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Zooplankton and *Karenia brevis* in the Gulf of Mexico

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Abstract

Blooms of the toxic dinoflagellate *Karenia brevis* are common in the Gulf of Mexico, yet no in situ studies of zooplankton and *K. brevis* have been conducted there. Zooplankton abundance and taxonomic composition at non-bloom and *K. brevis* bloom stations within the Ecology of Harmful Algal Blooms (ECOHAB) study area were 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 nine species contributing to 90% of abundance at both isobaths. At stations within *K. brevis* blooms however, *Acartia tonsa*, *Centropages velificatus*, *Temora turbinata*, *Evadne tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris* were dominant. Variations in abundance between non-bloom and bloom assemblages were evident, including the reduction in abundance of three key species within *K. brevis* blooms.

1. Introduction

Blooms of the toxic dinoflagellate *Karenia brevis* (previously *Gymnodinium breve*) frequently cause massive fish kills on the West Florida Shelf (WFS), with blooms reported by early Spanish explorers as far back as the 1500s (Steidinger et al., 1998). Previous research has identified possible links between *K. brevis* growth rates and nutrients, light

levels, *Trichodesmium* blooms, dinoflagellate life cycles, and hydrography of the Gulf of Mexico (Steidinger, et al., 1998 and references cited therein; Heil et al., 2001; Lenos et al., 2001; Lester et al., 2001; Vargo et al., 2001; Walsh and Steidinger, 2001; Walsh et al., 2002, 2003). To date, no studies have examined the potential changes to zooplankton populations within *K. brevis* blooms in the Gulf of Mexico.

Prior to identifying potential inter-relationships between the zooplankton assemblage and *K. brevis* blooms, taxonomic characterization of the normal

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(non-bloom) zooplankton assemblage in the study area was necessary. This 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 control volume.

Far more is known about the coastal and offshore regions that border the study area. Taxonomic analyses of the zooplankton assemblage have been conducted for many WFS estuaries (Hopkins, 1966, 1977; Weiss, 1978; Squires, 1984), as well as for areas further offshore (Hopkins, 1982; Morris and Hopkins, 1983; Hopkins and Lancroft, 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 et al., 1981), but all data acquired to date indicate that the zooplankton populations on the WFS are different than those found in estuaries and further offshore (Minello, 1980; Hopkins et al., 1981; Ortner et al., 1989; Sutton et al., 2001).

2. Methods

2.1. Study design

Sampling of the non-bloom 1999 and 2000 zooplankton assemblage took place during monthly ECOHAB cruises in the Gulf of Mexico (Fig. 1). Sampling was conducted at monthly intervals at the 5-m isobath (Stations 1 and 51) and at the 25-m isobath (Stations 5 and 46) from August 1999 through July 2000. A CTD profile was conducted at every station. Water samples were collected at 5-m intervals from the surface to the bottom to determine chlorophyll *a* concentration and *K. brevis* cell counts.

Sampling of the zooplankton assemblage within the 1999 and 2001 *K. brevis* blooms was conducted during October 1999 and September through December 2001. In October 1999 and September and December 2001, zooplankton tows were conducted on ECOHAB cruises at stations within the bloom. In October 2001, zooplankton tows were taken to the north of and within the ECOHAB study area on a National Science Foundation (NSF) research cruise. In November 2001, the Tampa Bay transect of the ECOHAB study area was sampled on a Hyperspectral Coastal Ocean Dynamics Experiments (HyCODE) cruise using a High

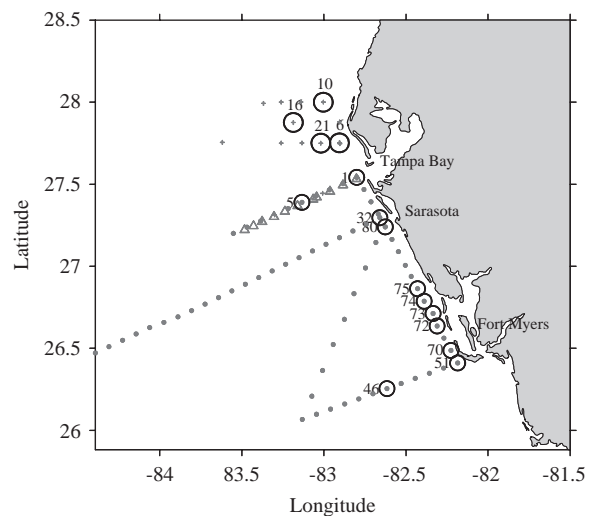


Fig. 1. Station locations for ECOHAB (●), NSF (+), and HyCODE (△) cruises. Stations on ECOHAB and NSF cruises where zooplankton tows were conducted are indicated by a number. On the November 2001 HyCODE cruise, zooplankton collections were conducted during every HRS deployment. NSF Station 5 is in the same location as ECOHAB Station 1 and the final HRS deployment.

Resolution Sampler (HRS) (see Sutton et al., 2001, for a complete description of sampling vehicle).

2.2. Collection of zooplankton

During the 1999–2000 ECOHAB cruises, 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 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.

During the 2001 ECOHAB, NSF, and HyCODE cruises, collection of zooplankton in September, October, and December 2001 was accomplished as described above, except that a single 153 μm mesh net was used instead of a bongo net. In November 2001, zooplankton were sampled with the HRS on a HyCODE cruise. Ten net samples (162 μm mesh) were taken during each deployment of the HRS.

