

Temporal variability in the night-time distribution of epipelagic siphonophores in the North Atlantic Ocean at Bermuda

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Abstract. The temporal variability of siphonophores was compared on night-to-night, month-to-month and year-to-year scales in open-net collections made at or near the Bermuda Atlantic Time Series (BATS) site. These collections were made as oblique tows to 100 m on (i) one summer night in each of 1986, 1989 and 1991, (ii) one night per month on 13 cruises between April 1991 and August 1992, and (iii) three consecutive summer nights of 1992. The mean wet displacement volume (WDV) of siphonophores in these collections was 1.4 ± 0.6 ml per 100 m³, or $20 \pm 10\%$ of the total catch biovolume. The most common species belonged to the Calycophorae families Diphyidae and Abylidae: the combined numerical abundance of *Chelophyes appendiculata*, *Eudoxoides mitra*, *Lensia subtilis*, *Eudoxoides spiralis*, *Bassia bassensis* and *Abylopsis eschscholtzi* averaged 300–400 per 100 m³. Combined numbers of these common species varied little when sampled hour by hour at the same location during consecutive summer nights or at different night-time sampling locations 10¹–10² km apart when these were sampled within 3–5 h. In contrast, most of these six species exhibited 2- to 3-fold differences in night-time abundance between summers of different years and between seasons. Three seasonal groups were detected, with a winter group being the most distinct from the others. Changes in the abundance of several species were correlated with seasonal changes in the depth of the mixed layer.

Introduction

Siphonophores are widespread in the ocean, with species known from the surface to the depths, from tropical to polar areas, and from neritic to oceanic water (Alvarino, 1971; Pugh, 1975). However, the majority are epipelagic (Alvarino, 1971; Daniel, 1974; Pugh, 1974; Musayeva, 1976) and they can comprise a significant portion of near-surface standing stocks when measured as volume. For instance, Grice and Hart (1962) reported that the displacement volume of siphonophores contributed between 1 and 18% of the total epizooplankton collected in net tows in the region between New York and Bermuda. Subsequent work by Deevey (1971) showed that, on average, dry weight and displacement volume of siphonophores in the Sargasso Sea accounted for 8 and 18% of the net zooplankton in the upper 500 m, respectively.

There have been few studies of siphonophores at Bermuda, even though numerous zooplankton collections have been made there in recent decades. Well-known and widely referenced interannual collections of zooplankton were made at biweekly intervals at Hydrostation-S of the Bermuda Biological Station for Research (BBSR) in 1957–1960 (Menzel and Ryther, 1961a,b), in 1961–1962 (Deevey, 1971), in 1976–1977 (Morris *et al.*, 1977), and at monthly intervals in 1968–1970 (Deevey and Brooks, 1977) and in 1979–1980 (Smith, 1982). However, siphonophores, like other gelatinous zooplankton groups, were usually neglected in most of these studies; moreover, in all of these studies zooplankton were usually

sampled only in the daytime, with remarkably few collections made at night. The only detailed study of siphonophores at Bermuda was carried out by Moore (1949). Moore was interested in whether there might be seasonal changes in the abundance of siphonophores at Bermuda, but he concluded that <50% of the siphonophore species showed any clear trends. While some species reached maximum numbers in winter, others had maxima at other seasons, apparently depending on the year of sampling. Such patterns appeared to Moore to reflect both the horizontal variability in the distribution of the animals and seasonal changes in hydrographical conditions that, Moore speculated, could be generated by local winds or currents transporting different plankton populations through a single sampling site. While localized peaks in biovolume were found at various stations during spring and autumn, Moore concluded that there were no marked seasonal changes in biovolume and that Bermuda was a single zoogeographic region. In contrast, Menzel and Ryther (1961a), when working two decades later, reported a zooplankton biomass peak in spring roughly coincident with the spring phytoplankton bloom. Deevey (1971) also reported the highest numerical abundance of zooplankton in April, with a secondary peak in October, in the top 500 m of the water column.

By enumerating siphonophores from zooplankton collections of opportunity at Hydrostation-S and the Bermuda Atlantic Time Series (BATS) station, over temporal scales varying from hours to years, the present research sought to determine whether siphonophore populations at the two stations would be similar and how the hour-to-hour variability of the more common species compared with that of month-to-month and year-to-year variability. By tracking the variations in standing stock of some 40 species of calycophoran siphonophores in the context of variations in near-surface hydrographic conditions, our goal was to correlate oceanographic processes with seasonal and interannual changes in siphonophore abundance.

Method

Field work

On summer nights of 17–18 July 1986, 24–25 July 1989 and 11–12 July 1991, 13 zooplankton samples were collected hour by hour from 1 h before sunset (20:00 h local) to 1 h after sunrise (06:00 h local) at Hydrostation-S. These samples were collected from R/V 'Weatherbird' and R/V 'Weatherbird-II' in oblique tows to 100 m with an open net of 333 μm mesh that measured 1 m in diameter and had a 5:1 aspect ratio. A General Oceanics flowmeter at the mouth of the net was used to calculate volume filtered; at tow speeds of 1–2 knots and winch speeds of 15–20 m min^{-1} , this volume generally ranged from 200 to 250 m^3 . All specimens were preserved on board by adding formaldehyde buffered with borax until the collections were ~5–10% formalin by volume.

Zooplankton were also collected every hour from before dusk to after dawn using the same sampling technique on three consecutive nights (28–29, 29–30 and 30–31 August) at the BATS station, during a 'Weatherbird-II' cruise in August 1992. On the first two evenings, the ship stayed within 10 km of the BATS station,

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while after 23:00 h local time on the third night it traversed from the BATS station to Hydrostation-S and then sampled there from 05:00 to 07:00 h (Figure 1). A limited number of collections were also made a few days before this time-intensive sampling: two during the day on 26 August and three on the night of 26–27 August. In addition, two night-time collections were made on each of 13 hydrographic cruises to the BATS station from April 1991 to August 1992. Unfortunately, the flowmeter was seldom attached to the net for these monthly collections, so there are no flow data on water volume filtered. To compare temporal variations in siphonophore abundance in different months, we normalized the abundance of each species to the total number of siphonophores collected.

