

A STOCHASTIC SIMULATION MODEL OF BROWN SHRIMP,
PENAEUS AZTECUS IVES, BURROWING BEHAVIOR

A Thesis

by

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Approved as to style and content by:



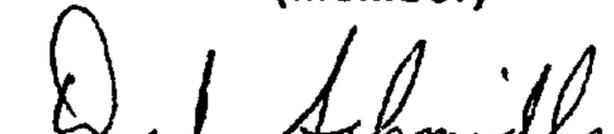
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ABSTRACT

A Stochastic Simulation Model of Brown Shrimp, *Penaeus aztecus* Ives, Burrowing Behavior. (December 1991).

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Burrowing behavior is important in regulating the availability of juvenile brown shrimp to predatory fishes in estuarine systems. Burrowing patterns are typically synchronized with diel fluctuations in light intensity. A model of shrimp burrowing was developed using light as the main driving variable. Water depth and turbidity variables are included because of their role in attenuation of light in the water column. Incident light, water depth, turbidity levels and their effect on subsurface light intensity were monitored at Jamaica Beach (Galveston), Texas. Material transfer rates were determined from a laboratory study examining subsurface light intensity on burrowing patterns of shrimp. Burrowing was classified into daytime, nighttime, predawn and transition periods. At night, and during predawn periods, burrowing levels were low. During the transition and daytime periods, burrowing was controlled by light intensity with the strongest effect occurring during the transition hours (dawn and dusk). Data from field observations on brown shrimp burrowing in estuaries were significantly different from baseline predictions during the daytime and transition periods. A 'modified baseline model' which used subsurface light intensity (measured in a separate field validation experiment) as the only driving variable was validated for the daytime period only. The final model was modified to include all data (results from laboratory and field experiments) for the purpose of parameterizing burrowing rates. The model can be integrated with more complex models to examine brown shrimp mortality by simulating burrowing patterns and encounter rates with predatory fishes.

DEDICATION

I would like to dedicate this research effort to several people. Without the love, patience, support and assistance of my wife Janet Lea, I would not have been able to complete this project. To our families and friends whose encouragement and moral support was always well timed. To the memories of my brothers and friends, Jody and Jimmy Hutchinson; they will always live in my heart. To the members of my graduate committee who served as my mentors and whose guidance will be with me forever, a special thank you is in order. Finally, I wish to acknowledge the courageous men and women of U. S. Armed Forces who serve during times of war, past and present. Only recently have they begun to receive the attention and praise that they have earned and deserve. Because of their efforts and sacrifices, I maintain the freedom and the time to apply myself in the disciplines I really enjoy.

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INTRODUCTION

The Gulf of Mexico shrimp stocks support the most valuable fishery in the United States (GMFMC 1981), and a major species in the fishery is the brown shrimp, *Penaeus aztecus*. Adult brown shrimp spawn in offshore waters primarily during the late winter of each year (Garcia and LeReste 1981), and the larvae are transported across the continental shelf into coastal bay systems during early spring (Baxter and Renfro 1967). Postlarvae and juveniles remain in shallow estuarine nurseries for approximately 2-4 months before returning to offshore waters as subadults (Trent 1966; Baxter and Renfro 1967; Garcia and LeReste 1981). Because recruitment to the fishable population is used as an indicator of the status of shrimp stocks, management of the fishery requires information on the magnitude of recruitment and on factors that modify recruitment.

The survival of young in estuarine nurseries is an important component of recruitment success, and Minello et al. (1989) report that predation by estuarine fish is the dominant factor affecting survival of juvenile brown shrimp in estuaries. The biotic and abiotic factors regulating predator-prey interactions among juvenile shrimp and fish in estuaries are complex. However, the availability of brown shrimp to predators is largely dependent on their diel behavior patterns because of their ability to burrow into the substrate.

A simulation model of brown shrimp burrowing behavior can be used to examine encounter rates with predators and consequently to help quantify predation mortality. A variety of predation schemes can be applied to the model to study the magnitude and variability of predation-related mortality in brown shrimp populations. Natural mortality estimates and recruitment or yield predictions may be

enhanced through incorporation of this information into current fishery models.

The objective of this study is to develop a simulation model representing the influence of major environmental factors on the burrowing behavior of brown shrimp in estuarine nursery areas. The model is based on results of laboratory experiments and field observations that determine the threshold light levels necessary to stimulate burrowing or elicit emergence from burrows.

The model is used to examine changes in burrowing patterns throughout the illuminated portion of the day under a variety of conditions, and to demonstrate possible effects of these conditions on brown shrimp mortality rates and population dynamics. The model will allow fishery managers to assess the activity of shrimp more accurately and provide valuable insight into factors regulating natural mortality and subsequent recruitment to the fishery.

LITERATURE REVIEW

Annual landings of brown shrimp off the Texas coast can be accurately predicted from an index using bait shrimp collected from Galveston Bay (Baxter and Sullivan 1986). This prediction however, cannot be made until bait shrimp data are collected and analyzed during the first half of each calendar year. Obtaining an earlier estimate requires information on natural mortality of young shrimp in estuarine nursery areas. Historically, most mortality estimates for shrimp have been for adult shrimp in offshore waters and these estimates are highly variable (Table 1). McCoy (1972) utilized mark-recapture data to estimate natural mortality of subadults in North Carolina estuaries at 91.6% (monthly). For juvenile brown shrimp in the Galveston Bay system, Minello et al. (1989) used a cohort analysis to provide variable estimates of actual mortality which ranged between 67.7% and 98.4% monthly. The large variability in estimates of mortality is probably due to methods of estimation as well as variability in natural mortality caused by environmental fluctuations (Rothschild and Brunenmeister 1984).

Table 1. Instantaneous and actual natural mortality estimates for brown shrimp.¹
Original estimates were converted to monthly values.

Growth Stage	Instantaneous Natural Mortality Rate (M)	Actual Natural Mortality Rate (%)	Source
Juvenile	1.13 - 4.17	67.7 - 98.4	Minello et al., 1989
Subadult	2.47	91.6	McCoy, 1972
Adult	0.91	59.7	Klime, 1964
Adult	0.15	13.9	Parrack, 1981
Adult	0.142	13.2	Rothschild & Brunenmeister, 1984

¹ Instantaneous natural mortality represents the ratio of the number of natural deaths (as opposed to those caused by fishing) per unit of time to population abundance during that time, if all deceased fish were to be immediately replaced so that the population size does not change.

A better understanding of the mechanisms causing mortality in penaeid shrimp is needed. Laboratory studies indicate that temperature, salinity, and dissolved oxygen content can cause mortality of penaeid shrimp (Zein-Eldin and Aldrich 1965; Zein-Eldin and Griffith 1966; Aldrich et al. 1968; Weispape et al. 1972; Copeland and Bechtel 1974; Kramer 1975; Wickham and Minkler 1975; Lakshmi et al. 1976; Renaud 1986), but levels of these parameters during the period when brown shrimp are in the nursery areas (March-June) seldom attain lethal limits. These physical factors along with starvation and disease may contribute to juvenile shrimp mortality, but the primary cause appears to be predation by estuarine fish (Minello et al. 1989). Research at the National Marine Fisheries Service in Galveston, Texas has provided insight into some important processes that regulate predation rates on shrimp.

In an estuary such as Galveston Bay, many biotic and abiotic factors affect predation mortality of brown shrimp. The presence and/or accessibility of vegetation is important because it provides a refuge from predators (Minello and Zimmerman 1983, 1985; Minello et al. 1989). Predator-prey size characteristics are important because very small or very large prey organisms can escape predation (Brooks and Dodson 1965; Edwards 1977; Nilson 1978; Zaret 1980) and because ingestion of prey by fish may be regulated by the size of their 'gape' or throat (Werner 1979; O'brien 1987). Water level, substrate type, water turbidity, and the burrowing behavior of shrimp are important because they can affect encounters among shrimp and fish (Fuss and Ogren 1966; Minello et al. 1987, 1989). The effects of each of these factors may vary for different predator species.

Burrowing by penaeid shrimp appears to be one of the most important behaviors regulating mortality. Fish predators on shrimp are often visual feeders (Chao and Musik 1977), and burrowing by shrimp can reduce shrimp detection.

Reduced activity of burrowed shrimp may also reduce encounter probabilities among shrimp and predatory fish (Gerritsen and Strickler 1977). Minello and Zimmerman (1984) and Minello et al. (1987) observed that burrowing by brown shrimp reduced their availability to some fish predators and decreased predation mortality. Increased knowledge of factors controlling burrowing behavior of penaeid shrimp should lead to a better understanding of the mechanisms regulating predation mortality.

Many factors have a direct effect on the burrowing behavior of penaeid shrimp and may consequently alter survival rates (Fuss and Ogren 1966; Wickham 1967; Hughes 1968; Moller and Jones 1975; Wickham and Minkler 1975). These factors can be classified as either physical or biological in nature. The single most important physical factor affecting burrowing is light intensity (Eldred et al. 1961; Fuss and Ogren 1966; Hughes 1966; 1968; Wickham and Minkler 1975; Lakshmi et al. 1976). Generally, penaeid shrimp burrow when light intensity is relatively high. A decrease in light intensity below a threshold level elicits the emergence of shrimp from burrows. In estuarine systems, the differences between diurnal and nocturnal light intensities are sufficient to evoke changes in burrowing patterns. Circadian activity rhythms in penaeid shrimp are synchronized with the daily illumination cycle. These activity patterns can be manipulated experimentally by altering the duration of the photoperiod (Hughes 1968; Moller and Jones 1975; Reynold and Casterlin 1979). Lunar cycles and tidal patterns are also correlated with burrowing behavior in penaeid shrimp (Aaron and Wisby 1964; Wickham 1967; Hughes 1968; Rulifson 1983). Aaron and Wisby (1964) and Wickham (1967) reported bimodal peaks of nocturnal activity by pink shrimp, *Penaeus duorarum*, during new and full moons. Rulifson (1983) observed that brown and pink shrimp utilize tidal currents for transport and thus emerge from burrows during flood and ebb tides. However, brown shrimp may burrow at any time during flood/ebb tides when they reach

favorable conditions such as optimal salinities or sediment characteristics (Rulifson 1983).

Temperature, salinity, dissolved oxygen, water turbidity, and substrate type are among other physical factors that affect burrowing in penaeid shrimp. *Penaeus aztecus* (Aldrich et al. 1968), *P. duorarum* (Fuss and Ogren 1966), and *P. esculentus* (Hill 1985) burrow when water temperatures decrease to 12-18 °C and re-emerge from burrows when temperatures rise above 18 °C. Conflicting data exist concerning the effects of salinity on shrimp activity. Lakshmi et al. (1976) contended that greater numbers of brown shrimp burrow at low salinities (8-17‰) in comparison to higher salinities (25-34‰). However, in previous unpublished studies, I have observed a significant decrease in burrowing by brown shrimp at low salinity (5‰) in comparison with higher salinities (25 & 40‰). The mean burrowing rates in this experiment suggest that reduced burrowing occurs at salinity extremes.

Venkataramiah et al. (1974) suggested that burrowing by brown shrimp can also be a response to physiological stress created by extreme salinities or temperatures.

Differences in experimental methods (e.g., acclimation time) may account for some of these apparent differences in burrowing patterns with changing salinity. In my unpublished experiments, shrimp were acclimated to test salinities for a minimum of three days; Lakshmi et al. (1976) acclimated shrimp for two days. Venkataramiah et al. (1974) also acclimated shrimp for two days but utilized a variety of salinity/temperature acclimation combinations.

Egusa and Yamamoto (1961) and Renaud (1986) reported that some penaeid species emerge from burrows or become more active at reduced levels of dissolved oxygen. NMFS experiments (unpublished) investigating the effect of rotenone on burrowed brown and white shrimp support their observations. Rotenone blocks oxygen transport across the gills which simulates anoxic environmental conditions and causes

shrimp to emerge from burrows. However, partially burrowed shrimp initially moved deeper into the substrate after application of rotenone and then emerged completely from burrows as apparent water quality deteriorated. This response may be stress-related, similar to that reported for temperature and salinity effects by Venkataramiah et al. (1974). However, increased burrowing may only be a short-term response to stress, and shrimp apparently emerge from burrows, presumably to seek habitats of better quality, when unfavorable conditions are prolonged (Tabb et al. 1962; Costello and Allen 1970).

Increased water turbidity significantly reduces burrowing of brown shrimp (Minello et al. 1987). This effect is apparently due to the reduction of light intensity near the substrate caused by turbid water. Turbidity also alters predation rates of fish on shrimp and other epibenthic prey (Moore and Moore 1976; Minello et al. 1987) which, at least in part, can be related to changes in burrowing behavior.

Burrowing rates are generally reduced as substrate grain size increases (Williams 1958; Fuss and Ogren 1966; Hughes 1968; Rulifson 1981, 1983; Moller and Jones 1975; Aziz and Greenwood 1982; Minello and Zimmerman 1984; Minello et al. 1987). Compaction and/or lithification of small grain sediment types, however, may suppress burrowing behavior of shrimp.

Population density, predators, and the presence of aquatic vegetation may all affect burrowing patterns in penaeid shrimp. Increasing shrimp density reduces burrowing by white shrimp, possibly due to overcrowding and social interaction (T.J. Minello, NMFS, Galveston, TX., personal communication, 1991). However, no significant density effects were observed for brown shrimp within the density range of 5.5-22.2 shrimp/m². The presence of predators elicits avoidance behavior in penaeid shrimp which commonly results in burrowing (Fuss and Ogren 1966; Hughes 1968; Moctezuma and Blake 1981). The presence of aquatic vegetation may

indirectly affect burrowing behavior by altering sediment characteristics and reducing turbidity (Thayer et al. 1984; Short and Short 1984), or providing an alternative refuge through increased habitat complexity (Minello and Zimmerman 1983, 1985).

Shrimp size and physiological condition can also affect burrowing. Small shrimp are more active and tend to burrow less than large shrimp (Eldred et al. 1961; Hughes 1968; Moctezuma and Blake 1981; Rulifson 1981). This is probably due to an increased need for foraging by small shrimp as a result of their higher nutritional requirements (Hughes 1968; Moctezuma and Blake 1981). Large *P. duorarum* have also been shown to be more sensitive to light than small individuals (Fuss and Ogren 1966). The effect of hunger (Hughes 1968; Ruello 1973) and molting processes (Wassenberg and Hill 1984) are important in determining activity rates in penaeid shrimp. Starved shrimp allow for more foraging time or emerge from burrows when food is present (Eldred et al. 1961, Costello and Allen 1970). Furthermore, penaeid shrimp will remain quiescent or burrowed during ecdysis, possibly to avoid predation during a period when they are most vulnerable (Eldred et al. 1961; Bishop and Herrnkind 1976; Lakshmi et al. 1976).

MODEL OVERVIEW

The ultimate goal in developing a burrowing model for brown shrimp is to provide information that can be used to explain the mechanisms regulating predation mortality of juveniles in estuaries. It is evident from the literature that many complex processes are interacting on shrimp and fish predators, and these are described in a conceptual model of shrimp mortality (Figure 1). The mortality model includes predator and prey populations and factors such as the physical environment, prey densities, and the presence of alternate prey. This conceptual model provides a general view of the estuarine ecosystem. Many important processes are aggregated within some of the variables shown. The effects of some factors (i.e., role of physical environment on recruitment) are not included in the conceptual mortality model; they are beyond the scope of this study and may provide the basis for future research.

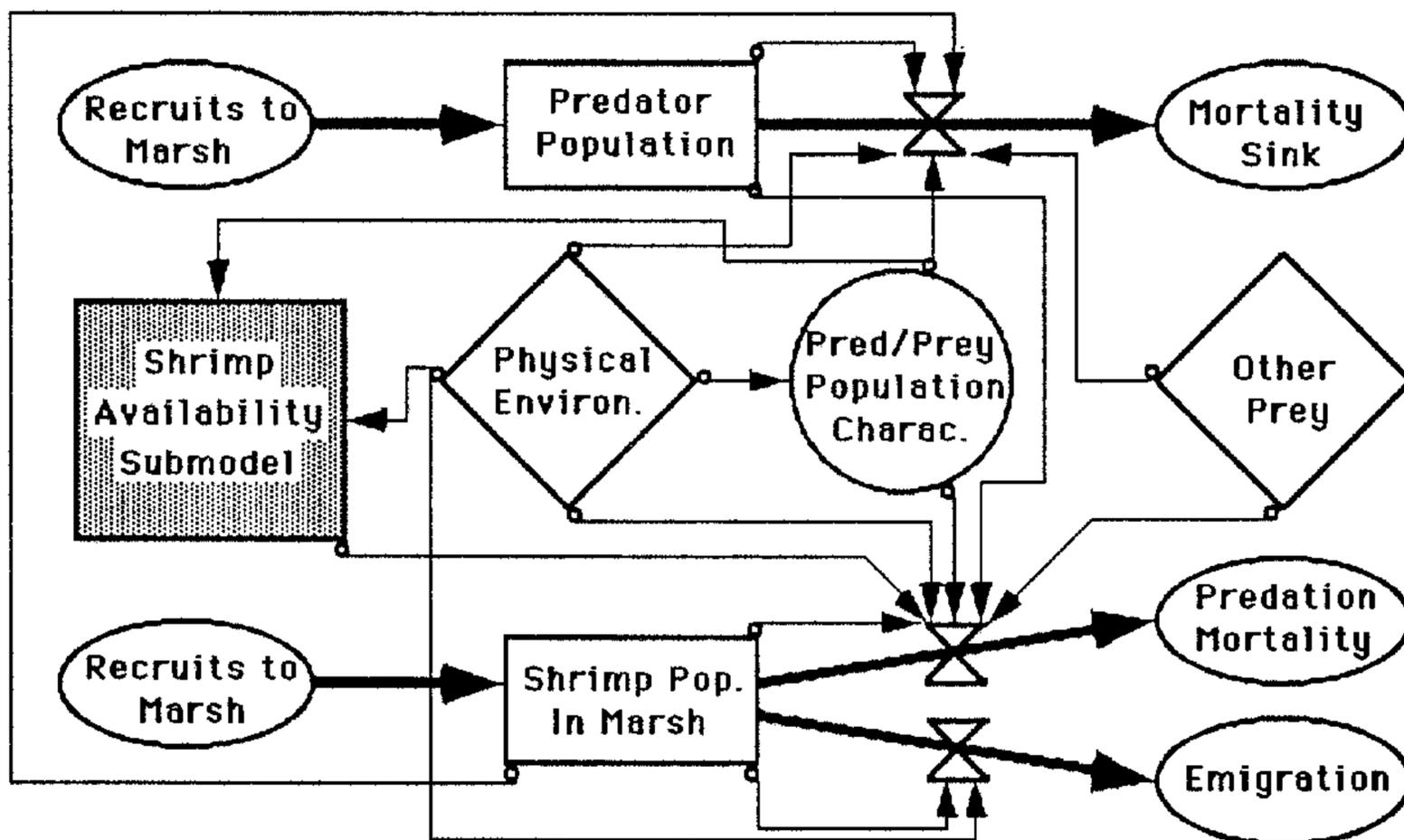


Figure 1. Conceptual model of shrimp mortality including predator and prey populations. Large arrows represent material transfers and thin arrows indicate information transfers. Symbols follow Forrester (1961).

