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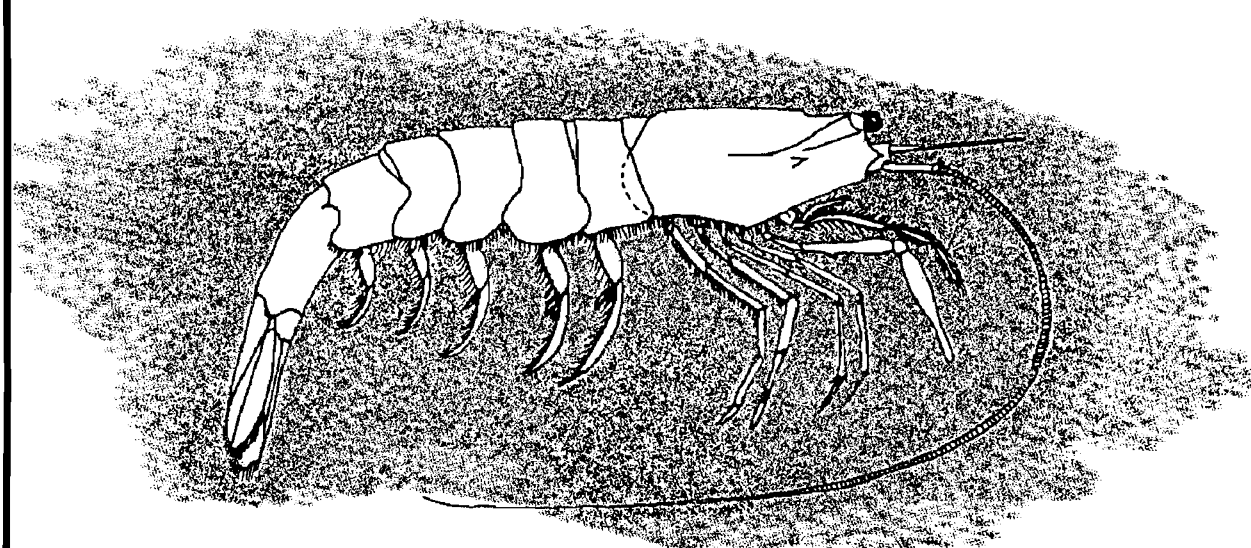

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest)

CRANGONID SHRIMP

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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Attention: WESER-C
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Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

Multiply	*By*	*To Obtain*
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (° C)	1.8 (° C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces	28.35	grams
pounds (lb)	0.4536	kilograms
pounds	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (° F)	0.5556 (° F - 32)	Celsius degrees

CONTENTS

ACKNOWLEDGMENTS

I am grateful for the reviews by Richard Wahle of the University of Maine and Kathy Hieb of the California Department of Fish and Game, Stockton, California, and helpful editorial comments by an unidentified reviewer, which greatly improved the readability of this work.

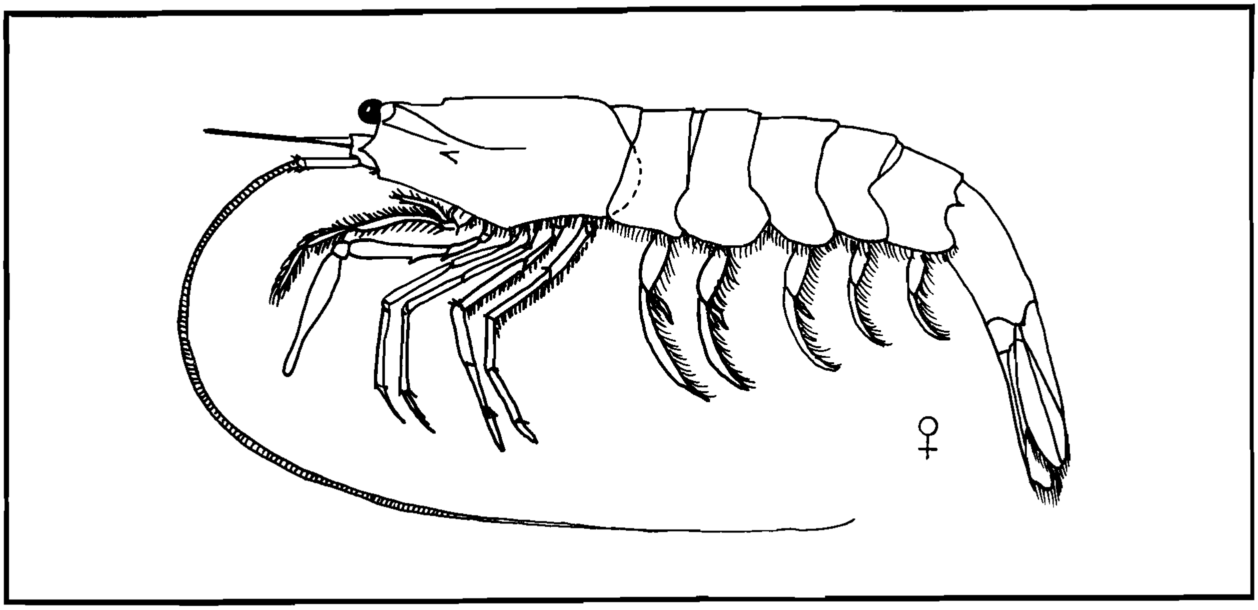

Figure 1. Representative crangonid shrimp (from Smith and Carlton 1975).

CRANGONID SHRIMP

NOMENCLATURE/TAXONOMY/RANGE

Three species of crangonid shrimp, commonly called bay shrimp (Figure 1), are important to epifaunal decapod shrimp communities of the Pacific Southwest.

Scientific name . . . . *Crangon franciscorum* (Stimpson)
Preferred common name . . . . sand shrimp
Other common names . . . grass shrimp, common shrimp.
Scientific name . . . . *Crangon nigricauda* (Stimpson)
Preferred common name . . . . black shrimp
Other common names . . . . deep-water shrimp, black-tailed shrimp
Scientific name . . . . . *Crangon nigromaculata* (Lockington)
Common name . . . . blue-spotted shrimp

Class . . . . Crustacea
Order . . . . Decapoda
Suborder . . . . Natantia
Tribe . . . . Caridea
Family . . . . Crangonidae

Geographic range: sand shrimp and black shrimp are widely distributed along the Pacific coast of North America--sand shrimp from southeastern Alaska to San Diego, California, and black shrimp from Alaska to Baja California (Figure 2) (Rathbun 1904) and possibly as far west as Japan (Schmitt 1921). Both shrimp are abundant in bays on mud and sand bottoms and offshore in deeper waters (Carlton and Kuris 1975). The range of blue-spotted shrimp is more restricted; it occurs from the Gulf of Farallons to Baja California (Rathbun 1904) (Figure 2). It is rarely abundant in embayments, living more commonly offshore on mud and sand bottoms.

