Stage-Structured Analysis and Modeling of the Pacific Razor Clam (*Siliqua patula*) in a Changing Environment:

Investigation of population dynamics and harvest strategies using process models and simulation.

by

John Warren Schlechte

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1996

Approved by: ______________________________
Chairperson of Supervisory Committee

____

____

Program Authorized to Offer Degree: Fisheries

Date: September 24, 1996

UMI Number: 9716916

UMI
300 North Zeeb Road
Ann Arbor, MI 48103

Doctoral Dissertation

In presenting this dissertation in partial fulfillment of the requirements for the Doctoral degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this dissertation is allowable for scholarly purposes only, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for copying or reproduction of this dissertation may be referred to University Microfilms, 1490 Eisenhower Place, P.O. Box 975, Ann Arbor, MI 48106, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in microform and/or (b) printed copies of the manuscript made from microform."

Signature: John Damm Scheuer

Date: September 23, 1996

University of Washington

Abstract

Stage-Structure Analysis and Modeling of the Pacific Razor Clam (*Siliqua patula*) in a Changing Environment: Investigation of population dynamics and harvest strategies using process models and simulation.

by John Warren Schlechte

Chairperson of the Supervisory Committee: Professor John R. Skalski

School of Fisheries

The Pacific Razor Clam (*Siliqua patula*) populations along the Washington coast have experienced massive fluctuations in abundance since the 1950s. Since the 1980s, it has been hypothesized that some of the declines in abundance might be related to the disease NIX (Nuclear Inclusion X; *Nucleobacter siliqua*). This study investigated the relationships between NIX and the processes of survival, growth and recruitment for razor clams along the Washington coast. This study suggests that NIX has not detrimentally affected the razor clam populations along the Washington coast. Contrary to the findings concerning NIX, this study suggests that the processes investigated were affected by the environmental conditions. In particular, survival and growth both showed seasonal components. Similarly, recruitment was correlated to the maximum mean-temperature. However, the degree and direction of the recruitment relationship was beach-specific.

Simulation models were constructed to determine whether alternative management strategies could provide greater harvest with little to no change in risk of extinction or loss of recreational harvest opportunity. The current management strategy is a harvest rate strategy in which 25.4% of all clams >3.5 inches may be harvested. The simulations suggested that the constant harvest rate strategy was a preferred strategy, but that the rate of harvest could be increased to 80% of the adults with little to no risk to the populations.

TABLE OF CONTENTS

Section Number	Section Title	Page

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Anyone who has ever gotten a Ph. D. degree realizes that no individual person can complete a degree without assistance from others. Although my name adorns the title, this is a community effort. Beginning with the professional acknowledgments: there are countless others who have provided assistance, insight, and support. I wish to express my deepest gratitude to the students, faculty and staff of the School of Fisheries and the Center for Quantitative Sciences with whom I interacted. Of special note, I wish to thank Dr. John Skalski and the other members of my committee for taking the patience to refine my work to the point it is today. A portion of this research was funded by the Washington Department of Fisheries. I appreciate their assistance in the field and elsewhere. Thanks also to my field crew who worked diligently through rain, sleet and snow (and also on those rare, sunny summer days). Frank Morado at NMFS - Sandpoint was generous enough to allow me to have lab space to process my tissue samples. Battelle Pacific Northwest Labs at Sequim, WA read my histological slides and provided me with my NIX Intensity values.

On a more personal note, I wish to thank family and friends. Special thanks goes to my wife Kristie. Without her constant love and support, this dissertation would not have been completed. And finally, I wish to acknowledge my son Gabriel. He has been a light in my life for the past two years.

Chapter 1

Introduction and Background

1.1 INTRODUCTION

The Pacific Razor Clam (*Siliqua patula*) can be found throughout the northern portion of the Eastern Pacific Rim, from northern California to Alaska (McMillin, 1924; Lassuy and Simons, 1989). Within their range, razor clam beds are located intertidally along shallow sloping sandy beaches. Because the clams are readily accessible during many low tides, razor clams have been utilized for food since prehistoric times. In fact, large quantities of razor clam shells have been discovered within Native American middens (Lassuy and Simons, 1989). Commercial harvest of the razor clam began in the 1890's and continued through the early 1900's. Quite early in the fishery, McMillin (1924) noticed population decreases along Washington beaches and sought regulatory changes. By the 1960's, populations had decreased significantly, and the fishery became solely recreational. Throughout recorded history, up until the 1980's, populations of razor clams have fluctuated dramatically (Figure 1.1). At Copalis, for instance, population estimates have varied between a high of 24 million (i.e., $4.85/m^2$), to a low of 400,000 (i.e., $0.08/m^2$) (Ayres and Simmons, 1991). This high variability is an indication that recruitment has probably always been sporadic. However, the mechanism which produces this variability has not yet been identified.

Over the past two decades, populations of razor clams along Washington beaches have been on a steady decline (Ayres and Simons, 1988). However, in 1983, following an El Nino event, razor clam populations within the state of Washington suffered tremendous declines that resulted in the closure of all razor clam harvest within Washington (Lassuy and Simons, 1989). The season was closed for the next two years (i.e., 1984 and 1985) and reopened in the spring of 1986 when managers believed populations had recovered

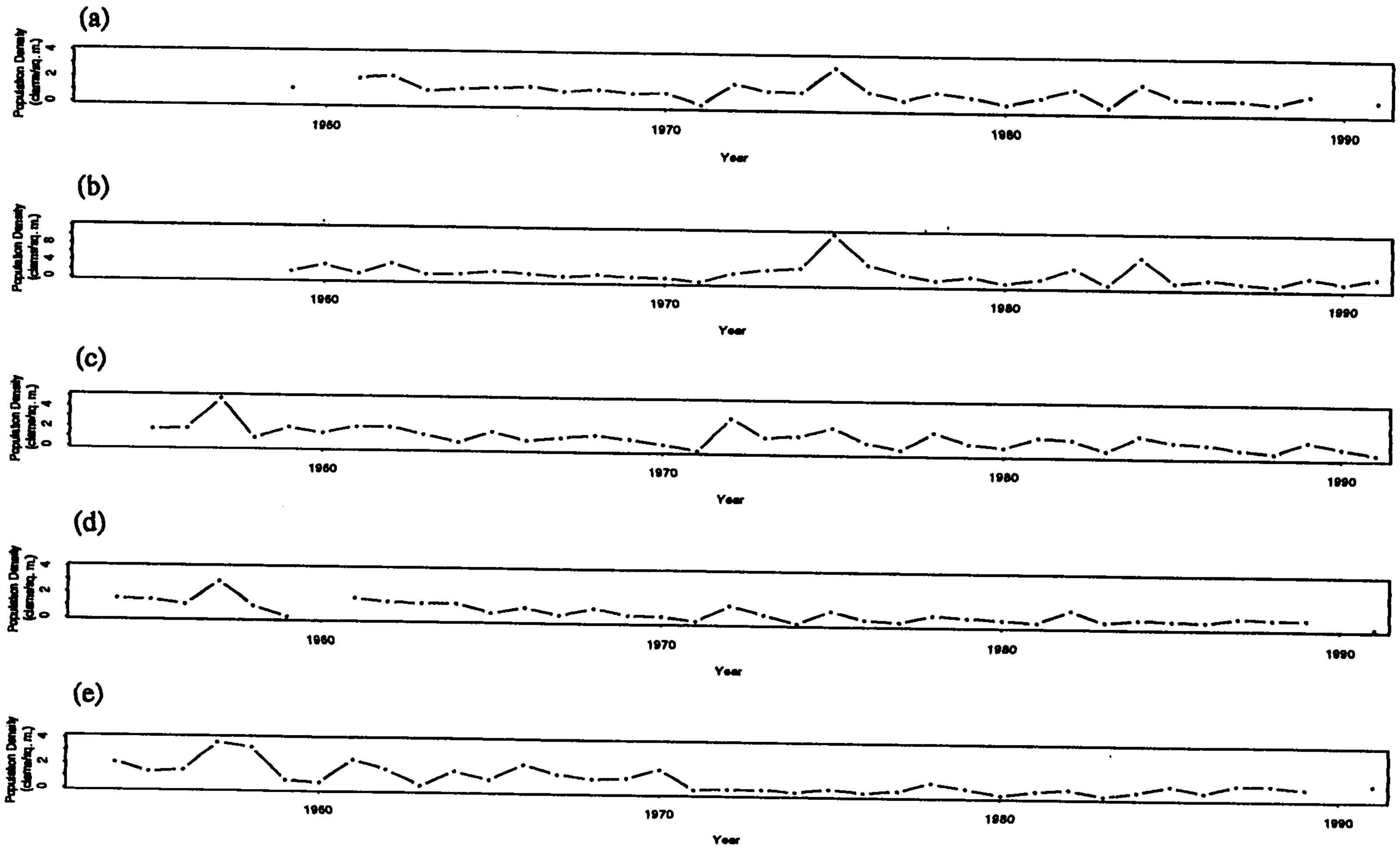


FIGURE 1.1 Time trend of the razor clam population estimates from the 1950's to the 1990's. The uppermost graph (a) is the average density of the population estimates for all Washington Beaches. Below, in geographical order, north to south, are the population estimates for the four beaches that the Washington Department of Fisheries surveys: (b) Mocrocks, (c) Copalis, (d) Twin Harbors, and (e) Long Beach.

substantially. When the fishery was reopened very strict catch quotas were imposed and the season was open for 2 months. Subsequent harvests have been allowed almost every year. However, seasons are open on a beach-by-beach basis and are typically short (i.e., < 2 months). In the mid-1990s, Washington beaches again faced closures. This time, however, the closures were implemented to protect the public, not the clams; for the first time since tests have been conducted, paralytic shellfish poison (PSP) and damoic acid had been detected in razor clam flesh. As both of these toxins are known to cause illness, and potentially death in humans, local health authorities prohibited harvest.

Most recently, the Quinault tribe has decided to exercise its tribal rights to the razor clam fishery. Beginning in 1994, the Quinault tribe began large-scale harvest of the razor clams along ancestral beaches. Under the Boldt decision (*United States vs. Washington*, 1974), one-half of the potential harvest can be allocated for indigenous peoples. Currently, the Quinault tribes are using the estimates from Washington Department of Fish and Wildlife (WDFW) to set their quotas, but the potential for future conflict does exist given the inherent errors associated with population estimates and poor understanding of the exploitative potential.

Shortly after the population decline in 1983, a previously unseen bacteria was discovered within the nuclear envelop of the gill tissue of the razor clam (Elston, 1984; Elston and Peacock, 1984; Elston, 1986a). This bacteria has since been classified as a Rickettsia-like bacterium, and is designated NIX for Nuclear Inclusion Factor X (*Nucleobacter siliqua*). Since the mid-1980s, WDFW has hypothesized that this newly discovered bacterium was a contributing factor in the massive population declines. According to WDFW, the time trajectory of NIX indicated that the highest NIX Intensities would occur during the late-summer and fall (Figure 1.2). By the following spring, when population surveys are conducted, the population of clams and the incidence of NIX often decline. (Ayres and Simons, 1991).

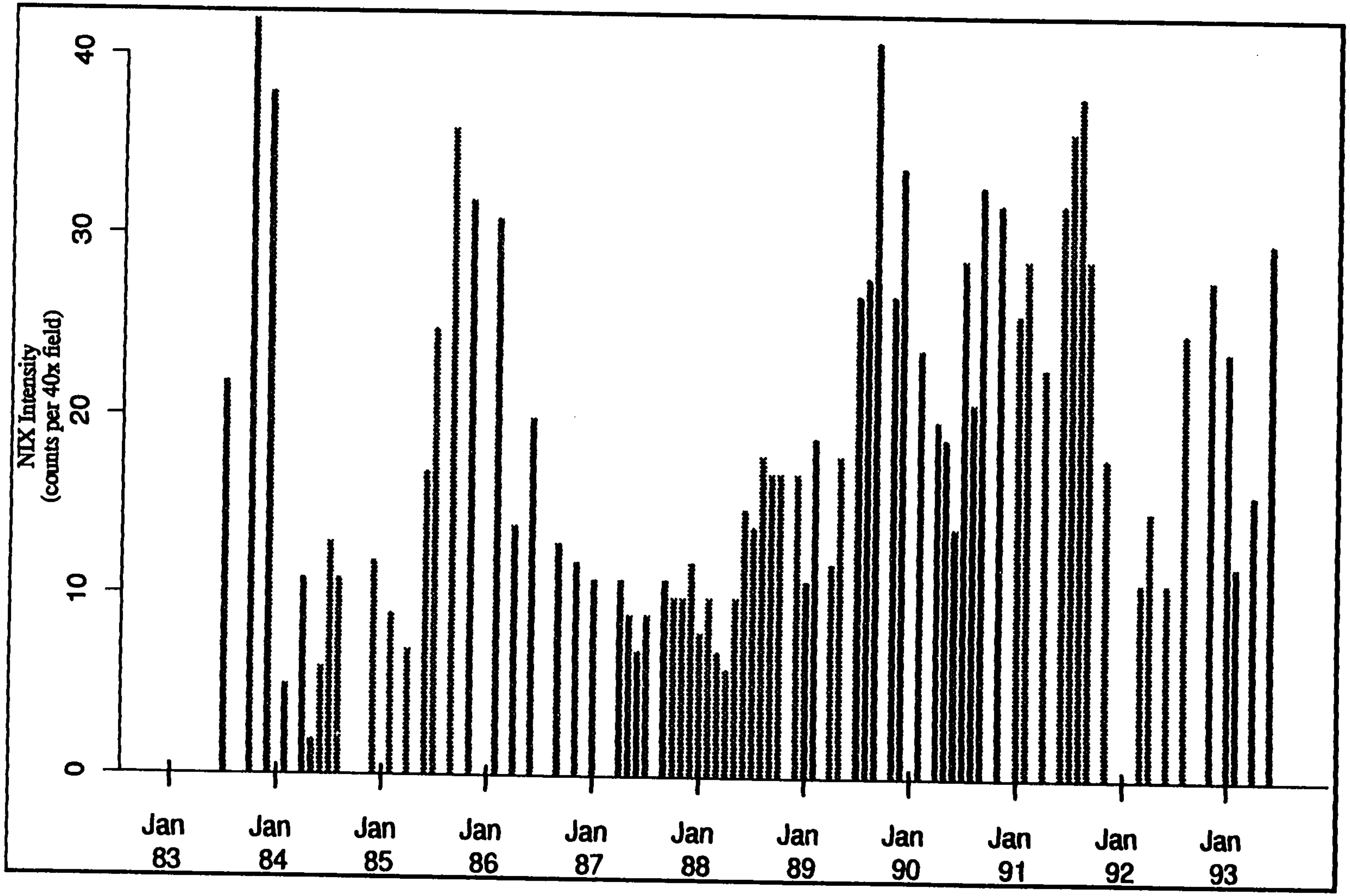


FIGURE 1.2 Time trend of the mean NIX Intensity at Copalis, as reported by WDFW.

These population declines have been troubling to WDFW because the razor clam is an important recreational fishery in Washington. The current management objective for WDFW is to maintain viable populations of razor clams for recreational harvest. As demands for raising harvest levels increase, there must be a fundamental understanding of the repercussions of such decisions. In view of the fact that populations have not responded to the beach closures with rapid increases in stock size, stock assessment has been concerned with estimating the number and size of clams on the beaches, the number and size of clams harvested, and the effort expended. However, many questions concerning the basic biological parameters of the razor clam remain to be answered, especially now that the disease NIX has infested the population.

At the beginning of this study, there was no evidence of NIX in clams found north of Vancouver Island, Canada, and little infection in clams found south of the Columbia River. The beaches at Copalis, Washington and Long Beach, Washington were chosen for this study because of their historical NIX intensities (high intensities at Copalis, lower intensities at Long Beach). Surveys conducted in 1992 indicated that clams in Alaska are now infected with NIX (Ayres, pers. comm). It is not known whether NIX has recently invaded Alaskan waters or whether previous sample sizes were too small to detect the bacteria. The samples taken from Alaskan clams have indicated that the endemic levels of NIX in Alaska are very low.

Quantitative stock assessment and modelling of finfish dynamics are common, but similar mathematical rigor has been less commonly applied to shellfisheries (Brousseau, 1978; Hall, 1983; Orensanz, 1986). Razor clam stocks along the Western coast of the United States and Canada are exploited for both recreational and commercial purposes. However, there have been few attempts to quantify the basic biological parameters within any of these stocks, and almost no work has been done on the stock(s) within Washington. There is little information on the longevity and no information on the intra-annual survival of razor clams within Washington waters. Additionally, there is no information about differences in survival along the coast, although anecdotal evidence indicates that differences between northern and southern beaches probably exist. Similarly, there has been limited work done on growth of razor clams, and none has been done since the infestation of NIX. In this dissertation I attempt to answer some of these basic questions through the combination of fieldwork and statistical modeling.

Similarly, there has been no work done on the stock-recruitment relationship for razor clams. The stock-recruitment relationship is especially interesting as it is unknown whether the entire coast of Washington operates as a single stock or whether each beach is reproductively isolated. In this dissertation I attempt to quantify the stock-recruitment relationship and determine the relationships between beaches.

Underpinning all this research is the investigation of the impact of NIX on the razor clam population. Although there is a theoretical basis for expecting disease processes to influence population dynamics, few studies have attempted to specifically incorporate such information with management models. No such studies exist on the impacts of NIX on razor clam stocks. The analyses within this dissertation investigate the influence of the disease NIX on the survival of the individual, and on the reproductive potential of the adults. The relationships between disease and survival/reproduction are incorporated within the simulation model to investigate how NIX and various harvest strategies may impact subsequent management of the razor clam.

The synthesis of the results into a simulation model formulation provides a coherent framework under which management strategies may be tested. Currently, no model exists that would allow the state shellfish manager to choose between alternative harvest strategies. Thus, the risk and subsequent repercussions of any strategic change are unknown, and can only be tested by submitting the stock to experimentation. The modeling framework allows the testing of these various scenarios to be conducted in the safety of the computer, without risk to the stock. Simulation studies allow replication of the stochastic population trajectory under a specific strategy, and thus allow probabilistic risk to be assigned to each strategy.

Finally, the analyses of existing data sets indicate which parameters are poorly understood and need further investigation. These analyses and subsequent modeling provide indications of further investigations that should be attempted to clarify the dynamics of the razor clam along the Washington coast.

To better manage the razor clam populations along the Washington coast, it is necessary to understand the population dynamics. And, given the current hypothesis that NIX is severely impacting the stock, it is imperative that the effect of NIX on the population dynamics of the razor clam be fully understood. Alternatively, stressors other than the disease process may be impacting the razor clam populations. These too shall be investigated.

1.2 OBJECTIVES

My goal is to assess possible mechanisms for the decline of the razor clam, with an intent to quantify the relationships involving survival, growth, and recruitment. Specific objectives for the study are as follows:

Chapter 2 - Estimate the monthly survival probabilities of razor clams at two beaches (i.e., Copalis and Long Beach) over an annual cycle. Relationships between survival and both population and individual covariates such as tidal height, size, and NIX intensity will be investigated.

Chapter 3 - Determine growth parameters of razor clams that are fully recruited to the fishery. Determine whether the effects of seasonal growth can be demonstrated and estimated.

Chapter 4 - Use length frequency and estimated population abundance estimates collected by WDFW to construct a stock-recruitment relationship. Determine how NIX and the water temperature may impact the stock-recruitment relationship.

Chapter 5 - Produce a discrete-time, stage-structured model of razor clam population dynamics that incorporates temporal and spatial components of survival, and empirically derived relationships between driving variables (environment, disease, and size) and population processes (growth, survival, and recruitment). Harvest strategies will be applied to the simulated population dynamics to generate alternative management scenarios. Results of these simulations will be used to quantify the risk of each harvest strategy.

It is hoped that through this exercise, the population dynamics of the razor clam can be better understood. Using the knowledge gained in this study, it is possible that effective utilization of the razor clam populations on the Washington beaches may be enhanced.

1.3 STRESS - LITERATURE REVIEW

The external physical environment often has dramatic effects upon mollusk physiology because of the close association between shellfish and their environment, and because molluscs are poikilothermic (Gabbott, P.A., 1976; Fisher *et al.*, 1987; Schoener, and Tufts, 1987; Allen and Turner, 1989; Thompson and MacDonald, 1991). One environmental force that could be of considerable importance is temperature (Orensanz *et al.*, 1991). Temperature can cause stresses that result in reduced growth or fecundity, and even death (Dickie and Medcof, 1963; Sayce and Tufts, 1971; Bayne *et al.*, 1985; Procarione, 1988). Razor clams could be particularly susceptible to alterations in their external environment because they lack a shell which closes completely, and their sole evasive tactic is limited to vertical migration in sand.

The association between environmental stress and disease in molluscs is also well documented (Thompson, 1983; Fischer *et al.*, 1987; Barber *et al.*, 1988 a&b). The paradigm of metabolic scope (Fry, 1947) states that there is a fixed energy budget, from which fixed costs due to standard metabolism are subtracted. When conditions deteriorate, more energy is allocated to maintenance, so less can be directed to growth and reproduction. Sub-lethal effects of stress which might alter population structure are reduced rates of growth, reduced fecundity, reduced egg viability, and reduced competitive ability (Bayne *et al.*, 1985). Warren and Davis (1967) subdivided metabolic requirements into:

1. Energy used for standard metabolism (i.e. the animal is at rest and digesting no food),
2. Energy used for the digestion of food, and
3. Energy used for routine activity (i.e. digging in the case of razor clams).

The amount of energy available to the organism after it has fulfilled its metabolic requirements is called its metabolic scope. Stresses that cause metabolism to increase cause the amount of energy available for other activities to decrease. Examples of stresses that can decrease the metabolic scope are non-optimal temperature regimes, movement, and disease. Under the metabolic scope model, an animal that is stressed will reduce its energy costs associated with reproduction and growth, until at some point, it reaches a negative balance. If the animal is forced to maintain a negative balance, it will die.

Many previous fisheries studies have explored the relationships between fisheries and the local environment (Gunter and Edwards, 1967; May, 1972; Peterson, 1973; Dow, 1977; Sutcliffe *et al.*, 1977; Lasker, 1978; Lasker 1982; Parrish, 1982; Peterson and Smith, 1982;; Garcia, 1983; Penn and Caputi, 1986). Previous large scale environmental perturbations, such as El Ninos, have had drastic effects upon bivalve condition indices (Schoener and Tufts, 1987), and have caused changes in the ecosystem composition

(Miller *et al.*, 1985). Although the environment surrounding the clams has many components that have been shown to cause stress (Bayne *et al.*, 1985), I will explore the importance of only temperature and the disease NIX.

This dissertation will investigate how the effects of the ambient water temperature and levels of the disease NIX may impact the processes that determine the dynamics of the razor clam. Specifically, this dissertation will investigate the impact of high summer temperatures on the survival, growth, and recruitment (i.e., to the one-year old juvenile stage) processes. Similarly, the impact of the disease NIX on the survival and recruitment processes will be quantified.

1.3.1 WATER TEMPERATURE

In poikilothermic animals, respiration will typically increase with increasing temperature. Over certain ranges of temperatures, many littoral invertebrates are capable of temperature acclimation. Thus, many physiological rates are maintained independent of temperature (Bayne *et al.*, 1985). Typically, however, the range of acclimation is not great. For example, the Baltic tellin (*Macoma balthica)* has optimal growth between 0-10 C, but does not grow at temperatures above 15 C (De Wilde, 1975). Likewise, laboratory studies of infected razor clams have shown death associated with temperatures above 16 C (Elston, pers comm.). Thus, although acclimation is evident within invertebrate populations, extremes in temperature can stress the organism. Previous studies have demonstrated that temperature-related stress can decrease survival and growth. Temperature-related stress is also implicated in decreased recruitment by either decreasing fecundity or by decreasing the survival and growth of the larvae.

In Chapter 2, I investigate whether an effect of water temperature on survival in the razor clam can be detected. Release-recapture methodology is used and seasonal survival probabilities are estimated. Previous work indicates that temperature mediated stress can affect survival directly or indirectly. Direct effects would consist of lethal temperatures (Fitch, 1950; Dickie and Medcof, 1963; Procarione, 1988). Indirect effects might include decreased resistance to disease, decreased food availability or increased predation (Anthony and Clark, 1982; Sissenwine, 1984). Fisher *et al.* (1987) demonstrated *in vitro* alterations in oyster resistance to disease caused by acute changes in temperature. These results supported similar *in vivo* experiments, also on oysters (Fisher and Tamplin, 1987).

In Chapter 3, I investigate the effect of temperature on growth in the razor clam. One of the most obvious measures of temperature-mediated growth is the occurrence of a seasonal cycle, which many bivalves demonstrate (Bayne *et al.* 1985). Although it could be argued that seasonality has more to do with food availability than increased stress, under the concept of metabolic scope, the primary metric is the magnitude of scope. For my purposes, I will not differentiate whether the magnitude of scope is reduced because of decreased food input or because of increased metabolism. The Baltic tellin is one shellfish which has demonstrated temperature-correlated growth (Beulema *et al.*, 1985; Harvey and Vincent, 1990). Oysters have also shown decreased growth and reproductive abilities in extreme high (> 32 C) and extreme low (< 6 C) temperatures (Allen and Turner, 1989). Finally, the fact that razor clams in Alaska can be aged using growth annuli (Nickerson, 1975) implies that temperature mediated growth occurs.

Finally, in Chapter 4 I investigate the relationship between temperature and recruitment. Most temperature-correlation studies have been concerned with the impacts of temperature on stock size. Oftentimes, the effect of temperature has been assumed to reflect alteration of recruitment potential. In fact, in some invertebrate fisheries, environmental factors, including temperature, appear to be the main controlling factor on recruitment, not stock size (Garcia and Le Reste, 1981; Bannister, 1986; Caddy, 1989). Temperature-mediated stress can reduce the condition of bivalves (Bayne *et al.*, 1985), which will leave less energy available to allocate for egg production. Bivalve examples of temperature-mediated decreases in fecundity include oysters (Allen and Turner, 1989) and mussels (Bayne, 1975; Bayne *et al.*, 1985; Barber *et al.*, 1988a). Again, as survival and recruitment are so closely linked, the effects of temperature may be direct (i.e. reduced fecundity) or indirect (e.g., mis-match of larvae and food source, increased predation) (Anthony and Clark, 1982). Bayne (1975) has also shown that even in the absence of decrease fecundity, when the adult stock is stressed, larval growth and survival are adversely affected.

1.3.2 NIX/DISEASE

NIX has the potential to influence all three processes (i.e., survival, growth, and recruitment) that will be modelled. As mentioned before, NIX is a bacteria which is found exclusively within the gill epithelium of razor clams. Virtually every individual clam along the Washington coast is infected, but at differing intensities. The dynamics of the NIX intensities throughout the year has appeared to be similar to the dynamics of MSX (*Haplosporidium (= Minchinia) nelsoni*), an oyster pathogen. MSX infections, like NIX infections, begin within the gill epithelium. Infection intensities increase in the late spring through early fall, then in late summer or fall, the infection breaks out of the gills, causing death and secondary infections (Ford, 1985). Disease effects in other bivalves have included reduced condition (Armstrong and Armstrong, 1974; Kent, 1979; Friedman *et al.*, 1989), reduced feeding (Newell, 1985), and reduced fecundity (Bayne *et al.*, 1985; Barber *et al.*, 1988a).

It is not currently possible to infect razor clams with NIX in the lab, nor is it possible to systematically vary the NIX intensity between individuals. Therefore, at this time, only observational and correlative studies are possible. In Chapter 2 I investigate whether the NIX Intensity of the individual or of the population can be correlated to survival. Mortality associated with disease and parasitism is well documented in shellfisheries. Thus, it is quite probable that the NIX bacterial pathogen will have a measurable effect on survival. In oysters, two of the most ubiquitous parasites that cause mortality are MSX (Ford, 1985) and *Dermocystidium (=Perkinsus) marinum* (Menzel and Hopkins, 1954; Hewett and Andrews, 1955; Mackin, 1962). It has been implied (Elston, 1984; Elston, 1986a) that the NIX pathogen was the causal agent in the decrease in razor clam numbers in 1983 and that NIX continues to cause significant mortality.

In Chapter 3, I investigate whether the NIX Intensity of the individual can be correlated to growth. Oysters infected with MSX show decreased feeding rates (Newell, 1985), and high NIX infection intensities restrict the effective diameter of gill epithelial channels. Thus, the potential exists for direct and indirect effects of NIX on growth. Infections by *Dermocystidium (=Perkinsus) marinum* and the trematode *Bucephalus cuclus*, when in high intensities, decreased growth (Menzel and Hopkins, 1954) of oysters. And, if one is willing to assume that the condition of a bivalve is closely related to its propensity for growth, then several studies have demonstrated that disease effects have the potential to decrease growth rates. Oysters infected by *Bonamia ostreae* were found to be in much poorer condition than uninfected oysters (Friedman *et al.*, 1989), and the blue mussel (*Mytilus edulis)*, when infected by the parasite *Polydora ciliata*, also displayed reduced condition (Kent, 1979).

Finally, in Chapter 4 I explore the relationship between NIX and recruitment. In MSX-infected oysters fecundity was significantly reduced (Barber *et al.*, 1988a). This result held even at sub-lethal levels of MSX. Elston (1986b) commented that the potentially lethal effects of rickettsiales-like infections, such as NIX, may not become apparent until the animal is under other stressful conditions. Hence, any noted effects on the clam population will probably be the result of a combination of factors. It has been suggested that both the prevalence and intensity of *Perkinsus marinus* in Gulf of Mexico oysters is strongly correlated to the El Nino Southern Oscillation (Gautheir *et al.*, 1990), and that death from contagious diseases is likely related to population density effects, as well as other factors (Sissenwine, 1984; Fogarty *et al.*, 1991). These examples make intuitive sense under the metabolic scope paradigm. Rickettsiales-like pathogens often infect the gill epithelial cells. Under light infection intensities, water flow through the gills is maintained and food is readily available. Thus the animal can survive and grow. However, under heavy infection intensities, water flow through the gills is reduced and access to food may be limited. These combined stresses can act to reduce the metabolic scope, and can even cause death.

1.4 ANTICIPATED BENEFITS

It is apparent from the literature that both the external environment and disease processes may affect the dynamics of shellfisheries. Prior to this dissertation, however, nothing was known about how the effects of temperature and the disease NIX impact the razor clam dynamics or subsequently how these external stressors may impact management of the stock. Although the razor clam is an important recreational fishery along the coast, very little quantitative work outside of this dissertation has been done on any aspect of this stock.

This dissertation provides a quantitative assessment of the current status of the razor clam population. In addition, this dissertation provides estimates of intra-annual adult survival, estimates of seasonal growth and estimates of the relationship between current adult density and subsequent recruitment. The impact of the disease NIX on survival and recruitment has investigated and quantified. Finally, this dissertation provides a spatial stage-structured simulation model of the razor clam population dynamics that was used to investigate the risk of different harvest strategies. These harvest strategies were applied to stocks responding to a normal environmental regime, as well as to stocks responding to environmental regimes that have been subjected to systematic changes (i.e., cooler or warmer than historical). These results should improve our understanding of how the razor clam has been and will be impacted by the actions of nature and the actions of man.

Chapter 2

Survival

2.1 INTRODUCTION

Populations of razor clams along Washington beaches have been on a steady decline over the past two decades (Ayres and Simons, 1988). However, in 1983, following an El Nino event, razor clam populations along the coast of Washington suffered tremendous declines. Subsequently, a previously unseen bacteria was discovered within the nuclear envelop of the gill tissue of the razor clam (Elston, 1986a). This bacteria has been classified a Rickettsia-like bacterium (*Nucleobacter siliqua*), and is designated NIX for Nuclear Inclusion Factor X (Ralph Elston, Pathologist of Battelle Pacific Northwest Labs- Sequim, WA, pers. comm). Since the discovery of NIX, Washington Department of Fish and Wildlife - Shellfish Division (WDFW) have hypothesized that this newly discovered bacterium was a contributing factor in the massive population declines. A pattern appeared to develop wherein each summer the intensity of NIX would increase and the clams would subsequently die (Ayres and Simons, 1992). In the winters the intensity of NIX fell (Ayres and Simons, 1992). At the beginning of this study (July 1990), there was no evidence of NIX in clams found north of Vancouver Island, Canada, and little infection in clams found south of the Columbia River. This distribution of NIX necessitated field work be confined to an area between these two borders of infection. The beaches at Copalis, Washington and Long Beach, Washington were chosen because of their historical NIX Intensities (i.e., high intensities at Copalis, lower intensities at Long Beach). New evidence indicates NIX is now infesting clams in Alaska (Dan Ayres, Shellfish Biologist of WDFW - Montesano, WA, pers. comm.).

To ascertain the effect of a disease process on a population, one can study changes in abundance or changes in survival. Changes in abundance estimates may be difficult to measure. Problems arise because the population is open to recruitment and mortality throughout much of the year and the variances of the abundance estimates are large. Changes in survival estimates should be easier to detect, for the population of interest will consist wholly of tagged individuals (Smith, 1991). This population of tagged clams is closed to immigration. Also, as adult razor clams do not experience horizontal movement along the beach, any clams that are tagged can only leave the study through mortality. Recent theoretical advances in release-recapture techniques now allow scientists to estimate how capture and survival probabilities might be related to concomitant factors, such as disease and environment (Smith, 1991; Smith *et al.*, 1994). For this study, the factors of interest that affected clams at the population level were beach location (i.e., whether Copalis, WA or Long Beach, WA), tidal height, and the biopsy procedure. The factors of interest that affected clams at the individual level were length and NIX Intensity (in counts per 40x microscope field).

Razor clams are an important recreational fishery along the Washington coast. Therefore, the endemic status of NIX and its effect on razor clam dynamics must be better understood. It is imperative that the exact effect NIX has on survival should be understood, so future management schemes might take this into account. The goal for this study was to better understand the decline of the razor clam, with an intent to quantify the relationships concerning survival. The specific objectives for the survival study were as follows:

1. Estimate the monthly survival and capture probabilities of razor clams on an annual cycle.

2. Compare survival probabilities of razor clams at the two beach locations.

3. Compare survival probabilities of razor clams across various beach tidal heights.

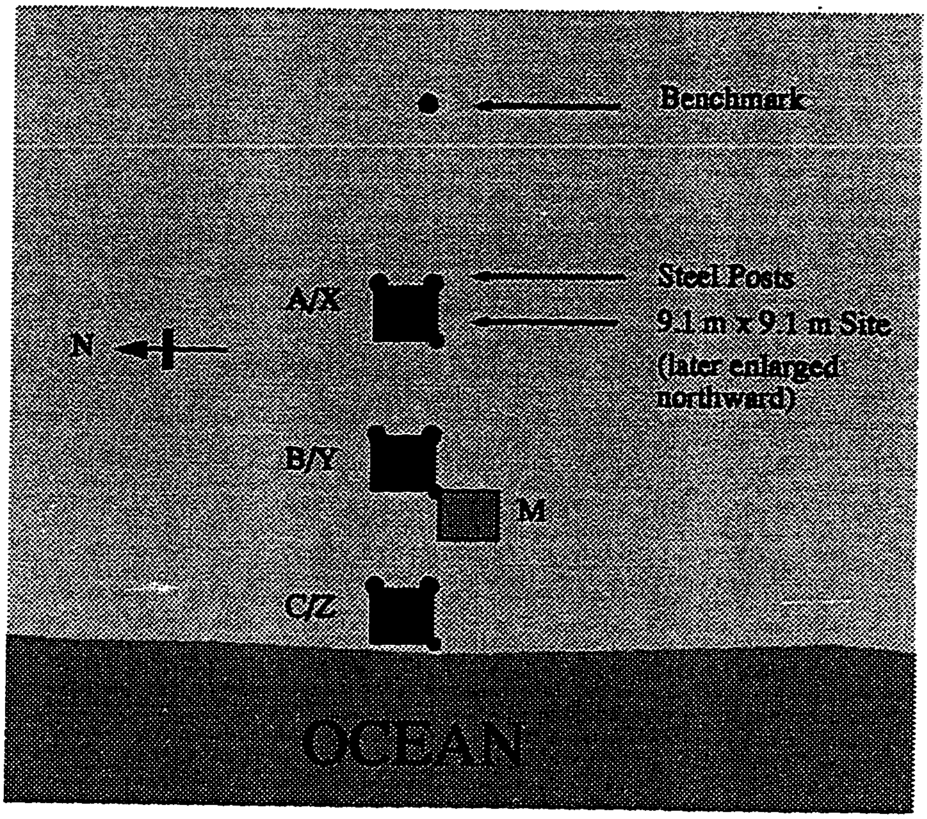
4. Determine the relationship between the size of razor clams and survival probabilities.

5. Determine the effects of NIX Intensity on razor clam survival probabilities.

2.2 STUDY SITES

Razor clams at two locations along the Washington coast were studied. The northern study site was at Copalis, Washington, in a razor clam reserve managed by the WDFW. The southern study area was at the northern end of Long Beach Peninsula, Washington; again in a razor clam reserve. Reserve areas are closed to harvest year-round. Three 9.1 m x 9.1 m plots were established at each site. As tagged clam densities inside the plots increased, the plots were expanded to 9.1 m x 18.3 m, then to 9.1 m x 27.4 m, and finally to 9.1 m x 45.5 m. Plots were expanded to keep clam densities within the plots within historical limits of published data (Ayres and Simons, 1991). Because razor clam densities vary according to tidal height, study plots were established at three different tidal heights (See Figure 2.1). Historical data from each beach (Dan Ayres, Shellfish Biologist of WDFW - Montesano, WA, pers. comm.) was used to determine at which tidal height each of the three plots would be placed. In general, clam densities have historically increased to a maximum density as one travels from the upper region of the beach to an intermediate region (i.e., going from area "A" to "B" or from "X" to "Y"), then decreased as one approaches the surf (i.e., going from area "B" to "C" or from "Y" to "Z"). The survey benchmarks, established behind the dunes by WDFW, marked the starting point for all measurements on the beaches.

(a)



(b)

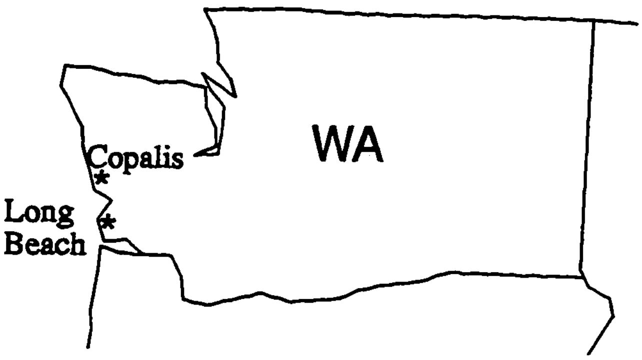


FIGURE 2.1 (a) Overhead view of a sample site. Note steel posts that mark the "top" of each of three 9.1 m x 9.1 m plots. At Copalis, Washington, the eastern-most site is designated "A", the next site would be "B", then "C" would be nearest the ocean. At Long Beach the sites were labelled "X", "Y", and "Z" respectively. Area "M" is at the southwest corner of the middle plot.

(b) Map of Washington indicating location of study sites.

At Copalis, Washington, the study plots were due west of the benchmark at 396 m from the benchmark (Area "A"), 457 m from the benchmark (Area "B"), and 488 m from the benchmark (Area "C"). At Long Beach, Washington, the study plots were due west of the benchmark at 335 m from the benchmark (Area "X"), 387 m from the benchmark (Area "Y"), and 408 m from the benchmark (Area "Z"). Although it would have been preferable to have sites "Y" and "Z" further apart, and "Z" further from the benchmark (i.e., approximately 500m from the benchmark), beach dynamics and beach availability above low water prohibited such a scheme. The boundary of each plot was marked with a row of steel posts that were spaced every 9.1 m.

At Copalis, during the second year, two additional study sites were established. One of the additional sites (i.e., Area "BS") was a 3 m x 3 m plot, just south of "B" plot. Area "BS" to established to investigate juvenile growth and survival. The other additional site (i.e., Area "M") was a 12.1 m x 12.1 m plot to the south and west of "B" plot. Area "M" was established to study growth (Chapter 3) and survival of newly recruited clams under reduced handling. The top boundary of Area "M" began at the southwestern most corner of "B" (Figure 2.1). The location of "M" was determined by two factors: (a) the site should be in an area of high survival in the absence of handling, and (b) the site should be comparable to other sites to determine handling mortality without undo assumptions. At the time when Area "M" was established, Area "B" had the highest survival probability. Therefore, Area "M" was located adjacent to Area "B".

2.3 METHODS

This section describes the marking (Section 2.3.1), tissue biopsy (Section 2.3.2), sampling methodology (Sections 2.3.3-2.3.5) and the statistical protocols (Sections 2.3.6 and 2.3.7) that were utilized in the analysis of data within this chapter. Multiple-release multiple-recapture techniques were used herein to quantify adult survival on a monthly basis and relate changes in survival to variables measured at the individual and group level. Juvenile survival was estimated using abundance data collected by WDFW.

2.3.1 MARKING

Unmarked clams were marked on one side of their shells using a Dremel® with an aluminum oxide grinding stone bit. The thin layer of periostracum was slit and the shell below was exposed. Each clam was assigned a unique number code, followed by a letter to indicate the plot, and then followed by either a space or a "C" to indicate either "biopsied" or "control" respectively. For example, the code "156AC", denotes "a control clam, number 156 in Area A." The length of the shell (along the longest axis) and the width of the shell (at the hinge) were measured and recorded for each marked clam.

2.3.2 TISSUE BIOPSY

Thirty-five of the previously unmarked clams were biopsied each month before they were released into the plots. A small section (i.e., approximately 3mm x 3mm) of gill tissue was removed from each clam using forceps. The tissue sample was secured in a labelled Tissue-Tek® III Biopsy Cassette (Miles Scientific, Part Number 4172 or 4174), and placed in Davidson's Solution for Shellfish (Shaw and Battle, 1957) for at least three days. Afterwards, gill tissue samples were placed in 70% ethanol for long-term storage. Slides were prepared and stained using the protocol of Elston *et al.* (1982).

Clams that had been biopsied on previous sampling occasions were not biopsied for at least 1 month. This precaution was instituted in hopes that it would allow a biopsied clam to recover from the stress of the biopsy, and thus diminish any biopsy-induced mortality.

2.3.3 SAMPLING AREAS "A", "B", "C", "X", "Y", AND "Z"

Sites "A-C" and "X-Z" were used to quantify the adult survival probabilities. Each site was sampled two successive days each month during the lowest tides. On the first day of each sample period, all plots were sampled for marked clams. Then, because time constraints did not allow for all three plots to be completed during one tidal sequence, clams from outside of the plots were marked, biopsied and released within only the uppermost plot (i.e., Area "A" at Copalis or Area "X" at Long Beach) during the first day. During the second day of sampling, clams at the two lower plots were resampled and newly marked clams were released. The uppermost plot was not resampled during the second day to eliminate the potential of killing newly-released individuals. Clams were located by minor spatial disturbances of the sand above them. Three such disturbance patterns were:

1. Keyhole - There are two holes in the sand surface that resemble a keyhole.

2. Depression - There is a minor depression in the sand, but no hole(s).

3. Doughnut - There is a slight circular mound with a minor depression in the center.

These three patterns indicate a clam is present below the surface. These disturbances are also called "shows." Once a "show" was noticed, the area was carefully dug using a shovel to recapture the clam. If the clam was accidentally broken during digging, or if excessive gill tissue was removed during the biopsy procedure, measurements were taken when possible (length, width and possibly NIX), but the clam was discarded and the mortality was recorded.

All "shows" within the plots were dug and the clams collected. The clams were separated into 2 groups on the basis of those that had been captured previously (marked) and those that had not been captured previously (unmarked). Those clams that had been captured previously were then further divided into three groups. The three groups were: (a) those clams that were biopsy-controls, (b) biopsied clams that had been biopsied on the previous sampling occasion, and (c) biopsied clams that had not been biopsied on the previous sampling occasion. The clams in the latter group (i.e., group "c") were re-biopsied before being released.

Unmarked clams were obtained from inside the plot and from areas adjacent to the plots. These unmarked clams were collected for marking and released. In the first year, we released a total of 70 clams from outside the plots within each plot during each sample period. In the second year, in an effort to increase precision, the release size was increased to 85 clams. Thirty-five of these 85 clams were biopsied (Section 2.3.2) to estimate the NIX Intensity. The remaining fifty were denoted controls. During some of the winter months (December 1990 - March 1991 and December 1991 - April 1992), due to weather conditions, I was unable to capture enough clams to fulfill my sampling requirements. During these months, variable numbers of newly-marked clams were released.

All marked clams (i.e., biopsies and controls) were released, unless they had been damaged during the digging or biopsy process. Newly-marked clams were released in each plot each sampling period (35 biopsied: remaining controls) along with any previously-marked clams recovered from within the plots during that sampling period. Holes, approximately two feet in depth, were dug in the sand and a clam secured within, with the hinge of the clam shell towards the ocean. The holes were then filled with sand. Damaged clams were not released and were taken from the sample area. Occasionally, clams were lost to seagull predation. When possible, the coded shell was recovered and the clam was either replaced (i.e., if it was a new release) or recorded as dead. The numbers of marked and unmarked clams dug from each plot were recorded each month.

Sites "A-C" and "X-Z" were sampled each month for two successive days during the lowest tides of the month from July 1990 - January 1992. In January 1992, sampling was discontinued at the Long Beach site due to insufficient funds, but the Copalis site was sampled each month through November 1992. The final sampling effort for Long Beach took place in July 1992, while the final sampling efforts at Copalis took place during March and April 1993. Unfortunately, due to weather complications, it was infeasible to complete a full sampling regime during some months (Table 2.1). Months with major difficulties included (a) December 1990 when Areas "A", 'B", 'C", and "X" were not sampled, (b) March 1991 when Areas "A", 'B", and "C" were not sampled, (c) a stretch from the beginning of March 1991 to April 1991, when tides were too high to permit sampling in any of the areas, (d) July 1991 - December 1991 when Area "Z" was unavailable, (e) December 1991 - April 1992 when Area "C" was unavailable, and (f) May 1992 when Area "B" was unavailable. Some areas were not sampled for several months due to insufficient drainage of the plots to permit recapture (See Appendix A for time between adjacent recaptures).

2.3.4 SAMPLING AREA "BS"

Unlike the studies in areas "A-C" and "X-Z", which focused on the survival of clams greater than 10cm in length, Area "BS" was established to estimate survival probabilities for smaller clams between 10-40 mm. Area "BS" (i.e., a 3 m x 3 m plot) was established south of Area "B". Newly set clams (15-40 mm) were captured using a screening tray. All undamaged clams were batch-marked using the technique discussed in Section 2.3.1 and measured. The site was flooded and the small clams were carefully introduced into the area. Any clams that did not dig into the sand under their own power were removed from the site. The site was drained and the area was guarded until the incoming tide covered the plot.

Area "BS" was sampled in subsequent months using three distinct techniques: shovels, a screening cart, and a high pressure water hose. A shovel was used to dig large "shows" as described in the field sampling section for Areas "A-C" and "X-Z". However, as the clams that had been marked were substantially smaller than those typically detected using "shows" (i.e., 10-40 mm versus >100mm respectively), two other techniques were

Table 2.1: Dates for releases and recaptures of clams at areas "A-C" and "X-Z". Dark-shaded cells indicate periods when clams were released. Light-shaded cells indicate periods when clams were recaptured. Open cells indicate an absence of a release or recapture respectively, typically related to inclement weather or high surf.

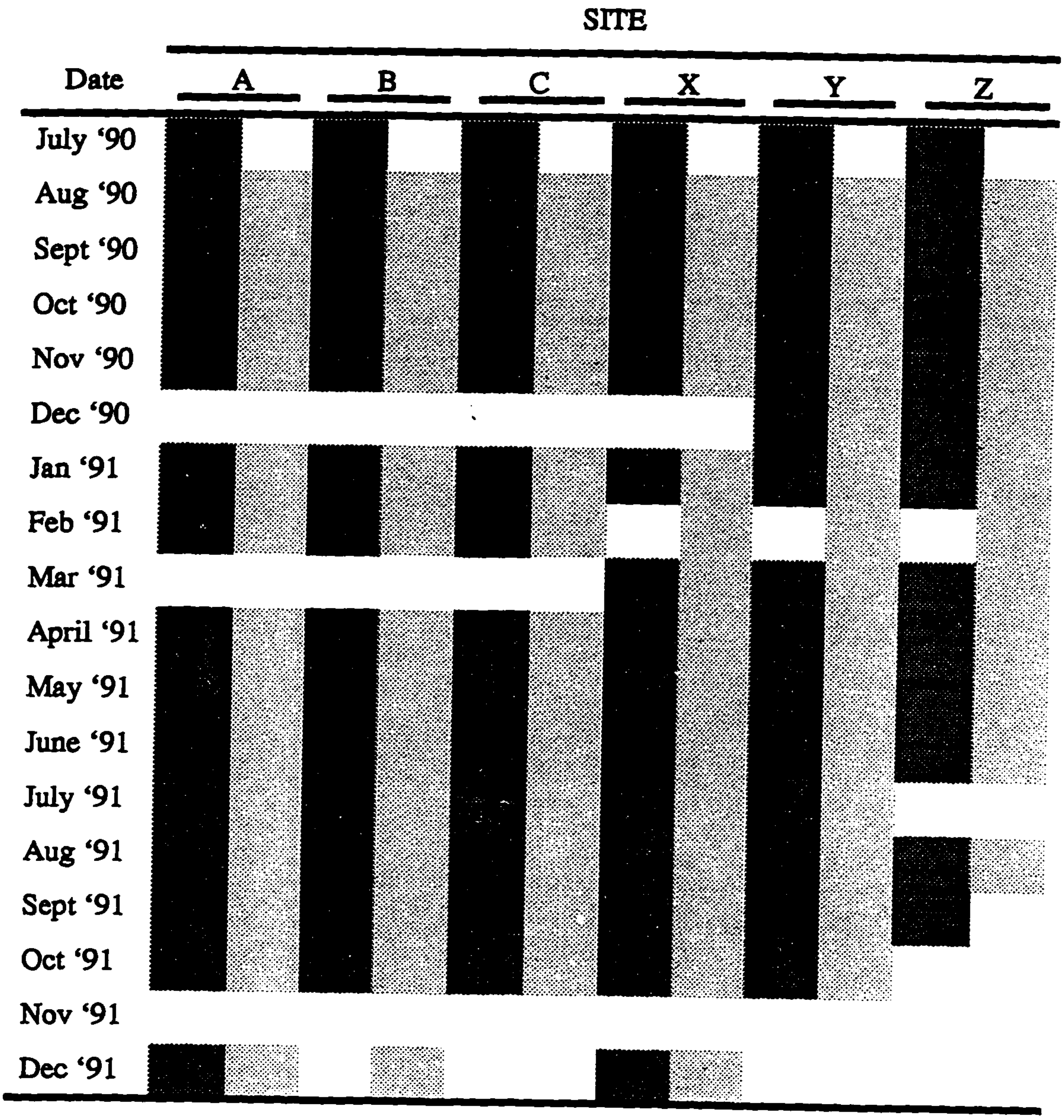
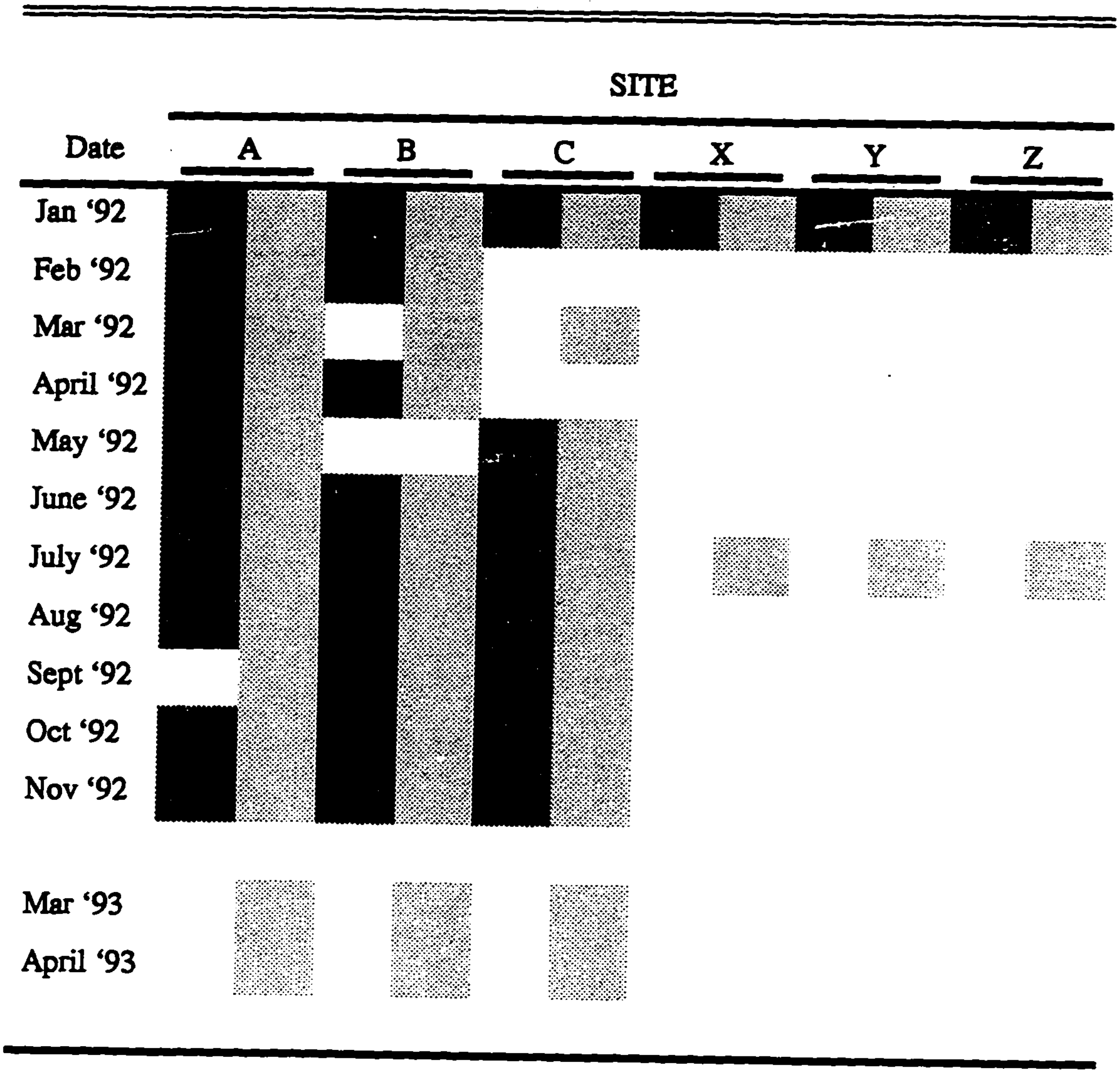


TABLE 2.1: (cont.)



utilized. These alternative techniques should have a higher capture rate for smaller clams, as they do not require searching for shows.

The screening cart is one technique used by WDFW to sample for small (10-80 mm) clams. All sand was removed from Area "BS", to a depth of 45 cm. This sand was placed in an open-topped box that had a mesh screen as its bottom. The mesh would retain any item greater than 1-2 mm. Water was poured over the sand; the sand and very small organisms were washed through the screen. Larger organisms and shells were retained. Any clams that were found were checked for a mark, measured and recorded.

The high-pressure water hose was used to sample for clams greater than 50 mm that did not display detectable "shows". A high-pressure water hose was inserted up to four feet into the sand. The water liquefied the sand and the clams floated to the surface. Clams were collected in a basket as they floated on top of the liquefied sand. Any clams that were found were checked for a mark, measured and recorded.

The three separate techniques were used at this plot because clams in this plot were much smaller than at other plots. It was feared that reliance upon one sampling technique could strongly bias the results.

2.3.5 SAMPLING AREA "M"

Area "M" was established in March 1992, and resampled in July and August 1992, and March and May 1993. In March 1992, 443 clams were marked, measured, and released into Area "M". In July 1992, clams from the area were recaptured using a shovel. These clams were measured and released. Seventy new clams were also marked and released at this time. All marking and handling procedures were the same as used in plots "A-C" and "X-Z". In August 1992, the high-pressure water-hose method was utilized for recapturing clams in Area "M" (Szarzi, 1991), but due to time, only a fraction of the total plot was sampled. The high-pressure water hose was inserted up to four feet into the sand, regardless of whether "shows" were present. The water liquefied the sand, and the clams floated to the surface. All clams recaptured in this method appeared highly stressed, as evidenced by an inability to withdraw the siphon when touched. Therefore, none of the clams extracted using the high-pressure water-hose technique were released.

In March 1993, the area was again sampled. This time, shovels were used to recapture the clams. All clams that were recaptured were measured and released. Finally, in May 1993, the entire area was sampled a final time using shovels first, followed by the high-pressure hose.

Area "M" was resampled three times in 1992 and twice in 1993. As noted before, during the final resampling periods of 1992 and 1993, a different method (i.e., a high-pressure hose) was used to extract the clams. In August 1992, only one-quarter of the entire area was sampled the final time due to technical and time related problems. The entire area was sampled using shovels in March 1993, and the entire area was pumped in May 1993.

2.3.6 STATISTICAL ANALYSES USING RELEASE-RECAPTURE DATA - ESTIMATION OF ADULT SURVIVAL

Release-recapture models have been used to study survival probabilities of various fauna. All release-recapture models have a similar formulation that states that the probability of sighting an animal in any period is a function of a capture probability and a survival probability (Cormack, 1964; Seber, 1982; White *et al.*, 1982; Burnham *et al.*, 1987). The purpose of the statistical analysis was to separately estimate the survival and capture probabilities for each sampling period and to relate changes in survival and capture to concomitant variables. The theory of proportional hazards was used to explore and explain these relationships (Smith, 1991).

The effects that the independent variables have on survival are being modelled using the SURPH (SURvival under Proportional Hazards) model (Smith, 1991; Hoffmann, 1993). SURPH (Smith *et al.*, 1994) utilizes a maximum likelihood approach for parameter estimation under a proportional hazards formulation to assess risk associated with independent covariates. Using SURPH, per-period estimates of capture and survival were calculated. Next, SURPH provided a framework to model capture and survival probabilities as functions of independent covariates measured at the group and individual level. The formulation of the effects on survival are modelled as:

$$S(\underset{\sim}{x}) = S^{exp(\underset{\sim}{x}'\underset{\sim}{\beta})} \quad \text{(EQ 2.1)}$$

where S is the baseline survival probability, the $\underset{\sim}{x}'$ are the levels of the covariate(s), and the $\underset{\sim}{\beta}$ are the slope terms.

Data were collected monthly using a multiple-release multiple-recapture protocol. I modelled the capture and survival probabilities of razor clam populations from the three plots at the two beaches using SURPH.1. Copalis was sampled monthly from July 1990 - November 1992, then again in March and April 1993 (Table 2.1). Long Beach was sampled monthly from July 1990 - January 1992, and again in July 1993. Population-wide covariates were modeled first to ascertain beach, monthly, intertidal location, and biopsy effects on razor clam survival. Then, using a fully-parameterized Cormack (1964)/Jolly (1965)-Seber (1965) model, individual-covariates were included to ascertain length and NIX effects on survival (Hoffmann, 1993). Data from the first month (July 1990) was deleted because the analysis indicated high mortality of biopsied clams. I feared this mortality was a direct result of inexperience on our part, and not a true indication of a mortality event.

The monthly survival was estimated rather than the traditional annual survival. The estimation of a monthly time-scale has several advantages. First, a greater understanding of the pattern of mortality can be gained when monthly survival probabilities are computed. NIX Intensities vary throughout the year, and because the effects of NIX are thought to be concentrated in summer months, it becomes imperative that the time scale for detection of effects be approximately monthly. Second, monthly survival probabilities can always be combined to give bimonthly, seasonal, or even annual survival probabilities. For example, the annual survival probability is simply the product of the monthly survival probabilities as follows:

$$\hat{S}_{\text{Annual}} = \prod_{i=1}^{12} \hat{S}_{\text{month}_i}. \qquad \text{(EQ 2.2)}$$

Third, any model that analyses release-recapture data will be unable to estimate survival probabilities in the final sampling period. Thus, under a sampling plan that estimates monthly survival probabilities, only survival in the last month is not estimable. Under an annual sampling scheme, the survival for the entire final year is not estimable. This would mean that with two years of field work, twenty-three monthly mortality probabilities will be estimable with a monthly sampling scheme, whereas only 1 annual estimate would be available from an annual sampling scheme.

The use of three intertidal locations, rather than one site at each beach, has similar benefits to the use of monthly survival probabilities as opposed to annual survival probabilities. Not only is greater accuracy achieved by stratifying the beach, but within-beach variation can also be investigated. If all beach levels have similar survival probabilities, the data can be pooled for greater precision. Additionally, during any one month, the beach dynamics may prohibit sampling from one or more areas of the beach. By having multiple sites, it is more likely that some data can be collected for each month.

Monthly survival and capture probabilities were estimated using SURPH (Smith, 1991). Although the recapture study was implemented for 30 periods, that data were analyzed in sequential subsets. There were two reasons for doing the analysis piece-wise. The first reason was that with 30 recapture periods, there are 2^{30} capture histories possible. As many of these capture histories will have few or no observations, there may be problems associated with the asymptotic assumptions that are utilized for testing hypotheses. The second reason was more pragmatic; the current version of SURPH can not handle data sets that span more than 9 periods. Instead, a series of data sets were constructed that jointly spanned the 30 sampling periods and the three areas within a beach. In many instances, data sets overlapped temporally and spatially. In this way, survival and capture estimates that were based on different portions of the data were available for comparison.

When more than one data set provided an estimate of the survival (or capture) probability at an area, the reported survival (or capture) probability was calculated as

$$\hat{Y}_{jk} = \frac{\sum_{i=1}^{n} w_{ijk}\hat{Y}_{ijk}}{\sum_{i=1}^{n} w_{ijk}} \qquad \text{(EQ 2.3)}$$

where

$\hat{Y}_{jk}$ = Weighted survival (or capture) estimate for area "j" in period "k"

$\hat{Y}_{ijk}$ = Unweighted survival (or capture) estimate from data set "i" for area "j" in period "k", and

w_{ijk} = Weight for the survival (or capture) from data set "i" for area "j" in period "k" = $\frac{1}{\left(\hat{var}\left(\hat{Y}_{ijk}\right)\right)}$.

Weighted estimates were computed because the different data sets and the different estimates varied in their level of precision. Both the SURPH estimates of survival/capture and the standard MLEs from the Cormack/Jolly Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965) were included in the estimation of the weighted survival/capture estimate. The weights that were assigned were inversely proportional to the estimated variance of the estimate. The variance of each weighted estimate was calculated analogously to the variance of a stratified sample (Hansen, Hurwitz and Madow, 1953; p. 182).

Due to the nature of tag-release data, survival and capture probabilities are highly correlated. The basic philosophy of the modelling procedure is to account for as much of the variability as possible in the capture probability parameters, before modelling survival probabilities. There are two approaches to modelling capture probabilities, termed conditionally-independent capture modeling and joint capture modeling (Smith, 1991).

For conditionally-independent capture modeling, capture probabilities are modeled using capture histories for clams known to be alive for multiple periods. The capture probabilities are computed using a Manly-Parr (1968) estimator. The Manly-Parr estimator of the capture probability in the i^{th} period is calculated as

$$\hat{p}_i = \frac{r_i}{r_i + z_i} \qquad \text{(EQ 2.4)}$$

where:

r_i = Animals seen in the i^{th} occasion that were also seen before and after the i^{th} occasion.

z_i = Animals not seen on the i^{th} occasion that were seen before and after the i^{th} occasion.

For example, if one was calculating the Manly-Parr capture probability in Period 2, the data would consist of animals that were recaptured in period 2 and sometime later (i.e., r_i), and those that were not recaptured in period 2, but were recaptured sometime later (i.e., z_i).

The alternative approach to conditionally-independent capture modeling is joint capture modeling. In this mode, capture and survival are modelled concurrently. The survival model may be altered, as well as the capture model. However, for the joint-analyses done herein, the capture model was found first while using a fully parameterized survival model. The survival model was then investigated, after specifying the capture model from the first stage of the analysis. Smith and Skalski (1993) have found that the power to model the capture probabilities is decreased only slightly by over-parameterization of the survival model. The joint-modeling approach was used for the analyses throughout this chapter.

In addition to modeling at the population-covariate level, it is also possible to model the capture probabilities as functions of the individual covariates. NIX Intensity and length were examined to ascertain if either or both affected the capture probability.

Once the capture model had been determined, the survival probabilities were modelled as functions of beach, month, intertidal location, and biopsy effects. An Analysis of Deviance (Smith, 1991) was used to ascertain significant differences among the variables. In using SURPH, a series of models were fit in a stepwise, forward selection manner. This technique allowed for determination of significant factors affecting survival during each time period. The final model that was fit included all factors deemed significant at $\alpha = 0.10$. Capture data from the release-recapture study are included in Appendix C.

Using SURPH, it was possible to use the data from clams knowingly removed from the population. Thus, estimates of survival and capture probabilities include data from clams that are known to have died during handling (i.e., right-censored data).

2.3.6.1 Estimation of survival probabilities at various intertidal locations

For the first 15 periods (i.e., August 1990 - October 1991), Areas "A", "B", and "C" at Copalis were analyzed simultaneously. However, after the 15th period, there were months when Area "B" or Area "C" could not be sampled due to insufficient drainage. When problems of this sort arose, data sets were constructed that combined areas of similar availability, while removing areas that were unavailable for sampling.

At Long Beach, for the first 11 periods (i.e., August 1990 - June 1991), Areas "X", "Y", and "Z" were analyzed simultaneously. However, after the 11th period, Area "Z" was unavailable too often to be included in a joint analysis, and so was analyzed separately from Areas "X" and "Y".

Survival estimates were standardized to a 30-day interval. If the survival probabilities were not standardized, periods with longer intervals between sampling would appear to have lower survival, even when survival probability through time was constant. For instance, suppose period "N" had 30 days between successive sampling periods and period "M" had 60 days between successive sampling periods. Even if survival was the same for both periods "N" and "M", say 0.90 over a 30-day period, the estimated survival over the interval M would be less than that for period N (i.e., 0.90^2 = 0.81 versus 0.90 for periods "M" and "N" respectively). Daily survivals were estimated as

$$\hat{S}_{jkm} = \hat{S}_{jk}^{\;1/n_{jk}} \qquad \text{(EQ 2.5)}$$

where

$\hat{S}_{jkm}$ = Daily survival estimate for day "m" in area "j" for period "k",

$\hat{S}_{jk}$ = Survival estimate in area "j" for period "k", and

n_{jk} = number of days in area "j" for period "k".

The daily survivals were ordered by date. Standardized survivals were then calculated by grouping the daily survivals into standard 30-day periods according to the formula

$$\hat{S}_{\text{Standard}_{jk}} = \prod_{m = 30(k-1)+1}^{30k} \hat{S}_{j \cdot m} \qquad \text{(EQ 2.6)}$$

where

$\hat{S}_{\text{Standard}_{jk}}$ = Standardized 30-day survival estimate for area “j” in period “k”, and

$\hat{S}_{j \cdot m}$ = Daily survival estimate for day “m” in area “j” for all periods.

The variances of the standardized estimates were calculated using the delta method for variance estimation (Seber, 1982). Standard errors of the estimates (se) are calculated as the square root of the variance.

Reporting the relative risk is an alternative to reporting the survival probability (Smith, 1991). Relative risk is a measure of how much more likely it is for an animal with covariate vector $\underset{\sim}{x}_1$ to have died in the interval than for an animal with covariate $\underset{\sim}{x}_2$ (Hosmer and Lemeshow, 1989; Smith, 1991). Relative risk under the hazard link is computed as

$$RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{\lambda_o e^{\underset{\sim}{x}'_1 \underset{\sim}{\beta}}}{\lambda_o e^{\underset{\sim}{x}'_2 \underset{\sim}{\beta}}} = e^{(\underset{\sim}{x}'_1 - \underset{\sim}{x}'_2)\underset{\sim}{\beta}} \qquad \text{(EQ 2.7)}$$

where

$RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2)$ = Relative Risk between animals with covariate vectors $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$,

λ_o = baseline hazard, and

$\underset{\sim}{\beta}$ = vector of regression parameters.

The relative risk is useful because it is a measure that is independent of the baseline survival, as can be seen in equation 2.6.

2.3.6.2 Estimation of survival probabilities at Copalis and Long Beach

Copalis and Long Beach were analyzed separately because there was no release data for several months at Copalis during the first year, and there was no release data at Long Beach after January 1992. The data from Copalis were incomplete because weather-related problems did not allow sampling of the beach every month. The data set for Long Beach ended in January 1992 because of insufficient funds. These gaps in the data resulted in fewer estimates of monthly survival probabilities for Copalis (Note bi-monthly rate for Dec-Jan and no estimate for March) in the first year, and much fewer estimates of monthly survival probabilities for Long Beach during the second year. Long Beach was not sampled after January 1992, whereas Copalis was sampled monthly until November 1992, and was sampled again in March and April 1993.

2.3.6.3 Assessment of Handling Mortality

Area "M" was used to investigate handling mortality. Whereas clams in the other plots were sampled monthly, clams in Area "M" were released, then not sampled for at least four months (Clams were released in March 1992, with recaptures attempted in July 1992, August 1992, March 1993 and May 1993). The survival analysis for Area "M" was conducted in the same manner as for Areas "A", "B", "C", "X", "Y", and "Z". The survival probability for Area "M" was then compared to the survival probability for Area "B" for the same period. Area "B" was chosen for the comparison because both "B" and "M" were located at Copalis, at approximately the same tidal height.

2.3.6.4 Assessment of Length Effects

The effect that length had on survival and capture were examined. In razor clams, length can be used as a surrogate for age. As such, relating length to survival will indicate how survival changes with age. In addition, as larger clams often make larger "shows", it is likely that sampling may be biased towards detection of the larger/older clams. Thus, it will be important to adjust for this bias in capture prior to estimating the survival.

Two techniques were used to assess the effect that the length of the clam had on survival. One technique that was used to estimate the effects of length was to compare the empirical cumulative distribution (i.e., cdf) of clams that had been recaptured to the distribution of clams that had not been recaptured. A Kolmogorov-Smirnov test (Zar, 1984) was used to tested whether the two cdf's were identical.

The problem with any analysis that solely uses the cdf's of recaptured and non-recaptured clams is that the cdf's fail to differentiate between the survival and capture processes. SURPH analysis provided an alternative means to measure the effect of length on capture and survival separately. Data sets were prepared that included recapture data for all calms released during the summers of 1990-1992. Capture models were fit using the joint-modeling option in SURPH.

Individual covariate effects were assessed following the modeling of all population effects (Hoffmann, 1993). SURPH was used to explore the effect of length on both the capture and survival processes. During the modeling, the effect that length had on the capture and/or survival process was allowed to vary across the different study sites and through time. A series of models were fit that modelled capture and survival as functions of length. Capture effects were modeled first (Smith *et al.*, 1994). Survival effects were modeled after significant capture effects had been included in the model. Model significance was assessed using a likelihood ratio test (LRT) among nested models. For non-nested models, Akaike's Information Criterion (AIC; Akaike, 1973) was used to determine the most parsimonious model.

2.3.6.5 Assessment of NIX Individual Level Effects

The effect of NIX on survival was assessed using the same statistical techniques that had been used to assess the effect of length on survival. Cdf's and SURPH modeling were utilized in an effort to determine the effect of NIX on survival. The NIX Intensity (Elston, 1984) for individual clams was measured for the summer-fall periods of 1990, 1991, and 1992. Because summer-fall months tended to show decreased survival (Section 2.4.3), these months were chosen for NIX analysis because if an effect existed, it would most likely appear during these times.

NIX effects are not orthogonal for this dataset. Thus, order of entry of a parameter may affect the significance of that effect. Models were fit using two techniques. For one technique, all of the period-specific effects were entered into the model simultaneously. Thus, if there were three periods in which NIX could affect survival, all three parameters were added to a single model and the model was estimated. For the second technique, a single period-specific effect was added to the model. Using this technique, if there were three periods in which NIX could affect survival, a single parameter would be added to each of three models and the models estimated. The significance and the direction of the effect were assessed for each period under each technique.

2.3.6.6 Assessment of NIX Population Level Effects

Even with high variability in the individual measures, it is possible to get a reasonable estimate of the average NIX Intensity for the population. The data used were the NIX Intensities that had been collected as part of this study during the summers of 1990, 1991, and 1992. The median value of NIX was computed at each beach during the summer months for which there was data. A multiple regression was used to test whether there was a decreasing linear relationship between the median NIX and the survival probabilities.

2.3.7 STATISTICAL ANALYSES USING POPULATION DATA - ESTIMATION OF JUVENILE SURVIVAL

Juvenile clams proved difficult to collect, but quantification of their survival probabilities is essential if a stage-structured population dynamics model is utilized. Following the complete failure of Area "BS" to provide any useful information on juvenile survival, alternative methods for estimating juvenile survival were used. All of the following methods relied upon the abundance data that are available from WDFW to estimate juvenile survival. Combining the abundance data with some modelling assumptions allowed the juvenile survival probabilities to be estimated. Abundance data of juveniles and adults through time were available from WDFW for two beaches (i.e., Mocrocks and Twin Harbors) besides Copalis and Long Beach. Mocrocks is located north of Copalis, whereas Twin Harbors is located between Copalis and Long Beach, south of Grays Harbor, WA.

2.3.7.1 Using an Exponential Decay Model

When survival is constant, the distribution of a year-class through time can be described using the exponential distribution (Aitkin *et al.*, 1989; pp. 256-258). This distribution is commonly used in fisheries modelling (Gulland, 1983) in the form

$$N_{yr,t} = N_{yr,0}e^{-Zt}, \qquad \text{(EQ 2.8)}$$

where:

$N_{yr,t}$ = the number of organisms observed at time "t" from year-class "yr",

$N_{yr,0}$ = the number of organisms observed at the initial time "0" from year-class "yr", and

Z = the instantaneous mortality rate.

From this equation, it is apparent that e^{-Z} is the annual survival probability.

The mean life expectancy is the expected value of the distribution (Seber, 1982; pp. 3-4), in this case the exponential distribution. The mean life expectancy for the exponential distribution can be calculated as

$$E(T) = \int_0^{\infty} Zte^{-Zt}dt$$
$$= 1/Z$$

Using the expected value of the exponential and assuming a life-span (i.e., $E(T)$), it is possible to estimate the instantaneous mortality by solving for "Z" in the above equation. Thus, if we assume that the exponential decay accurately describes the decline of a year-class of clams through time, then given a life-span, it will be possible to estimate an annual survival probability as

$$\hat{S} = e^{-Z} = e^{-(1/E(T))} \quad \text{(EQ 2.9)}$$

2.3.7.2 Using a Stock-Recruit Model

An alternative way to estimate the survival is to model the total observable density as

$$D_t = A_t + R_t, \quad \text{(EQ 2.10)}$$

where

D_t = the total observable density at time "t",

A_t = the observable density of adults at time "t", and

R_t = the recruitment at time "t".

In razor clams, it appears that there is a one-year lag between the time they are spawned and the time they appear as recruits (1+ year-olds) within the sample (See Chapter 4). The change in density can be estimated as

$$\begin{aligned}\Delta D_{t+1} &= D_{t+1} - D_t = (A_{t+1} + R_{t+1}) - (A_t + R_t) \\ &= (A_{t+1} + f_{SR}(A_t)) - (A_t + f_{SR}(A_{t-1}))\end{aligned}$$

where the number of recruits is estimated by $f_{SR}(A_t)$, the stock-recruitment relationship.

If it is further assumed that the majority of the adults do not survive after spawning, then the adults that are observed in the next time period are those juveniles that survived from this time to the next. Using this assumption, and the above equations yields

$$\begin{aligned}\Delta D_{t+1} &= (A_{t+1} + f_{SR}(A_t)) - (A_t + f_{SR}(A_{t-1})) \\ &= (S(R_t) + f_{SR}(A_t)) - (A_t + f_{SR}(A_{t-1})) \\ &= (S(f_{SR}(A_{t-1})) + f_{SR}(A_t)) - (A_t + f_{SR}(A_{t-1})) \\ &= f_{SR}(A_{t-1}) \cdot (S-1) + f_{SR}(A_t) - A_t\end{aligned}$$

where S is the estimated survival of the juvenile stage to the adult stage.

Finally, under the assumption that A_t can be measured without error, and that $f_{SR}(A_{t-1})$ and $f_{SR}(A_t)$ can be estimated, again without error, an equation that estimates the survival from the population data is derived. The straight line equation through the origin, with slope = $\hat{S}$ can be written as

$$Y = SX$$

where

$Y = \Delta D_{t+1} + A_t + f_{SR}(A_{t-1}) - f_{SR}(A_t)$, and

$X = f_{SR}(A_{t-1})$.

The current population data collected by WDFW will not allow estimation of 0-1 year old juveniles because no 0-year old clams are evident from the length frequency data. The current data will allow estimation of juvenile survival between ages 1 to 2, the juvenile stage to the adult stage.

2.4 RESULTS

Except for those months noted in Table 2.1, during the first year (i.e., July 1990 - July 1991), 35 biopsied and 35 control clams were released at each plot on each beach, each month; during the second and third years, 35 biopsied and 50 control clams were released at each plot on each beach, each month. A total of 3470 clams were placed within the plots during first ten months of the study (August 1990 - May 1991), half of which were biopsied at least once. In the second year (June 1991 - July 1992), an additional 3527 clams were released and in the third year (August 1992 - April 1993) an additional 1602 clams were released. Of 5314 clams that were marked, measured, and released at Copalis, 221 (4.2%) were damaged during a subsequent recapture attempt (Table 2.2). Of 3280 clams that were marked, measured, and released at Long Beach, 157 (4.8%) were damaged during a subsequent recapture attempt. A clam could become damaged during the recapture process or during the biopsy process.

2.4.1 MONTHLY ADULT SURVIVAL ESTIMATES

Monthly survival probabilities were estimated using SURPH.1 (Smith *et al.*, 1994) on a beach by tidal height basis. The estimated survival probabilities were then standardized to a 30-day survival (Section 2.3.6.1) to facilitate the comparison of survival across all months.

Table 2.2: A summary of clam release and recapture statistics for Copalis and Long Beach. Total number killed includes clams killed during the recapture process and clams killed during the biopsy process.

Action	Copalis	Long Beach
Control Clams		
Total Number Released	4258	2547
Total Number Recaptured	2010	1239
Percentage Recaptured	47%	49%
Biopsied Clams		
Total Number Released	1056	733
Total Number Recaptured	441	273
Percentage Recaptured	42%	37%
Control and Biopsied Clams		
Total Number Known Killed by Handling	221	157
Percentage Handling Mortality	4.2%	4.8%

Monthly survival probabilities varied throughout the years (Appendix A). However, it became apparent that when the survival probabilities were standardized, survival was greatest during the winter and spring months, at all tidal heights and beaches (Figures 2.2 - 2.4). Survival probabilities decreased most drastically during one or more of the late-summer to fall months, for all areas. Therefore, during the years studied, the annual cycle for clam survival was high survival in the winter and spring, with low survival sometime in the late-summer and fall. From this analysis, it appears that the mechanisms that decrease survival in the razor clams must operate primarily during the late-summer and fall.

2.4.1.1 Comparison of survival probabilities at various tidal heights

The location of the site within a beach was often a significant factor in clam survival. At Copalis, intertidal location was a significant factor during August 1990, April - October 1991, January 1992, June-August 1992, October 1992, and November 1992. During 1990 - 1991, Area "B" had the highest annual survival (Table 2.3). However, in 1992, the lowest tidal area, Area "C", had the highest annual survival. It was noted that during the period when the highest survival probability changed from Area "B" to Area "C", large numbers of red ghost shrimp (*Callianassa californiensis*) became apparent in Area "B". At the start of the study, the ghost shrimp were in Area "A" in very high densities, but they did not encroach into the razor clam habitats in Areas "B" and "C". By the end of the study, however, ghost shrimp densities were markedly increasing in Area "B". Ghost shrimp were not evident in Area "C" during any period of the study.

At Long Beach, tidal height was a significant factor in clam survival in August - October 1990, December 1990, March - May 1991, and July - September 1991. The middle area (i.e., Area "Y") typically had the highest population densities (WDFW abundance estimates) and this study found that Area "Y" shared the highest annual survival for 1991 (Appendix 2.3) with Area "X". Sampling at Long Beach was

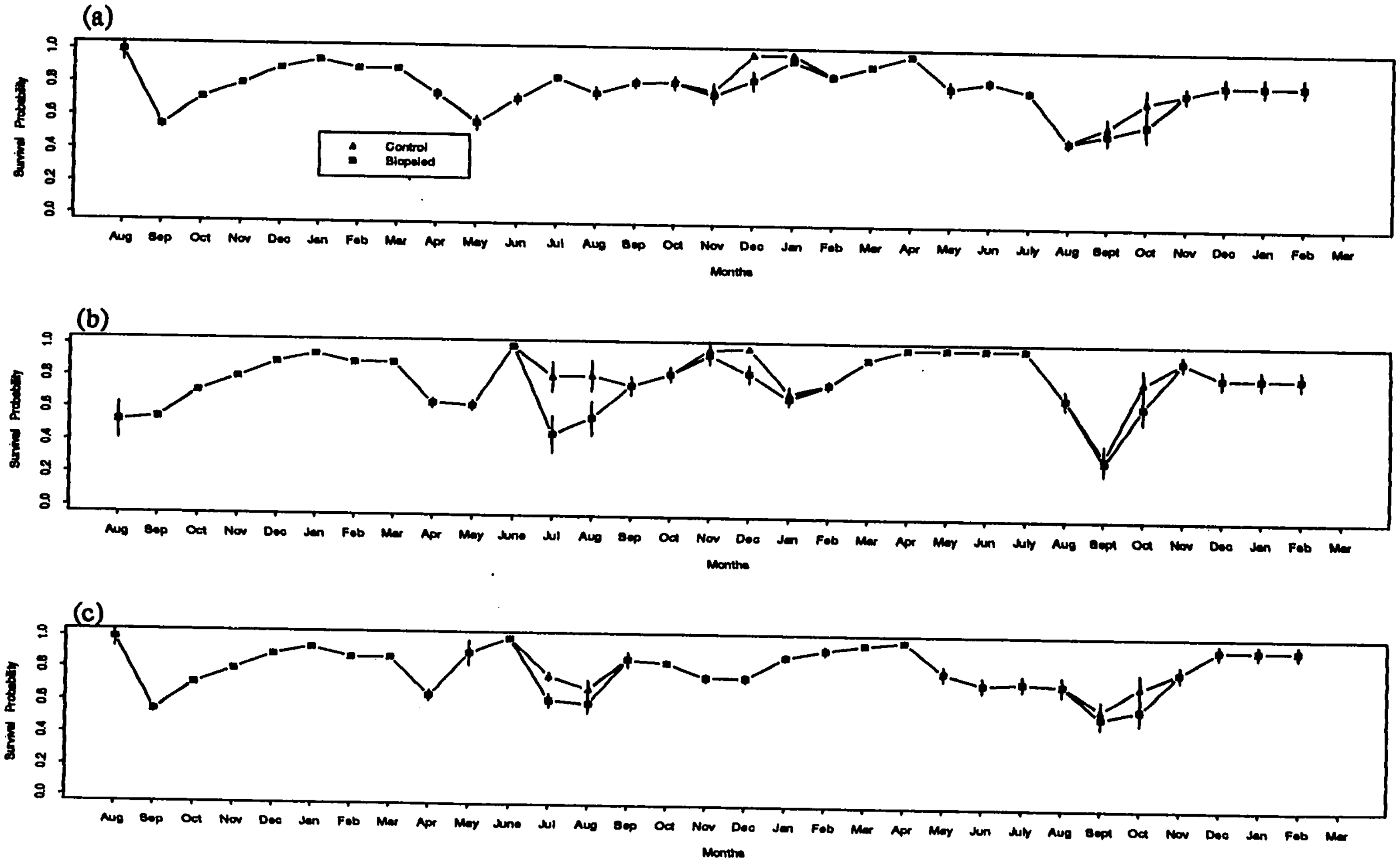


FIGURE 2.2 Monthly survival probabilities (± one standard error) for the Copalis Beach site at three tidal heights (i.e., (a) A, (b) B, and (c) C). The lines for the controls and biopsied clams overlap when SURPH found no statistical difference in survival probability for the two groups. The two treatment lines diverge when the survival probabilities were found to be statistically different.

