

Habitat Requirements and Environmental Factors Controlling Shrimp Production in the Brazil/Guiana Continental Shelf Area

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ABSTRACT

The hydrography of the Brazil/Guiana shelf is strongly influenced by freshwater run-off from major river systems extending from the Amazon on the northeast coast of Brazil to the Orinoco in Venezuela and the Gulf of Paria. Sediment, carbon and organic loads in freshwater discharge have a profound influence on the bathymetry and productivity of coastal habitats.

Four species of penaeid shrimp predominate commercial landings along the Brazil/Guiana continental shelf. Their recruitment into the commercial fishery appears to be influenced by coastal habitat type, environmental conditions (*e.g.* precipitation, temperature), freshwater runoff from river systems as well as biotic factors. Shrimp display considerable variation in seasonal and annual abundance. Much of this variability appears due to mortality during the planktonic larval and subsequent demersal estuarine juvenile stages when environmental factors are expected to determine cohort strength. These fluctuations, and the ability to predict them, are of interest to commercial large and small scale fishermen and resource managers. Traditional methods of stock assessment have proved inadequate, and more recent techniques that attempt to incorporate a series of environmental parameters have met with limited success. This study reviews the major factors affecting shrimp recruitment and production, and proposes monitoring methods and ecological approaches which may allow us to improve our understanding of the processes determining yields and our ability to predict them.

Keywords: Shrimp, Penaeidae, Recruitment, Habitat, Stock Assessment, Brazil/Guiana Continental Shelf, Amazon, Essequibo, Orinoco.

INTRODUCTION

The abundances of penaeid shrimp display substantial inter-annual variation which is reflected in their commercial landings. Much of this variability has been attributed to annual changes in environmental factors. Penaeid shrimp are particularly sensitive to environmental conditions since both marine and coastal habitats are exploited at different points in their life-history. Most commercial penaeids spawn at sea and their larvae migrate to a variety of coastal habitats where the juveniles develop for several months before returning offshore. Mangrove swamps, seagrass meadows, salt marshes and soft-bottom habitats are typical estuarine nursery grounds. Numerous variables are reported to play a role

in habitat selection by shrimp species. The effects of temperature, salinity, depth, turbidity, substrate characteristics, physical structure, and seasonal climatic variation are well documented (e.g. Garcia and Le Reste, 1981; Gulland and Rothschild, 1985; Rothlisberg *et al.*, 1985a; DeLoach *et al.*, 1991).

Many recommended management measures, such as protection of juvenile shrimp and groundfish, the protection of nursery grounds, and the estimation of annual maximum sustainable yields, can be enhanced if managers have an understanding of the relative value of habitats for designated species, and of the mechanisms through which habitats influence recruitment, growth and survival. This paper examines the habitat and environmental factors which are believed to affect shrimp productivity on the Brazil/Guiana continental shelf area, reviews methods of estimating recruitment strength to the commercial fishery, and proposes a stock assessment research program for the region.

Hydrology and Physical Oceanography of the Brazil-Guiana Shelf The hydrography of the Brazil-Guiana shelf is strongly influenced by the discharge of large river systems emptying from the northern coast of South America (Figure 1). The Amazon in Brazil and the Orinoco in Venezuela are the largest of these rivers, while the Essequibo in Guyana is the largest river in the three Guianas. The influence of the Amazon predominates along the coasts of northern Brazil, French Guiana and Suriname, while the Orinoco's discharge has a strong influence along the Atlantic coast of Venezuela and the southern coast and eastern shelf of Trinidad.

The equatorial trough and the disturbances associated determine the general weather patterns for the coastal regions along the Brazil/Guiana shelf. Data from nine coastal climatological stations, which register daily temperature and rainfall, were used to construct annual rainfall patterns (Figure 2). Maximum precipitation in northern Brazil (Belem) occurs in early March, whereas the maximum rainfall in the coastal regions north of the equator occur later in May and June. The rainfall peaks in May in Cayenne, June in Georgetown (Guyana) with a second peak in December, and in June/July in Venezuela. Correlations among the seven sites monitored are presented in Table 1. It is shown that the peak in rainfall in Venezuela is associated with the trough in Brazil. It would be interesting to know also if the amplitude of the rainfall in one sector can be a good predictor of the amplitude elsewhere afterwards but in the same season.

The total annual rainfall decreases gradually to the northwest, from a maximum of 3.75 m in Cayenne, French Guiana to 1.0-1.3 m in Trinidad and Venezuela (Rudloff, 1981). The relatively large difference between total rainfall in such close locations, as demonstrated between Cayenne and Paramaribo (in Suriname) makes interpolation difficult.

The seasonal and regional variability in rainfall is reflected in the runoff from the major rivers which lags behind peak precipitation by about one month. The flows of many of the regions rivers vary seasonally during the rainy season

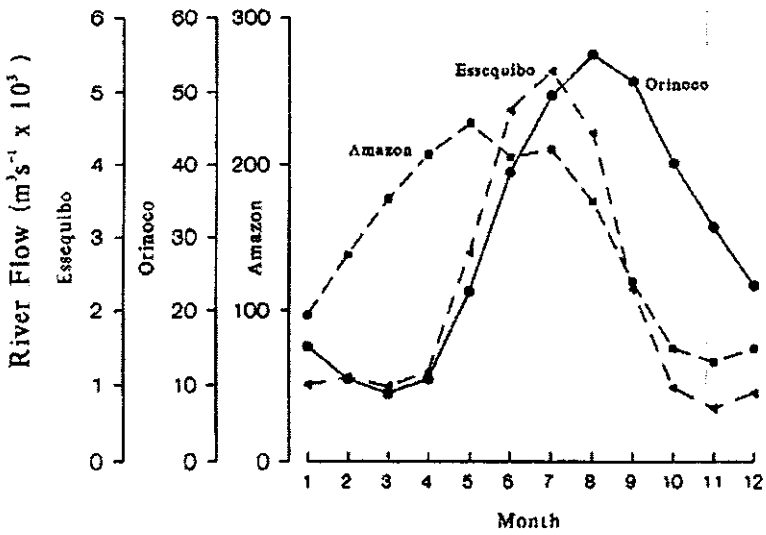


Figure 1. The Brazil-Guiana shelf region indicating the political boundaries, and the extent of the continental shelf as delimited by the 200 m isobath. Modified after (Cervign, 1993).

