Dynamics of meiobenthic copepod populations: a long-term study (1973–1983)*

Bruce C. Coull & Bettye W. Dudley

Belle W. Baruch Institute for Marine Biology and Coastal Research, Department of Biology, and Marine Science Program,
University of South Carolina, Columbia, South Carolina 29208, USA

ABSTRACT: Eleven years of monthly (or fortnightly) monitoring of meiobenthic copepods at 2 subtidal estuarine sites (sand and mud) in South Carolina, USA indicates that the 2 communities are controlled by different mechanisms. The mud community is distinctly seasonal, whereas at the sand site seasonality is not pronounced. Sand-site copepods have been declining over the 11 yr and their number of species has decreased at the rate of about 1 yr^{-1}. There has been no significant change at the mud site. The decrease in copepod species at the sand site was correlated with a concommitant decrease in sediment median grain size and sorting. There were no significant long-term abundance cycles at either site. Twelve mo was the maximum statistically reliable periodicity recorded at either site; although some of the sand species had no periodicity. It appears that meiobenthic copepods respond primarily to short-term seasonal events. Thus, a 2 yr monitoring period should be sufficient to determine meiobenthic copepod seasonality patterns.

INTRODUCTION

Temporal studies of marine meiobenthos have traditionally been directed toward describing trends in abundance variability at the major taxon level (e.g. nematode, copepod). When species composition and population life history stages (e.g. males, females, juveniles,) are included, the studies tend to be of short duration (< 2 yr) or limited to 1 or a few closely clustered points in time. The seasonal pattern(s) discerned in such short interval studies are typically inferred to be 'the' seasonal pattern(s) of the species in question. Except for the 7 yr data set of Heip (1980) and Herman & Heip (1983) and earlier reports on 2 to 3 yr of the present data set (Coull & Vernberg 1975, Coull & Fleeger 1977) we are unaware of meiofaunal studies where continuous species and life history information have been collected for longer periods.

We report on 11 yr (1973–1983) of continuous sampling of the meiobenthic copepod taxocene at 2 subtidal sites (sand and mud) in a Southeastern United States salt marsh complex. Copepods (including nauplii)

numerically comprise 17 and 13 % of the total meiofauna at the mud and sand site, respectively, and were second and third in abundance to nematodes and gastrotrichs at these sites (Coull 1985b). The present study examines copepod species abundance patterns over time and the inherent community patterns within these copepod taxocenes.

This research was conducted at the Belle W. Baruch Institute for Marine Biology and Coastal Research's North Inlet Estuarine system, the only marine/estuarine site in the National Science Foundation's Long-Term Ecological Research network. North Inlet is a natural undisturbed ecosystem maintained for conservation and research; thus an ideal setting to determine natural changes, fluctuations and trends in populations. The questions central to this research are: How do natural populations fluctuate, i.e. is there continuity over time in abundance and/or species abundance? What factors control the changes or the continuity? Are there different seasonal or long-term patterns in sand and mud assemblages separated by less than 2 km? Does ovigerous female abundance precede juvenile abundance, precede total abundance, etc., and how long must one sample to discern consistent seasonal patterns in meiobenthic populations?

METHODS AND MATERIALS

Field and laboratory. Details of meiofauna sampling/extraction and collection of the associated physical data are presented in Coull (1985b); we will not reiterate them here. Suffice it to say that sampling, with 2, 3 or 4 replicates on each sampling date, was performed in standard meiofaunal fashion. Samples were taken monthly 1973–80 and fortnightly 1981–83. Mud sample extraction was by Ludox centrifugation (deJonge & Boumann 1977); sand sample extraction by shaking-decantation (Wieser 1960).

Each copepod was removed identified to species, sexed, assessed as to status of eggs and defined as a juvenile or an adult. Prior to October 1975 all copepods from each of 4 replicates were placed in the same container to await identification. Thus between replicate variance could not be calculated for species data prior to that date. Starting October 1975 species were identified by replicate. All copepod data are presented as number 10 cm^{-2} following the admonishment of Hicks & Coull (1983, p. 83) to avoid percentage data.

Data analyses. All data have been stored on the University of South Carolina's IBM 3801 computer as SAS (SAS Institute, 1982) data sets. Autoregression analysis was used to determine whether the abundance of an individual species was increasing or decreasing through time. Autoregression was used because, as with most time series data, sampling dates were autocorrelated and the error term was not independent across time. Other statistical analyses are as outlined in Coull (1985b).

RESULTS

Details of the physical factors are provided in Coull (1985b). Briefly, temperature and salinity varied seasonally at both sites with maximum temperatures in August and minimum salinities in late winter/early spring (see Coull 1985b, Fig. 2). Neither temperature nor salinity was significantly different among years. At the mud site sediment, median grain size (mgs) ranged from 29 to 63 μm; sorting coefficient (S_o) from 0.95 to 2.50 ($\bar{x} = 1.46$) and percent silt-clay (% SC) from 59 to 69 %. There were no significant between year differences in any of these 3 parameters at the mud site. At the sand site, however, both median grain size and sorting coefficient decreased significantly (ANOVA, $p = 0.001$ and $p = 0.0002$ respectively) between the period 1973–79 and 1983. Median grain size decreased by ~ 93 μm and sorting coefficient by 0.22 units. See Coull (1985b) for details.

Seventy-three copepod species were identified from the 2 sites over the 11 yr; 47 at the mud site and 56 at the sand site (Tables 1 & 2). The mean number of copepod species per sampling date ranged from 2 to 15 at the mud site and 1 to 16 at the sand site. The mean number of species during the entire 11 yr was 6.9 at the mud site and 5.7 at the sand site. There was no significant difference between months in the number of species at either site (1-way ANOVA: mud, df = 11, F = 1.21, p = 0.24; sand, df = 11, F = 1.79, p = 0.06) nor was there any significant difference between years at the mud site (df = 10, F = 1.55, p = 0.12). There was a significant difference between years in the number of species (df = 10, F = 3.64, p ≤ 0.0001) at the sand site. Scheffé multiple comparisons indicate that there were significantly fewer species in 1981 and 1983 than in all other years at the sand site. Fig. 1 illustrates the yearly number of species at the sand site and their substantial decline over the study period.

The 6 most abundant species at each site were chosen for more detailed analysis. At the mud site these species comprised 88.5 % of all copepods collected (Table 1) and at the sand site made up 84.4 % (Table 2).

