Title

Biology and Long-Term Trends of Alien Hydromedusae and Striped Bass in a Brackish Tidal Marsh in the San Francisco Estuary

Author

Schroeter, Robert E.

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By

Robert Egon Schroeter
B.S. (University of California, Davis) 1993
M.S. (University of Nevada, Reno) 1998

DISSERTATION

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DAVIS

Approved:

William A Bennett
William A. Bennett

Edwin D. Grosholz
Edwin D. Grosholz

Peter B. Moyle

Committee in Charge

2008

ProQuest LLC
789 E. Eisenhower Parkway
PO Box 1346
Ann Arbor, MI 48106-1346

Robert Egon Schroeter
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ABSTRACT

Pelagic fish declines and increased abundance of gelatinous zooplankton are increasingly common in physically and ecologically disturbed estuaries. This dissertation investigates the ecology and trends of three alien hydromedusae (*Maeotias marginata, Blackfordia virginica,* and *Moerisia* sp.) and striped bass *Morone saxatilis* in Suisun Marsh in the upper San Francisco Estuary. Chapter one examines the ecology and long term (1981-2005) trends of *M. marginata* medusae using by-catch data from an otter trawl survey. *Maeotias marginata* increased in abundance with its greatest spatial occurrence and abundance after 1992. Salinity and temperature were significant predictors of medusae abundance with moderate salinity and high temperature resulting in their highest abundance. Water transparency was related to medusae abundance, but had a smaller effect. Medusae fed primarily on pelagic invertebrates, although benthic / epibenthic prey and larval fishes were also found in the gut contents. Chapter two reports the environmental relationships and abundance of three hydromedusae from a two year (February 2004 to January 2006) plankton study. *Moerisia* was the most abundant species, followed by *M. marginata* and *B. virginica.* Salinity and temperature had the largest effect on predicted occurrence and abundance although turbidity and dissolved oxygen were significant at times. *Maeotias marginata* was captured at the lowest salinity and temperature and was the first and last species captured each year. *Moerisia* was captured in samples with slightly higher salinity, but similar temperatures as *M. marginata. Blackfordia virginica* was captured in moderate to high salinity. Chapter three investigates the seasonal trends in striped bass young-of-year (YOY) abundance (1980 to 2005) and their environmental relationships, habitat use, and prey relationships. Striped bass YOY declined in deep water sites, but not in shallow tidal marsh sites. Environmental conditions were poorly correlated with striped bass abundance in all seasons. Prey species declined similarly in all depth groups. The declining abundance of mysids and adult copepods were correlated with the YOY decline in deep water sites only. Increased mean YOY length and seasonal recruitment shifts after the decline of mysids, suggests additional affects of changing prey abundance.

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Finally, to my daughter and son Gabriella and Justin, thank you for letting me see the world through your eyes, as you have continuously reminded me that life should be cherished, and filled with curiosity, excitement, and just enough comic relief to get through the rough spots; traits that any field ecologist would find useful.

DEDICATION

I dedicate this dissertation to you Gabriella and Justin Schroeter.
May you go forth and continue to explore all the world has to offer, with open hearts and minds.

TABLE OF CONTENTS

Chapter 1.
Ecology and Long Term Trends of the Invasive Gelatinous Zooplankton, *Maeotias marginata* in the San Francisco Estuary

Chapter 2.
Biology and Habitat Use of a Brackish Tidal Marsh in the San Francisco Estuary by a Trio of Alien Hydromedusae

TABLE OF CONTENTS cont.

ACRONYMS

Akaike's Information Criteria	AIC
All Time Period	ATP
Contra Costa Water District	CCWD
California Department of Fish and Game	CDFG
California Department of Water Resources	CDWR
Central Valley Project	CVP
Fairfield-Solano Sewer District	FSSD
Dissolved Oxygen	DO
Generalized Linear Models	GLM
Goodness of Fit	GIF
Honest Significant Difference	HSD
Inter-agency Ecological Program for the San Francisco Estuary	IEP
Likelihood Ratio	LR
Negative Binomial	NB
San Francisco Estuary	SFE
State Water Project	SWP
Suisun March Salinity Control Gates	SMSCG
Variance Inflation Factor	VIF
Yellow Springs Instruments	YSI
Young-of-Year	YOY

INTRODUCTION

Estuarine communities are increasingly being affected by a number of disturbances that alter community composition, population abundances and system productivity (Caddy 1993; Cohen and Carlton 1998). In some instances, alien species have altered the ecological function and structure of estuarine communities (Alpine and Cloern 1992; Kimmerer et al. 1994; Shiganova and Bulgakova 2000). Combined with additional anthropogenic impacts, estuarine communities are often significantly and negatively affected (Bennett and Moyle 1996; Bilio and Niermann 2004).

Estuaries are important aquatic habitats recognized for their high productivity and significant contribution to fisheries (Houde and Rutherford 1993). Tidal marshes are recognized as being an integral component of estuaries due to their complexity of habitat, large contribution of nutrients and productivity, and importance for rearing (McIvor and Odum 1988; Houde and Rutherford 1993; Beck et al. 2001). However, the proximity of estuarine tidal marshes to major urban centers often results in their extensive modification and loss (Nichols et al. 1986; Edgar et al. 2000).

In the San Francisco Estuary (SFE), more than 95% of the historic wetlands have been lost. This has likely resulted in significant impacts to aquatic species dependent upon these habitats, for at least a portion of their life. Furthermore, Cohen and Carlton (1998) identified the SFE as the most invaded estuary in the world stemming from the vast number of established alien species including flora and fauna (234 species with an additional 125 cryptogenic species). Several alien species have had a particularly large impact on the SFE food web, such as the overbite clam *Corbula amurensis* (Kimmerer et al. 1994; Kimmerer and Orsi 1996; Feyrer et al. 2003). The ecology and impacts of many of the alien invasive species are relatively unknown.

This work examines two components of a community of aquatic organisms that inhabit Suisun Marsh, a large brackish tidal marsh in the upper SFE. The first component of this work (Chapters 1 and 2) investigates the biology and habitat use of three alien invasive hydromedusae (*Maeotias marginata, Blackfordia virginica,* and *Moerisia* sp.) and in the case of one species, *Maeotias marginata,* the trends in abundance over 25 years of study (1981-2005). These three hydromedusae, native to the Black Sea, are becoming a prominent feature of many estuarine communities (Mills 2001). Yet, surprisingly little is known about their biological requirements, habitat use, and potential impacts where they have been introduced.

The second component of this work (Chapter 3) investigates the trends in abundance, habitat use, and prey relationships of striped bass young-of-year (YOY), an intentionally introduced game fish, which is extensively monitored and managed in the system, but has none-the-less declined in many habitats of the SFE. The striped bass is among many pelagic species that have declined in abundance in the low salinity zone of the SFE over the last three decades (Sommer et al. 2007). There are several plausible mechanisms for the observed pelagic organism decline and the low abundance of pelagic invertebrate prey, especially in the summer and fall months, has likely played a large role (Kimmerer 2000; Feyrer et al. 2003; Bennett 2005). Although the decline of striped bass in the SFE has been independently verified by many of the monitoring programs (Kimmerer 2000), most of these studies primarily sample the large bay and river channels, increasing the need for further study of the shallower tidal marshes.

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CHAPTER 1

Ecology and Long Term Trends of the Invasive Hydromedusa, *Maeotias Marginata*, in the San Francisco Estuary

1.1 INTRODUCTION

Estuaries are important aquatic habitats recognized for their high productivity and significant contribution to fisheries (Houde and Rutherford 1993). Estuarine communities are increasingly being affected by a number of disturbances that are altering community composition, population abundances and overall system productivity (Nichols et al. 1986; Caddy 1993; Cohen and Carlton 1998). Estuaries are inhabited by a diverse assemblage of aquatic organisms; therefore, any loss of system integrity and productivity can have wide ranging consequences. An area of estuarine ecology and conservation that has received increased attention in recent years is the ecosystem impact resulting from the introduction of alien species (Ruiz et al. 1997, 2000; Cohen and Carlton 1998; Moyle 1999; Carlton 2000; Grosholz 2002; Paavola 2005). It has been observed that these introductions can have major consequences, especially when acting together with other estuarine disturbances.

A group of alien invasive species (and native species) that are increasing in abundance in estuaries worldwide are the gelatinous zooplankton (Mills 1995; 2001). Numerous anthropogenic factors are fueling this increase, beginning with accelerated movement and introduction through shipping activities and associated ballast water transfer (Mills 1995; 2001) and through changes in the connectivity of estuaries and seas following removal of geophysical barriers (e.g., Grigorovich et al. 2002). Abiotic changes in estuaries are also contributing to the increasing trends of some alien invasive and native gelatinous zooplankton (Mills 2001). These changes include increased eutrophication following excess nutrient input and the resulting degradation of water quality (Arai 2001; Purcell et al. 2001b; Breitburg et al. 2003; Decker et al. 2004). In addition, salinity and temperature shifts resulting from both anthropogenic changes to freshwater flow (water diversion and flow alteration in tributaries) and climate fluctuations (eg. Pacific Decadal Oscillations, El Nino Southern Oscillation, and North Atlantic Oscillation) and climate change have also contributed to increasing populations of gelatinous zooplankton (Studenikina et al. 1991; Brodeur et al. 1999; Purcell et al. 1999; Vörösmarty et al. 2000; Graham 2001; Purcell 2005; Lynam et al. 2005a).

In addition, food web disruption and alteration stemming from the over-harvest of fish in marine and estuarine waters is likely contributing to the success of alternative or novel predator species such as gelatinous zooplankton (Caddy 1993; Mills 1995; 2001; Pauly et al. 1998; Link and Ford 2006; Lynam et al. 2006). This is likely a response to decreased competition for prey resources and the compensatory increase in invertebrate prey available to gelatinous zooplankton following reduced predation pressure by fishes.

The introduction of gelatinous zooplankton into estuaries and inland seas has, at times, resulted in significant ecological impacts such as in the Black Sea (e.g. Vinogradov et al.1989; Studenikina et al. 1991; Purcell et al. 2001a; Shiganova and Bulgakova 2000; Shiganova et al. 2003), Caspian Sea (Ivanov et al. 2000), Mediterranean (Lotan et al. 1992; Mills 2001), and the Gulf of Mexico (Graham et al. 2003). Gelatinous zooplankton can be significant pelagic predators with an ability to deplete fish stocks, reduce zooplankton abundance and alter community composition (Purcell 1992; Purcell et al. 1994; Schneider and Behrends 1998; Shiganova 1998; Brodeur et al. 1999; Purcell and Aria 2001; Purcell et al. 2001a; Brodeur et al. 2002; Lynam et al. 2005b). Estuaries are important nursery areas for oligohaline, mesohaline, and euryhaline fishes and invertebrates, whose eggs, larvae and juveniles are especially vulnerable to predation. Thus, the effects of predation and or competition by a novel predator can have wide ranging consequences. This is especially true in highly disturbed estuaries where vulnerable species may already be in a state of decline.

The purpose of this study is to examine the ecology of *Maeotias marginata*, an alien invasive hydromedusa, in order to determine if it may be having negative effects on zooplankton and fish in the San Francisco Estuary (SFE). Native to the Black Sea and Sea of Azov, *M. marginata* has been widely introduced into many different regions of the world with unknown consequences to the fish and invertebrate communities (Calder and Burrell 1967, 1969; Mills and Sommer 1995; Mills and Rees 2000; Rees and Gershwin 2000; Mills 2001; Vainola and Oulasvirta 2001). Here, I document the population trends, biology, and diet of *M. marginata* medusae and the factors contributing to its recent success in Suisun Marsh, part of the SFE, using data from a long term (25 year) monitoring study. My study was designed to answer the following questions: (1) Has the abundance, patterns of occurrence, and distribution of *M. marginata* medusae changed over the past 25 yrs? (2) How does the distribution and abundance of *M. marginata* vary with salinity, temperature, water clarity, and dissolved oxygen? (3) What environmental changes in Suisun Marsh and the larger SFE are contributing to the observed trends in abundance of *M. marginata*? (4) Does the spatial and temporal overlap with pelagic fishes in the system and diet of *M. marginata* medusae suggest potential competition with or predation on fishes?

1.1.1 Basic Biology of *Maeotias Marginata*

Maeotias marginata is a moderately sized hydrozoan reaching a maximum bell diameter of 40 mm in its native range (Black Sea - Ponto Caspian Region) and 50 mm in the SFE (Mills and Sommer 1995). The date of introduction of *M. marginata* into the SFE is unknown, but it is believed to have been present as early as 1959 based upon field notes from the California Department of Fish and Game and U. S. Fish and Wildlife (see Rees and Gershwin, 2000). The mode of introduction is also unknown, although ballast water transfer or attachment and transfer on ship hulls are the most likely mechanisms (Mills and Sommer 1995). The first published account of this species in the SFE was for a population occupying Petaluma Marsh, a system draining into San Pablo Bay (Mills and Sommer 1995). In the late 1990s, it was reported that the population began to invade, or more appropriately reinvade, low salinity tidal marshes, bays, and river systems adjacent to and upstream of Petaluma Marsh including the Napa River, Suisun Marsh, Grizzly Bay, and the lower reaches of the Sacramento River (Rees and Gershwin 2000).

The life cycle of *M. marginata* has been described in part by Rees and Gershwin (2000) and consists of two main stages including the free swimming medusa stage and the sessile polyp stage. The polyp stage of *M. marginata* is still poorly known, largely due to the difficulty of rearing them in the laboratory (Rees and Gershwin 2000). Cultured specimens in the early developmental stage are very small, simple in structure and are lacking tentacles (Rees and Gershwin 2000). Further structural changes during polyp development are possible.

Maeotias marginata can reproduce sexually during the medusa stage with fertilized eggs developing directly into polyps rather than passing through the planular larval phase (Rees and Gershwin 2000). Although it has not yet been observed for *M. marginata*, nearly all polyps are capable of reproducing asexually through a process termed budding. When environmental conditions become appropriate, polyps release larval medusae from medusa buds and this release of larvae drives rapid population increases called “blooms”. The time of development to the mature adult stage from larvae has not been reported for *M. marginata,* but is quite rapid for other gelatinous zooplankton under well fed conditions (Mills 1995; Ishii and Bâmstedt 1998; Ma and Purcell 2005). The medusa stage appears to be seasonal in the SFE with their presence reported between summer and fall (Rees and Gershwin 2000). The longevity of the polyp stage has not been reported.

Medusae of *M. marginata* have been found in a variety of habitats, but may prefer areas that are relatively shallow, generally < 10m depth (Vainola and Oulasvirta, 2001). *Maeotias marginata* is considered a true brackish water species, but temperature and salinity tolerances have been established only with anecdotal information and limited laboratory studies. Calder and Burrell (1967; 1969) reported that *M. marginata* was found in salinities as low as 1.2 ‰, although in Suisun Marsh they can be found at salinities as low as 0.9‰ (unpublished data). Mills and Sommer (1995) reported a range of salinities from field studies of 4.2 to 10.7‰ and laboratory-maintained specimens suffered mortality at salinities greater than 13‰. Observed water temperatures at site of capture were usually greater than 15 °C (Vainola and Oulasvirta, 2001; Rees and Gershwin 2000) although in Suisun Marsh they have been found at temperatures as low as 8.3°C (unpublished data). Reproduction has been noted under laboratory conditions at temperatures between 18 and 21 °C (Rees and Gershwin 2000). The effect of other water quality parameters on *M. marginata* medusae occurrence and abundance, including water transparency and dissolved oxygen (DO), have not been reported in the published literature.

Maeotias marginata have a typical hydromedusan vertical feeding migration, rising to the surface and drifting back to the bottom exumbrella down with tentacles outstretched where they may stay for a period of time (Mills and Sommer, 1995; Vainola and Oulasvirta, 2001). This behavior likely allows *M. marginata* the ability to catch both pelagic and benthic prey and increases the chance of finding patchy prey resources. From the single published diet study (Mills and Sommer 1995), it has been observed that *M. marginata* medusae have relatively high feeding rates (mean 37 prey·medusae^{-1}) and they had a wide variety of prey in their gut contents including pelagic, benthic and terrestrial organisms, with pelagic prey making up a majority of the diet. The most abundant taxonomic groups in their study (excluding copepod egg sacs from the total count) were the barnacle nauplii (39%), various stages of copepods (30%), and crab zoea (27%). No larval fish or juvenile fish were found in the gut contents of field caught medusae, although Mills and Sommer (1995) observed that medusae did prey upon guppies in laboratory aquaria, raising the possibility of predation on early stage fishes in the wild.

Aside from the diet work conducted by Mills and Sommer (1995), the feeding ecology of *M. marginata* is poorly known and its abundance has not been well studied, making its impact on the pelagic and benthic community difficult to determine. It appears that this species may occasionally become abundant enough to be a significant predator in the pelagic community, as Mills and Sommer (1995) suggest for the population occupying the Petaluma River, a tributary to the SFE. The high abundance of *M. marginata* in the SFE may be an exceptional case, since this species has not been reported as a nuisance organism in the published literature and may be quite rare even in its native habitat (see Mills and Sommer 1995; Mills and Rees 2000; Rees and Gershwin; Vainola and Oulasvirta 2001). Other locations where *M. marginata* has been introduced and detected include Chesapeake Bay and several other estuaries along the Atlantic Coast of North America, and the Baltic Sea (Calder and Burrell 1967, 1969; Mills and Sommer 1995; Mills and Rees 2000; Rees and Gershwin 2000; Mills 2001; Vainola and Oulasvirta 2001).

1.2 METHODS

The patterns of *M. marginata* medusae distribution, abundance and relationship to environmental conditions in Suisun Marsh were determined using data from a long term University of California, Davis monitoring program on the fishes and macro invertebrates in Suisun Marsh, Solano County, California. The results of the fish monitoring study have been published previously (e.g. Meng et al. 1994; Matern et al. 2002), but data on the population abundance and trends of *M. marginata* medusae have not been reported.

1.2.1 Study Area

Suisun Marsh (Figure 1.1) is a large brackish tidal marsh (approximately 340 km^2) in the upper SFE. Approximately one-third of the marsh is tidally influenced and the remainder consists primarily of diked wetlands managed to attract waterfowl. Water inputs to the marsh are provided by a number of sources including tidal intrusion from Grizzly Bay through lower Suisun and Montezuma Sloughs, river flow from the Sacramento and San Joaquin Rivers (i.e., inflow which is measured at Chipps Island near the start of Montezuma Slough), and several small local tributaries including Green Valley, Suisun, Ledgewood, Union and Denverton creeks. The majority of fresh water enters the upper SFE through the Sacramento and San Joaquin Rivers as winter rain pulses and a snow melt driven peak flow that usually occurs in spring. This is followed by reduced and more steady flow during the summer and fall dry-season. There is high annual variation in inflow that reflects the widely fluctuating precipitation and resulting runoff.

Inflow in the SFE has been significantly altered, particularly during the summer and fall dry-season to accommodate the high demand for freshwater by cities and farms (see Kimmerer 2002; Knowles 2002). A majority of diverted water is exported from the system at large pumping facilities located in the south western delta, although smaller irrigation diversions also remove a considerable volume of water from the system (Kimmerer 2002). There has been a large steady increase in combined export since the middle 1950s (Kimmerer 2002).

Environmental conditions within the marsh, including salinity, temperature, Secchi depth and DO, vary considerably depending upon season, location and the amount of fresh water entering the system (Matern et al. 2002; Figure 1.2). Freshwater inflow is usually at its highest from February to March and declines towards June with the lowest inflow occurring between July and November. As freshwater inflow decreases in late spring and early summer, more marine water intrudes into lower Suisun Marsh and salinity begins to increase. Salinity increases to its highest levels in the fall before declining in early to mid-winter as the winter rains begin. Salinity has ranged from zero to 17 ‰ during the study period (1980 to 2005).

Sloughs within the southwestern corner of the marsh have the highest salinities while sloughs in the southeastern portion of the marsh have the lowest salinities. Salinity within the northern area of Suisun Marsh is generally intermediate and strongly dependent upon local stream inflow. In an effort to reduce Suisun Marsh salinity during times of low inflow in the SFE, the Suisun Marsh Salinity Control Gates (SMSCG) were constructed in Montezuma Slough by the California Department of Water Resources and the United States Bureau of Reclamation and began operating in fall of 1988 (http://www.iep.ca.gov/suisun/facts/physicalfacilities.html).

Temperature is low in winter and increases to its highest levels in early summer before declining in the fall. Summer temperatures ranged from 17 to 29.5 °C with winter temperatures occasionally dropping below 5 °C. Summer water temperatures tend to be highest in the small shallow sloughs and lowest near Grizzly Bay and the upper reach of Montezuma Slough, but are more similar regionally during winter. Salinity typically increases in the summer months when temperature has already reached high levels and declines with temperature in the fall.

Secchi depth (a measure of water transparency) decreases at the onset of high freshwater inflow and declines to its lowest levels from March to June before increasing with salinity in late summer into fall. Dissolved oxygen concentrations are usually high ($\geq$6 mg·lO_2^{-1}) in Suisun Marsh except for seasonal declines in spring (June) and fall (October and November). Dissolved oxygen is usually highest ($\geq$ 7 mg·lO_2^{-1}) near the confluence of the Sacramento and San Joaquin Rivers and also near Grizzly Bay and lowest in the more isolated sloughs and upstream reaches of sloughs. In the fall, DO levels often become hypoxic ($<$ 2 mg·lO_2^{-1}) and occasionally anoxic (0 mg·lO_2^{-1}), especially in the northwestern area of the marsh where multiple anthropogenic stressors (urban runoff, sewage treatment discharge, seasonal wetland drainage, etc.) affect the water quality.

The proximity of Suisun Marsh to the large upper bay system (Grizzly, Suisun, and Honker Bay), its close proximity to the confluence of the Sacramento and San Joaquin Rivers, and its direct connection to numerous local tributaries have all strongly influenced the diversity of the aquatic community and the abundance of the various species (see Meng and Matern 2001 and Matern et al. 2002). Suisun Marsh is generally recognized as being an important low salinity nursery area for numerous fishes and important invertebrates (Meng et al. 1994; Meng and Matern 2001; Matern et al. 2002; Feyrer et al. 2003).

1.2.2 Field Methods

Medusae of *M. marginata* were captured by monthly otter trawl at 17 sites (core sites) in 7 Suisun Marsh sloughs from 1980 to 2005 (Figure 1). Data were further constrained to the 1981 to 2005 time period, based upon the likelihood of inconsistent reporting of medusae in the first complete year of the study (1980). Four additional sites in two sloughs in the northeastern region of the marsh were sampled from 1994 to 2005 (Figure 1.1; Table 1.1). Data from these additional sites supplemented the data from the core sites and was used in determining environmental relationships for *M. marginata* and trends in catch in that region only.

Field methods for the long-term fish monitoring program are provided in detail by Matern et al. (2002). Trawling was conducted using a four-seam otter trawl with a height of 1.5 m, a width of 4.3 m and a length of 5.3 m. The trawl was towed during day light hours at approximately 4 km/hr for either 5 or 10 minutes, dependent upon slough size (width and depth; Table 1.1). Small sloughs were sampled for 5 minutes (First Mallard, Peytonia, Boynton, Cutoff, Goodyear, Denverton and Nurse) and large sloughs (Suisun and Montezuma) were sampled for 10 minutes to adjust for low catch rates of fish. A single site in lower Goodyear Slough (GY3) was sampled for 10 minutes from 1980 to 1988 and for 5 minutes after 1988. At the end of each trawl, trawl contents were placed into large containers of water and the fishes and other by-catch including shrimp and jellyfish were identified, enumerated and released at the site of capture. All catch results were converted to catch per minute ($catch \cdot minute^{-1}$) to standardize catch in both small and large sized sloughs. The trawl mesh was 35 mm fully stretched, with a 17 mm rough opening and the cod–end was lined with a 6 mm fully stretched and 3 mm rough opening mesh. Mills and Sommer (1995) report the size range of collected *M. marginata* medusae from Petaluma Marsh in the SFE in July 1993 to be between 1 and 36 mm bell diameter with an approximate median size between 20 – 22 mm. The mesh size of the otter trawl used in this study likely retained medusae that were approximately 20 mm or larger in bell diameter throughout the body of the trawl down to a minimum size of approximately 5 mm bell diameter if retained by the smaller diameter mesh of the cod liner. As such, the results from this survey are likely an underestimate of the actual abundance of medusae in the system. None-the-less, the standardized sampling protocols and the large number of samples collected over the 25 year study (5274 samples) provides a robust measure of relative abundance and a useful indication of population shifts over time.

At each site, the water transparency (Secchi depth in centimeters), temperature (°C), and salinity (‰) were measured. Water temperature (°C) and salinity (‰) were measured using a Yellow Springs Instruments salinity-conductivity-temperature meter (YSI 85) and a Yellow Springs Instruments salinity-conductivity-temperature-DO meter (YSI 95). Dissolved oxygen ($mg \cdot l O_2^{-1}$ and % saturation) monitoring began in November 1999. A combination of meters was used to measure DO including Horiba Scientific Instruments temperature-specific conductance-pH-DO meter, the Yellow Springs Instruments multi-meter (YSI-95), and a Hydrolab 4a datasonde.

1.2.3 Analyses

Population Patterns

To address question 1 (Has the abundance, patterns of occurrence, and distribution of *M. marginata* medusae changed over the past 25 yrs?), several approaches were used. First, a series of correlations were conducted using the nonparametric Kendall's tau trend test (SAS software system; SAS Institute; Kendall and Gibbons 1990) to determine the likelihood of an increasing or decreasing annual trend in (1) catch (January to December), (2) regional catch (January to December), (3) annual percent site occurrence (% of total sites) and (4) annual bloom duration (months). The Kendall's tau test is rank based, thus is effective for identifying trends when extreme values and skewness are present in the data (Helsel and Hirsch 1992). Significance levels for all trend analyses (7 comparisons) were subject to a Bonferroni adjustment to reduce the Type 1 error rate resulting from multiple comparisons (i.e. $p_B = 0.05/7 = 0.007$).

The trends in annual regional catch were investigated in each of four regions in Suisun Marsh including the northwest (NW, n = 10), southwest (SW, n = 5), northeast (NE, n = 4) and southeast (SE, n = 2). The NE region of the marsh was first sampled after May 1994, thus trend results will reflect a shorter time period of study. The percent site occurrence, a measure of the spatial distribution of medusae across Suisun Marsh, was calculated using the total number of core sites where medusae were present for at least one sampling event in a given year. The duration of the annual *M. marginata* bloom in each sample year was determined by summing the number of months medusae were present in at least one of the 17 core sampling sites. Box plots were used to display the summary statistics for annual catch of medusae for the July to November time period, the 5 months of greatest abundance of medusae across all sampled years. The month of first catch (bloom onset), last catch (bloom termination) and the month of peak medusae abundance were also determined, to provide a better understanding of the temporal shifts in population patterns over the 25 year time period.

Environmental Relationships

Several approaches were used to answer question 2 (How does the distribution and abundance of *M. marginata* vary with salinity, temperature, water clarity, and DO). First, regression models were developed to determine if the environmental parameters salinity, temperature, and Secchi depth were significant predictors of *M. marginata* abundance in each of two time periods, 1981 to 2005 and 1996 to 2005. The two time periods were selected to test for the possibility that *M. marginata* was still expanding its range in the study area prior to 1996, as indicated by its limited spatial distribution. This could have resulted in biased environmental-abundance relationships due to lack of occurrence in potentially suitable habitats (Hirzel et al. 2001; Guisan et al. 2002). Similarity in model results for both time periods would suggest that environmental relationships and not a lack of habitat saturation was responsible for the observed patterns in annual catch.

Next, the data were divided into two intra-year time periods to determine (1) environmental conditions leading to the initiation of the medusae bloom (January to September) and (2) those leading to its bloom termination (October to December). For each time period and environmental variable (salinity, temperature, water transparency, and DO), the 5th and 95th percentiles of environmental data with medusae present were then used as an approximation of the suitable range of conditions for medusae. Using the estimated thresholds (5th and 95th percentiles) for medusae occurrence rather than the full range of data, allowed for a more conservative estimate of the suitable conditions, given that the edges of the distribution of medusae may consist of samples where few individuals are found or where medusae were recently displaced, due to tidal action in the system. The environmental thresholds corresponding to the 5th and 95th percentiles of medusae abundance were also determined for the same four environmental parameters to find out if abundance distributions were similarly related to environmental conditions. The relationship between the cumulative abundance of medusae and the environmental variables salinity, temperature, and Secchi depth were also plotted for each intra-year time period to visually inspect for changing slopes which may be indicative of conditions constraining medusae abundance. Additional summary statistics were also reported including the 10th and 90th percentiles, median, mean, minimum and maximum values and the range of observed environmental conditions in each time period.

Regression Model Selection and Development - The life history traits and the resulting seasonality of *M. marginata* medusae in this study resulted in abundance data distributions that did not meet the basic assumptions of general linear models including normal distribution of errors and constant variance, as is commonly the case for ecological data (McCune and Grace 2002; Guisan et al. 2002). Generalized linear models (GLMs) are mathematical extensions of linear models, but are more flexible allowing for non-linearity and non-constant variance structures in the data (Guisan et al. 2002). Generalized linear models are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables, with the relationship represented by a logarithmic link function (Guisan et al. 2002). Generalized linear models have the advantage of having a number of probability distributions that can be selected from, so a close match to the data of interest can usually be found.

Count data, as used in this study, are usually best represented by either a Poisson or negative binomial distribution (Jones et al. 2002; Hilbe 2007). The Poisson distribution assumes that the variance (V) is equal to the mean (μ). The negative binomial distribution is more appropriate in situations where the variance is considerably greater than the response mean ($V(\mu) > \mu$) resulting in overdispersion, as is commonly the case when count data includes large numbers of samples with zero catch. The hydromedusae data in this study were particularly well suited to Poisson and negative binomial regression given the count nature of the data (abundance per unit volume sampled) and the large number of zero catch records resulting from seasonal senescence and patchy occurrence distributions.

To determine which data distribution (Poisson or negative binomial) best fit the medusae abundance data, two approaches were used including a comparison of Akaike's information criterion (AIC; Akaike 1987) for each of the fitted models and by performing a likelihood ratio test (LR) for both competing models using the log likelihood from the intercept only models (i.e. -2[log likelihood Poisson – log likelihood negative binomial]; Cameron and Trivedi 1998). A low *p*-value (<0.05) would imply that the negative binomial distribution was a better fit to the abundance data while a large *p*-value (>0.05) would suggest that the Poisson distribution was more appropriate.

The Poisson and negative binomial distributions were analyzed using the PROC GENMOD procedures in SAS (SAS 9.1.3). A manual iterative parameter selection process was used to determine the best fit Poisson or negative binomial model to the abundance data. In both models, the first step assessed the univariate effect of each independent variable for the response variable medusae abundance. The independent variable that resulted in the lowest AIC was then selected and entered into the model. For both models, the Wald's X^2 significance level for entering an independent variable into the regression was 0.30 and for retaining the variable, 0.10 (Mickey and Greenland 1989; Hosmer and Lemeshow 1989). Independent variables were added to the regression in the stepwise fashion until none remained, or the selection criteria were no longer satisfied and the model with the lowest AIC was selected as the best fit model. The final model step was the inclusion of a quadratic term for salinity (i.e. Sal^2) to test for a non-linear response of medusae to the observed range of salinity. This was prompted by the observed negative salinity coefficient in the logistic regression model predicting occurrence of *M. marginata* medusae in the bloom termination time period (i.e. fall months) presented in Chapter 2. The quadratic term was first mean centered (salinity-mean salinity) prior to calculating the squared value, to reduce collinearity between the simple and quadratic term.

To determine the relative contribution of each independent variable to the best fit model, the standardized estimate (Stand. Est. = [independent variable coefficient * standard deviation of independent variable] / standard deviation of the dependent variable) was calculated (Nash and Bradford 2001; Bradford et al. 2003). The larger the standardized estimate the stronger the association between the independent and dependent variable in a given model.

Diagnostic Tests and Collinearity Checks - Several diagnostic checks were made for the regression models prior to analysis. First, plots were made of the estimated probability versus the deviance (difference in deviance) for each model to identify influential outliers and to check on their validity. Predictor variable collinearity, which can make model coefficients unstable and difficult to interpret (Allison 1999; Christensen 1997), was then evaluated in three ways. First, the pair-wise (Pearson) correlation coefficients (r) of the independent variables were examined and variables with r-values > 0.8 were considered for removal from the models (Berry and Felman 1985). Second, the variance inflation factor (VIF) was used to assess the level of multi-collinearity among the independent variables (Nash and Bradford 2001; Bradford et al. 2003). A VIF value of 1 indicates a non-linear relationship (r^2=0) between the independent variables. VIF values greater than 1 indicate increasingly linear relationships, with serious collinearity effects observed at VIF levels of 10 (Neter et al. 1996; Griffith and Amerhein 1997), the selected VIF criteria for this study. The final step in screening for collinearity effects was examining for changes in the value and sign of independent variable(s) already present in the model, when an additional independent variable was added. The presence of serial autocorrelation in the residuals was tested using the Durbin-Watson D test (Durbin and Watson 1951). All diagnostic tests were performed using SAS 9.1.3.

Environmental Changes and Relationships with Catch

To address question 3 (What environmental changes in Suisun Marsh and the larger SFE are contributing to the observed trends in abundance of *M. marginata*?), I used a combination of correlation analyses (Kendall's tau trend test), multiple comparisons (Tukey-Kramer Honest Significant Difference (HSD)), and visual comparisons of plots to explore whether changes in environmental conditions could be contributing to the observed temporal shifts in catch. First, the time series of mean annual salinity, temperature and Secchi depth from July to November, the time period of greatest medusae abundance, were plotted to visually examine for abiotic changes that have occurred over the 25 year time period. Included in each plot was a reference line for the estimated minimum threshold for medusae occurrence (i.e. 5th percentile for medusae presence). The temporal trends (i.e. significant increase or decrease) of the mean seasonal (July to November) environmental values (salinity, temperature and Secchi depth) were analyzed using Kendall's tau trend test with a Bonferroni adjustment for the 3 comparisons, which resulted in a significance level of $p_B = 0.017$.

To examine if environmental conditions were changing at a finer temporal scale, I analyzed for mean monthly trends in the environmental parameters salinity, temperature and Secchi depth using the Kendall's tau trend test and samples from the 17 core otter trawl sites. I restricted the analyses to the time period of May to December, since this included the full range of months with medusae present in Suisun Marsh over the 25 year study. The temporal trends in mean monthly catch were also analyzed for comparative purposes. This resulted in a total of 32 comparisons and a Bonferroni adjusted significance level of $p_B = 0.0015$.

To determine if environmental conditions could, in part, explain the observed differences in catch during this study, I plotted the mean monthly environmental values for all years (1981 to 2005) for two dominant abundance classes including (1) absent to very low catch (July to November seasonal average <0.1 medusae$\cdot$minute^{-1}) and (2) moderate to high catch (>0.1 medusae$\cdot$minute^{-1}). The group with medusae absent or in only low abundance was further divided into two subgroups based upon the water year type (http://cdec.water.ca.gov), a ranking of the amount of unimpaired runoff and an indirect measure of precipitation in the main river watersheds (Sacramento and San Joaquin River). The amount of unimpaired runoff in a given year affects the salinity, temperature and water clarity in the upper SFE. The absent to low catch years were then divided into (a) Wet and (b) Critical to Dry groups with the full range of rankings including Wet, Above Normal, Below Normal, Dry, and Critical. Because the total measure of water input into the SFE was of primary interest and in some instances water year classifications differed between the Sacramento and San Joaquin watersheds, I calculated a modified combined rank for both river watersheds by summing the individual index criteria and then used this new value to determine the combined water year type, which was heavily weighted for the larger Sacramento River.

Next, I used the three data groups [i.e. (I) absent to low catch – Critical to Dry; (II) moderate to high catch – Dry to Wet; and (III) absent to low catch – Wet], and tested for mean differences in the environmental variables salinity, temperature and Secchi depth with the Tukey-Kramer HSD multiple comparison procedure for unequal sample sizes using the JMPin statistical software application (JMPin 4.04). The time period of monthly comparisons was again May to December. The observed differences in the grouped monthly mean environmental conditions were then discussed in the context of the observed environmental thresholds and the changing environmental conditions in Suisun Marsh. I also plotted the mean monthly catch for each of the three groups for visual comparison.

Spatial and Temporal Overlap with Pelagic Fishes and Diet Analysis

I used two approaches to address question 4 (Does the spatial and temporal overlap with pelagic fishes in the system and diet of *M. marginata* suggest potential competition with or predation on fishes?). First the spatial and temporal overlap with key pelagic fishes in Suisun Marsh were determined for juveniles and adults using the otter trawl survey results to better identify pelagic species that may be negatively affected through potential competition. To evaluate the potential for predation on and competition with fish larvae, the temporal overlap of medusae and larval fishes were approximated for Suisun Marsh and other areas of the middle SFE using the monthly catch pattern determined from the otter trawl survey and the combined results from a previously conducted larval fish study in Suisun Marsh (Meng and Matern 1999) and the reported emergence times for larval fishes in the upper SFE (Wang 1986).

Next a diet study was conducted using field caught medusae from summer and fall. Medusae used in the diet study were collected from the field using a variety of methods including dip net, otter trawl, and zooplankton net. Because of the small size of medusae in the summer, all individuals were captured by stepped vertical zooplankton tows with a 300 mm diameter plankton net with 500 μm mesh. Dip net collected specimens were captured as *M. marginata* swam to the surface during its bottom to surface migrations. Medusae were immediately preserved with 70% ethanol, 5% formalin solution, or Lugol's solution depending upon the method of capture. All Lugol's preserved specimens were further preserved in 70% ethanol.

The diet of medusae was determined using methods similar to Mills and Sommer (1995). The gut content of each individual was obtained by first removing the entire stomach from the bell using forceps. The stomach was then viewed through a stereo microscope (Leica GZ7) with 70x magnification and opened from the backside (area previously in contact with the bell). There was generally a main bolus of prey in this area and it was removed and set aside. The remaining prey sticking to the sides of the four perradial stomach lobes were then removed and set aside. Only prey encountered up to the origination of the four frilly mouth lobes were included in the analysis to reduce the potential error of including net caught prey in the total count. The size (bell diameter in mm) was then determined for each preserved specimen using calipers.

The diet of medusae was summarized in table format with basic information recorded including prey water column position, total number of prey consumed, mean number of prey consumed, percent of total prey, number of medusae preying upon each taxa (frequency) and the percent frequency of medusae that consumed the given taxa. To determine if there was a size-based feeding relationship, a simple linear regression was performed (significance $P < 0.05$; SAS Institute) with size of medusae (bell diameter mm) and number of pelagic and benthic / epibenthic prey consumed, with prey from both seasons included in the analyses.

1.3 RESULTS

1.3.1 Population Patterns

The marsh was sampled in 290 out of 300 months (98%) with 5270 samples collected out of a possible 5660 samples (> 93%) from 1981 to 2005 (see appendix A for description and table of missing values). This sampling led to the capture of nearly 29,000 *M. marginata* medusae. Over 91% of medusae were captured after 1992 and over 80% were captured after 1998. Trend analyses results indicate that there is a significant ($P_B < 0.007$) increasing annual trend in catch of medusae at the core sites ($\tau = 0.28$, $n = 4735$). This trend was plotted for the July to November time period using box plots (Figure 1.2).

There were also significant increasing annual trends in regional medusae catch ($P_B < 0.007$) for all four regions sampled in the marsh (NW, $\tau = 0.25$, $n = 2811$; NE, $\tau = 0.14$, $n = 536$; SW, $\tau = 0.19$, $n = 1420$; and SE, $\tau = 0.25$, $n = 503$; Figure 1.3) and a significant increase in the annual percent site occurrence ($\tau = 0.62$, $n = 25$; Table 1.2). From 1981 to 1992, medusae were captured in all sampled sites in only 1 of 12 years. The percent site occurrence increased after 1992 with medusae being found in all core sites in 9 of 13 years and from 1996 to 2005, in 9 of 10 years.

There was also a significant ($P_B < 0.007$) increasing annual trend in bloom duration ($\tau = 0.53$, $n = 25$; Table 1.2). Bloom duration increased from a mean of 2.3 months from 1981 to 1992, to approximately 4.5 months from 1993 to 2005. There was a noteworthy reduction in variability of month of first appearance of medusae (bloom onset) after 1992. From 1993 to 2005, medusae were first captured in July and August in 11 of 13 years (85%) compared to 4 of 12 years (33%) in the preceding twelve-year time period (1981-1992). In the earlier time period (1981-1992), medusae first appeared either earlier than July (3 years), later than August (3 years), or they were not captured by otter trawl (2 years). The last month of catch (bloom termination) also changed during this study (Table 1.2). From 1981 to 1992, medusae were captured after September in only 4 of 10 years with medusae present (40%), 2 months in both October and November. However, from 1993 to 2005 medusae were captured after September in 13 of 13 years (100%). In the latter time period, medusae were last captured in October in 3 of 13 years (23%), November in 8 of 13 years (62%) and December in 2 of 13 years (15%). The delayed bloom termination and more consistent early bloom onset both contributed to the observed expanded bloom duration (Table 1.2).

The peak month of abundance also shifted to a later month in the latter half of this study (Table 1.2). In the early sampling time period (1981-1992), medusae were present in 10 of 12 years with August being the most frequent month of peak abundance (5 of 10 years or 50%). In that same time period, peaks in abundance occurred after August (September and October) in 3 of 10 years (30%) and in earlier months (May and June) in 2 of 10 years (20%). In the latter time period (1993-2005), peak abundance of medusae was in August 2 of 13 years (15%), after August in 10 of 13 years (77 %; September - November) and in an earlier month (July) in only 1 of 13 years (7.7%).

1.3.2 Environmental Relationships

Data Management

After conducting analyses for salinity, it became clear that nearly all samples collected from upper Boynton Slough (BY1) deviated considerably from other sites in regards to the low to moderate abundance of medusae and associated low salinity levels. Given that this site was in close proximity (200 m downstream) to a large volume low salinity inflow from a local sewage treatment facility and that there was a high abundance of medusae just downstream in lower Boynton Slough (BY3), it is likely that the presence of medusae in that area was due to tidal dispersion into low salinity areas, rather than the presence of a population maintaining themselves in that location. Thus, observations from the BY1 site were treated as outliers and were removed from the salinity analyses.

In addition, following some initial screening of the environmental data, inaccuracies were detected for salinity measurements throughout much of 1988, a critical water year marked by low precipitation (http://cdec.water.ca.gov). Salinity measurements in 1988 were routinely reported as being much lower (1 to 3 times) than they were based upon measurements taken at the site location or in adjacent locations over a similar time period by other sampling programs or fixed data recorders (Fairfield-Solano Sewer District water quality monitoring, California Department of Fish and Game (CDFG) -Summer Townet Survey and California Department of Water Resources fixed monitoring stations. As a result, the 1988 samples were removed from all analyses utilizing environmental data (i.e. regression and trend analyses).

The lack of sampling in October and most of November in 1989 resulted in an underestimate of salinity and overestimate of temperature for the bloom time period (July to November). Thus, the data were also removed from relevant analyses when seasonal means were used. The July to September data was included in the monthly trend analyses of environmental variables and in the calculation of suitable environmental conditions for medusae.

Regression Results

Model Diagnostic Tests and Collinearity Checks - All outliers identified in the deviance-probability plots were examined to ensure their validity and no data errors were found and all data points were retained in the final models. There was no evidence for collinearity between the independent variables (i.e. all Pearson correlations $r < 0.8$; range 0.01 to 0.62) and there was no indication of multi-collinearity of the independent variables (all VIF <10; range 1.1 to 2.0). The Durbin-Watson D test statistic was 1.4 for the 1981 to 2005 time period and 1.7 for the 1996 to 2005 time period, with a value of 2.0 indicating no serial autocorrelation and possible D values ranging from 0 to 4. The first order autocorrelation was low for the 1996 to 2005 time period (0.14), but somewhat higher for the full data set (i.e. 1981 to 2005; 0.29). Including the variable year in the model did not increase the D statistic suggesting that the observed autocorrelation may be due to some other missing term in the model.

Model Results - The negative binomial (NB) models were determined to have the most appropriate data distribution for the abundance of *M. marginata* for both the 1981 to 2005 and 1996 to 2005 time periods based upon the significant likelihood ratio test (LR) test (1981 to 2005; $X^2 = 19{,}382$, $df = 1$, $p<0.05$ and 1996 to 2005; $X^2 = 14{,}482$, $df = 1$, $p<0.05$) and the considerably lower AIC values (Table 1.3). All models in both time periods, including the intercept-only model were significant at the $p<0.01$ level (Table 1.3). The NB regression model with the lowest AIC was the same in both time periods with Medusae Abundance = Sal+Temp+Secchi Depth+Sal^2 and the model coefficients in the best fit models were similar in magnitude and sign (Table 1.2). All independent variables in both time periods were also significant (Wald's X^2 test; $p<0.01$). The criteria for goodness of fit (GFT; Pearson's test statistic / *df*) was 1.49 and 1.44 in the 1981 to 2005 and 1996 to 2005 time periods with a level near 1 indicating a good fit of the model. The positive coefficients of the independent variables temperature, salinity, and Secchi depth indicate that their increased values were associated with higher medusae abundance, while the negative coefficient of Sal^2 indicates a negative medusae abundance relationship. Salinity had the largest standardized estimate in both time periods (Table 1.4), thus was the most important predictor variable explaining *M.*

marginata abundance in the models. The quadratic term Sal^2 had the next highest standardized coefficient followed by temperature and Secchi depth (Table 1.4).

Bloom Initiation and Occurrence - The estimated suitable environmental ranges (5th and 95th percentiles) for salinity during the bloom initiation time period (January to September) was 2.8 to 9.9‰; temperature 19 to 24.1°C; water transparency 16 to 48 cm; and DO 5.3 to 9.2 $mg \cdot lO_2^{-1}$ (Table 1.5).

Bloom Initiation and Abundance - The estimated suitable range of environmental conditions for medusae corresponding to the 5th and 95th percentiles of medusae abundance, were similar to those observed for medusae presence but consisted of a narrower range in most instances (Table 1.6). The only exception was for temperature, which had an identical upper and lower threshold for the abundance data as for the occurrence data. The 5th and 95th percentiles of medusae abundance during the bloom initiation time period corresponded to a salinity of 3.4 and 9.4‰; temperature 19 and 24.1 °C, Secchi depth 19 and 47, cm and DO 5.7 to 9.4 $mg \cdot lO_2^{-1}$ (Table 1.6). The estimate of the lower thresholds (5th percentile) were much more robust than the upper estimates during the bloom initiation time period given that between 44 and 63% of all samples were found below the lower estimated suitable range and only 3% were found above the upper estimated range, with the exception of DO (10% of samples below and 12% of samples above the lower and upper thresholds; Table 1.6).

The cumulative abundance relationships for the environmental variables in the bloom initiation time period (Figure 1.5a-c) revealed fairly consistent increasing slopes between the upper and lower thresholds (5th and 95th percentiles) with the exception of salinity, which had a noteworthy change in slope at approximately 5.7‰.

Bloom Termination and Occurrence - The estimated suitable ranges of environmental variables (5th and 95th percentiles) during bloom termination (October to December) were 3.3 to 10.1‰ for salinity, 19 to 24.1°C for temperature, 16 to 48 cm for Secchi depth; and 2.8 to 9.6 $mg \cdot lO_2^{-1}$ for DO (Table 1.5).

Bloom Termination and Abundance - The estimated suitable range of environmental conditions for medusae corresponding to the 5th and 95th percentiles of medusae abundance in the bloom termination time period were 4.2 to 9.2‰ for salinity, 13.1 to 19.4 °C for temperature, 21 to 71 cm for Secchi depth, and 4.2 to 9.4 $mg \cdot lO_2^{-1}$ for DO (Table 1.6). These ranges were for the most part narrower than those observed for the occurrence data, although the upper abundance threshold for Secchi depth exceeded that for the occurrence data (Table 1.5 and 1.6), likely due to the low number of samples above the upper threshold (3.2%) and the continued high catch of medusae at those upper Secchi depths. The lower abundance thresholds were again represented by a large number of samples in the bloom termination time period, particularly for the variables of salinity (41.2% samples below lower threshold) and temperature (48.7% below the lower threshold). The upper threshold (95th percentile) for salinity was also well represented with over 13% of the samples occurring above that salinity level.

The cumulative abundance of *M. marginata* medusae between October and December was more variable than in the bloom initiation time period (Figure 1.5), particularly for temperature, which had a stepped pattern reflecting the large decrease in temperature between the months of October and December (Figure 1.4). There was also a decline in slope in the cumulative abundance salinity relationship occurring at approximately 7‰. In addition, there were several slope changes in the cumulative abundance relationship with Secchi depth, particularly above 45 cm, where there were also a low number of samples.

1.3.3 Environmental Changes and Relationship to Catch

Trends in Environmental Parameters by Season

There was no significant trend (p_B>0.017) in the annual mean July to November salinity (Kendall's $\tau = 0.07$, n = 23), but there was considerable annual variability with low, high, and more moderate salinity levels observed with moderate salinities becoming more common after 1992 (Figure 1.6). Similarly, there was no annual trend in mean July to November temperature (Kendall's τ = 0.22, n = 24), but there was a notable decrease in the seasonal variability of observed temperatures (i.e. standard deviation) beginning in the late 1980s (Figure 1.6). Mean July to November Secchi depth also did not increase or decrease significantly (Kendall's τ = 0.21, n = 24), even though there was a large increase in Secchi depth in the last five years of the study (2001 to 2005).

Monthly Trends in Environmental Parameters and Catch - The monthly trends indicate that environmental conditions and catch changed significantly (p_B<0.0015) in the months of May to December (Table 1.7). Temperature increased significantly in June, November and December. Salinity decreased significantly in May, but then increased in October and November. Secchi depth increased significantly from July through October. Catch of medusae increased significantly from July to December, with the largest increasing trend (i.e. positive correlation) in the late summer through fall (September to November).

Multiple Comparisons and Plots – The multiple comparison tests revealed that there were many significant differences in mean monthly salinity from May to December between the groups of years with none to few medusae present (Group I and III) and years in which medusae were present in moderate to high abundance (Group II; Table 1.8). Mean salinities in the Critical to Dry water years with none to few medusae present (Group I) were significantly higher than in the Dry to Wet water years with moderate to high catch of medusae (Group II) in all months but September. The mean salinities in Group I ranged from 4.5 in May to 9.8 in October before declining to 7.1 in December (Table 1.8). The mean salinities for Group II ranged from 1.7 in May to 6.3 in October before declining to 3.8 in December (Table 1.8). The mean monthly salinities in the Wet water years with none to few medusae present (Group III) were significantly lower than Group II from July to December with the mean salinities ranging from 0.8‰ in May to 1.9‰ in November before declining to 1.1‰ in December. These salinity differences were also evident in the annual monthly mean plots (Figure 1.7b).

There were no significant differences in mean monthly temperatures between Groups I, II, and III and only significant differences in mean Secchi depth in September and October (Table 1.8). In September, the mean Secchi depth was significantly higher in Group II than Group III and in October the mean Secchi depths in both Group I and II were significantly higher than Group III. The annual mean monthly plots revealed the similarity in temperature patterns (Figure 1.7c) among Groups I-III and the differences in Secchi depth (Figure 1.7d) particularly for the Wet, absent to low catch years in Group III.

1.3.4 Spatial and Temporal Overlap with Pelagic Fishes and Diet

Spatial and Temporal Overlap

The spatial comparison of *M. marginata* medusae and pelagic fishes was conducted at the regional level and the comparison was limited to the 1994 to 2005 time period, so that all regions could be included in the comparison (NE only sampled regularly beginning in 1994). The results indicate that there was considerable spatial overlap of *M. marginata* medusae and juvenile and adult pelagic fishes in Suisun Marsh (Figure 1.8). *Maeotias marginata* was the most abundant pelagic species captured in the NE and SE region of the marsh and was the second most abundant pelagic species, behind young of year (YOY) striped bass *Morone saxatilis* (alien), captured in the NW and SW. The catch of longfin smelt *Spirinchus thaleichthys* (native) was highest in the SW region near Grizzly Bay, but it was less than half as abundant as medusae in that region. Delta smelt *Hypomesus transpacificus* (endemic native) were rarely captured by otter trawl, but when captured they had slightly higher abundances in the NE region. Threadfin shad *Dorosoma petenense* (alien) were also captured in low abundance primarily in the NW and NE regions of the marsh.

Maeotias marginata medusae and several juvenile and adult pelagic fishes overlapped temporally in Suisun marsh, based upon the otter trawl catch (Figure 1.9), including (listed in order of abundance) striped bass young-of-year, longfin smelt, threadfin shad, and delta smelt. Larval fishes also overlapped temporally with *M. marginata* medusae (Figure 1.10), although only the larvae of alien species including inland silverside *Menidia beryllina*, threadfin shad, and various species of gobies (Gobiidae) are found in the marsh and other areas of the middle SFE during the summer and fall months when medusae are present.

Diet - A total of 95 *M. marginata* medusae were analyzed to determine diet in Suisun Marsh in two seasons including summer and fall. Summer caught medusae (n = 40) were collected on July 9, 11 and 12, 2004 from each of the 4 regions of the marsh. Given their small size, all medusae from the summer were collected by stepped vertical zooplankton tows with a 300 mm diameter plankton net with 500 μm mesh. Medusae collected in fall (n = 55) were captured by dip net (n = 22) and otter trawl (n = 33) on October 3 and 11, 2005 and November 1, 2005 from the same 4 regions of the marsh. The size distribution of medusae used in the diet study differed considerably between the summer and fall time period (Table 1.9). The mean bell diameter of medusae in summer was 4.7 mm, whereas in fall the mean size was 20.3 mm.

In summer, gut contents included a total of 121 prey items for the 40 medusae for a mean consumption of 3 prey·medusa^{-1} (Table 1.10a). The most abundant prey were calanoid copepods (59% of total) and crab zoea (27% of total) followed by larval fishes (5% of total) in the family Gobiidae (Table 1.10a). Calanoid copepods, crab zoea, and larval fishes were found in the gut contents of 62.5, 45 and 15 % of the medusae analyzed in summer. The majority of prey were pelagic taxa (115/121 or 95%) with very few epibenthic or benthic taxa (amphipods, n = 4 and harpacticoid copepods, n = 2) observed in the gut contents (6/121 or 5%; Table 1.10a).

In fall, gut contents included a total of 629 prey items for the 55 medusae for a mean consumption of 11.4 prey·medusa^{-1} (Table 1.10b). As in summer, calanoid copepods were the most abundant prey in fall (41.8% of total), with cyclopoid copepods and *Corophium* amphipods being the second (19.4% of total) and third (12.7% of total) most abundant prey found in the gut contents (Table 1.10b). Cladocera made up a total of 9.2% of the prey in the gut contents in fall. However, there was a much higher vulnerability of cladocerans to medusae predators than these results indicate; when cladocerans were locally available (e.g. Montezuma Slough, November 2005), they comprised 57% of the gut contents of medusae. Eleven of 12 (92%) medusae preyed upon them at a mean consumption of 4.8 cladocerans·medusa^{-1} and a maximum of 23 cladocerans·medusa^{-1}. A large number of copepod egg sacs (51 egg sacs or 8.1% of total diet contents), presumably from consumed copepods, were also found among the gut contents in fall (Table 1.10b). Calanoid copepods, cyclopoid copepods, and *Corophium* amphipods were found in the gut contents of 71, 52.7, and 65.5 % of the medusae in the fall. Both cladocerans and egg sacs were found in the guts of 21.8% of the medusae in fall. A majority of prey in fall were pelagic taxa (469/578 or 81.1% excluding copepod egg sacs). Epibenthic / benthic taxa were more abundant in the gut contents in fall (18.9%) than in summer (5%), with *Corophium* amphipods being the most abundant of the benthic and epibenthic group (80/109 = 73.3%). Other epibenthic and benthic taxa consumed included harpacticoid copepods (n = 19), gammarid amphipods (n = 3) and various other taxa including Cumacea, Chironomidae, Tanaidacea, and Hydracarina (mites).

There were highly variable, but significant (linear regression, $p < 0.05$) increasing linear relationships between number of prey in the gut contents and size (bell diameter) of medusae for both pelagic ($r^2 = 0.23$) and the grouped epibenthic and benthic prey ($r^2 = 0.18$), when diet data from both summer and fall were combined.

