

Effects of a Delayed Onset of Piscivory on the Size of Age-0 Bluefish

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Abstract.—Variation in advection or other physical forces may accelerate or delay arrival of young marine fishes into productive nearshore habitats, thereby affecting the length of the available growing season. The bluefish *Pomatomus saltatrix* is an oceanic spawner whose juvenile stages, upon entry into estuarine waters, become piscivorous and thereby experience greatly increased growth. Size attained during the growing season may therefore be determined by time of arrival into estuarine habitats. We exposed bluefish recently recruited to an estuary to three diet shift treatments in which test fish were fed adult brine shrimp *Artemia* sp. for 0, 10, or 20 d before they were switched to piscine prey. Bluefish that had a delayed onset of piscivory were smaller after 40 d of growth, indicating that they did not fully compensate for prior periods of slow growth. These bluefish did exhibit immediate moderate growth compensation (about 6% over 10 d) resulting from increased consumption rates, but relatively low growth efficiencies prevented full recovery of their growth losses. Low growth efficiencies may have resulted from an induced developmental handicap or an energetic penalty for prolonged feeding on an *Artemia* diet. The timing of age-0 bluefish recruitment into estuarine environments can have a lasting influence on size attained during the first growing season.

Many marine fishes spawn in offshore oceanic waters but have juvenile stages that occupy nearshore or estuarine zones. The timing and location of offshore spawning for some species appears to be “coupled” to local circulation patterns such that larvae and juveniles are transported into nearshore habitats, which may provide a different growth and predation environment (Parrish et al. 1981; Norcross and Shaw 1984; Sherman et al. 1984). Variations in flow patterns may directly affect survival and thereby contribute to variations in recruitment patterns (Cowen 1985; Sinclair and Iles 1985; Sinclair 1988). However, transport may also affect survival indirectly if physical mechanisms delay or accelerate the arrival of propagules into nearshore habitats.

For several freshwater piscivores, growth and survival depend on the timing of the ontogenetic shift to a piscine diet (Gutreuter and Anderson 1985; Wicker and Johnson 1987; Buijse and Houthuijzen 1992). The shift to piscivory results in elevated growth rates that appear to increase chances of survival by providing a refuge from

size-dependent mortality (e.g., overwinter or predation mortality; see Buijse and Houthuijzen 1992). The timing of the shift to piscivory may be influenced by timing of spawning, water temperature, and availability of piscine prey (Adams and DeAngelis 1987; Buijse and Houthuijzen 1992; Phillips et al. 1995). Marine piscivores also show an increase in growth coincident with diet shifts (Juanes and Conover 1994a), but much less is known about environmental factors that contribute to the variability in timing of a switch to a piscine diet.

The bluefish *Pomatomus saltatrix* is a marine piscivore with circumglobal distribution that has an estuarine or nearshore juvenile stage (Juanes et al. 1996). Along the east coast of the United States, spawning occurs offshore over the continental shelf, and juveniles migrate into estuaries when they are about 60 mm in fork length (Kendall and Walford 1979; Nyman and Conover 1988; McBride and Conover 1991). Bluefish spawned in the South Atlantic Bight (SAB) in spring are advected northward in waters associated with the Gulf Stream (Hare and Cowen 1996) and move into New York and New Jersey estuaries in June (Nyman and Conover 1988; McBride and Conover 1991). The offshore-to-inshore habitat shift coincides with a feeding shift from zooplanktivory to piscivory (Marks and Conover 1993) and an abrupt increase in growth rate (McBride and Conover 1991). Controlled diet studies in the laboratory

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suggest that the shift from invertebrate to piscine prey is at least partially responsible for the increase in growth rate (Juanes and Conover 1994a).

There are likely strong selective pressures for bluefish to attain a large size by the end of the growing season in order to migrate south and overwinter. Juanes et al. (1994) and Juanes and Conover (1995) hypothesized that the early life history of bluefish has evolved to allow spring-spawned bluefish to "accelerate the onset of piscivory" via early birth date in the south and advection northward from SAB spawning grounds into Middle Atlantic Bight estuaries. This ensures that the timing of estuarine entry of juvenile bluefish coincides with the availability of appropriately sized piscine prey such as Atlantic silversides *Menidia menidia* (Juanes and Conover 1995). Variation in advection or other physical forces, such as the onset of vernal warming (Hare and Cowen 1996), may accelerate or delay bluefish arrival in estuarine nursery habitats and thereby affect the timing of the onset of piscivory.

No data are available that describe the within-year time range over which spring-spawned bluefish move into estuaries. If we assume equal travel durations from spawning areas to estuaries, an extreme range of estuarine arrival dates would be based on the range of birthdates back-calculated from daily otolith increments (45–75 d; Nyman and Conover 1988; McBride and Conover 1991). Additionally, interannual variation in date of estuarine arrival is around 20 d (Nyman and Conover 1988; McBride and Conover 1991). These data point out the potential for large variation in arrival time within the spring-spawned cohort. Although arrival time sets initial bounds on size attainable at the end of the growing season, its effect will be modulated by the extent to which delayed bluefish are capable of growth compensation.