Laboratory work and data analysis

Biomass, as wet displacement volume (WDV) of total macrozooplankton, was measured following the method of Ahlstrom and Thraillkill (1960). Siphonophores were then separated and this siphonophore fraction was remeasured for WDV. The siphonophores were counted and identified from 1/4 or 1/8 subsamples, created using a Folsom plankton splitter. Polygastric and eudoxid nectophores were counted separately. Since some but not all of the common calycophoran siphonophores at Bermuda have anterior nectophores that are distinguishable at

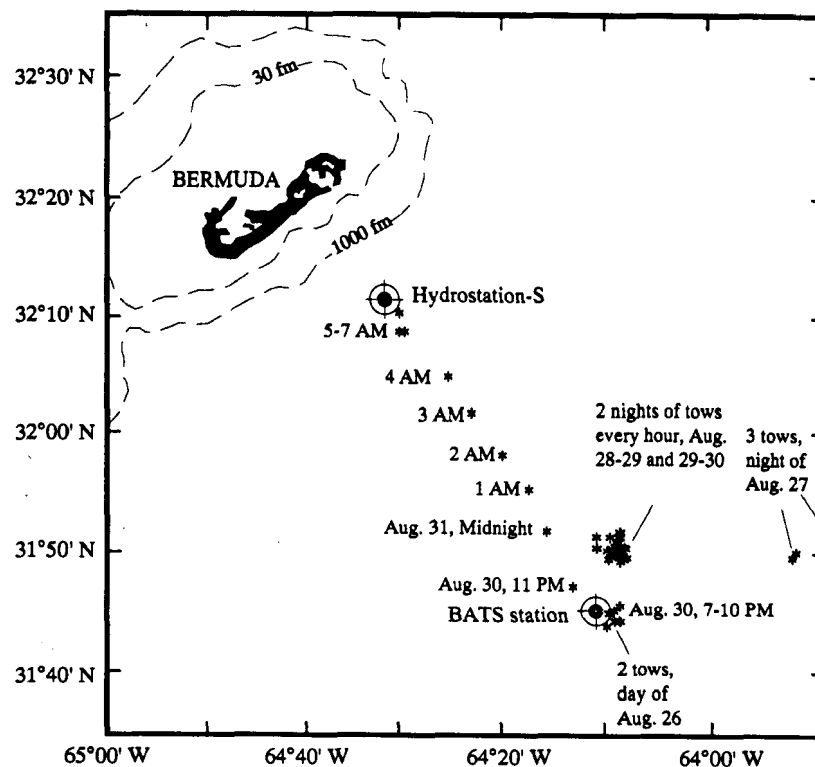


Fig. 1. Location of Hydrostation-S and the BATS station, annotated to show where meter net collections were made on 26–31 August 1992.

the species level from the corresponding posterior nectophores, the numbers of these two types of swimming bells were tallied separately. The numbers of each species in the sample were reported as the greater of the two counts.

We hypothesized that year-to-year and month-to-month differences in numerical abundance would exceed night-to-night and station-to-station differences. Accordingly, a three-factor analysis of variance (ANOVA) was performed to examine the significance of different time scales and stations on the numerical abundance of the 23 most common species (those present in $\geq 30\%$ of the total of 118 samples that were analyzed). The non-parametric Spearman rank order correlation coefficient was employed to test whether the distribution patterns of these species were similar between pairwise nights, among different nights of different years, or at the BATS versus Hydrostation-S locations. To further compare the similarity between BATS station/summer 1992 collections with those from Hydrostation-S/summers 1986, 1989 and 1991, principal components analysis (PCA) was run on the numerical abundance data for the 23 most common calyphorans using samples collected between 20:00 and 06:00 h local time on all six summer nights ($11 \text{ h} \times 6 \text{ nights} = 66$). The objective in applying PCA to the data was to determine how numerical abundance changed within this recurrent group of common species among different time scales (different consecutive nights versus nights of different years) and stations.

To compare differences in siphonophore groups with season, the relative abundances of the same 23 calyphoran species in the 13 pairs of monthly collections were first averaged and then cluster analysis was used to place similar species into groups or clusters using the minimum variance (or Ward) linkage. The pair of samples whose fusion results in the minimum variance (relative to the variances within each cluster taken separately) were first joined and then progressively enlarged by adding the second sample which results in the second lowest variance. The resultant groups were robust, as two different kinds of distance metric gave similar tree-diagram results [Pearson correlation coefficient and Euclidean distance; see Lo (1995) for details]. Finally, since temperature, salinity and sometimes other environmental parameters were measured on each cruise, multiple regression techniques were used to examine whether the relative abundance of any of the calyphoran species might co-vary with changes in mean temperature and mean salinity of the upper 100 m, and with depth of the seasonal mixed layer.

Results

Variations in biovolume

The mean WDV of the siphonophore fraction is given in Table I. During three consecutive nights of the same summer (August 1992), the mean WDV of the siphonophore fraction was quite similar ($1.7 \pm 0.4 \text{ ml per } 100 \text{ m}^3$). In contrast, means were significantly different ($P < 0.05$) between summer nights of different years. Siphonophore WDV averaged 50% lower on the night of 17–18 July 1986 than in August 1992, and 3-fold lower on the night of 24–25 July 1989 than in August 1992.

