Abstract—Daily and seasonal activity rhythms, swimming speed, and modes of swimming were studied in a school of spring-spawned age-0 bluefish *(Pomatomus saltatrix)* for nine months in a 121-kL research aquarium. Temperature was lowered from 20° to 15°C, then returned to 20°C to match the seasonal cycle. The fish grew from a mean 198 mm to 320 mm (*n*=67). Bluefish swam faster and in a more organized school during day (overall mean 47 cm/s) than at night (31 cm/s). Swimming speed declined in fall as temperature declined and accelerated in spring in response to change in photoperiod.

Besides powered swimming, bluefish used a gliding-upswimming mode, which has not been previously described for this species. To glide, a bluefish rolled onto its side, ceased body and tail beating, and coasted diagonally downward. Bluefish glided in all months of the study, usually in the dark, and most intensely in winter. Energy savings while the fish is gliding and upswimming may be as much as 20% of the energy used in powered swimming. Additional savings accrue from increased lift due to the hydrofoil created by the horizontal body orientation and slightly concave shape. Energy-saving swimming would be advantageous during migration and overwintering.

Effects of seasonal change on activity rhythms and swimming behavior of age-0 bluefish (*Pomatomus saltatrix*) and a description of gliding behavior

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Bluefish (*Pomatomus saltatrix*) are temperate-zone fish with seasonal cycles of activity that revolve around lengthy coastal migrations. Age-1 and older bluefish migrate northward from April through July along the continental shelf of the United States from Florida to as far north as Maine. They spawn in southern and middle-Atlantic waters. These bluefish are collected on the shelf in spring at a temperature range of 8–23°C, mainly 10–19°C (Shepherd and Packer, 2006). Spring- and summer-spawned cohorts of age-0 bluefish arrive in coastal waters and estuaries beginning in June and remain there throughout summer at temperatures of 14–25°C (Nyman and Conover, 1988; Able et al., 2003). Age-0 fish reside in estuaries and coastal waters until late October, whereas older age classes remain until late November (Scharf et al., 2004; Shepherd and Packer, 2006). Bluefish migrate southward along the Atlantic continental shelf from along the beaches to well offshore. Temperatures on the shelf where they are captured in fall are 10–27°C, mainly 17–25°C (Shepherd and Packer, 2006). Adults and the age-0 spring-spawned cohort spend winter on the outer continental shelf and slope from Virginia south to Florida (Shepherd and Packer, 2006; Shepherd et al., 2006). These lengthy migrations involve risks and are energetically costly.

With increasing temperature, the rates of metabolic processes of ectotherms increase (the bioenergetic response) (Fry, 1971; Brown et al., 2004). Within the thermal tolerance ranges of most fishes, as temperature increases, activity, food consumption, and growth increase (Beamish, 1978). Bluefish have a higher rate of increase in metabolism with temperature than their main competitors in the temperate zone, weakfish (*Cynoscion regalis*) and striped bass (*Morone saxatilis*) (Hartman and Brandt, 1995). The bioenergetic response in bluefish was observed experimentally in a school of 550–650 mm adults held in a 121-kL research aquarium under a summer photoperiod (Olla and Studholme, 1971). At 19.5°C, they swam at 40–60 cm/s. As the temperature increased to 30°C over a month, their swimming speed increased to 80–100 cm/s. The high food consumption rates of bluefish rival those of tropical species (Juanes and Conover, 1994; Buckel et al., 1995). Increased food consumption at higher temperatures is accompanied by increased growth rates in bluefish (Buckel et al., 1995; Hartman and Brant, 1995).

Diel activity cycles or rhythms in bluefish are known. Olla and Studholme (1972) examined effects of photoperiod upon the activity of six age-1+ bluefish in the aforementioned 121-kL aquarium. The mean swimming speed of the school increased after transition to daylight, peaked at midday, and slowed in afternoon. In darkness, the school was more dispersed, interfish distance increased, and speeds were more variable (Olla and Studholme, 1971, 1972). Less is known about seasonal rhythms in

bluefish. Under a winter photoperiod, as water temperature decreased, swimming speed correspondingly decreased (Olla and Studholme, 1971), but a longer study of behavior over a seasonal cycle has not been undertaken.

Bluefish use sustained or powered swimming for daily activity and long distance travel. They propel themselves by flexing the rear part of the body and tail and use their other fins mainly for stability and maneuvering. Powered swimming can be used for long periods without fatigue, although it has energetic costs (Beamish, 1978). For prey capture, bluefish use burst swimming at speeds recorded at up to 800–1000 cm/s (Olla et al., 1970). A novel and unexpected locomotory behavior was witnessed by Studholme and others during an unpublished study of a school of juvenile bluefish in the 12- kL research aquarium in 1984–85. At night, individual fish rolled onto their sides and, with their bodies and fins held still and slightly curved, glided downward diagonally, and then ascended. This behavior is remarkable in teleost fishes with laterally compressed bodies, because these fish are assumed to swim in a vertically oriented manner.

In 1995, a study was designed to expand upon previous bluefish research (Olla and Studholme, 1971, 1972; Olla et al., 1985) to examine in detail the seasonal cycle of activity in bluefish from fall through winter and spring. Unfortunately, the documentation of the cycle of behavior and gliding in age-0 bluefish from the 1984–85 study was lost in a fire. Therefore, a school of age-0 bluefish was brought to an aquarium of similar dimensions to that used earlier. Food consumption, swimming speed (as a measure of activity), and mode of swimming were recorded to determine their relationship to changing temperature and photoperiod. It was hoped that the previously observed but undescribed gliding behavior would recur. Particular attention was paid to changes in behavior that could be related to migration, overwintering, and the bioenergetic response.

Materials and methods

Source of fish and laboratory conditions

Spring-spawned age-0 bluefish were captured by hook and line from Sandy Hook Bay, NJ, over the period of a week. One hundred and five fish were placed in the research aquarium on 3 August 1995. The research aquarium, located at the National Oceanic and Atmospheric Administration James J. Howard Marine Sciences Laboratory, Sandy Hook, Highlands, NJ, held 121 kL (32,000 gallons), was 10.6 m by 4.5 m, and had a water depth of 2 m (Olla et al., 1967). Water originated from Sandy Hook Bay and salinity in the aquarium varied with ambient conditions (19 to 23 psu). The aquarium had a flow rate of 400 L /min and 10% of the water was replaced each week. Heaters and chillers were used to maintain the desired temperature (±0.5°C). Photoperiod matched that at the latitude of

North Carolina (35°N) with a minimum of 9.3 hr of light at winter solstice. Light intensity at the bottom was 206 lux (0.0027 mEinsteins PAR) at midday and 0.17 lux at night, which allowed for video recording.

Water temperature was controlled to approximate that in migration and at summering and wintering areas, as determined from historical data from the NOAA National Data Buoy Center. The temperature was set at 20°C from the start of the experiment through 9 October. Then it was decreased incrementally over 8 wk (0.105°C/d) until it reached 15°C, the average minimum temperature off North Carolina south of Cape Hatteras. The temperature in the aquarium was raised from 15 to 20°C (0.194°C/d) over the period from 24 May to 23 June, simulating temperature increases in New Jersey coastal waters.

Feeding and growth

Bluefish were usually fed each afternoon, 5 d/wk. Live mummichogs *(Fundulus heteroclitus)* were weighed and tossed into the middle of the aquarium until the bluefish had fed to satiation. In winter, the bluefish did not feed as readily and therefore were left undisturbed to feed for an hour. Then the uneaten mummichogs were removed. A subset of fish was seined from the aquarium, anaesthetized, measured by total length (TL, to ~1 mm), and weighed (to ~1 g) every two months. The total weight of food consumed each week was divided by the calculated weight of all fish in the aquarium that week, and then divided by seven, to obtain the consumption rate in g food per g body weight per day (BW/d).

