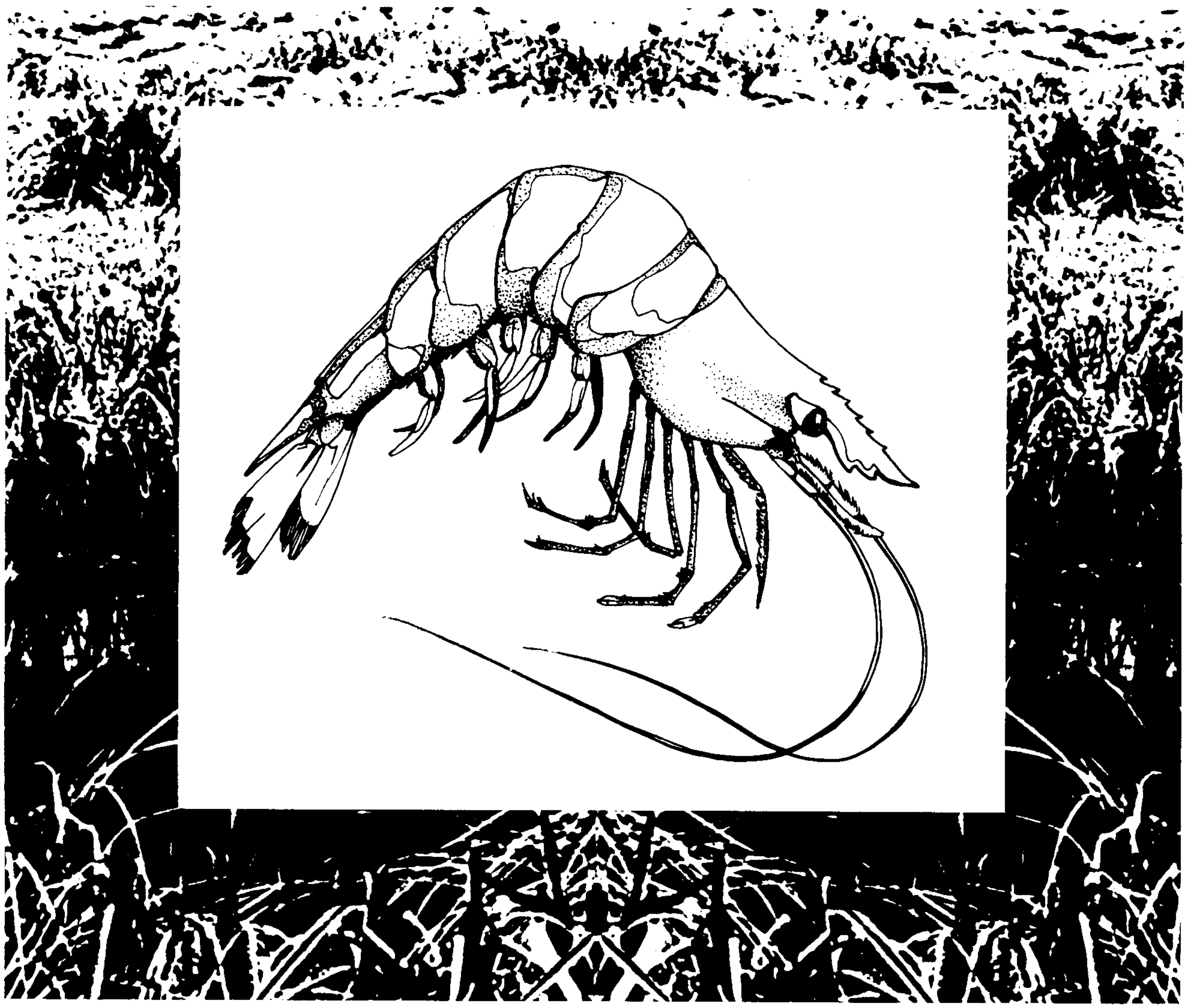
Biological Report 82 (11.35)
March 1985

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Gulf of Mexico)

GRASS SHRIMP



Coastal Ecology Group
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This is one of the first reports to be published in the new "Biological Report" series. This technical report series, published by the Research and Development branch of the U.S. Fish and Wildlife Service, replaces the "FWS/OBS" series published from 1976 to September 1984. The Biological Report series is designed for the rapid publication of reports with an application orientation, and it continues the focus of the FWS/OBS series on resource management issues and fish and wildlife needs.

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Gulf of Mexico)

GRASS SHRIMP

by

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Waterways Experiment Station
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National Coastal Ecosystems Team
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Research and Development
Fish and Wildlife Service
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Washington, DC 20240

This series should be referenced as follows:

U.S. Fish and Wildlife Service. 1983-19__. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. U.S. Fish Wildl. Serv. Biol. Rep. 82(11). U.S. Army Corps of Engineers, TR EL-82-4.

This profile should be cited as follows:

Anderson, G. 1985. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) -- grass shrimp. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.35) U.S. Army Corps of Engineers, TR EL-82-4. 19 pp.

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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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
kilometers (km)	0.6214	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	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

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

CONTENTS

ACKNOWLEDGMENTS

I am grateful for reviews and suggestions by Richard Heard, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; Henry Tatum, U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, Mississippi; and Steven Ross, Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, Mississippi.