We have plotted the mean abundance of total individuals, females, ovigerous females, and copepodites for *Leptastacus macronyx*, at the sand site for each sampling (Fig. 2) and in Fig. 3 we have plotted similar data for *Halicyclops coulli* from the mud site. We selected these species to plot the 'every-point' data because *L. macronyx* is the dominant sand site species (Table 2) and demonstrates a pattern of long-term decline common to all the interstitial species at the sand site. *H. coulli* was chosen because it is a species with 1 repeatable abundance peak per year (Fig. 3). Similar plots for the other 5 most abundant species at each site, while providing the mean ± SE for each sampling when replicates were maintained, are 'busy' and difficult to interpret. Thus, we have plotted the monthly means (i.e. the means of 11 January's, 11 February's, etc.) and the yearly means (i.e. mean for 1973, 1974, etc.) for the other 5 species at each site. In these plots (Fig. 4 & 5), only the total copepods values are plotted. Life history stages were not included because in every case the abundance patterns of the life history stages (females, ovigerous females, copepodites) were coincident in time with the 'total' abundance patterns. *A. priori* we expected time to be offset, e.g. first a peak (or lull) in ovigerous females, then copepodites, then totals but this was not the case when the every-point data for each category were overlain.

Each of the 6 most abundant species at the mud site (Fig. 3 & 4) varied seasonally (Months 1 to 3 = winter, Months 4 to 6 = spring, Months 7 to 9 = summer, Months 10 to 12 = autumn; 1-way ANOVA: season/abundance, p ≤ 0.0001 for all 6 species). Scheffé com-

Table 1. Eleven yr (Jan 1973 to Dec 1983) mean abundance of each copepod species collected at the mud site. Summary statistics are not provided for species which had a mean 11-yr total abundance of < 0.1 ind 10 cm^{-2}. All values (columns) – except for % abundance, SD of mean and ratio females/males – given as mean abundance 10 cm^{-2}

Species	% of Total copepods	Mean abun-dance	Range	SD of Mean	♀♀	Ovigerous ♀♀	Cope-podites	Ratio female/ males
Pseudobradya pulchella Sars	18.0	23.2	0–406	48.9	9.4	2.6	10.9	3.2
Microarthridion littorale (Poppe)	17.9	23.0	0–258	30.9	10.4	3.7	8.7	2.7
Halicyclops coulli Herbst	16.2	20.8	0–379	34.6	10.0	3.1	6.6	2.4
Enhydrosoma propinquum (Brady)	12.9	16.7	0–195	27.2	9.0	3.3	3.0	1.9
Paronychocamptus wilsoni (Coull)	12.9	16.7	0–406	38.1	7.8	3.7	5.5	2.4
Halectinosoma winonae Coull	10.6	13.8	0–244	28.6	6.5	0.8	6.4	6.8
Scottolana canadensis (Wilson)	3.4	4.4	0– 97	12.7	1.7	0.4	1.5	1.4
Enhydrosoma baruchi Coul	1.9	2.5	0– 44	5.1	1.7	0.2	0.4	4.0
Zausodes arenicolus Wilson	0.9	1.2	0– 28	3.2	0.8	0.01	0.2	4.4
Halectinosoma sp. 2	0.9	1.2	0– 38	4.3	0.5	0.8	0.6	7.6
Diarthrodes aegidius (Brian)	0.8	1.1	0– 62	4.6	0.6	0.02	0.3	2.8
Cyclopoid sp. 2	0.7	0.9	0–120	6.6	0.5	0.1	0.2	4.9
Nannopus palustris Brady	0.5	0.6	0– 13	1.5	0.4	0.04	0.1	4.8
Harpacticus sp.	0.3	0.4	0– 56	3.3	0.1	0.02	0.09	0.8
Cyclopoid sp. 3	0.2	0.3	0– 7	1.0	0.2	0.03	0.04	6.4
Clymenestra rostrata (Brady)	0.2	0.2	0– 5	2.1	0.1	0.01	0.08	4.6
Stenhelia (D) bifidia Coull	0.2	0.2	0– 2	0.1	0.1	0.01	0.04	18.5
Mesochra pygmaea (Claus)	0.2	0.2	0– 13	0.9	0.1	0.01	0.02	2.7
Longipedia americana Wells	0.1	0.1	0– 11	0.8	0.05	0	0	6.2
Ameira sp.	0.1	0.1	0– 6	0.6	0.09	0.05	0	3.4
Nitocra affinis Gurney	0.1	0.1	0– 17	1.1	0.09	0	0.02	5.4
Thompsonula hyaenae (Thompson)	0.1	0.1	0– 11	0.8	0.09	0.01	0.01	8.5

All following species had mean abundances of < 0.1 ind 10 cm^{-2}

Metis holothuriae (Edwards)	*Nitocra* sp.	*Eutepina acutifrons* (Dana)
Laophonte cornuta (Philippi)	*Stenhelia (D).* sp.	*Laophontidae* sp.
Cletoididae sp.	*Amphiascus* sp.	*Altheutha* sp.
Heteropsyllus nunni Coull	*Tegastes* sp.	*Tryphoema* sp.
Quinquelaophonte capillata (Wilson)	*Stenhelia (D) normani* Monard	*Rhizothrix* sp.
Leptocaris mangalis Por	*Amphiascopsis cinctus* (Claus)	*Phyllodopsyllus* sp.
Onychocamptus sp.	*Robertsonia propinquum* (Scott)	*Leptastacus macronyx* (Scott)
Tisbe sp.	*Diagoniceps bocki* Lang	*Diosaccidae* sp.
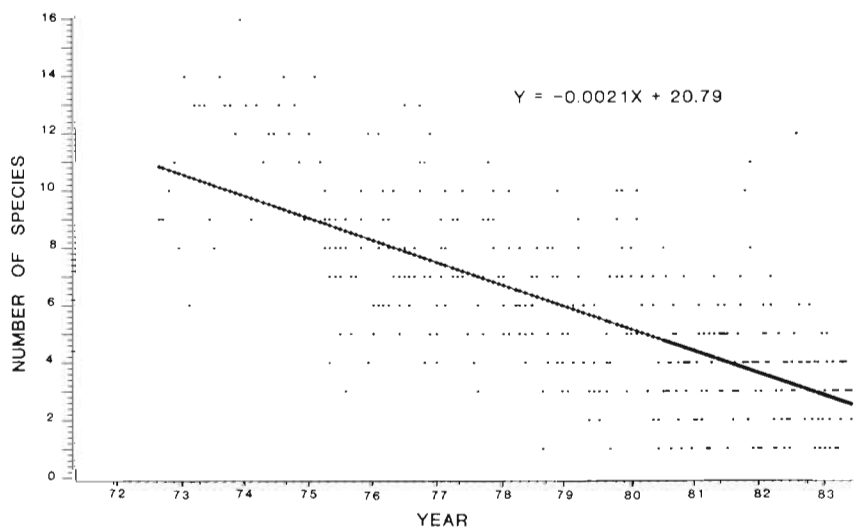
Fig. 1. Number of copepod species at sand site over the 11 yr. Note decrease in number of species

