Vol. 209: 71–84, 2001 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published January 5

Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA

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ABSTRACT: Throughout the eastern USA many *Spartina alterniflora* salt-marsh systems are being altered through the invasion of *Phragmites australis*. As a result, substantial declines in the areal distribution of *S. alterniflora*-dominated habitat have occurred in contrast to increases in *P. australis* dominated habitat. While information is scarce on nekton use of *P. australis* marsh, increases in the areal distribution of this species have concerned resource managers. Managers typically view the shift of *S. alterniflora* to *P. australis* marsh as a shift from a biologically diverse and productive marsh to one less biologically diverse and productive. We examined nekton use of *P. australis* marsh relative to *S. alterniflora* marsh with similar geographic location and physical conditions. We found no significant differences ($p > 0.05$) in the utilization of *P. australis* and *S. alterniflora* marsh by nekton in terms of abundance or biomass. Further, no significant difference ($p > 0.05$) in the total number of nekton species was evident between *P. australis* and *S. alterniflora* marsh. We postulate that under similar environmental and physical conditions these marsh types are equivalent in terms of nekton use. It may be necessary to reevaluate current wetland management practices which involve the elimination of *P. australis* in favor of *S. alterniflora* marsh in order to increase nekton use.

KEY WORDS: *Phragmites* · *Spartina* · Nekton · Fish · Shrimp · Fauna · Alteration · Invasion · Disruption · Utilization · Restoration · Marsh · *Fundulus* · *Palaemonetes*

INTRODUCTION

The loss of salt-marsh habitat is a concern to North American fishery managers because many coastal nekton species in North America rely on this habitat during some life-history stage. Although salt-marsh loss by natural processes such as erosion (Wray et al. 1995, Meyer et al. 1997) and sea-level change (Webb et al. 1995) is inevitable, additional loss or alteration due to direct and indirect human impact occurs (Sinicrope et al. 1990, Havens et al. 1997). While the physical alteration of marsh habitat is considered an immediate threat, the progressive change through indirect influences on the estuarine environment (such as water quality, water circulation impediments, freshwater runoff, etc.) can also be substantial and might shift ecosystem equilibrium. Once equilibrium shifts occur, changes in dominant floral and faunal species could follow.

Habitat alteration is occurring on a global scale, and shifts in macrophyte dominance have been observed throughout the world including those in Asia (Dudgeon 1992), Europe (Rico & Fernandez 1997) and North America (Keast 1984, Rice 1996). Throughout the eastern USA, the dominant floral composition of many salt-marsh systems is threatened by alteration. Invasive species including reed grass (*Phragmites australis*) may invade wetlands, spread, and reduce open-water habitat (Caffrey 1996, Broyer & Varagnat 1998), and/or replace dominant macrophyte species through natural habitat (Sinicrope et al. 1990, Havens et al.

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1997) or anthropogenically derived (Rice 1996, Havens et al. 1997) disturbances. Substantial declines in *Spartina alterniflora* areal coverage have occurred in the USA due to encroachment into mesohaline estuarine areas by *P. australis* (Rice 1996, Havens et al. 1997), a species typically thought to be native to oligohaline wetlands, including those of North America (Niering & Warren 1977, Orson et al. 1987). While the total amount of salt marsh might remain constant, there are general concerns by North American resource managers that the shift from *S. alterniflora*-dominated to *P. australis*-dominated marsh could result in a change from a biodiverse, fisheries-productive *S. alterniflora* marsh (Bozeman & Dean 1980, Boesch & Turner 1984, Zimmerman & Minello 1984, Hettler 1989, Minello & Zimmerman 1992, Minello et al. 1994) to a less biodiverse, unproductive *P. australis* marsh. While *P. australis* marsh may produce substantial vegetation biomass, North American *P. australis* marshes have been noted to be utilized by fewer avian species than *Spartina* spp. marshes (Benoit & Askins 1999), and are theorized to have little fisheries value (Hellings & Gallagher 1992, Kay 1995, Roman et al. 1997).

Differences in wetland management practices within North America and other continents do occur, because while globally *Phragmites australis* is considered a species which needs to be managed and controlled, outside of North America *P. australis* has also been considered an important habitat for fauna. Substantial information on the eradication of *P. australis* from North American marshes (van der Toorn & Mook 1982, Thompson & Shay 1985, 1989, Kay 1995) is available due to resource allocation for the elimination of *P. australis* in favor of *Spartina alterniflora* or some other more desirable marsh-grass species. While in other parts of the world there is affirmation of the importance of maintaining the integrity of other habitat types through the control of *P. australis* (Caffrey 1996, Broyer & Varagnat 1998), there is also concern for the loss (Newell 1978, Tscharntke 1992) and fragmentation of the endangered, rare, expansive monotypic *P. australis* wetlands, which are now often found only in reserves (Tscharntke 1992), as well as concern for the subsequent decline of biota associated with disruption of this habitat (Tscharntke 1992, Ostendorp 1993). Because of the broader view on the function of *P. australis* marshes in other parts of the world, information is available which not only targets control and maintenance of *P. australis* marshes (Cowie et al. 1992) but its potential importance to biota. *P. australis* has been noted to be an important vector for trophic energy exchange and a carbon source for fishes in Africa (Whitfield 1980, Doergeloh 1985), important in terms of avian (Tscharntke 1992, Ostendorp 1993, Balint et al. 1998, Broyer & Varagnat 1998) and macroinvertebrate use in Europe (Ostendorp 1993, Armitage et al. 1995, Arnold & Ormerod 1997), and fish use in Europe (Ostendorp 1993, Balint et al. 1998), Africa (Whitfield 1980, Blaber 1982) and Asia (Yu et al. 1994).

While it has been noted that the full importance of the *Phragmites australis* habitat for nekton is still not well known in Europe (Ostendorp 1993), information on the function of North American *P. australis* marsh is substantially lacking, but now coming to light. Numerous investigations are currently being undertaken to evaluate the function of the North American *P. australis* marsh. Work by Fell et al. (1998) has noted similarities in abundance and mummichog diet (*Fundulus heteroclitus*) from marsh creeks bisecting *P. australis*, and *P. australis*-free high marsh in Connecticut, USA. Similarly, the identification of *P. australis* isotope signatures in marsh nekton within Delaware Bay, USA, suggests that this macrophyte may be an important component of the estuarine food web (Wainright et al. 2000). It is evident that the information void on nekton use of North American *P. australis*-dominated marsh is now beginning to be filled with data indicating a potential importance of *P. australis* marsh in terms of fisheries habitat value.

In order to determine the potential affects that an invasive macrophyte species such as *Phragmites australis* may have on salt-marsh functions, we initiated this study. The objectives of the study were to: (1) increase our limited knowledge of the function of North American *P. australis* marshes in terms of nekton use, and (2) to compare nekton abundance, biomass and diversity for *P. australis* and *Spartina alterniflora* marshes with similar geographic locations and similar physical conditions.