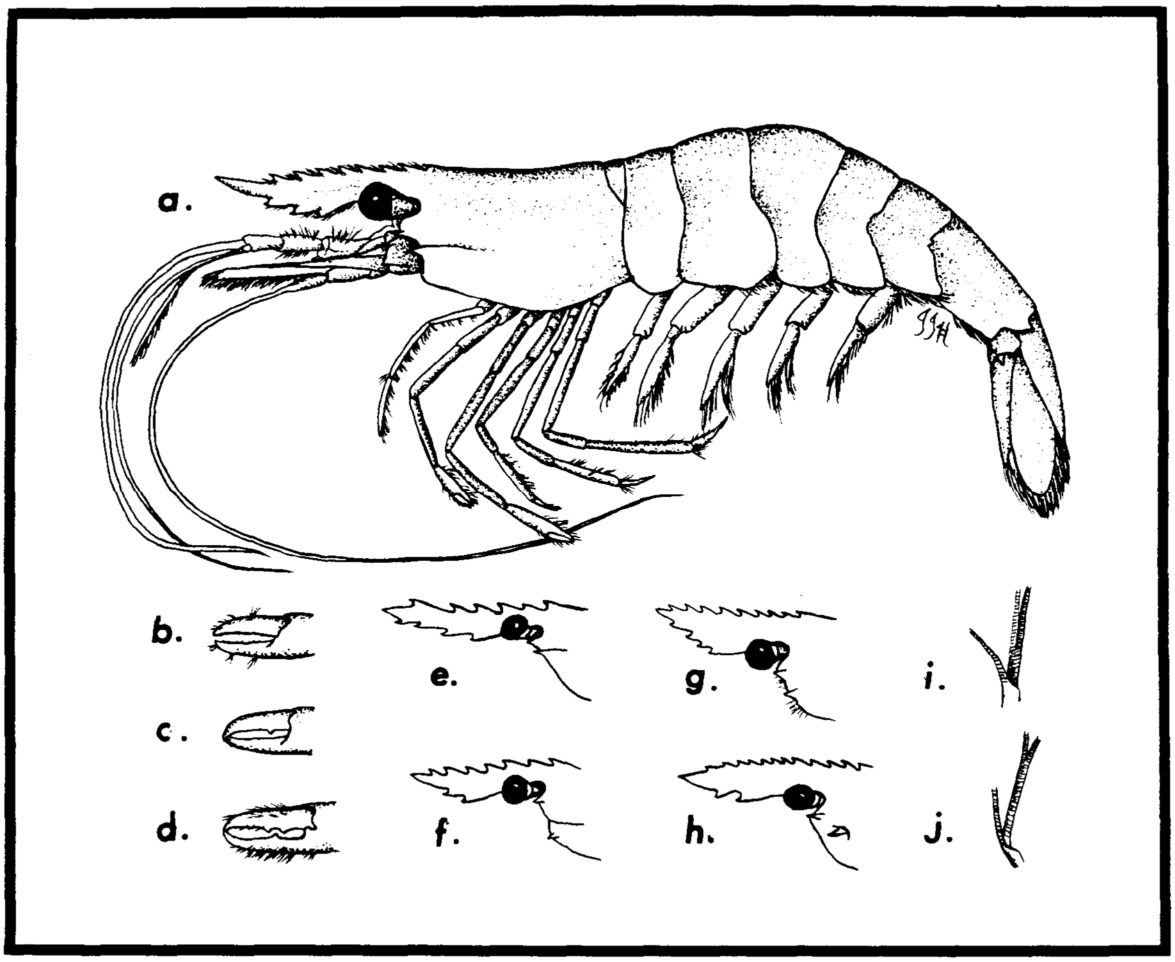

Figure 1. Grass shrimp. a. Palaemonetes pugio; b-d, second chela of P. pugio, P. intermedius and P. vulgaris, respectively; e-h, anterior carapace and rostrum of P. paludosus, P. kadiakensis, P. vulgaris, and Macrobrachium ohione, respectively; i-j, antennule of "brackish water" and "freshwater" grass shrimp, respectively. Scale of drawings to specimens in mm is (a) 7 to 1, (b-d) 16 to 1, (e-g) 4 to 1, (h) 1.6 to 1, and (i-j) 2 to 1.

GRASS SHRIMP

NOMENCLATURE/TAXONOMY/RANGE

Scientific names .... Palaemonetes pugio; P. vulgaris; P. intermedius; P. paludosus; P. kadiakensis.
Common name .... Grass shrimp (Figure 1).
Other names .... Jumpers, glass shrimp, popcorn shrimp, glass prawns, hardbacks.

Subphylum....................Crustacea
Class.....................Malacostraca
Order.........................Decapoda
Family....................Palaemonidae

Geographic range and speciation: The grass shrimp in the Gulf of Mexico area consist of five species, all relatively similar in morphological characteristics and most with overlapping distribution. Because of their similarities, these species are often misidentified or lumped as *P. vulgaris*.

Although *P. paludosus* and *P. kadiakensis* are primarily freshwater species, both are somewhat tolerant of mesohaline conditions (Maguire 1961; Dobkin and Manning 1964; Strenth 1976) and may be encountered in both freshwater and brackish-water tidal marshes (Swingle 1971; Christmas and Langley 1973; Heard 1982).

MORPHOLOGY/IDENTIFICATION AIDS

Most of the information summarized in this section is taken from Holthuis (1952), Williams (1965), Wood (1974), and Heard (1982).

Several diagnostic features distinguish the caridean shrimps, to which the genus *Palaemonetes* belongs, from the penaeidean shrimps. In the caridean forms, the pleura of the second abdominal somite overlap those of the first, and the third walking legs lack claws or chelae (Figure 1a). *Palaemonetes* spp. and other members of the family Palaemonidae may be distinguished from members of the families Alpheidae, Processidae, and Hippolytidae by having the second walking leg with an unjointed carpus (the segment just proximal to the chela). The absence of mandibular palps in *Palaemonetes* distinguishes this genus from the other palaemonid genera *Macrobrachium* and *Palaemon*. Furthermore, unlike *Palaemonetes*, *Macrobrachium* bears hepatic spines (Figure 1h) and *Palaemon floridanus* has a prominent striped pattern on the carapace and abdomen.