Daily and seasonal rhythms

Activity was measured by swimming speed. For each observation, an actively swimming bluefish was timed while it crossed a measured portion of the far wall of the aquarium. Only fish close to the wall were timed. During the first 5 minutes of each hour of the day, five randomly selected fish were timed and their speeds were averaged. When live observations could not be made, data were taken from videotapes made with a time-lapse video recorder and camera placed at a window opposite the far wall of the aquarium and set to record for five minutes at the start of each hour. Live observations were also made for longer periods during day and night. Every three or four weeks, or more often, a complete set of swimming speeds was recorded, in which 24 five-minute segments were observed on each of seven days, for a total of seventeen weeks. Speeds were expressed in cm/s and body lengths per second (BLl/s). For comparisons of day and night activity, a subset of the swimming speed observations were used, from 0900 through 1500 and 2100 through 0300.

Modes of swimming

The general behavior of the school, depth of swimming, and modes of swimming were noted in the first 5 min-

Table 1

Number of bluefish (*Pomatomus saltatrix*) measured, average total lengths (TL, mm), and weights (g), with ranges, at intervals during the activity rhythm experiment, 1995–96.

Date	Number of fish measured	Average total length (TL, mm)[1]	Length range (mm)	Average weight (g)	Weight range (g)
10 August 10 1995	110	161.5	125–192	34.8	16.6–60.5
12 October 1995	24	229.4	185–261	139.5	68.1–205.3
15 November 1995	26	251.8	210–278	196.7	100.7–259.5
17 January 1996	25	265.7	223–290	219.9	126.0–283.9
22 May 1996	27	302.6	268–334	285.2	186.7–389.7
28 June 1996	64	325.2	250–357	369.0	243.7–470.5

[1] Fork length = 0.8647 (TL) + 7.0656 for TL range 125 to 388 mm.

utes of each hour. During two weeks in January, counts were made to determine the proportion of fish that were gliding. All fish that passed in each 5-min observation period were counted, usually 300–600 observations. Then the videos were replayed and only the gliding fish were counted. Ascending fish were difficult to see and could not be counted.

Glide angles ($\acute{a}$), upswimming (returning to initial depth) angles (β), and glide and upswim distances (a_1, a_2) (Weihs, 1973; Magnuson, 1978) were determined for individual fish from videotapes from the first week of January 1996. Angles were determined from successive still images and reported as the angle deviating from a horizontal path. Speeds of individuals over ground were also obtained from successive images.

An additional study was conducted from November 2006 through May 2007, under the same experimental conditions, to focus on details of gliding behavior. Age-0 summer-spawned bluefish (n=71, length range 135–216 mm TL) were used. Glide angles were measured as before, and body roll angles were measured from images of these fish gliding straight toward a video camera.

Results

Feeding and growth

At the start of the experiment, the mean length of the bluefish was 162 mm total length (TL) (147 mm fork length) and the mean weight was 35 g (Table 1). Their condition factor (Fulton's K) averaged 1.08. The day after placement into the aquarium the fish fed readily. In early September, at 20°C, they consumed 13% body weight/d (BW/d) (Table 2). Consumption rates decreased thereafter, falling to 2.0–3.8% BW/d while the water temperature was 15°C. After the temperature was raised once again to 20°C, food consumption rose to 5.9% BW/d. Fish grew throughout the experiment, but the rate of increase in length and weight slowed as fish

size increased. At the end of the experiment on 28 June 1996, the mean length of the bluefish was 325 mm TL and the mean weight was 369 g (Table 2). At that time 67 bluefish survived in excellent health and their condition factor averaged 1.55. Growth rate over the entire experiment was 0.96 g/d.

From about 8 April to 4 May 1996, the fish were infested with the parasitic protozoa *Brooklynella hastili*. Swimming speed decreased, pale patches appeared on the skin, some scales were lost, and food consumption was unusually low (0.9% BW/d on week of 28 April to 4 May). Two fish died. The parasites were killed by lowering the salinity to 13 psu and then raising it to ambient psu from 1 May through 4 May. The following week the appetites and swimming speeds of the fish returned to levels similar to those before the infestation.

Daily and seasonal rhythms

After one week the bluefish settled into a pattern of swimming in a counterclockwise circle and individuals were spaced evenly around the aquarium perimeter. They occupied all depths of the aquarium. Individuals occasionally shot ahead or out of the circular path, but usually the fish remained apace with one another. In all months the bluefish swam faster during daylight than at night, accelerated each morning after light increased and usually attained maximum speed around noon. A representative diel rhythm during fall is shown for the week beginning 29 October 1995 (Fig. 1A). During the week of 31 December (Fig. 1B), the peaks of activity near noon were brief. Speeds in cm/s were highest when the fish had grown, as shown on the week of 26 May 1996 (Fig. 1C).

Activity varied seasonally in relation to water temperature and light in the aquarium. From early October through early December, mean swimming speeds decreased gradually from 38.3 to 31.2 cm/s (Fig. 2, Table 2). Mean speeds were irregular in winter, and at a minimum in early March (Fig. 2). Speeds increased

Table 2

Light, temperature, and biological measurements of bluefish (*Pomatomus saltatrix*), 1995–96. Seventeen weeks are presented in which observations of swimming were made at each hour of the day and averaged for the week. Total lengths and weights were calculated from subsamples measured on the dates in Table 1. All other quantities, hours of light per day, water temperature (°C), food consumption in percent body weight per day (% BW/d), and swimming speeds in cm/s and body lengths per second (BL/s), were averaged for the week.

Week	First day of week	Number of fish	Light (hr/d)	Mean temperature (°C)	Bluefish total length (mm)	Bluefish weight (g)	Food consumption (% BW/d)	Swimming speed (cm/s)	Swimming speed (BL/s)
7	10 Sep	89	12.6	20.7	198.3	78.8	13.0	35.8	1.81
11	8 Oct	72	11.4	19.2	228.2	137.3	8.8	38.3	1.68
14	29 Oct	72	10.5	17.9	242.0	170.0	9.3	40.0	1.65
18	26 Nov	71	9.6	15.3	254.7	201.3	4.1	33.6	1.32
20	10 Dec	71	9.4	15.1	257.7	206.3	3.8	31.2	1.21
23	31 Dec	71	9.4	15.0	262.3	214.1	2.5	35.0	1.33
27	28 Jan	71	10.1	15.0	269.3	225.9	3.1	38.5	1.43
31	25 Feb	71	11.2	15.0	277.2	239.3	3.1	34.8	1.25
32	3 Mar	71	11.6	15.0	279.2	242.8	2.0	34.3	1.23
33	10 Mar	71	11.9	15.0	281.2	246.3	2.2	31.1	1.11
34	17 Mar	71	12.2	15.0	283.3	249.9	3.6	37.0	1.31
35	24 Mar	70	12.5	15.0	285.3	253.6	2.1	46.0	1.61
36	31 Mar	69	12.8	15.0	287.4	257.2	3.2	45.0	1.56
40	28 Apr	67	13.9	15.5	295.8	272.5	0.9	38.2	1.29
44	26 May	67	14.8	17.2	306.3	298.1	4.7	44.2	1.44
46	9 Jun	67	15.0	19.2	315.3	330.4	4.5	51.2	1.62
47	16 Jun	67	15.0	20.4	319.9	347.9	5.9	53.3	1.67

