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Zooplankton of the West Florida Shelf: Relationships with *Karenia brevis* blooms

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Zooplankton of the West Florida Shelf:

Relationships with *Karenia brevis* blooms

by

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

to my husband, Sean

and my children, Joseph and Gabrielle

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ABSTRACT

Blooms of the toxic dinoflagellate *Karenia brevis* are common on the West Florida Shelf (WFS), yet little is known of the relationships between zooplankton and *K. brevis*. A comprehensive analysis was undertaken to examine 1) perturbations in zooplankton community composition within *K. brevis* blooms 2) the contribution of zooplankton ammonium and phosphate excretion to *K. brevis* bloom nutrient requirements, and 3) the role of zooplankton grazing in *K. brevis* bloom termination. Prior to undertaking the first portion of the study, an examination of the perturbations in the normal zooplankton assemblage within *K. brevis* blooms, it was first necessary to define the normal zooplankton assemblage on the WFS. To this end, a seasonal analysis of abundance, biomass and community composition of zooplankton was undertaken at 6 stations on the WFS. Monthly sampling was conducted for one year at the 5, 25 and 50-m isobaths. Two major groups in community composition were observed at the near shore (5-m and 25-m) and offshore (50-m) stations. Considerable overlap was seen in community composition between the 5-m to 25-m and 25-m to 50-m isobaths, but little overlap in community composition was observed between the 5-m and 50-m isobaths. Of the 95 species identified, only 25 proved to be important (>90%) contributors to community composition. Near shore, important contributors were *Parvocalanus*

crassirostris, *Penilia avirostris*, *Paracalanus quasimodo, Oithona colcarva*, *Oikopleura dioica, Centropages velificatus* and Pelecypod larvae. As distance offshore increased, important contributors to community composition were *Euchonchoichiea chierchiae, Clausocalanus furcatus*, *Oithona plumifera*, *Oithona frigida*, *Oncaea mediteranea*, *Calaocalanus pavoninius*, *Oithona similis,* and Gastropod larvae. Variations in abundance and biomass between non-bloom and bloom assemblages were evident, including the reduction in abundance of 3 key species within *K. brevis* blooms. One potential source of nutrients to support *K. brevis* blooms may be zooplankton regeneration of nutrients. To test this hypothesis, ammonium and phosphate excretion rates of several West Florida Shelf copepods (*Labidocera aestiva*, *Acartia tonsa*, *Temora turbinata*, and *Paracalanus quasimodo*) were measured and prorated to a 24-hour day. These excretion rates were then extrapolated to other West Florida Shelf zooplankton, combined with available literature excretion rates for some taxa, and applied to zooplankton abundances found for *K. brevis* blooms on the West Florida Shelf in 1999 and 2001. Ammonium excretion rates were found to be inadequate to support all but 10^4 cells l^{-1} of *K. brevis*, though phosphate excretion rates were adequate to support even 10^6 cells l^{-1} of *K. brevis*. Grazing assessment was conducted for three common zooplankton species that were found within two *K. brevis* blooms, *A. tonsa*, *P. quasimodo*, and *L. aestiva*, using ^{14}C labeled *K. brevis* cells. Grazing rates were then applied to the zooplankton community and grazing assessed. Grazing pressure was occasionally heavy, and was capable of reducing *K. brevis* to background concentrations at stations in the 1999 bloom and at 1 station in the 2001 bloom. Generally, however, grazing pressure

proved to be insufficient to reduce *K. brevis* to background concentrations during the 1999 and 2001 blooms.

CHAPTER ONE

INTRODUCTION

Early Spanish explorers in the Gulf of Mexico described events that suggest fish kills and aerosol production by blooms of the toxic dinoflagellate *Karenia brevis* (previously *Gymnodinium breve* Davis). Blooms occur most frequently on the West coast of Florida in an area extending from Tarpon Springs south to Sanibel, but are also known to occur on the east coast of Florida and as far north as Cape Hatteras (Tester et al., 1991; Tester and Steidinger, 1997; Steidinger et al., 1998). The economic impact of red tides in the Gulf of Mexico is estimated to range from $250,000 to $120,000,000 per event (Kusek, 1998). *K. brevis* blooms have been implicated in the mass mortalities of manatees and dolphins (Gunter, 1948; Layne, 1965; Geraci, 1989; Bossart et al., 1998, Flewelling et al., 2005), and can cause neurotoxic shellfish poisoning (NSP) in humans (Anderson, 1995). *K. brevis* is also an important contributor to the West Florida shelf (WFS) ecosystem. Steidinger (1975) suggested that it may play an important "forest fire" role in regulating the WFS ecosystem, and Vargo et al. (1987) calculated the total contribution of *K. brevis* carbon production can range from 10 to 40% of total carbon production for the WFS.

How *K. brevis* manages to out-compete other phytoplankton species and achieve numerical dominance in blooms is still not completely understood. Previous research has identified possible links between *K. brevis* growth rates and nutrients, light levels, *Trichodesmium* spp. blooms, dinoflagellate life cycles, and hydrography of the Gulf of Mexico (Steidinger, et al., 1998 and references cited therein; Lenes et al., 2001; Walsh

and Steidinger, 2001; Walsh et al., 2002; Lester et al., 2003; Heil et al., 2003; Vargo et al., 2003; Walsh et al., 2003). However, the ability of *K. brevis* to out-compete other phytoplankton species can only be understood in the context of losses (i.e. grazing rates) as well as growth rates.

Selective grazing of zooplankton on microalgal populations based on cell size, toxicity and nutritional quality is well documented, and can result in a dominance shift from edible to inedible species (Huntley, 1982; Lehman, 1984; Sterner, 1989; Turner and Tester, 1989; Banse, 1995; Kiorboe, 1993; Valiela, 1995). Some studies have suggested that differential mortality leads to the success of toxic phytoplankton blooms (Fiedler, 1982; Huntley, 1982; Smayda and Villareal, 1989; Buskey and Stockwell, 1993; Buskey and Hyatt, 1995) while Uye (1986) ascribed the termination of a toxic phytoplankton bloom to grazing. Turner and Anderson (1983) found that grazing was not able to deter initiation of a bloom of the toxic phytoplankter *Alexandrium tamarense*, but an increase in grazing pressure as the bloom progressed eventually resulted in bloom termination.

The impact of grazing on the aforementioned blooms is not fully understood, but it is clear that the interactions between toxic phytoplankton and their zooplankton grazers are complex and species specific, and depend on both the characteristics of the phycotoxin and the zooplankton species present (Huntley et al., 1986, Turner and Tester, 1989; Turner and Tester, 1997).

The only *in situ* study to date of zooplankton grazing on *K. brevis* generated intriguing questions about potential interactions between zooplankton and *K. brevis*. Turner and Tester (1989) exposed 5 dominant species of copepods from North Carolina waters to varying natural concentrations of *K. brevis*. All five species ingested the toxic

dinoflagellate, but the rates of ingestion tended to be variable and low. The three highest ingestion rates occurred for species that co-occur with *K. brevis* in the Gulf of Mexico (*Acartia tonsa*, *Oncaea venusta* and *Labidocera aestiva*), leading to speculation by the authors that *K. brevis* is most likely to be grazed by copepods that co-occur with it.

Anecdotal field observations made during red tide events, though subjective, indicate that other organisms may be able to ingest *K. brevis*. Woodcock and Anderson (cited in Galstoff, 1948) observed that large numbers of the cladoceran *Evadne* spp. captured in a red tide bloom had intestines stained deep red, presumably from ingestion of *K. brevis*. Dragovich and Kelly (1964) observed that a *K. brevis* bloom in Tampa Bay in 1963 coincided with high numbers of tintinnids. A preliminary report on *K. brevis* blooms by the University of Miami in 1954 (cited in Rounsefell and Nelson, 1966) reported that blooms of *K. brevis* often contained large numbers of the copepod *Acartia* spp. Martin et al. (1973) observed numerous ciliates within a *K. brevis* bloom. More recently, C. Heil (pers. comm.) observed an unidentified tintinnid ingesting *K. brevis* during a long-lived bloom off the coast of St. Petersburg, Florida.

Besides the question of loss rates of *K. brevis*, there are other enigmas surrounding the blooms and their relationships with zooplankton. Specifically, the source of nutrients available to *K. brevis* during long term bloom events remains uncertain (Vargo, et. al., in review). Zooplankton excretion rates, based on measured zooplankton population estimates and excretion rates from the literature, could supply all of the Nitrogen and Phosphorus required to support large populations of *K. brevis* (Vargo, et. al., review). However, no direct information on WFS zooplankton excretion rates is available.

The potential of zooplankton to ingest *K. brevis*, and the apparent ability of zooplankton to provide all of the nutrients required for a long term *K. brevis* bloom, generate three critical questions. First, what is the ecological impact of *K. brevis* blooms on the "normal" West Florida Shelf zooplankton assemblage? Second, what effect do potential grazers have on the termination of *K. brevis* blooms? Third, can zooplankton provide the daily turnover of nutrients required by long term *K. brevis* blooms?

METHODS

Study Design –Evaluation of community composition

This study dovetailed with the ECOHAB: Florida program, the objectives of which include modeling of initiation and transport of *K. brevis* blooms, description of physical habitat where blooms tend to occur, and determination of *K. brevis* community regulation processes. The ECOHAB: Florida study area extends from Tampa Bay to Charlotte Harbor and from shore to the 200-meter isobath (Figure 1).

Prior to addressing the relationship between *K. brevis* blooms and zooplankton assemblages on the WFS, it was first necessary to comprehensively define the normal zooplankton assemblage within the study area. This task proved to be difficult with the research at hand. Zooplankton studies previously conducted in or near the study area consisted of 1) analyses of total biomass variation with seasonality, 2) quantitative assessments of taxonomic composition at a single station at a single point in time, or 3)

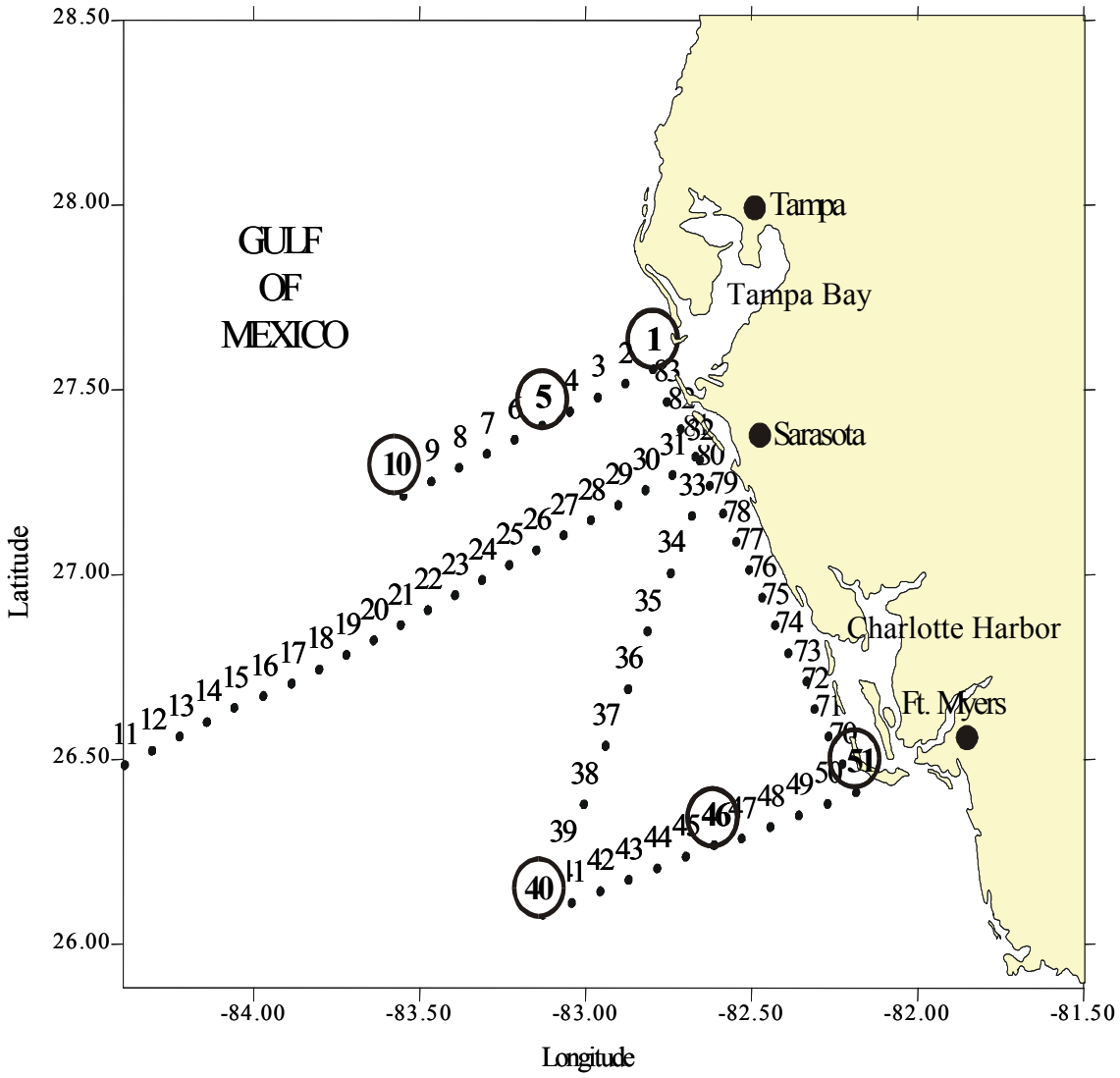

Figure 1. ECOHAB study area in the Gulf of Mexico. Station locations for ECOHAB cruises are indicated by a (•). Stations where zooplankton tows were conducted are circled and indicated by a number.

qualitative annual surveys (King, 1950; Bogdanov et al., 1968; Austin and Jones, 1974; Houde and Chitty, 1976; Hopkins, 1982). Sutton et al. (2001) examined spatial changes in taxonomic composition in the northern part of the area, but the study was to genus levels only, and consisted of a single transect.

Comprehensive taxonomic seasonal analyses of estuarine zooplankton assemblages in the Gulf of Mexico are more common (Hopkins, 1966; Hopkins, 1977; Weiss, 1978; Squires, 1984), but do not provide insight into composition of shelf communities. Likewise, offshore waters in the open Gulf of Mexico are relatively well studied (Hopkins et al., 1981; Morris and Hopkins, 1983; Hopkins and Lancraft, 1984), but do not include populations typically found shoreward of the 50-m isobath. Minello (1980) studied the neritic zooplankton of the Northwest Florida shelf, but it was unknown whether his findings could be extrapolated to the WFS study area, since the shelf is considerably narrower here and Gulf Stream dynamics bring open Gulf of Mexico waters closer to shore (Steidinger et al., 1998).

The evaluation of community composition then, had two primary components. The first was to characterize the zooplankton assemblage in the study area, including seasonal changes in abundance, biomass and community composition. The second component was to identify whether *K. brevis* blooms impacted the normal zooplankton assemblage.

Sampling took place in conjunction with monthly ECOHAB cruises on board the R/V Suncoaster and the R/V Bellows in the Gulf of Mexico (Figure 1). Stations were located approximately every 5 nautical miles. A CTD profile was conducted from bottom to surface at every station. At selected stations (usually every other station, but

occasionally more frequently) water samples were collected to determine chlorophyll *a* concentration, and *K. brevis* cell counts.

Zooplankton sampling for the characterization of the normal assemblage began in August of 1999 and continued through July of 2000 (Figure 2). Six stations (1, 5, 10, 40, 46, and 51) at three isobaths (5-, 25- and 50-meter) were chosen as representative zooplankton sampling stations. These three sets of stations were expected to provide three distinct zooplankton populations: a near shore population, a mixed population, and an offshore population, depending on time of year and intrusion of the Loop Current onto the shelf (Austin, 1971; Austin and Jones, 1974; Minello, 1980; Sutton et al., 2001). Additional zooplankton tows were conducted whenever possible at stations where *K. brevis* concentrations were found to be above background levels.

In the fall and winter of 2001, a major *K. brevis* bloom occurred within and around the study area. In September and December, zooplankton tows were conducted on ECOHAB cruises at stations where *K. brevis* concentrations were above background levels. In October, zooplankton samples were obtained in elevated *K. brevis* concentrations during a cruise conducted for a companion program with stations located north of the ECOHAB control volume (Figure 3).

Collection of Zooplankton

1999-2000 Zooplankton were collected with a 153 μm mesh bongo net, lowered closed through the water column, opened at depth and then towed obliquely from bottom to surface. A calibrated flow meter was used to calculate the volume of water filtered

		5-meter Isobath				25-meter Isobath				50-meter Isobath				Additional Stations					
		Station 1		Station 51		Station 5		Station 46		Station 10		Station 40							
		N1	N2	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2
1999	July	x	x	x	x	x	x	x	x	x	x	x	x	7	7	36	36	76	76
	August	x	x	x	x	x	x	x	x	x	x	x	x						
	September	x	x	x	x	x	x	x	x	x	x	x	x						
	October	**x**		**x**	**x**	x	x			x	x	x	x	**80**	**80**				
	November	x	x	x	x	x	x	x	x			x	x						
	December	x	x	x	x	x	x	x	x	x	x	x	x						
2000	January	x	x	x	x	x	x	x	x	x	x	x	x						
	February	83	83	70	70														
	March	x	x	x	x	x	x	x	x	x	x	x	x	23	23				
	April	x	x	x	x	x	x	x	x	x		x							
	May	x	x	x	x	x	x	x	x	x	x	x	x						
	June	x	x	x	x	x	x	x	x	x	x	x	x						
	July	x	x	x	x	x	x	x	x										

Notes: Bold face type indicates where *K. brevis* was found above background levels.
N1 and N2 refer to Net 1 and Net 2.
Numbers in lieu of x's indicate where additional samples were taken.

Figure 2. Sampling matrix for zooplankton samples taken during the 1999-2000 sampling period on the WFS.

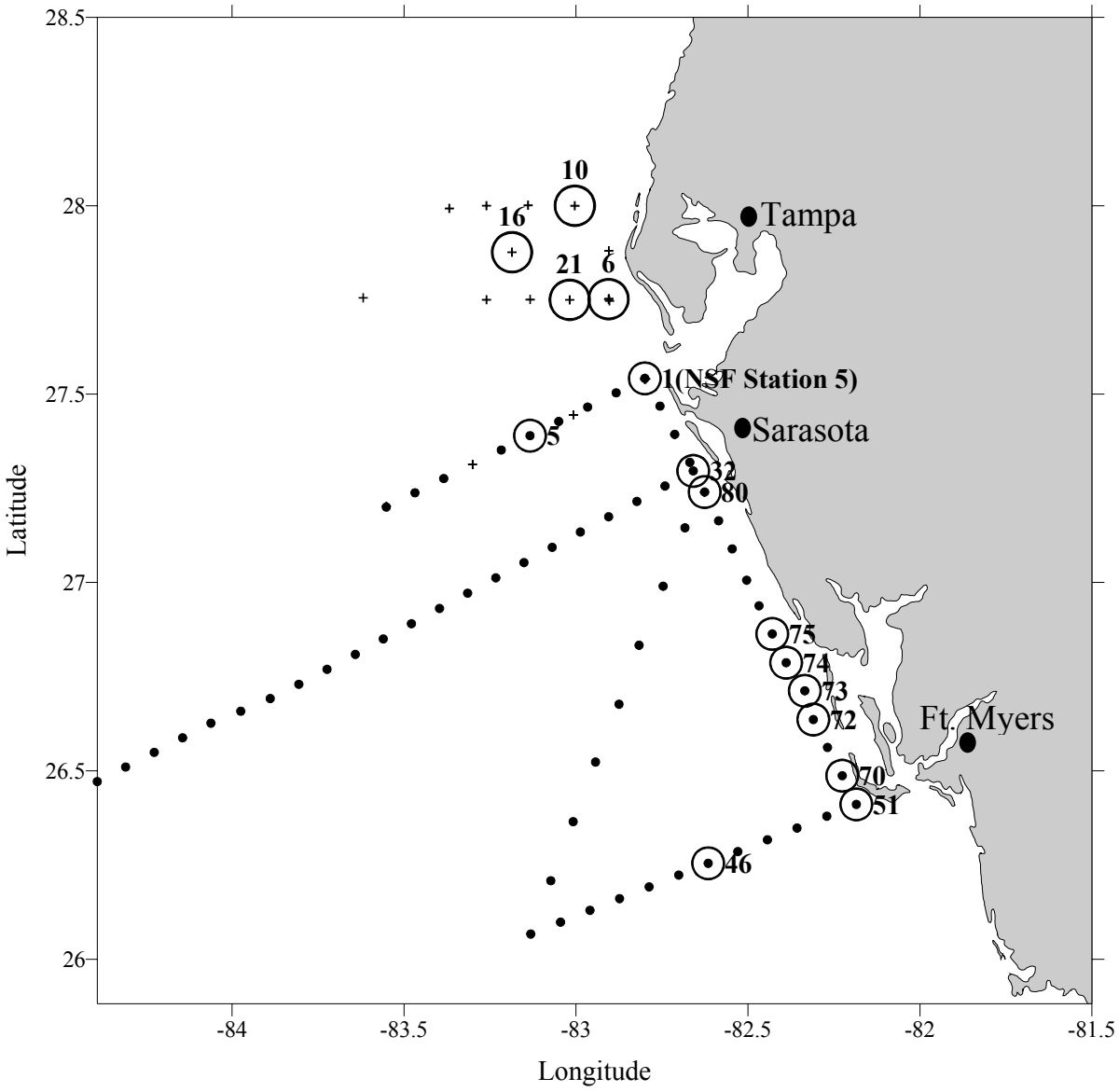

Figure 3. Station locations for ECOHAB cruises (•) and NSF cruises (+). Stations where zooplankton tows were conducted are circled and indicated by a number. NSF Station 5 is in the same location as ECOHAB Station 1.

during the oblique tow (Omori and Ikeda, 1992). The time of tow generally varied from 1 to 5 minutes, depending on the water column depth. The sides of each net were washed into the cod end prior to being brought on board. The cod ends were filtered through a 2000 μm mesh sieve to remove large gelatinous zooplankton. The filtered cod ends were then preserved on board in a 5% buffered formalin solution (Omori and Ikedo, 1992) for later counts of zooplankton species abundance.

2001 Collection of zooplankton in September, October, and December of 2001 was accomplished in an identical manner, except that a single 153 μm mesh net was used instead of a bongo net.

Chlorophyll a *concentration and* K. brevis *cell counts*

Zooplankton tows were conducted in conjunction with CTD casts, measurements of chlorophyll *a*, and *K. brevis* cell counts. Water column samples were collected from Niskin bottles mounted on a rosette sampler. During the October 2001 NSF cruise surface samples at selected stations were taken with a bucket, in addition to samples from Niskin bottles. Duplicate chlorophyll samples were filtered onto GF/F filters, placed in 10 ml methanol, stored at 4^{o}C in darkness for 3 days, and analyzed within one week using a Turner design fluorometer (Welschmeyer, 1994). *K. brevis* was counted live using a dissecting microscope within two hours of collection.

Zooplankton abundance and biomass

Zooplankton abundance Subsamples were obtained with a Stempel pipette; such that a typical sample contained ~500-600 animals (usually 1-5% of initial cod end volume). Zooplankton were then identified and counted using an Olympus dissecting microscope at 10-40x magnification, with critical taxonomic features observed on an Olympus compound microscope. Holoplankton were identified to species level whenever possible. Meroplankton were identified to major taxonomic group (e.g. pelecypod veligers, cirriped larvae). Copepod nauplii were not identified to species level but, when possible, were identified to family level.

Zooplankton biomass Dry weight contributions of each major species were either determined mathematically from regression equations or taken directly from available literature (Table 1 and references listed therein).

Grazing pressure determination

Grazing rates on cultured *K. brevis* populations were determined for three species of zooplankton: *Acartia tonsa*, *Paracalanus quasimodo* and *Labidocera aestiva*. Zooplankton were collected from the pier or a small boat with a 202 μm mesh net. Cod ends were immediately diluted with natural sea water and transported to the lab. After sorting, 3 replicates each of 2 adult female copepods were added to scintillation vials to which 20 ml filtered seawater was added. ^{14}C labeled *K. brevis* culture was added to each vial, such that the final *K. brevis* concentration was 5×10^3, 5×10^4, or 1×10^6 cells per liter. Vials were incubated for 30 minutes. After the incubation period, copepods were

Table 1
Sources of biomass values and length/width regression equations for WFS zooplankton taxa.

Taxon	Source	Comments
Undinula	Morris and Hopkins, 1983	
Eucalanus	Morris and Hopkins, 1983	
Acrocalanus	Weiss, 1978	Derived from *Paracalanus*
Calocalanus	"	
Paracalanus	"	
Clausocalanus	"	Derived from *Centropages*
Scolothrex	Morris and Hopkins, 1983	
Euchaeta	Morris and Hopkins, 1983	
Temora	Lester, unpub. Data	
Centropages	Weiss, 1978	
Calanopia	"	
Pseudodiaptomas	"	
Acartia	"	
Tortanus	"	
Labidocera	"	
Oithona	"	
Oncaeae	Squires, 1984	
Corycaeus	Weiss, 1978	
Farranula	"	
Euterpina	"	
Microsetaella	"	
Euchonchoichiea	Hopkins, 1984	
Penilia	Weiss, 1978	
Evadne	"	
Podon	"	*E. tergestina* value
Appendicularians	"	
Brachiopoda	"	
Bryozoa	"	
Cirripedia	"	
Decapoda	"	
Echinodermata	"	
Gastropoda	"	
Pelecypoda	"	
Platyhelminthe	Squires, 1984	
Polychaeta	Weiss, 1978	

filtered onto 12µm Nuclepore filters, rinsed with filtered seawater, and dissolved with were Hyamine Hydroxide. After addition of a scintillation fluor, vials were placed in the dark for two hours. CPM's were read on a Beta Scout scintillation counter. Adsorption controls were performed by placing 2 copepods each in scintillation vials with *K. brevis* concentrations reported above. The copepods were not incubated but instead immediately removed, filtered onto 12µm Nuclepore filters, rinsed with filtered seawater, dissolved with Hyamine hydroxide, and placed in the dark for 2 hours. CPM's were counted as described above on a Beta Scout scintillation counter.

Radioactivity of *K. brevis* cells was determined by filtering 0.1 ml of the labeled culture onto 1µm Nuclepore filters. Cells were dissolved in Hyamine hydroxide and CPM's recorded.

For remaining dominants within the blooms, the lowest published grazing rates reported for a variety of species that occur on the WFS were used (Table 2). Grazing rates for *Centropages velificatus* copepodites and *Oithona colcarva* and *Parvocalanus crassirostris* adults were determined using allometric derivations[1] based on the biomass of adult *C. velificatus, Oithona plumifera*, and *P. quasimodo,* respectively (Frost, 1980).

Excretion rates

Excretion rates were determined for *Acartia tonsa*, *Temora turbinata* and *Labidocera aestiva*. Zooplankton were collected with a 153µm mesh net. Tows were conducted from a boat, ship, and from the pier. If collected from a boat or ship, engines were cut and the tow collected with the drift of the boat or ship. Occasionally, it was

[1] Based on the allometric equations of Frost, 1980 $Y = \alpha m^b$, where $b = 0.75$.

Table 2
Taxon and life stage specific grazing rates for zooplankton taxa dominant within *K. brevis* blooms, pro-rated for a 24-hr day.

Taxon	Grazing rate	Source
O. colcarva	1.5 ng chl ind^{-1} day^{-1}	Dagg 1995, Sutton et al., 1999
Temora turbinata	41.5 ng chl ind^{-1} day^{-1}	Dagg 1995; Kirboe et al., 1985; Sutton et al., 1999
C. velificatus	16 "	Dagg 1995; Kirboe et al., 1985; Sutton et al., 1999
CV	2.8-6.4 "	
Evadne tergestina	.432 "	Sutton, 1999
Oikopleura dioica	92.9 "	Dagg 1995; Sutton et al., 1999

1. Cell Counts
2. Gut Fluorescence

a. Allometric derivation from *O. plumifera* (Frost, 1980)
b. Allometric derivation from *P. quasimodo*(Frost, 1980)
c. Allometric derivation from adult (Frost, 1980)

necessary to come ahead 1-2 knots to keep current flowing through the net. Typically, tows were conducted at the surface, though occasionally oblique tows from bottom to surface were conducted.

After being brought on board, cod ends were immediately diluted into a larger volume of natural seawater. The bucket was then covered with several layers of shade cloth to reduce light. Animals were sorted on an Olympus compound microscope. Animals were rinsed with filtered seawater and counted into 200 ml sealed chambers that contained either filtered seawater, natural seawater, or natural seawater with 10^4 cell l^{-1} concentration of *K. brevis* added. Zooplankton were incubated in the sealed chambers for two hours. Zooplankton were then transferred onto 60µm mesh net, rinsed with filtered seawater, and placed in filtered seawater in 60ml BOD bottles. The BOD bottles were wrapped in aluminum foil, placed in the incubator, and allowed to incubate for 8 hours. Controls consisted of BOD bottles filled with filtered sea water and incubated for 8 hours.

After the 8 hour incubation period, filtered seawater from the BOD bottles was filtered through a 60µm mesh net into 60ml acid cleaned bottles and frozen. Zooplankton were rinsed onto GF/F filters with filtered seawater and rinsed 3 times with ammonium formate. Zooplankton were then counted on the filter, wrapped in aluminum foil and frozen. At a later date, samples were dried in a drying oven to constant weight and weighed on a Cahn Electrobalance.

Statistical Analysis

After investigation of the data, a variety of statistical analyses were employed to quantify trends suggested by examination of raw data or shade matrices. Analyses consisted of comparing community composition between stations, clustering stations into observed groups, and relating environmental variables with community composition.

The use of univariate statistics was rejected in favor of multivariate statistics due to the nature of the data collected. The temporal and spatial spread of samples across isobaths resulted in a data set with a large number of zeros, even for common species. This made it impossible to reduce counts to the normality required for univariate statistics, and subsequently resulted in a right skewed abundance probability distribution (Clark and Warwick, 1994). Furthermore, univariate statistics require that the number of species be small in relation to the number of samples, a requirement that could not be met with the data presented here, where the number of species/taxa identified was greater than the number of samples (Clark and Warwick, 1994). An additional factor in deciding to use multivariate statistics was the nature of the study design. Because sampling location, times and the number of samples obtained were confined within the parameters of ECOHAB cruises, the data set was essentially composed of "convenience samples," and would not satisfy required a priori assumptions for univariate statistics (Motulsky, 1995).

Multivariate statistics utilizes comparisons between two samples based on the extent to which these samples share particular species at comparable levels of abundance (Clarke and Warwick, 1994). Though less rigorous than univariate statistics, the results obtained provided a truer picture of the variations in community composition for this data set. Multivariate statistics has become an increasingly common method to analyze

zooplankton community structure (see for example Jerling and Cyrus, 1998; Pakhomov et al., 1999; Hunt et al., 2001; Clark et al., 2001; Poulson and Reusse, 2002; Auel and Hagen, 2002).

Three statistical methods of the PRIMER (Plymouth Routines in Multivariate Ecological Research) program were employed (Clarke and Warwick, 1994). These were 1) hierarchal clustering into groups of samples, 2) calculation of species contributions (SIMPER) to each group, and 3) correlation between environmental data and community composition (BIOENV).

Hierarchal clustering of samples into groups Hierarchal clustering was used to identify groups of samples. The starting point for hierarchal cluster analysis was the calculation of Bray-Curtis (also known as Czekanaowski) similarity coefficients for every pair of samples, and the subsequent development of a triangular similarity matrix. Several methods of data transformation for calculation of similarity coefficients are available to emphasize certain aspects of the data set. At the two extremes of data transformation are no transformation and total transformation to presence/absence (Clarke and Warwick, 1994). No transformation of the data tends to give a greater emphasis to differences in absolute numerical abundance (Clarke and Warwick, 1994), a situation that was less than desirable here due to the decrease in numerical abundance of zooplankton with increasing distance offshore and the inherent variability of net tows. On the other end of the spectrum is transformation of the data to presence/absence only, which tends to over emphasize the contribution of rare species (Clarke and Warwick, 1994). This was also thought to be undesirable because the primary goal of the study was to analyze the typical zooplankton assemblage in the study area.

A fine balance was sought between minimizing variations in abundance to account for differences in near shore/offshore numerical abundance gradients and net tow variability without reducing the data to such an extent that rare species dominated the assemblage. Moderate transformation of absolute numerical abundance (square root transformation) was chosen because it reduced the importance of numerical abundance somewhat while still retaining enough information on the prevalence of a species that the more common species were given more weight then the rare ones (Clarke and Warwick, 1994).

Representation of the groups obtained through calculation of similarity coefficients was accomplished through the use of dendrograms, which allow for a visual interpretation of sample groups. In dendrograms, percent similarity is shown on the y-axis, with all samples represented on the x-axis. Similarity of 100% indicates that the samples are identical, while 0% similarity indicates that the samples are completely dissimilar. When transferred to a dendrogram, samples that are most similar to each other are grouped first, and the groups themselves form clusters at lower levels of similarity. The process ends with a single cluster containing all the samples (Clarke and Warwick, 1994).

Several linkage options, single, complete and group averaged, can be used for clustering samples. In single linkage, dissimilarity between the groups is shown as the maximum distance apart of the two groups. The pair with the highest similarity value is chosen and then adding the sample or species with the next highest similarity progressively enlarges the group. In practice, single linkage has a tendency to produce chains of linked samples with each successive stage just adding another single sample

onto a large group (Clarke and Warwick, 1994). In the case of the WFS data set the result was one large group that did not truly indicate the differences in community structure. Complete linkage tends to produce the opposite effect, with emphasis on small clusters at early stages (Clarke and Warwick, 1994). The result of using complete linkage for the WFS data set was numerous small groups that again did not adequately portray the observed patterns in the groups. As with the calculation of similarity coefficients, a compromise was sought that would give the maximum number of groups without compromising the overall observed structure. Therefore Group Averaged clustering was used, which is simply the average distance apart of the groups (Clarke and Warwick, 1994).

SIMPER: Calculation of species contributions to each group The SIMPER routine in PRIMER, which computes the average dissimilarity between all pairs of inter-group samples, was used to identify the primary species accounting for observed assemblage differences and to reduce the data set to those species that were responsible for >90% of the community composition. By looking at the overall percent contribution each species makes to the average dissimilarity between two groups, it is possible to list species in decreasing order of their importance in discriminating two or more sets of samples. One measure of how consistently a species contributes to the average contribution across all pairs is the standard deviation of the average contribution values. If the average contribution is large and the standard deviation small (resulting is a large ratio of average contribution to the standard deviation) then the species consistently contributes a large amount of the dissimilarity to the group. The final column in SIMPER analysis computes the percent of the total dissimilarity that is contributed by the

species, and cumulates these percentages down the rows of the table (Clarke and Warwick, 1994).

It is also possible, using SIMPER, to compute the contribution that each species makes to the average similarity *within* a group. The more abundant a species is the more it will contribute to the intra-group similarities. If it typifies the group, then the average contribution to the similarity will be high, and the standard deviation will be low. However, it is important to note that one species can typify more than one group, and that considerable overlap between groups can occur.

As with hierarchal cluster analysis, several options for transformation of raw data were available. The square root transformation used in the cluster analysis was retained for the SIMPER analysis, for the reasons described above. However in the SIMPER results tables, average abundance shown is for actual data, not for square root transformed data.

Matching of Environmental Variables to Community Composition The BIOENV routine of PRIMER attempts to match biotic variables (samples) with environmental data to determine which variable best matches community composition. Three factors were measured simultaneously with net tows: temperature, salinity and chlorophyll *a* concentration. Before analyzing data with the BIOENV routine, it was first necessary to ensure all measurements were on the same scale. This required some transformation since Chlorophyll *a* values tended to be much lower and more variable than temperature or salinity. Transformation of the environmental data was thus obtained by normalizing temperature and salinity (by subtracting lowest temperature and salinity values obtained) and then square root transforming all three variables. The transformed environmental

data was then compared to community composition using the BIOENV procedure, where combinations of environmental variables are considered at increasing levels of complexity.

The results of the BIOENV procedure do not imply causality, since several causal variables may not have been measured, but the results do imply a correlation between physical and biotic variables and sample community composition. Results of the BIOENV procedure are reported as correlation coefficients.

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CHAPTER 2

ZOOPLANKTON COMMUNITY COMPOSITION OF THE WEST FLORIDA SHELF

Abstract A comprehensive seasonal analysis of abundance, biomass and community composition of zooplankton was undertaken at 6 stations on the WFS. Monthly sampling was conducted for one year at the 5, 25 and 50-m isobaths. Abundance ranged from a low of 127 animals m^{-3} at the 50-m isobath in April 2000 to 15,179 animals m^{-3} at the 5-m isobath in August 1999. Abundance was always greatest at the 5-m isobath. Biomass ranged from 1.48 mg dry weight m^{-3} at the 50-m isobath in March 2000 to 40.93 mg m^{-3} at the 5-m isobath in August 1999. Abundance and biomass were greatest in the late summer and early fall, declining through the winter months. Two major groups in community composition were observed at the near shore (5-m and 25-m) and offshore (50-m) stations. Considerable overlap was seen in community composition between the 5-m to 25-m and 25-m to 50-m isobaths, but little overlap in community composition was observed between the 5-m and 50-m isobaths. Of the 95 species identified, only 25 proved to be important (>90%) contributors to community composition. Near shore, important contributors were *Parvocalanus crassirostris*, *Penilia avirostris*, *Paracalanus quasimodo, Oithona colcarva*, *Oikopleura dioica, Centropages velificatus* and Pelecypod larvae. As distance offshore increased, important contributors to community composition were *Euchonchoichiea chierchiae, Clausocalanus furcatus*, *Oithona plumifera*, *Oithona frigida*, *Oncaea mediteranea*, *Calaocalanus pavoninius*, *Oithona similis,* and Gastropod larvae.

INTRODUCTION

Zooplankton are important mediators of energy transfer from primary producers to higher trophic levels, and act as regulators of phytoplankton abundance, phytoplankton species structure, and seasonal phytoplankton succession (Banse, 1995; Sterner, 1989). Despite its high productivity and importance to the Gulf of Mexico (Austin and Jones, 1974), there is a paucity of zooplankton assemblage data for the West Florida shelf (WFS). *In situ* research of this trophic level on the WFS has generally taken one of two approaches. Those studies that report taxonomic composition of zooplankton assemblages are either 1) primarily descriptive (King 1950) or 2) are limited spatially and/or temporally (Hopkins et al., 1981; Sutton et al., 2001 Hopkins, 1973; Morris and Hopkins, 1981; Hopkins and Lancraft, 1984). Comprehensive taxonomic seasonal analysis of numerical abundance and biomass have been limited to estuaries of the WFS (Grice, 1956; Hopkins, 1966; Squires, 1974; Hopkins, 1977; Weiss, 1978).

Some overlap between estuarine, shelf and offshore zooplankton assemblages is expected due to mechanisms that periodically bring central Gulf water across the Florida shelf (Ortner et al., 1989; Hopkins, 1981), but accounts published to date indicate that the zooplankton populations on the WFS are different than those found in estuaries and offshore (Minello, 1980; Hopkins, 1981; Ortner et al., 1989; Sutton et al., 2001). The purpose of this chapter is to provide a comprehensive taxonomic seasonal analysis of the zooplankton assemblage of the WFS from coastal waters to the 50-meter isobath.

Methods

Sampling took place during monthly ECOHAB cruises on board the R/V Suncoaster and the R/V Bellows in the Gulf of Mexico (Figure 4). Stations were located approximately every 5 nautical miles. A CTD profile was conducted at every station. At selected stations (usually every other station, but occasionally more frequently) water samples were collected to determine chlorophyll *a* concentration and other parameters.

Zooplankton sampling began in August 1999 and continued through July 2000. The zooplankton assemblage at the 5-, 25-, and 50-meter isobaths were represented by Stations 1 and 51, Stations 5 and 46, and Stations 10 and 40, respectively (Austin, 1971; Austin and Jones, 1974; Minello, 1980; Sutton et al., 2001).

Collection of Zooplankton

1999-2000 Zooplankton were collected with a 153 μm mesh bongo net, lowered closed through the water column, opened at depth and then towed obliquely from bottom to surface. The volume of water filtered was calculated from a calibrated flow meter attached at the net mouth (Omori and Ikeda, 1992).

After being brought on board, the cod ends were filtered through a 2000 μm mesh sieve to remove large gelatinous zooplankton. Each filtered cod end was preserved on board in a 5% buffered formalin solution (Omori and Ikeda, 1992) for later counts of zooplankton species abundance.

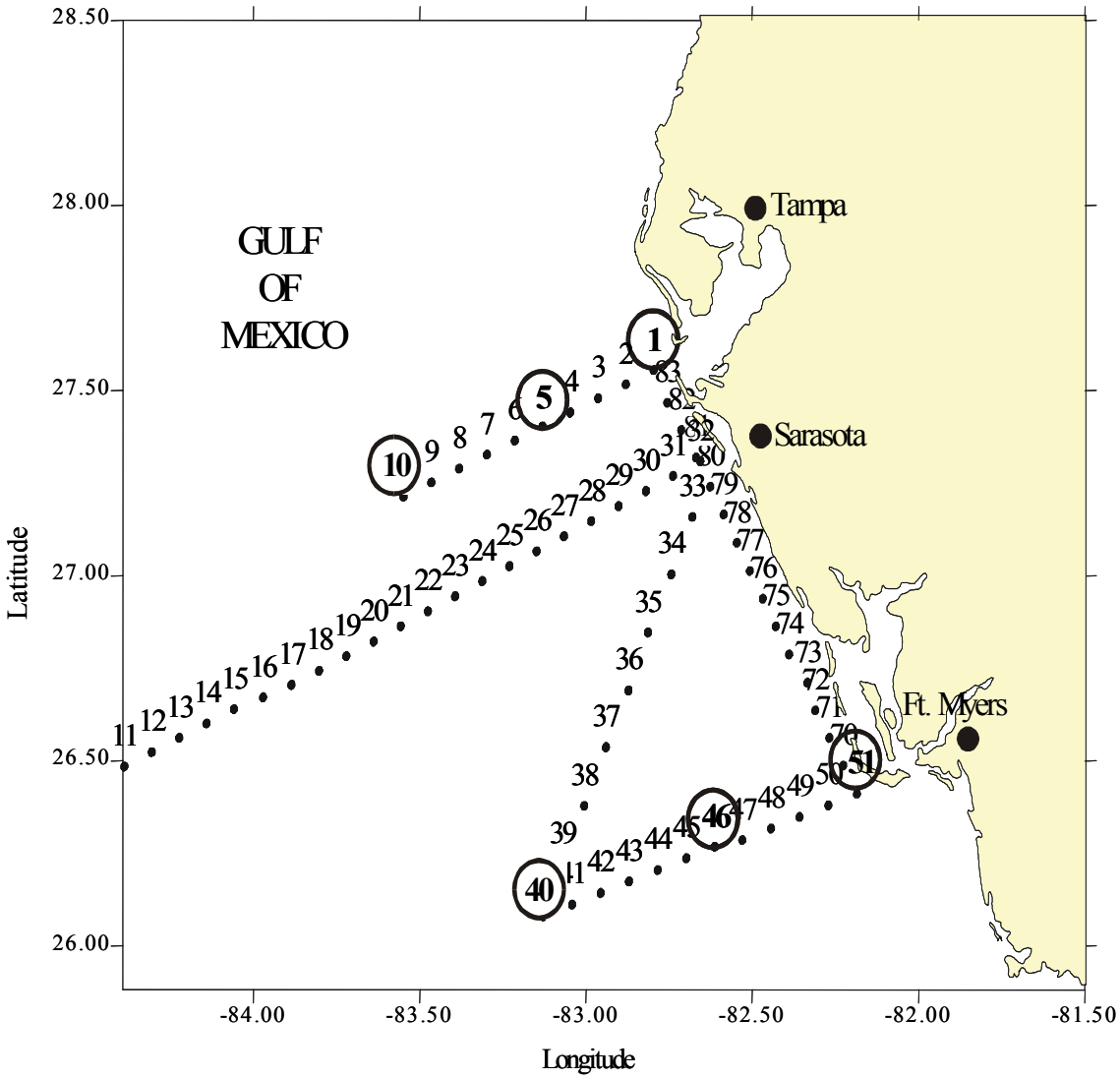

Figure 4. ECOHAB study area in the Gulf of Mexico. Station locations for ECOHAB cruises are indicated by a (•). Stations where zooplankton tows were conducted are circled and indicated by a number.

Zooplankton abundance and biomass

Representative subsamples of 500-600 animals were obtained with a Stempel pipette (usually 1-5% of initial cod end volume). Zooplankton were then identified and counted using an Olympus dissecting microscope at 10-40x magnification, with critical taxonomic features observed on an Olympus Canon dissecting microscope. Holoplankton were identified to species level whenever possible. Meroplankton were identified to major taxonomic group (e.g. Pelecypod veligers, Cirriped larvae). Copepod nauplii were not identified to species level but, when possible, were identified to family level. Replicate samples were averaged for each station. Biomass was determined using published length/width regression equations and values (Table 3 and references cited therein).

Abiotic and biotic factors

Zooplankton tows were conducted in conjunction with CTD casts and measurements of chlorophyll *a*. Water column samples were collected from Niskin bottles mounted on a rosette sampler. Duplicate chlorophyll samples were filtered onto GF/F filters, placed in 10 ml methanol and stored at -20^{o}C in darkness until later analysis with a Turner design fluorometer (Welschmeyer, 1994). Salinity, temperature and Chlorophyll *a* were averaged over the water column.