Other morphological features of *Palaemonetes*, as well as many other caridean genera and families, include the following: well-developed rostrum bearing both dorsal and ventral teeth, a smooth carapace and abdomen, rounded abdominal pleura 1-4, well-developed eyes with globular pigmented corneas, well-developed spines on the telson (two pairs dorsally, two pairs posteriorly), and chelate walking legs 1-2 (the second legs are stronger than the first). Grass shrimp are transparent to yellowish brown. Few exceed 50 mm in total length. Males can be separated from females by the presence of the appendix masculina attached to the appendix interna on the endopod of the second pair of pleopods. Also, the endopod of the first pleopod is larger in males than in females of the same age. Additional details were provided by Holthuis (1952) and Williams (1965). Selected morphological features of adults of the five species of *Palaemonetes* common to waters of the Gulf of Mexico are compared in Figure 1a through 1j and Table 1. However, these features cannot be used to distinguish between juveniles of the brackish-water forms of *P. vulgaris*, *P. intermedius*, and *P. pugio* (Boston and Provenzano 1982). External genitalic details of males may also be used to distinguish between the five species (Fleming 1969).

REASON FOR INCLUSION IN SERIES

Brackish water *Palaemonetes* are among the most widely distributed, abundant, and conspicuous of the shallow water benthic macroinvertebrates in the estuaries of the Atlantic and Gulf Coasts (Wood 1967; Odum and Heald 1972; Welsh 1975; Sikora 1977). Although grass shrimp have only limited value as fish bait (Huner 1979) or food for cultured fish or humans, their ecological importance is unquestioned. Grass shrimp have been extensively documented as prey of fishes (Gunter 1945; Darnell 1958; Diener et al. 1974; Overstreet and Heard 1982) and other carnivores (Heard 1982) and they are instrumental also in transporting energy and nutrients between various estuarine trophic levels: primary producers, decomposers, carnivores, and detritivores (Johannes and Satomi 1966;

Table 1. Summary of morphological differences between five species of *Palaemonetes* (grass shrimp) in the coastal waters of the Gulf of Mexico (Holthius 1952; Williams 1965).

Characters	*P. vulgaris*	*P. intermedius*	*P. pugio*	*P. paludosus*	*P. kadiakensis*
Number of teeth on dactylus; fixed finger of second leg	2/1 (Figure 1d)	1/0 (Figure 1c)	0/0 (Figure 1b)	0/0 (Figure 1b)	0/0 (Figure 1b)
Rostral teeth	8-11 on dorsal surface; 1 on tip; 3-5 on ventral surface (Figure 1g)	7-10 on dorsal surface; 1 on tip; 4-5 on ventral surface	7-10 on dorsal surface; tip naked; 2-4 on ventral surface (Figure 1a)	6-8 on dorsal surface; tip naked; 3-4 on ventral surface (Figure 1e)	6-8 on dorsal surface; tip naked; 2-3 on ventral surface (Figure 1f)
Upper antennular flagellum	Fused part of the two rami shorter than free part (Figure 1i)			Fused part of the two rami longer than free part (Figure 1j)	
Position of branchiostegal spine	On anteroventral part of branchiostegal groove (Figure 1a, 1e, 1g)				Considerably ventrad to branchiostegal groove (Figure 1f)
Approximate maximum total length (mm)	42	42	50	47	53
Number, size, and color of eggs	Numerous, small, usually grayish brown			Few, large, usually greenish	

Adams and Angelovic 1970; Welsh 1975; Morgan 1980).

LIFE HISTORY

Spawning

The spawning season of grass shrimp extends from February through October but may vary with species and geographical location. An exception is P. paludosus, which spawns all year in southern Florida (Dobkin 1963). In the prespawning female, the ripening ovaries are discernable as greenish or grayish brown masses of tissue dorsal and posterior to the stomach, and additional setae develop on the ventral surface of the abdomen and thorax. The female's molting condition and subsequent mating and spawning were described for P. vulgaris by Burkenroad (1947). He reported that after molting, the female is receptive to the male but that apparently the male recognizes her condition only if physical contact is made with her exoskeleton.

During copulation, which must occur within 7 h after molting, the ventral surfaces of the partners are positioned so that their genital apertures are close together. A spermatophore is quickly extruded by the male onto the genital sternites of the female where it remains until oviposition. Before oviposition, which occurs within 7 h after sperm transfer, part of the spermatophore dissolves (probably due to enzymatic secretions from the female's oviduct) and the spermatozoa are released. Ova are fertilized externally as they are extruded, then manipulated against the pleopods and setae on the ventral surface of the abdomen where they adhere.

The eggs hatch 12 to 60 days after fertilization, depending on species and geographical location. In warmer climates, the incubation period is usually shorter. Osmotic swelling of the inner membrane, struggling by the larva (protozoea), and ventilatory movements by the female assist in freeing the larva from the egg membrane (Davis 1965). The female molts again within a few days after spawning and may produce an additional brood, depending on the species or time of spawning (Broad and Hubschman 1963; Knowlton and Williams 1970; Beck and Cowell 1976).

Fecundity

The fecundity of P. pugio in Rhode Island is greater than that of other shrimp populations that have been studied. For example, in June, the average number of eggs per female was 486 in Rhode Island (Welsh 1975); 372 in Texas (Wood 1967); and up to 247 in South Carolina (Sikora 1977). There was a significant positive correlation between the length (X) of an ovigerous female and the number of eggs (Y). Wood (1967) reported the relation to be $\log Y = 1.19 + 0.0408 X$. Egg counts of P. paludosus in Florida ranged from only 8 to 85; $\log Y = 0.6288 + 0.0294 X$ (Beck and Cowell 1976).

