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DETECTING AND AVOIDING OXYGEN DEFICIENT SEA WATER BY BROWN SHRIMP, *PENAEUS AZTECUS* (Ives), AND WHITE SHRIMP *PENAEUS SETIFERUS* (Linnaeus)

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Abstract: Detection and avoidance of oxygen deficient sea water (≤ 3.0 ppm dissolved oxygen) by white shrimp, *Penaeus setiferus* (Linnaeus), and brown shrimp, *P. aztecus* (Ives), was measured under laboratory conditions. Shrimp were acclimated to control salinity (22‰) and temperature (22 °C) for a minimum of 2 days and to the test chamber for 1 h before recording data. A shrimp's response to treatment water was determined by its (1) response time, i.e., time in min to first entrance into the control side of the chamber, and (2) total time spent in the treatment side of the chamber.

White shrimp detected and significantly avoided intruding water containing ≤ 1.5 ppm dissolved oxygen. Brown shrimp were more sensitive and avoided water having dissolved oxygen concentrations ≤ 2.0 ppm. Behavioral responses of white shrimp and brown shrimp to hypoxic water included an initial increase in general level of activity, retreat from hypoxia by walking or swimming, rapid eye-stalk movements, and flexing of their antennal scales. In addition, white shrimp exhibited abdominal flexures and apparent exhaustion.

Hypoxia along coastal Louisiana, west of the Mississippi River Delta, could markedly affect shrimp stocks by increased natural mortality through (1) physiological stress, (2) increased inter- and conspecific competition, and (3) increased predation.

Key words: Avoidance; hypoxia; *Penaeus aztecus*; *Penaeus setiferus*

INTRODUCTION

Dissolved oxygen concentrations < 3.0 ppm occur at least intermittently in shallow (< 20 m) coastal regions of the northern Gulf of Mexico (Bedinger *et al.*, 1981; Stuntz *et al.*, 1982; Boesch, 1983; Leming & Stuntz, 1984; Rabalais *et al.*, 1985; Renaud, 1985, 1986). This condition, common during the summer and early fall, is most prevalent in Louisiana's nearshore waters. It is usually associated with stratification of the water column, phytoplankton blooms, and stable high pressure weather systems (Ragan *et al.*, 1978; Bedinger *et al.*, 1981; Harper *et al.*, 1981; Boesch, 1983; Renaud, 1985). Respiration by phytoplankton and organic decomposition possibly can reduce oxygen tensions to stressful levels for marine animals.

The effects of coastal hypoxia (≤ 2.0 ppm dissolved oxygen) on the movements of shrimp into and out of estuarine nurseries and to offshore spawning grounds is unknown. Several studies (Ragan & Harris, 1975; Ragan *et al.*, 1978; Fotheringham &

Weissberg, 1979; Reitsema *et al.*, 1982; Stuntz *et al.*, 1982; Renaud, 1986) make reference to reduced numbers of penaeid shrimp in hypoxic water. However, little or no data are present that relate growth, spawning, natural mortality, and behavior of shrimp to hypoxia. In this paper I (1) describe the laboratory behavior of brown shrimp, *Penaeus aztecus* (Ives) and white shrimp, *P. setiferus* (Linnaeus), with regard to specific levels of dissolved oxygen, (2) discuss the alternatives of shrimp confronted with hypoxia in nature, and (3) speculate on the outcome of their subsequent behavioral responses.

METHODS

Juvenile shrimp, 65–101 mm total length (tip of rostrum to tip of telson), obtained from Galveston Bay, Texas were transported to the laboratory in aerated, 28-l ice chests. Shrimp were acclimated to control conditions, 22 °C and 22‰ salinity, in 76-l aquaria for at least 2 days. They were fed dead shrimp daily and exposed to a photoperiod : scotoperiod of 12 h : 12 h. Thirty-two foot-candles of fluorescent background lighting filtered through beige-colored curtains were used during the photoperiod. An oxygen meter accurate to 0.1 ppm was used to measure dissolved oxygen.

