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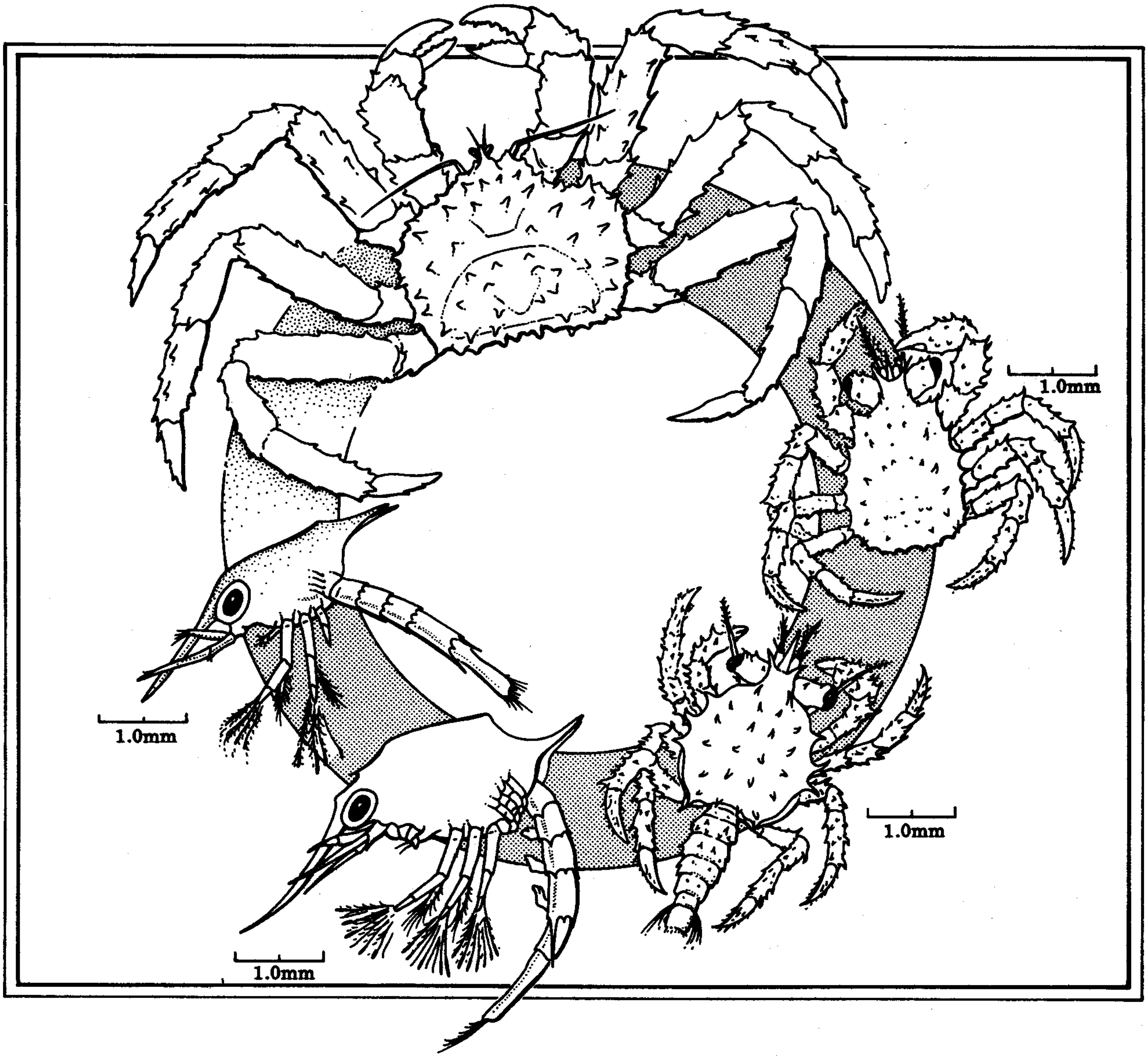

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Department of the Interior

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HABITAT SUITABILITY INDEX MODELS: RED KING CRAB

by

Stephen C. Jewett
Alaska Cooperative Fishery Research Unit
138 Arctic Health Research Building
University of Alaska
Fairbanks, AK 99775

and

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

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U.S. Department of the Interior
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Research and Development
National Wetlands Research Center
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PREFACE

This document is part of the habitat suitability index (HSI) model series and is designed for use with the U.S. Fish and Wildlife Service's (1980) habitat evaluation procedures in impact assessment and habitat management activities. The model was developed from a review and synthesis of existing information. It is not intended to be an exhaustive literature review. It is scaled to produce an index of habitat suitability between 0 (unsuitable habitat) and 1 (optimally suitable habitat). Model documentation and guidelines for model applications, including methods for measuring model variables, are provided.

Model documentation is provided for several reasons. First, it provides a means of explaining the model's structure and its inherent assumptions. Second, the model-building process involves considerable judgement on the part of the model builder, and documentation provides the insights necessary to modify the model when these judgements are inconsistent with local or new knowledge. Finally, the documentation should facilitate modification of the model to meet individual study constraints on time and human resources.

The model presented is a hypothesis of species-habitat relationships, not a statement of proven cause and effect. For this reason, users of the model are encouraged to suggest improvements that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife management. Please send suggestions to the following address:

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

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ACKNOWLEDGMENTS

The authors wish to thank Robert Otto and Bradley Stevens, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Kodiak, Alaska; A.J. Paul, University of Alaska, Institute of Marine Science, Seward; and Daniel Wickham, University of California, Bodega Marine Laboratories, Bodega Bay, for valuable comments on an earlier draft of this report. Evaluation of model structure and functional relationships was provided by personnel of the U.S. Fish and Wildlife Service's (FWS) National Wetlands Research Center and of the FWS Division of Ecological Services in Fairbanks and Juneau, Alaska. Funding was provided by U.S. Fish and Wildlife Service.

RED KING CRAB (Paralithodes camtschatica)

INTRODUCTION

The red king crab (Paralithodes camtschatica) belongs to the family Lithodidae and is one of three commercially exploited king crabs in the eastern North Pacific Ocean. Until recently this crab was the most valuable shellfish resource on Alaska's Continental Shelf. In the 1980-81 fishing season domestic fishermen harvested a record 81.6 thousand metric tons (t), which had an ex-vessel value of nearly $180 million. Landings plummeted annually thereafter to only 2.6 thousand t in 1985-86. In that season fishermen received only $14.8 million, even though the price per weight nearly tripled from 1980 to 1986 (Alaska Department of Fish and Game 1985a,b,c,d, 1986). Exact causes underlying the drastic decline of this species are unknown, although a combination of high natural mortality and variable year-class strength probably is involved (Otto 1986). Inadequate management practices are not blamed (Otto 1986). Possible causes for natural mortality are predation by Pacific cod (Gadus macrocephalus), Pacific halibut (Hippoglossus stenolepis), and yellowfin sole (Limanda aspera) on larval through adult life stages and by nemertean worms (Carcinonemertes spp.) on eggs (Armstrong 1983; Haflinger and McRoy 1983; Hayes 1983; Wickham et al. 1985; Blau 1986) and viral and microsporidan diseases (Sparks and Morado 1985) (see Fukuhara 1985 for a review on predation).

Distribution

The red king crab occurs on both sides of the North Pacific Ocean at depths <400 m. It is found from the Sea of Japan northward into the Sea of Okhotsk and along the shores of the Kamchatka Peninsula; the northern limit on the Asiatic coast is at Cape Olyutorskiy (60 °N latitude) (Vinogradov 1947). On the western coast of North America, the northern limit is Point Barrow, Alaska (71°25' N latitude) (MacGinitie 1955). The species occurs throughout the southeastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska to the southern limit off the Queen Charlotte Islands, British Columbia (54 °N latitude) (Butler and Hart 1962). A population of introduced red king crab also exists in the Barents Sea (Orlov and Ivanov 1978).

Historic major domestic fishery locations are Norton Sound in the northeast Bering Sea, the southeast Bering Sea, the Aleutian Islands, south of the Alaska Peninsula, near Kodiak Island, and Cook Inlet, while Prince William Sound and southeast Alaska support smaller fisheries (Alaska Department of Fish and Game 1985a,b,c,d). Major historic foreign fishing locations are on the west coast of the Kamchatka Peninsula, along Hokkaido and Sakhalin, and on the Japan Sea coast of the U.S.S.R. (Marukawa 1933; Vinogradov 1947). The commercial fishery is generally confined to depths <200 m. Adult king crab and those close to maturity use the deeper, offshore waters during most of the year; shallower waters (<50 m) are typically used during mating in the spring (Powell and Nickerson 1965a). Some deeper offshore areas (50-100 m) are also used for mating (McMullen 1967); however, the extent of offshore breeding is not known. Juveniles <4 years old (approximately 70-mm carapace length - CL) typically occur in depths <50 m (Powell and Nickerson 1965b; Sundberg and Clausen 1977; McMurray et al. 1984).

