Spatial dynamics of habitat suitability for the growth of newly settled winter flounder *Pseudopleuronectes americanus* in an estuarine nursery

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ABSTRACT: The relationship between the growth of early juvenile winter flounder (*Psuedopleuronectes americanus*, Walbaum; 17 to 27 mm standard length [SL]) and the spatial dynamics of estuarine gradients immediately following larval settlement was examined using field enclosure techniques in a temperate nursery. Enclosures (n = 60; 3 fish per enclosure) were deployed throughout the Navesink River/Sandy Hook Bay estuarine system, New Jersey, in a nested spatial design that allowed measurement of growth variation in time at 3 spatial scales (between regions: $\bar{x}$distance [D] = 12.3 km, SD = 3.6, n = 2; between sectors: $\bar{x}$D = 4.3 km, SD = 1.3, n = 6; between stations: $\bar{x}$D = 1.8 km, SD = 0.8, n = 12). Three 12 d enclosure experiments were performed over 40 consecutive days from mid-May through June 1999. Flounder growth (range = 0 to 0.9 mm SL d^{-1} enclosure^{-1}) was dynamic at a regional spatial scale. Generalized additive modeling indicated that growth was most rapid at relatively cool temperatures (<21°C) and low salinities (<24‰). However, spatial analysis of partial growth indicated that the relative influences of temperature and salinity changed over time. Salinity effects were strongest during the earliest experiment (May 20 to June 1) when temperatures were cool (<20°C) throughout the estuary. During this period, salinities were conducive for rapid growth throughout the river. From June 4 to 16, salinities remained optimal in the river, but as the system warmed, temperatures conducive for rapid growth contracted into the bay and temperature effects became stronger than salinity effects. Growth was more rapid in the bay, but not as high as that measured during the first experiment in the river where optimal salinities and temperatures overlapped within the estuary. With continued warming and curtailed freshwater runoff, temperatures were sub-optimal throughout the estuary, salinities were conducive for rapid growth only in the upper river, and from June 18 to 30 growth rates were relatively low. Our analysis suggests that habitat suitability for the growth of juvenile fish can be spatially dynamic because multiple regulatory factors vary simultaneously in space and time. Rapid growth occurs at sites and times when optimal conditions for regulatory factors intersect in space, but the spatial coincidence of optimal conditions can be ephemeral.

KEY WORDS: Essential fish habitat · Dynamic habitat · Spatial scale · Winter flounder · *Pleuronectes americanus*

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INTRODUCTION

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It is generally assumed that there is a positive relationship between the size of demersal fish populations and the availability of habitats promoting the growth and survivorship of critical early life history stages

(MacCall 1990, Rijnsdorp et al. 1992, Gibson 1994, 1997, Langton et al. 1996, Petitgas 1998, Ault et al. 1999, Nash & Geffen 2000, van der Veer et al. 2000a,b). Rapid growth is particularly important for newly settled fish which can suffer high mortality rates that typically vary inversely with body size (Victor 1986, Tanaka et al. 1989, Beverton & Iles 1992, Gibson et al. 1995, Sogard 1997, Schmitt & Holbrook 1999, Shima 2000). As a result, variation in the suitability of nursery habitats for early juvenile growth can strongly influence patterns of post-settlement survivorship.

Temperate nearshore areas serve as nurseries for a number of demersal fish species (Able & Fahay 1998). Within these systems, physical and biological factors that regulate the growth of fishes (e.g. temperature, salinity, dissolved oxygen, prey availability) vary substantially in space and time, particularly during periods of seasonal transition. Winter flounder *Pseudopleuronectes americanus* is a northwest Atlantic flatfish that uses estuaries as spawning and nursery grounds over much of its species range (Labrador to Georgia; Bigelow & Schroeder 1953). In the mid-Atlantic region, adults spawn during the winter and early spring. Pelagic larvae are retained within estuaries (Crawford & Kerrey 1985, Keller et al. 1999) and settle as benthic juveniles during the spring and early summer (April through June; Witting 1995, Sogard et al. 2001). Because environmental factors likely to regulate growth are highly variable during the winter flounder settlement period, patterns of habitat suitability for newly settled juveniles may also be dynamic. Previous studies show that growth rates of juvenile winter flounder vary over short periods of time at relatively coarse spatial scales (5 to 700 km, among estuaries, coastal ponds, embayments) and are not well explained by fine scale variability in natural habitat structure (e.g. vegetated beds, bare substratum; Sogard 1992, Meng et al. 2000, 2001, Phelan et al. 2000). While these studies suggest that habitat suitability for winter flounder growth is spatially dynamic, the relationship between early juvenile growth and the dynamics of important environmental factors within estuaries has not been studied.

In this study, enclosures were deployed throughout a winter flounder nursery ground to examine the relationship between the growth of recently settled fish and the dynamics of estuarine gradients over a 40 d period following larval settlement. We used a nested design to identify the spatial scale at which growth was most variable and to test the null hypothesis that growth rates were consistent in space and time. We then used generalized additive modeling to identify environmental variation related to the growth pattern. Finally, the growth model and maps of important environmental variables were used to describe the spatial dynamics of habitat suitability for growth.

MATERIALS AND METHODS

Study area and study design. A nested design was used to examine variability in recently settled winter flounder growth and its relationship to habitat heterogeneity in the Navesink River/Sandy Hook Bay estuarine system (NSHES), New Jersey (Fig. 1), a known spawning and nursery ground for the species (Scarlett 1991, Phelan 1992, Stoner et al. 1999, 2001, Sogard et al. 2001). The system is relatively small (3868 ha) with features typical of many riverine estuaries in the mid-
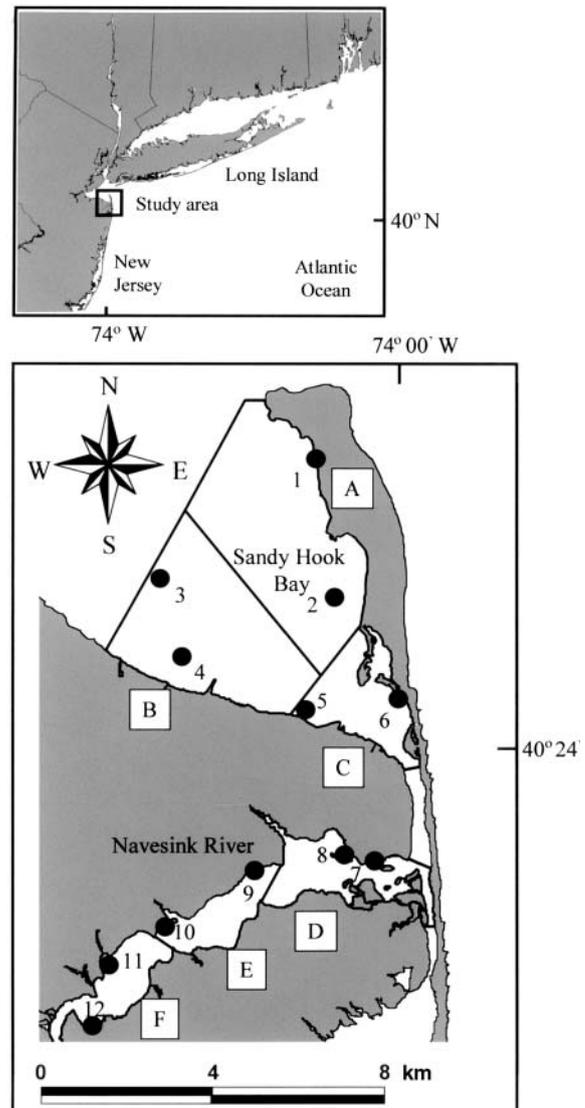

Fig. 1. Location of the study area on the mid-Atlantic coast of the United States (upper panel) and of the 12 stations in the Navesink River/Sandy Hook Bay estuarine system (NSHES, lower panel), New Jersey where the winter flounder growth experiments were performed. The study area was partitioned so that 3 sectors were nested within the bay (Sectors A, B and C) and river (Sectors D, E and F) regions

Atlantic region. Bottom water temperatures in the study area can exceed 30°C in the Navesink river during the summer and fall below 0°C during winter when the entire system can be covered with ice. The mean tidal range is 1.4 m. Because freshwater discharge into the study area is generally low (~2 m^3 s^{-1}; Chant & Stoner 2001), salinity variations associated with daily tidal cycles are small, ranging from a median of just 1.2‰ near the tip of the Sandy Hook peninsula to 2.3‰ in the western part of the Navesink.

