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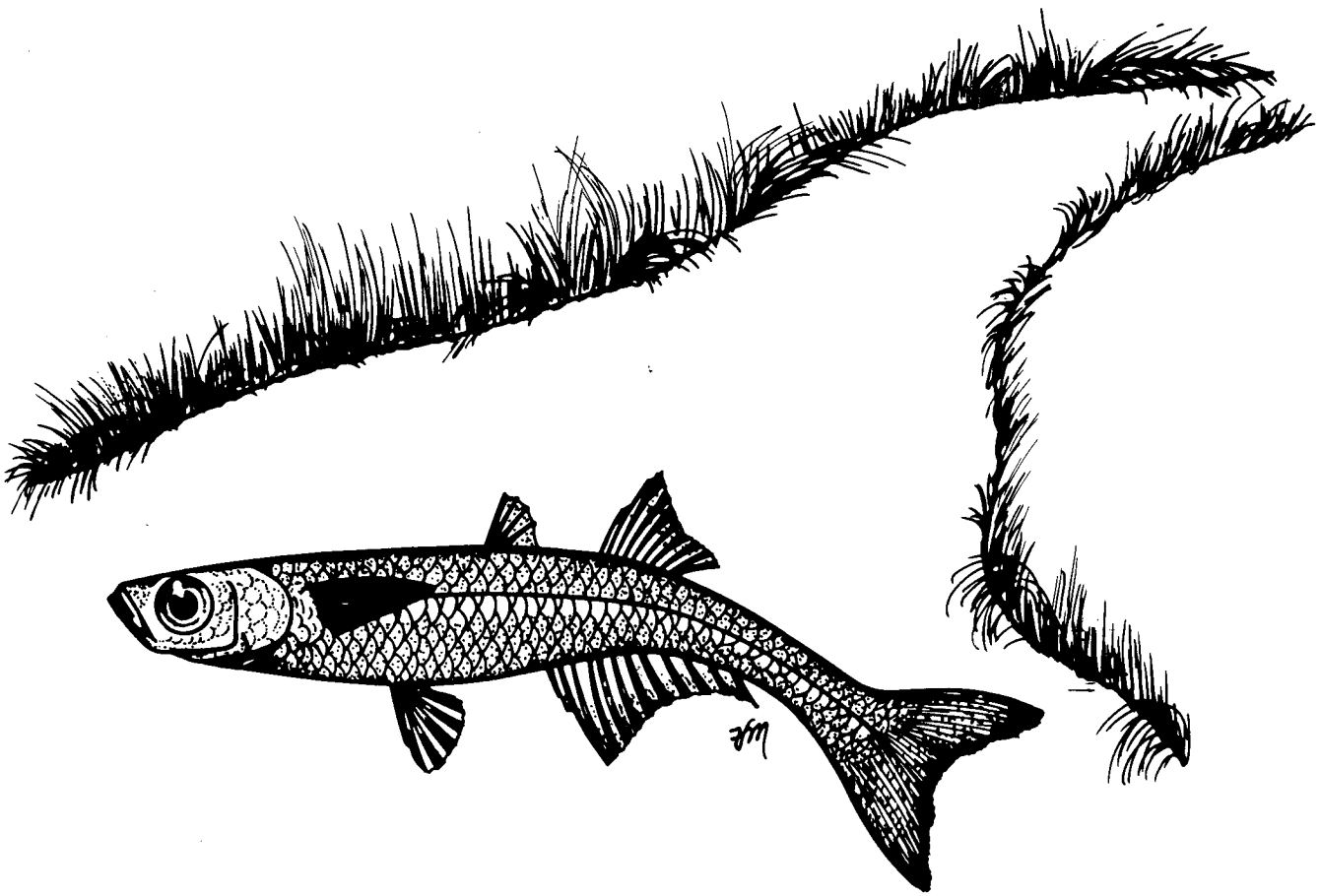
HABITAT SUITABILITY INDEX MODELS: INLAND SILVERSIDE



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HABITAT SUITABILITY INDEX MODELS: INLAND SILVERSIDE

by

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PREFACE

The habitat suitability index (HSI) models in this report on the inland silverside are intended for use in the habitat evaluation procedures (HEP) developed by the U.S. Fish and Wildlife Service (1980) for impact assessment and habitat management. The models were developed from a review and synthesis of existing information and are scaled to produce an index of habitat suitability between 0 (unsuitable habitat) and 1 (optimally suitable habitat). Assumptions involved in developing the HSI models and guidelines for their application, including methods for measuring model variables, are described.

These models are hypotheses of species-habitat relationships, not statements of proven cause and effect. The models have not been field-tested. The U.S. Fish and Wildlife Service encourages model users to convey comments and suggestions that may help increase the utility and effectiveness of this habitat-based approach to fish and wildlife management to the following address:

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INLAND SILVERSIDE (Menidia beryllina)

INTRODUCTION

The systematics of the Menidia complex have been evaluated by Johnson (1975), who could not distinguish biochemical differences between M. beryllina and M. audens, and by Chernoff et al. (1981), who concluded that M. audens is conspecific with M. beryllina. The two species have since been synonymized as M. beryllina, the inland silverside. The result is a considerable extension of M. beryllina's range into freshwater habitats.

Several previously reported studies of "Menidia beryllina" on the Florida peninsula are also suspect: it is likely that M. beryllina was at times confused with M. peninsulae (the latter form was elevated to species status by Johnson [1975]). Harrington and Harrington (1961, 1982) and Naughton and Saloman (1978) separated the two species, but it is possible that some of the Menidia present in the studies of Reid (1954), Kilby (1955), Springer and Woodburn (1960), Subrahmanyam and Drake (1975), Kinch (1979), and others were actually M. peninsulae.

Distribution

The inland silverside has been reported in estuarine habitat along the Atlantic coast from Massachusetts Bay at Cape Cod to the Gulf of Mexico at Vera Cruz, Mexico. It has been collected from freshwaters as far up the Mississippi drainage as Reelfoot Lake, Tennessee, and as far west in the Red River system as Lake Texoma, Oklahoma. Freshwater populations have also been established in lacustrine systems in South Carolina (Lakes Moultrie and Marion), Florida (St. Johns River reservoirs), Texas (reservoirs on the Colorado River and Rio Grande), and Clear Lake, California, where it was introduced as a pest control agent.

Life History Overview

Reproduction. In New England waters, gravid M. beryllina were first collected at 20 °C in June and July and young-of-year were initially captured in late July (Bengtson 1982). These data support the contention of Bigelow and Schroeder (1953) that M. beryllina spawns later in the year than its congener, M. menidia, the Atlantic silverside which is first observed in ripened condition in April. In Rhode Island, Bengtson (1982) reported that M. beryllina adults reach maximum abundance only after adult M. menidia leave the spawning area. He concluded that there was an apparent temporal partitioning of upper estuary spawning sites (where M. beryllina was most abundant): M. menidia used

these areas in April-May and M. beryllina used them in June-July, after M. menidia had begun to spawn farther down the estuary.