Several fish species are known to exhibit compensatory growth (Dobson and Holmes 1984; Miglav and Jobling 1989; Russell and Wootton 1992; Wieser et al. 1992). For our purposes, we define compensatory growth as the ability of a group of fish, temporarily delayed in growth, to "catch up" in size to a group of fish that was not delayed in growth. The authors cited just above compared fish fed ad libitum with fish that were starved or fed restricted rations of the same prey type. However, bluefish switch from an invertebrate to a piscine diet upon estuarine entry. Bluefish grow rapidly on an invertebrate diet, but not as fast as they do on a fish diet (Juanes and Conover 1994a). The

ability of fish to compensate for reduced growth under such conditions is unknown.

We examined the effects on body size of age-0 bluefish of a delayed onset of piscivory, in particular whether bluefish can compensate for an extended period of relatively slow growth. In laboratory mesocosm tanks, we exposed bluefish newly recruited to an estuary to three diet shift treatments: 0, 10, or 20 d of feeding on adult brine shrimp *Artemia* sp. before switching to fish prey. We then followed the growth of individual fish for 40 to 60 d. The results are discussed in terms of long-term effects of these growth regimes.

Methods

General considerations.—Our goal was to simulate the natural environment experienced by newly recruited bluefish as closely as possible. Age-0 bluefish that have a delayed estuarine entry will likely experience different temperature regimes and prey size distributions (see Juanes and Conover 1995) upon arrival than earlier immigrants had encountered.

To mimic the environment we began the experiment immediately after bluefish first recruited into local estuaries. This was done so that the period of time that bluefish had been eating fish in the field prior to being brought into the laboratory was nil or very short. Ambient water from Flax Pond (a salt marsh adjacent to the Flax Pond Marine Laboratory of the State University of New York at Stony Brook, Old Field, New York) was used so that fish experienced natural summer temperature fluctuations (Figure 1); photoperiod was also ambient because tanks were located in a greenhouse. We provided bluefish with live fish prey that had been collected in the field and that had size distributions normally encountered by young bluefish. Large tanks (about 800 L) were used because smaller tanks affect growth and consumption rates of bluefish (Buckel et al. 1995). However, bluefish densities in our tanks (10–200 g/m²) were still much higher than those measured by beach seining in the field (maximum, about 5.0 g/m²; calculated from McBride et al. 1995). Finally, we chose realistic delays in piscivory. As we described earlier, the only available data relevant to this choice were back-calculated range in birthdates of (45–75 d) and interannual variation in arrival times (20 d); conservatively, we chose 20 d as our longest delay.

Fish collection and acclimation.—Age-0 bluefish collection efforts began in late May 1995 in Great South Bay, Long Island, New York

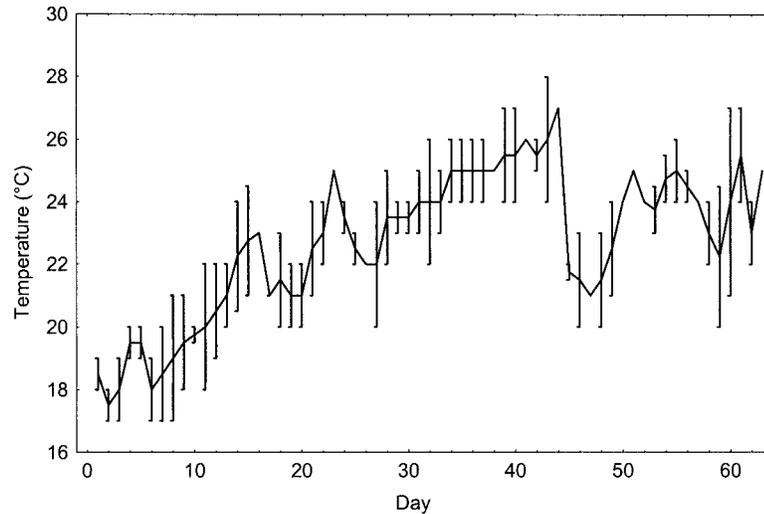


FIGURE 1.—Means and ranges of daily water temperatures in experimental bluefish tanks. Day 0 is June 23, 1995.

(40°10'N, 73°10'W). This represents the earliest time that age-0 bluefish have historically been observed to recruit into Great South Bay (Nyman and Conover 1988; McBride and Conover 1991). Bluefish sampling was conducted with a 30-m × 2-m beach seine (6-mm-mesh wings; 3-mm-mesh bag) on May 31, June 7, June 11, June 14, and June 16. Three seine hauls were completed on each date until age-0 bluefish were first encountered on June 14, 1995. At this point, a larger number of seine hauls were performed to obtain sufficient experimental fish (June 14: 7 bluefish in 9 hauls; June 16: 35 bluefish in 11 hauls).

Bluefish were transported immediately to the laboratory and stocked in a 183 × 92 × 72-cm-deep flow-through seawater tank. These fish were fed live adult brine shrimp *Artemia* sp. to satiation twice daily during a 3–4-d “laboratory” acclimation period. After laboratory acclimation, bluefish fork lengths (FL) were measured, a unique fin clip was given (top, bottom, or none), and fish were randomly assigned to treatments and experimental tanks (three fish per tank). Fin-clipped fish did not have significantly different growth rates over 40 d from unclipped fish (all treatment *P* values > 0.05, one-way analysis of variance). All fish were fed a mixture of live and dead adult brine shrimp ad libitum during a 4-d “experimental tank” acclimation period. After this acclimation (ending with a 12-h nonfeeding period), bluefish lengths (FL; ±1.0 mm) and wet weights (±0.01 g) were measured.