Development of Larvae

Larvae are planktonic and feed upon zooplankton, algae, and detritus. Depending on the species and environmental conditions, there may be from 3 to 11 morphologically distinct stages during larval development. Transition from one stage to the next occurs during molting. Intraspecific genotypic variability in the number of larvae and the morphology of different stages may enhance dispersal (Sandifer and Smith 1979).

Larval development has been described for each of the five species: P. vulgaris and P. pugio by Broad (1957), P. kadiakensis by Broad and Hubschman (1963), P. paludosus by Dobkin (1963), and P. intermedius by Hubschman and Broad (1974). Some additional interspecific differences in life histories, modified from Hubschman and Broad (1974), are shown in Table 2. The morphology and behavior of larvae and postlarvae differ. Larvae lack long appendages and swim almost continuously with the head down and the dorsal surface oriented toward the direction of horizontal movement. The duration of larval development may range from 11 days to several months for *P. pugio* (Floyd 1977), depending on environmental conditions. The final larval stage metamorphoses to a postlarva, which closely resembles the adult.

Maturation and Life Span

Juvenile *P. pugio* mature when they are 1.5 to 2 months old and about 15 to 18 mm long; their life span is 6 to 13 months (Alon and Stancyk 1982). The older, overwintering shrimp usually spawn early in the year and die by the next winter. Most young-of-the-year spawn late in the year as adults. Postlarvae that survive the fall and winter spawn in the following spring.

ECOLOGICAL ROLE

Food Habits

Grass shrimp eat a wide variety of aquatic foods. Depending on the availability of a particular food they may be detritivores, primary consumers, or secondary consumers (Odum and Heald 1972; Morgan 1980).

Table 2. Spawning season, fecundity, lengths (mm) at hatching and at metamorphosis, and number of larval molts for *Palaemonetes* spp. in the Gulf of Mexico.

Species	Spawning season	Fecundity (maximum observed)	Length (mm)[a] At hatching	At metamorphosis	Number of larval molts[a]
P. vulgaris	April-October[b]	No data	2.3	6.3	7-11
P. pugio	March-October[c]	486[d]	2.6	6.3	7-11
P. intermedius	May-September[b]	129[e]	3.5	7.0	6- 8
P. kadiakensis	February-October[f]	160[g]	4.4	7.5	5- 8
P. paludosus	Year round[h]	85[e]	3.8	4.5	3

[a]Data on length at hatching and metamorphosis and number of larval molts are from the following sources: *P. vulgaris* and *P. pugio*, Broad (1957); *P. intermedius*, Hubschman and Broad (1974); *P. kadiakensis*, Broad and Hubschman (1963); and *P. paludosus*, Dobkin (1963).
[b]Knowlton and Williams (1970).
[c]Wood (1967).
[d]Welsh (1975).
[e]Beck and Cowell (1976).
[f]White (1949).
[g]Meehean (1936).
[h]Dobkin (1963).

The fundamental role of grass shrimp as detritivores is explained by Odum and Heald (1972), Welsh (1975), and Adams and Angelovic (1970). As detritivores, grass shrimp aid in the mechanical breakdown of refractory organic material such as fibrous plant materials, as well as assimilate the associated microflora, microfauna, and fungi (Adams and Angelovic 1970). The assimilation of dissolved organic matter sorbed to finely divided particulate matter such as clay particles is important in grass shrimp nutrition (Odum and Heald 1972). Although grass shrimp often live among aquatic macrophytes (Adams and Angelovic 1970; Livingston et al. 1976; Heck and Orth 1980; Morgan 1980; Coen et al. 1981; Gore et al. 1981), there is little evidence that the macrophyte structure is actually consumed. More likely, grass shrimp eat and assimilate the epiphytic microalgae that coat the plant structure (Morgan 1980). Grass shrimp also are predators of meiofauna and small infaunal polychaetes, oligochaetes, nematodes (Sikora 1977; Bell and Coull 1978; Chambers 1981), epiphytic fauna (Odum and Heald 1972; Morgan 1980), and even motile prey such as mysids (Morgan 1980). As epibenthic predators and sediment disturbers, grass shrimp alter infaunal community structure (Bell and Coull 1978; Knieb and Stiven 1982). For example, in North Carolina a sharp decline in the abumdance of _P. pugio_ due to predation by mummichogs (_Fundulus heteroclitus_) brought about significant changes in infaunal composition.

Predation

In estuaries, numerous fish species and other aquatic carnivores, some of which are valuable sport and commercial fishes, eat large quantities of grass shrimp. Grass shrimp are also eaten by forage fishes such as _Fundulus_ spp. (Harrington and Harrington 1972; Welsh 1975; Knieb and Stiven 1982), which in turn are preyed upon by larger fishes. As prey, grass shrimp play an important role in the transfer of energy from the producer and decomposer levels to higher consumer levels.

Grass shrimp frequently inhabit water near underwater structures and are particularly attracted to dense stands of underwater macrophytes. These stands not only support an abundance and diversity of food for shrimp, but also provide a refuge from predators. Grass shrimp are more prone to predation when displaced from preferred substrata such as macrophytes (Coen et al. 1981; Heck and Thoman 1981) and oyster shells (Thorp 1976).

Parasites

Grass shrimp are hosts for numerous species of parasites and ectocommensals. The most abundant are coccidia (Solangi and Overstreet 1980), microsporidians (Overstreet and Weidner 1974), trematodes (Heard and Overstreet 1983), isopods (Anderson 1977), and leeches (Overstreet 1978). The biology of other host-parasite interrelationships involving _Palaemonetes_ spp. were summarized by Johnson (1977) and Overstreet (1978). Diseases and parasites do not appear to be major factors in limiting the abundance and growth of grass shrimp in the Gulf of Mexico.