The mean percentage of WDV of the siphonophore fraction relative to the WDV of the total macrozooplankton in summer was $20 \pm 10\%$. In monthly night-

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Table I. The mean \pm SD of wet displacement volume (WDV, as ml per 100 m³) of the siphonophore fraction versus total macroplankton in tows at 21:00–06:00 h local time at Hydrostation-S and the BATS station. The number of samples used for biovolume measurement is in parentheses

| Station/date | Total DV (ml) | Siphonophore DV (ml) | Siphonophore DV% |
|------------------------------|--------------------|----------------------|------------------|
| 17–18 July 1986 | 11 \pm 4.3 (10) | 1.2 \pm 0.6 (10) | 12 \pm 6 (10) |
| 24–25 July 1989 | 7.4 \pm 2.0 (10) | 0.6 \pm 0.3 (6) | 7 \pm 4 (6) |
| 11–12 July 1991 | 8.7 \pm 2.8 (10) | N/A | N/A |
| All Hydrostation-S | 8.9 \pm 3.4 (30) | 0.9 \pm 0.6 (16) | 10 \pm 5 (16) |
| 28–29 August 1992 | 7.5 \pm 1.5 (10) | 1.8 \pm 0.5 (9) | 25 \pm 8 (9) |
| 29–30 August 1992 | 7.6 \pm 0.8 (10) | 1.5 \pm 0.3 (10) | 20 \pm 4 (10) |
| 30–31 August 1992 | 8.1 \pm 1.6 (10) | 1.7 \pm 0.4 (10) | 21 \pm 5 (10) |
| BATS monthly samples 1991–92 | N/A | N/A | 31 \pm 8 (26) |
| All BATS station | 7.5 \pm 1.5 (30) | 1.7 \pm 0.4 (29) | 25 \pm 8 (55) |
| Overall mean | 8.2 \pm 2.6 (60) | 1.4 \pm 0.6 (45) | 20 \pm 10 (71) |

N/A, not available.

time sampling, this percentage ranged from 23 to 51 % (Figure 2): the highest percentages for WDV of the siphonophore fraction relative to that of the total macrozooplankton were found in November 1991 and August 1992; the lowest percentages were found from February to July in both years.

Variations in species composition

Sixty-eight species of siphonophores were identified in the open-net tows (Table II), comprised of 51 calyphoran species (plus 12 unidentified) and 17 physonect species (11 agalmid and four forskaliid species plus two unidentified). Fragments of a rhizophysid (suborder Cystonectae) were also present.

The calyphoran species present in the upper 100 m at night represent five out of six known families (Table III). Diphyidae predominated with 29 species, or just under half (29/68) of the total number of species that could be identified. Four of the diphyids, *Chelophyes appendiculata*, *Eudoxoides mitra*, *Lensia subtilis* and *Eudoxoides spiralis*, were generally the most common. In the summer collections from 1986, 1989, 1991 and 1992, the family Diphyidae comprised 73–81 % of numbers per 100 m³ at Hydrostation-S and 55–67 % at the BATS station. The next most common family was Abylidae, with *Bassia bassensis* and *Abylopsis eschscholtzi* the most abundant species. The two most common families, Diphyidae and Abylidae, together comprised 92–95 % of calyphore numbers at Hydrostation-S and 88–92 % at the BATS station (Table III). The family Clausophyidae is not represented, but most of these are midwater species and so are generally found in the 500–900 m depth range (Pugh, 1974).

The individual species ranking, however, varied from summer to summer (Table IV). *Bassia bassensis* was the most common species of all in the collections of the three consecutive nights of August 1992, while the night of 11–12 July 1991 was dominated by *E.mitra*. *Lensia subtilis* was the most common species in the summer

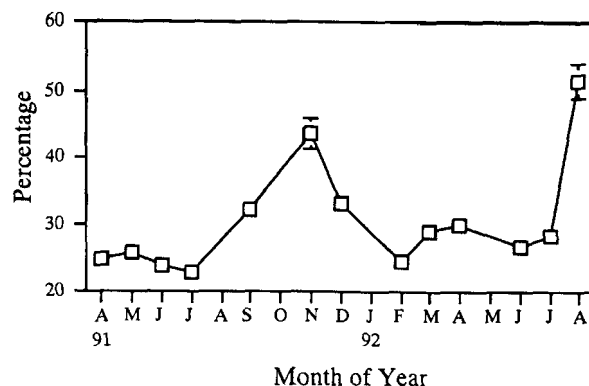


Fig. 2. Wet displacement volume of siphonophores relative to total macrozooplankton biovolume at the BATS station in 13 pairs of night-time tows of opportunity.

nights of July 1986 and July 1989, and overall was the most common species in the series of monthly collections in 1991–1992.

Similarity between sampling locations

Calycephoran species in net tows made on three July nights in 1986, 1989 and 1991 were combined for the calculation of mean abundance per 100 m³ (\pm SD) as 'Hydrostation-S'; those collected during three consecutive summer nights in August 1992 were combined as 'BATS station'. The overall means were 455 individuals per 100 m³ at BATS and 396 individuals per 100 m³ at Hydrostation-S (Table II). Generally, the correlation of species composition between the two stations was high, as well ($r = 0.77$, with Spearman rank order correlation). However, Table V shows that when the species are ranked in order of abundance, *L. subtilis* dominated at Hydrostation-S, with a mean density of 49 polygastric nectophores

Table II. Species number (plus number of unidentifiable species in parentheses) of siphonophores with the numerical abundance of all calycephorans (mean numbers per 100 m³ \pm SD in the summer night-time collections)

| Station/date | Species number of Siphonophorae | | | Total | Mean for Calycephorae |
|------------------------------|---------------------------------|-------------|-------------|---------|-----------------------|
| | Calycephorae | Physonectae | Cystonectae | | |
| 17–18 July 1986 | 32 (8) | 10 (2) | 0 (1) | 42 (11) | 338 \pm 91 |
| 24–25 July 1989 | 30 (10) | 6 (2) | 0 | 36 (12) | 336 \pm 130 |
| 11–12 July 1991 | 29 (9) | 6 (2) | 0 | 35 (11) | 501 \pm 150 |
| All Hydrostation-S | 38 (12) | 17 (2) | 0 (1) | 49 (15) | 396 \pm 147 |
| 28–29 August 1992 | 38 (8) | 12 (1) | 0 (1) | 50 (10) | 459 \pm 88 |
| 29–30 August 1992 | 34 (8) | 9 (1) | 0 (1) | 43 (10) | 471 \pm 44 |
| 30–31 August 1992 | 34 (9) | 9 (2) | 0 (1) | 43 (12) | 425 \pm 61 |
| BATS monthly samples 1991–92 | 38 (8) | 10 (2) | 0 (1) | 48 (11) | N/A |
| All BATS station | 50 (9) | 17 (2) | 0 (1) | 67 (12) | 455 \pm 76 |
| Overall mean | 51 (12) | 17 (2) | 0 (1) | 68 (15) | 422 \pm 118 |

