Return of foundation species: effects of large-scale seagrass restoration on hard clam population dynamics and secondary production across spatiotemporal scales

Michael Richard Cornish
Brookline, Vermont

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Committee:

Max C. N. Castorani, PhD (advisor)
Michael L. Pace, PhD
Patricia L. Wiberg, PhD
Edmund D. Brodie III, PhD

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Abstract

Foundation-species theory posits that habitat-forming organisms enhance consumer productivity by physically or chemically reshaping their environment and, in so doing, controlling major ecosystem functions, such as primary or secondary production. Other ecological frameworks—scale-transition, Moran-effect, and stress-gradient theories—suggest that this facilitation may not be universal or may depend on scale: non-linear local effects can change direction when averaged over larger areas or longer periods, region-wide climate signals can synchronize populations and override habitat differences, and the balance between facilitation and competition can shift with abiotic stress, predator pressure, or life stage. I evaluated these competing expectations in the world's largest restored seagrass meadow (exceeding 20 km²) on the Eastern Shore of Virginia, USA, pairing the foundational seagrass *Zostera marina* with a widespread and highly associated consumer, the hard clam *Mercenaria mercenaria*. Across a seascape that underwent a multidecadal transition from an unvegetated lagoon seafloor to a dense seagrass meadow, I combined centimeter-resolved phytoplankton profiling, seasonally replicated clam predation experiments, four-month clam growth assays, and a 45-year clam shell-growth chronology to quantify how seagrass habitat modification and regional climate interact across space, time, and life stage to affect hard clam secondary production and survivorship. Results reveal a driver hierarchy. Eelgrass canopies create a two-phase food pulse: a winter–spring reservoir of significant benthic (sediment) microalgal productivity followed by an eight- to ten-fold summer surge of near-bed suspended chlorophyll-*a.* The seagrass canopy—especially during spring and summer—significantly enhanced survival across life stages compared to unvegetated sites, with small newly-recruited individuals (~10 mm in length) benefitting most. While experimental observations of adult shell growth rates were marginally or entirely unexplained by variations in seagrass habitat or food availability,

juvenile clams deployed at seagrass sites grew 36% more faster and were spared notable tissue mass reductions per unit of shell growth exhibited by those at bare sites, indicating an energetic tradeoff/cost lessened by seagrass. At decadal scales, March–August sea surface temperature anomalies alone explained about one-third of annual shell-growth variance, while proximity to the expanding meadow had a relatively small positive effect, placing *M. mercenaria* among the most climate-sensitive marine bivalves. Collectively, these findings show that intrinsic habitat mechanisms operate as predicted but only when dense habitat, life stage, and seasonal windows align, whereas regional climate imposes a dominant, lagoon-scale synchronizing influence on growth over interannual to multidecadal scales regardless of seagrass presence. Hence, the effect of this foundational seagrass species on hard clams appears to be dominated by effects on recruitment through provisioning a predation refuge to small, young individuals while productivity is largely governed by climate.

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Introduction to the dissertation

Ecological theory casts foundation species as first-order controls on primary production: by virtue of their high abundance and generally large physical structure, they redirect light, flow, nutrients, and soils/sediments, and thereby determine the distribution and magnitude of basal energy in an ecosystem (Dayton 1972). Classic examples of foundation species—canopy-forming kelps, reef-building corals, and forest-forming trees—show that canopy height, reef architecture, or root mass can shape resource fields for entire consumer guilds (Jones et al. 1996). Ecosystem restoration projects often rely on this premise: re-establish the engineer and consumer production will track the recovery of physical habitat (Gagnon et al. 2020a).

Three lines of ecological theory may temper that expectation. *Scale-transition theory* demonstrates that non-linear local interactions—commonplace in ecological studies—do not aggregate predictably: effects measured at centimeter scales over weeks to months can strengthen, weaken, or reverse when observations extend to kilometers and decades (Holyoak et al. 2005). Relatedly, *Moran-effect theory* shows that spatially coherent climate anomalies synchronize populations across broad regions, potentially masking or overriding local habitat signals (i.e., assumptions of independent observations violated despite significant distance) (Koenig 2002; Castorani et al. 2022, Reuman et al. 2025). Lastly, *stress-gradient models* add that the outcome of habitat modification depends on abiotic stress, consumer pressure, and consumer life stage; facilitation can therefore switch to competition when background conditions change (Malkinson and Tielbörger 2010, Castorani et al. 2015). Together, these rising frameworks predict that the benefits of foundation species will vary sharply with scale and context—even when their physical presence is constant.

The interaction between the seagrass *Zostera marina* (eelgrass) and the hard clam *Mercenaria mercenaria* is a paradigmatic example of this idea (Fales et al. 2020). Eelgrass

canopies reduce near-bed flow velocities, facilitate deposition, and stabilize sediments (Bricelj and Malouf 1984; Lawson et al. 2007)—mechanisms expected to concentrate food near the seafloor for suspension feeders and dampen predation risk (Peterson 1984; Judge et al. 1993; Irlandi 1996). Clams, in turn, filter the water column and excrete bio-available nitrogen, found to significantly improve light availability and nutrient supply for seagrasses (Bell et al. 2016; Gagnon et al. 2020). Despite this apparent reciprocal coupling, empirical results remain inconsistent. Small-plot experiments frequently report higher juvenile growth and survival within vegetation (Irlandi 1996), yet others find the inverse or no significant effects of local habitat on clam performance or survival (Heck et al. 2003; Barber et al. 2019; Fales et al. 2020a), underscoring the need for scale-explicit tests.

Study system

Situated in the ≈950 km² back-barrier lagoons of Virginia's Eastern Shore (Delmarva Peninsula, USA), the Virginia Coast Reserve (VCR) hosts the world's largest successful seagrass (eelgrass *Zostera marina*) restoration. Over the past two decades, >30 km² of meadow have re-established from initial seeding (Orth et al. 2020). Across this expansive, tidally-driven system, strong inlet-to-interior gradients in flow, residence time, temperature, and wave energy—together with relatively low fishing pressure, coastal development, and other human impacts (Carr et al. 2012; Hondula and Pace 2014; Besterman et al. 2021)—provide a natural laboratory for testing habitat versus climate control on hard-clam performance. Annual mapping by the Virginia Institute of Marine Science (VIMS) Submerged Aquatic Vegetation Monitoring Program (VIMS 2025) now documents a near-annual chronosequence since initial restoration (2001–2024, ongoing) that ranges from unvegetated sand to young patches and mature canopy as the

meadows continues to expand. This spatial mosaic provides an ideal natural experiment for disentangling habitat- and climate-driven controls on benthic consumers.

To capitalize on this setting, each dissertation chapter was designed to address one overarching question directly while providing complementary evidence for the others:

1. How does modification of the benthic environment by eelgrass canopies affect the magnitude, vertical distribution, and seasonal timing of the food resources available to benthic consumers?

2. In what ways do local canopy architecture, predator activity, and clam ontogeny interact to determine clam survival outcomes within seagrass landscapes?

3. Over annual to multi-decadal horizons, how do local seagrass conditions compare with regional climate forcing in controlling hard-clam growth rates?

Chapter 1: *Benthic and pelagic primary production dynamics across a seagrass meadow*

Centimeter-stratified water samples, epiphyte biomass, and 1-cm deep sediment cores documented a two-phase sequence: (1) a winter–spring reservoir of benthic (sediment) chlorophyll-*a* concentrations (i.e., clam food abundance proxy) within the seagrass nearly double those collected at bare sites and (2) an eight- to ten-fold surge of near-bed (1–5 cm above the seafloor) chlorophyll-*a* (6–10 μg L^{-1}) during late-summer canopy senescence. Although the canopy concentrated chlorophyll-*a* in a seafloor-level layer (1–5 cm above benthos), peak values in this oligotrophic system rarely exceeded known saturation thresholds for hard clams (*Mercenaria mercenaria;* Kraeuter and Castagna 2001, Hondula and Pace 2014, McGlathery

2017), foreshadowing modest growth pay-offs. Hence, seagrass mediated a seasonally-elevated near-seafloor chlorophyll-*a* reservoir—the classic measure of basal food resources for filter-feeding invertebrates like infaunal bivalves (Griffiths et al. 2017, Cox et al. 2020).

Chapter 2: *Influence of seagrass habitat configuration, seasonality, and life stage on hard clam predation*

A fully factorial field experiment crossing habitat (bare, patchy seagrass, dense seagrass), season, and clam ontogeny showed that predation on hard clams depends jointly on vegetation density, season, and life stage: dense seagrass alone boosted uncaged juvenile (~10 mm) survival roughly five-fold over bare sites whereas patchy seagrass habitat offered no juvenile refuge; for adults (60–120 mm) dense and patchy seagrass raised survival about 20-fold during the late-spring canopy peak, while survivorship on an unvegetated seafloor was near zero at other times; summer predation intensified everywhere, yet seagrass still provided 4–7-fold protection compared to bare-sites—where survival dropped 88% from winter. Thus, refuge value is strong within the seagrass canopy, transient with canopy phenology, and most critical for the smallest clams when predator pressure peaks.

Chapter 3: *Effects of seagrass-mediated food sources, habitat configuration, and life stage on clam growth in a restored seagrass meadow*

A four-month caging experiment integrated centimeter-resolved chlorophyll-*a* profiles (food supply proxy) with spatial metrics of the meadow (shoot density, edge distance) to quantify growth responses across clam life stages. Juvenile *Mercenaria mercenaria* grew ~36 % faster inside the *Zostera marina* canopy than on adjacent bare sand, whereas adult growth rates

were near-uniform across habitats. Neither distance from the meadow edge nor modest differences in near-bed chlorophyll-a (≈ 6–10 μg L^{-1}) explained growth variation. Condition indices revealed a habitat-dependent trade-off: for juveniles deployed at bare-seafloor sites, condition declined by roughly 0.66 % for each cm^2 of accreted shell, whereas clams inside seagrass showed no such decline. These results indicate that eelgrass beds enhance juvenile shell extension and buffer juveniles against energetic costs from calcification, while adult growth is largely unaffected by habitat.

Chapter 4: *Climate variability, not ecosystem state, governs long-term productivity in seagrass-dwelling clams*

Rigorous sclerochronology methods and sample processing for extracting annually-resolved timeseries from bivalves (Schöne et al. 2005a; Black et al. 2008)—applied to hard clams (*Mercenaria mercenaria*) for the first time—were used to construct a long-term annual shell growth timeseries. This new application reveals that March–August sea-surface-temperature anomalies account for ~30% of annual shell-growth variance, and places hard clams among the most climate-sensitive marine bivalve—a significant and novel finding (Schöne et al. 2005; Mette et al. 2016). However, seagrass had a modest positive effect on growth indices, causing a small decrease in the growth of clams farther outside of the meadow. Thus, lagoon-scale temperature synchrony largely overrides local ecosystem state/habitat change at the temporal scale most relevant to lifetime growth and population dynamics of this long-lived bivalve.

Viewed through a scale-explicit lens, these chapters aimed to advance foundation-species theory by placing past, often contradictory, case studies into a coherent driver hierarchy. Intrinsic

canopy effects—flow attenuation, particle trapping, and structural refuge—operate as predicted, but are phase- and state-dependent, surfacing only where dense seagrass shoots, juvenile life stages, and narrow seasonal windows coincide. This places extrinsic climate forcing atop the hierarchy: local SST anomalies related to regional climate variability and basin-scale climate forcing synchronize growth and survival across habitats, satisfying Moran-effect expectations and overriding local habitat signals on annual to decadal horizons (Mette et al. 2016; Barber et al. 2019).

This scale-explicit hierarchy resolves earlier contradictions by revealing that each study observed a distinct blend of canopy structure, consumer life stage, and prevailing climate. Accounting for these interacting drivers will sharpen predictions of *M. mercenaria* survival and secondary production in *Z. marina* meadows. More broadly, the framework offers a template for investigating other, often under-studied, bivalve–foundation species pairings and the diverse response pathways highlighted by Fales et al. (2020). From a natural-resource-management perspective, eelgrass restoration projects are likely to enhance hard-clam recruitment by providing nursery habitat, which in turn can amplify nutrient recycling as a growing population of infaunal clams excretes bio-available nitrogen and phosphorus—a well-documented positive feedback between bivalves and seagrass (Griffiths et al. 2017, Gagnon et al. 2020).

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Chapter 1. Benthic and pelagic primary production dynamics across a seagrass meadow

Anticipated authors of peer-reviewed manuscript:

Michael R. Cornish

Katharine C. Schlachter

Michael L. Pace, PhD

Max C.N. Castorani, PhD

Abstract

Seagrass meadows are often noted for enhancing secondary production in shallow coastal marine ecosystems, yet the relative timing and magnitude of benthic versus pelagic (water-column) primary production that fuels consumers remain poorly constrained, particularly in oligotrophic systems. Here, we combined centimeter-resolved water-column sampling, epiphytic algal sampling, and benthic sediment cores to track chlorophyll-*a* and biomass dynamics across sites inside and outside a restored ~20 km² seagrass meadow (*Zostera marina*) in the Virginia Coast Reserve (Virginia, USA). We collected stratified water samples (1, 5, 15, and 45 cm above the seabed) and surface-sediment cores (1-cm deep) quarterly (2022–2023) and water samples weekly during summer/autumn 2021. We found that seagrass approximately doubled near-bed (1–5 cm) chlorophyll-*a* concentrations in autumn and reduced its within-year variability by ~35 %, indicating enhanced production, retention, and temporal stability within the benthic boundary layer. Across seasons, benthic microalgae dominated carbon stocks in both habitats; winter seagrass sediments supported 24 ±3 g C m^{-2}—three-fold more than the adjacent unvegetated seafloor. Epiphytes supplied a pronounced late-summer carbon pulse (18 ±3 g C m^{-2}), temporarily matching benthic stocks and accounting for ~56 % of total epiphyte, benthic, and water column algal carbon within the meadow. Integrated budgets indicated that bare flats remained benthic-dominated year-round, whereas meadows supported a diversified, seasonally shifting mix of significant benthic and epiphytic sources likely accessible to suspension and deposit feeders. Within the confines of our study, near-bed enrichment appears to elevate the biomass and stability of suspended algal material, a basal resource that may help fuel the significant suspension- and deposit-feeder communities associated with seagrass meadows. Hence, incorporating benthic and epiphytic sources alongside pelagic inputs may be

critical for evaluating the extent of seagrass-modulated contributions to this basal resource pool underpinning seagrass ecosystem food webs and functioning.

Introduction

Seagrass meadows are highly productive coastal ecosystems where foundational marine plants, such as eelgrass *Zostera marina*, stabilize sediments, attenuate flow, and facilitate diverse assemblages of invertebrates and fishes (Barbier et al., 2011; Gagnon et al., 2020; Orth et al., 1984, Hardison et al. 2023). The seagrass canopy creates a three-dimensional structure that supports both sessile and mobile organisms by offering food and refuge from hydrodynamic stress (Hansen & Reidenbach, 2013; Lewis & Anderson, 2012)**.**

Despite the physical dominance of seagrass and their major control over benthic metabolism (Berg et al. 2019, Berger et al. 2020), significant primary production within seagrass beds is not limited to the vascular plants themselves. Seagrass leaves host dense communities of epiphytic macroalgae and microalgae, while the underlying sediments support significant benthic microalgal stocks—often diatom-dominated (Duffy et al., 2001). These autochthonous producers, in combination with allochthonous (e.g., tidally delivered) phytoplankton inputs, form the energetic base for rich secondary producer communities associated with these systems. The seagrass canopy harbors amphipods, copepods, isopods, and other invertebrates; the seafloor supports abundant bivalves and polychaetes; other suspension feeders like tunicates, bryozoans, and sponges attach to seagrass and sediment surfaces (Irlandi 1996a, Heck et al. 2008, Whitlow and Grabowski 2012)**.**

Although the potential for mesograzer control of epiphytic production is well documented (Poore et al. 2009, Cook et al. 2011, Whalen et al. 2013) the contribution of autochthonous seagrass and benthic microalgal production to benthic secondary producers, such

as suspension-feeding infaunal bivalves remains underexplored—particularly in oligotrophic lagoons and oyster reef-fringed meadows—limiting robust estimates of seagrass-mediated secondary production across trophic guilds (Judge et al. 1993, Seitz and Lewis 2018, Rodil et al. 2022).

In the shallow, characteristically oligotrophic lagoons of the Virginia Coast Reserve (VCR), *Z. marina* coverage expanded over 25 years from ~0 to >30 km^2—the result of a significant restoration effort to re-populate the systems' light-and nitrogen-limited subtidal habitat (Hondula & Pace, 2020, Carr et al. 2012). These lagoons exhibit naturally low phytoplankton concentrations (Orth et al. 2020a, McGlathery and Christian 2024)—perhaps further depleted within seagrass meadows due to nutrient competition and efficient grazing by filter feeders (Allen and Williams 2003, de Wit et al. 2012, Fales et al. 2020). In such systems, highly abundant benthic filter feeders like hard clams (*Mercenaria mercenaria*), known to selectively feed on pelagic phytoplankton, may depend on 'alternative' food sources including benthic microalgae, detrital particles, and suspended epiphyte fragments (Peterson 1986, Judge et al. 1993, Carroll et al. 2008). Hence, understanding the spatiotemporal dynamics of benthic (attached to the seafloor and seagrass) and suspended primary production remains a significant gap in our knowledge of seagrass-fueled consumer productivity.

Methods

Stratified water column chlorophyll-a measurements

From June to September 2021, we collected vertically stratified water-column samples approximately once per week (weather and tides permitting), and then approximately quarterly from summer 2022 through early spring 2023, at 8 seagrass meadow sites and 8 unvegetated

‘bare’ sites (Fig. 4). A four-port PVC sampler modified from Judge et al. (1993) was deployed from an anchored skiff—held motionless for about 3 min to allow any disturbed particles to clear—before using a 60-mL polypropylene syringe attached to polyethylene tubing, to draw 180-mL water samples from four heights above the sediment–water interface (1, 5, 15, and 45-cm), thereby resolving centimeter-scale vertical heterogeneity in the benthic boundary layer. Samples were kept in a dark cooler on ice (< 2-h transit) before laboratory processing.

Following Judge et al. (1993) and methods used for long-term water quality datasets collected by the VCR LTER (McGlathery and Christian 2024), each sample was then vacuum-filtered (≤ 20 kPa) through pre-combusted 47-mm Whatman GF/C glass-fiber filters (1.2-µm nominal pore size). Afterward, filters were wrapped in aluminum foil and frozen at –20 °C until extraction (≤ 7 d). For pigment extraction, filters were ground by hand in a chilled mortar with 7 mL of 90% acetone, transferred to amber centrifuge tubes, and extracted for 24 hours at 4 °C in the dark. Extracts were clarified in a centrifuge (5 minutes at 7000 RPM corresponding to approximately 5000 g—where RPM = rotations per minute, g = relative centrifugal force) and the supernatant read spectrophotometrically at 664 and 750 nm before and after acidification with 0.1 N HCl.

Chlorophyll-*a* concentrations were calculated with the monochromatic equations of Lorenzen (1967) and corrected for pheophytin interference following U.S. EPA Method 445.0 (Arar & Collins 1997). Concentrations were normalized to the original sample volume and reported in µg L^{-1}, yielding high-resolution vertical profiles of chlorophyll-*a* suitable for detecting benthic boundary-layer enrichment and evaluating potential food availability for suspension feeders (Judge et al. 1993).

Seagrass algal epiphyte sampling

To quantify epiphytic macroalgal biomass throughout the summer growing season (June to September 2021), we haphazardly collected 10–15 seagrass shoots (~30-cm long) weekly from each of the 8 within-meadow sites, returned these to the lab on ice, and then scraped the leaves using methods described in Dauby and Poulicek (1995) to remove adhered sediment and occasional calcareous epifauna (e.g., spirorbid polychaetes) from epiphyte biomass measurements by using ash-free dry mass (AFDM) in place of dry weight. To convert seagrass leaf biomass to area, we photographed the seagrass leaves, measured their total (both sides of each leaf) surface area using ImageJ (Schneider et al., 2021), and acquired AFDM (dry mass – combusted mass) by following dry mass measurements (>48-h in a drying oven at 60 °C) with that following 12 hours in a 550 °C muffle furnace. Dividing leaf AFDM by leaf area generated a mean value of 1.702 mg cm^{-2} (standard deviation, σ = 0.21 mg cm^{-2}), which we applied to the epiphyte dataset to calculate epiphyte dry mass per unit seagrass leaf area.

Seagrass leaf dry mass (AFDM) and leaf surface area (cm^2) had a strong relationship (R^2 = 0.88, df = 8, p <0.001). Hence, to scale epiphyte biomass from leaf surface area to seafloor area (g DM m^{-2}), we used site-level estimates of total leaf area per square meter. These were calculated from July 2021 measurements of shoot density (shoots m^{-2}) and aboveground seagrass dry biomass (g DM m^{-2}) collected at long-term VCR LTER seagrass monitoring stations, located ~100 m from our sampling sites (McGlathery 2022). Then, we computed epiphyte ash-free dry mass per square meter of seafloor in the seagrass meadow ($\boldsymbol{E}_{\mathbf{seafloor}}$; g AFDM m^{-2}) as:

$$E_{seafloor} = E_{leaf} \times \left(\frac{B_{\text{seafloor}}}{b_{leaf}}\right), \text{ where:}$$

$\boldsymbol{E}_{\mathbf{leaf}}$ = epiphyte mass per cm^2 of leaf surface area (mg AFDM cm^{-2})

$\boldsymbol{B}_{\mathbf{seafloor}}$ = seagrass aboveground biomass per m^2 of seafloor (g DM m^{-2})

$\boldsymbol{b_{leaf}}$ = seagrass leaf biomass per cm^2 of leaf surface area (mg DM cm^{-2})

Sediment (benthic) chlorophyll-a measurements

During the 2022–2023 field campaign, we collected surface (0–1 cm) sediment samples with ~1-cm diameter corers (modified plastic syringes; n = 288 across 6 sampling events) at the seagrass and bare sites where water-column samples were taken. These field sample collections and laboratory analysis followed the long-term VCR LTER methods: sediment cores expressed into aluminum foil-wrapped 50 mL polypropylene centrifuge tubes (Falcon®, Corning Inc.) immediately after collection for transport on ice and frozen (−20 °C) within 2 hours, then pigments extracted overnight in 90% acetone at −20 °C in the dark, sonicated, and then—as described above for water column samples—clarified by centrifugation before chlorophyll-*a* concentrations were determined spectrophotometrically before and after acidification following Lorenzen (1967), as modified by Pinckney et al. (1994). Finally, these were converted to seafloor area units (mg cm^{-2}) by multiplying the extract chlorophyll-a concentration (μg L^{-1}) by the extraction volume (L), dividing by the corer footprint ($\pi \times 0.5$ cm^2), and then dividing by 1000 to express μg as mg (McGlathery 2017).

Effective-fetch distance (EFD)

Following Keddy's (1982) exposure index, we quantified site wave exposure with a novel computation of wind-weighted effective fetch because (1) we could compute this metric using wind data temporally-matched with the sampling effort, unlike existing study system fetch products based on 2013–2015 environmental data (Fonseca and Bell 1998, Kremer and Reidenbach 2021) and (2) we could exploit the meter-scale, nightly-updated OpenStreetMap shoreline—a high-resolution, community-digitized vector of the mean high-water (i.e., mean spring high tide line) from aggregated manually-traced coordinates, satellite, and aerial imagery–

–to capture fine-scale heterogeneity that commonly-used products such as the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) from the National Oceanic and Atmospheric Administration (NOAA) miss in complex coastal lagoon landscapes (Luijendijk et al. 2018, Mason et al. 2018, Zhai et al. 2025).

Using the R-package *waver* (v0.3.0; Marchand & Gill 2023), we traced 16 rays at 22.5° increments from each site centroid to the first land intersection in the OSM shoreline (EPSG: 32618), recording the over-water distance (d_i). Six-minute winds from NOAA station RPLV2 Rappahannock Light (NOAA National Data Buoy Center 2025) were binned into the same sectors to obtain relative frequency weights (f_i). Effective fetch was then: By combining the physical reach of open water with the directional probability of wind forcing this metric yields a more realistic estimate of wave-generation potential than fixed tables that assume isotropic winds and coarser shoreline resolution. All analyses were performed in R 4.3.0 (R Core Team 2024) with the *sf* (spatial objects; Pebesma 2018), and *circular* (Agostinelli and Lund 2024) R-packages.

Data analyses: water column chlorophyll-a

To examine how seagrass habitat modifies seasonal and vertical patterns in water-column chlorophyll-*a* concentrations, we modeled stratified chlorophyll-*a* samples collected at fixed depths (1, 5, 15, and 45 cm above the seafloor) across bare and seagrass habitats over four seasons and two years. The response variable was chlorophyll-*a* concentration (μg L^{-1}), and fixed effects included sampling height, habitat type (Bare vs. Seagrass), and season (Winter, Spring, Summer, or Autumn), with all two- and three-way interactions to capture context-dependent habitat effects.

To account for differences in data structure across time periods, we used separate models for each subset. For 2021 data (n = 463), we fit a Gamma generalized linear mixed-effects model (GLMM) with a log link function and included a random intercept for Site to account for repeated sampling. For 2022–2023 (n = 319), we used a Tweedie GLMM with a log link function, also including a random-intercept term for site. For the full combined dataset (n = 782), we fit a Tweedie generalized linear model (GLM) with the same fixed-effect structure but excluded random effects after model selection indicated negligible variance explained by site and no improvement in model fit (difference in Akaike Information Criterion, $\Delta AIC < 2$; Anderson and Burnham 2004). This allowed clearer estimation of group-level means and variances across depths, habitats, and seasons.

We fit all models using the *glmmTMB* package (Brooks et al. 2017) in R (R Core Team 2024). Model assumptions were evaluated using simulated residual diagnostics (uniformity, dispersion, and outlier rate) and inspected plots of residuals versus fitted values and individual predictors to verify homoscedasticity and independence in the *DHARMa* package (Hartig 2024). Estimated marginal means (EMMs) were computed using *emmeans* package (Lenth 2024) and back-transformed to the original scale for interpretation. Post-hoc comparisons used Tukey-adjusted *p*-values, and marginal R^2 values (when supported) were calculated using the *performance* package (Lüdecke et al. 2024).

To evaluate how chlorophyll-*a* concentrations varied between bare and seagrass habitats across seasons and depths, we calculated the coefficient of variation (CV) and a robust coefficient of variation (rCV), defined as: , where IQR is the interquartile range of chlorophyll-*a* and the constant 0.7413 scales IQR to approximate the standard deviation of a normally distributed dataset. Increasingly applied in coastal ecology and oceanography to analyze patchy

or non-normally distributed data that are challenging to appropriately transform (Atkinson et al. 2018, Bouchet et al. 2020, Rogers et al. 2023, Yokomatsu and Kida 2025), rCV captures the variability of the core part of the distribution (middle 50% of data) while resisting distortion from skew, zero inflation, and extreme values. In contrast, the conventional coefficient of variation (CV = standard deviation/mean) underestimates the variability of these distributions because both the mean and standard deviation are sensitive to long tails and zeros. Importantly, rCV retains the intuitive interpretability of CV as a measure of relative variability while preserving the data's original units and scale (Temnerud et al. 2013).

We computed the standard CV and rCV for each combination of Season × Habitat × Sampling Height, as well as for aggregated groupings: (1) by Season and Habitat (pooling across heights), (2) by Habitat and Depth (pooling across seasons), and (3) by Habitat overall (pooling across all depths and seasons (Temnerud et al. 2013).

To visualize habitat-level stability, we plotted the reciprocal of the robust coefficient of variation (Stability = 1 / rCV), so that larger values intuitively denote more stable (less variable) chlorophyll-*a* concentrations among samples, whereas smaller values indicate greater variability—conceptually identical to the inverse CV used to quantify community stability in ecological time-series analyses (Lamy et al. 2020).

Data analyses: benthic algal biomass

To assess how habitat and season influence benthic algal biomass, we modeled sediment chlorophyll-*a* concentrations (mg m^{-2} seafloor) measured from composite cores collected in seagrass and bare habitats across three seasons. Following the same modeling framework and diagnostics used described above the water-column analysis, we fit a Gamma GLMM with a log

link function using the *glmmTMB* package (Brooks et al. 2017), including fixed effects for habitat, season, and their interaction, and a random intercept for site. *DHARMa*-simulated residual diagnostics (Hartig 2024) confirmed adequate model fit, and estimated marginal means were computed and back-transformed using the *emmeans* package (Lenth 2024) to aid interpretation.

Data analyses: seagrass algal epiphyte biomass

To access the spatiotemporal variability of seagrass algal epiphytes (spatial distribution across meadow, biomass over summer growing season) and potential environmental drivers, we examined the influence of site wave exposure with the novel computation of wind-weighted effective fetch (EFD), distance to meadow edge (m), and sampling date. As done above, we fitted a variety of GLMMs, settling on a Gamma GLMM with a log link function and omitting the EFD (provided no additional explanatory power and induced significant complexity) using AIC and the beforementioned validation approaches.

Carbon biomass estimation

We converted pigment and biomass-based measurements (chlorophyll-*a* and AFDM) to carbon standing stock (mg C m^{-2}) so that biomass comparisons remain ecologically meaningful across habitats and seasons. Chlorophyll-*a* often serves as a convenient proxy for algal abundance, yet carbon biomass better represents the energy that higher trophic levels can exploit and thus reveals true differences in algal production among habitats (Cloern et al. 1995, Arteaga et al. 2016, Jakobsen and Markager 2016).

Using a real-time kinematic global positioning system (RTK-GPS; Emlid Reach RS2; WGS-84, mean-sea-level datum; Emlid Ltd. 2024), we determined that all sampling sites were

situated 1.48 ± 0.17 m below mean sea level (range = 1.23–1.74 m; n = 16). We combined these depths with a local long-term record of Secchi depth (m) readings (seasonally averaged) to calculate a diffuse attenuation coefficient of K_d = 2.1 m^{-1} (Poole and Atkins 1929). Then, we derived the 1%-light depth ($Z_{1\%} \approx$ 2.2 m) from the relation $Z_{1\%} = 4.6/K_d$ (Reinart et al. 2000), consistent with values reported for similarly turbid coastal lagoons (Brewin et al. 2023). Because every station was positioned at or shallower than 0.79 × $Z_{1\%}$, the seabed always received at least 1% of incident PAR, confirming the water column was optically shallow (Gattuso et al. 2006).

To calculate carbon-to-chlorophyll-*a* ratios for the water column, we used the Jakobsen and Markager (2016) model, which links the C:Chl-*a* ratio to temperature (T), photosynthetically active radiation (PAR), and dissolved inorganic nitrogen (DIN):

We averaged daily sea surface temperature observations from the NOAA Wachapreague, VA coastal station (37.61°N, 75.69°W; 1 m depth; Wiberg 2021) into monthly means; these averages differ from in-situ logger data by less than ±0.4°C (Wiberg 2021). We extracted daily incident PAR from a lagoon-edge VCR LTER meteorological station (Krovetz et al. 2024) and corrected it to 0–1 m depth with the seasonal K_d. We built seasonal DIN means (µM) by summing ammonium, nitrate, and nitrite concentrations obtained from the 30-year VCR LTER chemistry record (1992–2021; McGlathery and Christian 2024) following Grasshoff et al. (2009). These inputs produced C:Chl-*a* ratios between 165 and 231 g C g^{-1} Chl-*a*—values that match coastal estimates at similar latitudes (Miller and Harding Jr 2007, Wang et al. 2009, Son et al. 2014, Arteaga et al. 2016). We integrated discrete 1–45 cm chlorophyll-*a* profiles with the trapezoidal rule and multiplied each seasonal total by its ratio to obtain seasonal water-column carbon biomass (Walsby 1997, González-Gil et al. 2018).

We estimated carbon biomass in the benthic microphytobenthos by converting chlorophyll-*a* collected 0–1 cm surface-sediment cores (1 cm diameter) to carbon using 60 g C g^{-1} Chl-*a*, a mid-range factor for temperate lagoon sediments dominated by diatoms and cyanobacteria (MacIntyre et al. 1996, Cahoon 1999, McGlathery 2017).

Because we quantified seagrass (*Zostera marina*) blade epiphyte biomass as AFDM per m2 of seafloor (*see* epiphyte methods above; Dauby and Poulicek 1995), we applied a factor of 0.35 g C g^{-1} AFDM—representative of mixed macro- and microalgal epiphyte communities in temperate seagrass meadows (Duarte 1990). By expressing water-column, benthic, and epiphytic pools on a shared carbon basis, we created a unified framework for evaluating algal standing stocks and their seasonal dynamics across contrasting habitats.

