bull.* **138**: 35–46, doi:10.2307/1540289
- MARSH, G. A. 1973. The *Zostera* epifaunal community in the York River, Virginia. *Ches. Sci.* **14**: 87–97, doi:10.2307/1350873
- . 1976. Ecology of the gastropod epifauna of eelgrass in a Virginia estuary. *Ches. Sci.* **17**: 182–187, doi:10.2307/1351196
- MCCANN, K. S., J. B. RASMUSSEN, AND J. UMBANHOWAR. 2005. The dynamics of spatially coupled food webs. *Ecol. Lett.* **8**: 513–523, doi:10.1111/j.1461-0248.2005.00742.x
- MOKSNES, P. O., M. GULLSTRÖM, K. TRYMAN, AND S. BADEN. 2008. Trophic cascades in a temperate seagrass community. *Oikos* **117**: 763–777, doi:10.1111/j.0030-1299.2008.16521.x
- MOORE, K. A., AND J. C. JARVIS. 2008. Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: Implications for long-term persistence. *J. Coastal Res.* **55**: 135–147, doi:10.2112/SI55-014
- , H. A. NECKLES, AND R. J. ORTH. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **142**: 247–259, doi:10.3354/meps142247
- , D. J. WILCOX, AND R. J. ORTH. 2000. Analysis of the abundance of submerged aquatic vegetation in the Chesapeake Bay. *Estuaries* **23**: 115–127, doi:10.2307/1353229
- MUEHLSTEIN, L. K., D. PORTER, AND F. T. SHORT. 1988. *Labyrinthula* sp., a marine slime mold producing the symptoms of wasting disease in eelgrass, *Zostera marina*. *Marine Biology* **99**: 465–472.
- NAEEM, S., AND S. LI. 1997. Biodiversity enhances ecosystem reliability. *Science* **390**: 507–509.
- NECKLES, H. A., R. L. WETZEL, AND R. J. ORTH. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte *Zostera marina* L. dynamics. *Oecologia* **93**: 285–295, doi:10.1007/BF00317683
- NELSON, W. G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *J. Exp. Mar. Biol. Ecol.* **39**: 231–264, doi:10.1016/0022-0981(79)90129-1
- . 1980. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. *Bull. Mar. Sci.* **30**: 80–89.
- , K. D. CAIRNS, AND R. W. VIRNSTEIN. 1982. Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River lagoon, Florida. *Bull. Mar. Sci.* **32**: 121–129.
- ORTH, R. J. 1973. Benthic infauna of eelgrass, *Zostera marina*, beds. *Ches. Sci.* **14**: 258–269, doi:10.2307/1350754
- , AND K. L. HECK, JR. 1980. Structural components of eelgrass (*Zostera marina*) meadows of the lower Chesapeake Bay—fishes. *Estuaries* **3**: 278–288, doi:10.2307/1352083
- , AND K. A. MOORE. 1986. Seasonal and year-to-year variations in the growth of *Zostera marina* L. (eelgrass) in the lower Chesapeake. *Aquat. Bot.* **24**: 335–341, doi:10.1016/0304-3770(86)90100-2
- , AND OTHERS. 2006. A global crisis for seagrass ecosystems. *Bioscience* **56**: 987–996, doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2
- OSMAN, R. W., R. B. WHITLATCH, AND R. J. MALATESTA. 1992. Potential role of micro-predators in determining recruitment into a marine community. *Mar. Ecol. Prog. Ser.* **83**: 35–43, doi:10.3354/meps083035
- PARKER, J. D., J. E. DUFFY, AND R. J. ORTH. 2001. Plant species diversity and composition: Experimental effects on marine epifaunal assemblages. *Mar. Ecol. Prog. Ser.* **224**: 57–67, doi:10.3354/meps224055
- POLIS, G. A., AND D. R. STRONG. 1996. Food web complexity and community dynamics. *Am. Nat.* **147**: 813–846, doi:10.1086/285880
- SCHELTEMA, R. 1964. Feeding habits and growth in the mud snail *Nassarius obsoletus*. *Ches. Sci.* **5**: 161–166, doi:10.2307/1350560
- STONER, A. W. 1980. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. *Contr. Mar. Sci. Univ. Texas* **23**: 63–77.

- VALENTINE, J., AND J. E. DUFFY. 2006. The central role of grazing in seagrass ecology, p. 463–501. *In* A. W. D. Larkum, R. J. Orth and C. M. Duarte [eds.], *Seagrasses: Biology, ecology and conservation*. Springer.
- VAN MONTFRANS, J., R. J. ORTH, AND S. A. VAY. 1982. Preliminary studies of grazing by *Bittium varium* on eelgrass periphyton. *Aquat. Bot.* **14**: 75–89, doi:10.1016/0304-3770(82)90087-0
- , R. L. WETZEL, AND R. J. ORTH. 1984. Epiphyte-grazer relationships in seagrass meadows: Consequences for seagrass growth and production. *Estuaries* **7**: 289–309, doi:10.2307/1351615
- VIRNSTEIN, R. W., AND R. K. HOWARD. 1987. Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. I. Comparisons among three species of seagrasses from adjacent beds. *Bulletin of Marine Science* **41**: 1–12.
- WERNER, E. E., AND S. D. PEACOR. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**: 1083–1100, doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2
- WORM, B., H. K. LOTZE, H. HILLEBRAND, AND U. SOMMER. 2002. Consumer vs. resource control of species diversity and ecosystem functioning. *Nature* **417**: 848–851, doi:10.1038/nature00830
- , AND OTHERS. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**: 787–790, doi:10.1126/science.1132294
- ZIMMERMAN, R., R. GIBSON, AND J. HARRINGTON. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Mar. Biol.* **54**: 41–47, doi:10.1007/BF00387050

*Associate editor: Anthony Larkum*

*Received: 29 June 2009*

*Accepted: 16 February 2010*

*Amended: 09 March 2010*