

Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis

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ABSTRACT: We examined the nursery role of salt marshes for transient nekton by searching the literature for data on density, growth, and survival of juvenile fishes and decapod crustaceans in marshes and using meta-analyses to test hypotheses. We analyzed density data from 32 studies conducted throughout the world. Based on fish density, habitat types could be ranked from highest to lowest as: seagrass > vegetated marsh edge, nonvegetated marsh, open water, macroalgae, oyster reefs > vegetated inner marsh. However, patterns of habitat use varied among the 29 fish species represented. For decapod crustaceans (seven species), habitat types were ranked: seagrass > vegetated marsh edge > nonvegetated marsh, vegetated inner marsh, open water, macroalgae > oyster reef. We identified only 5 comparative studies on transient nekton growth in salt marshes. Fish growth in non-vegetated salt marsh was not significantly different from growth in open water or in macroalgae beds but was significantly lower than in seagrass. Growth of decapod crustaceans was higher in vegetated marsh than in nonvegetated marsh. Nekton survival in salt marsh (11 studies analyzed) was higher than in open water, lower than in oyster reef/cobble and not significantly different from survival in seagrass. When density, growth and survival are all considered, the relative nursery value of salt marshes for nekton appears higher than open water but lower than seagrass. Vegetated marsh appears to have a higher nursery value than nonvegetated marsh; however, tidal dynamics and nekton movement among marsh components complicates these comparisons. The available data have a strong geographical bias; most studies originated in the northern Gulf of Mexico or on the Atlantic coast of the United States. This bias may be significant because there is some evidence that salt marsh nursery value is dependent on geography, salinity regimes and tidal amplitude.

KEY WORDS: Salt marshes · Nekton · Meta-analysis · Decapod crustaceans · Habitat · Seagrass

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INTRODUCTION

Salt marshes are considered nurseries for many nekton species but the nursery concept itself has not been clearly or consistently defined. Beck et al. (2001) proposed that 'a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur'. They recognized

that production reaching adult populations is dependent on a combination of processes including: (1) successful recruitment to juvenile habitats; (2) adequate growth in these habitats; and (3) adequate survival both within juvenile habitats and during the migration to adult spawning habitats. The density of juveniles reflects recruitment, mortality and emigration; thus, density can be an important indicator of nursery habitat value (Minello 1999). Following the definition of Beck et al. (2001), we only apply the nursery concept to

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species that have separate juvenile and adult habitats, or habitats that are not completely overlapping.

Just as the term nursery can be confusing in marine ecological literature, other terms related to nekton use of salt marsh habitats also need clarification. The term 'habitat' has been used generally to mean a location where animals live, with the boundaries of the area defined by an author (rather than the animal) based on structure, plants or physicochemical descriptors. These areas usually support recognizable communities identified by their dominant components, such as coral reefs, seagrass beds, salt marshes, mangroves or oyster reefs. Whitaker et al. (1973) referred to these community habitats as biotopes. In general ecological literature, however, the 'habitat' of a species is the place where a population of that species (or life stage) lives at any particular time (Odum 1971, Whitaker & Levin 1975, Baltz 1990, Peters & Cross 1992, Ricklefs 1973); and often this habitat (defined by the animal) encompasses more than 1 biotope. Using the terms habitat and biotope interchangeably may be convenient but can cause confusion when the habitat of a particular species is considered. Herein, we use the term habitat to include all of the places that a life stage of a species lives; we use the term biotope to indicate a community habitat as in Whitaker et al. (1973). We use 'habitat type' generically to describe any particular place that organisms live. Thus, a species has an adult habitat, a juvenile habitat and a nursery habitat (a nursery habitat is a subset of a juvenile habitat); and all of these habitats may include many different biotopes and habitat types. We also broadly define nekton in this paper as organisms that are free swimming at some time in their life cycle. This usage allowed the inclusion of relatively benthic forms such as lobsters.

Salt marshes are generally recognized as areas that include intertidal, emergent, vascular plants, but a more specific definition is needed when making comparisons between marshes and other habitat types. We define a salt marsh as a complex that includes the vegetated marsh surface, marsh ponds and pools, intertidal creeks, and subtidal creeks. In the literature, salt marshes have been defined both broadly (e.g. Rountree & Able 1992, Deegan et al. 2000) and narrowly (e.g. Teal 1962, Kneib 2000); however, the broad definition acknowledges that nekton move among these marsh components at high tide and generally must move off the vegetated marsh surface at low tide (but see Kneib 1984, 1997a). The inherently different components of salt marshes and the different salt marsh definitions in use, have complicated comparisons of marshes with other biotopes.

In this review and meta-analysis, we examine the value of salt marshes as nurseries using the definition of Beck et al. (2001) and our broad definition of a salt

marsh. We divide salt marshes into 6 different components including 2 types of vegetated marsh (vegetated marsh edge and vegetated inner marsh) and 4 types of nonvegetated marsh (nonvegetated marsh edge, marsh pools and ponds, intertidal creeks and subtidal creeks). These terms and others are defined in the glossary (see Appendix 1). We test the hypotheses that the nursery value of different marsh components is similar and that the nursery value of the salt marsh is similar to that of other biotopes, such as seagrass beds and open water. The paper focuses on density, growth and survival in juvenile habitats as well as on motile invertebrates and fishes with complex life cycles in which larvae are transported to estuaries from coastal waters and live in salt marshes.

MATERIALS AND METHODS

Our intent was to review all available data on density, growth and survival of transient nekton in salt marshes worldwide. We searched our personal databases along with Aquatic Science and Fisheries Abstracts (Cambridge Scientific Abstracts, Bethesda, MD) and Current Contents/Agriculture, Biology & Environmental Sciences (ISI, Philadelphia, PA) for literature on abundance, growth and survival of nekton in salt marshes and found 800 to 900 potential studies for analysis. Most of these studies, however, were eliminated upon further examination with regard to our final selection criteria. We excluded studies with data solely on marsh resident species, because our nursery criteria requires that juvenile and adult habitats do not completely overlap. We excluded studies that did not provide a comparison of nursery functions either among salt marsh components or between one or more salt marsh component and another biotope. Because sampling limitations affect abundance comparisons in shallow water habitats (Kneib 1997b, Rozas & Minello 1997, Connolly 1999, Minello 1999), we only included such studies if nekton densities (animals per area of bottom) were reported. For example, we included data from enclosure samplers (e.g. drop samplers, throw traps, Wegener rings, lift nets, flume weirs) where the sampling area was reported but did not include data from sampling gear where the area sampled was not specified (mainly trawls, seines, gill nets, traps). If data from towed nets were reported as animals per area swept, we considered these density estimates. We excluded study results if measurements of nursery function could not be associated with our particular marsh habitat types. For estimates of survival or mortality, we only included studies where mortality could be separated from population losses due to emigration.

We assigned density values to our different habitat types based on information available in each paper; however, there may have been errors in this classification. The misidentification of habitat types is most likely between nonvegetated marsh and open water and among nonvegetated marsh types. We considered open water to be estuarine areas not within a salt marsh complex, including areas within open bays, inlets, coves, bayous, large subtidal channels and coastal lakes. Open water areas are not surrounded by salt marsh vegetation or are large enough (> several km in diameter) for the direct influence of marsh vegetation on nekton to be minimal. Within a salt marsh complex, we considered areas of nonvegetated bottom within approximately 10 m of marsh vegetation as non-vegetated marsh edge. This definition is tenuous and may overlap with open water or with other nonvegetated marsh categories, such as pools and ponds and intertidal creeks. See the glossary for additional definitions of habitat types (Appendix 1).

For each study, we recorded the species examined, the year and season of sampling, the location including latitude and longitude, the habitat types examined in addition to salt marsh, the method of data collection, the salinity regime and the tidal range. We classified study locations into the following salinity regimes: oligohaline (salinity between 0.5 and 5 ppt), mesohaline (5 to 18 ppt), and polyhaline (>18 ppt). If tidal range was not reported, we used the difference between mean low water and mean high water from the nearest US National Oceanic and Atmospheric Administration tide gauge to represent tidal range.

We developed databases on density, growth and survival that included mean values, standard deviations (SDs) and the number of observations. The number of independent comparisons between habitat types from any study (i.e. the number of rows in the database) was determined by the number of nekton species included, the number of habitat types examined and by certain subjective decisions on the independence of data. These decisions on the number of independent observations are important because they affect analytical power and the influence of a particular study on the overall analysis. Within a study, we considered data from different seasons and years to be independent. In the northern hemisphere, spring samples were those collected in March, April and May; summer in June, July and August; fall in September, October and November; and winter in December, January and February. The treatment of spatial (i.e. location or site) differences was based on the original author's analysis, and we considered locations to be independent if they were reported as such in the study. In some instances, values had to be estimated from figures or graphs. Infrequently, we also had to calculate SDs from sea-

sonal or spatial replicates presented. If we could not obtain an estimate of the SD or number of observations, the data were not included in our analyses. When data had to be combined, we use unweighted means and calculated a pooled standard deviation (Topping 1962).