The study area was partitioned into 6 sectors based on the spatial structure of environmental gradients strongly related to changes in fish and macro-invertebrate community structure (Manderson et al. 1997). A gradient defined by salinity and depth oriented along the downstream axis, and a gradient of sediment characteristics were used to delineate the sectors. Sectors A and B were located in Sandy Hook Bay, in deep, high salinity areas with generally fine sand and silty substrata (Fig. 1). Sediments are typically finer in Sector B than Sector A which contains the main navigational channel to the Atlantic Ocean. Substrata were also fine sands and silts in Sectors E and F, located in shallow, lower salinity areas of the Navesink River. The primary freshwater source for the river drains into Sector F which generally has lower salinities than Sector E. Networks of shallow sandbars and deep channels with high velocity tidal currents are characteristic of Sectors C in the bay and D in the river where sediments are coarse and medium sands. Three Sectors were located within each of 2 regions; the bay (Sectors A, B and C) and the river (Sectors D, E and F; Fig. 1).

Within each sector, 2 stations were randomly selected from transects used in large scale synoptic surveys of the system (Fig. 1; Stehlik & Meise 2000, Stoner et al. 2001). Five replicate enclosures were deployed at each of 12 stations for the growth experiments. This hierarchical design allowed us to examine growth variability in time and at 3 spatial scales; among regions ($\bar{x}$distance [D] = 12.3 km, SD = 3.6), among sectors within regions ($\bar{x}$D = 4.3 km, SD = 1.3) and among stations within sectors within regions ($\bar{x}$D = 1.8 km, SD = 0.8).

Enclosure techniques. *In situ* somatic growth rates of winter flounder were measured with enclosure techniques used in previous studies of habitat-specific growth for small demersal fishes (Sogard 1992, Guindon & Miller 1995, Able et al. 1999, Duffy-Anderson & Able 1999, Phelan et al. 2000, Spitzer et al. 2000). The enclosures were constructed of 3 mm nylon mesh bags (0.75 × 0.75 × 0.40 m) with zippered tops that were

Table 1. Details of the winter flounder growth experiments conducted in the Navesink River/Sandy Hook Bay estuarine system (NSHES) in 1999. During each experiment, 3 fish were contained within each of 5 enclosures deployed at each station (n = 12) (3 fish × 5 enclosures × 12 stations = 180 fish per experiment)

Experiment dates	Initial standard length (mm) Mean (range)	Number recovered after 12 d Enclosures	Fish
May 20 to Jun 1	22.4 (16.6–27.7)	55	147
Jun 4 to Jun 16	20.1 (16.5–24.8)	55	125
Jun 18 to Jun 30	23.5 (16.8–28.2)	56	123

tightly secured within rectangular steel reinforcing bar frames (0.85 × 0.85 × 0.45 m). The design retained fish but allowed sediment and prey to enter enclosures deployed on the substratum.

Similarly sized early juvenile flounder were used in all experiments ($\bar{x}$ = 22 mm standard length [SL], Range = 17 to 28; Table 1) to control for size-dependent growth variability (Sogard 1992, van der Veer et al. 1994). Fish were seined in the NSHES, transported to the James J. Howard Marine Sciences Laboratory, Highlands, New Jersey, and maintained <7 d in flow through aquaria supplied with ambient seawater from Sandy Hook Bay (temperature = 15.5 to 18.3°C, salinity = 20.3 to 25.2‰). The fish were fed live brine shrimp (*Artemia* sp.) *ad libitum* during the holding period.

Three 12 d experiments were conducted from May 20 to June 30, 1999 (Table 1). Before the start of each experiment, fish (n = 180) were marked 1 of 3 colors with subcutaneous injections of nontoxic acrylic paint (Createx). Marked fish were provided with a 24 h recovery period and measured for standard length (±0.1 mm). Groups of 3 uniquely marked and measured fish were placed in 1 l jars with mesh covers within aquaria without food for an additional 18 h period.

The fish were transported to the field in the jars within coolers filled with aerated seawater. Three fish from a randomly selected jar were placed in each enclosure which was then lowered to the substratum. Thus, 180 fish were deployed in each experiment (12 stations × 5 enclosures × 3 fish). After 12 d the fish were retrieved, remeasured alive and their stomachs were removed for dietary analysis. The enclosures were washed and dried between experiments to prevent fouling.

Changes in the standard lengths of fish per day (mm SL d^{-1}) were used as the index of relative growth. The duration of experiments was defined as 13 d; the period elapsing between initial and final measurement. Growth rates of fish recovered from each enclosure were averaged to ensure the independence of observations (Hurlbert 1984).

Physical and biological habitat parameters. Station depths were measured with an electronic depth finder (cm) and standardized to mean low water (MLW) with tidal prediction software (Tides and Currents 2.0, Nautical Software). Bottom water temperatures (°C) were monitored hourly with electronic recorders (Onset) attached to an enclosure at each station. Salinity (‰) and dissolved oxygen (mg l^{-1}) were measured with probes (Yellow Springs Instruments) at least 4 times at each station during each experiment.

Core samples for sediment (2.5 cm diameter, n = 3), sediment chemistry (7.0 cm diameter, n = 2) and benthic invertebrates (4.8 cm diameter, n = 3) were collected at the stations during each experiment by divers. Standard sieve fractionation was performed on sediments to calculate mean grain sizes and sorting coefficients (Folk 1980). Labile carbon (mmol dm^{-3}) was measured in the surface sediment (0 to 0.6 cm) as semi-ultimate BOD_{13} calibrated with glucose (Draxler 1995). Redox potential (E_H) was measured 0.5 cm below the surface of the substratum with a Pt electrode and calomel reference. Benthic invertebrate samples were sieved (0.5 mm) and the taxa identified to family and counted. Abundances of species collected in sediment cores that also occurred in the stomachs of flounder in enclosures (see 'Results') were pooled to calculate benthic prey densities (number cm^{-2}).

Statistical analysis. Variation in flounder growth ($\bar{x}$mm SL d^{-1} per enclosure) was analyzed with a nested analysis of covariance (ANCOVA) with experiment, region, and sector nested within region as fixed effects and station nested within sector and region as a random factor. The mean initial standard length (mm) of fish per enclosure served as the covariate. Expected mean squares were calculated to determine the appropriate error mean squares (MS) and degrees of freedom (df) for F-tests. Station nested within sector and region was used as the error for tests of region and sector nested within region. F-tests of experiment and interactions of experiment with region and sector within region used the MS and df for the interaction between experiment and station nested within sector and region. Finally, the interaction of experiment with station nested within sector and region was tested with the error MS and df.