MORPHOLOGY/IDENTIFICATION AIDS

The crangonid shrimp of the Pacific Southwest are easily distinguished from other members of the tribe Caridea by four features (Figure 3); (1)-the rostrum is very short, generally not extending beyond the eyestalks, (2)-the body is dorsally flattened, (3)-the chelipeds are not strongly developed, i.e., they

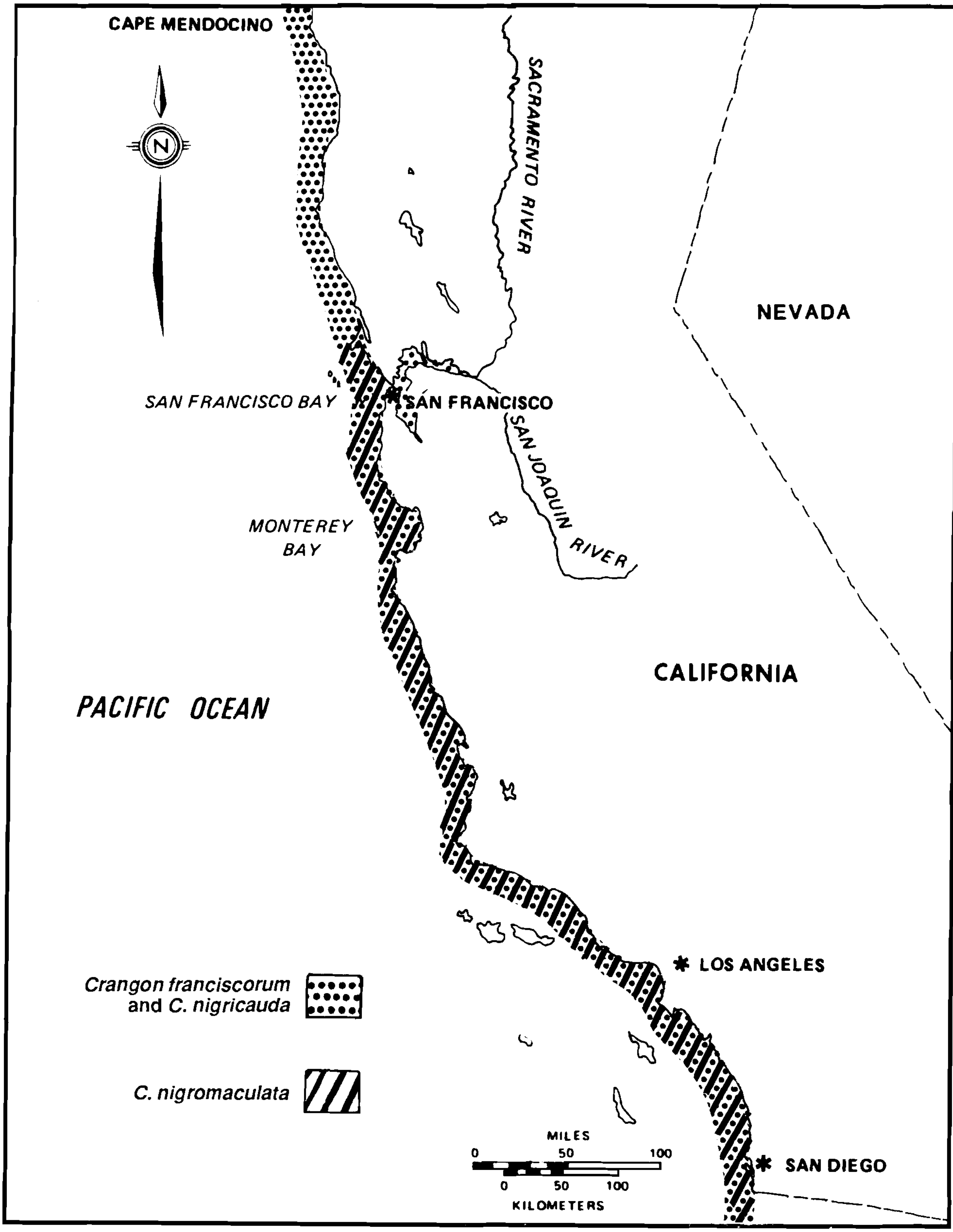

Figure 2. Distribution of crangonid shrimp in the Pacific Southwest.

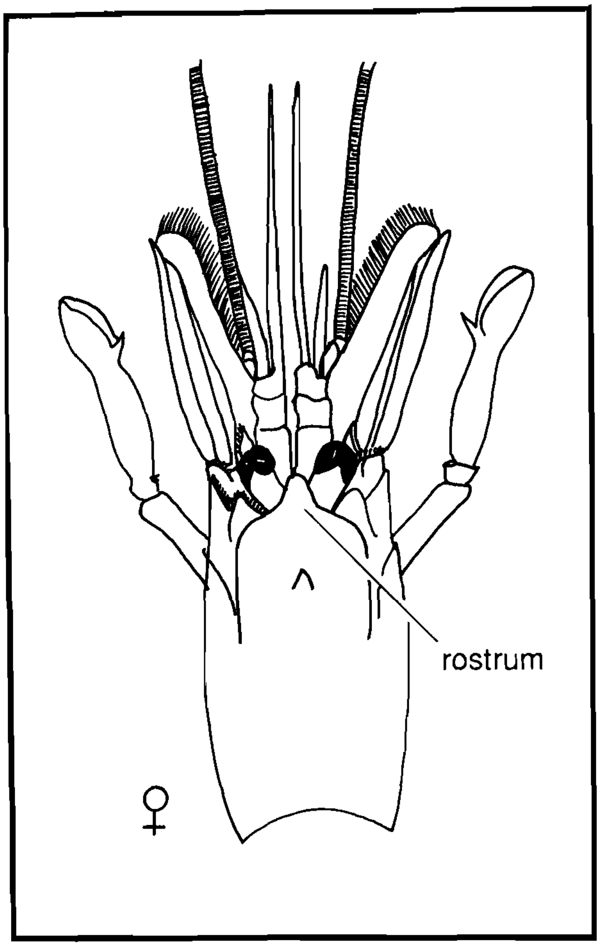

Figure 3. Distinguishing characteristics of crangonid shrimp (from Smith and Carlton 1975).

are subchelate in form, and (4)-the eyes are not covered by the carapace (Carlton and Kuris 1975). Shrimp of the genus *Crangon* are further distinguished by a single median spine in the gastric region of the carapace.