Life History Overview

Reproduction. Male red king crab are polygamous. Under confined conditions a male will mate with up to seven females annually (Powell et al. 1974). Under natural conditions the number of females mated by one male is unknown, although the sex ratio during the mating period suggests that one male may service as many as 11 females (McMullen 1967). The adult male to female ratio on the spawning grounds of outer Alitak Bay was 1:2 in May 1962 (Gray and Powell 1966) and 1:7 in March 1977 (Feder and Jewett 1977). Females mate annually with only one male (Powell and Nickerson 1965a). Adult males are typically larger than their female partners (Powell et al. 1973, 1974); however, no relationship between size of partners has been established. Reproductive activities (egg-hatching, female-molting, mating, and spawning) have been observed in shallow waters (<20 m) near Kodiak Island from January through June, but most activity is during March through May, specifically April (G. Powell, Alaska Department of Fish and Game [retired], Kodiak, pers. comm.; S. Jewett, pers. observ.). After egg hatching is nearly complete, each female is thought to chemically attract a male mate as lobsters do (Hughes and Mattiessen 1962). The male crab faces and grasps the female with his chelae at the base of her first appendage. This precopulatory embrace lasts anywhere from one to 16 days until the female molts (Powell et al. 1974). After the female molts, the male releases the cast shell, reclasps her, and spreads spermatophore bands (sperm) around her gonopores (genital openings). The male then releases her and she lays her eggs, depositing them externally on her abdomen. The eggs are fertilized externally as they emerge from the gonopores (Powell and Nickerson 1965a). Egg attachment to the abdominal pleopods occurs immediately upon extrusion (McMullen 1970).

Adult female red king crab typically produce a full clutch of eggs each year. The percentage of adult females carrying eggs near Kodiak Island in the fall of 1968 was 86.4%, with a range from 28% to 100% for different areas around the island (McMullen and Yoshihara 1969). Ovigerity among adult females in the southeastern Bering Sea was also examined for the years 1975-79 (Otto et al. 1980). The percentage of ovigerous females having a full clutch of eggs (defined as three-fourths full to full) exceeded 90 percent in four of five years, suggesting that clutch size was a stable population parameter.

Fecundity, measured within a few months after deposition, varies from 15,000 to nearly 447,000, depending on the area (Table 1). Incubation lasts 11 to 12 months before hatching begins (Haynes 1968).

Life stages. Red king crab pass through two distinct stages: a short pelagic stage and a long benthic stage. Upon hatching, the pre-zoeal larvae molt, usually within minutes, into the zoeal form (Weber 1967). The pelagic

Table 1. Fecundity of red king crab from various areas.

Area	No. of eggs	Carapace length, mm	Source
Hokkaido	62,500-345,900	118-158[a]	Nakazawa (1912)
Hokkaido	69,600-270,200	106-157[a]	Murukawa (1933)
Hokkaido	15,300-214,400	97-144[a]	Sato (1958)
S. Alaska Peninsula	148,300-446,600	128-145	Wallace et al. (1949)
Bristol Bay	55,400-444,700	85-162[a]	Rodin (1970)
Cook Inlet	30,000-390,000	100-170	Haynes (1968)

[a] Converted from carapace width after Wallace et al. (1949)

zoeae larvae molt through four stages, each lasting 2-4 weeks. A fifth larval stage is the semipelagic glaucothoe which lasts 3-4 weeks. The metamorphosis to first postlarval instar occurs 3-4.5 months after hatching (Marukawa 1933; Kurata 1960, 1961a,b; Weber 1967; Armstrong et al. 1981). Time of hatch within a region is not necessarily synchronous and multistage larval populations often occur simultaneously (Armstrong et al. 1981). Interannual timing of the onset of hatch and seasonal occurrence of pelagic larvae can vary by as much as 4-6 weeks (Armstrong et al. 1981; McMurray et al. 1984). A large interannual difference in apparent time of hatch in the southeastern Bering Sea was observed between the years 1976 and 1979. All larvae were Stage I zoeae in mid-May 1976, but all were Stage IV in mid-June 1979, indicating a very late and early hatch, respectively (Armstrong et al. 1981). This variability is presumably due, in part, to environmental conditions (mainly temperature) and timing of breeding among primiparous vs. multiparous females (Powell et al. 1973; Incze et al. 1986; Stevens and MacIntosh 1986). Larval densities in the southeastern Bering Sea are highest over bottom depths of 40-70 m, extending 20-50 km offshore along the Alaska Peninsula (Armstrong et al. 1981).

The benthic life stage may last 15 (McCaughran and Powell 1977) to 20 years (Kurata 1961b). By this age, crab are approximatey 220 mm CL and weigh approximately 10 kg (Wallace et al. 1949).

Growth. During pelagic development, growth of larvae is substantial, with increases from 0.2-0.3 mg dry weight as Stage I zoeae to >1.2 mg as glaucothoe (Armstrong et al. 1981). After settlement crab molt from 8 (Powell 1967) to 11 (Weber 1967) times in the first year. Between the end of the first year and the end of the third year, an additional eight molts occur; thereafter, typically only one molt a year occurs (Weber and Miyahara 1962; Weber 1967). Juveniles in the Kodiak Island vicinity and the southeastern Bering Sea reach about 11, 35, 60, and 80 mm CL at 1, 2, 3, and 4 years, respectively (Powell and Nickerson 1965b; Weber 1967; also see Incze et al. 1986 for size classes up to Age 6).

Red king crab are sexually mature at 5 to 6 years old or, depending on the area, between 60 and 112 mm CL (Tables 2 and 3). Maturity of males and females within an area is often attained at similar sizes. Based upon growth

Table 2. Size at maturity of red king crab from various areas.

Area	Carapace length, mm	Source
Kodiak Island	100[a]	Powell and Nickerson (1965a)
Pacific Ocean	93-112[b]	Wallace et al. (1949)
Sea of Nemuro	92- 96[a,c]	Marukawa (1933)
S.E. Bering Sea	85-102[a]	Wallace et al. (1949)
S.E. Bering Sea	90-105[a]	Weber (1967)
S.E. Bering Sea	76-105[b]	Otto et al. (1980)
Kamchatka Coast	78- 82[a]	Marukawa (1933)
W. Kamchatka	87- 92[b]	Matsuura et al. (1972)
Norton Sound	60- 79[b]	Powell et al. (1983)
Norton Sound	62- 82[b]	Stevens and MacIntosh (1986)

[a] Both sexes.
[b] Females only.
[c] Converted from carapace width after Wallace et al. (1949).

Table 3. Size at 50% maturity of female red king crab from various areas.

Area	Carapace length, mm	Source
Pacific Ocean	106	Wallace et al. (1949)
S.E. Bering Sea	97	Wallace et al. (1949)
S.E. Bering Sea	90- 97	Weber (1967)
S.E. Bering Sea	86- 90	Otto et al. (1980)
W. Kamchatka	80[a]	Matsuura et al. (1972)
Norton Sound	68	Powell et al. (1983)
Norton Sound	73	Stevens and MacIntosh (1986)

[a] Converted from carapace width after Wallace et al. (1949).

data obtained through tagging studies, the mean annual growth of adult male king crab near Kodiak Island (Powell 1967) and the southeastern Bering Sea (Weber and Miyahara 1962) is 20 and 16 mm CL, respectively. Simpson and Shippen (1968), however, maintained that since many of the larger crab do not molt annually, an average annual growth of 10 mm is more realistic for describing annual growth for the adult male population in the southeastern Bering Sea. Average annual growth for legal males in Norton Sound is 12.5 mm CL (Powell et al. 1983). Commercial size limits for the male-only fishery are set to ensure that males have two opportunities to mate before entering the fishery (Otto 1985). This measure serves to protect the reproductive potential of the population. Size at maturity within an area can be variable from year to year, presumably due to different environmental conditions. In the southeastern Bering Sea, Weber (1967) observed a change in the size at which 50% of females were mature from about 90 to 97 mm CL over 4 years. Otto et al. (1980) observed this value to vary from 86 to 90 mm CL over 5 years.

Growth models for the species have been developed by Weber and Miyahara (1962), Weber (1967), Balsiger (1974), McCaughran and Powell (1977), and Reeves and Marasco (1980). Growth data are also presented in Kurata (1961a,b) and Hayes and Montgomery (1963).

Mortality. Egg loss is closely related to the age of the eggs, trends in egg growth, structural changes in the embryo (Matsuura and Takeshita 1985), and egg predation (Wickham et al. 1985). Among laboratory-reared king crab, egg loss during incubation is reported to be 13%-24% in multiparous females (three individuals) and nearly 50% in a single primiparous female (Matsuura and Takeshita 1985). Matsuura and Takeshita (1985) noted that egg loss was greatest at the beginning of the incubation period, presumably due to unsuccessful egg attachment to the pleopods. Cumulative egg loss in a primiparous individual after 1 day, 5 days, and 3.5 months of incubation was 8%, 9%-20% and 50%, respectively. Egg loss appeared to decrease near the middle of the incubation period.

Egg mortality has recently been traced to predation by nemertean worms (Carcinonemertes). The number of nemerteans found in certain populations in the Gulf of Alaska represent the most massive infestation ever observed on any crab species (Wickham et al. 1985). Sample collections of red king crab were found with average densities up to 199 worms per 1,000 crab eggs; populations on individual crab reached over 250,000. Many populations have measured egg mortalities in excess of 90%. Populations from Cook Inlet lost their entire reproductive output by September, slightly more than halfway through their 11-month brooding period (Wickham et al. 1985). An annual survey by the Alaska Department of Fish and Game in September 1983 near Kodiak Island revealed that all adult females caught (n=341) were barren, having only empty egg cases attached to the pleopods (Blau 1986). This marked the first time in the 30 year history of Kodiak king crab research that a population of females around the island was found totally barren. Carcinonemertes was the major suspect for egg loss, but this was not corroborated.

Typically, at least 90% of the adult females carry a full clutch of eggs (see Reproduction section). However, in recent years the percentage of barren females may have increased in some areas (R. Otto, Northwest and Alaska Fisheries Center, Kodiak, AK; pers. comm.).

