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Contributions of Abiotic and Biotic Factors to Settlement in Summer Flounder, *Paralichthys dentatus*

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Metamorphic summer flounder, *Paralichthys dentatus*, enter Great Bay-Little Egg Harbor estuary in southern New Jersey prior to completion of metamorphosis and permanent settlement. Laboratory experiments indicate a preference by both juvenile and metamorphic summer flounder for sand over mud substrate. Metamorphic individuals do not appear to be capable of burial in the substrate when they enter the estuary. Complete burial was only observed in late-metamorphic and juvenile stages. A diel pattern of burying behavior was observed and was dependent upon several environmental variables, including substrate, water temperature, tide, and the presence and type of predator, all of which may effect growth and survival during metamorphosis.

ALTHOUGH the late larval and early juvenile periods of fishes are emerging as a focus of recruitment research, our knowledge of metamorphosis and settlement is generally poor. Metamorphosis in fishes often results in pronounced transitions in morphology, physiology, behavior, and habitat ecology (Youson, 1988). One of the most abrupt of these, especially for flatfishes, is the transition from the plankton to the benthos during settlement. During this transition, new behaviors develop as substrate selection occurs and burial eventually results. The timing of these events and the ability of the individual to appropriately conduct these behaviors can have significant impact on growth and survival.

Summer flounder, *Paralichthys dentatus,* undergo a dramatic morphological transformation, accompanied by a complex habitat shift from the plankton to the benthos presumably while leaving the ocean and entering estuaries (Able et al., 1990; Burke et al., 1991). They enter New Jersey estuaries from Oct. to April at sizes ranging from 11.2–15.1 mm standard length (SL) (mean = 13.1; Szedlmayer et al., 1992). Developmentally, these fish are in early to midmetamorphosis with eye migration in progress (Keefe and Able, 1993). The duration of these metamorphic stages appears to be dependent upon ambient water temperatures and can range from 25 days at 17 C average temperature to greater than 93 days at 10 C average temperature (Keefe and Able, 1993). Recently, laboratory preference tests on metamorphic summer flounder collected in North Carolina indicated a preference for sand substrate, but this choice may be complicated by local environmental conditions such as current flows and available food (Burke, 1991). In an attempt to further our understanding of the habitat-associated behavior of wild-caught metamorphic summer flounder, we examined substrate selection and the effects of various environmental and biological variables on burying behavior. The specific hypotheses we tested were (H1) metamorphic summer flounder exhibit no preference when given a choice between sand and mud substrates; (H2) the size and stage at the time of first burial for metamorphic summer flounder will not vary between mud and sand substrate; (H3a) burying behavior of metamorphic summer founder is independent of time of day, water temperature, substrate, salinity, and tide; (H3b) the pattern of burying behavior exhibited by metamorphic summer flounder will not change over time; and (H4) metamorphic summer flounder will bury in response to a potential predator regardless of predator type.

MATERIALS AND METHODS

Field collection and maintenance of experimental animals.—Metamorphic summer flounder were collected from plankton entering Great Bay-Little Egg Harbor estuary in southern New Jersey from Nov. 1990 to March 1991. Stationary plankton nets were set weekly at night from a bridge over Little Sheepshead Creek. To ensure sampling of Atlantic Ocean water as it enters the estuary and this creek (Charlesworth, 1968), these nets were set on night flood tides, at the water's surface just above the substrate at a 2–3 m depth (see Szedlmayer et al., 1992, for additional details). Plankton samples were transported immediately to the laboratory and were sorted. Live summer flounder metamorphs were enumerated and measured, and their metamorphic stage was determined as in Keefe and Able (1993). Summer flounder were maintained in the laboratory in unfiltered ambient bay water under a simulated natural photoperiod and were fed *Artemia* nauplii in excess unless otherwise indicated.