The relationship between flounder growth and habitat variation was examined with a generalized additive model (GAM). GAMs are non-parametric generalization of linear regression that iteratively fit scatter plot smoothers to relationships between dependent and independent variables (Hastie & Tibshirani 1990). Because GAMs assume the response is a function of the sum of unspecified smoothed functions, the approach allowed for the generation of data-defined partial growth response curves to important environmental variables. The GAM was constructed with S-Plus software (Math-Soft) using a cubic spline with 4 degrees of freedom which produced moderate smoothing (Hastie 1993, Venables & Ripley 1997). The model was constructed manually in a forward stepwise manner. The term added to model at each step resulted in the largest significant (p < 0.05) reduction in residual deviance when compared to the previous model using an approximate F-test in analysis of deviance (Hastie 1993). Deviance (≈variance) accounted for was calculated as null deviance minus residual deviance divided by null deviance. Average values for environmental variables measured at each station during each experiment were used as independent variables. First order interactions between significant variables in the model were also tested. Partial additive effects of the variables were plotted with ±2 SE confidence bands.

To compare the relative strengths of influence of environmental gradients on spatial growth patterns, the GAM was used to calculate partial growth predictions for the stations associated with each significant environmental variable. These partial growth rates were then used to calculate absolute values of between-station differences in growth associated with each variable. Linear regression was performed to estimate spatial rates of change in partial growth resulting from each environmental variable using growth differences as dependent and interstation distance (km) as independent variables. Spatial rates of change in partial growth were compared within experiments using F-tests for differences between slopes (Sokal & Rohlf 1995).

RESULTS

Habitat variation

Bottom water temperatures increased from 17°C on May 20, to 25°C on June 30 and mean daily warming rates increased with the distance of stations upstream (Table 2, Pearson's r = 0.81, p = 0.001). The lowest temperatures and slowest warming rates were generally recorded at deep bay stations while temperatures were consistently >2°C above the daily average at the westernmost station in the river (Stn 12, Fig. 1). Salinities ranged from 16 to 29‰ and were ≥5‰ lower in the western river than near the tip of Sandy Hook. As expected, the coefficient of variation (CV) for salinity increased with distance upstream (r = 0.65, p = 0.022).

Station depths were less than 3 m below MLW except at Stns 2 and 3 in Sandy Hook Bay (Table 2, Fig. 1). Labile carbon content and redox potential of the sediment were correlated with grain size (Pearson's r: –0.83, p ≪ 0.001; 0.67, p < 0.001, respectively).

Table 2. Environmental characteristics of the 12 stations in the NSHES during the flounder growth experiments. Depths were corrected to meters below mean low water (MLW). CV = % coefficient of variation, WR = mean daily warming rate (°C d^{-1})

Station	Km up-stream	Depth (m) MLW	Mean grain size (mm)	Labile carbon (mmol dm^{-3}) Mean	CV	Redox (E_H) Mean	CV	Prey (no. cm^{-2}) Range	Temperature (°C) Range	(°C d^{-1}) WR	Salinity (‰) Range	CV	Growth (mm SL d^{-1}) Range	CV
1	2.0	1.6	0.55	34	63	252	15	0.4–1.5	16–27	0.17	23–28	5.2	0.3–0.7	21
2	5.1	5.4	0.07	213	9	127	30	12.4–18.9	17–24	0.11	23–28	5.5	0.2–0.6	29
3	6.6	4.8	0.06	165	20	184	47	1.0–9.4	16–22	0.15	23–29	7.1	0.2–0.5	33
4	7.3	2.9	0.18	148	36	135	18	1.9–27.4	16–25	0.11	23–28	5.7	0.4–0.6	16
5	7.4	1.5	0.24	64	24	274	5	0.2–0.3	16–25	0.10	23–28	5.4	0.2–0.7	36
6	8.0	1.0	0.55	68	48	202	32	0.6–1.1	13–26	0.17	23–28	5.5	0.2–0.8	43
7	12.0	0.9	0.21	146	44	187	19	1.1–19.5	17–28	0.18	22–27	5.7	0.1–0.9	51
8	12.9	1.0	0.45	47	15	270	13	0.6–1.9	17–25	0.18	22–27	6.4	0.0–0.8	66
9	15.0	1.2	0.06	264	4	117	32	2.7–21.0	21–28	0.21	21–27	6.9	0.2–0.8	45
10	17.2	0.9	0.05	225	21	130	39	0.3–1.6	18–29	0.26	21–25	6.0	0.1–0.8	47
11	18.7	1.3	0.06	181	19	97	61	0.4–2.0	18–29	0.25	20–26	7.0	0.1–0.9	63
12	19.7	0.9	0.08	145	24	114	50	0.1–2.2	18–28	0.23	16–24	11.2	0.2–0.8	61

Stations in shallow bay habitats (<3 m MLW) and the lower river (Sector D) had sandy substrata with low labile carbon content and high redox potential, while stations in the western part of the river (Sectors E and F) and deep areas of the bay had fine-grained organically rich sediments with low redox potentials.

The dominant prey of fish in enclosures were Spionid polychaetes; amphipods in the families Ampeliscidae, Aoridae, and Gammaridae; and copepods (primarily *Eurytemora affinis*; Table 3). With the exception of copepods, these prey were collected in benthic samples and considered in the GAM of habitat effects on growth.

Benthic prey were generally more abundant at deeper stations (Table 2; Pearson's r = 0.50, p = 0.01) with fine grained sediments, but correlations of benthic prey densities with sediment characteristics were weak (r < 0.42, p ≥ 0.07). Densities of benthic prey did not co-vary with temperature and salinity (r < 0.21, p = 1).

Recovery of enclosures and fish

At least 4 of 60 enclosures deployed at the stations were missing at the end of each experiment (Table 1). When numbers of fish deployed were corrected for fish lost with these missing enclosures, recovery was 89% in the

May 20 to June 1 experiment, and approximately 75% from June 4 to 30. Proportions of fish recovered from the stations were not correlated with somatic growth rates (Pearson's r = 0.29, p = 0.10).

Table 3. Abundance of taxon collected in benthic cores and their contribution to the diets of winter flounder retrieved from enclosures during the growth experiments

Taxon	Benthic core samples n = 108 Mean no. cm^{-2} ± 1SE (% frequency)	Winter flounder stomachs n = 204 Mean % by no. ± 1SE (% frequency)
Polychaeta		
Spionidae	1.17 ± 0.31 (68)	19.8 ± 2.4 (26)
Capitellidae	0.13 ± 0.03 (42)	6.3 ± 1.6 (7)
Phyllodocidae	0.04 ± 0.01 (36)	4.8 ± 1.3 (8)
Polychaeta other	0.01 ± 0.00 (14)	4.6 ± 1.3 (8)
Mollusca		
Bivalvia unidentified	0.06 ± 0.02 (19)	1.7 ± 0.8 (3)
Crepidula sp.		0.4 ± 0.2 (4)
Gastropoda unidentified	0.00 ± 0.00 (3)	0.3 ± 0.2 (1)
Amphipoda		
Ampeliscidae	3.25 ± 0.74 (49)	8.2 ± 0.1 (18)
Aoridae	0.17 ± 0.05 (28)	30.8 ± 2.9 (37)
Corophiidae	0.04 ± 0.01 (19)	0.4 ± 0.3 (2)
Gammaridae	0.01 ± 0.00 (40)	6.6 ± 1.3 (17)
Amphipoda unidentified	0.01 ± 0.01 (9)	2.0 ± 0.9 (4)
Isopoda	0.00 ± 0.00 (3)	1.1 ± 0.3 (6)
Mysidaceae	0.04 ± 0.02 (18)	0.5 ± 0.3 (2)
Decapoda	0.00 ± 0.00 (3)	2.3 ± 0.9 (4)
Copepoda	0.00 ± 0.00 (0)	8.9 ± 1.6 (19)

Dynamic growth patterns

The pattern of flounder growth ($\bar{x}$mm SL d^{-1} enclosure^{-1}; range = 0.00 to 0.88 mm d^{-1}) was dynamic at a regional spatial scale. Experiment and the experiment × region interaction were significant in the ANCOVA, while the covariate, initial standard length, was not (Table 4). Flounder grew most rapidly during the May 20 to June 1 experiment when growth rates were significantly higher in the river than the bay (Fig. 2; Tukey HSD test, p < 0.001). However, growth declined rapidly in the river and from June 4 to 16, fish grew significantly (p = 0.017) faster in the bay than the river. From June 18 to 30, growth rates declined throughout the estuary and were not different (p = 0.08) in the 2 regions. The rapid decline in growth rates within the river was reflected in the high correlation between the CV for growth and distance upstream (Table 2; Pearson's r = 0.82, p = 0.001).

