



Evaluating estuarine habitats using secondary production as a proxy for food web support

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ABSTRACT: The management, restoration, and conservation of estuarine habitats would benefit from knowledge of habitat-specific functions that reflect important ecosystem services. Secondary production may provide a comprehensive metric of food web support because it synthesizes contributions of local primary production, food subsidies from other habitats, and the protective influences of habitat structure. Despite widespread perceptions of how habitats compare in food web contribution, few methodologically comparable studies on secondary production across multiple estuarine habitats exist. At field sites in North Carolina, USA, annual secondary production was estimated for macrobenthic infaunal and epifaunal communities in salt marshes, seagrass meadows, oyster reefs, intertidal and subtidal flats, and on shoreline stabilization structures. Habitats with hard emergent or biogenic structure generally exhibited higher secondary production than habitats lacking structure. Oyster reef had the highest secondary production, ranging from 467.3 to 853.7 g ash free dry mass (AFDM) m⁻² yr⁻¹, while shoreline stabilization structures ranked high because of dense epifaunal communities. Estimates of secondary production suggest ranking of natural habitats as oyster reef > salt marsh > seagrass > intertidal flat and subtidal flat. Undesirable impacts of shoreline stabilization structures on adjacent habitats made their inclusion in this ranking of food web support by habitat difficult. The importance of suspension feeders on oyster reefs, shoreline stabilization structures, and in some marshes suggests that secondary production patterns are partly influenced by external subsidies facilitated by support from habitat structure. Consequently, estuarine rehabilitation should include structural habitat elements that will contribute to ecosystem production at higher trophic levels. Without such habitat restoration, the fate of estuaries in the USA affected by anthropogenic stressors may be loss of habitat diversity and prevalence of low-trophic-supporting habitats.

KEY WORDS: Secondary production · Estuarine habitats · Food web support · Habitat value · Restoration · Shoreline stabilization structure · North Carolina

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INTRODUCTION

Estuarine habitats and their associated ecosystem services and functions are increasingly threatened by anthropogenic stressors, such as rising sea level, eutrophication, or shoreline development (Scavia et al. 2002, Orth et al. 2006, IPCC 2007). These stressors may influence the distribution and diversity of estu-

arine habitats, with potentially dramatic effects on habitat trophic structure and on total system productivity. Knowledge of how estuarine habitat change will affect ecosystem functioning depends on the ability to quantify habitat-specific functions that reflect important ecosystem services.

Restoration of estuarine habitats damaged or destroyed by anthropogenic impacts plays a pivotal

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role in maintaining ecological integrity of estuaries. Compensatory restoration is sometimes required to elevate lost ecosystem services by converting a less valued habitat into a more valued one (Peterson et al. 2003). Salt marshes have been preferentially restored in recognition of their high primary productivity and contributions to faunal abundance (Peterson et al. 2008a). Recently, seagrass, mangrove, and oyster reef have also been recognized as providing important ecosystem services and functions (Beck et al. 2001, Orth et al. 2006, Coen et al. 2007). Consequently, estuarine restorations generally target biogenically structured habitats, which are assumed to provide higher ecosystem services and functions per unit area. Metrics of ecosystem services that represent relative habitat value, when combined with information of habitat area and trajectory to full functional recovery, allow computation of the quantity of new habitat required to replace lost functions and services (Fonseca et al. 2000). These resource-based metrics depend on the ability to ascribe habitat value reflective of one or more important ecosystem services.

Such metrics have usually employed biological production to approximate ecosystem functions and services (Fonseca et al. 2000, Peterson et al. 2003). Biological production is a good proxy because many ecosystem services scale to increased biological production (Fonseca et al. 2000, Peterson et al. 2008a). Its effectiveness is, however, dependent on the trophic level chosen for assessment. Habitats with macrophytes provide many ecological functions and services, yet assessment of primary production does not always accurately represent services in all habitat types. Oyster reefs provide many ecological services despite having relatively low primary productivity (Lenihan & Peterson 1998, Coen et al. 2007). Also, compensating lost ecosystem services by stimulating primary production could lead to eutrophication and degradation of ecosystem functioning (Cloern 2001). Production at the secondary trophic level may better represent habitat value because it synthesizes contributions of local food production, food subsidies from other habitats, and the protective benefits of habitat structure. In fact, secondary production has been used to quantify benefits of habitat restoration (French McCay & Rowe 2003, Peterson et al. 2003). However, data of use in comparing estuarine habitat value are sparse, because few studies have quantified total secondary production across different estuarine habitats. Furthermore, no data are available for shoreline stabilization structures built to protect shorelines from erosion, such as bulkheads,

breakwaters, and stone sills. These structures are increasingly deployed on the southeast coast of the USA to protect property from rising sea level and increasing storm frequency resulting from climate change (NRC 2007).

Despite widespread perceptions of how different estuarine habitats compare in ecosystem functions and services, few data are available for habitat comparisons that can be used to predict consequences of anthropogenic impacts and the benefits of habitat restoration (NRC 2007). Our objective was to quantify food web support of the important estuarine shoreline habitats, using secondary production as a metric, by applying identical sampling in all habitats within a single estuarine system in North Carolina. Habitats sampled and compared were fringing salt marsh, intertidal flat, seagrass, shallow subtidal flat, oyster reef, and shoreline stabilization structures. Within each habitat, we (1) determined the seasonal biomass of the macrobenthic community, (2) estimated secondary production of the macrobenthic community, and (3) measured physical characteristics of the habitat. We then (4) compared the secondary production values across the different habitats, and (5) determined relative habitat value based on measures of secondary production.

MATERIALS AND METHODS

Study sites

Our field sites were at Harker's Island and Pine Knoll Shores located in Bogue Sound, and in Middle Marsh located in Back Sound, Carteret County, North Carolina, USA (Fig. 1). The mean tidal range for this region is ~1.0 m (NOAA tide datums, Beaufort, NC) and the salinity ranges from 20 to 34 (M. C. Wong pers. obs.). Mean water temperatures in March, June, September, and December of the years 2006 and 2007, the months when sampling occurred, were 12.5, 24.3, 27.5, 16°C (2006), and 13.5, 25.7, 26.3, 13.4°C (2007) (NOAA meteorological observations, Beaufort, NC).

At both Harker's Island and Pine Knoll Shores, 3 sites with different shoreline types were sampled: a natural shoreline, a stone sill, and a bulkhead. Hereafter, the sites will be referred to as Harker's Island-natural shoreline, -sill, -bulkhead, and Pine Knoll Shores-natural shoreline, -sill, and -bulkhead. All sites faced northeast. Both the stone sills were built ~10 yr ago, parallel to the natural shoreline. The stone sill at Harker's Island was 95 m in length, and

~10 m seaward from the marsh edge. The 100 m long stone sill at Pine Knoll Shores curved around an existing dock, and abutted directly against the marsh edge. To avoid confounding effects of the dock, our sampling site was the 30 m eastern portion of the sill. Both sills were constructed of large stone boulders and cobbles stacked vertically. The width of the sills was ~2 m. The base elevation was at low mean water, and the height extended to mean high water. The sills included two 2 m long openings to allow nekton access to the marsh during high tides. The openings were ~50 m apart at both sills. The portion of the sill sampled at Pine Knoll Shores incorporated 1 nekton opening. During sill construction at Pine Knoll Shores, *Spartina alterniflora* was transplanted by habitat managers in the low and mid-marsh, and *Spartina patens* in the high marsh to supplement existing plants. At the Harker's Island sill, marsh grasses were probably transplanted, but we are unable to confirm if a natural marsh existed prior to sill construction.

