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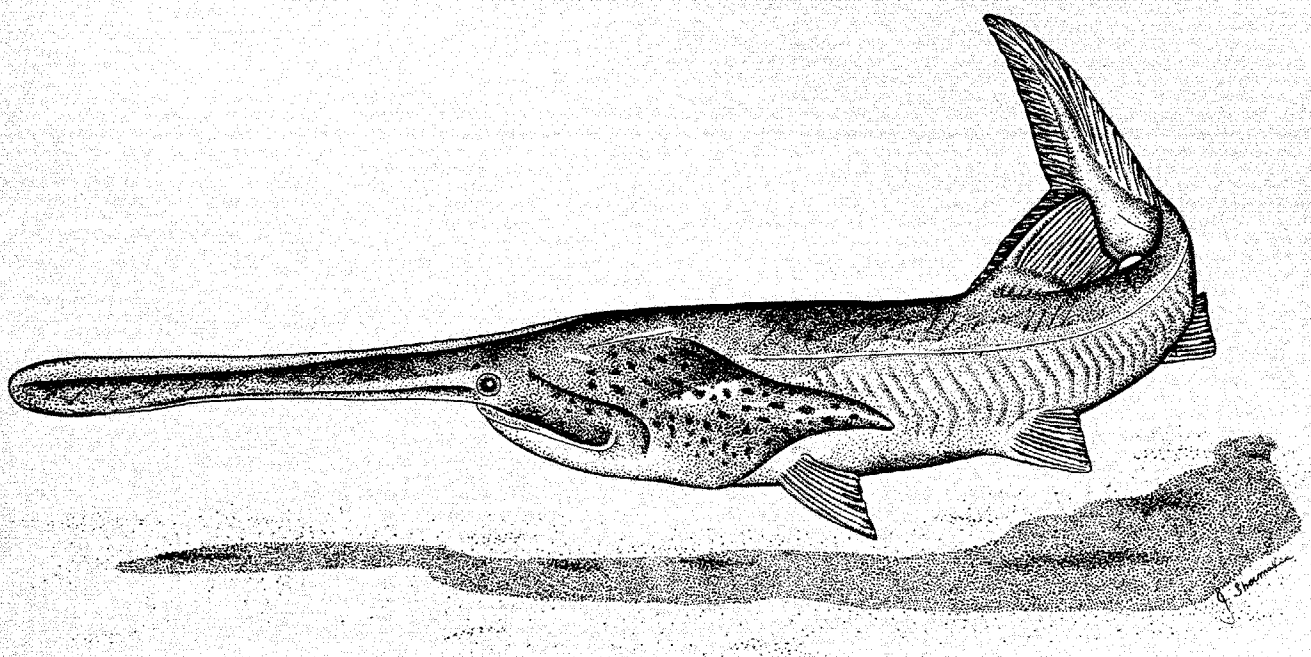
HABITAT SUITABILITY INDEX MODELS AND INSTREAM FLOW SUITABILITY CURVES: PADDLEFISH



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HABITAT SUITABILITY INDEX MODELS AND INSTREAM FLOW SUITABILITY CURVES: PADDLEFISH

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PREFACE

Paddlefish habitat suitability information presented in this document is for use with Habitat Evaluation Procedures (HEP) and the Instream Flow Incremental Methodology (IFIM). The information is useful for impact assessment and for developing management recommendations and mitigating alternatives for the species. Anyone who anticipates applying HEP or IFIM to paddlefish habitat should review the comparison and recommendations for use of HEP and IFIM (Armour et al. 1984).[1]

The Suitability Index (SI) curves and graphs and Habitat Suitability Index (HSI) models presented herein are based primarily on a synthesis of information obtained from a review of the literature concerning habitat requirements of the species. The HSI models are scaled to produce an index between 0 (unsuitable habitat) and 1 (optimal habitat). Assumptions used to transform habitat use information into HSI models are noted, and guidelines for application of the models are described. Discussions of IFIM and paddlefish SI curves available for use with IFIM are included.

Use of this habitat suitability information requires the setting of clear study objectives and may require modification of the SI curves or graphs and HSI models to meet those objectives. Users of the SI graphs and/or HSI models with HEP should be familiar with standards for developing HSI models (U.S. Fish and Wildlife Service 1981)[1] and guidelines for simplifying HSI models and recommended measurement techniques for model variables (Terrell et al. 1982).[1] Users of the SI curves with IFIM should be familiar with the guide to stream habitat analysis (Bovee 1982)[1] and the User's Guide to the Physical Habitat Simulation System [PHABSIM (Milhous et al. 1981)].[1]

The HSI models and SI curves presented herein are hypotheses of species-habitat relationships, not statements of proven cause and effect relationships. The curves and models are literature and professional judgment based. They have not been tested against field population data. For this reason, the U.S. Fish and Wildlife Service encourages model users to convey comments and suggestions that may help us increase the utility and effectiveness of this habitat-based approach to fisheries planning. Please send comments to:

Habitat Evaluation Procedures Group or
Instream Flow and Aquatic Systems Group
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Fort Collins, CO 80526-2899

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[1]Citation included in references.

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PADDLEFISH (Polyodon spathula)

HABITAT USE INFORMATION

General

The original range of the paddlefish was the Mississippi River drainage and adjacent Gulf Coast drainage. It was once found in some of the Great Lakes (Carlson and Bonislawsky 1981). The paddlefish is generally an inhabitant of large rivers, but it occurs in reservoirs and natural lakes connected to large rivers. Much of the original range has been reduced due to habitat alterations: (1) destruction of spawning areas; (2) blockage of movements by dams; (3) channelization and elimination of backwater areas; (4) dewatering of streams; and (5) pollution (Carlson and Bonislawsky 1981). Several States officially consider the paddlefish as rare or endangered (Miller 1972). An indexed bibliography of all known paddlefish work was prepared by Graham and Bonislawsky (1978) and recently updated to include more than 480 citations (Graham and Bonislawsky, in press).

Paddlefish supported a large commercial fishery in the Mississippi River basin in the early 1900's (Carlson and Bonislawsky 1981). As the most sought after species at that time, it was valued for its flesh, roe, and oil (Everman 1902; Hussakop 1910). Paddlefish fisheries have declined significantly through this century, but both commercial and sport fisheries still exist in some areas (Carlson and Bonislawsky 1981). A demand for paddlefish caviar has increased exploitation in several locations over recent years.

The paddlefish is primarily a large river species and travels extensively throughout a variety of riverine habitats. Paddlefish movements have been studied by mark and recapture techniques in the Osage River in Missouri (Purkett 1963b), the Missouri and Yellowstone Rivers (Robinson 1966; Rosen 1976; Elzer 1977; Rehwinkel 1978; Van Eeckhout 1980), the Cumberland River (Pasch et al. 1978, 1980), and the Mississippi River (Gengerke 1978). These investigations documented the high mobility of the species. One fish was observed to have moved nearly 2,000 km within 3 to 8 months of being tagged (Rosen et al. 1982). Telemetry has further confirmed these observations (Elzer 1977; Pasch et al. 1978, 1980; Russell et al. 1980; Unkenholz 1981; Southall and Hubert 1984). Southall (1982) observed paddlefish swimming as far as 12.8 km in 2.5 hours.

Age, Growth, and Food

Paddlefish are large fish with a life span exceeding 20 years. The largest paddlefish recorded was from an Iowa lake and weighed over 90 kg (Harlan and Speaker 1956). Paddlefish are sexually dimorphic with females being significantly larger than males (Gengerke 1978; Rosen et al. 1982). Sexual maturity is reached at 100 to 130 cm total length (TL) (6 to 12 years) in females; at about 115 cm TL (4 to 8 years) in males (Gengerke 1978). Females apparently spawn at 2 or more year intervals based upon observations of ova development patterns (Houser and Bross 1959; Vasetsky 1971; Gengerke 1978; Rosen et al. 1982). Meyer (1960) suggested that spawning may occur at 4 to 7 year intervals. As a result, periodicity of spawning runs has been suggested (Elser 1977).

Information on young-of-the-year growth in the Cumberland and Mississippi Rivers has been compared by Pasch et al. (1980) to information from other rivers and locations. In the Cumberland and Mississippi Rivers young paddlefish reached 200 to 350 mm TL by September of their first year and were 325 to 500 mm TL by June of the following year. The results were similar to observations from other river systems, but there are large variations in observed sizes at 1 year of age (Meyer 1960; Houser 1965; Bernet et al. 1977).

It appears to be advantageous to paddlefish to occupy still waters during the growing season. Fish from lake populations have been observed to grow faster than fish from riverine populations (Stockard 1907; Friberg 1974; Unkenholz 1979; Rosen et al. 1982).