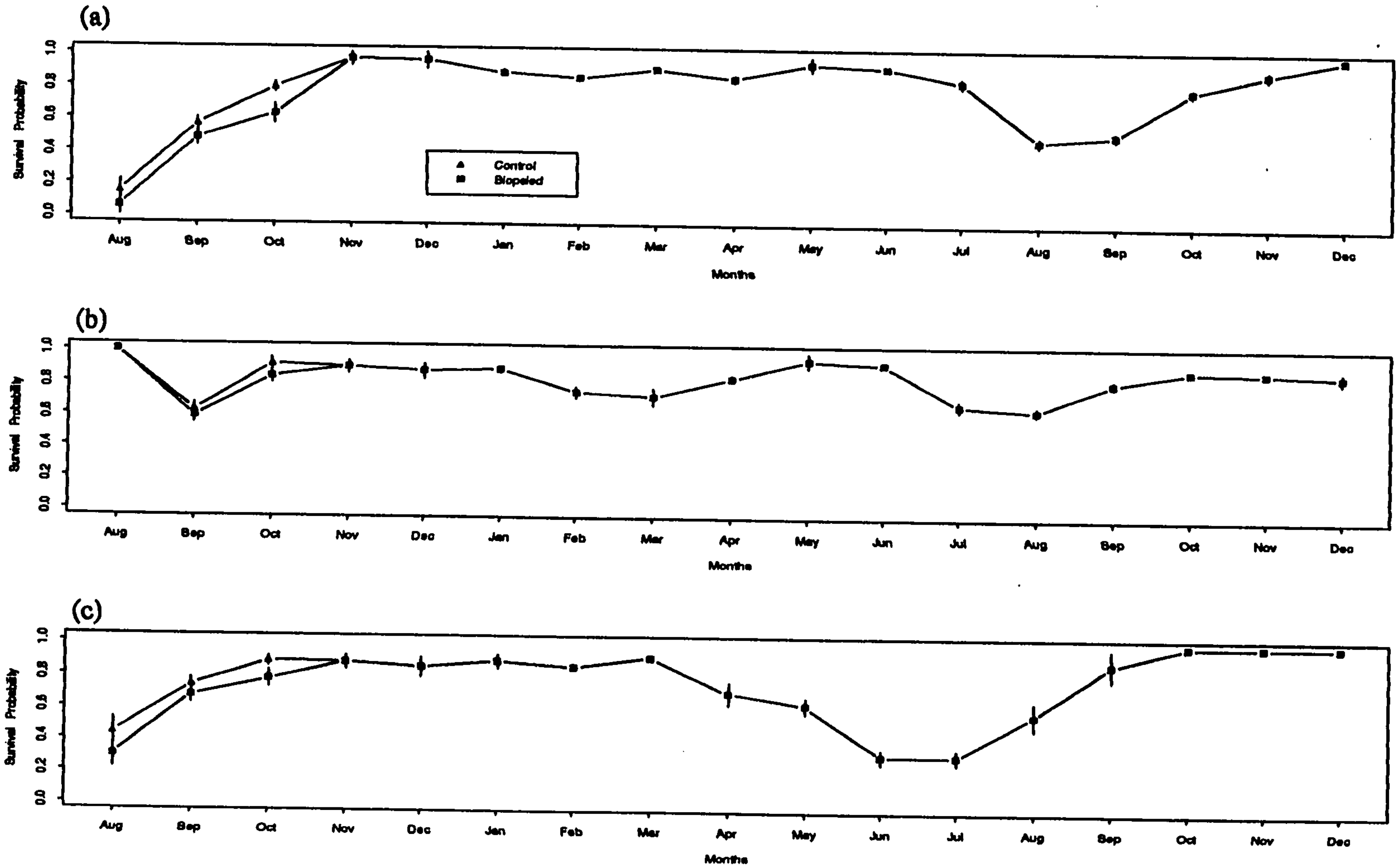


FIGURE 2.3 Monthly survival probabilities (± one standard error) for the Long Beach site at three tidal heights (i.e., (a) X, (b), Y, and (c) Z). The lines for the controls and biopsied clams overlap when SURPH found no statistical difference in survival probability for the two groups. The two treatment lines diverge when the survival probabilities were found to be statistically different.

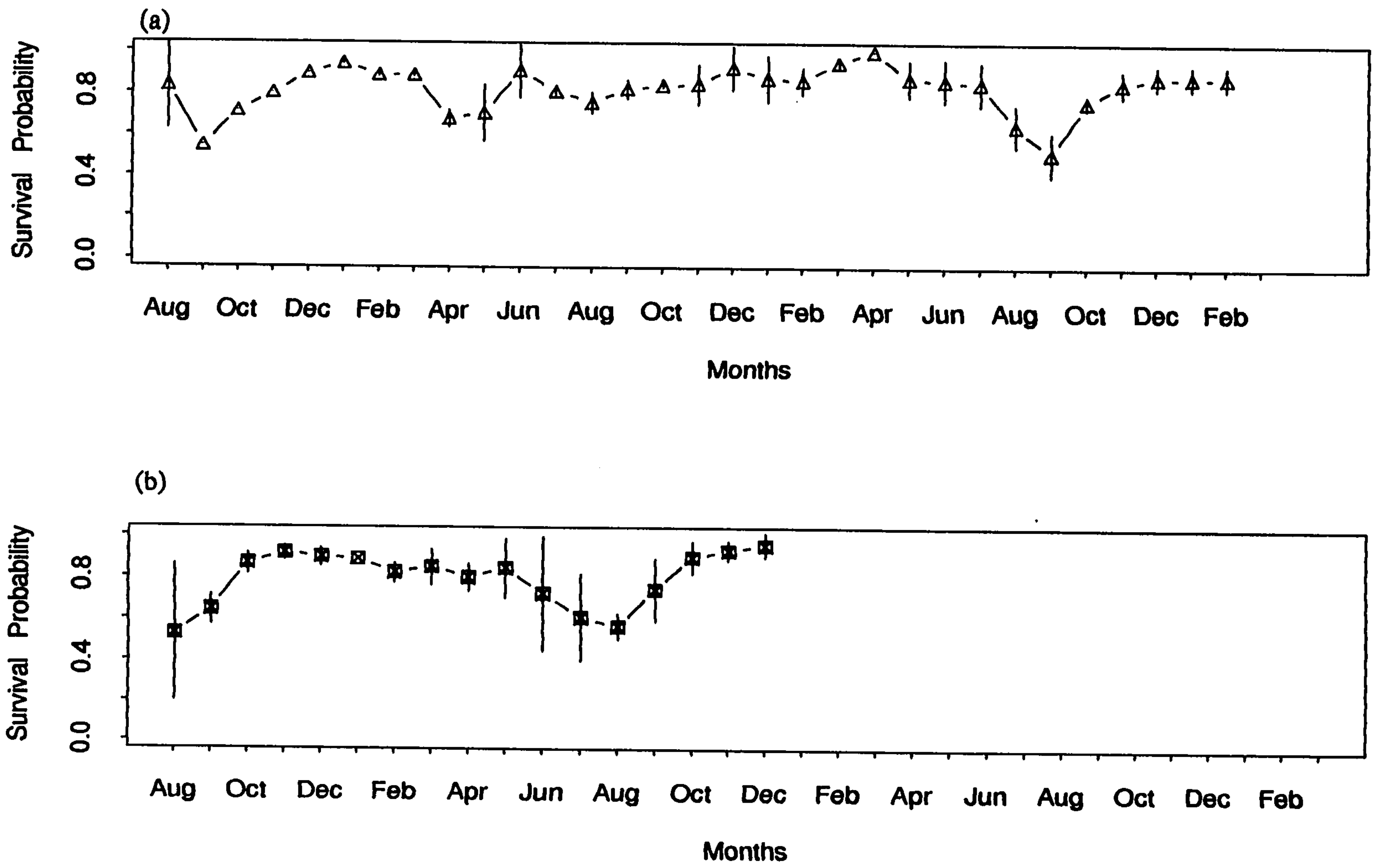


FIGURE 2.4 Time series of the standardized monthly survival probabilities (± one standard error) for (a) Copalis and (b) Long Beach. Each point represents the mean survival for control clams on that beach. The time series begins in August 1990 and continues through February 1992.

Table 2.3: Estimates of annual survival probabilities (and standard errors) for the period January 1991 to December 1992 by plot at Copalis and Long Beach for handling Controls (clams that were not biopsied).

Beach	Plot	1991 Survival	1992 Survival
Copalis	A	0.07 (0.014)	0.04 (0.014)
	B	0.13 (0.032)	0.05 (0.022)
	C	0.09 (0.017)	0.11 (0.089)
Long Beach	X	0.08* (0.010)	NA[1]
	Y	0.08* (0.014)	NA[1]
	Z	0.01* (0.006)	NA[1]

* Poor recaptures in December 1991 caused the survival to be estimated over a 13 month period, rather than a 12 month period. Thus annual survival will be negatively biased. However, as typical winter survival is high, the estimated survival will be very close to the anticipated annual survival.

[1] Long Beach was not sampled on a regular basis after January 1992.

discontinued in January 1992. Thus, annual survival probabilities are not available beyond 1991.

Regardless of the frequent differences in survival probability estimates among intertidal locations on a monthly basis, seasonal trends were similar within a beach, and across beaches. At both beaches, it appears that the annual survival is worst for clams in the upper tidal areas (Areas "A" and "X"), while clams in the areas of highest clam density (Areas "B","C", and "Y") experience the best annual survival (Table 2.3). During spring and winter months, all areas have similar survival probabilities. However, during the summer and fall, the clams in the upper tidal-height areas suffer greater mortality than the clams in the lower tidal-height areas. These few months account for the differences in survival observed among tidal heights (Table 2.3). Therefore, in general, the highest survival is found in clams in the areas of higher historical density (i.e., Areas "B" and "Y"), and this is due to better summer and fall survival. Because the major mortality event occurs in the summer and fall months, if NIX is causing a decrease in survival, it will be most likely detected during this period.

2.4.1.2 Comparison of survival probabilities at Copalis and Long Beach

To compute the survival for the entire beach for Copalis and Long Beach, all tidal areas were averaged. For the only year that data were available for both beaches, both beaches tended to have similar annual survival probabilities (Copalis 1991 - annual survival = 0.10, Long Beach 1991 - annual survival = 0.06; Table 2.3). The seasonal timing of both high and low survival at both beaches was also similar (Figures 2.2 - 2.4). These similarities were evident despite the differences in the length distributions, NIX Intensities, and location.

2.4.1.3 Assessment of Biopsy-Induced Mortality

The biopsy procedure could be expected to decrease the survival of the clams, as extra handling was involved. For the majority of the 30 months of the study, there was no difference between the survival probabilities of control clams versus biopsied clams. However, at Copalis a biopsy effect was significant in 7 of the 30 periods, although 3 of these 7 instances indicated increasing survival associated with the biopsy procedure. The biopsy effect was detrimental in July 1991 ($p=0.002$), December 1991 ($p=0.01$), February 1992 ($p=0.01$), and September 1992 ($p=0.08$). At Long Beach, the biopsy effect was a significant factor in survival in three periods, but in one period the survival of biopsied clams was higher than for the control clams. During the other two periods (i.e. August 1990 ($p=0.03$) and October 1990 ($p=0.001$)) survival for biopsied populations was lower than for control populations. These results indicate that there was an effect of the biopsy procedure, but the effect was not constant nor consistent.

There are other indications that the biopsy, although not often a significant factor during all periods, did decrease the survival slightly in all areas. Table 2.4 shows the mean and maximum number of months from first release to final recapture recorded for clams in this study (i.e., identified from here on as "mean time out" and "maximum time out" respectively). If survival was the same for the control groups and the biopsy groups, one would expect that the maximum time out and the mean time out would be similar for both groups. What is observed instead is that, in all cases, the maximum time out and the mean time out is greater for clams that were not biopsied. Using the nonparametric sign test (Daniel, 1978), and the following hypotheses

H_0: Biopsy and Control clams have identical survival

H_1: Biopsy clams have lower survival

we find that the probability of the null hypothesis being true is 0.02 for either metric (i.e., mean time out or maximum time out) ($P(k=0 \mid n=6, p=0.50) < 0.02$). This is an indication that the survival is slightly higher for the control groups.

Table 2.4: Maximum and mean time (in months) between initial release and final recapture. Populations are designated by a two-letter code. The first letter is the tidal height (i.e., "A-C" at Copalis, "X-Z" at Long Beach") while the second letter is the biopsy status (i.e., "C" indicates no biopsy procedure, "N" indicates biopsied).

Beach	Tidal Height	Treatment	Maximum Time Between Release and Final Recapture	Mean Time Between Release and Final Recapture
Copalis	A	C	16 months	1.5 months
	A	N	15 months	1.3 months
	B	C	23 months	2.3 months
	B	N	17 months	1.8 months
	C	C	20 months	2.5 months
	C	N	15 months	1.9 months
Long Beach	X	C	12 months	1.6 months
	X	N	10 months	1.3 months
	Y	C	17 months	2.3 months
	Y	N	14 months	1.9 months
	Z	C	13 months	1.8 months
	Z	N	10 months	1.5 months

Another indication that the biopsy procedure may have affected the survival of these clams comes from the recapture data. Table 2.2 shows that the percentage of biopsied clams recaptured (37% at Copalis, 42% at Long Beach) was lower than the percentage of control clams recaptured (46% at both Copalis and Long Beach). Thus, although the SURPH analysis indicated that the extra handling involved in taking a tissue biopsy did not appreciably decrease survival during most months, the recapture percentages indicate that the biopsy procedure may have decreased survival slightly. Therefore, only control clams should be used for the investigation of survival trends through space and time. Biopsied clams will be used to determine the relative effect of NIX on survival.

2.4.1.4 Assessment of Handling-Induced Mortality

Area "M" was used to investigate handling mortality. The best-fit model indicated that survival during the spring and early summer months (i.e., March - July) in Area "M" ($\hat{S}$ = 0.97; se($\hat{S}$) = NA) was much greater than that observed in Area "B" ($\hat{S}$ = 0.29; se$(\hat{S})$ = 0.05), for the same time span. During the second recapture phase at Area "M", which took place during March 1993 and May 1993, overall survival for the period between August 1992 and March 1993 was estimated as $\hat{S}$ = 0.36 (se($\hat{S}$) = NA). However, the results for these intermediate periods at area "M" were extremely model-dependent. In addition, there was a significant length effect evident in Area "M". Because SURPH does not provide standard errors for models that include individual covariates, standard errors for the intermediate periods are not available. The annual survival from March 1992 to March 1993 for Area "M" was estimated to be $\hat{S}$ = 0.35 (i.e., 0.97*0.36 = 0.35; se$(\hat{S})$ = 0.10), and was largely independent of the model chosen. The annual survival at area "M" is substantially higher than the annual March to March survival for Area "B", which was estimated to be $\hat{S}$=0.09 (se$(\hat{S})$ =0.03). This result suggests that handling is causing a mortality stress upon the clams.

2.4.1.5 Assessment of Length Effects

The potential relationship between clam length and survival were analyzed using three years of capture data on 5314 clams from Copalis and 3285 clams from Long Beach (Figure 2.5). KS-tests on the complete data sets (i.e., all tidal heights and all years combined) indicated that there were significant differences between the length distributions at both beaches ($p<0.001$ at both Copalis and Long Beach). Histograms of length distributions (Figures 2.5 - 2.8) for clams that were and were not recaptured (a.k.a. "known alive" and "not known alive" respectively) were used to more clearly illustrate where differences in the length frequencies exist. Chi-square tests of homogeneity were used to test whether the distribution of animals that were recaptured differed from the animals that were not recaptured (Zar, 1984 p. 49-52). At Copalis fewer clams of smaller sizes (<13 cm) than expected were recaptured, and more medium sized clams (13-14 cm) than expected were recaptured. At Long Beach the opposite held, where more clams of smaller sizes (<11 cm) than expected were recaptured, and fewer medium and large sized clams (12-16 cm) than expected were recaptured. There was a significant effect ($p < 0.004$) of length in all years of the study. In the first year at Long Beach, it appears as if two separate size classes were predominant, those clams < 11 cm, and those clams > 13 cm. Clams less than 10 cm were generally omitted from the marking study because of handling difficulties. However, because clams at Long Beach are typically of a smaller size than clams at Copalis, it was not always possible to obtain a complete sample without including the smaller clams.

Using SURPH, it was possible to model the survival and capture probabilities as functions of the length. A log-link was used to model the effect of length on the capture probabilities, whereas the hazard-link was used to model the effect of length on the survival probabilities. As stated earlier, the significance of nested models was tested using LRT, whereas non-nested models were assessed using the AIC. The SURPH analysis indicated that capture processes were affected by the length of the clam ($p < 0.005$) for two years at Copalis, and in the first year at Long Beach. During the second year there was

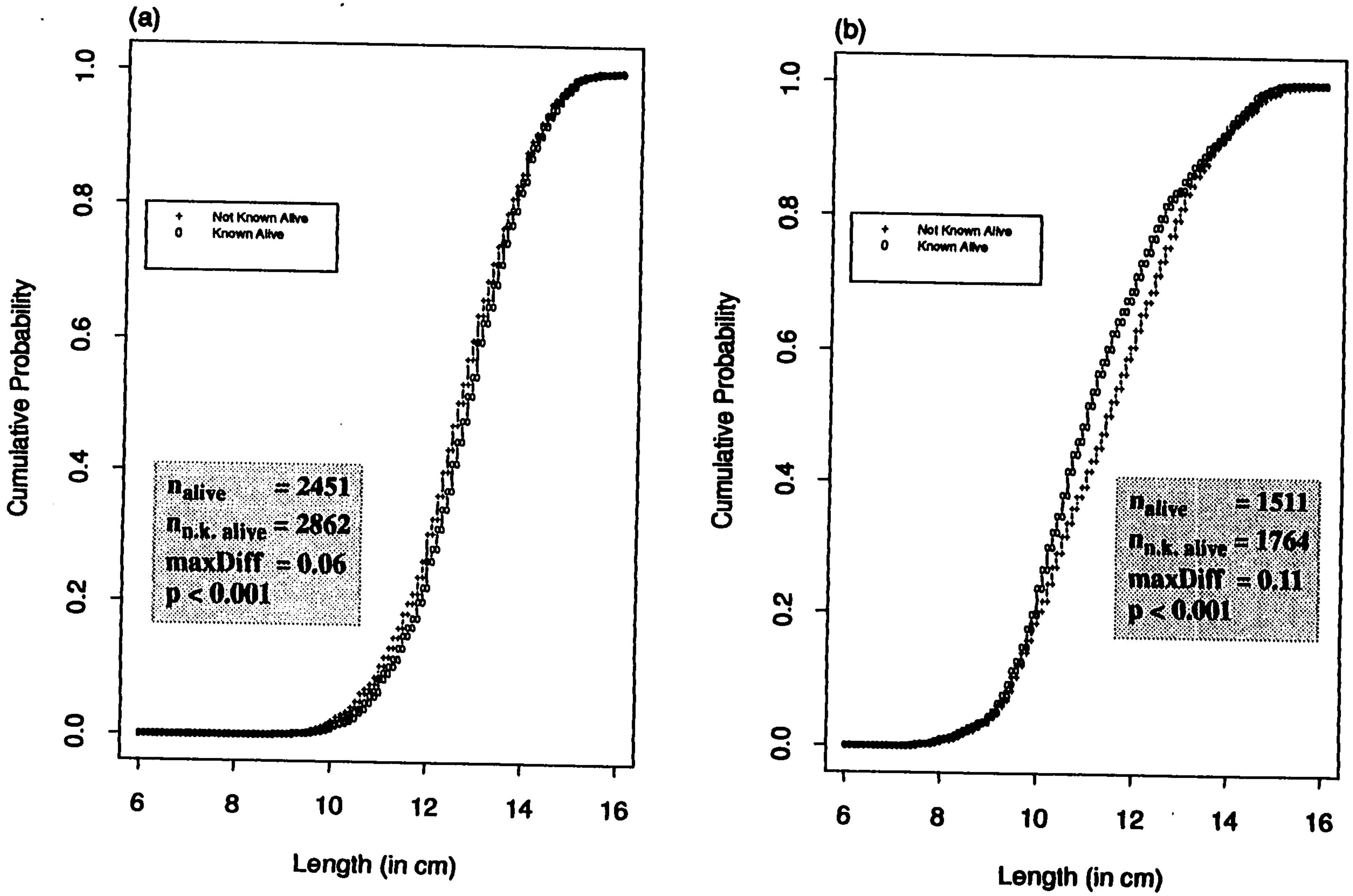


FIGURE 2.5 Cumulative Distribution Functions (cdf's) of Length at (a) Copalis and (b) Long Beach for clams that were and were not recaptured. Data come from all years and tidal heights combined.

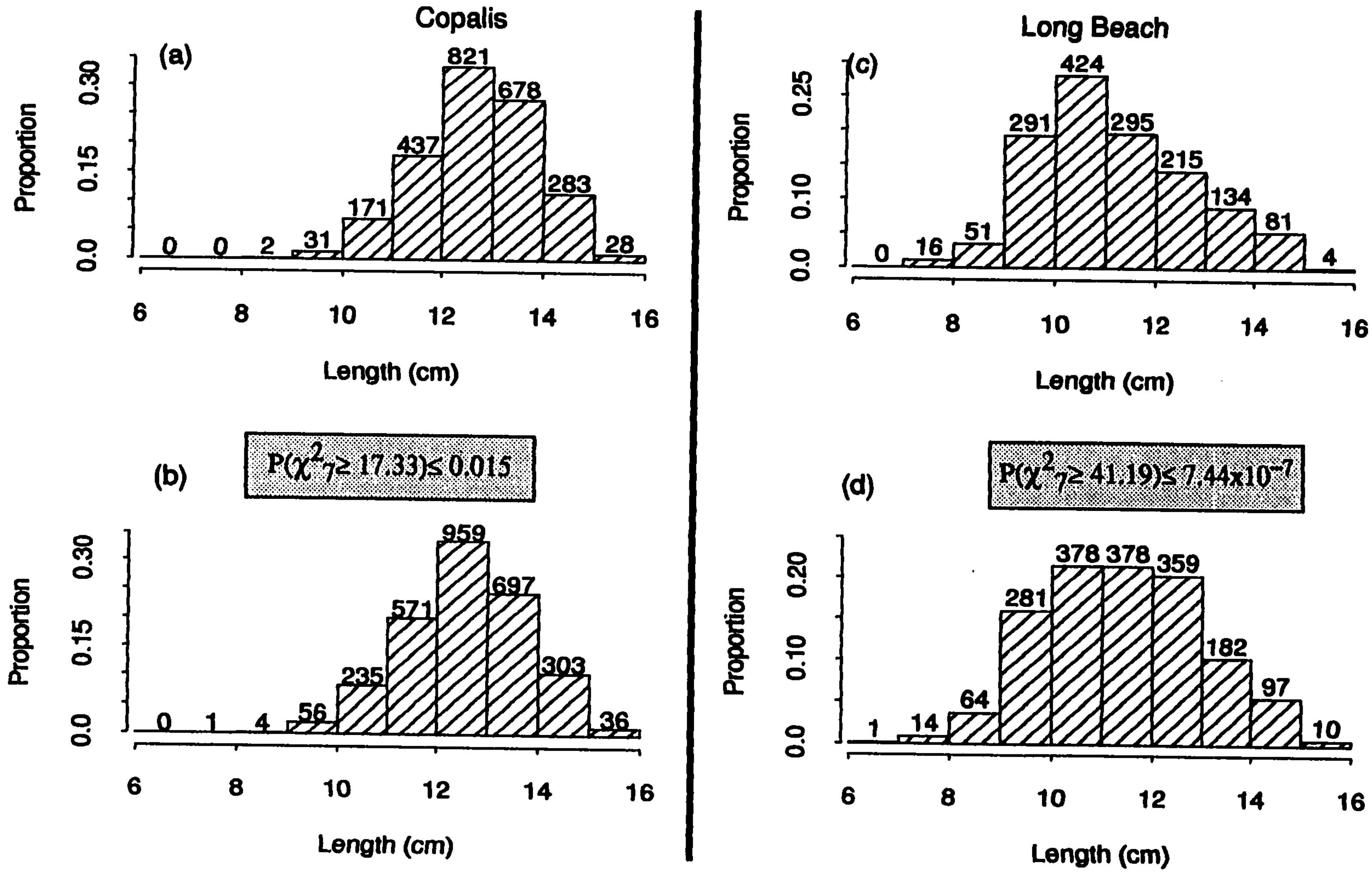


FIGURE 2.6 Histograms of lengths of clams that were subsequently recaptured (a and c) and were not subsequently recaptured (b and d) at Copalis and Long Beach. Data come from all years combined.

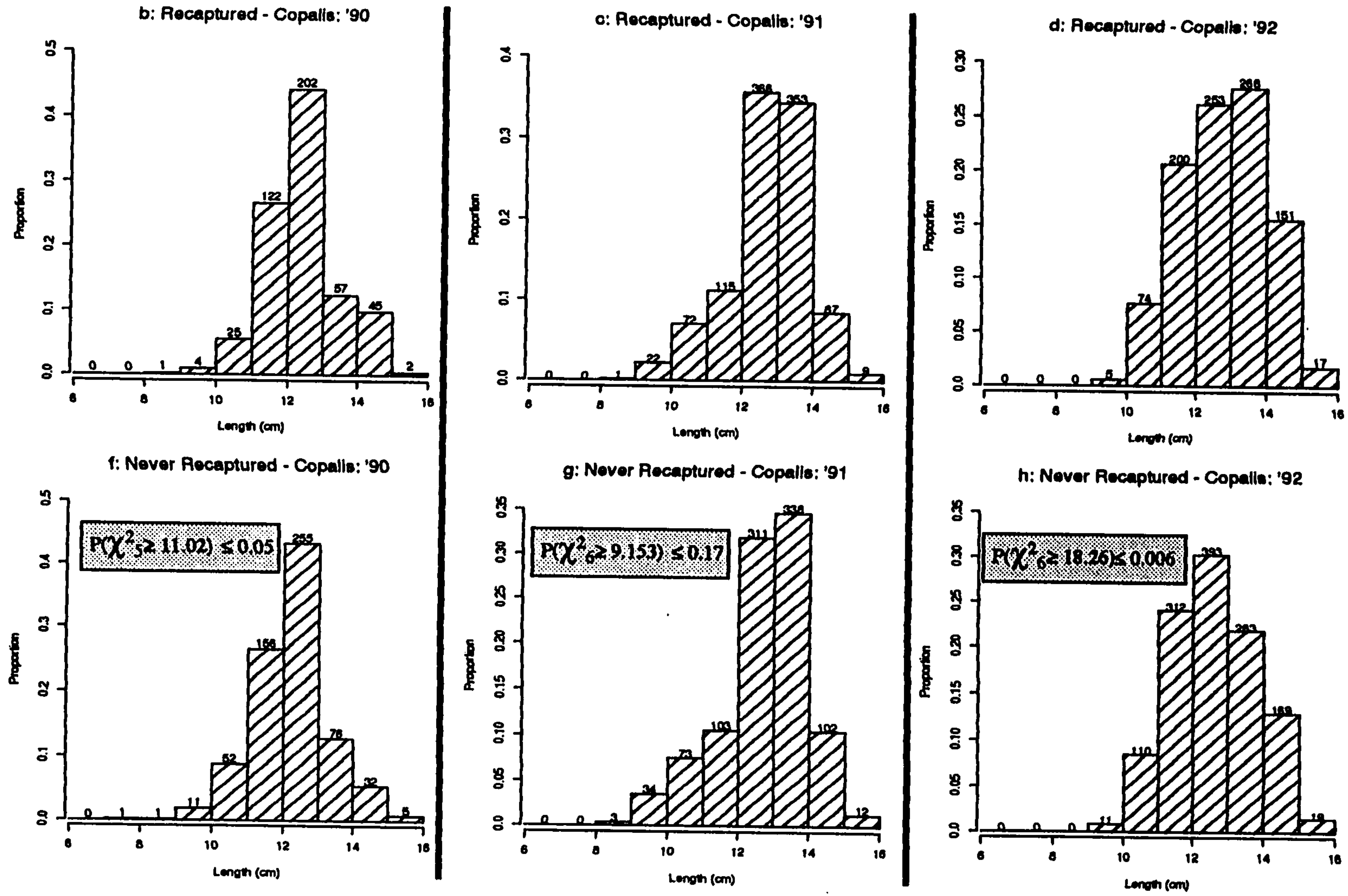


FIGURE 2.7 Histograms of lengths of clams that were (a-c) and were not (d-f) subsequently recaptured at Copalis by year.

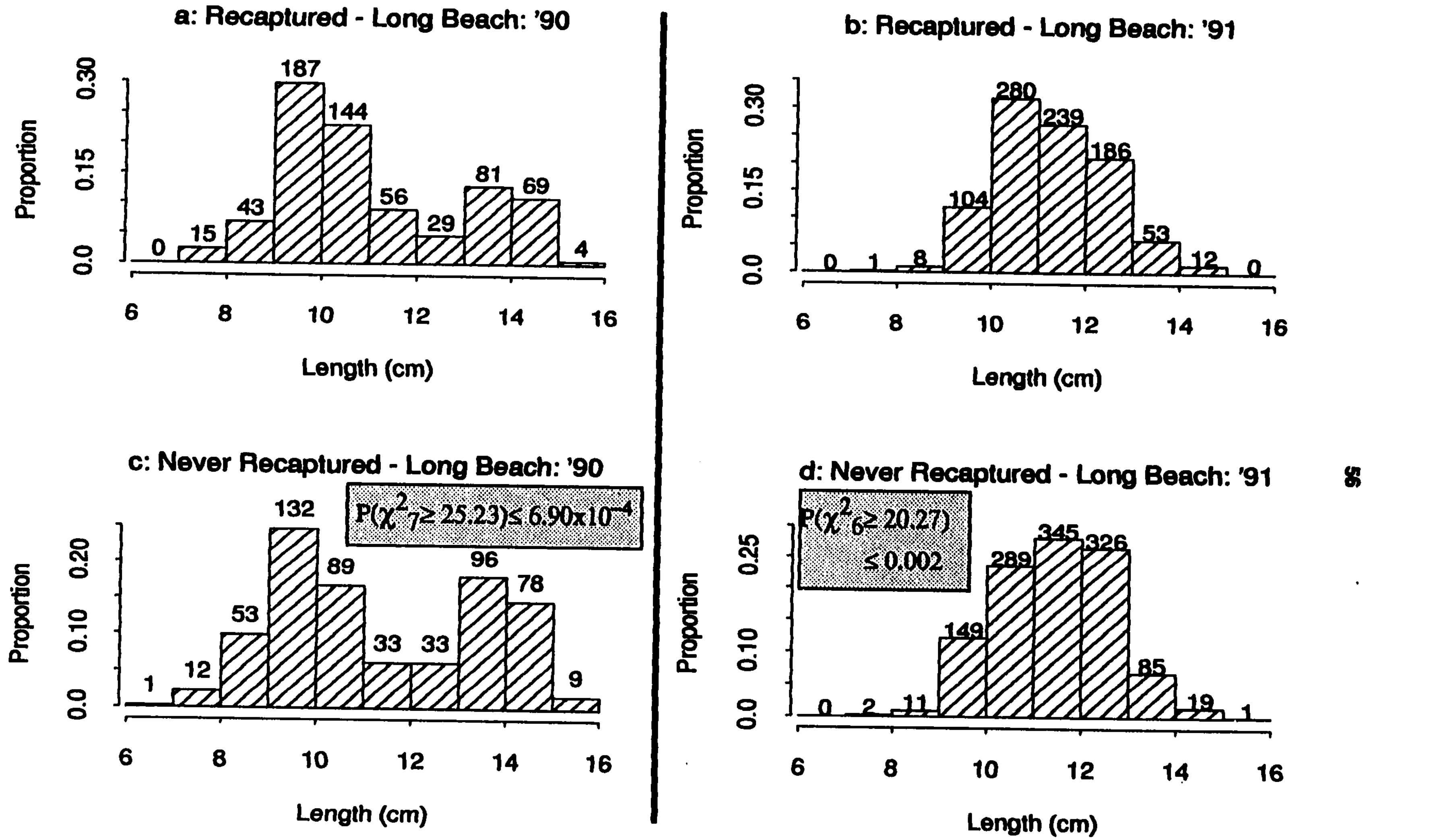


FIGURE 2.8 Histograms of lengths of clams that were (a-b) and were not (c-d) subsequently recaptured at Long Beach by year.

no evidence of a significant length effect on capture at either Copalis or Long Beach. At both Copalis and Long Beach, in most months, larger clams were more likely to be captured than smaller clams. Specifically, at Copalis for the summers of 1990 and 1992, and at Long Beach for the summer of 1990, larger clams were more likely ($p < 0.005$) to be captured than smaller clams (Figures 2.9 - 2.11).

The relationship between survival and length was rarely significant. Although in general, survival decreased with increasing length, this effect was only significant ($p=0.03$) at Copalis in 1992. At both Copalis and Long Beach, in most months, smaller clams were more likely to survive than larger clams. Specifically, at Copalis for the summers of 1990 and 1992, and at Long Beach for the summer of 1990, smaller clams were at slightly lower risk ($p > 0.39$) of mortality than larger clams (Figures 2.9 - 2.11).

The fact that size affects the capture probabilities may have impacts in sampling techniques that are prone to this bias. The SURPH analysis indicates that the differences between the distributions of those clams that were recaptured and those clams that were not recaptured is mostly due to the effect of length on capture, not an effect of length on survival.

In the second year I attempted to study survival of clams less than 10 cm at Area "BS" at Copalis. However, all clams from this plot disappeared. Either there was tremendous mortality on the smaller clams or they emigrated from the plot. It may well be that these smaller clams omitted from the study might be experiencing the greatest selection, yet go unnoticed in this investigation.

2.4.1.6 Assessment of NIX Individual Level Effects

The effect of NIX on the survival probabilities was analyzed using the individual-covariate routines in SURPH. The values of the NIX Intensities (counts per 40x field) at the time the clams were first biopsied were used as the predictor variables in the analysis. Biopsy data from the summer-fall months of 1990, 1991, and 1992 and recapture data

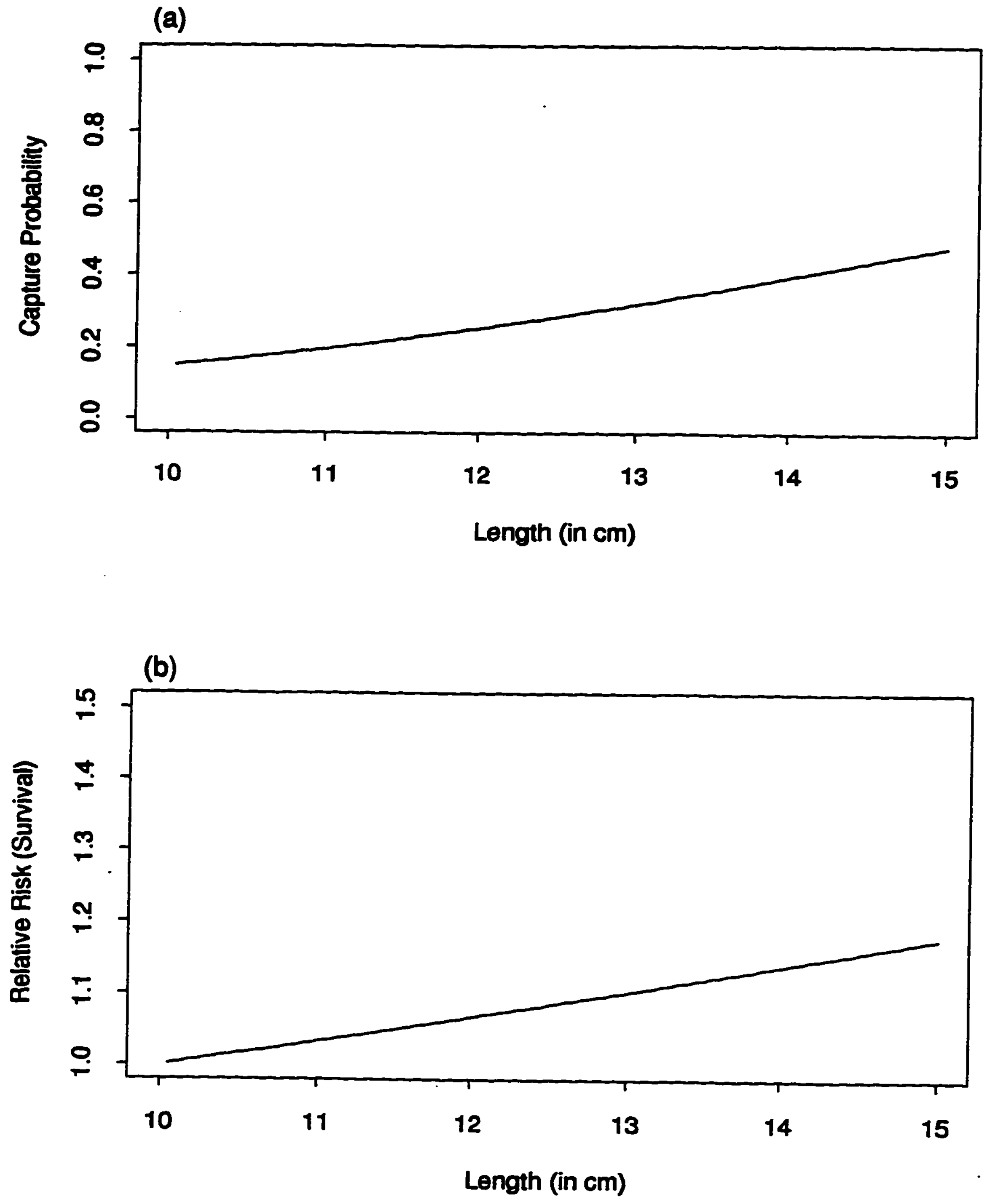


FIGURE 2.9 Representative plots of the (a) Capture Probability and (b) Relative Risk of Survival compared to a small (i.e., 10 cm) clam as estimated by SURPH for Copalis in the late-summer of 1990 for the individual covariate "length".

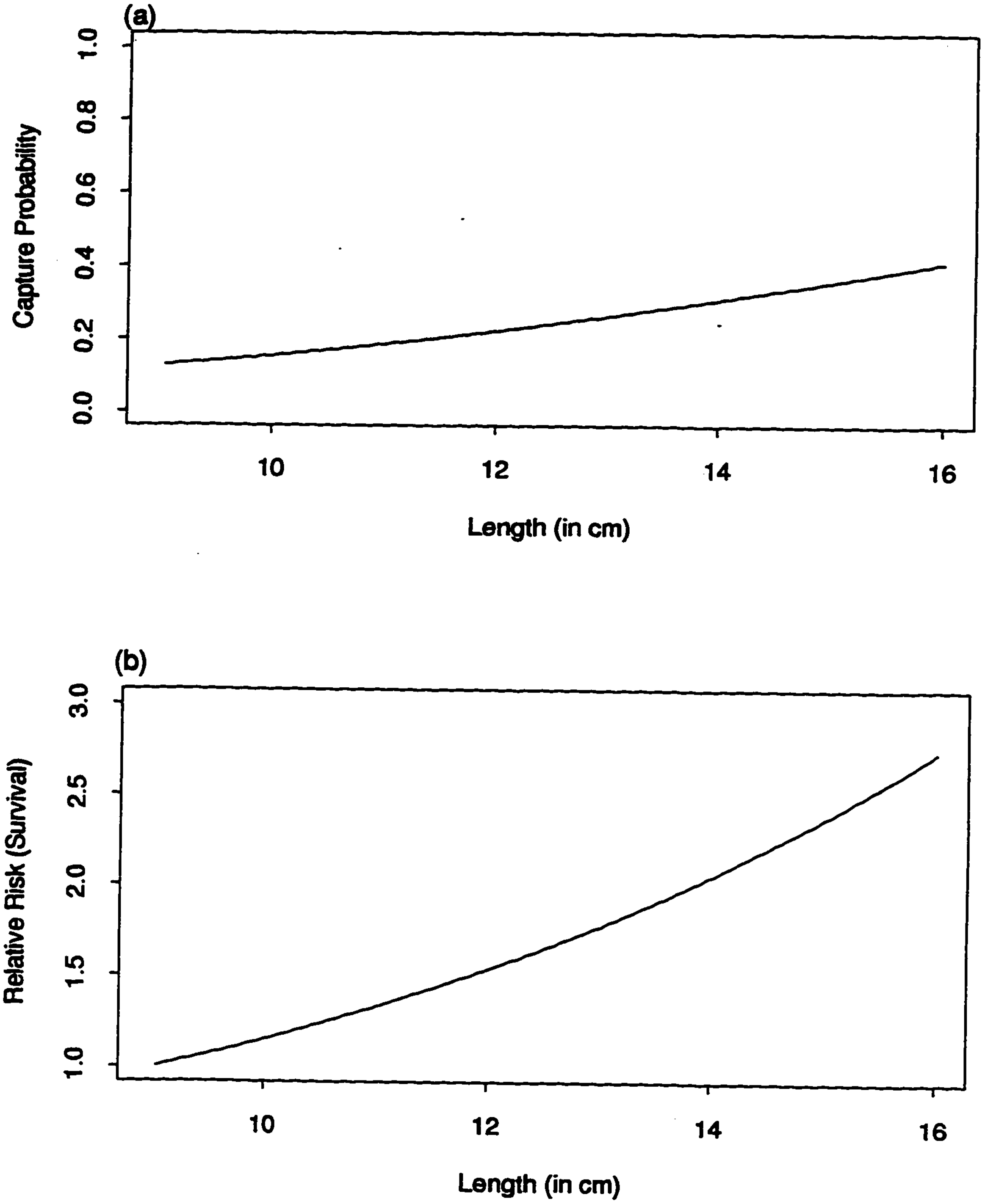


FIGURE 2.10 Representative plots of the (a) Capture Probability and (b) Relative Risk of Survival compared to a small (i.e., 9 cm) clam as estimated by SURPH for Copalis in the summer of 1992 for the individual covariate "length".

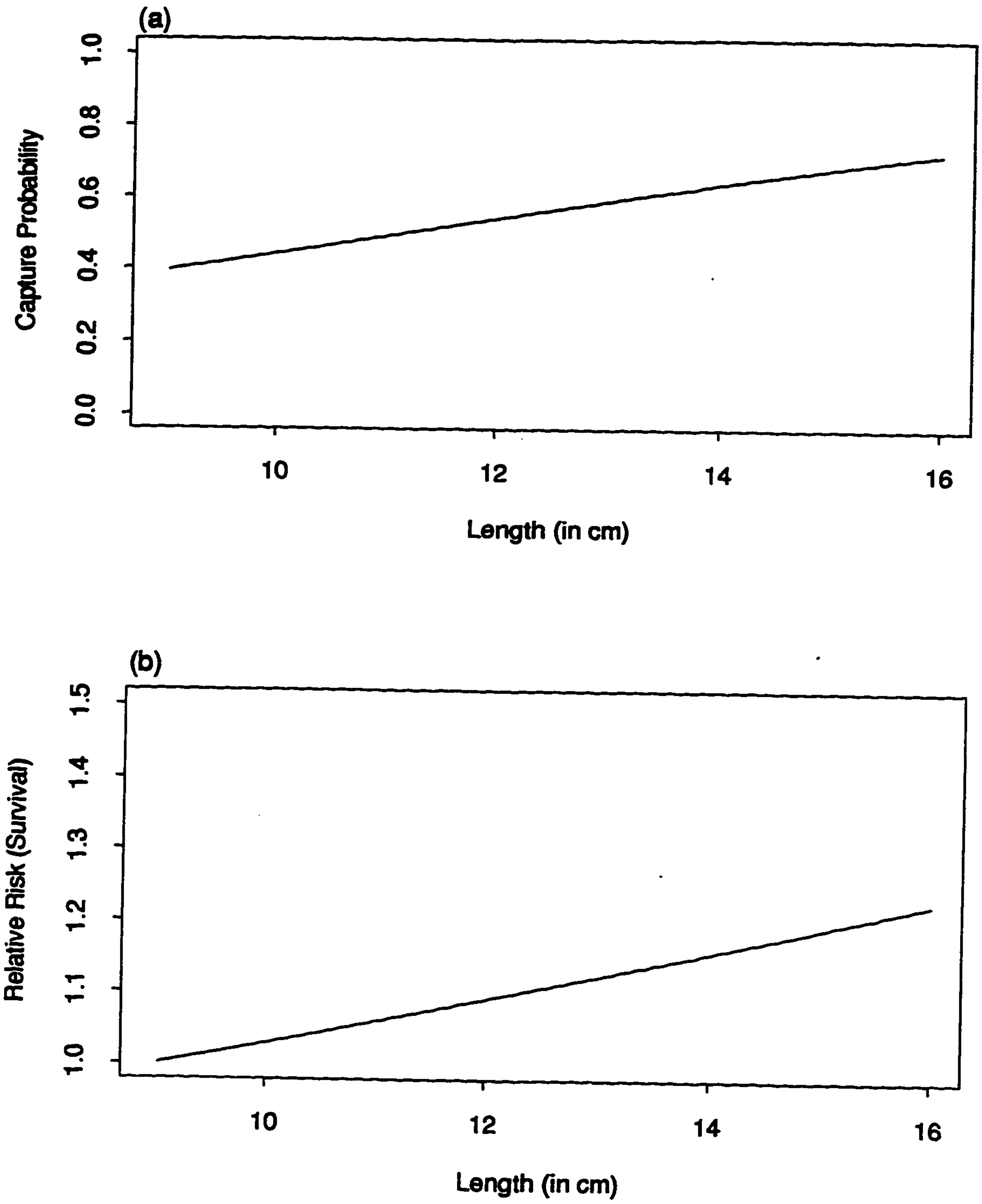


FIGURE 2.11 Representative plots of the (a) Capture Probability and (b) Relative Risk of Survival compared to a small (i.e., 9 cm) clam as estimated by SURPH for Long Beach in the summer of 1990 for the individual covariate "length".

from the summer-winter months of 1990, 1991, and 1992 were used in the analysis. Overall, the point estimates for the mean NIX Intensity sampled during the summers of this study were very similar to those that had been experienced during previous years (Ayres and Simons, 1991). The results of the analyses indicate that there were no significant NIX effects during the summers 1990-1992 for Copalis or for Long Beach. This is not to say that the inclusion of NIX within the modeling framework never provided a significant change in fit. In almost all summer months, the inclusion of NIX did significantly contribute to model fit. However, the direction of the significant fit was inconsistent, and was typically influenced mostly by NIX values between 10-40 counts per 40x field, not NIX values greater than 80 counts per 40x field (Table 2.5 and Appendix 2.4). For example, at Copalis in 1990, analysis of NIX data showed significant NIX effects ($p < 0.1$) in September. There was a general decrease in survival due to increasing NIX ($\beta_{NIX} = 0.01$), such that a clam with NIX > 100 has a 4 times greater risk than does a clam with a NIX Intensity of 20-30 counts per 40x field. However, during the same year, in October, the analysis found that there was a general increase in survival due to increasing NIX ($\beta_{NIX} = -1.73$), such that a clam with NIX > 100 counts per 40x field has no risk. These inconsistencies occur in all three years at both beaches.

Graphical inspection of the NIX Intensity values for clams that were and were not subsequently recaptured (Figures 2.13 - 2.16) also showed no significant differences in empirical cdf's. Kolmogorov-Smirnov (K-S) tests of the data (Appendix 2.4) on a monthly basis show that whenever there was a significant difference between the cumulative distribution functions of non-recaptured versus recaptured clams, the significant portion of the curve is not in the extremely high NIX regions, but in the intermediate levels. The only times the differences are significance, the significant portion of the cdfs occur when there were fewer clams with intermediate NIX being recaptured than expected, rather than fewer clams with high NIX being recaptured. These significant

Table 2.5: NIX Survival Effects - Slope Estimation Results for Razor Clam Recaptures with NIX Readings at Copalis and Long Beach.

Month	Beach	Tidal Height	Number Known Alive[1]	Estimated Slope for Survival ($\hat{\beta}$) due to NIX effect	P-value
1990					
August 1990	Copalis	All	31	-26.06^{S}	0.001**
September 1990	Copalis	All	29	0.014^{S}	0.001**
October 1990	Copalis	All	48	-47.80^{S}	0.001**
August 1990	Copalis	All	31	-0.604^{I}	0.41
September 1990	Copalis	All	29	0.011^{I}	0.10*
October 1990	Copalis	All	48	-1.725^{I}	0.002**
August 1990	Long Beach	All	32	-0.054^{S}	0.42
September 1990	Long Beach	All	57	0.017^{S}	0.42
October 1990	Long Beach	All	62	0.006^{S}	0.42
August 1990	Long Beach	All	32	-0.047^{I}	0.22
September 1990	Long Beach	All	57	0.018^{I}	0.31
October 1990	Long Beach	All	62	0.009^{I}	0.34
1991					
July 1991	Copalis	All	49	0.196^{S}	0.03*
August 1991	Copalis	All	38	0.004^{S}	0.03*
September 1991	Copalis	All	39	-0.035^{S}	0.03*
July 1991	Copalis	All	49	0.273^{I}	0.03*
August 1991	Copalis	All	38	0.006^{I}	0.01**
September 1991	Copalis	All	39	-0.032^{I}	0.02*

TABLE 2.5 (continued)

Month	Beach	Tidal Height	Number Known Alive[1]	Estimated Slope for Survival $(\hat{\beta})$ due to NIX effect	P-value
1991					
June 1991	Long Beach	All	38	-2.177^{S}	0.07*
July 1991	Long Beach	All	40	-0.008^{S}	0.07*
August 1991	Long Beach	All	37	-0.094^{S}	0.07*
September 1991	Long Beach	All	50	8.950^{S}	0.07*
October 1991	Long Beach	All	49	-0.021^{S}	0.07*
June 1991	Long Beach	All	38	-2.039^{I}	0.01**
July 1991	Long Beach	All	40	-0.007^{I}	0.10*
August 1991	Long Beach	All	37	-0.585^{I}	0.40
September 1991	Long Beach	All	50	0.188^{I}	0.59
October 1991	Long Beach	All	49	0.005^{I}	NA
1992					
June 1992	Copalis	All	26	0.016^{S}	0.69
July 1992	Copalis	All	37	0.008^{S}	0.69
August 1992	Copalis	All	43	0.435^{S}	0.69
September 1992	Copalis	All	30	-0.017^{S}	0.69
October 1992	Copalis	All	25	-0.016^{S}	0.69
June 1992	Copalis	All	26	0.022^{I}	0.11
July 1992	Copalis	All	37	0.015^{I}	0.14
August 1992	Copalis	All	43	2.122^{I}	0.24

TABLE 2.5 (continued)

Month	Beach	Tidal Height	Number Known Alive[1]	Estimated Slope for Survival ($\hat{\beta}$) due to NIX effect	P-value
1992					
September 1992	Copalis	All	30	-0.014[I]	0.12
October 1992	Copalis	All	25	-0.021[I]	0.10*

1 These are clams that were released on or before the month of the NIX effect and detected subsequent to that month.

S These are the parameter estimates and p-values from models that have all period-specific NIX effects estimated simultaneously.

I These are the parameter estimates and p-values from models that have each period-specific NIX effect estimated one at a time.

NA The estimation procedure had difficulties converging for this model. Hence, no p-value could be calculated.

* $p \leq 0.10$

** $p \leq 0.01$

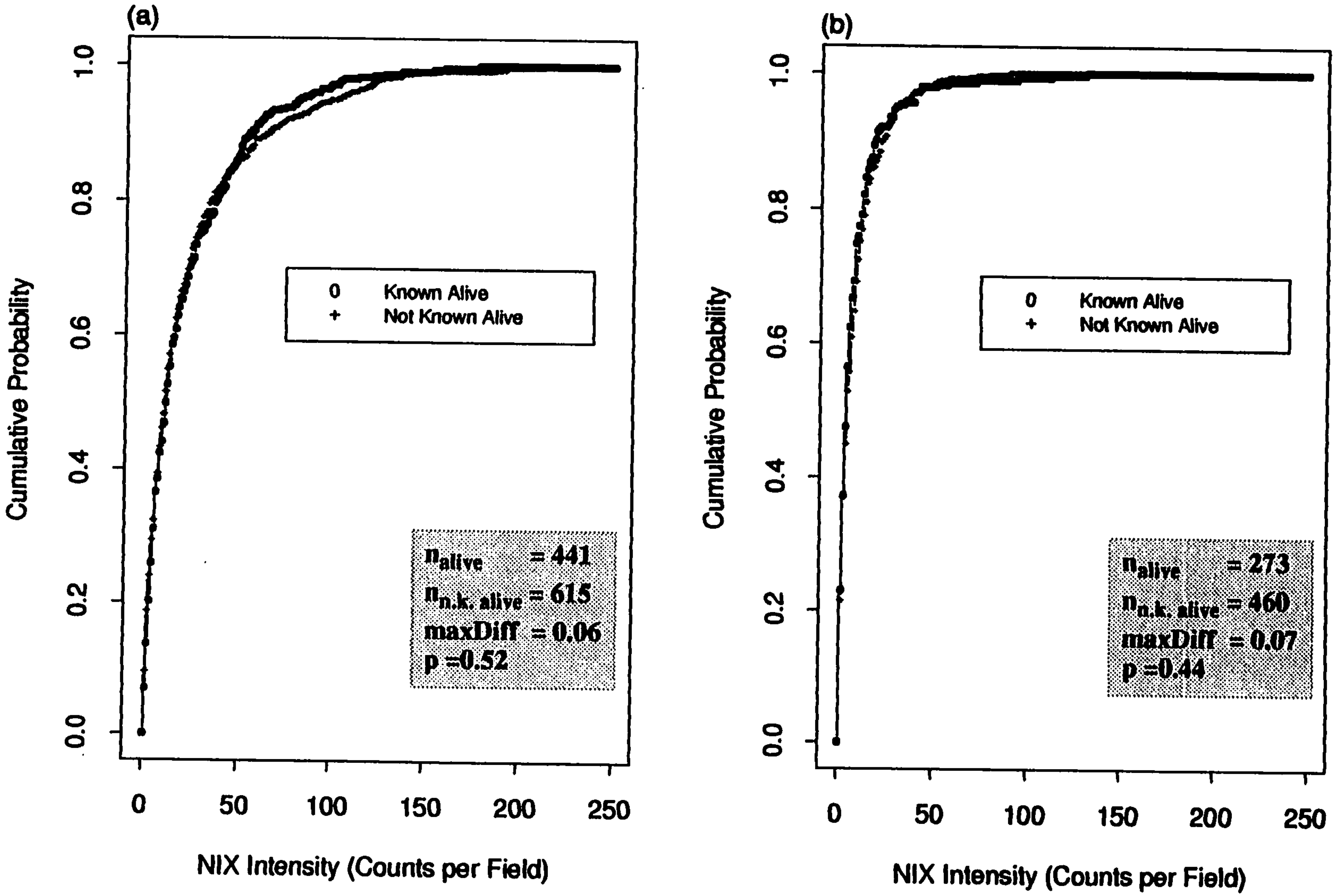


FIGURE 2.12 Cumulative Distribution Functions for NIX Intensity for clams that were and were not recaptured (a.k.a. "known alive" and "not known alive" respectively) at Copalis and Long Beach.

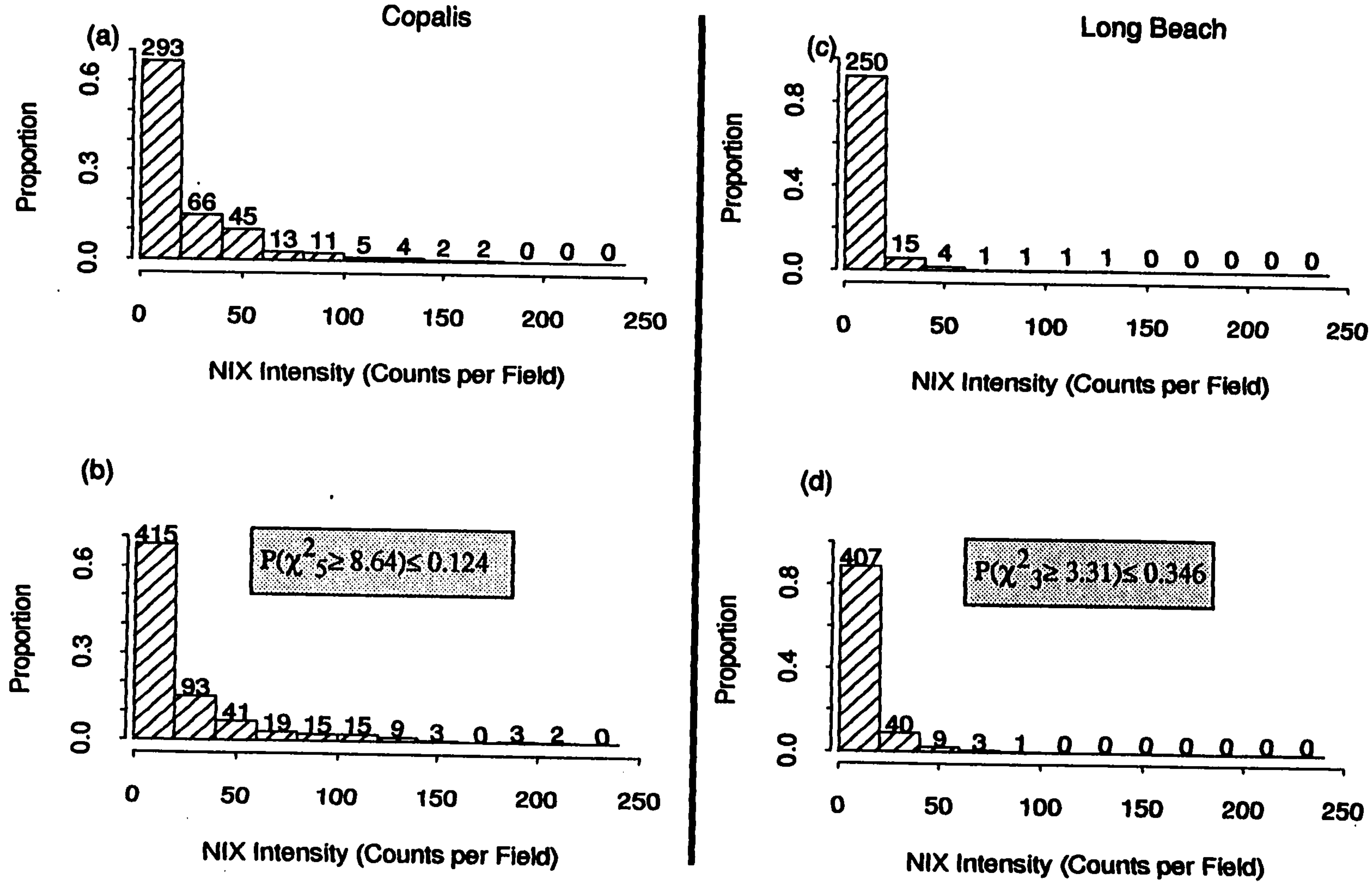


FIGURE 2.13 Histograms of NIX Intensities of clams that were subsequently recaptured (a and c) and were not subsequently recaptured (b and d) at Copalis and Long Beach. Data come from all years combined.

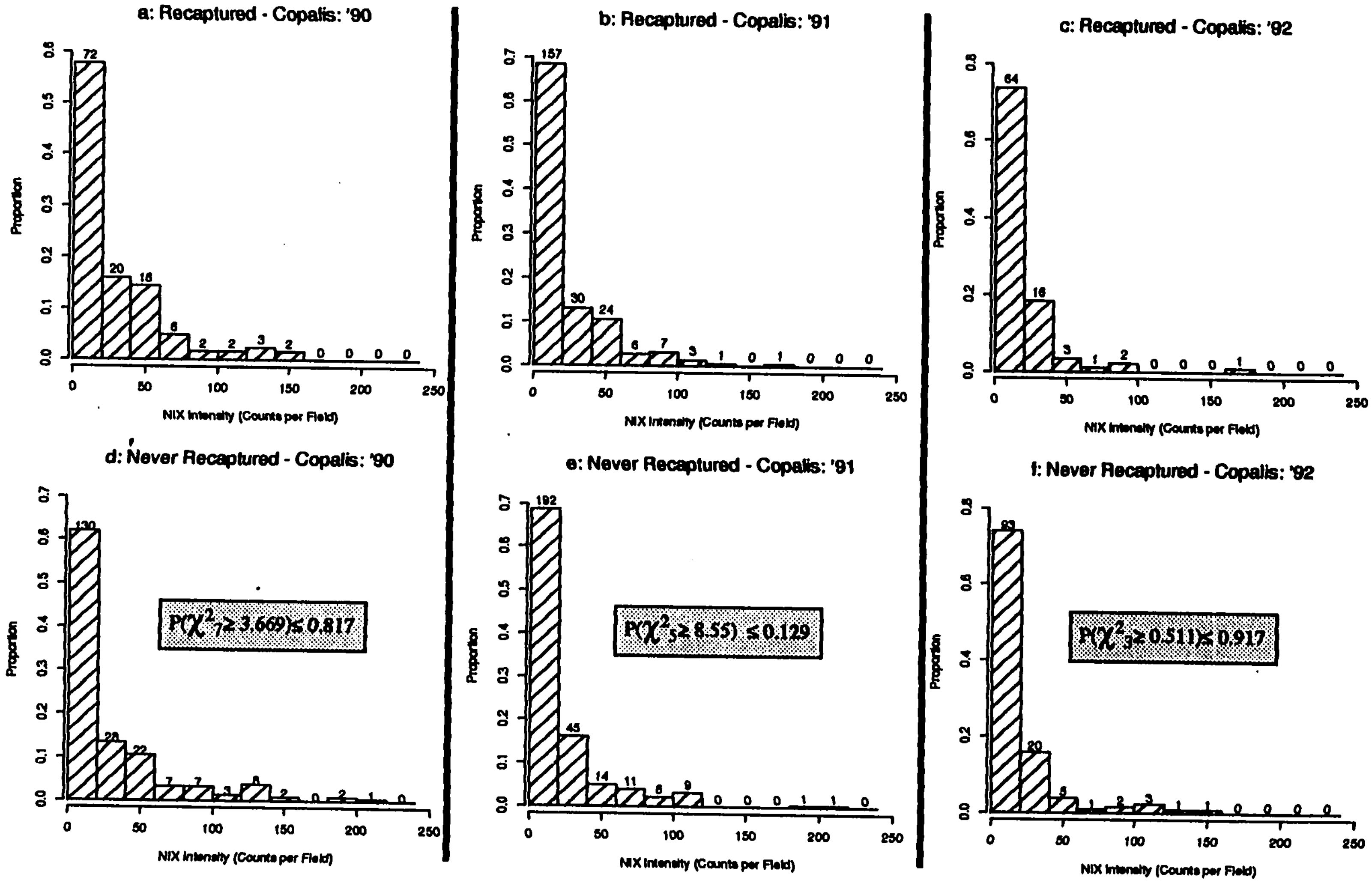


FIGURE 2.14 Histograms of NIX values measured in clams that were (a-c) and were not (d-f) subsequently recaptured at Copalis for each summer data were collected.

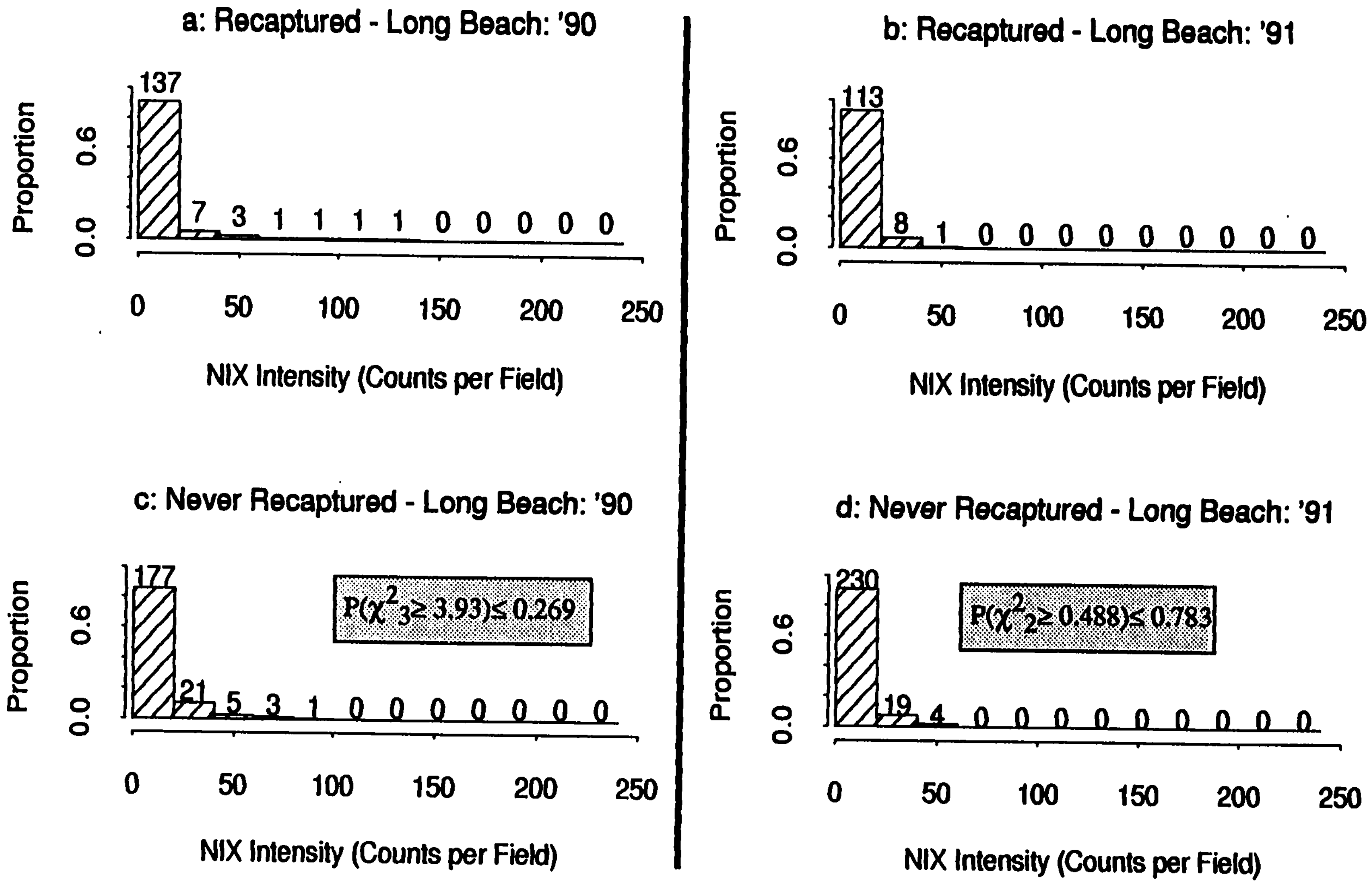


FIGURE 2.15 Histograms of NIX values measured in clams that were (a-b) and were not (c-d) subsequently recaptured at Long Beach for each summer data were collected.

differences, therefore, do not occur within the NIX Intensity region that would validate a "high-NIX/high-mortality" scenario (Figs. 2.17 - 2.18).

A K-S test across all years for Copalis [$P(D_{max}<=0.064;n_1=441;n_2=615) = 0.52$] and for Long Beach [$P(D_{max}<=0.066;n_1=273;n_2=460) = 0.44$] found no significant difference in the frequencies of NIX Intensity values between those clams that were released and never recaptured and those clams that were subsequently recaptured. When the data for NIX effects for each summer were analyzed individually, again, no significant differences in the cdfs were detected. Thus, regardless of year, regardless of beach, there were no significant differences in NIX distributions between the clams that survived to be recaptured (known alive) and those that were not recaptured (not known to be alive). Note that 8 of the 25 clams with NIX Intensity > 120 were recaptured at Copalis. This is a 32% recapture percentage, which is consistent with the recapture percentage (42% overall) of biopsied clams in general (Table 2.2). The 1 clam with NIX Intensity > 120 that was released at Long Beach was recaptured.

More clams at Copalis have higher NIX Intensities than at Long Beach. The median NIX Intensity at Copalis for all summers sampled was 11 ($\overline{\text{Nix Intensity}} = 23.1$, se($\overline{\text{Nix Intensity}}$)= 0.96), while the median intensity at Long Beach for all summers sampled was 4 ($\overline{\text{Nix Intensity}} = 8.6$, se($\overline{\text{Nix Intensity}}$)= 0.48)(Figure 2.19, Table 2.6). The mean NIX Intensities at Copalis during the summers of 1990-1992 were within the historical ranges that were thought to have caused population declines. The means during the summers of 1990-1992 were lower than the maximum NIX Intensity observed in 1983 ($\overline{\text{Nix Intensity}} \cong 43$). However, with the extremely skewed distribution and large variance that NIX Intensity readings exhibit, such a difference in means may be attributable to a very small portion of the population exhibiting very high NIX Intensities, not a major shift in the NIX Intensities throughout the population. Although both beaches have very

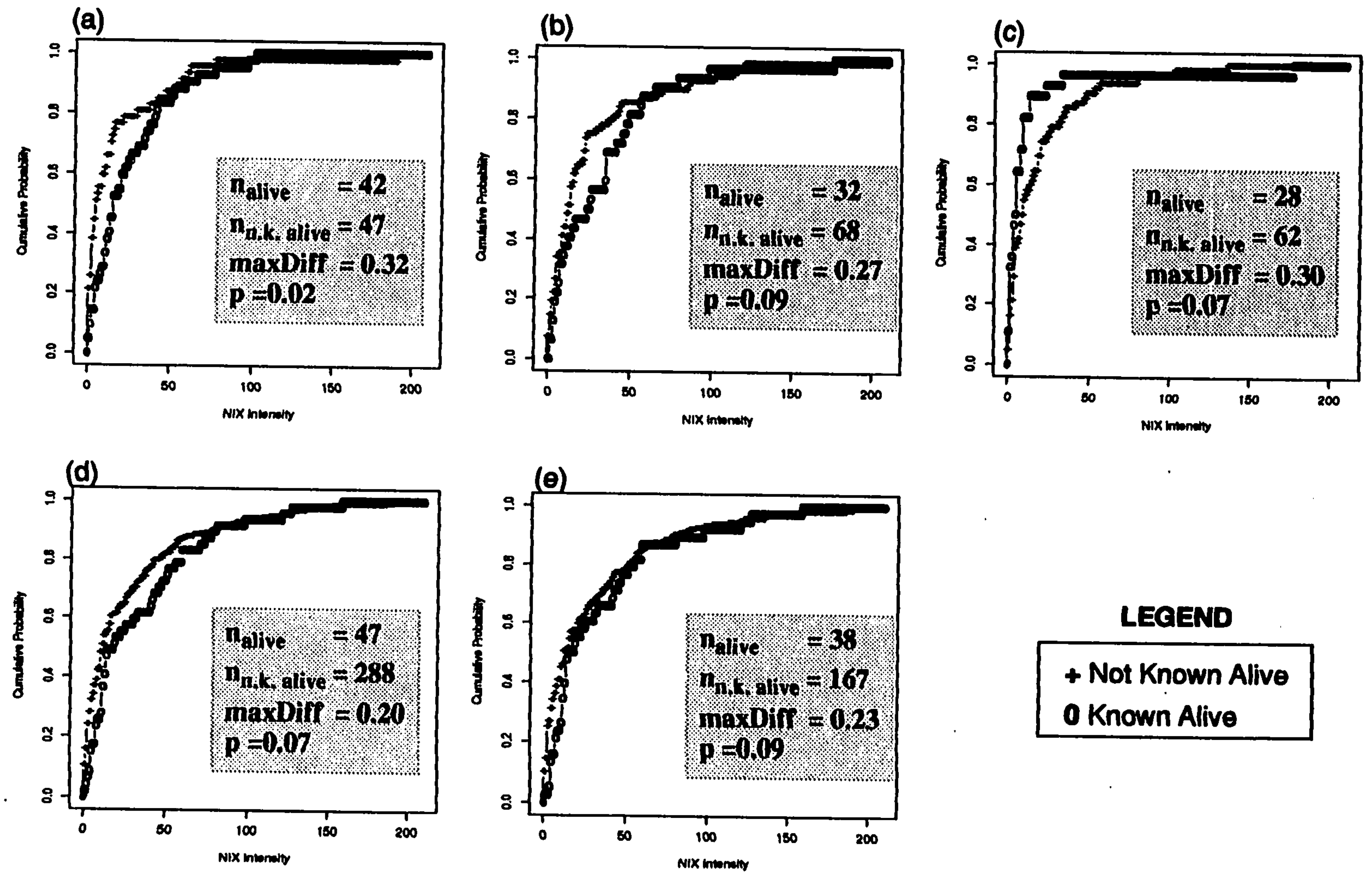


FIGURE 2.16 Empirical Cumulative Distribution Functions for significant ($p<0.10$) KS tests for clams that were (0) and were not (+) known to be alive at Copalis: (a) October 1990 - Area C, (b) September 1991 - Area C, (c) July 1992 - Area C, (d) December 1990 - All Areas, and (e) February 1991 - All Areas.

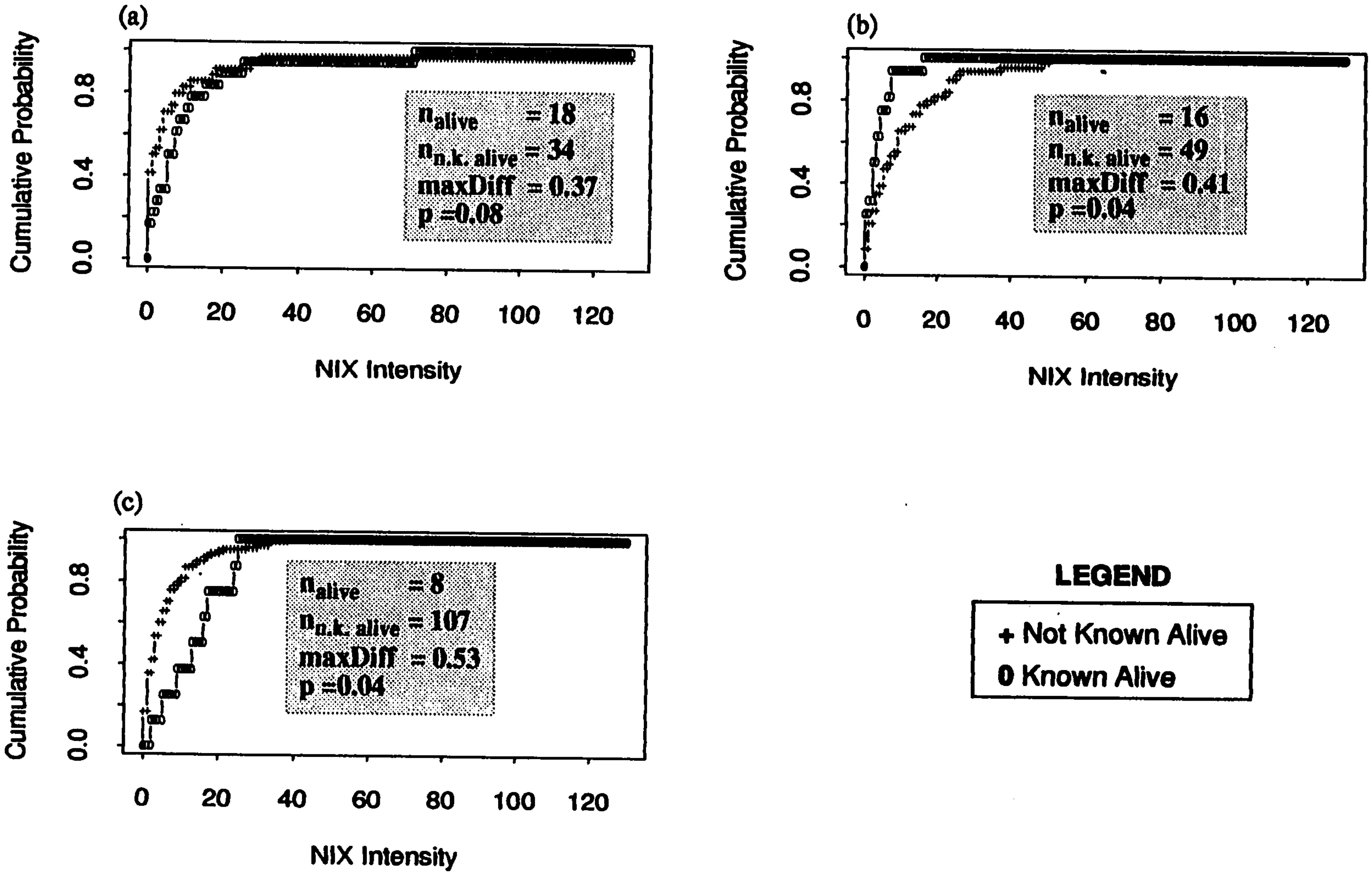


FIGURE 2.17 Empirical Cumulative Distribution Functions for significant ($p<0.10$) KS tests for clams that were (0) and were not (+) known to be alive at Long Beach: (a) April 1991 - Area Y, (b) January 1992 - Area Z, and (c) April 1992 - All Areas.

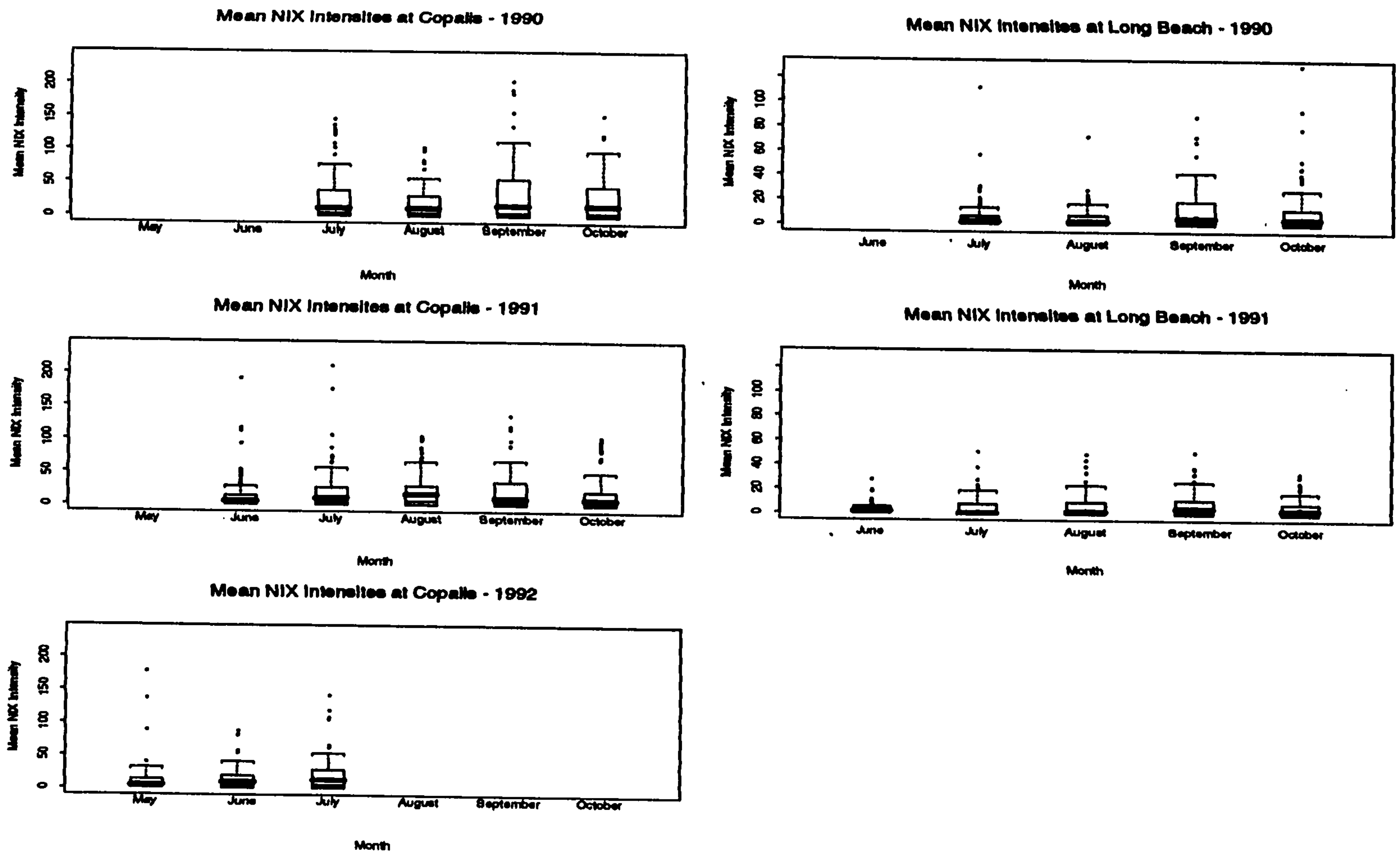


FIGURE 2.18 Box and whisker plots for NIX Intensities for clams at Copalis and Long Beach during the summer and fall of 1990 - 1992. The dark line indicates the median intensity, the box encloses the quartiles (i.e., 25% to 75%), and the whiskers extend 1.5 times the inter-quartile range (~90% CI). Points beyond the whiskers indicate extreme values(i.e., values beyond approximate 90% CI).

Table 2.6: Estimates of monthly NIX Intensity for the summer months of 1990-1992 at Copalis and Long Beach.

Beach	Date	Mean	SE (Mean)	Median	SE (Median)[1]	Maximum
	1990					
Copalis	July	28.5	3.92	11.5	0.48	146
Copalis	August	20.3	2.39	11.5	0.48	104
Copalis	September	37.1	5.37	16	1.51	204
Copalis	October	31.0	4.17	16	1.10	153
Copalis	Combined 1990	28.8	2.02	13	0.64	204
Long Beach	July	7.0	1.38	3	0.00	112
Long Beach	August	6.3	0.91	3	0.36	72
Long Beach	September	14.1	2.28	6	0.73	89
Long Beach	October	13.2	2.28	5	0.36	131
Long Beach	November	11.5	5.96	8	0.00	42
Long Beach	Combined 1990	9.8		4	0.09	131
	1991					
Copalis	June	18.3	3.21	6	0.28	192
Copalis	July	24.0	3.90	11	0.97	212
Copalis	August	23.5	2.45	17	0.72	105
Copalis	September	24.7	3.01	11	0.88	136
Copalis	October	19.1	2.52	9.5	1.00	104

TABLE 2.6 (continued)

Beach	Date	Mean	SE (Mean)	Median	SE (Median)[1]	Maximum
Copalis	Combined 1991	21.4	1.34	10	0.64	212
	1991					
Long Beach	June	3.4	0.40	2	0.00	28
Long Beach	July	8.0	1.13	3	0.47	51
Long Beach	August	10.3	0.98	7	0.33	49
Long Beach	September	9.4	0.99	6	0.39	51
Long Beach	October	7.6	0.90	5	0.46	34
Long Beach	Combined 1991	7.5	0.41	3	0.42	51
	1992[2]					
Copalis	May	14.4	3.96	5	0.74	178
Copalis	June	15.6	1.81	10	0.75	88
Copalis	July	24.2	3.69	13.5	0.81	142
Copalis	Combined 1992	17.8	1.75	10	0.65	178

[1] Estimated using bootstrap sampling.

[2] Long Beach was not sampled on a regular basis after January 1992.

different NIX Intensities, their annual survival estimates were very similar. This too indicates that high NIX does not directly translate into high mortality.

Of the 1053 clams at Copalis that yielded usable NIX readings, only 25 had NIX Intensities greater than 120, and less than 10% of the total clam population was ever found to have NIX Intensities greater than 80 counts. These data were collected exclusively during summer and fall months, when survival drops had been noted, and NIX Intensity increases had occurred previously (Ayres and Simons, 1991). Thus, even if every clam that had high NIX Intensity (NIX > 80) had died, only 10% of the population would have been killed. In order to lose 30-40% of the population due to a NIX-induced mortality event, all clams at Copalis that had NIX Intensities of greater than 20 counts, or all clams at Long Beach that had NIX Intensities of greater than 10 counts, would have to die. Death due to high NIX, therefore, cannot be the sole cause of the decreases in survival that were observed each summer, for there were far too few clams with high NIX to account for the large decreases in survival.

Finally, it was necessary to consider the possibility that length and NIX were highly correlated, such that if one were included in the survival model, the other would be unnecessary. When NIX was plotted against length, there was a small but significant correlation between the two variables ($r = 0.07$ for Copalis, $p = 0.018$; $r = 0.13$ for Long Beach, $p < 0.001$) (Figure 2.20). The square of the correlation coefficient is an estimate of the proportion of variability in one variable (Length) that is explained by its dependence on the other variable (NIX Intensity). The r^2 values for both Copalis and Long Beach are less than 2%. This indicates that length (or age) does not explain much of the variability of NIX within the population. Hence there does not appear to be a relationship between age and NIX that would be strong enough to causes problems in the analysis.

