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Effects of Bridge Shading on Estuarine Marsh Benthic Invertebrate Community Structure and Function

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ABSTRACT / The effect of bridge shading on estuarine marsh food webs was assessed by comparing benthic invertebrate communities beneath seven highway bridges with marshes outside of bridge-affected areas (reference marshes). We used light attenuation and height–width ratio (HW ratio), which takes into account the two main bridge characteristics that determine the degree of shading, to quantify the impact of shading on invertebrate communities. Low bridges, with HW ratio <0.7 and light attenuation greater than 85–90%, had benthic invertebrate densities and diversity that were significantly lower than reference marshes. Density of benthic invertebrates at low bridges was 25–52% (29,685–72,920 organisms/m^2) of densities measured in adjacent reference marshes (119,329–173,351 organisms/m^2). Likewise, there were fewer taxa under low bridges (5.8/11.35 cm^2 core) as compared to the reference marshes (9.0/11.35 cm^2 core). Density of numerically dominant taxa (e.g., oligochaetes and nematodes) as well as surface- and subsurface deposit feeders also were reduced under low bridges. Decreased invertebrate density, diversity, dominant taxa, and alterations of trophic feeding groups beneath low bridges was correlated with diminished above- and below-ground macrophyte biomass that presumably resulted in fewer food resources and available refuges from predators. With a greater knowledge of bridge shading effects, bridge construction and design may be improved to reduce the impacts on estuarine benthic invertebrate communities and overall ecosystem structure and function.

Coastal wetlands provide an important interface between terrestrial and marine habitats. Salt, brackish, and tidal freshwater marshes reduce erosion by protecting coastlines from storm surges and wave action (Broome and others 1986). These marshes also serve as a sink in the global carbon cycle and sequester organic matter and nutrients (Schlesinger 1977, Friedman and DeWitt 1978, Armentano 1980, Nixon 1980). Coastal wetlands play an important role in the human economy by offering habitat for commercially important juvenile fish and shellfish while contributing detritus to estuarine food webs (Teal 1962, de la Cruz 1973, Haines and Montague 1979, Peterson and others 1986, Peterson and Howarth 1987).

KEY WORDS: Bridge shading; Light attenuation; Benthic invertebrates; North Carolina; Ecosystem structure and function; Human impacts; Coastal wetlands

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With the expansion of human population and the demand for coastal dwellings and agricultural land, many coastal wetlands have been degraded or destroyed (Langis and others 1991, Moy and Levin 1991, Zedler 1992). Continuous population growth demands new construction and improvements to physical infrastructure such as bridges, docks, moorings, and marinas. These structures, however, can have an adverse impact on marsh structure and function. The initial construction of these structures may cause some short-term harm to marshes, but longer-term, chronic shading may have a greater impact on overall structure and function than the initial construction. Light attenuation is one of the principal limiting factors of primary productivity (microalgae and emergent macrophytic vegetation) in shallow and intertidal estuarine habitats (Heip and others 1995, MacIntyre and others 1996, Underwood and Kromkamp 1999). Therefore, shading by such structures may adversely affect vegetation and overall net primary production (NPP).

Whitney and Darley (1983) found that microalgal communities in shaded areas are generally less productive than unshaded areas, with productivity positively correlated with ambient irradiance. Likewise, net photosynthesis in *Spartina alterniflora, Juncus roemerianus* (Scheele), *Distichlis spicata* (L.), *Typha domingensis,* and *Cladium jamaicense* decreased with decreasing light intensity (Giurgevich and Dunn 1978, Giurgevich and Dunn 1979, Kemp and Cunningham 1981, Drake 1984, Pezeshki and others 1996). Similarly, shading by boat docks resulted in a decrease in shoot density and biomass in temperate, tropical, and subtropical species of eelgrass (*Zostera marina* L., *Thalassia testudinum, Halodule wrightii, Posidonia australis*) (Walker and others 1989, Czerny and Dunton 1995, Loflin 1995, Burdick and Short 1999, Shafer 1999).

Physical structures such as bridges, docks, moorings, and marinas can lead to a decrease in habitat degradation and local productivity of emergent vegetation and algal communities. Studies on shallow-water fish have looked at the impacts shading by manmade structures (pile-supported platforms or piers) have on habitat distribution and habitat quality in urban estuaries. Able and others (1998) found juvenile fish abundance and species richness was significantly lower under piers in urban estuaries. In another study, the same authors (Able and others 1999) found that caged fish under piers had growth rates similar to those held concurrently in the laboratory without food, whereas growth rates of fish caged in pile fields and open water were significantly higher. Similarly, a decrease in plant production in macrophytic vegetation can compromise the physical integrity of the remaining habitat by failing to attenuate wave energy and decreasing the stabilization of the marsh surface by root material, leaving shaded, unvegetated, or sparsely vegetated areas more susceptible to further habitat loss by erosion (Knutson 1988, Walker and others 1989). Other heterotrophic communities dependent on organic matter for food, substrate, and refuges from predation also may be adversely impacted.

Benthic invertebrates are an important component of the salt marsh ecosystem, feeding on vascular plant detritus and associated bacteria and microflora in the soil (Craft 2000). These organisms are involved in the mechanical breakdown and consumption of primary production (Lopez and Levinton 1987), soil bioturbation (Bertness 1985), and salt marsh biogeochemical cycling (Alkemade and others 1992). Levin and others (1998) found that macroinvertebrates play an important role in the mechanical breakdown and consumption of primary production and increase bioturbation through feeding and burrowing activities contributing to the complex elemental cycling that occurs in salt marshes. Because benthic invertebrates are a heterotrophic community intimately linked to marsh primary production, they may be adversely affected by disturbances (e.g., shading) that reduce NPP.

To date there have been relatively few studies exploring how shading may impact marsh benthic macroinvertebrate communities by reducing food sources and refuges from predators that emergent vegetation provide. Stocks and Grassle (2001) used shading (up to 60 days with light reduced to 8% compared to controls) as a means of reducing microalgae as a food limitation in order to study the recolonization of benthic invertebrates into *in situ* salt-marsh pond mesocosms. They found that the density of macrofauna in shaded plots was 62% lower than in controls with no shading. However, the goal of their study was to determine whether reduced microalgae, not shading, limited macrofaunal colonization and did not assess the effects of longer-term light attenuation on the estuarine benthic invertebrate community.