in late March with increase in day length, although temperature was unchanged. When bluefish measured about 285 mm in late March, their mean speeds rose above 40 cm/s and they became capable of much higher maximum speeds. In June 1996, swimming speeds in cm/s were significantly greater than those in September 1995 (*t*-test, $P<0.01$, both at 20°C). Speeds in body lengths/s, however, showed no trend during the experiment (Table 2), because larger fish can swim faster.
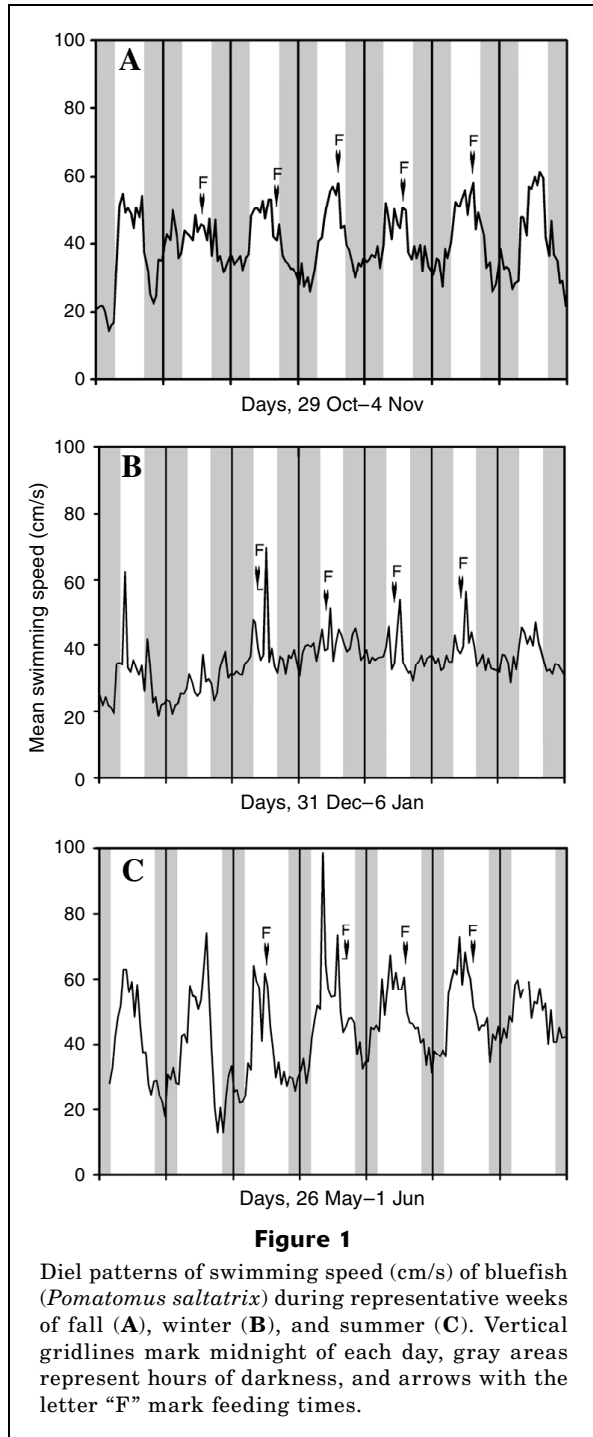
When twilight speeds were removed from the dataset, there was no overlap in day and night speeds (cm/s) or their standard deviations (Fig. 3). In fall, the mean speed during daylight was >52 cm/s, and the mean night speed was between 28 and 38 cm/s. The decrease in mean speed in winter (Fig. 2), particularly in January, was due only to decreased day speed and briefer periods of peak activity (Fig. 1B). Night speeds were similar all year, except for certain periods of extremely slow swimming in spring, as described below. By mid-June, at the end of the study, the difference between day and night activity was greater because the mean daylight speed increased to 68.6 cm/s.
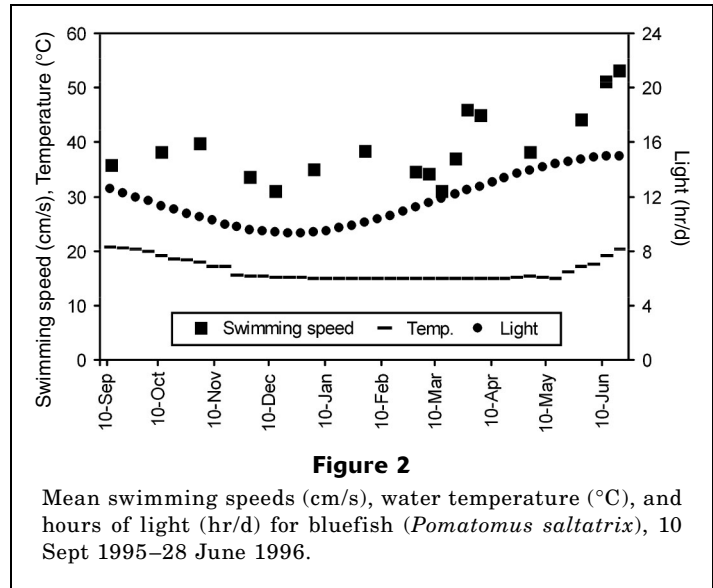
Modes of swimming

Bluefish used various modes of swimming in the research aquarium (Table 3). The most prevalent mode was pow-ered swimming, which they performed by propelling themselves by beats or contractions of the muscles of the rear of the body and caudal peduncle. During powered swimming, the body orientation was vertical, while the pectoral and pelvic fins were folded except to make adjustments in direction. Fish in the aquarium used this mode primarily while circling in a level horizontal ring. At other times, powered swimming in a vertically undulating or sine-wave-like pattern was observed at all depths of the aquarium. The entire school participated in this behavior, often for hours.

During periods of undulatory swimming, some fish glided on their sides. To glide, a bluefish rolled onto its side, ceased body and tail movement, and its momentum carried it gradually downward (Figs. 4 and 5). The body was held flat or in a slightly convex shape. The dorsal, anal, and pelvic fins were stretched out and curved up or down slightly in response to water flow or for changing direction. The pectoral fins were pointed outward and sometimes sculled or steered, the tail was still, and the tail fin lobes were curved up or down slightly. The body rolled by less than 90° (i.e., not parallel to the bottom). Either side might be oriented downward and a fish sometimes switched sides in mid-glide. A fish encountering a side of the aquarium sometimes turned and continued to glide downward. Only a few members of the school glided at one time, and they accompanied

Figure 1

Diel patterns of swimming speed (cm/s) of bluefish (*Pomatomus saltatrix*) during representative weeks of fall (**A**), winter (**B**), and summer (**C**). Vertical gridlines mark midnight of each day, gray areas represent hours of darkness, and arrows with the letter "F" mark feeding times.

Figure 2

Mean swimming speeds (cm/s), water temperature (°C), and hours of light (hr/d) for bluefish (*Pomatomus saltatrix*), 10 Sept 1995–28 June 1996.

Table 3

Modes of swimming behavior seen in bluefish (*Pomatomus saltatrix*) in a laboratory aquarium over an annual cycle.

Mode of swimming	Description
Powered	Horizontal swimming in upright orientation, propelled by body and tail
Undulating	Powered swimming while fish continually changed depth
Burst	Brief, high-speed swimming
Gliding	No propulsion, oriented on side, descending or sinking diagonally
Upswimming	Powered swimming to ascend from a glide to the initial level
Milling	Upright orientation, swimming very slowly or almost motionless
Side-swimming	Powered swimming, oriented on side

nongliding fish at approximately the same speed and along the same path. A fish righted itself by rolling smoothly or by flexing the body and turning abruptly. After righting itself, a fish returned to its initial level or briefly swam horizontally. Gliding occurred only when the school was swimming briskly and in an undulating path. Gliding nearly always occurred at night in this study. In the dark, fish gliding with their bellies facing the camera could be seen by the reflection of light off

their sides, but fish with their backs to the camera were difficult to detect.