Paddlefish feed primarily on zooplankton and immature aquatic insects (Eddy and Simer 1929; Ruelle and Hudson 1977). Young-of-the-year (< 120 mm TL) select individual large cladocerans, but at 120 mm TL they begin to switch to filter feeding (Michaletz et al. 1982). Adult paddlefish have been described as nonvisual filter feeders. The species of zooplankton consumed relates to the size, number and spacing of gill rakers (O'Brien 1979; Rosen and Hales 1981). Zooplankton has been found to be the most important food in most of the range (Meyer 1960; Rosen 1976; Rosen and Hales 1981), but immature insects can contribute significantly in some waters, such as the upper Mississippi River (Wagner 1908; Hoopes 1960; Meyer 1960). Adults may occasionally prey upon small fish (Meyer 1960; Fitz 1966).

Kofoid (1900) observed the feeding behavior of captive adults. These paddlefish appeared to locate concentrations of zooplankton and then swim in circles while opening and closing their mouths. This behavior continued until the zooplankton were consumed.

Reproduction

Paddlefish spawn over clean gravel bars in large rivers during spring periods of high water. Despite the economic importance of the species and searches for spawning sites (Stockard 1907; Alexander 1915), spawning was not observed until 1960 in the Osage River in Missouri (Purkett 1961). Purkett

recovered eggs and larvae from gravel substrate (13 to 38 mm diameter) immediately downstream from the spawning sites. Specific spawning sites have been located on the Missouri River (Berg 1981). Pasch et al. (1980) found a general spawning area below Cordell Hill Dam in the Cumberland River. The habitat in the rivers was similar to the Osage River with a large part of the streambed composed of gravel and rubble, ranging from 2 to 12 m deep. Unkenholz (1979, 1981) collected larvae 7.3 km downstream from Fort Randall Dam on the Missouri River, but the exact upstream spawning site was not located.

Paddlefish spawn when water temperatures exceed 10° C. There are observations of spawning activities at 10 to 15° C (Kallemeyn 1975; Pasch et al. 1980; Unkenholz 1981), but the usual spawning temperature given in the literature is 16 to 17° C (Alexander 1915; Purkett 1961).

A rapid increase in river discharge is a spawning stimulus for paddlefish. Purkett (1961) observed spawning in the Osage River on the seventh day after a water level rise of 2.7 m. Similar circumstances were associated with congregation of adult paddlefish below Cordell Hill Dam in the Cumberland River (Pasch et al. 1978). In the Yellowstone River, the duration of peak flow may be more critical to spawning success than the extent of the river rise (Elser 1977). Low water levels in spring may interfere with paddlefish spawning (Purkett 1961; Needham 1965) or limit the extent of migration to spawning areas (Elser 1977).

A spawning migration of adult paddlefish to upstream spawning areas occurs in the spring. The first observation of a spawning migration was made by Purkett (1961, 1963a) in the Osage River in Missouri. This spawning population migrated 80 km upstream from Lake-of-the-Ozarks to the spawning area in late February or March. Similar upstream migrations have been observed in the Missouri (Elser 1977; Rehwinkel 1978; Van Eeckhout 1980), Mississippi (Coker 1930; Meyer 1960; Southall 1982), Ohio (Everman 1902), and Cumberland (Pasch et al. 1980) River systems. Paddlefish do not move upstream until the river rises several meters and the water temperature is 10° C or greater (Purkett 1963a; Pasch et al. 1980). Upstream migrations appear to be an annual event. There is evidence that immature paddlefish may engage in group movements upstream during the spawning time (Meyer 1960; Purkett 1963a; Pasch et al. 1978).

As a result of the spring migratory patterns, paddlefish tend to congregate below dams on large rivers at that time (Coker 1929; Pasch et al. 1978, 1980; Southall 1982). Coker (1929) determined that very few fish use locks as a passageway upstream where they are present. In some cases, they apparently spawn in riverine areas downstream from large dams (Unkenholz 1979; 1980; Pasch et al. 1980), but suitable temperature, substrate, and hydrologic conditions must be present. On the Mississippi, where access through many of the dams is possible during high water periods, the fish apparently move upstream through the dams to suitable spawning areas (Gengerke 1978; Southall 1982; Southall and Hubert 1984).

Specific Habitat Requirements

In large rivers, paddlefish tend to inhabit slow moving waters with abundant zooplankton (Stockard 1907; Wagner 1908; Alexander 1915; Rosen 1976). Paddlefish in the upper Mississippi River have been observed to use a wide array of habitats, but the main channel border, tailwater, and backwater areas were frequented most (Southall 1982; Southall and Hubert 1984). In spring, tailwater use was great due to upstream movement tendencies, but a notable shift to use of backwater areas occurred following the spawning period. Other observers have seen shifts from riverine to more lentic areas following spawning, with movement into backwater lakes (Stockard 1907) and downstream reservoirs (Purkett 1963a).

Backwaters have been recognized as prime paddlefish habitat (Wagner 1908; Alexander 1915), especially during summer months (Marcoux 1966, Rosen et al. 1982). Backwaters are usually rich in zooplankton and immature aquatic insects (Kofoid 1903; Eckblad et al. 1984), therefore providing abundant food in an area of low current velocity.

In Pool 13 of the upper Mississippi River, all telemetry contacts with paddlefish in backwater areas were made in sloughs adjacent to the upstream riverine portions of the pool, no observations were made in the reservoir-like lower pool (Southall 1982; Southall and Hubert 1984). One large slough was used extensively by paddlefish. When river stage was low in summer, the slough waters became very warm (30° C), shallow, and beds of filamentous algae developed. Under these conditions, paddlefish were observed to congregate in the main channel border downstream from the slough. It is likely that invertebrate drift out of the slough was providing food, while the fish congregated in an area of reduced current velocity (< 35 cm/sec) resulting from wing dams along the main channel border.

Whereas a preference for backwaters has been indicated, their presence is not mandatory for paddlefish survival in riverine habitats. Paddlefish have been found to congregate in small areas of reduced current velocity downstream from sandbars in the Missouri River (Rosen et al. 1982) and man-made structures in the Mississippi River (Southall 1982; Southall and Hubert 1984). Paddlefish in the Missouri River preferred areas where the water was 1.5 to 4.5 m deep, with a current velocity of 0.0 to 0.3 m/sec (Rosen et al. 1982). These areas were near fast-flowing channels with 0.7 to 1.3 m/sec current velocities. Paddlefish in the upper Mississippi River were observed to frequent areas downstream from wing dams, bridge supports and rock piles with a current velocity of less than 0.35 m/sec (Southall 1982). Paddlefish found in these eddies often remained there for long periods.

During the winter, paddlefish apparently inhabit relatively deep, slow- or still-water areas (Kallemeyn and Novotny 1977). Rosen et al. (1982) observed Missouri River paddlefish congregating in areas greater than 3 m deep with little or no current.

Relatively little is known about the habitat requirements of embryonic and larval paddlefish. Despite searches for young paddlefish in the early

1900's (Stockard 1907; Alexander 1915), the smallest paddlefish found prior to 1958 were 17 mm individuals from the Mississippi River (Thompson 1933; Larimore 1949). Purkett (1961) found eggs and larvae in gravel substrate downstream from a spawning site on the Osage River in Missouri. Pasch et al. (1982) collected paddlefish eggs and larvae from a reach of the Cumberland River with gravel and rubble substrate.

Paddlefish eggs are adhesive after fertilization and become firmly attached to the substrate. Optimum embryonic development temperature is 14° C (Purkett 1961; Ballard and Needham 1964). Hatching takes place in 10 to 11 days at 14.0 to 14.5° C (Purkett 1963b). Ballard and Needham (1964) reported that 26 days after hatching (15 mm TL), larvae begin to feed. It appears that between hatching and the commencement of feeding, the young fish must drift or make their way into areas of low current velocity with abundant zooplankton.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. The models are applicable throughout the natural range of paddlefish in North America, i.e., the Mississippi River drainage and adjacent Gulf Coast drainages.

Season. The models provide a rating for a river system and associated reservoirs or lakes based on its ability to support a reproducing population of paddlefish.

Cover types. The models are applicable to riverine and connected lacustrine habitats as described by Cowardin et al. 1979.

Minimum habitat area. Minimum habitat area is defined as the minimum area of contiguous habitat that is required for the species to live and reproduce. No attempt has been made to establish a minimum habitat size for paddlefish, but it is often quite large (> 50 km of river length) based on the highly mobile nature of the animal and the size of the habitat areas where it is presently found.

Verification level. The goal of the paddlefish models is to produce an index between 0 and 1 that has a positive linear relationship between measurable habitat components and the carrying capacity of a river or associated reservoirs and lakes for spawning and adult fish. In order to verify the model, HSI's were calculated from hypothetical data sets based on actual conditions in the Mississippi, Missouri, and Osage River systems. These sample data sets and their relationships to model verification are discussed in greater detail following presentation of the model.

Model Description

The structure of the HSI models for paddlefish is represented in Figure 1. The analysis of paddlefish habitat quality is based on the ability of the habitat to meet spawning and adult habitat needs. The models are limited to these reproduction and adult habitat components due to the lack of information about other life history stages.