The three species of *Crangon* are easily distinguished by the structure of the cheliped or the presence of distinctive markings. The "hand" of the cheliped of sand shrimp is slender and elongate (Figure 3), and the "finger," when closed, turns back almost longitudinally. The hand of the cheliped of black shrimp is more robust: the closed finger of the hand is directed almost transversely. The hand of the cheliped of blue-spotted shrimp is intermediate in form--not as elongate as that of sand shrimp and not as robust as that of black shrimp. The differences in cheliped shape are not always distinctive in small shrimp but sand shrimp have a pair of spines on the fifth abdominal segment that can be used to separate small sand shrimp from small black shrimp. Blue-spotted shrimp are easily recognized (in life) by a prominent dark circular spot with a blue center surrounded by a black and then a yellow ring on each side of the 6th abdominal segment (Carlton and Kuris 1975).

The sexes of mature crangonid shrimp are easily distinguished. Sand shrimp sexes can be distinguished at about 26-30 mm while blue-spotted and black shrimp can be separated at 22-24 mm (Israel 1936; Krygier and Horton 1975; Siegfried 1980). The most distinguishing characteristic separating the sexes is the structure of the endopodite of the second pleopod (Lloyd and Yonge 1947; Meredith 1952). Males have an appendix masculina (Figure 4) on the endopodite of the second pleopod, whereas females do not, i.e., the first, second, and third pleopods look alike. The structure of the endopodite of the first pleopod is short and curved inward in males and long and straight in females. The location of the gonopore is still another distinguishing characteristic, but it is often difficult to recognize in preserved shrimp (Siegfried 1980). The gonopore is at the base of the fifth pair of walking legs in males and at the base of the third pair of walking legs in females.

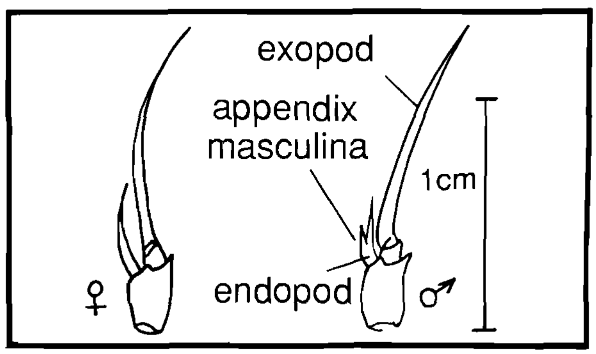

Figure 4. Sexual dimorphism in *Crangon franciscorum* (from Smith and Carlton 1975).

REASONS FOR INCLUSION IN SERIES

The crangonid shrimp of the California coast have been fished commercially since the 1800's. This commercial fishery was centered in San Francisco Bay. Before the 1960's, most of the catch was dried and shipped to the Orient, but part of it went to the fresh fish markets (Israel 1936). After the 1960's, the fishery became primarily a bait fishery, and annual harvests were less than 200,000 pounds.

The importance of crangonid shrimp in the food web of coastal estuaries is well documented. These shrimp are often the predominant food of the principal sport and commercial fishes of the Pacific coast estuaries (Johnson and Calhoun 1952; Ganssle 1966; Haertel and Osterberg 1966; Boothe 1967). Crangonids are opportunistic predators that feed on the most abundant small epibenthic and benthic fauna and thus serve as an important step in the transfer of energy from the primary consumers and detritivores to the top predators of estuarine food webs.

The agitation of bottom sediments by crangonids in search of food and protection may be important in the cycling of nutrients in coastal systems (Lloyd and Yonge 1947). Fecal pellets of crangonids are important substrates for bacterial colonization and may be important in nutrient regeneration in shallow water habitats (Knight 1978). Nitrogen excretion by large populations of crangonids in shallow water may have important influences on the nitrogen budget of coastal systems (Nelson et al. 1979). Crangonid shrimp have recently become the subject of research on aquaculture potential of native decapods (Knight 1978) and as a standard bioassay test organism for west coast estuaries (Dr. P. Sheehan, Aqua Terra Technical; pers. comm.).

LIFE HISTORY

Spawning and Larvae

Crangonid shrimp carry their eggs under the abdomen attached to and between the basal joints and inner rami of the pleopods. The distribution and abundance of ovigerous females is a useful index of reproductive activity. Several investigators have reported that the spawning season of crangonid shrimp is long. Ovigerous females have been reported to occur during 9 to 12 months of the year in various populations (Israel 1936; Lloyd and Yonge 1947; Meredith 1952; Price 1962; Krygier and Horton 1975).

Ovigerous females of the three species reviewed in this report can be found year-round along the California coast. Ovigerous sand shrimp are usually most abundant in the spring and summer in coastal embayments but are abundant offshore in winter (California Department of Fish and Game 1987). The abundance of ovigerous black shrimp is generally bimodal, peaking in winter-spring and summer-fall. They are usually found in embayments; few are collected in nearshore areas. Ovigerous blue-spotted shrimp are usually most abundant in nearshore coastal areas, peaking in winter (California Department of Fish and Game 1987).

Israel (1936) reported that both male and female sand shrimp live for about one year. More recent investigations suggest that females may live 1.5 to 2.5 years and males 1.5 years (Hatfield 1985; Kinnetic Laboratories 1987). Repeated spawning has been demonstrated by the presence of females bearing ovarian stages 5-7, early in the spawning season, as well as eggs on their egg pad (Israel 1936; Krygier and Horton 1975).

Ovigerous black shrimp females usually remain partly buried in the sediment during the day. The eggs usually hatch at night. Females emerge from the sediment and beat their pleopods, generating currents that release the newly hatched larvae. The females are usually free of eggs by dawn (Villamar and Brusca 1988).

