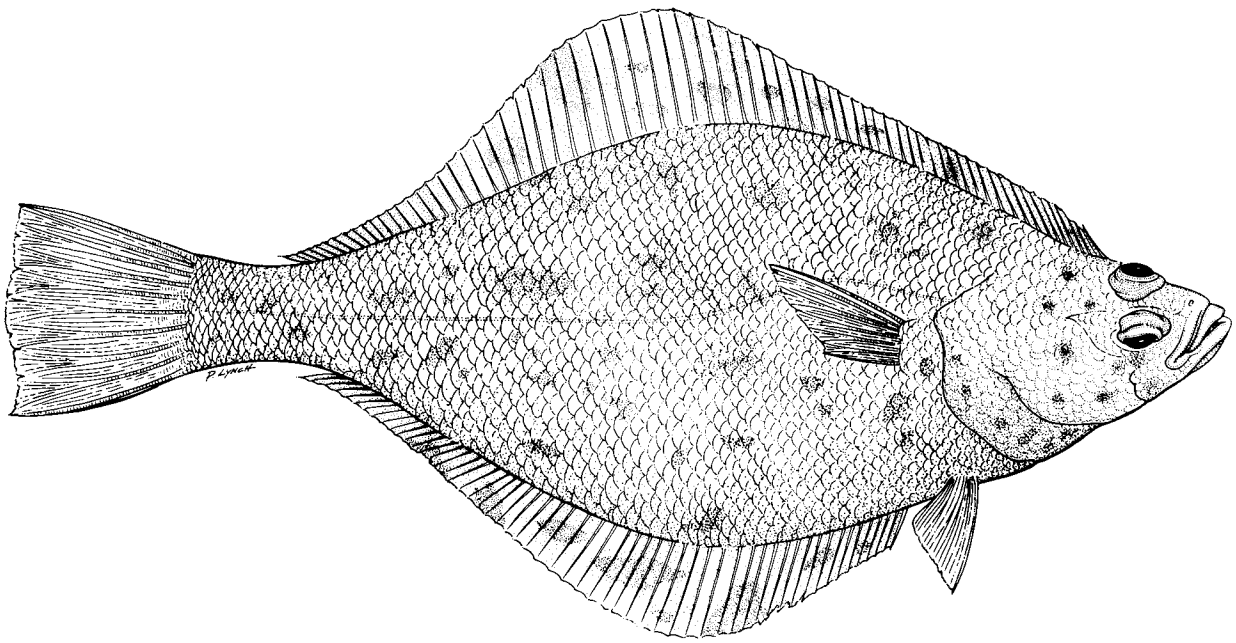
BIOLOGICAL REPORT 82(10.133)
FEBRUARY 1987

HABITAT SUITABILITY INDEX MODELS: JUVENILE ENGLISH SOLE



Fish and Wildlife Service

U.S. Department of the Interior

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February 1987

HABITAT SUITABILITY INDEX MODELS: JUVENILE ENGLISH SOLE

by

Christopher L. Toole
University of California Cooperative Extension
Sea Grant Marine Advisory Program
Foot of Commercial St.
Eureka, CA 95501

and

Roger A. Barnhart
U.S. Fish and Wildlife Service
California Cooperative Fishery Research Unit
Humboldt State University
Arcata, CA 95521

and

Christopher P. Onuf
U.S. Fish and Wildlife Service
National Wetlands Research Center
1010 Gause Boulevard
Slidell, LA 70458

Performed for
National Wetlands Research Center
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

This report may be cited as:

Toole, C.L., R.A. Barnhart, and C.P. Onuf. 1987. Habitat suitability index models: juvenile English sole. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.133). 27 pp.

PREFACE

The juvenile English sole habitat suitability index (HSI) model is intended for use in the habitat evaluation procedures (HEP) developed by the U.S. Fish and Wildlife Service (1980) for impact assessment and habitat management. The model was developed from a review and synthesis of existing information and is scaled to produce an index of habitat suitability between 0 (unsuitable habitat) and 1 (optimally suitable habitat). Assumptions involved in developing the HSI model and guidelines for model applications, including methods for measuring model variables, are described.

This model is a hypothesis of species-habitat relations, not a statement of proven cause and effect, and has not been field tested. For this reason the U.S. Fish and Wildlife Service encourages model users to convey comments and suggestions that may help increase the utility and effectiveness of this habitat-based approach to fish and wildlife management. Please send any comments or suggestions to the following address:

Information Transfer Specialist
National Wetlands Research Center
U.S. Fish and Wildlife Service
1010 Gause Blvd.
Slidell, LA 70458.

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ACKNOWLEDGMENTS

The authors wish to thank Gregor Cailliet, Moss Landing Marine Laboratories, Moss Landing, California; Perry Herrgesell, California Department of Fish and Game, Stockton; and William Pearcy, Oregon State University, Corvallis, for valuable comments on an earlier draft of this report. Other reviewers of the model were U.S. Fish and Wildlife Service personnel from the Ecological Services Field Offices of Sacramento, California, and Portland, Oregon. Christopher Dewees, Elizabeth Strange, and Debbie Marshall of the University of California Cooperative Extension assisted with the initial literature search and literature compilation. Word processing was provided by Mrs. Delores Neher of the California Cooperative Fishery Research Unit. A portion of this work was performed under grant number NA80AA-D-00120 through the Department of Commerce National Sea Grant College Program and through the California State Resources Agency, project number A/EA-1. Other funding was provided by U.S. Fish and Wildlife Service. Patrick J. Lynch illustrated the cover.

ENGLISH SOLE (Parophrys vetulus)

INTRODUCTION

English sole (Parophrys vetulus) is one of the major commercial groundfish species caught along the Pacific coast. Landings in the United States and Canada averaged 4,947 t/yr between 1975 and 1984, placing it third in importance among flatfish caught by Pacific coast trawlers (Pacific Marine Fisheries Commission 1985). Juvenile English sole are also among the most abundant fishes in many bays and estuaries along the Pacific (Westrheim 1955; Sopher 1974; Ambrose 1976; Rogers 1985). The English sole is not an important recreational species.