We conducted meta-analyses using MetaWin 2.0 (Sinauer Associates 1997, Rosenberg et al. 2000) and used Hedges' d (Hedges & Olkin 1985) as the metric to measure effect size. Hedges' d requires a mean, a SD and the number of observations for each value compared and is calculated as:

$$d = \frac{(\bar{X}^e - \bar{X}^c)}{S} J$$

where S is the pooled SD, \bar{X}^e and \bar{X}^c are the means of the experimental and control groups, respectively and

$$J = 1 - \frac{3}{4(N^c + N^e - 2) - 1}$$

where N^c and N^e are the numbers of observations in the control and experimental groups, respectively. Therefore, d describes the difference between an experimental and control group in terms of SD units. Thus, a positive value of d in our analyses reflects greater density, growth or survival of nekton in the experimental habitat type compared with the control habitat type. For growth, survival and one of our density analyses, salt marsh was the experimental habitat type and other biotopes (e.g. seagrass, open water) were the control. We also developed a second density database for meta-analysis that only included marsh data. In this analysis, vegetated marsh was the experimental group and nonvegetated marsh was the control.

Hedges' d was calculated for all habitat comparisons in the data sets and a weighted average effect size (E) was determined. Confidence intervals for these cumulative effect sizes were generated using bootstrapping methods (999 iterations) and used to test for significant differences from 0 with $\alpha = 0.05$. Confidence intervals generated through randomization techniques are considered more conservative than parametric methods, and there is no underlying assumption about normality of the data (Rosenberg et al. 2000). However, bootstrap confidence intervals do assume that the distribution of bootstrapped values is centered around the original mean value; we used bias-corrected bootstrap confidence intervals to ameliorate any bias due to small sample sizes (Efron 1987, Rosenberg et al. 2000).

In addition to estimating the cumulative or overall effect size across studies, MetaWin 2.0 also calculates Q_i , a measure of the variation in effect sizes for a set of studies (total heterogeneity). Q_i is a weighted sum of

squares and is analogous to the total sum of squares in an analysis of variance (Rosenberg et al. 2000). Similar to analysis of variance, Q_t can be partitioned in categorical or classified analyses into the variance in effect sizes between class variables (Q_b); comparisons of Q_b with the residual variance can then be used to test whether effect sizes are similar among the class variables. We ran categorical random-effects models to compare effect sizes among various habitat types and made specific habitat comparisons by conducting categorical analyses on subsets of the data. We also examined continuous models where we calculated a weighted least-squares regression between effect size and the continuous variables of latitude and tidal range.

RESULTS

Density

Thirty-two studies comparing nekton densities among habitat types met our criteria for analysis (Table 1). Most of the studies were conducted on the northern coast of the Gulf of Mexico (22) and more than half of these were conducted in the Galveston Bay system of Texas. An additional 8 studies were conducted on the Atlantic coast of the United States from Connecticut to South Carolina. Thus, 94 % of the studies included in our analysis of nekton densities were conducted in the US. Outside of the US., one study was conducted in

Table 1. List of studies included in the 2 meta-analyses on nekton density. The marsh versus marsh analysis compared different marsh components including vegetated edge (VE), vegetated inner (VI), nonvegetated edge (NVE), pools and ponds (PP), intertidal creeks (ITC) and subtidal creeks (STC). The marsh versus other analysis compared marsh and other biotopes including seagrass (SG), open water (OW), macroalgae (ALG) and oyster reefs (OR)

Location	Marsh vs marsh	Marsh vs other	Habitat types compared	Sampling technique	Source
Gulf coast, US					
TX		X	OW, SG, VE	Drop sampler	Rozas & Minello (1998)
TX	X	X	SG, NVE, VE	Drop sampler	Zimmerman et al. (1990c)
TX	X		NVE, PP, VE	Drop sampler	Zimmerman et al. (1990b)
TX		X	OW, SG, NVE	Sled, drop sampler	Petrik et al. (1999)
TX	X	X	OR, OW, ITC, NVE, VE, VI	Sled, drop sampler, lift net	Stunz et al. (2002b)
TX		X	OW, SG, VE	Drop sampler	Thomas et al. (1990)
TX	X		NVE, VE, VI	Drop sampler	Minello & Webb (1997)
TX	X	X	OW, ITC, PP, VE, VI	Drop sampler	Rozas & Zimmerman (2000)
TX	X	X	SG, NVE, VE	Drop sampler	Zimmerman et al. (1990a)
TX		X	OW, VE	Drop sampler	Zimmerman et al. (1992)
TX	X	X	OW, NVE, PP, VE, VI	Drop sampler	Minello et al. (1991)
TX	X		NVE, VE	Drop sampler	Zimmerman et al. (1984)
TX	X		NVE, VE	Drop sampler	Zimmerman & Minello (1984b)
TX	X		NVE, VE	Drop sampler	Zimmerman et al. (1991)
TX	X	X	OR, NVE, VE	Drop sampler	Zimmerman et al. (1989)
LA	X	X	SG, NVE, VE	Throw trap	Castellanos & Rozas (2001)
LA		X	OW, STC	Otter trawl	Deegan (1990)
LA	X	X	SG, PP, VE	Drop sampler	Rozas & Minello (1999)
LA	X		NVE, VE	Drop sampler	Zimmerman (1988)
AL		X	SG, VE	Enclosure cylinder	Heck et al. (2001)
AL	X		NVE, VE	Drop sampler	Howe et al. (1999)
AL		X	OW, SG, VE	Drop sampler	Howe & Wallace (2000)
Atlantic coast, US					
NJ, CT		X	ALG, OW, SG, STC	Beam trawl	Goldberg et al. (2002)
NJ		X	ALG, OW, SG, STC	Suction sampler	Able et al. (1989)
NJ		X	ALG, OW, SG, STC	Drop sampler	Wilson et al. (1990b)
NJ		X	ALG, OW, SG, STC	Throw trap	Sogard & Able (1991)
VA		X	SG, STC	Suction sampler	Orth & Van Montfrans (1987)
VA		X	SG, STC	Otter trawl, Wegener ring	Weinstein & Brooks (1983)
VA		X	OW, NVE, VE, VI	Drop sampler	Cicchetti (1998)
SC	X		STC, VE	Drop sampler	Mense & Wenner (1989)
Europe					
The Netherlands		X	OW, ITC	Fyke net, beam trawl	Cattrijsse et al. (1997)
Australia					
Queensland	X		PP, VI	Pop net	Thomas & Connally (2001)

Table 2. Comparison matrices for the meta-analysis of marsh versus marsh and marsh versus other habitat types. The number of independent comparisons is shown for each habitat type combination in the 2 analyses

Marsh vs marsh					
Vegetated marsh	Nonvegetated marsh				Total
	Intertidal creeks	Nonvegetated edge	Pools and ponds	Subtidal creeks	
Vegetated edge	19	407	55	2	483
Vegetated inner	19	18	23		60
Total	38	425	78	2	543
Marsh vs other					
Marsh type	Other habitat type				Total
	Open water	Seagrass	Macroalgae	Oyster reef	
Intertidal creeks	22	1			23
Nonvegetated edge	10	150		9	169
Pools and ponds	18	4			22
Subtidal creeks	29	38	32		99
Vegetated edge	77	175		11	263
Vegetated inner	31	4			35
Total	187	372	32	20	611

Europe (in the Westerschelde Estuary of The Netherlands) and one in South Queensland, Australia. Within salt marshes, most available comparisons were between vegetated marsh edge and nonvegetated marsh edge (Table 2). Most comparisons between salt marsh and other biotopes were with seagrass and open water.

In our initial density analysis, we included all nekton species and compared vegetated marsh (88.9% marsh edge) with different types of nonvegetated marsh; Q_b was significant, indicating that the effect size (E) differed among the nonvegetated marsh types (Table 3). Effect size was positive for nonvegetated edge and the 95% confidence interval did not overlap 0 (Table 3), indicating that overall nekton densities were significantly higher in vegetated marsh compared with nonvegetated edge. Densities in vegetated marsh were significantly lower than in subtidal creeks ($E = -0.63$), but this result was based on only 2 comparisons from 1 study of portunid crab densities (143 animals) in South Carolina (Mense & Wenner 1989). When compared with all nonvegetated marsh, the 2 types of vegetated marsh had significantly different effect sizes; densities in vegetated edge were higher than in nonvegetated marsh, while there was no significant difference between vegetated inner marsh and nonvegetated marsh (Table 3).

We also compared nekton densities in salt marshes with densities in other biotopes including open water, seagrass, macroalgae and oyster reef. For all nekton species combined, there was a significant difference among the effect sizes for these other biotopes; densities in salt marsh (all marsh components combined) were lower than in seagrass and higher than in oyster

reef, while there was no significant difference between nekton densities in marsh and in open water or macroalgae (Table 4). The pattern was similar when only vegetated marsh was included in comparisons. However, when only nonvegetated marsh was included, there were no significant differences between salt marsh and either open water, macroalgae or oyster reef. We compared different salt marsh components with open water and found no significant differences in density between open water and nonvegetated marsh; however, densities in vegetated marsh were significantly higher than in open water (Table 4). In a similar comparison with seagrass, nekton densities in seagrass were significantly higher than all types of salt marsh examined.

Overall fish densities were not significantly different between vegetated marsh and nonvegetated marsh edge or marsh pools and ponds, but densities were lower in vegetated marsh than in intertidal creeks (Table 3). Fish densities in vegetated inner marsh were significantly lower than in nonvegetated marsh. In comparison with other biotopes, fish densities in salt marshes were significantly lower than in seagrass but not significantly different from densities in open water, macroalgae or oyster reef. Densities in open water were significantly higher than in vegetated inner marsh but not significantly different from densities in other marsh types (Table 4).