Reproduction component. Temperature (V_1) is a critical variable in the reproductive component because failure to reach appropriate temperatures in the spring, or continuous temperatures exceeding those associated with spawning, can prevent or impair spawning activity, as well as survival of eggs and larvae. Access to a large river (V_2) is a critical requirement for spawning. Within the river, suitable spawning substrate (V_3) must be present at a sufficient water depth. A spring rise in water level (V_4) is needed to stimulate spawning activity and, in some cases, enable migration to spawning areas. A sufficient current velocity over the spawning gravels (V_5) is needed prior to spawning to flush accumulated silt from the spawning area. Dissolved oxygen levels (V_6) in the spawning areas must be sufficiently high for embryo survival and development.

Habitat component. Paddlefish occur in large rivers, as well as reservoirs and natural lakes connected to large rivers. The area of habitat (V_7) available is important, and a minimum average stream width (V_8) is needed for adults to utilize a stream reach during summer and winter. Abundant backwaters and other lentic habitats connected to the river channel (V_9) enhance paddlefish productivity, as do areas of low current velocity (V_{10}) within the river channel.

HSI determination. Two habitat suitability index models have been developed for paddlefish, one for spawning habitat and one for adult summer and winter habitat.

Spawning habitat (HSI_s)

$$HSI_s = (V_1 \cdot V_2 \cdot V_3 \cdot V_4 \cdot V_5 \cdot V_6)^{1/6}$$

Adult summer and winter habitat (HSI_a)

$$HSI_a = \{V_7 \cdot V_8 \cdot (V_9^2) \cdot V_{10}\}^{1/5}$$

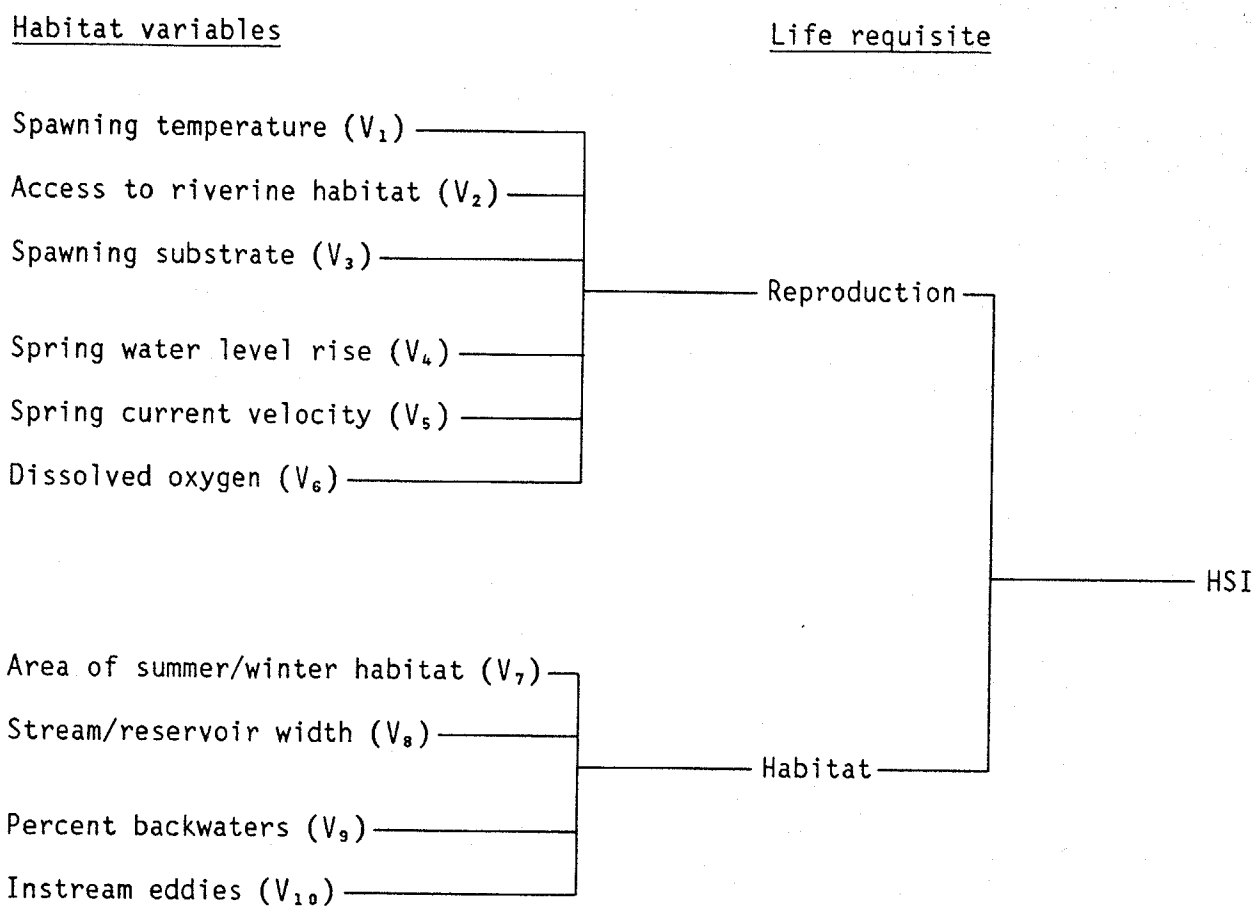


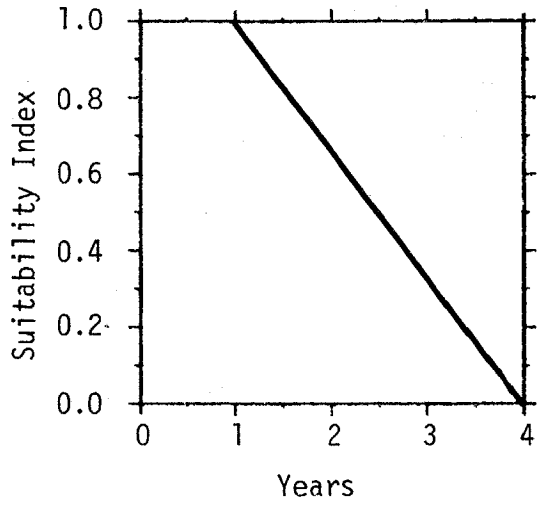
Figure 1. Tree diagram illustrating relationships of habitat variables and important life requisites for the paddlefish.

Suitability Index (SI) Graphs for Model Variables

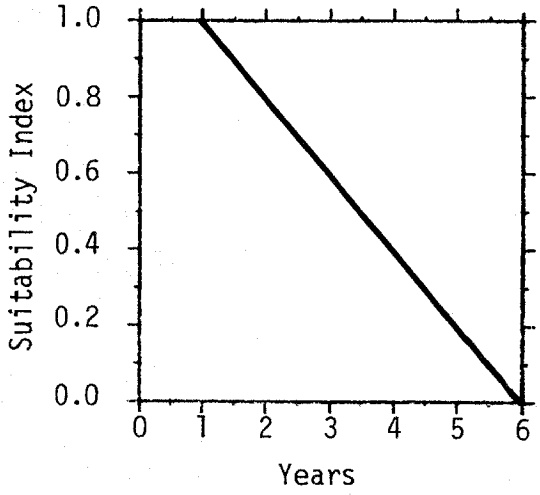
This section contains suitability index graphs for the 10 variables described above. The graphs and associated models can be applied to paddlefish populations that reside primarily in riverine or lentic habitats that are part of a large river system.

Variable

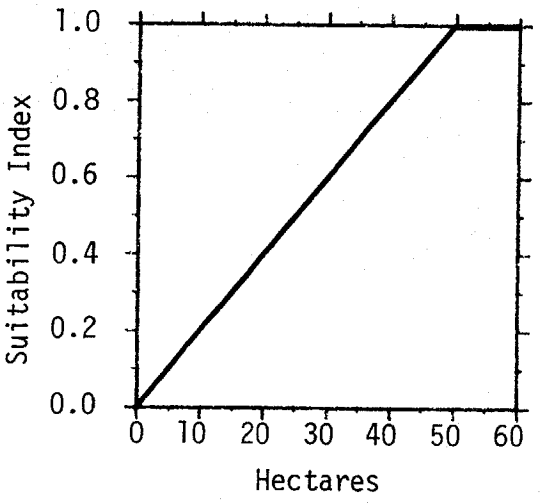
V_1 Yearly frequency of occurrence of at least a 21-day period of rising water temperatures between 10° C and 17° C.



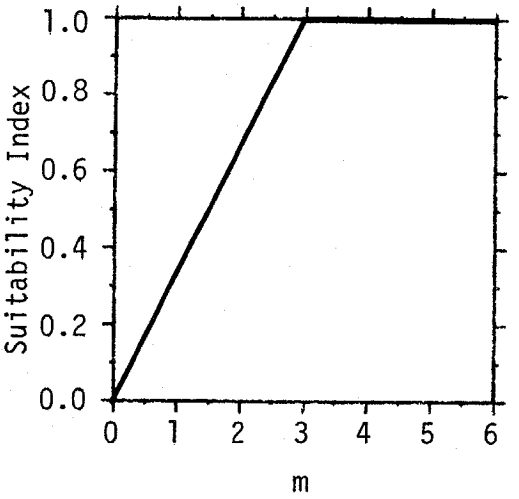
V_2 Yearly frequency of spring access to upstream spawning river (> 40 m average width, > 1 m depth).