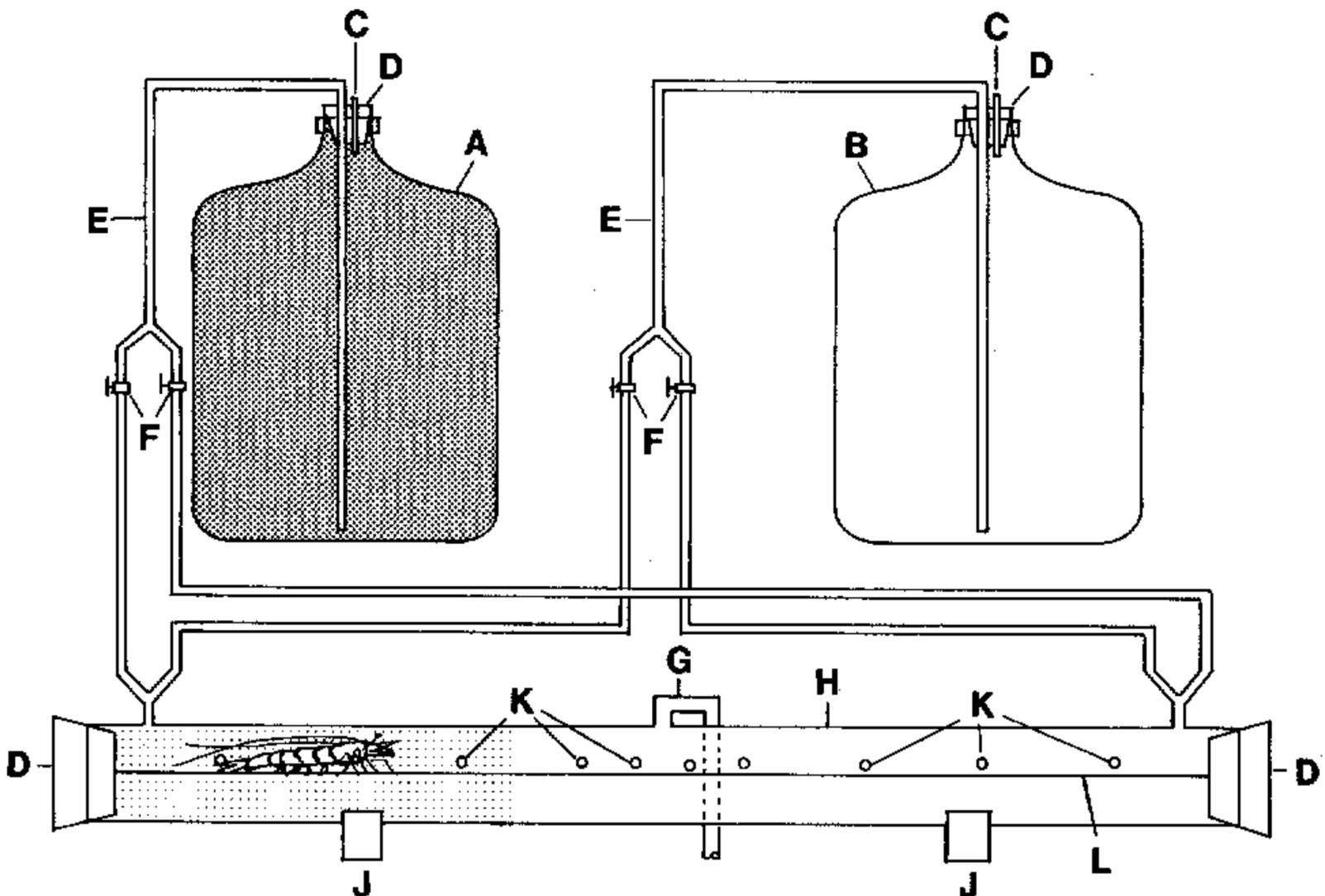


Fig. 1. Schematic diagram of avoidance apparatus: A, experimental seawater; B, control sea water; C, air vent; D, rubber stopper; E, inflow tubes; F, flow valves; G, water outflow tube; H, avoidance tube; J, support blocks; K, water sampling removal ports; L, raised mesh floor.