Behavioral Ecology

Field studies have shown that the movement and distributional patterns of grass shrimp may be influenced by both photoperiod and tidal cycles. Swimming of European species, _Palaemonetes varians_, peaked in morning and evening (Antheunisse et al. 1971). The only observation on nocturnal movement of _P. pugio_ was documented by Shenker and Dean (1979), who reported that some shrimp are buried in the sediments during daylight. These studies, as well as that of Sikora (1977), indicated that grass shrimp in tidal creeks migrate seaward (downstream) or drift with the current during ebb tides and migrate upstream into tidal creeks during incoming tides.

During laboratory experiments on agonistic behavior in P. pugio and P. vulgaris, females were dominant over males and large shrimp were dominant over smaller ones. In interspecific pairings, P. vulgaris generally dominated P. pugio (Chambers 1981), and P. vulgaris is known to displace P. pugio from the preferred shell substratum (Thorp 1976). Such displacement may favor coexistence between these two sympatric species by reducing the future potential for agonistic behavior. Distributional differences between two sympatric species are believed to be caused by displacement of P. vulgaris by Palaemon floridanus from the preferred red algal substratum (Coen et al. 1981).

GROWTH CHARACTERISTICS

Because populations of grass shrimp may produce more than two broods a year, length-frequency distributions may be polymodal and growth rates are difficult to characterize (Sikora 1977). Grass shrimp population growth characteristics have been described for P. pugio in Texas (Wood 1967), South Carolina (Sikora 1977; Alon and Stancyk 1982), North Carolina (Knowlton and Williams 1970), and Rhode Island (Welsh 1975); and for P. paludosus in Florida (Beck and Cowell 1976). Growth rates vary somewhat between species, sexes, habitats, and times of year. These differences are exemplified in part by the different daily growth rates of P. pugio from two populations in South Carolina (Table 3).

According to Beck and Cowell (1976), P. paludosus grows 3.25 mm per month in summer and fall. In Rhode Island, the length of P. pugio increased rapidly from July through September; females had then reached a total length of about 3 cm and males about 2.6 cm. The growth of grass shrimp was negligible from September to May in Rhode Island (Welsh 1975). In contrast, one group of P. pugio in South Carolina is born and recruited in early spring, grows rapidly during summer, and dies before winter. A second group is recruited in late summer, grows rapidly in autumn and again the following spring, and usually dies by midsummer (Alon and Stancyk 1982). These age and growth characteristics make it difficult to tabulate lengths of grass shrimp of different ages.

Table 3. Mean daily growth increments (mm) of Palaemonetes pugio from two habitats in South Carolina (data from Alon and Stancyk 1982).

Locality and sex	Season: Summer	Winter
North Inlet		
female	0.143 $\pm$ 0.111	0.090 $\pm$ 0.067
male	0.087 $\pm$ 0.060	0.086 $\pm$ 0.041
Minim Creek		
female	0.133 $\pm$ 0.109	0.089 $\pm$ 0.041
male	0.069 $\pm$ 0.036	0.068 $\pm$ 0.042

In the southern and southeastern coastal waters of the United States, overwintering P. pugio spawn in late February through March at water temperatures of 15° to 20°C. Juveniles from the February-March hatch mature and spawn from late summer (July-August) to November. By then the length distribution is highly bimodal. Shrimp of the summer-fall hatch mature from October to February and reproduce during the following spring. Shrimp hatched in spring grow faster than those hatched in summer and fall but have a shorter life span.

In colder coastal waters, growth patterns are different. In Rhode Island, this species spawns only once during May to July in any one year. Length distribution is consequently unimodal throughout the year (Welsh 1975).

Salinity is yet another factor that affects growth. In South Carolina, P. pugio matures and spawns at a younger age in habitats with relatively high salinity than in those with relatively low salinity (Alon and Stancyk 1982), but specimens collected in low salinity waters were smaller than those from more saline waters (Wood 1967).

ENVIRONMENTAL REQUIREMENTS

Aquatic Vegetation

Grass shrimp, macrophytes, and algae live in the same communities and are subject to many of the same environmental factors (Beck and Cowell 1976; Thorp 1976; Morgan 1980; Coen et al. 1981; Heck and Thoman 1981). Studies in Florida showed that P. pugio was most abundant in habitats characterized by aquatic macrophytes, relatively high turbidities, and low salinities (Livingston et al. 1976).

Because grass shrimp depend on aquatic vegetation in many coastal waters, alterations of estuaries that destroy vegetation could seriously reduce their abundance. In one instance, weirs built in marshes to benefit wildlife produced dense masses of aquatic vegetation that supported an abundance of grass shrimp far higher than that in nearby less densely vegetated waters (Weaver and Holloway 1974). In another study in West Bay, Texas, dredging, bulkheading, and filling of coastal marshes caused a permanent loss of intertidal vegetation. The reduction of detrital input into the adjoining aquatic systems caused a noticeable decrease in abundance of grass shrimp (Trent et al. 1976).

Salinity

The abundance of freshwater and brackish-water grass shrimp in estuaries is clear evidence of their survival in a wide range of salinities.

Brackish-water shrimp. Field and laboratory studies indicate that P. pugio adults tolerate salinities from 0 to 55 ppt but are most common in salinities of 2 ppt to 36 ppt (Wood 1967; Swingle 1971; Bowler and Seidenberg 1971; Christmas and Langley 1973; Kirby and Knowlton 1976; Morgan 1980). The 96 h LD_{50} values for adults are 0.5 and 44 ppt (Kirby and Knowlton 1976).