Our analyses on fish densities consolidated data on 29 species of transient fishes but density patterns varied among species (Table 5). In comparisons between vegetated and nonvegetated marsh, spotted seatrout *Cynoscion nebulosus*, striped mullet *Mugil cephalus*, pinfish *Lagodon rhomboides* and silver perch *Bair-*

Table 3. Results of meta-analysis comparing nekton densities among different salt marsh types. A significant Q_b indicates that the effect size (E) differs among the marsh types in that comparison. The effect size is based on Hedges' d and a positive value indicates relatively high densities in the experimental marsh type (vegetated marsh) compared with the control marsh type (non-vegetated marsh). An effect is considered significant if the 95% confidence interval does not overlap 0. Abbreviations for marsh types are in Table 1

Marsh type	No. of comparisons	E	95% CI
All nekton species			
Compared to all vegetated marsh (VE, VI) ($Q_b = 16.52$; $p = 0.014$; $df = 3,542$)			
Nonvegetated edge	425	0.458	+0.350 to +0.568
Subtidal creeks	2	-0.633	-0.880 to -0.632
Pools and ponds	78	0.092	-0.063 to +0.239
Intertidal creeks	38	-0.078	-0.388 to +0.207
Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 12.75$; $p = 0.002$; $df = 1,542$)			
Vegetated edge	483	0.419	+0.329 to +0.516
Vegetated inner	60	-0.110	-0.350 to +0.131
Fish			
Compared to all vegetated marsh (VE, VI) ($Q_b = 21.11$; $p = 0.001$; $df = 2,321$)			
Nonvegetated edge	256	0.009	-0.068 to +0.075
Pools and ponds	48	-0.094	-0.276 to +0.063
Intertidal creeks	18	-0.665	-0.985 to -0.313
Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 12.28$; $p = 0.002$; $df = 1,321$)			
Vegetated edge	289	0.005	-0.065 to +0.085
Vegetated inner	33	-0.449	-0.766 to -0.144
Decapod crustaceans			
Compared to all vegetated marsh (VE, VI) ($Q_b = 18.39$; $p = 0.008$; $df = 3,220$)			
Nonvegetated edge	169	0.958	+0.814 to +1.112
Pools and ponds	30	0.414	+0.189 to +0.654
Subtidal creeks	2	-0.628	-0.880 to -0.385
Intertidal creeks	20	0.474	+0.218 to +0.774
Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 8.52$; $p = 0.007$; $df = 1,220$)			
Vegetated edge	194	1.031	+0.855 to +1.231
Vegetated inner	27	0.291	+0.046 to +0.605

diella chrysoura appeared to select vegetated marsh, while blackcheek tonguefish *Symphurus plagiusa*, gulf menhaden *Brevoortia patronus*, spot *Leiostomus xanthurus*, speckled worm eel *Myrophis punctatus*, Atlantic croaker *Micropogonias undulatus* and spotfin mojarra *Eucinostomus argenteus* selected nonvegetated marsh. In comparisons between vegetated marsh and open water, *C. nebulosus*, *M. cephalus* and *B. chrysoura* selected vegetated marsh, and *L. xanthurus* and *M. undulatus* selected open water. Red drum *Sciaenops ocellatus* and *L. xanthurus* had higher densities in nonvegetated marsh compared with open water, but

M. undulatus and winter flounder *Pseudopleuronectes americanus* had higher densities in open water. When significant density differences occurred, all fish species appeared to select seagrass over both vegetated and nonvegetated marsh. However, there were no significant differences in density between vegetated marsh and seagrass for some fish species, such as *M. cephalus*, *L. xanthurus* and *L. rhomboides*.

Density trends for decapod crustaceans were similar to those for overall nekton, but more comparisons were statistically significant. Within marshes, overall crustacean densities in vegetation were significantly higher than in nonvegetated edge, pools and ponds or intertidal creeks (Table 3). In addition, densities in vegetated edge were significantly higher than in vegetated inner marsh. In comparison with other biotopes, crustacean densities in salt marshes (all marsh components included) were significantly higher than in open water and oyster reef, and significantly lower than in seagrass (Table 4). When compared with open water, densities in vegetated marsh edge were significantly higher, but there were no significant differences with other marsh types. Crustacean densities in seagrass were significantly higher than in all marsh types.

Seven species of decapod crustaceans occurred in the database (Table 5); species with the greatest number of independent habitat comparisons included blue crab *Callinectes sapidus*, brown shrimp *Farfantepenaeus aztecus* (formerly *Penaeus aztecus*, see Perez-Farfante & Kensley 1997 for changes in shrimp nomenclature), white shrimp *Litopenaeus setiferus* (formerly *Penaeus setiferus*) and pink shrimp *Farfantepenaeus duorarum* (formerly *Penaeus duorarum*). Patterns of habitat use (based on density differences) were generally consistent among crustacean species (Table 5). All species selected for vegetated marsh over nonvegetated marsh and open water. Most species selected seagrass over both vegetated and nonvegetated marsh. However, there was no significant difference in densities of *F. aztecus* between seagrass and vegetated marsh, and densities of *L. setiferus* were not significantly different between seagrass and either vegetated marsh or nonvegetated marsh.

Differences in density patterns were apparent between the US Atlantic and Gulf of Mexico coasts. Along the Atlantic, fish densities in open water were significantly higher than in either vegetated or nonvegetated marsh, while no significant difference occurred in the Gulf (Table 6). Decapod crustacean densities on the Atlantic coast were not significantly different between vegetated marsh and open water, while densities in vegetated marsh were significantly higher than in open water on the Gulf coast. In addition, the general pattern of higher fish and crustacean densities in seagrass compared with vegetated

marsh was stronger in the Atlantic compared with the Gulf.

We also examined density patterns in relation to salinity regimes and seasons. Although few strong interactions were apparent, habitat selection by fishes for seagrass (or submerged aquatic vegetation) over

nonvegetated marsh did not occur in oligohaline areas of estuaries as it did in other salinity regimes (Table 6). The pattern of higher juvenile crustacean densities in vegetated marsh compared with nonvegetated marsh was more pronounced in polyhaline salinity regimes and in the summer.

Table 4. Results of meta-analysis comparing nekton densities between salt marsh and other biotopes. A significant Q-value between habitat types (Q_b) indicates that the effect size (E) differs among the habitat types in that comparison. The effect size is based on Hedges' d , and a positive value indicates relatively high densities in the experimental habitat type (marsh) compared with the control habitat type (other biotopes). An effect is considered significant if the 95% confidence interval does not overlap 0. Abbreviations for habitat types are in Table 1

Habitat type	No. of comparisons	E	95% CI	Habitat type	No. of comparisons	E	95% CI				
All nekton species											
Compared to all marsh types (VE, VI, NVE, PP, ITC, STC) ($Q_b = 64.38$; $p = 0.001$; $df = 3,610$)											
Macroalgae	32	-0.255	-0.778 to +0.064	Subtidal creeks	21	-0.196	-0.841 to +0.145				
Open water	187	+0.189	-0.016 to +0.388	Vegetated edge	37	+0.245	-0.223 to +0.985				
Seagrass	372	-0.629	-0.779 to -0.464	Nonvegetated edge	6	+0.026	-1.463 to +1.471				
Oyster reef	20	+1.262	+0.587 to +1.953	Intertidal creeks	10	+0.878	-0.130 to +1.989				
Compared to all vegetated marsh (VE, VI) ($Q_b = 39.64$; $p = 0.006$; $df = 2,297$)											
Open water	108	+0.283	-0.022 to +0.571	Vegetated inner	17	-0.901	-1.634 to -0.260				
Seagrass	179	-0.690	-0.933 to -0.347	Pools and ponds	8	-0.364	-1.548 to +0.164				
Oyster reef	11	+1.642	+0.549 to +2.598	Compared to seagrass ($Q_b = 73.37$; $p = 0.009$; $df = 3,205$)							
Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 25.16$; $p = 0.001$; $df = 3,312$)											
Macroalgae	32	-0.233	-0.665 to +0.073	Subtidal creeks	26	-0.292	-0.781 to -0.058				
Open water	79	+0.060	-0.201 to +0.270	Vegetated edge	90	-0.521	-0.781 to -0.213				
Seagrass	193	-0.582	-0.756 to -0.436	Nonvegetated edge	88	-0.283	-0.549 to -0.120				
Oyster reef	9	+0.793	-0.125 to +1.535	Vegetated inner	2	-7.971	-19.306 to -2.998				
Decapod crustaceans											
Compared to open water ($Q_b = 23.22$; $p = 0.002$; $df = 5,186$)											
Subtidal creeks	29	-0.109	-0.604 to +0.158	Compared to all marsh types (VE, VI, NVE, PP, ITC, STC) ($Q_b = 62.30$; $p = 0.001$; $df = 3,271$)							
Vegetated edge	77	+0.620	+0.331 to +0.941	Macroalgae	7	-0.486	-1.881 to +0.234				
Nonvegetated edge	10	-0.162	-1.093 to +0.916	Open water	88	+0.447	+0.143 to +0.640				
Intertidal creeks	22	+0.437	-0.132 to +1.023	Seagrass	165	-0.822	-1.050 to -0.529				
Vegetated inner	31	-0.577	-1.053 to -0.138	Oyster reef	12	+1.467	+0.542 to +2.133				
Pools and ponds	18	-0.026	-0.665 to +0.311	Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 48.87$; $p = 0.001$; $df = 3,124$)							
Compared to seagrass ($Q_b = 148.27$; $p = 0.001$; $df = 4,370$)											
Subtidal creeks	38	-0.431	-0.902 to -0.165	Macroalgae	7	-0.406	-1.390 to +0.393				
Vegetated edge	175	-0.488	-0.703 to -0.205	Open water	34	+0.071	-0.273 to +0.283				
Nonvegetated edge	150	-0.610	-0.847 to -0.442	Seagrass	78	-1.009	-1.245 to -0.714				
Vegetated inner	4	-9.489	-11.824 to -4.509	Oyster reef	6	+1.298	+0.243 to +2.241				
Pools and ponds	4	-0.418	-2.598 to -0.308	Compared to open water ($Q_b = 34.52$; $p = 0.001$; $df = 5,87$)							
Fish											
Compared to all marsh types (VE, VI, NVE, PP, ITC, STC) ($Q_b = 12.84$; $p = 0.049$; $df = 3,338$)											
Macroalgae	25	-0.195	-0.780 to +0.165	Subtidal creeks	8	+0.145	-0.606 to +0.548				
Open water	99	-0.039	-0.317 to +0.301	Vegetated edge	40	+0.976	+0.720 to +1.225				
Seagrass	207	-0.474	-0.673 to -0.295	Nonvegetated edge	4	-0.505	-1.901 to +0.128				
Oyster reef	8	+0.957	-0.231 to +2.449	Intertidal creeks	12	+0.055	-0.473 to +0.341				
Compared to all nonvegetated marsh (NVE, PP, ITC, STC) ($Q_b = 2.71$; $p = 0.204$; $df = 3,187$)											
Macroalgae	25	-0.183	-0.691 to +0.142	Vegetated inner	14	-0.194	-0.679 to +0.371				
Open water	45	+0.050	-0.312 to +0.462	Pools and ponds	10	+0.243	-0.347 to +0.644				
Seagrass	115	-0.304	-0.538 to -0.171	Compared to seagrass ($Q_b = 82.11$; $p = 0.002$; $df = 4,164$)							
Oyster reef	3	-0.217	-3.296 to +0.498	Subtidal creeks	12	-0.721	-1.758 to -0.080				
				Vegetated edge	85	-0.449	-0.798 to -0.065				
				Nonvegetated edge	62	-1.078	-1.496 to -0.753				
				Vegetated inner	2	-10.950	-25.735 to -10.950				
				Pools and ponds	4	-0.418	-2.897 to -0.301				

