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Habitat Suitability Index Models for Eight Fish and Invertebrate Species in Casco and Sheepscot Bays, Maine

STEPHEN K. BROWN,*[1] KENNETH R. BUJA, STEVEN H. JURY,[2] AND MARK E. MONACO

Biogeographic Characterization Branch, Strategic Environmental Assessments Division,
National Oceanic and Atmospheric Administration,
1305 East-West Highway, Silver Spring, Maryland 20910, USA

ARNOLD BANNER

Gulf of Maine Coastal and Estuary Program, U.S. Fish and Wildlife Service,
4R Fundy Road, Falmouth, Maine 04105, USA

Abstract.—Habitat suitability index (HSI) models were used to map habitat quality for eight fish and invertebrate species in Casco Bay and Sheepscot Bay, Maine. Habitat suitability index modeling can be used to support a wide range of management needs involving species or habitat mapping, including analysis of essential fish habitat. The HSI values were calculated as a function of a species' habitat associations and mapped available habitat. Based on published information and expert review, models for two to four life stages were developed for alewives *Alosa psuedoharengus*, American sand lances *Ammodytes americanus*, Atlantic salmon *Salmo salar*, Atlantic tomcods *Microgadus tomcod*, common mummichogs *Fundulus heteroclitus*, winter flounder *Pleuronectes americanus*, American lobsters *Homarus americanus*, and softshell clams *Mya arenaria*. Using geographic information systems (GIS), habitat maps for each bay were developed consisting of 100 × 100-m grid cells for seasonal temperature and salinity and for depth and predominant substrate type. The HSI models were run in the GIS by reclassifying the habitat maps to a 0–1 suitability index scale, 1.0 representing the most suitable condition for each habitat variable. Following reclassification, the geometric mean of the suitability index values for the habitat variables was calculated by grid cell, and the results were mapped. Model performance was evaluated by expert reviewers and by using Kruskal–Wallis and Wilcoxon nonparametric statistical tests, which compared model outputs with available species catch data. Total suitable habitat on HSI maps ranged from 6% for American sand lance adults and juveniles to 95% for American lobster adults. Habitat importance was analyzed by mapping the arithmetic mean HSI value calculated from all models by season. Based on the mean of the HSI values from these models, which do not contain pollutant effects, shallow, nearshore areas and river mouths near Portland, Maine, provide the most important habitat in Casco Bay. These results suggest that remediation of degraded areas near Portland could restore valuable habitat.

Effective management and conservation of living resources requires knowledge of ecosystem structure and dynamics (Langton et al. 1995; Mangel et al. 1996), yet managers frequently must make decisions without the funding or time to conduct field studies or complex analyses. Moreover, even when field studies are conducted, they often do not provide comprehensive spatial or temporal coverage or fail to completely cover the range of available habitat. These problems can result in management decisions based on grossly inadequate information. The need for better fish habitat maps will probably increase as the Essential Fish Habitat (EFH) consultation process required by the Magnuson–Stevens Fishery Management and Conservation Act is implemented (NOAA 1997).

Habitat suitability index (HSI) modeling is a tool for developing maps and information upon which living-resource and environmental managers and conservationists can base decisions (USFWS 1980a, 1980b, 1981; Terrell 1984; Bovee and Zuboy 1988). Management applications include (1) developing maps in poorly sampled areas (Brown et al. 1997; Rubec et al. 1998); (2) evaluating impact scenarios of regulatory alternatives (Christensen et al. 1998), such as for EFH consultations; (3) identifying and prioritizing areas for

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* Corresponding author: stephen.k.brown@noaa.gov

[1] Present address: Research Analysis and Coordination Division, Office of Science and Technology, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 1315 East-West Highway, Silver Spring, Maryland 20910, USA.

[2] Present address: Caribbean Marine Research Center, National Undersea Research Program, 250 Teguesta Drive, Suite 304, Teguesta, Florida 33469, USA.

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conservation actions (Banner and Libby 1995; Banner and Hayes 1996), including protection or acquisition; and (4) predicting or assessing impacts of environmental change. In this paper, HSI models are simple mathematical expressions for calculating a unitless index of habitat quality as a function of one or more environmental variables that define habitat for a particular species or life history stage. The models are based on suitability indices that reflect habitat quality for a particular species or life stage over a range of possible environmental conditions, such as temperature or salinity. The indices for each habitat-defining variable are then combined yielding a composite HSI value. Using GIS, these values can then be mapped or analyzed as needed. High quality habitat may provide high carrying capacity and support high rates of growth, survival, or reproduction, whereas unsuitable habitat may have little or no carrying capacity.

The HSI modeling method used in this project was derived from the U.S. Fish and Wildlife Service (USFWS), Habitat Evaluation Procedures program (USFWS 1980a, 1980b, 1981; Terrell 1984; Bovee and Zuboy 1988), which has primarily focused on developing specific, detailed models for assessing relatively small areas in terrestrial or freshwater environments. These models have been used only occasionally in estuaries (Cordes et al. 1985; Krohn and Owen 1988; Soniat and Brody 1988; Gibson 1994; Reyes et al. 1994; Banner and Libby 1995; Banner and Hayes 1996; Brown et al. 1997; Christensen et al. 1997, 1998).

Development and testing of HSI models are described for the estuarine life history stages of eight fish and invertebrate species in Casco and Sheepscot bays, Maine. Casco Bay was chosen as a study site due to USFWS's commitment to map critical habitat for the U.S. Environmental Protection Agency, Casco Bay Estuary Program. Sheepscot Bay was added because it is near Casco Bay and has more available field data. The purpose of the modeling was to (1) generate habitat distribution maps for selected species, thereby supporting development of a critical habitat component for the Comprehensive Conservation and Management Plan by the Casco Bay Estuary Program, and (2) identify important habitat in the bays for prioritizing areas for possible protection or other management actions. Therefore, the HSI-modeling approach was adapted to address estuarine and marine issues at the local to regional scale (Brown et al. 1997). The models were designed to be developed, applied, and modified relatively quickly with minimal costs in terms of personnel and resources. No field studies were conducted. The models are simple, relying on a few key variables (for which data are usually available) to define habitat and simple arithmetic relationships between the environment and habitat suitability. As may often occur in situations requiring habitat management decisions, relatively little site-specific sampling data were available in the study area, which precluded development of highly detailed models. Therefore, information on species' habitat requirements was primarily derived from the scientific literature and supplemented by expert review. The limited sampling data that were available were used to evaluate performance of the models.

TABLE 1.—Depth and substrate characteristics of Casco Bay and Sheepscot Bay, based on maps developed in this project. The surface areas calculated for Casco Bay and Sheepscot Bay are 564 and 98 km^2, respectively.

	Percent area	
Variable	Casco Bay	Sheepscot Bay
Depth (m)		
Intertidal	6.7	13.1
0–3	23.6	33.9
3–10	10.2	5.5
10–20	24.8	1.2
20–50	32.4	43.0
50–100	2.3	3.3
Predominant substrate		
Vegetation	3.8	3.6
Rock	33.8	27.7
Gravel	4.9	3.5
Sand	6.1	5.2
Mud	51.5	60.2
Shell	0.0	0.0

Study Area

Based on the environmental maps developed in this project (see below), habitat characteristics of Casco and Sheepscot Bays are similar (Tables 1, 2). Both systems have maximum depths of approximately 75 m; contain a heterogeneous assortment of rocky and soft substrates (Barnhardt et al. 1998); have well-developed submerged and emergent vegetation in shallow, sheltered areas; experience semidiurnal tides ranging up to 4 m; and have seasonal mean water temperatures ranging from near freezing in winter to over 20°C in summer. Greatest freshwater inflow occurs during the spring or following storms. The bays' faunas are predominantly boreal, containing both resident and migratory species (Jury et al. 1994). Minor habitat differences are due primarily to differences in basin configuration, riverine influences, and urban development.

TABLE 2.—Mean bottom temperature and salinity characteristics of Casco Bay and Sheepscot Bay, based on maps developed in this project. The surface areas calculated for Casco Bay and Sheepscot Bay are 564 and 98 km², respectively.

	Percent area							
	Casco Bay				Sheepscot Bay			
Variable	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Temperature (°C)								
<0	0.0	0.0	0.0	14.1	0.0	0.0	0.0	2.0
0–2	0.0	0.0	0.0	60.8	0.0	0.0	0.0	34.4
2–4	34.1	0.0	0.1	25.1	22.3	0.0	0.0	63.6
4–6	13.5	0.0	2.9	0.0	17.8	0.0	2.1	0.0
6–8	12.5	21.4	26.2	0.0	25.9	12.6	45.2	0.0
8–10	11.3	14.0	49.8	0.0	20.1	14.6	39.1	0.0
10–12	14.5	10.0	20.3	0.0	10.2	20.7	13.6	0.0
12–14	11.3	12.1	0.7	0.0	3.4	13.2	0.0	0.0
14–16	2.5	11.3	0.1	0.0	0.3	9.1	0.0	0.0
16–18	0.4	20.0	0.0	0.0	0.1	18.8	0.0	0.0
18–20	0.0	10.3	0.0	0.0	0.0	8.4	0.0	0.0
20–22	0.0	0.8	0.0	0.0	0.0	2.5	0.0	0.0
22–24	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0
Salinity (‰)								
0–0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.5–5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
5–10	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.7
10–15	0.1	0.0	0.0	0.0	2.2	0.1	0.0	1.3
15–20	0.7	0.0	0.1	0.0	10.3	2.3	2.3	6.9
20–25	1.4	0.1	0.3	0.3	13.7	10.8	11.3	12.5
25–30	27.0	3.5	1.6	5.9	28.4	24.5	21.6	20.7
>30	70.8	96.4	98.0	93.8	44.4	62.3	64.8	57.7

The Casco Bay system is primarily a large marine embayment, with a total surface area of 564 km² (Table 1). Freshwater inflow averaging about 60 m³/s (M. D. Harris, National Oceanic and Atmospheric Administration [NOAA], personal communication) comes from several small rivers, but the Kennebec River plume also influences salinity and temperature in the northeastern and offshore portions of the bay. Subtidal substrates are primarily mud and rock with some sand; intertidal substrates are chiefly rock, cobble, and mud flat. Eelgrass *Zostera marina* beds occur on unconsolidated sediments, and kelp *Laminaria* spp. beds occur on rocky substrates. Blue mussel *Mytilus edulis* reefs, which may be important nursery habitats for some species, also occur in Casco Bay (Fefer and Schettig 1980). Portland, Maine, one of the largest population centers in the region, is located along the southwestern part of the Bay. Polluted sediments (Doggett and Smith 1992) and many treated and untreated municipal wastewater discharges (Ruffing 1991) exist in the Portland area.