1.4 DISCUSSION

1.4.1 Population Patterns

The results presented here indicate that *M. marginata* has been present in Suisun Marsh at least since 1981, although medusae blooms have been somewhat irregular and abundance has fluctuated considerably. The increased consistency of blooms, length of blooms, abundance of medusae, and spatial distribution of medusae in Suisun Marsh since 1993 are all an indication that conditions are becoming more favorable for them. *Maeotias marginata* medusae have been present in the SFE since at least 1959; thus the recent increase in occurrence and abundance is likely a reflection of changing estuarine conditions.

The pattern of increased abundance of medusae in Suisun Marsh and presumably in other areas of the middle SFE resembles a "net gain" increase, which has been observed and described for gelatinous zooplankton in other estuarine and marine habitats (Mills 2001). Several mechanisms could be contributing to the observed net gain including more moderate dry season salinities and warmer temperatures, but other unmeasured factors could also be playing a role including food web changes (Bouley and Kimmerer 2006) and expansion of polyp colonies, which primarily control the occurrence and abundance of gelatinous zooplankton medusae (Brewer and Feingold 1991; Lucas 2001).

Polyp abundance may be increasing as a result of more suitable conditions for their survival, growth and asexual budding. Asexual budding can occur even when conditions are not favorable for release of larval medusae (Ma and Purcell 2005). Thus, the establishment of polyps in a local area likely provides a foothold for continued production and future population expansion. For example, the dramatic decline in abundance of medusae in Suisun Marsh in very wet years with high inflow (1982, 1983, 1995 and 1998) was always followed by high abundance or increased abundance of medusae in subsequent years (1984, 1996 and 1999), indicating that polyps had survived the high flow low salinity conditions. In contrast, high salinity low inflow conditions from 1985 to 1992 resulted in the disappearance of medusae from most of Suisun Marsh even though conditions were suitable for a bloom to occur in the intervening moderate inflow years of 1986 and 1989. This may have been due to a number of factors including decreased production of medusae by polyps, reduced sexual reproduction and dispersal of medusae and polyps, and increased polyp mortality in the high salinity years.

Polyps of *M. marginata* have not been positively identified in Suisun Marsh, although the rapid increase in abundance of medusae in association with changing environmental conditions strongly suggests their local presence (e.g. this study and Chapter 2). Preliminary results from a benthic survey in Suisun Marsh conducted between 2003 and 2005, revealed a large number of polyps and hydroid colonies, but based upon morphology and structure most are likely polyps of the hydromedusa, *Moerisia* sp. and the non-medusa forming hydroid *Cordylophora caspia* (unpublished data). The lack of detailed descriptions of mature *M. marginata* polyps and their small size (Rees and Gershwin 2000) creates uncertainty with respect to their identification and detection in the field and increases the need for further research to verify their presence and determine their abundance.

Though difficult to verify, the recent increase in abundance of medusae in Suisun Marsh may also be attributed, in part, to increased sexual reproduction of medusae. The first reports of this species in the SFE indicated that only male specimens were found (Mills and Sommer 1995), although more recently, female specimens have also been collected (Rees and Gershwin 2000). If sexual reproduction has only recently been possible, perhaps as a result of the additional introduction of female *M. marginata*, then an increase in the distribution and abundance of medusa and polyps would be expected given the greater mobility of medusa and the increase in polyp abundance that would result from the combination of asexual and sexual reproduction.

Distributional shifts may also be playing a role in the observed increase in medusae abundance in Suisun Marsh (i.e. Graham et al. 2001). For instance, it is possible that the center of distribution for *M. marginata* was previously located in habitats down-estuary as higher dry-season inflows and lower salinities were more the norm in the upper SFE prior to the late 1970s (Appendix B2). More recently the population could have repositioned itself into upstream areas including Suisun Marsh and the surrounding bays (Grizzly Bay, Honker Bay, and Suisun Bay), as a result of shifting salinity. However, the absence of gelatinous zooplankton specific surveys in downstream regions of the SFE including San Pablo Bay and the surrounding marshes (Petaluma and Napa Marsh) prevents confirmation of such a population shift.

1.4.2 Environmental Relationships

The regression results from the 1981 to 2005 and 1996 to 2005 time periods indicate that salinity, temperature and Secchi depth are significant predictors of abundance for *M. marginata* medusae in Suisun Marsh. This is consistent with observations in other systems that salinity and temperature exert strong population controls over estuarine and marine gelatinous zooplankton (Graham et al. 2001; Purcell 2005; Decker et al. 2007; Purcell et al. 2007; Chapter 2) and that low water transparency may constrain medusae production by polyps due to low light levels (Chapter 2; Purcell 2007).

Salinity

The large effect of salinity in the regression models as both a main effect and a quadratic term (Salinity^2) suggests that salinity is a primary factor affecting the predicted abundance of medusae. Increased salinity resulted in increased abundance of medusae, as indicated by its positive main effect in the model. The consistent lower salinity threshold of ~3‰ for medusae occurrence in both the bloom initiation (2.8‰) and termination (3.3‰) time periods suggests that salinity levels associated with the production or release of medusae by the sessile polyps are likely similar to the physiological requirements of previously released medusae. A comparable, but slightly lower salinity threshold for occurrence (2.3 and 2.6‰ for bloom initiation and termination) was observed in a more spatially intensive (i.e. 36 sites) 2-year study (2004 to 2006) in Suisun Marsh (Chapter 2) that sampled with a finer mesh net (500µm).

This net was capable of catching smaller and younger medusae that were more recently released from polyps, which could account for the slightly lower salinity thresholds. The lower thresholds (5th percentile) for medusae abundance in this study (3.4 and 4.2‰ during bloom initiation and termination) were only slightly higher (<1‰) than for medusae occurrence, again indicating there was high consistency of the lower salinity threshold for medusae.

The upper salinity threshold for medusae occurrence (9.9 and 10.1‰ during bloom initiation and termination) and abundance (9.4 and 9.2‰ during bloom initiation and termination) were also similar, but the observed upper salinity limits may have been biased due to the low number of samples with salinities above the upper thresholds. In addition, several lines of evidence suggest that there were limitations to medusae abundance below the estimated upper thresholds. The first is the negative quadratic (Salinity^2) effect of salinity in the abundance models, which indicates that there was a non-linear effect of salinity that, in this case, resulted in lower abundance of medusae at higher salinities. The change (decrease) in slope in the cumulative abundance plots above 5.7‰ during the bloom initiation time period and above 7.0‰ in the bloom termination time period (Figure 1.5a) are consistent with the observed negative effect of the quadratic salinity term and they suggest that medusae abundance is maximized at more moderate salinities between 3 and 7‰. The near absence of medusae in the Critical to Dry water years, in which the annual mean monthly salinity was > 6‰ beginning in June and greater than 7‰ beginning in August, provides additional evidence that high salinity levels (> 6-7‰) may have limited medusae abundance and occurrence in the study area (Table 1.8). The years with moderate to high medusae abundance had mean monthly salinities from 2.5 to 6.3‰ from June to December (Table 1.8). The negative effect of elevated salinity on *M. marginata* medusae abundance was also observed in the study presented in Chapter 2. In that study, increased salinity resulted in the decreased probability of *M. marginata* medusae occurrence in the logistic regression model for the September to January time period, the time period with the highest salinity levels.

It is not possible to determine from this field study what life stage of *M. marginata* (polyps or medusae) was most negatively affected by the elevated salinities. However, given that adult medusae were captured in salinities as high as 12.9‰ in this study and mortality in laboratory reared medusae did not occur until salinity levels exceeded 13‰ (Mills and Sommer 1995), the observed decline in medusae abundance at salinities > 6-7‰ is likely a reflection of reduced production of medusae by polyps, rather than mortality of medusae.

Temperature

Temperature was also an important predictor of medusae abundance in the regression model, but its effect was secondary to salinity. The smaller effect of temperature was likely due, in part, to the consistent pattern of temperature increasing above the lower observed threshold of 19°C (this study and Chapter 2) in the early summer (May and June) regardless of water year type, whereas salinity was more variable and strongly affected by the annual climatic regime (Figure 1.7). Another factor that likely affected the strength of the predictor variable temperature was the widely divergent abundance-temperature response in early summer (bloom initiation time period) and late fall to winter (bloom termination time period). During the bloom initiation time period medusae were primarily captured at temperatures ≥ 19°C (5th percentile for occurrence and abundance), if salinity was also appropriate. However, in the fall the median temperature for medusae occurrence was 15.6°C, the 5th percentile was at 11.6°C and the lowest recorded temperature of occurrence was 8.3°C, indicating medusae could survive much cooler temperatures. The lower temperatures of occurrence in Suisun Marsh were below those previously reported (i.e. ~15°C; Vainola and Oulasvirta, 2001; Rees and Gershwin 2000).

The reason for the season specific response of *M. marginata* to temperature again can only be deduced from this study, but it is likely due to the differential environmental response of the sessile polyp and free-swimming medusa. *Maeotias marginata*, like many species of hydromedusa, over-winter as polyps and medusae are released from the polyps as conditions become appropriate in the spring to early summer. Thus, the lower bloom initiation temperature (19°C) likely corresponds to the minimum temperature required for either the production of medusa buds by the polyp or for the release of the larval medusae from the medusa bud. The production of medusae is energetically expensive, but required to obtain the benefits of sexual reproduction (e.g. increased dispersal and genetic diversity; Ma and Purcell 2005). Thus, it would be advantageous for polyps to withhold production of medusae until temperatures are suitable for reproductive success. The temperature range at which *M. marginata* medusae reproduced sexually under laboratory conditions (18 to 21°C; Rees and Gershwin 2000), is consistent with the observed minimum temperature thresholds for both occurrence and abundance in this study, which supports this possibility. The observed bloom termination thresholds for temperature (i.e. 11.6°C occurrence; 13.1°C abundance) would then likely relate specifically to temperatures affecting medusae survival, but further research is needed to verify the presumed temperature constraints for both polyps and medusae. In addition, other factors related to temperature including temperature controlled prey increases (e.g. pelagic copepod abundance) could also be contributing to the observed patterns, thus need to be investigated more thoroughly.

Secchi Depth

Secchi depth had the smallest positive effect on predicted abundance in the regression models. Low Secchi depth, which corresponds to low water transparency, may have directly affected the production of medusae by polyps if the resulting light levels inhibited medusae bud formation (i.e. Purcell 2007). In addition, low water transparency can also result in reduced primary productivity (Cloern 1987) and ultimately secondary productivity (i.e. zooplankton) that could, if prey abundance was sufficiently low, reduce the survival of medusae and polyps. Low prey availability could also reduce the number of medusae produced by polyps since prey availability is strongly tied to the production of medusae buds (Ma and Purcell 2005). Other studies have identified positive relationships between water transparency and medusae abundance (Arai 2001), but explanatory mechanisms were not investigated. Given that medusae are exclusively tactile feeders, it is unlikely that reduced water clarity alone would have much of an affect on their ability to forage effectively. In fact, in marine systems large aggregations of jellyfish are often found in areas of high turbidity and low light, where they have an advantage over visually feeding fishes (Eiane et al. 1999).

Dissolved Oxygen

The limited collection of DO data in this study (1999 to 2005) prevented the inclusion of this variable in the regression model. None-the-less, the thresholds of occurrence and abundance provided a reasonable approximation of how medusae may be affected by the observed range of DO. The suitable range (5th and 95th percentiles) of DO concentrations for medusae occurrence in Suisun Marsh during the fall months, when DO levels are often depressed, was 2.8 to 9.6 $mg{\cdot}lO_2^{-1}$. However, the low number of observations with DO concentrations less than 2 $mg{\cdot}lO_2^{-1}$ (n = 9 of 406 or 2.2%) affects the accuracy of the lower threshold estimate. In fact, live medusae were captured in sites with DO concentrations as low as 0 $mg{\cdot}lO_2^{-1}$. The 1st percentile of samples with medusae present occurred at a DO concentration of 0.5 $mg{\cdot}lO_2^{-1}$ and the mean catch of medusae between 0 and 1 $mg{\cdot}lO_2^{-1}$ was 4.6 $medusae{\cdot}minute^{-1}$. Thus, *M. marginata* medusae are capable of surviving the full range of anoxic to normoxic conditions found in Suisun Marsh, at least under acute exposure.

A high tolerance of gelatinous zooplankton to low DO levels has been observed in other systems (Purcell et al. 2001b; Condon et al. 2001). There is also evidence suggesting that medusae of gelatinous zooplankton species have a considerable advantage over zooplanktivorous fishes under low DO conditions, when it comes to feeding and processing captured prey (Decker et al. 2004). Certain areas of Suisun Marsh are becoming increasingly eutrophic (as measured by elevated phytoplankton biomass) with seasonal hypoxic and anoxic conditions becoming more common, (Appendix B1). Thus, if this trend in DO concentrations continues, gelatinous zooplankton, such as *M. marginata* may be at a competitive advantage over less tolerant pelagic species.

1.4.3 Environmental Changes and Relationship to Catch

Of the three environmental parameters measured throughout this study (salinity, temperature and Secchi depth), only the variability in salinity resulted in the significant separation of years with zero to near zero catch of medusae from years with moderate to high catch (Table 1.8 and Figure 1.7). The patterns in catch and monthly mean salinity indicate that moderate levels of salinity are associated with moderate to high catch of medusae, whereas both high (>6.3‰) and low salinity (<1.9‰) resulted in very low medusae catch. Since most years with high medusae abundance are in the latter half of this study (10 of 13 moderate to high catch years occur after 1993), this relationship further suggests that salinity conditions are becoming more moderate in Suisun Marsh during the bloom time period of May to December. This was also observed in the seasonal salinity plot (Figure 1.6) and is consistent with the lack of a significant seasonal (July to November) trend in salinity.

Although temperature variability does not appear to explain the major differences in abundance and occurrence of medusae (Table 1.8 and Figure 1.7), the significant increasing trend in fall temperatures (i.e. November and December; Table 1.7) is likely contributing to the significant increase in the November and December abundance of medusae, as well as the seasonal (July to November) abundance of medusae, the later bloom termination, and the increased duration of the medusae bloom. The continued increase in fall temperatures could lead to an even greater increase in medusae abundance if salinity remained appropriate and if temperatures remained at or above 19°C, the assumed critical lower level for production of medusae by polyps.

The variability in Secchi depth also does not appear to explain the large differences in abundance and occurrence of medusae (Figure 1.7), which is consistent with the small effect of Secchi depth in the regression models. The only significant differences in Secchi depth between the groups of years with zero to near zero catch and years with moderate to high catch of medusae occurred in the Wet water years (Group III; Table 1.8) that also had mean monthly salinities well below those needed for a bloom to occur (<2‰). The observed significant increase in Secchi depth in the months of July to October has likely had little direct effect on medusae abundance since Secchi depths were already above the minimum thresholds for occurrence (16 to 20 cm) and abundance (19 to 21 cm) during that time. An increase in Secchi depth in an earlier month (i.e. April or May) may have a much greater effect, if salinity and temperature were also favorable, since the secchi depths were either at or just below the observed lower thresholds.

1.4.4 Spatial and Temporal Overlap with Pelagic Fishes and Diet

The increasing abundance and widespread distribution of *M. marginata* medusae in Suisun Marsh and other areas of the SFE (Rees and Gershwin 2000; Rees and Kitting 2002) increases the likelihood of negative effects on the aquatic community. Pelagic invertebrates comprise a majority of the diet of *M. marginata* (Mills and Sommer 1995); thus their greatest impact would likely be on the pelagic invertebrate community. Pelagic prey species most frequently consumed by medusae are the calanoid and cyclopoid copepods and when there is spatial and temporal overlap, Cladocera. These invertebrates are also important prey for pelagic fishes in the system (Orsi and Mecum 1996; Kimmerer et al. 2000; Moyle 2002; Nobriga 2002; Feyrer et al. 2003) and there is some indication that they are in a current state of decline (Orsi and Mecum 1996; Kimmerer 2006; Cloern 2007). *Maeotias marginata* is currently the most abundant pelagic predator in Suisun Marsh throughout the late summer (August) and fall time period, increasing the possibility of negative interactions with fishes through competition for shared and declining prey resources.

Striped bass YOY have the greatest temporal and spatial overlap with medusae in Suisun Marsh, although juvenile and adult native longfin smelt and delta smelt and alien threadfin shad are also found in low abundance at the same time and locations. Striped bass YOY reach their peak abundance in Suisun Marsh in June and then decline dramatically into late summer and fall as mortality and recruitment affect their abundance and distribution (Chapter 3). The presence of an additional competitor (medusae) in the system during this important time period may adversely affect their recruitment success if food resources are limited. Density dependant relationships for pelagic feeding fishes such as striped bass young-of-year and delta smelt juveniles in the SFE have been found (Kimmerer et al. 2000; Bennett 2005). The density dependent effects are attributed, in part, to the reduced carrying capacity of the estuary as a result of reduced prey availability, increasing the possibility of adverse competitive effects.

The positive relationship between medusae size and number of pelagic and benthic prey in the gut contents suggests that in Suisun Marsh medusae presently have their greatest impact on the aquatic community during the late summer and early fall when medusae reach their largest size and greatest density. This can change if environmental conditions shift (e.g. inflow, salinity and temperature), as has already been observed with the month of peak abundance occurring later in the season in the latter half of this study. An earlier shift to dry season conditions (i.e. reduced inflow) could similarly shift the peak abundance of medusae as well as the overall seasonal abundance, since temperature conditions are usually favorable one to two months prior to salinity becoming appropriate. This would likely result in greater overlap of medusae and the more sensitive stages of fishes in the system (i.e. larval and juvenile fishes).

It is important to note that although the catch of medusae has extended into the late fall months in the latter half of the study, the late season conditions may be increasingly stressful for medusae and may have contributed to the observed decline in prey consumption from October (mean 12.8 prey·medusa^{-1}) to November (mean 7.9 prey·medusa^{-1}). The decline in prey consumption may have been due in part to reduced prey availability in the fall months and reduced metabolic requirements at cooler temperatures, but medusae collected in November were also beginning to show signs of decreased condition, such as discolored bells and loss of tentacles. Their declining condition in the fall months may have been due to cooler water temperatures and elevated salinities, but normal senescence following sexual reproduction may also have played a large role.

The diet results in this study differ somewhat from Mills and Sommer (1995), which observed a higher mean feeding rate of *M. marginata* medusae. Differences are likely due to the larger size of medusae used in their study and the timing of their investigation in relation to the bloom onset. Furthermore, a majority of prey consumed by medusae in the Mills and Sommer (1995) study were immature stages of invertebrates (67% of total excluding copepod eggs) including barnacle nauplii, crab zoea and copepod nauplii. In this study immature stage invertebrates accounted for 27.5% (all crab zoea) of the summer diet and < 1% (copepod nauplii) of the fall diet, when also excluding copepod egg sacs. Given that the immature stages of invertebrates in general have a low biomass, the biomass of consumed prey in both studies may be more similar.

Predation by *M. marginata* medusae on larval fishes has not previously been observed in natural systems, although they were observed feeding upon fishes (guppies) in the laboratory (Mills and Sommer 1995). The results from this study demonstrates that *M. marginata* medusae do in fact consume larval fishes, although the total number of medusae feeding upon larval fish (n = 6; 15% of medusae sampled in summer) and the number of larval fish consumed (n = 6; 5% of total diet in summer) was relatively low. Based upon emergence times, fish larvae most vulnerable to predation by medusae are alien species that, as a group, typically reproduce under warmer conditions when medusae are more likely to be found, such as the gobies consumed by medusae in this study. The small size of medusae (mean size 4.7 mm bell diameter) present in the summer of 2004 may have limited the potential for predation on larval fishes. Thus, it is possible that predation rates on larval fish would be higher if there was an earlier bloom of medusae and greater overlap between large medusae and larval fishes in the system. None-the-less, it was surprising that medusae as small as 4 mm and a mean size of 10 mm bell diameter were capable of capturing and consuming larval fishes.

In addition to direct effects of medusae on fishes, indirect effects may also negatively affect fishes in the SFE. For instance, fish avoidance behavior after encountering a large aggregation of jellyfish may contribute to a reduction in distribution and / or decreased abundance of pelagic fishes in certain locations. Purcell et al. (2000) first recognized that large aggregations of *Aurelia labiata* may in fact be serving a secondary role, primarily of defense against predators including other gelatinous species. Graham et al. (2001) further suggested that jellyfish aggregations may serve to deter competitors including zooplanktivorous fishes and other gelatinous species from entering an area, thus securing prey resources. The mechanism enabling this potential defense response has been suggested by Graham et al. (2001) to include the release of chemical scents or unfired nematocysts, as reported by Shanks and Graham (1988). Because medusae overlap spatially and temporally with high concentrations of pelagic invertebrates in the middle SFE (e.g. Suisun Marsh), fish avoidance of these areas would likely have considerable effects.

1.5 CONCLUSION

Although gelatinous zooplankton are by-catch in this study, the consistent monthly sampling of *M. marginata* medusae has yielded insights into possible mechanisms driving the increasing trends in abundance in the brackish region of the SFE. This study is unique in that there are relatively few long-term studies that have tracked the catch of gelatinous zooplankton, especially in estuarine waters (Mills 2001; Purcell 2005). The fact that *M. marginata* have apparently remained largely dormant in the SFE since their first reported occurrence in 1959 despite the extensive sampling of the rivers and estuarine habitats by various entities, suggests that until recently (i.e. after the 1980s) there has been a poor fit between the suitable environmental conditions for this species and the environmental conditions found in the estuary.

The more constant, but moderate dry-season inflow from 1978 to 1981 and again after 1992 (Appendix B2) has resulted in less variability in abiotic conditions, particularly salinity. In addition, the operation of the SMSCG in Montezuma Slough since the late 1980s (Figure 1.1) has likely further reduced the variability in salinity in Suisun Marsh in the late summer and fall months. More stable abiotic conditions tend to favor alien species and disadvantage native species, which may be adapted to and dependent on the more variable, yet predictable conditions that are often present in unaltered aquatic systems (Moyle and Light 1996; Gido and Brown 1999; Bunn and Arthington 2002). Thus, through managed flow conditions, the SFE is likely becoming more hospitable to previously established alien species and more invasible by the steady stream of exotic species that continue to be released into the system, primarily through shipping activities (Cohen and Carlton 1998; Carlton 2000; Choi et al. 2005). In the case of *M. marginata*, the narrow suitable salinity range for medusae (3 to 7‰ for bloom initiation and 3 to 10‰ for medusae survival) is likely the primary constraint for medusae abundance in the SFE at present, and these conditions are now regularly met in Suisun Marsh and surrounding areas during the dry-season, as moderate inflow conditions have prevailed.

The abundance and distribution of *M. marginata* in the SFE have changed considerably since the early 1990s and this species is now regularly captured in numerous locations in the system (Mills and Sommer 1995; Rees and Gerschwin 2000; Rees and Kitting 2002; Unpublished CDFG Fish Surveys). The freshwater conditions mixed with extensive drought in the first half of this study (1981 to 1992), likely prevented the regular occurrence of *M. marginata* in Suisun Marsh and may have resulted in a transient continuously shifting population in the SFE. In the latter half of this study (1993 to 2005), the return of more moderate and stable salinity conditions to the upper SFE likely contributed to the increased abundance of medusae and presumably the polyps that support the medusae blooms. Current climate patterns and water management in the SFE are likely playing a large role in the observed moderate salinity dry-season conditions (Knowles 2002; Knowles and Cayan 2002). As the human population and water demand increase in the State of California (Naiman and Turner 2000), there will be increased pressure to further alter the inflow regime, which could further benefit *M. marginata* if salinity remains favorable.

Increased fall water temperatures are also contributing to observed increases in abundance of medusae through extension of the bloom into the fall months. It is unclear if the warming fall temperatures are due to natural decadal shifts or are an indication of a larger global warming affect on the estuary (Cayan et al. 2008). Global warming scenarios are important to consider when predicting future biological changes in estuarine systems. In the SFE, these scenarios predict elevated temperatures in all seasons, increased rainfall versus snow and more variable annual precipitation totals, all of which will likely further affect the freshwater flow into the estuary (Naiman and Turner 2000; Knowles and Cayan 2002; Zhu et al. 2005; Cayan et al. 2008). The observed increasing temperatures in Suisun Marsh in the fall months during this study may be a foreshadowing of what is to come if the dry-season is prolonged and if warmer summer and fall conditions continue, as predicted under a regional global warming scenario (Knowles and Cayan 2002; Zhu et al. 2005; Cayan et al. 2008). Based upon these study results, increasing temperatures coupled with moderate inflow conditions and salinities resulting from altered runoff patterns, increased water export, and tidal modification by the salinity control structures will likely contribute to medusae blooms of greater duration, spatial extent and size in the SFE.

1.5.1 Relationship to Worldwide Patterns

The population increase of *M. marginata* medusae in Suisun Marsh and elsewhere in the SFE is one of many examples of jellyfish populations increasing worldwide in estuaries and marine waters. Although factors driving these increased abundance patterns likely vary for each species and region in which increases have been observed, many similarities also exist. For instance it is common for gelatinous zooplankton to increase in abundance in systems where there have been major changes to the trophic structure of aquatic ecosystems (Mills 1995, 2001; Pauley et al. 1998; Breitburg et al. 2003; Bilio and Niermann 2004; Lynam et al. 2006). The decline of pelagic fish predators through over-fishing, increased pollution and or degradation of the "natural" environmental conditions are the most common form of trophic disruption in estuaries and marine waters, although the introduction of alien invasive species are increasingly affecting the aquatic communities in receiving waters (Cohen and Carlton 1998; Moyle 1999).

Cohen and Carlton (1998) identified the SFE as the most invaded estuary in the world stemming from the vast number of established alien species including flora and fauna (234 species with an additional 125 cryptogenic species) and the aquatic community has become dominated numerically by alien invasive species, especially in the brackish upper estuary. The brackish portion of the SFE has been particularly affected by the introduction of the overbite clam *Corbula amurensis*, whose efficient filtering capacity and high density has contributed to the collapse of large phytoplankton blooms and either directly or indirectly has negatively affected the bacteria, meso and macrozooplankton and pelagic fishes (Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer and Orsi 1996; Orsi and Mecum 1996; Orsi and Ohtsuka 1999; Matern et al. 2002; Moyle 2002; Feyrer et al. 2003; Hoof and Bollens 2004; Kimmerer et al. 1994, 2000; Kimmerer 2006; Bouley and Kimmerer 2006).

It is also common for systems with large blooms of gelatinous zooplankton to have altered hydrology and disruption to the natural flow regime, which in most cases has resulted in increased salinity (Zaitsev and Mamaev 1997; Knowles 2002; Knowles and Cayan 2002; Oguz and Cokacar 2003; Bilio and Niermann 2004; Purcell 2005; Xiang et al. 2005). The SFE is unique in that the major water diversion system is positioned in the Sacramento-San Joaquin Delta just upstream of the estuary, rather than at the upstream water storage locations (i.e. reservoirs). In order for this system to function properly, a minimum inflow from the rivers is required to maintain water quality, primarily salinity, at the downstream water diversion locations (Kimmerer 2002; Knowles 2002). This minimum inflow keeps the intruding marine water "at bay" and has resulted in the more stable and moderate salinity in the upper SFE that has likely contributed to the increased abundance of *M. marginata* and other alien species.

It is also common for systems with expanding populations of gelatinous zooplankton to be increasingly eutrophic (Caddy 1993; Mills 1995; Arai 2001). As nutrient input increases in estuaries and marine waters, larger phytoplankton blooms often result, but they are usually dominated by species that are smaller, less nutritious, and less available to the macrozooplankton preferred by pelagic fishes. Microzooplankton usually dominate the zooplankton community under these conditions, as they have in the upper SFE, and although they tend to be highly abundant, their small size usually precludes visual pelagic predators from feeding upon them (Bouley and Kimmerer 2006; Kimmerer 2006). However, non-visually feeding gelatinous zooplankton often thrive in marine waters where microzooplankton dominate the community (Uye 1994; Uye and Sano 1995; Shiganova 1998; Orsi and Ohtsuka

1999; Purcell et al. 2007), although this relationship remains largely correlative. Microzooplankton (*Limnothoina* or *Oithona*), were found in the diet of *Maeotias marginata* medusae in this study, but their overall numbers were low (unpublished data). None-the-less, it is quite likely that both polyps and medusae would benefit from high densities of microzooplankton in eutrophic waters, while other visually feeding pelagic predators would not, but this relationship needs to be studied further.

In addition, the excess production of phytoplankton under eutrophic conditions can also lead to a biological oxygen demand and low DO levels when bacterial decomposition of the excess phytoplankton biomass occurs. In general, gelatinous zooplankton are less sensitive to the low DO conditions, compared to other estuarine predators (e.g. fishes) and may even feed more efficiently under moderately depressed DO levels (Purcell et al. 2001b; Breitburg et al. 2003; Decker et al. 2004). *Maeotias marginata* medusae in Suisun Marsh did not appear to be negatively affected by both hypoxic and anoxic conditions. Given that certain areas of the Sacramento-San Joaquin Delta (Lehman et al. 2004) and SFE (Suisun Marsh) are becoming increasingly eutrophic and deprived of DO in the fall months, medusae are likely to be at an advantage over other more sensitive pelagic fishes and invertebrates in areas where salinity and temperature are favorable.

Finally, the absence of an effective predator of gelatinous zooplankton often results in uncontrolled population increases and problematic blooms either at the time of introduction or when environmental conditions allow for rapid population increase. The best known example being the introduction of the alien ctenophore *Mnemiopsis leidyi* (Agassiz 1865) in the Black Sea, which along with several other ecosystem and habitat disturbances resulted in major alteration of the ecosystem (Vinogradov et al. 1989; Studenikina et al. 1991; Kideys et al. 2000; Shiganova and Bulgakova 2000; Mills 2001; Purcell 2001a; Shiganova et al. 2003; Bilio and Niermann 2004). It wasn't until the inadvertent introduction of another gelatinous zooplankter, the ctenophore *Beroe ovata*, a natural predator on *M. leidyi* in its native range that the community began to recover (Purcell et al. 2001a). Although many predators are well adapted for feeding on gelatinous zooplankton at both the medusa and polyp stage in marine waters, very few are likely to be found in estuaries where salinities are consistently <10‰, increasing the likelihood of negative effects of medusae on the associated fauna (Arai 1988; Purcell and Arai 2001; Arai 2005).

There are no known predators of *M. marginata* medusae or polyps in the upper SFE (Miller and Lea 1972; Smith and Carlton 1975; Rees and Gershwin 2000). The nearest potential fish predator in the SFE is the Pacific butterfish, *Peprilus simillimus* within the family Stromateidae (Harbison 1993; Mianzan et al. 1996), but this species is only found in high salinity areas including central and lower San Francisco Bay. Two other alien hydromedusae are found in association with *M. marginata* in the brackish region of the SFE including *Blackfordia virginica* and an unknown species in the genus *Moerisia*, but both are much smaller in size and are believed to feed primarily upon small invertebrates as medusae (Mills and Sommer 1995; Chapter 2). Larger alien and native gelatinous zooplankters that could feed upon *M. marginata* medusae are a component of the down-bay community in high salinity areas of the estuary (Rees and Kitting 2002). Common predators of polyps including nudibranchs, gastropods, and specialized invertebrates within the amphipoda (Arai 2005) are also largely absent from Suisun Marsh (unpublished data) and presumably other brackish areas of the SFE.

Since there are no known predators of *M. marginata* medusae in the system, much of the accumulated biomass of this species is likely lost from higher trophic levels during the important summer and fall growing season with the exception of waste products and occasional medusae mortality (e.g. Hansson and Norman 1995; Arai 2005; Lynam et al. 2005b; Titelman et al. 2006). The majority of biomass sequestered by medusae likely re-enters at the base of the food web as detritus, en masse during the late fall and winter die off, benefiting primarily the benthic and microbial community. This loss of pelagic biomass during the summer and fall seasons likely disrupts and further dilutes the productivity of the pelagic food web in the SFE, which already has been significantly disrupted by major habitat modification, flow alteration and the introduction of numerous alien species (Nichols et al. 1986, 1990; Alpine and Cloern 1992; Kimmerer and Orsi 1996; Orsi and Mecum 1996; Cohen and Carlton 1998; Orsi and Ohtsuka 1999; Hoof and Bollens 2004; Bouley and Kimmerer 2006).

The lack of predators in the SFE increases the likelihood that *M. marginata* is constrained primarily by abiotic conditions and prey availability. Changing abiotic conditions appear to be the most plausible explanation for the recent surge in medusae abundance since the availability of primary prey observed in this study (e.g. pelagic macrozooplankton [i.e. copepods], cladocerans and mysids) has actually declined since the middle to late 1980s (Orsi and Mecum 1996; Kimmerer 2006; Cloern 2007; Chapter 3). However, it is possible that the recent increase in microzooplankton densities in the upper SFE and other food web changes during roughly the same time period, could be contributing to the observed medusae increase (Orsi and Ohtsuka 1999; Bouley and Kimmerer 2006; Chapter 3).

Additional research is needed to address several shortcomings of this study. First, a more accurate estimate of the density of *M. marginata* in Suisun Marsh and the surrounding areas is needed to better assess the scope of possible impacts that this species may have on the aquatic community in the upper SFE. In addition, an improved understanding of the feeding ecology of this species, particularly on the highly abundant microzooplankton, would allow for a better understanding of its position and role in the SFE food web. Finally the environmental relationships observed in this study need to be further tested and validated under more controlled conditions for both the polyps and medusae of *M. marginata*.

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1.7 TABLES

Table 1.1 Slough and site characteristics and station details for otter trawl locations in Suisun Marsh, Solano County, California. The station code listed is followed (in parentheses) by the slough division for the depth / abundance relationship with U = Upper and L = Lower. Regions within Suisun Marsh are abbreviated as NW = North West, NE = North East, SW = South West, and SE = South East. Average Depth is the average station depth in meters with one standard deviation (s.d.) listed in parentheses. Slough Depth and Width refer to the average width and depth of the slough or reach if the slough was divided into upper (U) and lower reaches (L). The Slough Length is the estimated total length in kilometers.

Slough	Site	Region	Trawl Duration (minutes)	Average Depth (s.d.)	Slough Depth (m)	Slough Width (m)	Slough Length (km)
First Mallard	FM1	N.W.	5	1.2 (0.4)	1.3	30	1.9
	FM2	N.W.	5	1.5 (0.5)			
Cutoff	CO1	N.W.	5	1.9 (0.6)	2.0	39	6.4
	CO2	N.W.	5	2.0 (0.6)			
Boynton	BY1(U)	N.W.	5	3.0 (0.8)	3.0	33	5.1
	BY3(L)	N.W.	5	3.4 (1.2)	3.4	37	
Peytonia	PT1	N.W.	5	2.4 (0.9)	2.7	37	3.6
	PT2	N.W.	5	3.0 (0.7)			
Suisun	SU1(U)	N.W.	10	4.8 (1.1)	5.5	161	22.6
	SU2(U)	N.W.	10	6.3 (2.2)			
	SU3(L)	S.W.	10	2.5 (0.8)	3.0	205	
	SU4(L)	S.W.	10	3.5 (1.5)			
Goodyear	GY1(U)	S.W.	5	1.7 (0.6)	1.8	22	10.7
	GY2(U)	S.W.	5	1.8 (0.7)			
	GY3(L)	S.W.	5*	2.6 (0.7)	2.6	31	
Denverton	DV2	N.E.	5	2.4 (0.8)	2.7	68	4.9
	DV3	N.E.	5	3.1 (1.1)			
Nurse	NS2	N.E.	5	4.0 (1.0)	4.8	120	6.2
	NS3	N.E.	5	5.7 (2.4)			
Montezuma	MZ1(U)	S.E.	10	7.2 (2.1)	6.0	108	33.9
	MZ2(U)	S.E.	10	4.8 (1.0)			

*Goodyear Slough lower (GY3) trawl duration was 10 minutes from 1981 to 1988 and 5 minutes after 1988.

Table 1.2 Temporal and spatial patterns of *M. marginata* medusae in Suisun Marsh. Water Year Type is a rank value based on unimpaired runoff, a measure of precipitation in a given year, during the September to October time period with W – Wet, AN – Above normal, BN – below normal, D – Dry, and C – Critical. Bloom onset is the month of first occurrence and bloom termination is the last month of occurrence in any of the core sampling sites. Site Occurrence is the summed number of sites with at least one occurrence during the bloom season and the % Site Occurrence is the percent of samples with medusae present.

Year	Water Year Type	Bloom				Site Occurrence (Max = 17)	% Site Occurrence
		Onset	Termination	Duration (months)	Peak		
1981	D	July	Nov	5	Aug	16	94.1
1982	W	na	na	0	na	0	0.0
1983	W	na	na	0	na	0	0.0
1984	W	July-Aug*	Oct	*3 to 4	Sept	15/15	100.0
1985	D	July	Sept	3	Aug	7	41.2
1986	W	Aug-Sept*	Sept	*1 to 2	Aug-Sept*	2	11.8
1987	C	May	July	3	June	3/14	21.0
1988	C	June-July*	Oct	*4 to 5	Aug	14	82.4
1989	C	Aug	Aug	1	Aug	1	5.9
1990	C	Oct-Nov*	Nov	*1 to 2	Oct-Nov*	2	11.8
1991	C	Sept	Sept	1	Sept	2	11.8
1992	C	May	June	2	May	3	17.6
1993	AN	July	Oct	4	Aug	8	47.1
1994	C	July	Nov	5	Sept	13	76.5
1995	W	Aug	Oct	3	Oct	4	23.5
1996	W	Aug	Nov	4	Sept	17	100.0
1997	W	June	Nov	6	Sept	17	100.0
1998	W	Oct	Oct	1	Oct	1	5.9
1999	W	Aug	Nov	4	Nov	17	100.0
2000	AN	July	Nov	5	Oct	17	100.0
2001	D	July	Dec	6	July	17	100.0
2002	D	July	Nov	5	Aug	17	100.0
2003	AN	July	Dec	6	Sept	17	100.0
2004	BN	July	Nov	5	Sept	17	100.0
2005	W	Aug	Nov	4	Oct	17	100.0

na = Not Present. *Values with estimated range due to missing trawl data. For month of bloom onset, if a month was not sampled prior to the month of first occurrence, then the missing month was assumed to have had medusae present. The same data correction was applied to bloom duration. This may have resulted in an underestimate of bloom onset and overestimate of bloom duration in some instances. In 1986 and 1990 a range of months was listed for peak abundance due to missing data.

Table 1.3 Negative Binomial (NB) and Poisson (P) regression model results for the relationship between environmental predictor variables and the abundance of *M. marginata* for a) the full study time period, 1981 to 2005 and b) the years 1996 to 2005. The coefficient and standard error (in parentheses) are listed for each independent variable with Sal = salinity, Temp = water temperature, Secchi = end depth for the visibility of the Secchi disc [i.e. water transparency]. The selection of independent variables at each model step was based upon the lowest value of Aikake's information criterion (AIC). ΔAIC is the difference between the best-fit model and the AIC of the specified model. The model probability (*p*) was determined using the likelihood ratio test and the X^2 test statistic. The significance of each independent variable using Wald's X^2 test statistic with a level of significance indicated at $p<0.01$ (*). The model with independent variables that met the selection criteria and had the lowest AIC are indicated in bold and represent the best-fit model for the available data.

	Model	No. of terms	df	Sal	Temp	Secchi	Sal^2	*p*	AIC	ΔAIC
	P	4	4841	0.64(0.02)*	0.14(0.004)*	0.05(0.001)*	-0.11(0.003)*	<0.01	798	11842
	P	3	4842	0.10(0.005)*	0.16(0.004)*	0.06(0.001)*		<0.01	3286	14330
a.	**NB**	**4**	**4841**	**0.91(0.05)***	**0.24(0.01)***	**0.08(0.007)***	**-0.14(0.008)***	**<0.01**	**-11044**	**0**
	NB	3	4842	0.41(0.03)*	0.27(0.02)*	0.10(0.007)*		<0.01	-10700	344
	NB	2	4844	0.61(0.03)*	0.26(0.02)*	-		<0.01	-10466	578
	NB	1	4845	0.65(0.03)*	-	-		<0.01	-10194	850
	NB	0	4846	-	-	-		<0.01	-9760	1284

	Model	No. of terms	df	Sal	Temp	Secchi	Sal^2	*p*	AIC	ΔAIC
	P	4	2320	0.71(0.02)*	0.13(0.04)*	0.03(0.001)*	-0.10(0.003)*	<0.01	-3744	8236
	P	3	2321	0.22(0.01)*	0.16(0.004)*	0.04(0.001)*		<0.01	-2150	9830
	NB	**4**	**2320**	**1.07(0.05)***	**0.24(0.02)***	**0.03(0.006)***	**-0.15(0.009)***	**<0.01**	**-11980**	**0**
b.	NB	3	2321	0.61(0.02)*	0.27(0.01)*	0.06(0.005)*		<0.01	-11712	268
	NB	2	2322	0.76(0.04)*	0.26(0.02)*	-		<0.01	-11640	340
	NB	1	2323	0.81(0.04)*	-	-		<0.01	-11408	572
	NB	0	2324	-	-	-		<0.01	-10832	1148

Table 1.4 Standardized estimates for the best-fit negative binomial models for both 1981 to 2005 and 1996 to 2005 time periods. Salinity^2 is a quadratic term calculated by first mean centering the value (salinity-mean sal) prior to calculating its squared value. Standardized Estimate = [independent variable coefficient *x* standard deviation of the independent variable] / standard deviation of the dependent variable (Bradford et al. 2003).

Independent Variable	Standardized Estimate	
	1981-2005	1996-2005
Salinity	0.54	0.40
Temperature	0.22	0.15
Secchi	0.15	0.04
Salinity^2	-0.35	-0.19

Table 1.5 Environmental parameter summary values for samples collected from 1981 to 2005 with *M. marginata* present for (a) Bloom Initiation - January to September and (b) Bloom Termination - October to December. The lower threshold and upper threshold of environmental variables were estimated using the 5th and 95th percentiles of the samples with medusae present. The number of samples (n) with medusae present/absent are listed. Range refers to the maximum and minimum of field values in all samples in the respective season.

a. Bloom Initiation	Salinity (‰)	Temperature (°C)	Water Transparency (cm)	Dissolved Oxygen (mg·lO$_2$)
Mean(s.d.)	5.8(2.2)	21.3(1.7)	29.6(10)	7.4(1.2)
Minimum	0.9	16.5	8	3.7
5th	**2.8**	**19**	**16**	**5.3**
10th	3.2	19.3	19	5.8
Median	5.4	21.2	28	7.5
90th	9	23.6	43	8.9
95th	**9.9**	**24.1**	**48**	**9.2**
Maximum	12.9	27	75	11
Range	0 - 16	0 - 29.5	3 - 75	2 - 13.8
n	467/3683	467/3683	467/3683	257/1111

b. Bloom Termination	Salinity (‰)	Temperature (°C)	Water Transparency (cm)	Dissolved Oxygen (mg·lO$_2$)
Mean(s.d.)	6.3(2.1)	15.9(2.5)	34.2(10.6)	6.8(2.1)
Minimum	1	8.3	13	0
5th	**3.3**	**11.6**	**20**	**2.8**
10th	3.8	12.7	21	4
Median	5.9	15.6	33	7.1
90th	9.4	19.1	48	9.2
95th	**10.1**	**19.7**	**53**	**9.6**
Maximum	11.6	21.5	71	10.3
Range	0 - 14.8	2.9 - 23	2 - 74	0 - 12.5
n	303/1164	303/1164	303/1164	230/406

Table 1.6 Environmental parameter summary values for *M. marginata* abundance for (a) Bloom Initiation - January to September and (b) Bloom Termination - October to December. The lower threshold and upper threshold of environmental variables were estimated using the 5th and 95th percentiles of the total catch with the values in parentheses indicating the percent of samples occurring below and above the respective thresholds. Range refers to the maximum and minimum of field values in all samples in the respective season.

a. Bloom Initiation	Salinity (‰)	Temperature (°C)	Water Transparency (cm)	Dissolved Oxygen (mg·lO$_2$)
5th	**3.4(63.1%)**	**19.0(50.6%)**	**19(44.8%)**	**5.7(10%)**
10th	3.4	19.5	22	6.3
Median	5.3	21.5	31	7.4
90th	9	23.9	43	8.8
95th	**9.4(3.8%)**	**24.1(3%)**	**47(3.4%)**	**9.4(12%)**
Range	0 - 16	0 - 29.5	3 - 75	2 - 13.8
n	3683	3683	3683	1111

b. Bloom Termination	Salinity (‰)	Temperature (°C)	Water Transparency (cm)	Dissolved Oxygen (mg·lO$_2$)
5th	**4.2(41.2%)**	**13.1(48.7%)**	**21(25.3%)**	**4.2(9.1%)**
10th	4.6	13.5	23	5.1
Median	6.3	17.5	36	7
90th	8.5	19	64	8.8
95th	**9.2(13.7%)**	**19.4(5.5%)**	**71(3.2%)**	**9.3(16%)**
Range	0 - 14.8	2.9 - 23	2 - 74	0 - 12.5
n	1164	1164	1164	406

Table 1.7 Kendall's tau correlation for annual trends in monthly salinity, temperature, water transparency (i.e. Secchi depth), and catch of *M. marginata* medusae. The correlation coefficient and sample size are listed for each significant relationship with the Bonferroni adjusted $p = 0.0015$ (i.e. adjustment for 32 comparisons).

	Month							
Variable	May	June	July	Aug	Sept	Oct	Nov	Dec
Temp	ns	**0.17** **353**	ns	ns	ns	ns	**0.22** **363**	**0.18** **331**
Salinity	**-0.19** **367**	ns	ns	ns	ns	**0.18** **322**	**0.11** **363**	ns
Secchi	ns	ns	**0.21** **344**	**0.16** **361**	**0.14** **367**	**0.11** **310**	ns	ns
Catch	ns	ns	**0.32** **361**	**0.33** **362**	**0.49** **376**	**0.42** **322**	**0.52** **363**	**0.16** **331**

Table 1.8 Mean monthly environmental values for year groups with two dominant abundance classes (Absent-Low and Medium-High) with the Absent–Low abundance group further divided into two water year type groupings (Critical-Dry and Wet). Significant differences (Tukey-Kramer HSD test; $p<0.05$) for the between year group comparisons are indicated by the letters a-c. The absence of a letter or groups sharing a letter had mean values that were not statistically different.

Environmental Parameter	Group	Medusae Abundance Pattern	Water Year Type	Month							
				May	June	July	Aug	Sept	Oct	Nov	Dec
	I	Absent-Low	Critical-Dry	4.5(0.4)^{a}	6.3(0.6)^{a}	6.7(0.6)^{a}	7.6(0.6)^{a}	7.7(0.5)^{a}	9.8(0.1)^{a}	8.6(0.3)^{a}	7.1(0.6)^{a}
Salinity	II	Medium-High	Dry-Wet	1.7(0.2)^{b}	2.5(0.4)^{b}	4.1(0.4)^{b}	4.8(0.5)^{b}	5.7(0.5)^{a}	6.3(0.4)^{b}	6.0(0.4)^{b}	3.8(0.4)^{b}
	III	Absent-Low	Wet	0.8(0.2)^{b}	0.5(0.1)^{b}	0.4(0.1)^{c}	1.1(0.3)^{c}	1.0(0.3)^{b}	1.1(0.3)^{c}	1.9(0.8)^{c}	1.1(0.3)^{c}
	I	Absent-Low	Critical-Dry	19.8(0.6)	19.6(0.4)	22.1(0.6)	21.5(0.6)	19.9(0.3)	18.2(0.8)	13.5(1.2)	9.1(0.7)
Temperature	II	Medium-High	Dry-Wet	19.7(0.2)	21.8(0.4)	21.2(0.3)	21.8(0.4)	21.1(0.4)	17.3(0.5)	13.6(0.5)	10.3(0.3)
	III	Absent-Low	Wet	18.9(1.3)	20.1(0.9)	22.3(0.8)	20.6(0.7)	20.9(0.5)	17.1(0.3)	12.3(1.4)	9.6(0.6)
	I	Absent-Low	Critical-Dry	18.3(1.6)	18.6(1.2)	21.3(0.9)	23.7(1.8)	27.7(2.2)^{ab}	34.6(3.6)^{a}	32.2(4.2)	30.2(2.0)
Secchi	II	Medium-High	Dry-Wet	18.6(0.9)	21.9(2.3)	23.7(1.5)	25.7(1.6)	30.4(1.9)^{a}	31.2(1.4)^{ab}	30.2(1.1)	28.2(2.2)
	III	Absent-Low	Wet	16(1.7)	15.6(0.5)	15.1(1.3)	17.6(1.5)	16.1(1.9)^{b}	20.6(0.9)^{b}	21.9(0.8)	22.3(2.1)

Group I – 1985, 1987, 1989, 1990, 1991, 1992; Group II – 1981, 1984, 1993, 1994, 1996, 1997, 1999-2005; Group III – 1982, 1983, 1986, 1995, 1998

Table 1.9 Diet study details for *M. marginata* medusae for each season sampled. Standard deviations for Average Bell Diameter and Average Number of Prey are listed in parentheses. The average number of prey excludes the copepod egg sacs.

	Summer	Fall
Sample Size (n)	40	55
Average Bell Diameter (mm)	4.7 (3.8)	20.3 (5.0)
Min. Bell Dia. (mm)	1.5	9
Max. Bell Dia. (mm)	22	32
Average Number of Prey	3.0 (3.8)	10.5 (9.4)
Min. Number of Prey	0	1
Max. Number of Prey	16	49

Table 1.10 *Maeotias marginata* gut contents for Summer (July) and Fall (October and November). Taxa are listed in order of decreasing abundance. The water column position of prey are indicated in parentheses with P = Pelagic, E = Epibenthic, and B = Benthic. Uncertainty in water column position is indicated by a question mark (?). If a taxa is found in all water column positions, then the position of most frequent occurrence is in bold. Prey Abundance is the seasonal total of prey of a given taxa in the gut contents. P% is the percent of the seasonal total prey in the gut contents. Freq. is the number of medusae that fed upon the indicated taxa and F% is the percent of medusae that fed upon the taxa. Prey Avg. is the average number of prey found in the gut contents for the listed taxa and Season. Avg. is the total seasonal average including copepod egg sacs.

Season	Species	Prey Abundance	N%	Freq.	F%	Prey Avg.
(a) Summer n = 40	Calanoid Copepod (P)	71	58.7	25.0	62.5	1.8
	Crab Zoea (P)	33	27.3	18.0	45	0.8
	Larval Fish (Gobiidae; P)	6	5.0	6.0	15	0.2
	Amphipoda (Gammaridae; E,B)	4	3.3	1.0	2.5	0.1
	Mysids (P)	2	1.7	2.0	5	0.1
	Harpacticoid Copepod (B)	2	1.7	2.0	5	0.1
	Cladoceran (P)	1	0.8	1.0	2.5	0.0
	Cyclopoid Copepod (P)	1	0.8	1.0	2.5	0.0
	Copepod Egg Sacs (P?)	1	0.8	1.0	2.5	0.0
	Total	121			Avg.	3.0
(b) Fall n = 55	Calanoid Copepod (P)	263	41.8	39	71	4.8
	Cyclopoid Copepod (P)	122	19.4	29	52.7	2.2
	Amphipoda (Corophium; E,B)	80	12.7	36	65.5	1.5
	Cladoceran (P)	58	9.2	12	21.8	1.1
	Copepod Egg Sacs (P?)	51	8.1	12	21.8	0.9
	Harpacticoid Copepod (B)	19	3.0	9	16.4	0.3
	Mysids (P)	17	2.7	7	12.7	0.3
	Copepod Unknown (P?)	6	1.0	4	7.3	0.1
	Copepod Nauplii (P?)	3	0.5	3	5.5	0.1
	Amphipoda (Gammaridae; E,B)	3	0.5	2	3.6	0.1
	Cumacean (**E,B**,P)	2	0.3	2	3.6	0.0
	Chironomidae (B)	2	0.3	2	3.6	0.0
	Leptocheilea dubea (E,B)	2	0.3	1	1.8	0.0
	Mite (E,B)	1	0.2	1	1.8	0.0
	Total	629			Avg.	11.4

1.8 FIGURES

1.1 The San Francisco Bay, California and the upper San Francisco Estuary. The map of the upper San Francisco Estuary provides detail on the channels of Suisun Marsh including the 17 stations otter trawled monthly by U.C. Davis from 1980 to 2005 and 4 added stations trawled from 1994 to 2005. The Suisun Marsh Salinity Control Gates (SMSCG) in Montezuma Slough began operating in fall 1988. A measure of freshwater flow (inflow) entering the upper SFE is measured at Chipps Island near the entrance to Suisun Marsh (Montezuma Slough).

1.2 The annual average monthly patterns in environmental variables at the 17 core sampling stations in Suisun Marsh from 1981 to 2005 and the daily average freshwater inflow past Chipps Island in the middle SFE.

1.3 Annual July to November otter trawl catch of *M. marginata* medusae at the 17 core sampling stations in Suisun Marsh from 1981 to 2005. Data are illustrated by Box Plots which display the summary statistics including the Mean (dotted bar), Median (solid bar in box), 25th and 75th quartiles (top and bottom edges of box) and also the following percentiles: 10th and 90th (edge of whiskers) and 5th and 95th (open circles).

1.4 Regional annual catch of *M. marginata* medusae in Suisun Marsh otter trawls from July to November. The northeast region was only sampled from 1994 to 2005.

1.5 *Maeotias marginata* cumulative abundance plots for the 1981 to 2005 time period (1988 excluded) in both the January to September (a-c) and October to December (d-f) time periods for salinity (a and d), temperature (b and e) and Secchi depth (c and f). Reference lines for the level of the environmental variable that corresponds to the 5th (dotted) and 95th (dash-dot) percentiles of abundance are included. The percent of samples above and below the indicated thresholds are listed in Table 1.6. In (a), the dashed reference line indicates the change in slope of cumulative abundance at 5.7‰.

1.6 Annual average a) salinity, b) temperature and c) Secchi depth patterns in Suisun Marsh for the July to November time period. The annual variation (one standard deviation) is represented by error bars. The reference lines in a) represent the lower threshold (3‰, dotted line), upper threshold (10.3‰, dashed double dot line), and estimated upper threshold for larval medusae release (7‰, dashed single dot line). The reference lines in b) represent the estimated lower (~ 19 °C, dotted line) and upper threshold (~24 °C, dashed dot line). The year 1989 was removed because of incomplete sampling in the fall that would have skewed the results (no measurements in October and only 4 of 17 measurements in November). *Average salinity in 1988 was estimated using data from nearby continuous loggers and concurrent monitoring surveys for 13 of the 17 core sites.