The objectives of this study were to investigate the effects of shading on marsh benthic macroinvertebrate community structure and function by comparing light attenuation and benthic invertebrate communities beneath seven highway bridges of varying heights and widths with marshes outside of bridges not influenced by bridge shading. In this study, we hypothesized that a decrease in light availability would lead to a decrease in primary production. This, in turn, would result in a decrease in overall invertebrate density and taxa richness in sampling sites under lower bridges compared to sites from under higher bridges and natural reference marshes. We assessed functional capacity of the marsh through the analysis of four community attributes: total invertebrate density, invertebrate taxa richness, density of dominant invertebrate taxa, and proportion of invertebrate trophic feeding groups.

Research Methods

Site Description

We sampled estuarine marshes adjacent to and beneath seven bridges along the North Carolina coast (Figure 1). Bridges were selected based on varying bridge height, width, orientation, and presence of marsh macrophytes (Table 1). In 2000, benthic macroinvertebrates were sampled beneath seven bridges as well as unshaded reference marshes near each bridge (30–50 m). In 2001, we intensively sampled one site (Cedar Island) at four bridge heights to develop a predictive relationship between bridge height, width,

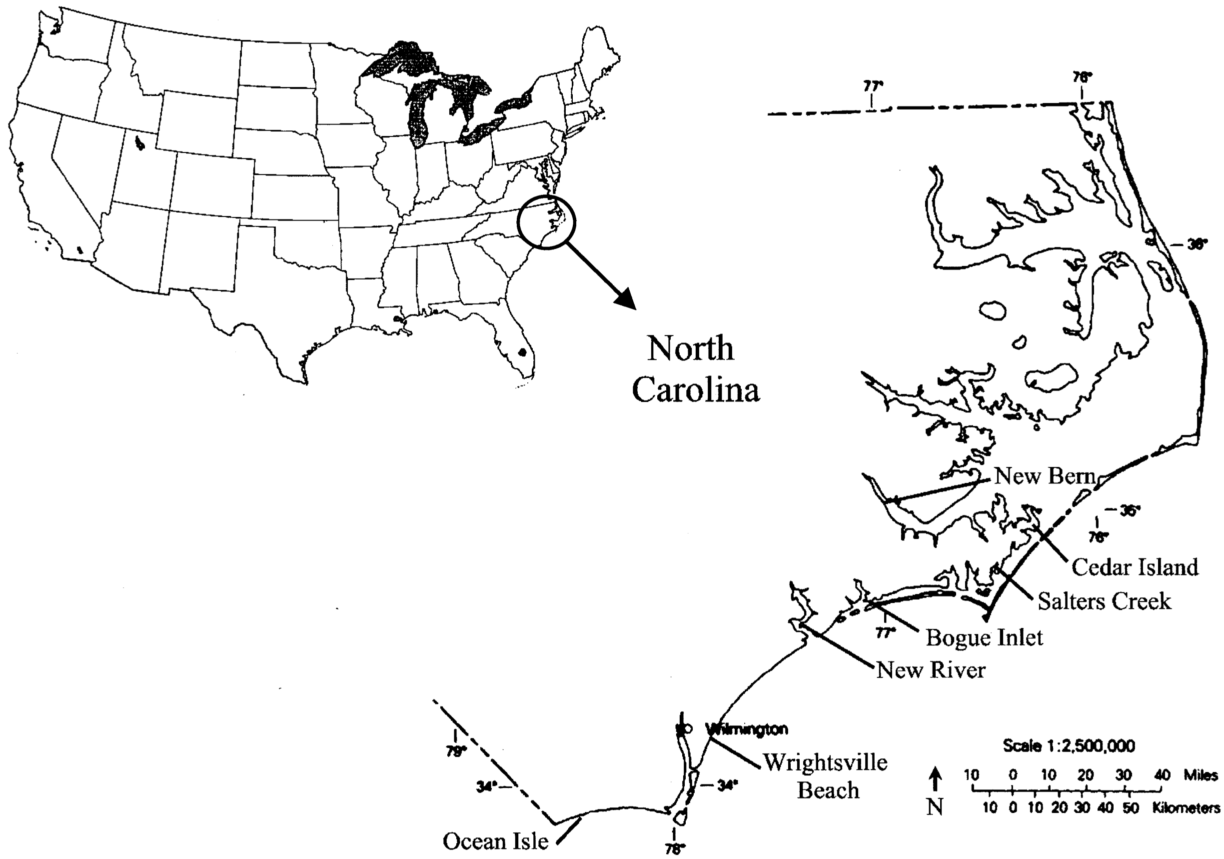

Figure 1. Map of eastern North Carolina showing the location of sampling sites. (Map modified from North Carolina Geological Survey 1984.)

Table 1. Bridge parameters, salinity, and dominant vegetation used to evaluate effects of shading on established marsh invertebrate communities (orientation is reported between 0° North and 180° South)

Location	Height (m)	Width (m)	HW ratio	Age (yrs)[a]	Orientation	Salinity (g/L)	Dominant vegetation
Wrightsville Beach	5.85	20.82	0.28	44	125° E-SE	32	*S. alterniflora*
Cedar Island	2.91	9.94	0.29	5	39° N-NE	29	*S. cynosuroides*
New Bern	8.53	12.59, 16.71[b]	0.68, 0.51[b]	24,2[b]	112° E-SE	3	*S. cynosuroides*
New River–Low	7.32	10.73	0.68	7	176° S-SE	4	*S. alterniflora*
Salter's Creek	11.58	10.70	1.08	18	125° E-SE	22	*J. roemarianus*
New River–High	14.63	10.73	1.36	7	176° S-SE	4	*S. alterniflora*
Ocean Isle	15.24	9.85	1.55	16	167° S-SE	39	*S. alterniflora*
Bogue Inlet	19.81	11.13	1.78	19	168° S-SE	34	*S. alterniflora*

[a]Age is calculated as the number of years after bridge construction finished until initial sampling in 2000.
[b]The New Bern bridge was widened by 4.12 m in 1998.

light attenuation, and benthic macroinvertebrate characteristics. Sampling sites were randomly selected in areas where vegetation, flooding depth and frequency, and sediment type were similar between bridge sampling sites and the corresponding natural reference marsh sites.