The bulkheads at Harker's Island and Pine Knoll Shores were constructed ~35 and 15 yr ago, respectively. A natural salt marsh was located seaward of the bulkhead at Pine Knoll Shores, but there was no marsh in front of the bulkhead at Harker's Island. The bulkhead at Harker's Island was constructed with vertical concrete slabs (~1.3 m high) on a base of horizontal concrete slabs (~1 m wide). The horizontal and vertical slabs and associated fauna were exposed at mean low water. During high tides, the water reached an elevation of ~0.40 m on the vertical slabs. The bulkhead at Pine Knoll Shores was constructed of corrugated plastic sheeting attached at the top of pressure-treated wood. Water reached the base of the wall only during extreme high tides or storm events. No fauna colonized this bulkhead.

An additional site was located at Middle Marsh, a complex of seagrass beds, salt marshes, oyster reefs, and mud flats. The habitats sampled were in a protected embayment at the southwestern end of the marsh complex. This site is part of the Rachel Carson National Estuarine Research Reserve, and no shoreline stabilization structures are present. Hereafter, this site is referred to as Middle Marsh-natural shoreline. This site was included because 3 habitats of particular interest in estuarine habitat restoration were present in combination: salt marsh, seagrass, and oyster reef.

At all sites, sampling for macroinfauna (>500 μm) in sediments and epifauna (>500 μm) on the shore-

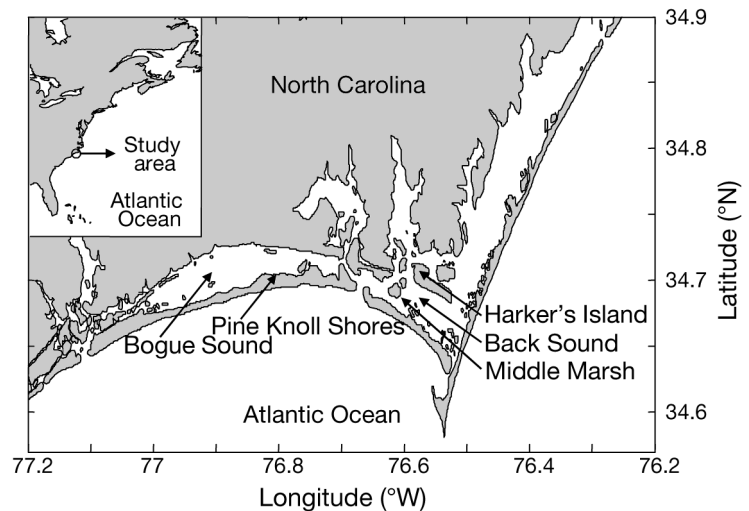


Fig. 1. Location of field sites in eastern North Carolina, USA

line stabilization structures was conducted in March, June, September, and December 2006. Marsh epifauna were sampled in the same months in 2007. Logistical constraints did not allow all sampling to be conducted in the same year.

Habitats sampled

Different combinations of salt marsh (M), oyster reef (OY), intertidal flat (IF), seagrass (SG), shallow subtidal flat (SF), and shoreline stabilization structures, i.e. sill (S) or bulkhead (B), were present at each site (Table 1). Salt marshes were sampled between the lower edge of the *Spartina patens* in the upper marsh and throughout the *Spartina alterniflora* to the lower marsh edge. The intertidal flats were exposed at mean low water in June and September, and covered with 5 to 10 cm of water in March and December. At sites without intertidal flats (i.e. Pine Knoll Shores-natural shoreline and -sill), the 0 to 10 m distance from the marsh or sill edge was sampled and called 'edge' habitat (E), and was usually covered by 10 to 15 cm water at mean low water. A natural oyster reef was present only at Middle Marsh-natural shoreline, and fringed the lower marsh edge. The overlaying oyster shell comprised of both living and non-living oysters and the underlying sediment matrix was sampled. Live oyster clumps were targeted for sampling. Seagrass (mixture of *Zostera marina* and *Halodule wrightii*) was defined as habitat between 0 and 0.6 m deep relative to mean low water. Live plants were targeted for sampling. We sampled shallow subtidal flats (sedimentary bottom

Table 1. Study sites and habitats in eastern North Carolina, USA. Habitats: B = bulkhead, S = sill, M = salt marsh, E = edge, OY = oyster, IF = intertidal flat, SG = seagrass, SF = subtidal flat. X = habitat sampled

Site	Shoreline length (m)	GPS coordinates	Habitat							
			B	S	M	E	OY	IF	SG	SF
Harker's Island										
Natural shoreline	25	34° 42.563' N, 76° 33.634' W			X			X	X	X
Sill	95	34° 42.696' N, 76° 33.962' W		X	X			X	X	X
Bulkhead	110	34° 42.577' N, 76° 33.663' W	X					X	X	X
Pine Knoll Shores										
Natural shoreline	30	34° 42.027' N, 76° 49.982' W			X	X			X	X
Sill	30	34° 42.079' N, 76° 49.894' W		X	X	X			X	X
Bulkhead	85	34° 42.238' N, 76° 49.196' W			X			X	X	X
Middle Marsh										
Natural shoreline	50	34° 41.479' N, 76° 37.229' W			X		X		X	

lacking macrophytes) between 0.6 and 1.0 m deep relative to mean low water. Shoreline stabilization structures supported dense epifaunal communities that were sampled.

Field and laboratory methods

During each sampling period, replicate core samples were taken from each habitat at each site. At Harker's Island and Pine Knoll Shores, samples were stratified throughout each habitat to span the elevation change of the habitat. Intertidal areas were visually divided into 3 equal zones parallel to the shore, while subtidal habitats were subdivided according to 3 equal depth zones. Four replicate samples were randomly taken from each of the 3 zones within each habitat, for a total of 12 replicates per habitat. At Middle Marsh, the elevation change across the habitats was negligible and so only 4 replicates were taken from the middle of each habitat type. All samples were spaced >5 m apart. Benthic macroinfauna were sampled using a 10 cm diameter hand core inserted 12 cm into the sediment. Each sample was sieved through a 0.5 mm sieve using salt water. Retained invertebrates were preserved in 5% buffered formalin with Rose Bengal stain sorted under a dissecting microscope and identified to phylum. We identified only to phylum because production can be adequately estimated from broad taxonomic categories, particularly when species body sizes are relatively similar (Brey 2001, Cusson & Bourget 2005, Dolbeth et al. 2005). We also wanted to represent a typical and realistic sampling scheme that might be employed by restoration managers. Species within each phylum had relatively similar

body size and ecology, with the exception of mollusca. Mollusca were further subdivided into small (≤ 10 mm shell length, SL) and large (> 10 mm SL) categories. In each replicate sample, the total abundance of organisms within each taxonomic category was determined. With the exception of large molluscs, dry mass (DM) per phylum was determined for each sample by drying at 60°C for 48 h. Ash free dry mass (AFDM) was then determined by combusting the dried samples in a muffle furnace at 500°C for 5 h, and subtracting the mass of the ash from the DM. Small molluscs were acidified in 10% HCl to remove the shells before drying. Biomass of large molluscs collected in cores was determined as for epifauna on shoreline stabilization structures and in marsh (see below).