1.7 Mean monthly (a) catch, (b) salinity, (c) temperature, and (d) Secchi depth for all sample years (1981-2005) at the core Suisun Marsh sites. Three groups of data are specified for each sub-figure with Group I represented by the Critical to Dry water years (1985, 1987, and 1989-1992) with medusae absent or only captured in very low abundance (mean July to November abundance <0.1 medusae·minute^{-1}). Group II – Dry to Wet water years (1981, 1984, 1993, 1994,

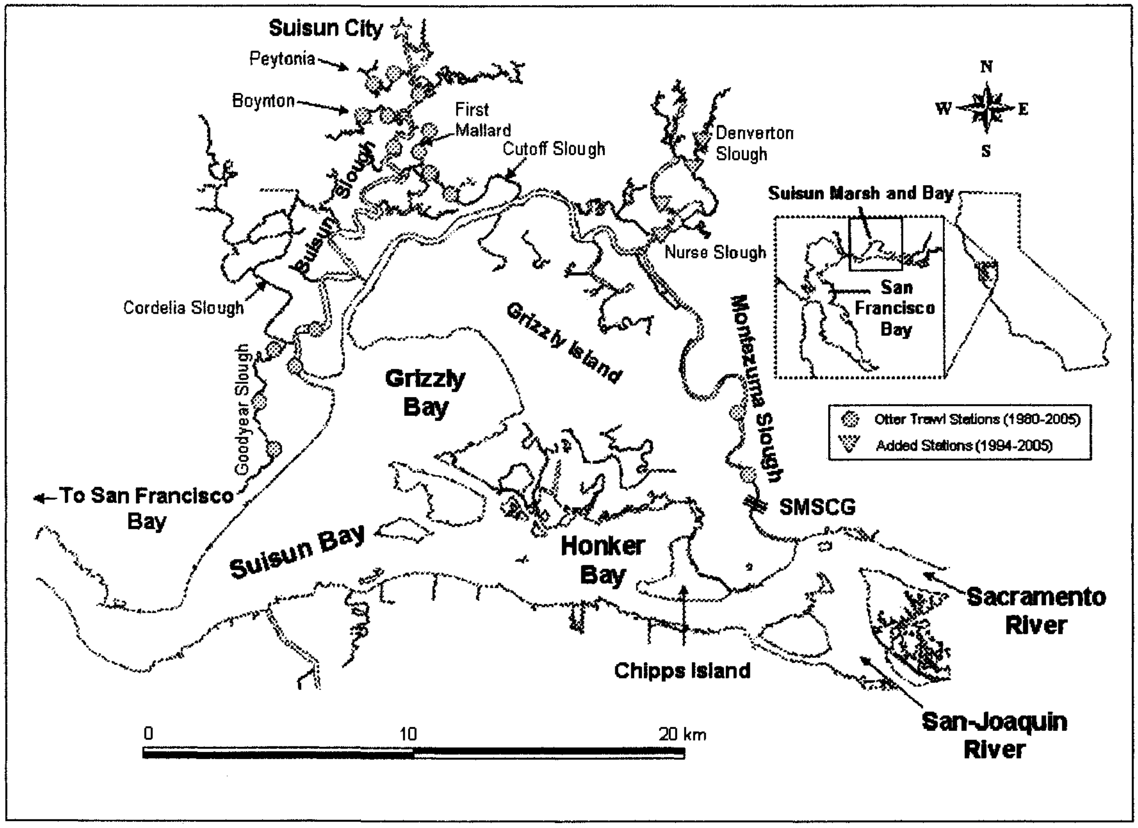


Figure 1.1

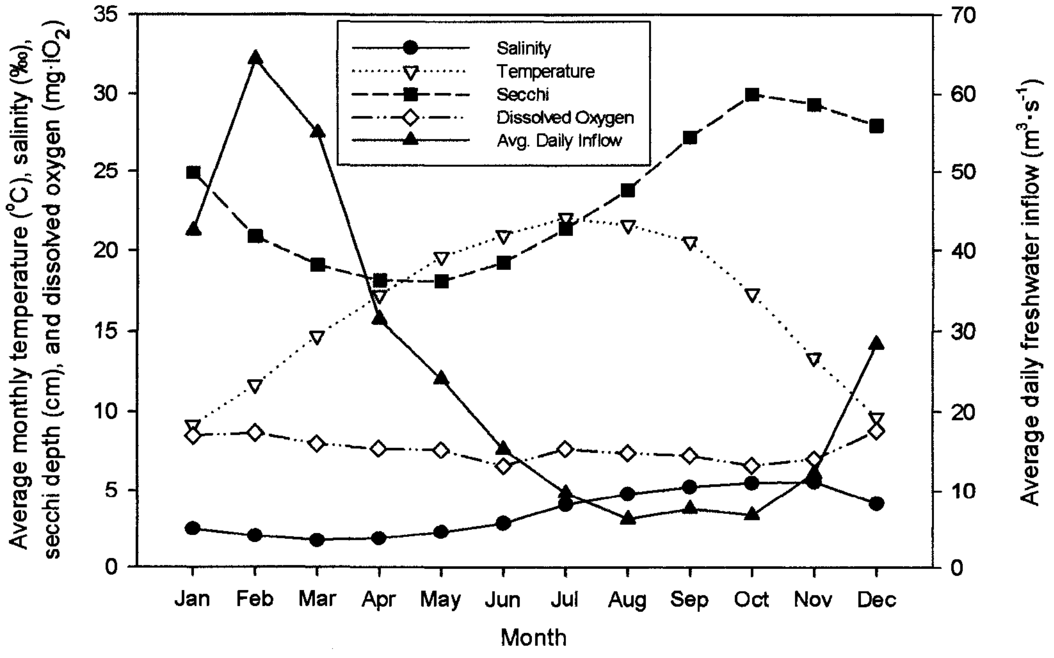


Figure 1.2

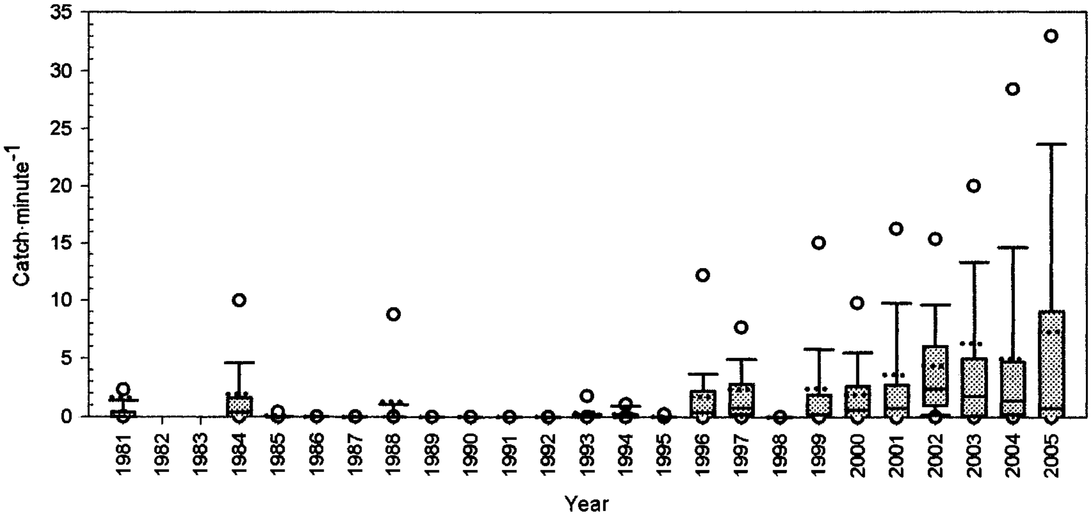


Figure 1.3

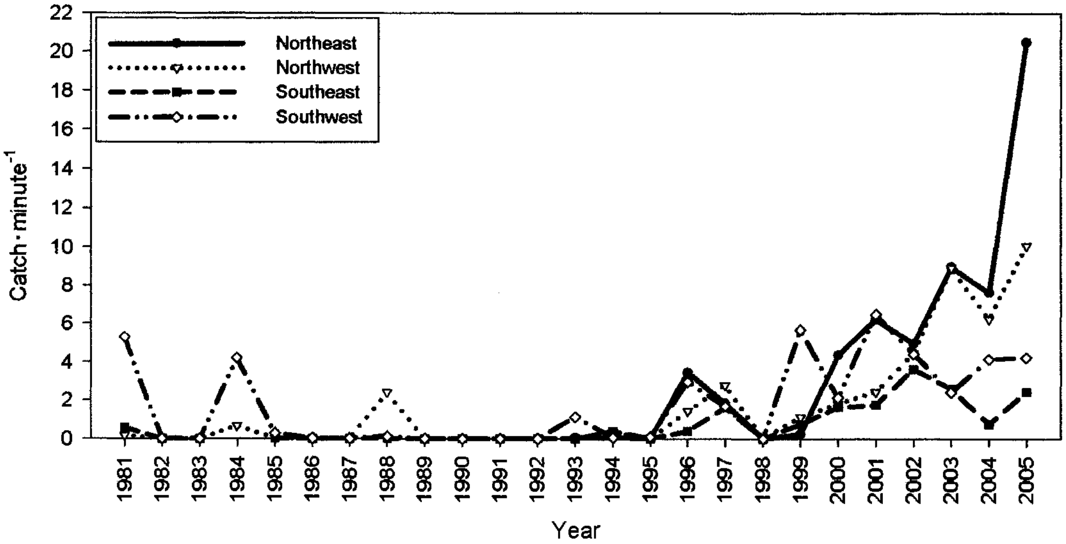


Figure 1.4

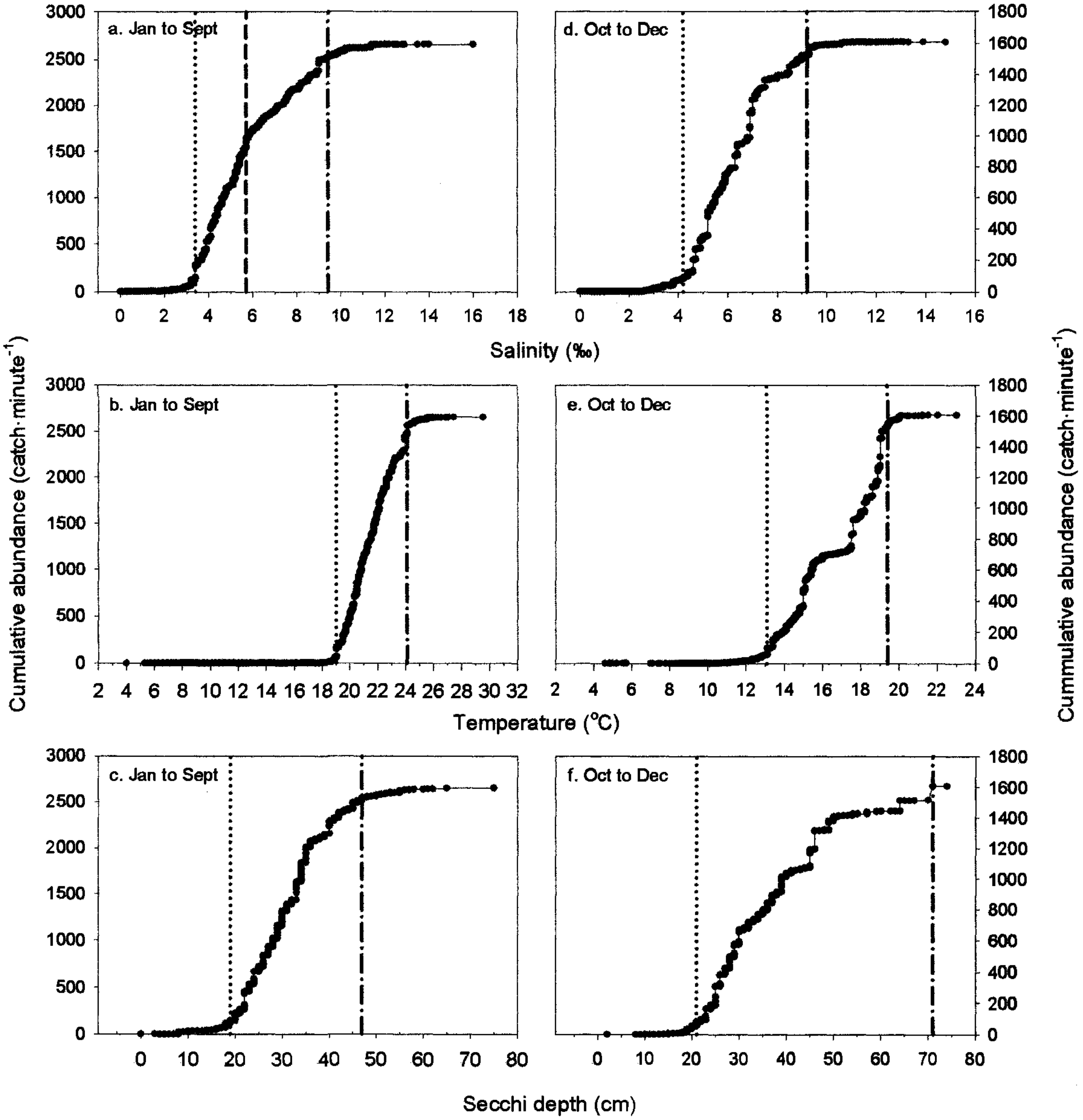

a. Jan to Sept
d. Oct to Dec
b. Jan to Sept
e. Oct to Dec
c. Jan to Sept
f. Oct to Dec
Salinity (‰)
Temperature (°C)
Secchi depth (cm)
Cumulative abundance (catch·minute-1)
Cummulative abundance (catch·minute-1)
0
500
1000
1500
2000
2500
3000
0
200
400
600
800
1000
1200
1400
1600
1800
0 2 4 6 8 10 12 14 16 18
0 2 4 6 8 10 12 14 16
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
2 4 6 8 10 12 14 16 18 20 22 24
0 10 20 30 40 50 60 70 80

Figure 1.5

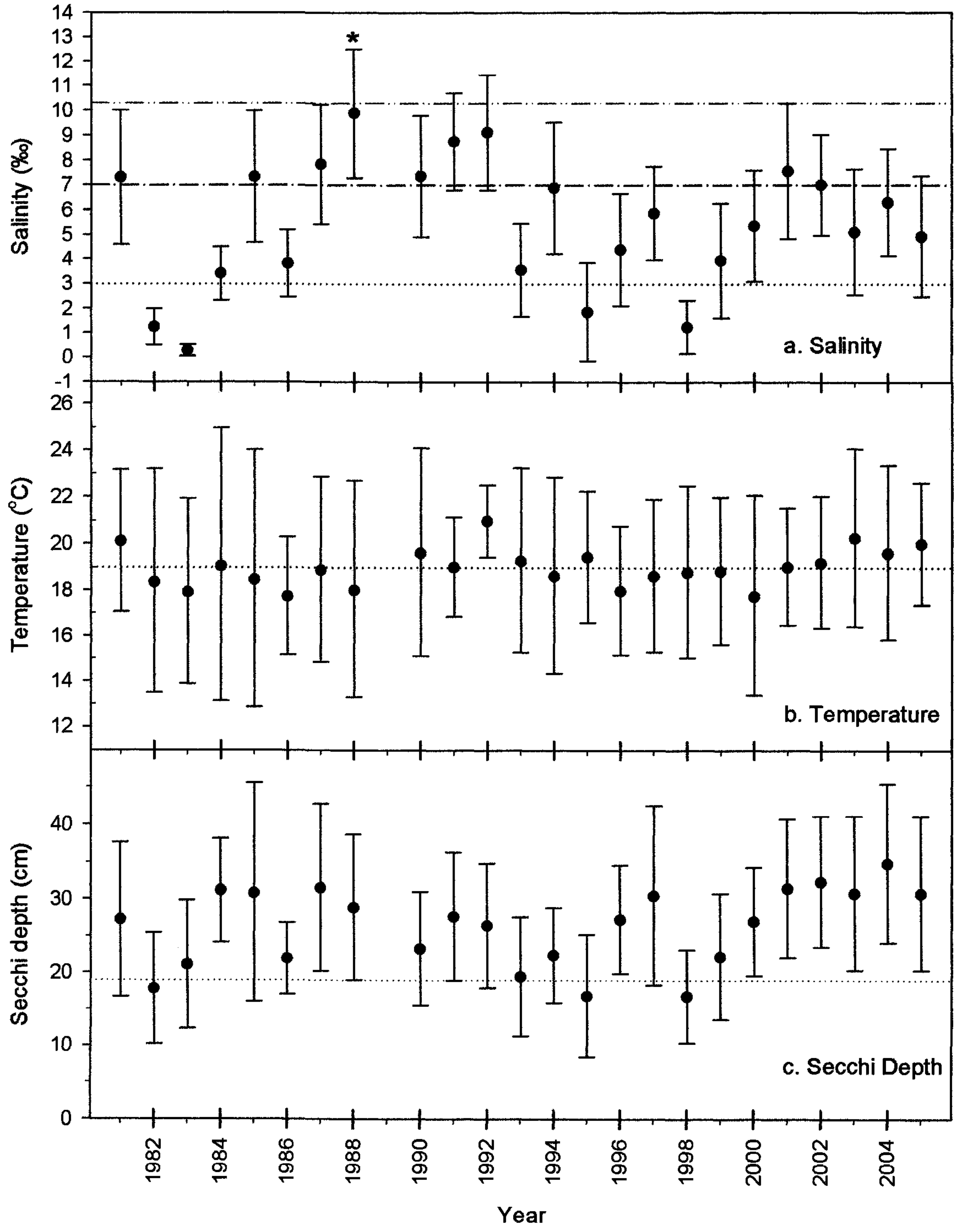

Salinity (‰)
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
*
a. Salinity
Temperature (°C)
26
24
22
20
18
16
14
12
b. Temperature
Secchi depth (cm)
40
30
20
10
0
c. Secchi Depth
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
Year

Figure 1.6

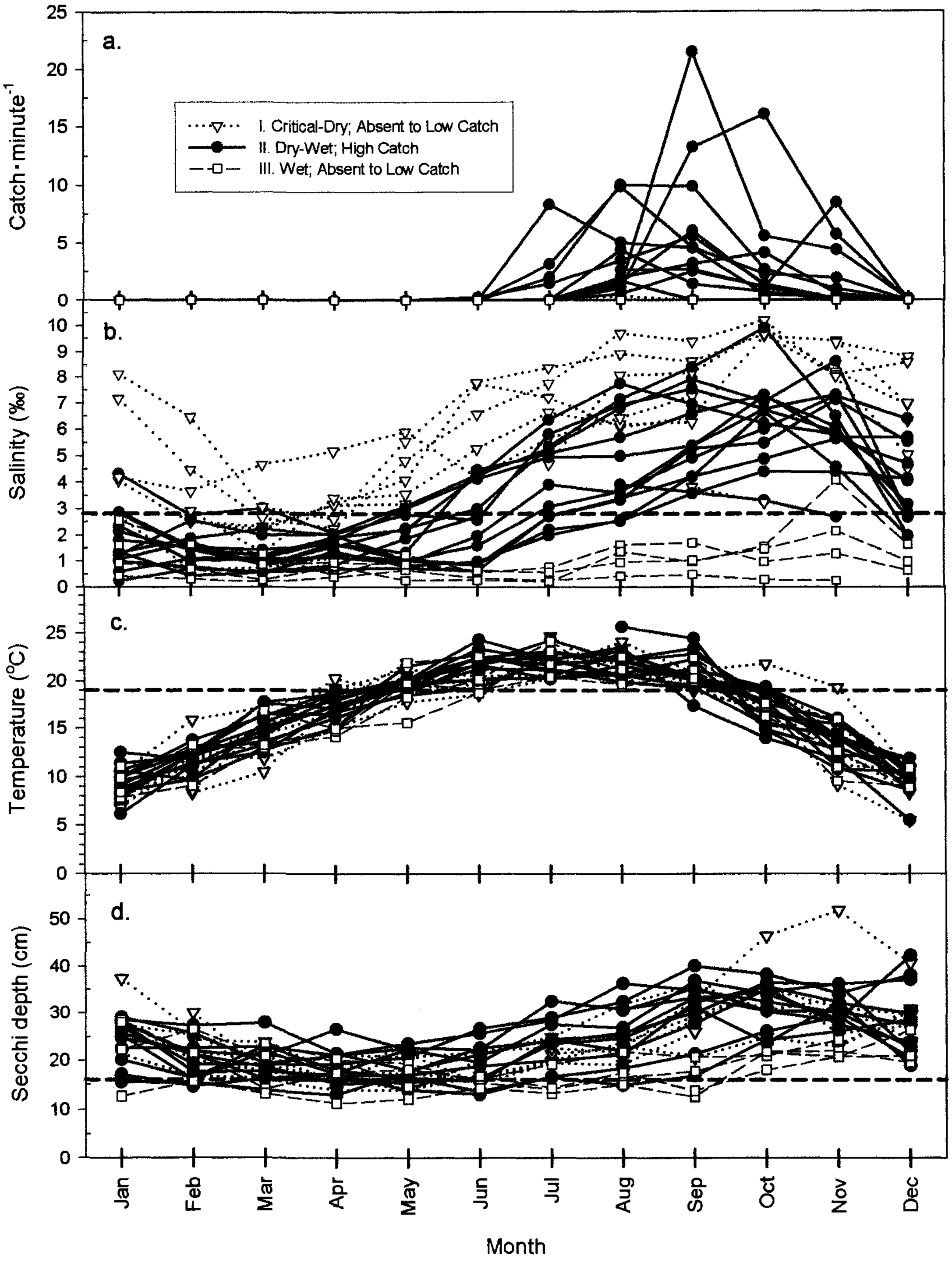

a.
b.
c.
d.
Catch·minute^{-1}
Salinity (‰)
Temperature (°C)
Secchi depth (cm)
I. Critical-Dry; Absent to Low Catch
II. Dry-Wet; High Catch
III. Wet; Absent to Low Catch
25
20
15
10
5
0
10
9
8
7
6
5
4
3
2
1
0
25
20
15
10
5
0
50
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 1.7

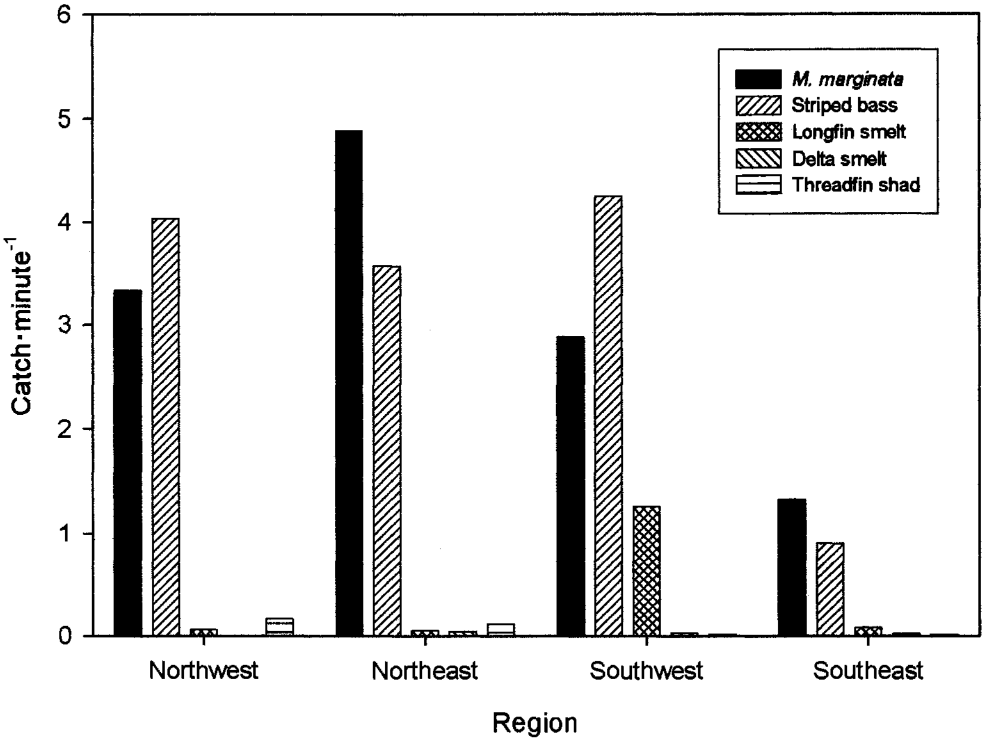


Figure 1.8

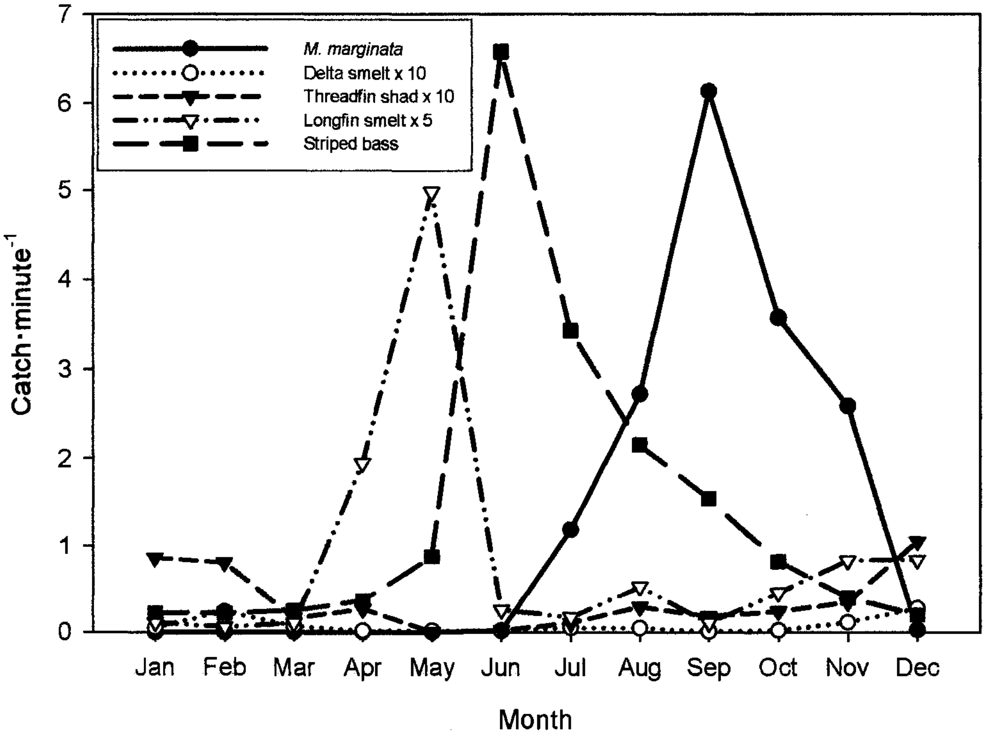


Figure 1.9

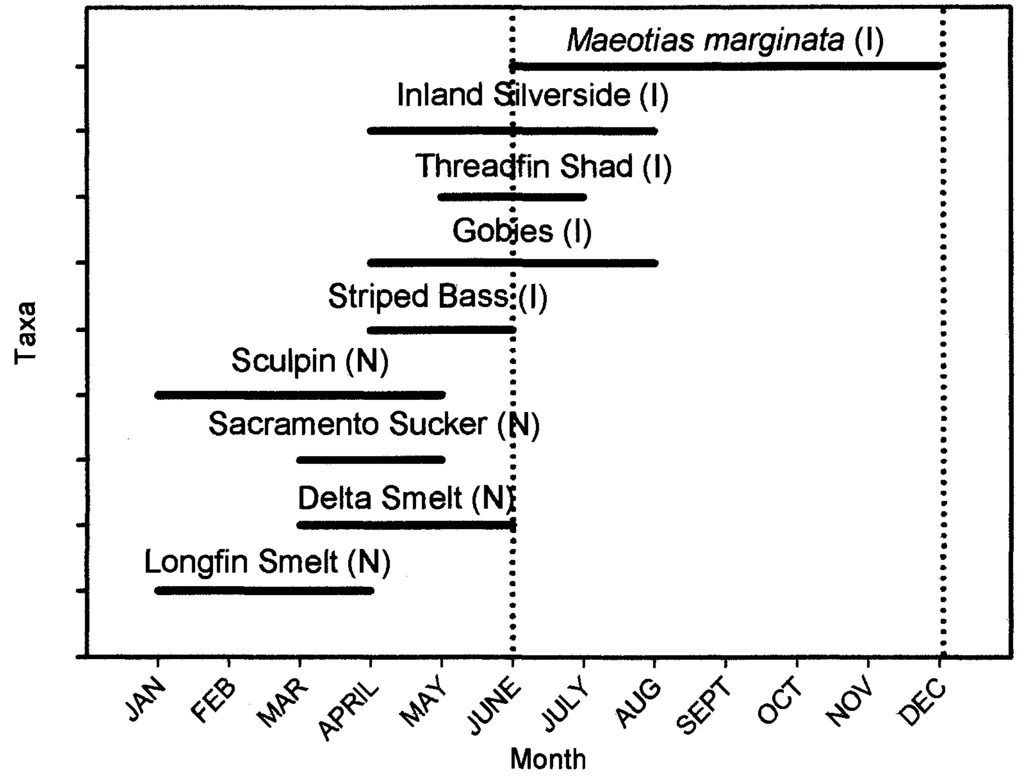

Maeotias marginata (I)
Inland Silverside (I)
Threadfin Shad (I)
Gobies (I)
Striped Bass (I)
Sculpin (N)
Sacramento Sucker (N)
Delta Smelt (N)
Longfin Smelt (N)
Taxa
JAN
FEB
MAR
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
Month

Figure 1.10

1.9 APPENDIX A

Missing Sample Description and Data Adjustments

Over the course of the 25 year study, some sampling stations were not sampled and on occasion, some months were not sampled. In total, 290 out of 300 (98%) months were sampled and 5270 out of 5660 samples were collected (> 93 %). Because some of the summary variables including month of bloom onset, duration, peak abundance, and site occurrence are sensitive to missing samples, data corrections were carried out using the following assumptions: First, if a bloom was detected in a month prior to or following the missing month, then medusae were recorded as being present in the missing month. For the summary of annual site occurrence, if fewer than 17 sites were sampled during the bloom period, as evidenced by medusae being present in the marsh at adjacent or nearby sites, then the total number of possible sites was adjusted before calculation of the % site occurrence. The adjustments made to the data may have the unintended effect of overestimating the bloom season in some sample years, but reduces the possibility of underestimating the bloom. The catch data is less sensitive to missing values given the large number of samples that represent the annual catch. In 1986 and 1990 the peak abundance may have been missed, due to incomplete sampling, which may have affected (i.e. decreased) the annual catch.

A-1 Sampling table for core otter trawl stations. Total station number = 17. Grey boxes indicate 16 to 17 sites sampled per month; white boxes indicate fewer than 16 sites sampled; and black boxes indicate no sample collected. Number inside the box refers to the number of samples collected, which may be greater than 17 due to some stations being sampled more than once.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1981	20	30	30	47	34	15	27	15	17	14	16	17
1982	14	18	15	6	16	16	16	16	21	22	16	16
1983	15	20	17	16	16	14	17	16	11	16	16	NS
1984	12	9	15	10	12	13	NS	15	15	15	18	NS
1985	NS	17	17	14	13	NS	18	17	18	3	16	14
1986	7	17	16	17	7	17	16	NS	17	17	15	16
1987	18	17	17	11	18	14	13	17	17	15	17	16
1988	17	17	18	17	15	2	17	16	18	9	17	15
1989	NS	15	17	16	17	17	16	17	16	NS	4	12
1990	17	16	17	18	17	17	17	17	17	NS	17	18
1991	17	17	16	16	16	16	17	17	17	16	17	16
1992	17	16	16	16	16	17	16	17	14	14	14	15
1993	15	16	15	17	17	17	17	17	17	14	17	16
1994	17	7	15	16	16	17	17	17	17	16	16	15
1995	17	15	17	17	17	17	10	17	17	13	17	17
1996	16	14	16	15	16	17	17	17	17	17	17	16
1997	17	17	16	17	17	17	17	17	17	17	17	17
1998	17	NS	17	17	6	17	17	17	17	17	17	17
1999	16	17	15	17	17	17	17	17	17	17	17	17
2000	17	17	17	17	17	17	17	17	17	17	17	17
2001	17	17	17	17	17	17	17	17	17	15	17	17
2002	17	17	17	17	17	17	17	17	17	15	17	16
2003	16	17	17	17	17	17	17	17	17	17	17	14
2004	17	17	17	17	17	17	16	17	17	17	17	16
2005	17	16	16	15	16	17	16	17	17	17	17	17

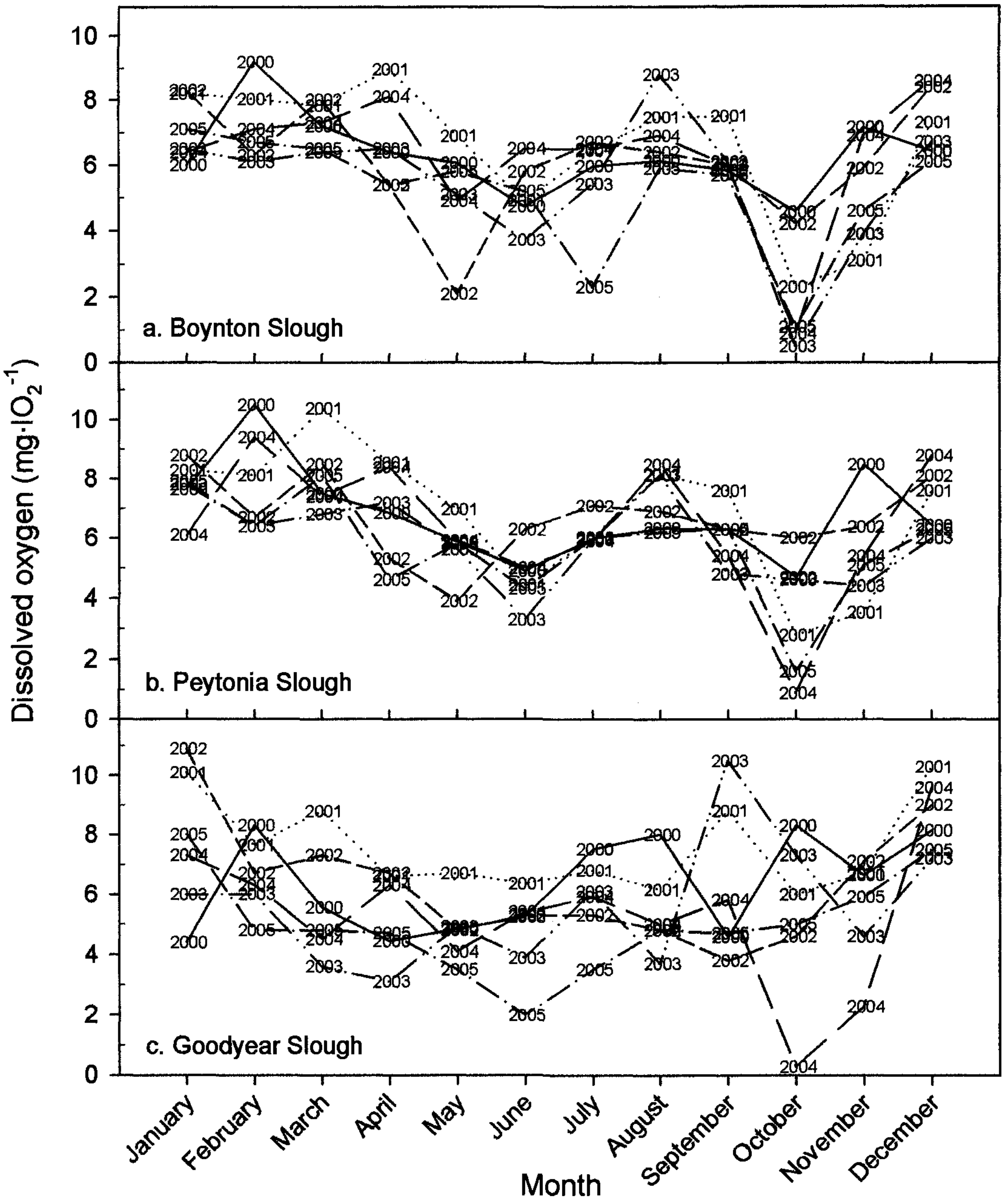
A-2 Sampling table for additional sampling stations in Suisun Marsh. Stations were sampled from May 1994 December 2005. Total station number = 4. Grey boxes indicate all 4 samples collected per month. White box indicates fewer than 4 sites sampled. Black box indicates no sample collected. Number inside the box refers to the number of samples collected.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1994					3	3	4	4	4	4	3	4
1995	4	4	4	4	4	4	4	4	4	4	4	4
1996	4	4	4	3	4	4	3	4	4	4	4	4
1997	3	3	4	4	4	4	4	4	4	3	4	4
1998	4		4	3		4	4	4	4	4	4	4
1999	4	4	4	4	4	4	4	4	2	4	4	4
2000	4	4	4	4	4	4	4	4	4	4	4	4
2001	4	4	4	4	4	4	4	4	4	4	4	4
2002	4	4	4	4	4		4	4	4	4	4	4
2003	4	4	4	4	4	4	4	4	4	4	4	4
2004	4	4	4	4	4	4	4	4	4	4	4	4
2005	4	3	4	4	4	4	4	4	4	4	4	4

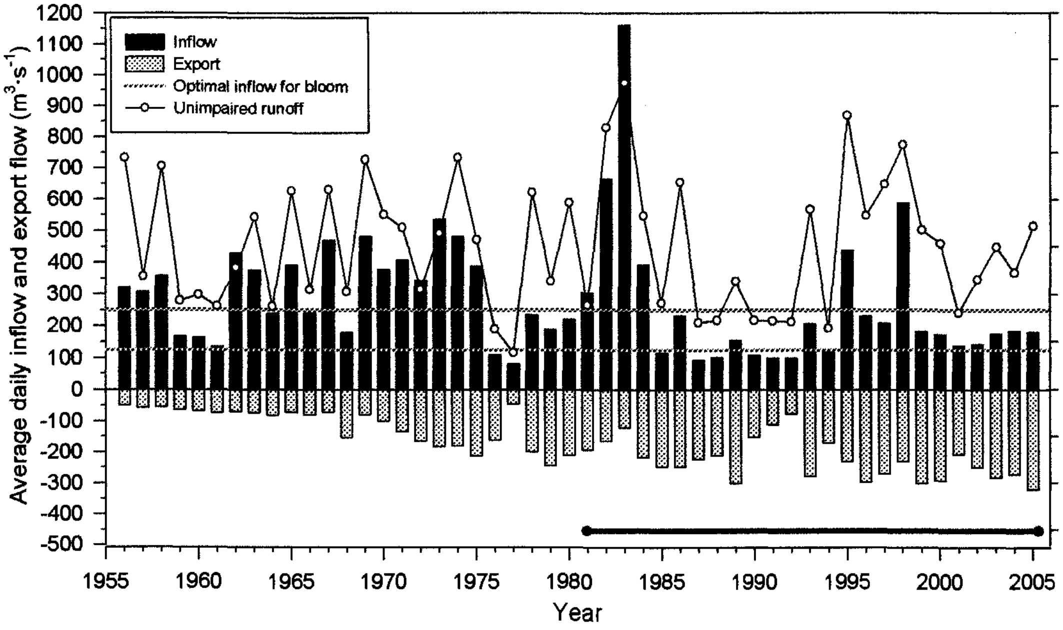
1.10 APPENDIX B

B1. Monthly patterns in minimum dissolved oxygen concentrations for (a) Boynton Slough, (b) Peytonia Slough and (c) Goodyear Slough for the years 2000-2006. Data are from three sources of monitoring including the UCD Otter Trawl Survey, CALFED Invertebrate Survey and supplemental dissolved oxygen monitoring surveys.

B2. Time series of inflow, export, and unimpaired runoff from 1956 to 2005. Export and inflow are mean values for July to November while unimpaired runoff is for the water year period of October 1 to September 30. The optimal inflow for bloom of medusae (125 to 250 m^3s^{-1}), indicated with grey reference lines, corresponds to an average July to November salinity of 3 to 10‰.


Dissolved oxygen (mg·lO$_2^{-1}$)
a. Boynton Slough
b. Peytonia Slough
c. Goodyear Slough
0
2
4
6
8
10
2000
2001
2002
2003
2004
2005
January
February
March
April
May
June
July
August
September
October
November
December
Month

B1


Inflow
Export
Optimal inflow for bloom
Unimpaired runoff
Average daily inflow and export flow ($m^3 \cdot s^{-1}$)
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
-100
-200
-300
-400
-500
Unimpaired runoff (km^3)
80
70
60
50
40
30
20
10
0
-10
-20
-30
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
Year

B2

CHAPTER 2

Biology and Habitat Use of a Brackish Tidal Marsh in the San Francisco Estuary by a Trio of Alien Hydromedusae

2.1 INTRODUCTION

Gelatinous zooplankton can severely alter marine communities as a result of high abundance, rapid response to favorable conditions, and efficient feeding (Mills 1995 and 2001; Purcell et al. 2007). Negative effects of alien gelatinous zooplankton invasions have been observed in the Black Sea (e.g. Studenikina et al. 1991; Purcell et al. 2001a; Shiganova and Bulgakova 2000; Shiganova et al. 2003), Caspian Sea (Ivanov et al. 2000), Mediterranean (Lotan et al. 1992; Mills 2001), and the Gulf of Mexico (Graham et al. 2003). The invasions appear to be especially a problem in waters that lack predators (Shiganova et al. 2003). Gelatinous zooplankton are increasing in abundance in marine and estuarine systems worldwide (Mills 1995 and 2001; Purcell et al. 2007), which is likely to result in further adverse impacts on the fish and invertebrate populations in waters in which they bloom.

There is a long list of explanatory factors and mechanisms and much debate over the causes for the recent success of gelatinous zooplankton (Arai 2001; Mills 1995 and 2001; Parsons and Lalli 2002; Purcell 2005; Purcell et al. 2007). Factors include both abiotic changes, such as temperature and salinity shifts, and biotic factors, such as reduction in top predator populations from overfishing and food web changes resulting from eutrophication and alien species introductions. The relative impact of any particular factor or combination of factors is likely to be both species and stage specific because polyps and medusae may respond to environmental changes independently (Ma and Purcell 2005a and 2005b).

One approach to identifying possible factors contributing to the recent surge in abundance and distribution of gelatinous zooplankton is to define abiotic conditions suitable for each species and then determine how biotic interactions are contributing to a particular species success. For alien estuarine gelatinous zooplankton, rigorous examination of the most suitable abiotic conditions for a species is rarely done, with a few notable exceptions such as the studies of *Mnemiopsis* introduced into the Black Sea (Purcell et al. 2001a; Purcell 2005). Environmental response is often gauged by studies conducted over a short duration, which may not necessarily reflect a species true response, given large seasonal changes and rapid shifts due to changing tides. This prevents or confuses the interpretation of conditions that are contributing to the first appearance (polyp release and / or successful recruitment of larvae), high abundance, and eventual disappearance (mortality of medusae) of gelatinous zooplankton.

Combining measurements of conditions when medusae are most abundant in the field with those obtained from laboratory work with medusae and polyps would provide a more complete picture of how a species responds to its environment. Recent studies have identified the biotic and abiotic conditions contributing to polyp growth and bud development for the hydrozoan *Moerisia lyonsi* (Purcell et al. 1999a; Ma and Purcell 2005a and 2005b) and the scyphozoan *Aurelia labiata* (Purcell 2007), which has significantly improved our understanding of how these species are likely to respond to varying environmental conditions. A solid understanding of abiotic factors limiting species abundance can lead to more accurate predictions as to how the species may respond to climate change and changes in estuarine conditions (Decker et al. 2007).

The purpose of this study is to examine the temporal and spatial distribution patterns of the medusa stage of a trio of alien hydromedusa in the San Francisco Estuary (SFE): *Blackfordia virginica, Maeotias marginata* and *Moerisia* sp. Rees and Gershwin (2000) report that this *Moerisia* sp. in the SFE most closely resembles *Moerisia lyonsi,* but a final species determination has not been made. *Moerisia* sp. will hereafter be referred to as *Moerisia.* All three species are believed to be native to the

Black and Caspian Seas and have been widely introduced into many different regions of the world (Rees and Gershwin 2000; Mills 2001; Vainola and Oulasvirta 2001; Genzano et al. 2006). All three species are well established in the San Francisco Estuary (Mills and Sommer 1995; Mills and Rees 2000; and Rees and Gershwin 2000), but their biology, distribution and abundance are not well known, making it difficult to assess their overall impact on the aquatic community. Furthermore, their uncertain biological response to environmental conditions hampers predictions of future population responses to changing environmental conditions and of where and when these species are likely to become problems. There is some indication that medusae of, *M. marginata,* have been increasing in abundance over the last two decades presumably in response to increasingly favorable environmental conditions (Chapter 1). It is unknown if *B. virginica* and *Moerisia* are following similar population trajectories in the system.

In this study, I document the temporal and spatial occurrence of the three species of hydromedusae in an important estuarine rearing area for fish and invertebrates in the brackish waters of the SFE. My study has been designed to answer the following questions: (1) What are the temporal and spatial patterns in occurrence and abundance of each hydromedusae species? (2) What environmental conditions affect the presence and abundance of hydromedusae? (3) What are suitable environmental conditions for each hydromedusae species? (4) What environmental conditions are currently limiting the hydromedusae blooms? Several alternative population trajectories for the hydromedusae are discussed in light of their estimated suitable environmental conditions and the predicted changes in climate and flow in the system.

2.1.1 Background

Basic Biology of *Maeotias Marginata, Blackfordia virginica, and Moerisia*

The mode and date of introduction for alien gelatinous zooplankton in the SFE are not well known. Shipping activities such as ballast water transfer and hull fouling are suspected to have played a role (Mills and Sommer 1995; Rees and Gershwin 2000). *Maeotias marginata* is believed to have been present as early as 1959 (Rees and Gershwin 2000). The earliest record of *B. virginica* in the SFE was in 1970 (Mills and Sommer 1995) and the earliest record for *Moerisia* was 1993 (Mills and Reese 2000). No native gelatinous zooplankton are known to have occurred in the low salinity region (< 10 ‰) of the SFE (Mills and Sommer 1995), thus these species are a novel predator guild that may be adversely affecting the fish and invertebrate community.

Maeotias marginata is the largest of the three hydrozoans introduced into the brackish region of the SFE, reaching a maximum bell diameter of 50 mm (Mills and Sommer 1995). Both *B. virginica* and *Moerisia* are considerably smaller with *B. virginica* reaching a maximum bell diameter of 10 mm (Mills and Sommer 1995; Genzano et al. 2006) and *Moerisia* sp. usually measuring between 4 to 4.5 mm bell diameter, although the largest individual captured in the SFE was 8.1 mm (Rees and Gershwin 2000)..

All three hydrozoans species have a life cycle with two main stages including the free swimming medusa stage and the sessile polyp stage, which has been described in part by Rees and Gershwin (2000) for *M. marginata*, Ma and Purcell (2005a) for *Moerisia lyonsi* and Mills and Rees (2000) for *B. virginica*. Sexual reproduction occurs during the medusa stage with fertilized eggs developing directly into polyps for *M. marginata* (Rees and Gershwin 2000). The medusa stage for all three species is seasonal and is typically restricted to the warm summer and fall months (Mills and Sommer 1995; Mills and Rees 2000; Rees and Gershwin 2000; Chapter 1).

All three hydromedusae are capable of reproducing sexually in the pelagic medusa stage and asexually as polyps through budding. Polyps release larval medusa when environmental conditions become favorable. The release of larvae by polyps, as environmental conditions become appropriate, produces a rapid population increase of medusae commonly referred to as a "bloom" (Brewer and Feingold 1991; Lucas 2001). Larval medusae can develop quickly and in *M. lyonsi*, larvae can reach sexual maturity in eight days under laboratory conditions (Ma and Purcell 2005a).

Both polyps and medusae of all three species feed primarily upon invertebrate prey. Mills and Sommer (1995) observed that gut contents from *M. marginata* medusae collected in the Petaluma River in the SFE included in order of most common, barnacle nauplii, copepods, crab zoea, copepod nauplii, Tanidacea and a variety of other prey only found in low abundance. In Suisun Marsh during summer 2004, gut contents of *M. marginata* medusae included copepods (60 % of diet) crab zoea (27 %), larval fish (5 %), amphipods (3 %), mysids (2 %) and a variety of other prey (< 2 %; Chapter 1). In fall 2005 when medusae were larger, *M. marginata* gut contents included copepods (74 % of diet), amphipods (13 %), cladoceran (9 %), mysids (3 %) and a variety of other prey (1 %; Chapter 1). *Moerisia lyonsi* medusae were successfully fed artemia (Rees and Gershwin 2000) and selectively fed upon copepods and their nauplii under laboratory conditions (Purcell et al. 1999a). The diet of *Moerisia* polyps are not known from the field, but Ma and Purcell (2005a and 2005b) fed cultured *M. lyonsi* polyps "natural" prey that primarily consisted of the copepod *Acartia tonsa*. Gut contents of field caught *B. virginica* medusae included in order of most common, copepods, copepod nauplii, and barnacle nauplii (Mills and Sommer 1995).

Population characteristics of the three species, in either the medusa or polyp form, are not well known, preventing a more accurate assessment of each species potential impacts on the invertebrate community. The limited sampling that has been done in the SFE indicates that *B. virginica* is generally found in very low abundance, with surface densities of 0.1 medusae·m^{-3} and a near bottom maximum density of 5 medusae·m^{-3} (Rees and Kitting 2002). *Blackfordia virginica* has been found at higher densities elsewhere, with abundances as high as 47 medusae·m^{-3} in estuaries along the coast of India and 67 medusae·m^{-3} in the Mira estuary in Portugal (Moore 1987). Few studies have reported the population abundances for *M. marginata*. Rees and Kitting (2002) observed maximum densities in the SFE were below 0.1 medusae·m^{-3}. The catch of *M. marginata* medusae in the Suisun Marsh study (Chapter 1) was based upon incidental take using an otter trawl, thus it was not possible to calculate a catch per unit volume estimate, but the catch was on average < 35 medusae·minute^{-1} trawled. *Moerisia lyonsi* was reported at a maximum density of 12 medusae·m^{-3} in the Choptank River, Maryland (Purcell et al. 1999a). In the SFE, Rees and Kitting (2002) reported the densities of *Moerisia* at ≥ 1 medusae·m^{-3}.

Environmental Conditions

Blackfordia virginica medusae are best described as a euryhaline species; they have been captured at salinities from 3 to 35 ‰ (Moore 1987; Mills and Sommer 1995; Genzano et al. 2006). In the Napa River of the SFE medusae of *B. virginica* had maximum abundances at salinities of 6.5 to 16 ‰, temperatures of 20 to 24 °C and water clarity of 27 to 50 cm secchi depth (Rees and Kitting 2002). In the Rio de la Plata estuary, Argentina, medusae were captured in waters with salinities of 23 to 30‰ and temperatures of 23 to 24 °C (Genzano et al. 2006).

Maeotias marginata medusae have been found in a variety of habitats, but may prefer areas that are relatively shallow, generally < 10 m depth (Vainola and Oulasvirta, 2001). Mills and Sommer (1995) summarized findings from several studies and reported that *M. marginata* medusae were found in salinities of 4 to 11 ‰ and that laboratory reared specimens suffered mortality at salinities greater than 13 ‰. These results are consistent with a long-term (25 year) study in Suisun Marsh, SFE which found suitable salinity conditions for medusae, based upon 5th and 95th percentiles of occurrence data, were 3 to 10 ‰, with the minimum and maximum observed salinities being 1 and 13 ‰, respectively (Chapter 1). In the same study, the range of salinities that resulted in the greatest abundance of medusae, possibly due to the highest rates of medusae production by polyps, was 3 to 7 ‰. Rees and Kitting (2002) reported catch of very small juvenile *M. marginata* medusae at salinities of 5 to 6 ‰ near Chipps Island in the SFE and based upon their size, concluded that salinities were suitable for release of medusae from the polyp. The minimum salinity reported for *M. marginata* in Chesapeake Bay by Calder and Burrell (1967; 1969) was 1.2 ‰.

Suitable temperatures (5th to 95th percentiles of occurrence data) for *M. marginata* in Suisun Marsh ranged from 19 to 24 °C (maximum = 27 °C) in the early bloom months (January to September) and a lower temperature range in the fall months (October to December) of 11.6 °C (minimum = 8.3 °C) to 19.7 °C (Chapter 1). A minimum bloom initiation temperature of approximately 19 °C was assumed for release of medusae from polyps, when salinities were also suitable (Chapter 1). The temperature range reported by Mills and Sommer (1995) of 11.3 to 27 °C were also consistent with those reported from Suisun Marsh (Chapter 1). Other studies observed that water temperatures at site of *M. marginata* capture were usually greater than 15 °C (Vainola and Oulasvirta, 2001; Suursaar et al. 1998; Rees and Gershwin 2000). Rees and Gershwin (2000) also noted that *M. marginata* reproduction occurred under lab conditions at temperatures between 18 and 21 °C.

Moerisia lyonsi medusae were found in salinities ranging from 2.3 to 9.3 ‰ and temperatures of 25 to 29 °C in the James and Pamunkey Rivers in Virginia, USA (Calder and Burrell 1967). In the Choptank River, Maryland USA, *M. lyonsi* medusae have been found in salinities from 0 to 5 ‰ with highest densities (12 medusae$\cdot$m^{-3}) observed at 4 ‰ (Purcell et al. 1999a). Thus based upon field results, it appears that *M. lyonsi* may have a similar salinity range to *M. marginata* (~2.3 to 10 ‰). However, in experimental mesocosms, *M. lyonsi* were found to thrive at salinities as highs as 12.5 ‰, where they reached densities as high as 13,600 medusae$\cdot$m^{-3} (Purcell et al. 1999a). Ma and Purcell (2005b) attributed the lack of medusae at salinities > 9 ‰ to the effects of the scyphomedusan predator *Chrysaora quinquecirrha*.

Laboratory studies by Ma and Purcell (2005a and 2005b), indicate that the polyps of *M. lyonsi* have their highest rates of asexual reproduction at salinities of 5 to 20 ‰, although they were observed reproducing asexually at salinities as high as 40‰, when temperatures were also high (20 to 29 °C). Polyps appeared to be more adversely affected by low temperatures with no asexual reproduction observed at 10 °C and a reduction at 15 °C versus the high temperature treatment of 20 to 29 °C. Medusa bud production was also reduced at temperatures of 20 °C compared to 29 °C and was greatest under conditions of high prey abundance and moderate to low salinity (5 and 15 ‰). The combination of low temperature and high salinity also resulted in low medusa bud development.

2.2 METHODS

2.2.1 Study Area

The study area was located primarily within Suisun Marsh, although adjacent sites were also sampled in Grizzly Bay and at Chain Island near the confluence of the Sacramento and San Joaquin Rivers (Figure 2.1; see Chapter 1 for a more detailed description of study area). Suisun Marsh is a large brackish tidal marsh (approximately 34,000 ha) at the downstream end of the Sacramento-San Joaquin Delta and at the upper end of the SFE.

Approximately one-third of the marsh is tidally influenced and the remainder consists primarily of diked wetlands managed to attract waterfowl. Water inflow to the marsh is provided by a number of sources including tidal inflow from Grizzly Bay through lower Suisun and Montezuma Slough, direct river inputs via the Sacramento and San Joaquin Rivers through upper Montezuma Slough and from a number of small tributaries to the marsh including Green Valley, Suisun, Ledgewood, Union, and Denverton creeks. Flow into the system is highly seasonal and is derived from winter rain pulses and increased flow in late winter through spring, as a result of snowmelt from the Sierra Nevada.

Temperature, salinity and dissolved oxygen (DO) vary considerably depending upon season, amount of freshwater inflow, and slough location. Sloughs in closer proximity to Grizzly Bay have higher salinities while sloughs in the southeastern and northwestern areas have lower salinities. Freshwater flow (inflow) strongly influences the pattern of salinity in the system. From 1980 to 2005, salinities ranged from 0 to 17 ‰, peaking in the summer and fall, particularly in drought years and declining during periods of high inflow in winter and spring. In an effort to reduce Suisun Marsh salinity during times of low inflow (reduced freshwater runoff due to low precipitation and/or increased water export and diversion), the Suisun Marsh Salinity Control Gates (SMSCG) were constructed in Montezuma Slough with operation beginning in fall 1988 (see http://www.iep.ca.gov/suisun/facts/physicalfacilities.html and Chapter 1 for more details).

Summer temperatures are usually highest in the small shallow sloughs and lowest near Grizzly Bay and the upper reach of Montezuma Slough, although differences between areas are generally small. Summer temperatures typically range from 17 to 29.5 °C with winter temperatures occasionally dropping below 5 °C. Dissolved oxygen is high (≥ 7 mg·lO_2^{-1}) near the confluence of the Sacramento and San Joaquin River and also near Grizzly Bay, with lower DO levels in the more isolated sloughs and upstream reaches of sloughs, especially in the spring and fall when episodic DO sags occur. In the fall, DO levels often approach 0 mg·lO_2^{-1}, especially in the northern area of Suisun Marsh.

The proximity of Suisun Marsh to the large upper bay system (Grizzly, Suisun, and Honker Bay), its close proximity to the confluence of the Sacramento and San Joaquin River, and its direct connection to numerous local tributaries have all strongly influenced the diversity and abundance of species (see Meng and Matern 2001 and Matern et al. 2002). Suisun Marsh is a major nursery area for numerous species of fishes, caridean shrimps, and mysids. In addition, numerous mesozooplankton species (copepods and cladocerans) are also found within Suisun Marsh reaching very high densities at times.

2.2.2 Field Methods

Hydromedusae were sampled monthly at 36 stations across Suisun Marsh and in adjacent waters beginning February 2004 and ending January 2006 (Yr1 = Feb 2004 to January 2005; Yr2 = Feb 2005 to January 2006). A 5-minute stepped horizontal plankton tow was conducted at each station using a 30 cm diameter, 500µm mesh, conical plankton net with sampling bucket. Net diameter to length ratio was 1 to 5 with a total length of 150 cm. The net was fastened to an inverted 1-meter height T-frame constructed from 2 cm diameter stainless steel tubing. Three 12-pound finned downrigger weights were attached to the bottom bar to reduce the tow angle in the line. The net and sampling apparatus were deployed using a manual winch and davit positioned off the starboard beam of the 22 foot research vessel. This forward position of the plankton net was required to prevent clogging of the net by the loose silt and bottom materials that are disturbed by the passing boat in the shallow water sites.