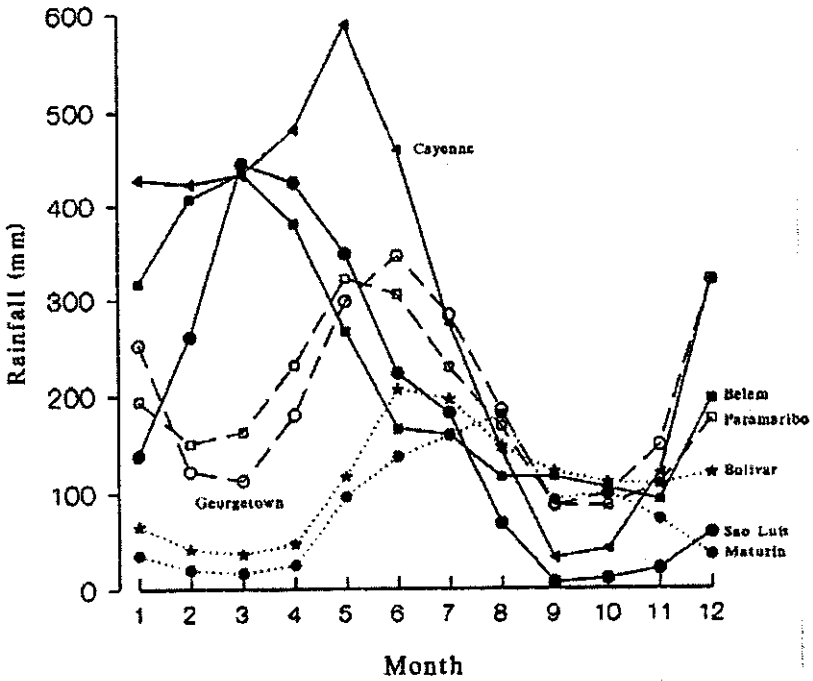


Figure 2. Annual rainfall patterns for several sites along the Guiana/Brazil continental shelf. The solid line represents sites most closely related geographically and hydrographically to the Amazon drainage basin. Similarly, the dashed line and the dotted line relates to the Essequibo and Orinoco rivers respectively. However, the Cayenne site seems intermediate between the Amazon and Essequibo rainfall patterns.

Table 1. Temporal correlation (monthly means within years) of rainfall pattern among the 7 monitoring sites along the Guiana/Brazil continental shelf.

n=12	Maturin	Bolivar	Georgetown	Paramaribo	Cayenne	Belem	Sao Luis
Maturin	1.000						
Bolivar	0.869	1.000					
Georgetown	0.559	0.270	1.000				
Paramaribo	0.319	0.193	0.804	1.000			
Cayenne	-0.250	-0.372	0.531	0.813	1.000		
Belem	-0.749	-0.727	-0.086	0.264	0.747	1.000	
Sao Luis	-0.413	-0.383	0.116	0.594	0.833	0.835	1.000

(April-May to October-November) and the dry season (November-December to March- April). The Amazon river, with an approximate drainage area of 5×10^6 km², discharges a peak flow of 2.4×10^5 m³·s⁻¹ in mid-May and a minimum of 9×10^5 m³·s⁻¹ in November (Figure 3). Similar patterns with diminished amplitude exist for the Essequibo and Orinoco rivers - the maximum discharges for these systems peak at 5.5×10^3 and 5.2×10^4 m³·s⁻¹, respectively (MARTEC, 1995). Interestingly, there is a gradual displacement pattern of peak discharge towards the northwest, with the Amazon, Essequibo and Orinoco peaking sequentially in mid-May, July, and August-September, respectively. Temporal correlations among the three rivers is shown in Table 2.

The runoff curves are smoother than those of rainfall because they integrate precipitation over relatively large catchment areas. These may therefore be used in place of rainfall if small-scale patterns are not of concern. Specific investigations, such as studies of sudden larval flushing from an estuary, would require local rainfall data.

Correlations of the inter-annual variations in rainfall in tropical America with the El Niño Southern Oscillation (ENSO) have been made by (Hastenrath, 1990). Results from that study indicate that the precipitation over northern South America is particularly correlated to the ENSO index. A 50% reduction in precipitation occurred in the southwest Caribbean Sea during the 1982-83 ENSO event. The opposite events (La Niña) appear associated with a strong discharge of the rivers from northern South America. The effects of these events on the hydrography of the Brazil/Guiana shelf are poorly understood.

Seasonal fluctuations in freshwater discharge shift the isohalines seaward or landward with consequent faunal shifts. Salinity measurements have primarily consisted of sea surface samples. The U.S. National Oceanographic Data Center maintains a database of these measurements collected from 3000-4000 stations along the shelf between 1911 and 1987. Most stations were located in Brazil, French Guiana and Suriname between the 20-100 m isobaths. The spatial and temporal variability in salinity patterns is a function of discharge from major river systems coupled with current patterns created by the interaction of rivers and oceanic currents (Neumann *et al.*, 1975; Levitus, 1986; Levitus, 1989).

The seasonal variation in the river outflow causes major salinity variability along the coastline (Dessier and Longuy, 1994). A regular annual feature is the presence of a high salinity tongue off the Guyana coast which begins in July and may be due to partial reversal of the Guiana current and upwelling of saltier water (Dessier and Longuy, 1994).

Lentz and Limeburner (1995) quantified the seasonal variations in the horizontal structure of the Amazon plume from historical oceanographic data and CTD surveys. Sea surface salinities of less than 33 psu were reported along the coast. The influence of freshwater flow is expected to extend to at least 20 m, however, little is known about the variation in salinity along the bottom, where