Attempts to assess salinity tolerances of larvae on a broad scale have yielded mixed results. McKenney and Neff (1979) were able to rear nearly 50% of the P. pugio larvae exposed to a salinity of 3 ppt, whereas, Broad and Hubschman (1962) reported poor survival of larvae at salinities less than 10 ppt. When larvae were exposed to a wide range of arbitrarily selected salinities, the low and high salinities required to kill 50% of the larvae during a 96-h exposure (LD50) were 16 ppt and 46 ppt, respectively (Kirby and Knowlton 1976). Optimum salinity for complete larval development is 20 to 25 ppt (Floyd 1977; McKenney and Neff 1979; Knowlton and Kirby 1984). Possible reasons for the conflicting findings are differences in populations in different geographic locations, and differences in laboratory procedures.

P. vulgaris is more tolerant of high salinity water and less tolerant of low salinity water than is P. pugio (Holthuis 1952; Knowlton and Williams 1970; Bowler and Seidenberg 1971; Thorp and Hoss 1975). Although Nagabushanam (1961) reported that salinities as low as 3 ppt were lethal to adult P. vulgaris, they have been collected in freshwater (Swingle 1971; Christmas and Langley 1973; Barrett et al. 1978). Schoen and Knowlton (1977) reported 96-h LD_{50} values of 0.8 and 51 ppt for adults. Larvae of P. vulgaris are less tolerant of low salinity than are adults. Larvae thrive at salinities between 10 ppt and 30 ppt; the optimum is 20 ppt (Sandifer 1973). Larvae do not survive at salinity extremes of 5 and 35 ppt (Knowlton 1965; Schoen and Knowlton 1977). Larvae of both P. pugio and P. vulgaris survive best, mature early, and often pass through fewer larval stages when salinities are near optimum (Sandifer 1973; Floyd 1977). Interspecific differences in salinity tolerance in estuaries are likely to segregate P. pugio and P. vulgaris (Bowler and Seidenberg 1971), although biotic interactions such as competition for food and space are probably more important for segregation and coexistence (Thorp 1976).

Although P. intermedius is euryhaline, it has been collected from waters with salinities of 5 to 39 ppt (Dobkin and Manning 1964). The larvae thrive at salinities of 20 ppt but survival is low at salinities less than 10 ppt (Broad and Hubschman 1962). The larvae have been reared at salinities near 30 ppt (Hubschman and Broad 1974).

Freshwater shrimp. The two freshwater species, P. paludosus and P. kadiakensis, often live in brackish waters (Christmas and Langley 1973). P. paludosus was reported in salinities of 0 ppt to 10 ppt by Tabb and Manning (1961), and one specimen was captured in a salinity of 25 ppt (Swingle 1971). In a laboratory experiment, P. paludosus survived for 7 days at a salinity of 30 ppt but died when the salinity was raised to 37 ppt. In another experiment, adult P. kadiakensis survived at salinities up to 20 ppt but died at 25 ppt (Maguire 1961; Strenth 1976). Larvae are relatively intolerant of salinities higher than 5 ppt (Hubschman 1975; Strenth 1976) but are more tolerant of higher salinities after they reach stage IV (Hubschman 1975).

The salinity tolerance of grass shrimp is summarized in Table 4.

Water Temperature

Grass shrimp are eurythermal. In coastal waters, P. pugio thrives at temperatures of 5° to 38°C (Wood 1967; Christmas and Langley 1973), but survival is greater at 18° to 25°C. Growth is most rapid in waters at temperatures above 30°C but drops rapidly at water temperature below 14°C (Wood 1967). This species breeds at

Table 4. Salinity tolerance limits and optima (ppt) reported by various investigators (see text discussion) for adult and larval Palaemonetes.

Form and species	Adults		Larvae	
	Limits	Optimum	Limits	Optimum
Freshwater forms				
P. kadiakensis	0-25	0	0-10	0
P. paludosus	0-30	0	No data	0
Brackish-water forms				
P. intermedius	5-39	No data	10-30	20
P. pugio	1-55	4-16	3-31	25
P. vulgaris	1-51	No data	5-35	20

temperatures of 22° to 27°C in Rhode Island (Sastry and Vargo 1977) and from 17° to 38°C in Texas (Wood 1967). Preferred water temperatures range from 5° to 35°C for P. vulgaris and P. paludosus and from 10° to 35°C for P. paludosus (Christmas and Langley 1973). Tolerance for warmer waters is greater for P. pugio than P. vulgaris, but both species are relatively tolerant of the heat stress of effluents from a power plant (Chung 1977). The breeding temperatures for P. paludosus range from 18° to 33°C (Beck and Cowell 1976).

Physiological responses of grass shrimp to temperature indicate that P. vulgaris adults (McFarland and Pickens 1965) and P. pugio larvae (Sastry and Vargo 1977) are metabolically active over a broad range of water temperatures, exhibiting physiological compensation to seasonal temperature changes.

Temperature tolerance data for grass shrimp are summarized in Table 5.

Dissolved Oxygen

Dissolved oxygen is another factor that helps regulate the distribution and abundance of grass shrimp. In Louisiana waters, P. vulgaris and P. pugio are common in dissolved oxygen (DO) concentrations of 6 to 11 ppm (Barrett et al. 1978). In Rhode Island, the mortality of P. vulgaris was higher than that of P. pugio, when both species were caged together in a hypoxic microhabitat (DO = 0.3 ppm) during a tidal cycle. In the laboratory, at oxygen concentrations lower than 1 ppm, survival was higher in P. pugio than in P. vulgaris at all test temperatures (10° to 30°C). In nature, grass shrimp sometimes climb out of the water during periods of oxygen deficiency, especially during warm summer nights, but such attempts to avoid hypoxia can be effective only for a few hours (Pomeroy and Wiegert 1981). Respiratory studies indicated that P. pugio is an oxyconformer; its oxygen uptake decreases as oxygen tension declines from 8 to 2 ppm (Welsh 1975; Dillon 1983).

