



Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries

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Abstract

Instantaneous growth rates of young-of-the-year winter flounder *Pseudopleuronectes americanus* (Walbaum) (12.0–60.4 mm standard length, SL) and tautog *Tautoga onitis* (Linnaeus) (21.4–73.8 mm total length, TL) from three estuarine systems in New Jersey (Great Bay–Little Egg Harbor and Navesink River) and Connecticut (Hammonasset River) were used in an attempt to assess the relative quality of selected nominal habitats. A series of short-term field caging experiments were conducted during 1994 and 1995 in: macroalgae (primarily, *Ulva lactuca*), eelgrass (*Zostera marina*), unvegetated areas adjacent to macroalgae and eelgrass and tidal creeks in *Spartina* dominated marsh. Growth rates varied with habitat, estuary and year. Comparisons across nominal habitats within and among estuaries did not show any one habitat with consistently higher growth, and growth was relatively independent of whether a habitat was vegetated or adjacent to vegetation. The growth rates of winter flounder and tautog from the Hammonasset River were not different among habitats in either year of the study. In the Great Bay–Little Egg Harbor, both winter flounder and tautog had higher growth rates in macroalgae with growth in eelgrass varying significantly between years. Conversely, in the Navesink River both species had higher growth rates in eelgrass. Environmental changes associated with temperature and dissolved oxygen appeared to influence growth rates. Winter flounder growth rate and survival was depressed in tidal marsh creeks in the three estuaries and in vegetated macroalgae habitats in the Navesink River where dissolved oxygen levels were often very low ($< 2 \text{ mg l}^{-1}$) for extended

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periods. In summary, the growth rates of the young-of-the-year of these two species varied temporally and were dependent on the interaction of both the specific estuary and habitat in which the experiments took place. Further, habitat quality, as defined by relative growth rate, was difficult to evaluate because it can be variable and nominal habitat designations are often not sufficient to define the boundaries of a species habitat requirements. Published by Elsevier Science B.V.

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1. Introduction

Estuaries along much of the northeastern coast of the United States provide nursery habitat for a wide variety of fish species (Able and Fahay, 1998), including those of commercial and recreational importance (Chambers, 1992). Within estuaries, a number of habitats, i.e. seagrasses, marshes, marsh creeks, have been identified as important fish nursery habitat. Seagrass habitats in the southeastern US (Hoss and Thayer, 1993; Heck et al. 1997) and marsh creek habitats (marsh surface, pools and creeks) along the east coast of the United States (Weinstein, 1979; Rountree and Able, 1992; Able et al., 1996) are considered high quality, in part because they support high abundances and densities of juvenile fish (Able, 1999). Seagrasses are known to provide refuge from predation (Heck and Orth, 1980; James and Heck, 1994) and food resources (Hoss and Thayer, 1993). The relative value of macroalgae, another macrophyte habitat in areas of the northeastern US (Short and Burdick, 1996; Timmons and Price, 1997), is somewhat debatable. Macroalgae are known to displace seagrasses (Short and Burdick, 1996), change the biogeochemistry of the water and sediment (Valiela et al., 1992), induce hypoxic conditions (D'Avanzo and Kremer, 1994) and alter benthic fauna (Valiela et al., 1997; Thiel et al., 1998). In laboratory experiments, a macroalgal (*Ulva lactuca*) exudate was toxic to invertebrates (Johnson and Welsh, 1985) and to larval winter flounder, *Pseudopleuronectes americanus*, but not to juvenile winter flounder (Johnson, 1980). In another study, *Ulva*-dominated habitats were comparable to eelgrass (*Zostera marina*) based on decapod crustacean abundance and were more important than areas lacking either type of vegetation (Sogard and Able, 1991). *Ulva* also provided a predator refuge for juvenile tautog, *Tautoga onitis* (Sogard and Able, 1991) and blue crabs, *Callinectes sapidus* (Wilson et al., 1990a,b).

High quality nursery habitats are those in which growth and survival of juvenile fish is enhanced and where ultimately reproductive potential is optimized (Houde, 1987; Gibson, 1994). Consequently, rapid growth can be used as one indicator of habitat quality because it implies that (1) there is sufficient food available, (2) individuals may achieve a size refuge from some predators, and (3) individuals may be larger at the end of the summer growing season, thus enhancing the chances of overwinter survival (Sogard, 1997; Able, 1999). Based on this, several studies have employed growth rates of juvenile fish in cages to evaluate habitat quality (Sogard, 1992; Guindon and Miller, 1995; Duffy-Anderson and Able, 1999; Able et al., 1999). Relative differences in growth

rates for selected species held in cages in southern New Jersey estuarine habitats were generally maintained across experiments suggesting a consistency in foraging value (Sogard, 1992). In the heavily impacted Hudson River estuary, growth of caged young-of-the-year winter flounder and tautog has been used to assess the quality of man-made habitats (e.g. piers and pile fields). These studies have shown negative somatic growth under piers, which may be related to factors such as available light and food (Duffy-Anderson and Able, 1999; Able et al., 1999).

While previous research has concentrated on habitat comparisons within a single estuary, (Sogard, 1992; Guindon and Miller, 1995; Duffy-Anderson and Able, 1999; Able et al., 1999), our study compares growth of young-of-the-year winter flounder and tautog among different habitats within an estuary and among similar habitats in three different estuaries in the southern New England–New York Bight coastal watershed (Fig. 1). Winter flounder adults occur in estuarine and continental shelf waters in the northwest Atlantic (Bigelow and Schroeder, 1953), with the largest fisheries from Canada through southern New England. Young-of-the-year winter flounder are known to occur across a variety of estuarine habitats (Sogard and Able, 1991; Able and Fahay, 1998). Tautog adults occur primarily on the inner continental shelf and the polyhaline portions of estuaries from Nova Scotia to South Carolina but is most abundant from Cape Cod to Delaware Bay (Bigelow and Schroeder, 1953). Young-of-the-year tautog occupies a variety of structured habitats and may be highly localized (Olla et al., 1979; Dixon, 1994; Able and Fahay, 1998). Both species, which are common in the study areas, have been shown to exhibit habitat related differences in growth in previous studies (Sogard, 1992; Duffy-Anderson and Able, 1999; Able et al., 1999). The nominal habitats studied, chosen for their emergent vegetation or proximity to vegetation and their common occurrence in each of the three estuaries, were evaluated for their ability to predict habitat growth both temporally and spatially. This study was part of a larger effort designed to examine several parameters that may be indicators of habitat quality within and among estuaries (Goldberg et al., 1993; Goldberg et al., 2000; Litvin et al., unpubl. data).

2. Materials and methods

2.1. Study sites

Three estuaries (all within 250 km) were selected for comparison: (1) Great Bay–Little Egg Harbor in southern New Jersey, (2) the Navesink River in northern New Jersey, and (3) the Hammonasset River on the Connecticut coast of Long Island Sound (Fig. 1). Great Bay–Little Egg Harbor is part of the Jacques Cousteau Estuarine Research Reserve and is located within the Mullica River watershed and drains through Little Egg Inlet into the Atlantic Ocean. Compared with the other estuaries it is relatively pristine (Psuty et al., 1993). In contrast, the Navesink River is a small estuary which joins the Shrewsbury River before entering the Atlantic Ocean through Sandy Hook Bay. Sandy Hook Bay mixes tidally with the highly urbanized and industrialized Raritan and New York Bays. The adjoining land areas are suburban and primarily residential.

