Inshore Environmental Effects on Brown Shrimp, *Penaeus aztecus*, and White Shrimp, *P. setiferus*, Populations in Coastal Waters, Particularly of Texas

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Introduction

Many states have instituted water management plans that may control freshwater inflow to various coastal bays and marshes, the normal estuarine habitat of species important to marine fisheries. Knowledge of the tolerance ranges and responses of estuarine fauna valuable to sport and commercial fishermen thus becomes increasingly important to advisors, decisionmakers, and scientists. Of this biota, the two commercial species of penaeid shrimp, the brown, Penaeus aztecus, and the white, P. setiferus, are of prime economic value in the coastal states of the southeastern United States.

Managers of coastal zones, water districts, or fisheries, require a direct avenue to pertinent literature, but biological data upon which to base decisions are scattered. This paper provides a brief overview of the more studied environmental parameters (temperature, salinity, rainfall, and their interactions) associated with ecological factors (location, vegetation, predation, substrate, etc.). Detailed tables and literature citations relate biological responses (growth, migration patterns, seasonal abundance, etc.) of various life stages of penaeid shrimp to particular environmental factors and interactions. Table 1 (brown shrimp), Table 2 (white shrimp), and Figure 1 may be used together to assess the present extent of this information; Figure 1 further identifies those areas and life stages requiring additional research. Each table contains information specific to either *P. aztecus* or *P. setiferus*.

Our discussion compares and contrasts responses of the two species to single factors and their interactions, giving only limited literature citations. Implications for the two species are then explored. The purposes of this paper are to 1) provide, in an easily accessed tabular format, representative information and literature sources relating environmental factors to several inshore life stages of brown and white shrimp and 2) bring attention to those factors, their interactions, and life stages for which information is lacking.

Materials and Methods

Information described in Tables 1 and 2 was derived both from laboratory studies, primarily upon postlarval and juvenile penaeids, and field observations of all stages including sexually mature adults. The quantity of sources cited in the tables indicate the intensity, relative importance, and ease of measurement (e.g., salinity and temperature), with which factors have been studied.

We have defined postlarvae as those less than 25 mm total length (TL = tip of rostrum to tip of telson), adults as animals which are sexually mature, and juveniles as those less than 100 mm total length, at which size offshore migration of brown shrimp occurs under normal conditions. Data from sources identifying animals only as "juvenile" shrimp without size classification have been included in defining field ranges of that stage.

Discussion

Early studies of the Penaeidae were limited chiefly to white shrimp (Lindner and Cook, 1970), the primary fishery source in most coastal states until the middle 1960's. Efforts were made to understand the causes of declining white shrimp harvest by relating it to environmental factors, primarily salinity, river flow, and rainfall (Gunter, 1950; Gunter and Hildebrand, 1954; Gunter and Edwards, 1969). The apparent decrease in population abundance of white shrimp may have accelerated the research on the brown shrimp, particularly in Texas where brown shrimp constituted the majority of the shrimp fishery (Cook and Lindner, 1970). Emphasis on the latter species continued, both because of its commercial importance and its longer seasonal availability to scientists, resulting in a larger body of data for brown shrimp.

Single Factors

Penaeid shrimp, like other estuarine biota, generally have a wide range of tolerance to many environmental factors commonly measured in inshore waters. *Penaeus setiferus* and *P. aztecus* have been reported in salinities of $1-45^{\circ}/\infty$; *P. aztecus* has been caught in salinities of $60-70^{\circ}/\infty$. In Texas, postlarvae (6-15 mm TL) of both species appear to be limited to a narrower salinity range of $15-35^{\circ}/\infty$. However, most of these

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animals have been collected at entrances or inlets to bays during sampling designed to determine the precise date of immigration into the estuary (Baxter, 1963; Baxter and Renfro, 1967; Copeland and Truitt, 1966). Caillouet et al. (1971), in contrast, documented the presence of white and brown postlarvae in Vermilion Bay, Louisiana, in salinities less than 1% on. Postlarvae also survive and grow at controlled salinities as low as 5% within a wide range of temperatures, and growth will occur even at lower salinities (Zein-Eldin, 1963; Zein-Eldin and Aldrich, 1965; Zein-Eldin and Griffith, 1969).