Distribution

English sole are found from San Cristobal Bay, Baja California, to Unimak Island, Alaska (Miller and Lea 1972; Hart 1973; Knaggs et al. 1976). Adults have been caught at depths of 550 m (Hart 1973), but are most common at depths between 40 and 150 m (Forrester 1969a; Demory et al. 1976; Pearcy 1978). Juveniles (0- and 1-age fish) are common in intertidal and subtidal waters of bays and estuaries from Elkhorn Slough, California, to at least Grays Harbor, Washington (Villadolid 1927; Westrheim 1955; Smith and Nitsos 1969; Olson and Pratt 1973; Samuelson 1973; Pearcy and Myers 1974; Sopher 1974; Ambrose 1976; Misitano 1976, 1977; Collins 1978; Hulberg and Oliver 1979; Toole 1980; Bayer 1981; Barry 1982; Rosenberg 1982; Yoklavich 1982; Rogers 1985; Krygier and Pearcy 1986). They are apparently not common in embayments south of Monterey (Fierstine et al. 1973; Horn 1980). In northern Washington and British Columbia juvenile English sole are common in shallow protected inland coastal areas (Ketchen 1956; Allen et al. 1959; Kendall 1966; English 1967; Alderdice and Forrester 1968; Forrester 1969a; Van Cleve and El-Sayed 1969; Moulton et al. 1974; Simenstad et al. 1977; Thornburgh 1978; Westrheim et al. 1981; Stocker et al. 1981; Fargo et al. 1982, 1983). Juveniles are also distributed in shallow waters in open coastal areas of Oregon and Washington (Laroche and Holton 1979; Rosenberg 1982; Rogers 1985; Krygier and Pearcy 1986).

Tagging and meristic studies indicate that at least eight separate stocks of English sole exist along the Pacific coast (Ketchen 1950; Ketchen and Forrester 1955; Van Cleve and Pruter 1956; Ketchen 1956; Forrester 1969b; Holland 1969; Jow 1969; Pattie 1969; Barss 1976; Day 1976). Stocks are currently separated for management purposes according to the International North Pacific Fisheries Commission geographical regions which, in some cases, may encompass two or more localized stocks (Pacific Fishery Management Council 1982).

Life History Overview

Measurements are of total length throughout this report unless indicated otherwise. Female English sole are usually mature at 3 years of age and 26-35 cm long. Median length at maturity has been reported as 29.5-31 cm. Males may mature when 2 years of age and 21-29 cm long. Median length at maturity is about 22-23 cm (Ketchen 1947; Harry 1959; Allen and Forrester 1966; Forrester 1969a).

Fecundity ranges from 150,000 eggs for 30 cm fish, 3 years of age, to 1.95 million eggs for 43.7 cm fish, 10 years of age. Fish of average size in the Strait of Georgia commercial fishery (33-38 cm, ages 4-6) produce between 0.5 and 1.0 million eggs (Ketchen 1947).

The spawning period in English sole is highly protracted and variable. Some spawning may occur in all months, but the peak season is September through April (Budd 1940; Ketchen 1956; Harry 1959; Jow 1969; Laroche and Richardson 1979). Examination of ovaries does not indicate serial spawning, so the protracted spawning season is probably due to the spawning of different individuals at different times (G. Hewitt, pers. comm., cited in Kruse and Tyler 1983). Kruse and Tyler (1983) showed that the spawning season is strongly correlated with bottom temperature and upwelling patterns, but the exact method of control was not determined. Hayman et al. (1980) showed a strong correlation between fall upwelling patterns and resulting cohort strength. They hypothesized that when upwelling persists into the fall, nearshore bottom temperatures are reduced, egg maturation is slowed, spawning is delayed, and larvae are ready to feed closer to the time of spring upwelling when feeding conditions are presumably more favorable.

Eggs are pelagic and hatch in 3.75 days at 13 °C to 11.8 days at 4 °C (Budd 1940; Ketchen 1956; Alderdice and Forrester 1968; Orsi 1968). Hatching rate is also dependent on salinity and dissolved oxygen levels (Alderdice and Forrester 1968). Embryology and larval development have been described by Budd (1940), Orsi (1968), and Ahlstrom and Moser (1975).

Duration of the pelagic larval phase was estimated at 6-10 weeks by Ketchen (1956) based on the time between peak spawning of adults and the appearance of transforming larvae in shallow waters. Laroche and Richardson (1979) estimated that this phase lasted about 18-22 weeks based on analysis of larval length frequency modes followed through time, but Laroche et al. (1982) corrected this to 8-10 weeks based on a later analysis of otolith-estimated age. During this time, larvae grow from approximately 2.8 mm standard length (SL) at hatching to 18-22 mm SL, the size at which metamorphosis to the benthic form occurs (Ahlstrom and Moser 1975; Misitano 1976; Laroche and Richardson 1979). Growth rate and feeding during the larval phase have been described by Laroche et al. (1982) and Gadomski and Boehlert (1984), respectively. Growth rate during metamorphosis has been described by Rosenberg and Laroche (1982).

Early stage larvae are rarely found in shallow water nursery areas, although some have been found throughout the brackish water areas of San Francisco Bay (P. Herrgesell, California Department of Fish and Game,

Stockton; pers. comm.) Transforming larvae (stages IV and V of Shelbourne 1957) and recently settled juveniles are common (Westrheim 1955; Ketchen 1956; Kendall 1966; Smith and Nitsos 1969; Van Cleve and El-Sayed 1969; Eldridge and Bryan 1972; Olson and Pratt 1973; Pearcy and Myers 1974; Simenstad et al. 1977; Misitano 1976, 1977; Thornburgh 1978; Laroche and Holton 1979; Toole 1980; Bayer 1981; Rosenberg 1982; Rosenberg and Laroche 1982; Rogers 1985). Transport of larvae into nursery grounds is poorly understood, although winter-spring oceanic onshore transport processes, such as those described by Wyatt et al. (1972) and Parrish et al. (1981), may bring them into nearshore areas, and "selective tidal transport," defined as the movement of young fish off the bottom during flood tides, may effect their movement into embayments (Pearcy and Myers 1974; Rogers 1985; Krygier and Pearcy 1986; Boehlert and Mundy, unpubl. MS.).

Growth rates of juveniles in both estuarine and nearshore nursery areas have been described by Westrheim (1955), Kendall (1966), Smith and Nitsos (1969), Van Cleve and El-Sayed (1969), Rosenberg (1982), Yoklavich (1982), Rogers (1985), and Krygier and Pearcy (1986). Growth rates of juveniles raised under laboratory conditions have been described by Williams and Caldwell (1978). Reported growth rates vary considerably, depending on location of the study and analytical methods. In those studies where the same methods were used to compare two areas, Rosenberg (1982) and Krygier and Pearcy (1986) found no significant differences between growth rates of juvenile English sole from Yaquina Bay and those from a nearshore open coastal area, while Rogers (1985) found that fish from an offshore nursery area in Washington had a higher growth rate than those from Grays Harbor. He noted, however, that his estimates were probably biased by emigration of the largest juveniles in the estuary to offshore areas.