Physical Factors

Grass shrimp usually inhabit the shallows near the water's edge but have been reported at depths as great as 8 fathoms (Williams 1965). In winter, during temperature lows and in summer, when water temperatures approach seasonal highs, P. pugio moves from shallow to relatively deep water (Wood 1967). Thorp (1976) noted that the extent of the movement of grass shrimp among various depths often coincides with the distribution of

Table 5. Temperature tolerance range and optima (°C) reported for adult and larval Palaemonetes.

Species	Adults Limits	Adults Optimum	Larvae Limits	Larvae Optimum
P. paludosus	10-35[b]	18-33[c]	No data	No data
P. pugio	5-38[a,b]	18-25[a]	15-35[d,f]	20-30[f]
P. vulgaris	5-35[b]	No data	20-30[e]	20[e]

Sources:
a - Christmas and Langley 1973; b - Beck and Cowell 1976; c - Wood 1967; d - McKenney and Neff 1979; e - Floyd 1977; f - Sandifer 1973

oyster shell substrates, which, in some waters, are preferred by P. pugio and P. vulgaris. Oyster beds provide food and protection.

Grass shrimp are abundant where turbidity is relatively high. This is particularly true in habitats where water currents tend to keep sediments suspended, such as in shallow tidal creeks or near river mouths. Turbidity may provide some degree of protection from predators in habitats with little vegetation. In less turbid habitats, macrophytes afford protection from predators. Although Livingston et al. (1976) found that grass shrimp abundance was positively correlated with turbidity, turbidity may not be an environmental requirement. In some habitats, grass shrimp have been observed in clear water such as is often associated with dense aquatic vegetation (Weaver and Holloway 1974).

Grass shrimp tend to avoid fast currents and migrate in the direction of tidal currents (Antheunisse et al. 1971; Sikora 1977; Shenker and Dean 1979).

Bioassays

In as much as grass shrimp have been recommended for use as bioassay test organisms (American Public Health Association 1975), much information has been published about mortality and sublethal effects of various toxicants on grass shrimp but only a few are mentioned here. Workers evaluating the effects of kepone and other insecticides (heptachlor, toxaphene, dieldrin, and endosulfan) conclude that P. pugio adults were usually less sensitive and showed a lesser tendency to bioconcentrate these toxicants than did the fish that were tested (Schimmel and Wilson 1977; Schimmel et al. 1977). For example, the 96-h LD_{50} values for kepone were 121 µg/l and 70 µg/l for P. pugio and for the sheepshead minnow (Cyprinodon variegatus). Bioconcentration factors were 698 for the shrimp and 1,548 for the minnow (Schimmel and Wilson 1977). On the other hand, grass shrimp are much more sensitive than fish to endrin (Tyler-Schroeder 1979), dithiocarbamates (Rao et al. 1982), various chlorophenols (Rao et al. 1981), and DDT and parathion (Sanders 1972). On the basis of a study of 12 insecticides, Eisler (1969) concluded that grass shrimp are more sensitive to organophosphorous insecticides, and less sensitive to several organochlorine insecticides at high salinity than at low salinity. Low temperatures enhanced the survival of shrimp exposed to both groups of insecticides. Also, for most organophosphorous compounds tested, crustaceans were more sensitive than marine fishes by several orders of magnitude.

Heavy metals such as cadmium are more toxic to grass shrimp than to mummichogs, Fundulus heteroclitus (Eisler 1971). Concentrations of heavy metals (mercury, cadmium, and chromium) are acutely toxic to adult grass shrimp, usually in the order of 100 to 1,000 ppb. Except in areas of sewage or industrial outfalls, such concentrations far exceed those in estuaries. Therefore, grass shrimp are too resistant to be of much value in heavy metal bioassays (Vernberg et al. 1977). Increased temperature or decreased salinity increases the sensitivity of grass shrimp to heavy metals (Fales 1978; Sunda et al. 1978). Sublethal effects of heavy metals on grass shrimp have included loss of a predator avoidance response (Barthalmus 1977), developmental abnormalities in larvae (Shealy and Sandifer 1975), and a reduced tolerance to salinity fluctuations (Middaugh and Floyd 1978).

Attempts have been made by Tatem (1976), Tatem et al. (1978), and Dillon (1982) to evaluate the effects of exposure to petroleum hydrocarbons on survival and various physiological phenomena in grass shrimp. Several conclusions have been drawn from this research: (1) concentrations of petroleum hydrocarbons normally found in saltwater (10 to 20 ppb) and its sediments are too low to have acutely toxic effects on grass shrimp; (2) when sediments and water are exposed chronically to oil pollution or during a large oil spill, hydrocarbon concentrations could cause acute toxicity; (3) metabolism, reproduction, and growth may be reduced or altered if oil concentrations persist near 1 ppm; (4) grass shrimp rapidly depurate accumulated petroleum hydrocarbons when they are returned to oil-free water; and (5) the toxicity of oil is correlated with the relative proportion of the aromatic fraction present.

Some investigators have evaluated the effects of biocides, such as those used to remove fouling organisms from cooling systems of powerplants (generally chlorine), on grass shrimp. In a review by Hall et al. (1979) it was concluded that the detrimental effects of chlorination on grass shrimp were negligible under normal powerplant operations.

Additional investigations indicated that P. pugio was less sensitive than mysid shrimp to drilling muds but that both were several orders of magnitude more sensitive than fishes (Conklin et al. 1980); grass shrimp were more sensitive than pinfish (Lagodon rhomboides) to a simulated refinery effluent containing phenol, sulfide, ammonia, and some other components (Hall et al. 1978); and grass shrimp were more sensitive than other crustaceans to ionizing radiation. Radiation affects metabolic pathways involved in the synthesis of non-essential amino acids used in osmotic regulation (Engel et al. 1974).