Epifauna on the shoreline stabilization structures were sampled using a 0.0625 m² quadrat. The quadrat was placed at random locations on the sill or bulkhead where large epifauna were present, and all organisms within the quadrat were removed from the structure and frozen until processed. Percent cover of epifauna on the structures was recorded during sample collection and used to adjust data for the total area of the structure. Epifaunal samples were washed over a 0.5 mm sieve, sorted, and the total abundance of organisms within each taxonomic category was determined. To determine AFDM, fauna excluding large molluscs (> 10 mm SL) were dried and combusted. Shell lengths of the large molluscs (mostly oysters *Crassostrea virginica*) were measured for each individual and used to determine biomass. The length–weight relationship used to do this was determined from random samples of 80 oysters ranging from 10 to 110 mm SL from Harker's Island-bulkhead at each sampling month. These oysters

were measured, shucked, and dried to determine SL–DM relationships using the allometric relationship $M = a L^b$, where M = dry mass (g), L = shell length (mm), and parameters a and b ranged from 2.9×10^{-6} to 6.9×10^{-7} , and from 2.556 to 2.901, respectively across the sampling periods. DM was converted to AFDM of oysters using AFDM/DM = 0.6, as determined from a sample of 20 oysters.

Epifauna in the salt marshes were sampled using a 0.25 m² quadrat following the sampling design used for macroinfauna. The number of epifauna (periwinkles *Littoraria irrorata*, mussels *Geukensia demissa*, oysters *Crassostrea virginica*), and fiddler crab (*Uca* spp.) holes within each quadrat were counted. In March 2007, epifauna were collected by hand, preserved, dried, and combusted to determine AFDM. To reduce further destructive sampling, in each remaining sampling period 20 to 30 periwinkles, mussels, and oysters of various sizes were collected from each marsh, measured, shucked, and dried to determine length to DM relationships. DM was converted to AFDM using AFDM/DM = 0.6 (*Crassostrea*), 0.81 (*Geukensia*), and 0.89 (*Littoraria*) determined from a sample of 20 individuals from each species. Each fiddler crab hole was assumed to represent 1 crab (Jordão & Oliveira 2003). The proportion of females to males was assumed to be 2:1 (Colby & Fonseca 1984). Samples of ~20 male and ~20 female fiddler crabs were collected during each sampling period from the middle of each marsh, and carapace width (CW) measured. Mean CW was used to determine DM from published CW–DM relationships (Cammen et al. 1980, Colby & Fonseca 1984). DM was converted to AFDM using AFDM/DM = 0.743 (Brey 2001). When biomass of epifauna was determined from length to weight relationships, mean individual DM was multiplied by species density to provide estimates of biomass per unit area.

Secondary production estimates

Traditional methods of calculating secondary production, such as cohort or size class methods, require species-specific data. When studying whole communities, particularly ones with high species diversity, it is usually not possible to measure secondary production of all individual species, and thus alternative methods must be employed. Commonly used methods include use of (1) published production to biomass (P/\bar{B}) ratios and (2) those estimated from empirical models (Gray & Elliott 2009). These methods allow calculation of secondary production for com-

posite groups of organisms. Although separate information for each species in the system is preferred, most ecosystem models utilize larger taxonomic groups, and the 2 methods for calculating secondary production are acceptable alternatives to more traditional approaches (Nilssen et al. 2006).

We calculated secondary production in each habitat using both published P/\bar{B} ratios and P/\bar{B} ratios estimated from an empirical model. Use of published P/\bar{B} ratios is a more general approach, and does not require additional measurements of environmental parameters. Inclusion of both methods in our study allowed us to compare their performance, and to determine if published P/\bar{B} ratios provide an easier and accurate alternative to estimation from empirical models for restoration managers. For the published P/\bar{B} ratio method, we calculated secondary production by multiplying mean annual AFDM of taxonomic groups by: 3.37 for Annelida, 4.85 for Arthropoda, 0.34 for Echinodermata, 2.3 for small Mollusca, 2.01 for large Mollusca, 1.20 for Bryozoa, 1.81 for Chordata (Ascidiacea), 1.81 for Cnidaria (Anthozoa), and 3.4 yr⁻¹ for Nemertea and Platyhelminthes (Dame 1976, Bader 2000, Cusson & Bourget 2005). These P/\bar{B} ratios were all determined using classical assessment methods (cohort- and size-based). Total secondary production in each habitat was determined by summing values for each taxonomic group. To account for the negative correlation between body size and P/\bar{B} ratios (Banse & Mosher 1980), and because largest body size differences were observed for molluscs, we calculated production separately for small (≤ 10 mm SL) and large (> 10 mm SL) molluscs.

For the empirical model method, P/\bar{B} ratios were estimated using Brey's (2001) model (v. 4–04):

$$\begin{aligned} \log(P/\bar{B}) = & 7.947 - [2.294 \times \log(M)] - \\ & [2409.856 \times 1/(T + 273)] + (0.168 \times 1/D) + \\ & (0.194 \times SubT) + (0.180 \times InEpi) + (0.277 \times \\ & MoEpi) + (0.174 \times Taxon1) - (0.188 \times Taxon2) \\ & + (0.330 \times Taxon3) - (0.062 \times Habitat1) + \\ & [582.851 \times \log(M) \times 1/(T + 273)] \end{aligned}$$

where M = mean individual body mass (kJ), T = bottom water temperature (°C), and D = water depth (m). Dummy variables are 1 (yes) or 0 (no) for subtidal species (*SubT*), infauna (*InEpi*), motile epifauna (*MoEpi*), Annelida or crustacea (*Taxon1*), Echinodermata (*Taxon2*), Insecta (*Taxon3*), and Lake (*Habitat1*). Calculations were implemented in the spreadsheet provided by Brey (2001). Mean individual body mass was computed by dividing mean annual biomass per phylum by mean annual density per phylum (Brey 2001, Nilssen et al. 2006). Colonial

organisms (i.e. bryozoans) were not included in the calculations. AFDM was converted to kJ using factors provided by Brey (2001). Production for each taxonomic group was derived by multiplying mean annual biomass by the P/B ratios generated by the model for the respective group in each habitat. Total secondary production of the benthic community in each habitat was determined by summing production of each taxonomic group. Separate estimates for small and large molluscs were calculated.

Habitat characteristics

To determine percent organic content of the surface sediments, 3 replicate samples (3 cm diameter \times 7 cm deep) were collected in September 2007 from the middle of every habitat at each site. The samples were oven dried at 60°C for 48 h, weighed, combusted at 500°C for 8 h, and reweighed. Percent organic content was calculated as $(DM - \text{weight after combustion})/DM \times 100$. Seagrass shoot density (*Zostera marina* and *Halodule wrightii*) was determined in July–August 2006 by counting the number of shoots in 5 to 10 quadrats (0.0156 m²) haphazardly spaced >10 m apart in the seagrass beds. Shoot density of *Spartina alterniflora* in marshes was determined by counting the number of live stems per 0.0625 m² quadrat in September 2007 and averaging across habitat. Oyster density was determined from the core samples in oyster habitats and from quadrats on shoreline stabilization structures, and averaged across dates.