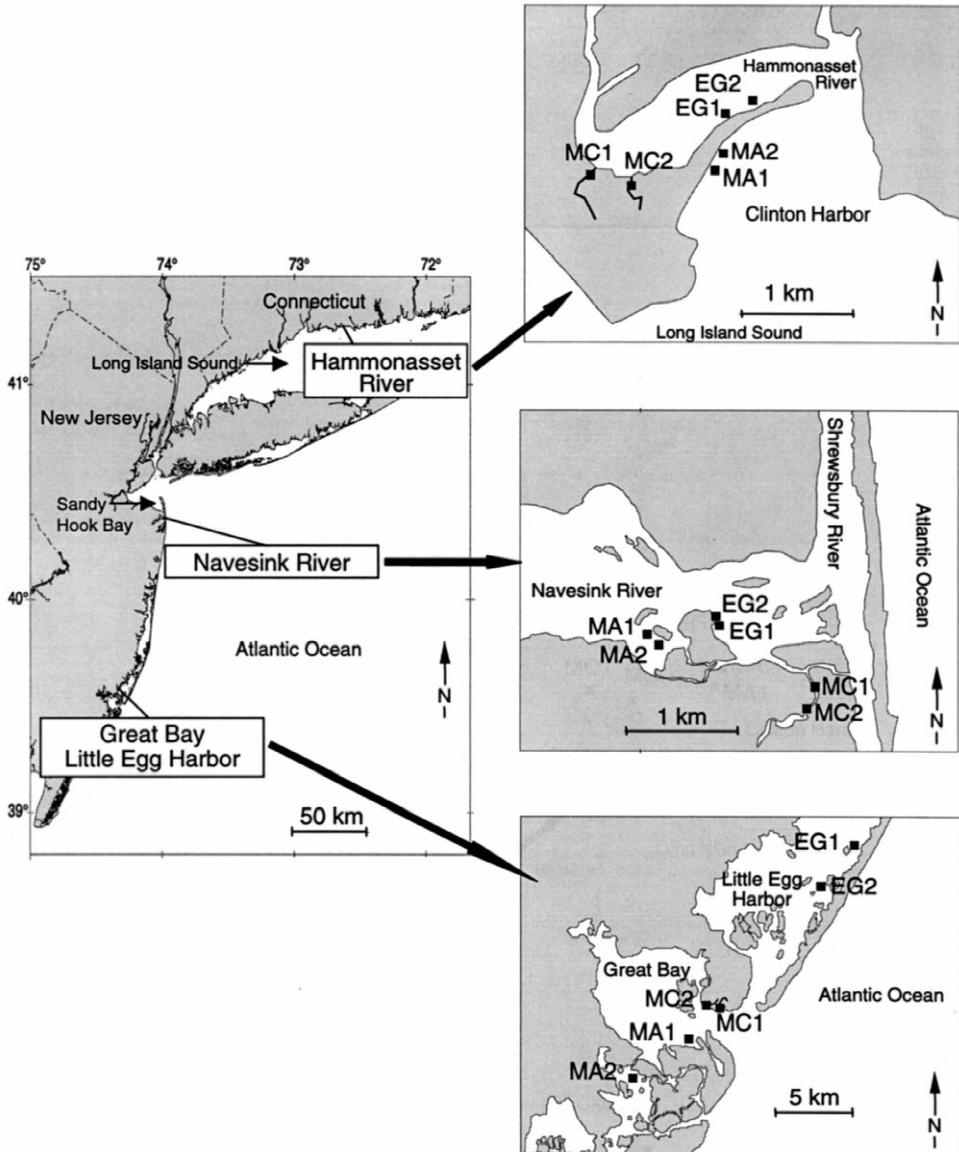


Fig. 1. Location and study site maps for Great Bay–Little Egg Harbor and the Navesink River in New Jersey and the Hammonasset River in Connecticut. EG, eelgrass; MA, macroalgae; MC, marsh creeks. Numbers refer to replicates. Unvegetated habitats associated with eelgrass and macroalgae are immediately adjacent to them.

Anthropogenic effects are reflected in elevated nutrient levels (Litvin et al., unpubl. data). In Connecticut, the mouth of the Hammonasset River and Clinton Harbor form a small estuary which empties into the eastern half of Long Island Sound. The surrounding area is suburban with light industry and a state recreation area. The study areas within

both the Navesink River and Hammonasset River were approximately 2 km² while Great Bay–Little Egg Harbor is larger (125 km²). All the study areas have similar temperature, salinity and tidal ranges (Table 1). Additional characteristics of these estuaries are available from a related study (Goldberg et al., 2000).

In the study areas, five nominal habitats were identified and selected, based on their emergent vegetation and proximity to each other: eelgrass (EG) (*Zostera marina*),

Table 1

Comparison of physical characteristics of Great Bay–Little Egg Harbor (GB), the Navesink River (NR), and the Hammonasset River (HR) estuarine study areas in 1994 and 1995 during the caging experiments^a

	Great Bay–Little Egg Harbor	Navesink River	Hammonasset River
Watershed area (km ²) ^b	40 000	246	128
Study area (km ²) ^b	125	2	2
Depth at MHHW (m) ^b	1.3	1.3	1.7
Tidal range (m) ^b	1.0	1.0	1.5
<i>Eelgrass (EG) and unvegetated areas (U-EG)</i>			
Salinity range (‰) ^c	29.0–30.5	14.7–28.4	16.3–30.0
Temperature range (°C) ^c	17.1–34.5	16.2–28.9	14.4–28.4
Dissolved oxygen range (mg l ⁻¹) ^c	3.4–7.8	0.9–11.8	2.5–11.7
Spatial coverage (km ²) ^{b,c}	7.0	0.1	1.0
Density (shoots m ⁻²) ^{b,c}	452.9	172.1	23.9
Distance (m) from EG to U-EG	10	10	20
Distance (m) between replicate habitat types	1000	5	500
<i>Macroalgae (MA) and unvegetated areas (U-MA)</i>			
Salinity range (‰) ^c	25.4–32.5	13.0–28.2	23.9–32.5
Temperature range (°C) ^b	16.2–34.3	16.6–29.7	14.5–26.7
Dissolved oxygen range (mg l ⁻¹) ^c	5.5–12.7	0.1–12.9	4.3–12.2
Spatial coverage (km ²) ^{b,c}	0.25	0.16	0.25
Density (g dw m ⁻²) ^{b,c}	12.0	366.1	10.8
Distance (m) from MA to U-MA	10	1	20
Distance (m) between replicate habitat types	1000	100	500
<i>Marsh creek^d</i>			
Salinity range (‰) ^c	19.0–31.5	15.8–22.4	16.0–29.4
Temperature range (°C) ^c	16.5–31.9	18.9–27.1	14.9–30.2
Dissolved oxygen range (mg l ⁻¹) ^c	0.1–9.3	0.1–9.8	0.1–12.8
Average length (km)	1.7	0.9	0.8
Distance (m) between replicate habitat types	500	200	300

^a Temperature, salinity and dissolved oxygen ranges were taken from continuous datalogger records. MHHW is the mean higher high water at each location. See Fig. 1 for locations.

^b From Goldberg et al. (2000).

^c Vegetated areas only.

^d 1994 only.

adjacent unvegetated habitat (U-EG), macroalgae (MA) (predominantly *Ulva lactuca*), adjacent unvegetated habitat (U-MA), and tidal marsh creeks (MC). Two replicate sets of these five habitats were selected in each of the three estuarine study sites (3 estuaries \times 5 habitats \times 2 replicates; $n = 30$ sites). All the sites were subtidal, with depths of 20–40 cm at mean low tide. Distance between replicates and between vegetated and unvegetated habitats was determined by the spatial coverage of vegetation and extent of the habitat type (Table 1).

In the Great Bay–Little Egg Harbor estuary, the eelgrass sites were composed of extensive *Zostera* beds in Little Egg Harbor with isolated patches of unvegetated fine sand. The macroalgae sites, located in Great Bay were fine sand substrates with varying densities of unattached *Ulva lactuca* mats. The eelgrass and macroalgae sites were used in prior habitat comparisons (Wilson et al., 1990a,b; Sogard and Able, 1991). Both marsh creek sites were located on a salt marsh peninsula dividing Great Bay and Little Egg Harbor. In the Navesink River estuary, the eelgrass sites had discontinuous but small dense patches of *Zostera*, interrupted by areas of unvegetated medium-coarse sand. The macroalgae sites had extensive dense accumulations of drifting macroalgal mats, occasionally broken by areas of fine-medium coarse sand. The marsh creeks were located in small fringing salt marshes that may have been altered in the past. The eelgrass sites in the Hammonasset River estuary were continuous but sparsely covered areas with a silt-clay substrate. The macroalgae sites had patchy accumulations and drifting pieces of *Ulva lactuca* on a fine sand substrate. The marsh creek sites were surrounded by extensive salt marshes altered by mosquito control efforts (Fig. 1, Table 1).

2.2. Growth experiments

In this study, we used somatic growth of caged young-of-the-year winter flounder and tautog to quantify relative estuary and habitat related differences over two years. Both species are small, demersal and relatively sedentary. The open-bottomed cages (adapted from a design by Sogard, 1992) were constructed of a welded metal base unit, supporting wooden frame ($0.72 \times 0.72 \times 0.45$ m) and removable lid, all covered with stiff plastic 2-mm mesh. This mesh was small enough to retain the fish but large enough to allow passage of prey. A 15-cm metal strip was attached to the bottom frame allowing the cage to be set into the substrate, thus preventing escape of experimental animals and the expected penetration of the cage by burrowers from outside, i.e. blue crabs (*Callinectes sapidus*) and toadfish (*Opsanus tau*). When initially deployed, the cages were swept repeatedly with a tightly fitting bar seine (3-mm mesh) to remove potential competitors and predators. At the macroalgae sites, a known biomass of macroalgae, representative of the species and abundance of the surrounding area (Table 1) was added to each cage at the start of each experiment. While in the field, the external surfaces of the cages were cleaned regularly to remove any fouling organisms or vegetation.

In 1994, there were three experiments for each species, where experiment is defined as a complete temporal replicate of the entire spatial design (3 estuaries \times 5 habitats \times 2

replicate locations \times 3 cages; $n = 90$ cages). In 1995, the marsh creek sites were discontinued and the number of replicate cages increased by one ($n = 4$) in the remaining four replicated habitats. In 1995, there were two experiments of the spatial design for each species (3 estuaries \times 4 habitats \times 2 replicate locations \times 4 cages; $n = 96$ cages). Within each estuary the experiment start date coincided with the availability of each species in each estuary. Winter flounder and tautog were collected with a 1-m beam trawl or a beach seine from locations outside the cage areas (Tables 2 and 3) to eliminate impact on a concurrent related project designed to determine the distribution and abundance of local fish assemblages (Goldberg et al., 2000). In 1995, to determine whether the estuary of origin influenced growth rates, all the tautog used in experiments were collected in Connecticut before transfer to the three estuaries (Table 3). After capture and before deployment in cages, the fish were held at ambient seawater temperatures and salinities particular to each of the estuaries for 1–7 days and fed daily on frozen brine shrimp (*Artemia* sp.).