Bridge Characteristics

Bridge width and height above the marsh soil surface were measured with a meter tape at each sampling point. Because both height and width variables contribute to bridge shading, they were combined to form a height:width ratio (HW ratio). Orientation of each bridge was recorded with a hand compass and checked with digital orthophoto quadrangle maps of each bridge (U.S. Geological Survey, Reston, VA 20192, USA). Bridge construction and improvement data were obtained through construction records provided by the North Carolina Department of Transportation.

HW ratios ranged from 0.28 at Wrightsville Beach, the second lowest but widest bridge, to 1.78 at Bogue Inlet, the highest measured bridge (Table 1). Bridge age varied from 5 to 44 years old. Bridge orientation of the seven bridges resulted in three bridges with roughly north/south orientations, three east-southeast/west-northwest orientations, and one with a northeast/southwest orientation (Table 1). Sample size and distribution of orientation measurements were not large enough to adequately assess the impacts of this variable.

Light Measurements

In July 2002, photosynthetically active radiation (PAR = 400–700 nm wavelengths), was estimated at each site by using a photosynthetic photon flux (PPF; μmol m^{-2} s^{-1} where 1 PPF = 5.01 foot-candles for sunlight) meter with a spherical quantum sensor (Li-Cor LI 190SA, Li-Cor, Inc., Lincoln, NE 68504, USA or BQM-SUN, Apogee Instruments, Logan, UT 84321, USA). Light data were collected simultaneously at or near the center of each bridge and outside of each bridge once during the growing season. Relative light attenuation—the percentage of surface irradiance compared to under bridge irradiance—was calculated by the quotient of paired "under bridge" light samples over "outside bridge" (natural sunlight) samples. Irradiance measurements were taken at 30-second intervals for at least 1.5 minutes when the ambient light outside of the bridge was in full or nearly full sunlight (1650–2000 μmol m^{-2} s^{-1}) between the hours of 10:00 AM and 3:00 PM.

Benthic Invertebrate Sampling

In the field, two soil cores each were collected from 10 to 20 0.25-m^2 quadrangular plots randomly selected under each bridge. Cores were collected near the center of the zone of bridge shading, and in reference marshes at the end of the growing season (early October). This timing coincides with a period of maximal recruitment for the most common invertebrate species in the region (Watzin 1986, Levin and Huggett 1990). We recognize that the most severe shading by bridges at this latitude may not occur directly beneath the bridges but lateral to them based on their orientation and sun angle. However, all samples were collected from shaded zones that, at times (November–February), may not be in shaded areas but are shaded throughout the growing season in North Carolina (March–October). Cores were extracted with a stainless steel corer with a diameter of 3.8 cm from the upper 5 cm of soil, resulting in a surface area equivalent to 11.35 cm^2 per core. Samples were immersed in 10% buffered formalin containing Rose Bengal (to stain the organisms) in the field to preserve invertebrates. In the laboratory, samples were washed on a 250-μm sieve. Animals retained on the screen were sorted under a dissecting microscope and identified to the lowest possible taxon, counted, and stored in 70% ethanol. Invertebrate data were sorted into trophic groups (surface feeders, subsurface deposit feeders, carnivores, and unknown) based on feeding strategy (Sacco and others 1994). The unknown feeding group included invertebrates in which food strategies were unknown in the literature or had several modes of feeding (i.e., nematodes, ostracods, copepods, *Acarina* sp., and bivalves).

Biomass and Soil C and N Measurements

Aboveground biomass was measured by clipping culms from the five randomly selected 0.25-m^2 quadrangular plots under each bridge and in unshaded reference marshes. Live standing material was dried in the laboratory at 70°C, and weighed. One soil core (8.5-cm diameter by 30-cm deep) was collected from each clipped plot for measurement of belowground biomass. Root material was separated from the soil by washing on a 2-mm-diameter mesh screen. The remaining roots and rhizomes retained on the screen were dried at 70°C and weighed.

A second soil core (8.5-cm diameter by 30-cm deep) was collected from each clipped plot and was analyzed for total organic carbon and total nitrogen content. Soil material was air dried, ground, and sieved through a 2-mm-mesh diameter screen. An aliquot taken from each plot was treated with acid to determine whether carbonates were present. No carbonates were detected; therefore, C values were assumed to be organic carbon. Organic C and total N were determined on material passing through the sieve using a Perkin-Elmer 2400 CHN analyzer (Perkin Elmer Life and Analytical Sciences, INC, Boston, MA, 02118).

Statistical Analyses

One-way analysis of variance (ANOVA) was used to compare benthic macroinvertebrate community composition and richness, functional feeding groups, densities of the six most common invertebrates, above- and below-ground biomass, and soil carbon and nitrogen of underbridge samples (shaded) with natural reference marsh samples (no shading). If data did not meet

Table 2. HW ratio, irradiance, aboveground and belowground biomass, and soil organic carbon and total nitrogen under each bridge compared to natural reference marshes[a]

Site	HW ratio	Avg. irradiance under bridge (μmol m^{-2}s^{-1})	Light attenuation (%)	Aboveground biomass under bridge (g/m^2)	Aboveground biomass natural marsh (g/m^2)
Wrightsville Beach	0.28	36	98.1	0***	838
New Bern	0.51	218	88.6	657**	1337
New River–Low	0.68	251	83.2	898	975
Salter's Creek	1.08	364	81.8	913	1051
New River–High	1.36	986	35.0	1137	1237
Ocean Isle	1.55	1788	5.9	839+	621
Bogue Inlet	1.78	1639	1.1	902	1043

Site	HW ratio	Belowground biomass under bridge (g/m^2/ 30-cm depth)	Belowground biomass natural marsh (g/m^2/ 30-cm depth)	Soil carbon under bridge (%)	Soil carbon natural marsh (%)	Soil nitrogen under bridge (%)	Soil nitrogen natural marsh (%)
Wrightsville Beach	0.28	0***	1082	0.35**	2.02	<0.04**	0.14
New Bern	0.51	837**	2162	20.48	24.04	1.44	1.70
New River–Low	0.68	1142	1519	0.26*	0.53	<0.04*	0.11
Salter's Creek	1.08	1167	1304	2.95**	6.16	0.19*	0.40
New River–High	1.36	1798	3080	4.27+	0.68	0.30+	0.07
Ocean Isle	1.55	892	830	1.94***	3.19	0.15***	0.26
Bogue Inlet	1.78	1507	1896	0.39	1.53	0.05	0.12