Results

Stratified water column chlorophyll-a

We analyzed seasonal and vertical patterns in water column chlorophyll-*a* concentrations across three years (see Figs. 1.2, 1.3, and 1.4) using statistical models describing the effects of habitat (Bare vs. Seagrass) on vertical stratification and temporal stability of algal material suspended in the water column. Because our primary goal was to assess how seagrass modifies vertical chlorophyll-a distribution across seasons, we first modeled each year separately (2021, 2022–2023; Figs. 1.2 and 1.3) to isolate within-year habitat effects, contend with uneven sampling effort across seasons between these and avoid confounding due to interannual variability in physical and biological conditions.

In June to November 2021, a Gamma GLMM (n = 463; marginal R^2 = 0.21) revealed strong vertical enrichment of chlorophyll-*a* in both habitat types, with particularly elevated

concentrations near the seafloor at seagrass sites (full model coefficients provided in Table S1). During summer (June–August), chlorophyll-*a* increased markedly from 4.06 (± 0.27 SD) μg L^{-1} at 45 cm to 5.79 (± 0.38) μg L^{-1} at 1 cm in seagrass, a significant bottom enhancement ($p < 0.001$). Measurements at bare, unvegetated sites showed a similar pattern, rising from 4.08 (± 0.27) μg L^{-1} to 5.82 (±0.39) μg L^{-1}. By autumn (September), differences were more pronounced. Seagrass sites exhibited uniformly elevated chlorophyll-*a*, with concentrations increasing from 3.38 (± 0.31) μg L^{-1} at 45 cm to 4.82 (± 0.41) μg L^{-1} at 1 cm. In contrast, bare sites had lower values throughout the column, ranging from 2.27 (±0.20) μg L^{-1} (45 cm) to 3.24 (± 0.28) μg L^{-1} (1 cm). Post-hoc contrasts confirmed significantly higher near-bottom concentrations in seagrass vs. bare habitat at 1 cm and 5 cm during approximately the second half of the summer (late July to mid-September; $p < 0.01$), supporting the hypothesis that seagrass canopies enhance near-bottom phytoplankton retention later in the growing season (Judge et al. 1993). All significant estimated marginal means are given in Appendix 1.A. and GLMM model outputs in Appendix 1.B.

For observations spanning April 2022 to February 2023, a Tweedie GLMM ($n = 319$; marginal $R^2 = 0.644$) revealed strong seasonal and vertical variation in water-column chlorophyll-a concentrations, with values in the seagrass meadow aligned with unvegetated sites in April, lower in the seagrass meadow during summer (July–August), and higher in the seagrass meadow during autumn (October–November) and winter (February) (full model coefficients given in Appendix 1.B). Specifically, chlorophyll-a peaked in summer across both habitats but remained relatively elevated near the seafloor in seagrass across seasons. At 1 cm—the height most relevant to food availability for suspension-feeding infauna—chlorophyll-*a* in the seagrass meadow matched or exceeded bare sites for all months except August, when both habitats had

high concentrations (> ~8 µg L^{-1}) but bare areas were exceedingly high (> ~12 µg L^{-1}). In autumn, concentrations at 1 cm height reached 6.66 (± 0.56) µg L^{-1} in seagrass compared to 3.24 (± 0.33) µg L^{-1} bare sites outside of the meadow. February, April, and July values at 1 cm were similar between the two habitats. Hence, seagrass enhanced stratification, with bottom-layer enrichment generally exceeding surface values.

The 2022–2023 model's estimated dispersion ($\varphi = 0.358$) and Tweedie power parameter ($p = 1.74$) indicated a right-skewed, overdispersed response distribution—characteristics commonly observed in pigment concentration datasets due to frequent low values punctuated by episodic peaks (Swarbrick et al. 2019)—justifying a Tweedie GLMM, which accommodates zero-inflated, positively skewed data structures without transformation (Zuur and Ieno 2021).

Finally, when we aggregated data across all sampling dates/years (2021–2023), enhanced chlorophyll-*a* at the near-seafloor level (1-cm height) within seagrass remained a prominent feature for some seasons (particularly autumn), supporting the notion that seagrass-mediated primary production, such as macroalgal fragments, should result in seasonally-enhanced biomass near the seafloor compared to unvegetated sites (Fig. 1.5C–D; Judge et al. 1993).

Across all years, chlorophyll-*a* variability—both spatial and temporal—differed markedly by habitat, depth, and season. When aggregated across seasons and sampling heights, seagrass sites generally exhibited higher stability (between-site; Fig. 1.5A) while seasonally, seagrass habitats exhibited greater spatial stability during summer and autumn compared to bare sites (Fig. 1.5B), suggesting a stabilizing influence during periods of high production (Fig. 1.5C–D). Notably, spatial variability across bare sites was lower than seagrass habitats in spring and winter when seagrass canopy structure is minimal yet rhizome biomass beneath the sediment surface remains significant (Widdows et al. 2008).

Temporally (across sampling dates), seagrass sites exhibited greater stability—suggesting a general stabilizing effect on suspended algal biomass at the meadow scale across seasons (Fig. 1.6). Depth-specific chlorophyll-*a* concentration temporal stability indicate that seagrass tends to reduce variability at mid and upper sampling heights (15–45 cm), while bare sediments showed lower stability at multiple depths over time (Fig. 1.6B). At 1 cm above the seafloor, stability was lower in seagrass—potentially due to detrital enrichment or fine-scale patchiness near the benthos as also indicated by significantly higher overall mean biomass in summer and autumn at this near-seafloor-level (see Fig. 1.2 through 1.4)

Benthic algal biomass

Benthic sediment-bound chlorophyll-a concentrations were significantly higher in seagrass than at bare sites across all seasons, with estimated means (±95% CI) of 399.0 (± 123.3) mg m^{-2} in winter, 160.2 (±35.1) mg m^{-2} in summer, and 203.9 (±62.7) mg m^{-2} in autumn. Bare sediments contained 143.2 (±44.2) mg m^{-2} in winter, 59.6 (±13.2) mg m^{-2} in summer, and 136.8 (±42.2) mg m^{-2} in autumn. This represented a 2.8-fold enhancement in seagrass relative to bare sediments during winter, a 2.7-fold difference in summer, and a 1.5-fold difference in autumn (Fig. 1.7). Habitat and season both had strong main effects on sediment chlorophyll-a ($p < 0.001$), and a significant two-way interaction in such that the seagrass advantage diminished during autumn (Gamma GLMM; $\beta = -0.63 \pm 0.13$ SE, $p = 0.041$) when compared with summer and winter.

Seagrass epiphyte biomass

The most parsimonious model by AIC rank (Gamma GLMM with a log link function) revealed a strong seasonal accumulation of epiphytes on seagrass leaves: a one-standard-deviation increase in sampling week (≈ 7 days) corresponded to a 0.81 mg cm^{-2} rise in mean epiphyte load (95 % CI: 0.73 – 0.89; $z = 19.47$, $p < 0.001$). Back-transformed estimated marginal means illustrate that, at an "early-season" point in June (–1 SD), mean biomass was only 0.173 mg cm^{-2} (95 % CI: 0.120–0.248), rising to 0.388 mg cm^{-2} by mid-season (0 SD; 0.272–0.553) and peaking at 0.872 mg cm^{-2} in the "late season" in September (+1 SD; 0.607–1.254). All pairwise comparisons between these three time-points were highly significant ($p < 0.0001$), with biomass at mid- and late season at least double that of early season (Fig. 1.8A).

Distance to the meadow edge (m) had a subtler influence on seagrass epiphyte biomass. After controlling for the effects of the month of sampling, sites deeper inside the meadow (–1 SD) averaged 0.535 mg cm^{-2} (95 % CI: 0.323–0.886), the meadow center (0 SD) averaged 0.397 mg cm^{-2} (0.278–0.565), and edge sites (+1 SD) averaged 0.294 mg cm^{-2} (0.178–0.486). None of the pairwise contrasts between these positions reached significance after Holm adjustment ($p \approx 0.30$ in all cases; Wright 1992), indicating that while epiphyte biomass tended to decline toward the meadow margin, the effect was not statistically robust at our eight sampling locations. Spatial mapping of raw model (GLMM) residuals from a model predicting epiphyte biomass as a function of month (Fig. 1.8B) revealed weak but significant positive autocorrelation (Moran's $I = 0.126$, $p = 0.007$), suggesting that unmeasured, fine-scale processes—such as localized hydrodynamics or grazing intensity—generated spatial structure beyond what seasonal, simplified edge-distance metrics, or fetch distance could explain.

Together, these estimates highlight that epiphyte biomass was overwhelmingly driven by seasonal progression, with strong late-summer peaks, and only modest spatial variation in relation to the meadow margin.

Total carbon standing stocks

Bare sediments were overwhelmingly dominated by estimated benthic carbon except in spring (Fig. 1.12). In summer, mean benthic (seafloor) microalgal carbon reached 3.67 ±0.38 g C m^{-2}, 8.9 × higher than the overlying water column (0.50 ±0.04 g C m^{-2}). Autumn and winter exhibited even larger contrasts (8.21 ± 0.98 g and 8.71 ±1.26 g C m^{-2}, respectively). Seagrass habitats exhibited a more diversified pool. During summer, epiphytes (9.97 ± 0.99 g C m^{-2}) and benthos (9.65 ±0.93 g C m^{-2}) contributed roughly equal fractions (49.8 % vs 48.3 %) of the total algal carbon budget (19.0 g C m^{-2}), whereas the water column accounted for only 1.9 %. In autumn, epiphytes remained the single largest compartment (18.1 ±3.31 g C m^{-2}; 59 %), but winter benthic stocks surged to 24.2 (±3.05) g C m^{-2}, representing 99 % of the seasonal total (Fig. 1.11 and 1.12; Table 1.1).

Discussion

Seagrass canopies restructure water-column productivity

Vertical water column profiles (Figs. 1.2 through 1.4) indicate that *Zostera marina* seagrass meadows fundamentally alter the spatiotemporal distribution suspended chlorophyll-*a* in the lower water column. In summer and early autumn, the canopy concentrated suspended algal material within a near-seafloor (1-5 cm above benthos) layer and enhanced its spatial (among-site) stability relative to bare seafloor sites, likely through canopy attenuation of

erosional bed shear-stress (Schanz et al. 2002, Noisette et al. 2020). These findings agree with flume and field studies demonstrating 40–60 % reductions in bed shear beneath *Z. marina* canopies (Widdows et al. 2008, Hansen and Reidenbach 2013) and extend them by revealing seasonal enrichment of chlorophyll-*a* at 1 cm above the seafloor (Fig. 1.4). By contrast, bare sites exhibited more vertically uniform and seasonally variable chlorophyll patterns, particularly during the summer and autumn (Fig. 1.3).

Hydrodynamic energy attenuation by seagrass therefore converts an otherwise pelagic energy pathway into a benthic subsidy as suspended algae, phytoplankton, and detritus are retained and concentrated where near-bed suspension feeders, such as bivalves, sponges, and tunicates can take advantage (Peterson 1984, Judge et al. 1993, Norkko et al. 2001). Our Tweedie GLMM quantified this effect, estimating that bottom-layer chlorophyll-*a* in seagrass was more than twice as high as bare sites during autumn (Table 1.1). Such canopy-mediated retention may explain cases of significantly-faster hard clam (*Mercenaria mercenaria*) growth inside *Z. marina* meadows (Peterson 1984) and highlights a potential food supply 'sink' that sustains secondary producers when pelagic phytoplankton abundance is low (Judge et al. 1993, Cox et al. 2020, Fales et al. 2020).

Benthic microalgae dominate carbon pools outside the spring bloom

Across seasons and habitats, benthic microalgae comprised either the largest pool of algal carbon, or co-equally largest carbon pool alongside summer epiphytes in the seagrass meadow (Figs. 11, 12). Bare flats relied almost exclusively on this compartment: benthic carbon exceeded pelagic carbon by 30–70-fold from summer through winter (Fig. 1.11). These data align with global syntheses showing that microphytobenthos support 30–50% of primary production in

shallow euphotic systems (MacIntyre et al. 1996, Cahoon 1999, Cox et al. 2020). Seagrass sediments contained still more chlorophyll-*a* (Fig. 1.11); mean winter values (~0.4 g m^{-2}) nearly tripled those on bare sediment, translating to 0.024 g C m^{-2} under a conservative 60 g C g^{-1} chlorophyll-a ratio (see Table 1.1). Stabilized sediments, oxygen leakage from roots, and rapid recycling of seagrass litter may act in-concert to maintain these high winter stocks when phytoplankton inputs are minimal (Cox et al. 2020).

Epiphytes deliver a seasonal carbon pulse

Epiphytic algae peaked at ~18 g C m^{-2} in August–September, contributing ~56 % of total algal carbon in seagrass habitat at that time (Fig. 1.12). Their biomass rose almost ten-fold from early summer to late summer (Fig. 1.11), consistent with temperature-controlled, nutrient-recycling epiphyte blooms reported elsewhere (Schanz et al. 2002, Poore et al. 2009). Spatially, the greatest positive residuals clustered in the sheltered interior of the meadow (Fig. 1.6B), suggesting hydrodynamic quiescence and perhaps grazer release foster epiphyte accrual there (Schanz et al. 2002, Whalen et al. 2013, Noisette et al. 2020), despite our models showing no trends related to distance from the meadow edge or wind-weighted effective fetch distance.

Once senescent or mechanically sloughed, a portion of this epiphytic material likely enters the near-bed suspended pool—as indicated by observations visualized in Fig. 1.2, 1.3, and 1.4—supplying labile detritus rich in essential fatty acids to winter suspension feeders (Judge et al. 1993, Hays 2005, Cook et al. 2011). The late-season epiphyte pulse may therefore offset declining phytoplankton production, lengthen the window of food availability.

Conclusions

Applying seasonally adjusted chlorophyll-to-carbon conversion factors revealed that the combined standing stock of benthic microalgae, epiphytes, and near-bed suspended material inside meadows can exceed one gram of carbon per square meter during both the spring accumulation phase and the late-summer suspension phase. Given published filtration rates (Kraeuter and Castagna 2001a), this standing stock could satisfy more than half of the daily carbon demand of an exceptionally-dense population of hard clams (*M. mercenaria*)—a canonical consumer in *Z. marina* beds (Kraeuter and Castagna 2001a, Fales et al. 2020b). This underscores the potential for a meadow to serve as a localized carbon pump sustaining secondary production under otherwise nutrient-poor conditions.

In summary, our study indicates that eelgrass canopies (1) seasonally enhance and spatially stabilize near-seafloor suspended algal concentrations, (2) boost microphytobenthic productivity, and (3) support seasonally abundant epiphytic algae. The net result is an organic carbon pool concentrated within the bottom few centimeters of the water column and in the surface sediment. Such near-bed enrichment appears to elevate the biomass and stability of algal material, a basal resource that may facilitate the significant suspension- and deposit-feeder communities associated with seagrass meadows (Orth et al. 1984a, Judge et al. 1993, Whalen et al. 2013, Rodil et al. 2022). Hence, quantifying benthic and epiphytic primary production alongside pelagic inputs (i.e., phytoplankton) may be critical when evaluating the extent of seagrass-modulated contributions to the basal resources underpinning seagrass ecosystem food webs and functioning.

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Figures and tables

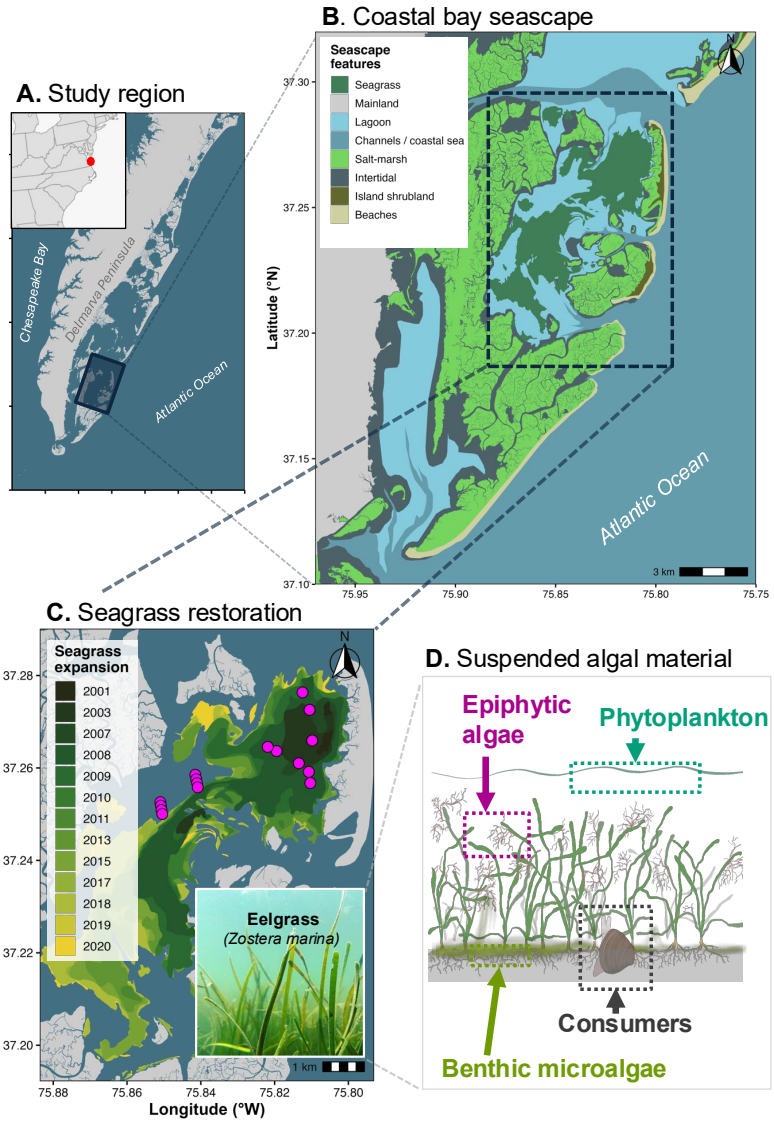


Figure 1.1. ***Study region, seascape context, and sources of suspended primary production.*** Study region (A), where the back-barrier island system shelters a complex seascape mosaic of marsh, creeks, larger channels, shallow subtidal and intertidal mudflats, and *Zostera marina* seagrass beds (B). Points in magenta (C) show sites sampled from 2021 to 2023 for algal material inside/outside expanding seagrass (green color-scale denotes year since restoration that began in the early 2000s). (D): Illustration of the sources of suspended local and pelagic (tidally mediated phytoplankton) food supply for filter-feeding consumers

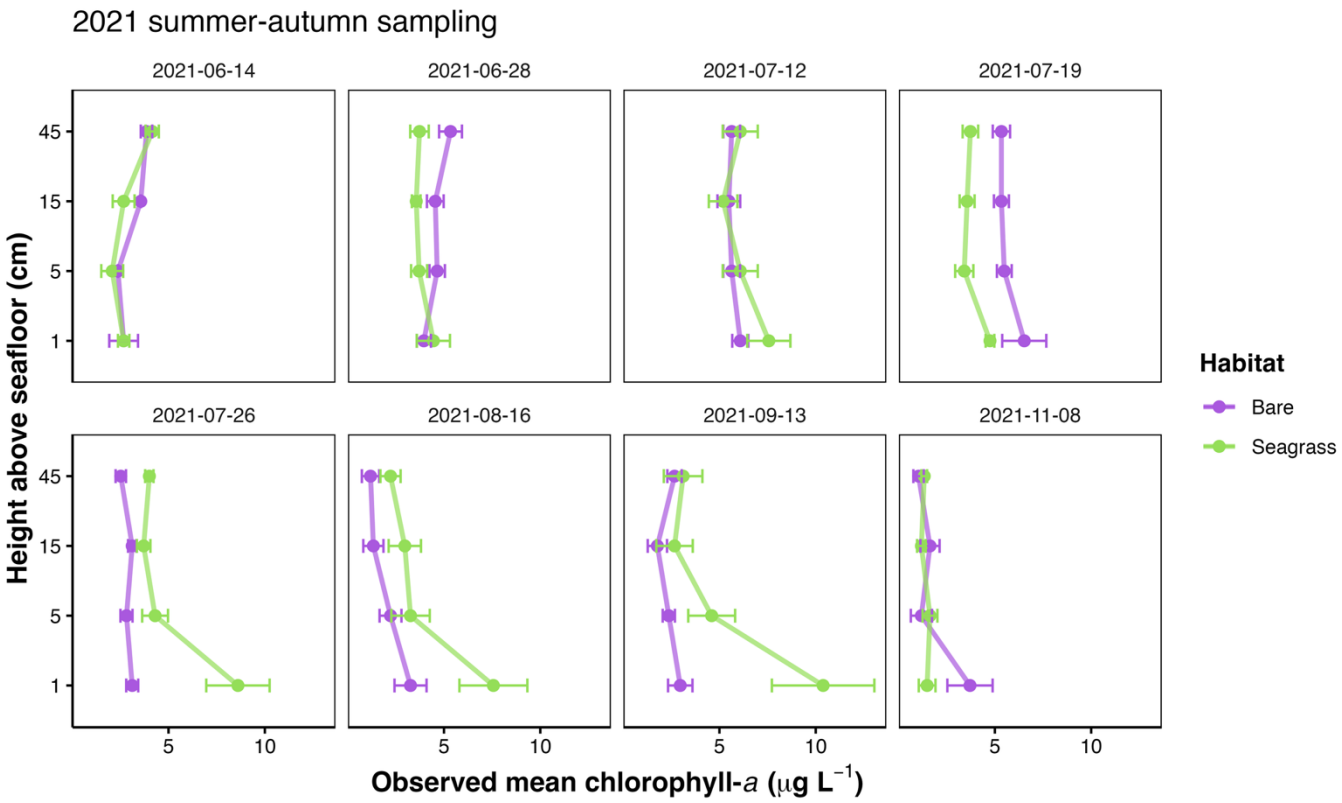


Figure 1.2. ***Vertical profiles of 2021 water-column chlorophyll-a by week and habitat.*** Mean chlorophyll-*a* values (±SE bars; μg L^{-1}) by sampling week for June–November of 2021 plotted as vertical profiles, with height above the seafloor (cm) on the y-axis and chlorophyll-*a* response on the x-axis. Color denotes habitat (purple = bare/unvegetated sites, green = within seagrass meadow). Note the relative increase in near-seafloor chlorophyll-*a* in seagrass vs. bare sites from late July to early September.

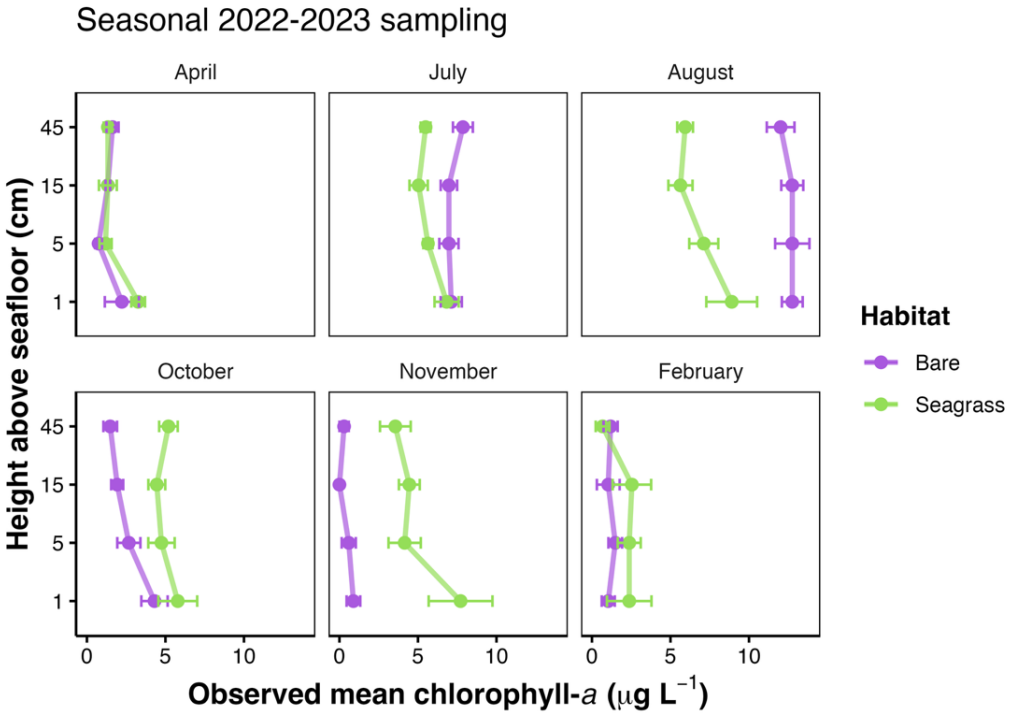


Figure 1.3. ***Vertical profiles of 2022-2023 water-column chlorophyll-a by month and habitat.*** Monthly mean chlorophyll-*a* values (±SE bars; μg L^{-1}) plotted as vertical profiles, with height above the seafloor (cm) on the y-axis and chlorophyll-*a* response on the x-axis. Color denotes habitat (purple = bare/unvegetated sites, green = within seagrass meadow). Notably, and regardless of the chlorophyll-*a* concentration difference between the habitats, vertical stratification appears more common and stronger within seagrass.

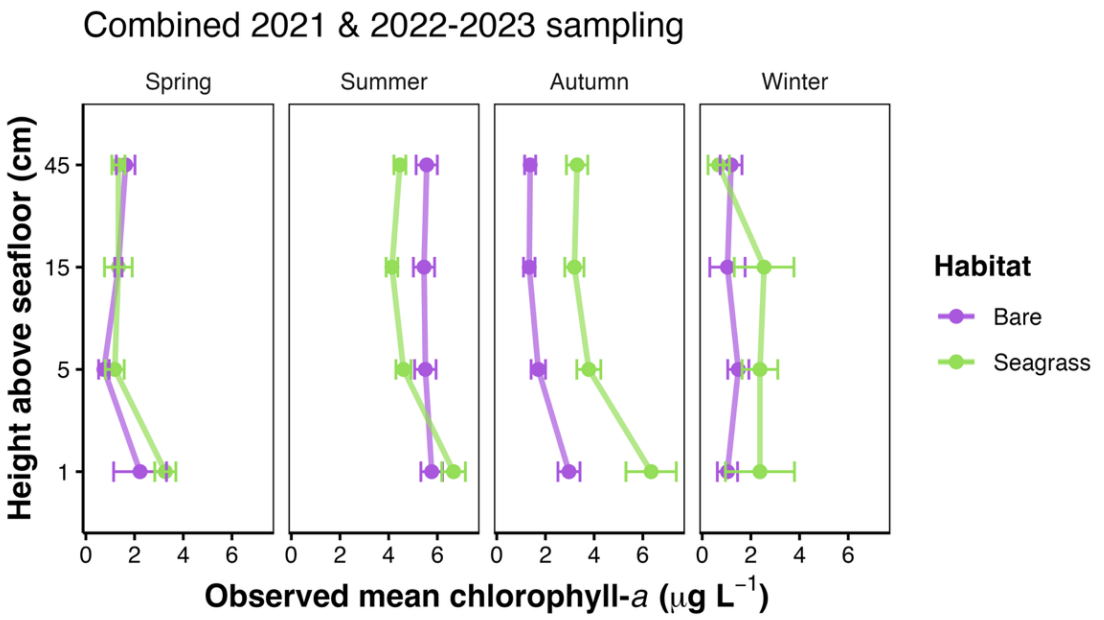


Figure 1.4. ***Seasonal vertical profiles of water-column chlorophyll-a from combined 2021–2023 sampling efforts.*** Mean chlorophyll-*a* values (±SE bars; μg L^{-1}) by sampling week for June- to November of 2021 plotted as vertical profiles, with height above the seafloor (cm) on the y-axis and chlorophyll-*a* response on the x-axis. Color denotes habitat (purple = bare/unvegetated sites, green = within seagrass meadow). Near-seafloor (1-cm height) within seagrass exhibits marginal to significant increased chlorophyll-*a* pigment concentrations across years compared to bare/unvegetated sites—particularly in autumn.

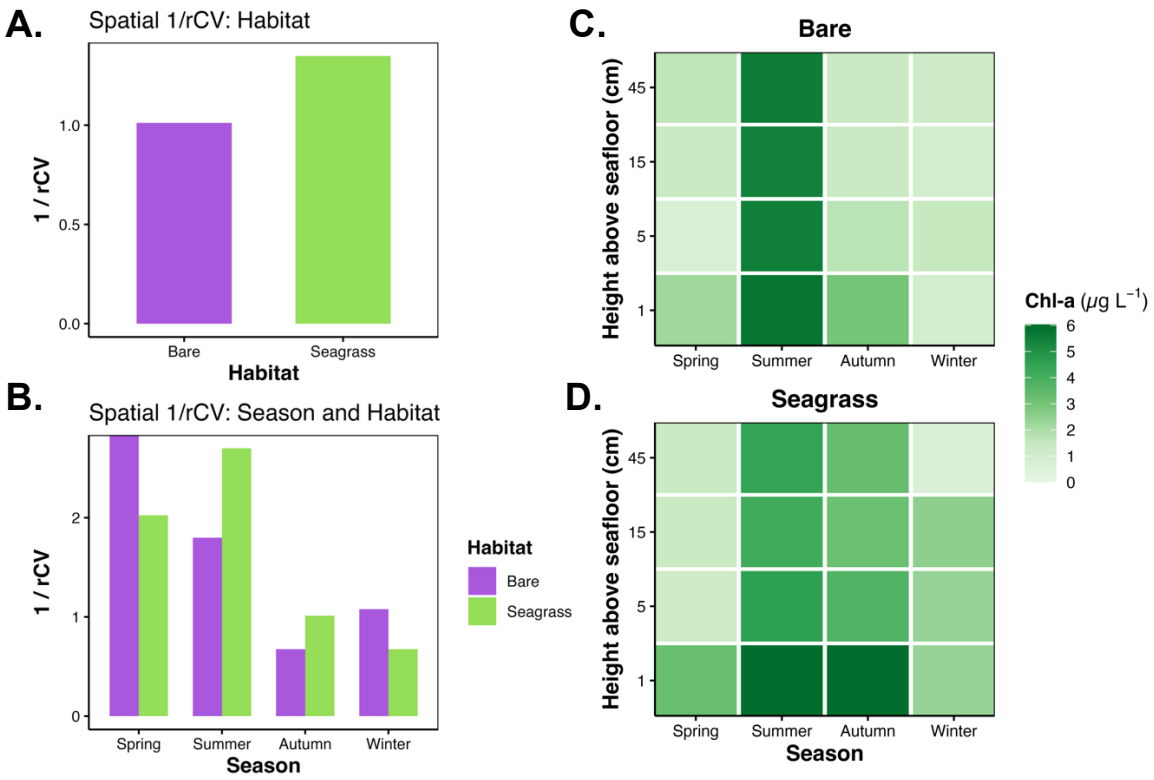


Figure 1.5. ***Spatial chlorophyll-a variability by habitat, collection height, and season.***

Chlorophyll-*a* concentration stability (1/rCV, where rCV is the robust coefficient of variation) by habitat is shown aggregated across seasons (A) and by season (B), with positive values indicating greater stability in seagrass while negative values indicate greater stability at bare sites. Overall, seagrass tended to increase the spatial stability of chlorophyll-*a* (A) while seasonally, seagrass habitats exhibited greater spatial stability during summer and autumn compared to bare sites, suggesting a stabilizing influence during periods of high production. Curtain plots of 2021–2023 season-averaged vertical chlorophyll-*a* concentrations (μg L^{-1}) in bare (C) and seagrass (D) habitats. Darker green shades indicate higher concentrations; the y-axis denotes sampling height above the seafloor (cm).