Table 5. Nekton species included in the density meta-analyses. For the comparisons of vegetated marsh with nonvegetated marsh, a positive effect size (E) indicates significantly ($p < 0.05$) higher densities in vegetated marsh. In other comparisons, a positive E indicates significantly higher density in marsh compared with either open water or seagrass. At least 2 comparisons were needed to record an effect size; ns = nonsignificant. *Brevoortia tyrannus* is not included under fishes because of too few comparisons

Species	Vegetated marsh vs Nonvegetated marsh		Vegetated marsh vs				Nonvegetated marsh vs			
	E	N	Open water E	N	Seagrass E	N	Open water E	N	Seagrass E	N
Fishes	ns	322	ns	54	-0.3937	92	ns	45	-0.29	115
<i>Acanthopagrus australis</i>		1								
<i>Anguilla rostrata</i>								1		1
<i>Archosargus probatocephalus</i>				1		1				
<i>Arius felis</i>	ns	7								
<i>Arrhamphus sclerolepis</i>		1								
<i>Bairdiella chrysoura</i>	+0.39	14	+0.44	3	ns	4			ns	5
<i>Brevoortia patronus</i>	-0.52	30	ns	5	ns	4	ns	6	ns	5
<i>Citharichthys spilopterus</i>	-0.25	9			ns	3			ns	4
<i>Cynoscion arenarius</i>			-0.28	2						
<i>Cynoscion nebulosus</i>	+0.18	30	+0.88	3	-0.41	13			-0.50	13
<i>Elops saurus</i>	ns	4								
<i>Eucinostomus argenteus</i>	-0.31	4								
<i>Gerres subfasciatus</i>		1								
<i>Lagodon rhomboides</i>	+0.62	39	ns	4	ns	17		1	-0.98	12
<i>Leiostomus xanthurus</i>	-0.51	32	-1.10	6	ns	10	+1.12	2	ns	14
<i>Micropogonias undulatus</i>	-0.49	19	-1.45	2	-1.19	2	-0.36	3	ns	4
<i>Mugil cephalus</i>	+0.18	40	+0.62	9	ns	10	ns	3	ns	9
<i>Mugil curema</i>	+0.45	2								
<i>Myrophis punctatus</i>	-0.16	26			-0.4186	15			-0.5147	14
<i>Opsanus beta</i>	ns	3								
<i>Orthopristis chrysoptera</i>	ns	4								
<i>Paralichthys dentatus</i>										1
<i>Paralichthys lethostigma</i>	ns	13								
<i>Pseudopleuronectes americanus</i>							-0.30	18	-0.29	19
<i>Sciaenops ocellatus</i>	ns	6	ns	6		1	+3.05	3		1
<i>Sillago maculata</i>		1								
<i>Symphurus plagiusa</i>	-0.32	36	-1.09	13	-2.1472	12	-0.71	8	ns	11
<i>Tautoga onitis</i>									-0.62	2
Decapod crustaceans	+0.82	221	+0.68	54	-0.34	87	ns	34	-0.91	78
<i>Callinectes sapidus</i>	+1.17	75	+0.57	24	-0.54	40	ns	18	-1.12	37
<i>Callinectes similis</i>		1						1		1
<i>Crangon crangon</i>								2		
<i>Farfantepenaeus aztecus</i>	+0.84	71	+0.59	15	ns	20	ns	8	-0.97	18
<i>Farfantepenaeus duorarum</i>	+0.87	19	+0.59	4	-0.42	11			-1.19	10
<i>Litopenaeus setiferus</i>	+0.38	51	+1.07	11	ns	13	-0.82	5	ns	11
<i>Macrobrachium ohione</i>	+0.82	4			ns	3				1

For overall nekton, we examined the relationships between latitude, tidal range and effect size. For comparisons of densities in salt marsh (all marsh components combined) versus open water, there was a significant negative relationship between tidal range and effect size (slope = -0.66 , $df = 1,186$, $p = 0.001$), indicating that selection for salt marsh over open water declined as tidal range increased (Fig. 1). A significant relationship was also present between latitude and effect size, but the slope was much closer to 0 (slope = -0.018 , $df = 1,186$, $p = 0.038$). For comparisons of densities in salt marsh (all marsh components) versus seagrass, there was also a significant negative relation-

ship between tidal range and effect size (slope = -0.39 , $df = 1,371$, $p = 0.009$), indicating that selection for seagrass over salt marsh was less intense at lower tidal ranges. There was no significant effect of latitude on selection for seagrass over salt marsh ($df = 1,371$, $p = 0.187$).

Growth

The 5 studies that met our criteria and provided growth rates in salt marshes varied in the species examined and in experimental approach (Table 7). The

Table 6. Meta-analysis comparisons of nekton densities in different coastal areas, salinity regimes and seasons. For the comparisons of vegetated marsh with nonvegetated marsh, a positive effect size (E) indicates significantly ($p < 0.05$) higher densities in vegetated marsh. In other comparisons, a positive E indicates significantly higher density in marsh compared with either open water or seagrass. At least 2 comparisons were needed to record an effect size; ns = nonsignificant. Results in bold print indicate that the Q_b (between treatments, e.g. coastal areas) was significant ($p < 0.05$), and the effect sizes were different for that comparison

Comparison	Vegetated marsh vs Nonvegetated marsh		Vegetated marsh vs				Nonvegetated marsh vs			
	E	N	Open water E	Open water N	Seagrass E	Seagrass N	Open water E	Open water N	Seagrass E	Seagrass N
Fishes	ns	322	ns	54	-0.3937	92	ns	45	-0.29	115
Coastal area										
US Atlantic			-1.71	8	-2.60	5	-0.38	21	-0.33	27
US Gulf of Mexico	ns	317	ns	46	-0.28	87	ns	24	-0.27	87
Salinity regime										
Oligohaline	ns	59	+0.54	3	ns	16	+0.80	2	ns	17
Mesohaline	ns	91	ns	14	-0.76	14	ns	8	-0.67	13
Polyhaline	ns	172	ns	37	-0.41	62	ns	35	-0.33	85
Season										
Spring	ns	163	ns	23	-0.33	40	ns	18	-0.2	48
Summer	ns	59	-1.18	4	ns	15	-0.54	7	ns	15
Fall	ns	84	ns	27	-0.43	37	ns	14	-0.37	42
Winter	ns	11								
Decapod crustaceans	+0.82	221	+0.68	54	-0.34	87	ns	34	-0.91	78
Coastal area										
US Atlantic	-0.63	2	ns	4	-6.37	4	ns	10	-1.07	14
US Gulf of Mexico	+0.83	219	+0.80	50	-0.23	83	ns	22	-0.88	64
Salinity regime										
Oligohaline	+0.57	35	+1.04	4	ns	17			-0.68	15
Mesohaline	+0.56	64	+0.55	17	-0.49	20	ns	12	-0.96	16
Polyhaline	+1.04	117	+0.73	33	-0.36	50	ns	22	-0.99	47
Season										
Spring	+0.81	81	+0.66	16	ns	25	ns	12	-0.65	23
Summer	+1.10	31	ns	4	ns	12	ns	3	-1.33	8
Fall	+0.81	98	+0.86	30	-0.59	42	ns	15	-0.88	41
Winter	ns	6								

most extensive study was conducted by Phelan et al. (2000) in estuaries of Connecticut and New Jersey. They measured growth of caged young-of-the-year tautog *Tautoga onitis* and winter flounder *Pseudopleuronectes americanus* in subtidal marsh creeks, seagrass, open water and macroalgae beds. Irlandi & Crawford (1997) compared growth of pinfish *Lagodon rhomboides* in enclosures between vegetated marsh edge with seagrass and vegetated marsh edge without seagrass in North River, North Carolina. We considered this study to be a comparison of vegetated marsh edge and seagrass, but it could also be considered a comparison of nonvegetated marsh edge and seagrass. On the US Gulf of Mexico Coast, Zimmerman & Minello (1984a) and Minello & Zimmerman (1991) reported results on caged brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus* in areas with and without access to marsh edge, and Stunz et al. (2002a) used solid walled field mesocosms to compare growth of juvenile red drum *Sciaenops ocellatus* in salt marsh (vegetated edge and nonvege-

tated edge), seagrass and oyster reef. Using a different approach, Whaley (1997) brought cores of marsh sediment into the laboratory to measure growth of brown shrimp and white shrimp in association with different marsh types. We entered growth into our database as mm d^{-1} except for values reported for pinfish by Irlandi & Crawford (1997) that were entered as a change in weight (g) over the 45 d experimental period.