[a]Cedar Island biomass and soil cores were not collected in the first year of sampling. Cedar Island values for four bridge heights are shown in Table 5. Average natural irradiance was 1770 μmol^{-1}m^{-2} (full sunlight = 2000 μmol^{-1}m^{-2}). Values with an asterisk(s) indicate significantly lower values in underbridge marshes versus natural reference marshes based on Student's *t*-test or Mann-Whitney Rank Sum test. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Values with a "+" indicate significantly ($p \leq 0.05$) higher density in under bridge marshes versus natural reference marshes. HW, height: width.

assumptions of equal variance (Levene Median test) or normality (Kolmogorov-Smirnov test with Lilliefors' correction and a *p* value of 0.05) then data were square root transformed and reanalyzed with one-way ANOVA. A nonparametric approach using Kruskal-Wallis one-way ANOVA on ranked values (for multiple experimental groups) or a Mann-Whitney Rank Sum test (for two experimental groups) was used with data that failed to meet normality or equal variance assumptions to make the above comparisons. A similar statistical approach was used for 2001 data to compare changes in HW ratios and benthic invertebrate community characteristics, biomass, and soil C and N at four bridge heights of varying light attenuation. Regression analysis was performed on all (2000 and 2001) data using HW ratio as the independent variable with relative invertebrate density and relative taxa richness to evaluate the relationships between bridge HW ratio and relative invertebrate community composition. Regression analysis also was employed to determine the relationship between HW ratio and light attenuation. All tests of significance were made at $\alpha = 0.05$. ANOVA analyses and regressions were done using commercial software from SPSS (version 10.0, SPSS Inc., Chicago, IL 60606, USA).

Results and Discussion

Survey of Six Bridges—Shading Impacts on Benthic Invertebrates in 2000

Photosynthetic photon flux was much lower at bridge sites with HW ratios less than 0.70 compared to bridges with an HW ratio greater than 0.7. Light attenuation at Wrightsville Beach, New Bern, and New River-Low averaged 98% (36 μmol m^{-2} s^{-1}), 89% (218 μmol m^{-2} s^{-1}), and 83% (251 μmol m^{-2} s^{-1}), respectively (Table 2). These same sites had 8%–100% less aboveground standing crop biomass and 25%–100% less belowground biomass compared to their respective reference marshes (Table 2). Results by Giurgevich and Dunn (1979) are similar in which net photosynthesis was approximately 60% to 75% lower for the tall form and 66% to 82% lower for the short form of *Spartina alterniflora* when *in situ* plants were measured under low light (PAR approximately 250–300 μmol m^{-2} s^{-1}) conditions compared to reference plants in full sunlight (2000 μmol m^{-2} s^{-1}) measured in March, July, and September. Little or no vegetation growth would be expected as the photosynthetic capacity of plants declined with light availability to the point that net pho-

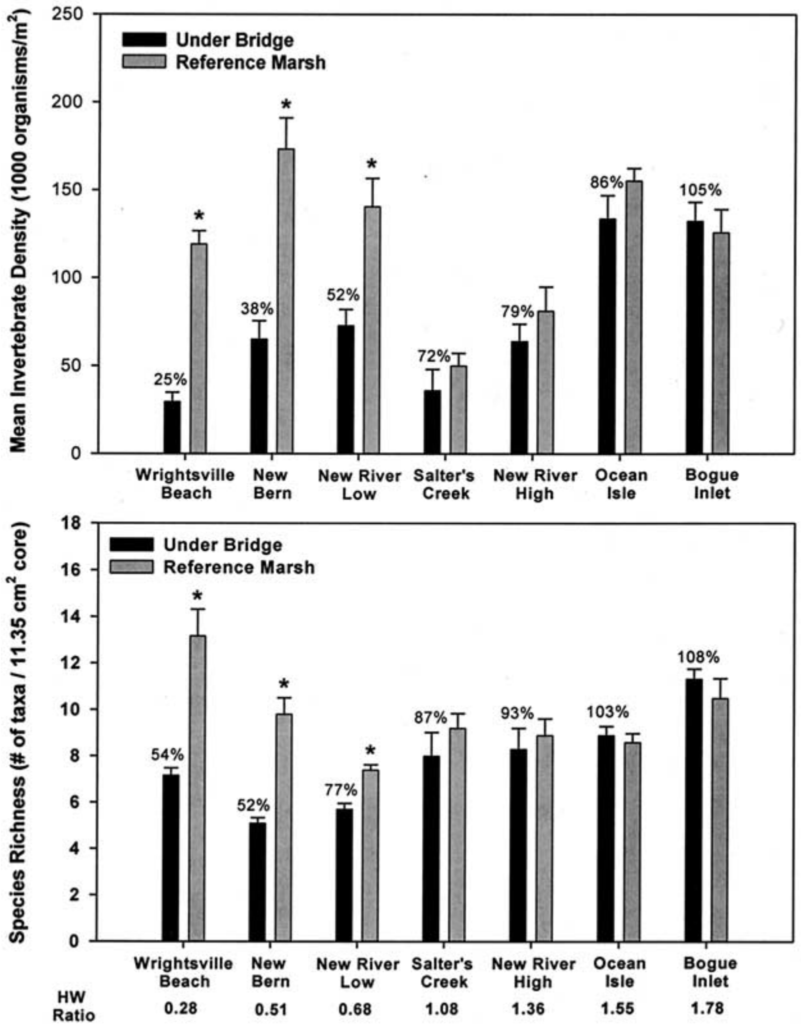

Figure 2. Composition of benthic invertebrate density and taxa richness under bridges (n = 10 for all sites except Wrightsville Beach and Bogue Inlet where n = 6; mean ± 1 SE) of varying height: width (HW) with natural reference areas outside of bridges (n = 10 for all sites except Bogue Inlet where n = 12; mean ± 1 SE). Values with an asterisk indicate significantly ($p < 0.05$) higher values in natural reference marshes versus underbridge marshes based on Student's *t*-test or Mann-Whitney Rank Sum test. Percentages indicate the percent of invertebrate density and richness under the bridges compared to their reference marshes (relative equivalence).

tosynthesis nears zero (light compensation point). Burdick and Short (1999) found that the light compensation point for the submerged seagrass *Zostera marina* was at a light attenuation of approximately 97.5%. Drake (1984) reported a light compensation point at a light attenuation of 91.6% when constructing a model using data for the brackish marsh species *Spartina patens, Distichlis spicata,* and *Scirpus olneyi.* Our light compensation points, where sites lacked aboveground macrophytic vegetation, are within these values (light attenuation greater than 95%).