2.3. Determination of zooplankton abundance

During the 1999–2001 ECOHAB and NSF cruises, 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.

November 2001 HyCode samples were split in a Folsom splitter to 1/8th or 1/16th of initial cod end volume, such that the total number of animals enumerated ranged from several hundred to the low thousands. Animals were identified with an Olympus dissecting scope to genus or major taxonomic group.

2.4. 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, except for November 2001, when water column samples were collected from HRS bottles triggered simultaneously with net samples. For all months, duplicate chlorophyll samples were filtered on GF/F filters, placed in 10 ml methanol and stored at -20°C in darkness for later analysis with a Turner Designs fluorometer (Welschmeyer, 1994). For ECOHAB and NSF cruises, *K. brevis* was counted live using a dissecting microscope within 2 h of collection. Typically five 0.2 ml subsamples were counted in duplicate well slides. Final abundance is expressed as the average of all values. For the HyCODE cruise in November 2001, aliquots from selected bottles were preserved using Lugols solution for phytoplankton identification at a later date.

2.5. Statistical analysis

Observed community associations were quantified using the multivariate statistical techniques of Plymouth Routines in Multivariate Ecological Research (PRIMER) software. Identification of trends in community distribution of the zooplankton assemblage was explored using hierarchal cluster analysis. 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). Due to differences in zooplankton collection and identification, it was not possible to include the November HyCODE data in the statistical analysis of the ECOHAB/NSF samples.

3. Results

3.1. Non-bloom zooplankton assemblage

Abundance ranged from 185 animals m^{-3} at Station 46 in June 2000 to 22×10^3 animals m^{-3} at Station 1 in September 1999 (Fig. 2). Isobath averaged abundance was always greatest at the 5-m isobath, where it peaked in late summer and early fall, increased again in December, and was at its lowest in early spring. At the 25-m isobath, abundance peaked in October and November decreased through April, and increased slightly through the summer.

Hierarchal cluster analysis showed two major communities at the 40% similarity level (Fig. 3). All 5-m isobath stations were included in a single group (identified as WFS1), and all 25-m isobath stations were included in a second group (identified as WFS2).

At both isobaths, six taxa were responsible for 60% of the community structure. At the 5-m isobath (WFS1), *Parvocalanus crassirostris*, *Oithona colcarva*, *Paracalanus quasimodo*, cirriped larvae

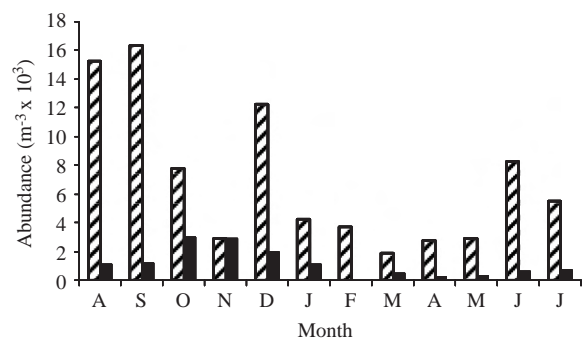


Fig. 2. Zooplankton abundance m^{-3} for the 5-m (hatched bars) and 25-m (solid bars) isobath.

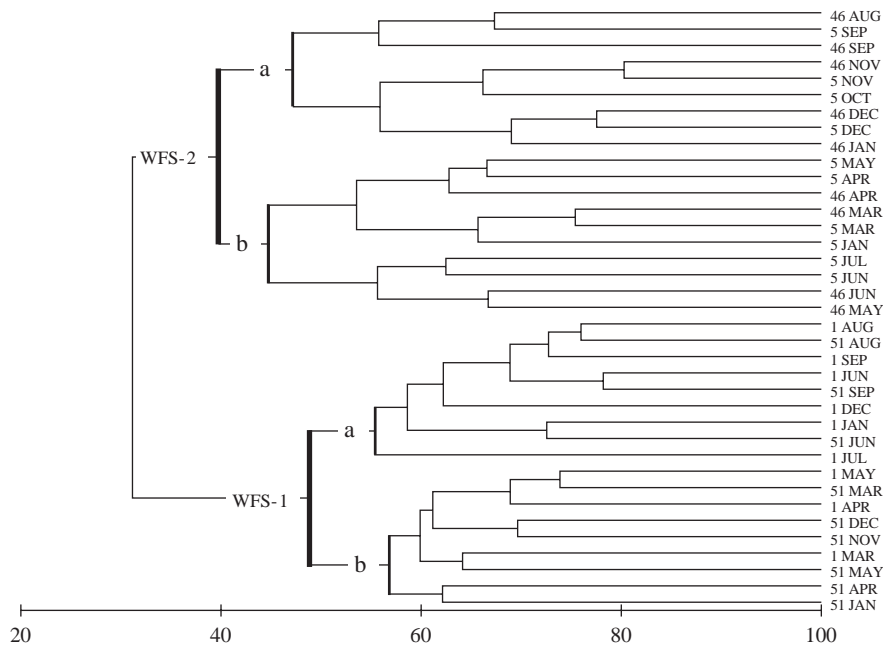


Fig. 3. Cluster-derived dendrogram for 37 stations at the 5- and 25-m isobaths, using group-averaged clustering from Bray-Curtis similarities on square root transformed abundance data.

(including nauplii and cyprids), *Euterpina acutifrons*, and the cladoceran *Penilia avirostris* were dominant (Table 1). Less abundant at this isobath were *Corycaeus americanus*, *Centropages velificatus*, *Oikopleura dioica*, *Acartia tonsa*, and the larvae of decapods, pelecypods, and gastropods.