Substrate preference.—Choice tests were conducted in a 240 × 60 × 15 cm flow-through tank divided into six alternating sections (60 × 22 cm) with 2 cm of mud or sand substrate and a water depth of 9 cm. The substrate was set in the experimental tanks and allowed to settle for 24 h. During this time, the experimental tanks also received flow-through unfiltered bay water. Groups of 14–18 wild-caught metamorphic summer flounder were released in the tank at 1400 h the next day. Half of the flounder were introduced over mud; the other half were introduced over sand. They were recovered 18 h later, and the number settled on sand and mud substrates was recorded. To minimize disturbing the flounder during recovery, the water was slowly siphoned off the table until the water level just covered the sediment. During this process, any flounder moving between substrates were recorded as being collected on the substrate from which the movement was initiated. Seven trials were conducted. Five were replicates with flounder in mid- to late metamorphosis (right eye located on the dorsal midline, stage H, H+), and two were replicates with flounder in late metamorphosis (eyes located as in adults, Stage I). As a precaution against any directional effect, the location of the substrate sections were haphazardly changed between each replicate. Recovery of summer flounder ranged from 94% in two trials to 100% in five trials. The proportions of fish found on each substrate type were analyzed using a binomial test. Preference was determined at alpha <0.05.

Size and stage at first burial.—This experiment was designed to examine the size and stage at which summer flounder first bury and the effect of substrate type. The experiment was conducted using two substrate treatments; sand (0.59% silt/clay) and mud (61.67% silt/clay). Six summer flounder, in early to midmetamorphosis (right eye approaching the dorsal midline, stages G, H−), were placed in glass bowls (197 diameter, 50 mm deep) that were supplied with ambient, flow-through bay water. The substrate depth in each bowl (0.5 cm) was sufficient to allow the flounder to bury after settling. Two replicate containers were used for each substrate treatment for a total of 24 fish per trial. During this experiment, the laboratory photoperiod was modified by using a dim nocturnal light source (2 lux at the water's surface). The fish were fed and mortalities removed and recorded daily. Preliminary observations indicated that summer flounder increased burying behavior during the day. Therefore, observations of burying were made once each day at 1200 h. If a fish was observed to be completely (with only its eyes visible) or partially buried, it was removed, staged with a stereomicroscope, and measured. To prevent confusion between initial and subsequent burial, the individuals that were partially buried were returned to the treatment container, whereas the completely buried individuals were removed permanently. The experiment was terminated when all of the fish had buried. This experiment was run in two trials using a total of 48 wild-caught summer flounder. When there were no significant differences between trials, the data were pooled. A student t-test was used to determine whether the mean size (SL) of flounder at first burial was different between substrates, whereas a binomial test was used to analyze the proportions of flounder burying in each metamorphic stage between substrates.

General aspects of burying behavior were observed occasionally during three years of observations of wild-caught individuals in the laboratory. To further describe burying behavior, four metamorphic flounder were recorded on videotape intermittently over a two-week period.

Effects of environmental variables on burial.—Tests were conducted on two developmental stages to investigate the effects of temperature, substrate, time of day, salinity, and tide on burial at different stages of metamorphosis. The summer flounder used in the first test (n = 28) were in stages G, H− at the onset of the experiment. The design incorporated two substrate treatments: mud and sand at ambient water temperatures. Ambient flow-through temperatures fluctuated from 4.3 to 13.2 and averaged 6.4 C. Each treatment contained two replicate glass bowls (197 mm diameter, 50 mm deep) that received flow-through bay water and housed seven summer flounder of known size and metamorphic stage. Each bowl was covered with two layers of plastic mesh, which provided shading and reduced the light entering the bowls. The second test was conducted using flounder in later stages of metamorphosis (stages H−, H, H+); and, in addition to the effect of substrate, we also examined the effect of temperature on burial. The flounder (n = 56) were equally divided among four substrate-temperature combination treatments: ambient-mud, ambient-sand, heated-mud, and heated-sand. Ambient temperatures were the same as reported for the first test. Heated treatments received ambient flow-through water that was heated to approximately 15 C. All other experimental conditions were the same as reported for the first test.