Table 4. Nested analysis of covariance of flounder growth ($\bar{x}$mm SL d^{-1} enclosure^{-1}) which was dynamic in time ($\approx$experiment) at a regional spatial scale

Source of variation	df	MS	F	p
Region	1	0.003	0.295	0.625
Sector (region)	4	0.019	2.191	0.273
Station (sector[region])	3	0.009	1.180	0.320
Experiment	2	0.399	58.73	<0.001
Experiment × Region	2	0.243	35.76	0.001
Experiment × Sector (region)	7	0.025	3.75	0.082
Experiment × Station (sector[region])	5	0.007	0.907	0.479
Covariate				
Initial standard length (mm)	1	0.003	0.355	0.553
Error	118	0.007		
Total	143			

Growth and habitat variation

GAM showed that flounder growth was related to bottom water temperature, salinity, sediment labile carbon content and redox potential which together explained nearly 79% of the variability (Table 5). Benthic prey density was a significant covariate (p = 0.02) in a pre-
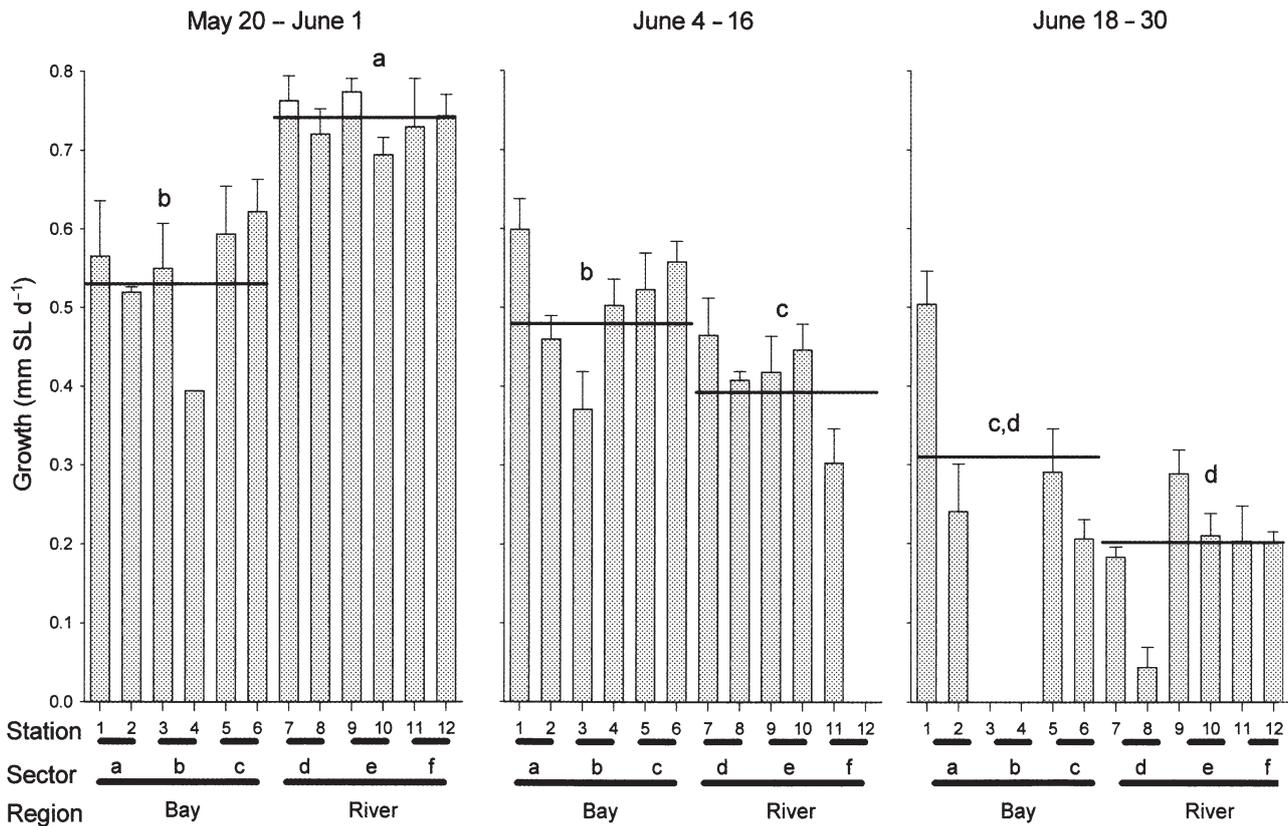

Fig. 2. Winter flounder growth rates ($\bar{x}$mm SL enclosure^{-1}) in the NSHES which varied in time at a regional spatial scale (see Table 4). Horizontal lines indicate regional mean growth while letters indicate significantly (p < 0.05) different groups in Tukey HSD tests. Error bars indicate 1 SE

Table 5. Generalized additive model for flounder growth ($\bar{x}$ mm SL d^{-1} enclosure^{-1}). Temperature and salinity accounted for the largest proportion of variation in growth which was not related to variability in depth, benthic prey density or sediment grain size (p > 0.08)

| Term | — Nonparametric — | | | Deviance accounted for | Independent effects (%) |
	df	F	p		
Null model				6.35	
Temperature	3	8.35	<0.001	1.77	27.77
Salinity	3	5.45	0.001	0.83	13.05
Sediment labile carbon	3	14.82	<0.001	0.36	5.74
Sediment redox potential	3	6.69	<0.001	0.18	2.86
Sum of independent effects				3.14	49.41
Intercorrelated effects				1.86	29.34
Total deviance explained				5.00	78.75

liminary GAM that also included temperature and salinity. However prey density ceased to account for a significant amount of growth variation when sediment labile carbon content was added to the model. Depth, sediment grain size or first order interactions did not increase (p > 0.08) the explanatory power of the final model.

Bottom water temperature followed by salinity produced the strongest independent effects on flounder growth (Table 5). Partial deviance plots derived from

the GAM showed that growth was most rapid at cool temperatures (16 to 18°C), decreased at higher values, and was relatively poor at temperatures above 21°C (Fig. 3). Flounder also grew rapidly at sites with relatively low salinities (20 to 23‰) and values ≥24‰ produced slower growth. The independent effects of sediment labile carbon content and redox potential were relatively weak (Table 5). Growth was marginally higher on oxidizing substrata with redox potentials ranging from 175 to 275 E_H (Fig. 3). The relationship between growth and sediment labile carbon content was unclear probably because the 2 sediment characteristics were inter-correlated (r = 0.63, p ≪ 0.001).