The brood sizes of crangonid shrimp are related to shrimp size and species. Siegfried (1980) determined the best fit relationship between brood size of sand shrimp from San Francisco Bay and total length to be:

$$\text{Log } N = -3.66 + 4.09 \text{ Log } TL,$$

where N = number of eggs and TL = total length (mm). (Lengths given refer to total length, from the tip of the rostrum to the distal end of the telson.) Brood size ranged from about 1,200 eggs for shrimp 48 mm long to about 7,000 eggs for females 65 mm long. Kinnetics Laboratories (1983) reported a linear relationship between sand shrimp brood size and length:

$$N = -16{,}542 + 339.6(TL).$$

Brood size ranged from 2,499 to 8,840 eggs for shrimp from 55 to 71 mm long. Both relationships account for 81% of the variation in brood size and predict similar brood sizes for shrimp >55 mm but differ in their predictions of brood sizes of smaller shrimp. Krygier and Horton (1975) reported a similar range of brood size for sand shrimp from Yaquina Bay, Oregon: brood sizes ranged from 1,900 to 4,800 eggs in shrimp of similar lengths. The relationship between length and brood size in blue-spotted and black shrimp of the California coast has not been investigated. Black shrimp in Yaquina Bay, Oregon, had length-brood size relations similar to those of sand shrimp, but broods were somewhat larger for each given length (Krygier and Horton 1975).

Eggs hatch directly into late zoea-stage larvae (Shaner 1978), which swim dorsal sides up and with abdomens hanging vertically. Sand shrimp are reported to require seven larval stages to complete metamorphosis to post-larva, which required 19-20 days at laboratory temperatures of 20 °C and 20-25 days 16 °C (Mondo 1980; Shaner 1978). The larval stages are believed to require 30-40 days at field temperatures (Hatfield 1985). The larvae of black shrimp molt to a megalops 24-30 days after hatching (Villamar and Brusca 1988).

Early-stage larvae are generally found in near-surface waters and late stage larvae near the bottom. Early larvae would be expected to occur in the nearshore zone, transported there by offshore surface currents or released from reproductive females. Late-stage larvae are more likely to be transported onshore or upstream in the shoreward moving lower layer of the water column (Siegfried et al. 1978; Hatfield 1985). Abundance of crangonid larvae generally corresponds to this expected pattern (California Department of Fish and Game 1987). Seasonal abundance of larvae is generally bimodal, with a large spring peak and a smaller fall peak (California Department of Fish and Game 1987).

Postlarvae and Juveniles

Postlarvae, the smallest juvenile stages of crangonid shrimp, are 5-10 mm long and cannot be distinguished to species (Siegfried 1980; California Department of Fish and Game 1987). Postlarvae occur over a wide range of salinity, from seawater to nearly fresh water, but are concentrated in more saline water (Siegfried et al. 1978; California Department of Fish and Game 1987). The preference of crangonid postlarvae for bottom waters places them in favorable currents for onshore and upstream transport. Postlarvae are abundant in San Francisco Bay in spring to early summer (California Department of Fish and Game 1987).

Crangonids longer than 10 mm can be identified to species and are considered juveniles. Most investigators have considered them to be juvenile or immature until they develop sexual characteristics, at lengths of 22-30 mm, although shrimp larger than this can still be immature. The abundance of juvenile crangonid shrimp commonly peaks in spring and summer; a smaller peak may develop in late summer and fall (California Department of Fish and Game 1987).

The abundance of juvenile sand shrimp generally peaks in spring and summer in low salinity waters of coastal embayments (Siegfried 1980; Hatfield 1985). Juveniles occur in nearly fresh water (<1 ppt) but move to water of higher salinity as they mature. Juveniles of blue-spotted and black shrimp generally have abundance peaks in spring but live in higher-salinity regions. Juvenile blue-spotted shrimp are uncommon in coastal embayments because they prefer the higher-salinity water offshore; they are rare in waters of <25 ppt salinity.

Juvenile (and adult) black shrimp are rare in waters of <10 ppt salinity (California Department of Fish and Game 1987).

Migrations

Both sand shrimp and black shrimp migrate to deeper, more saline water as they mature (Krygier and Horton 1975; Siegfried 1980; Hatfield 1985). This out-migration from low-salinity water appears to be related to reproduction, as it coincides with the development of sexual characteristics. The migration is particularly pronounced in sand shrimp. Juveniles are often found in the upper reaches of estuaries, in nearly fresh water. As the shrimp mature, they move to water of higher salinity, which may result in size gradients in sand shrimp populations. The mean length of sand shrimp collected in midsummer in the San Francisco Bay Estuary ranged from 31 mm near the upstream limit of their distribution (1 ppt) to >50 mm in the central bay (Siegfried et al. 1978; Siegfried 1980).

Further evidence for an outward migration related to reproductive state is provided by information on mean salinity of occurrence of females bearing eggs of various stages (California Department of Fish and Game 1987). The range of salinity for the three crangonid species is more restricted for ovigerous females than for other life stages. Females bearing stage-1 eggs are found at salinities of 0.1 to 33.8 ppt (mean 20 ppt). Ovigerous sand shrimp are generally found only at salinities greater than 14.6 ppt (Hatfield 1985; Krygier and Horton 1975). The average salinity appears to increase with egg stage (up to 24.6 ppt for those with stage-4 eggs; California Department of Fish and Game 1987). Females bearing stage-4 eggs were not collected from waters of salinity less than 3.7 ppt.

Ovigerous black shrimp apparently prefer somewhat higher salinities of about 25 ppt (California Department of Fish and Game 1987); their outward migration is less extensive because they do not penetrate as far inland as sand shrimp. Blue spotted shrimp prefer even higher salinities; ovigerous females are scarce in embayments but abundant offshore (>30 ppt; California Department of Fish and Game 1987).

The outward migration of crangonid shrimp is believed to be related to temperature-salinity interactions. Ovigerous females are found in coastal embayments in summer but are uncommon in them in winter; they seemingly migrate offshore in winter, possibly in response to water temperature fluctuation (Hatfield 1985). This offshore population then contributes larvae and postlarvae for the spring abundance peaks.

Sand shrimp also undergo diel vertical migrations. Siegfried et al. (1978) first reported a diel pattern in which the shrimp enters the water column and disperses through the water column at night but remains on or near the bottom during daylight. The ecological significance of this behavior remains unknown, but the habit may serve to allow feeding near the surface while protected by darkness from visual feeding predators (fish). Migration into the water column may also be a response to the movement of their primary food, *Neomysis mercedis*, into the water column (Welch 1970; Siegfried et al. 1979). Additional studies substantiated the diel activity patterns of sand shrimp and *N. mercedis* (Sitts 1978). There is no comparable information on the diel activity patterns of the other crangonids of the California coast.