Nine depth levels were sampled during each plankton tow with a net starting depth of 0.5 meters above the bottom (net was fastened 0.5 m above the downrigger weights). Depth intervals for each site were calculated based upon the total depth at that sampling location (depth interval = total depth / 9). Each depth interval was sampled for 30 seconds, with the first 30 seconds of the tow used to deploy the net to the deepest sampling depth. The final tow depth was 0.5 meters below the water surface. Speed of the tow was maintained by keeping the tow angle constant, which resulted in an average speed of 0.8 +/-0.07 $m \cdot s^{-1}$. A flow meter (General Oceanics Model #2030R) positioned inside the plankton net was used to calculate the speed of the tow and the volume of water sampled at each site.

Samples were collected within a 4 to 5 day period each month during a slack moderate low tide to ensure consistency across time and space. Sampling on a slack moderate low tide minimized the likelihood of advection by strong tides. Environmental data including temperature (°C), salinity (‰), turbidity (NTU), and DO (in mg·lO_2^{-1}) were measured at each station at 1 meter depth using a Hydrolab 4a Datasonde multi-meter. Periodic measurements along horizontal transects at 0.5 meter intervals were conducted to examine for water column stratification of the measured environmental parameters. Collected samples were preserved in 4% Lugols's solution and were later transferred to alcohol or 5% formalin solution depending upon the biomass of individuals in the sample and the time to identification. Medusae were identified to species in the laboratory using a stereo microscope with 70x magnification. Samples were processed in their entirety if less than 400 medusae (all species) were present. If greater than 400 medusae were present, the samples were sub-sampled using a randomized selection of grids within a 24 grid subdivided tray (6 x 9 inches). All individuals were removed from each selected grid until a minimum of 400 individuals were obtained. The total abundance was then extrapolated from the proportion of grids processed and the abundance per sample was then converted to catch·m^{-3} using the corresponding volume estimate.

2.2.3 Analyses

The two-year data set was analyzed by multiple regression analyses, graphical comparisons, correlations and multiple comparison procedures. Specific regression analyses used included Poisson and negative binomial regression for count data and multiple logistic regressions for presence absence data. Logistic regression, with a binary response of the dependent variable (hydromedusae presence or absence) was the primary tool for analyses because the abundance data were highly variable across time and space. Important variables known to strongly affect medusae abundance including prey availability and abundance of benthic polyps (Purcell et al. 1999a; Ma and Purcell 2005a; Decker et al. 2007), were unavailable at the time of analyses. Thus, I focused my efforts on determining what environmental parameters were contributing most to the occurrence of species within the sampled sites (logistic regression) and used Poisson and negative binomial regression as comparative tools to determine whether similar factors (independent variables) were also driving abundance patterns. A more detailed regression model for count data will be developed when additional independent variables are available, including a measure of prey abundance for medusae and benthic polyps and density of polyps.

Question 1: What are the temporal and spatial patterns in occurrence and abundance of each hydromedusae species?

In order to determine the temporal and spatial patterns in abundance of each species of hydromedusae, I first examined the temporal catch (monthly and annual patterns) of each species across all sites for overall marsh trends. Next, I grouped the 36 sampling sites into four areas based upon basic geographic layout of the study system (Figure 2.1). These areas reflected dominant salinity gradients in the study area from July to November (Figure 2.2), the time period of greatest medusae abundance, as well as strong chlorophyll a and mesozooplankton density gradients (unpublished data). Area 1 (A1) included stations in the southwest near to and located in Grizzly Bay, the main downstream (marine) entry point into Suisun Marsh. Sites situated in the central region of Suisun Marsh were included in Area 2 (A2). Area 3 (A3) included sites in the northwest portion of the marsh that are influenced by local freshwater inputs through several creeks including Ledgewood and Union Creeks and also a tertiary sewage treatment release (Fairfield Solano Sewer District) in Boynton Slough. Sites located near the confluence of the Sacramento and San Joaquin Rivers, the main freshwater entry point into Suisun Marsh, were included in Area 4 (A4). I then plotted the monthly average catch (catch·m^{-3}) of each species by area, so that both spatial and temporal trends in abundance could be visually inspected.

Question 2: What environmental conditions affect the presence and abundance of hydromedusae?

To determine the functional relationship between the environmental conditions and each species presence and abundance, I developed regression models (Poisson, negative binomial and logistic) for each species, using the full two year data set, with the following independent variables included: Area, Site, Temperature, Salinity, Turbidity, DO, and Depth. The variables Area and Site were included to determine if spatial effects were influencing the overall model. Occurrence (presence/absence) data were analyzed using logistic regression and abundance data were analyzed using Poisson and negative binomial regression models.

Using logistic regression, I also tested the relationship between season-specific changes in environmental conditions and medusae occurrence. Models were developed for two seasons including season 1 (S1) - February to September and season 2 (S2) - September to January, with Yr1 and Yr2 combined in the analyses. The separation of S1 and S2 was based upon the observation that peak abundance usually occurred in September in each of the study years and for all three species, suggesting that environmental conditions prior to, and including the peak abundance in September (S1) were likely to be favorable for medusae production and occurrence. The changing environmental conditions including and after the peak abundance in September (S2) were likely of decreasing quality for medusae, resulting in either direct (increased mortality of medusae and or larvae) or indirect (cessation of release of larval medusa from benthic polyps) effects on occurrence.

Model Description, Development and Analyses Steps

Abundance Models: Poisson and Negative Binomial Regression

The life history traits and the resulting seasonality of the medusae in this study resulted in abundance data distributions that did not meet the basic assumptions of general linear models including normal distribution of errors and constant variance, as is commonly the case for ecological data (McCune and Grace 2002; Guisan et al. 2002). Generalized linear models (GLMs) are mathematical extensions of linear models, but are more flexible allowing for non-linearity and non-constant variance structures in the data (Guisan et al. 2002). Generalized linear models are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables, with the relationship represented by a logarithmic link function (Guisan et al. 2002). Generalized linear models have the advantage of having a numbr of probability distributions that can be selected from, so a close match to the data of interest can usually be found.

Count data, as used in this study, are usually best represented by either a Poisson or negative binomial distribution (Jones et al. 2002; Hilbe 2007). The Poisson distribution assumes that the variance is equal to the mean. The negative binomial distribution is more appropriate in situations where the variance is considerably greater than the response mean resulting in overdispersion, as is commonly the case when count data includes large numbers of samples with zero catch. The hydromedusae data in this study were particularly well suited to Poisson and negative binomial regression given the count nature of the data (abundance per unit volume sampled) and the large number of zero catch records resulting from seasonal senescence and patchy occurrence distributions.

To determine which data distribution (Poisson or negative binomial) best fit the hydromedusae abundance data, two approaches were used including a comparison of Akaike's information criterion (AIC; Akaike 1987) for each of the fitted models and by performing a likelihood ratio (LR) test for both competing models using the log likelihood from the intercept only models (i.e. -2[log likelihood Poisson – log likelihood negative binomial]; Cameron and Trivedi 1998). A low *p*-value (<0.05) would imply that the negative binomial distribution was a better fit to the abundance data while a large *p*-value (>0.05) would suggest that the Poisson distribution was more appropriate.

The Poisson and negative binomial distributions were analyzed using the PROC GENMOD procedures in SAS (SAS 9.1.3). A manual iterative parameter selection process was used to determine the best fit Poisson or negative binomial model to the abundance data. In both models, the first step assessed the univariate effect of each independent variable for each of the response variables (3 hydromedusa species). The independent variable that resulted in the lowest AIC was then selected and entered into the model. Independent variables were added to the regression in the stepwise fashion until none remained, or the selection criteria were no longer satisfied and the model with the lowest AIC was selected as the best fit model. The Wald's X^2 significance level for entering an independent variable into the regression was $p<0.30$ and for retaining the variable, $p<0.10$ (Mickey and Greenland 1989; Hosmer and Lemeshow 1989). To determine the relative contribution of each independent variable to the best fit model, the standardized estimate (Stand. Est. = [independent variable coefficient * standard deviation of independent variable] / standard deviation of the dependent variable) was calculated (Nash and Bradford 2001; Bradford et al. 2003). The larger the standardized estimate the stronger the association between the independent and dependent variable in a given model.

Species Occurrence Models: Logistic Regression

The multiple logistic regression models were also analyzed using PROC GENMOD procedures in SAS (SAS 9.1.3) with the exception that a binomial distribution was specified and a logit link function was used. The selection of independent variables was performed in a stepwise fashion similar to the Poisson and negative binomial regression selection process with the independent variable with the lowest AIC selected and entered at each model step. The dependent variables in the logistic regression model were hydromedusa presence (1) or absence (0) and independent (predictor) variables were the environmental variables and the spatial variables Area and Site. The best fit logistic regression model for the included independent variables was determined using AIC. The overall model significance (Ho: all model coefficients are equal) was tested using the likelihood ratio test (LR) for the difference between the -2 log likelihood before (intercept only) and after including the independent variables. To determine the relative contribution of each independent variable to the best fit model, the standardized estimate was calculated, as described in the abundance regression models, with the largest standardized estimate representing the independent variable with the largest effect in a given model. The odds ratios were also presented for each independent variable.

Diagnostic Tests and Collinearity Checks: Logistic, Poisson and Negative Binomial Models

Several diagnostic checks were made for the regression models prior to analysis. First, plots were made of the estimated probability versus the deviance (difference in deviance) for each model to identify influential outliers and to check on their validity. Predictor variable collinearity, which can make model coefficients unstable and difficult to interpret (Allison 1999; Christensen 1997), was then evaluated in three ways. First, the pairwise (Pearson) correlation coefficients (r) of the independent variables were examined and variables with r-values > 0.8 were considered for removal from the models (Berry and Felman 1985). Second, the variance inflation factor (VIF) was used to assess the level of multicollinearity among the independent variables (Nash and Bradford 2001; Bradford et al. 2003). A VIF value of 1 indicates a non-linear relationship (r^2=0) between the independent variables. VIF values greater than 1 indicate increasingly linear relationships, with serious collinearity effects observed at VIF levels of 10 (Neter et al. 1996; Griffith and Amerhein 1997), the selected VIF criteria for this study. The final step in screening for collinearity effects was examining for changes in the value and sign of independent variable(s) already present in the model, when an additional independent variable was added.

Question 3: What are suitable environmental conditions for each hydromedusae species?

To determine the suitable environmental conditions for each hydromedusae species and differences among species, I first calculated the 5th and 95th percentiles for each environmental variable in each season (S1 and S2) for samples in which medusae were present. This range was selected because of high tidal dispersion in the area and strong salinity gradients and diel temperature variation that could, at times, result in individuals being captured in locations that may be chronically suboptimal. The occurrence data were then visually compared using boxplots with an additional boxplot of the full range of environmental conditions present in each season (all-sample). The deviation of the species-present environmental conditions from the all-sample environmental conditions was used to assess the general availability of suitable conditions for the occurrence of medusae in each season. These results were expected to be complimentary to the modeled logistic regression results by enabling a more visual interpretation of each species estimated range of suitable environmental conditions.

I tested differences among species means using the Tukey-Kramer Honest Significant Difference (HSD) multiple comparison procedure for unequal sample sizes using the JMPin statistical software application (JMPin 4.04). The similarities or differences in environmental conditions considered suitable for each species were then used to describe the current gelatinous zooplankton community structure in the brackish region of the SFE and to predict the community response under varying environmental conditions.

Differences between the suitable S1 and S2 temperatures, salinities, turbidities, and DO were also examined for each species to provide insight into the seasonal conditions associated with bloom initiation and bloom termination. The production and release of medusae by polyps is the primary trigger for the start of a medusae bloom and it commonly occurs during the spring and summer months (i.e. S1) as temperatures increase (Brewer and Feingold 1991; Lucas 2001; Purcell 2005). The decline of medusae during the fall months (i.e. S2) is likely due to the cessation of medusa production by polyps and increased mortality of medusae as temperatures cool in the fall and early winter (Purcell 2005). Thus, by investigating the season specific suitable environmental conditions for the trio of hydromedusae in this study, further insight can be obtained on the possibility of differential responses by the polyp and medusa life history stages (e.g. Chapter 1).

In order for this relationship to reflect a polyp response, polyps of each species need to be present throughout the study area. Preliminary results from a benthic survey in Suisun Marsh conducted between 2003 and 2005, revealed a large number of polyps and hydroid colonies are distributed throughout Suisun Marsh (unpublished data). A majority of the polyps were the hydromedusa, *Moerisia* sp. and the non-medusa forming hydroid *Cordylophora caspia*, although other unidentified polyps were also collected. The lack of detailed descriptions of mature *M. marginata* polyps and the small size of both *M. marginata* and *B. virginica* (Rees and Gershwin 2000; Mills and Reese 2000) creates uncertainty with respect to their identification and detection in the field and increases the need for further research to verify their presence and determine their abundance. None-the-less, the presence of very small *M. marginata* medusae (< 5mm bell diameter) in even the most isolated sloughs with presumably the least amount of tidal advection suggests a local presence of polyps (unpublished data). *Blackfordia virginica* medusae, on the other hand, are captured in estuarine waters with much higher salinities than *M. marginata* and *Moerisia*, thus their polyps may not be as widely distributed in the system. Thus, there is less certainty that estimated bloom initiation conditions for *B. virginica* are accurately reflecting conditions necessary for the release of medusae by their polyps.

I also plotted and visually compared average abundance patterns in relation to binned temperature (interval = 1 °C) and salinity (interval = 0.5 ‰) for all months combined to further identify a more specific range of environmental conditions associated with high abundance of medusae.

Question 4: What environmental conditions are currently limiting the hydromedusae blooms?

To determine environmental conditions that may limit medusae blooms in the study area, I used environmental variables found to have the strongest association with occurrence of each species in the logistic regression full model and seasonal model to develop limiting condition plots identifying when (months) and where (area) conditions were suitable for a given species. The range of suitable environmental conditions was again identified as the seasonal 5th to 95th percentiles for a given predictor when medusae of a given species were present. Each species' suitable seasonal range for the influential environmental variables was then compared to the observed monthly average value in a given area. The lack of overlap of environmental predictors found to be significantly related to medusae occurrence was then used as an indication of limiting conditions. The occurrence of each species was also indicated in the suitable condition plots with four levels of percent site occurrence (0-25, 25-50, 50-75 and 75-100%) within the indicated area. This was done to account for the variability of environmental conditions within a given area. The results from the suitable condition plots were then used to discuss the observed limiting factors for each species in the context of predicted climate change and possible flow alteration in the study area.

2.3 RESULTS

Question 1: What are the temporal and spatial patterns in occurrence and abundance of each hydromedusae species?

A total of 35,838 medusae were captured in 864 samples during the two year study (200. There was a large difference in catch between years, with over 86% of all medusae captured in the first year of the study (31,134 individuals). *Moerisia* dominated the catch in both years comprising 88 and 71% of the total medusae catch in Yr1 and Yr2 (Yr1 27,259 individuals; Yr2 3,352 individuals). *Maeotias marginata* was the next most abundant species comprising 11 (3,367individuals) and 27% (1,251 individuals) of the catch in years 1 and 2. *Blackfordia virginica* was the least abundant species comprising only 2% of the catch in both years 1 and 2 (Yr1 508 individuals; Yr2 101 individuals).

In addition to large differences in catch in Yr1 and Yr2, the timing of bloom initiation and termination also differed considerably between years, with a bloom defined as the large seasonal increase in abundance of medusae. Most notably, there was a Yr2 lag (+1 month) in the month of first catch for all species and in the case of *Moerisia* and *B. virginica*, a one month delay in bloom termination (Figure 2.3). *Maeotias marginata* had the longest bloom duration (6 months), June to November in Yr1 and July to November in Yr2. *Moerisia* had the next longest bloom duration (4 months), July to October in Yr1 and Aug to November in Yr2. *Blackfordia virginica* had the most restricted bloom duration (3 months), August to October in Yr1 and September to November in Yr2.

Occurrence by area and month further revealed spatial and temporal differences among species (see Figure 2.11). *Blackfordia virginica* exhibited the most limited spatial distribution and was captured almost exclusively in Areas 1 and 2 (A1, A2). *Maeotias marginata* and *Moerisia* had a broader spatial distribution, being found in all areas in both years, although their occurrence varied somewhat by month, area, and year. In general, there was a progressive (monthly) upstream spatial shift (A1 to A4) in occurrence for all species, with the first occurrence in each year being in A1 or A2 and most complete occurrence (highest % occurrence) usually occurring in downstream locations first. This pattern was most pronounced for areas 1 to 3, with some notable exceptions in occurrence in A4 for *M. marginata* and particularly *Moerisia.*

The abundance patterns of medusae were highly variable among species (Figure 2.3). *Moerisia* had the highest average monthly abundance for the 36 sites (25 medusae·m^{-3}), followed by *M. marginata* (2.2 m^{3}) and *B. virginica* (0.7 medusae·m^{-3}). The highest monthly abundance for all three species was in September of Yr1. *Moerisia* also had the highest maximum catch (102.3 medusae·m^{-3}), followed by *M. marginata* (12.3 medusae·m^{-3}) and *B. virginica* (5.7 medusae·m^{-3}).

Each species' abundance by area varied considerably by year and month (Figure 2.4a-c). The abundance of *B. virginica* was highest in A1 in Yr1 and Yr2 (Figure 2.4a). *Maeotias marginata* abundance in Yr1 was highest in A2 in July and August and more similar in all areas in September and October (Figure 2.4b). Abundance of *M. marginata* in Yr2 was lower and more variable, with medusae being most abundant in A1 and A2 in August and September and more similar in A1 to A3 in October and November. There was a considerable delay in the observed peak abundance of *M. marginata* in Yr1 in A4 and very low Yr2 catch in A4. In addition, abundance of *M. marginata* declined most rapidly in A1 in the fall months of S2 (October and November). In Yr1, the abundance of *Moerisia* was lowest in A1 and A4 and highest in A2 and A3 (Figure 2.4c). The abundance of *Moerisia* in Yr2 was significantly reduced from Yr1 with the highest abundance in August in A1 and September in A2. Very low *Moerisia* abundance was observed in A3 and A4 in Yr2.

2.3.1 Environmental conditions by year

Environmental conditions fluctuated seasonally (Figure 2.5) with salinity levels at their minimum (0.1 ‰) during high inflow in March and increasing to their maximum in summer to fall (11.4 ‰). A minimum temperature of 7.2 °C was observed during winter and a maximum of 25.9 °C was observed in the summer. Turbidities ranged from 12.3 to 287.2 NTU, with the highest turbidities observed from January to June and the lowest turbidities during the dry season base-line flow. DO levels fluctuated between 0.3 to 13 mg·lO_2^{-1}. The lowest DO levels were observed in the fall, particularly in upstream areas. Elevated DO levels, often exceeding super saturation, were observed in sites in or near Grizzly Bay. Depths varied between 0.78 m to 16.8 m with an average of 4 m (*s.d.* = 2.3 m).

Environmental conditions differed between the two years (Figure 2.5). Inflow in Yr1 was high in February to April and declined to low dry-season baseline inflow by May (Figure 2.5a). Year 1 inflow remained low until December resulting in dry-season baseline flows from May to December. Year 2 inflow was somewhat lower in February and March than in Yr1, but remained well above the baseline dry-season level until July. Dry-season baseline flow occurred between July and November in Yr2.

Salinity was higher in Yr1 from May to October, and then declined below Yr2 levels in November and December (Figure 2.5b). The large seasonal increase in salinity, which coincides with the seasonal decline in inflow, occurred in May in Yr1, but it was delayed 2 to 3 months in Yr2 with the seasonal increases in salinity not occurring until July and August. Temperature patterns were consistent in both years, although temperatures were somewhat higher in Yr2 of the study between February to April, June to August and in October and November (Figure 2.5c). There was a declining monthly trend in turbidity in both years, with the lowest turbidities occurring from September to December (Figure 2.5d). Differences between years were also evident with alternating peaks in turbidity between February to May and consistently higher turbidity in Yr2 from June to August. Turbidity was similar in each year from September to January. Turbidity patterns fluctuated inversely with salinity and directly with inflow. Dissolved oxygen patterns also differed considerably between years with the largest differences between February and July with Yr1 levels considerably higher than those in year 2 (Figure 2.5e). There was a weak inverse relationship between DO and temperature.

2.3.2 Environmental conditions by area

Differences in environmental conditions were also evident by area, with the largest differences observed for salinity, turbidity, and DO and only small differences observed for temperature (Figure 2.6). Salinity was consistently highest in A1 and increased earlier in the year than A2 to A4. Area 2 had intermediate salinities, with similar temporal patterns to those observed in A3 and A4. Salinity was more similar and lower in A3 and A4 for most of the year, with the exception of the spring and winter months when salinity in A4 was lower than A3 and averaged between 0 to 1 ppt. Turbidity patterns were not as consistent within and between areas, with large differences observed in most months. Area 4 had the lowest and most consistent turbidities in nearly all months sampled. DO levels were lowest in A3 with large seasonal declines evident in spring (May and June) and fall (October and November). DO levels were highest and most stable in A4. Intermediate DO levels were observed in A1 and A2.

Question 2: What environmental conditions affect the presence and abundance of hydromedusae?

2.3.3 Model Diagnostic Tests and Collinearity Checks

All outliers identified in the deviance-probability plots were examined to ensure their validity and no data errors were found and all data points were retained in the final models. There was no evidence for collinearity between the independent variables (Pearson correlation $r < 0.8$; range 0 to -0.48) and there was no indication of multi-collinearity of the independent variables (all VIF <10; range 1 to 4.14).

Regression Models

Blackfordia virginica

Abundance All Time Period (ATP) - The negative binomial (NB) was determined to be the most appropriate data distribution for abundance of *B. virginica* based upon the significant likelihood ratio test (LR; $X^2 = 20.8$, $df = 1$, $p<0.05$) and the lower AIC values (Table 2.1). All models including intercept-only were significant at the $p<0.01$ level (Table 2.1). There were two NB regression models with the lowest AIC value that also had independent variables with p-values that satisfied the model selection criteria

(*Abundance = Sal+Temp+DO* and *Sal+Temp+DO+Depth*). In order of entry and size of coefficient, salinity, temperature, and dissolved oxygen were significantly related to the abundance of *B. virginica* medusae (Wald's X^2 test) with depth also contributing to the overall model, although it was not significant ($0.05<p<0.10$). The criteria for goodness of fit (GFT; Pearsons Test Statistic / *df*) ranged from 0.12 to 0.13 for both best-fit NB models indicating the model results were affected by underdispersion. All four independent variables retained in the final model had positive coefficients indicating an increase in the variable resulted in an increase in medusae abundance. Based upon the standardized estimates, salinity and temperature were the most important predictor variables explaining *B. virginica* abundance, followed by DO and depth (Table 2.2). No spatial variables (i.e. site and area) were related to medusae abundance.

Occurrence ATP (Logistic Regression) - The logistic regression model for the full data set (i.e. all time periods or ATP) that resulted in the lowest AIC value when predicting the presence of *B. virginica* was *Presence = Sal+Temp+Turb+DO*, which was significant based upon the LR test ($X^2 = 205.4$, $df = 4$, $p<0.01$, Table 2.3a). Salinity, temperature turbidity, and DO contributed significantly in explaining the presence of *B. virginica* in the overall model (Wald's X^2 test; Table 2.3a). The Hosmer-Lemeshow goodness of fit test (GFT) did not indicate a lack of model fit ($X^2 = 2$, $df = 8$, $p>0.05$) and there was high concordance (94%). An increase in salinity, temperature, and DO resulted in a higher probability for the presence of *M. marginata*, while increasing turbidity resulted in a lower probability (Table 2.3a). Based upon the standardized estimates, salinity was the most important predictor variable explaining the occurrence of *B. virginica* followed by temperature and then turbidity and DO (Table 2.2).

Occurrence Seasonal Models (Logistic Regression)

Season 1 - The S1 logistic regression model that resulted in the lowest AIC value when predicting the presence of *B. virginica* was *Presence = Sal+Turb+Temp+ DO*, which was significant based upon the LR test ($X^2 = 140.4$, $df = 4$, $p<0.01$, Table 2.3b).

Salinity, turbidity, and temperature contributed significantly in explaining the presence of *B. virginica* in the overall model (Wald's X^2 test; Table 2.3b) while DO was not significant, but satisfied the criteria for remaining in the model ($p<0.10$). The Hosmer-Lemeshow GFT did not indicate a lack of fit ($X^2 = 0.4$, $df = 8$, $p>0.05$) and there was high concordance (96.6%). An increase in salinity, temperature, and DO resulted in a higher probability for the presence of *B. virginica*, while increasing turbidity and depth resulted in a lower probability (Table 2.3b). Salinity and temperature were the most important predictor variables for explaining occurrence of *B. virginica* in the S1 model followed by turbidity and DO (Table 2.2).

Season 2 - The S2 logistic regression model that resulted in the lowest AIC value when predicting the presence of *B. virginica* was *Presence = Temp+Sal+DO* and this model was significant based upon the LR test ($X^2 = 282.9$, $df = 3$, $p<0.01$, Table 2.3c). Temperature, salinity, and DO all contributed significantly in explaining the presence of *B. virginica* in the overall model (Wald's X^2 test; Table 2.3c). The Hosmer-Lemeshow GFT did not indicate a lack of fit ($X^2 = 4.9$, $df = 8$, $p>0.05$) and there was high concordance (93.2%). An increase in temperature, salinity and DO resulted in an increased probability for the presence of *B. virginica* (Table 2.3c). Temperature and salinity were the most important predictor variables explaining occurrence of *B. virginica* in the S2 logistic model followed by DO (Table 2.2).

Maeotias marginata

Abundance ATP - The negative binomial (NB) was also determined to be the most appropriate data distribution for abundance of *M. marginata* based upon the significant LR test ($X^2 = 333.4$, $df = 1$, $p<0.05$) and the lower AIC values (Table 2.4). All models including intercept-only were significant at the $p<0.01$ level (Table 2.4). The NB regression model with the lowest AIC value was *Abundance = Temp+Turb+Sal+Area+DO* and all independent variables were significant (Wald's X^2 test; $p\leq0.01$). The criteria for GFT (Pearson's test statistic / *df*) was 0.49 indicating moderate underdispersion. The positive coefficients of the independent variables temperature, salinity, dissolved oxygen and area (i.e. shift to upper Suisun Marsh) indicate that their increased values resulted in increased medusae abundance, while increased turbidity resulted in decreased abundance. Temperature had the largest standardized estimate, thus was the most important predictor variable explaining *M. marginata* abundance, followed by salinity, turbidity, area and DO (Table 2.2).

Occurrence ATP (Logistic Regression) - The logistic regression model for the full data set (i.e. all time periods or ATP) that resulted in the lowest AIC when predicting the presence of *M. marginata* was *Presence = Temp+Sal+Turb+Area+Depth+DO,* which was significant based upon the LR test ($X^2 = 484.7$, $df = 6$, $p<0.01$, Table 2.5a). Temperature, salinity, turbidity, area and depth contributed significantly in explaining the presence of *M. marginata* in the overall model (Wald's X^2 test; Table 2.5a) while DO was not significant, but met the criteria for remaining in the model ($p<0.10$). The Hosmer-Lemeshow GFT did not indicate a lack of fit ($X^2 = 8.5$, $df = 8$, $p>0.05$) and there was high concordance (92.3%). An increase in temperature, salinity, area and DO resulted in a higher probability for the presence of *M. marginata,* while increasing turbidity and depth resulted in a lower probability (Table 2.5a). Based upon the standardized estimates, temperature and salinity were the most important predictor variables for occurrence of *M. marginata* followed by turbidity and area and finally depth and DO (Table 2.2).

Occurrence Seasonal Models (Logistic Regression)

Season 1 - The logistic regression model with the lowest AIC when predicting presence of *M. marginata* in S1 was *Presence = Sal+Temp+Turb+Area+DO+Depth,* which was significant based upon the LR test ($X^2 = 388.4$, $df = 6$, $p<0.01$, Table 2.5b). Salinity, temperature, turbidity, area and DO contributed significantly in explaining the presence of *M. marginata* in the overall model (Wald's X^2 test; Table 2.5b) while depth was not significant, but met the criteria for remaining in the model ($p<0.10$). The

Hosmer-Lemeshow GFT did not indicate a lack of fit (X^2 = 15.6, *df* = 8, $p \geq 0.05$) and there was high concordance (95.1%). An increase in salinity, temperature, area and DO resulted in a higher probability for the presence of *M. marginata*, while increasing turbidity and depth resulted in a lower probability (Table 2.5b). Temperature and salinity were the most important predictor variables in explaining *M. marginata* occurrence followed by turbidity, area, DO and depth (Table 2.2).

Season 2 - The logistic regression model that resulted in the lowest AIC value when predicting the presence of *M. marginata* in S2 was *Presence = Temp+Sal+Area,* which was significant based upon the LR test (X^2 = 282.9, *df* = 3, $p < 0.01$, Table 2.5c). Temperature, salinity, and area all contributed significantly in explaining the presence of *M. marginata* in the overall model (Wald's X^2 test; Table 2.5c). The Hosmer-Lemeshow GFT did not indicate a lack of fit (X^2 = 12.1, *df* = 8, $p > 0.05$) and there was high concordance (95%). An increase in temperature and area resulted in a higher probability for the presence of *M. marginata,* while increasing salinity resulted in a lower probability (Table 2.5c). Temperature was the most important predictor variable explaining *M. marginata* occurrence with a much weaker association of both salinity and the spatial variable site (Table 2.2).

Moerisia

Abundance ATP - The negative binomial (NB) was also determined to be the most appropriate data distribution for abundance of *Moerisia* based upon the significant likelihood ratio test (LR; X^2 = 8699, *df* = 1, $p < 0.05$) and the low AIC values (Table 2.6). All models including intercept-only were significant at the $p < 0.01$ level (Table 2.6). The NB regression model with the lowest AIC was *Abundance = Temp+Sal+Area+Turb+Depth* and all independent variables were significant (Wald's X^2 test; $p \leq 0.01$). The criteria for goodness of fit (GFT; Pearson's test statistic / *df*) was 0.54 indicating moderate underdispersion. The positive coefficients of the independent variables temperature, salinity, and area (i.e. shift to upper Suisun Marsh) indicate that their increased values resulted in increased medusae abundance, while increased turbidity and depth resulted in decreased abundance. Based upon the standardized estimates, temperature and salinity were the most important predictor variables explaining *Moerisia* abundance, followed by turbidity, area, and depth (Table 2.2).

Occurrence ATP (Logistic Regression) - The logistic regression model for the full data set (i.e. all time periods or ATP) that resulted in the lowest AIC value when predicting the presence of *Moerisia* was *Presence = Sal+Temp+Area+Turb+Depth*, which was significant based upon the LR test (X^2 = 427, *df* = 5, $p<0.01$, Table 2.7a). Salinity, temperature, area, turbidity, and depth contributed significantly in explaining the presence of *Moerisia* in the overall model (Wald's X^2 test; Table 2.7a). The Hosmer-Lemeshow GFT did not indicate a lack of fit (X^2 = 8.2, *df* = 8, P>0.05) and there was a high degree of concordance (92.9%). An increase in salinity, temperature, and area resulted in a higher probability for the presence of *Moerisia*, while increasing turbidity and depth resulted in a lower probability (Table 2.7a). Based upon the standardized estimates, temperature and salinity were the most important predictors explaining occurrence of *M. marginata* followed by turbidity, area and finally depth (Table 2.2).

Occurrence Seasonal Models (Logistic Regression)

Season 1 - The S1 logistic regression model that resulted in the lowest AIC value when predicting the presence of *Moerisia* was *Presence = Sal+Turb+Temp+Area+DO*, which was significant based upon the LR test (X^2 = 363.6, *df* = 5, $p<0.01$, Table 2.7b). Salinity, turbidity, temperature, area, and DO contributed significantly in explaining the presence of *Moerisia* in the overall model (Wald's X^2 test; Table 2.7b). The Hosmer-Lemeshow GFT did not indicate a lack of fit (X^2 = 7.5, *df* = 8, $p>0.05$) and there was a high degree of concordance (95.9%). An increase in salinity, temperature, and area resulted in a higher probability for the presence of *Moerisia*, while increasing turbidity and DO resulted in a lower probability (Table 2.7b). Salinity was the most important predictor variable explaining *Moerisia* occurrence in S1 followed by turbidity, temperature and finally area and DO (Table 2.2).

Season 2 - The S2 logistic regression model that resulted in the lowest AIC value when predicting the presence of *Moerisia* was *Presence = Temp+Site*, which was significant based upon the LR test ($X^2 = 275.2$, $df = 2$, $p<0.01$, Table 2.7c). Only temperature contributed significantly in explaining the presence of *Moerisia* in the overall model (Wald's X^2 test; Table 2.7c), although site was included in the model since it satisfied the minimum criteria ($p<0.10$). The Hosmer-Lemeshow GFT did not indicate a lack of fit ($X^2 = 6.2$, $df = 8$, $p>0.05$) and there was a high degree of concordance (95.5%). An increase in temperature and site resulted in a higher probability of *Moerisia* presence (Table 2.7c). Temperature was the most important predictor variable explaining *Moerisia* occurrence in the S1 model (Table 2.2).

Question 3: What are the suitable environmental conditions for each hydromedusae species?

Season 1

Suitable environmental conditions (5th to 95th percentile range) and summary statistics for Season 1 are listed in Table 2.8. Suitable conditions (conditions in which species are collected most frequently) for *B. virginica* in Season 1 were temperatures of 19.4 to 22.8 °C, salinities of 5.6 to 10.3 ‰, turbidities of 17 to 68 NTUs, and DO levels of 5.4 to 7.7 $mg{\cdot}lO_2^{-1}$. Suitable conditions for *M. marginata* in Season 1 were temperatures of 19.4 to 22.8 °C, salinities of 2.3 to 8.5 ‰, turbidities of 20 to 86 NTUs, and DO levels of 4.9 to 8.1 $mg{\cdot}lO_2^{-1}$. Suitable conditions for *Moerisia* in Season 1 were identified as temperatures of 19.5 to 22.7 °C, salinities of 2.8 to 9.9 ‰, turbidities of 19 to 87 NTUs, and DO levels of 4.6 to 7.8 $mg{\cdot}lO_2^{-1}$.

The trio of hydromedusae responded similarly to environmental conditions within S1 (Figure 2.7) with all species exhibiting a strong trend for high temperature and salinity and low turbidity, which were only seasonally available and thus, presumably limiting in the study area. *Blackfordia virginica* exhibited the strongest salinity trend, being found in only the highest salinity samples. The species-presence patterns for DO and depth were closely matched to the all-sample pattern indicating those variables were generally non-limiting in the study area.

Significant species differences in the means of salinity and turbidity were detected in S1 (Tukey-Kramer HSD test, $p < 0.05$; Figure 2.7). *Blackfordia virginica* was captured in significantly higher salinity (mean = 7.4 ± 1.5 ‰) than both *M. marginata* (mean = 5.2 ± 2.0 ‰) and *Moerisia* (mean = 5.8 ± 2.0 ‰). There were also significant mean salinity differences between *M. marginata* and *Moerisia* with the prior species found in significantly lower salinities. Turbidity differences were detected for *B. virginica* (mean = 38.1 ± 15.4 NTU) and *M. marginata* (47.7 ± 23.2 NTU), with *B. virginica* found in sites with lower mean turbidities. No mean differences were detected for temperature, DO or depth.

Season 2

Suitable environmental conditions (5th to 95th percentile range) and summary statistics for Season 2 are listed in Table 2.9. The suitable environmental conditions for *B. virginica* in S2 were temperatures of 14.8 to 22 °C, salinities of 5.6 to 10.2 ‰, turbidities of 20 to 71 NTUs, and DO levels of 5.4 to 8 mg·lO_2^{-1}. Suitable conditions for *M. marginata* in Season 2 were temperatures of 13.8 to 21.9 °C, salinities of 2.6 to 9.1‰, turbidities of 18 to 71 NTUs, and DO levels of 4.4 to 8.1 mg·lO_2^{-1}. Suitable conditions for *Moerisia* in Season 2 were identified as temperatures of 15.7 to 22 °C, salinities of 3.1 to 9.3 ‰, turbidities of 21 to 71 NTUs, and DO levels of 4.6 to 7.8 mg·lO_2^{-1}.

In season 2, all species again responded similarly to environmental conditions with the exception of salinity (Figure 2.8). *Blackfordia virginica* exhibited a strong positive salinity trend, suggesting that this species was again salinity limited in S2 or was locally produced in higher salinity waters. Both *M. marginata* and *Moerisia* exhibited only a slight positive trend for salinity, indicating salinity was not a major limiting factor in season 2. All species exhibited a similar strong trend for a narrow range of high temperature, suggesting that temperature was a limiting factor in S2. There were only minor differences from the all sample data distribution and the species present distribution for turbidity, DO, and depth, with the exception of *B. virginica*, whose species-present values for DO were more closely matched to the all-sample mean.

Significant mean differences were detected in S2 for temperature, salinity and DO (Tukey-Kramer HSD test, $p < 0.05$), although differences with the exception of salinity were small (Figure 2.8). As in S1, *B. virginica* was captured at significantly higher mean salinity (mean = 7.7 ± 1.4 ‰) than both *M. marginata* (mean = 5.8 ± 2.0 ‰) and *Moerisia* (mean = 6.1 ± 1.8 ‰). Significant differences in mean temperature were detected for *M. marginata* (mean = 18.6 ± 2.5 °C) and *Moerisia* (mean = 19.4 ± 2 °C), with *Moerisia* being captured at higher mean temperatures in Season 2. Dissolved oxygen differences were also detected for *B. virginica* (mean = 7 ± 0.7 $\mathrm{mg \cdot lO_2^{-1}}$) and *Moerisia* (mean = 6.6 ± 1.1 $\mathrm{mg \cdot lO_2^{-1}}$). No mean differences were detected for turbidity and depth.

Examination of each species differences in suitable seasonal conditions revealed that temperature deviated considerably between seasons, whereas salinity was more similar (Table 2.8 and 2.9). The lower suitable temperatures for *B. virginica* in season 1 and 2 were 19.4 and 14.8 °C and the lower suitable salinities for S1 and S2 were both 5.6 ‰. For *M. marginata*, the lower suitable temperatures for S1 and S2 were 19.4 and 13.8 °C and the lower suitable salinities for S1 and S2 were 2.3 and 2.6 ‰. The lower suitable temperatures for *Moerisia* in S1 and S2 were 19.5 and 15.7 °C and the lower suitable salinities for S1 and S2 were 2.8 and 3.1 ‰. The lower suitable temperature in S1 was within 0.1 °C for all three species (19.4 to 19.5 °C).

Abundance patterns in relation to temperature (Figure 2.9) and salinity (Figure 2.10) were useful in further describing species differences. Temperature patterns were very similar for each species. The temperature range for the largest peak in *B. virginica* abundance was 18 to 23 °C. The temperature range for *M. marginata* was 19 to 24 °C and the temperature range for *Moerisia* was 19 to 23 °C. Salinity patterns were more variable, although large peaks were still evident. There were two peaks in *B. virginica* abundance, thus the full range including both peaks was used to represent favorable salinity conditions for medusae abundance. The salinity range for *B. virginica* was 7 to 11 ‰. The salinity range for *M. marginata* was 3 to 9 ‰ and the salinity range for *Moerisia* was 4 to 9 ‰.

Question 4: What environmental conditions are currently limiting the hydromedusae blooms?

Blackfordia virginica

Independent variables included in the limiting condition plot for *B. virginica* were salinity, temperature, and turbidity, as they had the highest standardized estimates from the logistic regressions (Table 2.2). Overall the limiting condition plots for *B. virginica* (Figure 2.11a) indicated that low salinity was likely limiting the occurrence of medusae in A3 and A4 in all months sampled. Low S1 salinity in A2 in Yr1 and A1 and A2 in Yr2, were also likely limiting the occurrence of medusae. Temperature was limiting in S2, as temperatures declined below the suitable range after October in Yr1 and after November in Yr2, while salinity usually remained suitable until December. The effects of turbidity were not as apparent, as conditions were usually classified as suitable for much of the season, with the exception of A1 in S1 of Yr1, where high turbidity may have limited the occurrence of *B. virginica* medusae. The occurrence of *B.*

virginica medusae was well matched to the overlap in limiting environmental conditions, with the exception of A3 in Yr1 when medusae were captured in what appeared to be unfavorable salinities, but this occurrence was limited to a single site within the area.

Maeotias marginata

Independent variables included in the limiting condition plots for *M. marginata* were salinity and temperature, based upon their high standardized estimates from the logistic regressions (Table 2.2). Overall, the limiting condition plots (Figure 2.11b) indicated that salinity was generally not limiting for *M. marginata* in Yr1, with the exception of A3 in June and A4 in July and August. However, low salinity (<2.3 ‰ in S1 and < 2.6 ‰ in S2) was likely limiting *M. marginata* occurrence in Yr2. Salinity limitation in Yr2 was most pronounced in S1 in all areas (A1 to A4) and in A4 in October (S2). Temperature limitation (< 19.4 °C in S1 and < 13.8 °C in S2) was most pronounced in S2 in both years, as temperatures usually cooled one to two months ahead of the salinity decline in January. Additional temperature limitation was also observed in May (S1) of Yr1 in A1. The occurrence of medusae in each area was closely matched to the overlap of suitable salinity and temperature conditions with only a few minor exceptions including A2 and A3 in November of Yr1 and A3 in August of Yr2 (Figure 2.11b). In each instance where occurrence was not well matched to the overlapping suitable environmental conditions, less than 25% of the sites in the given area had medusae present.

Moerisia

Independent variables included in the limiting condition plots for *Moerisia* were salinity and temperature, based upon their high standardized estimates from the logistic regressions (Table 2.2). Overall, the limiting condition plots (Figure 2.11c) indicate that low salinity (<2.8 ‰ in S1 and < 3.1 ‰ in S2) likely had a local effect in Yr1 in A3 and A4 while temperature remained suitable. However, in Yr2 low salinity was likely limiting the occurrence of *Moerisia* in S1 in all areas. Salinity was suitable for *Moerisia* in S2 in both years and in all areas. Temperatures were likely unsuitable (< 19.5 °C in S1 and < 14.9 °C in S2) in all areas after October in Yr1 and after November in Yr2. The average temperature in May (S1) in A1 of Yr1 was lower than the suitable range, at a time when salinity was considered suitable. The occurrence of medusae was well matched to the overlapping suitable salinity and temperature conditions, although in Yr1 there was a one month delay in first catch after temperature and salinity both became suitable and in Yr2 medusae were not captured in A1 and A4 in November even though temperature and salinity were considered suitable.

2.4 DISCUSSION

Question 1: What are the temporal and spatial patterns in occurrence and abundance of each hydromedusae species?

The temporal pattern of medusae occurrence in the study area indicates that all three species are seasonal, occurring primarily in the summer and fall with the onset of bloom and length of bloom largely dependent upon the year and area. The large difference in catch between years was likely due primarily to inflow differences, which resulted in a considerable delay in the onset of the dry season baseline flow in the second year of the study. The low salinity that resulted from the higher inflow likely delayed the onset of the medusae bloom, perhaps by inhibiting the production or release of medusae by polyps. The delay in baseline flow and low salinity levels resulted in the loss of one to three months (depending on study area) of warm water conditions believed to be suitable for production of medusae by polyps for all three species (i.e. > 19.4 °C), which likely contributed to the observed low annual catch. The late bloom termination in the second year of the study was likely the result of somewhat elevated

November temperatures (13.5 °C Yr1 and 15.5 Yr2), which may have delayed mortality of medusae already present by one month. Temperatures which resulted in the greatest abundance of medusae (>19 °C) were no longer available by October in both years (Yr1 average = 17.5 ± 0.5 °C and Yr2 18.1 ± 0.6 °C), which can in part explain the rapid decline in medusae abundance for all three species from September to October.

The temporal pattern of increasing occurrence by area for all three species was consistent with a shifting salinity gradient moving into Suisun Marsh as freshwater inflow into the middle SFE declined. However, the early season occurrence of *Moerisia* and to some extent *M. marginata* in A4 seems to deviate somewhat from the observed upstream shift in occurrence, with A4 being more similar to areas downstream (A1 and A2) in timing of first occurrence. The most likely explanation for this is the proximity of A4 to the occasionally higher salinity waters of upper Suisun Bay near Chipps Island. From the limiting conditions plot (Figure 2.11) it is apparent that in A4 in both years of the study, there was a short disconnected pattern of early suitable salinity conditions appearing shortly after inflow declined to the dry-season baseline level (Yr1 June; Yr2 August to September). This indicates that a pulse of higher salinity water entered A4 during this time, which could have either resulted in a local bloom in A4 as salinity conditions became appropriate, or alternatively, medusae may have been transported into the area by the incursion of higher salinity waters from an area down-bay where a local bloom had already begun (i.e. Suisun Bay near Chipps Island). *Blackfordia virginica, M. marginata* and *Moerisia* have all been captured in upper Suisun Bay near Chipps Island, which is just downstream from sites located in A4 (Rees and Kitting 2002).

Blackfordia virginica

Of the three species, *B. virginica* had the shortest bloom duration with medusae caught in only three months in each of the study years in middle to late summer. *B.*

virginica also had the most restricted spatial distribution, as it was primarily captured in areas near to Suisun Bay. The limited spatial distribution of *B. virginica* suggests that the study area was at this species upstream edge of distribution and it is possible that captured medusae may have been released from polyps in higher salinity habitats down-bay and were transported into the system by tides. The salinity range previously reported for this species is 3 to 35 ‰ (Moore 1987; Rees and Gershwin 2000; Genzano 2006). However, the highest reported abundance in the SFE has been at salinities between 7 to 16 ‰ (Rees and Kitting 2002). The maximum salinity observed during this study was 11 ‰, thus low salinity may have been inhibiting this species and was likely restricting its occurrence to the highest salinity sites near Grizzly Bay and areas farther downstream (Rees and Gershwin 2000; Rees and Kitting 2002).

The densities of *B. virginica* in this study were similar to those previously observed in the SFE. The maximum density of *B. virginica* in this study was 5.7 medusae$\cdot$m^{-3} and the maximum average monthly catch was 0.7 medusae$\cdot$m^{-3} in September of Yr1. The highest average monthly catch by area was 1.8 medusae m^{-3} in A1, also in September of Yr1. The maximum density of *B. virginica* previously reported in the SFE from a bottom sample was 5 medusae$\cdot$m^{-3} and densities from surface samples were usually < 0.1 medusae$\cdot$m^{-3} (Rees and Kitting 2002). It is likely that the abundance of *B. virginica* was greater in downstream areas where salinity may have been more favorable. *Blackfordia viriginica* has been found in higher abundance in other estuaries. Moore (1987) reported densities as high as 47 medusae$\cdot$m^{-3} in estuaries on the western coast of India and 67 medusae$\cdot$m^{-3} in the Mira Estuary in Portugal. Thus, *B. virginica* has the potential to reach much higher densities, particularly in areas of increased salinity, but the low salinity common in Suisun Marsh at present likely limits its occurrence and abundance.

Maeotias marginata

Maeotias marginata had the longest bloom duration, as it was the first species to appear in the system in late spring and was usually the last species to be captured in the fall. *M. marginata* medusae were evenly distributed across the study area with the exception of the first month of occurrence when they were primarily captured in areas closest to Suisun Bay. The earlier occurrence of medusae in sites nearest Suisun Bay may have been due to salinity shifts, since those same sites reached suitable salinity levels first, but medusae may also have been produced and released from polyps downstream of Suisun Marsh and entered Suisun Marsh following tidal advection. The densities of *M. marginata* in this study were higher than those previously reported in the SFE. Rees and Kitting (2002) observed that the maximum density of *M. marginata* in the SFE (Chipps Island and in Suisun Slough) was below 0.1 medusae·m^{-3}. The maximum abundance in this study was 12.3 medusae·m^{-3} and the highest average monthly catch was 2.2 medusae·m^{-3} in September of Yr1. The highest average monthly catch by area was 3.1 medusae·m^{-3} in A2 in August of Yr1.

Moerisia

Moerisia had a more restricted bloom duration with its bloom usually beginning one month later and ending one month sooner than *M. marginata*. *Moerisia* medusae were also more restricted spatially and temporally than *M. marginata*, but were none-the-less captured in all areas in each year. Despite having a reduced season length and more limited spatial distribution than *M. marginata*, *Moerisia* was by far the most abundant species captured with a maximum density of 102 medusae·m^{-3} in upper Suisun Slough (September 2004). In a nearby tributary to Suisun Slough (Shelldrake Slough - not included in the analyses due to incomplete sampling) the density of *Moerisia* was 197 medusae·m^{-3} in September 2004. The highest average monthly catch for all sites (September Yr1) was 25 medusae·m^{-3} and the highest average monthly catch by area was 45 medusae·m^{-3} in A3, in September of Yr1. The observed densities of *Moerisia* medusae were considerably higher than those observed previously in the SFE (≥ 1 medusae·m^{-3}; Rees and Kitting 2002) and in other systems where their densities have been reported (12 *M. lyonsi* medusae·m^{-3}; Purcell et al. 1999a). The rapid increase in abundance of *Moerisia* medusae, particularly in Yr1, suggests that a large number of sessile polyps were present in the benthos in each area and that release of medusae larvae occurred rapidly when conditions became appropriate. Polyps of *Moerisia* were captured throughout Suisun Marsh in a concurrent benthic survey, but numbers have yet to be quantified (unpublished data).

Question 2: What environmental conditions affect the presence and abundance of hydromedusae?

The negative binomial (abundance) and logistic (occurrence) regression models for the complete data set (ATP) revealed that the hydromedusae are responding to environmental conditions in the system. There were strong similarities (salinity, temperature and turbidity were all highly influential) and only minor differences (DO had a larger effect than turbidity for *B. virginica* in the ATP negative binomial model) between the abundance and occurrence models for each species. This is intuitive given that the presence and abundance of gelatinous zooplankton are often controlled by an initial and to some extent sustained release of medusae by polyps (Brewer and Feingold 1991; Lucas 2001). Although not measured in this study, it seems likely that the longer polyps release medusae, the longer a bloom will last if mortality and or dispersion from an area are occurring. It also follows that the longer polyps release medusae the greater medusa abundance will be, assuming medusae release is greater than the loss to mortality and dispersion. Given the rapid maturation (8 days) of larval *Moerisia* (Ma and Purcell 2005a), there may also be feedback responses of medusae producing new cohorts of polyps if environmental conditions remain appropriate for a long enough time period.

Salinity and water temperature were the most important predictor variables for both abundance and occurrence of medusae in the ATP models for all three species of hydromedusae. A thermal and salinity gradient response is common for gelatinous zooplankton in estuarine systems (Decker et al. 2007; Purcell 2005; Purcell et al. 2007). Temperature had a much larger positive effect in predicting the abundance of *M. marginata* and *Moerisia* and salinity was of secondary importance. For *B. virginica,* both salinity and temperature had similar positive effects in predicting abundance. Increased abundance of medusae at higher temperatures may be due to a number of factors including increased survival of medusae and greater medusae production by polyps (Purcell 2005). Ma and Purcell (2005a) found that the production of medusae buds by *M. lyonsi* polyps increased significantly at higher temperatures and at low to moderate salinities. The increased production of medusa buds at higher temperatures would likely result in a higher density of medusae, assuming survival is constant across the temperature range. The developmental response of *M. marginata* polyps to temperature and salinity has not been determined, but based upon the similarity in population response of *M. marginata* and *Moerisia,* it may be similar.

Indirect affects of elevated water temperature and salinity may also play a role in increased occurrence and abundance of medusae. For instance, higher summer water temperatures and moderate salinity in Suisun Marsh are associated with an increase in primary productivity and increased overall abundance of pelagic invertebrates (unpublished data), which are important in the diet of medusae and polyps of the hydromedusae (Chapter 1). Since increased food availability typically increases the production of medusae (Thiel 1962; Purcell et al. 1999a,b; Stibor and Tokle 2003; Ma and Purcell 2005a), it follows that increased prey availability is likely contributing somewhat to the seasonal increase in medusae abundance. This relationship needs to be more thoroughly investigated to determine the relative contribution of prey density and environmental conditions in the seasonal blooms of hydromedusae.

Turbidity was also found to be an important predictor variable for all species in both the ATP abundance and occurrence models, although turbidity effects were not as influential as salinity and temperature, in most instances. The mechanism by which turbidity could inhibit the abundance and occurrence of medusae is not known, but it is likely related to some type of inhibition of larval release from benthic polyps, because elevated turbidity usually occurs prior to the first catch of medusae in the system. It is possible that the observed turbidity effect may be due to the limited light conditions, because photoperiod and light intensity have been observed to positively affect the production of medusae by polyps (Purcell 2007). High turbidity is also likely to inhibit primary production in the system, which could indirectly affect prey abundance (Cloern 1987) and the number of medusae produced by polyps (Ma and Purcell 2005a; Purcell 2007). Thus, low light conditions associated with high turbidity may have both direct and indirect negative effects on medusae abundance.

Dissolved oxygen was found to be a significant predictor of *B. virginica* occurrence and abundance in all models and was occasionally significant in the *M. marginata* and *Moerisia* models. The reason for its positive affects (i.e. positive coefficients in all models) is not clear. It is possible that DO is correlated to some other measured (temperature and salinity) or unmeasured (e.g. primary productivity and prey abundance) environmental variable that is contributing to its significance in the models. None-the-less, low DO is unlikely a major controlling factor in the system, because gelatinous zooplankton in general appear to be very tolerant of low DO levels (Chapter 1; Purcell et al. 2001b) and medusae of all three species were captured at very low DO levels (minimum DO: *Moerisia* = 0.9, *M. marginata* = 2.8, and *B. virginica* = 4.3 $\text{mg}\cdot\text{l}O_2^{-1}$; Chapter 1). Dissolved oxygen concentrations and primary productivity in estuarine systems are often directly related (Cloern 1996), thus increased productivity and the resulting higher density of zooplankton prey that result, could be responsible for the observed relationship.

The lack of significant depth effects in nearly all the regression models (small negative effect for *M. marginata* and *Moerisia* in the ATP logistic and negative binomial regression models), suggests that general habitat characteristics are secondary to environmental conditions in determining the occurrence and abundance of medusae. However, it is possible that the continuous tidal mixing in the system may decrease the likelihood of detecting subtle habitat effects.

The spatial variable area was found to be an important predictor variable for *M. marginata* and *Moerisia* in both the ATP abundance and logistic models, but not for *B. virginica.* Area affects usually entered the model after the main effects of salinity temperature and turbidity were already included, suggesting that regional conditions, outside of what was measured during this study, are only minimally contributing to abundance and likelihood of occurrence of medusae. Several untested scenarios could be contributing to the area effect in the models including differential prey abundance, flow dynamics and their effects on dispersion (e.g. tidal transport), and localized or regional polyp distributions which give rise to regional medusae distributions following their production and release. The consistently positive coefficients for area indicate that medusae were generally found in greatest abundance in upstream areas of Suisun Marsh, where in general, mesozooplankton and benthic and epibenthic prey are at their highest density (unpublished data).

Seasonal Models - The seasonal influence of the predictor variables on the occurrence of medusae revealed additional information on important factors in each time period. Salinity, temperature and turbidity were the most important predictors for the occurrence of all three species of medusae in S1 (February to September). The occurrence of *Moerisia* and *B. virginica* in S1 was strongly associated with salinity and both species were first captured in the higher salinity areas and in the later months of the season as salinity began to intrude into the marsh. *Maeotias marginata* was more strongly associated with increasing temperature than salinity in S1. This is consistent with the observations that *M. marginata* was the first species captured in Suisun Marsh in both years of the study and also had a wider spatial distribution, particularly in areas of lower salinity. The predicted occurrence of all three species was negatively associated with turbidity in S1, particularly for *B. virginica* and *Moerisia*. As discussed previously, the low light conditions associated with high early season turbidity during periods of high inflow, may have inhibited the release of larval medusae by polyps, resulting in reduced medusae occurrence.

Of the significant predictors in S2 (September to January), temperature was the most important and it appeared to explain medusae occurrence for all three hydromedusae. This is consistent with the observation that by October temperature had declined below 19 °C, the level associated with the bloom initiation in S1 and the cool temperatures likely affected the production and release of medusae by all three species. In addition, the cooler temperatures in November and December likely increased medusae mortality for they were often below the minimum threshold for medusae occurrence (approximately 14 to 16 °C, depending upon species).