There does appear to be a somewhat stronger relationship between the maximum NIX Intensity and length. When the maximum NIX Intensity was correlated length, there

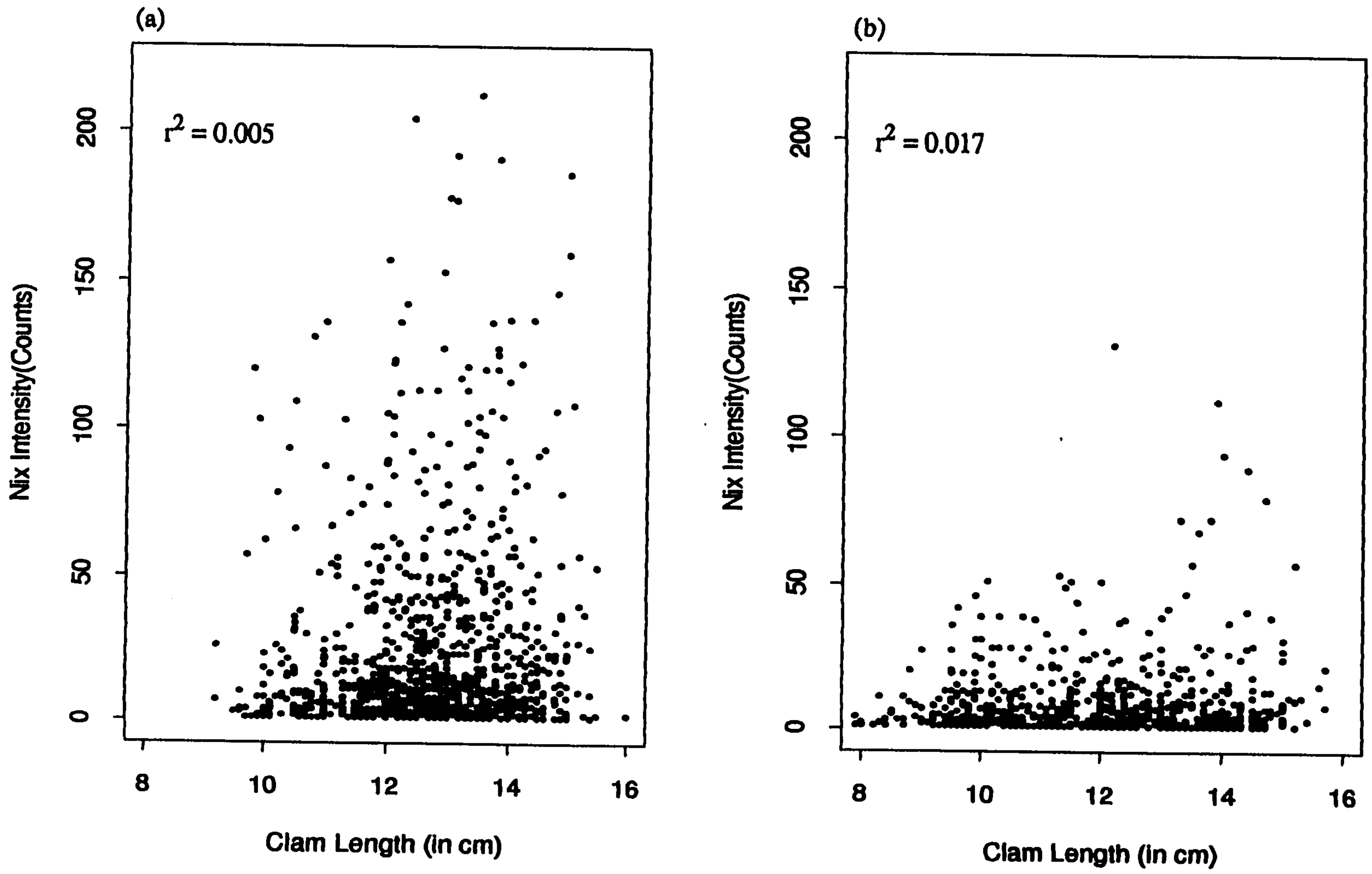


FIGURE 2.19 Correlation between NIX Intensity and Length for (a) Copalis and (b) Long Beach sites. The correlation coefficient ("r") is given for each relationship.

was a significant correlation between the two variables ($r = 0.31$ for Copalis, $p < 0.001$; $r = 0.37$ for Long Beach, $p < 0.001$). However, the relationship is more parabolic than linear, as with larger lengths the maximum NIX intensity begins to lessen. An F-test on the inclusion of the squared term indicates a highly significant ($p=1.84 \times 10^{-5}$ at Copalis and $p=0.001$ at Long Beach) nonlinear trend at both beaches.

2.4.1.7 Assessment of NIX Population Level Effects

The multiple regression analysis (Table 2.7, and Figure 2.21) indicated that there was no significant decrease in survival related to the median NIX Intensity ($p = 0.23$ for 1990, one-tailed; $p = 0.57$ for 1991, one-tailed; $p = 0.44$ for 1992, one-tailed). There appears to be a wide range of survivals associated with each analysis, regardless of the NIX Intensity. This is an indication that survival is largely independent of NIX Intensity. Unfortunately, in 1992 at Copalis, the analysis did not include NIX readings from August and beyond, when the decrease in survival was observed. Despite this shortcoming, given the overall lack of support of a relationship between NIX and survival, it is difficult to believe that a relationship between NIX and survival exists. The lack of a relationship between NIX and survival at the population level supports the findings at the individual level.

2.4.2 ANNUAL JUVENILE SURVIVAL ESTIMATES

2.4.2.1 Annual Juvenile Survival Estimates using the Exponential Decay Model

Evidence from this study indicates that the life-span of the average razor clam along the Washington Coast is three years (i.e., 2 years as a juvenile and 1 year as an adult). If the average life-span was assumed to be three years, the estimate of annual survival under the exponential decay model is 0.72. The theoretical variance under the exponential model is $1/\lambda^2$, which for this example is $1/3^2 = 0.11$. Likewise, if the

Table 2.7: Analysis of Variance Tables to test whether the median NIX Intensity (Table 2.6) is related to survival in razor clams.

a) Results of July - October 1990 at Both Beaches

Source	df	SS	MS	F	P(F)
Corr. Total	23	1.093			
Beach	1	0.025	0.025	0.477	0.498
Nix	1	0.015	0.363	0.287	0.600
Beach x Nix	1	0.000	0.000	0.002	0.965
Residual	20	1.053	0.053		

b) Results of June - October 1991 at Both Beaches

Source	df	SS	MS	F	P(F)
Corr. Total	24	0.639			
Beach	1	0.030	0.030	1.143	0.297
Nix	1	0.055	0.055	2.093	0.163
Beach x Nix	1	0.005	0.005	0.173	0.681
Residual	21	0.549	0.026		

c) Results of May - July 1992 at Copalis Beach

Source	df	SS	MS	F	P(F)
Corr. Total	7	0.			
Nix	1	0.000	0.000	0.025	0.881
Residual	6	0.086	0.014		

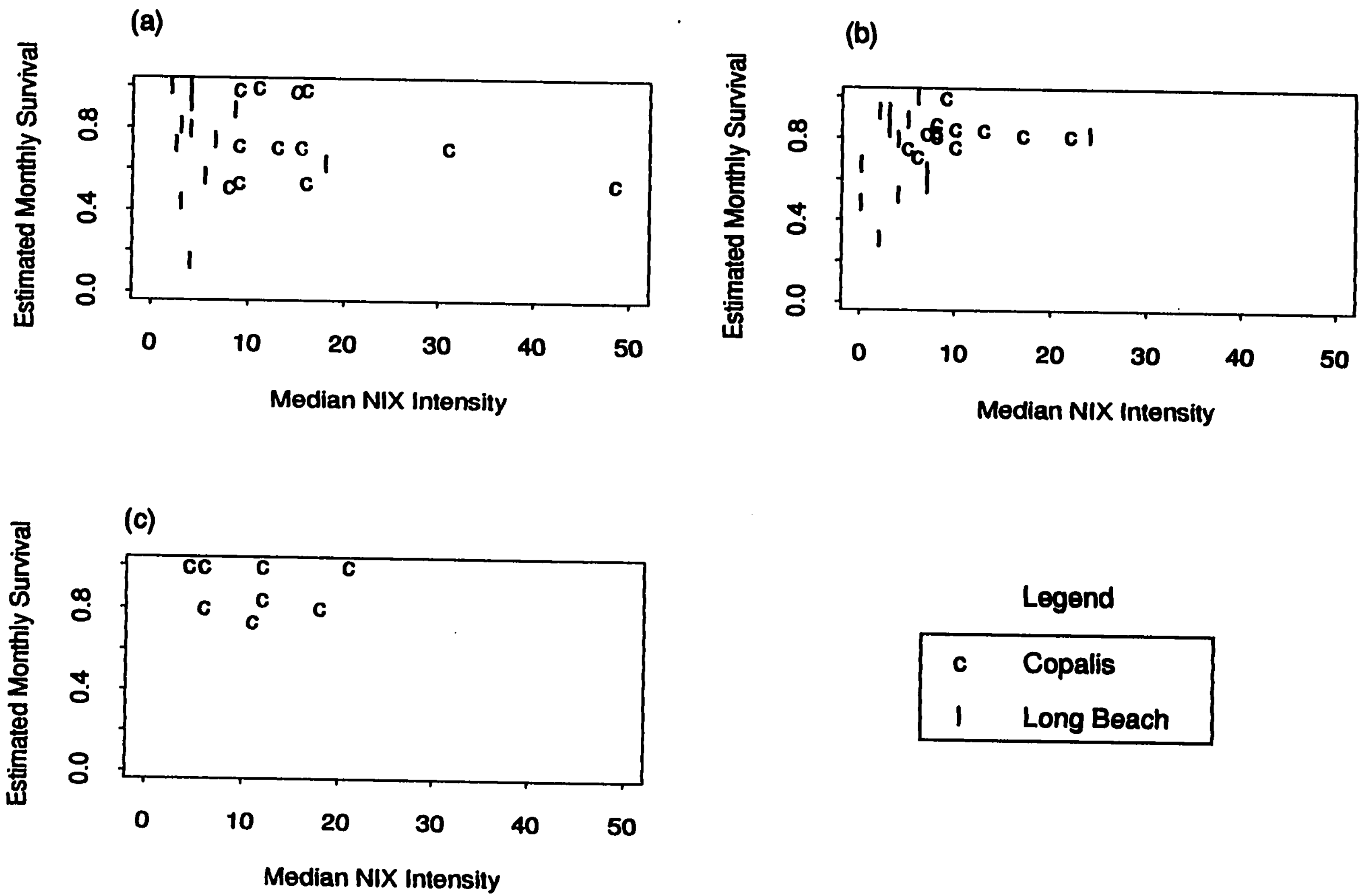


FIGURE 2.20 Relationship between the median NIX Intensity and survival for summer months (Table 2.6) during (a) 1990, (b) 1991, and (c) 1992.

average life-span was assumed to be four years, the estimate of annual survival under the exponential decay model is 0.78 and the theoretical variance is $1/4^2 = 0.06$.

The estimate of annual survival that is derived from the exponential decay model is much greater than the estimate that was derived using the SURPH model (i.e., 0.72 - 0.78 versus 0.36 for the clams from Area "M" (i.e., the handling-reduced case)). The estimate of annual survival that is derived from the exponential decay model, however, assumes constant survival throughout all life-stages, whereas the SURPH model looked specifically at adult survival. The results from the exponential decay model thus imply that juvenile survival is greater than adult survival.

2.4.2.2 Annual Juvenile Survival Estimates using Various Stock-Recruitment Models

The survival estimates that were derived from the population data are highly dependent upon the stock-recruitment model that is assumed. A variety of stock-recruitment models were used to estimate the annual juvenile survival. Parameters for the stock-recruitment models were estimated using the survey data collected by WDFW (See Chapter 4).

When it was assumed that recruitment followed a Ricker Stock-Recruitment Model (Equation 4.2), the estimates of annual survival for the juvenile stage were much higher than the adult survivals that were estimated by SURPH (Table 2.8). The estimates of juvenile annual survival for the two northern beaches (i.e., Mocrocks and Copalis) were approximately twice that of the estimates for the two southern beaches (i.e., Twin Harbors and Long Beach; $\hat{S}$ =1.09 and 0.81 versus 0.41 and 0.51 respectively). The model provided a significant fit at Mocrocks, Copalis, and Long Beach ($p < 0.10$), but the fit of the model to the data was poor (maximum r-squared was 0.19 at Copalis).

Table 2.8: Estimates of annual juvenile survival using the population data and assuming a stock-recruitment relationship.

Beach	Ricker Stock-Recruitment Model (Equation 4.2)	Mean Recruitment Model (Equation 4.27)	Mean Adult Density/ Mean Recruit Density
Mocrocks	1.09 (0.57)	0.51 (0.34)	0.52 (0.18)
Copalis	0.81 (0.30)	0.48 (0.25)	0.50 (0.27)
Twin Harbors	0.41 (0.26)	0.23 (0.21)	0.34 (0.31)
Long Beach	0.51 (0.22)	0.27 (0.22)	0.35 (0.33)

When constant recruitment model was assumed, again the estimates of annual survival for the juvenile stage were much higher than the adult survivals that were estimated by SURPH. However, the survival estimates from the mean-recruitment model (Equation 4.27) were approximately half the values of the estimates from the model that assumed a Ricker Stock-Recruitment Model (Table 2.8). As before, the estimates of juvenile annual survival for the two northern beaches (i.e., Mocrocks and Copalis) were approximately twice that of the estimates for the two southern beaches (i.e., Twin Harbors and Long Beach). The model did not provide a significant fit ($p > 0.14$) at Mocrocks, Twin Harbors, and Long Beach.

The final approach used to estimate the annual juvenile survival was to take the mean adult density at each beach and divide that by the mean juvenile density at that beach. This model assumes that all adults die after age three. The results from this analysis were very similar to the results from the mean recruitment model.

Overall, the model fit was rather poor, regardless of model used. Thus, all estimates of juvenile survival have large standard errors. However, the point estimates of juvenile survival did indicate that juveniles survival better than adults; all estimates from these analyses were higher than the SURPH estimates of adult survival. The estimates of juvenile survival also indicated that the northern beaches had higher juvenile survival than the southern beaches. The SURPH analysis did not indicate that the adult survival was different for Copalis and Long Beach. However, overall the northern beaches typically have greater densities of clams. The results from these models indicate that the reason for larger clam densities in the northern beaches is due to increased juvenile survival, not adult survival.

2.5 DISCUSSION

Factors that significantly affected survival over this three year study were time of the year (month), intertidal location (area), length of the clam, and histology (biopsy).

This implies that within a beach, survival varies according to month, location, and possibly size of the clam. Although each of these effects was significant in at least one period (i.e., month) studied, the only variable that consistently affected survival was month. Survival appears to be better in the winter and spring, and poorer in the late-summer and fall. NIX did not appear to been a significant factor affecting razor clam survival during the summers of 1990-1992.

The monthly survival probability had a typical range of between 0.40 and 1.00. At both Copalis and Long Beach, over the three year time series, a pattern appears evident in the survival. The minimum survival probabilities at both beaches occurred in late-summer or fall, for all Areas "A-C", "X-Z". This corresponds to previous reports of clam die-offs during the summer-fall periods (Doug Simons, WDFW Shellfish Biologist at Montesano, pers. comm.). Clams at both beaches exhibited higher survival in the winter and spring, with winter months the most favorable for survival (Figures 2.2 - 2.4). Both beaches have similar ranges of survival probabilities, similar annual survival, and similar timing of the lowest survival. Of interest is that even though there were declines in estimated survival probabilities in late summer 1990-92, WDFW's fall survey estimates showed no large decreases in clam population numbers across beaches (Dan Ayres, WDFW Shellfish Biologist at Montesano, pers. comm.). As all experimental areas showed decreases in survival, including Area "M", only the timing differed slightly as to which month was the worst for survival, one might expect to see corresponding declines in population levels. The probable reason that large decreases in population levels were not observed is that the timing of the sampling provides too coarse a scale.

The effect that tidal height had on survival probabilities was not constant throughout the study. At Copalis, tidal height was a significant factor during about half of the months. As one moved towards the dunes, the annual survival probability decreased slightly, but all of the point estimates of annual survival probabilities were very close (Table 2.2). Area "A" had many months with high survival, but when survival fell in Area

"A", it typically dropped to levels much lower than in Areas "B" or "C". Because Area "A" does not have many naturally occurring clams, the fact that any clams survived in this region of the beach was quite surprising. As Area "A" had the lowest survival in all years, it appears that this area is least suitable for razor clam habitat. This low survival in Area "A" could be due to a number of factors including the high ghost shrimp concentrations, the long exposure times during low tides and the lack of buffer from freshwater runoff. Regardless, there is little recruitment to this area, and even recruited clams (clams > 10 cm) do not survive in this area as well as in other areas on the beach. However, although the upper portion of the beach is generally considered to be poor razor clam habitat, it can support fully recruited razor clams as well as the other areas during the winter months. The fact that Area "C" had higher survival in 1992 was not only indicated by the survival analysis, but also by observations on the beach. Throughout 1991-1992, ghost shrimp populations expanded into Area "B". Ghost shrimp had been uncommon in the lower sections of the beach in 1990. Coincidentally, the highest densities of clams outside the experimental plots appeared to move seaward, from Area "B" to Area "C". It is unclear whether the appearance of ghost shrimp in an area previously occupied solely by razor clams is due to an environmental change that favors the ghost shrimp or whether ghost shrimp actively out-compete razor clams in areas that are suitable for both. Regardless, razor clams and ghost shrimp are rarely seen occupying the same region of the beach. Thus the increasing ghost shrimp concentrations in the upper beach regions of Copalis Beach do not bode well for razor clams within these same beach regions.

At Long Beach, intertidal location was a significant factor during 10 of 18 months. The two lowest survival estimates appeared in the upper region of the beach, but high survival estimates were evenly distributed among the three sites. Results on Long Beach suggest that the upper beach areas can support larger clams as well as lower beach areas during most months of the year, but that upper beach areas are poor areas for recruitment and suffer tremendous decreases in survival during the late summer-fall declines. These results are similar to those at Copalis.

Overall, annual survival probabilities appear low. The SURPH analyses estimate that the average annual survival probability for the optimal area at Copalis (Jan. 1991 - Dec. 1992) to be 0.11 and the average annual survival probability for the optimal area at Long Beach (Jan. - Dec. 1991) to be 0.08. These results are lower than two previously published estimates of annual survival, which were 0.30 - 0.40 (Nickerson,1975) and 0.48 (Hirschorn, 1962). It should be noted that the current study, like previous studies, was conducted using release-recapture methodology. Using this technique, it is not possible to completely isolate handling-induced mortality from natural mortality. Use of "M" plot has shown that the effects of handling are potentially great. Clams from Area "B" had an average survival probability from March 1991 to March 1992 of 0.09, whereas clams from Area "M" had a survival probability of 0.35. This result is in much closer agreement to the previously published results (Hirschorn, 1962; Nickerson,1975). The greatest decrease in survival at Area "M" apparently occurred in the fall. As the major difference between Area "B" and Area "M" was the difference in frequency of recapture, it appears that handling may induce substantial mortality for clams sampled monthly.

Results of the juvenile survival analyses indicated that survival may be higher for juveniles than for adults. The estimates for juvenile survival using the population data were two to ten times higher ($1.09 \le \hat{S} \le 0.23$) than the estimates of adult survival found using SURPH. Nickerson (1975), who studied clams in Alaska, found that survival increased with increasing age, whereas Link (1980), who studied clams in Oregon, found the opposite trend was evident. However, there is handling mortality associated with the release-recapture technique and this may have reduced the observed adult survival.

NIX and length were the two individual covariates of interest. The effect that length had on capture and survival was investigated using several different techniques. At Copalis, a K-S test of significance showed that the distributions were not similar (P(Dmax=)<0.02) for clams that were and clams that were not recaptured. Typically, smaller clams were recaptured less frequently than expected, and medium sized clams were captured more frequently than expected. At Long Beach, there were drastic differences between the distributions of clams released and clams recaptured (P(Dmax=)<0.001). In particular, smaller clams (9 - 10 cm) had a higher propensity for recapture than did medium clams (12-13 cm). At Copalis, such a trait would escape our detection since few clams smaller than 10 cm were utilized. At Long Beach, since the average size tends to be smaller, I was forced to use smaller clams. This K-S test, although useful, does not allow us to differentiate between length-mediated capture and survival processes.

In two of the summers studied (i.e., 1990 and 1992), survival decreased as size increased. However, only in 1992 at Copalis was the length effect on survival significant (p=0.03). During the summer of 1992, a 14-15 cm clam was half as likely to survive a given month as a 10-11 cm clam.

If NIX significantly reduces survival, the effect would be most likely detected during the late-summer to fall declines in survival. However, all efforts to quantify the effect of NIX on survival indicated no relationship. The evidence for no effect of NIX are as follows:

1. The K-S test showed no significant differences between the distributions of clams that were and were not recaptured at either Copalis (p=0.52) or Long Beach (p=0.44). At Copalis, the region where the two distributions were furthest apart was in the region (20 < NIX Intensity < 40), not the high NIX categories (i.e., NIX Intensity < 80).

2. Although there were SURPH survival-models in which the inclusion of NIX provided a significantly better fit to the model, for most periods and populations, the effects of NIX were in the wrong direction (Table 2.5) and the effects were acting within the wrong range of the data. For example, in Figure 2.18 and Table 2.5, notice that for October 1990, at Area "C", there is a

significant difference in the distributions of NIX for those clams that are known to be alive and those clams that are not known to be alive. However, upon closer examination, it becomes apparent that the significant difference between the two distributions occurs at low NIX Intensities (NIX < 40), and that the significant difference is in the wrong direction to indicate a NIX effect caused by high NIX Intensities. This data set shows that fewer of the low NIX individuals are known to be alive than would be expected if there were no NIX effect. What one would expect to see if there were truly a NIX effect would be no difference between the lines in the lower NIX Intensities, but large differences in the upper regions, with the "known alive" line to reach 1.00 at NIX values much lower than the "not known alive" line.

3. The data also indicate that clams at Long Beach have lower NIX Intensities than clams at Copalis. Clams from Long Beach have a lower mean and median NIX Intensity than do clams at Copalis. When the population-wide NIX Intensities were compared to survival, again no relationship between NIX and Survival emerged.

4. Of the 1053 clams at Copalis that yielded usable NIX readings, only 25 had NIX Intensities greater than 120, and less than 10% of the total clam population was ever found to have NIX Intensities greater than 80 counts. These data were collected exclusively during summer and fall months, when survival drops had been noted, and NIX Intensity increases had occurred previously (Ayres and Simons, 1991). Thus, even if every clam that had high NIX Intensity (NIX > 80) had died, only 10% of the population would have been killed. In order to lose 30-40% of the population due to a NIX-induced mortality event, all clams at Copalis that had NIX Intensities of greater than 20 counts or all clams at Long Beach that had NIX Intensities of greater than 10 counts would have to

die. Death due to high NIX, therefore, cannot be the sole cause of the decreases in survival that were observed each summer, for there were far too few clams with high NIX to account for the large decreases in survival.

5. Finally, the survival probabilities at both beaches are similar, yet the maximum intensity of NIX varies greatly between the two beaches. If NIX is to have a significant effect on survival, it cannot be solely a function of the absolute intensity (i.e., Survival = f(NIX Intensity)).

This study was initiated to quantify the effect of NIX on survival. The analyses in this chapter do not support the implication that NIX is detrimental to the survival of the razor clams. At the three scales (i.e., within an individual, within a beach population, and across beaches) that were studied, there was no evidence of decreased survival with increased NIX. The study did suggest that survival was seasonal, with decreased survival occurring during the late-summer and fall. The study also suggested that survival of the unfished adults was possibly lower ($0.10 < \hat{S} < 0.35$) than expected, although near the range of some other studies (Hirschorn, 1962; Nickerson,1975). These results suggest that adult razor clams along the Washington coast experience high natural mortality that is unrelated to NIX. Therefore, NIX can be ignored when future management policies are developed.

Chapter 3

Growth

3.1 INTRODUCTION TO RAZOR CLAM GROWTH

The idea of metabolic scope (Fry, 1947; Bayne *et al.*, 1985), implies that during times of high food supply and low stress, growth may be accelerated; while at times of either low food or high stress, growth may be limited. A commonly observed cycling of growth occurs due to seasonal availability of food. In many animals, seasonal growth is evident from annuli on hard parts (i.e., bones, scales). In fish, the scales and otoliths often show indications of annual growth patterns (Cushing, 1981; Gulland, 1983; Johnson and Stickney, 1989). The razor clam, like other molluscs, shows patterns of irregular growth on its shell. It is thought that during times of accelerated growth, the growth bands that are deposited are widely spaced. During times of reduced growth, however, growth bands are deposited closely, resulting in "growth checks". Both the periodicity of the growth checks evident on razor clam shells and their interpretation are uncertain (Ayres and Simons, 1991). However, based on these irregularly spaced growth rings, it is possible that razor clams along the Washington coast exhibit seasonal growth.

The analysis in this section attempts to characterize and estimate seasonal growth for the razor clams along the Washington coast. Hirschhorn (1962) observed that razor clams along the Oregon coast had accelerated growth in the spring and summer (March - July), and greatly reduced growth in the fall and winter (August-March). I use these cut-off dates and compare spring-summer versus fall-winter growth for clams along the Washington coast. I also attempt to determine whether handling and biopsy procedures that are part of the release-recapture study (Chapter 2) can affect growth. Finally, the effect of NIX on growth is examined. Management models that incorporate seasonal growth may behave quite differently than those that ignore the seasonality. If there is no growth, but high mortality during a certain portion of the year, harvesting before this time period will yield very different results than harvesting after this time period.

3.2 DESCRIPTION OF DATA

Two data sets were utilized to test whether seasonal growth of the razor clam along the Washington coast could be verified. The first data set was from area "M". Area "M" was established on Copalis Beach in March 1992, adjacent to Area "B" (Figure 2.1). Area "M" was established specifically to study growth and mortality of naturally recruited clams (i.e. clams > 70 mm) subjected to reduced handling. Clams from area "M" were used to measure growth of clams from March 1992 to either July or August 1992, and from March 1992 to either March or May 1993. The length of time between adjacent measures was dictated by the occasion on which a clam was recaptured. The length of each clam was measured along its longitudinal axis (Figure 3.1). The clams were then uniquely marked, released, and recaptured four, five, twelve, or thirteen months later. At each recapture occasion, the clams were measured. As handling is presumed to cause growth checks (i.e., evidence of decreased growth due to stress), growth data were collected only for the periods where the interval between a clam's release and its next recapture occasion exceeded three months. Thus, no growth data were collected for the interval from July 1992 to August 1992, nor were growth data collected for the interval March 1993 and May 1993. A total of 218 animals were used in the analysis.

The second data set that was utilized came from those animals that were used during the release-recapture survival study (Chapter 2). Animals at Copalis, from Areas "A", "B", and "C" (Figure 2.1), were extracted from the full data set using the following criteria:

1) Released during March, April, May, July or August, and

2) Recaptured more than 2 months after initial release, and

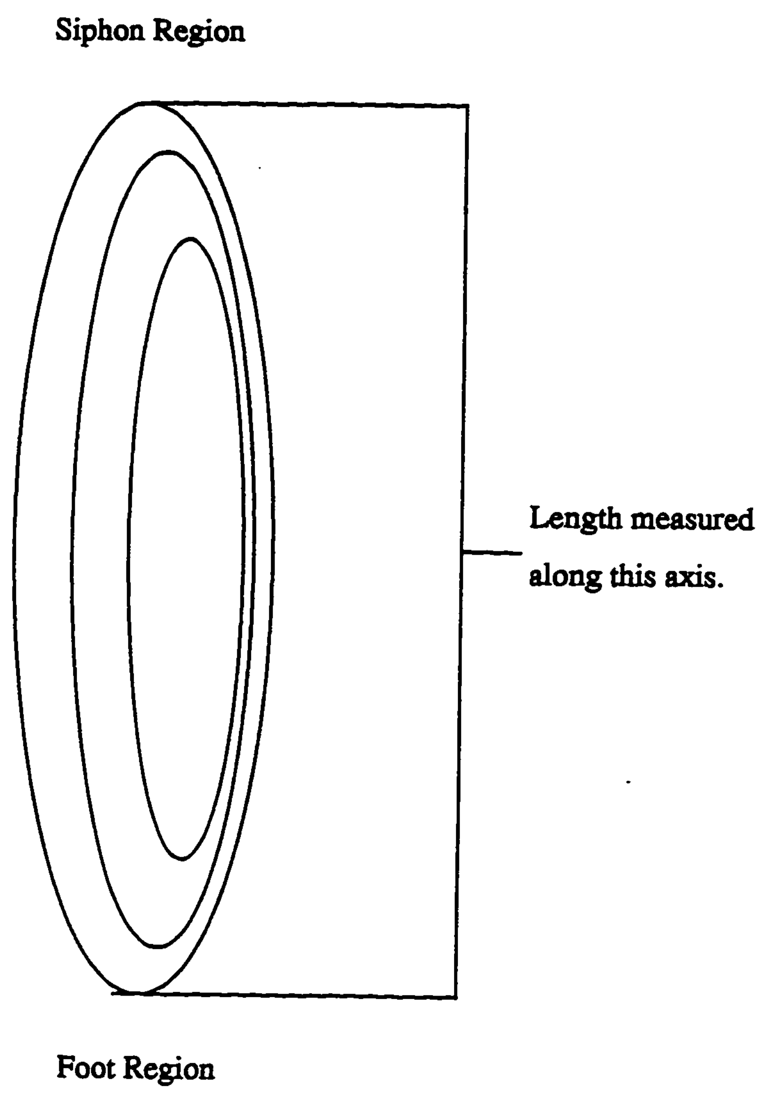


FIGURE 3.1 Schematic of an adult razor clam, showing axis used to measure length.

3) Recaptured at most 4 times from initial release to final recapture date.

These criteria were initiated in an effort to duplicate the conditions that were observed in Area "M". A total of 577 animals (96 with usable NIX readings) were extracted from Areas "A", "B", and "C" over the three years of the study. A fraction of the animals that were included in this data set were biopsied. Analysis of the biopsied animals was used to reveal whether the biopsy procedure had a measurable effect on the growth rate. Additionally, growth parameters for clams with multiple recapture histories were compared to those with single recapture histories over the same time interval. This comparison was used to give an estimate of the decrease in growth associated with a handling event.

Data collected during the release-recapture studies during 1990-93 come from larger clams (> 70 mm), and, thus, contain no information on growth in pre-recruited clams. However, estimates of monthly growth for smaller clams are available in the literature (Hirschhorn, 1962; Tegelberg, 1964; Tegelberg and Magoon, 1969). The published juvenile growth rate could be used in conjunction with the adult growth rates estimated from this study for use in a simulation model.

Using "change-in-length" as a proxy for growth is not without its problems, as shell growth and soft tissue growth in marine bivalves are not consistently co-occurring (Hilbish, 1986; Harvey and Vincent, 1990). However, for the purposes of this study, "change-in-length" will be used as a proxy for growth.There are good reasons for using the length as a growth surrogate. First, in the past, management decisions have been made based upon the strength of certain length classes in the population. There is reason to believe that future management decisions will continue to be based upon such a criterion. Second, measuring the length is both rapid and non-destructive. This allows for the collection of a large data set, without excessive adulteration of the metric being measured. And third, razor clams can retain large quantities of water within their viscera. Measures of wet-weight could be substantially affected by the amount of water retention, independent of dry-weight.

3.3 METHODS

3.3.1 OVERVIEW

Growth equations are often modelled with one of three functional forms, either the von Bertalanffy, the Gompertz, or the logistic (Cobb and Caddy, 1989). The von Bertalanffy growth equation is useful because it provides parameters with biological interpretations. The von Bertalanffy growth equation is described by three parameters, "L_∞", "k" and "t_0". The curve that is generated by the von Bertalanffy equation is typified by a strictly decreasing, positive first derivative with increasing age (length), and a single asymptotic maximum length. The parameter "L_∞" describes the maximum length of the organism, while the parameter "k" describes the annual rate at which the organism approaches this maximum (Ricker, 1975). Razor clam growth was modelled using variations on the von Bertalanffy growth equation (Equation 3.1).

$$l(t) = L_\infty [1 - e^{-k(t - t_0)}] \quad \text{(EQ 3.1)}$$

where

$l(t)$ = length at time "t",

L_∞ = maximal length attained,

k = intrinsic growth rate, and

t_0 = hypothetical age at time zero.

As there is a high correlation between L_∞ and k (Gallucci and Quinn, 1979), a reparameterization of the von Bertalanffy was used whenever possible. The reparameterized form of the equation is:

$$l(t) = \frac{\omega}{k}[1 - e^{-k(t-t_0)}] \quad \text{(EQ 3.2)}$$

where

$\omega = L_\infty k$ (Gallucci and Quinn, 1979),

and all other parameters are defined as previously.

3.3.2 MODIFIED FORD-WALFORD ANALYSIS (Area "M")

Data from Area "M" were analyzed using a modified Ford-Walford plot, which is derived from the von Bertalanffy equation (Equations 3.1 and 3.2). Because data consist of measurements over a known interval, the interval measurements can be substituted into Equation 3.3, and the linear relationship between l_t (i.e., the length of an individual at an initial point in time) and l_{t+T} (i.e., the length of an individual at some interval of time beyond the initial observation) derived (Gulland, 1983). The linearized form of this equation is

$$l_{t+T} = L_\infty(1 - e^{-kT}) + l_t e^{-kT}. \quad \text{(EQ 3.3)}$$

When T=1 year, and l_{t+T} is regressed on l_t, the regression is known as the Ford-Walford plot. A linear equation of the form Y = a + bX is produced. where the intercept "a" = $L_\infty(1 - e^{-kT})$ and the slope "b" = e^{-kT}. The "natural" parameters "k" and "L_∞" can be extracted algebraically.

In the modified Ford-Walford plot, the time "T" can be any interval of time. However, the value of "k" must be reinterpreted. The length of the clam at time "t+T" is regressed on the length at time "t", and the parameters "L_∞" and "k" (or "omega" and "k") are estimated from the regression. The procedure is termed "modified" because data were collected over non-standard intervals (i.e., time intervals that are not equal to one year), yet the final estimate will be an annual rate of increase. In order to computed the annual rate of growth, the parameter that is estimated from the regression procedure must be scaled by the inverse of the time interval over which the data was collected. For example, if the data were collected quarterly, then the estimate of "k" from the modified Ford-Walford would be the quarterly estimate. To get the annual rate of growth, the estimate must be multiplied by $\left(\frac{1}{4}\right)^{-1}$. The extrapolated estimate will approximate the annual growth rate if the growth rate is time-invariant. The non-standard growth rates that were estimated to annual growth rates were transformed for two reasons. First, the extrapolation from a non-standard growth rate to an annual growth rate is used to compare growth rates on a common time scale. Second, the standard growth rate parameter "k" in the literature is an annual rate.

To determine whether differences in seasonal growth were present, the omega (ω) parameter was utilized, as it contains information about both "k" and L_∞. The variance of omega was computed using the delta method of variance estimation (Seber, 1982). Previously, the estimates of omega were assumed to fit a normal distribution (Gallucci and Quinn, 1979). I used a weighted one-way ANOVA to test whether the estimates of spring-summer growth differed significantly from the estimates of fall-winter growth. The weights I used in the analysis were inversely proportional to the estimated variances of the omega (ω) parameters.

The modified Ford-Walford technique was used for the data from area "M" because all the clams were released in March 1992, and recaptured in either July 1992, August 1992, March 1993 or May 1993. A separate regression was produced for each of the time spans March-July, March-August, March-March and March-May.

Data from areas "A", "B", and "C" were not analyzed using the modified Ford-Walford technique. The primary reason for not using the Ford-Walford technique is that the time of initial release and the time of resighting were not constrained to the same intervals as in Area "M". Thus, very few clams would be available for any single regression analysis. There are also related problems associated with the timing of the seasonality, that cannot be sufficiently addressed using this second data source. In the area "M" data set, all clams were released in early March, then recaptured in July or August, then recaptured again in March-May of the subsequent year. Spring-summer growth for the area M clams was defined as growth that occurred between March and August, regardless of over which month(s) the growth occurred. Similarly, fall-winter growth was defined as growth that occurred between July-August and March-May. However, to get a large enough sample size from areas "A", "B", and "C", clams were selected from releases that occurred over a range of adjacent months. Because the temporal scale of seasonal growth is unknown, it was difficult to correctly classify the data. Any attempt to assign a fractional amount of growth to each month becomes arbitrary, and if the growth rate is time-variant, the assignment will influence the results. For example, if the spring-summer growth rate is constant from March-August, then a fractional assignment related to the amount of time exposed will be sufficient, because the growth rate is constant within the interval. If, however, all the spring-summer growth occurs between March and April, then only those clams released in March will experience spring-summer growth, while those released in April-August will not.

3.3.3 NONLINEAR ANALYSIS (Area "M"; Areas "A", "B", "C")

As an alternative to the modified Ford-Walford technique, a nonlinear regression analysis was also conducted. Equation 3.1 has three parameters that must be estimated, L_∞, "k", and "t_0". The parameter "t_0" is a nuisance parameter and has little application in my investigations. Rather than estimate an initial time of growth (i.e. "t_0"), as required in the typical von Bertalanffy growth equation, Equation 3.1 was rearranged and a variation of the form described in Gulland (1983) was used

$$\Delta l_{(T)} = (L_\infty - l_t) \cdot (1 - \exp(-(k \cdot [T_{SS} + T_{FW}]))) \qquad \text{(EQ 3.4)}$$

where:

$\Delta l_{(T)}$ = change in length observed from time "t" to time "t+(T_{SS}+T_{FW})",

L_∞ = asymptotic length,

l(t) = length at time "t",

T_{SS} = number of weeks that the clam was exposed to Spring-Summer conditions,

T_{FW} = number of weeks that the clam was exposed to Fall-Winter conditions, and

k = intrinsic rate of growth (or k_{SS} and k_{FW} if seasonal growth rates were appropriate).

This version (Equation 3.4) of the von Bertalanffy equation is more applicable to release-recapture data, as the change in length, the initial length, and the time between subsequent measurements are all observable quantities.

To account for changes in growth due to handling, biopsy or NIX, parameters were added to equation 3.3 in the following manner:

1. If the factors affecting growth change the maximum length attained, the effects could be modelled as a linear function of L_∞, as

$$\Delta l_{(T)} = (L_\infty + \underset{\sim}{\beta} \underset{\sim}{X} - l_t) \cdot (1 - \exp(-(k \cdot [T_{SS} + T_{FW}]))) \qquad \text{(EQ 3.5)}$$

2. If instead, the factors affecting growth change the growth rate, the effects could be modelled as a linear function of "k", as

$$\Delta l_{(T)} = (L_\infty - l_t) \cdot (1 - \exp(-(k \cdot [T_{SS} + T_{FW}] + \underset{\sim}{\beta} \underset{\sim}{X}))) . \qquad \text{(EQ 3.6)}$$

where:

$\underset{\sim}{X}$ = matrix of the number of times an individual clam was handled, an indicator of whether the clam was biopsied and the NIX Intensity.

The additional terms in the von Bertalanffy equation that allow for seasonality are similar to the generalized differential equation used to model seasonal effects in flathead sole (Hanumara and Hoenig, 1987) and have the effect of incrementally increasing the growth during the growing seasons, rather than simply allowing growth during some seasons and forcing no growth during other seasons. For the sake of completeness, changes in growth that are the result of handling, biopsy or NIX were modelled both as an effect on "L_∞" and as effect on "k". As mentioned previously, there is a strong correlation between the estimates of "L_∞" and "k". Therefore, although the model fitting routine may imply that a specific effect is best modelled solely as either a function of "L_∞" or a function of "k", to conclude that the effect is independent of the other parameter would be inappropriate.

The nonlinear analysis should give estimates of the seasonal growth parameters that are more precise than the estimates from the modified Ford-Walford analysis. First, the nonlinear analysis uses all the data in a single analysis. Thus the sample size for the single nonlinear analysis will be much greater than the sample size for any one of the modified Ford-Walford analyses. Second, the nonlinear analysis results in fewer parameters estimates overall. For each modified Ford-Walford analysis, the value of "k" and the value of "L_∞" are estimated. Thus, for the four periods that are investigated herein, a total of eight parameters are estimated. There is no reason to believe that there are four separate values of "L_∞", but in order to maintain the linear construct of the Ford-Walford, the analysis can only be conducted on releases which share the same "T" (i.e., the measure of time that has passed since the original release). The nonlinear analysis explicitly incorporates the time dimension into the analysis. Therefore, the nonlinear analysis estimates three parameters if growth varies seasonally (i.e., k_{SS},k_{FW}, and L_∞), and only two parameters (i.e., k and L_∞) if growth is not seasonally dependent.

I assumed an additive normally-distributed error about the change in length (Equation 3.4). Although the change in length should be strictly positive, measurements of the change in length are sometimes negative due to measurement errors. I used an F-test to test the significance of additional parameters (Bates and Watts, 1988; Seber and Wild, 1989) to a model that included an annual "k" and "L_∞". A forward stepwise procedure was followed and the order of entry for each of the additional parameters was based on the reduction of the sums of squares.

3.4 RESULTS

3.4.1 MODIFIED FORD-WALFORD ANALYSIS (Area "M")

The modified Ford-Walford regression provided reasonable fits to the data (Figure 3.2; Tables 3.1 and 3.2). Both estimates of the annual growth rate (k) extrapolated from the spring-summer intervals were similar ((a) $\hat{k} = 1.20 \cdot yr^{-1}$ March-July 1992; (b)

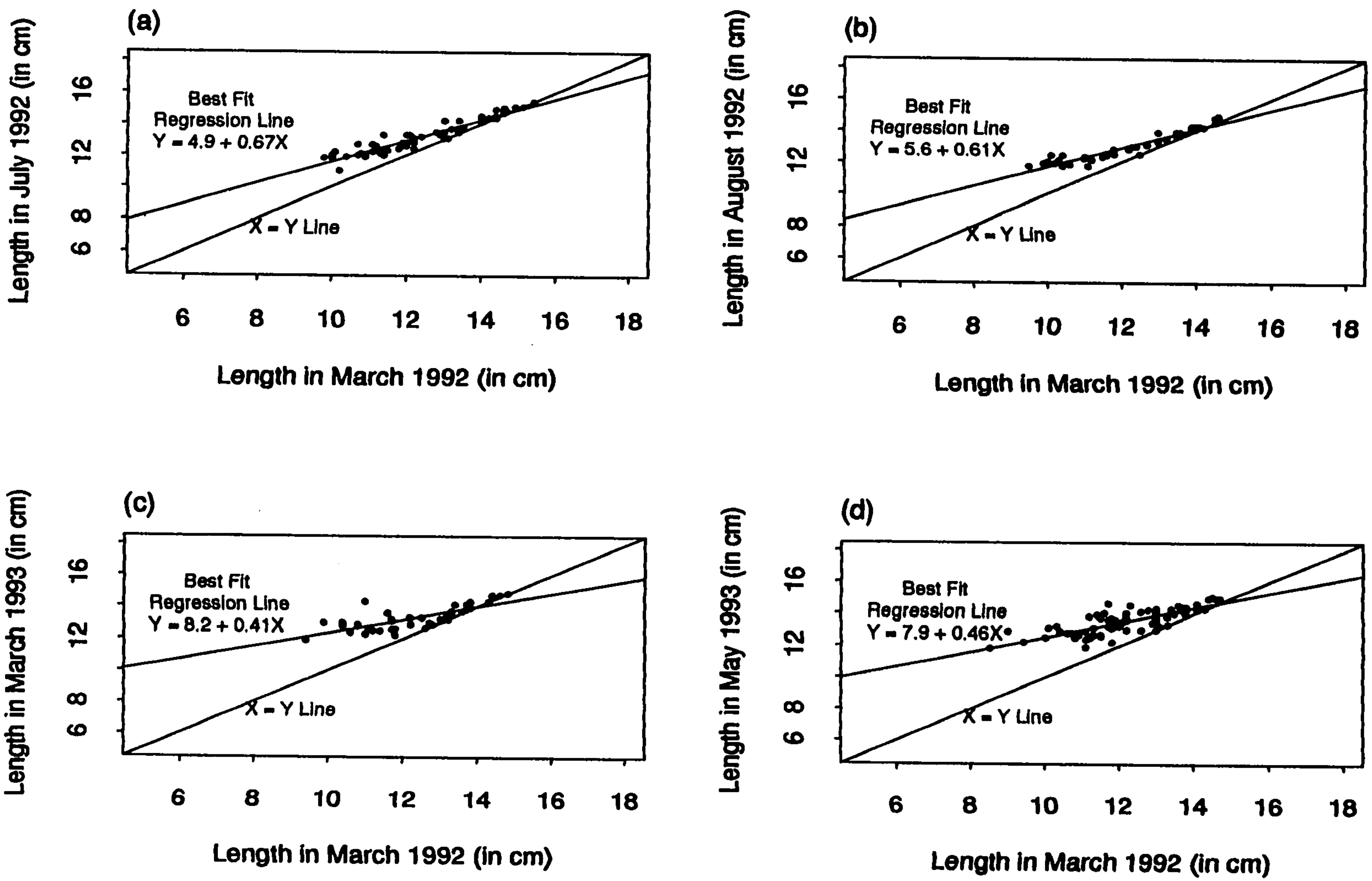


FIGURE 3.2 Modified Ford-Walford plots for razor clams (a) released in March 1992 and recaptured in July 1992, (b) released in March 1992 and recaptured in August 1992, (c) released in March 1992 and recaptured in March1993, and (d) released in March 1992 and recaptured in May 1993.

Table 3.1: ANOVA tables for the modified Ford-Walford analyses of Area "M".

(a) March 1992 - July 1992

Source	df	SS	MS	F	P(F)
Corrected Total	63	74.035			
Slope	1	67.269	67.269	616.43	<0.001
Residual	62	6.766	0.109		

(b) March 1992 - August 1992

Source	df	SS	MS	F	P(F)
Corrected Total	41	39.906			
Slope	1	36.694	36.694	457.00	<0.001
Residual	40	3.212	0.080		

(c) March 1992 - March 1993

Source	df	SS	MS	F	P(F)
Corrected Total	39	20.952			
Slope	1	12.552	12.552	56.80	<0.001
Residual	38	8.400	0.221		

(d) March 1992 - May 1993

Source	df	SS	MS	F	P(F)
Corrected Total	71	45.020			
Slope	1	29.642	29.642	134.93	<0.001
Residual	70	15.378	0.220		

Table 3.2: Estimated parameters of the von Bertalanffy growth equations from Area "M".

Season	Equation	Estimation Procedure	Parameter	Parameter Value	Standard Error
(a) Spring-Summer	3.3	Ford-Walford	k	1.20	0.12
(March-July)			L_∞	14.8	0.26
			ω	17.75	1.62
(b) Spring-Summer	3.3	Ford-Walford	k	1.21	0.11
(March - August)			L_∞	14.3	0.18
			ω	17.23	1.85
(c) Annual	3.3	Ford-Walford	k	0.89	0.13
(March-March)			L_∞	14.0	0.20
			ω	12.40	2.21
(d) Annual	3.3	Ford-Walford	k	0.72	0.08
(March - May)			L_∞	14.7	0.21
			ω	10.55	1.37
Spring -Summer	3.4	Nonlinear	k	1.14	0.08
			L_∞	14.5	0.11
			ω	16.53	1.15
Fall - Winter	3.4	Nonlinear	k	0.44	0.07
			L_∞	14.5	0.11
			ω	6.38	0.96

$\hat{k} = 1.21 \cdot yr^{-1}$ March - August 1992), as were both estimates of "L_∞" ((a) 14.8 cm March - July 1992; (b) 14.3 cm March-August 1992). Additionally, both estimates of the annual growth rate were similar ((c) $\hat{k} = 0.88 \cdot yr^{-1}$ March 1992 -March 1993; (d) $\hat{k} = 0.72 \cdot yr^{-1}$ March 1992 - May 1993), as were both estimates of "L_∞" ((c) 14.0 cm March 1992 - March 1993; (d) 14.7 cm March 1992 -May 1993). Mathematically, these growth rates imply that almost all growth occurs between March and August (i.e., k_{SS} is high), and no growth occurs between August and March (i.e., k_{FW} is low). Data from clams that were recaptured in July 1992 and again in May 1993 (n=7), had an estimated annual growth rate (i.e., k_{FW} extrapolated to an annual rate) for the fall-winter interval of $0.24 \cdot yr^{-1}$. This demonstrates that although the growth rate during the winter is not quite zero, it is much less than the growth rate experienced during the summer months. Although all estimates of "L_∞" are similar, they are smaller than the size of the largest clam observed (16.0 cm). This is because the "L_∞" that is computed is the average "L_∞" from the regression relationship, and can be smaller than the observed maximum. An alternative analysis can be constructed where "L_∞" is set as the maximum observed, and only "k" is estimated. When "L_∞" was fixed at the maximum observed value, the four estimates of "k" were very similar to the results when both parameters (i.e., "k" and "L_∞") were estimated (compare estimates in Table 3.2 to estimates in Table 3.3). In all cases, however, setting the maximal length and estimating only "k", rather than estimating the maximal length, caused the point estimate of "k" to drop. This occurs because of the strong negative correlation between the two parameters.

Using the four estimates of "k" and "L_∞" from the modified Ford-Walford regressions, values of omega (ω) were computed (Table 3.2) using Equation 3.2. A one-way weighted ANOVA was used to determine whether the estimates of the annual growth

Table 3.3: Estimated parameters of the von Bertalanffy growth equations from Area "M" with L_∞ fixed at the maximal length observed in the data set.

Season	Equation	Estimation Procedure	Parameter	Parameter Value	Standard Error
Spring-Summer	3.3	Ford-Walford	k	0.96	0.05
(March-July)			L_∞	15.40	0.00
			ω	14.83	0.77
Spring-Summer	3.3	Ford-Walford	k	0.95	0.05
(March - August)			L_∞	14.90	0.00
			ω	14.19	0.75
Annual	3.3	Ford-Walford	k	0.57	0.05
(March-March)			L_∞	14.80	0.00
			ω	8.43	0.74
Annual	3.3	Ford-Walford	k	0.57	0.03
(March - May)			L_∞	15.00	0.00
			ω	8.62	0.45
Spring -Summer	3.4	Nonlinear	k	0.80	0.04
			L_∞	15.40	0.00
			ω	8.62	0.62
Fall - Winter	3.4	Nonlinear	k	0.27	0.04
			L_∞	15.40	0.00
			ω	4.16	0.62

rate measured during the spring-summer period differed significantly from the estimates of annual growth rate measured on an annual time scale. The analysis indicated that the omega (ω) parameter for the extrapolated "k" based on spring-summer growth was significantly different than the omega for the observed annual growth (Table 3.4; $p = 0.018$).

3.4.2 NONLINEAR ANALYSIS (Area "M"; Areas "A - C")

The nonlinear analysis of data from Area "M" (Table 3.5) indicated that seasonal "k" parameters should be included in the model ($p < 0.001$). The analysis indicated that the spring-summer growth rate was 3 times faster than the fall-winter growth rate. The estimate for the spring-summer "k" was $1.14 \cdot yr^{-1}$, whereas the estimate of the fall-winter "k" was $0.44 \cdot yr^{-1}$ (Table 3.1). These parameters are slightly different than those estimated using the Ford-Walford plot, but the conclusions are similar. The major reason that the parameter estimates are different is that the modified Ford-Walford analyses consisted of four separate analyses, whereas the nonlinear analysis was a single analysis using all of the data. In the modified Ford-Walford analysis, four separate estimates of "L_∞" and four separate estimates of "k" (Table 3.2) were estimated. In the nonlinear analysis, a single estimate of "L_∞" and two seasonal estimates of "k" (Table 3.2) were estimated. There is no reason to expect that each interval should have a separate "L_∞". This was simply an artifact of the Ford-Walford procedure used to conduct the analysis. This artifact is not present in the nonlinear analysis, because the time interval is explicitly incorporated into the nonlinear analysis. As expected, the parameter estimates from the nonlinear analysis are more precise, which improved our ability to detect the seasonal difference ($p = 0.018$ for the modified Ford-Walford vs. $p < 0.001$ for the nonlinear analysis).

Table 3.4: ANOVA table to test whether the omega parameters from the spring-summer growth vary from those of annual growth. The values of the omega parameters were calculated from the modified Ford-Walford analyses of Area "M" (Table 3.2).

Source	df	SS	MS	F	P(F)
Corrected Total	3	15.157			
Season	1	14.616	14.616	53.99	0.018
Residual	2	0.541	0.271		

Table 3.5: ANOVA table for the nonlinear analysis of Area "M".

Source	df	SS	MS	F	P(F)
k_{Yr}, L_{∞}	2	315.949	157.975	$F_{2,215} = 940.32$	<0.001
k_{Season}	1	6.416	6.416	$F_{1,215} = 38.19$	<0.001
Residual	215	36.025	0.168		

The analysis indicated that for clams in Areas "A", "B", and "C", handling and biopsy procedures significantly decreased the growth rate ($p < 0.001$ and $p = 0.044$ respectively). The analysis (Table 3.6) indicated that the effect of a biopsy procedure was similar to that of a handling event, as the parameter estimates of the fitted equation

$$\Delta l_{(T)} = (14.59 - l_t) \cdot (1 - \exp(-(0.014 \cdot [T_{SS} + T_{FW}] + \quad)))$$

$$(-0.036)\, Biopsy + (-0.033)\, Handling$$

were almost identical. The estimated parameters were used in a simulation model to study the effects of handling on growth. The results from the simulation indicated that a 10 cm clam that was handled 4 times would grow approximately 0.5 cm less in a year than a clam that was not handled. However, there was only marginal ($p = 0.075$) evidence of seasonality in the growth rate after the effects of the handling and biopsy had been included in the model. A t-test on the estimates of omega (Table 3.7) from the analysis of Areas "A", "B", and "C" indicated that there was no seasonality in the growth rates. Similarly, NIX had no significant effect ($p = 0.84$) on growth.

3.5 CONCLUSIONS

Area "M" was used to calculate growth rates during two periods of the year, spring-summer (i.e., March - August) and fall-winter (i.e., September - February). This study suggests that the majority of the growth in razor clams occurs during the spring-summer portion of the year, whereas little growth occurs during the fall and winter periods. These results, combined with the survival trends (Chapter 2) would suggest that spring-summer has rapid growth, but that the late summer has the potential for very poor survival. Conversely, the winter has little to no growth, but the potential for survival is good.

Data from Areas "A", "B", and "C" suggest that handling and biopsy procedures decrease the growth rate. The parameter estimates from the regression indicate that the

Table 3.6: ANOVA table for the nonlinear analysis of Areas "A", "B", and "C".

Source	df	SS	MS	F	P(F)
k_{Yr}, L_∞	2	253.171	126.586	$F_{2,573} = 951.77$	<0.001
Handling	1	1.739	1.739	$F_{2,573} = 13.08$	<0.001
Biopsy	1	0.548	0.548	$F_{2,573} = 3.98$	0.044
k_{Season}	1	0.424	0.424	$F_{2,573} = 3.19$	0.075
Residual	573	76.449	0.133		

Table 3.7: Estimated parameters of the von Bertalanffy growth equations from Areas "A", "B", and "C".

Season	Equation	Estimation Procedure	Parameter	Parameter Value	Standard Error
Spring -Summer	3.4	Nonlinear	k	0.67	0.07
			L_∞	14.58	0.11
			ω	9.77	0.98
Fall - Winter	3.4	Nonlinear	k	0.75	0.06
			L_∞	14.58	0.11
			ω	10.94	0.83

stress from a biopsy procedure had about the same effect as a handling event. It is obvious, therefore, that clams that are handled frequently should not be used for estimating growth parameters, as the effect of the handling will result in decreased estimates of the growth rate. There was no indication of seasonal growth rates from data from Areas "A", "B", and "C".

The differences in the results from the two data sets are probably closely related to how the data were collected. The clams that were used to construct the data set for Areas "A", "B", and "C" were released at various times throughout the spring or fall months, and recaptured randomly throughout the year. Thus, assigning the time spent during the spring-summer, and during the fall-winter was much more difficult than with the controlled release-recapture at Area "M". The study at Area "M" demonstrated that on a coarse scale, growth varies according to the season. However, to get a large enough sample size from areas "A", "B", and "C", clams were selected from releases that occurred over a range of adjacent months. Because the temporal scale of seasonal growth is known at only a coarse scale (i.e., bi-seasonally), it was difficult to correctly classify the data from Areas "A, "B", and "C". Any attempt to assign a fractional amount of growth to each month becomes arbitrary, and if the growth rate is time-variant within the season, as has been demonstrated across seasons, the assignment will influence the results. For example, if the spring-summer growth rate is constant from March-August, then a fractional assignment related to the amount of time exposed will be sufficient, because the growth rate is constant within the interval. If, however, all the spring-summer growth occurs between March and April, then only those clams released in March will experience spring-summer growth, while those released in April-August will not. In addition, there is much more overlap across seasons and years with the data set composed of individuals from Areas "A", "B", and "C", which would tend to diminish the differences between the two growth rates.

These results suggest that there is strong seasonality in the metabolic responses of the razor clam along the Washington coast. Winter appears to be a time of high survival (Chapter 2), but limited growth. Recruitment (Chapter 4) and growth occur primarily in the spring. Survival during the spring remains high (Chapter 2). Growth may continue into the summer, but survival begins to decrease in late-spring through fall. These results indicate that the size of clam during harvest, the numbers of clams in the harvest, and the success of subsequent year-classes may be impacted by the timing of the harvest season.

Chapter 4

Recruitment Analysis using Stage-Classified Data

4.1 INTRODUCTION TO RAZOR CLAM RECRUITMENT

The Pacific razor clam is a broadcast spawner that inhabits sandy exposed beaches along the Pacific coast. Although evidence indicates that spawning can occur throughout the year (Ralph Elston, Pathologist at Battelle Pacific Northwest Labs - Sequim, WA, pers. comm), primary spawning probably occurs during the spring (McMillian, 1924; Weymouth, *et al.*, 1925; Bourne and Quayle, 1970). Larvae float within the water for 5-16 weeks (Lassuy and Simons, 1989) before settling upon a sandy oceanic beach. The duration of the planktonic stage suggests the potential for coastal transport of larvae from one beach to another. However, freshwater plumes from the major river systems in the area (e.g. Grays Harbor, Willipa Bay, and the Columbia River) may limit such a mechanism (Leclair and Phelps, 1994). In addition, near-shore geostrophic transport during the late spring (March-April) for the years 1983-1988 (McConnaughey *et al.*, 1992) shows a pattern that could keep juveniles near the area in which they were spawned. The geostrophic transport indicates periods of both northerly and southerly transport during the spring. The overall effect may be to allow limited mixing, but prohibit major movements of larvae.

Large numbers of larvae settle upon the beach in the early summer (McMillian, 1924; Tegelberg and Magoon, 1969). Juvenile razor clams may experience limited lateral movement, but once the clam reaches 2 cm, lateral movement usually ceases. There is no evidence that indicates that adult razor clams experience any lateral movement; all evidence indicates the contrary. Growth is rapid, although survival is poor (McMillian, 1924), and at the end of the first year, the mean size is approximately 3 cm. By the second year, the clam is approximately 10 cm long. It is during the second year that the clam becomes sexually active (Lassuy and Simons, 1989).

Recruitment into invertebrate fisheries is often highly variable (Naidu and Anderson, 1984; Bannister, 1986; Penn and Caputi, 1986). Razor clams seem to follow this pattern, as stock sizes have consistently fluctuated. Recruitment variability can be caused by several sources including variability in larval survival (Sissenwine, 1984; Fogarty, *et al.*, 1991), variability in oceanographic conditions (Coe, 1953 in Shaw and Hassler, 1989), or density dependent factors (Lett *et al.*, 1975).

Many authors (Beverton and Holt, 1957; Ricker, 1975; Cushing, 1981; Cushing, 1988) have suggested that the number/density of juveniles can be functionally related to the number/density of adults. In molluscs, the current adult density can often affect the recruitment of juveniles (Hancock, 1973; Caddy, 1975; Fogerty and Muraski, 1986). Where the current adult density is low, interference between adults is minimal, and juveniles can settle without interference from the adults. Where the current adult density is high, adults and juveniles must compete for resources. At high densities, the competition for resources between adults and juveniles can cause a decrease in the ratio of juveniles to adults. This competition can lead to either a constant level of recruitment over a large range of adult densities (e.g., Beverton-Holt Model) or it can lead to a decrease in recruitment with increasing adult densities (e.g., Ricker Model).

In addition to the parental stock density, environmental factors may also affect the success of recruitment. Many previous fisheries studies, both finfish and shellfish, have explored the relationships between fisheries and the local environment (Gunter and Edwards, 1967; May, 1972; Peterson, 1973; Dow, 1977; Sutcliffe, *et al.*, 1977; Lasker, 1978; Lasker, 1982; Parrish, 1982; Peterson and Smith, 1982; Garcia, 1983; Penn and Caputi, 1986). Large scale environmental perturbations, such as El Ninos, have had drastic effects upon bivalve condition indices (Schoener and Tufts, 1987), and have caused changes in the ecosystem composition (Miller *et al.*, 1985). El Nino events often cause elevated temperatures and alter the abiotic and biotic structures of the ocean ecosystem (Freeland, 1990). It would not be atypical, therefore, to expect that the razor clam too would respond to external cues.

There are three mechanisms by which the environment could influence the recruitment relationship. Poor environmental conditions could affect the survival of the adults, the fecundity of the adults, or the survival of the recruits.

The external environment can induce strong physiological responses in molluscs because of the close association between the molluscs and their environment, and because molluscs are poikilothermic (Schoener and Tufts, 1987; Allen and Turner, 1989; Thompson and McDonald, 1991). In poikilothermic animals, respiration will typically increase with increasing temperature. Over limited ranges of temperatures, many littoral invertebrates are capable of temperature acclimation. Thus, many physiological rates are maintained independent of temperature (Bayne *et al.*, 1985). The range of acclimation, however, is not typically great. For example, the Baltic tellin (*Macoma baltica*) has optimal growth between 0-10 C, but has no growth at all at temperatures above 15 C (De Wilde, 1975). Likewise, laboratory studies of NIX infected razor clams have shown death associated with temperatures above 16 C (Ralph Elston, Pathologist at Battelle Pacific Northwest Labs - Sequim, WA, pers comm.). Thus, although acclimation is evident within invertebrate populations, extremes in temperature have the ability to stress the organism.

Razor clams may be particularly susceptible to alterations in the external environment because they lack a shell that closes completely, and their sole evasive technique is limited to vertical migration. At all times, a large portion of the razor clam tissue is in direct contact with the sand and water in the surrounding region. Thus, whereas the oyster or mussel may isolate itself from harsh conditions, and await better conditions, the razor clam will remain exposed. The razor clam can migrate somewhat, unlike the sessile oyster, but previous studies (McMillian, 1924) have shown that typically, the maximum depth the clam may attain is 1 meter. The inability of the razor clams to isolate themselves from poor conditions implies that harsh conditions can not be avoided.

Most temperature correlation studies have been concerned with the impacts of temperature on stock size. Oftentimes, the effect of temperature has been assumed to reflect alteration of recruitment potential (Bayne, 1975; Bayne *et al.*, 1978; Barber *et al.*, 1988a; Allen and Turner, 1989). In some invertebrate fisheries environmental factors, including temperature, appear to be the main controlling factor on recruitment success (Garcia and Le Reste, 1981; Bannister, 1986; Caddy, 1989). Temperature-mediated stress can reduce the condition of bivalves (Bayne *et al.*, 1985), leaving less energy available to allocate for egg production. Bivalve mollusc examples of temperature-mediated decreases in fecundity include oysters (Allen and Turner, 1989) and mussels (Bayne, 1975; Bayne *et al.*, 1978; Barber *et al.*, 1988a). Bayne (1975) has also shown that even in the absence of decrease fecundity, when the adult stock is stressed, larval growth and survival are adversely affected. The overall conclusion from previous studies has been that the detrimental effects of temperature on the recruitment process may be direct (i.e. reduced fecundity) or indirect (i.e. mismatch of larvae and food source, increased predation) (Anthony and Clark, 1982).

For razor clams along the Washington coast, high summer temperatures will probably cause the most problems. High summer temperatures have been implicated in decreased survival in the Pacific razor clam. (Bourne and Quayle, 1970; Sayce and Tufts, 1971). In addition to the literature, there are two other reasons for believing that high summer temperatures may be problematic for the razor clam. First, razor clams within the lab have been shown to exhibit death in the presence of high temperatures (Ralph Elston, Pathologist at Battelle Pacific Northwest Labs - Sequim, WA, pers comm.). Second, razor clam survival at two beaches along the Washington coast decreased in the summer months (i.e., June - September) (Schlechte and Skalski, 1993).

As mentioned in Chapter 2, the disease process NIX was thought to cause mortality in the razor clams. However, no relationship was discovered between the point-in-time estimate of the disease level, and the subsequent survival of the individual clam. An alternative hypothesis is that the NIX could affect the clams, not through measurable decreases in survival of the adults, but through decreases in subsequent recruitment. The decrease in recruitment could be mediated through either a reduction in the spawning success of the clams that are infected with NIX, or by decreased survival of the juveniles. Therefore, NIX was included as a predictor variable to determine if the effect of NIX was pervasive and measurable at the population level, even if the effect of NIX was not measurable at the individual level.

It is the intent of this research to ascertain whether a stock-recruitment relationship exists, and whether a coastwide, or a beach-by-beach model of recruitment provides the best fit to the data at hand. Beyond this, I will attempt to ascertain whether the environment or NIX significantly influences the stock-recruitment relationship. Two classes of models were investigated. One class of models focuses upon the total density of razor clams of all sizes present upon a beach. The alternative class of models accounts for the size (age) differences within the population(s). Several different stock-recruitment relationships were investigated.

4.2 DATA SOURCES FOR THE RECRUITMENT MODELLING

Data used for the analysis of the recruitment process of the razor clam were obtained from two sources. Size and abundance data of the razor clams were obtained from the Washington Department of Fisheries (WDF) annual population surveys (Ayres and Simons, 1988). Estimates of the maximum NIX intensities and the yearly catch were also obtained from WDF. Mean monthly temperature data off the Washington Coast came from the National Oceanographic and Atmospheric Administration (NOAA).

Washington Department of Fisheries conducts annual release-recapture surveys to estimate the population of razor clams along the Washington Coast (Ayres and Simons, 1991). An estimate of razor clam abundance in each site is obtained using the formula (Bourne, 1969):

$$\hat{N} = \frac{n_1 \cdot (n_2 - m)}{(m+1)} \quad \text{(EQ 4.1)}$$

where $\hat{N}$ = total population estimate,

n_1 = number of marked razor clams released,

n_2 = total number of razor clams captured during the recapture process, and

m = number of marked razor clams recaptured.

From the mid-1950s through 1984, only fall surveys of abundance were available. In later years (1984 - 1991), both spring and fall surveys were undertaken to estimate clam abundance. Unfortunately, in the last few years, population estimates are available for spring surveys only; the fall data series does not exist. For this analysis of the recruitment process, only the fall survey data was used, even when the spring survey data existed.

The lengths of all razor clams that were captured during the population estimation surveys were measured. This provides the length frequencies that were used to separate juvenile from adult razor clams.

Monthly temperature data for the Washington Coast was collected and compiled by the National Oceanographic and Atmospheric Administration (Woodruff *et al.*, 1987). The primary source for the temperature data are ships in the area. The data set of temperatures used in this study for the Washington Coast was compared to other nearby regions in the NE Pacific (Woodruff *et al.*, 1987). All showed similar trends, with higher than average temperatures in the 1960's, lower than average temperatures in the 1970's, and average temperatures throughout the 1980's.

NIX intensities were measured on a random sample of approximately 50 clams that were collected at Copalis approximately monthly. These clams were taken to Battelle Pacific Northwest Laboratory, where the gill tissue was processed and the disease level was estimated (See methods in Section 2.3.4). Because NIX occludes the respiratory channels, it was assumed that high NIX intensities would cause the greatest degree of stress and possibly, mortality (Elston, 1986a). Therefore, I used the maximum yearly values of NIX to explore the relationship between NIX and recruitment.

4.3 METHODS OF MODELING RECRUITMENT

4.3.1 PRELIMINARY EXAMINATION OF THE DATA SETS

Population abundances were segregated into adults and pre-adults (recruits) on the basis of size (i.e., adults > 10cm). Initial data exploration showed that the northern three beaches (Mocrocks, Copalis, and Twin Harbors) all experienced strong recruitment in the early 1970's (Figure 4.1). In contrast, the clam populations at Long Beach did not respond positively to reduced temperatures during the 1970's. The population abundance at Long Beach has remained relatively low and stable since 1971 (Figure 4.2). The differential pattern of population abundance exhibited by Long Beach in the 1970's may make coastwide generalizations difficult.

The strong year-classes (1972-1975) at the three northern beaches maintained high population sizes into the mid-1970's. The occurrence of the strong year-classes coincided with the decrease in water temperatures experienced along the Washington Coast (Figure 4.3). Although very strong, and thus easy to follow, these year classes apparently only lasted for one to two years before disappearing completely (Figure 4.2). The disappearance of these large year classes within two years indicates that the life-span of the razor clam is only three to four years; the razor clam appears to spend two years as a juvenile, and one to two years as an adult.

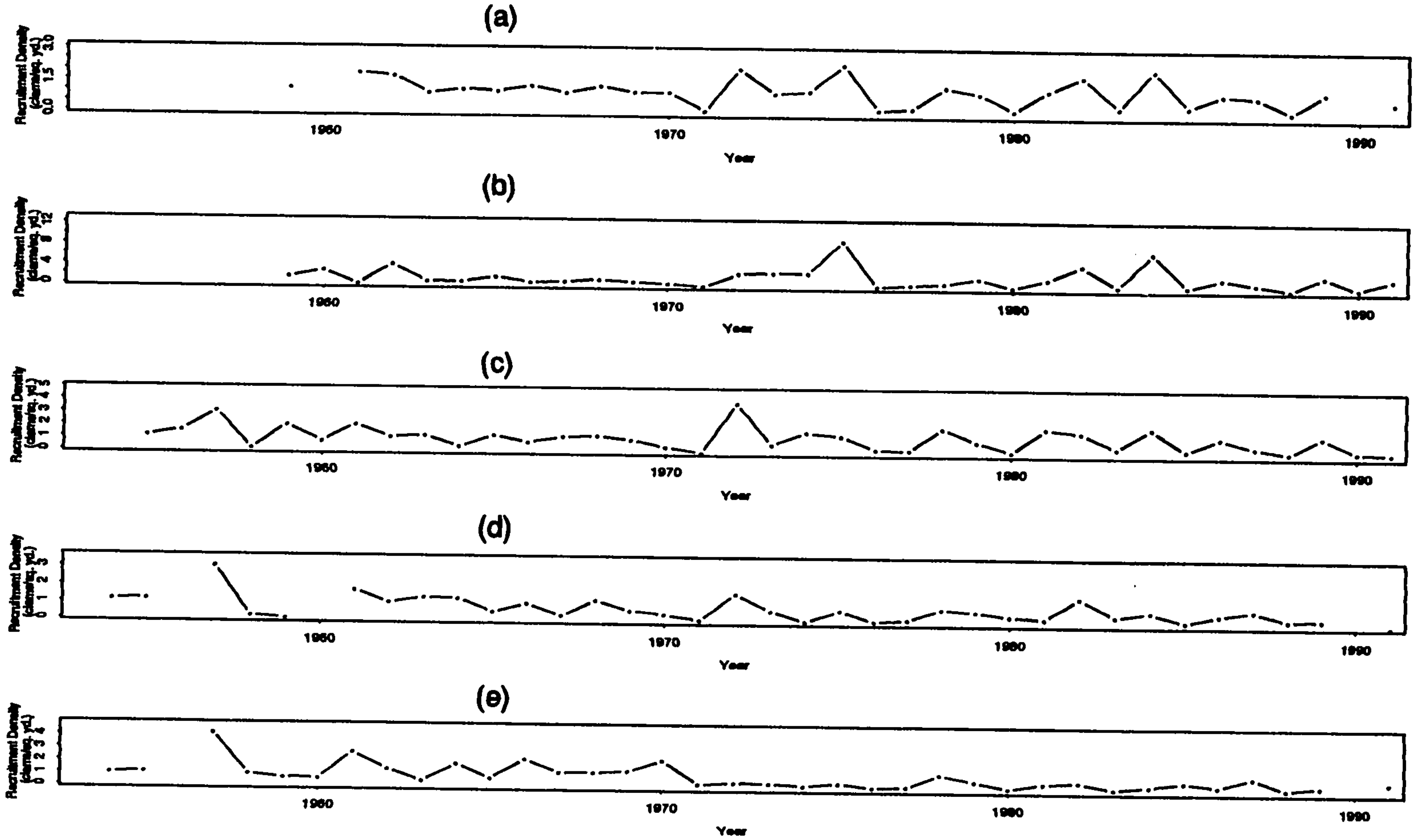


FIGURE 4.1 Trajectory of the razor clam recruitment estimates from the 1950's to the 1990's. The uppermost graph (a) is the average density of the recruitment estimates for all Washington Beaches. Below, in geographical order, north to south, are the recruitment estimates for the four beaches that the Washington Department of Fisheries surveys: (b) Mocrocks, (c) Copalis, (d) Twin Harbors, and (e) Long Beach.

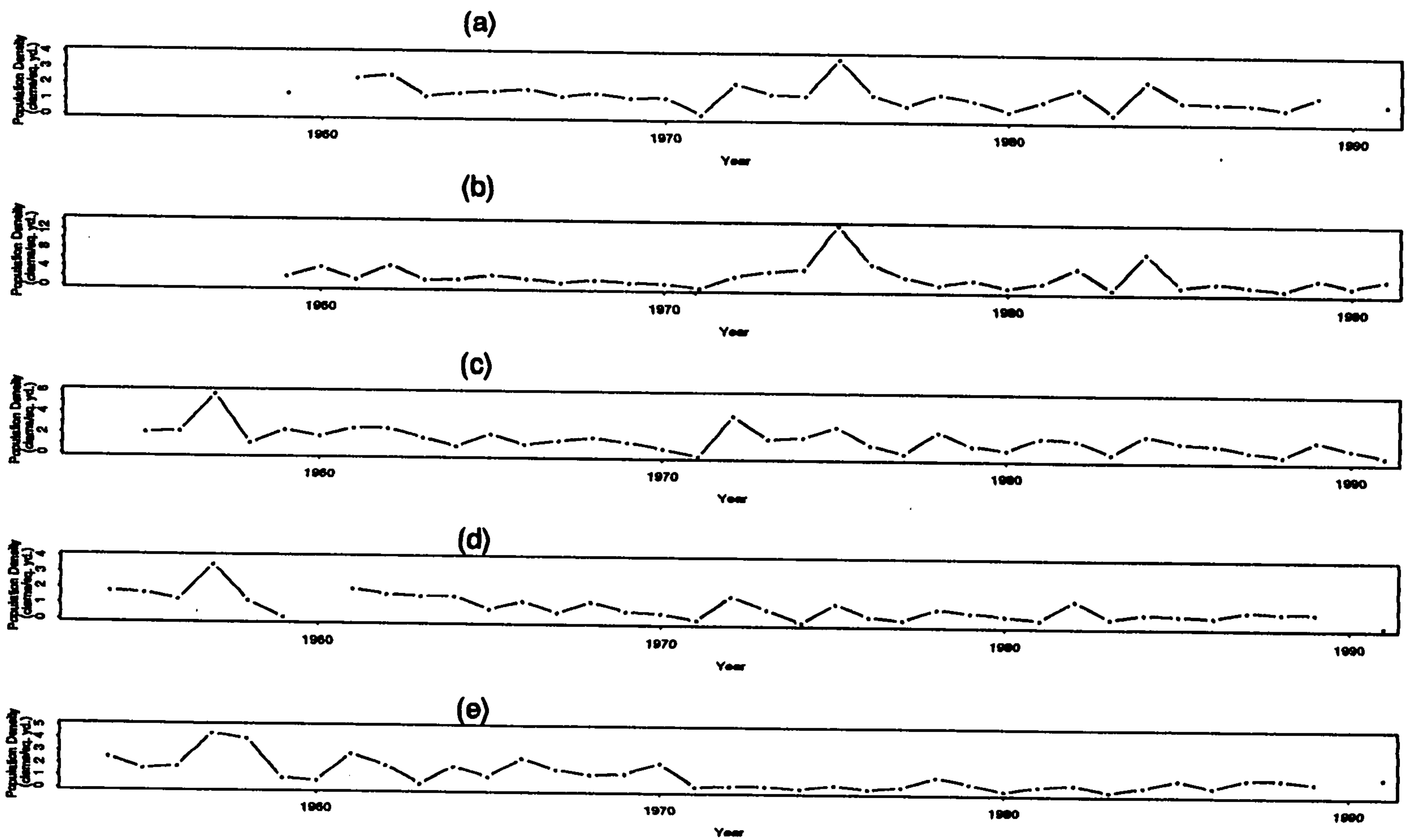


FIGURE 4.2 Trajectory of the razor clam population estimates from the 1950's to the 1990's. The uppermost graph (a) is the average density of the population estimates for all Washington Beaches. Below, in geographical order, north to south, are the population estimates for the four beaches that the Washington Department of Fisheries surveys: (b) Mocrocks, (c) Copalis, (d) Twin Harbors, and (e) Long Beach.

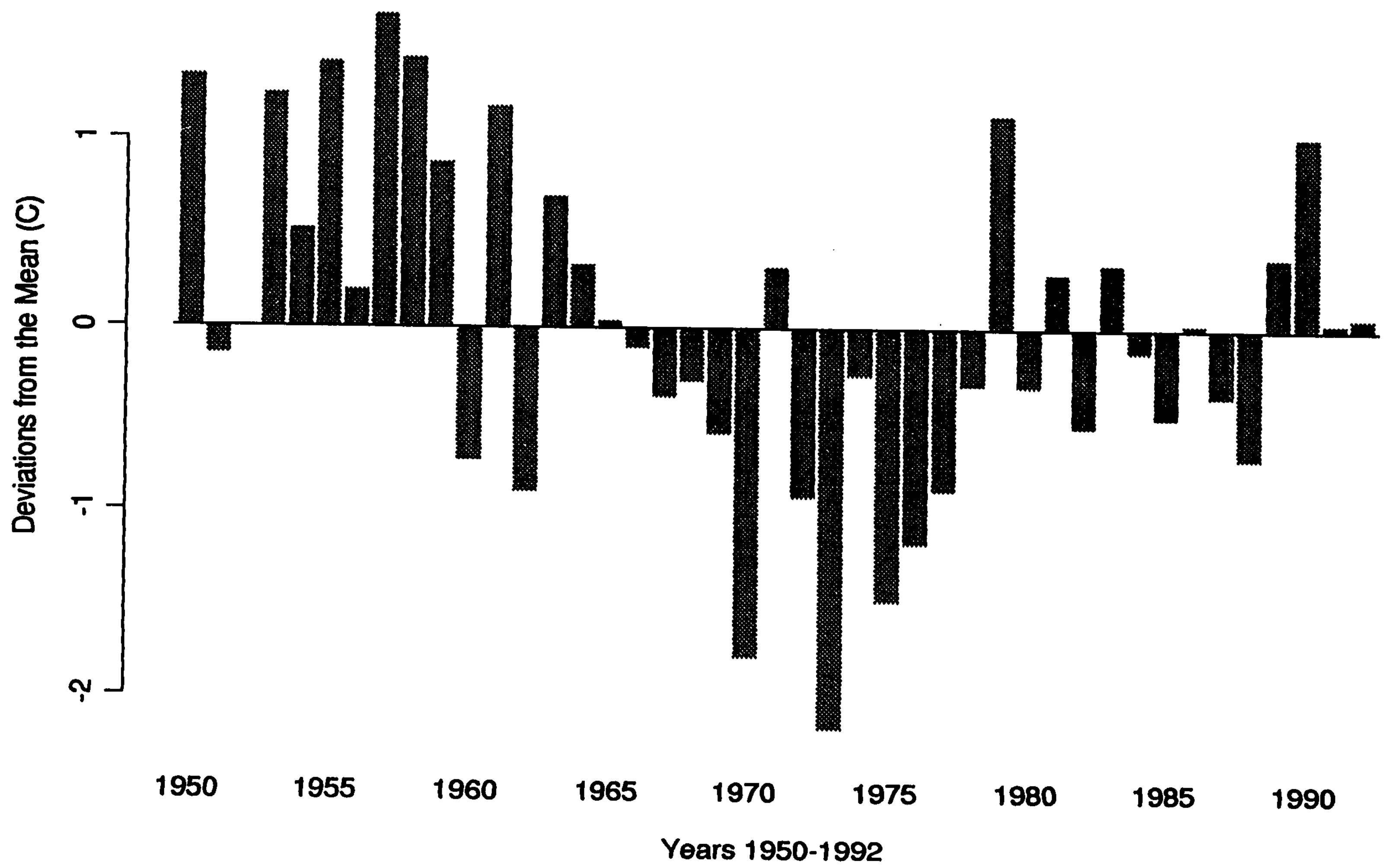


FIGURE 4.3 Time course of yearly maximum temperatures along the Washington coast. Maximum temperatures are plotted as deviations from the overall mean of all yearly maximum temperatures (1954-1992).

Another interesting trend in the population data is the indication of some cyclical behavior. All beaches typically show an increase in the total density of clams every 2-4 years, followed by a decline in the total density. The majority of the cycling can be attributed to the incoming recruits, as the adult population remains much more stable through time. This cycling may indicate some density-dependent factors that influence the success of the incoming recruitment classes.

Previous studies suggested that razor clams first spawn when they become 2 years old (McMillian, 1924). The approximate size of a 2 year old clam along the Washington Coast is estimated to be 10 cm (Lassuy and Simons, 1989). Newly recruited razor clams (0+ age class) are difficult to catch with the gear used during the WDF surveys because they are small and difficult to detect. Thus, the majority of the razor clams that are smaller than 10 cm in length should be the larger 1-year olds. This implied that with this data set, the stock-recruitment relationship should have a one year lag. If recruitment was auumed to follow a Ricker curve (Ricker, 1954), a plot of stock size and $\log_e$(recruits per spawner) should be linear and decreasing. Using the correlation coefficient (r) as the criterion, I found that the stock-recruitment relationship for all beaches was strongest with a one-year lag, and that there is a strong negative correlation between stock size and $\log_e$(recruits per spawner) (Figures 4.4 - 4.7 and Table 4.1). The one year lag implies that razor clams begin spawning at two years old (>10 cm), and that the majority of razor clams below 10 cm are one year olds.The negative correlation implies density-dependent processes are operating to maintain the population around some "ideal" stock size. The strong negative correlation continued with the two year lag (Table 4.1). This could indicate that more than one year class is important in determining the success of future recruitment.

The three northern-most beaches (Mocrocks (Figure 4.4), Copalis (Figure 4.5), and Twin Harbors (Figure 4.6)) show similar patterns in their regressions between $\log_e$(recruits per spawner) and the adult density. Long Beach (Figure 4.7), which had anomalous behavior when compared to the other three beaches during the 1970's, has a

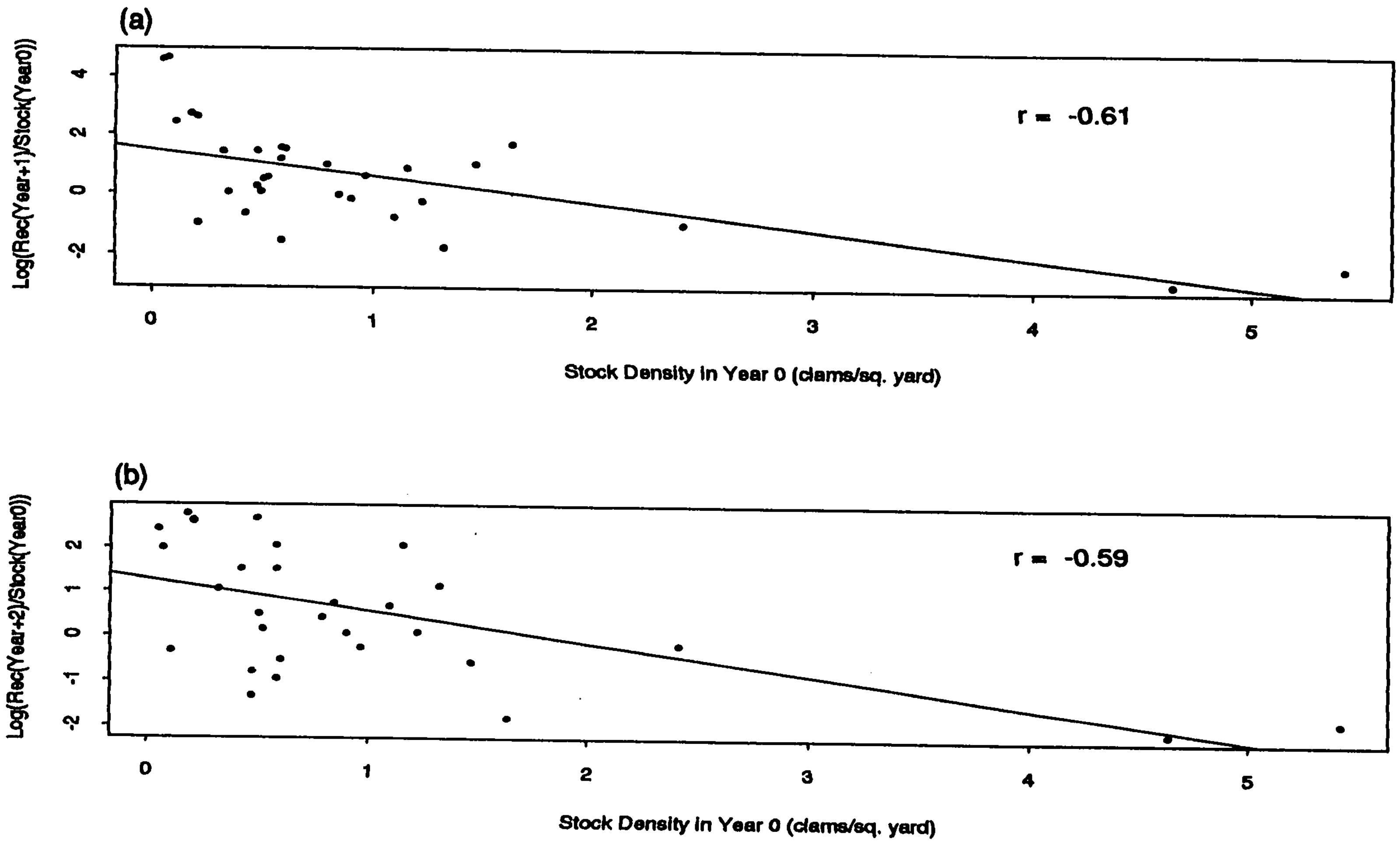


FIGURE 4.4 Relationship between current stock density and subsequent recruitment with lags of one or two years at Mocrocks. The horizontal axis is the estimated density of adults in year "t". The vertical axis is the natural log of the ratio (recruits/stock density) with a (a) one or (b)two year lag. If the recruitment relationship truly followed a Ricker Curve, the points would lie in a straight line. The line that is plotted is the best fit line for the scatter plot.