Adults

Male black shrimp in Yaquina Bay, Oregon, have been reported to be mature--i.e., to contain ripe sperm--at lengths of 26-28 mm; male sand shrimp matured at 34 mm (Krygier and Horton 1975). Ovigerous females as short as 36.2 mm for black shrimp and 43.6 mm for sand shrimp were reported by Krygier and Horton (1975) in Oregon waters. These lengths at maturity agree well with findings in California (Israel 1936; Siegfried 1980).

Israel (1936) reported a seasonal variation in the sex ratio of sand shrimp from San Francisco Bay: males predominated before the breeding season and females predominated during the peak of the breeding season. This variation can be attributed to the short life span of males, which are believed to die soon after copulation, and the longer life span of at least some of the breeding females. In general the sex ratios of crangonid populations of the Pacific Southwest appear to be about 1:1. This ratio is expected in nonsynchronously spawning populations in which a portion of the population has more than one brood (Krygier and Horton 1975).

GROWTH

In all crangonids, males and females grow at different rates (Lloyd and Yonge 1947; Meredith 1952; Allen 1960; Price 1962; Krygier and Horton 1975; Siegfried 1980). The length of male sand shrimp from San Francisco Bay rarely exceeded 50 mm although some individuals as long as 71 mm long have been collected (California Department of Fish and Game 1987). Female sand shrimp longer than 70 mm were commonly collected (Israel 1936; Siegfried 1980). In the somewhat smaller black shrimp, males generally reached 40 mm and females 60 mm (Israel 1936). The longest black shrimp reported from San Francisco Bay were 59 mm (male) and 64 mm (female) long. The maximum size of blue-spotted shrimp is believed to be similar to that of black shrimp. The length of crangonids in San Francisco Bay are somewhat greater than in Oregon, where Krygier and Horton (1975) reported maximum lengths of <40 mm for male and <55 mm for female black shrimp and 50 mm (males) and <62 mm (females) for sand shrimp. The shrimp may grow larger in San Francisco Bay because water temperatures are higher there than in Oregon, presumably leading to faster growth or longer growing seasons.

Offshore populations of crangonids may reach much larger lengths. Collections of sand shrimp off the mouth of the Columbia River indicate a population with a mean length >80 mm and maximum lengths of 110 mm (Durkin and Lipovsky 1977). Estuarine populations of the European species, *C. crangon*, attained smaller body sizes than nearby populations of the same species in marine habitats (Maucher 1961). Remane and Schlieper (1971) suggested that reduction in size of marine animals, although generally slight in higher Crustacea living in brackish water, is comparable to Bergmann's Law: size is related to features of the physical environment. The reduction may be attributable to the physiological effects of salinity, reduced food availability, or a combination of these and other factors. Studies of osmotic regulation indicated that smaller sand shrimp are capable of better hyper-regulation but larger ones are capable of better hypo-regulation (Shaner 1978). Thus, the migration of larger shrimp to high salinity waters would be energetically advantageous and may lead to faster growth.

Growth rates are extremely difficult to estimate from size-frequency histograms derived from field collections of crangonid shrimp. Immigration, emigration, temperature and salinity effects, and differential mortality combine to obscure growth patterns. Krygier and Horton (1975) estimated that the growth of juveniles ranged from 0.76 to 1.37 mm per week in Oregon. Growth rates of crangonids in California are somewhat higher. Kinnetics Laboratories (1984) estimated male and female sand shrimp >30 mm long to grow 1.7 to 2.4 mm per month.

Length-weight relationships for juvenile, male, and female sand shrimp were given by Siegfried (1980). The regression equations describing these relationships follow:

juveniles: $\text{Log } W = -5.41 + 2.58 \text{ LogTL}$
males: $\text{Log } W = -6.12 + 3.27 \text{ LogTL}$
females: $\text{Log } W = -6.62 + 3.57 \text{ LogTL}$

where W = dry weight in grams and TL = length in mm. Analysis of covariance revealed significant differences in slopes between the length-weight regressions of juvenile and mature shrimp. The difference is at least partly attributable to gonadal development.

Mortality

Annual abundance of crangonid shrimp varies widely (Siegfried 1980; California Department of Fish and Game 1987). Annual abundance indices for sand shrimp in San Francisco Bay were several orders of magnitude higher in some years than in others from 1980 to 1985, and that of blue-spotted and black shrimp varied by more than tenfold (California Department of Fish and Game 1987). Annual abundance of crangonid shrimp appears to be determined mostly by mortality of larvae and postlarvae. Mortality due to predation is undoubtedly high and may explain geographic patterns of abundance within embayments (Kinnetic Laboratories 1983; Kuipers and Dapper 1984). Recruitment to bay populations in any one year, however, appears to depend on environmental conditions.

Recruitment of crangonid shrimp to San Francisco Bay is independent of the abundance of ovigerous females, i.e., the parent stock. Correlations between annual abundance of crangonid larvae and postlarvae and of ovigerous females are non-significant (California Department of Fish and Game 1987), suggesting that environmental conditions play a major role in determining annual abundance. Thus, management to maintain crangonid populations should be aimed at maximizing recruitment (Christmas and Etzold 1977).

Annual abundance of crangonid shrimp has been linked to the volume of freshwater flow to San Francisco Bay (California Department of Fish and Game 1987). The volume of freshwater inflow determines the magnitude of seaward and landward currents, the salinity regime, temperature, and the distribution and abundance of other organisms including crangonid predators and prey (Siegfried et al. 1979; Armor and Herrgesell 1985). All of these factors play major roles in determining crangonid recruitment and mortality.

Disease and Parasites

Crustaceans are subject to infection by bacteria, fungi, protozoans, platyhelminths, and nematodes which can cause disease (Green 1968; Couch 1978; Overstreet 1978). Although infestation of crangonids by these groups has been observed (C.A. Siegfried, pers. obs.), there is little information on the incidence of infection or the effects on crangonid populations. In crangonids of San Francisco Bay, the incidence of infection by microsporidian protozoans is often high (C.A. Siegfried, pers. obs.).

