

Biodiversity and Conservation

December 2009, Volume 18 (14), Pages 3759-3784

<http://dx.doi.org/10.1007/s10531-009-9678-3>

© 2009 Springer. Part of Springer Science+Business Media

Archimer, archive institutionnelle de l'Ifremer

<http://www.ifremer.fr/docelec/>The original publication is available at <http://www.springerlink.com>**Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf**Stanislas Dubois^{1,2,3,*}, Carey G. Gelpi Jr.¹, Richard E. Condrey¹, Mark A. Grippo² and John W. Fleeger²¹ Department of Oceanography and Coastal Sciences, Louisiana State University, Energy Coast and Environment Building, Baton Rouge, LA 70803, USA² Department of Biological Sciences, Louisiana State University, 202 Life Sciences Building, Baton Rouge, LA 70803-1715, USA³ Present address : IFREMER, DYNECO Ecologie Benthique, Technopole de Brest-Iroise, BP 70, 29280 Plouzané, France*: Corresponding author : Dubois S., phone: +33 2 98 22 49 18, fax: +33 2 98 22 45 48 25, email address : sdubois@ifremer.fr**Abstract:**

Along the Louisiana, USA continental shelf, sandy shoals are shallow, possibly oxygen-rich “islands” surrounded by deeper muddy deposits prone to hypoxia. Shoals also contain significant quantities of fine sand that may be mined in the future for coastal restoration. The ecological role of shoals remains poorly understood and we hypothesized that shoals provide critical habitat for benthic invertebrates. Using Ship Shoal as a model system, we assessed the diversity and structure of macrobenthic assemblages and how community structure varies with season and environmental parameters. High biomass (averaging 26.7 g m⁻²) and high diversity (161 species) of macrobenthos was found in 2006. Polychaetes (45%—72 species) and crustaceans comprised most of the species (28%—46 species); spionids and amphipods dominated the polychaete and crustacean groups respectively, both in terms of number of species and abundances. Sharp decreases in diversity, abundance and biomass occurred from spring to autumn. Species diversity and total abundance significantly increased with decreasing sediment grain size and increasing bottom water dissolved oxygen. Across seasons, mole crabs *Albunea paretii* and amphioxus *Branchiostoma floridae* typified the community and contributed most of the biomass. The polychaetes *Nephtys simoni*, *Neanthes micromma*, *Dispio uncinata*, *Mediomastus californiensis* and *Magelona* sp. A, the amphipod *Acanthohaurorius* sp. A and the burrowing shrimp *Ogyrides alphaerostris* also contributed to variation in community composition. Cluster analyses quantified seasonal variation, mainly based on sharp decreases in abundance, as well as spatial differences in species composition oriented along both east–west and north–south gradients. Variation in benthic assemblages was correlated with water depth and sediment characteristics (mean grain size and percentage of gravel-sized shell debris). We conclude that Ship Shoal is an unrecognized biodiversity hotspot and a hypoxia refuge compared to the immediate surrounding area where the benthic community is affected by seasonal hypoxia events and we discuss how sand-mining may influence this community.

Keywords: Biodiversity hotspot - Continental shelf - Gulf of Mexico - Hypoxia refuge - Louisiana - Sand bank - Shallow habitat

Introduction

Recently, sandy shoals of the US continental shelf have received increased attention because they have been identified as potential exploitable sand deposits (Drucker et al. 2004). This is especially true for the Louisiana coast where a single shoal (Ship Shoal) is considered one of the largest sand sources in the Gulf of Mexico (Drucker et al. 2004), containing 1.6 billion cubic yards of fine sand intended for beach reinforcement and coastal stabilization projects designed to prevent coastal erosion due to storm damages and prevent wetland loss due to anthropogenic disturbances that induce sea-level rise (Michel et al. 2001). This increased interest in shoals highlights the observation that the benthic and nektonic composition of shoals is less well studied than other continental shelf environments (Brooks et al. 2006). Faunal composition may be important to predicting recovery after sand mining and to understanding ecological relationships on shoals. For example, benthic invertebrates are directly related to the sediment they inhabit (Gray 1974; Snelgrove and Butman 1994), and any sand-mining activity or associated human-related change in sediment features may negatively affect the resident community and consequently impact trophic relationships

1 within these communities. It is thus of primary importance to identify and characterize
2 75 macroinfaunal benthic assemblages associated with potential sand-mining sites.
3

4
5 The macrobenthos of some Louisiana – Texas shoals (i.e. Sabine and Healds Shoals)
6
7 have been recently investigated (Cheung et al. 2006) but these studies and a recent
8
9 macrobenthic survey of Louisiana in-shore and off-shore waters (Baustian 2005) did not
10
11 include Ship Shoal, partly because its shallow depth has discouraged access by large research
12
13 vessels. A habitat specific survey of the epifauna and fish fauna of several sandbanks off the
14 80 Welsh coast (UK) revealed that sandbanks were characterized by a unique (although low
15
16 diverse) epifauna and fish assemblages (Kaiser et al. 2004). But the authors also stated that
17
18 sandbanks are difficult habitats to sample and may have been overlooked by biologists. Ship
19
20 Shoal's benthic species assemblages might be used as a food source for numerous fishes or
21
22 large crustaceans that permanently or temporarily forage on this shoal, as suggested by
23
24 Thouzeau et al. (1991) for the Georges Bank, northeast coast of the United States. In
25
26 addition, because of its location in the north central Gulf of Mexico, and unlike the
27 85 continental shelf off of western Florida, Ship Shoal is surrounded by muddy soft-bottoms
28
29 affected by seasonal hypoxia events that causes drastic decreases in abundances of benthic
30
31 species inhabiting this “dead zone” (Rabalais et al. 1994; Justić et al. 1996). It is unknown
32
33 whether benthic populations living on Ship Shoal are affected by hypoxic events. It is
34
35 possible that Ship Shoal may serve as an hypoxia refuge for benthic populations or as a faunal
36
37 reserve from which larvae, juveniles and/or adults may disperse and recolonize the
38
39 90 surrounding hypoxic area when normoxia returns.
40
41
42
43
44
45
46
47
48
49

50
51 95 The overall objectives for this study are thus to better understand the potential role
52
53 Ship Shoal plays in the Louisiana's coastal ecosystem, and to address the potential effects of
54
55 sand-mining on the benthic community. Our approach is to describe spatial and seasonal
56
57 variations in diversity and structure of macrobenthic assemblages associated with Ship Shoal
58
59
60
61
62
63
64
65

1
2 100 over a relatively fine-scale latitudinal and longitudinal gradient and to link community
3 patterns with variation in environmental parameters.

4
5 On a broader scale, there is an increasing awareness of the ecological implications of
6 sand and gravel mining from land, river, and coastal-ocean systems (i.e. Peckenham et al.
7 2009; Pempel and Church 2009; Zeppelini et al. 2009). Though sand mining has historically
8 been associated with road and building construction, it has become one of the preferred
9 approaches in beach nourishment projects, despite the likelihood of broad ecological impacts
10 on both the extracted and receiving sites and the ephemeral beach-restoration expectations
11 (Defeo et al. 2009). Demands on coastal-ocean sand supplies are likely to increase as human
12 occupation of the coastal zone and sea level continue to rise, and land-based sand-supplies
13 decline. Lessons learned from careful studies of the impacts of current coastal-ocean sand
14 105 mining operations could prove valuable as extractions of other marine minerals begin and
15 increase (e.g., Rona 2008).
16
17
18
19
20
21
22
23
24
25
26
27 110
28
29
30
31
32
33
34
35

36 **Material and methods**

37 38 39 115 *Study site*

40
41
42
43
44
45
46 Samples were taken from 21 stations on Ship Shoal, located in the north-central Gulf
47 of Mexico approximately 20 km off-shore from Terrebonne Bay and Isles Dernieres,
48 Louisiana (28°54.092N , 91°00.989 W). The shape of this shoal is elongated, parallel to the
49 shore. It spans a 50 km distance along the east-west dimension and 1 to 10 km along the
50 north-south dimension (Figure 1). Based on depth contours available on existing sea charts,
51 120 stations were chosen according to an east-west distribution with three main north-south
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2 125 (latitude) transects, one in the east (stations 15-16-17), one in the west (stations 23-22-21),
3 and one in the middle (stations 24-25-26). Other stations were distributed along the spine
4 (longitude) of this sandy shoal in three main groups: east stations from station 18 to station
5 13, middle stations from station 12 to station 09 and 10, and west stations from stations 07
6 and 08 to station 01 and 19. The general bathymetry of the shoal is related to east-west and
7 north-south gradients: the western region is the shallowest (ca. 4 m) and the depth increase
8 toward the east (ca. 10 m). A north-south transect across the shoal shows that the northern
9 edge is well-defined with sharp slope while the slope of the southern edge is more gentle with
10 depth increasing slightly from the spine – i.e. middle – of the shoal toward the south, making
11 the definition of the southern edge difficult to discern.
12
13
14 130
15
16
17
18
19
20
21
22
23
24
25

26 135 *Field sampling*
27
28
29
30

31 Samples were collected during three cruises in 2006 using the Louisiana Universities
32 Marine Consortium (LUMCON) Research Vessel “ACADIANA”: May (21st to 24th; Spring),
33 August (19th to 21st; Summer) and October the 30th and November the 1st (Autumn). Because
34 of inclement weather, only 16 stations were sampled in October. Macrofauna was collected
35 using a GOMEX box corer which has been shown to efficiently sample muddy and very fine
36 to fine sandy sediments (Boland and Rowe 1991). Three replicates of 900 cm² (30 x 30 cm)
37 were taken at each station, for each of the three cruises. Subsamples for sediment analysis
38 and chlorophyll *a* sediment content were extracted from each box core with a 3 cm diameter
39 140 cylinder over ca. 5 cm depth. Sediment samples were frozen until ready for analysis. Water
40 characteristics (temperature, salinity, dissolved oxygen = DO) were monitored ca. 1 m above
41 the bottom.
42
43
44
45
46
47
48
49
50
51 145
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 Box core samples were sieved at sea on a 500 μm sieve using seawater. Retained
2 organisms, including sediment, was fixed and preserved in 5% buffered formalin and returned
3
4
5 150 to the laboratory.
6
7

8 9 *Laboratory analysis* 10

11
12
13
14 In the laboratory, macroinvertebrates were sorted to major taxon (i.e. polychaetes,
15 mollusks and others) and transferred to 70% ethanol. Bivalve and gastropod shells were
16
17 155 examined for the presence of tissue. Wet weight of each group (shells included for mollusks
18
19 and crustaceans) was taken before all individuals were sorted, identified to the species level
20
21
22 (or the lowest practical taxonomic level) and enumerated. Species were classified into five
23
24 feeding-guilds: (1) suspension-feeders, (2) surface deposit-feeders, (3) interface feeders (i.e.
25
26
27 species which can switch from suspension-feeding to surface deposit-feeding), (4) sub-surface
28
29 160 deposit-feeders, (5) predators or scavengers/detritivores, based on taxonomic affiliation of
30
31 families after Fauchald and Jumars (1979) for polychaetes, Yonge and Thompson (1976) for
32
33 mollusks, Lecroy (2000) for amphipod crustaceans and Pechenik (2005) for other taxonomic
34
35 groups. Some nematodes and planktonic copepods were retained but were excluded from
36
37
38
39
40
41 165 analysis following Rzeznik-Orignac et al. (2004).
42

43
44 Sediment particle size analysis was conducted for each station. Sediment samples
45
46 were washed with distilled water through a 63 μm sieve to separate sand from silt and clay
47
48 and to dissolve NaCl particles that may agglomerate smaller particles. The fraction <63 μm
49
50 was collected in a bowl with water and allowed to settle for 72 hours. The water was then
51
52
53 170 siphoned and the silt/clay fraction dried to constant weight in an oven at 60°C, then weighed.
54
55 The sand fraction was dried to constant weight in an oven at 60°C, and placed on a Ro-Tap
56
57 sieve shaker for 3 min (21 sieves from 2 mm to 63 μm mesh size with $\frac{1}{2} \Phi$ intervals). The
58
59
60
61
62
63
64
65

1 fraction retained on a 2 mm mesh size is the gravel fraction (consisting mostly of shell
2 debris). The average particle size and the sorting index σ were determined using the Folk and
3
4 175 Ward (1957) method. Results were processed by the Gradistat software (Blott and Pye 2001).
5
6
7
8

9 *Statistical analysis*

10
11
12
13
14 Data were analyzed using univariate and multivariate methods. Macrofauna species
15
16 180 diversity was estimated using species richness and Hill's (1973) heterogeneity of diversity
17
18 indices: $N1 = \exp(H')$, where H' is Shannon-Wiener diversity (\log_e - Shannon 1948); and $N2$
19
20 = $1/SI$, where SI is Simpson's index (Simpson 1949); $N1$ is sensitive to the number of
21
22 medium-density species whereas $N2$ is sensitive to the number of very abundant species
23
24 (Whittaker 1972). Species richness – i.e. the number of different species – is also called $N0$,
25
26 185 consistently with $N1$ and $N2$ indices. These indices are well suited to the analysis of diversity
27
28 of benthic macrofauna communities and, together with the equitability index J' (Sheldon
29
30 1969), are recommended by Gray (2000) to measure heterogeneity of marine coastal
31
32 diversity.
33
34
35
36
37

38
39 One-way ANOVA was used to test for geographic and seasonal trends in species
40
41 190 richness, diversity indices, and species abundances. Cochran's test was used to determine
42
43 homogeneity of variances and, if necessary, data were $\log_e (x+1)$ transformed. When
44
45 parametric ANOVA testing was acceptable, the Student-Newman-Keuls (SNK) test was used
46
47 for multiple comparisons. As recommended by Hsu (1996), post-hoc comparisons were
48
49 performed using Tukey HSD tests. A significance level of $p < 0.05$ was used in all tests.
50
51

52
53 195 Differences in the composition of the macrofaunal assemblages between sites were
54
55 determined using non-metric multidimensional scaling (nMDS) and cluster analysis (group
56
57 average mode), followed methods of Clarke and Warwick (1994), using the Primer package
58
59
60
61
62
63
64
65

(Clarke and Gorley 2001). Unstandardized multivariate data were $\log_e(1+x)$ transformed to downweigh the importance of the very abundant species, and similarity matrices were calculated with the Bray-Curtis similarity index. The statistical significance of differences among sites was assessed using analysis of similarities (ANOSIM), a non-metric method based on randomization of rank-similarities among all samples and multiple pair-wise comparisons (Clarke 1993). To build the matrix, species occurring in less than 5% of the samples, and with only one individual, were excluded. To identify within two different sample groups which species primarily accounted for the observed assemblage differences, SIMPER (similarity percentage) routines were performed using a decomposition of Bray-Curtis dissimilarity on $\log_e(x+1)$ transformed abundance data. Species were listed in decreasing order of their importance in discriminating the two sets of samples (Clarke and Gorley 2001).