A major component of the interaction between the predator and prey populations in the conceptual mortality model depends upon a submodel of shrimp "availability" (Figures 1, 2). The availability submodel reflects the factors involved in determining whether shrimp are available to predators, given their presence in the estuary. If shrimp are burrowed or otherwise undetectable by predators, then other factors that may affect their consumption (i.e., selection of alternate prey) by predators cannot be considered. Consequently, the burrowing behavior model is essentially a submodel 'nested' within the shrimp availability and mortality models.

The model for juvenile brown shrimp burrowing in an estuarine nursery area was formulated for conditions that are normally observed at the Galveston Island State Park at Jamaica Beach (Figure 3) in the spring and early summer. Bounding the

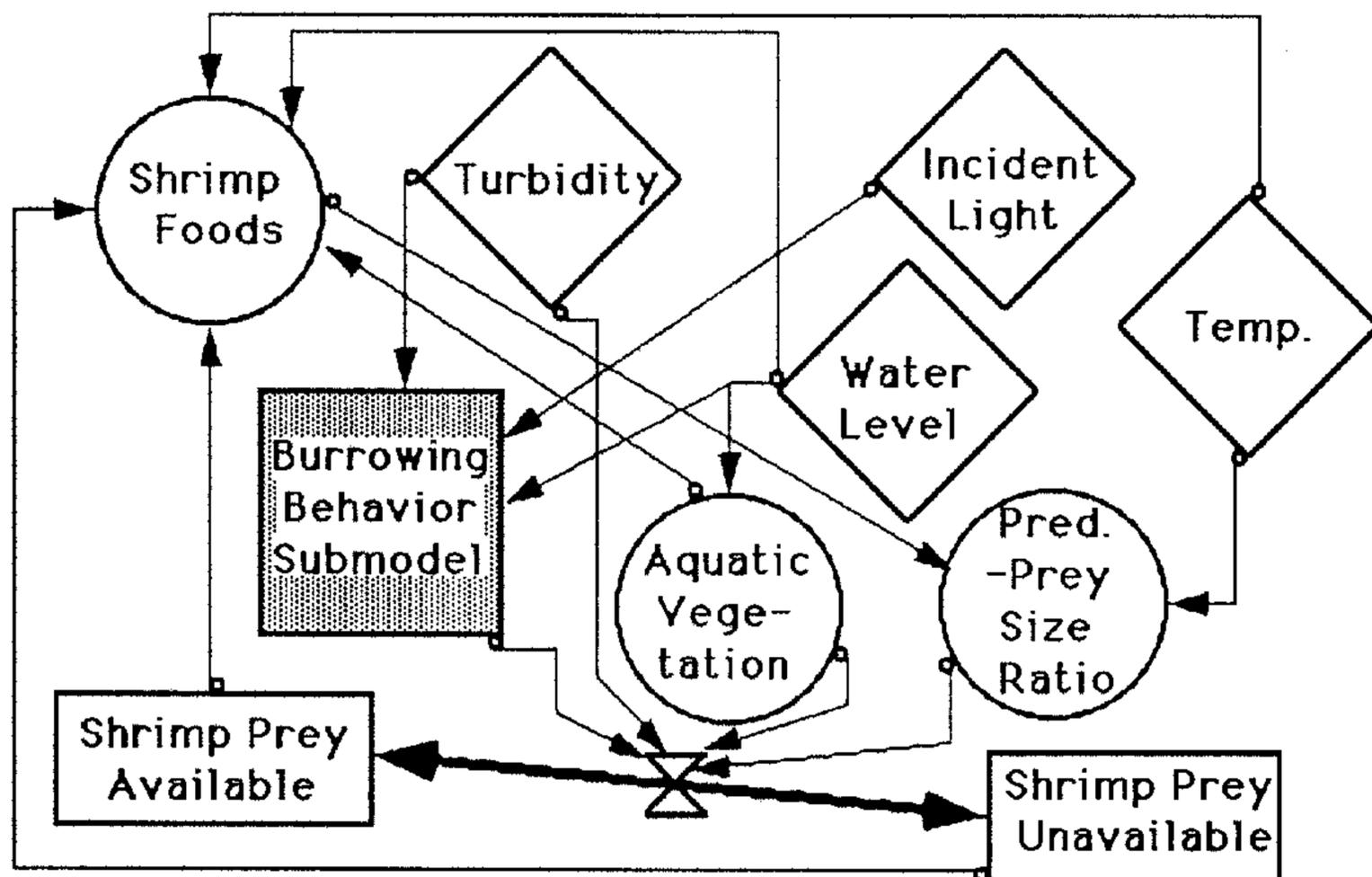


Figure 2. Conceptual model depicting major physical and biotic factors which affect the availability of shrimp to predators. Burrowing behavior of shrimp is a major factor regulating shrimp availability.

model to operate under these conditions (normally observed in Galveston Bay), resulted in the exclusion of some factors which may affect burrowing under different conditions (Table 2). Temperature-related processes are excluded from the model because estuarine water temperatures are unlikely to reach extremes that affect shrimp burrowing rates during the time when most brown shrimp utilize Galveston Bay nursery areas (March-July). Dissolved oxygen, salinity, population density, and nutritional considerations are excluded for the same reason.

Lunar effects and tidal patterns *per se* are not included in the present model because of their complexity, but the effects of these may be related to other factors in the model such as light intensity, water level, and water turbidity. Tidal patterns are therefore included implicitly in the model structure in the water level variable.

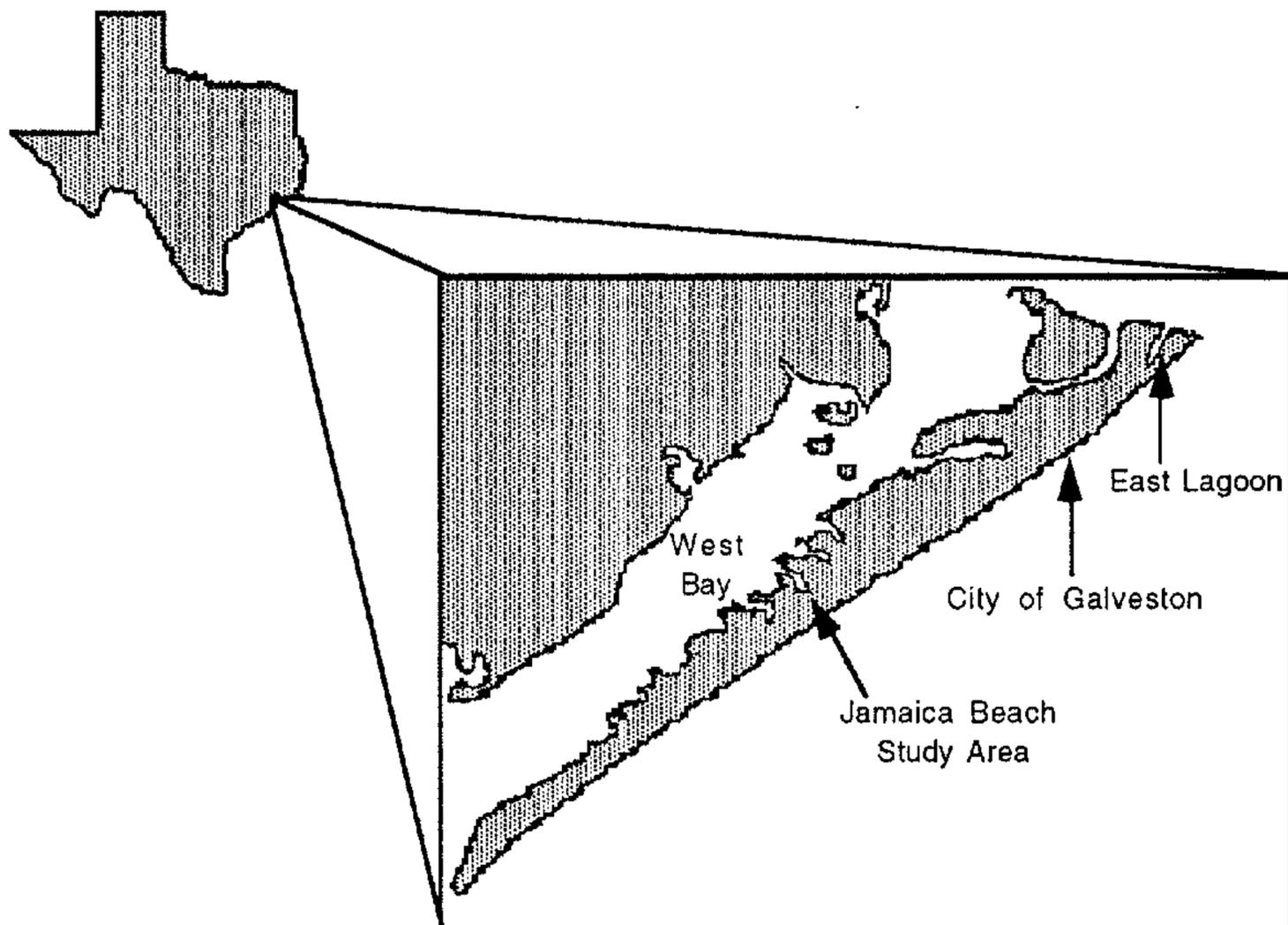


Figure 3. Map of Galveston Island showing study areas at Jamaica Beach and East Lagoon.

Table 2. Biotic and abiotic factors that may affect burrowing behavior of brown shrimp. Inclusion of factors which may be considered later depends on results from ongoing and future studies.

Presently In The Model:	Not Included In Model:
Incident Light	Temperature
Water Depth	Dissolved Oxygen
Water Turbidity	Salinity
	Shrimp Density
Can Be Considered Later:	Prey Abundance
Hunger Level	Lunar Effects
Circadian Rhythms	Winds / Climatic Effects
Substrate Type	Tides
Predators	Ecdysis / Physiological Effects
Shrimp Size	
Vegetation	

Burrowing behavior of brown shrimp is represented by a submodel consisting of two state variables, active and burrowed shrimp (Figure 4). There is a clock that influences burrowing rates and serves to drive incident light which is the primary input into the model. Water level and water turbidity control light intensity at the substrate surface through the attenuation of incident light via scattering and absorption.

Several factors not included in the model can be considered in later studies to determine how they affect model behavior. Addition of these factors may result in an improved version which can be applied to broader, generalized conditions. A vegetation component may be considered later because the presence of emergent vegetation may alter burrowing rates when brown shrimp move up into marshy areas during periods of high tide (Zimmerman et al. 1984; Zimmerman and Minello 1984a). The additional cover provided by the vegetation may elicit shrimp to emerge from burrows; emergent vegetation reduces fish predation on juvenile shrimp (Minello and Zimmerman 1983;

Minello et al. 1989). The effects of shrimp size, substrate type, and hunger may also be added later to determine if they enhance the accuracy of model predictions.

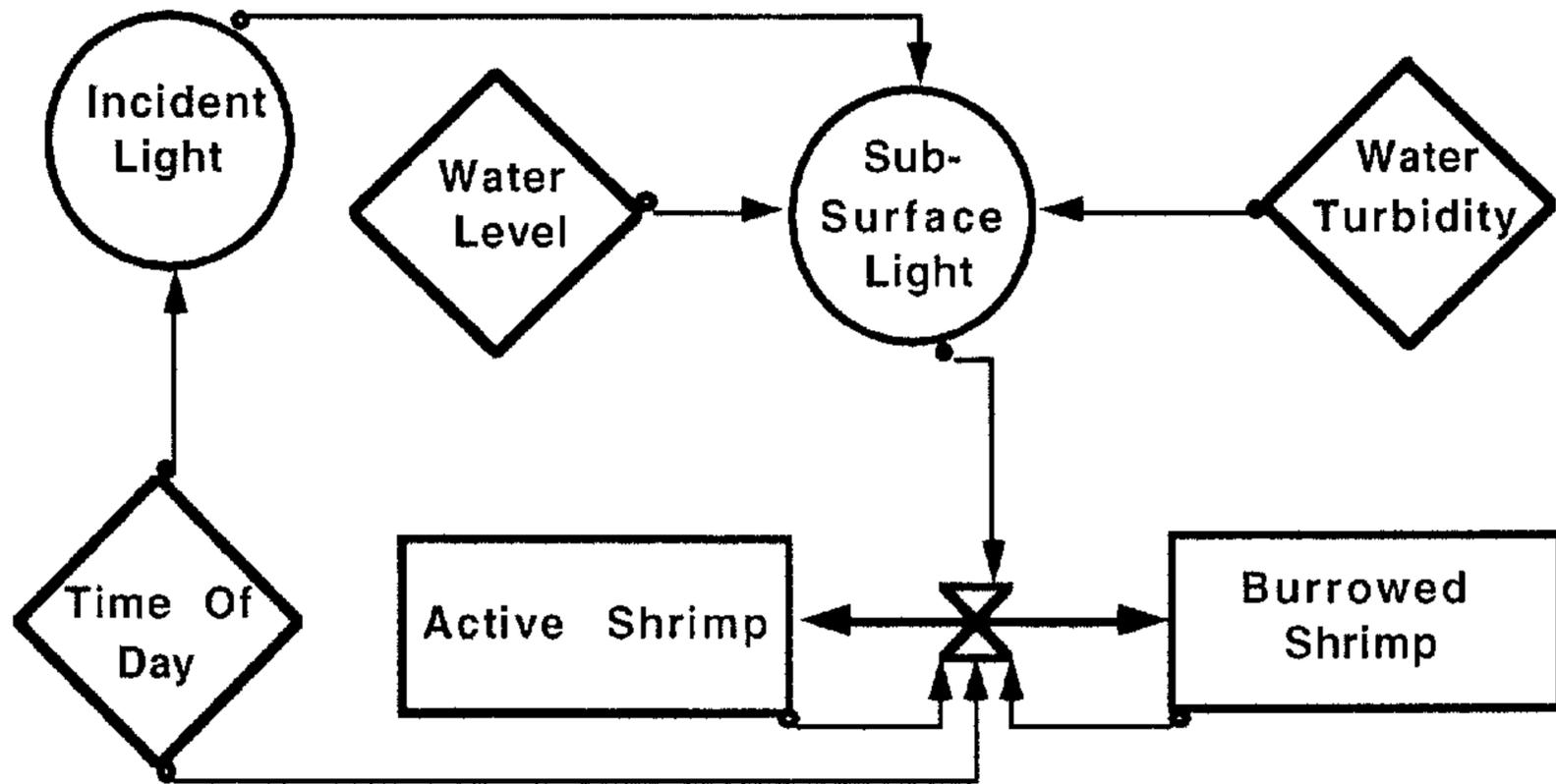


Figure 4. Conceptual model of brown shrimp burrowing behavior. Water level and turbidity are considered as driving variables here.

MODEL DEVELOPMENT

The model was developed in two stages. The first stage involved quantifying the driving variables (incident light, water level and water turbidity) and determining the effects of these on subsurface light intensity. The second stage in model development consisted of determining the effect of subsurface light intensity on movement between the two state variables, burrowed and emerged shrimp. The actual simulation model was programmed in the STELLA software package (High Performance Systems, Inc., 45 Lyme Rd., Hanover, NH 03755). STELLA is a graphics-based simulation environment for Macintosh computers that provides a programming framework for building and running simulation models.

Driving Variables

Incident Light

Diel incident light levels were measured with a LI-COR LI-1000 quantum meter/datalogger (LI-COR, Inc., Lincoln, Nebraska) during portions of the spring, summer and autumn of 1987 and during the spring and summer of 1988. The irradiation sensor used (model LI-192-SB) is capable of measuring light levels in the photosynthetically active range (PAR) of 400-700 nm wavelength. The unit of measure is in microEinsteins·meter⁻¹·second⁻² ($\mu\text{E}\cdot\text{m}^{-1}\cdot\text{sec}^{-2}$). Measurements of average light intensity were recorded every thirty minutes throughout each 24 hr. period. Only data collected during the month of May in 1988 and 1989 (n = 836) were used in the analysis because this represents the period when the majority of juvenile brown shrimp occur in Galveston Bay nurseries.