To follow growth of individuals each fish was marked subcutaneously with a nontoxic fluorescent material (Visible Implant Fluorescent Elastomer (VIE), Northwest Technologies Group) and anesthetized with MS-222 (3-aminobenzoic acid ethyl ester) prior to measuring and weighing except as noted in Table 2. Young-of-the-year winter flounder were marked on the unpigmented ventral surface and tautog were marked near the dorsal, ventral or caudal fins. Marked fish were measured (± 0.01 mm standard length, SL, for winter flounder; total length, TL, for tautog), weighed (± 0.001 g) except as noted in Table 2 and randomly assigned ($n = 3$ fish) to 0.95-l jars with mesh lids. The jars of three fish were placed in flow-through aquaria for approximately 6–18-h recovery periods before deployment. In the field, each cage received the contents of a randomly selected jar of three fish (1994: $n = 270$ fish [3 fish \times 90 cages]; 1995: $n = 288$ fish [3 fish \times 96 cages]). After 9–11 days, the fish were recovered from the cages with bar seines and transported to the laboratory for reweighing and remeasuring.

In July 1994, a separate experiment was performed to determine winter flounder mortality and rate of decomposition in marsh creeks. Six closed-bottom cages ($0.85 \times 0.85 \times 0.45$ m, Duffy-Anderson and Able, 1999), with three marked and measured winter flounder (22.5–36.2 mm) per cage, were deployed simultaneously with the open-bottomed cages in the second experiment in the Navesink River marsh creek and checked daily.

2.3. Physical characteristics

Water temperature, salinity and dissolved oxygen were recorded by dataloggers in the immediate sampling area of one of the eelgrass, macroalgae and marsh creek cages in each estuary when possible. There were no dataloggers placed in adjacent unvegetated habitats. In 1994, in Great Bay–Little Egg Harbor, Ryan Tempmentor recorders were used instead of dataloggers to record temperature. The dataloggers and tempmentors were deployed attached to concrete blocks and positioned near the sediment–water interface.

Table 2

Mean instantaneous daily growth rates in standard length ($\bar{x} G_{SL} \text{ day}^{-1}$) and mean somatic daily growth rates ($\bar{x} \text{ mm day}^{-1}$) of recovered winter flounder from cage experiments conducted in Great Bay–Little Egg Harbor (GB), the Navesink River (NR) and the Hammonasset River (HR) in 1994 and 1995^a

Year: Estuary experiment no.	Start of experiment (Date)	Experiment duration (days)	Temperature range (°C)	Initial size		Growth	
				Mean SL (mm) (range)	Mean wt (g) (range)	$\bar{x} G_{SL} \text{ day}^{-1}$	$\bar{x} \text{ mm day}^{-1}$
<i>1994</i>							
GB-1	June 3 ^{b,e,f}	10	16.7–29.5	16.0 (12.0–21.9)	NA	0.036	0.69
GB-2	June 14 ^{b,e,f}	10	16.2–34.3	19.6 (14.0–23.7)	NA	0.016	0.35
GB-3	June 28 ^b	9	17.1–34.5	34.9 (21.4–60.4)	0.92 (0.14–3.48)	0.005	0.15
NR-1	June 7 ^{c,e}	10	17.1–25.5	24.5 (16.5–31.2)	0.23 (0.06–0.45)	0.017	0.45
NR-2	June 21 ^c	10	20.8–27.1	26.0 (16.5–31.3)	0.27 (0.06–0.47)	0.015	0.43
NR-3	July 5 ^c	10	23.2–29.2	32.0 (24.0–41.2)	0.48 (0.15–1.17)	0.003	0.10
HR-1	June 27 ^{d,e}	10	19.4–30.0	30.6 (21.0–43.9)	0.50 (0.15–1.21)	0.007	0.21

HR-2	July 7 ^d	11	19.9–28.0	37.2 (23.5–53.0)	0.95 (0.26–2.66)	0.001	0.03
HR-3	July 26 ^d	10	22.2–30.2	41.0 (29.9–51.4)	1.28 (0.36–3.42)	–0.001	–0.03
<i>1995</i>							
GB-4	June 2 ^b	10	19.5–26.1	24.4 (15.0–38.6)	0.28 (0.04–0.94)	0.018	0.46
GB-5	June 12 ^b	10	17.8–27.9	27.8 (18.4–42.8)	0.40 (0.09–1.33)	0.002	0.09
NR-4	May 26 ^c	10	16.2–29.7	23.6 (15.8–32.4)	0.21 (0.06–0.50)	0.025	0.68
NR-5	June 9 ^c	10	18.4–24.3	26.3 (18.7–33.2)	0.31 (0.10–0.55)	0.018	0.54
HR-4	June 2 ^d	11	14.4–23.6	31.2 (22.2–37.8)	0.48 (0.18–0.81)	0.006	0.19
HR-5	June 26 ^d	10	15.7–24.2	45.7 (32.9–55.6)	1.62 (0.59–2.89)	0.002	0.01

^a Mean initial standard length and weights, where available, of winter flounder are indicated for each estuary in each experiment and ranges of initial sizes are given in parentheses. In 1994, there were three experiments (3 estuaries × 5 habitats × 2 replicate location × 3 cages; $n=90$ cages). In 1995, there were two experiments (3 estuaries × 4 habitats × 2 replicate locations × 4 cages; $n=96$ cages).

^b Fish collected in Great Bay, NJ.

^c Fish collected in Sandy Hook Bay, NJ.

^d Fish collected in New Haven Harbor, CT.

^e Fish not marked.

^f Fish not anesthetized.

Table 3

Mean instantaneous daily growth rates in total length ($\bar{x} G_{TL} \text{ day}^{-1}$) and mean somatic daily growth rates ($\bar{x} \text{ mm day}^{-1}$) of recovered tautog from cage experiments conducted in Great Bay–Little Egg Harbor (GB), the Navesink River (NR) and the Hammonasset River (HR) in 1994 and 1995^a

Year: Estuary experiment no.	Start of experiment (date)	Experiment duration (days)	Temperature range (°C)	Initial size		Growth	
				Mean TL (mm) (range)	Mean wt (g) (range)	$\bar{x} G_{TL} \text{ day}^{-1}$	$\bar{x} \text{ mm day}^{-1}$
<i>1994</i>							
GB-1	August 5 ^b	10	16.5–28.7	33.6 (21.4–54.3)	0.45 (0.09–2.04)	0.011	0.49
GB-2	August 16 ^c	10	17.9–27.3	41.9 (27.1–61.0)	1.06 (0.21–3.20)	0.012	0.60
GB-3	August 30 ^b	9	16.7–31.2	43.2 (23.5–72.2)	1.32 (0.14–5.78)	0.002	0.12
NR-1	July 22 ^b	10	24.5–28.9	31.2 (26.0–38.5)	0.34 (0.18–0.70)	0.001	0.10
NR-2	August 5 ^b	10	20.8–27.1	36.5 (24.1–46.8)	0.62 (0.15–1.28)	0.005	0.25
NR-3	August 19 ^b	10	18.9–32.1	44.1 (29.6–56.0)	1.14 (0.30–2.37)	0.005	0.25
HR-1	August 26 ^d	11	14.9–24.6	34.8 (22.1–51.4)	0.59 (0.12–1.86)	0.010	0.45
HR-2	September 13 ^d	11	16.4–23.8	45.2 (29.9–66.6)	1.32 (0.30–4.32)	0.002	0.07

HR-3	September 24 ^d	9	15.2–20.5	46.6 (28.3–73.8)	1.45 (0.26–5.43)	–0.002	–0.10
<i>1995</i>							
GB-4	August 11 ^d	11	20.7–28.9	39.9 (26.1–60.5)	0.81 (0.13–2.64)	0.013	0.53
GB-5	August 25 ^d	11	17.8–27.9	41.4 (23.9–59.3)	0.89 (0.14–2.38)	0.012	0.50
NR-4	August 11 ^d	10	23.3–28.8	41.3 (27.0–56.0)	0.95 (0.22–2.32)	0.005	0.26
NR-5	August 25 ^d	10	21.8–26.2	45.1 (28.4–68.4)	1.26 (0.25–4.21)	0.003	0.14
HR-4	August 4 ^d	10	17.3–28.0	42.3 (26.0–60.3)	1.05 (0.21–3.03)	0.010	0.54
HR-5	August 17 ^d	11	17.1–27.6	49.3 (29.4–67.1)	1.80 (0.29–4.50)	0.008	0.38

^a Mean initial total length and weights of tautog are indicated for each estuary in each experiment and ranges of initial sizes are given in parentheses. In 1994, there were three experiments (3 estuaries×5 habitats×2 replicate locations×3 cages; $n=90$ cages). In 1995, there were two experiments (3 estuaries×4 habitats×2 replicate locations×4 cages; $n=96$ cages).