At the 25-m isobath (WFS2), the most common zooplankton taxa were *P. quasimodo*, *O. colcarva*, *O. dioica*, *C. velificatus*, gastropod larvae, and *Oithona plumifera* (Table 2). Less frequent were *Oncaea mediterranea*, *P. crassirostris*, *E. acutifrons*, the ostracod *Euchonchoichiea chierchiae*, *Corycaeus amazonicus*, *Clausocalanus furcatus*, and the larvae of pelecypods and decapods.

Of the 13 taxa that accounted for 90% of abundance at the 5-m isobath, nine contributed to 90% of 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, five species (*C. amazonicus*, *E. chierchiae*, *O. mediterranea*, *O. plumifera*, and *C. furcatus*) were important contributors to abundance at the 25-m isobath only. Variations in the abundance of nine taxa (*P. crassirostris*, *O. colcarva*, *P. avirostris*, *E. acutifrons*, *P. quasimodo*, *A. tonsa* and the larvae of cirripeds, pelecypods and decapods) accounted

Table 1
Numerical abundance data square root transformed, $n = 18$

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

for 60% of the differences in community composition between the two isobaths (Table 3).

3.2. *K. brevis* bloom zooplankton assemblage

In October 1999, *K. brevis* concentration was very low at Stations 1 and 51 where the typical 5-m isobath assemblage of zooplankton was present and the most important contributors to abundance were

Table 2
Results of SIMPER analysis showing determinant species for WFS2

Taxon	Average abundance (m ⁻³)	Contribution (%)	Cum. (%)
<i>P. quasimodo</i>	123.05	12.22	12.22
<i>O. colcarva</i>	88.63	11.84	24.07
<i>O. dioica</i>	56.63	11.55	35.62
<i>C. velificatus</i>	82.55	8.20	43.82
Gastropod larvae	46.97	7.81	51.63
<i>O. plumifera</i>	19.87	7.57	59.20
Pelecypod larvae	63.97	6.71	65.91
<i>O. mediteranea</i>	53.24	4.61	70.52
<i>P. crassirostris</i>	29.13	4.60	75.12
<i>E. acutifrons</i>	32.97	3.72	78.84
<i>E. chierchiaie</i>	84.55	3.29	82.13
Decapod larvae	7.63	2.81	84.94
<i>C. amazonicus</i>	19.87	2.54	87.48
<i>C. furcatus</i>	26.66	2.47	89.95

Numerical abundance data square root transformed, $n = 19$.

Table 3
Results of SIMPER analysis showing average determinant dissimilarities between WFS1 and WFS2

Taxon	WFS1 average abundance (m ⁻³)	WFS2 average abundance (m ⁻³)	Average diss.	Cum. (%)
<i>P. crassirostris</i>	1655.08	29.13	8.39	12.19
<i>O. colcarva</i>	1224.78	88.63	6.43	21.53
<i>P. avirostris</i>	1105.17	4.95	6.24	30.60
Cirripid larvae	477.53	2.13	4.66	37.36
<i>E. acutifrons</i>	355.67	32.97	3.69	42.72
Pelecypod larvae	271.31	63.97	3.19	47.35
<i>P. quasimodo</i>	343.92	123.05	3.05	51.78
Decapoda	201.53	7.63	2.77	55.80
<i>A. tonsa</i>	243.50	1.61	2.71	59.73
<i>Oithona nana</i>	141.50	0.74	2.52	63.39
<i>C. americanus</i>	108.06	15.26	2.48	66.99
<i>T. turbinata</i>	165.42	36.11	2.20	70.19
<i>O. dioica</i>	176.31	56.63	1.80	72.80
<i>C. amazonicus</i>	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
<i>E. chierchiaie</i>	0.00	84.55	1.64	80.22
<i>C. velificatus</i>	70.14	82.55	1.63	82.58
<i>O. mediteranea</i>	0.00	53.24	1.52	87.11
<i>O. plumifera</i>	0.00	19.87	1.29	88.99
<i>C. furcatus</i>	2.14	26.66	1.05	90.52
Average dissimilarity	68.85			

Data square root transformed, WFS1 $n = 18$; WFS $n = 19$.

P. crassirostris and cirriped larvae (Table 4). At Station 80, where surface *K. brevis* exceeded $5 \times 10^6 \text{ l}^{-1}$, typical zooplankton species were either absent or significantly reduced in abundance. Instead, the dominant zooplankton species were *C. velificatus* and *T. turbinata* (Table 4). *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.

The zooplankton assemblage during September 2001 did not appear to diverge from a “normal” coastal assemblage on the WFS, except for lower abundance at most stations (Table 4). Major zooplankton species present were *A. tonsa* and *E. acutifrons* at Station 70, and *T. turbinata*, *P. crassirostris*, *O. dioica*, *O. colcarva*, and *A. tonsa* at Station 74. The dominant species at Station 75 was *P. crassirostris*. At Stations 72 and 73, *A. tonsa* was dominant.

As the bloom progressed in October, the zooplankton assemblage began to differ in both abundance and percent composition (Table 4). The greatest departure from previously observed zooplankton populations occurred at Stations 16, 10, and 21, when pelecypod larvae dominated the assemblage, in one case exceeding $8 \times 10^3 \text{ larvae m}^{-3}$ and comprising over 90% of the zooplankton assemblage. At Station 5, primary contributors to zooplankton abundance were *O. colcarva* and *Evadne tergestina*.