Two approaches were use to link environmental parameters - i.e. depth (m), sediment grain size (mean grain-size, sorting index), silt/clay and gravel (%) content, bottom DO (mg L^{-1}) and chlorophyll *a* ($\text{mg Chl } a \text{ g sediment}^{-1}$) sediment content - with the Ship Shoal macrobenthic community: (1) pair-wise regressions were used between environmental parameters and descriptors of benthic community (*i.e.* N0, N1, N2, taxonomic biomass or mean species abundances) to explore if the variation in one environmental parameter followed the variation in species richness and (2) multivariate BIOENV procedures (see Clarke and Ainsworth 1993 for details) were used to determine how spatial patterns in multivariate invertebrate community structure were related to spatial patterns in multivariate environmental structure, i.e. to what extent observed biological patterns fit with variations in environmental parameters.

Results

225 *General description*

1
 2
 3
 4
 5
 6
 7
 8
 9
 10 A total of 29331 macrofaunal individuals in 161 species were collected from Ship
 11 Shoal during the three cruises (see Appendix A). Polychaetes represented 45% (72 species)
 12 of the total species number, following by crustaceans (28%, 46 species) and mollusks (17%,
 13
 14 27 species). Other taxa (nemerteans, sipunculids, anthozoans etc.) represented 10% (16
 15
 16
 17 230 species). Global species richness exhibited a sharp decrease from spring to autumn, together
 18
 19 with the mean species richness ($p < 10^{-5}$). Except for a significant difference between N1 in
 20
 21 autumn and N1 in spring or summer ($p < 0.003$), heterogeneity indices and equitability did
 22
 23 not exhibit seasonal variation (Table 1). In terms of abundances, polychaetes and crustaceans
 24
 25
 26
 27
 28
 29 235 predominated the Ship Shoal community with mean abundances between 1500 and 2000
 30
 31 individuals m^{-2} in spring (Figure 2). Within these two taxonomic groups, spionids and
 32
 33 amphipods were respectively the largest component, representing more than 50% of
 34
 35 individual polychaetes and 80% of the crustaceans. *Amphioxus Branchistoma floridae*
 36
 37 (Cephalochordata) abundance peaked in summer. Community mean biomass (wet weight)
 38
 39 followed the same pattern, from 40.55 $g m^{-2}$ (SE = 5.22) in spring to 21.77 $g m^{-2}$ (SE = 2.88)
 40
 41 240 in summer and 15.44 $g m^{-2}$ (SE = 3.22) in autumn (Figure 3). While this decrease in biomass
 42
 43 occurred throughout the year for polychaetes, it was not significant between summer and
 44
 45 autumn for mollusks or between spring and summer for other taxa.
 46
 47
 48
 49
 50

51 In terms of the measured environmental parameters, Ship Shoal constituted a relatively
 52
 53 245 homogenous sandy habitat (Table 3). Sediment analysis revealed that the sediment in all 21
 54
 55 stations was well or very well sorted and unimodal. Sediment is classified as sand or slightly
 56
 57 gravelly sand for the most eastern stations (stations 14 to 18). Silt/clay (i.e. particles < 63
 58
 59
 60
 61
 62
 63
 64
 65

1
2
3
4
5 250
6
7
8
9
10
11
12
13
14
15
16
17 255
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41 265
42
43
44
45
46
47
48
49
50
51
52
53
54 270
55
56
57
58
59
60
61
62
63
64
65

μm) and gravel (i.e. particles $> 2 \text{ mm}$ - primarily shell fragments) were very low at each station. Mean grain size, smaller in the western part of the shoal and larger in the eastern, was significantly inversely correlated in spring with N0 ($r = 0.722$; $p < 0.001$), N1 ($r = 0.477$; $p < 0.05$), N2 ($r = 0.421$; $p < 0.05$) and species abundances ($r = 0.601$; $p < 0.01$). The DO at the sediment surface was also correlated with N0 ($r = 0.596$; $p < 0.01$) and species abundances ($r = 0.670$; $p < 0.01$) in spring. Dissolved oxygen and sediment grain size were autocorrelated ($r = 0.569$; $p < 0.01$). No significant relation was found between environmental parameters and any diversity indices in summer or autumn.

19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41 265
42
43
44
45
46
47
48
49
50
51
52
53
54 270
55
56
57
58
59
60
61
62
63
64
65

Significant differences in diversity and abundances between western, middle and eastern stations of Ship Shoal, as well as between northern and southern stations (ANOVA; Table 2) were observed. More precisely, species richness was significantly higher in the southernmost stations of the shoal in spring ($p = 0.032$), summer ($p = 0.002$) and autumn ($p = 0.030$) than in the middle or in the northernmost stations. Spring variations in global SR (i.e. total number of species for one station) and mean SR within the three transects across the shoal showed that both global and mean SR were higher at the southernmost stations (i.e. 17, 26 and 21) (Figure 4). The same pattern was indicated in summer and autumn. Mean species abundances were significantly higher in the southern edge in spring ($p = 0.018$), summer ($p < 10^{-6}$) and autumn ($p < 1.16 \cdot 10^{-4}$) but were also significantly higher in the western region in spring ($p = 0.004$), summer ($p < 10^{-6}$) and autumn ($p = 1.13 \cdot 10^{-4}$) than in the central or in the eastern region of the shoal. N1 and N2 indices exhibited more seasonal differences; in spring, both indices were significantly higher toward the west (N1, $p = 7.2 \cdot 10^{-5}$; N2, $p = 4.0 \cdot 10^{-4}$) and the southern edge (N1, $p = 0.012$; N2, $p = 0.029$) but both indices only exhibited a significant north-south gradient in summer (N1, $p = 6 \cdot 10^{-4}$; N2, $p = 4.4 \cdot 10^{-6}$) and no significant variation in autumn. While total biomass showed no significant variation, polychaete biomass was

significantly higher in the west and south in spring ($p = 0.013$ and $p < 10^{-7}$, respectively) and in summer ($p = 0.026$ and $p = 3 \cdot 10^{-4}$, respectively) (Table 2).

275 *Macrofaunal benthic assemblages*

Annual variability

Cluster analysis of the macrofauna abundance data showed a strong seasonal effect in sample composition (Figure 5), supported by ANOSIM (global $R = 0.684$; $p < 0.001$; Table 4). SIMPER results (Table 4) comparing seasons showed that a small number of species contributed most to the dissimilarity among seasons: the amphipods *Acanthohaustorius* sp.A and *Protohaustorius bousfieldi*, the polychaetes *Spiophanes bombyx* and *Dispio uncinata*, and the amphioxus *Branchiostoma floridae*. These species had a very high frequency of occurrence in samples each season but exhibited strong decreases in abundances, especially between spring and summer, with the exception of the amphioxus *B. floridae* which was more abundant in summer. Many species contributed to a smaller extent to the discrimination between spring and other seasons because they had low abundances and high frequency of occurrence in spring but occurred only in a few stations in summer and autumn. This was mainly the case for polychaetes such as *Scolelepis texana*, *S. squamata*, *Paraprionospio pinnata*, *Spiochaetopterus costarum*, *Phyllodoce mucosa*. In addition to *B. floridae*, a few species with a high frequency of occurrence were more abundant in summer, such as the polychaetes *Thalenessa spinosa* and *Eupolymnia nebulosa* or the nemertean *Micrura leidyi*. The polychaete *Paramphimone* sp.B and the shrimp *Acetes americanus* occurred almost exclusively in autumn. A few species, the polychaetes *Neanthes micromma* and *Nephtys simoni*, the gastropod *Oliva sayana*, the hermit crab *Pagurus annulipes* and the mole crab

Albunea paretii, did not vary through the spring, summer or autumn with a high frequency of occurrence throughout.

Spatial distribution in spring, summer and autumn

Cluster analyses also showed a clear difference in species assemblages among samples from the same season (Figure 6). SIMPER analyses revealed that in spring (global R = 0.564; $p < 0.001$) and summer (global R = 0.323; $p < 0.001$), samples from eastern, middle and western regions differed from each other mainly because of changes in species abundances. SIMPER also showed that discrepancies in species composition were predominately found between the eastern and the rest of the shoal, as the middle and western regions were similar in species composition. The MDS stress around 0.2 gives a useful 2-dimensional picture but an increase in MDS stress from 0.16 to 0.23 between spring and autumn is mainly due to the replicates without amphioxus *Branchiostoma floridae* that contributed for the largest part to the similarity between each station for summer and autumn.

In spring, the amphipod *Acanthohautorius* sp.A and spionids *Spiophanes bombyx* and *Dispio uncinata* contributed most to the dissimilarity among regions but also most to the similarity within each region. Amphipod species contributed the most to changes in species composition across the whole of the study area: *Protohaustorius bousfieldi* occurred almost only in western stations, while *Hartmanodes ranyei*, *Microprotopus ranyei* and *Ampelisca* sp.C were more abundant in the middle and western stations.

In summer, the amphioxus *Branchiostoma floridae*, the amphipod *Acanthohautorius* sp.A and the polychaete *Prionospio (Apoprionospio) pygmaea* contributed most to the dissimilarity between regions but also most to the similarity within each region. Polychaete species contributed most to the discrimination between groups: *Euplolymnia nebulosa*,

1 *Scoloplos* sp.B, *Tharyx annulosus* dominated abundances in the western stations, *Thalenessa*
 2 *spinosa* was more abundant in the middle region and *Nereis falsa*, *Neanthes micromma* and
 3
 4 *Travisia hobsonae* in the eastern region.
 5

6
 7 325 In autumn, similarity indices decreased, as displayed by the greater scatter in the MDS
 8
 9 plots of stations (Figure 6). This is due to larger discrepancies between species composition
 10
 11 of the samples between and within individual stations. As in summer, the amphioxus *B.*
 12
 13 *floridae* and the amphipod *Acanthohautorius* sp.A were the two structuring species. Also, *P.*
 14
 15 *bousfieldi* occurred mostly in the western stations, and the polychaetes *Magelona* sp.A and
 16
 17 *Magelona* sp.H occurred mostly in the northern and in the southern stations, respectively.
 18
 19 330
 20

21
 22 Though east-west changes were found, a high similarity threshold was also found
 23
 24 between all northern and all southern stations from the three transects (46.33%, 36.77% and
 25
 26 29.84%, 34.14% for spring and summer respectively, Figure 6). While this result was
 27
 28 supported by diversity indices, this was also due to species that exhibited higher abundances
 29
 30 in the southern stations, such as the polychaetes *Owenia fusiformis*, *Mediomastus*
 31
 32 335 *californiensis*, *Tharyx annulosus*, *Magelona* sp.H, *Spiophanes bombyx*, *Scoloplos* sp.B.,
 33
 34 *Paraprionospio pinnata* or higher abundances in the northern stations such as the polychaetes
 35
 36 *Nephtys simoni* and *Magelona* sp.A or the cumaceans *Oxyurostylis smithi* and *Cyclaspis*
 37
 38 *varians*.
 39
 40
 41
 42

43 340 BIOENV procedures showed that variations in macrobenthic assemblages were best
 44
 45 matched by a combination of three or four environmental variables in spring, that were depth /
 46
 47 grain size / % gravel (Spearman correlation = 0.687) or depth / grain size / % gravel / DO
 48
 49 (Spearman correlation = 0.682). In summer, depth provided the best match (Spearman
 50
 51 correlation = 0.505). No significant correlations were found in autumn.
 52
 53
 54
 55

56 345
 57
 58 **3.3. Feeding guilds**
 59
 60
 61
 62
 63
 64
 65

1
2 Species that are able to switch between suspension-feeding and surface deposit-
3
4 feeding dominated the trophic guild in spring (47%), and exhibited a decrease in summer
5
6 (31%) and autumn (30%) (Figure 7). True suspension-feeders almost disappeared in autumn
7 350 while the dominance of species relying on deposit-feeding varied but did not decrease. Only
8
9 the dominance of predators/scavengers increased with seasons, from 8% in spring to 30% in
10
11 the dominance of predators/scavengers increased with seasons, from 8% in spring to 30% in
12
13 autumn. In spring, abundance in sub-surface deposit-feeders were positively correlated with
14
15 water depth ($r = 0.545$; $p < 0.01$) and % silt/clay ($r = 0.524$; $p < 0.01$) but negatively
16
17 correlated with sediment mean grain size ($r = 0.471$; $p < 0.05$). On the contrary, abundance of
18
19 355 surface deposit-feeders was negatively correlated with water depth ($r = 0.747$; $p < 0.001$) and
20
21 % silt/clay ($r = 0.538$; $p < 0.01$). In summer, abundance in sub-surface deposit-feeders was
22
23 positively correlated with water depth ($r = 0.451$; $p < 0.05$) and abundance in surface deposit-
24
25 feeders was negatively correlated with depth ($r = 0.427$; $p < 0.05$). Abundance in suspension-
26
27 feeders or interface-feeders was positively correlated with chlorophyll *a* sediment content ($r =$
28
29 360 0.523 ; $p < 0.05$).
30
31
32
33
34
35
36
37
38
39
40

41 Discussion

42
43 365
44
45 Sandbanks and sandy shoals occur on continental shelves, in coastal embayments and
46
47 in estuaries throughout the world. Their associated mineral deposits represent potentially
48
49 valuable resources to help mitigate coastal erosion and to supply the raw material for beach
50
51 reinforcement and coastal stabilization projects (Michel et al. 2001). Demands on coastal-
52
53 ocean sand supplies are likely to increase as both human occupation of the coastal zone and
54
55 370 sea level continues to rise, and as land-based sand-supplies decline. Although a large number
56
57
58
59
60
61
62
63
64
65