^b Fish collected in Sandy Hook Bay, NJ.

^c Fish collected in Great Bay–Little Egg Harbor, NJ.

^d Fish collected in New Haven Harbor, CT.

2.4. Statistical analysis

Growth of caged winter flounder and tautog was calculated as a daily (day^{-1}) instantaneous growth rate (G) using the formula:

$$G = \ln(m_1/m_0)/t$$

where m_0 and m_1 are the initial and final standard length (winter flounder) or total length (tautog) in millimeters (mm) or weight in grams (g) and t is the duration of the experiment in days (Ricker, 1975). Mean G ($\bar{x} G \text{ cage}^{-1}$) in each cage was calculated to ensure statistical independence (Hurlbert, 1984) and since the number of fish recovered from a cage varied, a Wilcoxon signed-rank test was first conducted to determine if growth was related to the density of fish in a cage. There were no significant differences ($P > 0.05$) in the G values from cages having different numbers of fish recovered and thus, all the cages were included in subsequent analyses. A similar result was determined earlier (Sogard, 1992). A significant difference ($P < 0.05$) between the lengths and weights of fish used in the successive experiments indicated that an analysis of covariance was needed for this analysis. A nested factorial analysis of covariance (ANCOVA) (PC-SAS v. 6.12; SAS, 1989) was used to compare differences in mean growth of caged fish for each species among the three estuaries, the five habitat types, replicate habitats, and experiments. Substantial differences in the experimental design between years (i.e. cage and habitat number) lead us to analyze the years separately. The ANCOVA model was run using estuary and habitat as fixed and crossed main effects and replicates nested within the interaction of estuary and habitat applied to the data. A type III sums of squares analysis was used with replicate nested within estuary*habitat as an error term. Residual analysis and normal probability plots showed the data to be distributed homogeneously and normally. The length covariate for winter flounder was more stable when defined as a quadratic term in the model, while for tautog the length covariate was most stable as a linear term. In a posteriori comparisons, we tested the null hypothesis (H_0) that least square means were the same. Comparison of growth rates between habitats and estuaries focused on length as the growth parameter because weight was not measured in all experiments.

3. Results

3.1. Physical conditions

The physical parameters measured were similar in the three estuarine study sites. Temperature ranges in the three estuaries exhibited seasonal fluctuations typical of Mid-Atlantic and southern New England estuaries (Tables 2 and 3). Temperature was lower in early June, at the start of the winter flounder experiments, peaking in mid-summer at the end of the winter flounder and at the start of the tautog experiments before beginning to decline. Despite slight differences in the start date for each estuary within an experiment, there were relatively small differences in temperature ranges

during comparable experimental periods across estuaries (Tables 2 and 3). In 1994, comparisons of mean temperatures among estuaries showed no significant differences during the winter flounder experiments. During the tautog experiments, the mean Hammonasset River temperatures were significantly lower ($P=0.001$ ANOVA) than the other estuaries (Table 3). In 1995, mean temperatures were significantly different ($P=0.002$ ANOVA) among the three estuaries during the winter flounder experiments with Great Bay–Little Egg Harbor being warmer than the Navesink River which in turn was warmer than the Hammonasset River (Table 2). In 1995, mean temperatures were not significantly different among the estuaries during the tautog experiments.

Comparisons of temperature and salinity across the habitats in the three estuaries over the two years showed no major differences (Table 1). Salinity in the Hammonasset and Navesink rivers tended to have larger fluctuations than in Great Bay–Little Egg Harbor. The habitats in Great Bay–Little Egg Harbor had the highest temperatures and largest ranges while those in the Hammonasset River had the lowest minimum temperatures. The only significant temperature differences among the habitats in the three estuaries was in Great Bay–Little Egg Harbor. At this location in 1994 during the tautog experiments, the eelgrass habitats were significantly warmer ($P=0.020$ ANOVA) than the marsh creeks and in 1995 during the winter flounder experiments, eelgrass was significantly warmer than macroalgae ($P=0.030$ ANOVA). Dissolved oxygen ranges in all the habitats were broad and concentrations were as low as 0.1 mg l^{-1} in the macroalgae habitats of the Navesink River and in the marsh creek habitats of all three estuaries (Table 1). When complete datalogger records of dissolved oxygen were available, several showed that dissolved oxygen fell below 2 mg l^{-1} for 19–28% of the deployment time, i.e. in marsh creek habitat in Great Bay–Little Egg Harbor (June 1994) and in macroalgae habitat in the Navesink River (July 1994). The most extended period ($>76\%$ of the deployment time) of low dissolved oxygen $<2 \text{ mg l}^{-1}$ was recorded in the macroalgae habitat in the Navesink River during the first tautog experiment (July 1994).

3.2. Recovery from cages

Recovery of caged fish from habitats within estuaries was highly variable ranging from 16.7 to 91.7% ($\bar{x}=60.3\%$) for winter flounder and 20.0% to 82.3% ($\bar{x}=52.1\%$) for tautog, and recovery was higher in 1995 than in 1994. Except for marsh creeks, this variability in recovery resulted primarily from physical damage to cages from storms, vandalism and burrowing bivalves (*Teredo* sp.). In the Navesink River, cages were also occasionally undermined by waves, blue crabs (*Callinectes sapidus*) and toadfish (*Opsanus tau*) despite preventative measures. Recovery from marsh creeks in all three estuaries in 1994 was low ($<20\%$ for winter flounder; $<30\%$ for tautog) although the cages were not damaged or disturbed. Winter flounder mortality tests in closed bottom cages in the Navesink River marsh creek showed that winter flounder died within 24 h of deployment and fish tissues were undetectable after 48 h, and this response occurred in similar tests in another estuary (Able et al., 1999). Since it was unlikely the fish had escaped and because extended periods of low oxygen ($<2 \text{ mg l}^{-1}$) were recorded in the marsh creeks, it is speculated that recovery was affected by hypoxia-induced mortality.

Because of poor recovery and poor growth of survivors of both species (see below), no experiments were conducted in the marsh creeks in 1995. Consequently, in other habitats when intact cages were recovered but not all fish recaptured the loss of fish was suspected to result from mortality. Mortality of tautog from the macroalgae sites in the Hammonasset River and Great Bay–Little Egg Harbor in 1994 did not appear related to any available physical data. In 1995, when all experimental tautog were collected from a single site in Connecticut, recovery was higher in the Hammonasset River (74.5%) than from the Navesink River (52.1%) or Great Bay–Little Egg Harbor (51.8%).

3.3. Winter flounder growth

Growth rates of young-of-the year winter flounder varied among individuals, experiments, habitats and estuaries. Over the two years of the study, individual instantaneous growth rates in standard length (G_{SL}) ranged from -0.020 to 0.057 day⁻¹, and changes in standard length ranged from -0.66 to 1.20 mm SL day⁻¹. In 1995 when weight information was available, individual growth rates in weight (G_{WT}) followed trends in length ranging from -0.030 to 0.219 day⁻¹ (-0.03 – 0.13 g day⁻¹). Mean growth rates based on mean changes in standard length of all fish recovered from each cage ($\bar{x} G_{SL}$ cage⁻¹) ranged from -0.001 to 0.036 day⁻¹ (-0.03 – 0.69 mm SL day⁻¹) (Table 2). The fastest mean growth rates of juvenile winter flounder were always recorded in the first experiment within an estuary each year and usually corresponded to the smallest mean fish size tested (Table 2).

The results of the nested factorial ANCOVA for 1994 and 1995 (Table 4) showed that the estuary*experiment and habitat*experiment interactions were always significant ($P < 0.001$) indicating a temporal effect on growth within the estuaries and habitats. Also in both years, the significant estuary*habitat interaction ($P < 0.05$) suggested that the pattern in growth among the habitats differed among the three estuaries. In 1994, the largest proportion of the variation was attributable to the estuary ($F = 12.04$) as opposed to habitat ($F = 1.04$). In 1995, portions of the variation were attributable to both estuary ($F = 7.84$) and habitat ($F = 5.14$) (Table 4).

Inter-estuarine pairwise comparisons across habitats in 1994 indicated that growth rates were generally higher in habitats in Great Bay–Little Egg Harbor than in the other two estuaries (Fig. 2a–d) except for marsh creeks habitats where there were no significant differences ($P \geq 0.05$) (Fig. 2e). When all habitats were combined, growth rates were significantly higher in Great Bay–Little Egg Harbor than in the Navesink River which were significantly higher than growth rates in the Hammonasset River in 1994 (Fig. 2f). In 1995, inter-estuarine results were different from those of the previous year (Fig. 2g–k). Young-of-the-year winter flounder generally grew faster in the Navesink River habitats (Fig. 2g,h,j) than in the other two estuaries except for macroalgae habitats where there were no significant differences ($P \geq 0.05$) (Fig. 2i). When all habitats were combined, growth rates were significantly higher in the Navesink River than in either Great Bay–Little Egg Harbor or the Hammonasset River, which were not significantly different from each other in 1995 (Fig. 2k).