A protracted spawning period with multiple peaks has been reported for inland silversides in Mississippi Sound and other Gulf of Mexico waters. Ripe females were collected in March in Mississippi Sound at a temperature of about 24 °C (Garwood 1967). Spawning had tapered off by early April, only to resume again in May and continue through mid-July. Garwood (1967) attributed this lull in spawning to a period of cooler weather in April. In Texas, however, Gunter (1945) collected developing and ripe M. beryllina from mid-February to mid-August in two peaks; in southern Florida, Gunter and Hall (1963, 1965) and Springer and Woodburn (1960) noted that the chief spawning period involved two or three peaks in the spring and early summer, suggesting that reduced temperatures may not be required to cause multiple peaks in spawning.

Northward the qualitative pattern remains similar. Hildebrand (1922) found the spawning period to last from March to September near Beaufort, North Carolina. Hildebrand and Schroeder (1928) captured ripe adults from 10 April to 19 September in the Chesapeake Bay, and Rubinoff and Shaw (1960) noted that ripe specimens were present in the Cape Cod area in June and July, a pattern identical to that described by Bengtson (1982).

Extensive studies of M. beryllina spawning were conducted on Lake Texoma populations by Mense (1967) and Hubbs (1982). Males predominated in the spawning assemblages early in the season, giving way to larger numbers of females during peak and later spawning. Eggs are produced daily in gravid females. The eggs of M. beryllina are spherical to slightly ovoid and have adhesive filaments for attachment, with egg diameters variously reported as less than 0.75 mm (North Carolina), 0.96 mm (Oklahoma), and 0.9-1.0 mm (Massachusetts) (Martin and Drewry 1978). Hubbs (1982) demonstrated a slightly curvilinear relationship between length of female and fecundity: values ranged from 225 eggs produced per day for a 50-mm SL individual to 665 eggs produced per day at 70 mm to 1,700 eggs produced daily in a 90-mm fish. If an average 90-day spawning season is assumed, females may produce from 20,000 to 170,000 eggs during their reproductive lifetime. These values are similar to those Mense (1967) reported for the same waters.

Growth and survival. Menidia beryllina hatch at about 3.5 to 5 mm standard length (SL) (Hildebrand 1922; Hubbs 1982). In Lake Texoma, Mense (1967) collected fish averaging 14 mm SL on 14 May, 26 mm on 28 May, 38 mm on 10-12 June, 42 mm on 26 June, and 60 mm on 11 July. Growth over this 58-day period thus averaged about 0.79 mm/day. Similarly, Hubbs's (1982) data showed an average growth rate of 0.75 mm/day for the spring-summer growth stanza. Of course, these rates are influenced by temperature regimes and, perhaps, food availability. Growth of young fish has been shown to be density dependent (Hubbs and Dean 1979).

In Rhode Island, juveniles first appeared in fine-mesh seine collections in late July (Bengtson 1982). By the end of the month, they reached a mean length of about 20 mm SL. Bigelow and Schroeder (1953) reported the maximum size as about 3 inches (75 mm) in New England waters. The largest fish observed in New Jersey waters was 69 mm total length (TL) (Marcellus 1972;

Coorey et al. 1985). Marcellus (1972) also stated that growth was not rapid in New Jersey waters. Along the gulf coast of Florida, the species may reach nearly 100 mm SL.

Menidia beryllina young-of-year grow relatively rapidly, yet not quite so rapidly as their congener M. menidia. Bengtson (1982) conducted laboratory experiments on the two species and observed that M. menidia was the "better" competitor when initially slightly larger than M. beryllina. However, when M. beryllina was initially larger, it was not the better competitor. The M. beryllina tested required only 5% to 60% of their body weight per day for maintenance, compared to 20% to 135% for M. menidia. Thus, on a daily basis, the maximum food intake of M. menidia young-of-year was about double that of similarly sized M. beryllina.

In Rhode Island, peak abundance occurred in August at lower salinity stations in the upper estuaries. Young-of-year fish were usually found at densities of one or two individuals/m^2 in August, but densities rarely exceeded 0.5 individuals/m^2 by October. By the following spring, maturing M. beryllina were generally no more abundant than 0.1 fish/m^2 (Bengtson 1982).

Few, if any, inland silversides live more than 2 years. In New England waters, Bigelow and Schroeder (1953) reported that M. beryllina reaches adulthood in 1 year, and length-frequency data gathered by Bengtson (1982) indicated that few fish reach 2 years of age. Similar results have been observed elsewhere in M. beryllina's range; for example, Hubbs et al. (1971) found a few 2-year-old females in Lake Texoma, but no males of this age. They concluded that M. beryllina is essentially an annual fish in the lake. Mense (1967) reported differential growth rates for males and females in Lake Texoma: females were larger than males at 3 months. Adults of both sexes greatly diminished in numbers by July, indicating poor postspawning survival.

Movements. There is limited information on movements of M. beryllina in estuarine habitats. In Massachusetts, Hoff (1972) sampled extensively in the Slocum River Estuary and observed that (1) 81% of the 768 M. beryllina collected came from a particular location; (2) individuals were collected from this locality during 11 months of the year; and (3) although M. beryllina made up only 9.3% of approximately 9,000 Menidia spp. captured in the estuary, they made up 54% of the Menidia spp. taken at this location. Hoff (1972) interpreted these data to indicate that M. beryllina had a relatively small home range; this conclusion was supported by tagging studies in which about 1,000 marked M. beryllina were released at a single site in June 1970. All recoveries of tagged fish (up to 100 days after release) were within 100 m of the tagging site. Despite intense effort, none were recovered from other areas.

In the Cape Fear River Estuary, North Carolina, inland silversides were heavily concentrated in brackish waters of the upper half of the estuary, and the association of M. beryllina with low salinities was significant in multivariate analyses (Weinstein 1979; Weinstein et al. 1980). In North Carolina, M. beryllina tended to remain in brackish waters throughout the year, but in Rhode Island, Bengtson (1982) observed that adults and young-of-year undertook a down-estuary movement in the early fall. Unlike M. menidia, M. beryllina exhibited no offshore movements (Conover and Murawski 1982).

In the Delaware River Estuary, M. beryllina individuals were collected most often from late fall into early winter (deSylva et al. 1962) when they tended to penetrate farther into the bay. Thus, presence at several widespread localities in the lower estuary only in December suggests that these individuals may move downstream from upper bay tributaries.

SPECIFIC HABITAT REQUIREMENTS

Silversides are shallow-water estuarine species that frequent tidal salt marshes, seagrass meadows, and shore zones. Menidia beryllina generally prefer lower salinities (Weinstein 1979; Bengtson 1982), although they may be found seasonally along the entire salinity gradient and have been established in wholly freshwater systems. Menidia beryllina is most abundant over firm substrates (Weinstein 1979) with high sand content and low percentages of organics. These areas are usually located in moderate to fast tidal currents or along the sandy beaches (banks) of lakes or streams. Population densities are low where soft silts and reducing substrates (and consequently low dissolved oxygen) predominate.