Maximum values were fairly consistent between different days with most of the variability attributed to fluctuations in cloud cover. Seasonal measurements were quite similar with the main difference being the duration of sustained maximum light levels

as well as duration of the photoperiod. The relationship is characterized by a parabolic curve (Figure 5) which peaks at ~1300 hr's. and then drops to zero after sunset (~2000 hr's). Any reference to a specific time of day indicates central daylight time (CDT). In the model, at each thirty-minute time step, the mean light level (Figure 5, Table 3) is used as an input for incident light. Variability associated with each mean is incorporated into the model by factoring in the standard deviation of the parameter estimates (Table 3). This provides flexibility for using different ranges of incident light adjusted for varying cloud conditions. Thus the model equation for incident light is:

where Y_t = incident light intensity ($\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$) selected at time t , μ_t = mean

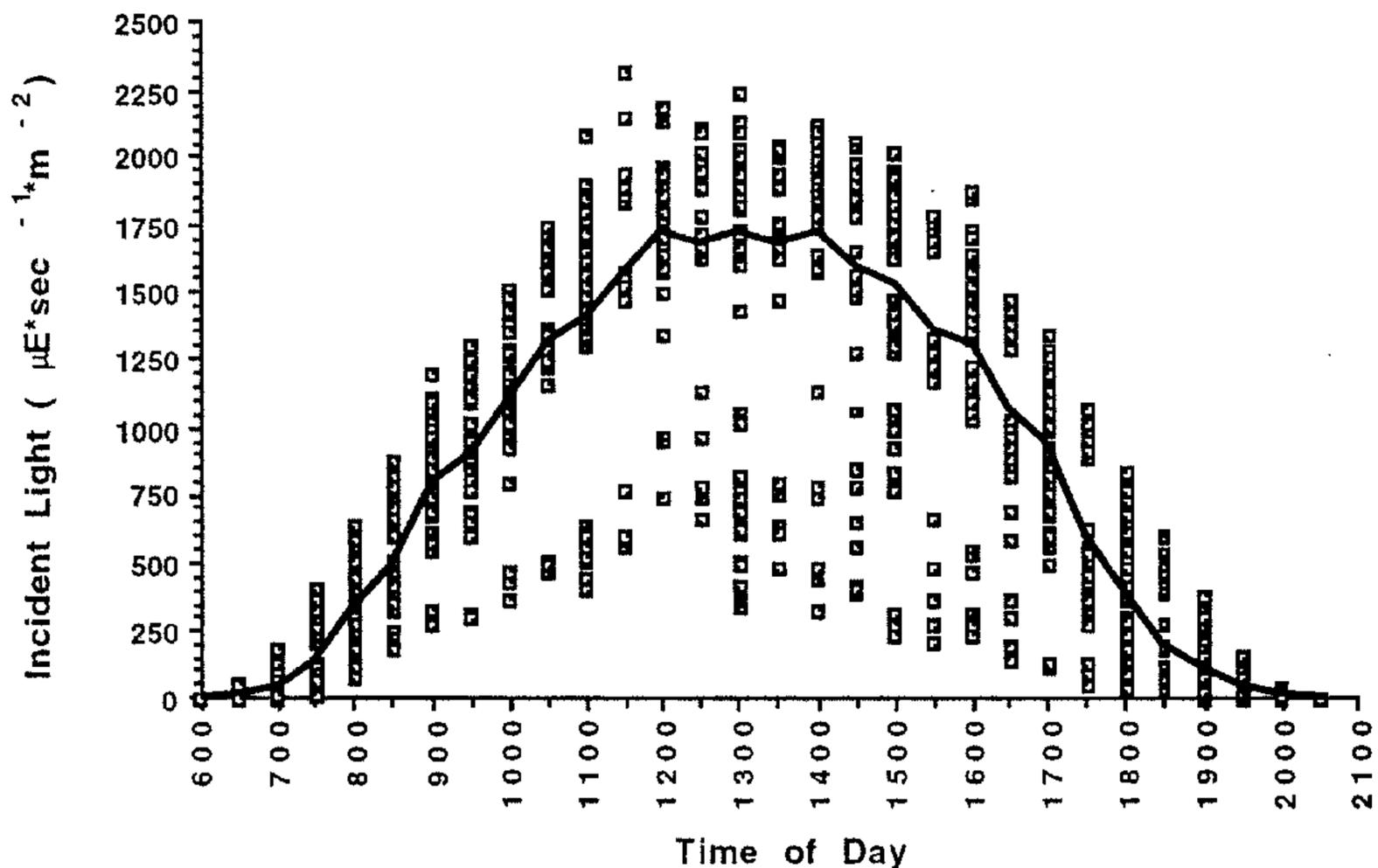


Figure 5. Incident light intensity vs. time of day for data collected during the month of May 1988-89 ($n=836$). Solid line represents mean incident light level during the day.

incident light intensity for time t (from field measurements), σ_t = the standard deviation of the mean light level and A = standard normal random variate (truncated such that $-1 < A < 1$). The truncated standard normal random variate (A) is selected at the beginning of each simulation day so that variations occur daily across the entire light range rather than at each time step.

Table 3. Mean light intensities ($\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^2$) used to parameterize incident light driving variable. Standard deviation for each mean is multiplied by a daily standard normal random variate (truncated) which serves to adjust incident light for cloudy days.

Time of Day	Mean Light Intensity (μ)	Standard Deviation (σ)
0600	2.34	1.42
0630	10.29	15.33
0700	36.19	47.05
0730	131.93	119.44
0800	330.60	143.81
0830	489.33	199.73
0900	805.63	231.00
0930	909.00	292.77
1000	1106.62	357.00
1030	1319.39	406.00
1100	1413.00	492.87
1130	1579.71	514.50
1200	1724.49	525.00
1230	1692.00	560.00
1300	1728.00	642.13
1330	1692.00	584.50
1400	1721.13	584.50
1430	1584.00	559.71
1500	1528.72	542.50
1530	1359.00	554.33
1600	1314.33	462.00
1630	1080.00	406.22
1700	940.69	336.00
1730	603.00	312.84
1800	400.02	252.00
1830	197.76	193.35
1900	107.52	115.50
1930	39.45	66.50
2000	5.15	9.85
2030	0.50	0.58

Water Turbidity

The role of water turbidity on attenuation of light in oceanic and estuarine waters is well documented. The effect of water on light is not limited to refraction, but also includes absorption and scattering of individual photons (Hogan 1983; Kirk 1977). In clear water, absorption involves the conversion of light into heat energy (Williams 1970; Kirk 1977; Duntley 1963), and up to half of the total radiant energy from sunlight is lost in the first meter of water (Jerlov 1976). Absorption is greatest for infrared light with wavelengths greater than 700 nm (Jerlov 1976).

Particulates in turbid water further amplify absorption of light as depth increases for two reasons: (1) Phytoplankton absorb light energy for photosynthesis. (2) Scattering of light photons off of suspended particulates increases light path length and consequently absorption (Jerlov 1976; Kirk 1977). The degree of scattering and absorption depends on the size, shape, density and chemical composition of the suspended particulates. Larger, irregularly-shaped particles have more surface area and thus deflect more photons (Hogan 1983; Kirk 1977). Dense concentrations of particles increase the probability of scattering and absorption, and chemicals in some particulates such as photosynthetic pigments may absorb light energy more readily (Kirk 1977).

In the model, changes in water turbidity occur daily. An analysis of data collected from NMFS field sampling at Jamaica Beach during 1980-89 provide the basis for quantifying turbidity as a driving variable. Water samples were analyzed with an HF-Instruments DRT 100B turbidimeter (model 20052, HF Scientific, Inc., Ft. Myers, FL). A mean and standard deviation was calculated for turbidity measurements (N=97) from water samples taken during the month of May (1980-1989). These were used as input for the model. The model equations for turbidity

also integrate the variability associated with these means through the use of a standard normal random variate (truncated). The model equation takes the form:

$$Y = 18.90 \pm 13.37*(A) \text{ (Eq. 2),}$$

where Y = turbidity (FTU's), which is based on the mean of turbidities observed at Jamaica Beach (18.90), the standard deviation associated with the mean (13.37) and a daily standard normal random variate (A) truncated between -1 and +1. During simulation, the model assigns a different turbidity value (mean FTU \pm s.d.) for each simulation day.

Water Level

Water level is an important variable in the model because it affects the path length of light as it passes through the water column; consequently, scattering and total absorption rapidly increases with increasing depth (Auer and Canale 1986; Jerlov 1976; Kirk 1977; Tyler 1958; Duntley 1962). Water levels in Galveston Bay are recorded hourly by NOAA's National Ocean Service at Galveston's Pier 21 which is located ~ 21-23 km east of the Jamaica Beach site. Water levels vary throughout the bay and predicted water heights for Jamaica Beach lag the Pier 21 levels by 2.5 and 3 hours for flood and ebb tides, respectively (NOAA 1989). In addition, wind speed and wind direction can have a major effect on tides in shallow bay systems such as Galveston Bay (Ward 1980a, 1980b; Hicks et al. 1983; Prandle 1986; Uncles et al. 1986; Duxbury 1987; Kuo & Neilson 1988).

A record of individual water level measurements taken at a fixed location at Jamaica Beach was compiled from field observations during 1985-88. Prior to, and at the end of each sampling trip during this period, distance to the water from the top of a concrete bulkhead was measured with a meter stick. Repeated measurement over time provided a long term, although discontinuous, record of water height. On several

occasions, measurements were taken every two hours throughout complete tidal cycles. These measurements (n=141) were compared with continuous tidal records from Galveston's Pier 21(converted to meters) which are monitored hourly by NOAA's National Ocean Service (NOAA, NOS, Sea & Lake Levels Branch, Datum and Information Section, Rockville, MD).

I attempted to use several regression models to determine the effect of wind speed and wind direction on tidal amplitude at Jamaica Beach. However, much of the variability remained unaccounted for with this method ($R^2 \leq 0.54$). I suspect that there were insufficient data to detect the effects of wind on tide height. The data did verify that tidal amplitude at Jamaica Beach lags Pier 21 by an average of three hours. Actual tide data from Pier 21, in the form of a lookup table, are used in the model. The differences among water level at Jamaica Beach and Pier 21 are accounted for through use of a correction factor. The simulation model checks the time of day, extracts the Pier 21 tidal amplitudes and converts them to levels comparable to those observed at Jamaica Beach. This method allows any or many daily records of tidal amplitude to be used for simulation purposes. To obtain the water levels at Jamaica Beach, measurements for tidal amplitude at Pier 21 are multiplied by 0.71 (NOAA 1989). An additional 0.45 m were subtracted from the calculated values to approximate tidal heights comparable to those observed in the area where incident and subsurface light measurements were recorded. The model equation for water level takes the form:

$$Y = (D*0.71)-0.45 \quad (\text{Eq. 3})$$

where Y = depth of water at Jamaica Beach near edge of salt marsh (meters) and D = hourly value for Pier 21 tidal height (meters).

Auxiliary Variables

Subsurface Light Intensity

In the model, subsurface light intensity is designated as an auxiliary variable that is a function of incident light level, water turbidity and depth. To quantify the effects of these factors on attenuation of light in the water column, the LI-1000 datalogger equipped with two light probes was used to simultaneously record incident and subsurface light intensities in ten minute intervals at Jamaica Beach. The datalogger remained in the field for periods of two to five days throughout the spring, summer and fall of 1988 and 1989. The submerged light probe was placed in a non-vegetated area with a tidal range of 0.27 - 0.90 meters while the other probe was fixed approximately one meter above the water surface. During periods of continuous light measurement, several water samples were obtained in the vicinity of the submerged light probe twice a day. A meter stick fixed in the substrate and used as a tide gauge provided point measurements of water depth. These point measurements were compared with continuous records of tidal amplitude at Pier 21 to calculate a continuous record of water depth at the submerged light probe.

On several occasions, measurements were recorded at various depths by raising and lowering the underwater light probe during flood tide and recording incident and submerged light intensities. This provided a 'profile' of light attenuation with increasing water depth (range = 0.02 - 0.89 m) while incident light remained constant. A similar profile of turbidity was obtained by collecting water samples at fixed depths immediately after recording light levels.

A total of 836 records were obtained for incident light, subsurface light and water depth in thirty minute intervals. Average daily values for turbidity were used when actual data were not recorded. Data were classified according to two distinct time periods:

- (1) A transition period that included data recorded at 0630-0700 and 2000 hours, and

(2) a daytime period that included data recorded between the hours of 0730 and 1930.

The reason for grouping data in this manner is related to results obtained from laboratory experiments for parameterizing the rate equations affecting movement between the state variables. Further explanation is provided in material transfer rates section of this chapter.

The GLM method in SAS was used to obtain multiple regressions for the effects of incident light, turbidity and depth on subsurface light (dependent variable) within each data group. Incident and subsurface light levels were log-transformed prior to the analysis. Log of incident light, turbidity and water depth were all significantly correlated with log of subsurface light ($p < 0.02$, Tables 4, 5). There were no significant interactions among incident light (log-transformed), turbidity and depth. Parameter estimates obtained from the solutions to the GLM method (Tables 4 and 5)

Table 4: Output from regression of subsurface light intensity against incident light, water turbidity and depth during the transition period ($R^2 = 0.934$).

Source	df	Sum of Squares	Mean Square	F	p
Model	3	504.969	168.323	321.04	<0.0001
Error	68	35.653	0.524		
Total	71	540.622			
Source	df	Type III Sum of Squares	Mean Square	F	p
Log Light	1	403.943	403.943	770.43	0.0001
Turbidity	1	3.118	3.118	5.95	0.0174
Depth	1	18.788	18.788	35.83	0.0001
Parameter		Estimate	Prob > T	Std. Err. of Estimate	
Intercept		-0.22574	0.2815	0.2080	
Log Light		0.97406	0.0001	0.3509	
Turbidity		-0.02445	0.0174	0.0100	
Depth		-2.06765	0.0001	0.3454	

Table 5 Output from regression of subsurface light intensity against incident light, water turbidity and depth during the daytime period ($R^2 = 0.827$).

Source	df	Sum of Squares	Mean Square	F	p
Model	3	1607.638	535.879	1190.17	<0.0001
Error	749	337.242	0.450		
Total	752	1944.880			

Source	df	Type III Sum of Squares	Mean Square	F	p
Log Light	1	1158.882	1158.882	2573.83	0.0001
Turbidity	1	23.859	23.859	52.99	0.0001
Depth	1	131.215	131.215	291.42	0.0001

Parameter	Estimate	Prob > T	Std. Err. of Estimate
Intercept	-0.36142	0.0279	0.1641
Log Light	1.00137	0.0001	0.0197
Turbidity	-0.01295	0.0001	0.0018
Depth	-2.19287	0.0001	0.1285

were used in a regression equation to parameterize subsurface light in the model. The model equations are shown below. For the transition period (0630-0700, 2000 hr's.),

$$Y = -0.22574 + 0.97406*(L) - 0.02445*(T) - 2.06765*(D) \quad (\text{Eq. 4}).$$

During the daytime period (0730-1930 hr's.),

$$Y = -0.36142 + 1.00137*(L) - 0.01295*(T) - 2.19287*(D) \quad (\text{Eq. 5}),$$

where Y = log transformed subsurface light intensity (μE), L = log transformed incident light (μE), T = turbidity in formazin turbidity units (ftu's) and D = water depth (meters).

Material Transfer Rates

The most important aspect of data collection involves the parameterization of the material transfer rates between the two state variables, the number of shrimp emerged and the number burrowed. Experiments were conducted in the laboratory to determine the effect of varying light intensity on burrowing rates. The data obtained from these experiments provide information on the diel fluctuations in burrowing patterns of brown shrimp and also on the threshold light levels that elicit movement between the two state variables.

Five experiments were conducted in a building with a translucent roof to allow for use of natural illumination and photoperiod. The translucent roof was composed of white plastic sheeting which reduced overall light levels by approximately 71-84%. The experiments were performed in twelve fiberglass tanks (bottom area = 0.405 m²) filled with filtered seawater to a depth of 25 cm (Figure 6). Each tank contained a 5 cm layer of washed beach sand as a substrate for burrowing. Previous experiments using this type of substrate indicate that shrimp are able to burrow into it without difficulty (Minello et al. 1987). Temperature and salinity of seawater were maintained at 24-27 °C and 25 ‰, respectively.

Filters made of tinted plastic sheets were used to reduce incident light by 0%, 83%, 95%, and 99% in experimental tanks, simulating varying degrees of light attenuation in the water column. Values for light intensity at the substrate surface were used in statistical analyses testing for main treatment effects. Four replicate tanks were randomly assigned to each light level. The clear covers (0% light reduction) on four of the tanks were used as controls and allowed animals to be exposed to unattenuated light conditions. Tinted covers reduced light levels by 83 and 95%. These attenuation levels were selected because preliminary field observations indicated that light during midday hours was reduced to approximately these levels when heavy cloud cover or

turbid water conditions prevailed. These attenuation levels were obtained by coating clear plastic sheets with sandy-colored spray paint. The sandy-colored paint simulated turbid water, and the amount of light reduction by any given filter was calibrated with a LI-COR integrating quantum photometer (model LI-188B) during application of the paint coatings.