1 of studies have examined sandbank formation, modeled sediment transport, and evaluated the
2 importance of shoals to local hydrodynamic conditions (e.g. Berthot and Pattiaratchi 2004),
3
4 few ecological studies have examined the functional value of these high-relief structures in
5
6
7 375 their ecosystems, especially in terms of biodiversity and associated ecological services. Even
8
9
10 so there is a growing awareness of the potential impact of sand and gravel mining, to both the
11
12 extracted and receiving sites, in coastal-ocean systems (i.e. Defeo et al. 2009; Peckenham et
13
14 al. 2009; Pempel and Church 2009; Zeppelini et al. 2009), and more studies are needed to aid
15
16 policy decisions. Finally, lessons learned from careful studies of the impacts of current
17
18
19 380 coastal-ocean sand mining operations could prove valuable as extractions of other marine
20
21 minerals begin and increase (e.g. Rona 2008).
22
23
24
25

26 *The Ship Shoal macrobenthic assemblage*

27
28
29
30

31 385 Ship Shoal is a large, discrete formation composed of fine to very fine sand (ca. 150
32
33 μm diameter) about 25 km offshore from the Louisiana coast. Environmental gradients of
34
35 water depth (increasing depth toward the east) and granulometry (increasing mean grain size
36
37 toward the east) characterize the Shoal. In terms of benthic macroinvertebrates, our results
38
39 suggest that Ship Shoal represents a faunally distinct habitat type in a transition between in-
40
41 shore and off-shore habitats. Species composition revealed differences between east and west
42
43 390 areas, along with differences between northern and southern edges of the shoal. Ship Shoal
44
45 hosted a unique combination of macroinfauna composed of species commonly found typically
46
47 in the swash zone of sandy beach communities associated with the Mississippi and northwest
48
49 Florida seashore (e.g. *Leitoscoloplos fragilis*, *Scolelepis squamata*, *Dispia uncinata*)
50
51 (Rakocinski et al. 1998), or abundant in shallow enclosed bays of the northern Gulf of Mexico
52
53
54
55 395 (e.g. *Paraprionospio pinnata*, *Gyptis vittata*, *Notomastus latericeus*, *Mulinia lateralis*)
56
57
58
59
60
61
62
63
64
65

(Mannino and Montagna 1997; Montagna and Ritter 2006), as well as species typically found in muddy off-shore environments south of Terrebonne Bay, Louisiana (e.g. *Armandia maculata*, *Magelona* sp.H, *Tellina versicolor*, *Nassarius acutus*) (Baustian et al 2009). More generally, shoals exhibit a unique physical regime, leading to special hydrodynamic and sedimentary patterns and to distinct species assemblages. But the extent to which associated fauna is distinct from surrounding environments is poorly known (Kaiser et al. 2004).

A significant number of species not reported previously for the Louisiana continental shelf were found on Ship Shoal. Uebelacker and Johnson (1984) provided a distribution range of polychaete species occurring on a large portion of the outer continental shelf of the northern Gulf of Mexico, e.g. south Texas (Texas), central Louisiana (Louisiana) and Mississippi-Alabama-west Florida (Florida) outer shelves. Based on that comprehensive work, we report that 50% of the polychaete species found on Ship Shoal (35 species) were recorded either from the Florida continental shelf only (23 species) or from both the Texas and Florida continental shelves (12 species). Thus half of the Ship Shoal polychaete species had not been recorded for the Louisiana continental shelf. While most of these polychaete species had a low density and widely scattered distribution on Ship Shoal (e.g. *Streptosyllis pettiboneae*, *Myriowenia* sp.A, *Anaitides groenlandica*), a few species (*Phyllodoce mucosa*, *Thalenessa spinosa*, *Nereis falsa* or *Nephtys simoni*) exhibited high frequency of occurrence with low density (ca. 10 individual m⁻²).

The Ship Shoal community appears to be a melange of species. Among species found throughout the year, with a high frequency of occurrence, mole crabs *Albunea paretii* and amphioxus *Branchiostoma floridae* best typified the very fine-sand shoal community and comprised most of the biomass. In this *Albunea-Branchiostoma* community, defined based on the two ubiquitous species which constitute the majority of the biomass on the shoal, we typically found the polychaetes *Nephtys simoni*, *Neanthes micromma*, *Dispio uncinata* and

1
2
3
4
5
6
7 425 *Magelona* sp.A, the amphipod *Acanthohautorius* sp.A and the burrowing shrimp *Ogyrides*
8
9
10
11
12 *alphaerostris*. They constituted the basis of the sandy shoal community, which exhibited
13
14 variation according to seasons or according to on-shore or off-shore influences. As expected,
15
16 the shoal community is typified by species that are adapted to changes in hydrography and are
17
18 able to re-burrow rapidly when washed out of the sediment during a storm event. Moreover,
19
20 Nephtyid or Magelonid polychaetes distinguish the fauna of sandbanks in the North-Sea
21
22 (Vanosmael et al., 1982).
23
24

25
26
27
28
29
30
31
32 430 The occurrence of amphioxus (*Branchiostoma floridae*) has been reported in sandy-
33
34 shore macrobenthic community of barrier islands to the west of the Mississippi river (Hefley
35
36 and Shoemaker 1952; Rakocinski et al. 1998), but this is the first report of high abundances of
37
38 amphioxus (up to 1250 ind m⁻²) off the Louisiana coast. In the spring, most individuals were
39
40 large ovigerous females. In the summer, many juveniles were present, suggesting Ship Shoal
41
42 is a locally important habitat for reproduction and early summer recruitment. The findings
43
44 435 presented here strongly suggest that Ship Shoal in particular and Louisiana sandy shoals in
45
46 general play an important role in the marine landscape ecology of the northern Gulf of
47
48 Mexico, by aiding dispersal and gene flow of benthic species over large spatial scales. The
49
50 sediment characteristics of Ship Shoal are similar to that of the Florida shelf (Posey et al.
51
52 1998). In addition, a recent large-scale study of current circulation in the northern Gulf of
53
54 440 Mexico (Ohlmann and Niiler 2005) found a strong inter-regional connectivity, especially
55
56 during passage of tropical storms that allowed particles to cross the Florida-Louisiana shelf-
57
58 break and the Mississippi river outflow. Thus, Ship Shoal represents a suitable area along the
59
60 Louisiana coast for larvae to settle and for a diverse group of species adapted to life in fine
61
62 sand to survive and develop.
63
64

65
66
67
68
69
70
71
72 445 More locally, Ship Shoal may serve as a source pool for recruitment of benthic
73
74 invertebrate larvae and adults to surrounding areas affected by seasonal hypoxia. Powilleit
75

1 and Kube (1999) found rapid recolonization by adult benthic macrofauna from an undisturbed
2 shallow coastal area with high macrofauna density to an area moderately affected by hypoxia
3
4 in the Pomeranian Bay in the Southern Baltic Sea. Ship Shoal may provide the same function
5
6
7 450 as abundances of benthic invertebrates on the hypoxia affected areas of the Louisiana shelf
8
9 increase after hypoxia ends (Rabalais et al., 2001). In addition, a study designed to study
10
11 hyperbenthic (=suprabenthic) species assemblages of subtidal sandbanks in the North Sea,
12
13 Dewicke et al. (2003) hypothesized that sandbanks might also sustain nursery areas for
14
15 several fish and crustacean species. Molecular tools would be of primary interest in testing
16
17
18
19 455 hypotheses regarding gene flow and dispersal.
20
21
22
23
24
25

26 *Is Ship Shoal a diversity hotspot?*
27
28
29
30

31 460 Few authors have focused specifically on sandbanks, employing multiple collections
32
33 with quantitative sampling devices (Kaiser et al. 2004). In the present study, the overall
34
35 species richness of macrobenthos on Ship Shoal totaled 118 species (with a mean per sample
36
37 of 23.71 ± 1.05). Benthic assemblages over a large sampling area off the central coast of
38
39 Louisiana surrounding Ship Shoal showed that the mean species richness for summer was
40
41
42
43 465 19.1 ± 2.3 (Baustian et al. 2009). This investigation covered a much broader area (ca. 4000
44
45 km^2) than the present study (ca. 200 km^2) and encountered a greater habitat variety (muddy
46
47 substrata through gravelly soft-bottoms). One would thus expect the off-shoal species
48
49 richness to be comparatively much higher than Ship Shoal for a similar number of stations
50
51
52
53 (Rosenzweig 1995). A comparable study was conducted on the Kwinte Bank in the Belgian
54
55
56 470 coastal waters on the area where the sediment is composed of coarse to fine grained sand
57
58
59
60
61
62
63
64
65 (Vanosmael et al. 1982). The Kwinte Bank was found to be more specious than the

1 surrounding habitat composed of finer grained sediment and considered a “biogeographical
2 island” located within the transition zone between the coastal zone and open sea.
3

4
5 In addition, Baustian (2005) studied seasonal variation in macrobenthic community at
6
7 475 one particular site that typifies muddy soft-bottom environments surrounding Ship Shoal (ca.
8
9 10 km off Ship Shoal). This seasonal survey provides a relevant comparison of seasonal
10
11 patterns with the present study. It showed a similar decrease in species richness and
12
13 abundances from spring to autumn: mean SR ranged from 14 to 4 species between May and
14
15 October, while the range was 33 to 13 species for the same months in Ship Shoal sediments.
16
17
18
19 480 Thus, Ship Shoal appears to maintain a higher number of species than nearby locations on the
20
21 Louisiana shelf. Biodiversity in benthic communities is often linked with many
22
23 environmental factors, of which sediment characteristic is of primary importance (Gray
24
25 1974). Traditionally, infaunal species richness is lower in muddy communities than in sandy
26
27 community but heterogeneous sands have typically more species than well-sorted mobile
28
29
30
31 485 sands, which are characterized by dominance of polychaetes and amphipods (e.g. Van Hoey
32
33 et al. 2004), as found in Ship Shoal.
34
35

36
37 Significant variation in species diversity occurred over a small latitudinal gradient
38
39 (less than 10 km) between the northern and southern edges of Ship Shoal (biodiversity in
40
41 southern stations was higher). This north-south gradient is characterized by the higher
42
43 490 abundances of large tube-building polychaete species at stations close to the southern edge in
44
45 deepening water. For example, average abundances for the main tube-building species
46
47 Onuphidae *Diopatra cuprea* and *Onuphis eremita oculata* and Oweniidae *Owenia fusiformis*
48
49 were 6.17 ± 6.17 , 74.03 ± 20.38 and 513.67 ± 482.31 individuals m^{-2} for the southern edge,
50
51 versus 0 , 4.90 ± 3.23 and 54.33 ± 54.33 individuals m^{-2} for the northern edge, respectively.
52
53
54
55 495 These tube-builders contribute to the high diversity on Ship Shoal compared to nearby non-
56
57 shoal habitats. Tubes that protrude several cm above the sediment surface are known to
58
59
60
61
62
63
64
65

1 increase surface heterogeneity and provide habitat for other small invertebrates (Zühlke 2001;
 2 Dubois et al 2002), as well as settlement surface for larval and postlarval benthic organisms
 3
 4 (Qian and Chia 1991). This last hypothesis was supported by high densities of spionid and
 5
 6
 7 500 oweniid juveniles in southern samples (e.g. up to 1478 ± 475 juveniles m^{-2} of *O. fusiformis* in
 8
 9 the station 21, Fig. 1).
 10

11 Baustian's (2005) seasonal study off Ship Shoal showed that, while polychaetes
 12 dominated (ca. 50%) throughout the year, mollusks were the second most important
 13
 14 taxonomic group (24% in May, 45% in August and 38% in October). *Nuculana acuta*, *Natica*
 15
 16
 17 505 *pusilla* and *Abra aequalis* were particularly abundant in Baustian's study but were found on
 18
 19 Ship Shoal in very low abundances (less than 3 ind. m^{-2}). We found that mollusks represented
 20
 21
 22 < 3% of the macroinfauna on Ship Shoal, but that crustaceans, and especially amphipods,
 23
 24
 25 were almost as abundant as polychaetes (even more abundant in spring), while it is
 26
 27
 28 traditionally assumed that polychaetes are the most diverse and dominant taxonomic group in
 29
 30
 31 510 most marine and estuarine environments (e.g. Hutchings 1998).
 32
 33
 34
 35

36 *Is Ship Shoal a local refuge from seasonal hypoxia?*

37
38
39
40

41 Ship Shoal is situated within one of the largest hypoxic areas in the world (Rabalais et
 42
 43 515 al. 2001). Mid-summer surveys from 1993 to 2000 revealed severe and persistent hypoxia
 44
 45 (i.e. $DO < 2$ mg L^{-1}) on the inner- to mid-Louisiana continental shelf (Rabalais et al. 2001).
 46
 47
 48 Yet, our estimates of bottom DO concentrations over the entire shoal were fairly high and
 49
 50
 51 constant in spring (6.1 ± 1.5 mg L^{-1}), summer (6.3 ± 1.1 mg L^{-1}) and autumn (6.9 ± 0.3 mg L^{-1}),
 52
 53
 54 with only one spring sample reaching 2.0 mg L^{-1} . Amphipods occurred in very high
 55
 56 520 abundance and diversity over Ship Shoal, with a total of 20 species identified.
 57

58 *Acanthohaustorius* sp.A, *Protohaustorius bousfieldi*, *Ampelisca* sp.C and *Hartmanodes nyei*
 59
60
61
62
63
64
65

1 were highly-ranked among the benthic assemblages throughout the year. In contrast,
2 complete and long lasting (one or more years) disappearance of amphipod communities was
3 recorded at stations in an area of severe oxygen depletion in the Pomeranian Bay of the
4
5
6
7 525 Southern Baltic Sea (Powilleit and Kube 1999). More locally, Baustian (2005) confirmed that
8
9 crustaceans in general and amphipods in particular are absent from muddy areas surrounding
10
11 Ship Shoal in summer and autumn. As amphipods are known to be affected by low oxygen
12
13 (Gaston 1985; Wu and Or 2005), together these results support the hypothesis that Ship Shoal
14
15 is a hypoxia refuge for benthic species.
16
17

18
19 530 Irregular bottom topography in shallow waters such as sand banks and shoals has been
20
21 known to influence coastal hydrodynamics and bottom boundary layer dynamics (Pepper and
22
23 Stone 2004). For instance, such bathymetric elevated areas act as submerged breakwaters,
24
25 mitigating wave energy, flow patterns, and consequently increase DO concentrations (e.g.
26
27 Kobashi et al. 2007) and the shoal is too shallow to facilitate local stratification (Grippio et al.,
28
29
30 535 2009). Moreover, biogenic activity exemplified by the high density of tubicolous polychaetes
31
32 (e.g. spionids, representing between 30% and 50% of polychaete density, as well as *Owenia*
33
34 *fusiformis*, or *Onuphis eremita oculata*) may enhance oxygen flux in sediment surface layer
35
36 (Jorgensen et al. 2005). Together, these factors may contribute to Ship Shoals high DO
37
38 concentrations.
39
40
41
42

43 540 Species abundances exhibited a steady but large rate of decline between spring,
44
45 summer and autumn, affecting amphipods as well as all other taxonomic groups (except
46
47 amphioxus). The magnitude and extent of these declines suggest an increase in the rate of
48
49 mortality that is most likely not due to a short life-span. The most abundant structuring
50
51 amphipod species – *Acanthohaustorius* sp. – exhibit a lifespan of 1.5 years (Sainte-Marie
52
53 545 1991) and the most abundant polychaete family – spionids – exhibit a mean life-span of 1.8
54
55 years (McHugh and Fong 2002). As indicated by our DO measurements (ca. 6 mg L⁻¹), a
56
57
58
59
60
61
62
63
64
65

hypoxia event is not likely the cause for such a decrease in species abundances on Ship Shoal.