By December, a strong estuarine signal characterized the bloom (Vargo et al., this volume), with the estuarine species *A. tonsa* and the cladoceran *E. tergestina* comprising the majority of the zooplankton assemblage (Table 4). Other taxa present at Stations 70 and 32 in December consisted of *A. tonsa*, *E. tergestina*, *O. colcarva*, *O. dioica*, and cirriped larvae.

3.3. Statistical comparison of bloom and non-bloom stations

With the exception of Station 1 in October 1999, all of the *K. brevis* bloom stations included in hierarchical cluster analysis fall outside the two groups in community composition previously found for the non-bloom stations sampled in

Table 4
 Zooplankton community composition, abundance, and biomass at stations sampled within 2001 *K. brevis* bloom

<i>K. brevis</i> ($\times 10^3$ cells l ⁻¹) Station	October 1999			September 2001					October 2001					December 2001		
	7.5	16	5270	8	200	500	75	15	1268	742	1320	1078	774	16	68	176
	51	1	80	70	72	73	74	75	6	10	16	21	5	70	32	1
<i>A. tonsa</i>	11	245	4	42	185	120	29	67	3	–	38	50	337	21447	145	16
<i>C. amazonicus</i>	39	98	–	8	–	–	2	1	2	141	–	225	56	–	–	–
<i>C. Americana</i>	56	–	–	7	3	4	3	17	–	–	–	0	–	–	–	–
<i>C. americanus</i>	7	–	–	12	–	–	5	0	–	–	–	112	112	48	18	24
<i>C. velificatus</i>	118	49	4569	2	–	–	4	41	1	–	2	25	112	–	–	–
<i>E. pileatus</i>	–	–	234	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>E. tergestina</i>	–	–	–	1	63	10	–	83	–	117	12	275	1516	1008	4462	621
<i>E. acutifrons</i>	25	405	–	23	4	–	9	18	–	23	24	–	–	–	–	–
<i>E. crassus</i>	57	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>L. aestiva</i>	–	–	112	4	1	–	1	3	1	23	–	50	56	–	–	–
<i>L. scotti</i>	–	25	55	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>O. nana</i>	52	172	–	–	–	–	–	–	–	–	–	–	–	–	48	0
<i>O. colcarva</i>	102	749	–	1	25	6	28	126	33	1081	38	4730	6121	–	289	24
<i>O. dioca</i>	150	–	–	–	–	26	39	100	1	47	108	2772	421	96	235	8
<i>O. similis</i>	–	–	–	–	–	–	–	–	–	–	–	826	–	–	–	–
<i>O. simplex</i>	–	25	–	19	19	4	5	60	–	–	–	–	337	–	–	–
<i>P. avirostris</i>	–	37	–	8	3	18	13	26	–	–	29	198	–	–	–	–
<i>P. crassirostris</i>	5553	2884	516	–	83	24	156	2711	30	681	–	826	1994	–	–	–
<i>P. quasimodo</i>	206	37	25	–	2	7	19	36	–	–	–	75	28	48	18	2
<i>T. setacaudatus</i>	18	–	–	2	–	–	–	–	–	–	23	–	75	–	–	–
<i>T. stylifera</i>	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–
<i>T. turbinata</i>	70	–	2341	2	–	0	37	29	–	–	–	–	–	–	–	–
Cirripid larvae	4	2037	59	6	8	7	–	1	1	234	216	2161	2161	432	217	21
Decapod larvae	43	650	179	–	56	81	–	1	6	164	120	590	590	96	18	–
Echinoderm larvae	4	–	–	–	–	–	–	–	0	658	41	197	197	–	–	–
Gastropod larvae	4	12	4	–	–	–	–	5	10	117	137	140	140	–	–	–
Pelecypod larvae	4	479	31	–	–	–	8	3	289	8366	5616	1685	1685	–	–	–
Polychaete larvae	14	123	–	24	8	16	1	5	12	141	225	505	505	192	54	10
Total numerical abundance (m ⁻³)	7069	1299	3542	219	531	325	635	3343	388	11866	6502	21580	16480	726	5456	23369
Biomass (mg m ⁻³)	24.50	3.13	62.02	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

