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Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh

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Abstract There has been much recent interest in restoration of salt-marsh habitats to their natural structure and function. However, the criteria for success of such restorations are not well-defined. As part of a larger program to evaluate the restoration of a former salt-hay farm bordering Delaware Bay, New Jersey, USA, we monitored the response of a large predator, the striped bass *Morone saxatilis*, to the restoration. During June to October 1998 we compared tidal and diel movements and food habits of juvenile and adult striped bass (n = 82, 212 to 670 mm fork length) between a restored marsh and an adjacent reference marsh with similar physical characteristics (depth, salinity, temperature). Striped bass movements at both sites were characterized by ultrasonic tracking with small, surgically implanted tags (21 d rated battery-life). Striped bass (n = 23, 421 to 610 mm fork length) were tagged and released near the main creek mouths at both the restored (n = 14) and reference (n = 9) marshes. At both sites, striped bass tended to move up the main creek during ebb tide. At the restored site, ebb tide upstream-movements ranged from 0.1 to 3.5 km from the main creek mouth (mean = 1.2 km). During the upstream movement, the fish typically stopped every 200 to 300 m (presumably to feed) for 1 to 2 h. At the reference site, few of the tagged fish moved farther than 100 to 200 m upstream from the main channel mouth at ebb tide, perhaps in response to somewhat lower dissolved oxygen at this site. During flood tide, tagged fish at both sites moved out into Delaware Bay, where they remained within 200 to 500 m of the creek mouth. Striped bass were sampled with gill nets to determine additional aspects of habitat use and food habits. Striped bass in both marshes were much more abundant at creek mouths (catch per unit effort, CPUE = 1.17) than in the upper reaches of the creeks (CPUE = 0.13). In the creek mouths, CPUE was greater at the restored site (CPUE = 1.8) than at the reference site (CPUE = 0.5). At both sites, most fish (approx. 80%) were collected on the late ebb or early flood tides, i.e. around low tide, when prey were presumably concentrated at the creek mouths. Stomach contents of bass from both restored and reference marshes (n = 59, 212 to 670 mm fork length) revealed that striped bass were eating mostly blue crab (*Callinectes sapidus*), grass shrimp (*Palaemonetes vulgaris*), sand shrimp (*Crangon septemspinosa*), mummichog (*Fundulus heteroclitus*), and various unidentifiable fishes (probably anchovies, *Anchoa mitchilli*, and Atlantic silverside *Menidia menidia*). In conclusion, the restored marsh supported larger numbers of striped bass than the reference marsh, but there was little difference in the pattern of creek utilization or food habits at either site. Thus, the restored marsh appears to be functioning in a similar manner to the reference marsh for these large predators.

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Introduction

Salt marshes are widely recognized as important nurseries for marine and estuarine fishes and invertebrates, including many economically important species (Gunter 1956, 1961; Nixon and Oviatt 1973; Weinstein 1979; Currin et al. 1984; Rountree and Able 1992; Kneib 1997). Moreover, the production of small fishes and crustaceans may directly affect growth and abundance of large predators that forage in tidal creeks in these marshes. Thus, successful restoration of salt marshes requires a thorough understanding of the utilization of marshes by both predators and prey.

In Delaware Bay (southern New Jersey, USA), many marshes have been diked for salt-hay farming (Sebold

1992). Restoration of these marshes to a more natural community dominated by *Spartina alterniflora* is being undertaken by the Estuary Enhancement Program of the Public Service Electric and Gas Company (Weinstein et al. 1997). This program is designed to restore tidal circulation in addition to marsh structure and function, through the opening of dikes and creation of a network of constructed "creeks." It is often difficult to determine the functional equivalency of restored marshes to natural marsh ecosystems because of the general scarcity of information on the basic habitat-use patterns of fish inhabiting subtidal and intertidal marsh creeks (Rountree and Able 1992, 1993; Kneib 1997) and a lack of understanding of the functions of marsh ecosystems in general (Zedler 1992; Zedler and Callaway 1999).

The objectives of this study were to compare the movements, habitat-use patterns, and food habits of a common Middle Atlantic Bight estuarine predator, the striped bass *Morone saxatilis*, in a restored marsh and an adjacent reference marsh. Our primary objective was to determine tidal and diel distribution patterns and movements of individual striped bass using ultrasonic tagging. Striped bass were chosen as the study species because they are abundant in Delaware Bay and have been the subject of several ultrasonic tracking studies in other regions (Dudley et al. 1977; Farquhar and Gutreuter 1989; Haeseker et al. 1996; Carmichael et al. 1998). However, nothing is known of the movements of striped bass in Delaware Bay, nor of the movements of adult striped bass in tidal marsh creeks in general. Our secondary objective was to determine if a restored marsh and a reference marsh are similar in another function – providing feeding areas for large predators such as striped bass. We examined stomach contents to determine if the prey eaten by these predators is linked to the marsh, in an attempt to provide an improved understanding of trophic linkages (food webs) in salt-marsh systems.

Materials and methods

Study sites

The reference marsh (Moores Beach) and the restored marsh, a former salt-hay farm (Dennis Township) are located in the mesohaline portion of lower Delaware Bay (39°11′ N; 74°49′ W), along the New Jersey shore (Fig. 1). Both marshes are bordered by large, natural creeks that connect them to Delaware Bay. The Moores Beach site was first diked for salt-hay farming in the 1950s, and these dikes were still present in aerial photographs in 1972 and 1977. As a result of large-scale breaches in the dikes, this site was open to tidal influence between 1977 and 1986, and has been largely revegetated since the early 1990s. In 1998, approx. 90% of the marsh plains was vegetated with *Spartina alterniflora* and other naturally occurring vegetation. Restoration of the Dennis Township site began in January 1996, and was completed in August 1996 (Weinstein et al. 1997). Prior to restoration, the salt-hay farm at Dennis Township consisted of a diked area that controlled access of tidal waters to the site. A series of linear ditches controlled water flow during fall/winter flooding of the salt-hay farm. Some of these ditches are still present at the site, and were incorporated into the flood/drain system when the dikes were opened during the restoration process. The restoration also included the creation of new creeks (Fig. 1), which were typically 700 to 1300 m in length, from the nearest natural creek to the upper limit of the created creeks (Able et al. 2000). The main channels were typically 500 to 700 m in length, with 1 or 2 branches measuring 100 to 400 m in length. Each channel was 6 to 10 m in width from bank to bank, and 2 to 3 m deep at high tide. The network of created creeks and existing ditches were engineered to provide the proper hydroperiod for regrowth of *S. alterniflora* (Weinstein et al. 1997). At Dennis Township, this consisted of six openings through the perimeter dike and 5500 m of channels inside the dike (Strait 1997).