Gliding was sometimes part of a sequence of side-oriented swimming behaviors. Side-swimming (Table 3) occurred during undulatory swimming, while a fish was descending, ascending, or moving horizontally, and often before or after a glide. Fish ascending from a glide sometimes side-swam up all or part of the distance. They usually returned smoothly along the undulating path of the rest of the school, but at times they ascended very steeply and swam against the direction of the school.

Gliding was prevalent throughout the study and occurred most frequently in fall and winter (Fig. 6). In

Table 4

Angles of gliding and upswimming, distances (cm), and horizontal speeds over ground (cm/s) of individual bluefish (*Pomatomus saltatrix*), January 1996, during the activity study. Angles of glides are in degrees below horizontal; angles of upswimming are in degrees above horizontal. Dashes indicate that no observations were available.

Angle of glide	Distance of glide (cm)	Horizontal speed (cm/s)	Angle of upswimming	Distance of upswimming (cm)	Horizontal speed (cm/s)
6.3	45	22.1	12.4	125	30.5
7.1	94	32.2	2.2	93	31.8
10.7	228	20.6	7.9	44	18.0
11.5	43	21.8	7.3	60	20.3
13.2	103	34.7	6.3	103	25.7
15.3	50	24.6	29.4	172	28.7
15.3	25	26.0	22.6	94	27.9
17.5	126	19.7	6.8	58	21.0
18.2	78	25.3	26.7	194	23.8
18.2	—	—	5.5	125	20.5
18.3	91	22.8	18.6	89	20.6
18.5	141	27.2	7.5	50	24.6
18.9	87	29.0	13.0	66	20.0
19.5	93	30.4	15.3	85	39.3
19.8	131	21.1	10.5	119	28.4
19.9	80	—	3.7	162	—
20.0	64	20.7	2.8	97	31.7
20.4	94	—	1.6	210	—
20.8	155	21.7	13.9	43	21.8
21.3	172	23.7	10.8	90	17.0
21.9	82	19.9	24.4	107	47.3
23.6	130	24.9	4.4	98	24.1

December and January, glides occurred during as many as 14 hr/d, even during daylight. During the greatest frequency of occurrence of the behavior in January, the proportion of fish gliding was also greatest, up to 14%.

Angles of descent during gliding ranged from 13–26° from the horizontal, and angles of ascent ranged from 2–29° (Table 4). The average angle of descent for all fish was 17.9° and for ascent by those that followed the undulating path of the school was 12.2°. The average speed of descent was 24.9 cm/s and of ascent was 26.3 cm/s. Using the gliding model of Weihs (1973), we diagrammed the path of a bluefish selected from Table 4. It glided at angle $\acute{a}$=19.8° for a distance a_1=131 cm and ascended at angle β=10.5° for a distance a_2=119 cm, a total distance of 250 cm. If it had actively swum, the horizontal distance would have been 240 cm.

Body roll angles were not measured in 1995–96, but in 2007 bluefish averaged 47° from vertical while gliding (n=33, maximum 65°). The glide angle $\acute{a}$ averaged 19.7° (n=23) in 2007.
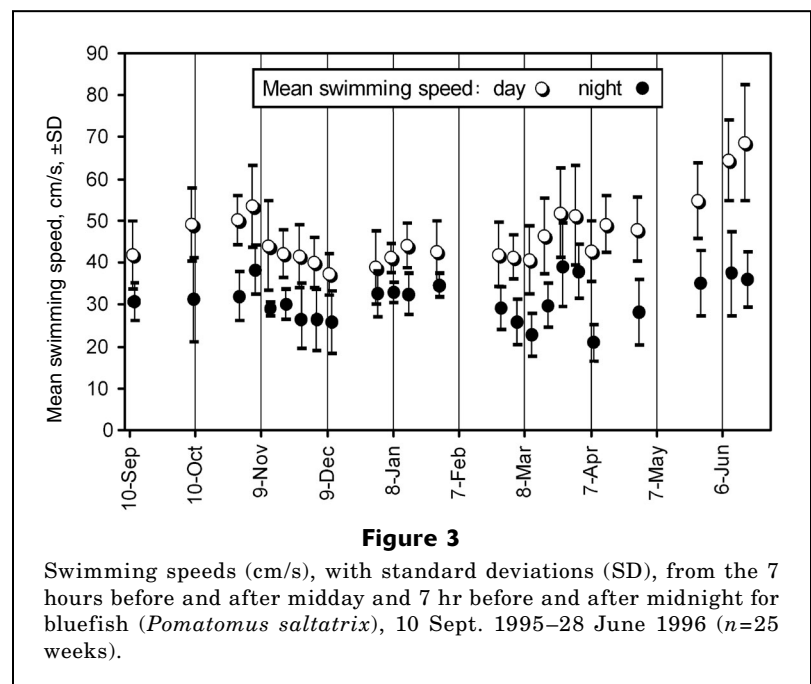
Figure 3

Swimming speeds (cm/s), with standard deviations (SD), from the 7 hours before and after midday and 7 hr before and after midnight for bluefish (*Pomatomus saltatrix*), 10 Sept. 1995–28 June 1996 (n=25 weeks).

During periods when gliding was rare, bluefish sometimes moved very slowly at night in a swimming mode that can be called "milling." The orderly spac-
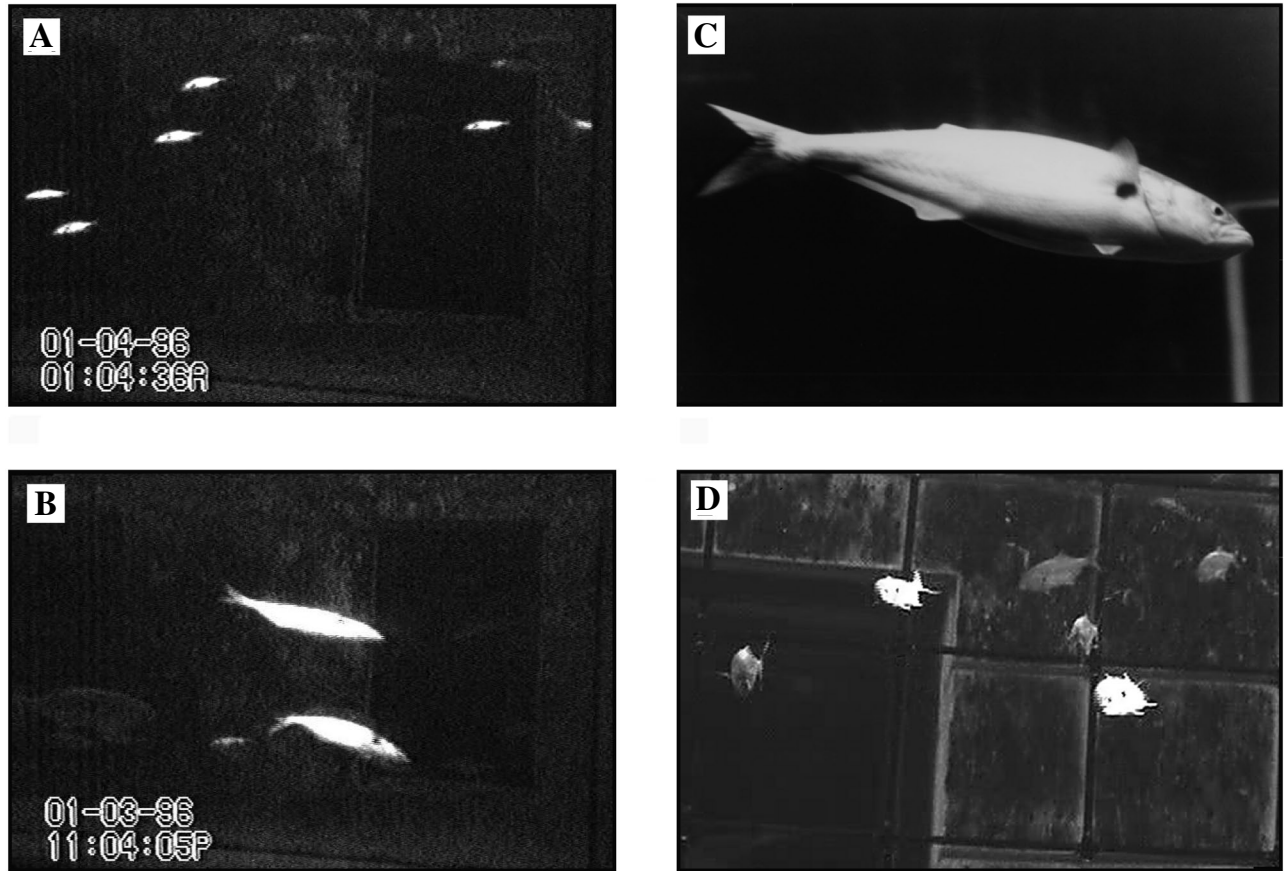
Figure 4