Statistical Analysis

Observed community associations were quantified using the multivariate statistical techniques of PRIMER (Plymouth Routines in Multivariate Ecological

Table 3
Sources of biomass values and length/width regression equations for WFS zooplankton taxa.

Taxon	Source	Comments
Undinula	Morris and Hopkins, 1983	
Eucalanus	Morris and Hopkins, 1983	
Acrocalanus	Weiss, 1978	Derived from *Paracalanus*
Calocalanus	"	
Paracalanus	"	
Clausocalanus	"	Derived from *Centropages*
Scolothrex	Morris and Hopkins, 1983	
Euchaeta	Morris and Hopkins, 1983	
Temora	Lester, unpub. Data	
Centropages	Weiss, 1978	
Calanopia	"	
Pseudodiaptomas	"	
Acartia	"	
Tortanus	"	
Labidocera	"	
Oithona	"	
Oncaeae	Squires, 1984	
Corycaeus	Weiss, 1978	
Farranula	"	
Euterpina	"	
Microsetaella	"	
Euchonchoichiea	Hopkins, 1984	
Penilia	Weiss, 1978	
Evadne	"	
Podon	"	*E. tergestina* value
Appendicularians	"	
Brachiopoda	"	
Bryozoa	"	
Cirripedia	"	
Decapoda	"	
Echinodermata	"	
Gastropoda	"	
Pelecypoda	"	
Platyhelminthe	Squires, 1984	
Polychaeta	Weiss, 1978	

Research) software. Hierarchal clustering analysis was used to identify trends in community distribution of the zooplankton assemblage. Bray-Curtis similarities (Clarke and Warwick, 1994) were calculated and subsequently ranked within a similarity matrix. Data were not standardized, since all stations were already on the same scale of abundance m^{-3}. However a square root transformation was performed to minimize variations in abundance (Clarke and Warwick, 1994). Similarity percentages within and between groups of zooplankton were determined using PRIMER's SIMPER routine, which calculates the average dissimilarity between inter-group samples and computes dissimilarities between groups (Clarke and Warwick, 1994). PRIMER'S BIOENV procedure was used to determine which measured variable contributed most to community composition. The BIOENV procedure matches transformed environmental data (in this case, salinity, temperature and chlorophyll *a* concentration) to changes in community composition. Environmental data were normalized and log transformed to ensure that all measurements were on the same scale.

RESULTS

Abiotic and Biotic Factors in the Study Area

Isobath averaged temperature ranged from 18.4 to 31.2 ^{o}C, with highest temperatures occurring from June through September, and lowest temperatures from December through March (Figure 5). Temperature fluctuations were most pronounced at the 5-meter isobath, where the highest (31.2 ^{o}C) and lowest (18.4 ^{o}C) surface temperatures recorded in the study area occurred. Temperature fluctuations from month

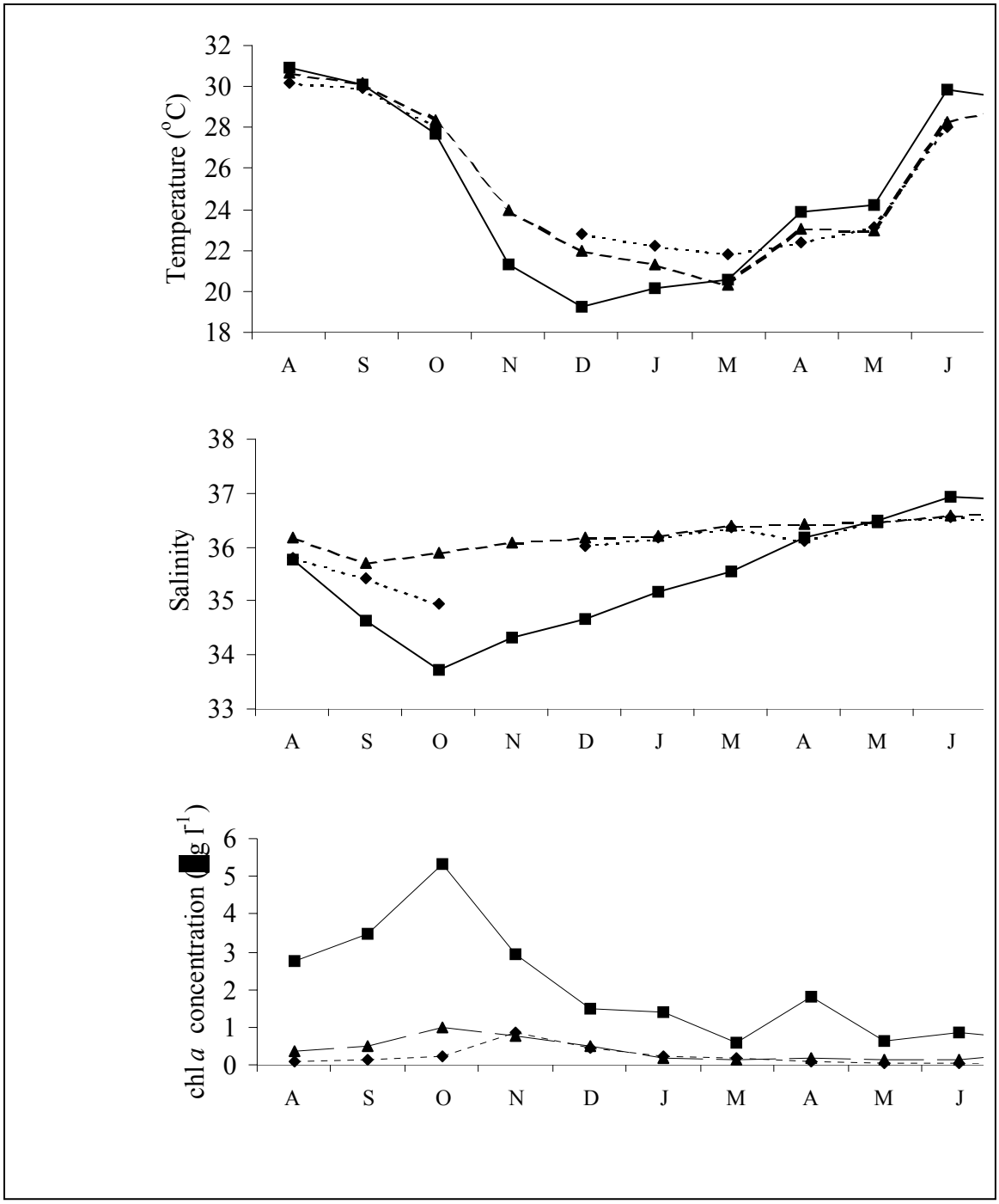

Figure 5. Temperature, Salinity and Chlorophyll *a* concentrations at the 5-meter (—■—), 25-meter- (—▲—), and 50-meter (--♦----) isobaths. Note that no data was collected in February of 2000.

to month became less pronounced as distance offshore increased. Temperature at the 25-meter isobath ranged from 19.2 to 30.4 ^{o}C, while temperature at the 50-meter isobath ranged from 19.9 to 28.6 ^{o}C. At all isobaths, the highest temperature occurred in August. At the 5-meter isobath, the lowest temperature occurred in December, while further offshore lowest temperatures occurred in March.

Isobath averaged salinity ranged from 34.2 to 37.1 ppt (Figure 5). The greatest range in salinity was found at the 5-meter isobath. Generally, salinity was lowest at the 5-meter isobath, while salinity at the 50-meter isobath followed the same trend and values as the 25-meter isobath throughout much of the year.

Isobath averaged chlorophyll *a* concentration ranged from less than 0.1 μg l^{-1} at the 50-meter isobath in spring and summer to 2.79 μg at^{-1} l^{-1} at the 5-meter isobath in October (Figure 5). Chlorophyll *a* concentration was highly variable at Stations 1 and 51, with a greater than two fold difference in chlorophyll *a* concentrations in October 2000 to January 2001. At offshore stations, chlorophyll *a* concentration was less variable, with the exception of April 2001 at the 50-meter isobath, where chlorophyll *a* concentration approached the near shore concentration, most likely due to influx of high chlorophyll Mississippi and Apalachicola river water to areas offshore in the Gulf of Mexico (Gilbes et al., 1996; Gilbes et al., 2002). This assertion is supported by the slight drop in salinity in April at Station 40 (Figure 6). Chlorophyll *a* concentration was usually highest at the 5-meter isobath, and dropped off significantly as distance offshore increased.

Chlorophyll *a* concentration was usually higher at the 25-meter isobath than at the 50-meter isobath, although there were sampling periods where the isobath averaged

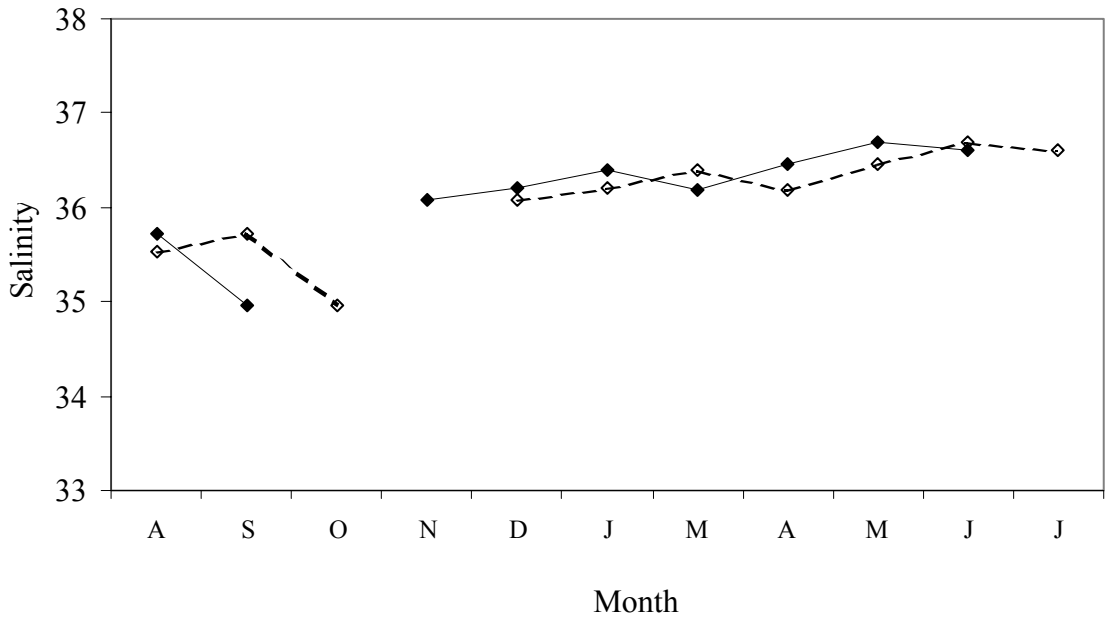

Figure 6. Salinity at Stations 10 (—◆—) and 40 (—◇—) for the 1999-2000 sampling period. No data was collected in February of 2000.

chlorophyll concentration at the 50-meter isobath either matched or exceeded the concentration at the 25-meter isobath. For all isobaths, chlorophyll *a* concentration was generally highest in the late summer and fall, declined through the winter, increased in April, and then declined again through the summer (Figure 5).

Zooplankton Abundance and Biomass

Isobath averaged zooplankton abundance ranged from a low of 127 m^{-3} animals at the 50-meter isobath in April 2000 to 15,179 m^{-3} animals at the 5-meter isobath in August 1999 (Figure 7). Abundance was always greatest at the 5-meter isobath and was generally higher in the late summer and early fall, declining through the winter months.

Isobath averaged zooplankton biomass ranged from 1.48 mg m^{-3} at the 50-meter isobath in March 2000 to 40.93 mg m^{-3} dry weight at the 5-meter isobath in August of 1999 (Figure 7). Biomass was usually greatest at the 5-meter isobath, except for January 2000, when biomass was higher at the 50-meter isobath. Biomass was usually greater at the 50-meter isobath than the 25-meter isobath, except for April, May and June 2000, when biomass was higher at the 25- isobath.

Zooplankton Community composition

Group determination - Cluster analysis Two groups of stations separated at the 35% similarity level (Figure 8). All of the 5-meter isobath stations are included in Group I, while all the 50-meter isobath stations are included in Group II. Stations at the 25-

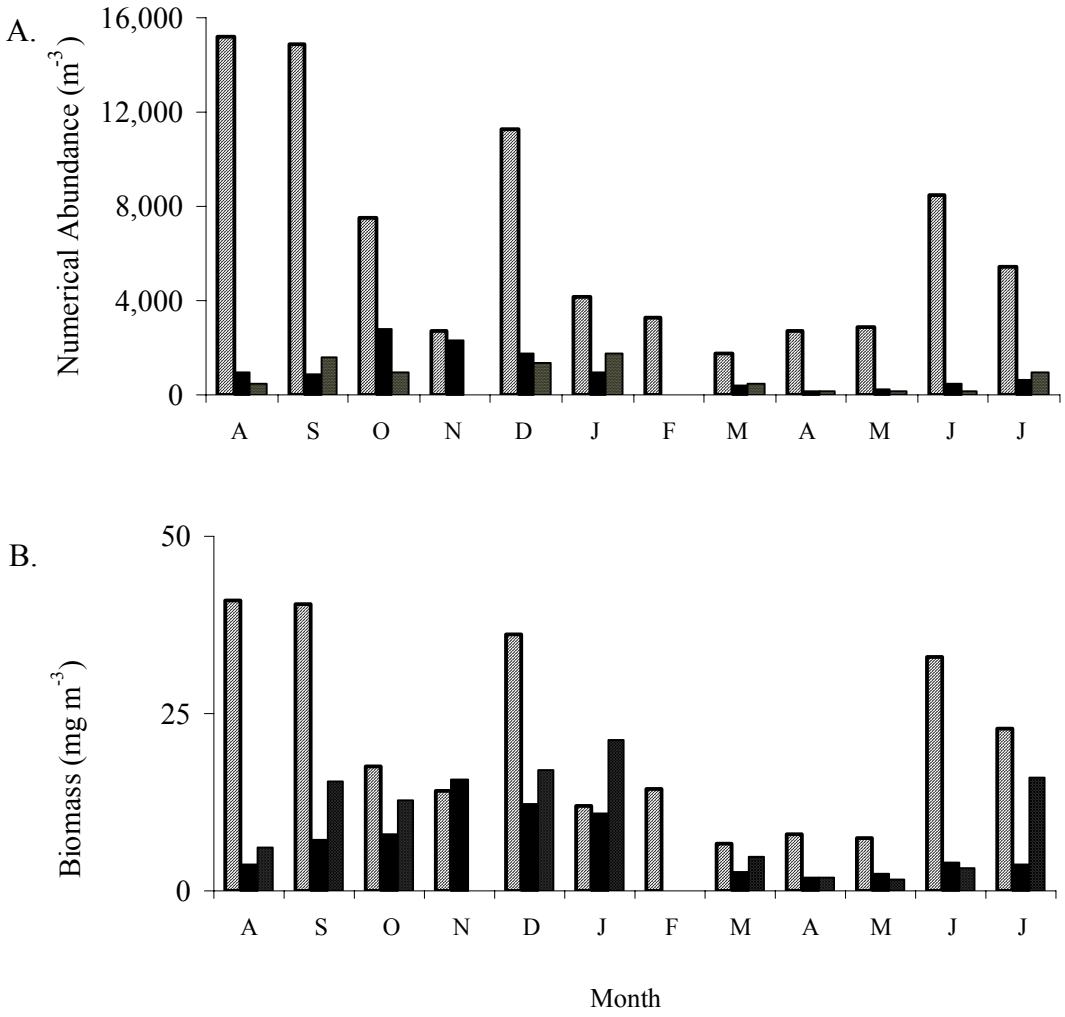

Figure 7. A. Total zooplankton abundance m^{-3} for the 5-m (hatched bars), 25-m (solid bars), and 50-m (dotted bars) isobaths. B. Total zooplankton biomass in dryweight mg^{-3} for the 5-m (hatched bars), 25-m (solid bars), and 50-m (dotted bars) isobaths.

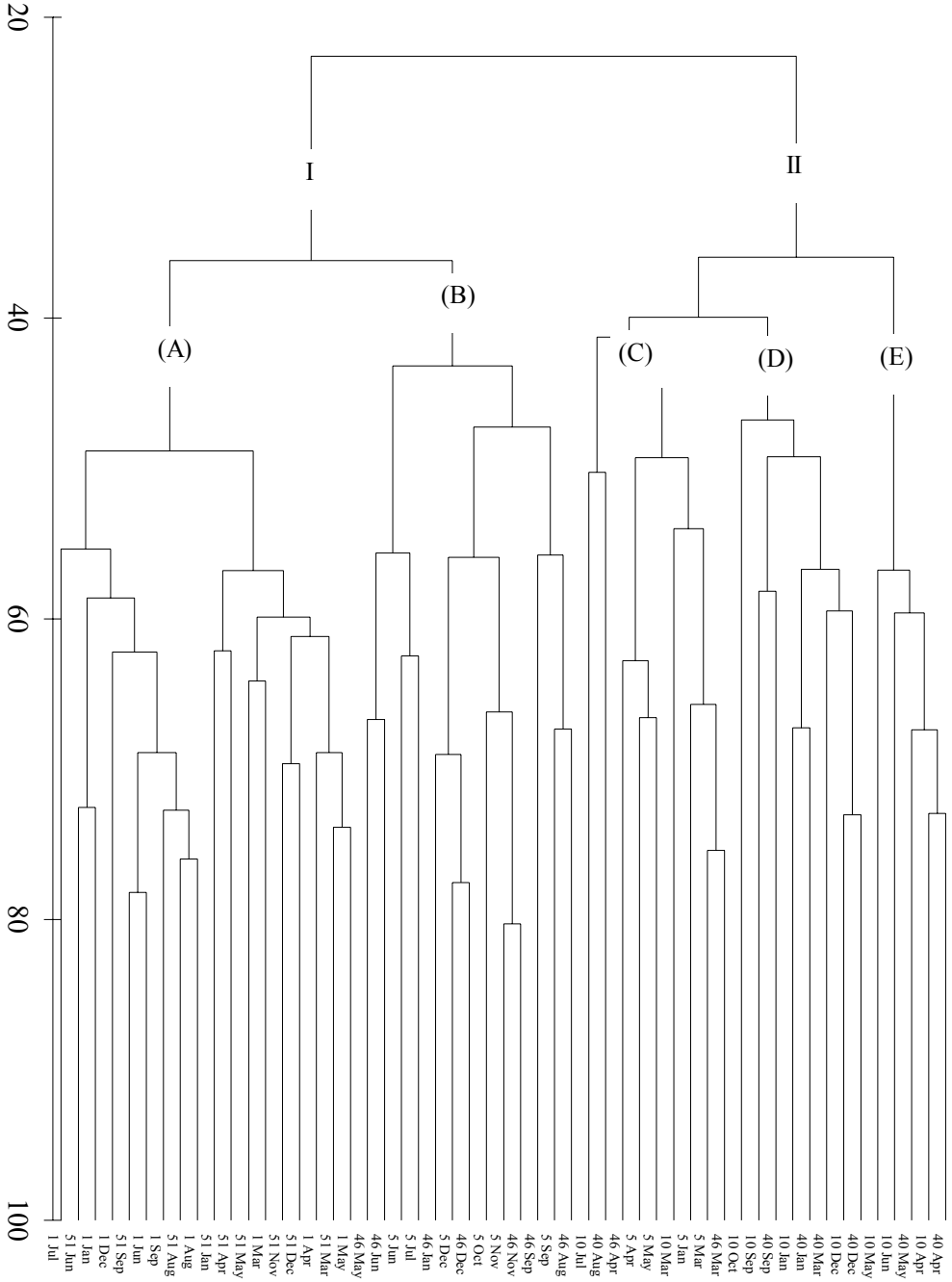

Figure 8. Cluster derived dendrogram for 53 stations at the 5, 25 and 50-meter isobaths, using group averaged clustering from Bray-Curtis similarities on square root transformed abundance data.

meter isobath are divided between Groups I and II, with the majority falling into Group I. Groups I and II separated at the 40% similarity level into 5 sub-groups. Subgroup A is comprised entirely of 5-meter isobath stations. Subgroup B is comprised of summer and fall 25-meter isobath stations, with all of the remaining 25-meter isobath stations falling into subgroup C. Subgroup D is comprised of a mix of winter/spring 25-meter isobath stations and winter/spring 50-meter stations. Only late spring/early summer 50-meter isobath stations are included in Subgroup E.

Determination of discriminating species – SIMPER analysis The SIMPER routine of primer was implemented to determine which zooplankton species were typical of each subgroup (Clarke and Warwick, 1994). Those species that contributed to 90% of the total abundance were included in the analysis. 4 species were responsible for 64% of the community composition of Subgroup A (Table 4). The copepods *Parvocalanus crassirostris* and *Oithona colcarva* were the primary species defining the group, contributing 26.64 and 19.28%, respectively, to community composition. The cladoceran *Penilia avirostris* contributed 11.00% to community composition, while the copepod *Paracalanus quasimodo* contributed 7.23%.

Considerable overlap in community composition was seen between Subgroups A and B, with 6 of the 11 species that contributed to 90% of the community composition of Subgroup A also contributing to 90% of the community composition of Subgroup B (Table 5). Two thirds (64.59%) of the community composition of Subgroup B was defined by 5 taxa: *P. quasimodo* (25.53%), *O. colcarva* (15.66%), the larvacean *Oikopleura dioica* (12.16%), the copepod *Centropages velificatus* (5.69%), and Pelecypod larvae (5.55%).

Table 4
Results of SIMPER analysis for Subgroup A.

Species	Av.Abund	Sim/SD	Contrib%	Cum.%
P. crassirostris	1655.08	1.55	26.64	26.64
O. colcarva	1224.78	0.87	19.28	45.92
P. avirostris	1105.17	0.47	11.00	56.92
P. quasimodo	343.92	1.11	7.23	64.15
Cirripedia	477.53	0.95	6.91	71.06
E. acutifrons	355.67	0.81	5.44	76.50
Pelecypoda	271.31	0.58	4.26	80.76
Decapoda	201.53	1.02	3.27	84.03
C. americanus	108.06	0.73	2.81	86.84
O. nana	141.5	0.51	2.20	89.04
Gastropoda	106.39	0.93	2.15	91.19

Table 5
Results of SIMPER analysis for Subgroup B.

Species	Av.Abund	Sim/SD	Contrib%	Cum.%
P. quasimodo	172.92	1.55	25.53	25.53
O. colcarva	121.85	1.24	15.66	41.19
O. dioica	72.08	1.5	12.16	53.35
C. velificatus	114.77	0.59	5.69	59.04
Pelecypoda	87.92	0.75	5.55	64.59
Gastropoda	59.5	0.91	5.47	70.06
P. crassirostris	41.12	1.07	5.31	75.37
O. mediteranea	71.15	0.64	4.27	79.64
O. plumifera	24.88	1.19	3.86	83.5
E. acutifrons	47.58	1.02	3.55	87.05
E. chierchiae	96.73	0.2	2.46	89.51
C. amazonicus	28.54	0.9	2.15	91.66

Only 4 out of 11 species from Subgroup A were responsible for the top 90% of community composition in Subgroup C, though 8 out of 12 species in Subgroup B proved to be important there (Table 6). Two thirds (65.07%) of the community composition of Subgroup C were defined by 5 species: the ostracod *Euchonchoichiea chierchiae* (21.01%), the copepod *Clausocalanus furcatus* (16.81%), *O. dioica* (10.86%), *C. velificatus* (8.45%), and the *Oithona Plumifera* (7.94%). Seven out of 11 species from Subgroup C were also important contributors to the community composition of Subgroup D (Table 7). Two thirds (64.43%) of the community composition of Subgroup D was defined by 4 species: *E. chierchiae* (30.06%), *Oithona frigida* (13.08%), *C. furcatus* (11.18%) and *Oncaea mediteranea* (10.12%).

Some overlap between Subgroups D and E was seen, with 6 out of 11 species from subgroup D included in the 9 species contributing to Group E (Table 8). Major contributors (63.47%) to community composition of Subgroup E were *C. furcatus* (19.06%), *Calaocalanus pavoninius* (18.13%), *Oithona similis* (15.17%) and Gastropod larvae (11.11%).

Determination of discriminating species – Shade Matrix The shade matrix compiled for the 5 subgroups confirms the considerable overlap in community composition between subgroups (Figure 9). In this figure, near shore groups trend to the upper left, offshore groups to the lower right. Represented this way, the considerable overlap between groups B, C and D is evident, as is the overlap between subgroups A and B and D and E. However, little overlap is observed between near shore subgroup A and offshore subgroup E.

Table 6
Results of SIMPER analysis for Subgroup C.

Species	Av.Abund	Sim/SD	Contrib%	Cum.%
E. chierchiae	65.39	0.75	21.01	21.01
C. furcatus	44.83	1.09	16.81	37.82
O. dioica	24.33	1.50	10.86	48.68
C. velificatus	11.50	2.58	8.45	57.13
O. plumifera	16.67	2.13	7.94	65.07
Gastropoda	17.61	1.34	6.75	71.82
O. colcarva	11.11	0.66	5.63	77.45
O. mediteranea	11.17	0.70	4.25	81.70
P. quasimodo	13.89	0.58	3.96	85.66
Pelecypoda	8.50	0.60	2.75	88.41
C. pavo	10.11	0.41	2.71	91.11

Table 7
Results of SIMPER analysis for Subgroup D.

Species	Av.Abund	Sim/SD	Contrib%	Cum.%
E. chierchiae	316.81	1.29	30.06	30.06
O. frigida	101.19	1.2	13.08	43.13
C. furcatus	114.56	1.98	11.18	54.31
O. mediteranea	100	1.76	10.12	64.43
O. dioica	68.75	1.14	7.19	71.62
Gastropoda	55.31	1.35	5.64	77.27
O. plumifera	64.25	1.03	5.23	82.5
C. velificatus	29.5	1.06	3.51	86.01
P. pygmaeus	43.38	0.51	2.02	88.03
P. aculeatus	41.63	0.53	1.52	89.55
C. limbatus	19.69	0.5	1.33	90.88

Table 8
Results of SIMPER analysis for Subgroup E.

Species	Av.Abund	Sim/SD	Contrib%	Cum.%
C. furcatus	18.8	2.35	19.06	19.06
C. pavoninius	19.5	1.57	18.13	37.19
O. similis	15.6	2.93	15.17	52.36
Gastropoda	11.7	1.33	11.11	63.47
E. chierchiae	12.7	1.30	10.12	73.59
O. mediteranea	13.0	0.81	7.69	81.28
O. dioica	5.8	1.20	4.21	85.50
O. plumifera	4.1	1.44	3.28	88.78

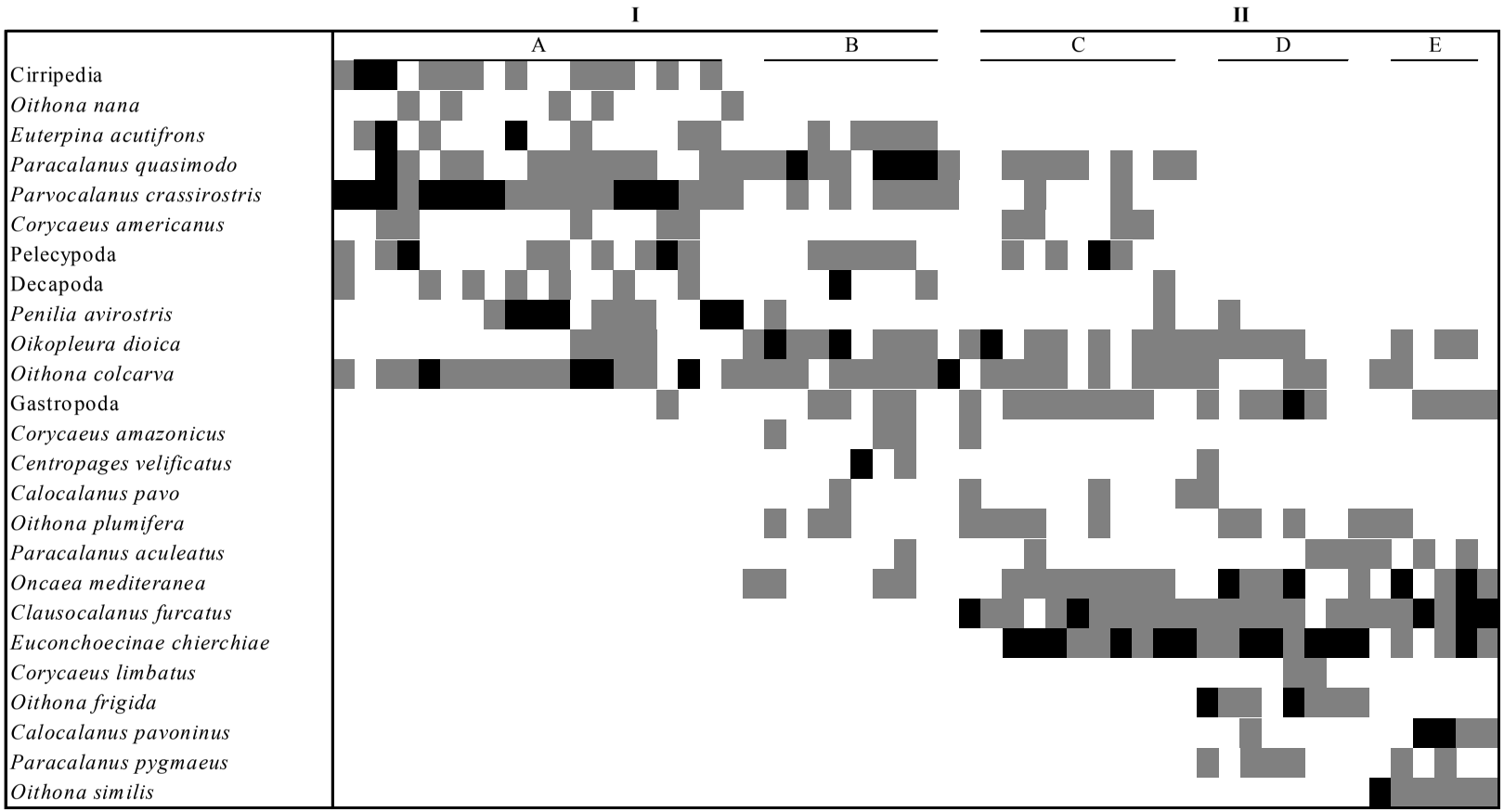

Figure 9. Shade matrix for WFS zooplankton subgroups A-E. Black squares indicate those months where the species was dominant. Gray squares indicate a species was present. White squares indicate the absence of a species. Near shore species trend to the upper left, offshore species to the lower right. Those species that showed considerable overlap between groups fall into the middle of the matrix.

Community associations with abiotic and biotic factors

Temperature All subgroups, with the exception of subgroup E, showed a wide range in temperature (Figures 10-14). The greatest range in temperature was observed for subgroups A and B, where highest mean temperatures were also observed (Figure 11, Table 9). As distance offshore increased, range in temperature and highest temperature observed decreased. Lowest mean temperature was observed for Subgroup C (Figure 12), while the narrowest range in temperature occurred in subgroup E, where only spring offshore stations are represented (Figure 14).

Salinity Range in salinity was greatest at subgroup A, with a range of 34.2 to 37.1 ppt (Figure 11). Lowest mean salinity was also seen for subgroup A (Table 9). A narrower range and higher mean were observed for subgroup B, where salinity ranged from 35.9 to 36.7 (Figure 12). The range in salinity narrowed as distance offshore increased, with the narrowest range in salinity, 36.4 to 36.6, observed for subgroup E (Figure 15).

Chlorophyll a The greatest range in chlorophyll *a* concentration was seen in near shore subgroup A, with mean chlorophyll *a* concentration and range of chlorophyll *a* concentration decreasing as distance offshore increased (Figure 11, Table 9). Chlorophyll *a* concentration decreased as distance offshore increased (Figures 11-15). The narrowest range in Chlorophyll *a* concentration occurred in subgroup E, where lowest mean Chlorophyll *a* concentration was also observed (Figure 15, Table 9).

BIOENV The BIOENV procedure of PRIMER was used to determine which of the three measured variables, Temperature, Salinity or Chlorophyll *a*, correlated best with

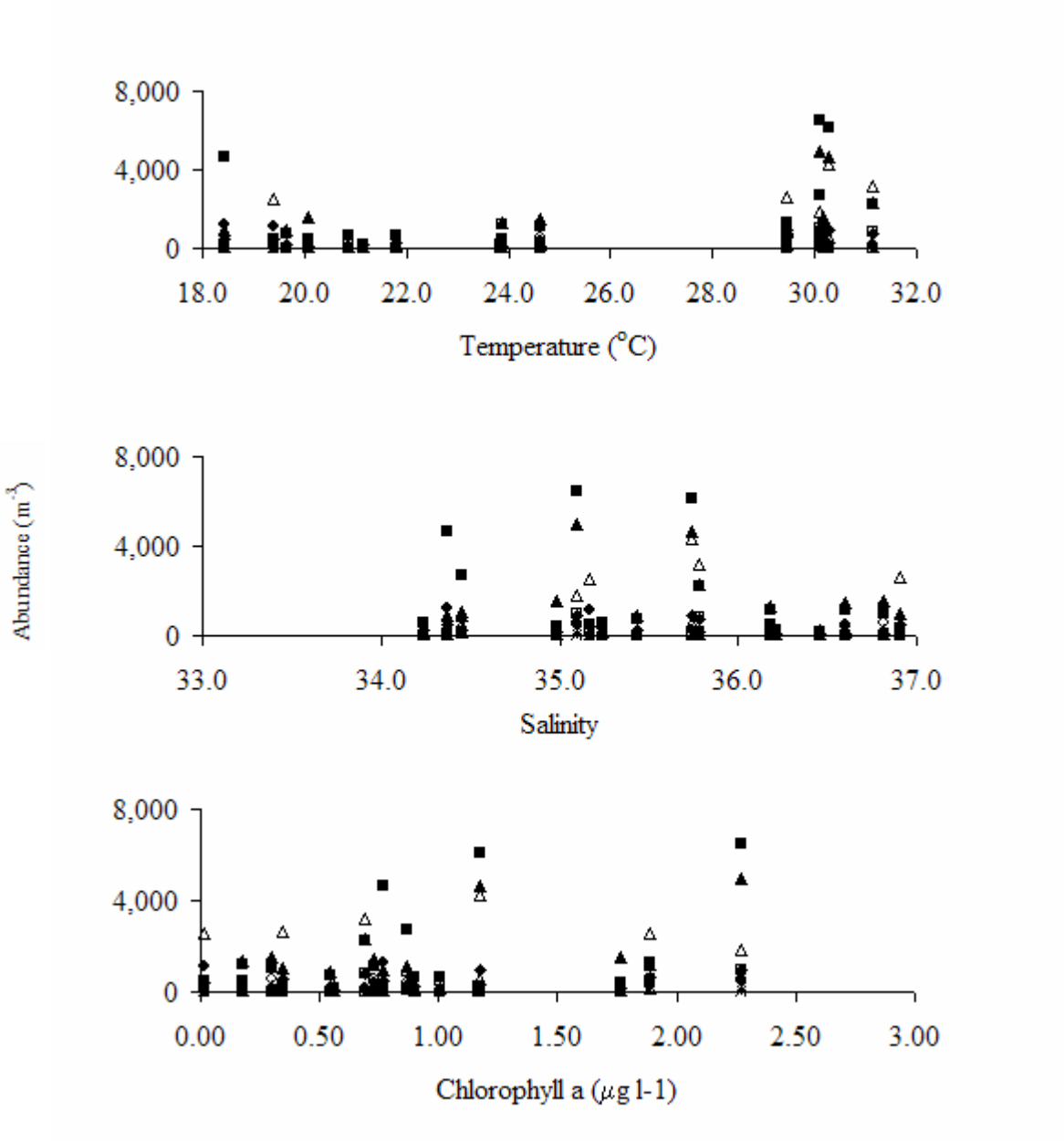

Figure 10. Distribution of a) Temperature, b) Salinity and c) Chlorophyll *a* for Subgroup A.

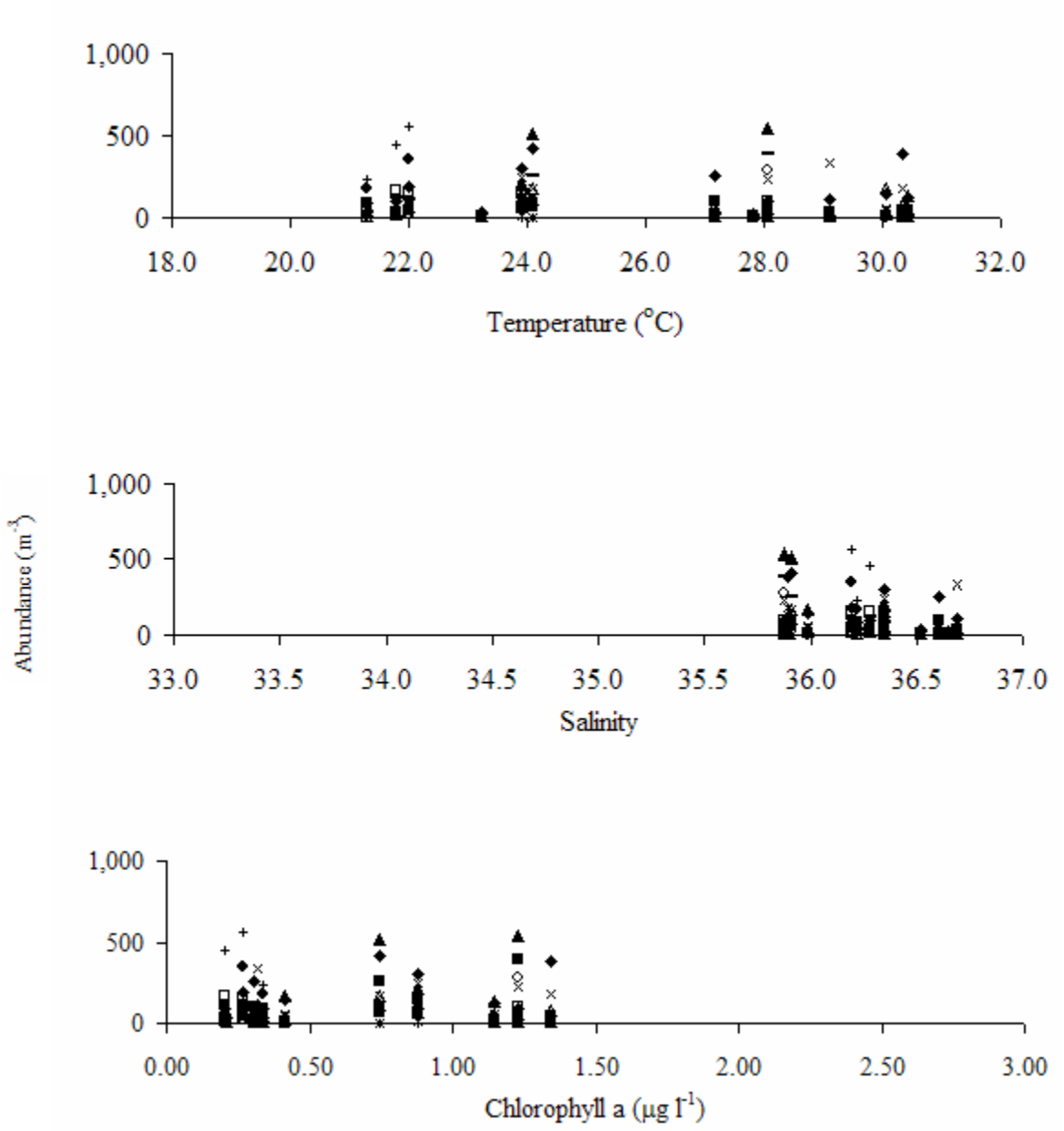

Figure 11. Distribution of a) Temperature, b) Salinity and c) Chlorophyll *a* for Subgroup B.

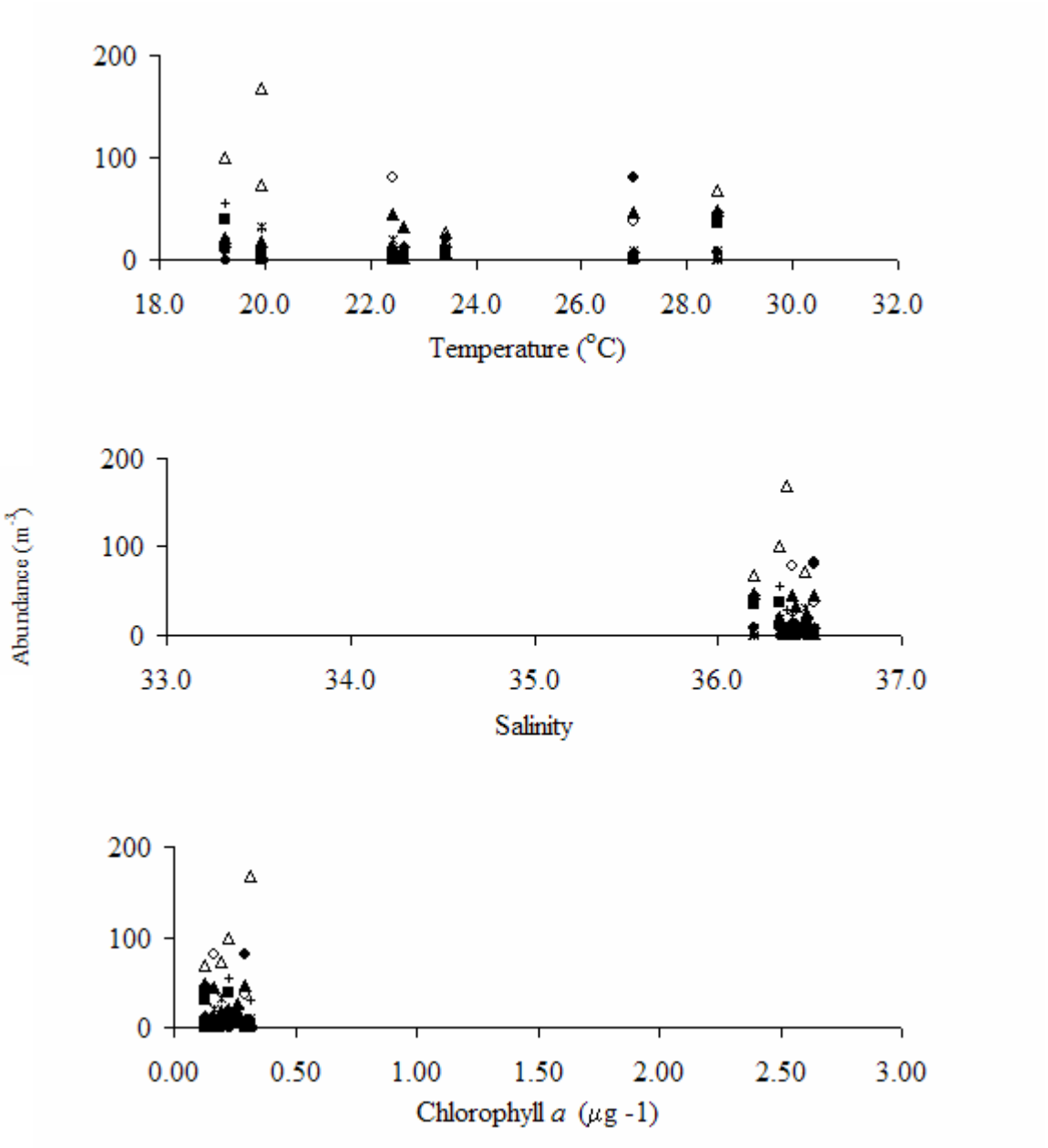

Figure 12. Distribution of a) Temperature, b) Salinity and c) Chlorophyll *a* for Subgroup C.

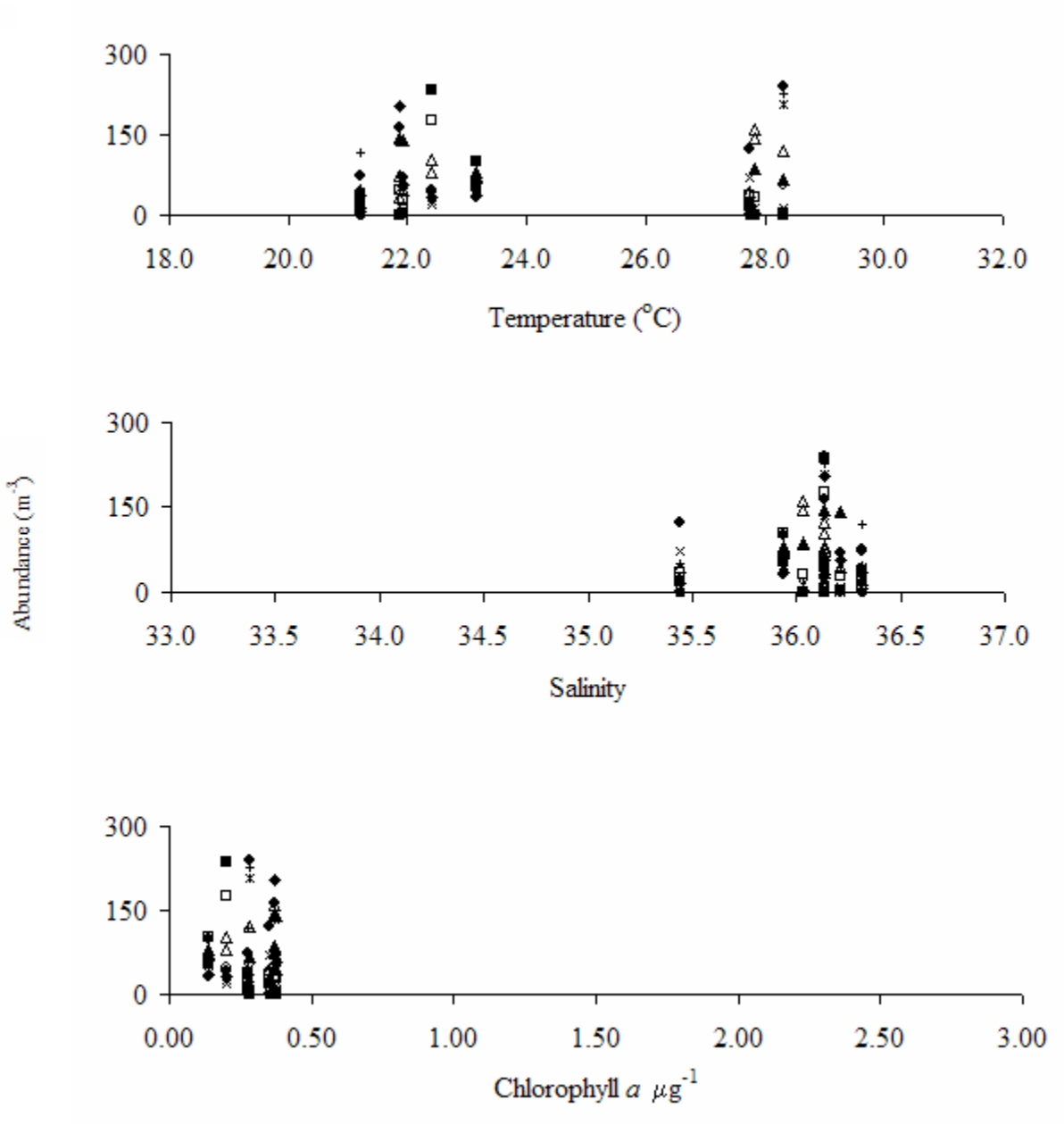

Figure 13. Distribution of a) Temperature, b) Salinity and c) Chlorophyll *a* for Subgroup D.