Cycles of abundance suggest that year-class success may depend on survival at a critical life stage such as the eggs, larvae, or young juveniles. However, the factors responsible for success are often unknown. The large year-classes of 1971 and 1978 in the southeastern Bering Sea were produced by two opposite extremes of adult female abundance (Incze et al. 1986). The large juvenile population observed during the middle 1970's led to abundant stocks of adults during the late 1970's. In contrast, the large year-class identified during 1982 did not show up in 1983, 1984, or 1985 (Incze et al. 1986). Year-class success is presumably related to water temperature. Long-term series temperature data are not available for the southeastern Bering Sea; however, such a series is available for the Gulf of Alaska (Royer 1985). During the 1971-84 period the water column temperature increased an average of 1.5 °C along the coast of the Gulf of Alaska (monitored at 59°50.8' N, 149°28' W) (Royer 1985).

The act of molting is physiologically stressing, and the high frequency of molting in the first few years could elevate mortality (Rice et al. 1985). Factors influencing molting rate, such as temperature, might therefore be responsible for some differences in year-class strength.

Instantaneous mortality rates of older juvenile and sublegal, sexually mature red king crab have been estimated to be low, about 10% per year until entering the fishery (Balsiger 1974; Reeves and Marasco 1980). Natural mortality for adult males (>135 mm CL) in the absence of a fishery generally increases with size to as high as 25% for crab of 170 mm CL (Hirschhorn 1966). Increased rates of natural mortality were undoubtedly the major cause of the recent recruitment failures in the southeastern Bering Sea, because the size limit and harvest quota on the fishery assured an adequate reproductive stock (Otto 1986).

Although one of the major mechanisms contributing to natural mortality is suspected to be predation, little specific information is available. An estimate of the magnitude of predation on larval red king crab is available in Haflinger and McRoy (1983). They conservatively estimated that 1.8×10^{10} king crab glaucothoe larvae were consumed by yellowfin sole in the southeastern Bering Sea in a one-month period. This consumption value may not be significant when one considers the number of glaucothoe that may have been available. The estimated number of adult females in the southeastern Bering Sea in 1982 was 5.48×10^7 (Incze et al. 1986). If one assumes that 90% of these adults had full clutches of 1×10^5 eggs and 75% hatched, then approximately 3.7×10^{12} larvae hatched. Assuming 10% of the larvae reached the glaucothoe stage, 3.7×10^{11} were available. Yellowfin sole consumed 1.8×10^{10} or only 5% of the available larvae.

Shimida and June (1982) sampled Pacific cod extensively throughout the eastern Bering Sea and found that over 10% of the cod stomachs examined in 1981 contained newly molted red king crab. Apparently cod do not prey on king crab except during molting, since studies conducted during other seasons have found few king crab in the cod stomachs (S. Jewett, pers. observ.).

Thousands of demersal fish stomachs were examined from the Gulf of Alaska and Bering Sea during 1975-1980, and king crab were rarely found as prey (Feder and Jewett 1981a). Other predators on king crab include Pacific halibut, sculpins (*Hemilepidotus* and *Myoxocephalus*), Korean hair crab (*Erimacrus isenbeckii*), and sea otters (*Enhydra lutris*). However, the extent of predation is not known.

Movement. Sampling of larval red king crab in the spring in the southeastern Bering Sea showed strong evidence of diel vertical migration (McMurray et al. 1984). The noon and midnight samples exhibited the greatest difference in vertical distribution, with higher densities at noonday at 40 m and at midnight at 10 m. This trend was not as apparent in two bays of Kodiak Island (Wolotira et al. 1984). During the day, most larvae were found 5-20 m below the surface in Kiliuda Bay and in the upper 60 m of the water column in Izhut Bay. Relatively few remained at or near the surface at night in both bays; most were at 40-100 m.

Based on data on development time (3-4.5 months) and current speeds in the southeastern Bering Sea, larvae could be transported over 200 km from hatch to metamorphosis (Armstrong et al. 1981). Since optimal bottom type does not occur uniformly along the North Aleutian Shelf into Bristol Bay, the location of spawning females and the dispersion of larvae by oceanographic factors (e.g., current speed and direction) are the major determinants of placement of larvae over optimal benthos at metamorphosis (Armstrong et al. 1981). This rationale also applies throughout the range of the red king crab.

When king crab are about 1 year old, they emerge from rock crevices, kelp patches, and other protective niches where they have been living since settling as glaucothoe larvae a year before (Jewett and Powell 1981). They gather with crab of similar size, and one small group meets another forming larger groups. As these groups join, mounds of crab or pods are formed, sometimes consisting of thousands of individuals. Juvenile crab in the 2+ to 3+ age classes are known to pod frequently throughout the year in the shallow water (<50 m). Most podding crab are smaller than 69 mm CL (Powell and Nickerson 1965b). Vinogradov (1969) reported that the maximum size of nonmigrating crab is about 65 mm CL (converted from 70-mm carapace width after Wallace et al. 1949).

At approximately 4 years old, king crab begin their onshore-offshore migration with the adults. The adults migrate to shallow waters generally during spring months, and then gradually return to deeper water. Tagging studies have revealed little about within-year movement. However, based on release and recovery data, migrations typically do not exceed 61 km in the Norton Sound crab stock (Powell et al. 1983), 185 km in the southeast Bering Sea stock (Simpson and Shippen 1968), and 65 km in the south Alaska Peninsula stock (Hayes and Montgomery 1963). The longest distance traveled by a crab during a single year was 426 km (Simpson and Shippen 1968). Sexes of the adults and subadults (usually refers to individuals that will reach maturity on the next molt) are normally segregated in deep water, but occur together in shallow water or in offshore breeding areas (Powell and Nickerson 1965a; McMullen 1967).

SPECIFIC HABITAT REQUIREMENTS

Substrate

The distribution of young-of-the-year red king crab is generally restricted to coarse substrates such as boulders, gravel, cobble, and shell debris with attached epifauna (Powell and Nickerson 1965b; Tsalkina 1969; Sundberg and Clausen 1977; McMurray et al. 1984). Dependence upon such a refuge substrate appears to progressively diminish for crab from Age 1 to Age 4. One area along the west Kamchatka Shelf that is especially important for young-of-the-year crab is the Cape Khairyuzovo coastline (57°06' N and 156°34' E) (Tsalkina 1969). Rocky bottoms predominate there, resulting in abundant sessile epifauna. Young crab in this area live mainly among an assemblage of hydroids (28 species), sponges (24 species), and bryozoans (10 species). Two-year-old crab were generally caught at locations where the epifauna was considerably sparser. The depth of the area surveyed was 1.5 to 20 m.

Statistical analyses indicate that juvenile crab distributions correlate better with biological parameters than physical parameters (McMurray et al. 1984). In the Bristol Bay region of the southeastern Bering Sea (mainly <50 m), strong, positive correlations were found between young-of-the-year crab and tube-building polychaete worm biomass and between juvenile crab through Age 2 and sea urchin (Strongylocentrotus droebachiensis) biomass. Older juvenile crab distributions correlated positively with tunicate (Boltenia ovifera) biomass (McMurray et al. 1984).

In Cook Inlet, an embayment of the northern Gulf of Alaska (<27 m), young-of-the-year crab were mainly found among coarse substrates (phi values <-3) containing dense refuge habitats of bryozoans (Flustrella sp. and Dendrobenia spp.), hydroids, sponges, and filamentous red algae (Sundberg and Clausen 1977). At five locations where postlarval crab were found, densities of 1.3/m^2 were observed (Sundberg and Clausen 1977).

Young crab depend on an environment which provides for adequate food (i.e., hydroids and bryozoans) and protection from predators (demersal fishes). The distribution of such suitable substrates in some locations (e.g., Bristol Bay) is extremely patchy, and it is believed that settling in areas where such substrates are absent or limited will hasten natural mortality. Settlement on unprotected bottom presumably will leave them exposed to predation, waves, and currents.

Shipboard substrate preference tests were conducted with Age 1+ crab (McMurray et al. 1984). These tests indicated that in the absence of epifauna, young crab preferred a medium-sized rock substrate over small rock, gravel, or sand. When small "reefs" of natural epifaunal materials were placed on the previously bare substrates, the highest percentages of crab were found on combinations of tube worms with sand and of mussels with small rocks. Erect bryozoans in combination with medium-sized rock attracted the smallest percentage of crab. Crab were observed during the experiments feeding directly on the tube worms and scavenging food from the spaces between mussels.

Subadult and adult red king crab populations reside on variable substrates from rocky, nearshore regions to mud, silt, or sand in deeper offshore and some nearshore areas. The latter substrate appears to be preferred (Korolev 1964; Powell et al. 1983; Feder and Jewett 1987). A historically important spawning area near the south end of Kodiak Island has substrates mainly consisting of mud, silt, and sand; however, some rocky areas also occur adjacent to the spawning ground (Kingsburg and James 1971; S. Jewett, pers. observ.). In April 1970, during the height of the king crab mating and spawning, an estimated 1.4 million red king crab occupied 208.7 km^2 of the above area between depths of 9 and 53 m. The average crab density was 6,722 per km^2 (Kingsbury and James 1971).

Vegetation

Spawning crab also occupy regions where kelp (i.e., Alaria, Costaria, and Laminaria) occurs (Powell and Nickerson 1965a). Numerous exoskeletons of recently molted crab were seen in a kelp bed near Kodiak Island (S. Jewett, pers. observ.). The rocks and kelp presumably give protection to the females while they are soft following ecdysis and during subsequent mating.