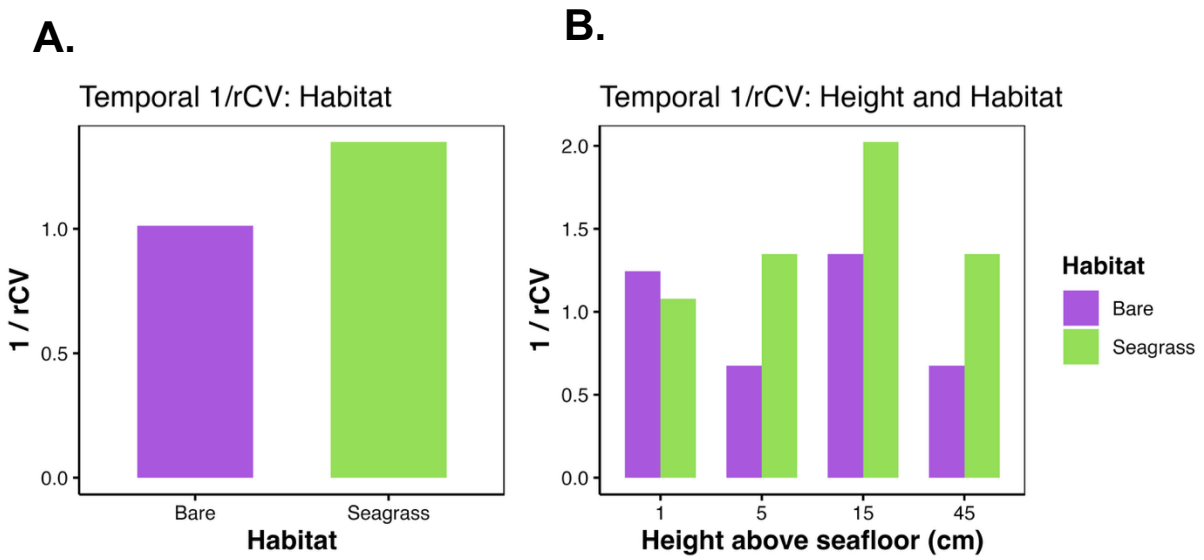


Figure 1.6. ***Summary of temporal chlorophyll-a stability (2021–2023).*** Panel A shows overall temporal chlorophyll-*a* stability (1/rCV, where rCV is the robust coefficient of variation) in bare and seagrass habitats, pooled across all sites, depths, and seasons. On average, seagrass habitats exhibited greater temporal stability (higher 1/rCV values), suggesting a general stabilizing effect on suspended algal biomass at the meadow scale. Depth-specific chlorophyll-*a* concentration stability in bare and seagrass habitats are shown in panel B. Seagrass tended to reduce variability at mid and upper sampling heights (15–45 cm), while bare sediments showed lower stability at multiple depths over time. At 1 cm above the seafloor, however, stability was slightly lower in seagrass habitat, potentially due to detrital enrichment or fine-scale patchiness near the benthos as also indicated by significantly higher overall mean biomass in summer and autumn at this near-seafloor-level (*see Figures 1.2 through 1.4*).

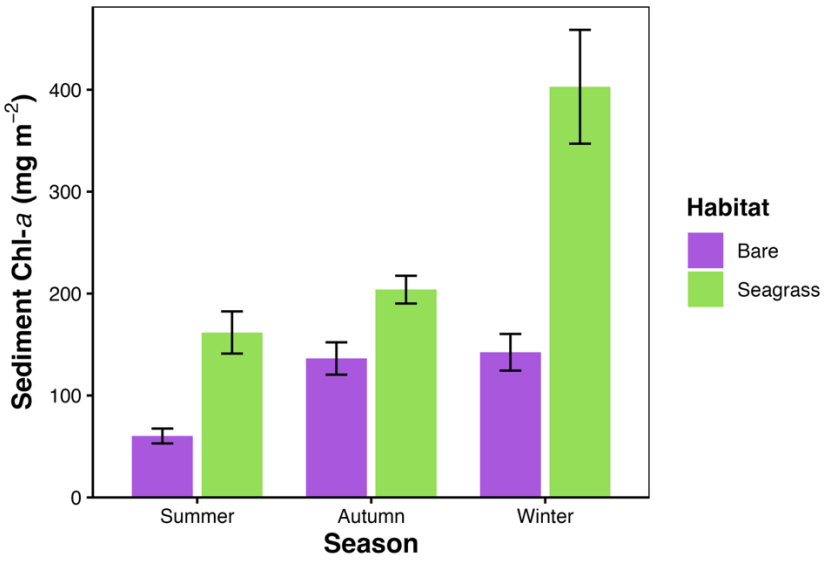


Figure 1.7. ***Benthic (sediment) chlorophyll-a concentrations by season and habitat (mean ± SE).*** Field data of benthic chlorophyll-*a* (1-cm deep surface sediment cores; mg m^{-2}) showed that sediments in the seagrass meadow consistently held more chlorophyll-*a* than adjacent unvegetated ('bare') areas, averaging ~150 mg m^{-2} in summer (bare ≈ 60 mg m^{-2}), ~200 mg m^{-2} in autumn (bare ≈ 140 mg m^{-2}), and peaking at ~400 mg m^{-2} in winter—nearly three-fold the winter value at bare sites (≈140 mg m^{-2}).

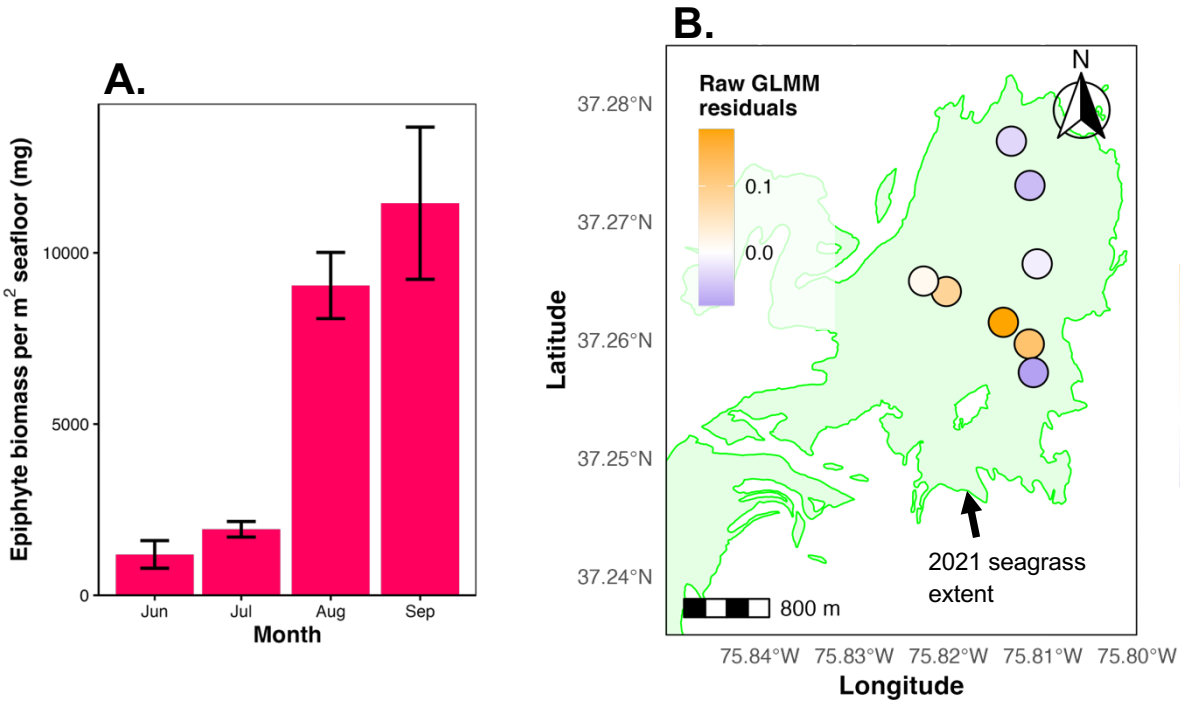


Figure 1.8. ***Epiphyte biomass and spatial variability of model residuals across the seagrass meadow.*** Mean epiphyte dry mass (mg ±SE) scaled to seafloor area (m^2) by sampling month (A). seagrass meadow footprint estimated from aerial imagery in 2021 (green layer—courtesy of the Virginia Institute of Marine Science 2025), with epiphyte sampling sites colored by their raw GLMM model residual values (blue = negative, white ≈ 0, orange = positive) highlight the parts of the interior meadow where biomass exceeded model predictions (B).

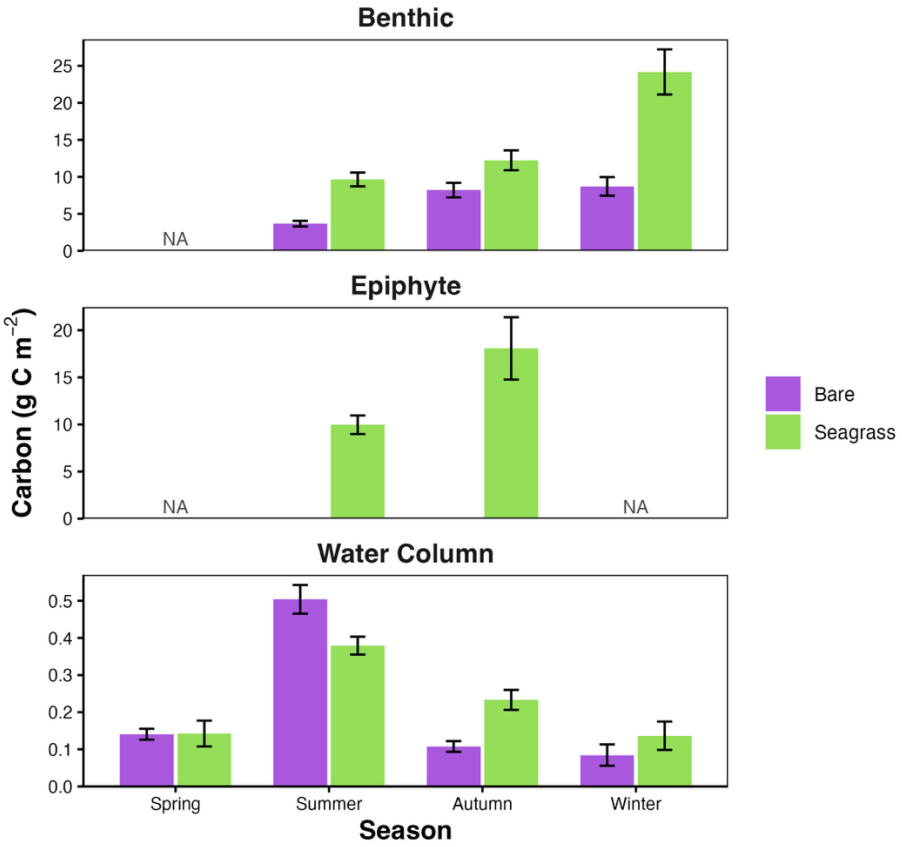


Figure 1.9. ***Seasonal standing stocks of algal carbon by habitat (2021–2023).*** Mean (±SE) carbon biomass (g C m^{-2}) for water-column phytoplankton/suspended algal material, seagrass-leaf epiphytes, and sediment-associated microphytobenthos. Water-column biomass was greatest at bare sites in summer but shifted toward seagrass habitats in autumn and winter. Benthic biomass consistently exceeded water-column biomass, reaching peaks in winter. Note that epiphyte biomass on seagrass blades peaked dramatically in autumn and substantially succeeded both water-column and benthic compartments beneath the seagrass canopy. Water-column biomass was computed from depth-resolved chlorophyll-*a* integrated between 1–45 cm above the seafloor. Seasons that lacked sampling efforts are denoted by "NA".

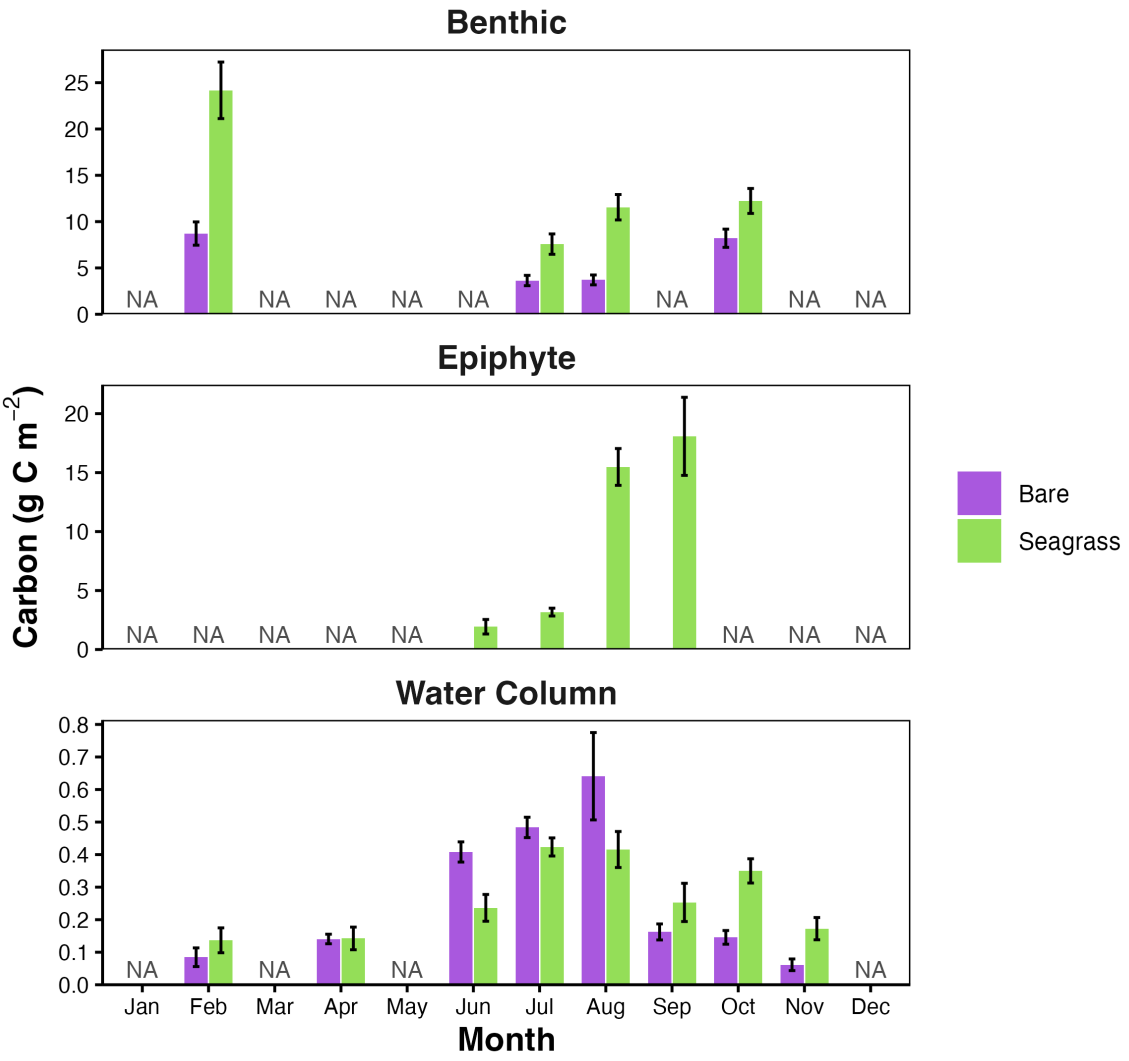


Figure 1.10. ***Monthly standing stocks of algal carbon by habitat (2021–2023).*** Mean (± SE) monthly carbon biomass (g C m^{-2}) across habitats for water-column, seagrass-leaf epiphytes, and sediment-associated microphytobenthos. Pelagic biomass over bare sediments peaked in August, while benthic carbon reached maximal values in February beneath seagrass. Epiphytes on seagrass blades surged from June to a September peak—during which the seagrass pelagic pool exceeded that outside the meadow (Sep–Nov). Months that lacked sampling efforts are denoted by "NA".

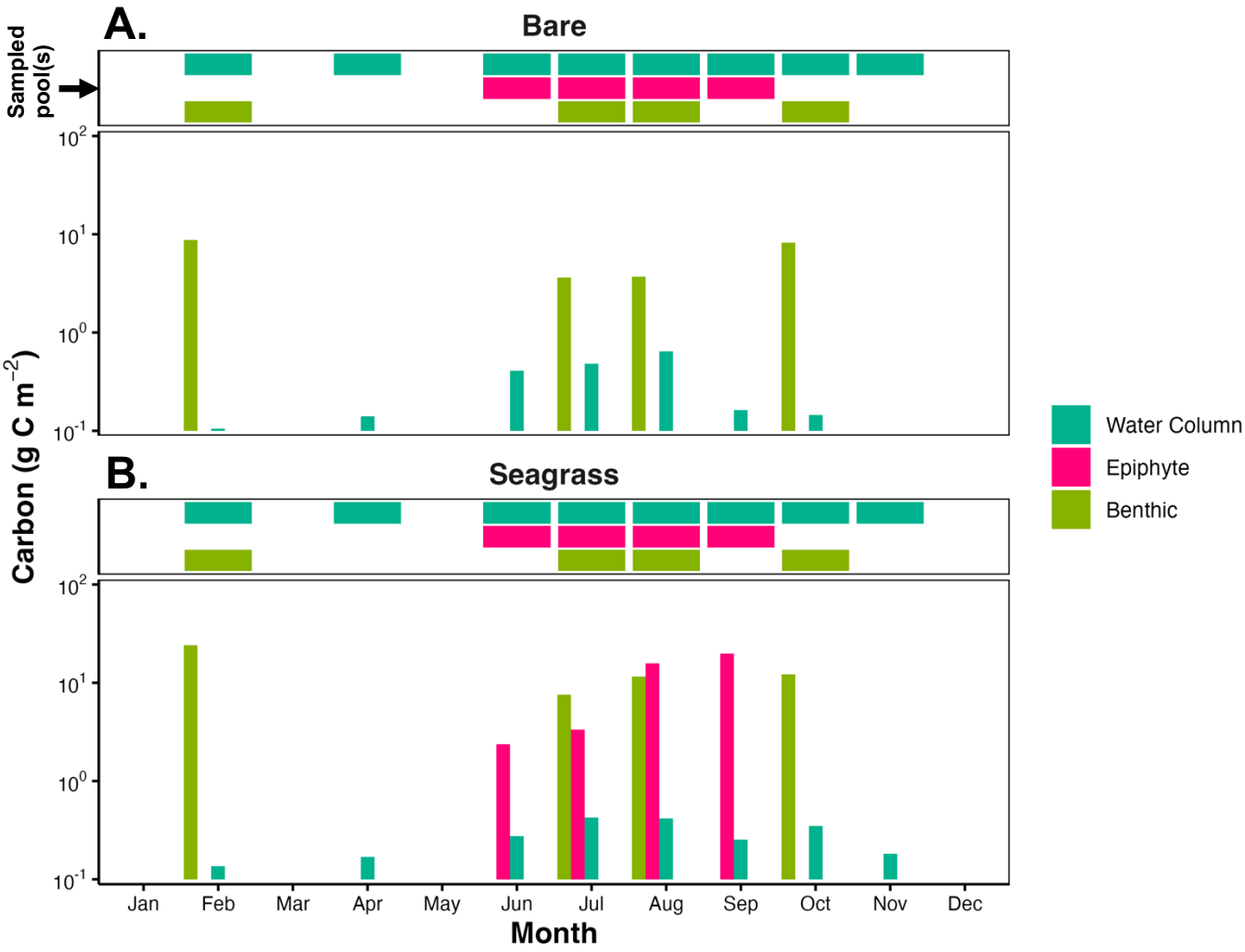


Figure 1.11. ***Monthly algal-carbon budgets on a log$_{10}$ scale (2021–2023).*** Log-scaled mean carbon biomass (g C m^{-2}) illustrating magnitude relative differences among algal sources by month of year. Small strip panels show which C-pools were sampled for a given month. Bare sites (A) were consistently dominated by benthic production, with summer and autumn ratios exceeding a 30-fold benthic-to-pelagic difference. In seagrass meadows (B), the combined benthic and epiphyte biomass exceeded water-column biomass by approximately 1–2 orders of magnitude, particularly pronounced in summer and winter. Epiphytes contributed significantly (>50%) to seagrass habitat carbon budgets during summer and autumn. Small panels atop each indicate which algal source/pool(s) were sampled for a given month.

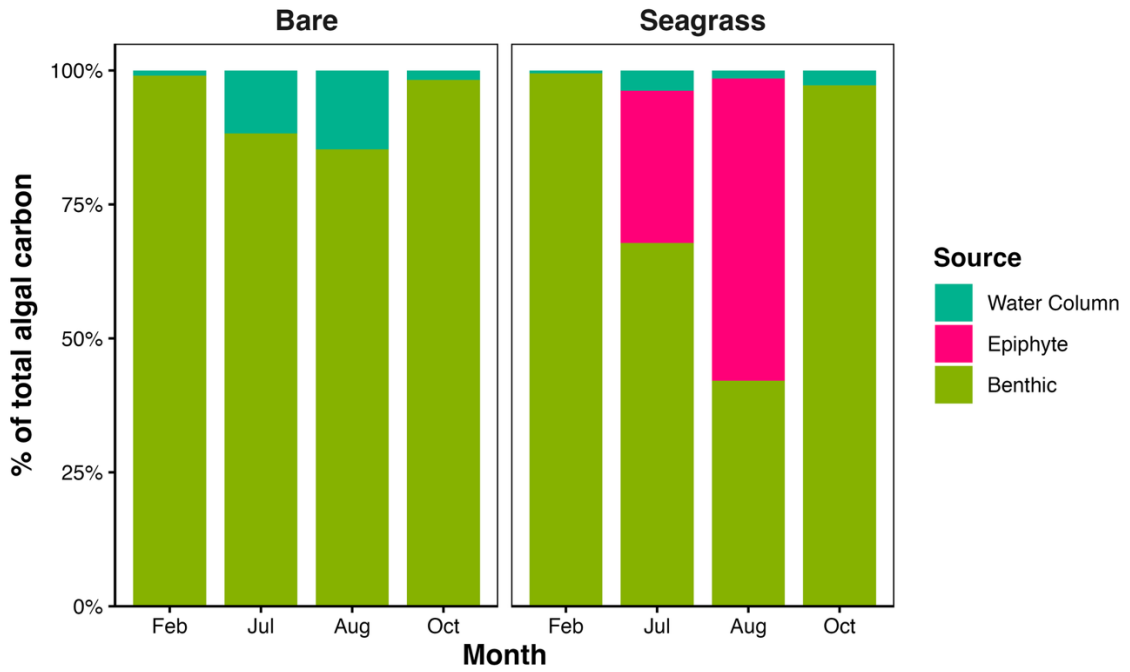


Figure 1.12. ***Relative contribution (%) by algal source to total carbon standing stock by month and habitat.*** Stacked bars represent the percentage of total algal carbon contributed by water-column phytoplankton/suspended material, seagrass-blade epiphytes, and benthic microalgae for months with sediment and water column chlorophyll-*a* data (epiphyte seasonality compressed into summer months). Benthic microalgae dominated in both bare and seagrass habitats throughout all months, accounting for 85–99% of total carbon. Epiphytes substantially contributed (~56%) to seagrass habitat carbon stocks at peak biomass in August (15.48 ±1.56 g C m^{-2}). The pelagic (water-column) fraction was consistently minor, ranging from <1% in winter (February) to approximately 15% in bare habitats in August.

Season	Habitat	Water column	Epiphyte	Benthos
Spring	Bare	141 (±15)	—	—
Spring	Seagrass	142 (±35)	—	—
Summer	Bare	504 (±39)	—	3,673 (±383)
Summer	Seagrass	379 (±24)	9,968 (±986)	9,650 (±927)
Autumn	Bare	108 (±14)	—	8,206 (±984)
Autumn	Seagrass	233 (±27)	18,077 (±3,310)	12,234 (±1,347)
Winter	Bare	84.6 (±28.7)	—	8,713 (±1,258)
Winter	Seagrass	137 (±38)	—	24,176 (±3,052)

Table 1.1. ***Seasonal-average carbon standing stocks (mean ±SE; g C m^{-2}).*** Bare-sediment sites were dominated by benthic productivity except in spring, whereas seagrass sites displayed a more even split between epiphytes and benthos in summer and a clear benthic dominance in winter. Peak values occurred in winter seagrass plots (24.2 ±3.05 g C m^{-2}) and autumn bare plots (8.21 ±0.98 g C m^{-2}), empirical evidence that carbon storage does not shut down outside the summer seagrass growing season. Dashes indicate habitats or sources not sampled. Benthic values use a conservative C:Chl-*a* ratio of 60-g C-g^{-1} Chl-*a*; epiphytes use 0.35 g C-g^{-1} Chl-*a*; water-column ratios are season-specific.

Appendix

Habitat	Season	Height (cm)	Estimate (Chl-*a;* µg L^{-1})	SE
Bare	Summer	45	4.08	0.26
Bare	Summer	1	5.82	0.39
Seagrass	Summer	45	4.06	0.27
Seagrass	Summer	1	5.79	0.38
Bare	Autumn	45	2.27	0.20
Bare	Autumn	1	3.24	0.28
Seagrass	Autumn	45	3.38	0.31
Seagrass	Autumn	1	4.82	0.41

Appendix 1.A. ***EEM table for 2021 water column chlorophyll-a gamma GLMM.*** Estimated marginal means (EMMs) of chlorophyll-a concentration (µg L^{-1}) across depths, habitats, and seasons for 2021. Seagrass plots maintained higher bottom-layer concentrations than Bare plots, particularly during autumn (4.82 ± 0.41 vs. 3.24 ± 0.28 µg L^{-1} at 1 cm), indicating enhanced retention of chlorophyll-*a* near the sediment surface.

Term	Estimate	Std. Error	*z*-value	*p*-value
(Intercept)	1.406	0.065	21.64	**<0.0001**
Height (15 cm)	–0.070	0.069	–1.02	0.308
Height (5 cm)	+0.010	0.069	+0.15	0.884
Height (1 cm)	+0.355	0.069	+5.16	**<0.0001**
Habitat (Seagrass)	–0.005	0.072	–0.07	0.943
Season (Autumn)	–0.586	0.081	–7.25	**<0.0001**
Seagrass × Autumn interaction	+0.404	0.115	+3.53	**0.0004**

Gamma GLMM; n = 463; $\sigma^2 = 0.27$; marginal $R^2 = 0.207$; conditional $R^2 = 0.233$)

Appendix 1.B. ***Fixed effects summary for 2021 water column chlorophyll-a.*** Gamma GLMM fixed-effects predicting chlorophyll-*a* concentration ($\mu g\ L^{-1}$) as a function of vertical height above the seafloor (1–45 cm), habitat (Bare vs. Seagrass), and season (Summer, Autumn). Significant positive coefficients for bottom depths (1 cm) reflect elevated concentrations relative to the upper-water column reference (45 cm), particularly in Seagrass habitats during autumn ($p = 0.0004$). The model used a log link function and included a random intercept for site ($n = 463$; marginal $R^2 = 0.207$; conditional $R^2 = 0.233$). Boldface denotes significant *p*-values (< 0.05).

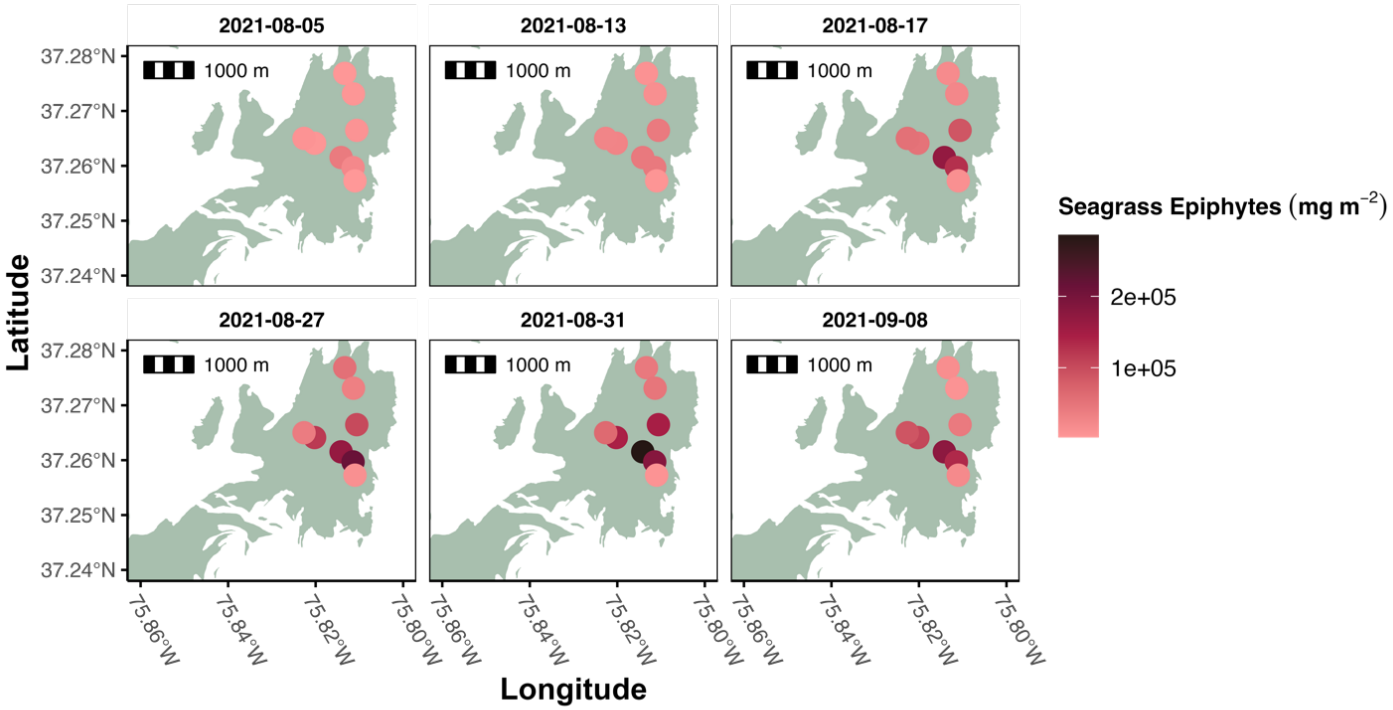
Term	Estimate	SE	*z*-value	*p*-value
(Intercept)	0.458	0.128	3.576	**0.00035**
Height (15 cm)	0.027	0.080	0.336	0.73668
Height (5 cm)	0.058	0.080	0.732	0.46445
Height (1 cm)	0.324	0.078	4.152	**<0.001**
Seagrass (vs. Bare)	0.424	0.168	2.522	**0.01168**
Season: Spring (vs. Winter)	0.008	0.159	0.052	0.95866
Season: Summer	1.734	0.127	13.66	**<0.001**
Season: Autumn	0.392	0.145	2.709	**0.00674**
Seagrass × Spring	-0.197	0.224	-0.879	0.37937
Seagrass × Summer	-0.882	0.182	-4.845	**<0.001**
Seagrass × Autumn	0.299	0.196	1.526	0.12706
GLMM; log link, φ = 0.358, power = 1.74; n = 319, marginal R^2 = 0.644				

Appendix 1.C. ***Fixed effects from 2022-2023 water column chlorophyll-a Tweedie GLMM***.

Estimated coefficients (± 95% confidence intervals) from a generalized linear mixed model using a Tweedie distribution (log link, φ = 0.358, power = 1.74; n = 319, marginal R^2 = 0.644) assessing effects of water-column height, habitat type, and season on chlorophyll-*a* concentration. Reference levels were Bare habitat, Winter, and 45 cm above the seafloor. Positive coefficients indicate increased chl-*a* relative to the reference, while negative values represent reductions. The interaction between Seagrass and Summer was strongly negative (–0.88), suggesting significantly lower chl-*a* during peak summer months in seagrass meadows. A random intercept for Site (SD = 0.085) accounted for repeated measures across 16 locations. Boldface denotes significant *p*-values (< 0.05).

Season	Height (cm)	Bare (Mean ± SE)	Seagrass (Mean ± SE)	Key insight
Summer	1	12.38 ± 0.99	7.83 ± 0.63	Seagrass reduced chl-*a* at 1 cm ($p < 0.001$)
Summer	45	8.95 ± 0.71	5.66 ± 0.47	Seagrass reduced surface chl-*a*
Autumn	1	3.24 ± 0.33	6.66 ± 0.56	Seagrass enhanced bottom chl-*a*
Autumn	45	2.34 ± 0.25	4.82 ± 0.41	Seagrass enhanced surface chl-*a*
Spring	1	2.20 ± 0.27	2.77 ± 0.33	Subtle enhancement at depth
Winter	1	2.19 ± 0.28	3.34 ± 0.43	Seagrass maintained elevated bottom values

Appendix 1.D. ***Estimated chlorophyll-a concentrations by height, season, and habitat (2022-2023).*** Predicted means (± SE) from a Tweedie GLMM (see Appendix 1.C) showing chlorophyll-*a* concentrations (μg L^{-1}) at four heights (1–45 cm above the seafloor) within Seagrass and Bare habitats across four seasons in 2022-2023. Seagrass plots exhibited pronounced seasonal modulation of chl-*a* vertical structure. In summer (July and August), seagrass reduced concentrations relative to Bare habitats at all depths (e.g., 1 cm: 7.83 ± 0.63 vs. 12.38 ± 0.99 μg L^{-1}), while in autumn, Seagrass maintained significantly higher chl-*a* at the bottom (6.66 ± 0.56 μg L^{-1} vs. 3.24 ±0.33) —the strongest difference across all estimate comparisons.



Appendix 1.E. ***Spatial distribution of epiphytic biomass across meadow sites.*** Seagrass algal epiphyte biomass (mg m^{-2}) by site, with darker red colors denoting increasing mass. As shown, the highest observed biomass occurred in central-meadow sites while all sites exhibited rapid increases in epiphyte load beginning around mid-August.