$Y = -0.0021X + 20.79$

Table 2. Eleven yr (Jan 1973 to Dec 1983) mean abundance of each copepod species collected at the sand site. Summary statistics are not provided for species which had a mean 11-yr total abundance of < 0.1 ind 10 cm^{-2}. All values (columns) – except for % abundance, SD of mean, and female/male ratio – are given as mean abundance 10 cm^{-2}

Species	% of Total copepods	Mean abundance	Range	SD of mean	♀♀	Ovigerous ♀♀	Copepodites	Ratio female/males
Leptastacus macronyx (Scott)	39.9	43.9	0–699	86.1	22.4	6.3	5.9	1.4
Thompsonula hyaenae (Thompson)	13.9	15.4	0–991	57.3	5.0	1.4	6.3	1.2
Kliopsyllus constrictus (Nicholls)	9.6	10.6	0–359	29.8	5.9	1.8	1.0	1.6
Arenostella spinicauda Wilson	8.7	9.6	0–220	20.6	7.4	2.0	1.1	7.2
Apodopsyllus unguiformis Coull & Hogue	8.7	8.4	0–410	27.9	4.2	0.8	1.1	1.3
Halectinosoma winonae Coull	4.7	5.1	0–105	11.6	3.7	0.6	0.01	4.6
Protosammotopa wilsoni (Wells)	3.4	3.7	0– 90	7.8	1.5	0.7	0.9	1.1
Ameira parvula (Claus)	2.9	3.2	0–257	16.4	1.7	0.5	0.4	1.5
Hastigerella leptoderma (Klie)	2.6	2.9	0–140	10.6	2.2	0.3	0.3	5.7
Zausodes arenicolus Wilson	1.3	1.4	0– 60	5.2	0.7	0.01	0.2	1.6
Heteropsyllus nunni Coull	1.1	1.2	0– 47	4.3	0.6	0.2	0.2	1.6
Paronychocamptus wilsoni (Coull)	0.8	0.8	0– 21	3.2	0.5	0.2	0.1	2.5
Pseudobradya pulchella Sars	0.7	0.8	0– 79	4.8	0.5	0.03	0.2	1.9
Laophonte cornuta Philippi	0.3	0.3	0– 15	1.3	0.2	0.03	0.03	6.4
Arenopontia arenardia (Pennak)	0.3	0.3	0– 8	1.2	0.2	0.04	0.01	3.2
Halicyclops coulli Herbst	0.3	0.3	0– 14	1.6	0.2	0.02	0.01	5.8
Mesochra pygmaea (Claus)	0.2	0.2	0– 17	1.3	0.1	0.02	0.02	3.6
Diathrodes aegidius (Brian)	0.1	0.1	0– 8	0.7	0.1	0	0.02	6.8
Enhydrosoma propinquum (Brady)	0.1	0.1	0– 1	0.8	0.05	0	0.05	1.6
Harpacticus sp.	0.1	0.1	0– 16	1.1	0.09	0.04	0.01	4.9
Rhizothrix gracilis (Scott)	0.1	0.1	0– 12	0.8	0.09	0.04	0	4.9
Longipedia americana Wells	0.1	0.1	0– 12	0.8	0.08	0	0.01	5.1
Microarthridion littorale (Poppe)	0.1	0.1	0– 12	0.7	0.03	0.02	0.1	1.8
Leptopontia curvicaudata (Scott)	0.1	0.1	0– 7	0.6	0.09	0.03	0	8.5
Rhizothrix sp.	0.1	0.1	0– 5	0.6	0.07	0.03	0.02	0
Stenhelia (D) bifidia Coull	0.1	0.1	0– 17	0.9	0.05	0	0.01	0
Stenocaris sp.	0.1	0.1	0– 4	0.4	0.05	0.02	0.01	0
Cyclopoid sp.	0.1	0.1	0– 14	0.8	0.06	0.04	0	0
Halectinosoma sp.	0.1	0.1	0– 10	0.6	0.04	0.01	0.01	2.6

All following species had mean abundances of < 0.1 ind 10 cm^{-2}

Enhydrosoma baruchi Coull	Cletoididae sp.	Robertsonia propinquum (Scott)
Tryphoema sp.	Nannopus palustris Brady	Nitocra affinis Gurney
Scottolana canadensis (Wilson)	Psyllocamptus sp.	Amphiascopsis cinctus (Claus)
Paraleptastacus spinicaudia (T & A Scott)	Arenopontia subterranea Kunz	Schizopera sp.
Onychocamptus sp.	Peltidium sp.	Leptocaris mangalis Por
Diosaccidae sp.	Normanella sp.	Amphiascus sp.
Metis holothuriae (Edwards)	Scottosyllus pararobertsonia Lang	Stenhelia (D) sp.
Phyllopodopsyllus sp.	Thalestridae sp.	Paralaophonte congenera (Sars)
Ameira sp.	Leptastacus minutus Chappuis	

parisons (Table 3) demonstrated which seasons were different for each species.

At the sand site there were no significant seasonal changes in Leptastacus macronyx (1-way ANOVA: season/abundance, p = 0.636) or Kliopsyllus constrictus (p = 0.717) (Fig. 2 & 5; Table 4). The remaining 4 dominant species, Thompsonula hyaenae, Apodopsyllus unguiformis, Halectinosoma winonae and Arenosetella spinicauda were seasonal (Fig. 5; Table 4). Note that H. winonae occurs among the

dominant species at both the sand and the mud site (Fig. 4 & 5), but reaches maximum abundance at different times of the year at each site, autumn in mud; summer in sand (Fig. 4 & 5; Tables 3 & 4).