Bridges with HW ratios greater than 1.50, such as Ocean Isle and Bogue Inlet, had the lowest average light attenuation under each bridge, with less than 6% of ambient light attenuated before reaching the marsh surface (Table 2). There also were no significant differences in aboveground and belowground biomass under these bridges with respect to the natural reference marshes.

There were no differences in benthic invertebrate densities in natural reference marshes and bridge shaded sites with an HW ratio greater than 0.70 (Salter's Creek, New River-High, Ocean Isle, and Bogue Inlet). However, bridges with an HW ratio less than 0.70 and light attenuation greater than 85–90% contained significantly fewer ($p < 0.001$) benthic invertebrates than unshaded areas outside of the bridges. Density of benthic invertebrates at Wrightsville Beach (HW = 0.28), New Bern (HW = 0.51), and New River-Low (HW = 0.68), were 48% to 75% (67,506–108,171 organisms/m^2) of the density measured in adjacent reference marshes (Figure 2).

The low (HW ratio < 0.70) HW bridges exhibited a similar trend with taxa richness. There were, on average, fewer taxa represented under the bridge as opposed to the natural reference marsh at Wrightsville Beach, New Bern, and New River–Low (Figure 2). No

Table 3. Mean total density of six dominant taxa (number per m^2) of underbridge marshes and natural reference marshes[a]

Site	HW ratio	N	Oligochaetes Bridge	Oligochaetes Reference	*Manayunkia aesturina* Bridge	*Manayunkia aesturina* Reference	*Steblospio benedicti* Bridge	*Steblospio benedicti* Reference
Wrightsville Beach	0.28	6	3233***	19,692	0*	8377	2351**	17,341
New Bern	0.51	10	7759***	28,480	0	0	0	0
New River–Low	0.68	10	5026	11,992	0	0	0	0
Salter's Creek	1.08	10	11,286	12,344	1763	353	0	0
New River–High	1.36	10	9082	20,986	0	0	8200	11,198
Ocean Isle	1.55	10	24,160	29,362	0	0	16,224	17,106
Bogue Inlet	1.78	12	17,044	16,603	15,431+	588	3233	4702

Site	HW ratio	N	*Capitella* sp. Bridge	*Capitella* sp. Reference	Nematodes Bridge	Nematodes Reference	*Nereidae* sp. Bridge	*Nereidae* sp. Reference
Wrightsville Beach	0.28	6	1617**	12,344	16,312*	35,417	1617	2351
New Bern	0.51	10	0***	1675,	50,348***	121,593	1587	1852
New River–Low	0.68	10	1146	617	31,302	47,791	353	176
Salter's Creek	1.08	10	794	705	12,168	9346	441*	2557
New River–High	1.36	10	4321	6613	28,833	31,831	803	88
Ocean Isle	1.55	10	2293	705	12,9705	16,0213	882	1411
Bogue Inlet	1.78	12	4115	3331	75,095	79,357	0	441

[a]N is the number of samples collected each at underbridge and reference sites. Values with an asterisk(s) indicate significantly lower, whereas values with a positive sign indicate significantly higher densities in underbridge marshes versus natural reference marshes based on Student's t-test or Mann-Whitney Rank Sum test. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. Values with a "+" indicate significantly ($p \leq 0.05$) higher density in underbridge marshes versus natural reference marshes. HW, height: width.

differences were found in the remaining high (HW ratio > 0.70) HW ratio bridge samples.

Bridges with low HW ratios had, on average, 45% less aboveground biomass compared to bridges with high HW ratios and 49% less aboveground biomass than the natural reference marshes. Likewise, belowground biomass was 51% to 61% less under low HW ratio bridges when compared to high HW ratio bridges and reference marshes, respectively (Table 2). Because salt marsh plants provide macroinvertebrates with protection from predation (Lopez and Levinton 1987), substrate and food (Zajac 1986, Gremare and others 1989, Marsh and Tenore 1990), while modifying temperature and humidity (Kraeter and Wolf 1974), sites with reduced or absent vegetation and algae may lead to fewer total macroinvertebrates. Levin and Talley (2000), however, have shown that macrofaunal densities were similar and species richness was higher in a mudflat compared to *S. foliosa*-vegetated sediments. We believe unvegetated areas resulting from light attenuation rather than other physical or chemical parameters represent a different environment than that of mudflats. Unvegetated areas beneath bridges as a result of reduced light may also limit microalgal growth, limiting this possible food source for invertebrates, which could lead to reduced macroinvertebrate density and richness.

Soil organic C and total N showed similar trends. Wrightsville Beach and New River–Low had significantly less soil C (0.35% and 0.26%, respectively) and soil N (<0.04% and <0.04%, respectively) compared to unshaded reference marshes (Wrightsville Beach reference marsh, soil organic C = 2.02%, total N = 0.14%; New River–Low reference marsh, soil organic C = 0.53%, total N = 0.11%). New Bern also had less soil C and N in samples from under the bridge compared to samples collected in the reference marsh (Table 2).

Invertebrate densities in our marshes ranged from 49,995 to 173,351 organisms/m^2. These invertebrate densities are similar to densities found in natural marshes of coastal North Carolina where nematodes were qualitatively enumerated (Craft and Sacco 2003) and in southern California *Spartina foliosa* marshes (Levin and others 1998). These densities are higher than those reported in other natural marshes in North Carolina (Moy and Levin 1991, Levin and others 1996). However, they reflect quantitative enumeration of nematodes that were retained on a 250-μm sieve or were in plant tissue that were excluded in other studies (Levin and others 1996) or were classified as meiofauna that were sieved through a 63–300-μm mesh screen (Moy and Levin 1991).