Historical evidence (Gunter and Hildebrand, 1954; Copeland and Bechtel, 1974) suggests that young white shrimp occur more frequently and grow faster when nursery areas are of lower (but undefined) salinity. White shrimp juveniles in the laboratory did not die at salinities of 35-40% after 30 days continuous exposure, but growth was retarded (Zein-Eldin and Griffith, 1969). Postlarval white shrimp also appear to grow less well, and survival is decreased at salinities of 35% compared with 25% (100; salinities between 5, 15, 25, and 35% have not been examined in detail, nor have juvenile shrimp (>25 mm) been tested in these higher salinities.

Both species occur in a broad temperature range, 5.2-38°C. Survival is reduced at low temperatures, however, and numerous reports document the winter kill of shrimp following cold fronts (Gunter and Hildebrand, 1951; Dahlberg and Smith, 1970; Whitaker, 1983). Laboratory studies have shown that postlarval growth of both species increases with temperature up to 32°C (Zein-Eldin and Griffith, 1969). Brown and white shrimp juveniles occur in water warmed by thermal effluents (Chung and Strawn, 1984), but field data relative to high temperature are generally sparse.

In the laboratory, survival of juveniles (<50 mm TL) exposed to controlled temperatures of 30°C and above varies between species. Small *P. setiferus* continue to grow and survive at constant temperatures approaching 35°C (Zein-

Eldin and Griffith, 1969). Survival of juvenile *P. aztecus*, however, decreases with temperatures above 30°C (Zein-Eldin and Griffith, 1969).

Rainfall and river outflow are major phenomena influencing estuarine salinity. Correlations of white shrimp harvests with these factors have been reported for Texas, but do not appear to be valid in some other Gulf states, nor do they apply to catches of the brown shrimp (Hildebrand and Gunter, 1953; Gunter and Hildebrand, 1954; Gunter and Edwards, 1969).

Other individual factors that may be of importance to penaeids during the estuarine phase have been less studied. Requirements for vegetation, substrate type, food, predators, and interactions of these parameters have received little attention. Of these, predation rates have been most discussed (Gunter, 1945; Darnell, 1958; Matlock and Garcia, 1983; Minello and Zimmerman, 1984). Substrate preferences also received early attention (Williams, 1958; Grady, 1971; Rulifson, 1981). Recently, relationships with vegetation and predators have been investigated (Minello and Zimmerman, 1984; Zimmerman and Minello, 1984; Zimmerman et al., 1984). As with studies of substrate, differences in species responses have been demonstrated; only brown shrimp prefer vegetation. Recent studies evaluating various estuarine food sources by carbon isotype techniques (Fry, 1983) supplement earlier assimilation studies and analyses of stomach contents (Condrey et al., 1972; Flint and Rabalais, 1981; Gleason and Zimmerman, 1984).

Interactions

Interactions of salinity with temperature may have more pronounced effects than either factor alone. For both species, the combination of low temperature with low salinity is more detrimental than other combinations (Zein-Eldin and Griffith, 1969). Shrimp are most susceptible to temperatures of 11-15°C at salinities of $5^{0}/\infty$ or less, but appear to be somewhat protected against such effects when salinities are nearer to or above those of the open Gulf (25, 35, and $40^{0}/\infty$). However, the young of the two species do respond differently to certain temperature and salinity combinations. Survival of postlarval and small juvenile brown shrimp is noticeably reduced by combinations of high temperatures (>30°C) with the salinities $\leq 5^{0/\infty}$. White shrimp at constant warm temperatures are adversely affected by high salinities ($35^{0/\infty}$ as compared with $25^{0/\infty}$; intermediate salinities untested).