Food

Investigations of the food habits or feeding behavior of king crab have been conducted in the following areas: the west Kamchatka Shelf, Okhotsk Sea, Sea of Japan, southeastern Bering Sea, and northern Gulf of Alaska (Cook Inlet and the Kodiak Island vicinity) (see Jewett and Feder 1982 for references relative to the above areas; Pearson et al. 1984).

The larvae are plankton feeders consuming both phytoplankton and zooplankton (Bright 1967). Therefore, the concurrence of the time of hatching and the spring phytoplankton and subsequent zooplankton blooms is important in determining larval feeding success. It appears that diatoms are an important energy source for first feeding larvae (A.J. Paul, University of Alaska, Seward, pers. comm.) with copepods (Paul and Paul 1980) and some meroplankton (A.J. Paul, pers. comm.) supplying additional energy.

First zoeae that received food within 60 hours of hatching were capable of capturing prey thereafter if prey concentrations were adequate. When feeding was delayed an additional 24 hours, the ability to capture prey was reduced, especially at water temperatures <4 °C (Paul and Paul 1980).

Paul et al. (1979) designed a laboratory study to determine zooplankton prey densities necessary to elicit a successful feeding response in first-feeding zoeae of red king crab (five zoeae per 500 ml of filtered seawater). Prey (copepod) densities had to equal 80 per liter before an average zoea was able to consistently capture at least one prey item each day. Prey densities of this magnitude are considerably higher than those in waters where larval king crab are known to occur (Paul et al. 1979). Prey consumption increased from 0.8 per day at a concentration of 20 prey items per liter to 7.6 at a concentration of 160 prey items per liter. The survival rate to day 11 in the container having 20 prey items per liter was 40%, and the survival rate to day 11 in beakers containing 40, 80, and 160 organisms per liter was 60%. In a beaker containing zoeae without prey, the first mortality occurred on day 4, and 100% mortality occurred by day 8 (Paul et al. 1979).

Although no quantitative information is available on the food of early postlarval king crab, some qualitative information is available. Young-of-the-year crab in a coastal region of the west Kamchatka Shelf were found to feed on hydroids, the dominant epifaunal component of the refuge substrate within the region (Tsalkina 1969). Young-of-the-year crab (172 between 3.2 and 5.0 mm CL) from the shallow (<27 m), rocky, bryozoan-dominated substrate of Cook Inlet most frequently contained diatoms, foraminifera, sponge spicules, bryozoans, polychaetes, and crustaceans (ostracods and harpacticoid copepods). Sediment was also found in 93% of these tiny crab (Feder et al. 1980). Pearson et al. (1984) reported that stomachs of 24 small juveniles (9-24 mm CL) from the southeastern Bering Sea were mainly full of sediment, in addition to unidentifiable organic matter. Although the discernible items were few, the most frequently occurring identifiable prey groups were pelecypods, gastropods, crustaceans, and sand dollars. These studies indicate that young crab feed on attached epifauna, as well as organisms within the sediment. It is not known if the high incidence of sediment represents accidental ingestion while taking larger organisms or deliberate ingestion for the extraction of bacteria, diatoms, foraminiferans, and meiofauna.

The calculated values for daily ration and caloric intake for juvenile king crab (53-80 mm CL) in the southeastern Bering Sea during June 1982 were 6.30 mg dry weight and 17.5 calories per g of crab wet weight, respectively. Similar values for August were higher with a daily ration of 11.92 mg dry weight and 42.2 calories per g of crab wet weight (Pearson et al. 1984). Two polychaetes, Pectinaria sp. and a sabellid, constituted over 50% of the caloric intake in June and August. The sand dollar Echinarachnius parma constituted 36% of the caloric intake in June, but only 2% in August. Bivalves constituted 3% of the caloric intake in June, but 25% in August. The major bivalve in the August diet was a small, thin-shelled clam, Tellina sp. The dietary differences between June and August were probably seasonal or temporal, but differences in geographic location or depth may have also been an important factor.

Cultured postlarval king crab are cannibalistic (Nakanishi 1985).

Mollusks (mainly bivalves), crustaceans (mainly barnacles, amphipods, and crabs), and echinoderms (mainly brittle stars, sand dollars, and sea urchins) are generally the dominant prey of adult and subadult red king crab nearshore as well as offshore (Feniuk 1945; Kun and Mikulich 1954; Kulichkova 1955; McLaughlin and Hebard 1961; Takeuchi 1967; Cunningham 1969; Tarverdieva 1976; Feder and Paul 1980; Feder and Jewett 1981b; Jewett and Feder 1982; Rusanowski et al. 1987). Adult and subadult crab were examined from three shallow (<20 m) areas around Kodiak Island in May and June 1978-79 (Feder and Jewett 1981b). Crab from these shallow waters contained 53 different prey taxa. All crab came from variable substrates, i.e., mud, silt, sand, firm bottoms with little or no apparent epifauna, and firm bottoms with lush, sessile epifauna. Although numerous prey types were taken, dominant prey, in terms of frequency of occurrence, biomass, and volume, were bivalves (clams and cockles) and barnacles (Table 4; Feder and Jewett 1981b; Feder and Jewett, unpubl.). Kulichkova (1955) also noted that the chief prey among recently molted red king crab from 16 m in the Okhotsk Sea were bivalves and barnacles. He suggested that the crab need to replace calcium carbonate lost during molting

Table 4. Dominant prey of adult and subadult red king crab from three shallow locations around Kodiak Island. All crab were collected in May and June. Prey are ranked by decreasing relative importance using an index calculated as % frequency of occurrence x (% weight + % volume).

Location	Near Island	McLinn Island	Anton Larsen Bay
Depth (m)	5-11	9-15	6-9
Number examined	88	65	69
% with food	98.8	87.7	92.7
Size range (mm CL)	85-148	84-149	95-173
Mean size (mm CL)	113	108	120
RANK	DOMINANT PREY		
1	Bivalves	Bivalves	Barnacles
2	Barnacles	Tanner crab	Bivalves
3	Polychaetes	Snails	Snails
4	Echinoids	Polychaetes	Polychaetes
5	Hydroids	Barnacles	Hydroids

and that young clams and barnacles in shallow waters during spring represent abundant resources to fulfill this need. Takeuchi (1959) and Jewett and Feder (1982) observed that red king crab feed most intensively in late spring.

Sessile epifauna taken by king crab in shallow Kodiak Island waters, in addition to barnacles, were hydroids. Crab that contained hydroids at a high frequency of occurrence came from locations which had high proportions of sessile organisms, including hydroids (S. Jewett, pers. observ.).

The mean weight of prey found in 713 feeding individuals (65-187 mm CL) from shallow and deep waters near Kodiak Island was 1.41 g wet weight, or 1 mg wet weight of prey per g of crab wet weight (Jewett and Feder 1982). Similar quantities of food have been reported in king crab of similar size from the west coast of the Kamchatka Peninsula. The mean quantities of stomach contents within crab of 75 and 165 mm CL approximated 0.3 and 2 g wet weight, respectively (Takeuchi 1967). Logvinovich (1945) reported the ratio of food weight to body weight to be much higher among smaller crab. Experiments indicate stomach residence time among juveniles (53-80 mm CL) is approximately 11 hours for soft tissue, whereas hard parts can remain in the stomach almost indefinitely, unless regurgitated (Pearson et al. 1984). Thus, the importance of prey possessing hard parts, i.e., mollusks, barnacles, and fishes, may tend to be overestimated in some studies, particularly those that rely exclusively on frequency of occurrence data.

Salinity

Little is known of the salinity tolerances of various stages of red king crab. Laboratory experiments have shown that the growth rate of zoeae is not affected by salinities within the range of 21.7 and 39.7 parts per thousand (ppt) (Kurata 1960). Further laboratory studies revealed that the optimal salinity for larvae, under various temperatures, is 26.8-40.2 ppt (Nakanishi 1985). Values approaching 40 ppt are unlikely to occur in natural areas. Nakanishi (1985) reported that the salinity optima narrow from first zoeae to first postlarvae, although no values were presented. Paul et al. (1979) reared Stage I zoeae at salinities of 32 to 33.5 ppt.

Sampling in Bristol Bay in April and June of 1983 revealed that the greatest densities of red king crab larvae occurred at salinities between 30 and 32 ppt (salinity measured at a depth of 10 m) (McMurray et al. 1984). Juveniles to Age 3 (approximately 67 mm CL) were most dense at bottom salinites between 26 and 32 ppt (April, June, and September). Crab >68 mm CL (including a few adults) were most dense at bottom salinities between 30 and 32 ppt.

Little salinity information is available concerning adult king crab. Adults are typically present in the shallow, coastal waters off Nome, Alaska (Norton Sound), during the ice-covered months. However, they are typically absent from these waters during the ice-free period (C. Lean, Alaska Department of Fish and Game, Nome; pers. comm.). Large differences in salinity and temperature have been observed between these two periods. The bottom salinity and temperature at 20 m during March 1971 (crab are usually caught through the ice in March) were 34 ppt and -1.8 °C (Hood et al. 1974). In contrast, bottom values at 10 m during August and September 1986 (crab are usually absent nearshore during these months) were 22-24.5 ppt and 8.5-11 °C (Rusanowski et al. 1987). It appears that salinity, more than temperature, may exclude king crab from the shallow waters near Nome during much of the ice-free period.

Although salinity data are meager, an optimal range from 26 to 34 ppt is indicated for larvae, juveniles, and adults.

Temperature

Temperature is considered one of the most crucial physical factors affecting survival and growth of red king crab of all stages. Regional and interannual differences in bottom water temperatures may significantly affect the rate of embryonic development in the egg and, in turn, the appropriate time of hatch each year.