Chapter 2. Influence of seagrass habitat configuration, seasonality, and life stage on hard clam predation

Anticipated authors of peer-reviewed manuscript:

Michael R. Cornish

Max C.N. Castorani, PhD

Abstract

Seagrass meadows are widely regarded as refuges that dampen predator pressure on benthic fauna. Because predation can limit prey recruitment and population persistence, the paradigm that seagrasses are a refuge predicts that seagrass meadows enhance prey abundances, especially for juveniles (the 'nursery habitat' hypothesis). However, tests of this theory rarely investigate the effects of meadow structure, seasonality, and prey ontogeny. We used a fully factorial field experiment in a 20 km² *Zostera marina* seagrass meadow at the Virginia Coast Reserve (Virginia, USA) to quantify how habitat configuration (bare sediment, patchy cover, dense cover), season (late winter, late spring, summer, autumn), and life stage (10 mm recruits vs. large 60–120 mm adults) interact to shape mortality of hard clams *Mercenaria mercenaria*, a common and widespread prey species that is critical to benthic-pelagic coupling, coastal food webs, and fisheries. Juvenile clams were transplanted into paired caged and uncaged plots; adult clams were tethered along replicated transects. We found that dense seagrass provided the strongest refuge across life stages. Predation appeared to have stark effects on juvenile survival: installing cages raised survival odds by 31-fold at sites without seagrass (bare seafloor) while, even without cages, dense seagrass quadrupled juvenile daily survival relative to bare sites (OR = 4.3). Notably, patchy seagrass conferred no detectable juvenile refuge. For adult clams, both dense and patchy seagrass increased daily survival 20-fold relative to bare sites. Summer intensified predation everywhere, yet dense and patchy seagrass habitats still elevated survival 7- and 4.5-fold, respectively, while winter mortality was negligible in all habitats. Survival at bare sites fell 88% from winter to summer, underscoring the strong seasonal effects. Adult shell length did not add predictive power once habitat and season were included, indicating that refuge effects outweighed any residual size refuge within the 20–123 mm size range examined. Together, these results support the paradigm that seagrass meadows serve as a prey refuge and

nursery habitat. However, our experiments also suggest habitat complexity, prey ontogeny, and seasonal dynamics interactively dictate predation outcomes within seagrass ecosystems—conditional maximized by dense vegetation during periods of intense predator activity and most important for the smallest clams.

Introduction

Temperate seagrass meadows (e.g., eelgrass *Zostera marina*) are widely recognized as important refuges that mediate predator–prey interactions in coastal ecosystems (Orth et al. 1984b). The structural complexity of the seagrass canopy, roots, and rhizomes can provide physical, chemosensory, and visual barriers that reduce predation risk for benthic prey (Main 1987, Chacin and Stallings 2016a). Classic studies demonstrated that hard clams (*Mercenaria mercenaria*) experience significantly higher mortality on unvegetated sand flats than within seagrass beds (Peterson 1986, Irlandi et al. 1999), thereby helping to establish the paradigm that seagrass is often critical refuge habitat for its associated infaunal bivalves (Fales et al. 2020b).

Habitat structure and configuration may be key drivers of predation intensity in seagrass systems across scales. At fine spatial scales, increased seagrass shoot density and canopy height tend to suppress predator foraging efficiency, thereby enhancing prey survival (e.g., reduced clam siphon nipping and mortality under dense seagrass canopies; Irlandi 1996a). At broader scales, habitat configuration (e.g., continuous vs. patchy meadows) can further influence outcomes, with seagrass patch size garnering significant attention by mediating encounter rates between predators and prey (Irlandi 1994, Smith et al. 2011, Fales et al. 2020b).

Seagrass structure heterogeneity and predator identity/life history strategies can interactively mediate clam predation rates, as different predators respond uniquely to seagrass structure across their life stages. For example, blue crabs (*Callinectes sapidus*)—a major benthic predator of hard clams—hunt largely by touch and chemical cues; dense seagrass can reduce predation success by hindering crab movement and dilute or confound water-borne hard-clam chemical cues amid that of other species (Main 1987). However, mesopredators (predators preyed upon by higher-order predators) like blue crabs also find refuge in seagrass habitats,

particularly as juveniles (Hovel and Fonseca 2005) when they are also primary predators of young and newly-recruited bivalves like hard clams (Irlandi 1994, Smee and Weissburg 2006, Meira et al. 2024). By contrast, predatory gastropods such as whelks (*Busycon* spp.) and large mobile predators like cownose rays (*Rhinoptera bonasus*)—while known to preferentially forage for bivalves—may be both attracted to seagrass habitat and inhibited by the dense seagrass rhizomes that encase infaunal clams (Hovel and Lipcius 2001). Hence, multiple pathways and outcomes are possible, suggesting that paradigmatic findings may be context-dependent (Peterson 1982, Fales et al. 2020b).

Like many organisms, hard clams also exhibit a strong ontogenetic shift in predation risk. Small juveniles (≲20 mm) are vulnerable to an array of seagrass-associated predators—blue crabs, whelks, and fishes—and experience high mortality outside and inside of seagrass meadows in their first year of life. However, as clams grow, they increasingly escape predation due to their size and thick shells. Classic studies (e.g., Peterson 1982; Irlandi 1994; Smee and Weissburg 2006) quantified this size refuge in different contexts, finding that clams above a certain size suffer very little predation, even outside of habitat refugia, as most predators are incapable of predating them due to the gape size, crushing strength, or prying force required for consumption. Consequently, vegetated habitats tend to contain disproportionately more large, older clams, since seagrass enhances juvenile recruitment and survival (Fales et al. 2020), and provides a haven for growing clams until they reach larger sizes (Irlandi and Peterson 1991). This ontogenetic dynamic illustrates the life stage-dependent effects of the seagrass-as-refuge paradigm—the habitat's protective value is highest for the smallest clams, whereas large adult clams cease to benefit.

Lastly, seasonal variability in predator–prey dynamics is a pivotal yet understudied factor in seagrass-mediated predatory-prey dynamics. In temperate ecosystems, predator density and activity vary by season, but for scientific and logistical reasons, most field campaigns are carried out during the summer. For example, blue crabs in the Mid-Atlantic region are active and abundant in warmer months and often burrow or migrate to deeper waters in winter (Hovel and Fonseca 2005), while cownose rays migrate into coastal bays bay in late spring and depart by early fall (Orth 1976, Fisher et al. 2011, Bade et al. 2014). These shifts can cause seasonal peaks in predation risk. Moreover, habitat "refuge value" may likewise change with seasons as seagrass biomass varies (e.g., canopy height and density peak in summer and decline in fall) (Hansen and Reidenbach 2013, Rheuban et al. 2014). Yet, most studies are based in the summer when predator densities and predation risk may be highest (Orth et al. 1984b, Chacin and Stallings 2016a). If extrapolated to longer timescales, such short-term studies may misrepresent how habitat structure affects predation risk across prey life stages.

Despite over four decades of research and an increasing number of complex field experiments (Witman et al. 2015), most seagrass-predation studies still test a single driver at a time (Fales et al. 2020b), pointing to Heck and Orth's (2006) unresolved call for experiments that unite habitat complexity with seasonal dynamics and prey ontogeny. Peterson's (1986) conclusion that greater clam densities in seagrass arise from higher post-settlement survival instead of higher larval supply underscores the need to track cohorts through time and consider interactive drivers—yet studies that simultaneously examine season, clam size (ontogeny), and habitat structure in hard clam predation experiments have not been published in the scientific literature. This study carried out a fully factorial manipulation of these factors to help close this gap.

We conducted two field experiments in a large (~20 km^2) U.S. Mid-Atlantic eelgrass meadow: a tethering assay for adult clams and a caging experiment for small clams that represent new recruits (10–15 mm shell length, SL). We deployed these studies in unvegetated ('bare') seafloor sites, patchy seagrass, and dense seagrass during different seasonal windows to evaluate the experimental evidence for: (1) the seagrass-as-refuge paradigm across hard clam life stages, (2) seagrass habitat-structure effects on refuge quality, and (3) seasonal-dependencies for these factors.

Methods

Study system and habitat characterization

We carried out our study in a ~20 km^2 restored eelgrass (*Zostera marina*) meadow within the coastal bays of the Virginia Coast Reserve (VCR)—a back-barrier island system on the Eastern Shore of Virginia, USA (Fig. 2.1). The VCR lagoons were carpeted by eelgrass until a 1933 wasting-disease outbreak and hurricane extirpated the meadows, leaving the bays entirely unvegetated for at least 60 years. Beginning in 1999, the Virginia Institute of Marine Science, the University of Virginia, and The Nature Conservancy broadcast more than 70 million seeds across bays, catalyzing a rebound to ~3,600 ha (≈ 36 km^2) of continuous seagrass in Virginia's coastal bays—the largest and most successful restoration of its kind worldwide (Orth et al. 2020b).

To identify and characterize experimental sites by landscape-scale seagrass coverage, we used a DJI Phantom 4 RTK (real-time kinematic) (Taddia et al. 2020) unoccupied aerial system to fly gridded missions over meadow areas that ground-truth surveys indicated would meet our habitat targets (bare = 0%, patchy = 10–50%, dense > 70%). We processed the raw images in Agisoft Metashape Professional v2.2.1 (Agisoft LLC 2025) to generate orthorectified

GeoTIFF mosaics (Fig. 2.1, Panel A). From these, we produced percent-cover rasters in QGIS 3.36 (Ventura et al. 2022) using the "Semi-Automatic Classification" function to summarize seagrass cover for the transect area (200-m buffer) around each fixed 50-m transect described below (Nahirnick et al. 2019).

Adult clam predation experiment

We quantified size-specific predation on adult hard clams (*Mercenaria mercenaria*) with four successive tethering experiment deployments at nine 50-m transects in South Bay, Virginia, USA: three in unvegetated sites (0% cover), three in patchy seagrass (Zostera marina) sites (10–40% cover) and three in the continuous canopy found at the center of the meadow (>70% cover) (Irlandi et al. 1999). A minimum of two days before deployment, we marked all individuals with a unique ID using a permanent maker, measured the dimensions of each (shell height, width, and length) and glued its tether (Carroll et al. 2012, Baker and Waltham 2020). Tethers were attached to clams with rapid-curing cyanoacrylate glue—commonly used in this manner (Micheli 1997, Baker and Waltham 2020). We kept all clams in aquaria (1 m deep, 2 m wide, 2 m long, with 20 cm of sand at the bottom) supplied with flowing unfiltered seawater at Oyster Harbor, Virginia, for observation to ensure that we only used individuals seen actively filter-feeding the day of deployment.

At each field site (three sites per habitat type), we distributed 10 clams at 5-m intervals along a 50 m transect, fixing each to the seafloor with a 10 cm aluminum turf staple tied to the 50 cm monofilament tethers, allowing clams to burrow but preventing emigration (Smith et al. 2011). Clams were sorted into three significant length (SL) size classes: small (20–35 mm), medium (40–60 mm), and large (60–123 mm) to ensure an even distribution of shell sizes

deployed across transects, sites, and habitats (shell significant lengths = 19-123 mm ±24.48 mm standard deviation; n = 359). We obtained hatchery-reared clams 35 mm-SL and smaller from a nearby aquaculture facility because it is not feasible to collect large numbers of small clams from the field. We conducted field-collections for the larger sizes not available from farms. After testing different trial periods, ~25-day deployments were targeted to ensure sufficient time for predation to occur. Following this deployment period, we carefully searched by snorkel at low tide for tethered clams and noted their unique-IDs and evidence of predation surrounding the transect (e.g., crushed shells, shell fragments, foraging pits).

To quantify adult-clam predation, we recorded the number of days in which clams remained in the field ('exposure time') and classified their survival status at the time of survey (alive = 1, dead/missing = 0) to use as the response in mixed models. Dead/missing clams represent those where the tether and staple were found without a live clam attached. To ensure "lost" individuals would not be considered predated (i.e., those we could not locate but may have been present/eluded predation), we disregarded deployed individuals that lacked a tether and staple upon retrieval from analyses.

Following Zuur et al. (2009), we modeled daily survival probability with a binomial generalized linear mixed-effects model (GLMM). The fixed effects included habitat (Bare, Patchy, or Dense), season (spring, summer, autumn, winter), their interaction, and shell length (significant length; SL). An offset of the natural log of the deployment duration (no. days) converted survival counts to per-day probabilities. Random intercepts for transect plus an observation-level random effect (one level per clam) accommodated spatial clustering and variation among individuals deployed on the same transect (i.e., site effects; Zuur et al. 2009).

We assessed model fit with simulated residual diagnostics in R using the *DHARMa* (Hartig 2024) and *performance* (Lüdecke et al. 2024) packages.

Juvenile/young recruit predation experiment

To examine the role of life stage on seagrass-mediated predation, we deployed juvenile clams representing new recruits in predation trials at either end of the transect sites described above. Following Castorani & Hovel (2015), we used small, self-contained plots constructed from 15 cm-diameter × 5 cm-high cylindrical sections of PVC with a 1-mm fiberglass-mesh screen fixed to the base (hereafter, 'plots'). During deployments, we used a PVC-corer to excavate pits in the seafloor for each of the juvenile plots. After excavations, plots were filled with pre-sieved, dried sediment from a nearby beach, and pressed flush with the surrounding seabed. Then, twenty small (SL = 10–15 mm) hard clams, acquired from a local hatchery, were gently pushed posterior-end first into each plot so that the dorsal margin lay ~2 mm below the sediment surface—the settled depth that maximizes feeding while matching natural burial of recruits. We observed the plots to confirm that the clams righted themselves and began feeding shortly after. They did this within 10–15 min—unsurprising as small juvenile hard clams, unlike adults, are highly mobile (Tettelbach et al. 2017). At each transect terminus, we installed one plot with a randomly selected treatment (predator-exposed control vs. predator-exclusion cage) and applied the opposite treatment to the plot on the other end of the transect (i.e., two plots per transect, one of each treatment). Enclosures consisted of galvanized-steel mesh cages (25 cm diameter × 30 cm height; 1.3 cm edge-length of the square apertures) buried 15 cm deep, a design shown to prevent access by crabs, demersal fishes, and whelks without substantially altering flow or light regimes (Castorani and Hovel 2015). Biofouling of the cages was minimal.

After ~5 days (chosen based on trial deployments), we retrieved each ring by inserting a 15 cm diameter corer beneath the mesh base and sieving its contents (1 mm). Clams were classified as alive, dead but intact, or predated (as evidenced by crushed, drilled, or missing valves). Missing individuals were treated as predator removals, a conservative approach that captured mobile predator effects documented for juvenile clams in similar assays (Kushner and Hovel 2006, Castorani and Hovel 2015)

We analyzed juvenile predation—expressed as the percentage of the 20 deployed clams per plot recovered alive after 5 days—with a binomial generalized linear mixed-effects model (logit link) fitted by maximum likelihood with the R package *glmmTMB* v1.2-5 (Brooks et al. 2017, Hesterberg et al. 2017). Our fixed-effects structure matched the experimental design: habitat (Bare, Patchy, or Dense), predator exposure (Uncaged or Caged), and their interaction. We added the natural logarithm of deployment duration (no. days) as an offset to express survival on a per-day basis. To account for spatial and temporal clustering, we included random intercepts for transect and deployment date. Simulation-based residual diagnostics in *DHARMa* (Hartig 2024) showed no systematic patterns, confirming that the estimated dispersion term captured overdispersion. We summarized model fit and pseudo-R^2 with the *performance* package (Lüdecke et al. 2024).

Results

Adult-clam predation

A binomial GLMM that included habitat, season, their interaction, and shell length detected a strong habitat × season interaction (Type III Wald $\chi^2 = 19.35$, df = 6, $p = 0.0036$; Table 2.1). Season remained an important main effect ($\chi^2 = 11.29$, df = 3, $p = 0.010$), whereas

habitat lost main-effect significance once its interaction with season was modeled ($\chi^2 = 5.57$, df = 2, $p = 0.062$; Fig. 2.2). Shell length did not improve model fit ($\chi^2 = 0.35$, $p = 0.55$) and none of its possible interactions were retained (all $p \geq 0.09$; Table 2.1).

During spring, dense and patchy seagrass increased daily survival roughly twenty-fold relative to bare sand (Dense versus Bare site odds ratio [OR] ≈ 19.7; Patchy versus Bare OR ≈ 19.3; both $p = 0.015$), raising mean predicted survival from 0.04 to 0.72 clam day^{-1}. In summer, predation intensified in every habitat, yet seagrass still conferred a marked refuge: dense grass elevated survival just over seven-fold (OR ≈ 7.1, $p = 0.010$) and patchy grass about four-and-a-half-fold (OR ≈ 4.6, $p = 0.039$) compared with bare sites. Survival on bare sand dropped by 88 % from winter to summer (OR = 0.12, $p = 0.004$), a seasonal decline mirrored in patchy grass but dampened in dense seagrass. In autumn, survival in patchy grass fell sharply; dense grass outperformed patchy sites six-fold (OR ≈ 6.3, $p = 0.020$), whereas neither seagrass treatment differed statistically from bare sand. Winter predation was minimal in all habitats, with daily survival exceeding 99% and no contrasts reaching significance (all $p > 0.11$; Table 2.3). Collectively, these patterns identify summer as the period of greatest risk and highlight dense seagrass as the most effective refuge, whereas winter mortality is intrinsically low and largely habitat-independent (see Table 2.3 for full GLMM outputs; raw observation summaries in Appendix 2.A).

Juvenile-clam predation

A binomial GLMM predicting daily survival (% of deployed individuals per plot) by habitat, predator exposure (caged vs. exposed), and their interaction revealed strong main effects of both factors and a marginally significant interaction (Type III Wald χ^2:

Habitat = 11.83, df = 2, p = 0.0027; Treatment = 44.82, df = 1, p < 0.0001; Habitat × Treatment = 5.02, df = 2, p = 0.081; Table 2.4).

For predator exposed (uncaged) plots on bare sediment, daily survival probability was 0.033 (logit = −3.37 ± 0.46 SE, z = −7.34, p < 0.001; Table 2.4), equivalent to 0.66 juveniles plot^{-1} day^{-1}. Installing a cage increased the odds of survival 31-fold (β = +3.45 ± 0.58, z = +5.96, p < 0.0001; OR = 31.4, 95 % CI = 10.1–97.6), raising expected survival to 10.4 clams plot^{-1} day^{-1}. Even without predator exclusion cages, dense seagrass quadrupled survival relative to those at bare sites (β = +1.45 ± 0.55, z = +2.65, p = 0.008; OR = 4.26, 95 % CI = 1.46–12.5), yielding a mean daily survival of 2.6 clams plot^{-1}. Consequently, the dense-grass × cage interaction was weak and negative (β = −2.36 ± 1.09, p = 0.031, OR = 0.09, 95 % CI = 0.01–0.81), indicating that the significant protection afforded by dense grass rendered cage minimal. Conversely, patchy seagrass offered no detectable refuge (β = +0.12 ± 0.63, p = 0.85, OR = 1.12, 95 % CI = 0.06–4.35). Random-effect variances were negligible for transect (< 4 × 10^{-5}) and modest for deployment date (σ = 0.33), suggesting that short-term (summertime; May–September) temporal conditions, rather than site effects, slightly modulated outcomes.

Collectively, these results show that predators account for nearly all juvenile mortality, that dense seagrass substantially buffers recruits from predators, and that patchy cover confers little protection (Fig. 2.3).

Discussion

Our findings give strong support for—and indicate ecological nuance about—the paradigm that seagrass meadows are predation refuges and juvenile nurseries for hard clams

(Orth et al. 1984b, Fales et al. 2020b). By introducing the interactive effects of habitat complexity, prey size, and seasonal dynamics, our results highlight that mechanistically grounded context-dependence, rather than generality, is the emergent property of these species interactions.

Both adult tethering and juvenile caging experiments demonstrated significantly higher survival rates for hard clams in seagrass habitats compared to unvegetated areas, aligning with prior observations that vegetation and other physically complex structures substantially reduce benthic predation risk (Peterson 1986; Irlandi et al. 1999). Dense seagrass canopies impede predator movements and obscure prey detection via visual and chemical cues (Main 1987; Chacin and Stallings 2016), markedly enhancing prey survival. Our results indicate increased clam survivorship with increasing seagrass density, consistent with findings by Irlandi (1996) that greater structural complexity reduces predator foraging efficiency.

Habitat configuration emerged as an important modulator of refuge efficacy. Continuous, densely vegetated meadows offered maximal protection, whereas patchy seagrass beds provided intermediate refuge benefits (Fig. 2.2). Specifically, adult tethering experiments revealed substantially higher clam survival within meadow interiors (>70% cover) compared to patchy meadows (10–40% cover) and bare areas (0% cover). Hence, not all seagrass habitats confer equal protection. Instead, we found that seagrass bed configuration fundamentally influences predator-prey dynamics, aligning with foundational work in this field (Peterson 1986, Irlandi 1994, Irlandi et al. 1999, Carroll et al. 2012).

Predator identity and behavior likely modulate these habitat-mediated interactions further. For example, blue crabs (*Callinectes sapidus*)—significant predators of juvenile hard clams (Kraeuter and Castagna 2001a)—are inhibited by dense seagrass that interferes with their ability

to track chemical-cues to locate prey (Main 1987). This may well explain why particularly intense predation rates in summer, when blue crab populations peak (Lipcius et al. 2005, Rielly-Carroll and Freestone 2017, Cheng et al. 2022), yielded the strongest refuge effect in dense seagrass (Smee and Weissburg 2006). We also observed evidence of predator-specific clam mortality; chipped shell margins were common and indicated crab predation, while some spring/summer tether locations had large pits and crushed shells characteristic of cownose rays (*Rhinoptera bonasus*). Notably, both of these predators are less effective at foraging in dense seagrass—albeit for different reasons (Hovel and Lipcius 2001, Ajemian and Powers 2013). Our results are also consistent with the prior finding that seagrass reduces predation on hard clams by two species of large predatory gastropods common in our system, knobbed whelks (*Busycon carica*) and channel whelks (*Busycotypus canaliculatus*) (Peterson 1982).

We also observed significant ontogenetic shifts in predation risk; small juvenile clams (10–15 mm) exhibited near-complete mortality in bare habitats but gained considerable protection in dense seagrass regardless of protection by experimental cages. Conversely, larger adult clams in the tethering experiment (>20 mm) had substantially lower loss rates, even at bare sites. While our inclusion of these larger size classes is novel among seagrass-bivalve predation experiments (Fales et al. 2020b), this size-refuge effect has been long postulated (Peterson 1982, Hovel and Lipcius 2001, Smee and Weissburg 2006, Ajemian and Powers 2013).

Seasonality strongly influenced patterns of adult mortality, with peak predator activity in late spring and summer markedly elevating the risk of clam death. Conversely, winter months exhibited negligible mortality regardless of habitat, evidence likely attributable to reduced predator activity(Orth 1976, Hovel and Fonseca 2005, Fisher et al. 2011) The temporal alignment of peak seagrass structural complexity in summer (Berger et al. 2020) when predator abundance

is highest (Orth et al. 1984b, Canion and Heck 2009) highlights a dynamic seasonal interaction wherein seagrass refuge benefits are amplified when predation pressure is highest. Consequently, seasonal fluctuations in habitat structure and predator abundance demand year-round investigations to accurately assess the functional importance of seagrass as a predation refuge (Orth et al. 1984b, Lipcius et al. 2005, Carr et al. 2012, Hansen and Reidenbach 2013).

In sum, our experiments demonstrate that habitat complexity, prey ontogeny, and seasonal dynamics interactively dictate predation outcomes in coastal ecosystems. By adopting a factorial experimental design, we addressed calls to simultaneously examine the effects of these drivers (Larkum et al. 2006, Witman et al. 2015, Fales et al. 2020b). Our findings emphasize that the efficacy of the seagrass-as-refuge paradigm is highly dependent on the ecological context, requiring explicit consideration of recruitment pulses, habitat persistence, and predator assemblages to achieve predictive generality. Moreover, our results are consistent with the notion that seagrass conservation and restoration can yield long-term population-level benefits for consumers by enhancing juvenile survival and sustaining significant populations of large individuals that contribute disproportionately to reproductive output (Peterson 1986; Fales et al. 2020).

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Figures and tables

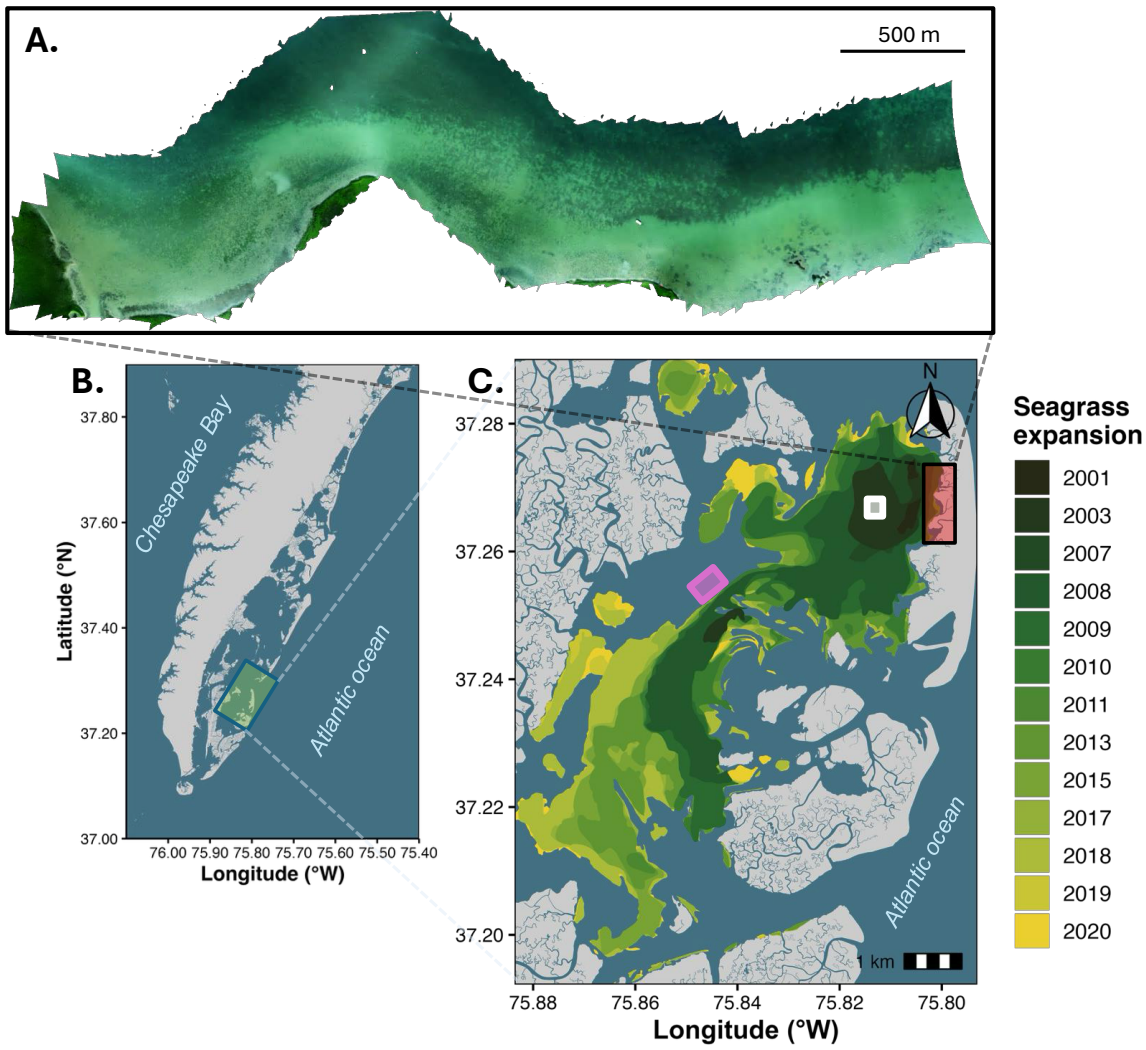


Figure 2.1. ***Study region, locations, and habitat-characterization photomosaic.*** (A) Photomosaic of eastern edge of the studied seagrass meadow. Darker areas show dense seagrass and light areas show unvegetated sandy seafloor; note the patchy areas between these two habitats. (B) Location of South Bay within the coastal bays of Virginia, USA. (C) Composite map of the restored seagrass meadow from 2001 (dark green) to 2020 (yellow) following seed restoration.

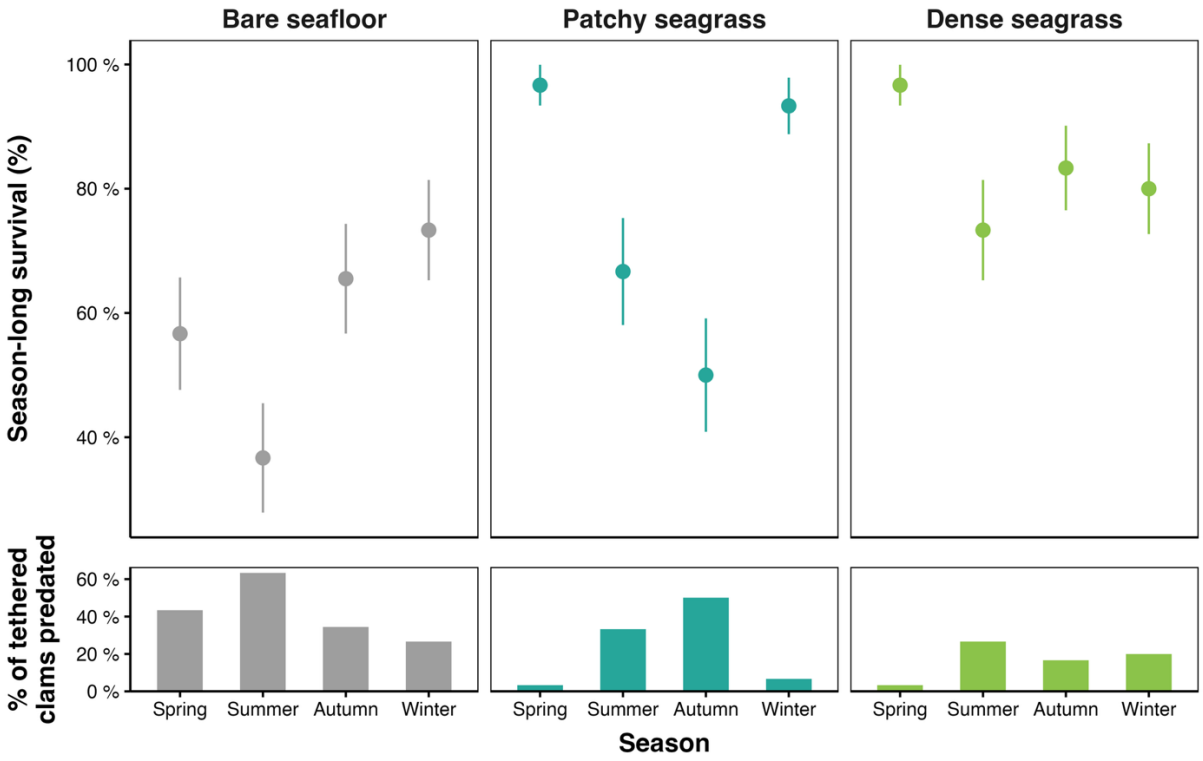


Figure 2.2. ***Observed adult clam survival percentages across habitats and seasons.***

Top panels: mean (±SE bars) observed season-long survival (%) of tethered clams by habitat (i.e., treatment). Bottom panels: proportion of deployments in which clams were predated (% of deployed individuals tether and staple were retrieved without a live clam attached) for the same habitat × season combinations.

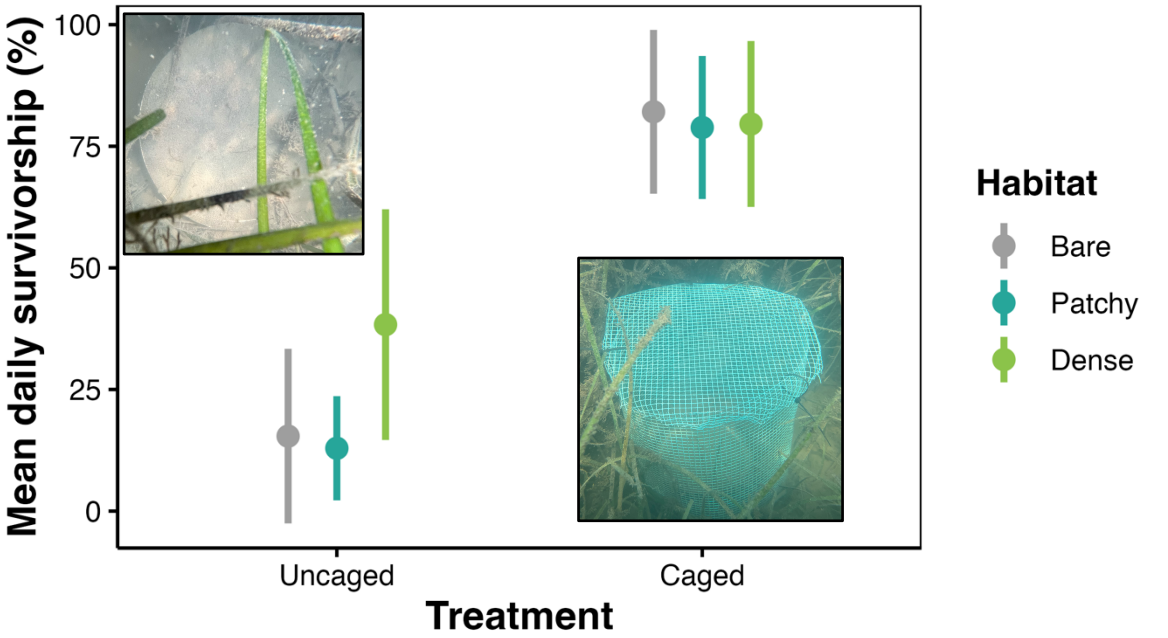


Figure 2.3. ***Observed juvenile clam survival percentages across habitats and treatments.*** Mean daily survivorship (with 95% CI) of juvenile hard clams (*Mercenaria mercenaria*) after ~5-day field deployments in three habitat types—bare seafloor (grey) patchy seagrass (teal), and dense seagrass (green)—under two treatments: predator-exposed ("Uncaged") and predator-excluded ("Caged").