Embayments appear to be important rearing areas for juvenile English sole. Using a Peterson mark-recapture estimate, Misitano (1970) determined that more than 100,000 juveniles were in the channels of Humboldt Bay in September, 1969. Sole out-migration was already in progress at that time. Using catch-per-effort data, Rogers (1985) calculated total juvenile English sole populations of 4.8 million in 1983 and 10.9 million in 1984 in the 8,500 ha of Grays Harbor. In the adjacent offshore study area, which spanned about 70 km of the coastline and was 18 times the Grays Harbor area, the total juvenile English sole population was 3.0 million in 1983 and 16.6 million in 1984. In a survey of the shallow waters off the Oregon coast between Tillamook Bay and the Umpqua River estuary, Krygier and Pearcy (1986) reported a total population of 64.3 million 0-age English sole in May-early June 1978, which declined by almost 90% to 7 million by the end of June. The total number of juvenile sole for five estuaries along the same 448 km stretch of coast was 14 million in May. The estuaries were not sampled again at the end of June; however, the results of other studies indicate that abundances either decline much less rapidly in estuaries at this time of year (approximately 50% in Grays Harbor [Rogers 1985]), change little (Yaquina Bay [Olsen and Pratt 1973]), or even increase (Yaquina Bay [Westrheim 1955]). Assuming a 50% reduction in abundance within the estuaries, the same number of 0-age sole were in estuaries as offshore by the end of June 1978 in Krygier and Pearcy's (1986) study area. This analysis suggests that estuaries and embayments may provide rearing habitat for half the juvenile English sole population, at

least between the Umpqua estuary, Oregon, and Grays Harbor, Washington, while occupying only about 5% of the area in which juveniles are found offshore. Observations offshore of Yaquina Bay on the incidence of infection by parasites that can only develop during estuarine residence led Olson and Pratt (1973) to conclude that virtually all English sole surviving their first year had reared in the estuary.

No data are available to make offshore-estuary comparisons for the remaining four-fifths of the Pacific coast where English sole are common. Some documented estuarine rearing areas such as Elkhorn Slough, San Francisco Bay, and Humboldt Bay are present along this part of the coast. However, relatively long stretches are devoid of suitable estuarine rearing areas, possibly increasing the proportionate contribution of offshore rearing.

Most English sole leave shallow water nursery areas and emigrate to deeper waters during the fall of their first year at an average size of 110-150 mm, although some 1-age fish remain in the nursery areas through the winter (Westrheim 1955; Ketchen 1956; Olson and Pratt 1973; Samuelson 1973; Sopher 1974; Ambrose 1976; Simenstad et al. 1977; Rogers 1985). When English sole reach deeper water their movements become fairly localized, although there is evidence that adults make seasonal inshore-offshore migrations and that a small proportion of the population makes extensive coastal movements (Ketchen 1950; Ketchen and Forrester 1955; Van Cleve and Pruter 1956; Ketchen 1956; Alverson 1960; Forrester 1969b; Jow 1969; Pattie 1969; Barss 1976; Day 1976; Hewitt 1980).

Growth rates of adult English sole have been described by Manzer and Taylor (1947), Holland (1969), Van Cleve and El-Sayed (1969), Smith and Nitsos (1969), and Kreuz et al. (1982). Kreuz et al. (1982) demonstrated both seasonal and annual variations in growth rates within a single population. Variations were most strongly correlated with temperature. The maximum recorded age of English sole is 22 years (Leaman and Beamish 1984). The largest male recorded was 57 cm and the largest female 49 cm (Forrester 1969a).

Adult English sole are opportunistic feeders and prey on benthic mollusks, ophiuroids, polychaetes, crustaceans (particularly amphipods), squid, and small fish (Villadolid 1927; Forrester 1969a; Hilasky 1972; Pearcy and Vanderploeg 1973; Kravitz et al. 1976; Hulberg and Oliver 1979).

English sole are capable of hybridizing with starry flounder (Platichthys stellatus); the resulting offspring are known as forkline sole or (hybrid) sole (Inopsetta ischyra) (Aron 1958; Hart 1973).

SPECIFIC HABITAT REQUIREMENTS

Cover and Substrate

Rosenberg (1982) compared growth of English sole in estuarine and coastal areas and suggested that the primary value of estuaries for English sole is not abundant food and enhanced growth, but escape from predation. Kendall

(1966), Toole (1980), Bayer (1981), and Borton (1982) have described the use of intertidal habitats by recently metamorphosed English sole. Relatively few piscivorous fish have been collected intertidally with English sole and, in spite of possible increased predation by birds (Talent 1984), Toole (1980) hypothesized that intertidal areas give recently metamorphosed English sole protection from predation as well as decreased competition for food from larger flatfish in channels.

Misitano (1970) found that, among intertidal habitats, areas with mud and sparse eelgrass (Zostera marina) had the densest concentrations of English sole in Humboldt Bay. Phillips (1984), in reviewing the use of eelgrass beds by fish, noted that English sole are generally included among the eelgrass fauna and pointed out the advantages of this cover to juvenile fish. Bayer (1981), however, did not find English sole to be more abundant in eelgrass beds than on mud flats in Yaquina Bay. Borton (1982) also found no significant difference between catch per haul of 0-age English sole in eelgrass and sand habitats of Alki Point in Puget Sound. Toole (1980) found that juvenile English sole were common over an intertidal sand flat, but made no comparison with other habitats. Kendall (1966) also found English sole to be common in sandy intertidal areas.

Barry and Cailliet (1981) and Barry (1982) reported juvenile English sole from shallow marshes and tidal creeks in Elkhorn Slough, and noted that cover from plants and turbidity of the water helped to make this habitat ideal for juvenile fish rearing. The numbers of English sole reported from these habitats are very low, however, possibly because of the extremes of temperature and salinity. Chamberlain (in prep.) collected no juvenile English sole from salt marshes in Humboldt Bay.