Information from factor-interaction studies, in particular of salinity and temperature, has been combined with data from postlarval monitoring to provide annual harvest predictions for brown shrimp. This measurement of the abundance of postlarval brown shrimp (Baxter, 1963) entering the bays and passes was adopted by most states, with various modifications correcting for environmental factors that affect the young brown shrimp in the nursery areas. Thus, Louisiana biologists correct for the number of hours water temperatures are below 20°C (Barrett and Gillespie, 1973; Gaidry and White, 1973). In Mississippi, a more complex formula considers salinity and a salinity-temperature interaction factor, together with a postlarval abundance term based on collections within nursery areas (Christmas and Van Devender, 1981; Sutter and Christmas, 1983).

A somewhat similar formula has been proposed for a limited area of North Carolina (Pamlico Sound: Hunt et al., 1980). Evaluation of white shrimp production based upon a postlarval index has not been attempted, but effects of low temperature on stocks have been described (Whitaker, 1983). Most recently, Garcia (1983) has proposed that an environmental factor be included in stock recruitment analysis of the penaeid fisheries, although few real data are available relating environmental effects to juvenile penaeids of either species (Fig. 1).

Interactions of most other factors are not well documented (Tables 1 and 2). Little is known of the effect of seawater intrusion on the other biota, although changes in species composition during periods of high salinity have been recorded (Parker, 1955; Hoese, 1960). The decrease in abundance and com-





mercial catch recorded during drought (Gunter and Hildebrand, 1954) may indicate more complex ecological or biological relationships, as in the effects of competition and predation by increasing numbers of crabs (Parker, 1955).

In the oyster, laboratory-determined physiological tolerances far exceed the ecological tolerances of the species established by interactions with parasites and predators. Such relationships, as well as those of salinity to vegetation and cover, natural riverine sediments and turbidity, remain to be investigated for penaeids. More detailed ecological examinations might result in a reduction of the broad biological tolerance ranges of these two penaeid species.

Implications

If decisions are made to control estuarine water flow, managers should con-

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sider the biological requirements of the penaeids. Based on interaction of only temperature and salinity, without regard to other ecological tolerances, population response would vary with season. Runoff of low salinity waters during colder periods may be detrimental to postlarval browns, as at times of "blue northers" accompanied by heavy spring rains. Young white shrimp occur in nursery areas of lower salinity somewhat later in the spring, however.

Based on the limited data for juvenile shrimp, it would appear that water flow could be restricted during the early spring months, when cold fronts are still likely, to minimize the negative effects of the combination of cold and low salinity on young brown shrimp. Conversely, water inflow would be most necessary during the late spring and summer in the presence of young white shrimp needing salinities below $25^{0}/_{00}$ and perhaps less, during the warmer months (August-September) of the year. As temperatures decrease in the fall, control of water flow might again be important, since it appears that in postlarvae of both species, survival is better at higher salinities than at $5^{0}/_{00}$ or less as temperatures decrease to 18° C or less. Penaeids may require variable water flow into nursery areas depending on season, and perhaps on particular year, e.g., early or late entrances of postlarvae into a given system.

Rate of change and length of exposure to the new conditions should also be considered if discharges are designed. Gradual release would be preferred to provide time for the animals to acclimate to the new regime and prevent additional stress from current effects.

Although all of these factors (salin-

ity, temperature, water flow, vegetative cover, food supply, presence of predators and parasites, and concentration of pollutants (heavy metals, etc.)) need to be evaluated for determining the amount of water required for commercial and sport fisheries in the various bays, practicality may demand that only the most stressful factors be included. Thus, consideration must be given not only to 1) the total volume of water to be released, 2) the time of release in relationship to the arrival of young of the year, and also 3) the interaction of temperature and salinity: Maintain higher salinities in cold temperatures, but to simultaneously providing marsh areas with sufficient covering water for the young while lowering salinities ($<20-25^{\circ}/\infty$) during hotter summer months when young white shrimp are most numerous in the estuarine areas.

In summary, the biological tolerances to commonly measured environmental factors of both species of penaeid shrimp appear to be broad. The ecological interactions of the animals with other fauna and flora are less well understood. and these latter may play important roles in determining the success of the species in nursery areas and bays, particularly during periods of stress from temperature or salinity.