The Sheepscot Bay system is a smaller (98 km²), drowned river valley, located in a predominantly rural watershed. This system has a relatively greater freshwater inflow than does Casco Bay, averaging approximately 18 m³/s (M. D. Harris, NOAA, Strategic Environmental Assessments Division, personal communication). The major freshwater sources are the Sheepscot and Sasanoa rivers. There are several dams on the Sheepscot River, but anadromous fish restoration has resulted in the return of small, but apparently sustainable, runs of Atlantic salmon *Salmo salar* and alewives *Alosa psuedoharengus*, (Meister 1982; L. Flagg, Maine Department of Marine Resources, personal communication). The shores are relatively steep and rocky with extensive mud flats and salt marshes in the intertidal zone of the upper estuary and along small tributaries (Stickney 1959; Ruffing 1991). The bottom sediments are primarily muddy silt with some clay, sand, or organic fraction. Large pockets of sand or bedrock are interspersed throughout the mud bottom, and pockets of sawdust are present near former sawmill operations. Subtidal aquatic vegetation is primarily eelgrass on muddy sediments (Fefer and Schettig 1980; Ruffing 1991). The upper estuary has stronger currents, greater variation in salinity and temperature, and stronger tidal exchange than the lower estuary. The hydrography, flora, and fauna of this system were extensively described during environmental impact studies for the Maine Yankee Nuclear Pow-

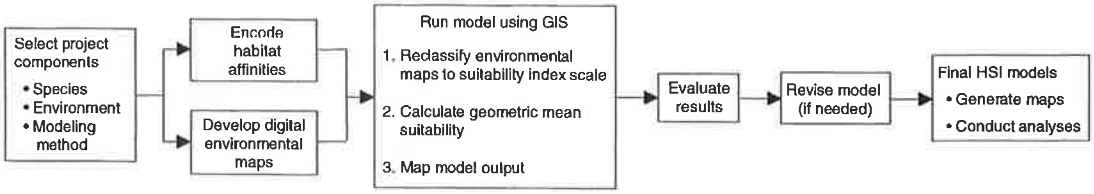

FIGURE 1.—Processes followed for developing and running habitat suitability index models.

er Plant, located on Montsweag Bay, and in studies by the Maine Department of Marine Resources (Maine Yankee Power Company 1976, 1977, 1978, 1979, 1980; Maine Department of Marine Resources 1993).

Methods

The process for developing and running the HSI models began with selecting the species to be modeled, the environmental variables upon which the models would be run, and the modeling method (Figure 1). The next phase contained two elements conducted in parallel: (1) encoding the habitat affinities of the species and life stages being modeled, combined with the selected modeling method, yielded the HSI models, and (2) developing digital environmental maps provided the mapped habitat characteristics upon which the HSI models were run. The environmental maps were converted to a raster (i.e., grid) format, and all GIS operations were performed on a grid cell-by-grid cell basis. Running the HSI models using the GIS consisted of three steps. First, each environmental map was reclassified by grid cell to the suitability index scale (e.g., temperature in degrees centigrade was converted to a 0–1 suitability scale) based on habitat affinities of the organism being modeled. Second, the model calculations were run. In this case the calculation was the geometric mean of the suitability index values, which was obtained by overlaying the environmental maps and running the calculation by grid cell. Third, the results of this calculation were then mapped. After a model was run, its output was evaluated, and, if necessary, the model and environmental maps were modified, and the process was repeated until a satisfactory model and HSI map were completed. The same models were run for both Casco and Sheepscot bays.

Selecting Project Components

Species.—Habitat suitability index models were developed for alewives, American sand lances *Ammodytes americanus,* Atlantic salmon, Atlantic tomcods *Microgadus tomcod,* common mummichogs *Fundulus heteroclitus,* winter flounder *Pleuronectes americanus,* American lobsters *Homarus americanus,* and softshell clams *Mya arenaria* (Appendix 1). These species were chosen because of their commercial, recreational, or ecological value. All use estuaries or coastal bays at some point in their life cycles, and they represent a wide range of life modes, life histories, and ecological niches. Each has been identified as a species of concern in the area by the USFWS's Gulf of Maine Project, the Gulf of Maine Council on the Marine Environment, and NOAA's Estuarine Living Marine Resources program (Jury et al. 1994).

Twenty-one models were developed for species and life history stages with unique habitat requirements (Table 3). Single models were developed for combined life history stages with the same habitat or for stages that were not separated in the available field data sets, such as adult and older juvenile softshells. Models were developed only for life history stages that occur in the study area and were run only for seasons in which they occur. In addition, models were not developed for certain life history stages for which little or no information is available in the region (e.g., American sand lance eggs).

Environment.—Temperature, salinity, depth, and predominant substrate were chosen as the environmental characteristics to be included in the models (Table 4). Selection of these variables was based on their importance for defining estuarine habitat in the Gulf of Maine (Bigelow and Schroeder 1953; Stickney 1959; Targett and McCleave 1974; Fefer and Schettig 1980; Larsen et al. 1983; MacDonald et al. 1984; Langton et al. 1989; Ruffing 1991; Tort 1993) and on the feasibility of developing comprehensive digital maps with no new field studies.

Modeling Method.—The calculation used for the models was an unweighted geometric mean (Layher and Maughan 1985). The following was the initial model for every species and life history stage:

$$\mathrm{HSI} = (\mathrm{SI}_{\mathrm{salinity}} \cdot \mathrm{SI}_{\mathrm{temperature}} \cdot \mathrm{SI}_{\mathrm{substrate}} \cdot \mathrm{SI}_{\mathrm{depth}})^{1/4},$$

TABLE 3.—The habitat suitability index (HSI) models developed and seasons in which they were run.

Species and life stage	Winter	Spring	Summer	Fall
Alewife				
Spawning migrant		X		
Coastal adult		X	X	X
Juvenile outmigrant			X	X
American sand lance				
Adult–juvenile	X	X	X	X
Spawning–egg	X			
Atlantic salmon				
Spawning migrant		X	X	X
Smolt outmigrant		X		
Atlantic tomcod				
Adult–juvenile	X	X	X	X
Spawning–eggs	X[a]			X[a]
Larva	X	X		
Common mummichog				
Adult–juvenile	X	X	X	X
Spawning–eggs			X	
Winter flounder				
Adult	X	X	X	X
Spawning–eggs	X[b]	X[b]		
Larva		X		
Juvenile	X	X	X	X
American lobster				
Adult	X	X	X	X
Larva			X	
Juvenile	X	X	X	X
Softshell clam				
Adult–juvenile	X	X	X	X
Spawning		X	X	

[a] Final HSI maps contain the maximum of the fall and winter HSI values.

[b] Final HSI maps contain the maximum of the winter and spring HSI values.

TABLE 4.—Environmental variables included in the habitat suitability index models and the data resolution incorporated into the models.

Variable	Resolution
Temperature	Mean surface and bottom by season at increments of 2°C
Salinity	Mean surface and bottom by season for 0, >0–0.5, >0.5–5, >5–10, >10–15, >15–20, >20–25, >25–30, >30‰
Depth	Intertidal, 0–3 m, 3–10 m, 10–20 m, 20–50 m, 50–100 m, 100–200 m (Depths from 3 m above mean low water to 5 m below mean low water are broken out in 1-m intervals for shallow-water species)
Predominant substrate	Rock, gravel, sand, mud, shell (≤2-m depth only), submerged–emergent vegetation

where SI_x is the suitability index for environmental variable x. In some cases, the final HSI models were based on a reduced number of habitat variables. For example, the distribution of Atlantic tomcod larvae is not known to be influenced by substrate, so this variable was dropped from the final model.

For each model, SI values from 0 to 1 were assigned to ranges of each environmental variable, depending on how favorable the range is for survival, growth, and reproduction (Table 5). An SI of 1.0 was assigned to the most favorable conditions. An SI of 0.5 was assigned to an environmental range of approximately average suitability, which was intended to represent habitat about half as suitable as the most favorable habitat. An SI of 0.1 was assigned to that portion of a range in conditions in which the species or life stage can occur but is rare. This SI value represents habitat about 1/10 as suitable as the most favorable habitat. An SI of 0 was assigned to environmental parameters outside the range naturally used by the the particular species or life stage. The intermediate SI values were chosen to enable the HSI models to generate a wide range of output values. However, this decision was based on judgment, rather than on analytical criteria, and different intermediate SI values might be appropriate for studies with different needs for resolution in the models.

The models generated a geometric mean or average suitability, with all environmental variables included in a model weighted equally. Because all terms in the models ranged from 0 to 1, model outputs also ranged from 0 to 1. The geometric mean was used instead of an arithmetic mean because the geometric mean is calculated multiplicatively and goes to zero if any term in the model is zero. Habitat with any single environmental characteristic outside the range used by a species should be identified as unsuitable, regardless of the values of the other environmental characteristics.

The values obtained from running the HSI models were consolidated into four HSI classes rep-

TABLE 5.—Definitions of suitability index values.

Suitability index value	Description of habitat use
1	High density or relative abundance in field studies; high reproductive or growth potential; active preference in behavioral studies
0.5	Common occurrence or average density in field studies; average reproductive or growth potential
0.1	Rare occurrence or low density in field studies; tolerance documented in field or laboratory studies; little potential for growth or reproduction
0	Little or no occurrence in field studies; mortality may occur in laboratory or field studies; active avoidance in behavioral studies

resenting high (HSI ≥ 0.84), medium ($0.84 > \text{HSI} \geq 0.5$), and low suitability ($0.5 > \text{HSI} \geq 0.1$), and unsuitable (HSI = 0). A model with four variables could generate 16 unique HSI values, depending on the SI values of each environmental variable. For mapping, the HSI values were consolidated as above because maps depicting 16 habitat suitability classes were deemed too complex for management purposes. Also, because of data limitations and assumptions inherent in the models, mapping 16 distinct classes of habitat suitability would overinterpret model accuracy. No statistical criterion was used to define cutoffs between the HSI classes. The cutoffs were chosen to provide HSI maps with substantial amounts of area in each suitability class. Other cutoffs could be more appropriate for particular objectives. For example, a map intended to depict only the best habitat might emphasize details in the high-suitability range, while a map intended to depict only where a species would not be expected to occur might emphasize details in the low-suitability range.

Model assumptions.—Four assumptions are inherent in the modeling method used in this study, although approaches are available to relax these assumptions.

(1) Each environmental variable is equally important in determining habitat suitability for a species. This assumption is caused by the equal treatment of each environmental variable in calculating the geometric mean of habitat suitability (Layher and Maughan 1985). It could be relaxed by weighting terms in the model or by limiting the range of SI values for a variable (Christensen et al. 1997). For example, if the SI value for an environmental variable were limited to 0.1 and 0.5, the influence of that particular variable over the calculated result would be less than if the SI value ranged between 0.0 and 1.0. Because of the lack of site-specific information for designing the models, the absence of recommendations from the review panels, and the requirement for simplicity, none of these explicit approaches for adjusting the importance of a single variable was used in this study. This is a reasonable approximation here because the ranges of every variable in the study area are sufficient that each has the potential to limit distribution.

(2) The relationships between habitat quality for a species and each environmental variable are independent. This assumption is a consequence of the mathematical structure of the models because the SI value of each environmental variable is entered separately into the geometric mean calculation and no interaction terms are included. This assumption could be tested statistically using a synoptic data set of abundance and environmental data. In such a case, more sophisticated models could be developed using multiple regression or multivariate techniques. Because of the lack of appropriate data, this assumption could not be tested in this study.

(3) The environmental associations of a species or life stage are constant throughout the period modeled. This assumption can be relaxed by developing models for specific periods or narrowly defined activities, as was done for 13 of the models developed in this study (Table 3).

(4) Species distributions are independent across seasons. This assumption is required, because each season was modeled and mapped by itself. For sedentary species, distribution may be limited by mortality during periods of environmental stress or high predation. In this case, maps developed from models run for periods of greatest environmental stress may correspond most closely to actual distribution. Softshell clam is the only sedentary species in this study, and its distribution is primarily controlled by depth (mediated by high predation rates below the intertidal zone) and substrate (Newell and Hidu 1986), which do not vary by season. However, this issue could affect habitat suitability maps of a species that is limited by temporally varying factors, such as temperature or salinity.