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50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO. Biol. Rep. 82(11.35)*

2.

3. Recipient's Accession No.

4. Title and Subtitle

Species profiles: life histories and environmental require ments of coastal fishes and invertebrates (Gulf of Mexico)-- grass shrimp

5. Report Date

March 1985

6.

7. Author(s)

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8. Performing Organization Rept. No.

9. Performing Organization Name and Address

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10. Project/Task/Work Unit No.

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

(C)

(G)

12. Sponsoring Organization Name and Address

National Coastal Ecosystems Team
Division of Biological Services
Fish and Wildlife Service
U.S. Department of Interior
Washington, DC 20240

U.S. Army Corps of Engineers
Waterways Experiment Station
P.O. Box 631
Vicksburg, MS 39180

13. Type of Report & Period Covered

14.

15. Supplementary Notes

*U.S. Army Corps of Engineers Report No. TR EL-82-4

16. Abstract (Limit: 200 words)

This species profile summarizes much of the literature published about the biology of grass shrimp, *Palaemonetes* spp. Five species (*P. pugio*, *P. vulgaris*, *P. intermedius*, *P. paludosus*, and *P. kadiakensis*) are common in coastal waters of the northern Gulf of Mexico, although the last two are primarily freshwater forms. The brackish-water species are among the most abundant shallow-water benthic decopods in estuaries and play important roles as food for fishes and as transporters of nutrients among various trophic levels. They spawn from spring to autumn and the growth of planktonic larvae is normally completed in 7 to 12 molts. Postlarvae of 7-10 mm are 1.5 to 2 months old. The life span of grass shrimp is 6 to 13 months (maximum size rarely exceeds 50 mm). *Palaemonetes* spp. are eurythermal, euryhaline, and are relatively tolerant to hypoxia and a variety of pollutants. Grass shrimp feed on detritus, epiphytes, and meiofauna. They tend to concentrate near underwater structures and plants, especially in dense stands of underwater macrophytes.

17. Document Analysis a. Descriptors

Estuaries
Fishes
Growth
Feeding

b. Identifiers/Open-Ended Terms

Grass shrimp
Palaemonetes spp.
Temperature requirements
Life history
Habitat requirements
Spawning

c. COSATI Field/Group

18. Availability Statement

Unlimited

19. Security Class (This Report)

Unclassified

20. Security Class (This Page)

Unclassified

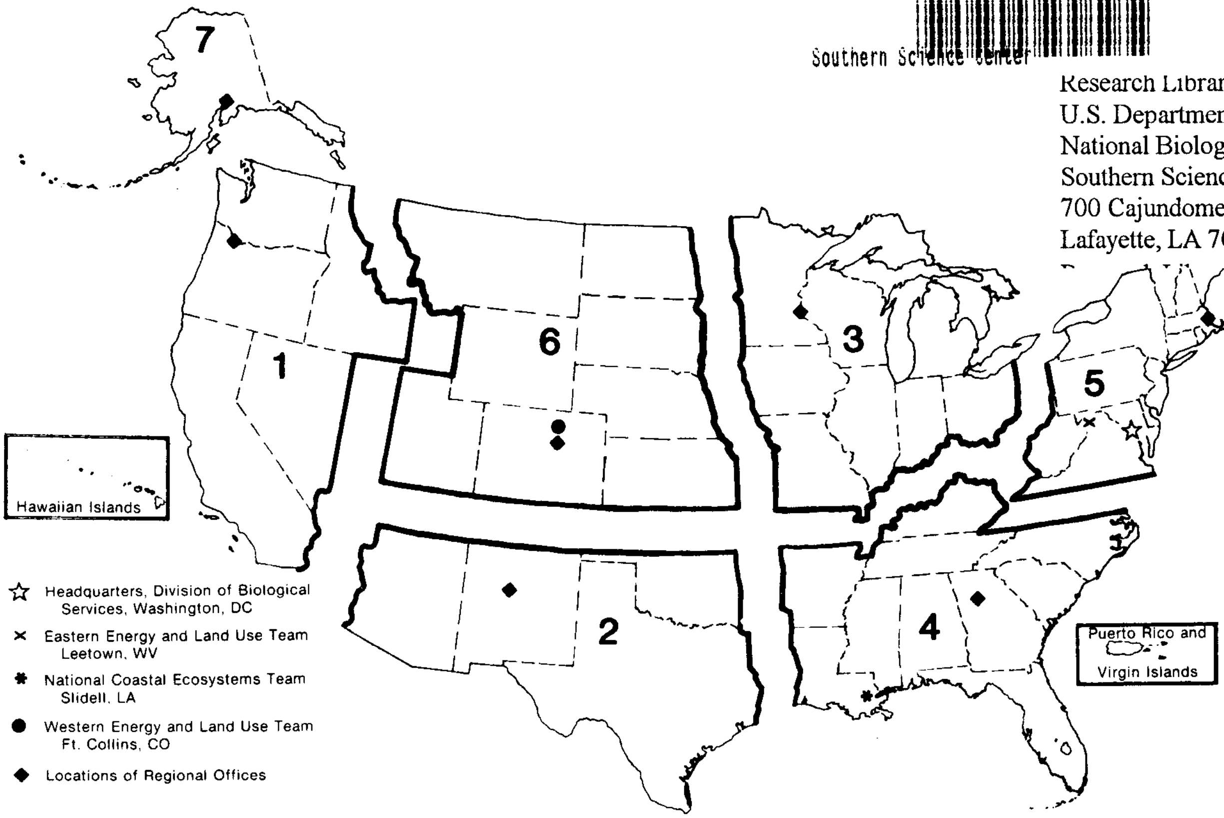
21. No. of Pages

19

22. Price

(See ANSI-Z39.18)

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



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DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.