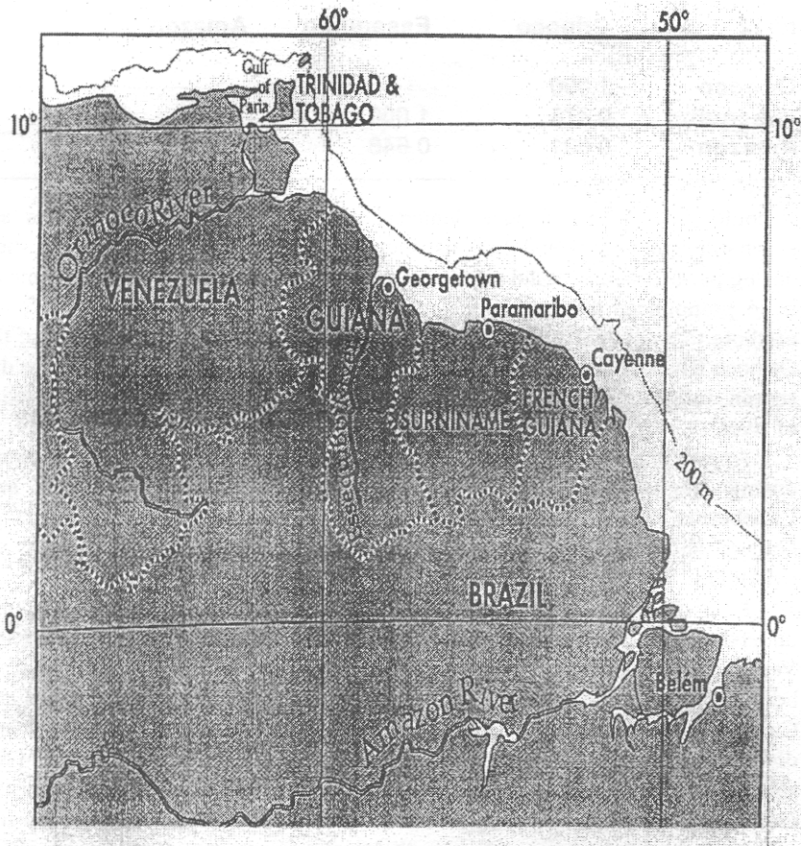


Figure 3. Seasonal variation in river discharge for the Amazon, Essequibo and Orinoco rivers. The scale for the river flows are different for each river to emphasize the differences in the timing of the river flow cycles.

Table 2. Temporal correlation (monthly means within years) of river flow patterns among 3 major rivers on the Guiana/Brazil continental shelf.

n=12	Orinoco	Essequibo	Amazon
Orinoco	1.000		
Essequibo	0.676	1.000	
Amazon	0.001	0.646	1.000

it could potentially influence demersal species. Most estuarine species are euryhaline and may extend their distributions seaward over the continental shelf during periods when coastal salinities are low. The extent of these displacements is so pronounced that during the rainy season, brackish fauna may be found offshore to a depth of 20 m or more and surface salinities 40 km seaward of the Orinoco River drop to 10 psu (Cervigon *et al.*, 1993). Conversely, during the dry season, salinities increase and marine fauna may be found in the lower reaches of river.

Approximately 70% of the Amazon's freshwater plume is carried eastward during August-October with the remainder going westward (Lentz and Limeburner, 1995). The maximum and minimum salinities along the Brazil-Guiana shelf occur in December/January and June-August, respectively (MARTEC, 1995).

Near-shore variation in salinity due to rainfall and coastal runoff is poorly understood as few data are available. Within the Gulf of Paria off Trinidad and Venezuela, it is difficult to determine the seasonal pattern of salinity variation because of the paucity of data. Evidence from sediment patterns (Van Andel and Curray, 1960) suggests that a substantial amount of freshwater is trapped and diverted into the Gulf by the strong Guiana current flowing along the edge of the shelf. Significant research has been carried out on the Guiana and North Brazil currents over the past 50 years due to their uniqueness in spreading freshwater inflows to higher latitudes of the North Atlantic (Neumann, 1969; Gibbs, 1982; Flagg *et al.*, 1986; Reverdin and McPhaden, 1986; Geyer *et al.*, 1991; Geyer and Kinaka, 1995). The Guiana current flows northwesterly along the coasts of French Guiana, Suriname, Guyana and Trinidad with its central axis generally lying along the continental shelf. The current is characterized by frequent topographically-induced meanders with wavelengths of 400-600 km and rotation periods of 8-13 d (Febres-Ortega and Herrera, 1976; Johns *et al.*, 1990; Richardson *et al.*, 1994; Limeburner *et al.*, 1995). Tidal currents at the mouth of the Amazon river range from 0.7-2.0 m·s⁻¹ (Eisma *et al.*, 1978). Current velocities over the shelf range from 0.11 m·s⁻¹ in September to 0.71 m·s⁻¹ in April-May with an annual mean velocity of 0.42 m·s⁻¹ (Febres-Ortega and

Herrera, 1976). The proximity of the current to the coasts of French Guiana and Suriname, coupled with the somewhat reduced riverine influence along their coasts, results in an increased marine character to their waters. Off the coast of Venezuela, the Guiana current deflects the Orinoco's plume to the west forcing it into the Gulf of Paria south of Trinidad (Serpent's Mouth) or into the Caribbean between Trinidad and Tobago. Within the Gulf of Paria, water flows northward between Venezuela and Trinidad (Dragon's Mouth) while an anti-cyclonic gyre exists in the Gulf of Paria off the west coast of Trinidad (Cervigon *et al.*, 1993).

Trade winds blow from the east-northeast throughout the year but are strongest from January-June. During this period of maximal winds, sea-surface temperatures are normally between 26.5-28.0°C, although they may be slightly cooler off Suriname (Cervigon *et al.*, 1993). Gradients in sea-surface temperature do not appear to influence fish distributions but they have been used to track water movements along the continental shelf.

Evidence exists which suggests that long-term shifts in shrimp production vary in relation to large-scale climatological factors (Garcia and Le Reste, 1981).

Unfortunately, good fisheries data sets which are sufficiently complete to allow the long-term variability in stock abundance to be followed are rare. (Staples *et al.*, 1985b; Staples *et al.*, 1985a) provided evidence that long-term reductions in shrimp landings in the Gulf of Carpentaria were related to cyclical drought conditions. Presumably cyclical phenomena such as the ENSO, which alters precipitation and temperatures for extended periods, can have an effect on penaeid stock sizes.

VARIABILITY IN SHRIMP ABUNDANCE

Penaeid shrimp are short-lived (1-2 yr) decapods. Although life-histories vary among species, most of the commercially important penaeids have a life-cycle which includes a period of estuarine residence. Adult shrimp spawn offshore and release demersal eggs that hatch and pass through a series of planktonic larval stages. Transport towards the coast, during this larval phase normally takes 3-4 weeks (Garcia, 1985). The larvae are weak swimmers, and their transport is likely a combination of active vertical movements and passive horizontal displacement by favorable onshore currents. In such life-histories, coastal dispersal and larval drift are likely to be very important, and mortality rates of larvae are probably very high.