Still images of gliding bluefish (*Pomatomus saltatrix*) during the activity study. (**A**) Numerous gliding fish near the far side of the aquarium at night, recorded with a video camera, winter 1996, (**B**) one gliding (top fish) and one side-swimming fish (lower fish) close to the window near the video camera, winter 1996, (**C**) photograph from below a gliding fish, spring 1995, (**D**) gliding fish (lighter fish) are keeping pace with vertically oriented fish (gray-toned individuals) in the school, recorded with a video camera, spring 2007.

ing of the school was disrupted and fish dispersed with no common direction. Milling fish stayed near the water surface, apparently neutrally buoyant, and moved extremely slowly, propelled by occasional gentle flexes of the pectoral fins and tail. Milling was noticed beginning 6 February and was common through mid-March. Another period of milling occurred in the last week of April and the beginning of May during the parasite infestation.

Discussion

Feeding and growth

The period of extremely high food consumption and growth per body weight does not last very long in young bluefish. In this experiment, food consumption was greatest when the fish were smallest, as was anticipated from the literature. From 16% body weight per day (BW/d) in 35-g fish, food consumption rate decreased to 1–5% BW/d in 369-g fish the following spring. Similarly, in laboratory mesocosms at 21°C, growth rates of the smallest, (mean 2.6 g), age-0 fish were as high as 9.2% BW/d, but those of larger (mean 10.2-g) fish were 2.7% BW/d (Buckel et al., 1995). In small age-0 field-caught bluefish, food consumption rates were >30% BW/d (Juanes and Conover, 1994; Buckel et al., 1995). Rapid food intake permits rapid growth to a size where fish are less vulnerable to predators.

Growth in the research aquarium was continuous, and the increase in length was comparable to that of wild bluefish in the middle-Atlantic states. The fish in the aquarium grew to a mean total length of 300 mm (265 mm FL) by 22 May, whereas wild age-1 fish originating from a spring-spawned cohort are about 250 mm FL when they are caught in spring (Shepherd and Packer, 2006).

Daily and seasonal rhythms

In this and earlier studies (Olla and Stud-holme, 1972), bluefish in the laboratory were active during the day and schooled more cohesively during day than at night. Gliding and milling occurred at night. This timing of passive behaviors may alternate with active behaviors such as feeding during the day. Field studies corroborate these laboratory-observed rhythms. Stomach fullness in bluefish was greatest in the afternoon (Marks and Conover, 1993; Juanes and Conover, 1994). Bluefish were more vulnerable to otter trawls during daylight hours than at night (Munch, 1977; Wiedenmann and Essington, 2006). The latter authors hypothesized that bluefish descend to near-bottom during the day to feed upon schools of anchovies, *Anchoa* spp., and then ascend at night to where they are less accessible to otter trawls.

The present study is the first ever published on the behavior of bluefish over a yearly cycle in real time in a research aquarium. Bluefish changed activity patterns by season, as exemplified in the fall, when their swimming speeds and the day-night differences in speeds gradually decreased as temperature decreased. No period of restlessness or accelerated swimming was seen during the fall, as had been seen in an earlier study (Olla and Studholme, 1971). In that study, a school of adult bluefish was acclimated to 19.5°C, under a winter photoperiod, and were swimming at a mean speed of 20–30 cm/s. When the water was chilled to 11.5°C over 29 days (0.25°C/d), the fish, instead of swimming more slowly as predicted by the bioenergetic response, swam dramatically faster at 60–100 cm/s. Increased activity in reaction to chilling was also seen in tautog (*Tautoga onitis*) and sablefish (*Anoplopoma fimbria*) (Olla et al., 1980; Sogard and Olla, 1998). The fish in these latter studies may have been undergoing short-term stress responses associated with the urge to migrate or escape. In the present study, temperature was lowered half as fast (0.105°C/d in 57 days) as in the earlier study (Olla and Studholme, 1971), and the fish could adjust to the temperature change without a stress response.

In spring, the bluefish in the present study accelerated their swimming speed in response to the cue of increased daylength, without any cue of increased temperature. Similarly, bluefish on their wintering grounds respond to changes in day length and begin migration in time to arrive at their summer grounds when tolerable temperatures are available.