Bridges with an HW ratio less than 0.70 contained fewer dominant taxa compared to bridges with an HW ratio greater than 0.70 (Table 3). Significantly fewer oligochaetes were observed at Wrightsville Beach and New Bern under the bridges as opposed to natural

Table 4. Mean total density of benthic invertebrate community feeding groups (number per m^2) in underbridge marshes and natural reference marshes[a]

			Surface feeders		Subsurface feeders	
Site	HW ratio	N	Bridge	Reference	Bridge	Reference
Wrightsville Beach	0.28	6	3968***	31,008	5143**	32,918
New River–Low	0.51	10	353*	3262	22,749*	38,180
New Bern	0.68	10	2028*	4232	7759**	30,861
Salter's Creek	1.08	10	6437	10,052	12,697	14,637
New River–High	1.36	10	10,581	12,609	15,342	30,156
Ocean Isle	1.55	10	20,016	20,456	26,629	26,717
Bogue Inlet	1.78	6,12	20,427	16,753	23,072	17,782
			Carnivores		Unknown feeders	
Site	HW ratio	N	Bridge	Reference	Bridge	Reference
Wrightsville Beach	0.28	6	1470	2645	19,105**	53,199
New River–Low	0.51	10	88	0	49,730**	99,373
New Bern	0.68	10	0	0	55,374***	138,258
Salter's Creek	1.08	10	0	0	16,841	25,306
New River–High	1.36	10	176	441	33,771	34,653
Ocean Isle	1.55	10	0	0	174,762	197,864
Bogue Inlet	1.78	6,12	0	0	88,909	91,554

[a]Values with an asterisk(s) indicate significantly lower density in underbridge marshes versus natural reference marshes based on Student's *t*-test or Mann-Whitney Rank Sum test. *$p < 0.05$; **$p < 0.01$; *** $p < 0.001$. HW, height: width.

reference marshes (Table 3). Wrightsville Beach also had significantly fewer *Manayunkia aestuarina, Streblospio benedicti, Capitella* sp., and nematodes under the bridge compared to the reference marsh, whereas New Bern had significantly fewer *Capitella* sp. and nematodes. In general, bridges with an HW ratio less than 0.70 had 77% fewer oligochaetes and 51% fewer nematodes when compared to natural reference marshes. These two taxa were numerically dominant, constituting nearly 60% of the total invertebrate density; therefore, they are likely to show the greatest decline in population with decreased food and substrate and less protection from predators.

Similar to total density, taxa richness, and dominant taxa, bridges with an HW ratio less than 0.70 adversely affected trophic composition. Wrightsville Beach, New River-Low, and New Bern sites contained fewer surface (52%–89%), subsurface (40%–84%), and unknown feeders (50%–64%) (Table 4). There was no significant relationship between the densities of carnivores found in under-bridge samples compared to reference marsh samples.

The reduction or absence of plant biomass beneath bridges leads to reduced inputs of organic matter that serve as food sources for the suspension- and deposit-feeding detritivores, including those categorized in this study into the surface and subsurface feeding groups. Similarly, reduced levels of soil C (with the exception of the high nutrient pools at New Bern) found under bridges versus the natural reference marshes may contribute to the reduction in benthic invertebrates beneath bridges. Craft (2000) reported that benthic invertebrate communities developed concurrently with accumulating soil organic carbon along a 25-year-old chronosequence of created *S. alterniflora* marshes, emphasizing the role organic matter plays in benthic invertebrate structure and function.

The unknown feeding strategy trophic group dominated with 63.5% of the total invertebrates collected. This is likely due to the number of organisms identified with multiple feeding strategies (classified as unknown) such as nematodes and copepods (63% and 12%, respectively). Subsurface (25.8%), surface (10.5%), and carnivore (0.2%) feeding groups comprised the rest of the trophic groups.

Predictive Relationship Between Bridge Height and Benthic Invertebrates—Based on 2001 Data

Light attenuation under the Cedar Island Bridge ranged from 99% (18 μmol m^{-2} s^{-1}) at a HW ratio of 0.29% to 10% (1803 μmol m^{-2} s^{-1}) at a HW ratio of 1.56. Regression analysis using HW data and light attenuation at 12 bridge elevations (from low to high) at Cedar Island revealed a significant negative relationship between bridge HW ratio and light attenuation under the bridge (Figure 3).

Aboveground biomass was 0%, 62%, and 72% at the low, medium-low, and medium-high sampling sites, re-

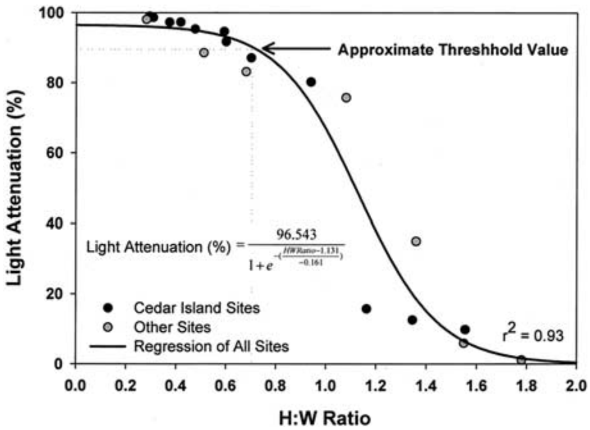

Figure 3. Light attenuation of natural available light based on the height and width (HW ratio) of bridges. The regression uses HW ratio as the independent variable and is based on a sigmoidal curve. The approximate threshold value indicates the point at which greater light attenuation results in a significant negative impact to the benthic invertebrate community.

spectively, compared to the natural reference marsh biomass (Table 5). These same sites had an average belowground biomass of 0%, 16%, and 21%, respectively, compared to the natural reference marsh. Soil organic C was 32% (low), 39% (medium-low), and 70% (medium-high) of the levels measured in the unshaded reference marsh (Table 5). Likewise, the percentages of soil total N at these respective sites were 25%, 40%, and 62% of the soil nitrogen levels measured in the reference marsh.

Total invertebrate density was 4% of the reference marsh invertebrate density at the low (HW = 0.29) bridge site and 57% at the medium-low (HW = 0.41) bridge site (Figure 4). Similarly, invertebrate taxa richness at the low and medium-low bridge sampling locations were 16% and 70%, respectively, of the reference marsh taxa richness. Invertebrate density and taxa richness at the medium-high and high sites did not differ significantly from the reference marshes (Figure 4). The observed reduction in invertebrate density and species richness at the low and medium-low bridge elevations is likely the result of reduced levels or absence of plant biomass and low levels of soil organic carbon and nitrogen.

As with total density, significantly fewer oligochaetes were present at the low bridge elevation compared to the reference marshes. Similarly, low and medium-low elevations had significantly fewer nematodes than were found in the reference marsh (Table 6). These two taxa are numerically dominant, making up 61% of the total invertebrate density (35% for oligochaetes and 26% for nematodes).