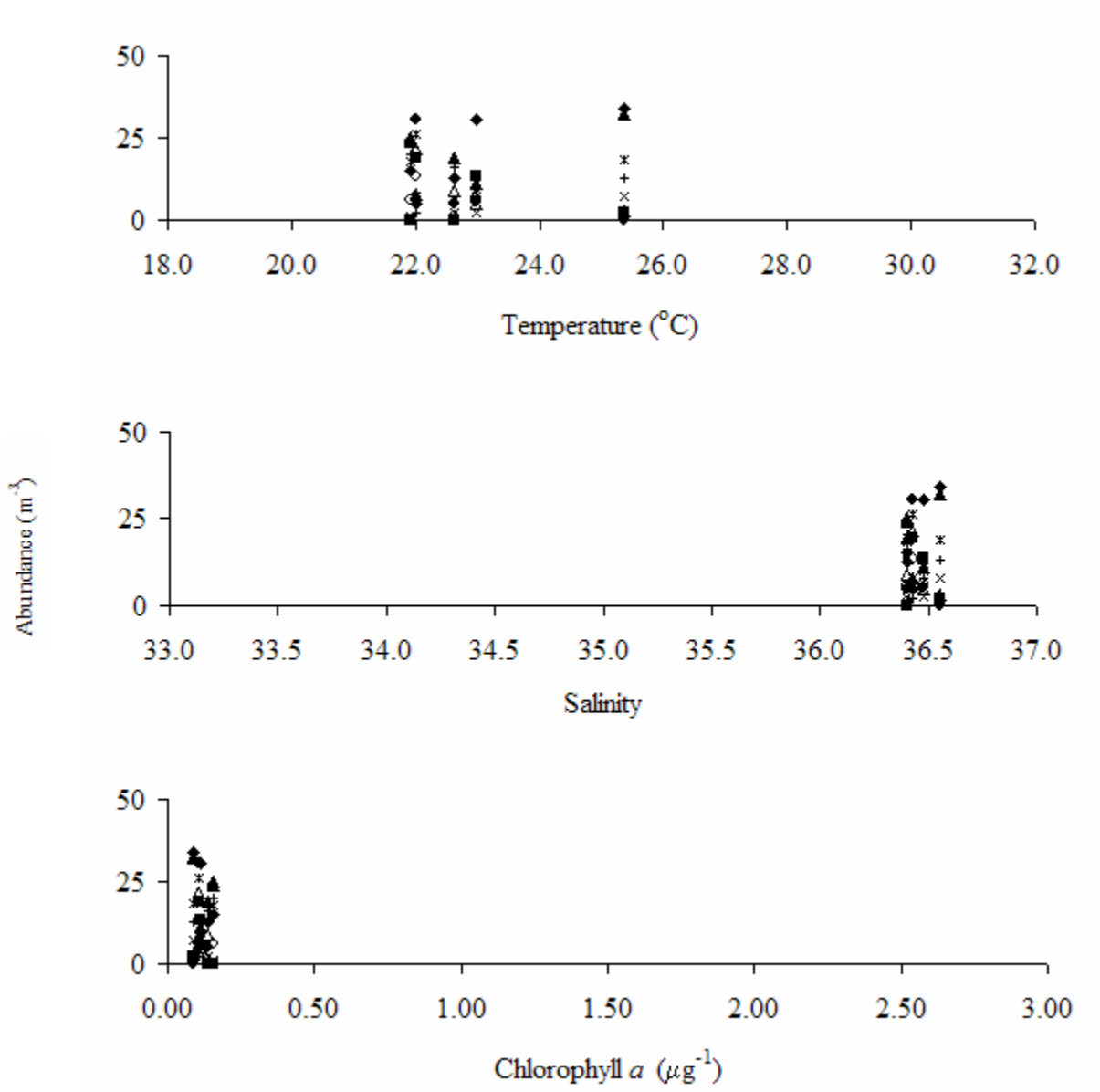

Figure 14. Distribution of a) Temperature, b) Salinity and c) Chlorophyll *a* for Subgroup E.

Table 9
Environmental and biotic variables for subgroups A-E.

	Temperature			Salinity			Chlorophyll *a*		
Subgroup	Range	Mean	St Dev	Range	Mean	St Dev	Range	Mean	St Dev
A	18.4- 31.3	24.91	4.59	34.2- 37.1	35.70	0.89	.27- 4.47	1.72	1.33
B	21.3- 30.4	26.10	3.47	35.9- 36.7	36.27	0.29	.20- 1.34	0.59	0.42
C	19.2- 28.6	22.89	3.39	36.2- 36.5	36.40	0.10	.13- 0.31	0.21	0.07
D	21.2- 28.3	24.30	3.09	35.4- 36.3	36.04	0.27	.14- 0.38	0.30	0.09
E	21.9- 25.4	22.98	1.41	36.4- 36.6	36.45	0.07	.09- 0.15	0.12	0.03

community composition (Table 10). The single variable which correlated best with community composition was Chlorophyll *a* concentration (corr. of .353).

DISCUSSION

Abundance

Comparison of zooplankton abundance between studies is often difficult due to variations in sampling methods such as mesh size and seasonality, as well as error associated with the patchiness and variability of zooplankton population sampling. However, it can be useful to compare overall abundance with similar studies, if available, to assess the validity of a chosen sampling method. The data obtained in this study agrees well with data found in other portions of the Gulf of Mexico (Table 11), with one notable exception. Although the abundance numbers found in this study and Ortner et al. (1989) are similar for April, the data diverge significantly from each other in December at the 5- and 25-meter isobaths, where the numerical abundance found in this study is a full order of magnitude greater. This may be due to a combination of the larger mesh size used by Ortner et al. (1989) (333 μm vice 153μm) and the prevalence in December of smaller zooplankton forms such as *P. crassirostris* and *O. colcarva*, which would easily be extruded through the larger mesh net (Calbet, 2001).

Table 10

Results of BIOENV Procedure on log transformed data. n=53

Correlation	Variables
0.353	Chl *a*
0.345	Chl *a*, Salinity
0.275	Chl *a*, Salinity, Temperature
0.255	Chl *a*, Temperature
0.236	Salinity
0.153	Temperature, Salinity
0.103	Temperature

Table 11
Comparison of results found with this study and those from other studies in Gulf of Mexico and Mediterranean Sea.

	Mesh Size (μm)	Location	Time of Year	Bottom Depth (m)	Abundance (# m^{-3})
5-Meter Isobath comparison					
This study	153	WFS	April	5	2773
Ortner , 1989	333	NGOMX		4.5	3124
This study	153	WFS	December	5	12227
Ortner, 1989	333	NGOMX		5.3	1298
This study	153	WFS	Averaged over year	5	6915
Minello, 1980	200	NWFS		8	3412
25-Meter Isobath comparison					
This study	153	WFS	December	25	2066
Ortner, 1989	333	NWGOMX		30	484
This study	153	WFS	April	25	212
Ortner, 1989	333	NGOMX		35	212
Ortner, 1989	333	CGOMX		38	76
This study	153	WFS	Averaged over year	25	1289
Calbet et al., 2001	200	Mediterranean		20-25	43865
50-Meter Isobath comparison					
This study	153	WFS	Averaged over year	50	1114
Minello, 1980	200	NWFS		73	1131

Community Composition

Of the 95 species and taxa identified in this study, only 25 were found to contribute to the top 90% of community composition. The community composition found here is consistent with that previously reported for other areas of the Florida shelf (King 1950; Hopkins, 1966; Hopkins, 1977; Weiss,1978; Minello, 1980; Squires 1984; Dagg, 1995).

Subgroup A Only All stations in subgroup A were at the 5-meter isobath. Four taxa, *P. avirostris*, *C. americanus*, *O. nana* and Cirriped larvae were significant (top 90%) contributors to community composition in subgroup A, but not B, C, D or E.

The cladoceran *P. avirostris* is circumglobally distributed in tropical and subtropical areas, and can demonstrate intermittent abundance and explosive population growth (Paffenhoffer, 1983; Paffenhoffer and Knowles, 1984; Turner and Tester, 1988). On the West Florida Shelf, *P. avirostris* is present in high concentrations near shore (Minello, 1980; Paffenhoffer 1984), with highest concentrations typically occurring in August and September (Minello, 1980; Paffenhoffer, 1984; Hopkins, 1984) though secondary peaks have been noted in late spring and early summer (Minello, 1980; Squires 1984). The very high populations of *P. avirostris* found at the 5-meter isobath in this study are a full order of magnitude higher than reported by Minello (1980) on the NWFS, though Squires (1984) occasionally found populations of this cladoceran exceeding 6,000 animals l^{-1} in Charlotte Harbor. The highest numbers reported here were on the same order of magnitude as that found by Squires (1984) (Figure 15).

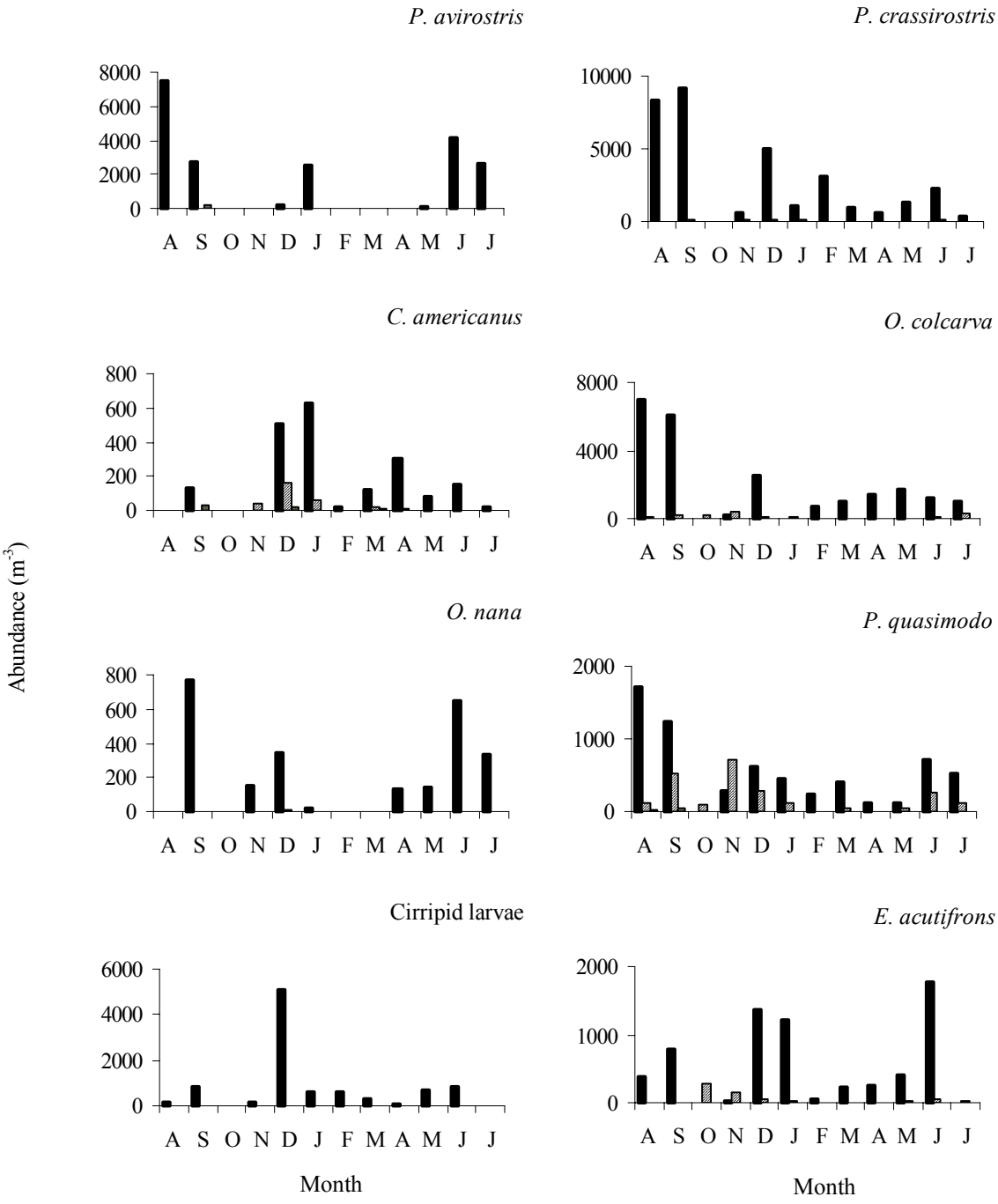

Figure 15. Abundance distribution of selected WFS zooplankton taxa. 5-m (solid bars), 25-m (hatched bars), and 50-m (dotted bars).

Surface temperature appears to be the most important factor in determining *P. avirostris* distribution. Minello found that above 28°C there appeared to be a correlation with *P. avirostris* distribution. My study confirms these findings. The maximum *P. avirostris* populations in this study occurred at temperatures between 30 and 31° C (Figure 16). In most studies performed to date, the temporal occurrence of *P. avirostris* is especially related to temperature (Marazzo and Valentin, 2001).

C. americanus is more abundant at coastal stations on the NWFS and the WFS than within estuaries (Weiss, 1977; Minello, 1980; Hopkins, 1981; Hopkins, 1984; Squires, 1984). *C. americanus* was present only intermittently and in low concentration in the St. Andrew's Bay system and the Anclote Estuary, and was not a major contributor to zooplankton assemblages in Tampa Bay (Hopkins, 1966; Hopkins, 1977; Weiss, 1977). In Charlotte Harbor, *C. americanus* was present in slightly higher concentrations, but was absent from the assemblage for 6 months out of the year (Squires, 1984). On the NWFS, populations never exceeded 40 animals m^{-3} (Minello, 1980). Populations in my study were much higher, with a peak concentration in December and January of over 500 animals m^{-3} (Figure 15).

The primary factor describing the distribution of *C. americanus* was surface temperature, though high concentration of chl *a* also appeared to be a factor. Minello reported highest numbers between temperatures of 10-22 ^{0}C. Highest abundances in my study were found between 18 and 24°C (Figure 17).

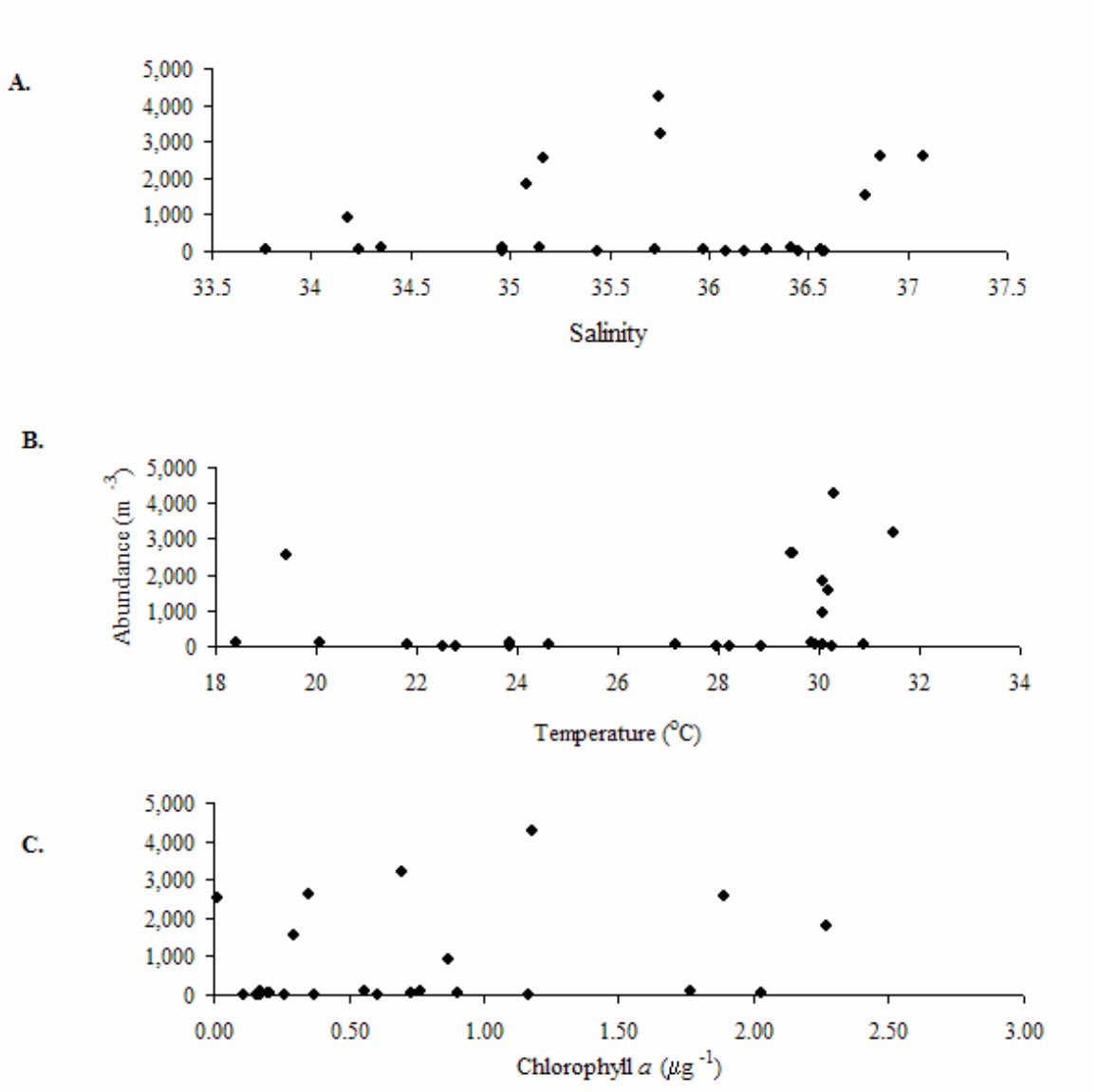

Figure 16. Distribution of *P. avirostris* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

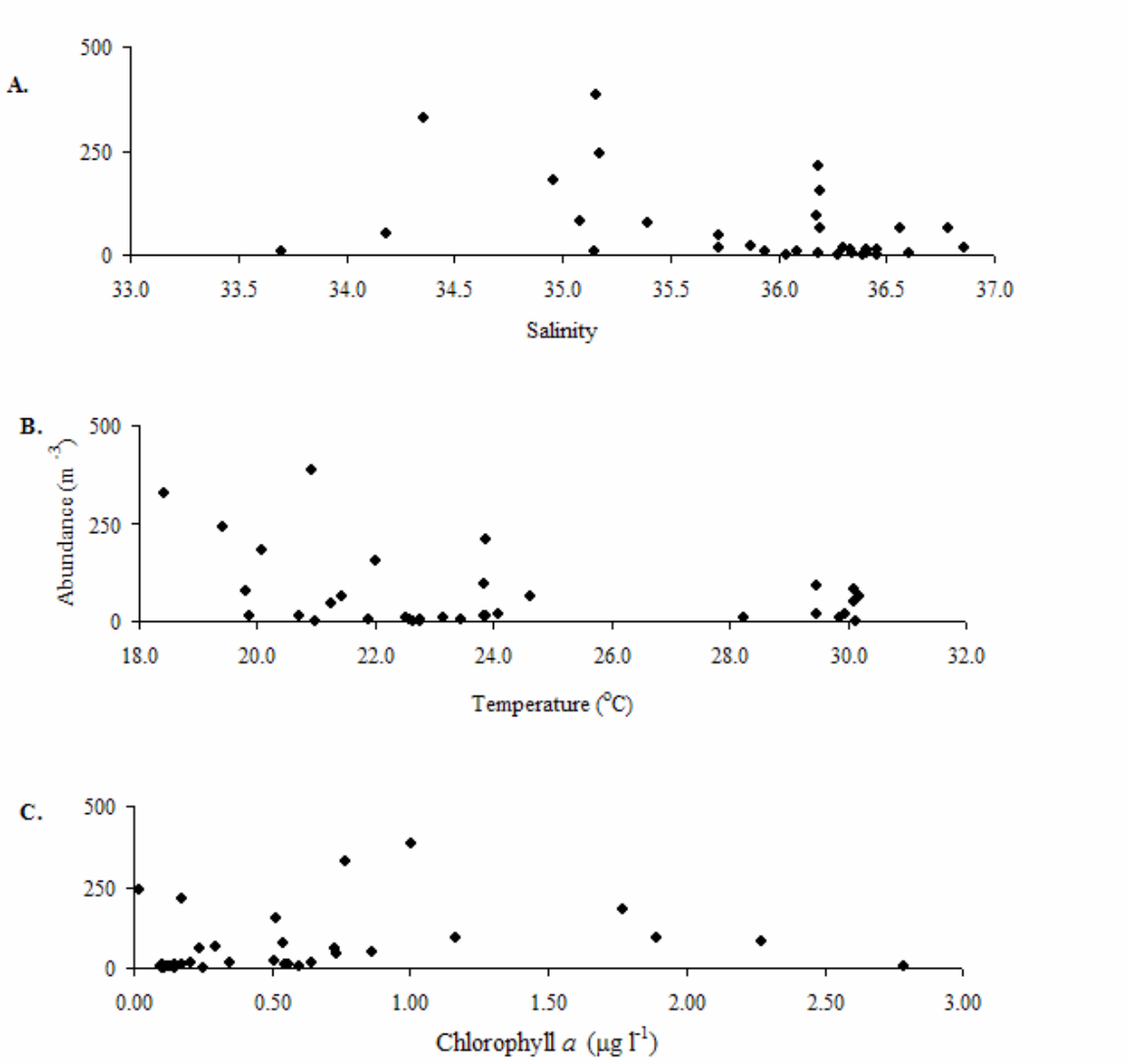

Figure 17. Distribution of *C. americanus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

O. nana is most abundant in the summer and fall in higher salinity regions of WFS estuaries (Hopkins, 1966; Weiss, 1977; Hopkins, 1977; Squires, 1984), though Weiss (1977) reported highest numbers in spring and summer. In my study, *O. nana* was most abundant in summer and fall, and never occurred at the 25 or 50-meter isobaths (Figure 15).

Minello (1980) determined that salinity was the primary variable defining this copepod's distribution. In my study, salinity did not appear to be an important factor in its distribution. *O. nana* occurred in greatest numbers at temperatures exceeding 30^0C and chlorophyll *a* concentrations between .5 and 1 $\mu g\ l^{-1}$ (Figure 18).

Cirriped larvae are common year round in the estuaries of the West Florida coast, with no pattern in seasonal distribution evident (Hopkins, 1966; Weiss, 1977; Hopkins, 1977; Squires, 1984). In this study, Cirriped larvae were never found past the 5-meter isobath (Figure 16), though there are reports of Cirriped larvae occurring further offshore in other studies (King 1950; Minello, 1980). A peak in Cirriped larvae was observed in December (Figure 15).

A strong correlation between Cirriped larvae abundance and temperature were observed in this study (Figure 19). Peak populations occurred between 33 and 38^oC. No strong correlation was seen between salinity or chlorophyll *a* concentration and Cirriped concentration.

Salinity and chlorophyll *a* concentration were not significant factors in the distribution of those species represented only in subgroup A. Instead, temperature was the major factor contributing to community distribution. The lack of salinity or

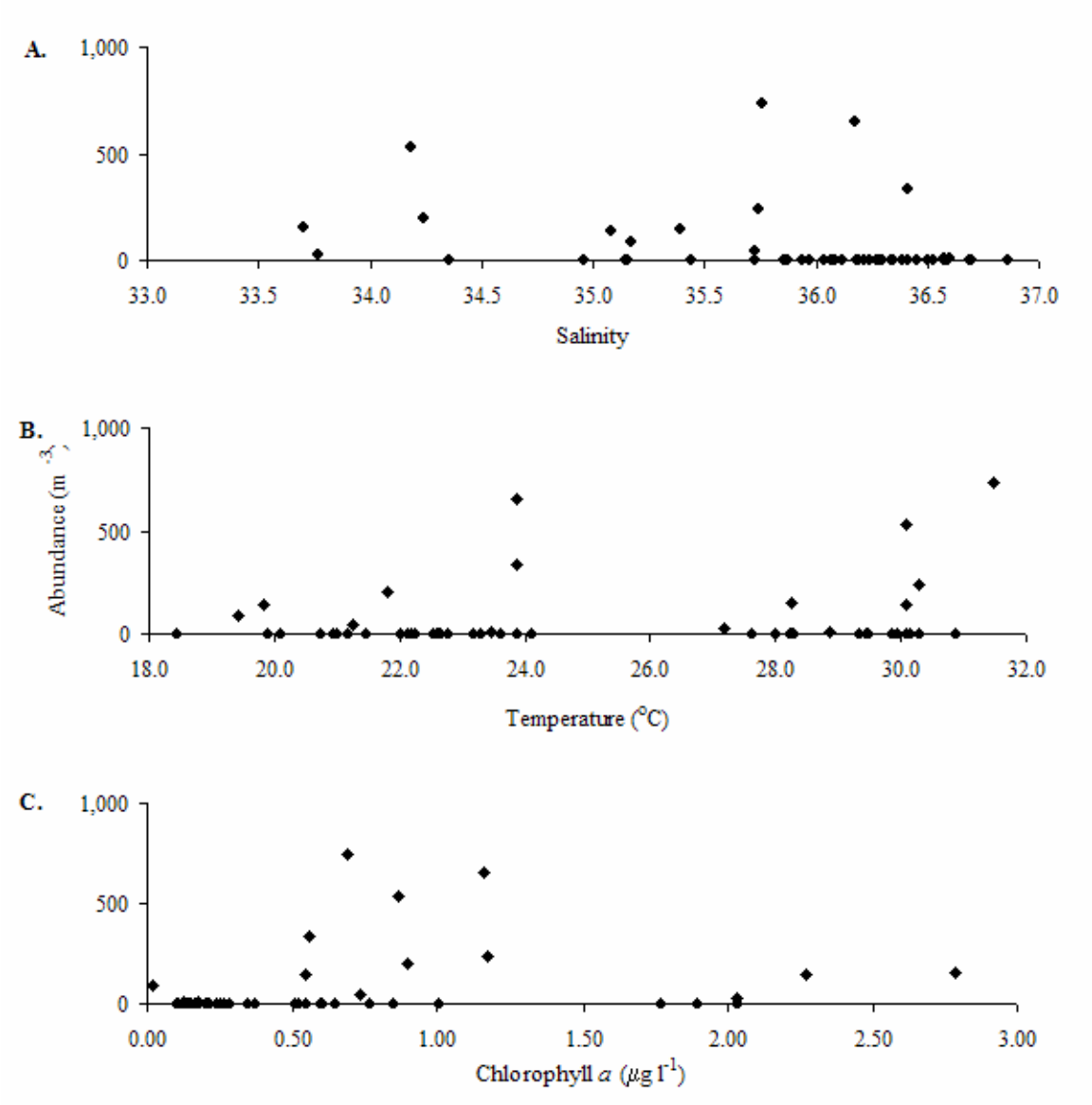

Figure 18. Distribution of *O. nana* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

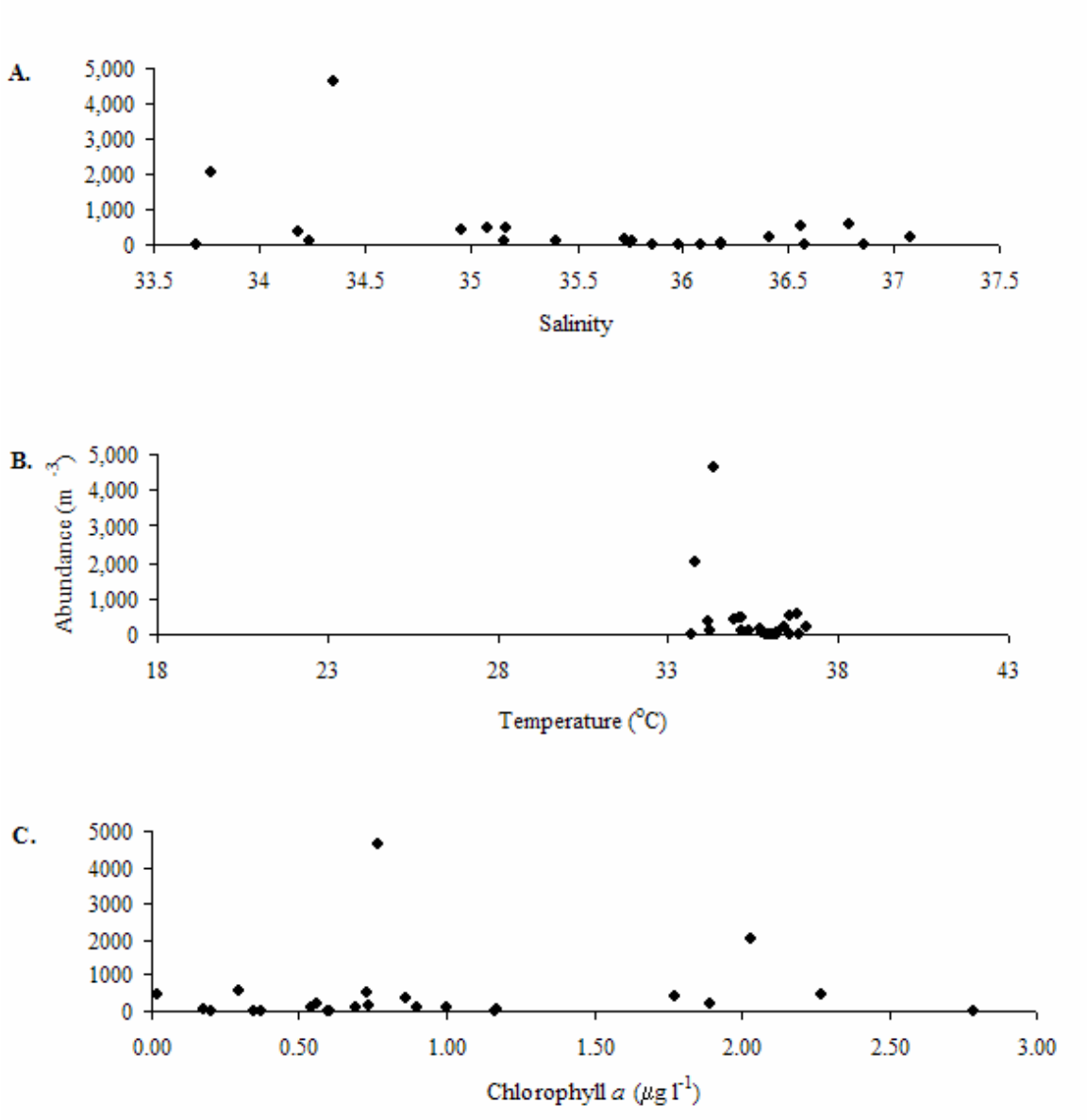

Figure 19. Distribution of Cirripid larvae in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

chlorophyll *a* concentration as contributing factors suggests that these organisms are well adapted to the continually changing biotic and abiotic variables in an estuarine environment.

Subgroup A and B All stations in subgroup B were at the 25–meter isobath. Six taxa, *P. crassirostris*, *O. colcarva*, *P. quasimodo*, *Euterpina acutifrons*, Pelecypod larvae and Gastropod larvae were primary contributors to community composition in subgroups A and B, indicating significant overlap in community composition between the 5 and 25-meter isobaths. *P. crassirostris* was abundant and frequently dominant in all areas of Tampa Bay, Charlotte Harbor, the Anclote Estuary, and the St. Andrew's Bay System (Hopkins, 1966; Hopkins, 1977; Weiss, 1977; Squires, 1984). Numerical abundance peaked in late summer, and was generally greatest at the mouths of the estuaries. Minello (1980) reported *P. crassirostris* abundant at the 8- and 14-meter isobaths, with numerical abundance dropping off sharply with increasing distance offshore. Numerical abundance of *P. crassirostris* in this study (Figure 15) was typically an order of magnitude lower than that found in the WFS estuaries, and a full order of magnitude higher than that found by Minello (1980) at the 8- and 14-meter isobaths on the NWFS. This is possibly due to the differences in mesh size used (70 μm in estuarine studies, 153μ in this study, 200 μm in NWFS study) since *P. crassirostris* is a small (~.5mm) copepod that is easily extruded through larger size nets (Calbet, 2001).

Minello (1980) reported a strong correlation between both salinity and temperature for this species. In that study, highest concentrations were found at salinities from 29 to 35, with abundance dropping off sharply at salinities greater than 35. Greatest

abundances were at lower temperatures of 10 to 20 ^{o}C, with a secondary peak at 31^{o}C. In my study, *P. crassirostris* distribution peaked between salinities of 33.5 to 35.5 and temperatures of 27 to 32 ^{o}C (Figure 20).

O. colcarva is a primary dominant species in WFS estuaries (Hopkins, 1966 ; Weiss, 1977; Hopkins, 1977; Squires, 1984). This numerically important copepod tends to be least abundant at the mouths of bays, where it can still be present in tens of thousands of cells m^{-3} (Hopkins, 1966 ; Weiss, 1977; Hopkins, 1977; Squires, 1984). In this study, lowest abundance occurred in the winter, with highest populations occurring in late summer (Figure 16). Although *O. colcarva* was found out to the 25-meter isobath, populations there were typically low.

Highest populations of *O. colcarva* were found at salinities of 35.5 to 36.5, though lowest abundances were also found at these salinities. There was a strong correlation with temperature and abundance of *O. colcarva*, with highest populations occurring at 20^{o}C (Figure 21).

P. quasimodo populations peak at the mouths of WFS estuaries, and the species is usually absent from lower salinity areas at the heads of estuaries (Hopkins, 1966; Weiss, 1977; Hopkins, 1977; Squires, 1984). *P. quasimodo* was reported to be less abundant at offshore isobaths by Minello (1980), with highest populations found at the 8-meter isobath in late summer and early fall. In this study, peak abundances also occurred in late summer and early fall at the 5-meter isobath (Figure 16).

Minello (1980) found no relationship between the distribution of *P. quasimodo* with any of the physical or chemical factors measured. However, in this study lower

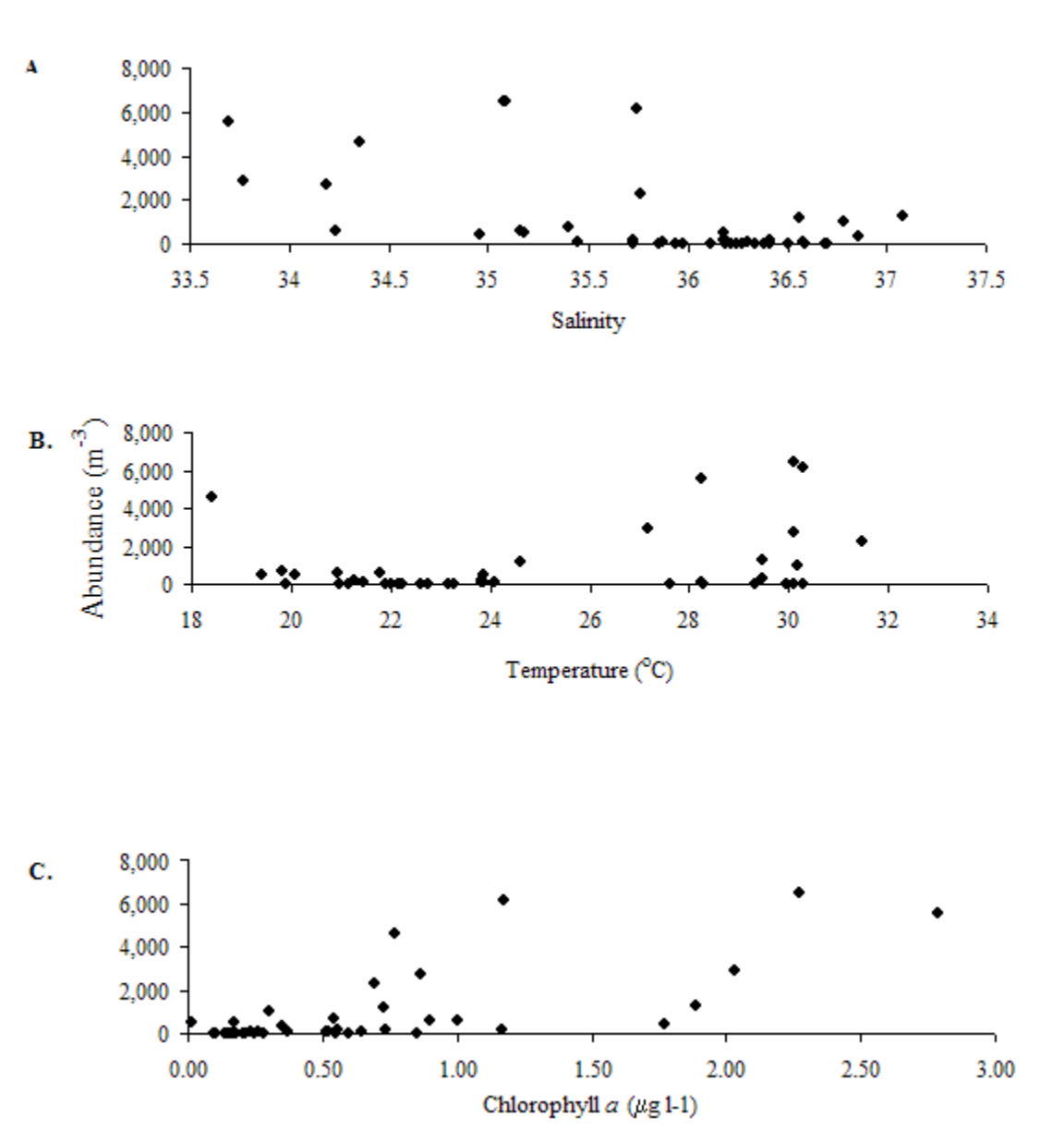

Figure 20. Distribution of *P. crassirostris* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

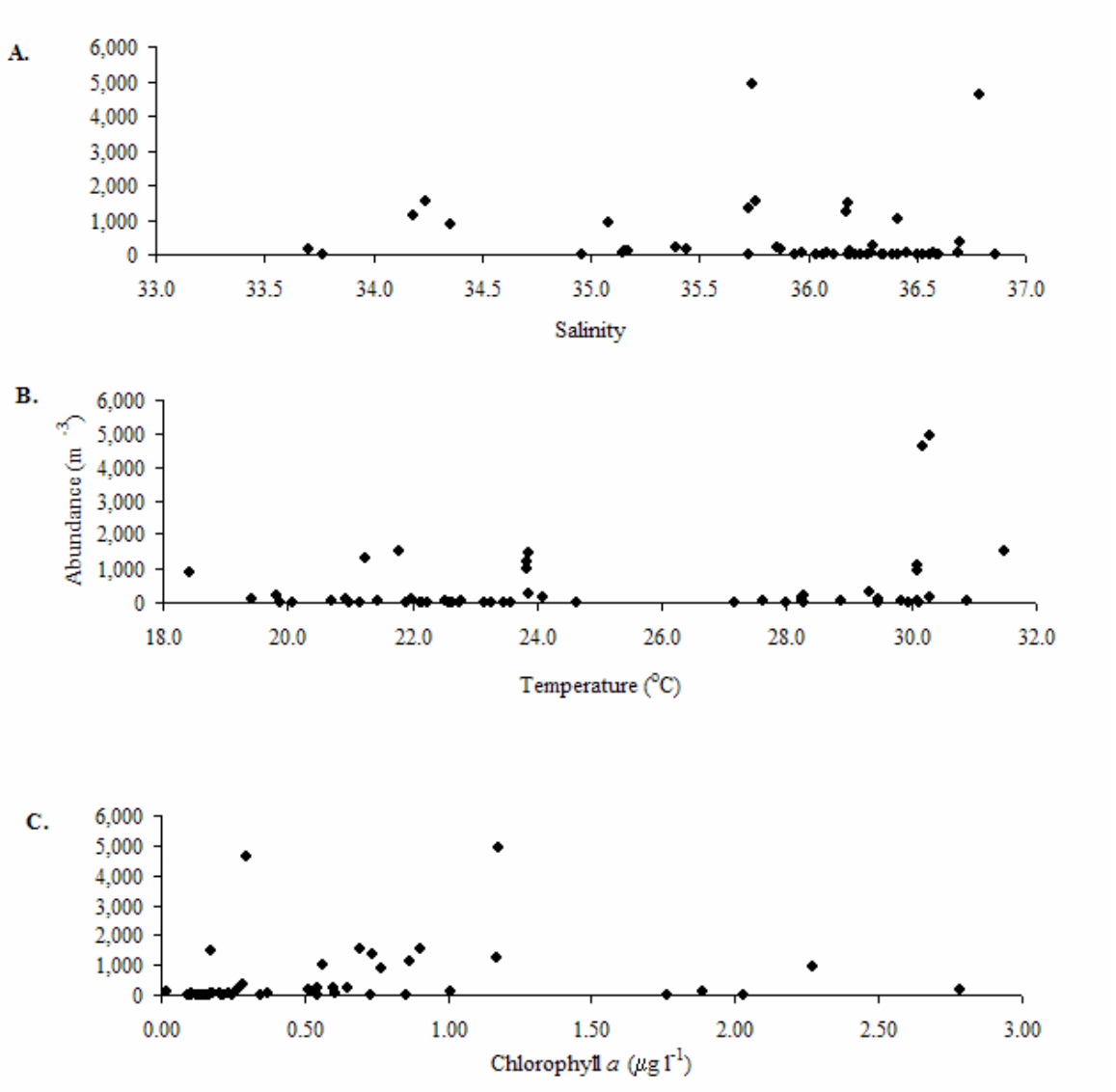

Figure 21. Distribution of *O. colcarva* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

salinities and higher temperatures were correlated with *P. quasimodo* abundance (Figure 22).

E. acutifrons was an important contributor to Groups A and B. This harpacticoid copepod is typically present near the mouths of estuaries on the WFS, though highest populations typically occurred in the upper and middle portions of the Anclote estuary and Charlotte Harbor (Hopkins, 1966; Weiss, 1974; Hopkins, 1977; Squires, 1984). Highest abundances in estuaries occurred in the winter and spring (Hopkins, 1966; Weiss, 1974; Hopkins, 1977; Squires, 1984). King (1950) reported finding *E. acutifrons* out to the 40- meter isobath. In this study, highest populations occurred in winter and in summer at the 5-meter isobath (Figure 15). *E. acutifrons* occurred only occasionally at the 25-meter isobath.

Salinity and chlorophyll *a* concentration did not affect the distribution of *E. acutifrons*, however there did appear to be some correlation with temperature, with maximum populations occurring at temperatures greater than 24^{o}C (Figure 23).

Not surprisingly, Pelecypod larvae and Gastropod larvae contributed to community composition across a range of subgroups, since each of these taxa represent larval forms of multiple species. Pelecypod larvae contributed significantly only to subgroups A, B, and C, though it was present at all isobaths for at least one sampling period (Figure 24, Tables 3-5). Gastropod larvae contributed significantly to abundance and community composition at all subgroups (Figure 24, Tables 3-7). Minello found that intermediate depths (28- to 46-meters) had higher numbers of Gastropod larvae than near shore or offshore depths.