Term	χ^2	*df*	*p*
Length	0.35	1	0.554
Habitat	5.57	2	0.062
Season	11.29	3	**0.010**
Length × Habitat	0.38	2	0.828
Length × Season	6.44	3	0.092
Habitat × Season	19.35	6	**0.0036**

Table 2.1. ***Adult predation χ^2 test outputs.*** Type-III Wald χ^2 tests for fixed effects in the binomial GLMM described in Table 2.2. Boldface denotes significant *p*-values (< 0.05).

Term	**β**	**SE**	***z***	***p*-value**	**OR** (95%CI)
(Intercept)	4.079	1.028	3.97	**7.23×10^{-5}**	59.11 (7.88–443)
Length	−0.009	0.016	−0.59	0.554	0.99 (0.96–1.02)
Habitat Patchy seagrass	2.852	1.403	2.03	**0.0420**	17.32 (1.11–271)
Habitat Dense seagrass	2.458	1.476	1.66	0.0960	11.68 (0.65-211)
Season Summer	−4.031	1.348	−2.99	**0.00278**	0.02 (0.00–0.25)
Season Autumn	−1.118	1.273	−0.88	0.380	0.33 (0.03–3.96)
Season Winter	−2.295	1.408	−1.63	0.103	0.10 (0.01–1.59)
Length × Habitat Patchy	0.003	0.015	0.23	0.815	1.00 (0.97–1.03)
Length × Habitat Dense	0.010	0.017	0.61	0.539	1.01 (0.98–1.04)
Length × Season Summer	0.045	0.020	2.22	**0.0262**	1.05 (1.01–1.09)
Length × Season Autumn	0.028	0.019	1.47	0.141	1.03 (0.99–1.07)
Length × Season Winter	0.052	0.024	2.15	**0.0316**	1.05 (1.00–1.10)
Habitat Patchy × Season Summer	−1.548	1.244	−1.24	0.213	0.21 (0.02–2.44)
Habitat Dense × Season Summer	−1.123	1.267	−0.89	0.376	0.33 (0.03–3.90)
Habitat Patchy × Season Autumn	−3.762	1.228	−3.06	**0.00219**	0.02 (0.00–0.26)
Habitat Dense × Season Autumn	−1.968	1.275	−1.54	0.123	0.14 (0.01–1.70)
Habitat Patchy × Season Winter	−1.259	1.412	−0.89	0.373	0.28 (0.02–4.52)
Habitat Dense × Season Winter	−2.555	1.291	−1.98	**0.0478**	0.08 (0.01–0.98)

Table 2.2. ***Adult predation mixed-model effect estimates.*** Fixed-effect estimates from a binomial GLMM for daily survival as a function of shell length (continuous), habitat configuration (Bare, Patchy, Dense seagrass), season, and all two-way interactions, with an offset for log exposure-time (days) and random intercepts for transect and clam identity nested within transect. β = log-odds estimate (logit link); SE = standard error; OR = odds ratio (e^{β}) with 95 % CI. Boldface denotes significant *p*-values (< 0.05).

Season	Contrast	OR	95 % CI	*z*	*p*
Spring	Bare / Patchy	0.05	0.00–0.62	−2.78	**0.015**
Spring	Bare / Dense	0.05	0.00–0.61	−2.79	**0.014**
Summer	Bare / Patchy	0.22	0.05–0.94	−2.44	**0.039**
Summer	Bare / Dense	0.14	0.03–0.68	−2.92	**0.010**
Autumn	Patchy / Dense	0.16	0.03–0.79	−2.69	**0.020**
Winter	(none were significant at $p < 0.05$)				

Table 2.3. ***Adult predation odds ratios by habitat configuration.*** Pairwise habitat contrasts (odds ratios) within each season derived from marginal means at mean shell length (57 mm).

β = log-odds estimate (logit link); SE = standard error; OR = odds ratio (e^{β}) with Wald 95 % CI.

Odds ratios < 1 indicate higher survival in seagrass relative to unvegetated (bare) seafloor sites.

Boldface denotes significant *p*-values (< 0.05).

Term	β	SE	*z*	*p*	OR (95 % CI)
Intercept (Bare × Uncaged)	–1.725	0.894	–1.93	**0.0538**	0.18 (0.03–1.03)
Habitat Patchy	–0.213	0.860	–0.25	0.8050	0.81 (0.15–4.36)
Habitat Dense	2.196	0.781	2.81	**0.0049**	8.99 (1.95–41.50)
Treatment Caged	5.471	0.817	6.70	**< 0.0001**	238 (48–1,179)
Patchy × Caged	–0.700	1.107	–0.63	0.5270	0.50 (0.06–4.35)
Dense × Caged	–2.358	1.093	–2.16	**0.0310**	0.09 (0.01–0.81)

Table 2.4. ***Juvenile clam predation odds ratios by habitat and cage treatment.*** Fixed-effect coefficients for the juvenile binomial GLMM. β = log-odds estimate (logit link); SE = standard error; OR = odds ratio (e^{β}) with Wald 95 % CI. Boldface denotes significant *p*-values (< 0.05).

Appendix

Habitat	Season	Alive (1)	Dead/missing (0)	*n*
Bare seafloor	Spring	17	13	30
Bare seafloor	Summer	11	19	30
Bare seafloor	Autumn	19	10	29
Bare seafloor	Winter	22	8	30
Patchy seagrass	Spring	29	1	30
Patchy seagrass	Summer	20	10	30
Patchy seagrass	Autumn	15	15	30
Patchy seagrass	Winter	28	2	30
Dense seagrass	Spring	29	1	30
Dense seagrass	Summer	22	8	30
Dense seagrass	Autumn	25	5	30
Dense seagrass	Winter	24	6	30

Appendix 2.A. ***Adult predation observation summary.*** Number of tethered adult *M. mercenaria* recovered alive versus dead or missing in each habitat–season combination. Counts represent unique individuals deployed for 30- to 33-day intervals; missing clams were classified as predated only when the tether and staple were present.

Chapter 3. Effects of seagrass-mediated food sources, habitat configuration, and life stage on clam growth in a restored seagrass meadow

Anticipated authors of peer-reviewed manuscript:

Michael R. Cornish

Max C.N. Castorani, PhD

Abstract

Seagrass meadows and associated suspension-feeding bivalves often influence benthic–pelagic coupling in shallow coastal ecosystems, yet their interactions can shift from positive to negative as environmental conditions change and organisms age—a context dependence that remains poorly understood. To clarify how seagrass-mediated food supply, habitat configuration, and life stage affect bivalve productivity in seagrass meadows, we quantified hard clam (*Mercenaria mercenaria*) growth and condition across a 20 km² *Zostera marina* meadow. We paired centimeter-resolved vertical chlorophyll-*a* profiles with individually tagged juveniles and adults deployed in caged plots located inside, at the edge of, and outside the seagrass meadow from May to September 2024. We found that juvenile clams grew ~36 % faster inside the meadow, while adult growth did not differ by habitat. Distance away from the meadow edge and near-bed chlorophyll-*a* concentrations (6–10 μg L^{-1}) were not predictive of growth for either life stage. Despite similar mean condition index values between habitats, the percentage of tissue declined by ~0.66 % for each cm^2 of shell accreted for juvenile clams at bare seafloor sites; those inside seagrass showed no such decline. These results indicate that seagrass meadows enhance juvenile clam shell growth and buffer them against energetic costs induced by calcification, while adult clam growth is largely independent of habitat. Moreover, these findings underscore that shell-growth metrics alone may miss significant habitat effects, thereby emphasizing the need to consider condition, energetics, and life stage when evaluating seagrass–bivalve interactions.

Introduction

Seagrass meadows and suspension-feeding bivalves are emblematic of benthic–pelagic coupling in shallow-water ecosystems. By drawing down phytoplankton and fine particulates, clams and other filter feeders increase light penetration and regenerate dissolved nitrogen and phosphorus that can be taken up by nutrient-limited seagrasses. Conversely, the seagrass canopy damps near-bed flow and, with the roots and rhizomes, enhances sediment stability; together these conditions foster the growth of benthic microalgae that supplement the bivalve diet (Irlandi 1996; Gagnon et al. 2020). Early enclosure studies in Florida and North Carolina, USA, suggested that a broadly positive feedback: juvenile *Mercenaria mercenaria* survived better and grew faster within *Zostera marina* patches than on adjacent bare sand, a posited result of vegetation-hindered blue crab foraging, enhanced food supply, and reduced hydrodynamic stress (Peterson 1984, Arnold et al. 1991, Judge et al. 1993). Yet, subsequent experiments and surveys reported neutral or even negative effects of seagrass on bivalves, particularly at high clam densities or in quiescent coves where slowed flow limits food delivery and biodeposition smothers shoots (Schanz et al. 2002; Ruesink et al. 2018). A growing body of work therefore frames the seagrass–bivalve interaction as highly context dependent, modulated by current velocity, nutrient status, patch size, predator assemblage, and organismal life stage (Fales et al. 2020).

Two leading, and sometimes opposing, hypotheses dominate debates the outcomes for bivalves of seagrass and bare habitat. The predation-refuge (or nursery) hypothesis posits that vegetated habitat reduces encounter rates between juvenile clams and visual predators, tipping the balance toward facilitation. This mechanism is well supported for small size classes in moderately energetic lagoons and is strengthened by the additional benefit of reduced sub-lethal

"siphon-nipping": pinfish cropping of clam siphons—known to slow growth by up to 30 %—occurs far less often inside dense eelgrass (Coen and Heck 1991). In contrast, the flow-delivery hypothesis argues that the same structural complexity that hinders predators also thickens the diffusive boundary layer, restricting food supply to suspension feeders. Patch-manipulation experiments demonstrate that large clams (> 40 mm shell length) frequently grow faster at meadow edges or on unvegetated sand where currents are stronger (Irlandi 1994, 1996). Meta-analyses synthesize these findings into a coherent pattern: facilitation dominates under oligotrophic, high-energy conditions and for early ontogenetic stages, whereas competition emerges in eutrophic or low-flow settings and at high bivalve biomass, when excessive biodeposits and sulfide accumulation can suppress shoot density (Ruesink et al. 2018).

Progress towards resolving this ecological puzzle has been hampered by two pervasive sources of uncertainty. First, most manipulative studies are conducted in plots only tens of meters across, yet climatic and oceanographic drivers such as temperature anomalies, nutrient pulses, and basin-wide phytoplankton blooms vary coherently over tens of kilometers. This Moran-type synchrony can inflate or depress growth at all sites simultaneously, thereby masking local habitat effects (Ranta et al. 1997, Massie et al. 2015, Chacin and Stallings 2016). Second, bivalve ontogenetic shifts may fundamentally alter the interaction: juveniles forage entirely within the canopy boundary layer, whereas adults can extend siphons above that layer, as well as channel an increasing fraction of energy into reproduction (Ansell 1968, Kraeuter and Castagna 2001). Therefore, whether the benefits conferred by seagrass persist throughout the bivalve life cycle and under varying environmental conditions remains an open question.

To disentangle these interacting drivers, we coupled centimeter-scale spatial data with a lagoon-wide field experiment within the Virginia Coast Reserve (VCR)—an oligotrophic back-

barrier lagoon system on the Eastern Shore of Virginia, USA (McGlathery 2017). We caged cohorts of juveniles and adults at sixteen sites that collectively spanned a 20-km^2 eelgrass meadow and the adjacent unvegetated benthos. Precise real-time kinematic global positioning system (RTK GPS) measurements overlaid on a map of the seagrass meadow distribution over time (Virginia Institute of Marine Science Submerged Aquatic Vegetation Monitoring Network [VIMS SAV], 2025) enabled us to describe each cage's position as a signed distance from the meadow edge—negative values positioned inside the canopy and positive values outside. Approximately every two weeks we sampled chlorophyll-*a* concentrations at 1 cm, 5 cm, 15 cm, and 45 cm above the bed, providing a vertically resolved, time-integrated measure of potential food supply at each location. Finally, mixed-effects models with site as a random intercept partitioned local habitat and edge effects from broader lagoon-scale environmental variability while explicitly testing for differences between life stages.

Methods

Clam growth experiment

To examine the effects of habitat and spatial metrics (e.g., distance from edge habitat), we deployed a 4-month caged clam growth experiment at 16-sites (8 seagrass, 8 unvegetated) across a 20 km^2 *Zostera marina* meadow within the study region of the VCR Long Term Ecological Research project (VCR LTER).

At each site we made two (1 adult, 1 juvenile treatment), ~15 cm-diameter × ~5 cm-deep excavations to place same-sized PVC plots with a 1-mm nylon-mesh screen fixed to the base—following Castorani and Hovel (2015). We filled plots with pre-sieved, dried sand from a nearby beach and pressed flush with the surrounding seabed to eliminate edge refugia. To exclude

predators while minimizing effects on ambient flow, we enclosed each experimental plot in a wire cage patterned after the design used by Castorani & Hovel (2015). Galvanized hardware cloth cages (25 cm internal diameter, 30 cm height, 1.3-cm mesh) were pushed 10–15 cm into the sediment so that a significant wire barrier was completely buried around the treatment ring. Then, 5 adult or 10 juvenile hard clams sourced from a local hatchery (Cherrystone Aqua-Farms, Oyster VA, USA)—each marked with a unique polymer-paint identification number—were distributed evenly within each plot/enclosure. Cage walls were scrubbed free of fouling organisms weekly with a wire brush and inspected for breaches; any colonizing predators found to enter cages were promptly removed.

Cages were spaced ≥ 5 m apart at each site and marked with a color-coded 4-meter PVC pole. Site coordinates were surveyed with an Emlid Reach RS2 multi-band RTK-GNSS rover receiving real-time corrections from a Virginia Coast Reserve LTER-curated NTRIP caster; the RTK solution routinely delivered ~3 cm horizontal and ~8 cm vertical precision, well within the receiver's published RTK specifications of 7 mm + 1 ppm horizontally and 14 mm + 1 ppm vertically (Emlid Ltd. 2024).We restricted the juvenile cohort to 18–32 mm shell length because hard clams do not initiate gametogenesis until they surpass ~33–35 mm SL (Kraeuter and Castagna 2001); keeping animals below this maturity threshold enabled us to target somatic accretion, avoiding the seasonal diversion of energy into gonad production that depresses growth in reproductively active adults (Ansell 1968).

Chlorophyll-a sampling

At each of the 16 field sites, we used a four-port PVC sampling device (modified from Judge et al. 1993) to draw water (120 mL) samples from different heights above the seafloor (1,

5, 15, 45 cm) for subsequent chlorophyll-*a* pigment concentration measurement. We did so from a skiff anchored at bow and stern, holding the sampling device motionless for ≈ 3 min before sampling water by suction to allow any disturbed particles to clear. Using a 60 mL polypropylene syringe attached to polyethylene tubing, we drew 180 mL of water from the four heights above the sediment–water interface, thereby resolving centimeter-scale vertical heterogeneity in the benthic boundary layer. Samples were kept in a dark cooler on ice (< 2 h transit) before laboratory processing.

Following methods used by the VCR LTER for a long-term water quality dataset (McGlathery and Christian 2024), we immediately vacuum-filtered (≤ 20 kPa) each water sample through pre-combusted 47-mm Whatman GF/C glass-fiber filters (1.2-µm nominal pore size) after returning from the field. Then, we wrapped the filters in aluminum foil and froze at –20 °C until extraction (≤ 7 d). For pigment extraction, we ground filters by hand in a chilled mortar with 7 mL of 90% acetone, transferred to amber centrifuge tubes, and extracted for 24 hours at 4 °C in the dark. Extracts were clarified in a centrifuge (5 minutes at 7000 RPM corresponding to approximately 5000 g—where RPM = rotations per minute, g = relative centrifugal force expressed as a multiple of Earth's gravitational force) and the supernatant read spectrophotometrically at 664 nm and 750 nm before and after acidification with 0.1 N HCl.

We calculated chlorophyll-*a* concentrations with the monochromatic equations of Lorenzen (1967), corrected for pheophytin interference (Arar and Collins 1997) and normalized to the original sample volume and reported in µg L^{-1}, yielding high-resolution vertical profiles of chlorophyll-*a* suitable for detecting benthic boundary-layer enrichment and evaluating potential food availability for suspension feeders (Judge et al. 1993).

Growth and condition metrics

At deployment and recovery, we measured shell length and width (0.1 mm resolution). From those measurements we derived three field-standard metrics: (1) Shell accretion was the change in elliptical surface area, $\Delta SA = \pi LW/4$, where "L" = shell length and "W" = shell width (both in mm), scaled to a common 120-day interval; (2) We summarized linear shell extension as a daily specific growth rate (SGR) = $100 \times [\ln L_{end} - \ln L_{start}]/t$; (3) We dried and combusted juvenile soft tissue to obtain ash-free dry weight (AFDW); (4) Used these to compute a Walne–Mann condition index (CI) = $1000 \times AFDW / M_{shell}$, where M_{shell} = shell dry mass (mg) was estimated using shell length: $9.8 \times 10^{-5} \times L^{2.97}$ (Lucas and Beninger 1985).

Statistical modeling

To determine how habitat and individual traits influence clam performance, we asked whether juvenile and adult shell accretion (specific growth rate, SGR) differed between clams deployed in plots inside the seagrass canopy and those outside the meadow at bare sites, and whether the relationship between shell accretion and Walne–Mann condition index (CI) varied by habitat. Preliminary analyses showed that our signed-distance metric (distance into or out of the meadow) was near-perfectly correlated with habitat (Inside vs. Outside of the seagrass meadow), and that including chlorophyll-*a* concentration as a covariate did not improve model fit ($\Delta AIC < 2$ and $p > 0.2$). We therefore excluded distance and chlorophyll-*a* as predictors or SGR and CI from the final models (Zuur et al. 2009). To directly compare effect sizes, we rescaled continuous predictors by dividing by their standard deviation (i.e., converted to Z-scores).

We analyzed the daily specific growth rate (SGR) separately for juveniles and adults using generalized linear mixed models (GLMMs) fitted in R 4.3.1 with the *lme4* package (Bates 2010, R Core Team 2024). In both juvenile and adult GLMMs, we regressed SGR vs. habitat with a random intercept for Site to account for unmeasured patch-level heterogeneity. To verify that conclusions were not an artefact of the rate formulation (SGR calculations), we also fit "robustness-check" GLMM models that replaced SGR values with deployment start-end absolute shell length change measurements (mm, ΔL; Table 3.1).

To assess potential drivers of juvenile tissue condition index (CI), we modelled CI as a function of standardized shell surface area accretion (ΔSA), habitat, their interaction, and juvenile SGR, again with a random intercept term for Site. We followed the model-selection protocol of Zuur et al. (2009), beginning with a 'maximal' model that included habitat and the interaction with ΔSA, refitting with maximum likelihood to compare nested candidates, and retaining terms only when they reduced AIC by at least two units or when likelihood-ratio tests indicated significance at the 0.05 level.

Diagnostic plots of residuals and quantile–quantile plots were inspected, and marginal and conditional R^2 values were computed using the *performance* and *DHARMa* R-packages (Lüdecke et al. 2024; Hartig 2024). We report fixed-effect estimates as slopes with 95 % Wald confidence intervals and Satterthwaite-adjusted *p*-values obtained with *lmerTest* (Kuznetsova et al. 2017).

Results

Habitat and shell growth

Juvenile clams grew (daily shell specific growth rate, SGR) significantly faster inside the seagrass meadow than at bare sites outside the meadow. In the mixed model with only a habitat factor ("Inside" or "Outside") and a random "Site" intercept, the mean SGR inside the meadow was 0.125 mm day^{-1}, whereas clams on bare sand grew 0.033 mm day^{-1} (26%) slower (estimate = –0.0329 ± 0.0065 mm d^{-1}, $p = 0.0002$; Table 3.2). The site random effect was very small (SD = 0.0048 mm day^{-1}), and the fixed habitat effect explained about 16% of the variance in juvenile growth (marginal $R^2 \approx 0.17$); adding the random effect increased the conditional R^2 only marginally.

The GLMM accessing adult growth showed no effect of habitat (caged inside vs. outside the seagrass meadow) on adult clam SGR (estimate = –0.01 ± 0.005 mm d^{-1}, $p = 0.334$; Table 3.2). The random "Site" intercept (SD ≈0.012 mm day^{-1}) accounted for about 22% of the total variance (marginal $R^2 = 0.024$, conditional $R^2 = 0.24$), suggesting modest site-to-site heterogeneity related to unmeasured factors.

For both adults and juveniles, "robustness-check" GLMMs using measurements of the absolute shell length change from the start to the end of deployment (mm, ΔL) for both adults and juveniles instead of SGR produced highly similar results (see Table 3.2).

Chlorophyll-a and shell growth (SGR)

Near-bed chlorophyll-*a* concentrations—a proxy for food supply—showed no discernible relationship with juvenile or adult shell growth (SGR). Separate univariate models produced trivial, non-significant slopes for chlorophyll-*a* measured 1-cm and 5-cm above the seabed

(*juvenile SGR vs. 1-cm chl-a:* $\beta = +0.0069 \pm 0.0053$ mm d^{-1} SD^{-1}, $p = 0.22$; *juvenile SGR vs. 5-cm chl-a:* $\beta = -0.0025 \pm 0.0056$ mm d^{-1} SD^{-1}, $p = 0.66$; *adult SGR vs. 1-cm chl-a:* 1-cm $\beta = -0.0045 \pm 0.0039$ mm d^{-1} SD^{-1}, $p = 0.27$; *adult SGR vs. 5-cm chl-a:* $\beta = +0.0004 \pm 0.0041$mm d^{-1} SD^{-1}, $p = 0.92$; Appendix 3.1; Figs 3.3C & 3.4C). Each term increased the marginal R^2 by <1% and failed to reduce AIC ($\Delta AIC < 2$), thus we omitted chlorophyll-*a* from the final mixed-effects models presented in Table 3.2 and from the candidate-model set described in Table 3.1.

Condition index

We calculated Walne–Mann condition indices as 1000 × (ash-free dry tissue weight ÷ predicted shell dry mass), expressing metabolically active tissue as parts per thousand of shell mass. Juvenile *M. mercenaria* deployed at bare sites exhibited higher condition indices (≈55 ± 4‰) than those inside the seagrass meadow (≈32 ± 4‰) after controlling for the shell accretion rate, ΔSA ($p < 0.001$; Table 3.2). However, vegetation strongly influenced how tissue condition responded to shell accretion (ΔSA × habitat interaction $p < 0.001$; Table 3.2). Specifically, in seagrass, CI did not decline with increasing shell surface area ($\beta = -0.0006 \pm 0.002$‰ per 100 mm^2, $p = 0.72$; Table 3.2), indicating that shell growth incurred negligible energetic cost. Conversely, bare-site clams experienced a steep reduction in condition: the ΔSA × habitat interaction term shows that each additional 10 cm^2 of shell area accreted reduced CI by about 6‰ ($\beta = -0.0060 \pm 0.0009$, $p < 0.001$; Table 3.2).

Juvenile SGR had no detectable effect on CI ($\beta = +0.007 \pm 0.071$‰ per mm day^{-1}, $p = 0.92$). Thus, although juvenile clams on bare substrate began the experiment with more tissue

relative to shell, they lost condition as they invested in shell growth, whereas juveniles within the seagrass meadow maintained their tissue reserves across the range of shell accretion observed.

Discussion

This study aimed to address a longstanding question in foundation-species ecology: does seagrass facilitate or inhibit the growth of suspension-feeding bivalves, and does that balance change with life stage or depend on the way in which growth is measured? By coupling centimeter-scale food-supply profiles with a growth experiment of tagged clams held in caged plots arrayed across and outside a 20 km² meadow, we tested the mechanisms proposed for facilitation of juvenile and adult cohorts (Griffiths et al. 2017, Gagnon et al. 2020, Fales et al. 2020). Our experiment revealed that: (1) juvenile clams grew their shells significantly faster inside the seagrass meadow than on bare sediment, whereas adult shell growth rates were uniform across habitats; (2) neither distance from the seagrass meadow edge nor water-column chlorophyll-*a* concentrations explained variability in growth for either life stage; and (3) a trade-off between shell accretion and tissue condition occurred at bare sites—juveniles that invested more in shell growth ended the season with proportionally less tissue—whereas juveniles inside the meadow indicated no such cost.

Juvenile shell growth (SGR) differed habitat, adults did not

Juvenile and adult hard clams (*M. mercenaria*) exhibited differing growth responses based on benthic habitat: juvenile shell growth (SGR) was ~36% faster inside the seagrass meadow than at bare sites over the four-month (May–September) experimental deployment, while adult shell growth did not differ by habitat. However, a random effect (intercept) for site

did slightly improve the adult mixed model fit, suggesting there were weak site-level influences not captured by habitat or location on the landscape in relation to the meadow edge.

Chlorophyll-a: food supply not predictive of growth

Chlorophyll-*a* was unrelated to shell growth (SGR) for either life stage. Univariate models produced trivial, non-significant slopes for samples collected both 1-cm and 5-cm above the seabed, in zone accessible by hard clam suspension feeding (juveniles: $p = 0.22–0.66$; adults: $p = 0.27–0.92$). Including these terms raised marginal R^2 by <1% and failed to reduce AIC ($\Delta AIC < 2$), so they were excluded from final mixed-effects models.

Condition index: seagrass reduces shell growth costs

At retrieval, juvenile clams from bare sites had, on average, soft tissue comprising about 8.4 % of shell mass (range = 2.43–38.6 %), whereas clams from seagrass beds were slightly lower on average (8.05 %) but less variable (range = 5.98–10.8 %). Clams at bare sediment sites exhibited a negative relationship between shell accretion and condition: for every additional square centimeter of shell surface area gained, the percentage of soft tissue fell by approximately 0.66 %, while there was no detectable decline for clams growing inside the seagrass meadow. Thus, although all clams ended the experiment with a similar proportion of tissue, bare site individuals appeared to trade off tissue reserves against shell growth, whereas clams inside seagrass were able to add shell without sacrificing body condition.

Synthesis and conclusions

Together, these results bolster and integrate multiple literature-reported and theorized relationships between bivalves and seagrass. First, they support the notion that *Z. marina* seagrass effects on *M. mercenaria* clam growth are neither universally positive nor strong, instead being highly context-dependent and variable (Gagnon et al. 2020, Fales et al. 2020). Second, while the lack of chlorophyll-*a* effects on clam growth we observed undermine studies suggesting that seagrass-associated food sources (e.g., algal epiphyte sloughed off of seagrass blades; Judge et al. 1993) should benefit these bivalves—especially in oligotrophic settings like our study system (Irlandi and Peterson 1991, McGlathery et al. 2001, Carroll et al. 2008)—other studies indicate that the mean chlorophyll-*a* value range we observed (6–10 $\mu g\ L^{-1}$) may be too low to elicit hard clam growth responses, as it lies completely within the lower shoulder of published growth curves where added phytoplankton has yet to drive sharp increases in deposition or tissue addition—typically at and above 20-$\mu g\ L^{-1}$ (Bricelj and Malouf 1984, Casper et al. 2002, Carmichael et al. 2004). Moreover, a stable-isotope diet analysis indicated that hard clams depend heavily on macroalgae (>50% diet) in our system—which are also highly abundant on intertidal and subtidal mudflats, not just in seagrass meadows (McGlathery 2017, Cox et al. 2020, Besterman et al. 2021). Lastly, life stage adds a possible mechanistic explanation for the high variability among experimental findings. If seagrass-governed growth effects (or relationships between condition and shell accretion rates) are strongest in young, pre-reproductive clams, habitat effects could remain undetected if shell growth measurements are the only response variable—as is common in prior studies (Ansell 1968, Peterson 1984, Arnold et al. 1991, Irlandi and Peterson 1991, Irlandi et al. 1999, Allen and Williams 2003, Carroll et al. 2008, Galván and Puente 2023). However, it is important to consider that clam tissue condition

indices likely reflect late-season (primarily September) chlorophyll-*a* (i.e., food supply) concentrations—which differed between habitats (Fig. 3.2)—whereas shell growth occurred throughout the growing season. Hence, this mismatch in timing may help explain the observed divergence between tissue and shell accretion.

Our findings also echo classic expectations that bivalve growth rates differ with life stage. Small, thin-shelled bivalves typically exhibit growth rates far greater than later-life growth rates—an ontogenetic growth response to extremely-high juvenile mortality (Lucas and Beninger 1985, Peterson and Heck Jr 2001, Abele et al. 2009). In addition, many bivalves—including hard clams—delay reproduction to prioritize shell growth until they attain a size (~30-mm shell length for hard clams *M. mercenaria*) at which predation risk declines significantly (Richards et al. 1999, Kraeuter and Castagna 2001, Meira et al. 2024). The finding that juvenile hard clams exhibited significantly faster shell growth (SGR) in seagrass, while showing reduced metabolic condition outside the meadow, suggests they experienced habitat-related stressors unrelated to predation risk (as all clams were caged), such as reduced food availability (Fig. 3.2). Clam growth may also be suppressed outside of the meadow due to higher suspended sediment concentrations, which require significant energetic expenditure to sort from digestible algae/seston and excrete as pseudofeces (Dame and Kenneth 2011, Specht 2017, Gagnon et al. 2020). Additionally, significantly higher hydrodynamic stressors outside of the flow- and wave-attenuating seagrass canopy may reduce clam growth (Hansen and Reidenbach 2013, Fales et al. 2020).

In sum, our field experiment reveals that *Zostera marina* meadows do not consistently accelerate *Mercenaria mercenaria* shell accretion. While seagrass significantly enhanced juvenile shell growth and appeared to buffer young clams from the tissue-condition costs

incurred at bare sites, habitat failed to elicit a significant response by adults. Growth rates were insensitive to modest differences in chlorophyll-*a* (6–10 μg L^{-1}) across sites, implying that other habitat-mediated processes, such as changes in hydrodynamics or sediment load, rather than just simple food limitation, mediated the observed patterns. These findings caution against evaluating seagrass influence solely through shell accretion and highlight the value of integrating condition indices and life-stage energetics. More broadly, the results suggest that the ecological role of seagrass for suspension feeders may lie less in directly boosting shell growth via autochthonous food resources and more (or equally) in modulating energetic investment strategies and trade-offs that shape juvenile survival and population resilience in these dynamic coastal ecosystems (Griffiths et al. 2017, Gagnon et al. 2020, Fales et al. 2020).

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Figures and tables

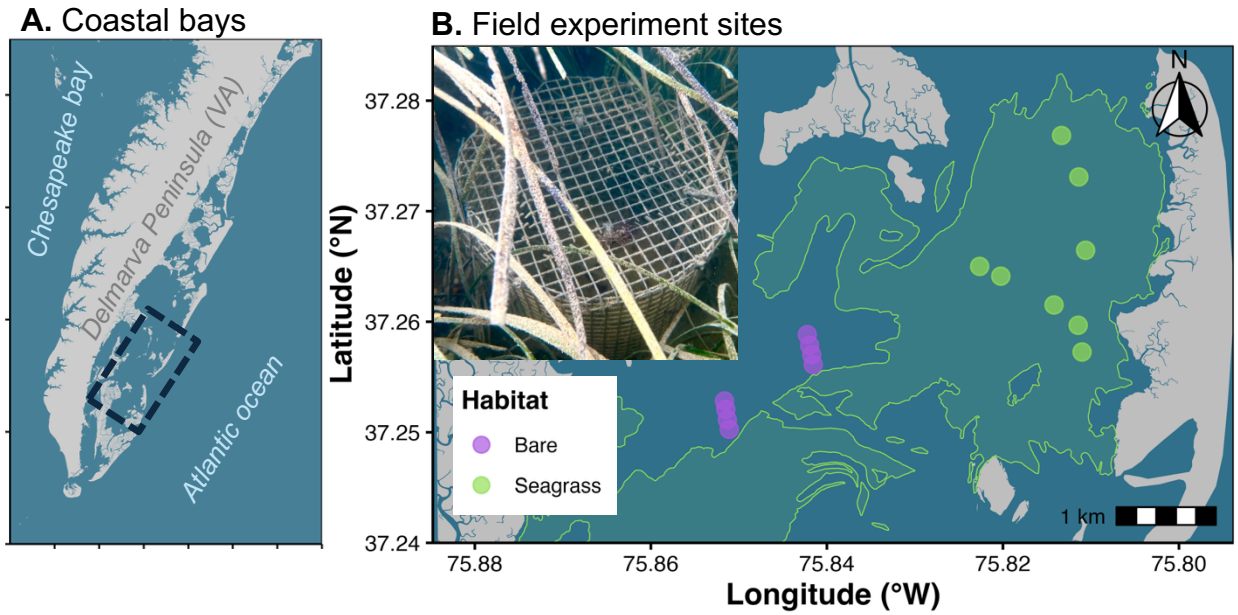


Figure 3.1. ***Coastal bays, seagrass extent, and study sites.*** (A) Delmarva Peninsula, Virginia USA, and the coastal bays on its eastern shore formed by a barrier island system. (B) Seagrass extent (faint green line) within the coastal bay study-system with seagrass-present experimental sites throughout (green) and bare sites (purple) in transects (100-meter) away from meadow edge. Panel B inset in upper left shows a top-down view of a predator-exclusion cage.