Postlarvae move into estuaries (salt marshes, mangroves, lagoons) where they become benthic and metamorphose into juveniles. Shrimp remain in these nursery areas for approximately 3 months, after which they begin to move into progressively deeper water and emigrate offshore. This emigration often coincides with reductions in salinity in the estuaries (Rothlisberg *et al.*, 1985b; Staples and Vance, 1986; Jayakody and Costa, 1988) or lunar phases (King,

1971). Temperature is important in more northerly estuaries, but is unlikely to be so along the warm Brazil-Guiana continental shelf. There is an artisanal interception fishery which targets emigrating juveniles/subadults with fyke nets (Chinese seines) in Guyana. An offshore commercial fishery targeting subadults and adults has been in operation throughout the Brazil-Guiana shelf, including Trinidad, since the late 1960's.

Penaeid stocks display substantial inter-annual variability (Garcia and Le Reste, 1981; Staples, 1985; Nance *et al.*, 1989) and Kirkegaard (1975) has suggested that estuarine-dependent species are subject to the greatest stock-size fluctuations. Species which spawn offshore and undertake cross-shelf migrations as planktonic larvae are subject to high natural mortality rates which may be environmentally mediated by shifts in hydrographic and meteorological conditions, and biologically influenced by food supply and predation pressure. Once shrimp gain access to estuarine, their survival is dependent on physical conditions, habitat availability, food supply, predation pressure, anthropogenic influences and artisanal fishing mortality. Following estuarine development, shrimp must migrate offshore and complete maturation during which time both natural and fishing mortality as well as food supply contribute to variation in the size of the fishable adult stock. Given their planktonic larval phase and subsequent multiple sources of mortality, it is not surprising that penaeid stocks exhibit high variability. Larval recruitment variability is one of the single least understood problems in fisheries science (Houde, 1987).

Habitat Preferences

Detailed ecological studies of penaeids in many different regions have determined that each species is generally associated with a particular habitat type within an estuary. For example, quantitative sampling along the Gulf of Mexico has demonstrated that brown shrimp *Penaeus aztecus* are associated with emergent aquatic vegetation while white shrimp *P. setiferus* are more abundant in non-vegetated soft bottom areas (Zimmerman and Minello, 1984; Zimmerman and Minello, 1984; Zimmerman *et al.*, 1984; Minello and Zimmerman, 1985; Minello and Zimmerman, 1991; Minello *et al.*, 1989a). Pink shrimp *P. duorarum* appear to be abundant only where seagrasses are present (Costello *et al.*, 1986). Data on the densities of five penaeid species from Australia indicated that three were most abundant in seagrasses, one species was most abundant along mud-mangrove banks and the fifth species was equally abundant in seagrasses and mangroves (Staples *et al.*, 1985b). The value of such habitat specificity may be reduced predation pressure due to structural protection or elevated food availability (Minello and Zimmerman, 1983; Minello and Zimmerman, 1985; Minello and Zimmerman, 1991). Minello and Zimmerman (1991) have pointed out that density alone may not be an indicator of habitat preference because density is affected by both biotic and abiotic factors. For example, Talbot (in

press) pointed out that the used of secondary habitat may result in higher densities than in the primary habitat if the density in the latter is limited by some biological (competition or predation) or physical (space, shelter) factor.

Long-term studies relating the area of available wetland habitat to offshore shrimp landings suggest a direct relationship (Doi *et al.*, 1973; Turner, 1977; Wadie and Abdel-Razek, 1985) and numerous examples of reductions in offshore and artisanal landings in response to reclamation of intertidal wetlands have been documented by Turner (1990). What constitutes quality habitat for many species of penaeid shrimp is not well defined, however, habitat quality and availability appear to be two of the long-term factors influencing sustained shrimp harvests (Turner, 1986). It appears that nursery habitat availability is a limiting factor for shrimp production. Habitat-based management strategies should focus on this area.

Four species belonging to the genus *Penaeus* are commercially exploited along the Brazil-Guiana shelf: southern brown shrimp *P. subtilis*, pink-potted shrimp *P. brasiliensis*, southern pink shrimp *P. notialis* and southern white shrimp *P. schmitti*. Our current understanding of the estuarine habitat requirements of the penaeids along the Brazil-Guiana shelf is limited. Fortunately, there appear to be some strong similarities among the white, brown and pink shrimp of the region and their ecological counterparts in the Gulf of Mexico. Both the northern brown shrimp *P. aztecus* and southern brown shrimp *P. subtilis* appear to be associated with aquatic vegetation while northern white shrimp *P. setiferus* and southern white shrimp *P. schmitti* are more common on non-vegetated soft-bottom areas. Further sampling in the estuaries along the Brazil-Guiana shelf is needed to confirm these similarities and determine which habitats are important for *P. brasiliensis* and *P. notialis*.

Loss of mangrove and seagrass habitat is a potential problem along the Brazil-Guiana shelf and adverse impacts on fisheries have been reported in the region (*e.g.* Mutunhu, 1984). Protection of nursery grounds by controlling fishing in their vicinity, pollution abatement and restrictions on engineering projects with adverse impacts have been advocated (Villegas and Dragovich., 1984). Determination of the habitat requirements of coastal penaeids and finfish will provide a basis for habitat-based conservation of juvenile stocks. The protection of nursery habitat is necessary to maintain overall yields and ensure the sustainability of stocks.

Juveniles live in estuaries for an average of three months before migrating to offshore habitats. For most species there are peak migrations periods during which large concentrations of juveniles can be found along emigration routes. Growth overfishing occurs when artisanal and inshore fisheries heavily exploit these concentrations. Fishery closures during the offshore recruitment phase is a management tactic which would help reduce growth overfishing (Coles and Lee Long, 1985). For this type of management, it is necessary to identify the location

of the primary nursery grounds, distribution of juveniles within nurseries, migration routes and migratory timing. This method of management has successfully reduced growth overfishing in Louisiana where closures of the inshore fishery during May to July have been instituted to prevent exploitation of juvenile *P. aztecus* and to allow them to reach larger sizes before recruitment (Ford and St. Amant, 1977). A similar strategy, termed the Texas Closure, has been employed off Texas during the brown shrimp emigration (Nance, 1994). While the stated goal of such management is to allow the juveniles to grow to a larger, more valuable size prior to harvest, it probably also reduces growth overfishing.