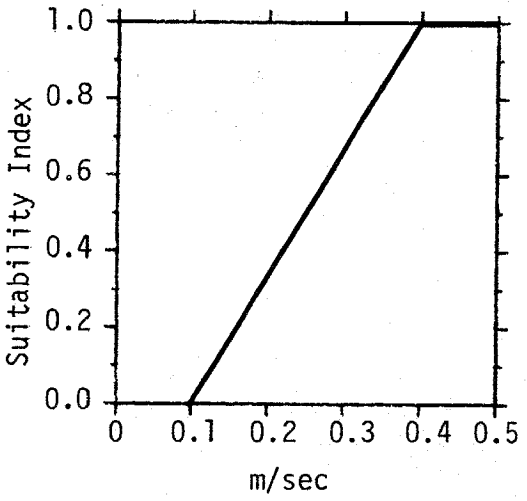
V_3 Accessible area of gravel and cobble substrate (> 80% of substrate 15 to 100 mm diameter particles) in spawning river(s) within 200 km of winter habitat.



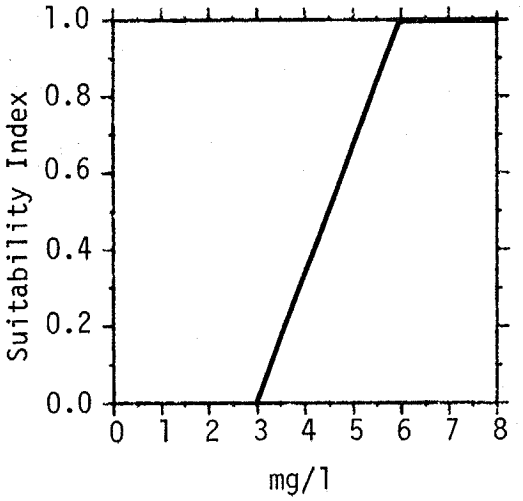
V_4 Average magnitude of spring water rise in the river over average midwinter flow for a period exceeding 10 days while water temperatures are 10 to 17° C.



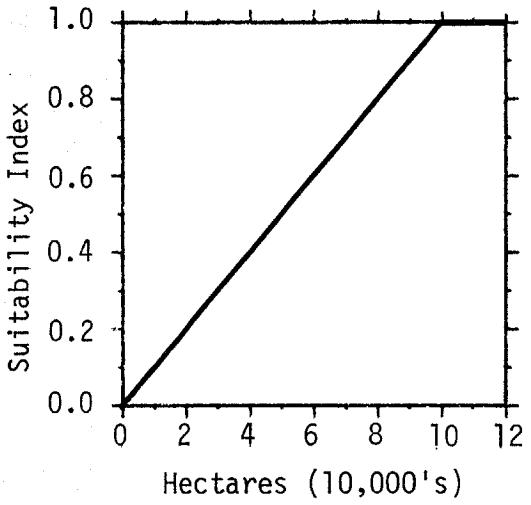
V_5 Average current velocity (0.3 m above substrate over potential spawning substrates) during spring water rise.



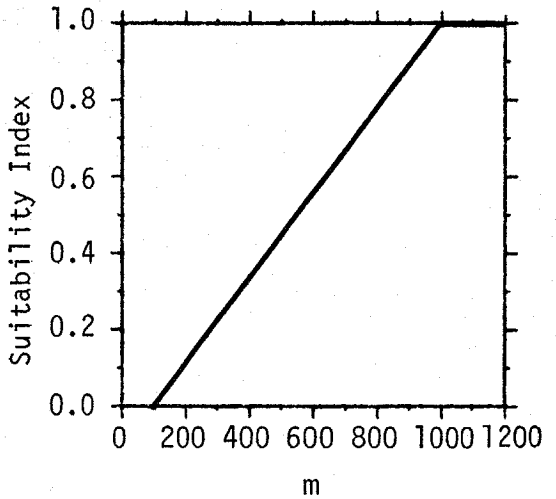
V_6 Minimum dissolved oxygen level in potential spawning areas while water temperatures are 10 to 17° C.



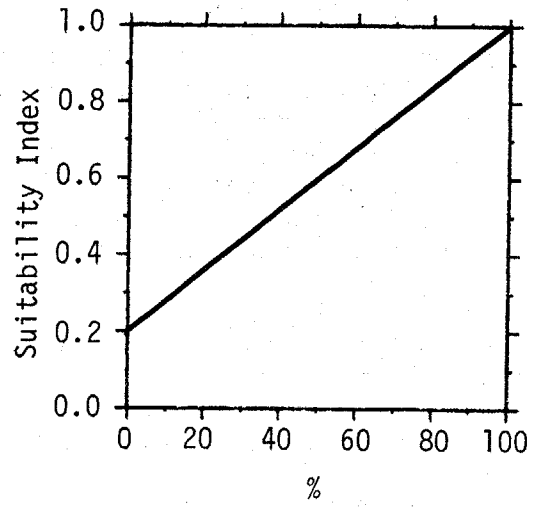
V_7 Area of possible summer and winter habitat.



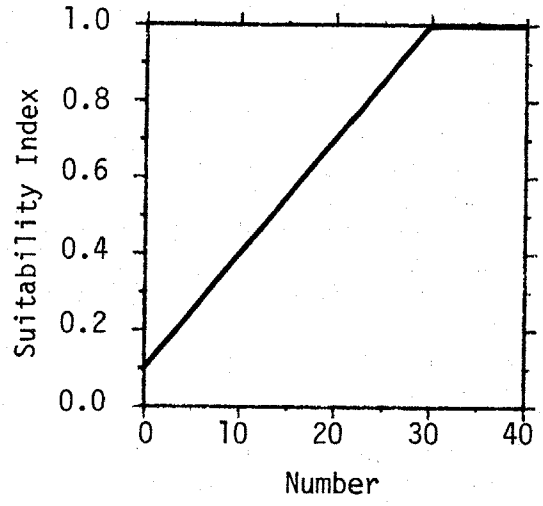
V_8 Average width of river channel, reservoir or lake inhabited during summer and winter (average channel depth > 1.0 m).



V_9 Percentage of water area continuous with summer and winter habitat with a current velocity of < 0.05 m/sec in the river system (backwaters, reservoirs, accessible lakes).



V_{10} Number of eddies within summer and winter channel habitats (0.0 to 0.3 m/sec current, 1.5 m water depth, > 25 m^2 area) per kilometer of river. SI = 1.0 if V_9 > 0.3.



Development of Suitability Index Graphs: Rationale and Assumptions

The preceding suitability index graphs should be regarded as tentative and open to modification. The prospective user should understand that the curves are not the products of extensive laboratory or field investigations. Rather, they reflect the authors' subjective integration of the literature, personal experience, and reviewers' comments. The following discussion documents the thought process used in constructing the curves. Some curves are better documented than others. In many cases, there is information about preferred and limiting or unsuitable conditions, but little information on which to base ratings of intermediate conditions. The model is offered as a starting point, with the hope that refinements will be made as additional information becomes available, including results of model testing.

Spawning temperature (V_1). A rising water temperature in the spring associated with increased discharge is an environmental stimulus for spawning migrations and direct spawning activities. Paddlefish begin to move upstream when water temperature is 10° C or greater (Purkett 1963a; Pasch et al. 1980) and spawn between 10 and 17° C (Kallemeyn 1975; Unkenholz 1981; Pasch et al. 1980). They appear to be most active at 16 to 17° C (Alexander 1915; Purkett 1961). A minimum period of 3 weeks with temperatures between 10 and 17° C appears to be necessary to enable upstream migration, spawning and embryonic development to occur (Purkett 1961, 1963a,b; Ballard and Needham 1964; Pasch et al. 1978, 1980). Based on these observations it is assumed that annual spring periods of rising water temperatures between 10 and 17° C for a period of at least 21 days are required for spawning success. If the frequency of such an occurrence is less than yearly, recruitment should be reduced proportionately to incidence of occurrence.

Access to riverine habitat (V_2). Migration of adult paddlefish to upstream spawning areas of large rivers occurs in the spring. Migrations have been observed in the Osage River in Missouri (Purkett 1961, 1963a), the Missouri River Drainage (Elser 1977; Rehwinkel 1978; Van Eeckhout 1980), the Mississippi River (Coker 1930; Meyer 1960; Southall 1982), the Ohio River (Everman 1902), and the Cumberland River (Pasch et al. 1980). The smallest of these rivers was the Osage River which was approximately 90 m wide at the spawning sites (Purkett 1961; 1963a). Both deep pools (5 to 7 m deep) and submerged bars (1 to 4 m deep) with a gravel and cobble substrate (13 to 38 mm diameter) appear to be important to spawning behavior and larval fish survival (Purkett 1961, 1963a; Pasch et al. 1978, 1980). It seems unlikely that a river with an average width of less than 40 m in the Mississippi River drainage could supply the array of environmental conditions needed for spawning success. As a result it is assumed that the spawning stream must average at least 40 m in width in order to be suitable.