One of the dominant species at the mud site (Halicyclops coulli) and 3 at the sand site (Leptastacus macronyx, Kliopsyllus constrictus, Arenosetella spinicauda) declined significantly in abundance over the 11 yr. The autoregression slopes and significance for the 4 species are: H. coulli (slope = −0.050;
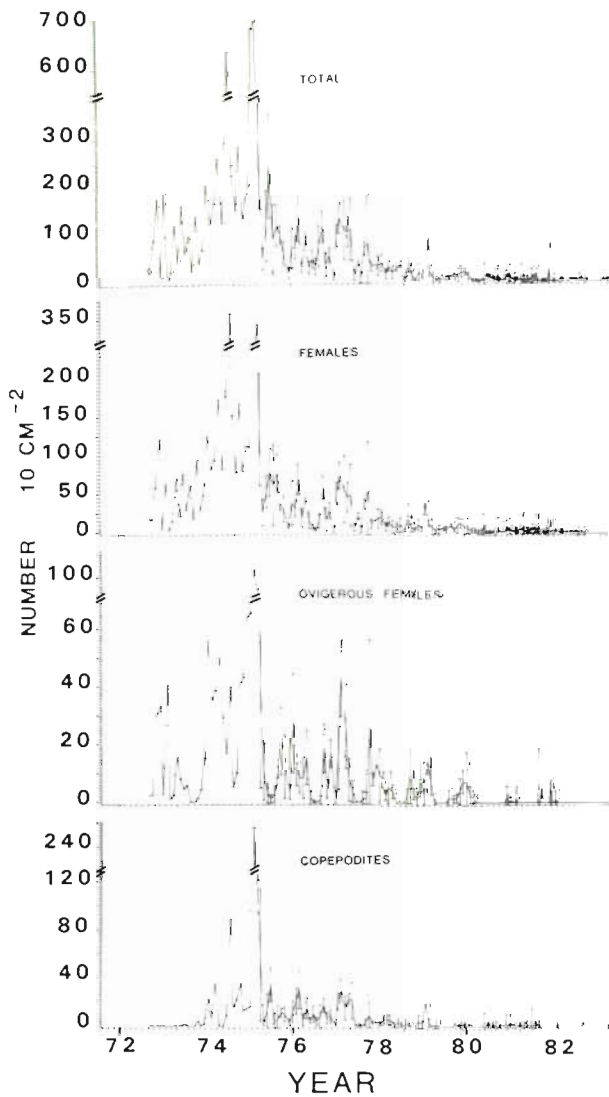
Fig. 2. *Leptastacus macronyx.* Mean abundance (± SE) of total number, females, ovigerous females, and copepodites for each sampling time at sand site (Jan 1973 to Dec 1983). Year labels, e.g 72, 74, 76, are placed at yearly midpoints (1 Jul)

Fig. 3. *Halicyclops coulli.* Mean abundance (± SE) of total number, females, ovigerous females, and copepodites for each sampling time at mud site (Jan 1973 to Dec 1983). Year labels, e.g. 73, 75, 77, are placed at yearly midpoints (1 Jul)

p = 0.013); *L. macronyx* (slope = −0.047; p = 0.006); *K. constrictus* (slope = −0.012; p = 0.009) and *A. spinicauda* (slope = −0.067; p ≤ 0.001). All 3 declining sand species are interstitial forms as they occupy the spaces between sand grains, whereas 2 of the 3 species that did not decline significantly (*T. hyaenae* and *H. winonae*) were epibenthic forms which occupy the sediment surface. *Apodopsyllus unguiformis* (no significant decline) is also an interstitial species.

Time series (spectral) analyses indicated no periodicity of greater than 1 yr in the abundance of the dominant and dwelling species (Fig. 6). Two of the 6 mud species (*Pseudobradya pulchella* and *Halectinosoma winonae*) also had cycles at 6 mo, as did the
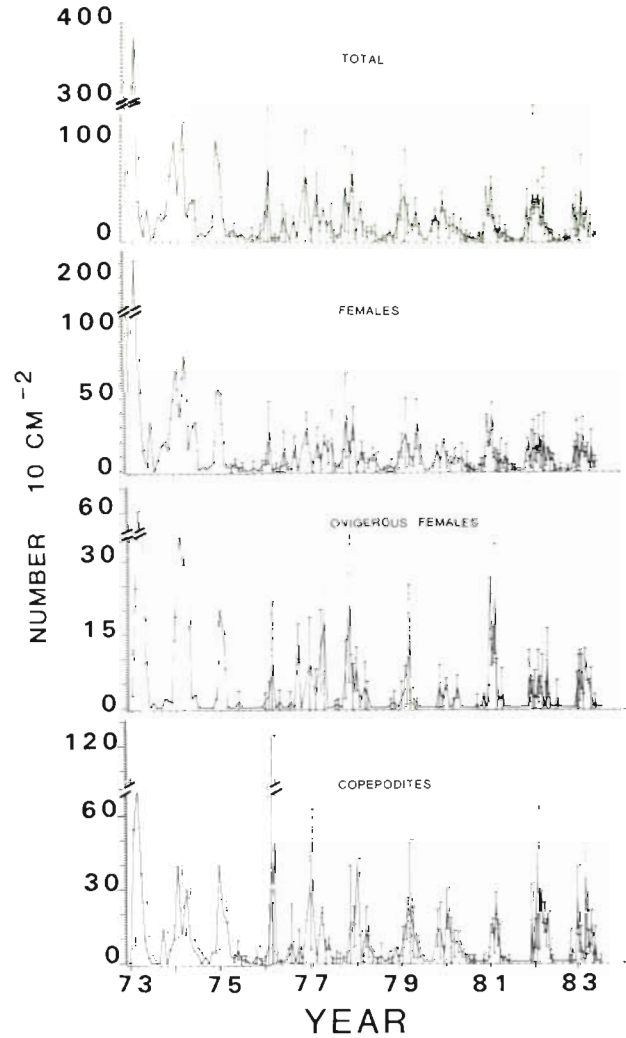
abundance of total copepods at the mud site (Coull 1985b).