Habitat preferences of the principal penaeid species are not well understood. The adults appear to favor mud or mud-sand bottoms. Some species burrow during the day while others remain exposed. Burrowing appears inversely related to turbidity suggesting that burrowing is a predator avoidance mechanism (Minello *et al.*, 1991). The coast from eastern Suriname to Brazil is dominated by *P. subtilis*, while the Orinoco Delta region and Guyana coast are dominated by *P. brasiliensis* (Jones and Dragovich., 1977; Willman and Garcia, 1985) with some overlap among the two species. *Penaeus subtilis* is typically associated with seagrass beds and mangroves (Fabres, 1988) while *P. brasiliensis* may be associated with mangrove swamps. There are no data on comparative growth rates and mortality in different nursery habitats for the Brazil-Guiana shelf penaeids.

There has been some speculation concerning the distribution of *P. brasiliensis*, which extends well into Surinamese waters despite the absence of identified nurseries for this species in that country. (Willman and Garcia, 1985) speculated that the adults migrate southeast down the coast from Guyana towards Brazil, and a similarly directed migration from Guyana towards French Guiana has been suggested (Kawahara, 1989; WECAFC, 1989). Such a migration would run counter to the Guiana Current unless a counter-current could be exploited. The presence of a tongue of high salinity water off Guyana may indicate such a counter-current which would facilitate return of subadults to their hypothesized spawning grounds off eastern Suriname. The timing of the subadult recruitment to the offshore fishery correlates well with this hypothesis since juveniles would enter the sea at a time when the current velocity is maximal.

Factors Influencing Survival

The two processes that determine the absolute abundance of any population of penaeid shrimp are: (1) the total number of viable eggs produced by the adult females; and (2) the survival of those eggs through the larval and juvenile stages to adulthood. This should not be confused with variability induced by changes in local abundances. The precision of any measurement of the abundance of a particular life stage will be influenced by a range of local or microhabitat

physical and biological factors, and the susceptibility of the shrimp to the sampling gear.

Penaeid shrimp are highly fecund with individual females capable of producing hundreds of thousands of eggs (Neal and Maris, 1985). Fecundity estimates for *P. brasiliensis* ranges from $0.5-1.5 \times 10^6$ eggs·female⁻¹ (Lares, 1985). Such fecundity has lead many fisheries biologists to believe that recruitment overfishing is uncommon given the high reproductive potential of the survivors (Garcia, 1983). Little is known about the factors which determine the onset of reproduction, the level of spawning activity in a population, or the age- specific fecundity. The survival rate and hatching success of penaeid eggs in the wild is unknown.

Viable eggs and their resultant larvae face a high risk of mortality during their cross-shelf migration and concurrent development (Turner, 1990). Predation risk to eggs and planktonic larval stages is high and dependent upon the time spent at each stage. Variability in planktonic food resources can lead to starvation while unfavorable shifts in oceanic current patterns can result in the loss of entrained eggs or larvae (Houde, 1987). Low temperatures or inadequate food supplies can reduce growth rates of meroplankton and prolong the larval stage. While some studies have attempted to examine the distribution of penaeid larval stages over the shelf (Temple and Fischer, 1965; Jones *et al.*, 1970; Staples and Vance, 1986; Rogers *et al.*, 1993), most assessments of the vertical distribution and migratory pathways of shrimp have generally been unsuccessful because of low larval densities, patchiness and limited taxonomic resolution of the early larval stages.

Heavy precipitation associated with tropical storms can reduce salinities to near 0 psu in a matter of hours and flush many organisms out of estuaries. This effect has been documented by (Forbes and Hay, 1988) and observed by one of the current authors (M.C. Benfield, pers. comm.) in the same South African estuary. Post cyclone sampling confirmed that penaeid shrimp were virtually absent from areas where, prior to the storm, abundances had been high. The capacity of estuarine populations to rebound after catastrophic weather events was suggested by the renewed abundance of penaeids and other estuarine fauna within a month of the storm. Witzell and Allen (1982) reviewed the effects of hurricanes on shrimp production in North America and found isolated reports of early emigration from estuaries at a small size, low subsequent harvests, and occasional beneficial reductions in estuarine salinity.

Low dissolved oxygen induced by eutrophication or other factors can potentially kill shrimp, however, unpublished studies in Florida Bay (P.F. Sheridan, National Marine Fisheries Service) suggest that penaeids can persist despite nocturnal hypoxic conditions. Juvenile mortality in estuaries can have a large impact on adult populations. Measurements of *P. aztecus* mortality in Galveston Bay ranged from 33-61% over a two week period (Minello *et al.*,

1989b). Estimates from other systems adjusted to two week rates were 52% for *P. aztecus* and 65% for *P. vannamei* (Minello *et al.*, 1989b). Predation appeared to have been the major factor contributing to brown shrimp mortality because mortality rates in predator exclusion cages over a comparable two week period were <3%. Once shrimp emigrate from estuaries and begin to recruit into commercial fisheries, natural mortality rates are probably low. Fishing mortality appears to be the major risk encountered by shrimp on re-entry to the ocean and becomes a factor at a size range of 50-70 mm TL. Prediction of Shrimp Abundance The relatively short life-spans of penaeids (1-2 yr), means that the annual catch is primarily derived from the recruitment of a single year class (Garcia and Le Reste, 1981). The establishment of predictive models are essential for the rational exploitation of these resources (Garcia and Le Reste, 1981; Matthews,). In general there are three types of models which predict the annual abundance of juvenile or adult penaeids: (1) those which relate abundance to a climatological factor such as temperature; (2) models which relate abundance to a biological factor such as the abundance of an earlier life-stage; and (3) stock-recruitment models which attempt to relate the abundance of reproductive age shrimp in one generation to the number of new recruits of the next generation entering the fishery. Predictive models which use the abundance of an earlier life-stage as a predictor tend to be superior to environmental indices (Garcia, 1983), but their usefulness in terms of a management tool decreases as the time interval between the sampled phase and the fishery phase is reduced. The long-term utility of environmental indices is difficult to evaluate because all available is generally used to develop formulate the model leaving little or no independent data for model validation (Garcia, 1985). Further, the causal mechanisms behind the correlations are often not understood although this does not appear to preclude their employment (Garcia and Le Reste, 1981). Stock recruitment models have limited utility for penaeid shrimp (Garcia, 1983).

The 1-1.5 year generation time of most penaeids simplifies prediction somewhat because events need only be considered for the preceding 12-18 months. (Staples *et al.*, 1985b) argue that in a geographically stable environment, the high fecundity of penaeids ensures a fairly reliable return of postlarvae to estuaries. Therefore, processes which determine survival of shrimp after postlarval settlement will often determine the size of the commercial stock from the same generation. Predictions based entirely on the abundances of juveniles assume unrealistic uniform year-to-year environmental influences and Staples *et al.* (1985b) suggest that weather induced effects (temperature and salinity fluctuations) need to be included in predictive models. Despite this criticism, juvenile abundance indices appear to work well and can provide reasonable predictive power.