Ideally, outflows should be planned to minimize stress to penaeid species by carefully monitoring the time of entry of the young shrimp together with the evaluation of actual conditions in the areas of planned waterflow. Temperature records would be important during late February through early April so that effects of low temperature-low salinity interaction upon the brown shrimp population could be reduced. Similarly, estuarine and marsh salinity records during August and September would determine outflow necessary to protect the population of white shrimp.

Table 1.—Inshore environmental effects on brown shrimp, <i>Penaeus aztecus</i> .						
tem	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources	
Temperature	Collection range: 12.6-30.6°C (8-13 mm); burrow from 12-17°C emerge >18°C; 36.6-36.8°C lethal if acclimated at 24°C.	Collection range: 2-38°C; stressed $>$ 32°C and <10°C; growth slow <18°C; 10-37°C in ponds if acclimated.	10-37°C in ponds if accli- mated.	Total penaeid catch related to net heating days over geogra- phic area; optimum catch 20- 38° C; catch range 5-38^{\circ}C; max. summer resistance at 40° C in 5-14% or 1035 min., low catch ratio below 15°C, optimum 20-35°C.	2, 3, 8, 9, 12, 13, 14, 18 20, 22, 23, 24, 25, 26 55, 59, 64, 65, 71, 72 75, 81, 83, 95, 114 127, 128, 134, 138	
	Growth rate (30 days) increases between 18 and 27.5°C; de- creases at 32°C.	Tolerances to extremes: summer 3 h $LD_{50} = 38^{\circ}C$; nonsummer 3 h LD_{50} $= 36^{\circ}$; optimum catch 20-35°C.			140, 142, 143, 144, 147 148, 150, 151, 152, 154 155, 156	
		Time below 20°C may be important for population survival.				
Salinity	Collection range: 0.10-69.0%, good growth at 2-40%.	Range 0-45% (is tributed over en- tire range; no relation between catch and salinity; burrowing decreased at 34% vs. 8.5 or 17%; prefer 10- 20%?	2-35 ⁹ / ₁₀₀ in ponds; less exposed to salinity variation after emigration.	Collection range 0.5-45.3 ⁹ / ₀₀ ; no preference within estuary.	3, 8, 9, 11, 12, 13, 14 17, 18, 22, 23, 24, 25, 48, 49, 50, 51, 52, 53 54, 57, 59, 61, 62, 64 65, 71, 73, 81, 84, 93 95, 98, 109, 110, 114 134, 138, 140, 141, 142 143, 144, 147, 148, 150 152, 153, 154, 156	
Rainfall		May leave estuaries prematurely if large freshwater inflow occurs.		Catch unrelated to rainfall in Texas or to river discharge in Louisiana.	3, 12, 53, 61, 138, 147	
Dissolved O ₂		65-86 mm: avoid 1.5 and 2.0 ppm; mean lethal D.O. is 0.8 ppm (1.4 ppm/ h reduction) or 0.5 ppm (2.6 ppm/h reduction).	<2.0 ppm = stress. >4.0 ppm = no stress.		11, 13, 80, 85, 94, 97 114, 118, 121, 122, 142 157	
Substrate	Collected in soft, muddy sub- strates.	Prefer soft muddy substrates vs. sand or shell; serves as protection from predators.	Prefers sand-silt-clay high in- organic content.		23, 39, 46, 70, 81, 102 103, 114, 125, 134, 140 149	
Vegetation	Prefer vegetated areas over open areas; use <i>Spartina</i> epi- phytes for food and stems for cover.	Prefer vegetated areas over open areas; use <i>Spartina</i> epiphytes for food and stems for cover; reduced predation observed in <i>Spartina</i> vs. open areas.	Do not use vegetation per se; found offshore on sandy-silt- clay bottoms.	Occurs in areas from zero to dense vegetation.	23, 44, 45, 81, 100, 101 103, 113, 137, 140, 158 159	
Food	Spartina epiphytes, Skeletone- ma, and detritus; growth better on animal food than on plant; omnivorous.	Omnivorous: Diatoms, detritus, Spar- tina epiphytes, Artemia, polychaetes, fecal pellets; progress from encoun- ter feeders to selective feeders; less selective than white shrimp.	Omnivorous: Polychaetes, amphipods, detritus; detrital- based food web is dependent on 80% of primary producer's biomass being directed to bot-		21, 23, 32, 45, 70, 72 113, 140	
	Larvae: Planktonic feeders.	isso selective than write simmp.	tom in shallow shelf.			