During both tests, observations of burying behavior were made six times per day at 0600, 0700, 1200, 1700, 1800, and 2300 h. To allow for diel observation, the simulated natural photoperiod was modified with a dim night light (2 lux at the water's surface). Observations were continued for 15 consecutive days for the test with developmentally younger fish (stage G, H−) and for 12 consecutive days with older fish (stage H−, H, H+). The behavior of the fish was recorded as follows: buried, indicating complete coverage with sand except that the eyes and mouth were exposed; partially buried, variable coverage with sand ranging from only the edges of the fish covered to all except the head covered; and unburied, no sand covering any portion of the body (with possible exception of a few sand grains on the exposed surface). During each observation, the number of flounder that were buried, partially buried, and unburied was recorded. Measurements of water temperature and salinity were made and recorded at each observation. To evaluate the possibility of earlier larval entrainment to a circatidal rhythm, the stage of the tide in the bay was matched to the date and time of each laboratory observation record. It is important to note that test 1 using earlier metamorphic stages was completed within 16 days from when these individuals were collected from the plankton.

A discrete response variable, degree of burial, was chosen for this experiment and prevented the use of analysis of variance and regression analysis. In a log-linear analysis, the response function is a logit generated from the log of the ratio of dependent variables (for example, a ratio of the number of buried to unburied observations). In this way, a discrete variable is converted to something that approximates a continuous model. Thus, a log-linear model analysis was chosen for the multiway analysis of the effects of several environmental variables on burying behavior.

A Statistical Analysis Systems Institute log-linear analysis (SAS Institute, 1988) was used for test 1 to determine whether burying behavior was independent of substrate type, time of day, tide, salinity, and length of time in the laboratory. The only interaction in which we were interested, and thus tested for, was an interaction between temperature and substrate. The same analysis was completed for test 2 with the exception that we included the effect of a substrate factor and a temperature/substrate interaction in the analysis. In addition, we omitted the effect of time in the laboratory from the analysis from test 2 because these fish had already exhibited burial at the time the test was initiated.

Burial as a response to potential predators.—Selection of potential predators was based on our knowledge of species that co-occur both temporally and spatially with metamorphic summer flounder in Great Bay and prior laboratory observations (Witting and Able, 1993). Two potential predators, sevenspine bay shrimp (*Crangon septemspinosa*) and mummichog (*Fundulus heteroclitus*), were collected from Great Bay and maintained in the laboratory on a diet of chopped fish and shrimp. The body size of both predators and prey was recorded as standard length (mm) for fish and total length (mm) (Price, 1962) for sevenspine bay shrimp. Individual summer flounder were staged just prior to the onset of the experiment and both mid- (stage H, H+) and late-metamorphic (stage I) individuals were used. Three trials of this experiment were conducted with each predator type using a total of 36 individuals in treatment groups and 18 controls.

Each trial was conducted with new flounder and predators over a four-day time frame. An individual trial was conducted using either all shrimp or all mummichog predators. On day one (1400 h) of each trial, 18 summer flounder (12 treatment and six controls) were placed in individual experimental arenas that were immersed in an ambient water bath (6–9 C). The arena size varied with the predator. Trials with shrimp were conducted in glass bowls (197 mm diameter, 50 mm deep). Trials with mummichogs were conducted in 305-mm diameter opaque, plastic bowls containing a water column 90 mm deep. Each arena contained sand (2 cm deep), which allowed both the summer flounder and shrimp predators to bury.

Summer flounder were allowed to acclimate in the arenas for 24 h. At 1400 h on day two, predators were introduced. Shrimp were tethered to a monofilament line (Barshaw and Able, 1990) which limited their access to approximately half the experimental arena and ensured that the flounder had an area of refuge from predation. In an attempt to prevent immediate predation by mummichogs and thus allow observation of flounder behavior, mummichogs were fed to satiation prior to release into the experimental arena. Twelve treatments and six controls were run simultaneously. Each treatment contained one summer flounder and one predator, whereas the controls contained isolated summer flounder. Observations of burying behavior were made at approximately 1700 h on day two. The number of flounder completely buried, partially buried, and unburied was recorded. The number of completely and partially buried flounder were combined for analysis.

The third day of this experiment allowed us to determine whether the potential predators actually represented a threat to the summer flounder. The shrimp were cut free of the tether line at 1400 h; and, by this time, mummichogs had not received food for 24 h. Neither species of predator was given an alternative food source. After an additional 24 h (day four), the predators were removed from the arena, and flounder mortalities were recorded. Mortality was determined by the presence of partial remains or the total absence of a summer flounder in the experimental arena. In the arenas where summer flounder were initially observed to be absent, the sand was washed through a fine-mesh net to make sure flounder were not buried. For analysis of this data, if there were no significant differences between trials with one predator type, the data were pooled. The data were analyzed using a binomial test.