Sedimentation in the form of an ephemeral fluiditic flood layer has been reported to have a dramatic effect on benthic species abundances on the US Pacific Northwest coast (e.g.

550 Wheatcroft 2005). However, a 2006 survey done by US Army Corps of Engineers (data available at www.mvn.usace.army.mil/eng/edhd/watercon) did not reveal summer and/or

autumn flooding of the Atchafalaya and Mississippi Rivers on the adjacent Louisiana

continental shelf that could lead to a large-scale mud-layer deposition. Furthermore, our

sediment analyses over the entire Ship Shoal area found that silt and clay was always < 2% of

555 the total sediment. Flooding events are most likely to affect Ship Shoal in the winter and spring when continental cold fronts occur and when river flow is high (Allison et al 2005).

Recent modeling investigations showed that ephemeral and patchy fluiditic mud may occur in

spring on Ship Shoal (Kobashi et al. 2007). While we did not find evidence of this in our

seasonal survey, it may have had adversely affected the benthic populations on a small-scale.

560 Lastly, a seasonal influx of benthic predators may strongly affect benthic populations (e.g.

Langlois et al 2006). Gelpi et al. (in review) found expectedly high concentrations of

spawning/hatching blue crabs *Callinectes sapidus* in summer 2006 in Ship Shoal, but not in

spring trawls. Stable isotopes and gut content data (Gelpi et al., in prep.) showed that these

blue crabs actively fed on Ship Shoal. *C. sapidus* is known to be an important benthic

565 predator which may have a strong influence on polychaete and bivalve populations (Bell et al.

2003). We suggest here that seasonal blue crab predation (perhaps supplemented by other

predators such as white, brown shrimp and croaker) on Ship Shoal may contribute to the

observed seasonal decline in the macroinfaunal community.

570 *Is Ship Shoal macrofauna sensitive to sand-mining disturbance?*

1 Ship Shoal has been identified as perhaps the most significant sand resource (ca. 1.6
2 billion cubic yards of fine sand) in the northern Gulf of Mexico (Brooks et al. 1999).

3
4 Dredged sand may be used to supply beach reinforcement and coastal stabilization projects
5
6
7 575 and mitigate Louisiana coastal erosion and wetland loss (Michel et al. 2001). Much previous
8
9
10 research suggests that dredging and mining activities negatively affect, at least temporarily,
11
12 shoal benthic communities (Newell et al. 1998). Our study provides baseline information to
13
14 better understand the ecological services provided by Ship Shoal and to predict its sensitivity
15
16 to human disturbances in general and sand-mining disturbances in particular. Given the size
17
18
19 580 of Ship Shoal, it is likely that mining would remove only a fraction of the available sand but
20
21 localized effects may be strong and similar to responses experienced by sandbanks
22
23
24 worldwide.

25
26
27 Newell et al. (1998) estimated that the rate of recovery for sandy environments after
28
29 sediment extraction is much longer (2 to 3 years) than the rate for muddy environments (6 to
30
31 585 8 months), and may be even longer depending on the amount of sand removed, the proportion
32
33 of slow-growing species and the intensity of environmental disturbance. Palmer et al. (2008)
34
35 found that macrofauna off the western coast of Louisiana were not fully recovered three years
36
37 after dredging a sand excavation pit. The macrofauna assemblage of Ship Shoal is species-
38
39 rich with strongly contrasting life history characteristics compared to the surrounding off-
40
41
42 shoal community (Palmer et al. 2008; Baustian et al 2009). Many of Ship Shoal's more
43 590 abundant species (including *Branchisotoma floridae*, *Scoloplos* sp., *Sabellides* sp.,
44
45
46
47 *Terebellides* sp. and *Dosinia* sp., *Tellina* sp., *Ensis* sp.) have been designated "equilibrium
48
49 species" (K-strategists) (Newell et al. 1998) because they are relatively large in body size,
50
51 have a slow reproduction rate and a long life-cycle. These species, and the amphipod fauna as
52
53
54
55
56 595 a whole, are considered sensitive species (Geistera and Dauvin 2000), and are probably
57
58 controlled by biological interactions rather than extreme changes in environmental conditions
59
60
61
62
63
64
65

1 on Ship Shoal. Large species accounted for most of the biomass on Ship Shoal, which is high
2 (37.3 g wet weight m⁻²) compared to other areas of similar water depth (Pinn and Roberson
3
4 2003; Thouzeau et al. 1991). These observations suggest that Ship Shoal's macrofauna will
5
6
7 600 be strongly affected by and slow to recover from sand extraction. We predict that sand
8
9 extraction on Ship Shoal and other sandbanks will cause a shift in dominance to small,
10
11 rapidly-growing species including spionid polychaetes. These "disturbance specialists" or
12
13 "opportunistic species" (r-selected species, Pianka 1970) are found throughout the world.
14
15
16 They have a rapid rate of reproduction and body growth which facilitates colonization of
17
18
19 605 disturbed habitats (e.g. Dubois et al. 2002; Palmer et al. 2008), and are less sensitive to sand-
20
21 mining. The resulting reduction in macrofaunal biomass may elicit indirect effects at higher
22
23 trophic levels, for example on fishes and crustaceans using Ship Shoal as a foraging ground.
24
25

26 Sand mining will also impact physical factors that have direct and indirect effects on
27
28 ecological services. Variation in water depth and mean particle size was closely associated
29
30
31 610 with changes in benthic communities across Ship Shoal. Excavation of sand will lead to
32
33 localized increases in water depth and turbidity (due to the overflow of fine particles). Even
34
35 small changes in water depth may influence primary production on Ship Shoal. Grippo et al.
36
37 (2009) found that benthic microalgae may have higher biomass than phytoplankton integrated
38
39 through the water column on Ship Shoal, suggesting benthic primary production contributes
40
41
42 significantly to the shoal's food web. For example, the high macrofaunal biomass we
43
44 615 observed may be attributed to high levels of *in situ* primary production (e.g., our observed
45
46 correlation between chl *a* and benthic interface feeders). Changes in primary production and
47
48 a finer particle size will likely influence the benthic community by reducing community
49
50 biomass and altering community composition. Higher trophic levels may be influenced by
51
52
53 resulting bottom-up effects induced by changes in the biomass or community composition of
54
55
56 620 macrofauna.
57
58
59
60
61
62
63
64
65

Conclusion

625 Sandy shoals appear to provide key ecological services at multiple trophic
630 levels from all localities studied so far. For example, Vanaverbeke et al. (2007) showed that
635 sand extraction affected the nematode community at the base of the food web from the
Kwinte sandbank (Southern Bight of the North Sea). Kaiser et al. (2004) showed that
sandbanks on the Welsh coastline (United Kingdom) hosted distinct fish assemblages
foraging on benthic species colonizing the sandbanks. McGuire and Winemiller (1998)
demonstrated that the presence of sandbanks in the Cinaruco estuary (Venezuela) was
associated with a greater frequency of dolphin sightings. Our work suggests that larvae
spawned by benthic invertebrates living on Ship Shoal contribute to the recolonization of a
nearby seasonally hypoxic “dead zone” and that this sandy habitat is a species richness
hotspot that hosts a unique macrobenthic community that contrasts strongly with the
surrounding deeper muddy community. Ship Shoal offers a hypoxia refuge for benthic
species, as well as a settlement area for postlarvae and juveniles, enhancing the survival
probability for newly settled species. Ship Shoal might also be an important foraging ground
for fishes or large crustaceans preying upon benthic invertebrates, especially when nearby
severe hypoxia reduces essential habitat.

The effects of sand-mining on Ship Shoal benthos would likely last for months to
years and effects may extend to shoal-dependent nekton by food web interactions. In general,
human interventions to combat coastal erosion and shoreline retreat have been shown to cause
local ecological impacts and a loss of biodiversity that may have cumulative large-scale
645 consequences (Schlacher et al. 2007). Because of the scale of this problem, the continued
existence of sandy shoals - the main sand resource all over the world - as functional

1 ecosystems is likely to depend on direct conservation efforts. Our work, although not a
2 before-after study, suggests that shoals are more than mineral resources and that sand-mining
3 activities should be carried out with caution, especially where sandy shoals differ markedly
4
5
6
7 650 from surrounding benthic habitats.

8 9 10 11 **Acknowledgements** 12

13
14
15
16
17 This study was jointly funded by the U.S. Department of Interior Minerals
18
19 655 Management Services (contract number 1435-01-04-CA-35162) and by the Louisiana
20
21 Department of Natural Resources (contract number 2513-04-02/613082). We wish to thank
22
23 the Drs. Nancy Rabelais, Darryl Felder, Sara Lecroy, Felix Jose and Richard Shaw; the crew
24
25 of the Acadiana; and Mss Sara Arndt and Elaine D. Evers for their advise and assistance.
26
27
28
29
30

31 660
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Appendix A. Families and species identified from the GOMEX box core samples. Core