Extrusion of eggs has been observed at a water temperature of 0-2.7 °C (McMullen 1970; Powell et al. 1973). McMullen (1970) reported the 8-blastomere stage was attained 5-7 days after fertilization at temperatures of 2.8-4.4 °C. Powell et al (1973) observed the 8-blastomere stage after 10-14 days at 0-1.7 °C. The first appearance of the zoeae in the eggs normally occurs in the late fall, approximately 6 months after fertilization (Nakanishi 1985). In laboratory trials, the optimal temperature from fertilization to the egg-zoeae stage is 3-8 °C (Nakanishi 1985). The zoeae then overwinters in the egg, and the optimal temperature in the laboratory is correspondingly lower: 3 °C (Nakanishi 1985). The thermal tolerance of free-swimming zoeae has been determined to be between 0.5 and 15 °C (unspecified salinity) (Kurata 1960) and -1.8 and 18 °C at a salinity of 33.5 ppt (Nakanishi 1985). Duration of the first free-swimming stage varies from 24 days at 2 °C to 9 days at 8 °C (Kurata 1960). It took 84 days to raise crab to first postlarvae at water temperatures between 3.8 and 7.8 °C (Marukawa 1933). Nakanishi (1985) stated that the optimal water temperature for survival and growth of laboratory-reared larvae is 8 °C. Kurata (1960) found the greatest survival of zoeae to be between 5 and 10 °C and formulated an equation that relates developmental time to temperature. Larval development time can double with a decrease of temperature from 10 to 5 °C (Kurata 1960), and an average of 460 degree days (= cumulative average daily temperature) is required for development from hatch of egg to metamorphosis of glaucothoe (Kurata 1961a).

Paul and Paul (1980) studied the effect of temperature and starvation on subsequent ability to capture food, and found that prey availability when zoeae first begin to feed had more effect on later feeding success than water temperature. First zoeae held at 2, 4, and 6 °C and first fed after 12 and 60 hours were able to successfully capture copepod prey. Zoeae held at 6 °C and starved for 84 hours retained the ability to capture prey; however, there was a significant reduction in predation rates in comparison to zoeae starved for shorter periods at this temperature. Zoeae held at 2 °C and 4 °C without food for 84 hours were unable to capture copepod prey when later presented.

Takeuchi (1962) collected larvae in the southeastern Bering Sea in April-June 1960. During this period temperatures at 10 and 50 m depths were 1.5-5.5 °C and 1.5-2.8 °C, respectively. Larval densities in Bristol Bay in April and

June 1983 were highest at 1-3 °C and 5-7 °C, respectively (temperature measured at 10 m depth) (McMurray et al. 1984).

The effect of temperature on juvenile (30-40 mm CL) king crab was examined in a 90-day laboratory study (Rice et al. 1985). Crab held at 5 °C had high overall survival (88%) because the crab had a moderate amount of molting attempts (46%) and the highest molting success (75%). Crab at 10 °C had good overall survival (65%); all attempted to molt and 65% were successful. Survival at 15 °C was poor (46%) because a high percentage of crab attempted to molt (62%) and survival of molting crab was only 12%. Crab at 1 and 20 °C had high survival (92% and 81%, respectively), but few attempted to molt and none succeeded. Food consumption in these crab increased linearly with increasing temperature. At 1 °C, crab ate a daily average of 0.09 g of fish, and at 20 °C, 1.0 g. There was no significant difference in growth among crab held at 5 and 10 °C (Rice et al. 1985). The optimal water temperature for long-term rearing of juvenile crab (30-40 mm CL) was concluded to be 10 °C, because it allowed relatively rapid molting and reasonably good survival.

Numerous young-of-the-year crab were observed beneath rocks at 6 m in an embayment of Kodiak Island (S. Jewett, pers. observ.). The bottom temperature during this observation in May 1978 was 5.5 °C. The distribution of juveniles up to Age 3 (approximately 67 mm CL) within Bristol Bay in 1983 was generally restricted to the coastal region (<50 m) (McMurray et al. 1984). Juvenile crab of this size had their highest concentrations at bottom temperatures of 1-3 °C in April, 4-10 °C in June, and 10-11 °C in September 1983 (McMurray et al. 1984). Red king crab older than Age 3 (>67 mm CL) (including a few adults) were mainly located at depths of 50-70 m in temperatures of 1-3 °C in April, 4-7 °C in June, and 9 °C in September (McMurray et al. 1984).

The known temperatures in shallow coastal areas where adult red king crab molt, mate, and spawn are mainly from the Kodiak Island area. Primiparous females in holding pens molted and mated at temperatures between -0.3 and 1.7 °C during February and March 1971 (Powell et al. 1973). Adults were observed where bottom water temperatures at 6-12 m ranged between 5.5 and 7.0 °C in May and June 1978 and 1979 (S. Jewett, pers. observ.). Activity mainly observed at this time was feeding, although some molting and mating also occurred. Much information is available on temperatures in deeper, offshore waters where adults reside during most of the year. The bottom temperatures associated with sublegal and legal-sized male crab at depths averaging between 50 and 60 m in the southeastern Bering Sea in June and July of 1975-85 ranged between -1.5 and 8 °C, with most found between 2 and 5 °C (Otto et al. 1982, 1983, 1984; Stevens and MacIntosh 1985). Although there were peaks in catch rates associated with a narrow temperature range in each year, peak catches were associated with different temperatures in different years. Stinson (1975) correlated male and female abundance with temperature and, from several years of National Marine Fisheries Service (NMFS) survey data, located most sexually mature females inshore of the 4 °C isotherm in the southeastern Bering Sea. Surveys of red king crab populations in Norton Sound in September-October 1976 and 1985 found most adults dispersed at 18-22 m, where temperatures were between 6 and 8 °C (Wolotira et al. 1977; Stevens and MacIntosh 1986). Sato (1958) reported that in Asiatic waters, commercial concentrations of king crab were not found where bottom temperatures exceeded 12 °C.

In summary, based on laboratory and field data, king crab of different life stages have specific temperature tolerances and optima. Optimal temperatures for eggs are 3-8 °C. Although larvae may tolerate water-column temperatures of -1.8 to 18 °C, survival appears to be best at 5-10 °C. Juveniles can tolerate temperatures at least 0-15 °C, but their optimal temperatures are thought to be 5-10 °C. While adults are in shallow waters, mainly from March through May, they may be exposed to temperatures -1.8 to 9 °C, but 2-7 °C is assumed to be optimal, based on our interpretation of the NMFS survey analyses.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. The red king crab model is applicable to the Continental Shelf of the North Pacific Ocean (54° to 71°25' N latitude), with emphasis on coastal waters of the Gulf of Alaska and the southeastern Bering Sea, from the intertidal zone to around 50 m. The crab population in Norton Sound, an embayment of the northeastern Bering Sea, is subjected to a suite of environmental conditions unlike the conditions known for other populations. Anomalies in depth (<30 m depths throughout the Sound) and ice-covered conditions (up to 6 months per year) suggest that the timing of various activities, e.g., mating, may differ from populations elsewhere. Therefore, the model should not be applied to this northern population.

Season. The model can be applied throughout the year for juveniles to Age 4. It is designed to be used for larvae for about 6 months, from March through August. This is approximately 6 weeks longer than the longest time suspected for larval existence (approximately 4.5 months) so that interannual variability can be taken into account. Similarly, the model is designed for seasonal use for adults and subadults (Age 4+ juveniles). They typically use the coastal waters for not more that three months in spring (mainly March-May).

Minimum habitat area. This is defined as the minimum area of contiguous suitable habitat required for a species to live and reproduce successfully. No attempt has been made to establish a minimum habitat area for this species.

Verification level. The model output is an index value between 0.0 and 1.0 that reflects the habitat potential for all life stages of the crab after the egg. The model has not been field tested. Hypothetical data sets were used to verify the acceptability of the model output.

The following biologists have reviewed this model for accuracy and applicability to various Alaskan coastal water areas: Robert Otto and Bradley Stevens, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Kodiak, Alaska; A.J. Paul, Institute of Marine Science, University of Alaska, Seward; and Daniel Wickham, Bodega Marine Laboratories, University of California, Bodega Bay. Their comments have been incorporated, but the authors are responsible for the final version of this model.