Table 4

Results of the nested factorial ANCOVA on the mean instantaneous growth rates ($\bar{x} G_{SL}$ day⁻¹) of winter flounder recovered from cages in Great Bay–Little Egg Harbor (GB), the Navesink River (NR) and the Hammonasset River (HR) estuaries in 1994 and 1995^a

Source	df	MS	F	P
<i>1994</i>				
Estuary ^b	2	6.220	12.04	0.001
Habitat ^b	4	0.537	1.04	0.427
Estuary*Habitat ^b	8	1.553	3.01	0.042
Rep (Estuary*Habitat) ^c	12	0.516	2.09	0.001
Experiment ^c	2	7.055	39.66	0.0001
Estuary*Experiment ^c	4	6.154	34.60	0.0001
Habitat*Experiment ^c	8	0.563	3.17	0.002
Linear covariate ^c (Initial SL)	1	2.821	15.86	0.0001
Error	140	0.178		
<i>1995</i>				
Estuary ^b	2	2.447	7.84	0.007
Habitat ^b	3	1.605	5.14	0.016
Estuary*Habitat ^b	6	3.458	11.08	0.0003
Rep (Estuary*Habitat) ^c	12	0.312	2.08	0.021
Experiment ^c	1	2.790	18.62	0.0001
Estuary*Experiment ^c	2	4.684	31.25	0.0001
Habitat*Experiment ^c	3	0.835	5.57	0.001
Linear covariate ^c (Initial SL)	1	3.373	22.51	0.0001
Quadratic covariate ^c (Initial SL ²)	1	2.106	14.05	0.0003
Error	144	0.150		

^a Initial standard length (SL) was used as a linear covariate in 1994 and 1995 and as a quadratic covariate in 1995.

^b Rep (Estuary*Habitat) used as error term.

^c General model error term used.

In 1994, intra-estuarine pairwise comparisons among habitats indicated few habitat differences in growth (Fig. 3). In Great Bay–Little Egg Harbor, growth was significantly lower ($P < 0.05$) in marsh creeks compared with all habitats except eelgrass ($P = 0.08$). In the Navesink River, macroalgae, its adjacent unvegetated area and marsh creeks supported the lowest growth rates. In the Hammonasset River there were no significant differences ($P \geq 0.05$) in growth rates among habitats. In 1995, significant habitat differences were observed in the intra-estuarine comparisons (Fig. 3). In Great Bay–Little Egg Harbor, the highest growth rates were recorded in macroalgae and its adjacent unvegetated area while significantly lower ($P < 0.001$) growth was measured in eelgrass and its adjacent unvegetated area. In contrast, in the Navesink River, fish held in macroalgae habitat grew significantly slower ($P < 0.05$) than in the other three habitat types. As in 1994, there were no significant differences ($P \geq 0.05$) in winter flounder growth among any of the habitats in the Hammonasset River.

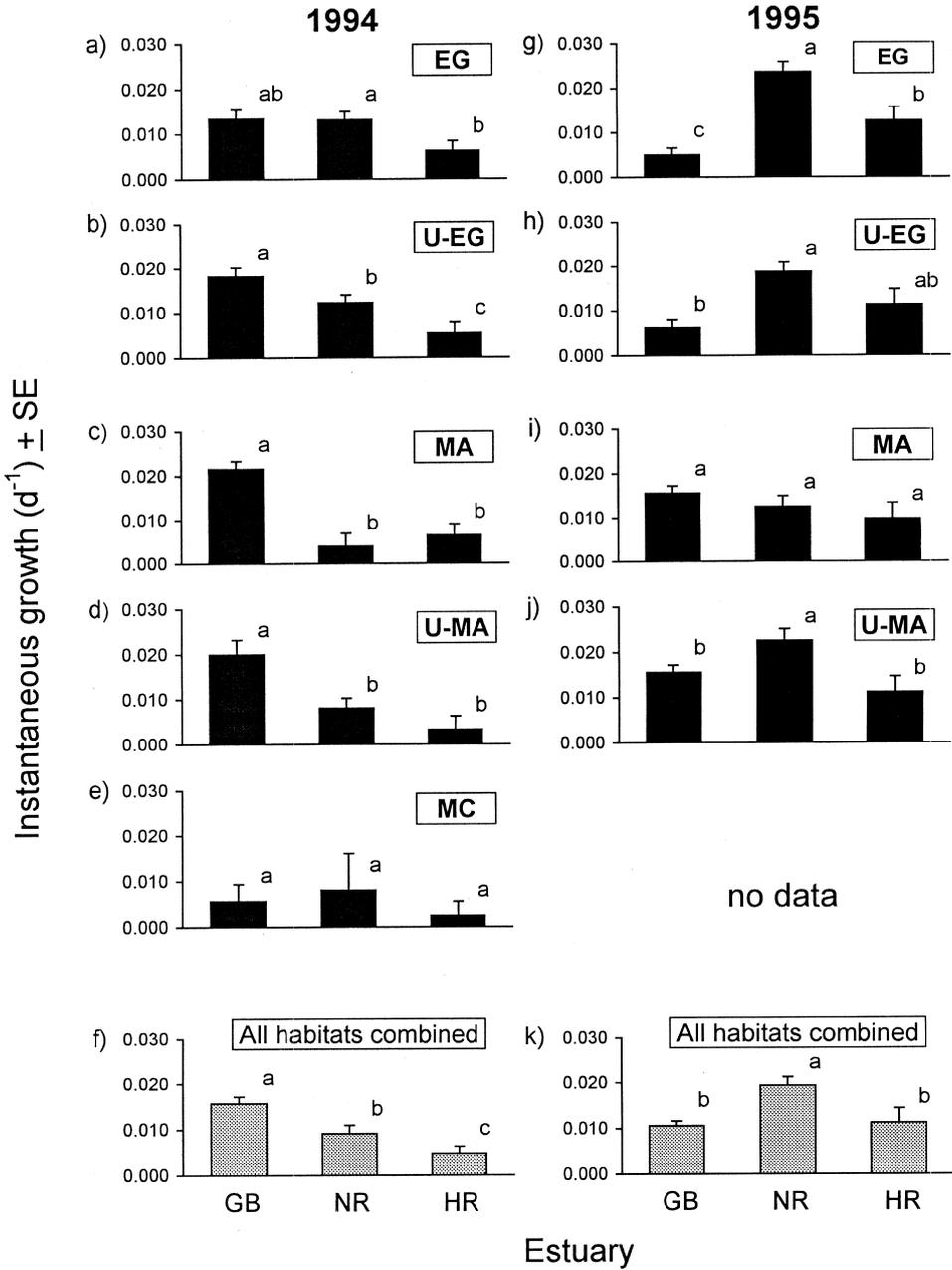


Fig. 2. Comparison of inter-estuarine instantaneous growth rates in length (least-square mean $G_{SL} \pm 1$ S.E.) of caged winter flounder in 1994 (a–f) and 1995 (g–k) in the three estuaries: Great Bay–Little Egg Harbor (GB), the Navesink River (NR), and the Hammonasset River (HR) in selected habitats (eelgrass (EG), unvegetated areas adjacent to eelgrass (U-EG), macroalgae (MA), unvegetated areas adjacent to macroalgae (U-MA), and marsh creeks (MC)). Panels f and k illustrate all the habitats combined. Estuaries which do not share a letter are statistically different ($P < 0.05$).