At the sand site the spectral plots indicated that *Apodopsyllus unguiformis* and *Halectinosoma winonae* had major periodicities at 1 yr. The other 4 dominant species have spectral density maxima at varying periodicities: *Leptastacus macronyx* (33 to 66 mo), *Thompsonula hyaenae* (6, 12, 33, 66 mo), *Kliopsyllus constrictus* (6, 44 mo), *Arenosetella spinicauda* (6, 12, 33, 44 mo) (Fig. 7). The data-set length is 132 mo and the coincidence of spectral density maxima at 66 mo ($^1/_2$ the wave length), 44 mo ($^1/_3$ the wave length) or 33 mo ($^1/_4$ the wave) suggested that these supposed 'long term' periodicities may have been harmonics of the total data set, i.e. an interaction between data-set length and analysis procedure. To
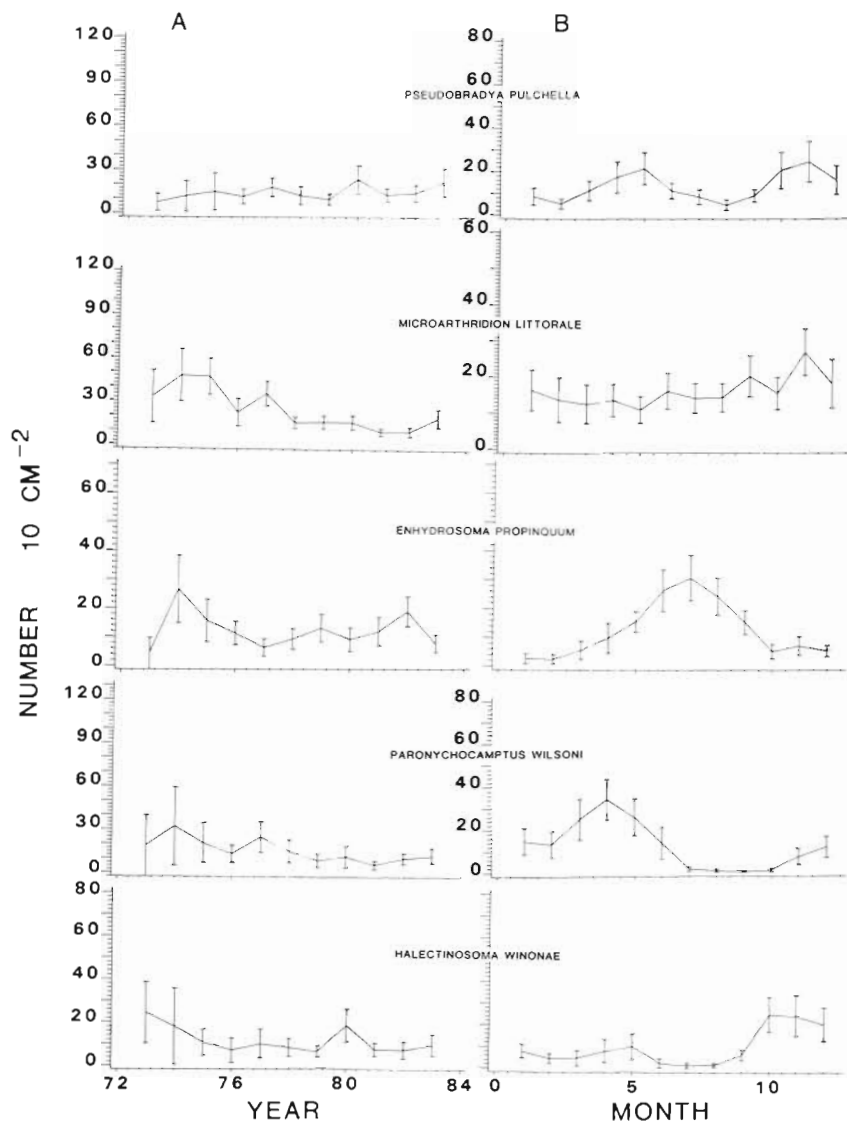
Fig. 4. (A) Yearly mean total abundances (± SE) of the other 5 most abundant copepod species at mud site. (B) Monthly mean abundances (± SE) of 5 species at mud site

test whether this was an artifact of record length, we ran 96 continuous mo (8 yr); 84 continuous mo (7 yr); and 72 continuous mo (6 yr) of individual abundance data to determine if the supposed 'long-term' cycles were real or a function of the total data-set length (a harmonic). Indeed, in all cases, spectral density maxima were obtained at the predicted harmonic interval, with only the 6 mo cycle persisting for *Arenosetella spinicauda* and *Thomsonula hyaenae*. All other peaks then were artifacts of the analysis and we could not discern any cycles longer than 1 yr. While we have already demonstrated the distinct seasonality within the mud species and relative lack of distinct seasonality in the sand dwellers (Fig. 2 to 5; Tables 3 & 4), spectral analysis allows a view of potential longer term periodicities; there appears to be little long-term periodicity at either site.

DISCUSSION

Number of species

The number of species did not change seasonally or over the 11 yr at the mud site, but while there was no seasonal change at the sand site, the number of species decreased over the study period (Fig. 1). This decrease of approximately 1 species per year may well be due to the decreasing trend in total copepod abundance at the sand site concomitant with the lower median grain size and increased sediment sorting (Coull 1985a, b). The finer, better sorted sediments have apparently eliminated the interstitial habitat for *Leptastacus macronyx, Kliopsyllus constrictus, Arenosetella spinicauda* and other less abundant species not discussed individually.
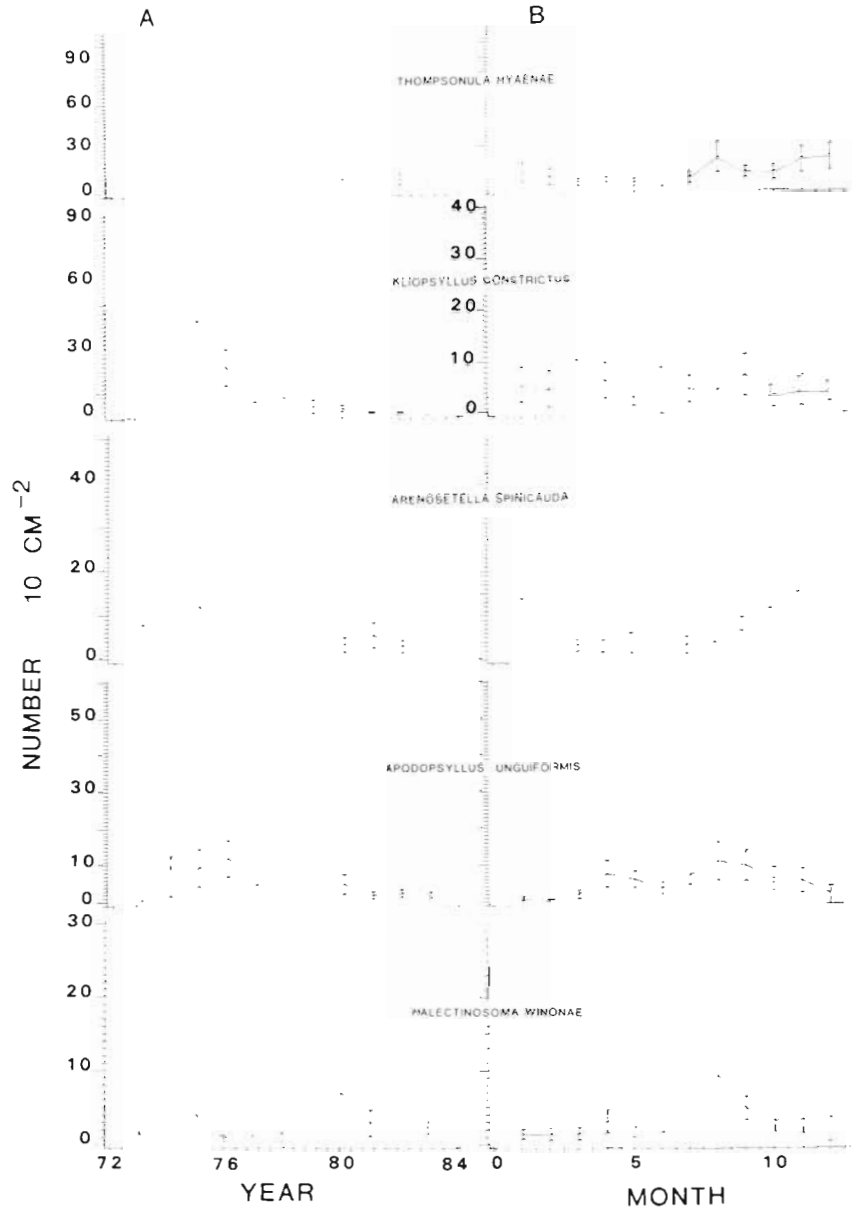
Fig. 5. (A) Yearly mean total abundances (± SE) of the other 5 most abundant copepod species at sand site. (B) Monthly mean abundances (± SE) of 5 species at sand site