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Item	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources
Predators on Shrimp	Spotted seatrout, crab mega- lops, southern flounder, pinfish, spot, bighead searobin.	Spotted seatrout, sea catfish, red drum, southern flounder, ladyfish, sea birds, pinfish, Atlantic sharp- nose shark, blue crab, Atlantic croaker, black drum, silver perch, sand seatrout.	Spotted seatrout, sea catfish, red drum, southern flounder, ladyfish, croaker, pinfish, At- lantic sharpnose shark, blue crab, sea birds.	Information on predation rates in the field is lacking. Pena- eids in stomach contents of predatory fishes are seldom identified to species. Preda- tion on offshore populations may not be a significant source of mortality. Little infor- mation is available concerning predation on postlarvae in estuaries, but juveniles are frequently fed upon by fish predators.	4, 23, 28, 29, 30, 33, 47 58, 68, 74, 78, 84, 96 99, 100, 101, 102, 107 108, 111, 129, 130, 133 135, 140, 159
Growth	Almost none <16°C; rapid (1 mm/day) only >20°C; >0.5 mm/ day at 26°C; 1.4 mm/day at 32°C; max. growth between 25- 27°C; max. growth on <i>Skeleto- nema costatum</i> and <i>Spartina</i> epiphyte diet; shrimp in labora- tory grow faster when buried for long periods of time (energy conservation).	Lab growth: 12-35 mm/mo. in winter, 24-43 mm/mo. in summer, 50 mm/mo. in spring. Field growth: <0.1 mm/day at <20°C, 1.7 mm/day at <20°SC, 3.3 mm/day at <25°C. Mark-recapture: 0-0.77 mm/day (males), 0.11-0.89 mm/day (females). Growth decreases at 29-33°C.			12, 23, 25, 38, 42, 43 45, 63, 66, 68, 70, 71 79, 83, 93, 112, 124 127, 128, 138, 140, 141 142, 143, 145, 147, 153 154, 155, 156
Migration	Offshore planktonic stages re- cruit to estuaries from Jan. to June (La.); Feb. to Apr. (Galves- ton). Positive correlation with wind direction and recruitment (Cedar Bayou); capable of 4.8 cm/sec. salinity independent descent.	Migrate offshore w/new moon Apr. to July (Tex.); June = peak migration time; prefer sides of channels; can descend vertically at about 27 cm/sec. Emigration size approximately 80-100 mm; may be as high as 135 mm; may leave estuaries prematurely if large freshwater in- flow occurs.	Remain offshore to grow and spawn. Carbon isotopes in tissues generally converge with that in offshore sediments.		6, 7, 9, 10, 23, 25, 35 38, 43, 68, 75, 126, 127 134
Location	Planktonic to demersal; tidal passes to interior marsh.	Range: Secondary streams out to con- tinental shelf; no optimum within range.	Offshore spawning grounds at 25-110 m.		6, 7, 10, 16, 22, 23, 31, 59, 82, 103, 104, 105, 120, 123, 124, 152
Season	Abundant Feb. thru early June; secondary peak SeptOct.	Catch Range: MarDec.; optimum catch is MarSept.	Gonads mature in all months offshore; high abundance: May-Sept.; peak abundance: June-Aug.; generally higher catches at night.		6, 7, 9, 10, 12, 16, 23, 24, 39, 63, 75, 82, 105, 114, 120, 123, 124, 134, 158
Prediction	Abundance of postlarvae and juv	reniles has been used to predict offsh	ore catches of adults with some	success.	19, 34, 40, 41, 65
Interactions Salinity-Tem- perature	 24-h survival: 80% at 4-35°C and 5-40^{*0}/∞; dependent on acclimation period. 30-day survival: <80% at combinations of approximately 11°C × 12⁰/∞, 15°C × 7⁰/∞, and 18°C × 2⁰/∞. Growth: Increases markedly at 18-20°C; relatively constant in both tissue production and daily growth over salinity range 5-35⁰/∞ at any given temperature. Effects of temperature and salinity combinations used in models to predict harvest based on postlarval occurrence indices. 	Salinity not important during period of juvenile abundance unless temperatures <20°C; de- crease in temperature decreases ability to osmoregulate; oxygen consumption increases with tem- perature, varies with salinity.		Simultaneous changes in salinity and temperature have more influence on physiologi- cal responses than single alteration; most effect at com- binations of extremes.	9, 11, 24, 43, 50, 64, 65, 80, 83, 119, 136, 140, 142, 143, 144, 148, 150, 152, 155, 156, 158
Salinity-Loca- tion		Present in all estuarine areas re- gardless of salinity if temperature is tolerable.			24
Salinity-Sea- son		Catch ratio similar at all salinities during seasons of availability.			24, 158
Salinity-Size		Juveniles better osmoregulators than adults; regulate better at salinities >20%.			11, 64, 150