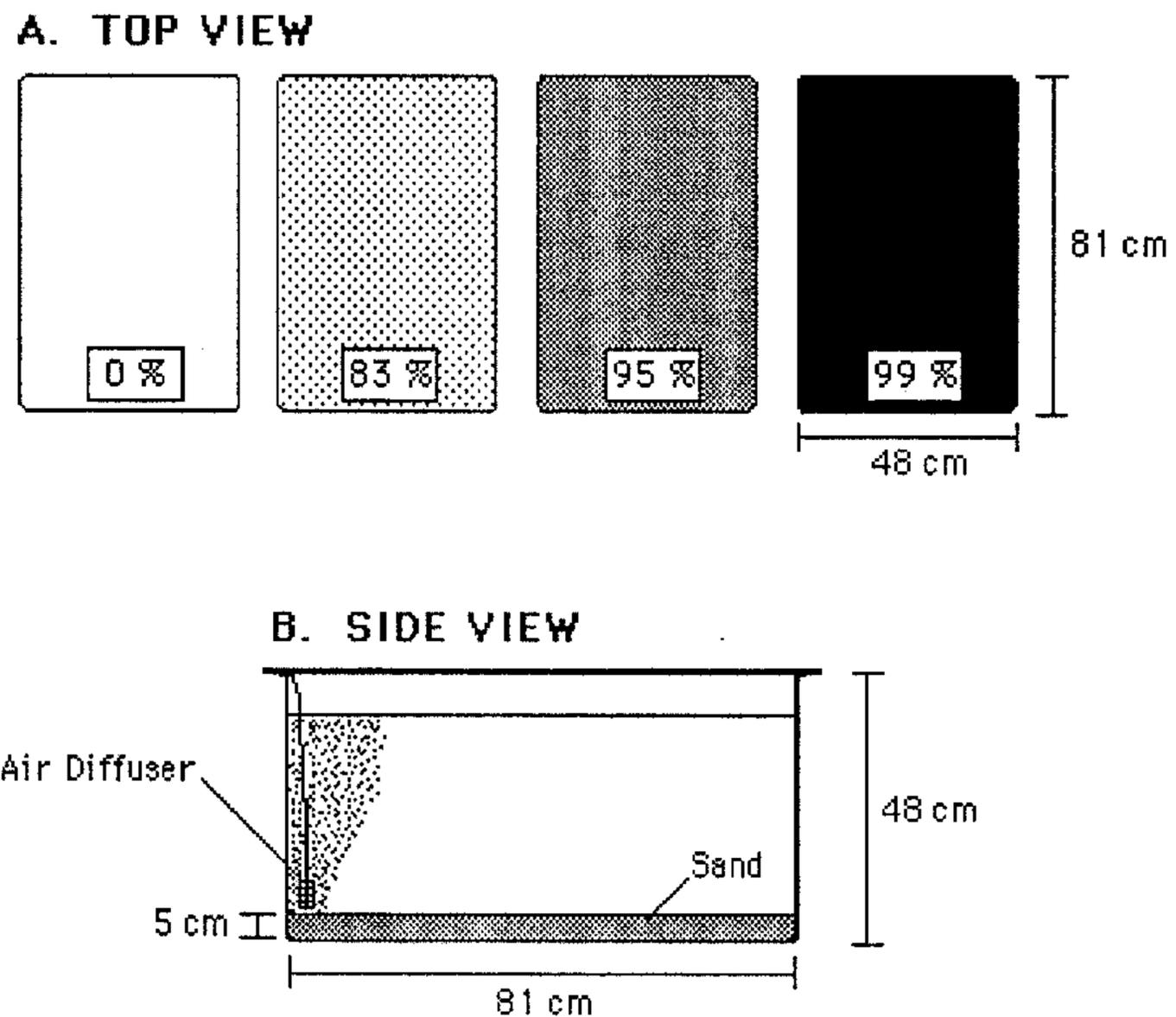


Figure 6. Diagram of experimental burrowing tanks depicting differences among the light attenuation filters (A). 5 cm of washed beach sand was used as a substrate (drawings not to scale).

Filters allowing 99% light reduction were made of three sheets of black plastic. This treatment was included to test shrimp behavior under constant, or nearly constant dark conditions. Observations from treatment tanks with the 99% attenuation filters should show burrowing patterns driven by circadian rhythms and

thus can also be used to reduce the confounding effects due to the persistence of circadian rhythms.

Brown shrimp (40-60 mmTL) were collected with an otter trawl at Jamaica Beach. Ten shrimp were added to each tank resulting in a density of 24.7 shrimp/m². This density is comparable to estimates of natural abundance during periods of highest utilization of nursery areas in west Galveston bay by juvenile brown shrimp (Zimmerman & Minello 1984a, 1984b). In each of the five experiments, changes in the number of shrimp active or burrowed were recorded over a 24-hour period in each tank. Observations were taken every 30 minutes during sunrise and sunset transition periods when shrimp typically are burrowing or emerging from the substrate. Observations were recorded every two hours throughout the rest of the 24-hour experiment. One hour after sunset, the entire experimental area was covered with a black plastic sheet to extinguish any additional light from external sources (i.e., street lights, security lights from nearby buildings) that penetrated through the translucent greenhouse roof. The black plastic cover was removed before sunrise, at the first appearance of light which was barely bright enough to cancel out the effects of the external artificial light sources.

Measurements of incident light intensity were continuously recorded near the experimental tanks with the LI-1000 datalogger. These values were multiplied by attenuation percentages for each filter type to determine light levels at the substrate surface in each treatment. It was assumed that light attenuation caused by the water column was negligible because of the clarity of the seawater used and the shallowness of the water in the tanks (depth = 25 cm). This technique reduced disturbance of shrimp in experimental tanks. Occasionally, bottom light levels were measured in the experimental tanks for verification purposes and light reduction was within $\pm 2.1\%$ of the treatment value.

Data from the laboratory experiments were analyzed with a two-way ANOVA in SAS using percent of shrimp burrowed as the dependent variable. Time of day and light intensity were the main effects tested, and experiment was used as a blocking variable. Regressions were also obtained for percent of shrimp burrowed vs. light intensity; these regressions and parameter estimates would be used to quantify the rate equations for the state variables.

The results from the ANOVA indicated a significant interaction between the filter type (which represents light attenuation) and the time of day (Figures 7, 8). The lowest burrowing rates observed were during times of low light. The effect of

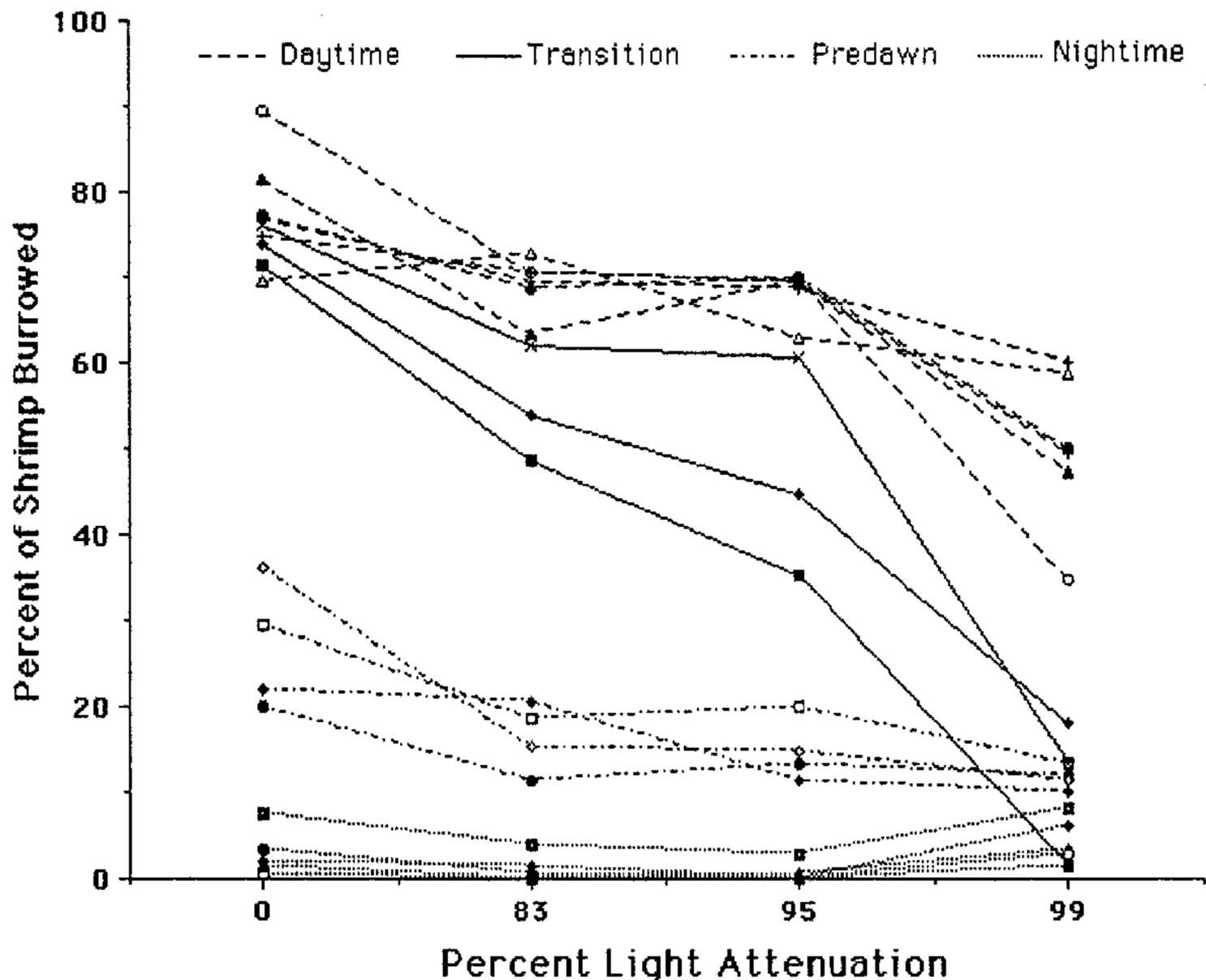


Figure 7: Mean percent of shrimp burrowed vs. light attenuation. Burrowing is divided among four categories: Daytime (0700-1930), transition (0630-0700, 2000), predawn (0430-0600) and nighttime (2030-0400).

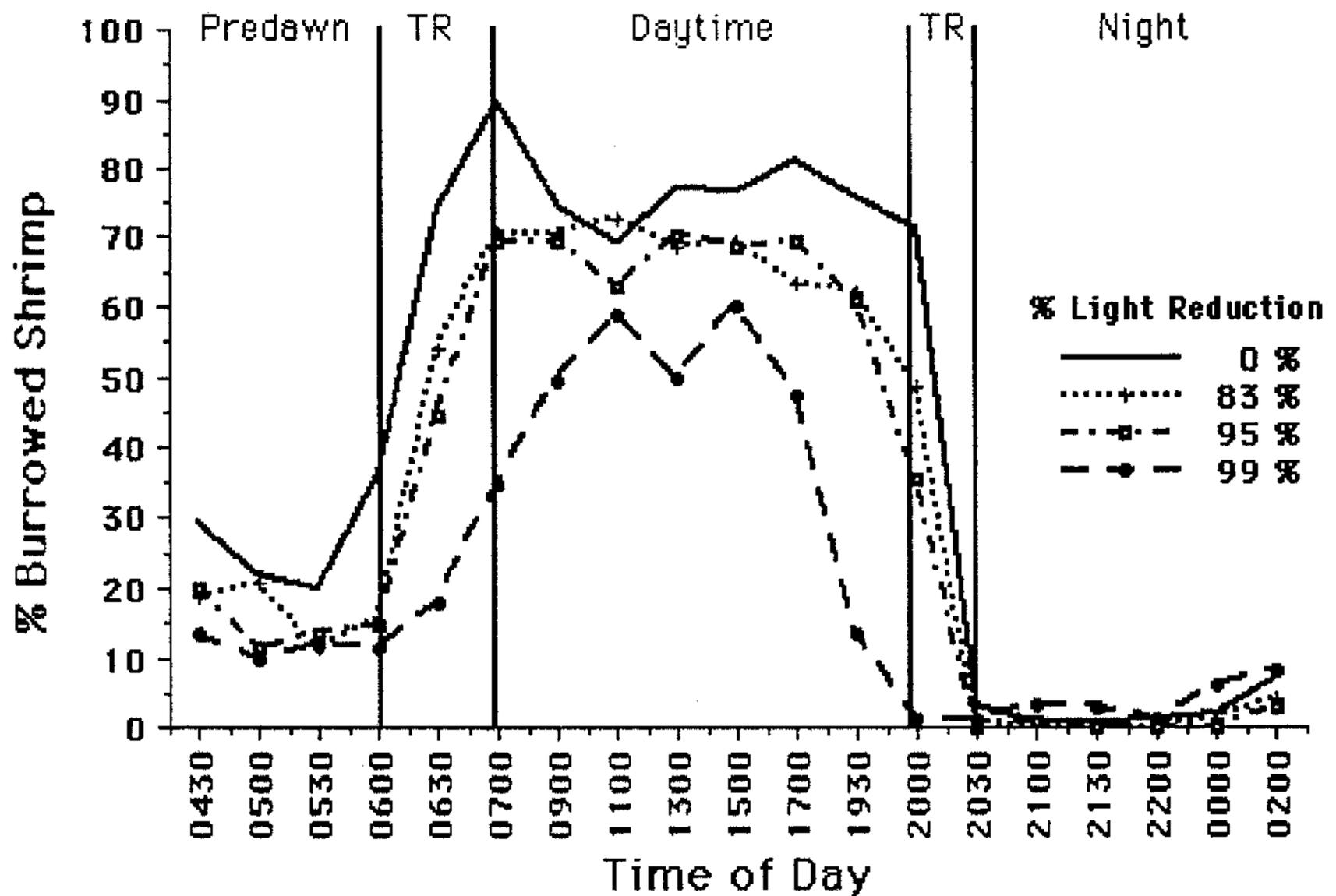


Figure 8: Mean percent of shrimp burrowed vs. time of day for shrimp in tanks with light attenuated by 0, 83, 95 and 99 percent. Each data point is a mean of three replicates for each treatment and five experimental replicates. Burrowing is classified into four periods: Predawn, daytime, nighttime and transition periods.

light filters is greatest during the transition hours of 0630, 1930 and 2000 (Figure 7). There was also a significant effect of the blocking variable (experiment) indicating that overall, mean burrowing levels were higher on some days. Mean percent of shrimp burrowed vs. time of day is shown in Figure 8.

Mean burrowing rates for each observation period (time of day) were calculated and multiple t-tests were performed on adjacent means. Data from means with no significant differences were grouped and tested against data from adjacent time periods. This process was continued until only four distinct burrowing groups remained, classified according to time of day, with each group being significantly different from the others. The four burrowing periods included a predawn and a nighttime period when no light was available. During these two periods, burrowing rates were low and fairly

constant. Mean number of burrowed shrimp was 19.4% during the predawn hours (4:30-6:00 am) and 1.4% during the nighttime period (8:30 pm - 4:30 am). In addition, there was a slight reduction in the number of shrimp burrowed between 5:00 and 6:00 am (predawn) in tanks with 0% and 83% light reduction filters, indicating a small burst of activity. This observation parallels results of other studies which show a second smaller activity peak in a bimodal pattern observed for some shrimp (Wickham 1967; Hughes 1966, 1968; Moller and Jones 1975; Wickham and Minkler 1975; Lakshmi et al. 1976).

In the transition periods which occur at dawn and dusk (6:30-7:00 am and 8:00-8:30 pm), and in the daytime period (7:00 am - 8:00 pm), burrowing rates changed with light intensity. Logistic curves were fitted to the relationships between log-transformed (base e) light and the percent of shrimp burrowed (Figure 9). These curves are characterized by a rapid increase in burrowing at low light which then level off to an asymptotic limit as light continues to increase. At sunrise, around 6:00-7:00 am, the shrimp move into the substrate very quickly (transition period). During the day, the burrowing levels reach the flat area of the relationship. In the evening, at sunset, burrowing follows the transition curve, moving downwards as light levels decrease. In the tanks with clear filters (0% light reduction), highest burrowing levels were observed during the morning transition period (Figure 7). Mean burrowing rates reached up to 90% at 0700 hours and decreased to ~70-80% through the remainder of the daytime period.