METHODS

Study sites. The study sites were located within the Chester River and Prospect Bay regions of Chesapeake Bay, Maryland, USA, along a meso-oligohaline interface. Two low-marsh stations of the same stream order (Rozas & Odum 1987, Hettler 1989), 1 of *Phragmites australis* and 1 of *Spartina alterniflora* were selected within each of the 5 study sites (Fig. 1). The paired marsh stations within a study site were a minimum of 100 m (Marshy Creek South) and a maximum of ~400 m (Piney Creek, Muddy Creek, Marshy Creek North and Marshy Creek East) apart. All marsh stations were typically gently sloping and contained numerous vegetated hummocks interspersed by small (~20 to 30 cm wide) sinuous channels. Paired marsh stations were located on the same creek, with separate pairs being at least 1 km apart, and located on separate creeks or tributaries. All study sites and marsh stations

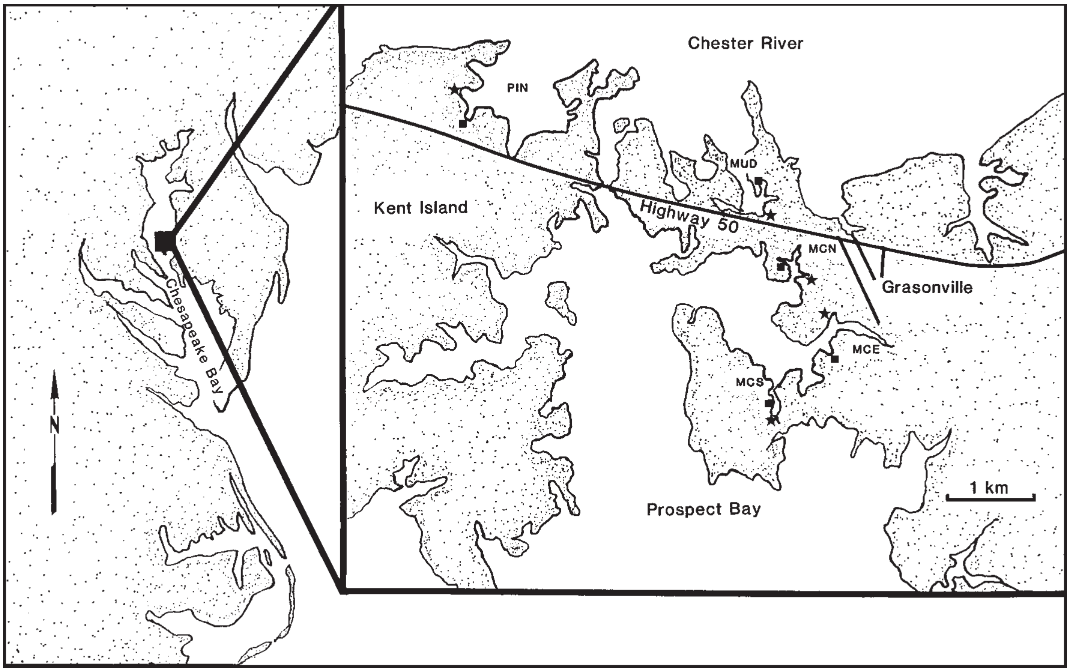

Fig. 1. Study-site locations in Chesapeake Bay, Maryland. Each of the 5 sites is designated by a 3-letter designation. PIN = Piney Creek; MUD = Muddy Creek; MCN = Marshy Creek North; MCE = Marshy Creek East; MCS = Marshy Creek South. Locations of *Phragmites australis* (★) and *Spartina alterniflora* (■) sample areas within each site

were selected during initial site surveys, based on the occurrence of the dominant vegetation and apparent similarities in salinity, elevation, topographical slopes and hydroperiod.

Vegetation. Marsh stations at each study site were characterized for vegetation dominance through stem-density counts and morphometrics, based on methodology used by Cowie et al. (1992), during each collection period (May, July and October 1997). To account for vegetation zonation within each of the 6 m deep × 10 m wide nekton collection areas, which encompassed each marsh station, each marsh station was divided into two 3 m deep × 10 m wide sections: the lower marsh section, which encompassed an area from the lower marsh fringe up to 3 m into the marsh, and the upper marsh section which encompassed the area from 3 to 6 m from the lower fringe. Within each 6 m × 10 m nekton collection area at a marsh station, 4 randomly selected vegetation count locations were located: 2 count locations within the lower marsh section and 2 within the upper section. Within each count location, the number of live and dead plant stems within a 0.25 m^2 quadrat were recorded for each plant species.

Percent areal stem coverage was estimated for each stem-count quadrat by measuring the diameter for up to 10 live and 10 dead stems (at 10 cm) of each macrophyte species encountered within the quadrat with a vernier caliper to the nearest 0.1 mm. Stems were chosen based on closest proximity to a pre-determined quadrate corner. Areal stem coverage was then estimated for each quadrate by multiplying the mean stem diameter for each macrophyte species by the number of stems observed for that species.

Environment. Salinity, water temperature, elevation at the marsh fringe and 6 m landward of the marsh fringe and marsh slope were measured for each macrophyte marsh station at each study site during each collection period, and the frontal marsh slope was measured during the fall. Both salinity (measured with a temperature-compensated refractometer, accuracy of 0.1 %), and temperature were measured once the fyke and block nets used to collect nekton had been set. Relative marsh elevations for each macrophyte marsh station were measured during high tide to the nearest 1 cm following a method employed by Meyer (1994), using the water surface as a level. Once nets had been set, the water depth was measured at 3 points along both sides of the 10 m wide collection plots; at the mouth of the fyke net, at the fyke net stakes on the front fringe of the marsh, and at the block net stakes located 6 m back into the marsh. The 2 sets of measurements collected for each macrophyte marsh station were averaged to estimate marsh fringe elevation, frontal marsh slope (slope along the 3 m distance between the mouth of the fyke net and the marsh fringe) and the marsh slope (between the fringe to 6 m into the marsh) for the marsh station at each study site. Distance of water incursion from the marsh fringe into each macrophyte marsh station was also measured, to the nearest 0.1 m, during each collection period.

Marsh fauna. During May, July and October 1997, nekton collections were made at each marsh station within each study site using methods similar to those of Hettler (1989). These collection dates were used in order to examine marsh usage by nekton during different critical life-history stages. Fyke nets with a mouth measuring 1 m^2 with 3.4 m wings in combination with 6 m block nets were used. Nets were constructed of black 3.2 mm stretch-mesh netting. At each site, 10 contiguous linear meters of marsh fringe were demarcated and sampled using paired fyke nets. On the day prior to nekton collections, paired sets of fyke-net attachment poles were set along the marsh fringe so that when fyke nets were set and attached to the poles 10 contiguous meters of marsh edge would be fished. One 6 m long block net was attached to each of the outer fyke-net attachment poles. In addition to fyke-net attachment poles, block-net attachment poles were set 6 m into the marsh from the fringe and 10 m apart. Block nets were folded and bundled to each outer fyke-net attachment pole in preparation for marsh-fauna collection. During site preparation, debris which might hinder the net lead line set on the bottom was removed from the area along which the nets would be deployed. Preparation included the connection of each block-net top to guidelines which were strung between the fyke net and back block-net poles. To reduce disturbance when sampling, a pull line was connected to the free end of each block net. When this line was pulled, the block net would slide along a guideline to the back pole and block off the lateral movement of nekton within the 10 × 6 m nekton collection area of the marsh station. While there is a recognized potential for nekton movement in and out of the back of the cordoned-off 6 m deep nekton collection area, such movement was considered to have a minimal effect on marsh-use comparisons because of the potential of nekton-movement similarities for the *Phragmites australis* and *Spartina alterniflora* marshes sampled. Further, notations in other studies suggest that the majority of nekton collected within marshes utilize the area within 3 m (Peterson & Turner 1994) to 5 m (Minello et al. 1994) of the marsh fringe, and that up to 98% of total nekton abundance is concentrated within 2 m of the marsh fringe (Baltz et al. 1993). Once a site was prepared, it was allowed to settle for at least 1 complete tidal cycle prior to sampling. Fyke and block nets were deployed at a site during a morning high tide for same-day sampling of paired marsh stations within a study site. Nekton were collected once the tide had evacuated from the fyke nets during the subsequent low tide, and the collection areas were surveyed for nekton stranded on the marsh surface. Nekton were preserved in 95% ethanol, and later all fishes, shrimps and crabs were identified to species. For each marsh station, the number of individuals and wet-weight biomass for each species were recorded. All individuals for a species were measured or, if numerically abundant, a randomly selected subsample of at least 100 individuals or 10% of the total (whichever was higher) was measured (standard length for fishes, total length for shrimps and carapace width for crabs).