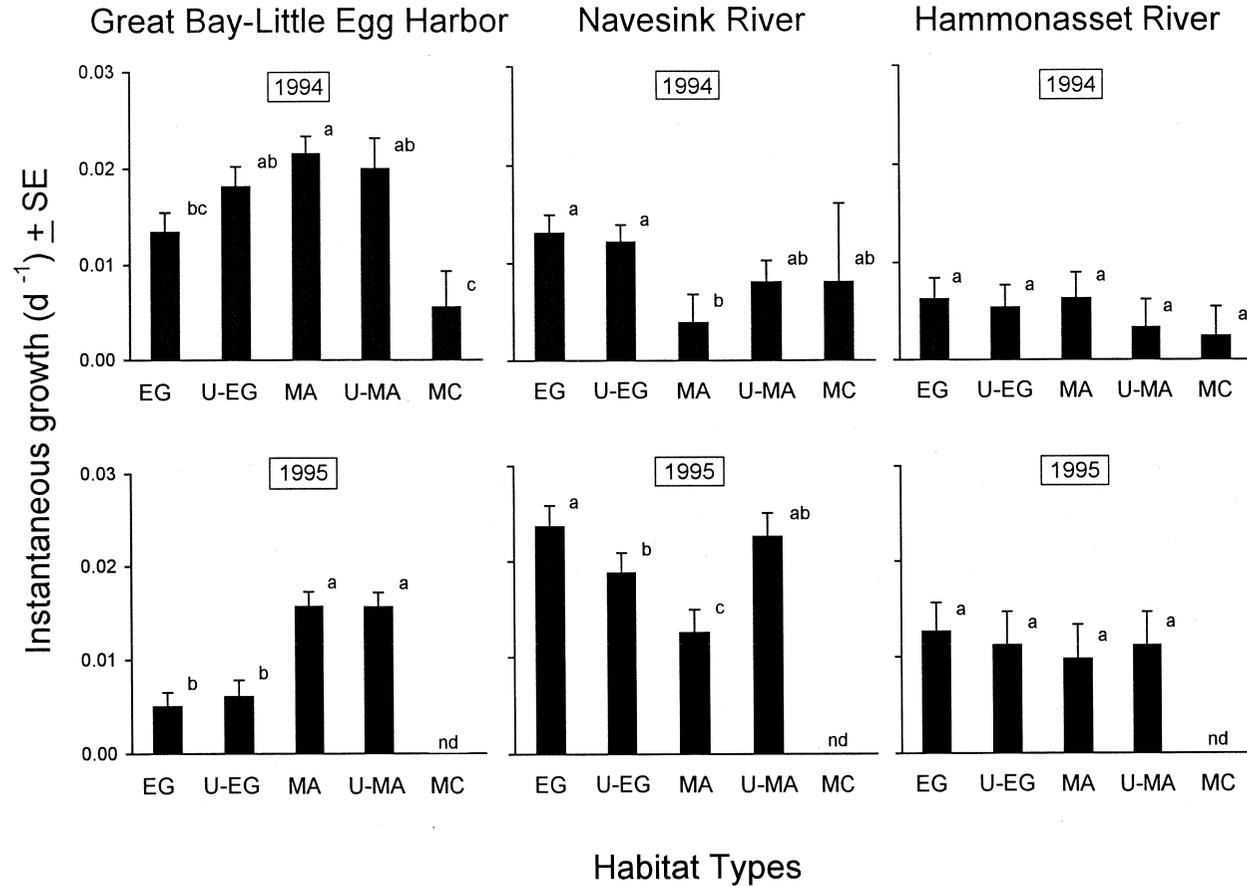


Fig. 3. Comparison of intra-estuarine instantaneous growth rates in length (least-square mean $G_{SL} \pm 1$ S.E.) of caged winter flounder in 1994 (upper panels) and 1995 (lower panels) in selected habitats (eelgrass (EG), unvegetated areas adjacent to eelgrass (U-EG), macroalgae (MA), unvegetated areas adjacent to macroalgae (U-MA), and marsh creeks (MC)) in the three estuaries: Great Bay–Little Egg Harbor (GB), the Navesink River (NR), and the Hammonasset River (HR). Habitats which do not share a letter are statistically different ($P < 0.05$).

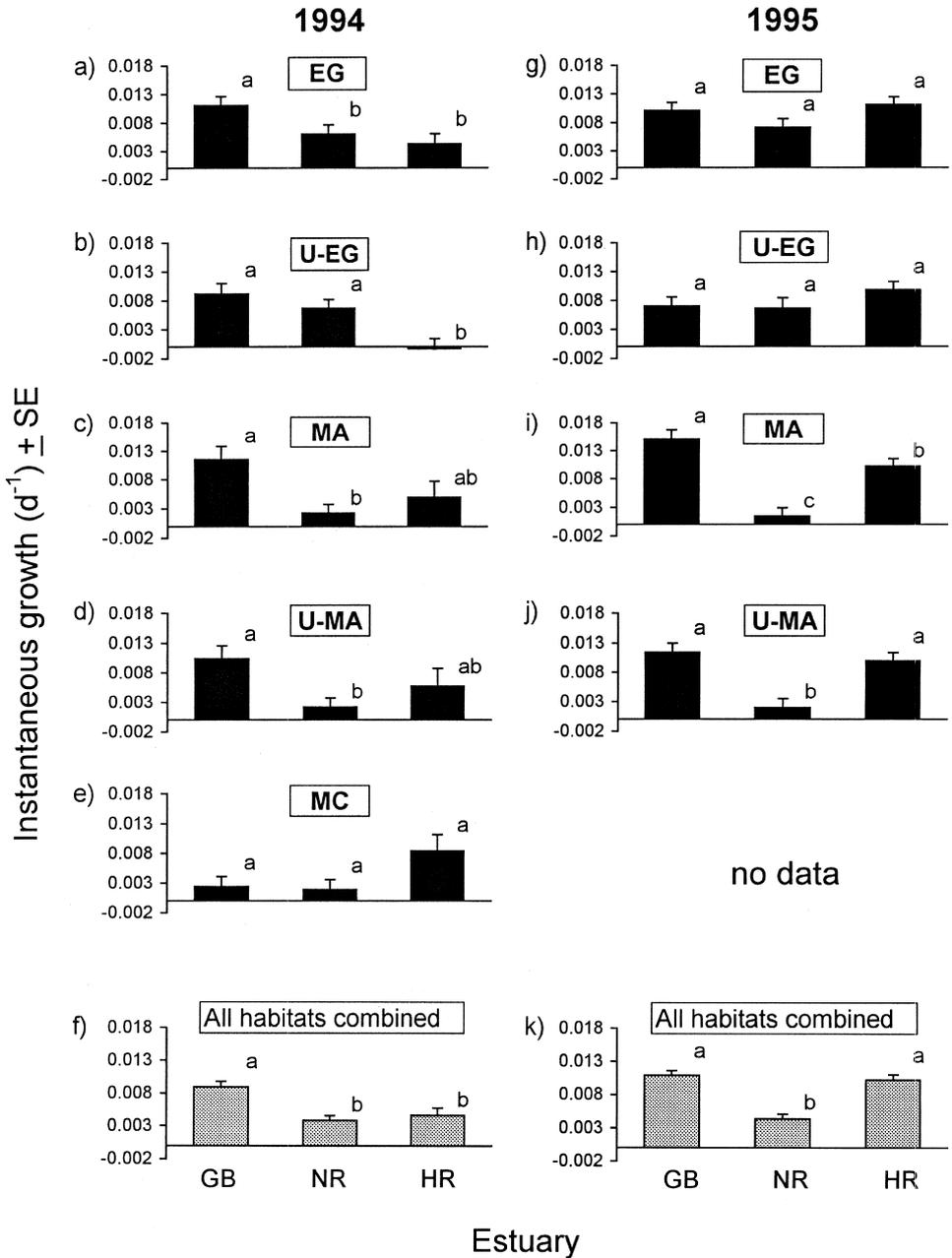


Fig. 4. Comparison of inter-estuarine instantaneous growth rates in length (least-square mean $G_{TL} \pm 1$ S.E.) of caged tautog in 1994 (a–f) and 1995 (g–k) in the three estuaries: Great Bay–Little Egg Harbor (GB), the Navesink River (NR), and the Hammonasset River (HR) in selected habitats (eelgrass (EG), unvegetated areas adjacent to eelgrass (U-EG), macroalgae (MA), unvegetated areas adjacent to macroalgae (U-MA), and marsh creeks (MC). Panels f and k illustrate all the habitats combined. Estuaries which do not share a letter are statistically different ($P < 0.05$).

3.4. *Tautog* growth

Similar to winter flounder, growth of young-of-the-year tautog varied among individuals, experiments, habitats and estuaries. Over the 2 years of the study, individual instantaneous growth rates in total length (G_{TL}) ranged from -0.020 to 0.033 day⁻¹ and changes in total length ranged from -0.42 to 1.18 mm TL day⁻¹. Individual growth rates in weight followed trends in length with G_{WT} ranging from -0.133 to 0.118 day⁻¹ (-0.09 – 0.20 g day⁻¹). Growth rates, based on the mean growth in total length of all tautog recovered from each cage ($\bar{x} G_{TL}$ cage⁻¹) ranged from -0.002 to 0.013 day⁻¹ (-0.10 – 0.60 mm TL day⁻¹) (Table 3). Also, as was characteristic of winter flounder, the highest growth rates were usually recorded in the first experiment within an estuary. There were two exceptions to this; the growth rates ($\bar{x} G_{TL}$ cage⁻¹) in the second experiment of 1994 in Great Bay–Little Egg Harbor and the Navesink River were slightly higher than during the first experiment which used smaller fish.

Results of the nested factorial ANCOVA showed that the covariate of total length was not significant ($P \geq 0.05$) in 1994 but was in 1995 ($P < 0.001$) (Table 5). In 1994, the interactions of estuary*experiment and habitat*experiment were significant ($P < 0.0001$)

Table 5

Results of the nested factorial ANCOVA on the instantaneous growth rates ($\bar{x} G_{TL}$ day⁻¹) of tautog recovered from cages in Great Bay–Little Egg Harbor (GB), the Navesink River (NR) and the Hammonasset River (HR) estuaries in 1994 and 1995^a

Source	df	MS	F	p
<i>1994</i>				
Estuary ^b	2	4.069	10.93	0.001
Habitat ^b	4	0.380	1.02	0.429
Estuary**Habitat ^b	8	1.221	3.28	0.023
Rep (Estuary*Habitat) ^c	15	0.372	2.29	0.006
Experiment ^c	2	4.521	27.87	0.0001
Estuary*Experiment ^c	4	4.556	28.08	0.0001
Habitat*Experiment ^c	8	0.923	5.69	0.0001
Error	138	0.162		
<i>1995</i>				
Estuary ^b	2	3.690	13.48	0.0009
Habitat ^b	3	0.257	0.94	0.452
Estuary*Habitat ^b	6	0.984	3.60	0.028
Rep (Estuary*Habitat) ^c	12	0.274	1.66	0.083
Experiment ^c	1	0.091	0.55	0.459
Estuary*Experiment ^c	2	0.557	3.38	0.037
Habitat*Experiment ^c	3	0.402	2.44	0.067
Linear covariate ^c (Initial TL)	1	11.766	71.44	0.0001
Linear covariate ^c Estuary ^c	2	2.227	13.53	0.0001
Error	128	0.165		

^a Initial total length (ITL) was used as a linear covariate in 1995 but was not significant in 1994.