Statistical analyses

Analyses of biomass were conducted for each site because suites of habitats differed at each. Two-way ANOVAs with habitat and date as fixed factors and biomass as the dependent variable were used. Type III sums of squares based on unweighted marginal means were used to account for the unequal number of replicates per habitat (Quinn & Keough 2002). Secondary production estimates were compared visually. Habitat characteristics were compared across habitats within each site using 1-way ANOVAs with habitat as the fixed factor, and percent organic content of surface sediments, *Spartina alterniflora* shoot density, seagrass (*Zostera marina* and *Halodule wrightii*) shoot density, or oyster density as the dependent variable. Seagrass shoot density, marsh plant shoot density, or oyster density were compared

across sites using 1-way ANOVAs. For all ANOVAs, residual plots were examined to determine if the underlying assumptions of homogeneity of variance and normality were violated. Violations were corrected by transforming data using $\log(x + 1)$ and by weighting the analyses by the replicate variance⁻¹ (Draper & Smith 1998). Significant main effects and interactions were examined using Tukey's HSD test. All statistical analyses were done using R v.2.8.1 statistical software (www.r-project.org).

RESULTS

General faunal description

Macrobenthic fauna (≥ 0.5 mm) from phyla Annelida, Arthropoda, and Mollusca comprised >80% of the total biomass and >95% of the estimated secondary production in most habitats at each site (Figs. 2 to 4). Remaining biomass and production was from Bryozoa, Chordata, Cnidaria, Echinodermata, Nemertea, and Platyhelminthes. At all sites, the highest number of phyla was observed in the seagrass and oyster reef (8 to 9 phyla per habitat). At Middle Marsh-natural shoreline, molluscs (mainly *Crassostrea virginica*) comprised >90% of the biomass and >70% of the secondary production in the oyster reef across all dates. At sites with shoreline stabilization structures, molluscs comprised >92% of the biomass and >90% secondary production on the stone sills or bulkheads across all dates. Marsh epifauna constituted 54 to 78% of the biomass and 64 to 74% of the secondary production in the marsh at most dates at each site, except at Harker's Island-sill. Marsh epifauna were dominated by fiddler crabs (*Uca* spp.) and suspension feeders (*C. virginica* and *Geukensia demissa*) at all sites except Harker's Island-sill, where *Littoraria irrorata* and *Uca* spp. were dominant.

Biomass across habitats

Total biomass of macrobenthic communities across habitats and months ranged from 0.220 to 713.5 g AFDM m⁻² (Fig. 2). At all sites, the interaction between habitat and date was significant (Table 2). Biomass of macrobenthic communities was consistently higher in structured habitats than unstructured habitats at all Harker's Island and Pine Knoll Shores sites (Table 2, Fig. 2). At Middle Marsh, macrobenthic biomass was significantly highest in the oyster habitat

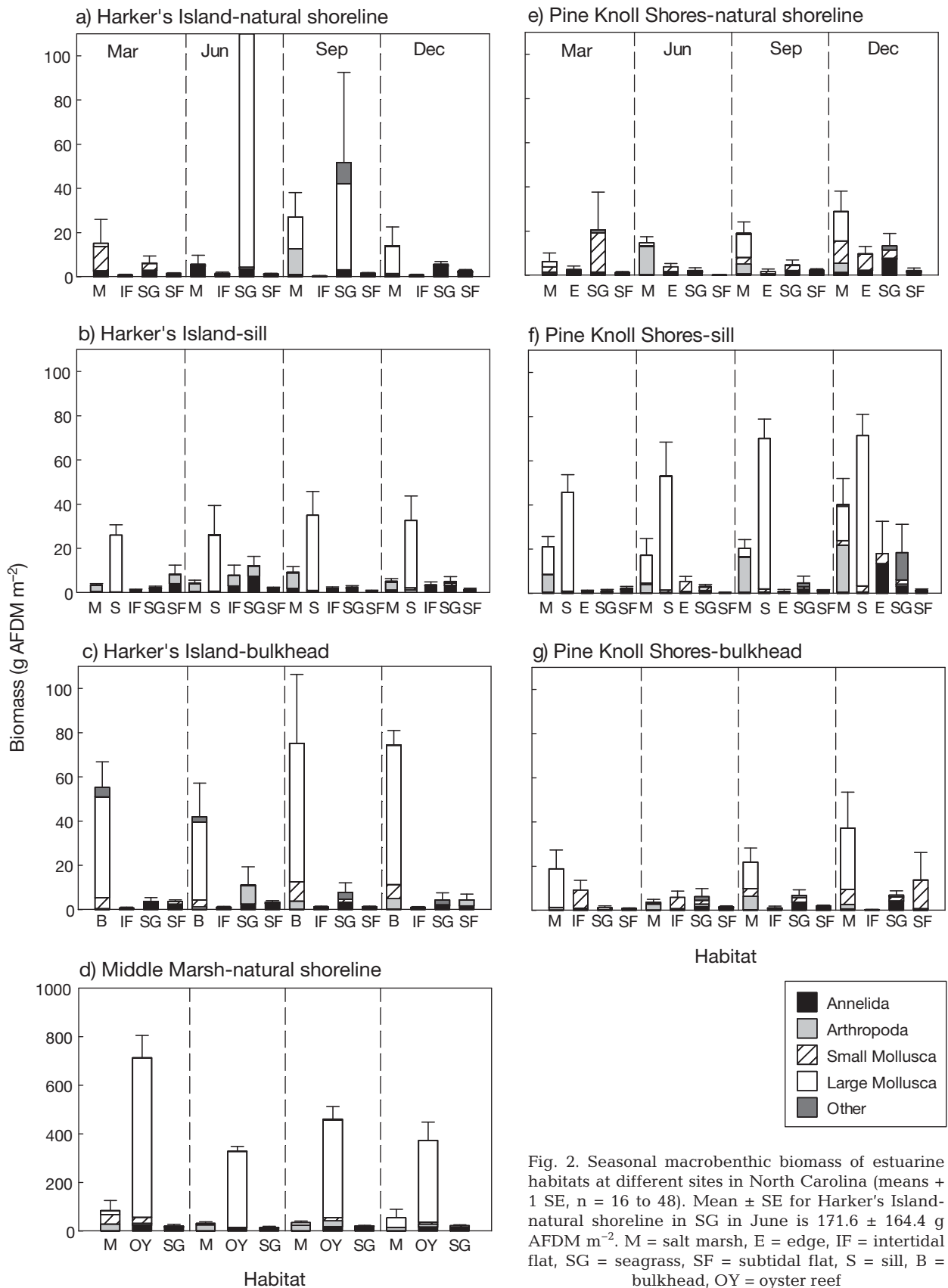


Table 2. Fixed factor ANOVA results for total macrobenthic biomass (g AFDM m⁻²). Data were log(x + 1) transformed. H = habitat, D = date. See Table 1 for habitat abbreviations. For post-hoc comparisons, treatment level means are listed in increasing magnitude; those sharing a common underline do not differ significantly