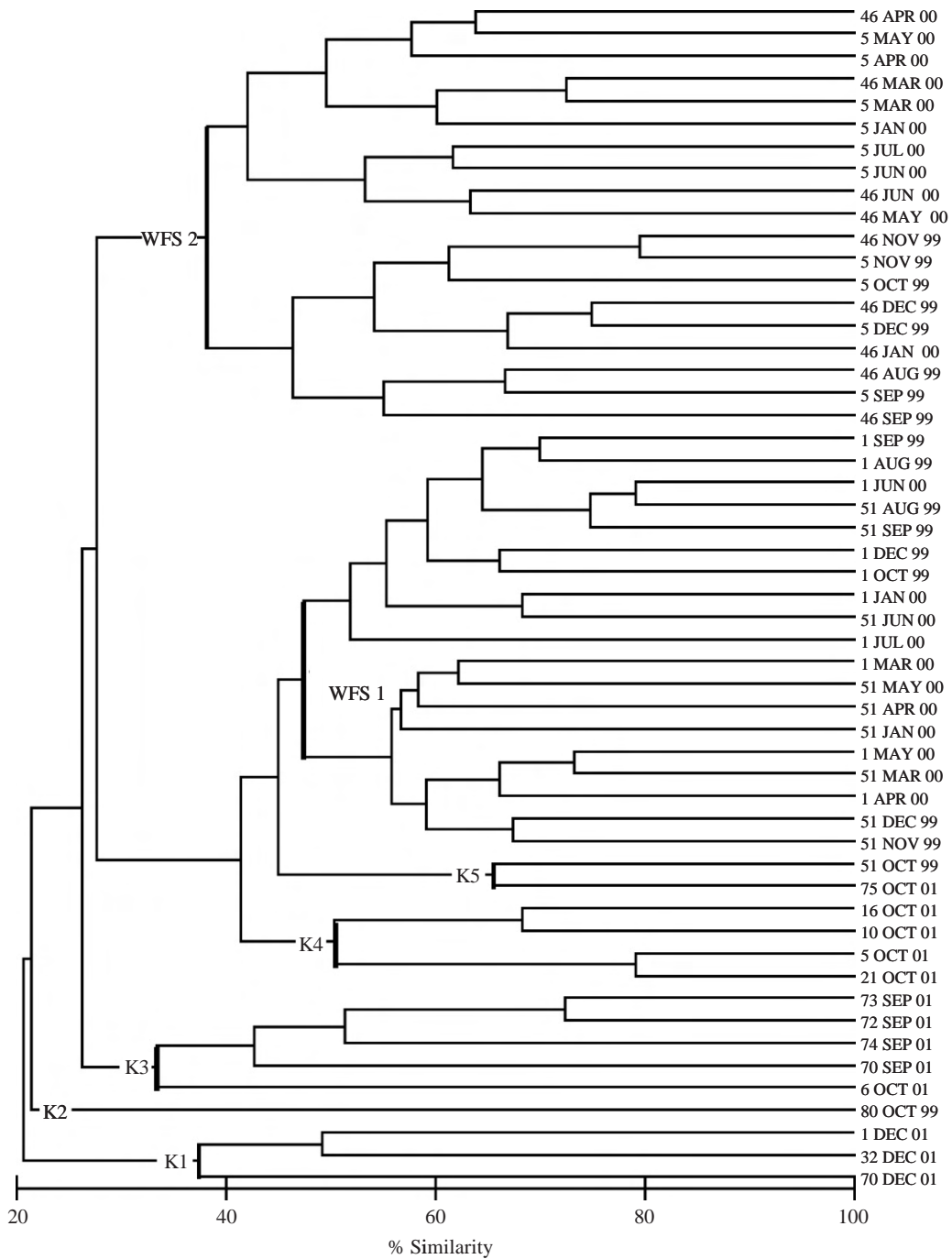


Fig. 4. Cluster-derived dendrogram for 37 stations at the 5- and 25-m isobaths and 16 stations within the 1999 and 2001 *K. brevis* blooms, using group-average clustering from Bray-Curtis similarities on square root transformed data. $n = 53$.

1999 and 2000 (WFS1 and WFS2) (Fig. 4). The hierarchical cluster analysis of the stations within *K. brevis* blooms revealed five separate groups. Groups K1, K2, and K3 were different from the rest of the assemblages at the 20%, 25%, and

30% similarity levels, respectively. Groups K4 and K5 were more closely associated with the WFS1 assemblage, but were distinct from that assemblage at the 40% and 45% similarity levels, respectively.

Table 5
Results of SIMPER analysis showing dissimilarities between *K. brevis* and WFS stations

Taxon	K1		K2		K3		K4		K5		WFS1	
	Average abundance	%	Abundance	%	Average abundance	%	Average abundance	%	Average abundance	%	Average abundance	%
<i>A. tonsa</i>	7203	10.2	–	–	76	20.9	–	–	39	2.9	244	3.2
<i>C. americana</i>	–	–	3	4.5	–	–	–	–	37	3.7	–	–
<i>C. americanus</i>	30	7.7	–	–	–	–	–	–	–	–	108	4.4
<i>C. velificatus</i>	–	–	4569	56.2	–	–	–	–	80	5.8	70	4.2
<i>E. acutifrons</i>	–	–	7	3.0	–	–	–	–	22	3.8	356	6.9
<i>E. tergestina</i>	2030	46.0	–	–	480	4.0	–	–	–	–	–	–
<i>L. aestiva</i>	–	–	–	–	1	2.7	–	–	–	–	–	–
<i>O. colcarva</i>	–	–	18	49.6	–	–	2993	12.0	114	9.2	1225	12.4
<i>O. dioica</i>	113	7.7	13	3.0	–	–	837	5.4	125	9.1	176	4.1
<i>O. simplex</i>	–	–	9	6.3	–	–	–	–	–	–	–	–
<i>P. avirostris</i>	–	–	8	6.2	–	–	–	–	–	–	1105	6.8
<i>P. crassirostris</i>	–	–	516	6.4	59	14.6	875	6.2	4132	30.9	1655	17.1
<i>P. quasimodo</i>	–	–	–	–	–	–	–	–	121	5.4	344	8.2
<i>T. turbinata</i>	–	–	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	–	–	–	–

