Deep-Sea Research II 56 (2009) 1763–1774

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Benthic species diversity along a depth gradient: Boston Harbor to Lydonia Canyon

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ARTICLE INFO

Available online 23 June 2009

Keywords:
Continental shelf
Continental slope
Log-series *alpha*
Expected species diversity
Massachusetts Bay
Georges Bank

ABSTRACT

Benthic infaunal samples collected from depths ranging from 5.9 to 2180 m, from nearshore in Boston Harbor to offshore on the continental slope off the coast of Massachusetts, USA, were evaluated for changes in diversity with depth using expected species at a subsample size of 100, ES(100), as well as Fisher's log-series *alpha*. All samples were processed with fine mesh (0.3 mm) screens and identified by the same team of researchers, who provided a high and comparable level of expertise. Both measures of diversity were made at the single sample level. An analysis of the variation in these measures, based on a linear mixed model, showed that the largest source of variation was due to depth followed by stations within the same depth range. Variation between cruises/years was relatively small. Communities from the shallowest harbor stations out to 168 m at the edge of the continental shelf had a wide range of diversities, but exhibited no apparent pattern of change with depth or sediment type. The highest diversities were found at mid-slope depths (1220–1350 m). Diversities at 2065–2180 m overlapped with those from mid-slope depths, but were generally lower.

1. Introduction

Measurement of marine benthic species diversity and the pattern of change in the diversity of soft-sediment marine benthic communities with depth has now been debated in the literature for several decades (Sanders, 1968; Gray, 1994; Gray et al., 1997; Rex et al.. 2000; Levin et al., 2001). Large-scale global patterns, for at least a portion of the infauna, have been discussed by Rex et al. (1993). Data sets for the purpose of comparing communities at different depths in the same geographical region or between regions in different parts of the world were provided by Gray (1994) and Gray et al. (1997), who argued that the diversity of shallow-water and deep-sea communities did not differ as much as previously proposed by, for example, Grassle and Maciolek (1992). The debate is hindered, however, by the use of different methods, especially the mesh size of screens used to process samples, and uncertainty concerning the validity of comparing samples identified by different teams of researchers with possibly differing levels of taxonomic expertise. For example, Gray's studies are based on samples processed with 0.5- or 1.0-mm-mesh sieves and cannot be compared directly with samples from similar depths processed on finer 0.3-mm-mesh screens, which sample the entire macrofaunal community. As pointed out by Levin et al. (2001), samples collected on Georges Bank and along the east coast of the United States during the Minerals Management Service's (MMS's) Atlantic Continental Slope and Rise (ACSAR) program of the 1980s were unique in terms of consistency of sample collection and preparation as well as taxonomic analysis.

In addition to inconsistent methodology, benthic ecologists have used a variety of statistical measures of diversity, each measure having specific strengths and weakness (Carney, 2007). Magurran (1988) classifies diversity indices into three categories: (1) indices based on the proportional abundances of species (e.g., the Shannon [1948] information index); (2) species richness indices, e.g., rarefaction, developed by Sanders (1968) and modified by Hurlbert (1971); and (3) species abundance indices, e.g., Fisher's log-series *alpha* (Fisher et al., 1943). All diversity indices, including Fisher's log-series *alpha*, the Shannon index, and expected species (Smith and Grassle, 1977) are defined in terms of individuals randomly sampled from a large population (Pielou, 1975; Magurran, 1988): this assumption clearly does not describe environmental samples collected from a patchy marine benthic environment. However, diversity at the sediment core or sample level satisfies these conditions, at least approximately, since there is little environmental variation within a single small sample.

The rarefaction method is considered an unbiased estimator useful for comparing samples of different sizes by reducing each sample to a uniform number of individuals, usually 100 (Smith

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doi:10.1016/j.dsr2.2009.05.031

et al., 1979). One problem with the use of this index is that it does not consider the composition of the entire sample; rather, it measures a point on the steep slope of the rarefaction curve rather than at the asymptote (Levin et al., 2001). The Shannon information index has been shown to have a strong linear relationship with ES(10) (Smith et al., 1979).

Fisher's log-series model, which is based on a parametric model of species abundance, has been widely used by entomologists and botanists but not by marine benthic ecologists, even though May (1975) demonstrated that Sanders–Hurlbert rarefaction curves for marine communities are often identical to those produced under the assumption that the distribution of individuals among species follows a log-series distribution. Taylor's (1978) studies of the properties of this index found that it was the best index for discriminating among subtly different sites. Hubbell (2001) considers *alpha* the fundamental biodiversity parameter and promoted the use of this index for studies of diversity in all environments.

Rex et al. (1997) and Levin et al. (2001), using data developed by Blake et al. (1987), Blake and Grassle (1994), Maciolek et al. (1987a, b), and Grassle and Maciolek (1992) from the ACSAR programs, confirmed maximum infaunal species diversity at mid-slope depths in the areas off the coasts of Massachusetts, New Jersey, and Delaware; patterns in the areas off North and South Carolina were not as clear. In this paper, we extend into shallow water the range of samples collected and identified by the research team that developed the ACSAR data. Although some identifications of the deep-sea material may eventually be refined as additional material is examined, the level of expertise applied to all samples is high and comparable across all studies. Samples were collected and analyzed between 1981 and 2007 from depths ranging from 5.9 m in Boston Harbor, Massachusetts, to 168 m on Georges Bank, to 2180 m on the continental slope off New England (Table 1). We consider species diversity based on ES(100) and log-series *alpha* within single samples, thus all regions and depths are compared in terms of local or small-scale diversity within a single and uniform benthic environment.

Table 1
Samples used for diversity estimates.