Salinity had a reduced and more variable influence on the probability of medusae occurrence in S2. For instance, there was a lack of an association with salinity by Moerisia in S2 likely due to the fact that salinity remained at moderate to high levels (monthly average > 3 ‰) that were largely favorable throughout most of the fall and early winter. The probability of occurrence of *M. marginata* was negatively associated with salinity in S2, suggesting that the upper salinity levels observed were detrimental to this species and were limiting its distribution. The negative salinity association on the probability of medusae occurrence may have been due to unfavorable conditions for the production of medusae by polyps or for medusae survival, but this was not tested in this study. In contrast, salinity remained an important predictor for *Blackfordia virginica* occurrence in S2, which is consistent with this species higher salinity requirement (> 6 ‰) and the limited regional availability of those higher salinities. Thus medusae in the fall to winter months (S2) during this two year study can best be classified as being temperature limited with low salinity further limiting the occurrence of *B. virginica* and high salinity limiting the occurrence of *M. marginata*.

Question 3: What are the suitable environmental conditions for each hydromedusae species?

Of the three species, *M. marginata* and *Moerisia* responded most similarly to environmental conditions and both appear to be well suited for the conditions found within Suisun Marsh and Grizzly Bay. *Blackfordia virginica* had a more restricted spatial distribution and was primarily captured in the higher salinity downstream areas of Suisun Marsh and Grizzly Bay, suggesting conditions in Suisun Marsh were less suitable.

The observed seasonal response of each species allowed for a better estimate of suitable environmental conditions for medusae and provided insight into possible conditions that may affect the release or production of medusae by polyps. For instance, the differential temperature response of medusae between the spring and summer and fall and winter months suggests different mechanisms are contributing to the observed occurrence of medusae. The similarity in the lower suitable temperatures in S1 (19 °C) for all three hydromedusae either suggests a similar temperature requirement for survival of larval medusae or for the production of medusae by polyps. However, it is possible that other unmeasured factors including prey availability could have contributed to the consistent temperature response among medusae in the spring and early summer months. The large decline in abundance of all three hydromedusae in S2, usually beginning in October, is consistent with a temperature influenced increase in mortality of medusae and possibly a decline in larval medusae production since temperatures were well below the minimum bloom initiation temperature of 19 °C.

Of the three species, medusae of *M. marginata* were captured in the coldest water temperatures and were the last species captured in the fall and early winter months, thus likely had the greatest tolerance to low water temperatures. Although other factors including greater tolerance to low food availability, that also occurred in the late fall and winter months, may also have played a role in their increased longevity.

High temperatures did not appear to affect medusae abundance in either season. In fact, medusae of all three species were captured most frequently and in greatest abundance at the highest temperatures recorded during the study, when salinity was also appropriate. Medusae of all three species have been reported in temperatures as high or higher than those observed in Suisun Marsh (Mills and Summer 1995; Genzano et al. 2006; Chapter 1), which suggests that the estimate of upper suitable temperatures in this study were likely an artifact of the limited environmental variation during this two-year study, rather than physiological limitation. Higher temperatures may even facilitate a larger bloom, at least for *Moerisia*, as Ma and Purcell (2005a) observed a greater production of medusa buds at temperatures of 29 °C compared to 20 °C in their laboratory experiments.

The S1 differences in the lower salinity thresholds (5th percentile) indicate a more species-specific salinity response. *Blackfordia virginica* were associated with higher salinity conditions (> 5.6 ‰) than both *M. marginata* (> 2.6 ‰) and *Moerisia* (> 3.1 ‰), which is consistent with its limited spatial distribution in the study area. It is not known if the medusae of *B. virginica* are adversely affected by low salinity or if production of larval medusae by polyps is inhibited. The lack of *B. virginica* dispersal into areas of lower salinity in all but one instance in this study is highly suggestive that at least part of the limitation occurs at the medusa stage, perhaps due to medusae mortality. This finding differs somewhat from the lower range of salinities reported for *B. virginica* medusae (3 ‰) in studies conducted outside of the SFE and summarized by Mills and Sommer (1995), but is consistent with the observed salinities at which medusae reached their greatest abundance (6 to 16 ‰) in the SFE (Rees and Kitting 2002).

Maeotias marginata appears to be the most tolerant of the three hydromedusae to low salinity conditions although the difference in the lower suitable salinity threshold for *M. marginata* compared to *Moerisia* is small (< 1 ‰). None-the-less, the lower suitable salinity threshold appears to explain the observed pattern of earliest occurrence of *M. marginata* medusae in the spring and early summer. *Maeotias marginata* also appears to be the most restricted hydromedusae by high salinities. In addition to having the lowest upper suitable salinity thresholds in both S1 and S2, there were also significant negative effects of salinity on the probability of occurrence of *M. marginata* medusae in the S2 logistic model. A large negative effect of high salinity on predicted medusae abundance was also observed in Chapter 1, as indicated by the large quadratic effect of salinity in the medusae abundance models.

Maeotias marginata medusae had similar salinity thresholds for occurrence in the long-term study presented in Chapter 1 (January to September 5th to 95th percentile = 3 to 10 ‰ and October to December 5th to 95th percentile = 3 to 10.1 ‰), but their greatest abundance occurred at a narrower salinity range of 3 to 7 ‰ that was assumed to be favorable for production of larval medusae by polyps. A similar peak in *M. marginata* medusae abundance was observed in this study (4 to 7 ‰), although the data were variable. The mechanism resulting in the decline in abundance and occurrence of *M. marginata* medusae at salinities >7 and >9-10 ‰ is unknown, but may be due to increased mortality of medusae and a possible decrease in production of larval medusae by polyps.

Moerisia had a similar salinity related abundance pattern with the largest peak in abundance occurring at salinities between 4 and 9 ‰, which is consistent with that reported by Purcell et al. (1999a) for the population in the Choptank River (highest abundance at 4 ‰) and by Calder and Burrell (1967) in the James and Pamunkey Rivers (salinity range of 2 to 9 ‰). These results differ somewhat from the observed maximal production of medusa buds by *M. lyonsi* polyps at salinities of 5 to 15 ‰ under laboratory conditions (Ma and Purcell 2005a). This difference may be explained, in part, by the lower temperatures (< 26 °C) and salinities (<11.4‰) observed in this study, the mismatch between high temperatures and moderate to high salinities in the summer to fall, differences in laboratory conditions versus field conditions, and perhaps species differences, because a final identification of the species in the SFE has not been made. If the *Moerisia sp.* in the SFE is in fact *M. lyonsi*, then physiological limitation by elevated salinity and not predation, as suggested by Ma and Purcell (2005a), may be limiting its occurrence in the field at salinities greater than 9 ‰. There are no known predators of the hydromedusae in the middle SFE (Chapter 1). The only gelatinous zooplankton predator in the SFE that could exert population control over *Moerisia* would be *M. marginata*, given their co-occurrence, but the lack of medusae in its diet (Mills and Sommer 1995; Chapter 1) and its low abundance, especially at the higher salinities, suggests that this scenario is unlikely.

Question 4: What environmental conditions are currently limiting the hydromedusae blooms?

Fluctuating flow conditions in the system during the two years of this study resulted in large differences in medusae occurrence and abundance. This provided valuable insight into how hydromedusae may respond to a variety of conditions including altered inflow and climate change. In summary, low early season salinities associated with high inflow appear to have negatively affected all species, particularly *B. virginica*, while reduced early season inflow and elevated salinities likely resulted in greater abundance of medusae. Areas farthest upstream from Suisun Bay had the lowest salinity in the late spring and early summer and thus may have been the least hospitable for medusae, particularly *B. virginica* and *Moerisia*. Early season temperatures (June to September) were generally above 19.5 °C, in all areas, thus were unlikely to be limiting medusae production and survival. Fall and winter salinities were generally favorable for all species except *B. virginica*, which continued to be salinity limited in upstream areas. Medusae occurrence and abundance were negatively associated with low fall temperatures and positively associated with high fall temperatures. High turbidity was negatively associated with medusae occurrence and abundance in the early season months under conditions of high inflow, but was not associated with turbidity during the late summer and fall months.

The predicted effects of climate change in the SFE include increased temperatures in all seasons, increased rainfall versus snow, earlier snowmelt and peak runoff, and more variable annual precipitation totals (Knowles and Cayan 2002; Howat and Tulaczyk 2005; Zhu et al. 2005). These climate induced changes will likely lead to shifts in the availability of water for inflow. However, it is unlikely that the dry-season baseline inflow will decrease below current levels because of the need to maintain salinity levels near the pumping facilities in the south delta (Dettinger and Cayan 1995; Knowles 2002). However, this scenario is based upon the assumption that conditions in the estuary remain stable, which is unlikely in the long term (Lund et al. 2007). Given limited water availability for inflow and earlier snowmelt, it is probable that the dry-season will begin earlier in the spring, extending its duration (Chapter 1). A reduction in variation in summer and fall inflow has already been observed in the SFE, which has resulted in more stable and more saline waters in the middle estuary (Feyrer et al. 2007). This is likely due to climate induced effects as well as increased human demand for water resources as California's population and water needs continue to grow (Naiman and Turner 2000). The observed increasing fall and winter temperatures in Suisun Marsh from 1981 to 2005 (Chapter 1) are consistent with the predictions of climate change, although decadal climate cycles are likely playing a role (Dettinger and Cayan 1995). It is possible that temperatures will continue to increase as predicted under a regional global warming scenario (Knowles and Cayan 2002; Zhu et al. 2005).

Because environmental conditions including salinity, temperature, and turbidity were strong predictors of hydromedusae occurrence and abundance, it is possible to make further predictions concerning future population shifts under varying inflow and warming regimes as described above. Possible scenarios likely to affect medusae occurrence and abundance in the study area are: (1) Decreased spring and early summer inflow; (2) Decreased dry-season base line inflow below current levels; (3) Increased spring and summer temperatures; (4) Increased fall temperatures; (5) Decreased spring and early summer inflow and increased spring and summer temperatures; (6) Increased inflow and decreased temperatures. These scenarios are discussed in greater detail in the following paragraphs.

Decreased spring and early summer inflow - maintained dry-season outflow

Reduced spring and early summer inflow, resulting from reduced precipitation, climate altered snowmelt or increased anthropogenic water use would result in highly favorable conditions for both *M. marginata* and *Moerisia* by increasing early season salinity, which would extend the bloom season to months in which temperatures were already favorable for medusae production (May and June). A similar scenario was observed in Yr1 of this study when temperature and salinity conditions were both suitable early in the season, which resulted in very high abundances of all three species, particularly *Moerisia.* Under this scenario, conditions for *B. virginica* medusae would likely remain somewhat limiting since salinity would be at or near the levels observed in this study (< 11 ‰), which resulted in only a low abundance of medusae.

Decreased dry-season inflow

A lower dry-season inflow would result in elevated salinities and adverse conditions for *M. marginata* and possibly *Moerisia* by limiting the production of larval medusae and increasing mortality of medusae. *Moerisia* was captured in higher salinity than *M. marginata,* thus may not be as adversely affected. The low catch of *M. marginata* medusae was attributed to high salinity conditions (> 7‰) during the drought years 1985 to 1993, which may have inhibited the production of medusae by polyps (Chapter 1). *Blackfordia virginica* would likely respond favorably to reduced dry-season inflow, as salinity would increase to levels closer to those at which this species has been found to occur in greatest abundance in the SFE (6 to 16 ‰; Rees and Kitting 2002). Medusae of all three species would likely shift their population distribution upstream, resulting in greater distribution of *B. virginica* in Suisun Marsh and a reduced distribution of *M. marginata* and *Moerisia.*

Increased spring and summer temperatures - maintained dry-season inflow

An increase in spring and summer temperatures associated with climate warming and earlier snowmelt would likely benefit both *M. marginata* and *Moerisia,* but would likely have little effect on *B. virginica* since salinity would remain unfavorable in much of Suisun Marsh. Increased temperatures would likely increase production of larval medusae by polyps of *M. marginata* and *Moerisia* in downstream areas with suitable salinity conditions in the early spring and summer months. Higher spring temperatures would also likely result in a larger bloom in upstream areas as salinity increased, especially if temperatures approached 29 °C, the temperature that resulted in the highest production of medusa buds by *M. lyonsi* (Ma and Purcell 2005a; Purcell 2005).

Increased fall temperatures – maintained dry-season inflow

An increase in fall temperatures would likely extend the bloom of medusae of all three species. A longer bloom occurring into the fall and early winter months has been observed for *M. marginata* in Suisun Marsh over the last 15 years as fall temperatures have increased (Chapter 1). However, unless fall temperatures remained high (i.e. above 19.5 °C, the assumed minimum temperature for larval medusae production by polyps) the fall abundance of all three species would likely remain low.

Decreased spring and early summer inflow and increased spring and summer temperature-maintained dry-season inflow

The combination of decreased spring and early summer inflow (i.e. increased early season salinity) and increased spring and summer temperatures would make early season conditions in Suisun Marsh more favorable for both *M. marginata* and *Moerisia* medusae. Assuming turbidity was not limiting, the production of medusae by polyps would likely occur earlier in the spring and would continue until temperatures were no longer favorable in the early fall. An earlier and extended bloom would increase the opportunity for both asexual and sexual reproduction, which could lead to the further production of additional polyps and medusae. It is unlikely that *B. virginica* would benefit from these conditions since salinity would remain at levels observed in this study.

Increased dry-season outflow and decreased temperatures

Increased inflow and decreased temperatures would adversely affect all species, especially if temperature and salinity declined below 19.5 °C and 3 ‰. In the long term study in Suisun Marsh, there were four years that had high summer and fall inflow and low average salinity (< 3 ‰) during the July to November time period (Chapter 1). These conditions resulted in the absence of *M. marginata* medusae or their significant reduction in abundance (Chapter 1). Average summer and fall water temperatures within Suisun Marsh are usually not much above the lower temperatures required for production of medusae (19.5 °C; Chapter 1). In Yr1 and Yr2 of this study, the highest average monthly temperatures observed during a bloom were 21.8 °C and 22.1 °C. Thus a reduction in average temperatures of only 3 °C would likely have inhibited a bloom. Two cooler climate cycles have been observed in Suisun Marsh from 1982 to 1988 and 1996 to 2000 during which July to November average water temperatures were usually < 19 °C (Chapter 1). In each of those years medusae abundance was generally low, especially in the early season months of June and July and late season months of October and November.

2.5 CONCLUSION

This trio of alien hydromedusae has been broadly distributed to estuaries worldwide, yet little is known of their population characteristics, factors affecting abundance, and impacts on aquatic communities, due mainly to the limited number of studies targeting these small and seemingly innocuous species. Within the SFE, this trio represents a novel predator group; no native gelatinous zooplankton were present in the low salinity reaches prior to their invasion and at present there are no known natural predators. Their spatial and temporal occurrence and high abundance suggests that they are well established in the system and they appear to be responding favorably to changing estuarine conditions.

Environmental conditions including salinity, temperature, and turbidity were of primary importance in predicting their occurrence and abundance, while depth had little effect. It appears that stable low salinity conditions (3 to 10 ‰) are ideal for *M. marginata* and *Moerisia*, while *B. virginica* is better suited for higher salinity conditions (> 6 ‰). Baseline dry-season inflow in the SFE from late spring to early winter resulted in the greatest abundance and most widespread occurrence of all three species. Due to flow management and precipitation changes, a more stable and longer dry-season is becoming increasingly common in the SFE (Chapter 1; Feyrer et al. 2007), thus it can be predicted that these hydromedusae will continue to increase in abundance, if prey are sufficiently abundant. Predicted warming trends in the system will likely have a positive affect on medusae abundance, because temperatures are presumably limiting in the spring and fall months. A shift to warmer fall temperatures in Suisun Marsh has already extended the bloom of medusae of *M. marginata* by 1 to 2 months over the last two decades (Chapter 1). Higher summer temperatures would also likely benefit each species, by increasing the potential for a larger bloom through developmental changes in the benthic polyps (Ma and Purcell 2005a). However, increased warming and changes in inflow will also likely affect turbidity, CO^2 levels, primary production, and secondary production, which may indirectly and directly affect the abundance of medusae in a less predictable way.

The high densities of hydromedusae in Suisun Marsh are likely to be adversely affecting the aquatic community through their predation on invertebrates and their removal of energy from the system (Chapter 1). Their greatest impact is likely on the pelagic community, given their copepod dominated diet (Chapter 1; Mills and Sommer 1995). The pelagic community in the SFE has already undergone significant changes over the last few decades with well documented declines in important phytoplankton, invertebrates and fish (Bennett and Moyle 1996; Kimmerer and Orsi 1996; Orsi and Mecum 1996; Lehman 2000; Jassby et al. 2002; Kimmerer 2002; Matern et al. 2002; Feyrer et al. 2007; Sommer et al. 2007). At the same time there has been a notable increase in less beneficial organisms including the microzooplankter *Limnothoina tetraspina,* which now dominates the zooplankton community in the low salinity zone (LSZ) of the SFE from spring through late fall (Orsi and Ohtsuka 1999; Bouley and Kimmerer 2006). Presumably due to its small size, *L. tetraspina* has not been found to be an important prey species for visually feeding pelagic fishes and there are, at present, no abundant filter feeding fishes which frequent the middle SFE (Kimmerer 2006). Thus, Bouley and Kimmerer (2006) suggest that *L. tetraspina* represents an energetic dead end in the metazoan food web.

The increasing abundance of *M. marginata* in the SFE since 1995 is well matched to the observed increase of *L. tetraspina* (Chapter 1; Bouley and Kimmerer 2006). Long term records of catch in the SFE are unavailable for *B. virginica* and *Moerisia,* but their observed densities in this study were significantly higher than those reported from the 1990s (Mills and Sommer 1995; Rees and Kitting 2002). It is possible that the hydromedusae are increasing in abundance in response to this readily available prey species that often makes up 80% of the SFE plankton community in the summer and fall months (Bouley and Kimmerer 2006). It has been observed that non-visually feeding gelatinous zooplankton often thrive in coastal waters dominated by small microzooplankton (Uye 1994; Uye and Sano 1995; Shiganova 1998; Purcell et al. 2007). Microzooplankton (Limnothoina or Oithona cyclopoid copepods) were observed in the diet of *M. marginata* and *Moerisia* in Suisun Marsh, but their overall numbers were low (unpublished data).

At present, both hydromedusae and *L. tetraspina* represent apparent energetic dead ends. If the hydromedusae in the LSZ of the SFE are deriving much of their biomass from *L. tetraspina*, then both predator and prey comprise a more complex and largely inaccessible (no predators of and few predators of *L. tetraspina*) portion of the SFE pelagic foodweb during the usually productive summer and fall months. The only exception would be the detrital contribution resulting from the release of waste products and the occasional mortality of medusae. Given the lack of predators, it can be assumed that the majority of the accumulated biomass of the hydromeduae only re-enters at the base of the food web as detritus, which would primarily occur following their mass die off as temperatures cool in late fall. This cycle of energy loss during the summer and fall months has many ecological ramifications for an already struggling community of pelagic invertebrates and fish in this energy poor system. The most significant of which would be the redirection of pelagic biomass by the hydromedusae and microzooplankton to the detrital loop of the food web. This would primarily benefit filter feeding organisms such as the introduced overbite clam *Corbula amurensis*, and indirectly the microbial community. Increased microbial production would further benefit the microzooplankton community and in turn the hydromedusae, assuming they comprise an important component of their diet.

Additional research is needed to better understand the role and impacts of hydromedusae in the system. First, a system wide survey of hydromedusae would greatly improve our knowledge of the current abundance and distribution of each species and it could serve as a valuable reference point in the SFE, for the system will undoubtedly continue to change as anthropogenic influences accumulate and climate change sets in. Second, the biology and ecology of each species polyps needs to be further investigated with the goal of improving our understanding of their role in the production of medusae, their limiting factors for growth, and their impact on the benthos and plankton community. Third, the feeding ecology of all species of medusae needs to be more closely examined to allow for an improved understanding of their position and influence in the aquatic foodweb of the SFE.

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2.7 TABLES

Table 2.1 Poisson (P) and Negative Binomial (NB) regression model results for abundance of *B. virginica* for the full two year data set (ATP = All Time Periods; n = 864 samples). The coefficient and standard error (in parentheses) are listed for each independent variable with Sal = salinity, Temp = water temperature, DO = dissolved oxygen, Depth = average depth, Site/Area = numerical values for sites 1-36 or areas 1-4, and Turb = turbidity. The selection and order of independent variables at each model step, unless noted otherwise, was based upon the lowest value of Aikake's information criterion (AIC). The change in AIC (ΔAIC) indicates the difference between the lowest AIC of all of the independent variable combinations and the AIC of the specified model. The spatial variable used in each model (i.e. Site or Area) is indicated. p = probability of the model using the likelihood ratio test and the X^2 test statistic. The significance of each independent variable was determined using Wald's X^2 test statistic with a level of significance indicated at both $p<0.05$ (*) and $p<0.01$ (**); ns = not significant. The model with independent variables that met all selection criteria and had the lowest AIC is indicated in bold.

Model	No. of terms	Spatial var.	Sal	Temp	DO	Depth	Site/Area	Turb	*p*	AIC	ΔAIC
P	6	Area[1]	1.00(0.157)**	0.55(0.101)**	0.55(0.160)**	0.10(0.080)ns[b]	0.21(0.433)ns[c]	-0.01(0.010)ns[b]	<0.01	141	3
P	6	Site[1]	0.99(0.132)**	0.57(0.101)**	0.61(0.167)**	0.12(0.079)ns[b]	-0.04(0.021)ns[a]	-0.01(0.010)ns[b]	<0.01	138	0
NB	6	Area[1]	0.99(0.163)**	0.55(0.106)**	0.53(0.175)**	0.10(0.082)ns[b]	0.20(0.442)ns[c]	-0.01(0.011)ns[c]	<0.01	140	2
NB	6	Site	0.98(0.136)**	0.57(0.104)**	0.60(0.176)**	0.12(0.080)ns[b]	-0.04(0.022)ns[a]	-0.01(0.010)ns[b]	<0.01	138	0
NB	5	Site	0.96(0.133)**	0.54(0.102)**	0.52(0.163)**	0.15(0.074)ns[a]	-0.03(0.022)ns[b]	-	<0.01	138	0
NB	**4**	**na**	**0.94(0.129)****	**0.52(0.102)****	**0.47(0.161)****	**0.13(0.076)ns**[a]	-	-	**<0.01**	**138**	**0**
NB	**3**	**na**	**0.88(0.115)****	**0.51(0.101)****	**0.49(0.156)****	-	-	-	**<0.01**	**138**	**0**
NB	2	na	0.77(0.104)**	0.47(0.104)**	-	-	-	-	<0.01	146	8
NB	1	na	0.72(0.103)**	-	-	-	-	-	<0.01	180	42
NB	0	na	-	-	-	-	-	-	<0.01	299	161

Note: The negative binomial was the most appropriate data distribution based upon the significant LR test (X^2 test statistic = 20.8, df = 1, $p<0.05$; reject H_o: k=0).

[a] $p>0.5$ and <0.10, the minimum criteria for independent variable retention in the model.

[b] $p>0.1$ and <0.30, the minimum criteria for adding the independent variable to the model.

[c] $p>0.3$.

Table 2.2 Standardized estimates and odds ratios for the independent variables in the best-fit (i.e. lowest AIC) negative binomial (abundance; Neg. Bin.) and logistic regression models (presence / absence). Ind. Var. = independent variable. Std. Est. = standardized estimate calculated by: (Stand. Est. = [ind. var. coefficient * standard deviation of ind. var.] / standard deviation of the dependent variable]; Bradford et al. 2003). Independent variables indicated as not significant (^{ns}) were not significant in the final model (p>0.05) but satisfied the minimum criteria for inclusion (p<0.10).

	B. virginica			***M. marginata***			***Moerisia***		
Model	Ind. Var.	Std. Est.	Odds Ratio	Ind. Var.	Std. Est.	Odds Ratio	Ind. Var.	Std. Est.	Odds Ratio
All Data - Neg. Bin.	**Sal**	8.62		**Temp**	2.06		**Temp**	0.39	
	Temp	7.89		**Sal**	0.96		**Sal**	0.24	
	DO	2.54		**Turb**	-0.72		**Turb**	-0.16	
	Depth^{ns}	1.01		**Area**	0.35		**Area**	0.14	
				DO	0.32		**Depth**	-0.04	
All Data - Logistic	**Sal**	7.23	2.03	**Temp**	4.25	1.52	**Temp**	5.33	1.61
	Temp	5.22	1.36	**Sal**	3.36	1.74	**Sal**	4.43	1.93
	Turb	-2.83	0.98	**Turb**	-1.70	0.98	**Turb**	-1.86	0.98
	DO	2.46	1.50	**Area**	1.58	2.06	**Area**	1.84	2.13
				Depth	-0.52	0.90	Depth^{ns}	-0.68	0.89
				DO^{ns}	0.50	1.15			
Season 1 - Logistic	**Sal**	8.60	2.37	**Temp**	4.67	1.71	**Sal**	5.49	2.61
	Temp	7.29	1.58	**Sal**	3.68	1.99	**Turb**	-2.91	0.98
	Turb	-6.80	0.96	**Turb**	-1.81	0.98	**Temp**	2.87	1.37
	DO^{ns}	2.97	1.56	**Area**	1.23	1.75	**Area**	1.84	2.19
				DO	1.19	1.39	**DO**	-1.35	0.70
				Depth^{ns}	-0.66	0.88			
Season 2 - Logistic	**Temp**	6.24	1.66	**Temp**	6.47	2.02	**Temp**	7.90	2.27
	Sal	5.73	2.14	**Sal**	-0.97	0.85	Site^{ns}	0.66	1.03
	DO	2.69	1.93	**Site**	0.85	1.04			

Table 2.3 Logistic regression results for presence/absence of *B. virginica* for (a) full two year data set (ATP = All Time Periods; n = 864 samples), (b) Season 1 (February to September; n = 576) and (c) Season 2 (September to January; n = 360). Column labels, model details, and data subscripts are as described in Table 2.1.

a. *B. virginica* - All Data (ATP)

No. of terms	Spatial var.	Sal	Temp	Turb	DO	Depth	Site/Area	*p*	AIC	ΔAIC
6	Area	0.71(0.106)**	0.31(0.055)**	-0.02(0.009)**	0.40(0.141)**	0.01(0.07)ns^{c}	-0.01(0.245)ns^{c}	<0.01	280	4
6	Site	0.71(0.087)**	0.31(0.055)**	-0.02(0.009)**	0.40(0.142)**	0.01(0.07)ns^{c}	0.00(0.017)ns^{c}	<0.01	280	4
5	na	0.71(0.086)**	0.31(0.055)**	-0.02(0.009)**	0.40(0.140)**	0.01(0.07)ns^{c}	-	<0.01	278	2
4	**na**	**0.71(0.086)****	**0.31(0.055)****	**-0.02(0.009)****	**0.41(0.137)****	**-**	**-**	**<0.01**	**276**	**0**
3	na	0.65(0.081)**	0.28(0.053)**	-0.03(0.009)**	-	-	-	<0.01	284	8
2	na	0.68(0.075)**	0.26(0.052)**	-	-	-	-	<0.01	294	18
1	na	0.59(0.061)**	-	-	-	-	-	<0.01	328	52
0	na	-	-	-	-	-	-	<0.01	474	198

b. *B. virginica* - Season 1

No. of terms	Spatial var.	Sal	Turb	Temp	DO	Site/Area	Depth	*p*	AIC	ΔAIC
6	Area	0.78(0.165)**	-0.05(0.017)**	0.42(0.218)ns^{a}	0.42(0.236)ns^{a}	-0.35(0.386)ns^{c}	0.01(0.114)ns^{c}	<0.01	136	2
5	Area	0.78(0.164)**	-0.04(0.015)**	0.42(0.218)ns^{a}	0.42(0.225)ns^{a}	-0.35(0.385)ns^{c}	-	<0.01	134	0
6	Site	0.87(0.146)**	-0.04(0.017)**	0.47(0.229)*	0.47(0.246)ns^{a}	-0.01(0.025)ns^{c}	0.00(0.112)ns^{c}	<0.01	138	4
5	Site	0.87(0.146)**	-0.04(0.016)**	0.47(0.228)*	0.46(0.234)*	-0.01(0.025)ns^{c}	-	<0.01	136	2
4	**na**	**0.86(0.144)****	**-0.04(0.015)****	**0.45(0.224)***	**0.44(0.227)ns**^{a}	**-**	**-**	**<0.01**	**134**	**0**
3	na	0.79(0.134)**	-0.04(0.015)**	0.40(0.211)ns^{a}	-	-	-	<0.01	136	2
2	na	0.76(0.118)**	-0.05(0.015)**	-	-	-	-	<0.01	138	4
1	na	0.79(0.103)**	-	-	-	-	-	<0.01	152	18
0	na	-	-	-	-	-	-	<0.01	266	132

c. *B. virginica* - Season 2

No. of terms	Spatial var.	Temp	Sal	DO	Turb	Depth	Site/Area	*p*	AIC	ΔAIC
6	Area^{1}	0.51(0.081)**	0.60(0.151)**	0.62(0.203)**	0.01(0.014)ns^{c}	0.07(0.087)ns^{c}	-0.57(0.350)ns^{b}	<0.01	176	2
5	Area^{1}	0.51(0.081)**	0.59(0.151)**	0.61(0.201)**	-	0.07(0.087)ns^{c}	-0.60(0.347)ns^{a}	<0.01	174	0
4	Area^{1}	0.51(0.081)**	0.60(0.151)**	0.64(0.196)**	-	-	-0.56(0.343)ns^{b}	<0.01	174	0
6	Site	0.51(0.083)**	0.76(0.122)**	0.66(0.202)**	0.01(0.014)ns^{c}	0.06(0.086)ns^{c}	-0.01(0.02)ns^{c}	<0.01	180	6
5	na	0.51(0.082)**	0.76(0.122)**	0.65(0.201)**	0.01(0.014)ns^{c}	0.05(0.085)ns^{c}	-	<0.01	178	4
4	na	0.51(0.082)**	0.76(0.122)**	0.68(0.197)**	0.01(0.013)ns^{c}	-	-	<0.01	176	2
3	**na**	**0.51(0.082)****	**0.76(0.123)****	**0.66(0.193)****	**-**	**-**	**-**	**<0.01**	**174**	**0**
2	na	0.44(0.076)**	0.65(0.107)**	-	-	-	-	<0.01	186	12
1	na	0.36(0.052)**	-	-	-	-	-	<0.01	242	68
0	na	-	-	-	-	-	-	<0.01	320	146

Table 2.4 Poisson (P) and Negative Binomial (NB) regression model results for abundance of *M. marginata* for the full two year data set (n = 864 samples). Column labels, model details and data subscripts are as described in Table 2.1.

Model	No. of terms	Spatial var.	Temp	Turb	Sal	DO	Site/Area	Depth	*p*	AIC	ΔAIC
P	6	Area^{1}	0.45(0.03)**	-0.02(0.004)**	0.33(0.034)**	0.22(0.059)**	0.35(0.076)**	0.01(0.027)ns^{c}	<0.01	554	86
P	6	Site	0.40(0.03)**	-0.02(0.003)**	0.22(0.025)**	0.19(0.055)**	0.02(0.006)*	0.01(0.025)ns^{c}	<0.01	568	100
NB	6	Area^{1}	0.48(0.04)**	-0.02(0.005)**	0.37(0.053)**	0.23(0.088)**	0.37(0.122)**	-0.02(0.042)ns^{c}	<0.01	470	2
NB	**5**	**Area^{1}**	**0.48(0.043)****	**-0.02(0.005)****	**0.37(0.053)****	**0.21(0.083)***	**0.37(0.122)****	**-**	**<0.01**	**468**	**0**
NB	6	Site	0.45(0.04)**	-0.03(0.005)**	0.25(0.042)**	0.22(0.090)*	0.02(0.009)ns^{a}	-0.03(0.043)ns^{c}	<0.01	476	8
NB	5	Site	0.44(0.04)**	-0.03(0.004)**	0.26(0.041)**	0.20(0.085)*	0.01(0.009)ns^{a}	-	<0.01	475	7
NB	4	na	0.45(0.04)**	-0.03(0.004)**	0.27(0.040)**	0.22(0.085)*	-	-	<0.01	476	8
NB	3	na	0.44(0.04)**	-0.03(0.004)**	0.27(0.041)**	-	-	-	<0.01	481	13
NB	2	na	0.42(0.04)**	-0.04(0.004)**	-	-	-	-	<0.01	527	59
NB	1	na	0.44(0.04)**	-	-	-	-	-	<0.01	621	153
NB	0	na	-	-	-	-	-	-	<0.01	845	377

Note: The negative binomial was the most appropriate data distribution based upon the significant LR test (X^2 test statistic = 333.4, df = 1, $p<0.01$; reject H_o: k=0) and the low AIC values.

Table 2.5 Logistic regression results for presence/absence of *M. marginata* for (a) the full two year data set (ATP = All Time Periods; n = 864 samples), (b) Season 1 (February to September; n = 576) and (c) Season 2 (September to January; n = 360). Column labels, model details and data subscripts are as described in Table 2.1

a. *M. marginata* - All Data (ATP)

No. of terms	Spatial Var.	Temp	Sal	Turb	Site/Area	Depth	DO	*p*	AIC	ΔAIC
6	**Area**	0.42(0.037)**	0.55(0.063)**	-0.02(0.005)**	0.72(0.151)**	-0.10(0.053)*	**0.14(0.084)ns^{a}**	**<0.01**	**554**	**0**
5	Area	0.41(0.037)**	0.55(0.064)**	-0.02(0.005)**	0.72(0.151)**	-0.08(0.050)ns^{b}	-	<0.01	554	0
4	Area	0.41(0.037)**	0.55(0.063)**	-0.02(0.005)**	0.69(0.149)**	-	-	<0.01	556	2
6	Site	0.39(0.034)**	0.33(0.045)**	-0.03(0.005)**	0.02(0.011)*	-0.09(0.052)ns^{a}	0.12(0.083)ns^{b}	<0.01	574	20
5	Site	0.39(0.034)**	0.33(0.045)**	-0.04(0.005)**	0.02(0.011)*	-0.07(0.049)ns^{b}	-	<0.01	574	20
4	Site	0.39(0.034)**	0.34(0.044)**	-0.03(0.005)**	0.02(0.010)*	-	-	<0.01	574	20
3	na	0.39(0.034)**	0.35(0.043)**	-0.03(0.005)**	-	-	-	<0.01	576	22
2	na	0.35(0.031)**	0.48(0.041)**	-	-	-	-	<0.01	636	82
1	na	0.30(0.025)**	-	-	-	-	-	<0.01	820	266
0	na	-	-	-	-	-	-	<0.01	1026	472

b. *M. marginata* - Season 1

No. of terms	Spatial Var.	Sal	Temp	Turb	DO	Depth	Site/Area	*p*	AIC	ΔAIC
6	**Area^{1}**	0.69(0.092)**	0.54(0.086)**	-0.02(0.006)**	0.33(0.142)*	**-0.13(0.076)ns^{a}**	0.56(0.194)**	**<0.01**	**306**	**0**
5	Area^{1}	0.71(0.091)**	0.53(0.085)**	-0.02(0.006)**	0.24(0.130)ns^{a}	-	0.55(0.192)**	<0.01	308	2
4	Area^{1}	0.73(0.092)**	0.48(0.078)**	-0.02(0.006)**	-	-	0.58(0.192)**	<0.01	308	2
6	Site	0.51(0.072)**	0.51(0.079)**	-0.03(0.006)**	0.34(0.140)*	-0.13(0.078)ns^{a}	0.02(0.014)ns^{c}	<0.01	314	8
5	na	0.53(0.071)**	0.51(0.079)**	-0.03(0.006)**	0.35(0.140)*	-0.12(0.076)ns^{b}	-	<0.01	314	8
4	na	0.55(0.070)**	0.50(0.079)**	-0.02(0.006)**	0.27(0.128)*	-	-	<0.01	314	8
3	na	0.56(0.071)**	0.45(0.072)**	-0.03(0.006)**	-	-	-	<0.01	316	10
2	na	0.67(0.068)**	0.45(0.066)**	-	-	-	-	<0.01	344	38
1	na	0.78(0.064)**	-	-	-	-	-	<0.01	422	116
0	na	-	-	-	-	-	-	<0.01	682	376

c. *M. marginata* - Season 2

No. of terms	Spatial Var.	Temp	Sal	Site/Area	DO	Depth	Turb	*p*	AIC	ΔAIC
6	Area^{1}	0.68(0.072)**	-0.09(0.111)ns^{c}	0.23(0.271)ns^{c}	0.15(0.116)ns^{b}	-0.00(0.010)ns^{c}	-0.04(0.087)ns^{c}	<0.01	224	10
6	Site	0.71(0.075)**	-0.19(0.080)*	0.05(0.019)*	0.14(0.119)ns^{b}	-0.01(0.010)ns^{c}	-0.06(0.088)ns^{c}	<0.01	218	4
5	Site	0.71(0.075)**	-0.18(0.079)*	0.04(0.018)*	0.11(0.111)ns^{c}	-0.01(0.010)ns^{c}	-	<0.01	216	2
4	Site	0.72(0.073)**	-0.17(0.077)*	0.04(0.018)*	0.13(0.107)ns^{b}	-	-	<0.01	214	0
3	**Site**	0.70(0.072)**	-0.17(0.077)*	0.04(0.018)*	-	-	-	**<0.01**	**214**	**0**
2	na	0.68(0.069)**	-0.15(0.076)*	-	-	-	-	<0.01	218	4
1	na	0.64(0.064)**	-	-	-	-	-	<0.01	220	6
0	na	-	-	-	-	-	-	<0.01	492	278

Table 2.6 Poisson (P) and Negative Binomial (NB) regression model results for abundance of Moerisia for the full two year data set (n = 864 samples). Column labels, model details and data subscripts are as described in Table 2.1.

Model	No. of terms	Spatial var.	Temp	Sal	Turb	Depth	Site/Area	DO	*p*	AIC	ΔAIC
P	6	Area^{1}	0.59(0.016)**	0.43(0.013)**	-0.04(0.002)**	-0.10(0.013)**	0.83(0.028)**	-0.02(0.021)ns^{c}	<0.01	-4730	3474
P	6	Site	0.45(0.012)**	0.20(0.011)**	-0.04(0.002)**	-0.08(0.012)**	0.01(0.003)**	-0.02(0.021)ns^{c}	<0.01	-3931	4273
NB	6	Area^{1}	0.83(0.066)**	0.86(0.097)**	-0.04(0.008)**	-0.17(0.068)*	1.38(0.214)**	0.05(0.146)ns^{c}	<0.01	-8200	4
NB	**5**	**Area^{1}**	**0.83(0.066)****	**0.86(0.096)****	**-0.04(0.008)****	**-0.15(0.060)***	**1.38(0.213)****	**-**	**<0.01**	**-8204**	**0**
NB	6	Site	0.73(0.061)**	0.48(0.08)**	-0.06(0.008)**	-0.24(0.073)**	0.02(0.012)ns^{b}	0.01(0.150)ns^{c}	<0.01	-8159	45
NB	5	Site	0.73(0.060)**	0.48(0.08)**	-0.06(0.008)**	-0.23(0.065)**	0.02(0.012)ns^{b}	-	<0.01	-8161	43
NB	4	na	0.73(0.061)**	0.51(0.079)**	-0.06(0.008)**	-0.21(0.063)**	-	-	<0.01	-8161	43
NB	3	na	0.73(0.061)**	0.56(0.08)**	-0.047(0.007)**	-	-	-	<0.01	-8152	52
NB	2	na	0.76(0.067)**	0.80(0.083)**	-	-	-	-	<0.01	-8102	102
NB	1	na	0.75(0.057)**	-	-	-	-	-	<0.01	-7993	211
NB	0	na	-	-	-	-	-	-	<0.01	-7754	450

Note: The negative binomial was the most appropriate data distribution based upon the significant LR test (X^2 test statistic = 8,699, df = 1, $p<0.01$; reject H_o: k=0) and the low AIC values.

Table 2.7 Logistic regression results for presence/absence of *Moerisia* for (a) the full two year data set (ATP = All Time Periods; n = 864 samples), (b) Season 1 (February to September; n = 576) and (c) Season 2 (September to January; n = 360). Column labels, model details and data subscripts are as described in Table 2.1

a. *Moerisia* - All Data (ATP)

No. of terms	Spatial Var.	Sal	Temp	Turb	Depth	DO	Site/Area	*p*	AIC	ΔAIC
6	Area^{1}	0.67(0.079)**	0.48(0.050)**	-0.03(0.006)**	-0.09(0.057)ns^{a}	-0.13(0.095)ns^{b}	0.77(0.170)**	<0.01	470	0
5	**Area^{1}**	**0.66(0.076)****	**0.48(0.049)****	**-0.02(0.006)****	**-0.12(0.055)ns***	**-**	**0.76(0.168)****	**<0.01**	**470**	**0**
6	Site	0.43(0.053)**	0.42(0.043)**	-0.03(0.006)**	-0.08(0.056)ns^{b}	-0.12(0.092)ns^{b}	0.01(0.011)ns^{c}	<0.01	492	22
5	na	0.43(0.052)**	0.43(0.043)**	-0.03(0.006)**	-0.07(0.056)ns^{b}	-0.11(0.092)ns^{b}	-	<0.01	490	20
4	na	0.43(0.052)**	0.43(0.042)**	-0.03(0.006)**	-0.09(0.053)ns^{a}	-	-	<0.01	490	20
3	na	0.44(0.051)**	0.43(0.042)**	-0.03(0.005)**	-	-	-	<0.01	490	20
2	na	0.54(0.047)**	0.40(0.040)**	-	-	-	-	<0.01	526	56
1	na	0.42(0.035)**	-	-	-	-	-	<0.01	708	238
0	na	-	-	-	-	-	-	<0.01	886	416

b. *Moerisia* - Season 1

No. of terms	Spatial Var.	Sal	Turb	Temp	DO	Depth	Site/Area	*p*	AIC	ΔAIC
6	Area^{1}	0.95(0.116)**	-0.03(0.008)**	0.31(0.093)**	-0.31(0.146)*	-0.07(0.083)ns	0.79(0.224)**	<0.01	260	2
5	**Area^{1}**	**0.96(0.115)****	**-0.03(0.007)****	**0.31(0.093)****	**-0.35(0.139)***	**-**	**0.78(0.223)****	**<0.01**	**258**	**0**
4	Area^{1}	0.89(0.103)**	-0.02(0.007)**	0.35(0.092)**	-	-	0.66(0.207)**	<0.01	264	6
6	Site	0.71(0.084)**	-0.04(0.008)**	0.27(0.078)**	-0.21(0.137)ns^{b}	-0.06(0.082)ns^{c}	-0.01(0.016)ns^{c}	<0.01	274	16
5	na	0.70(0.083)**	-0.04(0.008)**	0.27(0.078)**	-0.21(0.136)ns^{b}	-0.06(0.083)ns^{c}	-	<0.01	272	14
4	na	0.71(0.082)**	-0.03(0.007)**	0.27(0.079)**	-0.25(0.129)ns^{a}	-	-	<0.01	270	12
3	na	0.70(0.080)**	-0.03(0.007)**	0.30(0.078)**	-	-	-	<0.01	272	14
2	na	0.77(0.076)**	-0.04(0.006)**	-	-	-	-	<0.01	290	32
1	na	0.88(0.074)**	-	-	-	-	-	<0.01	328	70
0	na	-	-	-	-	-	-	<0.01	612	354

c. *Moerisia* - Season 2

No. of terms	Spatial Var.	Temp	Site/Area	Depth	Sal	Turb	DO	*p*	AIC	ΔAIC
6	Area^{1}	0.84(0.105)**	0.05(0.321)ns^{c}	-0.10(0.095)ns^{b}	0.11(0.136)ns^{c}	0.01(0.013)ns^{c}	-0.00(0.137)ns^{c}	<0.01	192	8
6	Site	0.85(0.106)**	0.03(0.019)ns^{b}	-0.12(0.095)ns^{b}	0.08(0.083)ns^{c}	0.01(0.013)ns^{c}	-0.02(0.136)ns^{c}	<0.01	188	4
5	Site	0.85(0.105)**	0.03(0.019)ns^{b}	-0.13(0.089)ns^{b}	0.08(0.082)ns^{c}	0.01(0.012)ns^{c}	-	<0.01	186	2
4	Site	0.84(0.104)**	0.03(0.019)ns^{a}	-0.14(0.087)ns^{b}	0.08(0.083)ns^{c}	-	-	<0.01	184	0
3	**Site**	**0.83(0.100)****	**0.04(0.019)ns^{a}**	**-0.15(0.087)ns^{a}**	**-**	**-**	**-**	**<0.01**	**184**	**0**
2	**Site**	**0.82(0.098)****	**0.03(0.019)ns^{a}**	**-**	**-**	**-**	**-**	**<0.01**	**184**	**0**
1	na	0.81(0.096)**	-	-	-	-	-	<0.01	186	2
0	na	-	-	-	-	-	-	<0.01	456	272

Table 2.8 Season 1 (February to September) summary statistics including suitable environmental conditions (5th and 95th percentiles in bold) for *B. virginica*, *M. marginata* and *Moerisia* when medusae were present for (a)salinity, (b) temperature, (c) turbidity, (d) DO = dissolved oxygen, and (e) depth. SD = standard deviation. n = the number of samples with medusae present. Results from the Tukey-Kramer HSD test are indicated as superscripts on the mean value. Species means sharing a letter are not statistically different. The absence of superscripts indicates no means were statistically different.

Variable	**Estimate**	***B. virginica*** **(n=35)**	***M. marginata*** **(n=160)**	***Moerisia*** **(n=128)**
Temperature (°C)	**Mean (SD)**	21.3(1.0)	21.4(1.1)	21.2(0.9)
	Minimum	19.3	18.9	18.9
	5th	***19.4***	***19.4***	***19.5***
	10th	19.6	19.8	19.8
	Median	21.5	21.6	21.4
	90th	22.5	22.6	22.4
	95th	***22.8***	***22.8***	***22.7***
	Maximum	22.9	25	23.3
Salinity (‰)	**Mean (SD)**	7.4(1.5)^{a}	5.2(2.01)^{b}	5.8(2.0)^{c}
	Minimum	***5.1***	***1***	***1.5***
	5th	***5.6***	***2.3***	***2.8***
	10th	5.7	2.6	3.5
	Median	7.3	5.2	5.6
	90th	9.7	8	8.5
	95th	***10.3***	***8.5***	***9.9***
	Maximum	11.3	11.3	11.4
Turbidity (NTU)	**Mean (SD)**	38.1(15.4)^{a}	47.7(23.2)^{b}	44.6(20.9)^{ab}
	Minimum	12.3	12.3	12.3
	5th	***17.1***	***19.9***	***18.9***
	10th	21.2	23.6	22.8
	Median	35.5	45.2	41.1
	90th	64.2	70.3	68.5
	95th	***68.1***	***85.7***	***86.9***
	Maximum	68.4	182	121.3
DO (mg·lO$_2^{-1}$)	**Mean (SD)**	6.8(0.7)	6.7(0.9)	6.5(1.0)
	Minimum	4.3	4.3	3.6
	5th	***5.4***	***4.9***	***4.6***
	10th	5.8	5.5	5.1
	Median	6.9	6.8	6.7
	90th	7.5	7.9	7.7
	95th	***7.7***	***8.1***	***7.8***
	Maximum	7.7	8.9	8.7
Depth (m)	**Mean (SD)**	4.1(2.4)	3.8(2.4)	3.8(2.5)
	Minimum	1	0.8	0.8
	5th	***1.1***	***1.1***	***1.1***
	10th	1.4	1.3	1.3
	Median	4	3	2.9
	90th	7.9	6.6	6.6
	95th	***9.3***	***8.2***	***8.3***
	Maximum	9.9	16.8	16.8

Table 2.9 Season 2 (September to January) summary statistics including suitable environmental conditions (5th and 95th percentiles in bold) for *B. virginica*, *M. marginata* and *Moerisia* when medusae were present for (a)salinity, (b) temperature, (c) turbidity, (d) DO = dissolved oxygen, and (e) depth. SD = standard deviation. n = the number of samples with medusae present. Results from the Tukey-Kramer HSD test are indicated as superscripts on the mean value. Species means sharing a letter are not statistically different. The absence of superscripts indicates no means were statistically different.

Variable	**Estimate**	***B. virginica*** **(n=58)**	***M. marginata*** **(n=150)**	***Moerisia*** **(n=117)**
Temperature (°C)	**Mean (SD)**	19(2.1)^{a}	18.6(2.5)^{a}	19.4(2)^{b}
	Minimum	14.6	13	14.9
	5th	***14.8***	***13.8***	***15.7***
	10th	16	15	16.7
	Median	18.7	18.6	19.6
	90th	21.7	21.7	21.7
	95th	***22***	***21.9***	***22***
	Maximum	22.9	22.9	22.9
Salinity (‰)	**Mean (SD)**	7.7(1.4)^{a}	5.8(2)^{b}	6.1(1.8)^{b}
	Minimum	5	1	2
	5th	***5.6***	***2.6***	***3.1***
	10th	6	3.1	3.6
	Median	7.6	6	6.2
	90th	9.6	8.3	8.3
	95th	***10.2***	***9.1***	***9.3***
	Maximum	11.3	11.3	11.3
Turbidity (NTU)	**Mean (SD)**	39.7(15.1)	39.2(15.8)	39.9(14.6)
	Minimum	18.5	13.1	16.1
	5th	***20.1***	***17.5***	***20.9***
	10th	22.5	21.3	23.4
	Median	37.5	35.9	36.5
	90th	63.7	60.8	62.6
	95th	***71.3***	***71.3***	***71.3***
	Maximum	71.3	97.4	81.6
DO (mg·lO$_2^{-1}$)	**Mean (SD)**	7(0.7)^{a}	6.6(1.1)^{ab}	6.6(1.1)^{b}
	Minimum	4.3	2.8	0.9
	5th	***5.4***	***4.4***	***4.6***
	10th	6.2	5.4	5.4
	Median	7	6.8	6.7
	90th	7.7	7.8	7.7
	95th	***8***	***8.1***	***7.8***
	Maximum	9	10.1	8.3
Depth (m)	**Mean (SD)**	4.1(2.5)	4.0(2.2)	3.8(2.2)
	Minimum	0.9	1	1
	5th	***1.1***	***1.3***	***1.1***
	10th	1.5	1.5	1.4
	Median	3.3	3.4	3
	90th	8.3	6.9	6.6
	95th	***9.3***	***8.1***	***8.2***
	Maximum	9.9	11.8	11.8

2.8 FIGURES

2.1. The San Francisco Bay, California and the upper San Francisco Estuary. The map of the upper San Francisco Estuary provides detail on the channels of Suisun Marsh including the 36 sites sampled by plankton tow from February 2004 to January 2006 Suisun Marsh Salinity Control Gates = SMSCG are located in Montezuma Slough. Inflow, a measure of freshwater flow entering the middle SFE is measured at Chipps Island near the entrance to Suisun Marsh (Montezuma Slough).

2.2. Salinity range for the 36 sites and four areas sampled in Suisun Marsh from July to November in sample years 1 and 2 (2004 and 2005). Data are illustrated by Box Plots which display the summary statistics including the, Median (solid bar in box), 25th and 75th quartiles (top and bottom edges of box) the 10th and 90th percentiles (edge of whiskers), 5th and 95th percentiles (circles). Sampling areas are indicated by the color of the shaded box with (A1) black; (A2) light grey; (A3) white; and (A4) dark grey.

2.3. Average monthly catch in year 1 (Feb 2004 to Jan 2005) and year 2 (Feb 2005 to Jan 2006) for (a) *B. virginica*, (b) *M. marginata* and (c) *Moerisia* medusae at the 36 plankton sampling sites in and adjacent to Suisun Marsh. When medusae were present, but only in low abundance, their presence was indicated with the symbol P and the year of their presence was indicated.

2.4. Average monthly catch of (a) *B. virginica*, (b) *M. marginata*, (c) *Moerisia* medusae by area. Area 1 = southwest Suisun Marsh; Area 2 = central; Area 3 = northwest; Area 4 = southeast. Year 1 - Feb 2004 to Jan 2005 and year 2 - Feb 2005 to Jan 2006.

2.5. Average monthly (a) inflow (measured at Chipps Island), (b) salinity, (c) temperature, (d) turbidity, (e) dissolved oxygen for year 1 (Feb 2004 to Jan 2005) and year 2 (Feb 2005 to Jan 2006). For b - e average monthly values are for all 36 plankton tow sites.

2.6. Average monthly (a) temperature, (b) DO = dissolved oxygen, (c) salinity, and (d) turbidity by area. Area 1 = southwest Suisun Marsh; Area 2 = central; Area 3 = northwest; Area 4 = southeast. Year 1 - Feb 2004 to Jan 2005 and Year 2 -Feb 2005 to Jan 2006).

2.7. Season 1 (February to September for Year 1 and Year 2) environmental relationships for all data (All) and when only medusae (*Black* = *B. virginica*, *Maeotias* = *M. marginata* and *Moerisia* = *Moerisia sp.*) were present for (a) salinity, (b) temperature, (c) turbidity, (d) DO = dissolved oxygen, and (e) depth. Data are illustrated by Box Plots which display the summary statistics including the mean (dotted bar), median (solid bar in box), 25th and 75th quartiles (top and bottom edges of box) the 10th and 90th percentiles (edge of whiskers), 5th and 95th percentiles (squares) and the outlier points (solid circles). Species boxplots sharing a letter were not found to be statistically different using the Tukey-Kramer HSD test. The absence of letters indicates no means were statistically different.

2.8. Season 2 (September to January for Year 1 and Year 2) environmental relationships for all data (All) and when only medusae (*Black* = *B. virginica*, *Maeotias* = *M. marginata* and *Moerisia* = *Moerisia sp.*) were present for (a) salinity, (b) temperature, (c) turbidity, (d) DO = dissolved oxygen, and (e) depth. Data are illustrated by Box Plots, which display the summary statistics including the mean (dotted bar), median (solid bar in box), 25th and 75th quartiles (top and bottom edges of box) the 10th and 90th percentiles (edge of whiskers), 5th and 95th percentiles (squares) and the outlier points (solid circles). Species boxplots sharing a letter were not found to be statistically different using the Tukey-Kramer HSD test. The absence of letters indicates no means were statistically different.

2.9. Medusae (abundance) response to temperature in all months. Data are temperature bin (1°C) averages. Lines are spline-smoothed.

2.10. Medusae (abundance) response to salinity in all months. Data are salinity bin (0.5 ‰) averages. Lines are spline-smoothed.

2.11. Limiting condition plots by year for (a) *B. virginica*, (b) *M. marginata*, (c) *Moerisia*. Solid bars indicate that for the listed area, the average values for turbidity (*B. virginica* only), salinity and temperature (temp) were within the estimated suitable range (5th to 95th percentiles) within the specific season. Season 1 = February to September and Season 2 = September to January. Occurrence = the presence of medusae in the specified area and month and is indicated by the following symbols representing the % site occurrence at four levels: ⊙ = 0-25%, ◉ = 25-50%, ◙ = 50-75% and ● = 75-100%. A1 = Area 1, A2 = Area 2, A3 = Area 3 and A4 = Area 4.