Spawning migrations occur on an annual basis, but reproducing stocks can still occur in rivers where annual access to upstream spawning areas is not possible. Such was the case in the Osage River (Purkett 1961, 1963a), and is currently the situation in some sections of the Mississippi River (Southall 1982) and the Yellowstone River (Elser 1977). It is assumed that the more frequently that access is blocked to spawning areas, the less productive the stock will become, and if access is permanently blocked the stock will eventually be extirpated.

Spawning substrate (V_3). Paddlefish spawn over gravel bars in large rivers. Purkett (1961, 1963a) observed spawning over large gravel substrate in the Osage River. Gravel bars were prominent in the areas used by sexually mature fish during spawning season in the Cumberland River (Pasch et al. 1980), the Missouri River (Berg 1981), and the Mississippi River (Southall 1982). It is assumed that areas of gravel and cobble (15 to 100 mm diameter) in the spawning rivers are required for successful reproduction and that, while the bars can be isolated patches in the river, the greater the abundance of gravel/cobble substrate the better the reproductive success will be.

Spring water level rise (V_4). A rapid increase in river discharge in association with suitable spawning temperatures (V_1) is a stimulus for spawning. Purkett (1961) observed spawning in the Osage River on the seventh day after a water level rise. Similar circumstances have been associated with congregation of adults and probable spawning sites in both the Cumberland River (Pasch et al. 1978) and the Mississippi River (Southall 1982). Both the magnitude and duration of the high flows may be critical to spawning success (Needham 1965; Elser 1977). It is assumed that the greater the spring water rise, the better the access and the stronger the environmental stimulus for spawning. If the duration of gravel bar flushing is sufficient to allow congregation of fish on the spawning sites, spawning and development of larvae to the point where they can drift to downstream nursery areas, then spawning should be successful. It is assumed that a water level rise for at least 10 days with water temperatures optimum for spawning (10 to 17° C) is necessary for success.

Spring current velocity (V_5). Paddlefish spawn over silt-free gravel bars (Purkett 1961, 1963a). A prespawning current velocity of sufficient velocity to flush the gravel of silt is needed for successful spawning. It is assumed that a current velocity of 0.4 m/sec at 0.3 m above the substrate is optimum for flushing silt and a velocity of less than 0.1 m/sec would achieve no silt dispersion.

Dissolved oxygen (V_6). Paddlefish eggs and larvae require a dissolved oxygen level similar to that of other warmwater stream fishes in order to survive. It is assumed that optimum is a constant 6 mg/l or higher, while survival would be zero at less than 3 mg/l for more than a few minutes.

Area of summer/winter habitat (V_7). Backwater areas are prime paddlefish habitat during summer months (Wagner 1908; Alexander 1915; Marcoux 1966; Rosen et al. 1982). Within river channels paddlefish seek areas of reduced current velocity (< 0.3 m/sec) in protected areas downstream from sandbars, wing dams and other structures (Rosen et al. 1982; Southall 1982; Southall and Hubert 1984). During winter paddlefish apparently inhabit slow water areas that are relatively deep (> 3 m) (Kallemeyn and Novotny 1977; Rosen et al. 1982). It is assumed that areas inhabited by paddlefish will possess such characteristics and the greater the total surface area of possible habitat, the greater the carrying capacity for paddlefish.

Stream/reservoir width (V_8). Paddlefish are inhabitants of large rivers. It is assumed that the smallest rivers supporting paddlefish are about 40 m in width with an average depth exceeding 1.0 m (Purkett 1961, 1963a; Pasch et al. 1980; Carlson and Bonislawsky 1981) and the larger the river the greater the percentage of habitat suitable for paddlefish.

Percent backwaters (V_9). Because backwater areas are especially important to paddlefish (Wagner 1908; Alexander 1915; Marcoux 1966; Rosen et al. 1982; Southall 1982; Southall and Hubert 1984) during the growing season as sources of food (Kofoid 1903; Eckblad et al. 1984) and as refuges from current

(Southall 1982; Rosen et al. 1982) they are emphasized in this model. It is assumed that the greater the proportion of backwater area (< 0.05 m/sec current velocity) within the total surface area of water continuous to the summer/winter habitat, the greater the carrying capacity for paddlefish.

Instream eddies (V_{10}). Areas of reduced current velocity (< 0.3 m/sec) in rivers with few backwaters are important to paddlefish. Rosen et al. (1982) and Southall (1982) found that paddlefish in riverine areas select eddies downstream from sandbars, wing dams, and other major structures. It is assumed that the greater the percent area of refuges from high current velocity in river channels, the greater the carrying capacity for paddlefish. A suitable refuge would have a current velocity of 0.0 to 0.3 m/sec, a water depth of > 1.5 m, and a surface area > 25 m^2 (Rosen et al. 1982; Southall 1982; Southall and Hubert 1984).

Field Use of the Model

Variation in river conditions can complicate the application of these models. The models are constructed to incorporate variations between years by obtaining average values for the variables and considering the range of variation from year to year. The user must decide what part of the river system is to qualify as "spawning habitat" and as "summer/winter habitat" based on sport and commercial fishing patterns, and possibly tagging studies. The area may be subdivided based on a particular understanding of a population's behavior, the magnitude of the area, or the nature of a proposed water development project for which the HSI model is to be applied.

Interpreting Model Output

Paddlefish may be present even if the HSI determined is 0. For example, if a zero value is obtained due to a recent blockage of upstream passage to spawning areas, a remnant population of nonreproducing fish may still occur in the system. Likewise, habitat with a high HSI may contain few fish due to pollution, over-exploitation, or a low level of primary productivity in lentic water. If the model is a good representation of paddlefish habitat, the HSI should be positively correlated with long term average sport and commercial harvest levels in areas where population levels are influenced primarily by habitat related factors. Estimates of abundance for paddlefish populations are difficult and time consuming to make as a result of the wide range and congregating behavior of the species.

The sample data sets are not actual field measurements, but represent combinations of variable values that are likely to occur in the river systems based on published information and personal contact with biologists familiar with the rivers (Table 1). These computations suggest that similar densities of paddlefish would occur in Pools 12 and 13 of the Upper Mississippi River and in the Osage River-Lake of the Ozarks habitats. Abundance would be less in the channelized Missouri River and the population in the Osage River-Lake of the Ozarks would be completely eliminated by Truman's Dam blockage of migration to spawning areas. Artificial propagation of paddlefish could maintain populations in Lake of the Ozarks since the components of adult habitat are minimally affected by the upstream dam.

Table 1. Sample data set using paddlefish HSI model.

Variable	Data set 1[a]	Data set 2[b]	Data set 3[c]	Data set 4[d]
V_1	1.00	1.00	1.00	1.00
V_2	0.90	1.00	1.00	0.00
V_3	0.60	0.40	0.20	0.00
V_4	0.80	0.50	0.60	0.60
V_5	1.00	1.00	1.00	0.00
V_6	1.00	1.00	1.00	1.00
V_7	0.16	0.50	0.25	0.22
V_8	0.60	0.20	0.80	0.80
V_9	0.50	0.10	0.80	0.80
V_{10}	1.00	0.10	1.00	1.00
HSI_s	0.87	0.76	0.70	0.00
HSI_a	0.47	0.16	0.66	0.65

[a]Pools 12 and 13, Mississippi River (Southall 1982).

[b]Channelized Missouri River downstream from Sioux City, Iowa (Rosen 1976; Rosen et al. 1982).

[c]Osage River and Lake-of-the-Ozarks, Missouri (Purkett 1961, 1963a).

[d]Osage River following construction of Truman Dam (Purkett 1961, 1963; Carlson 1977; Sparrowe 1977).

We believe the HSI's calculated from the sample data represent carrying capacity of the habitats with the listed characteristics. The true relation between the model-generated index to measurable indices of carrying capacity, such as production or standing crop, is unknown. The model must be viewed as conceptual. Any attempt to use the model, or model components, as predictive tools should be preceded by validation of the model with actual field measurements.

ADDITIONAL HABITAT MODELS

No additional habitat models were found in the literature.

INSTREAM FLOW INCREMENTAL METHODOLOGY

Instream Flow Incremental Methodology (IFIM) is a process of stepwise analyses used to assess instream flow problems (Bovee 1982). The Physical Habitat Simulation System (PHABSIM) model (Milhous et al. 1981), a component of IFIM, is used to compute the amount of available instream habitat for life stages of a species as a function of streamflow.

The output generated by the PHABSIM component of IFIM can be used for several IFIM habitat display and interpretation techniques, including:

1. Habitat Time Series. Determination of impact of a project on a species life stage habitat by imposing project operation curves over baseline flow time series conditions and integrating the difference between the corresponding time series;

2. Effective Habitat Time Series. Calculation of the habitat requirements of each life stage of a single species at a given time by using habitat ratios (relative spatial requirements of various life stages); and

3. Optimization. Determination of flows (daily, weekly, monthly) that minimize habitat reductions for a complex of species and life stages of interest.