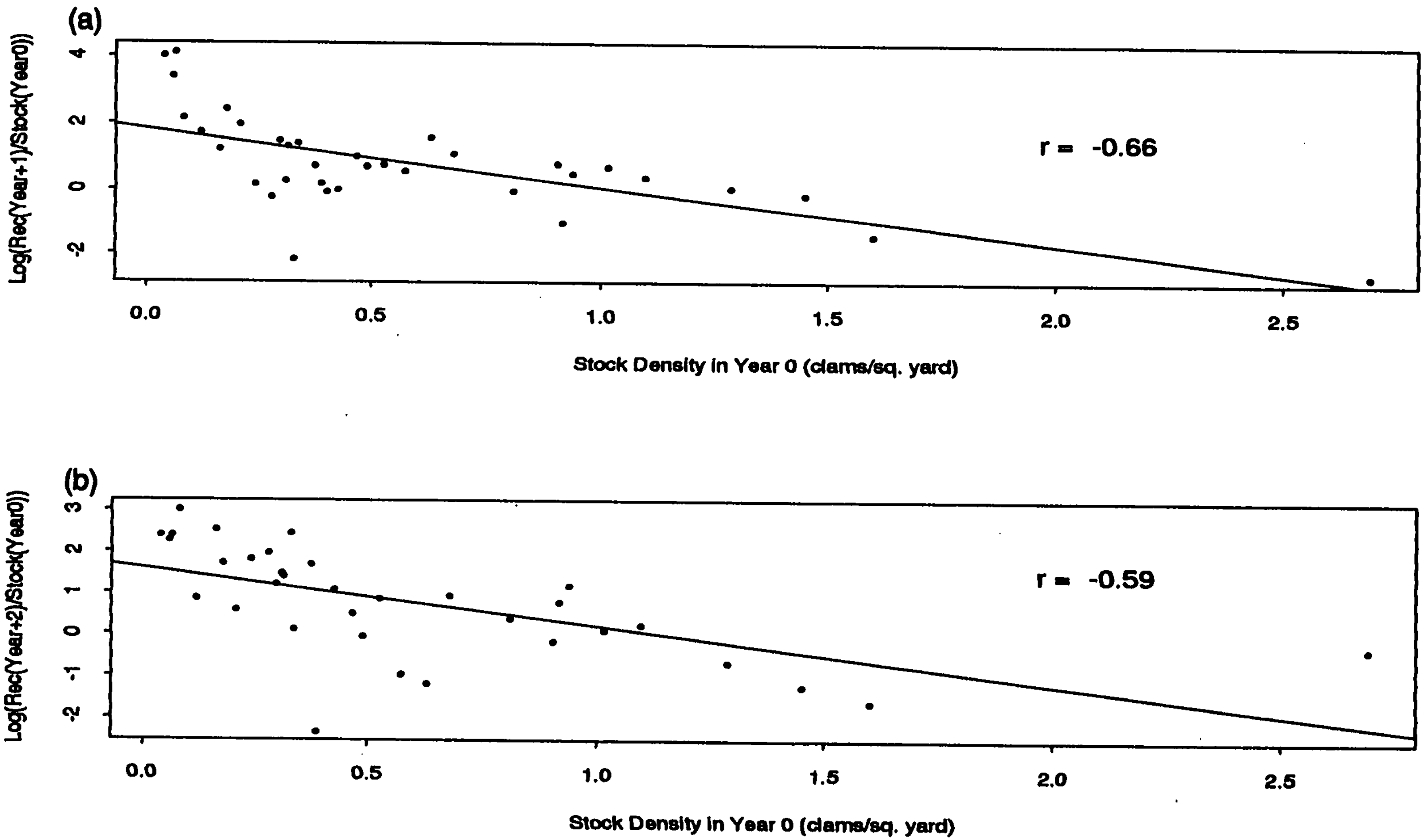


FIGURE 4.5 Relationship between current stock density and subsequent recruitment with lags of one or two years at Copalis. The horizontal axis is the estimated density of adults in year "t". The vertical axis is the natural log of the ratio (recruits/stock density) with a (a) one or (b) two year lag. If the recruitment relationship truly followed a Ricker Curve, the points would lie in a straight line. The line that is plotted is the best fit line for the scatter plot.

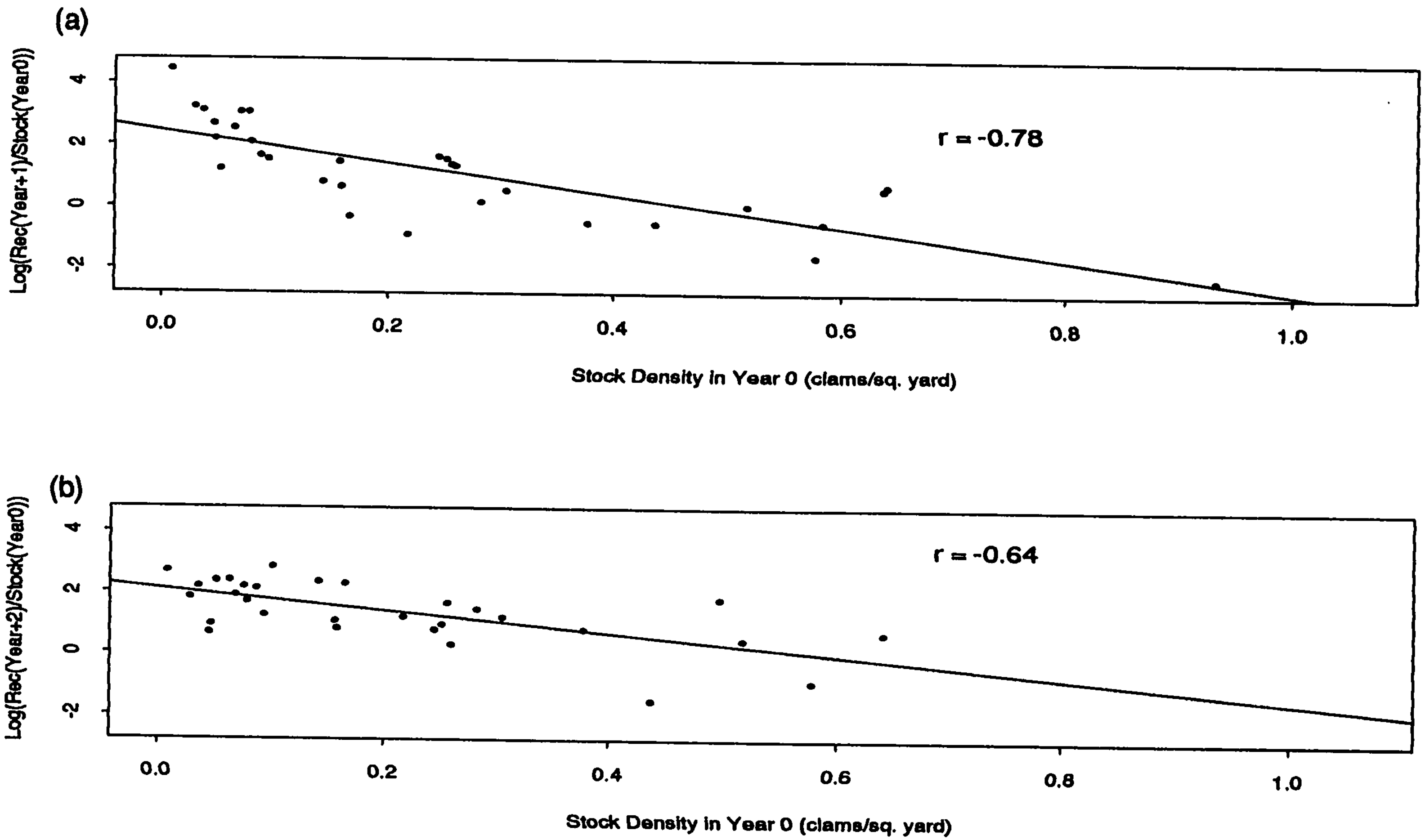


FIGURE 4.6 Relationship between current stock density and subsequent recruitment with lags of *one or two* years at Twin Harbors. The horizontal axis is the estimated density of adults in year "t". The vertical axis is the natural log of the ratio (recruits/stock density) with a (a) one or (b) two year lag. If the recruitment relationship truly followed a Ricker Curve, the points would lie in a straight line. The line that is plotted is the best fit line for the scatter plot.

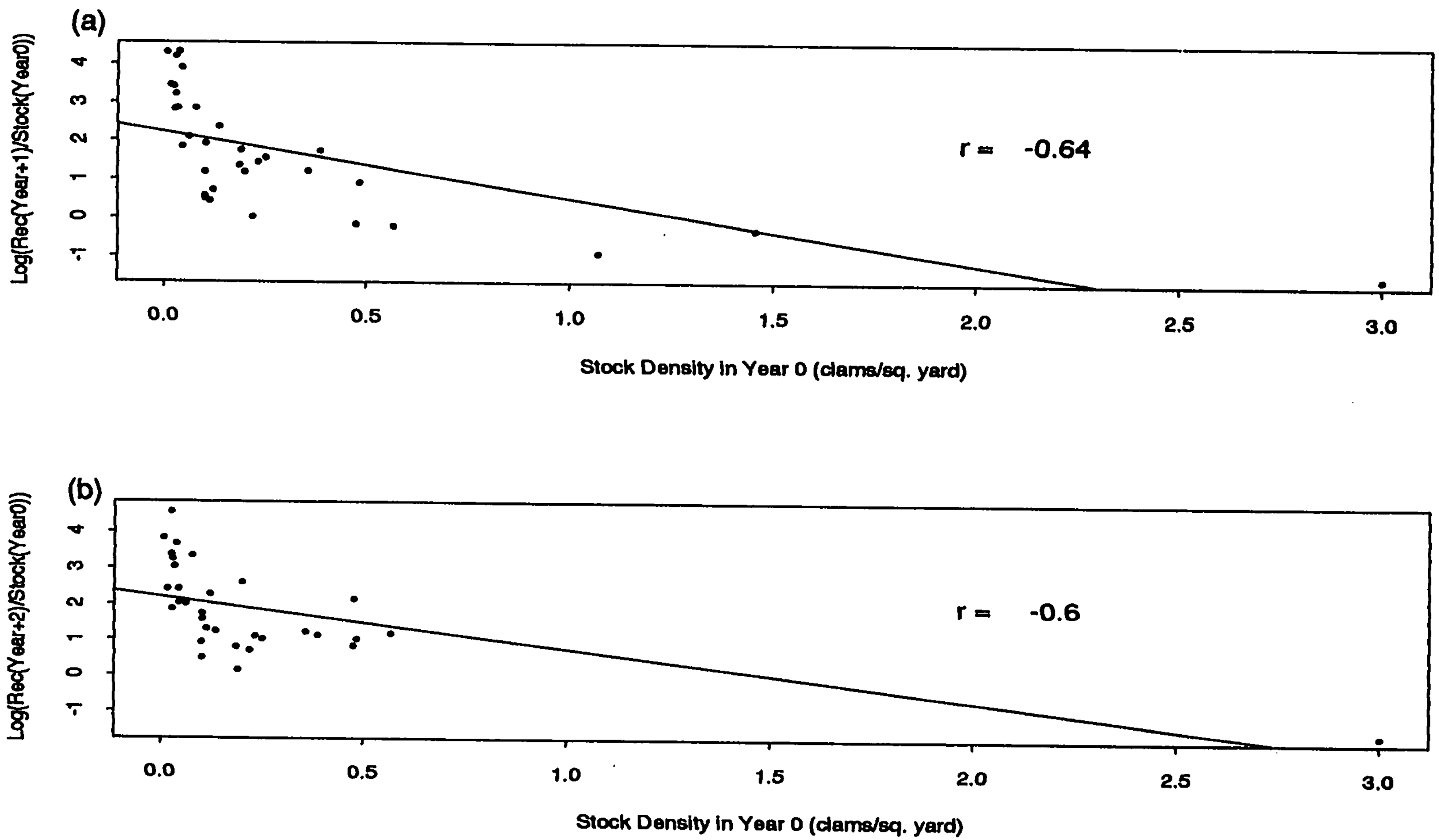


FIGURE 4.7 Relationship between current stock density and subsequent recruitment with lags of one or two years at Long Beach. The horizontal axis is the estimated density of adults in year "t". The vertical axis is the natural log of the ratio (recruits/stock density) with a (a) one or (b) two year lag. If the recruitment relationship truly followed a Ricker Curve, the points would lie in a straight line. The line that is plotted is the best fit line for the scatter plot.

Table 4.1: Comparison of correlation coefficients for Ricker Stock-Recruit models with a one year lag versus models with a two-year lag. Individual beaches are listed in order from North to South. The final category, "All Beaches Combined", uses the data from all four beaches.

Beach	Correlation Coefficient with a One-Year Lag	Correlation Coefficient with a Two-Year Lag
Mocrocks	-0.61	-0.59
Copalis	-0.66	-0.59
Twin Harbors	-0.78	-0.64
Long Beach	-0.64	-0.60
All Beaches Combined	-0.76	-0.71

much poorer linear fit. This is a further indication that it may be necessary to model each beach uniquely.

As it is unclear whether each beach is a self-sustaining stock, or whether the entire coast is a single stock, the relationship between the total coastal adult population and the total coastal recruits was also examined. This relationship also indicated a one-year lag, and a negative correlation between the adult density and the $\log_e$(recruits per spawner) ($r = -0.76$; Figure 4.8). The fit of the regression line again is quite strong, suggesting a relationship between current stock size and the number of one-year old recruits in the following year. As occurred with several of the individual beaches, the regression line underestimates the number of observed recruits at low stock values, but fits the observed recruits well at high stock values.

To characterize the degree of interaction between beaches, at each beach recruitment deviations from the median recruitment for that beach were calculated and all pairwise correlations (i.e., between beaches) were computed. The deviations from the median recruitment were used because each beach has a separate median recruitment, and the deviation metric helps to standardize the direction and degree of change in a given year. The median was used, as opposed to the mean, because the distribution of recruitment was skewed. For skewed distributions, the median is a better descriptor of the central tendency of the distribution. The absence of correlation between beaches could imply that each beach behaves independently. This could imply that each beach responds to either internal or external cues independent of other beaches. Under this scenario, each beach should be modelled separately. If correlations are detected, this implies some type of large scale phenomenon. A positive correlation could either occur if the beaches were responding similarly to external cues, but had independent, self-sustaining stocks, or if the beaches contributed to a pool of larvae, that then either did well or did poorly. A negative correlation could either occur if beaches have larvae that are competing for resources while they are in the planktonic stage or if the beaches have unlimited areas to settle in,

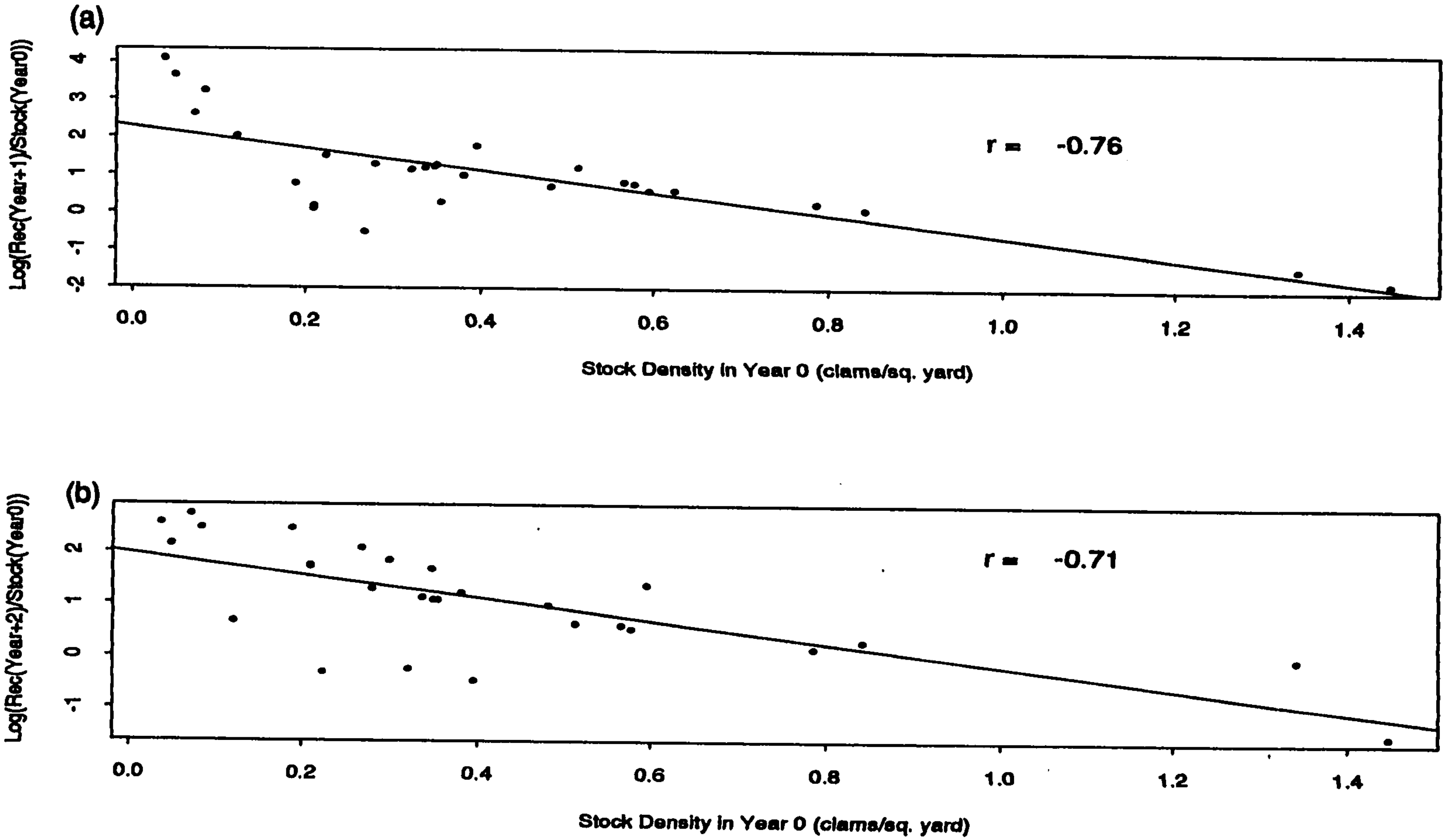


FIGURE 4.8 Relationship between current stock density and subsequent recruitment with lags of one or two years at all four beaches combined. The horizontal axis is the estimated density of adults in year "t". The vertical axis is the natural log of the ratio (recruits/stock density) with a (a) one or (b) two year lag. If the recruitment relationship truly followed a Ricker Curve, the points would lie in a straight line. The line that is plotted is the best fit line for the scatter plot.

but are competing for a fixed pool of larvae. In either case, if there is strong correlation, some interaction between the beaches is implied. Under this scenario, beaches would be modelled together. A nonparametric correlation (Kendall's tau) was computed that only used the direction of deviation; either positive one (e.g., "+1") for recruitment greater than the median recruitment or negative one (e.g., "-1") for recruitment less than the median recruitment.

The result of the Kendall's tau correlation analyses showed that beaches that were geographically closer had higher positive correlations than those beaches that were distant (Figure 4.9, Table 4.2). The only negative correlation that appeared in the pairwise comparisons of all four beaches was the relationship between the northern-most beach (Mocrocks) and the southern-most beach (Long Beach). In this instance, the nonparametric correlation coefficient indicated almost no correlation. Significant correlations ($p<0.05$) occurred only among beaches that were adjacent.

The positive correlation implies that when conditions are good or poor for one beach, the conditions are also good or poor, respectively, for adjacent beaches. The fact that the correlation decreases with distance implies that the scale of the recruitment process is less than coast-wide. As an example of the type of mechanism that could drive this correlation, good environmental years could allow for strong spawning success throughout the coast, but local conditions may determine the success of the larvae settlement. The lack of significant correlation among non-adjacent beaches gives credence to the idea of individual spawner-recruit relationships for each beach.

For the models that did not differentiate between juveniles and adults, it was necessary to include the catch in the models. A problem arose at this juncture, for there have been several occasions when the total catch from a beach has exceeded the total estimated population (Figure 4.10). This problem occurs through a combination of measurement error associated with the estimation techniques used to measure abundance, and the selectivity of the sampling techniques used to enumerate the clams prior to the

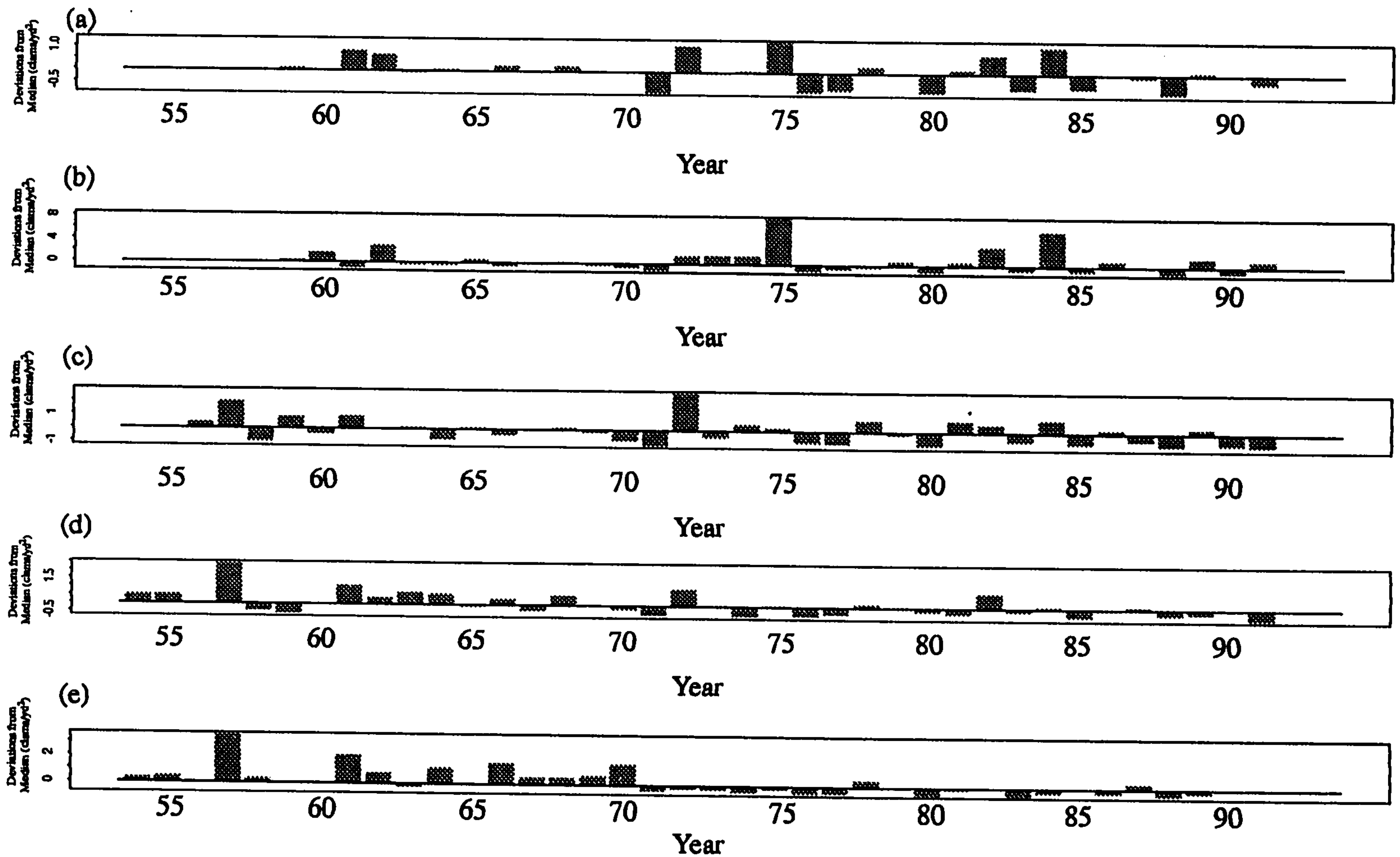


FIGURE 4.9 Deviations of recruitment from the median through time. The uppermost graph (a) is the combined recruitment estimates for all Washington Beaches. In geographical order, north to south, are the recruitment estimates for the four beaches that the Washington Department of Fisheries surveys (b) Mocrocks, (c) Copalis, (d) Twin Harbors, and (e) Long Beach.

Table 4.2: Kendall's Tau Correlations Between Recruitment Deviations for the Four Washington Beaches. Beaches are organized from north to south.

Beach	Mocrocks	Copalis	Twin Harbors	Long Beach
Mocrocks	1.000	0.520**	0.186*	-0.045
Copalis		1.000	0.348**	0.137
Twin Harbors			1.000	0.379**
Long Beach				1.000

* Significant at the p=0.1 level.

** Significant at the p=0.01 level.

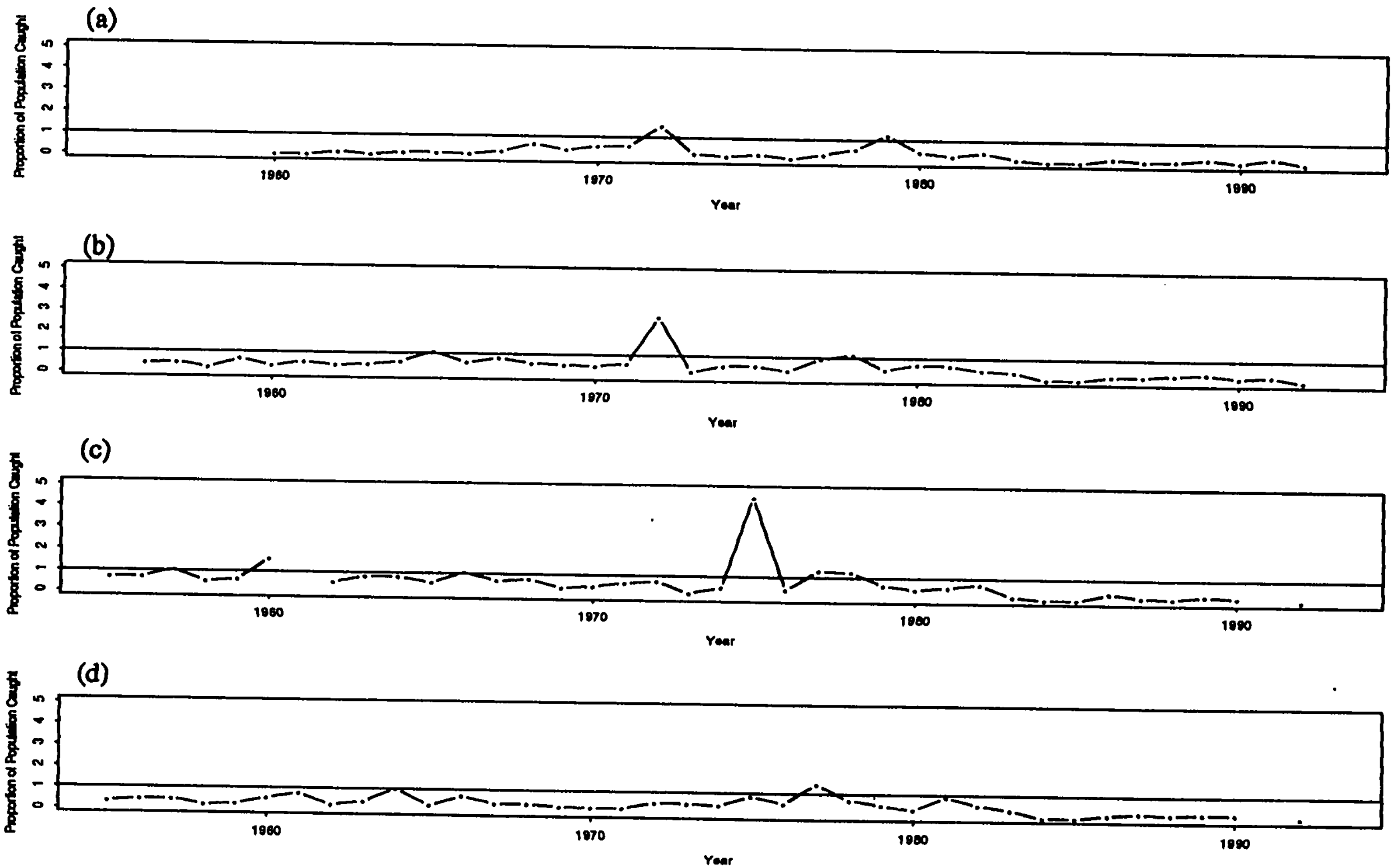


FIGURE 4.10 Proportion of the stock that was taken as sport harvest. Any values above 1.0 indicate a problem with either the estimate of abundance or the estimate of catch. Beaches are displayed in geographic order from north to south (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach.).

season. Although problematic, the fact that catch has exceeded the estimated population size provides some insight into the dynamics of the stock. The size of the stock is estimated prior to the season, but after the spawning. Apparently, in certain years, most of the harvestable population has been removed without any great detriment to the subsequent populations. Recall too, that the total population estimate consists not only of reproductive adults, but pre-reproductive juveniles. In many years, the pre-reproductive juveniles contribute a major proportion of the individuals upon the beach. However, harvest is typically selective; primary focus is on the larger adults. Therefore, in many instances, even when the entire estimable population was not harvested, the majority of the adults could have been harvested.

Survival of both the adults and juveniles may be related to changes in temperature. Exploratory graphics (Figures 4.1 and 4.2) indicated that strong year classes in the razor clam population coincided with reduced maximum temperatures off the coast of Washington. The most pronounced feature that appeared when the razor clam abundance data were compared to the temperature data was that parental stock size and recruitment both showed substantial increases during the early 1970's, because of a sequence of strong year-classes. The combination of increased population densities during the cooler years and the survival studies (Ralph Elston, Pathologist at Battelle Pacific Northwest Labs - Sequim, WA, pers. comm.; Schlechte and Skalski, 1993) mentioned in Section 4.1, were reasons for believing that the maximum yearly temperature could influence the stock-recruitment relationship.

The temperature data that were available consisted of the mean temperature of the sea surface along the Washington coast for each month between 1946 and 1992. The metric that was used throughout the analysis was the maximum value of the mean temperature for each year (MMT). The pattern of the MMT through time suggested that the MMT captured the general pattern of the temperature regime for the coast. However, other measures of the summer temperature were also examined. One measure was the mean summer temperature within a year (i.e., arithmetic mean of July, August and September). This measure could provide better fit if the effect of temperature is chronic throughout the summer, rather than simply the effect of one month. Another set of measures, the mean temperature for either July or August or September, could provide better fit if the timing of the maximum mean temperature within the summer was important. These metrics were strongly correlated with the MMT (Figure 4.11). After these initial investigations, the MMT was chosen as the environmental metric throughout. However, because of the correlation among the various temperature metrics (Figure 4.11), conclusions based on correlations with the MMT may be due instead to other correlated metrics.

Finally, one cause of elevated sea surface temperature is an El Nino event (Freeland, 1990). El Nino events often cause elevated temperatures, and in addition alter the abiotic and biotic structures of the ocean ecosystem. Thus, an indicator variable was constructed that did not use the actual temperature, but instead, identified those years when El Nino events were measured off the Washington coast. Because the timing of the El Nino event and the timing of the sampling of the razor clam population may cause the effect to be measured during the year of the event or the year after the event, the effect of the El Nino was tested with various lags.

I also conducted some preliminary investigation on the relationship between NIX and the razor clam population numbers at Copalis. NIX could affect either the adults in the current year (by causing mortality) or the recruits in the next year (by mortality or by decreased fitness and/or quantities of gametes). I compared the observed estimates of the adult and recruit populations to the observed values for the maximum and mean NIX Intensities for each year. There are no NIX observations prior to 1983. Under the assumption that NIX was not established in the razor clam population before 1983 (Elston, 1986a), all values for years prior to 1983 were set to zero. The highest observed population of razor clams occurred prior to 1983. Therefore, the least-squares line showed

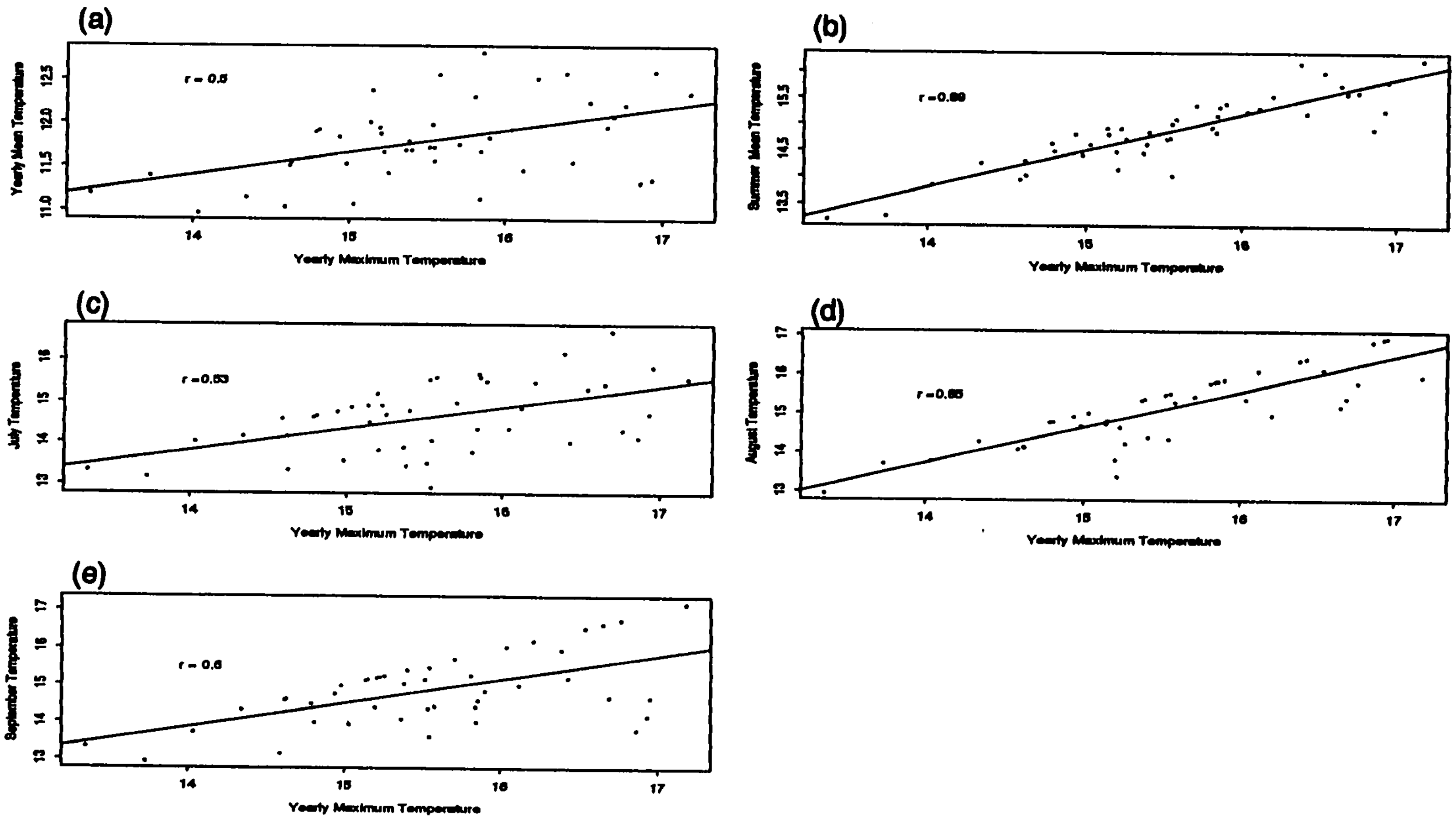


FIGURE 4.11 Correlation structure of various measures of temperature from 1948 - 1992. The comparisons are: (a) yearly mean temperature versus yearly maximum temperature, (b) summertime mean temperature versus yearly maximum temperature, (c) maximum temperature in July versus yearly maximum temperature, (d) maximum temperature in August versus yearly maximum temperature, and (e) maximum temperature in September versus yearly maximum temperature. Each plot also includes the best-fit line to the data.

a slight decline in both the numbers recruited and the population size as a function of the maximum NIX Intensity (Figure 4.12). However, this relationship is not statistically significant for either the adults ($p=0.35$) or the recruits ($p=0.54$). Similar results were noted when the mean annual NIX Intensity was used. The slope of the regression was negative for both adults and recruits, but the relationship was not significant for either the adults ($p=0.28$) or the recruits ($p=0.62$)

Rather than assuming that the NIX intensity was zero for all years prior to its discovery, an alternative approach ignored all years prior to 1983. Again, the relationship between the maximum NIX Intensity and either the adults ($p=0.52$) or the recruits ($p=0.33$) was not statistically significant. Finally, the relationship between the mean annual NIX Intensity and either the adults ($p=0.97$) or the recruits ($p=0.23$) was not statistically significant. Therefore, using this simple correlation analysis, there does not appear to be a relationship between either the mean annual or the maximum NIX intensity and the population of adults during the current year or the population of recruits in the following year.

4.3.2 RECRUITMENT MODELS

Fisheries scientists often assume that there is a relationship between the parental number, and the number of offspring produced (Beverton and Holt, 1957; Ricker, 1975; Cushing, 1981; Cushing, 1988). Many models have been proposed to account for this relationship. The majority of recruitment models have a few characteristics in common. Generally, these models assume that with no measurable parental stock, recruitment is zero. A few specialized models assume that before the stock size is zero, recruitment can no longer sustain the stock (e.g., an Allee effect). A second general characteristic is that as the parental stock increases, up to a point, so does the potential recruitment. Finally, for many models, at some high parental stock level, there is a density-dependent feedback that suppresses further increases in recruitment. For some models, not only is there no increase in recruitment with increasing parental stock size, but the larger parental stocks actually

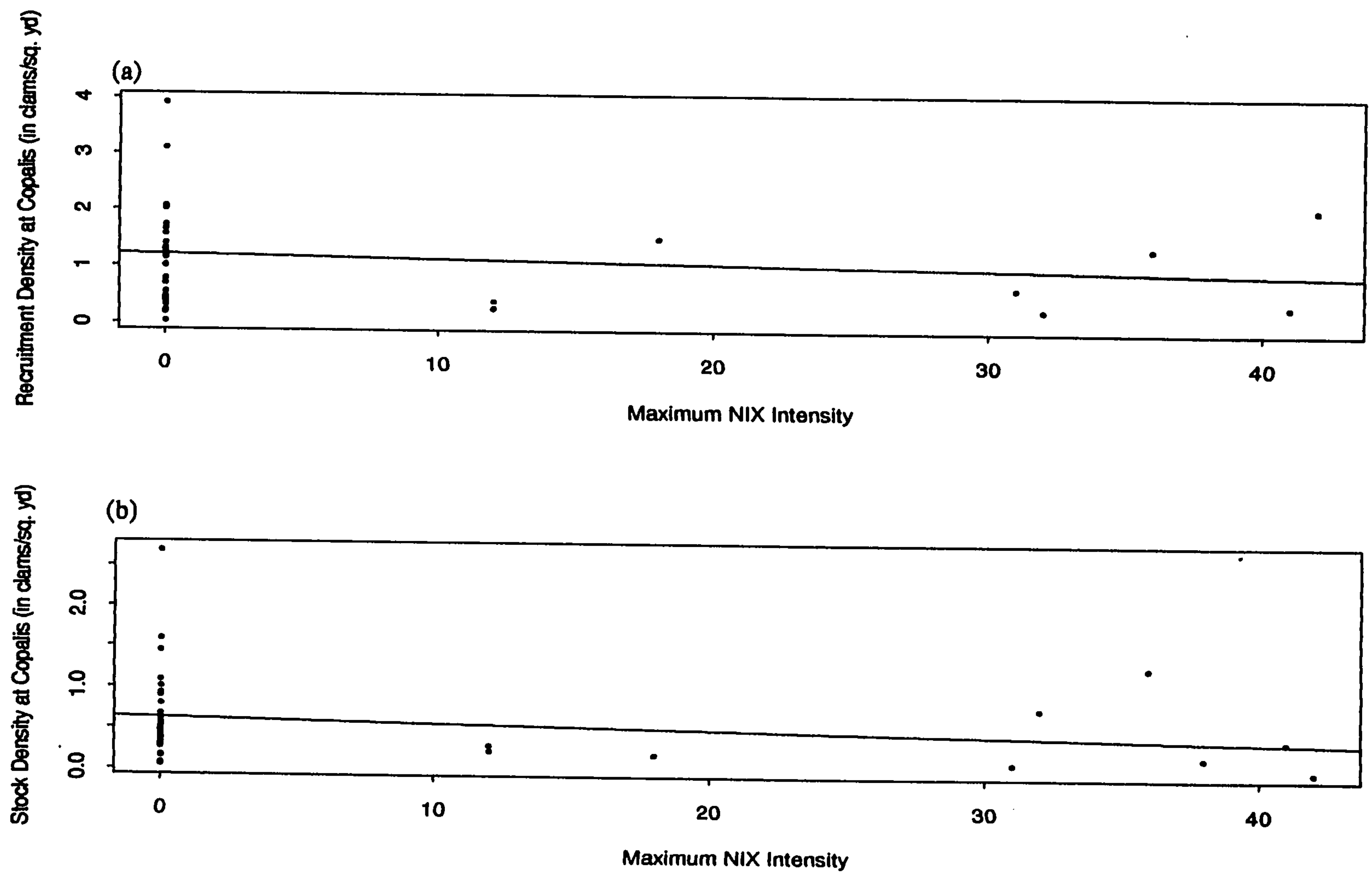


FIGURE 4.12 Relationship between maximum yearly NIX intensity and (a) recruitment or (b) adult population size. Although the best-fit least-squares line does indicate a decrease in population size with an increase in the NIX intensity, this relationship is not statistically significant ((a) $p=0.54$; (b) $p=0.35$).

cause a decrease in the expected number of recruits. Although razor clams are not sessile, they are known to show only vertical movement once they become adults. Therefore, space for settlement could be a limiting factor, resulting in a strong density-dependent relationship between the adults and future recruitment success. For the razor clam, the recruitment relationship should meet the following criteria:

1) There is a compensatory mechanism at low parental stock sizes. This is evident by high recruitment success at times of low stock size.

2) At high parental stock sizes, there is a spatial limit to the number of new recruits that can establish upon a beach. This is the density-dependent feedback.

3) Beyond the parental influence, there is probably an influence of external stresses.

The support for the above criteria are:

1) Without compensation, no fishery could exist. If reproduction simply replaced the adults in the stock at all levels of the adult stock, then any fishing would drive the population down, and the population would stay at that level. With compensation, however, the potential exists for the recruits to not only replace the adults, but to supplement their numbers.

2) At all beaches, the highest historical stock densities showed poor recruitment. Also, the cyclical behavior of the stock indicates that strong recruitment success follows a series of poor (i.e., low density) years.

3) External stresses may or may not be correlated to parental stock size, and can significantly alter the stock-recruitment relationship. A stress such as temperature may act independent of parental stock size, if death of the recruits is due to temperature mediated stress, or dependent upon parental stock size, if death of the recruit is due to limited food supply.

Evidence from growth data, as well as anecdotal evidence, indicated that it takes approximately 2 years for a razor clam to become sexually mature and to reach ~10cm. As it is not possible to accurately age razor clams, length surrogates for age must be used. Thus, for all analyses that account for the two classes (adult and juvenile), this 10 cm boundary was used.

Three major classes of models were investigated. In the first class of models, the razor clam recruitment was investigated using size classified data that distinguished between adults and juveniles. For this set of models, it is assumed that the number of juveniles in future generations is related to the current number of adults that are reproductive. In the second and third classes of models, the size classification was dropped, and the total density of clams was used. The second and third classes of models require less information, and have slightly different assumptions. For the second set of models, it is assumed that the total number of clams (adults and juveniles) in future generations is related to the current number of clams that have already settled upon the beach. For the third set of models, it is assumed that the total number of clams (adults and juveniles) in future generations is not related to the current or past number of clams. However, very strong density-dependent mechanisms are assumed that maintain the population at a fairly constant level. A mean recruitment is modelled, and variations around this mean recruitment is controlled by external variables.

The release-recapture data described in section 4.2 provided the annual population of clams for each beach, along with the number of juveniles and adults within the population. Using these data, a series of potential models were constructed. Of these, a subset looked at the relationships between stock and recruitment, in the absence of any environmental data, whereas the others looked at not only the stock-recruitment relationship, but how this relationship was altered by the environment. As the life-span of the razor clam seems to be on the order of 3-4 years, environmental data for both the year in which the clam was spawned, and the first year of juvenile life were included in the models. It was hoped that by doing so, a critical stage might be assessed. Supposing a model could be found that incorporated both stock abundance and temperature, future stock abundance could be estimated based on current stock sizes and environmental factors within the year of the critical stage.

The first class of models have the Ricker model as their basis. The Ricker model was chosen because initial graphics from all beaches indicated that at very high stock densities, reproductive success was poor. This result is consistent with the Ricker formulation. All models based upon variations of the Ricker model were transformed before the parameters were estimated. This was done to accommodate the assumption of log-normal errors in the original formulation (Ricker, 1975). As a by-product, this transformation made all equations linear.

The second and third classes of models use either the Schaefer (Hilborn and Walters, 1992) model, a differenced regression model or a mean recruitment model as their basis. Some of these models are also transformed to accommodate a normal error structure.

4.3.2.1 Stock-Recruitment Relationships Using Stage-Structured Data

The first class of models rely upon stage-structured data, and imply that the number of spawning adults currently on the beach is the driving force behind the success of future recruitment. At low stock densities, an increase in adults will be beneficial to the stock, for more adults create more recruits. Beyond some density, however, density-dependent mechanisms cause the per capita mortality of the juveniles to increase. The models in this section assume that recruitment is related to stock density through some form of the Ricker model. The most typical form of the Ricker model is parameterized as

$$R = \alpha A \exp(-\beta A) \cdot \varepsilon \qquad \text{(EQ 4.2)}$$

whereas the generalized form may be represented as

$$R = \alpha A \exp(\underline{X}'\underline{\beta}) \cdot \varepsilon \qquad \text{(EQ 4.3)}$$

where R = number or density of recruits,

A = number or density of adults,

$\underline{X}$ = matrix of independent variables (e.g., indicator variable of beach, the stock density, the NIX intensity, or the maximum temperature)

$\alpha, \underset{\sim}{\beta}$ = parameters to be estimated,

ε = error term.

The assumption of a log-normal error allowed the Ricker equation to be linearized. The linearized version of the general Ricker model is represented as

$$\ln(R) = \ln(\alpha) + \ln(A) + \underline{X}'\underline{\beta} + \ln(\varepsilon) \qquad \text{(EQ 4.4)}$$

All models in this section use the general format of the Ricker equation (Equation 4.3). The different models are created by changing which independent variables are included in the exponent. This created a series of hierarchical regression models that were tested using a step-wise procedure (Tables 4.3 and 4.4).

The data used in model 4.3 were parsed into parental stock (i.e., adults) and new recruits based upon length, as mentioned previously. Although there is a 2 year delay between the time a razor clam is spawned and it first spawns, capture of yearling razor clams (0-year old clams) is difficult due to gear selectivity. Therefore, within the data series, the proportion of 0-year old clams that were caught was typically insignificant. The

Table 4.3: Listing of Variables Used in the Recruitment Models

Variable Symbol	Variable Name	Variable Description
	Ricker-Based Models	
R	Recruit Density	Density (in clams per square yard) of clams that are below 10 cm in length.
A	Adult Density	Density (in clams per square yard) of clams that are above 10 cm in length.
T_j	Maximal-Mean Yearly Temperature with lag "j"	The maximum value of the mean-monthly sea-surface water temperature off the Washington coast (in Celsius) for a given year.
E_j	El Nino Indicator with lag "j"	Indicator variable for years when El Nino effects occurred off the Washington coast.
N_j	Maximal-Mean Yearly NIX Intensity with lag "j"	The maximum value of the mean-monthly NIX Intensity for a given year. The NIX Intensity was measured at Copalis Beach.
B	Subscript indicating Beach	This subscript is used to designate from which beach the data were collected. The values of "B" are integers from [1,4] for the four beaches (i.e., Mocrocks, Copalis, Twin Harbors and Long Beach).
j	Subscript indicating lag	This subscript is used to designate the lag between the data and when the effect was operational. The values of "j" are the integers 1 and 2; where 1 = two years before adulthood, and 2 = one year adulthood
β_i	Parameters	Slope/Effect parameters estimated using least-squares.

Table 4.3 (cont.): Listing of Variables Used in the Recruitment Models

Variable Symbol	Variable Name	Variable Description
	Schaefer-Based and Regression Models	
$\Delta D_{k,t+i}$	Change in Total Density	Change in the total density of clams from time step "t" to time step "ti"
D_t	Total Density	Total density of clams (in clams per square yard) on beach "B" at time "t"
$C_{B,t}$	Catch Density	Total density of clams that were caught at beach "B" during the autumn of time "t" and the spring of time "t+1"
T_j	Maximal-Mean Yearly Temperature with lag "j"	The maximum value of the mean-monthly sea-surface water temperature off the Washington coast (in Celsius) for a given year.
E_j	El Nino Indicator with lag "j"	Indicator variable for years when El Nino effects occurred off the Washington coast.
N_j	Maximal-Mean Yearly NIX Intensity with lag "j"	The maximum value of the mean-monthly NIX Intensity for a given year. The NIX Intensity was measured at Copalis Beach.
B	Subscript indicating Beach	This subscript is used to designate from which beach the data were collected. The values of "B" are integers from [1,4] for the four beaches (i.e., Mocrocks, Copalis, Twin Harbors and Long Beach).
j	Subscript indicating lag	This subscript is used to designate the lag between the data and when the effect was operational. The values of "j" are the integers 1 and 2; where 1 = two years before adulthood, and 2 = one year adulthood

Table 4.3 (cont.): Listing of Variables Used in the Recruitment Models

Variable Symbol	Variable Name	Variable Description
	Schaefer-Based and Regression Models (continued)	
r_B	Intrinsic Rate of Growth Parameter	Rate at which the population will grow in the absence of any limiting factors. The "B" subscript indicates that each beach may have a separate estimate of this parameter.
K_B	Carry Capacity Parameter	The estimated maximum density of clams that can be supported on any beach. The "B" subscript indicates that each beach may have a separate estimate of this parameter.
β_i	Parameters	Slope/Effect parameters estimated using least-squares.
	Stage Structured Ricker-Based Models	
D_{t+1}	Total Density	Total density of clams (in clams per square yard) at time "t"
A_t/A_{t-1}	Adult Density	Density of clams (per square yard) that are greater than 10 cm in length at time "t" or time "t-1" respectively.
$C_{B,t}$	Catch Density	Total density of clams that were caught at beach "B" during the autumn of time "t" and the spring of time "t+1"
T_j	Maximal-Mean Yearly Temperature with lag "j"	The maximum value of the mean-monthly sea-surface water temperature off the Washington coast (in Celsius) for a given year.
E_j	El Nino Indicator with lag "j"	Indicator variable for years when El Nino effects occurred off the Washington coast.

Table 4.3 (cont.): Listing of Variables Used in the Recruitment Models

Variable Symbol	Variable Name	Variable Description
	Stage Structured Ricker-Based Models (continued)	
N_j	Maximal-Mean Yearly NIX Intensity with lag "j"	The maximum value of the mean-monthly NIX Intensity for a given year. The NIX Intensity was measured at Copalis Beach.
B	Subscript indicating Beach	This subscript is used to designate from which beach the data were collected. The values of "B" are integers from [1,4] for the four beaches (i.e., Mocrocks, Copalis, Twin Harbors and Long Beach).
j	Subscript indicating lag	This subscript is used to designate the lag between the data and when the effect was operational. The values of "j" are the integers 1 and 2; where 1 = two years before adulthood, and 2 = one year adulthood
S_B	Survival Estimate	Survival probability of adults that are not caught. The "B" subscript indicates that each beach may have a separate estimate of this parameter.
α,β_i	Parameters	Slope/Effect parameters estimated using least-squares.

Table 4.4: Recruitment Model Formulations.

Model Name		Dependent Variable	Linear/Nonlinear Predictor
Ricker-Based Models			
Classical Ricker Model	(EQ. 4.5)	$\log_e(R)$	$\beta_1 A$
Full Model - Based on Ricker Formulation	(EQ. 4.6)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2 + \beta_{3_B} T_j + \beta_{4_B} T_j^2 + \beta_{5_B} E_j +$ $\beta_{6_B} N_j + \beta_{7_B} (N_j T_j) + \beta_{8_B} \left(N_j T_j^2\right)$
Ricker Stock-Recruitment Model	(EQ. 4.7)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2$
Ricker Environmental- Recruitment Model	(EQ. 4.8)	$\log_e(R)$	$\beta_{0_B} + \beta_{3_B} T_j + \beta_{4_B} T_j^2$
Ricker Stock-Environmental Model	(EQ. 4.9)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2 + \beta_{3_B} T_j + \beta_{4_B} T_j^2$
Ricker Stock-El Nino Model	(EQ. 4.10)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2 + \beta_{5_B} E_j$
Ricker Stock-NIX Model	(EQ. 4.11)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2 + \beta_{6_B} N_j$
Ricker Stock-Environmental NIX Model	(EQ. 4.12)	$\log_e(R)$	$\beta_{0_B} + \beta_{1_B} A + \beta_{2_B} A^2 + \beta_{3_B} T_j + \beta_{4_B} T_j^2 +$ $\beta_{6_B} N_j + \beta_{7_B} (N_j T_j) + \beta_{8_B} \left(N_j T_j^2\right)$

Table 4.4 (cont.): Recruitment Model Formulations.

Model Name	Dependent Variable	Linear/Nonlinear Predictor
Schaefer-Based Models		
Classic Schaefer Model (EQ. 4.13)	ΔD_{t+1}	$r_B D_t\left(\frac{K_B - D_t}{K_B}\right) - C_{B,t}$
Schaefer Model, Including Density-Independent Temperature Factors (EQ. 4.14)	ΔD_{t+1}	$r_B D_t\left(\frac{K_B - D_t}{K_B}\right) - C_{B,t} + \beta_{3_B}(D_t T_j) + \beta_{4_B}\left(D_t T_j^2\right)$
Schaefer Model, Including Density-Dependent Temperature Factors (EQ. 4.15)	$\Delta D_{k,t+1}$	$r_B D_t\left(\frac{K_B + \beta_{3_B} T_j + \beta_{4_B} T_j^2 - D_t}{K_B + \beta_{3_B} T_j + \beta_{4_B} T_j^2}\right) - C_{B,t}$
Schaefer Model, Including Density-Independent El Nino Factor (EQ. 4.16)	ΔD_{t+1}	$r_B D_t\left(\frac{K_B - D_t}{K_B}\right) - C_{B,t} + \beta_{3_B}(D_t E_j)$
Schaefer Model, Including Density-Dependent El Nino Factor (EQ. 4.17)	$\Delta D_{k,t+1}$	$r_B D_t\left(\frac{K_B + \beta_{3_B} E_j - D_t}{K_B + \beta_{3_B} E_j}\right) - C_{B,t}$

Table 4.4 (cont.): Recruitment Model Formulations.

Model Name	Dependent Variable	Linear/Nonlinear Predictor
Differenced Regression Models		
Basic Differenced Regression Model (EQ. 4.18)	ΔD_{t+2}	$r_B(K_B - D_t) + \beta_{2_B} C_{B,t}$
Differenced Regression Model, Including Density-Dependent Temperature Factors (EQ. 4.19)	ΔD_{t+2}	$r_B(K_B - D_t) + \beta_{2_B} C_{B,t} + \beta_{3_B}(D_t T_j) + \beta_{4_B}\left(D_t T_j^2\right)$
Differenced Regression Model, Including Density-Independent Environmental Factors (EQ. 4.20)	ΔD_{t+2}	$r_B(K_B - D_{k,t}) + \beta_{2_B} C_{B,t} + \beta_{3_B} T_j + \beta_{4_B} T_j^2$
Differenced Regression Model, Including Density-Dependent El Nino Factor (EQ. 4.21)	ΔD_{t+2}	$r_B(K_B - D_t) + \beta_{2_B} C_{B,t} + \beta_{3_B}(D_t E_j)$
Differenced Regression Model, Including Density-Independent El Nino Factor (EQ. 4.22)	ΔD_{t+2}	$r_B(K_B - D_{k,t}) + \beta_{2_B} C_{B,t} + \beta_{3_B} E_j$

Table 4.4 (cont.): Recruitment Model Formulations.

Model Name	Dependent Variable	Linear/Nonlinear Predictor
Stage-Structured Ricker-Based Models		
Stage-Structured Ricker-Based Model (EQ. 4.23)	D_{t+1}	$S_B(A_t - C_{B,t}) + \alpha_B A_t \cdot \exp\left(-\left(\beta_{1_B} \cdot A_t\right)\right) +$ $\beta_{2_B} A_{t-1} \cdot \exp\left(-\left(\beta_{1_B} \cdot A_{t-1}\right)\right)$
Stage-Structured Ricker-Based Model with Temperature Factors (EQ. 4.24)	D_{t+1}	$S_B(A_t - C_{B,t}) + \alpha_B A_t \cdot \exp\left(-\left(\beta_{1_B} \cdot A_t\right)\right) +$ $\beta_{2_B} A_{t-1} \cdot \exp\left(-\left(\beta_{1_B} \cdot A_{t-1}\right)\right) +$ $\beta_{3_B} T_j + \beta_{4_B} T_j^2$
Stage-Structured Ricker-Based Model with an El Nino Factor (EQ. 4.25)	D_{t+1}	$S_B(A_t - C_{B,t}) + \alpha_B A_t \cdot \exp\left(-\left(\beta_{1_B} \cdot A_t\right)\right) +$ $\beta_{2_B} A_{t-1} \cdot \exp\left(-\left(\beta_{1_B} \cdot A_{t-1}\right)\right) +$ $\beta_{5_B} E_j$
Stage-Structured Ricker-Based Model with NIX Intensity (EQ. 4.26)	D_{t+1}	$S_B(A_t - C_{B,t}) + \alpha_B A_t \cdot \exp\left(-\left(\beta_{1_B} \cdot A_t\right)\right) +$ $\beta_{2_B} A_{t-1} \cdot \exp\left(-\left(\beta_{1_B} \cdot A_{t-1}\right)\right) + \beta_{6_B} N$

Table 4.4 (cont.): Recruitment Model Formulations.

Model Name		Dependent Variable	Linear/Nonlinear Predictor
Mean Recruitment Regression Models			
Mean Recruitment Regression Model	(EQ. 4.27)	D_{t+1}	$\alpha_B + \beta_{2_B} C_{B,t}$
Mean Recruitment Regression Model with Temperature Factors	(EQ. 4.28)	D_{t+1}	$\alpha_B + \beta_{2_B} C_{B,t} + \beta_{3_B} T_j + \beta_{4_B} T_j^2 + \beta_{5_B} (D_t T_j) + \beta_{6_B} \left(D_t T_j^2 \right)$
Mean Recruitment Regression Model with El Nino Factors	(EQ. 4.29)	D_{t+1}	$\alpha_B + \beta_{2_B} C_{B,t} + \beta_{3_B} E_j + \beta_{4_B} (D_t E_j)$
Mean Recruitment Regression Model with NIX Intensity	(EQ. 4.30)	D_{t+1}	$\alpha_B + \beta_{2_B} C_{B,t} + \beta_{7_B} N$

conclusions of the statistical analysis mentioned in Section 4.2 also lead me to use a one year lag. Thus, all razor clams that were below the 10cm cutoff were assumed to be 1 year olds. The numbers of razor clams were converted into densities using the estimated area of each beach, as supplied by the Washington Department of Fisheries. Data for all beaches were analyzed using regression analysis.

The traditional Ricker model is that subset of the Full Model (Equation 4.6 in Table 4.4) that includes only the independent variables associated with the adult density. The traditional Ricker model (Ricker, 1954) (Equation 4.5 in Table 4.4) meets several of the criteria mentioned in the introduction to this section (Section 4.3). As typically parameterized, the Ricker model does not include environmental influences. The traditional Ricker model does, however, produce a stock-recruitment relationship that has a maximum recruitment at an intermediate stock size, and has decreased recruitment beyond that stock size in either direction (Figure 4.13). This dome-shaped response is expected if an increase of spawners results in an increase of recruits, but the success of a recruitment class is affected by density-dependent competition for space. For this portion of the analysis, the Ricker model was parameterized as Equation 4.7 (Table 4.4), which includes both the adult density and the square of the adult density.

The purpose of the analysis was to determine whether the four beaches had a single stock-recruitment relationship, a stock-recruitment relationship that varied only in the per capita recruitment at low stock densities (alpha), a stock-recruitment relationship that varied only in the effect of the density-dependence (beta), or a stock-recruitment relationship that was different for each beach.

An alternative approach is to model the recruits solely as a function of an environmental variable (i.e., the maximal mean temperature (MMT)). When the MMT was used as the environmental variable, the independent variables for this subset of the Full Model were either both the maximum mean temperature and the maximum mean temperature squared, or the running average of maximum mean temperatures over 2 or 3

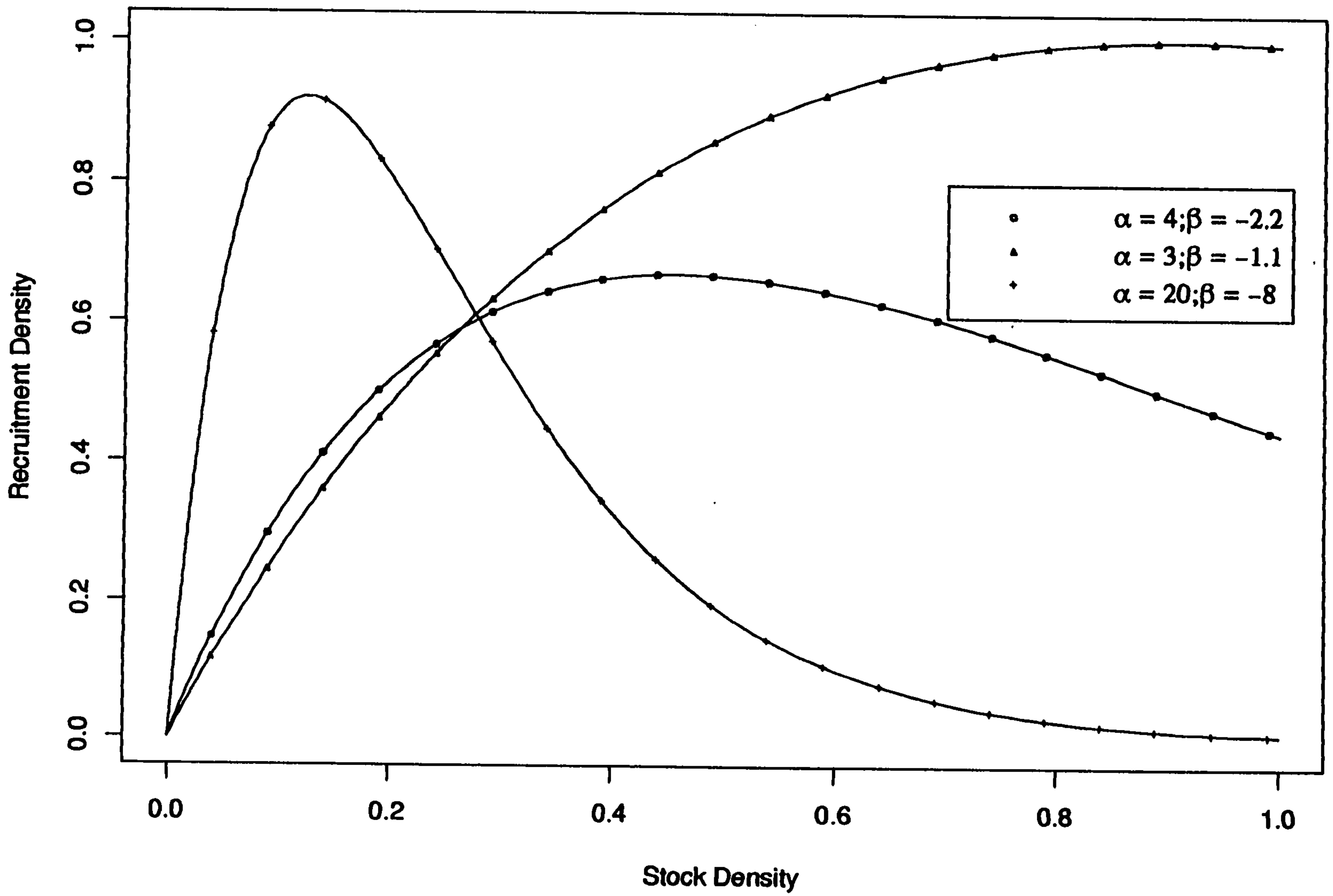


FIGURE 4.13 Shapes of the traditional Ricker Stock-Recruitment Model (Eq. 4.3). For the example, axes are unitless.

years. The linearized form of the Full Model that was used to estimate parameter values was Equation 4.8 (Table 4.4).

Equation 4.8 allows a maximum recruitment at some intermediate level of the independent variable (i.e., maximum mean temperature). A maximum recruitment at some intermediate level of temperature would be expected, as animals typically have a domed (i.e., quadratic) response curve to external stresses (Fry, 1947; Rounsefell, 1958; Ricker, 1975; Hilborn and Walters, 1992). At either extreme of the stressor, the stress level is high, and the recruitment tends to zero, but in the mid-range of the stressor is the optimal regime, where the recruitment is maximized.

Combining the two ideas in Equations 4.7 and 4.8 (Table 4.4) allows both the parental stock size and the maximal mean temperature to impact the production of juvenile razor clams (Equation 4.9). Similarly, combining the two ideas in Equations 4.7 and an El Nino Indicator variable (Table 4.4) allows both the parental stock size and the El Nino to impact the production of juvenile razor clams (Equation 4.10).

In an effort to determine whether the relationship has been stable through time, I also analyzed a subset of the data that did not include the data from the 1980's and 1990's. A significant change in parameter values would have indicated an altered response model, and may affect which data would be used to characterize the current stock-recruit relationship.

To determine whether the NIX intensity significantly altered the stock-recruitment relationship, the recruits were modelled as a function of both the adult density and the NIX intensity. The linearized form of the Full Model that was used to estimate parameter values was Equation 4.11 (Table 4.4).

As high NIX intensities are thought to be problematic, the slope term for the NIX intensity should be negative. A negative slope in the exponent term would imply that as the NIX intensity increased, the production of recruits would decrease. This decrease in production could be due to decreased fitness of the young or the gametes, or due to decreased fecundity of the adults.

WDF data for NIX intensities were primarily available for Copalis. Therefore, the NIX-recruitment relationship was only tested using the data from Copalis. NIX intensity data that I collected at Long Beach was significantly different from that obtained at Copalis, indicating that at any given time, each beach has a unique level of NIX intensity. Thus, using the data for Copalis as a measure of NIX intensity across all beaches does not seem appropriate.

4.3.2.2 Stock-Recruitment Relationships Using Density Data

The Ricker-based models rely upon stage-structured data, and imply that the number of adults on the beach determine recruitment success. An alternative hypothesis is that the total density of both adults and juveniles upon the beach at any one time would be a better descriptor of the spatial pressures that would influence recruitment success. The previous stock-recruitment relationships ignore the spatial contributions made by the juveniles (0-year old clams that recruit during the same season and 1-year old clams that are already present upon the beach). Using the total density implies that living space is a limiting resource. When either juveniles or adults occupy some space, that space is not available to future recruits. Alternatively, interference to settlement may not be spatial, but may instead be due to ingestion of plantonic larvae as they pass over areas with high densities of feeding clams (Dr. Vincent Gallucci, University of Washington School of Fisheries, pers comm.).

As mentioned in Section 4.2, the harvest from the sport fishery (i.e., catch) becomes an important component in the density-based models. The catch is computed using WDF estimates of catch per unit effort and effort statistics. In certain circumstances, the total estimated catch exceeds the estimated population. This problem arises because the estimate of abundance is from a point in time before the season begins, whereas the estimate of catch occurs over an extended time. Selectivity of the smaller clams prior to the season may prohibit an accurate count of them. However, as the season progresses, the smaller clams grow to become clams that are large enough to enter into the catch. Prior to 1986, the catch statistic that was used for the models was the catch that was recorded in the year following the population estimate. For example, for the data associated with 1967 the population density estimate came from the 1967 population estimate. The population was estimated during fall of 1967. The catch estimate for 1967 came from the 1968 estimate of catch, because the catch was harvested from the fall of 1967 to the spring of 1968. After 1985, often, rather than having one long season that progressed from the fall of one year to the spring of the next year, two separate seasons were opened. To keep the data consistent, the catch data from the fall of one year was combined with the catch data from the spring of the next year. For example, for 1990, the population estimate is taken from the fall 1990 estimate, whereas the catch estimate is the combined fall 1990 estimate and the spring 1991 estimate.

4.3.2.2.1 Total Density Relationship Using the Schaefer Model

One model that uses the approach of total density rather than just parental density is the logistic (Emlen, 1984). The logistic equation has a sigmoidal shape, with an asymptotic value of "K", the carrying capacity, and is forced through zero when the total density goes to zero (Equation 4.13 in Table 4.4). The term "K" is the natural upper bound of this equation.The term "r" in the logistic equation is typically referred to as the intrinsic growth rate, and is the growth rate of the population in the absence of any limiting factors. The logistic equation assumes that the measure of density and catch are taken at the same point in time. This would preclude the catch from ever being larger than the total population density. As mentioned in Section 4.2, however, in certain circumstances, the catch does exceed the population estimate. This equation is also known as the Schaefer model (Hilborn and Walters, 1992) in fisheries literature. The form of the equation used in this analysis was Equation 4.13 (Table 4.4).

4.3.2.2.2 Total Density Relationship Using the Schaefer Model, Including Density-Independent Environmental Factors

Previous studies (Section 4.1) have indicated that the temperature can have an impact on the success of the spawning in various other invertebrates. Because I thought that razor clams might behave similarly, I included either temperature (i.e., the MMT) or the El Nino Indicator as a density-independent factor in the Schaefer relationship (Emlen, 1984) as an additive term on the per capita change in density (Equations 4.14 and 4.16 in Table 4.4). As written, these models imply that the environmental factors are density-independent events that act to change the population growth (Emlen, 1984). The "beta" terms in these models indicate sensitivity of the species to the changes in the environment.

4.3.2.2.3 Total Density Relationship Using the Schaefer Model, Including Density-Dependent Environmental Factors

Environmental factors may impact the carrying capacity of a beach, which would imply that the effect of the environmental factor is density-dependent. To add either temperature or the El Nino Indicator as a density-dependent effect to the Schaefer model, the environmental factor is modelled as an additive effect on the carrying capacity (Equations 4.15 and 4.17 in Table 4.4). These models imply that the environmental factors are density-dependent events that act to change the population's carrying capacity (Emlen, 1984). The "beta" terms in this model indicate the sensitivity of the carrying capacity to changes in the environment. In the ideal situation, Equation 4.15 would allow for estimation of the temperature that gives the maximum carrying capacity.

4.3.2.2.4 Total Density Relationship Using the Differenced Regression Model

The differenced regression model is a delay difference equation that has a monotonic convex shape, with an asymptotic value of "K", the carrying capacity

(Equation 4.18). However, unlike the Schaefer and Ricker models, which are forced through zero when the density goes to zero, the differenced regression form allows recruitment in the absence of any indication of animals; sort of an anti-Allee effect (Boyce and DiPrima, 1986, p.61). This scenario is possible for this species under the current sampling scheme. Only razor clams that are accessible during low tide are counted and included in the density estimates. However, Nickerson (1975) and Szarzi (1991) have explored the distribution of razor clams in Alaska and have found that limited populations do exist below the low-tide mark. Similarly, there is evidence from Lassuy and Simons (1989) that suggests a similar distribution pattern for the razor clams along the coast of Washington; although much of the evidence is anecdotal. Therefore, as not all razor clams are included within the population survey, even when the observed density goes to zero, there may still be reproductive adults available to replenish the beaches. The differenced regression model also implies that the success of the future recruitment is determined when the young begin to settle, before the adults are harvested in the fall. The parameters "r" and "K" assume the same definitions as in Section 4.3.5. The form of the equation used in this analysis was the differential form (Equation 4.18 in Table 4.4). Under the assumption of equilibrium conditions, the "beta" parameter before the catch term (Equation 4.18) should be equal to "-1". However, because the actual catch term is an estimate, and there is little evidence to support the equilibrium hypothesis, this parameter will be estimated instead.

4.3.2.2.5 Total Density Relationship Using the Differenced Regression Model, Including Density-Independent and Density-Dependent Environmental Factors

One of my hypotheses is that temperature should affect subsequent recruitment. The temperature could affect the clams in either a density-dependent manner (Equations 4.19 and 4.21 in Table 4.4) or in a density-independent manner (Equations 4.20 and 4.22 in Table 4.4). The value of the X-vector is the only difference between the density-dependent and the density-independent models. In the density-dependent model, the X-vector is the product of the total clam density and either the MMT and the square of the MMT in the previous 2 years, or the indicator of an El Nino event The effect of the temperature metric is a density-dependent factor that alters the rate of population growth. Under this formulation the "betas" measure the sensitivity of the species to changes in the temperature.

In the density-independent model, the X-vector is either the MMT and the square of the MMT in the previous 2 years, or it is the indicator of an El Nino event. In the density-independent parameterization, the effect of the temperature metric is a factor that changes the carrying capacity. With this formulation, the maximum carrying capacity occurs at some intermediate temperature, and decreases quadratically as you either increase or decrease the temperature. This formulation should allow for the estimation of parameters "r", "K". When the MMT is used as the independent variable, this formulation should allow for the estimation of the temperature at which the maximum value of "K" occurs.

4.3.2.2.6 Total Density Relationship Using a Stage-Structured Ricker Stock-Recruitment Relationship

Previous models in this chapter have concentrated on either traditional stock recruitment relationships (i.e., variations of the Ricker Model), or have used the approach of total density in the absence of any stock-recruitment relationship (e.g., the Schaefer Model and Differenced Regression Model). However, dynamics within the systems appeared to show a series of strong recruitments, followed by a series of poor recruitments. This indicates that some age-structure mechanism could be acting within the population to determine the success of future populations In addition, previous correlation results (Section 4.2.1) indicated that multiple year lags may be valid. This model, which I call the Stage-Structured Ricker Stock-Recruitment (SSRSR) Model, attempts to merge the traditional stock recruitment relationship and the total density relationship into one model. Rather than assume that the success of future recruits is defined solely by the numbers of parental stock, this model assumes that both the adults and the juveniles exert a pressure on the success of future recruitment. In many shellfish, this pressure is assumed to be a density-dependent relationship that is related to an area of influence due to disturbance or food allocation. This model also explicitly incorporates the age structure that is present within the population by using the current adult and juvenile densities to construct the prediction of the future densities.

The form of the equation used in this analysis was Equation 4.23 (Table 4.4). Equation 4.23 implies that in the next time period, there will be contributions to the total population from the past two generations, as well as survival of adults not caught. This relationship assumes that the form of the stock-recruitment relationship takes the shape of a Ricker curve, and that survival for adults has been constant throughout the history of the data series. I assumed a normal error about the observed density. The equation was fit using nonlinear least squares. In one version of the fitting, the survival parameter "S" was constrained using a logistic transform, but in a second version, the survival parameter was unconstrained. All other parameters were unconstrained.

4.3.2.2.7 Total Density Relationship Using the a Stage-Structured Ricker Stock-Recruitment Relationship, Including Temperature and NIX

Rather than including the temperature and/or the NIX Intensity into the SSRSR Model arbitrarily, the residuals of the model (Equation 4.23) will be used to suggest how temperature and/or the NIX Intensity may enter the above model. This is a slightly different technique than was used before, but in many cases will yield exactly the same model. The cases when this technique will yield the same model are cases when the temperature and/or the NIX Intensity is linearly related to the dependent-variable. This was the case in the linearized Ricker (Equation 4.11) and in the density-independent temperature effects to the differenced regression model (Equation 4.20). The cases when the this technique will not yield the same results are cases when the temperature and/or the NIX Intensity is nonlinearly related to the dependent variable. This was the case for both the density independent and the density dependent temperature relationships under the Schaefer model (Equations 4.14 and 4.15) and for the density-dependent temperature effects under the Differenced Regression model (Equation 4.19).

Unless there is some extremely compelling reason to fit complicated response models to the temperature and/or the NIX Intensity data, fitting the residuals will probably yield a model in which the density in the next time-step can be modelled as a linear model in response to temperature and/or the NIX Intensity. This would be analogous to appending an additive temperature (Equation 4.24) and/or the NIX Intensity (Equation 4.26) effect to Equation 4.23. Similarly, the indicator variable for El Nino events will also be fitted (Equation 4.25) using the residuals of the fitted model (Equation 4.23).

4.3.2.2.8 Mean Recruitment Regression Model, Including Temperature and NIX

The mean recruitment regression model assumes a constant positive recruitment at all levels of the stock. Deviations from the mean recruitment level are modelled one time step into the future as linear functions of catch, MMT, and NIX Intensity. The use of the mean recruitment regression model has two important implications: (a) there are always enough recruits to maintain the population, regardless of current stock density, and (b) there are strong density-dependent mechanisms that operate to limit the maximum number of recruits that survive. For the razor clam population, the first point could be an indication of either large numbers of gametes produced by a small number of adults or a portion of the population that can contribute to the recruitment pool, but is not included in the stock assessment. The second point could be an indication of space-limiting mechanisms. Combined, these two points imply that there will always be recruitment regardless of the measured stock density, and that reducing harvest to attain higher stock densities will not translate into stronger recruitment classes.

All four beaches were fit individually. The best-fit model was selected using both forward single-step additions and backward single-step deletions of the independent variables. The criteria for model fit are described in the next section (Section 4.4).

4.4 METHODS FOR ASSESSING MODEL FIT

Three measures of model fit (Neter *et al.*, 1983) were computed for each model. These metrics can be used across all models, regardless of whether models are nested or not. The measures of model fit areas follows:

1. Fitting Multiple R-square, calculated as the percentage of the total variability in the transformed "Y" explained by the model, $R^2 = \left(1 - \frac{SSError}{SSTotal}\right) \times 100\%$,

2. Fitted Multiple R-square, calculated as the percentage of the total variability in the back-transformed "Y" explained by the model, and

3. Adjusted Fitted Multiple R-square, calculated as the percentage of the total variability explained by the model during the prediction phase, but with a penalty that accounts for the number of parameters ("*p*") that are estimated,
$$R^2 = \left(1 - \left(\frac{n-1}{n-p}\right) \cdot \left(\frac{SSError}{SSTotal}\right)\right) \times 100\%.$$

If the dependent variable in the fitting process is the same as the dependent variable in the prediction phase (i.e., no transform was performed on the "Y" variable prior to fitting the model), then the Fitting R-square and the Fitted R-square will be equal. In many cases, however, the fitting procedure used a transformed variable as the dependent variable.

When using regression analysis, it is important to understand whether the fit of the model is being strongly affected by a few points. Influence is a statistical measure that quantifies the potential effect a point could have on the fit of a line. The influence of a point is obtained from the diagonal elements of the hat matrix in regression, where the hat matrix is defined as $H = X\left(X^T X\right)^{-1} X^T$ (Hoaglin and Welsch, 1978). The influence statistic is a function of the independent variables only; the dependent variable does not enter into the calculation of the influence. Because influence does not account for the effect the point truly has on the line, only the potential effect, it is useful to also examine the leverage statistic (McCullagh and Nelder, 1989). The leverage statistic summarizes the effect that a single point has on the effect of the fitted line. I examined the leverage by looking at how the removal of an individual point would affect the slope parameter for the effect of interest within the regression analysis.

4.5 RESULTS OF ANALYSIS

4.5.1 STOCK-RECRUITMENT RELATIONSHIP USING THE RICKER MODEL

The analysis of the stock-recruitment relationship using the Ricker Model (Equation 4.7 in Table 4.4) revealed there is a strong stock-recruitment relationship ($p<0.01$), and that this relationship varies for each of the four beaches ($p<0.1$) (Table 4.5). The significance of the "Beach" term indicates that each beach has a separate intercept term; a separate value of "α" in the Ricker model. The "BeachxStock" interaction term indicates that each beach has a separate slope term; a separate value of "β" in the exponent of the Ricker model. These two terms, the "Beach" and the "BeachxStock" interaction term, indicate that each beach has a significantly different ($p<0.10$) stock-recruitment relationship. The following are the fitted model for each beach:

a) Mocrocks: $\ln\left(\frac{R}{A}\right) = 2.07 - (1.97 \cdot A) + \left(0.217 \cdot A^2\right)$

Table 4.5: Analysis of Variance Table for the Linearized Ricker Stock-Recruitment Relationship (Equation 4.7 in Table 4.4). The "Beach" term tests for individual intercept terms. The "BeachxStock" term tests for individual slope terms.

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Total Corr. Sum Sq.	11				
Stock Density	1	117.910	117.910	93.729	< 0.001
(Stock Density)^2	1	35.102	35.102	27.904	< 0.001
Beach	3	8.414	2.805	2.229	0.088
Beach x Stock Density	3	12.076	4.025	3.200	0.026
Beach x (Stock Density)^2	3	10.269	3.423	2.721	0.047
Residual	120	150.958	1.258		

Multiple R-Square = 0.4962

b) Copalis: $\ln\left(\frac{R}{A}\right) = 2.13 - (2.84 \cdot A) + \left(0.472 \cdot A^2\right)$

c) Twin Harbors: $\ln\left(\frac{R}{A}\right) = 2.89 - (9.27 \cdot A) + \left(5.34 \cdot A^2\right)$

d) Long Beach: $\ln\left(\frac{R}{A}\right) = 2.68 - (4.76 \cdot A) + \left(1.17 \cdot A^2\right)$

Both the stock density, and the square of the stock density had statistically significant contributions to model fit ($p<0.001$). Models that are fit with and without the stock squared term are essentially the same (Figures 4.14 and 4.15), except for at extremely large stock densities. The stock squared term enters into the model because, when the model includes only the stock density, recruitment declines too rapidly at very high stock densities. The squared stock density term brings the right tail of the model into closer agreement with the observed values. Beyond the highest observed stock sizes, the squared term causes the numbers of recruits to increase with increasing stock size, resulting in a total disintegration of the depensatory density-dependent relationship. In fact, recommendations from the extrapolated model would indicate that the higher the stock density, the higher the subsequent recruitment. In the extreme, as the stock density goes to infinity, so does the subsequent recruitment. This trend is not observed in the data. Accordingly, it would be very foolish to extrapolate much beyond the bounds of the historical densities. Given the fit, it is not surprising to discover that a few points that have very high leverage also exert a strong influence upon the fit of the stock squared term (Figures 4.16 and 4.17).

Figures 4.16 and 4.17 indicate that those stock densities that were the highest on each beach have high leverage and high influence on the stock-recruit relationship. Notice that in Figure 4.16, the influential points (values distant from zero) for Copalis (Point #35), Twin Harbors (Point #71), and Long Beach (Point #102) are the points that are the

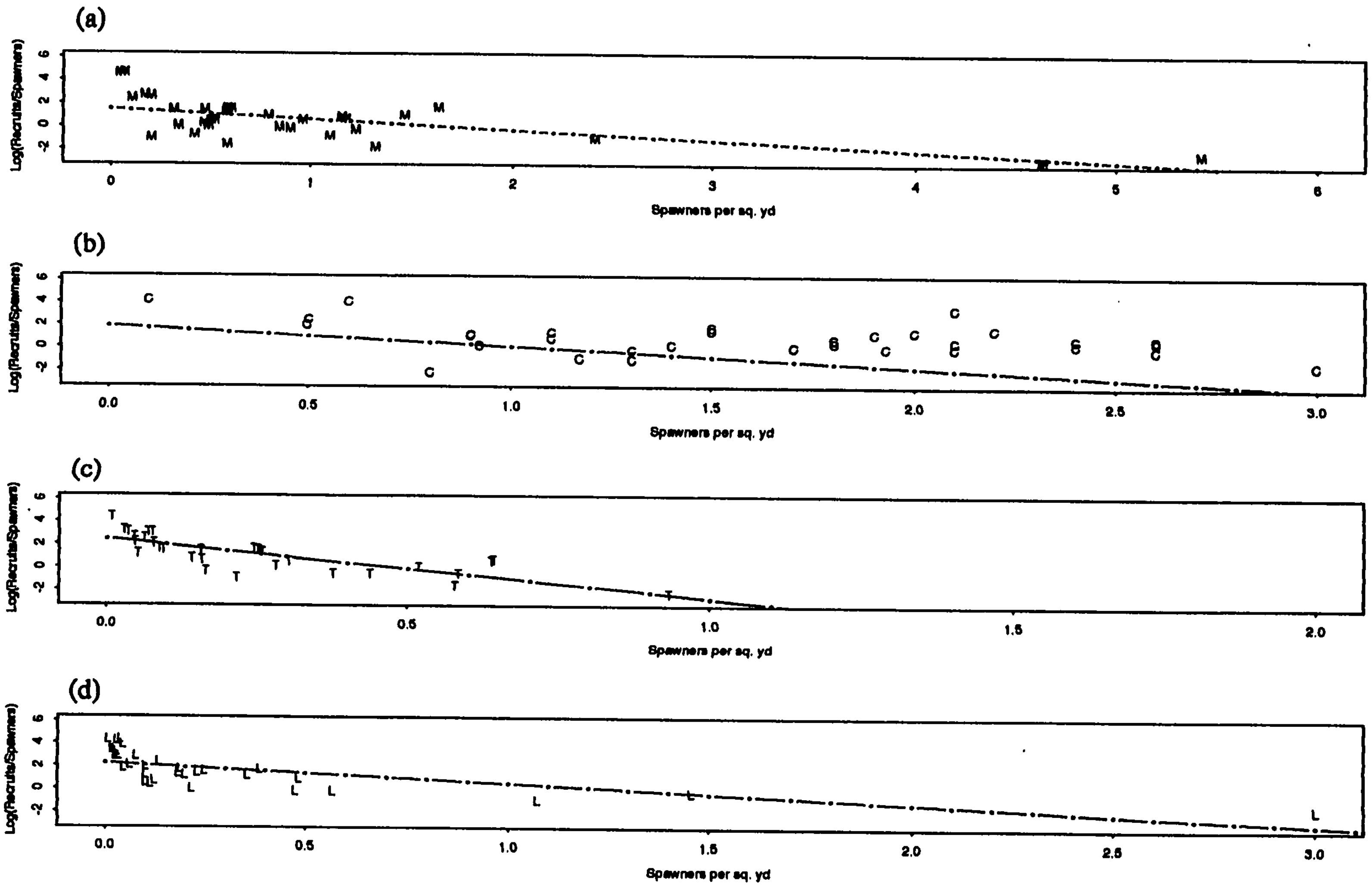


FIGURE 4.14 Best fit line for the linearized Ricker curve for (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. This fit is from the model that uses stock size as the only independent variable (Eq. 4.5).