Most growth comparisons between marshes and other habitat types were based on fish in subtidal marsh creeks (Phelan et al. 2000) or nonvegetated marsh edge (Stunz et al. 2002a). A meta-analysis of these comparisons indicated that growth in nonvegetated marsh was not significantly different from growth in open water or in macroalgae beds, but was significantly lower than growth in seagrass ($E = -1.253$). Nekton growth (mainly penaeid shrimp) in vegetated marsh edge and nonvegetated marsh edge has been measured in Texas using 3 different approaches (Zimmerman & Minello 1984a, Whaley 1997, Stunz et al. 2002a). Although results appeared to

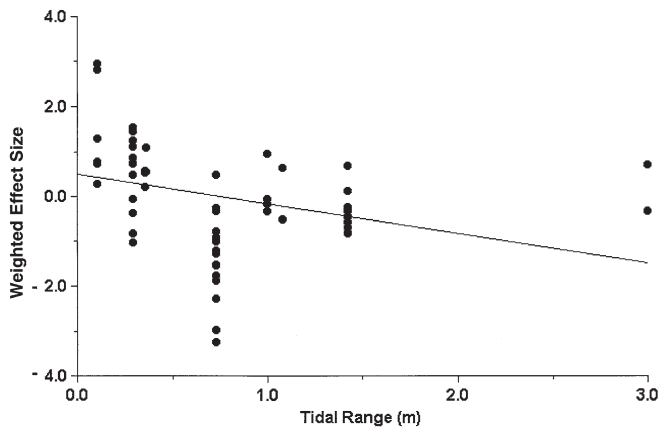


Fig. 1. Relationship between tidal range and nekton selection (based on density) for salt marsh over open water. Larger effect sizes indicate a stronger selection for marsh

vary with species (Table 7), a meta-analysis of 7 comparisons indicated that overall growth was significantly higher in vegetated marsh compared with non-vegetated marsh ($E = +0.58$). We found only 2 studies where growth was compared between vegetated salt marsh and non-marsh habitat types. Irlandi & Crawford (1997) reported negative growth (measured as biomass) of *Lagodon rhomboides* in vegetated marsh (with nonvegetated marsh) compared with positive growth in seagrass (and vegetated marsh). Stunz et al. (2002a), found no significant difference in growth of young *Sciaenops ocellatus* between vegetated marsh edge and seagrass, while growth rates in these vegetated habitat types were significantly higher than in nonvegetated marsh edge and oyster reefs.

Survival

We identified 11 studies that compared nekton survival in salt marshes with other habitat types (Table 8). Mortality in all of these studies was attributed to predation, although other sources could have been important in tethering studies. Five of the studies were field tethering experiments using either young blue crabs (4 studies) or brown shrimp as the prey. Survival in subtidal marsh creeks was compared with open water and seagrass in Chesapeake Bay and New Jersey (Shirley et al. 1990, Wilson et al. 1990a, Ryer et al. 1997). Survival within marsh edge vegetation was compared with open water and seagrass in Mobile Bay and Mississippi Sound, AL (Heck et al. 1994) and Christmas Bay, TX (Minello 1993). In laboratory studies, prey consisted of juvenile decapod crustaceans (American lobster *Homarus americanus*, *Farfantepenaeus aztecus*, *Litopenaeus setiferus*, *Callinectes sapidus*)

and 1 species of fish (*Sciaenops ocellatus*). Predators consisted mainly of fishes although crabs were occasionally used (Table 8). Marsh treatments consisted of marsh peat reefs, planted *Spartina alterniflora*, or green straws that simulated the structure of emergent marsh vegetation. The data from all studies were converted to percent survival in each habitat type.

Our meta-analysis of the entire data set indicated that survival in salt marsh was significantly higher than survival in open water, significantly lower than in oyster reef/cobble and not significantly different from seagrass (Table 9). Results from field tethering studies were similar. If we limited the analysis to laboratory studies, the same patterns were apparent, but survival attributed to salt marsh vegetative structure was lower than survival in seagrass.

DISCUSSION

Density patterns

Nekton densities should be one indicator of habitat value and by far, most of the data available to assess the nursery value of salt marshes is on density. Our meta-analyses of density patterns allowed us to generally rank habitat types. For all nekton (fishes and decapod crustaceans), densities in salt marshes appeared similar to densities in open water and macroalgae beds. These densities, however, were lower than those in seagrass and higher than those in oyster reefs. Vegetated marsh edge generally had higher densities than other marsh types and overall rankings appeared to be: seagrass > vegetated marsh edge > nonvegetated marsh, open water, macroalgae > vegetated inner marsh > oyster reef. For fishes alone, this ranking differed slightly: seagrass > vegetated marsh edge, nonvegetated marsh, open water, macroalgae, oyster reefs > vegetated inner marsh. We graphically represented these density relationships among some different habitat types by calculating effect sizes in comparison with vegetated marsh edge and modifying results to eliminate negative values (Fig. 2). Fishes in our analysis were represented by 29 species and patterns of habitat use varied among species. However, the relative value of salt marsh and seagrass beds was consistent; densities were higher in seagrass for all fish species where a significant difference occurred between these habitat types. Density patterns for decapod crustaceans indicated a ranking of: seagrass > vegetated marsh edge > nonvegetated marsh, vegetated inner marsh, open water, macroalgae > oyster reef (Fig. 2). Although 7 species of crustaceans were included in the analysis, most comparisons were for blue crabs, brown shrimp and white shrimp. Densities of the 2 shrimp species were not significantly differ-

Table 7. Mean nekton growth rates and SE in different habitat types. All growth is in mm d⁻¹ except for the data of Irlandi & Crawford (1997) where growth was measured in weight (g) over 45 d. Experiment types include field caging (FC), field mesocosms (FM) and laboratory (L)

Species	Salt marsh		Seagrass	Open water	Oyster reef	Macro-algae	Experiment type	Location	Source
	Vegetated edge	Nonveg-Subtidal inner etated edge creek							
<i>Lagodon rhomboides</i>	Mean (SE)	-4.30 (0.20)	0.80 (1.00)				FC	North River, NC	Irlandi & Crawford (1997)
<i>Tautoga onitis</i>	Mean (SE)	0.46 (0.24)	0.22 (0.04)	0.09 (0.06)		0.21 (0.17)	FC	Hammonasset River, CT	Phelan et al. (2000)
<i>Tautoga onitis</i>	Mean (SE)	0.06 (0.03)	0.25 (0.04)	0.20 (0.03)		0.09 (0.03)	FC	Navesink River, NJ	Phelan et al. (2000)
<i>Tautoga onitis</i>	Mean (SE)	0.11 (0.02)	0.47 (0.04)	0.42 (0.03)		0.43 (0.07)	FC	Great Bay-Little Egg Harbor, NJ	Phelan et al. (2000)
<i>Pseudopleuronectes americanus</i>	Mean (SE)	0.13 (0.04)	0.24 (0.07)	0.10 (0.04)		0.04 (0.07)	FC	Hammonasset River, CT	Phelan et al. (2000)
<i>Pseudopleuronectes americanus</i>	Mean (SE)	0.35 (0.25)	0.61 (0.03)	0.72 (0.04)	0.12 (0.01)	0.81 (0.04)	FC	Great Bay-Little Egg Harbor, NJ	Phelan et al. (2000)
<i>Sciaenops ocellatus</i>	Mean (SE)	0.40 (0.10)	0.42 (0.05)				FM	Galveston Bay, TX	Stunz et al. (2002a)
<i>Farfantepenaeus aztecus (spring)</i>	Mean (SE)	0.18 (0.07)					L	Galveston Bay, TX	Whaley (1997)
<i>Farfantepenaeus aztecus (summer)</i>	Mean (SE)	0.18 (0.03)					L	Galveston Bay, TX	Whaley (1997)
<i>Litopenaeus setiferus</i>	Mean (SE)	0.11 (0.03)					L	Galveston Bay, TX	Whaley (1997)
<i>Farfantepenaeus aztecus</i>	Mean (SE)	0.98 (0.02)					FC	Galveston Bay, TX	Minello & Zimmerman (1991)
<i>Farfantepenaeus aztecus</i>	Mean (SE)	1.41 (0.05)					FC	Galveston Bay, TX	Minello & Zimmerman (1991)
<i>Litopenaeus setiferus</i>	Mean (SE)	1.04 (0.03)					FC	Galveston Bay, TX	Minello & Zimmerman (1991)

Table 8. Mean percent survival and SE of transient nekton prey in salt marsh and other biotopes