Statistical analysis. A Student's *t*-test for paired data comparisons was used to test the mean differences between the marsh types in this study (Ott 1993) using the SAS Statistical Analysis System (SAS Institute Inc 1985). Each fyke/block-net pair within a marsh station (marsh type) at each of the sites was considered a replicate for nekton (n = 5) and was analyzed as such during each collection period. This included comparisons of lengths, biomass and abundances of individual species, and biomass and total abundances for groupings of fishes, shrimps and crabs. A replicate for vegetation parameters including, stem-density counts and estimates of areal stem coverages was considered to be the marsh area encompassed within the fyke-net collections for a marsh type at each site (n = 5) and analyzed as such. Physical parameters including salinities, temperatures, mean marsh elevations, and frontal marsh and marsh slopes (all sites included, n = 5) were compared between macrophyte marsh types.

RESULTS

Vegetation

Based on vegetation surveys, 8 macrophyte species were common within marshes sampled with a total of 7 species observed within each marsh type. Of the 8 species, 6 were observed in both *Phragmites australis* and *Spartina alterniflora* dominated marshes. Of the remaining 2 species, 1 (*Iva frutescens*) was only observed in the *P. australis* marshes, and the other (*Distichlis spicata*) was only observed in the *S. alterniflora* marshes. *P. australis* and *S. alterniflora* had a minor presence in opposing marsh types. Within the *P. australis*-dominated marshes, 1 species (*P. australis*) was numerous, and the 6 other species comprising *Solidago sempervirens*, *Aster tenuifolius*, *Scirpus americanus*, *I. frutescens* and *S. alterniflora* were less numerous (Fig. 2). Within the *S. alterniflora*-dominated marshes, 3 species were numerous, *S. alterniflora*, *D. spicata* and *Spartina patens*, while the other 4 species, *S. sem-*

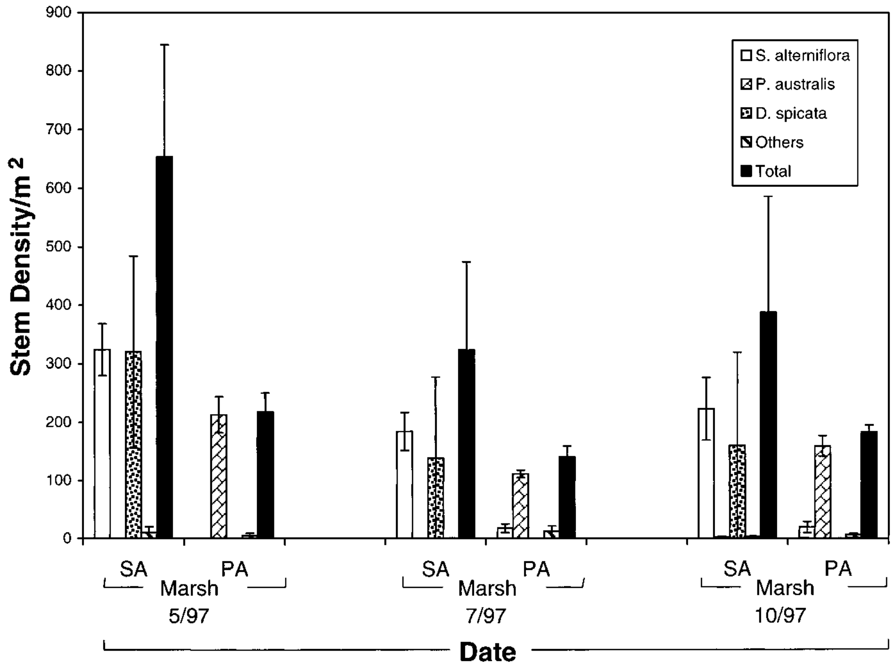

Fig. 2. Mean vegetation stem-density m^{-2} (±1 SE) by date, for dominant species, and stem density for all species combined, within *Spartina alterniflora* (SA), and *Phragmites australis* (PA) marsh types. n = 5 for the means of both *S. alterniflora* and *P. australis* marsh types. *D. spicata*: *Distichlis spicata*

pervirens, S. americanus, A. tenuifolius and *P. australis* were less numerous (Fig. 2). During each collection period, significantly higher *P. australis* stem densities were observed within the *P. australis* compared to the *S. alterniflora* marshes (spring p = 0.0001, summer p = 0.0001, fall p = 0.0009), and significantly higher stem densities of *S. alterniflora* were observed within the *S. alterniflora* compared to the *P. australis* marshes (spring p = 0.0001, summer p = 0.006 and fall p = 0.002) (Fig. 2). Total stem density, all species combined, tended to be consistently higher in the *S. alterniflora* than in the *P. australis* marshes; however, no significant differences were detected between marsh types (spring p = 0.08, summer p = 0.30, fall p = 0.36).

Areal stem coverage varied little between *Phragmites australis*- and *Spartina alterniflora*-dominated marshes. A high of ~3.3 to 3.6% of the marsh area was taken up by stems during spring, and ~0.7 to 1.2% during the summer and fall periods (Table 1). No significant difference (p > 0.05) was observed between marsh types in regard to areal stem coverage during any collection period (Table 1).

Environment

Salinities and temperatures measured during faunal collections did not significantly differ (p > 0.05) between *Phragmites australis* and *Spartina alterniflora* marshes during spring, summer or fall collections (Table 1). Topographical marsh features were also similar between the macrophyte marsh types. Marsh-fringe elevation (as measured from mean high water) did not differ significantly between the *P. australis* and *S. alterniflora* marshes during any of the collection periods nor did elevations observed at a distance of 6 m into the marsh (Table 1). Similarly, no significant differences between *P. australis* and *S. alterniflora* marsh types were evident in terms of marsh slopes during spring, summer or fall collections (p = 0.27, p = 0.08, p = 0.08, respectively) nor for the frontal marsh slope during fall (p > 0.05), (Table 1). No significant differences in terms of distance of water incursion into the *P. australis* and *S. alterniflora* marsh types were evident during spring, summer or fall collections (Table 1).

Marsh fauna

A total of 21 fish, 1 shrimp and 3 crab species were collected over the course of this study (Tables 2 & 3). The crab species collected made a relatively small contribution to overall faunal abundance and biomass. Two crab species collected, *Rithropanopeus harrisii* and *Callinecties sapidus*, were common to both *Phragmites australis* and *Spartina alterniflora* marshes, while the third, *Dyspanopeus sayi* was observed only within the *S. alterniflora* marshes. The grass shrimp *Palae-*

Table 1. *Phragmites australis* and *Spartina alterniflora.* Mean physical parameters measured for the marsh types in 1997. No significant differences (p > 0.05) were observed between marsh types for any of the parameters measured. –: no observations taken during sampling period