cross-sectional area = 0.09 m². Mesh size 500 µm

| Plathelminthes | | Polychaeta (cont.) | | Crustacea (cont.) | |
|-------------------|-----------------------------------|--------------------|------------------------------------|----------------------|---|
| - | <i>Probursa veneris</i> | Goniadidae | <i>Goniada littorea</i> | Xanthidae | <i>Xanthidae</i> sp. |
| Plehnidae | <i>Discocelides ellipsoides</i> | Nephtyidae | <i>Nephtys simoni</i> | Majidae | <i>Libinia dubia</i> |
| | | | <i>Aglaophamus verrilli</i> | | <i>Mithrax acuticornis</i> |
| Cnidaria | | Amphinomidae | <i>Paramphinoe</i> sp.B | Paguridae | <i>Pagurus annulipes</i> |
| Actinostolidae | <i>Paranthurus rapiformis</i> | Onuphidae | <i>Diopatra cuprea</i> | Albuneidae | <i>Albunea paretii</i> |
| | <i>burrowing Anemone</i> sp.2 | | <i>Onuphis eremita oculata</i> | | <i>Lepidopa benedicti</i> |
| | <i>burrowing Anemone</i> sp.3 | Lumbrineridae | <i>Lumbrineris latreilli</i> | Porcellanidae | <i>Euceramus praelongus</i> |
| | | | <i>Lumbrineris tenuis</i> | - | <i>Thalassinidea</i> sp. |
| Nemertea | | Oweniidae | <i>Owenia fusiformis</i> | Callianassidae | <i>Glypturus</i> nr. <i>acanthochirus</i> |
| Lineidae | <i>Micrura leidyi</i> | | <i>Myriowenia</i> sp.A | Pasiphaeidae | <i>Leptochela serratorbita</i> |
| - | <i>Nemertea</i> sp.1 | Ampharetidae | <i>Sabellides</i> sp.A | Processidae | <i>Processa hemphilli</i> |
| - | <i>Nemertea</i> sp.2 | | <i>Ampharete</i> sp.A | Hippolytidae | <i>Latreutes parvulus</i> |
| - | <i>Nemertea</i> sp.3 | Terebellidae | <i>Loimia viridis</i> | Panaeidae | <i>Solenocera vioscai</i> |
| | | | <i>Eupolytmia nebulosa</i> | Sergestidae | <i>Lucifer faxoni</i> |
| Polychaeta | | Sabellidae | <i>Chone americana</i> | | <i>Acetes americanus</i> |
| Orbiniidae | <i>Leitoscoloplos fragilis</i> | | | Ogyrididae | <i>Ogyrides alphaeostriis</i> |
| | <i>Scoloplos rubra</i> | Mollusca | | Nannosquillidae | <i>Coronis scolopendra</i> |
| | <i>Scoloplos</i> sp.B | Olividae | <i>Oliva sayana</i> | | <i>Squilla</i> sp.A |
| | <i>Phylo felix</i> | | <i>Olivella mutica</i> | Diastylidae | <i>Oxyurostylis smithi</i> |
| Paraonidae | <i>Cirrophorus forticirratu</i> | Nassariidae | <i>Nassarius acutus</i> | Bodotriidae | <i>Cyclaspis varians</i> |
| | <i>Aricidea fragilis</i> | Fasciariidae | <i>Latirus carinifer</i> | | |
| | <i>Aricidea suecica</i> | Columbellidae | <i>Anachis obesa</i> | Echinodermata | |
| | <i>Aricidea alisdairi</i> | Naticidae | <i>Polinices duplicatus</i> | Amphiuridae | <i>Amphipholis squamata</i> |
| | <i>Aricidea quadrilobata</i> | | <i>Natica pusilla</i> | | |
| | <i>Paraonis pygoenigmatica</i> | | <i>Sinum maculatum</i> | Sipuncula | |
| Spionidae | <i>Spiophanes bombyx</i> | Litiopinae | <i>Epitonium multistriatum</i> | Golfingiidae | <i>Phascolion strombi</i> |
| | <i>Boccardiella</i> sp.A | Calyptraeidae | <i>Crepidula plana</i> | | <i>Golfingia tenuissima</i> |
| | <i>Polydora ligni</i> | Cyclostremellinae | <i>Cyclostremella humilis</i> | Sipunculidae | <i>Sipunculus</i> sp. |
| | <i>Polydora socialis</i> | Tellinidae | <i>Strigilla pisiformis</i> | | |
| | <i>Dispia uncinata</i> | | <i>Tellina iris</i> | Echiura | |
| | <i>Aonides paucibranchiata</i> | | <i>Tellina versicolor</i> | Echiuridae | <i>Thalassema</i> sp. |
| | <i>Scolecopsis texana</i> | | <i>Macoma pulleyi</i> | | |
| | <i>Scolecopsis squamata</i> | Mactridae | <i>Mulinia lateralis</i> | Phoronida | |
| | <i>Paraprionospio pinnata</i> | | <i>Raeta plicatella</i> | Phoronidae | <i>Phoronis architecta</i> |
| | <i>Prionospio cristata</i> | Cardiidae | <i>Americardia media</i> | | |
| | <i>Prionospio pygmaea</i> | Solecurtidae | <i>Abra aequalis</i> | Chordata | |
| | <i>Prionospio cirrobranchiata</i> | Ungulinidae | <i>Diplodonta soror</i> | Branchiostomatidae | <i>Branchiostoma floridae</i> |
| | <i>Spio pettiboneae</i> | Lucinidae | <i>Parvilucina multilineata</i> | | |
| | <i>Microspio pigmentata</i> | | <i>Linga amiantus</i> | | |
| Magelonidae | <i>Magelona</i> sp.A | Veneridae | <i>Chione clenchi</i> | | |
| | <i>Magelona</i> sp.H | Solenioidea | <i>Solen viridis</i> | | |
| Poecilochaetidae | <i>Poecilochaetus johnsoni</i> | Dosiniinae | <i>Dosinia discus</i> | | |
| Chaetopteridae | <i>Spiochaetopterus costarum</i> | Pandoridae | <i>Pandora trilineata</i> | | |
| | <i>Mesochaetopterus capensis</i> | Arcidae | <i>Anadara transversa</i> | | |
| Cirratulidae | <i>Tharyx annulosus</i> | | | | |
| | <i>Chaetozone</i> sp.A | Crustacea | | | |
| | <i>Cirriformia</i> sp.B | Haustoriidae | <i>Acanthohaustorius</i> sp. A | | |
| Capitellidae | <i>Mediomastus californiensis</i> | | <i>Protohaustorius bousfieldi</i> | | |
| | <i>Mastobranthus</i> sp.A | | <i>Pseudohaustorius americanus</i> | | |
| | <i>Notomastus latericeus</i> | Synopiidae | <i>Metatiron triocellatus</i> | | |
| Arenicolidae | <i>Arenicola</i> sp. | | <i>Metatiron tropakis</i> | | |
| Opheliidae | <i>Armandia maculata</i> | Liljeborgiidae | <i>Listriella barnardi</i> | | |
| | <i>Travisia hobsonae</i> | Isaeidae | <i>Microprotopus raneyi</i> | | |
| Phyllodoceidae | <i>Phyllodoce mucosa</i> | Corophiidae | <i>Monoconophium</i> sp. A | | |
| | <i>Anatides groenlandica</i> | | <i>Monocorophium tuberculatum</i> | | |
| Polynoidae | <i>Malmgreniella</i> sp.C | Ampelisca | <i>Ampelisca</i> sp. C | | |
| | <i>Lepidonotus sublevis</i> | Oedicerotidae | <i>Hartmanodes nyei</i> | | |
| | <i>Perolepis</i> sp.A | | <i>Americhelidium americanum</i> | | |
| | <i>Polynoidae</i> sp. | Ischyroceridae | <i>Erichthonius brasiliensis</i> | | |
| Eulepethidae | <i>Grubeulepis</i> sp.A | | <i>Cerapus tubularis</i> | | |
| Sigalionidae | <i>Thalenessa spinosa</i> | Argissidae | <i>Argissa hamatipes</i> | | |
| | <i>Fimbriosthenelais minor</i> | Stenothoidae | <i>Parametopella cypris</i> | | |
| Hesionidae | <i>Podarke</i> sp.A | Caprellidae | <i>Unknown species</i> | | |
| | <i>Gyptis brevipalpa</i> | Platyischnopidae | <i>Eudevenopus honduranus</i> | | |
| Pilargiidae | <i>Sigambra tentaculata</i> | Phoxocephalidae | <i>Trichophoxus</i> sp. | | |
| | <i>Synelmis klatti</i> | - | <i>unknown Amphipod</i> | | |
| Syllidae | <i>Streptosyllis pettiboneae</i> | Portunidae | <i>Portunus gibbesii</i> | | |
| Nereidae | <i>Neanthes micromma</i> | | <i>Ovalipes floridanus</i> | | |
| | <i>Nereis falsa</i> | | <i>Callinectes similis</i> | | |

| | | | |
|------------|----------------------------------|---------------|-----------------------|
| | <i>Websterinereis tridentata</i> | | <i>Portunidae</i> sp |
| Glyceridae | <i>Glycera americana</i> | Pinnotheridae | <i>Pinnixa chacei</i> |
| | <i>Glycera abbranchiata</i> | | <i>Pinnixa sayana</i> |

7 665 **References**

- 8
- 9
- 10
- 11
- 12 Allison MA, Sheremet A, Goni MA, Stone GW (2005) Storm layer deposition on the
- 13
- 14 Mississippi-Atchafalaya subaqueous delta generated by Hurricane Lili in 2002. Cont
- 15
- 16 Shelf Res 25:2213-2232
- 17
- 18
- 19 670 Berthot A, Pattiaratchi C (2004) Maintenance of headland-associated linear sandbanks:
- 20
- 21 modelling the secondary flows and sediment transport. 12th International Biennial
- 22
- 23 Conference on Physics of Estuaries and Coastal Seas. Springer Heidelberg, Merida,
- 24
- 25 Mexico, pp526-540
- 26
- 27
- 28
- 29 Baustian MM (2005) Benthic communities in the northern Gulf of Mexico hypoxic area:
- 30
- 31 675 potential prey for demersal fish. Master Thesis, Louisiana State University.
- 32
- 33 <http://etd.lsu.edu/docs/available/etd-07142005-082657>
- 34
- 35
- 36 Baustian MM, Craig JK Rabalais NN (2009) Effects of summer 2003 hypoxia on
- 37
- 38 macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of
- 39
- 40 Mexico. J Exp Mar Biol Ecol *in press*
- 41
- 42
- 43 680 Bell GW, Eggleston DB, Wolcott TG (2003) Behavioral responses of free-ranging blue crabs
- 44
- 45 to episodic hypoxia. II. Feeding. Mar Ecol Prog Ser 259:227-235
- 46
- 47
- 48 Blott SJ, Pye K (2001) GRADISTAT: a grain size distribution and statistics package for the
- 49
- 50 analysis of unconsolidated sediments. Earth Surf Proc Land 26:1237-1248
- 51
- 52
- 53 Boland GS, Rowe GT (1991) Deep-Sea Benthic Sampling with the Gomex Box Corer.
- 54
- 55
- 56 685 Limnol Oceanogr 36:1015-1020
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- 1
2
3
4
5
6
7
8
9
10 690
11
12
13
14
15
16
17
18
19
20
21
22 695
23
24
25
26
27
28
29
30
31
32
33
34 700
35
36
37
38
39
40
41
42
43
44
45
46 705
47
48
49
50
51
52
53
54
55
56
57
58 710
59
60
61
62
63
64
65
- Brooks RA, Purdy CN, Bell SS, Sulak KJ (2006) The benthic community of the eastern US continental shelf: A literature synopsis of benthic faunal resources. *Cont Shelf Res* 26:804-818
- Cheung MM, Brooks RA, Sulak KJ (2006) Benthic polychaete assemblages on Sabine and Heald sand banks, northern Gulf of Mexico: a pre-disturbance study on a sand extraction site, USGS Outer Continental Shelf Ecosystem Studies Program Report, Gainesville, FL
- Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117-143
- Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Mar Ecol Prog Ser* 92:205-219
- Clarke KR, Gorley RN (2001) *PRIMER v5 : User Manual/Tutorial*. PRRIMER-E Ltd, Plymouth
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Report No. 144, Plymouth Marine Laboratory, Plymouth
- Defeo O, McLachlan A, Schoeman DS, Schlacher TA, Dugan J, Jones A, Lastra M, Scapini F (2009) Threats to sandy beach ecosystems: A review. *Est Coast Shelf Sci* 81:1-12
- Dewicke A, Cattrijsse A, Mees J, Vincx M (2003) Spatial patterns of the hyperbenthos of subtidal sandbanks in the southern North Sea. *J Sea Res* 49:27-45
- Drucker BS, Waskes W, Byrnes MR (2004) The US minerals management service outer continental shelf sand and gravel program: Environmental studies to assess the potential effects of offshore dredging operations in federal waters. *J Coast Res* 20:1-5
- Dubois S, Retiere C, Olivier F (2002) Biodiversity associated with *Sabellaria alveolata* (Polychaeta : Sabellariidae) reefs: effects of human disturbances. *J Mar Biol Ass UK* 82:817-826

1 Fauchald K, Jumars PA (1979) The diet of worms: A study of polychaete feeding guilds.

2 Oceanogr Mar Biol Ann Rev 17:193-284

3
4 Folk RL, Ward WC (1957) Brazos River bar: a study in the significance of grain size

5 parameters. J Sed Pet 27:3-26

6
7
8
9 715 Gaston GR (1985) Effects of Hypoxia on macrobenthos of the inner shelf off Cameron,
10 Louisiana. Est Coast Shelf Sci 20:603-613

11
12 Gesteira JLG, Dauvin JC (2000) Amphipods are good bioindicators of the impact of oil spills
13 on soft-bottom macrobenthic communities. Mar Poll Bull 40:1017-1027

14
15 Gray JS (1974) Animal-sediment relationships. Oceanogr Mar Biol 12:223-261

16
17
18 720 Gray JS (2000) The measurement of marine species diversity, with an application to the
19 benthic fauna of the Norwegian continental shelf. J Exp Mar Biol Ecol 250:23-49

20
21
22
23 Grippio MA, Fleeger JW, Condrey RE, Carman KR (2009) High biomass of benthic
24 microalgae found on Ship Shoal, north-central Gulf of Mexico. Bull Mar Sci 84:237-
25 256

26
27
28
29
30 725 Hefley HM, Shoemaker H (1952) The occurrence of *Branchiostoma* (Amphioxus) in
31 Mississippi and Louisiana. Science 115:48

32
33
34
35 Hill MO (1973) Diversity and evenness: a unifying notation and its consequence. Ecology
36 54:427-432

37
38
39
40
41 Hutchings PA (1998) Biodiversity and functioning of polychaetes in benthic sediments.

42
43 730 Biodiv Conserv 7:1133-1145

44
45 Jorgensen BB, Glud RN, Holby O (2005) Oxygen distribution and bioirrigation in Arctic
46 fjord sediments (Svalbard, Barents Sea). Mar Ecol Prog Ser 292:85-95

47
48
49
50
51 Justic D, Rabalais NN, Turner RE (1996) Effects of climate change on hypoxia in coastal
52 waters: A doubled CO₂ scenario for the northern Gulf of Mexico. Limnol Oceanogr
53 41:992-1003

54
55 735

56
57
58
59
60
61
62
63
64
65

- 1 Kaiser MJ, Bergmann M, Hinz H, Galanidi M, Shucksmith R, Rees EIS, Darbyshire T,
2 Ramsay K (2004) Demersal fish and epifauna associated with sandbank habitats. Est
3 Coast Shelf Sci 60:445-456
4
5
6
7 Kobashi D, Jose F, Stone GW (2007) Impacts of fluvial fine sediments and winter storms on a
8
9
10 740 transgressive shoal, off south-central Louisiana, U.S.A. Proceedings of the 9th
11 International Coastal Symposium. J Coast Res, Gold Coast, Australia, p858-862
12
13
14 Langlois TJ, Anderson MJ, Babcock RC (2005) Reef-associated predators influence adjacent
15 soft-sediment communities. Ecology 86:1508-1519
16
17
18
19 Lecroy S (2000) An illustrated identification guide to the nearshore marine and estuarine
20
21
22 745 Gammaridean Amphipoda of Florida, vol 1. Families Gammaridae, Hadziidae,
23 Isaeidae, Melitidae and Oedicerotidae. Tallahassee. Florida Department of
24 Environmental Protection, Florida
25
26
27
28
29 Mannino A, Montagna PA (1997) Small-scale spatial variation of macrobenthic community
30 structure. Estuaries 20:159-173
31
32
33
34 750 McGuire TL, Winemiller KO (1998) Occurrence patterns, habitat associations, and potential
35 prey of the river dolphin, *Inia geoffrensis*, in the Cinaruco river, Venezuela. Biotropica
36 30:625-638
37
38
39
40
41 McHugh D, Fong PP (2002) Do life history traits account for diversity of polychaete
42 annelids? Invert Biol 121:325-338
43
44
45
46 755 Michel J, Nairn R, Johnson JA, Hardin D (2001) Development and design of biological and
47 physical monitoring protocols to evaluate the long-term impacts of offshore dredging
48 operations on the marine environment, U.S. Department of the Interior, Mineral
49 Management Service, International Activities and Marine Minerals Division
50
51
52
53
54
55
56 (INTERMAR), Herndon, VA
57
58
59
60
61
62
63
64
65