Prey species	Predator species	Experiment type	Marsh		% Survival		Open water	Oyster/cobble	Marsh type	Location	Source
			Mean (SE)	SE	Seagrass	Mean (SE)					
<i>Callinectes sapidus</i>	Natural	Tethering	0.12 (0.06)		0.07 (0.04)		0.03 (0.02)		Vegetated marsh edge	Mobile Bay, AL	Heck et al. (1994)
<i>Callinectes sapidus</i>	Natural	Tethering	0.23 (0.13)		0.22 (0.09)		0.13 (0.08)		Vegetated marsh edge	Mobile Bay, AL	Heck et al. (1994)
<i>Fairfantepenaeus aztecus</i>	Natural	Tethering	0.56 (0.25)		0.46 (0.17)		0.21 (0.07)		Vegetated marsh edge	Christmas Bay, TX	Minello (1993)
<i>Callinectes sapidus</i>	Natural	Tethering	0.23 (0.13)		0.22 (0.13)				Subtidal creek	Chesapeake Bay	Ryer et al. (1997)
<i>Callinectes sapidus</i>	Natural	Tethering	0.53 (0.31)		0.58 (0.34)				Subtidal creek	Chesapeake Bay	Ryer et al. (1997)
<i>Callinectes sapidus</i>	Natural	Tethering	0.74 (0.52)				0.44 (0.31)		Subtidal creek	Chesapeake Bay	Shirley et al. (1990)
<i>Callinectes sapidus</i>	Natural	Tethering	0.57 (0.33)		0.81 (0.47)		0.64 (0.29)		Subtidal creek	Chesapeake Bay	Wilson et al. (1990a)
<i>Homarus americanus</i>	<i>Carcinus maenas</i>	Laboratory	0.15 (0.09)				0.20 (0.11)	0.71 (0.41)	Marsh peat	Little Egg Harbor, NJ	Barshaw et al. (1994)
<i>Homarus americanus</i>	<i>Tautoglabrus adspersus</i>	Laboratory	0.19 (0.11)				0.00 (0.00)	0.46 (0.27)	Marsh peat	Tuckerton, NJ	Barshaw et al. (1994)
<i>Fairfantepenaeus aztecus</i>	<i>Cynoscion nebulosus</i>	Laboratory	0.62 (0.36)				0.62 (0.36)		Green straws	Tuckerton, NJ	Barshaw et al. (1994)
<i>Fairfantepenaeus aztecus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.67 (0.03)				0.33 (0.07)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.55 (0.02)				0.30 (0.06)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.53 (0.05)				0.43 (0.15)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Micropogonias undulatus</i>	Laboratory	0.66 (0.04)				0.48 (0.02)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Sciaenops ocellatus</i>	Laboratory	0.43 (0.31)				0.36 (0.21)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Sciaenops ocellatus</i>	Laboratory	0.53 (0.31)				0.48 (0.28)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
<i>Fairfantepenaeus aztecus</i>	<i>Sciaenops ocellatus</i>	Laboratory	0.68 (0.39)				0.67 (0.38)		Green straws	Galveston, TX	Minello & Zimmerman (1983)
Pensaeid shrimp	<i>Micropogonias undulatus</i>	Laboratory	0.47 (0.27)				0.45 (0.26)		Green straws	Galveston, TX	Minello & Zimmerman (1985)
Pensaeid shrimp	<i>Micropogonias undulatus</i>	Laboratory	0.57 (0.33)				0.48 (0.28)		Green straws	Galveston, TX	Minello & Zimmerman (1985)
<i>Fairfantepenaeus aztecus</i>	<i>Fundulus grandis</i>	Laboratory	0.88 (0.29)				0.77 (0.26)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Fundulus grandis</i>	Laboratory	0.90 (0.30)				0.97 (0.32)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.62 (0.15)				0.41 (0.10)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.70 (0.16)				0.47 (0.11)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Micropogonias undulatus</i>	Laboratory	0.80 (0.27)				0.90 (0.30)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Micropogonias undulatus</i>	Laboratory	0.87 (0.29)				0.71 (0.24)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Paralichthys lethostigma</i>	Laboratory	0.80 (0.30)				0.59 (0.22)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Sciaenops ocellatus</i>	Laboratory	0.87 (0.29)				0.53 (0.18)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Fairfantepenaeus aztecus</i>	<i>Sciaenops ocellatus</i>	Laboratory	0.88 (0.29)				0.74 (0.25)		Planted <i>S. alterniflora</i>	Galveston, TX	Minello et al. (1989)
<i>Sciaenops ocellatus</i>	<i>Cynoscion nebulosus</i>	Laboratory	0.38 (0.13)		0.64 (0.21)		0.24 (0.08)	0.51 (0.17)	Planted <i>S. alterniflora</i>	Galveston, TX	Stunz & Minello (2000)
<i>Sciaenops ocellatus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.41 (0.13)		0.51 (0.16)		0.20 (0.06)	0.73 (0.23)	Planted <i>S. alterniflora</i>	Galveston, TX	Stunz & Minello (2000)
<i>Callinectes sapidus</i>	<i>Callinectes sapidus</i>	Laboratory	0.76 (0.17)		0.72 (0.16)		0.53 (0.12)		Planted <i>S. alterniflora</i>	Galveston, TX	Thomas (1989)
<i>Callinectes sapidus</i>	<i>Lagodon rhomboides</i>	Laboratory	0.77 (0.17)		0.89 (0.20)		0.37 (0.08)		Planted <i>S. alterniflora</i>	Galveston, TX	Thomas (1989)

Table 9. Results of meta-analysis comparing nekton survival between salt marsh and other biotopes. A significant Q_b indicates that the effect size (E) differs among the biotopes in that comparison. The effect size is based on Hedges' d , and a positive value indicates relatively high survival in the experimental habitat type (marsh) compared with the control habitat type (other biotopes). An effect is considered significant if the 95% confidence interval does not overlap 0

Biotope	No. of comparisons	E	95% CI
All data included ($Q_b = 28.73$; $p = 0.001$; $df = 2,43$)			
Open water	30	+0.64	+0.440 to +0.885
Oyster/cobble	4	-1.005	-2.204 to -0.608
Seagrass	10	-0.28	-0.657 to +0.029
Only comparisons with structured marsh ($Q_b = 27.52$; $p = 0.001$; $df = 2,38$)			
Open water	28	+0.651	+0.432 to +0.885
Oyster/cobble	4	-0.996	-2.990 to -0.608
Seagrass	7	-0.223	-0.588 to +0.138
Only comparisons with subtidal marsh creeks ($Q_b = 0.98$; $p = 0.480$; $df = 1,4$)			
Open water	2	+0.543	-0.530 to +2.427
Seagrass	3	-0.712	-1.401 to +0.013
Only laboratory comparisons ($Q_b = 25.65$; $p = 0.001$; $df = 2,32$)			
Open water	25	+0.622	+0.406 to +0.890
Oyster/cobble	4	-1.014	-2.211 to -0.608
Seagrass	4	-0.401	-0.894 to -0.034
Only field tethering comparisons ($Q_b = 2.93$; $p = 0.083$; $df = 1,10$)			
Open water	5	+0.808	+0.031 to +1.632
Seagrass	6	-0.068	-0.878 to +0.238

ent between seagrass and vegetated marsh edge. Our meta-analysis of nekton density patterns indicates that species selectively use different components of salt marshes and therefore, comparisons of salt marshes with other habitat types are strongly affected by the marsh components examined. Because salt marshes are intertidal, there is also a temporal complexity inherent in density comparisons. Information on tidal stage at the time of collection was not always available, but most comparisons were made at high tide when marsh vegetation was flooded. During low tide, densities in nonvegetated marsh will be elevated for most nekton and comparisons among habitat types may differ (Cicchetti & Diaz 2000).

There are many variables that can affect nekton density patterns in estuaries (Craig & Crowder 2000) and that may interact with utilization of different biotopes. Our meta-analyses indicated that habitat use was affected by salinity regime, tidal range, season and geographic location. Salinity patterns in estuaries often have been shown to coincide with dramatic shifts

in the distribution and abundance of young nekton (Weinstein et al. 1980b, Zimmerman et al. 1990a,b, Baltz et al. 1993, Bulger et al. 1993, Whitfield 1994). The location of salt marshes in the estuarine landscape is also important, and proximity to barrier islands (Weinstein et al. 1980b) and seagrass beds (Rozas & Odum 1987, Irlandi & Crawford 1997) appears to affect marsh use.