Eggs

Spawning occurs in fresh or brackish shallow waters (up to 15 parts per thousand [ppt]), and eggs may become exposed in tidal waters. Vegetation, whether dead leaves, tree roots, algal mats, or rooted aquatic plants of the marshes, is the preferred spawning habitat (Hildebrand 1922; Wang 1971). On a daily basis, spawning in Lake Texoma took place at about 0900-1000 h each morning from March through July at temperatures ranging from 13 to 34 °C (Hubbs 1982). Large females predominated on the spawning grounds in the early morning hours, with smaller females reproducing during the afternoon. A similar pattern was evident for males: maximum sizes were observed in spawning areas before noon. Hubbs (1982) concluded that the functional breeding population was therefore reflected by the prenoon population on the spawning beaches.

The number of clutches per female varied with the number of days in the spawning season; thus, the number of clutches approximated the number of days a female lived after 1 April (Hubbs 1982). The termination of spawning in Lake Texoma seemed temperature dependent; i.e., reproduction slowed or ceased soon after water temperatures exceeded 30 °C. If this temperature was attained by 1 July, surviving females would produce about 90 clutches. Hubbs and Bailey (1977) reported that this temperature did not occur until early August in 1976. During this spawning season, therefore, females produced about 120 clutches.

Eggs from Lake Texoma (lat. 34 °N) populations developed successfully at incubation temperatures between 13.0 and 34.0 °C (Hubbs et al. 1971). Egg survival was highest between 17 and 33.5 °C. Optimal development occurred over the range 20.0-25.0 °C. Parental thermal conditions (acclimation history) were thought to influence temperature tolerance of embryos (Hubbs et al. 1971); consequently, temperature limits to survival, development rates, size at hatch, etc., may be expected to differ qualitatively at higher latitudes.

Salinity has varying interactive effects with temperature on survival of embryos and larvae. A concentration of 25% seawater had no noticeable effect on development and hatching of M. beryllina eggs. At 50% seawater concentration, hatching was restricted to temperatures between 19 and 33 °C; however, all but one of the young died within 24 h. This individual survived until its yolk was absorbed. In 75% seawater, hatching was restricted to temperatures between 22.0 and 31.3 °C, with similar survival of a single individual at the lowest temperature in the range. In full seawater, only a single egg hatched, at 20.9 °C, and it died the next day. Death was associated with starvation due to temperature/salinity-induced stress on metabolism during development (Hubbs et al. 1971). These studies were conducted on freshwater populations. It is expected that salinity tolerances would be higher in estuarine populations, though optimum salinities are probably in the brackish range.

Juveniles

The preferred habitats of juveniles overlap broadly with those of adults, although young M. beryllina may enter habitats, such as the high marsh, not frequented by larger specimens (Talbot and Able 1984). In the Talbot and Able (1984) study, juvenile M. beryllina were abundant in very shallow water (a few cm deep) in small pools as well as among Spartina culms on the flooded marsh. Many of these individuals would remain during low water periods. Whether or not this behavior was adaptive (e.g., to avoid predators) could not be ascertained.

By comparison, small juveniles were taken in Mississippi Sound from 5 April through 26 April at temperatures of 26.4-28.4 °C and at salinities of 3.3-19.4 ppt (Garwood 1967). Juveniles up to 36 mm TL were collected until 26 June in water temperatures of 21.0-31.8 °C and salinities of 2.2-23.8 ppt. Individuals approaching the arbitrary upper limit of juveniles (~49 mm TL) were captured from 6 April through 29 July in temperatures of 21.0-32.5 °C and salinities of 2.2-28.3 ppt.

In laboratory experiments by Bengtson (1982), postlarval M. beryllina consumed about 80% of their body weight per day, up to a maximum of about 160% of body weight. Maintenance ration was estimated at 5%-60% of body weight per day, with the remainder being devoted to growth. Young-of-year inland silversides apparently consume greater proportions of copepods than do adults (Kinch 1979).

Adults

The propensity of M. beryllina to form dense schools, combined with their high mobility, results in a tendency to treat their preferred habitats as fine grained (Levins 1968). Within brackish shallow waters, silversides may occur equally in vegetation, sandy areas, marshes, or shore zones (Reid 1954; Kilby 1955; Briggs and O'Connor 1971). They do not seem to do well in impounded coastal marshes (Harrington and Harrington 1982; Coorey et al. 1985). They may be captured well up into tidal creeks, over seagrass meadows, around sandy spoil islands, and over firm substrates along sandbars or banks. Subrahmanyam and Drake (1975) suggested that Florida tidal marsh fish communities be

designated as Fundulus-Menidia communities. Among the Atlantic coast drainages, however, M. beryllina is also distributed in tidal river channels below the fall line, estuaries, and upper bays (Martin and Drewry 1978).

Although captured at times virtually anywhere in the estuary, M. beryllina seems to be transient in many areas. However, on the basis of frequency of occurrence, preferred food types, and abundance, there is little doubt that M. beryllina is, as Bengtson (1982) describes it, a "denizen of the upper estuary," found in areas where substrates are sufficiently firm for seining. Weinstein (1979) and Weinstein et al. (1980) did not collect M. beryllina in soft bottom tidal creeks of the Cape Fear River Estuary (North Carolina) where rotenone was used, but they were common at all sandy-bottom brackish seining localities. Overall, M. beryllina displayed a significant negative correlation with the percentage of organics in the substrate (Weinstein 1979). High organic content is indicative of areas of deposition and reducing environments (Mills 1975).

Bengtson (1982) suggested that winter temperatures may adversely affect the survival of M. beryllina, particularly because, unlike M. menidia (Conover and Murawski 1982), they apparently do not migrate offshore. Overwintering mortality in the 80%-90% range has been reported for M. beryllina in Rhode Island waters (Bengtson 1982). In the warmer waters of Lake Texoma, Hubbs (1982) did not find significant winter mortality (minimum water temperature ~10 °C). The weekly mortality rate was about 19% during summer (maximum temperature ~30 °C). High predation rates, especially during the spawning season, were assumed to be responsible for the warm weather mortality rates. Thus, although few Menidia survive to age II throughout their range, the limiting factors for survival may differ with latitude, predation being more important farther south.

Inland silversides are fully adapted to freshwater (Minckley 1965; Cook and Moore 1970; Echelle et al. 1971; Gomez and Lindsay 1972; Meinz and Mecum 1977; Hubbs 1982) and are reported to tolerate salinities at least up to 75 ppt (Simmons 1957). Fish at higher salinities were reported to be "slightly" larger (Gunter 1945), probably because of seasonal down-estuary movements of young-of-year (Bengtson 1982). Weinstein et al. (1980) observed maximum abundance of M. beryllina at about 3 ppt salinity. Abundance decreased closer to the estuary mouth.

Reid (1954) and Kilby (1955) found that M. beryllina in Florida gulf coast populations were usually associated with some sort of "shelter" - islands, piers, oyster bars, pools containing rubbish, or near submerged vegetation. At Bayport, Florida, specimens were most often collected in the upper water column above dense seagrass meadows (Kilby 1955). Similar habitat requirements have been reported for populations of M. beryllina in Lake Texoma (Hubbs et al. 1971): fish occurred in schools of similar-sized individuals near the surface, typically in the upper 10 cm of the water column, and either near the shore (during the breeding season), or farther offshore (>30 m) at other times. Sandy bottom and gradual slope were deemed optimal habitat.