Sampling techniques

Distribution and abundance of striped bass, Morone saxatilis

The occurrence, distribution, relative abundance and size (mm fork length, FL) of striped bass were determined from June through October 1998 by gill-netting at the Dennis Township restored marsh and the Moores Beach reference marsh sites. Gill nets were 37 m in length, 2.5 m in height, and had five panels of different mesh size, increasing from 7.5 to 11.5 cm in 1 cm increments. At both sites, gill nets were deployed in the upper and lower portions of two creeks (Creeks 2 and 4 at the restored marsh and Creeks 2 and 7 at the reference marsh; see Fig. 1). The nets were stretched across the creek and anchored by poles embedded vertically in the sediment. Nets were deployed during daylight hours twice monthly for 3 h on each of four tidal regimens: low tide to mid-flood tide (early flood), mid-flood tide to high tide (late flood), high tide to mid-ebb tide (early ebb) and mid-ebb tide to low tide (late ebb). Mean abundance, lengths and weights of striped bass from the two restored and two reference marsh creeks were $\log(x + 1)$-transformed to ensure homogeneity of variance (Sokal and Rohlf 1981), and compared using ANOVA. Catch per unit effort (CPUE) data were arcsine-transformed prior to analysis. Each time a gill net was deployed or hauled, water temperature, salinity and dissolved oxygen concentration were measured with a hand-held temperature, salinity and oxygen meter (YSI Model 85) by lowering the probe into the water and recording surface and bottom values.

Ultrasonic tracking

Movements of individual striped bass were determined using ultrasonic tags with unique combinations of frequency and interval. Prior to tracking fish in the field, a laboratory study was conducted to determine tag retention and mortality associated with the implantation of tags into the body cavity of striped bass ($n = 15$). Each individual was anaesthetized in a cooler containing 120 mg l^{-1} MS-222 (Sigma). A dummy transmitter, identical in size and shape to the real tag, was then surgically implanted into the body cavity (Mulford 1984). The fish were then held in outdoor tanks (1.5 m diam × 1 m high) with flow-through, ambient estuarine water for 21 d, after which the incision was reopened and the transmitter removed. All fish survived the 21 d period in good condition and retained their tags.

In July to September 1998, striped bass ($n = 23$) were collected by hook and line and by cast net in the large, natural creeks bordering the Dennis Township restored marsh and the Moores Beach reference marsh (Fig. 1). The implantation procedure employed in the field was identical to that used for the tag-retention study. The transmitters used (Sonotronics IBT96-1) were 18 mm in length and had a nominal battery life of 21 d. Based on our retention studies and field-tracking results, the implantation procedure we used did not lead to mortality of striped bass. With the exception of Haeseker et al. (1996), other studies have not reported high mortality of adult striped bass following implantation of ultrasonic transmitters (e.g. Farquhar and Gutreuter 1989). Of the 23 striped bass we tagged in the field, only 1 was never relocated. A strong downriver flight response following ultrasonic tagging has been reported