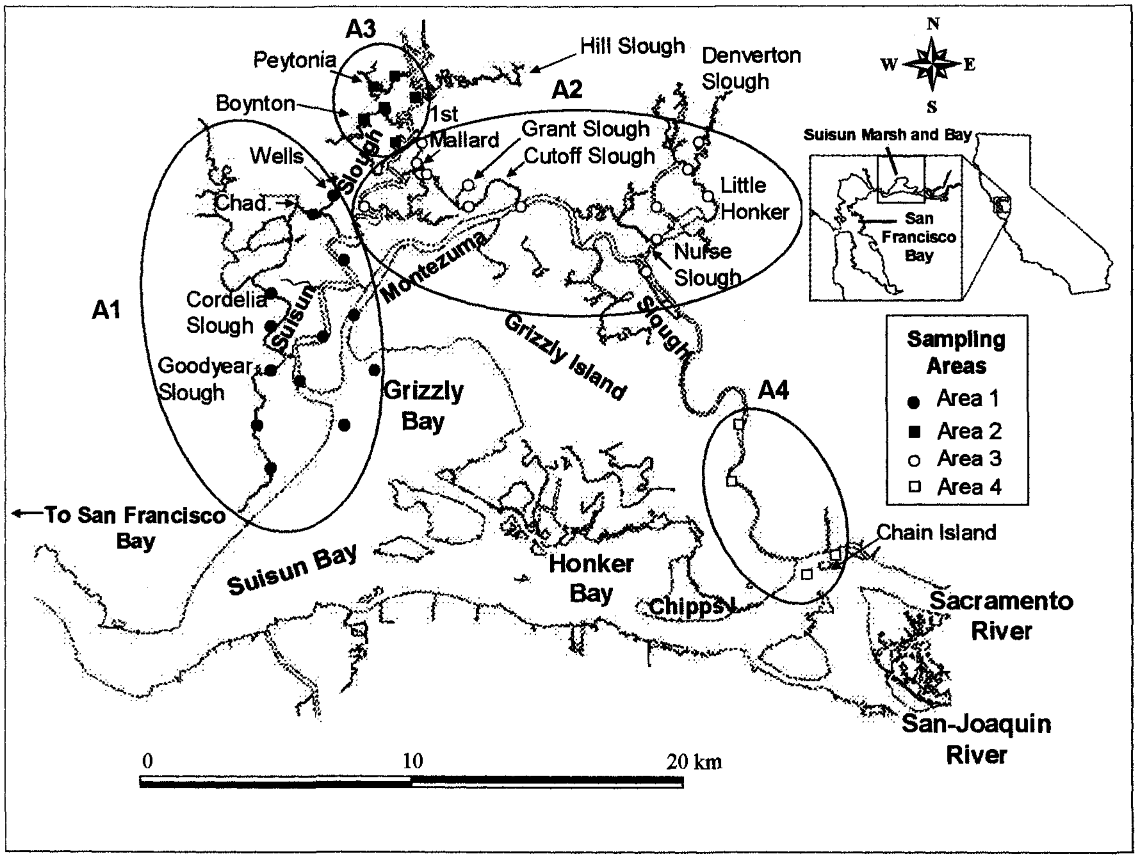


Figure 2.1

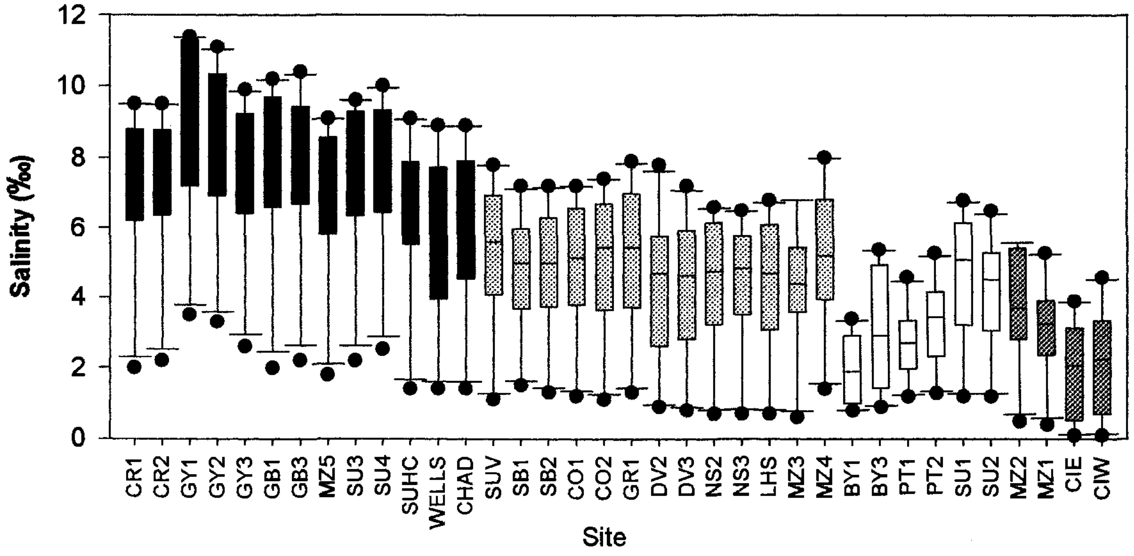


Figure 2.2

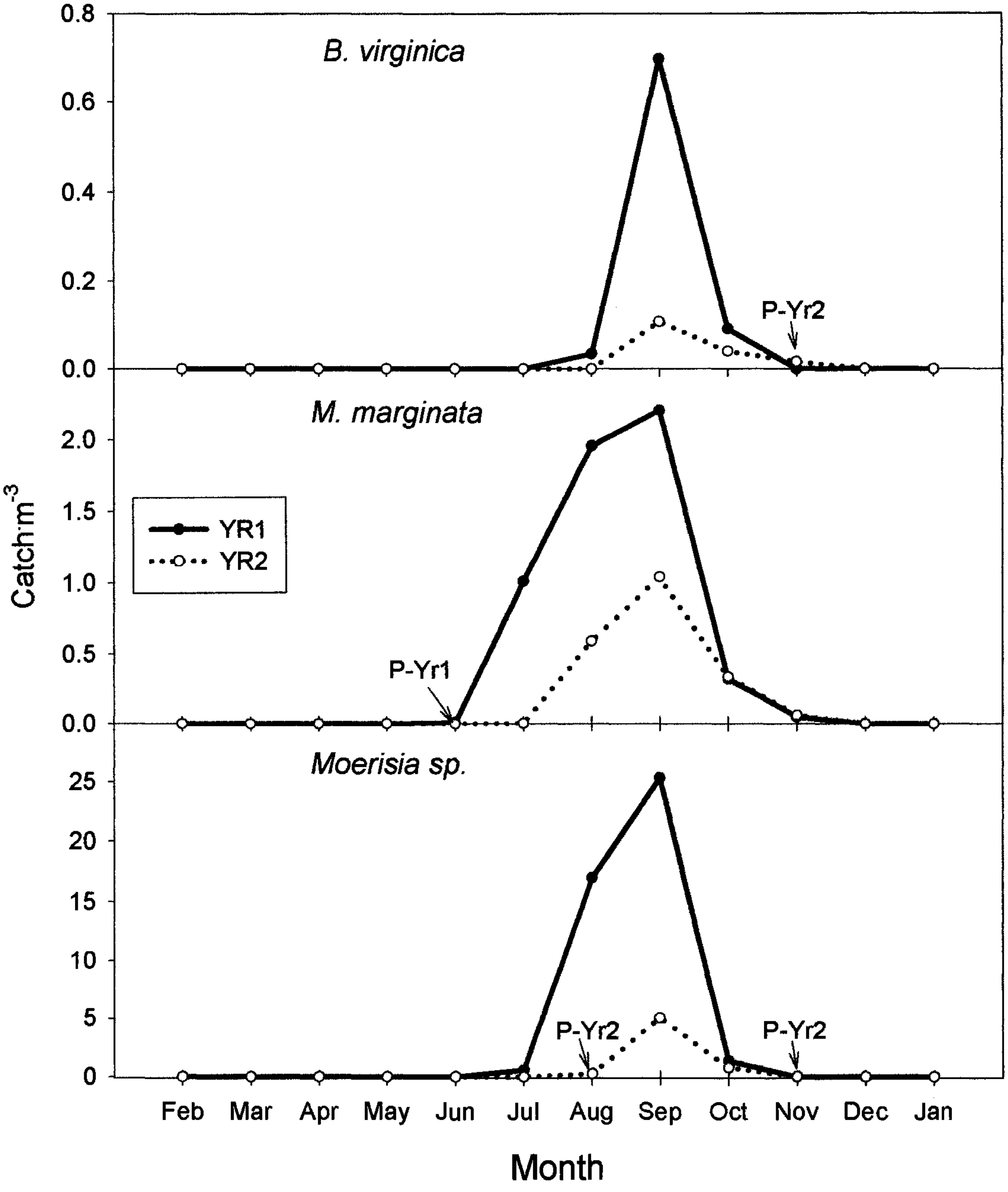
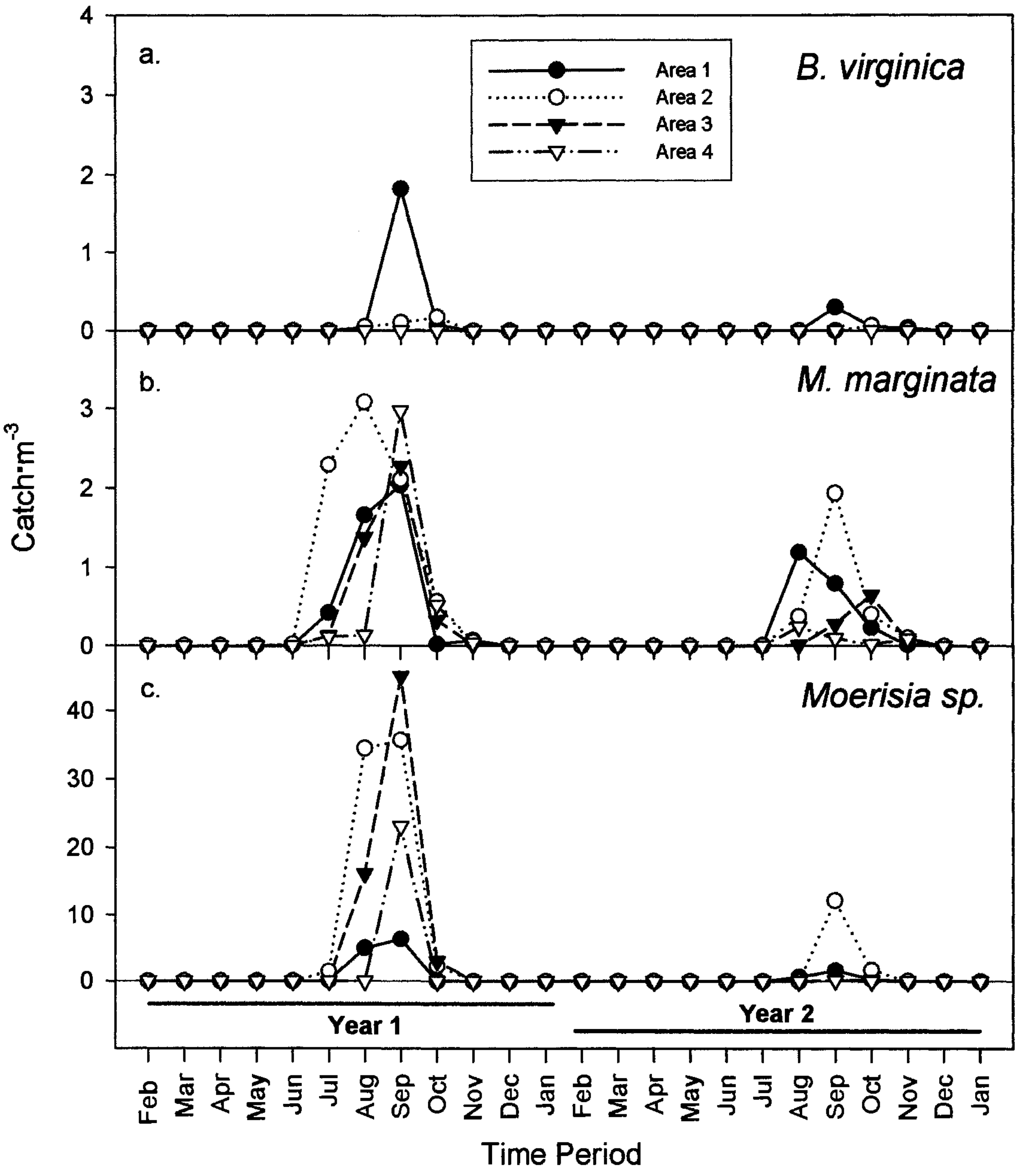

B. virginica
M. marginata
Moerisia sp.
Catch·m-3
0.8
0.6
0.4
0.2
0.0
2.0
1.5
1.0
0.5
0.0
25
20
15
10
5
0
YR1
YR2
P-Yr2
P-Yr1
P-Yr2
P-Yr2
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month

Figure 2.3



a.
B. virginica
b.
M. marginata
c.
Moerisia sp.
Area 1
Area 2
Area 3
Area 4
Catch·m^{-3}
0
1
2
3
4
10
20
30
40
Year 1
Year 2
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Time Period

Figure 2.4

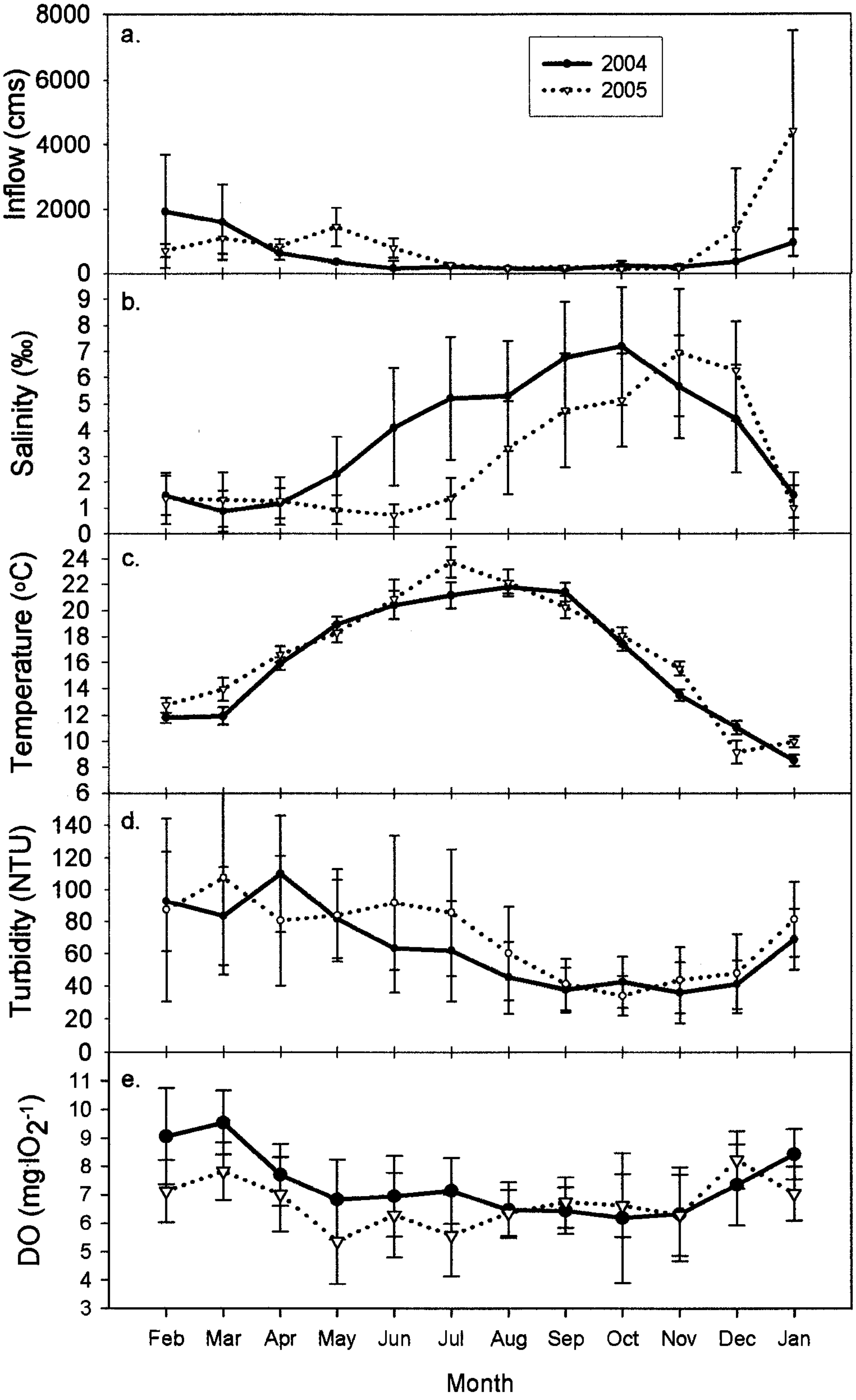

a.
2004
2005
Inflow (cms)
8000
6000
4000
2000
0
b.
Salinity (‰)
9
8
7
6
5
4
3
2
1
0
c.
Temperature (°C)
24
22
20
18
16
14
12
10
8
6
d.
Turbidity (NTU)
140
120
100
80
60
40
20
0
e.
DO (mg·lO2-1)
11
10
9
8
7
6
5
4
3
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month

Figure 2.5

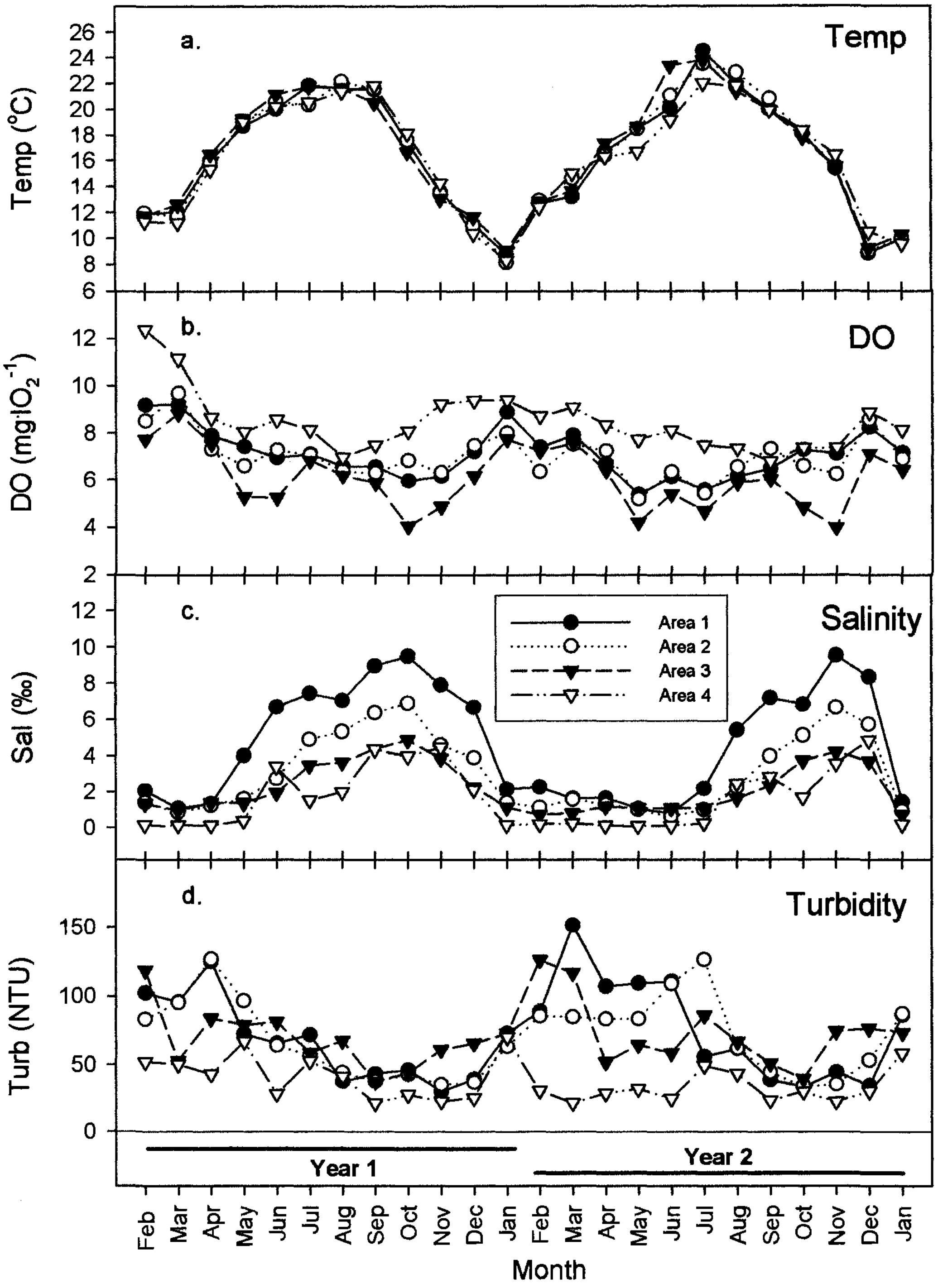

a.
Temp
Temp (°C)
26
24
22
20
18
16
14
12
10
8
6
b.
DO
DO (mg·lO$_2^{-1}$)
12
10
8
6
4
2
c.
Salinity
Sal (‰)
12
10
8
6
4
2
0
Area 1
Area 2
Area 3
Area 4
d.
Turbidity
Turb (NTU)
150
100
50
0
Year 1
Year 2
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month

Figure 2.6

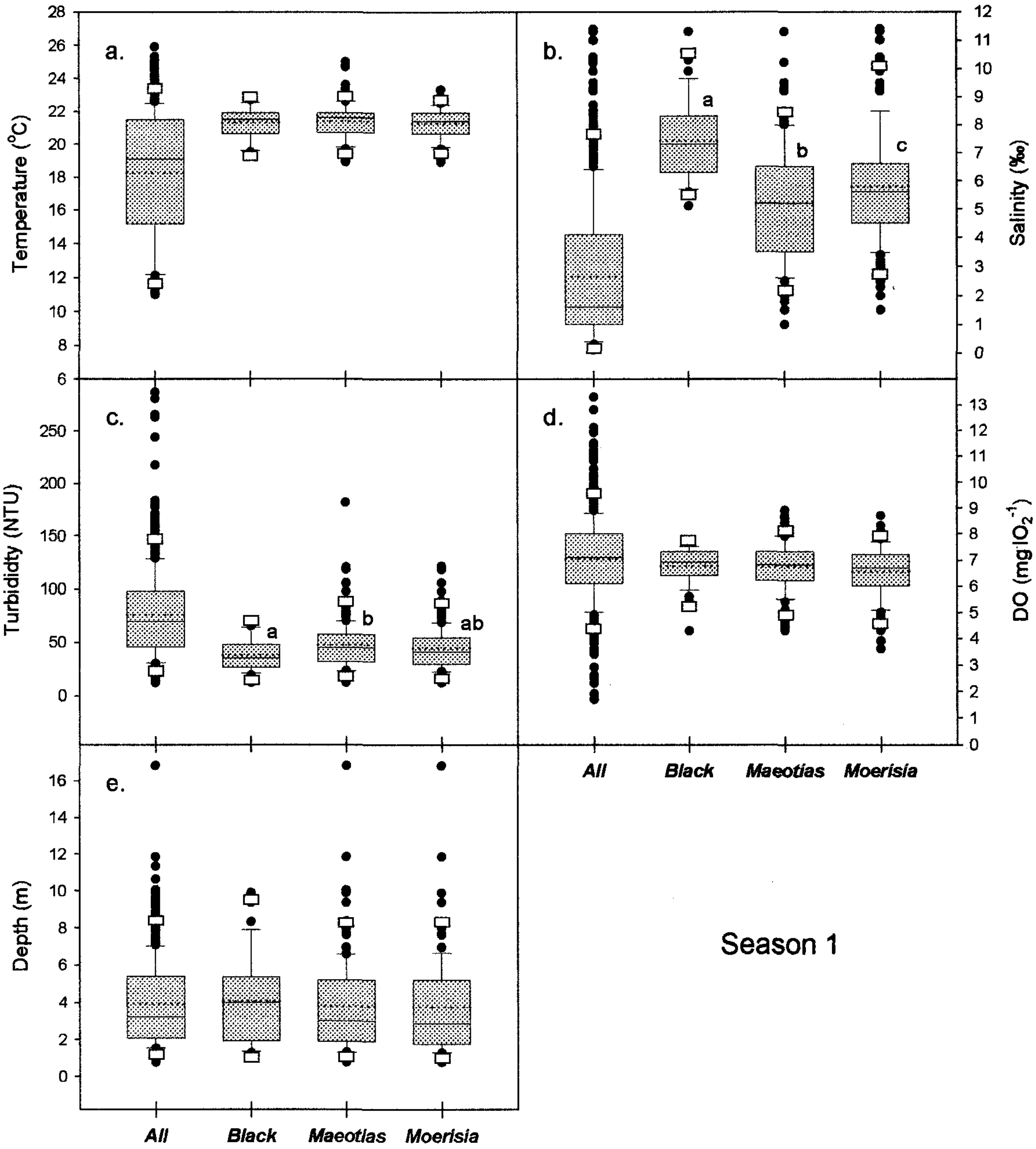

a.
b.
c.
d.
e.
Temperature (°C)
Salinity (‰)
Turbididty (NTU)
DO (mg·lO$_2^{-1}$)
Depth (m)
28
26
24
22
20
18
16
14
12
10
8
6
12
11
10
9
8
7
6
5
4
3
2
1
0
250
200
150
100
50
0
13
12
11
10
9
8
7
6
5
4
3
2
1
0
16
14
12
10
8
6
4
2
0
a
b
c
a
b
ab
All
Black
Maeotias
Moerisia
All
Black
Maeotias
Moerisia
Season 1

Figure 2.7

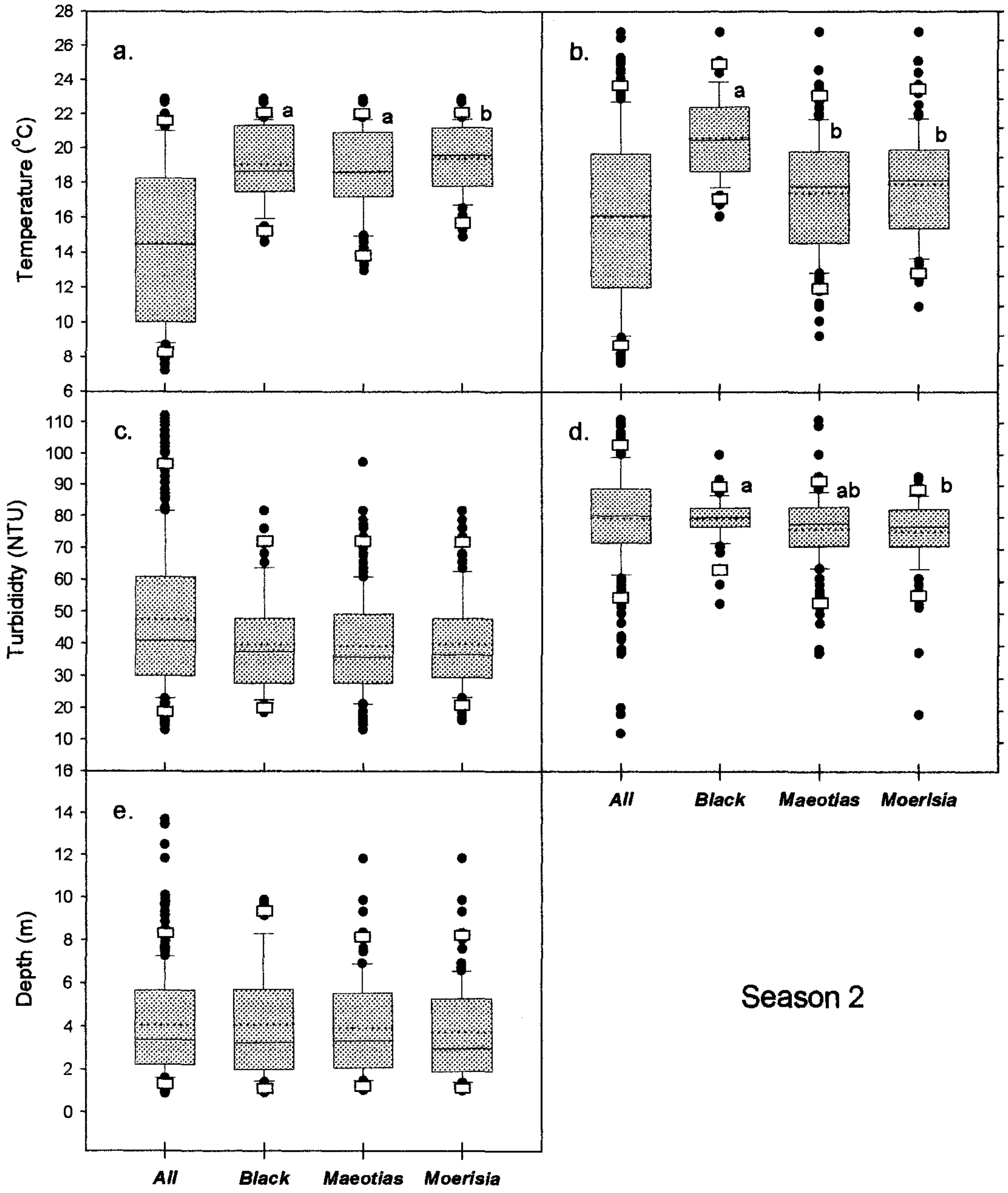

a.
b.
c.
d.
e.
Temperature (°C)
Salinity (‰)
Turbididty (NTU)
DO (mg·lO2-1)
Depth (m)
a
a
b
a
b
b
a
ab
b
All
Black
Maeotias
Moerisia
Season 2

Figure 2.8

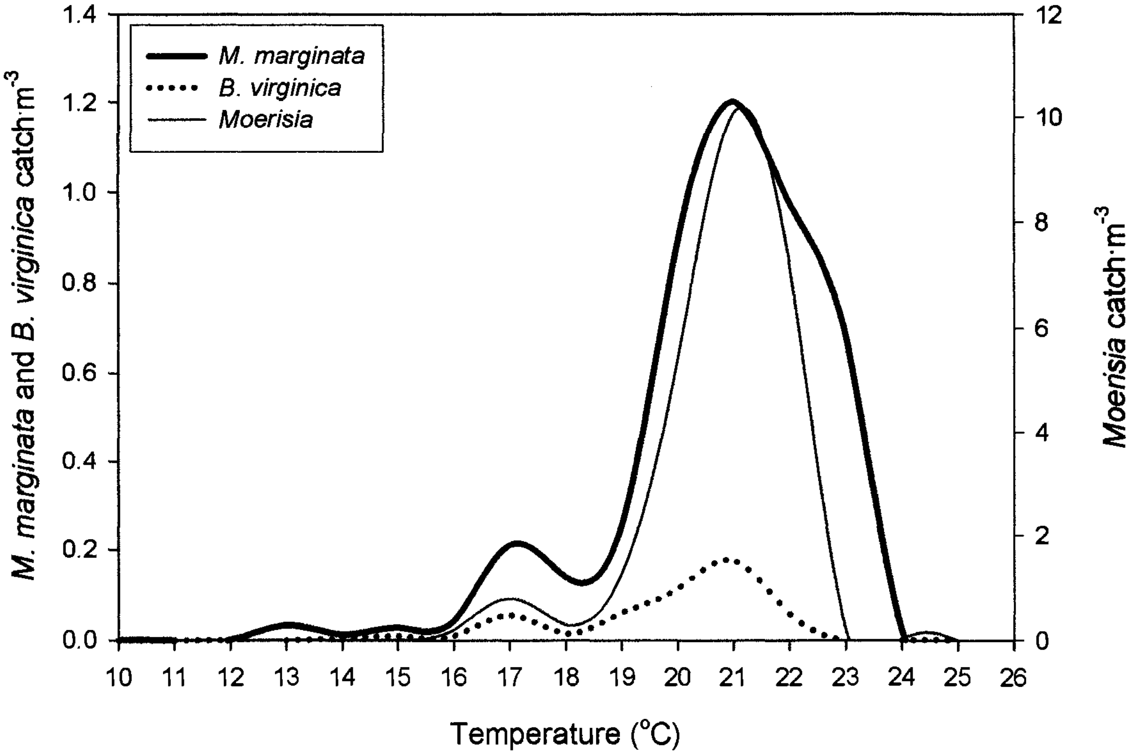

M. marginata
B. virginica
Moerisia
M. marginata and B. virginica catch·m-3
Moerisia catch·m-3
Temperature (°C)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
12
10
8
6
4
2
0
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

Figure 2.9

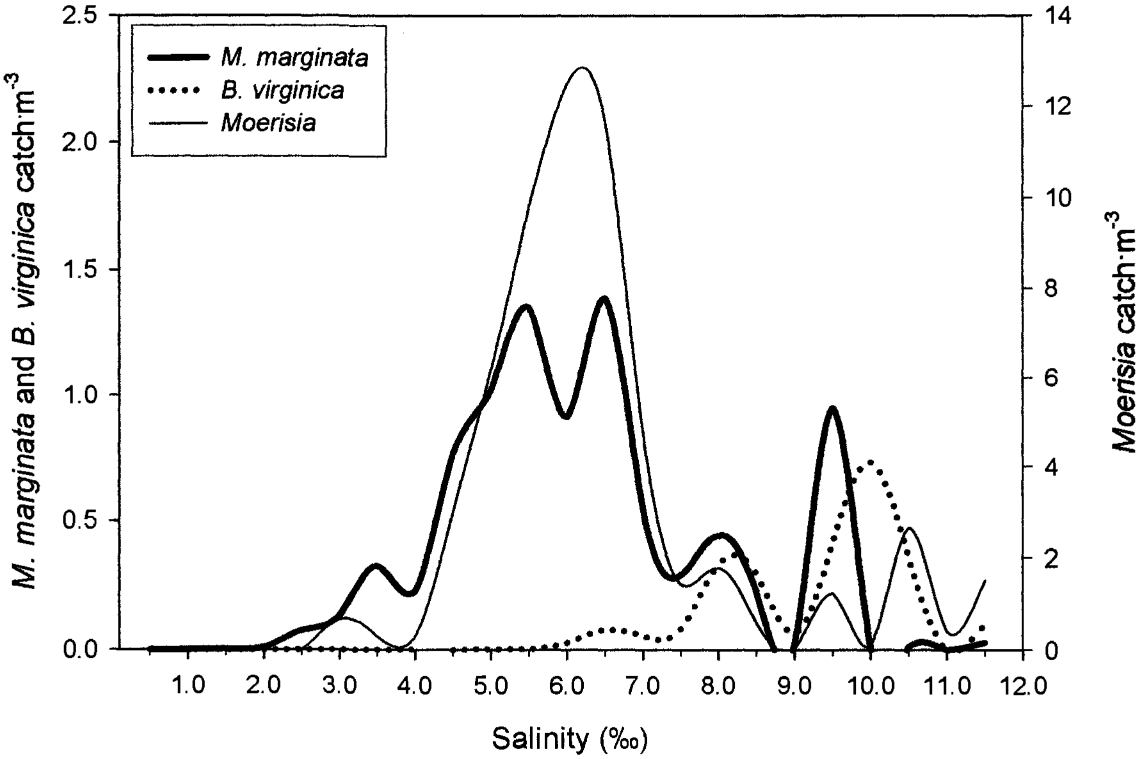
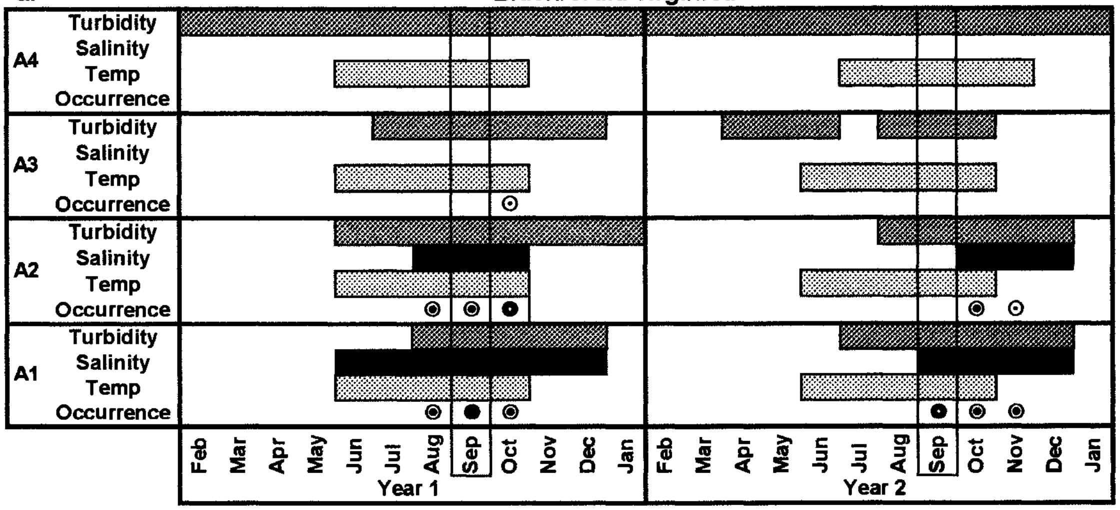
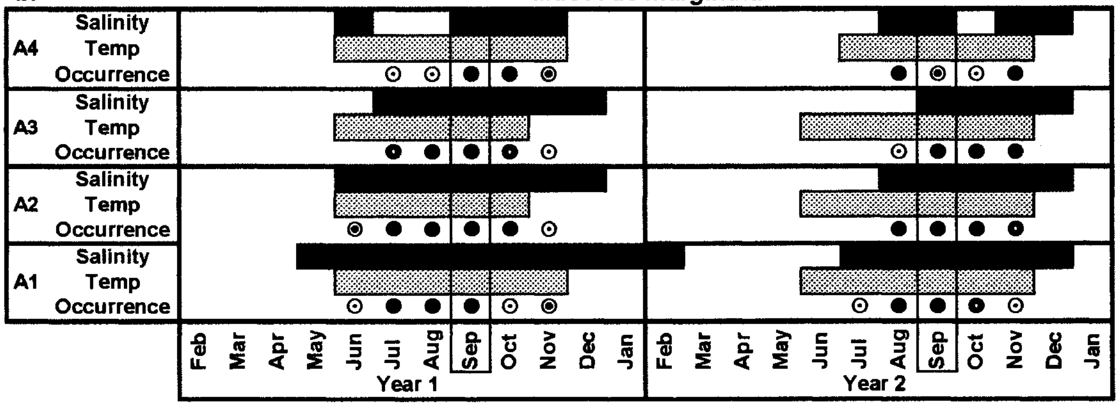

M. marginata and B. virginica catch·m⁻³
Moerisia catch·m⁻³
Salinity (‰)
M. marginata
B. virginica
Moerisia
0.0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
12
14
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0

Figure 2.10

a. *Blackfordia virginica*



b. *Maeotias marginata*



c. *Moerisia sp.*

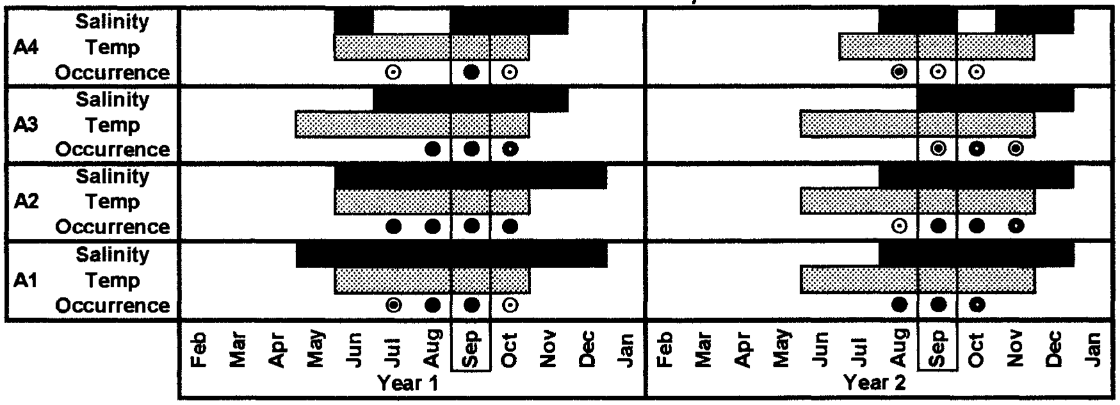


Figure 2.11

CHAPTER 3

The Importance of Shallow Water Habitat for Striped Bass Young-of-Year in the San Francisco Estuary

3.1 INTRODUCTION

Estuaries are extensively used for rearing by early life stages of many fish species (Boesch and Turner 1984; McIvor and Odum 1988; Nemerson and Able 2004; Hampel et al. 2005). Ecological suitability for different life stages, however, can vary considerably along an estuary's length, given the strong physical and chemical gradients that result in differential prey availability and restricted fish distributions (Jassby et al. 1995; North and Houde 2001 and 2003; Kimmerer 2004; Feyrer et al. 2007). At a local scale, fish abundance is influenced by the variety and complexity of physical habitats (Rountree and Able 2007). Physical habitat complexity such as off-channel habitats, instream structure, and depth variability can positively affect fishes by providing refuges from predation (Crowder and Cooper 1982; McIvor and Odum 1988; Ruiz et al. 1993; Beukers and Jones 1997; Paterson and Whitfield 2000) and by increasing prey availability (Boesch and Turner 1984; McIvor and Odum 1988; Hampel et al. 2005).

Although estuaries provide many benefits to early life stages of fishes, human-caused perturbations often make them less suitable for rearing (Nichols et al. 1986; Caddy 1993; Cohen and Carlton 1998; Dahl 2000; Kennish 2002; Lotz et al. 2006). In the case of the San Francisco Estuary (SFE), there has been a significant disruption of the pelagic (open water) food web as a result of numerous anthropogenic impacts (e.g. species introductions, habitat loss, excess nutrients), which have contributed to decreased primary production (Nichols et al. 1986; Alpine and Cloern 1992; Cohen and Carlton 1998; Lopez et al. 2006; Dugdale et al. 2007), reduced pelagic prey abundances

(Orsi and Mecum 1996; Kimmerer and Orsi 1996; Kimmerer et al. 2000), and a significant reduction in abundance of pelagic fishes (Kimmerer 2006; Sommer et al. 2007).

The disruption of the pelagic food web has had a particularly large and negative affect on the juvenile stages of striped bass *Morone saxatilis*, an extensively monitored and managed sport fish first introduced into the SFE in 1879 (Dill and Cardone 1997). Striped bass juveniles have declined significantly in abundance in the SFE over the last three decades with notable step reductions in abundance occurring in the early 1970s, middle 1980s, and from 2000 to 2005 (Kimmerer et al. 2001; Kimmerer 2004; Sommer et al. 2007; Feyrer et al. 2007). The decline in striped bass young-of-year (YOY) has been attributed in large part to a decline in carrying capacity and increased density dependence resulting from prey limitation (Kimmerer et al. 2000), although other factors including declining environmental quality, reduced egg production (low adult returns), contaminants, altered river flow and entrainment at numerous water diversions have also negatively affected the SFE population (Stevens et al. 1985; Bennett and Moyle 1996; Kimmerer 2004; Feyrer et al. 2007). The decline in abundance of striped bass YOY is similar to declines in other fishes in the SFE that also feed upon pelagic prey and is consistent with observations that the carrying capacity of the pelagic system has declined since the late 1970s (Bennett and Moyle 1996; Kimmerer et al. 2000; Kimmerer 2004 and 2006; Sommer et al. 2007).

Our current understanding of population trends of striped bass YOY in the SFE is the result of seven monitoring studies with their associated long-term data sets (see Kimmerer et al. 2001 and Kimmerer 2004 for general discussion). However, the studies most widely used to monitor striped bass populations have, for the most part, focused their sampling on large rivers, tidal channels and bays, primarily for logistical reasons (i.e., they can be accessed by the large research vessels used). As a result, the status and historical trends of striped bass juveniles using shallow water areas and smaller tidal channels is less well understood. This is a problem because striped bass YOY often preferentially use shallow water habitat (Boynton et al. 1981; Hartman and Brandt 1995; Nemerson and Able 2003) and in general increasingly favor shallow habitats during their first year of life (Robichaud-Leblanc et al. 1998). Shoreward ontogenetic habitat shifts are thought to be due to fishes taking advantage of areas of higher productivity and thus prey availability (Kernehan et al. 1981; Rulifson and Dadswell 1995). Boynton et al. (1981) observed that a greater proportion of fish in near-shore habitats had high feeding success (greater weight of food items per individual) compared to those captured off-shore. Other factors may also contribute to the observed near-shore shifts by striped bass YOY such as avoidance of predators and transport factors (e.g., Robichaud-LeBlanc et al. 1998).

Given that striped bass YOY can preferentially use shallow water habitats (Boynton et al. 1981; Hartman and Brandt 1995) where there is often a high abundance and diversity of prey (McIvor and Odum 1988; Ruiz et al. 1993; Cattrijsse et al. 1997), it is possible that the decline in YOY striped bass in the SFE is less evident in shallow water habitats than observed in deep water areas. In this chapter, I examine striped bass abundance patterns in a brackish tidal marsh in the middle SFE, using a long-term (26 year) otter trawl survey dataset. My primary objective is to examine YOY abundance trends in habitats with different depths to determine if there has been a differential abundance response to changing conditions. I hypothesize that striped bass YOY using shallow waters areas are less affected by the widespread decline in pelagic prey in the SFE, as reflected by their higher abundance.

I specifically investigate depth-based abundance patterns of striped bass YOY in Suisun Marsh, an important estuarine rearing area for many species of fishes (Meng and Matern 2001; Matern et al. 2002). I designed this study to answer the following questions: (1) What are the long-term trends and seasonal patterns in abundance of striped bass YOY and prey species relative to depth? (2) Are prey abundance and environmental parameters important predictors of striped bass YOY abundance? (3) Has a decline in prey abundance affected the seasonal abundance and size of striped bass YOY? The patterns of catch in the tidal channels of Suisun Marsh are compared with results of other studies in the larger channels of the SFE.

3.1.1 Background

Study Area

Suisun Marsh (Figure 3.1) is a large brackish tidal marsh (approximately 34,000 ha or 340 km^2) located in the upper SFE. It is the largest contiguous wetland along the Pacific coast of the western United States. Approximately one-third of the marsh is tidally influenced and the remainder consists primarily of diked wetlands managed to attract waterfowl. Water inputs to the marsh are from a number of sources including tidal inflow from Grizzly Bay through lower Suisun and Montezuma Sloughs, fresh water from the Sacramento River, and fresh water from a number of small local tributaries including Green Valley, Suisun, Ledgewood, Union and Denverton creeks.

Environmental conditions within Suisun Marsh vary considerably depending upon season, slough location and the amount of freshwater entering the system (Matern et al. 2002). Based on an evaluation of data collected since 1980, salinity in Suisun Marsh ranges from zero to near 17 ‰, peaking in the autumn of drought years and declining during periods of high outflow in winter and spring. Summer temperatures typically range from 17 to 29.5 °C and winter temperatures occasionally drop below 5 °C. Secchi depth, a measure of water transparency, ranges from 2 to 75 cm with the lowest levels occurring during periods of high river flows in spring and highest levels during the fall. Dissolved oxygen is usually close to saturation (~7 $mg \cdot l^{-1}$) in the main sloughs where river influence is high, but lower dissolved oxygen levels occur in the more isolated sloughs and upper ends of sloughs, especially in spring and fall when episodic dissolved oxygen sags occur (Chapter 1).

The proximity of Suisun Marsh to the large upper bay system (Grizzly, Suisun, and Honker Bay), its close proximity to the confluence of the Sacramento and San

Joaquin rivers, and its direct connection to numerous local tributaries have all strongly influenced the diversity and abundance of its fishes and invertebrates (see Meng and Matern 2001 and Matern et al. 2002). Suisun Marsh is an important low salinity nursery area for numerous fishes including striped bass YOY (Meng et al. 1994; Meng and Matern 2001; Matern et al. 2002; Feyrer et al. 2003). Large invertebrate species that are abundant in marsh for at least a portion of their life include the native mysids *Neomysis mercedis* and *N. kadiakensis,* the introduced mysid *Hyperacanthomysis longirostris,* the crangonid shrimp *Crangon franciscorum,* and the introduced palaemonid shrimps *Palaemon macrodactylus* and *Exopalaemon modestus.*

Striped bass

Striped bass spawn in spring in rivers and their negatively-buoyant eggs and larvae drift downstream into the SFE. They accumulate just upstream and within the freshwater-saltwater mixing zone at salinities between 0-2 ‰ (Turner and Chadwick 1972; Rutherford et al. 1997; Dege and Brown 2004). Post-larvae and juvenile striped bass continue moving downstream and are found with sub-adults in brackish areas, such as Suisun Marsh. Adults occur throughout the SFE and lower reaches of inflowing rivers and may use the open ocean for at least a portion of their life cycle (Calhoun 1952; Turner and Chadwick 1972; Moyle 2002).

The early season (May to August) abundance and distribution of striped bass YOY in the SFE are strongly affected by river flow (Turner and Chadwick 1972; Stevens 1977; Kimmerer et al. 2000). Extreme high flow events result in displacement of YOY into downstream areas near or below San Pablo Bay (Stevens 1977; Moyle et al. 1986) and low outflow results in a larger percentage of the striped bass population positioned farther upstream, in the Sacramento-San Joaquin Delta (Turner and Chadwick 1972; Chadwick 1964; Dege and Brown 2004).

Striped bass YOY are highly flexible in diet and are known to undergo ontogenetic shifts in feeding (Cooper et al. 1998; Bryant and Arnold 2007). Early stage juveniles < 25 mm fork length (FL) feed primarily on copepods followed by corophiid amphipods, mysids and cladocerans in spring and early summer. As they reach sizes >25 mm FL by summer and fall, they shift their diet to larger invertebrates such as mysids and amphipods. In late fall and winter they increasingly feed upon larger crangonid and palaemonid shrimps and fishes (Heubach et al. 1963; Stevens 1966; Cooper et al. 1998; Feyrer et al. 2003; Bryant and Arnold 2007). The timing and nature of the observed diet shift is strongly influenced by striped bass YOY size and the availability of prey at a given time and location (Heubach et al. 1963; Cooper et al. 1998; Bryant and Arnold 2007).

Despite the observed flexibility in striped bass YOY diet, mysids are their primary prey (by weight) in both the SFE and in Atlantic Coast estuaries (Heubach et al. 1963; Stevens 1966; Boynton et al. 1981; Feyrer et al. 2003; Bryant and Arnold 2007). However, when mysid abundance levels are low, striped bass YOY in both the SFE and Atlantic Coast estuaries shift their feeding to other prey, particularly corophiid and gammarid amphipods and YOY fishes (Heubach et al. 1963; Stevens 1966; Boynton et al. 1981; Gartz 1999; Feyrer et al. 2003). A feeding shift to amphipods suggests a shift of position in the water column as well as in habitat, because amphipods are most abundant in benthic habitats in low velocity, shallow, near-shore areas (Hazel and Kelley 1966), while mysids are found in greatest abundance in open water areas at water depths usually > 5 meters (Turner and Heubach 1966). Habitat specific prey consumption was observed by Boynton et al. (1981) in Chesapeake Bay. In this case, mysids dominated YOY diet in off-shore habitats, but in near-shore habitats a greater diversity of prey was consumed including amphipods, insects, polychaetes, and YOY fishes.

In the SFE, there is evidence of a decline in the carrying capacity for striped bass YOY at an age when juveniles begin to consume greater numbers of mysids and small fishes in the summer to fall months (Kimmerer et al. 2000). Feyrer et al. (2003) documented shifts in the diet of striped bass YOY in Suisun Marsh in years with high and low mysid availability and observed striped bass YOY consumed a greater variety of prey and switched to piscivory at a smaller size (> 80 mm standard length (SL) versus > 120 mm SL) when mysids were in low abundance. Thus the change in availability of mysids in Suisun Marsh, and presumably other brackish areas of the SFE, has had measurable effects on the feeding ecology of striped bass YOY.

3.2 METHODS

The patterns of striped bass YOY abundance and distribution and their relationship to prey abundance and environmental conditions in Suisun Marsh were determined using data from a long term (1980 to 2005) University of California, Davis monitoring program on the fishes and macro invertebrates of Suisun Marsh, Solano County, California. Meng et al. (1994) and Matern et al. (2002) investigated the general relationships of environmental factors to striped bass catch, but the factors contributing to the more recent changes in striped bass abundance within the marsh have not been reported.

3.2.1 Field Methods

Striped bass were captured in monthly otter trawls in 15 sites in 6 sloughs from 1980 to 2005 (Figure 3.1). Study methods are provided in detail in Chapter 1 and Matern et al. (2002). Trawling was conducted using a four-seam otter trawl with a height of 1.5 m, a 4.3 m head-rope and a length of 5.3 m. The trawl mesh of the Suisun Marsh Fish Survey was 35 mm fully stretched, with a 17 mm rough opening and the cod-end was lined with a 6 mm fully stretched and 3 mm rough opening mesh. The trawl was towed during day light hours at approximately 4 km/hr for either 5 or 10 minutes, dependent upon slough size. Small sloughs were sampled for 5 minutes (First Mallard, Cutoff, Peytonia and Goodyear) and large sloughs (Suisun and Montezuma) were sampled for 10 minutes to account for low catch rates of fish. A single site in lower Goodyear Slough was sampled for 10 minutes from 1980 to 1988 and for 5 minutes after 1988.

At the end of each trawl, trawl contents were placed into large containers of water and the fishes and shrimp including mysids, *C. franciscorum* and the palaemonid shrimps *P. macrodactylus* and the more recently introduced (2000) *E. modestus* were identified, enumerated and released at the site of capture. The total catch per trawl of striped bass, *C. franciscorum* and the palaemonid shrimps was converted to catch·minute^{-1} (hereafter referred to as abundance) to adjust for the different trawl durations (5 or 10 minutes). The palaemonid shrimps *P. macrodactylus* and *E. modestus* were treated together because *E. modestus* was not distinguished early in its invasion. Striped bass were also measured to the nearest mm SL prior to release and were later assigned a YOY age classification using monthly length frequency distributions for the first year of life (May to April of the subsequent year). Mysids were pooled into one category and given an abundance ranking: 1 = 1-3 mysids, 2 = 4-50, 3 = 51-200, 4 = 201-500, 5 = >500. The index was necessary because most mysids pass through the trawl and those that remain in the net are difficult to accurately count. Species included in the mysids group were the native *N. mercedis* and *N. kadiakensis* and several introduced species, primarily *H. longirostris* (formerly *Acanthomysis bowmani*), which largely replaced *N. mercedis* after its introduction in 1992 (Modlin and Orsi 1997).

At each site, the water transparency (Secchi depth in centimeters), temperature (°C), salinity (‰), and depth were measured. Salinity and temperature were measured using a Yellow Springs Instruments (YSI) salinity-conductivity-temperature meter (YSI 85) and a YSI 95 salinity-conductivity-temperature-dissolved oxygen meter. Site depth was measured with a Lowrance X85 depth finder beginning in 2001. Site averages were used for all samples prior to 2001, but given the fixed trawl location, depth is unlikely to have changed over the course of the study.

Adult copepod abundances in Suisun Marsh were obtained from two long-term Interagency Ecological Program (IEP) zooplankton monitoring stations in Suisun Slough (CDFG S42) and Montezuma Slough (CDFG 32; Orsi and Mecum 1996). Values used were the site averages for the combined adult calanoid copepods and the cyclopoid *Acanthocyclops sp.*, both important taxa consumed by striped bass YOY in the system (Kimmerer and Orsi 1996; Bryant and Arnold 2007).

3.2.2 Analyses

Question 1: What are the long-term trends and seasonal patterns in abundance of striped bass YOY and prey species relative to depth?

To determine the long-term depth trends in seasonal abundance of striped bass YOY and important prey species, I first divided the data into three groups based upon depth and location in Suisun Marsh (Figure 3.1). The first group consisted of four sites with water depths >4 m with two sites each in upper Suisun Slough (avg. depth = 5.5 m) and upper Montezuma Slough (avg. depth = 6.0 m). The other two groups consisted of sites with water depths < 4 m. The first < 4 m depth group was located in the upstream northern region of Suisun Marsh and included six sites in three sloughs (two sites in each slough) including Peytonia (avg. depth = 2.7 m), Cutoff (avg. depth = 2.0 m), and First Mallard Slough (avg. depth = 2.0 m). The second <4 meter depth group included 5 sites in the southwestern region of Suisun Marsh with 2 sites in lower Suisun Slough (avg. depth = 3.0 m) and three sites in Goodyear Slough (avg. depth = 2.1 m). The sites with depths < 4m were divided to take into account local environmental conditions and prey abundance differences, given that they were separated by a distance of approximately 10 kilometers and at opposite ends of a strong gradient in salinity (Figure 3.1). Spearman rank correlation analyses on YOY abundances indicated that sites within each of the three depth groups were significantly correlated ($p<0.05$) and the strength of the correlations were usually the highest within the employed divisions (unreported analyses).

I then divided the data into seasons to take into account the large seasonal shifts in abundance of striped bass YOY and their prey that occur during their first year of life and to better determine when shifts in abundance have occurred in the system. Average annual catch was calculated for three seasons, each four months in duration, including *Season 1* - May to August (S1), *Season 2* - September to December (S2), and *Season 3* - January to April (S3). The largest pulse of immature stages of striped bass enter the system in the spring and recruit to a size vulnerable to the otter trawl (~20mm standard length) in the May to August time period (S1), thus the observed abundances in S1 provide a useful measure of reproductive success in a given year. Striped bass YOY decline in abundance between S1 and S2 as environmental conditions shift (river flow decreases, salinity increases, temperature decreases) and prey abundance (i.e. mysids) declines (Moyle et al. 1986). Striped bass YOY continue to decline between S2 and S3 as river flow increases, temperatures decrease and salinity and Secchi depth decrease.