The experimental apparatus (Fig. 1), modified from that developed by Matthews (1969), consisted of a clear plastic tube 8 cm in diameter \times 90 cm long, marked at 5-cm intervals. A raised floor of semipliable black plastic mesh (0.6 cm) was placed in the tube. Two water inlets, one at each end of the tube, and a single centrally positioned outflow were present. Experimental and control water introduced into the apparatus through a gravity flow system, could be directed toward either end of the apparatus. Ports positioned at 10-cm intervals along the length of the apparatus permitted monitoring of dissolved oxygen levels. Behavior was observed through slits in the curtains to prevent outside movement or shadows from influencing shrimp behavior.

Sea water from the Gulf of Mexico was passed through 5 μ m polyethylene filters to remove suspended particles. Test concentrations of dissolved oxygen (1.0, 1.5, 2.0, and 3.0 ppm) were prepared by bubbling nitrogen gas through sea water in 50-l carboys. This is a common procedure for removing oxygen from water and has been used in experiments with fish (Jones, 1952; Whitmore *et al.*, 1960), penaeid shrimp (Kramer, 1975) and sea stars (Shick, 1976).

Seventy-five white shrimp were individually tested at 1.0, 1.5, or 2.0 ppm dissolved oxygen, 25 randomly assigned to each level. Similarly, 75 brown shrimp were tested at 1.5, 2.0, or 3.0 ppm. Shrimp were initially placed in the right end of the apparatus for one experiment, the left end for the next, and so on to reduce the chance of developing a starting preference. The acclimation period was started when the chamber was full of water. Following 1 h of acclimation to the test chamber, an additional hour of exposure to control conditions provided a period for comparison with tests. Well-aerated sea water (6.0–7.4 ppm dissolved oxygen) was introduced at both ends of the tube during the acclimation and control periods. These oxygen levels were well above those possibly causing low-oxygen stress in penaeid shrimp (Broom, 1971). Upon completion of the control period, test water of a selected dissolved oxygen level was introduced into the end of the test chamber nearest the shrimp, and behavior of the animal was observed. Each shrimp was used for two 30-min tests and then discarded. The position of each shrimp was recorded at 1-min intervals during both control and treatment tests; location of the gills was used as an index of a shrimp's position. The average shrimp position during the control period determined its side-preference in the chamber. Side-preference during a treatment was based on the average position of a shrimp during the final 20 min of each 30-min test.

After the first 30-min test, the apparatus was flushed with control sea water. Test and control sea-water inflows were reversed for the second test, so that behavior was observed under conditions of exposure from both ends of the tube. Laminar flow, 650 ± 100 ml/min, was maintained by inline valves (Fig. 1) and was monitored at 10-min intervals during the tests. All experiments were carried out between 0700 and 1800. Sex, weight, and length of each shrimp were recorded following each experiment.

A χ^2 analysis of average shrimp position, treatment versus control side of the apparatus, was used to determine if shrimp avoided the end of the apparatus in which test sea water was introduced. Analysis of variance (ANOVA) and Student–New-

man-Keuls multiple range test (SNK) were used to detect variation among treatments and between species for shrimp response times and time spent in the treatment side of the apparatus.

RESULTS

Both brown and white shrimp detected and avoided low oxygen levels under laboratory conditions. Avoidance by white shrimp was significant at 1.0 ppm ($\chi^2 = 26.06$, $P < 0.001$) and 1.5 ppm ($\chi^2 = 35.28$, $P < 0.001$) dissolved oxygen but not at 2.0 ppm (Table I). Avoidance by brown shrimp was significant at 1.5 ppm ($\chi^2 = 37.73$, $P < 0.001$) and 2.0 ppm ($\chi^2 = 42.32$, $P < 0.001$) but not at 3.0 ppm (Table I). The average position of brown and white shrimp was equally distributed between the right and left sides of the apparatus during the controls, i.e., no preference for either side of the test chamber was exhibited. Therefore, shrimp behavior during the treatment experiments was affected only by changes in dissolved oxygen concentration.