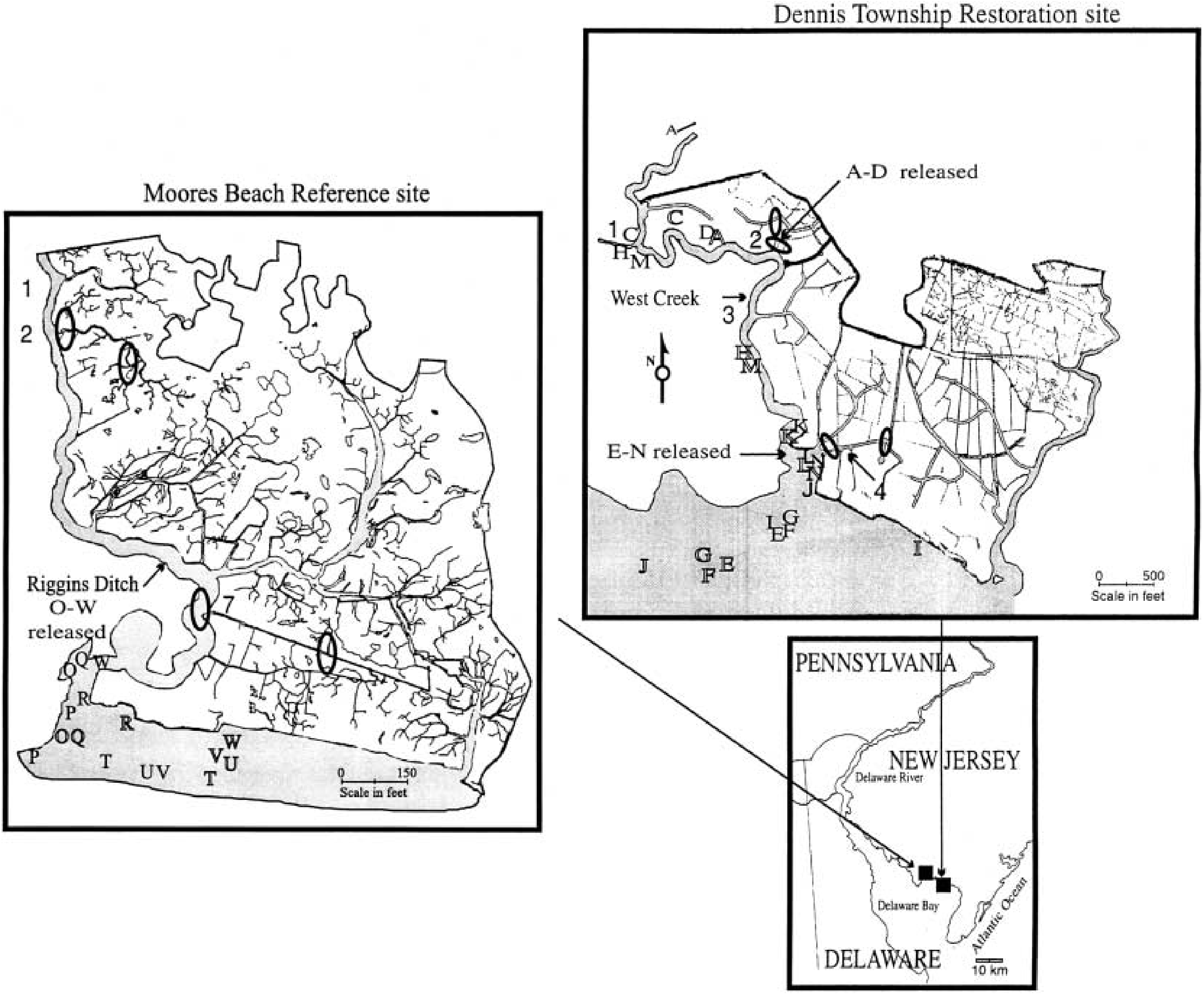

Fig. 1 Map of restored and reference-marsh study sites in lower Delaware Bay, New Jersey. [*Oval symbols* location of gill net sets; *numbers* specific creeks; *Letters* areas where specific tagged fish were most often located at high tide (*outlined characters*) and at low tide (*filled-in characters*) in their respective systems]

in a number of telemetry studies of anadromous fishes (Gray and Haynes 1979; Hall et al. 1991; Moser and Ross 1995; Carmichael et al. 1998). However, we did not observe this behavior in striped bass tagged in Delaware Bay salt marshes; in fact, the majority of fish either took cover in submerged structures for 2 to 3 h or swam upstream after tagging.

Whenever multiple fish were caught at a given site, the tagged individuals were held in 100-liter coolers until all fish could be released simultaneously, then released at the point of capture. In no case were fish held for more than 15 min before release. In order to determine if there were effects of capture, surgery, and release on fish movement patterns, all individuals were tracked continuously for a 4 h period after their release. Location and tracking of tagged fish was then attempted daily for the following 4 d and twice weekly for the next 3 wks. In addition, night-time tracking was conducted twice each month. Tracking consisted of systematically searching an area until a fish was located. After locating a tagged fish, the fish was followed from a small boat using a directional hydrophone mounted on a 1.5 m length of PVC pipe. The hydrophone was connected to a receiver (Sonotronics USR-5W). At 15 min intervals, we recorded the transmitter frequency and pulse interval, time, date, precise location using a differentially corrected hand-held GPS unit (Garmin Model 45), tidal stage (early ebb, late ebb, early flood, late flood), water temperature, salinity and dissolved oxygen (using a YSI Model 85). Because of the narrowness of the creeks, it was usually not possible to fix the location of a fish by triangulation; locations were fixed using a one-directional hydrophone. The location of the fish was then recorded on a waterproof map of the marsh creek system. Data collection was continued at 15 min intervals for a period of 4 h or until the fish was lost.

Distances between consecutive locations of a fish were calculated from the positions recorded by the GPS. Distance and time data did not meet the assumptions of parametric analyses, despite the application of several data-transformation techniques. Nonparametric analyses were therefore used to analyze these data.

Several types of habitat were available to striped bass in both the restored and reference marshes. Habitat types were defined as follows: (a) the open waters of Delaware Bay, (b) main creek mouth (the mouth of Riggins Ditch at the Moores Beach reference marsh and the mouth of West Creek at Dennis Township restored marsh; see Fig. 1), (c) main channel, the largest natural creek in each marsh (Riggins Ditch in the reference marsh, West Creek in the restored marsh), (d) tributary mouth, the mouths of created or natural creeks draining into the main channel, and (e) tributary channels, the subtidal areas of created or natural creeks draining into the main channel. The mean number of hours fish spent in different habitats was compared using the Kruskal–Wallis test (Sokal and Rohlf 1981).

We compared diel variation in swimming activity (distance traveled during 15 min intervals between position fixes) to a theoretical uniform distribution using a Kolmogorov-Smirnov one-sample test (Sokal and Rohlf 1981). Hydrographic data (water temperature, salinity and dissolved oxygen) were normally distributed and were compared between the restored and reference marshes using Student's *t*-tests (Sokal and Rohlf 1981).

Food habits

In order to determine food habits of juvenile and adult striped bass (n = 59, 212 to 670 mm FL) in the study creeks, each fish collected in the gill nets was measured to the nearest mm FL, labeled, and then placed on ice in an insulated cooler for transport back to the laboratory. In the laboratory, fish were weighed to the nearest gram and frozen until the stomachs were removed for examination. Upon removal, the stomachs were stored in 10% formalin for at least 48 h and then the contents were examined under microscopes and identified to the lowest possible taxon. The individual taxa were then dried in an oven and weighed in order to compare the weight of the stomach contents to the total fish weight. This allowed the relative contribution of each prey species or prey category to be expressed as both percent frequencies of occurrence and percent by weight. Relative abundance of taxa from striped bass stomach-contents was compared among creeks using Costello graphical analysis (Costello 1990) and Spearman rank correlation. All data were arcsine-transformed prior to analysis.

Results

Physical characteristics of study sites

The physical characteristics of the study sites were generally similar, with the exception of dissolved oxygen (Table 1). Water temperature did not differ significantly between the restored and reference marsh (Student's *t*-test, $t = 1.7, p > 0.25$) nor did salinity (*t*-test, $t = 0.4$, $p > 0.6$). Mean dissolved oxygen, however, was significantly higher at the restored marsh (4.9 ppm) than at the reference marsh (3.5 ppm: Table 1) (*t*-test, $t = 4.6$, $p < 0.05$). Mean dissolved oxygen was generally lower in the upper reaches of the tributary creeks than in West Creek or Riggins Ditch, and was particularly low in Creeks 2 and 7 in the reference marsh at Moores Beach (range 0.03 to 5.4 ppm).