Site	Source of variation	Effect MS	df	F	p	Post-hoc comparison (H × D)	
Harker's Island							
Natural shoreline	H	26.76	3	26.78	<0.0001	Mar: <u>IF SF M SG</u>	M: <u>Jun Mar Dec Sep</u>
	D	1.845	3	1.84	0.140	Jun: <u>IF SF M SG</u>	IF: <u>Sep Dec Mar Jun</u>
	H × D	2.042	9	2.044	0.037	Sep: <u>IF SF SG M</u>	SG: <u>Mar Dec Jun Sep</u>
						Dec: <u>IF SF M SG</u>	SF: <u>Jun Sep Mar Dec</u>
Residual	0.999	176					
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Sill	H	18.63	4	18.6	<0.0001	Mar: <u>IF SG M SF S</u>	M: <u>Jun Mar Dec Sep</u>
	D	0.625	3	0.63	0.600	Jun: <u>SF IF M SG S</u>	S: <u>Jun Dec Mar Sep</u>
	H × D	2.806	12	2.80	0.002	Sep: <u>SF IF SG M S</u>	IF: <u>Mar Sep Dec Jun</u>
						Dec: <u>SF IF SG M S</u>	SG: <u>Mar Sep Dec Jun</u>
Residual	1.000	188				SF: <u>Sep Dec Jun Mar</u>	
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Bulkhead	H	99.26	3	99.26	<0.0001	Mar: <u>IF SG SF B</u>	B: <u>Jun Mar Sep Dec</u>
	D	0.403	3	0.403	0.750	Jun: <u>IF SF SG B</u>	IF: <u>Mar Jun Dec Sep</u>
	H × D	2.040	9	2.040	0.039	Sep: <u>IF SF SG B</u>	SG: <u>Mar Dec Jun Sep</u>
						Dec: <u>IF SF SG B</u>	SF: <u>Sep Dec Mar Jun</u>
Residual	1.000	144					
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Pine Knoll Shores							
Natural shoreline	H	22.31	3	22.9	<0.0001	Mar: <u>SF E M SG</u>	M: <u>Mar Jun Sep Dec</u>
	D	8.143	3	8.14	<0.0001	Jun: <u>SF SG E M</u>	E: <u>Sep Mar Jun Dec</u>
	H × D	3.336	9	3.33	0.0009	Sep: <u>E SF SG M</u>	SG: <u>Jun Sep Mar Dec</u>
						Dec: <u>SF E SG M</u>	SF: <u>Jun Mar Dec Sep</u>
Residual	1.001	176					
<hr/>							
Sill	H	170.3	4	170.3	<0.0001	Mar: <u>E SG SF M S</u>	M: <u>Jun Mar Sep Dec</u>
	D	7.857	3	7.857	<0.0001	Jun: <u>SF E SG M S</u>	S: <u>Mar Jun Sep Dec</u>
	H × D	3.682	12	3.682	<0.0001	Sep: <u>E SF SG M S</u>	E: <u>Sep Mar Jun Dec</u>
						Dec: <u>SF E SG M S</u>	SG: <u>Mar Jun Sep Dec</u>
Residual	1.000	188				SF: <u>Jun Dec Sep Mar</u>	
<hr/>							
Bulkhead	H	12.85	3	12.9	<0.0001	Mar: <u>SG SF IF M</u>	M: <u>Jun Mar Sep Dec</u>
	D	1.810	3	1.82	0.1445	Jun: <u>SF IF M SG</u>	IF: <u>Dec Sep Jun Mar</u>
	H × D	4.849	9	4.88	<0.0001	Sep: <u>IF SF SG M</u>	SG: <u>Mar Jun Sep Dec</u>
						Dec: <u>IF SF SG M</u>	SF: <u>Mar Jun Dec Sep</u>
Residual	0.993	175					
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Middle Marsh							
Natural shoreline	H	101.9	2	102.1	<0.0001	Mar: <u>SG M OY</u>	M: <u>Jun Dec Sep Mar</u>
	D	12.53	3	12.55	<0.0001	Jun: <u>SG M OY</u>	OY: <u>Jun Dec Sep Mar</u>
	H × D	6.650	6	6.66	<0.0001	Sep: <u>SG M OY</u>	SG: <u>Jun Mar Sep Dec</u>
						Dec: <u>SG M OY</u>	
Residual	0.998	36					

compared to marsh or seagrass. Macrobenthic biomass in the marsh at Middle Marsh was higher than in seagrass, a pattern also observed at all other sites except Harker's Island-natural shoreline, where the opposite trend was observed because of the patchy distribution of molluscs in seagrass (Table 2, Fig. 2). At sites with shoreline stabilization structures, highest macrobenthic community biomass was on the structures themselves compared to all other habitats. Seasonal patterns of macrobenthic community biomass were not evident (Table 2, Fig. 2).

Secondary production across habitats

Secondary production calculated using published P/\bar{B} ratios ranged across habitats from 3.253 to 853.7 g AFDM $m^{-2} yr^{-1}$ when large molluscs were

included, and from 3.253 to 147.0 g AFDM $m^{-2} yr^{-1}$ when large molluscs were excluded (Fig. 3). Secondary production calculated using P/\bar{B} ratios from the empirical model when large molluscs were included ranged from 4.945 to 467.3 g AFDM $m^{-2} yr^{-2}$, and from 2.592 to 160.0 g AFDM $m^{-2} yr^{-2}$ when large molluscs were excluded (Fig. 4). At sites with shoreline stabilization structures, secondary production calculated using both methods was consistently higher on the structures than in other habitats when large molluscs were included (Figs. 3 & 4). When large molluscs were excluded, secondary production on the shoreline stabilization structures was either similar to or less than secondary production in other habitats (Figs. 3 & 4). The importance of large molluscs to overall secondary production was also illustrated at Middle Marsh-natural shoreline, where secondary production was 5 times higher in the