Burrowing during the daytime period (7:00 am - 8:00 pm) was highly variable ($R^2 = 0.254$) when compared to regressions for the transition periods ($R^2 = 0.683$). Some possible explanations for this are suggested later in the Discussion and Conclusions section. The prominence of two distinct burrowing levels throughout the

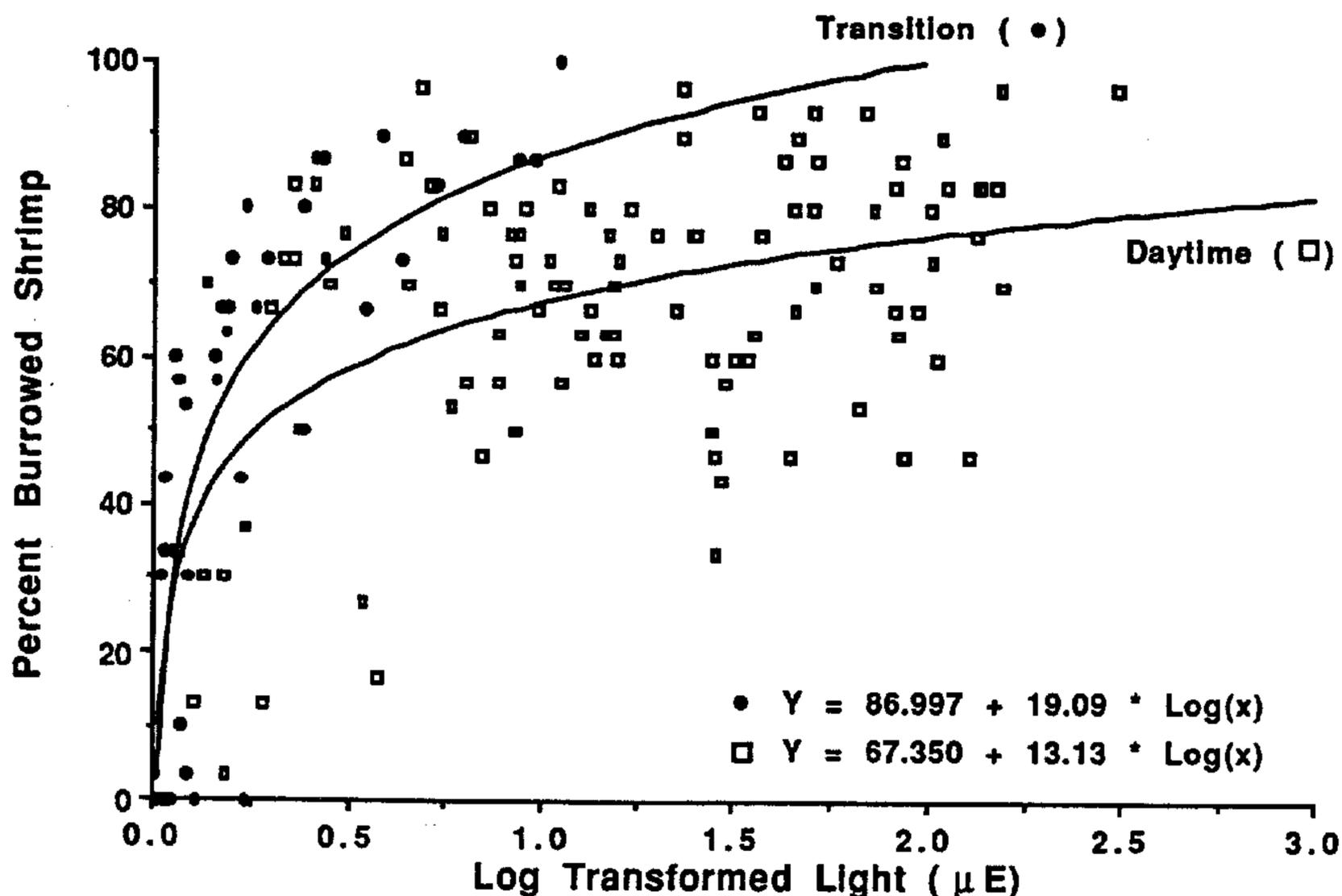


Figure 9: Graph of shrimp burrowing vs. log-transformed light during transition and daytime hours. Solutions to logistic fits are provided for each relationship.

day is also the main reason for grouping data used in parameterizing Equations 4 and 5 (effect of water level and turbidity on attenuation of light).

In the simulation model, predictions for brown shrimp burrowing during nighttime and predawn hours are based on the mean burrowing rates (μ) during those periods. The variance ($\sigma = \text{std. dev.}$) associated with the mean percent of shrimp burrowed is also incorporated into the model through the use of a standard normal random variate similar to that described for parameterization of incident light and water turbidity. The estimates for μ and σ were calculated from the experimental data and used as parameters in the simulation model as shown in Table 6. The equations take the form:

Nighttime 2030-0400 hrs., $Y = [1.387 \pm 2.72 * (A)]$ (Eq. 6).

cases, the equations calculating the percent of shrimp burrowed are restricted to within 0 and 100. Adding in the variability to achieve stochasticity sometimes results in predictions beyond these limits; negative values are designated as 0% burrowing and values greater than 100 are limited to 100% burrowing. It is important to note that the percent of shrimp burrowed at any given time (t) is not dependent on the amount of shrimp burrowed during the previous time period ($t-1$).

Baseline Simulations

A series of baseline simulations were conducted to examine the average diel changes in burrowing patterns over a one-month period. The simulation time-step was thirty minutes. The reason for simulating an entire month is that due to the stochastic nature of the burrowing model, specific results reflect only one of many possible conditions; primarily due to the incorporation of the variability associated with driving variables (incident light, turbidity) and rate equations (effect of subsurface light on burrowing during daytime periods). Simulation results were grouped into the four time periods observed in the laboratory experiments (daytime, nighttime, transition and predawn) to obtain mean burrowing rates (Table 7). Simulation results also were grouped by hour to examine mean burrowing patterns and mean values for driving variables throughout the 24-hour day (Figures 10-12).

The results indicate a slightly higher burrowing rate during the transition period (88.71%) in comparison to the daytime period. Overall, burrowing rates during the photopic portion of the day were higher than those observed in the laboratory experiments (Figure 12). This is most likely due to the fact that the burrowing rate equations (Equations 8-9) were parameterized with relatively low light levels observed in the laboratory yet the incident light driving variable (quantified from field measurements) produced much higher intensities.

Table 7. Mean output values during the four time periods from thirty-one day simulation using May 1988 tidal records from Galveston's Pier 21. Values in parentheses are standard deviation.

	Daytime	Nighttime	Predawn	Transition
% Burrowed	86.57 (11.68)	1.38 (0.11)	19.38 (0.10)	88.71 (10.97)
Incident Light	1011.99 (647.88)	0.00 (0.00)	0.00 (0.00)	22.03 (22.97)
Subsurface Light	118.30 (72.69)	0.00 (0.00)	0.00 (0.00)	2.57 (2.06)
Turbidity (FTU's)	18.14 (10.10)	-	-	18.14 (10.10)
Depth (m)	0.69 (0.11)	0.57 (0.15)	0.67 (0.16)	0.65 (0.15)

Consequently, burrowing levels in relation to light fall at the upper extreme of the logistic curves (Figure 9) and predictions reached the 100% (burrowed) limit more often during the simulations. However, the mean percent of shrimp burrowed (Figure 12) exhibits a pattern similar to that observed in experimental tanks with clear filters (Figure 8). In the simulation results, mean burrowing rates were highest during the early transition period (~94%) and then decreased (to ~87-88%) through the rest of the daytime period. The low values for mean percent burrowed at 0730 and 1830 hours may have been due to several factors but variance in predictions also is greatest during these periods (Figure 12).

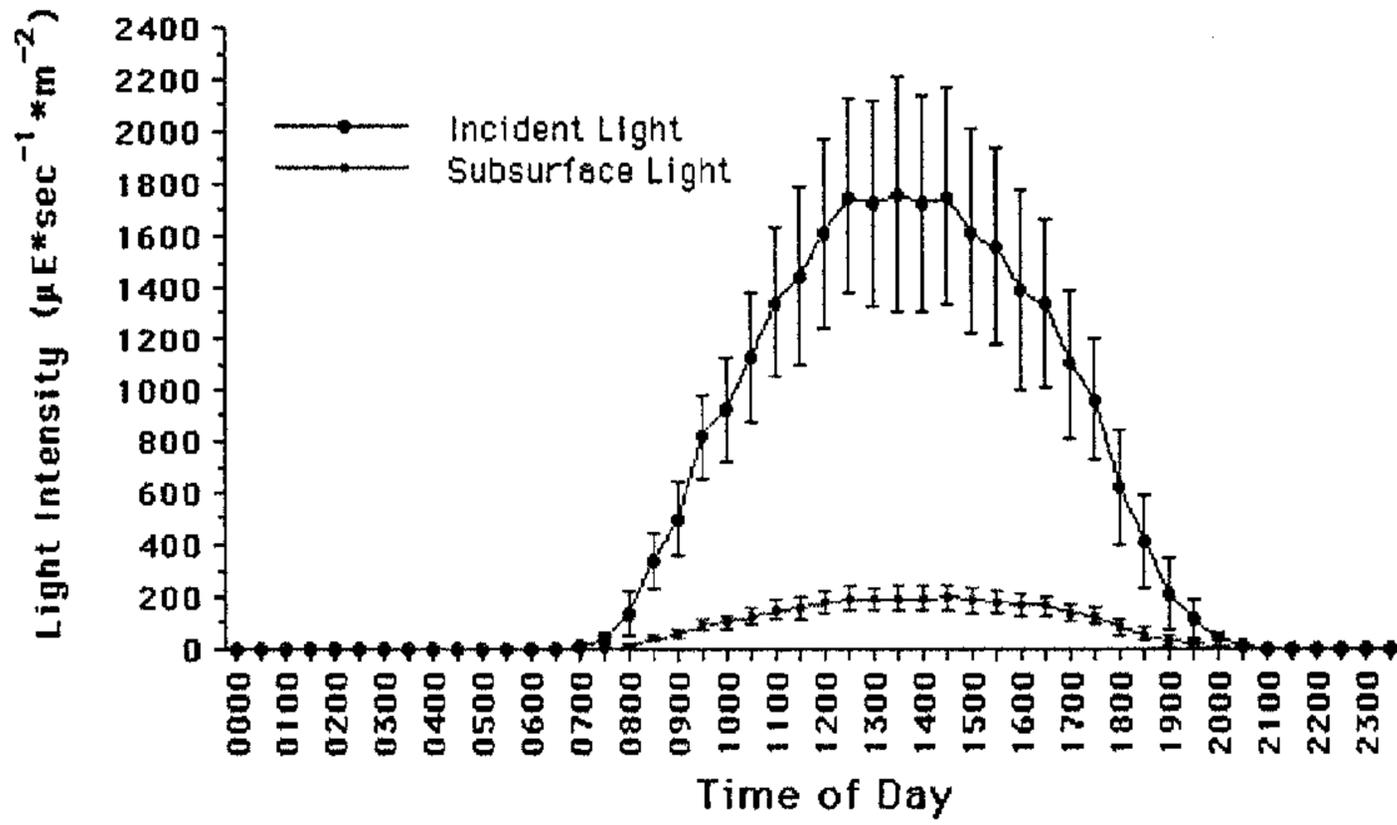


Figure 10. Graph of mean incident and subsurface light intensities vs. time from the simulation output ($n=31$). Error bars represent standard deviation.

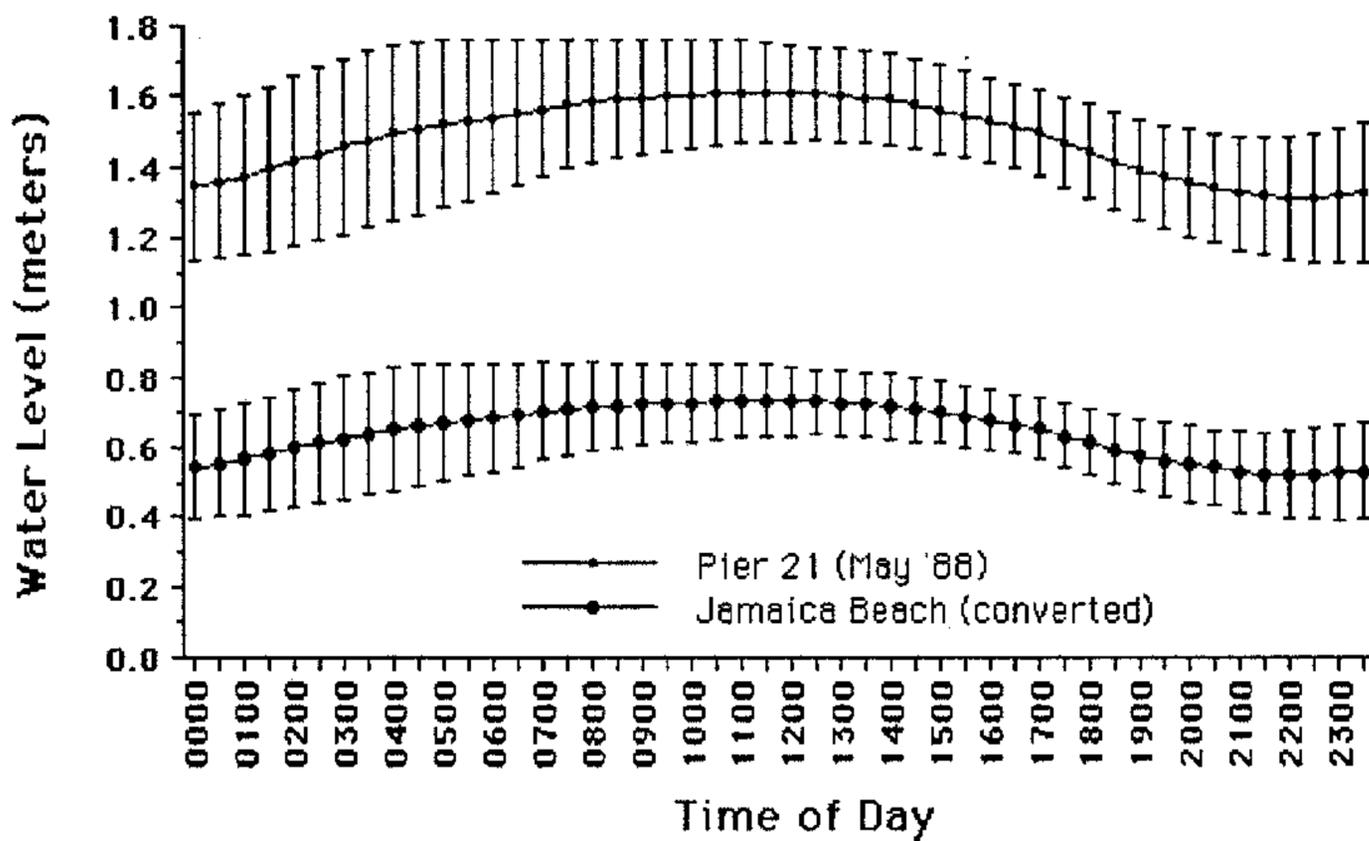


Figure 11. Mean water levels from baseline simulations of thirty-one days. Pier 21 levels from May 1988 data; Jamaica Beach water levels converted using Equation 3. Error bars represent standard deviation.

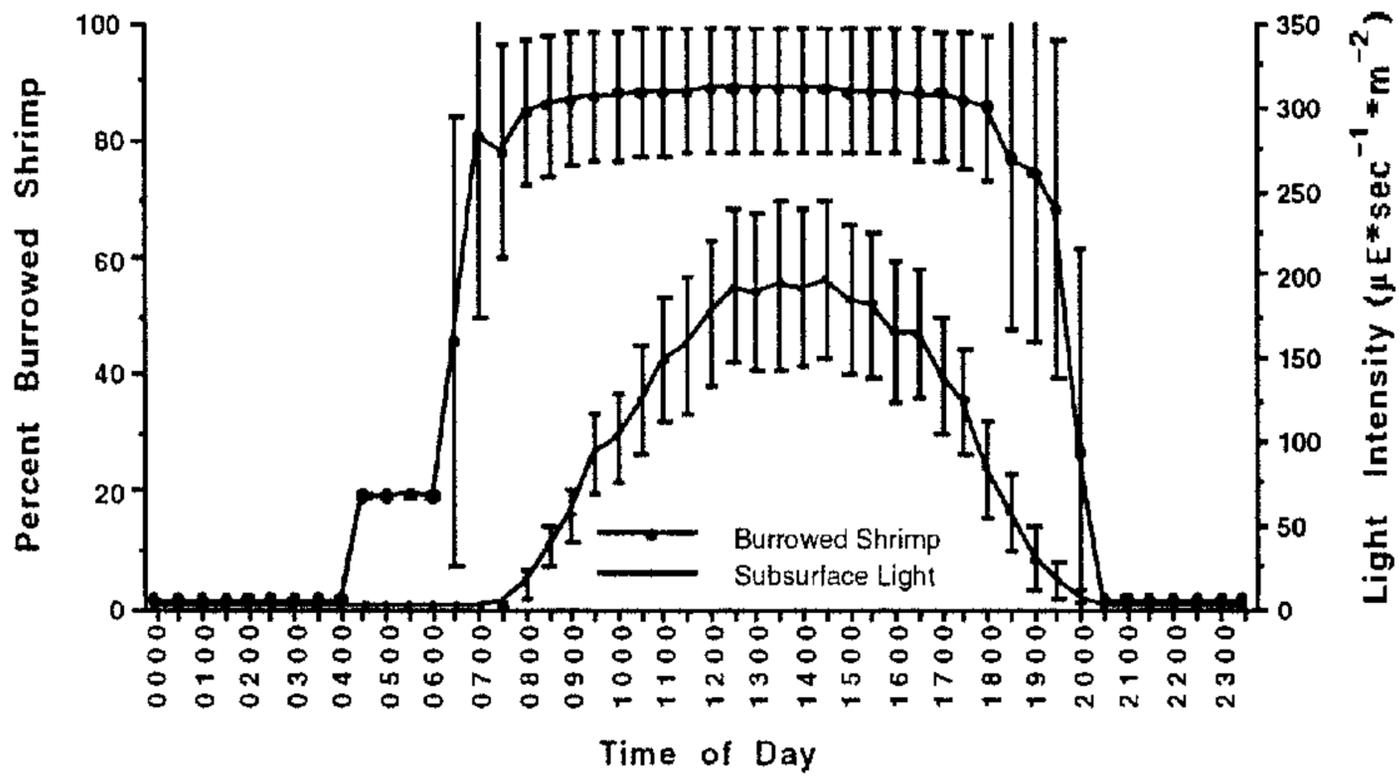


Figure 12. Mean subsurface light and percent of shrimp burrowed vs. time of day. Burrowing during transition (0630, 0700, 2000 hr's.) and daytime (0730-1930) periods are light dependent. Error bars represent standard deviation during transition and daytime periods.