Menidia beryllina may be characterized as a daytime predator that primarily locates its prey by sight. It takes food in the water column and, at

times, on or near the bottom. Some nighttime feeding has been reported (predominantly on large food items), but it is an activity that was greatly reduced on new moons, according to Elston and Bachen (1976). Nightly benthic feeding has also been reported in clear Florida waters (Odum 1971; Brook 1977; Kinch 1979).

Dominant food items in the diet of M. beryllina include copepods, mysids, amphipods, isopods, veligers, and insects (Reid 1954; Springer and Woodburn 1960; Darnell 1961; Harrington and Harrington 1961; Odum 1971; Carr and Adams 1973; Brook 1977; Kinch 1979; Bengtson 1982). Inland silversides confined to reservoirs preyed upon zooplankton, mostly Ceriodaphnia sp., Daphnia pulex, and emerging diptera (Elston and Bachen 1976; Hubbs 1982). In Clear Lake, California, Elston and Bachen (1976) found that M. audens (= M. beryllina) consumes 86%-95% of its daily ration during daylight, with peak feeding activity at 0800-0900 h. Virtually everywhere that diet has been examined, the presence of sand, algae, and detritus in the gut of M. beryllina suggests a substantial amount of benthic feeding.

Seasonality in the diets of M. beryllina and M. menidia was examined and compared in Rhode Island estuaries by Bengtson (1982). Members of both species exhibited seasonal changes in diet, largely brought about by temporal changes in food availability and simultaneous movements of fish that enabled them to feed in different areas of the estuary. Guts of M. beryllina, like those of its congener, were fullest during spring, but the percentage of fullness declined substantially in June and remained low during summer. Menidia beryllina collected at upper estuary sites during fall had relatively empty guts. In general, when compared with those of M. beryllina, the guts of M. menidia were relatively fuller at all times of the year. The slower rate of growth of M. beryllina in late summer has been attributed to this phenomenon (Bengtson 1982), indicating seasonal food limitation for this species.

Bengtson's (1984) data on gut contents showed that, overall, the most abundant food items eaten by both species were the copepodite and adult stages of calanoid copepods. At upper estuary stations in the spring, both species primarily consumed polychaete larvae and zooplankton. As food became scarce in late summer, resource partitioning was observed: Menidia beryllina switched to epibenthic invertebrates and insects while M. menidia still concentrated on zooplankton (Bengtson 1984). Competition experiments conducted by Bengtson (1982) suggested that M. beryllina is an inferior competitor to M. menidia. It should be noted, however, that M. beryllina has virtually extirpated a related atherinid, Labidesthes sicculus, where the former has been introduced (McComas and Drenner 1982).

Parasites

Parasites of M. beryllina were examined in the Escambia Bay region of Florida, where individual fish were infested by a parasitic copepod, Ergasilus manicatus, at two locations, Mulatto Bayou and Catfish Basin (Bortone et al. 1978). At the former site, 13.2% of the fish were infected at an intensity of 1.9; at Catfish Basin the infestation rate exceeded 50%, with an intensity of 2.3. Fish with parasites were significantly longer than fish without

parasites. Levels of incidence and intensity of parasite infestation were lowest in winter and gradually increased to maximum levels in May.

Special Considerations

Numbers of juvenile M. beryllina were apparently reduced in tidal creeks affected by heated cooling waters from a steam-electric station (Carr and Giesel 1975). At that study site, temperatures routinely exceeded 35 °C from June through September. With only one exception, the July average daytime temperatures at all stations in the primary sampling area, San Carlos Creek, were greater than 35 °C. Although the overall population of fishes found in San Carlos Creek was neither "large nor very diverse" (Carr and Giesel 1975), 15 out of 48 species displayed no marked decrease in numbers, and a few species were actually more abundant here than in the ambient temperature (control) creek. The majority of these taxa were highly resistant cyprinodontiform forms, a result that was not surprising given the extreme adaptability of these species. The results of Chung and Strawn (1977, 1978) demonstrate that juvenile M. beryllina may be regarded as an intermediately temperature-resistant species in marshland nurseries. In their studies of the temperature effects of heated effluents on estuarine fishes, the modal 3-h LC_{50} for M. beryllina exposed to heated effluent at a Texas generating station was 37 °C, independent of season and at ΔT's ranging from 13.7 to 17 °C. Of the 54 species tested, only 15 (6 cyprinodonts) had modal values higher than M. beryllina, which placed M. beryllina in the intermediate temperature-resistance range.

Menidia beryllina has recently become an increasingly popular subject for bioassay and toxicological studies (Bengtson 1982). Time-related responses to chlorine (an environmental pollutant), for example, have been observed (Morgan and Prince 1977) in the eggs of M. beryllina. The general response for fertilized eggs was decreasing sensitivity with egg age. Two-hour-old eggs had LC_{50} values of about 0.25 parts per million (ppm) chlorine; 24-hour-old eggs, 0.32 ppm. The species has been shown to bioaccumulate PCB's to high levels (Nimmo et al. 1975), and among six species of fishes and crustaceans examined for sensitivity to water-soluble extracts of crude oil, M. beryllina ranked fifth in sensitivity, with only Cyprinodon variegatus more resistant (Anderson et al. 1974). Other studies with crude oil and its water-soluble fractions (Solangi and Overstreet 1982) indicated that relatively brief exposure to whole crude oil (WCO) at 5 ppm concentrations and 5% water-soluble fractions temporarily disrupted schooling patterns and feeding did not occur up to 6 h after exposure. Some M. beryllina exposed to 5 ppm WCO died on the fifth day of exposure, and deaths increased steadily until termination of the tests at day 30, by which time 42% of the fish had died (Solangi and Overstreet 1982). A similar mortality rate occurred in fish exposed to 5% and 50% water-soluble fractions. Initial deaths in these groups were at days 2 and 4 and, after a consistent increase in death rate, about 56% of the fish died by day 27. Histological effects were also noted, and pathological effects were linked to mortality. At the relatively low concentrations noted above, hyperplasia intensified by day 30 and many gill lamellae were fused at their bases. Olfactory organs and livers were similarly affected. However, degenerative changes were reversed if, after 20 days of exposure, fish were transferred to clean water (Solangi and Overstreet 1982).

The apparent "intermediate" sensitivity of M. beryllina to toxic substances in the environment may make it a more suitable indicator species to pollution-induced stress than previously utilized species such as C. variegatus and Fundulus sp. Menidia beryllina is currently being tested as a "standard" bioassay organism by the U.S. Environmental Protection Agency (C. Cordes, U.S. Fish and Wildlife Service; pers. comm.).

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

This model applies to all life stages of the inland silverside found in tidal creeks and flats, marsh pools, and all shallow subtidal (to 3 m deep at low tide) estuarine habitats, including tidal freshwaters. Model application is not always appropriate where habitats have been severely altered by impounding or influenced by other anthropogenic activities, including toxicant additions, cultural eutrophication, or thermal discharges. In many of these situations, water quality has so deteriorated as to make model use moot. The model does not apply in water deeper than 3 m at low tide.

Geographic area. This model is applicable to M. beryllina populations occupying estuarine habitats from Massachusetts to New Jersey. However, the model is sufficiently general so that, with only minor adjustments (for latitudinal acclimation histories), it can apply virtually anywhere M. beryllina is found. This is also partly because the species is a habitat generalist and is endemic to estuaries, a trait by itself indicating that M. beryllina has a wide range of environmental tolerances.