Table 1.—Brown shrimp data continued.

tem	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources
Salinity-Vege- tation		Spartina adversely affected by salinity intrusion; intertidal condi- tion necessary for germination.			1, 61, 62, 81, 116, 131 158
Season-Loca- tion			Shallower waters (25 m) dur- ing spring and summer; deep- er during autumn and winter.		24, 105
Vegetation- Abundance	90% postlarvae in Galveston salt marsh occurred in Spartina vs. unvegetated areas from Mar. to July; no apparent selection for vegetation DecMar.	75-95% found in Spartina vs. un- vegetated habitat.	Worldwide commercial shrimp harvest proportional to area of vegetated cover in nursery grounds.		81, 101, 139, 140, 158, 159
Vegetation- Substrate availability		Channeling of river, dikes, levees, etc. prevent natural sediment dis- persal during spring river floods, losing marsh sediments offshore; results in marsh subsidence and loss of vegetated habitat.			
Chemical Effects		Most sensitive estuarine organ- isms to pesticides: Organochlor- ines, DDT, dieldrin, mirex (delayed toxic effect). 0.9 ppb PCB for 2 weeks affects premolt.	Malathion: Mortality in marshes when applied by air. No. 2 fuel oil 24-h TLM: 0.77-25 ppm.	Effluents (sulfides, phenols, oils): Toxic lethal mean = 4.8% for brown shrimp. Cadmium: LC ₅₀ for 30 days = 718 ppb, causes blackgill disease.	26, 69, 132
		Malathion: Mortality in marshes when applied by air.		Formalin: 96 h LC ₅₀ at 28°C = 235-270 ppm.	
		No. 2 fuel oil: 24-h TLM: 0.77-2.51 ppm.		$KMnO_4$. 95 h $LC_{50} = 6$ ppm. Aroclor 1254: 1 μ g/liter is lethal in 2 weeks.	
		Carbamate: toxic in lab.			
Disease and Parasites	Several representatives of fungi, more details and extensive biblic	nicrosporidia, trematodes, cestodes, r graphies see Literature Cited	ematodes, barnacles, bacteria, a	nd viruses infect P. aztecus. For	24, 26, 69, 86, 87, 89 90, 106, 137

¹Total length = tip of rostrum to tip of telson. ²Sexually mature.