Experimental design and maintenance.—The ex-

periment consisted of three treatments. Fish were fed either (1) a piscine diet immediately (delay = 0 d), (2) *Artemia* for 10 d followed by a piscine diet (delay = 10 d), or (3) *Artemia* for 20 d followed by a fish diet (delay = 20 d). Age-0 bluefish are known to abruptly leave the shore zone at the end of the growing season (Nyman and Conover 1988; McBride and Conover 1991). Therefore, all treatments lasted until day 40 measured from June 23; this was considered the hypothetical end of summer. Fish in the 10- and 20-d-delay treatments were allowed an additional 10 (50 d total) and 20 (60 d total) days growth, respectively, merely to see how many days it would take them to reach a size comparable to that of fish in the 0-d-delay treatment at day 40. Each treatment was replicated three times; each replicate consisted of three fish in either a 122 × 92 × 72-cm (seven tanks) or a 183 × 92 × 72-cm (two tanks) flow-through seawater tank (no differences in fish growth were seen between tank sizes within a treatment). Bluefish that were fed an *Artemia* diet received a mixture of live and dead adult brine shrimp ad libitum. Bluefish receiving a piscine diet were fed daily, ad libitum, weighed amounts of live Atlantic silversides, which are a dominant prey of juvenile bluefish in Great South Bay (Juanes and Conover 1995). Fish prey were captured by beach seining at 3–4-d intervals; this ensured ambient prey size distributions as prey grew throughout the summer. Prey in bluefish tanks were never allowed to be depleted completely. Dead fish prey were removed

and weighed daily. Temperature was measured twice daily.

Individual bluefish FL and wet weights were measured every 10 d. Fins were reclipped during fish measurement. Only two fish died during the experiment, one (partly eaten) in the 10-d-delay treatment at day 10 and one (not recovered) in the 0-d-delay treatment between days 30 and 40.

Analysis.—Absolute growth rate was calculated as $(L_f - L_i)/d$, where L_f = final fork length (mm), L_i = initial fork length (mm), and d = number of days. Daily weight-specific growth rate was calculated as $(W_f - W_i) \cdot (\text{geometric mean fish weight})^{-1} \cdot d^{-1}$, where W_f = final wet weight (g) and W_i = initial wet weight (g). Growth rates for individual fish and mean growth rates by tank were calculated. Mean growth rates for each treatment were calculated from the three replicate tank means. Daily consumption rate was calculated as (amount of prey consumed, g) \cdot (geometric mean fish weight) $^{-1} \cdot d^{-1}$. Geometric mean fish weight, calculated as $e^{[\log_e(W_i) + \log_e(W_f)]/2}$, was used to estimate the size of fish between actual measurements because fish growth was exponential. Gross growth efficiency (GGE) was calculated as $\text{GGE} = (\text{fish weight gain, g})/(\text{prey biomass consumed, g})$.

We performed a repeated-measures analysis of variance of delay treatments (0, 10, and 20 d) in which body size (\log_e [weight] or FL) was the dependent variable and day was the independent variable. Temperature-adjusted consumption and growth rates were standardized to the mean experimental temperature (22.7°C). This was required because temperature varied throughout the course of the experiment making it difficult to compare rates between time periods (Figure 1). The adjustment of consumption and growth rates was $(a/b) \times (\text{unadjusted rate})$, where a = growth or consumption rate calculated at the average experimental temperature (22.7°C) and b = growth or consumption rate calculated at the average temperature over a 10-d period. Both a and b were calculated from equations describing weight-specific growth rate (SGR) and consumption rate (CR) as a function of temperature (T) developed from data on small juvenile bluefish reported by Buckel et al. (1995): $\text{SGR} (\%/d) = -0.4480 + 0.0433T - 0.000835T^2$, $r^2 = 0.95$; $\text{CR} (\%/d) = -0.7191 + 0.0775T - 0.00138T^2$, $r^2 = 0.78$. We were unable to adjust for the effect of body size on growth and consumption rates using a functional relationship so we limited statistical comparisons to fish of similar size.

TABLE 1.—Repeated-measures analysis of variance with treatment (piscivory delay) and time (days) as independent variables and bluefish fork length or \log_e (weight) as dependent variables.