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Table III. Percentages of calyccophoran species by family at Hydrostation-S versus the BATS station

| Family | Hydrostation-S | | | BATS station | |
|---------------------|--------------------|--------------------|--------------------|---------------------------------|-------------------------|
| | 17–18 July 1986 | 24–25 July 1989 | 11–12 July 1991 | Monthly samples 1991–1992 | 28–30 August 1992 |
| Diphyidae | 72.6 | 80.6 | 77.1 | 67.0 | 54.5 |
| Abylidae | 19.5 | 14.3 | 17.2 | 20.8 | 37.5 |
| Prayidae | 6.8 | 3.8 | 3.7 | 3.6 | 6.4 |
| Hippopodiidae | 0.6 | 0.3 | 0.1 | 1.0 | 0.8 |
| Sphaeronectidae | 0.3 | 0.03 | 0.1 | 5.9 | 0 |
| (unidentified spp.) | (0.2) | (0.9) | (1.7) | (1.6) | (0.7) |

and 42 eudoxid nectophores per 100 m³. At the BATS station, by contrast, *B. bassensis* dominated, with a mean density of 38 polygastric nectophores and 48 eudoxid nectophores per 100 m³. These ‘station-to-station’ differences in numerical abundance apparently reflect differences between summers of different years, though, rather than spatial differences on a scale of tens of kilometers. When both the BATS station and Hydrostation-S were sampled on the same night of 30–31 August 1992, while the ship traversed from the BATS station to Hydrostation-S, the mean numerical abundance of the calyccophoran species in Table V was not significantly different between the two stations (Lo, 1995).

The results of the PCA that was run on the numerical abundance data for the 23 most common species further illustrate the difference between the summer 1992 collections and those from the summers of 1986, 1989 and 1991. The first two principal components accounted for a combined total of 43% of the variance and, when plotted, it can be seen that the 4 years separate almost completely (Figure 3). The summer 1986, 1989 and 1991 collections have negative scores for PC-1, while the summer 1992 collections have positive scores. The plot also illustrates that samples from summers 1986 and 1991 show more scatter (variation) along principal component axis 2 than those from summers 1989 and 1992. That the three tows made at Hydrostation-S on the third consecutive night of sampling in August 1992 (individually circled as n5 in Figure 3) grouped with samples collected earlier that

Table IV. The species rank and relative abundance (as percentage in parentheses) of the six most common calyccophoran species at Hydrostation-S versus the BATS station

| Species | Hydrostation-S | | | BATS station | |
|---------------------------------|--------------------|--------------------|--------------------|-------------------------------------|-------------------------|
| | 17–18 July 1986 | 24–25 July 1989 | 11–12 July 1991 | Monthly samples 1991– 1992 | 28–30 August 1992 |
| <i>Lensia subtilis</i> | 1 (18.1) | 1 (50.0) | 5 (5.3) | 1 (17.3) | 5 (8.7) |
| <i>Eudoxoides mitra</i> | 2 (12.5) | 6 (3.5) | 1 (31.7) | 2 (14.6) | 4 (8.7) |
| <i>Chelophyes appendiculata</i> | 3 (11.6) | 2 (7.7) | 6 (4.7) | 8 (4.6) | 3 (9.7) |
| <i>Bassia bassensis</i> | 4 (10.2) | 3 (7.6) | 3 (10.7) | 3 (14.2) | 1 (19.2) |
| <i>Eudoxoides spiralis</i> | 5 (8.7) | 5 (4.0) | 2 (15.3) | 4 (11.0) | 6 (6.6) |
| <i>Abylopsis eschscholtzi</i> | 6 (7.7) | 4 (5.5) | 4 (5.3) | 6 (5.6) | 2 (15.0) |

Table V. Presense-absense occurrence rate compared with mean numerical abundance \pm SD of the eight most common calyophoran species in summer night-time collections at the BATS station compared to Hydrostation-S

| Calycophore species | Occurrence (%) | | Abundance (individuals per 100 m ³) | | |
|-----------------------------------|------------------|---------------------|---|---------------------|-------------------|
| | BATS (n = 30) | Hydro-S (n = 30) | BATS (n = 30) | Hydro-S (n = 30) | F_{ob} value |
| <i>Bassia bassensis</i> P | 100 | 100 | 38 \pm 14 | 17 \pm 9 | 55* |
| <i>B.bassensis</i> E | 100 | 100 | 48 \pm 14 | 22 \pm 13 | 57* |
| <i>Lensia subtilis</i> P | 100 | 100 | 24 \pm 11 | 49 \pm 36 | 16* |
| <i>L.subtilis</i> E | 100 | 100 | 15 \pm 8 | 42 \pm 47 | 11* |
| <i>Eudoxoides mitra</i> P | 100 | 97 | 13 \pm 8 | 22 \pm 19 | 7* |
| <i>E.mitra</i> E | 100 | 90 | 30 \pm 17 | 57 \pm 64 | 6* |
| <i>Abylopsis eschscholtzi</i> P | 100 | 97 | 26 \pm 8 | 8 \pm 5 | 108* |
| <i>A.eschscholtzi</i> E | 100 | 97 | 39 \pm 11 | 16 \pm 8 | 93* |
| <i>Chelophyes appendiculata</i> P | 100 | 100 | 14 \pm 7 | 11 \pm 6 | 6* |
| <i>C.appendiculata</i> E | 100 | 100 | 26 \pm 10 | 18 \pm 12 | 8* |
| <i>Eudoxoides spiralis</i> P | 100 | 93 | 7 \pm 5 | 8 \pm 6 | 1 |
| <i>E.spiralis</i> E | 100 | 100 | 22 \pm 9 | 32 \pm 28 | 4 |
| <i>Diphyes bojani</i> P | 97 | 57 | 10 \pm 5 | 2 \pm 2 | 67* |
| <i>D.bojani</i> E | 97 | 43 | 13 \pm 7 | 1 \pm 1 | 95* |
| <i>Abylopsis tetragona</i> P | 100 | 50 | 9 \pm 6 | 1 \pm 2 | 54* |
| <i>A.tetragona</i> E | 100 | 67 | 6 \pm 3 | 2 \pm 3 | 29* |

P, polygastric generation; E, eudoxid generation; F_{ob} = Fisher statistic (ANOVA with one fixed factor).