Coull & Fleeger (1977), utilizing the first 3 yr (1973–75) of this present data set, concluded that the number of species did not change seasonally, or over a 3 yr period, at either site. However, they suggested that the mechanisms controlling diversity constancy were different, i.e. varied microhabitats (= spatial heterogeneity) in sand and distinct seasonal suites of species (temporal separation) in mud. Since that time, decreased grain size and increased sorting ($S_o \sim 1$) have apparently reduced the sand microhabitat heterogeneity and thus the diversity observed by Coull & Fleeger (1977). With no sedimentological or apparent physical changes at the mud site, the pattern persists and the seasonal switching of species suites continues to maintain constant species numbers.

Seasonal abundance

Coull & Vernberg (1975) reported on seasonal abundance and reproductive patterns of the dominant species at both sites for 28 mo (Sep 1972 to Dec 1974). The thrust of their discussion was directed at whether the dominant species during the 2.3 yr period reproduced continuously or cyclically, as well as observation on the seasonal cycling of abundances. At the mud site the seasonal abundance patterns based on the full 11 yr are the same as reported by Coull & Vernberg for 2.3 yr, with the exception of *Pseudobradya pulchella*. There have been some nomenclatural changes and additions of species since the Coull & Vernberg report; *Halectinosoma* sp. of Coull & Vernberg is now *H.*

Table 3. Seasonal rank abundance of the 6 most abundant copepod species at the mud site. Seasons with common underlines are not significantly different in abundance (Scheffé multiple comparison method; experiment wise error rate p ≦ 0.05). Seasons are W: winter; Sp: spring; Su: summer; A: autumn. The 1-way ANOVA, comparing a species abundance and season, indicated there were significant differences between seasons (p ≦ 0.0001 in every case)

Species	Season (mean abundance 10 cm⁻² for that season)			
Pseudobradya pulchella	Sp (42)	A (32)	W (12)	Su (7)
Microarthridion littorale	A (35)	W (20)	Su (19)	Sp (17)
Halicyclops coulli	Su (45)	Sp (17)	Au (16)	W (5)
Enhydrosoma propinquum	Su (30)	Sp (28)	A (7)	W (4)
Paronychocamptus wilsoni	Sp (36)	W (26)	A (6)	Su (1)
Halectinosoma winonae	A (35)	Sp (7)	W (7)	Su (4)

Table 4. Seasonal rank abundance of the 6 most abundant copepod species at the sand site. Seasons with common underlines are not significantly different in abundance (Scheffé multiple comparison method; experiment wise error rate p ≦ 0.05). Seasons are W: winter; Sp: spring; Su: summer; A: autumn. The p value next to the species name is the probability that there are differences between seasons (from the 1-way ANOVA comparing abundance and season)

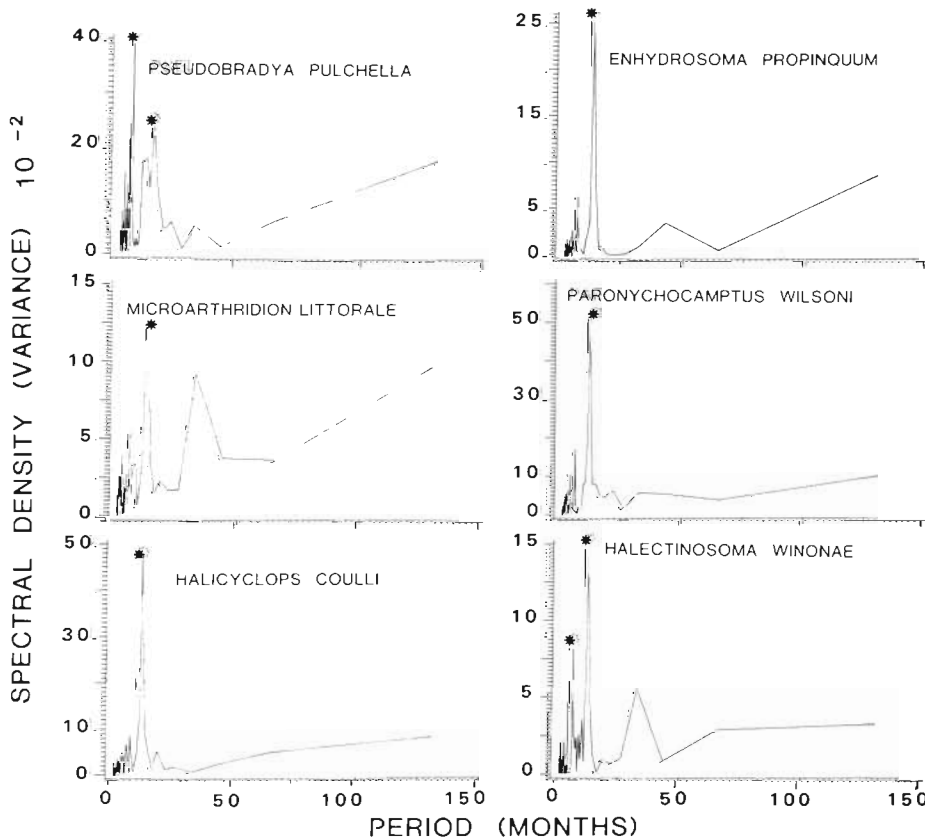| Species (p > F)		Season (mean abundance 10 cm⁻² for that season)			
Leptastacus macronyx	(p = 0.636)	Su (56)	A (45)	W (36)	Sp (29)
Thompsonula hyaenae	(p ≦ 0.0001)	A (23)	Su (18)	W (10)	Sp (4)
Kliopsyllus constrictus	(p = 0.7173)	A (13)	Su (12)	W (11)	Sp (4)
Arenostella spinicauda	(p = 0.0031)	A (15)	W (10)	Su (5)	Sp (4)
Apodopsyllus unguiformis	(p ≦ 0.0001)	Su (15)	Sp (12)	A (6)	W (1)
Halectinosoma winonae	(p = 0.0004)	Su (10)	A (4)	Sp (3)	W (1)