Distribution and abundance of striped bass, *Morone saxatilis* from gill-net samples

The distribution and abundance of juvenile and adult striped bass, determined from gill-net collections, varied between and within marsh study sites. A total of 59 striped bass (FL = 212 to 670 mm) were collected in gill-net samples during June to November 1998. Of these, 56 were caught at the mouths of creeks (CPUE = 1.17); only 3 fish were collected from the upper reaches of the study creeks (CPUE = 0.13).

Striped bass were significantly more abundant in the restored marsh at Dennis Township than in the reference marsh at Moores Beach (*t*-test, $t = 5.4, p < 0.001$). As an example, in the creek mouths, CPUE was greater at the restored site (CPUE = 1.8) than the reference site (CPUE = 0.5). Striped bass were most abundant at Creek 4 in Dennis Township, and least abundant in Creek 7 at Moores Beach (Fig. 2). Analysis-of-variance indicated significant among-creek variation in CPUE of striped bass ($F = 16.3, p < 0.001$). Post-hoc analyses (Bonferroni) indicated no difference in CPUE between Creeks 2 and 4 at Dennis Township, however all other pairwise comparisons were significantly different.

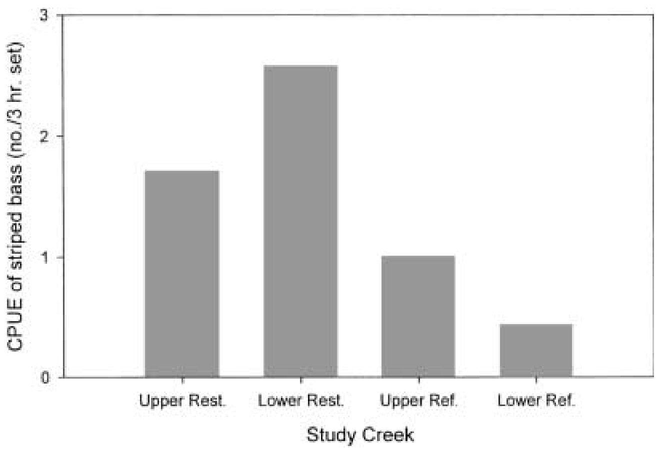

Fig. 2 *Morone saxatilis*. Abundance (count per unit effort, CPUE) in restored and reference-marsh tidal creeks in lower Delaware Bay, New Jersey, based on gill-net collections (*Upper Rest* = upper restored Dennis Township creek, Site 2; *Lower Rest* = lower restored, Dennis Township creek, Site 4; *Upper Ref* = upper reference, Moores Beach creek, Site 2; *Lower Ref* = lower reference, Moores Beach creek, Site 7; see Fig. 1 for location of creeks)

Table 1 Sampling effort (gill net) for striped bass (*Morone saxatilis*) and physical characteristics of tidal creeks at time of fish collection in restored and reference marshes in lower Delaware Bay, New Jersey, (*CPUE* catch per unit effort)

Marsh type	Duration	No. of 3 h sets	No. of fish collected	Overall CPUE (fish/set)	Temperature (°C)	Salinity (‰)	Dissolved oxygen (mg l^{-1})
Reference marsh (Moores Beach)	Jun–Oct	36	23	0.6	17.8–30.2 ($\bar{X}$ = 23.5)	13.7–22.0 ($\bar{X}$ = 19.7)	0.3–5.9 ($\bar{X}$ = 3.5)
Restored marsh (Dennis Township)	Jun–Oct	36	36	1.0	19.7–30.5 ($\bar{X}$ = 25.2)	17.6–20.8 ($\bar{X}$ = 19.0)	1.6-8.0 ($\bar{X}$ = 4.9)

Tidal stage had a profound influence on abundance of striped bass at both the restored and reference marshes (Fig. 3). Catches were near zero at times of high water (late flood and early-ebb tide), were highest on the early-flood tide, and moderate on the late-ebb tide (including low tide). At all stages of the tide except late flood, CPUE of striped bass was significantly higher at Dennis Township than at Moores Beach (Bonferroni test, $p < 0.05$; Fig. 3). Since the gill nets were deep enough to reach from the surface to the bottom at all stages of the tide, this pattern is unlikely to have been caused by tidal variation in gear efficiency.

Movements

The movements of juvenile and adult striped bass with ultrasonic tags varied between marsh sites and with tidal stage. Twenty-three striped bass (421 to 610 mm FL) were successfully tagged during June to September 1998. Of these, 22 fish were tracked for a total of 140 h over a distance of 21303 m, based on 569 position fixes. Fish B was lost 10 min after release and its signal could not be relocated. This fish was excluded from all analyses. At the restored marsh, 14 fish (421 to 450 mm FL) were released and tracked for a total of 99 h over a distance of 17774 m, based on 395 position fixes. At the reference marsh, 9 fish (438 to 610 mm FL) were released and tracked for a total of 41 h over a distance of 3529 m, based on 164 position fixes.

There was no significant difference between the restored and reference marshes (or the adjacent Delaware Bay waters) in the temperature (t-test, $t = 1.83, p = 0.12$), salinity ($t = -1.58, p = 0.17$), or dissolved oxygen concentration ($t = 0.66, p = 0.54$) of the water in which tagged striped bass were located (Table 2). However, concurrent studies indicated that dissolved oxygen concentrations in August were as low as 0.9 mg l^{-1} in tributary channels in the restored marsh (Creeks 2, 3 and 4; see Fig. 1) and <0.1 mg l^{-1} in tributary channels in the reference marsh (Creeks 1, 2 and 7; see Fig. 1) (Miller and Able unpublished data). Thus, very low dissolved-oxygen readings in the upper reaches of tributaries of the main creeks may explain why tagged fish did not move there in either the restored or reference marshes.