- 760 Montagna PA, Ritter C (2006) Direct and indirect effects of hypoxia on benthos in Corpus
1 Christi Bay, Texas, USA. *J Exp Mar Biol Ecol* 330:119-131
2
3
4
5 Newell RC, Seiderer LJ, Hitchcock DR (1998) The impact of dredging works in coastal
6
7 waters: a review of the sensitivity to disturbance and subsequent recovery of
8
9 biological resources on the seabed. *Oceanogr Mar Biol Ann Rev* 36:127-178
10
11
12 765 Ohlmann JC, Niiler PP (2005) Circulation over the continental shelf in the northern Gulf of
13
14 Mexico. *Progr Oceanogr* 64:45-81
15
16
17 Palmer TA, Montagna PA, Nairn RB (2008) The effects of a dredge excavation pit on benthic
18
19 macrofauna in offshore Louisiana. *Environ Manag*, 41:573-583
20
21
22 Pechenik JA (2005) *Biology of the invertebrates*, McGraw-Hill, New York
23
24 770 Peckenham JM, Thornton T, Whalen WB (2009) Sand and gravel mining: Effects on ground
25
26 water resources in Hancock County, Maine, USA. *Env Geol* 56:1103-1114
27
28
29 Pempel LL, Church M (2009) Physical and ecological response to disturbance by gravel
30
31 mining in a large alluvial river. *Can J Fish Aquat Sci* 66:52-71
32
33
34 Pepper DA, Stone GW (2004) Hydrodynamic and sedimentary responses to two contrasting
35
36 775 winter storms on the inner shelf of the northern Gulf of Mexico. *Mar Geol* 210:43-62
37
38
39 Pianka ER (1970) R-Selection and K-Selection. *Am Nat* 104:592-597
40
41
42 Pinn EH, Robertson MR (2003) Macro-infaunal biodiversity and analysis of associated
43
44 feeding guilds in the Greater Minch area, Scottish west coast. *J Mar Biol Ass UK*
45
46 83:433-443
47
48 780 Posey MH, Alphin TD, Banner S, Vose F, Lindberg W (1998) Temporal variability, diversity
49
50 and guild structure of a benthic community in the northeastern Gulf of Mexico. *Bull*
51
52 *Mar Sci* 63:143-155
53
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Powilleit M, Kube J (1999) Effects of severe oxygen depletion on macrobenthos in the
2 Pomeranian Bay (southern Baltic Sea): a case study in a shallow, sublittoral habitat
3 characterised by low species richness. J Sea Res 42:221-234
4 785
5
6
7 Qian PY, Chia FS (1991) Effects of food concentration on larval growth and development of
8 two polychaete worms, *Capitella capitata* (Fabricius) and *Polydora ligni* (Webster).
9 Bull Mar Sci 48:477-484
10
11
12 Rabalais NN, Smith LE, Harper Jr DE, Justic D (2001) Effects of seasonal hypoxia on
13 continental shelf benthos. In: Rabalais NN and Turner RE (eds) Coastal hypoxia:
14 790 consequences for living resources and ecosystems, coastal and estuarine studies,
15 American Geophysical Union, Washington D.C., pp211-240
16
17
18 Rabalais NN, Wiseman WJ, Turner RE (1994) Comparison of continuous records of near-
19 bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. Estuaries
20 17:850-861
21 795
22
23
24 Rakocinski CF, LeCroy SE, McLelland JA, Heard RW (1998) Nested spatiotemporal scales
25 of variation in sandy-shore macrobenthic community structure. Bull Mar Sci 63:343-
26 362
27
28
29
30
31 Rona PA (2008) The changing vision of marine minerals. Ore Geol Rev 33:618-666
32
33
34
35
36
37
38
39
40
41 800 Rosenzweig ML (1995) Species diversity in space and time, Cambridge University Press,
42 Cambridge
43
44
45
46 Rzeznik-Orignac J, Fichet D, Boucher G (2004) Extracting massive numbers of nematodes
47 from muddy marine deposits: efficiency and selectivity. Nematology 6:605-616
48
49
50
51 Sainte-Marie B (1990) A review of the reproductive bionomics of aquatic gammaridean
52 amphipods. Variation of life-history traits with latitude, depth, salinity and
53 805 superfamily. 7th International Colloquium on Amphipoda. Walpole, Me, pp189-227
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Shannon CE (1948) A mathematical theory of communications. *Bell Sys Tech Jour* 27:379-
2 423
3
4 Sheldon AL (1969) Equitability indices: dependence on the species count. *Ecology* 50:466-
5 467
6
7 810
8
9 Simpson EH (1949) Measurement of diversity. *Nature* 163:688
10
11 Snelgrove PVR, Butman CA (1994) Animal-sediment relationships revisited: cause versus
12 effect. *Oceanogr Mar Biol Ann Rev* 32:111-177
13
14
15
16
17 Thouzeau G, Robert G, Ugarte R (1991) Faunal assemblages of benthic megainvertebrates
18 inhabiting sea scallop grounds from eastern Georges Bank, in relation to
19 815 environmental factors. *Mar Ecol Progr Ser* 74:61-82
20
21
22
23
24 Uebelacker JM, Johnson PG (1984) Taxonomic guide to the polychaetes of the northern Gulf
25 of Mexico, Vol.1-7 Barry A. Vittor & Associates, Inc., Mobile, Alabama
26
27
28
29 Van Hoey G, Degraer S, Vincx M (2004) Macrobenthic community structure of soft-bottom
30 sediments at the Belgian continental shelf. *Est Coast Shelf Sci* 59:599-613
31 820
32
33
34 Vanaverbeke J, Deprez T, Vincx M (2007) Changes site in nematode communities at the
35 long-term sand extraction of the Kwintebank (Southern Bight of the North Sea). *Mar*
36
37
38
39
40
41 Pol Bull 54:1351-1360
42
43
44 825
45
46 Vanosmael C, Willems KA, Claeys D, Vincx M, Heip C (1982) Macrobenthos of a sublittoral
47 sandbank in the southern Bight of the North Sea. *J Mar Biol Ass UK* 62:521-534
48
49
50
51 Wheatcroft RA, Sommerfield CK (2005) River sediment flux and shelf sediment
52 accumulation rates on the Pacific Northwest margin. *Cont Shelf Res* 25:311-332
53
54
55
56 830
57
58 Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21:213-251
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295
296
297
298
299
300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355
356
357
358
359
360
361
362
363
364
365
366
367
368
369
370
371
372
373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394
395
396
397
398
399
400
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432
433
434
435
436
437
438
439
440
441
442
443
444
445
446
447
448
449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
483
484
485
486
487
488
489
490
491
492
493
494
495
496
497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631
632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651
652
653
654
655
656
657
658
659
660
661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698
699
700
701
702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733
734
735
736
737
738
739
740
741
742
743
744
745
746
747
748
749
750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808
809
810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826
827
828
829
830
831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863
864
865
866
867
868
869
870
871
872
873
874
875
876
877
878
879
880
881
882
883
884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946
947
948
949
950
951
952
953
954
955
956
957
958
959
960
961
962
963
964
965
966
967
968
969
970
971
972
973
974
975
976
977
978
979
980
981
982
983
984
985
986
987
988
989
990
991
992
993
994
995
996
997
998
999
1000

1 Zeppelini D, Bellini BC, Creato-Duarte AJ (2009) Collembola as bioindicators of restoration
2 in mined sand dunes of Northeastern Brazil. Biodiv Conserv 18:1161-1170
3

4 Zühlke R (2001) Polychaete tubes create ephemeral community patterns: *Lanice conchilega*
5

6
7 835 (Pallas, 1766) associations studied over six years. J Sea Res 46:261-272
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Figure captions

1
2
3
4
5 840 *Figure 1.* Geographic position of the 21 sampling stations on Ship Shoal, off Louisiana.

6
7 Detailed bathymetry outlining the shoal and surrounding area is given. Depths in
8
9 meters (m). Coordinates in NTF (system) Lambert (projection). Data for the
10
11 bathymetry provided by Divins D.L. and Metzger D., National Geophysical Data
12
13 Center (NOAA) <http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>
14
15

16
17 845 *Figure 2.* Seasonal variations in abundances (individuals m^{-2} ; mean \pm SE) of main taxonomic
18
19 groups, with emphasis on spionids and amphipods. Core cross-sectional area = 0.09
20
21 m^2 .
22
23

24
25 *Figure 3.* Mean biomass (wet weight; g m^{-2} ; mean \pm SE) of polychaetes, mollusks (including
26
27 shells) and other taxonomic groups according to seasonality. Core cross-sectional area
28
29 850 = 0.09 m^2 . Letters a, b and c refers to statistical differences between the 3 seasons for
30
31 total biomass, polychaetes, mollusks and others.
32
33

34
35 *Figure 4.* Global and mean (\pm SE) species richness in spring on Ship Shoal within the east,
36
37 middle and west transects on the Ship Shoal. Core cross-sectional area = 0.09 m^2 . See
38
39 Figure 1 for precise location of the stations.
40

41 855 *Figure 5.* Multi-dimensional scaling ordination diagram of all samples of all stations showing
42
43 seasonal changes in species composition and assemblages. Ordination was based on
44
45 unstandardized log-transformed abundances matrix.
46
47

48
49 *Figure 6.* Multi-dimensional scaling ordination diagrams based showing, for spring (top),
50
51 summer (middle) and autumn (bottom) samples east-west variations (left panels) or
52
53 860 north-south variations (right panels). A schematic of the shoal is provided to illustrate
54
55 the position of the stations on the east-west and north-south transects (see Figure 1 and
56
57
58
59
60
61
62
63
64
65

description of study site for details). Ordination was based on unstandardized log-transformed abundances matrix.

Figure 7. Seasonal variations in dominance (%) of the five feeding guilds. Interface feeders are species which can switch between suspension-feeding and surface deposit-feeding.

1
2
3
4
5
6
7 865
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3
4 870 *Table 1.* Species richness and heterogeneity of diversity and equitability (mean \pm SE) for
5
6 each season. Core cross-sectional area = 0.09 m². Results of one-way ANOVA for each
7
8 measurement, where same letters indicate non-significant differences at p -level = 0.05
9
10
11
12
13

| | Seasonal global species richness | Species Richness | Heterogeneity of diversity N1 = exp (H') | Heterogeneity of diversity N2 = 1/SI | Equitability J' |
|-----------|---|-------------------------------|--|--|-----------------|
| 19 Spring | 134 | 33.19 \pm 1.53 ^a | 13.90 \pm 1.15 ^a | 8.67 \pm 0.86 | 0.72 \pm 0.10 |
| 20 Summer | 118 | 23.71 \pm 1.05 ^b | 12.40 \pm 0.96 ^a | 8.19 \pm 0.73 | 0.77 \pm 0.08 |
| 21 Autumn | 91 | 13.54 \pm 1.01 ^c | 8.38 \pm 0.80 ^b | 6.08 \pm 0.58 | 0.78 \pm 0.11 |

22
23
24
25 875
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2 *Table 2.* Results of ANOVA tests showing east-west gradient and north-south gradient within
3
4 Ship Shoal area according to diversity indices, species abundance and biomass for each
5
6 season. SR = species richness (N0), N1 and N2 = heterogeneity of diversity. Post-hoc
7
8 columns indicated results of post-hoc comparisons between E (east), M (middle) and W
9
10 880 (west) or between N (north), M (middle) and S (south), with “ = ” indicating non-significant
11
12 difference and “ < ” indicating significant difference at p -level = 0.05
13
14
15
16
17
18
19

| Spring | east - west gradient | | | north - south gradient | | |
|--------------------|----------------------|----------------------|-----------|------------------------|----------------------|-----------|
| | F | p-level | post-hoc | F | p-level | post-hoc |
| SR | 2.91 | NS | - | 4.27 | 0.032 | N = M < S |
| N1 | 18.35 | $7.2 \cdot 10^{-5}$ | E < M < W | 5.91 | 0.012 | N < M < S |
| N2 | 13.05 | $4.0 \cdot 10^{-4}$ | E < M < W | 4.41 | 0.029 | N < M = S |
| abundances | 13.06 | $4.0 \cdot 10^{-3}$ | E = M < W | 5.19 | 0.018 | N < M = S |
| total biomass | 1.07 | NS | - | 2.09 | NS | - |
| polychaete biomass | 5.77 | 0.013 | E < M = W | 39.29 | $1.0 \cdot 10^{-7}$ | N = M < S |
| Summer | east - west gradient | | | north - south gradient | | |
| | F | p-level | post-hoc | F | p-level | post-hoc |
| SR | 2.85 | NS | - | 8.83 | 0.002 | N < M < S |
| N1 | 1.52 | NS | - | 11.40 | $6 \cdot 10^{-4}$ | N = M < S |
| N2 | 3.17 | NS | - | 15.04 | $4.4 \cdot 10^{-6}$ | N = M < S |
| abundances | 58.82 | $1 \cdot 10^{-6}$ | E < M < W | 37.42 | $1 \cdot 10^{-6}$ | N < M < S |
| total biomass | 2.13 | NS | - | 0.15 | NS | - |
| polychaete biomass | 4.47 | 0.026 | E = M < W | 13.15 | $3 \cdot 10^{-4}$ | N = M < S |
| Autumn | east - west gradient | | | north - south gradient | | |
| | F | p-level | post-hoc | F | p-level | post-hoc |
| SR | 11.32 | $6.54 \cdot 10^{-4}$ | E = M < W | 4.26 | 0.030 | N = M < S |
| N1 | 2.80 | NS | - | 1.93 | NS | - |
| N2 | 1.11 | NS | - | 1.16 | NS | - |
| abundances | 15.71 | $1.13 \cdot 10^{-4}$ | E < M < W | 9.39 | $1.16 \cdot 10^{-4}$ | N < M < S |
| total biomass | 0.47 | NS | - | 1.15 | NS | - |
| polychaete biomass | 0.06 | NS | - | 0.06 | NS | - |

885

Table 3. Seasonal variations in monitored environmental parameters over Ship Shoal

| | Spring | | Summer | | Autumn | |
|---|---------------|------------------|---------------|------------------|---------------|------------------|
| | min - max | mean \pm sd | min - max | mean \pm sd | min - max | mean \pm sd |
| Depth (m) | 4.2 - 10.2 | 6.9 \pm 1.6 | 4.2 - 9.4 | 6.4 \pm 1.5 | 4.9 - 10.5 | 7.2 \pm 1.7 |
| Mean grain size (μm) | 127.7 - 198.1 | 159.9 \pm 20.6 | 118.1 - 323.3 | 170.0 \pm 39.5 | 115.6 - 320.6 | 174.3 \pm 46.2 |
| Silt/clay content (%) | 0.3 - 3.4 | 1.4 \pm 1.0 | 0.3 - 4.5 | 1.4 \pm 1.1 | 0.3 - 18.1 | 1.9 \pm 4.2 |
| Gravel content (%) | 0.0 - 3.7 | 0.5 \pm 1.0 | 0.1 - 11 | 1.2 \pm 2.6 | 0.1 - 11.8 | 1.4 \pm 3.1 |
| Sorting index | 1.2 - 1.7 | 1.2 \pm 0.1 | 1.2 - 2.5 | 1.3 \pm 0.3 | 1.3 - 2.4 | 1.3 \pm 0.3 |
| Chlorophyll <i>a</i> (mg m^{-2}) | 12.0 - 120.1 | 41.8 \pm 27.4 | 2.7 - 122.0 | 37.0 \pm 31.5 | 1.8 - 94.0 | 30.2 \pm 21.8 |
| Dissolved oxygen (mg L^{-1}) | 2.0 - 8.4 | 6.1 \pm 1.5 | 4.5 - 8.3 | 6.3 \pm 1.1 | 6.3 - 7.2 | 6.9 \pm 0.3 |

890

Table 4. ANOSIM and SIMPER results comparing species composition according to seasons.