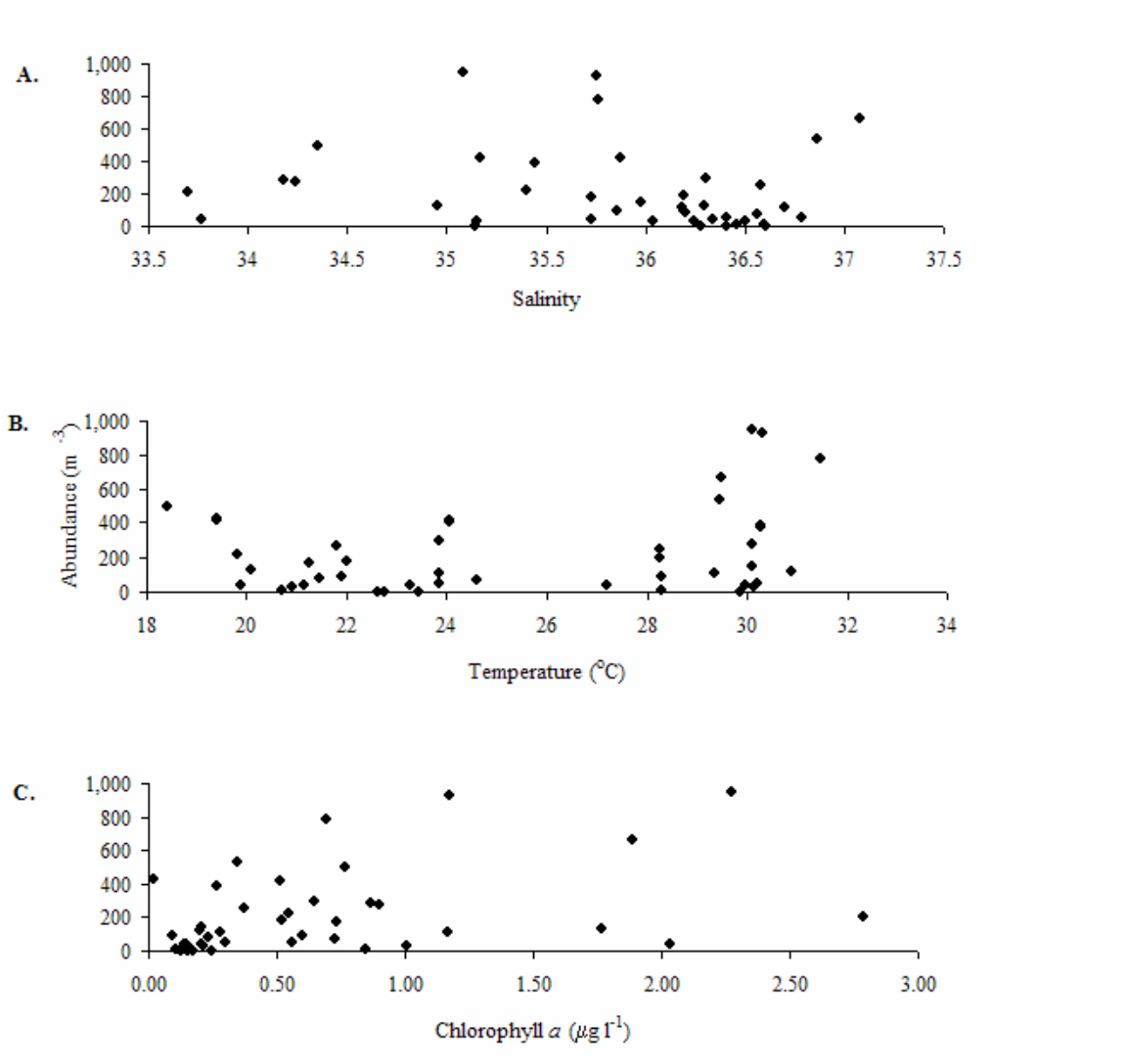

Figure 22 Distribution of *P. quasimodo* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

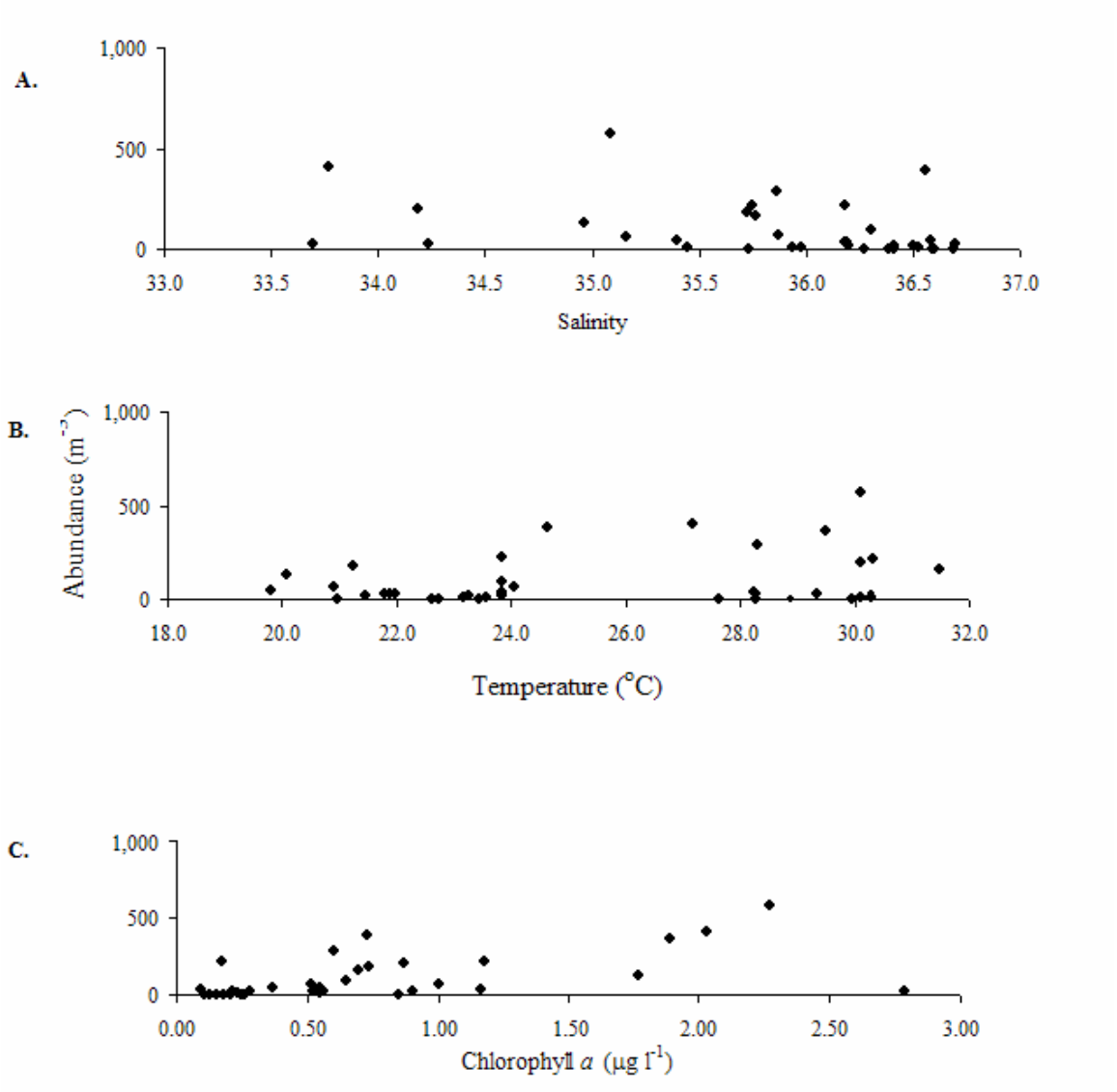

Figure 23. Distribution of *E. acutifrons* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

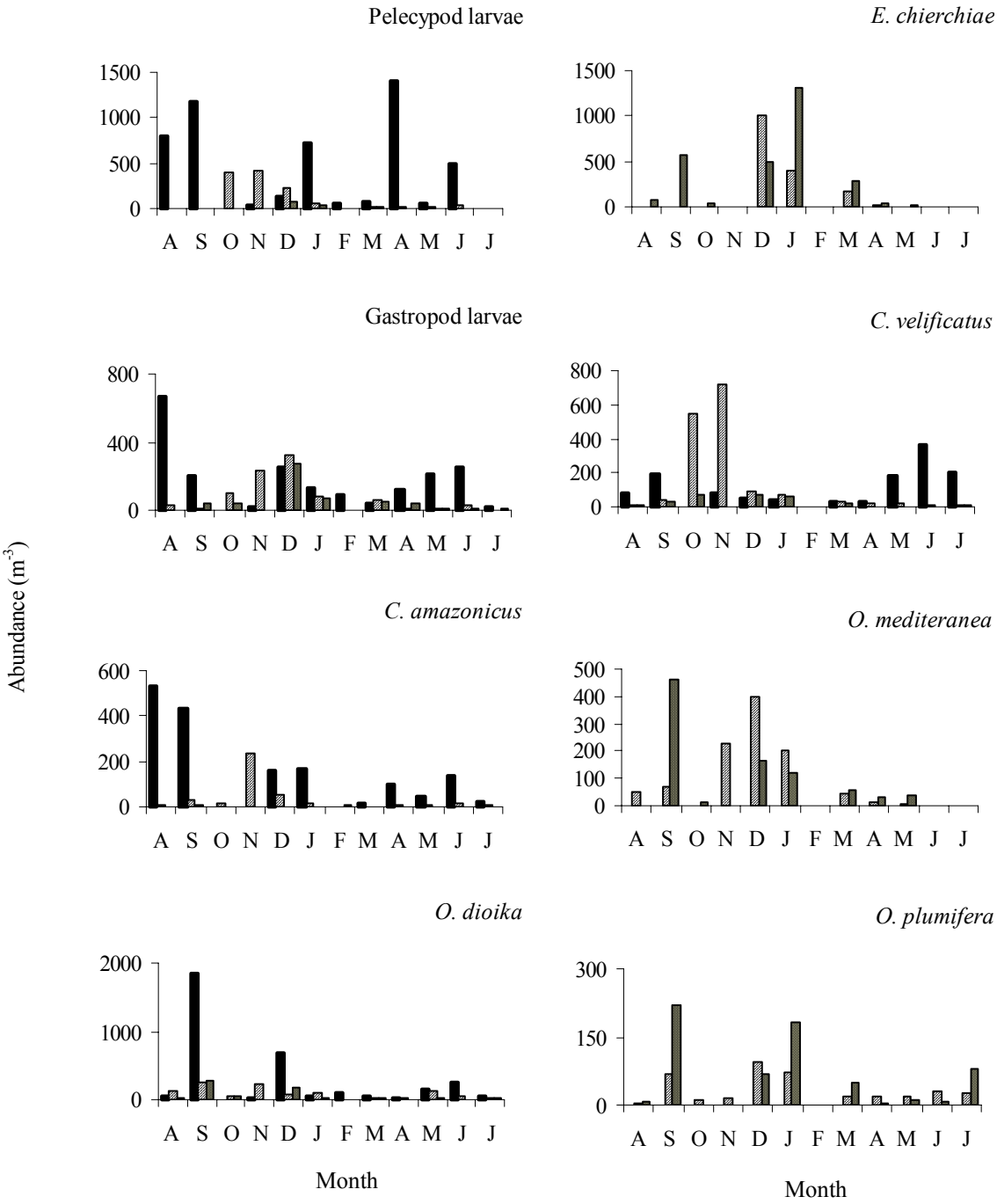

Figure 24. Abundance distribution of selected WFS zooplankton taxa. 5-m (solid bars), 25-m (hatched bars), and 50-m (dotted bars).

There was no correlation with salinity, temperature, or chlorophyll *a* concentration with pelecypod or Gastropod larvae in the Minello (1980) study, nor in this study (Figures 25 and 26). This is most likely do to the fact that each larval taxa represents many species, all of whom have different exogenous factors that induce spawning.

Subgroup B only One species, *Corycaeus amazonicus*, contributed only to subgroup B but not to subgroups A, C, D or E. *C. amazonicus* is a common contributor to zooplankton assemblages in higher salinity regions of WFS estuaries in late spring and summer (Hopkins, 1966; Weiss, 1974; Squires, 1984). Minello (1980) reported highest populations in September, with minor peaks in spring. On the WFS, *C. amazonicus* occurred most often at the 5-meter isobath, with highest numbers occurring in late summer/early fall (Figure 24). Minello (1980) found that surface temperature was the most important contributor to *C. amazonicus* distribution, with peak abundances occurring at temperatures higher than 26^{o}C. In my study, peak abundances occurred at temperatures higher than 28^{o}C (Figure 27). Although Minello (1980) did not find a strong correlation between the distribution of *C. amazonicus* and salinity, there was some evidence from my study that maximum populations occurred at intermediate salinities o35 to 36 (Figure 27).

Of the above species that contributed to Subgroups A and B, salinity played a greater role in distribution than it did in those species represented in Subgroup A alone, indicating that the species in subgroup B become less euryhaline as distance offshore increases. Temperature still proved to be an important contributing factor to distribution. Chlorophyll *a* concentration was important only in the distribution of *P. quasimodo*.

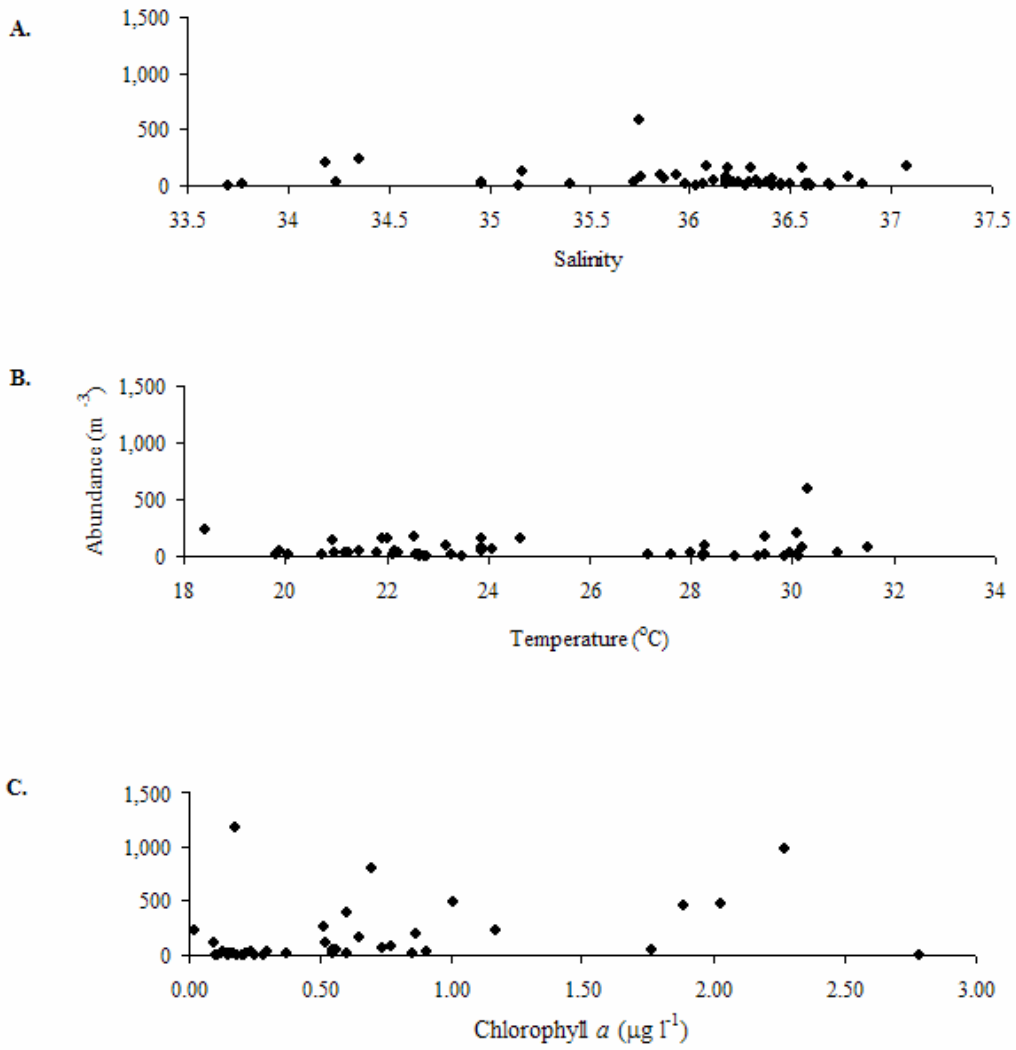

Figure 25. Distribution of Pelecypod larvae in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

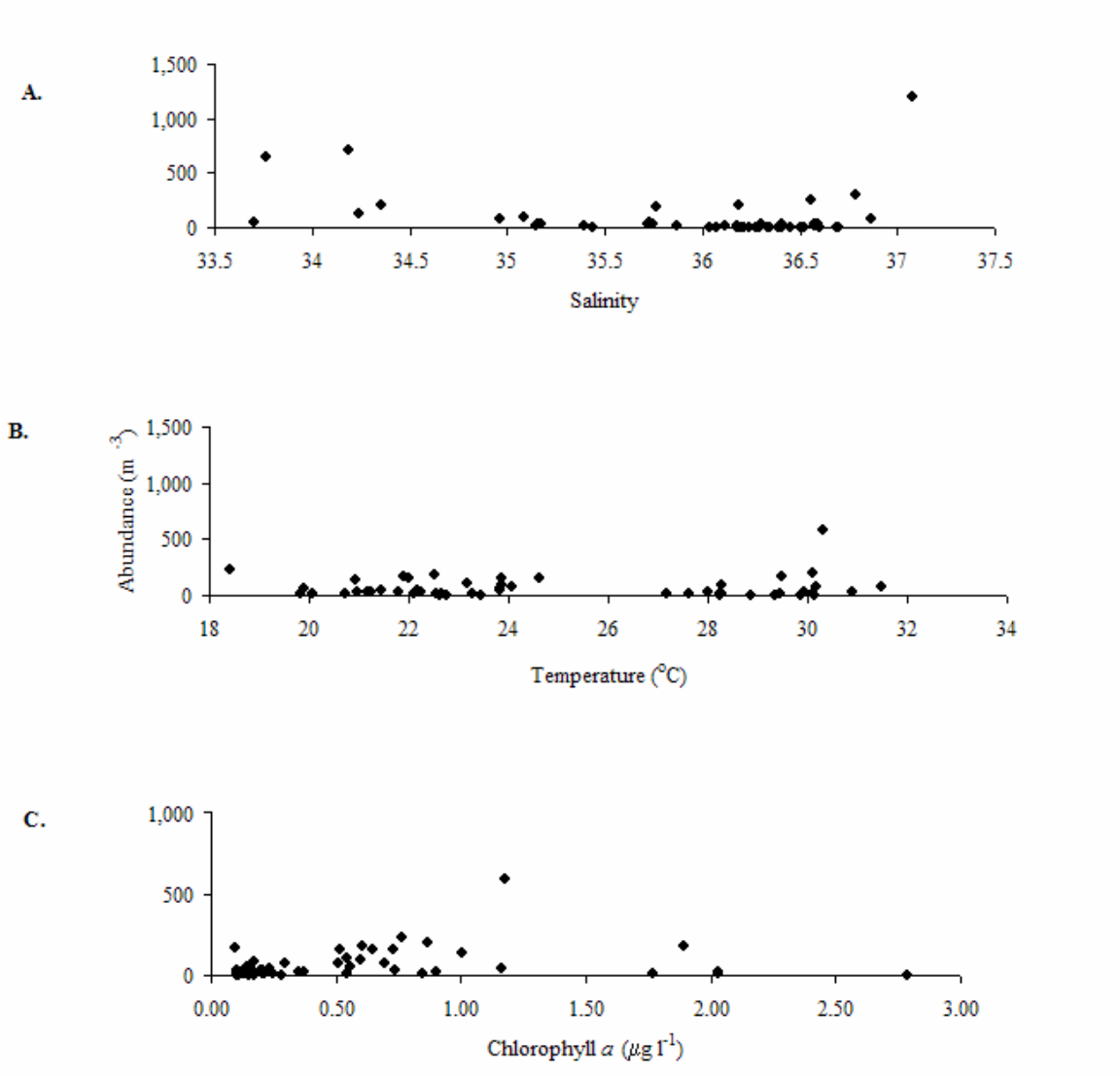

Figure 26. Distribution of Gastropod larvae in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

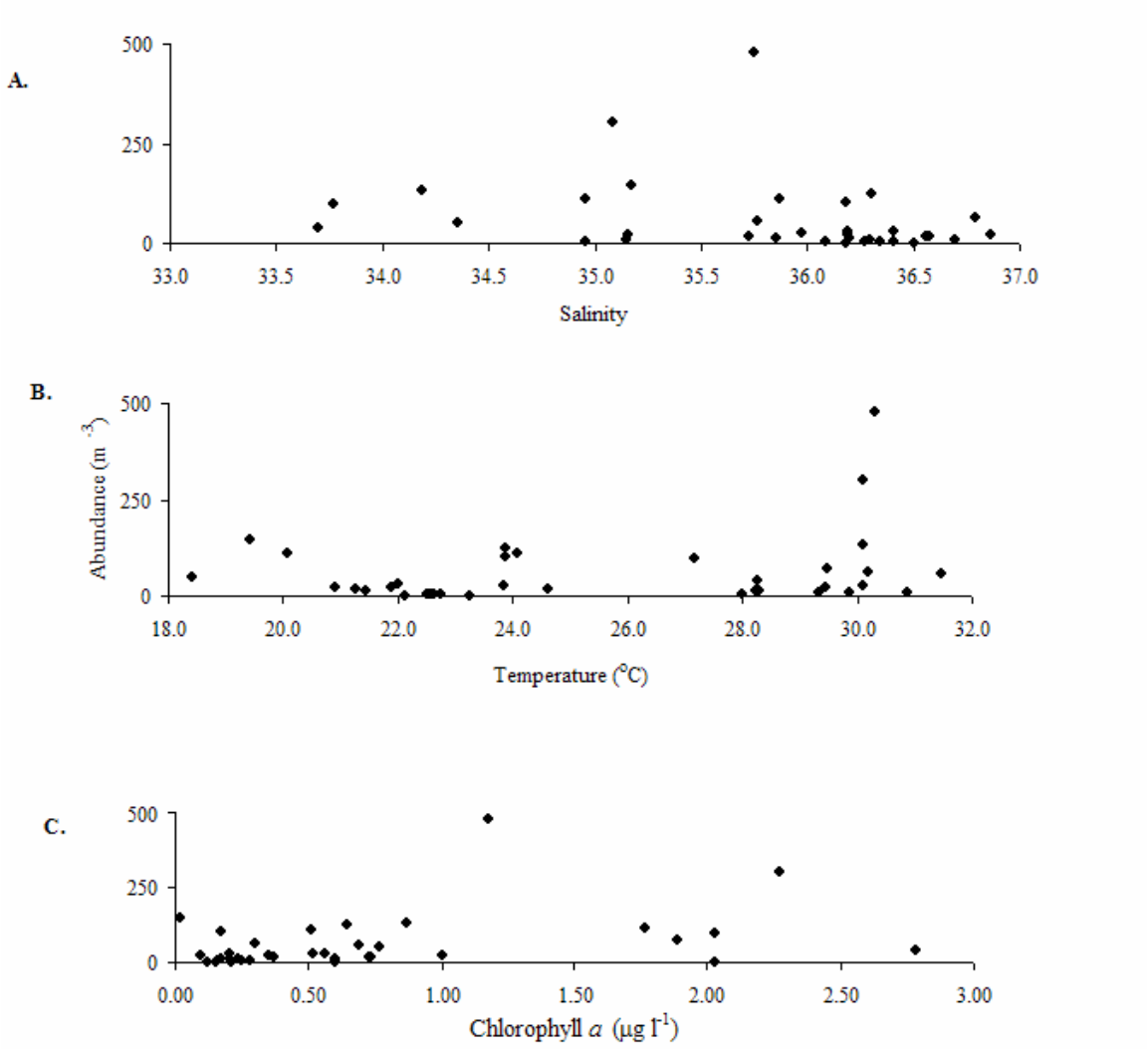

Figure 27. Distribution of *C. amazonicus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

Subgroups B, C, D and E Six taxa, *O. dioica*, Gastropod larvae, *O. mediteranea*, *C. velificatus*, *O. plumifera*, and *E. chierchiae*, contributed significantly to community composition in subgroups B, C and D. Five of these taxa, *O. dioica*, Gastropod larvae, *O. mediteranea*, *O. plumifera*, and *E. chierchiae* also contributed to subgroup E.

O. dioica, a temperate tropical euryhaline species often reported at the heads and mouths of estuaries, is the most abundant appendicularian in coastal areas and estuaries of the NWFS and WFS, and can reach populations of thousands m^{-3} (Hopkins 1966; Weiss, 1977; Hopkins, 1977; Minello, 1980; Squires, 1984; Dagg, 1995). In this study *O. dioica* was found in greatest abundance at the 5-meter isobath, but was also frequently present at the 25- and 50-meter isobaths (Figure 24). Salinity appeared to be the greatest determining factor in explaining the distribution of *O. dioica* in my study, with highest populations occurring at lower salinities of 34.0 to 35.0 (Figure 28).

Sutton et al. (2001) noted that the importance of the pelagic ostracod *E. chierchiae* to the WFS ecosystem has been overlooked in the past, and ranked it as second in abundance at the 40-meter isobath, but absent shoreward of the 25-meter isobath. Minello reported populations that were a full order of magnitude lower than that reported here (Figure 24), with peaks in winter and spring. In this study, *E. chierchiae* never occurred shoreward of the 25-meter isobath, though Hopkins (1966) reported its presence in the high salinity regions of the St. Andrew's Bay system. Minello (1980) reported a peak in September in some years, an observation confirmed by Sutton et al. (2001), also working in September. A small peak of *E. chierchiae* in September was observed in this study at the 50-meter isobath, but highest abundances occurred in winter months at the 25- and 50-meter isobaths (Figure 24).

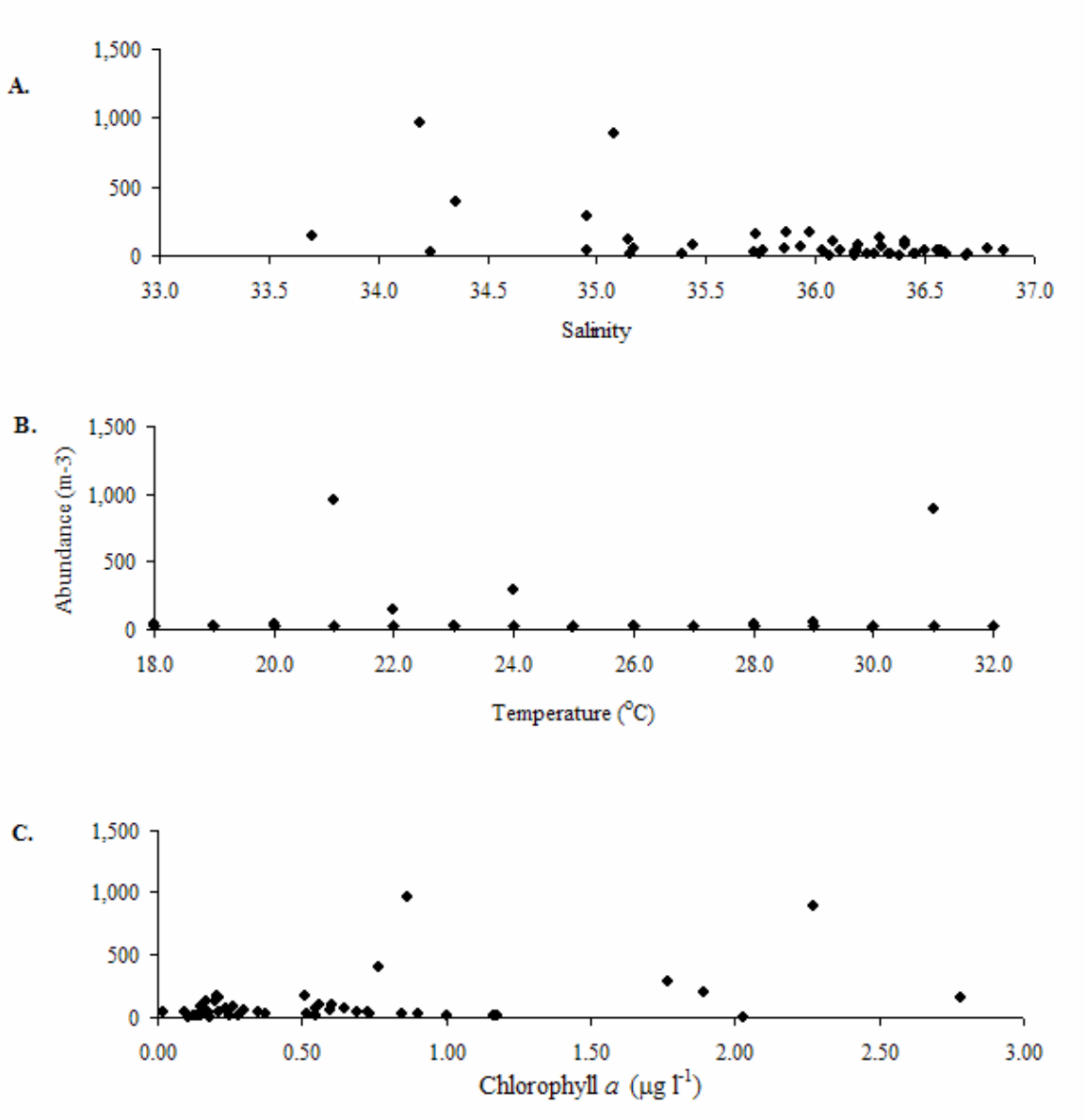

Figure 28. Distribution of *O. dioica* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

Using regression models, Minello (1980) determined that the greatest factor contributing to *E. chierchiae* distribution was salinity. These findings were confirmed by my study, where maximum abundance of *E. chierchiae* occurred between salinities of 35-36.5 (Figure 29). Low chlorophyll *a* concentration also appeared to be a factor in *E. chierchiae* distribution, with peak numbers occurring at chlorophyll *a* concentrations of .50 $\mu g\ l^{-1}$ or less.

Like *P. quasimodo, C. velificatus* shows abundance peaks at the mouths of WFS estuaries, and is often absent from lower salinity areas at the heads of estuaries (Squires, 1984; Weiss, 1977; Hopkins, 1977; Hopkins, 1966). *C. velificatus* was reported to be less abundant at offshore isobaths by Minello (1980) where it was most abundant at the 8-meter isobath. *C. velificatus* was a frequent contributor at the 5 and 25-meter isobaths in my study, with peak numbers occurring at the 5-meter isobath in early summer and at the 25-meter isobath in October and November (Figure 24).

Minello found that abundance of *C. velificatus* decreased with increasing temperature. In this study, maximum populations of *C. velificatus* occurred between 24 and 28^{o}C (Figure 30). Neither salinity nor chlorophyll *a* concentration appeared to play a role in the distribution of *C. velificatus*.

Ortner (1989) found *O. mediteranea* and *O. plumifera* most abundant in transition waters of the Mississippi River outflow. Minello (1980) reported *O. mediteranea* only rarely shoreward of the 14-meter isobath. Sutton et al. (2001) found members of the genus *Oncaea* (presumably *O. mediteranea*) present in high numbers at the 40-meter isobath in September. Minello (1980) reported peaks of *O. mediteranea* in April and early summer. In this study, *O. mediteranea* was found as far offshore as 50-meter

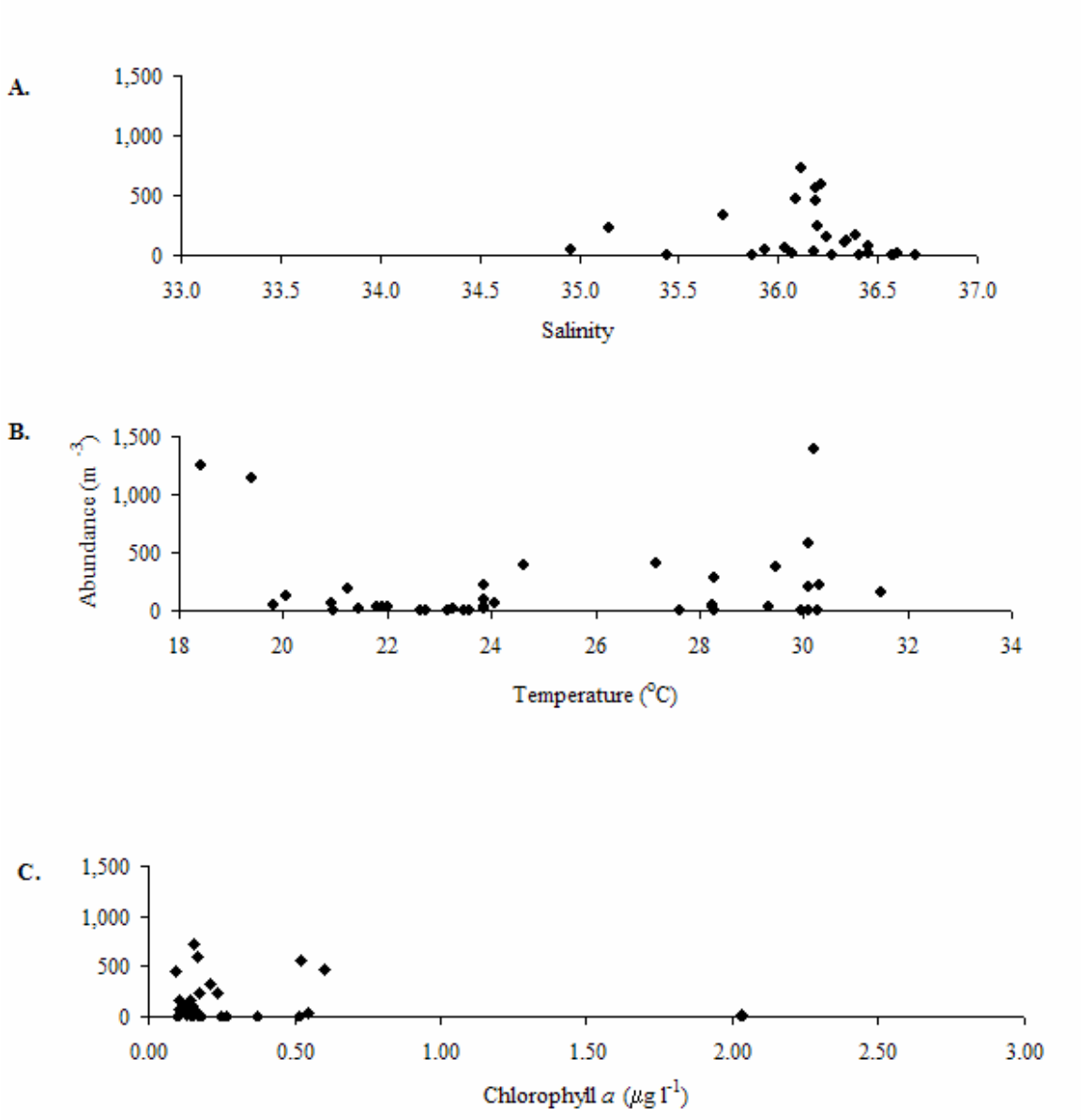

Figure 29. Distribution of *E. chierchiae* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

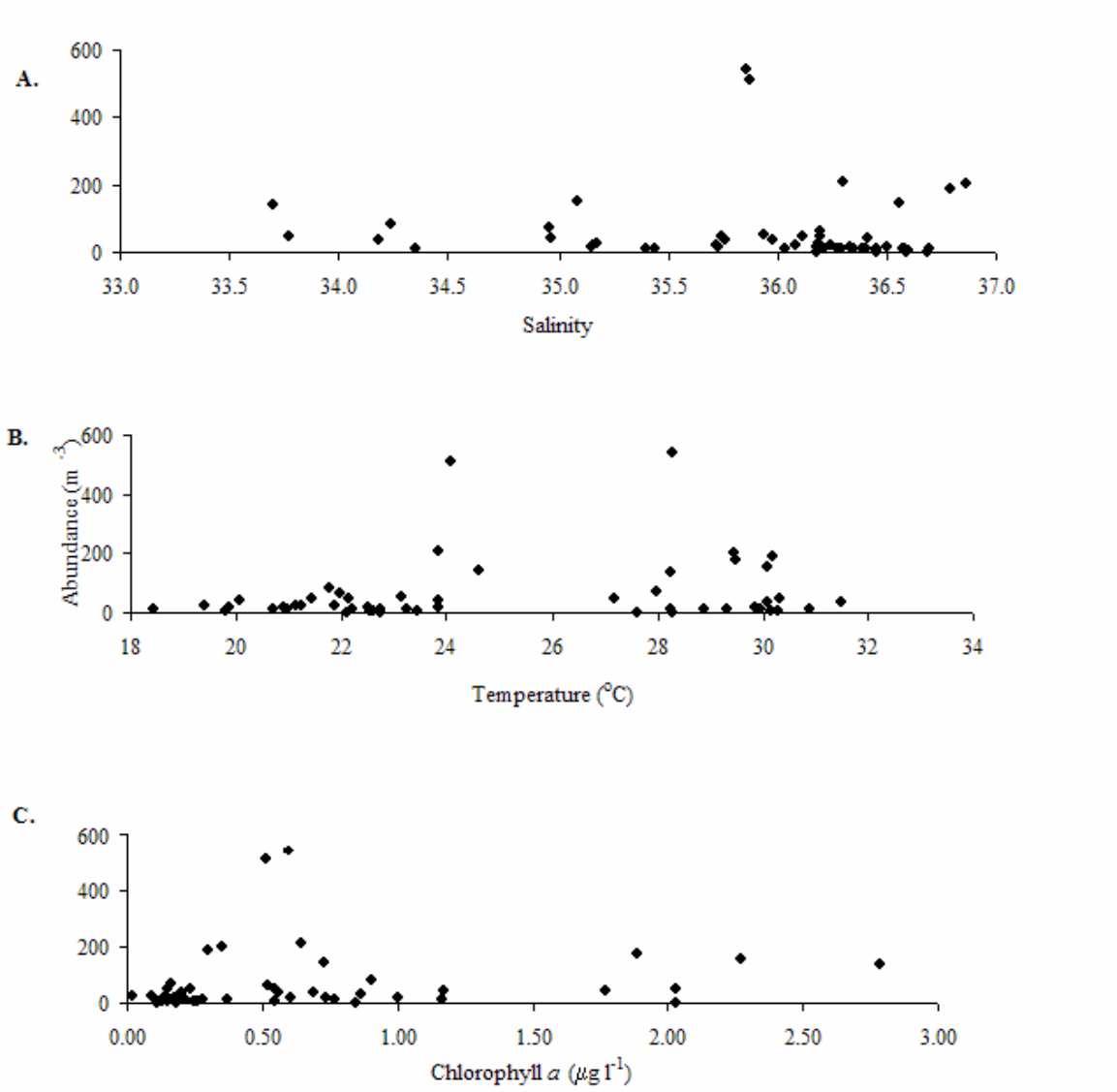

Figure 30. Distribution of *C. velificatus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

isobath (Figure 24), with peak abundances observed at the 50-meter isobath in September and at the 25-meter isobath in winter.

A significant correlation with salinity was found in my study, with high numbers of *O. mediteranea* occurring at salinities between 36 and 36.5 (Figure 31). Minello (1980) reported similar findings with peak populations occurring between salinities of 35 and 37. No correlation was found between the occurrence of *O. mediteranea* and temperature, though there was some indication that lower chlorophyll *a* concentrations were correlated with higher populations.

O. plumifera was mostly absent at the 5-meter isobath and was most abundant at the 25-meter isobath (Figure 24). High numbers of *O. plumifera* were occasionally found at the 50-meter isobath. Minello (1980) reported *O. plumifera* only occasionally shoreward of the 28-meter isobath.

Minello (1980) reported that abundance of *O. plumifera* was highest at salinities higher than 35 and surface temperatures of greater than 21^{o}C. In this study, *O. plumifera* occurred only between salinities of 35 to 37 (Figure 32). Temperatures that resulted in the highest numbers ranged from 24 to 30^{o}C, though low populations also occurred at these temperatures . There was also some indication that low chlorophyll *a* concentration was correlated with *O. plumifera* distribution, since highest numbers occurred at concentrations of less than .5 μg l^{-1}.

Clausocalanus furcatus was found in Subgroups C and E (Figure 33). In the St. Andrews Bay system, this species was present in July and October at higher salinity stations (Hopkins, 1966). Minello (1980) found *C. furcatus* abundant at the 28-, 46- and 73-meter stations. Mean densities in that study were greatest in July at the deepest b

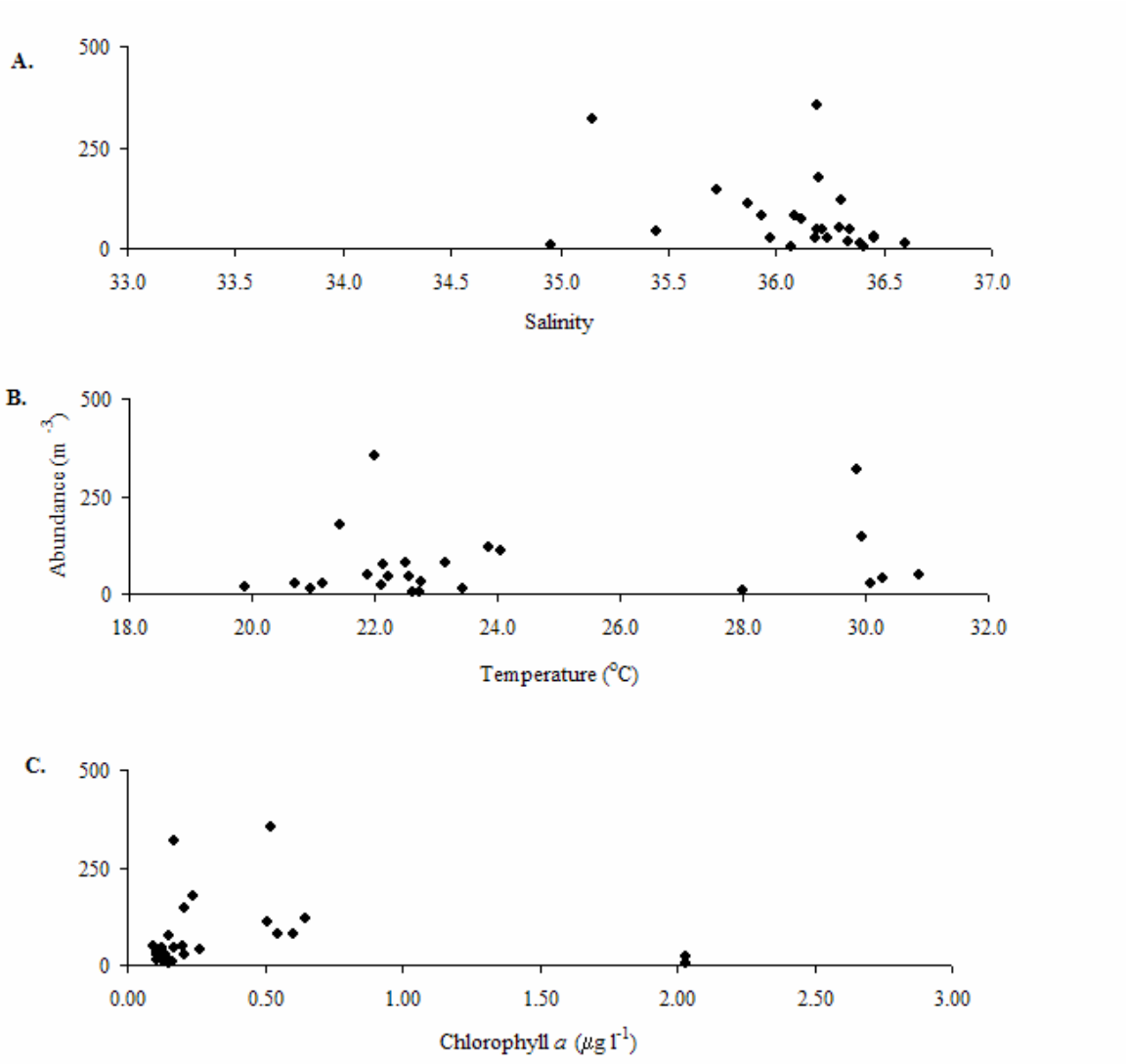

Figure 31. Distribution of *O. mediteranea* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

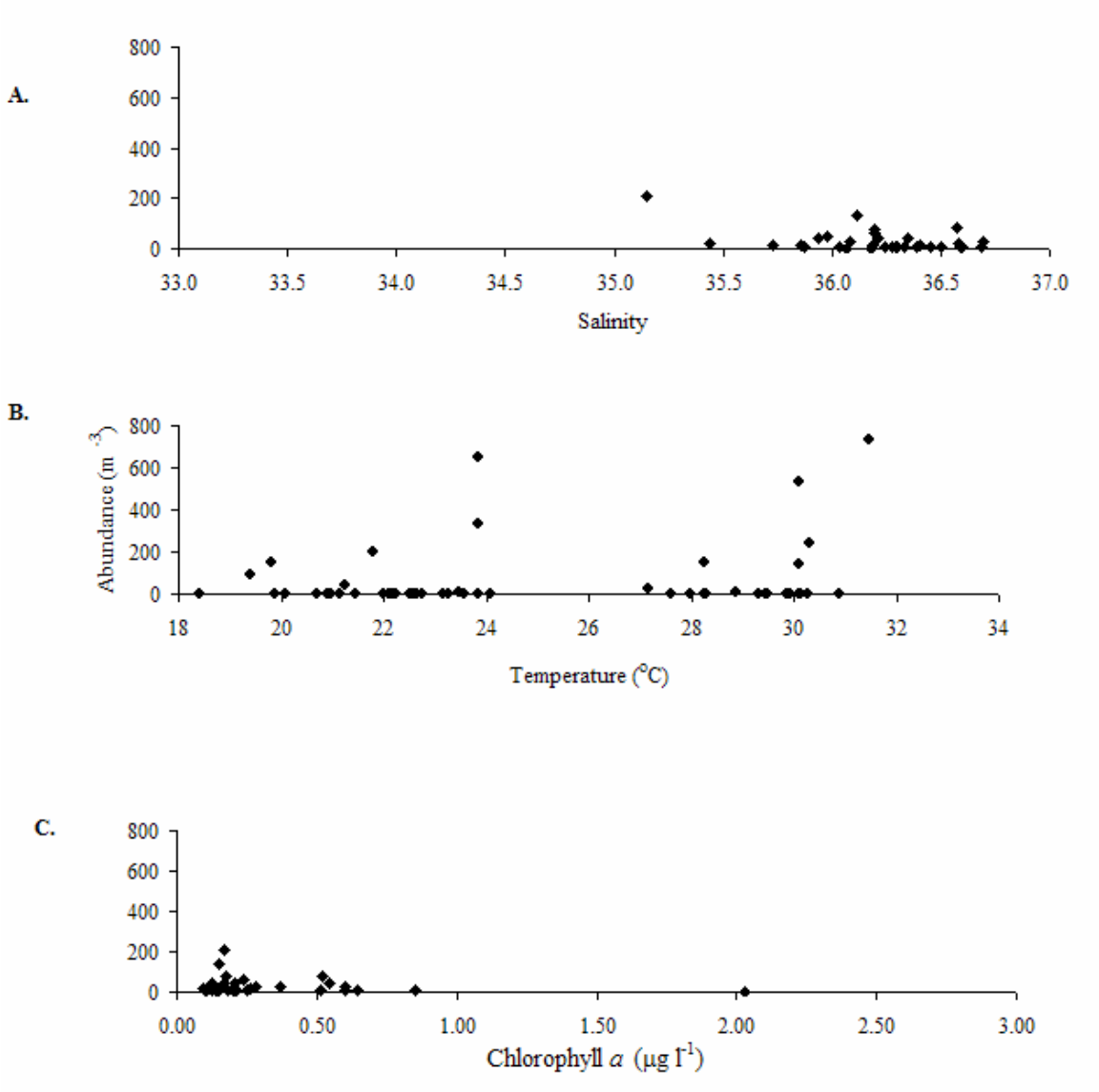

Figure 32. Distribution of *O. plumifera* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

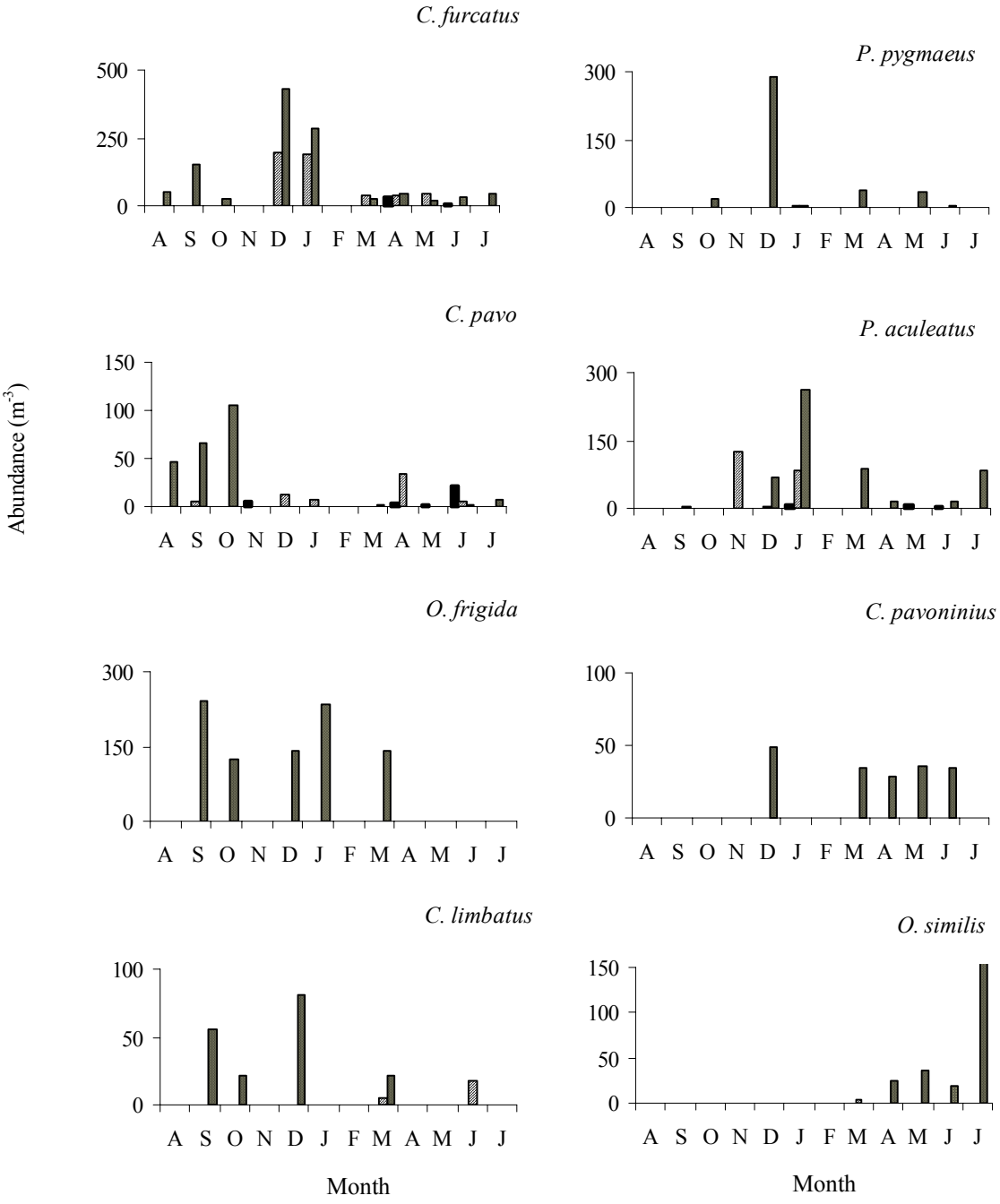

Figure 33. Abundance distribution of selected WFS zooplankton taxa. 5-m (solid bars), 25-m (hatched bars), and 50-m (dotted bars).

stations, with *C. furcatus* only occasionally occurring at the 8- and 14-meter isobaths. In my study, *C. furcatus* was found consistently at the 25- and 50- meter isobaths, with highest populations occurring in December and January (Figure 33).