Marsh type	Marsh fringe elevation(cm)	Marsh elevation at 6 m (cm)	Distance of water incursion(m)	Frontal marsh slope	Marsh slope	Salinity (‰)	Temp. (°C)	% areal stem coverage
May								
P. australis	–26.8	–11.9	22.1	–	0.027	5.4	13.1	3.3
S. alterniflora	–28.0	–18.6	36.8	–	0.017	5.2	13.2	3.6
July								
P. australis	–45.4	–20.2	33.1	–	0.046	8.0	26.7	0.7
S. alterniflora	–42.8	–30.7	45.8	–	0.022	8.2	26.7	1.2
October								
P. australis	–34.5	–15.2	37.5	0.051	0.035	10.0	13.2	1.0
S. alterniflora	–31.6	–21.2	41.7	0.052	0.019	10.0	13.1	1.2
Average for year								
P. australis	–35.6	–15.8	30.9	0.051	0.036	7.8	17.7	1.7
S. alterniflora	–34.1	–23.5	41.4	0.052	0.019	7.8	17.7	2.0

monetes pugio was common to both marsh types, and accounted for a substantial amount of the overall catch during fall. A total of 15 fish species were common to both marsh types overall, with 5 species collected only in *P. australis* and 1 species collected only in *S. alterniflora* (Tables 2 & 3). While more species were collected within the *P. australis* marsh during spring (15), and summer (19) than within the *S. alterniflora* marsh (10 spring, 17 summer) no significant differences (p > 0.05) based on mean number of species present were detected (Tables 2 & 3). During the fall, the total number of species collected was 16 for both the *P. australis* and *S. alterniflora*, and the total number of species collected for the year overall was higher in the *P. australis* marsh (23), than in the *S. alterniflora* marsh (20); however, again no significant difference based on mean number of species present was detected (p > 0.05).

Ranking nekton species based on the percent of the catch which they comprised in abundance and biomass during each collection period revealed substantial similarities in the composition of the species complement for *Phragmites australis*- and *Spartina alterniflora*-dominated marshes. In general, 3 to 6 of the species present within *P. australis* and *S. alterniflora* marshes during each collection period composed 95% of the nekton abundance and biomass (Table 2). Species which were consistently among the more dominant in terms of abundance and biomass included *Fundulus heteroclitus*, *Cyprinodon variegatus*, *Palaemonetes pugio* and *Fundulus diaphanus*. Seasonal dominance was evident for other species including *Menidia beryllina*, *Fundulus luciae*, *Morone americanus*, *Lepomis gibbosus*, *Anguilla rostrata and Callinecties sapidus* during the summer and *Lucania parva* and *Fundulus majalis* during the fall (Table 2). Among the more evident differences in use patterns between *P. australis*- and *S. alterniflora*-dominated marshes were the consistently higher percentages of catch that *C. variegatus* made up within *S. alterniflora* compared to *P. australis* marshes throughout the year and the higher proportion of catch that *P. pugio* made up within *P. australis* during the spring and fall compared to *S. alterniflora* marshes (Table 2).

The abundances of total nekton (all species combined) and total fishes (all fish species combined), did not significantly differ (p > 0.05) between the *Phragmites australis* and *Spartina alterniflora* marshes during any collection period (Fig. 3). Significantly different abundances were evident for only 2 species: *Cyprinodon variegatus*, which was present in higher abundance in *S. alterniflora* than in *P. australis* marshes during summer and fall (p = 0.02, p = 0.03, respectively); and *Lepomis gibbosus*, which was present in higher abundance in *P. australis* than in *S. alterniflora* marshes during fall (p = 0.05) (Table 3).

No significant differences (p > 0.05) in the abundances of the 1 shrimp species collected (*Palaemonetes pugio*), were detected between *Phragmites australis* and *Spartina alterniflora* marshes for any collection period (Table 3, Fig. 3). No significant differences between *P. australis* and *S. alterniflora* marshes were observed for the abundances of the 3 crab species collected (*Rithropanopeus harrisii*, *Callinecties sapidus* and *Dyspanopeus sayi*), nor for total crab abundances (all crab species combined) for any collection date (Table 3, Fig. 3).

Total wet-weight biomass for all species combined, all fish species combined, shrimp, and all crab species combined did not significantly differ between the *Phragmites australis* and *Spartina alterniflora* marshes for any collection date (Fig. 4). Significant differences

Table 2. Rank of fish and decapod species observed in fyke- and block-net collections in *Phragmites australis* and *Spartina alterniflora* marshes based on percent abundance and biomas