RESULTS

Two hundred sixteen summer flounder were collected from Nov. 1990 to April 1991. All flounder collected were in early (stage G) to midmetamorphosis (stage H, H−) and ranged from 10.0–15.6 mm SL with a mean of 12.8 mm SL (1.04 SD). A more detailed breakdown and size of metamorphic stage of summer flounder entering Little Egg Harbor-Great Bay Estuary can be found in Keefe and Able (1993).

Substrate preference and size and stage at first burial.—There were no significant differences in proportions of flounder found on each substrate type between replicates of the same metamorphic stage; therefore, these replicates were pooled for analysis. A binomial test of pooled data indicated that significantly greater proportions of flounder were collected from sand substrate, 61% (51 out of 83) for individuals in midmetamorphosis (stages H−, H) and 68% (19 out of 28) in late metamorphosis (stage I).

Although choice tests indicated a preference for sand substrate by summer flounder, there was no significant effect of substrate on the size (t-test, $P > 0.05$) or metamorphic stage (binomial, $P > 0.05$) at first burial. Size at first burial ranged from 12.1–16.9 mm SL, with a mean of 14.1 mm SL in mud treatment and a mean of 14.0 mm SL in the sand treatment ($n = 37$). The majority (69%) of flounder that were observed buried for the first time were stage H+. The remainder of fish were identified as stage H at first burial. Flounder in earlier stages of metamorphosis (stages G and H−) were never seen completely buried. They did exhibit partial burial with sediment covering different portions of their body but never with the anterior portion of their body buried.

Burial for settled individuals (late- or post-metamorphic) was rapid but variable in the degree to which sediment covered the body regardless of substrate. Burial occurred after swimming along the bottom or while resting in place. Sediment was resuspended by rapid (<1 sec) fluttering movement of a portion of or the entire body. Rapid fluttering of the caudal fin and the caudal peduncle resulted in those portions of the body being covered with sediment. More exaggerated movement by larger portions of the body and head resulted in a greater covering of sediment. Frequently after complete burial, the eyes and gill openings remained uncovered, and the eyes continued to move.

Effects of environmental variables on burial.—Burying behavior of metamorphic individuals was dependent upon several environmental variables. The data from the first test (Table 1A) with early- to midmetamorphic flounder (G, H) indicated a significant effect of substrate on burying behavior. These flounder exhibited significantly more burying in mud substrate. Time of day, tide, and time in laboratory had a significant effect on burying, but salinity did not. The significant effect of tide can be explained by more burying during the period of flood tide. The significant effect of time of day is attributable to more burying during the daylight hours (Fig. 1A). In addition, these fish, which were at earlier metamorphic stages at the onset of the experiment, demonstrated an increase in burial over time (Fig. 1A).

The second test using individuals in mid- to late metamorphosis (stages H−, H, and H+) showed an overall significant effect of both temperature and substrate on burying (log-linear analysis, $P < 0.05$; Table 1B). The analysis of contrasts indicated that metamorphic individuals were completely buried significantly more in heated, as opposed to ambient, water temperature and buried significantly more in sand, as opposed to mud, substrate. The overall significant effect of substrate was a result of the effect of substrate within the heated treatment. There was no significant difference in burying

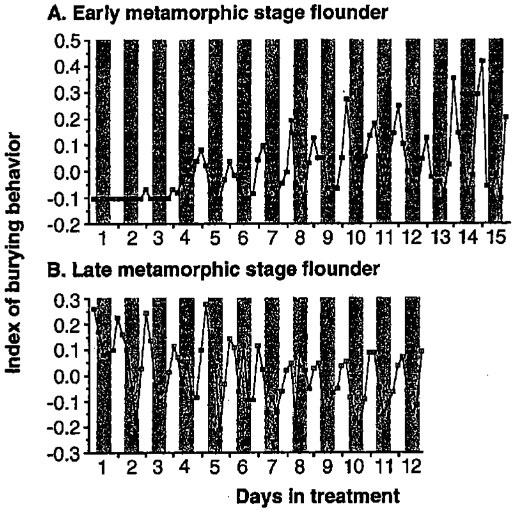

Fig. 1. The pattern of burying activity by metamorphic summer flounder held in the laboratory: (A) stage G, H−, and H individuals; and (B) stage H, H+, and I individuals. Index of burying behavior was derived by a log-linear analysis of weighted-least-squares estimates; a higher index represents greater numbers of fish buried. Day/night are indicated by alternating light/dark bands.