The bopyroidean branchial isopod, *Argeia pugettensis*, an ectoparasite in the branchial chamber, often infects crangonids in San Francisco Bay (Nelson and Simmons 1978) and in Yaquina Bay, Oregon (Krygier and Horton 1975). It attacks shrimp in San Francisco Bay only in higher-salinity waters. Krygier and Horton (1975) reported only female parasitized sand shrimp in Yaquina Bay, Oregon; however, no parasitized ovigerous females were found. In San Francisco Bay almost all parasitized shrimp appeared to be females (Nelson and Simmons 1978). Since it is unlikely that the isopod would attack only females, and since castration by parasites is reported for other crustacean species, it is likely that the attachment of *A. pugettensis* results in castration in sand shrimp (Nelson and Simmons 1978). Castration would inhibit gonadogenesis and castrated male shrimp would take on feminizing characteristics, including larger size. A larger host would presumably make more energy available to the parasitic isopod. Since host and parasite weights are positively correlated, early attachment of the parasite and growth with the host is indicated (Nelson and Simmons 1978; Kinnetics Laboratories 1987; Jay 1989).

Whether female or castrated male, parasitized crangonid shrimp are still significantly smaller than nonparasitized shrimp, as shown in a field study conducted in Humboldt Bay. The study suggests that there are slower growth rates in the parasitized shrimp (Jay 1980). Preliminary laboratory investigation reveals that parasitism by *A. pugettensis* depresses metabolic rates (oxygen consumption) in sand shrimp but does not affect excretion rates (Nelson and Simmons 1978).

THE FISHERY

The earliest commercial fishing for crangonid shrimp along the California coast is believed to have been done in San Francisco Bay in the late 1860's by Italian fishermen (Scofield 1919; Bonnot 1932; Israel 1936). The shrimp were taken in bag seines 18.3 m long by 2.4 m deep. The catch of crangonid shrimp greatly increased when Chinese fishing camps appeared in 1871. The Chinese introduced the use of the Chinese shrimp net, a funnel-shaped net 12.1 m long with a mouth 9.1 m wide. These nets were held stationary by a system of lines and anchors, and shrimp were captured as they were carried into the net by the tide. Chinese nets were set during a single ebb or flood tide and then lifted just before the tide turned. By 1897, 26 Chinese fishing camps operated 20 to 50 nets each in San Francisco Bay, landing 400 to 8,000 pounds of shrimp per camp per day. In the early 1890's, crangonid shrimp were also caught in Tomales Bay, north of San Francisco, but the fishery was abandoned by about 1895 (Bonnot 1932).

The local market for crangonid shrimp was saturated soon after the Chinese began shrimp fishing. However, a profitable export trade soon developed, based on the shipment of dried shrimp to the Orient. The use of Chinese shrimp nets was investigated by the California Fish and Game Commission in 1897 and again in 1910, largely to assess the loss of young fish (particularly striped bass, *Morone saxatilis*) in the Chinese nets. In 1901 the California State Legislature established a closed season to shrimp fishing from May to August. By 1911 the Chinese shrimp nets were prohibited, but in 1915 a law was passed to allow limited use of the nets in parts of San Francisco Bay (Scofield 1919).

Trawl shrimp fishermen began operating in San Francisco Bay in about 1910. Trawl fishermen used trawls with beams of 5.5 to 6.1 m and an 18.3-m funnel-shaped net. The trawl was dragged over the bottom in the direction of the tide. A single haul lasted from 40 min to 2 h, and a day's work consisted of making 2-4 hauls and catching a total of 100 to 1,000 pounds of shrimp (Fry 1933).

The annual shrimp catch in San Francisco Bay exceeded 720 t for much of the 1920's and 1930's; the peak catch of more than 1,591 t was made in 1935 (California Department of Fish and Game 1987). The annual catch did not exceed 455 t during the 1940's and 1950's, and had declined to less than 45 t by the late 1950's, it did not exceed 114 t except in 1978 when 216 t were landed (California Department of Fish and Game 1987).

The catch of crangonid shrimp continued to be used for fresh or dried food until the 1960's. However, the demand declined steadily after the 1930's and the fishery became a bait fishery, supplying sport fishermen. Crangonid shrimp are too small to shell and market economically. The bait fishery relies entirely on trawls to capture shrimp.

The sport fishermen of the region will probably continue to support a bait fishery landing 68-91 t of crangonid shrimp annually. The prospect of expansion of the fishery is poor.

ECOLOGICAL ROLE

Little is known about the ecology of larval and postlarval crangonids. The larvae are presumably predators on small zooplankters, such as copepods. Larvae have been maintained in the laboratory on a diet of *Artemia* nauplii (Shaner 1978).

Juvenile and adult crangonids are predaceous, their dietary differences being related to shrimp size and prey availability (Siegfried 1982; Wahle 1985). Seasonal and geographical dietary studies have indicated that crangonid prey in the diet is generally proportional to their occurrence in an estuary (Siegfried 1982; Wahle 1985). Wahle (1985), who studied the feeding ecology of sand shrimp and black shrimp in San Francisco Bay, found that these species feed on a similar array of benthic prey made up of crustaceans, polychaetes, mollusks, foraminiferans, and plant material. Amphipods were the most frequently ingested; barnacle exuvia, fish eggs, bryozoans, hydrozoans, and mites were occasionally ingested. Black shrimp ate significantly more amphipods than did sand shrimp. Larger crangonids ate larger prey. Foraminiferans, copepods, and ostracods were taken by small shrimp, while shrimp, polychaetes, and isopods were taken by large shrimp.

In the less saline regions of the San Francisco Bay Estuary--the delta region--the most important food of sand shrimp is the opossum shrimp, *Neomysis mercedis*, which occurred in

62%-84% of all sand shrimp gastric mills containing prey (Siegfried 1982). Larger crangonids ate larger mysids. Sitts and Knight (1979) suggested that predation by sand shrimp affected the population structure and abundance of mysids in the delta.

The distribution of *N. mercedis* does affect the distribution of sand shrimp in the San Francisco Bay Delta (Siegfried 1980). Not only is crangonid density much greater in locations where mysids are abundant, but crangonids in areas of high mysid density take more prey than those in areas of low prey density (Siegfried 1982). The delta region of San Francisco Bay has impoverished benthic communities (Nichols 1979) and thus the region has few potential prey organisms. This may be an important factor linking the distributions of crangonids and mysids in the delta region of San Francisco Bay.