Effect	df	Sum of squares	F	P
Length				
Treatment	2	333.22	2.03	0.21
Time	4	36437.80	1101.00	<0.0001
Treatment \times time	8	228.00	3.44	0.0088
Weight				
Treatment	2	0.28	1.27	0.35
Time	4	36.60	2115.58	<0.0001
Treatment \times time	8	0.10	3.12	0.015

Results

Initial mean bluefish sizes (SEs) were 71 (1.0) mm FL and 3.61 (0.16) g in the 0-d-delay treatment, 73 (2.1) mm and 3.76 (0.41) g in the 10-d-delay treatment, and 73 (1.6) mm and 3.66 (0.29) g in the 20-d-delay treatment; these values did not differ between treatments (length: $F = 0.314$, $P = 0.734$; weight: $F = 0.062$, $P = 0.940$; one-way analysis of variance). Over the course of the trial, however, fish sizes became significantly different among treatments (Table 1; Figure 2). By day 40 of the experiment, fish from the 0-d-delay treatment were 8.3% longer and 26.1% heavier than fish from the 20-d-delay treatment, and fish from the 10-d-delay treatment were intermediate in size (bold line connects day-40 data in Figure 2). Delayed-piscivory fish did not appear to compensate sufficiently for slow early growth and did not “catch up” to undelayed fish.

Growth rates of fish feeding on *Artemia* were much lower—1.0–1.6 mm/d—than those of piscivorous fish, which often exceeded 2 mm/d (Figure 3). Immediately following a switch to piscivory, growth rates were often substantially higher than they were before and after the switch.

Corrections for the effects of temperature and allometry on growth over the course of the trials were required. Temperature-adjusted growth rates plotted as functions of bluefish weight indicated that delayed-piscivory fish briefly compensated for slow initial growth (Figure 4). However, such compensations never brought significantly higher growth rates than shown by 0-delay fish of similar size. Growth in the 0-d-delay treatment (Figure 4) followed the linear relation $0.129 - 0.049 \cdot \log_{10}(\text{weight})$, for which $F = 60.741$; $df = 1, 10$; $P < 0.00001$; and $r^2 = 0.86$. Maximum compensatory growth rates of 10- and 20-d-delay fish were 6.12 and 6.06% greater, respectively, than values pre-

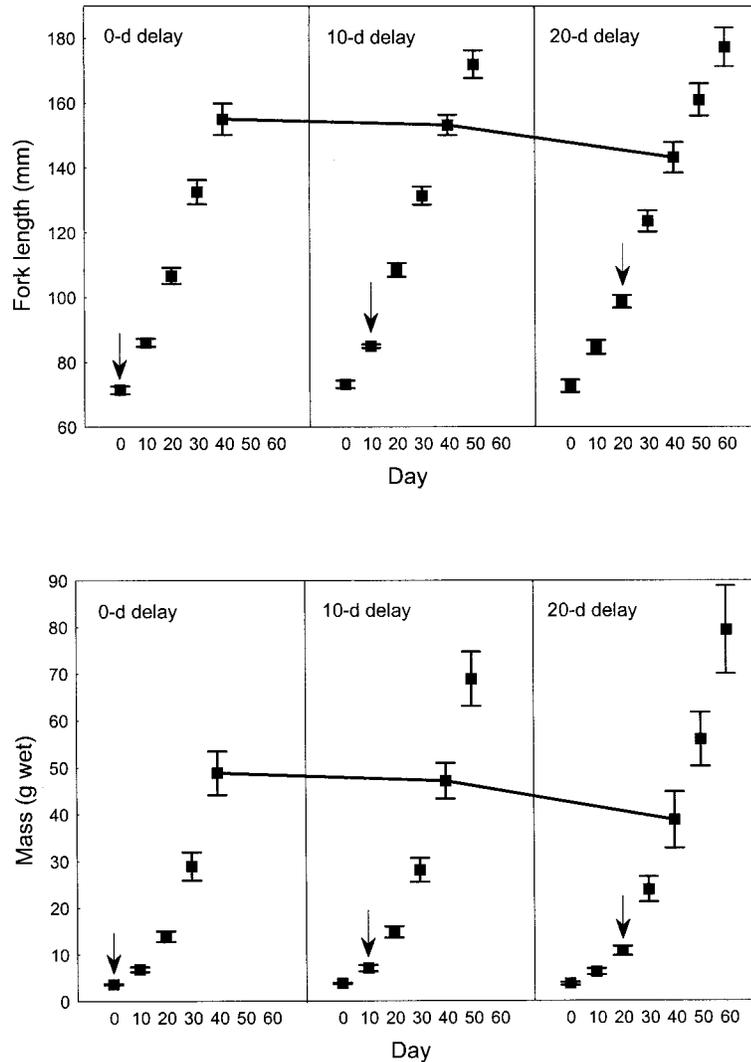


FIGURE 2.—Means and SEs of age-0 bluefish lengths and weights (masses) for three treatments in which bluefish were delayed from switching to a piscivorous diet. Delay periods were 0, 10 or 20 d. Arrows indicate the switch to piscivory. Mean fish sizes at the hypothetical end of the growing season (day 40) are connected by a bold line. Day 0 is June 23, 1995.

dicted from the 0-d-delay regression, but statistical analysis (Sokal and Rohlf 1981) showed the differences were nonsignificant (10-d delay: $t = 1.531$, $P = 0.150$; 20-d delay: $t = 1.770$, $P = 0.100$). Over the 10 d following initial switches to piscivory, growth rates of delayed-piscivory fish became significantly lower than that of 0-d-delay fish of similar size (10-d delay: $t = 3.052$, $P = 0.009$; 20-d delay: $t = 3.856$, $P = 0.002$). Had delayed-piscivory fish been able to maintain the high growth rates, they would have been 126%

(10-d delay) and 18% (20-d delay) heavier than the undelayed fish by day 40.