Table 1. Results of Log-Linear Analysis of Variance Testing the Effects of Environmental Variables on Burying Behavior of Summer Flounder. (A) Test 1: Early- to midmetamorphic stages G and H. (B) Test 2: Mid- to late-metamorphic stages, H−, H, and H+.

Variable	Degrees of freedom	Chi-square	Probability
(A) Test 1			
Substrate	1	63.86	0.0000
Salinity	1	0.75	0.3860
Tide	3	10.10	0.0178
Time of day	1	30.32	0.0000
Time in laboratory	89	469.91	0.0000
(B) Test 2			
Substrate	1	144.60	0.0000
Temperature	1	10.95	0.0009
Salinity	1	49.62	0.0000
Tide	3	5.19	0.1585
Time of day	1	248.07	0.0000
Temperature × substrate	3	303.27	0.0000

among flounder in ambient substrate treatments. There was also a significant interaction between temperature and substrate that influenced burial. In addition, there was an overall effect of salinity and time of day but no effect of tidal stage (Table 1B). Flounder clearly buried more during the daylight hours (Fig. 1B).

Burial as a response to potential predators.—The burial of metamorphic summer flounder exposed to potential predators was significantly different from that of controls and also differed between predators. In the treatments with tethered shrimp predators, significantly fewer flounder ($n = 36$) were buried than in controls (binomial, $P < 0.0002$). An average of 50% were buried in the presence of shrimp as opposed to 78% of controls buried. The response to mummichogs was the opposite, with significantly more flounder than the solitary controls (binomial, $P < 10^{-5}$) burying in the presence of the potential predator. An average of 77% of flounder buried in mummichog predator treatment whereas only 44%, on average, buried in the controls.

Mortality with both fish and shrimp predators was significantly greater in treatments than were controls (binomial, $P < 10^{-6}$). There was no mortality in the controls. Treatment mortality averaged 25% with shrimp predators and 38% with fish predators. The majority of flounder mortalities found in the treatment arenas were partially or totally consumed. However, during one trial with mummichogs, 21% of the mortalities were not consumed by the predators. These prey were observed to have considerable fin damage that may have resulted from unsuccessful predation attempts. Fin damage was never observed in summer flounder controls. The mean size of the flounder preyed upon was 16.2 mm SL (3.0 SD) in shrimp treatments and 14.2 mm SL (1.27 SD) in fish treatments. The size range of predators associated with flounder mortalities was 45–58 mm TL for shrimp and 45–72 mm SL for mummichog.

DISCUSSION

Substrate choice.—The preference for sand by metamorphic summer flounder seen in this study is consistent with the findings of Burke et al. (1991). However, these laboratory studies are not wholly consistent with recent field investigations on the distribution of juvenile summer flounder (Wyanski, 1988; Burke et al., 1991). Burke et al. (1991) found recently settled juveniles to be abundant on mixed substrates with slightly higher probabilities on sandy relative to muddy substrates, whereas Wyanski (1988) found juveniles over a larger size range on fine substrates (defined as >50% very fine sand, silt, and clay). The inconsistency between laboratory and field studies may, in part, be related to the distribution and abundance of prey in the field. Burke et al. (1991) observed a decrease in the precision of summer flounder substrate selection when they used substrates which contained prey organisms. The experimental arena used for choice test in this study received unfiltered bay water for 24 h prior to the tests. Therefore, prey species may have been available to colonize both substrate types. The presence of a predator may also play a role in substrate choice (see below). Substrate choice, as measured by varying grain sizes, has little effect on growth and metamorphosis in *Pleuronectes platessa* (Becker, 1988; Gibson and Batty, 1990). However, if there is a correlation between substrate type and associated food or other factors, then substrate characteristics would indirectly affect substrate choice. For some species other than flatfishes, the substrate preferences of settling fishes varied in a specific manner with tactile cues, light transmission, current speed, and salinity affecting ultimate choice (Marliave, 1977).