Table 2.—Inshore env	ironmental effects	on white shrimp.	Penaeus setiferus.
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Item	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources
Temperature	Collection range: 12.6-30.6°C (6-8 mm). Growth rate (30 days) increases with temperature between 18° and 32.5°C; decreases at 35°C.	10-37°C in ponds if acclimated; growth slow <18°C; Louisiana col- lected 9-33°C, peaks in abundance 15-33°C. Tolerance to extremes: Summer 3 h LD ₅₀ = 37°C, nonsummer 3 h LD ₅₀ = 36°C. Catch ratio increases with tempera- ture <5° \geq 35°C; catch range <5°- 40°C; optimum catch 20-38°C; lower limit 4.5°C Georgia.	10-37°C in ponds if accli- mated; growth slow <18°C.	Max. summer resistance time at 40° C = 29.5 min. when salinity $>10^{9}/_{00} < 25^{9}/_{00}$. Collection range for animals >20 mm: 6.5-39.0°C.	2, 3, 8, 12, 13, 14, 18, 20, 22, 24, 25, 27, 55, 59, 64, 71, 72, 75, 81, 91, 92, 95, 114, 115, 134, 138, 140, 146, 151, 156
Salinity	Collection range: 0.4-37.4°/ (6-8 mm). Growth less at 35°/ compared with 25°/ or lower. Survive salinities of 40°/ for 30 days.	Prefer <10°/ $_{00}$; Louisiana collection range: 5-26°/ $_{00}$, peaks 5-21°/ $_{00}$; Mobile Bay peak 1-15°/ $_{00}$; S. Texas 5-10°/ $_{00}$; no relation between catch and salinity in range 0-38°/ $_{00}$; opti- mum catch over entire range.	2-35%/00 in ponds.	Collection range: 0.4-47.96 ⁰ /∞; "prefer lower end of salinity gradient, whatever it may be" (49).	3, 8, 9, 12, 13, 14, 15, 17, 18, 22, 24, 25, 48, 49, 50, 51, 52, 53, 54, 56, 57, 59, 60, 61, 62, 64, 67, 71, 73, 81, 92, 93, 95, 98, 110, 114, 134, 138, 140, 156
Rainfall				Direct correlation between shrimp catch and average state rainfall for previous 2 years (Tex.); 1937-51 $r = 0.83$, 1927-51 $r = 0.80$, 1927-64 $r =$ 0.67; not correlated with river discharge in Louisiana.	3, 9, 53, 56, 60, 61, 92, 138
Dissolved O ₂		Avoids 1.0, 1.5 ppm.	Stressed ≤2.0 ppm, no stress >4.0 ppm.		13, 85, 94, 97, 114, 118, 121, 122