Abundance						Biomass					
Phragmites australis			*Spartina alterniflora*			*Phragmites australis*			*Spartina alterniflora*		
Rank	Species	%	Rank	Species	%	Rank	Species	%	Rank	Species	%
May 1997											
1	*Fundulus heteroclitus*	54.3	1	*Fundulus heteroclitus*	63.3	1	*Fundulus heteroclitus*	84.1	1	*Fundulus heteroclitus*	78.8
2	*Palaemonetes pugio*	34.8	2	*Palaemonetes pugio*	21.0	2	*Fundulus diaphanus*	9.3	2	*Fundulus diaphanus*	15.3
3	*Fundulus diaphanus*	7.4	3	*Fundulus diaphanus*	11.7	3	*Palaemonetes pugio*	3.6	3	*Cyprinodon variegatus*	2.7
4	*Cyprinodon variegatus*	0.9	4	*Cyprinodon variegatus*	3.0	4	*Lepomis gibbosus*	1.4	4	*Palaemonetes pugio*	2.4
5	*Lucania parva*	0.8	5	*Lucania parva*	0.7	5	*Cyprinodon variegatus*	0.7	5	*Lepomis gibbosus*	0.3
6	*Apeltes quadracus*	0.7	6	*Lepomis gibbosus*	0.1	6	*Anguilla rostrata*	0.3	6	*Menidia beryllina*	0.1
7	*Lepomis gibbosus*	0.6	6	*Rithropanopeus harrisii*	0.1	7	*Lucania parva*	0.2	6	*Lucania parva*	0.1
8	*Rithropanopeus harrisii*	0.1	7	*Fundulus majalis*	<0.1	8	*Perca flavescens*	0.1	7	*Rithropanopeus harrisii*	<0.1
9	*Menidia beryllina*	<0.1	7	*Fundulus luciae*	<0.1	8	*Apeltes quadracus*	0.1	7	*Fundulus majalis*	<0.1
9	*Anguilla rostrata*	<0.1	7	*Menidia beryllina*	<0.1	9	*Rithropanopeus harrisii*	<0.1	7	*Fundulus luciae*	<0.1
9	*Brevoortia tyrannus*	<0.1				9	*Menidia beryllina*	<0.1			
9	*Fundulus luciae*	<0.1				9	*Menidia menidia*	<0.1			
9	*Lepomis macrochirus*	<0.1				9	*Lepomis macrochirus*	<0.1			
9	*Menidia menidia*	<0.1				9	*Brevoortia tyrannus*	<0.1			
9	*Perca flavescens*	<0.1				9	*Fundulus luciae*	<0.1			
July 1997											
1	*Fundulus heteroclitus*	84.5	1	*Fundulus heteroclitus*	75.5	1	*Fundulus heteroclitus*	66.1	1	*Fundulus heteroclitus*	61.2
2	*Cyprinodon variegatus*	5.0	2	*Cyprinodon variegatus*	14.4	2	*Morone americanus*	16.0	2	*Morone americanus*	21.6
3	*Fundulus luciae*	3.1	3	*Menidia beryllina*	5.1	3	*Lepomis gibbosus*	6.3	3	*Lepomis gibbosus*	8.3
4	*Menidia beryllina*	3.0	4	*Menidia menidia*	1.2	4	*Anguilla rostrata*	6.2	4	*Cyprinodon variegatus*	3.2
5	*Morone americanus*	1.1	5	*Morone americanus*	1.0	5	*Callinecties sapidus*	1.4	5	*Menidia beryllina*	1.4
6	*Fundulus majalis*	0.8	6	*Lepomis gibbosus*	0.7	6	*Fundulus luciae*	1.0	6	*Perca flavescens*	1.0
6	*Palaemonetes pugio*	0.8	7	*Gambusia affinis*	0.5	7	*Cyprinodon variegatus*	0.9	7	*Menidia menidia*	0.8
7	*Lepomis gibbosus*	0.5	8	*Fundulus luciae*	0.4	8	*Menidia beryllina*	0.6	8	*Alosa aestivalis*	0.7
8	*Gambusia affinis*	0.4	9	*Alosa aestivalis*	0.3	9	*Perca flavescens*	0.5	9	*Fundulus majalis*	0.6
9	*Anguilla rostrata*	0.2	9	*Lucania parva*	0.3	10	*Morone saxatilis*	0.2	10	*Anguilla rostrata*	0.5
10	*Rithropanopeus harrisii*	0.1	9	*Palaemonetes pugio*	0.3	10	*Fundulus diaphanus*	0.2	11	*Fundulus diaphanus*	0.4
10	*Lucania parva*	0.1	10	*Fundulus majalis*	0.2	10	*Fundulus majalis*	0.2	12	*Fundulus luciae*	0.2
10	*Menidia menidia*	0.1	11	*Fundulus diaphanus*	0.1	11	*Leiostomus xanthurus*	0.1	13	*Gambusia affinis*	0.1
10	*Fundulus diaphanus*	0.1	12	*Rithropanopeus harrisii*	<0.1	12	*Menidia menidia*	<0.1	14	*Rithropanopeus harrisii*	<0.1
11	*Callinecties sapidus*	<0.1	12	*Anguilla rostrata*	<0.1	12	*Palaemonetes pugio*	<0.1	14	*Lucania parva*	<0.1
11	*Leiostomus xanthurus*	<0.1	12	*Perca flavescens*	<0.1	12	*Gambusia affinis*	<0.1	14	*Palaemonetes pugio*	<0.1
11	*Morone saxatilis*	<0.1				12	*Rithropanopeus harrisii*	<0.1			
11	*Perca flavescens*	<0.1				12	*Lucania parva*	<0.1			
11	*Strongylura marina*	<0.1				12	*Strongylura marina*	<0.1			
October 1997											
1	*Palaemonetes pugio*	80.9	1	*Palaemonetes pugio*	45.7	1	*Fundulus heteroclitus*	45.2	1	*Fundulus heteroclitus*	44.0
2	*Fundulus heteroclitus*	10.8	2	*Fundulus heteroclitus*	21.0	2	*Palaemonetes pugio*	32.6	2	*Fundulus diaphanus*	19.6
3	*Cyprinodon variegatus*	3.0	3	*Cyprinodon variegatus*	12.2	3	*Cyprinodon variegatus*	5.9	3	*Palaemonetes pugio*	11.7
4	*Fundulus diaphanus*	2.4	4	*Fundulus diaphanus*	10.1	3	*Fundulus diaphanus*	5.9	4	*Cyprinodon variegatus*	10.8
5	*Lucania parva*	1.7	5	*Menidia beryllina*	5.3	4	*Fundulus luciae*	3.7	5	*Fundulus majalis*	4.4
6	*Menidia beryllina*	0.8	6	*Lucania parva*	4.5	5	*Morone americanus*	3.1	6	*Menidia beryllina*	4.2
7	*Fundulus majalis*	0.2	7	*Fundulus majalis*	0.6	6	*Lepomis gibbosus*	1.5	7	*Lucania parva*	1.9
8	*Rithropanopeus harrisii*	0.1	8	*Menidia menidia*	0.4	7	*Menidia beryllina*	1.0	8	*Morone americanus*	1.9
9	*Lepomis gibbosus*	<0.1	9	*Rithropanopeus harrisii*	0.1	7	*Lucania parva*	1.0	9	*Menidia menidia*	1.2
9	*Morone americanus*	<0.1	9	*Gambusia affinis*	0.1	8	*Rithropanopeus harrisii*	0.1	10	*Rithropanopeus harrisii*	0.1
9	*Apeltes quadracus*	<0.1	10	*Morone americanus*	<0.1	9	*Menidia menidia*	<0.1	11	*Lepomis gibbosus*	0.1
9	*Fundulus luciae*	<0.1	10	*Lepomis gibbosus*	<0.1	9	*Gobiosoma bosci*	<0.1	12	*Gambusia affinis*	<0.1
9	*Gambusia affinis*	<0.1	10	*Fundulus luciae*	<0.1	9	*Fundulus luciae*	<0.1	13	*Gobiosoma bosci*	<0.1
9	*Gobiosoma bosci*	<0.1	10	*Gobiosoma bosci*	<0.1	9	*Lepomis macrochirus*	<0.1	13	*Lepomis macrochirus*	<0.1
9	*Lepomis macrochirus*	<0.1	10	*Lepomis macrochirus*	<0.1	9	*Apeltes quadracus*	<0.1	14	*Fundulus luciae*	<0.1
9	*Menidia menidia*	<0.1	10	*Dyspanopeus sayi*	<0.1	9	*Gambusia affinis*	<0.1	14	*Dyspanopeus sayi*	<0.1

in wet-weight biomass (WWB) for individual species were only detected for *Lepomis gibbosus* during fall, with *P. australis* having significantly ($p = 0.03$) higher WWB g^{-1} linear m of marsh edge than *S. alterniflora* marshes (Table 3).

Among the more dominant fish species, including *Fundulus heteroclitus*, *Cyprinodon variegatus*, *F. diaphanus*, *F. majalis* and *Lepomis gibbosus*, a trend of larger individuals per species based on average WWB ind.$^{-1}$ (AWWBI = mean of the replicate total wet weight/number of individuals) (Fig. 5) and mean size, as measured by mean standard length (Fig. 6), was generally observed within *Phragmites australis* relative to *Spartina alterniflora* (although not significant in most cases) throughout the 3 collection periods. Differences were noted to be significant during the spring, with *F. heteroclitus* AWWBI higher ($p < 0.04$) within *P. australis* than within *S. alterniflora* (Fig. 5). Exceptions to this

Table 3. Fish and decapod species observed during fyke- and block-net collections in *Phragmites australis* and *Spartina alterniflora* marshes. No.: number of individuals per linear meter of marsh fringe (±1 SE); Biomass: g wet weight biomass per linear meter of marsh fringe (±1 SE). *Significant difference ($p \leq 0.05$) between means of the marsh types for that species; –: relevant species was not observed in that marsh type during that collection period