^b Rep (Estuary*Habitat) used as error term.

^c General model error term used.

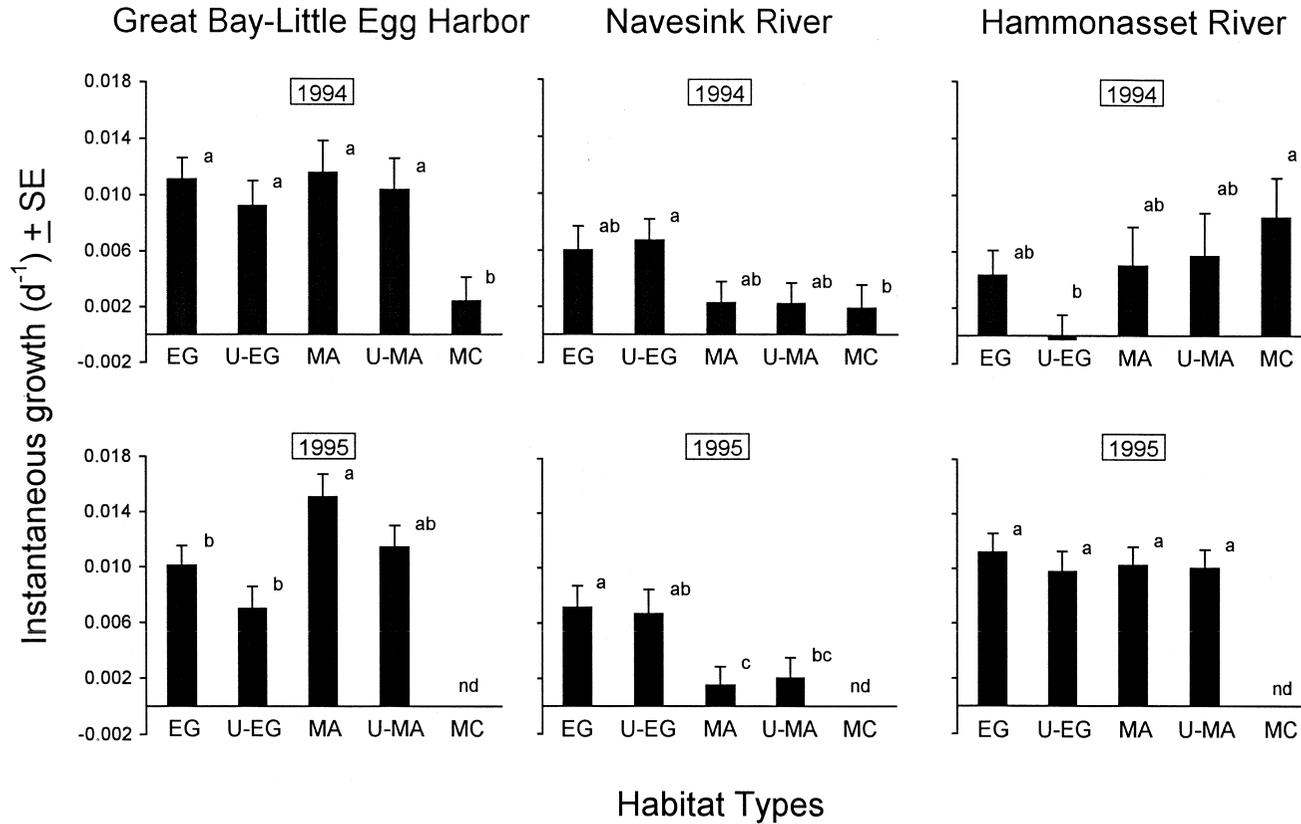


Fig. 5. Comparison of intra-estuarine instantaneous growth rates in length (least square mean $G_{TL} \pm 1$ SE) of caged tautog in 1994 (upper panels) and 1995 (lower panels) in selected habitats (eelgrass (EG), unvegetated areas adjacent to eelgrass (U-EG), macroalgae (MA), unvegetated areas adjacent to macroalgae (U-MA) and marsh creeks (MC) in the three estuaries: Great Bay-Little Egg Harbor (GB), the Navesink River (NR) and the Hammonasset River (HR). Habitats which do not share a letter are statistically different ($P < 0.05$).

indicating a temporal effect on growth. In 1995, while estuary*experiment was significant ($P=0.037$), the habitat*experiment interaction was not significant ($P=0.067$) perhaps due to a decrease in the number of experiments thereby reducing the probability of detecting significant differences. In both years, however, the estuary*habitat interaction was significant ($P<0.05$) indicating that the patterns in growth among the habitats differed among the three estuaries. As was seen for winter flounder in 1994, the largest amount of variation was attributable to estuary ($F=10.93$ [1994], 13.48 [1995]) as opposed to habitat ($F=1.02$ [1994], 0.94 [1995]).

Inter-estuarine pairwise comparisons across habitats in 1994 indicated that like winter flounder, tautog growth rates were generally higher in Great Bay–Little Egg Harbor than in the Navesink River or Hammonasset River (Fig. 4a–d) except for marsh creeks (Fig. 4e) where there were no significant differences ($P\geq 0.05$). In macroalgae and its adjacent unvegetated habitat, growth rates were significantly lower ($P<0.05$) in the Navesink River than in Great Bay–Little Egg Harbor while Hammonasset River fish grew at intermediate rates (Fig. 4c,d). In 1995, the general pattern was similar to the previous year (Fig. 4i,j) but there were no significant differences ($P\geq 0.05$) in growth rates among eelgrass habitats and its adjacent unvegetated sites across the three estuaries (Fig. 4g,h). When all habitats were combined, growth rates in 1994 and 1995 were significantly higher in Great Bay–Little Egg Harbor than in the Navesink River. Growth rates in the Hammonasset River were similar to those in the Navesink River in 1994 but were more similar to Great Bay–Little Egg Harbor in 1995 (Fig. 4f,k).

In 1994, intra-estuarine pairwise comparisons among habitats indicated that there were few significant differences in growth (Fig. 5). In Great Bay–Little Egg Harbor and the Navesink River tautog growth rates were lowest in marsh creeks ($P<0.05$) in contrast to the Hammonasset River, where tautog growth rates were highest in marsh creeks. In 1995, there were no significant differences ($P\geq 0.05$) in growth rates among any of the Hammonasset River habitats. In the Navesink River, the highest growth rate was in eelgrass habitat and the lowest in macroalgae habitat ($P<0.05$). In Great Bay–Little Egg Harbor growth rates were significantly ($P<0.05$) higher in macroalgae than in eelgrass and its adjacent unvegetated sites (Fig. 5).

4. Discussion

4.1. Artifacts of caging

Cages are a valuable tool for comparing the relative growth of small juvenile fish in different habitats but are also known to have certain limitations (Peterson and Black, 1994; Able, 1999). Cages confine fish to a small space, preventing movements to surrounding areas i.e. for food searching or to avoid areas of poor water quality. In general, this may be less of an issue for the target species in this study. Juvenile winter flounder are reported to make relatively limited movements (<100 m) from summer nursery habitats (Saucerman and Deegan, 1991), and tag–recapture studies (Able and Fahay, 1998) have shown that juvenile tautog have strong site fidelity associated with structure (Dixon, 1994). Yet, cage confinement probably had a negative affect on fish

held in the marsh creek cages and some Navesink River macroalgae cages. Low recovery rates indicated poor survival and low growth rates of surviving fish implied a negative habitat effect probably due to extended periods of low dissolved oxygen ($<2 \text{ mg l}^{-1}$). Avoidance of low oxygen has been described for a number of fish species (Bejda et al., 1987; Kramer, 1987; Pihl et al., 1991; Breitbart, 1992, 1994) but studies in western Long Island Sound indicated that smaller winter flounder seem to remain in certain habitats even when exposed to stressful low oxygen conditions (Howell and Simpson, 1994). Cages can also potentially affect food availability by filtering or concentrating prey, however, in an earlier study (Sogard, 1992) there was no consistent relationship between prey densities and growth in cages and food limitation was also not detected in a caging study using southern flounder (*Paralichthys lethostigma*) (Kamer-mans et al., 1995). Others (Sogard, 1992; Duffy-Anderson and Able, 1999; Able et al., 1999) have found that cage confinement did not seem to alter growth of either winter flounder or tautog relative to wild populations. Somatic growth rates in cages for winter flounder and tautog have been found comparable to those under natural conditions (Sogard, 1992) and to those estimated from otolith increment widths (winter flounder; Sogard and Able, 1992) and increment counts (tautog; Sogard et al., 1992). Caging experiments therefore, can provide a useful measure of relative differences in growth of winter flounder and tautog.