Core cross-sectional area = 0.09 m². SIMPER cumulative dissimilarity cut-off = 50%. See

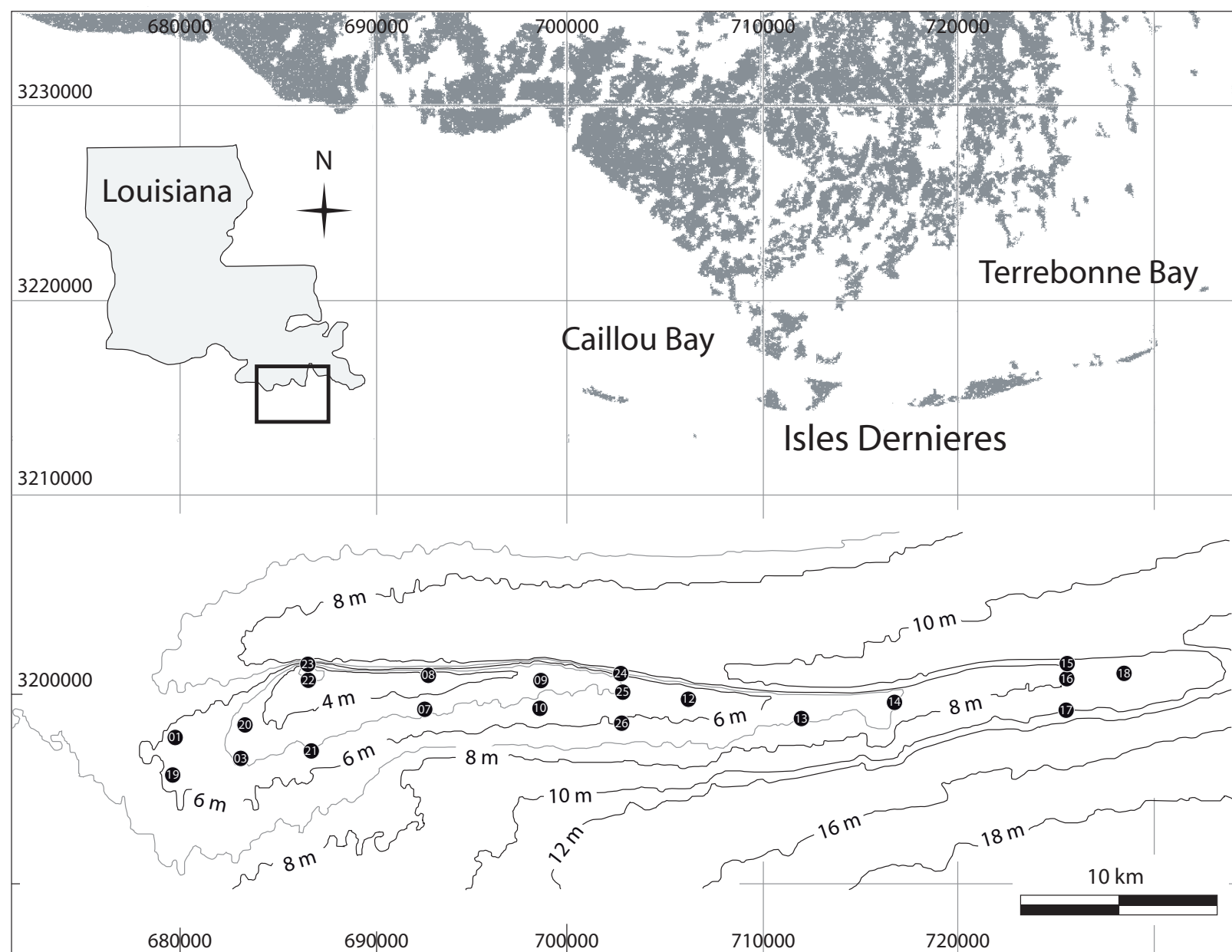
Figure 6 for nMDS plots

| | Spring | Summer | Spring | Autumn |
|-----------------------------------|-----------------------------------|--------|-----------------------------------|--------|
| R statistic | 0.733 | | 0.861 | |
| p-value | 0.001 | | 0.001 | |
| Similarity (%) | 38.34 | 33.97 | 33.97 | 28.55 |
| Bray-Curtis dissimilarity (%) | 81.38 | | 88.35 | |
| Contribution to dissimilarity (%) | <i>Acanthohaustorius</i> sp. A | 14.85 | <i>Acanthohaustorius</i> sp. A | 18.69 |
| | <i>Protohaustorius bousfieldi</i> | 8.41 | <i>Spiophanes bombyx</i> | 8.83 |
| | <i>Branchiostoma floridae</i> | 7.66 | <i>Protohaustorius bousfieldi</i> | 8.26 |
| | <i>Spiophanes bombyx</i> | 7.04 | <i>Dispia uncinata</i> | 4.44 |
| | <i>Dispia uncinata</i> | 3.84 | <i>Microprotopus raneyi</i> | 3.83 |
| | <i>Prionospio pygmaea</i> | 3.74 | <i>Ampelisca</i> sp. C | 3.70 |
| | <i>Microprotopus raneyi</i> | 3.41 | <i>Branchiostoma floridae</i> | 3.41 |
| | <i>Ampelisca</i> sp. C | 3.34 | | |
| | Summer | Autumn | | |
| R statistic | 0.459 | | | |
| p-value | 0.001 | | | |
| Similarity (%) | 33.97 | 28.55 | | |
| Bray-Curtis dissimilarity (%) | 76.70 | | | |
| Contribution to dissimilarity (%) | <i>Branchiostoma floridae</i> | 16.12 | | |
| | <i>Acanthohaustorius</i> sp. A | 10.51 | | |
| | <i>Prionospio pygmaea</i> | 9.18 | | |
| | <i>Protohaustorius bousfieldi</i> | 6.37 | | |
| | <i>Scoloplos</i> sp.B | 3.82 | | |
| | <i>Mediomastus californiensis</i> | 2.86 | | |
| | <i>Magelona</i> sp.A | 2.64 | | |

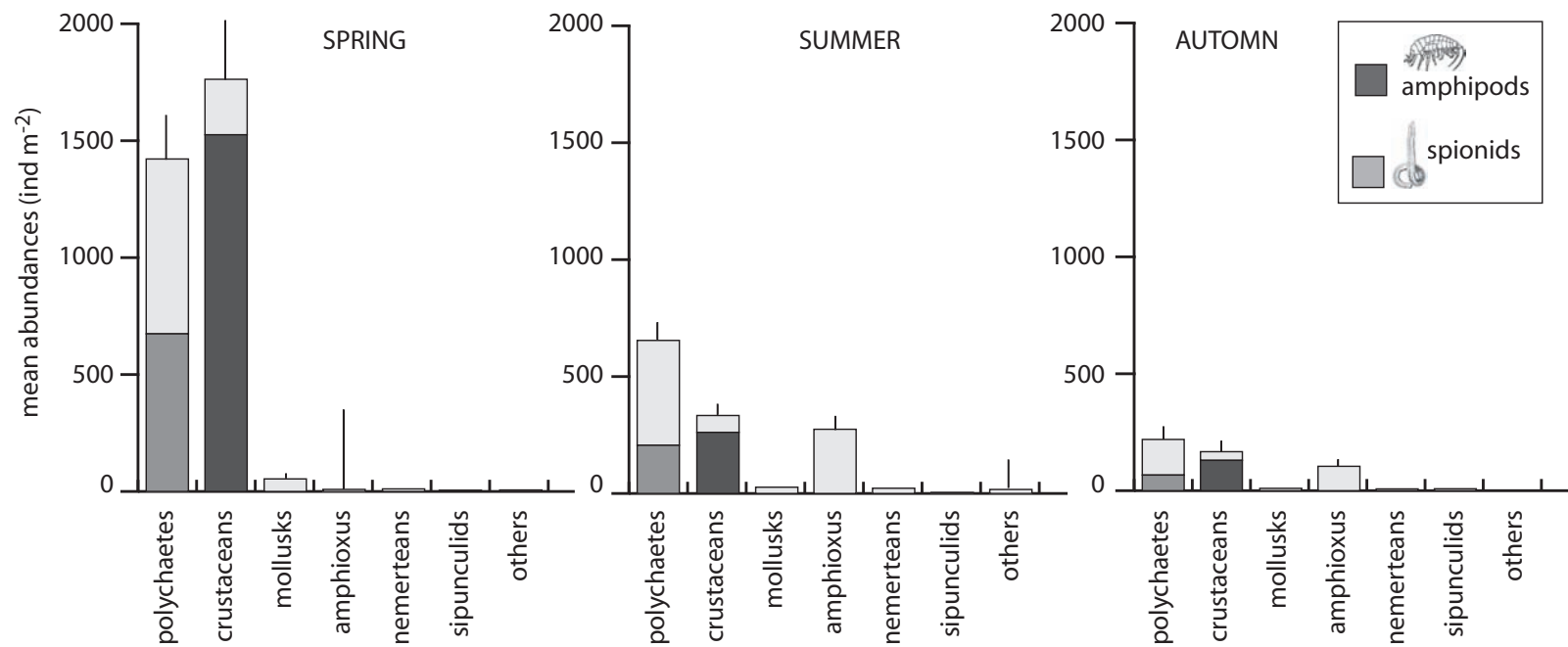
895

line figure 1

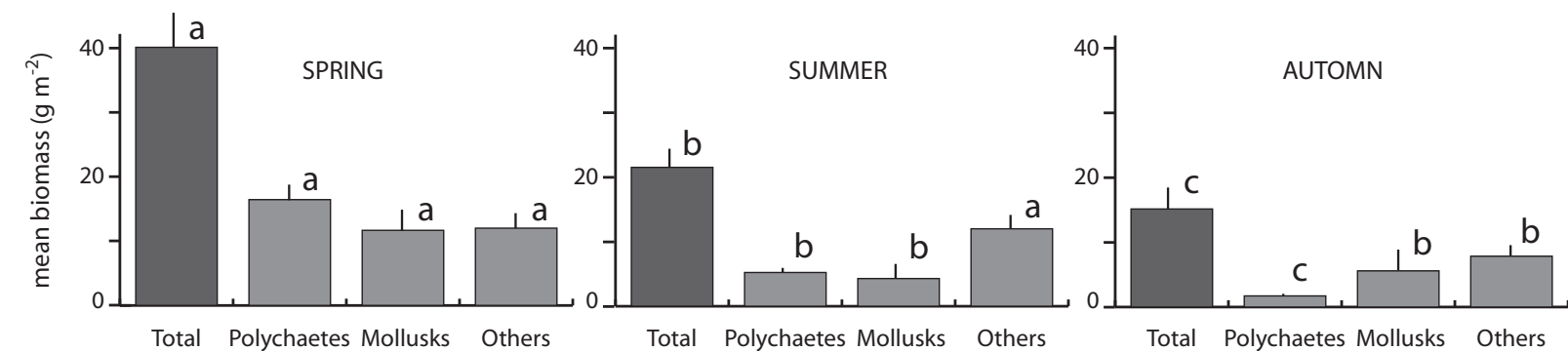
[Click here to download line figure: Fig 1revised.eps](#)