Growth and the spatial dynamics of temperature and salinity gradients

Analysis of spatial trends in the partial effects of environmental variables included in the GAM sug-
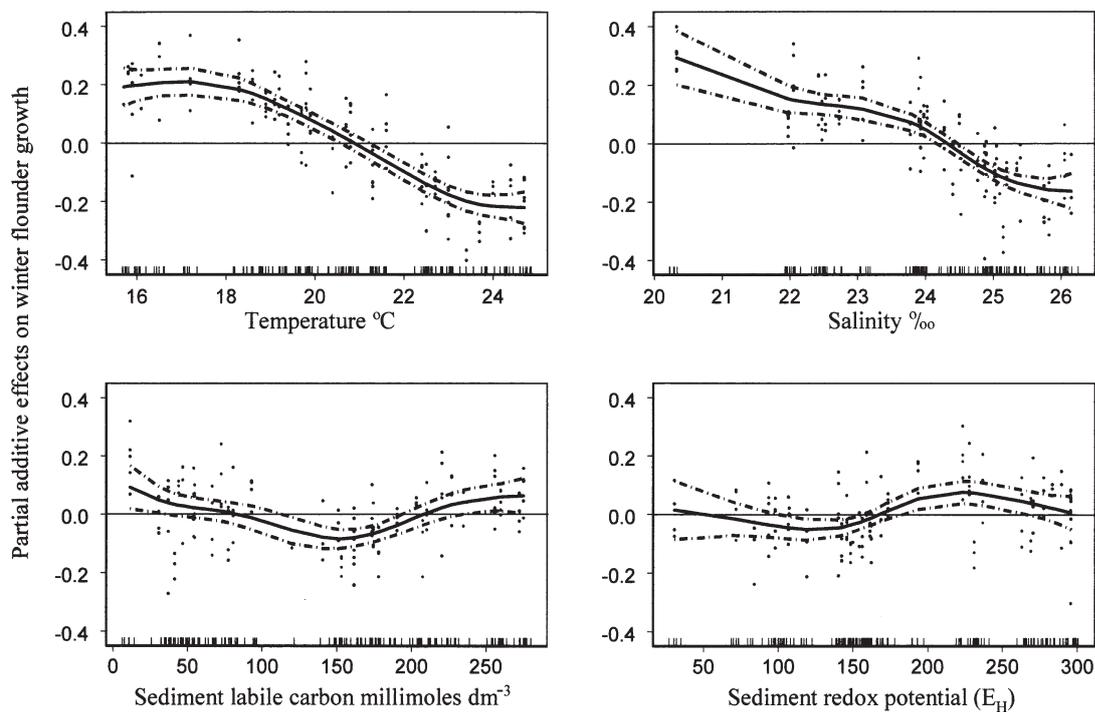

Fig. 3. Deviance plots derived from the generalized additive model (Table 5) showing the partial additive effects of temperature, salinity, sediment labile carbon, and sediment redox potential on the growth of flounder in enclosures. Horizontal lines indicate thresholds for positive and negative effects while vertical dashes along abscissa show the distribution of values for each environmental variable. Dashed lines represent 2 standard error confidence bands
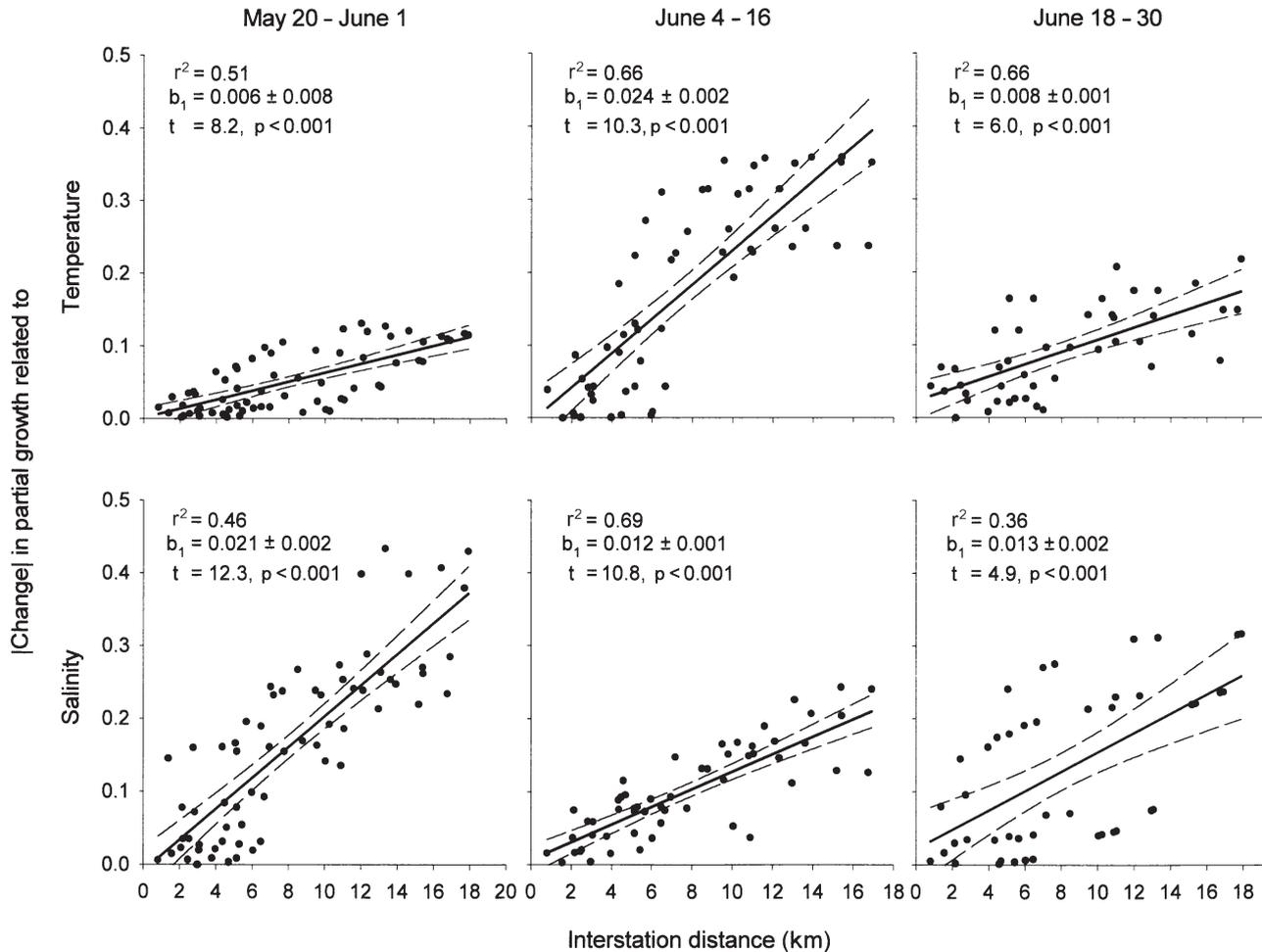
Fig. 4. Absolute values of between station differences in partial growth predictions related to temperature and salinity as a function interstation distance (km). r^2 and t-tests for slope coefficients (b_1) of regressions are indicated in the plots. Analysis of slope coefficients showed that the change in growth per unit distance was greater for salinity than temperature during the May 20 to June 30 experiment ($F_{1,128} = 63.7$, p $\ll$ 0.001), while the converse was the case from June 4 to 16 ($F_{1,106} = 20.5$, p < 0.001). Slopes were not different from June 18 to 20 ($F_{1,86} = 2.6$, p = 0.110)

gested that changes in salinity and temperature were primarily responsible for the dynamic regional scale spatial variability in flounder growth identified in the ANCOVA. Regression analysis showed that between station differences in partial growth related to temperature and salinity increased with interstation distance (Fig. 4) while deviations associated with sediment labile carbon, redox potential and residual growth variation did not (regression slopes ≤ 0.002, t ≤ 2.9, p ≥ 0.13).