Encoding Habitat Affinities

The ranges of environmental conditions assigned to the SI values (Appendix 1) were determined from a comprehensive review of the available literature on habitat associations of the species in the study. The draft models, their output maps, and the statistical results were subsequently reviewed by two expert-review panels (see Evaluating the Results below). Because the models were to be applied to the environmental maps, the environmental ranges for the models were the same as those used for the environmental maps. The choices for environmental ranges were based on two factors. First was the resolution with which the study species are distributed over environmental gradients. Because of the minimal sampling data available for the study area, this was based on literature review. Second was the resolution of the information available for developing the environmental maps.

The treatment of depth illustrates the approach. Bathymetric contours were initially generated at 1-m intervals. For most species in the study, 1-m

TABLE 6.—Data sources used for developing seasonal temperature and salinity maps; CB = Casco Bay, SB = Sheepscot Bay.

Water body	Period of record	N	Data source
CB, SB	1991–1993	8,736	Shellfish bed surveys, Maine Department of Marine Resources
CB, SB	1992–1994	3,945	Shrimp surveys, Maine Department of Marine Resources
CB	1993–1994	4,023	Volunteer monitoring program, Friends of Casco Bay
CB, SB	1933–1934, 1979–1991	183	Gulf of Maine nutrient study, Bigelow Laboratory for Ocean Sciences
CB, SB	1912–1936, 1953–1985	527	Atlantic Fisheries Adjustment Program, Bedford Institute of Oceanography
CB	April 1980	56	Northeast Monitoring Program, National Marine Fisheries Service
CB, SB	1971–1983	330	STORET, U.S. Environmental Protection Agency
CB, SB	1992–1993	15,627	Oceanography Department, University of Maine
SB	1975–1977	1,880	Maine Yankee Atomic Power Company
SB	1984–1985	387	Maine Department of Marine Resources, unpublished plankton survey

resolution is not needed for habitat mapping, so broader ranges were chosen: intertidal, mean low tide to 3, 3–10, 10–20, 20–50, 50–100, 100–200, 200–400, and 400–500 m. However, two species in the study, softshell clam and common mummichog, primarily occur in intertidal habitats (Bigelow and Schroeder 1953; Newell and Hidu 1986; Hawkins 1994; C. S. Heinig, MER Assessment Corporation, personal communication). For these species, the intertidal and shallow subtidal depths were partitioned into 1-m intervals (Appendix 1). Also, juvenile American lobsters occur in the lower intertidal (Lawton and Lavalli 1995), so the intertidal depths also were partitioned in 1-m increments for this species.

Developing Digital Environmental Maps

The processes used to develop the environmental maps differed by variable (Brown et al. 1997). Maine's official 1:24,000-scale digital coastline for the study area was obtained from the Maine Office of Geographic Information Systems. When necessary, source maps with different scales were converted to the 1:24,000 scale using the GIS.

Similar processes were used to develop contour maps for depth and predominant substrate. Depth contours at 10-m intervals were obtained from a draft digital contour map provided by the Maine State Geological Survey (J. Kelley, Maine State Geological Survey, personal communication), which was developed from the Coastal Marine Geologic Environments maps (Timson 1976). These contours were supplemented by digitizing the 1.8-m contour below mean low water from NOAA's National Ocean Service nautical charts 13290 and 13293. Mean low water itself was mapped by selecting the most offshore boundary of intertidal habitats from the USFWS's National Wetlands Inventory maps (Cowardin et al. 1979) or the Coastal Marine Geologic Environments map. Intermediate depth contours were developed by interpolation using the GIS. All information for the predominant substrate maps was obtained from the Maine State Geological Survey's Seafloor Atlas program (J. Kelley, Maine State Geological Survey, personal communication), the National Wetlands Inventory maps (Cowardin et al. 1979), and the NOAA's National Ocean Service nautical charts 13290 and 13293.

Temperature and salinity contour maps were developed to represent average seasonal conditions for the surface and the bottom. Ten sources of raw data were used for generating these maps (Table 6). Substantial efforts were required to identify appropriate data sets, digitize some of the data sets, and conduct quality control checks. Quality control checks included checking (1) ranges, to ensure that impossible values were excluded; (2) locations, to ensure that reported sample positions were reasonable (and not on land); and (3) depths, to ensure that reported sample depths were consistent with mapped bathymetry. Questionable data points were dropped. Over 35,000 points were obtained, but because many points were for water column profiles, a considerably smaller data set was available for developing the seasonal surface and bottom contours. For temperature the seasonal data sets used for generating the maps contained between 43 and 571 points/bay (mean of 243). For salinity the seasonal data sets used for generating the maps contained between 64 and 533 points/bay (mean of 254).

To develop the temperature and salinity maps, typical years were identified by season using data from nearby stations that had long-term data records. For these stations, comparisons of seasonal temperature and river flow means for each year were made to their long-term seasonal means. For each variable the seasons from all years with means falling within 1 SD of the long-term seasonal means were considered to be typical. Season definitions were defined temporally: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). For each season, the point data from the typical years were then selected from the hydrographic data sets for Casco and Sheepscot bays. These selected data were then contoured using the Arc/Info TIN procedure, resulting in Arc/Info thematic covers consisting of vector-based contours.

For Casco Bay, years with typical seasonal temperatures were identified using data from Station 8418150 (Portland, Maine) of the National Water Level Observation Network (NOAA, National Ocean Service). Years with typical seasonal salinities were identified using freshwater inflow data from the U.S. Geological Survey's gauging stations in the Casco Bay watershed (Station 01064000, Presumpscot River at Sebago Lake outlet, and Station 01060000, Royal River at Yarmouth). For Sheepscot Bay, years with typical seasonal temperatures were identified using data from the Maine Department of Marine Resources Boothbay Harbor station. For identifying the typical salinity seasons, freshwater inflow data were used from the U.S. Geological Survey's Station 0103800, Sheepscot River at North Whitefield.

Before running the HSI models, all the environmental maps were converted from the vector to the raster format using the Arc/Info GRID module. The raster maps all contained 100 × 100-m (1 ha) grid cells. Modeling computations are more efficient in the raster than in the vector format, though data storage requirements may be greater (Isaak and Hubert 1997).

Running the HSI Models Using GIS

An Arc/Info Arc Macro Language program (AML) called HSI was developed for this project. It starts by bringing up a series of menus for defining the model: species and life stage, season, strata (for choosing surface or bottom temperature and salinity maps), type of classification to be used on the output map (all 16 unique calculated HSI values or the consolidated set of four HSI classes: high, medium, low suitability, and unsuitable), and output type (file or screen display). Following these selections, the AML begins to construct and run the model.

The AML reclassifies the grid coverage for each environmental map according to previously constructed reclassification tables (Appendix 1). For each species and life history stage, these tables specified the SI values over the possible range for each environmental variable. For example, the SI values for depth in the adult lobster model are 0.0 for the intertidal zone, 0.5 for depths of 0–3 m, 1.0 for depths of 3–200 m, and 0.5 for depths of 200–400 m. Calculations began with reclassifying the depth grid. Then the salinity grid was reclassified and multiplied by the depth grid. This resultant grid was multiplied by the reclassified substrate grid, and finally by the reclassified temperature grid. The last steps were to calculate the fourth root of the final grid, reclassify it according to the 4 or 16 output-class scheme, and either print the resulting map or write it to a file.

For models that did not include all four environmental variables, the reclassification tables for the variables excluded from the particular model contained a marker showing that the table was invalid and which variable was left out of the calculations. A counter kept track of how many reclassified grids were used in the model, so that the appropriate root could be calculated for the geometric mean.

Evaluating the Results and Revising the Models

The models, their mapped outputs, and the environmental maps upon which the models were run were repeatedly evaluated and revised to correct shortcomings identified through detailed inspection and statistical analysis and in two expert review workshops. To detect systematic biases, such as a model under or overestimating the habitat suitability for a particular environmental condition (e.g., temperature or predominant substrate), the project team examined graphs of HSI values plotted against the mapped values of the environmental variables and graphs of catch-per-unit-effort (CPUE) data plotted against HSI values. When such biases were suspected, an investigation was undertaken to determine whether this bias was due to anomalies in the field data (e.g., error in sample location or sampling during unseasonably warm or cold conditions), inaccuracies of an environmental map, or problems with the model (e.g., inappropriate SI values). Where possible, changes in the models and environmental maps were made to eliminate the problem. During the expert review workshops, biologists working in the study area suggested changes in the SI values assigned to environmental ranges and suggested changes in model structure, such as dropping substrate from models for pelagic species. Based on their familiarity with the study area, the expert reviewers also were able to provide information to improve the environmental maps, primarily by filling in missing or incorrect information.

Statistical analyses.—Statistical analyses were used to compare mapped model outputs with CPUE data from the study area. Because the carrying capacity of a habitat should increase with increasing habitat suitability (USFWS 1980a, 1980b, 1981; Rubec et al. 1999), there should be a close correspondence between CPUE data and HSI values. This was tested statistically with comparisons of mean CPUE for the HSI classes (i.e., high, medium, and low suitability, and unsuitable). Where significant differences were found, a visual inspection was performed to determine whether the differences showed increasing CPUE with increasing HSI class.

Data sets for the statistical analyses were prepared by overlaying point CPUE data on the appropriate HSI model output map and by extracting data sets containing the CPUE values and the calculated HSI value for the grid cell corresponding to the sampling point location and season. To facilitate interpretation, these data sets also contained mean seasonal temperature and salinity, predominant substrate, and depth values for the corresponding grid cell.

The HSI values were grouped into the high, medium, low, and unsuitable HSI classes for the statistical analyses. Because of nonnormality of data distributions and heterogeneity of variances, nonparametric statistical tests were used. Each data set was examined for overall differences in CPUE among the HSI classes using the Kruskal–Wallis (H) test (Steel and Torrie 1960). When overall differences in CPUE were found among the HSI classes, the CPUEs in pairs of HSI classes were compared using Wilcoxon two-sample rank tests (equivalent to Mann–Whitney tests; Snedecor and Cochran 1967). For these Wilcoxon tests, experimentwise type I error rate was constrained to $P < 0.05$, which meant that the significance level for comparing catches for a particular pair of HSI classes was adjusted using the formula

$$1 - (1 - \alpha)^c = 0.05,$$

where α is the significance level required for the pairwise comparisons of CPUE per HSI class to preserve the 0.05 experimentwise significance level and c is the number of pairwise comparisons (SAS Institute 1989). In this study, data sets contained from two to four HSI classes. Solving the above equation results in pairwise-comparison α levels of 0.05 for two HSI classes (total of one comparison), 0.017 for three HSI classes (total of three comparisons), and 0.0085 for four HSI classes (total of six comparisons). Following the Wilcoxon two-sample rank tests, the overall numerical order of the CPUE per HSI class was determined by visual inspection of the HSI class means.

Ideally, field data sets for testing HSI models would combine CPUE data with environmental data, would be based on frequent and replicated sampling over many years, and would cover the complete range of available habitat. Unfortunately, the data sets available for this project were far from this ideal (see next paragraph). Because several data problems complicated interpretation of the statistics, the statistical results were interpreted as supporting evidence for the existence and strength of a relationship between model outputs and catch data, rather than as a definitive test. The expert review panels were the final authority for modification, acceptance, or rejection of a model. No model approved by the expert review panels was discarded solely because of the lack of significance in the statistical tests.