Certain data limitations need to be considered in assessing the value of our meta-analyses on nekton densities. The data used in these comparisons are highly biased towards the Atlantic and Gulf of Mexico coasts of the US. However, salt marsh systems are distributed throughout the world (Chapman 1960); and young transient nekton have been collected in salt marshes on the western coast of the US (Shreffler et al. 1990, Chamberlain & Barnhart 1993, Desmond et al. 2000), in Europe (Drake & Arias 1991, Cattrijsse et al. 1994, Costa et al. 1994, Laffaille et al. 1998, Mathieson et al. 2000), Africa (Whitfield 1994, Paterson & Whitfield 1996) and Australia (Connolly 1999). The prepon-

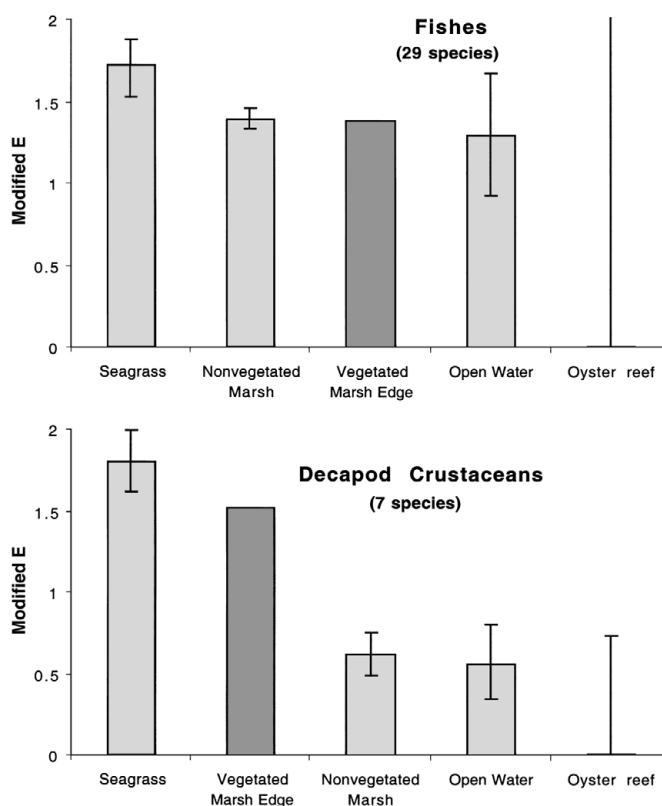


Fig. 2. Density relationships among habitat types based on meta-analysis effect sizes. All habitat types are compared with vegetated marsh edge. The absolute value of the lowest effect size (oyster reef) was added to each effect size to convert all values to positive numbers. Error bars are 95% confidence intervals and can be used to compare habitat types with vegetated marsh edge

derance of studies in our analyses from the northern Gulf of Mexico should be noted because extended tidal flooding in these salt marshes may increase use of the marsh surface (Rozas 1993, 1995, Zimmerman et al. 2000) and density patterns in the Gulf may not be similar to patterns in other coastal regions of the world. We could not directly address hypotheses regarding flooding duration and nekton use of the marsh surface, because these data have been infrequently measured outside the northern Gulf of Mexico where tidal range is low and flooding duration is often high (Rozas & Reed 1993, Rozas 1995). However, nekton use of salt marshes in relation to open water appeared to be greater in the Gulf of Mexico than along the Atlantic coast of the US (Table 6) and was negatively related to tidal range (Fig. 1). Density comparisons may also be affected by errors in our assignment of data to habitat types and by the spatial scale of our habitat classification. For example, we assigned nekton densities to nonvegetated marsh edge if they were obtained on nonvegetated bottom within approximately 10 m of marsh vegetation. There is some evidence, however, that within this marsh type, some fishes selectively use a much narrower band just outside of the vegetation (Baltz et al. 1993, Stunz et al. 2002b). In addition, comparisons from our data are limited by the relative lack of information on nekton densities in water deeper than about 1 m due to gear restrictions (Rozas & Minello 1997, Connolly 1999).

Growth and survival

The nursery function of a habitat is related to the export of secondary production (Beck et al. 2001). Thus, growth and survival within habitats are important characteristics defining nursery value for nekton. The measurement of these variables, however, has been problematic, especially with regard to specific habitat types.

Relatively few studies have examined growth rates of transient nekton species in salt marshes. The comparisons we found were mainly restricted to measurements of fish growth in subtidal marsh creeks and penaeid shrimp growth in vegetated and nonvegetated marsh edge. Fish growth in subtidal marsh creeks was similar to growth in open water and macroalgae beds, but lower than in seagrass. Most of these data were from an extensive field caging study by Phelan et al. (2000) in New Jersey and Connecticut, and they concluded that growth rates varied with fish species, habitat type, estuary and year. Low growth rates of *Pseudopleuronectes americanus* in marsh creeks were attributed to low dissolved oxygen levels (<2 mg l⁻¹). Experimental data on growth of penaeid

shrimps in salt marshes suggest that while overall growth rates appear higher in vegetated marsh edge compared with nonvegetated marsh edge, results vary with shrimp species and experimental techniques. Growth rates reported by Zimmerman & Minello (1984a) and Minello & Zimmerman (1991) appear to approach natural shrimp growth rates (Knudsen et al. 1977), and they found that *Farfantepenaeus aztecus* grew better in vegetated marsh but *Litopenaeus setiferus* did not. Whaley (1997) brought cores of marsh sediment into the laboratory and obtained different results for the same 2 shrimp species. Overall growth in her experiments was relatively low, and food limitation may have occurred (Whaley 1997). In a study on juvenile *Sciaenops ocellatus* growth, Stunz et al. (2002a) found no significant differences between vegetated marsh edge and seagrass, while growth rates in these vegetated habitat types were significantly higher than in nonvegetated marsh edge (sand bottom) or on oyster reefs. Overall, these data indicate that the type of marsh included in a study affects comparisons of nekton growth: growth in nonvegetated marsh may be similar to open water, oyster reef and macroalgae beds, while growth in vegetated marsh can be similar to growth in seagrass beds. However, the limited availability of data makes these conclusions highly speculative. Additionally, there is evidence for species-specific differences in growth patterns.

No single technique appears to adequately address experimental difficulties and artifacts encountered in the measurement of habitat-specific growth rates of nekton (Peterson & Black 1994, Underwood 1997). In salt marshes, experimental problems are exacerbated by tidal dynamics. Enclosures or cages have been used to limit nekton movement and relate growth to a particular habitat type, but this restriction is unnatural for highly mobile organisms and may affect results. As an example, apparent low growth rates in marsh creeks observed by Phelan et al. (2000) may have been caused by forcing fish in cages to endure periodic low dissolved oxygen conditions in creeks; under free ranging conditions, fish may have escaped effects of hypoxia. Similarly, caging nekton on the marsh surface prevents normal access to low tide refuges. In addition, if growth is food limited, the size of enclosures, wall construction, type of food required and density of experimental animals can interact with results. Growth of shrimp in marsh cores measured by Whaley (1997) was apparently food limited, and this limitation may have prevented the detection of some differences among her treatments. The interpretation of habitat-specific growth rates is also made difficult by extensive variation between years and estuaries such as that observed by Phelan et al. (2000). In summary, while habitat-specific growth should be an important measure of

nursery value (Beck et al. 2001), there are insufficient data available to use growth rates for effectively comparing marshes with other habitat types. In the future, mark–recapture and remote sensing studies on tagged and free-ranging juvenile nekton should improve our ability to measure habitat-related growth by allowing us to relate growth to home range and site fidelity. Recent growth rates of captured nekton can be assessed through measurements of otolith microstructure (Baltz et al. 1998, Rooker et al. 1999), accumulation rates of cellular pigments (Vila et al. 2000) and metabolic processes (Rooker et al. 1997, Buckley et al. 1999, Westerman et al. 1999); however, problems determining where nekton have been before capture restrict the utility of these techniques for measuring habitat-specific growth (Stunz et al. 2002a).

Habitat-specific estimates of survival may be one of the most useful ways to measure habitat quality for nekton and thus, help to identify nursery habitats. In our meta-analysis, nekton survival in salt marshes was significantly higher than survival in open water, significantly lower than in oyster reef/cobble and not significantly different from seagrass (Table 9). Similar to growth measurements, comparisons of survival in salt marshes with other habitat types are limited by experimental restrictions; only 2 approaches were used to estimate survival, laboratory predation experiments on the effects of vegetative structure and field tethering experiments. In laboratory experiments, survival was best in structured habitats, but salt marsh structure did not appear to offer as much protection as seagrass and oyster reef/cobble. However, structural complexity of habitats is difficult to reproduce in the laboratory and difficult to quantify (Nelson & Bonsdorff 1990, Bartholomew et al. 2000). Although controlled laboratory experiments can eliminate confounding variables, results of these studies may not reflect actual survival rates in habitats where environmental conditions and predator abundances may co-vary with habitat types. Tethering experiments have been used to take this natural variability into account, and these experiments indicate that survival in salt marsh and seagrass is better than in open water (Table 9). However, survival of tethered prey may not always reflect survival of untethered prey (Peterson & Black 1994, Aronson & Heck 1995, Micheli 1996, Kneib & Scheele 2000), and tethering generally has been limited to invertebrates because of concerns regarding abnormal behavior of tethered fishes (Minello 1993, Curran & Able 1998). Advances in the miniaturization of sonic tags and the development of other means of tracking individual organisms may provide techniques to examine both growth and mortality in specific habitat types.

Production of adult nekton that is derived from nursery habitats (as defined by Beck et al. 2001) is difficult

to measure, because it depends on density, growth and survival in nurseries. Cicchetti (1998) provides an excellent literature review of salt marsh production estimates for nekton (mainly small resident species) and discusses difficulties in generating these estimates. His production estimate for transient nekton from vegetated salt marsh edge in Chesapeake Bay was $6.6 \text{ g dry wt m}^{-2} 150 \text{ d}^{-1}$ and was mostly from blue crabs *Callinectes sapidus* (6.0 g). He noted that this production of blue crabs was comparable to estimates from a Virginia seagrass bed (Fredette et al. 1990). We found no direct comparisons of transient nekton production between salt marshes and other habitat types in the literature. Estimates of spot *Leiostomus xanthurus* production have been derived from subtidal marsh creeks in North Carolina ($0.05 \text{ g dry wt m}^{-2} \text{ mo}^{-1}$) by Weinstein & Walters (1981) and in Virginia ($4.6 \text{ g dry wt m}^{-2} 90 \text{ d}^{-1}$) by Weinstein et al. (1984). Deegan & Thompson (1985) estimated production of Atlantic croaker *Micropogonias undulatus* ($23 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$) and gulf menhaden *Brevoortia patronus* ($13 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$) from estuaries of coastal Louisiana, and they suggested (based on standing crop estimates) that productivity was highest in estuarine systems that were in early stages of marsh disintegration. Herke et al. (1992) estimated production from a 35 ha area of impounded marsh (75% marsh pond and 25% *Spartina patens* vegetation) in Louisiana by assuming that biomass recruiting into the system was negligible and measuring the biomass of emigrating nekton; these annual production estimates were $7.8 \text{ g wet wt m}^{-2}$ for *C. sapidus*, 4.5 g m^{-2} for *B. patronus*, 3.2 g m^{-2} for *M. undulatus*, 2.4 g m^{-2} for *Farfantepenaeus aztecus* and 2.2 g m^{-2} for *Litopenaeus setiferus*. Natural mortality and movement within marsh ecosystems complicates these production measurements, and Deegan (1990) discusses these and additional problems encountered estimating production of estuarine nekton.