MODEL VALIDATION

The validation (or invalidation) procedure used for the brown shrimp burrowing model was a multi-step process. Field experiments were conducted in special enclosures that enabled measurement of shrimp burrowing under turbid water conditions. Data from field experiments were then compared with results from baseline simulations as the first test on model predictions. However, comparing field observations to baseline simulation data may cause misleading results. The inclusion of variability in the stochastic model can result in a wide range of predictions thus reducing the ability to detect differences among field data and baseline simulations (type II error). A 'modified baseline model', which utilized subsurface light measured during field experiments as the main driving variables, was therefore used to perform a second set of simulations for daytime and transition periods.² This ensured a direct comparison of burrowing rates in the field with model predictions which are driven by field conditions (subsurface light intensities). The result was a more rigorous test of equations for the material transfer rates during the daytime and transition periods (Equations 8 and 9).

Field Validation Experiments

Validation data were collected in the field by measuring light levels, water depth, turbidity and brown shrimp burrowing on forty occasions near the marsh edge

² The baseline model utilizes field data collected from Jamaica Beach to parameterize subsurface light intensity; subsurface light depends on incident light, water depth and turbidity. In addition, the effect of subsurface light on material transfer rates in the baseline model is determined from results of the laboratory experiments. However, the modified baseline model presented here utilizes only the subsurface light levels measured in the field enclosures at East Lagoon as the main driving variable. Incident light, water depth and turbidity variables are removed from the 'modified baseline model'.

in shallow waters of East Lagoon on Galveston Island (Figure 3). This site was chosen because of its' sandy substrate, easy access from shore and its utilization as a nursery by juvenile shrimp. Measuring burrowing in the field is difficult because brown shrimp cannot be observed easily in turbid water. To solve this problem, observations were made in clear plexiglas enclosures with a sliding 'trap door' designed to permit easy capture of non-burrowed shrimp without disturbing burrowed individuals (Figure 13).

The enclosures were pushed into the substrate to within 1 cm of the trap door. The substrate was leveled and environmental data inside the enclosures were recorded (salinity, temperature, depth and incident and subsurface light intensity). Water samples were taken for later analysis of water turbidity. Shrimp were collected immediately prior to use with a beam trawl or otter trawl and were marked by clipping a small edge of their right uropod. Clipping the uropods did not injure the shrimp yet made it possible to distinguish experimental shrimp from those trapped inside the enclosure during deployment. Only healthy shrimp within a size range of 45-65 mmTL were used in the treatment enclosures. Fourteen shrimp were added to the enclosures for a density of 24.6 shrimp/m^2 , equivalent to that of the laboratory experiments.

After 3 hours, the trap door was closed, sealing off the substrate from the water column. The 1 cm space between the substrate and the trap door prevented disturbance of burrowed or partially burrowed shrimp in the sand, but shrimp on top of the substrate surface were captured. Environmental data in the tank were measured again, and the tank was removed from the water with the trap door locked firmly in place. Any shrimp caught in the device were assumed to be in the water column and not burrowed. During preliminary trials, I tested this assumption by snorkeling up to the tank and visually observing the number of emerged shrimp while a co-worker

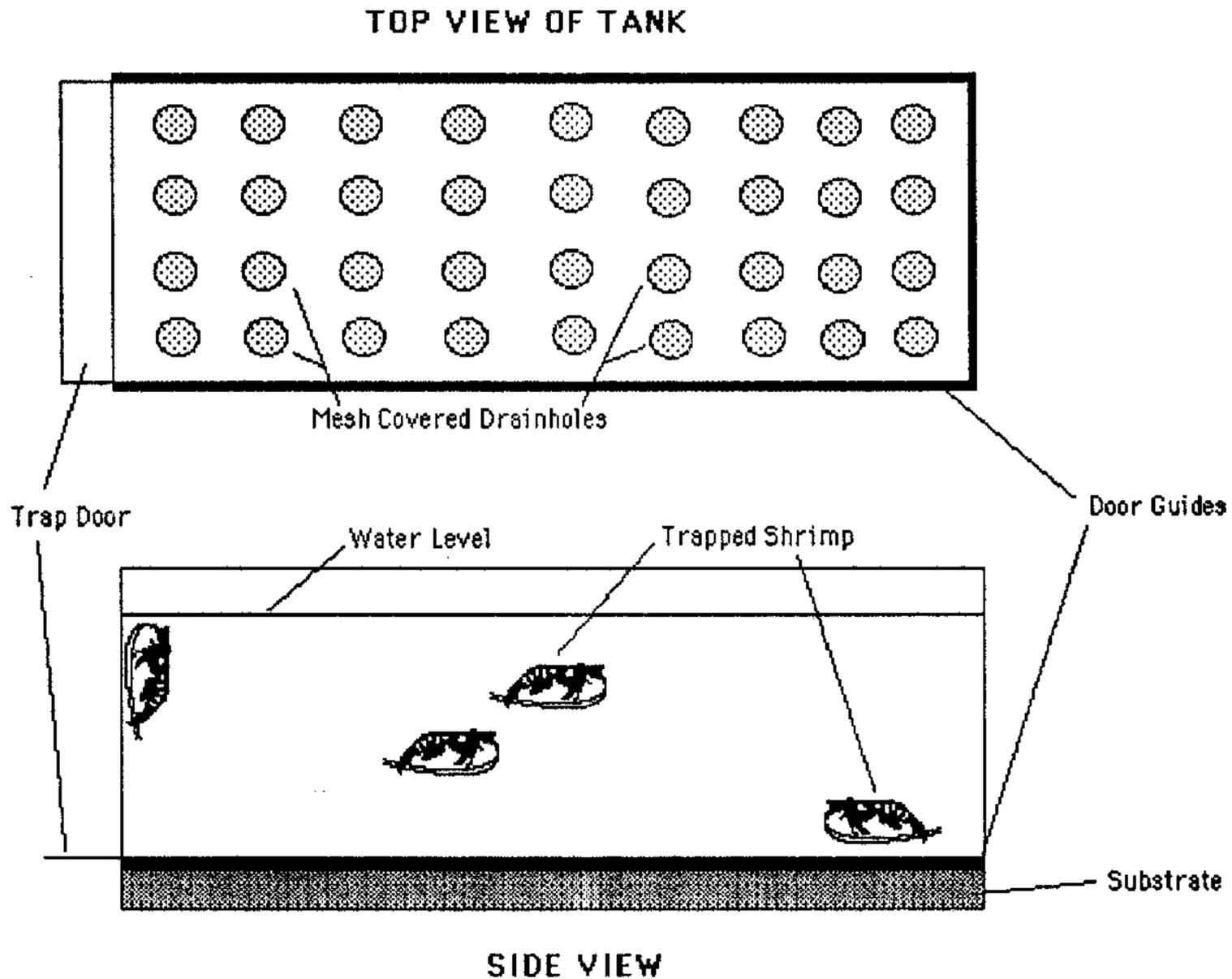


Figure 13. Diagram showing top and side views of the field experiment enclosure. When the sliding door is closed, any shrimp remaining above the substrate surface are trapped within the tank. When the tank is removed from the substrate, water escapes through the mesh covered drainholes, and marked shrimp are counted as recaptures. Dimensions of the tank are 1.25 m long x 0.455 m wide x 0.5 m deep (diagram is not to scale).

closed the trap door. In eight trials, I observed 100% catch efficiency of non-burrowed shrimp.

Within a day, burrowing frequency was measured at randomly selected times within the four time periods identified in laboratory experiments (Figures 8, 14). This procedure was repeated on ten subsequent days. Mean percent of shrimp burrowed in the field studies was 72.1% during the daytime, 76.4% in the transition period, 18.6% at night and 11.4% during the predawn period (Table 8). Overall, mean burrowing rates in the field were lower during the predawn, transition and

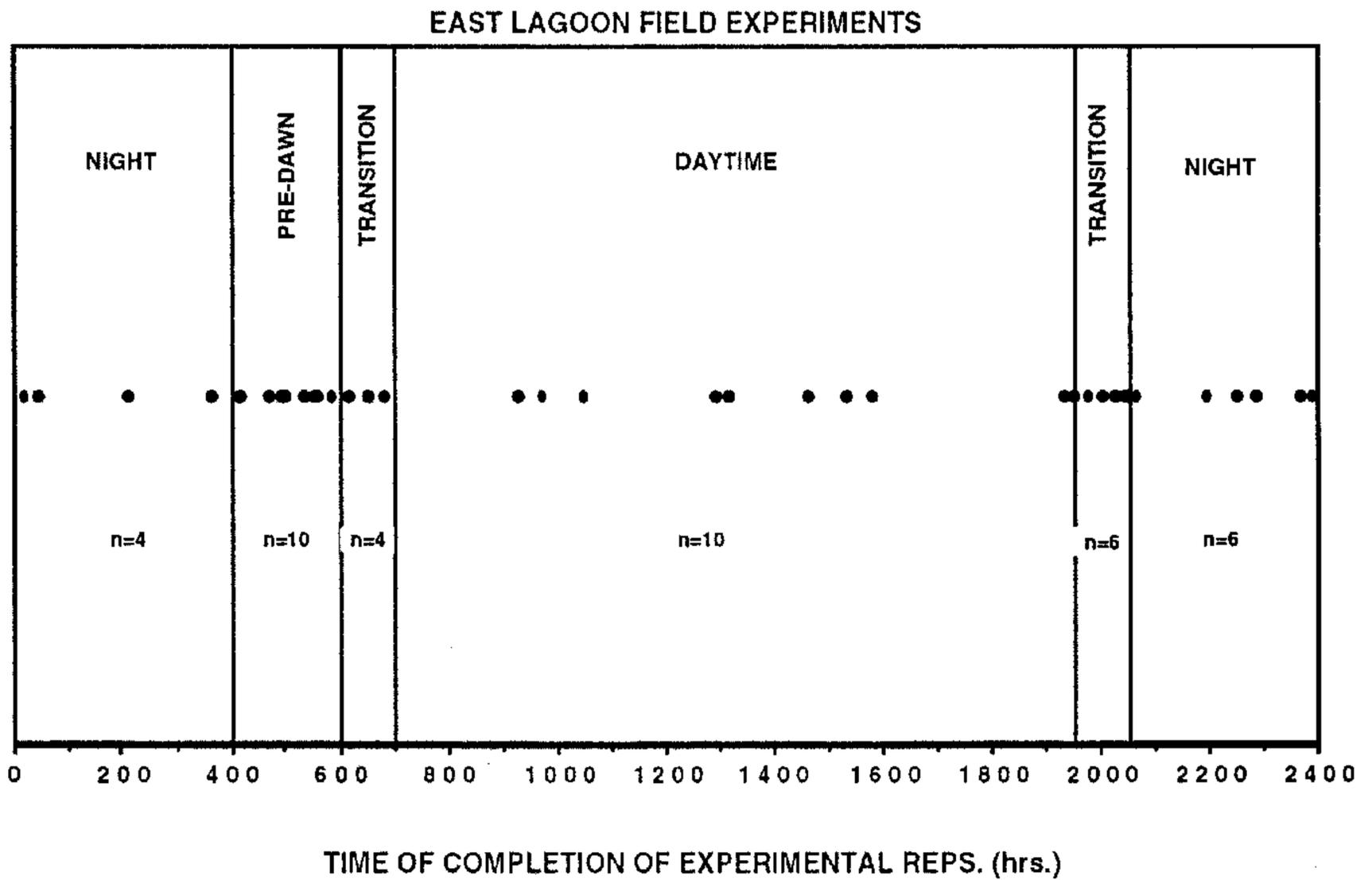


Figure 14. Randomly selected times for deployment of field enclosures to measure burrowing.

Table 8: Mean percent of shrimp burrowed by time group in laboratory and field experiments as well as from thirty-one day baseline simulation using the stochastic model.

Time Group	LABORATORY EXPERIMENTS		STOCHASTIC MODEL		FIELD EXPERIMENTS	
	N	Mean ± s.d.	N	Mean ± s.d.	N	Mean ± s.d.
Daytime	40	86.99 (18.12)	775	85.67 (15.44)	10	72.14 (25.52)
Transition	15	67.35 (21.31)	93	61.04 (22.66)	10	76.43 (21.04)
Nighttime	25	1.30 (2.72)	496	1.39 (1.87)	10	18.57 (20.26)
Predawn	15	19.40 (14.33)	124	19.39 (10.49)	10	11.43 (8.38)

daytime periods when compared to data from laboratory experiments (Table 8). However, burrowing at night was much higher in the field than in the laboratory. There are numerous factors interacting on shrimp in the field studies (i.e., presence of prey items, olfactants, turbid water, etc.) that were not present in the laboratory experiments. In addition, subsurface light levels measured in the field experiments were greater than those observed in the laboratory (Table 9). These factors may account for differences among the two sets of burrowing observations from laboratory and field experiments. This problem is examined in greater detail in the Discussion section.

Comparison of Model Results with Field Data

Ten predicted values for percent of shrimp burrowed for each time group (daytime, transition, nighttime, predawn) were randomly selected from baseline simulation results. Multiple t-tests were used to compare the mean burrowing rates between field experiments and baseline simulations (Table 10). Significant differences were observed in the nighttime and predawn periods ($p \leq 0.015$). The lack of detectable differences during the daytime and transition periods ($p \geq 0.10$) may be due to the large variability incorporated into the predictions via the stochastic process of the model.

The subsurface light intensities measured in the field experiments (Table 9) were used as the only input variable in the 'modified baseline model'. The 'modified baseline model' was used in a second set of simulations which were performed only for daytime and transition groups. This provides a more rigorous test of the rate equations. The only sources of variability in the predictions are determined by the different subsurface light intensities used as input (Table 9) and the variance associated with the rate equations (Equations 8-9). Ten predictions were obtained for the daytime period.

Table 9. Data from field experiments examining burrowing in experimental enclosures. Presence of light during the last nighttime experiments (marked by asterisks) was caused by a full moon.

EXP. #	DATE (1989)	TIME OF RECOVERY	DEPTH (cm)	TURBIDITY (FTU's)	INCIDENT LIGHT (mE)	SUBSURFACE LIGHT (mE)	% SHRIMP BURROWED
DAYTIME							
1	May 24-25	1519	35.25	4.50	2160.000	911.700	35.71
2	May 29-30	1601	33.50	4.85	1861.750	521.350	28.57
3	Jun 5-6	1921	30.50	4.95	832.125	394.478	78.57
4	Jun 8-9	1438	32.75	5.50	1989.500	1377.750	71.43
5	Jun 13-14	0945	44.00	3.03	1443.500	959.800	78.57
6	Jun 16-17	1030	37.00	5.95	880.548	499.320	71.43
7	Jul 11-12	0918	43.00	1.76	615.140	288.164	57.14
8	Jul 11-12	1255	31.50	3.00	1642.000	1164.725	100.00
9	Jul 17-18	1607	24.50	2.90	1568.500	1066.450	100.00
10	Jul 17-18	1610	25.50	2.45	1634.500	1206.000	100.00
TRANSITION							
1	May 24-25	0630	31.00	-	-	-	42.86
2	May 29-30	2002	22.25	4.00	337.933	210.050	92.86
3	June 5-6	2010	28.50	7.95	580.742	132.379	92.86
4	June 8-9	1950	38.00	10.95	725.873	217.430	92.86
5	June 13-14	0650	28.00	0.13	205.200	114.250	50.00
6	June 16-17	1955	31.75	12.05	815.325	184.828	64.29
7	July 11-12	2004	22.75	8.11	648.131	430.356	78.57
8	July 11-12	0640	39.50	5.80	19.475	8.718	57.14
9	July 17-18	0632	29.75	5.20	31.470	17.380	92.86
10	July 17-18	2005	22.25	3.95	639.250	377.916	100.00
NIGHTTIME							
1	May 24-25	2045	38.00	2.25	0.000	0.000	35.71
2	May 29-30	2157	39.25	10.90	0.000	0.000	14.29
3	June 5-6	0338	30.25	12.15	0.000	0.000	7.14
4	June 8-9	2353	25.25	6.10	0.000	0.000	57.14
5	June 13-14	0206	28.50	7.13	0.000	0.000	7.14
6	June 16-17	0030	30.50	9.18	0.000	0.000	0.00
7	July 11-12	2230	47.00	7.00	0.000	0.000	0.00
8	July 11-12	0013	52.50	4.05	0.000	0.000	0.00
9	July 17-18	2253	23.50	8.40	0.000	0.000	21.43
10	July 17-18	2340	17.50	13.00	4.999*	3.781*	42.86
PREDAWN							
1	May 24-25	0409	37.75	0.38	0.000	0.000	7.14
2	May 29-30	0535	25.25	7.75	0.000	0.000	14.29
3	June 5-6	0521	35.75	9.00	0.000	0.000	7.14
4	June 8-9	0410	27.50	17.45	0.000	0.000	7.14
5	June 13-14	0550	46.75	8.45	0.000	0.000	7.14
6	June 16-17	0443	34.00	6.57	0.000	0.000	0.00
7	July 11-12	0530	40.00	8.05	0.000	0.000	7.14
8	July 11-12	0500	39.50	4.40	0.000	0.000	28.57
9	July 17-18	0500	35.00	6.20	0.000	0.000	21.43
10	July 17-18	0455	37.00	5.70	0.000	0.000	14.29

Table 10: Results from t-tests comparing mean burrowing rates from initial baseline simulations of stochastic model and field experiments. Negative values indicate lower mean burrowing rates during field experiments in comparison with model predictions.