Season. The model is designed for year-round use but can be readily adapted for seasonal applications or for a single life stage. If the model is adapted for one season or life stage, it is assumed that necessary life requisites in other seasons or for other life stages can be obtained at the same site or by routinely migrating to other locations.

Habitat types. Inland silversides use nearshore habitats (to depths of 3 m at low tide) that usually have some sort of vegetation nearby, such as marshgrasses or submerged aquatic vegetation (SAV). They seem to prefer flowing water. Different life stages overlap in the use of these habitats; however, early life stages sometimes frequent microhabitats, such as high marsh pools surrounded by vegetation, where adults are not found. Inland silversides occur in all estuarine subtidal and intertidal habitat classes as defined by Cowardin et al. (1979).

Minimum habitat area. The minimum habitat area is the contiguous suitable habitat required for inland silversides to live and reproduce. No minimum spatial requirements for this species have been reported to date.

Verification level. The acceptable output for this model is an index between 0 and 1 that is believed to have a positive relationship to carrying capacity. Hypothetical data sets were used to verify that the HSI's determined with the inland silversides model were reasonable and accurate. These data sets and their relationship to model verification are discussed later.

Model Description

Because all life stages of the inland silversides share nearly identical habitats, a single model may be used to adequately predict habitat suitability. Three habitat components are important: water quality, food, and cover (Figure 1). Collectively they identify those habitats and conditions that maximize fitness (reproductive success) and production in the species. Physicochemical variables define minimum requisites for the presence of a species. Within this framework, differences between sites in interactions with competitors and predators may alter overall suitability from that predicted by this model from physicochemical characteristics alone.

The following sections describe the conceptual framework and assumptions used to construct the HSI model. Although model calculations are based on discrete variables, it should be emphasized that these variables are not mutually exclusive nor are their life requisite combinations independent. There is a great deal of overlap and correlation between the habitat variables and life requisites. For example, substrate characteristics and current velocities are directly related, as are water depth and distance from shore. Nevertheless, HSI's are useful first approximations of habitat suitability. The model should be modified as applications provide additional information about how variables act together to determine habitat suitability.

Water quality component. No field or laboratory experimental data are available for judging dissolved oxygen effects on inland silversides. However, data for a wide variety of other fishes (Doudoroff and Shumway 1970) suggest that values below 3.0 mg/l exert significant negative effects on growth and production rates. Detectable metabolic changes also occur at levels below about 5.0 mg/l (Doudoroff and Shumway 1970). For these reasons, lowest monthly mean dissolved oxygen levels (V_1) above 5.0 mg/l are considered suitable and nonlimiting for M. beryllina. Although low levels of dissolved oxygen may make a site unavailable only temporarily, it is assumed that elimination of less mobile food organisms will prolong the harmful effects of low oxygen and reduce suitability to 0 when the lowest monthly mean for dissolved oxygen reaches 0.

Inland silversides can tolerate a wide range of salinities; however, high salinities are harmful, at least to early developmental stages. Individuals from a freshwater population did not survive past the yolk sac stage in 50% seawater (~17 ppt) and showed no adverse effects in 25% seawater (~8 ppt) (Hubbs et al. 1971). Estuarine populations probably tolerate somewhat higher salinities. Juveniles and adults are most abundant in the oligo-mesohaline range (0.5-18 ppt, Cowardin et al. [1979]). Based on this and the presence of flourishing lake populations, salinity (V_2) is assumed to be optimally suitable at 0 ppt and to remain optimal to 10 ppt, above which eggs and larvae begin to be affected. The presence of M. beryllina in the higher salinity reaches of estuaries usually occurs only at cool temperatures, when metabolic demand for osmoregulation and other physiological activities is reduced. This suggests that mean salinities approaching that of the ocean are unsuitable for all life stages, even though much higher salinities can be tolerated for brief periods. Accordingly, suitability is assumed to decline to 0 at 30 ppt salinity.

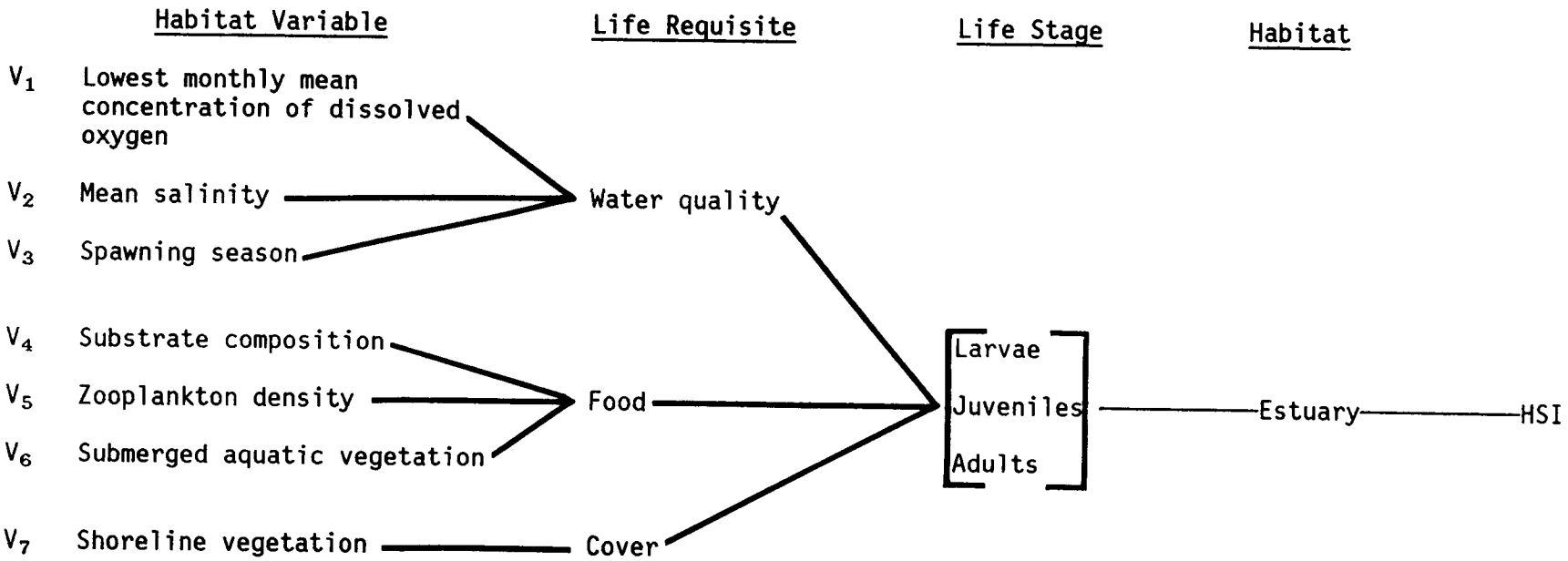


Figure 1. Relationship of habitat variables and life requisites to the habitat suitability index (HSI) for inland silversides in estuarine habitats.