Minello (1980) reported that a number of factors contributed to the distribution of *C. furcatus*, with salinity being most important. Peak abundances of *C. furcatus* in the Minello (1980) study occurred at salinities greater than 35 and temperatures from 20 to 30^{o}C. Highest populations in my study occurred between salinities of 35 and 37, temperatures from 24 to 30^{o}C, and chlorophyll *a* concentrations of .5 μgl^{-1} or less (Figure 34).

Subgroup C Only C. pavo is widely distributed in temperate and tropical waters where the populations occur mostly in the upper levels (Owre and Foyo, 1967). Jones (1952) reported it throughout the year but in widely varying abundances. King (1950) reported the presence of *C. pavo* from 10 to 100 fathoms as well as inshore of the 10 fathom mark. In my study, *C. pavo* occurred at the 25- and 50-meter isobaths, with highest populations occurring in late summer and fall at the 50-meter isobath (Figure 33).

Little correlation was seen between the distribution of *C. pavo* and salinity, temperature or chlorophyll *a* concentration. Peak abundances tended to occur at intermediate salinities, but the copepod was also present at higher salinities (Figure 35). This may explain the wide distribution of this species (Owre and Foyo, 1967).

Overall, salinity was a greater factor in describing species distribution in subgroups B and C than in A, indicating that these species may not be as euryhaline and are more limited in spatial distribution by salinity. Chlorophyll *a* concentration appeared to be a greater factor in Subgroups B and C than in A.

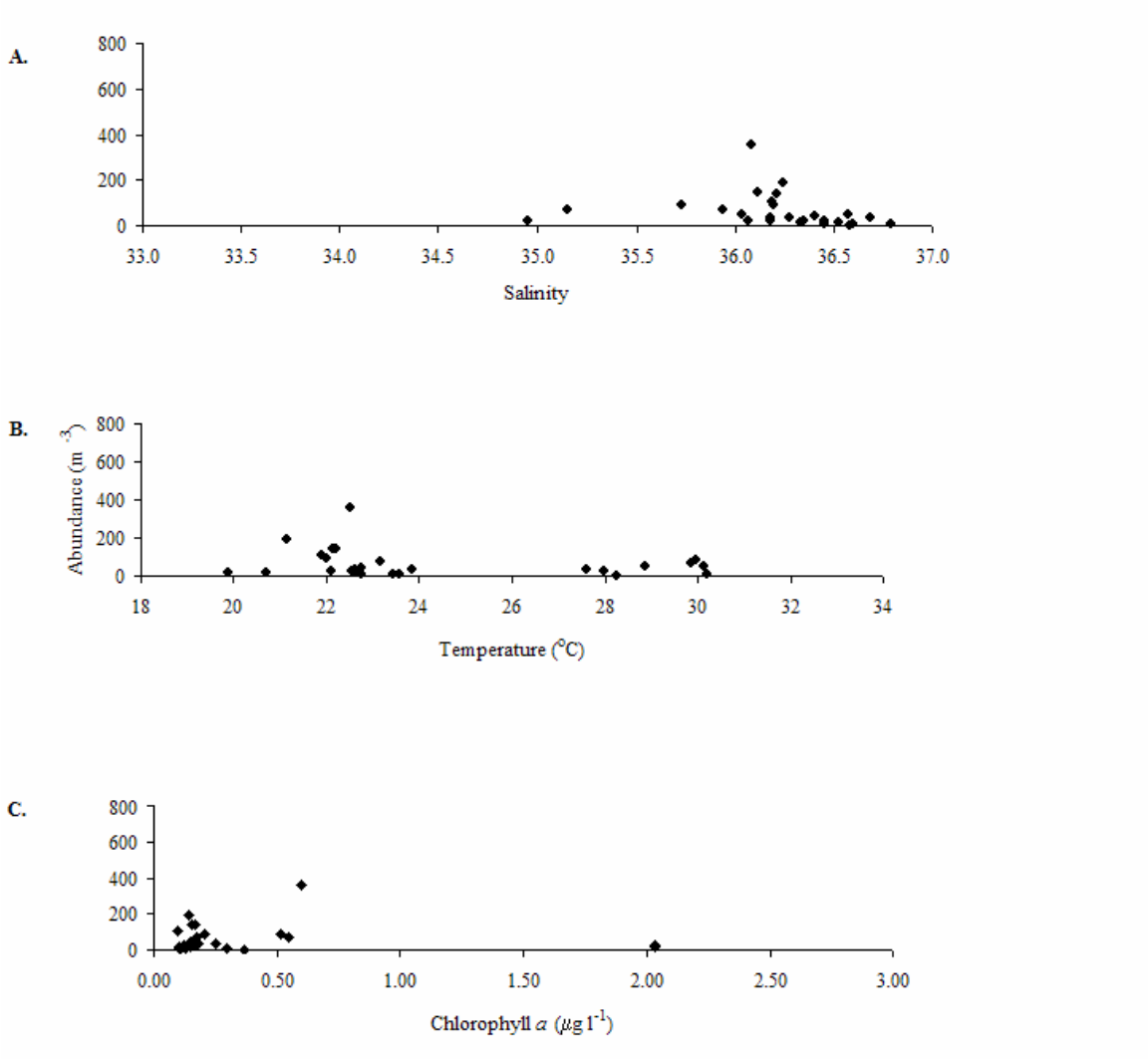

Figure 34. Distribution of *C. furcatus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

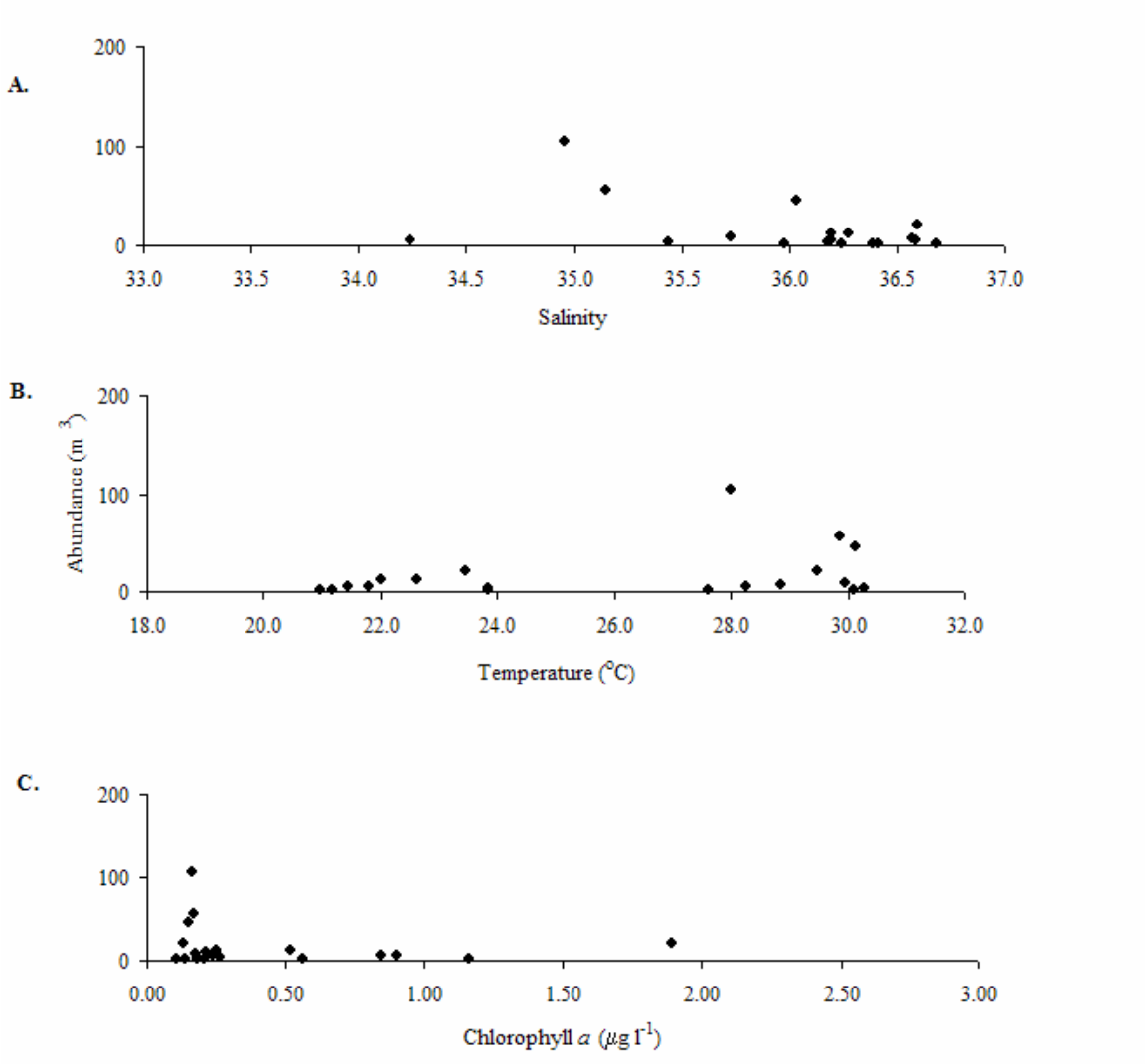

Figure 35. Distribution of *C. pavo* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

Subgroup D only O. frigida (Figure 33) was found only at the 50-meter isobath from late fall though early spring. Owre and Foyo (1964) reported this species in the Florida Current, but little is known of its distribution in the Gulf of Mexico. Distribution of *O. frigida* appeared to be correlated with high salinity and low chlorophyll *a* concentrations (Figure 36).

P. pygmaeus (Figure 33) in this study was found at the 50-meter isobath only, with highest populations occurring in December. Distribution of *P. pygmaeus* was associated with high salinity and low chlorophyll *a* concentrations (Figure 37).

P. aculeatus was reported by Minello (1980) from June through December at the 28- and 46-meter stations. Davis (1950) reported it from a sample taken 60 miles west of Anclote light. Grice (1960) found it at stations off Pensacola and Panama city. This study found *P. aculeatus* only at the 25- and 50-meter isobaths, with highest populations found at the 50-meter isobath in January (Figure 33). Bowman (1971) reported that *P. aculeatus* was a common constituent of oceanic associations, but was also tolerant of shelf waters.

Both temperature and salinity were important in the distribution of *P. aculeatus*. Minello (1980) found highest numbers at salinities greater than 30 and temperatures between 20 and 25^{o}C. In my study, *P. aculeatus* rarely occurred at salinities less than 35.5. Peak abundances were found at salinities ranging from 35.5 to 36.6 and temperatures lower than 24^{o}C (Figure 38). A correlation between *P. aculeatus* and chlorophyll *a* concentration was not observed.

C. limbatus (Figure 33) was found mostly at the 50-meter isobath in late fall through December. Owre and Foyo (1967) reported the presence of this copepod at the

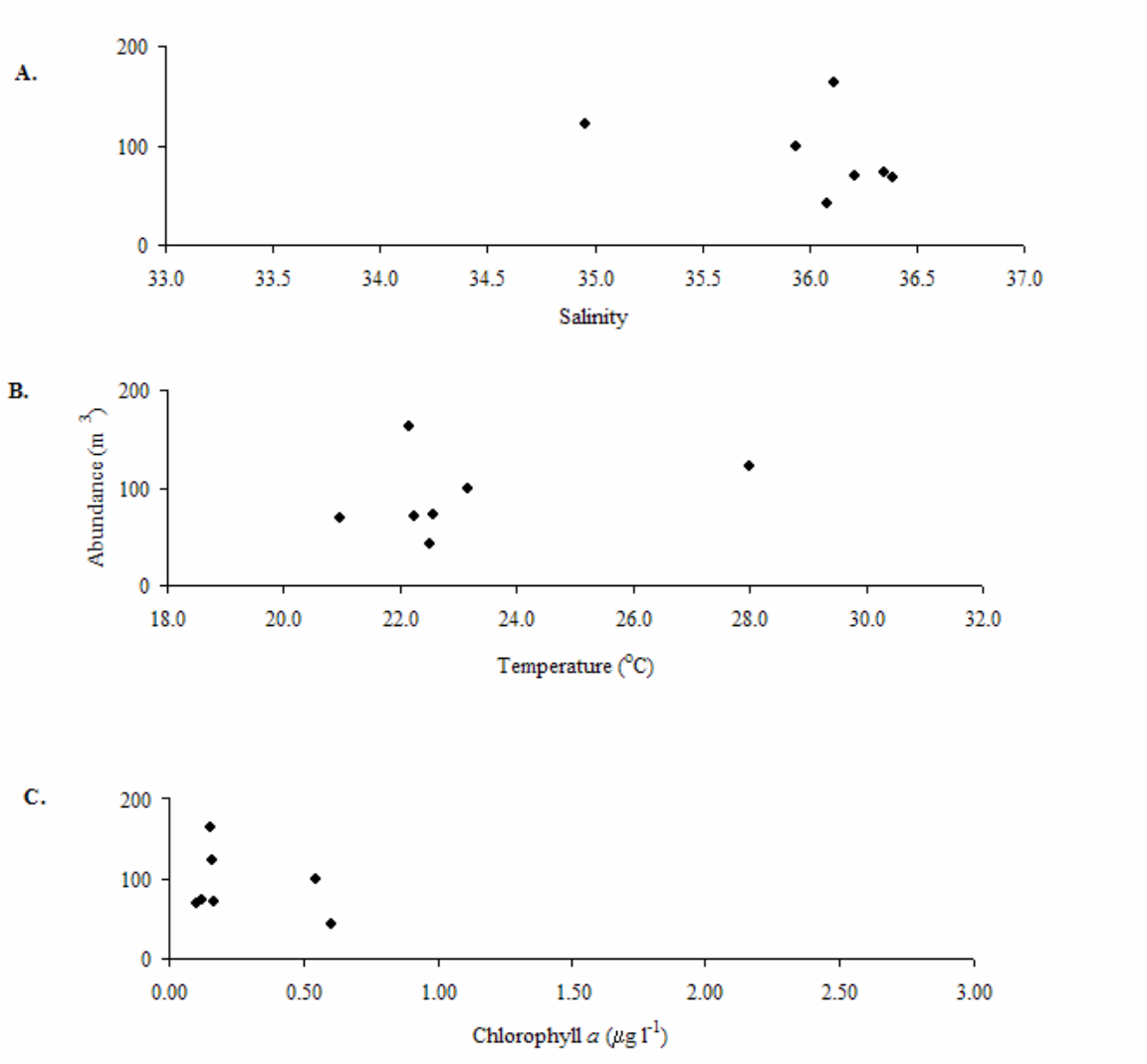

Figure 36. Distribution of *O. frigida* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

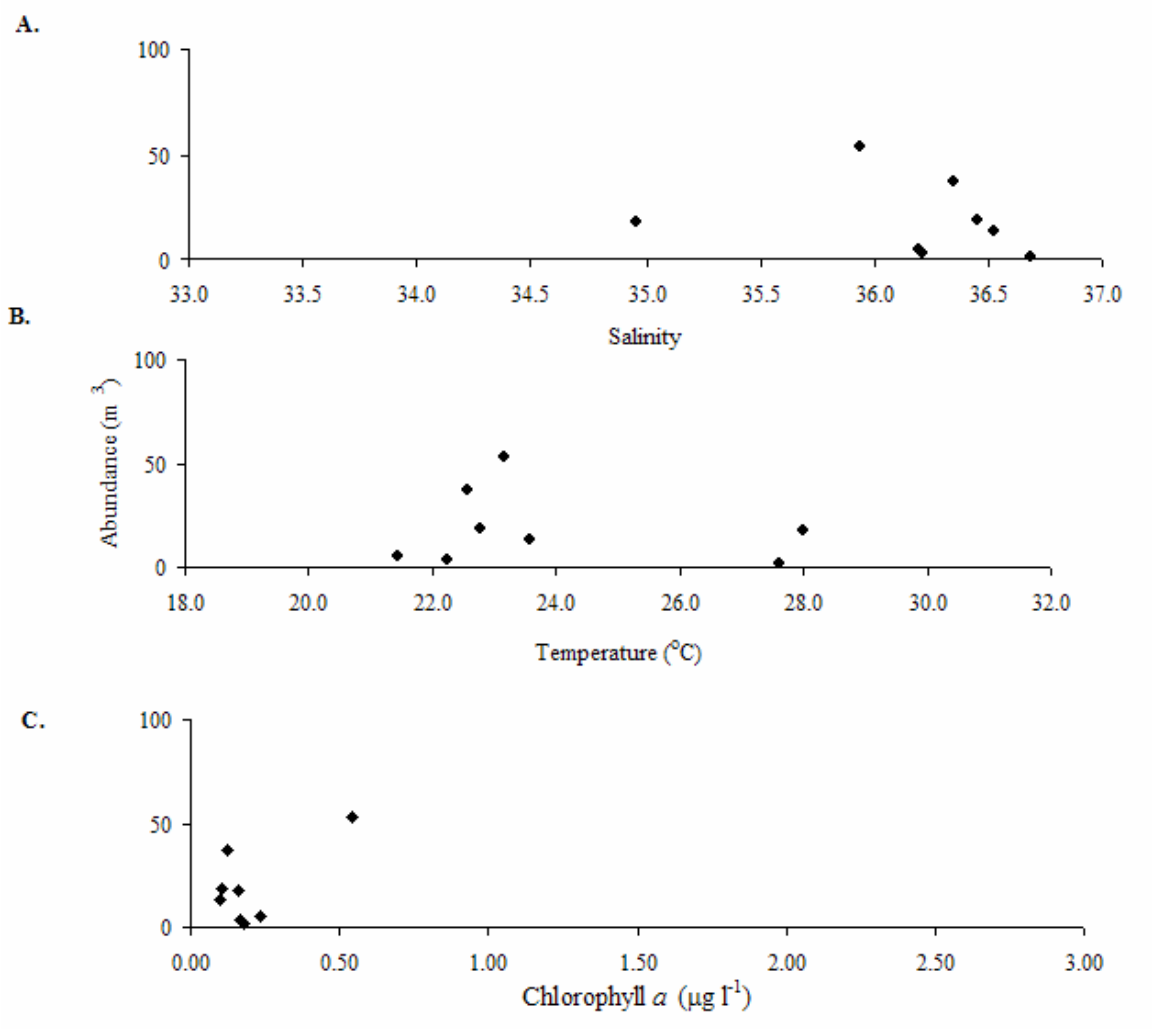

Figure 37. Distribution of *P. pygmaeus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

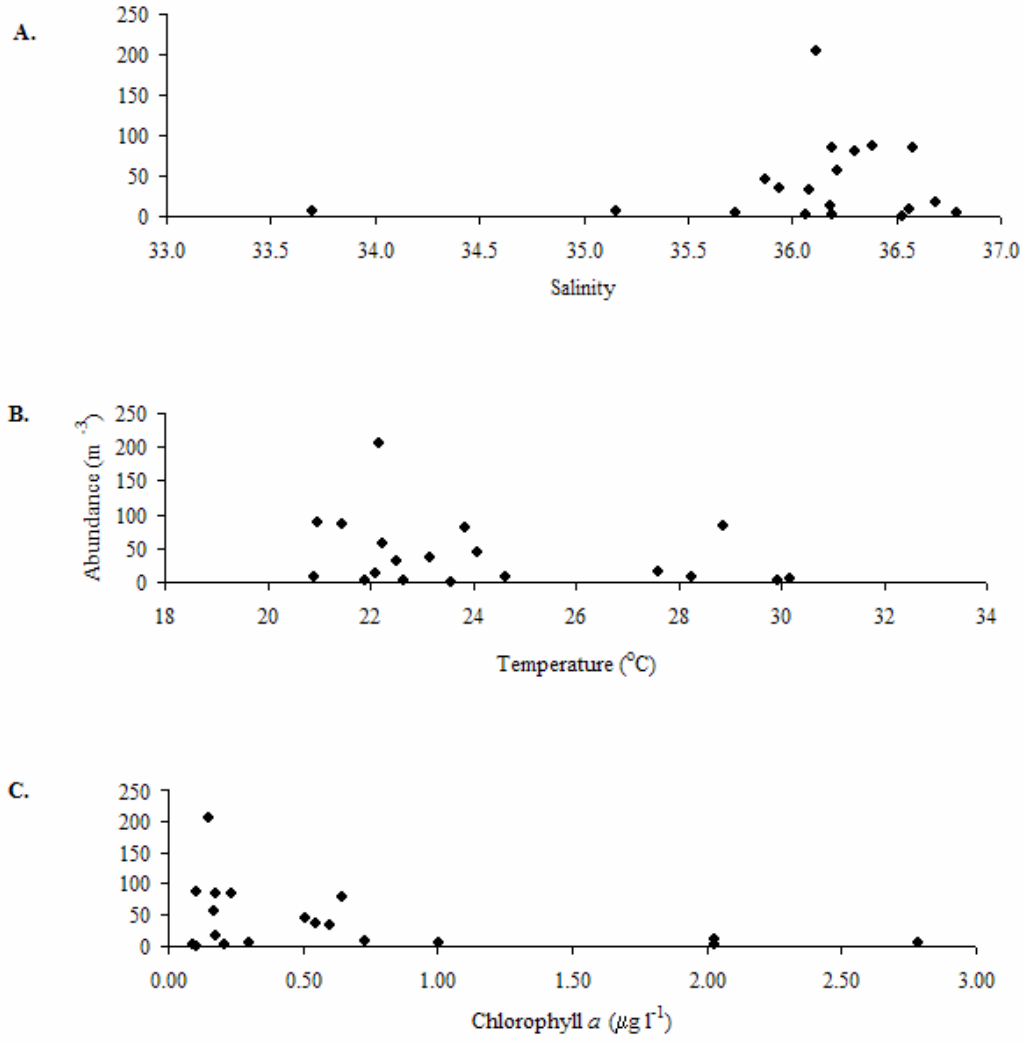

Figure 38. Distribution of *P. aculeatus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

40 mile station in the Florida Current. Little is known about the distribution of this species elsewhere in the Gulf of Mexico, which may be due to the fact that most taxonomists do not attempt to identify *Corycaeus* to species level due to difficulty in identification. There appeared to be an association between distribution of *C. limbatus* and high salinity and low chlorophyll *a* concentrations (Figure 39), though there appeared to be little association between distribution of *C. limbatus* and temperature. This association should be interpreted with caution however, due to the low number of samples containing this species.

Subgroup E only C. pavoninius (Figure 40) was found in this study at the 50 – meter isobath only. A peak in abundance occurred in December, but minor peaks were observed in spring and early summer. Distribution was associated with high (36.0 to 36.5) salinities and temperatures of 22-23^{o}C.

O. similis (Figure 33) was found in greatest concentration in July at the 50-meter isobath. No strong correlation was indicated with salinity, temperature or chlorophyll *a* concentration. However, the low number of samples of this species make analysis of contributing factors difficult. (Figure 41).

The preference for and tolerance of environmental factors differs between zooplankton species. Organisms can be classified by the extent to which they may be widely or narrowly tolerant of such factors as salinity, temperature and chlorophyll *a* concentration (Omori and Ikeda, 1992). On the WFS, such differences in distribution based on environmental factors is evident. The two major groups seen in community composition (Figure 9) show a clear disassociation with onshore and offshore environmental factors. Park and Turk (1980) found similar results working on the

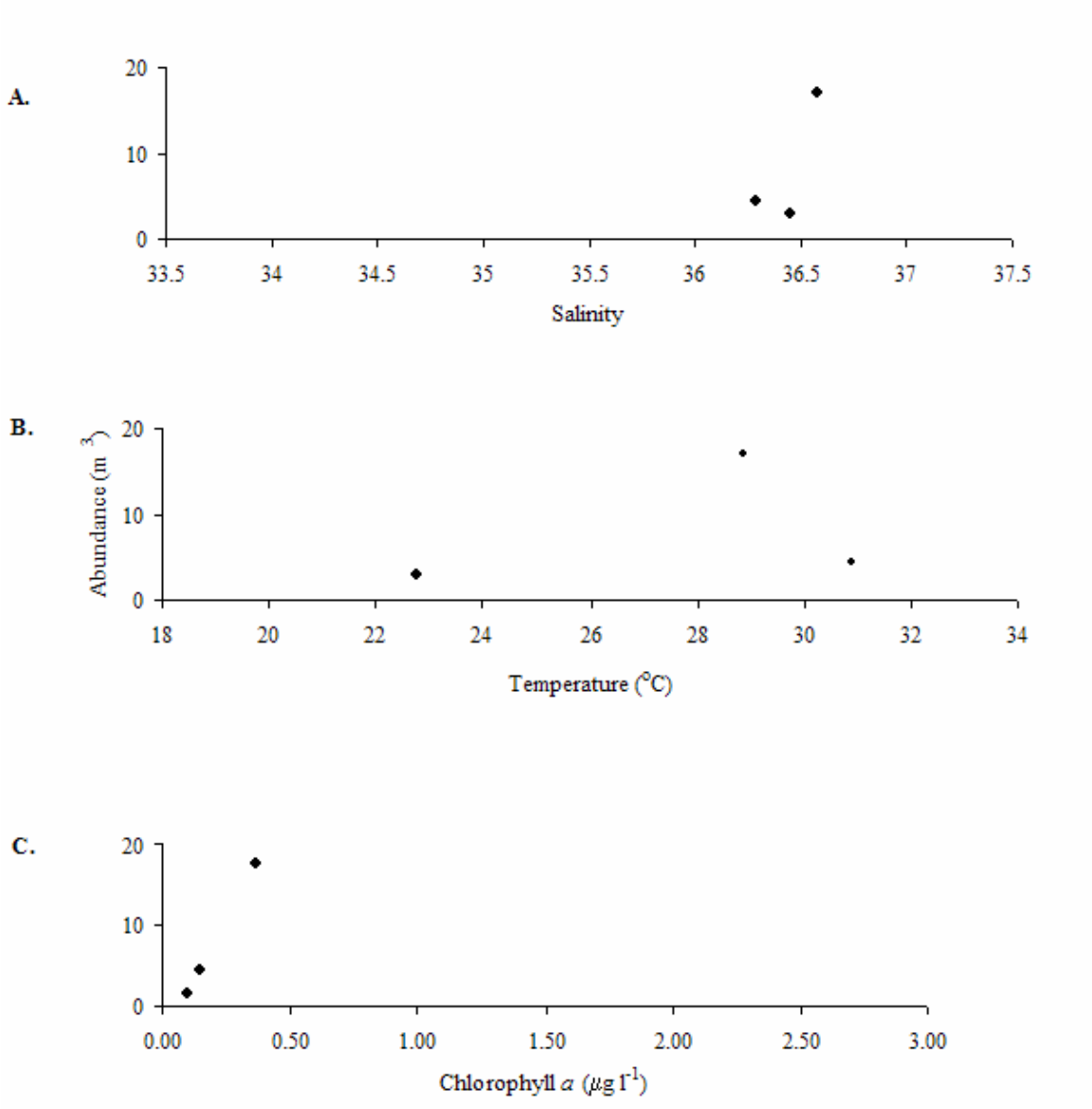

Figure 39. Distribution of *C. limbatus* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

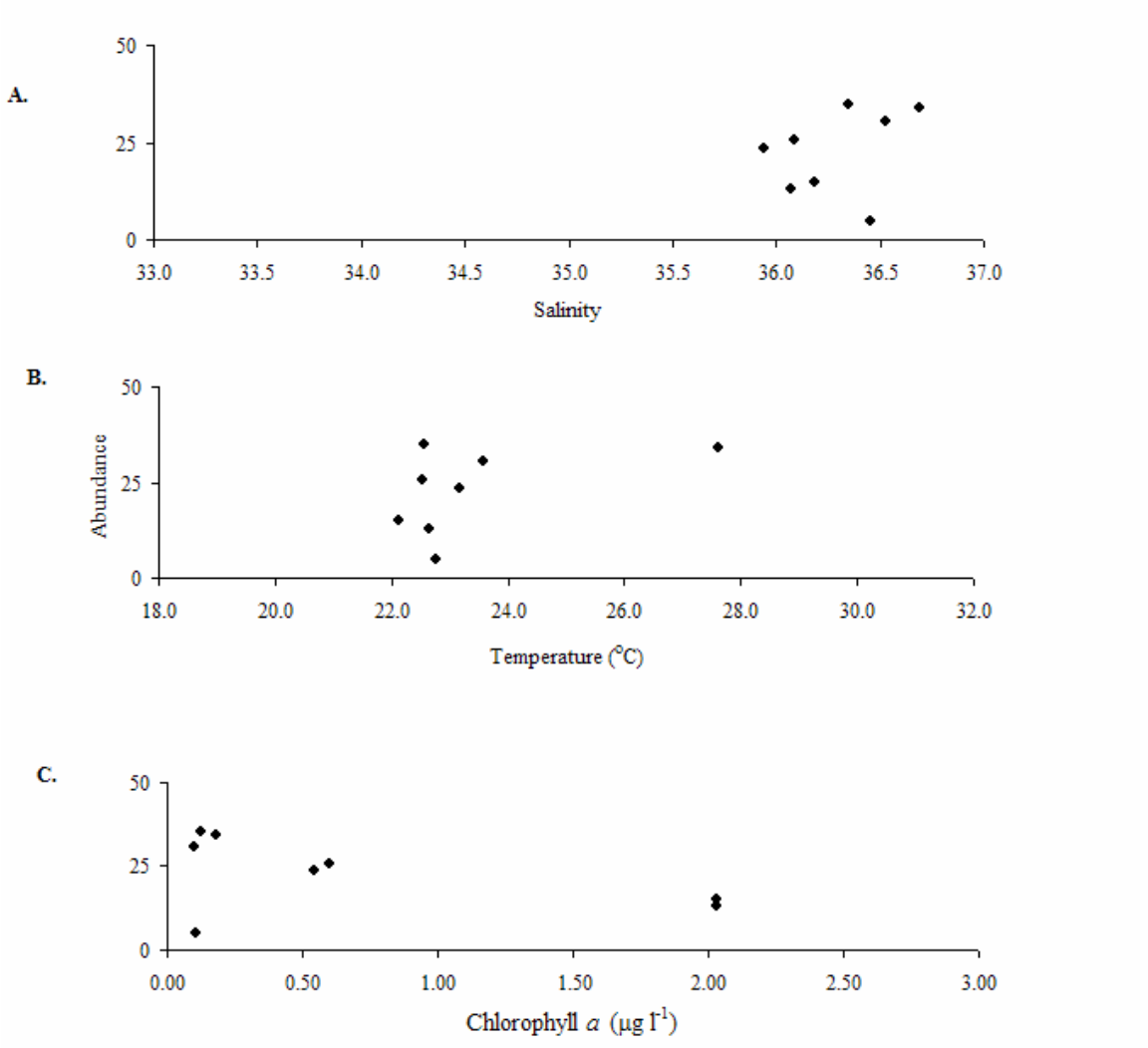

Figure 40. Distribution of *C. pavoninius* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

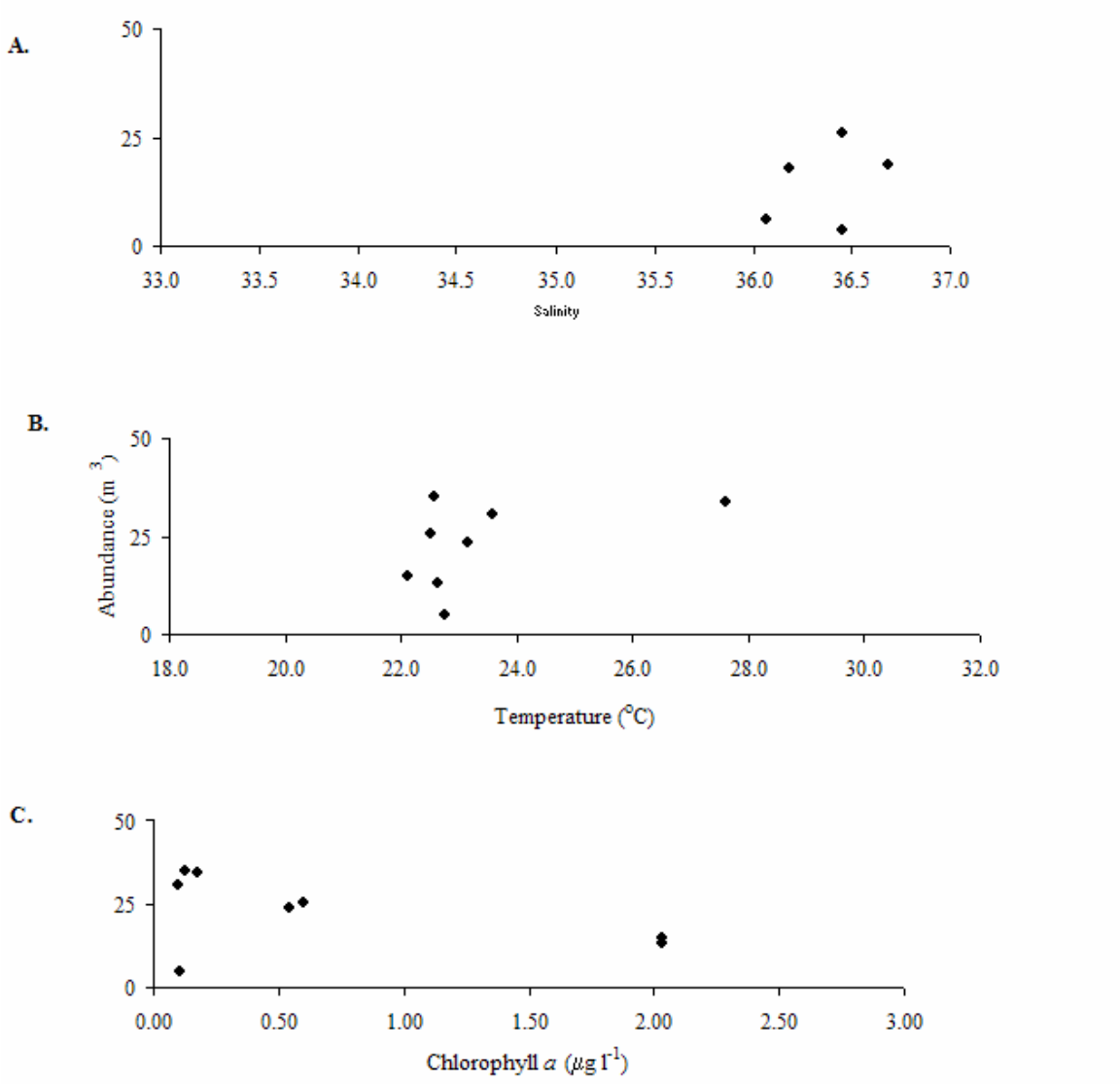

Figure 41. Distribution of *O. similis* in relation to a) salinity, b) temperature, and c) chlorophyll *a* concentration.

NWFS, as did Minello (1980). Bowman (1971) reported a marked inshore-offshore zonation working off the west coast of Florida. Sutton (2001) reported that zonation was the most prominent feature of the zooplankton community, and observed a tight correlation with physical oceanographic factors. In that study, offshore areas were dominated by Oncaea and Ostracods, while inshore areas were dominated by *O. dioica*, *Corycaeus*, *Oithona*, *Temora* and *Paracalanus*.

Upon closer examination of subgroups within these two onshore/offshore groupings, it becomes apparent that across the shelf there is significant overlap between bordering subgroups, but little overlap between near shore subgroup A and offshore subgroup E. A range of environmental factors were associated with distribution, with temperature being the most important factor associated with distribution near shore. As distance offshore increased, salinity and chlorophyll *a* concentration became increasingly important factors.

CONCLUSIONS

Abundance, biomass and community composition of zooplankton on the WFS compares well to other studies performed on the Florida shelf. The community composition found in this study mirrors that found by Minello (1980) on the NWFS. Since Minello's (1980) study encompassed 5 years of sampling, the data found here can reasonably be assumed to reflect the zooplankton assemblage of the WFS for years other than this sampling period.

At the 5-meter isobath, the copepods *O. colcarva* and *P. crassirostris* were the most important contributors to abundance and community composition. Other important and intermittent contributors to abundance and community composition at the 5-meter isobath were *P. avirostris* and *P. quasimodo*.

At the 25-meter isobath for much of the year the zooplankton assemblage was dominated by *P. quasimodo*, *O. colcarva* and the larvacean *O. dioica*. In the winter and spring, *E. chierchiae* and *C. furcatus* were dominant.

At the 50-meter isobath, fall, winter and early spring assemblages were dominated by *E. chierchiae*, *O. frigida*, *C. furcatus* and *O. mediteranea*. In the late spring, the assemblage was dominated by *C. furcatus*, *C. pavoninius*, *O. similis* and Gastropod larvae.

The importance of *E. chierchiae* to the WFS ecosystem is clearly more important than previously realized (Sutton, 2001). The ostracod dominated the zooplankton assemblage at the 25 and 50-meter isobaths for much of the year. Little is known about the ecology of *E. chierchiae*, yet it's prevalence on the WFS suggests that further study is warranted.

The 5 subgroups in community composition were tightly coupled with temperature, salinity and chlorophyll *a* concentration. A range of environmental factors defined distribution, with temperature being the most important factor defining distribution near shore. As distance offshore increased, salinity and chlorophyll *a* concentration became increasingly important as factors defining distribution.

The shade matrix developed for the 25 species that contributed to 90% of community composition supports the assertion that many species occur across a range of

subgroups (Figure 7). Considerable overlap is observed for subgroups A and B, Subgroups B, C and D, and Subgroups C, D and E. However, no overlap is observed for near shore subgroup A and offshore subgroup E. Range in chlorophyll *a* concentration, temperature, and salinity decreased as distance offshore increased. Chlorophyll *a* was found to be the most important in relation to zooplankton community composition.

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CHAPTER 3

ZOOPLANKTON AND KARENIA BREVIS IN THE GULF OF MEXICO

Abstract Blooms of the toxic dinoflagellate *K. brevis* are common in the Gulf of Mexico, yet no *in situ* studies of zooplankton and *K. brevis* interactions have been conducted. Zooplankton abundance, biomass and taxonomic composition of non-bloom and *K. brevis* bloom stations within the ECOHAB study area were thus compared. At non-bloom stations, the most abundant species of zooplankton were *Parvocalanus crassirostris*, *Oithona colcarva* and *Paracalanus quasimodo* at the 5-m isobath and *P. quasimodo*, *O. colcarva* and *Oikopleura dioica* at the 25-m isobath. There was considerable overlap in dominance of zooplankton species between the 5 and 25-m isobaths, with 9 species contributing to the top 90% of abundance at both isobaths. Within *K. brevis* blooms however, *Acartia tonsa*, *Centropages velificatus*, *Temora turbinata*, *Evadne tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris* were instead dominant. Variations in abundance and biomass between non-bloom and bloom assemblages were evident, including the reduction in abundance of 3 key species within *K. brevis* blooms.

INTRODUCTION

Blooms of the toxic dinoflagellate *K. brevis* (previously *Gymnodinium breve* Davis) frequently cause massive fish kills on the West Florida Shelf (WFS), with blooms reported by early Spanish explorers as far back as the 1500's (Steidinger et al., 1998). Previous research has identified possible links between *K. brevis* growth rates and nutrients, light levels, *Trichodesmium* spp. blooms, dinoflagellate life cycles, and hydrography of the Gulf of Mexico (Steidinger et al., 1998 and references cited therein; Lenes et al., 2001; Walsh and Steidinger, 2001; Walsh et al., 2002; Walsh et al., 2003; Heil et al., 2003; Vargo et al., 2003; Lester et al., 2003). To date, no studies have examined the qualitative and quantitative relationship between *K. brevis* and zooplankton in the Gulf of Mexico.

Studies of interactions between *K. brevis* and zooplankters invariably indicate that co-occurrence with and ingestion of *K. brevis* are associated with some physiological cost (i.e. reduced grazing, regurgitation, paralysis, twitching, and reduced fecundity), and that zooplankton will avoid ingesting it whenever alternative food sources are present (Huntley et al., 1986; Huntley et al., 1987; Sykes and Huntley, 1987; Turner and Tester, 1989). However, many zooplankton species present in the Gulf of Mexico ingest *K. brevis* (Galstoff, 1948; Dragovich and Kelly, 1964; Rounsefell and Nelson, 1966; Martin et al., 1973; Turner and Tester, 1989; Tester et al., 2000). These arguments lead to the question: what effect does the presence of *K. brevis* have on the subsequent distribution of co-occurring zooplankton?