The final choice of settlement substrate may be controlled by a period of testing the substrate. *Solea solea* settle on the substrate numerous times and then reenter the water column (Flüchter, 1965) whereas *Pleuronectes platessa* apparently reenters the water column if starving (Creutzberg et al., 1978), thus providing an appropriate means of choosing a profitable substrate. Burke (1991) suggested that *P. dentatus* may also sample the benthic habitat before final settlement, using grain size of the sediment as an indicator of preferred habitat.

Burial.—The results of this study indicate that summer flounder entering the estuary may not exhibit complete burial until they have reached mid- to late metamorphosis when eye migration is complete. The size distribution of flounder at first burial was on average 1 mm (7.1% of SL) larger than that of planktonic individuals, suggesting an initial period of growth and development may occur before these fish are capable of complete burial. This idea is supported by both the increase in burying behavior over time seen in the developmentally younger flounder in the diel activity experiment (Fig. 1A) and the finding that the fish held in the heated treatment, which developed more rapidly than those in the ambient treatment, also exhibited a higher incidence of burying behavior.

Substrate type, water temperature, time of day, tide, and salinity had significant effects on the burying behavior in metamorphic summer flounder. The effect of substrate was only evident for developmentally advanced fish (heated treatment), which buried more in sand than in mud. This finding corroborates research on Japanese flounder (*P. olivaceus*), which suggested that an increased ability to bury was associated with growth, because there was a higher degree of burying in larger size fish. A similar relationship has been shown for *P. platessa* (Gibson and Robb, 1992). Tanda (1990) observed increased burying of juvenile *P. olivaceus* in preferred substrate.

Metamorphic summer flounder exhibited a diel pattern in burying with a higher incidence of burying occurring during the day. This increased nocturnal activity of metamorphic individuals corresponds well with the field collections in which metamorphic summer flounder are frequently collected (Able et al., 1990; Szedlmayer et al., 1992; Keefe and Able, 1993) and most abundant during night flood tides (Weinstein et al., 1980). A similar pattern occurs for *P. olivaceus* (Tanaka et al., 1989a, 1989b), and this pattern may begin at metamorphosis (Kawamura and Ishida, 1985). It also agrees with other laboratory observations on the diel activity of larger juveniles held in the laboratory (Klein-McPhee, 1979) but is in contrast to observed activity patterns in adults which are primarily day active in captivity (Olla et al., 1972). This suggests a period of transition from night-active metamorphic individuals to day-active adults.

An effect of tide on burying behavior was evident for the early metamorphic individuals, thus supporting the possibility of tidal entrainment. The larvae of several marine fishes (Creutzberg, 1961; Creutzberg et al., 1978), including paralichthid flounders (Weinstein et al., 1980) utilize selective tidal transport as an energetically advantageous means of entering an estuary. There is also evidence for tide-associated movements in juvenile plaice (Gibson, 1973; Gibson and Blaxter, 1978) and in larger juvenile summer flounder (Rountree and Able, 1993; Szedlmayer and Able, 1993). The increased burial at flood tide seen in this study, although perhaps a laboratory artifact, may be likened to the decrease in pelagic swimming and increase in bottom activity of *P. platessa* once settled in a habitat with plentiful food (Creutzberg et al., 1978). Thus, increased burying on a flood tide may represent a means for retention in a favorable habitat.

The burial behavior of metamorphs is similar or identical to that of adults (Olla et al., 1972) even though the metamorphs had not completed formation of all adult characters. For example, lateral line and scale formation occur during stage I (Keefe and Able, 1993), after burial begins (stages H, H+). However, unlike the adults, our observations suggest that recently buried individuals frequently maintain eye movements.