TABLE I

Avoidance of oxygen-depleted water by brown shrimp and white shrimp: average shrimp position during the final 20 min of each treatment experiment was used to differentiate control or test water preferences.

	Test water (ppm)	Observed distribution of shrimp during experiments			χ^2	<i>P</i>
		Control water	Test water	Percent avoidance		
Brown shrimp	1.5	46	3	94	37.73	<0.001
	2.0	48	2	96	42.32	<0.001
	≤ 2.0	94	5	95	100.12	<0.001
	3.0	31	19	62	2.88	0.120
White shrimp	1.0	41	6	87	26.06	<0.001
	1.5	46	4	92	35.28	<0.001
	≤ 1.5	87	10	90	61.12	<0.001
	2.0	25	24	51	0.02	0.890

The total time spent in the treatment side of the chamber (TT) and the time in min before a shrimp's initial entry into the control side of the chamber (RT, response time) varied among treatments and between species (Tables II and III). Brown shrimp RT and TT did not vary significantly between 1.5 ppm and 2.0 ppm treatments, but these values were significantly shorter than those from the 3.0 ppm treatment (ANOVA, SNK, $P < 0.05$). No difference was indicated in RT or TT between 1.0 ppm and 1.5 ppm tests for white shrimp, although these times were significantly shorter than

TABLE II

Response time (RT) and total time spent by shrimp in treatment water (TT): RT is the time to first entrance into control seawater; TT is the number of times a shrimp was recorded in the test end of the chamber; all times (means \pm SD) are expressed in minutes; ^a variation between species: time in this treatment level was significantly lower for brown shrimp than for white shrimp (ANOVA, SNK, $P < 0.05$); no species differences were noted in the 1.5 ppm treatments; ^b variation within species: time in this treatment level was significantly higher than that in other treatments for the same species (ANOVA, SNK, $P < 0.05$).

	Dissolved oxygen treatments (ppm)			
	1.0	1.5	2.0 ^a	3.0
Brown shrimp				
RT	no data	5.7 \pm 1.2	5.0 \pm 1.2	10.7 \pm 1.2 ^b
(95% CI)		(3.4 - 8.0)	(2.7 - 7.3)	(8.4 - 13.0)
TT	no data	6.3 \pm 1.2	6.7 \pm 1.2	11.8 \pm 1.2 ^b
(95% CI)		(3.9 - 8.6)	(4.4 - 9.1)	(9.5 - 14.2)
White shrimp				
RT	8.3 \pm 1.2	7.9 \pm 1.2	19.2 \pm 1.2 ^b	no data
(95% CI)	(5.7 - 9.0)	(4.9 - 8.0)	(8.3 - 12.5)	
TT	9.3 \pm 1.2	8.6 \pm 1.2	19.5 \pm 1.2 ^b	no data
(95% CI)	(6.7 - 11.8)	(5.4 - 10.2)	(16.9 - 21.8)	

TABLE III

ANOVA and SNK summaries for response time (RT) and total time (TT): ^a B, brown shrimp; W, white shrimp; number following B or W is the dissolved oxygen concentration (ppm) for that treatment.

ANOVA table					Significant differences determined by SNK ^a					
Source of variation	d.f.	SS	MS	F						
TT										
Total	293	26435			<u>B1.5</u>	<u>B2.0</u>	<u>W1.5</u>	<u>W.10</u>	<u>B3.0</u>	<u>W2.0</u>
Group	5	6000	1200							
Error	288	20435	71	16.9						
RT										
Total	293	26989			<u>B1.5</u>	<u>B2.0</u>	<u>W1.5</u>	<u>W.10</u>	<u>B3.0</u>	<u>W2.0</u>
Group	5	6561	1312							
Error	288	20429	71	18.5						

those from the 2.0 ppm treatment ($P < 0.05$). No significant interspecific variation in TT or RT was noted in the 1.5 ppm treatments, but both RT and TT for brown shrimp were significantly shorter than those for white shrimp in the 2.0 ppm treatment (ANOVA, SNK, $P < 0.05$). Brown shrimp and white shrimp responded similarly at lower oxygen levels, however, brown shrimp appear to be more sensitive than white

shrimp, exhibiting a quicker avoidance behavior at marginally stressful oxygen concentrations.