In addition to oligochaetes, nematodes and *Capitella* sp., the meiofauna *Harpacticoid* sp., the gastropod *Spiratella inflata,* and the mite *Acarina* sp. were numerically important taxa in the Cedar Island samples. These species are more common in brackish marshes than in salt marshes (S. D. Struck, unpublished data). Similar to other taxa, significantly fewer *S. inflata* and *Acarina* species were observed at the low bridge site compared to the reference marsh (Table 6). Density of *Acarina* sp. also was lower in the low bridge samples compared to the high bridge samples.

Low and medium-low bridge elevations had lower densities of surface deposit (4% and 84%, respectively), subsurface deposit (5% and 62%), and unknown (2% and 50%) feeding strategists when compared to densities found in the reference marsh (Table 7). The low bridge elevation also had significantly fewer unknown feeding strategists compared to the medium-high and high bridge sites (Table 7). Reduced plant biomass, organic C, and total N in the low and medium low bridge elevations are likely the reason for the trophic differences observed. Relative proportions of trophic feeding groups were similar between under-bridge sites and the reference marsh. Subsurface deposit feeders and unknown feeders, respectively, dominated the overall trophic feeding structure composing 46% and 42% of the under-bridge samples and 45% and 43% of the reference marsh samples at Cedar Island. As in the year 2000 sampling of invertebrates, there was insufficient data representing the carnivorous trophic feeding group to contribute to the analyses.

Combined Results of 2000 and 2001 Data

When we compared invertebrate data across all sites and years, the relative equivalence of invertebrate density and taxa richness were significantly reduced under bridges with a HW ratio less than 0.70 (Figure 5) and light attenuation greater than 85% to 90% (Figure 3). Impacted sites included Wrightsville Beach, New Bern, the low sampling site at New River, as well as the low and medium-low bridge heights at Cedar Island. Indeed, the sites in which the benthic invertebrate community was significantly reduced include the medium-low bridge height at Cedar Island (HW ratio of 0.41, light attenuation = 97%) and New River-Low (HW ratio of 0.68, light attenuation = 83%). However, at sites with an HW ratio of greater or equal to 0.70 and light attenuation of less than 82%, the benthic invertebrate density and taxa richness were not significantly impacted by shading (Figure 5). One exception to this was the Cedar Island medium-high site, which had a light attenuation of 87% but did not have significantly lower invertebrate density or taxa richness from the

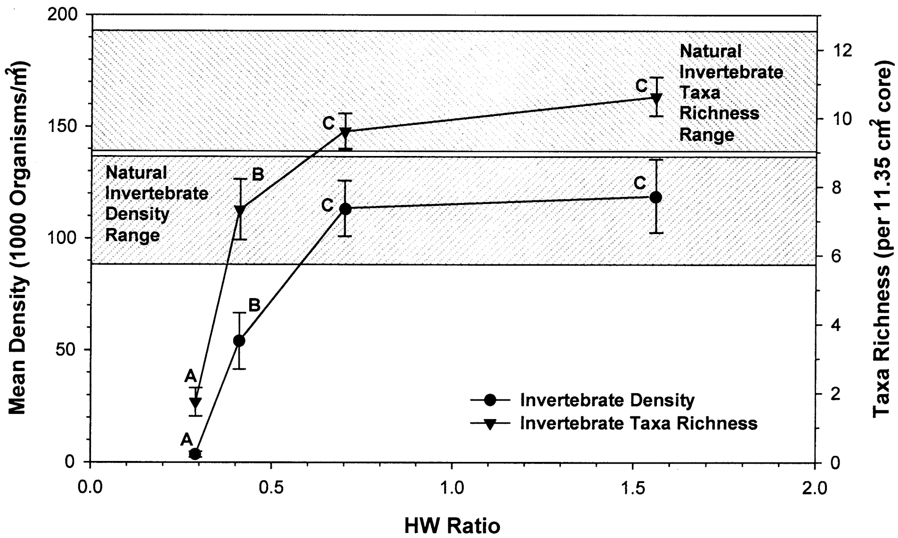

Figure 4. Mean total density and taxa richness for Cedar Island samples and nearby natural reference marshes. Capital letters denote significant differences ($p <$ 0.05 using Student's t-test or Mann-Whitney Rank Sum test) from each mean. Error bars = ± 1 SE. Shaded areas represent the range of total density and taxa richness measured in the natural marsh.

Table 5. Percent organic carbon, percent total nitrogen, below and aboveground biomass of samples collected at four separate HW (height: width) ratios (by increasing bridge height) and the natural reference marsh at Cedar Island in 2000[a]

Site	HW ratio	N	Average irradiance (μmol m^{-2} s^{-1})	Light attenuation	Carbon in soil (%)	Nitrogen in soil	Aboveground biomass (g/m^2)	Belowground biomass (g/m^2/30-cm depth)
Low	0.29	10	18	99.0	1.18**a**	0.065**a**	0.00**a**	0.00**a**
Medium low	0.41	4	52	97.3	1.42**a**	0.105**a**	305.55**a,b**	347.61**b**
Medium high	0.70	6	200	87.2	2.54**b**	0.163**b**	352.57**a,b**	467.58**b**
High	1.56	10	1803	9.8	6.41**d**	0.481**d**	474.65**c**	2738.36**c**
Natural marsh	na	10	1936	0	3.63**c**	0.265**c**	490.84**b,c**	2133.76**c**

[a]Lower-case letters denote significant differences between sampling sites based on analysis of variance with Tukey's HSD post hoc test or Mann-Whitney Rank Sum test.

Table 6. Mean total density of dominant taxa (number per m^2) of a single marsh at four bridge heights and natural reference marshes[a]

Site	Height (m)	HW ratio	N	Oligochaetes	*Capitella* sp.	Nematodes
Low	2.9	0.29	8	2498**	882*	1470**
Medium Low	4.1	0.41	3	24,689	4409	7054*
Medium High	7.0	0.70	5	45,674	3527	32,977
High	15.5	1.56	8	39,127	13,887	37,474
Natural Marsh	na	na	16	39,318	10,856	33,366
Site	**Height (m)**	**HW ratio**	**N**	***Calanoid* sp.**	***Spiratella inflata***	***Acarina* sp.**
Low	2.9	0.29	8	220	0***	0**
Medium low	4.1	0.41	3	1226	1470*	588
Medium High	7.0	0.70	5	1108	7936	705
High	15.5	1.56	8	2535	15,982	2755
Natural marsh	na	na	16	2149	11,022	3086

[a]Values with an asterisk(s) indicate significantly lower density in underbridge marshes versus the natural reference marsh based on Student's t-test or or Mann-Whitney Rank Sum test. *$p < 0.05$; **$p < 0.01$. HW, height: width.