MUD SITE

Fig. 6. Spectra of the species abundance at mud site. * Peaks that are significant (by Fishers G_{crit} statistic) and are not harmonics (see text)
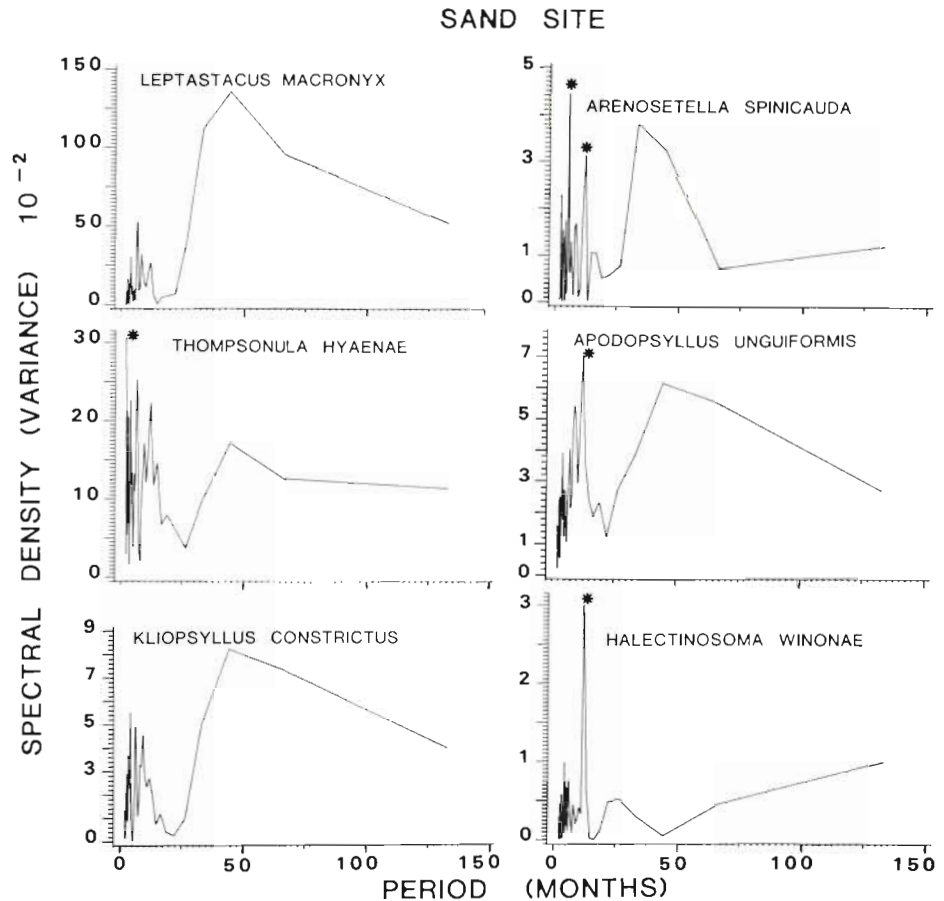
SAND SITE

Fig. 7. Spectra of the species abundance at the sand site. * Peaks that are significant (by Fishers G_{crit} statistic) and are not harmonics (see text)

winonae; Paronychocamptus sp. is now *P. wilsoni* and *Paracyclopina* sp. is now *Halicyclops coulli*. The 2.3 yr study indicated that *Pseudobradya pulchella* reached maximum abundance once a year in spring, whereas it is now clear that *P. pulchella* has a bi-modal distribution peaking in the spring and autumn (Fig. 4 & 6; Table 3).

The seasonal patterns of the dominant sand species (note that the 3rd ranked species of Coull & Vernberg, *Hastigerella leptoderma*, did not even rank in the top 6 for the entire 11 yr), is confounded by the general decline in copepod abundances. *Leptastacus macronyx* was not distinctly seasonal in the 2.3 yr study; nor was it during 11 yr (Fig. 2 & 7; Table 4). *Thompsonula hyaenae* was irregular the first 2.3 yr (Coull & Vernberg 1975), but over the 11 yr reached maximum abundance regularly in the autumn. *Arenosetella spinicauda*'s seasonality over 11 yr is essentially as reported by Coull & Vernberg for 2.3 yr with peak abundance in autumn and winter. The other species, *Apodopsyllus unguiformis, Halectinosoma winonae* and *Kliopsyllus constrictus,* were not included in the Coull & Vernberg report of sand dwelling species.

Halectinosoma winonae occurs at both sites, but reaches maximum abundance earlier (summer) at the sand site than at the mud site (autumn). This epibenthic, highly motile species may well enter the North Inlet system from the open ocean and migrate into the estuary. The sand site, just inside the inlet mouth, receives *H. winonae* first; it then, we suspect, migrates further into the system to the mud site, where it reaches maximum abundance in autumn.