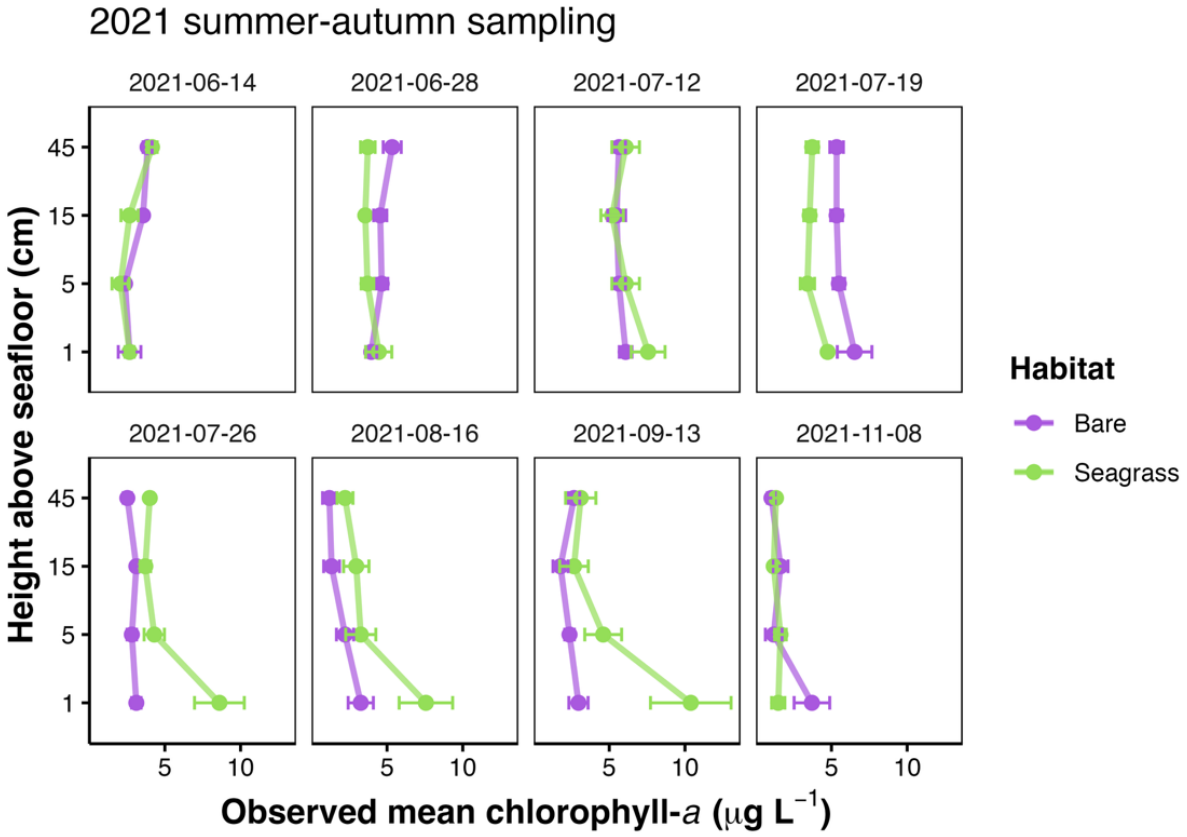


Figure 3.2. ***Stratified water-column chlorophyll-a differed by date & habitat.*** Chlorophyll-*a* (µg L^{-}) water samples taken at 1-cm, 5-cm, 15-cm, and 45-cm above the seafloor revealed habitat and sampling date differences across the clam growth experiment. Most prominent of these was the elevated near-seafloor (1-cm) feature within seagrass between late July and mid-September. Generally, regardless of chlorophyll-*a* concentration differences, a notable observation well-captured in this growth experiment-supporting (and thus summer-biased) sampling regime was the vertical stratification of suspended algal material apparent within the seagrass canopy.

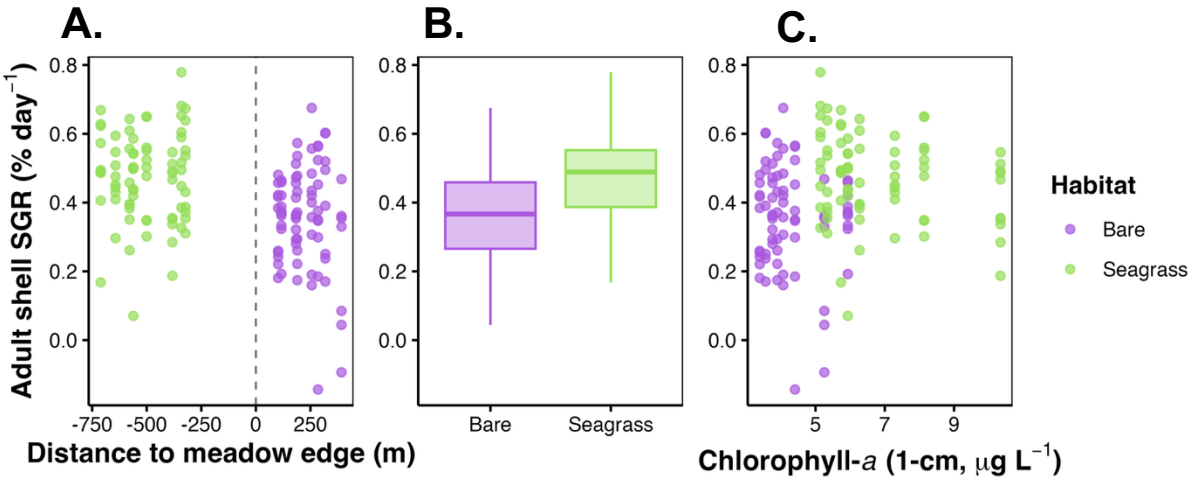


Figure 3.3. ***Juvenile growth by edge distance, habitat, and food supply.*** Juvenile clam shell specific growth rate (SGR; % day^{-1}) by habitat (bare = purple, seagrass = green) and mean observed food supply in the form of chlorophyll-*a* concentrations. (A) SGR of individual clams plotted against the Euclidean distance from the nearest edge of the seagrass meadow; dashed line at 0-m marks the meadow boundary. (B) Distribution of SGR in seagrass versus adjacent bare-seafloor sites. Box plots show the median (center line), inter-quartile range (box), and 1.5 × IQR whiskers. (C) SGR vs. mean near-bottom chlorophyll-*a* concentrations at 1-cm above seafloor during May–October (μg L^{-1}).

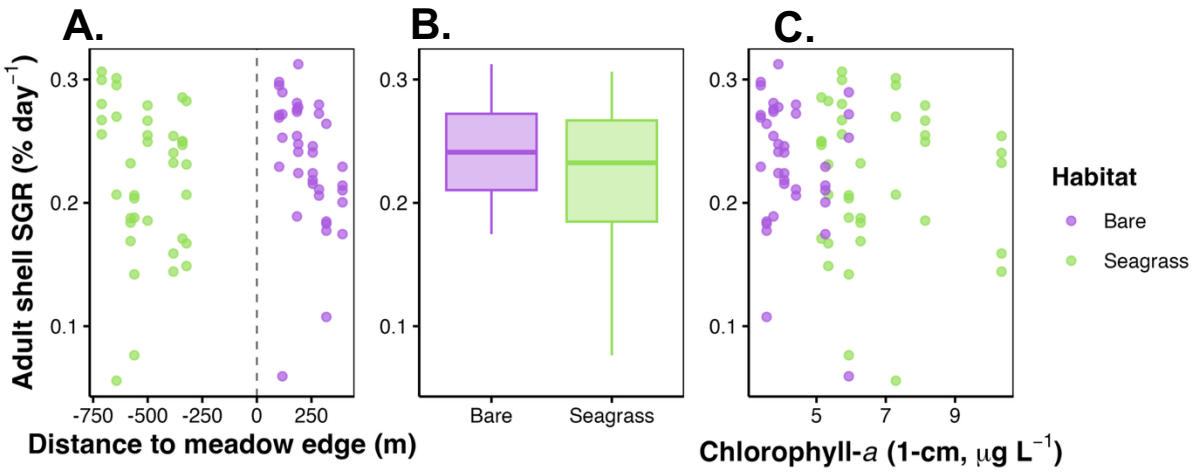


Figure 3.4. ***Adult growth by edge distance, habitat, and food supply.*** Adult clam shell specific growth rate (SGR; % day^{-1}) by habitat (bare = purple, seagrass = green) and observed food supply in the form of chlorophyll-*a* concentrations. **(A)** SGR of individual clams plotted against the Euclidean distance from the nearest edge of the meadow; vertical dashed line at 0-m marks the meadow boundary. **(B)** Distribution of SGR in seagrass versus bare-seafloor sites. Box plots show the median (center line), inter-quartile range (box), and 1.5 × IQR whiskers. **(C)** SGR versus mean near-bottom chlorophyll-*a* concentrations at 1-cm above seafloor during May–October (μg L^{-1}).

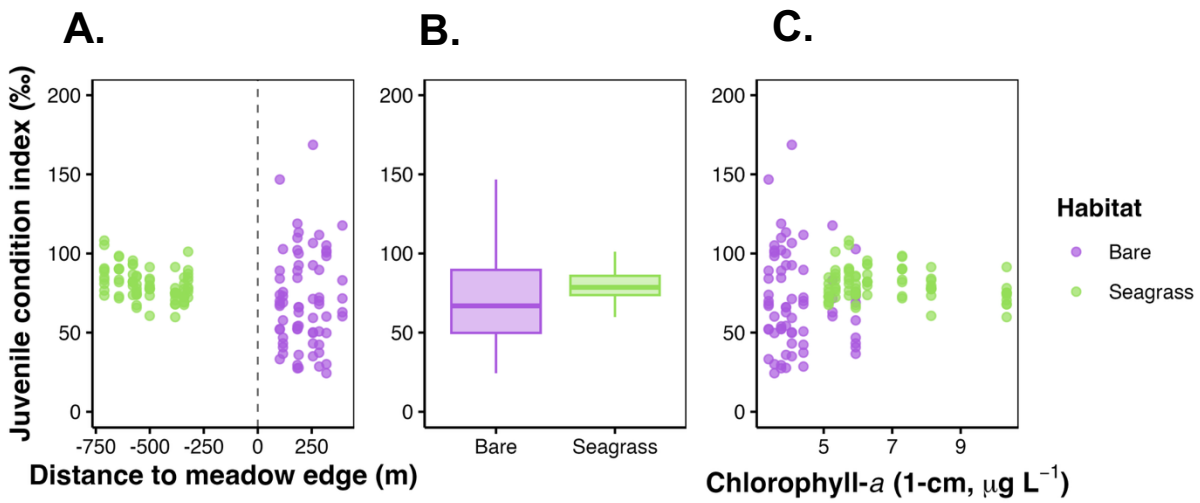


Figure 3.5. ***Juvenile condition indices by edge distance and habitat.*** (A) Walne–Mann condition indices (CI, ‰ = 0.1 % tissue per unit mass of shell) at experiment end for each individual juvenile plotted against the Euclidean distance from the nearest seagrass meadow edge; the dashed vertical line at 0-m marks the meadow boundary, bare = purple, seagrass = green. (B) Distribution of CI in seagrass versus bare sites. Box plots show the median (center line), inter-quartile range (box), and 1.5 × IQR whisker. **(C)** CI versus mean near-bottom chlorophyll-*a* concentrations at 1-cm above seafloor during May–October (μg L^{-1}).

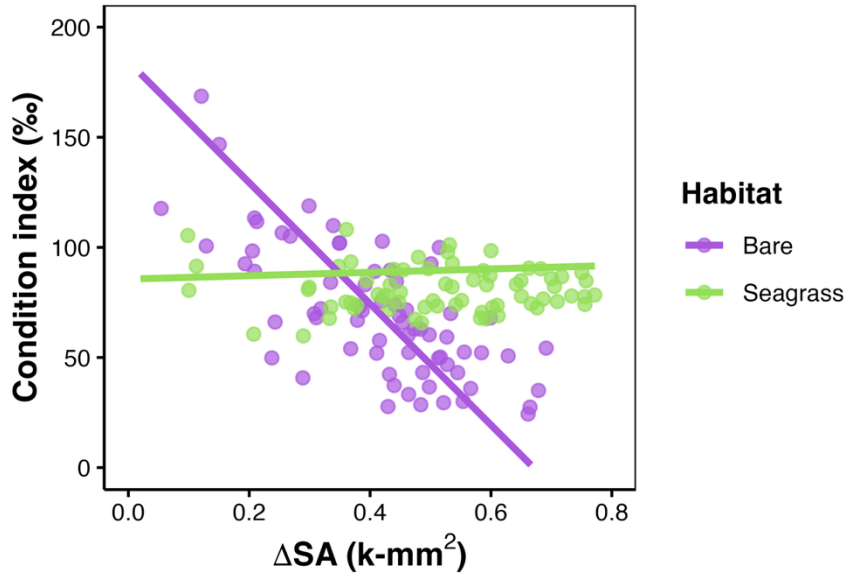


Figure 3.6. ***Condition index vs. shell accretion: a habitat-driven tradeoff.*** Each point represents the final condition index (CI) of an individual juvenile hard clam, solid lines show the fitted mixed-effects models for bare (purple) and seagrass (green) habitats. The *x*-axis is shell accretion (ΔSA), expressed as the change in elliptical surface area per clam and scaled to 1-cm² increments (100 mm²); the *y*-axis is the Walne–Mann condition index expressed as a percentage of soft tissue relative to shell mass. On bare sand, CI declines by roughly 0.66 % for each additional cm^2 of shell accreted ($\beta \approx -0.0066 \pm 0.0009$ % cm^{-2}, $p < 0.001$), suggesting an energetic cost of calcification. The habitat × ΔSA interaction term shows that this decline is absent within the seagrass meadow; clams inside the canopy can enlarge their shells without the drop in condition those at bare sites exhibited.

Model	Response (units)	Fixed effects† (all *z*-scored)	Interaction(s)	Random intercept terms	*n*
Juvenile SGR	Length SGR (mm day^{-1})	Habitat	—	Site	151
Adult SGR	Length SGR (mm day^{-1})	Habitat	—	Site	77
Juvenile CI	Walne–Mann CI (ratio)	ΔSA (k mm^2 120 days^{-1}), Habitat, SGR	ΔSA × Habitat	Site	151
Juvenile and Adult ΔL‡	Length gain (mm per 120 days)	Habitat	—	Site	151

Table 3.1. ***Model structures testing habitat-scale controls on hard-clam performance.*** Model structures testing the controls on hard-clam growth performance. Habitat denotes a binary variable representing clams grown inside vs. outside of the seagrass meadow (reported as Outside – Inside). Continuous covariates were Z-scored (centered and scaled to mean = 0 and SD = 1) to directly compare effect sizes across predictors. Signed distance to the meadow edge and chlorophyll-*a* covariates were dropped from the specific growth-rate models because they neither reduced AIC (ΔAIC < 2) nor reached significance. The "ΔL" models (for juvenile and adults) replaces the specific growth-rate (SGR) response with absolute length gain to verify that conclusions are not an artefact of the rate formulation.

Model	Term	Estimate (±SE)	*t* (df)	p-value	R^2_m	R^2_c
Juvenile SGR	Intercept	0.125 ± 0.005	27.6 (12.5)	**< 0.001**	0.165	0.179
	Habitat (Outside – Inside)	–0.033 ± 0.006	–5.11 (12.9)	**0.0002**		
Adult SGR	Intercept	0.099 ± 0.004	25.3 (15.2)	**< 0.001**	0.000	0.223
	Habitat (Outside – Inside)	–0.01 ± 0.005	–1.00 (14.25)	0.334	0.024	0.24
Juvenile CI	Intercept	0.032 ± 0.004	8.93 (124)	**< 0.001**	0.438	N/A
	ΔSA (100 mm²)	–0.00061 ± 0.00171	–0.36 (130)	0.72		
	Habitat (Outside – Inside)	+0.023 ± 0.00436	5.31 (115)	**< 0.001**		
	SGR (len_day)	+0.0073 ± 0.0710	0.10 (128)	0.92		
	ΔSA × (Outside – Inside)	–0.00597 ± 0.00090	–6.64 (146)	**< 0.001**		
Juvenile ΔL‡	Intercept	12.98 ± 0.56	23.13 (12.1)	**< 0.001**	0.034	0.073
	Habitat (Outside – Inside)	–1.60 ± 0.80	–2.00 (12.4)	0.068		

Table 3.2. ***Final mixed-model outputs***. Coefficients and goodness-of-fit statistics for the final mixed models. Each row gives the estimate (β ± standard error, SE), the *t*-statistic with estimated degrees of freedom in parentheses, the two-tailed *p*-value, and marginal (R^2_m) and conditional (R^2_c) R-squared values. Both the juvenile and adult SGR models compare growth inside (baseline) vs. outside the seagrass meadow such that a negative coefficient indicates slower growth outside. The juvenile CI model showed that although baseline condition is higher outside the meadow, condition declines steeply with increasing shell accretion outside, whereas the slope is much shallower inside the meadow. The robustness ΔL model shows that using absolute length gain instead of SGR yielded a qualitatively similar habitat effect, albeit marginally non-significant (p = 0.07). ‡ ΔL = shell length (mm) over the deployment period. Boldface denotes significant *p*-values (< 0.05).

Appendix

Life stage	Depth	Term	Estimate ± SE	*t* (df)	*p*-value	R^2_m	R^2_c
Juvenile	1 cm	Intercept	**0.108 ± 0.005**	20.69 (13.5)	**< 0.001**	< 0.01	**0.18**
		scale(chl_1)	+0.0069 ± 0.0053	1.30 (13.2)	0.22		
Juvenile	5 cm	Intercept	**0.108 ± 0.006**	19.63 (13.6)	**< 0.001**	< 0.01	**0.20**
		scale(chl_5)	–0.0025 ± 0.0056	–0.46 (13.3)	0.66		
Adult	1 cm	Intercept	**0.099 ± 0.004**	25.51 (14.3)	**< 0.001**	< 0.01	**0.22**
		scale(chl_1)	–0.0045 ± 0.0039	–1.15 (13.9)	0.27		
Adult	5 cm	Intercept	**0.099 ± 0.004**	24.42 (14.2)	**< 0.001**	< 0.01	**0.24**
		scale(chl_5)	+0.0004 ± 0.0041	0.11 (13.8)	0.92		

Appendix 3.1. ***Near-bed chlorophyll-a and clam growth (SGR).*** Univariate mixed-effects models assessing whether water-column chlorophyll-*a* concentration at 1-cm or 5-cm above the seabed explains length specific-growth rate (SGR) in juvenile or adult hard clams. Each model consists of a single scaled chlorophyll-*a* term and a random intercept for Site (16 levels; $n = 151$ juveniles, 77 adults). Values shown are the fixed-effect estimate ($\beta \pm SE$), the *t*-statistic with estimated degrees of freedom (in parentheses), *p*-value, and marginal (R^2_m) and conditional (R^2_c) R-squared value. Across both life stages and depths, chlorophyll-*a* terms are small ($|\beta| \leq 0.007$ mm d^{-1} SD^{-1}), non-significant ($p \geq 0.22$), and raise R^2_m by <1%. Thus, variation in near-bed food supply as indexed by chlorophyll-*a* does not explain clam growth; hence, these chlorophyll covariates were excluded from the multivariate habitat–distance models in the main text (Table 3.2). Boldface denotes significant *p*-values (< 0.05).

Chapter 4. Climate variability, not ecosystem state, governs long-term productivity in seagrass-dwelling clams

Anticipated authors of peer-reviewed manuscript:

Michael R. Cornish

Max C.N. Castorani, PhD

Abstract

Species-habitat associations and short-term experiments suggest that seagrass meadows generally enhance bivalve growth, but this topic is unexamined over long timescales relevant to organismal lifespans and population dynamics. We used sclerochronology methods to construct a novel > 40-year (1976–2020) shell-growth chronology from the growth increment widths of 77 hard clams (*Mercenaria mercenaria*) collected from coastal bays in Virginia, USA, across a 20 km^2 chronosequence of restored *Zostera marina* seagrass expansion. March–August SST anomalies alone explained 50–57 % of standardized growth index (SGI) variance; a +1 °C anomaly increased shell deposition by ~6–8 %. Adding contemporaneous or lagged seagrass meadow area, year-to-year meadow extent change, or distance to the meadow edge did not improve model nor explain enough to variance to distinguish from background variability (R^2 <1 %). In a population-level master growth chronology, the interannual SST anomaly link was stronger before 1999, but remained significant thereafter despite regional warming of ~0.25 °C $decade^{-1}$. Nine site-level chronologies across the lagoon replicated the pattern: SST effects dwarfed habitat terms by two to three orders of magnitude. Hence, regional climate variability emerged as a strong predictor of annual shell deposition whereas a system-wide state change from an unvegetated seafloor to recovery of the world's largest restored seagrass meadow had minimal influence. This study provides novel long-term empirical evidence that climate forcing can outweigh local habitat effects in seagrass–bivalve interactions—underscoring the dominant role of large-scale climate forcing in controlling and synchronizing coastal organismal growth and secondary productivity.

Introduction

Benthic-pelagic coupling—the bidirectional exchange of nutrients, mass, and energy between the water column and seafloor—underpins the high productivity of many coastal ecosystems (Nixon 1988, Griffiths et al. 2017). Among the classic examples of this process are suspension-feeding bivalves that transfer pelagic nutrients to benthic plants and energy to higher-order consumers (Norkko et al. 2001, Griffiths et al. 2017, Peters et al. 2019). For instance, hard clams (*Mercenaria mercenaria*) enhance seagrass productivity by clarifying bottom light and excreting nutrients that can limit plant growth (Orth et al. 1984, Irlandi 1997, Barbier et al. 2011, Fales et al. 2020). However, evidence that seagrass reciprocates benefits to clams has mixed support. Field predation and growth experiments (all <2 years) suggest that seagrass reduces hard clam predation and may boost growth rates (Irlandi and Peterson 1991a, Irlandi 1996b, 1997). However, other studies find no effect or even negative growth rate responses to seagrass (e.g., Johnson and Heck 2007). Notably, studies following clam growth over longer durations are lacking, despite the long lifespan of hard clams—which can live for decades to more than a century (Ridgway et al. 2011). And, because clam growth slows dramatically as clams age, and wild clams are challenging to source from natural populations in numbers needed for experimental replication, growth studies have focused on very young hatchery-reared clams (usually <3 years) whose growth responses may not represent those at the population scale. Moreover, multiyear to multidecadal climate oscillations that govern growth in many long-lived bivalves over broad spatial scales (Black 2009) have not been explicitly considered in seagrass-bivalve studies (Fales et al. 2020).

Instead, seagrass-bivalve studies have largely centered on ecological processes over local to landscape scales (e.g., centimeters to hundreds of meters), such as habitat structure,

hydrodynamics, predator density, and food availability (Fales et al. 2020). These are difficult to manipulate in situ at relevant scales (Judge et al. 1993, Chacin and Stallings 2016) without creating confounding effects (e.g., seagrass density affects predator density and behavior; Lannin and Hovel 2011, Mccloskey and Unsworth 2015). Thus, results from one locale may not translate to others (Peterson & Beal 1989; Irlandi 1996; Johnson & Heck 2007). Additionally, ontogenetic growth deceleration is region-specific and may contribute to among-study variability (Ansell 1968; Heino & Kaitala 1996). Collectively, these challenges to studying seagrass-bivalve interactions may help explain why short-term, small-scale experiments have yielded inconsistent outcomes and underscore the need for long-term, broad-scale observations to disentangle habitat and climate effects (Fales et al. 2020).

To help close these knowledge gaps and resolve how clam shell growth responds to interannual climate variability and a large-scale ecosystem state change to seagrass dominance in a coastal lagoon, we collected hard clams of various ages across a historically documented chronosequence representing the world's largest successful seagrass restoration (Fig. 4.1). We then applied shell sectioning (Hemeon et al. 2021) and increment time-series-validation methods (i.e., "crossdating"; Black et al. 2008) to extract a 45-year record (1976–2020) of highly-resolved annual shell growth measures. As detailed below, we fit multiple statistical models across various spatial and temporal scales to quantify and, to the extent possible, disentangle the possible effects of temperature and seagrass restoration on clam growth. Our novel approach revealed that local to regional climate variability over interannual and decadal timescales, not ecosystem state, dominates long-term hard clam growth.

Methods

Seagrass data and clam collection

In October 2020, we collected 197 hard clams from 50 sites distributed across a ~20 km² seagrass (*Zostera marina*) meadow within South Bay, Virginia, USA, a lagoon focal to the Virginia Coast Reserve Long Term Ecological Research project (VCR LTER; Fig. 4.1). The bays are shallow (~1 m mean sea level), high-salinity (29–32 PSU), and oligotrophic (McGlathery et al. 2007; McGlathery & Christian 2024). Disease extirpated seagrass from the region in the 1930s. In the early-2000s, a reseeding campaign yielded the world's largest successful seagrass restoration (Orth et al. 2022). The gradual expansion of the meadow created a unique time-since-restoration chronosequence ('meadow age') over which we stratified our sampling sites with restricted randomization (5 sites within each of 10 meadow-age layers, 2001–2019; Fig. 4.1). We determined meadow age using 13 seagrass polygon layers that we developed using QGIS from aerial imagery collected by low-altitude airplane every 1–4 years by the Virginia Institute of Marine Science Submerged Aquatic Vegetation Monitoring Program (VIMS SAV; 2024). At each site, we collected all live clams by snorkel along a 100-m × 0.5 m swath-transect using a 14-cm clamming fork (50 m^2 per site; 2,500 m^2 total).

In a preliminary investigation into the effect of bay-wide meadow extent on clam growth, we found a significant relationship between the overall extent of the meadow (from the VIMS SAV time series maps) and the distance of each sampling site from the meadow edge. To avoid conflation between these two variables in subsequent models predicting clam growth, we computed the 'residual' seagrass area—statistically independent of a site's position relative to the meadow edge—by extracting the raw residuals from an ordinary least-squares regression of total meadow area in a given year on the signed edge distance for each site in each year (negative =

distance into the meadow from the edge; positive = distance away from the meadow edge). In doing so, we eliminated the collinearity that arises as sites become closer to the meadow interior as the seagrass meadow expanded (Fig. 4.1). The result were two orthogonal predictors: signed edge distance described the distance from the meadow edge while residual seagrass area captured year-to-year expansion (or, sometimes, contraction) of the entire meadow across the bay. This separation allowed us ask in an unbiased way whether clam growth responds to structural refuge at the patch edge, broader fluctuations in the amount of habitat, or both (Jelbart et al. 2006, Boström et al. 2011).

Sample preparation

We removed soft tissues from all specimens and dried valves at 60 °C. We sectioned each left valve from hinge to growing edge with a wet tile saw. We sanded and polished these using a Buehler® EcoMet 30 grinding/polishing machine with sequential 240-, 320-, 400-, and 600-grit sanding papers followed by 6-µm and 1-µm polycrystalline diamond-suspensions (Hemeon et al. 2021).

To quantify annual growth in each shell section, we measured annual increment widths to the nearest 0.5-µm from photomosaics constructed (using Nikon® NIS-Elements D® software) from a camera-mounted dissecting microscope (Nikon® DS-Fi3 with 1X-zoom SMZ 800N). While acetate peel replicas of sectioned value are traditionally used for age/growth determinations of hard clams (Fritz 1982, Arnold et al. 1991, Kraeuter and Castagna 2001a), we found these to be unreliable for many samples—indicated by poor agreement among shell timeseries during initial cross dating steps (described below). However, terminal bands—small, translucent increments deposited from late autumn to early spring in the U.S. Mid-Atlantic (Fritz

1982)—were significantly enhanced by immersion for 5–15 min in Mutvei's solution (Schöne et al. 2005), which lightly etches calcium carbonate and preferentially stains the organic matrix most-prevalent in fast-growth shell deposition. This method proved best at consistently revealing the autumn/winter annuli increments (Fig. 4.1B) by enhancing the contrast between etch/stain-resistant cessation lines and dark blue growth bands that largely correspond with spring (Fritz 1982).

Cross-dating and growth chronology construction

First, we visually cross-dated annual increments by iteratively identifying and aligning anchor years among individuals, using this to begin initial timeseries-shifts, identify missing or erroneous increments, and resolve their temporal range/location. After repeating this process numerous times and obtaining initial groups of visually-synchronous timeseries, we used the standard dendrochronology-derived methods in the *dplR* R-package (Bunn 2008) to build preliminary standardized growth chronologies from 50%-frequency spline–detrends of the individual time series before subjecting them to quality control thresholds (Fig. 4.2-A: inter-series correlation (*R-bar*) ≥ 0.20, expressed population signal (EPS) ≥ 0.85— both computed with 15-yr sliding windows—and Gleichläufigkeit (GLK), a field-standard measure of interannual synchrony (Fig. 2; Wigley et al. 1984; Black et al. 2010). Because over half (112/197) of the processed valves were <10 years old and <5% of valves (8/197) exhibited unclear annual increments (and therefore were unsuitable for chronology reconstruction; Black et al. 2008), we restricted subsequent analyses to the remaining 77 shells (77/197 = 39% of total) that yielded the high quality timeseries (age range = 14–45 years). These were detrended with a negative-exponential function, converted to standardized growth indices (SGIs), and combined

with Tukey's bi-weight robust mean (using the R-package *dplR;* (Bunn 2008) to produce a single population-level master SGI chronology (representing all 77 shells) and 9 site-level master SGI chronologies (one for each of 9 sites from which the 77 shells were collected; 5–23 shells per site).

Ocean climate data

We compiled a novel daily sea surface temperature (SST) array for 1961–2021 by merging records from the Virginia Institute of Marine Science Eastern Shore Laboratory (1961–1981; Ross & Snyder 2024) with daily means from NOAA station 831044 in Wachapreague, Virginia (37.61 °N, 75.69 °W; 1982–2021; Wiberg 2021) based on their mean daily value. The composite series tracked temperatures of the lagoon in which we made collections (Wiberg 2023). We converted monthly means to anomalies (SSTA) by subtracting the 1961–2020 climatological mean for the matching calendar month.

To identify the thermal seasonality most-predictive of annual hard clam growth (SGI), we leveraged the *climwin* R-package (Bailey and Van De Pol 2016) to apply a "climate window sweep" approach in which all possible month combinations summing to a 3–6-month window are correlated with an SGI chronology (whole-population or site-level) towards finding the Pearson-r correlation-maximizing "best" window. Before conducting these climate sweeps, we pre-whitened both the anomaly and SGI using AR(1) residuals—i.e., fitting a first-order autoregressive model to address spurious relationships from serial dependence (Wigley et al. 1984, Black 2009).

To extend this further and investigate whether hard-clam growth integrates discrete spring and autumn thermal cues, we exhaustively assessed every possible pair of non-

overlapping 3-month SST-anomaly windows within each calendar year (Fritz 1982, Shirai et al. 2018). For each candidate pair, anomalies were first averaged within each window and then combined (simple mean) to form a composite annual SSTA index. Hence, we compared Pearson-r between the pre-whitened residuals of each composite index and the lagoon-wide SGI chronology.

Overview to the statistical analyses

We carried out three sets of statistical analyses to determine how SST and seagrass restoration affected clam growth, each differing in the spatial and temporal scale of the data and predictor variables (summarized in Tables 4.1–4.2). These decisions are explained in detail below, but presented here at a high level to justify our modeling choices and explain why they increase the robustness of our conclusions.