The first task of this study, comprehensively defining the non-bloom WFS zooplankton assemblage, proved to be very difficult with the available information. Despite its high productivity and importance to the Gulf of Mexico (Austin and Jones, 1974), there is a paucity of zooplankton assemblage data for the ECOHAB study area. King (1950) described zooplankton species found from January through October 1949, but did not report quantities or seasonal data. Hopkins et al. (1981) examined the landward distribution of crustacean species of zooplankton from the 15 to the 3000 m isobath in the summer only. A more recent study (Sutton et al., 2001) focused on spatial changes in taxonomic composition within the northern portion of the ECOHAB study area, but was limited to a single transect, with identifications made to genera only.

Far more is known about the areas that border the study area. Taxonomic seasonal analysis of abundance and biomass have been conducted for Tampa Bay (Hopkins, 1977), the Anclote estuary (Weiss, 1974), Charlotte Harbor (Squires, 1977), Alligator Harbor (Grice, 1956), and the St. Andrew Bay system (Hopkins, 1966). Seasonal changes in taxonomic composition in offshore areas of the WFS are less known due to logistical constraints, though several studies have been conducted (Hopkins, 1973; Morris and Hopkins, 1981; Hopkins and Lancraft, 1984). Some overlap between estuarine, shelf and offshore zooplankton assemblages is expected due to intrusions of central Gulf water across the Florida shelf (Ortner et al., 1989; Hopkins, 1981), but all data acquired to date indicate that the zooplankton populations on the WFS are different than those found in estuaries and offshore (Minello, 1980; Hopkins, 1981; Ortner et al., 1989; Sutton et al., 2001). Prior to identifying potential interrelationships between the

zooplankton assemblage and *K. brevis* blooms, taxonomic characterization of the zooplankton assemblage in the study area was necessary.

METHODS

Zooplankton sampling took place during monthly ECOHAB cruises on board the R/V Suncoaster and the R/V Bellows in the Gulf of Mexico (Figure 42). Stations were located approximately every 5 nautical miles. A CTD profile was conducted at every station. At selected stations (usually every other station, but occasionally more frequently) water samples were collected to determine chlorophyll *a* concentration and *K. brevis* cell counts.

Zooplankton sampling began in August 1999 and continued through July 2000. Stations 1 and 51 were chosen to represent the zooplankton assemblage at the 5-m isobath, while Stations 5 and 46 represented the zooplankton assemblage at the 25-m isobath. Although most blooms occur inshore of the 25 m-isobath (Steidinger et al., 1998), the analysis of zooplankton community composition at that isobath was assessed to ensure that advected offshore populations were not responsible for any of observed changes in zooplankton community structure. In addition to the fixed stations, during the first year of sampling zooplankton tows were also conducted at stations where *K. brevis* concentrations were found to be above a background concentration of 1,000 cells l^{-1}.

During the fall and winter of 2001, a *K. brevis* bloom occurred in the study area. In September and December 2001, zooplankton tows were conducted on ECOHAB

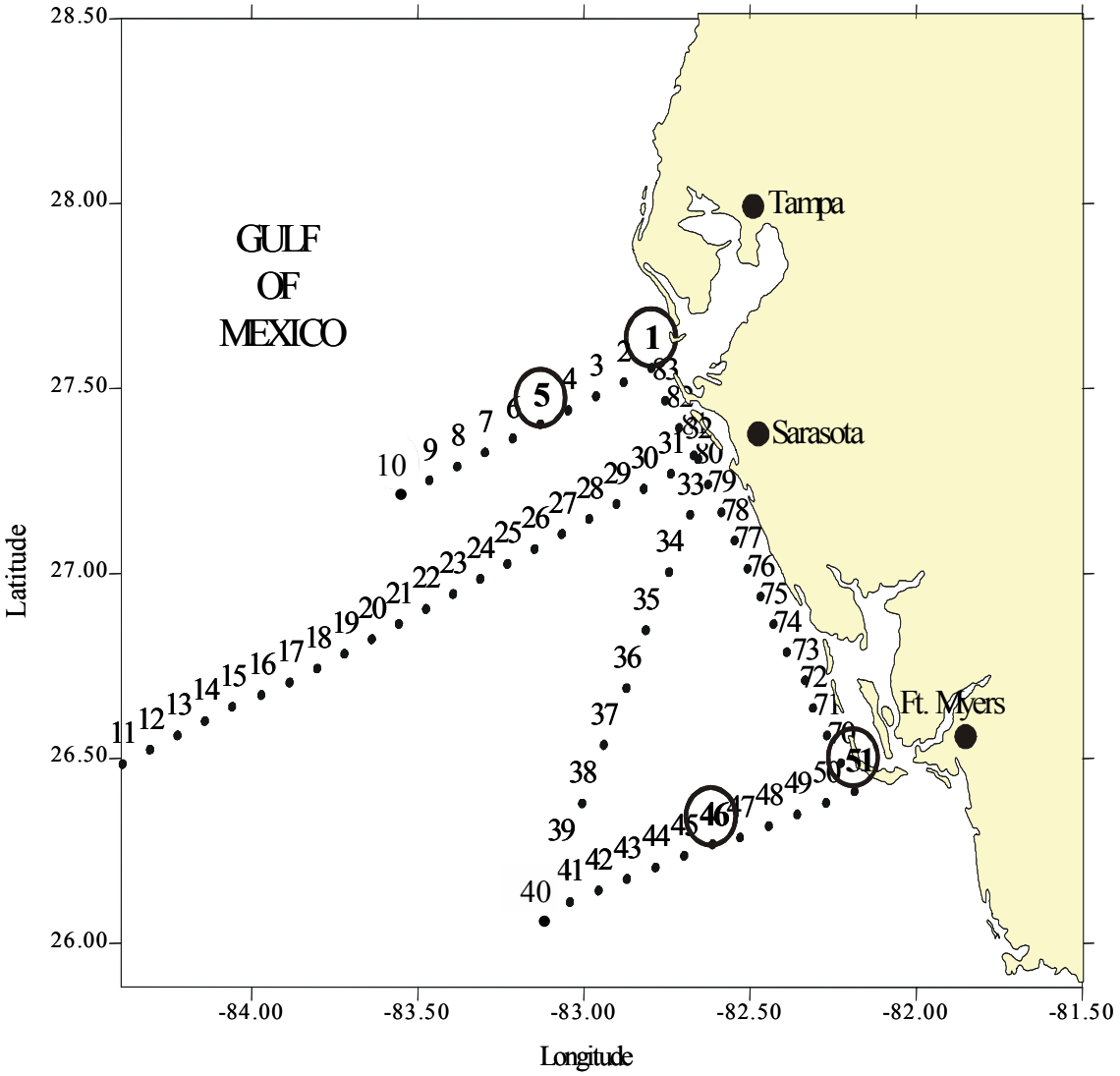

Figure 42. ECOHAB study area in the Gulf of Mexico. Station locations for ECOHAB cruises are indicated by a (•). Stations where zooplankton tows were conducted are indicated by a circle.

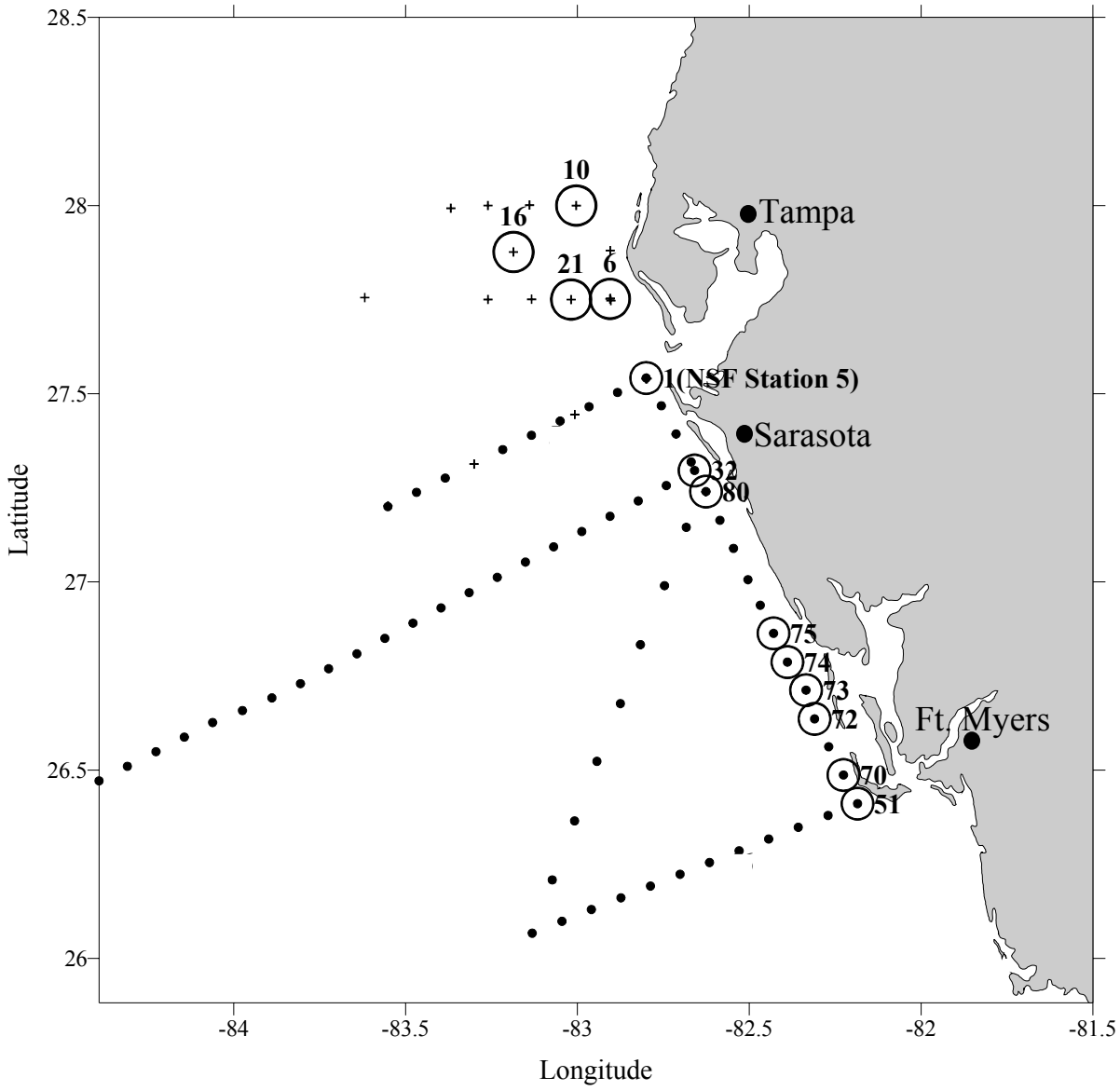

Figure 43. Station locations for ECOHAB cruises (•) and NSF cruises (+). Stations where zooplankton tows were conducted are circled and indicated by a number. NSF Station 5 is in the same location as ECOHAB Station 1.

cruises at stations within the bloom, while in October, the zooplankton tows within the bloom were taken to the north of the ECOHAB study area (Figure 43).

Collection of Zooplankton

1999-2000 Zooplankton were collected with a 153 μm mesh bongo net, lowered closed through the water column, opened at depth and then towed obliquely from bottom to surface. The volume of water filtered was calculated with a calibrated flow meter attached at the net mouth (Omori and Ikeda, 1992).

The cod ends were filtered through a 2000 μm mesh sieve to remove macrozooplankton and large gelatinous zooplankton. Each filtered cod end was preserved on board in a 5% buffered formalin solution (Omori and Ikeda, 1992) for later counts of zooplankton species abundance.

2001 Collection of zooplankton in 2001 was accomplished in an identical manner, except that a single 153 μm mesh net was used instead of a bongo net, because statistical analysis conducted in 1999-2000 had shown that a single tow could adequately sample the zooplankton population.

Zooplankton abundance and biomass

Representative subsamples of 500-600 animals were obtained with a Stempel pipette (usually 1-5% of initial cod end volume). Zooplankton were identified and counted using an Olympus dissecting microscope. Holoplankton were identified to species level. Meroplankton were identified to major taxonomic group (e.g. Pelecypod veligers, Cirriped larvae). Copepod nauplii were not identified to species level but, when

possible, were identified to family level. Replicate samples were averaged for each station. Biomass was determined using published length/width data (Table 12).

Chlorophyll a *concentration and K. brevis cell counts*

Zooplankton tows were conducted in conjunction with CTD casts, measurements of chlorophyll *a*, and *K. brevis* cell counts. Water column samples were collected from Niskin bottles of a rosette sampler. Duplicate chlorophyll samples were filtered on GF/F filters, placed in 10 ml methanol and stored at -20^{o}C in darkness for later analysis with a Turner design fluorometer (Welschmeyer, 1994). *K. brevis* was counted live using a dissecting microscope within two hours of collection. Typically 5 0.2 ml subsamples were counted in duplicate well slides. Final abundance is expressed as the average of all values.

Statistical Analysis

Observed community associations were quantified using the multivariate statistical techniques of PRIMER (Plymouth Routines in Multivariate Ecological Research) software. Hierarchal clustering analysis was used to identify trends in community distribution of the zooplankton assemblage. Bray-Curtis similarities (Clarke and Warwick, 1994) were calculated and subsequently ranked within a similarity matrix. Data were not standardized, since all stations were already on the same scale of abundance m^{-3}. However a square root transformation was performed to minimize variations in abundance (Clarke and Warwick, 1994).

Table 12
Sources of biomass values and length/width regression equations for WFS zooplankton taxa.

Taxon	Source	Comments
Undinula	Morris and Hopkins, 1983	
Eucalanus	Morris and Hopkins, 1983	
Acrocalanus	Weiss, 1978	Derived from *Paracalanus*
Calocalanus	"	
Paracalanus	"	
Clausocalanus	"	Derived from *Centropages*
Scolothrex	Morris and Hopkins, 1983	
Euchaeta	Morris and Hopkins, 1983	
Temora	Lester, unpub. data	
Centropages	Weiss, 1978	
Calanopia	"	
Pseudodiaptomas	"	
Acartia	"	
Tortanus	"	
Labidocera	"	
Oithona	"	
Oncaeae	Squires, 1984	
Corycaeus	Weiss, 1978	
Farranula	"	
Euterpina	"	
Microsetaella	"	
Euchonchoichiea	Hopkins, 1984	
Penilia	Weiss, 1978	
Evadne	"	
Podon	"	*E. tergestina* value
Appendicularians	"	
Brachiopoda	"	
Bryozoa	"	
Cirripedia	"	
Decapoda	"	
Echinodermata	"	
Gastropoda	"	
Pelecypoda	"	
Platyhelminthe	Squires, 1984	
Polychaeta	Weiss, 1978	

Similarity percentages within and between groups of zooplankton were determined using PRIMER's SIMPER routine, which calculates the average dissimilarity between inter-group samples and computes dissimilarities between groups.

RESULTS

WFS Zooplankton Assemblage – 1999-2000

Abundance and Biomass Abundance ranged from 185 animals m^{-3} (at Station 46 in June 2000) to 22 x 10^3 animals m^{-3} (at Station 1 in September 1999) (Table 13). Depth-averaged abundance was always greatest at the 5-meter isobath, where it peaked in late summer and early fall, increased again in December, and was at its lowest in early spring (Figure 44). At the 25-m isobath, abundance peaked in October and November, decreased through April, and increased slightly through the summer.

Biomass ranged from 0.91 mg m^{-3} (at Station 46 in June 2000) to 62.12 mg m^{-3} dry weight (at Station 1 in December) (Table 13). Depth-averaged biomass at the 5-m isobath showed the same trends as abundance, with highest biomass occurring in August, September, and December, decreasing through the spring, and increasing again through the summer (Figure 45). At the 25-m isobath, biomass was highest in November, remained high through January, declined in the spring and increased through the summer and fall.

Statistical Analysis and Community Composition Hierarchal cluster analysis showed two major groups of community composition at the 30% similarity level. All 5-m isobath stations were included in WFS 1, and all 25-m isobath stations were included

Table 13
Numerical abundance and biomass for non-red tide 5-m and 25-m isobath stations sampled on the WFS in 1999 and 2000.

	5-m isobath			25-m isobath		
Month	Station	Abund. (m^{-3})	Biomass (mg m^{-3})	Station	Abund. (m^{-3})	Biomass (mg m^{-3})
August	1	18995	44.47	5	--	--
1999	51	11469	37.40	46	1105	3.79
September	1	22135	53.81	5	845	5.92
1999	51	10547	26.91	46	1501	8.63
October	1	9020	18.34	5	3013	7.91
1999	51	6613	16.62	46	--	--
November	1	--	--	5	2628	15.31
1999	51	2886	14.04	46	3154	15.93
December	1	20021	62.12	5	1494	10.39
1999	51	4425	10.48	46	2502	14.19
January	1	6312	20.16	5	703	12.07
2000	51	2121	3.59	46	1501	9.67
March	1	2463	6.14	5	503	2.96
2000	51	1311	7.06	46	424	2.24
April	1	1099	12.25	5	224	2.44
2000	51	4446	3.76	46	194	1.42
May	1	1389	4.27	5	301	3.38
2000	51	4499	10.79	46	292	1.57
June	1	10452	45.24	5	1015	7.04
2000	51	6031	20.88	46	185	0.91
July 2000	1	5472	22.95	5	721	3.81

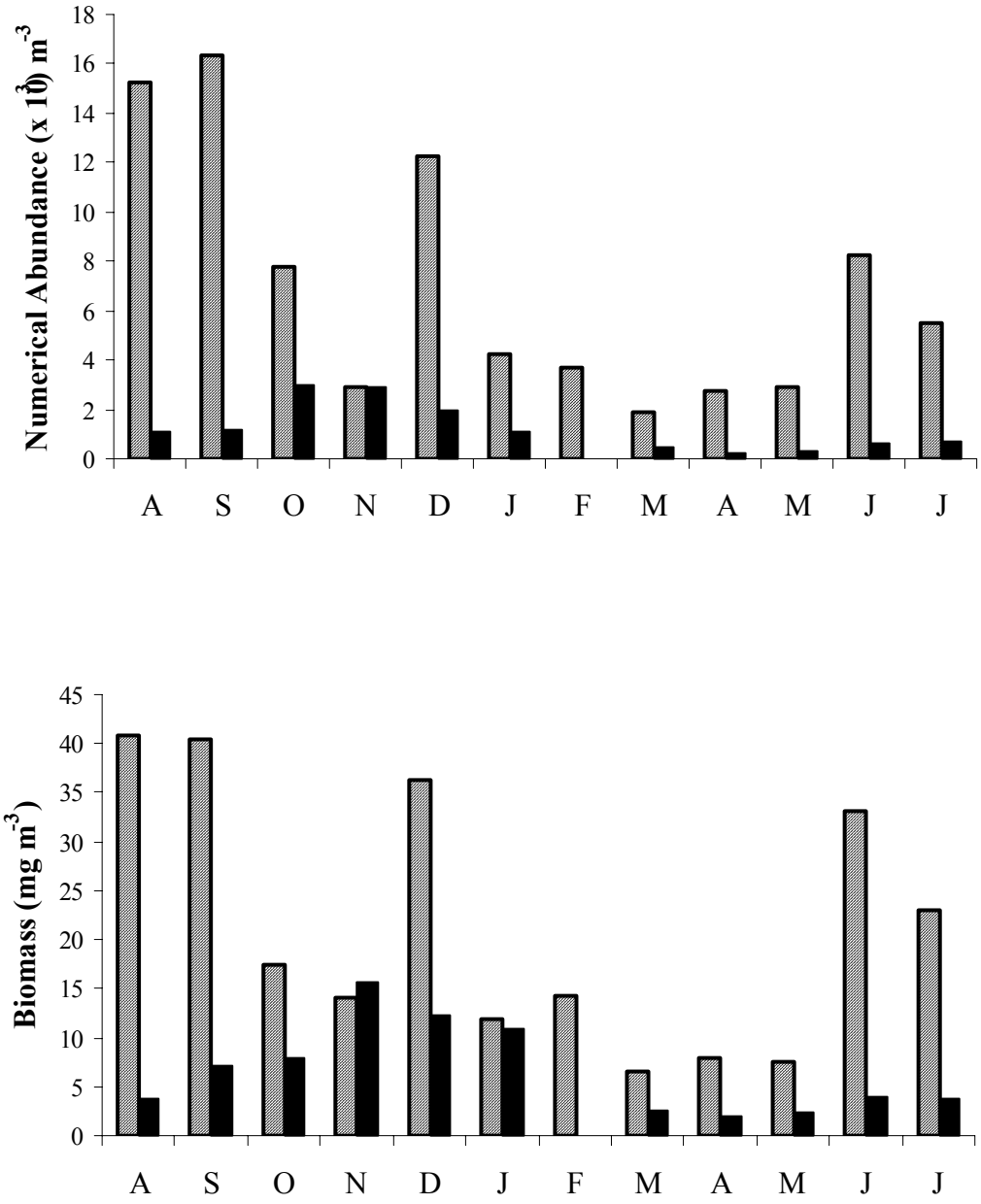

Figure 44. a) Total zooplankton abundance m^{-3} for the 5-m (hatched bars) and 25-m (solid bars) isobath. b) Total zooplankton biomass in dryweight mg^{-3} for the 5-m (hatched bars) and 25-m (solid bars) isobath.

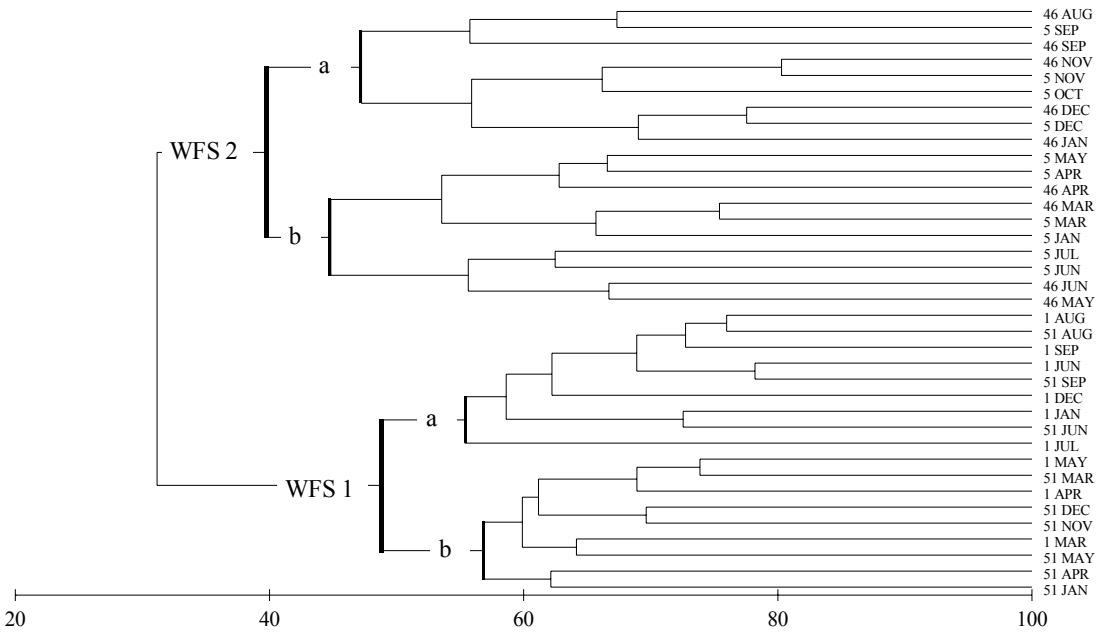

Figure 45. Cluster derived dendrogram for 37 stations at the 5 and 25-m isobaths, using group-averaged clustering from Bray-Curtis similarities on square root transformed abundance data.

in WFS 2 (Figure 45). Groups WFS 1 and WFS 2 consisted of two seasonal subgroups each at the 40 and 50% similarity levels, respectively.

At both isobaths, 6 taxa were responsible for 60% of the community structure. At the 5-m isobath, *P. crassirostris*, *O. colcarva*, *P. quasimodo*, Cirriped larvae, *Euterpina acutifrons* and the cladoceran *Penilia avirostris* were dominant (Table 14). Less abundant at this isobath were *C. velificatus*, *A. tonsa*, *Corycaeus americanus*, *O. dioica*, and the larvae of Gastropods, Decapods and Pelecypods. At the 25-m isobath (Table 15), the most abundant zooplankton were *P. quasimodo*, *O. colcarva*, *O. dioica*, *C. velificatus*, Gastropod larvae and *O. plumifera*. Lesser contributors were *P. crassirostris*, *Oncaea mediteranea*, *E. acutifrons*, the ostracod *Euchonchoichiea chierchiae*, and the larvae of Pelecypods and Decapods.

Of the 13 taxa that accounted for 90% of the abundance at the 5-m isobath, 9 contributed to 90% of total abundance at the 25-m isobath as well, indicating significant overlap in community structure. Four taxa, Cirriped larvae, *A. tonsa*, *P. avirostris* and *C. americanus*, were dominant at the 5-m isobath but not at the 25-m isobath. Similarly, 5 species, *O. plumifera*, *O. mediteranea*, *E. chierchiae*, *C. amazonicus*, and *C. furcatus*, contributed significantly to abundance at the 25-m isobath only.

Variations in the amount contributed by *P. crassirostris*, *O. colcarva*, *P. avirostris*, *E. acutifrons*, *P. quasimodo*, *A. tonsa* and the larvae of Cirripeds, Pelecypods and Decapods accounted for 60% of the differences in community composition between the two isobaths (Table 16). The 5 species characteristic of 25-m isobath assemblages, *O. plumifera*, *O. mediteranea*, *E. chierchiae*, *C. amazonicus*, and *C. furcatus*, accounted for only 7.98% of the difference in community composition between the two groups.

Table 14

Results of SIMPER analysis showing determinant species for WFS 1. Abundance data square root transformed, n=18.

Taxon	Av. Abund. (m^{-3})	Contrib. (%)	Cum. (%)
P. crassirostris	1655.08	17.07	17.07
O. colcarva	1224.78	12.35	29.42
P. quasimodo	343.92	8.23	37.65
Cirriped larvae	477.53	7.74	45.39
E. acutifrons	355.67	6.87	52.26
P. avirostris	1105.17	6.77	59.03
Decapod larvae	201.53	5.67	64.70
Pelecypod larvae	271.31	4.97	69.67
C. americanus	108.06	4.35	74.02
C. velificatus	70.14	4.17	78.19
Gastropod larvae	106.39	4.16	82.36
O. dioica	176.31	4.08	86.44
A. tonsa	243.5	3.15	89.59

Table 15

Results of SIMPER analysis showing determinant species for WFS 2. Abundance data square root transformed, n=19.

Taxon	Av. Abund. (m^{-3})	Contrib. (%)	Cum. (%)
P. quasimodo	123.05	12.22	12.22
O. colcarva	88.63	11.84	24.07
O. dioica	56.63	11.55	35.62
C. velificatus	82.55	8.20	43.82
Gastropod larvae	46.97	7.81	51.63
O. plumifera	19.87	7.57	59.20
Pelecypod larvae	63.97	6.71	65.91
O. mediteranea	53.24	4.61	70.52
P. crassirostris	29.13	4.60	75.12
E. acutifrons	32.97	3.72	78.84
E. chierchiae	84.55	3.29	82.13
Decapod larvae	7.63	2.81	84.94
C. amazonicus	19.87	2.54	87.48
C. furcatus	26.66	2.47	89.95

Table 16
Results of SIMPER analysis showing average determinant dissimilarities between WFS 1 and WFS 2. Abundance data square root transformed, WFS 1 n = 18; WFS n=19.

Taxon	WFS 1 Av. Abund. (m-3)	WFS 2 Av. Abund. (m-3)	Av.Diss	Cum. (%)
P. crassirostris	1655.08	29.13	8.39	12.19
O. colcarva	1224.78	88.63	6.43	21.53
P. avirostris	1105.17	4.95	6.24	30.60
Cirriped larvae	477.53	2.13	4.66	37.36
E. acutifrons	355.67	32.97	3.69	42.72
Pelecypod larvae	271.31	63.97	3.19	47.35
P. quasimodo	343.92	123.05	3.05	51.78
Decapoda	201.53	7.63	2.77	55.80
A. tonsa	243.50	1.61	2.71	59.73
Oithona nana	141.50	0.74	2.52	63.39
C. americanus	108.06	15.26	2.48	66.99
T. turbinata	165.42	36.11	2.20	70.19
O. dioica	176.31	56.63	1.80	72.80
C. amazonicus	90.28	19.87	1.75	75.35
Gastropod larvae	106.39	46.97	1.71	77.83
Polychaete larvae	124.42	13.45	1.59	84.90
E. chierchiae	0.00	84.55	1.64	80.22
C. velificatus	70.14	82.55	1.63	82.58
O. mediteranea	0.00	53.24	1.52	87.11
O. plumifera	0.00	19.87	1.29	88.99
C. furcatus	2.14	26.66	1.05	90.52

Average dissimilarity 68.85

Zooplankton Assemblage - K. brevis *Blooms*

Abundance and Biomass Zooplankton abundance and community composition at each station sampled during the 1999 and 2001 *K brevis* blooms are given in Tables 17 and 18. In October 1999, the highest abundance and biomass occurred at Station 80, where *K. brevis* exceeded 5 X10^6 cells l^{-1}. In 2001, greatest abundance was found at Station 70 in December, when *K. brevis* was 1.7 X 10^5 cells l^{-1}, and at Station 21 in October, with a *K. brevis* stock of 1 X 10^6 cells l^{-1}. The lowest abundance in 2001 was 219 animals m^{-3} at Station 70 in September, at a *K. brevis* population of only 8 X 10^3 cells l^{-1}.

Maximum zooplankton abundance during the 2001 *K. brevis* bloom occurred in December at Station 70, when biomass exceeded 355 mg m^{-3}, 5 times greater than the highest biomass at non-bloom stations in 1999-2000.

Community Composition In October 1999, *K. brevis* populations were very low at Stations 1 and 51 where the typical near shore assemblage of zooplankton was present and the most important contributors to abundance were *P. crassirostris* and Cirriped larvae. At near shore Station 80, where surface *K. brevis* exceeded 5 million cells l^{-1}, typical near shore zooplankton species were either absent or were significantly reduced in importance. *A. tonsa*, *P. quasimodo*, *P. crassirostris*, decapod larvae and pelecypod larvae were >80% less abundant at Station 80 than at Station 51. *O. colcarva*, *O. dioica*, and *E. acutifrons*, all present at Stations 1 and 51, were absent from the assemblage at Station 80.

Table 17
Zooplankton community composition, numerical abundance and biomass at stations sampled within 1999 *K. brevis* bloom.

	October-99		
K. brevis cells l^{-1} x 10^3	7.5	16	5270
Station	51	1	80
A. tonsa	11	245	4
C. amazonicus	39	98	--
C. americana	56	--	--
C. americanus	7	--	--
C. velificatus	118	49	4569
E. pileatus	--	--	234
E. tergestina	--	--	--
E. acutifrons	25	405	--
E. crassus	57	--	--
L. aestiva	--	--	112
L. scotti	--	25	55
O. nana	52	172	--
O. colcarva	102	749	--
O .dioica	150	--	--
O. similis	--	--	--
O. simplex	--	25	--
P. avirostris	--	37	--
P. crassirostris	5553	2884	516
P. quasimodo	206	37	25
T. setacaudatus	18	--	--
T. stylifera	--	--	--
T. turbinata	70	--	2341
Cirriped larvae	4	2037	59
Decapod larvae	43	650	179
Echinoderm larvae	4	--	--
Gastropod larvae	4	12	4
Pelecypod larvae	4	479	31
Polychaete larvae	14	123	--
Total Num Abund. m^{-3}	7069	1299	3542
Biomass (mg m^{-3})	24.50	3.13	62.02

Table 18
Zooplankton community composition, numerical abundance and biomass at stations sampled within 2001 *K. brevis* bloom.

	September-01					October-01					December-01		
K. brevis cells l^{-1} x 10^3	8	200	500	75	15	1268	742	1320	1078	774	16	68	176
Station	70	72	73	74	75	6	10	16	21	5	70	32	1
A. tonsa	42	185	120	29	67	3	--	38	50	337	21447	145	16
C. amazonicus	8	--	--	2	1	2	141	--	225	56	--	--	--
C. americana	7	3	4	3	17	--	--	--	0	--	--	--	--
C. americanus	12	--	--	5	0	--	--	--	112	112	48	18	24
C. velificatus	2	--	--	4	41	1	--	2	25	112	--	--	--
E. pileatus	--	--	--	--	--	--	--	--	--	--	--	--	--
E. tergestina	1	63	10	--	83	--	117	12	275	1516	1008	4462	621
E.acutifrons	23	4	--	9	18	--	23	24	--	--	--	--	--
E. crassus	--	--	--	--	--	--	--	--	--	--	--	--	--
L.aestiva	4	1	--	1	3	1	23	--	50	56	--	--	--
L.scotti	--	--	--	--	--	--	--	--	--	--	--	--	--
O. nana	--	--	--	--	--	--	--	--	--	--	--	48	0
O.colcarva	1	25	6	28	126	33	1081	38	4730	6121	--	289	24
O.dioka	--	--	26	39	100	1	47	108	2772	421	96	235	8
O.similis	--	--	--	--	--	--	--	--	826	--	--	--	--
O.simplex	19	19	4	5	60	--	--	--	--	337	--	--	--
P. avirostris	8	3	18	13	26	--	--	29	198	--	--	--	--
P. crassirostris	--	83	24	156	2711	30	681	--	826	1994	--	--	--
P. quasimodo	--	2	7	19	36	--	--	--	75	28	48	18	2
T. setacaudatus	2	--	--	--	--	--	23	--	75	--	2	--	--
T. stylifera	9	--	--	--	--	--	--	--	--	--	--	--	--
T. turbinata	2	--	0	37	29	--	--	--	--	--	--	--	--
Cirripid larvae	6	8	7	--	1	1	234	216	2161	2161	432	217	21
Decapod larvae	--	56	81	--	1	6	164	120	590	590	96	18	--
Echinoderm larvae	--	--	--	--	--	0	658	41	197	197	--	--	--
Gastropod larvae	--	--	--	--	5	10	117	137	140	140	--	--	--
Pelecypod larvae	--	--	--	8	3	289	8366	5616	1685	1685	--	--	--
Polychaete larvae	24	8	16	1	5	12	141	225	505	505	192	54	10
Total Num Abund. m^{-3}	219	531	325	635	3343	388	11866	6502	21580	16480	726	5456	23369
Biomass (mg m^{-3})	1.24	3.95	2.81	1.80	5.77	0.64	17.18	10.59	38.64	31.07	1.15	9.77	355.40

Dominant zooplankton species in October were instead *C. velificatus* and *T. turbinata*. *C. velificatus* was 39 times more abundant at Station 80 than at Station 51, and 93 times more abundant here than at Station 1. The majority of *C. velificatus* at Station 80 were Stage III and IV copepodites. *T. turbinata* was 14 times more abundant at Station 80 than at Station 51 and 98 times more abundant at Station 80 than at Station 1. No copepodite stages of *T. turbinata* were observed. *E. pileatus*, absent at Stations 1 and 51, was a major contributor to biomass at Station 80.

During the early stages of the 2001 bloom in September, the zooplankton assemblage did not appear to diverge from a "normal" coastal assemblage on the WFS, except for lower abundance at most stations. At low *K. brevis* concentrations, *P. crassirostris* dominated at Station 75, *P. avirostris* at Station 72, and *A. tonsa* and *E. acutifrons* at Station 70. At Stations 72 and 73, where *K. brevis* concentrations were 2 X 10^5 and 5 X 10^5 cells l^{-1}, respectively, *A. tonsa* was dominant. Other major contributors at stations 72 and 73 were Decapod larvae, *P. crassirostris* and *O. dioica*.

As the bloom progressed through October, the zooplankton assemblage changed in both abundance and percent composition. Abundance was high at all stations except Station 6. The greatest departure from zooplankton populations observed in 2001 occurred at stations 16, 10 and 21, when pelecypod larvae dominated the assemblage, in one case exceeding 8,000 larvae l^{-1} and comprising over 90% of the zooplankton assemblage. At Station 6 most near shore species were present, and Station 5 was characterized by very high concentrations of *O. colcarva* and Cirriped larvae. By December, a strong estuarine signal characterized the bloom (Vargo et al., in press), with

the estuarine species *A. tonsa* and the cladoceran *Evadne tergestina* comprising the majority of the zooplankton assemblage.

In October 2001, Pelecypod larvae dominated the assemblage, presumably those of the calico scallop, *Argopecten gibbus*. Due to the inherent difficulty in identifying early scallop larvae to species this identification should be interpreted with caution. By December, Pelecypod larvae were absent from the assemblage, and meroplankton contributed 3-5% of total abundance.

Statistical analysis With the exception of Station 1 in October 1999, all of the *K. brevis* bloom stations fall outside the two groups in community composition formed by the non-bloom WFS 1999-2000 stations (Figure 46). Groups K1, K2 and K3 are different from the rest of the assemblages at the 20, 25 and 30% similarity levels, respectively. Groups K4 and K5 are more closely associated with the WFS 1 assemblage, but are distinct from that assemblage at the 40 and 45% similarity levels, respectively.

The results of the SIMPER analysis showing the average abundance of important (>90%) species and their percent contribution to community composition for groups K1-5 and WFS 1 are presented in Table 19. Group K1 was characterized by higher abundances of *A. tonsa*, *E. tergestina* and Polychaete larvae and lower abundances of *C. americanus* and Cirriped larvae. Group K2 consisted of a single station, Station 80 in October 99. It was separated from the rest of the stations by high concentrations of *C. velificatus*, *T. turbinata* and *E. pileatus*, and by low concentrations of typical coastal zooplankton such as *O. colcarva* and *P. avirostris*. K3 was characterized by very low abundances of *P. crassirostris*, *O. colcarva*, *P. avirostris*, Cirriped larvae and *E. acutifrons* and by the presence of *L. aestiva*. Group K4 was characterized by higher

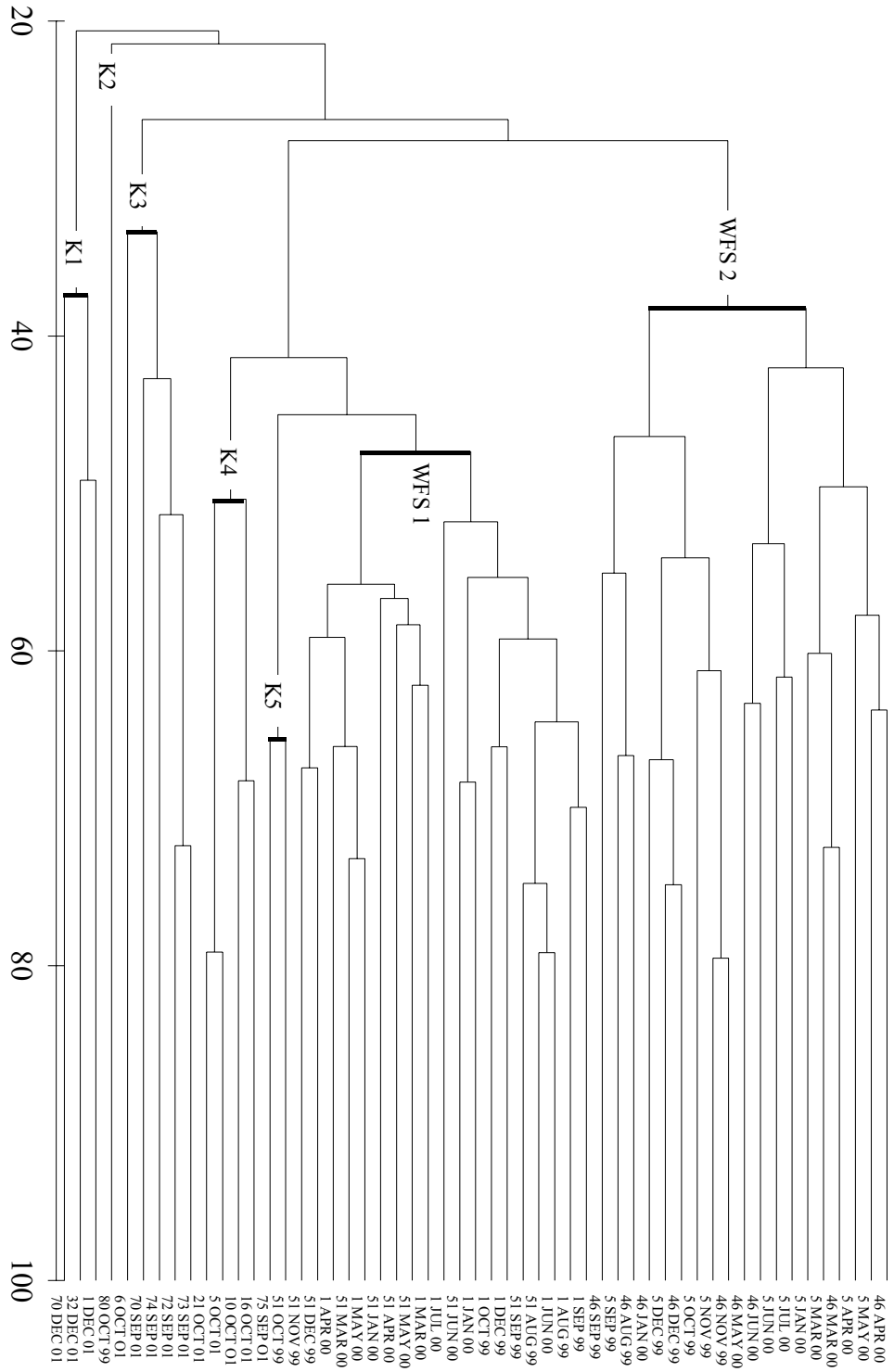

Figure 46. Cluster derived dendrogram for 37 stations at the 5 and 25-m isobaths and 16 stations within the 1999 and 2001 *K. brevis* blooms, using group-average clustering from Bray-Curtis similarities on square root transformed data. n=53

Table 19
Results of SIMPER analysis showing dissimilarities between *K. brevis* and WFS stations.

Taxon	K1		K2		K3		K4		K5		WFS1	
	Av.	%	Abund	%	Av.	%	Av.	%	Av.	%	Av.	%
A. tonsa	7203	10.2	--	--	76	20.9	--	--	39	2.9	244	3.2
C. americana	--	--	3	4.5	--	--			37	3.7	--	--
C. americanus	30	7.7	--	--	--	--	--	--	--	--	108	4.4
C. velificatus	--	--	4569	56.2	--	--	--	--	80	5.8	70	4.2
E. acutifrons	--	--	7	3.0	--	--	--	--	22	3.8	356	6.9
E. tergestina	2030	46.0	--	--	480	4.0	--	--	--	--	--	--
Labidocera aestiva	--	--	--	--	1	2.7			--	--		
O. colcarva	--	--	18	49.6	--	--	2993	12.0	114	9.2	1225	12.4
O. dioika	113	7.7	13	3.0	--	--	837	5.4	125	9.1	176	4.1
O. simplex	--	--	9	6.3	--	--	--	--	--	--	--	--
P. avirostris	--	--	8	6.2	--	--	--	--	--	--	1105	6.8
P. crassirostris			516	6.4	59	14.6	875	6.2	4132	30.9	1655	17.1
P. quasimodo	--	--	--	--	--	--	--	--	121	5.4	344	8.2
T. turbinata	--	--	2341	28.8	--	--	--	--	50	4.9	--	--
Cirriped larvae	233	12.0	4	4.7	--	--	1193	10.4	--	--	478	7.7
Decapod larvae	--	--	29	5.2	--	--	366	7.3	--	--	202	5.7
Echinoderm larvae	--	--	--	--	273	5.3	--	--	--	--	--	--
Gastropod larvae	--	--	--	--	--	--	134	6.2	--	--	106	4.2
Pelecypod larvae	--	--	--	--	--	--	4338	27.1	--	--	271	5.0
Polychaeta larvae	85	7.2	--	--	12	10.5	344	7.9	--	--	--	--

concentrations of pelecypod larvae, *O. colcarva* and Cirriped larvae and lower abundances of *P. crassirostris*, *P. avirostris*, and Decapod larvae. Group K5 was distinguished by very high concentrations of *P. crassirostris*, and by lower than normal concentrations of *O. colcarva*, *E acutifrons* and meroplankton.

DISCUSSION

WFS Zooplankton Taxonomic Composition

The zooplankton community compositions at the 5-m and 25-m isobaths for non-red tide stations are consistent with other observations on the Florida shelf (King 1950; Minello, 1980; Ortner et al., 1989; Dagg, 1995, Sutton et al., 2001). Of the 4 taxa that were important at the 5-m isobath only, 3 (A. *tonsa*, *P. avirostris*, and Cirriped larvae) are abundant within WFS estuaries (Hopkins, 1966; Hopkins, 1977; Weiss, 1977; Squires, 1984), their concentration decreasing seaward (King, 1950; Minello, 1980; Ortner et al., 1989; Dagg, 1995). The cyclopoid copepod *C. americanus* was more abundant at coastal stations on the NWFS and the WFS than within estuaries (Hopkins, 1977; Weiss, 1977; Minello, 1980).