*Significant at the 0.05 level.

night and from the two previous nights at the BATS station is additional evidence that PC-1 variability represents differences between summers rather than between the two station locations.

By species, the first component had higher loadings for most Abylidae species and some of the Diphyidae species. In other words, much of the variability between years was explained by variations in the abundance of these groups. Overall calyophore species composition was compared among summers of different years using two kinds of correlation methods (Lo, 1995). Both Spearman rank order correlation and multiple regression showed higher correlation values between summer nights of the same year (0.92–0.95 and 0.95–0.97) than between summer nights of different years (0.71–0.88 and 0.07–0.72).

Similarity between nights

Samples from the three consecutive summer nights of August 1992 were used to examine night-to-night similarity in numerical abundance among the calyophoran species. Generally, most species did not show significant differences in mean night-time abundance (20:00–06:00 h) between the three consecutive nights; most means varied <30% among the three different nights, and both Spearman rank order correlation and multiple regression produced correlations >0.92 (Lo, 1995).

Figure 4A illustrates that samples from the three consecutive nights of 28–29, 29–30 and 30–31 August clustered strongly together, with >70% overlap. To better illustrate the similarities among calyophore species groups, collections from August 1992 have also been grouped into one of four time periods: (A) 19:00, 20:00

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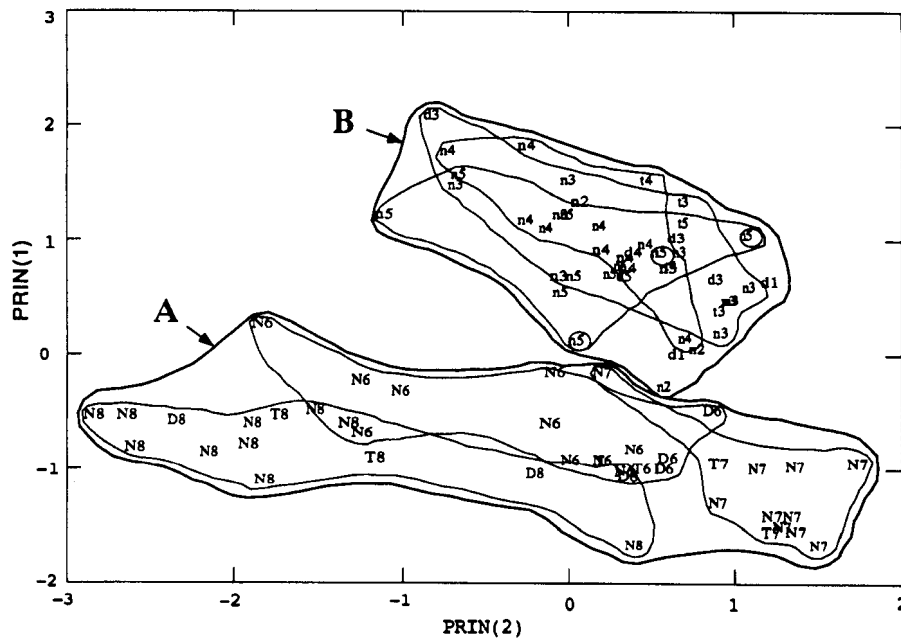


Fig. 3. PCA plot of the similarity in calyophoran species composition among various summer collections. Compound symbols summarize when each collection was made, by diel period (alphabet) and night (number): N(n) = night; D(d) = day; T(t) = twilight; 1 = August 26, 1992; 2 = August 27, 1992; 3 = August 28, 1992; 4 = August 29, 1992; 5 = August 30, 1992; 6 = July 17, 1986; 7 = July 24, 1989; 8 = July 11, 1991. Collections at Hydrostation-S in July of 1986, 1989 and 1991 are encircled as group A; collections at the BATS station in August 1992, including three collections at Hydrostation-S that are circled individually within night 5, are encircled as group B.

and 21:00 h; (B) 22:00, 23:00 h and midnight; (C) 01:00, 02:00 and 03:00 h; (D) 05:00, 06:00 and 07:00 h (Figure 4B). Note that group A is well separated from groups C and D. While groups B and C mostly overlap, they exhibit less variation in PC-1 space (nearly zero loading) than shown by groups A (positive loading) or D (negative loading). In other words, night-time species groups collected at 22:00–03:00 h are less variable than those collected near dusk (group A) and dawn (group D).

Differences between seasons

The species most common in the summer night collections occur throughout the year at Bermuda (Figure 5). However, there were marked differences in the relative abundance of most of these between April 1991 and August 1992. Five species, *B. bassensis*, *E. spiralis*, *Abylopsis eschscholtzi*, *A. tetragona* and *Diphyes bojani*, exhibited maximum relative abundance in winter (December–March). Two other species (*L. subtilis* and *C. appendiculata*) had maxima during summer (June–September).

Among the ‘winter’ species, both *B. bassensis* and *A. eschscholtzi* exhibited maxima in relative abundance in December. During this winter peak, both the eudoxid and the polygastric generations were abundant. In contrast, only one of the gener-