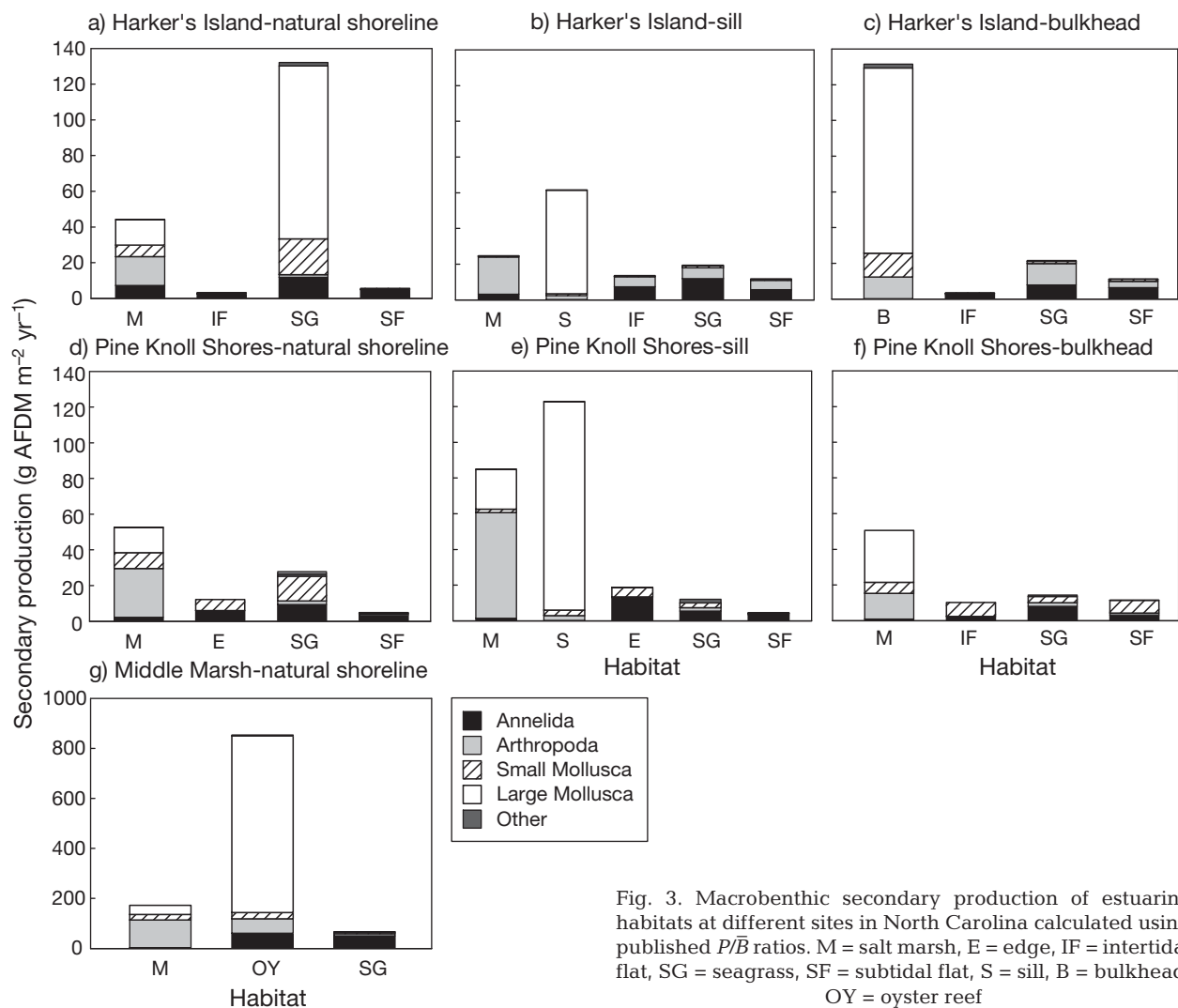


Fig. 3. Macrobenthic secondary production of estuarine habitats at different sites in North Carolina calculated using published P/\bar{B} ratios. M = salt marsh, E = edge, IF = intertidal flat, SG = seagrass, SF = subtidal flat, S = sill, B = bulkhead, OY = oyster reef

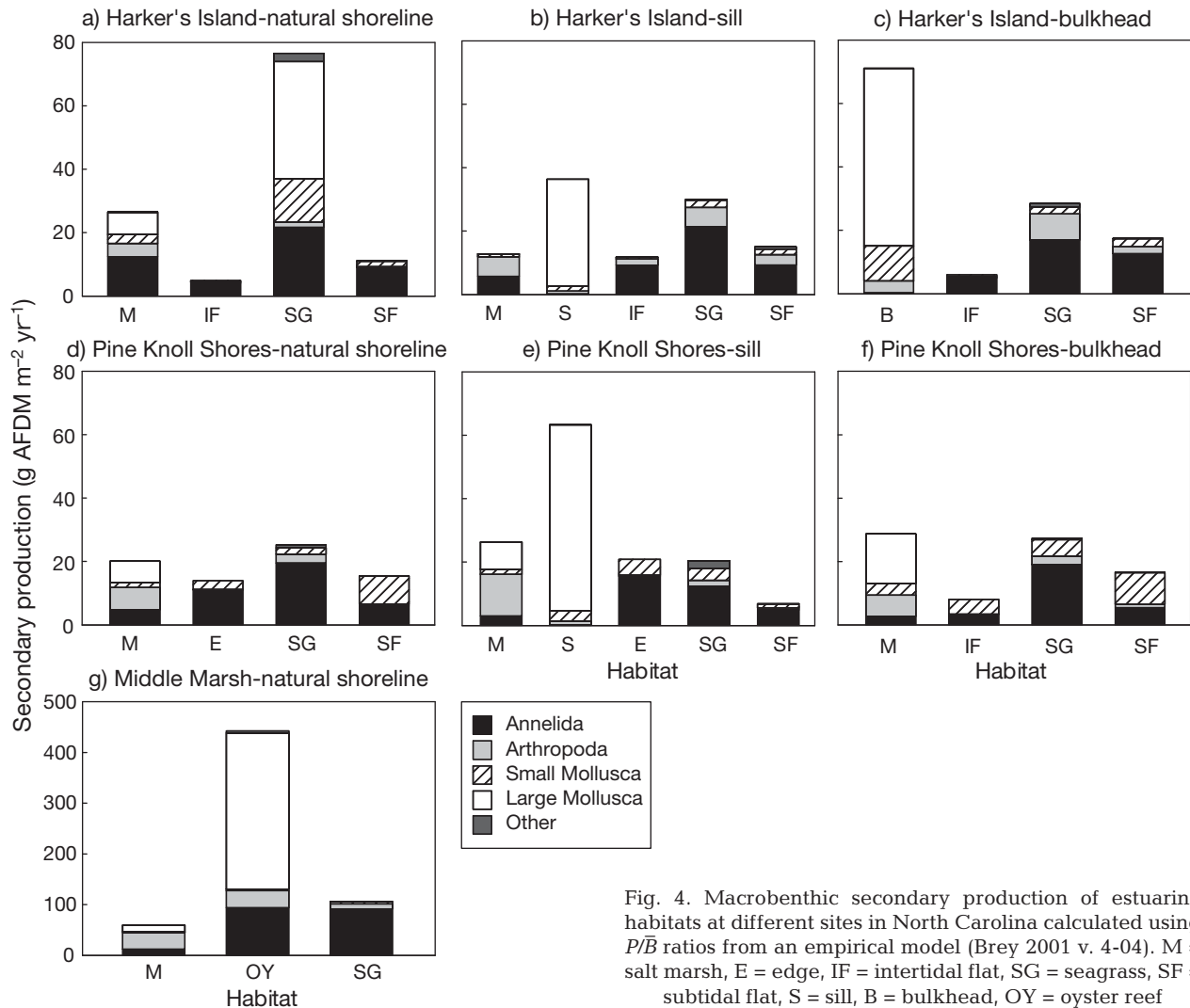


Fig. 4. Macrobenthic secondary production of estuarine habitats at different sites in North Carolina calculated using P/\bar{B} ratios from an empirical model (Brey 2001 v. 4-04). M = salt marsh, E = edge, IF = intertidal flat, SG = seagrass, SF = subtidal flat, S = sill, B = bulkhead, OY = oyster reef

oyster reef than in the marsh or seagrass when large oysters were included in the calculations (Figs. 3 & 4). At sites where both structured and non-structured habitats were sampled, secondary production in the marsh was usually higher than in the unstructured habitats, particularly when calculated using published P/\bar{B} ratios (Fig. 3). Secondary production in seagrass was also higher than in unstructured habitats, except at Pine Knoll Shores-sill where it was lower (published P/\bar{B} ratios) or equivalent (P/\bar{B} ratios from the empirical model) to edge habitat (Figs. 3 & 4).

P/\bar{B} ratios for the main taxonomic groups calculated using the empirical model varied across habitat (Table 3). Mean P/\bar{B} ratios across habitats and sites were 5.58, 3.32, 0.98, and 3.03 for Annelida, Arthropoda, large Mollusca, and small Mollusca, respectively. P/\bar{B} ratios calculated using the empirical

model were higher than those used from the literature for Annelida and small Mollusca, while they were lower for Arthropoda and large Mollusca.