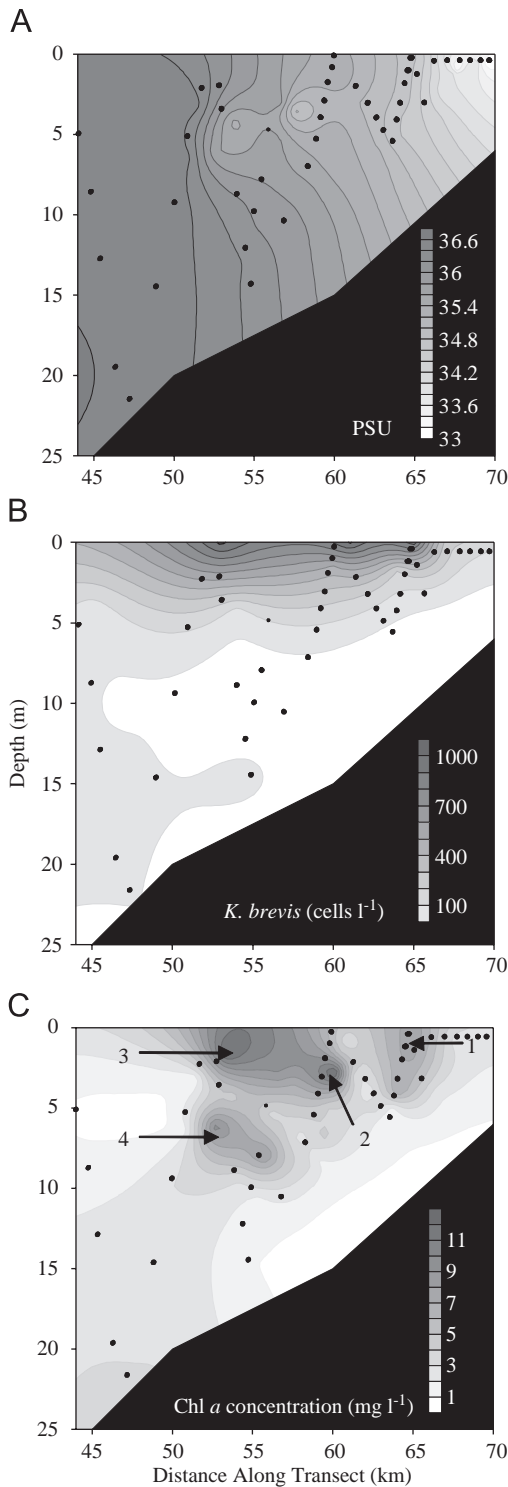


Fig. 5. November 2001 depth profiles for (A) salinity, (B) *K. brevis* ($\times 10^3$ cells l⁻¹), and (C) chlorophyll *a* (mg l⁻¹). Blackened circles indicate sampling locations.

The results of the SIMPER analysis showing average abundances of important (>90%) species and their percent contribution to community composition demonstrated five groups of taxonomic composition within *K. brevis* blooms on the WFS (Table 5). 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, *E. acutifrons*, and by the presence of *L. aestiva*. Group K4 was characterized by higher 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.

3.4. November HRS cruise

In November 2001, *K. brevis* was present in high concentrations on both sides of a strong salinity front located at the 25-m isobath off of Tampa Bay (Fig. 5). Highest cell counts at the surface exceeded 1×10^6 cells l⁻¹, with decreasing concentration near the bottom. The bloom was monospecific at only one location; at transect kilometer 47.7 and a depth of 13 m (Table 6). Otherwise, the phytoplankton population was comprised of a mixed assemblage of *K. brevis*, other *Karenia*, other dinoflagellates, diatoms, and flagellates.

Chlorophyll *a* distribution in November was highly localized, with four primary areas of concentration (Fig. 6). Chlorophyll *a* concentration area 1, at transect kilometer 65 and 0 m, was associated with *K. brevis* concentrations of less than 2×10^5 cells l⁻¹ and high percentages of diatoms (60–68%) nearer shore (Table 6). Chlorophyll *a* concentration area 2, located at transect kilometer 60 and a depth of 2 m, was associated with *K. brevis* concentrations exceeding 1×10^6 cells l⁻¹. The phytoplankton assemblage here was comprised of *K. brevis* (81%) and other dinoflagellates. Chlorophyll *a* concentration area 3, at transect kilometer

Table 6

Phytoplankton population ($\times 10^3 \text{ cells l}^{-1}$) sampled from 25 to 6 m isobath in November 2001

Distance along transect	Depth	<i>K. brevis</i>	Other <i>Karenia</i>	Other dino-flagellates	Diatoms	Flagellates	Total
45	4	24	6	1	20	4	55
44	5	66	30	–	7	–	103
47	8	6	2	–	2	–	9
47.7	13	6	–	–	–	–	6
48	20	2	–	7	–	6	15
48	23	–	–	–	2	7	9
53	0	1029	143	17	28	11	1227
54	4	55	15	–	20	2	92
55	15	17	20	–	7	–	29
60	2	459	55	25	8	17	564
61	0	1019	81	7	44	9	1161
64	2	204	25	–	28	3	259
65	0	964	92	11	161	7	1236
66.5	0	256	25	14	451	3	748
70.5	0	123	11	4	317	11	466

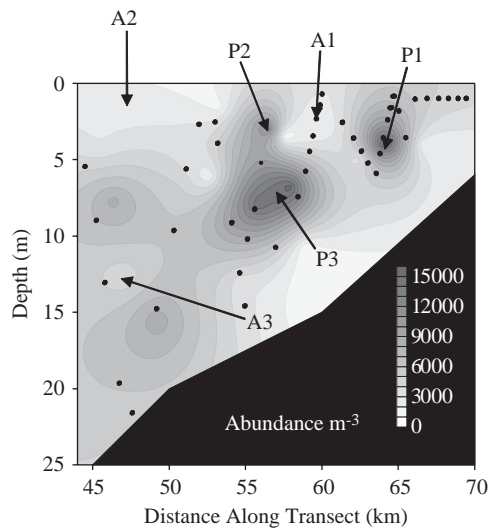


Fig. 6. Zooplankton abundance in November 2001. P indicates zooplankton population center, and A indicates low zooplankton population center. Blackened circles indicate sampling locations.