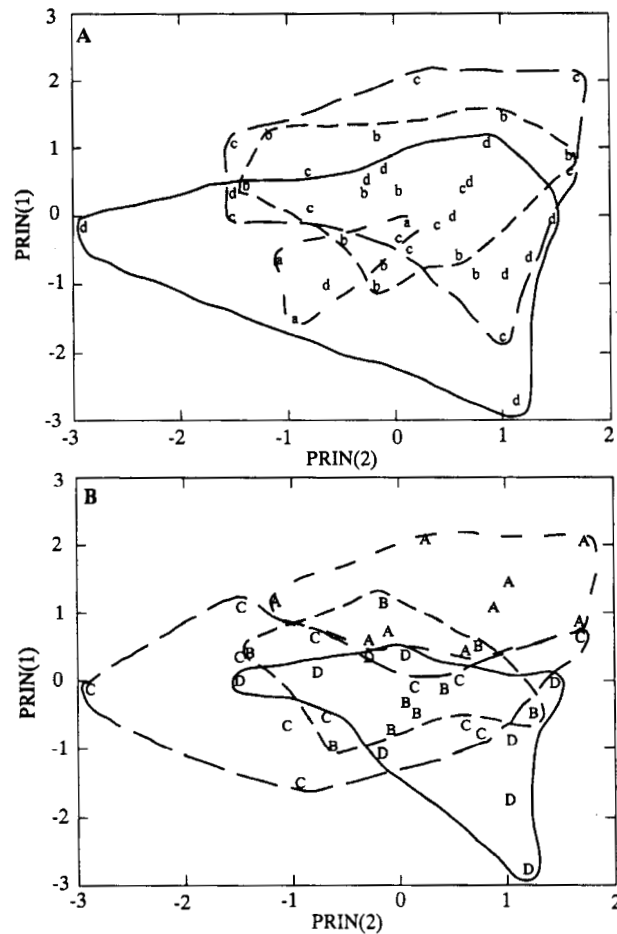


Fig. 4. PCA plot of the similarity in calyophoran species composition among the August 1992 collections. In (A), the symbols summarize the night each collection was made: a = 26–27 August; b = 28–29 August; c = 29–30 August; d = 30–31 August. In (B), the symbols summarize the local time of collection: A = 19:00–21:00 h; B = 22:00 h–midnight; C = 01:00–03:00 h; D = 05:00–07:00 h.

ations of other species was responsible for winter maxima. For *E. spiralis*, it was the eudoxid phase; for *A. tetragona*, it was the polygastric phase. Among the 'summer' species, *C. appendiculata* and *L. subtilis* reached maximum relative abundance in early and late summer in each year. These maxima in relative abundance are evident in polygastric as well as eudoxid generations of these two species, respectively. In contrast, *E. mitra* was quite common (5–22% relative abundance) in all 13 pairs of open-net tows, but showed no clear peaks in relative abundance in any single season.

As other ways to visualize differences in siphonophore groups with season, the relative abundances of each species of calyophore in the two night-time collections in each month were first averaged and then cluster analysis (CA), Spearman rank order correlation and multiple regression were run on the mean relative

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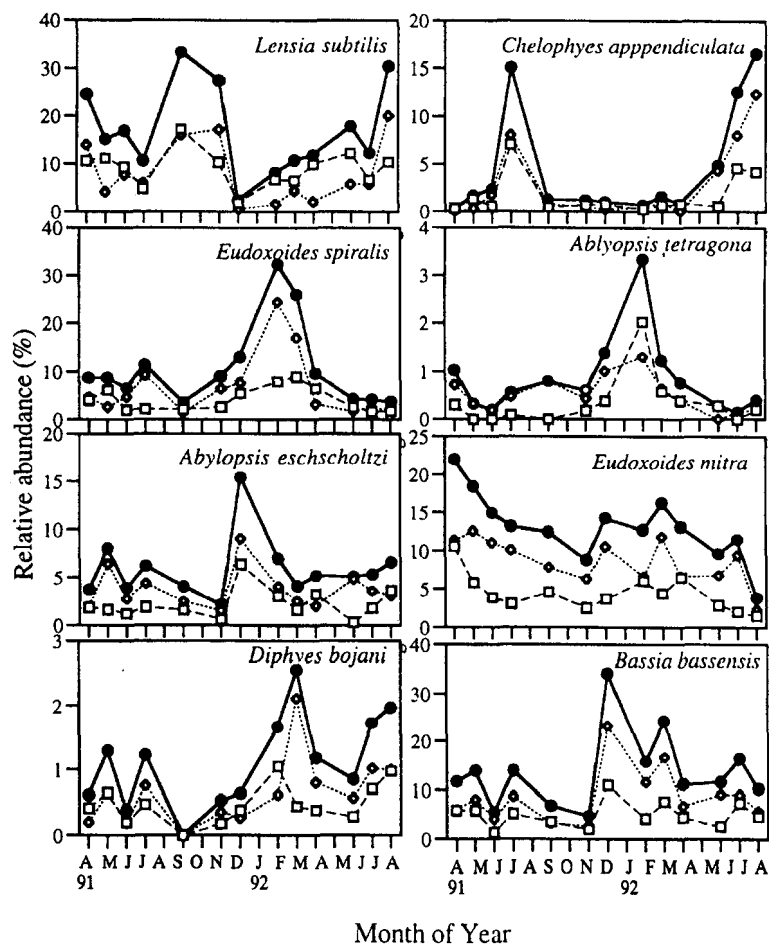


Fig. 5. Comparison of the relative abundance of the polygastric generation (open squares) and eudoxid generation (open circles) for the eight most common calycophorans at the BATS station. Solid circles are the sum of polygastric plus eudoxid occurrence.

abundance data. From the CA results (Figure 6), it is apparent that there are three seasonal groups: winter (December–March), spring–summer (April–July) and summer–fall (June–November). Note, however, that it is the three winter month samples that are separated most strongly from the rest of the months. This can also be seen from the results of Spearman and multiple regression correlation, in which the winter group consistently had lower values than other seasons (Lo, 1995).