Overwintering mortality in northeastern Atlantic coast populations of M. beryllina is reportedly high (Bengtson 1982). Nevertheless, the strongest influence of temperature on habitat suitability appears to be by determining the length of the spawning season. Gravid females are first collected at about 20 °C (V_3) in Rhode Island estuaries (Bengtson 1982). Spawning is reduced at temperatures exceeding 30 °C, thereby setting an upper limit for the success of the species. Optimum conditions for development and hatching occurred over the range 20-25 °C in Lake Texoma (Hubbs et al. 1971). Since inland silversides are daily spawners, the length of the spawning season, or number of days in the year that water temperature is between 20 and 30 °C (V_3), determines fecundity. It is assumed that a minimum of 15 days within this temperature range is required to assure survival of the most sensitive early developmental stages and that populations are not limited by production and early survival of young beyond a 75-day period with temperatures between 20 and 30 °C. It is also assumed that temperatures approaching the upper lethal limit of 36 °C (Chung and Strawn 1977, 1978) are never reached in the region of application of this model; however, this assumption must be reconsidered where thermal discharges are being assessed.

Food component. Weinstein (1979) and Weinstein et al. (1980) reported a significant negative correlation between the percentage of organics in the substrate and the abundance of M. beryllina. Rather than being a direct influence, the low percentage of organics is indicative of preferred habitat associated with scouring tidal flows and sandy substrates. Mild tidal currents may also supplement the foraging activities of M. beryllina by carrying food items into the area at an energy savings to the species; in addition, nonreducing substrates may provide more suitable habitat for the seasonal benthic component of the M. beryllina diet. Percentage of silt plus clay in the substrate (V_4) is used as an indicator of these conditions influencing suitability for feeding. For most of the year, zooplankton in the water column provide the largest component of this diet. In Rhode Island, weekly mean zooplankton densities in the littoral zone (V_5) reached a maximum of about 160 individuals per liter in each of the 2 years sampled (Bengtson 1982). For purposes of this model, >160 zooplankters/liter will be considered optimum for M. beryllina growth and fitness; values below this level will eventually become limiting. Bengtson (1982) observed that guts were less full in late summer when zooplankton abundance declined, and suggested that slower rates of growth during this period may be due in part to reduced food intake.

Submerged vegetation (V_6) apparently provides supplementary food resources in the form of epibenthic organisms that reach high areal densities in seagrass meadows or among marshgrass culms. The frequent association of M. beryllina with this habitat may be a product of food availability and the diel vertical migration of zooplankton (partly from seagrasses); inland silversides may take advantage of these migrations by crepuscular and nighttime feeding during periods of the full moon (K. Sulak, Huntsman Marine Laboratory, St. Andrews, New Brunswick; pers. comm.).

Cover component. The most important aspects of cover for M. beryllina are associated with reproduction and perhaps also with survival of juveniles. In general, the species occupies shallow water near shorelines, a trait that may result in reduced predation on this important forage species. Inland

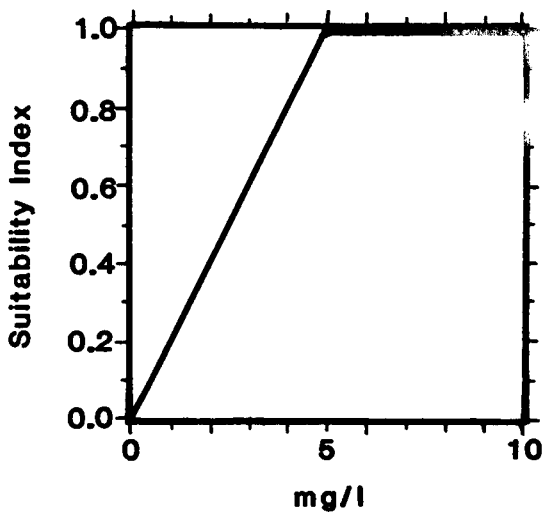
silversides are most abundant within 30 m of the shore during the breeding season (Hubbs et al. 1971; Fisher 1973). At other times they apparently venture farther offshore but are not commonly found at water depths greater than about 2 m. Therefore, only areas shallower than 3 m deep are evaluated in applications of this model. They generally reside near the surface in the vicinity of some sort of "shelter" (Reid 1954; Kilby 1955), such as oyster reefs, vegetation, or artificial structures. Shoreline vegetation (V_7), especially emergent marshgrasses, seems critical to egg survival in estuarine habitats. Eggs are most often laid with their adhesive filaments in this substrate, which reduces predation. Juveniles may also use the shallow pools and vegetated areas of the high marsh as a refuge from predators. Individuals <20 mm SL are at times abundant in these microhabitats (Talbot and Able 1984; M.P. Weinstein, pers. obs.).

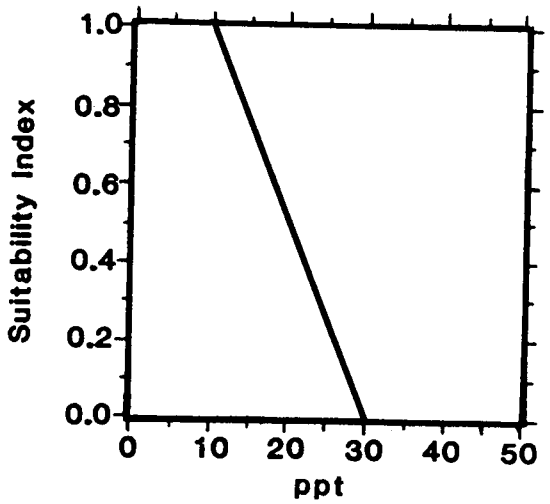
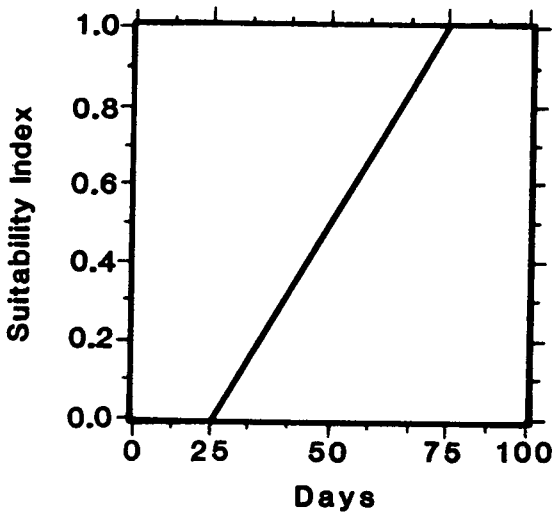
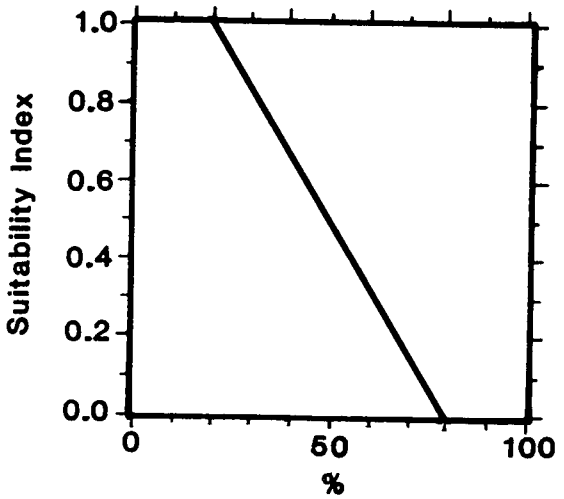
Model variables and sources for HSI calculations are listed in Table 1. Graphic representation of these variables as they are related to habitat suitability is shown below.