Environmental Indices

Environmental models depend heavily on one or two driving variables which presumably control the survival of earlier life history stages. They also assume that there is no relationship between the stock density of one generation, and the recruitment of the following generation (Staples, 1985). In other words, environmentally mediated processes determine survival through to the adult stock. Coastal precipitation and air temperature will determine the prevailing estuarine salinity and temperature regimes which will then determine the amount of high quality nursery area available to juvenile shrimp (Witzell and Allen, 1982). The precision of these environmental relationships increases with the amplitude of the environmental phenomenon. When conditions are average, the strongest variance is often linked to biotic factors (Garcia and Le Reste, 1981). The mechanisms behind the relationships are poorly understood. They seldom involve the direct physiological effects of salinity and temperature but probably operate via a variety of intermediate physical (e.g. turbidity, area inundated, period of time shrimp are at a size vulnerable to predators) and biological (e.g. pathogens, predator abundance, availability of vegetated refuges, prey quality and quantity) processes affecting shrimp production.

Both temperature and salinity have been correlated with shrimp landings in a variety of regions. The relative importance of these two environmental factors depends on the geographic area and species being considered. Given the tropical climate of the region, seasonal temperature variation is unlikely to be sufficiently large to be well correlated with landings. The seasonal precipitation pattern certainly influences salinity, however, we have not focused on salinity because a more proximate indicator of rainfall such as river discharge is more likely to be correlated with landings. In regions of high seasonal rainfall, salinities in estuaries may fall to the point that low salinity becomes the dominating environmental factor influencing shrimp abundance (Staples *et al.*, 1985b). The effect of low salinity is species dependent. Some species such as white shrimp *P. setiferus* (and presumably its ecological equivalent - *P. schmitti*) are very euryhaline and do well in low salinity systems. Other species such as *P. aztecus* (and perhaps *P. subtilis* and *P. notialis*), prefer higher salinities and are more strongly influenced by rainfall and consequent reductions in salinity. (Hildebrand and Gunter, 1953; Gunter and Edwards, 1969) demonstrated that there was a positive relationship between the annual offshore catches of *P. setiferus* in Texas and the average annual rainfall over Texas for the two previous years ($r=0.66$), or the two previous years and the current year ($r=0.70$). No relationship was found for white shrimp production and rainfall or river discharge in Louisiana, presumably because the strong influence of the Mississippi and Atchafalaya rivers kept salinities below limiting levels in most years. Staples *et al.* (1985b)

cite work by Vance who found a significant positive relationship ($r=0.864$) between summer monsoonal rainfall and the catch of *P. merguensis* during the following autumn in the Karumba region of the Gulf of Carpentaria.

The only study which appears to have evaluated the influence of rainfall on shrimp landings in South America was that of Castello and Müller (1978). They reported a negative relationship between rainfall in the catchments flowing into the Patos Lagoon, Brazil and the landings of *P. paulensis* in the artisanal fishery during the subsequent year. Their best correlation was between landings and the rainfall from July-December ($r=-0.703$). Periods of heavy rainfall were hypothesized to increase flow rates in the access channel (up to 1.5-2.0 m·s⁻¹) which would limit access by recruiting postlarvae. River discharge has been used as another proxy variable for salinity. An example from a tropical region is discussed by Jorge da Silva (1986). That author reported a strong positive correlation ($r=0.898$) between the catch rate of subadult *P. indicus* (<13.5 cm TL) on the Sofala Bank, Mozambique (September - April) expressed as number of shrimp·hr⁻¹ and the Zambesi River discharge rate (km³) between August-March at a gauged station. Yield models which include effort data and river discharge have been developed for the Gulf of Mexico shrimp fishery with improved predictive power ($R^2=0.78$) (Griffin and Beattie, 1978).

Multivariate models which utilize more than one environmental variables are rare and offer little improvement of single variable predictors. Vance et al. (1985) developed a multistage model to offshore landings of *P. merguensis* in the Gulf of Carpentaria. The predictive success of this multistage model was similar ($r=0.865$) to the rainfall model ($r=0.864$). Ulanowicz et al. (1982) report that a model developed by Hunt et al. (1979) which used both temperature and salinity as independent variables in a multiple regression, was a useful predictor of shrimp landings. Ulanowicz et al. (1982) also developed a stepwise multiple linear regression model which used air and water temperature, salinity and precipitation as dependent variables. The model provided reasonably accurate prediction ($R^2=0.45-0.60$) of historical landings of a bivalve and four marine fishes, however, validation data sets were not available.

Biological Indices

These models attempt to relate the abundance of one life stage of shrimp to that of an earlier stage (e.g. predicting the abundance of adults from the abundance of postlarvae of the same generation). Given the complex life history of penaeid shrimp with large spatial and temporal distances between the eggs and their subsequent adults, stages which are far apart are unlikely to be correlated in a simple fashion. The more closely related the life history stages, the higher the chance that their abundances are correlated predictably (Staples, 1985).

Predicting Larval or Postlarval Abundance from Adult Abundance

Mortality rates of planktonic larvae are very high and variability at the larval and postlarval stage is related essentially to environmental factors and predation. For these reasons, Neal (1975) argues that it is not possible to show a useful correlation. The primary obstacles to the development of a production model are the difficulty in obtaining a reliable measure of larval abundance at sea, and the short duration of each larval stage against extended periods of egg and larval production. The concentrations of eggs, nauplius, protozoal and mysis stages in shelf waters are extremely low with high variances. A similar problem exists for predicting the abundance of adults from larval abundance of the same generation at sea - inadequate data on larval abundances at sea (Garcia and Le Reste, 1981). The large separation in life history stages during which time many different mortality factors can alter survivorship, makes it unlikely that a useful relationship exists.