Discussion

Relationships with environmental variables

In summer, the seasonal mixed-layer depth averaged 30 m. A composite 67 h plot of temperature and salinity in the upper 200 m from CTD casts done before, during and after each night of net tows on 28–31 August 1992 showed that mean mixed-

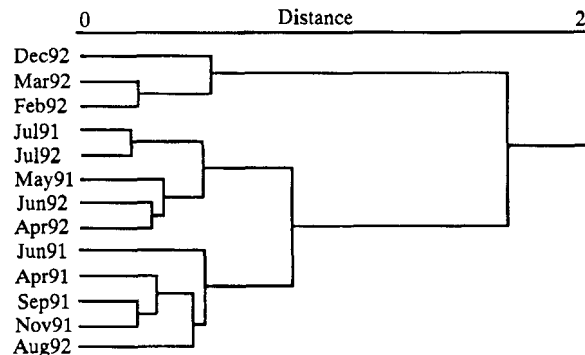


Fig. 6. Tree diagram obtained by minimum variance linkage cluster analysis, based on a Pearson correlation matrix of the relative abundances of calycophoran species in monthly samples.

layer temperature varied by only 0.5°C and mean mixed-layer salinity by only 0.1 (Figure 4 in Lo, 1995). Below this seasonal mixed layer, there was about an 8°C temperature gradient between 30 and 160 m, which marked the top of the $18 \pm 1^{\circ}\text{C}$ 'Sargasso Sea Water'. Because all of the open-net tows were fished obliquely from the surface to 100 m, they had the potential to integrate zooplankton stocks in the mixed layer with those which might seek out the seasonal thermocline. However, by comparing the temperature/salinity (T/S) profiles versus depth from night-to-night with those collected on the year-to-year scale, Lo (1995) concluded that in an environment in which temperature and salinity varied little on a night-to-night scale, species composition and numerical abundance also varied little. Conversely, the greater variability of T/S profiles on the year-to-year scale correlated with more diverse species groups and greater year-to-year variability in numerical abundance.

Using the monthly data from 1991–92, multiple linear regression and CA were employed to determine whether there were positive or negative associations between the numerical abundance of common calycophore species and five environmental variables. Multiple linear regression used five variables: mixed-layer depth (MLD), temperature (T), salinity (S), stratification of temperature (T_s), stratification of salinity (S_s), and two cross-product terms ($T \times S$ and $T_s \times S_s$), and used stepwise forward selection to choose the best regression model based on minimum mean square error (MSE) or a large R^2 .

The results of modeling how the relative abundance of the eight most common calycophore species in the monthly collections might vary with these seven variables are presented in Table VI. The overall regression F -values for half of the species were significant at the 0.05 level; R^2 values ranged from 0.18 (for the polygastric phase of *B. bassensis*) to 0.91 (for the polygastric phase of *A. tetragona*). The residual plots of most species exhibited random scatter in a horizontal band centered around zero residual, suggesting that assumptions of normality were appropriate. Note, however, that the relative abundance of most species exhibited significant relationships with just one (or two) environmental variables and that few species exhibited associations with the same environmental variable. For example, the relative abundance of both generations of *A. tetragona* was positively

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Table VI. Correlation coefficients for the eight most common calyophore species in the 1991–92 monthly sampling with various environmental factors. Species as dependent variables are listed in rows and hydrographic parameters as independent variables are listed in columns. See the first paragraph of the Discussion for an explanation of abbreviations

| Calyophore species | MLD | T | S | Ts | Ss | T × S | Ts × Ss | R ² |
|-----------------------------------|-------|--------|-------|--------|-------|-------|---------|----------------|
| <i>Lensia subtilis</i> P | –0.6 | | –3.4 | | | | | 0.32 |
| <i>L.subtilis</i> E | –1.2 | 4.9 | –4.5 | –2.8 | | | | 0.55 |
| <i>Eudoxoides mitra</i> P | –3.3 | –10.6* | | –4.1 | –6.1* | | 6.1* | 0.83 |
| <i>E.mitra</i> E | –2.3 | | | | | | 5.8* | 0.40 |
| <i>Bassia bassensis</i> P | | | 2.4 | | | | | 0.18 |
| <i>B.bassensis</i> E | 0.6 | | 4.0 | | | | | 0.31 |
| <i>Eudoxoides spiralis</i> P | 0.5 | | | –24.7* | | | | 0.75 |
| <i>E.spiralis</i> E | 11.5* | | | | | –2.4 | | 0.62 |
| <i>Abylopsis eschscholtzi</i> P | 1.2 | 2.2 | 15.5* | –3.6 | | | | 0.79 |
| <i>A.eschscholtzi</i> E | | | 1.0 | | | | | 0.37 |
| <i>Chelophyes appendiculata</i> P | | | | | –0.6 | | 8.2* | 0.46 |
| <i>C.appendiculata</i> E | | | 0.9 | | 34.2* | | | 0.78 |
| <i>Abylopsis tetragona</i> P | 68.2* | –11.2* | | | 1.7 | | | 0.91 |
| <i>A.tetragona</i> E | 15.6* | 1.1 | 0.8 | –0.9 | –2.9 | –1.8 | 1.1 | 0.85 |
| <i>Diphyes bojani</i> P | 1.9 | | | –6.1* | –0.4 | | 2.2 | 0.65 |
| <i>D.bojani</i> E | | –3.3 | | | 3.1 | | | 0.28 |

*Significant at the 0.05 level.

related with MLD, that of *A.eschscholtzi* was positively related with salinity, and that of *D.bojani* was negatively related with stratification of temperature. On the other hand, the relative abundance of *B.bassensis* exhibited no significant relationships with any of these variables.

Haury *et al.* (1978) popularized the use of the three-dimensional plots of environmental parameters first presented by Stommel (1963) to illustrate how spatial and temporal scales often interrelate fairly predictably in biological aggregations. They described seven time/space combinations, spanning distances from millimeters to hundreds of kilometers and times from minutes to hundreds of years. Their ‘coarse’ spatial scale (1–100 km) and their ‘weather-random’ temporal scale (hours–days) are the scales most appropriate to the open-net collections of the present study.

On these scales of time/space, the biovolume of macrozooplankton and siphonophores and the abundance of most calyophore species showed no significant differences during consecutive summer nights of 1992, and similar species composition also occurred in coarse space (tens of kilometers) scales when on the night of 30–31 August the ship sampled Hydrostation-S as well as the BATS station. In other words, the siphonophore population was very stable on spatial scales of 50–100 km and during the temporal scale of three consecutive summer nights. Low variability in near-surface environmental conditions on this coarse spatial/weather-random temporal scale presumably played an important role in creating low nightly variations in numerical abundance. Otherwise, biological populations can be dispersed by cascade mechanisms (Mackas *et al.*, 1985), such as the passage of mesoscale eddies (Michaels *et al.*, 1994).