Nine taxa contributed to 90% of the community structure at both the 5 and the 25-m isobaths. Both *P. crassirostris* and *O. colcarva* are dominant in WFS estuaries. *P. crassirostris* is also present in high salinity areas of the estuaries, and is frequently abundant out to the 14-m isobath (Minello, 1980). The abundance of *O. colcarva* was lowest at the mouths of bays, where it can still amount to tens of thousands of animals m^{-3} (Hopkins, 1966; Weiss, 1977; Squires 1984; Hopkins, 1984). *P. crassirostris* and *O.*

colcarva were probably under-sampled in this study, due to the large mesh size of the nets. Actual abundance of these two important species may be 4 times those reported here (Calbet et al., 2001).

P. quasimodo, *C. velificatus*, and *C. amazonicus* are typical of near shore zooplankton assemblages on the Florida shelf (Weiss, 1977; Hopkins, 1977; Squires 1984; Ortner et al., 1989; Minello, 1980; Sutton et al., 2001). The pelagic harpacticoid copepod *Euterpina acutifrons* is a major dominant in WFS estuaries (Hopkins, 1966; Weiss, 1977; Hopkins, 1977; Squires, 1984), and has been observed out to the 50-m isobath (King, 1950). *O. dioica* is the most abundant appendicularian in coastal areas and estuaries of the NWFS and WFS, reaching populations of thousands m^{-3} (Hopkins, 1966; Hopkins, 1977; Weiss, 1977; Minello, 1980; Squires, 1984; Dagg, 1995).

Five species, *E. chierchiae*, *O. plumifera*, *O. mediteranea*, *C. furcatus*, and *C. amazonicus*, were important components of total abundance at the 25-m isobath, but were either absent or infrequent contributors at the 5-m isobath. *O. plumifera*, *O. mediteranea* and *C. furcatus* are associated with transition waters on the Florida shelf, where the three species are closely associated (Minello, 1980; Ortner et al., 1989). The pelagic ostracod *E. chierchiae* is typically associated with offshore water masses (Minello, 1980; Sutton et al., 2001), though it has been reported in the higher salinity areas of the St. Andrew's Bay system (Hopkins, 1966).

Comparison of bloom and non-bloom community composition

Three zooplankton species, *C. americanus*, *P. avirostris* and *E. acutifrons*, had reduced abundance in all *K. brevis* blooms. Seven species, *A. tonsa*, *C. velificatus*, *T.*

turbinata, *E. tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris*, were important (>4% of total abundance) in two or more of the *K. brevis* groups. Each of these species were also numerically dominant at least one bloom station within the 1999 and 2001 blooms, suggesting that they may be important contributors to *K. brevis* bloom dynamics on the WFS.

Previous associations of K. brevis *blooms with zooplankton*

Far more is known about the interactions of *A. tonsa* with *K. brevis* than any other of the species described above. A preliminary report by investigators at the University of Miami in 1954 (cited by Rounsefell and Nelson, 1966) indicated that members of the genus *Acartia* were usually present within a *K. brevis* bloom. *In situ* grazing studies during a novel occurrence of *K. brevis* in North Carolina waters indicate that *A. tonsa* will ingest *K. brevis* if no other food is available (Turner and Tester, 1989), though the ingestion rates were low and variable. Subsequently, the ingestion of *K. brevis* was found to reduce fecundity of *A. tonsa* (Turner and Tester, 1998).

No previous research has indicated an association between *C. velificatus* and *K. brevis*, though two studies have examined the grazing rates of congeners on brevetoxin producing phytoplankton. During the *K. brevis* bloom off North Carolina, *Centropages typicus* (an ephemeral northern transient in those waters) did not ingest *K. brevis*, suggesting that co-occurrence with *K. brevis* in nature may be an indicator of a species' ability to ingest it (Turner and Tester, 1989). In Japan, *Centropages yamadai* ingested the brevetoxin producing raphidophyte *Chatanella subsalsa* (previously *C. antiqua*) indicating that other copepods of the genus *Centropages* may have the capacity to ingest

brevetoxins (Uye, 1986). The high numbers of *C. velificatus* copepodites within the October 1999 bloom imply that the *K. brevis* red tide provided ample food for reproduction, though carnivory cannot be eliminated for this species (Kleppel, 1996; Paffenhöfer and Knowles, 1980).

T. turbinata was not an important component of the non-bloom WFS groups, despite its presence in 39% of the samples. Very high abundances of this copepod have been reported previously on the Florida shelf (Dagg, 1995; Paffenhöffer and Knowles, 1980). No in-situ grazing studies of this species or its congeners on brevetoxin producing phytoplankton have been conducted, but in a toxin vector study *T. turbinata* ingested an average of 72 *K. brevis* cells copepod h^{-1} (Tester et al., 2001). In this study, *K. brevis* cells were observed trapped in the feeding appendages of *T. turbinata* specimens at Station 80 in October 1999, where *K. brevis* concentration exceeded 5 x 10^6 cells l^{-1} and abundance of *T. turbinata* was
2, 341 animals m^{-3}.

The cladoceran *E. tergestina* is a dominant of WFS estuaries (Hopkins, 1966; Weiss, 1977, Hopkins, 1977, Squires, 1984). *E. tergestina* was not a major contributor to abundance in the non-bloom WFS samples, but was present in 13% of the 5-m isobath stations. Direct evidence of *K. brevis* ingestion by *E. tergestina* is not available, though Woodcock and Anderson (cited in Galstoff, 1948) reported large numbers of *E. tergestina* within a *K. brevis* bloom had intestines stained deep red, presumably from ingestion of *K. brevis*.

Copepods of the genus *Paracalanus* will ingest *K. brevis* (Tester and Turner, 1989), suggesting that *Parvocalanus* (a subgenus of *Paracalanus*) may also have the

capability to ingest *K. brevis*. No congeners of *O. colcarva* have been examined with respect to grazing on toxic phytoplankton, though the preference of this genus for motile prey implies that dinoflagellates may comprise a portion of their *in-situ* diet (see discussion in Paffenhöffer, 1993).

The high concentration of scallop larvae found within the 2001 *K. brevis* bloom is puzzling, since reduced clearance rates, decreased size, impaired metamorphosis and increased mortality of bay scallop (*A. irradian concentricus*) larvae exposed to very low concentrations of *K. brevis* have been reported (J. Leverone, *pers. comm*.). The predominant spawn of the calico scallop occurs in April, and usually involves the majority of the population (Moyer and Blake, 1986). When a fall spawn does occur, it comprises a very small portion of the total population (Blake and Moyer, 1991).

The highest total Pelecypod larvae concentrations found in the ECOHAB study area prior to this study were 900 larvae m^{-3} in September of 1999, and on the Northwest Florida Shelf, highest average pelecypod larvae concentrations were 400 larvae m^{-3} (Figure 47). Minello (1980) found evidence of an April spawn on the NWFS, but did not report a major fall spawn over a five-year sampling period.

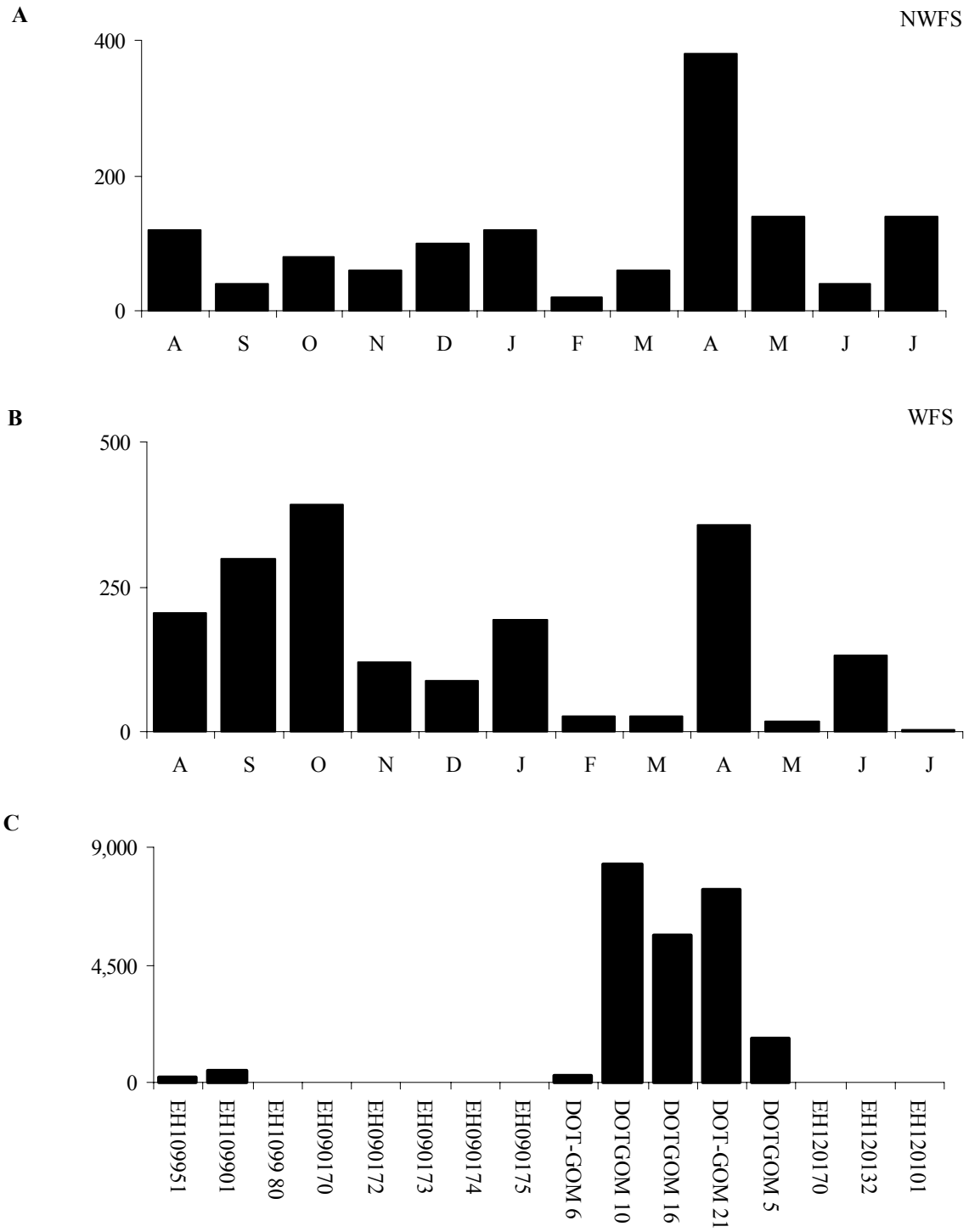

Figure 47. Abundance (m^{-3}) of pelecypod larvae a) on the NWFS averaged over 5 years and 5 stations, b) on the WFS averaged over 1 year and 4 stations and c) within the *K. brevis* blooms on the WFS in 1999 and 2001.

Aside from age, temperature and food are the most important exogenous controls for scallop reproduction (Blake and Moyer, 1991). The water temperature range of 24° to 27°C found in October was higher than the ideal spawning range of 19° to 20°C and the 22°C cutoff temperature for spawning (Miller et al, 1981). Given the reduced clearance rates of the congener *A. irradians* in the presence of *K. brevis* (Jay Leverone, pers. comm.), it is unlikely that *K. brevis* is an adequate food source for scallop larvae.

In the absence of ideal temperatures and adequate food, the most likely explanation for the magnitude of the fall spawn may be the stressful conditions of the *K. brevis* bloom (N. Blake, *pers. comm*.). Other meroplankton taxa were also abundant in October 2001, most notably Cirriped, Polychaete and Echinoderm larvae, all of which were more abundant here than in the non-bloom WFS samples. An explanation for this phenomenon is not forthcoming from this analysis, other than the suggestion that increased stress may have been responsible for the increased spawning of benthic forms.

CONCLUSIONS

The objective of this study was to determine if there were perturbations in the zooplankton community composition associated within *K. brevis* blooms. Only one *K. brevis* bloom station was statistically indistinguishable from non-bloom WFS stations. The remaining stations differed significantly from non-bloom stations in abundance or community composition. No one response by the zooplankton community was evident, but some consistencies between bloom stations occurred, including decreased abundance of three important WFS coastal species, *C. americanus*, *P. avirostris* and *E. acutifrons*,

and numerical dominance by *A. tonsa*, *C. velificatus*, *T. turbinata*, *E. tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris*, which were consistently found in high concentrations inside *K. brevis* blooms. Of these, only *T. turbinata* and *E. tergestina* were not major contributors to normal WFS zooplankton assemblages at the 5-m isobath.

Perturbations in meroplankton contribution to community structure also were evident. In October 2001 there were higher than normal abundances of most meroplankton forms, with the most obvious of these being the Pelecypods. The impact of the increased meroplankton abundances are not clear, since the Pelecypod larvae found in October 2001 almost certainly did not survive the bloom (N. Blake, *pers. comm*.).

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CHAPTER 4

ZOOPLANKTON NUTRIENT REGENERATION WITHIN *KARENIA BREVIS* BLOOMS

Abstract The source of nutrients required to support long lived, high-concentration blooms of the toxic dinoflagellate *Karenia brevis* on the West Florida Shelf are unknown. One potential source of nutrients to support these blooms may be zooplankton regeneration of nutrients. To test this hypothesis, ammonium and phosphate excretion rates of several West Florida Shelf copepods (*Labidocera aestiva*, *Acartia tonsa*, *Temora turbinata*, and *Paracalanus quasimodo*) were measured. These excretion rates were then applied to other species of West Florida Shelf zooplankton, combined with available literature excretion rates for some taxa, and used in conjunction with zooplankton populations found for *K. brevis* blooms on the West Florida Shelf in 1999 and 2001 to estimate Nitrogen and Phosphorus. Ammonium excretion rates were found to be inadequate to support > 10^4 cells l^{-1} of *K. brevis*, though phosphate excretion rates were adequate to support 10^6 cells l^{-1} of *K. brevis*.

INTRODUCTION

The source of nutrients required to support long lived, high-concentration blooms of the red tide dinoflagellate *K. brevis* on the West Florida Shelf are enigmatic. Blooms of this dinoflagellate may reach concentrations of 10^6 cells l^{-1} within weeks of bloom initiation when inorganic nutrients are at or below the limits of detection (Steidinger et al., 1998; Vargo et al., in review). The question of which nutrient sources are supporting these blooms remains (Vargo et al., in review).

Both inorganic and organic nutrient sources can be used by *K. brevis*. The major nutrients required by *K. brevis* for growth and reproduction are nitrogen and phosphorus (Steidinger et al., 1998).

Reports of uptake and growth rates for *K. brevis* as a function of nitrate, nitrite, ammonium and urea availability are rare. In a series of preliminary experiments, growth rates were reported to be from 0.16 to 0.2 div day^{-1} and were independent of ammonia or urea concentration over a range of .5 to 7 μM l^{-1} (Steidinger et al., 1998). K_s values were calculated to be 0.47 for ammonia and 1.07 for urea. Calculated K_s values for nitrate of 0.42 were similar to that of ammonia. Both values are indicative of a species with a high affinity for inorganic nitrogen and suggest that *K. brevis* is a species adapted for growth in low-nutrient environments (Steidinger et al., 1998). Doig (1973) reported use of ammonia as an N source for growth by *K. brevis*, and Dragovich et al. (1961) suggest that ammonia could be the primary N source for *K. brevis*. In culture studies, *K. brevis* has been shown to utilize organic N sources, urea, glycine, leucine, and aspartic acid (Baden and Mende, 1979; Shimizu and Wrensford, 1993; Shimizu et al., 1995).

K. brevis is highly efficient in the acquisition and utilization of available inorganic phosphate (Steidinger et al., 1998). A K_s of 0.18 μM l^{-1} day^{-1} suggests that *K. brevis* is adapted for growth at the low P concentrations commonly found in coastal waters (Vargo and Howard-Shamblott, 1990). Vargo (1988) determined that sufficient P was available in the water column to meet the daily requirements of a 1986 bloom off of Tampa Bay, and that K. *brevis* does not require high nutrient levels to support normal growth rates and relatively high abundances (Steidinger et al., 1998). However the two stations with the highest population density (10^6 cells l^{-1}) would have depleted the water column supply in one day (Vargo et al., in review). Vargo and Shanley (1985) demonstrated production of alkaline phosphatase within a *K. brevis* bloom in situ, suggesting that DOP sources are also available to blooms.

Potential sources of nutrients for *K. brevis* blooms include aerial deposition, estuarine flux, benthic flux, zooplankton excretion, N_2 fixation and subsequent release of organic and inorganic N by *Trichodesmium spp*., and release of N and P from dead and decaying fish within blooms (Vargo et al., in review). Vargo et al. (in review) determined that atmospheric deposition, benthic flux, and N_2 fixation were minor contributors to the flux required to support growth of populations >2.6 x 10^4 cells l^{-1}. Estuarine loadings may not contribute significantly to the growth requirements of *K. brevis* blooms in coastal waters, but DON levels were high and could not be ruled out as a source of N for coastal blooms (Vargo et al., in review). However, no near shore source of DON or DOP was detected during a 1998-1999 bloom, though both were found in higher concentrations near shore at various times over the course of the bloom (Lester et al., 2003). N and P from decaying fish could theoretically maintain populations at

moderate concentrations, but there is insufficient data on flux and mixing rates to determine this decisively (Vargo et al., in review).

Inputs of new nitrogen are often insufficient to support requirements of primary production (Valiela, 1995). Instead, several pathways by which regenerated nitrogen can be recycled in the water column are of primary importance. One pathway, the regeneration of nitrogen by zooplankton and its potential contribution to *K. brevis* bloom nutrient requirements, will be the focus of this chapter.

Zooplankton produce various substances as end products of metabolism. Excretia for most zooplankton include solid and liquid forms (Ikeda et al., 2000). Liquid forms of nitrogen excreted by zooplankton include free amino acids and ammonia, with urea making up some of the difference (Corner and Newell, 1967). Nitrogen compounds have been measured in terms of total N, ammonia-N, amino-N and urea N (Ikeda et al., 2000). Ammonia is the major form of dissolved nitrogen excreted by marine zooplankton (Ikeda et al., 2000; Wright, 1995), with urea constituting from 0-40% of excreted N (Jawed, 1969; Ikeda and Skjoldal, 1989; Corner and Newell, 1967; Corner et al., 1976).

Phosphorus compounds have been measured in terms of total-P, inorganic-P and organic-P. Dissolved phosphorus compounds in zooplankton excretia can be separated into inorganic and organic fractions (Ikeda et al., 2000). Pomeroy et al. (1963) reported that 33-35% of total phosphorus excreted by mixed zooplankton was inorganic. In another study, as much as 75% of phosphorus was excreted as DOP and total DIP excreted by zooplankton exceeded daily algal requirements (Hargrave and Geen, 1968). Measurements of this source of regenerated nutrients show that it is potentially capable of

providing substantial amounts of nutrients relative to the amounts assimilated by producers (Ikeda et al., 2000).

Zooplankton excretion rates could supply all of the N and P required to support *K. brevis* populations >10^6 cells l^{-1} (Vargo et al., in review). However, the excretion rates used to determine the potential for regenerated nutrients to support a bloom >10^6 cells l^{-1} were from literature values determined for only two species, *Acartia tonsa* and *Centropages velificatus*. No other measurements of zooplankton excretion rates are available for the WFS.

The purpose of this chapter is to examine the role of zooplankton regeneration in the nitrogen and phosphorus dynamics of *K. brevis* blooms by incorporating direct measurements of excretion rates into calculations of bloom nutrient dynamics.

METHODS

Zooplankton Abundance Sampling within K. brevis blooms

Sampling was conducted in October 1999 and September, October, and December 2001 during *K. brevis* blooms on the WFS. In October 1999 and September and December 2001, zooplankton tows were conducted on ECOHAB cruises at stations within blooms (Figure 48). In October 2001, zooplankton tows were taken to the north of and within the ECOHAB study area on an NSF research cruise.

Zooplankton were collected with a 153 μm mesh towed obliquely from bottom to surface. The volume of water filtered was measured with a flow meter attached at the net mouth (Omori and Ikeda, 1992). The cod ends were filtered through a 2000 μm mesh

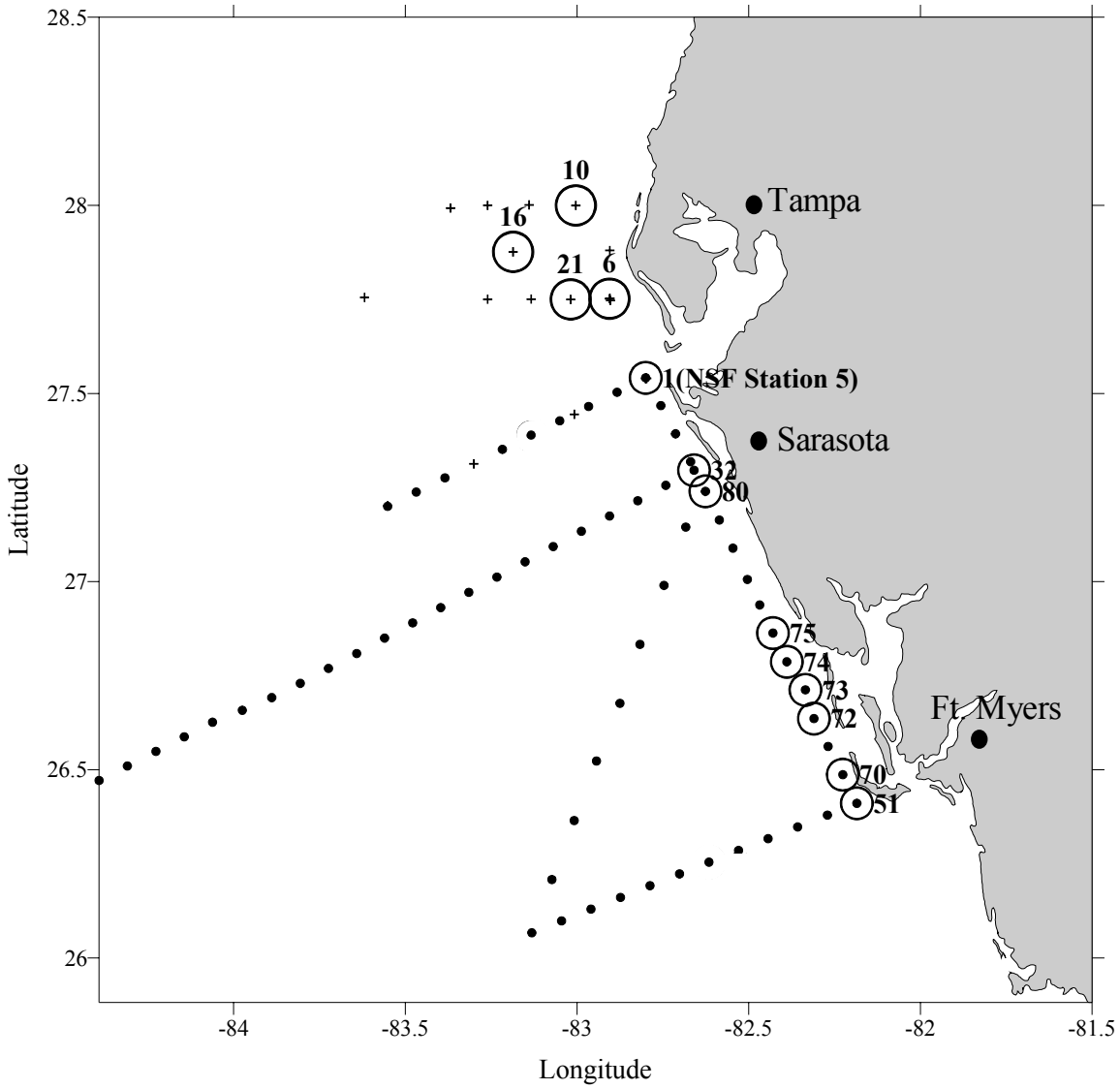

Figure 48. Station locations for ECOHAB cruises (•) and NSF cruises (+). Stations where zooplankton tows were conducted are indicated by a number. NSF Station 5 is in the same location as ECOHAB Station 1.

sieve to remove macrozooplankton and large gelatinous zooplankton. Each filtered cod end was preserved on board in a 5% buffered formalin solution (Omori and Ikeda, 1992) for later counts of zooplankton species abundance. Representative subsamples of 500-600 animals were obtained with a Stempel pipette (usually 1-5% of initial cod end volume). Zooplankton were identified and counted using an Olympus dissecting microscope. Holoplankton were identified to species level.

Meroplankton were identified to major taxonomic group (e.g. Pelecypod veligers, Cirriped larvae). Replicate samples were averaged for each station. Zooplankton tows were conducted in conjunction with *K. brevis* cell counts. *K. brevis* was counted live using a dissecting microscope within two hours of collection.

Excretion experiments

Underway procedures In 2005, zooplankton were collected from a ship, boat or from the pier with a 153μm mesh net in areas normally impacted by *K. brevis* blooms. Tows were conducted after sunset with deck lights dimmed. The engines of the ship or boat were cut and the tow collected with the drift of the ship. Occasionally, it was necessary to come ahead 1-2 knots to keep current flowing through the net. Typically, tows were conducted at the surface, though occasionally oblique tows from bottom to surface were conducted. After being brought on board, cod ends were immediately diluted into a larger volume of natural seawater. The bucket was then covered with several layers of shade cloth to reduce light.

Animals were sorted on an Olympus dissecting scope, rinsed with filtered seawater and counted into 200 ml sealed chambers that contained either filtered seawater,

natural seawater, or natural seawater with 10^4 concentration of *K. brevis* added. Zooplankton were incubated in the sealed chambers for two hours. Zooplankton were then transferred onto 60µm mesh net, rinsed with filtered seawater, and placed in filtered seawater in 60ml BOD bottles. The BOD bottles were wrapped in aluminum foil and allowed to incubate for 8 hours. Controls consisted of BOD bottles filled with filtered sea water and incubated for 8 hours. After the 8 hour incubation period, filtered seawater from the BOD bottles was filtered through a 60µm mesh net into 60ml acid cleaned bottles and frozen. Zooplankton were rinsed onto GF/F filters with filtered seawater and rinsed 3 times with ammonium formate. Zooplankton were then counted on the filter, wrapped in aluminum foil and frozen. At a later date, samples were dried to a constant weight and weighed on a Cahn Electrobalance.

Ammonium and Phosphate Sample Analysis

Samples were analyzed for total ammonium and total phosphate on a Technicon Autoanalyzer II continuous flow analyzer using the methods of Grashoff (1976) as modified by Gordon et al. (1993).

Nutrient requirements of blooms

Bloom nutrient requirements were calculated using an assumed growth rate of 0.2 divisions day^{-1} and N and P cell content of 1.08×10^{-5} µmoles and 4.88×10^{-7} µmoles per cell, respectively (Heil, 1986).

RESULTS

Zooplankton Abundance and Community Composition

Zooplankton abundance and community composition sampled on ECOHAB and NSF cruises for the 1999 and 2001 *K brevis* blooms are given in Table 20. In October 1999, the highest zooplankton abundance occurred at Station 80, where *K. brevis* concentrations exceeded 5 X 10^6 cells l^{-1}. The zooplankton assemblage here deviated from a normal WFS assemblage and consisted almost entirely of *Centropages velificatus* copepodites and *Temora turbinata* adults. At Stations 51 and 1, in the northern and southern portions of the study area, the *K. brevis* concentration was low, and the normal WFS zooplankton assemblage was present.

The *K. brevis* concentration was low at most stations in September 2001, with greatest concentration (10^5 cells l^{-1}) occurring at stations 72 and 73. Zooplankton abundances were relatively low, except at Station 75, where the common, small copepod *Parvocalanus crassirostris* was dominant. All zooplankton assemblages in September were normal WFS zooplankton assemblages.

In October 2001 *K. brevis* was present in concentrations exceeding 10^6 cells l^{-1} at most zooplankton stations sampled. The zooplankton assemblages sampled deviated from those normally found on the WFS in October. The most radical departure from a normal WFS zooplankton assemblage (see Chapter 2) occurred at Stations 10, 16 and 5, when pelecypod larvae dominated the assemblages and were present in concentrations of 10^3 larvae m^{-3}. Other important components of the zooplankton assemblage in October

Table 20

Top 80% of contributors to zooplankton abundance (m^{-3}) at red tide stations sampled during 1999 and 2001.

	October-99			September-01					October-01					December-01		
K. brevis cells l^{-1} x 10^3	7.5	16	5270	8	200	500	75	15	1268	742	1320	1078	774	16	68	176
Station	51	1	80	70	72	73	74	75	6	10	16	21	5	70	32	1
A. tonsa	--	245	--	42	185	120	29	67	3	--	--	--	337	21447	145	16
C. americana	--	--	--	7	--	--	--	--	--	--	--	--	--	--	--	--
C. americanus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
C. velificatus	118	--	4569	--	--	--	--	41	--	--	--	--	112	--	--	--
E. tergestina	--	--	--	--	--	--	--	--	--	--	--	--	1516	--	4462	621
E.acutifrons	--	405	--	23	--	--	--	--	--	--	--	--	--	--	--	--
E. crassus	57	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
O.colcarva	--	749	--	--	--	--	--	--	33	1081	--	4730	6121	--	--	--
O.dioka	--	--	--	--	--	26	39	100	--	--	--	2772	--	--	--	--
O.similis	--	--	--	--	--	--	--	--	--	--	--	826	--	--	--	--
P. avirostris	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
P. crassirostris	5553	2884	--	--	--	--	--	2711	--	--	--	--	1994	--	--	--
P. quasimodo	206	--	--	--	--	7	19	36	--	--	--	--	--	--	--	--
T. turbinata	70	--	2341	2	--	--	37	29	--	--	--	--	--	--	--	--
Decapod larvae	--	650	--	--	--	81	--	--	--	--	--	590	590	--	--	--
Pelecypod larvae	--	--	--	--	--	--	--	--	289	8366	5616	--	1685	--	--	--

were the common copepods *Oithona colcarva* and *P. crassirostris* and the larvacean *Oikopleura dioica*, which is normally present in WFS zooplankton assemblages.

By December an estuarine signature characterized the bloom (Vargo et al., in press). The copepod *Acartia tonsa* and the cladoceran *Evadne tergestina*, both associated with estuaries on the WFS (Hopkins, 1977; Weiss, 1978; Squires, 1984) were the main contributors to the zooplankton assemblage in December.

Excretion rates of WFS zooplankton

Ammonium and phosphate excretion rates were determined for 4 WFS copepods, *A. tonsa*, *P. quasimodo*, *L. aestiva*, and *T. turbinata* (Figure 49). Highest ammonium excretion rates were observed for the large copepod *L. aestiva*, while lowest excretion rates were observed for the relatively small copepod *T. turbinata*. Phosphate excretion rates followed the same trend, with *L. aestiva* demonstrating the highest phosphate excretion rate, and *T. turbinata* demonstrating the lowest phosphate excretion rate (Figure 50). No correlation was observed between the presence of *K. brevis* and ammonium excretion rates. With phosphate excretion rates, there did appear to be a trend to lower excretion rates in the presence of *K. brevis*, but this was never significant. Generally, excretion rates for starved copepods were lower than excretion rates for fed copepods.

The excretion rates found here were prorated to a 24-hour day using the results of Checkley et al, (1992) who found that excretion rates were approximately 2 times greater during the day than at night. These prorated excretion rates were extrapolated to other WFS zooplankton found within the 1999 and 2001 *K. brevis* blooms (Tables 21 and 22),

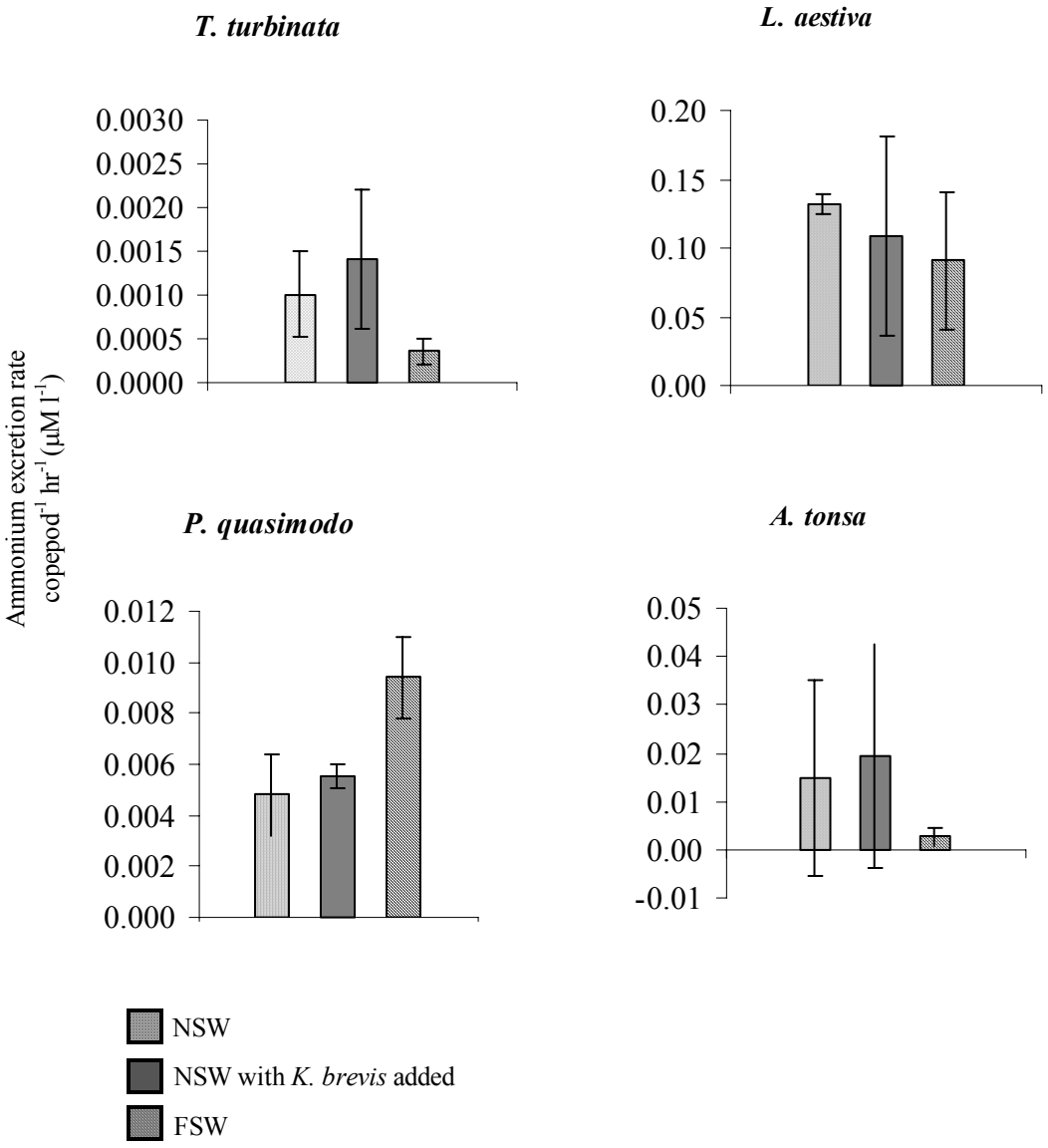

Figure 49. Ammonium excretion rates of selected WFS copepods.

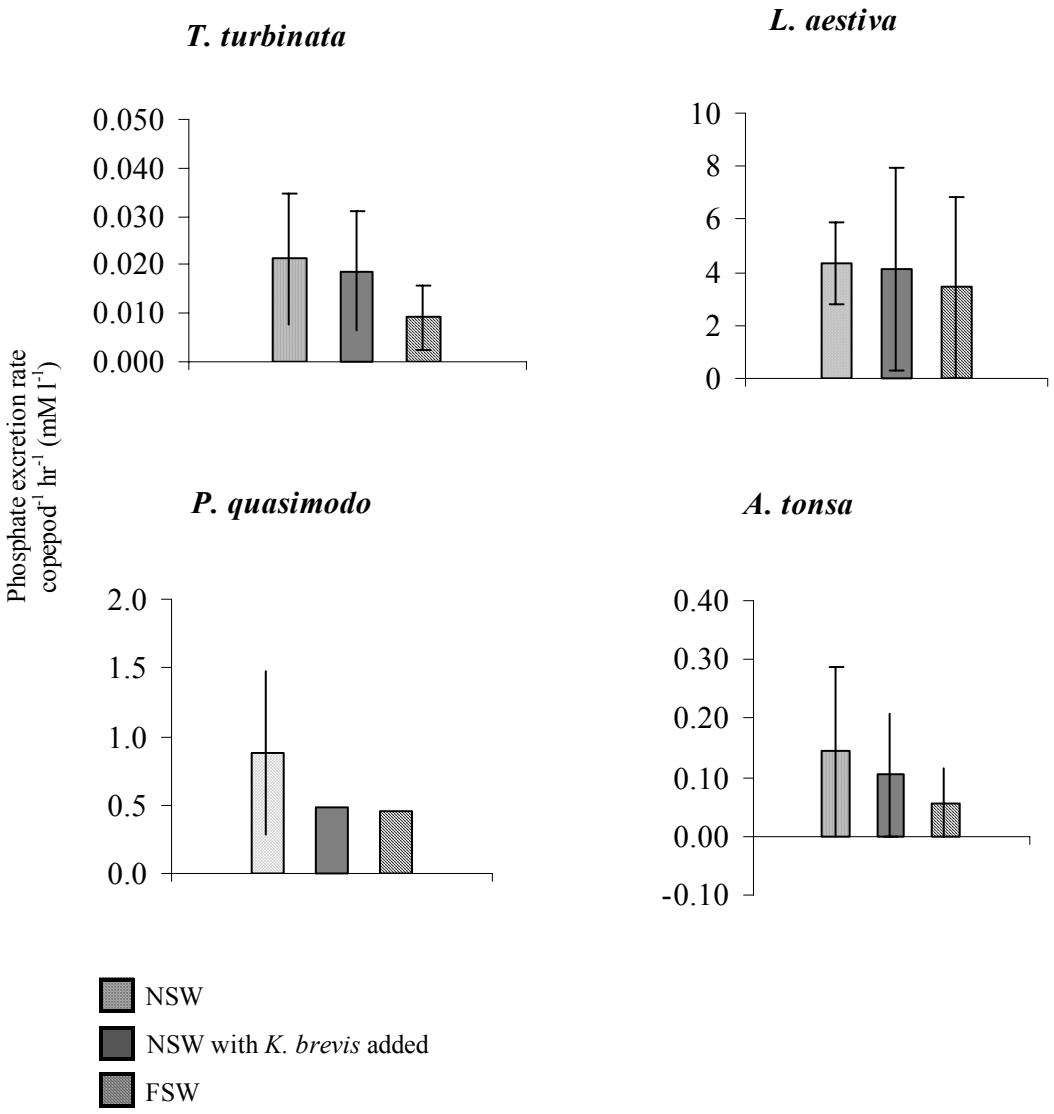

Figure 50. Phosphate excretion rates of selected WFS copepods.

Table 21
Ammonium excretion rates used in bloom nutrient calculations.

Taxa	Excretion rate (μM animal^{-1} day^{-1})	Based on	Source
Acartia tonsa	0.318	Actual	Present study
Calanopia americana	1.963	*L. aestiva*	Present study
Centropages velificatus	0.039	Actual	Checkley et al, 1992
Corycaeus americanus	0.115	*T. turbinata*	Present study
Eucalanus crassus	1.963	*L. aestiva*	Present study
Euterpina acutifrons	0.115	*T. turbinata*	Present study
Evadne tergestina	0.048	Daphnia	Martinez and Gulati, 1999
Labidocera aestiva	1.963	Actual	Present study
Oikopleura dioica	0.026	*Mnemiopsis ledyii*	Nemazie et al., 1993
Oithona colcarva	0.115	*T. turbinata*	Present study
Oithona similis	0.318	*A. tonsa*	Present study
Penilia avirostris	0.048	*Daphnia* spp.	Martinez and Gulati, 1999
Parvocalanus crassirostris	0.059	1/2 *P. quasimodo*	Present study
Paracalanus quasimodo	0.118	Actual	Present study
Temora turbinata	0.115	Actual	Present study
Decapod larvae	0.003	Actual	Schmitt and Santos, 1998
Pelecypod larvae	0.010	Actual	Yantian et al, 1999

Table 22
Phosphate excretion rates used in bloom nutrient calculations.

Taxa	Excretion rate (μM animal^{-1} day^{-1} x 10^{-3})	Based on	Source
Acartia tonsa	1.82685	Actual	Present study
Calanopia americana	71.80433	*L. aestiva*	Present study
Centropages velificatus	1.82685	*L. aestiva*	Present study
Corycaeus americanus	3.59312	*T. turbinata*	Present study
Eucalanus crassus	71.80433	*L. aestiva*	Present study
Euterpina acutifrons	3.59312	*T. turbinata*	Present study
Evadne tergestina	0.20000	*Daphnia* spp.	Martinez and Gulati, 1999
Labidocera aestiva	71.80433	Actual	Present study
Oikopleura dioica	1.82685	.5 * *A. tonsa*	Present study
Oithona colcarva	3.59312	*T. turbinata*	Present study
Oithona similis	1.82685	*A. tonsa*	Present study
Penilia avirostris	0.20000	*Daphnia* spp.	Martinez and Gulati, 1999
Parvocalanus crassirostris	5.42666	*P. quasimodo*	Present study
Paracalanus quasimodo	10.85332	Actual	Present study
Temora turbinata	3.59312	Actual	Present study
Decapod larvae	0.03593	*T. turbinata*	Present study
Pelecypod larvae	0.03593	.01 * *T. turbinata*	Present study

applied to zooplankton abundance numbers obtained within the blooms, and compared to bloom nutrient requirements (Tables 23 and 24).

Highest prorated ammonium and phosphate excretion rates were observed for larger copepods such as L. aestiva. Lowest prorated ammonium and phosphate excretion rates were found for Decapod and Pelecypod larvae. Zooplankton community ammonium excretion rates for the 1999 and 2001 blooms ranged from a low of 0.0076 $\mu M\ l^{-1}\ day^{-1}$ at Station 6 in October 2001 to a high of 6.8192 $\mu M\ l^{-1}\ day^{-1}$ at Station 70 in December 2001. Zooplankton community phosphate excretion rates ranged from a low of 0.0059 mM l-1 day-1 at Station 6 in October 2001 to a high of 0.5144 mM l-1 day-1 at Station 80 in October 1999.

DISCUSSION

Zooplankton nutrient regeneration as a source of nutrients for K. brevis *blooms*

Generally, zooplankton ammonium excretion rates were adequate to support the nutrient requirements of blooms that were 10^4 cells l^{-1}. However, ammonium excretion rates proved to be an inadequate nutrient source for the booms with a 10^5 or 10^6 cells l^{-1} concentration. There were several stations where ammonium excretion proved to be inadequate in providing enough nutrients to support even a 10^4 cells l^{-1} bloom. At Station 74 in September 2001 the presence of high concentrations of *O. dioica*, an animal with a relatively low ammonium excretion rate compared to WFS copepods, resulted in a low total ammonium excretion rate for the zooplankton community and subsequently there

Table 23
Zooplankton community ammonium excretion rates for 1999 and 2001 blooms and *K. brevis* bloom requirements

	K. brevis Concentration (cells L^{-1} X 10^{-3})	Ammonium Excretion Rate (µM $liter^{-1}$ day^{-1})	Bloom Requirements (µM $liter^{-1}$ day^{-1})	% of Bloom Nitrogen Requirements Provided By Zooplankton
October 1999				
51	7.5	0.3644	0.1620	224.93%
1	16	0.3832	0.0346	1108.85%
80	5270	0.4454	11.3832	3.91%
September 2001				
70	8	0.3615	0.0173	2092.24%
72	200	0.1293	0.4320	29.93%
73	500	0.0140	1.0800	1.30%
74	75	0.0400	0.1620	24.71%
75	15	0.2584	0.0324	797.45%
October 2001				
6	1268	0.0076	2.7389	0.28%
10	742	0.2079	1.6027	12.97%
16	1320	0.0562	2.8512	1.97%
21	1078	0.8800	2.3285	37.79%
5	744	1.0243	1.6718	61.27%
December 2001				
1	16	0.0349	0.3802	9.18%
32	68	0.2603	0.1469	177.21%
70	176	6.8192	0.0346	19731.61%

Table 24
Zooplankton community phosphate excretion rates for 1999 and 2001 blooms and *K. brevis* bloom requirements

	K. brevis Concentration (cells L^{-1} X 10^{-3})	Zooplankton Excretion Rate (μM $liter^{-1}$ day^{-1})	Bloom Requirements (μM $liter^{-1}$ day^{-1})	% of Bloom Phosphate Requirements Provided by Zooplankton
October 1999				
51	7.5	0.4977	0.00732000	6799.67%
1	16	0.6360	0.00156160	40727.46%
80	5270	0.6762	0.51435200	131.47%
September 2001				
70	8	0.0156	0.00078080	1995.85%
72	200	0.0266	0.01952000	136.48%
73	500	0.0298	0.04880000	61.01%
74	75	0.0074	0.00732000	101.35%
75	15	0.3555	0.00146400	24284.85%
October 2001				
6	1268	0.0059	0.12375680	4.74%
10	742	0.1748	0.07241920	241.32%
16	1320	0.0157	0.12883200	12.21%
21	1078	0.8793	0.10521280	835.70%
5	744	1.1528	0.07554240	1526.01%
December 2001				
1	16	0.0243	0.01717760	141.36%
32	68	0.2177	0.00663680	3280.56%
70	176	3.0884	0.00156160	197769.47%

was not enough ammonium present to support the *K. brevis* population at this station. At Station 1 in December 2001 the zooplankton abundance was very low. The major zooplankton taxa present was the cladoceran *Evadne tergestina*, which like *O. dioica* has a relatively low ammonium excretion rate. These two factors combined resulted in a low total zooplankton ammonium rate. The percentage of ammonium supplied by zooplankton at this station was only 28%. At Station 70 in December 2001, a very high concentration of the copepod *A. tonsa* resulted in enough ammonium to support a 10^5 concentration bloom. This was the only situation during the 1999 or 2001 blooms where zooplankton excretion provided enough ammonium to support a bloom of greater than 10^4 cells l^{-1}.