Model Description

Overview. The requirements of red king crab differ considerably according to life stage. Therefore, separate models are developed for larval, young-of-the-year juvenile, Age 1 to Age 4 juvenile, and Age 4+ juvenile (subadult) through adult life stages. Red king crab larvae are pelagic, and the model for larval stages has only a water quality component with temperature and salinity variables (Figure 1). All other stages are benthic. The models for benthic stages all have the same structure, with a food/cover component derived from one substrate variable and a water quality component consisting of temperature and salinity variables (Figure 1). Existing salinity data are too limited to detect differences among life stages, but tolerances are broad. In these

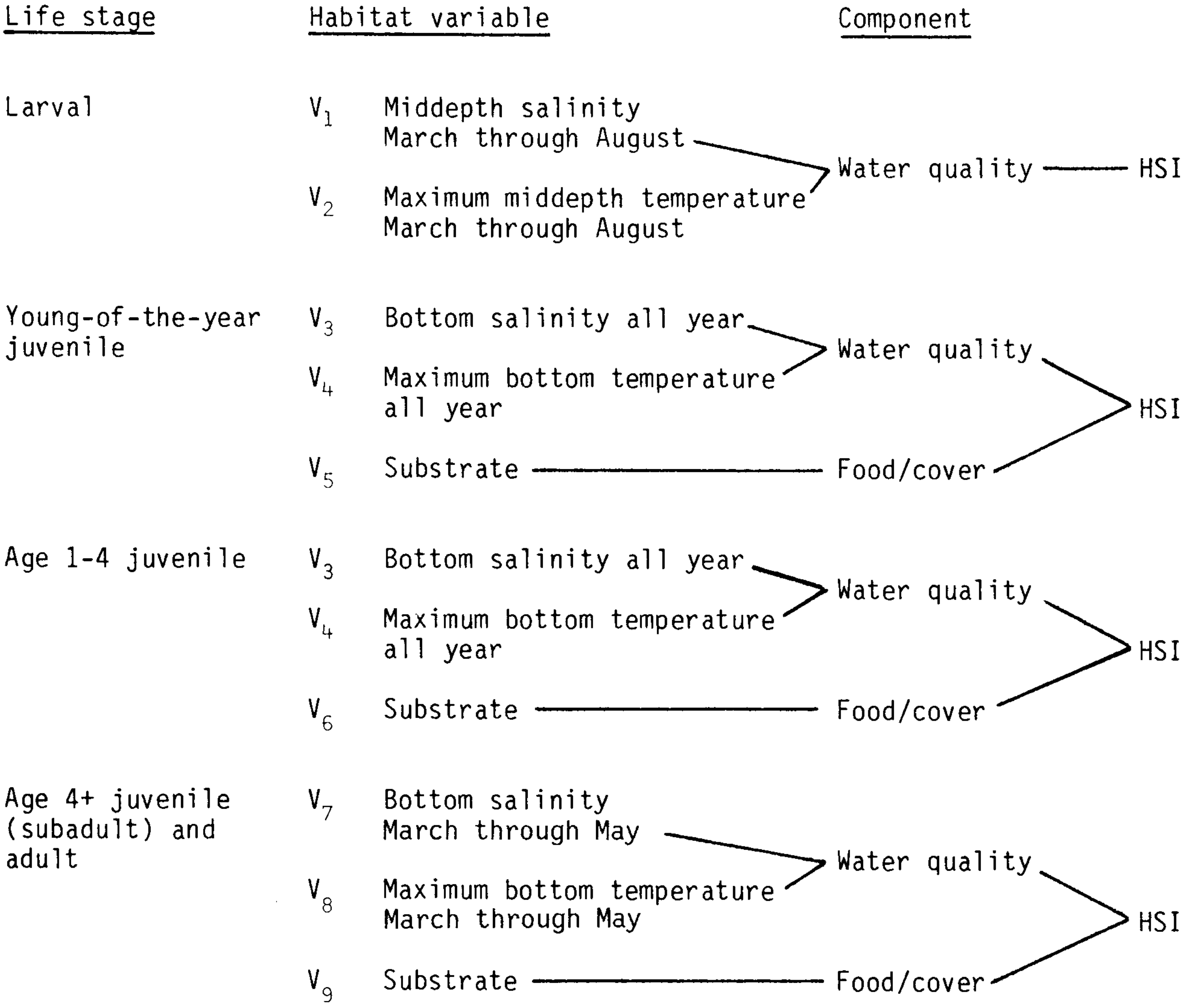


Figure 1. Relationship of habitat variables and life requisites to the Habitat Suitability Index (HSI) values for different life stages of red king crab.

models, salinites between 26 and 40 ppt are assumed optimal for all life stages. Because the crab are so unresponsive to this factor, temperature is assumed to be the more important determinant of water quality. The models differ in their season of application and the specific relationships between other measured variables and suitability. Usually it is inappropriate to use all models at the same site because the requirements of some stages are mutually exclusive. Guidance about application of models is provided under Field Use of the Models.

Larval life stage. Conditions in the water column determine habitat suitability for the pelagic larvae of king crab. The model has only a water quality component, where salinity during the larval period from March through August can range quite broadly without adversely affecting suitability. Since the period that larvae are present in the water column is much longer than that required for an individual to complete development (3-4.5 months), it is possible for segments of the population to successfully complete development even if conditions were lethal much of the March-August period before or after they were in the water column. Therefore, the duration of the period that salinities are in the optimal range between 26 and 34 ppt from March through August (V_1) is a good indicator of suitability. Under ideal conditions, larval development is completed in approximately 90 days (Marukawa 1933). It is assumed in this model that salinities in the optimal range for at least half this long (>45 days) are required for any successful development. Above that threshold, the longer the duration of optimal salinities, the higher the suitablity will be.

The temperature variable (V_2) must take into account three responses. (1) Starvation is likely to occur before first successful feeding below 4 °C (Paul and Paul 1980). (2) In the laboratory, survival is high between 5 °C and 10 °C (Kurata 1960) and developmental time is half as long at 10 °C as at 5 °C (Kurata 1961a). Nakanishi (1985) reported 8 °C as optimal. (3) Survival decreases as temperature increases above 10 °C, presumably because metabolism is so high that further increase in the molt rate is physiologically stressful. If the high risk of predation in the water column under natural conditions is taken into account, optimal temperatures would appear to be near 10 °C, where the length of the larval period is minimized while viability remains high.

The maximum middepth water temperature during the larval period of March through August is an easily obtained field measurement that nevertheless can be used to express these complex relations. If the highest temperature achieved during the larval period is 4 °C or lower, starvation probably will occur. If not, development will take so long that predation will be severe. Between the two effects, unsuitability is assumed. If a maximum temperature of 7 °C is reached, survival is high and developmental time is intermediate, but the time that these conditions prevailed probably would be short. Therefore, suitability would be intermediate for the whole larval period. For a maximum of 10 °C, shortest development time compatible with high survival probably would prevail for the longest time. For still higher maxima, some larvae will complete development before conditions become unsuitable. It is assumed that the higher the maximum, the sooner in the larval period unsuitable conditions will ensue and the fewer larvae will complete development, to the point that none are successful at a maximum of 20 °C.

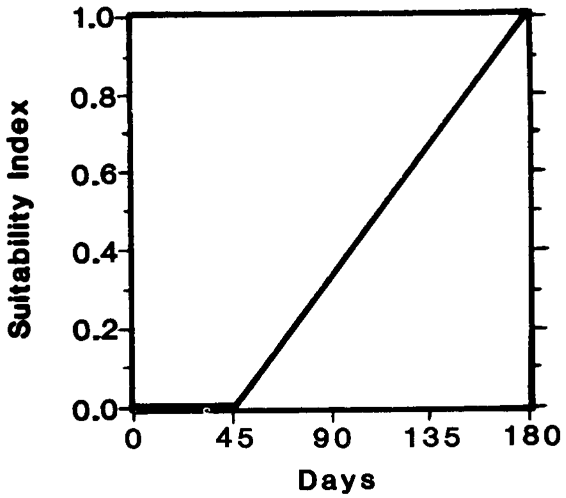
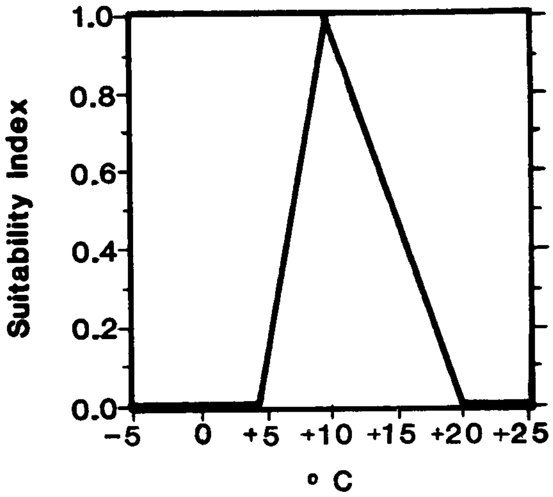
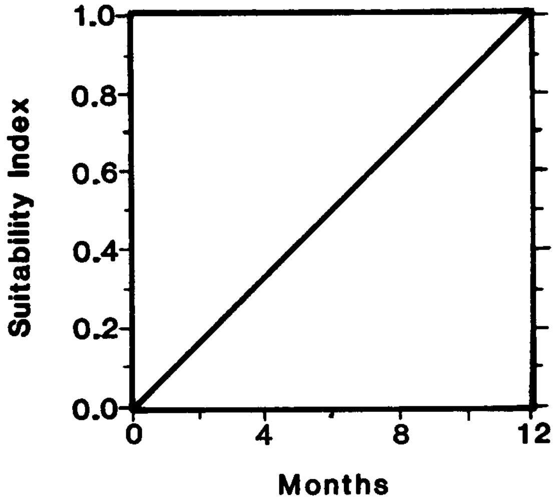
Young-of-the-year and young juvenile (Age 1-4) life stages. The same water quality component applies in both juvenile stage HSI models. Similar water quality variables apply as for the larval life stage, except that the measurements are for conditions on the bottom and year-round. It is assumed that considerably longer periods in the 26- to 34-ppt salinity range (V_3) are required for high suitability than is the case for the larval stage and that suitability decreases linearly from 1.0 at 12 months in the optimal range to 0 when salinities are never in the optimal range. Since juveniles reared at 5 and 10 °C had high molting success (Rice et al. 1985), maximum temperatures (V_4) of 5-10 °C appear to be optimal. Unsuitable conditions presumably exist when maximum temperatures are <1 °C or >16 °C (Rice et al. 1985). Suitability decreases more rapidly at high maximum temperatures than is the case for larvae, because the whole population of juveniles, but not of larvae, is at risk at the same time. In contrast, many larvae may have successfully completed development and may no longer be in the water column when unsuitable temperatures are reached there.