Modes of swimming

Bluefish exhibit speed and swimming endurance although they do not have the body and caudal-fin shapes
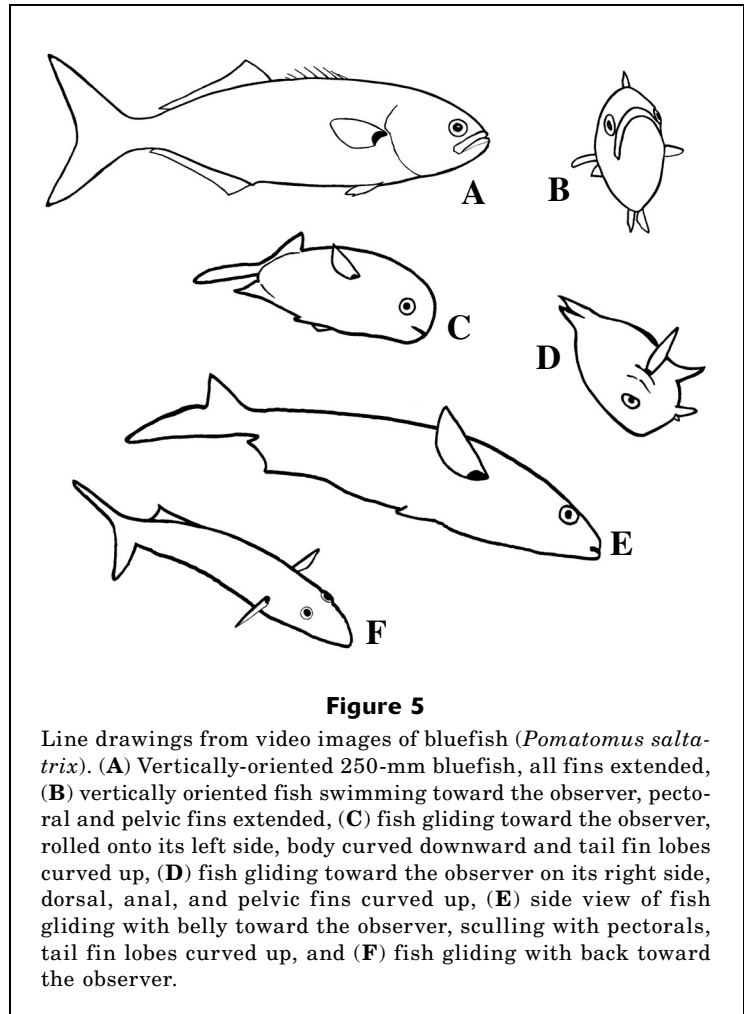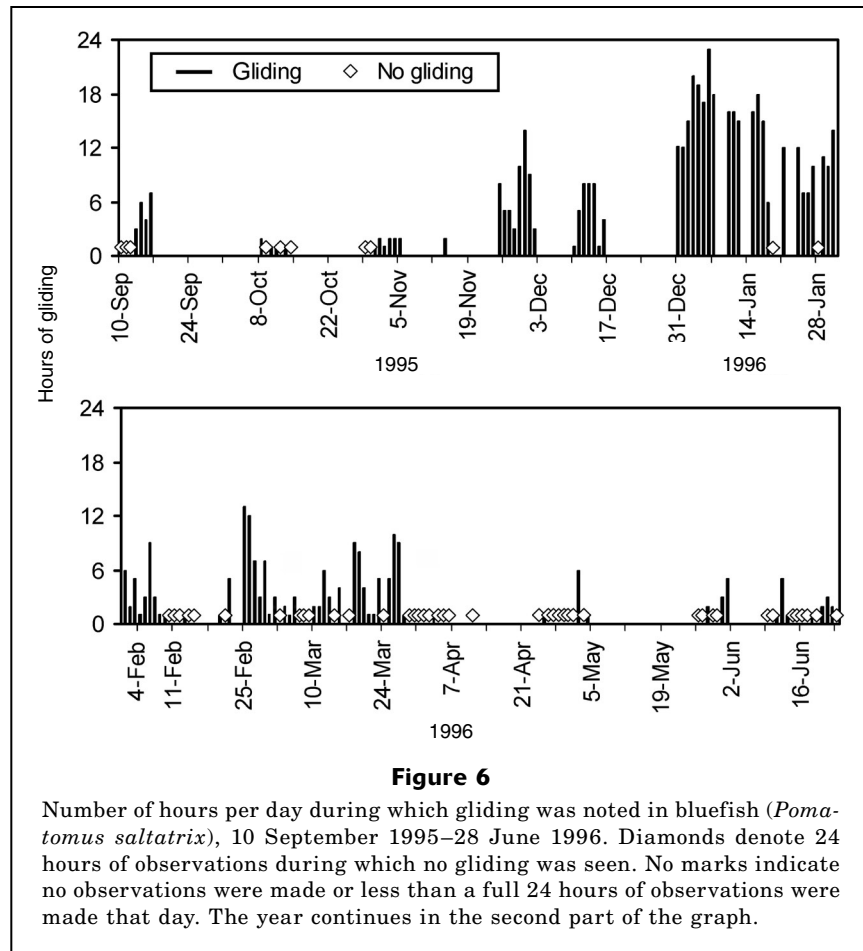

Figure 5

Line drawings from video images of bluefish (*Pomatomus saltatrix*). (**A**) Vertically-oriented 250-mm bluefish, all fins extended, (**B**) vertically oriented fish swimming toward the observer, pectoral and pelvic fins extended, (**C**) fish gliding toward the observer, rolled onto its left side, body curved downward and tail fin lobes curved up, (**D**) fish gliding toward the observer on its right side, dorsal, anal, and pelvic fins curved up, (**E**) side view of fish gliding with belly toward the observer, sculling with pectorals, tail fin lobes curved up, and (**F**) fish gliding with back toward the observer.

optimally adapted for sustained swimming performance, as are found in pelagic taxa such as scombrids (Webb, 1978). The bodies of scombrids are cylindrical, elliptical in cross-section, and highly streamlined to minimize frictional drag. The optimal caudal fin for sustained swimming is stiff, has a high aspect ratio, and a lunate shape that reduces drag produced by the wake of the fish (Nursall, 1958; Webb, 1978). In the scombriform mode of propulsion, thrust is generated by the caudal peduncle and tail only (Blake, 2002). In contrast, bluefish use the anguilliform swimming mode, in which thrust is generated by muscular contractions along the body and tail (Webb, 1978). The tail of a bluefish produces 65% of the total thrust (Ogilvy and DuBois, 1982). Like scombrids, bluefish are streamlined and have elliptical body cross sections, but their tails are flexible and semilunate, suited for burst swimming as well.

To glide, an aquatic animal must be negatively buoyant, have sufficient forward momentum, and possess a foil shape that produces lift to counteract sinking. A foil has a downward-facing arch and an asymmetrical camber ratio that produces less pressure below it than above it. At sufficient speed, the horizontal body plan

Figure 6

Number of hours per day during which gliding was noted in bluefish (*Pomatomus saltatrix*), 10 September 1995–28 June 1996. Diamonds denote 24 hours of observations during which no gliding was seen. No marks indicate no observations were made or less than a full 24 hours of observations were made that day. The year continues in the second part of the graph.

of flatfishes and the large area of the pectoral fins of certain sharks generate enough lift to permit gliding without stalling (Weihs, 1973). Sharks and flatfishes, which have no swim bladders, are always negatively buoyant. The shortfin mako (*Isurus oxyrinchus*), great white shark (*Carcharodon carcharias*), and blue shark (*Prionace glauca*) use bouts of gliding and upswimming in undulatory patterns over tens of meters (Klimley et al., 2002). Tuna (*Thunnus* spp.), billfish (Istiophoridae), and marine mammals glide while performing diving oscillations (Weihs, 1973; Klimley et al., 2002).

Reports of gliding in teleosts are scarce, and such reports have mostly been based on observations of flatfishes. American plaice (*Hippoglossoides platessoides*) used a glide-and-settle mode of swimming, gliding over 50 m while avoiding simulated trawl gear (Winger et al., 2004). Japanese flounder (*Paralichthys olivaceus*) used bouts of gliding and powered ascent in the field and in the laboratory (Kawabe et al., 2003, 2004). Ogilvy and DuBois (1982) stated that bluefish cannot glide, because the surface area of their pectoral fins is not enough to produce much lift, and if they stopped propelling themselves, they would stall. However, bluefish do not stall because they turn onto their sides and increase their horizontal surface area.

Energetics

Force required by a fish to swim forward must overcome pressure drag in front of the fish, frictional drag from distortion of water flow over the body, and turbulence from the swimming movements themselves. The drag in powered swimming is related to the drag created by gliding by a ratio, k: (Weihs, 1973; Magnuson, 1978),

$$k = Fs/Fg,$$

where Fs = the drag force of swimming; and
Fg = the drag force of gliding.

The ratio, k, varies between 1 and 4 (Weihs, 1973). In a scombriform lunate-tailed tuna, the kawakawa (*Euthynnus affinis*), k has been estimated at 1.2 (Magnuson, 1978). The streamlined body of the kawakawa generates relatively little drag during swimming; therefore gliding does not save it much energy. In contrast, a fish that uses anguilliform propulsion, such as a trout, dace, flatfish, or bluefish, may have a k of 3 to 4 (Weihs, 1973). A fish uses less energy or thrust during a cycle of gliding and upswimming than during horizontal powered swim-

ming over the same distance (Weihs, 1973; Webb, 1978). The smallest possible glide angle produces the greatest energy benefits. A fish having $k=3$, that achieves a glide angle $\acute{\alpha}$ of 11°, and uses the most advantageous upswim angle β of 37° saves 49% of the energy needed for a straight swim over the same distance, although it covers the distance in 12% more time (Weihs, 1973).

If $k=3$ for a bluefish and the glide and ascent angles are those measured in this study, namely, $\acute{\alpha}$ = 18° and β = 12°, a bluefish would save 20% of the energy it would use to actively swim the same horizontal distance. In January 1996, 14% of the bluefish in the aquarium were gliding at once, and if one multiplies by two to include the ascending fish that were unseen, more than one-quarter of the school was using this energy-saving mode at one time.