The data sets compiled for evaluating model performance (Table 7) have several shortcomings. With the exception of the American lobster data set, the CPUE data obtained from the Maine Yankee studies (Maine Yankee Power Company 1976, 1977, 1978, 1979, 1980) did not contain size information, so data for adults and juveniles could not be separated. Also, environmental data were not associated with the CPUE data in these Maine Yankee reports, so samples collected during atypical temperature or salinity conditions could not be removed from the data sets. A number of problems with station location were encountered. Any ambiguity in station location could have affected the statistical analyses because the HSI value determined for the station could have been taken from the wrong location. With the exception of the Tort (1993) and Wippelhauser (G. S. Wippelhau-

TABLE 7.—Summary of statistical analyses for evaluating habitat suitability index (HSI) models using field data. Catches for HSI classes along a row not followed by a common letter are significantly different (Wilcoxon two-sample rank test, experimentwise $P < 0.05$). Classes without values did not occur in the data set.

Species and life stage	Data source	N	Kruskal-Wallis Chi-square	Experimentwise P	Catch by HSI class			
					Unsuitable	Low	Medium	High
Alewife								
Spawning Migrant	Maine Yankee gill net (Spring data)	49	5.8	>0.05	1.4 z	9.3 z	6.3 z	
Coastal adult	Maine Yankee gill net	172	50.9	<0.001	0.3 z	5.9 y	24.1 x	3.7 xy
Juvenile	Seine surveys reported by Tort (1993) and G. S. Wipplehauser (Maine Natural Areas Program, personal communication)	26	11.5	>0.05	0.0 z	1.7 z	1,548 z	2,128 z
Juvenile	Maine Yankee intake channel	91	42.0	<0.001	0.04 z	1.2 y		1.9 y
Atlantic tomcod								
Adult–juvenile	Maine Yankee trawl survey	177	34.0	<0.001	5 z	85 y	137 y	182 y
Larva	Maine Yankee plankton tows	10	6.5	<0.01	0.3 z		21.6 y	
Larva	Maine Yankee stationary plankton nets (bottom data)	32	22.7	<0.001	0.0 z	0.4 y	6.5 x	
Common mummichog								
Adult-juvenile	Tort (1993) seine survey	20	6.2	>0.05	778 z	9,501 z	1,536 z	8,806 z
Winter flounder								
Adult	Maine Yankee trawl survey	180	54.3	<0.0001	3.3 z	33 y	65 x	
Juvenile	Maine Yankee trawl survey	185	32.3	<0.0001		26 z	73 y	
Juvenile	Seine surveys reported by Tort (1993) and Wipplehauser (Maine Natural Areas Program, personal communication)	21	6.0	<0.01		1.8 z	7.6 y	
Larva	Maine Yankee stationary plankton nets	32	18.9	<0.001	0.2 z		2.4 y	6.9 y
Larva	Maine Yankee plankton tows	14	3.8	>0.05	0.4 z		23 z	
American lobster								
Adult	Maine Yankee pot survey	106	18.0	<0.001		0.04 z	0.3 y	0.1 z
Softshell clam								
Adult–juvenile	Maine Yankee clam survey	142	12.2	<0.05		24 z	53 yz	98 y
Adult–juvenile	Heinig (1993), Heinig et al. (1995), Larsen et al. (1983)	83	48.2	<0.001	4 z	33 yz	123 xy	101 x

ser, Maine Natural Areas Program, personal communication) seine surveys and the Larsen et al. (1983) data set, none of the data sets contained positional data, so station locations had to be estimated from maps of varying quality and differing coastlines. Several of the positions estimated for the Maine Yankee stations were located on land on the official coastline used in this study. This problem also affected some of the stations sampled by Tort (1993) and Wippelhauser (G. S. Wippelhauser, Maine Natural Areas Program, personal communication). Several of the positions given in Larsen et al. (1983) are clearly inaccurate, the tabular positional data and mapped locations differing for several stations. One of the investigators from the Larsen et al. (1983) team (L. Doggett, Maine Department of Environmental Protection, personal communication) recommended using the station map in the report, rather than the tabular positional data. Some stations occurred at impossible depths or over incorrect substrates, and were dropped. Some of the position problems may have been due to the methods used to determine location in the original studies. Positions determined using LORAN or triangulation are subject to considerable, but unknown, variation.

Because of the paucity of available field data, attempts were made to resolve positional questions. Using the GIS and the environmental maps developed for this project, stations with associated depth or substrate information were replotted to an adjacent location with the appropriate conditions. If an adjacent location with these conditions did not exist on the project maps, the station was dropped.

Expert review workshops.—In the expert review workshops, all environmental maps, models, maps of model outputs, and statistical tests of the models were posted on a wall. These products were grouped by variable for the environmental variables and by species for the models. Following a verbal introduction on the goals of the project and objectives of the workshop (i.e., reviewing environmental maps, HSI models, statistical tests, and mapped model outputs), the review teams focused on one group of products at a time and provided verbal and written commentary. Care was taken to ensure that all reviewers who felt competent to review a particular map or model expressed themselves fully. A computer with all the necessary GIS software, programs, and data sets was brought to the reviews, so that possible modifications to the models could be evaluated during the workshops. The review process was designed to be detailed, and each workshop took an entire work day to complete. The final models and maps were completed following the second workshop.

Reviewers had specific comments on model design and species distribution for every species. Also, several comments focused on the environmental maps. Additional information was provided by reviewers for substrate in Sheepscot Bay, and some anomalous values were corrected in the Casco Bay temperature maps. Reviewer comments incorporated into the models were as follows. Because alewives and Atlantic salmon are pelagic, reviewers suggested that depth and substrate be removed from the models for these species. In addition, the reviewers suggested developing models specific to certain activities for these species, both of which are anadromous. Therefore, specific models were developed for alewife spawning migrants, coastal adults (i.e., adults outside of the spawning season), and juvenile emigrants (from fresh to salt water) and for Atlantic salmon spawning migrants (passing through estuaries) and smolt emigrants (passing through estuaries). For American sand lance, the reviewers agreed that little information was available, except that the species favors sandy substrates. For Atlantic tomcod, reviewers noted that spawning and egg deposition can occur on muddy substrates, so the SI of predominantly mud was increased from 0.0 to 0.1 for the spawning–eggs model. Also, because this species spawns in late fall and early winter, the final HSI map for the spawning–eggs model contains the maximum of the fall and winter HSI values. Reviewers suggested that the SIs for lower salinity categories in the common mummichog models be increased. For the winter flounder models, the reviewers suggested widening the range of suitable salinities and, because this species spawns in late winter and spring, using the maximum of the winter and spring HSI values for the final spawning–egg maps. The SIs for temperature were also modified to reflect seasonal distributional patterns in which winter flounder adults and juveniles tend to move out of the nearshore zone during the warmest and coldest months (R. Langton, Maine Department of Marine Resources, personal communication). Reviewers requested only minor changes in substrate SIs for the American lobster adult model and noted that habitat suitability is generally lowest during the winter. The reviewers also noted that trap data may not be an accurate measurement of abundance. For the softshell clam models, the reviewers suggested changing the SIs for depth and substrate.

The consensus of the reviewers was that, with the recommended revisions, all the models described in this paper could generate credible maps that would be useful for assessing habitat in the study area. Models were retained for the project, even if the statistical tests for evaluating model performance were equivocal or not significant. Models were also retained for which no field data were available from the study area for evaluating model performance.

Developing the softshell clam and winter flounder models.—To illustrate model development, the model development process is described in detail for softshell clam and winter flounder. Model development proceeded similarly for the other species, and more comprehensive information for all species is available in Brown et al. (1997).

For softshell clam, adult–juvenile and spawning models were developed (Appendix 1). Model characteristics follow the ecological associations of the species (see references cited in Appendix 1). The adult–juvenile model is for sizes greater than 10 mm shell length. The SI values used in both models demonstrate a strong association with intertidal depths. Although this species is capable of growth in subtidal waters in the Gulf of Maine, predation rates on spat and small juveniles by bottom feeders are very high, greatly reducing habitat suitability below the intertidal (Newell and Hidu 1986). The SI values used in the models also reflect an association with soft sediments. However, because spatial variability in bottom type can occur at a smaller scale than was mapped, soft sediments may exist even in areas that were mapped as having predominantly hard substrate. Therefore, firmer substrates are assigned low, but not zero, SI values. Because of temperature, spring, summer, and fall are the most favorable seasons for growth and survival in the Gulf of Maine. The SI values for the adult–juvenile model are consistent with this pattern. Spawning occurs only during the late spring and summer, so the spawning model was only run during these seasons.

For winter flounder, models were developed for adults, juveniles, spawning–eggs, and larvae. Information on the ecological associations of this species was obtained from the references cited in Appendix 1. The size cutoff between the adult and juvenile stages was 20 cm total length. The larva model was designed for mid and late larval stages, which have left the plankton and adopted a primarily benthic habit. The spawning and egg stages were combined because demersal eggs are deposited on the bottom where spawning occurs and little independent information is available for eggs. The SI values reflect the species' association with relatively shallow waters above 15 ppt salinity (Appendix 1). The species occurs over nearly all substrates, with sand and gravel being most suitable. Adults and older juveniles tend to move somewhat offshore to avoid cold winter temperatures and, to a lesser extent, hot summer temperatures (Bigelow and Schroeder 1953; R. Langton, Maine Department of Marine Resources, personal communication). The high SI values for low temperatures for spawning, eggs, and larvae are a consequence of these stages occurring in late winter and spring.

Using Final HSI Models Analytically: Mapping Important Habitat

A simple approach for integrating the results of the individual models was used to identify and map important habitats. Using the GIS, the final HSI maps for all models were overlain by season, and the arithmetic mean HSI value was calculated by grid cell. These means were then consolidated into the HSI classes (unsuitable, and low, medium, and high suitability). The resulting maps depict spatial distribution of average habitat suitability class by season based on all the species and life stages included in this study.

Results

Statistical Analyses

Catch data were available for conducting statistical analyses for certain life stages of alewives, Atlantic tomcods, common mummichogs, winter flounder, American lobsters, and softshell clams. Sixteen data sets were prepared for evaluating 11 models. Results of the Kruskal–Wallis and Wilcoxon two-sample rank tests for differences in mean CPUE by HSI class are given in Table 7. Most of the data were obtained from the siting and monitoring studies for the Maine Yankee Atomic Power Plant (Maine Yankee Power Company 1976, 1977, 1978, 1979, 1980) in the Sheepscot Bay system. The data set from Heinig (1993), Heinig et al. (1995), and Larsen et al. (1983) for softshell clam was the only data set available for Casco Bay. No data sets with more than a very few observations were found for any life stage of American sand lances and Atlantic salmon, nor for the egg stages of any of the species in the study. Larval data were only found for Atlantic tomcods and winter flounder. When field data do not exist, expert review is the only source available for assessing model performance.

The statistical results (Table 7) from 12 of the 16 data sets directly support 8 of the 11 models for which tests could be performed: alewife coastal adult and juvenile; Atlantic tomcod adult–juvenile and larva; winter flounder adult, juvenile, and larva; and softshell clam adult–juvenile. In these cases, the Kruskal–Wallis tests were significant for the overall data set, and significant differences between CPUEs per HSI class were determined by the pairwise Wilcoxon two-sample rank tests for at least one of the data sets: the lowest mean CPUE grouped with the lowest suitability class and the highest mean CPUE grouped with the highest suitability class. However, for the test of the alewife coastal adult model, using the Maine Yankee gillnet data, the mean abundance for the high habitat suitability class was considerably lower than the mean abundance for the medium habitat suitability class. The abundance data for the high suitability class consisted of only six points from one station, which typically had very high currents (B. Hanson, Central Maine Power Company, personal communication); this inconsistency could be due to shortcomings in the model, which is based only on temperature and salinity (currents are not included), or shortcomings of the data set, or both.

While statistically significant, the results of the tests of the American lobster adult model using the Maine Yankee pot survey data did not indicate a clear relationship between CPUE and HSI class (Table 7). The Kruskal–Wallis test for overall differences in the CPUEs per HSI class was highly significant ($P < 0.0001$), but the pairwise Wilcoxon two-sample rank tests indicated that the mean CPUE for the medium HSI class is significantly higher than the mean CPUEs for the low and high HSI classes. Possible explanations include complexity of the behavior of this species, which may complicate representation by a simple,

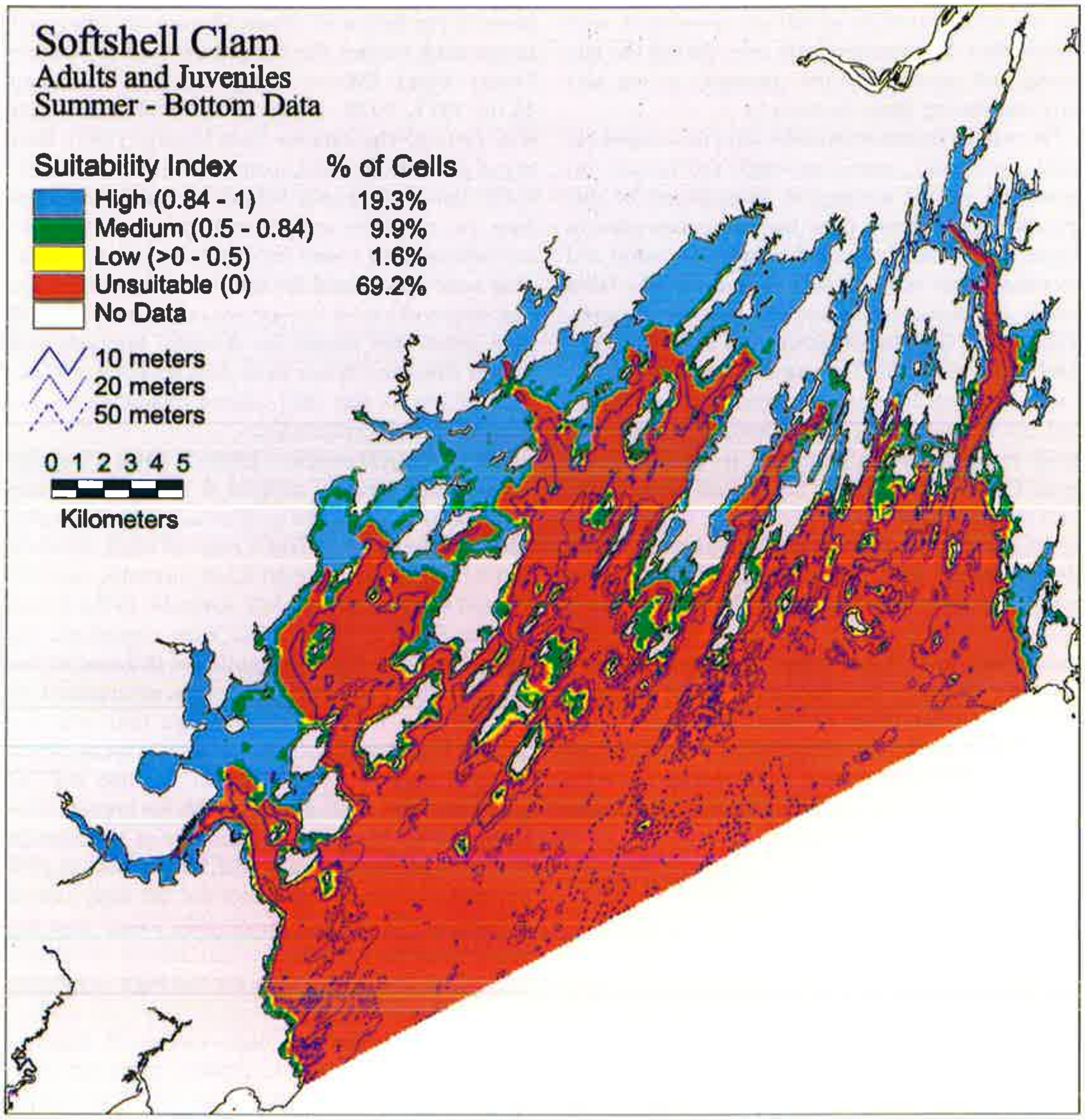

FIGURE 2.—Map of habitat suitability index classes for softshell clam adult–juvenile habitat suitability index model in Casco Bay under summer conditions.

generalized model, or inadequacy of the data set, which may have been effected by trap saturation or disruption of behavior due to the presence of bait (Krouse 1989; Fogarty and Addison 1997).

Three of the data sets did not provide statistically significant results (Table 7). For the test of the alewife spawning migrant model using the Maine Yankee gill net data, the nonsignificant Kruskal–Wallis test and inconsistent relationship between CPUE and HSI class suggest that the model, which is based only on temperature and salinity, may lack an important variable, such as currents. However, only seven data points were available above the low-suitability range, so this test was fairly weak. There was considerable scatter in the test of the common mummichog adult–juvenile model using the Tort (1993) seine survey data. This scatter could be due to shortcomings in the model, the data set, which contains only 20 unreplicated and highly variable observations, or both. For the test of the winter flounder larva model using the Maine Yankee plankton tow data, the results are in the correct direction, so increasing the number of observations substantially above 14

TABLE 8.—Percentages of softshell clam adult–juvenile and winter flounder adult habitat per habitat suitability index (HSI) class mapped in Casco Bay, by season.

HSI class	Percent softshell clam adult–juvenile habitat				Percent winter flounder adult habitat			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
High (HSI ≥ 0.84)	0	15	19	5	0	7	20	18
Medium (0.5 ≤ HSI < 0.84)	16	12	10	19	16	70	57	62
Low (0.1 < HSI < 0.5)	11	4	2	7	8	17	17	15
Unsuitable (HSI = 0.0)	73	69	69	69	76	6	7	6

points would probably yield a statistically significant result. The other test of this model, with the Maine Yankee stationary plankton net data, had a highly significant Kruskal–Wallis test ($P < 0.0001$), the mean CPUEs per HSI class differing in the correct order.

The Final Models

The final SI values used in the HSI model calculations for each species and life stage are provided in Appendix 1. To illustrate statistical evaluation and interpretation of the model outputs, the softshell clam and winter flounder results are covered in some detail below. More comprehensive information for all species and the environmental characteristics of the study area is available in Brown et al. (1997).

Evaluation and interpretation of softshell clam models.—Examination of the statistical results (Table 7) can provide insight into both model performance and characteristics of the data sets used to evaluate model performance. The overall relationship between model outputs and CPUE data is stronger for the data set of Heinig (1993), Heinig et al. (1995), Larsen et al. (1983) for Casco Bay (Kruskal–Wallis test, $\chi^2 = 48.2$, $P < 0.0001$) than for the Maine Yankee data set for the Sheepscot system (Kruskal–Wallis test, $\chi^2 = 12.2$, $P = 0.002$), possibly because the former data set covered the complete range of habitat suitability, including unsuitable habitat. For both data sets, the pairwise Wilcoxon two-sample rank tests for differences among mean CPUEs for the HSI classes and the visual inspections of those results provided strong support for this model. However, for the data set of Heinig (1993), Heinig et al. (1995), Larsen et al. (1983), CPUE dropped off slightly in the highest suitability class, probably due to commercial harvesting in the most productive areas (C. Heinig, MER Assessment Corporation, personal communication). The model appears to have misclassified Maine Yankee Station C3 (not shown) in Young Point Cove, a small, shallow, marshy embayment in the Sheepscot system that had relatively high HSI values but relatively low CPUE. The model may lack a variable that affects softshell clam density in this area, possibly involving restricted larval access. In addition, inaccuracy of the estimated station coordinates and erroneous substrate or bathymetry maps could have affected the data for this station.

The softshell clam adult–juvenile model mapped high-suitability habitat in the shallows around the shoreline and near major islands. In Casco Bay, high-suitability habitat ranged from 19% of the bay's area under summer conditions (Figure 2; Table 8) to 0% under winter conditions (not shown). Unsuitable habitat covers 69% of the bay in summer and 73% in the winter. These figures correspond closely to the percentage of the bay deeper than 3 m (69%; Table 1). Most of the suitable habitat falls in the high- and medium-suitability ranges in the summer (29% of total area and only 2% of total area modeled as low-suitability habitat), and in the medium- and low-suitability ranges in the winter (27% of total area and 0% modeled as high-suitability habitat). Essentially all the high-suitability adult–juvenile habitat in the summer is also high-suitability spawning habitat (not shown), whereas under spring conditions the amount of high-suitability spawning habitat (7% of total area, not shown) is only about half of the amount of high-suitability adult–juvenile habitat (14% of total area). Similar results were obtained for the Sheepscot system, 45% of this system being modeled as high- or medium-suitability adult–juvenile habitat under summer conditions (not shown).

Evaluation and interpretation of winter flounder models.—Several data sets were available for evaluating performance of the winter flounder HSI models (Table 7). Because the data from the Maine Yankee trawl surveys do not contain size information, interpreting the statistical analyses based on this data set is ambiguous. The statistical tests were run with this data set using outputs from both the adult and juvenile models. In both cases, the overall results from the Kruskal–Wallis tests were highly significant ($\chi^2 = 54.3$, $P < 0.0001$ for the adult model; $\chi^2 = 32.3$, $P < 0.0001$ for the juvenile model), and all mean CPUEs per HSI class were significantly different from one another (pairwise Wilcoxon two-sample rank tests) and ordered in the correct sequence (visual inspection). The Kruskal–Wallis test run for the juvenile model using the Tort (1993) and Wippelhauser (G. Wippelhauser, Maine Natural Areas Program, personal communication) seine data were significant ($\chi^2 = 6.0$, $P = 0.01$), the pairwise test and visual inspection indicating significantly different mean CPUEs per HSI class in the correct sequence. The Kruskal–Wallis test for the larva model using the Maine Yankee stationary plankton net data were significant ($\chi^2 = 18.9$, $P < 0.0001$). The pairwise Wilcoxon two-sample rank tests and visual inspection indicated the mean CPUEs for the medium and high HSI classes were significantly higher than the mean CPUE for the unsuitable HSI class, but the CPUEs for the mean and high HSI classes, while in the correct numerical order, were not significantly different from one another. Although higher catches were made in higher suitability locations in the smaller Maine Yankee plankton tows data set (14 observations), the differences were not quite significant (Kruskal–Wallis test, $\chi^2 = 3.8$, $P = 0.052$).

The temporal and spatial patterns of habitat suitability shown on maps of HSI classes were consistent with this species' known distributional patterns. Under spring, summer, and fall conditions, suitable adult habitat was modeled for all but about 6% of Casco Bay (Table 8), unsuitable habitat being located only in the shallowest areas along the shore. Highly suitable winter flounder adult habitat was modeled for moderate depths in the middle of the bay during the summer (Figure 3). Although the total amount of highly suitable adult habitat is greater for the summer (20% of the bay) than for the spring (7% of the bay; Figure 4), the suitability of nearshore areas was lower in the summer than in the spring. This result is probably due to temperature, which exceeds the highly suitable range in nearshore areas during the summer. Under winter conditions (not shown), only one-fourth of the bay, primarily in offshore, deeper areas, was modeled as having suitable adult habitat, and none of this area was modeled in the high-suitability range. Just over half of Casco Bay contains suitable spawning–egg habitat (not shown), approximately 5% of the bay being modeled as highly suitable spawning–egg habitat, primarily in coastal areas with moderate depths near Portland and Cape Small. Similar results were apparent on the HSI maps for the Sheepscot system (Brown et al. 1997).

Using Final HSI Models Analytically: Mapping Habitat Importance

Depending on the season (Table 3), 12–16 HSI maps were overlain using the GIS and averaged by grid cell to evaluate habitat importance. During the spring, habitat with a mean suitability in the high range (HSI = 0.84) was mapped in shallow, nearshore areas, including Portland Harbor, Back Cove, and the mouths of the Presumpscot and Royal rivers (Figure 5). No habitat was mapped that had a mean habitat suitability in the unsuitable range (HSI = 0.0). Similar results were obtained for the Sheepscot system.

Discussion

The HSI modeling methodology developed for this project was generally successful for its intended use of mapping habitat for selected species and of mapping important habitat in the study area. The models produced habitat maps that agreed well with the limited sampling data and with the expert reviewers' collective knowledge of species distributions.

Models for well-known species and life stages with strong affinities for the bottom appeared to perform better than the other models. Substrate and depth were judged to not be relevant for models of the pelagic species, alewives and Atlantic salmon, and were dropped from the final models. Also, some species have very complex patterns of habitat use (e.g., American lobster, Atlantic salmon), which apparently cannot be completely accounted for using the existing variables. In addition, the possible effects of pollutants and other anthropogenic impacts have not been included in the models.

Data and Statistical Issues

Many of the available field data sets had significant shortcomings for testing the HSI models, such as the lack of size data to assign life stage, the lack of environmental data associated with catches, and inaccurate or erroneous station positions. Such problems may be common for any data set developed for purposes other than testing HSI models, especially for older data sets.

Three generic data issues may affect statistical testing of HSI models in studies dependant on using existing data. The first issue is that most data sets consist of point data, but the models are intended for broader characterizations of long-term average conditions for areas and seasons, rather than for specific locations and times. Thus, using point data to test the models implies a greater spatial accuracy than the models and seasonal maps are intended to provide and potentially represents an overinterpretation of the model results. In addition, chance and sampling variability, which are not included in the models, can have major effects on small sets of point data (Neill and Gallaway 1989). For example, species may move in and out of suitable habitat and may not be encountered during a survey with limited sampling. Also, sampling may occur under atypical conditions (e.g., a drought that raises salinity in an estuary) or in an area with an unrecognized contaminant problem so that some data may be correct for a particular point in space and time but not appropriate for testing a model of typical conditions. Because most of the data sets available for this study did not include associated environmental or contaminant data, screening the data sets for atypical environmental conditions or contamination was not possible.

The second generic data issue is that many data sets do not cover the complete range of available habitats. Resource surveys often focus on areas of known high abundance (e.g., Maine Yankee clam survey) or where harvests occur (Heinig 1993; Heinig et al. 1995). Because the areas omitted from such studies would probably have both low abundance and low HSI values, the complete range of a model cannot be tested. In addition, because of the lack of data from low quality habitat, the effect of sampling variability in the higher quality habitat is exaggerated, which may further obscure relationships.

The third generic data issue is that species occurring in numbers below carrying capacity may not occupy all suitable habitat in numbers proportional to habitat quality, thus reducing the relationship between habitat quality and abundance. The impact of this problem may be greatest for highly mobile species and for species with patchy or aggregated distributions. Also, during periods of very high abundance, species may occur in low-quality habitats not normally used.

Potential Enhancements to the Models

This project was designed to be completed relatively quickly and was conducted in an area for which only small amounts of field data were available. The HSI modeling methods developed are therefore appropriate for this situation, which may often exist in an environmental or resource management context. However, several approaches are available for enhancing the models, including adding environmental variables and using more sophisticated algorithms to model patterns of habitat associations or interactions among environmental variables. To add an environmental variable to an HSI model requires access to or creation of a comprehensive digital map. Developing more sophisticated models would require statistical analysis (e.g., stepwise regression, polynomial regression, principal components analysis) of a robust data set that covered complete ranges of habitat use by the species and life stages of interest. Such a data set would have to include not only abundance and accurate positional data, but also associated data for all the environmental variables in the model.

Two approaches are available for assessing species interactions (e.g., predation, competition) using simple HSI models. One approach is to map distribution of one species (e.g., a prey species) and include a measure of its potential availability in the model of another species (e.g., a predator). A second approach would be to develop maps based on suitability of the physical environment and analyze patterns of co-occurrence of the interacting species. The logic underlying this approach is that interactions can only occur where the habitat is suitable for both species.

Developing spatially explicit models may be appropriate when it is necessary to characterize not only spatial patterns, but also dynamics through space and time (Brandt and Kirsch 1993; Dunning et al. 1995; Hermann et al. 1996; Kolody and Healey 1998). These models may include multiple components and feedback loops for species interactions, population spatial and age structure, trophic relationships, bioenergetics, and hydrography. Because of their complexity, using spatially explicit models may be impractical in many management situations, and the level of detail they provide may not be needed to address many management questions that focus on basic issues of habitat location and quality.

Assessing Management Implications

Habitat suitability index maps can be used in a broad range of assessments requiring information on habitat distribution and quality. A major early use of HSI models was to calculate "habitat units" for evaluating the impacts of actions on habitat (USFWS 1980b). Habitat unit analyses were used to estimate gains or losses of habitat over a period

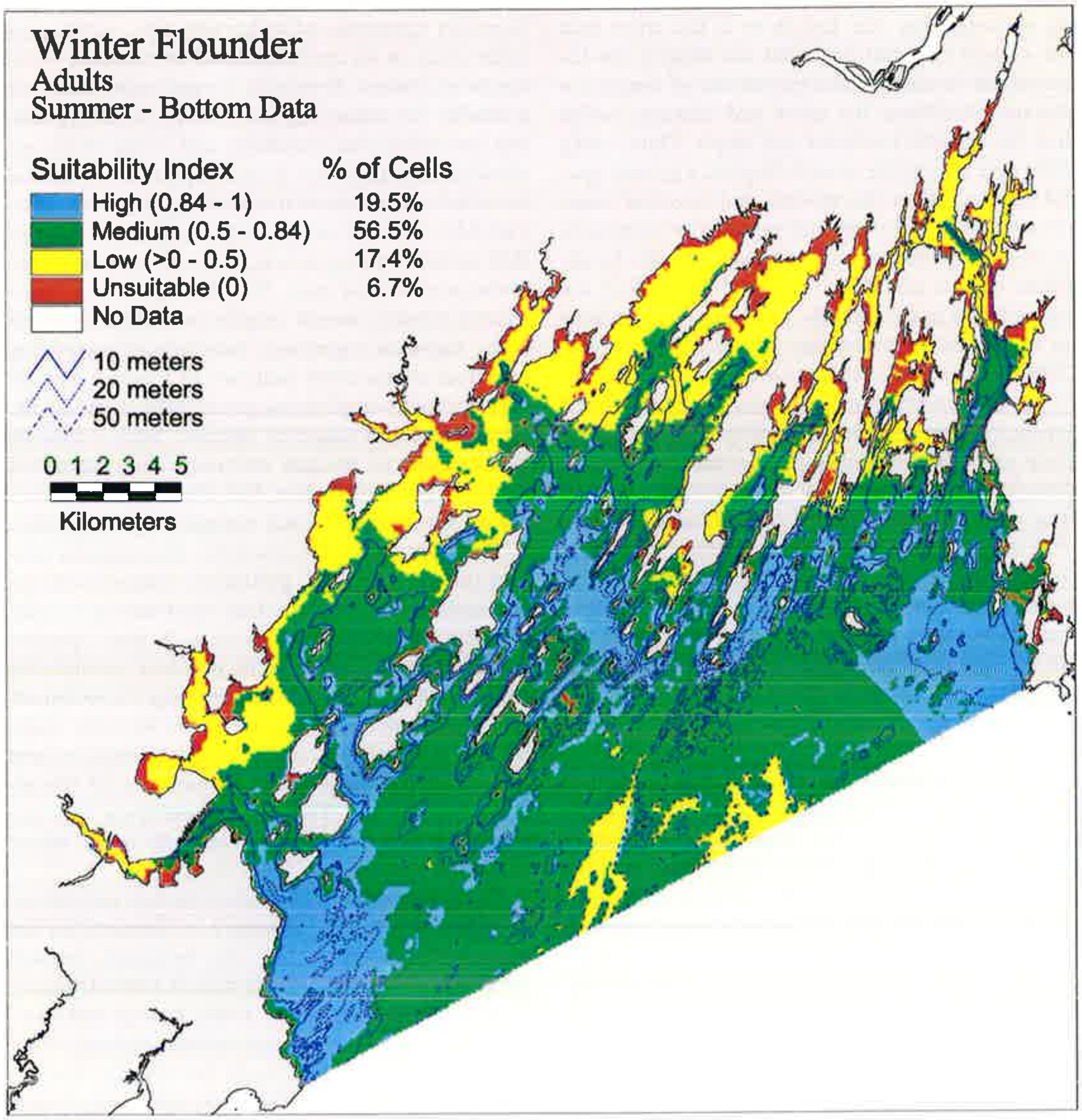

FIGURE 3.—Map of habitat suitability index classes for winter flounder adult habitat suitability index model in Casco Bay under summer conditions.

of time. The use of GIS with HSI models increases the power and flexibility of such analyses. At the most basic level, individual species maps (Figures 2–4) can be used to identify areas of high and low quality habitat and to develop quantitative estimates of amounts and quality of available habitat (Table 8) in support of decisions affecting the particular species (Banner and Libby 1995; Rubec et al. 1998). In addition, HSI maps enable identification of species and life stages with severely limited areas of suitable habitat. Because of the lack of alternative habitat, these species may be particularly sensitive to habitat loss. For example, approximately 94% of Casco Bay is modeled as unsuitable habitat for adult and juvenile American sand lance, most of the highly suitable habitat being found in two patches of sandy substrate near Portland and Cape Small (Brown et al. 1997). Loss of one of these patches would only represent a loss of 2–3% of the bay's area but would represent a loss of about half of the suitable habitat available for this species.

Scenario analysis can be based on comparisons of HSI maps developed under different environ-

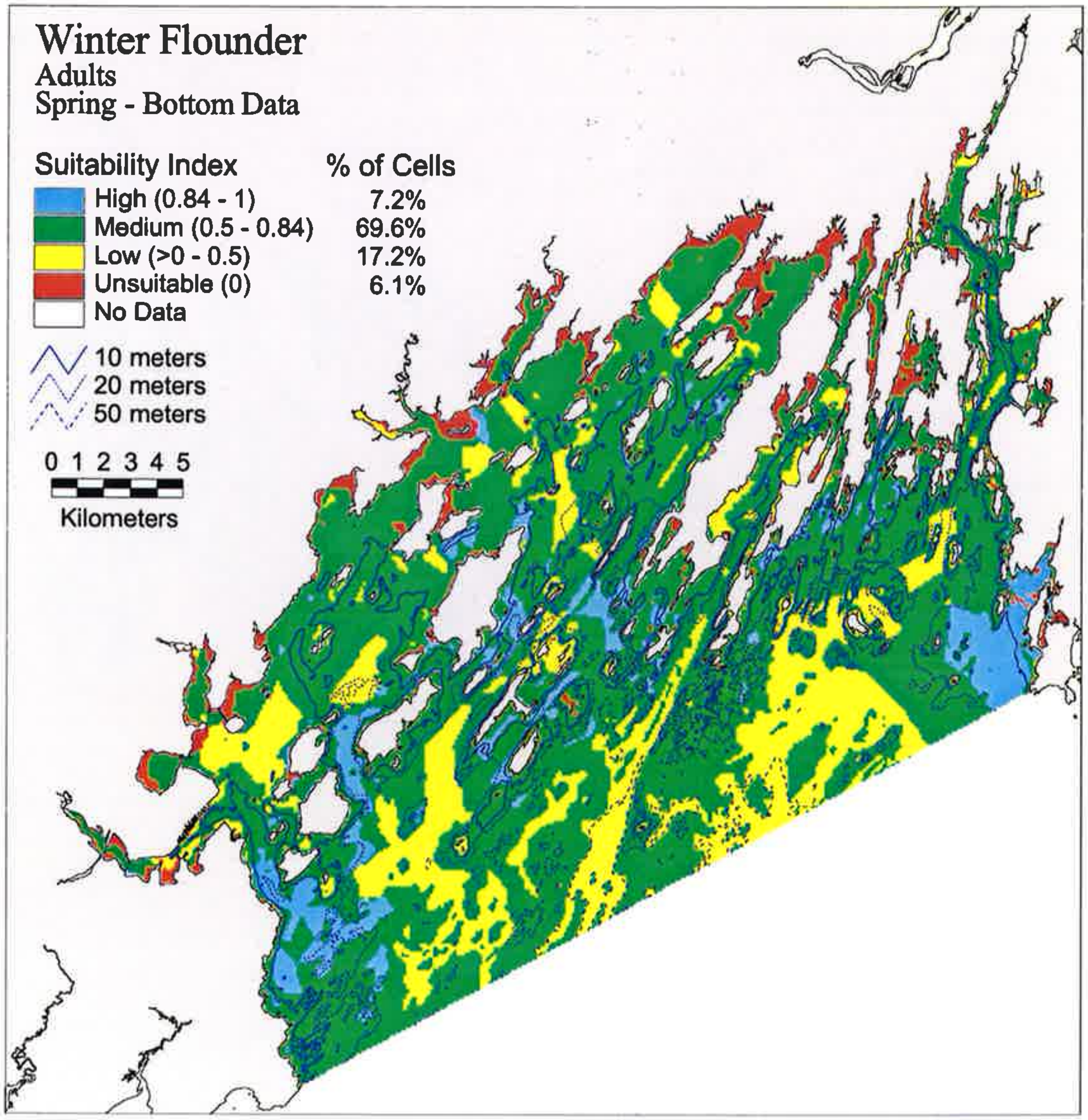

FIGURE 4.—Map of habitat suitability index classes for winter flounder adult habitat suitability index model in Casco Bay under spring conditions.

mental regimes, such as different salinity distributions that could occur as a result of alternative patterns of freshwater diversion (Christensen et al. 1997, 1998). The scenario analysis could be extended to assess impacts on species interactions because an analysis could be made of effects of changed environmental patterns on the spatial and temporal patterns of species co-occurrence.

Identification of candidate areas for conservation or restoration is another potential use of HSI models. In Figure 5, most of the area in Casco Bay with an overall mean habitat suitability in the highly suitable range is near the City of Portland. The models used to generate this map contain only temperature, salinity, depth, and substrate, and including pollutants would probably have changed these results (Doggett and Smith 1992). Even without the inclusion of pollutants in the models, the results suggest that restoration of areas such as Portland Harbor and Back Cove could yield substantial benefits for improving habitat and ultimately increasing species abundances.

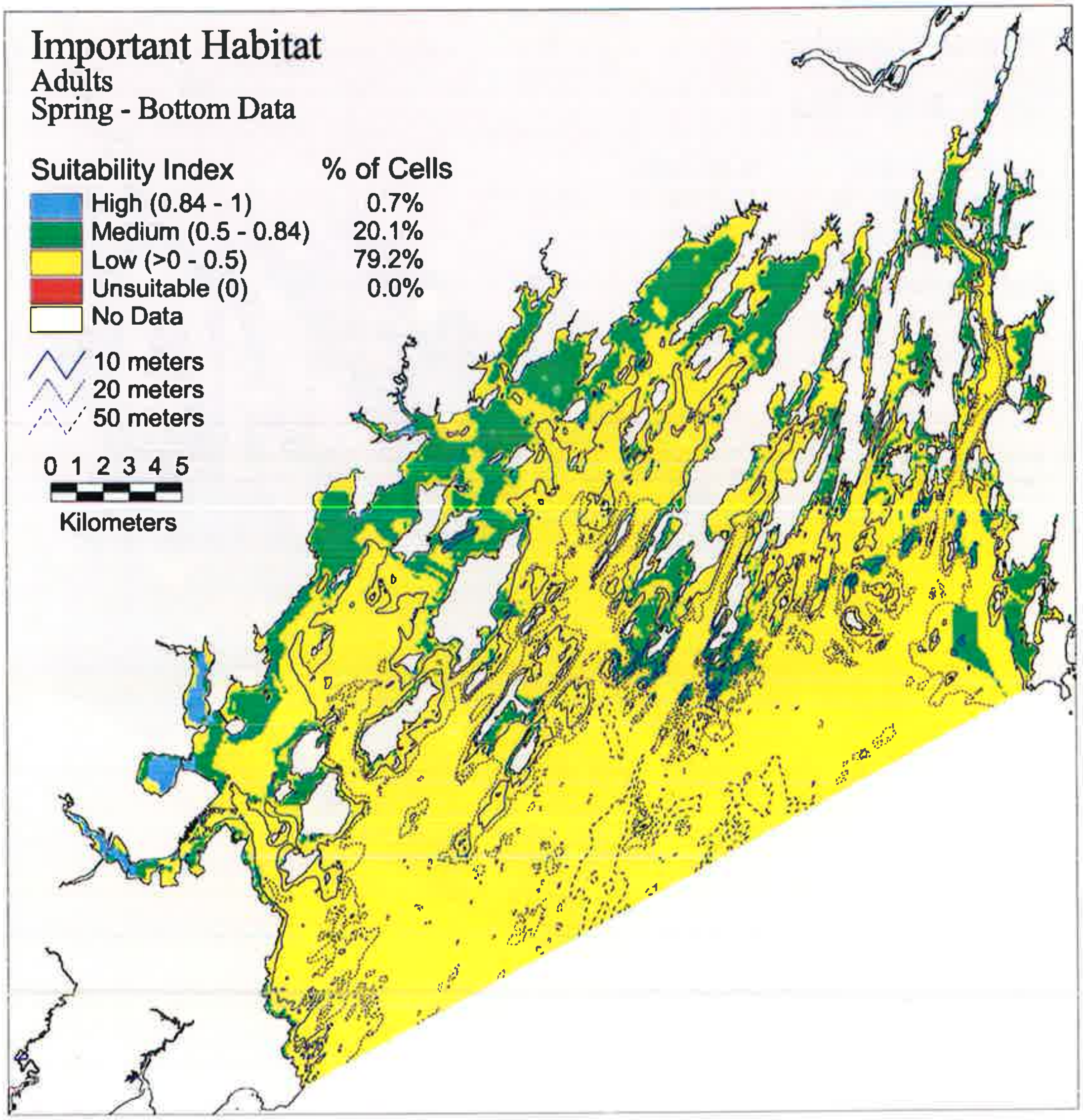

FIGURE 5.—Map of important habitat in Casco Bay during the spring, equal to the mean of the spring habitat suitability index values for all species and life stages included in this study.

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Appendix follows

Appendix 1: Suitability index values used in the habitat suitability index models

TABLE A.1.—Alewife[a]

	Suitability index[b]		
Variable	Spawning migrant	Coastal adult	Juvenile
Depth (m)			
Intertidal	0.5	NA[b]	0.5
MLT–3[c]	1	NA	1
3–10	1	NA	1
10–20	0.1	NA	0.1
20–50	0	NA	0
50–100	0	NA	0
100–200	0	NA	0
200–400	0	NA	0
400–500	0	NA	0
Salinity (‰)			
0–0.5	1	0	0.1
0.5–5	1	0	0.1
5–10	1	0	0.5
10–15	1	0	1
15–20	0.5	0.1	1
20–25	0.1	0.5	1
25–30	0	1	1
>30	0	1	1
Temperature (°C)			
<0	0	0	0
0–2	0	0	0
2–4	0	0	0
4–6	0	0	0
6–8	0	0.1	0.1
8–10	0.1	0.1	0.1
10–12	0.5	0.5	0.5
12–14	1	1	1
14–16	1	1	1
16–18	0.5	0.5	1
18–20	0.1	0.5	1
20–22	0	0.1	1
22–24	0	0.1	0.5
24–26	0	0	0.1
26–28	0	0	0.1
28–30	0	0	0.1
30–32	0	0	0
>32	0	0	0
All substrates	NA	NA	NA

[a] References used for model development: Bigelow and Schroeder (1953); Card, Aho and Gillespie (1981); Fried (1973); Loesch (1987); MacDonald et al. (1984); Maine Department of Marine Resources (1993); Mullen et al. (1986); Recksiek and McCleave (1973); Scott and Scott (1988); Stickney (1959); Targett and McCleave (1974), Tyler (1971a); L. Flagg, Maine Department of Marine Resources, personal communication; B. Hanson, Central Maine Power Company, personal communication.

[b] NA = not applicable.

[c] MLT = mean low tide.

TABLE A.2.—American sand lance.[a]

	Suitability index[b]	
Variable	Adult–juvenile	Spawning–egg
Depth (m)		
Intertidal	0	0
MLT–3[b]	1	0.5
3–10	1	1
10–20	1	1
20–50	0.5	0.5
50–100	0.5	0.5
100–200	0.1	0.1
200–400	0	0
400–500	0	0
Salinity (‰)		
0–0.5	0	0
0.5–5	0	0
5–10	0	0
10–15	0	0
15–20	0	0
20–25	0.1	0
25–30	1	0.5
>30	1	1
Temperature (°C)		
<0	0.1	0.1
0–2	0.5	0.5
2–4	1	1
4–6	1	1
6–8	1	0.5
8–10	1	0
10–12	1	0
12–14	1	0
14–16	1	0
16–18	0.5	0
18–20	0.5	0
20–22	0.1	0
22–24	0.1	0
24–26	0	0
26–28	0	0
28–30	0	0
30–32	0	0
>32	0	0
Predominant substrate		
Mud	0	0
Sand	1	1
Gravel	0	0.1
Rock	0	0
Shell	0	0
Vegetation	0	0

[a] References used for model development: Auster and Stewart (1986); Bigelow and Schroeder (1953); Fefer and Schettig (1980); Meyer et al. (1979); Nizinski et al. (1990); Richards (1982); Scott and Scott (1988); Smigileski et al. (1984); Stickney (1959); Westin et al. (1979); Winters (1989).

[b] MLT = mean low tide.

TABLE A.3.—Atlantic salmon.[a]

Variable	Suitability index[b] Spawning migrant	 Smolt outmigrant
Depth (m)		
Intertidal	0	0
MLT–3[c]	1	1
3–10	1	1
10–20	0.1	0.1
20–50	0	0
50–100	0	0
100–200	0	0
200–400	0	0
400–500	0	0
Salinity (‰)		
0–0.5	1	1
0.5–5	1	1
5–10	1	0.5
10–15	1	0.5
15–20	0.5	0.1
20–25	0.1	0.1
25–30	0	0
>30	0	0
Temperature (°C)		
<0	0	0
0–2	0	0
2–4	0	0
4–6	0.1	0
6–8	0.5	0.5
8–10	1	1
10–12	1	1
12–14	0.5	0.5
14–16	0.5	0.1
16–18	0.1	0
18–20	0.1	0
20–22	0.1	0
22–24	0	0
24–26	0	0
26–28	0	0
28–30	0	0
30–32	0	0
>32	0	0
Predominant substrate		
Mud	0.5	NA
Sand	0.5	NA
Gravel	0.5	NA
Rock	1	NA
Shell	0.5	NA
Vegetation	0	NA

[a] References used for model development: Baum (1993); Beland (1984); Beland et al. (1982); Bigelow and Schroeder (1953); Cunjak et al. (1990); Danie et al. (1984); Fefer and Schettig (1980); Fried (1973); Gustafson-Greenwood and Moring (1990); Meister (1982); Mills (1989); Scott and Scott (1988); L. Flagg, Maine Department of Marine Resources, personal communication.

[b] NA = not applicable.

[c] MLT = mean low tide.

TABLE A.4.—Atlantic tomcod.[a]

Variable	Suitability index[b] Adult–juvenile	 Spawning–egg	 Larva
Depth (m)			
Intertidal	0	0	0
MLT–3[c]	1	1	1
3–10	1	1	1
10–20	0.1	0	0
20–50	0.1	0	0
50–100	0	0	0
100–200	0	0	0
200–400	0	0	0
400–500	0	0	0
Salinity (‰)			
0–0.5	0	0.5	0.5
0.5–5	0.1	1	1
5–10	0.1	1	1
10–15	0.5	0.5	1
15–20	1	0.1	0.5
20–25	1	0.1	0.5
25–30	0.5	0	0.1
>30	0.1	0	0
Temperature (°C)			
<0	0	0	0
0–2	0	1	0.5
2–4	0.1	1	0.5
4–6	0.1	0.5	1
6–8	0.1	0.1	1
8–10	0.5	0	1
10–12	1	0	1
12–14	1	0	0.5
14–16	1	0	0.1
16–18	0.5	0	0
18–20	0.5	0	0
20–22	0.1	0	0
22–24	0.1	0	0
24–26	0.1	0	0
26–28	0	0	0
28–30	0	0	0
30–32	0	0	0
>32	0	0	0
Predominant substrate			
Mud	1	0.1	NA
Sand	0.5	1	NA
Gravel	0.1	1	NA
Rock	0.1	1	NA
Shell	0.1	0.5	NA
Vegetation	1	1	NA

[a] References used for model development: Bigelow and Schroeder (1953); Card et al. (1981); Dew and Hecht (1994); Fefer and Schettig (1980); Fried (1973); Laprise and Dodson (1990); MacDonald et al. (1984); Peterson et al. (1980); Recksiek and McLeave (1973); Scott and Scott (1988); Stewart and Auster (1987); Stickney (1959); Targett and McCleave (1974); R. Langton, Maine Department of Marine Resources, personal communication; L. Mercer, Maine Department of Marine Resources, personal communication.

[b] NA = not applicable.

[c] MLT = mean low tide.

TABLE A.5.—Common mummichog.[a]

Variable	Suitability index[b]	
	Adult–juvenile	Swimming–egg
Depth (m)		
(+)2–(+)3	0.5	0.5
(+)1–(+2)	1	1
0–(+)1	1	0.5
1–0	1	0
1–2	0.5	0
2–4	0.1	0
4–10	0	0
10–20	0	0
20–50	0	0
50–100	0	0
100–200	0	0
200–400	0	0
400–500	0	0
Salinity (‰)		
0–0.5	0.5	0.1
0.5–5	0.5	0.5
5–10	0.5	0.5
10–15	1	1
15–20	1	1
20–25	1	1
25–30	0.5	0.5
>30	0.1	0.1
Temperature (°C)		
<0	0	0
0–2	0.1	0
2–4	0.1	0
4–6	0.1	0
6–8	0.1	0
8–10	0.5	0
10–12	0.5	0
12–14	1	0.1
14–16	1	0.5
16–18	1	1
18–20	1	1
20–22	1	1
22–24	1	1
24–26	1	1
26–28	0.5	0.5
28–30	0.5	0.1
30–32	0.1	0
>32	0.1	0
Predominant substrate		
Mud	1	0.5
Sand	0.1	0.1
Gravel	0.1	0
Rock	0	0
Shell	0	0.5
Vegetation	1	1

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[a] References used for model development: Abraham (1985); Bigelow and Schroeder (1953); Card et al. (1981); MacDonald et al. (1984); Scott and Scott (1988); Stickney (1959); Targett and McCleave (1974).

[b] Plus sign signifies above mean low tide.

TABLE A.6.—Winter flounder.[a]

Variable	Suitability index			
	Adult	Spawning–egg	Larva	Juvenile
Depth (m)				
Intertidal	0	0	0	0.5
MLT–3[b]	0.5	1	0.5	1
3–10	1	1	1	1
10–20	1	0.5	0.5	0.5
20–50	1	0	0	0.5
50–100	0.5	0	0	0.1
100–200	0.1	0	0	0
200–400	0	0	0	0
400–500	0	0	0	0
Salinity (‰)				
0–0.5	0	0	0	0
0.5–5	0	0	0	0.1
5–10	0.1	0	0	0.5
10–15	0.5	0.1	0.5	1
15–20	1	0.5	1	1
20–25	1	1	1	0.5
25–30	1	1	1	0.5
>30	1	1	0.1	0.1
Temperature (°C)				
<0	0	0.1	0	0
0–2	0	1	0	0.1
2–4	0.1	1	0.1	0.1
4–6	0.5	1	1	0.1
6–8	0.5	0.1	1	0.5
8–10	0.5	0	1	0.5
10–12	1	0	0.5	0.5
12–14	1	0	0.1	1
14–16	1	0	0	1
16–18	0.5	0	0	1
18–20	0.1	0	0	1
20–22	0	0	0	0.5
22–24	0	0	0	0.1
24–26	0	0	0	0.1
26–28	0	0	0	0.1
28–30	0	0	0	0
30–32	0	0	0	0
>32	0	0	0	0
Predominant substrate				
Mud	0.1	0.1	0.5	0.1
Sand	1	1	1	1
Gravel	1	1	1	1
Rock	0.5	0.1	0.5	0.5
Shell	0.1	0.1	0.1	0.1
Vegetation	0.5	0.1	0.5	0.5

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[a] References used for model development: Bigelow and Schroeder (1953); Buckley (1982, 1989); Casterlin and Reynolds (1982); Fefer and Schettig (1980); Fried (1973); Gray (1990); Langton et al. (1989); MacDonald et al. (1984); McCracken (1963); Reynolds and Casterlin (1985); Rogers (1976); Stickney (1959); Scott (1982); Scott and Scott (1988); Targett and McCleave (1974); Tyler (1971a, 1971b); Van Guelpen and Davis (1979); Witherell and Burnett (1993); L. Mercer, Maine Department of Marine Resources, personal communication; R. Langton, Maine Department of Marine Resources, personal communication.

[b] MLT = mean low tide.

TABLE A.7.—American lobster.[a]

Variable	Suitability index[b] Adult	Larva	Juvenile
Depth (m)			
(+)3–(+)2	0	0	0
(+)2–(+)1	0	0	0.1
(+)1–0	0	0	0.5
mlt-3	0.5	0.5	1
3–10	1	1	1
10–20	1	0.1	1
20–50	1	0	1
50–100	1	0	1
100–200	1	0	0.5
200–400	0.5	0	0.5
400–500	0.5	0	0.1
Salinity (‰)			
0–0.5	0	0	0
0.5–5	0	0	0
5–10	0	0	0
10–15	0	0	0
15–20	0.1	0	0.1
20–25	0.5	0.5	0.5
25–30	0.5	1	0.5
>30	1	1	1
Temperature (°C)			
<0	0.1	0	0.1
0–2	0.1	0	0.1
2–4	0.1	0	0.1
4–6	0.5	0	0.5
6–8	1	0	0.5
8–10	1	0.1	1
10–12	1	0.5	1
12–14	1	0.5	1
14–16	0.5	1	1
16–18	0.5	1	0.5
18–20	0.5	1	0.5
20–22	0.5	0.5	0.5
22–24	0.5	0.1	0.5
24–26	0.5	0	0.5
26–28	0.1	0	0.1
28–30	0.1	0	0.1
30–32	0	0	0
>32	0	0	0
Predominant substrate			
Mud	0.5	0.1	0.1
Sand	0.5	0	0.1
Gravel	1	1	1
Rock	1	0.5	1
Shell	0.1	0.5	0.5
Vegetation	0.5	0.5	0.5

[a] References used for model development: Able et al. (1988); Aiken and Waddy (1986); Barshaw and Bryant-Rich (1988); Berrill and Stewart (1973); Botero and Atema (1982); Boudreau et al. (1990); Campbell (1990, 1992); Charmantier et al. (1988); Cobb and Wahle (1994); Dibacco and Pringle (1992); Ennis (1986); Fefer and Schettig (1980); Fogarty and Lawton (1983); Harding (1992); Hudon and Lamarch (1989); Incze and Whale (1991); Johns and Mann (1987); Junio and Cobb (1992); Jury et al. (1994); Karnofsky et al. (1989a, 1989b); Krouse (1973, 1981); Lawton and Lavalli (1995); MacKenzie and Moring (1985); McCleese (1956); McCleese and Wilder (1958); Pottle and Elner (1982); Reynolds and Casterlin (1985); Scarrat and Raine (1967); Stickney (1959); Thomas (1968); Wahle (1993); Wahle and Steneck (1992).

[b] Plus signs represent above mean low tide.

TABLE A.8.—Softshell clam.[a]

Variable	Suitability index[b] Adult–juvenile	Spawning
Depth (m)		
(+)3–(+)2	0.5	0.5
(+)2–(+)1	1	1
(+)1–0	1	1
0–1	1	1
1–2	0.5	0.5
2–3	0.1	0.1
3–4	0.1	0.1
4–5	0	0
5–10	0	0
10–20	0	0
20–50	0	0
50–100	0	0
100–200	0	0
200–400	0	0
400–500	0	0
Salinity (‰)		
0–0.5	0	0
0.5–5	0	0
5–10	0	0
10–15	0.1	0.1
15–20	0.5	0.5
20–25	1	1
25–30	1	1
>30	1	1
Temperature (°C)		
<0	0.1	0
0–2	0.1	0
2–4	0.1	0
4–6	0.1	0
6–8	0.1	0
8–10	0.5	0
10–12	0.5	0
12–14	1	0.5
14–16	1	1
16–18	1	1
18–20	1	1
20–22	0.5	1
22–24	0.1	0.5
24–26	0	0
26–28	0	0
28–30	0	0
30–32	0	0
>32	0	0
Predominant substrate		
Mud	1	1
Sand	0.5	0.5
Gravel	0.1	0.1
Rock	0.1	0.1
Shell	0.1	0.1
Vegetation	0.1	0.1

[a] References used for model development: Appledorn (1983); Arbuckle (1982); Brousseau (1978); Card et al. (1981); Creaser and Clifford (1977); Fefer and Schettig (1980); Hawkins (1994); Newell and Hidu (1986); Ropes and Stickney (1965); Stickney (1959); C. Heinig, MER Assessment Corporation, personal communication.

[b] Plus signs represent above mean low tide.