In subtidal channels, larger piscivorous fish and marine mammals (Brown and Mate 1983) contribute to increased predation, but by virtue of the strong predominance of small, young fish in shallow embayments, the rate is probably lower than in offshore habitats. Rogers (1985) collected juvenile English sole over sand, silty sand, and mud bottoms, either bare or with varying types of epibenthic materials (e.g., shell hash, eelgrass). He found no obvious differences in abundance attributable to substrate or bottom cover. Similarly, surveys by Sopher (1974) and Ambrose (1976) indicate that trends in abundance at stations in Humboldt Bay and Elkhorn Slough are controlled by factors other than substrate.

Food

Recently metamorphosed English sole occur in intertidal and shallow subtidal sand, sand/eelgrass, and mud/eelgrass habitats, where they feed primarily on small epibenthic crustaceans such as calanoid and harpacticoid copepods and cumaceans (Simenstad et al. 1977; Toole 1980). At lengths of approximately 50-65 mm English sole begin to feed primarily on polychaetes and other infaunal organisms. English sole exceeding 85 mm rarely feed in intertidal areas (Toole 1980). In the subtidal channels of Elkhorn Slough and Humboldt Bay, larger English sole (generally between 70 and 150 mm) feed primarily on infaunal polychaetes and bivalves, but also on amphipods and a variety of other organisms (Ambrose 1976; Collins 1978). On the basis of

comparisons between available prey items and composition of prey organisms in stomach contents, juvenile English sole in estuarine channels are considered non-selective feeders (Collins 1978).

Analyses of stomach contents by Collins (1978) showed that English sole collected from stations near the entrance to Humboldt Bay consumed fewer species, smaller numbers, and lower volumes of prey than elsewhere in the bay. The percentage of English sole stomachs containing food times the percentage fullness of those stomachs averaged 38.4% for collections from the entrance channel, and densities of sole were low. Values for the other areas of the bay ranged from 61.6% to 77.6%, and averaged 69.7%. Also, densities of English sole were 1.5 to 5 times higher in these other areas of the bay. The substrate at stations near the entrance channel was shifting gravel and coarse sand. The reduced suitability of the entrance channel as a feeding environment was attributed to sediment instability rather than to the coarseness of the sediment, because at one sampling area with an even coarser but stable substrate, densities and stomach fullness were the highest sampled anywhere in the bay. Benthic samples collected by Boyd et al. (1975) and analyzed by principal components analysis by Collins (1978) demonstrated that the entrance channel of Humboldt Bay, with its coarse shifting sediments and high current velocities, has sparse populations of invertebrate species consumed by juvenile English sole. Gravel and coarser materials alone can reduce suitability when they are the dominant substrate types, however, as reported by Rogers (1985) for offshore sampling.

Temperature

High water temperatures are important in limiting the growth and production of English sole. Sopher's (1974) lowest abundance stations for English sole in Humboldt Bay had summer bottom temperatures between 16.7 and 20.3 °C, while bottom temperatures at his highest abundance stations were 13.9-17.3 °C. Yoklavich (1982), using Ambrose's (1976) distributional analysis of English sole in Elkhorn Slough and records of temperatures during the same period (Nybakken et al. 1977), noted that the fish tended to avoid waters which warmed to 17-20 °C. Barry (1982) also found relatively few juvenile English sole in marshes and tidal channels of Elkhorn Slough, which often have summer temperatures exceeding 18 °C (G. Cailliet, Moss Landing Marine Laboratories, Moss Landing, California; pers. comm. 1985).

Yoklavich's (1982) laboratory experiments showed that growth rates at 17 °C were reduced 30% below growth rates at 13 °C. Similarly, Williams and Caldwell (1978) found in laboratory experiments that growth of juvenile English sole slowed 28%-47% at 18 °C compared to growth at 15 °C, and stopped completely at 21 °C. Stober et al. (1971) and Ames et al. (1978) found the mean upper lethal temperatures to be between 25.7 and 27.0 °C when juvenile and adult English sole were subjected to a gradual rise in temperature.

High water temperatures also may be implicated in increased mortality caused by parasitism. Olson (1976, 1981) has documented temperature dependence in the infection of English sole by the microsporidean protozoan Glugea stephani. The upper estuary is the only part of Yaquina Bay where

water temperature appreciably exceeds that of the ocean, and this is where juveniles become infected. Approximately 17% of infected fish die (Olson 1976).

Low temperatures encountered in estuaries are probably not limiting. In Humboldt Bay, most English sole emigrate to offshore waters in the fall when bottom temperatures range from 12 to 16 °C; however, some English sole remain in the bay all winter and are found at stations where bottom temperatures are as low as 9.4 °C (Sopher 1974). Ambrose (1976) was not able to correlate the emigration of English sole from Elkhorn Slough with marked changes in temperature. Although he found no English sole at any stations between November and January, the lowest temperature at any station during that time was 11.5 °C (Nybakken et al. 1977). Rogers (1985) found juvenile English sole at offshore stations with bottom temperatures as low as 7.6 °C. Mean bottom temperatures in the offshore nursery area ranged from 9.2 to 11.3 °C.

Salinity

Olson and Pratt (1973) considered salinity to be the major factor explaining the low density of English sole in the upper estuary of Yaquina Bay versus the high density in the lower estuary. The lower estuary had bottom salinities ranging from 25 to 35 ppt while the upper estuary had extremely variable salinities ranging from 0 to 34 ppt. Densities of English sole in the lower estuary averaged 9-120 times greater than upper estuary stations during April-October and 3-10 times greater during November-March.

Rogers (1985) collected English sole in Grays Harbor at salinities ranging from 15 to 34 ppt. Over the whole April to October sampling period in 1983, density was not different among the three sampling areas where mean salinity exceeded 23 ppt, but density was 63% lower in the one sampling area where mean salinity was <23 ppt.

In Humboldt Bay, bottom salinities at Sopher's (1974) stations with the lowest numbers of English sole ranged from 21.8 to 29.3 ppt during the rainy season of October-March and from 31.7 to 32.9 ppt during April-September. In contrast, stations with highest sole abundance ranged from 27.4 to 31.9 ppt during the rainy season and from 31.8 to 33.8 ppt during the remainder of the year. Catch per effort was approximately three times greater at high sole abundance stations than at the low sole abundance stations.