The function of gliding in migration has been studied outside the phylum of fishes. Some birds, particularly raptors, minimize the use of powered flight in migration by soaring upward on a rising heated air current and then gliding as far as possible to the next thermal current (Kerlinger, 1989). While soaring, birds flatten and extend their wings to increase their surface area. While gliding, they partially fold their wings to adjust their wing area and foil shape, to control the angle and speed of descent. Energy used in the soar and glide mode of flight for a hypothetical raptor, depending on its weight and wing area, is 10–40% of the energy used in powered flight. A broad-winged hawk (*Buteo platypterus*) in migration, given atmospheric conditions that produce consistent thermal currents, can fly 8 hr/d and travel 320 km/d with only occasional wing flapping (Kerlinger, 1989).

If a bluefish is turned onto its side, its tail shape is similar to that of the most energy-efficient tail shape of birds that glide. The most efficient lift-to-drag ratio is produced with a forked tail, the outermost feathers of which are twice the length of the innermost, and by a 120° angle when the tail is spread (Thomas, 1997). In juvenile bluefish, the ratio of the lengths of the outer to inner caudal fin rays (measured from a straight line across the narrowest part of the caudal peduncle) is about 2:1. The angle of the fork, however, is 65–80°.

Migration capability and swimming speed

When one compares information from bluefish tagging data with information on swimming capability ascertained in the laboratory, one concludes that migration is not a continuous activity. Recently, bluefish migration data from years of tagging studies along the U.S. eastern coast were summarized, and recoveries were grouped by season and distance (Shepherd et al., 2006). Among the southward-traveling bluefish, one group had a relatively short migratory path (about 600 km), having been tagged in the middle-Atlantic region and recaptured off North Carolina. Longer movements (up to 2000 km) were made by another group of fish tagged in the northern region (New England through

New York Bight) and recaptured from the Carolinas south to Florida. The speeds calculated from the tag recoveries from fish at large for 2–3 mo, averaged 5.9 km/d (Shepherd et al., 2006), which are much less than speeds observed in laboratory studies. In the research aquarium, spring-spawned age-0 fish, in the late fall, including all hours of day and night and periods of gliding, averaged 33.6 cm/s (29 km/d). They would be able to travel the 600 km from the New York Bight to just south of Cape Hatteras, where age-0 fish overwinter, in 22 d. Older fish (500–550 mm) swim at sustained speeds up to 60 cm/s (52 km/d) (Olla et al., 1970) and could travel 2000 km in a minimum of 31 days. Age-2+ bluefish are the only fish captured regularly on Georges Bank and northward, and therefore would travel the farthest (Shepherd and Packer, 2006). Although a few tagged bluefish have attained speeds >20 km/d and one has attained >48 km/d (Shepherd et al., 2006), they are in the minority. Bluefish may not migrate directly, but intermittently. Their paths include detours, feeding stops, and searches for tolerable water conditions.

Little has been published on northward migration routes of bluefish. The timing of these migrations can be inferred from ichthyoplankton collections. From these, it is known that bluefish spawn in southeast U.S. continental shelf waters from March through May and continue to spawn in northeast U.S. continental shelf waters through August (Hare and Cowen, 1996; Berrien and Sibunka, 1999). Eggs from the spring spawning are entrained in currents off the southeast U.S. outer continental shelf waters and in the Gulf Stream (Kendall and Walford, 1979; Hare and Cowen, 1996). These currents travel northward at 50–100 cm/s (Hare and Cowen, 1996; Hare et al., 2002), and perhaps the bluefish themselves use them to migrate. Energy-conserving behavior would be extremely valuable to bluefish when they must migrate and produce eggs and sperm at the same time.

Overwintering

Bluefish are intolerant of cold, as is evident from their distribution range and from laboratory studies. A bluefish transferred from water 19.5°C to 10°C loses equilibrium and motor control, sinks, and soon dies (Olla et al., 1985). Gradual acclimation however allows them to endure longer. In North Carolina, age-0 bluefish survived for weeks in outdoor enclosures as temperatures declined gradually to 10°C, but a rapid temperature decline to 6°C killed many (Slater et al., 2007). The majority of bluefish, from age-0 spring-spawned to adults <45 cm, winter from south of Cape Hatteras, NC, to Florida (Shepherd et al., 2006; Morley et al., 2007), where surface waters do not decline below 15°C. Large adults, particularly >45 cm, also winter on the outer continental shelf and slope off Virginia and North Carolina (Shepherd et al., 2006). On the shelf-slope edge in that area, winter bottom temperatures vary among years from 10°C to >12°C (Bigelow, 1933). Age-0 bluefish can

endure more cold than adults and may not winter as far south as other age classes (Slater et al., 2007).

When fish cannot escape unfavorable temperatures, they resort to behavioral thermoregulation (Olla et al., 1985; Sogard and Olla, 1998). Starved walleye pollock (*Theragra chalcogramma*) reduce swimming speed and spend most of their time in colder waters below a thermocline, thus decreasing their metabolic cost (Sogard and Olla, 1996). Summer-spawned age-0 bluefish may use the same strategy to suppress metabolic rates by wintering in colder waters off North Carolina just south of Cape Hatteras instead of farther south (Morley et al., 2007; Slater et al., 2007). Milling is certainly another way in which bluefish reduce their activity in winter.

The 121-kL research aquarium is a large experimental space, but confinement may potentially alter fish behavior. Despite qualifications, the author believes gliding behavior in bluefish is authentic natural behavior. This behavior began in the first few weeks of captivity and persisted throughout the experiment. The researchers who initiated this line of investigation observed gliding in the aforementioned unpublished experiment in 1984–85, and the author witnessed it in a seven-month experiment in 2006–07. The behavior each time was composed of similar elements of body curvature, fin extension, glide distance, and glide angle. It is unknown, however, how far bluefish would glide given unlimited space.

Bluefish may be unique among laterally compressed teleosts in gliding on their sides, thus radically changing their hydrodynamic profiles. Although gliding has been witnessed in more than one group of age-0 bluefish in the laboratory, it has not been studied in very small age-0 fish or older age classes. Energy benefits may be different according to the age of a fish, because the bodies of adult bluefish are relatively more cylindrical and less flexible than age-0 fish, and perhaps cannot attain as efficient a foil shape.

Much remains to be discovered about daily behavior routines, migration routes, and overwintering in various cohorts and age classes of bluefish. Considerably less energy is spent during the glide and upswim mode, possibly comparable to energy savings by migrating raptors, and should be quantified or modeled. Internal archival tags that record depth would be valuable for field studies of gliding, in places where recovery is possible, such as a migration corridor. Bluefish with acoustic tags could be detected at strings of fixed or roving receivers at ocean observatories. Information from such tags may locate concentrations of milling bluefish in areas offshore that would be accessible to fishing. Daily vertical migrations of bluefish on the continental shelf should be investigated to determine their relation to feeding and long-distance travel. It was surprising that bluefish in the laboratory continued to glide briskly during midwinter when they would have reached wintering grounds in the wild. Perhaps the modes of swimming, speeds, and routes during migration and wintering in bluefish are more variable than we suspect.