The relatively slow growth of delayed-piscivory fish after the transient compensatory surges could have been due to declines in consumption rate or growth efficiency. Immediately after the switch to piscivory, temperature-adjusted consumption rates of delayed-piscivory fish were 8% (10-d delay) and 20% (20-d) higher than those of undelayed fish of comparable weight, but the rates became similar among treatments in subsequent weeks

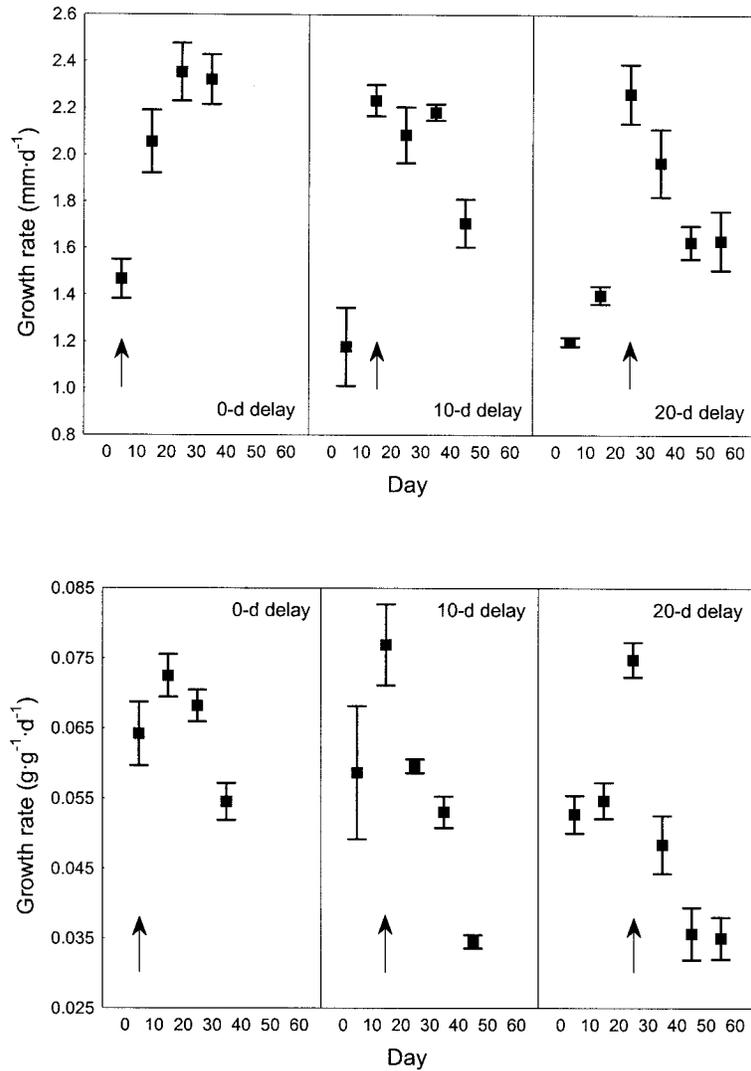


FIGURE 3.—Growth rates (fork length and specific weight) and SEs of age-0 bluefish for three treatments in which bluefish were delayed from switching to a piscine diet. Delay periods were 0, 10 or 20 d. Arrows indicate the switch to piscivory. Day 0 is June 23, 1995.

(Figure 5). Growth efficiencies, in contrast, varied substantially among treatments; efficiencies of undelayed fish were the highest, efficiencies of 10-d-delay fish were intermediate, and efficiencies of 20-d-delay fish were the lowest at comparable weights (Figure 5).

However, these gross growth efficiency estimates are not adjusted for temperature. In order to interpret the results further, we directly compared growth rate with consumption rate—both temperature adjusted—for the three treatments. Higher growth per unit consumption implies greater efficiency. Growth rates differed significantly

among treatments when consumption rate was the covariate in an analysis of covariance (slopes: $F = 1.04$, $df = 2, 30$, $P = 0.365$; intercepts: $F = 14.78$, $df = 2, 32$, $P < 0.0001$; Figure 6). Highest growth per unit ingestion was found in 0-d-delay fish; 10-d-delay fish had intermediate growth, and 20-d-delay fish exhibited the lowest growth over a wide range of consumption rates.

Discussion

Age-0 bluefish that underwent periods of slow growth as a result of a delayed onset of piscivory were unable to catch up in size to undelayed blue-