Ambrose (1976) never encountered salinities below 25.9 ppt at any of his stations in Elkhorn Slough (Nybakken et al. 1977), and no correlations between salinity and catch of English sole are apparent. Analysis of the numbers of English sole versus salinity at stations in Netarts Bay, Oregon, also showed no obvious correlations between salinity and catch (W. Pearcy, College of Oceanography, Oregon State University, Corvallis; pers. comm. 1986).

Dissolved Oxygen

Levings (1980) demonstrated the response of adult English sole to changes in dissolved oxygen under natural conditions. A normal density was maintained

until dissolved oxygen dropped below about 3 mg/l. English sole density continued to decline as dissolved oxygen decreased, until all English sole had either left the area or died by the time dissolved oxygen reached 1.0 mg/l. It was unknown whether the English sole were physically impaired by low dissolved oxygen levels or left the areas as their infaunal prey items died. Stations containing English sole outside of the oxygen-depleted area had dissolved oxygen levels up to 6.0 mg/l.

Special Considerations

In discussing declines in the commercial fishery for English sole in the Strait of Georgia, Ketchen et al. (1983) proposed that pollution of the intertidal and shallow subtidal habitats occupied by 0- and 1-year age group fish may have increased the mortality of these juveniles and reduced recruitment to the fishable stocks. Cancerous tumors were noted in English sole over 50 years ago (Pacis 1932), and in recent years a large body of literature has developed regarding the possible causes, mechanisms of transmittal, and degree of mortality associated with the condition (e.g., Angell et al. 1975; Stitch et al. 1976; Varanasi and Gmur 1981; Krahn et al. 1984; Malins et al. 1984). Carcinogenic agents most closely examined in recent studies were hydrocarbon derivatives.

Stitch et al. (1977) demonstrated that the incidence of skin tumors on juvenile English sole in the Strait of Georgia is inversely related to distance from major urban centers, the proposed sources of carcinogenic contamination. However, other studies such as those of Cooper and Keller (1969) and Kelly (1971) in San Francisco Bay have not shown this relationship.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area and cover types. This model is designed to apply to juvenile English sole in estuaries and coastal lagoons year-round. The use of estuarine areas by juvenile English sole begins with the immigration of metamorphosing postlarvae and recently metamorphosed juveniles in late winter and spring and ends with the emigration of most juveniles in the fall. Small numbers overwinter in estuaries and emigrate the following spring. The major area of application is along the Pacific coast from central California to northern Washington. Marsh and marsh creek habitat are used to such a minor extent (Barry and Cailliet 1981; Barry 1982; Chamberlain, in prep.) that they are excluded from consideration in this model.

Minimum habitat area. This is defined as the minimum area of contiguous suitable habitat required for a species to successfully live and reproduce. No attempt has been made to establish a minimum habitat area for English sole because they must migrate between inshore nursery areas and offshore spawning grounds. This model only applies to estuarine nursery areas.

Verification level. This model has not been verified in the field. It is based upon existing information documented in the literature; however, none of

the studies examined were designed to compare different habitats within an estuary in the comprehensive manner addressed in this model. Adjustments to the model will undoubtedly be required if adequate field tests are conducted.

The following biologists have reviewed this model for accuracy and applicability to various areas of the Pacific coast: Gregor Cailliet, Moss Landing Marine Laboratories; William Pearcy, Oregon State University College of Oceanography; and Perry Herrgesell, California Department of Fish and Game, Stockton. Their comments have been incorporated when feasible, but the authors are responsible for the final version of the model.

Model Description

Overview. The model is based upon the assumption that any environmental variable that has an impact on the growth, survival, distribution, or abundance of juvenile English sole can be expected to have an impact on the carrying capacity of its habitat. Juvenile English sole habitat is assumed to consist of two major life requisite components: food and water quality. Variables contributing to each of these components are described below and the relationships between habitat variables, habitat components, and habitat suitability are described in Figure 1. Cover was not included as a component in the model because the importance of cover in reducing predation and influencing the abundance of English sole has not been demonstrated in the existing literature.

Food Component. English sole are generalized benthic feeders. By the criteria of stomach fullness and density, the suitability of a site for English sole is positively correlated with prey abundance (Collins 1978); however, measurement of prey density is usually beyond the capabilities of a HEP assessment team and is only possible for baseline assessments. Where predictions of future conditions are required, the state of the food resource would have to be estimated in terms of responses to alterations in the

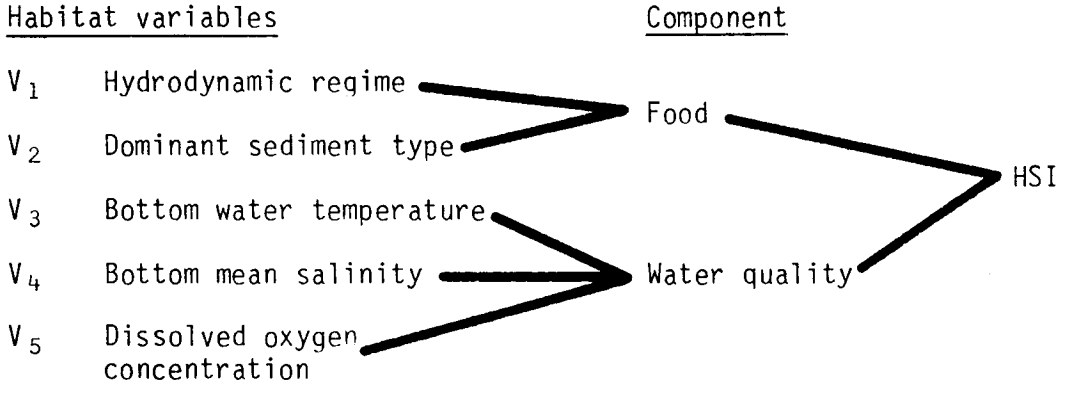


Figure 1. The relation of habitat variables, life requisite components, and the habitat suitability index (HSI) for juvenile English sole in estuaries and coastal lagoons.

physical environment. Water velocity and substrate type probably are the two most important factors influencing the food resource for English sole. The suitable ranges are broad. High water velocities can limit the food resource by making the substrate so unstable as to prevent the development of a dense benthic community (Collins 1978). Low velocities become limiting by not providing sufficient exchange of materials to support a dense benthic assemblage. Weak currents may also limit the accessibility of the interior parts of large systems such as San Francisco Bay. There, only in years when high freshwater inflow induces a countercurrent of marine water at the bottom, do substantial numbers of English sole get beyond the Central Bay (Armor and Herrgesell 1985). However, the actual velocities at which suitability diminishes have not been determined. High densities of food organisms and English sole have been found associated with substrates containing as much as 20% gravel (>2 mm diameter particles) (Collins 1978); but English sole densities were low where gravel or rocks predominated (Rogers 1985), presumably because prey either were not abundant or were not accessible. There is no indication of a decrease in suitability directly as a result of very fine sediments.