Item	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources
Substrate	Collected in mud habitat.	Prefer sandy-mud; preference in- creases with time = offshore train- ing; collected from shallow mud flats to deep channel (loose peat, sand).	Galveston: Prefer sand-silt- clay areas of high organic content.	Prefer sediments with higher organic content than brown shrimp; collected in mud and peat.	39, 46, 81, 92, 103, 113 125, 134, 140, 149
Vegetation	Collected in <i>Spartina</i> .	No consistent pattern of vegetation selection (day or night in lab);pre- fer vegetation if no other species are present; displaced from vege- tation by brown shrimp, and then eaten more by croaker (lab).			1, 44, 81, 92, 101, 103 113, 140, 158
Food	Omnivorous; prefers Artemia over artificial food.	Omnivorous: Organic-inorganic detritus, fecal pellets, diatoms, polychaetes; lab-reared prefer <i>Artemia</i> vs. artificial; not as selec- tive as brown shrimp = coexis- tence.	Omnivorous: Polychaetes, or- ganic-inorganic detritus.		21, 32, 70, 72, 92, 113 140
Predators on Shrimp	Spotted seatrout, crab mega- lops, southern flounder, spot, killifish.	Spotted seatrout, sea catfish, red drum, southern flounder, ladyfish, sea birds, pinfish, Atlantic sharp- nose shark, blue crab, Atlantic croaker, black drum, silver perch, sand seatrout.	Spotted seatrout, sea catfish, red drum, southern flounder, ladyfish, croaker, pinfish, At- lantic sharpnose shark, blue crab, sea birds.	Information on predation rates in the field is lacking. Pena- eids in stomach contents of predatory fishes are seldom identified to species. Preda- tion on offshore populations may not be a significant source of mortality. Little infor- mation is available concerning predation on postlarvae in estuaries, but juveniles are frequently fed upon by fish predators.	28, 30, 33, 47, 68, 74 76, 84, 92, 96, 99, 101 107, 108, 111, 129, 130 133, 135, 140, 159
Growth	No growth at 15°C; slow below 18°C; max. = 1.7-2.0 mm/day at 30.5-34.1°/w and 25-31°C.	Mean growth range mm/day (mark- recapture data): 0.0-0.8 (males), 0.03-2.3 (females). 98-133 mm in 4 weeks, 98-146 mm in 6 weeks.		mean mm/wkAugOct.1.3OctFeb.0.9FebApril2.0April-Aug.1.7	12, 38, 42, 63, 67, 68 72, 76, 77, 91, 92, 93 112, 138, 140, 156
Migration	Recruit June-Sept. to bays (Loui- siana); recruit late spring-fall (Galveston); recruit May-Oct. (Texas, Mississippi).	Overwinter offshore when bay temp. gets too low; small shrimp reenter bays the following spring when temperatures rise; migrate offshore Aug.Oct.	Stay nearshore to grow and spawn; tissues generally show no convergence of car- bon isotopes with any region of sediments.		7, 9, 25, 35, 37, 38, 68 75, 77, 82, 91, 92, 93 117
Location	Near sides of channels vs. mid- channel; planktonic to demersal; tidal passes to interior marsh.	All estuary locations; optimum catch in secondary streams, marshes, and in tertiary, secon- dary, and primary bays.	Principal spawning depth is 10-15 m (Texas); 15-30 m (Loui- siana).		7, 12, 16, 22, 24, 25, 31 59, 91, 92, 93, 103, 104 120, 123
Season	Mean size at entry, Aransas Pass: 7 mm—May 8 mm—July 6 mm—Sept.	Caught in all months; optimum catch July-Dec., absent from marshes Jan. thru April; peak abundance = spring, late summer, and fall (inshore Louisiana).	Strong gonadal development May-Sept., peak abundance fall-winter offshore (Texas).		7, 9, 12, 16, 24, 25, 39 63, 75, 82, 92, 114, 120 123, 134, 158
	Enter during late spring and summer.				
Interactions Salinity-Tem- perature	80% survival over 50 days at temperatures >33°C and salin- ity approximately 3-40%; lower limits approximately 15°C and salinity less than 5%.	Catch ratio low at all salinities if temperature below 15-20°C; at higher temperature generally dis- tributed in less than 25%.		Simultaneous change in salin- ity and temperature has more influence on physiological responses than a single alter- ation; most effect at combina-	24, 92, 119, 140, 156, 158
	Growth reduced at 35% at all temperatures tested.			tion of extremes.	
	Less tolerant of cold than post- larval browns; at lowest temper- atures (11-15°C) survival better at higher salinities.				
Salinity-Loca- tion		Occupy upper estuarine areas dur- ing warm season; relying on "con- tents" of inflowing water.			24
Salinity-Sea- son		Found in all salinities during months when available.			24, 158
Salinity-Size		Better osmotic regulators than adults; hemolymph concentrations may decline below 10 ⁰ / ₀₀ .			15, 64, 92, 117

Table 2.-White shrimp continued.

Item	Postlarvae (<25 mm ¹)	Juveniles	Adults ²	General comments	Sources
Salinity-Vege- tation		Spartina adversely affected by salinity intrusion; intertidal condi- tion necessary for germination.			1, 62, 81, 116, 131, 158
Temperature- Migration		Overwinter offshore when bay tem- peratures drop; may return to bays as temperature rises.			37, 117
Vegetation- Abundance		Not dependent on vegetation; equally abundant in nonvegetated areas.			81, 101, 139, 140, 158
Vegetation- Substrate availability		Channeling of river, dikes, levees, etc. prevent natural sediment dis- persal during spring river floods, losing marsh sediments offshore; results in marsh subsidence and loss of vegetated habitat.			1, 5, 36, 81, 131
Chemical Effects		Malathion: Mortality in marshes when applied by air; No. 2 fuel oil: 24-h TLM=0.77-25 ppm; Quinaldine: 25 ppm is the mini- mum effective anesthetic concen- tration; 10-20% concentrations cause death in 48 h.			26, 69
Disease and Parasites		i, microsporidia, trematodes, cestodes, nemat liographies, see Literature Cited.	odes, barnacles, bacteria	, and viruses infect <i>P. setiferus</i> . For	26, 69, 86, 87, 88, 89, 106

¹Total length = tip of rostrum to tip of telson. ²Sexually mature

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