The relative strengths of influence of temperature and salinity on coarse scale growth patterns varied as areas in which temperatures and salinities were conducive for growth changed over time. Analysis of slopes showed that salinity produced greater changes in partial growth per unit distance than temperature in the May 20 to June 1 experiment (Fig. 4; $F_{1,128} = 63.7$,

p $\ll$ 0.001). During this period, temperatures were within the range of positive effects in the GAM (< 21°C) throughout the study area, while salinities were conducive for rapid growth (< 24‰) throughout the river (Fig. 5) where the highest growth rates were recorded (Fig. 2). From June 4 to 16, temperature produced significantly larger changes in partial growth per unit distance than salinity (Fig. 4; $F_{1,106} = 20$, p < 0.001). During that experiment, the area in which temperatures were conducive for growth was confined to the bay while salinities remained within range of positive effects throughout the river (Fig. 5). Thus, in contrast with the first experiment, locations in which temperatures and salinities promoted rapid growth did not overlap within the study area, and growth rates were significantly lower in the river than the bay. From June 18 to 30, rates of spatial change in partial growth
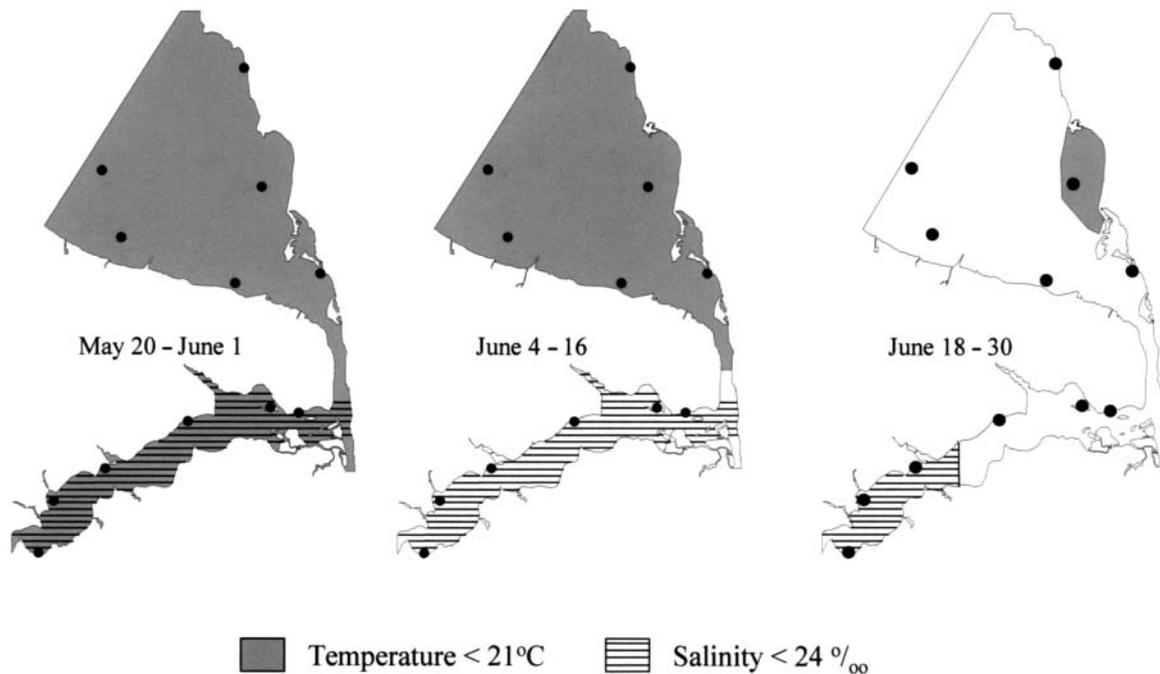
Fig. 5. Maps showing areas (•: Stations) in which temperatures and salinities were within the range of positive effects in the GAM for winter flounder growth (see Fig. 4) during the experiments. Areas in which temperatures and salinities were conducive for rapid growth overlapped within the study area during the first experiment when maximum growth rates were measured in the river (see Fig. 2)

related to temperature and salinity were not different (Fig. 4; $F_{1,86}$ = 63.7, p = 0.11). Areas in which temperature and salinity were conducive for rapid growth contracted into the northeastern part of the bay and upper river, respectively (Fig. 5). Growth was relatively poor throughout the estuary.

DISCUSSION

Scales of variability in biological responses typically reflect the scales of influence of dominant controlling processes (Haury et al. 1978, Wiens 1989, Levin 1992, Schneider 1994, Legendre et al. 1997). The results of our experiments suggest that habitat suitability for the growth of recently settled winter flounder is primarily determined by environmental factors that change rapidly in time and produce significant differences in growth at a relatively coarse spatial scale (~10 km) within the estuary. Experiment (≈time) and the interaction between experiment and region were the only significant sources of variation in the nested analysis of covariance. Extrinsic environmental factors were primarily responsible for growth differences since initial body size was not a significant covariate in the model. This pattern of variation is consistent with previous field studies in which growth rates were repeatedly measured in nearby habitat types (e.g. vegetated beds

vs bare substrata) replicated at more distant locations (Sogard 1992, Able et al. 1999, Meng et al. 2000, Phelan et al. 2000). In those experiments, significant differences in juvenile flounder growth were also measured over short time periods (wk) at coarse (i.e. locations: 5 to 200 km, among coastal ponds, embayments, estuaries) rather than fine (<1 km; among habitat types) spatial scales.

Our GAM showed that the dynamic growth pattern was strongly related to bottom water temperature which is considered to be the most important factor controlling growth rates in poikilotherms (Fry 1971, Laudien 1973, Brett 1979, Brett & Groves 1979) including flatfishes (Fonds et al. 1992, Malloy & Targett 1994a,b, Neill et al. 1994, Rose et al. 1996). In the NSHES, early juvenile flounder grew fastest at the coolest temperatures measured (17°C) and growth was suppressed at values higher than 21°C. The temperature response curve derived in our GAM agrees closely with previous laboratory and field observations. Winter flounder is a 'cold water' species (Magnuson et al. 1979, Jobling 1981) and the juvenile growth response to temperature is thought to be unimodal with an optima at approximately 15°C (Armstrong 1995, Rose et al. 1996). Young fish exposed to temperatures higher than 20°C in the laboratory show feeding inhibition, lower food conversion efficiencies and slower growth rates than fish exposed to cooler water (Frame 1973,

Casterlin & Reynolds 1982). Without exception, field studies of juvenile winter flounder growth have been performed in temperate estuaries during the early summer warming period (Sogard 1992, Able et al. 1999, Duffy-Anderson & Able 1999, Meng et al. 2000, 2001, Phelan et al. 2000). Reductions in growth rates over time and increasing water temperature have been observed in all investigations. Although temperature and size effects were confounded in several studies in which increasingly large fish were used in successive experiments, most authors have concluded that temperature probably contributed to temporal as well as spatial growth patterns. In field enclosure studies that used similarly sized fish in all experiments, temperature appeared to have the strongest effects on growth rates (Meng et al. 2000; this study).

Salinity variations within the estuary also influenced flounder growth rates which were relatively rapid at values ≤24‰. Salinity is rarely considered in assessments of winter flounder nursery habitat because the animals are euryhaline with broad salinity tolerance (4 to 30‰; Bigelow & Schroeder 1953, Pearcy 1962, Mulkana 1966). However, exposure to sub-optimal salinities can 'mask' growth when metabolic energy is used for osmoregulation (Fry 1971). In the laboratory, juvenile winter flounder exposed to salinities ≤20‰ exhibit lower respiration rates and osmoregulatory energy expenditures than those exposed to higher salinities (Frame 1973). Furthermore, in another enclosure study conducted at 3 sites along an estuarine gradient in Rhode Island, fish also grew more rapidly at sites with salinities <25‰ (Meng et al. 2001).