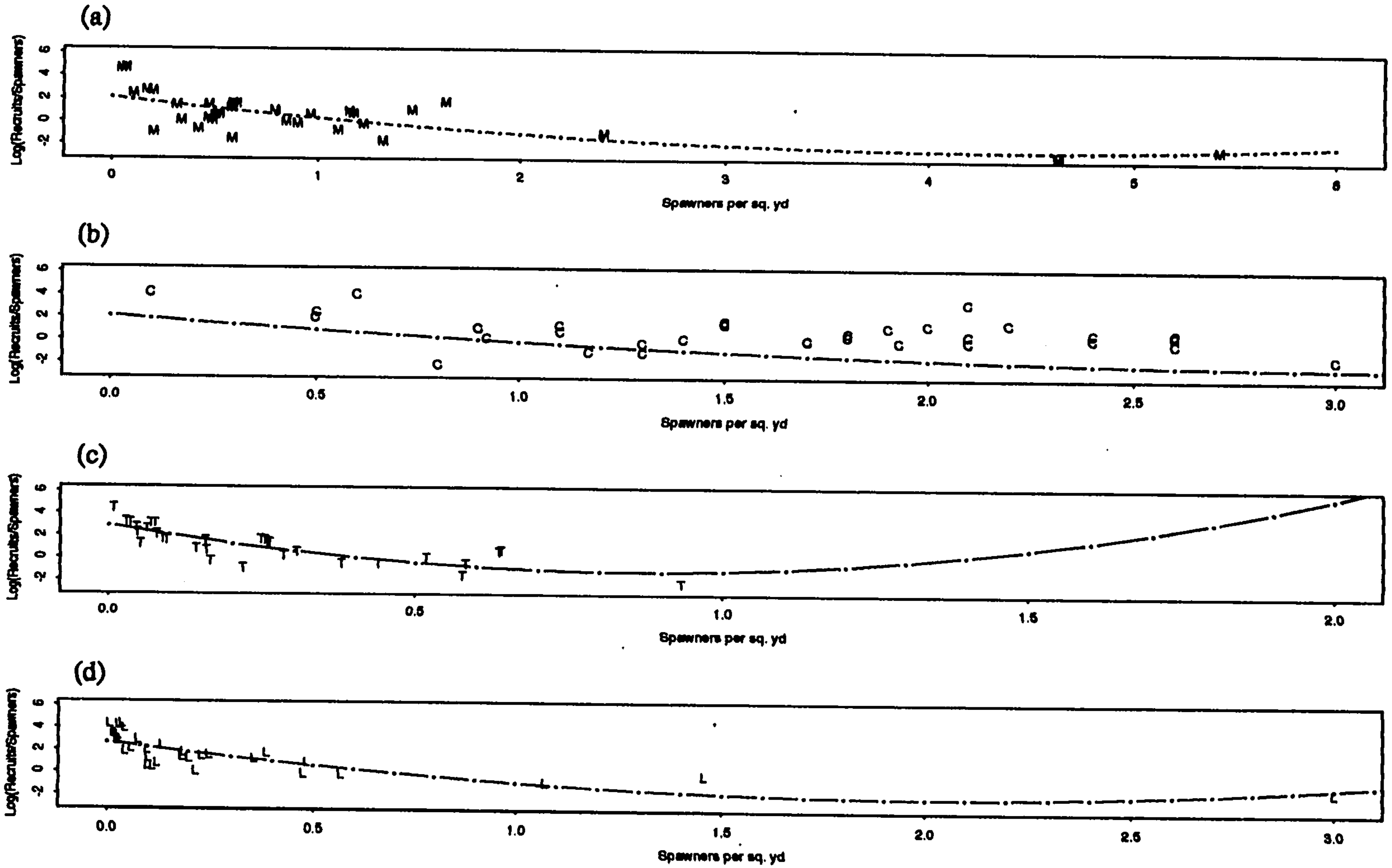


FIGURE 4.15 Best fit line for the linearized Ricker curve for (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. This fit is from the model that uses stock size and the squared stock size as the independent variables (Eq. 4.7; no temperature effects included). Including the squared term allows a curvilinear fit.

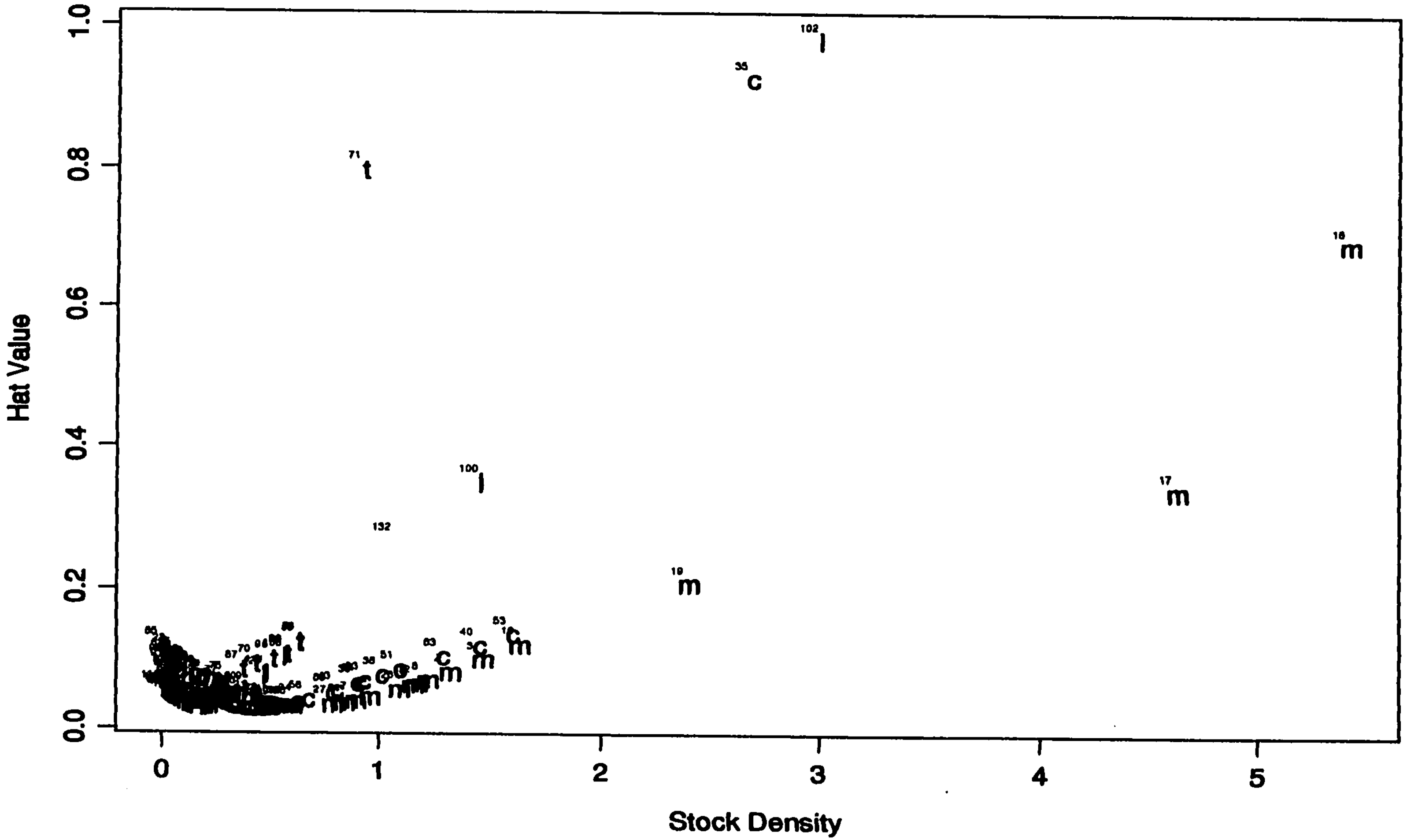


FIGURE 4.16 Influential data points in the stock-recruit relationship (Eq. 4.7). Points from each beach are plotted using the first initial of that beach (e.g., Mocrocks = "m"). Notice that, in general, for all beaches, the points on that beach with the highest densities are the points that have the highest influence. The numbers beside each point are used only as reference numbers for this and the next figure.

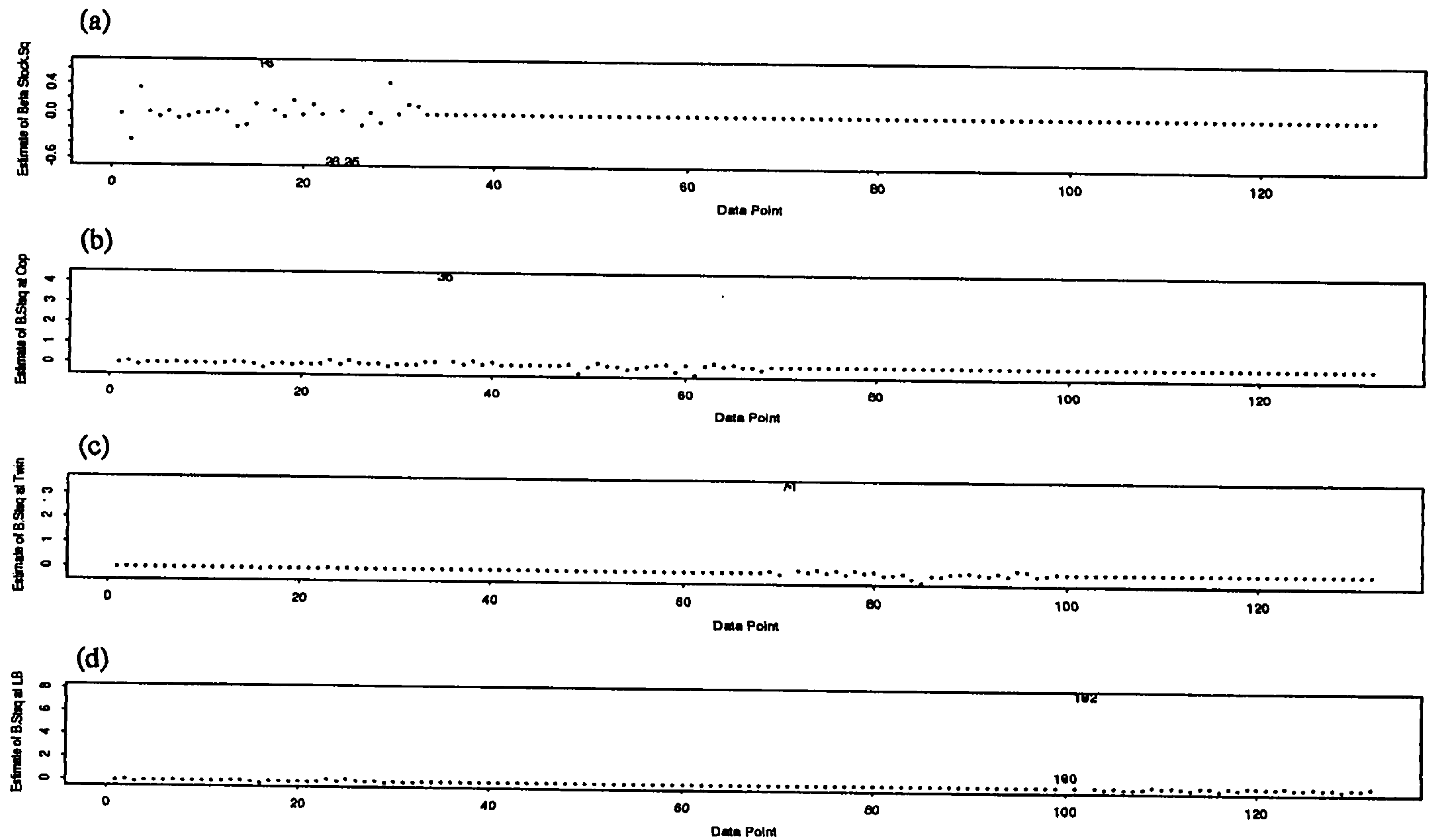


FIGURE 4.17 Effect of individual data points on the standardized coefficient for the stock-squared term at each beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach). Notice that, in general, those points that alter the standardized coefficient greatest are those points that had greatest influence (Figure 4.16).

highest density upon that beach (i.e., the point farthest to the right for that beach). These same points (i.e., Point #35 at Copalis, point #71 at Twin Harbors, and point #102 at Long Beach) also change the estimate of the slope parameters most dramatically when they are removed from the data set (Figure 4.17). At all beaches, the recruitment that was associated with the highest density of stock was very poor. As the Ricker assumes a depensatory density-dependent effect with increasing stock density, these high stock densities are the values that are defining the shape of the curve. Adding the squared term of the stock as a second independent variable allows the curve to fit the higher leverage points very well, but the consequence is that beyond the limits of the data, the stock-recruit relationship becomes nonsensical.

The parameter values for the models that used either stock density or both the stock density and the square of the stock density were used to estimate the stock density that gave the maximum recruitment, and the stock density that gave the greatest positive difference between expected recruitment and current stock size (i.e., the stock size that would give the MSY for a stock that is stable). I found that the stock densities for maximum recruitment and "MSY" varied greatly across the beaches (Table 4.6). Because of the form of the Ricker equation, the stock density for the "MSY" is always less than the stock density for the maximum recruitment. For all beaches, the addition of the stock squared term shifted the value of the stock density for the maximum recruitment and the "MSY" to the left (i.e., smaller densities maximized the relationship). The addition of the stock squared term also lowered the subsequent recruitment from a given stock density for all values to the left of the stock density at maximum recruitment. Because the squared term becomes highly influential in stock densities beyond those typically observed, and because the relationship between stock and recruitment changes drastically because of the squared term, conclusions were only drawn for the range of densities that had been observed.

Table 4.6: Estimated Stock Densities to Achieve Maximum Recruitment and Maximum Sustainable Yield Using the Estimated Parameters Associated with Equations 4.7.

Beach	Stock Density for Maximum Recruitment Using Eq. 4.4 without $Stock^2$ term included.	Stock Density for Maximum Recruitment Using Eq. 4.4 with $Stock^2$ term included.	Stock Density for MSY Using Eq. 4.4 without $Stock^2$ term included.	Stock Density for MSY Using Eq. 4.4 with $Stock^2$ term included.
Mocrocks	$1.14/yd^2$	$0.56/yd^2$	$0.68/yd^2$	$0.39/yd^2$
	(i.e., $0.95/m^2$)	(i.e., $0.47/m^2$)	(i.e., $0.57/m^2$)	(i.e., $0.33/m^2$)
Copalis	$0.56/yd^2$	$0.43/yd^2$	$0.38/yd^2$	$0.30/yd^2$
	(i.e., $0.47/m^2$)	(i.e., $0.36/m^2$)	(i.e., $0.32/m^2$)	(i.e., $0.25/m^2$)
Twin Harbors	$0.19/yd^2$	$0.13/yd^2$	$0.16/yd^2$	$0.11/yd^2$
	(i.e., $0.16/m^2$)	(i.e., $0.11/m^2$)	(i.e., $0.13/m^2$)	(i.e., $0.09/m^2$)
Long Beach	$0.59/yd^2$	$0.24/yd^2$	$0.45/yd^2$	$0.19/yd^2$
	(i.e., $0.49/m^2$)	(i.e., $0.20/m^2$)	(i.e., $0.38/m^2$)	(i.e., $0.16/m^2$)

After the least squares estimates for the parameters of the stock-recruit models had been estimated, both models (i.e., the model that used the stock density as the sole independent variable and the model that used both stock density and squared value of stock density as the independent variables) were used to fit the time series of recruitments (Figure 4.18). The fitting was done on a beach by beach basis, because the analysis had indicated that the parameters for the stock recruitment relationship varied by beach. Regardless, the fit of the models to the data was very poor (Table 4.7). The models did not appear to capture much beyond the mean recruitment. At no beach could either model explain the large recruitments. Finally, the models did not typically capture the 2-3 year decay in population density that follows the very large recruitment classes in the observed time series.

The models for Mocrocks and Copalis do not have very different predictions of subsequent recruitment regardless of the model used. Both the model with only stock density and the model with both the stock density and the squared value of stock density predict relatively stable recruitment throughout the period observed. The models for Twin Harbors and Long Beach that had stock density as the only independent variable indicated a very strong density dependent mechanism at high stock densities. The strong density dependent mechanism causes highly variable predictions of recruitment throughout the time series. Inclusion of the stock squared term in the model at Twin Harbors and Long Beach reduced the effect of high stock sizes to predict drastically reduced recruitment.

4.5.2 ENVIRONMENTAL-RECRUITMENT RELATIONSHIP USING THE RICKER MODEL

The fit of the maximum mean-yearly temperature (MMT), and the MMT squared for the two years prior to adulthood was investigated. Again, the linearized form of the relationship (Equation 4.8) was used to achieve a linear model and an additive error. Stock was included within the relationship only to standardize the recruitment. The relationship between the MMT and recruitment was significant ($p < 0.10$) for all beaches. However, at

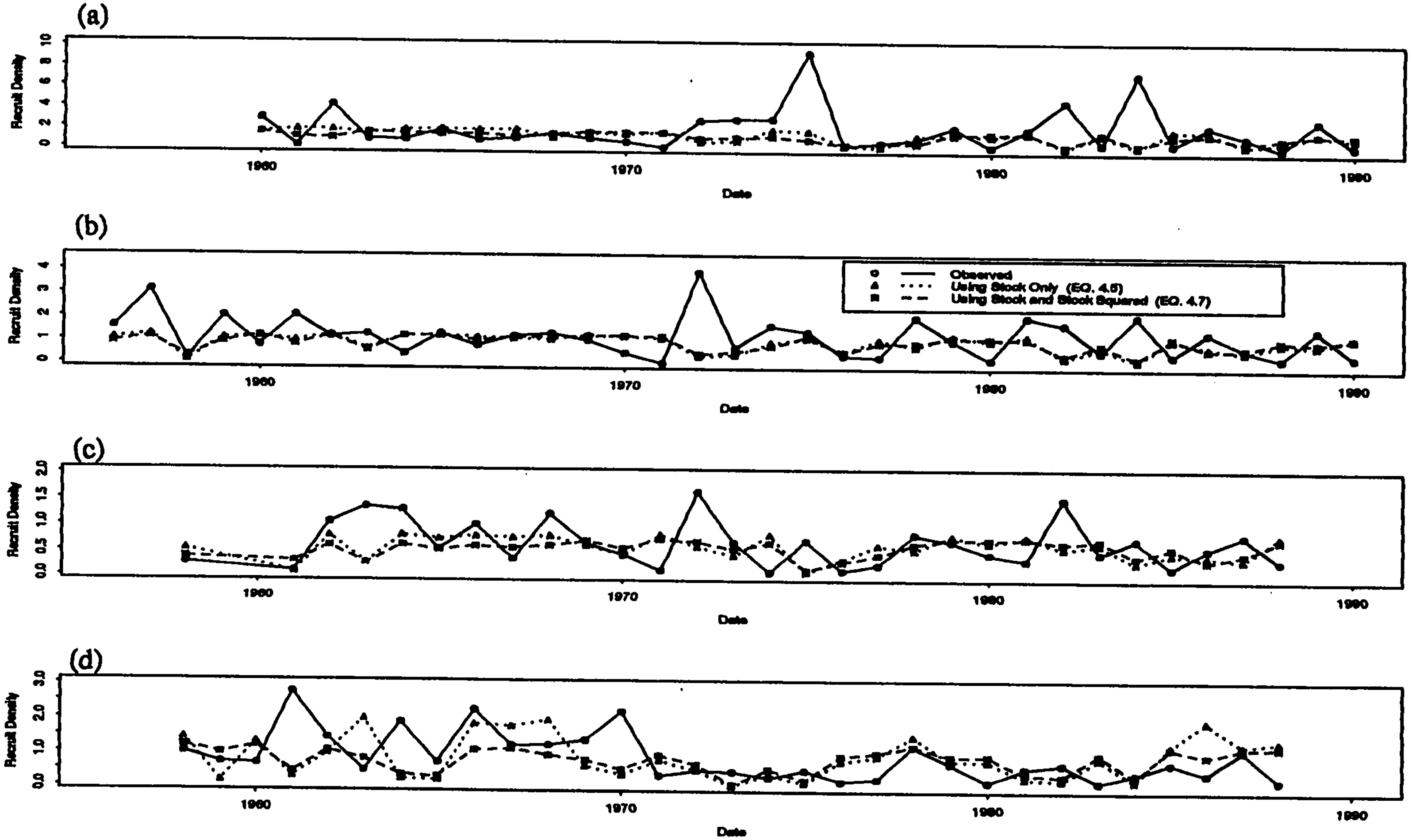


FIGURE 4.18 Fit of the Ricker model at each beach to the time series of recruitments (in clams/sq. yd.)at that beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach). On each plot are two lines; one line shows the fit for the model that uses only the stock density as the independent variable (Eq. 4.5), the other line shows the fit for the model that uses both stock density and the squared term of stock density as the independent variables (Eq. 4.7).

Table 4.7: Fit Statistics for the various recruitment models. Darker cells indicate models that best fit at each beach based on each metric.

Model		Beach	Fitting r^2	Fitted r^2	Adjusted Fitted r^2
Ricker S-R Model	(EQ. 4.7)	Mocrocks	0.549	0.302	0.224
Ricker S-R Model	(EQ. 4.7)	Copalis	0.549	0.360	0.286
Ricker S-R Model	(EQ. 4.7)	Twin Harbors	0.549	0.648	0.607
Ricker S-R Model	(EQ. 4.7)	Long Beach	0.549	0.523	0.468
Ricker S-R w/ Temp	(EQ. 4.10)	Mocrocks	0.613	0.352	0.163
Ricker S-R w/ Temp	(EQ. 4.10)	Copalis	0.613	0.544	0.411
Ricker S-R w/ Temp	(EQ. 4.10)	Twin Harbors	0.613	0.709	0.624
Ricker S-R w/ Temp	(EQ. 4.10)	Long Beach	0.613	0.608	0.494
Differenced Regression Model	(EQ. 4.18)	Mocrocks	0.420	0.558	0.542
Differenced Regression Model	(EQ. 4.18)	Copalis	0.420	0.717	0.708
Differenced Regression Model	(EQ. 4.18)	Twin Harbors	0.420	0.674	0.670
Differenced Regression Model	(EQ. 4.18)	Long Beach	0.420	0.623	0.612
Differenced Regression w/ Density Independent Temp. Effect	(EQ. 4.20)	Mocrocks	0.482	0.670	0.662
Differenced Regression w/ Density Independent Temp. Effect	(EQ. 4.20)	Copalis	0.482	0.818	0.812
Differenced Regression w/ Density Independent Temp. Effect	(EQ. 4.20)	Twin Harbors	0.482	0.717	0.708
Differenced Regression w/ Density Independent Temp. Effect	(EQ. 4.20)	Long Beach	0.482	0.650	0.639

Table 4.7 (cont.):

Model		Beach	Fitting r^2	Fitted r^2	Adjusted Fitted r^2
Differenced Regression w/ Density Dependent Temp. Effect	(EQ. 4.19)	Mocrocks	0.420	0.696	0.685
Differenced Regression w/ Density Dependent. Temp. Effect	(EQ. 4.19)	Copalis	0.420	0.818	0.812
Differenced Regression w/ Density Dependent Temp. Effect	(EQ. 4.19)	Twin Harbors	0.420	0.717	0.708
Differenced Regression w/ Density Dependent Temp. Effect	(EQ. 4.19)	Long Beach	0.420	0.650	0.639
SSRSS Model	(EQ. 4.23)	Mocrocks	0.584	0.584	0.522
SSRSS Model	(EQ. 4.23)	Copalis	0.704	0.704	0.663
SSRSS Model	(EQ. 4.23)	Twin Harbors	0.815	0.815	0.785
SSRSS Model	(EQ. 4.23)	Long Beach	0.704	0.704	0.662
SSRSS Model w/ Temp	(EQ. 4.24)	Mocrocks	0.707	0.707	0.637
SSRSS Model w/ Temp	(EQ. 4.24)	Copalis	0.786	0.786	0.722
Mean Regression Model	(EQ. 4.27)	Mocrocks	0.569	0.569	0.554
Mean Regression Model	(EQ. 4.27)	Copalis	0.732	0.732	0.727
Mean Regression Model	(EQ. 4.27)	Twin Harbors	0.757	0.757	0.749
Mean Regression Model	(EQ. 4.27)	Long Beach	0.748	0.748	0.740

Table 4.7 (cont.):

Model	Beach	Fitting r^2	Fitted r^2	Adjusted Fitted r^2
Mean Regression Model w/ Temp. Effect (EQ. 4.28)	Mocrocks	0.710	0.710	0.689
Mean Regression Model w/ Temp. Effect (EQ. 4.28)	Copalis	0.821	0.821	0.810
Mean Regression Model w/ Temp. Effect (EQ. 4.28)	Twin Harbors	0.829	0.829	0.811
Mean Regression Model w/ Temp. Effect (EQ. 4.28)	Long Beach	0.776	0.776	0.754

Mocrocks and Copalis the one-year lag was the significant lag, whereas at Long Beach, the two-year lag was the significant lag. At Twin Harbors, both the one-year and the two-year lags were significant. Therefore, there was no discernible pattern as to the critical year in the juvenile stage evident from the environment-recruitment relationship. The fit of this model was rather poor (0.13 < fitted r-square < 0.51); therefore no attempt was made to fit the predicted time-series of recruitments using this model.

An alternative relationship was investigated using the running average of the maximum mean temperature over the two years of the juvenile life-span or over the three years of total life-span, rather than the maximum mean temperature in a specific year. None of the analyses for any of the four beaches demonstrated a significant relationship ($p > 0.10$) between the running averages of the maximum mean temperature and the recruitment. This implies that the effect of temperature on the stock-recruit relationship is probably acute, rather than chronic. No attempt was made to fit the time-series of recruitments using the model that used the running average of the maximum mean temperature because none of the analyses for any of the four beaches demonstrated a significant relationship between the running averages of the maximum mean temperature and the recruitment.

4.5.3 STOCK-RECRUITMENT RELATIONSHIP USING THE RICKER MODEL, INCLUDING ENVIRONMENTAL FACTORS

Equation. 4.9 included both effects of stock, and the MMT. A multiple regression analysis found that each beach had an independent stock-recruitment relationship. There was no "BeachxTemperature" interaction ($p>0.48$). Both the MMT and the MMT squared for both years during the juvenile stage made significant contributions to the stock-recruitment relationship (Table 4.8). Regardless of the order in which the MMT effects were added to the model, the effects of temperature during the first year of the juvenile

Table 4.8: Analysis of Variance Table for the Linearized Ricker Stock-Recruitment Relationship Including Maximum Temperature (Equation 4.10).

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Total Corr. Sum of Squares	15				
Stock Density	1	117.910	117.910	93.729	< 0.001
(Stock Density)^2	1	35.102	35.102	27.904	< 0.001
Beach	3	8.414	2.805	2.229	0.088
Beach x Stock Density	3	12.076	4.025	3.200	0.026
Beach x (Stock Density)^2	3	10.269	3.423	2.721	0.047
Max. Temp. Yr 1	1	5.337	5.337	4.761	0.031
(Max. Temp. Yr. 1)^2	1	10.729	10.729	9.571	0.002
Max. Temp. Yr. 2	1	1.321	1.321	1.178	0.280
(Max. Temp. Yr. 2)^2	1	3.546	3.546	3.163	0.078
Residual	116	130.025	1.122		

Multiple R-Squared = 0.6128

stage accounted for more of the sums of squares than the effects during the second year. The following are the fitted model for each beach:

a) Mocrocks:

$$\ln\left(\frac{R}{A}\right) = -29.536 - (1.716 \cdot A) + \left(0.187 \cdot A^2\right) + (9.434 \cdot T_1) - \left(0.299 \cdot T^2{}_1\right) - (5.478 \cdot T_2) + \left(0.175 \cdot T^2{}_2\right)$$

b) Copalis:

$$\ln\left(\frac{R}{A}\right) = -29.576 - (2.182 \cdot A) + \left(0.301 \cdot A^2\right) + (9.434 \cdot T_1) - \left(0.299 \cdot T^2{}_1\right) - (5.478 \cdot T_2) + \left(0.175 \cdot T^2{}_2\right)$$

c) Twin Harbors:

$$\ln\left(\frac{R}{A}\right) = -28.471 - (7.530 \cdot A) + \left(3.672 \cdot A^2\right) + (9.434 \cdot T_1) - \left(0.299 \cdot T^2{}_1\right) - (5.478 \cdot T_2) + \left(0.175 \cdot T^2{}_2\right)$$

d) Long Beach:

$$\ln\left(\frac{R}{A}\right) = -28.723 - (4.855 \cdot A) + \left(1.208 \cdot A^2\right) + (9.434 \cdot T_1) - \left(0.299 \cdot T^2{}_1\right) - (5.478 \cdot T_2) + \left(0.175 \cdot T^2{}_2\right)$$

Interestingly, parameter values for the effect of temperature during the two years were not consistent. Even though both the maximum temperature, and the squared term showed significant contributions to the model fit, the coefficients within the first year are opposite of those within the second year. During the first year, the model fits a positive partial regression coefficient value to the maximum temperature and a negative partial regression coefficient value to the squared term. In the second year, the signs of the parameters are reversed, such that the model fits a negative partial regression coefficient to the maximum temperature, and a positive partial regression coefficient to the squared term. The overall effect of this parameterization is to narrow the range of temperatures with positive effects on recruitment, and implies that temperatures above and below some optimum results in decreased spawning success. Of course, care must be taken when attempting to interpret the individual coefficients in a multiple regression, as all of the coefficients are correlated with one another.

To make certain that the relationship with the temperature metric was not being solely defined by extreme values such as the maximum temperature in 1957 (17.18 C), the extremes were removed, and the model fit again. The conclusions concerning which effects should be in the model were identical. The parameter values changed somewhat, but the signs remained the same. Thus, the relationship does not appear to be governed simply by a few strongly influential outliers, and because of this, the entire data set was utilized.

Often, one stressor may make an organism more susceptible to other stresses. NIX was first detected in the early 1980's, and was thought to be a disease stressor. It would be conceivable that the onset of NIX could increase the susceptibility of the clams to temperature extremes. Therefore, I compared the results from the entire time series to the results from the entire time series up to the 1980's. Those variables that significantly affected the fit for the pre-1980's data set had similar effects for the entire data set. It does not appear that the onset of NIX has significantly influenced the response of the razor clam to temperature (Also see Section 4.5.4).

The indicator variable for the El Nino events was found to significantly improve the fit of the Ricker model (Equation 4.10 in Table 4.4). The effect was significant in both the year of the event (p=0.052), and the year following the event (p=0.028), although the signs of the coefficients are different. In the year of the event, the estimated coefficient has a positive sign, and in the year following the event, the estimated coefficient has a negative sign. Overall, although the indicator variable for El Nino did provide a significant addition to the Ricker model, the coefficient of partial determination (Neter, *et al.*, 1983) of the indicator variable (partial $r^2 = 0.055$) was much less than that of the quantitative temperature metrics (partial $r^2 = 0.139$). Therefore, the quantitative temperature metrics were used for model predictions instead of the indicator variable of El Nino.

The parameter values for the model that used the stock density, the square of the stock density and the temperature metrics were used to estimate the stock density that gave the maximum recruitment, and the stock density that gave the greatest positive difference between expected recruitment and current stock size (i.e., the stock size that would give the MSY for a stock that is stable). I used the same temperature for both years during the estimation procedure. I found that the stock densities for maximum recruitment and "MSY" varied greatly across the beaches (Table 4.9). Temperature did not affect the estimate of the stock density needed for the maximum recruitment, but the temperature did affect the estimate of the stock density that provided the "MSY". When compared to the Ricker model that included both stock density and the squared value of the stock density (Equation 4.7), the model with temperature effects (Equation 4.9) suggested that slightly higher stock densities should be maintained to achieve the maximum recruitment. Overall, however, the suggested density increases were slight. The temperature did affect the results for the "MSY" stock density. The optimal temperature was 15-16 C, with decreases in recruitment beyond this range. The effect of temperature beyond the optimum was to reduce recruitment and flatten the curve. In all cases, the model with temperature suggested that the stock density to achieve "MSY" should be slightly higher than the model with stock density and the squared value of stock density suggested.

The observed densities were compared to densities that the model (Equation 4.9) predicted would provide the maximum recruitment and the MSY. This comparison would

Table 4.9: Estimated Stock Densities (in clams per unit area) to achieve Maximum Recruitment and Maximum Sustainable Yield using the estimated parameters from Equation 4.6. The results are reported for the best environmental conditions, which occurred at 15-16 C according to the model fitting procedure.

Beach	Stock Density to attain the Maximum Recruitment Using Equation 4.6	Stock Density for MSY Using Equation 4.6
Mocrocks	0.68 clams/yd^2	0.46 clams/yd^2
	(i.e., 0.57 clams/m^2)	(i.e., 0.39 clams/m^2)
Copalis	0.54 clams/yd^2	0.36 clams/yd^2
	(i.e., 0.45 clams/m^2)	(i.e., 0.30 clams/m^2)
Twin Harbors	0.16 clams/yd^2	0.12 clams/yd^2
	(i.e., 0.13 clams/m^2)	(i.e., 0.10 clams/m^2)
Long Beach	0.24 clams/yd^2	0.20 clams/yd^2
	(i.e., 0.20 clams/m^2)	(i.e., 0.17 clams/m^2)

indicate whether the stocks were near the target densities that the model indicated were optimal. For the three northern beaches (i.e., Mocrocks, Copalis, and Twin Harbors), during the past 20 years the stock densities have been sufficient to achieve "MSY" about 50% of the time. The stock densities to achieve maximum recruitment are higher than the stock densities to achieve "MSY". Thus, the stock densities have been sufficiently high on average to achieve maximum recruitment only about 40% of the time. For Long Beach, the situation has been worse. During the past 20 years, only 25% of the time have the stock densities been high enough to achieve the "MSY"; the majority of the high stock densities have been in the past 5 years. The stock density to attain "MSY" and the stock density to attain maximum recruitment at Long Beach are very close (0.23 clams/yd^2 (i.e., 0.19 clams/m^2) versus 0.20 clams/yd^2 (i.e., 0.17 clams/m^2)). In the past 20 years, again only 25% of the time have the stock densities been high enough to achieve the maximum recruitment. These results indicate that the potential exists at each beach to improve the harvest.

The least squares estimates of the parameters were inserted into the model and the historical stock size was used with the model to try to predict the recruitment. This was done on a beach by beach basis, because the analysis had indicated that the parameters for the stock-recruitment relationship varied by beach. Regardless, the fit of the models to the data was very poor (Table 4.7, Figure 4.19) and had fitted r^2 values of between 0.35 (Mocrocks) and 0.71 (Twin Harbors). Although the models captured the average recruitment relationship fairly well at the three southern beaches (Copalis to Long Beach), the model could not capture any of the extremely large recruitments, even with the inclusion of the temperature variables. In fact, despite the fact that the addition of stock squared terms and temperature terms to the model were statistically significant, the general results of models with and without parameters for the stock squared and the temperature terms were very similar. The inclusion of the slope parameters for the stock squared term and the temperature terms in the models tended to smooth the recruitment

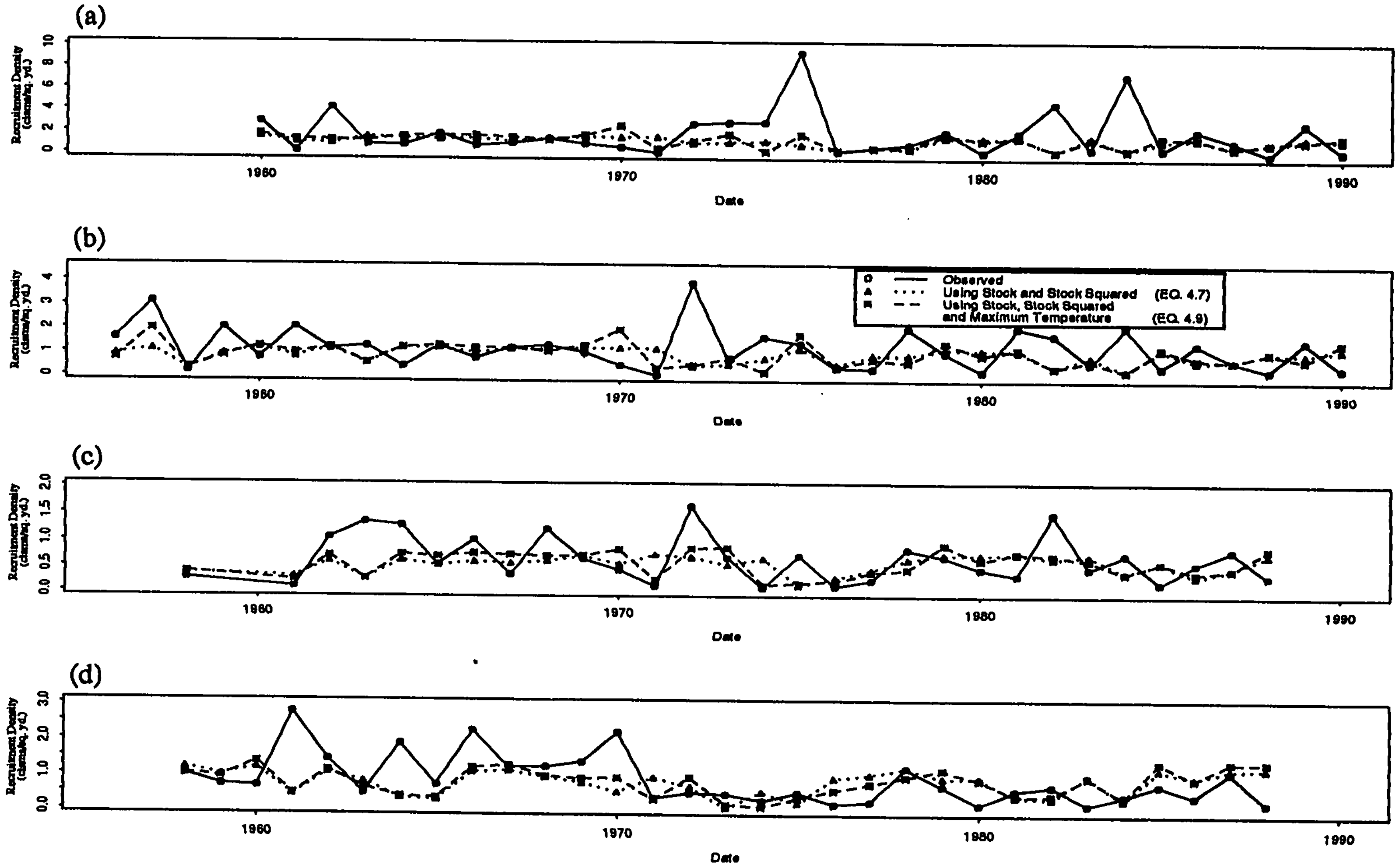


FIGURE 4.19 Prediction of subsequent recruitment using the Ricker model that includes the independent variables stock, stock-squared, the maximum temperature for both years, and the maximum temperature squared for both years (Eq. 4.9). The solid line indicates the observed pattern of recruitment through time at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach.

variability. All models tended to remain near the mean level of recruitment, and did not vary much from that level.

Most distressing is the lack of coincidence between large recruitment classes and this model. The model was formulated in such a way that the environmental variables were supposed to provide the missing data source that would explain the extremely strong year classes and the extremely poor year classes. However, as is evident from Figure 4.19, the inclusion of the temperature variables, although statistically significant ($p < 0.004$), does not provide the improvement where it was anticipated.

An encouraging note is that the model does anticipate very small year classes throughout the history of the fishery. For example, in 1983, the year when the disease NIX was first noted, and the year when there was much concern about the stock, the model indicates that given the current stock density and temperature regime, a low recruitment class was anticipated.

4.5.4 STOCK-RECRUITMENT RELATIONSHIP USING THE RICKER MODEL, INCLUDING NIX INTENSITY FACTORS

The inclusion of NIX into the stock-recruitment relationship did not significantly improve the fit of either the stock-recruitment model ($p = 0.87$) or the model that had both stock and stock squared as the independent variables ($p = 0.90$). Therefore, there appears to be no evidence that NIX has had a significant impact on the stock-recruitment relationship.

Another way of analyzing whether NIX had influenced the relationship was to measure whether there was a NIX by temperature interaction effect. I analyzed the interaction of NIX and temperature in the linearized Ricker Model (Equation 4.12). When the NIX values prior to 1983 were set to zero, no significant interaction was observed between either the mean annual NIX Intensity ($p>0.26$) or the maximum annual NIX

Intensity ($p>0.24$) and temperature. The results were identical ($p>0.29$) when the NIX Intensity values prior to 1983 were ignored.

4.5.5 TOTAL DENSITY RELATIONSHIP USING THE SCHAEFER MODEL

Three versions of the Schaefer model were investigated. The first version used only the total densities of the razor clam and fit the change in densities between two adjacent years as a function of the current density (Equation 4.13). The second and third versions of the Schaefer model included the temperature metric as an independent variable, and will be discussed in section 4.5.6. Various parameterizations of the Schaefer model were fit. One parameterization had a common "r" and a common "K" term for all beaches. Other parameterizations had either individual estimates of "r" for each beach, individual estimates of "K" for each beach or both individual estimates of "r" and "K" for each beach. The nonlinear least-squares fit of the Schaefer model indicated that all beaches shared a common "r" and a common "K" parameter. The Schaefer model in its various forms provided a statistically significant model, but had a very low explanatory power (Multiple r^2 of 0.26 - 0.30 depending on the parameterization) and did not behave well at lower stock sizes (Figure 4.20). Residuals from the model fit indicated a linear relationship was being fit with a curvilinear model. For all beaches, the model underestimated ΔD_{t+1} at the extremely low densities, and overestimated ΔD_{t+1} at the intermediate densities and extremely high densities. In fact, the data suggested that ΔD_{t+1} was linearly related to D_t, not curvilinearly related, as is assumed in the Schaefer equation. This linear relationship between ΔD_{t+1} and D_t was explored further using the Differenced Regression Model (Section 4.5.7). Based upon overall fit of the model, I would not recommend this model.

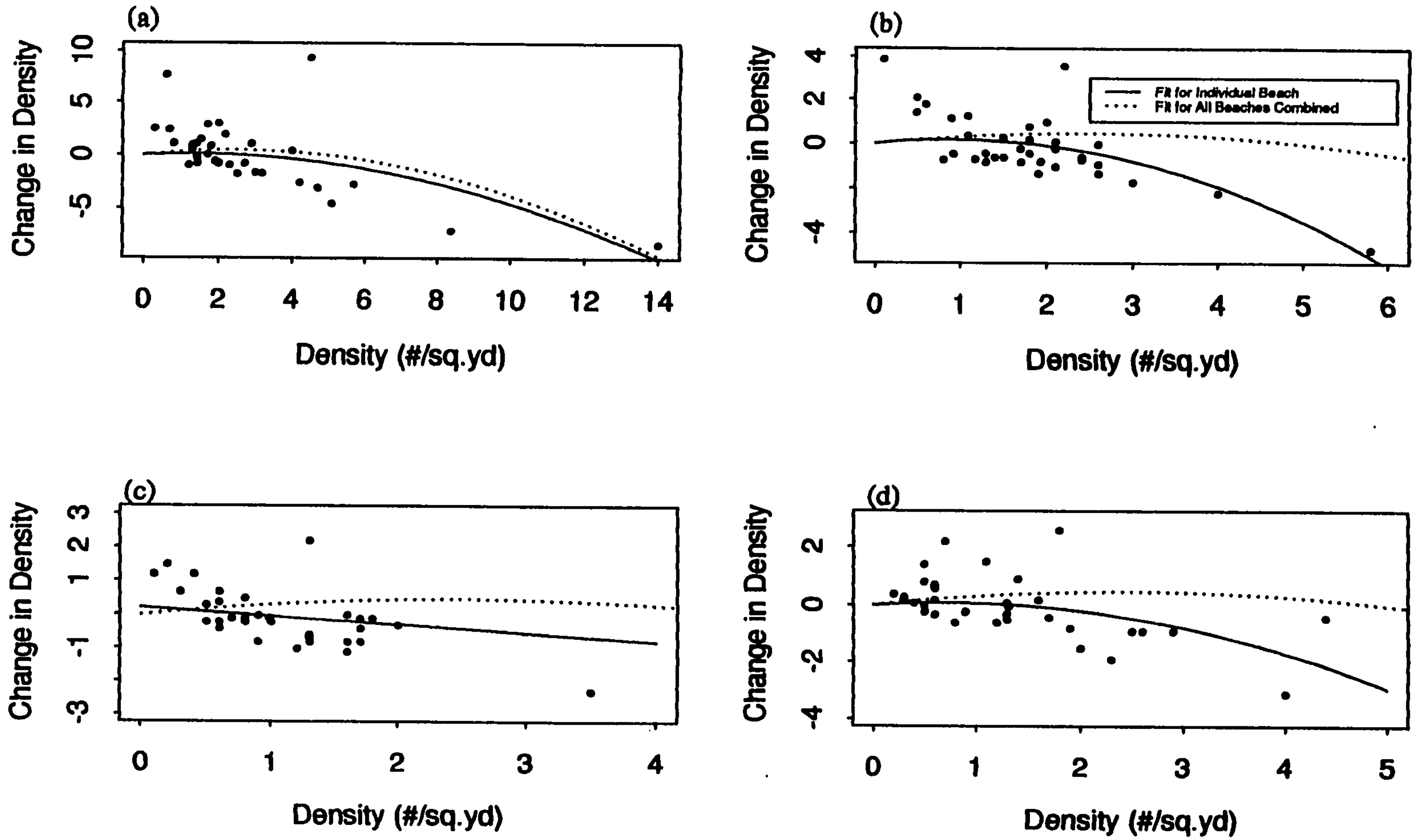


FIGURE 4.20 The best fit lines from the nonlinear fit of the Schaefer model (Eq. 4.13) at (a) Mocrocks, (b) Copalis, (c) Twin Harbors and (d) Long Beach. The solid line reflects the best fit line when data from each beach are analyzed individually (i.e., Unique "r" and unique "K"). The dotted line reflects the best-fit line when data from all beaches are analyzed concurrently (i.e., Common "r" and common "K").

4.5.6 TOTAL DENSITY RELATIONSHIP USING THE SCHAEFER MODEL, INCLUDING DENSITY INDEPENDENT AND DENSITY DEPENDENT ENVIRONMENTAL FACTORS

The temperature metrics (i.e., maximum yearly temperature$_{t-1}$ and maximum yearly temperature$_{t-2}$) were added to the Schaefer model under two hypotheses of how temperature could affect the clams. The first hypothesis was that temperature had a density-independent effect on the clam population (Equations 4.14 and 4.16). Under this hypothesis, the temperature alters the growth rate of the population. The inclusion of temperature$_{t-1}$ to the base model did not significantly improved the fit, whereas the inclusion of temperature$_{t-2}$ to the base model did significantly improved the fit. However, the overall fit of the model remained poor (Multiple r^2=0.33).

The second hypothesis was that temperature had a density dependent effect on the clam population (Equations 4.15 and 4.17). Under this hypothesis, the temperature alters the carrying capacity of the population. I experienced problems in the nonlinear convergence under this model, and was unable to assess the fit.

The fit of the Schaefer model in general and especially at low stock sizes, even with the addition of the density-independent temperature metric, was poor (Multiple $r^2 \leq 0.33$). Therefore, no further investigations of the Schaefer model and its derivatives were performed.

4.5.7 TOTAL DENSITY RELATIONSHIP USING THE DIFFERENCED REGRESSION MODEL

Evidence in the data set suggested high recruitment during times of low parental stock size, but strongly reduced recruitment at times of high stock density. The Differenced Regression model (Equation 4.18) was formulated to fit this observed pattern. The four beaches (i.e., Mocrocks, Copalis, Twin Harbors and Long Beach) were analyzed both separately and combined together in a multiple regression analysis to discern the stock-recruitment relationship. The combined analysis would provide evidence of whether there are four separate stock-recruitment relationships, or whether there is a coastwide relationship. The model (Equation 4.18) fit the change in density two years into the future as a function of the independent variables. The two-year time step is consistent with the idea that it takes two years to become an adult. The model that was found to be highly significant ($p < 0.001$) for all four beaches (Table 4.10), and had r-square value of 0.42 (Table 4.11, Figure 4.21).

The fit of the Differenced Regression model (Equation 4.18) showed that the total density (i.e., the sum of the juvenile and adult densities) was a significant factor in predicting subsequent densities, and that each beach had its own baseline recruitment when the value of the spawning stock fell to zero. However, in the Differenced Regression model, unlike the Ricker model, there was no significant beach by density interaction. In practice this means that the effect of change in density is constant for all beaches, only the total maximum density differs for each beach.

The catch was included as a predictor variable because it was thought that future densities should be affected by the total catch that is taken. However, for the two northern beaches, this was not evident in the analysis. For Mocrocks and Copalis, the inclusion of the catch term, after the stock density had been added to the model, did not significantly improve the fit of the model; the parameter estimate for the catch term was not significantly different from "0" ($p>0.46$). For Twin Harbors and Long Beach, although the inclusion of the catch term significant improved the model fit ($p=0.03$ and $p=0.02$ respectively), the parameter estimate at both beaches was positive, suggesting that increases in catch during the current year would benefit the population in the future. At the two northern beaches, where the catch term was not significant, the amount of explanatory power associated with the catch term, after having already included the stock density, was slight (partial r^2 for catch < 0.02). At the two southern beaches, where the catch term was significant, the amount of explanatory power associated with the catch term, after having

Table 4.10: Analysis of Variance Table for the Differenced Regression Model for Each Beach Individually (Equation 4.18). The dependent variable for this analysis is the change density two years in the future.

Mocrocks Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Stock Density	1	140.100	140.100	18.857	<0.001
Catch	1	1.596	1.596	0.215	0.647
Residual	28	208.034	7.430		

Copalis Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Stock Density	1	36.713	36.713	29.869	<0.001
Catch	1	0.658	0.658	0.536	0.470
Residual	32	39.333	1.229		

Table 4.10 (cont.): Analysis of Variance Table for the Differenced Regression Model for Each Beach Individually (Equation 4.18). The dependent variable for this analysis is the change density two years in the future.

Twin Harbors Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Stock Density	1	13.647	13.647	33.668	<0.001
Catch	1	2.174	2.174	5.364	0.028
Residual	30	12.161	0.405		

Long Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Stock Density	1	27.038	27.038	30.981	<0.001
Catch	1	5.730	5.730	6.566	0.015
Residual	32	27.927	0.873		

Table 4.11: Analysis of Variance Table for the Differenced Regression Model for All Beaches Fit Simultaneously (Equation 4.18). The dependent variable for this analysis is the change density two years in the future.

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Total Corr. Sum Squares	5				
Stock Density	1	176.976	176.976	75.819	<0.001
Beach	3	39.292	13.097	5.611	0.001
Catch	1	0.119	0.119	0.051	0.822
Residual	128	298.777	2.334		

Multiple R-Square = 0.42

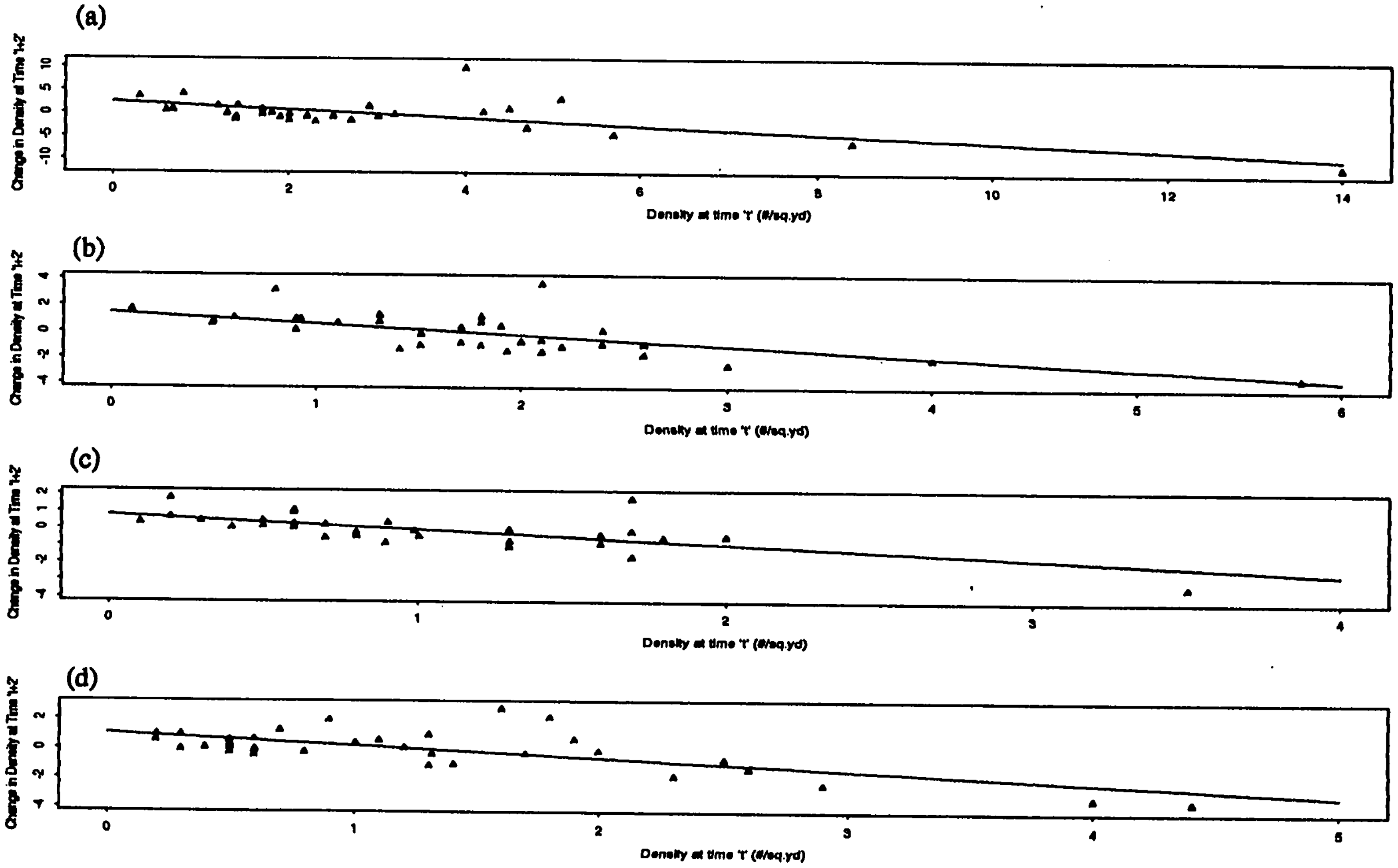


FIGURE 4.21 The best fit line for the Differenced Regression model at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. The dependent variable is the change in density (in clams/sq.yd.) in the next year, and the independent variable is the current density (Eq. 4.18). This fit is based on the multiple regression results (Table 4.9).

already included the stock density, was higher (partial r^2 for catch < 0.17). However, at all beaches the total density provided the greatest reduction in the sums of squares. The following are the fitted models for each beach when the model was fit to the data from each beach individually:

a) Mocrocks: $\Delta D_{t+2} = 2.52 - 0.78D_t - 0.49C_t$

b) Copalis: $\Delta D_{t+2} = 1.49 - 1.07D_t + 0.45C_t$

c) Twin Harbors: $\Delta D_{t+2} = 0.87 - 1.37D_t + 0.84C_t$

d) Long Beach: $\Delta D_{t+2} = 0.68 - 1.39D_t + 2.38C_t$

whereas when the data from all of the beaches are combined, the fitted models are:

a) Mocrocks: $\Delta D_{t+2} = 2.40 - 0.838 \cdot D_t$

b) Copalis: $\Delta D_{t+2} = 1.43 - 0.838 \cdot D_t$

c) Twin Harbors: $\Delta D_{t+2} = 0.79 - 0.838 \cdot D_t$

a) Long Beach: $\Delta D_{t+2} = 1.05 - 0.838 \cdot D_t$

The Differenced Regression model formulation provided estimated values of "r" and "K" (See Section 4.3.6). The estimates of "r" and "K" were within the range expected from historical records (Table 4.12). The estimated values for "K" are for average conditions at each beach. Therefore, the estimated values for "K" were lower than the historical maxima. The pattern in the estimates of "K" reflects what is observed on the beaches; the most densely populated beach is Mocrocks, followed by Copalis, with Twin

Table 4.12: Estimates of "r" and "K", and estimated standard errors, under the Differenced Regression Model (Equation 4.18). Units are razor clams per square yard.

Beach	r	K
Mocrocks	0.847 (0.09)	2.807 (0.434)
Copalis	0.847 (0.09)	1.636 (0.423)
Twin Harbors	0.847 (0.09)	0.886 (0.389)
Long Beach	0.847 (0.09)	1.205 (0.371)

Harbors and Long Beach exhibiting much lower densities. Estimates of the variance were computed using the delta method approximation (Seber, 1982).

The differenced regression model uses total density instead of recruit densities and stock densities. Thus, it is not possible to obtain densities that will give maximum recruitment or the density of recruits at MSY. Therefore, other measures of stock health were investigated. By definition, the stock density that gives the "MSY" is calculated by finding the point on the stock density axis where the greatest difference between the "x=y line" (i.e., the stock density = recruit density line) and the recruitment curve exists. The analogue for "MSY" under the Differenced Regression model should be that population that gives the largest change in expected density. For this model, the largest change in expected density always occurs at an estimated population density of zero. Beyond zero, the change in density is a decreasing function of current population density. Similarly, the stock density that gives the maximum recruitment is calculated by finding the point on the stock density axis where the greatest difference between the "y=0 line" and the recruitment curve exists. The analogue for maximum recruitment should be that population that gives the largest expected density in the following time period. For the Differenced Regression model, that value always occurs at the equilibrium situation. The equilibrium situation occurs at the carrying capacity, or "K" (Table 4.12). For these calculations, the catch was assumed to be zero. If the catch was included in the calculations as the individual regression analyses indicated (i.e., with a positive parameter before the catch term), inclusion of the catch caused an increase in the size of the equilibrium population.

After the least squares estimates for the parameters had been obtained, the historical population size was used with the model to try to predict the future population size. This was done on a beach by beach basis, because the analyses indicated that the parameters for the relationship varied by beach (Figure 4.22). This model shows marked improvement (based on the fitted r-square; Table 4.7) over the Ricker models. The greatest

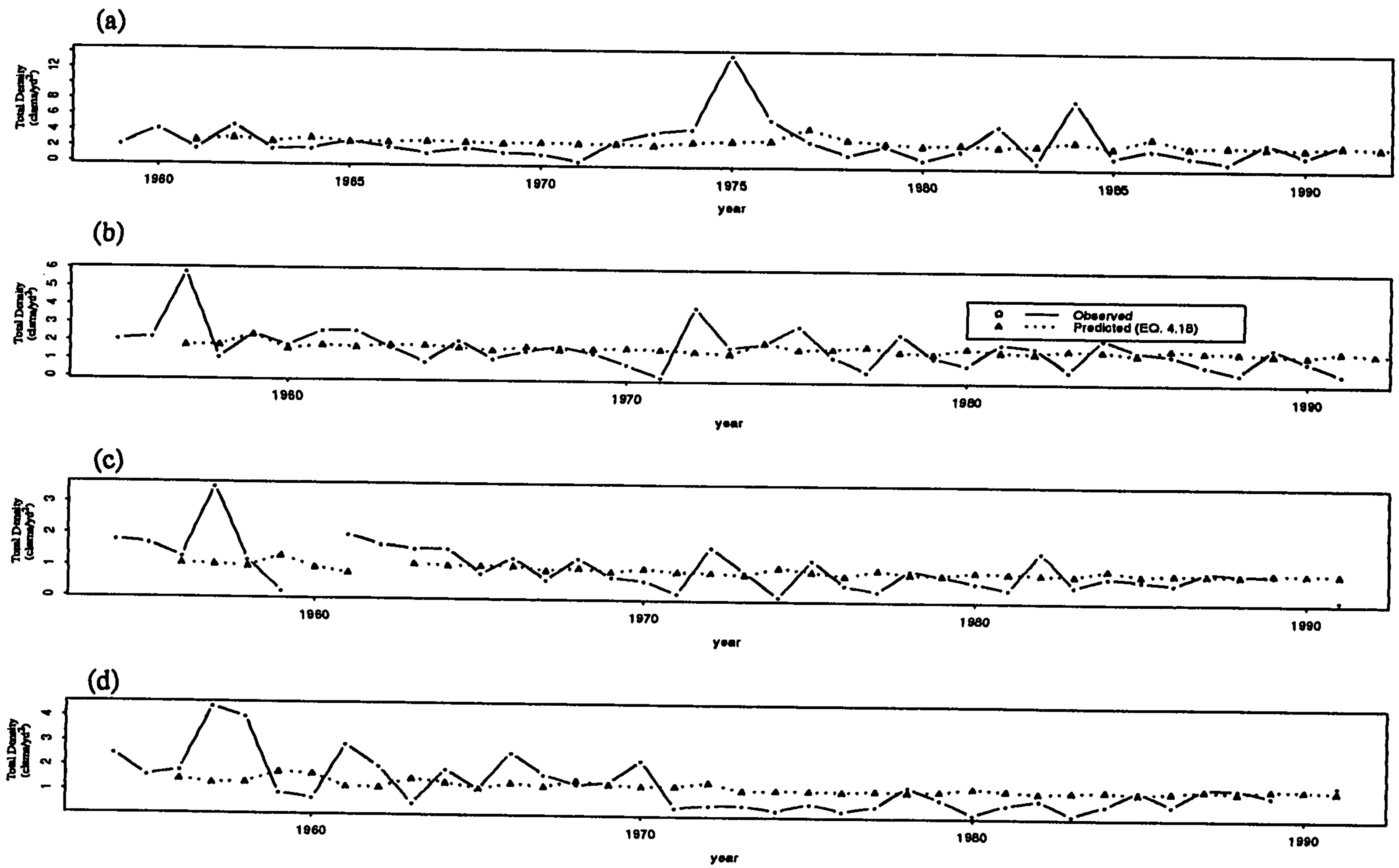


FIGURE 4.22 Prediction of subsequent population density using the Differenced regression model that includes the independent variable density at time "t" (Eq. 4.18). The solid line indicates the observed pattern of abundance through time at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach.

improvement occurred at Copalis, where the difference in the r^2 for the Ricker model versus the Differenced Regression model was 0.360 versus 0.818 respectively. The least improvement occurred at Twin Harbors, where the difference in the r^2 for the Ricker model versus the Differenced Regression model was 0.648 versus 0.717 respectively. Even the addition of the temperature metric to the Ricker framework did not fit the data as well as the Differenced Regression model, despite the fact that the Ricker model with the temperature metric had four more parameters. Despite the improvement in the r-square, the fit of the models to the data was not very good. The models captured only the mean population density well, and little of the variability. The model could not capture the general relationship through time. In several instances, the observed data show a strong increase in population followed by a gradual decrease in population size through time. This decay was missing in the predicted data sets. This implies that the dynamic mechanism in the Differenced Regression model is not formulated correctly.

4.5.8 TOTAL DENSITY RELATIONSHIP USING THE DIFFERENCED REGRESSION MODEL, INCLUDING ENVIRONMENTAL FACTORS

The inclusion of environmental factors to the Differenced Regression model (Equations 4.19 - 4.22) indicated that a variety of functional forms of the maximal mean-yearly temperature (MMT) during the previous two years significantly improved the fit of the model. The form of the relationship between MMT and subsequent density was beach-specific. For the model that included density-independent environmental effects, the MMT and the square of the MMT during the first year had a significant effect. The inclusion of the temperature data statistically improved the fit of the model ($p < 0.01$). The inclusion of the temperature data increased the fit of the model quite substantially (partial r-squared = 0.28). The significant effect of the temperature in the first year was due, in large part, to the 1973 data point. However, even with the removal of this data point, the conclusions were identical, only the level of significance was altered. All beaches had unique intercepts ($p<0.001$), but shared a common slope term ($p>0.43$). The largest contribution to explaining the variability was the current density (Table 4.11). The following are the fitted models for each beach:

a) Mocrocks: $$\Delta D_{t+2} = 302.266 - 1.027 \cdot D_t - 38.061 \cdot T_t + 1.206 \cdot T_t^2 .$$

b) Copalis: $$\Delta D_{t+2} = 138.902 - 1.027 \cdot D_t - 18.003 \cdot T_t + 0.589 \cdot T_t^2 .$$

c) Twin Harbors: $$\Delta D_{t+2} = 45.837 - 1.027 \cdot D_t - 6.001 \cdot T_t + 0.200 \cdot T_t^2 .$$

d) Long Beach: $$\Delta D_{t+2} = -13.863 - 1.027 \cdot D_t + 1.632 \cdot T_t - 0.042 \cdot T_t^2 .$$

The Differenced Regression model that included temperature as a density-independent effect (DRMDI) did not respond to temperature as expected. The model was formulated to have an optimal temperature. This optimal temperature would correspond to the maximal response (i.e., change in density). To either side of the optimal temperature, a movement away from the optimal temperature would result in a decrease in the response variable (i.e., the change in density). However, using the least-squares parameter estimates, that response is not obtained. Instead, using the least-squares parameterization, there exists some minimal change in density at an intermediate temperature, and in either direction from this temperature, the change in density increases. This response implies that as the hotter or colder the temperature, the stronger the response of the model, and that the optima exist at plus and minus infinity. Although it would have been more satisfactory had the parameter estimates held to the theoretically preconceived construct of how temperature should affect the density, such problems will exist when multiple, correlated variables are used as predictor variables in a multiple regression analysis. This is one problem with using observational data, not experimental data, to create a multiple regression model. This result argues that extrapolation beyond the bounds of the problem could be inaccurate and misleading, and should be avoided.

Table 4.13: Analysis of Variance Table for the Differenced Regression model Including Density-Independent Effects of the Maximal Mean Yearly Temperature (Equation 4.19). The dependent variable for this analysis is the change in density two years in the future.

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Total Corr. Sum Squares					
Stock Density	1	176.976	176.976	82.211	<0.001
Beach	3	39.292	13.097	6.084	<0.001
Catch	1	0.119	0.119	0.055	0.815
Max. Temp. Yr. 1	1	2.027	2.027	0.942	0.334
(Max. Temp. Yr. 1)^2	1	25.045	25.045	11.634	<0.001
Max. Temp. Yr. 2	1	3.949	3.949	1.834	0.178
(Max. Temp. Yr. 2)^2	1	0.822	0.822	0.382	0.538
Beach x Max. Temp. Yr. 1	3	33.151	11.050	6.023	<0.001
Beach x (Max. Temp. Yr. 1)^2	3	24.121	8.040	4.382	0.005
Beach x Max. Temp. Yr. 2	3	1.683	0.561	0.306	0.821
Beach x (Max. Temp. Yr. 2)^2	3	2.481	0.827	0.451	0.717
Residual	112	205.497	1.835		

Multiple R-Square - 0.602

Alternatively, although the maximum temperature should behave exactly the same as the mean temperature in a physiological response model (i.e., there should be a domed response over the range of maxima, with an optimum maximum somewhere between two extremes), it is quite possible that the current temperature data only give us information about one side of the domed response. Within the range of temperatures observed, there may exist an optimum temperature below 13 C, while temperatures of 15 - 16 C and above, may cause decreased reproductive potential. The problem with fitting the current temperature metric to the domed-response theory is two-fold. First, there is a very narrow range of maximum temperatures throughout the time series (13-17 C), with the majority of temperatures between 14.5 and 16.5 C; only one observation is below 13.5 C and one observation is above 17 C. Second, the temperature metric being examined is the maximum temperature. The physiological response to the maximum temperature may not behave quite the same as the physiological response to mean temperature.

Although the removal of the 1973 density at Mocrocks did not affect which predictors were included in the DRMDI model, the removal of the 1973 point did alter the shape of the response that temperature had on the subsequent density. When the 1973 point was included, the response of the model to temperature was an inverted dome, with optima at plus and minus infinity. When the 1973 point was deleted, the response of the model to temperature was a dome, with an optimum near 14 C. To either side of 14 C the equilibrium density declined. Regardless of whether the 1973 data point is retained, there will still be problems with extrapolation. However, at least the result based on the data set without the 1973 data point is more consistent with theory, and the effect from the previous fit has been explained. Overall, regardless of whether or not the 1973 data point is retained, the predicted densities are very similar for the range of observed temperatures. Therefore, because the results are qualitatively similar throughout the observed range of temperatures, rather than deleting this point arbitrarily, a very similar result will be obtained by refusing to extrapolate beyond the bounds of the data.

The Differenced Regression model that included temperature as a density-dependent effect (DRMDD) had different results than the model that included the temperature as a density-independent effect. The inclusion of the MMT variable from the first year significantly improved the fit of this model ($p \leq 0.002$) (Table 4.14). The inclusion of the MMT for the second year of the juvenile stage also significantly improved the fit of the model ($p \leq 0.06$). As with the Differenced Regression model with density-independent temperature effects, the Differenced Regression model with density-dependent temperature effects also found that all beaches had unique intercepts ($p<0.001$), but shared a common slope term ($p>0.89$). The addition of the catch term into either model did not improve the fit ($p>0.56$) once the effect of the current density had been added. Although in the full model (i.e., the model that included all potential predictor variables), the effect of the MMT was beach specific, when the reduced model (i.e., that model that was fit using only those predictor variables that appeared to be significant ($p<0.10$) in the full model) was fit, the effect of the "BeachxMMT" interaction term was no longer significant ($p>0.83$). From step-wise additions and removals, it became apparent that the "beach by temperature" interaction effect in the density-dependent model was significant only when it entered the model in conjunction with the "beach by density" interaction effect. When both terms were added simultaneously, and their total contribution to the sums of squares was calculated, the combined effect was not significant ($p > 0.17$). Based on this analysis, both the "beach by density" interaction and the "beach by temperature" interaction terms were dropped from the final model.

The inclusion of the temperature data in a density-dependent fashion increased the fit of the model a little (partial r-squared = 0.11), but not as much as the inclusion of temperature in a density-independent fashion. An examination of the influence statistics indicated that the significant effect of the temperature might be due, in large part, to the 1973 data point (i.e., a year with low temperature and high recruitment at Mocrocks). With the removal of this data point, the density-dependent temperature effects were no longer

Table 4.14: Analysis of Variance Table for the Differenced Regression model Including Density-Dependent Effects of the Maximal Mean Yearly Temperature (Equation 4.19). The dependent variable for this analysis is the change in density in the subsequent year.

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Total Corr. Sum Squares					
Stock Density	1	176.976	176.976	81.497	<0.001
Beach	3	39.292	13.097	6.0313	<0.001
BeachxStock	3	1.282	0.427	0.197	0.898
Catch	1	0.734	0.734	0.338	0.562
(MMT Yr. 1)* (Stock Dens.)	1	2.689	2.689	1.238	0.268
(MMT Yr. 1)^2 *(Stock Dens.)	1	21.259	21.259	9.788	0.002
(MMT Yr. 2)* (Stock Dens.)	1	8.782	8.782	4.043	0.047
(MMT Yr. 2)^2 *(Stock Dens.)	1	1.391	1.391	0.640	0.425
Beachx(MMT Yr. 1)* (Stock Dens.)	3	2.235	0.745	0.357	0.784
Beachx(MMT Yr. 1)^2 *(Stock Dens.)	3	15.565	5.188	2.483	0.065
Beachx(MMT Yr. 2)* (Stock Dens.)	3	12.448	4.149	1.986	0.120
Beachx(MMT Yr. 2)^2 *(Stock Dens.)	3	4.764	1.588	0.760	0.519
Residual	109	227.746	2.089		

Multiple R-Square - 0.524

significant ($p>0.26$). Rather than basing all conclusions on the influence of a single point, it appears instead that there is little evidence for density-dependent temperature effects on the razor clam under this model. Thus, the Difference Regression model with density-dependent temperature effects collapses to the Difference Regression model without temperature effects.

The overall fit of the model that included temperature as a density-independent effect is substantially better ($r^2=0.58$) than the fit of the model that did not include temperature ($r^2=0.42$). Therefore, on the basis of the multiple r-square, there is evidence that temperature affects future densities, and that the effect of the temperature acts in an independent nature with the stock density.

Recall that the temperature variable was included under the hypothesis that high summer temperatures reduce survival. An alternative hypothesis suggested that the presence of an El Nino event, which often causes high sea surface temperatures, might drive stock dynamics. The inclusion of the indicator variable for El Nino was not significant ($p>0.17$).

In all versions of the Differenced Regression models that modelled all four beaches concurrently, the effect of taking a catch from the current population had no measurable effect on the change in density two years into the future. This implies that future densities are not influenced by the current level of harvest.

As with the Differenced Regression Model (Equation 4.18), these models (Equation 4.19-4.22) also have the greatest recruitment when the current stock size is zero. This is an artifact of the way in which the equation was formulated. As with the discussion concerning the Differenced Regression Model, it may be of more interest to discuss other features of the model, such as the effect of temperature and the equilibrium population. Given that the analysis indicated a unique relationship for each beaches, the results are beach-dependent.

The Differenced Regression Model that included temperature as a density-independent (DRMDI) effect (Equation 4.20) typically has a higher predicted equilibrium density than the equilibrium density (i.e., "K") estimated using the Differenced Regression Model (Equation 4.18) without temperature effects. As discussed above, the temperature entered the Differenced Regression Model that included temperature as a density-independent effect in a fashion that was not wholly consistent with the preconceived theory. Only at the intermediate temperatures observed (15-16 C) does the equilibrium population of this model (i.e., DRMDI) approach the equilibrium of the Differenced Regression model. To either side of this temperature, the equilibrium population increases slightly.

After the Differenced Regression model that included temperature as a density-independent (DRMDI) effect had been parameterized, the historical population size was used with the model to try to predict the future population size. This was done on a beach by beach basis, because the analysis had indicated that the parameters for the relationships varied by beach (Figures 4.23). The fit of the models to the data was fair to good, depending upon the beach (Table 4.7).

At both Mocrocks and Copalis, the model that included temperature as a density-independent effect (DRMDI - Equation 4.19) generally did not predict the same pattern of recruitment that was observed. The model (DRMDI) did fit the mean recruitment, and appeared to capture the high densities that were apparently due to temperature effects. The peaks and troughs of the 1970's were captured much better than the peaks and troughs of the 1980's. However, the model was not as dynamic as the observations, and indicated a tendency to stay near the mean. At the two southern beaches, the addition of the temperature metrics to the relationship did not have much effect on the predicted line. At Twin Harbors, the model did not show the variability that the observations showed. Also, regardless of whether or not temperature was added, the DRMDI model consistently stayed near the mean value. At Long Beach, the model again appeared to capture the mean

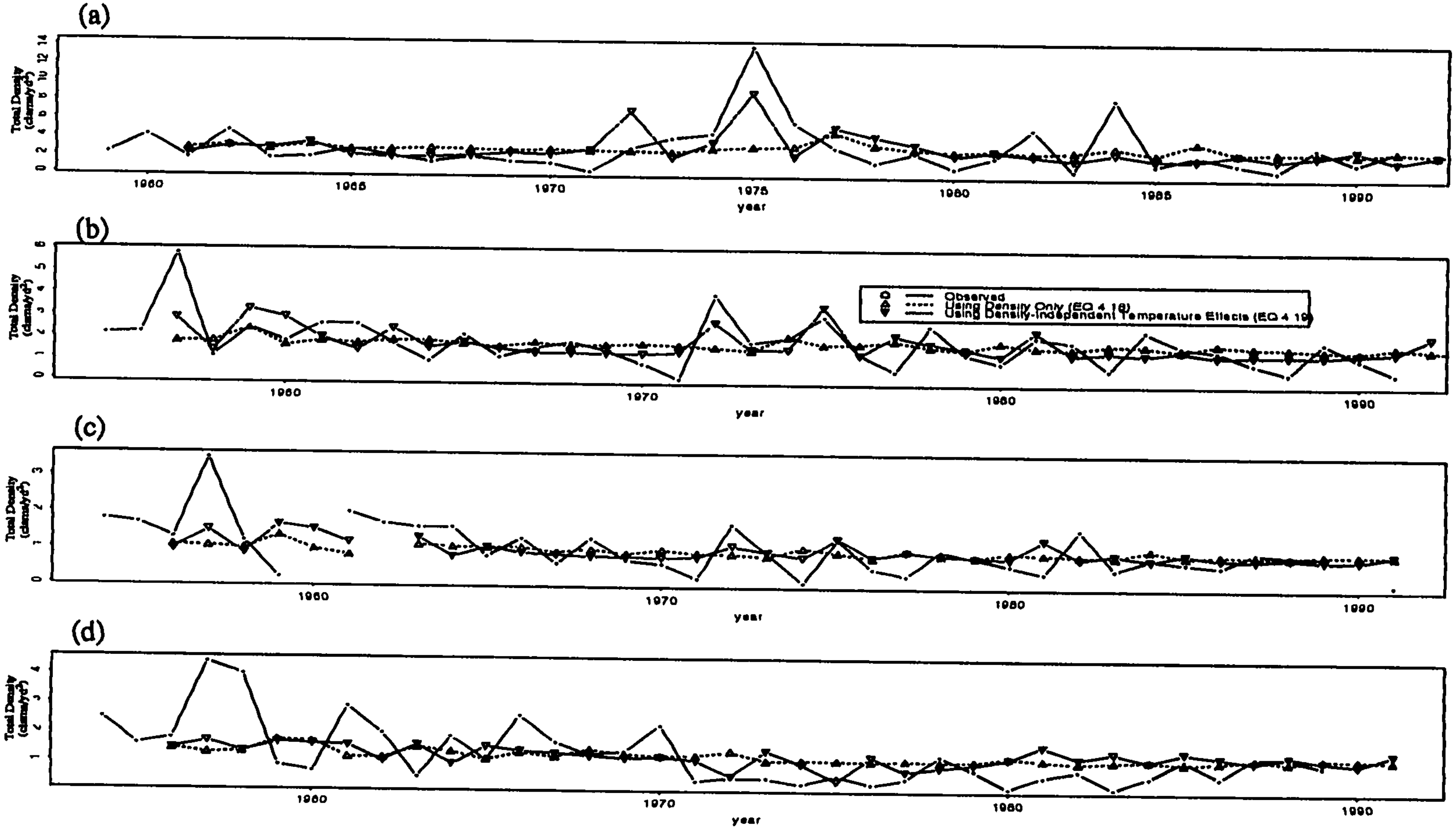


FIGURE 4.23 Prediction of subsequent population density using the Differenced Regression model with density-independent temperature effects at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach (Eq. 4.20). The independent variables are the density and temperature measures at time "t". Two predicted fits are shown. In the first, temperature is not included. In the second, the temperature is included in the model. The solid line indicates the observed pattern of recruitment through time.

clam density through the 1950's and 1960's fairly well, but tended to overestimate the densities observed during the 1970's, with the exception of a couple years in which the model and the observed agree. In addition, the model showed much more variability than the observations from the 1970's onward. By the mid-1980's and 1990's, the model for Long Beach again came into agreement with the observations. Overall, the DRMDI model appeared to capture the observed pattern of a recruitment spike followed by a gradual decrease in density over time better than previous models. However, in general it suffers from not being dynamic enough in years where there are no strong environmental signals.

4.5.9 TOTAL DENSITY RELATIONSHIP USING THE STAGE-STRUCTURED RICKER STOCK-RECRUITMENT MODEL

Under this model, because of the nonlinearity, all four beaches were modelled individually. The parameters of the model were estimated using nonlinear least squares (Table 4.15). The survival parameter indicated that there has been little to no survival (i.e., Fail to reject null hypothesis of $S=0$ at alpha $= 0.05$) of adults from time "t" to time "t+1"; the adults are either all caught or die of natural mortality. Conversely, the beta2 parameter indicates that the juveniles have high survival from their first to second years. High standard errors on the alpha parameter at all beaches indicates that the effect of the stock density at time "t" on subsequent densities is much less influential than the stock density at time "t-1". As with other models, this implies that a two-year lag is the stronger lag. However, the inclusion if the one-year lag was incorporated to complete the conceptual model, and to create the decay that is apparent within the data set. The model was highly significant at all beaches, and had fairly high r-squared values.

For the Stage-Structured Ricker Stock-Recruitment (SSRSR) model (Equation 4.23), two year classes affect the final result, not one year class as in all previous models. Thus, it became necessary to optimize the model over two year classes, and to understand how each of those year classes affected the density in the future. Rather than using an analytical solution, a simulation was run that estimated the density in the next year given

Table 4.15: Parameter estimates and their standard errors (in parentheses) for the Stage-Structured Ricker Stock-Recruitment Model (Equation 4.23). In the upper table (a) the parameter estimates are associated with an "S" that is allowed to take on any value; in the lower table (b) the parameter estimates are associated with an "S" that is constrained to "0" after failing to reject the hypothesis H_0: S=0.

(a)

Beach	alpha	Beta1	Beta2	Unconstrained S	Multiple R-square
Mocrocks	-1.27	-0.99	10.44	0.70	0.584
	(3.64)	(0.40)	(5.33)	(0.45)	
Copalis	2.53	-1.26	4.98	-0.34	0.704
	(2.10)	(0.43)	(2.52)	(0.36)	
Twin Harbors	1.67	-3.61	9.81	-0.04	0.815
	(2.25)	(0.76)	(2.88)	(0.28)	
Long Beach	4.67	-2.42	6.88	-0.33	0.694
	(2.64)	(0.88)	(2.84)	(0.27)	

(b)

Beach	alpha	Beta1	Beta2	Constrained S	Multiple R-square
Mocrocks	1.60	-0.53	5.11	0.00	0.564
	(2.02)	(0.19)	(2.37)		
Copalis	2.47	-1.29	5.44	0.00	0.704
	(2.29)	(0.44)	(2.46)		
Twin Harbors	1.63	-3.55	9.86	0.00	0.828
	(2.25)	(0.82)	(2.84)		
Long Beach	6.42	-2.77	6.91	0.00	0.678
	(4.42)	(1.26)	(2.88)		

the adult densities from the previous two years. The results are illustrated as contour plots (Figure 4.24). The results indicate that although the optimal stock density is different for each beach, the effect of the two years is very similar across all beaches. For all beaches, maintaining the stock at the optimum adult density can cause the total density of clams on the beach in the future to be two to three times larger than the current adult stock density. For example, at Mocrocks, any stock density at time "t-1" that is between approximately 1.5 and 3 clams/yd^2 (i.e., 1.25-2.51 clams/m^2), when combined with a stock density at time "t" of between approximately 0.5 and 6 clams/yd^2 (i.e., 0.42-5.02 clams/m^2), will produce a density in time "t+1" of around 4 clams/yd^2 (i.e., 3.35 clams/m^2).

For all beaches, the density at time "t-1" is more crucial than the density at time "t". This is illustrated by the longer tail to the left than to the top in the contour plot. The implication of this result is that under this model, clams need to be managed on a two-year time span, rather than simply using the in-season management style that is currently pursued. A second implication is that this year's management will have repercussions two years from now, not next year. This implication is consistent with the idea of a two year time span between birth and entering the fishery.