Coull & Vernberg (1975) also reported that the dominant species at each site (*Leptastacus macronyx* in sand; *Microarthridion littorale* in mud) were present and ovigerous all year round. Based on the 11 yr data set, we cannot evaluate whether this would continue to be true for *L. macronyx* since this species has been eliminated at the sand site (Fig. 1). *M. littorale* is now the co-dominant at the mud site with *Pseudobradya pulchella* (Table 1). *M. littorale* was present on 165 of 170 sampling dates and had ovigerous females in the population 78.7 % of the time. Thus, while not ovigerous all the time, as reported for the first 2.3 yr, it should still be considered a continuous breeder *sensu* Hicks (1979). The other dominant species at each site had discrete breeding periods coinciding with their maximum abundance illustrated in Fig. 1 to 4. Our inability to distinguish a peak in ovigerous female abundance preceding both a juvenile and total population

abundance maximum for any species is due, we feel, to 2 factors. First, all the eggs of a female or a population do not hatch simultaneously nor is the development rate of individual juveniles from the same clutch synchronous after the eggs are hatched (Coull & Dudley 1976). Thus hatching and development are spread out over some time period (days to weeks?). Secondly, our shortest sampling interval of 2 wk in 1981–83 was not sufficient to distinguish either those species with protracted development or those with 2 or more cohorts within our sampling interval. Accurate determination of sequencing of life history stages would require many replicated short interval samples (daily to weekly). Since most harpacticoids progressively increase their stage duration during development, i.e. a proportionately greater part of the total development is spent in the latter stages (Hicks & Coull 1983), and since cohorts are known to overlap in time (Fleeger 1979), it may well be impossible to accurately assess life history sequencing from even short interval field data. Lab rearings would be necessary.

Long-term abundance

The absence of any long-term period in individual species abundance at the mud site is indicative of the consistent seasonality inherent in this community. That no species has a period longer than 1 yr, and that 2 of the top 6 have 6 mo and 1 yr periods, allows accurate (± 1 mo) prediction of when each species will be present. This regular, consistent pattern is not surprising. The relative constancy of the habitat has apparently allowed development of an assemblage well tuned to recurring environmental parameters; thus maintaining definitive seasonal suites of meiobenthic copepods.

At the sand site, there was also no long-term periodicity in any species (once the spurious harmonics from the spectral analysis were removed). This lack of long-term periodicity does not appear to be a function of distinct seasonality since seasonality was not marked at the sand site. Three of the 6 top species significantly declined in abundance over the 11 yr: these 3, all interstitial, species have apparently had their preferred habitat (interstitial space) removed. The lack of long-term cycles is thus confounded at the sand site by a declining number of interstitial species and repeatable cyclicity in the epibenthic forms (*Thompsonula hyaenae, Halectinosoma winonae*; Fig. 5; Table 4). Regardless of the reasons, we can discern no long-term periodicity in abundance of any of the top 12 species (both sites).

Herman & Heip (1983) reported on long-term trends (spectral analysis) for 3 species from a Belgian brack-ish water pond and found that 1 species had a significant periodicity of longer than 1 yr. They correlated the reported 3.5 yr periodicity of *Canuella perplexa* to a 3.5 yr cycle in ammonium concentration (it is not clear if this ammonium was in the overlying water or in the sediment) and speculated that since ammonium is an indicator of decomposition rate, it may be an important forcing function for *C. perplexa* abundance. Combining the Herman & Heip (1983) data (3 species) with ours (12 species), only 1 *(Canuella perplexa)* of the 15 species monitored regularly over the long term has any long-term periodicity. That 14 of the 15 species have annual or no detectable cycles suggests that meiobenthic copepods harpacticoids primarily respond to short-term (1 yr or less) seasonal events and because of this, long-term population cycles do not occur.

It appears that seasonality of individual species can be accurately determined in a sampling regime of much less than 11 yr. The patterns reported by Coull & Vernberg (1975) on 2.3 yr of this data set are essentially the same as those recorded over the 11 yr. Two yr, with adequate sampling frequency and assuming no unusual climatic or perturbation events, appears sufficient to track seasonal patterns. Only with such a long-term data set as reported here, which shows repeatable year-to-year constancy could one verify such a statement. Additionally, while there were no long-term population cycles there were long-term trends in abundance, i.e. the disappearance of the interstitial species at the sand site which could not have been detected with only 2 to 3 yr of sampling. Thus, the value of long-term research very much depends on the questions being asked. We are convinced that 2 yr (one must at least replicate years) of technically accurate sampling and sorting should provide species seasonal patterns; patterns which seem to be the dominant cycling periodicity in harpacticoids. Definition of long-term trends and seasonal patterns obviously requires sampling on a longer time scale.

LITERATURE CITED

Coull, B. C. (1985a). The use of long-term biological data to generate testable hypotheses. Estuaries 8: 84–92

Coull, B. C. (1985b). Long-term variability of estuarine meiobenthos: an 11 year study. Mar. Ecol. Prog. Ser. 24: 205–218

Coull, B. C., Dudley, B. W. (1976). Delayed naupliar development of meiobenthic copepods. Biol. Bull. mar. biol. Lab., Woods Hole 150: 38–46

Coull, B. C., Fleeger, J. W. (1977). Long-term temporal variation and community dynamics of meiobenthic copepods. Ecology 58: 1136–1143

Coull, B. C., Vernberg, W. B. (1975). Reproductive periodicity of meiobenthic copepods: seasonal or continuous? Mar. Biol. 32: 289–293

Fleeger, J. W. (1979). Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. Mar. Biol. 52: 147–156

Heip, C. (1980). The influence of competition and predation on production of meiobenthic copepods. In: Tenore, K. R.,

Coull, B. C. (ed.) Marine benthic dynamics. University of South Carolina Press, Columbia, S.C., p. 167–177

Herman, P. M. J., Heip, C. (1983). Long-term dynamics of meiobenthic populations. Oceanologica Acta 1983: 109–112

Hicks, G. R. F. (1979). Pattern and strategy in the reproductive cycles of benthic harpacticoid copepods. In: Naylor, E., Hartnoll, R. G. (ed.) Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, p. 139–147

Hicks, G. R. F., Coull, B. C. (1983). The ecology of marine meiobenthic harpacticoid copepods. Oceanogr. mar. biol. A. Rev. 21: 67–125

deJonge, V. N., Bouman, L. A. (1977). A simple density separation technique for quantitative isolation of meiobenthos using the colloidal silica Ludox-TM. Mar. Biol. 42: 143–148

SAS Institute Inc. (1982). SAS user's guide: statistics, 1982 ed. SAS Institute Inc., Cary, N.C.

Wieser, W. (1960). Benthic studies in Buzzards Bay II. The meiofauna. Limnol. Oceanogr. 5: 121–137