Predation.—In forced interactions with predators, the burying of metamorphic individuals varied with predator type. Although the shrimp predator, *Crangon septemspinosa,* may occur in the water column (Dodson et al., 1989) and bury in the substrate (Witting and Able, 1993), they are more likely to be buried during the day (D. A. Witting and KWA, pers. obs.). During our observation period (1700 h), the majority of shrimp were buried in the substrate. This may have reduced burying by the summer flounder. The opposite response to the mummichog (i.e., more summer flounder buried during the day) suggests that exposure to this predator, which swims in the water column, may have caused more burying, at least during the day. Thus, the type, and presumably abundance, of predators could determine whether a metamorphic individual stays in the substrate or returns to the water column. This response could play an important role in substrate selection and settlement of individuals that are being transported into an estuary during metamorphosis.

Mortality by both predators, as observed in the laboratory in this and prior experiments, is likely to occur in nature as well. Large *C. septemspinosa* (>35 mm) that can prey upon metamorphic summer flounder (Witting and Able, 1993) are abundant during the winter (D. A. Witting, pers. obs.) when metamorphic summer flounder enter New Jersey estuaries (Szedlmayer et al., 1992; Keefe and Able, 1993). Thus, encounters with these predators are likely, especially if low temperatures delay metamorphosis and growth (Keefe and Able, 1993), which would make them susceptible to this mortality for a longer period of time before they can reach a size refuge (Witting and Able, 1993). Clearly, the potential for *Crangon crangon* to play a significant role in the survival of plaice has been demonstrated in the North Sea (Veer and Bergman, 1987). Predation by *F. heteroclitus* on metamorphic summer flounder may only occur in the fall and spring because the predator is relatively inactive and not feeding at winter water temperatures (KWA, pers. obs.).

In summary, metamorphic summer flounder undergo a number of significant transitions as they enter estuarine nurseries, including the change of habitat associated with leaving the plankton and becoming benthic. Burying in the substrate first occurs during late metamorphosis and appears to have a diel pattern that differs from the adults. The occurrence, frequency, and pattern of burying is affected by several abiotic and biotic factors that may contribute to growth and survival during metamorphosis.

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LITERATURE CITED

ABLE, K. W., R. E. MATHESON, W. W. MORSE, M. P. FAHAY, AND G. P. SHEPHERD. 1990. Patterns of summer flounder (*Paralichthys dentatus*) early life history in the Mid-Atlantic Bight and New Jersey estuaries. Fish. Bull. 88:1–12.

BARSHAW, D. E., AND K. W. ABLE. 1990. Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters, *Homarus americanus. Ibid.* 88:415–417.

BECKER, D. S. 1988. Relationship between sediment character and sex segregation in English sole, *Parophrys vetulus. Ibid.* 86:517–524.

BURKE, J. S. 1991. Influence of abiotic factors in feeding on habitat selection of summer and southern flounder during colonization of nursery grounds. Unpubl. Ph.D. diss., North Carolina State Univ., Raleigh.

———, J. M. MILLER, AND D. E. HOSS. 1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Netherlands J. Sea Res. 27:393–405.

CHARLESWORTH, L. J., JR. 1968. Bay, inlet and nearshore marine sedimentation: Beach Haven-Little Egg Inlet Region, New Jersey. Unpubl. Ph.D. diss., Univ. of Michigan, Ann Arbor.

CREUTZBERG, F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. Netherlands J. Sea Res. 1:257–338.

———, A. TH. G. W. ELTINK, AND G. J. VAN NOORT. 1978. The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea, p. 243–252. *In:* Physiology and behavior of marine organisms. D. S. McLusky and A. J. Berry (eds.). Proceedings 12th European Marine Biological Symposium. Pergamon Press, Oxford, England.

DODSON, J. J., J. DAUVIN, R. G. INGRAM, AND B.

D'ANGLEJAN. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplankton fauna of the middle St. Lawrence estuary. Estuaries 12: 66–81.

FLÜCHTER, J. 1965. Versuche zur Brutaufzucht der Seezunge *Solea solea* in Kleinen Aquarien. Helgoländer wiss. Meeresunters. 12:395–403.

GIBSON, R. N. 1973. Tidal and circadian activity rhythms in juvenile plaice, *Pleuronectes platessa*. Mar. Biol. 22:379–386.