Another common feature of the SSRSR that occurs at all four beaches, is that the stock-recruitment relationship has a much steeper ascending limb than a descending limb (i.e., the slope of the stock-recruitment model from the point (0,0) to the maximum recruitment is much steeper than the slope from the maximum recruitment to the extremes of the observed stock densities.). This feature implies that it would be better to err on the side of conservative policies, for having too many clams has a lesser impact on the subsequent recruitment than having too few clams. However, based on other models (e.g., Differenced Regression Model (Section 4.5.7) and the Mean Recruitment Model (Section 4.5.12)), the steeper ascending limb is undoubtedly an artifact that is created by the Ricker model formulation, which forces the model through the point (0 $stock_t$,0 $recruit_{t+1}$). At all beaches there is a range of densities that, if the adult stock were maintained at those

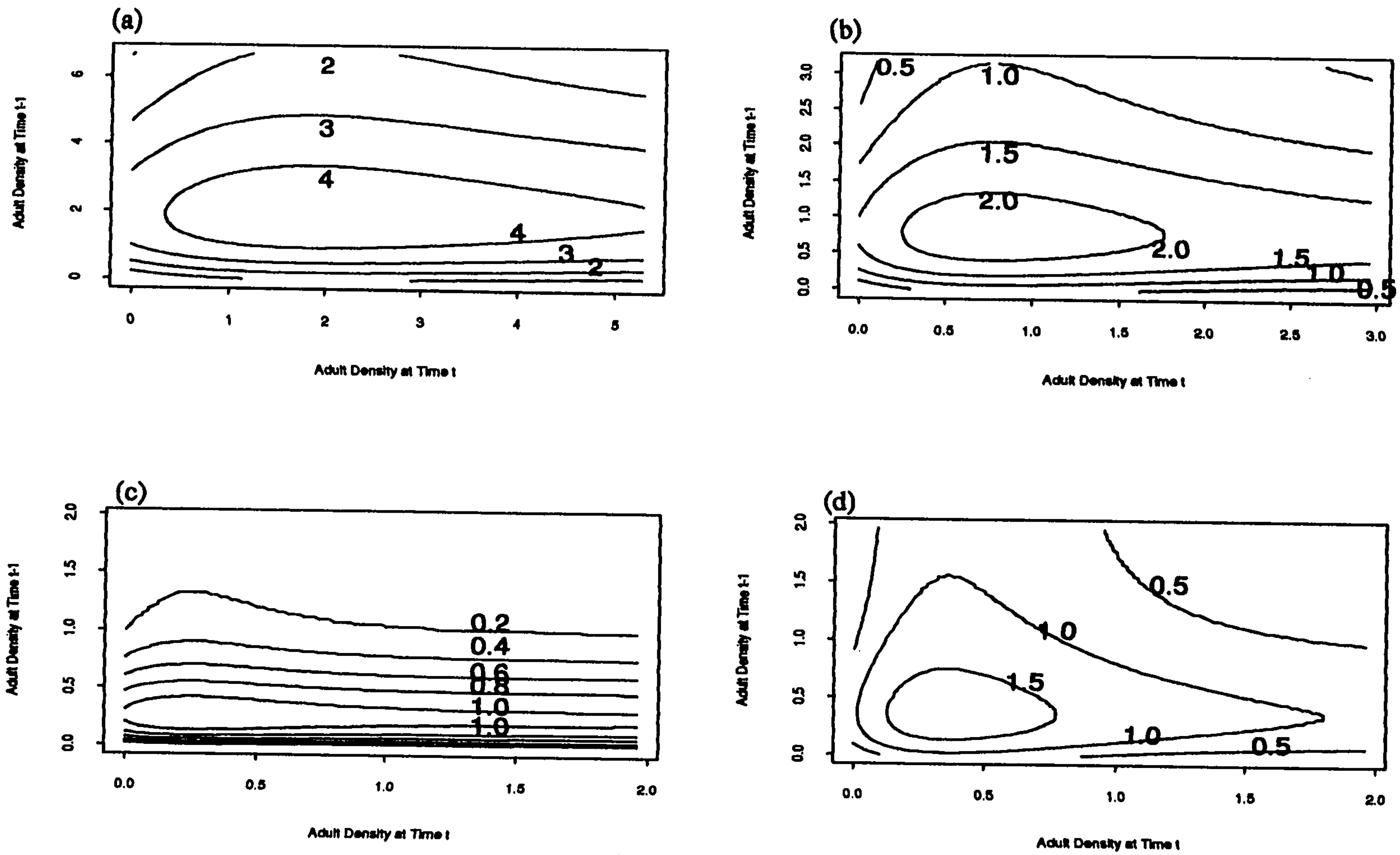


FIGURE 4.24 Contour plots that show the estimated total density (in clams/sq. yd.) y at time "t+1", given the adult densities at time "t" and "t-1" at the four major beaches in Washington (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach). The greater the value of the contour, the greater the density at time "t+1" (From Eq. 4.23).

densities, would produce the maximum future stock density. At Mocrocks, for example, if the adult stocks were maintained near 2 clams/yd^2 (i.e., 1.67 clams/m^2), the maximum density from this model would be realized.

Comparing the SSRSR model results with the past observations, the stocks have often been kept too low to allow maximal densities to recruit. For example, at Mocrocks, the adult stock density has only seldom (10 years out of 33) been high enough to allow the stock to produce its maximum density. The results from the other three beaches indicate that the adult densities have been sufficiently high to allow the stock to produce its maximum density about half of the time. Even at these beaches, however, the results indicate that within recent history (late 1970's through 1990), the stocks have been kept too low to allow maximal densities to recruit.

In addition to simulating the results of the model to attain optimal adult stock densities, I also used the estimated parameters, and fit the model to the time series. The overall fit for all beaches was fairly good (Figure 4.25). Based on the various statistics to measure the fit, at Mocrocks, Copalis and Twin Harbors, the fits for the SSRSR model and the SSRSR model with the environmental metrics included were better than any of the other models (See Table 4.7). The fit for Long Beach was comparable to the fits of the various Differenced Regression models (See Table 4.7). Even when the r-squared of the SSRSR model was not better than previous models, the overall qualitative look of the predictions was better than the other models. Of greatest interest is that this model appears to capture both the peaks and troughs of the beach dynamics, along with the three to four year decay that is often evident within the time series.

One interesting feature of the SSRSR model is that it explains the poor recruitment in 1983. This model indicates that given the two good year classes of 1981 and 1982, the combined effect would be to cause a decrease in the clam population density in 1983. The model prediction is very close to the population estimate that was observed. This is further

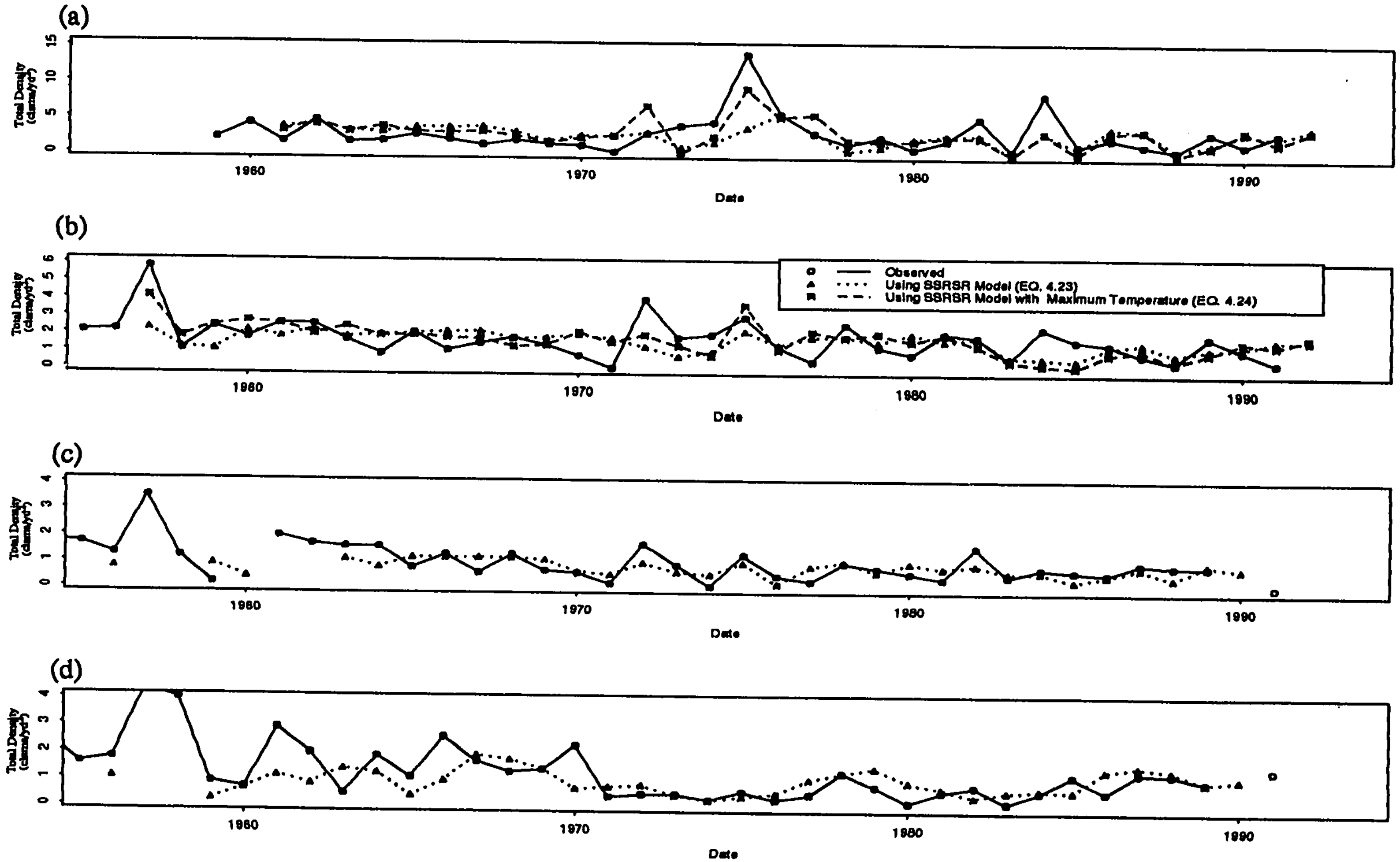


FIGURE 4.25 Prediction of subsequent population density using the Stage-Structured Ricker Stock-Recruitment models (Eqs. 4.23 and 4.24). The independent variables are the density of adults at time "t" and time "t-1", and the maximum annual temperature. The solid line indicates the observed pattern of recruitment through time at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach.

evidence that the decrease in population densities in 1983 could have been general razor clam dynamics, and not related to any outside disease factor. At the same time, however, the model predicts low populations in 1984 and 1985, which was not the case. There was no catch allowed in 1983 or 1984, and this apparently aided the population at Copalis, although the effects at the other three beaches are ambiguous.

4.5.10 TOTAL DENSITY RELATIONSHIP USING THE STAGE-STRUCTURED RICKER STOCK-RECRUITMENT MODEL, INCLUDING STOCK-RECRUITMENT RELATIONSHIP AND TEMPERATURE

The addition of temperature to the Stage-Structured Ricker Stock-Recruitment Model was investigated. As mentioned in section 4.3.11, temperature was added by fitting the temperature effect to the residuals from the SSRSR model (Equation 4.24). An alternative approach, which fit the temperature in the exponent of the Ricker model, was attempted, but the nonlinear fitting routine would not converge. For the two northern beaches, the addition of the MMT data for the year prior to the current year significantly improved the model fit ($p < 0.10$; Table 4.7, Figure 4.25). For Mocrocks, the temperature and temperature squared from the year prior to the current year was added to the model as a linear effect as indicated in Equation 4.24 (Table 4.4).

At Copalis, not only was the temperature and temperature squared from the previous year added, but the temperature and the temperature squared for the current year was added as well. However, the reason that the addition of temperature for the current year (i.e., time "t") was significant was due to one very influential point from the 1950's. This is similar to the situation that arose with the Differenced Regression model that included the MMT data as a density-dependent effect (Section 4.5.8). Because the inclusion of the extra two terms for the temperature in this year is due to one point, I prefer to keep the models for both Mocrocks and Copalis the same, with the inclusion of the MMT and MMT-squared in the previous year only. The actual parameterizations for these two models are:

a) Mocrocks:

$$D_{t+1} = 228.83 + 0.00 \cdot (A_t - C_t) + 1.60 \cdot A_t \cdot \exp(-(0.53 \cdot A_t)) + 5.11 \cdot A_{t-1} \cdot \exp(-(0.53 \cdot A_{t-1})) + (-28.86) \cdot E_{t-1} + 0.91 \cdot E^2_{t-1}, \text{ and}$$

b) Copalis:

$$D_{t+1} = 92.85 + 0.00 \cdot (A_t - C_t) + 2.47 \cdot A_t \cdot \exp(-(1.29 \cdot A_t)) + 5.44 \cdot A_{t-1} \cdot \exp(-(1.29 \cdot A_{t-1})) + (-12.13) \cdot E_{t-1} + 0.39 \cdot E^2_{t-1}.$$

For the two southern beaches, the addition of temperature to the SSRSR model did not significantly improve the fit of the model ($p > 0.16$ at Twin Harbors and $p > 0.17$ at Long Beach). The lack of a significant temperature effect with the SSRSR model at the two southern beaches was surprising because both the Ricker and the Differenced Regression models had found that the inclusion of the temperature did improve the model fit. Of course, at the two southern beaches, the fit of the SSRSR model is good, so the additional information that the temperature data could provide is limited.

The addition of the indicator variable for El Nino to the SSRSR model, instead of the quantitative temperature metric, was not significant for either Mocrocks ($p = 0.37$) or Long Beach ($p = 0.16$), but was significant for Copalis ($p = 0.07$) and Twin Harbors ($p < 0.06$). The significant fit at Copalis was due to one large population in a non-El Nino year (1956). If this point was removed, the effect became nonsignificant ($p = 0.38$). The fit at Twin Harbors was significant, and was not due to just one point that had high leverage. The inclusion of the El Nino indicator had a partial r-square of 0.12. Because none of the other beaches indicated a significant effect due to the El Nino variable, and because of the small increase in precision gained while including an extra parameter, I have chosen not to include the predicted fit of the model including the El Nino indicator variable at Twin Harbors.

As with several other models that included temperature, at Mocrocks and Copalis, the temperature enters the model in such a fashion that the extremes of the temperature result in greater densities, not lesser densities as theory predicted. This means that at very low temperatures, and at very high temperatures, the density in the next year is expected to increase more than if the temperature were average. This result explains why the model can now fit the large peak in the 1970's, an era with cool temperatures. However, although 1983 was an El Nino year, and had a slightly elevated mean temperature, the temperature that was experienced falls right within the range of temperatures where the stock densities experience the greatest reduction under this model. Over the range of temperatures reported in the time series, the squared term appears to enter into the model because at higher temperatures (16 - 17 C), the effect of temperature does not continue to cause a decrease in the subsequent density, but instead approaches an asymptotic value.

The addition of the temperature metric at Mocrocks helped to explain some of the peaks that had been missed by the model that did not include temperature (Figure 4.26). This was especially true concerning the massive peaks in 1974 and 1975. Similarly, at Copalis, peaks in 1972 and 1975 were explained by adding the temperature metric. This model also predicts a low population density during 1983, a result that seems driven by population size and temperature, rather than the emergence of a new disease. There are still peaks and troughs within the observed data that are not sufficiently accounted for by the model. Apparently, these cannot be attributed to the effect of the temperature metric. This implies that either something other than temperature is causing these deviations from the current model.

4.5.11 TOTAL DENSITY RELATIONSHIP USING THE STAGE-STRUCTURED RICKER STOCK-RECRUITMENT MODEL, INCLUDING STOCK-RECRUITMENT RELATIONSHIP AND NIX

The effect of the NIX intensity on the future density of razor clams was investigated at Copalis. Similar to the temperature metric, the relationship between NIX and the population density was explored using the residuals of the SSRSR model that used the adult stock only. There was no relationship evident between NIX and the residuals ($p=0.93$). This result, in concert with the results from the SSRSR model with temperature effects, indicates that the future population density is driven by historical population densities and temperature, rather than the disease NIX.

4.5.12 MEAN RECRUITMENT MODEL

The mean recruitment model (Equation 4.27) was a very basic model, but provided a very good fit to the time series at all four beaches. Prior to the addition of the temperature metrics, the mean recruitment model showed limited dynamic behavior. Throughout the investigations that used the mean recruitment model as their basis, it appeared that the two northern beaches were closely related, and the two southern beaches were closely related. For example, "catch" was included in the mean recruitment model, and a parameter estimated to assess whether the inclusion of "catch" provided any information on subsequent population densities. At both Mocrocks and Copalis, the inclusion of the "catch" term was not significant ($p > 0.46$) (Table 4.16). However, at both Twin Harbors and at Long Beach, the inclusion of the "catch" at time "t", was a significant addition to the model ($p < 0.01$). At both Twin Harbors and at Long Beach, the catch at time "t" was positively correlated to the subsequent density at time "t+1". The relationship between catch and subsequent populations at all four beaches imply that taking a large catch from the beach will not have a negative impact on future populations.

Table 4.16: Analysis of Variance Table for the Mean Recruitment Regression Model for Each Beach Individually (Equation 4.27). The dependent variable for this analysis is the density in the subsequent year.

Mocrocks Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	4.102	4.102	0.555	0.462
Residual	29	214.221	7.387		

Copalis Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	0.174	0.174	0.144	0.707
Residual	33	39.836	1.207		

Twin Harbors Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	2.846	2.846	7.655	0.01
Residual	31	11.527	0.372		

Long Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	11.740	11.740	17.188	<0.001
Residual	33	22.539	0.683		

4.5.13 MEAN RECRUITMENT MODEL WITH TEMPERATURE

The mean recruitment model with temperature fit the data surprisingly well, and in fact, based on the r-squared statistic, outperformed every other model that was estimated (Table 4.7). The investigations imply that much of the deviations that are experienced by the razor clam stocks along the coast of Washington are due to the MMT. At the two northern beaches, a two year lag between the MMT and the density was the most significant ($p < 0.02$) lag (Table 4.17). In the absence of the "catch" term, at the two southern beaches, the most significant ($p<0.01$) lag was the 0-year lag (Table 4.18), which indicates that the year-class strength is not fully determined until the current summer effects have been experienced. The next most significant ($p<0.03$) lag at the two southern beaches was the 1-year lag. Even after fitting the 1-year lag, the 0-year lag was still significant ($p<0.02$). The pattern of when year-class strength is determined indicates that there is a possible geographic link to the stock dynamics. When the "catch" term is include in the model for the two southern beaches, if catch is added before temperature, the significant temperature effects drop out at Long Beach, but remain at Twin Harbors. Since the MMT for the 0-year lag is not known until late in the summer of the current year, this relationship between temperature and stock density would not be helpful for predictive management purposes. Therefore, the models that are selected have at least a 1-year lag.

The parameterizations of the models that were selected for each beach are:

a) Mocrocks: $$D_{t+1} = 300.01 - 37.81 \cdot \mathrm{T}_{t-1} + 1.20 \cdot \mathrm{T}_{t-1}^2$$

b) Copalis: $$D_{t+1} = 137.02 - 17.76 \cdot \mathrm{T}_{t-1} + 0.58 \cdot \mathrm{T}_{t-1}^2$$

c) Twin Harbors: $$D_{t+1} = -73.71 + 0.88 \cdot \mathrm{C}_t + 9.66 \cdot \mathrm{T}_t - 0.31 \cdot \mathrm{T}_t^2$$

Table 4.17: Analysis of Variance Table for the Mean Recruitment Regression Model with MMT for Each Beach Individually (Equation 4.28). The dependent variable for this analysis is the density in the subsequent year.

Mocrocks Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	4.102	4.102	0.779	0.385
MMT_{t-1}	1	41.135	41.135	7.814	0.009
$(MMT_{t-1})^2$	1	30.954	30.954	5.880	0.022
Residual	27	142.133	5.264		

Copalis Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	0.174	0.174	0.204	0.655
MMT_{t-1}	1	0.403	0.403	0.4730	0.497
$(MMT_{t-1})^2$	1	12.999	12.999	15.245	<0.001
Residual	31	26.434	0.853		

Table 4.17 (cont.): Analysis of Variance Table for the Mean Recruitment Regression Model with MMT for Each Beach Individually (Equation 4.28). The dependent variable for this analysis is the density in the subsequent year.

Twin Harbors Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	2.846	2.846	10.167	0.003
MMT_t	1	0.064	0.064	0.228	0.636
$(MMT_t)^2$	1	3.345	3.345	11.947	0.002
Residual	29	8.118	0.280		

Long Beach

Source	df	Sum of Squares	Mean Square	F Value	P(F)
Catch	1	11.740	11.740	19.777	<0.001
MMT_{t+1}	1	1.024	1.024	1.725	0.199
$(MMT_{t+1})^2$	1	3.114	3.114	5.246	0.029
Residual	31	18.401	0.594		

d) Long Beach: $D_{t+1} = 0.54 + 1.32 \cdot C_t$

The alternative to fitting the actual temperatures was to fit the indicator variable for an El Nino event. In no case did the indicator variable for an El Nino event fit the data better than the quantitative temperature metrics. At Copalis and Twin Harbors, the inclusion of the El Nino indicator was significant, indicating that at least a portion of the temperature effect that was significant might be attributable to the El Nino events.

The final parameterizations of the Mean Recruitment model were compared to the historical time series to understand how the various model components affected the fit. The comparison was conducted on an individual-beach basis. The graphics (Figure 4.26) showed that for the two northern beaches, the temperature component caused the model to fit the peaks in the 1970's. However, as with the Differenced Regression models, which are closely related to the Mean Recruitment models, the troughs were not explained as well. As with several of the other models, the variability of the model was seemingly less than the variability of the observations. This implies that the model would predict a future time series that was much more stable than the observed time series.

At the two southern beaches, the models fit the data series fairly well, but again showed less variability than the observations. At Twin Harbors, the model predictions are generally quite good. A couple of the dominant peaks are explained by the model, as are some of the troughs. At Long Beach,.the fit, although fairly good, is less appealing than at the other beaches. The predictions are a little high in the 1970's and show almost no variability. This is probably a reflection of the fact that the data series at Long Beach responded so differently to the reduced temperatures of the 1970's than did the other beaches.

The fit of the Mean Recruitment model with temperature effects (Equation 4.28) and the fit of the SSRSR Model with temperature effects (Equation 4.24) to the historical time series are remarkably similar (Figures 4.25 and 4.26). This is somewhat surprising,

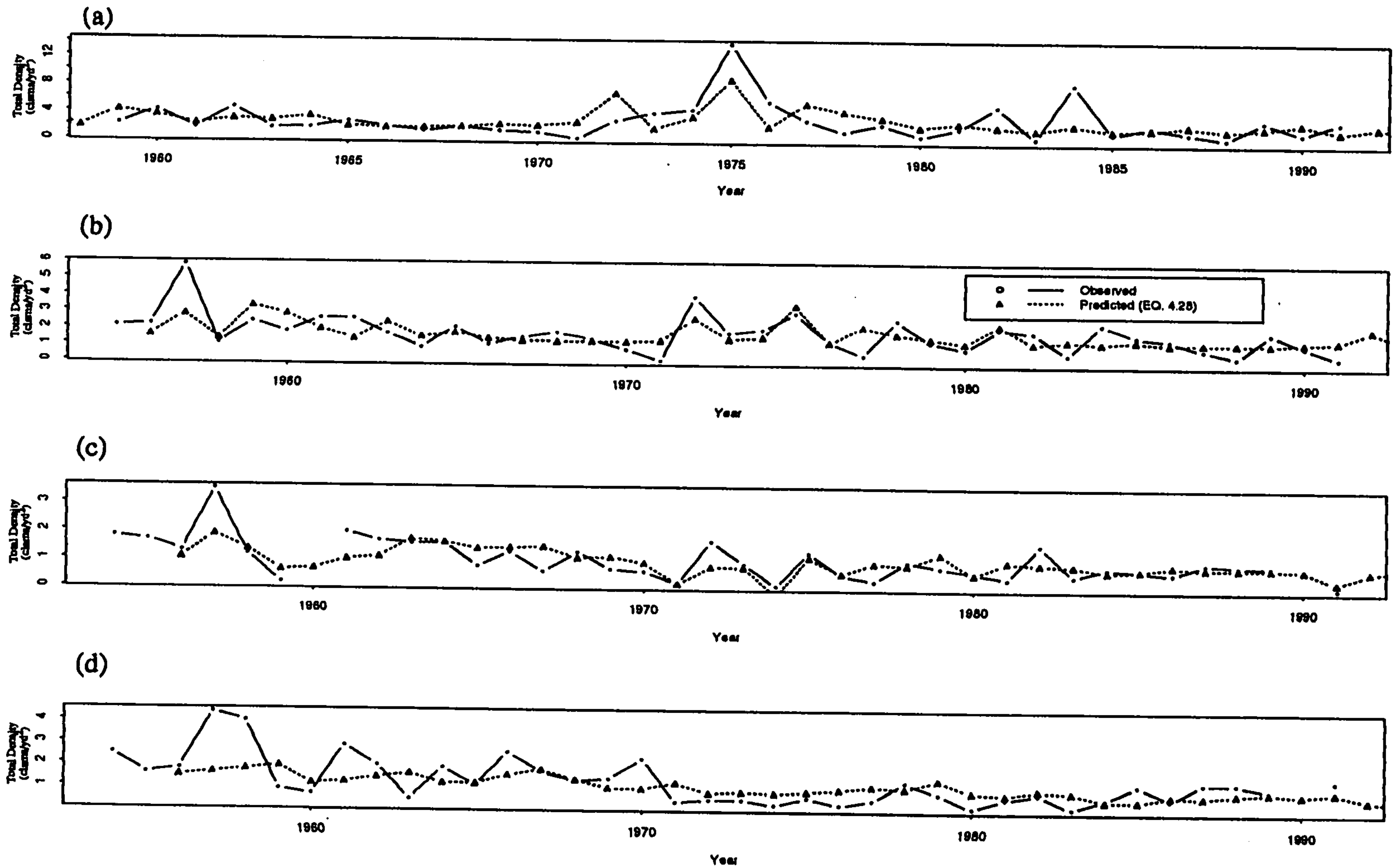


FIGURE 4.26 Prediction of subsequent population density using the Mean Recruitment models (Eq. 4.28). The independent variables are the catch density and the maximum annual temperature. The solid line indicates the observed pattern of total clam densities through time at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. The dashed line indicates the model predictions.

given the extreme differences in the assumptions of the two models. In the Mean Recruitment model, there is no stock-recruitment relationship (i.e., as the stock increases and decreases, recruitment stays constant) and the dynamics are generally provided by the temperature effects. In the SSRSR model, there is a stock-recruitment relationship (i.e., as the stock increases to infinity and decreases to zero, recruitment goes to zero) and the dynamics are driven by both the stock densities in the past as well as the temperature. The fact that the fits are similar, even though the model assumptions are very different implies the following:

a) that the majority of the time, the stock has not been near the extremes, where differences would allow clear delineation between the two models, and

b) that the temperature provides much of the dynamics associated with population fluctuations in the razor clam.

4.5.14 MEAN RECRUITMENT MODEL WITH NIX

The effect of the NIX intensity on the future density of razor clams was investigated at Copalis. The effect of NIX was explored with both the assumption that prior to 1983, the NIX Intensity had been zero, and with the assumption that prior to 1983, the NIX Intensity was unavailable. Unlike all other models that investigated the influence of NIX, the Mean Recruitment model indicated that there was a significant relationship evident between NIX (when the NIX Intensity was assumed to be zero prior to 1983) and the density ($p=0.08$) at the next time step. However, when the significant temperature effects were added to the model in a forward step-wise fashion, the NIX effect became non-significant ($p=0.27$), indicating that the NIX and the MMT are correlated. The NIX effect was not significant ($p=0.25$) under the assumption that NIX Intensity was unavailable prior to 1983. Even when the fit was statistically significant, the partial r-square was rather low (partial r-square = 0.09). These results, in concert with the results from the Mean Recruitment model with temperature effects, indicates that the future population density is driven largely by the mean recruitment and temperature, rather than the disease NIX.

4.6 CONCLUSIONS OF THE RECRUITMENT ANALYSIS

A series of models were fit, each of which had different assumptions. Traditional fisheries models (e.g., the Ricker model and the Schaefer model) were pursued originally, but poor fit from these models necessitated different model formulations. In several cases, the models that were investigated consisted of a hierarchical series. With hierarchical models, statistical tests can be constructed to determine the significance of the addition and deletion of a specific effect. Among the non-hierarchical models, the models had very different assumptions and drastically different parameterizations. These differences among the non-hierarchical models made comparisons across the various models somewhat difficult. I chose to use the r-squared statistic and general dynamic behavior as the bases for model selection. The r-squared statistic describes how well the model fits the current data, regardless of the assumptions or the choice of the response/dependent variable (i.e., y-axis). In addition, with some of the models, even some of the traditional fisheries statistics were meaningless (e.g., maximum recruitment under the Differenced Regression Model).

Two models provided superior fit to the data series, although assumptions associated with the two models provide for vastly different ideas about stock dynamics. The greatest difference between the Mean Recruitment model and the Stage-Structured Ricker Stock-Recruitment model is that with the Mean Recruitment model, there is no relationship between current stock density and subsequent recruitment. Thus, if the measurable stock is driven to zero, there is no impact on subsequent densities. In the SSRSR model, the Ricker form of the stock-recruitment equation is utilized. The Ricker formulation specifies that as the stock density goes to zero, the subsequent recruitment will also be zero. Despite this major difference, the current data do not provide sufficient evidence for support or refutation of either model exclusively. Overall, although the Mean Recruitment model provided a slightly better fit (based on the r-squared statistic) to the data, the SSRSR model appeared to better capture the dynamics of the stock through time. Despite these noted differences, several general themes appeared throughout the investigations.

The total variability that is still not accounted for after the best models are fit is substantial (i.e., 0.18 < 1-(Sum of Squares for Model)/(Sum of Squares Total) < 0.29). This is probably a combination of several factors. One factor that induces error in the regressions is measurement error from the release-recapture surveys. Measurement error is associated with both the dependent and independent variables (i.e., total and adult densities per beach respectively), which induces error into the regression (Ludwig and Walters, 1981). Spatial analyses that I have undertaken have indicated that both the size distributions of clams and the densities of clams within an area vary greatly across even small areas of the beach. This spatial variability within a survey area adds to the variability in the estimate of the abundance which were used to construct the models within this section. Error could also be induced if other processes are at work to define the success/failure of the recruitment year-class. The correlation structure of the recruitment deviations along the Washington coast (Section 4.3.1) indicates that some local conditions that have not been inserted into the model may contribute to the spawning success.

Investigations of the four beaches for the years 1954-1991 indicate several important factors are at work along the Washington coast. These can be summarized as follows:

1) There are some local-scale phenomena. Recruitment deviations at adjacent beaches are significantly correlated ($p < 0.01$), but recruitment deviations for non-adjacent beaches are not significantly correlated ($p > 0.10$). The suite of recruitment models that were investigated indicated that this interaction is not strong enough to allow the beaches to be jointly modelled.

2) The total density of the razor clam population can vary substantially through time. In addition, due to the interactions among adults, juveniles and newly settled larvae, a cyclical pattern is observed at all beaches. This cyclical behavior was somewhat captured in the Stage-Structured Ricker Stock-Recruitment model.

3) A stock-recruit relationship does exist within the razor clams. Based on the decay trends that are observed in the data series, the stock-recruit relationship appears to be governed by the density of the within-beach spawning stock over the two previous years. However, as mentioned, the relationship between stock and recruitment at very low densities is poorly defined. Whatever the form of this relationship, strong density-dependent pressures appear to be present. These density-dependent pressures maintain the stock density around a mean density at all beaches. Despite the strong contribution of the within-beach spawning stock to the stock-recruitment relationship, no evidence exists to ascertain the origin of the recruits. The sole genetic study (Leclair and Phelps, 1994) that has compared the various stocks of razor clams along the Washington coast also does not give a strong indication as to whether or not the beaches are separate stocks.

4) The maximal mean-yearly temperature, which occurred in July, August or September for the years 1954-1991, can significantly ($p < 0.10$) help to improve the fit of the stock-recruitment relationship. The results from the Stage-Structured Ricker Stock-Recruitment model, which is a hybrid of the Ricker-based models and the density models, indicates that the significance of the temperature effect on the stock-recruit relationship is beach-specific. In the case of Copalis and Mocrocks, the addition of temperature to the Stage-Structured Ricker Stock-Recruitment model substantiated the hypothesis that several of the extremely large year classes that occurred in the past were in large part a function of good environmental conditions combined with optimal stock densities. The improvement in predictive power of any of the stock-recruit relationships when the environmental variables are added is rather low ($0.08 <$ partial $r^2 < 0.17$). In general,

however, the major increases in the population density appear to be highly linked to the temperature metric.

The fact that the effect of temperature is not consistent across models or beaches does cause some concern. In the case of the Stage-Structured Ricker Stock-Recruitment model, the result of adding the temperature metric to the model indicated a general decrease in reproductive success from 13 C to 16 C. A problem arises with the model at higher temperatures. The SSRSR model predicts that higher temperatures (i.e. temperatures greater than 16 C) cause increases in future reproductive success. Only once during the time series has the maximum temperature gotten above 17 C. When the data associated with this point was removed the increase in reproductive success with increasing temperature above 16 C was eliminated from the model. This implied that the inclusion of the squared term was simply the way the model could fit the highly influential point above 17 C. Thus, the SSRSR model implies that the reproductive success decreases as the maximum temperature increases, but that the decrease may asymptote within the range of maximum temperatures typically observed, and not continue downward.

5) The indicator for El Nino sometimes provided a significant improvement in model fit. However, the effect was not apparent at all beaches, nor was the effect as informative as the quantitative measure of temperature. In general, because there are mechanisms other than El Ninos that can influence the water temperature, it appears that the quantitative measure (i.e., maximal mean-yearly temperature) provides a better descriptor of the environmental stress.

6) The NIX intensity metric is typically a poor predictor of subsequent stock density. Only in one model (Mean Recruitment) did the NIX Intensity appear to provide a significant ($p=0.08$) improvement in the fit of the base model. However, even in this case, the inclusion of the temperature metric provided a much better fit to the data than the NIX Intensity. When the highly significant ($p<0.001$) temperature metric was included, the NIX Intensity was no longer significant ($p=0.27$).

7) No analysis indicated that large catches in the past have had detrimental effects on the population. Some analyses indicated that catch did not significantly influence the subsequent populations, while other analyses indicated that taking adults from the population this year increased the density in the next year. This result, combined with the evidence of low adult survival (Chapter 2 and Section 4.5.10), indicates that attempts to increase the population by limiting harvest may not succeed.

8) The Stage-Structured Ricker Stock-Recruitment model indicated that the number of adults that survive the fishery and the subsequent summer is very small. The model estimate of adult survival suggested that none of the adults survived both the fishery and the subsequent summer at any beach. This result is consistent with the low survival estimates that were observed in the mark-release study. This result also indicates that on the majority of Washington Beaches, adult razor clams do not survive much beyond 3 years of age.

Overall, the Stage-Structured Ricker Stock-Recruitment model provided a satisfactory fit to the data. The Stage-Structured Ricker Stock-Recruitment model was extremely useful, for it allows us to estimate the relative effects of the current adults and juveniles on the subsequent recruitment. It also provides an estimate of survival for the adults currently on the beach. According to the SSRSR model, success of future recruitment is highly dependent upon the current density of adults and juveniles already established upon the beach. The model implies that the razor clams along the Pacific Coast of Washington experience strong density dependency. Temperature did improve the fit of the models to the large recruitments of the early 1970's at Mocrocks and Copalis. The inclusion of the temperature metric does not appear to be strongly related to decreases in population densities. The disease NIX does not appear to strongly influence the beach density. The small predictive improvement that comes from including temperature in the models, along with the high degree of heterogeneity measured within the genome, implies that the Pacific razor clam has very strong adaptive responses and can tolerate a wide variety of environmental regimes.

Chapter 5

Population Dynamic Simulations

5.1 INTRODUCTION

Following the 1983 decline, WDFW became very concerned about overharvest of the razor clam stocks. For two years following the decline in 1983, no harvest was allowed at all. Since then, the harvest has been highly regulated. The current management strategy is to limit effort and total harvests by setting seasons, during which the number of clams removed is enumerated on a daily basis. The season is then lengthened or shortened based upon the manager's idea of how many clams were there before the season began and how many he hopes to allow in the catch. Under the current policy, Washington Department of Fish and Wildlife (WDFW) personnel allow a harvest rate of 25.4% of all clams greater than 3 inches (7.6 cm). It is not always possible to limit the catch to such a precise fraction of the stock, as catch-effort relationships are neither temporally nor spatially stable along the coast. However, the stock is watched closely and closures have been implemented in the past when overharvest (as defined under WDFW guidelines) has been detected.

There are two ways to investigate whether overharvest is a problem in the razor clam stocks along the Washington coast. One could subject the populations along the coast to several different harvest levels over a number of years to determine the effect of increased harvest. However, this technique would take many years and could deplete the stock (See Hilborn and Walters, 1992 for more about adaptive management and experimentation with stocks). Thus, the risk and subsequent repercussions of any strategic change are unknown. Alternatively, one could create a model to simulate the populations and subject the model to different harvest levels and different harvest strategies. Prior to this dissertation, no model existed that would allow the state shellfish manager to choose between alternative harvest strategies. The advantages to the simulation modeling approach are that the model formulation will provide a coherent framework under which management strategies may be tested, the population is unaffected by strategies that could deplete the stock and the time span between implementation of the strategy and the results is greatly reduced. Simulation studies also allow replication of the stochastic population trajectory under a specific strategy and will thus allow probabilistic risk to be assigned to each strategy. Finally, the modeling will provide indications of further investigations that should be attempted to clarify the dynamics of the razor clam along the Washington coast.

Discussions were carried out with the WDFW to discover their preferences about how the model should be constructed and which metrics should be evaluated. WDFW indicated that they were interested in managing each beach independently. As the data analyses (Chapter 4) indicated that recruitment relationships varied according to the beach, such beach-by-beach management appears to be a logical choice. However, it is possible that there is crossover of recruits from adjacent beaches. The model simulations within this chapter ignore this contribution to the recruitment pool.

WDFW are also very concerned with avoiding very low population densities while maintaining a regular annual harvest. This may be problematic, as indications from the time series are that significant decreases in abundance occur rather often. Additionally, data analyses (Chapter 4) indicated that high catches did not significantly decrease subsequent populations. This implies that controlling for year-class failure may be outside the realm of control by the manager. From these discussions, it is apparent that there are two measures of interest to the WDFW personnel. WDFW desire a strategy that (1) protects the resource from collapse and (2) allows harvest on an annual basis.

A simulation model was constructed to test whether overharvest was a problem and whether alternative harvest strategies could provide greater harvest with similar or reduced levels of risk. The simulation exercise consisted of three separate steps. In the first step, the various mathematical parameters which describe the underlying processes that governed the population dynamics of the razor clam were quantified (i.e., Chapters 2-4).

In the second step, a conceptual and mathematical model was constructed. Finally, the parameters estimates were used in the mathematical model to simulate the repercussions of various harvest strategies. In a few cases in Chapters 2-4, different approaches resulted in estimates of parameters that were widely variable. For these cases, sensitivity analyses were carried out to determine the effect of parameter values on various model outputs. The final step in this modelling exercise was to subject the simulated populations to simulated harvest and assessment.

5.2 DEVELOPMENT OF POPULATION DYNAMICS MODEL

The model was formulated as illustrated in Figure 5.1. Essentially, this model states that the number of animals in stage "i", during time "t+1", will be composed of those animals who were less than or equal to stage "i" at time "t", that grew into or remained in stage class "i" and survived, or were recruited directly into stage "i". Stages are length-based classifications that separate the total population into (a) one-year old juveniles and (b) adults. The processes of survival, growth and recruitment were modelled separately.

5.2.1 SURVIVAL MODEL

Adult and juvenile survival were estimated in Chapters 2 and 4. However, for both adults and juveniles, different approaches provided different estimates of survival. Survival estimates for the adults ranged from 0.00/year (Section 4.5.9) to 0.35/year (Section 2.4.1.4). Adult survival appeared to be independent of the beach from which the data had been collected. The estimates of the juvenile survival were beach-dependent and had a wide range (i.e., 0.24/year; $\text{s.e.}(S_j) = 0.18$ to 1.09/year; $\text{s.e.}(S_j) = 0.57$) of values. The modelling will use a range of possible survivals and evaluate the impact of the alternative estimates on simulation results and on subsequent management recommendations.

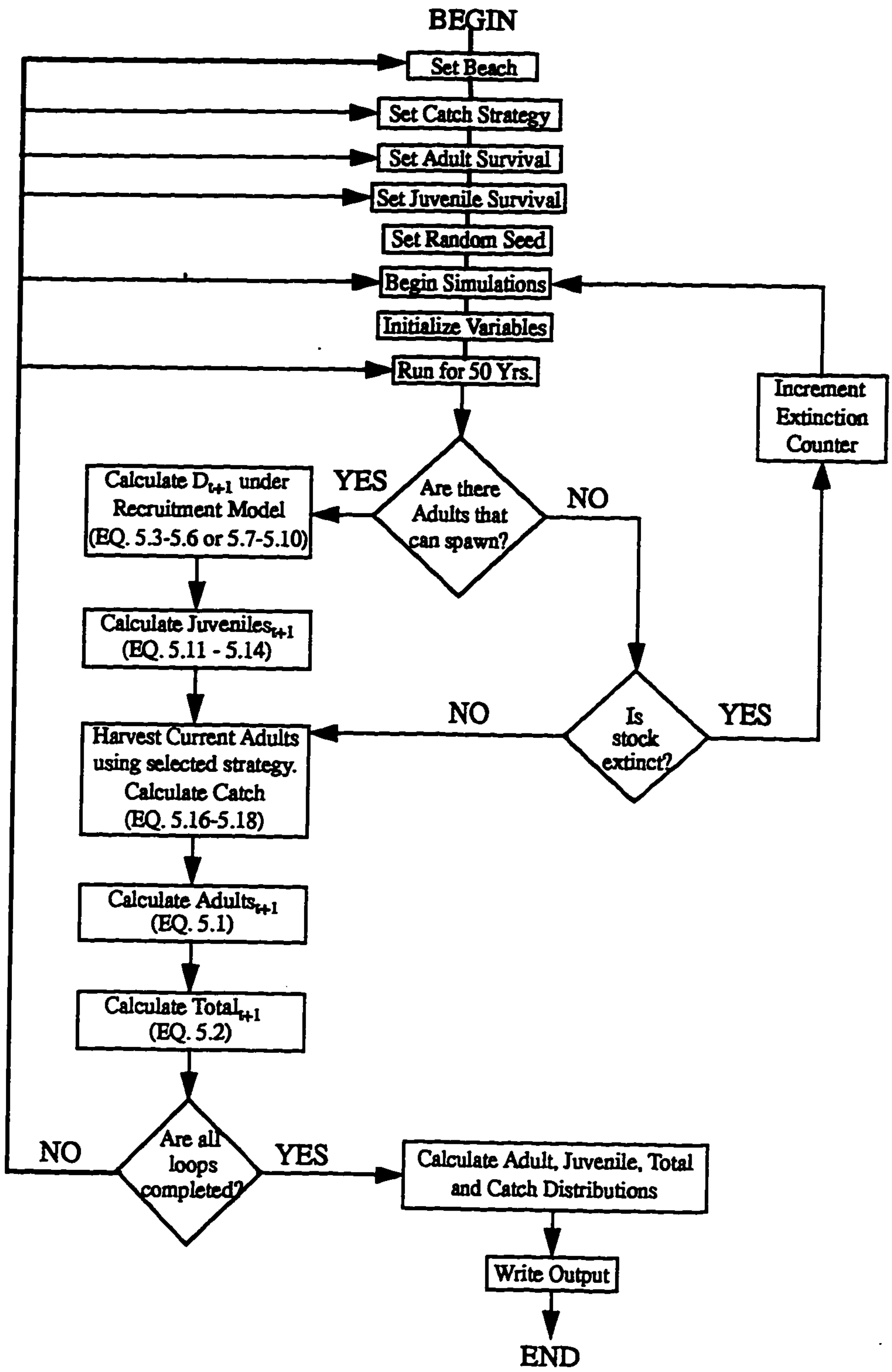


FIGURE 5.1 Flowchart of simulation model.

In the case of constant catch policies, the clam population was subjected to harvest and then the remaining individuals were subjected to the survival process. In the case of constant harvest rate and escapement policies, the natural mortality and the fishing mortality were assumed independent. Thus, total survival was adjusted using the following probability relationship for independent processes:

$$S_{Total} = 1 - M_{Total} = M_{Natural} + M_{Fishing} - M_{Natural}M_{Fishing}$$

where

S = survival probability, and

M = mortality probability.

Although the SURPH model indicated that adult survival was somewhat dependent on size, this effect was typically nonsignificant. The effect of length on survival has, therefore, been ignored within these simulations. Similarly, because no significant ($p>0.10$) NIX effects were evident in any of the statistical analyses, the affect of NIX has not been included in any process in the simulation model.

5.2.2 GROWTH MODEL

Growth was modelled as a gross transition from one stage to another. The two stages that were modelled were (a) one-year old juveniles and (b) adults. All juvenile clams progressed to adults within a time step. Adult clams stayed within the adult stage if they survived throughout the time step. Thus, the density of adult clams in the next time step was calculated as

$$A_{t+1} = A_t S_A + J_t S_J \qquad \text{(EQ 5.5)}$$

where

A = adult clam density,

J = juvenile clam density,

S_A = survival probability of the adults,

S_J = survival probability of the juveniles, and

t = relative designation of time.

To calculate the total density of clams in the next time step, the adult density and the juvenile density were summed as

$$D_{t+1} = A_{t+1} + J_{t+1} \qquad \text{(EQ 5.6)}$$

where

D = total clam density.

The time step for all simulations was one year.

5.2.3 RECRUITMENT MODEL

Recruitment was modelled on a beach-by-beach basis, as this was the conclusion reached in Chapter 4. Two models were used to introduce recruitment into the simulation. The two recruitment models were (a) the Stage-Structured Ricker Stock-Recruitment model (SSRSR) (Equations 5.7 - 5.10) and (b) the Mean Recruitment model (Equations 5.11 - 5.14). Although these two models indicate vastly different behavior when there are no spawners and when there are infinite spawners, the fit of either to the data was almost identical. Using the current data set, it is difficult to objectively choose one particular recruitment model to the exclusion of the other. Simulations were run using each recruitment model independently to determine the influence of the recruitment model on the results. At each time step during a simulation, the population was checked to determine whether there were any adults. If there were no adults from the previous two time steps, the recruitment was set to zero. If adults were present in the population, the recruitment was predicted under whichever recruitment model (i.e., SSRSR or Mean Recruitment) was being investigated during that simulation.

The parameterizations for the Stage-Structured Ricker Stock-Recruitment model including the significant temperature effects (Sections 4.5.9 and 4.5.10) for each beach were as follows:

Mocrocks:
$$\begin{aligned} D_{t+1} = {} & 228.83 + 0.00 \cdot (A_t - C_t) + \\ & 1.60 \cdot A_t \cdot \exp(-(0.53 \cdot A_t)) + \\ & 5.11 \cdot A_{t-1} \cdot \exp(-(0.53 \cdot A_{t-1})) + \\ & (-28.86) \cdot T_{t-1} + 0.91 \cdot T^2_{t-1} + \varepsilon, \end{aligned} \quad \text{(EQ 5.7)}$$

Copalis:
$$\begin{aligned} D_{t+1} = {} & 92.85 + 0.00 \cdot (A_t - C_t) + \\ & 2.47 \cdot A_t \cdot \exp(-(1.29 \cdot A_t)) + \\ & 5.44 \cdot A_{t-1} \cdot \exp(-(1.29 \cdot A_{t-1})) + \\ & (-12.13) \cdot T_{t-1} + 0.39 \cdot T^2_{t-1} + \varepsilon, \end{aligned} \quad \text{(EQ 5.8)}$$

Twin Harbors:
$$\begin{aligned} D_{t+1} = {} & 0.00 \cdot (A_t - C_t) + 1.63 \cdot A_t \cdot \exp(-(3.55 \cdot A_t)) + \\ & 9.86 \cdot A_{t-1} \cdot \exp(-(3.55 \cdot A_{t-1})) + \varepsilon, \text{ and} \end{aligned} \quad \text{(EQ 5.9)}$$

Long Beach:
$$\begin{aligned} D_{t+1} = {} & 0.00 \cdot (A_t - C_t) + 6.42 \cdot A_t \cdot \exp(-(2.77 \cdot A_t)) + \\ & 6.91 \cdot A_{t-1} \cdot \exp(-(2.77 \cdot A_{t-1})) + \varepsilon. \end{aligned} \quad \text{(EQ 5.10)}$$

where

D = density of adult and juvenile clams,

A = density of adult clams,

C = density of the catch,

T= maximum mean annual temperature, and

t = relative indicator of time (i.e., "t" is the current time; "t-1" is one time step into the past).

For the simulations in this chapter, the parameterizations for the Mean Recruitment model included significant temperature effects (Section 4.5.13). The models that were used during the simulations for each beach were as follows:

$$\text{Mocrocks:} \begin{cases} D_t > 0.00 & D_{t+1} = 300.01 - 37.81 \cdot T_{t-1} + 1.20 \cdot T_{t-1}^2 + \varepsilon \\ D_t \leq 0.00 & D_{t+1} = 0.00 \end{cases} \quad \text{(EQ 5.11)}$$

$$\text{Copalis:} \begin{cases} D_t > 0.00 & D_{t+1} = 137.02 - 17.76 \cdot T_t + 0.58 \cdot T_t^2 + \varepsilon \\ D_t \leq 0.00 & D_{t+1} = 0.00 \end{cases} \quad \text{(EQ 5.12)}$$

$$\text{Twin Harbors:} \begin{cases} D_t > 0.00 & D_{t+1} = -49.882 + 6.47 \cdot T_t - 0.21 \cdot T_t^2 + \varepsilon \\ D_t \leq 0.00 & D_{t+1} = 0.00 \end{cases} \quad \text{(EQ 5.13)}$$

$$\text{Long Beach:} \begin{cases} D_t > 0.00 & D_{t+1} = -5.04 + 0.408 \cdot T_t + \varepsilon \\ D_t \leq 0.00 & D_{t+1} = 0.00 \end{cases} \quad \text{(EQ 5.14)}$$

The Mean Recruitment models are parameterized somewhat different from the models that were described in Chapter 4. First, the Mean Recruitment model used in the simulations was a step function with a zero-zero intercept imposed. Imposing the zero-zero intercept implies that if there are no adults that could spawn, there will be no recruitment. If the zero-zero intercept was not imposed, recruitment would occur even in the absence of measurable adults. The net result of not imposing the zero-zero intercept would be to select for harvest strategies that took all adults, for there would be no relationship between adults and recruitment at any level. The zero-zero intercept was imposed because the contributions of recruits from the offshore and adjacent beaches is unknown. This zero-zero intercept may affect the conclusions by implying that more conservative harvest strategies might be found than would be necessary in practice. However, to impose a non-zero intercept would imply that contributions from offshore and adjacent beaches would be sufficient to repopulate the harvested beach. The assumption that contributions from offshore and adjacent beaches would be sufficient to repopulate the harvested beach is risky and is beyond the scope of the existing data. I chose the risk-averse scenario because it is more in keeping with the philosophy generally espoused by WDFW. Second, in Chapter 4 (Section 4.5.13), the models for Twin Harbors and Long Beach both included a significant "catch" term. This "catch" term indicated that high "catches" this year would positively impact the expected density next year. Therefore, models that included the "catch" term would impose strategies that would harvest the entire adult population this year so as to increase the expected density in the following year. However, under the correlative structure of the analysis, the correlation between high catches this year and increased density in the following year could be a function of simply having cycles of good and bad years, with associated good and bad catches. Rather than force a risky scenario by including "catch" as a causative agent for increased densities in the future, I chose to ignore models that included "catch", thereby again taking a more risk-averse approach. The model without "catch" which best fit the available data was used instead. Stochasticity was added to the recruitment models as an additive error term, with mean zero and variance estimated by the MSE of the fitted model (Table 5.1). For Mocrocks, the MSE under both recruitment models was inflated by two

Table 5.1: Mean squared errors used to induce stochasticity in the simulations.

Beach	MSE of Fitted Model		
	SSRSR Model	Mean Recruitment Model	Juvenile Density Model
Mocrocks	2.218 (EQ. 5.7)	2.170 (EQ. 5.11)	0.339 (EQ. 5.15)
Copalis	1.119 (EQ. 5.8)	0.853 (EQ. 5.12)	0.178 (EQ. 5.16)
Twin Harbors	0.166 (EQ. 5.9)	0.405 (EQ. 5.13)	0.047 (EQ. 5.17)
Long Beach	0.441 (EQ. 5.10)	0.896 (EQ. 5.14)	0.081 (EQ. 5.18)

extremely large outliers due to highly successful years. When a model was run with the MSE that included these outliers, the model produced too many extremely low year classes. Thus, the MSE that is reported and that was used in the simulations was a MSE calculated without these two outliers. The MSE is typically an overestimate of the inherent variability, for the MSE includes not only natural variability, but measurement error as well.

5.2.4 MODEL SELECTION FOR SIMULATION

In Chapter 4, all of the recruitment models that were considered fit predicted quantities based upon observed quantities, with the observed quantities updated throughout the time series. The procedure used what is called process error noise (Ludwig and Walters, 1989; Hilborn and Walters, 1992 pp. 224-226), and as such, must have feedback from the current state of the system in order to continue. During the fitting routine, the current state of the system was the observed predictor variables (i.e., observed adult densities). However, in the simulation model, it would no longer be possible to observe the current state independent of the model and it becomes necessary to build some relationships into the model that did not exist during the fitting procedure. For example, in the SSRSR model, given the adult densities at times "t" and "t-1" are known, the total density in the next time span can be calculated. However, nowhere within this equation is the relationship between the current total density and the current adult density formally stated. Such a statement is not necessary during the fitting phase, for adult densities are measured at almost every point in time. However, during the simulation phase, it becomes necessary to account for the adult densities at times "t" and "t-1" using some formal construct.

The survival estimates for the adults and the juveniles obtained in Chapter 2 were used to retain adults in the system and to calculate the percentage of juvenile that would survive to adults. Using the survival parameters along with the SSRSR model provided the mechanism needed to account for the time series of adult densities.

A similar problem arose with respect to the juveniles. Both of the recruitment models that are used herein (i.e., those models that were deemed to fit best in Chapter 4) predicted not juvenile recruitment, but total density in the following period. Subsequent analysis (Appendix A.3) has shown that the density of juveniles increased in a linear fashion with respect to the total density. The equations for the relationship between total density and the juvenile density used in the simulations, by beach, were:

Mocrocks: $$J_{t+1} = 0.723 \cdot D_{t+1} + \varepsilon \qquad \text{(EQ 5.15)}$$

Copalis: $$J_{t+1} = 0.671 \cdot D_{t+1} + \varepsilon \qquad \text{(EQ 5.16)}$$

Twin Harbors: $$J_{t+1} = 0.780 \cdot D_{t+1} + \varepsilon \qquad \text{(EQ 5.17)}$$

Long Beach: $$J_{t+1} = 0.776 \cdot D_{t+1} + \varepsilon \qquad \text{(EQ 5.18)}$$

The fit of this relationship was quite strong at all four beaches ($0.87 \le r^2 \le 0.96$). The combination of the stock-recruitment relationship (Equations 5.5 - 5.8) and this linear relationship between total predicted density and juvenile density (Equations 5.9 - 5.12) was used to predict the strength of subsequent recruitment year-classes. Stochasticity was added to this portion of the recruitment process as an additive effect, with mean zero and variance estimated by the MSE (Table 5.1) from the fitted model. As mentioned before, the MSE is typically an overestimate of the inherent variability.

Two types of simulations were investigated, deterministic and stochastic. To understand general model behavior, and to look at the sensitivity of the model to adult and juvenile survivals, a deterministic model was used initially. For deterministic simulations, survival, growth and recruitment processes were deterministic and no influence of temperature was included in the simulation model.

Stochastic models were used to study the variability of the population density, the variability of the catch and the risk. Stochasticity was added to the recruitment process and to the temperature-generating process. Stochasticity was added to the stock-recruitment relationship in two places. First, the MSE (Sections 4.5.9 and 4.5.10; Table 5.1) from the fitted stock-recruitment relationship was used as an estimate of variability inherent in the population and in our ability to predict subsequent populations based on the model. This component of the variance affected the total predicted density. To predict the number of recruits from the number total, a second component of variance, the MSE from the fitted total-recruitment relationship (EQ. 5.9 - 5.12; Table 5.1), was added.

To estimate the future time series of maximum temperatures, the time series of maximum annual temperatures from 1947 to 1994 was fit using a series of sine functions. The fitted model was:

$$\hat{MaxT} = 15.600 + 0.776\sin\left(\frac{2\pi t}{48.471}\right) + 0.214\sin\left(\frac{2\pi t}{0.838}\right) + \varepsilon \qquad \text{(EQ 5.19)}$$

This technique provided a very good fit to the observed maximum temperatures. Stochasticity was added to the temperature as an additive effect, with mean zero and the variance estimated by the MSE ($\sigma^2 \equiv \varepsilon = 0.45$) from the fitting routine.

5.2.5 MODEL OUTPUT AND MANAGEMENT CRITERIA

To determine the harvest strategy and harvest level that best met WDFW criteria, three different harvest strategies, each with a range of harvest levels, were used to harvest clams from the beaches. The time series for each beach was simulated 1000 times for a 50 year sequence. Recruitment and temperature were stochastic throughout the time series. Only adult clams were harvested. The different harvest strategies were: (a) constant catch that removed from 0.1 clams/yd^2 - 1.9 clams/yd^2 (i.e., 0.083 clams/m^2 - 1.59 clams/m^2) each year, (b) constant harvest rate that removed from 10% to 100% of the adult population each year, and (c) constant escapement policies that allowed from 0 clams/yd^2 to 2.0 clams/yd^2 (i.e., 0.00 clams/m^2 - 1.67 clams/m^2) to escape harvest. When adult densities were greater than the escapement, a harvest rate strategy with a range of harvest rates from 0%-100% was imposed on those adult clams that were not protected. Under the constant catch strategy, the total catch was calculated as

$$C_t = \max(0.00, \min(A_t, \text{Harvest Level})) . \qquad \text{(EQ 5.20)}$$

Equation 5.20 states that if there were no adults in the population, then there was no catch. If there were adults in the population, then the amount that were caught was either the prescribed allowance or all of the adults, whichever was less. For example, if there were 20 adults, but the harvest level was 30, then all 20 adults would be harvested. If, however, there were 30 adults and the harvest level was 20, then 20 adults would be caught.

Under the constant harvest rate strategy, the total catch was calculated as

$$C_t = \max(0.00, (A_t \cdot \text{Harvest Rate})) . \qquad \text{(EQ 5.21)}$$

Equation 5.21 states that if there are no adults in the population, then there is no catch. If there are adults in the population, then the amount that is taken as catch is the fraction prescribed by the harvest rate. For example, if the harvest rate is 10% and there are 20 adults, then 2 adults would be caught (i.e., $20 \cdot 10\% = 2$).

And under the constant escapement strategy, the total catch was calculated as

$$C_t = \max(0.00, (A_t - \text{Escapement}) \cdot \text{Harvest Rate})) . \qquad \text{(EQ 5.22)}$$

Equation 5.22 acted like equation 5.21, but under equation 5.22, there were two scenarios that would result in no catch. First, as with the other two equations (EQs. 5.20 and 5.21) used for calculating the catch, there is no catch if there are no adults. Second, if the escapement is higher than the number of adults, again there is no catch. The catch is positive only if there are more adults in the population than the escapement level. If there are more adults in the population than the escapement level, the catch is the fraction prescribed by the harvest rate. For example, if the harvest rate is 10% and there are 20 adults, but the escapement was 10, then 1 adult would be caught (i.e., $(20-10) \cdot 10\% = 1$).

The results were examined at 5, 10, and 50 years into the simulations to observe whether certain strategies had short-term success, but were not viable for the long-term health of the stock. A plot of Catch vs. Coefficient of Variation of the Catch was used to indicate which strategies yielded the largest catch with the least variability. Results were integrated over all survivals to determine which catch strategies provided the greatest catch, regardless of the underlying survival relationships. To integrate results across all survival possibilities, the metric of interest was evaluated at each pair of adult-juvenile survival probabilities. The results from all adult-juvenile survival probabilities were pooled to form a distribution of the metric, with equal weight given each result regardless of the survival. The final output was a distribution of the metric that was independent of the assumed survivals.

The overall amount of catch removed from the stock is but one indicator of the strength of a strategy. Other indicators that are important are indicators of risk. For this stock, the measures of risk that were examined were the probability that a given strategy would drive a stock to extinction and the probability that a given strategy would result in no catch in a given year. These measures of risk were calculated as

$$\text{Risk of Extinction} = \frac{\begin{pmatrix}\text{Number of simulations in which stock}\\ \text{density} \equiv 0 \text{ prior to 50 yr time horizon}\end{pmatrix}}{\text{Total Number of Simulations}} \qquad \text{(EQ 5.23)}$$

$$\text{Risk of No Catch} = \frac{\text{Number of years in which the estimated catch} \equiv 0}{\text{Total Number of Years Simulated}} \quad \text{(EQ 5.24)}$$

These two measures of risk are important to WDFW (Doug Simons, WDFW Shellfish Biologist at Montesano, WA, pers. comm.). All risks were evaluated for the entire range of juvenile and adult survival probabilities.

5.2.6 EFFECT OF CLIMATE SHIFTS ON HARVEST POLICIES

Aside from purely stochastic temperature effects based upon the historical data, two additional scenarios where established. Warming/cooling scenarios abound in the literature (Welsch, 1992; Schneider, 1994; Mitchell *et al.*, 1995; Pearce, 1995; Monastersky, 1996; to cite a few). Some of these changes are expected due to established regime shifts, others are anticipated results of anthropogenic effects (i.e., global climate change due to pollutants). In the face of uncertain changes in the climate and its effects on temperatures along the Washington coast, both scenarios were explored. It was hoped that these scenarios would provide guidance concerning the impacts of uncertain regime shifts along the Washington coast. For the cooling scenario, the intercept of the temperature equation was decreased by 0.5 Celsius. The amplitude, period and variance of the computed temperatures remained the same as the base model (EQ 5.19). For the warming scenario, the intercept of the temperature equation was increased by 0.5 Celsius. As with the global cooling scenario, the amplitude, period and variance of the computed temperatures remained the same as the base model (EQ 5.19).

5.2.7 RETROSPECTIVE COMPARISON OF HARVEST POLICIES

Recall that this study was initiated following the decline of the razor clam stocks in the 1980s. Contrary to the hypothesis that the declines in the 1980s were a result of NIX, the SSRSR model (Section 4.5.9) implied that the 1980s decline could be a phenomenon that was driven by the stock density and temperatures of that era. Similarly, the Mean Recruitment model indicated that the declines in the 1980s were independent of NIX. In an effort to increase stock densities following this decline, WDFW has established a policy to allow 25.4% of all clams greater than 3 inches (7.6 cm) to be harvested. For the retrospective analysis, a data series will be generated using the recruitment models (i.e., SSRSR and Mean Recruitment) and the observed temperatures from the 1980s. This data series will be subjected to harvest under the WDFW policy and under the policies suggested by the results of the prospective simulation model (Section 5.2.5). The resulting catch, population density and risk metrics discussed previously (Section 5.2.5) will be used as endpoints to determine the effect of the alternative harvest strategies. These results will be used to determine whether the current WDFW strategy of harvesting 25.4% of the adult population is liberal, conservative or close to optimal. These results will also be used to determine whether curtailing the harvest could be expected to increase future clam densities.

5.3 SIMULATION RESULTS

The results in the following section (i.e., Section 5.3) reflect simulations that began when the current time series of data ended (i.e., in the early 1990s). Projection simulations incorporated the estimated temperatures for the next fifty years based on the temperature model that was developed in section 5.2.4.

5.3.1 DETERMINISTIC BEHAVIOR-SSRSR MODEL

The simulation was run over a variety of adult and juvenile survivals to indicate the impact of the different survivals on the model outputs. The results of these runs indicated that (Figures 5.2 - 5.5) at the two northern beaches (i.e., Mocrocks and Copalis), sustained oscillations were unattainable without either some stochasticity or the inclusion of temperature in the model. The deterministic models at the two northern beaches (i.e., Mocrocks and Copalis) either decayed to extinction or stabilized to some positive density. At the two southern beaches (i.e., Twin Harbors and Long Beach), oscillations were achievable with high juvenile survival (S_j=0.96). At all four beaches, populations were

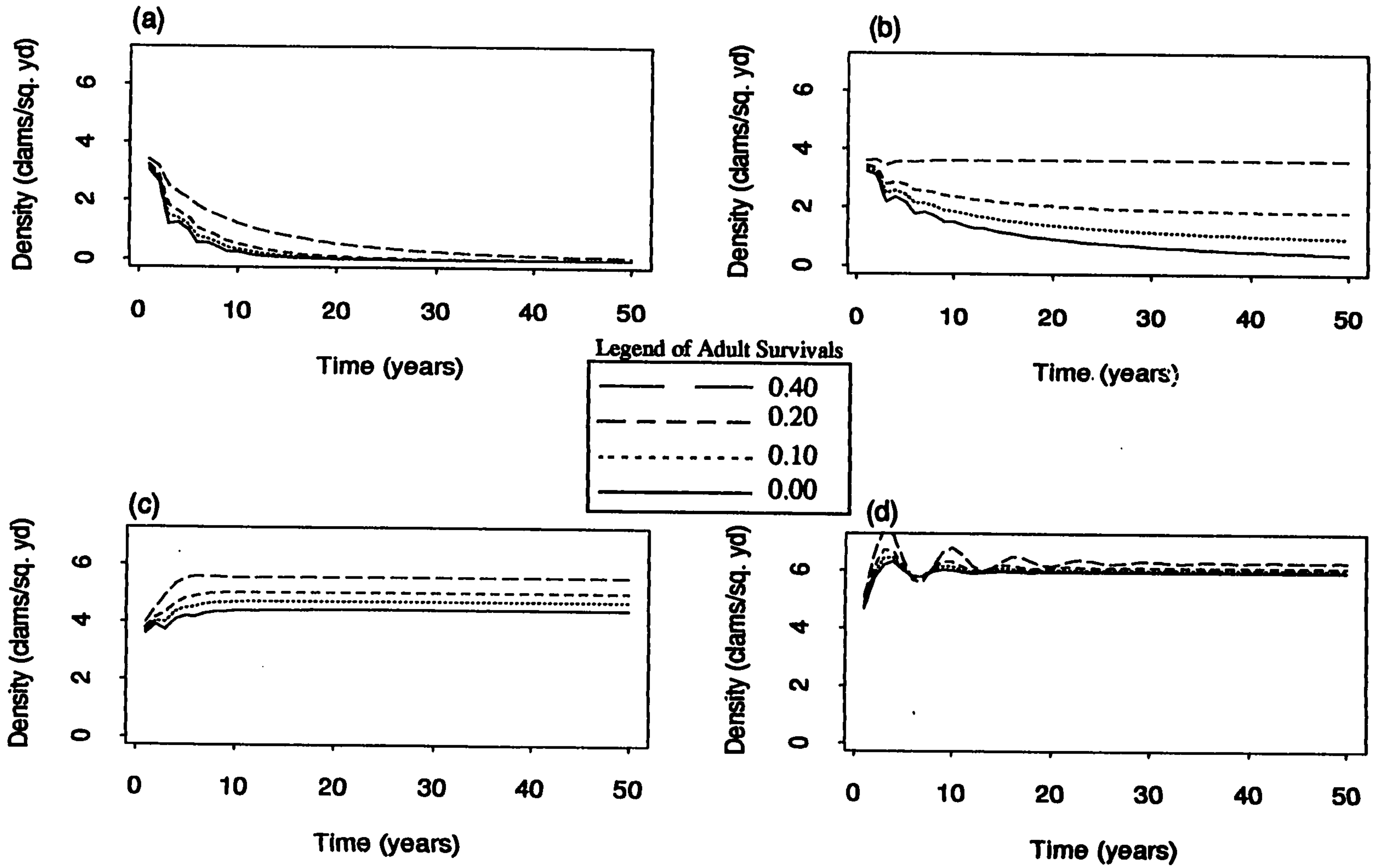


FIGURE 5.2 Time series of total (i.e., adult and juvenile) clam densities at Mocrocks under the deterministic SSRSR model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory under adult survivals of 0.40, 0.20, 0.10, and 0.00.

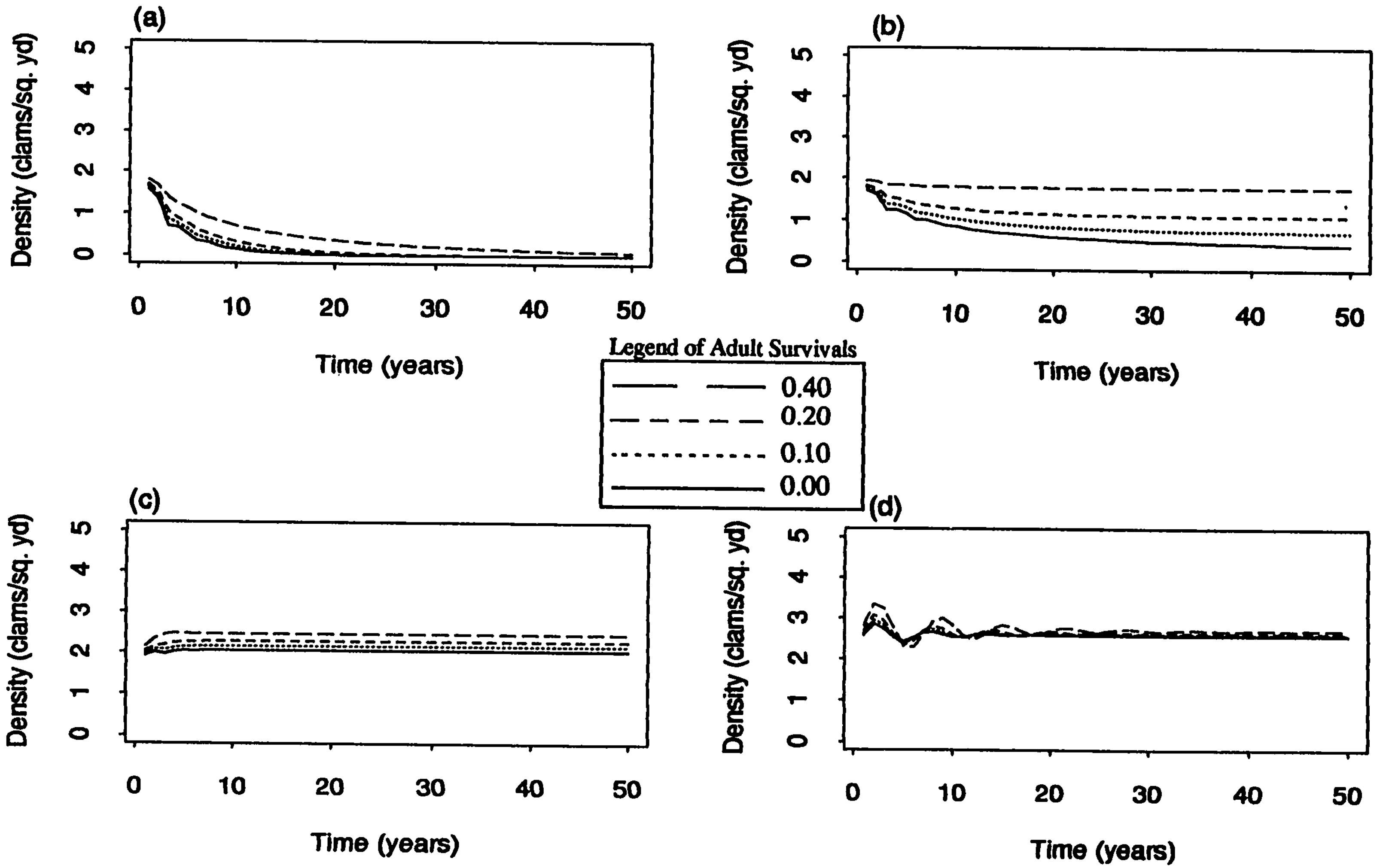


FIGURE 5.3 Time series of total (i.e., adult and juvenile) clam densities at Copalis under the deterministic SSRSR model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory under adult survivals of 0.40, 0.20, 0.10, and 0.00.

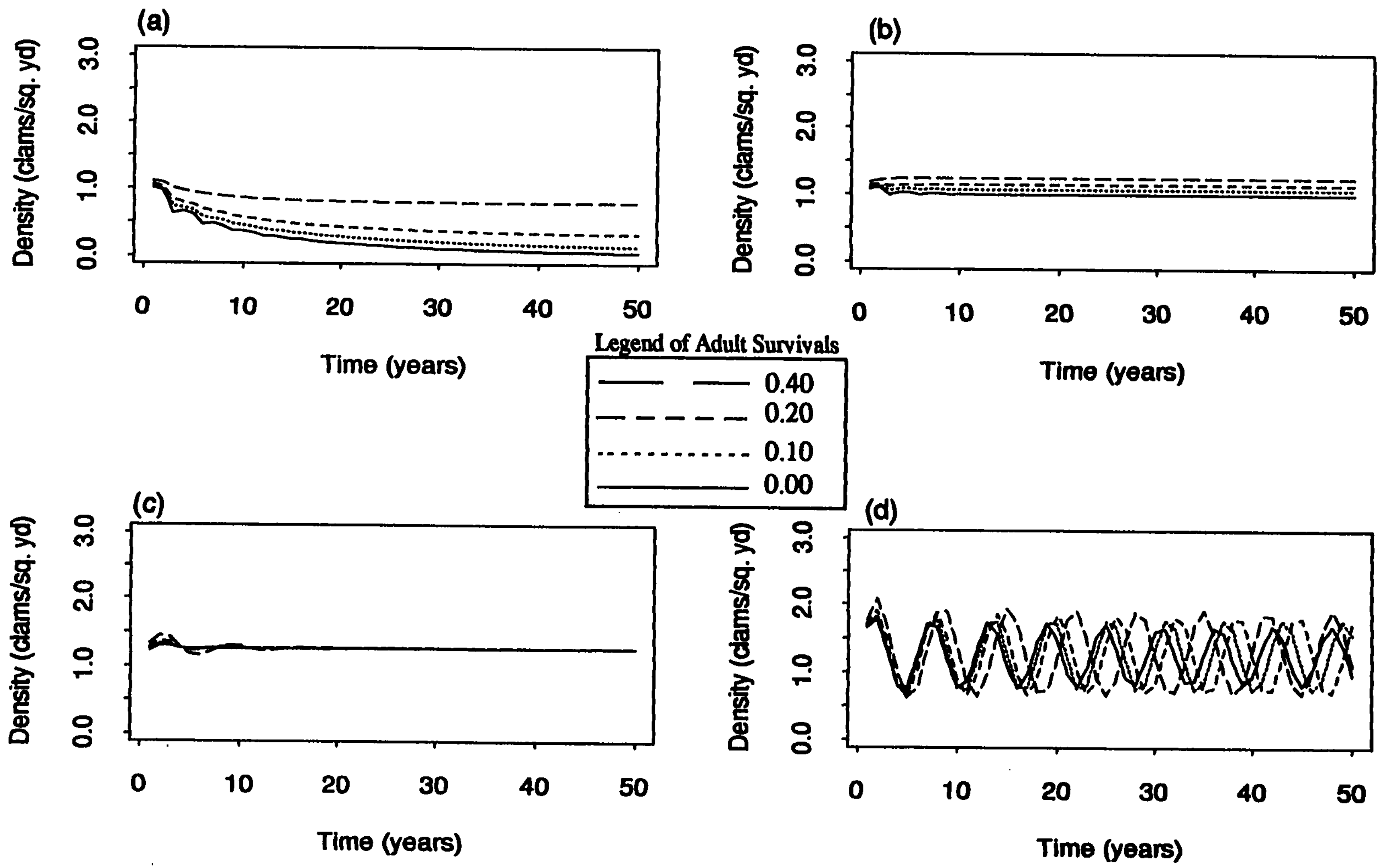


FIGURE 5.4 Time series of total (i.e., adult and juvenile) clam densities at Twin Harbors under the deterministic SSRSR model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory under adult survivals of 0.40, 0.20, 0.10, and 0.00.

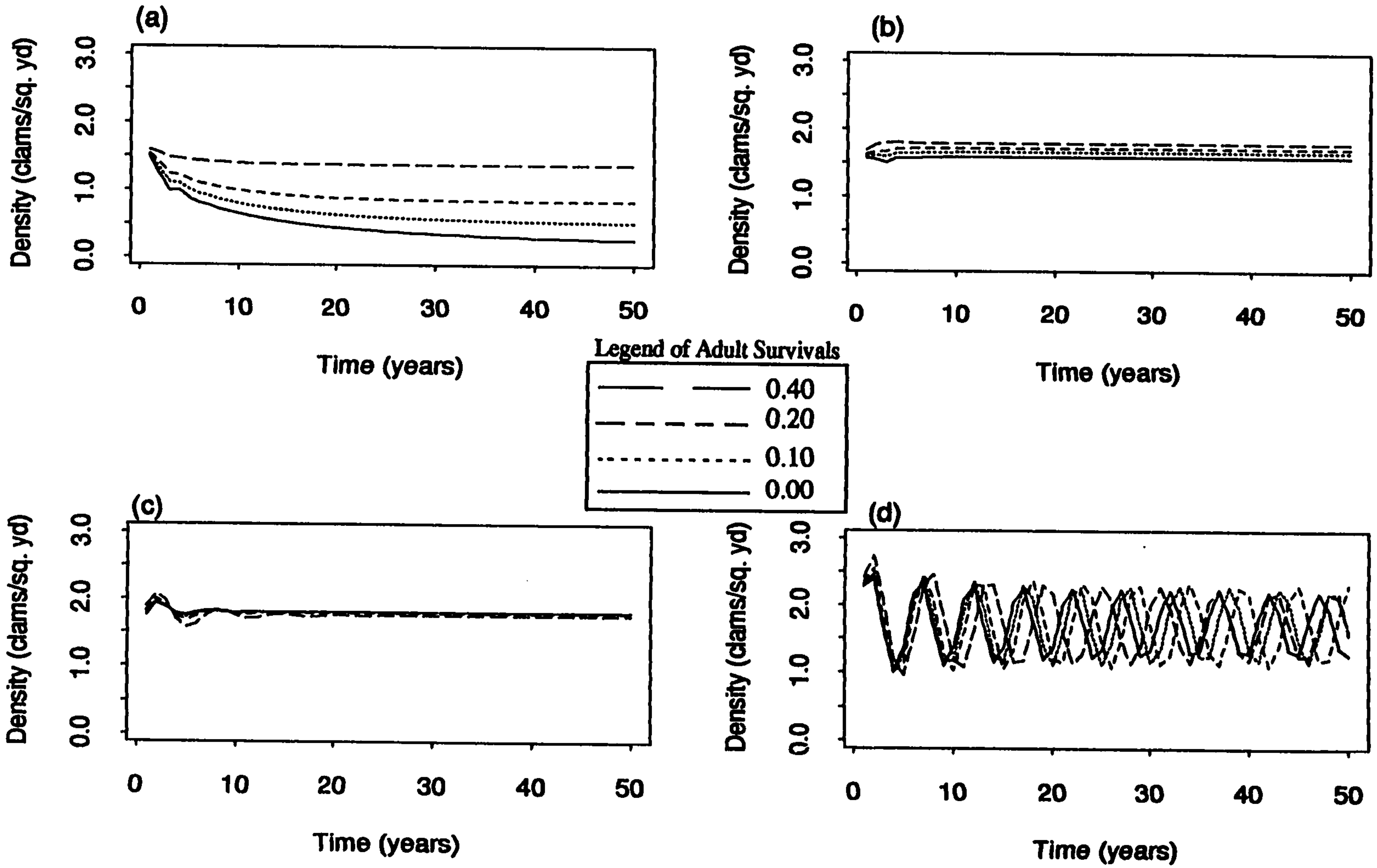


FIGURE 5.5 Time series of total (i.e., adult and juvenile) clam densities at Long Beach under the deterministic SSRSR model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory under adult survivals of 0.40, 0.20, 0.10, and 0.00.

sustainable as long as juvenile survival was greater than 0.30, regardless of adult survival. At the three southern beaches (Copalis, Twin Harbors and Long Beach), the model results indicate that the model is insensitive to adult survivals. Similarly, there is a wide range of juvenile survivals that exhibit similar behavior. Comparing the stabilized populations from the model to the observed populations, it appears that the most likely range of juvenile survivals (where S_J are juvenile survival probabilities) are ($0.20 \le S_J \le 0.40$) for Mocrocks, ($0.20 \le S_J \le 0.80$) for Copalis, ($0.20 \le S_J \le 1.00$) for Twin Harbors, and ($0.10 \le S_J \le 1.00$) for Long Beach. The adult survivals were $0.01 \le S_A \le 0.40$ (where S_A are adult survival probabilities) regardless of the beach.

5.3.2 STOCHASTIC BEHAVIOR (using SSRSR MODEL for recruitment)

The simulation model was run without harvest to provide a baseline scenario, to which the effects of the various harvest strategies could be compared. After stochastic recruitment and temperature were added to the deterministic model, it was discovered that the SSRSR model was unable to simulate a 50 year time span at Copalis without causing the population to remain at very low levels (total density < 1.5 clams/yd^2 (i.e., 1.25 clams/m^2)) and/or go extinct regardless of the adult or juvenile survival. It was further discovered that the formulation of the SSRSR model at Copalis was able to attain greater densities only with regular inputs of strong year-classes that would then decay at a rate determined by the adult survival probability. This result may imply an exterior source of recruits to Copalis. Alternately, this result may imply that the current parameterization of the SSRSR model provides a poor explanation of the data from Copalis. The other three beaches were sustainable over 50 years the majority of the simulations. Comparison of the observed data with the predicted data indicated that the SSRSR model tended to overestimate low densities and underestimate large densities. This was not totally unexpected, as this behavior was noted in Chapter 4. In the absence of harvest, under the SSRSR model at no time did any beach go extinct during the 50 year time horizon.

However, the excessively low predictions and high extinction probabilities for Copalis may make it pointless to consider subsequent analyses on harvest strategies at Copalis. Future work should be directed at developing a better prediction model for Copalis.

5.3.3 STOCHASTIC BEHAVIOR WITH CATCH (using SSRSR MODEL for recruitment)

The results at all beaches, regardless of adult or juvenile survival, and despite the time horizon, indicated that harvest strategies that took all post-spawning adults provided the highest catch with the lowest coefficient of variation. However, at such high harvest pressure, the level of risk (i.e., either of extinction or of foregoing harvest) was often quite high.

The results indicated that the constant catch strategy provided the greatest catch with the lowest CV for all beaches the majority of the time. However, the constant catch strategies were often more risky than constant harvest rate strategies or escapement strategies. The results also indicated that the best strategy (i.e., greatest catch with the lowest CV) was not particularly sensitive to adult or juvenile survival. At any particular level of juvenile survival (where $(0.20 \leq S_J \leq 0.80)$), the amount of catch and the harvest strategy that provided the most catch with the lowest CV did not change dramatically. As juvenile survival increased, the amount of catch increased, but the harvest strategies that provided the most catch with the lowest CV typically remained the same. This can be illustrated using the results of 50 years of simulations at Mocrocks (Figure 5.6). Each point represents the results of 1000 simulations. In Figure 5.6, circles are used to illustrate results associated with constant catch strategies, triangles indicate results associated with constant harvest rate strategies, and crosses are used to indicate results associated constant escapement policies. For the majority of the juvenile-adult survival pairs, the highest constant catch strategies (O) provide the greatest catch with the lowest CV. As the juvenile survival increases to 0.60 and 0.80, the constant catch strategies still provide very

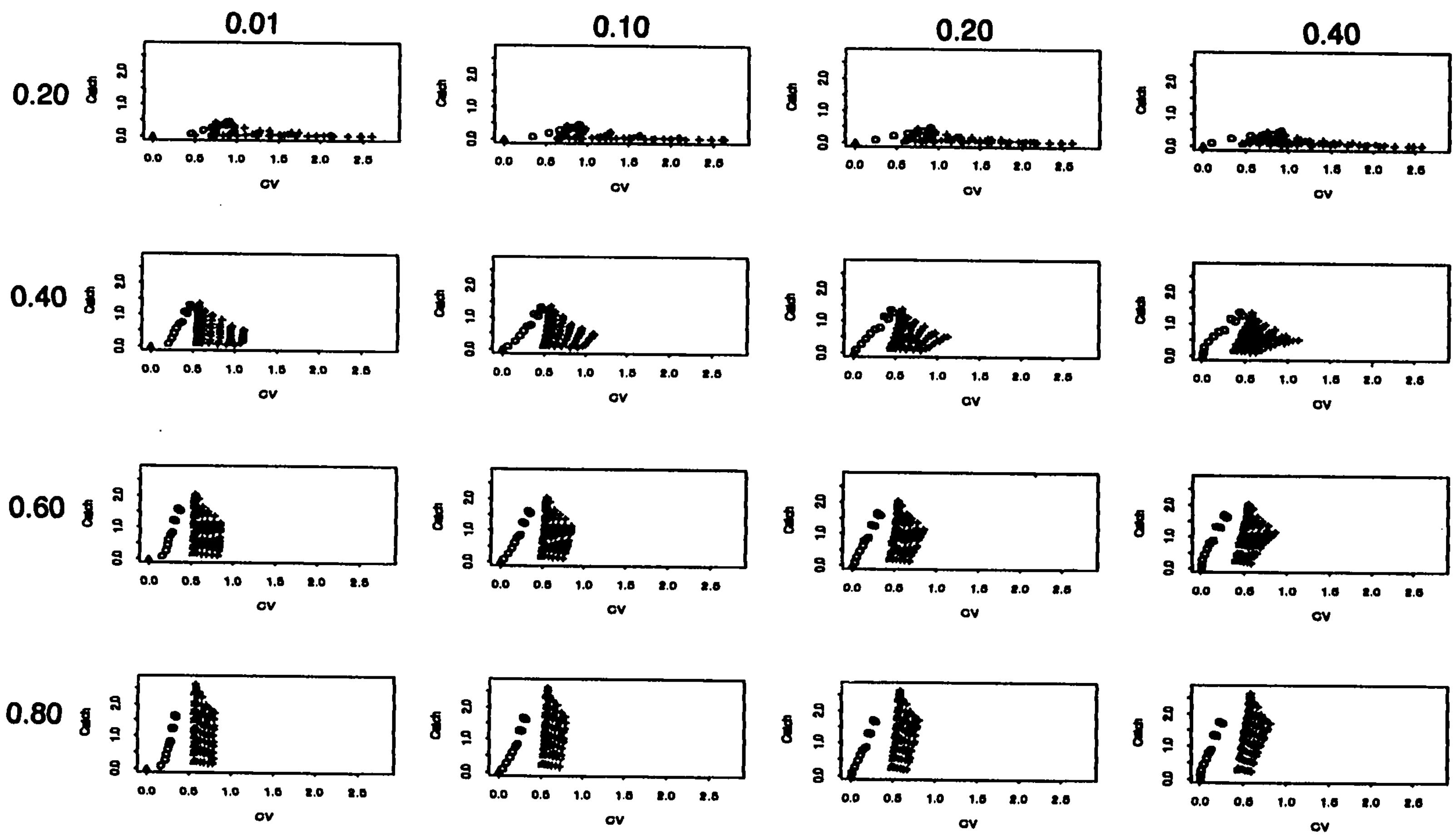


FIGURE 5.6 Catch (in clams/yd^2) vs. CV plots for Mocrocks after 50 years of simulated data. Adult survival increases from left to right (i.e., 0.01, 0.10, 0.20, 0.40); juvenile survival increases from top to bottom (i.e., 0.20, 0.40, 0.60, 0.80). Circles (o) indicate constant catch policies, triangles (Δ) represent constant harvest rate policies and crosses (+) indicate escapement policies.

high catches with low CV. However, the maximal catches are now being taken using constant harvest rate (▲) and escapement (+) strategies. The constant harvest rate and escapement strategies suffer from having higher associated CV's than the constant catch strategies. All of the escapement policies have higher CV's than the constant catch strategies or the constant harvest rate strategies. Results at the other beaches indicated a similar choice of optimal strategy, only the level of catch and the value for the estimated CV differed.