Table 3. Habitat-specific P/\bar{B} ratios estimated from the empirical model for the 4 major taxonomic groups. Habitat abbreviations are given in Table 1. nd = no data

Habitat	Annelida	Arthropoda	Mollusca	
			Large	Small
B	4.17	1.52	1.08	1.91
S	3.89	2.08	1.09	2.65
M	8.20	1.44	0.97	1.63
E	5.17	5.01	nd	2.28
IF	5.38	3.59	nd	3.61
OY	5.19	2.86	0.87	2.49
SG	6.89	5.30	0.93	3.36
SF	5.76	4.77	nd	6.32

Habitat characteristics

Percent organic content of surface sediments ranged across habitats from 0.36 to 16.1% (Table 4). It differed significantly across habitats at Harker's Island-sill, Middle Marsh-natural shoreline, Pine Knoll Shores-natural shoreline, and Pine Knoll Shores-sill ($F_{2-3, 6-8} = 6.32$ to 96.8 , $p < 0.0001$ to $p = 0.016$), driven by higher organic content in marsh sediments than in other habitats (Tukey's test, $p < 0.05$). Seagrass shoot density ranged from 874 to 2971 shoots m^{-2} (Table 4) and differed significantly among sites ($F_{6, 79} = 4.74$,

$p = 0.0004$), being highest at Middle Marsh-natural shoreline than at other sites (Tukey's test, $p < 0.05$). Stem density of *Spartina alterniflora* ranged from 140 to 259 stems m^{-2} , and did not differ significantly among sites (Table 4, $F_{5, 51} = 2.01$, $p = 0.093$). Oyster density was significantly affected by site when oyster density at Middle Marsh-natural shoreline and on the shoreline stabilization structures were compared ($F_{3, 59} = 3.9 \times 10^6$, $p < 0.0001$). Oyster density was highest in the oyster reef at Middle Marsh, while it did not differ among shoreline stabilization structures (Tukey's test, $p < 0.05$).

Table 4. Physical characteristics of the different habitats sampled at each site. The salt marsh macrophyte was *Spartina alterniflora*, seagrasses were *Zostera marina* and *Halodule wrightii*. Oysters were *Crassostrea virginica*. Data are mean \pm 1 SE. $n = 3, 12, 4-30$ for sediment organic content, marsh grass shoot density, and seagrass shoot density, respectively. Habitat abbreviations are given in Table 1

Site	Habitat	Sediment organic content (%)	Density		
			Macrophyte (shoots m^{-2})	Oyster (ind. m^{-2})	
Pine Knoll Shores					
Natural shoreline	M	3.87 \pm 0.31	259 \pm 50		
	E	0.74 \pm 0.10			
Sill	SG	0.58 \pm 0.02	1560 \pm 151		
	SF	0.54 \pm 0.02			
	M	2.06 \pm 0.39	275 \pm 65		
	S			382 \pm 38	
	E	0.53 \pm 0.06			
Bulkhead	SG	0.73 \pm 0.02	1749 \pm 172		
	SF	0.36 \pm 0.02			
	B			0	
	M	2.34 \pm 1.32	277 \pm 52		
	IF	0.63 \pm 0.04			
Harker's Island	SG	0.64 \pm 0.17	1680 \pm 303		
	SF	0.56 \pm 0.03			
	Natural shoreline	M	0.43 \pm 0.06	140 \pm 36	
	IF	0.47 \pm 0.04			
	SG	0.82 \pm 0.20	1929 \pm 401		
Sill	SF	0.65 \pm 0.17			
	M	0.56 \pm 0.01	152 \pm 28		
	S			332 \pm 45	
	IF	0.47 \pm 0.07			
	SG	0.68 \pm 0.03	874 \pm 113		
Bulkhead	SF	0.44 \pm 0.03			
	B			451 \pm 80	
	IF	0.49 \pm 0.04			
	SF	0.60 \pm 0.03			
	SG	0.53 \pm 0.02	1888 \pm 193		
Middle Marsh					
Natural shoreline	M	16.1 \pm 0.88	152 \pm 34		
	OY	7.4 \pm 1.01		1411 \pm 325	
	SG	3.9 \pm 0.33	2971 \pm 363		

DISCUSSION

Our field study used secondary production as a metric of food web support to evaluate different estuarine habitats. Comparisons of secondary production across habitats were similar between methods of calculation, despite absolute values differing. Comparisons among habitats suggest that certain habitats provide more food web support to higher trophic levels than others. In particular, secondary production in habitats with hard emergent structure (i.e. oyster reef, stone sills, and bulkheads) was consistently higher than in other habitats. In fact, the oyster reef at Middle Marsh-natural shoreline had the highest secondary production of any habitat sampled, with mean annual values of 853.7 (from published P/\bar{B} ratios) and 467.3 (P/\bar{B} ratios from the empirical model) g AFDM $m^{-2} yr^{-1}$. Comparable values of high secondary production in oyster reefs ranging from 243 to 2282 g AFDM $m^{-2} yr^{-1}$ have been found in other studies from the southeastern USA (using estimated P/\bar{B} ratio of 2.01; Bahr 1976, Dame 1979, Nestlerode 2004). In our study, we were able to directly compare secondary production in the oyster reef to other habitats at Middle Marsh-natural shoreline. Annual secondary production in the oyster reef was 5.0 (from published P/\bar{B} ratios) and 7.0 (P/\bar{B} ratios from the empirical model) times higher than in the salt marsh. When compared to seagrass, oyster reef production was 13.0 (from published P/\bar{B} ratios) and 4.2 (P/\bar{B} ratios from the empirical model) times higher. The high secondary production of oyster habitats compared to other habitats was also observed by Peterson et al. (2008b), where annual secondary production of oyster reefs was 24.8, 20.7, 21.8, and 22.4 times higher than in salt marsh, seagrass *Zostera marina*, intertidal flat, and subtidal flat, respectively. In our current study, large molluscs (mainly oysters) comprised 86 to 97% of the total sec-

ondary production in the oyster reef. Arthropods, annelids, and small molluscs constituted the remaining production. Bahr (1976) found that oysters comprised the majority (~95%) of the total secondary production of an oyster reef in Sapelo Island, GA. While the oysters themselves provide food web support to higher trophic levels, the associated macroinvertebrates also contribute important trophic linkages (Grabowski et al. 2005), and tertiary consumers are often higher in abundance on oyster reefs than nearby sand flats (Lenihan et al. 2001). The high secondary production of oyster reefs thus provides quantitative evidence that this estuarine habitat delivers the greatest food web support per unit area than any other natural estuarine habitat.

The shoreline stabilization structures also supported highly productive epibenthic communities relative to all other habitats lacking hard vertically emergent structure. Annual secondary production on the shoreline stabilization structures at Harker's Island-sill, -bulkhead, and Pine Knoll Shores-sill ranged from 61.5 to 131.4 (from published P/\bar{B} ratios) and 36 to 71 (P/\bar{B} ratios from empirical model) g AFDM $m^{-2} yr^{-1}$. Secondary production on the shoreline stabilization structures was consistently higher on the structures than in other habitats within each site. This pattern was evident even for comparisons with habitats traditionally considered to provide high food web support (i.e. salt marsh and seagrass). However, annual estimates of secondary production from the shoreline stabilizations were 6.5 to 13.9 (from both methods of calculation) times lower than in the oyster reef at Middle Marsh. This pattern emerged even though oysters themselves constituted >79% of the total secondary production on the shoreline stabilization structures. Oyster density was higher at Middle Marsh than on the shoreline stabilization structures, and may have lead to this pattern. The absence of a sediment matrix on the shoreline stabilization structures had little effect on total secondary production, because the majority of production was from the oysters themselves.