We first fit a (1) 'lagoon-scale' model to an among-sample average of all data available from suitable specimens (n = 77 clams gathered from 9 sites) across all possible years (1976–2020). The goal of this model was to quantify how SST and restoration-driven seagrass recovery at the scale of the entire system affect clam growth based on a single time series that represented the longest duration of available data and minimized the influence of site- and individual-level variability (at the cost of spatial replication). Because distance to the seagrass meadow edge could not be calculated prior to the restoration of seagrass in 2001, site-level variation in the distance to the seagrass meadow could not be considered in this first modeling framework and, moreover, we used all samples pooled together as an average for each time point. Thus, only the bay-wide extent of seagrass or its year-to-year change could be included.

Therefore, we also fit two types of 'within site-scale' models: (2) First, we build individual models for each of the 9 sites to ask how SST, distance to the seagrass meadow edge, and the residual area of seagrass affect clam growth during the period 2001–2020 (after the start of restoration and when maps of the seagrass meadow distribution were available). Data from each site was modeled independently based on the assumption that if seagrass effects are strong, they should be quantifiable in clam growth at all or most sites. Thus, we compared the results of individual models fitted to data for each of the 9 sites to evaluate the weight of evidence in favor of an effect of a predictor.

Lastly, (3) we fit 'among site-scale' models by analyzing data from all 9 sites (2001–2020) in a single model. The data between the 'within site-scale' and 'among site-scale' models were the same, except in the former each site was modeled separately and in the latter all sites were pooled as replicates in the same model.

This bifurcating site-scale analysis approach balanced two risks: First, when fitting multiple models there is an increased risk of committing Type I errors—rejecting a true null hypothesis (e.g., "proximity to seagrass has no effect on clam growth") and concluding that there is a significant effect or relationship when there is not one. If an observed relationship between clam growth and a predictor is significant for one site, but rarely found at other sites, we may conclude that the relationship is spurious. Therefore, the first set of site-scale models fit to data from individual sites ('2', above) could be considered conservative when conclusions are drawn from the aggregate behavior of all 9 models (e.g., asking, 'Is a certain predictor statistically important to clam growth in all or most models?'). The second risk, however, is that limitations in the amount of data (low statistical power), constraints to the distribution of data with respect to both response and predictor variables (e.g., Simpson's Paradox), and potential conflation

between variables increases the risk of committing Type II errors—failing to reject a false null hypothesis and thereby missing a significant effect that is actually present. The second set of site-scale models is better suited to overcoming these challenges. Hence, exploring both 'site-scale' modeling frameworks balanced these tradeoffs.

Lagoon-scale chronology analysis

We constructed a single, lagoon-wide hard-clam growth chronology to evaluate how multi-decadal climate variability and the 20 km² seagrass expansion (Fig. 4.1) modulated clam productivity over larger spatiotemporal scales. To this end, we aggregated all detrended increment series (n = 77) for three key purposes. First, it maximized temporal coverage; the oldest shells, which extend the record back to 1976, seldom co-occurred with the ≥ 5-clam threshold necessary for robust site-level chronologies (as determined by the beforementioned R-bar, EPS, and GLK thresholds; Fig. 4.2-C,D; Black et al. 2008). Second, this whole-dataset aggregation dampened small-scale, site-level variability in favor of synchronized lagoon- or basin-scale driver signals (that may represent a Moran effect; Moran 1953). Third, because each individual series was detrended with a modified negative-exponential function, a procedure that retains both inter-annual variability and some of the low-frequency (decadal) component of growth, multidecadal ecosystem state and oceanographic climate effects might be found in this bivalve growth record (Black et al. 2008, Black 2009, Campana et al. 2023).

To do this, we compiled all cross-dated individual-clam timeseries (n = 77), spanning the years 1976 to 2020, to produce a single, population-level standardized growth index timeseries (Fig. 4.2-A) in R using the *dplR* package (Bunn 2008) "master chronology" building functionality—a Tukey's bi-weight robust mean-based population signal. To obtain a continuous

annual bay-wide seagrass meadow area time series aligned with the entire modeling period, we generated a complete annual sequence spanning the earliest to latest years of the clam growth chronology; pre-2001 values for seagrass area were set at 0-ha because seagrass was absent from the 1930s until restoration was initiated in 2001 (Orth et al. 2022). Because VIMS SAV flights were not completed in some years, we gap-filled missing measurements of annual seagrass area by linear interpolation in R with the *zoo* package (Zeileis et al. 2004).

We evaluated the lagoon-wide chronology with a nested sequence of generalized least-squares (GLS) models (shown in Table 4.1), each fitted with a first-order autoregressive residual structure (corAR(1)) to accommodate temporal autocorrelation (Wigley et al. 1984, Barber et al. 2019). The baseline model, GLS1, tested how ocean temperature alone affects shell growth by regressing the standardized growth index (SGI) on the late-spring–summer SST anomaly ($SSTA_{(z)}$). To directly compare effect sizes of different variables, we Z-scored all predictors in this and in subsequent models (i.e., centered by subtracting the mean and normalized dividing by the standard deviation). GLS2 added as a predictor the Z-scored contemporaneous, bay-wide residual seagrass area ($SG_{(area\ z)}$; described above) to evaluate whether absolute habitat extent affects growth. GLS3 substituted $SG_{(area\ z)}$ with the annual change in area ($\Delta SG_{(area)}$) to gauge sensitivity to year-to-year meadow expansion or contraction. To estimate potential physiological or trophic carry-over effects from year to year, GLS4 and GLS5 modeled shell growth as a function of $SSTA_{(z)}$ and the one- or two-year lags of $SG_{(area\ z)}$, respectively. GLS6 combined both main effects of $SSTA_{(z)}$ and $SG_{(area\ z)}$ with their two-way interaction to test meadow area and temperature sensitivity mediate each other's effects. These models are compared in Table 4.1.

At each step, we retained the more complex model only when the additional term(s) were significant ($p < 0.05$) and lowered AIC relative to the simpler model fitted to identical observations. To evaluate whether a more flexible, non-linear approach would outperform our GLS model, we also fit a thin-plate spline generalized additive mixed-effects model (GAMM) with $SSTA_{(Z)}$ as the predictor. We retained the GAMM only when leave-one-year-out cross-validation (LOOCV) increased predictive R^2 by ≥ 0.02 relative to the best GLS formulation; we calculated LOOCV R^2 from predicted versus observed SGI (Zuur et al. 2009, Bueno de Mesquita et al. 2021).

To test for non-stationary relationships—characteristic of ecological responses to climate (Bueno de Mesquita et al. 2021), we split the master SGI series into two periods of nearly equal duration: early (1976–1998) and late (1999–2020) (Gröger et al. 2011). Within each, we repeated the window sweep and GLS procedures (AR(1) pre-whitening and correlation) to detect period-specific SSTA predictors and slope differences between periods. We further examined the stability of the climate–growth relationship over time using a 15-year moving window analysis: for each centered period we computed absolute pre-whitened correlation and GLS-derived slopes with AR(1).

For all GLMMs and GAMMs, we ensured that residuals conformed with model assumptions using diagnostics on simulated residuals in R using the *DHARMa* package (Hartig 2024; full sensitivity analyses in Appendix 4.1B). These diagnostics showed no issues with normality, uniformity, or dispersion issues (Table 4.3).

Within site-scale GLS modeling

For the shorter 2001–2020 site-level chronologies (after seagrass restoration was initiated and for which data on the seagrass distribution were available), we adopted a streamlined modeling hierarchy to conserve statistical power (shown in Table 4.2; Black 2009). For each of the 9 site-level chronologies, we fit the following types of models (i.e., 9 models fit for each type of model below denoted C_1, C_2, and C_3, yielding 27 total models). The baseline model (C_1) mirrored the lagoon-scale modeling approach by regressing each site's standardized growth index (SGI) on the Z-scored late-spring–summer SST anomaly ($SSTA_{(z)}$). Model C_2 added the Z-scored signed distance from each site to the nearest meadow edge estimated for each year ($Distance_{(z)}$) to test whether clam shell growth varies with distance from the ecotone. We hypothesized that growth would have a negative relationship with distance outside the meadow (a negative coefficient) if beneficial flow attenuation or predator refuge strengthens towards the meadow interior. Model C_3 replaced $Distance_{(z)}$ with meadow area ($Area_{(res)}$), asking whether the estimated bay-wide area of the meadow for each year conveys information beyond spatial position of a site relative to the meadow edge; a positive slope might indicate food-retention benefits of larger patches. This model used the 'residual' seagrass area (defined above) to avoid conflation between the meadow area and the distance to the meadow edge.

As in the lagoon-scale analysis, we retained an added predictor only when it both reduced AIC ($\Delta AIC < 0$) and remained individually significant ($p < 0.05$). Every model incorporated a corAR(1) residual structure to absorb first-order temporal autocorrelation. Because each GLS was fit to a single site and thus within-model spatial autocorrelation impossible, we conducted a Moran's I test on the pooled residuals. All site-level GLS models were specified and evaluated using the same structure and diagnostics as the lagoon-scale models (see above). As with GLMM

and GAMM diagnostics, we found no issues with the normality, uniformity, or dispersion of GLS model residuals (Table 4.3).

Among site-scale GLS modeling

To further evaluate whether proximity to the seagrass meadow margin exerted an influence on clam growth, we analyzed all 9 site-level SGI timeseries in a single GLS model framework (Table 4.5). Pooling preserved the full year-to-year variability at each location while an AR(1) structure nested by Site accounted for repeated measures and residual autocorrelation without imposing separate fits for each chronology.

All analyses were conducted in R using the *nlme, MuMIn, zoo, mgcv,* and *DHARMa packages* (Bates et al. 2003, Zeileis et al. 2004, Bartoń 2025, Hartig 2024).

Results

Lagoon-scale chronology

A GLS model with an AR(1) residual structure linking the population-level SGI chronology to March–August SST anomalies ($SSTA_{Mar–Aug}$) explained 50% of the likelihood-based variance ($R^2_{LR} \approx 0.50$) and had Pearson r = 0.61, $p < 0.0001$ (Fig 4.3B). The slope was strongly positive ($\beta = 0.25 \pm 0.05$ SE, $p < 0.001$) and remained robust after cross-validation (RMSE ≈ 0.62 z units; LOOCV $R^2 \approx 0.20$). An exhaustive block search (i.e., repeated testing of different month combinations for 2- and 3-month windows) identified a Mar–Apr–May plus Sep–Oct–Nov anomaly pair as the optimal six-month composite. Replacing $SSTA_{Mar–Aug}$ with this dual-window index increased explanatory power from 50% to 57% ($\Delta AIC = –7.7$; $\beta = 0.33 \pm 0.06$, $p < 10^{–6}$; Table 4.4). Adding contemporaneous seagrass area ($SSTA_{Mar–Aug}$ + Area)

did not improve fit (ΔAIC = +3.6; β_{Area} = –0.03 ± 0.18; likelihood-ratio test, p = 0.87). This result held when the dataset was restricted to 2001–2020, the period with complete habitat data: the temperate-only model (β = 0.24 ± 0.06) outperformed all variants that included residual seagrass meadow area, the year-to-year change in residual seagrass meadow area, 1–2 year lags of residual meadow area, or an interaction term between residual seagrass meadow area and temperature (each ΔAIC ≥ +1.8: Table 4.4).

Dividing the chronology in half revealed stronger temperature control before 1999 (β = 0.42 ± 0.09, R^2_{LR}≈ 0.66) than after (β = 0.23 ± 0.09, R^2_{LR} ≈ 0.60). A 15-year moving-window analysis confirmed this change: The absolute value of the Pearson correlation coefficient (|r|) peaked at 0.80 in 1985–1995 and declined to 0.55 in the 2000s (1995–2015). Spring anomalies explained most shared variance in both eras (unique R^2 ≈ 0.28 pre-1999; R^2 ≈ 0.21 post-1999), with autumn contributing a smaller but consistent share (≈ 0.08; Appendix 4.A).

Site-level SGI chronologies

Nine site-level chronologies (2001–2020; Fig. 4.2B) analyzed in the 'within site-scale' framework echoed the lagoon-wide pattern. Climate-only GLS models were best at every site; adding signed distance to the seagrass meadow edge worsened model parsimony (ΔAIC = +13–17; Appendix 4.B) and adding meadow extent further diminished model parsimony (ΔAIC = +13–15; Appendix 4.B). SSTA slopes were positive and similar among sites (β = 0.11 – 0.27, all p <0.01); seagrass-distance slopes were negative and similar among sites (-1.00 × 10^{-3} to –0.000 SGI m^{-1}, p = 0.032–0.773) and seagrass-area slopes were highly inconsistent, near zero (-0.001 to 0.001 SGI km^{-2} , p = 0.263–0.959). Semi-partial R^2 quantified the contrast: SST anomaly explained an average of 18% (i.e., R^2 =0.18) of the variance (range 2.6–18.4 %), distance 1.0

% (0.2–11.4 %), and seagrass area < 0.1 % at eight sites. Fifteen-year running correlations between pre-whitened SGI and $SSTA_{Mar–Aug}$ (Pearson r = 0.27–0.73) tracked the corresponding GLS slopes, showing the climate signal persisted through rapid meadow expansion (see summary of model outputs for each site in Appendix 4.B). A Moran's I test on the pooled residuals ($I \approx 0.03$, $p = 0.42$) confirmed that between-site correlation was low.

Finally, when we pooled site-level chronologies (2001–2020, 9 sites) for the 'among site-scale' framework and fitted their SGI values with and without SST anomaly and/or signed distance from the eelgrass meadow edge in GLS models (with AR(1) error structures; Table 4.5), distance emerged as a statistically significant but secondary driver of growth. In a distance-only model (M2; Table 4.5) SGI declined by 0.21 SD for every 1 SD increase in distance away from the meadow edge (i.e., towards bare habitat; $t = –2.7$, df = 2, $p = 0.008$). However, this model was inferior to an SST-only model (i.e., it came with a significant AIC penalty; $\Delta AIC = +35.5$; M1 in Table 4.5) while a model retaining both SST anomaly and edge distance as predictors (M3) retained a significant negative effect of distance on growth (-0.17 SD, df = 5, $p = 0.017$; Table 4.5), but improved fit by less than one AIC unit, suggesting that march-to-August SST anomalies are the dominant year-to-year control (Fig. 4.5A), while habitat position explains a relatively modest portion of the variance (Fig. 4.5B).

Discussion

Our study establishes a novel, annually resolved 45-year shell-growth chronology (Fig. 4.2A) for the hard clam *Mercenaria mercenaria,* built from increment-width series that were rigorously cross-dated and detrended to isolate environmental signals (Black et al. 2008, 2016). Across both lagoon-wide and site-level analyses, a single regional driver—late-spring

sea-surface temperature anomalies ($SSTA_{Mar–Aug}$)—emerged as the dominant control on inter-annual growth, while the two-decade, 20 km² expansion of *Zostera marina* exerted a significant yet relatively modest influence that slightly enhanced growth for clams within the expanding seagrass meadow from 2001–2020 (Table 4.5; Figure 4.5B) . In the best-supported lagoon-scale model of a single average chronology for the region (GLS1), a one-standard-deviation rise in $SSTA_{Mar–Aug}$ increased standardized growth indices (SGI) by $\beta = 0.25 \pm 0.05$ SE (*z*-scaled $SSTA_{Mar–Aug}$; ≈ 3–4 % wider increments °C⁻¹), explaining roughly half of the likelihood-based variance ($R^2_{LR} \approx 0.50$). Refining the temperature window to a dual spring + autumn composite boosted explanatory power to 57 % ($\Delta AIC = -7.7$; $\beta \approx 0.33$), yet temperature remained the sole driver.

None of the six lagoon-scale models that included seagrass terms (GLS2–GLS6) passed a $\Delta AIC < 2$ retention criterion: adding contemporaneous meadow area, its annual change, one- or two-year lags, or an SST × area interaction all greatly reduced model parsimony, indicating that none of these seagrass variables sufficiently improved explanatory power to justify their inclusion as predictors in the information-theoretic approach to predictive modeling (Anderson and Burnham 2004). Moreover, these more complex models produced standardized (Z-scored) coefficients for the seagrass variables that were much smaller than those for temperature ($|\beta| \leq 0.07$ for seagrass variables vs. $\beta = 0.24–0.25$ for temperature). A thin-plate-spline GAMM yielded edf ≈ 1.2, indicating near-linearity of the temperature term and leaving cross-validated R^2 unchanged.

Partitioning the chronology in half at 1999 showed that temperature control weakened modestly after rapid meadow expansion ($\beta \approx 0.42$ before 1999 vs. $\beta \approx 0.23$ after), yet climate still

explained ~60 % of SGI variance in both time periods, confirming that the seagrass regime-shift left clam growth relatively unaltered at lagoon scale.

Analysis of the nine site-level chronologies echoed this pattern—indicating that the effects of local habitat on clam growth are weaker than those of the basin-wide climate signal via temperature, even at spatial scales <2 km. When fitting models to data from individual sites, the climate-only model (C_1) outperformed alternatives for every site: adding distance to the meadow edge raised ΔAIC by +13–18 units and adding local patch area by a further +13–15 units. SST slopes were uniformly positive and significant ($\beta = 0.11 – 0.27$, all $p < 0.01$), whereas relationships with distance from the meadow edge and overall seagrass meadow area were modest or near-zero and most all were non-significant ($p > 0.05$). Semi-partial R^2 values underscored the contrast: $SSTA_{Mar–Aug}$ explained a median ≈ 5 % of site-level variance (range = 2.6–18.4 %), seagrass distance ≈ 1 % (0.2–11.4 %), and seagrass area <1 %). Fifteen-year running correlations between pre-whitened SGI and $SSTA_{Mar–Aug}$ ($r = 0.27–0.73$) persisted through meadow expansion, reinforcing the conclusion that temperature largely modulates growth variability while seagrass may impose a slight, secondary effect. Unexplained residual variance (~40–50%) may reflect episodic food supply, disease, predation attempts, measurement error, or other factors (Judge et al. 1993, Perrigault et al. 2011).

When we pooled the 9 site-level SGI chronologies and examined the relative influence(s) of distance from meadow edge (m) and SST anomaly in a single statistical model (Table 4.5), meadow edge was a significant but secondary predictor (Fig. 4.4). Distance from the meadow edge had a negative effect on growth with or without SST anomaly included as a model covariate ($p < 0.017$). Notably, when SST anomaly was included, the effect of distance to the seagrass meadow edge weakened in slope (a change in β from –0.213 to –0.168) and statistical

significance (a change in p from 0.008 to 0.017). This indicates that a substantial amount of variance in clam growth that might have been attributed to seagrass effects (in the model without SST anomaly) are instead attributable to temperature; coincidental timing between the restoration and expansion of the seagrass meadow and interannual temperature changes apparently caused minor conflation between these two variables (Fig. 4.5B). In summary, this modeling framework isolated the unique contribution of the habitat gradient while controlling for the dominant climatic signal in the pooled SGI record (Fig. 4.5A), finding a modest yet significant decrease in SGI with distance away from the meadow interior (Table 4.5, Figs. 4.4, 4.5B), indicating a positive effect of seagrass on clam growth that generally aligns with previous research (Fales et al. 2020).

Although warming within the hard clam's 10–25 °C optimum promotes calcification, observed trends now exceed 0.30 °C decade^{-1} in summer and 0.27 °C decade^{-1} in spring (Fig. 4.6). Continued acceleration—as indicated by the strong relationship with $SSTA_{Mar–Aug}$ —will shift the peak-growth window earlier, risk phenological mismatches between clam larval release and plankton blooms, and periodically push clams beyond their upper thermal threshold, amplifying metabolic stress and disease exposure (Ansell 1968, Kraeuter and Castagna 2001). Hence climatic warming—rather than the management and further restoration of submerged aquatic vegetation—will likely dictate future clam production. This poses growing challenges for Virginia's hard-clam aquaculture industry—which generated US $57.8 million in 2021 (Hudson and McCarty 2023)—as well as a smaller but significant recreational fishery for wild hard clams.

Our findings align with the conclusions of a recent seagrass-bivalve meta-analysis (Fales et al. 2020): pronounced yet contradictory effects in short-term manipulations reflect pathway complexity rather than dominant drivers, which are set by spatially coherent climate

forcing (Witman et al. 2015, Barber et al. 2019). By scaling up to a lagoon-wide, 45-year perspective, we make that hierarchy explicit—regional climate dominates while local to mesoscale habitat effects remain secondary—and reconcile divergent short-term results with macro-ecological expectations (Brown 1995, Campana et al. 2023).

Acknowledgements

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Figures and tables

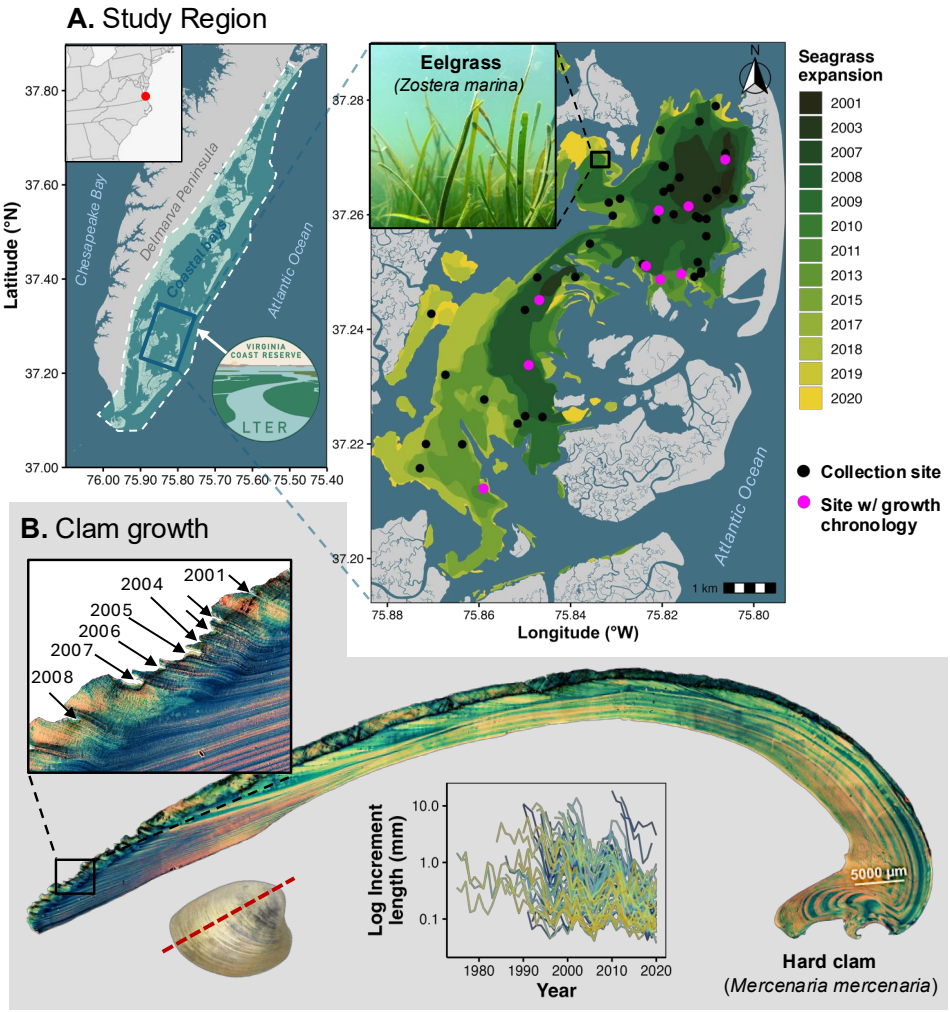


Figure 4.1. ***Study region, system, and hard clam growth increments.*** Panel A: Study domain of the Virginia Coast Reserve Long Term Ecological Research (VCR LTER) in coastal Virginia, USA, and the associated ~20-km^2 seagrass meadow expansion following restoration. Fifty clam collection sites (black points) were distributed with restricted randomization across 13 seagrass expansion layers (2001 to 2020). Pink points show 9 sites where sufficient replication of >15 yr-old clams enabled the constructing of a site-level growth chronology. Panel B shows Mutvei's solution-stained sample with clear, well-defined annual growth increments and their widths as plotted time series with synchronous patterns in clam growth (log scale).

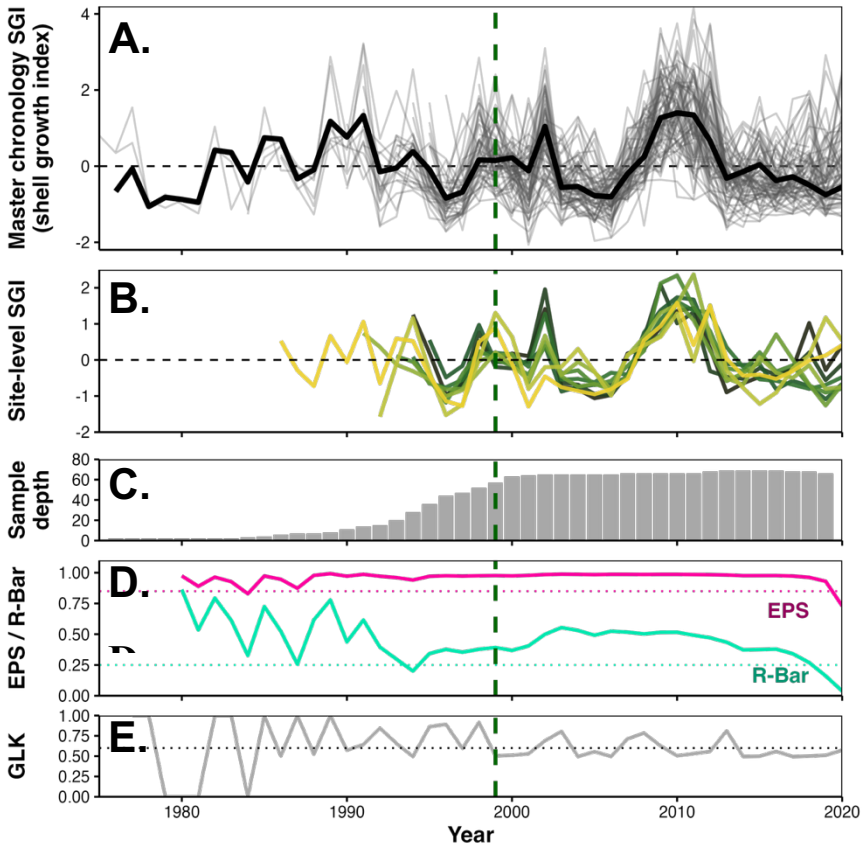


Figure 4.2. ***Hard clam chronology construction and quality-assessment.*** (A) Master chronology standardized shell-growth index (SGI; thick black line) overlaid on all individual-level detrended series (grey), illustrating year-to-year coherence among the 77 shells retained after detrending. (B) Site-level chronologies: color-coded SGIs for each of the 9 collection sites (pink points in Fig. 4.1A) highlight modest spatial variability around the regional signal; dashed line marks zero growth anomaly. (C) Sample depth, (D) 15-yr inter-series correlation (R-Bar, colored teal) and expressed population signal (EPS, colored magenta); dotted reference lines denote standard thresholds of 0.25 (R-Bar) and 0.85 (EPS). (E) Gleichläufigkeit (GLK), proportion of pairwise series that agree in the sign of year-to-year change; the dotted line at 0.60 marks the benchmark for strong common forcing. Vertical dashed green line denotes year of seagrass restoration start (2001).

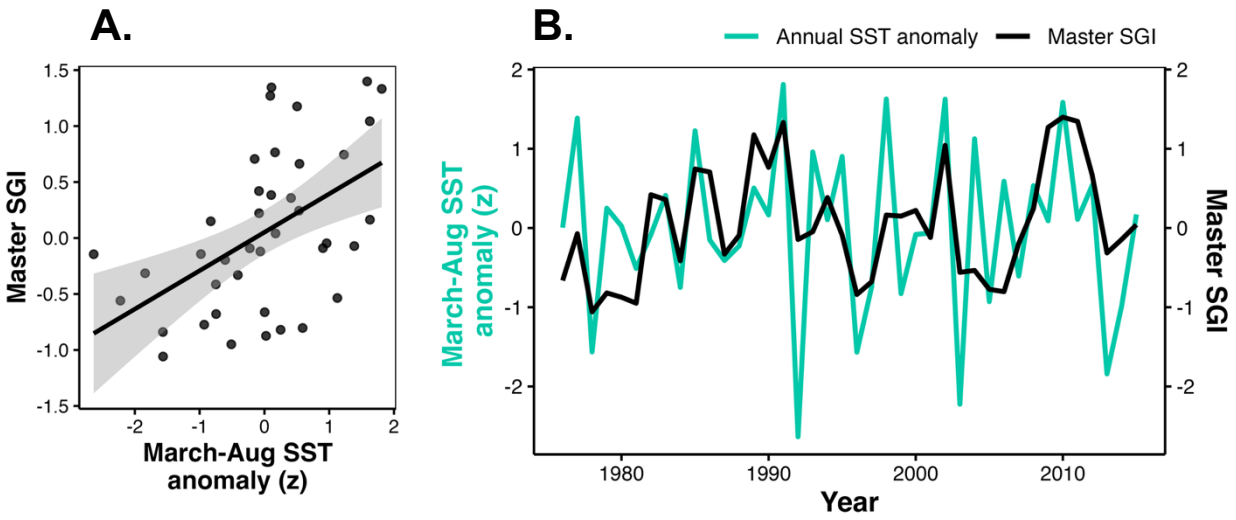


Figure 4.3. ***March-August SST anomaly population-level SGI (1974–2020).*** Annual March-August mean SST anomaly (z-scored) and master (average population-level) shell-growth index (SGI; z-scored) as: ordinary least-squares regression (A; $R^2 = 0.25$, $p = 0.001$) and timeseries (B; Pearson r = 0.61, $p < 0.0001$). All model statistics and coefficients reflect pre-whitened growth chronology and climate series to account for serial temporal autocorrelation.

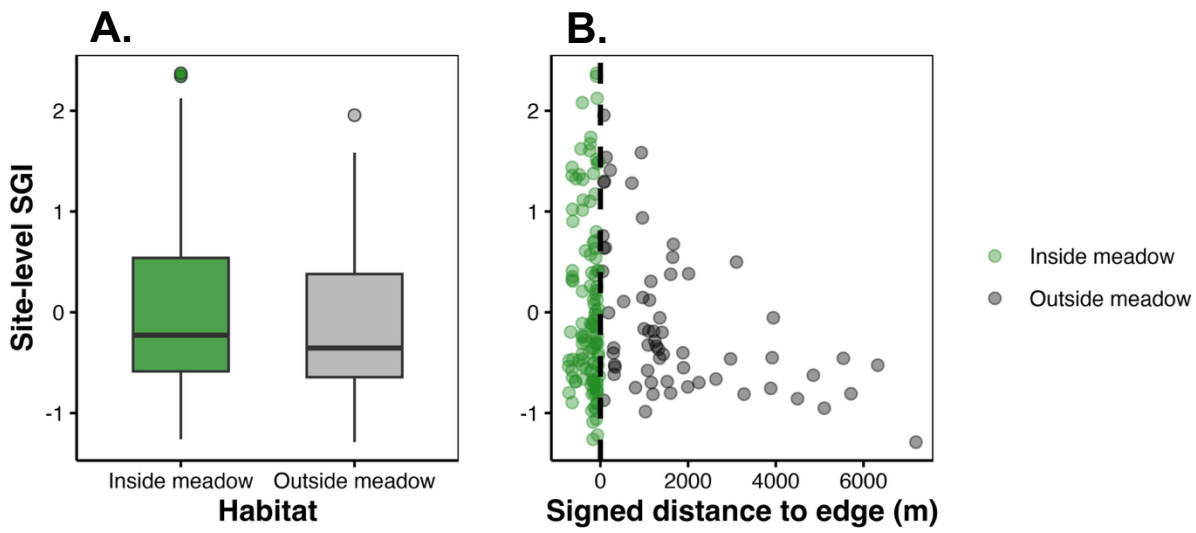


Figure 4.4. ***Site-level chronology indices (SGI) vs. seagrass presence and distance (2001-2020).*** Box-and-whisker (A) comparison of clam SGI distributions for site–year SGI value ($n = 180$) observations, grouped by the binary habitat classifier. Boxes show the inter-quartile range (IQR) with the median; whiskers extend to 1.5 × IQR; points denote outliers. (B) Scatterplot of site–year SGI values ($n = 180$) against signed distance to the nearest meadow edge. Negative values on the x-axis indicate sampling points located within the contiguous meadow footprint; positive values indicate points outside the meadow. The vertical dashed line marks the meadow boundary (0 m).