A small but significant proportion of growth variability in our study was related to substrate characteristics, particularly redox potential. Fish grew slightly faster on oxidizing substrata (>175 EH). Water overlying sediments with high redox potentials is generally less prone to hypoxia (Draxler 1995, Davis et al. 1998) and the relationship may have reflected the importance of dissolved oxygen as a limiting growth factor (Fry 1971, Taylor & Miller 2001). In the laboratory, winter flounder growth rates are suppressed at low dissolved oxygen concentrations (Bejda et al. 1992) and poor growth in the field has frequently been attributed to hypoxic conditions (Phelan et al. 2000, Meng et al. 2001). The species richness of benthic invertebrate communities is also positively related to sediment redox potential (Draxler 1996), which may therefore have served as a surrogate for food availability in our analysis. Benthic prey density was a significant covariate in a preliminary GAM in which the deviance plot showed that flounder growth increased with increasing prey densities up to 2.5 prey cm^{-2}. However, the effects of prey density were eliminated when sediment characteristics, which had greater explanatory power, were in-

cluded in the model. Marginal increases in the growth of juvenile flatfish have been related to food availability and consumption in several other studies (Kamermans et al. 1995, Malloy & Targett 1994a). However, we were unable to control for the inter-correlated effects of sediment characteristics and benthic prey densities in our field study. As a result, it not clear whether the marginal effects of sediment characteristics on growth identified in our final model were related to variations in prey density and/or to the potential of habitats to become hypoxic.

The relationship between the dynamic coarse scale spatial growth pattern identified in the ANCOVA and the dynamics of temperature and salinity gradients was confirmed by our spatial analysis of partial growth deviations. Growth deviations associated with temperature and salinity showed significant spatial trends while those related to sediment characteristics and residual growth did not. However, the relative strengths of influence of temperature and salinity on growth changed rapidly in time. When temperatures throughout the estuary were lower than values that appear to inhibit growth, salinity influenced the spatial growth pattern more strongly. Fish grew rapidly in the river where salinities were below values that appear to 'mask' growth. As the estuary warmed more rapidly in the river than the bay, temperatures conducive for rapid growth became confined to the bay. Under these conditions, growth was more rapid in the bay, but not as high as that recorded within the river when regions of 'optimal' salinity and temperature overlapped within the estuary. With continued warming and curtailed freshwater runoff, temperatures and salinities conducive for rapid growth were limited to small patches in bay and upper river, respectively, and growth was generally low. Thus, winter flounder growth was most rapid at sites and times when optimal conditions for temperature and salinity intersected in space, but the spatial coincidence of optimal conditions was ephemeral.

Although estuarine temperatures and salinities are extremely variable, the geographic and hydrographic structure of estuaries is likely to produce relatively predicable patterns of spring warming and salinity profiles. Within the NSHES, temperatures and salinities optimal for the growth of early juvenile winter flounder are more likely to coincide during late spring and early summer within the river than in the bay where relatively cool seawater mixes with estuarine water. During periods when optimal temperatures and salinities overlap within the estuary, sufficiently high dissolved oxygen and prey concentrations could further enhance growth rates within the region of overlap. Although habitat suitability for the juvenile winter flounder growth is spatially dynamic, optimal condi-

tions for factors regulating growth may be more likely to coincide within a specific region of the estuary during the spring and early summer when winter flounder begin their early juvenile growth phase.

CONCLUSION

Current strategies of marine habitat conservation typically involve the preservation of areas defined by relatively stable fine-scale variability in habitat structure (e.g. vegetated beds, oyster reefs). Our study suggests that nursery habitat suitability for the growth of a commercially important flatfish is defined by multiple environmental factors that vary simultaneously in space and time and as a result the location and suitability of nursery areas can change rapidly in time. Similar dynamics have been observed in the growth of pacific herring in Alaska embayments (Stokesbury et al. 1999), and in spatially explicit models of fish and invertebrate growth and production that incorporate spatio-temporal variability in multiple regulatory factors (Brandt & Kirsch 1993, Ault et al. 1999). Although the spatial dynamics of habitat suitability can be complex, optimal values for critical regulatory factors may be more likely to coincide during limited periods of time within specific areas as a result of the geological and hydrographic structural characteristics of nearshore ecosystems.

LITERATURE CITED

Able KW, Fahay MP (1998) The first year in the life of estuarine fishes in the middle Atlantic Bight. Rutgers University Press, New Brunswick

Able KW, Manderson JP, Studholme AL (1999) Habitat quality for shallow water juvenile fishes in an urban estuary: the effects of manmade structures on the growth of winter flounder and tautog in the lower Hudson River estuary. Mar Ecol Prog Ser 187:227–235

Armstrong MP (1995) A comparative study of the ecology of smooth flounder *Pleuronectes putami*, and winter flounder, *Pleuronectes americanus* from Great Bay, New Hampshire. PhD dissertation, University of New Hampshire

Ault JS, Luo J, Smith SG, Serafy JE, Wang JD, Humston R, Diaz GA (1999) A spatially dynamic multistock production model. Can J Fish Aquat Sci 56(Suppl 1):4–25

Bejda AJ, Phelan BA, Studholme AL (1992) The effects of dissolved oxygen on the growth of young-of-the-year winter flounder, *Pseudopleuronectes americanus*. Environ Biol Fishes 34:321–327

Beverton RJH, Iles TC (1992) Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda*) and turbot (*Scopthalmus maximus* L.) in European waters. III. Density dependent mortality rates of 0-group plaice and some demographic implications. Neth J Sea Res 29:61–79

Bigelow HB, Schroeder WC (1953) Fishes of the gulf of Maine. Fishery Bulletin of the Fish and Wildlife Service, No. 53. Washington DC

Brandt SB, Kirsch J (1993) Spatially explicit models of striped bass growth potential in Chesapeake bay. Trans Am Fish Soc 122:845–869

Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology. III. Bioenergetics and growth. Academic Press, New York, p 599–675

Brett JR, Groves TDD (1979) Physiological energetics. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology. III. Bioenergetics and growth. Academic Press, New York, p 280–352

Casterlin ME, Reynolds WW (1982) Thermoregulatory behavior and diel activity of yearling winter flounder, *Pseudopleuronectes americanus* (Walbaum). Environ Biol Fishes 7:177–180

Chant RJ, Stoner A (2001) Particle trapping in a stratified flood dominated estuary. J Mar Res 59:29–51

Crawford RE, Kerry CG (1985) Retention of winter flounder larvae within a Rhode Island salt pond. Estuaries 8(28):217–227

Davis WR, Draxler AFJ, Paul JF, Vitaliano JJ (1998) Benthic biological processes and E_H as a basis for a benthic index. Environ Monit Assess 51:259–268

Draxler AFJ (1995) Changes in sediment biogeochemistry resulting from cessation of sewage sludge dumping in the New York Bight. NOAA Tech Rep NMFS 124:133–143

Draxler AFJ, Studholme AL, Zdanowicz VS, Reid RN, Vitaliano JJ, Wilk SJ, Katz I, O'Reilly JE (1996) Closure of the New York bight 12-mile sewage sludge dumpsite: ecosystem responses with implications for resource management. Northeast Geol Environ Sci 18(4):293–303

Duffy-Anderson JT, Able KW (1999) Effects of municipal piers on the growth of juvenile fishes in the Hudson River estuary: A study across a pier edge. Mar Biol 133:409–418

Folk RL (1980) Petrology of sedimentary rocks. Hemphill Publishing Company, Austin

Fonds MR, Cronie A, Vethaak KW, Van Der Puyl P (1992) Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Neth J Sea Res 29(1–3):127–143

Frame DW (1973) Biology of young winter flounder *Pseudopleuronectes americanus* (Walbaum); Metabolism under simulated estuarine conditions. Trans Am Fish Soc 2:423–430

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds.) Fish physiology VI. Academic Press, New York, p 1–98

Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfish. Neth J Sea Res 32(2):191–206

Gibson RN (1997) Behavior and the distribution of flatfishes. J Sea Res 37(3–4):241–256

Gibson RN, Yin MC, Robb L (1995) The behavioral basis of predator-prey size relationships between shrimp (*Crangon crangon*) and juvenile plaice (*Pleuronectes platessa*). J Mar Biol Assoc UK 75:337–349

Guindon KY, Miller JM (1995) Growth potential of juvenile southern flounder, *Paralichthys lethostigmata*, in low sal-

inity nursery areas of Pamlico Sound, North Carolina, USA. Neth J Sea Res 34(1–3):89–100