The food/cover component is defined by slightly different substrate variables for young-of-the-year (V_5) and Age 1-4 (V_6) juveniles, as a consequence of the decreasing need for cover as juveniles grow. The decreased vulnerability of larger individuals allows them to exploit the alternative food resources provided by adjacent soft-bottom areas, and these changes are reflected in different suitability index values for the same substrate classes, depending on age.

Subadult (Age 4+) and adult life stages. Subadult and adult red king crab engage in inshore-offshore migrations and are typically only present in shallow coastal waters from March through May. The water quality variables are adjusted accordingly. Suitability is assumed to increase linearly the longer that salinities are in the 26- to 34-ppt range (V_7). Maximum temperatures (V_8) are assumed unsuitable below 2 °C and above 15 °C, optimal at 7 °C, and to change linearly between 2 and 7 °C and between 7 and 15 °C. The food/cover component is determined by a substrate variable (V_9), with finer substrates assigned slightly higher suitabilities than for Age 1-4 juveniles.

Suitability Index (SI) Graphs for Model Variables

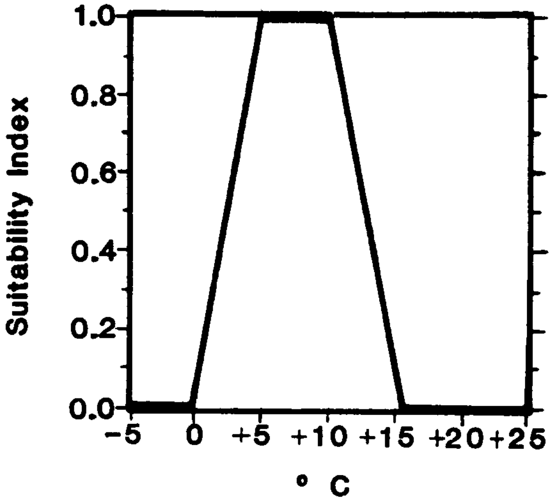
This section provides graphic representations of the relations previously described between the habitat variables (V_1-V_9) and habitat suitability for different life stages of red king crab in coastal waters. An SI value of 1.0 indicates optimal conditions and a value of 0 indicates unsuitable conditions. Data sources and assumptions associated with documentation of the SI graphs are listed in Table 5.

Variable	Suitability Graph
V_1 Salinity - number of days March through August with 26- to 34-ppt middepth salinity - larvae.	
V_2 Maximum middepth water temperature March through August - larvae.	
V_3 Salinity - number of months during the year with 26- to 34-ppt bottom salinity - young-of-the-year juveniles.	

Variable

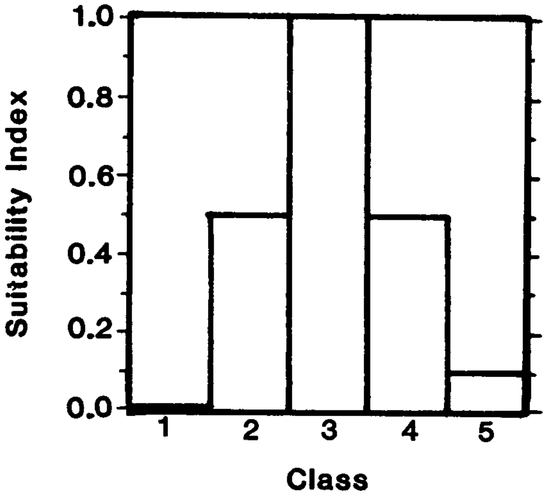
Suitability Graph

V_4 Maximum bottom water temperature during year - young-of-the-year and Age 1-4 juveniles.



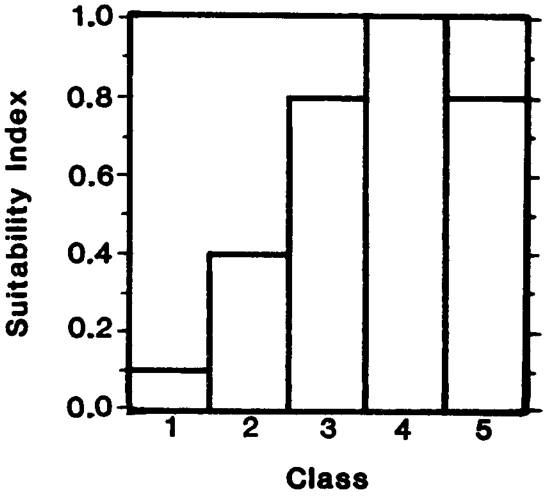
V_5 Substrate class - young-of-the-year juveniles.

1) Bare bedrock
2) Bare rocks, gravel, shell
3) Bedrock, rocks, gravel, shell with sessile epifauna/flora
4) Substrate with sessile epifauna/flora adjacent to soft bottom areas
5) Soft bottom - sand, mud.



V_6 Substrate class - Age 1-4 juveniles.

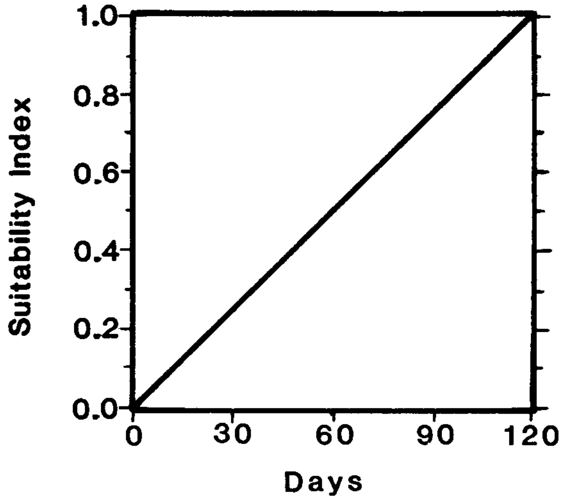
1) Bare bedrock
2) Bare rocks, gravel, shell
3) Bedrock, rocks, gravel, shell with sessile epifauna/flora
4) Substrate with sessile epifauna/flora adjacent to soft bottom areas
5) Soft bottom - sand, mud.



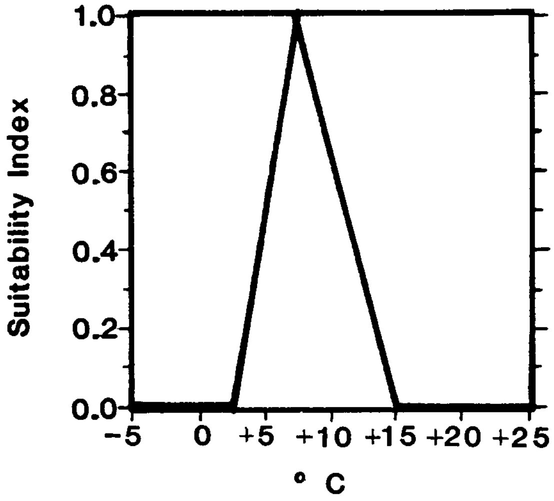
Variable

Suitability Graph

V_7 Salinity - number of days March through May with 26- to 34-ppt bottom salinity - subadults and adults.



V_8 Maximum bottom water temperature March through May - subadults and adults.



V_9 Substrate class - subadults and adults.

1) Bare bedrock
2) Bare rocks, gravel, shell
3) Bedrock, rocks, gravel, shell with sessile epifauna/flora
4) Substrate with sessile epifauna/flora adjacent to soft bottom areas
5) Soft bottom - sand, mud.

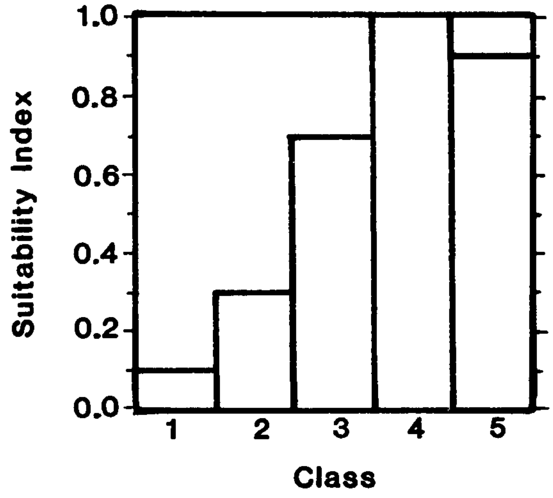


Table 5. Data sources and assumptions for red king crab suitability indices.

Variable and source		Assumptions
$V_{1,3,7}$	Kurata 1960 Paul et al. 1979 McMurray et al. 1984 Nakanishi 1985	Probable optimal salinities for larvae, juveniles, and adults are 26-34 ppt.
V_2	Marukawa 1933 Kurata 1960, 1961a Takeuchi 1962 Paul and Paul 1980 McMurray et al. 1984 Nakanishi 1985	Tolerance is reported variously as -1.8 to +18 °C or 0.5-15 °C; survival is best at 5-10 °C; development is twice as fast at 10 °C as at 5 °C; development is optimal in the laboratory at 8 °C; starvation before first meal is likely at <4 °C.
V_4	McMurray et al. 1984 Rice et al. 1985 Jewett, unpubl.	Molting success is high in the laboratory at 5-10 °C; survival is better at 5 °C than at 10 °C, but frequency of molting at 5 °C is half that at 10 °C; only 12% of crab molting at 15 °C survive; no molting occurs at 1 and 20 °C; field observations are consistent with these laboratory determinations.
V_5	Powell and Nickerson 1965b Tsalkina 1969 Sundberg and Clausen 1977 McMurray et al. 1984	Coarse substrates with sessile epifauna/flora are optimal by providing food and cover; soft bottoms are low in suitability; bare bedrock is unsuitable.
V_6	Feder et al. 1980 McMurray et al. 1984 Pearson et al. 1984	Soft bottoms are more suitable for Age 1-4 juveniles than for the young of the year, because larger individuals can forage more successfully in the surface layers of the sediment and are less vulnerable to predators; however, coarse material with epifauna/flora is still valuable for food and cover.
V_8	Sato 1958 Wolotira et al. 1977 Otto et al. 1982, 1983, 1984 Stevens and MacIntosh 1985 Jewett, unpubl.	Subadults and adults are exposed to temperatures from -1.8 to 9 °C; the optimal range is 2-7 °C.