Species	May 1997							
	P. australis				*S. alterniflora*			
	No.		Biomass		No.		Biomass	
Fishes								
Alosa aestivalis	–	–	–	–	–	–	–	–
Anguilla rostrata	<0.1	–	0.81	(±0.81)	0.0	–	0.00	–
Apeltes quadracus	1.5	(±1.5)	0.41	(±0.40)	0.0	–	0.00	–
Brevoortia tyrannus	<0.1	–	<0.01	0.0	–	0.00	–	
Cyprinodon variegatus	2.0	(±1.1)	2.37	(±1.47)	7.1	(±4.7)	8.68	(±6.49)
Fundulus diaphanus	15.8	(±9.4)	29.58	(±18.83)	27.6	(±16.0)	48.62	(±28.77)
Fundulus heteroclitus	115.2	(±34.4)	267.00	(±87.65)	149.8	(±73.1)	249.90	(±127.63)
Fundulus luciae	<0.1	–	<0.01	–	<0.1	–	<0.01	–
Fundulus majalis	0.0	–	0.00	–	0.1	(±0.1)	0.10	(±0.10)
Gambusia affinis	–	–	–	–	–	–	–	–
Gobiosoma bosci	–	–	–	–	–	–	–	–
Leiostomus xanthurus	–	–	–	–	–	–	–	–
Lepomis gibbosus	1.3	(±1.3)	4.57	(±4.56)	0.3	(±0.3)	1.07	(±0.95)
Lepomis macrochirus	<0.1	–	0.01	(±0.01)	0.0	–	0.00	–
Lucania parva	1.8	(±1.0)	0.53	(±0.30)	1.6	(±0.6)	0.39	(±0.16)
Menidia beryllina	0.1	(±0.1)	0.12	(±0.12)	<0.1	–	0.44	(±0.44)
Menidia menidia	<0.1	–	0.07	(±0.07)	0.0	–	0.00	–
Morone americanus	–	–	–	–	–	–	–	–
Morone saxatilis	–	–	–	–	–	–	–	–
Perca flavescens	<0.1	–	0.42	(±0.42)	0.0	–	0.00	–
Strongylura marina	–	–	–	–	–	–	–	–
Decapods								
Callinecties sapidus	–	–	–	–	–	–	–	–
Dyspanopeus sayi	–	–	–	–	–	–	–	–
Palaemonetes pugio	73.9	(±25.8)	11.58	(±4.37)	49.7	(±15.7)	7.59	(±2.70)
Rithropanopeus harrisii	0.3	(±0.1)	0.13	(±0.09)	0.3	(±0.27)	0.12	(±0.09)

trend were *L. gibbosus* during the spring, where both AWWBI and mean size were greater within *S. alterniflora* compared to *P. australis*, although not significantly for either ($p > 0.05$); and for *F. majalis* during the summer, where AWWBI and mean size were significantly greater ($p < 0.002$) within the *S. alterniflora* than within *P. australis* (Figs. 5 & 6).

DISCUSSION

Because ecosystems are not static, and natural changes occur (Kelley et al. 1995, Wray et al. 1995), it is often difficult to discern natural from anthropogenic alterations. Consequently, many perceived ecosystem changes have been attributed to human activities. On the eastern coast of the USA, a noticeable structural change associated with some marsh habitat has been the invasion and subsequent dominance of *Spartina alterniflora* marsh by *Phragmites australis*. In such cases, the general opinion is that habitat function has been diminished due to the change in macrophyte dominance. However, this evaluation may not be valid.

Numerous studies have examined the important fisheries functions of *Spartina alterniflora* marshes (e.g., Kneib & Stiven 1978, Kneib 1984, Zimmerman & Minello 1984, McIvor & Odum 1986, Rozas et al. 1988, Hettler 1989, Minello & Zimmerman 1992, Meyer et al. 1993, Minello et al. 1994, Rozas 1995), nekton utilization patterns (Meyer et al. 1993), and factors which may affect nekton utilization (Meyer et al. 1993, Rozas 1995). However, published information on the functions of North American *Phragmites australis* marshes is lacking. Information on *P. australis* marsh has generally described growth patterns (Hellings & Gallagher 1992), its expanding areal distribution within North America (Haslam 1971, Rice 1996, Havens et al. 1997), methods of eradication and distribution control (van der Toorn & Mook 1982, Thompson & Shay 1985, 1989, Cowie et al. 1992), and speculation on its non-use by nekton (Hellings & Gallager 1992, Roman et al. 1997).

The data from this study represents information on nekton use of *Phragmites australis* and *Spartina alterniflora* marshes over 3 seasons. This time frame was selected because it encompassed known peak recruitment and growth periods for dominant nekton species associated with *S. alterniflora*- and potentially *P. australis*-dominated marshes. Few significant differences in nekton species use were evident between the 2 marsh types, and neither exhibited significantly

Table 3 (continued)

July 1997								October 1997							
P. australis				*S. alterniflora*				*P. australis*				*S. alterniflora*			
No.		Biomass		No.		Biomass		No.		Biomass		No.		Biomass	
0.0	–	0.0	–	1.2	(±1.2)	2.15	(±2.15)	–	–	–	–	–	–	–	–
0.5	(±0.2)	21.93	(±21.6)	0.1	(±0.1)	1.78	(±1.03)	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	<0.1	–	<0.01	–	0.0	–	0.00	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
15.0*	(±6.2)	3.15	(±1.32)	54.0*	(±10.9)	10.32	(±4.72)	24.6*	(±11.0)	14.03	(±7.74)	62.8*	(±9.8)	25.03	(±3.54)
0.2	(±0.1)	0.73	(±0.45)	0.4	(±0.3)	1.22	(±1.11)	20.0	(±8.2)	13.88	(±5.89)	51.8	–	45.35	(±26.45)
253.2	(±71.8)	231.70	(±79.34)	282.3	(±09.5)	199.40	(±83.93)	90.1	(±62.0)	106.85	(±76.66)	108.0	(±18.1)	101.90	(±21.42)
9.3	(±9.0)	3.70	(±3.59)	1.4	(±0.8)	0.55	(±0.34)	<0.1	–	0.02	(±0.01)	<0.1	–	<0.01	–
2.5	(±2.3)	0.68	(±0.60)	0.8	(±0.3)	1.88	(±0.64)	1.4	(±1.1)	8.73	(±6.24)	3.0	(±0.9)	10.26	(±4.00)
1.2	(±0.7)	0.13	(±0.09)	2.0	(±1.4)	0.26	(±0.16)	<0.1	–	<0.01	–	0.4	(±0.2)	0.05	(±0.02)
–	–	–	–	–	–	–		–	<0.1–	0.03	(±0.02)	<0.1	–	0.02	(±0.02)
<0.1	–	0.35	(±0.35)	0.0	–	0.00	–	–	–	–	–	–	–	–	–
1.6	(±0.8)	22.20	(±12.78)	2.5	(±2.3)	26.96	(±24.00)	0.4*	(±0.1)	3.49*	(±1.01)	0.1*	(±0.1)	0.25*	(±0.17)
–	–	–	–	–	–	–	–	<0.1	–	0.02	(±0.01)	<0.1	–	0.02	(±0.01)
0.3	(±0.2)	0.02	(±0.02)	1.2	(±0.6)	0.08	(±0.04)	14.1	(±7.3)	2.25	(±1.14)	23.0	(±17.5)	4.42	(±3.15)
8.9	(±3.3)	1.93	(±0.66)	19.0	(±13.4)	4.66	(±2.60)	6.6	(±2.4)	2.26	(±0.95)	27.2	(±15.4)	9.62	(±5.23)
0.3	(±0.1)	0.20	(±0.07)	4.3	(±1.8)	2.56	(±1.04)	<0.1	–	0.04	(±0.02)	2.0	(±1.7)	2.78	(±2.39)
3.4	(±0.4)	56.29	(±15.50)	3.4	(±1.2)	70.41	(±40.73)	0.3	(±0.2)	7.41	(±0.45)	0.2	(±0.1)	4.38	(±2.65)
<0.1	–	0.89	(±0.89)	0.0	–	0.00	–	–	–	–	–	–	–	–	–
<0.1	–	1.70	(±1.70)	<0.1	–	3.35	(±0.84)	–	–	–	–	–	–	–	–
<0.1	–	0.01	(±0.01)	0.0	–	0.00	–	–	–	–	–	–	–	–	–
0.1	(+0.1)	4.83	(±390)	0.0	–	0.00	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	0.0	–	0.00	–	<0.1	–	<0.01	–
2.4	(+0.18)	0.14	(±0.10)	1.0	(±0.7)	0.06	(±0.04)	671.0	(±347.6)	76.91	(±42.19)	235.0	(±12.2)	27.13	(±12.22)
0.4	(+0.3)	0.12	(±0.09)	0.2	(±0.2)	0.10	(±0.09)	0.9	(±0.3)	0.22	(±0.09)	0.7	(±0.7)	0.32	(±0.17)