Habitat-use by ultrasonically-tagged striped bass was relatively localized, with movements restricted to the creek system in which they were captured and the adjacent bay. Tagged striped bass remained in the marsh-creek system or just outside the mouths of the main creeks for 1 to 16 d, with a mean of 4.5 d at the restored marsh and 6.2 d at the reference marsh. Habitat-use varied somewhat between restored and reference marshes. At the restored marsh, tagged striped bass were located in West Creek about 76% of the time (34% in the main channel, 22% in the mouth and 20% in

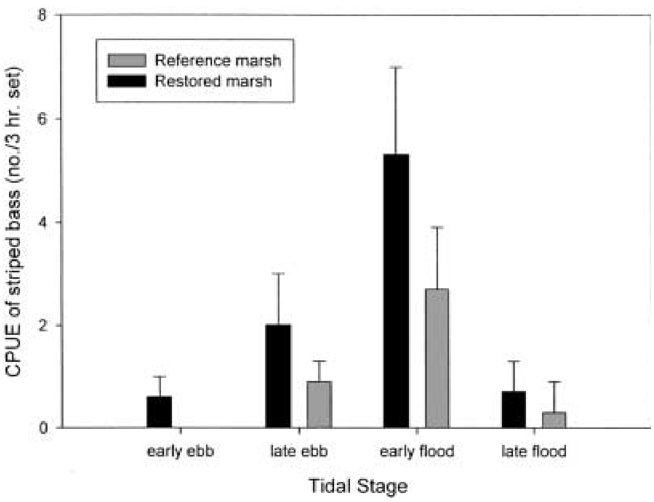

Fig. 3 *Morone saxatilis*. Abundance (CPUE) in lower Delaware Bay tidal creeks as a function of tidal stage, based on gill-net collections. Data from all study creeks at each site pooled

Table 2 *Morone saxatilis*. Water temperature, salinity and dissolved oxygen each time an individual striped bass (designated by letters) was located (*N* number of relocations)

Location	Fish ref.	(*N*)	Water temperature (°C)			Salinity (‰)			Dissolved oxygen (ppm)		
			Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Restored marsh	A	(34)	27.9–28.4	28.1	0.2	13.7–14.8	14.2	0.5	3.6–5.1	4.3	0.4
(Dennis Township)	C	(19)	28.4–29.5	28.9	0.3	15.2–17.9	16.1	1.7	3.7–4.9	4.4	0.6
	D	(14)	28.4–29.5	28.9	0.3	15.2–17.9	16.2	1.9	3.7–4.9	4.3	0.5
	G	(49)	22.3–25.5	23.8	2.8	19.7–21.1	20.6	0.7	3.0–4.9	4.1	1.2
	J	(49)	20.0–21.4	20.9	0.7	19.2–21.1	20.4	0.9	4.4–8.0	5.6	1.7
	K	(49)	20.0–21.4	20.8	0.7	19.2–21.1	20.2	0.9	5.1–7.9	5.9	1.2
(Total)		(214)	(20.0–29.5)	(25.2)	(1.9)	(13.7–21.1)	(18.0)	(1.4)	(3.0–8.0)	(4.8)	(0.7)
Reference marsh	O	(26)	24.3–28.1	25.7	1.6	18.6–20.1	19.6	0.6	3.3–5.8	4.3	1.2
(Moores Beach)	P	(17)	24.3–28.1	26.5	1.6	18.6–20.1	19.4	0.7	3.3–5.8	4.2	1.2
	Q	(32)	25.2–26.0	25.4	0.5	18.8–21.4	19.8	1.3	4.3–7.5	5.9	1.5
	R	(14)	19.4–24.4	21.1	2.9	17.9–20.8	19.2	1.5	2.9–5.7	3.7	1.3
	T	(17)	19.4–24.7	21.4	3.1	19.8–20.9	20.1	0.4	3.3–5.7	4.4	1.1
	W	(44)	19.4–24.6	22.3	2.3	19.8–20.9	20.1	0.3	3.3–5.7	4.3	1.1
(Total)		(150)	(19.4–28.1)	(23.7)	(1.8)	(17.9–21.4)	(19.7)	(0.4)	(2.9–7.5)	(4.5)	(1.2)

tributary mouths; Table 3, Fig. 1). The remaining 25% of the time was spent in Delaware Bay, within 200 to 500 m of the mouth of West Creek. Tagged striped bass were never located within any of the tributary creeks at Dennis Township. Among the four habitats that tagged fish occupied (Delaware Bay, mouth of West Creek, West Creek proper, and creek mouths along West Creek), there was no significant difference in the mean number of hours spent in each habitat (Kruskal–Wallis test, $H = 0.4$, $p = 0.76$).

At the reference marsh, striped bass did not utilize the main channel (Riggins Ditch) to the extent that they used the main channel of the restored marsh (Tables 3 and 4; Fig. 1). The time spent in Delaware Bay was similar for the reference marsh (30%) and the restored marsh (25%), but fish from the reference marsh appeared to remain much longer at the mouth of the main creek (49% of the time) as compared to the restored marsh (22% of the time). Similar to the restored marsh, striped bass were not located within any of the tributary creeks at the reference marsh. In contrast to the restored marsh, tagged fish spent significantly more time in the mouth of Riggins Ditch than in any other habitat, and significantly less time in the channel of Riggins Ditch and in tributary mouths than in Delaware Bay [Kruskal–Wallis H-statistic, $H = 3.3$, $p = 0.03$, post-hoc comparisons by STP (Simultaneous test procedure)].

At the restored marsh, three fish (A, C, D; Fig. 1) traveled upstream on the ebb tide after release, making frequent stops along the way, usually at tributary creek mouths or undercut sections of the creek bank or in rips or eddies caused by sharp bends in the creek. These stops became longer in duration as the afternoon progressed. All three fish halted their movements at sundown. The greatest distance traveled in 1 d was 3.5 km upstream (Fish A). The remainder of fish tagged at the restored marsh (E through M) were caught and released at a sandy beach along the mouth of West Creek. With the exception of Fish H and M, both of which traveled 2 km upstream, this group did not travel as far into the marsh system as the previous group (Fig. 1). Five individuals moved out into Delaware Bay and remained just outside the creek mouth for the remainder of the study.