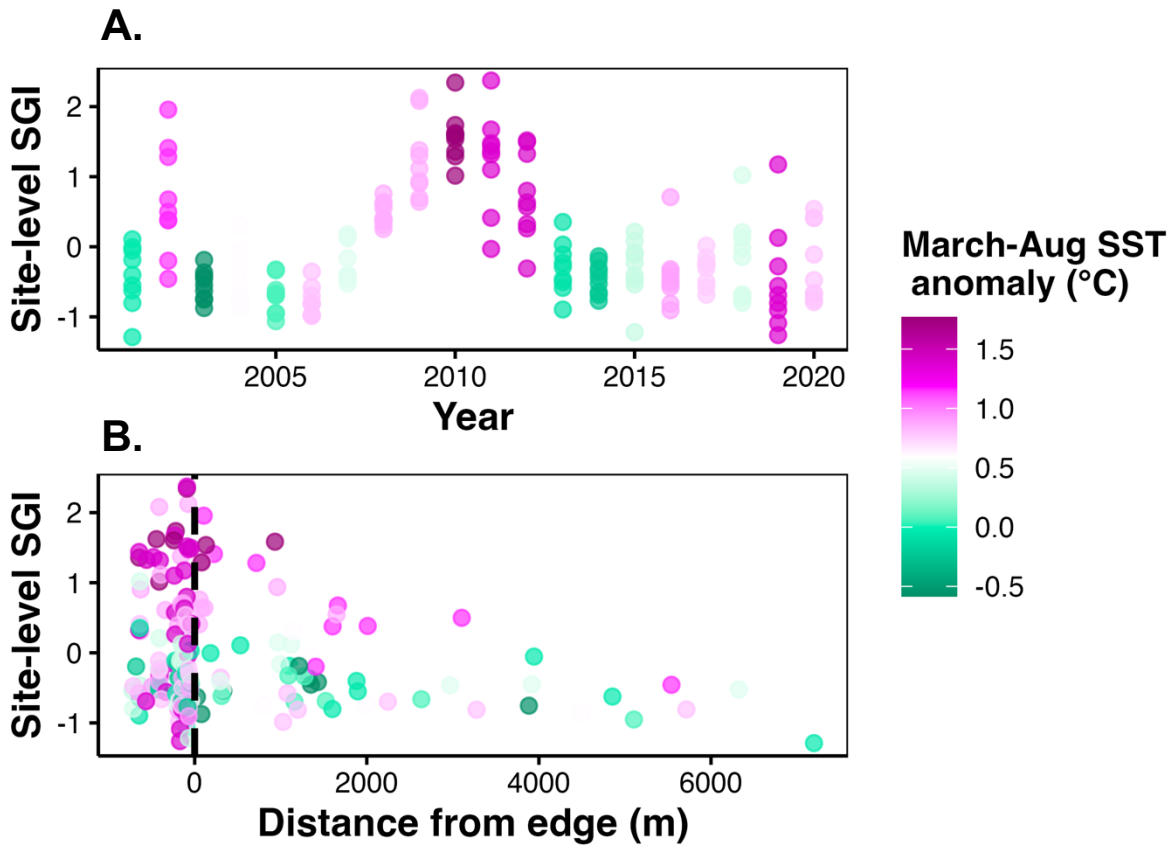


Figure 4.5. ***Interannual and spatial controls on site-level clam shell-growth indices (SGI) from 2001 to 2020.*** (A) Site-level annual SGI values (2001–2020) colored by the March–August SST anomaly, visualizing that SGI values increased in years with warm anomalies post-seagrass restoration. (B) Within-meadow spatial perspective: site level SGI observations plotted against its signed annual distance (meters) from the nearest meadow edge, where positive values = interior (right), 0 m = edge (dashed line), and negative values (left) are within seagrass. Note that, while points in panel B are consistent with a decrease in SGI values away from the edge, many of the low values right of 0-m (dashed line) correspond to low SST anomaly values (green points). This is also illustrated in panel A; while variability exists—likely influenced by the small yet robust effects of seagrass (*see Table 4.5*)—SST anomaly still holds clear impacts on annual SGI values.

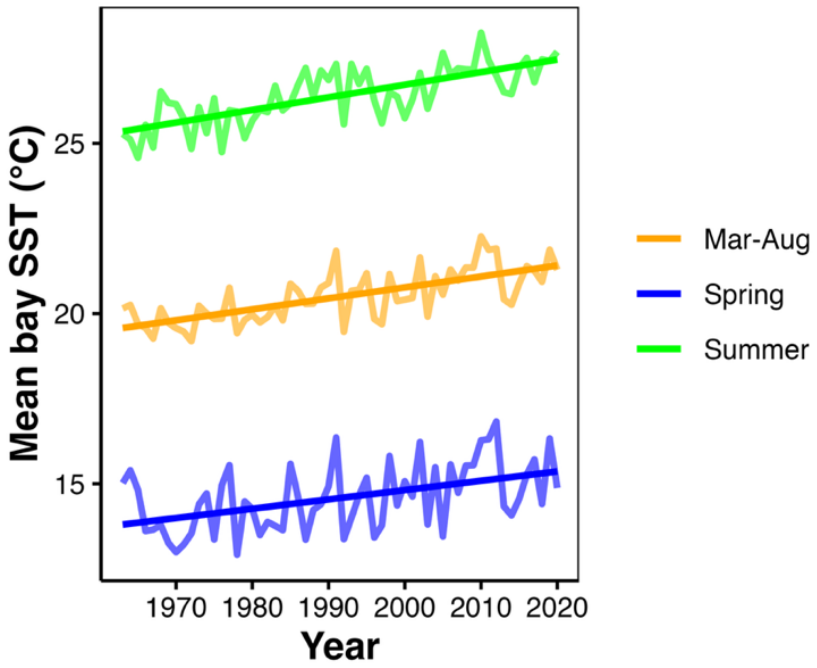


Figure 4.6. ***Long-term mean SST trends for March-August window.*** Linear trends (°C/year) by season and SGI climate window (orange) of mean annual coastal bay sea surface temperatures (SST) from 1963 to 2020 (Wiberg 2021). March–August held highest decadal increase (linear model: 0.37 °C/10 yrs, $p < 0.001$, $R^2 = 0.50$), with summer SST a close-second (linear model: 0.32 °C/10 yrs, $p < 0.001$, $R^2 = 0.50$) and spring third (linear model: 0.22°C/10 yrs, $p < 0.001$, $R^2 = 0.54$).

Model	Fixed effects	Ecological question	A-priori expectation	Retention criterion*
GLS1	standardized SST anomaly (SSTA_z)	Does late-spring–summer temperature govern growth?	Positive slope, reflecting faster calcification in warm years.	Baseline
GLS2	SSTA_z + contemporaneous seagrass area (SG_{area}_z)	Does the absolute size of the meadow enhance growth via food, hydrodynamics, predator refuge, etc.?	Positive SG_{area} effect if habitat matters.	$\Delta AIC < 0$ *and* $p < 0.05$ for SG_{area}_z
GLS3	SSTA_z + annual change in area (ΔSG_{area})	Is growth sensitive to rapid expansion or contraction of habitat?	Positive effect if expansion boosts resources; negative if disturbance costs dominate.	As above
GLS4 & GLS5	SSTA_z + 1- or 2-year lag of SG_{area}	Do physiological carry-over or food-web lags link past habitat to current growth?	Detectable positive lagged slopes.	As above
GLS6	(SSTA_z + SG_{area}_z) + (SSTA_z × SG_{area}_z)	Does seagrass modify thermal sensitivity (e.g., buffer stress at high *T*)?	Significant interaction: slope of SSTA depends on meadow size.	As above
GAMM	thin-plate spline of SSTA_z	Is the temperature effect non-linear (e.g., optimum then decline)?	Spline estimated degrees of freedom > 1; lower cross-validated RMSE than GLS1.	LOOCV R^2 improves by ≥ 0.02

*ΔAIC values are computed against the next-simplest nested model using identical rows; likelihood-ratio tests provide parallel.

Table 4.1. ***Lagoon-scale chronology (1974–2020) candidate model set and hierarchy.*** Ordered set of increasingly complex models, starting with the simplest biologically plausible hypothesis (temperature alone; GLS1) and adding habitat terms only when they demonstrably improved fit. All models were fitted with the *nlme* R-package using generalized least squares (GLS) and a first-order autoregressive AR(1) residual structure, which accounts for temporal dependence while leaving fixed-effect estimates unbiased. SSTA_z = SST anomaly (z-scored annual mean), SG_{area}_z = lagoon-wide seagrass cover (ha).

Model	Fixed terms	Ecological question	Expected sign*	Retention criterion†
C_1	SSTA_z	Does basin-scale temperature alone explain within-site growth?	Positive	Baseline
C_2	SSTA_z + Distance_z	Does proximity to the meadow edge modify growth (e.g., reduced predation or altered flow inside the canopy)?	Negative slope if growth is higher inside the meadow	$\Delta AIC < 0$ and $p < 0.05$ for Distance_z
C_3	SSTA_z + Distance_z + Area_res	Does the absolute local footprint add information beyond spatial position?	Positive if larger patches enhance food retention; could be negative if self-shading reduces seston	Same as above

*Signs are hypothesized a priori from previous field experiments (Irlandi 1997; Johnson & Heck 2007).
†ΔAIC values are computed against the next-simplest nested model using identical rows; likelihood-ratio tests provide parallel inference.

Table 4.2. ***Within site-scale chronology (2001–2020) candidate model set and hierarchy.*** GLS models with a corAR1(Year) residual structure; log-likelihoods were calculated with restricted maximum likelihood. The ladder is intentionally simple to preserve power in the relatively short site time series (2001–2020, $n = 20$ yrs for each of 9 sites; one model fitted per site): Distance_z = signed distance (shortest straight-line path from collection site to the seagrass meadow edge in the year of growth).

Model	Fixed effects (beyond SST_A)	β_{SST} ± SE (*p*)	ΔAIC	Decision	Key inference
GLS1	– (baseline SST_A_z only)	0.247 ± 0.054 (**<0.001**)	—	**Retained**	**Late-spring SST alone explains ≈ 50 % of SGI variance**
GLS2	+ SG_area_z	0.246 ± 0.054 (**<0.001**)	**+3.6**	Rejected	Meadow size adds no explanatory power
GLS3	+ ΔSG_area	0.244 ± 0.055 (**<0.001**)	**+2.3**	Rejected	Rapid expansion/contraction not reflected in growth
GLS4	+ SG_area(t-1)	0.245 ± 0.055 (**<0.001**)	**+2.7**	Rejected	One-year habitat memory absent
GLS5	+ SG_area(t-2)	0.245 ± 0.055 (**<0.001**)	**+3.1**	Rejected	Two-year habitat memory absent
GLS6	+ SG_area_z × SST_A_z	0.245 ± 0.054 (**<0.001**)	**+4.5**	Rejected	Seagrass does not modulate thermal sensitivity
GAMM	Thin-plate spline of SST_A_z	edf = 1.2 (≈ linear) (*p* for non-linearity = 0.29)	–0.4	Tie with GLS1 (no LOOCV gain)	Relationship is effectively linear; GLS1 preferred

*ΔAIC values are relative to the next-simplest model fitted to identical data rows (criterion for
**Retention criteria: ΔAIC < 0 *and* added term $p < 0.05$).
***"Rejected" indicates failure to meet the retention criterion.

Table 4.3 ***Lagoon-scale (1974–2020) GLS/GAMM models and outputs.*** None of the habitat additions (GLS2–GLS6) lowered AIC or produced significant coefficients; the GAMM revealed no nonlinear relationship (curvature). Consequently, GLS1—late-spring SST anomaly (SST_A, SST_A_z = z-scored SST anomaly) with an AR(1) error structure—was the most parsimonious and biologically supported model for lagoon-wide clam growth.

Metric	**GLS1** ($SSTA_{March-Aug}$)	**GLS2** ($SSTA_{MAM + SON}$)
Period included	1976 – 2020	1976 – 2020
SST_A window	Mar–Aug	Mar–May + Sep–Nov
Sample size (*n* years)	45	45
β SSTA	**0.247**	**0.327**
SE (*β*)	0.054	0.056
p-value	**<0.001**	**<0.001**
φ (AR:1)	0.619	0.699
AIC / BIC	76.21 / 83.25	68.47 / 75.51
log-likelihood	−34.10	−30.23
σ (residual SD)	0.629	0.634
R^2_{LR}	0.496	0.573
KS p / Disp p	0.863 / 0.800	0.987 / 0.732
RMSE / LOOCV R^2	0.615 / 0.20	—
Notes	headline linear model	dual-season alternative

Abbreviations: β = slope; SE = standard error; φ = AR(1) parameter; σ = residual SD; R^2_{LR} = likelihood-ratio pseudo-R^2; KS p / Disp p = *DHARMa* uniformity and dispersion tests (Hartig 2024); RMSE / LOOCV R^2 = leave-one-year-out skill.

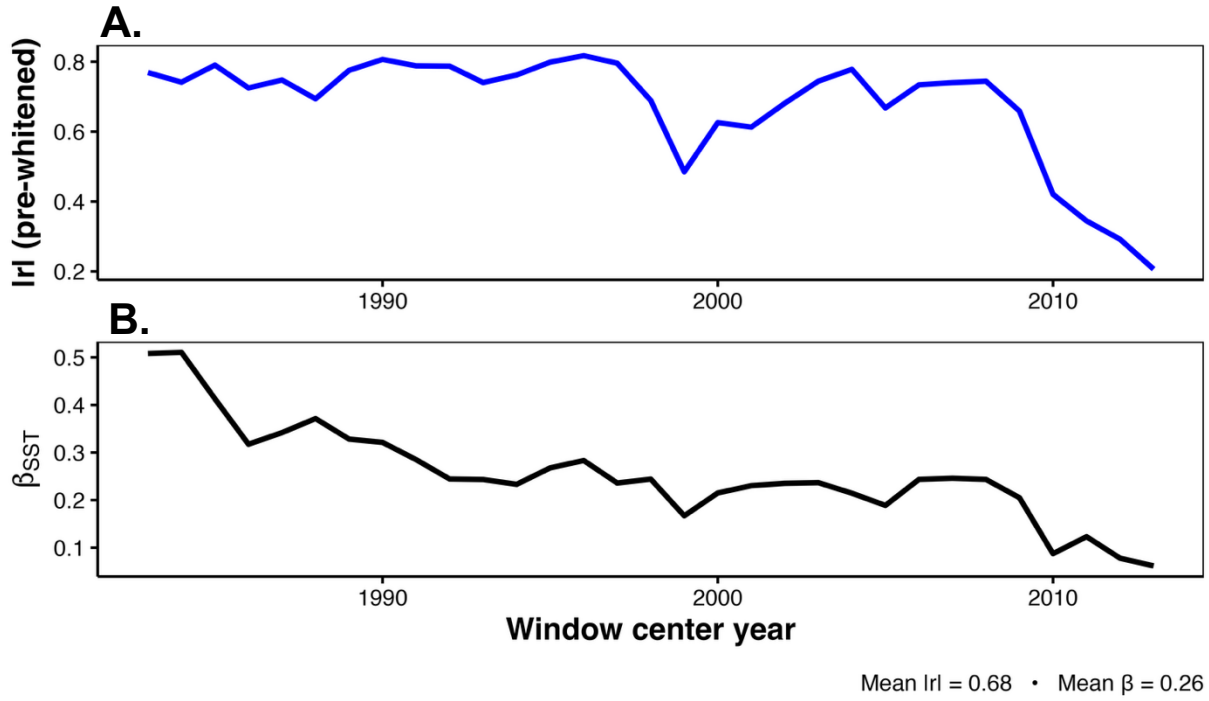
Table 4.4 ***Lagoon-scale clam SGI chronology (1974–2020) and SST anomaly GLS models.***

Metrics for the two principal GLS(AR1) models linking detrended, z-standardized *M. mercenaria* growth index (SGI) to coastal bay SST anomaly (SSTA). The *GLS1* model uses a single continuous six-month window climate-sweep that maximized pre-whitened Pearson |r|; *GLS2* exploited the best dual-season (March-April-May, and September-October-November) SST_A combination identified by exhaustive search. RMSE (root mean square error) and cross-validated R^2 are only shown where leave-one-year-out predictions were calculated (i.e., *GLS1*). Both models passed *DHARMa* R-package residual checks (KS and dispersion p > 0.7).

Model	Fixed effect	Estimate	SE	*t*	*p*	*df* (REML)	AIC
M1	Intercept	–0.017	0.090	–0.19	0.851	4	338.86
	$SSTA_{Mar–Aug}$	+0.293	0.041	7.07	**< 0.001**		
M2	Intercept	–0.023	0.106	–0.21	0.832	4	374.39
	Dist. edge	–0.213	0.080	–2.67	**0.008**		
M3	Intercept	–0.009	0.089	–0.10	0.922	5	338.59
	$SSTA_{Mar–Aug}$	+0.284	0.041	6.91	**< 0.001**		
	Dist. edge	–0.168	0.070	–2.41	**0.017**		

Table 4.5. ***Among site-level chronology GLS models*.** Model structures (M1–M3) for pooled site-level SGI chronologies (9 site time series spanning 2001–2020) as predicted by SST anomaly (annual March through August SST window) and/or signed distance to the seagrass meadow edge ('dist edge'; m), and model fixed-effect coefficients. All models include an AR(1) residual structure nested within Site ($\rho \approx 0.54$). Model M1 shows that warmer March–August SST anomalies strongly enhance the standardized growth index (SGI). Model M2 reveals a negative relationship between SGI and distance from the seagrass meadow edge (i.e., a positive effect of proximity to the meadow edge). Model M3 combines both predictors; its ΔAIC relative to M1 is < 2, indicating that temperature remains the dominant driver while distance adds a modest but significant secondary effect. Boldface denotes significant p-values (< 0.05).

Appendix



Appendix 4.A. ***Running correlations (15-yr) between clam growth and March–Aug SST anomaly.*** (A) Fifteen-year running correlations between pre-whitened SGI and $SSTA_{March\text{-}Aug}$ (centered on 2020), were moderate to strong (|r| = 0.27–0.73). (B) GLS slopes (SGI~ $SSTA_{March\text{-}Aug}$) on same timescale as Pearson r above, indicating that the climate signal weakened but remained coherent through the period of rapid meadow expansion (2001–2010).

Site	yrs	AIC (C1)	ΔAIC_{Dist}	ΔAIC_{Area}	β_{SSTA}	$\beta_{Dist}(\times 10^{-4})$	$\beta_{Area}(\times 10^{4})$	R^2_{SSTA}	R^2_{Dist}	R^2_{Area}	$r_{2006\text{-}2020}$
2007-1	20	54.0	+14.2	+14.8	**0.144**	–6.7	–0.4	0.042	0.010	0.001	0.36
2007-2	20	57.6	+13.2	+14.6	**0.161**	–7.8	–0.5	0.038	0.002	0.001	0.27
2008-4	20	41.4	+17.5	+14.0	**0.123**	–2.8	+8.9	0.078	0.017	0.001	0.36
2009-1	20	41.7	+14.6	+13.9	**0.222**	–5.3	+3.2	0.184	0.016	0.006	0.73
2011-4	20	46.4	+15.3	+13.9	**0.119**	–2.9	–2.3	0.038	0.038	0.030	0.31
2012-2	20	44.8	+17.0	+14.5	**0.112**	–0.9	–4.7	0.056	0.035	0.041	0.37
2013-5	20	51.3	+15.3	+13.2	**0.092**	–7.3	–10.6	0.026	0.070	0.064	0.42
2015-3	20	51.2	+15.2	+14.3	**0.171**	–2.6	+1.0	0.048	0.010	0.000	0.61
2017-2	20	44.8	+14.7	+14.6	**0.134**	**–2.4**	+5.0	0.075	0.114	0.000	0.53

ΔAIC values are relative to the climate-only baseline (C1). Positive ΔAIC indicates poorer fit; no habitat term meets the retention criterion ($\Delta AIC < 0$ and $p < 0.05$).

Appendix 4.B. ***Within site-scale GLS model set hierarchy.*** Climate baseline (C1) vs. habitat additions (C2 = + Distance, C3 = + Residual Area) for the 2001–2020 period following seagrass restoration. All models include an AR(1) residual structure and the March–August SST anomaly identified at the lagoon scale (via climate sweep across site-level chronologies). Model coefficients (β) for Temperature Anomaly are per degree C, for Distance are expressed $\times 10^{-4}$ per m, and for Area $\times 10^{4}$ per km^2. Semi-partial R^2 values quantify the unique variance of each term. Boldface denotes model coefficients (β) with significant *p*-values (< 0.05).

Model code	Period	*n*	SST window	β_{SST} (SE)	$\beta_{SG\ area}$ (SE)	φ	σ	AIC / BIC	log L	KS p / Disp p
M1 Climate + SG area	1976–2020	*45*	Mar-Aug	**0.246 (0.054)**	–0.030 (0.179)	0.648	0.656	79.9 / 88.5	–34.92	0.949 / 0.564
M2 Climate-only, data-matched subset	2001–2020	*42*	Mar-Aug	**0.242 (0.058)**	—	0.590	0.608	69.3 / 76.3	–30.64	0.929 / 0.800
M3 Early era	1976–1998	*23*	Feb-Jul	**0.424 (0.092)**	—	0.487	0.526	40.3 / 44.5	–16.15	0.827 / 0.760
M4 Late era	1999–2020	*22*	Mar-Jun	**0.228 (0.090)**	—	0.656	0.645	41.0 / 45.0	–16.51	0.822 / 0.712

KS and Disp are Kolmogorov–Smirnov and dispersion tests from *DHARMa*; values > 0.05 denote no diagnostic problems.

Appendix 4.C. ***Performance of alternative lagoon-wide GLS models used in sensitivity analyses***. Each model includes an AR(1) residual structure; all coefficients are standardized (z-scores). β values refer to the SST anomaly term except where indicated. Boldface denotes model coefficients (β) with significant *p*-values (< 0.05). Parentheses show standard errors; Model codes correspond to those discussed in the text:

M1 = *gls_area* (full record, SST + contemporaneous seagrass area);

M2 = *hab_fast_only* (climate only, harmonized habitat-data subset);

M3 = *GLSEarly*;

M4 = *GLSLate*. No model surpasses the headline climate-only fit in parsimony; seagrass terms never explain > 1 % additional variance.

Site	β_{SSTa}	β_{dist} ($\times 10^{-4}$)	β_{area} ($\times 10^{4}$)	r_{2020}	R^2_{SSTA}	R^2_{dist}	R^2_{area}
2007-1	**0.144**	–6.7	–0.04	0.36	0.042	0.010	0.000
2007-2	**0.161**	–7.8	–0.05	0.27	0.038	0.002	0.001
2008-4	**0.123**	–2.8	+8.9	0.36	0.078	0.017	0.001
2009-1	**0.222**	–5.3	+3.2	0.73	0.184	0.016	0.006
2011-4	**0.119**	–2.9	–2.3	0.31	0.038	0.038	0.030
2012-2	**0.112**	–0.9	–4.7	0.37	0.055	0.035	0

Appendix 4.D. ***Site-level influence of climate vs. post-restoration habitat geometry (2001–2020) GLS outputs.*** Best-window (March-August) mean SST anomaly slopes (β_{SSTA}) are uniformly positive and, together with their semi-partial R^2, show that late-spring temperature dominates shell-growth variance. In contrast, signed-distance and meadow-area terms have order-of-magnitude smaller slopes and near-zero unique R^2 at every site. Values are site-specific GLS estimates; r_{2020} is the centered 15-yr running correlation (2006-2020) between pre-whitened SGI and $SSTA_{March\text{-}Aug}$. Boldface denotes model coefficients (β) with significant *p*-values (< 0.05).

Summary and Conclusions

This dissertation examined how the presence of a foundational seagrass species—eelgrass *Zostera marina*—influences ecosystem processes and an associated consumer, the hard clam *Mercenaria mercenaria*, across multiple spatial and temporal scales. Foundation species like seagrasses, corals, and canopy-forming trees and kelps physically engineer environments in ways that alter resource availability for other organisms (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011). In eelgrass meadows, dense underwater canopies attenuate water flow, facilitate suspended sediment deposition, and provide refuge from predators (Orth et al. 1984, Larkum et al. 2006, Lawson et al. 2007, Hansen and Reidenbach 2013). These mechanisms are expected to enhance food supply and survival for benthic filter-feeders like clams, explaining their often-high abundance in these habitats (Peterson 1986, Judge et al. 1993, Meira et al. 2024). How common and consequential these purported benefits are, however, remained uncertain; empirical studies yield mixed outcomes for clam growth and survival, ranging from strongly positive to neutral or negative effects, and highlighting a need for the scale-explicit tests presented here (Coen and Heck 1991, Irlandi 1996, Canion and Heck 2009, Fales et al. 2020).

I posit that three ecological theories help explain this lack of predictive power: scale-transition theory predicts that effects observed in small-scale experiments may change direction or intensity at larger scales (Holyoak et al. 2005), Moran effect theory highlights that regionally synchronous environmental variability can drive broad-scale population trends independent of local habitat (Ranta et al. 1997, Hansen et al. 2020, Castorani et al. 2022), and stress-gradient theory predicts that habitat benefits (e.g., facilitation) can shift to costs (e.g., competition) under shifting environmental conditions (Malkinson and Tielbörger 2010, Castorani et al. 2015). Incorporating these frameworks, this research investigated eelgrass–clam interactions from centimeters to kilometers and months to decades, aiming to disentangle

intrinsic habitat effects from extrinsic climate forces.

In Chapter 1, I showed that seagrass canopies altered the vertical distribution and timing of microalgal food abundance for clams. Within seagrass beds, water column chlorophyll-*a* (a proxy for high-quality microalgal food availability; Judge et al. 1993) accumulated in a 1-cm to 5-cm benthic layer near the seabed. Sediment-bound microalgae (chlorophyll-*a* concentrations from cores of the upper 1 cm of sediment)—likely dominated by benthic diatoms (McGlathery 2017, Cox et al. 2020)—peaked in late-winter while a mid-to-late summer surge of near-bed suspended chlorophyll-*a* occurred inside the seagrass meadow, both reaching concentrations several-fold higher than bare site observations. Moreover, this mid-to-late summer near-bed pulse coincided with peak epiphytic algal biomass accumulation on seagrass blades—likely contributing to near-bed seagrass chlorophyll-*a* (Irlandi and Peterson 1991, Judge et al. 1993, Poore et al. 2009). However, near-bed water column chlorophyll-*a* concentrations (~6 to10-µg L^{-1}) rarely approached hard clam feeding saturation thresholds—reported to occur at or above 15-µg L^{-1} (Kraeuter and Castagna 2001, Silva and Gobler 2023). Consequently, food-driven growth enhancement within seagrass is likely limited in extent and confined to brief seasonal windows.

In Chapter 2, I found that the structural complexity of eelgrass provided a strong refuge from predation for hard clams, but this benefit was highly dependent on seagrass density, clam size, and season. Our experiments showed that in at sites in dense, continuous seagrass habitat, small, newly recruited juvenile clams (<1-year old, ~10-mm significant shell length) experienced survival rates up to five times higher than those at bare-seafloor sites. In contrast, sparse/patchy seagrass habitats offered little to no protection for these juveniles—with predation rates largely mirroring unvegetated areas. Adult clams (60–120 mm) also benefited: during spring when U.S.

Mid-Atlantic canopy growth rates peak (Carr et al. 2012, Berger et al. 2020), adult survival was 20-fold higher in seagrass than bare site deployments—where adults had near-zero survival. By late summer, however, predation pressure intensified in all habitats, likely tracking peak abundances of blue crabs and cownose rays (Orth et al. 1984, Irlandi 1994, Lipcius et al. 2005). Despite this, vegetated sites still had 4–7 times higher clam survival. Hence, seagrass meadows served as a significant "nursery", enhancing the survival of young clams during periods of intense predation, whereas larger clams gained seasonal benefits. In sum, value of habitat structure appears to peak when and where it is needed most—for small, vulnerable life stages and during high predator activity.

In Chapter 3, I found life-stage dependent growth responses to seagrass and evidence of an energetic trade-off between shell accretion and tissue mass. While juvenile *Mercenaria mercenaria* grew ≈36 % faster inside the *Zostera marina* canopy than on adjacent bare sand, adult growth rates were near-uniform across habitats. Neither distance from the meadow edge nor modest differences in near-bed chlorophyll-a (≈6–10 μg L^{-1}) explained growth variation. Condition indices suggest a habitat-dependent trade-off: juveniles at bare sites exhibited condition declines of roughly 0.66 % for each cm^2 of accreted shell, whereas clams inside seagrass showed no such decline. Together, these findings suggest that juvenile clams gain a net growth advantage in seagrass habitats while adult clams are relatively indifferent or slightly disadvantaged in dense vegetation, indicating that seagrass facilitation may be stronger under higher stress conditions (e.g., high suspended sediment concentrations, increased predator activity, low food abundance, etc.), turning neutral or negative when stress is low or organisms are larger and less-vulnerable—as predicted by the stress-gradient hypothesis (Bertness and Callaway 1994, Malkinson and Tielbörger 2010).

Finally, in Chapter 4 I found that over annual to decadal scales, regional climate variability in the form of sea-surface temperature was the dominant driver of clam growth, overwhelming local seagrass habitat effects. Using sclerochronology methods to extract annual shell growth increment measurements from hard clam shell samples—many of which were several decades old—I constructed multi-decade annual shell growth records for hard clams extending back over a decade before seagrass restoration and captured its expansion to over 20 km^2. This study revealed that spring–summer (March–August) sea surface temperature anomalies alone explained over 30% of the variance in annual shell growth. Particularly warm years caused highly synchronous increases in growth across the coastal bay system, whereas cooler years depressed growth rates—these occurring when forcing from the North Atlantic Oscillation (NAO) modified Mid-Atlantic sea-surface temperatures (Thomas et al. 2017, Poitevin et al. 2019). Crucially, whether a clam grew at the center of the expanding seagrass or outside the meadow had a modest but significant influence on interannual growth rates and long-term trends. Hence, during the two decades of seagrass expansion (from zero to >20 km^2), we found significant yet small—especially relative to the effect of SST—long-term growth trend attributable to habitat restoration, generally consistent with evidence from several previous, short-term studies (including my own study in Ch. 3) suggesting that seagrass benefits clam growth (summarized in Fales et al. 2020). Clam shell accretion rates were highly synchronized across the coastal bay to regional climate forcing. This is likely evidence of strong Moran effects, wherein spatially synchronized climate/environmental drivers induce synchronous population dynamics over space and time (Ranta et al. 1997, Barber et al. 2019, Hansen et al. 2020). In sum, unusually warm spring and summer conditions can suppress regional clam growth, regardless of local habitat conditions.

Viewed through a scale-focused lens, these findings present a picture in which intrinsic habitat effects operate within clear limits set by dominant extrinsic factors. At fine scales (centimeters to meters, days to months), eelgrass appeared to act as a facilitator of hard clams: its physical structure attenuates currents, increases epiphytic and benthic primary production, and reduces predation, yielding measurable increases in food availability near the seafloor and substantial boosts clam survival and growth. These positive local-scale effects confirm the classic role of foundation species in mediating basal resources for associated fauna (Ellison et al. 2005, Gagnon et al. 2020a). However, the strength of these effects proved highly context-dependent—manifesting strongest only under certain seagrass configurations (continuous, high-density meadows), during specific phenological windows (e.g. spring to mid-summer before senescence diminishes cover), and for specific life stages (i.e., small juveniles benefitted the most). On broader scales (hundreds of meters to kilometers, years to decades), the direct influence of this seagrass-driven ecosystem state change dilutes to weak signals while regional climate drivers elicited stronger and more consistent effects.

The synchronous, climate-driven interannual growth patterns we observed in clams collected across a 20 km^2 coastal seascape illustrate how large-scale variability may mask or override local habitat differences (Arnold et al. 1991, Brown 1995, Lawton 1999). This hierarchical interplay—with local biogenic habitat setting the stage for small-scale outcomes captured in field experiments (Witman et al. 2015), and climate oscillations orchestrating the larger picture (Bueno de Mesquita et al. 2021, Campana et al. 2023)—may help reconcile the conflicting results of past studies. Previous research on bivalves in seagrass reported responses ranging from strong positive effects (i.e., significantly increased growth related to seagrass) to negligible or negative effects (Peterson 1986, Coen and Heck 1991, Arnold et al. 1991, Irlandi

and Peterson 1991, Gagnon et al. 2020, Fales et al. 2020). Our findings predict these discrepancies on the basis that each study isolated and captured different positions on the scale and context spectrum. For example, short-term experiments deploying juvenile clams inside and outside of dense seagrass patches (Peterson 1984, Irlandi 1996, Galván and Puente 2023) might find positive effects because of the clam life-stage examined or the season or regional climate conditions under in which they were studied. Such are the general logistical constraints of most experimental studies (e Knapp et al. 2012). Conversely, long-term observations, by integrating over small spatiotemporal-scale effects to better capture low-frequency (longer-term) signals, may capture the opposite, or weakened seagrass/habitat effects, despite their inherent limitations for testing hypotheses.

By explicitly evaluating seagrass-bivalve interactions across multiple scales, this dissertation unifies those disparate observations into a single framework: foundation species effects are real but conditional, and their net impact is the result of an interplay between habitat structure and the environmental context.

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