Unlike ammonium excretion rates, phosphate excretion rates generally proved to be adequate to support blooms of even 10^6 concentrations. There were however a few exceptions. At Station 73 in September 2001 high concentrations of Decapod larvae with their low phosphate excretion rates resulted in low excretion rates for the zooplankton community at that station and subsequently, there was not enough phosphate to support a 10^5 concentration of *K. brevis*. Similarly, at Stations 6 and 16 in October 2001 the zooplankton community was dominated by small pelecypod larvae with a low phosphate excretion rate. This resulted in a low total phosphate excretion rate for the zooplankton community and an inadequate amount of phosphate to support the 10^6 concentration of *K. brevis* located at those stations.

Comparison of excretion rates with other studies

The ammonium excretion rates found here were normalized to mg body weight and compared to other studies examining excretion rates of copepods and general zooplankton populations (Table 25). The numbers obtained here are on the high end of those found in the literature, and compare well to those found by Martin (1968) working with the total zooplankton community in Narragansett Bay. It is interesting to note that despite the high excretion rates found here, ammonium excretion rates were still not adequate to provide nutrients for a 10^5 or 10^6 cells l^{-1} bloom. This is probably due to the fact that, when calculating the ammonium excretion load of the zooplankton community as a whole, literature values were used for several important zooplankton taxa, including pelecypod larvae, *O. dioica* and *E. tergestina*. The excretion rates for these three taxa tended to be low and kept the total zooplankton community excretion rate low. The range of ammonium excretion for the entire zooplankton community was generally on the same order of magnitude as that found in Narragansett Bay (Vargo, 1976; Vargo, 1979) where ammonium excretion for the zooplankton community ranged from 0.56 to 1.66 μg mg dry wt^{-1} day^{-1}.

The situation for phosphate excretion rates was quite different. Phosphate excretion rates were generally high enough to provide enough phosphate for the bloom, even at 10^6 l^{-1} concentrations. Compared with Narragansett Bay, where phosphate excretion rates for the zooplankton community ranged from 0.03 to 0.19 μM phosphate mg dry wt^{-1} day^{-1}, the phosphate excretion rates for the zooplankton community on the

Table 25
Comparison of ammonium excretion rates for various taxa between this study and other studies

Study	Taxa	Average Ammonium Excretion Rate (µM mg body weight)	Range	Temperature
Present study	*Temora turbina*	1.596	0.314-5.166	22°C
Present study	*Labidocera aestiva*	4.488	2.365-5.783	22°C
Present study	*Paracalanus quasimodo*	0.401	0.224-2.335	22°C
Present study	*Acartia tonsa*	1.077	0.006-5.035	22°C
Checkley et al, 1992	*Acartia tonsa*	0.120	0.05-0.21	25°C
Miller and Glibert, 1998	*Acartia tonsa*	0.001	0.00-0.002	Not available
Kirboe et al., 1985	*Acartia tonsa*	0.150	0.06-0.25	18°C
Checkley et al, 1992	*Centropages velificatus*	0.127	0.09-0.22	22-30°C
Martin, 1968	Total zooplankton community	1.123	0.25-2.42	Not available
Isla et al., 2004	Small size fraction of zooplankton community[1,2]	0.100	0.04-0.16	Not available

1. Those zooplankton that passed through a 200µ mesh net
2. Assuming a carbon content of 44.7% (Mauchline, 1998)

WFS during *K. brevis* blooms had a wider range, with values ranging from 0.0059 to 3.0884 μM l^{-1} day^{-1} (Vargo, 1976).

Phosphate excretion rates for pelecypod larvae and *O. dioica* were not available from the literature, and therefore phosphate excretion rates for these taxa were extrapolated from WFS copepod excretion rates. For pelecypod larvae, this was accomplished by multiplying the *T. turbinata* excretion rate by 10^{-3}, the same ratio observed for ammonium excretion rates. The three stations where pelecypod larvae were important contributors to the zooplankton community were stations 6 and 16 in October 2001 where phosphate excretion by zooplankton contributed 5 and 12%, respectively, of the phosphate required by the *K. brevis* bloom. These low numbers indicate that the phosphate excretion rates of pelecypod larvae were likely not overestimated.

For *O. dioica*, phosphate excretion rates were ½ the value of *A. tonsa*, due to the size ratio between the two species. This may have resulted in an overestimation of *O. dioica* phosphate excretion rates. The station where this overestimation would have been a factor was Station 21 in October 2001, when the *O. dioica* population was quite high. The phosphate excretion rates for the total zooplankton community resulted in 836% of the required phosphate for the bloom being provided by zooplankton. However, 75% of the zooplankton excretion rate at that station was provided by the small cyclopoid copepod *Oithona colcarva*, with only 0.02% of the total phosphate excretion rate supplied by *O. dioica*, indicating that the larvacean was not an important contributor to the phosphate requirements of the bloom.

CONCLUSIONS

The values calculated here for ammonium and phosphate excretion for the total zooplankton community indicate that *K. brevis* blooms could be obtaining their phosphate from zooplankton excretion, though ammonium excretion rates proved to be too low to support all but a 10^4 cells l^{-1} concentration of *K. brevis*.

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CHAPTER 5

ZOOPLANKTON GRAZING ON *KARENIA BREVIS* BLOOMS OF THE WEST FLORIDA SHELF

Abstract Blooms of the toxic dinoflagellate *K. brevis* are common in the Gulf of Mexico. An *in situ* study of two of these blooms that occurred during 1999 and 2001 was conducted to determine whether zooplankton grazing could prove sufficient to terminate *K. brevis* blooms. Sampling was conducted to determine zooplankton abundance and community composition during bloom periods. A grazing assessment was conducted for three common zooplankton species that were found within the blooms, *A. tonsa*, *P. quasimodo*, and *L. aestiva*, using ^{14}C labeled *K. brevis*. Grazing rates were then applied to the zooplankton community and grazing assessed. Grazing pressure was capable of reducing *K. brevis* to background concentrations at only one station, Station 1 in December 2001. Generally, however, grazing pressure proved to be insufficient to reduce *K. brevis* to background concentrations during the 1999 and 2001 blooms.

INTRODUCTION

Blooms of the toxic dinoflagellate *K. brevis* are common in the Gulf of Mexico, where populations can reach concentrations in the millions of cells per liter within weeks of detection. Prior to my study, no *in situ* studies of zooplankton and *K. brevis* have been conducted in the Gulf of Mexico. Previous research has examined numerous factors affecting growth rates (Steidinger et al., 1998 and references cited therein; Lenes et al., 2001; Walsh and Steidinger, 2001; Walsh et al., 2002; Lester et al., 2003; Heil et al., 2003; Vargo et al., 2003; Walsh et al., 2003), yet the ability of *K. brevis* to out-compete other phytoplankton species can only be understood in the context of losses as well as growth rates.

Differential mortality can lead to the success (Fiedler, 1982; Huntley, 1982; Smayda and Villareal, 1989; Buskey and Stockwell, 1993; Buskey and Hyatt, 1995) or failure of toxic phytoplankton blooms (Uye, 1986). In the only *in situ* study to date of zooplankton grazing on *K. brevis,* 5 species of zooplankton ingested the toxic dinoflagellate, but the rates of ingestion tended to be variable and low (Turner and Tester, 1989). Anecdotal field observations indicate that cladocerans, tintinnids, and ciliates may also have the ability to ingest *K. brevis*. (Woodcock and Anderson (cited in Galstoff, 1948); Dragovich and Kelly, 1964; Rounsefell and Nelson, 1966; Martin et al., 1973; C. Heil, *pers. comm*.).

Lester et al. (in review) calculated *K. brevis* grazing rates based on literature values and reported that grazing had little effect on *K. brevis* blooms. However, the grazing rates used for the calculations were derived from zooplankton feeding on natural

non-toxic populations, or from North Carolina copepods feeding on *K. brevis*, and were difficult to extrapolate to Gulf of Mexico *K. brevis* blooms. Experimentally derived ingestion rates of naturally occurring zooplankton in the Gulf of Mexico on *K. brevis* populations are needed to determine the impact of zooplankton grazing rates on *K. brevis* bloom termination.

METHODS

Zooplankton Sampling

Sampling was conducted as a component of the ECOHAB:Florida program in October 1999 and September, October, and December of 2001 during *K. brevis* blooms on the WFS. In October 1999 and September and December 2001, zooplankton tows were conducted on ECOHAB cruises at stations within blooms (Figure 51). In October 2001, zooplankton tows were taken to the north of and within the ECOHAB study area on an NSF research cruise.

Zooplankton were collected with a 153 μm mesh towed obliquely from bottom to surface. The volume of water filtered was measured with a flow meter attached at the net mouth (Omori and Ikeda, 1992). The cod ends were filtered through a 2000 μm mesh sieve to remove macrozooplankton and large gelatinous zooplankton. Each filtered cod end was preserved on board in a 5% buffered formalin solution (Omori and Ikeda, 1992) for later counts of zooplankton species abundance.

Representative subsamples of 500-600 animals were obtained with a Stempel pipette (usually 1-5% of initial cod end volume). Zooplankton were identified and

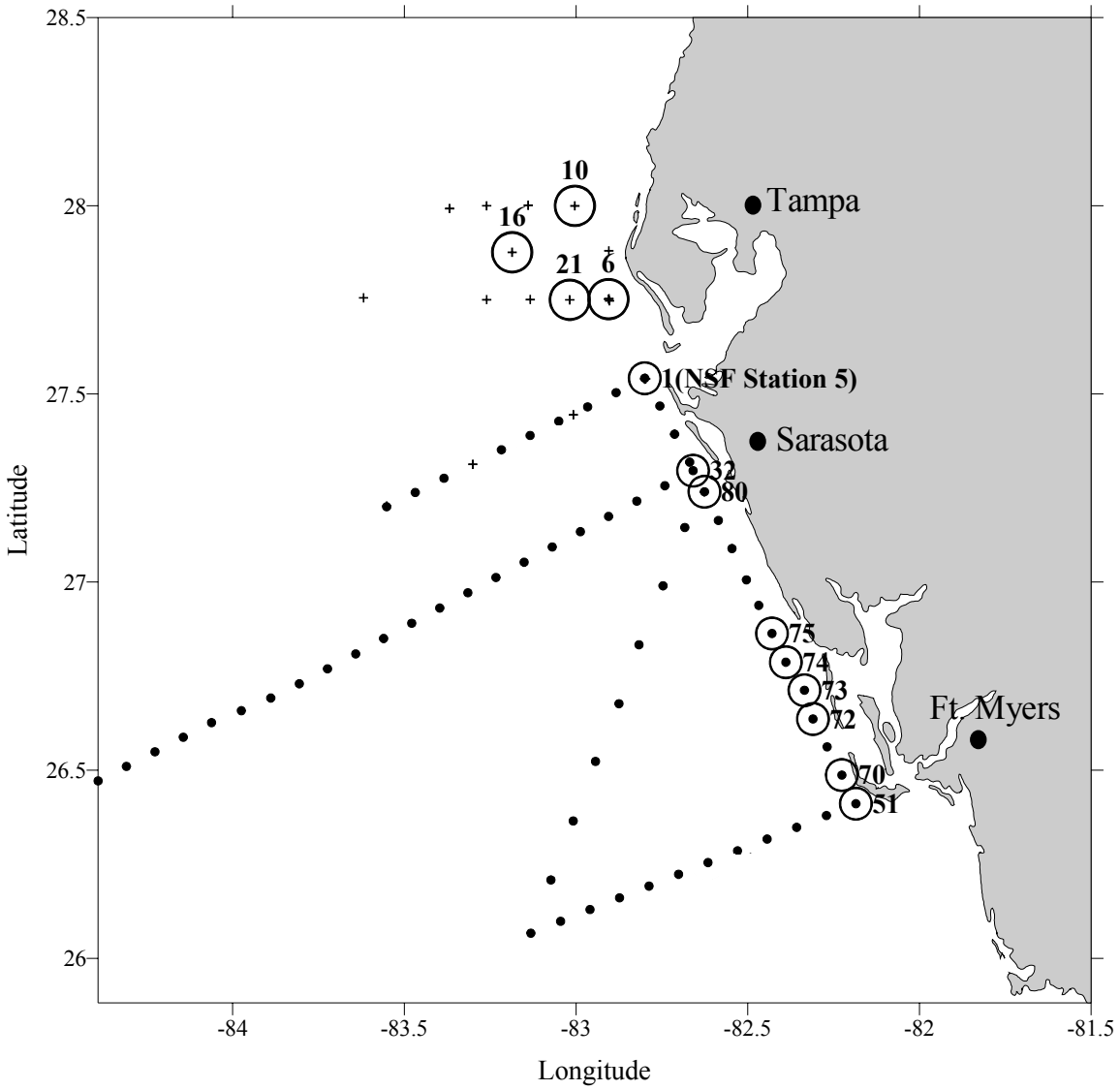

Figure 51. Station locations for ECOHAB cruises (•) and NSF cruises (+). Stations where zooplankton tows were conducted are indicated by a number. NSF Station 5 is in the same location as ECOHAB Station 1.

counted using an Olympus dissecting microscope. Holoplankton were identified to species level. Meroplankton were identified to major taxonomic group (e.g. Pelecypod veligers, Cirriped larvae). Replicate samples were averaged for each station.

K. brevis *cell counts*

Zooplankton tows were conducted in conjunction with CTD casts and *K. brevis* cell counts. Water column samples were collected from Niskin bottles mounted on a rosette sampler. During the October 2001 NSF cruise surface samples at selected stations were taken with a bucket, in addition to samples from Niskin bottles. *K. brevis* was counted live using a dissecting microscope within two hours of collection.

Grazing assessment

Grazing studies were conducted in 2005 using cultured *K. brevis* and the copepods *Acartia tonsa*, *Labidocera aestiva*, and *Paracalanus quasimodo*. Zooplankton were collected from the pier or a small boat with a 202 μm mesh net. Cod ends were immediately diluted with natural sea water, covered with shade cloth and transported to the lab. After sorting, 2 adult female copepods were added to scintillation vials to which 20 ml filtered seawater was added. ^{14}C labeled *K. brevis* culture was added to each vial, such that the final *K. brevis* concentration was 5×10^3, 5×10^4, or 1×10^6 cells per liter. Vials were incubated for 30 minutes. After the incubation period, copepods were filtered onto 12μm Nuclepore filters, rinsed with filtered seawater, and dissolved with Hyamine Hydroxide. After addition of a scintillation fluor, vials were placed in the dark for two hours. CPM's were read on a Beta Scout scintillation counter.

Adsorption controls were performed by placing 2 copepods each in scintillation vials with *K. brevis* concentrations reported above. The copepods were not incubated but were instead immediately removed, filtered onto 12µm Nuclepore filters, rinsed with filtered seawater, dissolved with Hyamine hydroxide, and placed in the dark for 2 hours. CPM's were counted as described above on a Beta Scout scintillation counter.

Radioactivity of *K. brevis* cells was determined by filtering 0.1 ml of the labeled culture onto 1µm Nuclepore filters. Cells were dissolved in Hyamine hydroxide and CPM's recorded.

Clearance rate (F in ml animal^{-1} h^{-1}) was calculated as:

$$F=(\mathrm{dpm}_{animal} \times v)/(\mathrm{dpm}_{algae} \times t)$$

where dpm_{animal} is the radioactivity of one animal, dpm_{algae} is the radioactivity of v ml of the phytoplankton suspension, and t is the incubation time in hours (Bamstedt et al., 2000). Ingestion rate (in cells ingested per hour) was calculated by multiplying the clearance rate by the phytoplankton concentration during incubation (Bamstedt et al., 2000).

For remaining dominants within the blooms, grazing pressure was calculated using published grazing rates (Table 26). Grazing rates of *Centropages velificatus* copepodites and *Oithona colcarva* and *Parvocalanus crassirostris* adults were determined using allometric derivations[2] based on the biomass of adult *C. velificatus, Oithona plumifera*, and *P. quasimodo,* respectively (Frost, 1980).

Several assumptions were made to assess the impact of grazing pressure on *K. brevis* blooms. First, if other phytoplankton species were present, grazing on *K. brevis*

[2] Based on the allometric equations of Frost, 1980 $Y = \alpha m^b$, where b = 0.75.

Table 26
Taxon and life stage specific grazing rates for zooplankton taxa dominant within *K. brevis* blooms, pro-rated for a 24-hr day.

Taxon	Grazing rate	Source	Comments
O. colcarva	1.5 ng chl ind^{-1} day^{-1}	Dagg 1995, Sutton et al., 1999	2,a
P. crassirostris	.05 x 10^3 cells ind^{-1} day^{-1}	Turner and Tester, 1989	1,b
Temora turbinata	41.5 ng chl ind^{-1} day^{-1}	Dagg 1995; Kirboe et al., 1985; Sutton et al., 1999	2
C. velificatus	16 "	Dagg 1995; Kirboe et al., 1985; Sutton et al., 1999	2
CV	2.8-6.4 "		2,c
Evadne tergestina	.432 "	Sutton, 1999	2
Oikopleura dioica	92.9 "	Dagg 1995; Sutton et al., 1999	2

1. Cell Counts
2. Gut Fluorescence

a. Allometric derivation from *O. plumifera* (Frost, 1981)
b. Allometric derivation from *P. quasimodo*(Frost, 1981)
c. Allometric derivation from adult (Frost, 1981)

was assumed to be negligible since copepods will avoid ingesting *K. brevis* if alternate food is available (Turner and Tester, 1989). Second, carnivory and diel variation in feeding rates were not considered, resulting in a probable overestimation of the grazing pressure. In addition to the numerically dominant species, 2 additional species, *L. aestiva* and *P. quasimodo*, were incorporated into the grazing analysis because they have been shown to ingest *K. brevis* (Turner and Tester; 1989, this study). Pelecypod larvae were not included in the analysis, due to the apparent inability of scallop larvae to ingest *K. brevis* (J. Leverone, *pers. comm*.).

RESULTS

Two separate *K. brevis* blooms were sampled during the course of the ECOHAB:Florida program. The first bloom occurred in October of 1999 and was relatively short lived (Figure 52). Near shore stations 1 and 51 both had low *K. brevis* concentrations and were dominated by typical near shore WFS zooplankton assemblages (Table 27). Station 80, also near shore, and with a very high *K. brevis* concentration of over 5 million cells l^{-1}, had a zooplankton assemblage dominated by *Centropages velificatus* and *Temora turbinata*, with much of the assemblage consisting of *C. velificatus* copepodites (Table 28).

The second bloom spanned a four month sampling period from September to December, 2001 (Figures 53-55). In September the bloom was present in very low concentrations, and the typical WFS zooplankton assemblage was present (Table 29). As the bloom progressed through October, the bloom was present at several stations at

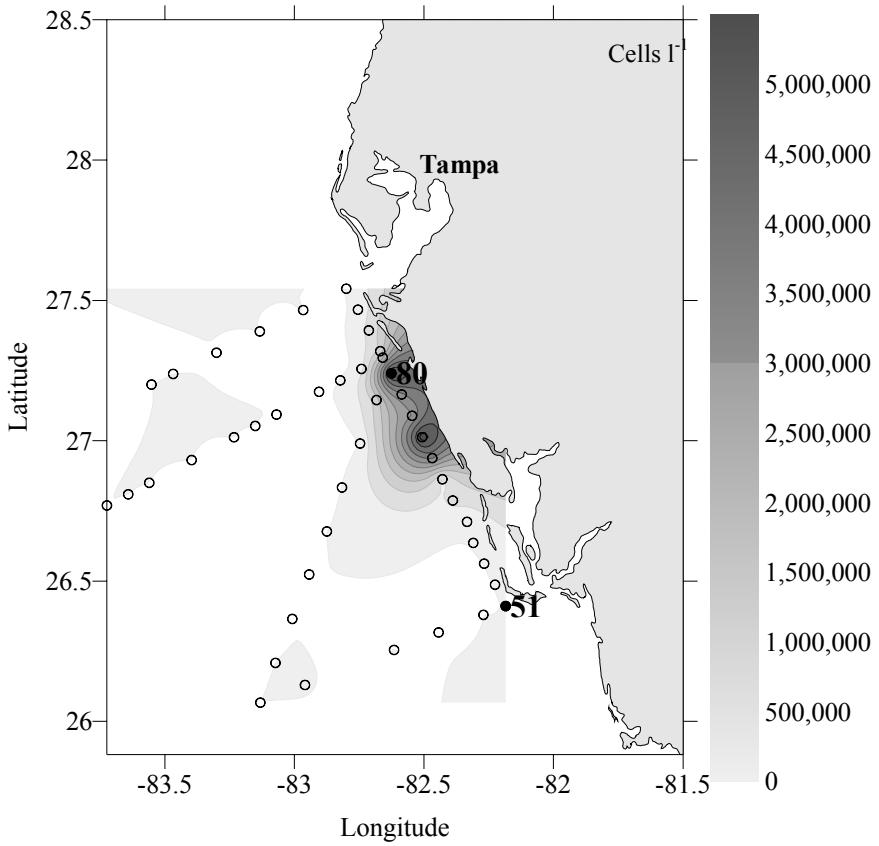

Figure 52. Surface *K. brevis* concentrations for October 1999.

Table 27
Zooplankton abundance and community composition sampled in October 1999

	October-99		
K. brevis cells l^{-1} x 10^3	7.5	16	5270
Station	51	1	80
A. tonsa	11	245	4
C. amazonicus	39	98	--
C. americana	56	--	--
C. americanus	7	--	--
C. velificatus	118	49	4569
E. pileatus	--	--	234
E. acutifrons	25	405	--
E. crassus	57	--	--
L. aestiva	--	--	112
L. scotti	--	25	55
O. nana	52	172	--
O. colcarva	102	749	--
O. dioica	150	--	--
O. simplex	--	25	--
P. avirostris	--	37	--
P. crassirostris	5553	2884	516
P. quasimodo	206	37	25
T. setacaudatus	18	--	--
T. turbinata	70	--	2341
Cirriped larvae	4	2037	59
Decapod larvae	43	650	179
Echinoderm larvae	4	--	--
Gastropod larvae	4	12	4
Pelecypod larvae	4	479	31
Polychaete larvae	14	123	--
Total Num Abund. m^{-3}	7069	1299	3542

Table 28

C. *velificatus* copepodite abundance at Station 80 in October 99

Stage	Abund. (m^{-3})
I	92
II	506
III	2177
IV	2667
V	410
Adult	355

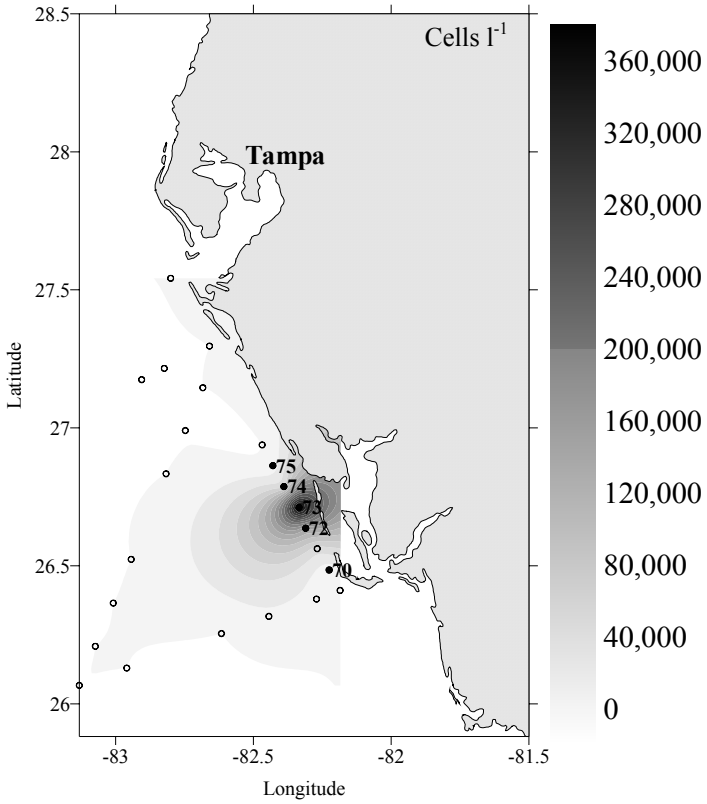

Figure 53. Surface *K. brevis* concentrations for September 2001.

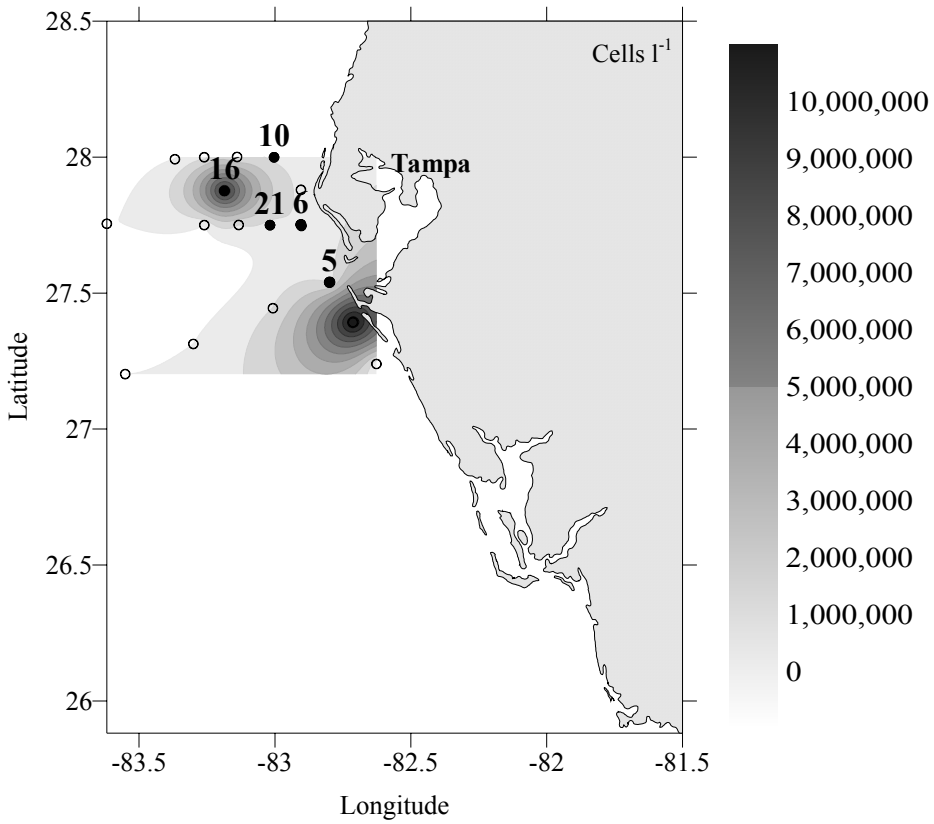

Figure 54. Surface *K. brevis* concentrations for October 2001.

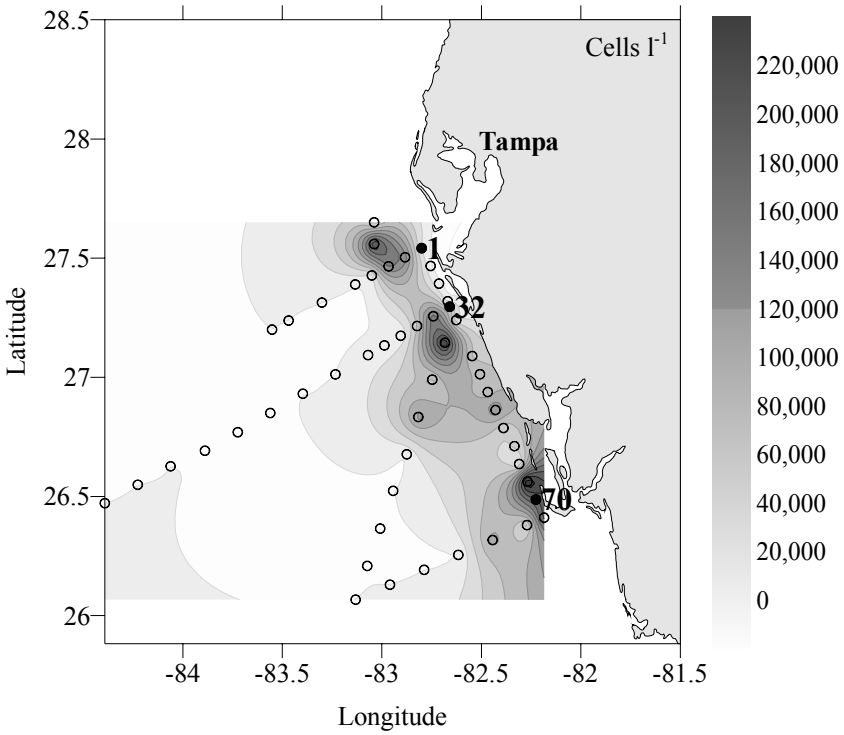

Figure 55. Surface *K. brevis* concentrations for December 2001.

concentrations of over 1 million cells liter (Figure 55). The zooplankton assemblage in October changed in both abundance and percent composition (Table 29). The greatest departure from normal WFS zooplankton populations occurred at stations 16, 10 and 5, when pelecypod larvae dominated the assemblage. By December, an estuarine signature characterized the bloom (Vargo et al., in press). The copepod *A. tonsa* and the cladoceran *E. tergestina* dominated the assemblage.

Grazing experiments

All three experimental animals, *A. tonsa*, *P. quasimodo*, and *L. aestiva*, ingested *K. brevis* (Figure 56). For all three species, highest ingestion rates were observed when *K. brevis* concentrations were at 10^6 cells liter, though variability was high. Lowest ingestion rates were found at lowest *K. brevis* cell concentrations. *P. quasimodo* ingested the lowest number of *K. brevis*. One of the species examined, *L. aestiva*, ingested negligible quantities of *K. brevis* at 10^4 concentrations.

Grazing assessment

The results of the grazing assessment indicate that heavy grazing pressure occurred at one station in the 1999 and 2001 blooms. At Station 1 in December 2001, grazing pressure was 34.52% of the *K. brevis* population. Taking into account an assumed growth rate of 0.2 divisions day^{-1}, the zooplankton assemblage at Station 1 in December 2001 could have reduced the *K. brevis* concentration to background levels in 7 days. For the remainder of the stations, grazing pressure was negligible, and was never above 2%.

Table 29
Zooplankton abundance and community composition at stations sampled within the 2001 *K. brevis* bloom

	September-01					October-01					December-01		
K. brevis cells l^{-1} x 10^3	8	200	500	75	15	1268	742	1320	1078	774	16	68	176
Station	70	72	73	74	75	6	10	16	21	5	70	32	1
A. tonsa	42	185	120	29	67	3	--	38	50	337	21447	145	16
C. amazonicus	8	--	--	2	1	2	141	--	225	56	--	--	--
C. americana	7	3	4	3	17	--	--	--	0	--	--	--	--
C. americanus	12	--	--	5	0	--	--	--	112	112	48	18	24
C. velificatus	2	--	--	4	41	1	--	2	25	112	--	--	--
E. tergestina	1	63	10	--	83	--	117	12	275	1516	1008	4462	621
E.acutifrons	23	4	--	9	18	--	23	24	--	--	--	--	--
L.aestiva	4	1	--	1	3	1	23	--	50	56	--	--	--
O. nana	--	--	--	--	--	--	--	--	--	--	--	48	0
O.colcarva	1	25	6	28	126	33	1081	38	4730	6121	--	289	24
O.dioka	--	--	26	39	100	1	47	108	2772	421	96	235	8
O.similis	--	--	--	--	--	--	--	--	826	--	--	--	--
O.simplex	19	19	4	5	60	--	--	--	--	337	--	--	--
P. avirostris	8	3	18	13	26	--	--	29	198	--	--	--	--
P. crassirostris	--	83	24	156	2711	30	681	--	826	1994	--	--	--
P. quasimodo	--	2	7	19	36	--	--	--	75	28	48	18	2
T. setacaudatus	2	--	--	--	--	--	23	--	75	--	2	--	--
T. stylifera	9	--	--	--	--	--	--	--	--	--	--	--	--
T. turbinata	2	--	0	37	29	--	--	--	--	--	--	--	--
Cirripid larvae	6	8	7	--	1	1	234	216	2161	2161	432	217	21
Decapod larvae	--	56	81	--	1	6	164	120	590	590	96	18	--
Echinoderm larvae	--	--	--	--	--	0	658	41	197	197	--	--	--
Gastropod larvae	--	--	--	--	5	10	117	137	140	140	--	--	--
Pelecypod larvae	--	--	--	8	3	289	8366	5616	1685	1685	--	--	--
Polychaete larvae	24	8	16	1	5	12	141	225	505	505	192	54	10
Total Num Abund. m^{-3}	219	531	325	635	3343	388	11866	6502	15517	16368	23369	5456	726

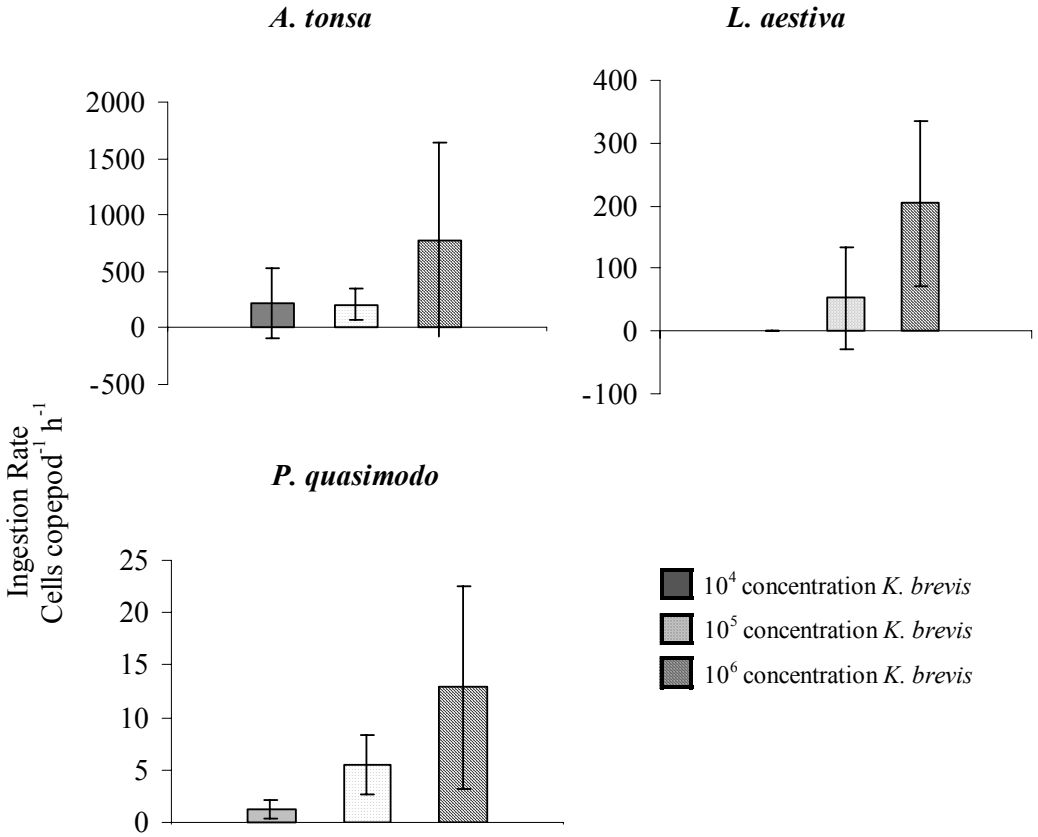

Figure 56. Grazing rates of selected WFS copepods on *K. brevis*.

Table 30
Assessment of grazing pressure on 1999 and 2001 *K. brevis* blooms on the WFS.

Month	Station	*K. brevis* cells l^{-1} (x 10^{-3})	Phytoplankton assmblage	Dominant grazer(s)	Grazing pressure (% of *K. brevis* population)
Oct-99	51	7.5	Monospecific	*P. quasimodo*	1.64
	1	16	Monospecific	*A. tonsa , P. quasimodo*	0.37
	80	5270	Monospecific	*T. turbinata, C. velificatus*	0.82
Sep-01	70	8	Monospecific	*A. tonsa*	0.12
	72	200	Diatoms		--
	73	500	Microflagellates, *Bellerochea*		--
	74	75	Monospecific	*A. tonsa*	0.17
	75	15	Dinoflagellates		--
Oct-01	6	1268	Diatoms		--
	10	742	Microflagellates, *Bellerochea*		--
	16	1320	Monospecific	*O. dioica*	0.15
	21	1078	Dinoflagellates		--
	5	774	Monospecific	*O. dioica*	0.51
Dec-01	70	16	Dinoflagellates, *Thalassiosira* spp.		--
	32	68	Small dinoflagellates, flagellates		--
	1	176	Monospecific	*O. dioica, A. tonsa*	34.52

DISCUSSION

The ingestion numbers obtained here for WFS copepods grazing on cultured *K. brevis* are lower than those found by Turner and Tester (1989) (Table 31). There are three potential reasons for this. The first is the difference in methodology between the two studies. The Turner and Tester (1989) study used cell counts to determine ingestion rates of naturally occurring *K. brevis*, and it is possible that the difference in methodology between that study and this one resulted in the discrepancies in grazing rate. Secondly, the very high concentrations of *K. brevis* used by Turner and Tester (1989) in their study (as high as 20 million cells l^{-1}) could explain the discrepancies between our studies, since ingestion rate for all species examined appears to increase with increasing concentrations of *K. brevis*. A third explanation is the potential resistance to brevetoxins developed by copepods that have been exposed to brevetoxins for some time. The *K. brevis* bloom studied by Turner and Tester (1989) was an expatriate red tide, new to North Carolina waters, but had reportedly been in the area for at least a month (Turner and Tester, 1989). It is possible then, that the North Carolina copepods studied by Turner and Tester (1989) had developed resistance to brevetoxins, resulting in a higher grazing rate. Most of the animals examined in my study were taken from waters that were free of brevetoxins. The *P. quasimodo* specimens were taken from waters with high *K. brevis* concentrations (>100,000 cells l^{-1}), but this bloom had been in the area for less than one month. Resistance to algal toxins in copepods has been demonstrated for other species of toxic algae (Colin and Dam, 2005), while rejection of *K. brevis* as a food source has been

Table 31

Comparison of *K. brevis* grazing activity between this study and Turner and Tester (1989)

	This Study			Turner and Tester		
	K. brevis concentration			*K. brevis* concentration		
	$10X10^3$	$10X10^4$	$10X10^5$	$10X10^3$	$10X10^4$	$10X10^5$
	Ingestion Rate			Ingestion Rate		
A. tonsa	220	210	780	929	8,129	80,129
P. quasimodo	1	6	13	--	--	1,000
L. aestiva	1	53	203	1,015	10,285	102,985

shown by copepods that do not normally co-occur with *K. brevis* in nature (Huntley et al., 1986).

The grazing numbers found here represent carbon ingestion rates that are lower than the typical carbon ingestion ranges found for these species (Table 32), indicating that there are factors present that reduce copepod grazing on *K. brevis*. Carbon ingestion values were at least one order of magnitude lower than the lowest carbon ingestion rates reported.

Sutton et al. (2001) found that an average of 7.9% of phytoplankton standing stock was grazed by the zooplankton assemblage on the WFS sampled during a September 1999 cruise, with occasional heavy concentration of grazing depending on zooplankton taxa present. Dagg (1995), working in the Northern Gulf of Mexico during September, found that ingestion removed 14-62% of phytoplankton biomass in Mississippi river plume waters. My rates are much lower, suggesting that grazing rates on *K. brevis* blooms by the mesozooplankton community are lower than grazing rates for non-bloom phytoplankton assemblages.

Teegarden (2001) and Turner and Tester (1997) suggested that the effect of grazing on toxic algae blooms could be species specific, with the impact of grazing on the bloom dependent on species present. In this study, highest ingestion rates for copepods feeding on cultured *K. brevis* were found for *A. tonsa*, yet the dominance of the zooplankton assemblage by *A. tonsa* appeared to less important than the total number of zooplankton present and the concentration of *K. brevis*.

Table 32

Comparison of carbon ingestion for *K. brevis* grazing experiments and literature carbon ingestion values[1]

	Carbon ingested (μg day^{-1}) at varying *K. brevis* concentrations			Typical non red-tide ingestion values (μg day carbon ingestion)			
	10X10^3	10X10^4	10X10^5	min	max	mean	
A. tonsa	0.0046	0.0044	0.0163	0.01	0.09	0.05	[2,3]
P. quasimodo	0.0000	0.0001	0.0003	--	--	0.05	[4]
L. aestiva	0.0000	0.0011	0.0042	0.4	1.2	0.8	[5,6]

1. Based on Carbon concentration of *K. brevis* of 7.25 x 10^{-5} μM cell (Heil, 1986)
2. Irigoien et al., 1993
3. Roman, 1977
4. Based on the values for *Paracalanus parvus* from Checkley, 1980
5. Conley and Turner, 1985
6. Based on assumed carbon value of 44% (Bamstedt, 1986)

CONCLUSIONS

The results of the grazing assessment suggest that grazing pressure from the mesozooplankton community during the 1999 and 2001 blooms was not sufficient for *K. brevis* bloom termination. However, other components of the zooplankton community that may have contributed to total grazing pressure, such as tintinnids and ciliates, were not assessed in this analysis. These components may prove to be important grazers of *K. brevis*, since tintinnids were observed to ingest *K. brevis* during the 2001 bloom (C. Heil, *pers. comm.*).

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CHAPTER 6

CONCLUSIONS

The purpose of this study was to examine the relationships between zooplankton and *K. brevis* blooms on the West Florida Shelf. To this end, a sampling program was undertaken to assess the normal zooplankton assemblage of the WFS on a seasonal and taxonomically distinct basis. The results of this assessment were compared to the zooplankton assemblage sampled during red-tide events on the WFS. The abundance and community composition found during *K. brevis* blooms on the WFS during 1999 and 2001 were used to assess the effects of zooplankton nutrient regeneration and grazing on *K. brevis* blooms.

The community composition found here agrees well with other studies conducted in the Gulf of Mexico. At the 5-meter isobath, the copepods *O. colcarva* and *P. crassirostris* were the most important contributors to abundance and community composition. Despite their high abundances in this study, both *P. crassirostris* and *O. colcarva* are probably present in even greater amounts, but were underrepresented due to the relatively large mesh size used. Other important and intermittent contributors to abundance and community composition at the 5-meter isobath were *P. avirostris* and *P. quasimodo*.

At the 25-meter isobath for much of the year the zooplankton assemblage was dominated by *P. quasimodo*, *O. colcarva* and the larvacean *O. dioica*. In the winter and spring, *E. chierchiae* and *C. furcatus* were dominant.

At the 50-meter isobath, fall, winter and early spring assemblages were dominated by *E. chierchiae*, *O. frigida*, *C. furcatus* and *O. mediteranea*. In the late spring, the assemblage was dominated by *C. furcatus*, *C. pavoninius*, *O. similis* and Gastropod larvae.

The importance of *E. chierchiae* to the WFS ecosystem needs to be explored further. The ostracod dominated the zooplankton assemblage at the 25 and 50-meter isobaths for much of the year. Little is known about the ecology of *E. chierchiae*, yet it's prevalence on the WFS suggests that further study is warranted.

The 5 subgroups (A-E) in community composition were tightly coupled with temperature, salinity and chlorophyll *a* concentration. A range of environmental factors defined distribution, with temperature being the most important factor defining distribution near shore. As distance offshore increased, salinity and chlorophyll *a* concentration became increasingly important as factors defining distribution. Considerable overlap in community composition was observed for subgroups A and B, Subgroups B, C and D, and Subgroups C, D and E. However, virtually no overlap was observed for near shore subgroup A and offshore subgroup E.

Range in chlorophyll *a* concentration, temperature, and salinity decreased as distance offshore increased. Chlorophyll *a* was found to be the most important contributing factor to zooplankton community composition.

Statistical analysis of *K. brevis* bloom stations and non-bloom near shore stations showed that most *K. brevis* bloom stations differed significantly from non-bloom stations in abundance or community composition. Some of the consistent differences observed between bloom and non-bloom stations were decreased abundance of three important

WFS coastal species, *C. americanus*, *P. avirostris* and *E. acutifrons*, and numerical dominance by *A. tonsa*, *C. velificatus*, *T. turbinata*, *E. tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris*, which were consistently found in high concentrations inside *K. brevis* blooms. Of the 7 species found in high concentration inside *K. brevis* blooms, only *T. turbinata* and *E. tergestina* were not major contributors to normal WFS zooplankton assemblages at the 5-m isobath. Perturbations in meroplankton contribution to community structure also were evident. In October 2001 there were higher than normal abundances of most meroplankton forms, with the most obvious of these being the Pelecypods.

The values calculated here for ammonium and phosphate excretion for the total zooplankton community indicate that *K. brevis* blooms could be obtaining their phosphate from zooplankton excretion, though ammonium excretion rates proved to be too low to support all but a 10^4 cells l^{-1} concentration of *K. brevis*.

The results of the grazing assessment suggest that grazing pressure from the mesozooplankton community during the 1999 and 2001 blooms was not sufficient for *K. brevis* bloom termination. There was only one station where grazing pressure exceeded the assumed growth rate of 0.2 divisions day^{-1}, however grazing pressure was not consistently heavy across stations. At most stations, grazing pressure was 1.64% or less of the *K. brevis* population. It is important to note that other components of the zooplankton community that may have contributed to total grazing pressure, such as tintinnids and ciliates, may prove to be important grazers of *K. brevis*.