At the reference marsh, Fish O through W were caught and released near the mouth of Riggins Ditch. None of these fish moved more than 200 m into the

Table 3 *Morone saxatilis*. Distributions (time, h) by habitat type of tagged individuals in and out of restored marsh at Dennis Township. Letters designate individual fish

Fish ref.	Delaware Bay	West Creek				Total
		Creek mouth	Main channel	Tributary mouth	Tributary channel	
A	0	0	6.6	2	0	8.6
B	0	0	0	0	0.1	0.1
C	0	0	2.0	2.3	0	4.3
D	0	0	1.2	2.3	0	3.5
E	0	1.0	0.3	0	0	1.3
F	0	0.7	1.7	0	0	2.4
G	0	0.4	10.4	1.5	0	12.3
H	0	2.5	8.7	1.1	0	12.3
I	0	0	2.0	2.8	0	4.8
J	7.5	4.6	0.2	0	0	12.3
K	7.5	4.6	0.2	0	0	12.3
L	2.3	2.5	0	0	0	4.8
M	0	2.5	0.3	7.5	0	10.3
N	7.0	2.5	0	0	0	9.5
Total hours	24.3	21.3	33.6	19.5	0.1	98.8
% of time	24.6	21.6	34.0	19.7	0.1	

Table 4 *Morone saxatilis*. Distributions (time, h) by habitat type of tagged individuals in and out of reference marsh at Moores Beach. Letters designate individual fish

Fish ref.	Delaware Bay	Riggins Ditch				Total
		Creek mouth	Main channel	Tributary mouth	Tributary channel	
O	3.0	3.5	0	0	0	6.5
P	0	1.2	3.0	0	0	4.2
Q	0	4.7	0.2	3	0	7.9
R	0	3.5	0	0	0	3.5
S	2.1	0	0	0	0	2.1
T	0	4.2	0	0	0	4.2
U	2.1	0	0	0	0	2.1
V	2.1	0	0	0	0	2.1
W	2.8	3.1	0.2	2.2	0	8.3
Total hours	12.1	20.2	3.4	5.2	0	40.9
% of time	29.6	49.4	8.3	12.7	0	

marsh system, although they moved a similar distance into Delaware Bay as fish tagged in the restored marsh (Fig. 1).

Tidal movements were consistent between tagged striped bass in both restored and reference marsh creeks. In both marsh types, fish moved primarily upstream on the ebb tide and downstream on the flood tide (i.e. against the current), and spent about 20 to 30% of the time stationary (Table 5). During these stops, particularly on the ebb tide, striped bass were observed feeding on baitfish at the surface; however, it was not apparent whether the fish feeding were tagged fish. Fish moved with the current only 1 to 3% of the time in the restored marsh and not at all in the reference marsh. At low tide, tagged fish in the restored marsh spent roughly equal amounts of time swimming upstream or downstream or remaining stationary, whereas striped bass in the reference marsh spent more time stationary. At high tide, striped bass from both marshes were mainly stationary, usually at the creek mouth or in Delaware Bay.

Food habits

Stomach-content analysis revealed that the major prey items of striped bass in Delaware Bay tidal creeks were blue crab (*Callinectes sapidus*), grass shrimp (*Palaemonetes vulgaris*), sand shrimp (*Crangon septemspinosa*), mummichog (*Fundulus heteroclitus*), and various small pelagic fishes, which were difficult to identify but these were probably bay anchovy (*Anchoa mitchilli*) and Atlantic silverside (*Menidia menidia*) (Fig. 4). Of the 59 fish collected for diet analysis, 7 had empty stomachs. All of these were collected at times of high water, i.e. late flood or early-ebb tide. All fish collected on the late ebb and early-flood tides had food in their stomachs.

The overall diet composition of juvenile and adult striped bass was similar between the restored and reference marshes, in terms of percent frequency of prey items by weight (Spearman rank correlation, $R^2 = 0.66$, $p < 0.01$) and percent frequency of occurrence ($R^2 = 0.70$, $p < 0.01$). In both marshes, *Callinectes sapidus* and *Crangon septemspinosa* were major prey items, while *Fundulus heteroclitus* was important only in the reference marsh (Fig. 4). Variation in diet was more striking between creeks in the reference marsh than between marsh types (i.e. restored vs. reference marshes). Within the restored marsh, diet composition was slightly less similar between striped bass collected in Creeks 2 and 4 (Spearman rank correlation, $R^2 = 0.57, p < 0.05$ for diet composition by weight; $R^2 = 0.61, p < 0.01$ for diet composition by frequency of occurrence). The most common prey item in Creek 2 was *Callinectes sapidus* followed by *Crangon septemspinosa* (Fig. 4). In Creek 4, the most common prey item was *C. septemspinosa*, followed distantly by nearly equal proportions of *Callinectes sapidus*, *F. heteroclitus* and unidentified fishes (Fig. 4). Within the reference marsh, there were large differences between Creeks 2 and 7 in diet of striped bass (Spearman rank correlation, $R^2 = 0.0$, $p > 0.75$ for diet composition by weight; $R^2 = 0.11$, $p > 0.50$ for diet composition by frequency of occurrence). In Creek 2 the most common prey item was *C. sapidus*, whereas in Creek 7 the diet of striped bass was dominated by *F. heteroclitus*.