53 and 0 m, consisted of *K. brevis* concentrations exceeding $1 \times 10^6 \text{ cells l}^{-1}$ and was again characterized by a phytoplankton population of *K. brevis* (84%) and other dinoflagellates. Chlorophyll *a* concentration area 4, at transect kilometer 54–55 and a depth of 5–10 m, was associated with concentrations of *K. brevis* lower than $5.6 \times 10^4 \text{ cells l}^{-1}$ and the presence of other *Karenia* (13–17%) and diatoms (21–25%).

Zooplankton abundance was concentrated in three major zooplankton population centers (Fig. 6). Zooplankton population center 1 (P1)

was coincident with the chlorophyll *a* density area nearest to shore (Fig. 5), where *K. brevis* concentration exceeded $9 \times 10^5 \text{ cells l}^{-1}$ in a mixed assemblage. Primary contributors to total zooplankton abundance were typical coastal genera: *Acartia*, *Oithona*, *Paracalanidae*, *Corycaeus*, larvaceans, and cirriped larvae (Fig. 7). Zooplankton population center 2 (P2) was located between high chlorophyll *a* areas 2 and 3. The phytoplankton assemblage here consisted of low concentrations of *K. brevis* ($1.7 \times 10^3 \text{ cells l}^{-1}$) and other dinoflagellates and diatoms. Primary contributors to zooplankton abundance were *Temora* and *Oithona*. Zooplankton population center 3 (P3) was coincident with chlorophyll *a* density area 4, where concentrations of *K. brevis* were lower than $5.6 \times 10^4 \text{ cells l}^{-1}$ and other dinoflagellates and diatoms were present. Primary contributors to total zooplankton abundance were *Centropages*, *Corycaeus*, and *Paracalanidae*.

Three areas of low zooplankton abundance were synchronous with high *K. brevis* concentration areas (Fig. 6). Area 1 (A1) coincided with chlorophyll *a* density area 2, where concentrations of *K. brevis* exceeded $1 \times 10^6 \text{ cells l}^{-1}$. Area 2 (A2) coincided with the surface waters west of the salinity front. East of the salinity front, population centers of all taxa were found away from the high *K. brevis* cell counts at the surface. Area 3 (A3) coincided with the only monospecific portion of the bloom, and occurred at transect kilometer 47 and 13 m depth, where the *K. brevis* concentration was a low $6 \times 10^3 \text{ cells l}^{-1}$. Abundances of *Centropages*, *Paracalanidae*, and *Temora* were all reduced in this area. *Corycaeus*

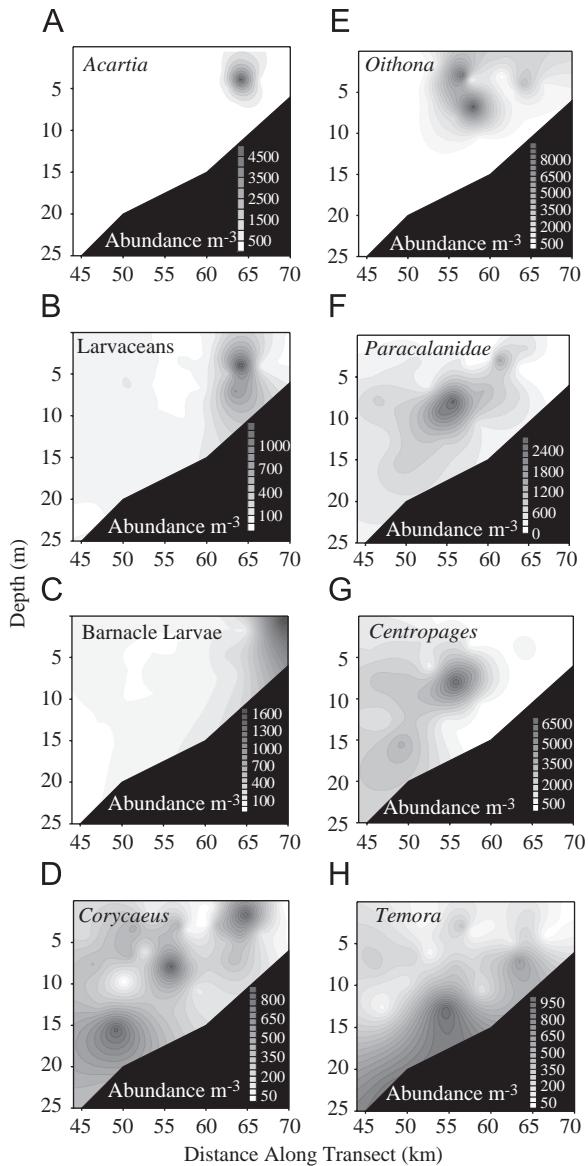


Fig. 7. Major taxa contributing to zooplankton total abundance in November 2001. (A) *Acartia*, (B) Larvaceans, (C) Barnacle larvae, (D) *Corycaeus*, (E) *Oithona*, (F) *Paracalanidae*, (G) *Centropages*, and (H) *Temora*.

abundance was also reduced in comparison to areas immediately adjoining the monospecific patch.