Crangonid shrimp are important food for many estuarine fish. They have been reported to be important in the diets of striped bass (Johnson and Calhoun 1952; Huebach et al. 1963; Ganssle 1966; Kinnetic Laboratories 1983); white sturgeon, *Acipenser transmontanus* and green sturgeon, *A. medirostris* (Ganssle 1966; McKechnie and Fenner 1971); and staghorn sculpin, *Leptocottus armatus*, (Ganssle 1966; Boothe 1967; Kinnetic Laboratories 1983). They are also an important food of American shad, *Alosa sapidissima*; brown smoothhound, *Mustelus henlei*; Pacific tomcod, *Microgadus proximus*; and white catfish, *Ictalurus catus* (Ganssle 1966).

Crangonid shrimp recycle nutrients during their feeding activities. Agitation of bottom sediments by crangonids searching for food and shelter has been suggested as an important mechanism of nutrient recycling in estuaries (Lloyd and Yonge 1947). Nitrogen excretion by large populations of crangonids can have important effects on the nitrogen budget of estuarine systems (Nelson et al. 1979).

ENVIRONMENTAL REQUIREMENTS

Temperature

Water temperature is a critical factor not only in survival but in the regulation of most life functions of cold-blooded organisms such as crangonid shrimp. Water temperature affects metabolic, growth, and feeding rates, osmoregulation, movement, habitat selection, and survival (Prosser 1950). The discharge of heated effluents may restrict the distribution of crangonids or other cold-blooded organisms in estuarine systems, and sudden temperature changes may be lethal.

The seasonal migrations of crangonids have been linked to changing water temperatures. The spring onshore migration of juveniles may be a migration to warmer waters and the fall-winter offshore movement of mature shrimp may be a migration to cooler waters (Israel 1936; Krygier and Horton 1975; Siegfried 1980; Hatfield 1985). Decreasing water temperature resulted in the movement of *C. septimspinosa* from shallow to deeper areas of Chesapeake Bay (Haefner 1976). Havinga (1930) suggests that the seasonal migrations of *C. crangon* can be explained as a search for the warmest water mass.

Crangonids of the Pacific Southwest have been collected over a wide range of temperatures; sand shrimp, 6.3 to 23.9 °C, black shrimp, 6.7 to 22.1 °C; and blue-spotted shrimp, 7.8 to 20.2 °C (California Department of Fish and Game 1987). Sand shrimp are abundant at >15 °C, black shrimp at <18 °C, and blue-spotted shrimp at 14-18 °C.

Temperature tolerance in adult sand shrimp under laboratory conditions was reported by Khorram and Knight (1977a). The research indicated a significant interaction between temperature and salinity on survival: water temperature affected survival at different salinities and salinity affected survival at different temperatures. In general, survival of adult sand shrimp was poor at water temperatures below 10 °C or above 20 °C, and decreased with decreasing salinity. The optimum ranges of temperature and salinity for adult sand shrimp, as determined by response surface analysis (a statistical technique that determines optimum response to more than one variable), was 14.5-17.0 °C and 18-20 ppt. The authors concluded that temperature was slightly more important than salinity in determining adult survival (Khorram and Knight 1977a).

Salinity

Crangonids are euryhaline, occurring at salinities from nearly fresh water to seawater (Siegfried 1980; Hatfield 1985). Sand and black shrimp have been collected from San Francisco Bay at salinities of 0.1-34.3 ppt and blue-spotted shrimp at the somewhat narrower range of 4.5-34.3 ppt (California Department of Fish and Game 1987). Blue-spotted shrimp are generally abundant only in water with salinity >23 ppt. Black shrimp are generally more abundant in water with salinity >23 ppt. Black shrimp are generally most abundant in waters of salinity >10 ppt and sand shrimp at salinities <19 ppt (California Department of Fish and Game 1987). These salinity ranges are based on the abundance of juvenile and adult stages. Adult crangonids, and particularly ovigerous females, prefer the higher end of the salinity range.

The seasonal distribution of crangonids, particularly sand shrimp, along the California coast is closely related to salinity. Although the sand shrimp inhabits brackish water during much of its life cycle, it requires relatively high salinities for reproduction. Ovigerous females are rarely collected where salinity is low. Ovigerous females are found year-round in San Francisco Bay, but almost never in the less saline portions of the bay (Israel 1936; Siegfried 1980; Hatfield 1985). Energetic demands of osmoregulation at low salinities may preclude egg development and thus reproduction in low salinity waters. Broekema (1941) showed that low salinities retard egg development in crangonids. Salinity is thus important in larval survival; preliminary investigations suggested that survival of larval sand shrimp declined at salinities below 12 ppt (S.W. Shaner, Univ. Calif., Davis, unpubl.)

Salinity tolerance was significantly affected by water temperature. At 5 ppt salinity, the 96-h survival was zero at 5 °C and 25 °C, but ranged from 30% to 42% at intermediate temperatures; in waters of 25 ppt salinity, survival after 96 h was >80% at 10 °C and 15 °C but 60% at 5 °C (Khorram and Knight 1977a). More recent salinity tolerance investigations indicated that juvenile sand shrimp were more tolerant of low salinity; survival was 100% in water of 2 ppt salinity (S.W. Shaner, unpubl.) Sand shrimp from high salinity waters (20-30 ppt) acclimated to low salinity (2.2-5.5 ppt) in the laboratory within 5-6 weeks. At this time, they physiologically resembled sand shrimp from low salinity (1-7 ppt) waters (Shaner et al. 1985).

The upstream distribution of sand shrimp in the San Francisco Bay Estuary is limited by low salinity. In extensive collections from this system between 1976 and 1985, almost no crangonids were taken in water of <1 ppt salinity (Siegfried 1980; California Department of Fish and Game 1987).

Temperature-Salinity Interactions

The response of crangonids to changes in temperature and salinity are highly interdependent (Khorram and Knight 1977a). Researchers disagree about the relative importance of each of these factors in crangonid distribution. Havinga (1930) and Haefner (1976) suggsted that temperature is the most important factor. Krygier and Horton (1975), Siegfried (1980), and Hatfield (1985), indicated that salinity was the most important factor determining sand shrimp distribution. Both factors are important in determining black shrimp distribution; temperature is most important in summer and salinity in the winter (Krygier and Horton 1975).

Laboratory investigations of the interactive effect of temperature and salinity on the survival of adult sand shrimp indicated optimum temperature and salinity ranges of 14.5-17.0 °C and 18-20 ppt (Khorram and Knight 1977a). The range of temperature and salinity optima decreased with increasing exposure times. The optimum ranges of temperature and salinity were 8.0-22.5 °C and 13-25 ppt for a 24 h exposure; 9.5-21.0 °C and 14.0-24.5 ppt after 48 h; and 12-19 °C and 15.5-22.0 ppt after 72 h.