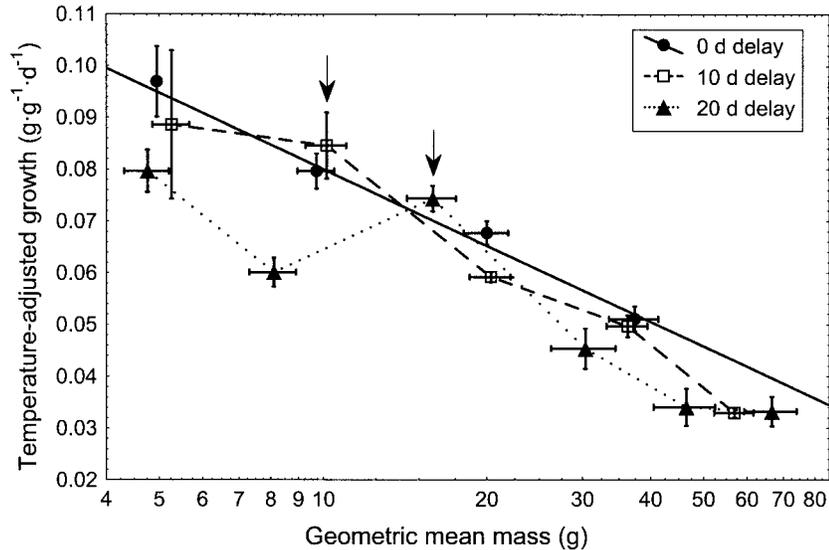


FIGURE 4.—Temperature-adjusted specific weight growth of age-0 bluefish as functions of geometric mean weight (mass) in three diet-switching treatments. Error bars are SEs. Linear regression (solid line) describes the relationship for fish immediately switched to a piscine diet (0-d delay), and broken lines connect means for fish in the 10-d-delay and 20-d-delay treatments.

fish. They showed slight evidence of brief compensatory growth when first given a piscine diet, but they could not sustain it, and the relatively low growth rates that followed limited bluefish from completely recovering growth losses resulting from the *Artemia* diet. The low growth of the delayed-piscivory fish after the switch resulted from lower growth efficiencies, suggesting an induced developmental handicap or energetic penalty for prolonged feeding on an *Artemia* diet. Our results suggest that if the timing of their entry into an estuary causes age-0 bluefish to delay their shift to a piscine diet, their size at the end of the growing season will be smaller than normal.

Physiological Mechanisms

The physiological mechanisms underlying growth compensation are not well understood. In previous research, fish have shown increased growth following starvation or limited rations (Dobson and Holmes 1984; Wieser et al. 1992; Jobling et al. 1993). This increased growth is usually a result of increased consumption, increased gross growth efficiency (GGE), or both (Miglav and Jobling 1989; Russell and Wootton 1992; Jobling 1994). We found only a temporary growth compensation that was best attributed to a brief increase in consumption rate. The inability of bluefish in the delayed-piscivory treatments to main-

tain higher or comparable growth rates relative to undelayed fish was a result of decreased GGE.

These findings suggest either a developmental handicap or energetic cost associated with an *Artemia* diet. It is possible that delayed-piscivory bluefish had lower GGEs because they failed to initiate production of some critical digestive enzyme during development as a result of exclusive feeding on *Artemia*. We believe this is unlikely for two reasons. Fish in all treatments (including 0-d-delay) were given an exclusive *Artemia* diet for 7 or 8 d during laboratory and tank acclimation periods prior to the start of the experiment. Furthermore bluefish grew well on the *Artemia* diet, suggesting that it was energetically adequate (*Artemia*-fed bluefish growth rates were 1.0–1.6 mm/d; Figure 3).

An energetic cost might have been responsible for the lowered growth efficiencies in delayed-piscivory treatments if (for example) smaller bluefish had to expend more energy capturing prey than larger fish (Juanes and Conover 1994b). Energetic problems were unlikely, however, because delayed-piscivory fish had consumption rates similar to (and briefly higher than) those of control fish, and bluefish in the 0- and 10-d-delay treatments were similar in size.

A more likely explanation for the differences in GGE is that delayed-piscivory fish required more