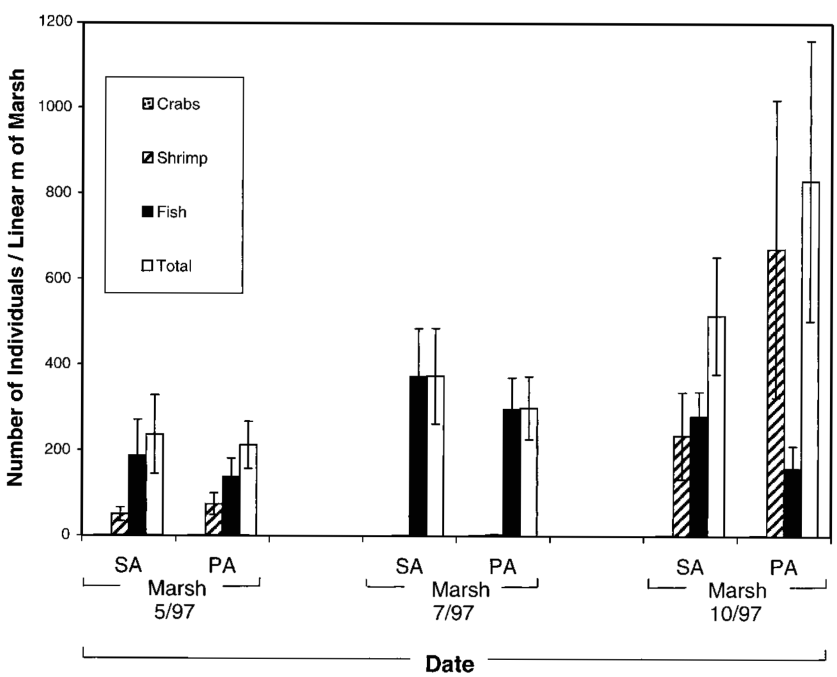

Fig. 3. Mean abundance per linear meter of marsh fringe (±1 SE) by date, for fish, shrimp and crab taxonomic groups, and totals for all combined, within *Spartina alterniflora* (SA), and *Phragmites australis* (PA) marsh types. n = 5 for the means of both *S. alterniflora* and *P. australis* marsh types

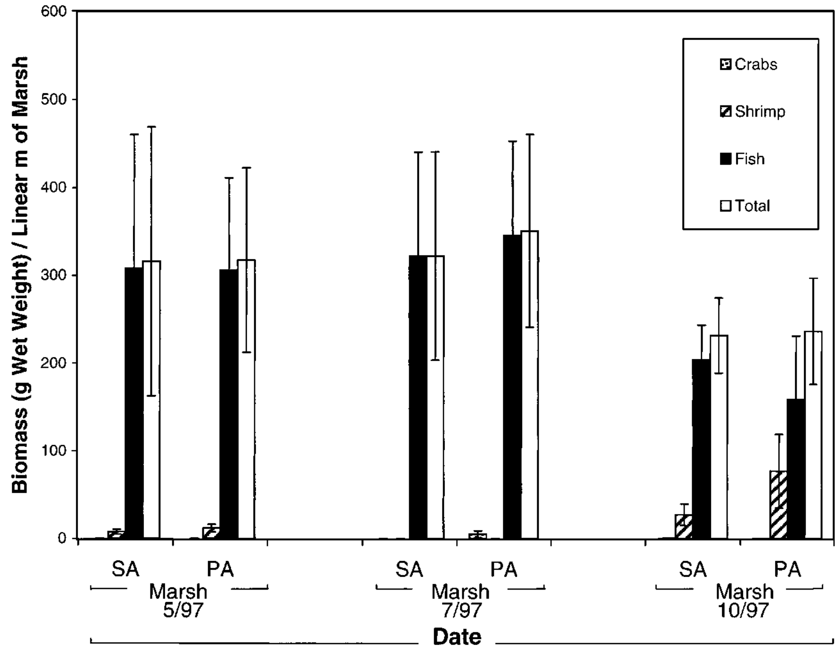

Fig. 4. Mean wet weight biomass, per linear meter of marsh fringe (±1 SE) by date, for fish, shrimp and crab taxonomic groups, and totals for all combined, within *Spartina alterniflora* (SA), and *Phragmites australis* (PA) marsh types. n = 5 for the means of both *S. alterniflora* and *P. australis* marsh types

higher nekton species diversity (number of species), total nekton abundance or biomass than the other. However, trends which might be indicative of potentially divergent utilization patterns by nekton were observed. For example, killifish (*Fundulus heteroclitus*, *F. diaphanus*, *F. majalis* and *Cyprinodon variegatus*), were typically more abundant in *S. alterniflora*- than in *P. australis*-dominated marshes. In contrast, shrimp (*Palaemonetes pugio*) abundances were reciprocal. We suspect this differential use pattern might be

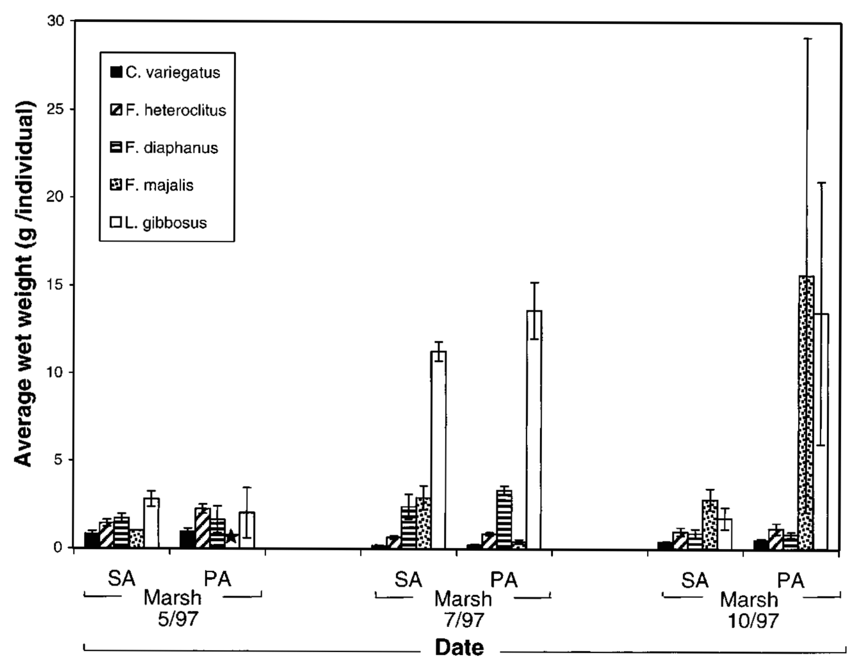

Fig. 5. Average wet weight biomass per individual (±1 SE) by date, for the dominant fish species within *Spartina alterniflora* (SA), and *Phragmites australis* (PA) marsh types. (★) No individuals of that species were collected within that marsh type at that collection date. Full specific names in Table 2