Table 5 *Morone saxatilis*. Proportion of time (%) tagged individuals spent moving upstream or downstream or were stationary as a function of tidal phase; and total distance (m) covered during each tidal phase. "Upstream" movements include movements in Delaware Bay toward main creek mouth. "Downstream" movements include movements away from main creek mouth and into bay

Location	Ebb	Low	Flood	High
Restored marsh (Dennis Township)				
Upstream	77	32	1	0
Downstream	3	38	81	35
Stationary	20	30	18	65
Total distance (m)	9696	1154	6954	270
Reference marsh (Moores Beach)				
Upstream	75	29	0	0
Downstream	0	21	30	0
Stationary	25	50	70	100
Total distance (m)	2208	90	1231	0

Discussion

Distribution and habitat use

Tagged striped bass, *Morone saxatilis* exhibited a high degree of site-fidelity; all were re-located within the creek system where they were released or in adjacent bay waters. Striped bass appeared to make similar use of tidal creeks in the restored and reference marshes, except that striped bass ventured farther into the restored marsh (i.e. farther up the main channel) than the reference marsh. In this study, temperature and salinity did not vary widely between marsh types or between creeks within a marsh, and appeared to have little effect on the abundance or distribution of striped bass or their food habits. However, dissolved oxygen was much lower in the upper (intertidal) reaches of the tidal creeks than near the mouths, particularly at the Moores Beach reference marsh, and catches of striped bass in intertidal creek areas were near zero in both the restored and the reference marsh. One explanation for the lower abundance of striped bass in the reference marsh may be that water containing low levels of dissolved oxygen flowed out of the upper reaches of the creeks on the ebb tide, resulting in a lower overall mean dissolved oxygen value for the reference marsh. This pattern of lower dissolved oxygen in the reference marsh at Moores Beach was true for 1997 as well (Able et al. 2000), but not as obvious in other studies in this same marsh during 1998 (Able et al. in preparation, Miller and Able in preparation).

Axon and Whitehurst (1985) cited the most frequent problem in management of striped bass populations in

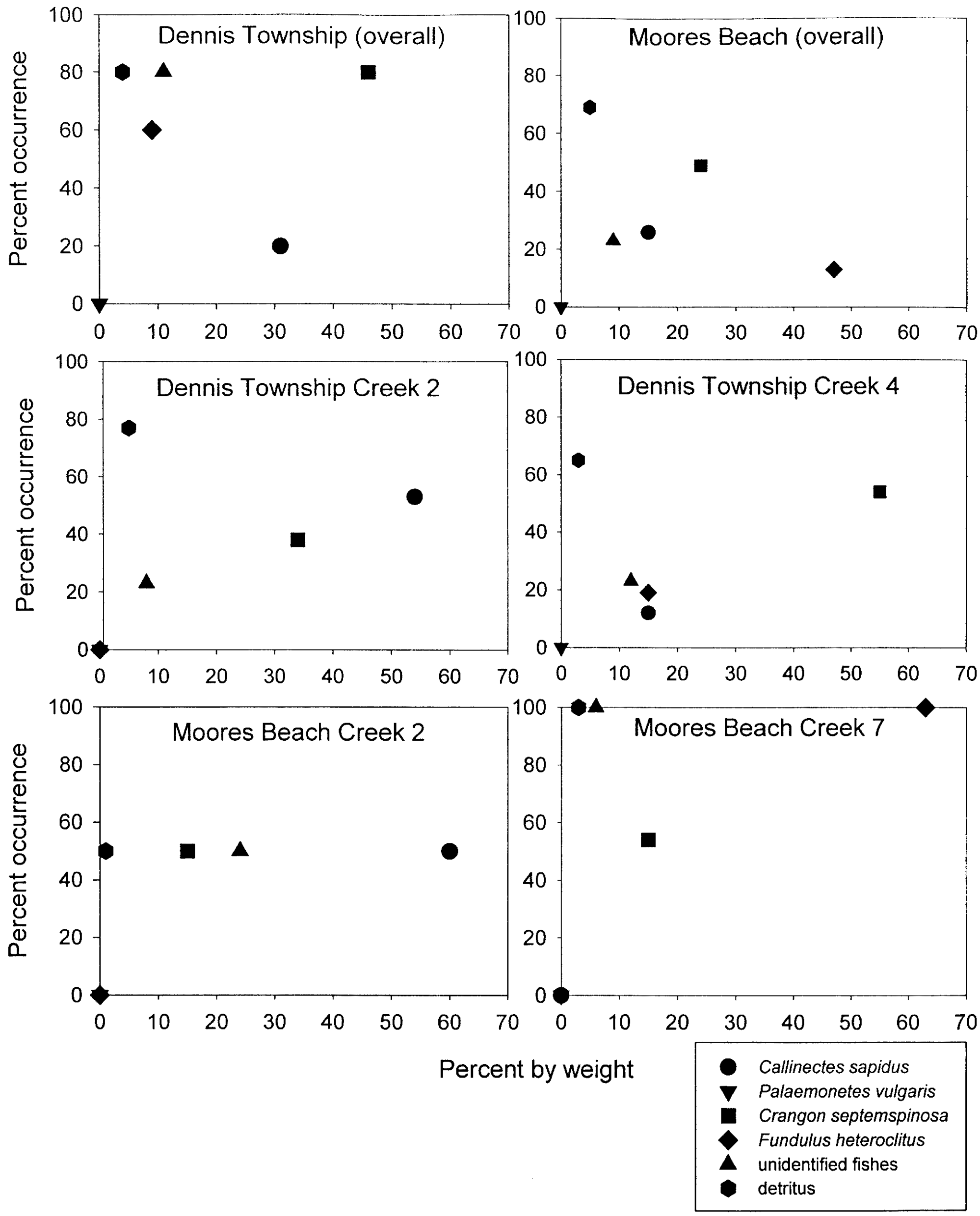

Fig. 4 *Morone saxatilis*. Costello diagrams of diet composition in restored (Dennis Township) and reference (Moores Beach) tidal creeks in lower Delaware Bay, New Jersey

reservoirs as mortality of adult fish due to summer thermal stress and low dissolved oxygen concentrations. Farquhar and Gutreuter (1989) reported that striped bass in Lake Whitney (Texas) preferred the coolest water available (27 to 29 °C) that contained adequate dissolved oxygen (>4.0 mg l^{-1}). In general, the upper thermal limit of striped bass decreases with age (Coutant 1985). As a result, adult striped bass are forced into restricted areas to avoid high temperatures and low dissolved oxygen. These areas often lack adequate prey. Striped bass restricted to waters of low dissolved oxygen are generally in poor condition compared with individuals from normoxic waters (Coutant 1985). In tidal marsh systems, however, striped bass are less likely to be restricted to a given area, because of the connection of marshes with cooler, more oxygen-rich estuarine and ocean waters. These conditions may partially explain the movements of striped bass into Delaware Bay and the longer residence of fish in the lower portions of tidal creeks. Moreover, the high level of production in tidal marsh systems means that food is unlikely to be limiting even in conditions of high temperature and lower dissolved oxygen.