Table 7. Mean total density of benthic invertebrate community feeding groups (number per m^2) of a single marsh at four bridge heights and natural reference marshes[a]

Site	Height (m)	HW ratio	N	Subsurface feeders	Surface feeders	Carnivores	Unknown
Low	2.9	0.29	8	1984**	772**	0	770***
Medium low	4.1	0.41	3	26,159*	4702*	294	23,807*
Medium high	7.0	0.70	5	49,554	12697	0	51,318
High	15.5	1.56	8	55,219	281,056	0	47,835
Natural marsh	na	na	16	42,489	17,958	0	47,229

[a]Values with an asterisk(s) indicate significantly lower density in underbridge marshes versus the natural reference marsh based on Student's *t*-test or Mann-Whitney Rank Sum test. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. HW, height: width.

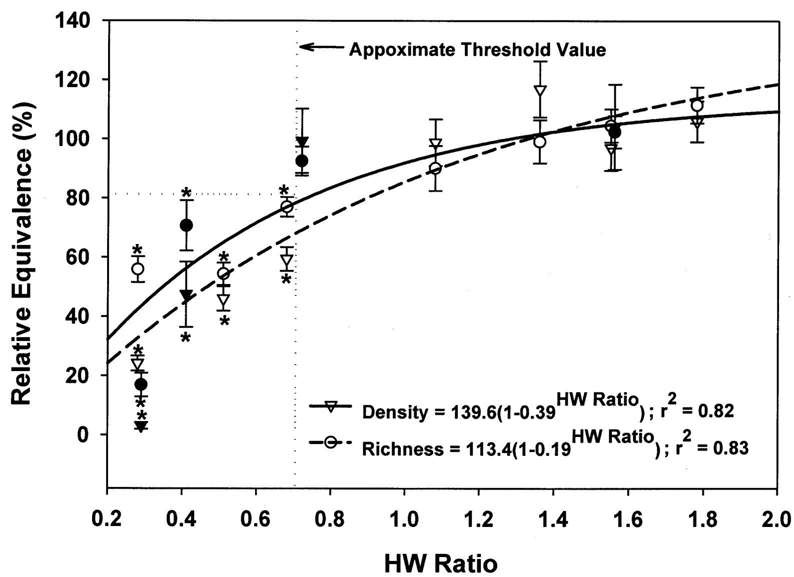

Figure 5. Relative equivalence (underbridge sample/reference sample expressed as a percent) of invertebrate density and richness of all samples with height: width (HW) ratio. Asterisks denote a significant difference ($p < 0.05$ using Student's *t*-test or Mann-Whitney Rank Sum test) between the mean of underbridge samples and reference marsh samples. The vertical dashed line indicates an HW ratio of 0.7. Darkened triangles/circles indicate samples from Cedar Island (year 2 of the study).

natural marsh. Therefore, our data indicate that light attenuation between 83% and 87%, which corresponds to a bridge HW ratio of approximately 0.7, results in benthic invertebrate density and taxa richness under bridges that are less than 80% of levels found in unshaded marshes and are adversely impacted compared to natural reference marshes (Figure 5).

We recognize that other environmental and physical variables may contribute to the patterns in invertebrate density and taxa richness we observed under bridges compared to the reference marshes. Increased predation in shaded areas that lack vegetation may contribute to reduced density and richness of invertebrates under bridges. Although predation of invertebrates can be greater in unvegetated or thinly vegetated areas (Minello and Zimmerman 1983, McIvor and Rozas 1996, Kneib 1997), rates of predation are mostly based on depth and duration of submergence relating to the number of predators and length of time to prey on the invertebrates. Most of the marshes sampled in this study are located in areas with irregular microtidal fluctuations leading to minimal depth of inundation and reduced frequency of tidal inundation relative to regularly flooded marshes. Likewise, the abundance and growth rate of juvenile fish has been shown to be lower under man-made structures such as piers (Able and others 1998, Able and others 1999). Also, the presence of vegetation, especially belowground biomass, is a primary determinant of benthic invertebrate community composition, leading to greater invertebrate densities in vegetated versus unvegetated intertidal zones (Levin and Talley 2000). Alterations in hydrodynamics by bridge pylons leading to increased scouring of the bottom could also result in reduced macrophytic vegetation and recruitment of larvae, as well as inhibit some trophic feeding groups such as deposit feeders. However, all sampling sites, save one (Wrightsville Beach), were located in areas with low hydrodynamic energy (channel flow, surface slope, depth and frequency of inundation). Similarly, samples were collected at least 5 m from bridge pylons to avoid any influence of these structures.

Conclusions

Of seven bridges spanning salt and brackish water marshes sampled in North Carolina, those with a HW ratio less than 0.70 and light attenuation of 85% to 90%, had a significant negative impact on under-bridge invertebrate density, taxa richness, dominant taxa (oligochaetes, nematodes, and *Capitella* sp.) as well as trophic feeding groups (surface and subsurface deposit feeders). Results from the year 2001 study of Cedar Island, assessing the role of bridge height, are similar, with additional impacts to densities of *Spiratella inflata* and *Acarina* species that are more characteristic of brackish marsh areas. Our results suggest that low bridges, which attenuate light more than 85% to 90%, may adversely affect estuarine marsh food webs by reducing macrophyte growth, soil organic carbon, and density and diversity of benthic invertebrates. With a greater knowledge of bridge shading effects, bridge design and construction may be improved to reduce the impacts on estuarine marsh ecosystem structure and function. More recently constructed bridges are taller to avoid the expense involved with drawbridges and to accommodate boat traffic, particularly high-mast sailboats. However, the impacts of lower, older bridges remain. Although the overall area impacted by bridge shading may be relatively small, increased development in coastal areas may increase the number of bridges and similar man-made structures (e.g., docks, moorings, piers, and marinas) that shade the marsh and have cumulative impacts and can cause lasting destruction of coastal wetland habitat.

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