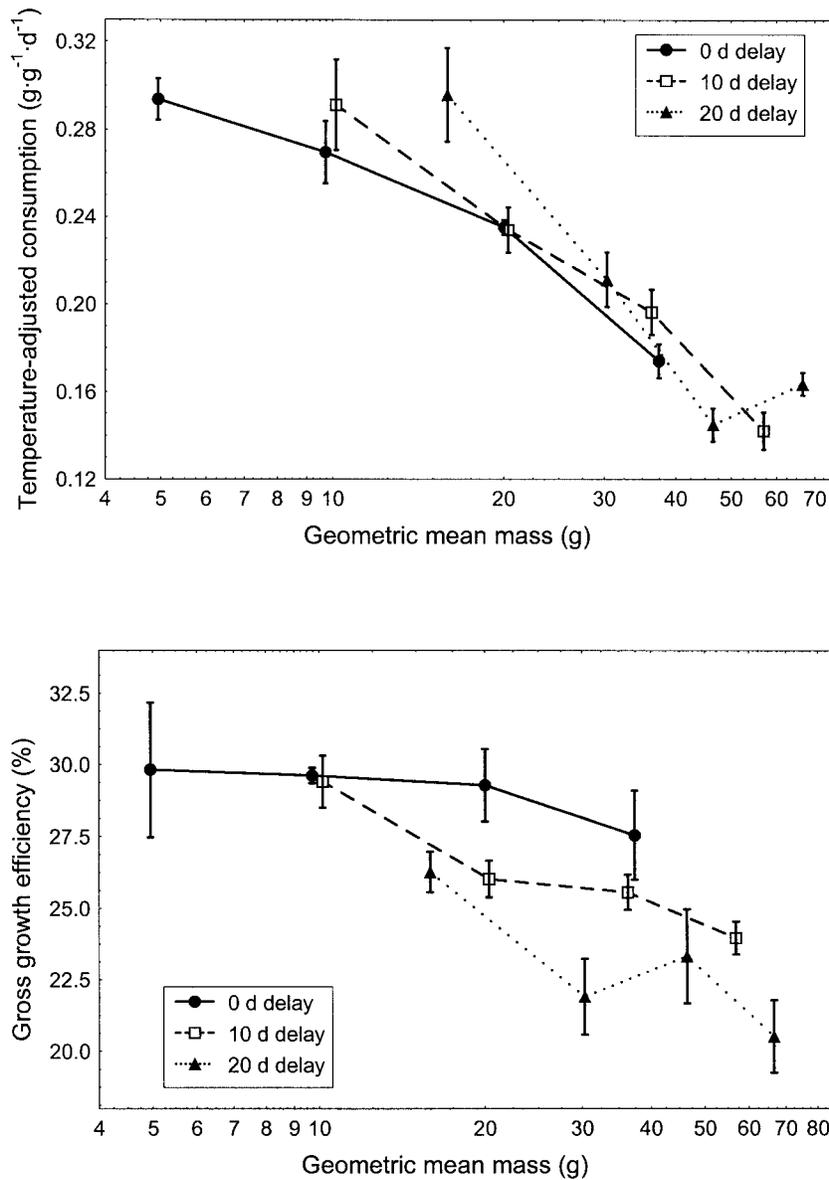


FIGURE 5.—Consumption rates and gross growth efficiencies of age-0 bluefish as functions of geometric mean weight (mass) in three treatments involving delays in the switch to a piscine diet. Error bars are SEs; horizontal error bars are shown in Figure 4 and are omitted here for clarity.

energy because they were synthesizing different body constituents from control fish. Several researchers examining body composition (carbohydrates, proteins, lipids) of fish with different feeding histories have found dissimilarities in mobilization and remobilization of body constituents (McCormick and Molony 1992; Mendez and Wieser 1993; Molony 1993; Kerrigan 1994). Our experiment did not address this possibility, and the

effect of delayed onset of piscivory on gut development and body composition should be examined in future work.

Investigators typically examine compensatory responses by comparing responses after the extremes of starvation and ad libitum feeding (Russell and Wootton 1992; Wieser et al. 1992). We compared fish fed ad libitum on diets of differing quality, which led to short-term reductions in

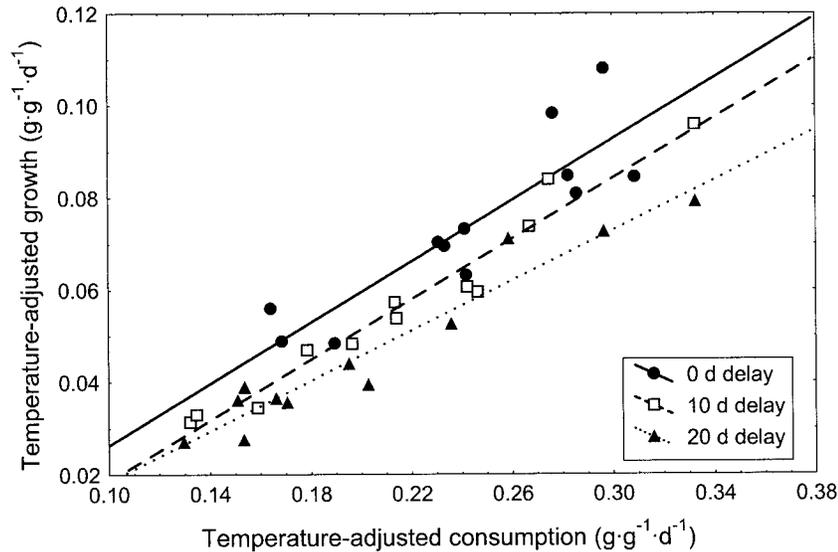


FIGURE 6.—Temperature-adjusted growth rates as functions of temperature-adjusted consumption rates for age-0 bluefish in three treatments involving delays in the shift to piscivory. Linear regressions describe the relationships for 0-d, 10-d, and 20-d-delay treatments.

growth (1.0–1.6 mm/d for delayed-piscivory fish versus >2.0 mm/d for controls). We still detected compensatory growth when deprived fish were given piscine diets, though the responses were modest and transitory. However, they helped move fish into faster growth modes. After the experiment's day 40 checkpoint, only 5 and 10 d of continued growth were necessary for fish in the 10-d and 20-d-delay treatments, respectively, to reach the size control fish had attained at day 40.

Growth compensation is often time dependent; the longer the period of food deprivation, the higher the magnitude of compensatory growth (Wieser et al. 1992). There was slight compensatory growth in both delay treatments but it was not time dependent; it reached about 6% above the control in both cases. However, the magnitude of gross growth efficiency variation in the different treatments was dependent on the length of the delay to piscivory.