Time Group	df	T-value	p-value
Daytime	18	-0.876	0.393
Transition	16	1.577	0.134
Nighttime	18	-0.299	0.008
Predawn	18	2.682	0.015

Only nine predictions were obtained for the transition group due to equipment failure which resulted in a lack of light data during one of the field replicates (Table 9). In the 'modified baseline model', simulations for both the daytime and transition periods almost always resulted in a prediction of 100% shrimp burrowed. Comparison with burrowing rates in the field using paired t-tests resulted in detection of a significant difference during the transition period only ($p = 0.013$, Table 11). Thus, the rate equations (Equations 6-9) fail to accurately predict burrowing patterns during the transition period but not during the daytime period.

The most plausible explanation for significant differences among predicted and observed burrowing rates (from field studies) is provided by the differences in light intensities among laboratory and field experiments. Data from the laboratory experiments were used to quantify the rate equations (Equations 8-9) determined from the light-burrowing relationships (Figure 9). Light intensities in the laboratory were much lower than in the field due to artificial light attenuation from the roof in the greenhouse-type lab. When naturally occurring light levels are applied to the regression models in Equations 8 and 9, predicted burrowing rates exceeded the 100% level. The simulation model then set the prediction at the 100% maximum.

Table 11: Results of paired t-tests comparing mean burrowing rates from simulations of the 'modified baseline model' and field experiments.

Time Group	df	Mean X-Y	Paired T-value	p-value
Daytime	9	11.199	1.290	0.229
Transition	8	18.796	3.182	0.013

From Figure 9, it is evident that the rate of increase in burrowing is highest near the threshold light intensity. Equations 8 and 9 which set the burrowing rates during the illuminated portion of the day must be modified in the final model to accommodate light intensities of the magnitude observed in estuaries. All data from laboratory and field studies were therefore grouped to obtain new solutions to the logistic curves shown in Figure 9 (Equations 8 and 9). Figure 15 shows the new logistic curves using the modified data set. Log-transformed light intensities (x-axis) which were previously limited to values less than three (Figure 9) now extend out to ~7.5. Data from field studies are easily seen on the extreme right portions of the curves (Figure 15). The solutions to the regressions are used to modify Equations 8 and 9 so that they take the form:

$$\begin{array}{ll} \text{Transition} & 0630-0700 \text{ hr's.}, \\ & 2000 \text{ hr's.} \end{array} \quad Y = [73.41 + 14.24*\text{Log}(x) \pm 21.51*(A)] \quad (\text{Eq. 10})$$

$$\begin{array}{ll} \text{Daytime} & 0730-1930 \text{ hr's.} \end{array} \quad Y = [66.27 + 9.40*\text{Log}(x) \pm 18.12*(A)] \quad (\text{Eq. 11})$$

The rate equations for burrowing during nighttime and predawn periods in the final model also were modified to include results from field experiments. Thus, Equations 6 and 7 now take the form:

$$\begin{array}{ll} \text{Nighttime} & 2030-0400 \text{ hr's.}, \end{array} \quad Y = [3.41 \pm 9.03*(A)] \quad (\text{Eq. 12}).$$

$$\begin{array}{ll} \text{Predawn} & 0430-0600 \text{ hr's.}, \end{array} \quad Y = [18.25 \pm 13.88*(A)] \quad (\text{Eq. 13}).$$

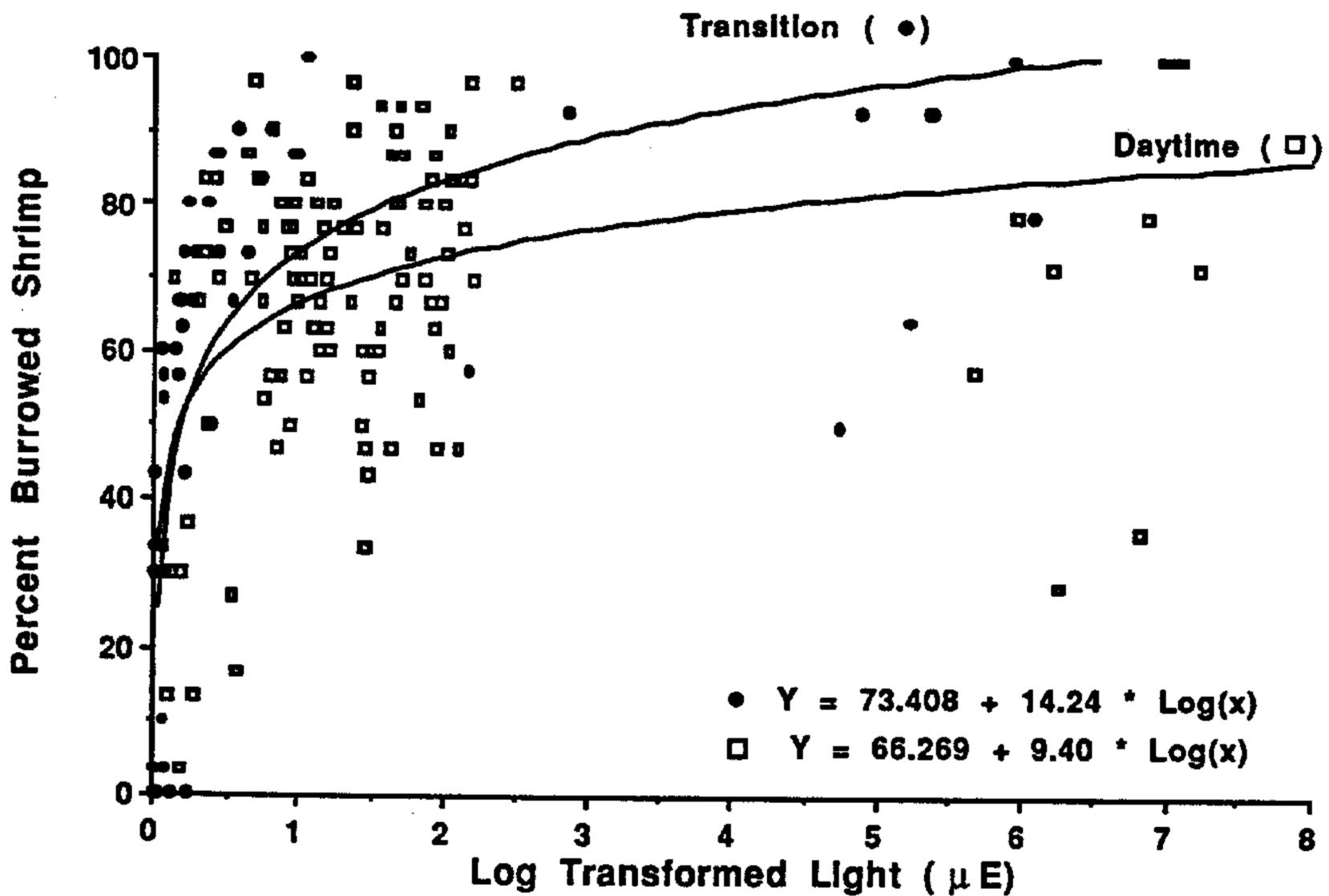


Figure 15. Graph of shrimp burrowing vs. log-transformed light during transition and daytime hours using all available data (laboratory and field experiments combined). Solutions to logistic fits are used to parameterize material transfer rates in the final model.

In Equations 10-13 above, Y = percent of shrimp burrowed and x = the log transformed subsurface light intensity. The variable A represents the standard normal random variate truncated between -1 and +1 which is selected once a day.

Sensitivity Analysis

A new set of simulations were conducted using the final burrowing model. The results and burrowing patterns are shown in Table 12 and Figure 16. Generally, burrowing decreased about 5-8% in the predawn and daytime periods (Table 12) when compared to the initial model. Mean burrowing decreased almost 50% during

the transition period and burrowing increased ~1.5x to 3.41% shrimp burrowed at night (Table 12).

To determine sensitivity of the model to driving variables, water depth and turbidity were varied in 25% increments up to $\pm 100\%$, and also tested at 3x their normal rates (200% increase). The effects of these changes in water depth and turbidity are reflected in changes in subsurface light intensity and burrowing rates (Figures 17-18, Table 13). As depth or turbidity increase over baseline levels, subsurface light levels and mean burrowing rates decrease. The opposite holds true as depth and turbidity levels decrease. The effects of water depth and turbidity on burrowing are more dramatic during the transition period (Figures 17-18). During the daytime period, a larger amount of light enters the water column, thus a greater proportion of light reaches the substrate surface. When subsurface light intensities decrease to extremely low levels, burrowing rates decrease rapidly. This suggests that an extremely low threshold light level is needed to elicit a change in burrowing of brown shrimp. When water depth and turbidity are simultaneously increased at equal rates, their synergistic effects result in a sharper decline in subsurface light intensity and consequently, burrowing levels (Table 14).

Table 12. Mean subsurface light intensity ($\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$) and percent burrowed shrimp during the four time periods from thirty-one day simulation using the final model. Standard deviations are in parentheses. The percent change reflects the difference between means from the modified in comparison with baseline simulations from the initial model.

Time Group	N	Mean Subsurface Light Intensity	% Change From Initial Model	Mean % Burrowed Shrimp	% Change From Initial Model
Daytime	775	121.17 (73.28)	2.426	80.16 (16.07)	-7.399
Transition	93	2.97 (2.43)	15.435	46.30 (36.91)	-47.809
Nighttime	496	-	-	3.41 (2.64)	147.273
Predawn	124	-	-	18.25 (10.35)	-5.837

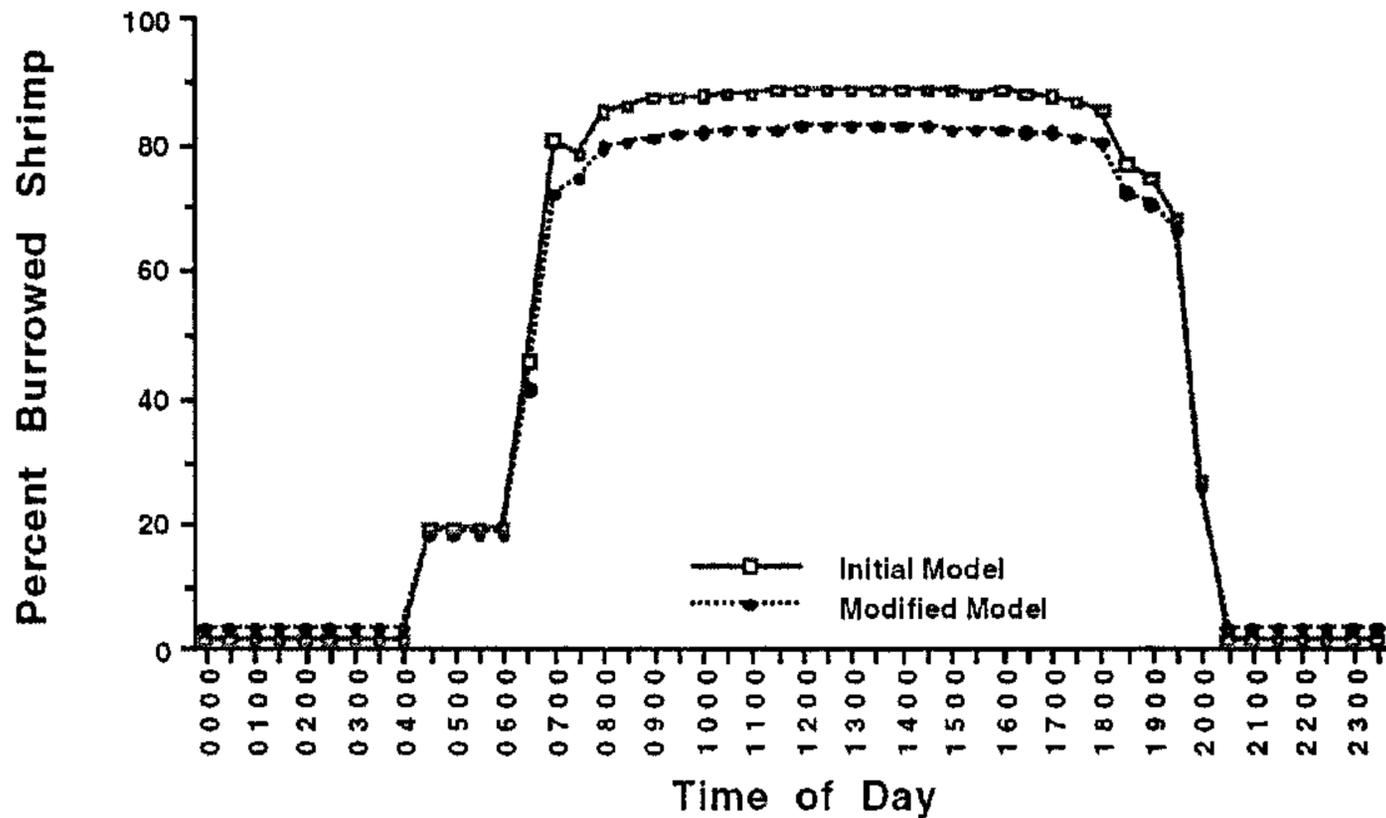


Figure 16. Mean percent of shrimp burrowed vs. time of day in the initial and final models. Burrowing during transition (0630, 0700, 2000 hr's.) and daytime (0730-1930) periods are light dependent.

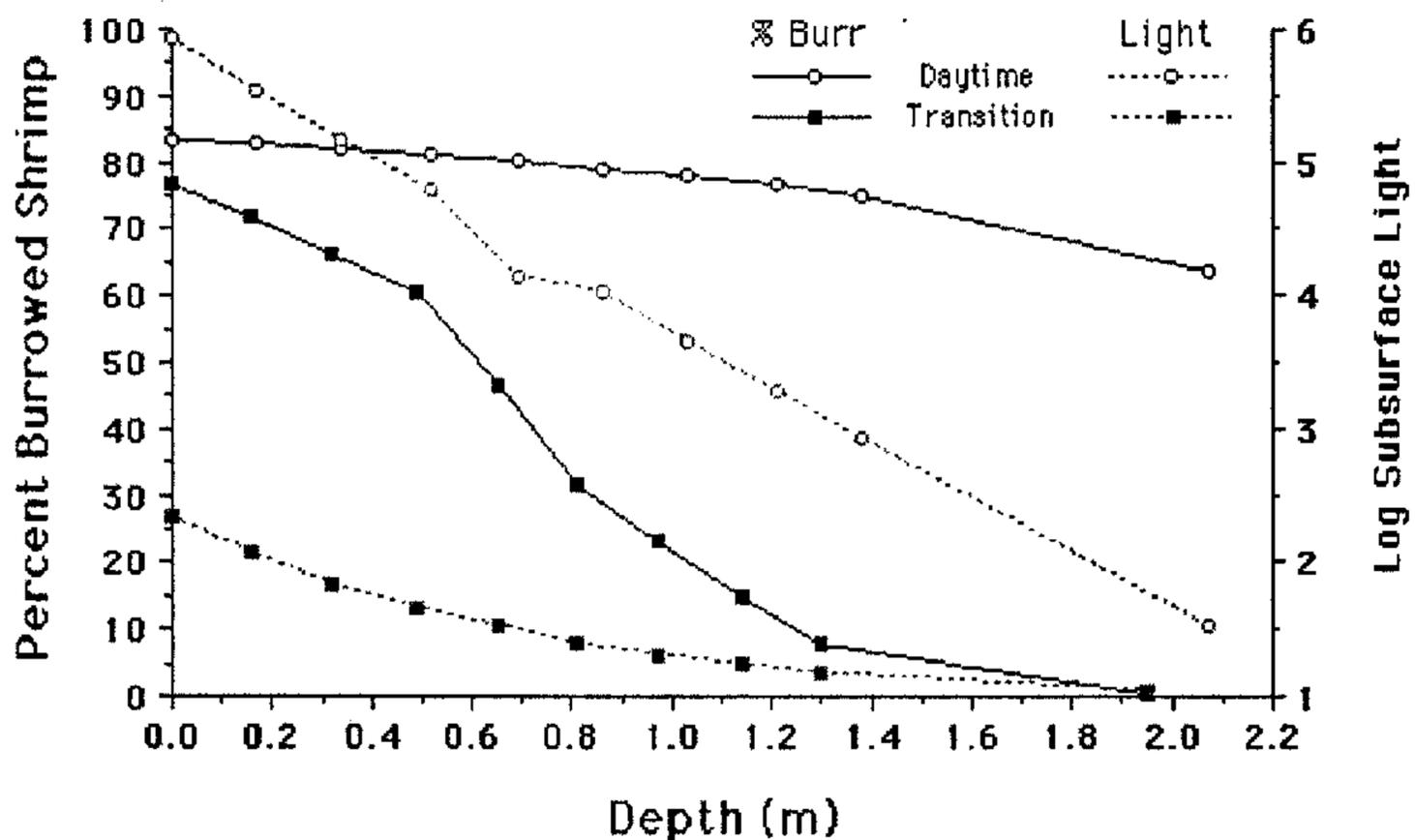


Figure 17. Graph of water depth (m) vs. log subsurface light intensity and percent of burrowed shrimp for daytime and transition periods. Data are from sensitivity analysis simulation using the final model. Light is in units of $\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$. The solid line represents burrowing during daytime (—○—) and transition (—■—) periods. The broken lines are subsurface light intensity (---○--- = daytime, ---■--- = transition).