Suitability Index Curves Required for IFIM Analysis

PHABSIM utilizes Suitability Index (SI) curves that describe the instream suitability of the habitat variables most clearly related to stream hydraulics and channel structure (e.g., velocity, depth, substrate, cover, and temperature) for each major life stage of a given species (spawning, egg incubation, larval, juvenile, and adult). Four categories of curves and standardized terminology pertaining to the curves are described below. The designations of a curve as belonging to a particular category does not imply that there are differences in the quality or accuracy of curves among the four categories.

Category one SI curves are the most common type presently available for use with IFIM. Category one curves usually have as their basis one or more literature sources. Some may be derived from general statements made in the literature about fishes (e.g., rainbow trout spawn in gravel; fry prefer shallow water). Others may come from literature sources which include variable amounts of field data (e.g., from a sample size of 300, fry were observed in velocities ranging 0.0 to 3.0 ft/s, and 80% were found in velocities less than 1.0 ft/s). Other category one curves may be based entirely on professional opinion, obtained by using the Delphi technique (i.e., the concensus of a panel of experts may be that velocities ranging from 1.0 to 4.0 ft/s are necessary for successful spawning of striped bass). Most category one curves are the result of a combination of sources; an individual curve may include information from the literature, combined with field data, and smoothed or modified using professional judgment. Category one curves usually are intended to reflect general habitat suitability throughout the entire geographic range of the species and throughout the year, unless they are identified as being applicable only to a given area or season. In the latter case, curves developed for a specific area or stream area may not accurately reflect habitat utilization in other areas. Curves meant to describe the general habitat suitability of a variable throughout the entire range of a species may not be as sensitive to small changes of the variable within a specific stream (i.e., rainbow trout will utilize silt, sand, gravel, and cobble for spawning substrate, but utilize only cobble in Willow Creek, Colorado).

Category two SI curves are derived from frequency analyses of field data, and basically are curves fit to a frequency histogram. Each curve describes the observed utilization of a habitat variable by a life stage of the evaluation species. Category two curves, unaltered by professional judgment or other sources of information, are referred to as utilization curves. When modified by judgment they are considered category one curves. Utilization curves from one set of data are not applicable for all streams and situations (i.e., a depth utilization curve from a shallow stream cannot be used for the Mississippi River). Category two curves, therefore, are usually biased because of limited habitat availability. An ideal study stream design would have all substrate and cover types present in equal amounts; all depth, velocity, and percent cover intervals available in equal proportions; and all combinations of all variables in equal proportions. Utilization curves from such a perfectly designed study theoretically should be transferable to any stream within the geographical range of the species. Curves from streams with high habitat diversity are generally more transferrable than curves from streams with low habitat diversity. Users of category two curves should first review the stream description to see if conditions are similar to those present in the stream segment to be investigated. Some variables to consider include stream width, depth, discharge, gradient, elevation, latitude, and longitude, temperature, water quality, substrate and cover diversity, fish species associations, and data collection descriptors (e.g., time of day, season of year, sample size, and sampling methods). If one or more of these factors deviate significantly from those of the proposed study site, curve transference is not advised, and the investigator should develop his or her own curves.

Category three SI curves are derived from utilization curves that have been corrected for environmental bias and, therefore, represent the preference of the species. Habitat utilization data and habitat availability data must simultaneously be collected from the same area in order to generate a preference curve. Habitat availability information should reflect the relative amount of different habitat types in the same proportions as they exist throughout the stream study area. A curve is then developed for the habitat frequency distribution in the same way as for fish utilization observations. The equation coefficients of the availability curve are subtracted from the equation coefficients of the utilization curve, resulting in preference curve coefficients. Theoretically, category three curves should be unconditionally transferrable to any stream. But at present, very few category three curves exist because most habitat utilization data sets are without concomitant habitat availability data sets. In the future, investigators will be encouraged to collect habitat availability data.

Category four SI curves (conditions preference curves) describe habitat preferences as a function of interaction among variables. For example, fish depth utilization may depend on the presence of cover, or velocity utilization may depend on time of day or season of year. Category four curves are just beginning to be developed and are still largely conceptual.

IFIM analyses may utilize any or all categories of curves, but category three and four curves yield the most precise results. Category two curves yield accurate results if they are transferrable to the stream segment under investigation. If no category three or four curves are available and category two curves are transferable for a particular application, category one curves may be the better choice. A basic underlying assumption of the IFIM is that the evaluation species exhibits a desirable preference/avoidance behavior for one or more of the microhabitat variables of depth, velocity, substrate, and cover.

Paddlefish SI Curves Available for Use with IFIM

There are insufficient data available on the relationship of velocity, depth, substrate, cover, and temperature to habitat suitability for paddlefish spawning, egg incubation, larvae, juveniles, and adults to develop all of the SI curves likely needed for a complete IFIM analysis of habitat for all life stages of paddlefish (Table 2). SI curves presented in Figures 2 through 4 are based on very limited information. If a SI curve for a variable/life stage of interest is not available, it must be developed if an analysis of the effects of the variable on habitat suitability is the objective.

All paddlefish SI curves available to date are category one curves. They are based on a combination of published and nonpublished reports, expert opinion, and judgment of the author. The curves should be considered for interim use until improved or new field studies directed toward SI curve development are undertaken. Before investigators undertake an IFIM analysis of paddlefish riverine habitat they should use the best professional judgment available to determine: which SI curves are needed; which of the available curves are appropriate for the IFIM study planned; if existing curves should

Table 2. Availability of SI curves for use with the IFIM analyses of paddlefish riverine habitat.

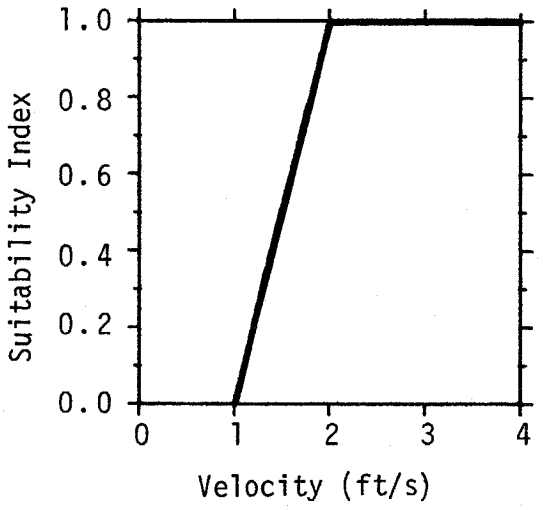
Activity/ life stage	Velocity	Depth	Substrate[a]	Cover	Temperature
Spawning	Use SI curve, Fig. 2.	Use SI curve, Fig. 2.	Use SI curve, Fig. 2.	Curve not necessary.	Use SI curve, Fig. 2.
Egg incubation	Use SI curve, Fig. 3.	Use SI curve, Fig. 3.	Use SI curve, Fig. 3.	Curve not necessary.	Curve not available.
Fry	Curve not available.	Curve not available.	Curve not available.	Curve not available.	Curve not available.
Juvenile	Curve not available.	Curve not available.	Curve not available.	Curve not available.	Curve not available.
Adult	Use SI curve, Fig. 4.	Use SI curve, Fig. 4.	Curve not available.	Curve not available.	Use SI curve, Fig. 4.

[a]The following codes for substrate were used for SI curves in Figures 2 and 3.

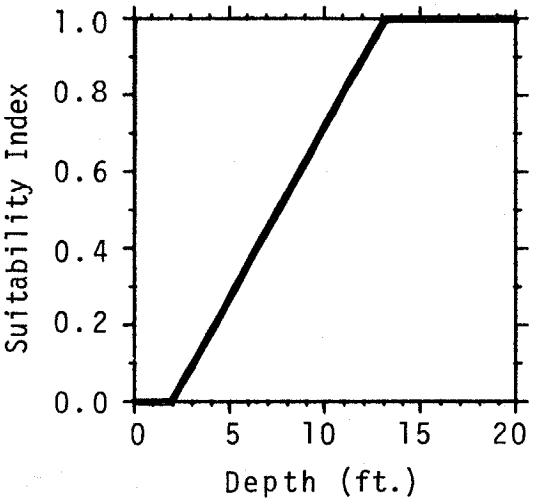
1 = plant detritus/organic material
2 = mud/soft clay
3 = silt (particle size <0.062 mm)
4 = sand (particle size 0.062 to 2.0 mm)
5 = gravel (particle size 2.0 to 64.0 mm)
6 = cobble/rubble (particle size 64.0 to 250.0 mm)
7 = boulder (particle size 250.0 to 4000.0 mm)
8 = bedrock (solid rock)

Coordinates

x (ft/s)	y (SI)
0.0	0.0
1.0	0.0
2.0	1.0
12.0	1.0
15.0	0.0
16.0	0.0



x (feet)	y (SI)
0.0	0.0
1.9	0.0
13.1	1.0
20.0	1.0
100.0	1.0



x (substrate)	y (SI)
1	0
2	0
3	0
4	0
5	1
6	0.5
7	0.2
8	0.0

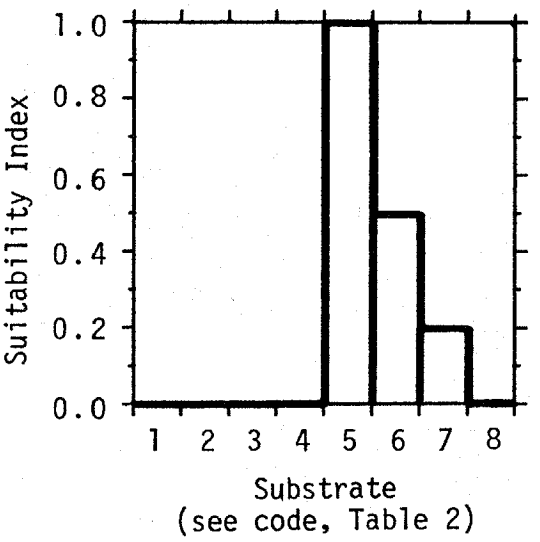


Figure 2. SI curves for IFIM analyses of paddlefish riverine spawning habitat.