Hastie TJ (1993) Generalized additive models. In: Chambers JM, Hastie TJ (eds) Statistical models. Chapman and Hall, London, p 249–307

Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman and Hall, London

Haury LR, McGowan JA, Weibe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele JH (ed) Spatial pattern in plankton communities. Plenum Press, New York, p 277–327

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Jobling M (1981) Temperature tolerance and the final preferendum: rapid methods for the assessment of optimal growth temperatures. J Fish Biol 19:439–445

Kamermans P, Guindon KY, Miller JM (1995) Importance of food availability for the growth of juvenile southern flounder (*Paralichthys lethostigma*) in the Pamlico River estuary, North Carolina, USA. Neth J Sea Res 34(1–3):101–109

Keller AA, Klein-MacPhee G, Burns JS (1999) Abundance and distribution of ichthyoplankton in Narragansett, Bay Rhode Island, 1989–1990. Estuaries 22:149–163

Langton RW, Steneck RS, Gotceitas V, Juanes F, Lawton P (1996) The interface between fisheries research and habitat management. North Am J Fish Manage 16(1):1–7

Laudien H (1973) Changing reaction systems. In: Precht H, Christopherson J, Hansel H, Larcher W (eds) Temperature and life. Springer Verlag, Berlin, p 255–397

Legendre P, Thrush SF, Cummings VJ, Dayton PK and 9 others (1997) Spatial structure of bivalves in a sandflat: scale and generating processes. J Exp Mar Biol Ecol 216: 99–128

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

MacCall AD (1990) Dynamic geography of fish populations. University of Washington Press, Seattle

Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. Am Zool 19:331–343

Malloy KD, Targett TE (1994a) Effects of ration limitation and low temperature on growth, biochemical condition, and survival of juvenile summer flounder from two Atlantic Coast estuaries. Trans Am Fish Soc 123:182–193

Malloy KD, Targett TE (1994b) The use of RNA:DNA ratios to predict growth limitation of juvenile summer flounder (*Paralichthys dentatus*) from Delaware and North Carolina estuaries. Mar Biol 118:367–375

Manderson JP, Stoner AW, Stehlik, LL (1997) Species responses to environmental gradients and the description of estuarine landscape patterns. ICES Annual Science Conference, Baltimore, ICES CM.S15

Meng L, Gray C, Taplin B, Kupcha E (2000) Using winter flounder growth rates to assess habitat quality in Rhode Island's coastal Lagoons. Mar Ecol Prog Ser 201:287–299

Meng L, Powell JC, Taplin B (2001) Using winter flounder growth rates to assess habitat quality across an anthropogenic gradient in Narragansett bay, Rhode Island. Estuaries 24:575–583

Mulkana MS (1966) The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res Rep 2: 97–168

Nash RDM, Geffen AJ (2000) The influence of nursery ground processes in the determination of year class strength in juvenile plaice, *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. J Sea Res 44:101–110

Neill WH, Miller JM, van der Veer HW, Winemiller KO (1994) Ecophysiology of marine fish recruitment: a conceptual framework for understanding inter-annual variability. Neth J Sea Res 32(2):135–152

Pearcy WG (1962) Ecology of an estuarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum) Parts I-IV. Bull Bingham Oceanogr Collect 18(1):1–77

Petitgas P (1998) Biomass-dependent dynamics of fish spatial distributions characterized geostatistical aggregation curves. ICES J Mar Sci 55:443–453

Phelan BA (1992) Winter flounder movements in the inner New York Bight. Trans Am Fish Soc 121:777–784

Phelan BA, Goldberg R, Bejda AJ, Pereira J, Hagan S, Clark P, Studholme AL, Calabrese A, Able KW (2000) 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. J Exp Mar Biol Ecol 247:1–28

Rijnsdorp AD, Van Beek FA, Flatman S, Millner RM, Riley JD, Giret M, DeClerk R (1992) Recruitment of sole stocks, *Solea solea* (L.) in the northeast Atlantic. Neth J Sea Res 29:173–192

Rose KA, Tyler JA, Chambers RC, Klein-MacPhee G, Danilla DJ (1996) Simulating winter flounder population dynamics using coupled individual-based young-of-the-year and age-structured adult models. Can J Fish Aquat Sci 53: 1071–1091

Scarlett PG (1991) Relative abundance of winter flounder (*Pseudopleuronectes americanus*) in nine inshore areas in New Jersey. Bull NJ Acad Sci 36(2):1–5

Schmitt RJ, Holbrook SJ (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80(1):35–50

Schneider DC (1994) Quantitative ecology: spatial and temporal scaling. Academic Press, San Diego, CA

Shima JS (2000) Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality. Oecologia 126:58–65

Sokal RR, Rohlf FJ (1995) Biometry: the principals and practice of statistics in biological research. WH Freeman and Co, New York

Sogard SM (1992) Variability in growth rates of juvenile fishes in different estuarine habitats. Mar Ecol Prog Ser 85: 35–53

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60(3): 1129–1157

Sogard SM, Able KW, Hagan SM (2001) Long term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. Neth J Sea Res 45:189–201

Spitzer PM, Matilla J, Heck KL Jr (2000) The effects of vegetation density on the relative growth rates of juvenile pinfish, *Lagodon rhomboides* (Linneaus), in Big Lagoon, Florida. J Exp Mar Biol Ecol 244:67–86

S-Plus (2000) Guide to statistics, Vol. 2. Data Analysis Products Division, Mathsoft, Seattle

Stehlik LL, Meise CJ (2000) Diet of winter flounder in a New Jersey estuary: ontogenic change and spatial variation. Estuaries 28(3):381–391

Stokesbury KDE, Foy RJ, Norcross BL (1999) Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasi*, growth in Prince William Sound, Alaska. Environ Biol Fishes 56:409–418

Stoner AW, Bejda A, Manderson JP, Phelan BA, Stehlik LL, Pessutti JP (1999) Behavior of winter flounder (*Pseudopleuronectes americanus*) during the reproductive season: laboratory and field observations on spawning, feeding, and locomotion. Fish Bull 97:999–1016

Stoner AW, Manderson JP, Pessutti J (2001) Spatially-explicit analysis of estuarine habitat for juvenile winter flounder (*Pseudopleuronectes americanus*): combining generalized additive models and geographic information systems. Mar Ecol Prog Ser 213:253–271

Tanaka M, Goto T, Tomiyama M, Sudo H (1989) Immigration, settlement and mortality of flounder (*Paralichthys oliva-ceus*) larvae and juveniles in nursery ground, Shijiki Bay, Japan. Neth J Sea Res 24:57–67

Taylor CJ, Miller JM (2001) Physiological performance of juvenile southern flounder, *Paralichthys lethostigma* (Jor-dan and Gilbert, 1884), in chronic and episodic hypoxia. J Exp Mar Biol Ecol 258:195–214

van der Veer HW, Bergman R, Rijnsdorp AD (1994) Impact of juvenile growth on recruitment in flatfish. Neth J Sea Res 32(2):153–173

van der Veer HW, Geffen AJ, Witte JIJ (2000a) Exceptionally strong year classes in plaice *Pleuronectes platessa*: are they generated during the pelagic stage only, or also in the juvenile stage. Mar Ecol Prog Ser 199:255–262

van der Veer HW, Berghahn R, Miller JM, Rijnsdorp AD (2000b) Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. ICES J Mar Sci 57(2):202–215

Venables WN, Ripley BD (1997) Modern applied statistics with S-Plus. Springer-Verlag, New York

Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol Monogr 56(2):145–160

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3: 385–397

Witting DA (1995) Settlement of winter flounder, Pleuro-nectes americanus, in a southern New Jersey Estuary: Spatial and Temporal dynamics and the effect of deca-pod predation. PhD thesis, Rutgers University, New Brunswick