Suitability Index (SI) Graphs for Model Variables

This section illustrates the relationships between the value of estuarine (E) habitat variables and habitat suitability for inland silversides. The SI values are read directly off the graph (1.0 = optimum suitability; 0.0 = no suitability) for any variable value.

Although there are interdependencies and correlations between many habitat variables, it is assumed for purposes of model construction that each variable operates independently over the range of other variables under consideration. Furthermore, there is no significance attributed to the order in which these variables and their associated curves are presented.

Habitat	Variable		Suitability Graph
E	V_1	Lowest monthly mean concentration of dissolved oxygen (mg/l) at middepth.	

Habitat	Variable		Suitability Graph
E	V_2	Mean middepth salinity (ppt), 21 March through 21 September.	
E	V_3	Length of spawning season. Number of days in year that water temperature (°C) is greater than or equal to 20° and less than or equal to 30°.	
E	V_4	Percentage of silt plus clay in substrate.	

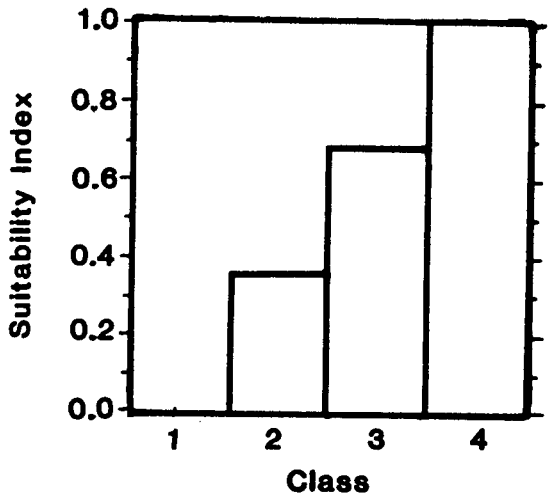
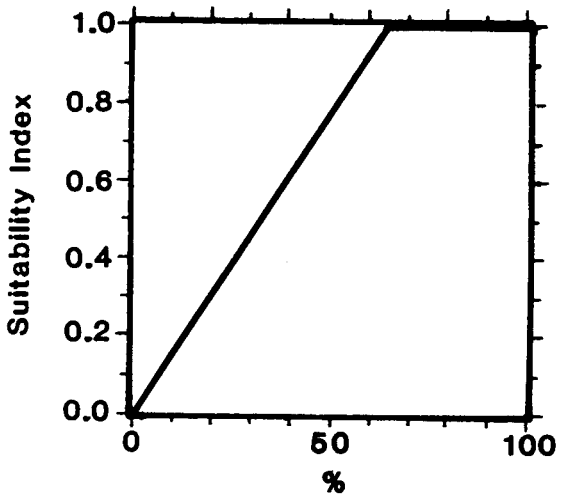
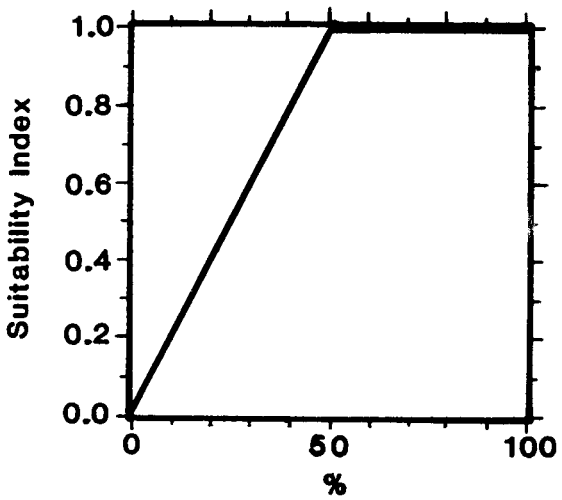
Habitat	Variable		Suitability Graph
E	V_5	Zooplankton density (no./l) in July and and August (period of peak M. beryllina abundance). 1) <40 2) 40-79 3) 80-159 4) ≥160	
E	V_6	Percentage of sub-tidal area covered by submerged aquatic vegetation.	
E	V_7	Percentage of tidal creek/bay shoreline vegetated by marsh-grasses.	

Table 1. Primary data sources for inland silverside habitat variables.

Variable and sources		Assumptions
V_1	Doudoroff and Shumway 1970	Significant reductions in growth rates and production may occur at dissolved oxygen concentrations of 3 mg/l or less. Concentrations of dissolved oxygen above 5 mg/l are optimal.
V_2	Hubbs et al. 1971 Weinstein 1979 Weinstein et al. 1980 Bengtson 1982	Salinities less than 10 ppt are optimal. Adults are not usually found in polyhaline salinities until October (after the season for which this variable is determined), when temperatures are cooler and metabolic demands are lower.
V_3	Hubbs et al. 1971 Carr and Giesel 1975 Chung and Strawn 1977, 1978 Bengtson 1982	The onset of reproduction in New England occurs at temperatures above 20 °C; spawning is reduced at temperatures above 30 °C; lethal limits are approached at temperatures exceeding 36 °C.
V_4	Hubbs et al. 1971 Martin and Drewry 1978 Weinstein 1979	Sediment texture does not influence habitat quality for inland silversides directly; however, grain size is a good indicator of the prevailing current regime, which is important. Water movements fast enough to scour fine particles are most suitable; therefore, suitability decreases as the percentage of fine particles increases.
V_5	Elston and Bachen 1976 Bengtson 1982	From data developed for the littoral zone of Rhode Island estuaries, it is assumed that summertime average concentrations exceeding 160 individuals/l are optimal food densities.
V_6	Reid 1954 Kilby 1955 Briggs and O'Connor 1971 Wang 1971	Submerged vegetation provides a supplementary food resource in the form of associated epibenthic fauna.
V_7	Reid 1954 Kilby 1955 Hubbs et al. 1971	No information is available on substrate requirements for spawning in northern estuaries. Based on the cited references for other regions, emergent shoreline vegetation (marshgrasses) is assumed to be required as a spawning substrate in northern estuaries.

Component Index (CI) Equations and HSI Determination

To calculate HSI scores for inland silversides, the individual SI values must be composited. This approach requires two steps: first, a CI score is calculated for the water quality, food, and cover components, then a single HSI score is calculated by compositing these values. A weighting procedure is employed to give added emphasis to the most important habitat variables. The CI may be composited in several ways, depending on whether variables are seen as limiting factors, in which case the CI takes the value of the lowest SI, or whether compensatory relationships exist among variables such that a variable with low suitability can be offset by the high suitability of other variables. Arithmetic means (AM) give equal weight to high and low constituent values, while geometric means (GM) are more influenced by low values, becoming a limiting factor approach when one variable has an SI of 0.

$$AM = \frac{(SI_{V_1} + SI_{V_2} + \ldots + SI_{V_n})}{n} \qquad GM = (SI_{V_1} \times SI_{V_2} \times \ldots \times SI_{V_n})^{1/n}$$

In this model, variables have been weighted according to their relative importance in determining suitability in the judgment of the author. Arithmetic and geometric means were used in combination to express the different levels of compensation believed to operate among variables and CI values.