The starting positions of shrimp could conceivably have affected RT and TT if the distances from the hypoxic source were significantly different. However, the starting positions of both shrimp species in all treatments were not significantly different (ANOVA, $P > 0.05$). In addition, there were no detectable differences in avoidance reactions based on sex (ANOVA, $P > 0.05$). Avoidance was not analyzed with respect to weight or length of shrimp because the range of these data were so small that any groupings would have been arbitrary (Table IV).

TABLE IV
Weights and lengths of shrimp used in experiments.

	Weight (g)	Length (mm)
Brown shrimp		
Mean \pm SD	3.6 \pm 0.7	75.2 \pm 4.6
Range	3.2 - 5.6	65.0 - 86.0
White shrimp		
Mean \pm SD	4.1 \pm 0.9	80.4 \pm 6.6
Range	2.7 - 7.0	66.0 - 101.1

Noted behavioral responses of white shrimp to hypoxic water (≤ 2.0 ppm dissolved oxygen) were: (1) an initial increase in their general level of activity, (2) retreat from hypoxia by walking or swimming, (3) rapid eye-stalk movements, (4) flexing of their antennal scales, and (5) abdominal flexures followed often by "exhaustion". Reactions of brown shrimp to hypoxic water included only the first four responses mentioned above. The major behavioral difference between brown shrimp and white shrimp was the absence of abdominal flexures by brown shrimp exposed to hypoxic water. This is noteworthy even though brown shrimp were only tested in oxygen concentrations as low as 1.5 ppm. White shrimp exhibited abdominal flexing in all oxygen concentrations tested but more frequently in the lower concentrations. Perhaps the quicker response times, shorter residence times in 2.0 ppm water, and infrequent returns by brown shrimp into the test water partially explain this result. Brown shrimp that remained in test water for extended periods of time, and those that returned to this water during a test, retreated by walking or swimming. White shrimp moved out of hypoxic water by abdominal flexing 78% of the time. The behavior of shrimp during controls varied from total "inactivity" to constant swimming within the chamber. Rapid eye-stalk movements, antennal scale flexing, and abdominal flexing were not observed during 150 h of control observations. These behaviors appear to result from stress caused by unsuitable oxygen concentrations.

DISCUSSION

Survival of organisms exposed to stressful conditions is dependent on their ability to recognize these conditions and alter their behavior to avoid or physiologically cope with them. The ability to detect or avoid oxygen deficient water has been reported in many aquatic and marine species including European brown shrimp, *Crangon crangon* (Dyer, in Hagerman & Uglow, 1982), southern flounder, *Paralichthys lethostigma* (Deubler & Posner, 1963), Kumura prawn, *Penaeus japonicus* (Egusa & Yamamoto, 1961), blue crab, *Callinectes sapidus*, several unidentified species of crustaceans and fish (Loesch, 1960; May, 1973), bluefish, *Pomatomus saltatrix*, summer flounder, *Paralichthys dentatus* (Swanson & Sindermann, 1979), gold fish, *Carassius auratus* (Olgilve, 1982), minnows, *Phoxinus phoxinus*, and stickleback, *Gasterosteus aculeatus* (Jones, 1952).

Minimum dissolved oxygen requirements for various aquatic organisms vary widely among species. For example, summer flounder become stressed at 5.1 ppm dissolved oxygen while goldfish tolerate levels as low as 0.5 ppm (Davis, 1975). Brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, are able to tolerate oxygen levels as low as 2.0 ppm in rearing ponds, although they show some indications of stress (Broom, 1971). No problems were noted at or above 4.0 ppm.