Some aspects of the local movements and behavior of striped bass may be influenced by submerged structures. Several of the creek mouths in the restored marsh contained wooden pilings and other remains of water-control structures in the former salt-hay farm. In contrast, the only structure found in the reference marsh was a group of large cedar stumps just inside the mouth of Riggins Ditch. In both marsh types, tagged striped bass were often found in association with these structures. Haeseker et al. (1996) also reported that structures represented important habitat for striped bass in Albemarle Sound. If structure is an important feature of preferred striped-bass habitat, then the larger amount of structure available in the Dennis Township restored marsh may partially explain the greater use of the restored marsh system by tagged striped bass.

Movements

Data from gill-net samples and ultrasonic tracking indicated a clear association of striped bass movements into and out of the restored and reference marshes with tides. Most fish moved up the creek on ebb tides and down the creek on flood tides, apparently to feed on prey items concentrated in the creek mouths at low tide. Movements of striped bass in tidal creeks have not previously been investigated, and therefore we cannot compare our results to other studies of this species. However, ultrasonic telemetry has been used to document the tidal movements of flatfishes in the Bann estuary, Ireland (Wirjoatmodjo and Pitcher 1984), and in tidal creeks of the Great Bay/Mullica River, in southern New Jersey (Szedlmayer and Able 1993).

In the Bann estuary, movements of European flounder (*Platichthys flesus*) were most strongly linked to the tidal cycle, although there was some evidence of increased activity at dusk, indicating that diurnal light levels may also have an influence (Wirjoatmodjo and Pitcher 1984). Wirjoatmodjo and Pitcher suggested that estuarine flounder movements were governed more by the tidal availability of food than by any physical factor. Juvenile (Age 0) summer flounder (*Paralichthys dentatus*) in a southern New Jersey tidal creek also moved upstream with flood tide and downstream with the ebb tide (Szedlmayer and Able 1993). These latter authors suggested that summer flounder employed selective tidal-stream transport as a means of maximizing energy efficiency, as has been reported for other flatfishes (Greer-Walker et al. 1978; Harden-Jones et al. 1979; Metcalfe et al. 1990). They further suggested that habitat use within the creek also might have served to maximize energy efficiency. Similar to striped bass, juvenile summer flounder were often found in creek mouths. Szedlmayer and Able (1993) suggested that creek mouths may serve as a low-energy holding area because the physical configuration probably produced a low-current area during both flood and ebb tides. Moreover, creek mouths may be a refuge from low dissolved-oxygen conditions that typically occur in the upper reaches of tidal creeks. Digestion of food is an energetically expensive activity, and oxygen consumption following a meal may rise to double the routine rate in teleosts (Jobling 1981). Thus, conditions of low dissolved oxygen in the upper reaches of tidal creeks may strictly curtail feeding in these areas. While it is unknown whether adult striped bass would gain any energetic benefit from stationing themselves at creek mouths, it is clear that aggregations of juvenile fish and shrimp that occur there at low tide (Able unpublished data) might provide a concentrated prey source.

There was a striking difference between the restored and reference marsh in the average distance moved by striped bass. In the restored marsh, striped bass moved much farther into the marsh system than in the reference marsh. Conversely, the average distance moved out into Delaware Bay from the main channel mouth did not differ between marsh types. It is possible that low dissolved oxygen levels in the upper reaches of the reference marsh deterred striped bass from moving farther upstream. Alternatively, between-marsh differences in prey distribution and abundance may account for the difference in creek-utilization patterns by striped bass.

Food habits

Diet composition of striped bass differed little between the restored and reference marsh creeks during 1998. The pattern of dominance by weight of items that were relatively infrequent in occurrence is a result of large quantities of a particular prey item being eaten by only a few fish. This, in turn, may result from within-creek or within-marsh differences in prey preference. For example, *Fundulus heteroclitus* were absent from the diet of striped bass at both upper marsh creeks (Creek 2 in the restored marsh and Creek 2 in the reference marsh). In these creeks, *Callinectes sapidus* were the dominant prey item. In the lower marsh creeks (Creek 4 in the restored marsh and Creek 7 in the reference marsh), *C. sapidus* were a much less important diet component, while *F. heteroclitus* increased in importance. Alternatively, some individual striped bass may select a narrow prey field and focus on these, resulting in within-creek and/or within-marsh differences in diet composition. However, striped bass in estuarine waters are usually considered to be opportunistic or nonselective feeders, consuming prey in accordance with the local prey availability (Manooch 1973; Cooper et al. 1998).

Significant variation in diet between upper and lower creeks occurred only in the reference marsh. This may result from a difference in prey availability between the upper and lower reaches of the restored marsh. However, assessment of these and nearby creeks suggest that fish/shrimp abundance is relatively similar across the upper and lower areas of both the restored and reference marshes (Able et al. 2000). The upstream/downstream variation in diet in the reference marsh could result from lower dissolved oxygen in the upper reaches of the reference marsh that occurred during this study, part of which was conducted at night. These differences in dissolved oxygen were not as obvious in other studies in the same marsh during the same year (Able et al. in preparation, Miller and Able in preparation).

One point that must be made with regard to our results is that our small sample size necessitated pooling unequal sample sizes across seasons and across size classes of striped bass. Thus, we could neither determine nor correct for possible size-related or seasonal differences in the diet composition of striped bass. Further data are needed to more fully examine the feeding habits of striped bass in Delaware Bay tidal marshes. However, our data on movements and habitat use, coupled with diet compositions, strongly suggest that striped bass used the restored and reference marshes in a similar manner. This has important implications for the management of commercially important large predators in restored coastal marshes.

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