I then analyzed the long-term (1980 to 2005) seasonal time trends in average annual abundance of striped bass YOY and prey species including copepods, mysids, *C. franciscorum,* and palaemonid shrimps in each depth group using the nonparametric Kendall's tau trend test (SAS software system; SAS Institute; Kendall and Gibbons, 1990). Kendall's tau trend test is rank based and thus effective for identifying trends when extreme values and skewness are present in the data (Helsel and Hirsch 1992). A non-parametric test was needed because catch was highly variable and extreme abundance values were commonly observed during the late spring and summer months when large numbers of YOY recruit to the otter trawl. The level of significance for the Kendall's tau trend test was set at $p < 0.05$, but a more conservative level of significance ($p < 0.01$) was also reported. I also plotted the log+1 transformed average annual seasonal abundance for striped bass YOY and prey species, so that the long-term trends for each depth group could be visually compared.

To determine if the seasonal patterns in abundance of striped bass YOY and prey species were similar in the three depth groups, Spearman's rank correlation analyses was used on the average annual log+1 seasonal abundance (n = 26 years). The level of significance was set at $p < 0.05$. A rank-based non-parametric test was necessary because of the large variation in abundance, extreme outliers, and skewness of the data.

Question 2: Are prey abundance and environmental parameters important predictors of striped bass YOY abundance?

I used Spearman's rank correlation to determine whether average prey abundance and environmental conditions were correlated with average striped bass YOY abundance in each season and depth group. Prey groups included adult copepods, mysids, *C. franciscorum*, and palaemonid shrimps. The correlation between adult copepods and striped bass YOY was only analyzed for in the deep water sites (i.e. >4 meter depth group), given the similar depths and spatial proximity of the sampling sites (Figure 3.1). Environmental parameters included in the analyses were temperature, salinity and Secchi depth.

I also investigated the correlation between striped bass YOY abundance and the distance in kilometers (absolute value) of the position of the 2 ‰ near-bottom isohaline position from the main opening to Suisun Marsh at the mouths of Suisun and Montezuma Slough from April to June, the time period when striped bass are most vulnerable to the effects of flow (Kimmerer et al. 2000). The location of the 2 ‰ near-bottom isohaline was estimated from X^2, a widely used integrator of flow in the SFE, which is expressed as kilometers (km) from the mouth of the estuary (Jassby et al. 1995; Kimmerer et al. 2000). Striped bass eggs, larvae and post-larvae typically reach their greatest densities within the freshwater-saltwater mixing zone at salinities of 0-2

‰, the position of which is strongly affected by outflow and is well represented by X^2 (Turner and Chadwick 1972; Jassby et al. 1995; Rutherford et al. 1997; Dege and Brown 2004). The main downstream opening to Suisun Marsh was estimated to be at an X^2 position of 70 km, near the upstream edge of Ryer Island (Figure 3.1). The level of significance for the Spearman's rank test was set at $p < 0.05$, but a more conservative level of significance ($p < 0.01$) was also reported. All data were analyzed using SAS systems software (SAS 9.1.3).

Question 3: Has a decline in prey abundance affected the seasonal abundance and size of striped bass YOY?

To determine whether reduced prey availability (i.e. mysids) in Suisun Marsh affected striped bass YOY abundance patterns and size, I first selected two time periods of high and low mysid abundance for comparison (Feyrer et al. 2003) and then analyzed the seasonal striped bass YOY abundance patterns for each time period and depth group. My hypothesis was that striped bass YOY in Suisun Marsh would be food limited during time periods of low mysid availability, thus would undergo more dramatic abundance declines, especially in the deeper habitats where mysids are assumed to be the primary prey species. I used linear regression to examine the relationship between the log (x+1) transformed abundance of striped bass YOY in S1 (May to August) and S2 (September to December) and S2 and S3 (January to April of the following year), to determine if initial densities of striped bass YOY were a significant predictor of abundance in the following season in both the pre-mysid decline and mysid decline time periods. Statistical significance was indicated at $p = 0.05$.

To determine if the decline in mysid abundance affected the size of striped bass YOY, I analyzed for differences in the seasonal mean length between the pre-mysid decline and mysid decline time periods within each depth group and also between depth groups within each time period. I first plotted the data using box plots for visual comparison and analyzed for mean length differences using the Tukey-Kramer HSD multiple comparison procedure for uneven sample sizes using the JMPin statistical software application (JMPin 4.04). Statistical significance was assessed at $p = 0.05$. The Tukey-Kramer method considers all possible pair-wise differences of means simultaneously and controls the significance level for multiple comparisons.

My hypothesis was that striped bass YOY would have a reduced mean length, particularly in the >4m depth group, after their preferred prey (mysids) were no longer readily available. This hypothesis is largely based upon observations by Feyrer et al. (2003) that striped bass was the only fish species in Suisun Marsh that continued to feed on mysids, albeit at a significantly reduced rate (>80% of diet to <40%) after an estuary-wide decline in availability. Thus, I assumed that striped bass YOY would expend additional energy searching for rare but preferred prey, which could result in decreased growth rates and ultimately fish of smaller size.

However, Feyrer et al. (2003) also observed a significant increase in niche breadth of striped bass YOY in Suisun Marsh at low mysid abundance and also provided evidence that striped bass YOY switched to piscivory at a smaller size. It has been observed that YOY fishes that switch to piscivory earlier eventually become larger than those feeding on a non-fish diet and these size differences often carry through to older age classes (Mittelbach and Persson 1998). Thus, an alternative hypothesis was that surviving striped bass YOY would have had faster growth and larger mean length after the decline of mysids, due to a shift in diet that provided greater nutritional value at a reduced cost of foraging (i.e. benthic and epibenthic invertebrates and YOY fishes).

3.3 RESULTS

A total of 48,278 striped bass YOY were captured in 4,358 otter trawls in the 15 sites sampled monthly in Suisun Marsh from 1980 to 2005. A majority of the striped bass YOY were captured in S1 (35,074 individuals) with an approximate 70% reduction in abundance, on average, in each subsequent season (S2 – 10,125 and S3 – 3,078 individuals).

Question 1: What are the long-term trends and seasonal patterns in abundance of striped bass YOY and prey species relative to depth?

Striped bass YOY

Striped bass YOY declined significantly (Kendall's tau, $p<0.05$) in all seasons in the >4 meter depth group (Table 3.1). In contrast, there were no significant trends in abundance in all three seasons in the <4 meter depth group in the upstream northern region of Suisun Marsh and in S1 and S2 in the <4 meter depth group in the downstream southwestern region of Suisun Marsh (Table 3.1). However, there was a significant decline in striped bass YOY abundance in S3 in the downstream southwestern region.

The average annual striped bass YOY abundance patterns revealed that there was considerable variability in catch throughout the 26-year study and some notable changes (Figure 3.2). The largest change was a step like decline in abundance beginning in the early 1990s in the >4 meter depth group, especially in S1 and S2, although notable declines were also evident during the drought years (1986 to 1992) in both S2 and S3. The average annual abundance patterns in the >4 meter depth group were similar to the <4 meter depth groups until the early 1990s, but deviated considerably afterwards when the >4 meter depth group abundances were lower in almost all years.

Striped bass YOY abundance in S1 in the <4m depth groups was the most stable, remaining high except during the drought and in 1998, and 2002 (Figure 3.2a). In S2, striped bass YOY abundances in the <4 meter depth groups were more variable with high abundances observed in the early to middle 1980s, intermittently throughout the drought years, and more consistently from the middle 1990s to the end of the study, with 1998 being a notable exception (Figure 3.2b). In S3, the abundances of striped bass YOY in the <4 meter depth groups declined similarly from high levels in the early 1980s to low levels through the drought (Figure 3.2c). After the drought, there was a general increase in abundance in the upstream <4 meter depth group, particularly from 2001 to 2005, although there were several notable exceptions (1996, 1997, 1999, and 2000). The striped bass YOY abundance in the downstream <4 meter depth group increased similarly with the upstream <4 meter depth group in 1993 and 1995, but then remained at low levels until it increased again from 2002 to 2004.

The seasonal average abundance in the <4 meter depth groups tracked each other closely and were significantly correlated in all three seasons (Spearman's correlation, $p<0.05$), but there was poor correlation between the abundance in the >4m depth group and the <4m meter depth groups, with significant correlations in only 1 of 6 seasonal comparisons (i.e. downstream < 4m depth group in S3; Table 3.2).

Trends in Prey Species

Copepods - There was a significant decline (Kendall's tau, $p<0.05$) in adult copepod abundance in the Suisun Marsh IEP sampling stations in both S2 and S3 and a negative but non-significant trend in S1 (Table 3.1). The average annual abundance patterns indicate that the time periods of greatest copepod decline varied by season (Figure 3.3a-c). In S1, copepods were least abundant in the last 5 years of the study (2001 to 2005), although they were also captured in low abundance in 1987, 1988 and 1994 (Figure 3.3a). There was a step-like decline in copepod abundance in S2 post-1990 and in S3 post-1989, after which copepods remained at relatively low levels of abundance (Figure 3.3b,c).

Mysids - Mysids declined significantly (Kendall's tau, $p<0.05$) from 1980 to 2005 in each season and depth group, with the only exception being the upstream <4 meter depth group in S1 (Table 3.1). There was a step like decline in average mysid rank abundance after the early 1990s in each season (Figure 3.4a-c). The step decline was most pronounced for the >4m depth group, since this group had the highest rank abundance prior to 1992 and the lowest rank abundance afterwards, particularly in S2 and S3. The mysid rank abundances for all depth groups in each season were significantly correlated (Spearman's correlation, $p<0.05$; Table 3.2).

Crangon franciscorum - Trend analyses (Kendall's tau, $p<0.05$) of the average annual seasonal abundance of the crangonid shrimp *C. franciscorum* indicated only one significant trend (decreasing) for the >4 meter depth group in S2 (Table 3.1). The annual average abundance patterns for the >4 meter depth group in S2 revealed that *C. franciscorum* declined from high abundance levels after the middle 1990s to very low abundance levels from 2000 to 2005 (Figure 3.5b). The abundance of *C. franciscorum* in the upstream <4 meter depth group declined similarly in S2 from a peak in 1995 to very low levels from 2001 to 2004, but the abundance pattern for this depth group was more variable, which contributed to the lack of a statistically significant trend. The catch of *C. franciscorum* in the downstream <4 meter depth group was less variable and somewhat higher than the other depth groups, especially after the early 1990s. The annual average catch patterns for all three depth groups were significantly correlated in all seasons (Spearman's rank correlation, $p<0.05$; Table 3.2).

Palaemonid Shrimps - There were no significant declines in average annual seasonal abundance of palaemonid shrimps in Suisun Marsh (Kendall's tau, $p<0.05$; Table 3.2), but this was largely due to the introduction and dramatic increase in abundance of *E. modestus* from 2000 to 2005 (Figure 3.6a-c). Prior to the introduction of *E. modestus* (1980 to 1999), *P. macrodactylus* had declined significantly (Kendall's tau, $p<0.05$) in abundance in all but one depth group and season (S3 in the downstream <4 meter group; Table 3.1). After its introduction, *E. modestus* dominated the catch, making up over 95% of the combined catch. The abundance of palaemonid shrimp after 2000 increased dramatically to levels rarely reached by only *P. macrodactylus,* particularly in S3. There were significant correlations (Spearman's correlation, $p<0.05$) between the average annual abundance of palaemonid shrimp in all three depth groups within each season (Table 3.2)

Question 2: Are prey abundance and environmental parameters important predictors of striped bass YOY abundance?

Striped Bass YOY - Prey Species Correlations

Copepod abundances at the IEP monitoring stations in Suisun Marsh were significantly and positively correlated (Spearman's correlation; $p<0.05$) with striped bass YOY abundance in the >4 meter depth group in S2 and S3 (Table 3.3). Mysids were significantly and positively correlated (Spearman's correlation, $p<0.05$) with striped bass YOY abundance in all three seasons in the >4 meter depth group, but there were no significant correlations in the <4 meter depth groups in any season (Table 3.3). The correlations between *C. franciscorum* and striped bass YOY abundance were mixed (both positive and negative) and were only significantly correlated (Spearman's correlation, $p<0.05$) in the upstream <4 meter depth group in S2 and the downstream < 4m depth group in S3 (Table 3.3). The significant correlations were both negative indicating that higher *C. franciscorum* abundance was associated with lower striped bass YOY abundance. There were positive correlations between palaemonid shrimp and striped bass YOY abundances in all depth groups and seasons, with the positive correlations increasing in strength towards S3 as striped bass YOY increased in size, but only the correlation for the upstream <4 meter depth group in S3 was significant (Spearman's correlation, $p<0.05$; Table 3.3).

Striped Bass YOY - Environmental Parameter Trends and Correlations

Average water temperatures in all depth groups tracked each other well and were similar in S2 and S3, but they were somewhat elevated in the <4 meter depth groups in S1 (Figure 3.7a-c). Average water temperatures were temporally variable with no clear patterns, with the exception of the more stable and somewhat elevated temperatures in S2 beginning in the early 1990s (Figure 3.7b). Average salinities in all depth groups also tracked each other closely, but average salinity levels were highest in nearly all instances in the downstream <4 meter depth group and very similar in the upstream <4 meter and >4 meter depth group (Figure 3.8a-c). Average salinity levels were highest during the drought years (all seasons) from the middle 1980s to the early 1990s, but were also somewhat elevated after 2000 in S1 and S2 (Figure 3.8a,b). Salinity was most stable and low in S3 from the early 1990s to 2005 (Figure 3.8c). Water clarity (as measured by Secchi depth) patterns were again similar for the three depth groups with the >4 meter depth group having the highest water clarity in all three seasons, particularly after the early 1990s (Figure 3.9a-c). Average water clarity was the least variable of the measured environmental parameters, but recent increases were evident in all seasons after the late 1990s, especially in the deep water sites.

There were no significant correlations (Spearman's correlation, $p<0.05$) between striped bass YOY and temperature or salinity and only a single significant correlation (positive) between striped bass YOY and Secchi depth in the upstream < 4m depth group in S2 (Table 3.4). However, there were significant negative correlations (Spearman's correlation; $p<0.05$) between the abundance of striped bass YOY and the average distance of X^2 (April to June) from the downstream opening of Suisun Marsh in both <4 meter depth groups in S1 (Table 3.4). Negative correlations between the April to June X^2 position persisted in S2 and S3 in the <4 meter depth groups, but they were not significant. There was no correlation between position of X^2 and the seasonal abundance of striped bass YOY in the >4 meter depth group.

Question 3: Has a decline in prey abundance affected the seasonal abundance and size of striped bass YOY

A step-like decline in mysid abundance occurred after 1991 in each of the three seasons, although it was most pronounced in the May to August (Season 1) and January to April (Season 3) time periods (Figure 3.4). The step decline in mysid abundance was used to divide the data into two time periods, including a pre-mysid decline (1980 to 1991) and mysid decline (1992 to 2005) time period, for the seasonal abundance relationships and growth comparisons.

Striped Bass YOY Seasonal Abundance Relationships

Season 1 vs. Season 2 - There were only weak linear relationships between the seasonal log abundance of striped bass YOY in both the pre-mysid decline (1980 to 1991) and mysid decline (1992 to 2005) time periods (Figure 3.10a-c). This prevented a comparison of slopes between the two time periods, but several important patterns were still evident. The only significant S1-S2 relationship (simple linear regression; $p<0.05$) was in the upstream <4 meter depth group during the mysid decline time period, in which a positive linear relationship was observed (Figure 3.10a). In that same depth group (US<4m), the pre-mysid decline plot revealed that the following season's (S2) striped bass YOY log abundance was usually higher than that for the mysid decline time period and in two years the striped bass YOY log abundance exceeded the 1:1 line, indicating that the striped bass YOY abundance in S2 was greater than in S1.

The S1-S2 striped bass YOY log abundance plots for the downstream <4 meter depth group were not significant and the data were highly variable in both the pre-mysid decline and mysid decline time periods (Figure 3.10b). In addition, there were five years that had a seasonal striped bass YOY log abundance greater than the 1:1 line (three in the pre–mysid decline time period and two after the mysid decline), indicating there was considerable movement of striped bass YOY in the area.

In the >4m depth group in the pre-mysid decline time period, there was also considerable variability and a lack of a significant linear relationship in the S1-S2 comparison of YOY log abundance (Figure 3.10c). In the mysid decline time period there was low S1 and S2 YOY log abundance in all but one year (1992), resulting in a cluster of data points well below those in the pre-mysid decline time period (Figure 3.10c). In addition to having generally higher YOY log abundance in the pre-mysid decline time period in the >4m depth group, there were five years in which abundances exceeded the 1:1 line.

Season 2 vs. Season 3 - The striped bass YOY S2-S3 log abundance plots for the pre-mysid decline and mysid decline time periods revealed stronger linear patterns (Figure 3.11a-c). However, there was only one pair of significant relationships (simple linear regression; $p<0.05$) in the downstream <4 meter depth group, which again prevented the direct comparison of slopes. In the upstream <4 meter depth group, there was a significant linear relationship for YOY log abundance in only the mysid decline time period (Figure 3.11a). In addition, the S3 YOY log abundance was generally higher in the mysid decline time period than in the pre-mysid decline time period and most of the data points for the mysid decline time period were close to or above the 1:1 line, as was the regression line fitted to those data points. In the downstream <4 meter depth group, both S2-S3 pre-mysid decline and mysid decline relationships for striped bass YOY log abundance were significant (simple linear regression; $p<0.05$) and the slopes were very similar (Figure 3.11b).

The S2- S3 striped bass YOY log abundance plots for the >4m depth group revealed large differences in the pre-mysid decline and mysid decline time periods, although the seasonal relationships were either not significant, as in the pre-mysid decline time period, or were significant, but heavily influenced by a single outlier (1992) in the mysid decline time period (Figure 3.11c). There was very low striped bass YOY log abundance in the mysid decline time period in both S2 and S3, which led to a large cluster of data points near zero with the exception of 1992, which had an average mysid rank abundance more similar to the pre-mysid decline time period (Figure 3.4). The S2 YOY log abundance in the pre-mysid decline time period was much higher than the post mysid decline time period, but was similar and low in both pre-mysid decline and mysid decline time periods in S3.

Growth Changes – There were many significant differences in the striped bass YOY length comparisons (Tukey-Kramer HSD test; $p<0.05$; Figure 3.12a-c). Comparing the S1 mean lengths between the pre-mysid decline and mysid decline time periods within each depth group, revealed that striped bass YOY were significantly larger in the <4 meter depth groups in the mysid decline time period, while the mean length was smaller in the >4 meter depth group in the mysid decline time period (Figure 3.12a). The between depth group comparisons in S1 revealed that in the pre-mysid decline time period, the mean length of striped bass YOY was significantly smaller in the upstream <4 meter depth group than in the downstream <4 meter and >4 meter depth groups, which were both similar and did not differ statistically. In the S1 mysid decline time period, the mean lengths of striped bass YOY in both <4 meter depth groups were similar and significantly larger than the >4 meter depth group.

In the S2 (September to December) comparisons, the mean lengths of striped bass YOY were significantly larger in the mysid decline time period in all depth groups (Figure 3.12b). In the S2 pre-mysid decline time period the mean lengths of striped bass YOY were similar in the <4 meter depth groups and they were both significantly larger than the mean lengths in the >4 meter depth group. In the mysid decline time period, striped bass YOY were significantly larger in the upstream <4 meter depth group than both the downstream <4 meter depth group and the >4 meter depth group, which were more similar and did not differ statistically.

The S3 (January to April) mean lengths were again significantly larger in the mysid decline time period compared to the pre-mysid decline time period for both <4 meter depth groups, but not in the >4 meter depth group (Figure 3.12c). In the S3 pre-mysid decline time period, the mean striped bass YOY lengths were similar in all depth groups and they did not differ statistically. However, in the mysid decline time period all depth groups were statistically different from each other and there was a successive decline in mean lengths in the following order; upstream <4 meter, downstream <4 meter, and >4 meter depth groups (Figure 3.12c).

3.4 DISCUSSION

Question 1: What are the long-term trends and seasonal patterns in abundance of striped bass YOY and prey species relative to depth?

Trends in Striped Bass YOY

The decline in striped bass YOY in the deep water sites, but not in the shallow water sites, in Suisun Marsh indicates that depth-specific conditions are affecting the abundance and or catchability of striped bass. These results are consistent with the initial prediction that local abundance of striped bass YOY would be differentially affected by the decrease in availability of pelagic prey in habitats of differing depth. The significant decline in abundance of striped bass YOY in the deep water sites in Suisun Marsh since the early 1990s is consistent with reported declines in other areas of the SFE (Kimmerer et al. 2004; Feyrer et al. 2007; Sommer et al. 2007), although the decline in Suisun Marsh was somewhat delayed. The lack of significant striped bass YOY abundance changes in the shallow water sites in Suisun Marsh strongly contrast with the trends observed in other areas of the SFE, suggesting that shallow water conditions in Suisun Marsh have remained more favorable for them.

Seasonal Patterns in Striped Bass YOY Abundance

The decline in striped bass YOY in only the deep water sites in late spring and early summer (S1) indicates that there was either increasingly poor survival of striped bass YOY, or there was reduced recruitment and/or reduced movement into Suisun Marsh by larval and post-larval bass. The lack of a consistent decline during S1 in the shallow water (<4 meter) depth groups indicates that recruitment of larval and postlarval bass has not declined. Given close proximity of the deep water sites to the shallow water sites, particularly the upstream sites, the influx of these early stage fishes should have been similar. If this is the case, the S1 decline in abundance of striped bass YOY in deep water sites is likely due to increased mortality or exodus from the region occurring sometime after the immature stages entered Suisun Marsh, but before the end of S1 (August). Although there were no significant S1 time trends in abundance of striped bass YOY in the shallow water depth groups, there were still notable, if temporary, declines, particularly from the middle 1980s to middle 1990s. This was likely due to fewer striped bass spawners and thus reduced egg production throughout the SFE (Kimmerer 2004), as well as the tendency of larval and postlarval bass to remain upstream under low flow conditions (Turner and Chadwick 1972; Chadwick 1964; Dege and Brown 2004).

Striped bass YOY in S2 (September to December) are survivors from S1 and are subjected to more food limited conditions in the fall months, especially after the decline in pelagic prey in the early 1990s (Moyle 1986; Hennessey and Hieb 2007). The significant decline in abundance of striped bass YOY in S2 in the deep water sites (>4 m) is again consistent with declines reported in other areas of the SFE (Feyrer et al. 2007). The lack of a significant decline in abundance of striped bass YOY in S2 in the shallow water sites indicates that conditions in Suisun Marsh have remained suitable for striped bass YOY in most years, although occasional declines were again evident from the middle 1980s through middle 1990s. This was likely due, in large part, to the low recruitment of YOY from S1, although other drought related conditions (i.e. elevated salinity, reduced flow etc.) may also have made conditions more stressful for YOY. The increase in striped bass YOY abundance in S2 in the shallow water sites beginning in the middle to late 1990s, indicates a recovery from the less favorable drought conditions, which again strongly contrasts with the observed low abundance in the deep water sites in Suisun Marsh and the continued decline in other sampled areas of the SFE, especially from 2001 to 2005 (Feyrer et al. 2007; Sommer et al 2007).

The abundance of striped bass YOY in the January to April time period (S3) again shifted downward from S2 levels, likely due in part to increasing mortality, emigration, and a decreasing vulnerability to the otter trawl. Striped bass YOY were least abundant in the deep water sites in S3, which was likely the result of poor recruitment from S2 and low prey availability. The S3 abundance pattern for striped bass YOY in the shallow water sites was similar to S2, as indicated by the significant linear relationships observed in the seasonal comparisons (Figure 3.11). This suggests the S3 abundances of striped bass YOY in the shallow water sites are largely reflecting earlier population constraints in both S1 and S2. The high abundance of striped bass YOY in S3 from 2001 to 2005 in the shallow water sites is consistent with the increased abundance observed in S2, indicating that conditions were suitable for survival and retention of striped bass YOY in the shallow water sites from fall through early spring. These results strongly contrast with the observed declines in the deep water sites in Suisun Marsh and other areas in the SFE (Feyrer et al. 2007; Sommer et al. 2007).

Trends in Prey Species

The significant declines in adult copepods (S2 and S3), mysids (S1 to S3), palaemonid shrimp *P. macrodactylus* (S1 to S3 after 1990), and *C. franciscorum* (S2 in deep water sites after 2000), considerably reduced availability of prey for striped bass YOY. The decline in prey abundance in the shallow water sites was not as extensive as in the deep water sites, but none-the-less resulted in a decline in prey availability. The similar intra-specific abundance patterns of monitored prey species across the sampled depth groups in Suisun Marsh suggests that marsh-wide or estuary-wide abiotic and biotic conditions were of greater importance in determining local prey abundance than local depth-specific conditions. Similar declines in the above mentioned prey species, including calanoid copepods, mysids, and *C. franciscorum,* were observed in sampling areas outside of Suisun Marsh (Hennessy and Hieb 2007; Hieb 2007), which further indicates that estuary wide conditions are contributing to the observed reduction in local prey abundances in Suisun Marsh. It is notable that the introduced mysid *H. longirsotris* is considerably smaller in size than the native *N. mercedis,* thus is less vulnerable to the otter trawl, given the large mesh size (6 mm stretch). However, the step declines in otter trawl catch of mysids are similar to those observed in the IEP macro-zooplankton monitoring survey stations in Suisun Marsh (Figure 3.1), which used a 500µm mesh conical zooplankton net (Appendix A.1). This indicates that the declines in Suisun Marsh were likely not due to size based sampling bias.

The cause of the declines in prey abundance were not investigated in this study, but are likely due to the general deterioration of the SFE pelagic food web beginning with decreased primary productivity as a result of extensive grazing by introduced bivalves (Alpine and Cloern 1992; Cohen and Carlton 1998) and elevated and inhibitory nutrient levels (Dugdale et al. 2007). The declining trend in copepods, mysids and *P. macrodactylus* were likely linked given that each species feeds at a successively higher trophic level (i.e. copepods feed upon phytoplankton; *N. mercedis* feeds heavily on copepods and diatoms and *P. macrodactylus* feeds heavily on mysids; Kost and Knight 1975; Sitts and Knight 1979; Siegfried and Kopache 1980). The S2 decline in *C. franciscorum* after 2000 may also be due in part to poor prey availability, since it also feeds extensively upon mysids and other small invertebrates (Siegfried 1982; Wahl 1985), but Hieb (2007) reported that high river flow during the years of decline (2000 to 2005) had shifted the population to a location farther downstream of Suisun Marsh.

The palaemonid shrimp *E. modestus* was the only monitored prey species to increase in abundance in the latter years of this study, and its high abundance after its introduction in 2000 resulted in the increased availability of relatively large (average length 40 mm) year-round prey for fishes large enough to feed upon them. Similar increases in abundance of *E. modestus* in fresh to brackish water areas outside of Suisun Marsh and upstream of Suisun Bay have also been reported (Hieb 2007). The recent increase in *E. modestus* is unusual in that pelagic copepods and mysids were in low abundance at the time of its population increase, suggesting that it may have a less restrictive and more omnivorous diet than *P. macrodactylus*. No published diet studies have been conducted for *E. modestus* in the SFE, but Weigang (1995) observed that their diet in Taihu Lake in the Yangtze River delta, China, was very diverse, consisting of invertebrates, algae, and aquatic macrophytes. Furthermore, isotopic analyses on two populations of *E. modestus* inhabiting Lake Taihu and Chaohu in China revealed that they derived a majority of their energy from the benthic food web (Xu et al. 2008). Given a diet dominated by benthic prey, *E. modestus* should be less affected by the deteriorating pelagic food web in the SFE, which is consistent with its current high abundance in areas of moderate to low salinity.

Question 2: Are prey abundance and environmental parameters important predictors of striped bass YOY abundance?

Striped Bass YOY Abundance Relationship to Prey Species

The large decline in abundance of striped bass YOY in the deep water sites and the strong positive correlation between abundances of striped bass YOY and prey species including copepods and mysids are consistent with a decline resulting from prey limitation. Because pelagic organisms are the primary prey of striped bass YOY in open water habitats (Boynton et al 1981), their low abundance has likely contributed to reduced striped bass YOY abundance. Low prey availability in the deep water sites could have resulted in increased striped bass YOY mortality, due to starvation, or increased emigration into habitats with greater prey availability, which is consistent with general theories of optimal foraging theory (Werner and Mittelbach 1981; Werner et al. 1983). Deep water habitats also tend to carry an added risk of predation (McIvor and Odum 1988; Ruiz et al. 1993; Paterson and Whitfield 2000), which may make them especially unfavorable at low prey levels.

The lack of a significant relationship between abundances of striped bass YOY and mysids in shallow water sites of Suisun Marsh and the continued moderate to high abundance of YOY in those sites, suggests that YOY in shallow water areas are less dependent upon pelagic prey such as mysids. This conclusion is consistent with striped bass feeding patterns in their native range, where striped bass YOY in near-shore habitats consume far fewer mysids (<20 % of the diet) than YOY feeding in off-shore habitats (40-50% of the diet)(Boynton et al. 1981). Shallow water bass also exhibited greater feeding success in general.

In the shallow water habitats in Suisun Marsh and other areas of the SFE, there is a wide diversity of prey species available to striped bass YOY including many species of benthic (e.g. oligochaetes, polychaetes), epibenthic (e.g. corophiid and gammarid amphipods, cumaceans) and pelagic invertebrates (copepods and mysids), as well as large numbers of YOY fishes (unpublished data: Meng and Matern 1999; Matern et al. 2002). Collectively, the high diversity and abundance of prey in shallow water habitats has likely reduced the overall impact of reduced mysid availability. The single striped bass diet study conducted in Suisun Marsh before and after the significant decline in mysids (Feyrer et al. 2003), revealed that striped bass significantly reduced their consumption of mysids (decrease of >40%), had increased dietary breadth, and shifted to earlier piscivory during the time period of reduced mysid abundance. This is consistent with feeding in near-shore or shallow water areas where prey diversity is the highest (unpublished data); however, no distinction was made among diets of fish collected from different habitats within Suisun Marsh.

Although the timing of the striped bass YOY decline matches that of several important prey species and the abundance patterns of bass and prey are well correlated in the deep water sites in Suisun Marsh, it is difficult to determine whether the observed striped bass YOY-prey relationships are correlative or causative. The lack of direct evidence of food limitation or starvation of striped bass YOY in the SFE (Bennett et al. 1995; Bryant and Arnold 2007) adds to this uncertainty. Although not discussed in their study, Bryant and Arnold (2007) actually do provide evidence of a step-like decline in the percent of striped bass YOY with food in their stomachs in Montezuma Slough in Suisun Marsh (decline of 80% to 60%) from 1987 to the end of their study in 2002 and in Suisun Bay (70% down to 60%) from 1987 to 1997 (Figure 2 in Bryant and Arnold 2007). These results support the hypothesis that reduced prey abundance may be an increasing problem for striped bass YOY in the vicinity of Suisun Bay and in the deeper sloughs in Suisun Marsh (i.e. Suisun and Montezuma Slough).

There is also indication that average prey size of striped bass YOY has been declining during this same time period (1987 to 2002). Bryant and Arnold (2007) observed that copepods were consumed in greater abundance, while fewer amphipods and mysids were consumed, aside from the years 1996, 1997 and 2002 in which abundances of striped bass were low and sample sizes were small. Increased incidence of empty stomachs and feeding upon smaller prey such as copepods instead of larger amphipods and mysids would likely have negative consequences at the population level through slower growth and increased vulnerability to predators (Houde 1987). Growth data for striped bass YOY is limited in the SFE, but a recent unpublished study from samples collected in the bay and river habitats suggests that the end of the year YOY striped bass length has become more variable and has on average increased since the 1970s (K. Hieb, CDFG, personal communication). This is inconsistent with a hypothesis of slower growth during years with reduced prey size, but this may be due in part to size selective mortality and the very low catch of striped bass during this same time period.

The lack of evidence of prey limitation and starvation for striped bass YOY in the SFE is likely due to the difficulty of observing such an event with monitoring surveys that only take monthly samples of the population. In addition, the continuous decline of striped bass (and other pelagic fishes) over the last several decades has likely decreased competition for prey among fish that made it past the constraining life stage. None-the-less, it is well documented that copepods and mysids are important prey for striped bass YOY (Heubach et al. 1963; Feyrer et al. 2003; Bryant and Arnold 2007) and declines in striped bass YOY abundance in the SFE since the 1970s are correlated with reduced prey abundance and hence reduced carrying capacity (Stevens et al. 1985; Kimmerer et al. 2000; Kimmerer 2004). Further reduction in carrying capacity could become a serious problem in the SFE, given that by all measures it is already relatively low (Foss and Miller 2004).

Seasonal Prey Correlations with Striped Bass YOY Abundance

The seasonal prey correlations provide insight into striped bass YOY life stages that may be particularly sensitive to changes in prey availability. Striped bass in S1 ranged in average length (SL) from 20 mm in June to 60 mm in August. Important prey for striped bass YOY < 25 mm FL (~23 mm SL) in the SFE includes copepods and amphipods and to a lesser extent mysids, while mysids followed by amphipods dominated the diet (mean weight) of YOY > 25 mm FL (Bryant and Arnold 2007). Thus, if prey limitation is controlling striped bass YOY abundance in S1, then the decline in YOY may be attributed initially to the limited availability of copepods and smaller crustaceans and towards the end of S1, mysids. The significant positive correlation between S1 abundance of YOY and mysids supports the prey limitation hypothesis, but there was no significant correlation with adult copepods in deep water sites. The lack of a copepod correlation may have been due to the spatial separation of the copepod and fish sampling sites in the deep water sloughs (Figure 3.1). It is also possible that copepods may have been limiting at an earlier time period such as when immature larvae first enter Suisun Marsh prior to S1 (i.e. April). The large step decline in copepod abundance in S3 (January to April), particularly after the early 1990s, could have contributed to decreased survival of larval and postlarval striped bass and thus the reduced abundances of juveniles in S1. Bryant and Arnold (2007) also suggest the possibility of prey limitation occurring at the larval fish stage in the SFE.

In S2 and S3, striped bass YOY had a similar average size range (60 to 120 mm SL from Sept. to Dec. and 70 to 130 mm from Jan. to Apr.). Important prey for fish of this size in the SFE are mysids, amphipods, juvenile fishes, crangonid shrimp, palaemonid shrimp, and, to a lesser extent, copepods (Heubach et al. 1963; Feyrer et al. 2003; Bryant and Arnold 2007). The abundance of copepods and mysids were significantly correlated with striped bass YOY in deep water sites, where pelagic prey limitation may have the largest negative effect. In the deep water sites there was also overlap between the time period of low abundance of striped bass YOY (after the early 1990s) and the decline and low abundance of palaemonid shrimp (*P. macrodactylus* in the 1990s and *C. franciscorum* after 2000), although the correlations were not significant. Despite the lack of significance for some of these prey groups, the collective decline in abundance of prey species in S2 and S3 in the deep water sites and to some extent in shallow water sites in Suisun Marsh has almost certainly contributed to the general deterioration of feeding conditions for striped bass YOY, which has likely played a role in their observed decline.

The recent invasion and high abundance (2001 to 2005) of *E. modestus* in Suisun Marsh, however, may have benefited striped bass YOY, because this relatively large shrimp became abundant after other prey species declined. Positive correlations between striped bass YOY and palaemonid shrimp were observed in all depth groups in S2 and S3, although there was a lack of statistical significance in all but the upstream shallow water sites in winter and early spring (S3) where striped bass also did not decline statistically. None-the-less, the large increase in both *E. modestus* and striped bass YOY in Suisun Marsh from 2001 to 2005 is suggestive that this prey species at least partially compensated for the loss of mysids, *C. franciscorum* and *P. macrodactylus*. The extent of predation by striped bass YOY on *E. modestus* in the SFE is not well known. In Suisun Marsh, *E. modestus* was preyed upon by striped bass YOY as small as 70 mm SL (unpublished data), which demonstrates that striped bass are capable of feeding upon this new prey source in their first year of life. Age 1 and older striped bass in the upper SFE have also been observed feeding upon *E. modestus* (Nobriga and Feyrer 2007).

Correlation between Striped Bass YOY Abundance and Environmental Parameters

The lack of correlation between striped bass YOY abundance and environmental parameters (i.e. salinity, temperature, and Secchi depth), suggests that the abiotic conditions in Suisun Marsh were either favorable in most years or were not as important as other factors in determining the seasonal abundance of striped bass YOY. This is likely due to the fact that the range of environmental variation that striped bass YOY experienced during this study was well within their physiological limits (Turner and Chadwick 1972; Matern et al. 2002). For salinity the observed range in Suisun Marsh is considered optimal for growth (Secor et al. 2000; Altinok and Grizzle 2001). These results run counter to the findings by Feyrer et al. (2007), which found that increasing fall salinity (i.e. specific conductance) and water clarity (i.e. Secchi depth) likely played a role in the decreasing environmental quality for striped bass YOY in Suisun Bay and San Pablo Bay. Differences between studies are likely due to the more limited environmental variation and geographic coverage in this study compared to the study conducted by Feyrer et al. (2007).

The significant negative correlation between abundance of striped bass YOY in S1 and the distance of X^2 from the main entry point into Suisun Marsh (lower Suisun and Montezuma Sloughs) during the time period of maximum larval fish transport and recruitment (April to June) in the SFE (Kimmerer et al. 2000), indicates that striped bass YOY have maximized access to Suisun Marsh sloughs under moderate flow conditions. This is consistent with the results from past studies investigating flow effects on the position of the striped bass population in the SFE (Chadwick 1964; Turner and Chadwick 1972; Dege and Brown 2004). The continued negative, but not significant correlations between the April to June X^2 distances from Suisun Marsh and the S2 and S3 striped bass YOY abundances, suggests that limited access and reduced entry by immature stages of striped bass during low outflow periods extend into the fall and winter months. The lack of correlation between striped bass YOY abundance and distance of X^2 in the deep water sites was likely due to other more influential factors (e.g., prey availability).

Question 3: Has a decline in prey abundance affected the seasonal abundance and size of striped bass YOY?

Growth Changes in Striped Bass YOY

The significant increase in mean lengths of striped bass YOY in all three seasons in the mysid decline time period in the shallow water sites suggests that striped bass have not been negatively affected by the decline in mysids and other prey species (copepods, *C. franciscorum*, and *P. macrodactylus*). This is consistent with the alternative hypothesis that striped bass YOY exhibit increased growth under a more diverse diet. However, several interacting scenarios, discussed below, could have contributed to the observed changes in mean lengths of striped bass in shallow water sites during the mysid decline time periods. Discussed separately, the high seasonal variability in mean striped bass length in deep water sites in the mysid decline time period is likely due to a number of factors, particularly the low abundance of YOY after the early 1990s.

Scenario 1 - Striped Bass YOY Diet Shifts to Alternative Prey Species

Under this scenario, striped bass YOY shift their feeding to alternative prey such as smaller fish (including other striped bass YOY) and near-shore or shallow water invertebrates including amphipods, to compensate for the low availability of mysids (Heubach et al. 1963; Stevens 1966; Gartz 1999; Feyrer et al. 2003). This leads to increased growth and YOY length if the prey species that replaced mysids are sufficiently abundant and provide high nutritional value along with reduced cost of foraging. This scenario is consistent with the study results reported by Feyrer et al. (2003), which found that striped bass YOY in Suisun Marsh had increased dietary breadth and shifted to piscivory at a smaller size under conditions of low mysid abundance. YOY fishes that switch to piscivory earlier usually become larger than those feeding on a non-fish diet and the size differences often carry through to older age classes (Mittelbach and Persson 1998). The increased mean length and reduced gape limitations of striped bass YOY residing in Suisun Marsh since the early 1990s, has likely resulted in the ability of YOY to feed on a larger size range of prey including other YOY fishes and larger shrimp species, such as *E. modestus*. The ability to consume larger prey may further contribute to faster growth and length increases.

Striped bass diet shifts have also been observed outside of Suisun Marsh. Gartz (1999) detected a large decrease in the consumption of mysids and an increase in amphipod consumption after the decline of mysids. Bryant and Arnold (2007) studied the diet of striped bass YOY in the SFE at a larger temporal (1972 to 2002) and spatial scale (upper SFE and Sacramento San Joaquin Delta). They observed a decline in the consumption of mysids and amphipods since the middle 1980s by YOY between 0 and 50 mm SL and more variable consumption of those two prey groups by YOY >50 mm SL. They also observed an increase in consumption of copepods over the course of their study, especially after 1987 and for YOY <50mm SL. Increased consumption of the much smaller copepods and decreased consumption of larger amphipods and mysids would undoubtedly have negative growth consequences, since copepods have considerably lower biomass relative to mysids and amphipods, but differences in mean weight of diet contents were less clear over the long term study (Bryant and Arnold 2007). Differences between the reported diet studies in the SFE are likely due to the spatial and temporal differences in the investigations as well as the differing microhabitats sampled and the methodology used.

Scenario 2 - Reduced Survival of Small Striped Bass YOY

A second scenario is that there has been an increased loss of the smallest individuals from the population perhaps due to starvation under conditions of low prey abundance (i.e. copepods, mysids and amphipods) or increased predation (*Scenario 1*). This results in an increase in observed mean length of striped bass independent of an increase in growth rates. The reduced abundance of striped bass YOY in the shallow water sites sometime between the end of summer (S1) and the end off fall (S2), after mysids had declined in the system (Figure 3.10), indicates a possible time period when smaller striped bass YOY could have suffered increased mortality. Analyzing for changes in striped bass length at a finer temporal scale (monthly versus seasonal trend), reveals that there has been a significant increasing linear relationship (simple linear regression, $p < 0.05$) in mean standard length (response variable) over time (year = predictor variable) in each month from September through April, with the largest length increases beginning in the early 1990s (Appendix 1.2). Mysids are increasingly important in the diet of striped bass YOY as they reach lengths >25 mm TL (Bryant and Arnold 2007), which represents the lower size range of striped bass YOY in the S1 time period. Thus, it is possible that low mysid availability in S1 may have contributed to increased mortality of the smaller YOY, but more research is needed to determine if size-based mortality could result in the observed increase in length.

Scenario 3 - Density Dependence Release

A third scenario is that the reduced abundance of striped bass YOY, beginning sometime between S1 and S2 in the mysid decline time period, decreases competition among the surviving fish, given the strong density dependence observed for striped bass populations in the SFE (Kimmerer et al. 2000 and 2004). Decreased striped bass YOY abundance, presumably would lead to increased growth rates and size of the remaining striped bass YOY. The evidence for density dependent growth of striped bass YOY in the SFE is limited (Gartz 1999) and it was not specifically investigated for in this study, thus further research is needed to fully address this possibility.

Scenario 4 – Reduced Emigration and Increased Immigration

A final scenario is that given reduced availability of pelagic prey in deep water sites and sufficient prey availability in the shallow water sites, there is reduced emigration from shallow water sites and increased immigration into shallow water sites by the larger and presumably more mobile striped bass YOY. Both of these situations could result in increased mean length of fishes without an increase in growth. Consistent with this scenario is the finding that there was low seasonal loss of striped bass YOY between S2 and S3 in the upstream shallow water sites after mysids had declined in abundance, which suggests that there was either increased survival, or migration patterns had changed.

Deep Water Changes in Length

The observed decrease in mean length of striped bass YOY in S1 (May to August) in the deep water sites in Suisun Marsh may be due to decreased growth rates resulting from prey limitation, following the decline in mysid abundance and to some extent copepod abundance after the early 1990s. These results are consistent with the observed step decline in striped bass with prey in their stomachs in Suisun Marsh (i.e. Montezuma Slough) and Suisun Bay in roughly the same time period and the increased consumption of smaller prey estuary wide after 1987 (Bryant and Arnold 2007). The results contrast with the observed increase in mean length of YOY striped bass in the shallow water sites, which suggests there is greater prey availability in shallow water habitats.

The increased mean length during S2 in the deep water sites during the mysid decline time period is not consistent with the pattern during S1. One explanation is a rapid increase in growth rates between S1 and S2. This is unlikely given the low prey availability for striped bass in the deep water sites in the late summer and fall months. A more plausible explanation is that size dependent mortality is disproportionately affecting the survival of small striped bass YOY, which are likely more dependent upon mysids and copepod prey (i.e. *Scenario 2*). In addition, immigration by large YOY striped bass from surrounding areas (i.e. shallow water habitats) could also be contributing to the observed increase in mean lengths. The mean lengths of striped bass YOY in S2 in the deep water sites were similar to the downstream shallow water sites and were smaller than the upstream shallow water sites, suggesting that shallow water areas could have been a potential source of larger immigrants. Prey for larger striped bass YOY including *C. franciscorum* and *E. modestus* were still available, albeit less consistently, in the deep water sites in S2 during the mysid decline time period (Figure 3.5 and 3.6), but only for the YOY large enough to feed upon them (i.e. > 70 mm SL).

The lack of a significant difference in mean lengths of striped bass YOY in S3 in the pre-mysid decline and mysid decline time periods in the deep water sites runs counter to the observed shorter mean lengths in S1 and the longer mean lengths in S2 in the mysid decline time period. This may be due to greater emigration by the larger striped bass YOY in S3, which could have contributed to a shift back to a lower mean length. However, the low abundance of YOY in S2 and especially in S3 in the deep water sites has likely contributed to the large variation in YOY length, as the mean of a smaller sample size is much more sensitive to the addition of outlier values, such as the larger dispersing fishes moving through the system.

3.5 CONCLUSION

The results from this study indicate that striped bass YOY in shallow and deep water habitats in Suisun Marsh have been differentially affected by the changing ecological conditions. The significant decline in YOY striped bass in deep water habitats and lack of decline in shallow water habitats indicates that YOY receive some advantage by rearing in shallow water areas. Shallow water sites in Suisun Marsh maintain high densities of YOY fishes and a diverse assemblage of invertebrates, which has likely provided sufficient alternative prey for striped bass YOY after the decline in availability of pelagic prey. In contrast, pelagic invertebrates are the primary prey in deepwater habitats (Hazel and Kelley 1966; Turner and Heubach 1966; Boynton et al. 1981). Thus, their decline in abundance in the SFE has likely had profound impacts on striped bass YOY abundance. This is consistent with the significant decline and strong positive correlation between the abundance of pelagic copepods and mysids and striped bass YOY in deepwater habitats.

The increasing lengths of striped bass YOY in Suisun Marsh since the decline in pelagic prey in the early 1990s provides further evidence that the ecological conditions have changed in the system. The length increases in Suisun Marsh are consistent with those observed in the bay and river habitats in the SFE, as discussed earlier. The mechanism(s) behind the observed length changes are difficult to determine, because there are likely multiple and interacting factors responsible (see discussion). In general, size selective mortality is likely contributing to the loss of the smallest striped bass, due to the lack of suitable densities of small prey such as copepods and mysids. Reduced densities of smaller striped bass numerically shifts the mean length to a larger size, but may also relieve some of the density dependent effects on growth, resulting in the larger size of surviving individuals. The large surviving YOY likely benefit from the continuous availability of prey such as small fish and the more recent increased availability of larger prey such as *E. modestus*, especially in shallow water habitats where this species is most abundant.

The continued moderate to high catch of striped bass YOY in the shallow tidal channels of Suisun Marsh and presumably other shallow water areas in the brackish region of the SFE, has likely buffered the SFE population from a more catastrophic decline by providing the suitable conditions and prey resources needed for striped bass to survive and recruit to an older age class. However, the total contribution of shallow water reared striped bass to the larger SFE population is largely unknown and cannot be determined until more detailed investigations (e.g. marking and tagging) are conducted. The large and widespread decline in abundance of striped bass YOY in the bay and river channels in the SFE (Kimmerer 2004; Feyrer et al. 2007; Sommer et al. 2007), increases the importance of shallow water rearing.

The significant decline in striped bass YOY abundance in the bay and river channels in the SFE contrasts with increasing adult abundance estimates since the middle 1990s (Kimmerer 2004). The increase in adult abundance has been attributed to the greater survival of the few striped bass YOY that are still being produced in the system (Kimmerer 2004). However, it is possible that the adult population may be more accurately reflecting recruitment from shallow water reared YOY, such as in Suisun Marsh, where striped bass YOY have fared much better. The poor representation of shallow water habitats (i.e. <4 meters) in the monitoring surveys sampling the bays and rivers in the SFE likely contributes to the reported poor correlation between the abundance of YOY and adult striped bass.

Thus, the question arises: *Are the depth-based abundance trends unique to Suisun Marsh or are they also evident in other areas of the SFE?* The published results from long-term studies reporting on the declines in striped bass abundance in the SFE (Kimmerer et al. 2000; Kimmerer 2002 and 2004; Feyrer et al. 2007) did not differentiate catch by sampling depth. Thus, comparing the observed patterns with the published literature is not possible. The most comparable survey in the SFE to this study is the CDFG Bay Study otter trawl survey (Baxter et al. 1999), which sampled the bay and river channels sites from 1980 to 2005. Preliminary analyses of this data suggest that striped bass YOY have declined significantly in both the deep water channels (>7 meters depth) and shallow water shoals (<4 m) in Suisun and Grizzly Bay, although the decline in shoal catch has been less extensive and now comprises a majority of the striped bass catch in the monitoring survey (unpublished data; K. Hieb CDFG personal communication).

Taken together, the evidence from both Suisun Marsh and Bay suggests that striped bass YOY in deep water areas within the brackish region of the SFE have been disproportionately and adversely affected by changing conditions in the system, while YOY in the shallow water areas remain somewhat resilient to these changes. The abundance of striped bass YOY in shallow water areas did not increase in either Suisun Bay or Suisun Marsh following the decline in pelagic prey, suggesting a lack of a behavioral shift to alternative habitats. However, it is possible that there was an undetected shift, but limited carrying capacity and strong density dependence within those more restricted (by area) shallow water habitats prevented their sustained high abundance.

Given the deteriorating conditions of the pelagic food web in the SFE, a species must be flexible in both its habitat use and response to the available prey in order to continue to be successful. Spreading of risk is a mechanism by which a species can ensure its persistence in a highly variable environment. Bennett and Moyle (1996) suggest that a species with large spatial distribution, ontogenetic change in habitat, and variable seasonal patterns reduce risks to the effects of adverse conditions; at the same time these population attributes also make it difficult to accurately detect and understand how a species functions in a complex system (Kimmerer 2002). The results from this study reaffirm that striped bass YOY are well suited to the dynamic and often stressful conditions found in estuaries, given their high adaptability to changing conditions and flexibility in habitat use, but their continued resilience and success in SFE may well be dependent upon the availability and access to diverse habitats including shallow brackish tidal marsh.

Understanding the contribution of shallow water tidal habitats to estuarine fishes is an important goal for population managers and estuarine ecologists, as these habitats are increasingly being lost through various anthropogenic activities (Nichols et al. 1986; Dahl 2000; Kennish 2002; Lotz et al. 2006) and are further threatened by climate change and rising sea levels (Adam 2002; Scavia et al. 2002). In the SFE, approximately 95% of the original tidal marshes and their associated shallow water habitat have been lost (Nichols et al.1986). The current patchwork arrangement of the remaining tidal marshes increases the likelihood of a mismatch between the location of the shallow tidal habitat and the species dependent upon them, especially for fishes that have distribution patterns largely controlled by river flow.

Reduced prey availability in pelagic open-water habitats intensifies the need and importance of shallow water areas for species such as striped bass, because greater densities of fishes likely move to these habitats to satisfy their basic ecological needs. However, given strong density dependent population characteristics of striped bass (Kimmerer et al 2000; Kimmerer 2004), the limited availability of shallow water habitats may constrain the overall size of the SFE population. These results provide further evidence that habitat complexity is a key element in changing ecosystems, by helping to ensure persistence and stability of populations of striped bass and other species.

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3.7 TABLES

Table 3.1 Kendall's *tau* time series trends (1980 to 2005) for average annual seasonal abundance (n = 26 years). Table values are Kendall's tau coefficients. Coefficients with significant trends are indicated in bold with a single asterisk indicating significance at $p < 0.05$ and a double asterisk at the $p < 0.01$ level. The direction of the trend is indicated by the + and – sign of the coefficient. Sites are divided into three groups including upstream sites < 4 meters (US < 4m; n = 6), downstream sites < 4 meters (DS < 4m; n = 4), and main channel sites > 4 meters deep (>4m; n = 3). Time periods are May to August (S1), September to December (S2), and January to April (S3). The trend for the category Mysids is based upon a rank abundance for all mysid species combined. Palaemonid Shrimp includes *E. modestus* and *P. macrodactylus*.

Taxa	Depth	May to Aug	Sept to Dec	Jan to Apr
Striped Bass YOY	US < 4m	+0.13	-0.15	+0.03
	DS < 4m	-0.05	-0.13	**-0.30***
	> 4m	**-0.47****	**-0.58****	**-0.43****
Copepods[1]	> 4m	-0.24	**-0.34***	**-0.40****
Mysids	US < 4m	-0.04	**-0.30***	**-0.46****
	DS < 4m	**-0.46****	**-0.50****	**-0.60****
	> 4m	**-0.41****	**-0.35***	**-0.47****
C. franciscorum	US < 4m	-0.06	-0.25	-0.08
	DS < 4m	-0.02	-0.14	+0.25
	> 4m	+0.01	**-0.34***	+0.03
Palaemonid Shrimp	US < 4m	-0.05	+0.10	-0.05
	DS < 4m	-0.13	-0.13	+0.07
	> 4m	-0.16	-0.12	-0.10
P. macrodactylus[2]	US < 4m	**-0.48****	**-0.41***	**-0.48****
	DS < 4m	**-0.50****	**-0.43****	-0.27
	> 4m	**-0.41***	**-0.55****	**-0.44****

Table 3.2 Spearman's rank correlations for the seasonal similarities in abundance of striped bass (YOY) and potential shrimp prey species between the three depth groups (n = 26 years). Table values are Spearman's rank correlation coefficients (r). Significant correlations are indicated in bold with a single asterisk indicating significance at $p < 0.05$ and a double asterisk at the $p < 0.01$ level. Depth Group Comparisons indicate the pair of depth groups for which the abundance correlations were calculated. The time periods, and taxa are as in Table 3.1.

Taxa	Depth Group Comparisons	May to Aug	Sept to Dec	Jan to Apr
Striped Bass YOY	US < 4m vs. DS < 4m	+0.71**	+0.73**	+0.65**
	> 4m vs. DS < 4m	+0.34	+0.18	+0.44*
	> 4m vs. US < 4m	+0.12	+0.39	+0.11
Mysids	US < 4m vs. DS < 4m	+0.32	+0.67**	+0.83**
	> 4m vs. DS < 4m	+0.70**	+0.75*	+0.82**
	> 4m vs. US < 4m	+0.51**	+0.76**	+0.77**
C. franciscorum	US < 4m vs. DS < 4m	+0.72**	+0.60**	+0.62**
	> 4m vs. DS < 4m	+0.55**	+0.40*	+0.73**
	> 4m vs. US < 4m	+0.89**	+0.66**	+0.68**
Palaemonid Shrimp	US < 4m vs. DS < 4m	+0.71**	+0.60**	+0.74**
	> 4m vs. DS < 4m	+0.47*	+0.67*	+0.81**
	> 4m vs. US < 4m	+0.61**	+0.70**	+0.73**

Table 3.3 Spearman's rank correlations for striped bass (YOY) average annual seasonal abundance (n = 26 years) and abundance of potential prey species. Table values are Spearman's rank correlation coefficients (r). Significant correlations are indicated in bold with a single asterisk indicating significance at $p < 0.05$ and a double asterisk at the $p < 0.01$ level. Depth groups, time periods, and taxa are as in Table 3.1.

Taxa	Depth Group	May to Aug	Sept to Dec	Jan to Apr
Copepods[1]	> 4m	+0.26	+0.53**	+0.47*
Mysids	US < 4m	-0.20	-0.08	-0.26
	DS < 4m	+0.18	+0.16	+0.27
	> 4m	+0.52**	+0.59**	+0.46**
C. franciscorum	US < 4m	+0.01	-0.40*	-0.15
	DS < 4m	+0.11	+0.16	-0.47*
	> 4m	-0.11	+0.21	+0.27
Palaemonid Shrimp	US < 4m	+0.14	+0.20	+0.43*
	DS < 4m	+0.03	+0.34	+0.31
	> 4m	+0.13	+0.17	+0.32

Table 3.4 Spearman's rank correlations for striped bass YOY average annual seasonal abundance versus average seasonal environmental parameters (n = 26 years). Table values are Spearman's rank correlation coefficients (r). Significant correlations are indicated in bold with a single asterisk indicating significance at $p < 0.05$ and a double asterisk at the $p < 0.01$ level. Depth groups and time periods are as in Table 3.1. The parameter X^2 Distance from SB refers to the average distance of X^2 (2 ‰ isohaline position) from Suisun Bay near Ryer Island from April to June, the time period of greatest larval striped bass abundance.