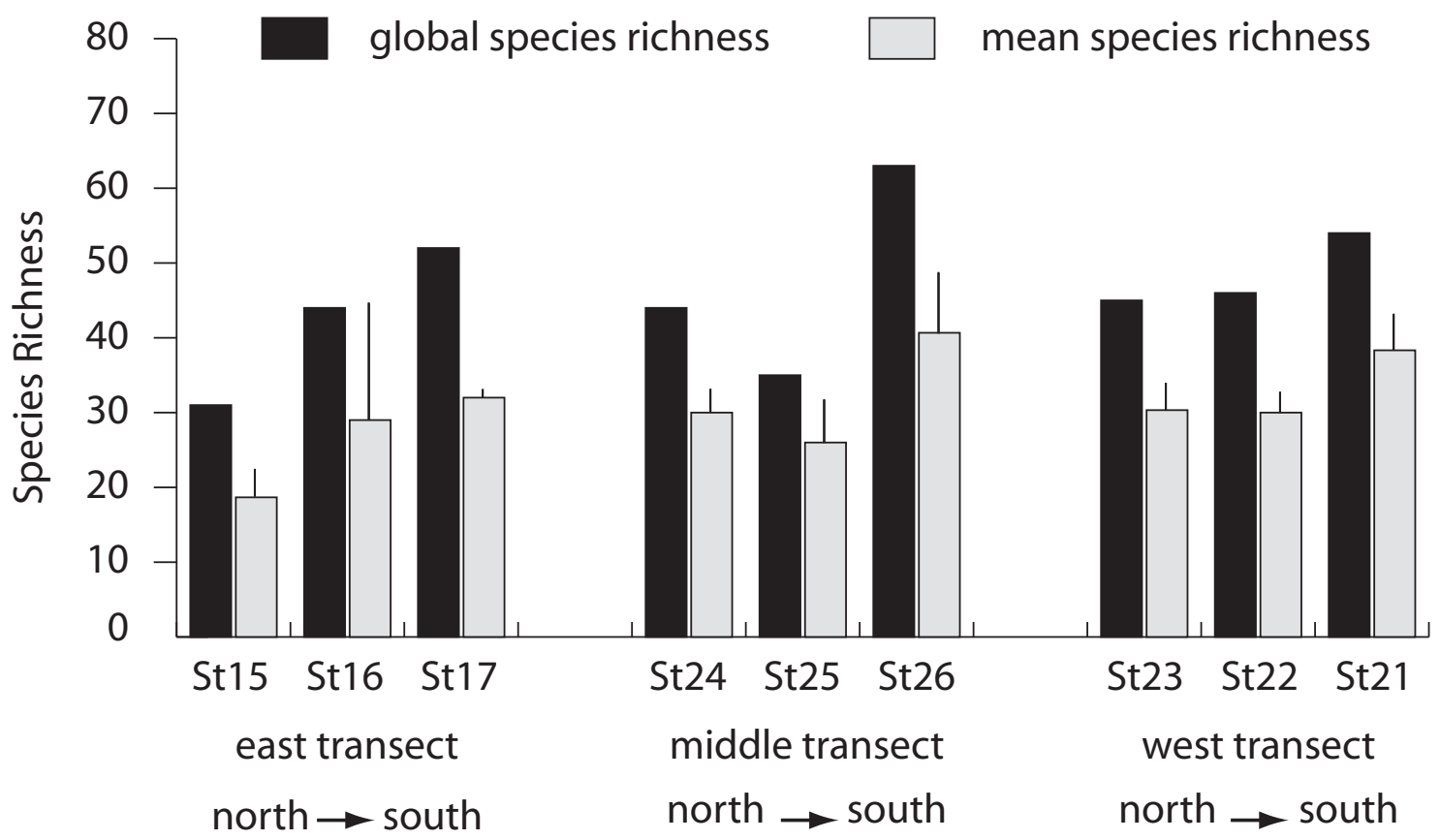
line figure 2
[Click here to download line figure: Fig 2review.eps](#)



line figure 3
[Click here to download line figure: Fig 3review.eps](#)

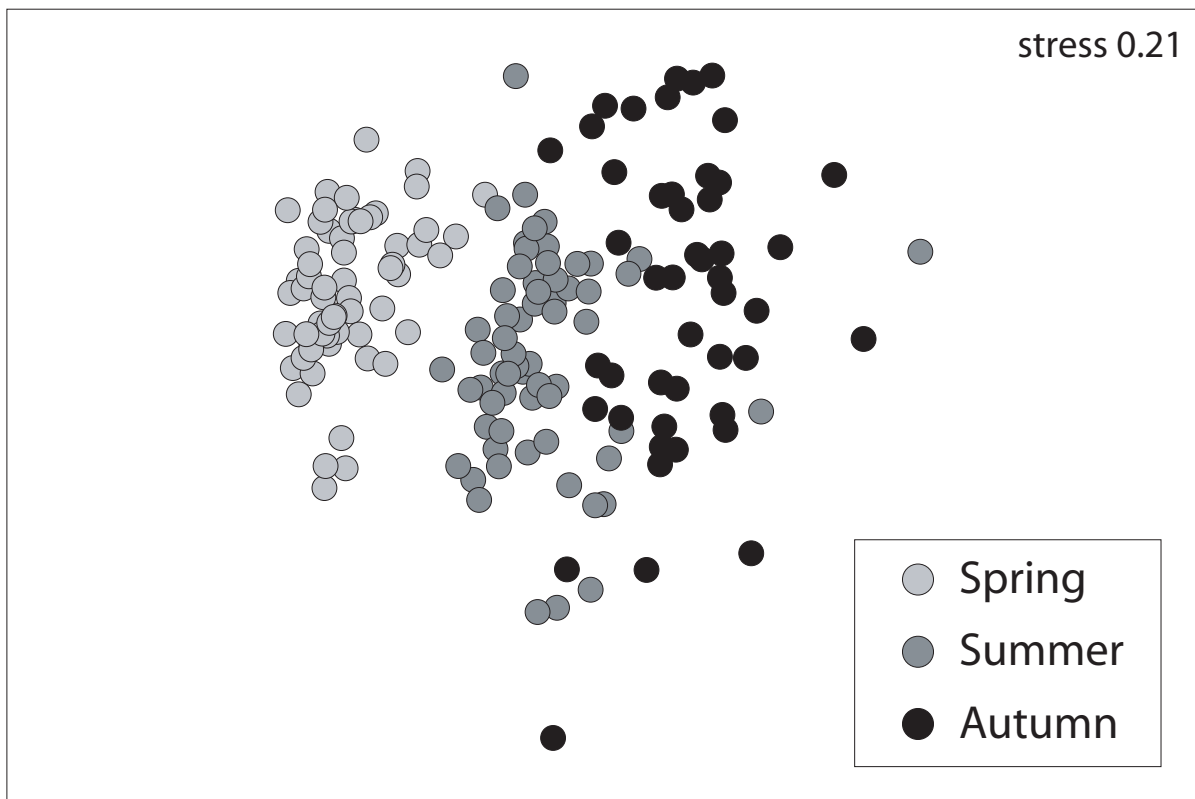


line figure 4
[Click here to download line figure: Fig 4review.eps](#)

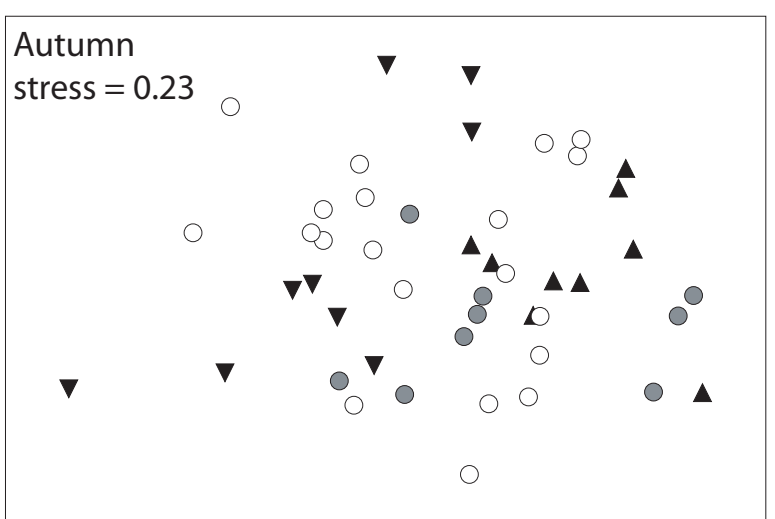
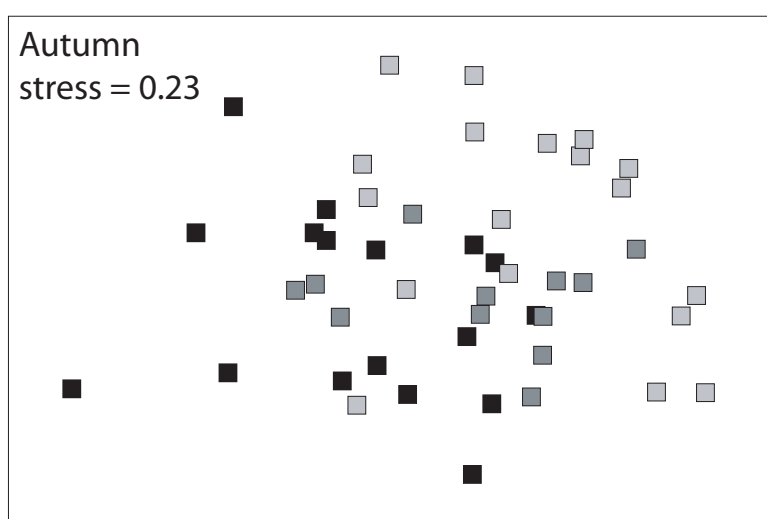
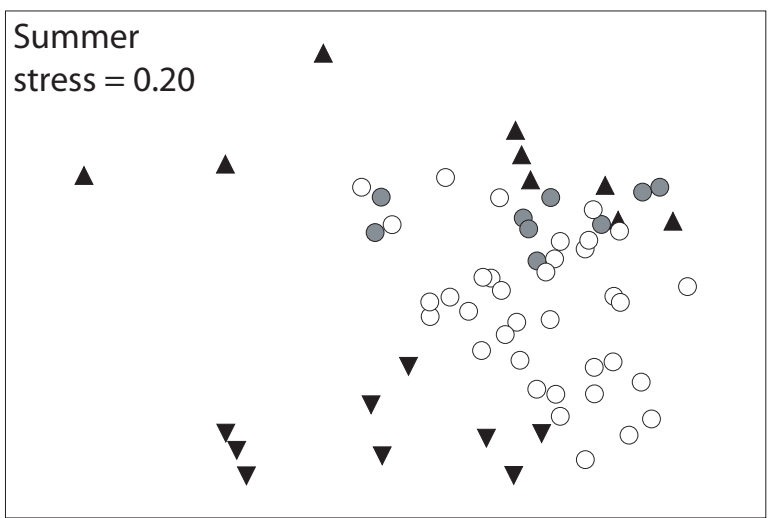
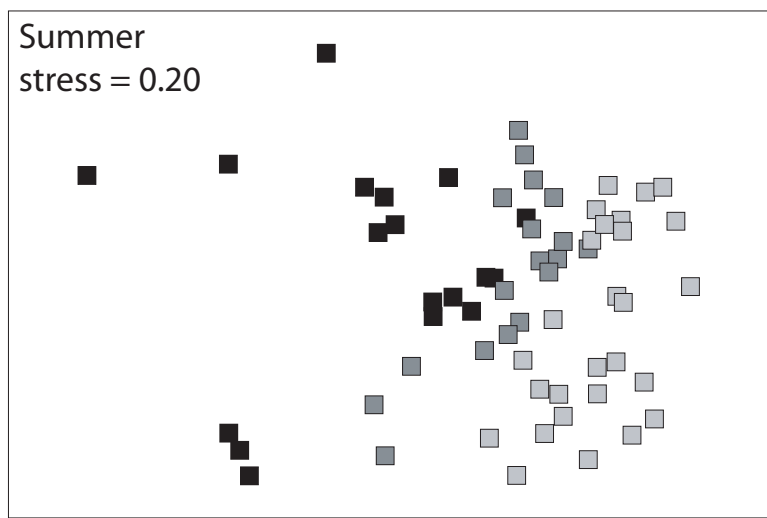
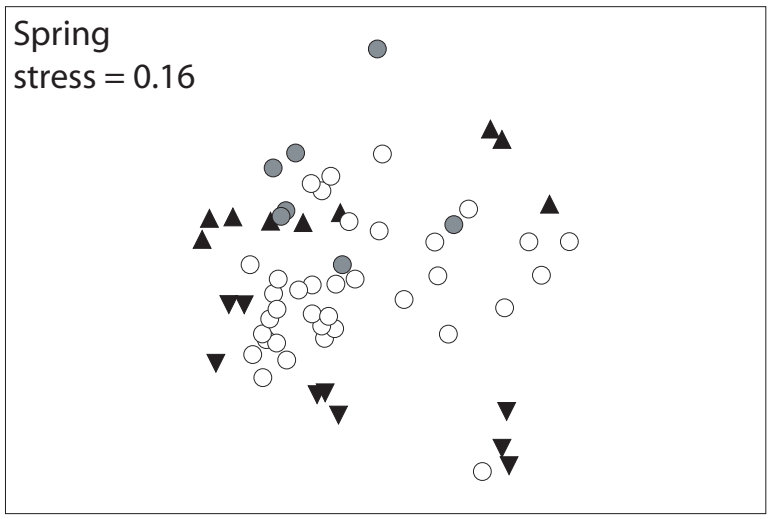
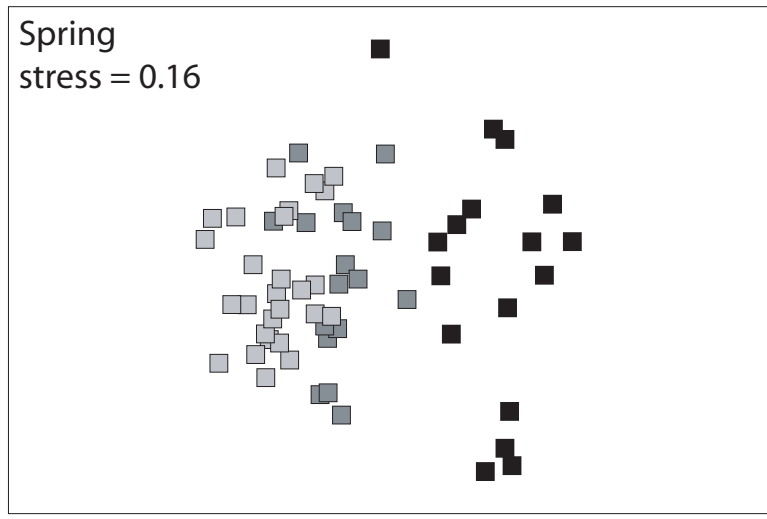
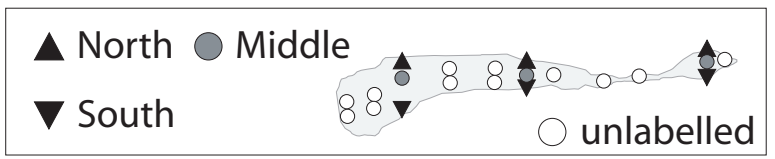


line figure 5

[Click here to download line figure: Fig 5review.eps](#)



line figure 6
[Click here to download line figure: Fig 6review.eps](#)



line figure 7

[Click here to download line figure: Fig 7review.eps](#)