(continued)

Table 5. Concluded.

	Variable and source	Assumptions
V_9	Feniuk 1945 Kun and Mikulich 1954 Kulichkova 1955 McLaughlin and Hebard 1961 Korolev 1964 Powell and Nickerson 1965a Takeuchi 1967 Cunningham 1969 Kingsbury and James 1971 Tarverdieva 1976 Feder and Paul 1980 Feder and Jewett 1981b Jewett and Feder 1982 Powell et al. 1983 Feder and Jewett 1987	Subadult and adult red king crab reside on substrates ranging from rock to mud; soft bottoms seem to be preferred slightly offshore, but coarse substrate with sessile epifauna/flora adjacent to soft bottom is assumed optimal inshore for feeding and allowing protection for females during the necessary molt for reproduction.

Component Index Equations and HSI Determination

The Habitat Suitability Index (HSI) model for the larval life stage of red king crab has only a water quality component in which temperature is considered to be more important than salinity. It is assumed that high suitability for one variable can partially compensate for low suitability for the other variable, except that unsuitable conditions for one variable will be limiting. Therefore, a weighted geometric mean is used to combine salinity and temperature SI values into the water quality component index (CI) and HSI. The HSI models for juvenile and adult life stages are composed of water quality components of the same form as for the larval stage, plus a food/cover component equal to the SI for the substrate variable. No compensatory relationships between water quality and food/cover components are assumed to operate. Therefore, the HSI for these stages is the lower of the two CI values. Examples of model outputs using hypothetical data sets appear in Table 6.

Life Stage	Component	Equation
Larval	Water quality (WQ)	$[SI_{V_1} \times (SI_{V_2})^2]^{1/3}$
	HSI = WQ	
Young-of-the-year juvenile	WQ	$[SI_{V_3} \times (SI_{V_4})^2]^{1/3}$
	Food/cover (FC)	SI_{V_5}
	HSI = WQ or FC, whichever is lower	

Life Stage	Component	Equation
Age 1-4 juvenile	WQ	$[SI_{V_3} \times (SI_{V_4})^2]^{1/3}$
	FC	SI_{V_6}
	HSI = WQ or FC, whichever is lower	
Age 4+ juvenile and adult	WQ	$[SI_{V_7} \times (SI_{V_8})^2]^{1/3}$
	FC	SI_{V_9}
	HSI = WQ or FC, whichever is lower	

Table 6. Calculation of suitability indices (SI), component indices (CI), and habitat suitability indices (HSI) for three hypothetical data sets using habitat variable (V) measurements and red king crab HSI model equations.

Model component		Data set 1		Data set 2		Data set 3	
		Data	SI	Data	SI	Data	SI
V_1	days	180	1.00	150	0.78	90	0.33
V_2	°C	8	0.67	6	0.33	4	0.00
V_3	months	10	0.83	6	0.50	4	0.33
V_4	°C	8	1.00	4	0.80	1	0.20
V_5	Class	3	1.00	2	0.50	5	0.10
V_6	Class	3	0.80	2	0.40	5	0.80
V_7	days	120	1.00	60	0.50	30	0.25
V_8	°C	7	1.00	4	0.40	1	0.00
V_9	Class	3	0.70	2	0.30	5	0.90
WQ	larvae	0.77		0.44		0.00	
	young-of-the-year	0.94		0.68		0.24	
	Age 1-4	0.94		0.68		0.24	
	Age 4+	1.00		0.43		0.00	
FC	young-of-the-year	1.00		0.50		0.10	
	Age 1-4	0.80		0.40		0.80	
	Age 4+	0.70		0.30		0.90	
HSI	larvae	0.77		0.44		0.00	
	young-of-the-year	0.94		0.50		0.10	
	Age 1-4	0.80		0.40		0.24	
	Age 4+	0.70		0.30		0.00	

Field Use of the Models

The most important step in the proper application of the red king crab HSI models is model selection. Usually it is inappropriate to aggregate results of models for different life stages applied at the same location.

Since the different life stages have conflicting requirements, most approaches to aggregation will yield intermediate results that are unresponsive to changes in conditions. Changes that increase suitability for one life stage decrease suitability for another. The lack of response of the aggregate HSI could be very misleading if the life stage that was adversely affected was limiting the population.

In many cases, knowledge about the biology of the crab in the proposed study area will provide the needed guidance for proper model selection. Almost certainly an area will not be equally important for all life stages. If it is known or strongly suspected that an area is especially significant for a life stage, then this should dictate the choice of models. Alternatively, even though an area is known to be particularly important for one life stage, another life stage might be selected for evaluation if it is known to be limiting for the population as a whole. The young-of-the-year life stage is the most likely candidate.

Two other options are available when prior knowledge is insufficient to rank the importance of a location for different life stages. All the models can be applied for baseline conditions and the model selected for the life stage that has the highest HSI. In this case, the assumption is that the study area is most important to the life stage that does best there under baseline conditions. In the absence of other information, this assumption may be acceptable, but even here judgment should be exercised. A relatively poor area for a life stage may nevertheless be the best there is and critical for the population, a possibility that would not be accounted for with this approach.

The other option is to perform before and after comparisons using all life stages and select the life stage most adversely affected for assessing project impacts. This approach also has the drawback that the life stage suffering the largest impact may not be the stage for which habitat is limiting to the stock as a whole.

It should be recognized that these models do not take into account some aspects of red king crab habitat that may be more critical than those addressed. Among these, factors responsible for water column stability and upwelling are critical in determining the availabilty of the planktonic food supply for larval stages. Currents and local patterns of water circulation will determine whether or not larvae will be carried to areas suitable for juvenile rearing after settlement. Probably both of these aspects are more important influences on habitat suitability for the larval stage than the water quality factors included in this model. Unfortunately, data are not available to formulate models that incorporate larval food supply and access to juvenile rearing areas, and general models will never be feasible. In local situations, these factors may be amenable to analysis and users should take them into consideration. Guidance on obtaining the necessary information to apply the models is provided in Table 7.

Interpreting Model Outputs

The proper interpretation of the red king crab HSI models is one of comparison. The models can be used to compare different areas at the same time or the same area at different times. Provided that the model for the limiting life stage was selected and that larval food and larval access to juvenile-rearing areas do not overwhelm the effects measured by these models, areas with higher HSI values should support larger red king crab populations.

Table 7. Suggested techniques for obtaining the data necessary to apply the red king crab HSI models.

Variable	Techniques
V_1	Long-term salinity records are desirable. Surveys of the National Marine Fisheries Service, Alaska Department of Fish and Game, and University of Alaska Institute of Marine Science may be the best sources of this information. Field measurements should be made at middepth with a probe or from water samples collected at middepth by titration, refractometer, hydrometer, or conductivity meter (Strickland and Parsons 1968). Limited observations will be adequate, if they are made at the known time of most extreme salinity conditions and values still are in the 26- to 34-ppt range. When measurements fall outside this range, monthly or more frequent sampling from March through August is desirable.
V_2	Long-term temperature records are desirable. The same sources listed for V_1 should be consulted. In addition, satellite remote monitoring of sea surface temperature is being conducted. The National Ocean Survey or National Weather Service should be contacted about the availability of monitoring records for Alaskan coastal waters. If surface temperatures are available, it will be necessary to determine the relationship between surface and middepth temperatures before application in the model. When only limited field measurements are possible, the measurements should be made in July and August, when maximum temperature during the larval period is bound to occur. Temperature should be measured with a probe at middepth or with a thermometer in a water sample immediately after collection at middepth.
V_3	Same as V_1, except measurements should be at the bottom and for the whole year.
V_4	Same as V_2, except measurements should be at the bottom and for the whole year.
$V_{5,6,9}$	Three grab samples should be collected while the boat is anchored at the same location. The substrate is Class 1 if all three samples are empty; Class 2 if bare coarse material is dominant in all three samples; Class 3 if coarse material with sessile epifauna or sessile epifauna alone is dominant in all three samples; Class 4 if mud and coarse material with sessile epifauna are dominant in different samples from the same location; Class 5 if mud or sand is dominant

(continued)

Table 7. Concluded.

Variable	Techniques
$V_{5,6,9}$ (cont'd)	in all three samples. Intermediate values should be assigned when different substrates are dominant among samples collected at the same location, except as specified for Class 4. Users should have little difficulty in adapting these criteria for visual determinations made by diving.
V_7	Same as V_1, except measurements should be at the bottom and for March through May.
V_8	Same as V_2, except measurements should be at the bottom and for March through May.

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U.S. Fish and Wildlife Service
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138 Arctic Health Research Bldg., University of Alaska
Fairbanks, AK 99775

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A review and synthesis of existing information were used to develop models for evaluating habitat of different life stages of red king crab. The model is scaled to produce an index between 0 (unsuitable habitat) and 1 (optimal habitat) in Alaskan coastal waters, especially in the Gulf of Alaska and the southeastern Bering Sea. 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.

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