Env. Parameter	Depth Group	May to Aug	Sept to Dec	Jan to Apr
Temperature	US < 4m	+0.08	+0.20	-0.01
	DS < 4m	-0.09	+0.28	-0.18
	> 4m	-0.27	+0.07	-0.35
Salinity	US < 4m	-0.18	+0.30	-0.12
	DS < 4m	-0.12	+0.13	-0.19
	> 4m	-0.21	+0.11	+0.27
Secchi	US < 4m	+0.22	**+0.60****	+0.10
	DS < 4m	+0.11	+0.15	-0.13
	> 4m	-0.04	-0.09	-0.21
X2 Distance from SB	US < 4m	**-0.48***	-0.18	-0.10
	DS < 4m	**-0.42***	-0.27	-0.27
	> 4m	+0.06	+0.11	+0.05

3.8 FIGURES

3.1. Location of Suisun Marsh within the upper San Francisco Estuary with otter trawl and zooplankton monitoring station locations. The dotted outline provides the approximate boundaries to Suisun Marsh. Several X^2 position transects are noted (dashed lines) including an X^2 of 70 km near the upstream edge of Ryer Island, which indicates the main downstream entry point into Suisun Marsh.

3.2. Time series of average striped bass YOY catch·min^{-1} (log(x+1) transformed) for the three depth groups in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* Depth groups are identified by > 4m = deep water depth group with site depths > 4 meters; DS < 4m = downstream shallow water sites with depths < 4 meters; and US < 4m = upstream shallow water sites with depths < 4 meters. The time period of the extended drought (1986-1992), the mysid decline (1992-2005), and the introduction and high abundance of *E. modestus* (2000-2005), are also indicated in the figure.

3.3. Time series of average adult copepod (calanoid and *Acanthocyclops sp.*) catch·meter^{-3} (log (x+1) transformed) from 1972-2005 at the two IEP/CDFG monitoring stations located in Suisun Marsh in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* The study time period 1980-2005 is indicated by the lower reference line.

3.4. Time series of average mysid rank abundance for the three depth groups in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* Depth groups are abbreviated, as in Figure 3.2. The time period in which *H. longirostris* replaced *N. mercedis* as the dominant species (1992-2005) is indicated. The step-like decline is indicated by the drop in combined depth group averages between the pre-mysid decline (1980-1991) and mysid decline (1992-2005) time periods (dot-dash lines).

3.5. Time series of average *C. franciscorum* catch·min^{-1} (log(x+1) transformed) for the three depth groups in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* Depth groups are abbreviated, as in Figure 3.2.

3.6. Time series of average palaemonid shrimp (*P. macrodactylus* and *E. modestus*) catch·min^{-1} (log(x+1) transformed) for the three depth groups in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* Depth groups are abbreviated, as in Figure 3.2. *Palaemon macrodactylus* was largely replaced by *E. modestus* beginning in 2000, as indicated in the figure.

3.7. Time series of temperature for the three depth groups in each of the following seasons: (a) May to August - *Season 1,* (b) September to December - *Season 2,* and (c) January to April - *Season 3.* Depth groups are abbreviated, as in Figure 3.2.

3.8. Time series of salinity for the three depth groups in each of the following seasons: (a) May to August - *Season 1*, (b) September to December - *Season 2*, and (c) January to April - *Season 3*. Depth groups are abbreviated, as in Figure 3.2.

3.9. Time series of turbidity for the three depth groups in each of the following seasons: (a) May to August - *Season 1*, (b) September to December - *Season 2*, and (c) January to April - *Season 3*. Depth groups are abbreviated, as in Figure 3.2.

3.10. The seasonal comparisons of striped bass YOY catch·min^{-1} (log(x+1) for the pre-mysid decline (1980-1991) and mysid decline time periods (1992-2005) in *Season 1* (May to August) and *Season 2* (September to December) for (a) US < 4m, (b) DS < 4m, and (c) > 4m (abbreviations as in Figure 3.2). Significant (p<0.05) simple linear regression lines are indicated by a solid and dotted line, for the pre-mysid decline and mysid decline time periods, respectively. The 1:1 line (i.e. S1 abundance = S2 abundance) is indicated by the dash-double dot line.

3.11. The seasonal comparisons of striped bass YOY catch·min^{-1} (log(x+1) for the pre-mysid decline (1980-1991) and mysid decline time periods (1992-2005) in *Season 2* (September to December) and *Season 3* (January to April) for (a) US < 4m, (b) DS < 4m, and (c) > 4m (abbreviations as in Figure 3.2). Significant (p<0.05) simple linear regression lines are indicated by a solid and dotted line, for the pre-mysid decline and mysid decline time periods, respectively. The 1:1 line (i.e. S2 abundance = S3 abundance) is indicated by the dash-double dot line.

3.12. Striped bass YOY standard length comparisons for each depth group and time period. Depth group abbreviations are as in Figure 3.2. T1 = pre-mysid decline and T2 = mysid decline time periods. Data are illustrated by Box Plots, which display the summary statistics including the Mean (dotted bar), Median (solid bar in box), 25th and 75th quartiles (top and bottom edges of box) the 10th and 90th percentiles (edge of whiskers) and the 5th and 95th percentiles (solid circles). Significant results (p<0.05) from the Tukey-Kramer HSD test are indicated by an asterisk (*) for the within depth group comparisons between T1 and T2. Significant results for the between depth group comparisons within each time period are indicated by the letters a-c located above the corresponding box plot for T1 and d-e located below the box plots for T2. Depth groups sharing a letter were not found to be statistically different using the Tukey-Kramer HSD test. The absence of letters and asterisks indicate no means were statistically different.

FIGURES

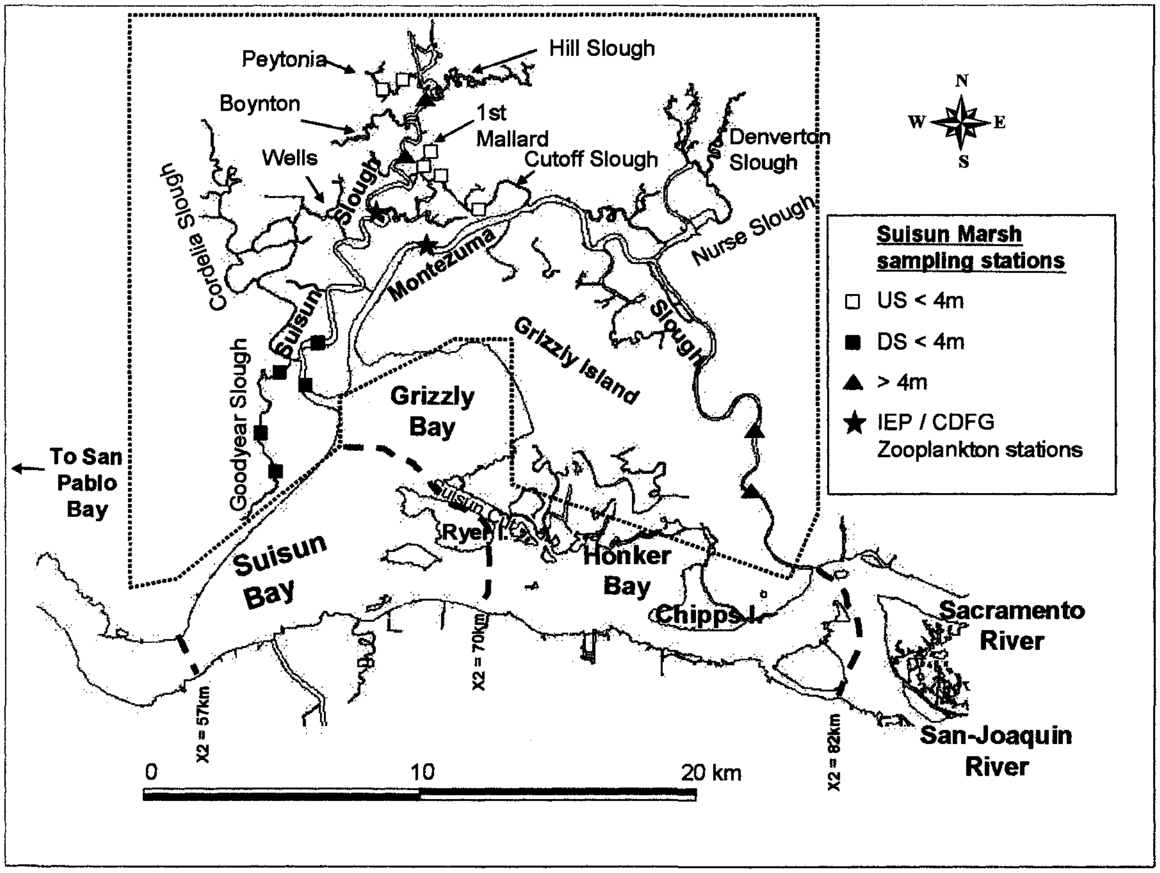


Figure 3.1

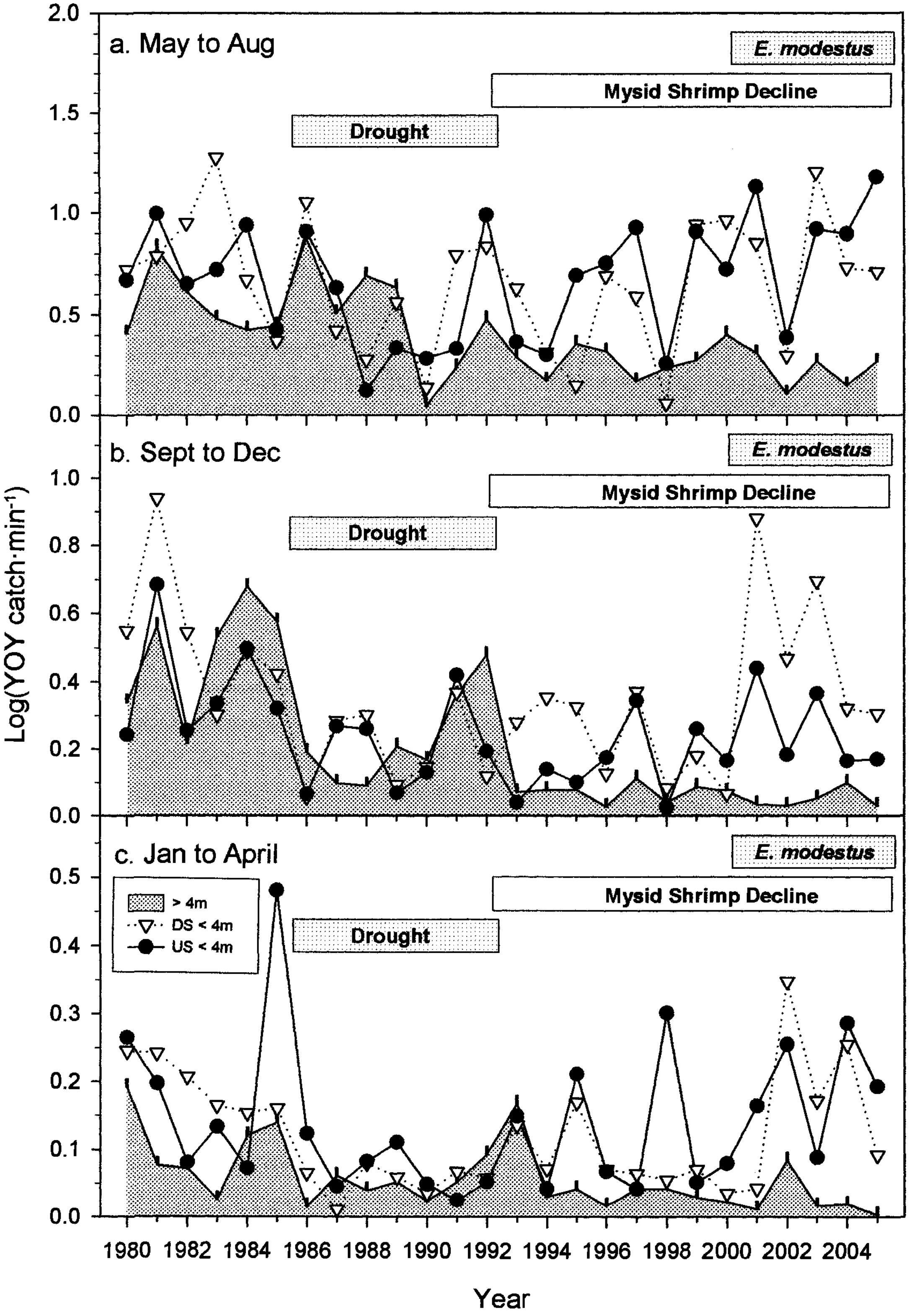

a. May to Aug
b. Sept to Dec
c. Jan to April
E. modestus
Mysid Shrimp Decline
Drought
> 4m
DS < 4m
US < 4m
Log(YOY catch·min⁻¹)
Year
2.0
1.5
1.0
0.5
0.0
0.8
0.6
0.4
0.2
0.3
0.1
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004

Figure 3.2

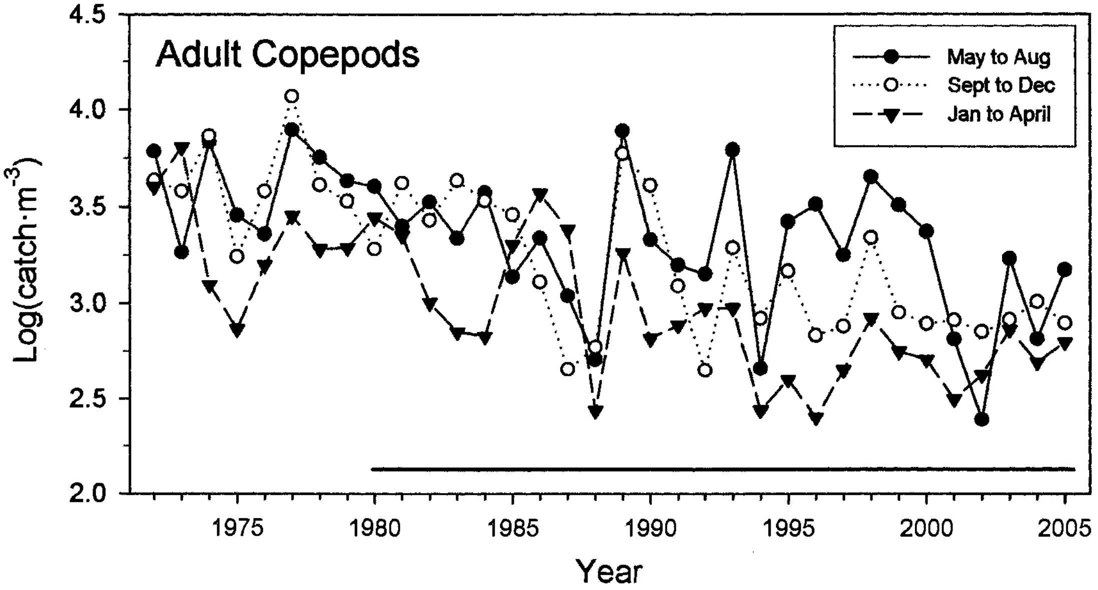

Adult Copepods
May to Aug
Sept to Dec
Jan to April
Log(catch·m-3)
4.5
4.0
3.5
3.0
2.5
2.0
1975
1980
1985
1990
1995
2000
2005
Year

Figure 3.3

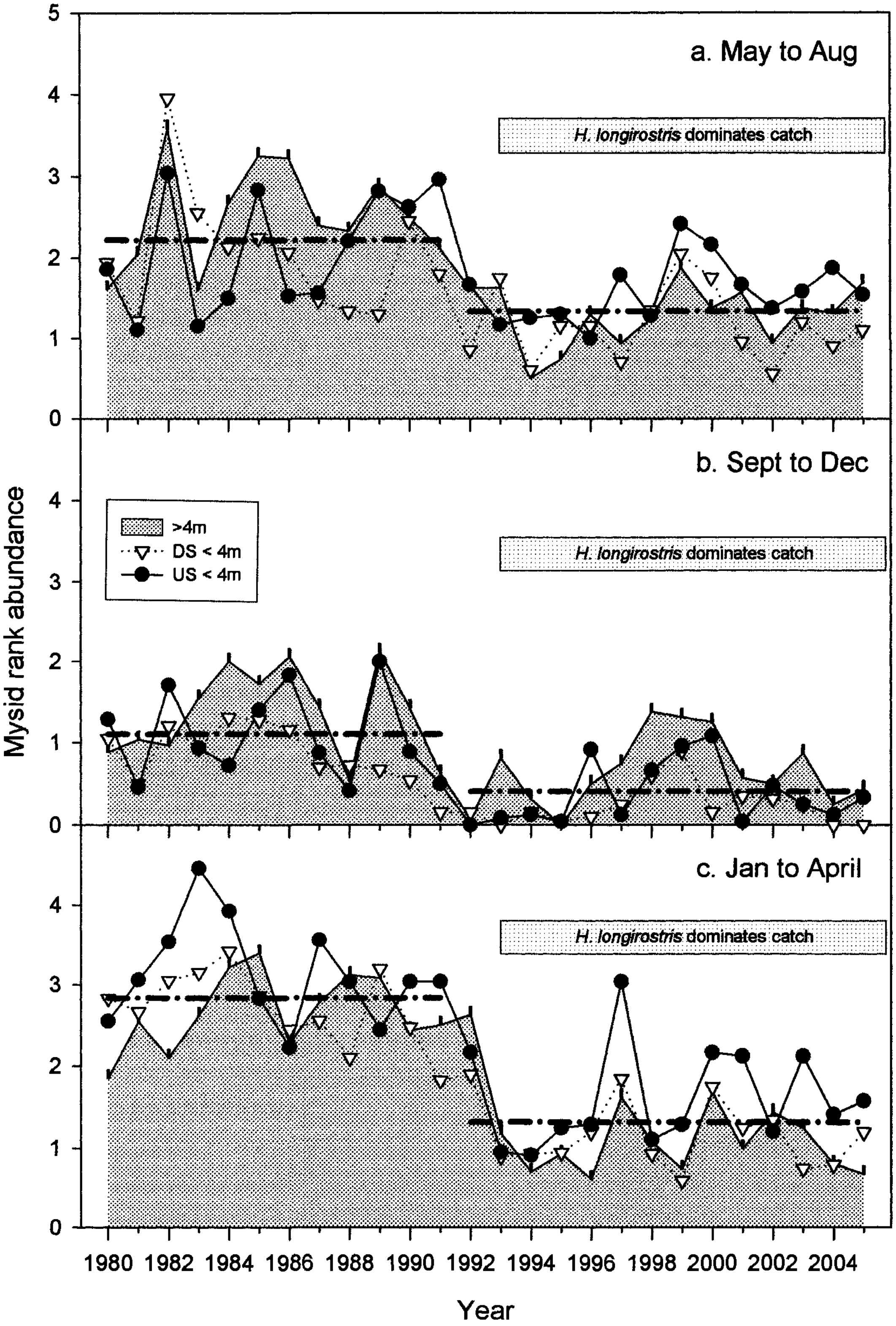

a. May to Aug
H. longirostris dominates catch
b. Sept to Dec
H. longirostris dominates catch
c. Jan to April
H. longirostris dominates catch
>4m
DS < 4m
US < 4m
Mysid rank abundance
0
1
2
3
4
5
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
Year

Figure 3.4

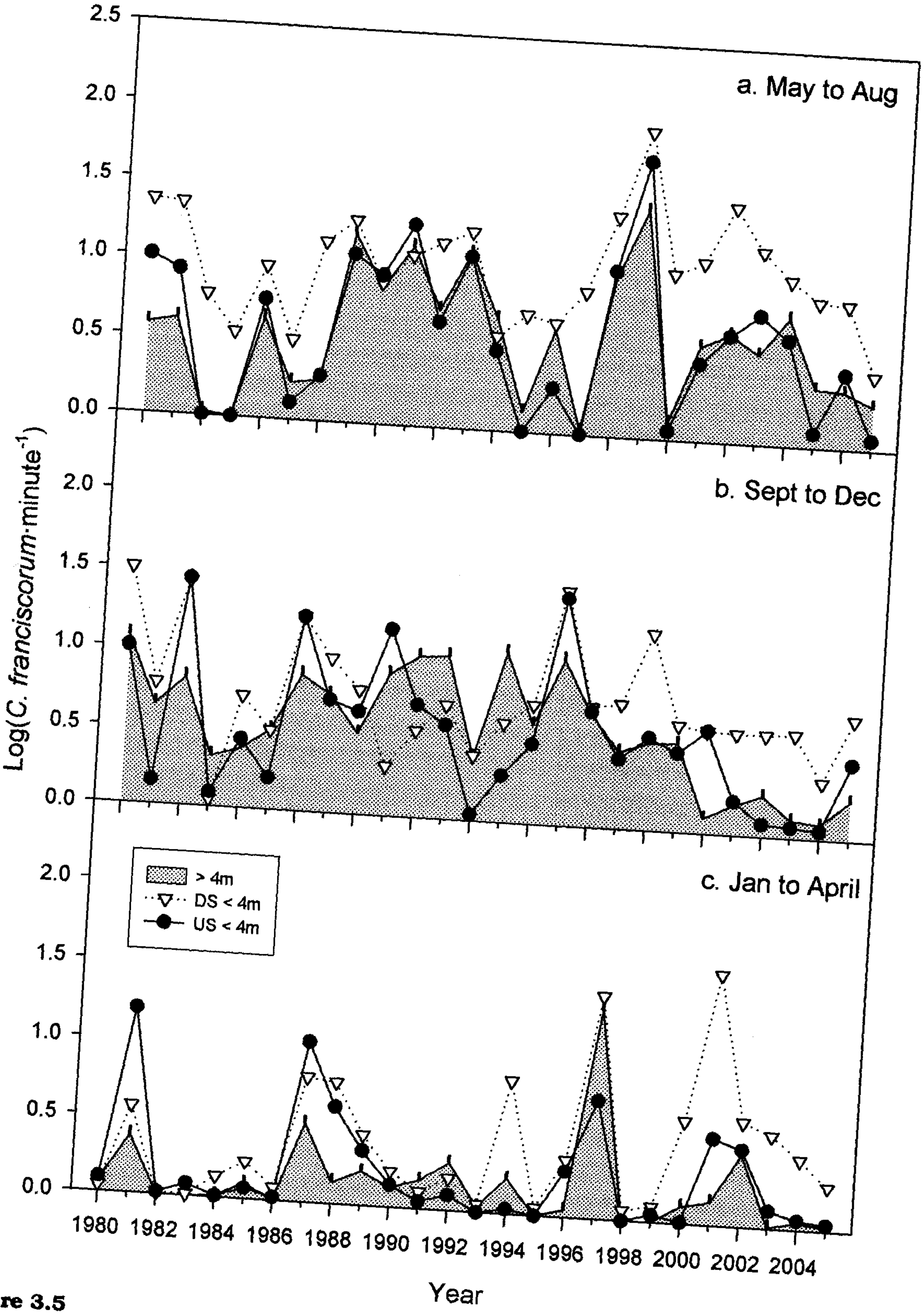

a. May to Aug
b. Sept to Dec
c. Jan to April
▨ > 4m
DS < 4m
US < 4m
Log(*C. franciscorum*·minute^{-1})
0.0
0.5
1.0
1.5
2.0
2.5
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
Year

Figure 3.5

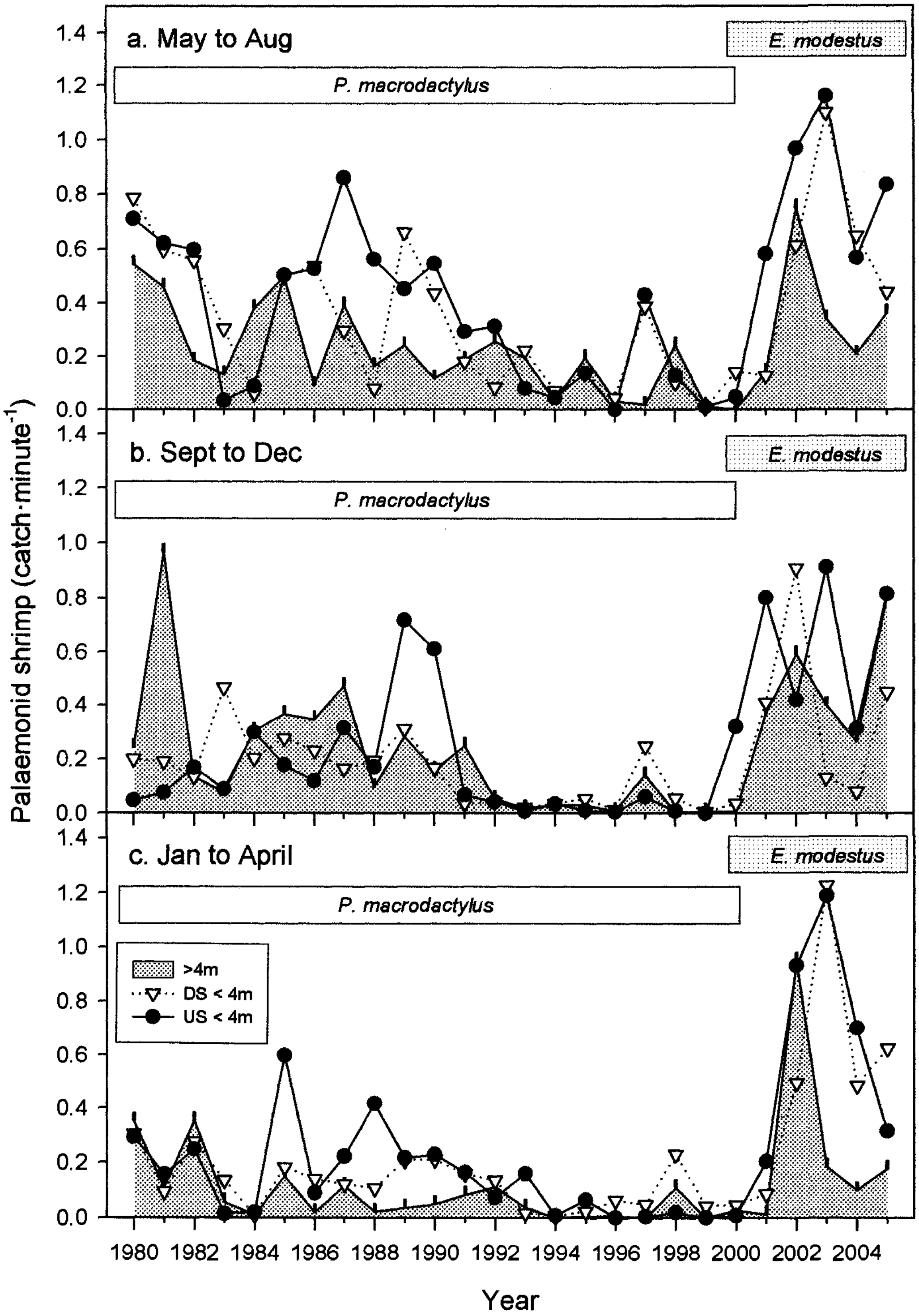

a. May to Aug
E. modestus
P. macrodactylus
b. Sept to Dec
E. modestus
P. macrodactylus
c. Jan to April
E. modestus
P. macrodactylus
>4m
DS < 4m
US < 4m
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Palaemonid shrimp (catch·minute-1)
1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004
Year

Figure 3.6

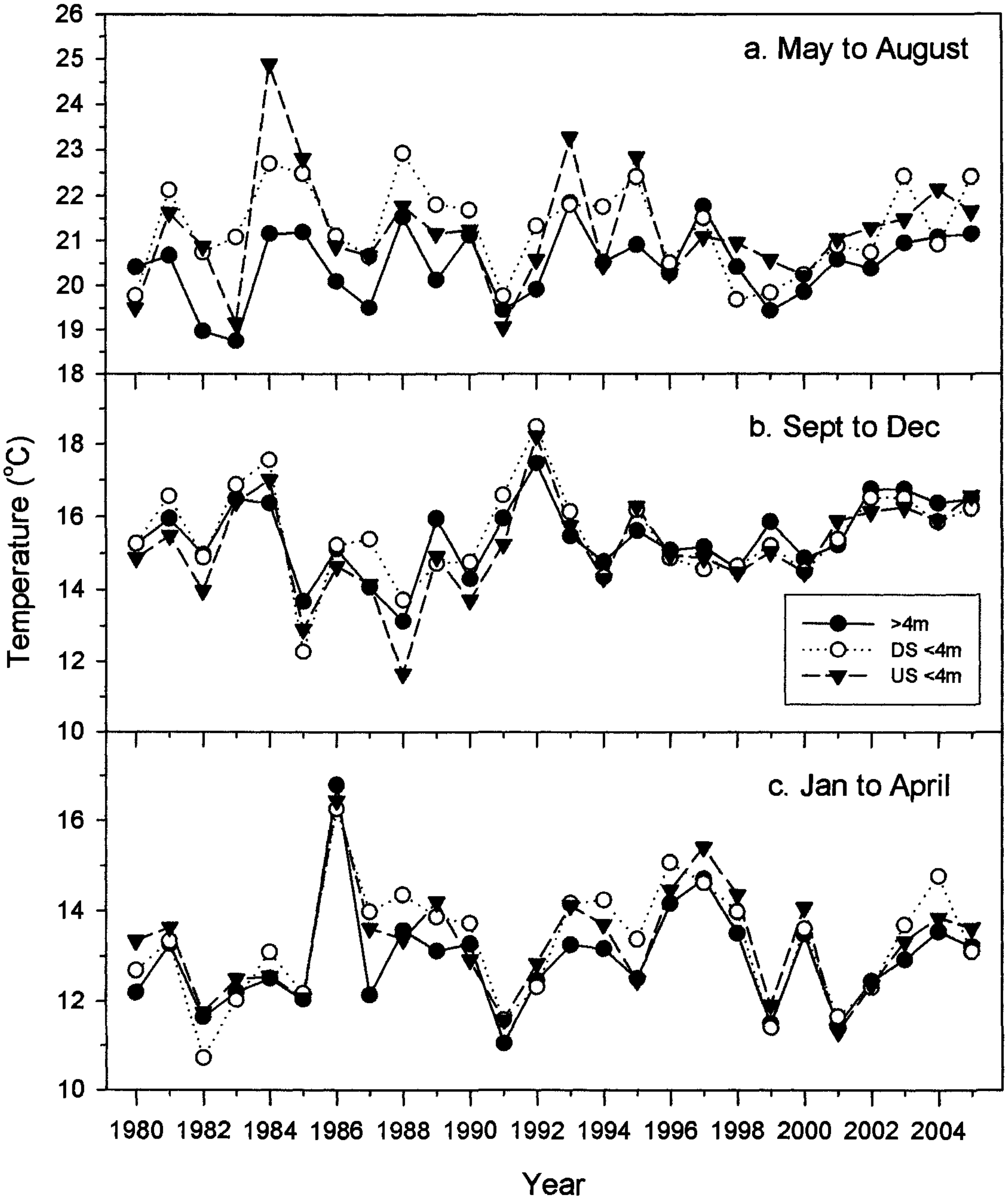

a. May to August
b. Sept to Dec
c. Jan to April
Temperature (°C)
Year
>4m
DS <4m
US <4m
26
25
24
23
22
21
20
19
18
16
14
12
10
1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004

Figure 3.7

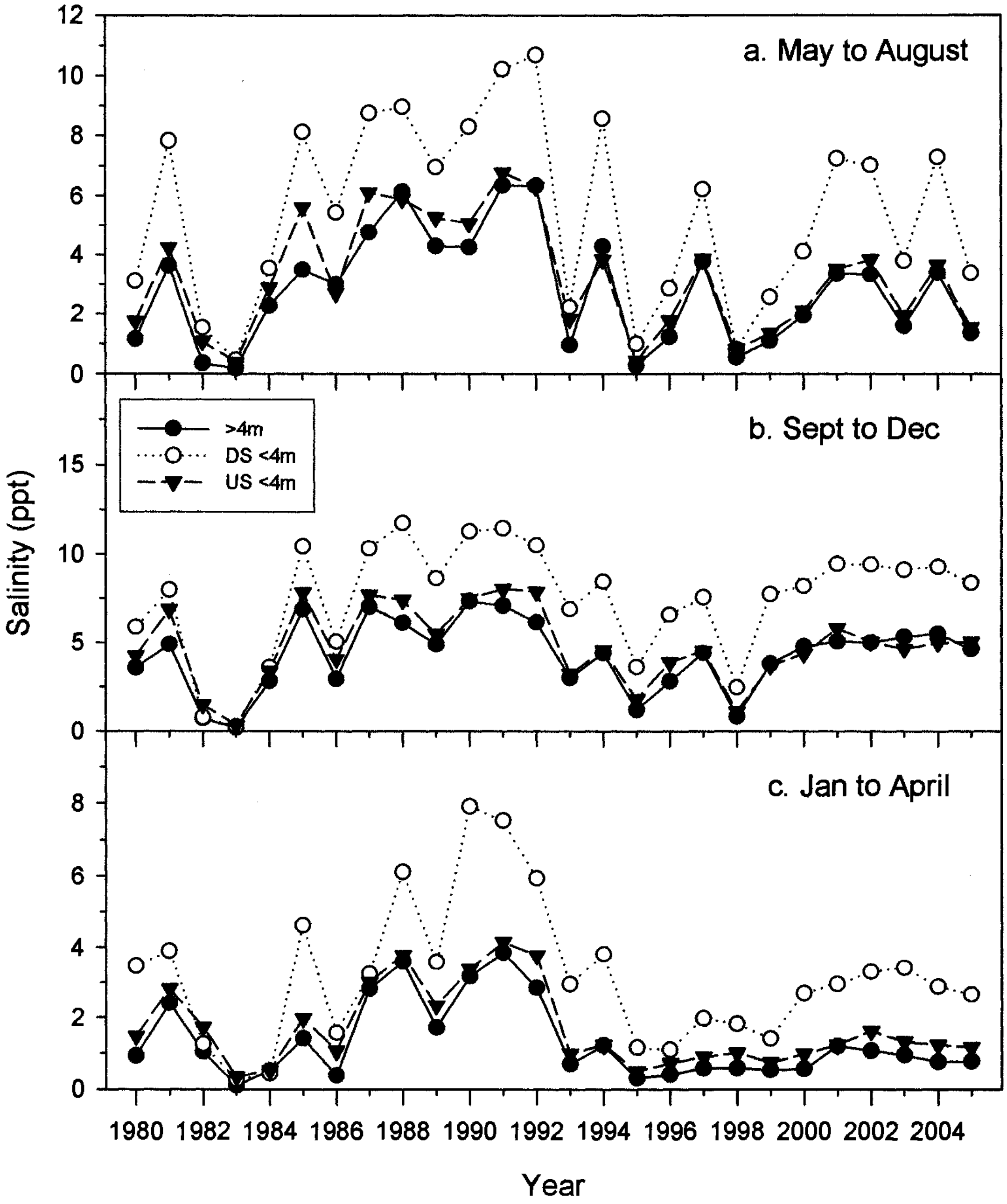

a. May to August
b. Sept to Dec
c. Jan to April
>4m
DS <4m
US <4m
Salinity (ppt)
Year
0
2
4
6
8
10
12
0
5
10
15
0
2
4
6
8
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004

Figure 3.8

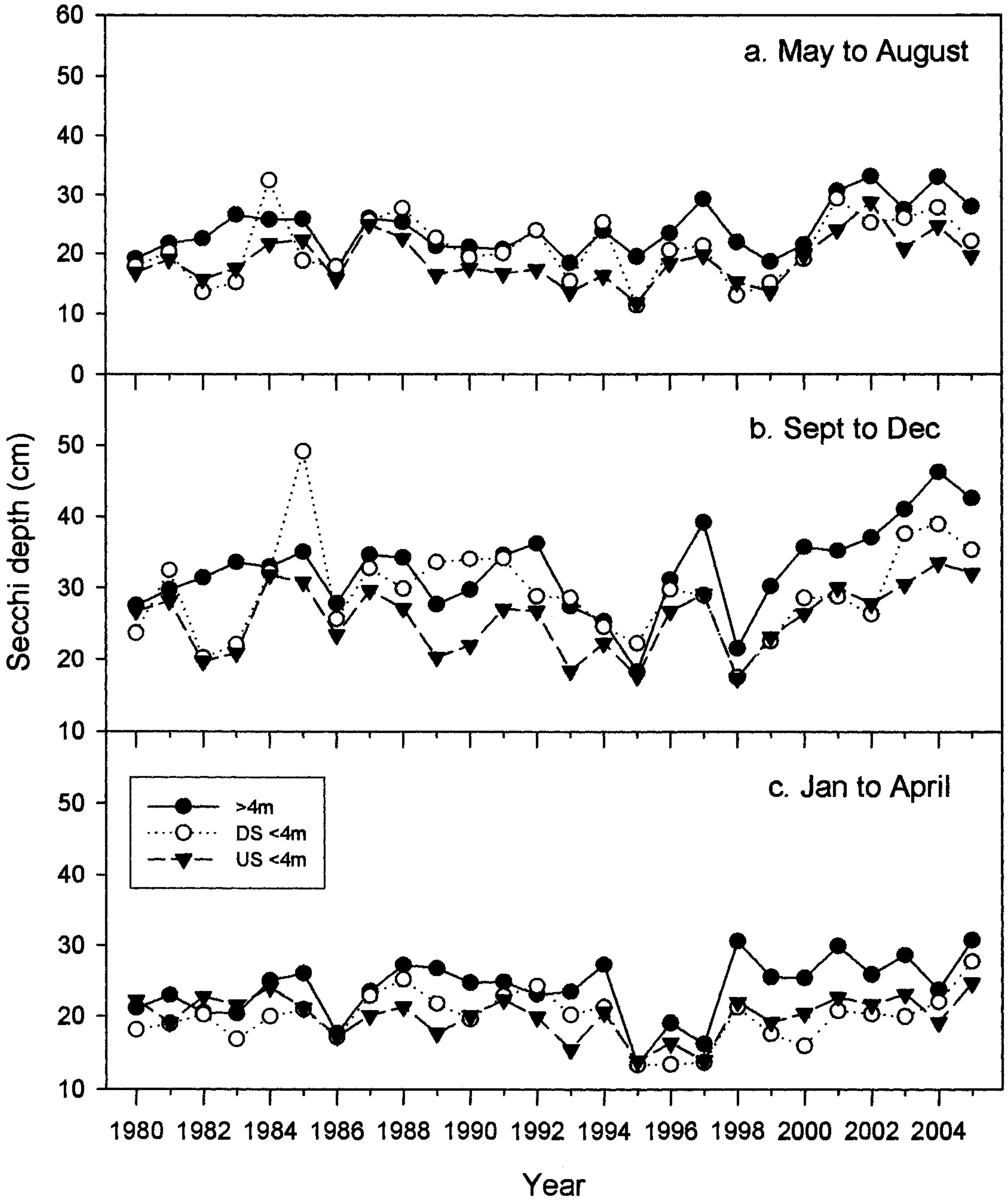

a. May to August
b. Sept to Dec
c. Jan to April
Secchi depth (cm)
Year
>4m
DS <4m
US <4m
0
10
20
30
40
50
60
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004

Figure 3.9

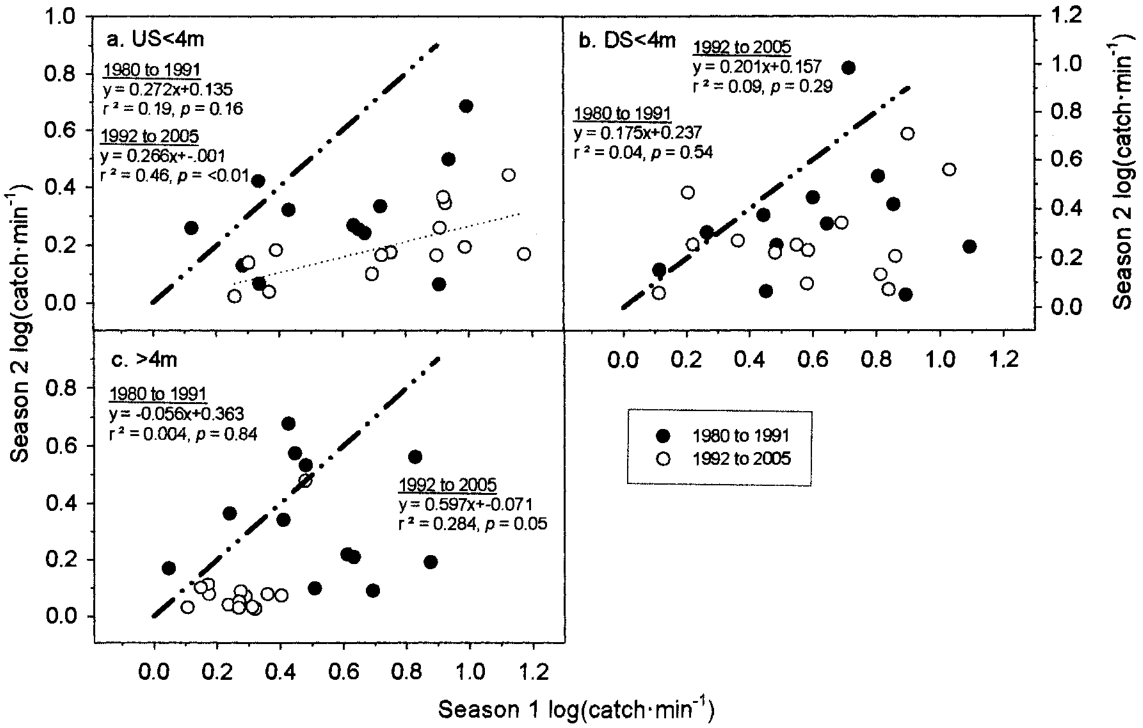


Figure 3.10

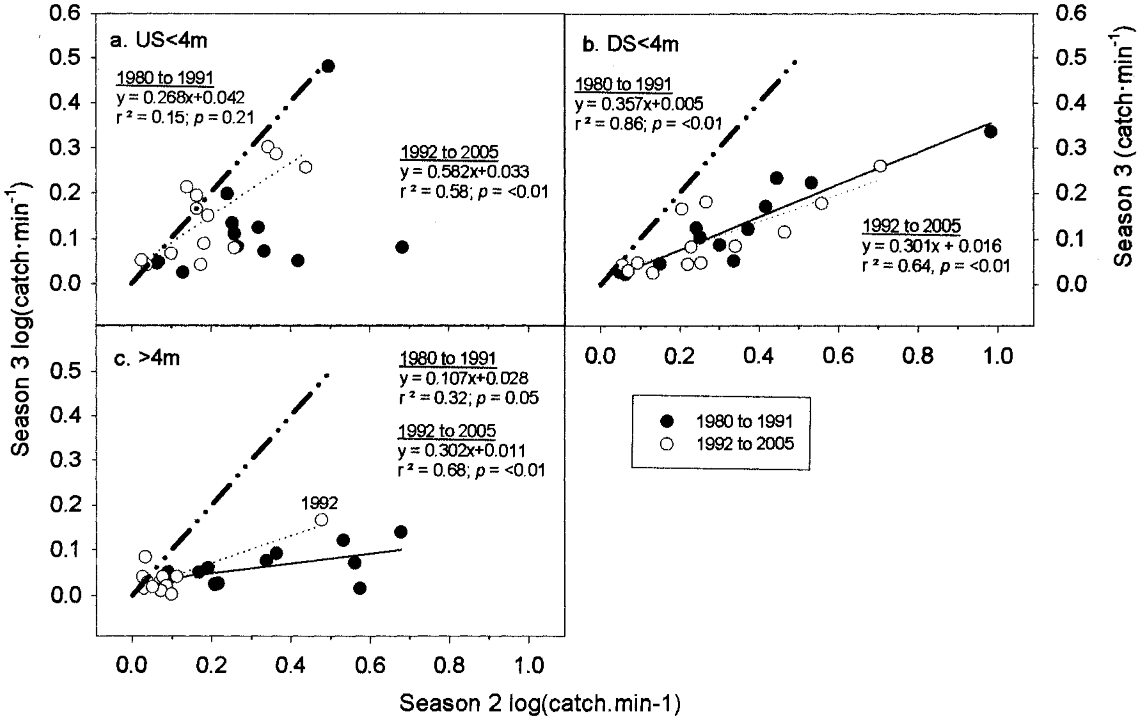


Figure 3.11

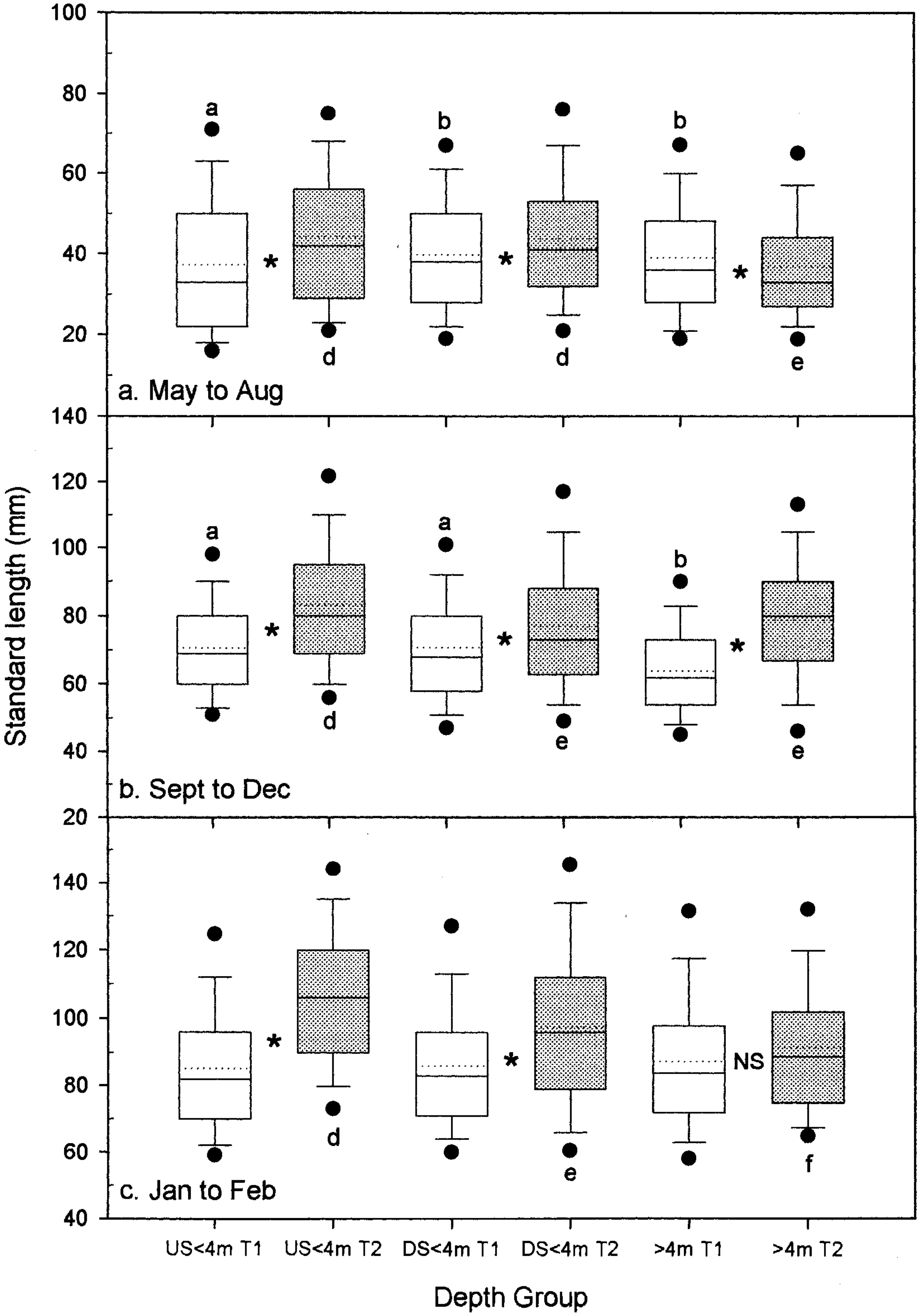
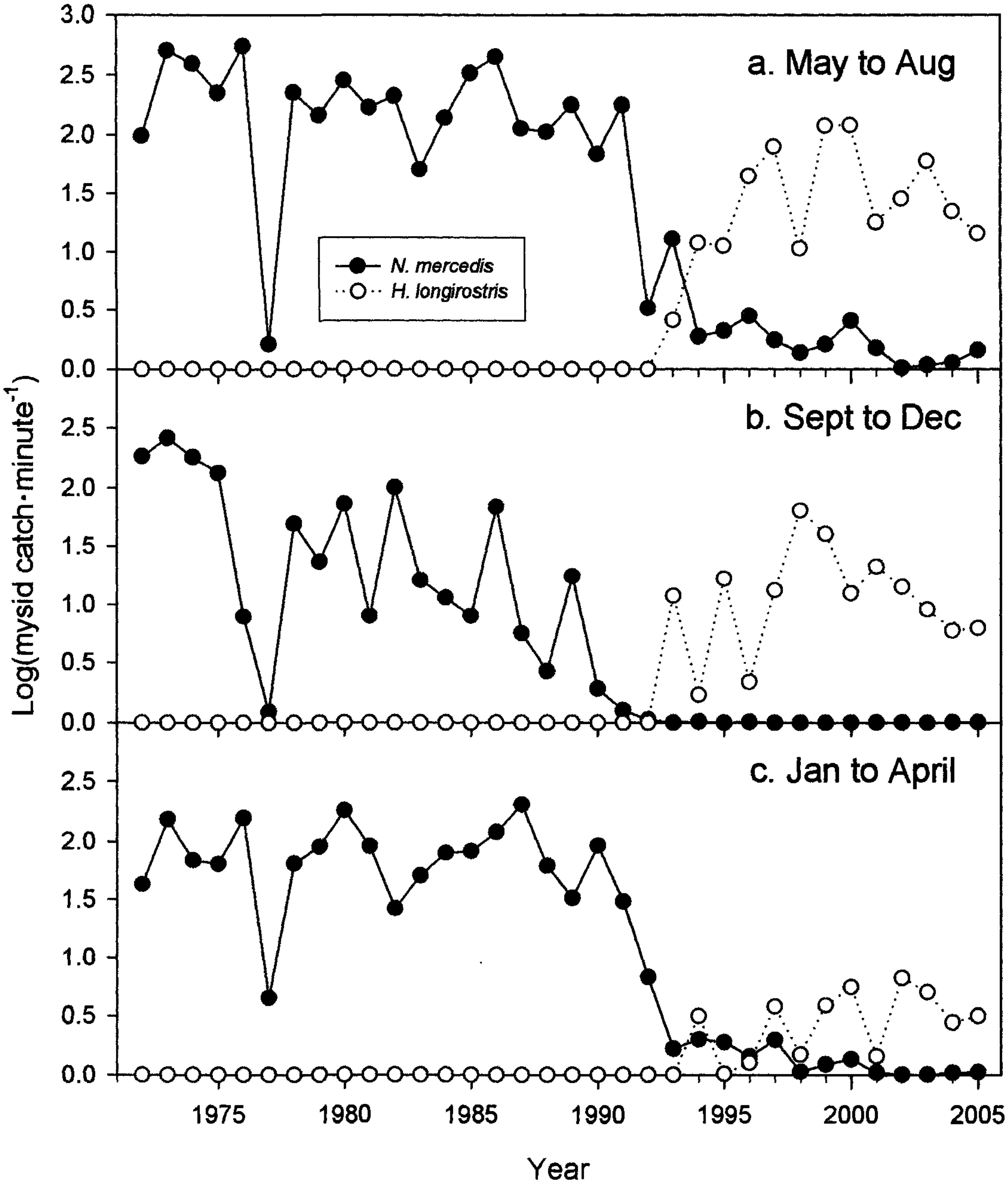
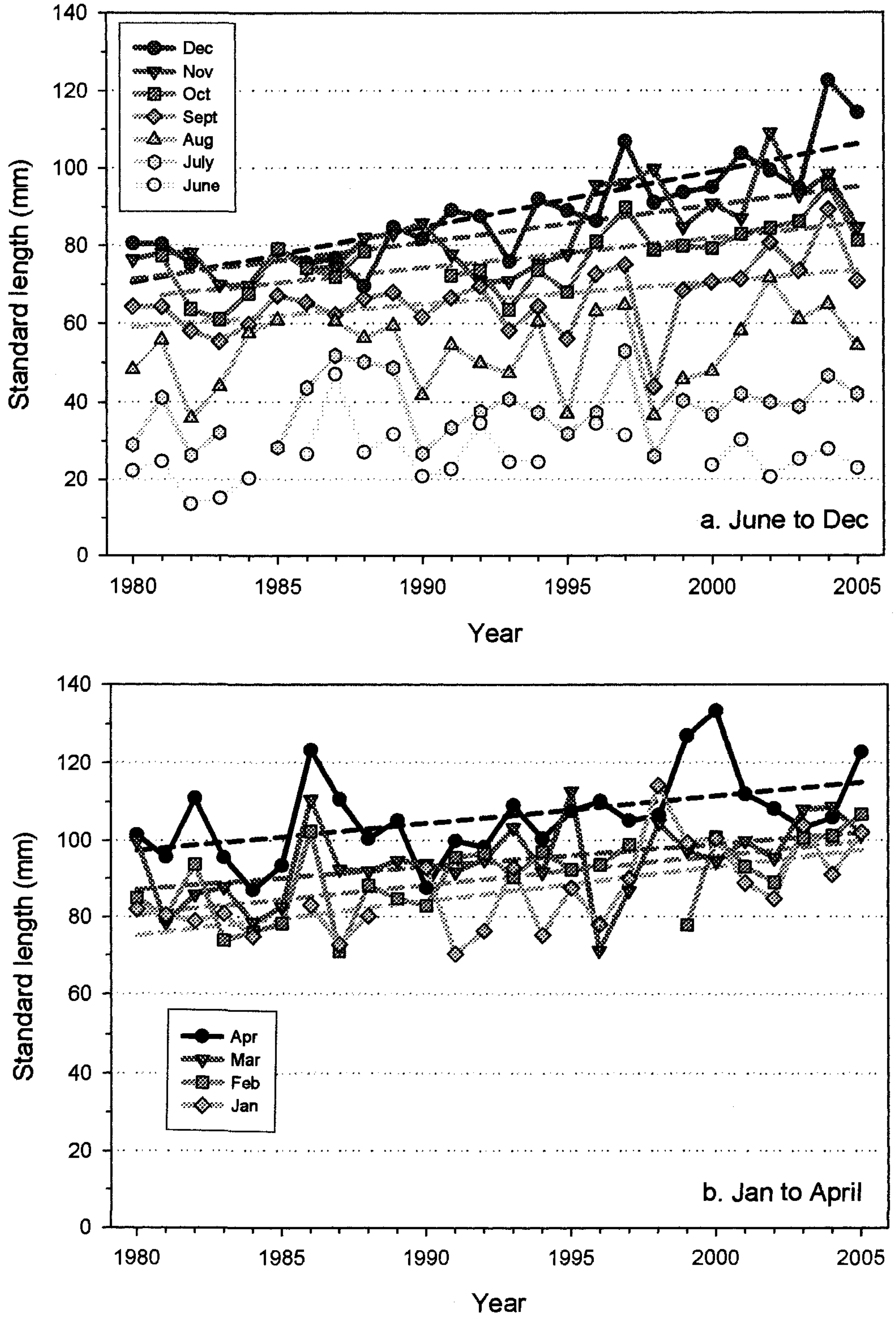

Standard length (mm)
100
80
60
40
20
a. May to Aug
140
120
100
80
60
40
b. Sept to Dec
20
140
120
100
80
60
c. Jan to Feb
40
a
b
b
d
d
e
a
a
b
d
e
e
d
e
f
*
NS
US<4m T1
US<4m T2
DS<4m T1
DS<4m T2
>4m T1
>4m T2
Depth Group

Figure 3.12

3.9 APPENDIX A



Appendix A.1 Mysids log (x+1) transformed catch·meter^{-3} from 1972-2005 at the two IEP/CDFG monitoring stations located in Suisun Marsh in each of the following seasons: (a) May to August - *Season 1*, (b) September to December - *Season 2*, and (c) January to April - *Season 3*.



Appendix A.2 Time series of the monthly average striped bass YOY standard length (mm) from the Suisun Marsh otter trawl sampling sites in each of the following seasons: (a) May to August - *Season 1*, (b) September to December - *Season 2*, and (c) January to April - *Season 3*. Dashed lines represent significant linear relationships (simple linear regression, $p<0.05$).