Predicting Juvenile or Adult Abundance from Postlarval Abundance

In a frequently cited paper, (Baxter, 1963; but see also Baxter, 1969) showed some correlation between seasonal variations in the abundance of postlarval brown shrimp *P. aztecus*, and the abundance of their juveniles and adults in Galveston Bay, Texas. Essentially he demonstrated that cohorts of postlarvae could be identified in the subsequent juvenile and adult fishery samples, and that these could also be linked to overall commercial landings. Abundance of postlarval brown shrimp caught during their spring migration into estuaries was proposed as a tool to forecast subsequent landings. Since postlarvae migration occurs in advance of the commercial fishery, it would give sufficient warning for the industry to adjust and maximize their investment (Matthews, in review). Several short-term studies have shown a positive relationship between postlarval and juvenile abundances (Christmas *et al.*, 1966; Subrahmanyam, 1966; Subrahmanyam and Rao, 1970; Roessler and Rehrer, 1971). Longer data sets have not supported this relationship. Results from Louisiana by St. Amant *et al.* (1965) suggested that there was no good relationship between postlarval abundance and juvenile abundance. Later, Berry and Baxter (1969) examined seven years of postlarval data and could not find a useful relationship between the postlarval CPUE and the bait (juvenile) or offshore commercial CPUEs. These results suggest that, at least for *P. aztecus*, production depends heavily on juvenile survival in the estuary. Attempts to use only the abundance of postlarval brown shrimp as a forecasting index have generally been unsuccessful. The lack of success using postlarvae is probably due to: (1) the difficulty in accurately estimating abundances of postlarvae migrating into bays from the Gulf of Mexico (2) varying mortality rates for small brown shrimp in the nursery areas; and (3) climatically-induced mortality early in the season when cold-fronts are frequent (Matthews, under review).

In an attempt to address the problems which have limited the utility of postlarval-based forecasting models, Geoff Matthews at NMFS has developed a model which combines the postlarval abundance index with environmental parameters to predict the annual landings of adult *P. aztecus* in the Gulf of Mexico (Matthews *et al.*, 1994; Matthews, 1995). The Matthews Environmental and Postlarval Model (MEP) utilizes three environmental variables: the mean daily air temperatures (°F) for Galveston, Texas during April 9-22, the rainfall (inches) for the day that had the most rainfall between February 26-March 11, the mean water height (feet) at a tide gauge in Galveston Channel between April 23-May 6, and the mean of the lowest of the daily mean catches of postlarval brown shrimp for each of the periods February 26-March 11 and March 12-25. The model was developed using a subset of the complete data set and validated using the remaining data. The regression coefficient of the model for hindcast data was $R^2=0.90$, with 19 years of data. The predictive capability of the model ranges from excellent to pathetic, to quote Matthews, who expects the R^2 to stabilize around 0.70 with additional years of data. This model does suggest that for certain fisheries, the combined use of postlarval abundance and environmental data can provide a reasonable predictive capability.

Predicting the Abundance of Adult Stocks from Juvenile Abundances.

The most successful biologically-based forecasting tools utilize the abundance of resident or emigrating juvenile shrimp to predict adult landings offshore (Table 3). The advantages of such an index are obvious. The temporal and spatial separation of juveniles and harvested subadult/adult shrimp are close, and large juveniles have developed past the stages where environmentally mediated and predator mortality are highest. The potential disadvantage of such an index is the relatively short lead time for prediction. For juvenile abundance indices to be useful, they must be collected sufficiently early in the season to provide the commercial fishery with advance warning (Berry and Baxter, 1969).

(Yokel, 1969) showed that by taking seasonal variations in size at migration into account, there was good correlation between the numerical abundances of migrating juvenile pink shrimp *P. duorarum* and young recruits on the Tortugas fishing grounds. High correlation (not published but calculated from their data was $r=0.7$) was found between catches of juvenile *P. aztecus* in the Galveston Bay, Texas bait fishery between April 25-August 31, and the catch of adults at sea from July-September, and for similar indices derived from Louisiana waters (Berry and Baxter, 1969). Caillouet and Baxter (1973) used longer time-series to estimate a model for *P. aztecus* in Texas and Louisiana. When the annual catch at sea off Texas was correlated with the juvenile abundance index in one major estuary - Galveston Bay from 25 April-12 June, the model had a correlation coefficient of 0.85. This correlation dropped ($r=0.28$) when the estimate was based on the annual estuarine catch of juvenile brown shrimp. *Penaeus setiferus*

Table 3. Parameters used in the prediction of shrimp abundance from juvenile stages.

Location	Parameter	Variance Explained (R ²)	Author(s)
Barataria Bay (Northern Gulf of Mexico)	Water Temp.	High	(Barrett and Ralph, 1977)
Texas	Latitude		(Turner, 1977)
Gulf of Carpentaria	Rainfall	0.44 to 0.49	(Gunter and Edwards, 1969)
Patos Lagoon, Brazil	Monsoonal rainfall	0.75	(Staples et al., 1985a)
Gulf of Mexico	Rainfall	-0.49	(Castello and Müller, 1978)
Mozambique	River Discharge	0.78	(Griffin and Beattie, 1978)
Gulf of Carpentaria (Australia)	River Discharge	0.81	(Jorge da Silva, 1986)
North Carolina	Multistage (with rainfall)	0.75	(Vance et al., 1985)
	Air temperature		
	Water temperature	0.45 to 0.60	(Ulanowicz et al., 1982)
	Salinity		
	Rainfall		
Gulf of Mexico	Air temperature	Hindcast: 0.90	(Matthews, 1995)
	Rainfall	Forecast: ??	
	Water height		
Gulf of Mexico	Postlarval abundance		
	Juvenile abundance	0.72	(Matthews et al., 1994)

yielded a correlation of $r=0.58$ for the same kind of data. In Louisiana the correlation between the annual estuarine and marine catch was $r=0.73$ for *P. aztecus*, and $r=0.86$ for *P. setiferus* (Barrett and Gillespie, 1975). NMFS biologists currently employ the Baxter Bait Shrimp Index (BBSI) to predict commercial landings. The model yielded a fit $R^2=0.72$, with 18 years of data (Matthews *et al.*, 1994). The bait shrimp index is the mean CPUE (lbs·hr fished⁻¹) from Galveston Bay's bait shrimp fishery. The performance of the model for forecasts and hindcasts of annual Texas offshore landings during a biological year (12 months beginning in July and running through the following June) is reasonable - for 10 of the 18 hindcast years the BBSI predictions were within $\pm 10\%$ of actual landings. The model's predictions are poor during years when Galveston Bay receives heavy rain (Matthews *et al.*, 1994). Under these conditions (e.g. 1966, 1979), juvenile brown shrimp congregate in the lower bay where the salinities are higher. These concentrations are more easily fished which leads to inflation of the BBSI and under these circumstances, the model is not used predictively. In other cases, heavy flooding results in the early emigration of large numbers of small shrimp which may survive offshore. Their absence from the bay leads to an unrealistically low BBSI and an underestimate of the stock.