When juvenile and adult survivals were integrated out (Section 5.2.5), the catch strategies that provided the greatest catch with the lowest coefficient of variation tended to be those strategies that removed a large majority of the adults from the population (Figure 5.7 - 5.10). Figures 5.7-5.10 were generated by selecting the twenty strategies that provided the largest catch. From the shape of plots in Figure 5.6, it is apparent that selecting the strategies that provide the largest catches regardless of the CV will ultimately select the largest catches with the lowest CV's. All escapement policies tended to have lower catch and higher CV (Figure 5.6). This is expected, as these policies force there to be no catch in years with low adult densities. Thus, from a catch standpoint, at no time did an escapement policy behave optimally. These results did not change whether the time horizon was 5, 10 or 50 years. For all policies, the CV was quite high (Figure 5.6). This is a reflection of the high variability in the recruitment. Thus, regardless of the harvest policy implemented, catch cannot be expected to be very stable.

As with the deterministic model, the stochastic models indicated that the amount of catch and the harvest strategy that yielded the highest yield were insensitive to the adult survival. The catch was somewhat more sensitive to the juvenile survival, but above a juvenile survival of 0.20, the amount of catch and the harvest strategy that generated the highest yield were very insensitive. The sensitivity of the model to the juvenile survival indicates that this aspect should be studied in the field more, but the insensitivity of the

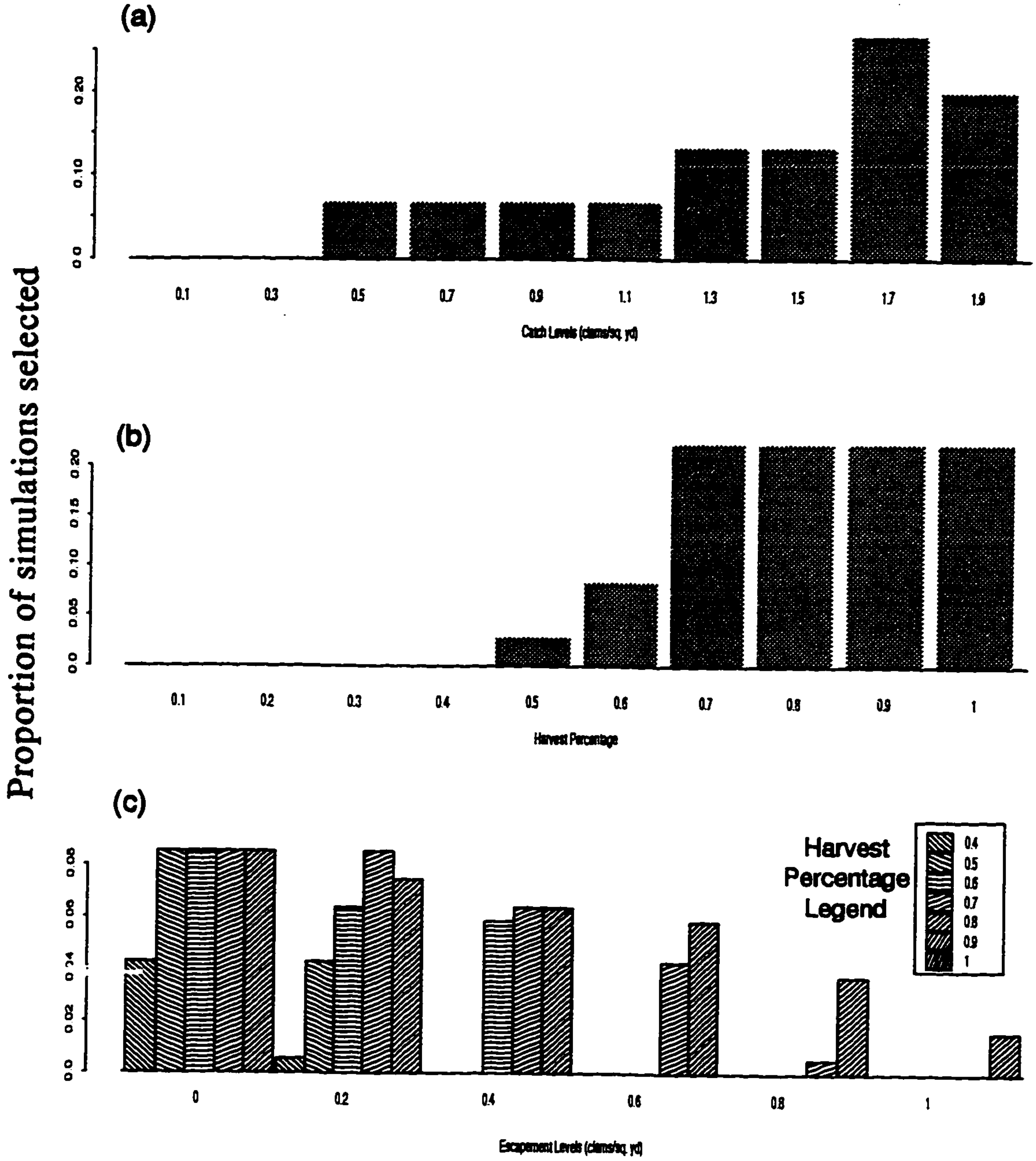


FIGURE 5.7 Strategies that provided the largest catch at Mocrocks. Results are integrated across all juvenile and adult survivals. The x-axis of each plot indicates the level of the harvest strategy (i.e., (a) Constant Catch, (b) Constant Harvest Rate, and (c) Escapement). The y-axis of each plot indicates the proportion of times a particular strategy was selected as one of the top strategies. The highest harvest pressures resulted in the greatest catch.

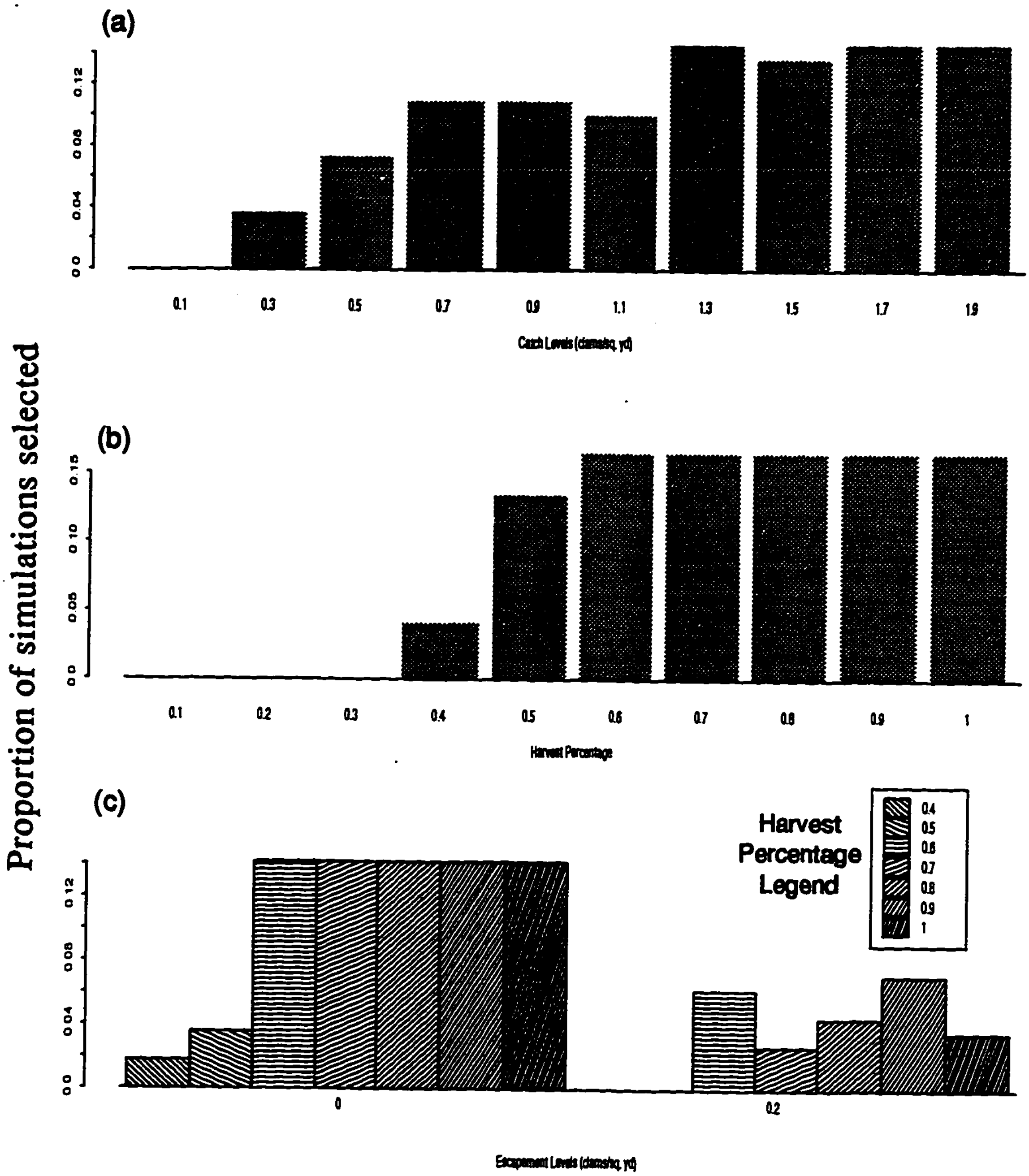


FIGURE 5.8 Strategies that provided the largest catch at Copalis. Results are integrated across all juvenile and adult survivals. The x-axis of each plot indicates the level of the harvest strategy (i.e., (a) Constant Catch, (b) Constant Harvest Rate, and (c) Escapement). The y-axis of each plot indicates the proportion of times a particular strategy was selected as one of the top strategies. The highest harvest pressures resulted in the greatest catch.

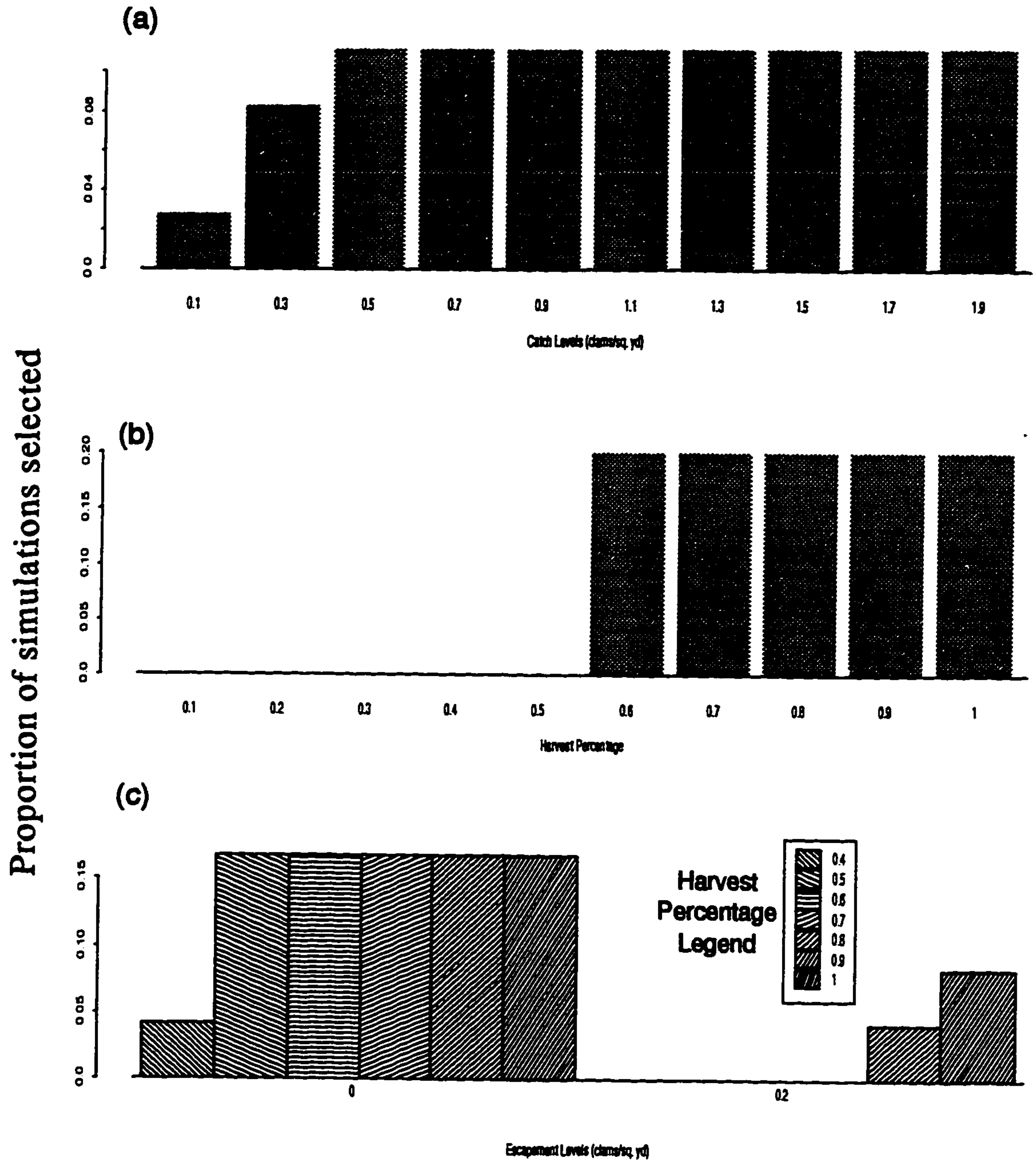


FIGURE 5.9 Strategies that provided the largest catch at Twin Harbors. Results are integrated across all juvenile and adult survivals. The x-axis of each plot indicates the level of the harvest strategy (i.e., (a) Constant Catch, (b) Constant Harvest Rate, and (c) Escapement). The y-axis of each plot indicates the proportion of times a particular strategy was selected as one of the top strategies. The highest harvest pressures resulted in the greatest catch.

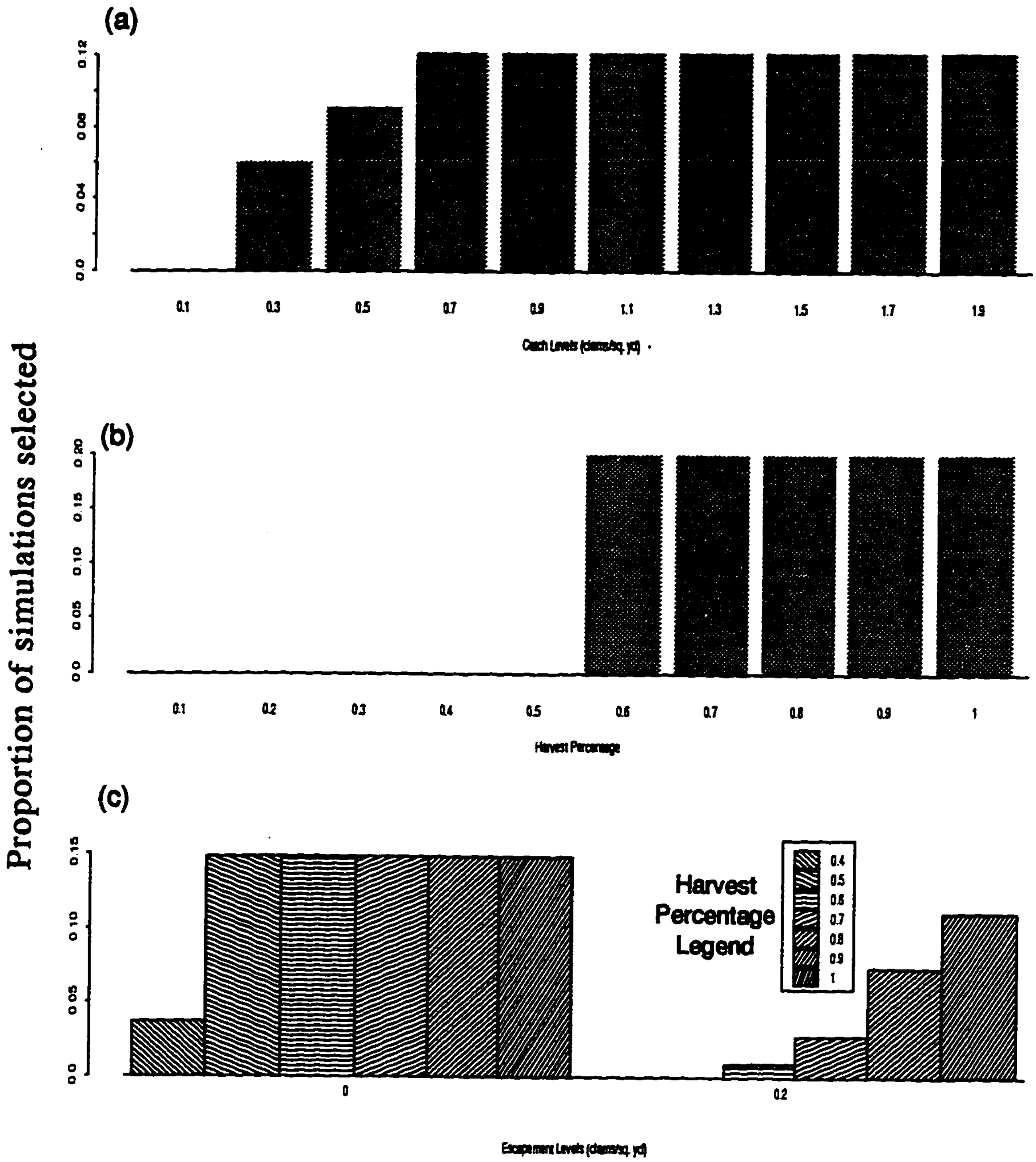


FIGURE 5.10 Strategies that provided the largest catch at Long Beach. Results are integrated across all juvenile and adult survivals. The x-axis of each plot indicates the level of the harvest strategy (i.e., (a) Constant Catch, (b) Constant Harvest Rate, and (c) Escapement). The y-axis of each plot indicates the proportion of times a particular strategy was selected as one of the top strategies. The highest harvest pressures resulted in the greatest catch.

model to the juvenile survival over a large range of survivals indicates that if juvenile survival is fairly high (i.e., >0.20), high harvest rates can be sustained.

As catch is not the only metric of interest, the measures of risk were also evaluated (Figures 5.11 and 5.12). The risk metrics were computed for each juvenile and adult survival probability. In addition to the two risk metrics, the distribution of the total population density (Figure 5.13) and the distribution of the catch density (Figure 5.14) were examined under each catch scenario.

At Mocrocks, using the constant harvest rate and constant harvest level strategies, the simulations indicated that as the harvest increased, the population would be forced into lower levels. At a 100% harvest rate of post-spawning adults, ~18% of the time the stock would be between 0-1 clams/yd^2 (i.e., 0-0.84clams/m^2). With no harvest, only ~4% of the time the stock would be between 0-1 clams/yd^2 (i.e., 0-0.84clams/m^2). Even low levels of the constant catch strategy quickly forced the population into low total densities. This is illustrated in Figure 5.13 were there is a definite left-skew to the distribution. This skew gets more pronounced with increasing harvest.

However, having a low "standing stock" is not necessarily bad. When the risk of extinction under the model was examined (Figure 5.11), the simulations indicated that there was a definite bifurcation in possible results with intense pressure. If the clams have low juvenile survival (i.e., $S_j \leq 0.20$), then the constant harvest rate strategies might be best employed to avoid possible extinction; the constant harvest level strategy quickly caused high extinction probabilities. Although the variability of harvest is much higher under a harvest rate strategy, there is no risk of driving the stock extinct until 100% of the adults are taken. At the same time, below an 80% harvest rate, there is low probability ($P \leq 0.07$) of having to forego harvest.

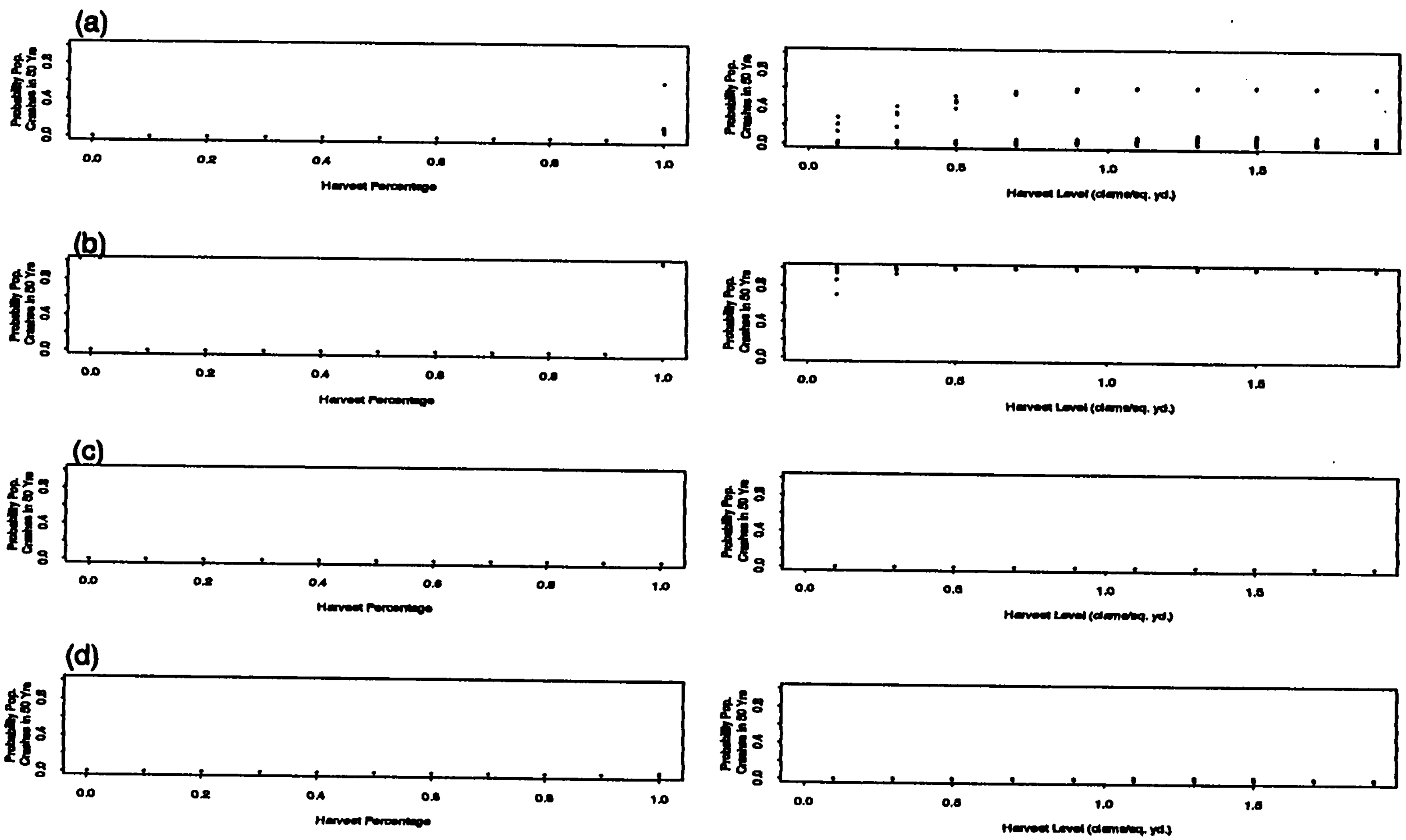


FIGURE 5.11 Probability of extinction under the SSRSR model. Within each row, the left column summarizes results under constant harvest rate strategies; the right column summarizes results under constant catch strategies. The results from each beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach) are arranged by row. Each dot on the graph represents a different juvenile/ adult survival pair.

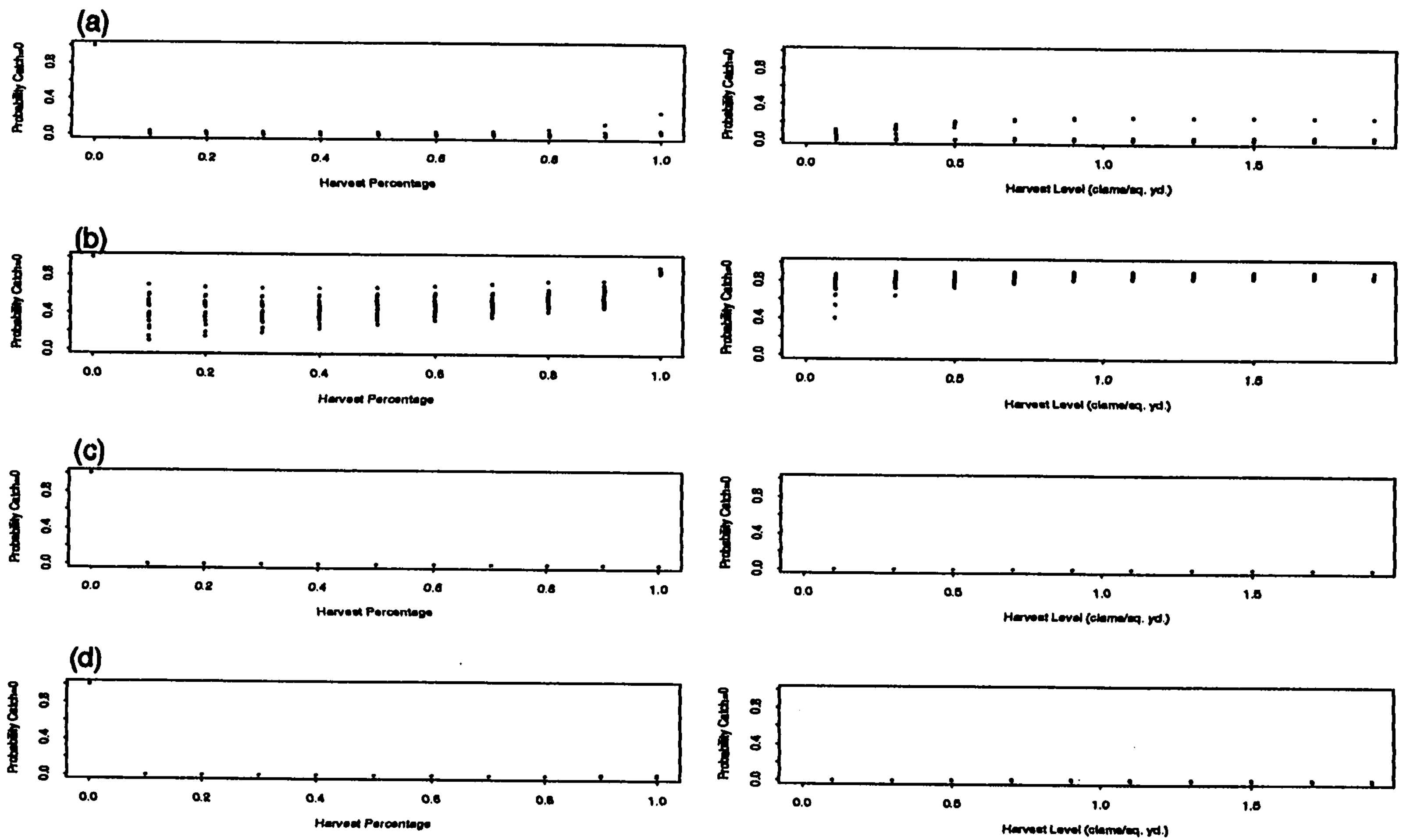


FIGURE 5.12 Probability that annual catch will be interrupted under the SSRSR model. Within each row, the left column summarizes results under constant harvest rate strategies; the right columns summarizes results under constant catch strategies. The results from each beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach) are arranged by row. Each dot on the graph represents a different juvenile/adult survival pair.

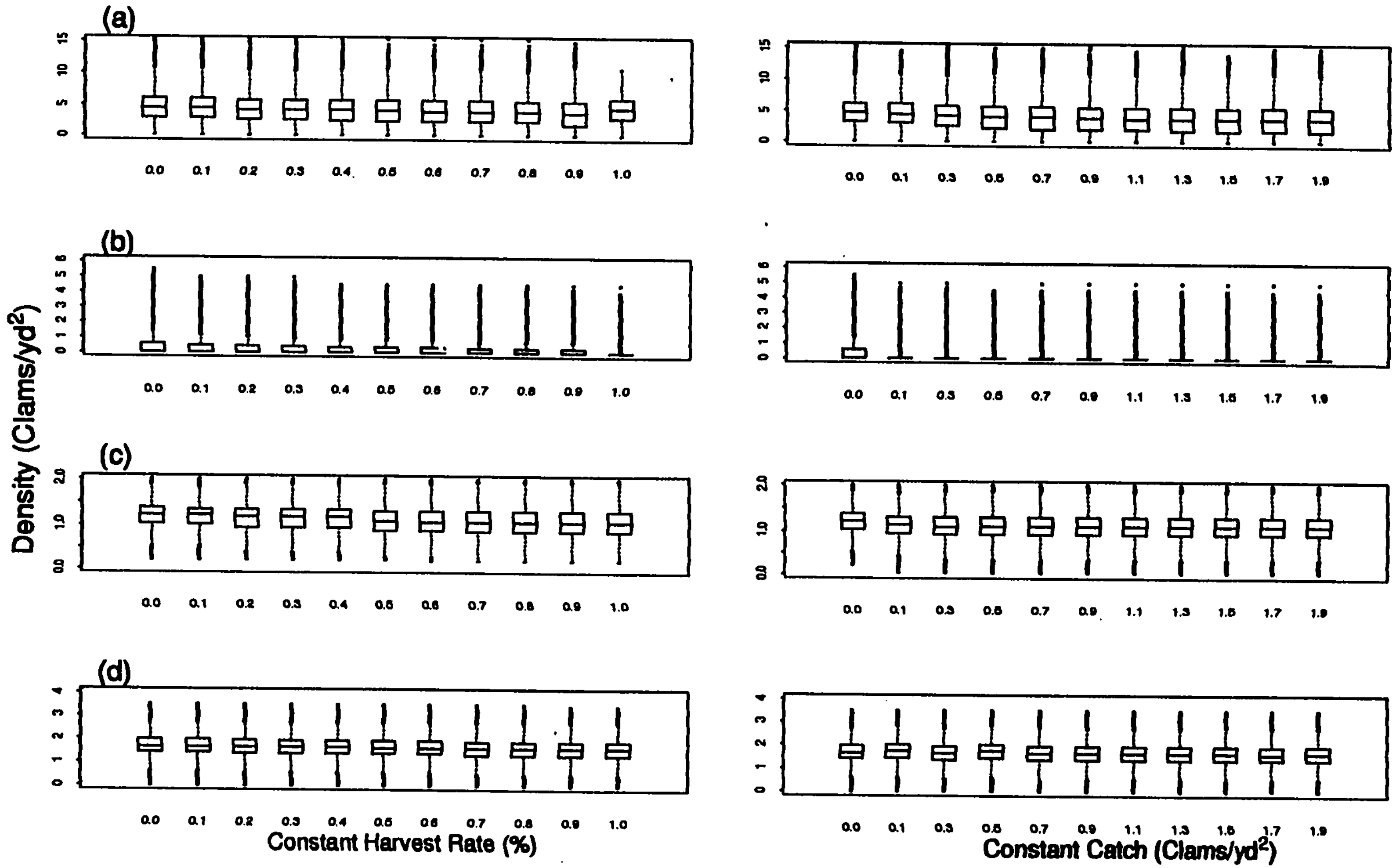


FIGURE 5.13 Distributions of total densities from 50 years of simulations as a function of either constant harvest rate or constant catch strategies at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. In each plot, the black bar in the box indicates the median, the box encloses the quartiles (i.e., 25% to 75%), the whiskers enclose the middle 90% and points indicate extreme values.

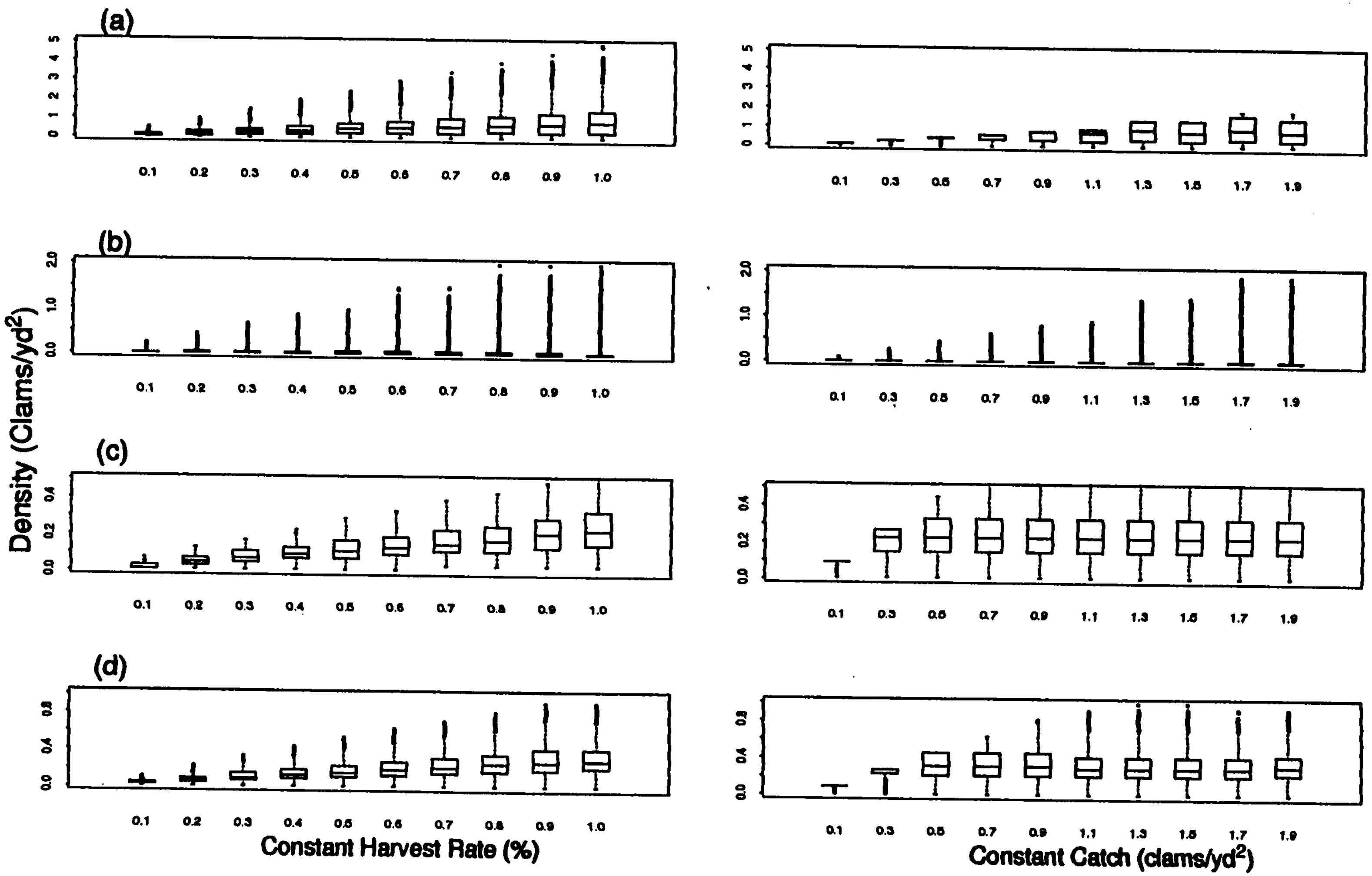


FIGURE 5.14 Distributions of catch densities from 50 years of simulations as a function of either constant harvest rate or constant catch strategies at (a) *Mocrocks*, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. In each plot, the black bar in the box indicates the *median*, the box encloses the quartiles (i.e., 25% to 75%), the whiskers enclose the middle 90% and points indicate extreme values.

If a constant catch policy is initiated, and there is very low adult survival (i.e., $S_a \leq 0.01$) and low juvenile survival (i.e., $S_j \leq 0.20$), there is a high risk (~60%) of collapse of the stock. This is an artifact of the fact that the SSRSR model does not persist at Mocrocks under low juvenile and low adult survival (Section 5.3.1; Figure 5.2). If instead, adult and juvenile survival are high, constant harvest strategies below 1.0 clam/ yd^2 (i.e., 0.84 clams/m^2) have a low risk of causing a population extinction (~10% compared to 0% without harvest). Above a harvest rate of 1.3 clams/yd^2 (i.e., 1.09 clams/ m^2), the risk of population extinction remains constant at around 10%. This indicates that only rarely will the catch be much higher than 1.3 clams/yd^2 (i.e., 1.09 clams/m^2), and corresponds to a 100% harvest rate in most years.

It is apparent (Figure 5.14) that the constant harvest rate strategy is foregoing quite a lot of catch in comparison to the constant harvest level strategy. In doing so, the median total density (Figure 5.13) is not greatly affected, but more of the distribution is shifted towards zero. This again indicates the importance of allowing influxes of the larger year classes that can sustain the population. Without these occasional large recruitment classes, the model predicts that the population at Mocrocks would go extinct under intensive harvest pressures.

At both Twin Harbors and Long Beach, the results of the simulations indicated that these beaches could be exploited as heavily as desired, with almost no risk to stock. This result indicates a very strong density-dependent relationship, such that at low levels of adult stock density, subsequent recruitment classes will be sufficient to replenish the beach. Increased fishing pressure does tend to skew the distribution of the populations at Twin Harbors and Long Beach to the left (towards zero; Figure 5.13), but the populations never goes extinct within the simulated 50 year time horizon (Figure 5.11).

These results indicate that the stocks on Mocrocks, Twin Harbors and Long Beach are best exploited using a constant harvest rate policy, like that currently implemented by

WDFW. However, unlike the 25.4% rate imposed by WDFW, the simulation model results indicate that harvest rates in the range of 80% can be sustained, with increased catch and no increased risk of extinction.

As mentioned earlier (Section 5.3.2), the SSRSR model did not behave well at Copalis. Even in the absence of harvest, in the majority of the simulations for Copalis under the SSRSR model, the total clam density decayed to <1.5 clams/yd^2 (i.e., 1.25 clams/m^2) and often went extinct. Therefore, there are no useful results associated with the SSRSR model for Copalis.

5.3.4 STOCHASTIC BEHAVIOR (using Mean Recruitment model for recruitment)

The results for the simulations that used the Mean Recruitment model were compared to the observed densities. For a wide range of survivals, the results were very similar. Overall, the stochastic behavior of this model appeared to mimic the time series that had been observed (Figures 5.15 - 5.18). The simulations at Mocrocks indicated occasional peaks, but few troughs. Depending upon the juvenile survival, strong year classes appeared between every 20 to 30 years. The simulations at Copalis indicated more peaks (i.e., more strong year classes) than were apparent at Mocrocks. As at Mocrocks, the simulations at Copalis indicated that very strong year classes appeared about every 20 years. The simulations at Twin Harbors indicated few peaks and troughs. Finally, it is evident from both the model equation (Equation 5.14) and the graphic (Figure 5.18) that the recruitment at Long Beach tends to track the temperature closely. Thus, the simulations follow the same sinusoidal oscillation that the temperature series follows. The simulations at Long Beach predict higher than average recruitment during one region during the 50-year simulation. As with the SSRSR model, there was almost no chance that the population at any of the four beaches would crash in the absence of catch under the Mean Recruitment model. This result was consistent across all four beaches at all levels of juvenile and adult survival.

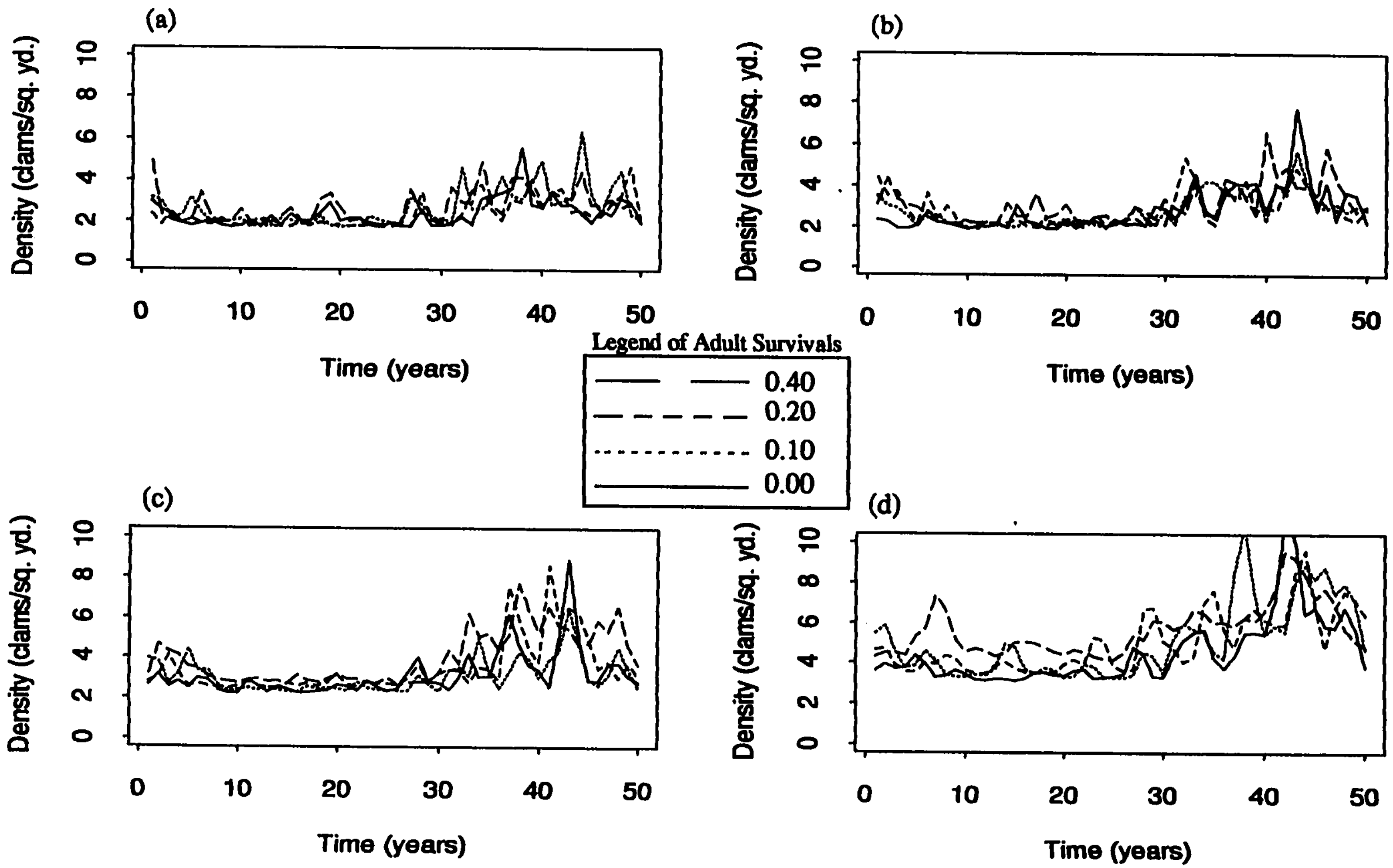


FIGURE 5.15 Stochastic behavior of the time series of adult and juvenile clam densities at Mocrocks under the Mean Recruitment model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory for densities of adult and juvenile clams for adult survivals of 0.40, 0.20, 0.10, and 0.00 (see legend).

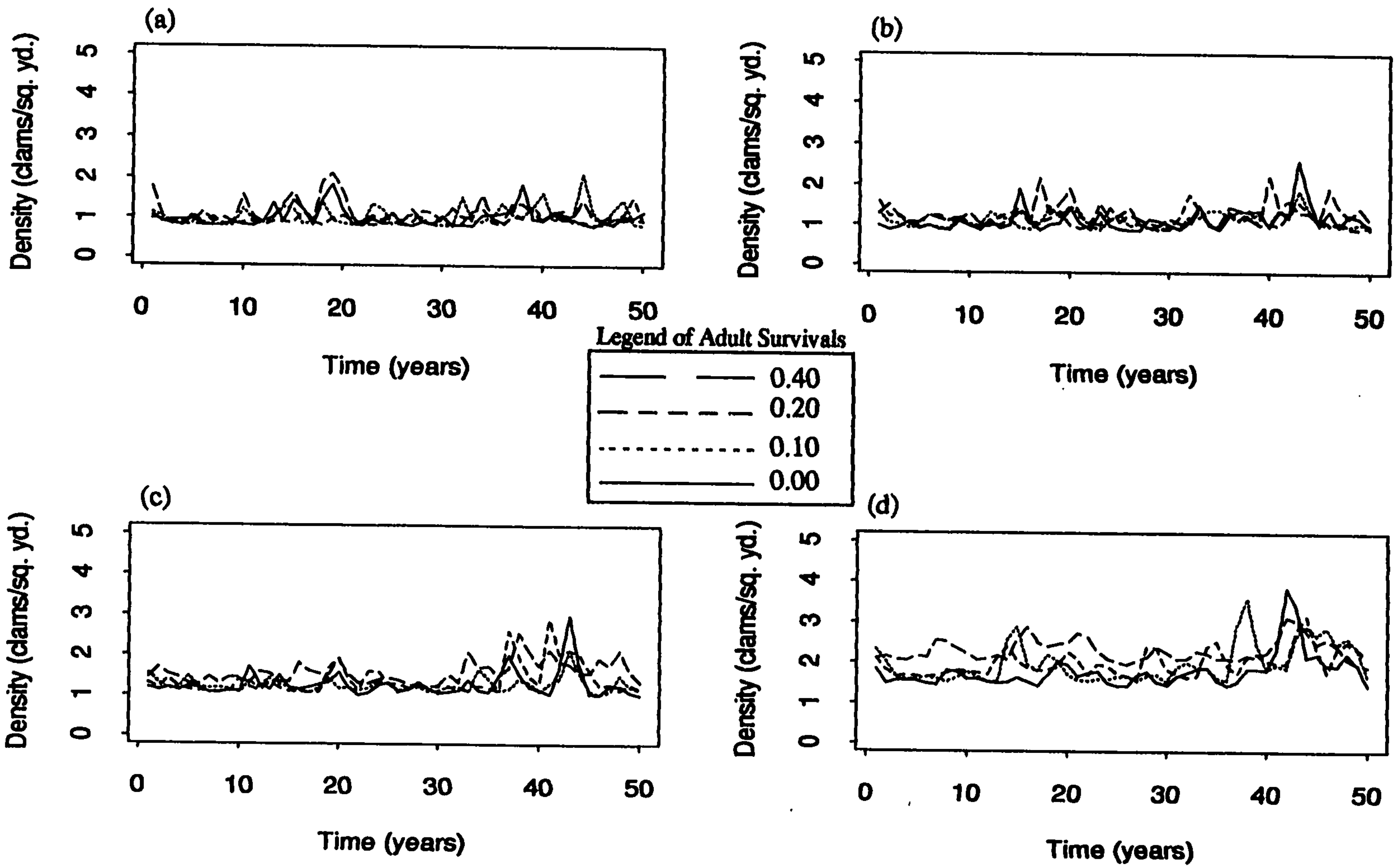


FIGURE 5.16 Stochastic behavior of the time series of adult and juvenile clam densities at Copalis under the Mean Recruitment model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory for densities of adult and juvenile clams for adult survivals of 0.40, 0.20, 0.10, and 0.00 (see legend).

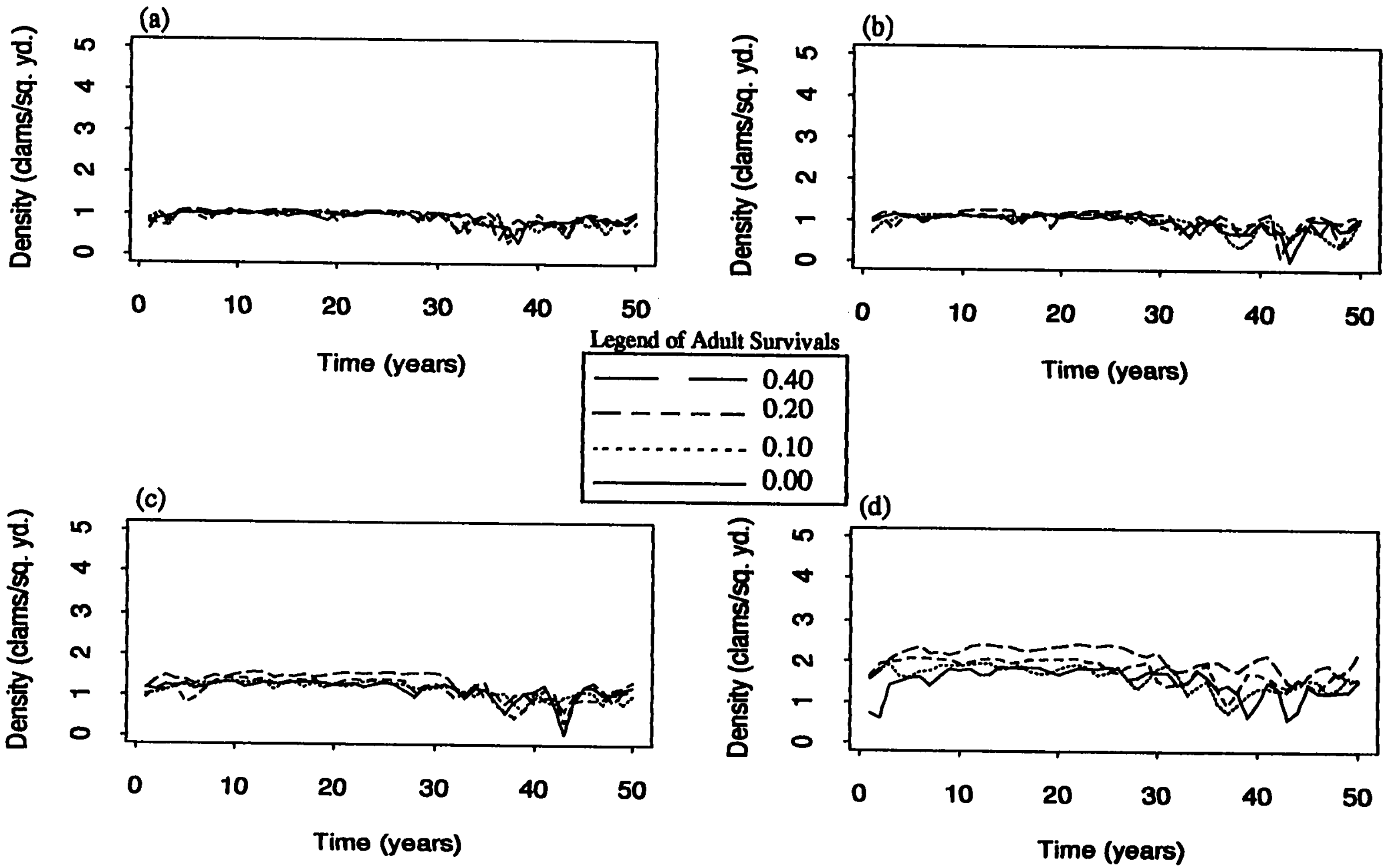


FIGURE 5.17 Stochastic behavior of the time series of adult and juvenile clam densities at Twin Harbors under the Mean Recruitment model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory for densities of adult and juvenile clams for adult survivals of 0.40, 0.20, 0.10, and 0.00 (see legend).

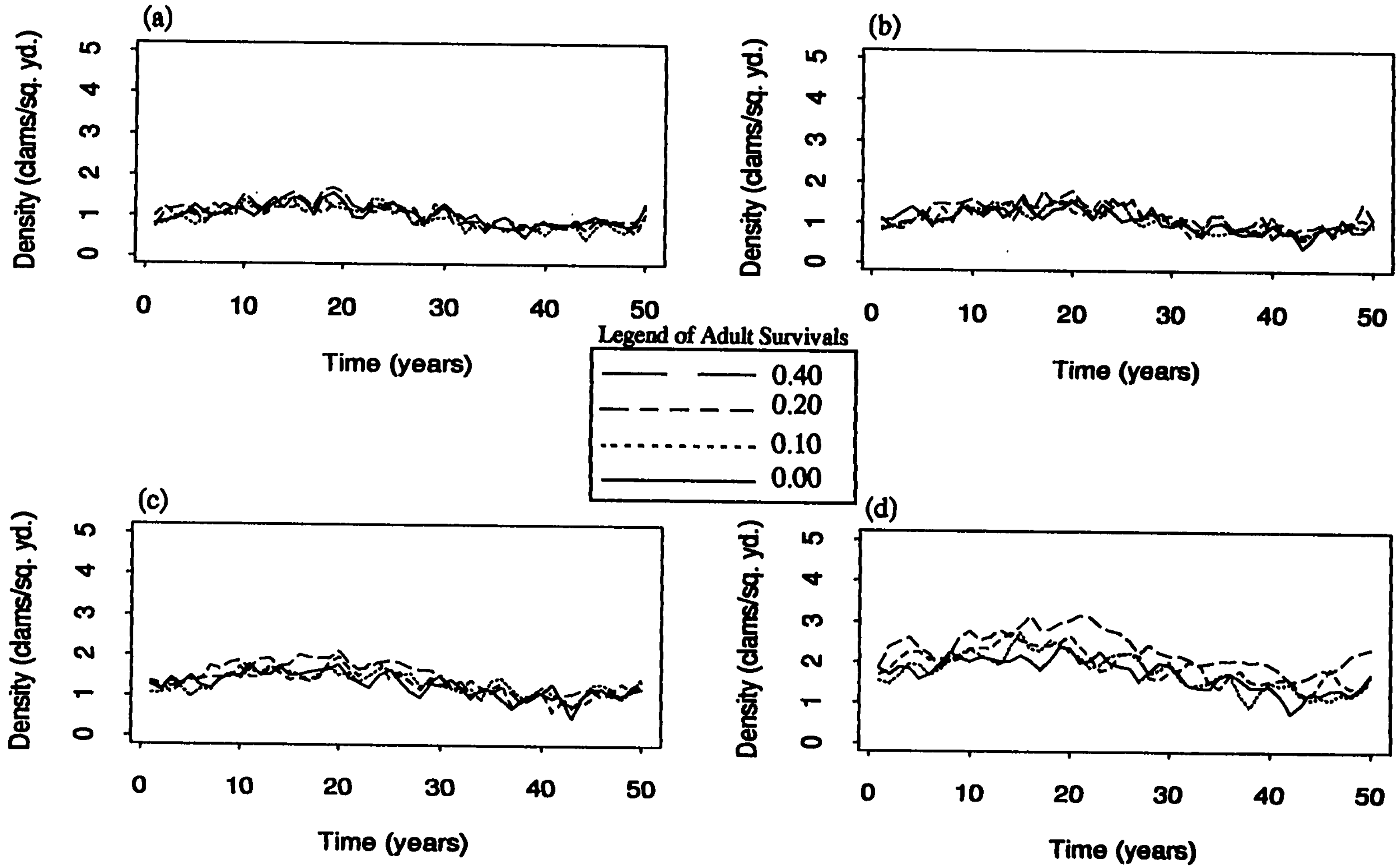


FIGURE 5.18 Stochastic behavior of the time series of adult and juvenile clam densities at Long Beach under the Mean Recruitment model for four juvenile survivals (i.e., (a) 0.10, (b) 0.20, (c) 0.40, and (d) 0.96). Within each graphic, the four lines represent the trajectory for densities of adult and juvenile clams for adult survivals of 0.40, 0.20, 0.10, and 0.00 (see legend).

5.3.5 STOCHASTIC BEHAVIOR WITH CATCH (using Mean Recruitment model for recruitment)

The simulation results using the Mean Recruitment model indicated that the constant catch strategy provided the highest catch with the lowest CV for all beaches the majority of the time. However, constant catch strategies were often more likely to cause extinction than were constant harvest rate and escapement policies. The results also indicated that the strategies that yielded the greatest catch with lowest CV were not particularly sensitive to adult or juvenile survival. Within a particular level of juvenile survival, the amount of catch and the strategy which worked the best remained mostly constant. As juvenile survival increased, the amount of harvest increased, but the harvest strategy that provided the highest catch with the lowest CV typically remained the constant catch strategy.

When the results were integrated over all juvenile and adult survivals, the catch strategies that provided the highest catch with the lowest coefficient of variation tended to be those strategies that removed a large majority of the adults from the population. These results did not change whether the time horizon was 5, 10 or 50 years. These results are consistent with the results under the simulations that used the SSRSR model of recruitment.

The measures of risk (i.e., probability of extinction and probability of foregoing an annual season) were also evaluated at all beaches for each juvenile and adult survival probability (Figures 5.19 and 5.20). In addition to the two risk metrics, the distribution of the total population density (Figure 5.21) and the distribution of the catch density (Figure 5.22) were examined under each catch scenario. These metrics are the identical metrics that were examined when the SSRSR model was used.

Under the Mean Recruitment model, Mocrocks appeared to be somewhat more vulnerable to exploitation than was apparent under the SSRSR model. At even relatively low levels of harvest under a constant catch policy, the population went extinct >10% of

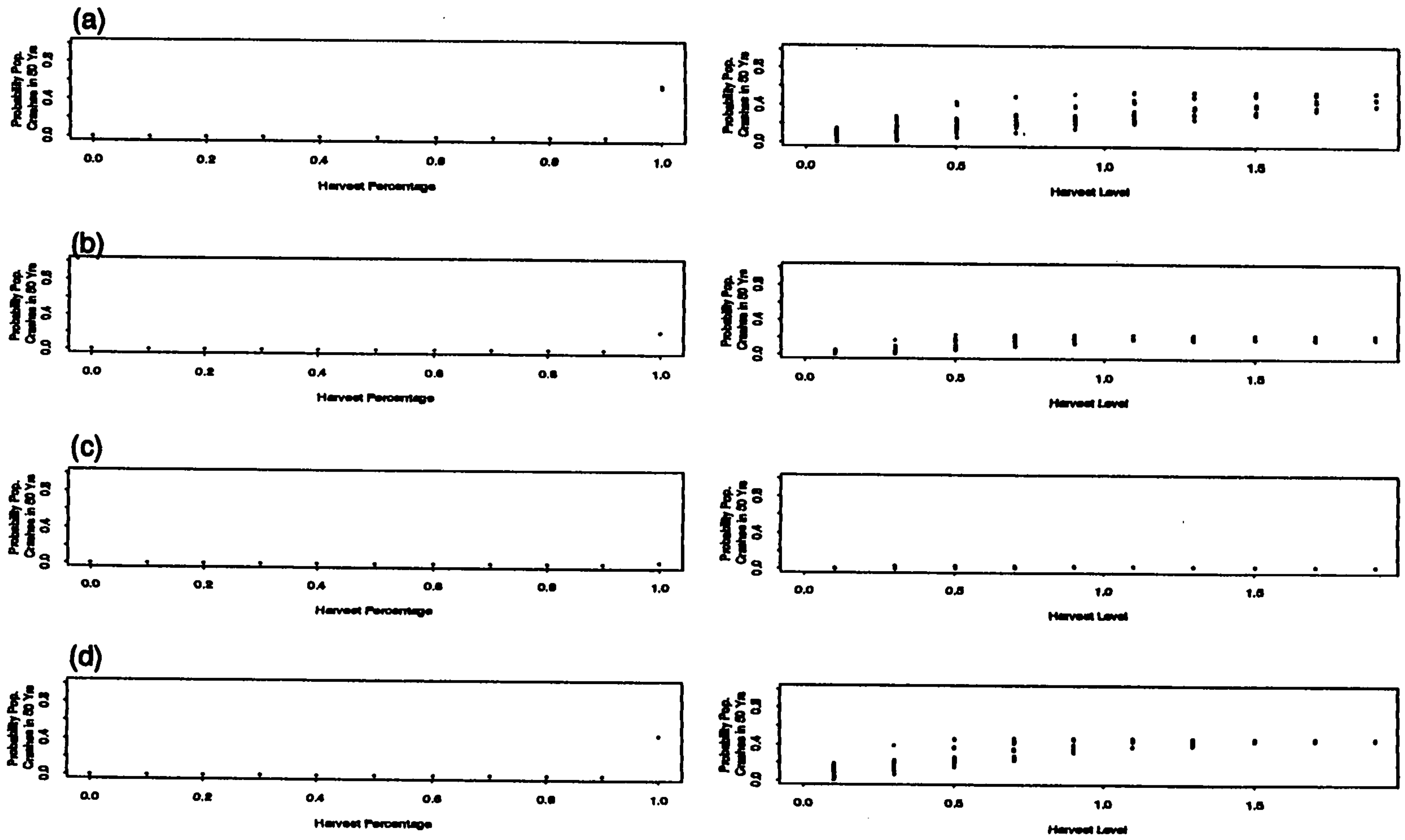


FIGURE 5.19 Probability of extinction under the Mean Recruitment model. Within each row, the left column summarizes results under constant harvest rate strategies; the right column summarizes results under constant catch strategies. The results from each beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach) are arranged by row. Each dot on the graph represents a different juvenile/adult survival pair.

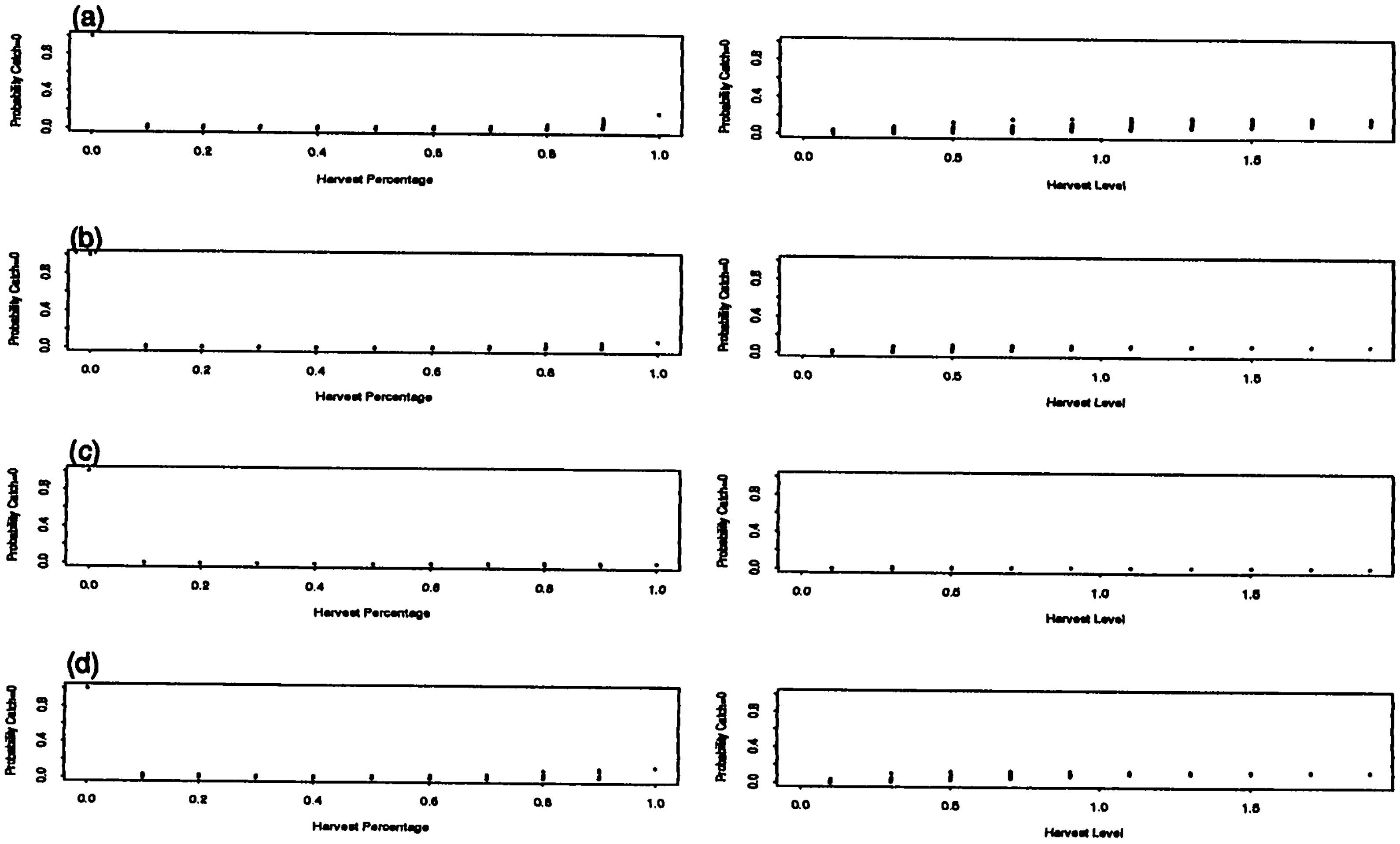


FIGURE 5.20 Probability that annual catch will be interrupted under the Mean Recruitment model. Within each row, the left column summarizes results under constant harvest rate strategies; the right column summarizes results under constant catch strategies. The results from each beach (i.e., (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach) are arranged by row. Each dot on the graph represents a different juvenile/adult survival pair.

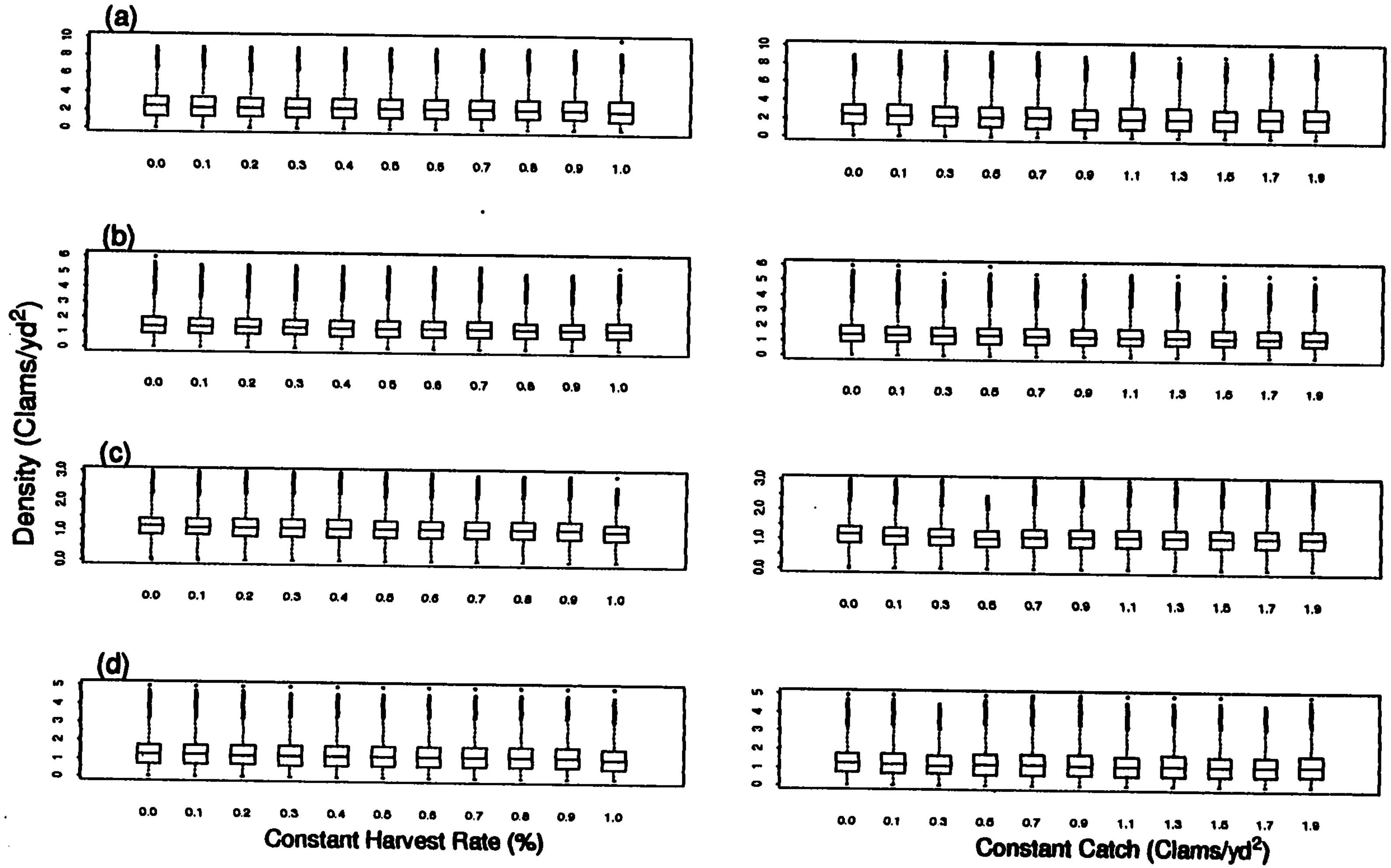


FIGURE 5.21 Distributions of total densities from 50 years of simulations as a function of either constant harvest rate or constant catch strategies at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. In each plot, the black bar in the box indicates the median, the box encloses the quartiles (i.e., 25% to 75%), the whiskers enclose the middle 90% CI and points indicate extreme values.

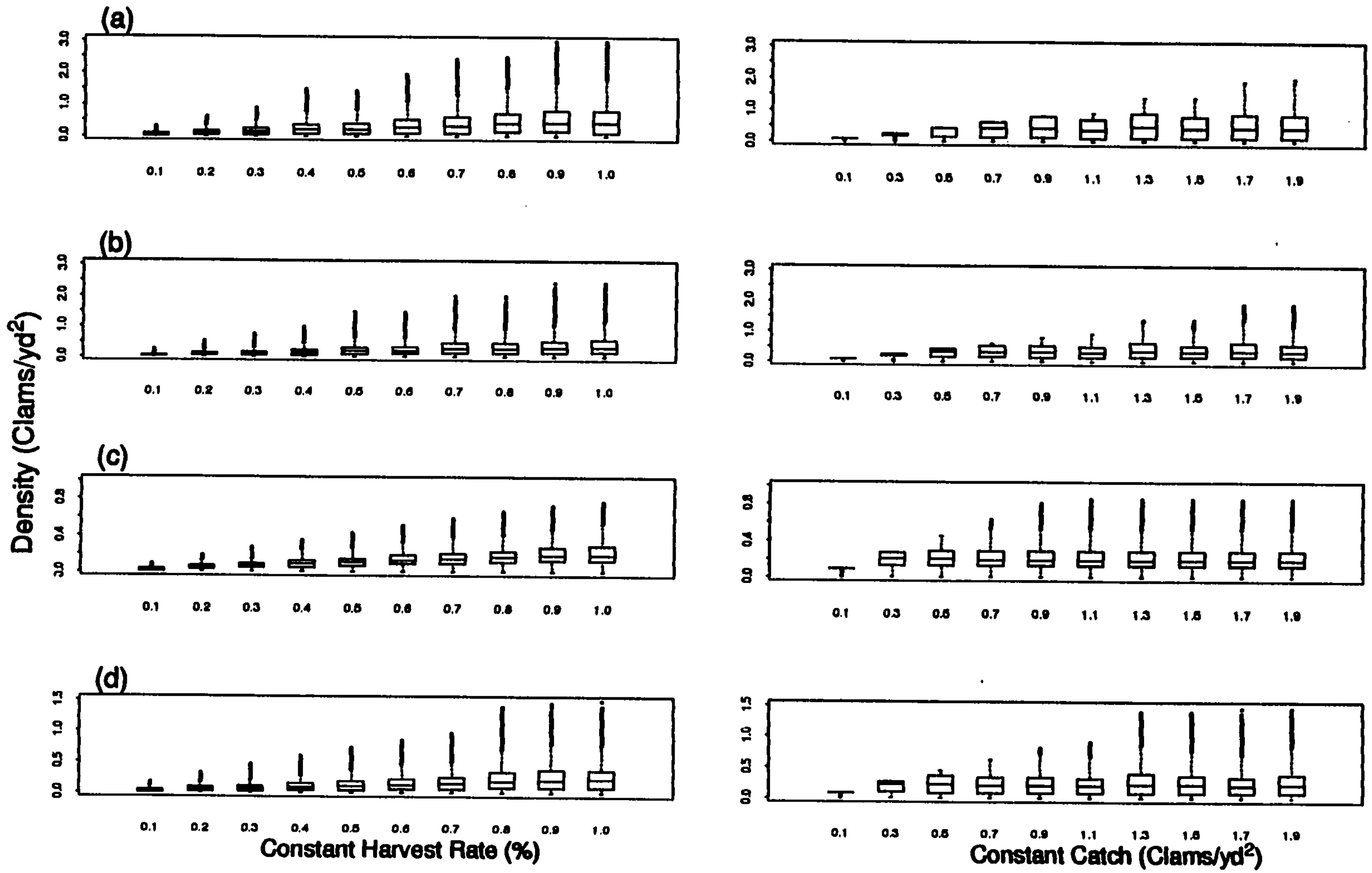


FIGURE 5.22 Distributions of catch densities from 50 years of simulations as a function of either constant harvest rate or constant catch strategies at (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach. In each plot, the black bar in the box indicates the median, the box encloses the quartiles (i.e., 25% to 75%), the whiskers enclose the middle 90% and points indicate extreme values.

the time. This effect occurred regardless of the level of adult and juvenile survival. At the lowest levels of survival and the highest rates of exploitation, the model predicted a high probability (~45%) of extinction. If extinction is the major criterion, then a constant harvest rate policy or an escapement policy is preferable, as adults are always retained for future generations. A constant harvest rate strategy forces a lower median catch over the 50 year time horizon than does a constant catch strategy. Thus, constant harvest rate policies forego catch to decrease the odds of extinction. With higher harvest pressure the probability distribution of the expected population densities is forced slightly to the left (towards zero).

Copalis behaved very similarly to Mocrocks. At even relatively low levels of harvest under a constant harvest policy, the population went extinct ~20% of the time. Again, if extinction is the major criterion, then a constant harvest rate policy or an escapement is preferable, as adults are always retained for future generations. Also, there is little to be gained in catch by the constant harvest level policies.

Contrary to the results at the northern beaches, simulations under the mean recruitment model indicated that Twin Harbors was not vulnerable to extinction or catch failures, even under intense fishing pressure. Intense fishing pressures did skew the distribution of the population somewhat to the left (i.e., towards zero), but this effect was minimal. These results are consistent with those under the SSRSR model.

Long Beach showed a marked increase in risk of extinction under the Mean Recruitment model at all levels of adult and juvenile survival. Even low levels of the constant catch strategy caused drastically increased risk. At the highest levels of the constant catch strategy, the model estimated that there was a 40% chance that the population would go extinct within 50 years. A constant harvest rate policy showed no increased risk of extinction if the rate was less than 100%. At Long Beach, neither the total density (Figure 5.21) nor catch (Figure 5.22) increased sufficiently to outweigh the increased risk inherent in utilizing a constant catch strategy. Thus, the constant harvest rate strategy would be preferred, although the amount of catch allowed each year would be more variable.

The simulation results under the Mean Recruitment model indicate that the stocks on all four beaches are best exploited using a constant harvest rate policy with harvest rates in the range of 80%. The simulation model results suggest that increasing the harvest rate from 25.4% (i.e., the harvest rate policy currently employed by WDFW) will allow increased catch with no increased risk of extinction.

5.4 CLIMATE-SHIFT SIMULATION RESULTS

For the simulations that used the SSRSR model, temperature was a significant factor at Mocrocks and Copalis (Equations 5.7 and 5.8), but not at Twin Harbors and Long Beach (Equations 5.9 and 5.10). Thus, increasing/decreasing the maximum temperature would not impact the conclusions at either Twin Harbors or Long Beach under the SSRSR model.

In general, a decrease in the maximum temperature increased the total stock densities at both Mocrocks and Copalis. This is not totally unexpected, as good year-classes in the 1970's at both beaches corresponded to decreased temperatures (See Chapter 4). An increase in the maximum temperature caused decreases in the total stock densities and slight increases in the probability of extinction. These effects were more pronounced at lower survivals. The benefit resulted from increasing recruitment associated with the lower maximum temperatures. The model was unable to realistically simulate the population at Copalis. The model tended to force the density of clams to very low levels (<1.5 clams/yd^2 (i.e., 1.25 clams/m^2)) and remain there or go extinct. Therefore, only results from Mocrocks will be discussed.

For the simulations that used the Mean Recruitment model, temperature was a significant factor at all beaches. However, the effect that temperature had at each beach was somewhat different (Section 5.2.3). This meant that temperatures that were beneficial for the clams on one beach could be inconsequential or even detrimental to the clams on other beaches.

At Mocrocks, there was a slight increase (0.2-0.3 clams/yd^2 (i.e., 0.17- 0.25 clams/m^2)) in total density with the decreasing temperatures. However, increasing temperatures did not affect the stock. At Copalis, both cooler and warmer temperatures increased the expected total densities. Cooler temperatures were somewhat more beneficial, resulting in 0.6-0.8 clams/yd^2 (i.e., 0.50-0.67 clams/m^2) increase. At Twin Harbors there was little to no change in the densities expected. And at Long Beach, recall that the temperature entered into the model as a linearly increasing function. Thus, it was not surprising to see that expected densities increased with increasing temperatures. The warmer temperatures had a slightly beneficial effect, while the cooler temperatures caused a decrease of 0.2-0.4 clams/yd^2 (i.e., 0.17-0.33 clams/m^2).

5.4.1 CATCH STRATEGIES (using the SSRSR model for recruitment)

Simulations at Mocrocks indicated that an increase of 0.5 C in the maximum annual temperature would result in a slightly larger catches. In addition, the constant harvest rate strategy appears to be a potentially better strategy, especially at high juvenile and adult survivals. A decrease in temperature of the same magnitude did not affect the mean catch very much.

The warming and cooling scenarios at Mocrocks affected the risk of extinction and the risk that harvest would not occur (Figures 5.23 and 5.24). A cooler regime would reduce the risk that constant catch policies would cause extinction. At the highest levels of harvest and the lowest levels of survival, the risk of extinction is reduced ~25% from 65%

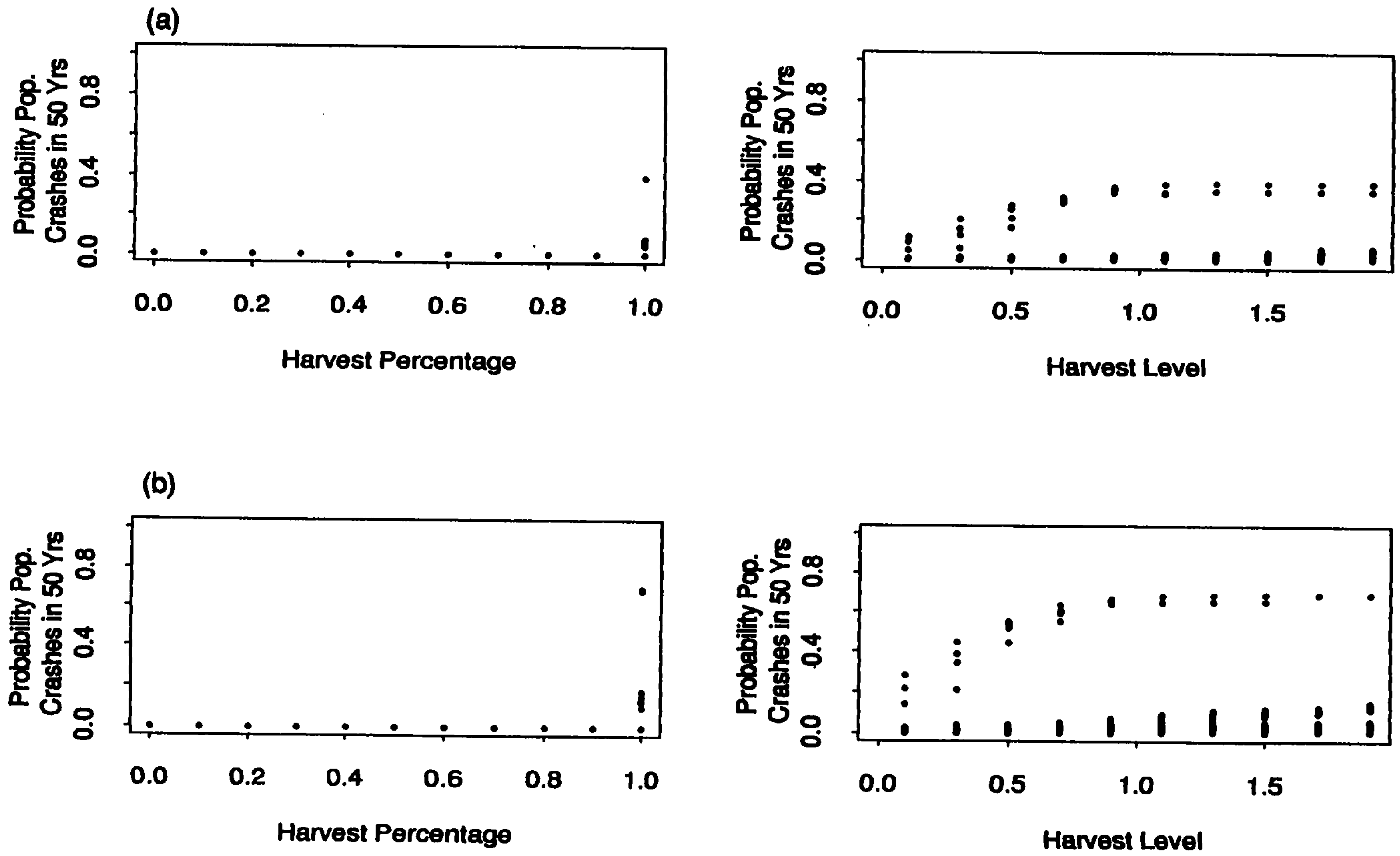


FIGURE 5.23 Probability of extinction under the SSRSR model at Mocrocks. Within each row, the left column summarizes results under constant harvest rate strategies; the right column summarizes results under constant catch strategies. The results from Mocrocks for (a) cooler and (b) warmer scenarios are arranged by row. Each dot on the graph represents a juvenile-adult survival pair.