For the purposes of this model, it is sufficient to characterize the hydrodynamic regime in terms of the gross morphology and surficial characteristics of the estuary (V_1). The shifting deposits of the tidal deltas at the mouths of estuaries are low in suitability, as are any other areas where rapid erosion or deposition is occurring. At the other extreme, suitability is low in peripheral areas where tidal exchange is impeded or the turnover rate of the water is low, as in a deep cul-de-sac. In San Francisco Bay, it will also be necessary to take account of distance from the mouth. Results of the Bay-Delta study will allow quantification of this factor in the near future (P. Herrgesell, pers. comm.). The substrate variable (V_2) indicates the reduced suitability of areas with substantial amounts of gravel or rocks.

Water Quality Component. Water quality variables used for the English sole HSI model are bottom water temperature (V_3), bottom mean salinity (V_4), and dissolved oxygen concentration (V_5), all of which affect growth, survival, and abundance. Because of the high mobility of English sole and their ability to temporarily avoid suboptimal conditions, the duration of stressful high temperatures and low oxygen concentrations was regarded as more important than how stressful those conditions may be. Therefore, the temperature variable (V_3) was constructed as the number of months in which bottom mean temperature is high enough to reduce suitability and presumably induce avoidance, as inferred by Yoklavich (1982). The threshold for suboptimal temperature was selected as 15 °C, approximately midway between the highest temperature without and the lowest temperature with detectable effects on growth in the experiments of Williams and Caldwell (1978) and Yoklavich (1982).

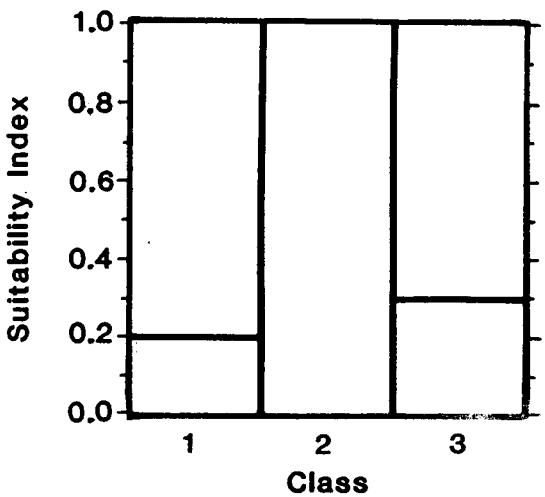
The oxygen variable (V_5) was constructed as the number of months in which the mean concentration was below the threshold level of 3 mg/l (Levings 1980). Note that this measure will overestimate suitability where anaerobic conditions cause a die-off of food organisms. In this case, unsuitable conditions will persist until prey populations recolonize, and an adjustment should be made.

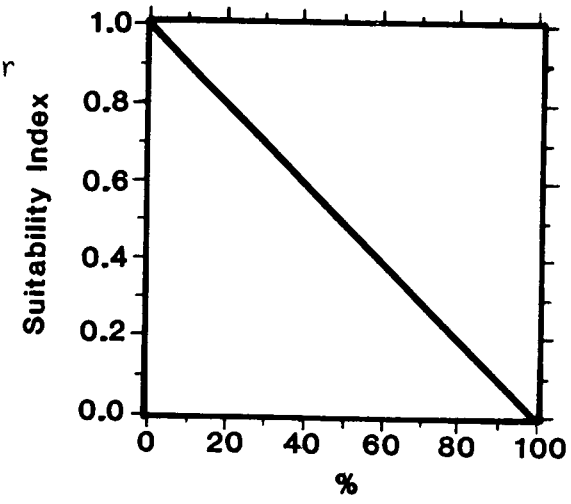
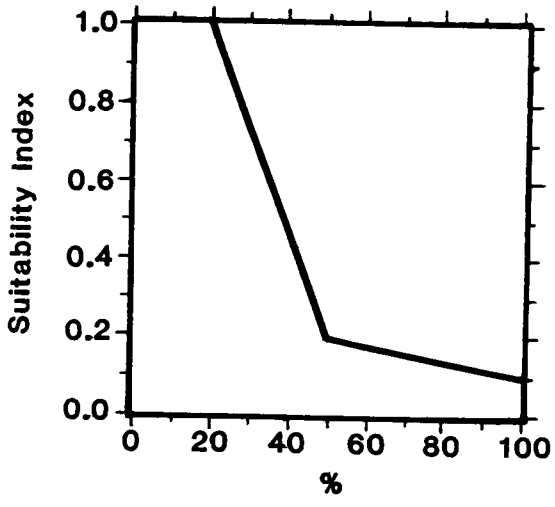
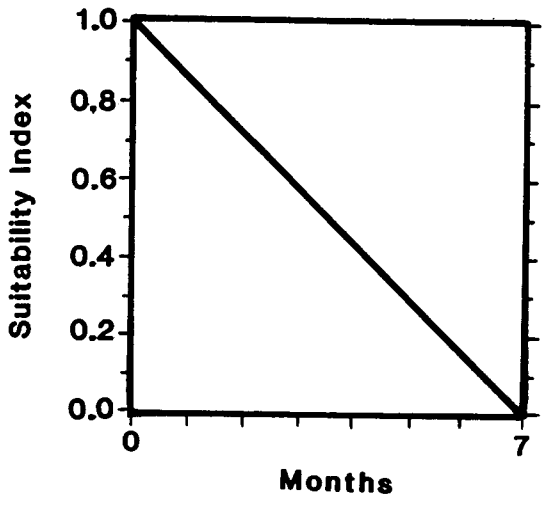
Classes 1 and 2 of the salinity variable (V_4) are based on data for Elkhorn Slough, California (Ambrose 1976; Nybakken et al. 1977), and Grays Harbor, Washington (Rogers 1985). We are aware of no reports of English sole from sites where mean salinity from April to October was <15 ppt and have defined Class 3 accordingly.

Distance from sources of environmental contaminants was not included as a variable because the clearest evidence of this relationship is based on a relatively large section of coastline (Stitch et al. 1977). Within a given estuary, this relationship has not been demonstrated (e.g., Cooper and Keller 1969; Kelly 1971; discussion in Angell et al. 1975).