It is assumed that cover is unimportant to or not used by paddlefish for spawning and, therefore, a cover SI curve for spawning is not necessary.

Coordinates	
x (F°)	y (SI)
0.0	0.0
50.0	0.0
55.4	1.0
62.6	1.0
68.0	0.0
100.0	0.0

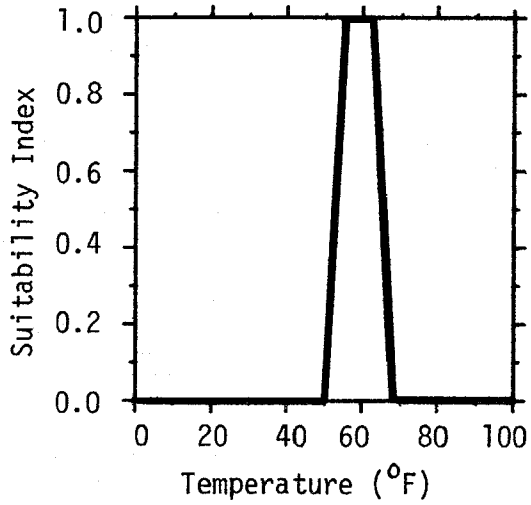
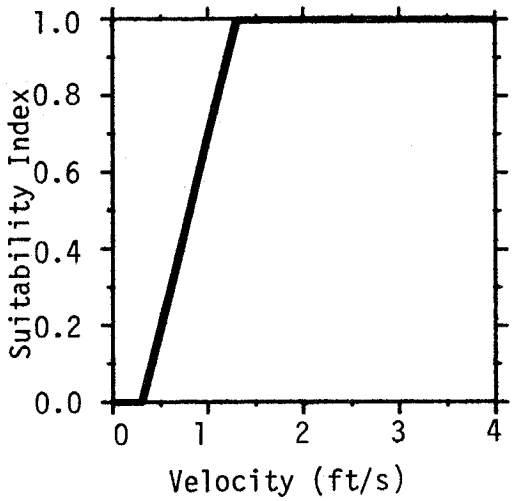


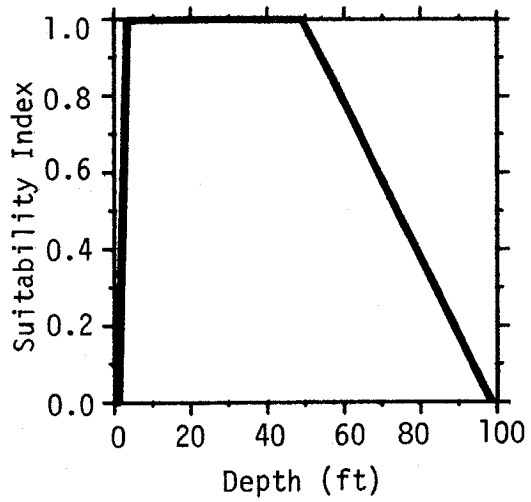
Figure 2. (concluded).

Coordinates

x (ft/s)	y (SI)
0.0	0.0
0.3	0.0
1.3	1.0
12.0	1.0
15.0	0.0
16.0	0.0



x (feet)	y (SI)
0.0	0.0
0.9	0.0
3.3	1.0
49.2	1.0
98.4	0.0
100.0	0.0



x (substrate)	y (SI)
1	0
2	0
3	0
4	0
5	1
6	0.5
7	0.2
8	0.0

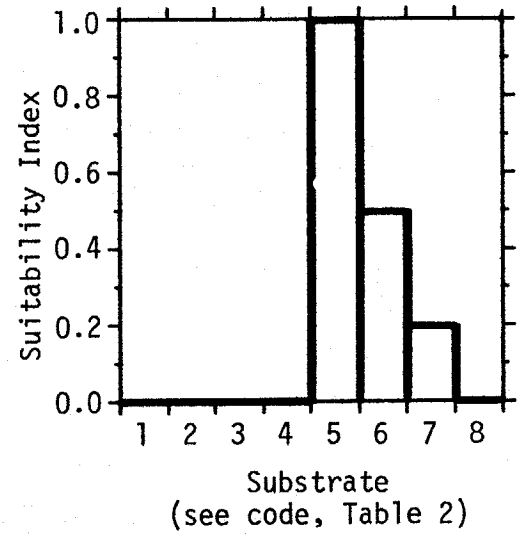
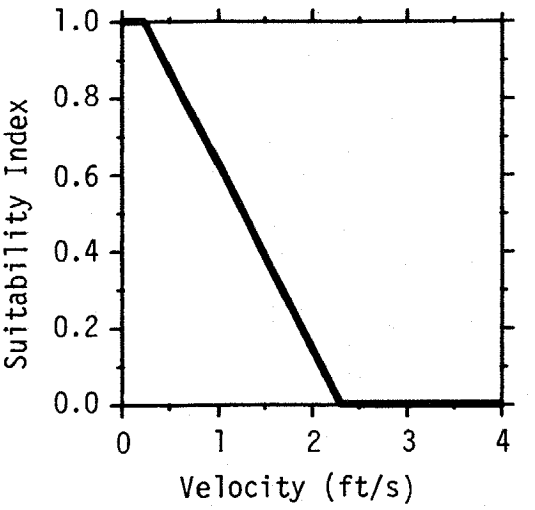


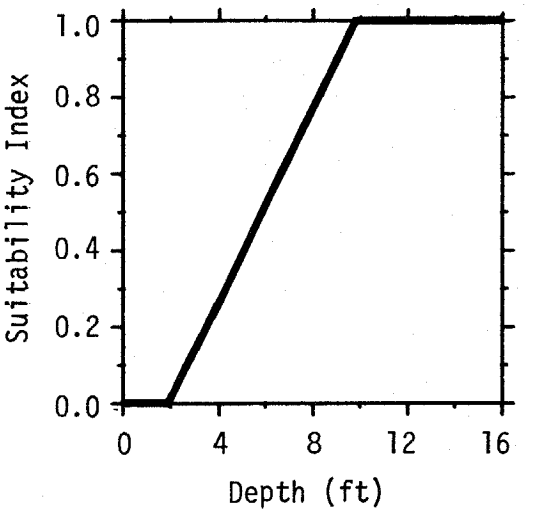
Figure 3. SI curves for IFIM analyses of paddlefish riverine habitat - egg incubation.

Coordinates

x (feet)	y (SI)
0.0	1.0
0.23	1.0
2.3	0.0
4.0	0.0



x (feet)	y (SI)
0.0	0.0
1.0	0.0
9.8	1.0
100.0	1.0



Coordinates

x (F°)	y (SI)
0.0	0.0
33.0	0.0
44.6	1.0
68.0	1.0
86.0	0.0
100.0	0.0

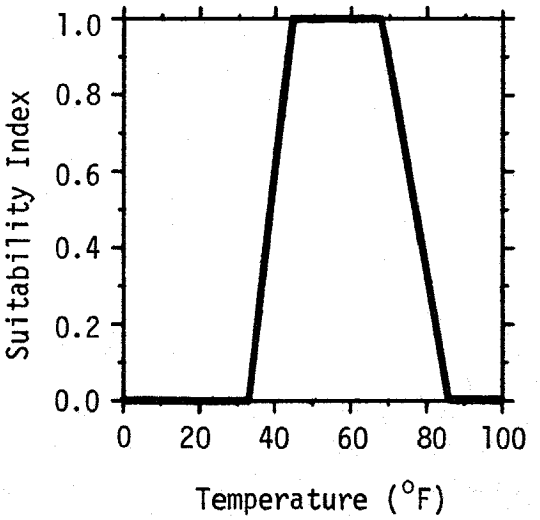


Figure 4. SI curves for IFIM analyses of paddlefish riverine habitat - adult.

be altered based on new information; and/or if data must be collected in the field to develop the SI curves needed. For example, if an investigator is aware that paddlefish use spawning habitat in the study stream differently from what is represented by the SI curves presented herein, he may want to modify the curves or collect data to generate new curves. Once curves to be used are agreed upon and are available, curve coordinates are used to build a computer file (FISHFIL) which becomes a necessary component of PHABSIM analyses (Milhous et al. 1981). Coordinates for the SI curves developed and presented in Figures 2 through 4 are given in U.S. units rather than in metric units, to facilitate entering data into the computer programs for IFIM analyses.

Spawning

SI curves for paddlefish spawning (Figure 2) are for IFIM analyses of spawning habitat during the spawning season which is sometime during March to June, depending on the locale. Spawning sites are usually located several miles upstream from nonspawning habitat and are generally characterized as having fast flowing water, varying water depths, clean-swept gravel substrate, and temperatures above 10° C (50° F). Eggs are released in the water column, and after fertilization occurs the eggs settle into the substrate until hatching. Depending on current velocity, depth, and other factors, egg incubation habitat may be located a considerable distance downstream from the spawning site. Therefore, the two habitats should be considered separately.

Velocity. Water velocities crucial for paddlefish spawning are unknown. Sufficient current velocity over gravel beds where eggs incubate is needed prior to spawning to flush accumulated silt from the gravel. Based on unpublished information obtained from biologists employed by the Tennessee Valley Authority, it is assumed that velocities slightly higher than those for flushing silt from the egg incubation substrate are suitable for spawning. Therefore, the SI velocity curve (V_s) used as a component of the HSI model was modified for IFIM analyses of spawning habitat.

Depth. Pasch et al. (1978) reported water depths at spawning sites ranging from 2 to 12 m (6.6 to 39.4 ft) but were generally 4 m (13.1 ft). Purkett (1961) reported that spawning occurred where water depth ranged from 4.6 to 6.1 m (15 to 20 ft). It is assumed that a depth less than 0.6 m (2 ft) is unsuitable for unimpeded movement by adults and for spawning and that depths of 4 m (13.1 ft) and above are optimum. If maximum depths suitable for spawning exists, they are unknown. It is assumed that all depths above 4 m (13.1 ft) are equally suitable.

Substrate. Spawning is reported to occur over clean gravel or gravel/cobble substrate (Purkett 1961, 1963a; Pasch et al. 1980; Carlson and Bonislawsky 1981; Southall 1982). Substrate is a requirement for egg incubation. It is assumed that spawning occurs near the site of egg incubation and that substrate suitability for spawning and egg incubation are equal (see discussion on substrate under egg incubation).

Cover. No information was available to indicate the use of cover by paddlefish for spawning. It is assumed that a cover SI curve for spawning is not necessary.

Temperature. Spawning may occur when water temperature is as low as 10° C (50° F) (Unkenholz 1981; Wallus, unpublished) but spawning may not be successful when temperature is below about 12° C (53.6° F) (Pasch et al. 1978, 1980; Alexander and McDonough, unpublished). The highest temperature reported for spwaning is about 16 to 17° C (60.8 to 62.6° F) (Alexander 1915; Purkett 1961, Unkenholz 1981). Kallemeyn (1975) reported spawning at 13.9 to 15.6° C (57.1 to 60.1° F). The majority of paddlefish eggs were collected by Pasch et al. (1980) at 13° C (55.4° F). It is assumed that the optimum temperature range for spawning is about 13 to 17° C (55.4 to 62.6° F). Maximum water temperatures unsuitable for spawning are unknown; it is assumed to be 20° C (68° F).

Egg Incubation

Paddlefish eggs hatch in 10 to 11 days at 14.5° C (58.1° F) (Purkett 1963a). The egg incubation SI curves (Figure 3) are for IFIM analyses of egg incubation habitat from the beginning of spawning to about 14 days beyond the end of spawning.

Velocity. The velocity SI curve for egg incubation is based on the SI velocity curve (V_5) used as a component of the HSI model.

Depth. Depth suitability for egg incubation is unclear. Paddlefish eggs apparently desiccate and die if the water level drops rapidly below the gravel substrate to which they are attached (Purkett 1961). Presumably, reduced dissolved oxygen concentration could become a problem at extreme depths. Assumptions used to develop the SI curve for depth are: (1) water depth 0.3 m (1 ft) or less is unsuitable; (2) depths 1 to 15 m (3.3 to 49.2 ft) are optimum; and (3) suitability decreases at depths over 15 m and becomes unsuitable at 30 m (98.4 ft).

Substrate. Purkett (1961) reported that clean swept gravel bars provided the most favorable substrate for paddlefish egg incubation. He did not find paddlefish eggs on substrate composed of large rubble or on boulders. Paddlefish eggs will likely adhere to clean surface of substrate particles larger than gravel. However, it is assumed that bedrock and particles smaller than gravel are unsuitable substrate.

Cover. No information was available to indicate the importance of cover to egg incubation. It is assumed that a cover SI curve is not necessary. If it is assumed that substrate provides some degree of cover for egg incubation, refer to the substrate SI graph for egg incubation.

Temperature. Optimum embryonic development is reported to occur at about 14° C (15.2° F) (Purkett 1961; Ballard and Needham 1964) but the suitability of higher and lower temperatures for egg incubation is unclear. Therefore, a SI curve for the variable was not developed.

Larvae

No SI curves for larval paddlefish were developed because the relationships of the variables (velocity, depth, substrate, cover and temperature) to habitat suitability are unclear. Current velocity is probably important for helping to move larvae out of spawning areas before the water level recedes and leaves the fish stranded to die. Current also helps move the larvae to slow moving or still water where food would likely be more abundant.

Depth suitability for larvae may be similar to that for eggs but additional information is needed to support depth suitability.

Substrate probably provides larvae cover for resting and for protection from predators during the first few hours following hatching.

Pasch et al. (1980) did not collect larvae below 12.2° C (54° F) or above 18.6° C (65.5° F) while Wallus (unpublished) reported that larvae were collected over a range of 11 to 21° C (51.8 to 69.8° F).

Juveniles

No SI curves for juvenile paddlefish are available. Little is known about habitat suitability for this life stage. Juveniles reach maturity at about 4 to 6 years of age. Some juveniles may participate in spawning migrations before they are capable of reproducing (Purkett 1963a).

Adults

SI curves for adult paddlefish (Figure 6) are for IFIM analyses of non-spawning habitat. Adults may occupy definite summer and winter habitats in some stream systems (Rosen 1976; Rosen et al. 1982; Southall and Hubert 1984). The potential for such seasonal habitat preferences should be considered for each adult paddlefish population of interest. If seasonal habitat selection occurs, then a set of SI curves for each season is needed for IFIM analyses.

Velocity. It appears advantageous for adult paddlefish to occupy slow moving or still water (Stockard 1907; Friberg 1974; Unkenholz 1979; Resen et al. 1982). Rosen et al. (1982) reported that most paddlefish were found where current velocity was 0 to 30 cm/s (0 to 1 ft/s) and that the fish likely avoided nearby areas where current velocities were 70 to 130 cm/s (2.2 to 4.3 ft/s). Southall and Hubert (1984) reported mean current velocity at telemetry location sites of paddlefish ranged from 6.4 to 63.6 cm/s (0.21 to 2.1 ft/s). Assumptions used to develop the velocity SI curves for adults are: (1) 0 to 7 cm/s (0 to 0.23 ft/s) is optimum; (2) suitability decreases as current velocity increases above 7 cm/s (0.23 ft/s); and (3) water velocity above 70 cm/s (2.3 ft/s) is unsuitable.

Depth. Rosen et al. (1982) reported that paddlefish were most often found during summer in areas with water depths of 2 to 3 m (6.6 to 9.8 ft) and that during winter the fish were located in areas with depths of at least 3 m (9.8 ft). Southall and Hubert (1984) reported mean water depth at telemetry location sites to vary from 2.2 to 14.8 m (7.2 to 48.6 ft). The depth SI

curve for adults is based on the assumptions that a depth of 0.61 m (2 ft) is minimum for unimpeded movement by adults, and that depths of 3 m (9.8 ft) and above are optimum.

Substrate. Sufficient information on substrate preferences or utilization by adult paddlefish was unavailable to develop a SI curve for the variable.

Cover. No SI curve was developed for cover preference by adult paddlefish. Rosen et al. (1982), Southall (1982) and Southall and Hubert (1984) present evidence that paddlefish often locate near sand bars or man-made structures that create eddies and reduce current velocities. Further information is needed to identify the quality and quantity of cover types preferred by paddlefish.

Temperature. Rosen and Hales (1981) reported that the temperature of habitat occupied by adult paddlefish ranged from near 0° C (32° F) when ice formed on the river to about 28° C (82.4° F) during late summer, and that feeding was optimum between 7 to 20° C (44.6 to 68.0° F). Paddlefish appeared to move out of backwater with temperatures as high as 30° C (86° F) (Southall 1982). The temperature SI curve for adults is based on the above information and the assumption that temperatures of 0.5° C (33° F) and below are unsuitable.

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