In addition to habitats with hard structure, our study showed that habitats with emergent macrophytes were often higher in secondary production than habitats without structural elements. Seagrass at all Harker's Island and Pine Knoll Shores sites showed this pattern well, particularly when secondary production was calculated using P/\bar{B} ratios from the empirical model. Several studies have also found higher secondary production in seagrass beds when compared to non-structured sand and mud flats (e.g. Heck et al. 1995, Dolbeth et al. 2003,

Bologna 2006). Our results reflect the long-held paradigm that seagrass beds provide high ecosystem services. Our values of secondary production in seagrass are comparable to those in other studies which range from 20 to 240 g AFDM $m^{-2} yr^{-1}$ (Bologna & Heck 2002, Dolbeth et al. 2003, Dolbeth et al. 2005, Bologna 2006). Differences in magnitude of secondary production among studies may be partially related to seagrass bed characteristics. We found that secondary production in seagrass at Middle Marsh, which had highest shoot density, was higher than at other sites. Seagrass shoot density is sometimes positively correlated with macrofaunal abundance and thus secondary production (e.g. Homziak et al. 1982, Boström & Bonsdorff 2000; but see Boström et al. 2006).

Secondary production in salt marsh was also higher than in most non-structured habitats. This was particularly observed at all sites at Pine Knoll Shores, which had higher epifaunal densities compared to marshes at Harker's Island (not shown). High *Spartina alterniflora* density at both Pine Knoll Shores and Middle Marsh may have provided protection from predators (Lin 1989) or increased surface area for attachment of epifauna (Bertness 1984). High organic content of marsh sediments at the Pine Knoll Shores sites may have also enhanced diets of fiddler crabs and suspension feeders (Kreeger & Newell 2000).

In general, our field sampling demonstrated that structured estuarine habitats provide high food web support when compared to unstructured habitats. Suspension feeders were highly productive on oyster reefs, shoreline stabilization structures, and in marshes, suggesting production is partly influenced by external food subsidies and facilitated by support from habitat structure. Natural habitats can be ranked in our results from highest secondary production to lowest as follows: oyster reef > salt marsh > seagrass > intertidal flat and subtidal flat. Undesirable aspects of shoreline stabilization structures make their inclusion difficult in this ranking of food web support by habitat (further discussed below). We are aware of only 2 other field studies that compare macrobenthic communities across different estuarine habitats that include reef building organisms. Ferraro & Cole (2007) used macrobenthic diversity, density, and biomass to rank habitat value as: seagrass *Zostera marina* and oyster reef *Crassostrea gigas* \geq salt marsh *Spartina alterniflora* \geq mud shrimp *Upogebia pugettensis* habitat \geq bare mud/sand \geq ghost shrimp *Neotrypaea californiensis* habitat and subtidal flat. Hosack et al. (2006) found that epifaunal

density was higher in seagrass *Zostera marina* and oyster reef *Crassostrea gigas* than in bare mud, and that macroinfaunal density was highest in seagrass, intermediate in oyster reef, and lowest in bare mud. These results resemble ours, except that our sampling reveals a stronger dominance by oyster reef.

While stone sills and bulkheads are built primarily for erosion control of shorelines, our study shows that associated epifaunal communities may provide important food web support if accessible to consumers. The value of shoreline stabilization structures in terms of food web support depends on the fate of the organic matter produced. There is some evidence that organic matter from the structures can be transported by water currents to adjacent habitats (Schaal et al. 2008) or is consumed by birds (M. C. Wong unpubl. data). In this manner, shoreline stabilization structures could provide a food web benefit in addition to protecting shorelines from erosion. However, the effects of the structures on the macrobenthos and predators in nearby habitats may reduce or even negate these benefits. Macrobenthic abundance and biomass are often highest in the subtidal adjacent to natural marsh shorelines, intermediate in the subtidal adjacent to sills, and lowest in the subtidal adjacent to bulkheads (Seitz et al. 2006). Fish and crab abundance and diversity are often higher at natural shorelines than at sills or bulkheads (Peterson et al. 2000, Seitz et al. 2006), suggesting that export of organic material from shoreline stabilization structures via direct consumption by nekton may not be readily achieved. Additionally, shoreline stabilization structures can have negative impacts on associated salt marshes. Bulkheads prevent marsh transgression in response to sea level rise, resulting in loss of marsh habitat and food web benefits (Peterson et al. 2008a). Stone sills allow marsh transgression because they are constructed seaward of the marsh, but potentially reduce nekton access during high tides, disrupting important habitat linkages (although see Currin et al. 2007). Calculation of net food web support from epifaunal communities on the shoreline stabilization structures must take into account services lost from adjacent habitats affected by the structures.

Comparison of our secondary production values estimated using the 2 sources of P/\bar{B} ratios indicated that absolute values differed according to the method of calculation. Generally, secondary production estimates from published P/\bar{B} ratios were approximately 1.5 to 3 times higher than estimates from the empirical model. These discrepancies are related in part to the difference in P/\bar{B} ratios for large molluscs

between the 2 methods (0.998 yr⁻¹ from the empirical model [averaged across habitat] and 2.01 yr⁻¹ from the literature). The literature value is likely more accurate because it was calculated for adult oysters, the main organism that comprised our large mollusc category, in nearby South Carolina (Dame 1976). The mean P/\bar{B} ratio for large molluscs from the empirical model is also lower than those calculated for mollusca (1.77 yr⁻¹) and filter feeders (1.82 yr⁻¹) in a recent review (Cusson & Bourget 2005). The difference in absolute production estimates between the 2 methods may have also resulted from using the same published P/\bar{B} ratios across all habitat types. P/\bar{B} ratios calculated using the empirical model differed across habitats, a pattern observed in other studies (Tumbiolo & Downing 1994, Dolbeth et al. 2003, Cusson & Bourget 2005). Because our absolute values of secondary production depended in part on the method of calculation, we caution against using these secondary production estimates as benchmarks for future studies that do not use similar calculation methods. However, relative patterns of secondary production across habitats were not influenced by the calculation method, and these robust relationships indicate relative habitat values and provide important information for future restoration of estuarine habitats.

While the focus of our study was on habitat-specific secondary production, the biomass data also provided the opportunity to gain insight into the seasonal dynamics of macrobenthic invertebrates. Contrary to other studies (e.g. Dolbeth et al. 2003, Bologna 2006), clear patterns in macrobenthic invertebrate biomass across seasons were not observed. Seasonal signals may have been dampened by large-bodied molluscs, by our inability to catch the small new recruits, or by our level of taxonomic resolution. More importantly, better characterization of the short- and long-term temporal variability in the various habitats would have enhanced our ability to detect seasonal patterns (Morrisey et al. 1992, Thrush et al. 1994).

The distribution and diversity of estuarine habitats in the southeastern USA will increasingly be influenced by anthropogenic stressors (Scavia et al. 2002, Orth et al. 2006, IPCC 2007). Our study shows that a decrease in the extent of highly productive biogenically structured habitats represents a substantial loss of food web support. Conversion of these habitats to ones ranking lower in habitat value, through processes such as rising sea level or eutrophication, will not fully replace lost food web support. Thus, without appropriate habitat restoration that includes

structural habitat elements, the fate of southeastern USA estuaries impacted by anthropogenic stressors will be loss of habitat diversity and prevalence of low-trophic-supporting habitats. Our confirmation of habitats with vertical emergent structure as providing high food web support could greatly enhance the success of restoration projects and overall management and conservation of estuarine habitats.

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