———, AND R. S. BATTY. 1990. Lack of substratum effect on the growth and metamorphosis of larval plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Series 66:219–223.

———, AND J. H. S. BLAXTER. 1978. Developmental changes in the activity rhythms of the plaice (*Pleuronectes platessa* L.), p. 169–186. *In:* Rhythmic activity of fishes, J. Thorpe (ed.). Academic Press, London, England.

———, AND L. ROBB. 1992. The relationship between body size, sediment grain and the burying ability of juvenile plaice, *Pleuronectes platessa* L. J. Fish. Biol. 40:771–778.

KAWAMURA, G., AND K. ISHIDA. 1985. Changes in sense organ morphology and behavior with growth in the flounder *Paralichthys olivaceus*. Bull. Jap. Soc. Sci. Fish. 51:155–165.

KEEFE, M., AND K. W. ABLE. 1993. Patterns of metamorphosis in the summer flounder (*Paralichthys dentatus*). J. Fish. Biol. 42:713–728.

KLEIN-MCPHEE, G. 1979. Growth, activity and metabolism studies of summer flounder, *Paralichthys dentatus* (L.) under laboratory conditions. Unpubl. Ph.D. diss., Univ. of Rhode Island, Kingston.

MARLIAVE, J. B. 1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. J. Exp. Mar. Biol. Ecol. 27:47–60.

OLLA, B. L, C. E. SAMET, AND A. L. STUDHOLME. 1972. Activity and feeding behavior of the summer flounder (*Paralichthys dentatus*) under controlled laboratory conditions. Fish. Bull. 70:1127–1136.

PRICE, K. S. 1962. Biology of the sand shrimp, *Crangon septemspinosa* in the shore zone of the Delaware Bay region. Ches. Sci. 3:244–255.

ROUNTREE, R. A., AND K. W. ABLE. 1993. Foraging habits, growth and temporal patterns of salt marsh creek habitat use by juvenile summer flounder in New Jersey. Trans. Amer. Fish. Soc. 121:247–253.

SAS INSTITUTE, INC. 1988. SAS/STAT® user's guide, release 6.03 edition. Statistical Analysis Systems Institute, Cary, North Carolina.

SZEDLMAYER, S. T., AND K. W. ABLE. 1993. Ultrasonic telemetry of Age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia 1993:728–736.

———, ———, AND R. A. ROUNTREE. 1992. Growth and temperature induced mortality of 0-age summer flounder, *Paralichthys dentatus* in southern New Jersey. Copeia 1992:120–128.

TANAKA, M., T. GOTO, AND M. TOMIYAMA. 1989a. Immigration, settlement, and mortality of flounder (*Paralichthys olivaceus*) larvae and juveniles in a nursery ground Shiiki Bay, Japan. Netherlands J. Sea Res. 24:57–67.

———, ———, ———, H. SUDO, AND M. AZUMA. 1989b. Lunar-phased immigration and settlement of metamorphosing Japanese flounder larvae into the near-shore nursery ground. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 191:303–310.

TANDA, M. 1990. Studies of burying ability in sand and selection to the grain size for hatchery reared marbled sole and Japanese flounder. Nipp. Suison. Gakkaishi 56:1543–1548.

VEER, H. W. VAN DER, AND M. J. N. BERGMAN. 1987. Predation by crustaceans on a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 35:203–215.

WEINSTEIN, M. P., S. L. WEISS, R. G. HODSON, AND L. R. GERRY. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull. 78:419–446.

WITTING, D. A., AND K. W. ABLE. 1993. Effects of body size on probability of predation on juvenile winter and summer flounder. *Ibid.* 91:577–581.

WYANSKI, D. J. 1988. Depth and substrate characteristics of age 0 summer flounder (*Paralichthys dentatus*) habitat in Virginia estuaries. Unpubl. master's thesis, School of Marine Science, College of William and Mary, Williamsburg, Virginia.

YOUSON, J. H. 1988. First metamorphosis, p. 135–136. *In:* Fish physiology, Vol XIB. W. S. Hoar and D. J. Randall (eds.). Academic Press, Chicago, Illinois.

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