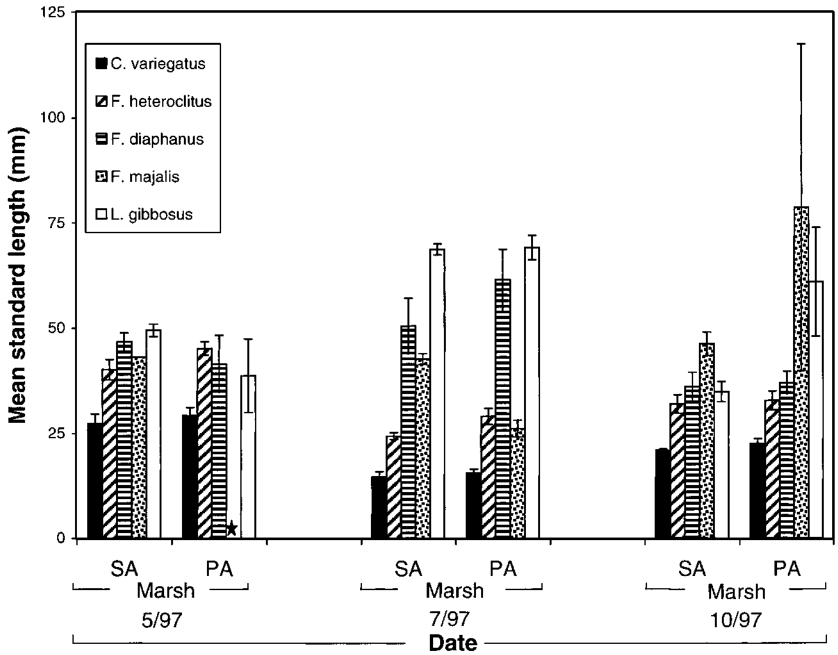

Fig. 6. Mean standard length per individual (±1 SE) by date, for the dominant fish species within *Spartina alterniflora* (SA), and *Phragmites australis* (PA) marsh types. (★) No individuals of that species were collected within that marsh type at that collection date. Full specific names in Table 2

best explained by predator/prey interactions including prey-habitat shifts due to predator occurrence, as noted for *Lepomis macrochirus* when in the presence of *Micropterus salmoides* (Wenner et al. 1983) and *P. pugio* when in the presence of *F. heteroclitus* (Posey & Hines 1991). Posey & Hines (1991) further noted that within aquaria *P. pugio* does shift from deeper-water habitat to shallow-water habitat in the presence of a predator, in particular *F. heteroclitus.* This interaction-based model probably best explains the trend of higher abundances of *P. pugio* in the *P. australis* compared to *S. alterniflora* marshes because of the slightly shallower water closer to the marsh edge in the *P. australis* than the *S. alterniflora* marshes sampled. The potential of predator/prey interactions is further supported by fish size-distribution trends within the *P. australis* and *S. alterniflora* marshes, particularly during the fall (peak *P. pugio* abundance), when more known predators of *Palaemonetes* spp., larger-sized *Fundulus* spp. (Kneib 1988, Cross & Stiven 1999), and *Lepomis* spp. (Rottmann & Anderson 1976) were observed within *P. australis* than within *S. alterniflora* marshes.

While potential differences in nekton utilization patterns might occur between *Phragmites australis* and *Spartina alterniflora* marshes there were substantial similarities among these marsh types. Both marsh types supported diverse nekton populations, with the nekton species comprising 95% of the abundance and biomass typical of 'highly productive' *S. alterniflora* marshes within the southeastern USA (Hettler 1989) and Chesapeake Bay (McIvor & Odum 1986, Rozas & Odum 1987, Rozas et al. 1988). It was also evident that both the *P. australis*- and *S. alterniflora*-dominated marsh habitats we sampled were highly productive and supported an order of magnitude higher nekton abundance than observed for *S. alterniflora* marshes in the southeastern USA sampled with similar gear during the same months by Hettler (1989).

Although vegetation structure is important for nekton (Heck & Thoman 1981), other physical parameters have substantial effects on nekton habitat-use (Rozas 1995) and might strongly influence fisheries use. The collection of substantial densities of numerous estuarine salt-marsh species by Rozas & Hackney (1984) in intertidal oligohaline bulrush (*Scirpus* spp.) and cattail (*Typha* spp.) marshes also indicates that physical conditions of wetlands (elevation, salinity, slope etc.) might be more important than the occurrence of a particular macrophyte species. Noted similarities in diet and feeding potential for *Fundulus heteroclitus* between high marsh habitat with and without *Phragmites australis* (Fell et al. 1998) further supports this assertion. Hence, a shift in marsh vegetation dominance in a particular area may not indicate that habitat value for nekton has significantly changed.

Ecosystem disturbance has occurred throughout the world due to natural (Kelley et al. 1995) and anthropogenic processes at scales ranging from entire river systems in Asia (Dudgeon 1992) and North America (Serafy et al. 1994), to coastal oceans of Europe (Rico & Fernandez 1997), to small individual marshes and creeks within the Chesapeake Bay of North America (Rice 1996). These disruptions have typically been considered detrimental to ecological processes important for ecosystem function. Cases supporting this assertion include the effects on the Asian river systems noted by Dudgeon (1992), and introduction of the macrophyte *Myriophyllum spicatum* into North America, which encroaches upon aquatic *Potamogeton* spp.-*Vallisneria* spp. communities, making the habitat less supportive of nekton (Keast 1984). However, perceived change in an ecosystem or locale may not necessarily have disastrous effects. Alterations might be more cosmetic in nature than disruptive, with the basic functions that drive the system still in good order. For example, habitats with different dominant macrophytes or undergoing a change in macrophyte dominance may not equate with change or difference in habitat function as observed by Fonseca et al. (1996) for nekton use of different seagrass species in the southeastern USA and by Fell et al. (1998) for high-marsh macrophytes in the northeastern USA. Similarly, the presence of the invasive macrophyte *Hydrilla verticillata* in the waterways of temperate North America has been noted to provide a high-quality habitat for nekton species (Killgore et al. 1989, Serafy et al. 1994) as has Eurasian water-milfoil (Borawa et al. 1979).

The contention that within North America only *Spartina* spp. marshes can provide quality salt-marsh habitat for nekton needs to be reevaluated. Current efforts to eliminate *Phragmites australis* from regularly flooded salt marshes to establish *S. alterniflora* plantings may not increase nekton use. *P. australis* invasion and spread to areas through anthropogenic changes in physical or environmental factors (Roman et al. 1984, Havens et al. 1997) may be inevitable, and efforts to control the *P. australis* spread may consume resources and not influence vegetation change. Perhaps, instead of altering existing marshes in an attempt to provide the functions valued, resources might be better used to conserve, restore or create salt marsh.

Because environmental managers and regulators must consider benefits of habitat use by a wide range of users, including nekton, avian and mammalian, the ultimate goal of a wetland's function needs to be considered to best use resources to attain well defined objectives. To attain these functional objectives, it is essential that reliable information on the functional value of wetland habitats be available. It is evident that information on faunal use of many habitat types is limited and often generalized. Additionally, the physical factors that influence the utilization, production and functions of habitats including salt marshes are poorly understood. It is easier to assign higher value to a habitat that is better understood than to a habitat which is not. As a result, when decisions are made on how to best manage habitat resources to provide high yields, habitats with known functional attributes are often chosen over habitats for which functional attributes are unknown. The information gaps on the functions of all habitat types, including salt marshes, need to be filled if good environmental management decisions are to be made.

Acknowledgements. The authors wish to thank Chris Doley, Raymond Li, Laura Hamilton, Bob Murphy and Derek Orner for assistance in the field, rain or shine. We also thank Glen Montgomery for sorting and identifying all those thousands of fishes and shrimps and Fred (Fritz) Rohde for validating fish identification. Gordon Thayer, William Hettler Jr, Allyn Powell, Alan Stoner and 3 anonymous reviewers provided valuable comments that substantially improved this manuscript. This project was funded by NOAA's National Marine Fisheries Service Restoration Center. This manuscript is dedicated to the memory of Eunice R. Meyer (1919–1999), the senior author's first mentor.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: July 6, 1999; Accepted: June 27, 2000
Proofs received from author(s): December 14, 2000