Literature cited

Able, K. W., P. Rowe, M. Burlas, and D. Byrne.
    2003.   Use of ocean and estuarine habitats by young-of-year bluefish (*Pomatomus saltatrix*) in the New York Bight.   Fish. Bull. 101:201–214.
Beamish, F. W. H.
    1978.   Swimming capacity.   *In* Fish physiology, vol. 7 (W. S. Hoar, and D. J. Randall, eds.), p. 101–187.   Academic Press, New York, NY.
Berrien, P., and J. Sibunka.
    1999.   Distribution patterns of fish eggs in the United States northeast continental shelf ecosystem, 1977–1987.   NOAA Tech. Rep. NMFS 145, 301 p.
Bigelow, H. B.
    1933.   Studies of waters on the continental shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature.   Papers Phys. Oceanogr. Meteorol. 2:1–135.
Blake, R. W.
    2002.   Fish functional design and swimming performance.   J. Fish Biol. 65:1193–1222.
Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West.
    2004.   Toward a metabolic theory of ecology.   Ecology 85:1771–1785.
Buckel, J. A., N. D. Steinberg, and D. O. Conover.
    1995.   Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish.   J. Fish Biol. 47:696–706.
Fry, F. E. J.
    1971.   The effect of environmental factors on the physiology of fish.   *In* Fish physiology, vol. 6 (W. S. Hoar, and D. J. Randall, eds.), p. 1–98.   Academic Press, New York, NY.
Hare, J. A., and R. K. Cowen.
    1996.   Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats.   Limnol. Oceanogr. 41:1264–1280.
Hare, J. A., J. H. Churchill, R. K. Cowen, T. J. Berger, P. C. Cornillon, P. Dragos, S. M. Glenn, J. J. Govoni, and T. N. Lee.
    2002.   Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf.   Limnol. Oceanogr. 47:1774–1789.
Hartman, K. J., and S. B. Brandt.
    1995.   Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores.   Can. J. Fish. Aquat. Sci. 52:1647–1666.
Juanes, F., and D. O. Conover.
    1994.   Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*).   Can. J. Fish. Aquat. Sci. 51:1752–1761.

Kawabe, R., Y. Naito, K. Sato, K. Miyashita, and H. Yamashita.
　2004.　Direct measurement of the swimming speed, tail-beat, and body angle of Japanese flounder (*Paralichthys olivaceus*). ICES J.　Mar. Sci. 61:1080–1087.

Kawabe, R., K. Nashimoto, T. Hiraishi, Y. Naito, and K. Sato.
　2003.　A new device for monitoring the activity of freely swimming flatfish, Japanese flounder (*Paralichthys olivaceus*).　Fish. Sci. 69:3–10.

Kendall, A. W., Jr., and L. A. Walford.
　1979.　Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States.　Fish. Bull. 77:213–227.

Kerlinger, P.
　1989.　Flight strategies of migrating hawks, 375 p.　Univ. Chicago Press, Chicago, IL.

Klimley, A. P., S. C. Beavers, T. H. Curtis, and S. J. Jorgensen.
　2002.　Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ.　Biol. Fishes 63:117–135.

Magnuson, J. J.
　1978.　Locomotion by scombrid fishes: hydromechanics, morphology, and behavior.　*In* Fish physiology, vol. 7 (W. S. Hoar, and D. J. Randall, eds.) p. 239–313.　Academic Press, New York, NY.

Marks, R. E., and D. O. Conover.
　1993.　Ontogenetic shift in the diet of young-of-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history.　Fish. Bull. 91:97–106.

Morley, J. W., J. A. Buckel, and T. E. Langford.
　2007.　Winter energy dynamics and cohort structure of young-of-the-year bluefish (*Pomatomus saltatrix*) off North Carolina.　Mar. Ecol. Prog. Ser. 334:273–286.

Munch, S. B.
　1997.　Recruitment dynamics of bluefish, *Pomatomus saltatrix,* from Cape Fear to Cape Cod, 1973–1995.　M.S. thesis, 127 p.　State Univ. New York, Stony Brook, NY.

Nursall, J. R.
　1958.　The caudal fin as a hydrofoil.　Evolution 12:116–120.

Nyman, R. N., and D. O. Conover.
　1988.　The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York.　Fish. Bull. 86:237–250.

Ogilvy, C. S., and A. B. DuBois.
　1982.　Tail thrust of bluefish *Pomatomus saltatrix* at different buoyancies, speeds, and swimming angles.　J. Exp. Biol. 98:105–117.

Olla, B. L., H. M. Katz, and A. L. Studholme.
　1970.　Prey capture and feeding motivation in the bluefish *Pomatomus saltatrix*.　Copeia 1970:360–362.

Olla, B. L., W. W. Marchioni, and H. M. Katz.
　1967.　A large experimental aquarium system for marine pelagic fishes.　Trans. Am. Fish. Soc. 96:143–150.

Olla, B. L., and A. L. Studholme.
　1971.　The effect of temperature on the activity of bluefish, *Pomatomus saltatrix* L.　Biol. Bull. 141:337–349.
　1972.　Daily and seasonal rhythms of activity in the bluefish (*Pomatomus saltatrix*).　*In* Behavior of marine animals, vol. 2: Vertebrates (H. E. Winn, and B. L. Olla, eds.), p. 303–326.　Plenum Press, New York, NY.

Olla, B. L., A. L. Studholme, and A. J. Bejda.
　1985.　Behavior of juvenile bluefish *Pomatomus saltatrix* in vertical thermal gradients: influence of season, temperature acclimation and food.　Mar. Ecol. Prog. Ser. 23:165–177.

Olla, B. L., A. L. Studholme, A. J. Bejda, and C. Samet.
　1980.　Role of temperature in triggering migratory behavior of the adult tautog *Tautoga onitis* under laboratory conditions.　Mar. Biol. 59:23–30.

Scharf, F. S., J. P. Manderson, M. C. Fabrizio, J. P. Pessutti, J. E. Rosendale, R. J. Chant, and A. J. Bejda.
　2004.　Seasonal and interannual patterns of distribution and diet of bluefish within a middle Atlantic Bight estuary in relation to biotic and abiotic factors.　Estuaries 27:426–436.

Shepherd, G. R., J. Moser, D. Deuel, and P. Carlsen.
　2006.　The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries.　Fish. Bull. 104:559–570.

Shepherd, G. R., and D. B. Packer.
　2006.　Essential fish habitat source document: Bluefish, *Pomatomus saltatrix*, life history and habitat characteristics.　NOAA Tech. Memo. NMFS-NE-198, 89 p.

Slater, J. J., T. E. Lankford Jr., and J. A. Buckel.
　2007.　Overwintering ability of young-of-the-year bluefish (*Pomatomus saltatrix*): effects of ration and cohort of origin on survival.　Mar. Ecol. Prog. Ser. 339:259–269.

Sogard, S. M., and B. L. Olla.
　1996.　Food deprivation affects vertical distribution and activity on a marine fish in a thermal gradient: potential energy-conserving mechanisms.　Mar. Ecol. Prog. Ser. 133:43–55.
　1998.　Contrasting behavioral responses to cold temperatures by two marine fish species during their pelagic juvenile interval.　Environ. Biol. Fishes 53:405–412.

Thomas, A. L. R.
　1997.　On the tails of birds.　BioScience 47:215–225.

Webb, P. W.
　1978.　Hydrodynamics: nonscombroid fish.　*In* Fish physiology, vol. 7 (W. S. Hoar, and D. J. Randall, eds.), p. 189–237.　Academic Press, New York, NY.

Weihs, D.
　1973.　Mechanically efficient swimming techniques for fish with negative buoyancy.　J. Mar. Res. 31:194–209.

Wiedenmann, J., and T. E. Essington.
　2006.　Density-dependent overwinter survival in young-of-year bluefish (*Pomatomus saltatrix*)? A new approach for assessing stage-structured survival.　Can. J. Fish. Aquat. Sci. 63:1934–1943.

Winger, P. D., S. J. Walsh, P. He, and J. A. Brown.
　2004.　Simulating trawl herding in flatfish: the role of fish length in behaviour and swimming characteristics.　ICES J. Mar. Sci. 61:1179–1185.