4. Discussion

4.1. Community composition—comparison of bloom and non-bloom stations

The zooplankton community composition found at the 5-m isobath for non-red tide stations is

consistent with other observations on the Florida shelf (King, 1950; Hopkins, 1966, 1977; Weiss, 1978; Minello, 1980; Squires, 1984; Sutton et al., 2001). *P. quasimodo*, *C. velificatus*, *C. amazonicus*, *E. acutifrons*, and *O. dioica* are typical of zooplankton assemblages on the Florida shelf (Weiss, 1978; Hopkins, 1977; Squires, 1984; Minello, 1980; Sutton et al., 2001), while the poecilostomatoid copepod *C. americanus* is more abundant at coastal stations than within estuaries (Hopkins, 1977; Weiss, 1978; Minello, 1980). Both *P. crassirostris* and *O. colcarva* are dominant in WFS estuaries, and can also be found in higher salinity areas (Hopkins, 1966; Weiss, 1978; Minello, 1980; Squires 1984; Hopkins and Lancroft, 1984).

Five species (*E. chierchiaie*, *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). The pelagic ostracod *E. cheierchaie* is typically associated with offshore water masses (Minello, 1980; Sutton et al., 2001).

4.2. Effect of *K. brevis* concentration on zooplankton abundance

Many species of coastal zooplankton were present during *K. brevis* blooms. Some species were routinely found within high-concentration areas of the *K. brevis* blooms, while others were found only in the lower concentration portions of the bloom. *T. turbinata* was found only twice during the sampling period. In both cases, the *K. brevis* bloom was nearly monospecific. *C. velificatus* was present only once, when bloom concentrations exceeded $5 \times 10^6 \text{ cell l}^{-1}$ and the *K. brevis* bloom was nearly monospecific. Pelecypod larvae were found in very high concentrations in blooms that were over $1 \times 10^6 \text{ cells l}^{-1}$. Also found within the densest blooms were cirriped larvae, *O. colcarva*, *O. dioica*, and *P. crassirostris*. At intermediate and lower concentrations, species present included *O. colcarva*, *P. crassirostris*, *O. dioica*, *A. tonsa*, decapod larvae, *E. tergestina*, *E. acutifrons*, and cirriped larvae.

Three zooplankton species (*C. americanus*, *P. avirostris*, and *E. acutifrons*) had reduced abundance in all *K. brevis* blooms, while 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 was also numerically dominant in 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. In November 2001, where identification was only made to genus or taxa level, the most abundant taxa near shore were Larvaceans, Acartia, Cirriped larvae, Oithona, Corycaeus, Paracalanidae, and Temora.

4.3. November 2001 HyCODE cruise

The zooplankton population centers present in November 2001 were offset from two chlorophyll areas associated with high *K. brevis* concentrations. Nearer to shore, zooplankton were present in a third *K. brevis* patch, but that portion of the bloom was associated with low concentration of *K. brevis* and high diatom concentrations. Of the seven taxa indicated earlier as being present consistently within *K. brevis* blooms, four were found within the high chlorophyll area near to shore, including *Acartia*, larvaceans, *Oithona*, and *Paracalanidae*.

Two genera, *Temora* and *Oithona*, were found between high chlorophyll *K. brevis* patches near the surface. The concentration of *K. brevis* in this zooplankton population center was much lower than that found in surrounding areas (17 and 55×10^3 cells l⁻¹), suggesting that both genera may have been avoiding the high concentration areas. However, patchiness of zooplankton distribution cannot be ruled out as an explanation for this distribution pattern.

Offshore, most taxa were found away from areas that had high concentrations of *K. brevis*. The taxa found outside the bloom areas included *Paracalanidae*, *Centropages*, some population centers of *Temora*, and *Corycaeus*.

5. Conclusions

The objective of this study was to determine perturbations to normal zooplankton community compositions within *K. brevis* blooms. Only one *K. brevis* bloom station was statistically indistinguishable from non-bloom stations. The remaining stations differed significantly from non-bloom stations in abundance or community composition. Although no single response by the zooplankton community was evident, some consistencies between

bloom stations occurred, including decreased abundance of three important WFS coastal species, *C. americanus*, *P. avirostris*, and *E. acutifrons*, and the numerical dominance by *A. tonsa*, *C. velificatus*, *T. turbinata*, *E. tergestina*, *O. colcarva*, *O. dioica*, and *P. crassirostris*. Of these, only *T. turbinata* and *E. tergestina* were not major contributors to normal WFS zooplankton assemblages at the 5-m isobath.

Offshore, areas with low numbers of zooplankton were coincident with high concentrations and monospecific areas of *K. brevis* blooms. However, in lower concentration areas of the bloom where the phytoplankton assemblage was mixed, high abundances of certain zooplankton genera were present, including *Oithona*, *Temora*, *Acartia*, and near shore populations of *Corycaeus* and *Paracalanidae*.

Acknowledgments

Funding was provided by ECOHAB Florida (NOAA/ECOHAB NA96P00084 and USEPA/ECOHAB CR826792-01-0), Office of Naval Research (N000149615024 and N000149910212), the National Science Foundation (NSF OCE 0095970), and the Florida Fish and Wildlife Conservation Commission. The USF College of Marine Science Murtagh Fellowship provided additional funding. Thanks is also extended to the Florida Institute of Oceanography, and the crew and scientific staff of the R/V *Suncoaster* and the R/V *Bellows*.

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