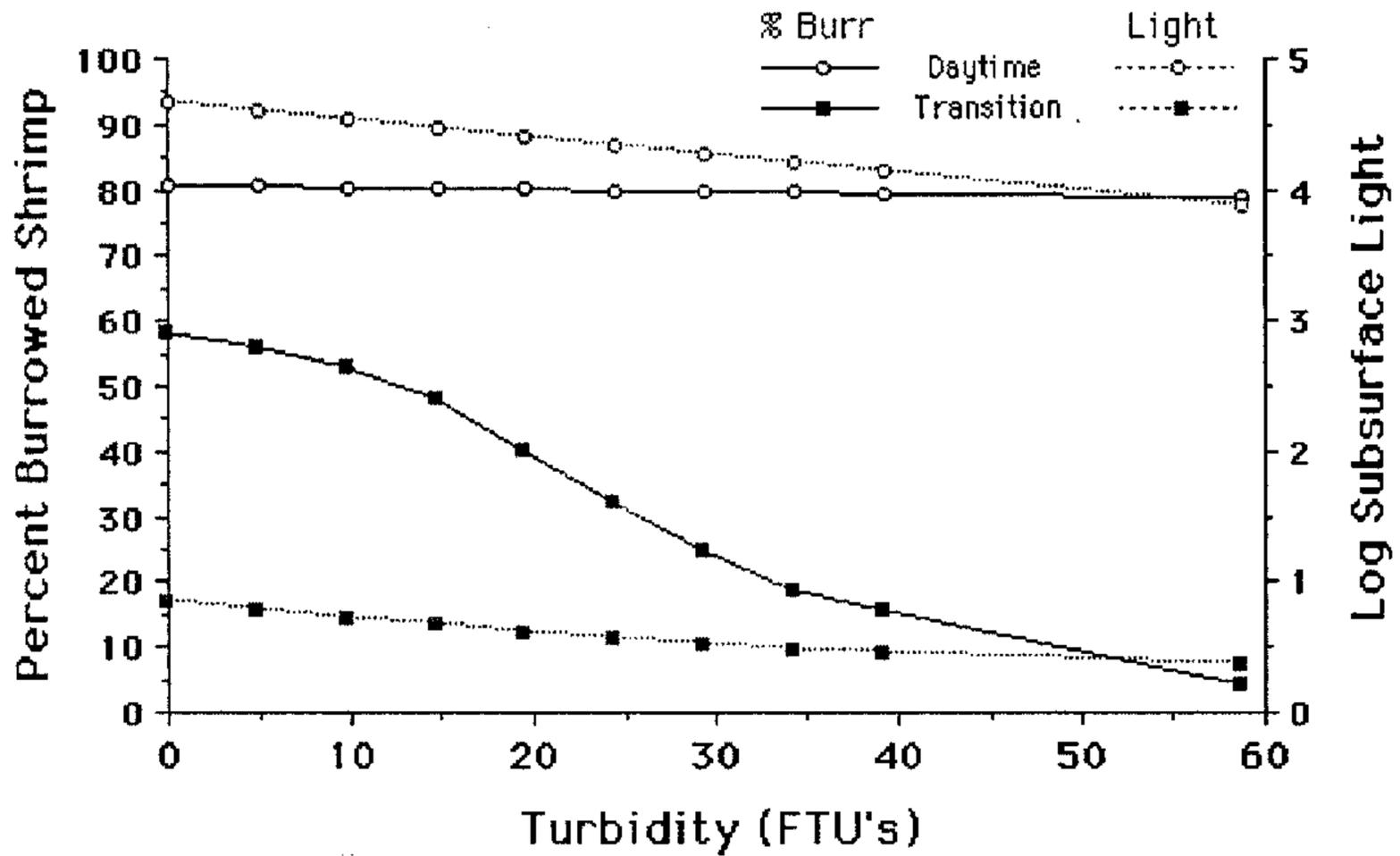


Figure 18. Graph of water turbidity (formazin turbidity units) vs. log subsurface light intensity and percent of burrowed shrimp for daytime and transition periods. $\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$. The solid line represents burrowing during daytime (—○—) and transition (—■—) periods. The broken lines are subsurface light intensity (---○--- = daytime, ---■--- = transition).

Data from

Table 13. Results from sensitivity analysis simulations using the final model. Changes in mean subsurface light intensity (microEinsteins/sec/sq. meter) and percent of shrimp burrowed during daytime and transition periods with varying levels of water depth and turbidity. The percent change reflects difference from baseline conditions.

		Effect of Depth Changes				Effect of Turbidity Changes			
	Variable Difference	Mean Subsurface Light Intensity	% Change	Mean Percent Shrimp Burrowed	% Change	Mean Subsurface Light Intensity	% Change	Mean Percent Shrimp Burrowed	% Change
Daytime Period	-100%	560.71	362.7	83.41	4.1	159.77	31.9	80.69	0.7
	-75%	380.56	214.1	82.82	3.3	148.92	22.9	80.57	0.5
	-50%	259.07	113.8	82.13	2.5	138.91	14.6	80.44	0.3
	-25%	176.90	46.0	81.13	1.2	129.68	7.0	80.30	0.2
	Baseline	121.17	-	80.16	-	121.17	-	80.16	-
	+25%	83.24	-31.3	79.12	-1.3	113.30	-6.5	80.02	-0.2
	+50%	57.37	-52.7	77.89	-2.8	106.03	-12.5	79.87	-0.4
	+75%	39.66	-67.3	76.61	-4.4	99.31	-18.0	79.72	-0.5
	+100%	27.50	-77.3	75.09	-6.3	93.09	-23.2	79.55	-0.8
+200%	6.61	-94.5	63.68	-20.6	72.48	-40.2	78.87	-1.6	
Transition Period	-100%	9.38	215.8	76.90	66.1	4.10	38.0	62.60	35.2
	-75%	6.86	131.0	71.89	55.3	3.77	26.9	60.66	31.0
	-50%	5.08	71.0	66.36	43.3	3.47	16.8	57.78	24.8
	-25%	3.85	29.6	60.45	30.6	3.21	8.1	53.60	15.8
	Baseline	2.97	-	46.30	-	2.97	-	46.30	-
	+25%	2.35	-20.9	31.75	-31.4	2.76	-7.1	39.13	-15.5
	+50%	1.93	-35.0	23.28	-49.7	2.57	-13.5	32.42	-30.0
	+75%	1.64	-44.8	14.95	-67.7	2.42	-18.5	26.95	-41.8
	+100%	1.42	-52.2	7.97	-82.8	2.27	-23.6	24.19	-47.8
+200%	1.06	-64.3	0.53	-98.9	1.85	-37.7	14.01	-69.7	

Table 14. Mean subsurface light intensity ($\mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$) and percent of shrimp burrowed due to combined increases in water depth and turbidity. Means are from a thirty-one day simulation using the final model. Number of observations per mean are 775 and 93 for daytime and transition periods, respectively.

	Variable Difference	Mean Subsurface Light Intensity	% Change	Mean Percent Shrimp Burrowed	% Change
Daytime Period	Baseline	121.17	-	80.16	-
	+25%	77.84	-35.8	78.96	-1.5
	+50%	50.21	-58.6	77.49	-3.3
	+75%	32.52	-73.2	75.93	-5.3
	+100%	21.15	-82.5	73.96	-7.7
	+200%	4.01	-96.7	55.51	-30.8
Transition Period	Baseline	2.97	-	46.30	-
	+25%	2.21	-25.6	26.55	-42.7
	+50%	1.74	-41.4	15.82	-65.8
	+75%	1.44	-51.5	5.61	-87.9
	+100%	1.23	-58.6	1.83	-96.0
	+200%	1.00	-66.3	0.00	-100.0

MODEL USE

Development of the burrowing model is the initial step of a continuing effort to examine predation mortality of juvenile brown shrimp in estuaries. Numerous factors are involved in regulating predation mortality of juvenile shrimp; the burrowing model eventually will be used as a submodel in a larger, more complex mortality model. However, the value of the model can be demonstrated in a simple predator-prey system.

In this exercise, the number of shrimp eaten by the predator (southern flounder) will depend on a linear relationship with 'apparent density'.³ Mortality of shrimp due to predation by southern flounder is positively correlated with shrimp density (T. J. Minello, NMFS, Galveston, TX, personal communication). In an unpublished experiment with white shrimp, densities of 2.8 and 16.7 shrimp/m² were used to examine predation by southern flounder (T. J. Minello, NMFS, Galveston, TX, personal communication). The mean number of shrimp eaten per fish at those densities was 3.2 and 5.6, respectively (0.13 and 0.23 shrimp eaten per 30-minute period). Assuming predation rates increased linearly with prey density, the slope of a regression of shrimp density against the number of shrimp eaten (per 30-minute period) is 0.0072. In other experiments, burrowing by brown shrimp reduced predation rates of southern flounder, suggesting that burrowed shrimp were not susceptible to predators (Minello et al. 1987). Subsurface light in itself does not appear to affect predation rates of southern flounder; there is virtually no difference in flounder feeding rates during daytime and nighttime periods (Minello et al. 1989). Assuming that only non-burrowed shrimp are available to predators, changes in

³ The term 'apparent density' is used because only non-burrowed shrimp are included. True density includes the total number of shrimp (burrowed and non-burrowed).

burrowing frequency affect the density of shrimp available to predators. By combining model output with density-dependent predation, the effect of environmental conditions on shrimp mortality can be simulated.

A true density of 10 shrimp/m² was arbitrarily selected, and the model was used to predict changes in burrowing (and apparent density) by increasing turbidity (similar to the method used for sensitivity analysis). As turbidity increases, subsurface light intensity decreases and shrimp should emerge from burrows. The duration of model simulations was limited to one day, with a time-step of thirty minutes. Mortality of shrimp at each time step was calculated by using the solution to the linear equation for density-dependent predation (described above): $Y = 0.1131 + 0.0072 \cdot x$, where Y is the number of shrimp eaten per fish (in each 30-minute period) and x is the number of non-burrowed shrimp (apparent density) which is available to predators.

Under the initial conditions of 20.6 FTU's, the model predicted 7.15 shrimp would be consumed during one day. A 2x or 3x increase in turbidity (41.3, 61.9 FTU's) resulted in 7.18 and 7.25 shrimp eaten per fish for one day. Thus, a large increase in water turbidity appears to have little effect on predation of brown shrimp by southern flounder. This response is not surprising because sensitivity analysis showed little effect of increasing turbidity on burrowing rates (and apparent density) during the daytime period (Figure 18). In addition, the effect of turbidity on mortality rates is somewhat diluted by the method used here to quantify predation. Predation pressure is equal throughout the day but mortality of shrimp depends on their availability to predators and is controlled by shrimp density. Predation is high during nighttime periods when burrowing is low and is not affected by turbidity levels or subsurface light intensities.

The effect of turbidity (or depth) may be amplified for other predators which concentrate feeding during the illuminated portion of the day. For example, pinfish (*Lagodon rhomboides*), are abundant in Galveston Bay and primarily utilize visual stimuli to detect shrimp prey (Minello and Zimmerman 1983). Changes in burrowing and apparent density during the daytime period, would have a greater effect on predation rates by this species.

The best application of the burrowing model should be in its use as a submodel in the mortality model described earlier (model overview section). This research effort was a prelude to developing the mortality model. The numerous complex factors that affect predator-prey populations in an estuary must be examined in detail and quantified prior to inclusion in the brown shrimp mortality model.

DISCUSSION AND CONCLUSIONS

The shrimp fishery in the Gulf of Mexico remains the most valuable fishery in the U.S. Brown shrimp, *P. aztecus* make up the bulk of the Gulf stocks and annual variation in landings ranges in the tens of millions of pounds. Consequently, brown shrimp have been the subject of extensive research during the past 40 years. Finfish predation on postlarval and juvenile shrimp is important in determining the recruitment of brown shrimp to the fishery (Minello et al. 1989).

Recent studies have increased the knowledge of the factors regulating predator and prey interaction. Behavior of shrimp (and fish) is of primary concern in examining the mechanisms controlling predator-prey relationships (Minello et al. 1989). However, biotic and abiotic factors are equally important in 'adjusting' the response of organisms to their environment (Venkataramiah et al 1974; Zein-Eldin and Aldrich 1965; Trent 1966; Zimmerman et al. 1984). A simulation model is an effective tool for examining the relative importance of all factors interacting on juvenile brown shrimp. Previous studies outline the effect of individual factors on burrowing rates of brown shrimp. Not all studies, however, agree on the effects of specific conditions. One factor prevails as the most important; burrowing among brown shrimp is a direct result of (or at least synchronized with) underwater light conditions (Wickham and Minkler 1975; Rulifson 1983)

The conceptual burrowing model presented here is nested as a submodel within a larger conceptual model of mortality. The simulation model uses light as the main factor forcing movement between the emerged and burrowed conditions. Water depth and turbidity are included due to their effect on light attenuation. The model was developed using field data for input parameters and forcing functions. Laboratory experiments were conducted to determine the threshold levels of light required to stimulate

burrowing or elicit emergence of shrimp from the substrate. Special light filters were constructed to artificially attenuate incident light in experimental tanks.

Similar burrowing patterns were observed in all treatments. The persistence of burrowing in tanks with little or no light indicated a circadian rhythm effect. Continued observation indicated that the circadian rhythm effects dissipated after shrimp endured a second day in complete darkness. The translucent roof covering the greenhouse-type structure in which experiments were conducted also reduced incident light, sometimes by an order of magnitude. Nevertheless, changes in burrowing at sunrise and sunset persisted under extremely low light conditions (compared to naturally occurring conditions). This suggests a very small threshold light level forcing movement of shrimp between active and passive conditions. Examination of the logistic curves describing the light-burrowing relationship reveals the threshold light intensity to be within $0-3.0 \mu\text{E}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$.

Several different types of curve fitting techniques were initially used to parameterize the light-burrowing relationships in an attempt to find the regression model that best predicted burrowing in the laboratory experiments. Although several regressions using combinations of transformations or curve-fitting methods resulted in higher R^2 values, a logistic fit to the effect of log-transformed light on burrowing was used. A large portion of the variability remained unaccounted for during the daytime period but this variability was incorporated into model predictions using stochastic simulation. Unexplained variability may be caused by other factors not examined such as physiological condition (hunger level, molt stage, etc.) circadian rhythms or lunar phase. I attempted to minimize handling of shrimp prior to, and during experiments in order to reduce confounding effects, but this factor also may have had an impact on within treatment variability. Physical condition and stress due to handling are probably the most important factors regarding variability of results.

The enclosure developed for the purpose of collecting validation data provided good information on burrowing rates in the field where direct observations are limited by turbid water conditions. Randomly selected predictions from the nighttime and predawn baseline simulations were significantly different from field experimental data. No significant differences were detected during the daytime period, and data for the transition period were nearly significant at the 95% level ($p=0.072$). The lack of significant differences between field and baseline simulation data for daytime and transition periods did not allow me to refute or invalidate the model. However, the lack of significant differences was likely due to the large amount of variability incorporated into simulation predictions.

A second, more rigorous test of predictions using light intensities from field experiments support this conclusion. In the 'modified baseline model', comparisons were made only for the daytime and transition periods. Comparisons of field burrowing rates and the new predictions were significantly different for both time periods, thus the original baseline model was considered to be invalid. The reason for significant differences is identified through closer inspection of the logistic curves governing model predictions. Light intensities from the field experiments extend beyond the range of those measured in the laboratory which were used to parameterize the rate equations. Model predictions thus reflect high end conditions which are limited by the 100% maximum burrowing rate.

This comparison provides a good example of problems associated with ecological studies. Hairston's (1989) treatise on tradeoffs in ecological research outlines the dilemma. Laboratory studies associated with ecological studies allow for better control over experimental design, data collection and analysis. Field experiments provide more realism over the sometimes sterile environment observed in laboratory studies, but usually at the expense of precision. The best possible

situation is a middle ground where information from both laboratory and field studies are integrated, thereby providing better insight into the subject being examined. In the case of this study on burrowing shrimp, grouping data from the laboratory and field studies results in a more robust model. Ideally, the final model should be compared with another independent data set for validation purposes but resource and logistical problems prevented me from doing so. Future studies can help determine the sources of variability associated with burrowing that remain unaccounted for in this study. This would provide the basis for a shift away from an empirical towards a more mechanistic model.

I am confident that the modified model provides realistic and plausible predictions of burrowing behavior in brown shrimp. The stochasticity of the model adds some flexibility and realism. Achieving realism in modelling animal behavior remains a controversial subject but all organisms are governed by specific ecological rules and relationships. Random events are also a fact in real world situations and the stochastic burrowing model utilizes this in predictions.

Changes in water depth during illuminated periods (transition, daytime) result in greater changes in burrowing in comparison to proportional changes in turbidity. From this study, it is evident that water depth plays a large role in attenuating light in the water column. The role of suspended particulates in light attenuation is primarily one of scattering light photons. In a shallow estuarine system, there may be enough down scattering to reduce the role of turbidity on light attenuation. As expected, concurrent increases in water turbidity and depth result in even greater changes in burrowing levels, but only slightly higher than those observed with increases in water depth only.

The model developed here, together with past studies on shrimp predators, provides a foundation for examination of juvenile shrimp mortality in estuaries.

Collectively, these investigations greatly increase the knowledge of the factors regulating penaeid shrimp populations in the Gulf of Mexico.

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