The abundance of emigrating juveniles appears to be a useful index for timely prediction of adult landings (3 months in advance). These models may not be suitable for all fisheries. It should be noted that the brown shrimp fishery along the coast of Texas is a simple system which is amenable to modeling (Matthews *et al.*, 1994). This is because: (1) heavy fishing pressure means over 99% of shrimp harvested are <1 year old; (2) 75% of the Gulf brown shrimp harvest occurs in July, August and September; and (3) the harvested stock is derived from late-winter/early-spring spawned shrimp. Thus, events which are confined to the first few months of the year shape the size of the exploited stock. The problems associated with natural environmental variation, spatial and temporal variations in biological populations (eg. multiple year classes) which can complicate forecasting are minimized in the Texas case. This type of forecasting has not been widely evaluated and the development of a bait shrimp-type index for other fisheries, such as those along the Brazil-Guiana shelf, merits consideration. A BBSI-type index should be considered for the Brazil-Guiana shelf. The artisanal fisheries in the lagoons and coastal waters already exploit juvenile shrimp using Chinese seines and small vessels (eg. Gulf of Paria). Catches from these fisheries may provide an index analogous to that of the bay shrimpers in Texas. If historical landings data are available for the artisanal fisheries, correlation analyses may suggest potential sites for development of a functional relationship.

Factors Influencing Abundance Estimates The factors which contribute to variability in estimates of postlarval or juvenile abundance are highly variable

and in many cases - species, habitat and gear specific. The distributions of these animals are patchy in time and space. As a consequence, short-term samples are unlikely to be representative of seasonal trends. Most of the early-life stage indices which have been examined rely on means of estimates for several weeks or months. A sound understanding of the regional periodicity of the species of interest appears to be a prerequisite for development of any predictive index. For example, when does the major period of postlarval recruitment occur? The brown shrimp fishery in Texas is well studied and the peak recruitment is generally agreed to occur during early April (Matthews, 1995). Historical data on postlarval abundance reveal a wide degree of scatter. Estimates of postlarval abundances need to be taken over an extended period around the historical mean. Further investigations revealed that postlarval abundance varies on a diel basis with greatest catches occurring at night, and on a tidal basis with greatest catches on flood tides. These, and other factors are responsible for variations in the postlarval abundance of almost all estuarine-dependent penaeid species (see reviews in Staples, 1980; Staples and Vance, 1986; Lochmann, 1990; Matthews *et al.*, 1991). Matthews (1995) suggests that estimates of postlarval could be improved by sampling (1) each day, (2) during both day and night, (3) at two or more sites, (4) taking triplicate samples and (5) on flood and ebb tides. Similar considerations are important when estimating the abundance of juvenile shrimp (Staples and Vance, 1979).

In a fisheries context, recruitment refers to the numbers of new individuals entering the fishable stock and for this reason recruitment is operationally defined in relation to specific fisheries. In many regions, penaeids are targeted at various ages and sizes by successive fisheries (artisanal then commercial trawlers) and thus recruitment into each fishery occurs at different times. Most stock-recruitment models attempt to define the relationship between the abundance of the spawning stock of generation t , and that of the subsequent recruits to the commercial fishery from generation $t+1$.

Stock recruitment models assume that the number of recruits is fixed at some earlier life-history stage and tend to ignore subsequent environmental and biological effects (Staples, 1985). The success of stock-recruitment models for species such as penaeid shrimp, where recruitment is related to biomass of the spawning stock some 6-12 months earlier is dubious (Staples, 1985), and many published penaeid stock-recruitment relationships could easily be artifacts of serial changes in environmental variables (Garcia, 1983).

Garcia (Garcia, 1983; Garcia, 1985) reviews evidence for stock-recruitment relationships in penaeids and suggests that in most cases, there is no strong evidence that recruitment strength is determined by stock size. Stock-recruitment relationships in penaeids may be complex because: (1) annual landings are strongly influenced by environmental factors and predation; (2) environmentally driven changes in stock size are often serially correlated which may produce an

artificial stock-recruitment relationship; and (3) pre-recruit mortality is likely to vary seasonally for different cohorts (Garcia, 1985). The presence of poorly documented inshore fisheries exploiting juveniles and subadults further complicates the use of stock-recruitment indices for offshore trawl fisheries.

CONCLUSIONS

Substantial gaps exist in our understanding of the life history patterns of all of the commercially important shrimps along the Brazil-Guiana shelf. Basic information on mortality, growth rates, age and size at maturation, and periodicity of spawning and recruitment is required. This information is required for each species individually as the literature suggest that there are important differences among species. Development of a predictive model based on juvenile abundances in the artisanal fishery coupled with one or more environmental parameters appears to be the best strategy for management of the shrimp fishery along the Brazil-Guiana shelf. Selection of appropriate sites for model data collection and formulation will require an understanding of (1) the distribution of juvenile shrimp by species among the estuaries of the shelf; (2) the seasonal periodicity of emigration from those estuaries; and (3) the migration pathways leading from estuaries to offshore fishing grounds. These three issues should receive the highest priority. Habitat mapping should also be accorded a high priority so that productive nursery areas can be identified and preserved, and appropriate sampling sites can be selected. The remaining life-history considerations (location of spawning sites and larval migration pathways) are important because they directly link the offshore commercial stocks with their estuarine nurseries. Given the need for management of shrimp stocks which almost certainly cross national boundaries, identification of these pathways is an important step. To fully permit management of the shrimp species in the above fashion, we need to determine the species distribution and seasonal periodicity of juvenile shrimp in coastal estuaries. This includes the determination of the relative abundance of each species of shrimp in the system; the times of the year when they arrive, reach peak abundance, and emigrate; and the nature and distribution of the substratum. The development of a monitoring system using artisanal gear (fyke nets or outboard trawlers) to confirm emigration periodicity, and estimate the species composition and size-frequency distribution of emigrating shrimp is required. Meteorological records and other environmental parameters which are recorded with sufficient continuity for each region of interest should be assembled. While the juvenile shrimp index may indeed be correlated with offshore landings and thus prove to be effective, the addition of one or more environmental parameters to the juvenile index model may improve its predictive power. Both river discharge and precipitation appear to have potential as environmental indicators. Finally, all hydrographic and fisheries survey cruise data from the region should be gathered and merged, so that some synthesis of existing data can be developed.

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