The levels of dissolved oxygen that shrimp can detect affect their behavior and subsequent survival. It would be advantageous for shrimp to respond quickly, although not vigorously, as brown shrimp do. White shrimp, apparently more tolerant to low oxygen levels than brown shrimp, exhibited a delayed avoidance response which usually included abdominal flexures. This delay might be disadvantageous since shrimp were in a more stressful environment when they began to avoid hypoxic water.

Hypoxia is most chronic and widespread during the summer in Louisiana coastal waters. This time frame overlaps with the offshore migration of juvenile brown shrimp and white shrimp (Baxter & Renfro, 1967; Cook & Lindner, 1970; Lindner & Cook, 1970), nearshore spawning of white shrimp, and postlarval migrations of white shrimp into coastal estuaries (Lindner & Anderson, 1956; Lindner & Cook, 1970). Therefore, it is fair to assume that shrimp may be exposed to hypoxia of coastal waters. Two behavioral options for shrimp confronted with masses of hypoxic water would seem to be: (1) no response, or (2) active avoidance.

It is clear from my laboratory experiments that brown shrimp and white shrimp avoid hypoxic water. They moved into areas with a more favorable oxygen regime. Shrimp unsuccessful in this endeavor became exhausted and died within 15 min. Abdominal flexing toward the wrong end of the avoidance tube prevented shrimp from escaping the stressful condition. Similar errors in escape behavior could take place in the natural environment where hypoxic water masses are much larger than those created under laboratory conditions.

Possible methods of avoidance of hypoxic water by shrimp include: (1) burrowing into the substratum, (2) swimming above the water mass, (3) swimming around it, or (4) delaying their offshore migration. Burrowing to avoid hypoxia is apparently not a

viable option, in fact, the opposite occurs with *P. japonicus* (Egusa & Yamamoto, 1961). Shrimp came out of their burrows when dissolved oxygen was lowered to 0.7 ppm.

Ocean currents are thought to aid shrimp in their migrations (Hughes, 1969; Salia *et al.*, 1982). Shrimp that swim above hypoxic bottom water place an increased stress on their energy budget by having to maintain swimming activity. At the same time, they are removed from food sources, and are susceptible to pelagic carnivores. When shrimp tire of active swimming, they will be forced to return to the bottom and face the consequences of lower oxygen concentrations. Midwater sampling above hypoxic bottom water did not indicate that shrimp migrate en masse above oxygen depleted water (Renaud, 1986). Lowery (1983) also indicated that shrimp were not capable of swimming above hypoxic water for extended periods of time and that they became trapped in shallow water during "jubilees". So it is unlikely that shrimp could avoid hypoxic water by these means.

It is possible that shrimp can alter their migration patterns to move around hypoxic water. Hypoxia, originally thought to exist over wide regions of the Louisiana coast (Flowers *et al.*, 1975; Bedinger *et al.*, 1981; Stuntz *et al.*, 1982) has also been shown to have patchy distributions (Renaud, 1986). Higher catches of shrimp between the zones of hypoxia suggest that shrimp can avoid small oxygen depleted areas. Avoiding hypoxia in this manner or delaying offshore migrations should concentrate animals and may result in increased competition and predation. Although no specific spawning grounds have been identified for white shrimp (Reitsema *et al.*, 1982), migratory patterns altered by hypoxia may result in gravid shrimp, their eggs, and their larvae occupying a less than suitable habitat.

Physiological stress derived from exposure to hypoxia and resultant abnormal behaviors may make shrimp more vulnerable to predators that are more tolerant to low oxygen levels than shrimp. Predators near the fringe of the hypoxic area may also be able to take advantage of shrimp incapacitated by low oxygen as they escape it. Therefore, hypoxia may be a factor leading to the reduction in shrimp stocks through increased mortality due to physiological stress, increased competition, and increased predation.

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