The relationships between nekton production and coastal salt marshes can also be examined by looking for large-scale correlative trends. Positive relationships have been observed between the area of coastal wetlands and the landings of commercial shrimp (Turner 1977, 1992, Turner & Boesch 1988). Our meta-analyses suggest that salt marshes are important nurseries for decapod crustaceans, such as penaeid shrimp and blue crabs, and therefore, we might expect declines in these fishery species to coincide with the loss of coastal wetlands. In this regard, the northern Gulf of Mexico is of interest because of extensive wetland loss ($>70 \text{ km}^2 \text{ yr}^{-1}$ over several decades) in the region and because of the abundance of estuarine-dependent fishery species, including decapod crustaceans. However, fishery declines are

not yet apparent in the northern Gulf, and the complexity of ecological interactions between wetlands and nekton may be affecting such relationships (Boesch & Turner 1984, Chesney et al. 2000, Zimmerman et al. 2000).

Other considerations

The ability of nekton to move into and out of biotopes can affect nursery values. The level of successful recruitment bringing larvae and postlarvae into estuaries is an important component of habitat use, controlling initial densities of juveniles in different habitat types. Certain characteristics, such as orientation to shoreline, extent and direction of wind induced currents as well as tidal dynamics, appear to promote successful recruitment into particular estuaries (Weinstein et al. 1980a, Rothlisberg et al. 1983, Weinstein 1988, Rogers et al. 1993, Epifanio 1995, Olmi 1995, Morgan et al. 1996, Wenner et al. 1998). Thus, location with respect to a source of recruits (e.g. tidal passes, inlets) may affect density patterns within habitats and therefore, potential nursery value may never be realized. As an example, Guindon & Miller (1995) showed that abundance of juvenile southern flounder in marsh creeks was not always related to production potential. The contribution of a biotope to nekton production reaching adult populations is also highly dependent on the successful movement of animals from a potential nursery area to the adult habitat (Beck et al. 2001). Poor survival during this movement, perhaps due to the physical location of the biotope and the distribution of predators, can influence nursery value. This aspect of nurseries is difficult to examine, and we know of no studies on survival of nekton during movement from salt marshes to adult habitats (Gillanders et al. 2003). The importance of movement into and out of nurseries reinforces the necessity to view nursery habitats within the context of the landscape (Simenstad et al. 2000).

Insights into the relative nursery value of habitat types also have been obtained from analyses of diet (Rozas & LaSalle 1990, Moy & Levin 1991), bioenergetics (Nixon & Oviatt 1973, Deegan 1993, Madon et al. 2001), ecophysiological responses (Miller et al. 2000), stable isotopes (Fry & Sherr 1984, Deegan & Garritt 1997, Kwak & Zedler 1997, Wainright et al. 2000, Weinstein et al. 2000), otolith microchemistry (Secor & Zdanowicz 1998, Campana 1999, Thresher 1999, Gillanders & Kingsford 2000) and trace elements in body tissues (Courtney et al. 1994). For example, stable isotope analyses have demonstrated that nutrient sources for fishes and crustaceans vary with estuarine location, habitat type, dominant vegetation type and season (Currin et al. 1995, Deegan & Garritt 1997,

Hughes et al. 2000, Wainright et al. 2000, Weinstein et al. 2000). The assessment of nursery value is an ecosystem problem that will require a basic understanding of trophic relationships and other ecological linkages within and between biotopes. For example, the abundant resident nekton in salt marshes are likely to play an important role in estuarine nursery functions for transient nekton (Kneib & Wagner 1994, Kneib 1997b, 2000). Ecosystem modeling will be needed to address this complexity.

We found evidence that geographic location (East US coast vs Gulf coast), tidal range and salinity regime affected nekton density patterns and the nursery value of salt marshes. Other landscape level factors may also be important, including the presence or proximity of other habitat types (Weinstein et al. 1980b, Irlandi & Crawford 1997, Micheli & Peterson 1999), marsh drainage patterns (Desmond et al. 2000, Simenstad et al. 2000, Webb & Kneib 2002), connectivity with coastal waters (Herke et al. 1992, Rogers et al. 1994, Rozas & Minello 1999) and physicochemical gradients (Weinstein et al. 1981, Baltz et al. 1993, Miller et al. 2000). Landscape level salinity patterns also have been shown to affect nekton growth (Baltz et al. 1998) and survival (Weinstein & Walters 1981); and both salinity and temperature have been associated with productivity of brown shrimp in salt marshes (Ford & St. Amant 1971).

Salt marshes are really mosaics of different habitat types and hence, we divided marshes into 6 components for analysis. For some nekton, densities varied among all of these marsh types. These distribution patterns, the intertidal nature of salt marshes and the ability of nekton to move among marsh types, suggest that abundance comparisons with other habitat types should really be made at a different spatial scale, rather than on the basis of nekton per m². Such analyses, however, require the sampling of entire marsh systems or combining small-scale density patterns with landscape pattern analyses. Estimates of average population size in marsh complexes are relatively rare. Havens et al. (1995) sampled an entire marsh system (excluding subtidal creeks) using block nets and calculated overall densities based on the aerial extent of the flooded marsh at mean high tide. This approach will not include nekton that remain on the vegetated marsh surface at low tide, but most of these animals are small resident species (Kneib 1984, 1997a). An alternative approach involves sampling each habitat type within a marsh complex and using a geographic information system to estimate cover of different marsh types and to extrapolate densities to overall marsh populations (Rozas & Minello 1999, Clark et al. 1999, Minello & Rozas 2002).

Appendix 1. Glossary of terms as used in this paper

Biotope. An area or location that is characterized by a recognizable community and is defined by dominant components of structure, plants or physicochemical variables (e.g. coral reefs, seagrass beds, salt marshes, mangroves and oyster reefs)

Density. The number of animals per area of bottom

Enclosure sampler. A sampling device that encloses a known area of bottom and allows the removal of nekton and calculation of density (e.g. drop samplers, throw traps, Wegener rings, lift nets and flume weirs)

Habitat. All places that a population of a species (or life stage of a species) lives

Habitat type. A generic term used to describe any particular place that organisms live

Intertidal creeks. Nonvegetated creeks within a salt marsh complex that drain at low tide

Juvenile habitat. All places that the juveniles of a species occur (see 'Habitat')

Marsh pools and ponds. Nonvegetated open water areas within a salt marsh complex that can range in diameter from m to several km. These areas are generally surrounded by marsh vegetation (see 'Nonvegetated marsh')

Nekton. Organisms that are free swimming and independent of water currents at some time in their life cycle

Nonvegetated marsh. The areas within a salt marsh complex that are not vegetated with emergent or submerged vascular plants. Areas of submerged aquatic vegetation within the marsh complex were not considered to be marsh in our analyses but considered to be seagrass

Nonvegetated marsh edge. A generic term for areas of non-vegetated bottom (often intertidal) within a salt marsh complex that are within approximately 10 m of marsh vegetation. There may be overlap between nonvegetated marsh edge and marsh pools and ponds, intertidal and subtidal creeks (see 'Nonvegetated marsh')

Nursery habitat. An area of a juvenile habitat that is especially productive for a species. The contribution per unit area of nursery habitat to the production of individuals that recruit to adult populations is greater, on average, than production from other juvenile habitat areas (Beck et al. 2001)

Open water. A nonvegetated habitat type that is not within a salt marsh complex. These areas within open bays, inlets, coves, bayous, large subtidal channels and coastal lakes are not surrounded by salt marsh vegetation or are large enough (>several km in diameter) for the direct influence of marsh vegetation on nekton to be minimal

Salt marsh. A complex of vegetated and nonvegetated habitat types that includes the intertidal vegetated marsh surface, marsh pools and ponds, intertidal and subtidal creeks. Areas of submerged aquatic vegetation and oyster reef can occur within a salt marsh complex, but we considered these areas to be distinct habitat types

Seagrass. Areas populated by submerged vascular plants

Subtidal creeks. Nonvegetated creeks within a salt marsh complex that do not completely drain at low tide

Transient nekton. Nekton species with juvenile and adult habitats that are not completely overlapping

Vegetated inner marsh. The intertidal vegetated surface area of a salt marsh complex that is farther than approximately 5 m from any nonvegetated bottom. Inner marsh vegetation can be similar to that of the vegetated edge but often includes additional plant species

Vegetated marsh edge. The intertidal vegetated surface area of a salt marsh complex that is within approximately 5 m from any nonvegetated bottom. In the eastern US, the marsh edge is usually vegetated with *Spartina alterniflora*, *S. patens*, *Juncus roemerianus*, *Scirpus* spp. or *Phragmites australis*

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