Station	Latitude (N)	Longitude (W)	Reference depth (m)	No. of samples used	Sample size (m^2)
Boston Harbor (2002–2007): 90 samples from 5 stations					
T07	42°17.36′	70°58.71′	5.9	18	0.04
T06	42°17.61′	70°56.66′	6.6	18	0.04
T03	42°19.81′	70°57.72′	8.7	18	0.04
T08	42°17.12′	70°54.75′	11.3	18	0.04
T05A	42°20.38′	70°57.64′	17.5	18	0.04
Massachusetts Bay Nearfield (2002–2007): 91 samples from 12 stations					
FF12	42°23.40′	70°53.98′	23.5	12	0.04
NF02	42°20.31′	70°49.69′	26.0	4	0.04
NF20	42°22.69′	70°50.69′	28.9	4	0.04
NF21	42°24.16′	70°50.19′	30.0	4	0.04
NF17	42°22.88′	70°48.89′	30.6	18	0.04
NF15	42°22.93′	70°49.67′	32.7	4	0.04
NF10	42°23.57′	70°50.29′	32.9	4	0.04
NF13	42°23.40′	70°49.35′	33.8	4	0.04
NF04	42°24.93′	70°48.39′	34.0	4	0.04
NF14	42°23.20′	70°49.36′	34.1	3	0.04
NF12	42°23.40′	70°49.83′	34.9	18	0.04
NF24	42°22.83′	70°48.10′	37.0	12	0.04
Massachusetts Bay Farfield (2002–2007: 48 samples from 4 stations					
F9	42°18.75′	70°39.40′	50	12	0.04
F5	42°08.00′	70°25.35′	65	12	0.04
F14	42°25.00′	70°39.29′	73.3	12	0.04
F4	42°17.30′	70°25.50′	90	12	0.04
Georges Bank (1981–1984): 1170 samples from 20 stations (# samples with <100 individuals)					
G15	41°27.5′	68°00.7′	38	24 (6)	<0.04
G1	41°13.0′	67°15.3′	55	72 (5)	<0.04
G10	40°42.0′	68°35.3′	66	71 (5)	<0.04
G4	40°50.7′	68°00.2′	67	66	<0.04
G13	40°29.5′	70°12.6′	70	72	<0.04
G2	40°59.0′	66°55.8′	79	72	<0.04
G13A	40°30.0′	71°00.5′	80	42	<0.04
G5	40°39.5′	67°46.2′	84	71	<0.04
G11	40°30.8′	68°33.7′	86	66	<0.04
G3	40°53.7′	66°46.5′	100	72 (1)	<0.04
G6	40°34.3′	67°45.3′	102	72 (71)	<0.04
G12	40°22.2′	68°30.2′	108	65	<0.04
G17	40°35.0′	67°11.7′	141	48 (14)	<0.04
G16	40°34.2′	67°12.3′	142	72 (3)	<0.04
G9	40°26.7′	68°09.8′	144	66	<0.04
G8	40°27.1′	67°37.4′	152	71	<0.04
G18	40°33.5′	67°13.7′	152	46 (3)	<0.04
G7	40°28.8′	67°43.2′	165	24	<0.04
G7A	40°32.1′	67°44.2′	167	48 (1)	<0.04
G14A	41°57.5′	68°31.0′	168	30 (1)	<0.04
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North Atlantic (1984–1986): 190 samples from 14 stations (# samples with <100 individuals)					
N11	40°01.30′	70°55.14′	255	6	0.09
N4	40°21.24′	67°32.31′	550	9	0.09
N12	39°54.32′	70°55.09′	550	15	0.09
N7	40°27.54′	67°40.34′	560	8	0.09
N9	39°50.48′	70°01.73′	1220	15	0.09
N10	39°48.16′	70°05.37′	1220	15	0.09
N13	39°48.39′	70°54.98′	1250	15	0.09
N3	41°01.40′	66°20.20′	1350	18	0.09
N5	40°05.15′	67°29.99′	2065	18	0.09
N2	40°57.21′	66°13.85′	2100	18 (2)	0.09
N14	39°40.95′	70°54.29′	2105	6	0.09
N6	40°05.10′	67°29.30′	2115	15 (1)	0.09
N15	39°40.05′	70°54.27′	2155	14 (1)	0.09
N8	40°10.32′	67°37.37′	2180	18	0.09

2. Materials and methods

A subset of 1589 samples was used for the present analyses (Table 1). All samples were processed using 0.3-μm-mesh screens and the fauna identified by a group of taxonomists who, with few exceptions, worked together on all four studies. When necessary, experts in certain faunal groups were consulted to verify identifications. In all studies, animals attached to hard surfaces such as rocks and shells, and parasitic and planktonic species were not included in calculations of diversity. Infaunal species for which the identification was uncertain (e.g., juveniles, anterior fragments) were not included in diversity estimates. The database includes 741,555 individual organisms in 1879 taxa. Sediment composition was measured in each of the study areas (see Maciolek-Blake et al., 1985; Maciolek et al., 1987b, 2008a, b for methods and detailed results). These four benthic surveys provide insight into the natural variation in small-scale benthic diversity across time, space, and depth.

2.1. Boston Harbor

Boston Harbor had a long history of anthropogenic impacts dating back at least to colonial times (Loud, 1923). In addition to the damming of rivers and the filling of salt marshes and shallow embayments to create the present footprint of the city, the direct discharge of waste products had a profound impact on the composition of the biological communities in the harbor. Prior to the 1950s, raw sewage was discharged into Boston Harbor. In 1972, the Federal Clean Water Act (CWA) mandated secondary treatment for all sewage discharges to coastal waters, and the State of Massachusetts ultimately complied with this order. The