Seasonal and interannual differences

Winter (December–March), spring–summer (April–July) and summer–fall (August–November) groups were recognized by cluster analysis. Winter species (*B.bassensis*, *E.spiralis*, *A.tetragona* and *A.eschscholtzi*) exhibited a positive correlation with the depth of the mixed layer (MLD), but a negative correlation with the stratification of temperature (thermocline). In other words, these species were most abundant when the depth of the mixed layer was deep during winter and decreased in abundance in summer when a seasonal thermocline developed. Spring–summer species (*E.mitra*, *D.bojani* and *L.hotspur*) exhibited a negative correlation with temperature and stratification (thermocline or halocline). They were most abundant in spring, but populations decreased when summer stratification intensified. Summer–fall species (*L.subtilis*, *C.appendiculata* and *D.dispar*) showed a negative or low correlation with MLD and a negative correlation with salinity, suggesting that they fared best during the strongly stratified, oligotrophic months characterized by lower surface salinity at the BATS station (Michaels *et al.*, 1994).

A likely explanation of why the spring–summer and summer–fall groups were more closely related to each other than either of them was to the winter group is that the seasonal variation in calycophore populations may be related to the annual cycle of 18°C water formation. With the deepening of the wind-mixed layer, the seasonal thermocline can be destroyed so that 18°C water may extend to the surface, as discussed by Deevey (1971) and Michaels *et al.* (1994). In general, the seasonal changes in vertical profiles of temperature and salinity are larger than the cast-to-cast variations during a single cruise (Michaels *et al.*, 1994), and also larger than the variations within the same month (season), but in different years. The fact that the calycophores in collections made in the same month, but in different years (i.e. July 1991 and July 1992) or in the same season, but in different years (i.e. May 1991, April 1992, and June 1992), clustered together is strong evidence that species groups were similar during the same month (or season) in both 1991 and 1992.

Only relative differences in abundance of the three seasonal species groups have been discussed because the water volume fished was not known for most of the monthly open-net collections. However, one of the more common species exhibited measurable differences in nectophore size in spring–summer versus summer–fall or winter. The overall length of the anterior nectophore of *C.appendiculata* in the 1991–92 open-net collections was generally large (70% of them were 6–9 mm long) in collections during April–July, but small (<6 mm) later in the summer and in fall and winter. The larger size of these polygastric generation nectophores in spring may reflect more frequent or better feeding by *C.appendiculata* on grazers of the spring phytoplankton bloom. As a corollary, the high relative abundance in summer of the even smaller size eudoxid phase in the monthly meter net data might be an additional adaptation for survival in food-poor, stratified surface water. Roman *et al.* (1993) reported similar results for a zooplankton study in the same area. Their overall zooplankton biomass retained by 333 µm mesh nets in the upper 500 m was 4–6 times higher in spring (March) than in summer (August); the smaller size zooplankton fraction (<200 µm) showed the opposite trend.

Most species in the present study had >50% eudoxid phase for most of the year, although this varied up to $\pm 25\%$ and both generations generally co-occurred seasonally. From numerical abundance, it can be seen that the eudoxid phase of *C. appendiculata* usually exhibited a peak around July in each year, which suggests that this species has a breeding period in early summer. Bigelow and Sears (1937) and Pugh (1974) also reported a similar breeding season for this species, reaching maximum abundance in the spring and early summer, and minimum abundance in the winter. Other common species, like *L. subtilis* and *D. dispar*, also reached peak abundance in summer, while *E. spiralis* had a bimodal distribution of abundance, with a major peak in winter and a minor peak in summer.

Although most of the common species could be found in the night-time plankton throughout the year, most of them varied markedly in numerical abundance in different years. In July 1989, when *L. subtilis* was the most common siphonophore overall, the mean numerical abundances of both the polygastric and eudoxid phases were 2- to 7-fold higher than in other years. Similarly, when *E. mitra* was overall the most common siphonophore in July 1991, the mean numerical abundances of both the polygastric and eudoxid phases were 2- to 70-fold higher than in summers of other years. Four other species—*B. bassensis*, *A. tetragona*, *A. eschscholtzi* and *D. bojani*—were 2–20 times more abundant in August 1992 than in summer open-net collections from other years.

These variations between years may have been forced by interannual differences in local hydrographic conditions. Zooplankton collections from 1991 were made in early July, while the 1989 collections were in late July. The temperature and salinity of the upper 100 m were different between these two years (Lo, 1995). Near-surface temperatures in late July 1989 were more typical of summer than those of early July 1991: temperature throughout the upper 100 m in July 1989 averaged 1°C warmer than in July 1991. Supporting evidence is the 5-fold greater numerical abundance of *L. subtilis* in July 1989 versus July 1991. *Lensia subtilis*, which has smaller sized nectophores than do most of the other calycophore species, may be more competitive in the food-poor summer season in the oligotrophic Sargasso Sea. That *E. mitra* surpassed *L. subtilis* in abundance in July 1991 may have been a consequence of lower mean surface temperatures (lower near-surface stratification) in July 1991, particularly if lower temperatures facilitated its vertical migration up into surface water.

The interannual variability of hydrographic conditions at Bermuda can be seen in the data reports for the first 4 years of BATS CTD data (Knap *et al.*, 1991, 1992, 1993, 1994). Michaels *et al.* (1994) used these data, along with the four decades of bottle data collected at Hydrostation-S from 1954 to 1994, to argue that the depth of wintertime mixing has been highly variable from one year to the next. For example, they noted that winter mixing by wind and winter storms was more energetic during the period 1954–1969 than it has been since 1970. In the early 1980s, in fact, the depth of winter mixing was <100 m in some years. The depth to which mixing occurs in winter in this area is the most important physical process involved in renewing nutrients to the surface water and thereby stimulating the spring plankton bloom (Bissett *et al.*, 1994; Michaels *et al.*, 1994). When winter mixing extended deeper than 150 m, this usually correlated with a well-developed phytoplankton

bloom that could persist for 2–3 months, lasting until late spring or early summer. Thus, interannual changes in the depth of the mixed layer may be an important forcing factor for the interannual and seasonal variability of siphonophore abundance, if these result in marked changes in the abundance of copepods and other potential prey.

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