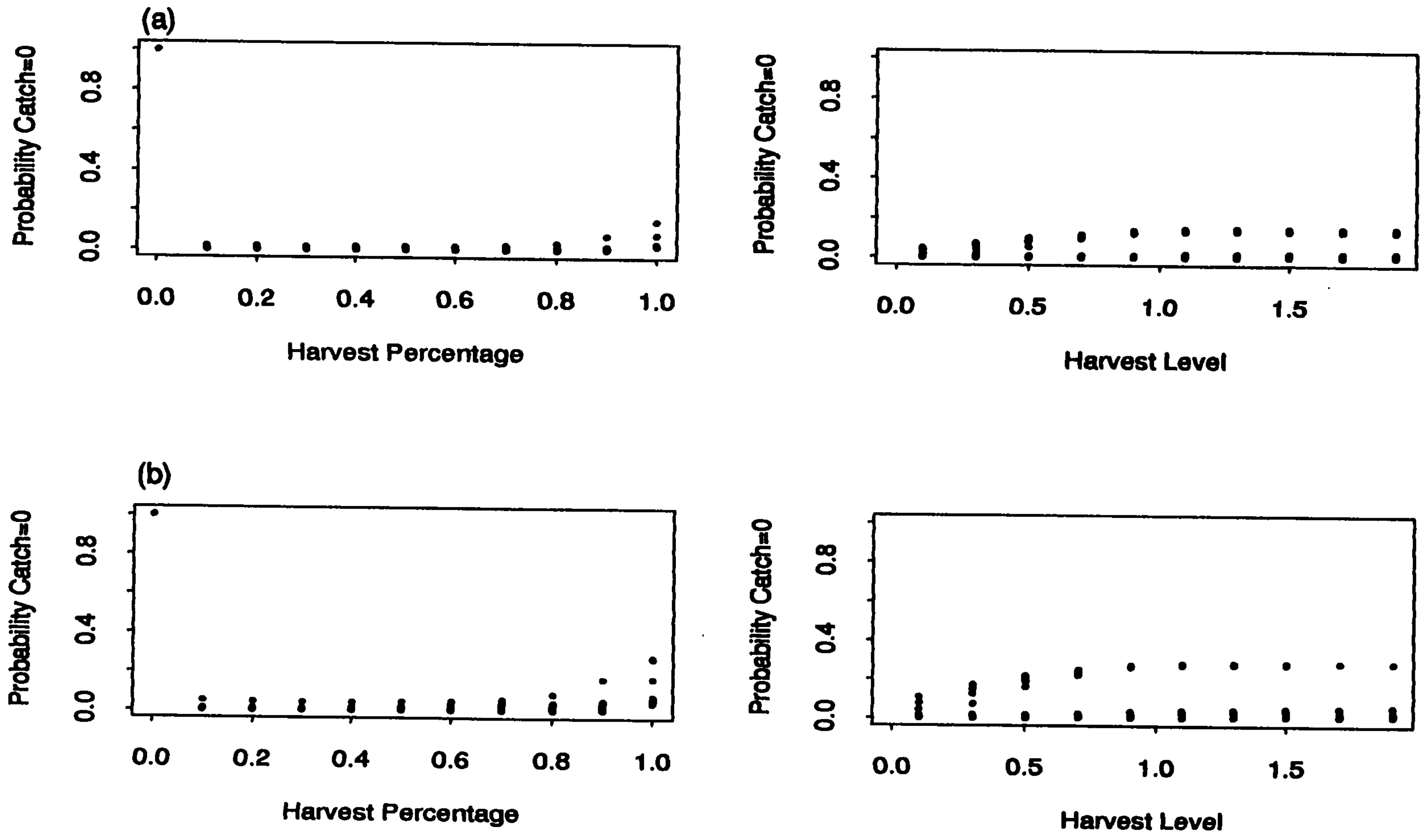


FIGURE 5.24 Probability that the annual catch will be interrupted under the SSRSR model at Mocrocks. Within each row, the left column summarizes results under constant harvest rate strategies; the right column summarizes results under constant catch strategies. The results from Mocrocks for (a) cooler and (b) warmer scenarios are arranged by row. Each dot on the graph represents a juvenile-adult survival pair.

to 40%. Under a constant harvest rate policy, the risk of extinction at 100% harvest is reduced from a maximum of 25% to ~15%. Otherwise, the response under the cool regime is similar to that observed under the simulations that did not have a systematic change in the expected temperature.

Contrarily, a warmer regime does not substantially impact the risk metrics. There is a slight increase in risk of extinction under the constant catch strategies for intermediate survivals. However, the risk of extinction for low and high survival pairs behaved very similar to the simulations that did not have a systematic change in the expected temperature.

The simulation results indicate that a warmer regime would be detrimental to the stock at Mocrocks, but a cooler regime would be beneficial. Regardless, constant harvest rate strategies still retain the ability to harvest a high percentage of the vulnerable clams without causing the population to go extinct.

5.4.2 CATCH STRATEGIES (using Mean Recruitment model for recruitment)

At all four beaches, despite the direction of the temperature change, the catch strategies that were recommended from the simulations were constant harvest rate strategies that took the majority of the adult clams. In general, the constant catch strategies had the lower CV's, but higher risk of extinction. These results were consistent with the results from the simulations that did not have systematic temperature changes imposed.

Although the catch strategies that were recommended at Mocrocks did not change with changing environment, the measures of risk did. With a cooler maximum temperature, there was less risk of extinction overall (5-10% decrease). Constant catch policies were more likely to run the risk of extinction than were the constant harvest rate policies. Only the 100% constant harvest rate policy led to substantial risk of extinction. With the warmer temperatures, the risk at Mocrocks was almost identical to the simulations without systematic changes in the temperature. This follows as the stock was not affected greatly by the increase in temperature.

At Copalis, although the expected densities were affected slightly by the changes in temperature. The risks to the stock did not change much. The constant harvest rate strategy is still the preferred harvest policy based on either risk of extinction or risk of foregoing catch.

At Twin Harbors, the systematic changes in the temperature did not affect the total densities much, but there was a change in the risk associated with cooler temperatures. Constant catch strategies caused increased risk of extinction at the cooler temperatures. This is noteworthy, for this is the only result that indicates that Twin Harbors is ever at risk. This risk can be averted by using constant harvest rate strategies that do not take 100% of the adults.

Finally, at Long Beach, the risk of extinction was impacted by changes in the temperature. With cooler temperatures, the risk of extinction increased under constant catch policy. With warmer temperatures, the risk of extinction decreased. The risk could largely be avoided if a constant harvest rate policy was implemented.

5.5 RESULTS OF RETROSPECTIVE SIMULATION

The retrospective simulation, which simulated recruitment, growth and survival processes under the temperatures that were observed during the 1980s, indicated that the increased harvest would not severely impact the stock. The simulations indicate that recruitment would be sufficient to maintain the population even under harvest rates that are much higher (i.e., 75%) than the harvest rate (25.4%) currently instituted by WDFW. Recall that under the SSRSR model, the simulations did a poor job of recreating the conditions at Copalis. Therefore, reliable information is only available for the other three beaches. A plot of the observed time series (Figure 5.25) is contrasted to the mean of the

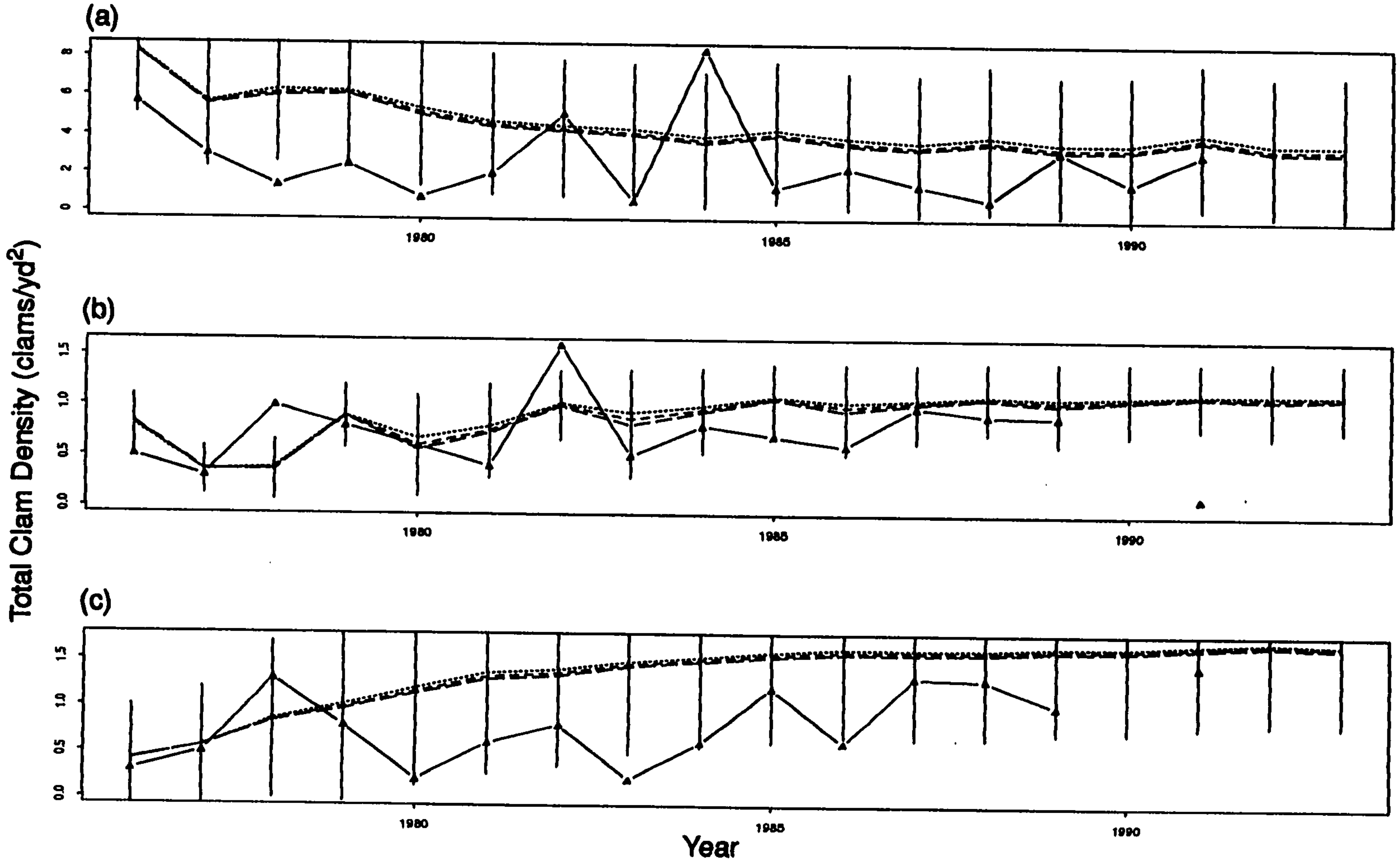


FIGURE 5.25 Time series of the observed (Δ) total densities and the mean of the simulated time series (i.e., dotted lines for 25%, 50% and 75% harvest rates with theoretical 95% tolerance intervals denoted by vertical bars) under the SSRSR model for (a) Mocrocks, (b) Twin Harbors, and (c) Long Beach.

simulated time series under the three harvest strategies (i.e., 25%, 50%, and 75% harvest of the adults). At all three beaches, the mean of the simulations generally overestimated the observed time series during the 1980s. Several points of the observed time series lie outside the tolerance limits. This indicates that the theoretical 95% coverage did not enclose 95% of the data for the 1980s. The fact that the SSRSR model does tend to overestimate the observations under the simulation, but not in Chapter 4 indicates that the transition from an annually-updated time series model to a simulation model may not have been totally successful. However, the small relative change in the model output over the three harvest strategies indicates that the population can withstand much higher levels of harvest than are typically allowed (i.e., 25.4%), without drastic changes in the total density.

Under the Mean Recruitment model, the simulations produced results that were in close agreement to the observations at all four beaches (Figure 5.26). The elements (i.e., harvest rates, tolerance intervals) of Figure 5.26 are consistent with the elements of Figure 5.25. At the two northern beaches, the mean of the simulations generally came very close to the observed time series. At the two southern beaches, the mean of the simulations slightly overestimated the observed time series. In almost all cases, the observed time series fell within the tolerance limits of the simulation, indicating that the observed time series could be one realization of the model output. The mean total density under all three harvest strategies are very close to one another, thus only one line is observable within the graphic. Regardless of the level of harvest, there was no adverse impact on the populations under this model. This result agrees with the results from the projective simulations. Again, the model indicates that harvest levels that are greater than 25.4% would not adversely impact the populations.

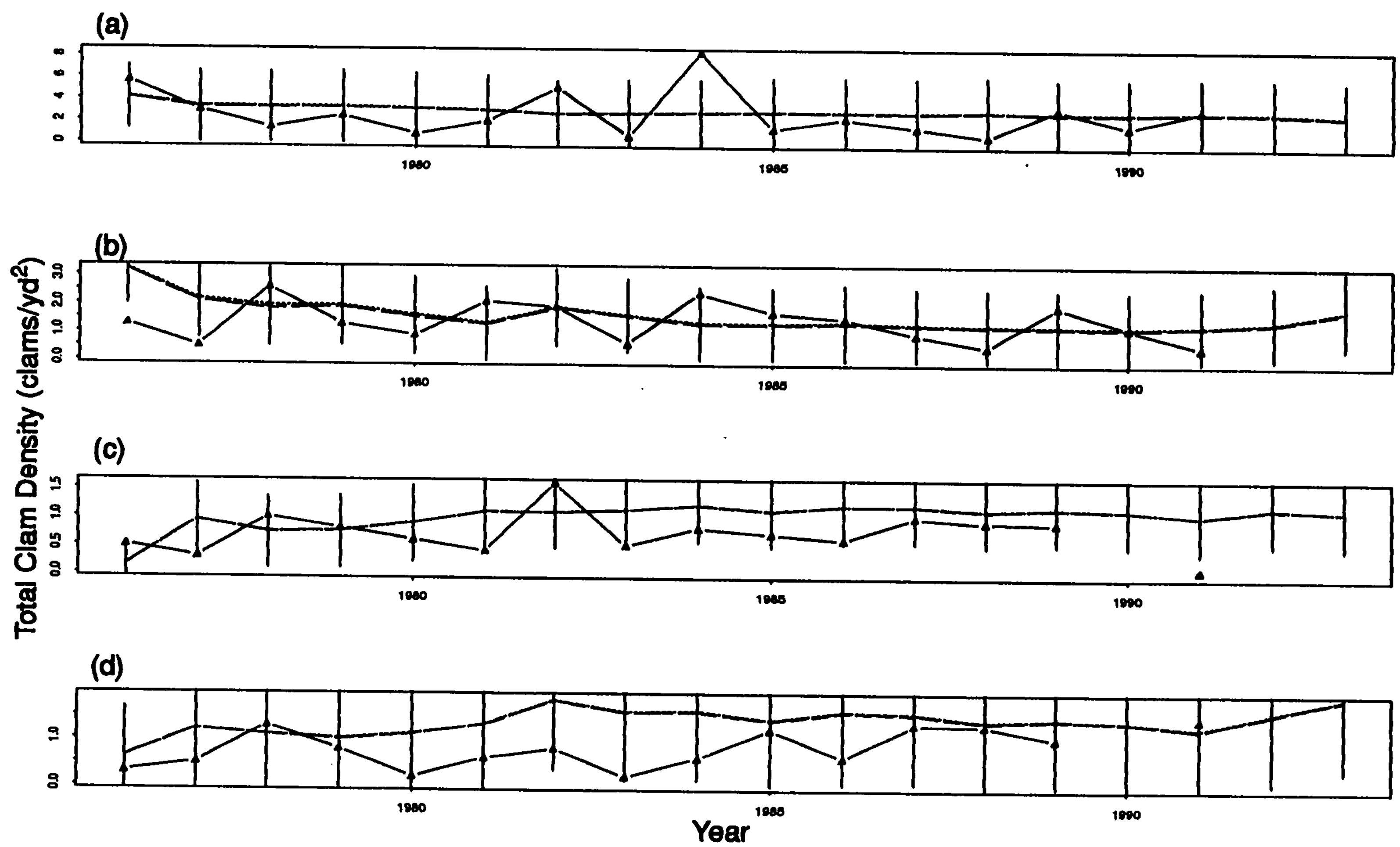


FIGURE 5.26 Time series of the observed (Δ) total densities and the mean of the simulated time series (i.e., dotted lines for 25%, 50%, and 75% harvest rates with ~95% tolerance intervals denoted by error bars) under the Mean Recruitment model for (a) Mocrocks, (b) Copalis, (c) Twin Harbors, and (d) Long Beach.

5.6 CONCLUSIONS

The results of these simulations indicate that a harvest rate policy would probably be best suited for the needs of WDFW. Although the catch varies greatly, as does the population density, it is apparent from the simulations that high levels of exploitation are possible. Whereas WDFW currently imposes a 25.4% harvest rate policy, the simulation results indicted that higher rates could be possible without endangering the stocks. As long as the harvest rate of the adults was less than 80%, there was no indication of an increased risk of extinction. In addition, annual harvest is almost always possible. Other than the level at which clams may be harvested, the policy advocated by the simulation is very similar to the policies already implemented by WDFW.

Although not totally model-independent, many of the results were similar regardless of the model used to generate the recruitment. Overall, the models were more sensitive to juvenile survival than adult survival. Adult survival, within the range considered, had very little impact on the conclusions of the model. This was because the juveniles from the previous year typically make up the larger fraction of the adult class in the following year. These incoming adults then provide the bulk of the spawning biomass, and subsequently, the bulk of the catch. Only if adult survivals were considerably higher than those that were observed in this study (Section 2.4.1.4: $S_A \leq 0.35$) would the impact of the surviving adults become an important component to the catch. However, the analyses in this dissertation do not support such a contention (i.e., high adult survival).

Constant catch policies that took a large proportion of the clams on the beach provide the largest amount of catch with the lowest annual variability, regardless of beach, time horizon, survival or model used to generate recruitment. However, it is apparent that at Mocrocks, Copalis and Long Beach, these strategies must provide outstanding catches only in the short-term, for the extinction probability increases with increasing exploitation. The increasing extinction probabilities with increasing constant harvest indicate that as the populations are being driven to very low levels for a number of subsequent years, random effects are causing the populations to succumb. The constant harvest rate policies, by always taking a fixed percentage of the clams, allow for occasional strong year classes, that replenish the population. Escapement policies always had poorer catch with a higher CV than either the constant catch or the constant harvest rate policies. Although conservative in nature, there appears to be limited benefit to the escapement strategies, for constant harvest rate strategies provide higher overall catch, with no increased risk of extinction. At the same time, there is rarely a year when catch is not allowed. At Twin Harbors, the simulations indicated that regardless of the harvest strategy, there was no increased risk to the stock. This indicates a highly effective compensatory mechanism.

The effect that temperature had on the results varied according to the underlying recruitment model. For example, the SSRSR model at both Twin Harbors and Long Beach did not include any temperature effects. Thus, any increase or decrease in the temperature did not affect these stocks under the SSRSR model. Mocrocks and Copalis, however, did have temperature effects within the model. Both Mocrocks and Copalis responded to the decrease in temperature with increase stock productivity, whereas increased temperatures decreased stock productivity slightly. The harvest strategies that were recommended were not affected greatly by changes in the temperature, but the two measures of risk to the stock were affected. In general, according to the SSRSR model, a cooler regime would be beneficial for the stock, whereas a warmer regime would be detrimental.

Under the Mean Recruitment model, each beach behaved somewhat differently. This was expected because temperature entered the model in different functional forms at each beach. In general, the two northern beaches (i.e., Mocrocks and Copalis) responded positively to cooler temperatures, while the two southern beaches responded positively to warmer temperatures. Overall, the conclusions were not impacted drastically by the changes in temperature. The risk of extinction did change with the changing temperatures, but this was mostly for the constant catch strategies. If constant harvest rate policies were pursued, there still appeared to be little risk to the stock.

These simulations tended to support the contention that the razor clam stocks along the Washington coast can withstand high levels of exploitation. In light of these findings, the assumptions that are driving some of the mechanisms should be reiterated. There are two assumptions that were made that could actually imply that the harvest strategies that are recommended are conservative policies. First, each model simulated a single beach. Thus, the model did not incorporate the contributions of spawners from adjacent beaches. Second, the contribution of offshore spawners was not incorporated into the model. Both of these factors (i.e., spawners on adjacent beaches and offshore spawners) could potentially increase the number of recruits that are produced. However, as I have been unable to quantify the contributions of these two extra sources of recruits, they have been ignored in this model. Ignoring these potential spawners will probably lead to a more conservative strategy than had they been incorporated.

Conversely, there are also a couple of assumptions that suggest that the harvest strategies that are recommended are liberal policies. First, the SSRSR model assumed that all spawners were allowed to spawn prior to harvest. This assumption, in effect, implies that the season was closed throughout the winter and early spring. Of potentially greater importance, there was no harvest of juveniles. Because the majority of the spawners in year "t" were those juveniles that escaped harvest the in year "t-1", harvest of juvenile stocks would decrease the number of spawners which could possibly result in decreased recruitment. In addition, as the model is more sensitive to juvenile survival than adult survival, it would appear that harvesting juveniles, even incidentally, is something that should be avoided. The simulations suggest that as long as the net juvenile survival is >20%, there is little to no risk of extinction. However, the simulations also suggest that the quantity of subsequent adult harvests will decrease with increasing harvest of juveniles.

The results of the simulations agreed with WDFW's policies of protecting the juveniles and using the harvest rate policy. The major difference between the results of the simulation and the current WDFW policy is that the simulation indicated that the adults in the population can be harvested at a greater rate without risk to the stock. In general, the results from the simulations reflect the fact that if most of the adults are not going to survive until next year, there is no risk in harvesting them.

Chapter 6

Conclusions and Discussion

This study was initiated to understand the impacts of the disease NIX on the management of the razor clam stocks along the Washington coast. In order to ascertain the impact on the population dynamics of the razor clam, this study quantified the impact of NIX on survival (Chapter 2), growth (Chapter 3) and recruitment (Chapter 4). Studies were carried out to understand the impact of NIX at both the individual and at the population level. The survival studies measured the impact of NIX at the individual level within a beach, at the population level within a beach and at the population level across beaches. The research in this dissertation did not find a significant impact of NIX in any of the processes (i.e., survival, growth and recruitment) investigated. The results from this study suggest that decreases in the populations along the Washington coast are probably unrelated to NIX and are more likely the result of density-dependent effects and environmental conditions. Therefore, within the range of NIX intensities that were observed during this study, management can proceed without undue concerns for the disease the population or subsequent harvests.

Although NIX did not affect the processes studied, some of the auxiliary findings could be quite valuable. Specifically, this study found that both adult survival and growth exhibited seasonal components. Survival of the adults was lowest during the late summer and fall and highest during the winter at both Long Beach and Copalis during all three years (i.e., 1990-1993) that were studied (Chapter 2). Growth was highest during the spring and summer (Chapter 3). In addition, recruitment success was correlated to temperature. Regardless of the model that was used to explain the recruitment relationship, recruitment was almost always significantly impacted by the maximum mean-temperature in one or both of the previous two years. However, the direction and strength of the recruitment relationship to temperature was dependent on the beach and on the specific recruitment model analyzed.

Using the statistical relationships that were developed in Chapters 2-4, a simulation model was constructed to determine the harvest strategy that provided the best compromise between harvest and risk (i.e., the probability of extinction or the probability of not having an annual season). Conclusions based on the historic catch statistics and on the simulation results (Chapter 5) suggest that the stock density is not negatively impacted by intense harvest. The simulations indicated that constant harvest rate strategies could take up to 80% of the adult population annually without risk to the stock. Similarly, the historic record has noted occasional harvest rates of 100% of the adults. The fact that the population can sustain high harvest of the adults is consistent with the findings indicating high natural mortality (Chapters 2 and 4) of adults in the population. Reducing the harvest to protect the adults is not advantageous because many of the adults are destined to die of natural causes before the next season.

Of the three different harvest strategies that were simulated (i.e., constant catch, constant harvest rate and constant escapement), the constant harvest rate strategy appeared to be the best compromise between harvest and risk. Although the constant catch strategy typically had highest harvest and lowest CV of the three strategies, the constant catch strategy often experienced the highest risk of extinction. At the other extreme, the constant escapement strategy had the lowest harvest and the highest CV, but no risk of extinction. The constant harvest rate strategy offered a compromise of high harvest, an intermediate CV and little to no risk. The simulations indicated that the clams could undergo high harvest (80% of the adults) under the constant harvest rate strategy with no risk of extinction. The constant catch and constant escapement strategies also had a higher risk of foregoing annual harvests than did the constant harvest rate strategy. Thus, the constant harvest rate strategy met the criteria set by WDFW. The constant harvest rate strategy maximizes harvest on an annual basis, while minimizing risk of extinction or loss of recreational harvest opportunities.

Although, in general, the simulation models in Chapter 5 suggest that high harvest rates would not be detrimental to the stock, this conclusion is valid only if harvest is focused on post-spawning adults. If juveniles are harvested as well, the simulations suggest that the average catch will decline and the risk of extinction could increase. Unfortunately, safe rates of harvest for juveniles are currently unavailable because the natural mortality rate of juveniles remains poorly understood. The simulations in Chapter 5 suggest that as long as the net juvenile survival is >20%, there is little to no risk of extinction. However, the simulations also suggest that the quantity of subsequent adult harvests will decrease with increasing harvest of juveniles.

As mentioned previously, this study indicates that summer seems to be a time of greatest mortality, while winter seems to be a time of greatest survival (Chapter 2). Spring and summer provide the best times for growth (Chapter 3). Combining the results of the survival, growth and recruitment processes (i.e., Chapters 2-4) with the simulation results (Chapter 5) suggests a harvest strategy that would allow harvests in late spring and summer, until ~80% of the adults that just spawned have been harvested. The season would then be closed to protect the next spawning class from harvest until they had spawned the following spring. An 80% harvest rate is much higher than the 25.4% harvest rate that is currently imposed by WDFW. According to the simulation results, the higher fishing pressure will allow for increased harvest, with no increased risk to the stock. This in turn should lead to longer annual seasons.

One domain that remains unexplored concerns the stocks of clams that are located offshore (i.e., subtidally) of the survey areas. Currently, the influence of the subtidal populations on intertidal production is unknown and was ignored in the simulation modeling (Chapter 5). There are several indications that such a subtidal population exists and it is reasonable to think that the subtidal population may recruit onshore. Given that the simulation model indicated that 20% of the adults should not harvested, protection of the subtidal population may be sufficient to maintain viable populations for recreational harvests. Before such a strategy is pursued, it would be advisable to confirm the existence of the subtidal populations, to estimate the density of these populations and to estimate the contributions of these populations to the intertidal populations.

In general, it appears that the razor clam stocks along the Washington coast are composed of individuals that are short-lived (~2-3 years old), experience rapid growth and are extremely fecund. The low survival of the adults, combined with the high potential for recruitment, results in stocks with high turnover, regardless of harvest pressures. This study suggests that NIX has not influenced the population dynamics of the razor clam stocks along the Washington coast. Fluctuations in population abundance appear to be primarily the result of interactions between the stock density and temperature. This study also suggests that the current harvest poiicy can be adjusted. Although the simulation model confirmed that the harvest rate strategy best suits the desires of WDFW, the models and the historic record suggest that the current harvest rates may be increased without harming the stock.

REFERENCES

Aitkin, M., D. Anderson, B. Frances, and J. Hinde. 1989. Statistical Modelling in GLIM. Ney York: Oxford University Press. 374 p.

Allen, R.L. and R.E. Turner. 1989. Environmental influences on the oyster industry along the west coast of Florida. *Journal of Shellfish Res.* **8(1)**. p. 95-104.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In*: B.N. Prtrov and F. Csaki [ed.] 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest.

Anthony, V.C. and S. Clark. 1982. A description of the northern shrimp fishery and its decline in relation to water temperature. *In*: Climate and Fisheries. Cushing, D.H. ed. New York, NY: Academic Press. p. 119 - 21.

Armstrong, David A. and J. L. Armstrong. 1974. A Haplosporidan infection in gaper clams, *Tresus capax* (Gould), from Yaquina Bay, Oregon. *Proc. Natl. Shellfish Ass.* **64**:68-72.

Ayres, D.L. and D.D. Simons. 1988. The Spring and Fall 1988 recreational razor clam fisheries with a review of razor clam sampling methodology. *Prog. Rept.* **276**. *Washington Dept. Fish.*

Ayres, D.L. and D.D. Simons. 1991. The Spring and Fall 1990 recreational razor clam fisheries and status of the razor clam stocks. *Prog. Rept.* **293**. *Washington Dept. Fish.*

Ayres, D. L. and D.D. Simons. 1992. The Spring and Fall 1991 recreational razor clam fisheries and status of the razor clam stocks. *Prog. Rept.* **300**. *Washington Dept. Fish.*

Bannister, R.C.A. 1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales. *In*: North Pacific Workshop on Stock Assessment and Management of Invertebrates. Jamieson, G.S. and N. Bourne, eds. *Can. Spec. Publ. Fish. Aquatic Sciences.* **92**:182-194.

Barber, B.J. 1988. Reduced fecundity in scallops in Maine. *Marine Ecol. Prog. Ser.* **42**:207-212.

Barber, B.J., S. E. Ford, and H.H. Haskin. 1988a. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism I. Condition index and relative fecundity. *J. Shellfish Res.* **7**:25-31.

Barber, B.J., S. E. Ford, and H.H. Haskin. 1988b. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassotrea virginica*) energy metabolism II. Tissue biochemical composition. *Comp. Biochem. Physiol. A Comp. Physiol.* **91**:603-608.

Bates, D.M. and D.G. Watts. 1988. Nonlinear Regression Analysis and Its Applications. John Wiley and Sons, Inc., New York, NY. 365 p.

Bayne, B.L. 1975. Reproduction in bivalve molluscs under environmental stress. *In*: Physiological Ecology of Estuarine Org. p. 259-277.

Bayne, B.L., D.A. Brown, K. Burns, D.R. Dixon, A. Ivanovici, D.R. Livingstone, D.M. Lowe, M.N. Moore, A.R.D. Stebbing, and J. Widdows. 1985. *In*: The Effects of Stress and Pollution on Marine Animals. New York, NY: Praeger Pub. p. 3-45.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth. *Human Biol.* **10**:181-213.

Beukema, J. J., E. Knol and G.C. Cadee. 1985. Effect of temperature on the length of the annual growing season in the tellinid bivalve *Macoma balthica* living on tidal flats in the Dutch Wadden Sea. *J. Exp. Mar. Biol. Ecol.* **90**:129-144.

Beverton, R.J.H. and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. *Fish. Invest. London. Ser. II.* **19**: p.533.

Bourne, N. 1969. Population studies on razor clams at Masset, British Columbia. *Tech. Rpt.* **118**. *Fish. Res. Bd. Can.* p. 24.

Bourne, N. and D.B. Quayle. 1970. Breeding and growth of razor clams in British Columbia. *Tech. Rept.* **232**. *Fish. Res. Bd. Can.* p. 42.

Boyce, W.E. and R.C. DiPrima. 1986. Elementary Differential Equations. 4th Ed. John Wiley and Sons, Inc. New York, NY. 512 p.

Brousseau, D.J. 1978. Population dynamics of the soft-shell clam *Mya arenaria*. *Mar. Biol.* 50:63-71.

Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie and K.H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monographs* 5. 437 p.

Caddy, John F. 1975. Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. *J. Fish Res. Bd. Can.* 32:1305-1328.

Caddy, John F. 1989. Marine invertebrate fisheries: their assessment and management New York: Wiley, c1989.

Cobb, J.S. and J.F. Caddy. 1989. The population biology of decapods. *In*: Marine invertebrate fisheries: their assessment and management. Caddy, J.F. ed. p. 327-374.

Coe, W.R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology.* 34:225-229.

Cormack, R.M. 1964. Estimates of survival from sighting of marked animals. *Biometrika.* 51:429-438.

Cushing, D.H. 1981. Fisheries Biology: A Study in Population Dynamics. 2nd Ed. University of Wisconsin Press, Madison, WI. 295 p.

Cushing, D.H. 1988. The study of stock and recruitment. *In*: J.A. Gulland (Ed.) Fish Population Dynamics. John Wiley and Sons, Inc., New York, NY. p. 105-128.

Daniel, W.W. 1978. Applied Nonparametric Statistics. Houghton Mifflin Co., Dallas, TX. 510 p.

Dickie, L.M. and J.C. Medcof. 1963. Causes of mass mortalities of scallops (*Placopecten magellanius*) in the southwest gulf of St. Lawrence. *J. Fish. Res. Bd. Canada.* 20:451-482.

Dow, R.L. 1977. Effects of climate cycles on relative abundance of marine and estuarine species. *J. Cons. Perm. Int. Explor. Mer.* 37(3):272-80.

Elston, R.A. 1984. Pacific razor clam mortalities: pathology, distribution of disease, and apparent cause. *Proc. Natl. Shellf. Assoc. West Coast Meeting*. p. 51-52.

Elston, R.A. 1986a. An intranuclear pathogen [Nuclear Inclusion X (NIX)] associated with massive mortalities of the Pacific razor clam, *Siliqua patula*. *Journ. Invert. Pathol.* 47:93-104.

Elston, R.A. 1986b. Occurrence of branchial rickettsia-like infections in two bivalve molluscs, *Tapes japonica* and *Patinopecten yessoensis* with comments on their significance. *J. Fish Disease*. 9:69-71.

Elston, R.A., E.L. Elliot and R.R. Colwell. 1982. Conchiolin infection and surface coating in Vibrio: Shell fragility, growth depression and mortalities in cultured oysters and clams, *Crassostrea virginica*, *Ostrea edulis*, and *Mercenaria mercenaria*. *J. Fish Disease*. 5:265-284.

Elston, R.A. and M.G. Peacock. 1984. A Rickettsiales-like infection in the Pacific razor clam, *Siliqua patula*. *Journ. Invert. Pathol.* 44:84-96.

Emlen, J. M. 1984. **Population Biology: coevolution of Population Dynamics and Behavior**. MacMillan Pub. Co., New York, NY. 547 p.

Fisher, W.S., M. Auffret, and G. Balouet. 1987. Response of oyster to acute salinity and temperature. *Aquaculture* 67:179-190.

Fisher,W.S. and M. Tamplin. 1988. Environmental influence on activity and foreign-particle adherence by hemocytes by American oyster *Crassostrea virginica*. *Can. Journ. Fish. Aquat. Sci.* 45(7):1309-15.

Fitch, 1950. The pismo clam. *Calif. Fish Game* 36(3):285-312.

Fogerty, M.J. and S.A. Muraski. 1986. Population Dynamics and Assessment of Exploited Invertebrate Stocks. *In*: G.S. Jamieson and N. Bourne (Ed.) **North Pacific Workshop on Stock Assessment and Management of Invertebrates**. *Can. Spec. Publ. Fish. Aquat. Sci.* 92:228-244.

Fogarty, M.J., M.P. Sissenwine, and E.B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends Ecol. Evol.* **6(8)**:241-48.

Ford, S.E. 1985. Chronic infections of *Haplosporidium nelsoni* (MSX) in the oyster *Crassotrea virginica. Journ. Invert. Pathology.* **45**:94-107.

Freeland, H.J. 1990. Sea surface temperature along the coast of British Columbia: Regional evidence for a warming trend. *Can. J. Fish. Aquat. Sci.* **47(2)**:346-350.

Friedman, C.S., T. McDowell, J.M. Groff, J.T. Hollibaugh, D. Manzer, and R.P. Hedrick. 1989. Presence of *Bonamia osteae* among populations of the European flat oyster, *Ostrea edulis* (Linne), in California, USA. *Journ. Shellfish Res.* **8(1)**:133-137.

Fry, F.E.J. 1947. Effects of the environment on animal activity. *Univ. Toronto Stud. Biol., Ser.* **55**:1-62.

Gabbot, P.A. 1976. Energy metabolism. *In*: Marine Mussels. Bayne, B.L. ed. Cambridge: Cambridge University Press. p. 293-355.

Gallucci, V.F. and T.J. Quinn II. 1979. Reparameterizing, fitting, and testing a simple growth model. *Trans. Am. Fish. Soc.* **108**:14-25.

Garcia, S. 1983. The stock-recruitment relationships in shrimp: reality or artifacts and misinterpretations? *Oceanog. Trop.* **18**:25-48.

Garcia, S. and L. LeReste. 1981. Dynamics, exploitation, and management of coastal shrimp. *FAO Tech. Paper.* **203**.

Gauthier, J.D., E.N. Powell, E.A. Wilson, and J.M. Brooks. 1990. "DERMO" an the Southern Oscillation? *Journ Shell Res.* **9**:451.

Gulland, J.A. 1983. Fish Stock Assessment: A Manual of Basic Methods. John Wiley and Sons, Inc., New York, NY. 223 p.

Gunter, G. and J.C. Edwards. 1967. Relation of rainfall and freshwater drainage in penaeid shrimp. *FAO Fish Report.* **57(3)**: 875-92.

Hall, M.A. 1983. A spatial approach to the population dynamics of the manila clam (*Tapes philipinarum*). Ph.D. Dissertation, Univ. of Washington, Seattle, WA. 240 p.

Hancock, D.A. 1973. The relationship between stock and recruitment in exploited invertebrates. *Rapp. P.V. Reun. Cons. Int. Explor. Mer.* **164**: 113-131.

Hansen, M.H., W.N. Hurwitz and W.G. Madow. 1953. Sample Survey Methods and Theory, Vol. 1. John Wiley and Sons, Inc., New York, NY. 638 p.

Hanumara, R.C. and N.A. Hoenig. 1987. An empirical comparison of a fit of linear and non-linear models for seasonal growth in fish. *Fish. Res.* **5**:359-381.

Harvey, M. and B. Vincent. 1990. Density, size distribution, energy allocation and seasonal variations in shell and soft tissue growth at two tidal levels of a *Macoma balthica* population. *J. Exp. Mar. Biol. Ecol.* **142**:151-168.

Hewett, W.G. and J.D. Andrews. 1955. Temperature control experiments on the fungus disease, *Dermocystidium marinum*, of oysters. *Proc. Natl. Shellf. Assoc.* **46**:129-133.

Hilbish, T.J. 1986. Growth trajectory of shell and soft tissue in bivalves: seasonal variations in *Mytilus edulis* (L). *Journ. Exp. Mar. Biol. Ecol.* **96**:103-113.

Hilborn, R. and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York, NY. 570 p.

Hirschhorn, G. 1962. Growth and mortality rates of the razor clam (*Siliqua patula*) on Clatsop Beaches, Oregon. *Fish. Comm. Oregon.* **No. 27**. 55 p.

Hoaglin, D.C. and R.E. Welsch. 1978. The hat matrix in regression and ANOVA. *The Am. Statistician.* **32**:17-22.

Hoffmann, A. 1993. Quantifying selection in wild populations using known fate and mark-recapture designs. Ph.D. Diss. University of Wash. 260 p.

Hosmer, D.W., Jr. and S. Lemeshow. Applied logistic regression. New York: Wiley, 1989. 307 p.

Johnson, F.G. and R.R. Stickney. 1989. Fisheries: Harvesting Life from Water. Kendall/ Hunt Pub. Co., Dubuque, IA. 423 p.

Jolly, G.M. 1965. Explicit measures from capture-recapture data with both death and immigration -- stochastic model. *Biometrika.* **52**:225-247.

Kent, R.M.L. 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of Mytilus edulis. *J. Mar. Biol. Assoc. UK.* **59**:289-297.

Lasker, R. 1978. Ocean variability and its biological effects in the NE Pacific. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* **173**:168-181.

Lasker, R. 1982. The effect of weather and other environmental variables upon larval fish survival leading to recruitment of northern anchovy. In **Climate and Fisheries**. Cushing, D.H. ed. New York, NY: Academic Press. p. 127-129.

Lassuy, D.R. and D.D. Simons. 1989. Species Profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) -- Pacific razor clam. *U.S. Fish. Wildl. Serv. Biol. Rept.* **82(11.89)**. U.S. Army Corps of Eng., **TR-EL-82-4**. 16 p.

Leclair, L.L. and S.R. Phelps. 1994. Genetic characteristics and relationships of five razor clam (*Siliqua patula*, Dixon) populations along the Pacific Coast of North America. *J. Shellfish Res.* **13**:207-216.

Lett, P.F., A.C. Kohler, and D.N. Fitzgerald. 1975. Role of stock biomass and temperature in recruitment of Southern Gulf of St. Lawrence Atlantic cod *Gadus morhua. J. Fish. Res. Bd. Can.* **32**:1613-28.

Link, T. 1980. Mortality rates of the razor clam based upon the 1973 tagging study on Gearhart Beach. *Oregon Dept. Fish Wildl. Info. Rep.*

Ludwig D. and C.J. Walters. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. *Can. J. Fish. Aquat. Sci.* **38**:711-720.

Ludwig D. and C.J. Walters. 1989. A robust method for parameter estimation from catch and effort data. *Can. J. Fish. Aquat. Sci.* **46**:137-144.

Mackin, J.G. 1962. Oyster disease caused by *Dermocystidium marinum* and other organisms in Louisiana. *Public. Institute Mar. Sci. Univ. Texas.* **7**:1-131.

Mackin J.G. and S.H. Hopkins. 1962. Studies on oyster mortality in relation to natural environments and to oil field in Louisiana. *Public. Institute Mar. Sci. Univ. Texas.* 7:1-131.

Manly, B.F.J. and M.J. Parr. 1968. A new method for estimating population size, survivorship and birth rate from capture-recapture data. *Trans. Soc. Brit. Ent.* 18:81-89.

May, E.B. 1972. Effects of floodwaters on oysters. *Proceedings Natl. Shellfish Assoc.* 62:67-71.

McConnaughey, R.A., D.A. Armstrong, B.M. Hickey and D.R. Gunderson. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Can. J. Fish Aquat. Sci.* 49:2028-2044.

McCullagh, P. and J.A. Nelder. 1989. Generalized Linear Models, 2nd Ed. Chapman and Hall, New York, NY. 511 p.

McMillin, H.C. 1924. The life history and growth of the razor clam. *Wash. Dept. Fish.* Olympia, WA. 52 p.

Menzel, R.W. and S.H. Hopkins. 1954. Effects of two parasites on the growth of oysters. *Proc. Natl. Shellf. Assoc.* 45:184-86.

Miller, C.B., H.D. Batchelder, R.D. Brodeur, and W.G. Pearcy. 1985. Response of the zooplankton and ichthyoplankton off Oregon to the El Nino event of 1983. *In:* El Nino North: Nino Effects in the Eastern Subarctic Pacific Ocean. Wooster, W.S. and D.L. Fluharty, ed. p. 185-187.

Mitchell, J.F.B., T.C. Johns, J.M. Gregory and S.F.B. Tett. 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature.* 376:501-504.

Monastersky, R. 1996. The loitering El Nino: greenhouse guest. *Science News.* 149:54.

Naidu, K.S. and J.T. Anderson. 1984. Aspects of scallop recruitment and its relation to oceanography and its implications for resource management. *CAFSAC Res. Doc.* 84/29:1-15.

Neter, J., W. Wasseman and M.H. Kutner. 1983. Applied Linear Regression Models. Richard D. Irwin, Inc., Homewood, IL. 547 p.

Newell, R.I.E. 1985. Physiological effects of the MSX parasite *Haplosporidium nelsoni* (Haskin, Stauber, and Mackin) on the American oyster *Crassotrea virginica* (Gmelin). *J. Shellfish Res.* 5:91-95.

Nickerson, Richard B. 1975. A critical analysis of some razor clam (*Siliqua patula*, Dixon) populations [Juneau]: State of Alaska, Dept. of Fish and Game.

Orensanz, J.M., A.M. Parma, and O.O. Iribarne. 1991. Population dynamics and management of natural stocks. *In*: Scallops: biology, ecology, and aquaculture. Shumway, S.E. ed. New York: Elsevier. p. 625-713.

Orensanz, J.M. 1986. Size, environment and density: The regulation of a scallop stock and its management implications. *In*: North Pacific Workshop on stock assessment and management of invertebrates. G.S. Jamieson and N. Bourne ed. *Can. Spec. Publ. Fish. Aquat. Sci.* p. 195-227.

Parrish, R.H. 1982. Climatic variation and the Pacific mackerel fishery. In Climate and Fisheries. Cushing, D.H. ed. New York, NY: Academic Press. p. 130-131.

Parrish, R.H. and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Fish. Bull.* **167**.

Pearce, F. 1995. Not warming, but cooling. *New Scientist.* 143:37-41.

Penn, J. W. and N. Caputi. 1986. Spawning stock-recruitment relationships and environmental influences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia. *Aust. Journ. Mar. Freshwater Res.* 37:491-506.

Peterson, W.T. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the West Coast of the United States. *U.S. Fish. Bull.* 71:902-910.

Peterson, W.T. and R.L. Smith. 1982. Upwelling indices and the Oregon Dungeness crab fishery catches. *In*: Climate and Fisheries. Cushing, D.H. ed. New York, NY: Academic Press. p. 132-133.

Procarione, L. 1988. The effect of salinity and water hardness concentration on the lower lethal temperature in juvenile red drum *Sciaenops ocellatus*. MS. Thesis. Texas A&M University.

Ricker, W.E. 1954. Stock and Recruitment. *J. Fish. Res. Board. Can.* **11**:559-623.

Ricker, W.E. 1975. **Computation and Interpretation of Biological Statistics of Fish Populations**. *Bulletin of the Fish. Res. Bd. Can.* 382 p.

Rounsefell, G.A. 1958. Factors causing decline in sockeye salmon of Karluk River AK. *U.S.F.W.S. Bull.* **58(130)**:83-169.

Sayce, C.S. and D.F. Tufts. 1971. The effect of high water temperature on the razor clam, *Siliqua patula* (Dixon). *Proceedings Natl. Shellf. Assoc.* **62**:31-34.

Schlechte, J.W. and J.R. Skalski. 1993. NIX Annual Report - Year 2. *Prog. Report Wash. Dept. Fish.* 46 p.

Schneider, S.H. 1994. Detecting climatic change signals: are there any "fingerprints". *Science.* **263**:341-347.

Schoener, A. and D.F. Tufts. 1987. Changes in oyster condition index with El Nino-Southern Oscillation events at 46 N in the eastern Pacific Bay. *Journ. Geophys. Res.* **92(C13)**:14429 - 14435.

Seber, G.A.F. 1965. A note of the multiple recapture census. *Biometrika.* **49**:330-349.

Seber, G.A.F. 1982. **Estimation of animals abundance and related parameters - 2nd edition**. London: Charles Griffin and Company Ltd. 654 p.

Seber, G.A.F. and C.J. Wild. 1989. **Nonlinear Regression.** John Wiley and Sons, Inc., New York, NY. 768 p.

Shaw, B.L. and H.I Battle. 1957. The gross and microscopic anatomy of the oyster *Crassostrea virginica* (Gmelin). *Canadian Journal Zool.* **35**:325-347.

Shaw, W.N. and T.J. Hassler. 1989. Species Profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)- Pismo Clam. *U.S. Fish. Wildl. Serv. Biol. Rept.* **82**(11.95). U.S. Army Corps of Eng., **TR-EL-82-4**. 12 p.

Sissenwine, M.P. 1984. Why do fish populations vary? Report of the Dalhem Workshop on Exploitation of Marine Communities. *Life Sci. Res. Rep.* 32:59-94.

Smith, Steven G. 1991. Assessing Hazards in Wild Populations Using Auxiliary Variables in Tag-Release Models. Ph. D. Diss. University of Washington. 338 p.

Smith, S.G. and J.R. Skalski. 1993. Assessing the statistical significance of group covariate effects on survival using analysis of deviance of release-recapture data. *J. Applied Ecol.* (Under Revision)

Smith, S.G., J.R. Skalski, J.W. Schlechte, A. Hoffmann, and V. Cassen. 1994. Statistical Survival Analysis of Fish and Wildlife Tagging Studies: Surph.1 Manual. 526 p.

Sutcliffe, Jr., W.H., K. Drinkwater, and B.S. Muir. 1977. Correlation of fish catch and environmental factors. *J. Fish. Res. Bd. Can.* 34: 19-30.

Szarzi, N.J. 1991. Distribution and Abundance of the Pacific Razor Clam, *Siliqua patula* (Dixon), on the Eastside Cook Inlet Beaches, Alaska. M.S. Thesis. University of Alaska. 166 p.

Tegelberg, H.C. 1964. Growth and ring formation of Washington razor clams. *Wash. Dept. Fish. Fish. Res. Papers.* 2(3):69-103.

Tegelberg, H.C. and C.D. Magoon. 1969. Growth, survival and some effects of a dense razor clam set in Washington. *Proc. Natl. Shell. Assoc.* 59:126-135.

Thompson, R.N. and B.A. MacDonald. 1991. Physiological integrations and energy partitioning. *In*: Scallops: biology, ecology, and aquaculture. Shumway, S.E. ed. New York: Elsevier. p. 347-376.

Thompson, S.N. 1983. Biochemical and physiological effects of parasites on hosts. *Comparative Biochemical Physiology.* 74B:183-211.

US v. Washington. 1974. 384 F.Suppl. 312 (Western District of Washington), *affirmed* 500 F.2nd 676 (9th Circuit 1975), *certiorari denied*, 423 US 1086 (1976), Seattle, Washington.

Warren, C.E. and G.E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth in fish. *In*: The Biological Basis of Freshwater Fish Production. ed. Gerking, S.D. Oxford: Blackwell Scientific Publ. p. 175-214.

Welsch, R.L. 1992. Food for thought. *Natural History*. **8**:26-27.

Weymouth, F., H.C. McMillin, and H.B. Holmes. 1925. Growth and age at maturity of the Pacific razor clam, *Siliqua patula* (Dixon). *Bull. U.S. Bureau Fish.*, **41**:201-236.

White, G.G., D.R. Anderson, K.P. Burnham and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP, Los Alamos National Laboratory. Los Alamos, NM. 235 p.

Wilde, P.A.W.J. De, 1975. Influence of temperature on behaviour, energy metabolism and growth of *Macoma balthica*. *In*: Proc. 9th Eur. Mar. Biol. Symp. Barnes, H. ed. Aberdeen: Aberdeen University Press. p. 239-256.

Woodruff, S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-Atmosphere Data Set. *Bull. Am. Meteorol. Soc.* **68(10)**:1239-1250.

Zar, J.H. 1984. Biostatistical Analysis, 2nd Ed. Prentice Hall, Inc. Englewood Cliffs, NJ. 718 p.

Appendix A - Estimated Capture and Survival Probabilities

Table A.1: Estimated Capture and Survival Probabilities at Copalis and Long Beach

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
1990								
August	4	Copalis	A	No	0.99	0.06	NA	NA
August	4	Copalis	A	Yes	0.99	0.06	NA	NA
August	4	Copalis	B	No	0.52	0.11	NA	NA
August	4	Copalis	B	Yes	0.52	0.11	NA	NA
August	4	Copalis	C	No	0.99	0.06	NA	NA
August	4	Copalis	C	Yes	0.99	0.06	NA	NA
August	4	Long Beach	X	No	0.15	0.07	NA	NA
August	4	Long Beach	X	Yes	0.06	0.05	NA	NA
August	4	Long Beach	Y	No	1.00	0.00	NA	NA
August	4	Long Beach	Y	Yes	1.00	0.00	NA	NA
August	4	Long Beach	Z	No	0.44	0.09	NA	NA
August	4	Long Beach	Z	Yes	0.30	0.08	NA	NA
September	4	Copalis	A	No	0.65	0.02	0.10	0.02
September	4	Copalis	A	Yes	0.65	0.02	0.10	0.02
September	4	Copalis	B	No	0.65	0.02	0.27	0.04
September	4	Copalis	B	Yes	0.65	0.02	0.27	0.04
September	4	Copalis	C	No	0.65	0.02	0.10	0.02
September	4	Copalis	C	Yes	0.65	0.02	0.10	0.02
September	4	Long Beach	X	No	0.67	0.04	0.34	0.07
September	4	Long Beach	X	Yes	0.67	0.04	0.34	0.07
September	4	Long Beach	Y	No	0.67	0.04	0.49	0.06
September	4	Long Beach	Y	Yes	0.67	0.04	0.49	0.06
September	4	Long Beach	Z	No	0.81	0.04	0.78	0.11
September	4	Long Beach	Z	Yes	0.81	0.04	0.78	0.11

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
October	4	Copalis	A	No	0.65	0.02	0.10	0.02
October	4	Copalis	A	Yes	0.65	0.02	0.10	0.02
October	4	Copalis	B	No	0.65	0.02	0.10	0.02
October	4	Copalis	B	Yes	0.65	0.02	0.10	0.02
October	4	Copalis	C	No	0.65	0.02	0.48	0.06
October	4	Copalis	C	Yes	0.65	0.02	0.48	0.06
October	4	Long Beach	X	No	0.67	0.04	0.34	0.07
October	4	Long Beach	X	Yes	0.45	0.07	0.34	0.07
October	4	Long Beach	Y	No	0.86	0.06	0.42	0.06
October	4	Long Beach	Y	Yes	0.74	0.09	0.42	0.06
October	4	Long Beach	Z	No	0.81	0.04	0.22	0.05
October	4	Long Beach	Z	Yes	0.65	0.07	0.22	0.05
Nov - Jan[a]	8	Copalis	A	No	0.65	0.02	0.24	0.03
Nov - Jan[a]	8	Copalis	A	Yes	0.65	0.02	0.24	0.03
Nov - Jan[a]	8	Copalis	B	No	0.65	0.02	0.47	0.04
Nov - Jan[a]	8	Copalis	B	Yes	0.65	0.02	0.47	0.04
Nov - Jan[a]	8	Copalis	C	No	0.65	0.02	0.24	0.03
Nov - Jan[a]	8	Copalis	C	Yes	0.65	0.02	0.24	0.03
November	4	Long Beach	X	No	1.00	0.00	0.89	0.07
November	4	Long Beach	X	Yes	1.00	0.00	0.89	0.07
November	4	Long Beach	Y	No	1.00	0.00	0.61	0.06
November	4	Long Beach	Y	Yes	1.00	0.00	0.61	0.06
November	4	Long Beach	Z	No	1.00	0.00	0.58	0.06
November	4	Long Beach	Z	Yes	1.00	0.00	0.58	0.06
December	4	Long Beach	X	No	0.93	0.08	0.00	0.00
December	4	Long Beach	X	Yes	0.93	0.08	0.00	0.00
December	4	Long Beach	Y	No	0.79	0.07	0.10	0.04

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
December	4	Long Beach	Y	Yes	0.79	0.07	0.10	0.04
December	4	Long Beach	Z	No	0.75	0.07	0.21	0.05
December	4	Long Beach	Z	Yes	0.75	0.07	0.21	0.05
1991								
January	4	Copalis	A	No	1.00	0.00	0.10	0.02
January	4	Copalis	A	Yes	1.00	0.00	0.10	0.02
January	4	Copalis	B	No	1.00	0.00	0.27	0.04
January	4	Copalis	B	Yes	1.00	0.00	0.27	0.04
January	4	Copalis	C	No	1.00	0.00	0.50	0.05
January	4	Copalis	C	Yes	1.00	0.00	0.50	0.05
January	4	Long Beach	X	No	1.00	0.00	0.22	0.05
January	4	Long Beach	X	Yes	1.00	0.00	0.22	0.05
January	4	Long Beach	Y	No	1.00	0.00	0.38	0.06
January	4	Long Beach	Y	Yes	1.00	0.00	0.38	0.06
January	4	Long Beach	Z	No	1.00	0.08	0.36	0.06
January	4	Long Beach	Z	Yes	1.00	0.08	0.36	0.06
Feb - April[a]	11	Copalis	A	No	0.74	0.03	0.24	0.03
Feb - April[a]	11	Copalis	A	Yes	0.74	0.03	0.24	0.03
Feb - April[a]	11	Copalis	B	No	0.74	0.03	0.47	0.04
Feb - April[a]	11	Copalis	B	Yes	0.74	0.03	0.47	0.04
Feb - April[a]	11	Copalis	C	No	0.71	0.02	0.64	0.05
Feb - April[a]	11	Copalis	C	Yes	0.71	0.02	0.64	0.05
February	4	Long Beach	X	No	0.80	0.03	0.25	0.04
February	4	Long Beach	X	Yes	0.80	0.03	0.25	0.04
February	4	Long Beach	Y	No	0.80	0.03	0.11	0.03
February	4	Long Beach	Y	Yes	0.80	0.03	0.11	0.03
February	4	Long Beach	Z	No	0.80	0.03	0.02	0.01

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
February	4	Long Beach	Z	Yes	0.80	0.03	0.02	0.01
March	7	Long Beach	X	No	0.86	0.02	0.43	0.05
March	7	Long Beach	X	Yes	0.86	0.02	0.43	0.05
March	7	Long Beach	Y	No	0.58	0.07	0.26	0.04
March	7	Long Beach	Y	Yes	0.58	0.07	0.26	0.04
March	7	Long Beach	Z	No	0.86	0.02	0.29	0.04
March	7	Long Beach	Z	Yes	0.86	0.02	0.29	0.04
April	4	Copalis	A	No	0.74	0.03	0.19	0.03
April	4	Copalis	A	Yes	0.74	0.03	0.19	0.03
April	4	Copalis	B	No	0.64	0.03	0.54	0.05
April	4	Copalis	B	Yes	0.64	0.03	0.54	0.05
April	4	Copalis	C	No	0.64	0.03	0.17	0.02
April	4	Copalis	C	Yes	0.64	0.03	0.17	0.02
April	4	Long Beach	X	No	0.86	0.02	0.37	0.03
April	4	Long Beach	X	Yes	0.86	0.02	0.37	0.03
April	4	Long Beach	Y	No	0.86	0.02	0.47	0.04
April	4	Long Beach	Y	Yes	0.86	0.02	0.47	0.04
April	4	Long Beach	Z	No	0.70	0.07	0.37	0.03
April	4	Long Beach	Z	Yes	0.70	0.07	0.37	0.03
May	4	Copalis	A	No	0.59	0.04	0.34	0.05
May	4	Copalis	A	Yes	0.59	0.04	0.34	0.05
May	4	Copalis	B	No	0.64	0.03	0.65	0.05
May	4	Copalis	B	Yes	0.64	0.03	0.65	0.05
May	4	Copalis	C	No	0.92	0.08	0.65	0.05
May	4	Copalis	C	Yes	0.92	0.08	0.65	0.05
May	4	Long Beach	X	No	0.96	0.04	0.57	0.04
May	4	Long Beach	X	Yes	0.96	0.04	0.57	0.04

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
May	4	Long Beach	Y	No	0.96	0.04	0.50	0.04
May	4	Long Beach	Y	Yes	0.96	0.04	0.50	0.04
May	4	Long Beach	Z	No	0.69	0.05	0.57	0.04
May	4	Long Beach	Z	Yes	0.69	0.05	0.57	0.04
June	6	Copalis	A	No	0.59	0.04	0.19	0.03
June	6	Copalis	A	Yes	0.59	0.04	0.19	0.03
June	6	Copalis	B	No	1.00	0.00	0.44	0.05
June	6	Copalis	B	Yes	1.00	0.00	0.44	0.05
June	6	Copalis	C	No	1.00	0.00	0.27	0.05
June	6	Copalis	C	Yes	1.00	0.00	0.27	0.05
June	6	Long Beach	X	No	0.89	0.02	0.42	0.04
June	6	Long Beach	X	Yes	0.89	0.02	0.42	0.04
June	6	Long Beach	Y	No	0.89	0.02	0.42	0.04
June	6	Long Beach	Y	Yes	0.89	0.02	0.42	0.04
June - Aug[a]	10	Long Beach	Z	No	0.06	0.02	0.36	0.02
June - Aug[a]	10	Long Beach	Z	Yes	0.06	0.02	0.36	0.02
July	4	Copalis	A	No	1.00	0.00	0.44	0.04
July	4	Copalis	A	Yes	1.00	0.00	0.44	0.04
July	4	Copalis	B	No	0.71	0.13	0.44	0.03
July	4	Copalis	B	Yes	0.27	0.11	0.44	0.03
July	4	Copalis	C	No	0.64	0.03	0.44	0.03
July	4	Copalis	C	Yes	0.45	0.05	0.44	0.03
July	4	Long Beach	X	No	0.80	0.04	0.54	0.02
July	4	Long Beach	X	Yes	0.80	0.04	0.54	0.02
July	4	Long Beach	Y	No	0.55	0.04	0.54	0.02
July	4	Long Beach	Y	Yes	0.55	0.04	0.54	0.02
July	4	Long Beach	Z	No	NA	NA	0.00	0.00

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
July	4	Long Beach	Z	Yes	NA	NA	0.00	0.00
August	5	Copalis	A	No	0.62	0.05	0.05	0.01
August	5	Copalis	A	Yes	0.62	0.05	0.05	0.01
August	5	Copalis	B	No	0.90	0.13	0.38	0.10
August	5	Copalis	B	Yes	0.90	0.13	0.38	0.10
August	5	Copalis	C	No	0.72	0.09	0.18	0.04
August	5	Copalis	C	Yes	0.72	0.09	0.18	0.04
August	5	Long Beach	X	No	0.34	0.03	0.08	0.01
August	5	Long Beach	X	Yes	0.34	0.03	0.08	0.01
August	5	Long Beach	Y	No	0.71	0.04	0.09	0.01
August	5	Long Beach	Y	Yes	0.71	0.04	0.09	0.01
August	5	Long Beach	Z	No	0.75	0.18	0.79	0.09
August	5	Long Beach	Z	Yes	0.75	0.18	0.79	0.09
September	4	Copalis	A	No	1.00	0.00	0.05	0.01
September	4	Copalis	A	Yes	1.00	0.00	0.05	0.01
September	4	Copalis	B	No	0.67	0.05	0.17	0.05
September	4	Copalis	B	Yes	0.67	0.05	0.17	0.05
September	4	Copalis	C	No	1.00	0.00	0.17	0.02
September	4	Copalis	C	Yes	1.00	0.00	0.17	0.02
September	4	Long Beach	X	No	0.70	0.03	0.39	0.02
September	4	Long Beach	X	Yes	0.70	0.03	0.39	0.02
September	4	Long Beach	Y	No	0.77	0.03	0.64	0.02
September	4	Long Beach	Y	Yes	0.77	0.03	0.64	0.02
September	4	Long Beach	Z	No	1.00	NA	0.00	0.00
September	4	Long Beach	Z	Yes	1.00	NA	0.00	0.00
Oct - Dec[a]	6	Copalis	A	No	0.64	0.07	0.05	0.01
Oct - Dec[a]	6	Copalis	A	Yes	0.64	0.07	0.05	0.01

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
Oct - Dec[a]	6	Copalis	B	No	0.98	0.09	0.04	0.01
Oct - Dec[a]	6	Copalis	B	Yes	0.98	0.09	0.04	0.01
Oct - Jan[a]	12	Copalis	C	No	0.47	0.04	0.47	0.06
Oct - Jan[a]	12	Copalis	C	Yes	0.47	0.04	0.47	0.06
Oct - Dec[a]	6	Long Beach	X	No	0.84	0.04	0.43	0.02
Oct - Dec[a]	6	Long Beach	X	Yes	0.84	0.04	0.43	0.02
Oct - Jan[a]	12	Long Beach	Y	No	0.82	0.04	0.40	0.02
Oct - Jan[a]	12	Long Beach	Y	Yes	0.82	0.04	0.40	0.02
Oct - Jan[a]	12	Long Beach	Z	No	1.00	NA	0.00	0.00
Oct - Jan[a]	12	Long Beach	Z	Yes	1.00	NA	0.00	0.00
December	6	Copalis	A	No	1.00	0.00	0.04	0.01
December	6	Copalis	A	Yes	0.78	0.07	0.04	0.01
December	6	Copalis	B	No	1.00	0.00	0.10	0.03
December	6	Copalis	B	Yes	0.78	0.07	0.10	0.03
December	6	Copalis	C	No	NA	NA	0.00	0.00
December	6	Copalis	C	Yes	NA	NA	0.00	0.00
December	6	Long Beach	X	No	1.00	NA	0.00	0.00
December	6	Long Beach	X	Yes	1.00	NA	0.00	0.00
December	6	Long Beach	Y	No	NA	NA	0.00	0.00
December	6	Long Beach	Y	Yes	NA	NA	0.00	0.00
December	6	Long Beach	Z	No	NA	NA	0.00	0.00
December	6	Long Beach	Z	Yes	NA	NA	0.00	0.00
1992								
January	4	Copalis	A	No	1.00	0.00	0.04	0.01
January	4	Copalis	A	Yes	1.00	0.00	0.04	0.01
January	4	Copalis	B	No	0.64	0.05	0.45	0.06

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
January	4	Copalis	B	Yes	0.64	0.05	0.45	0.06
Jan - March[a]	8	Copalis	C	No	0.88	0.05	0.38	0.06
Jan - March[aa]	8	Copalis	C	Yes	0.88	0.05	0.38	0.06
February	4	Copalis	A	No	0.81	0.03	0.23	0.02
February	4	Copalis	A	Yes	0.81	0.03	0.23	0.02
February	4	Copalis	B	No	0.81	0.03	0.59	0.05
February	4	Copalis	B	Yes	0.81	0.03	0.59	0.05
February	4	Copalis	C	No	NA	NA	0.00	0.00
February	4	Copalis	C	Yes	NA	NA	0.00	0.00
March	4	Copalis	A	No	1.00	0.00	0.23	0.02
March	4	Copalis	A	Yes	1.00	0.00	0.23	0.02
March	4	Copalis	B	No	1.00	0.00	0.23	0.02
March	4	Copalis	B	Yes	1.00	0.00	0.23	0.02
March - May[a]	8	Copalis	C	No	1.00	0.00	0.54	0.05
March - May[a]	8	Copalis	C	Yes	1.00	0.00	0.54	0.05
April	4	Copalis	A	No	1.00	0.00	0.09	0.02
April	4	Copalis	A	Yes	1.00	0.00	0.09	0.02
April - June[a]	8	Copalis	B	No	1.00	0.00	0.47	0.04
April - June[a]	8	Copalis	B	Yes	1.00	0.00	0.47	0.04
April	4	Copalis	C	No	NA	NA	0.00	0.00
April	4	Copalis	C	Yes	NA	NA	0.00	0.00
May	4	Copalis	A	No	0.76	0.05	0.27	0.02
May	4	Copalis	A	Yes	0.76	0.05	0.27	0.02
May	4	Copalis	B	No	NA	NA	0.00	0.00
May	4	Copalis	B	Yes	NA	NA	0.00	0.00
May	4	Copalis	C	No	0.76	0.05	0.40	0.05
May	4	Copalis	C	Yes	0.76	0.05	0.40	0.05

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
June	6	Copalis	A	No	0.80	0.04	0.38	0.04
June	6	Copalis	A	Yes	0.80	0.04	0.38	0.04
June	6	Copalis	B	No	1.00	0.00	0.35	0.05
June	6	Copalis	B	Yes	1.00	0.00	0.35	0.05
June	6	Copalis	C	No	0.61	0.07	0.38	0.04
June	6	Copalis	C	Yes	0.61	0.07	0.38	0.04
July	4	Copalis	A	No	0.51	0.03	0.22	0.02
July	4	Copalis	A	Yes	0.51	0.03	0.22	0.02
July	4	Copalis	B	No	1.00	0.00	0.16	0.03
July	4	Copalis	B	Yes	1.00	0.00	0.16	0.03
July	4	Copalis	C	No	0.84	0.07	0.39	0.06
July	4	Copalis	C	Yes	0.84	0.07	0.39	0.06
August	4	Copalis	A	No	0.54	0.06	0.36	0.03
August	4	Copalis	A	Yes	0.54	0.06	0.36	0.03
August	4	Copalis	B	No	0.26	0.08	0.02	0.01
August	4	Copalis	B	Yes	0.26	0.08	0.02	0.01
August	4	Copalis	C	No	0.55	0.07	0.43	0.04
August	4	Copalis	C	Yes	0.55	0.07	0.43	0.04
September	4	Copalis	A	No	0.74	0.11	0.14	0.03
September	4	Copalis	A	Yes	0.55	0.11	0.14	0.03
September	4	Copalis	B	No	0.74	0.11	0.14	0.02
September	4	Copalis	B	Yes	0.55	0.11	0.14	0.02
September	4	Copalis	C	No	0.74	0.11	0.14	0.02
September	4	Copalis	C	Yes	0.55	0.11	0.14	0.02
October	4	Copalis	A	No	0.76	0.06	0.14	0.02
October	4	Copalis	A	Yes	0.76	0.06	0.14	0.02
October	4	Copalis	B	No	1.00	0.06	0.14	0.02

Table A.1 (continued):

Month	Weeks Between	Beach	Level	Biopsy	Survival Probability	S.E.	Capture Probability	S.E.
October	4	Copalis	B	Yes	1.00	0.06	0.14	0.02
October	4	Copalis	C	No	0.76	0.06	0.14	0.02
October	4	Copalis	C	Yes	0.76	0.06	0.14	0.02
Nov-March[a]	16	Copalis	A	No	0.55	0.12	0.14	0.02
Nov-March[a]	16	Copalis	A	Yes	0.55	0.12	0.14	0.02
Nov-March[a]	16	Copalis	B	No	0.55	0.12	0.30	0.04
Nov-March[a]	16	Copalis	B	Yes	0.55	0.12	0.30	0.04
Nov-March[a]	16	Copalis	C	No	0.88	0.12	0.56	0.06
Nov-March[a]	16	Copalis	C	Yes	0.88	0.12	0.56	0.06
1993								
March	4	Copalis	A	No	NA	NA	0.14	0.02
March	4	Copalis	A	Yes	NA	NA	0.14	0.02
March	4	Copalis	B	No	NA	NA	0.26	0.05
March	4	Copalis	B	Yes	NA	NA	0.26	0.05
March	4	Copalis	C	No	NA	NA	0.25	0.05
March	4	Copalis	C	Yes	NA	NA	0.25	0.05

a. Note that these areas had zero recaptures during the interval. Thus, we can only get multi-monthly estimates of survival during these intervals. Capture probabilities reflect the probability of being recaptured in the terminal month of the interval.

Appendix B - Kolmogorov-Smirnov Test Results

Table B.1: Kolmogorov-Smirnov Test Results for Razor Clam Recaptures with NIX Readings at Copalis and Long Beach

Month	Beach	Level	Number Recaptured	KS Test Max Difference	KS Test P-value
1990					
August 1990	Copalis	All	31	0.14	0.81
August 1990	Copalis	A	4	0.52	0.31
August 1990	Copalis	B	10	0.23	0.87
August 1990	Copalis	C	17	0.31	0.49
August 1990	Long Beach	All	32	0.11	0.96
August 1990	Long Beach	X	13	0.28	0.64
August 1990	Long Beach	Y	13	0.15	0.99
August 1990	Long Beach	Z	6	0.46	0.23
September 1990	Copalis	All	29	0.14	0.81
September 1990	Copalis	A	11	0.25	0.74
September 1990	Copalis	B	5	0.37	0.61
September 1990	Copalis	C	13	0.42	0.15
September 1990	Long Beach	All	57	0.14	0.39
September 1990	Long Beach	X	6	0.31	0.67
September 1990	Long Beach	Y	37	0.31	0.67
September 1990	Long Beach	Z	14	0.43	0.16
October 1990	Copalis	All	48	0.15	0.42
October 1990	Copalis	A	14	0.33	0.20
October 1990	Copalis	B	9	0.22	0.41
October 1990	Copalis	C	25	0.41	0.01**

Table B.1 (continued):

Month	Beach	Level	Number Recaptured	KS Test Max Difference	KS Test P-value
October 1990	Long Beach	All	62	0.13	0.38
October 1990	Long Beach	X	14	0.37	0.08*
October 1990	Long Beach	Y	26	0.12	1.00
October 1990	Long Beach	Z	16	0.09	1.00
November 1990	Copalis	All	49	0.16	0.26
November 1990	Copalis	A	15	0.14	0.98
November 1990	Copalis	B	15	0.28	0.30
November 1990	Copalis	C	19	0.36	0.04*
November 1990	Long Beach	All	88	0.16	0.08*
November 1990	Long Beach	X	21	0.26	0.21
November 1990	Long Beach	Y	37	0.13	0.89
November 1990	Long Beach	Z	26	0.16	0.79
December 1990	Long Beach	All	50	0.17	0.18
December 1990	Long Beach	X	8	0.58	0.01**
December 1990	Long Beach	Y	31	0.11	0.97
December 1990	Long Beach	Z	17	0.19	0.73
1991					
July 1991	Copalis	All	49	0.09	0.99
July 1991	Copalis	A	8	0.26	0.82
July 1991	Copalis	B	20	0.42	0.13
July 1991	Copalis	C	21	0.21	0.87
July 1991	Long Beach	All	40	0.14	0.70
July 1991	Long Beach	X	18	0.24	0.73

Table B.1 (continued):

Month	Beach	Level	Number Recaptured	KS Test Max Difference	KS Test P-value
July 1991	Long Beach	Y	20	0.58	0.01**
July 1991	Long Beach	Z	2	0.32	0.99
August 1991	Copalis	All	38	0.20	0.19
August 1991	Copalis	A	8	0.40	0.21
August 1991	Copalis	B	14	0.14	0.98
August 1991	Copalis	C	16	0.23	0.53
August 1991	Long Beach	All	37	0.14	0.62
August 1991	Long Beach	X	15	0.17	0.89
August 1991	Long Beach	Y	20	0.29	0.30
August 1991	Long Beach	Z	2	0.32	0.99
September 1991	Copalis	All	39	0.26	0.02*
September 1991	Copalis	A	5	0.46	0.28
September 1991	Copalis	B	9	0.24	0.72
September 1991	Copalis	C	25	0.37	0.02*
September 1991	Long Beach	All	50	0.15	0.36
September 1991	Long Beach	X	11	0.18	0.91
September 1991	Long Beach	Y	36	0.31	0.05*
September 1991	Long Beach	Z	5	0.42	0.39
October 1991	Long Beach	All	49	0.17	0.21
October 1991	Long Beach	X	13	0.25	0.44
October 1991	Long Beach	Y	32	0.33	0.02*
October 1991	Long Beach	Z	11	0.17	0.94

Table B.1 (continued):

Month	Beach	Level	Number Recaptured	KS Test Max Difference	KS Test P-value
1992					
June 1992	Copalis	C	17	0.28	0.64
July 1992	Copalis	All	37	0.11	0.97
July 1992	Copalis	A	11	0.18	0.98
July 1992	Copalis	B	15	0.23	0.76
July 1992	Copalis	C	11	0.25	0.38
August 1992	Copalis	All	43	0.15	0.45
August 1992	Copalis	A	11	0.35	0.24
August 1992	Copalis	B	12	0.40	0.18
August 1992	Copalis	C	20	0.17	0.69
September 1992	Copalis	All	30	0.14	0.70
September 1992	Copalis	A	3	0.67	0.16
September 1992	Copalis	B	11	0.32	0.32
September 1992	Copalis	C	16	0.23	0.40
October 1992	Copalis	All	25	0.18	0.52
October 1992	Copalis	A	2	0.78	0.20
October 1992	Copalis	B	8	0.37	0.32
October 1992	Copalis	C	15	0.30	0.15
November 1992	Copalis	All	17	0.17	0.79
November 1992	Copalis	A	0	NA	NA
November 1992	Copalis	B	6	0.53	0.09*
November 1992	Copalis	C	11	0.28	0.50

Appendix C - Data Layout

A diskette that contains all the release-recapture data is included (See Pocket Material). Length and release-recapture data from Long Beach can be found under lb0on.dat. Length and release-recapture data from Copalis can be found under cop0on.dat. NIX Intensity data for both beaches is also included on the disk. NIX Intensity data for Long Beach can be found under lbnix0.dat. NIX Intensity data for Copalis can be found under copnix0.dat.

All data begin at the first release (July 1990) and continue until April 1993. Entries in the datafiles that contain length resemble the following:

```
35 35 35 35 35 0 35 0 35 35 35 35 35 35 50 35 29 50

1XC   1 0 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0   9.00
2XC   1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0   8.20
3XC   1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0   14.60
```

where the first line is the number of newly-marked clams released on each occasion and subsequent lines contain the capture histories. The first entry in each line of capture histories is the unique clam ID. The ID is followed by the capture history. The final entry in each line is the length that was measured at the first release.

All datafiles that contain NIX data look slightly different. As before, the first entry in each line of capture histories is the unique clam ID, the ID is followed by the capture history, and the final entry in each line is the length that was measured at the first release. However, between the final capture and the length, the NIX Intensity is recorded (i.e., clam 2XN has length of 8.30 and NIX Intensity of 2).

```
2XN   1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0   2   8.30
```

Appendix D - Estimating Proportion of Juveniles

The density of recruits at time "t" was regressed against the total clam density at time "t" to determine whether a linear relationship existed between these two variables. The analysis indicated that the linear relationship provided a very good fit to the data (Table D.1). In all cases but one, the inclusion of a non-zero intercept term did not significantly ($p=0.10$) improve the fit of the model. At Twin Harbors, the non-zero intercept was significant. However, the explanatory power was not improved much ($r^2 = 0.95$ with zero-zero intercept vs. $r^2 = 0.96$ with non-zero intercept), so the zero-zero intercept was retained. Nonlinear models of the forms

$$R = \frac{\alpha T}{\beta + T} + \gamma \text{ and}$$

$$R = \alpha T \cdot \exp(\beta T) + \gamma$$

where

R = Recruits,

T= Total, and

α, β, γ = Parameters to be estimated

were tested, but did not provide improved fits. For nested models, an F-test was used to determine the significant model. For cases in which the linear and nonlinear models were not nested, improved fit was assessed visually.

At Mocrocks, data from 1976 was an outlier that suggested a higher than usual percentage of recruits to adults than was typical for the rest of the data. This point was removed from the analysis to provide a better description of the typical proportion of juveniles to adults. At Long Beach, data from 1957 and 1958 suggested a lower than usual

Table D.1: ANOVA tables for the linear regression results relating current recruitment density to current total density.

Mocrocks

Source	df	SS	MS	F	P(F)
Total Density	1	243.158	243.158	717.68	0
Error	31	10.03	0.339		

Copalis

Source	df	SS	MS	F	P(F)
Total Density	1	69.700	69.700	387.07	0
Error	36	6.424	0.178		

Twin Harbors

Source	df	SS	MS	F	P(F)
Total Density	1	31.568	31.568	668.12	0
Error	34	1.606	0.047		

Long Beach

Source	df	SS	MS	F	P(F)
Total Density	1	35.902	35.902	441.14	0
Error	33	2.686	0.081		

percentage of recruits to adults than was typical for the rest of the data. These points were removed from the analysis to provide a better description of the typical proportion of juveniles to adults.

Name: J. Warren Schlechte, Ph.D.

Goals:

My primary interest is the study of interactions between environmental variables and fisheries population dynamics. I am interested in how these processes can affect the design of subsequent harvest management strategies. Finally, I am interested in quantifying the uncertainty associated with stock assessment models and assessing the risk of different management policies. I have included all of these interests in my dissertation.

Education:

BS - Marine Biology from Texas A&M University - 1985

GPA - 3.8

Honors:

Marine Science Award

Swetnam Memorial Scholarship

Who's Who in American College Students

National Dean's List

Texas A&M University Dean's List

Spring Awards 1982-1985

MS - Wildlife and Fisheries Sciences from Texas A&M University - 1989

Thesis Title: "Routine Metabolism and Critical Oxygen Concentration for Juvenile Red Drum (*Sciaenops ocellatus*) as Functions of Water Hardness and Salinity."

GPA - 3.6

Honors:

Lechner Fellowship

Ph.D. - Fisheries from University of Washington

Dissertation Title: "Stage-Structured Analysis and Modeling of the Pacific Razor Clam (Siliqua patula) in a Changing Environment: Investigation of population dynamics and harvest strategies using process models and simulation."

GPA - 3.6

Honors:

Melvin G. Anderson Memorial Scholarship

Richard van Cleve Memorial Scholarship

Finalist for Keeler Fellowship

Professional Experience:

Date: Present

Employer: University of Washington **Title:** Graduate Research Assistant

Responsibilities: I am currently working on a project that will incorporate Markov Chain Monte Carlo modeling to study salmon movement around dams. My primary responsibilities will be to build the mathematical model and to analyze the data. I am writing the code and developing the user interface in Excel/Visual Basic.

Date: Fall 1993 - Present

Employer: University of Washington **Title:** Graduate Research Assistant

Responsibilities: I did the example analyses on known-fate and release-recapture data for the SURPH.1 manual. I wrote the chapters in the SURPH.1 manual that dealt with how to implement all the various options of the SURPH program, how to format the data files, and how to analyze example data sets using the SURPH program. I also wrote several chapters on new utilities in SURPH.1 and a chapter on how to use SURPH-PC (i.e., the Windows version of SURPH).

Date: Summer 1995

Employer: Skalski Statistics Inc. **Title:** Consultant - Subcontractor

Responsibilities: I analyzed harvest data from mule deer to determine whether habitat improvements had resulted in increased buck abundance. I wrote two reports characterizing our findings.

Date: 1990 - Present

Employer: University of Washington **Title:** Graduate Research Assistant

Responsibilities: I studied the population dynamics of the Pacific razor clam (*Siliqua patula*) along 4 Washington beaches. I gathered data on survival, disease intensity and growth through three years of field work. I established disease intensity levels within individual clams through 1 year of lab work. I analyzed data using various statistical and modelling techniques. I have defined the relationships between disease and survival, growth, and recruitment in population dynamics models. I created a simulation model and simulated the dynamics under various management strategies. I have written three reports detailing earlier work and my dissertation.

Date: Fall 1993 (Intermittently)

Employer: University of Washington **Title:** Teaching Assistant

Responsibilities: I substitute taught several different classes whenever the professors had other obligations. The classes that I taught were Introduction to Biostatistical Analysis I and II (senior and graduate level introductory statistical classes), and Calculus I (a sophomore level introductory calculus class).

Date: Summer 1993

Employer: University of Washington **Title:** Teaching Assistant

Responsibilities: I taught Introduction to Biostatistical Analysis I, a senior and graduate level introductory statistical class. I taught four one hour classes and a two-hour lab each week. I wrote and graded homework problems and tests.

Date: 1988 - 1990

Employer: Baylor College of Medicine - Pharmacology

Beginning Title: Research Technician II.

Ending Title: Research Technician III

Responsibilities: I used molecular biological techniques (i.e., Western blots, Northerns, Southerns) to analyze the effects of receptor-bound urokinase in colon cancer cell lines. The results of these studies were published in 3 journal articles. I also kept track of the budget and ordering for the project. I taught molecular biological techniques to a visiting graduate student and I supervised a summer work student.

Date: 1985 - 1988

Employer: Texas A&M University **Title:** Graduate Research Assistant

Responsibilities: I modified a computer program that automated control of and took readings from multiple respirometers. I examined the effects of salinity and water hardness on the routine metabolic rates and critical oxygen concentration in juvenile red drum. I analyzed the data using analysis of covariance. I reported the results of the study in the form of a thesis.

Publications/Reports:

Steven G. Smith, John R. Skalski, J. Warren Schlechte, Annette Hoffmann, and Victor Cassen. Submitted. Introduction to SURPH.1 analysis of release-recapture data for survival studies. Report to the Bonneville Power Administration. 300 pp.

Steven G. Smith, John R. Skalski, J. Warren Schlechte, Annette Hoffmann, and Victor Cassen. 1994. Statistical Survival Analysis of Fish and Wildlife Tagging Studies. SURPH.1 manual. 526 pp.

J. Warren Schlechte and John R. Skalski. 1995. Abundance Trends of Mule Deer Bucks in GMUs 248, 254 and 272. Report for the Washington Department of Fish and Wildlife. 36 pp.

J. Warren Schlechte and John R. Skalski. 1995. Harvest Trends of Trophy Mule Deer Bucks in GMU 136. Report for the Washington Department of Fish and Wildlife. 12 pp.

W. Schlechte and J. R. Skalski. 1991. Estimates of razor clam survival probabilities and risk factors associated with NIX. 1991 Annual Report to Washington Department of Fisheries. 27 pp.

W. Schlechte and J. R. Skalski. 1993. NIX Annual Report. 1992 Annual Report to Washington Department of Fisheries. 39 pp.

W. Schlechte and J. R. Skalski. 1993. Estimates of razor clam survival rates and risk factors associated with Size and NIX. 1993 Annual Report to Washington Department of Fisheries. 73 pp.

W. Schlechte, M. Brattain, and D. Boyd. 1990. "Invasion of extracellular matrix by cultured colon cancer cells: dependence on urokinase receptor display." Cancer Communications 2(5). pp. 173-9.

J. W. Schlechte, D. D. Boyd. 1990. "Insensitivity of laminin degradation by receptor bound urokinase to PAI-1 in cultured colon cancer." Cancer Communications 2(8). pp. 261-9.

W. Schlechte, G. Murano, and D. Boyd. 1989. "Examination of the role of the urokinase receptor in human colon cancer mediated laminin degradation." Cancer Research 49(21). pp. 6064-69.

J. Warren Schlechte. 1989. "Routine Metabolism and Critical Oxygen Concentration for Juvenile Red Drum (*Sciaenops ocellatus*) as Functions of Water Hardness and Salinity." MS thesis, Texas A&M University, College Station.

Meetings:

1995 Graduate Student Symposium, University of Washington - "Nix on NIX: Research on Disease Effects on the Pacific Razor Clam."

14th Pacific Coast Resource Modelling Conference, Juneau, AK - "Modelling Razor Clam Survival and Recruitment."

1995 Graduate Student Symposium on Fish Population Dynamics and Management, University of British Columbia - "Investigations into the Dynamics of the Pacific Razor Clam along the Washington Coast."

45th Annual Meeting - National Shellfisheries Association - Pacific Coast Section. - "Pacific Razor Clam Survival and Capture on Two Washington Beaches"

Texas Academy of Sciences - 1989. "Routine Metabolism and Critical Oxygen Concentration for Juvenile Red Drum (*Sciaenops ocellatus*) as Functions of Water Hardness and Salinity."

References:

Dr. J. R. Skalski - University of Washington
Columbia Basin Research
Box 358218
Seattle, WA 98195-8218

jrs@cqs.washington.edu

(206)616-7455

Dr. Steven G. Smith - Northwest Fisheries Science Center
2725 Montlake Blvd.
Seattle, WA 98112

sgs@tyee.nwfsc.noaa.gov

(206)860-3352

Dr. Vincent Gallucci- University of Washington
Center for Quantitative Sciences
Box 355230
Seattle, WA 98195-5230

gallucci@cqs.washington.edu

(206)543-1191

Dr. William H. Neill- Texas A&M University
Dept. of Wildlife and Fisheries Sciences
210 Nagle Hall
College Station, TX 77840

w-neill@tamu.edu

(409)845-5777

Dan Ayres - Washington Dept. Fish and Wildlife
48A Devonshire Rd.
Montesano, WA 98563

ayresdla@dfw.wa.gov

(360)249-4628