Component		Component Index Equation
Water Quality		$\frac{SI_{V_1} + 2SI_{V_2} + SI_{V_3}}{4}$
Food:	with V_5	$\frac{2[SI_{V_4} \times (SI_{V_5})^2]^{1/3} + SI_{V_6}}{3}$
	without V_5	$\frac{2SI_{V_4} + SI_{V_6}}{3}$
Cover		SI_{V_7}

$$HSI = [\text{Water Quality} \times \text{Food} \times \text{Cover}]^{1/3}$$

In summary, the following steps are required to determine an HSI for any application:

1. Review the section on model applicability for validity of the model for the intended application.

2. Identify the boundaries of the evaluation area or areas and obtain data for each variable used in the model. Using the SI graphs and proper equation, calculate the component indices.

3. Determine the HSI by calculating the geometric mean of the respective component indices.

Three sample data sets, from which suitability indices, component indices, and habitat suitability index values have been generated, are shown in Table 2. Although the data sets are not actual field measurements, they do represent the kinds of values expected for estuarine habitats used by inland silversides. The HSI's calculated from these hypothetical data reflect the relative abundance of silversides in habitats with the characteristics listed in Table 2.

Field Use of the Model

This HSI model is designed for application to all life stages of the inland silversides found along the Atlantic coast from Massachusetts to New Jersey. To ensure the most reproducible and meaningful results from model output, sampling should be conducted at least monthly during spring and summer. Detailed evaluation of all variables in the actual project area will produce the most reliable and reproducible HSI values. Unfortunately, long-term means probably are more critical for achieving reliability in HSI determinations than the most exhaustive determination of habitat variables in a short span of time. Field measurements for a HEP analysis probably never will be made over several years before a project. Therefore, other sources of environmental data, such as State and Federal monitoring programs or long-term research projects conducted by academic institutions, may be more valuable for a HEP application than the limited field measurements that could be made during a HEP analysis. However, these alternative sources of data are unlikely to be specific to the project area. The user must decide whether extrapolation to a project site is justified. Field observations should be used to check the appropriateness of extrapolation from these other sources.

The time and effort required to determine zooplankton density (V_5) adequately for use in this model are likely to exceed the resources available for many applications. A variant of the model may be used in this case, where the substrate variable (V_4) and the submerged aquatic vegetation variable (V_6) serve as predictors of food availability, rather than as modifiers of the more direct measure provided by zooplankton density (V_5). Greater uncertainty in the calculated HSI value for existing conditions will result when V_5 is not measured; however, this qualification does not apply in predicting future conditions. Future zooplankton density would have to be predicted based on more easily predicted changes in other variables. Therefore, the alternative HSI model including V_5 will be no more reliable than the alternative excluding V_5 for future conditions. See Table 3 for suggested methods of measuring the variables of this HSI model in the field.

Limitations. The natural geographic range of M. beryllina is extensive and has been expanded by various introductions into lakes and reservoirs nationwide. The controversy concerning the taxonomic status of the genus is unique to this species among those used in HSI models to date. Consequently,

much of the data base is in confusion; for example, many studies on "M. beryllina" in Florida likely involved M. peninsulae partly or entirely. The synonymy between M. beryllina and M. audens has extended the range of the former into wholly freshwaters with substantially different habitat types, food, etc. Some of the most extensive studies on the species come from these habitats, particularly from Lake Texoma. This model is developed for application to M. beryllina populations occurring along the northeastern Atlantic coast, specifically in estuarine habitats. Because the best information on life requisites frequently comes from other geographic areas, it will be necessary to make some assumptions to allow extrapolation to the geographic area of interest. Most of these assumptions are simply based on latitudinal adjustments of parameters and do not require changes in the parameters themselves (e.g., time or temperature of spawning, temperature tolerance).

Table 2. Hypothetical data sets for suitability indices (SI) in selected inland silverside localities. Associated component indices (CI) for water quality (WQ), food (F), and cover (C) are shown along with habitat suitability index (HSI) values.

Model component	Cattus Island (NJ)		Great South Bay (NY)		Point Judith (RI)	
	Data	SI	Data	SI	Data	SI
V_1 (mg/l)	4	0.8	8	1.0	7	1.0
V_2 (ppt)	22	0.4	25	0.25	4	1.0
V_3 (days)	50	0.5	75	1.0	70	0.9
V_4 (% fines)	50	0.5	5	1.0	40	0.67
V_5 (no. per liter)	50	0.33	310	1.0	--	----
V_6 (% cover by SAV)	0	0.0	60	0.92	0	0.0
V_7 (% vegetated shoreline)	75	1.0	35	0.7	90	1.0
WQ		0.53		0.63		0.98
F		0.25		0.97		0.44
C		1.0		0.7		1.0
HSI		0.51		0.75		0.76

Interpreting Model Outputs

An inland silverside HSI determined by field application of this model may not reflect the population density of inland silversides in the study area because factors other then habitat quality have significant influence on the abundance of a species at any one time. In coastal areas where inland silverside populations are primarily regulated by habitat-based factors, the model should yield HSI values that have positive correlations with long-term

abundance. This correlation has not been tested. The proper interpretation of the HSI is one of comparison. If two different areas have different HSI's, then the area with the higher HSI should have the potential to support more inland silversides than the one with the lower HSI.

Table 3. Suggested methods[a] for field measurements of variables used in the inland silverside HSI model.

Variable	Methods
V_1	Dissolved oxygen (DO) at middepth can be measured using Winkler titrations or an oxygen electrode.
V_2	Salinity at middepth can be measured by a temperature-compensated refractometer or salinity meter.
V_3	Temperature can be measured by thermometer or temperature probe.
V_4	Percentage silt plus clay in substrate can be measured by wet sieving.
V_5	Zooplankton production can be estimated by field sampling with plankton nets. Suction samplers (in seagrass meadows), and bottom grabs (or cores) must be used to sample for demersal zooplankton and epifauna, if these alternative sources proved to be important locally. Care must be exercised to ensure that the field sampling design is adequate to account for the abundance and distribution (often contagious) of dominant taxa.
V_6	Percentage submerged aquatic vegetation can be determined from aerial surveys or field sampling.
V_7	Percentage of shoreline vegetated by marshgrasses can be determined from aerial surveys or field sampling.

[a]Detailed procedures for measuring water quality can be found in Standard Method for Examination of Water and Wastewater (Anonymous 1981). Previously collected data may be available in published literature and/or technical reports for many areas.

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16. Abstract (Limit: 200 words)

A review and synthesis of existing information were used to develop a model for evaluating inland silverside habitat quality. The model is scaled to produce an index of habitat suitability between 0 (unsuitable habitat) and 1.0 (optimal habitat) along the Atlantic coast of the United States from Massachusetts to New Jersey. Habitat suitability index models are designed for use with the Habitat Evaluation Procedures previously developed by the U.S. Fish and Wildlife Service. Guidelines for model application and technique for measuring model variables are provided.

17. Document Analysis a. Descriptors

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