Implications for Recruitment

Bluefish year-class strength likely depends on survival not only during the initial oceanic transport phase (Hare and Cowen 1993, 1996), but also during estuarine residence and subsequent out-migration (Juanes et al. 1994; Juanes and Conover 1995; McBride et al. 1995). In Narragansett Bay, Rhode Island, growth and loss rates (mortality and sum of immigration and emigration) of estuarine

juvenile bluefish were correlated with bluefish density, suggesting density-dependent regulation (McBride et al. 1995). Our results suggest that variation in the timing of estuarine arrival may further affect the size that bluefish attain by the end of the summer growing season and potentially a cohort's survival over the next winter.

Juanes et al. (1994) and Juanes and Conover (1995) hypothesized that the advection and migration of spring-spawned bluefish northward from South Atlantic Bight spawning areas gives them a size advantage over inshore fish that become their principal prey. They argued that an early estuarine arrival and an early onset of piscivory should be favored by natural selection because the resulting strong increase in growth rate may confer increased survival and fitness. Because bluefish do not show prominent growth compensation, selection for timing of estuarine arrival should be strong.

Bluefish grow exponentially in length during the larval and pelagic juvenile stages of their early life history (Hare and Cowen 1995). Based on otolith analyses, larvae grow at 0.3 mm/d (Hare and Cowen 1995) and pelagic juveniles grow at 0.8–1.0 mm/d (McBride and Conover 1991; Hare and Cowen 1995). Juveniles arrive in estuarine nursery areas in June at a size of about 60 mm FL, at which time growth rates increase to 1.3–2.1 mm/d. Sizes exceeding 250 mm FL are attained by the time

juveniles leave estuaries in the autumn during their migration southward (McBride and Conover 1991; McBride et al. 1995). The estuarine increase in growth rate is likely due to warmer waters and the switch to a fish diet. Results from our experiment confirmed previous findings that bluefish growth on an *Artemia* diet was lower than growth on a fish diet (Juanes and Conover 1994a).

The switch by bluefish from invertebrate to piscine prey coincides with a change in habitat from cooler shelf waters to warmer estuarine waters. We did not examine the effects of the change in temperature on growth directly, but it probably explains why our fish, which were kept in relatively warm estuarine water, grew faster on an *Artemia* diet (1.0–1.6 mm/d) than juvenile bluefish do on the shelf (0.8–1.0 mm/d). Therefore, delayed-piscivory fish had a better chance of catching up in our experiment than they would in the wild.

Juveniles arriving late at an estuary likely will encounter higher temperatures than their predecessors of the year had found. Upon shifting to piscivory, therefore, they may grow faster than their predecessors had grown immediately after dietary shifts and might thereby make up some of their growth disadvantage—if they can find fish prey of appropriate sizes. Late-arriving bluefish may find that prey fish have grown to sizes difficult to capture and consume. Young bluefish generally consume the smaller of the range of prey sizes available in the field (Juanes et al. 1994; Juanes and Conover 1995; Scharf et al. 1997; but see Gleason and Bengston 1996). Juanes and Conover (1994b) found that small bluefish captured 30-mm Atlantic silversides more than twice as successfully (65%) as they did 60-mm silversides (30%). Poor prey availability may negate any compensatory response that otherwise might be enhanced by higher temperatures.

Size during the summer estuarine growth phase, autumn southward shelf migration, and periods of overwintering may be important to young bluefish for both predator avoidance and foraging efficiency. If we use temperature-adjusted growth rates on day 40 to extrapolate experimental bluefish weights to September 15, when most age-0 bluefish have emigrated from estuaries (McBride and Conover 1991), we obtain bluefish sizes of 160 g for fish whose switch to piscivory was not delayed, 150 g for 10-d-delay fish, and 120 g for 20-d-delay fish. Therefore, the cost of a 20-d-delayed onset of piscivory would be about a 25% reduction in size. The larger the bluefish, the greater will be the size range of prey they can capture (Juanes and

Conover 1994b) and the lower the risk of mortality from gape-limited piscivores such as even larger bluefish.

Compensatory growth has important implications for understanding size-dependent processes thought to influence recruitment dynamics of fish (Houde 1987; Anderson 1988; Miller et al. 1988; Rice et al. 1997). For example, Bertram et al. (1993) found that slow-growing larvae of winter flounder *Pleuronectes americanus* that were small after metamorphosis stage could catch up in growth as juveniles; fast larval growth did not convey a sustainable size advantage to juveniles (but see Bertram et al. 1997). Larval Atlantic cod *Gadus morhua* that were switched from a low- to a high-food regime at day 11 posthatch were able to catch up in size by day 30 to larvae fed high food continuously (Gotceitas et al. 1996). Therefore, larvae and juveniles with different feeding regimes and growth trajectories can ultimately reach comparable size. Because bluefish did not exhibit complete growth compensation, an earlier switch to a faster growth rate on a piscine diet will provide a long-term size advantage.

Our data support the importance of the timing of habitat and diet shifts in determining subsequent fish size (Werner and Gilliam 1984). In freshwater systems, the timing of the shift to piscivory and its consequences for growth and body size affects survival and recruitment (Gutreuter and Anderson 1985; Buijse and Houthuijzen 1992). There are virtually no published examples of an increase in growth rate associated with the onset of piscivory in marine fishes other than bluefish (Juanes and Conover 1994a). The variability in the timing of habitat shifts by marine piscivores may also have lasting influences on body size and survival.

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