Suitability Index (SI) Graphs for Model Variables

This section provides graphic representations of the relations previously described between the habitat variables (V_1-V_5) and estuarine (E) habitat suitability for juvenile English sole. An SI value of 1.0 indicates optimal conditions and a value of 0 indicates unsuitable conditions. Data sources and assumptions associated with documentation of the SI graphs are listed in Table 1.

Habitat	Variable		Suitability Graph
E	V_1	Hydrodynamic regime 1) High energy (tidal delta, areas of rapid erosion or deposition) 2) Intermediate energy (main body of estuary with stable substrates) 3) Low energy (peripheral areas with impacted tidal exchange or deep cul-de-sacs).	

Habitat	Variable		Suitability Graph
E	V_1*	Percent reduction in tidal range (alternative to V_1 for peripheral areas with impacted tidal exchange).	
E	V_2	Substrate composition - percentage by weight of a sample >2 mm in diameter.	
E	V_3	Water temperature - number of months of sub-optimal bottom temperature from April to October (mean temperature >15 °C).	

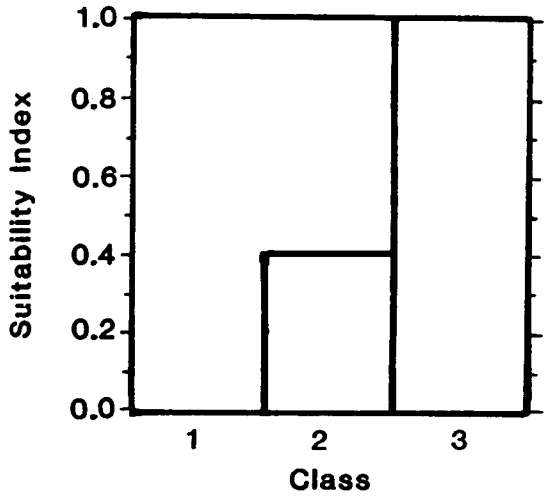
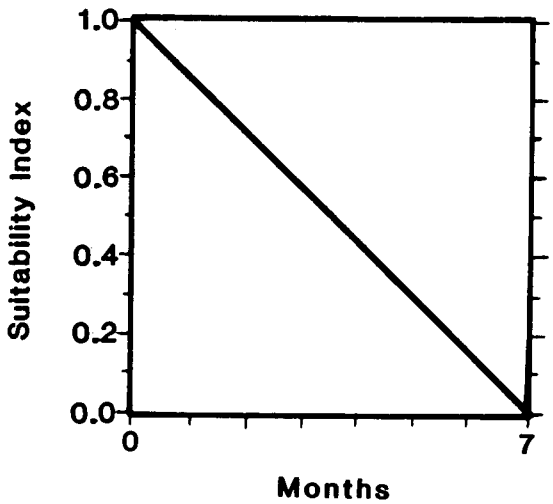
Habitat	Variable		Suitability Graph
E	V_4	Bottom mean salinity April to October 1) <15 ppt 2) 15-23 ppt 3) >23 ppt	
E	V_5	Dissolved oxygen concentration - number of months of suboptimal dissolved oxygen (mean dissolved oxygen <3 mg/l).	

Table 1. Data sources and assumptions for habitat variables included in the juvenile English sole HSI model.

Variable and source	Assumptions
V_1 Boyd et al. (1975) Collins (1978) G. Cailliet (pers. comm.) W. Pearcy (pers. comm.)	High energy areas are low in suitability because the substrate is not stable enough for a dense benthic assemblage to develop. Peripheral areas with impeded tidal exchange or low rates of turnover of water are low in suitability because the exchange

(continued)

Table 1. (Concluded)

Variable and source		Assumptions
V_1	(continued)	of materials is too slow to support a productive benthic community. Also, access by larval or weak-swimming young juvenile English sole may be impaired.
V_2	Boyd et al. (1975) Collins (1978) Rogers (1985)	Sediments with as much as 20% gravel were suitable by the criteria of stomach fullness and density of English sole. Densities were low where gravel and rocks were the dominant substrate type; however, even 100% gravel or coarser substrate is assumed to provide some food for English sole.
V_3	Stober et al. (1971) Sopher (1974) Ambrose (1976) Olson (1976) Nybakken et al. (1977) Ames et al. (1978) Williams and Caldwell (1978) Olson (1981) Barry (1982) Yoklavich (1982)	Infection by a parasite that only develops at water temperatures >15 °C can cause 17% mortality of English sole. Growth rates are 30%-50% less at temperatures >17-18 °C as compared to lower temperatures, and English sole avoid this range. Death occurs between 25.7 and 27.0 °C. Duration of suboptimal conditions is assumed to be more important than the severity of suboptimal conditions on the grounds that English sole are highly mobile, will avoid even moderately stressful temperatures, and can quickly return when temperatures cease to be stressful.
V_4	Nybakken et al. (1977) Rogers (1985)	On average, locations in Grays Harbor with mean salinities <23 ppt from April to October supported only 40% of the densities of English sole that higher salinity areas supported. In Elkhorn Slough, salinities <25 ppt were not observed, and densities at different sampling locations were not correlated with salinity.
V_5	Levings (1980)	Suitability is optimal with a dissolved oxygen concentration above 3 mg/l. Habitat is unsuitable at 1 mg/l. Duration of suboptimal conditions is assumed to be more important than the severity of suboptimal conditions for reasons described for V_3.

Component Index Equations and HSI Determination

The SI values for the habitat variables are combined so component scores for juvenile English sole can be obtained. The suggested equations for obtaining food or water quality values for juvenile English sole follow.

Component		Equation
Food (F)		V_1 or V_2, whichever is lower
	or	V_{1*} or V_2, whichever is lower
Water quality (WQ)		V_3, V_4, or V_5, whichever is lowest

HSI = F or WQ, whichever is lower

The equation for determining HSI is based on the limiting factor concept. No cumulative or compensatory relationships between variables are assumed.

Sample data sets from which HSI values have been generated are given in Table 2. Data set 1 represents a site on the tidal delta where the instability of the substrate is the limiting factor; data set 2, a site in the main body of the estuary where all conditions are satisfactory; and data set 3, a site in a shallow tributary embayment connected to the main stem of the estuary through a culvert, where the impairment of tidal exchange probably is the limiting factor, which in turn causes suboptimal conditions of salinity and temperature. Although the data sets are not actual field measurements, they do represent the kinds of values expected for estuarine habitats used by English sole. The HSI's calculated from these hypothetical data reflect the relative abundance of English sole in habitats with the characteristics listed in Table 2.