4.2. Inter-estuarine comparisons

Estuary and habitat effects interacted and influenced somatic growth rates of caged young-of-the-year winter flounder and tautog, however these effects were not the same among the estuaries or habitats studied and they varied between years. Overall, we found a large part of the variability in growth rates of both species attributable to the estuary in which the fish grew, especially in 1994 when habitat effects were few. Further, in the 1995 tautog experiments a significant difference in growth rates among estuaries was demonstrated despite having an identical source of experimental animals. Differences in estuarine growth rates also varied interannually among the study estuaries. Winter flounder growth rates in 1994 were significantly higher in southern New Jersey (Great Bay–Little Egg Harbor) but in 1995 were significantly higher in northern New Jersey (Navesink River). Interannual variability in juvenile winter flounder growth was first documented for winter flounder in a Connecticut estuary (Pearcy, 1962).

Significant differences in the average temperatures among the estuaries was probably the cause of some of the variation in somatic growth rates of winter flounder among estuaries and between years. Great Bay–Little Egg Harbor temperatures were significantly warmer in 1995 and since winter flounder is near the southern limit of its range (Bigelow and Schroeder, 1953) the warmer temperatures could have resulted in lower growth rates. Temperature effects were considered a potential factor in an earlier study of winter flounder growth conducted in Great Bay–Little Egg Harbor (Sogard, 1992). In addition, variation in growth rates between European flatfish nurseries areas was most frequently explained in terms of temperature differences (Gibson, 1994). Temperature could also have been related to a significant difference in tautog growth

rates among the estuaries in 1994. Significantly lower tautog growth rates occurred in the Hammonasset River when average estuarine temperatures were significantly lower compared to the two estuaries in New Jersey. Other studies suggest that tautog growth rates are generally higher in southern locations, where seawater temperatures are warmer and there is an extended summer season (Sogard et al., 1992; Hostetter and Munroe, 1993). Estuarine differences in juvenile winter flounder growth have also been demonstrated with otolith microstructure analysis among four New Jersey coastal sites (including Great Bay–Little Egg Harbor) (Sogard and Able, 1992).

Winter flounder and tautog had consistently higher growth rates in specific but different habitat types in the two New Jersey estuaries. In both years of this study, Great Bay–Little Egg Harbor tended to have higher winter flounder and tautog growth rates in macroalgae and its adjacent unvegetated areas while in the Navesink River significantly higher winter flounder and tautog growth rates occurred in eelgrass and its adjacent unvegetated areas. Potential factors causing these habitat related differences are discussed in the next section. In a related study, another measure of growth (RNA) based on these same species and specimens showed similar differences in growth of winter flounder and tautog among years, estuaries and habitats (Kuropat et al., unpubl. data).

4.3. *Intra-estuarine comparisons*

Winter flounder and tautog growth rates often varied among the habitats within an estuary and between years but were also somewhat consistent in that, the habitats with the highest growth were the same in both years of the study. In the two New Jersey estuaries, significant habitat-related differences in growth rates occurred in 1995, but few differences were present in 1994. The Hammonasset River rarely had a significant habitat-related difference which might have been due to the close proximity of the habitats. Yet, similar distances between habitats occurred in the Navesink River and relative differences in growth were still detectable. Distance between habitat types may also have been a factor in differences in fish growth between Great Bay and Little Egg Harbor. Located in different embayments and separated by a narrow peninsula, fish may have been exposed to sufficiently different environmental conditions to affect their growth. Yet, both caging locations are located within the same watershed and share a number of similar characteristics (Able et al., 1996). Differences in winter flounder and tautog growth in cages have been shown to occur over distances of only 20 m along a transitional zone that passed under a pier, the pier edge and beyond pier habitats in the Hudson River (Duffy-Anderson and Able, 1999).

Physical parameters (i.e. temperature, dissolved oxygen) at each site are likely the potential factors causing the relative differences detected in growth rates. Significantly higher growth rates for winter flounder and tautog in Great Bay–Little Egg Harbor usually occurred in macroalgae habitats and its adjacent unvegetated habitats compared to the other habitats. In contrast, significantly higher temperatures measured in the eelgrass habitats could have been detrimental to winter flounder growth rates. Juvenile winter flounder are known to avoid high water temperatures (Bigelow and Schroeder, 1953; Percy, 1962). A similar pattern of higher growth for both species in macroalgae habitats and lower growth for winter flounder due to elevated temperatures was seen in

an earlier study (Sogard, 1992) indicating consistency in the relative quality of the Great Bay–Little Egg Harbor sites despite a number of years between the two studies.

The presence or absence of vegetation appeared significant to growth rates only in macroalgae sites in the Navesink River where extremely low dissolved oxygen ($<2 \text{ mg l}^{-1}$) appeared to be the significant factor. In contrast, significantly higher growth rates of winter flounder and tautog in the Navesink River usually occurred in eelgrass and its adjacent unvegetated areas. Dense macroalgae ($366.3 \text{ g dw m}^{-2}$) caused extreme diel fluctuations in dissolved oxygen levels that at times resulted in hypoxic conditions ($<2 \text{ mg l}^{-1}$) known to affect the growth of YOY winter flounder (Bejda et al., 1992) and YOY black sea bass (*Centropristis striata*) (Hales and Able, 1995). Physiologically limiting oxygen concentrations vary among fish species but generally range from 1 to 3 mg l^{-1} (Neill et al., 1994). Behavioral changes in activity (i.e. increased respiration, decreased feeding) associated with low oxygen conditions would have expended metabolic energy eventually lowering growth rates (Kramer, 1987). The effects of macroalgae therefore, seem to be estuarine specific and are related to its density. As a result, habitat quality based on fish growth, was high in low density macroalgae in Great Bay–Little Egg Harbor, but low where it was dense in the Navesink River.

4.4. Factors affecting fish growth

Growth of flatfishes and other juvenile fishes is affected by a number of factors in the nursery habitat. The major factors known to contribute to habitat quality are temperature, oxygen, salinity, predators, water depth, food, habitat structure and hydrodynamics (Gibson, 1994; Van der Veer et al., 1994). Temperature and oxygen have already been discussed as important parameters in observed estuarine and habitat-related differences in winter flounder and tautog growth rates. Salinity, which did not vary significantly among estuaries, did not seem related to any observed differences in growth for either species, which have a wide range of salinity tolerances (Bigelow and Schroeder, 1953; Pearcy, 1962). In our study, cages were designed to exclude predators and depth was controlled by placing cages just within the shallow subtidal zone in all estuaries.

Food quality and quantity is considered a critical limiting factor in flatfish growth (Neill et al., 1994; Van der Veer et al., 1994) and may be an element in estuarine and habitat-related differences in growth (Gibson, 1994). Small juvenile winter flounder and tautog eat primarily copepods and amphipods and polychaetes (Pearcy, 1962, Richards, 1963; Grover, 1982). Prey density data were not collected in our study, but Sogard (1992) found that winter flounder cage growth did not appear to be related to prey densities inside field cages although tautog may have been influenced by prey densities.

Flatfish growth has also been associated with sediment type. In a concurrent study (Goldberg et al., 2000), high total organic carbon and silt/clay were found in the Hammonasset River eelgrass sites but growth in these sites did not significantly differ from other sites in the Hammonasset River. A relationship between winter flounder growth and coarser sediments was noted in one study (Sogard, 1992), but lower growth has also been found in habitats with silt/clay sediment and high total organic carbon (Saucerman, 1990).

Some environmental conditions can have an indirect effect on growth. Tissues from

winter flounder and tautog caged in our study in 1994 and analyzed for stable isotopes demonstrated lower nitrogen isotope values ($\delta^{15}\text{N}$) in Great Bay–Little Egg Harbor, indicating a lower input of anthropogenic nitrogen, than in either the Navesink and Hammonasset estuaries (Litvin et al., unpubl. data). Anthropogenic nitrogen entering from sewage or non-point runoff would increase nutrient loading in estuarine systems and potentially favor rapid growth of macroalgae (Lavery et al., 1991) and thus negatively effect dissolved oxygen levels, indirectly causing negative effects in growth that could differ between estuaries. Hydrodynamic conditions can also indirectly promote changes in temperature and low dissolved oxygen (Gibson, 1994). Further, both hydrodynamics and nutrients can vary over time within a habitat and estuary. Man-made piers in the highly impacted Hudson River estuary (Able et al., 1999) significantly decreased growth in cages for both winter flounder and tautog compared to nearby open-water habitats in part due to decreased light levels affecting feeding success (Duffy-Anderson and Able, 1999). Thus, winter flounder and tautog growth apparently responds to interacting estuarine and habitat-related factors.

Recent interest in essential fish habitat as a result of amendments in the Magnuson–Stevens Fishery Conservation and Management Act (NOAA, 1996) has inspired attempts to identify, classify and define essential fish habitat by easily described physical structure. Essential fish habitat and critical nursery habitat designations may not be readily defined by current knowledge for many species, including winter flounder and tautog. In this study, nominal habitat classifications were not adequate predictors of habitat quality in different estuaries where a variety of biotic and abiotic factors may affect juvenile fish growth. A more comprehensive approach requires more extensive, long-term comparative studies of habitat use and a better understanding of subtidal habitats and the habitat specific-behavior of juvenile fish (Able, 1999).

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