Substrate

Little information is available relating crangonid distribution to substrate type. Crangonids are found on substrates ranging from mud to peat to sand (Israel 1936; Carlton and Kuris 1975). They appear to be particularly suited to sand-mud substrates by being able to nestle and bury themselves into the substratum using their pleopods and walking legs. Some crangonid species are reported from the rocky intertidal zone (Carlton and Kuris 1975).

The dorsally flattened crangonids usually spend days in shallow depressions in the substrate with just the eyes above the substrate. In laboratory aquaria this behavior occurs on sand as well as on softer substrates. Substrate selection by crangonids is undoubtedly influenced by prey availability as well as habitat considerations. Benthic prey is generally not abundant on coarse sediments in San Francisco Bay but is abundant and diverse on softer, more organic sediments (Nichols 1979). These richer sediments are often the preferred substrates of crangonids.

Freshwater Flow

Freshwater flow to estuarine systems affects water temperature, salinity, substrates, seaward and landward currents, and the distribution of potential prey and predators. During periods of high freshwater flows, seaward and residual landward currents are high and salinity intrusion is low. During periods of low freshwater flows, currents are reduced, high salinity waters intrude higher into the estuary, and water temperatures tend to be higher. These differences in current patterns and temperature-salinity regimes lead to important differences in recruitment and habitat availability for crangonids and their prey and predators.

The recruitment of crangonids to the San Francisco Bay Estuary appears to be linked to variations in current patterns related to freshwater flow. Ovigerous females occur in high salinity portions of the estuary and in the offshore region (California Department of Fish and Game 1987). Larvae are released in these regions, and since they are generally in the water column they can be entrained by surface currents moving seaward. Crangonid postlarvae congregate near bottom and are thus more likely to be transported upstream or landward in the landward flowing lower layer of water (Siegfried et al. 1978). The interaction of currents flowing seaward and landward thus determines recruitment of crangonids to the estuary.

Correlation analysis of annual abundance of sand shrimp in relation to freshwater flow to San Francisco Bay indicates some highly positive relations (California Department of Fish and Game 1987). The annual abundances of postlarvae, juveniles, and all sand shrimp stages combined were positively correlated with freshwater flows during the period from 1980 to 1985. The abundances of early and mid-stage crangonid larvae in San Francisco Bay were negatively correlated with freshwater flow. This is consistent with a life history pattern in which larvae are planktonic in the upper layers of the water column and are carried offshore during high freshwater flows. In years of high freshwater outflow, a larger proportion of the reproductive population moves from embayments to the nearshore coastal area, resulting in more larvae hatched outside the embayments (K. Hieb, California Department of Fish and Game, Stockton, CA; pers. comm.). The annual abundance of black shrimp is also correlated with freshwater inflow, but the relation is not as strong as that of sand shrimp (California Department of Fish and Game 1987). The annual abundance of blue-spotted shrimp, which does not show the extensive migration associated with development of sexual characteristics, is not correlated with freshwater outflows.

The volume of freshwater outflow, and thus the location of the sediment entrapment zone associated with the salinity gradient in the San Francisco Bay Estuary, has been linked to variations in the annual abundance and distribution of *N. mercedis*, the principal food of sand shrimp in the upper estuary (Siegfried et al. 1979). The distribution of sand shrimp in the upper estuary has in turn been related to the distribution of *N. mercedis* (Siegfried 1980). Thus, the distribution of crangonids can also be affected indirectly as well as directly by freshwater flow. The distributions and abundances of many species of fishes in the San Francisco Bay system are also influenced by freshwater flows (Armor and Herrgesell 1985). Abundance of fishes appears to be higher during years of high freshwater flows. Potential predators as well as the prey of crangonid shrimp are thus affected by freshwater flow to the San Francisco Bay system.

Other Environmental Requirements

Other environmental factors, such as dissolved oxygen concentration, metals concentrations, pesticides, and other agricultural, municipal, and industrial pollutants may affect the distribution and abundance of crangonids. Khorram and Knight (1977b) reported the toxicity to sand shrimp of Kelthane, an organochlorine miticide once commonly used on vegetable, fruit, and grain crops in regions tributary to San Francisco Bay. The lethal threshold was estimated to be about 100 ppb. Kelthane and its breakdown products bioaccumulate in body tissue (Khorram and Knight 1977b). Shrimp exposed to this pesticide showed a characteristic sublethal response, including increased physical activity, and decreased feeding and molting rates.

Low dissolved oxygen concentrations, in combination with high water temperatures, are believed to limit the occurrence of crangonids in several streams tributary to San Francisco Bay (Israel 1936; Nichols 1979; Kinnetic Laboratories 1983). Sand shrimp were abundant upstream from San Francisco Bay, into the Sacramento River, during years of low freshwater flows (Siegfried 1980). Crangonid shrimp were not collected from the San Joaquin River in Siegfried's study (1980) even though the temperature and salinity regimes in each river are similar. The San Joaquin River receives more industrial and agricultural effluent than the Sacramento River, relative to its discharge. This increased effluent may create water quality differences between the two rivers that limit shrimp distribution.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are prepared to assist in environmental impact assessments. Crangonid shrimp once were important in an export fishery but are now the basis of a bait fishery in San Francisco Bay. The shrimp are important components of the estuarine system, serving as an important food of almost all sport and commercial fishes of west coast estuaries. Spawning occurs in waters of >15 ppt salinity. Ovigerous females are found year-round; abundance peaks in spring and summer in embayments and in winter offshore. Eggs hatch directly into planktonic zoea which require 30-40 days to develop into postlarvae. Larvae prefer surface waters, while postlarvae prefer bottom waters. Larvae are exposed to predominantly seaward currents and postlarvae to landward moving bottom currents. Juvenile crangonids are generally found in brackish to nearly fresh water but move to more saline waters as they mature. Crangonids are opportunistic predators of epibenthic and benthic forms. Annual abundance of crangonids in San Francisco Bay has been linked to the volume of freshwater flow to the estuary. Maintaining adequate freshwater flows to the estuary to ensure successful recruitment is vital to maintaining populations of this important component of the estuarine system.

17. Document Analysis a. Descriptors
Estuaries
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