Field Use of the Model

Small (<85 mm) juvenile English sole are found in both intertidal and subtidal areas within bays and estuaries. The importance of intertidal areas for feeding and possibly refuge for small English sole has been described by Toole (1980). Large (85-140 mm) juvenile English sole are rarely found intertidally, consume different prey items, and exhibit different foraging strategies from small juveniles collected intertidally. Because intertidal and subtidal habitats play different but equally important roles in the ecology of juvenile English sole, they should be treated separately when applying this model. Losses of shallow water habitat (to 1 m below Mean Lower Low Water) can only be compensated by replacement or improvement of shallow water habitat. Similarly, losses in deep water habitat can only be compensated by replacement or improvement of subtidal areas.

The HSI model for English sole is simple. Nevertheless, it demands considerable field sampling. An application using all five variables requires at least monthly, and preferably more frequent, sampling of the water quality variables from April to October. Rarely, a university study or a major

monitoring program may provide the necessary information, but only if the timing and location of samples are appropriate. Extrapolation from outside the project area should not be considered except in consultation with experts.

Alternatively, the model can be applied using primarily aerial photography, maps, and existing data compilations. In this case, only Variables 1 and 2 would be evaluated. Field observations would be used to verify and update interpretations from these secondary sources. Applications scaled down in this fashion will sacrifice some resolution but will still be valid in our opinion, because the hydrodynamic regime is the driving force determining water quality in most instances. Thus, where water quality limits habitat suitability, some impediment to water exchange usually is responsible for the impairment of water quality. Close monitoring of water quality will yield a more precise determination of habitat suitability than hydrodynamic regime and substrate can provide by themselves, but this greater sensitivity may not always be necessary. The abbreviated version of the model is most likely to be in error at the southern end of English sole's geographic range, where limiting temperatures may not be adequately predicted by the hydrodynamic regime, and in areas receiving major allogenic discharges. Suggested methods for measuring the variables are presented in Table 3.

Interpreting Model Outputs

The proper interpretation of the English sole HSI is one of comparison. This model can be used to compare different habitats or the same habitat at different times. The habitat with the higher HSI should be the area that could potentially support more juvenile English sole.

Table 2. Calculations for food (F) and water quality (WQ) suitability indices (SI) and the habitat suitability index (HSI) for three sample data sets, using the juvenile English sole variables (V) and model equations.

Component	Data set 1		Data set 2		Data set 3	
	Data	SI	Data	SI	Data	SI
V_1	1	0.2	2	1.0	-	-
V_{1*}	-	-	-	-	70%	0.3
V_2	30%	0.73	10%	1.0	0%	1.0
V_3	0 mo	1.0	1 mo	0.86	3 mo	0.57
V_4	32 ppt	1.0	25 ppt	1.0	20 ppt	0.4
V_5	0 mo	1.0	0 mo	1.0	2 mo	0.72
F		0.2		1.0		0.3
WQ		1.0		0.86		0.4
HSI		0.2		0.86		0.3

Table 3. Suggested techniques for field measurements of variables used in the English sole HSI model.

Variable	Techniques
V_1	The shifting deposits of tidal deltas at the mouths of estuaries are evident in aerial photographs. Other areas subject to rapid erosion and depositions can be identified from time series of aerial photographs and by boaters familiar with the estuary. Areas with impeded tidal exchange or a low turnover rate of the water usually are the result of human activities. Look for linear features at the periphery of the estuary - causeways partially separating peripheral areas from the main body of the estuary, box-ended deep areas abutting the shore. For peripheral areas with impeded tidal exchange, an alternative, V_{1*} - percent reduction in the tidal range, provides a more precise criterion for evaluating suitability. It requires measurement of high and low water levels on a spring tide sequence inside and immediately outside the area of suspected impeded tidal exchange. The tidal range inside is expressed as a % of the tidal range outside.
V_2	Substrate samples can be obtained with an Ekman or a Ponar grab. Substrate composition can be determined from the proportion of known weight of substrate retained by a screen with 2 mm openings. If a graded series of sieves is used, an analysis for skewness will indicate areas of rapid erosion or deposition (Folk 1974). See V_1.
V_3	Bottom water temperatures can be obtained by using either a thermistor or a thermometer and a water sample collected with a water bottle (American Public Health Association et al. 1976).
V_4	Salinity can be measured by titration or by a refractometer, hydrometer, or conductivity meter (Strickland and Parsons 1968).
V_5	Dissolved oxygen can be measured by Winkler titration or with an oxygen meter (Strickland and Parsons 1968; American Public Health Association 1976).

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50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. Biological Report 82(10.133)	2.	3. Recipient's Accession No.

4. Title and Subtitle

Habitat Suitability Index Models: Juvenile English Sole

5. Report Date February 1987

6.

7. Author(s)

C.L. Toole, R.A. Barnhart, and C.P. Onuf

8. Performing Organization Rept. No.

9. Performing Organization Name and Address

U.S. Fish and Wildlife Service
California Cooperative Fishery Research Unit
Humboldt State University
Arcata, CA 95521

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.

(C)

(G)

12. Sponsoring Organization Name and Address

National Wetlands Research Center
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

A review and synthesis of existing information were used to develop a model for evaluating juvenile English sole habitat. The model is scaled to produce an index between 0 (unsuitable habitat) and 1 (optimal habitat) along the Pacific coast of North America from central California to southern British Columbia in estuaries and lagoons. Habitat suitability models are designed for use with the Habitat Evaluation Procedures previously developed by the U.S. Fish and Wildlife Service. Guidelines for model application and techniques for measuring model variables are provided.

17. Document Analysis a. Descriptors

Estuaries
Fishes
Habitat
Mathematical models

b. Identifiers/Open-Ended Terms

Habitat Suitability Index
Impact assessment
English sole
Parophrys vetulus

c. COSATI Field/Group

18. Availability Statement	19. Security Class (This Report)	21. No. of Pages
Unlimited	Unclassified	27
	20. Security Class (This Page) Unclassified	22. Price

(See ANSI-Z39.18)

U.S. GOVERNMENT PRINTING OFFICE: 1987—761-070/40006

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce