Population Density of Gelatinous Macrozooplankton: *In Situ* Estimation in Oceanic Surface Waters

Douglas C. Biggs
Robert R. Bidigare
David E. Smith

Department of Oceanography
Texas A&M University
College Station, Texas

Abstract   SCUBA divers counted the number and kinds of open-ocean gelatinous zooplankton that passed through 5m × 5m reference grids suspended beneath a floating raft. Scales of horizontal and vertical patchiness were evaluated by recording how organism abundance changed temporally and spatially. Population abundance estimates made on a transect of the North Atlantic Ocean at 40°N were compared with those made in subtropical Bahamian waters. In both areas, variability in abundance reflected different scales of time and space. Abundance of the more common taxa generally varied horizontally by less than two-fold on a distance scale of tens-of-meters or on a time scale of tens-of-minutes. However, numerical abundance could vary by an order of magnitude when dives separated by several miles or several hours were compared. Vertically, there were order-of-magnitude variations in numerical abundance within the upper 15 m.

Quantitative information on the population density of gelatinous zooplankton is needed to verify the trophodynamic impact postulated for these organisms in oceanic zooplankton communities (see review by

Hamner *et al.*, 1975). While simple calculations predict that individual gelatinous zooplankton may have the feeding impact (Harbison and Gilmer, 1976; Biggs, 1977*a*) or excretion impact (Biggs, 1977*b*) of all of the non-gelatinous zooplankton biomass in 1–5 m^3 of oligotrophic oceanic surface waters, such impacts might be important only on local microscales if gelatinous population densities averaged less than, for example, one individual per 1,000 m^3.

Nets can be used to sample populations of smaller gelatinous or- gamisms, such as larvaceans and chaetognaths, and estimates of the. population abundance and production of these forms can be found in the literature (Reeve, 1970; Reeve and Walter, 1972; Buckman, 1973; Sameoto, 1973; Fenaux, 1976; Esnal and Castro, 1977). It is statistically ineffective to use plankton nets to quantitatively sample gelatinous taxa like salps, ctenophores, siphonophores, medusae and pseudothecosomatous pteropods. Individuals of these taxa are generally larger and rarer than chaetognaths, larvaceans, and most non-gelatinous plankton. Since most plankton nets are 1 m^2 or less in mouth area, a standard tow samples less than 1,000 m^3. While trawls can sample a larger volume of water, they do not sample the common gelatinous taxa with equal effectiveness. Taxa like pseudothecosomatous pteropods may successfully avoid oncoming trawls (Gilmer, 1974), while other taxa fragment easily, even when captured in trawls fitted with protective cod ends.

An alternative means of studying surface living populations of large gelatinous zooplankton is by the use of SCUBA (Hamner *et al.*, 1975; Harbison *et al.*, 1977, 1978). Divers tethered on 10-m leads may view 10^4–10^5 m^3 of water during a 20–30 minute dive because of the excellent visibility in oligotrophic surface water. Since most of the gelatinous macrozooplankton taxa common there have characteristic shapes, swimming behavior, or fishing postures (Biggs, 1977*a*; Madin and Harbison, 1978*a*; Harbison *et al.*, 1978), divers can readily identify them to suborder (and often to genus) *in situ*. However, the lack of reference boundaries in oceanic surface waters makes it difficult for oceanic divers to estimate the volume of water they search per dive.

The present study reports attempts to quantify the abundance of gelatinous organisms in oceanic surface waters by recording the rate at which animals passed through one or more reference grids suspended

beneath a floating raft. The method is simple, appears to be highly repeatable, and can be carried out by one to three observers.

Materials and Methods

Our *in situ* estimates of gelatinous macrozooplankton abundance were made: (1) during a month-long transect of the North Atlantic Ocean at 40°N during June–July, 1978 (R/V *Atlantis-II* cruise 101), and (2) within a 10 × 50-km corridor in oceanic Bahamian waters occupied for six days during June, 1979 (R/V *Johnson* cruise 80). Reference grids used for both studies measured 5m × 5m and were constructed as follows: Two nylon lines 5 mm in diameter and weighted with 3-kg weights were suspended laterally on booms extending amidships from a rubber support raft. These lines were connected at 5-m intervals with nylon snap-on horizontal lines to define a series of vertically arrayed reference grids (Figure 1).
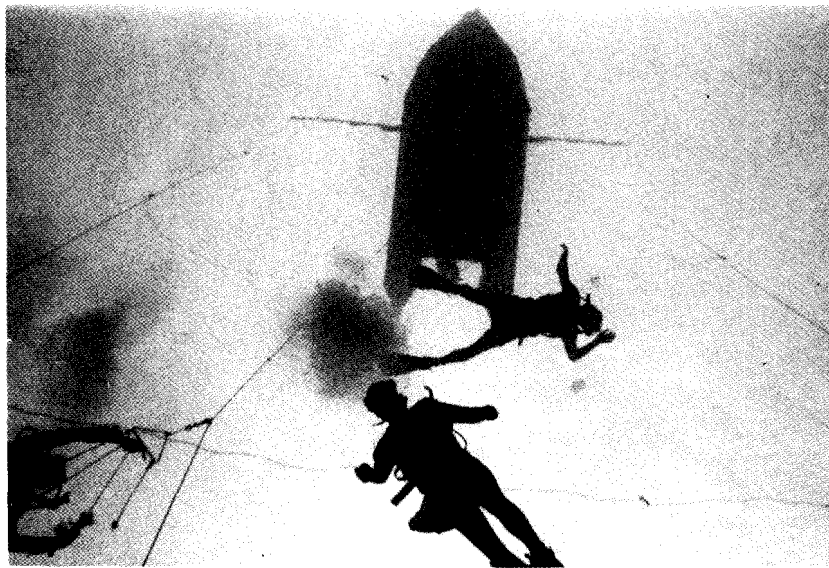

FIGURE 1. Underwater photo of three 5m × 5m grids arrayed below surface raft.

Transect of North Atlantic Ocean

On all dives during *Atlantis-II* cruise 101 (Figure 2), the raft drifted in response to wind and surface currents. When divers tethered off the bow of the raft on a third weighted-down line (as described by Hamner, 1975), they acted as a sea anchor. The effective result was a net drift of water directly through the reference plane of the grid(s) and toward the divers. Underwater cassette tape recorders (Sound Wave Systems, Costa Mesa, CA) were used to record the sightings of large gelatinous zooplankton drifting through the grid(s).
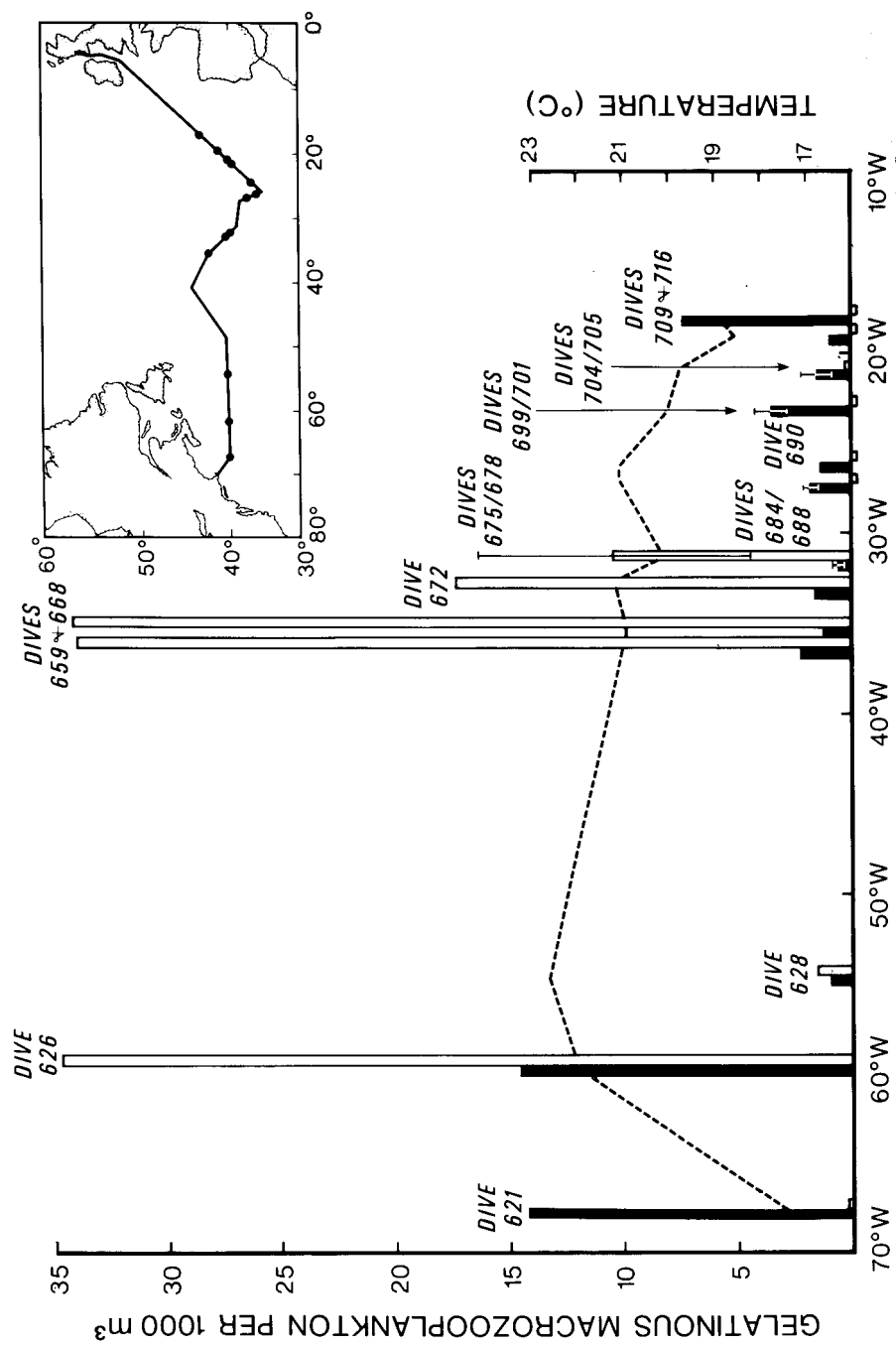
When the wind opposed the current, the grid booms on the raft were rotated to align the plane of the grid(s) normal to the net drift. Since the lateral lines were of narrow diameter, weighted, and supported above the sea surface, a grid presented very little drag and did not noticeably change its orientation over the range of drift rates (1–10 m min^{-1}) and sea states (0–2 m) encountered. The volume searched was calculated by multiplying the grid area by the product of the drift rate and the time of the search interval. Drift was measured at each grid depth separately at the beginning and end of every dive.

Three different methods were used to compare the net drift rate of water through a grid: (1) Divers measured flow rate for 30–60-second intervals with a hand-held TSK flow meter (Trent *et al.*, 1978). (2) Divers, starting at a grid, released concentrated fluorescein dye from syringes and then timed its drifting traverse along the 10-m length of their tether lines. (3) Dye was released at the grid at 30–60-second intervals, and the distance between dye patches was measured by swimming it with a TSK flowmeter (Trent *et al.*, 1978).

To tabulate the ocean-wide survey of data, we have clustered our 17 dives by regions which are broadly temperate, temperate–subtropical transition, or subtropical. These included dives in Slope Water (621), Northern Gyre (659), and Azores–Britain (709, 716) temperate faunal

---

FIGURE 2. Transect averages of the numerical abundance of macrogelatinous carnivores (ctenophores + siphonophores + medusae + gymnosome pteropods + heteropods) versus macrogelatinous herbivores (salps + pseudothecosome pteropods) in the upper 15m of the North Atlantic Ocean.

Legend: Carnivores = solid bars, herbivores = open bars, surface temperature = dashed line. Open bars below abscissa denote dives where no organisms were seen. For dive pairs 675/678, 684/688, 699/701, and 704/705, abundance reflects the average ($\pm$ range) of a late morning and an early afternoon estimate.

TEMPERATURE (°C)

23 21 19 17

10°W 20°W 30°W 40°W 50°W 60°W 70°W

0° 20° 40° 60° 80°

30°W 40° 50° 60°

DIVES 709+716
DIVES 704/705
DIVES 699/701
DIVE 690
DIVES 684/688
DIVES 675/678
DIVE 672
DIVES 659+668
DIVE 628
DIVE 626
DIVE 621

35 30 25 20 15 10 5

GELATINOUS MACROZOOPLANKTON PER 1000 m³

provinces (according to Backus and Craddock, 1977) and in the North-ern Sargasso Sea (628), and Northern North African Subtropical (672, 675/678, 684/688, 690) subtropical faunal provinces.

Bahamas

Six dives were made in a subtropical oceanic area seaward of the 1,000-m isobath, where the southern edge of Little Bahama Bank intersects the Northwest Providence Channel (Figure 3). On three suc-cessive days, Dives A, B, and C were made in early morning (5 hours before local noon). Dives D, E, and F were made in late afternoon (6½ hours after local noon) on three subsequent days.

The volume of water searched on these dives was increased by motoring the raft forward slowly. Observers, tethered off its stern, swam behind the series of grids. The motoring rate was monitored throughout each 20-minute counting period by a surface tender, who recorded the time required for markers placed astern of the raft to drift the distance of a towed 10-m floating line. Temporal changes in or-ganism abundance were examined during each dive by recording obser-vations at each grid depth in four consecutive 5-minute tally intervals (Figue 3).

Taxonomic Identification

The salient features of morphology and swimming–fishing posture of gelatinous zooplankton which permit their generic identification *in situ* have been given in previous reports (Biggs, 1977*a*; Madin and Harbi-son, 1978*a*; Harbison *et al.*, 1978). In summarizing our raw data, we have lumped most taxa at the level of order or suborder or, in the case of salps, by life-history stage. The genera within each taxonomic group show more similarities in feeding biology than others in different groups. Pooling of individual genera into a relatively few groups based on order or suborder also facilitates broad comparisons of the abundance and distribution of herbivores versus carnivores, or between different phyla.

Juvenile forms were too small to be counted effectively and have been ignored in this report, although ephyrae and juvenile medusae were
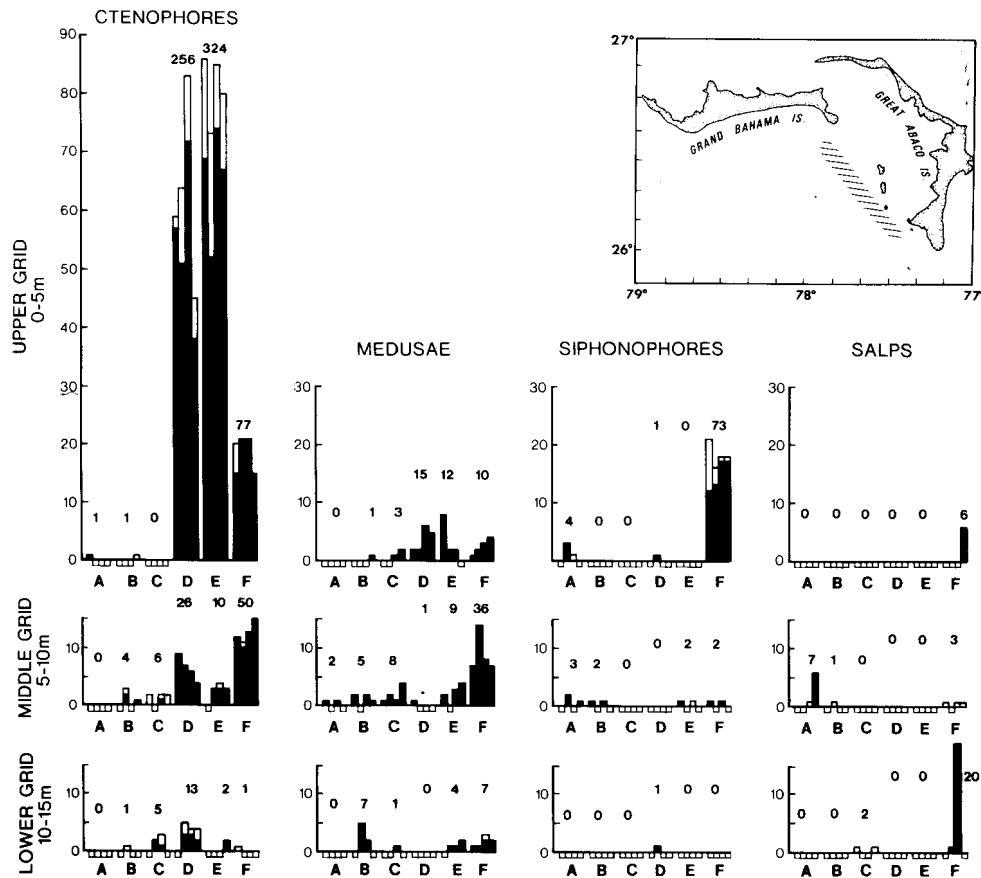
FIGURE 3. Numbers of gelatinous macrozooplankton encountered per dive in each of four consecutive 5-minute tally intervals, with dive totals for six dives (A–F) in Bahamian surface waters. See Table 3 for details of time and volume searched. Shaded corridor on map denotes operations area.

Legend: For ctenophores, shaded bars = lobates, open bars = all other taxa. For medusae, shaded bars = hydromedusae, open bars = scyphomedusae. For siphonophores, shaded bars = calycophores, open bars = all other taxa. For salps, shaded bars = aggregate individuals, open bars = solitary individuals. Open bars below abscissa denote tally intervals in which no organisms were seen.

abundant at times. Among siphonophores of the suborder Ca-
lycophorae, only large common genera were enumerated (*Diphyes,
Chelophyes, Rosacea*). Among the pelagic tunicates, only salps of the
genera *Pegea, Salpa, Cyclosalpa, Ihlea,* and *Iasis* were enumerated.
Doliolids, larvaceans, and salps of the genus *Thalia* were frequently
present, but were too small to be enumerated on a 5m × 5m scale.

Results

North Atlantic Ocean

The three methods used to estimate drift rate agreed to within 15%. Drift
rate was sometimes more variable when drift determined at the start of
the dive was compared with drift estimated 20–30 minutes later. How-
ever, the standard error in drift rate, due to measurement error com-
pounded by variability of drift with depth or through time, averaged
only 20% of the mean (Table 1).

The data presented for the North Atlantic focus on the 17-grid dives
which allowed us to survey at least 2,000 m³ (Table 1). Woods Hole
Oceanographic Institution dive numbers were assigned to each dive and
are shown graphically in Figure 2. Detailed location data have been
published elsewhere (Swanberg and Harbison, 1980). Eight of these 17
dives represent pairs of dives conducted on the same day at essentially
the same geographic location (675/678, 684/688, 699/701, and 704/
705, which were 2.5, 3.1, 3.4, and 37.6 miles apart, respectively). The
dives in each pair were separated in time by 3–5 hours.

The most numerous organisms seldom differed in abundance between
first and second halves of the same dive by more than a factor of two
(Table 2). The average daytime density of macrogelatinous carnivores
(ctenophores, siphonophores, medusae, gymnosome pteropods, and
heteropods) did not exceed 5–10 of any one type per 1,000 m³, or a total
of 15 per 1,000 m³ in all classes (Table 1; Figure 2). Large gelatinous
herbivores, on the other hand, were encountered only sporadically at the
17 grid stations.

Bahamas

During these grid dives the motor speed remained uniform to within
about 8% (range 6–10%, n = 6). Consequently, the mean error in the

Table 1

Volume searched per dive and calculated average numerical abundance (individuals per 1,000 m³) of gelatinous macrozooplankton present during the daytime in the upper 15 m of North Atlantic Ocean surface waters. See text for details of station code.

	Temperate Region				Temperate—Subtropical Transitional Region						Subtropical Region						
	621	659	709	716	626	668	699	701	704	705	628	672	675	678	684	688	690
Volume Searched per Dive																	
Grid area (m²)	25	50	50	50	25	50	50	25	50	50	25	50	50	75	50	50	50
Minutes searched	25	20	20	20	15	25	20	25	20	20	20	30	35	10	25	20	20
Drift rate (m/rm)	7±1	6±2	10±1	7±1	7±1	7±1	7±1	5±1	6±1	5±1	4±1	7±2	4±1	5±1	3±1	6±1	5±1
Volume searched (m³)	4,400	6,000	10,000	7,000	2,600	8,800	7,000	3,100	6,000	5,000	2,000	10,500	7,000	3,800	3,800	6,000	5,000
Numerical Abundance (Individuals/1,000m³, 0–15)																	
Ctenophores	8.4	1.5	1.8	3.7	9.6	0.1	·2.6	1.3	1.0	0.2	0	0.9	0.1	0.3	0	0.2	0
Sipnonephores	5.2	0.3	0.2	0.4	2.7	0.1	0	0	0.5	0.4	0.5	0.8	0.6	0.3	1.6	1.2	0.6
Madusae	0.7	0.5	1.1	3.4	1.5	1.1	0.3	2.9	0.7	0.4	0	0	0	0.3	0.5	0.2	0.8
Gymnosomes/Heteropods	0	0	0	0	0.8	0	0	0	0	0	0.5	0	0	0	0	0	0
Pseudothecosomes	0	0	0	0	1.2	0	0	0	0	0	1.5	0	0	0	0	0	0
Salps	0.2	34.0	0.1	0	33.5	34.2	0	0	0.2	0	0	17.3	4.4	16.3	0	0	.0
Time Difference from Local Noon (hours)																	
	+3	-2	+1½	+3	+3	-3	-2	+1½	-2	+3	-2	+2	-2	+2	-2	+1	-2

Table 2

Numbers of gelatinous macrozooplankton encountered per dive on a transect of the North Atlantic Ocean at 40°N. Each entry is the sum of individuals encountered in all grids during the first half of a dive plus those encountered during the second half of that same dive. See Table 1 for details of time and volume searched; see text for details of station code.

	Temperate Region				Temperate–Subtropical Transitional Region						Subtropical Region						
	621	659	709	716	626	668	699	701	704	705	628	672	675	678	684	688	690
Ctenophores																	
Cydippid	1+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cestid	0	0	0	0	8+7	0+1	1+0	0	0	0	0	0	0	0	0	0	0
Lobate	5+5	4+5	12+6	7+13	0	0	10+6	3+1	4+2	0+1	0	3+5	0+1	0	0	0+1	0
Beroid	12+13	0	0	3+3	4+6	0	0+1	0	0	0	0	0+1	0	1+0	0	0	0
Siphonophores																	
Calycophore	2+0	0+1	0+2	2+1	1+1	1+0	0	0	1+2	1+1	0	6+2	2+2	1+0	3+2	3+3	1+2
Physonect	14+7	0	0	0	1+4	0	0	0	0	0	0+1	0	0	0	0+1	0+1	0
Cystonect	0	0+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Madusae																	
Scyphozoan	0+1	2+1	3+8	12+12	0	4+6	1+1	4+5	2+2	0+2	0	0	0	0+1	0+1	0	3+1
Hydrozoan	1+1	0	0	0	2+2	0	0	0	0	0	0	0	0	0	1+0	0+1	0
Gelatinous Molluscs																	
Gymnosome	0	0	0	0	0+2	0	0	0	0	0	0	0	0	0	0	0	0
Heteropod	0	0	0	0	0	0	0	0	0	0	0+1	0	0	0	0	0	0
Pseudothecosome	0	0	0	0	1+2	0	0	0	0	0	1+2	0	0	0	0	0	0
Salps																	
Solitary	1+0	0+2	1+0	0	0	3+3	0	0	0	0	0	1+1	0+1	1+0	0	0	0
Aggregate	0	120+82	0	0	27+60	206+89	0	0	0+1	0	0	108+72	18+12	37+24	0	0	0

volume of water searched on these dives is 2½ times lower than reported for our North Atlantic transect work (8% vs. 20%).

As in the North Atlantic transect data, the abundance of the more common non-salp taxa in Bahamian waters rarely differed by more than a factor of two between halves (or even quarters) of any given dive (Figure 3). Moreover, on dives A–C as in the subtropical region of the North Atlantic transect, numerical abundance of macrogelatinous carnivores was uniformly low ($x \pm s_x = 0.9 \pm 0.4$ individuals 1,000 m^{-3}; Table 3). At these low densities, no consistent vertical stratification of numerical abundance was apparent (Figure 3).

In sharp contrast to dives A–C and to the North Atlantic subtropical dives, numerical abundance of macrogelatinous carnivores on late afternoon dives D–F was consistently more than an order of magnitude greater ($x \pm s_x = 12.7 \pm 1.8$ individuals 1,000 m^{-3}; Table 3). In addition, vertical stratification of the ctenophores was apparent (Figure 3). Lobates were most abundant in the uppermost 5m, with mean densities calculated to be 31 and 26 individuals per 1,000 m^3 on dives D and E, respectively. On dive F, lobate density was lower (10 individuals per 1,000 m^3), but was spread more evenly between the uppermost and middle grids.

Discussion

Horizontal Patchiness

The relative scale length of horizontal patchiness of the more common taxa of gelatinous macrozooplankton can be estimated by using the appropriate drift rate and search time data. We traversed average distances of 65 m (range 25–100 m, n = 17) and 146 m (range 115–208 m, n = 6) during half of an average dive in the North Atlantic and Bahamas, respectively (Tables 1 and 3). That the more common gelatinous macrozooplankton varied in abundance by less than two-fold between the two halves of a dive implies that patch-creating processes operate on these organisms at scales markedly greater (or markedly smaller) than tens-of-meters or tens-of-minutes. As Figure 3 indicates, such a generalization remains substantiated if the Bahamian data are analyzed by five-minute (about 73 m) path length intervals.

Between-dive variation in abundance of the more common taxa, as

Table 3

Volume searched per dive and calculated average numerical abundance (individuals per 1,000 m³) of gelatinous macrozoo-plankton present during the daytime in the upper 15 m of Bahamian surface waters. See text for details of station code.

	Early Morning Dives			Late Afternoon Dives		
	A	B	C	D	E	F
Volume Searched per Dive						
Grid Area (m²)	75	75	75	75	75	75
Minutes Searched	20	20	20	20	20	20
Motor Rate (m/min)	11.5 ± 1.1	14.2 ± 1.4	12.2 ± 0.7	14.2 ± 1.0	20.8 ± 1.3	14.6 ± 1.4
Volume Searched (m³)	17,300	21,300	18,300	21,300	31,200	21,900
Numerical Abundance (Individuals/1,000 m³, 0–15 m)						
Ctenophores	0.1	0.2	0.6	13.9	10.8	5.8
Siphonophores	0.4	0.1	0	0.1	0.1	3.4
Medusae	0.1	0.6	0.7	0.8	0.8	2.4
Gelatinous Molluscs	0	0	0	0	0	0
Salps	0.4	0.1	0.1	0	0	1.3
Time Difference from Local Noon (hours)						
	-5	-5	-5	+6 1/2	+6 1/2	+6 1/2

calculated from the paired dives separated by less than 40 miles and 5 hours in the North Atlantic, was more pronounced than within-dive variation. There was two-fold and five-fold variation, respectively, in ctenophore abundance between dives of pairs 699/701 and 704/705 in the temperate–subtropical transition zone. Similarly, abundance of medusae varied ten-fold and two-fold between dives of these same pairs. In subtropical regions, the abundance of siphonophores and salps varied by two-fold and four-fold, respectively, between the paired dives 675/678. However, in the other subtropical pair of dives (684/688); siphonophores varied by only about 25%, and salps were absent.

Order-of-magnitude and larger variations in population abundance were observed over larger distances (and/or longer time periods), when occasional local aggregations were documented on the North Atlantic cruise. For example, on dive 637 at a station in the western Northern Sargasso Sea, aggregate and solitary salps of the genus *Thalia* were locally abundant below 5 m to a depth of at least 15 m. Also, on dive 726 at a station in slope water off the Bay of Biscay, doliolids and aggregate salps of the genus *Ihlea* were abundant from the surface to a depth of at least 20 m. In both cases the aggregations of pelagic tunicates were too dense to be counted accurately on a 5m × 5m scale, and we estimate that salp densities at these stations were at least 1–2 orders of magnitude higher than those recorded in Table 2.

Vertical Patchiness

We documented order-of-magnitude variations in abundance of lobate ctenophores on a vertical fine-scale of 5m in surface waters of the Bahamas. Such patchiness has a strong diel component and might be created if most or all of a normally daytime-diffuse population of epipelagic ctenophores become positively buoyant. An alteration in buoyancy, or any other mechanism that creates microscale variability in vertical population density, may influence the community structure and stability of gelatinous plankton assemblages. For example, sharp gradients in population abundance which change on a diel basis (see Table 3) may allow two or more epipelagic species to coexist in a "contemporaneous disequilibrium" (Richerson *et al.*, 1970) solution to Hutchinson's (1961) "paradox of the plankton."

Geographic Variations

Pugh (1975) investigated the distribution of siphonophores in a transect of the North Atlantic Ocean at 32°N. Since his samples were derived from RMT-8 trawl collections (0–1,000m), the fragmented condition of most siphonophores captured in the nets allowed Pugh to estimate numerical abundance for small calycophore species only. Pugh did determine the total biomass of the fragmented gelatinous components (displacement volume per two-hour haul), however, and his 0–1,000 m. biomass data support our *in situ* observations of the upper 15 m that siphonophores were more abundant in the eastern and western margins of the North Atlantic than in the central regions.

While most of the siphonophore species that were most common in Pugh's (1975) collections live either deeper than 15 m (Alvariño, 1967; Pugh, 1975) or are too tiny to be enumerated on a grid size of 5m × 5m, we did encounter *Chelophyes appendiculata* in common with Pugh. Like him, we found this species more abundantly in the eastern half of the transect than in the Sargasso Sea.

Comparisons with Alternative Methods

We thought initially of using a less fragile "index species" able to be sampled by conventional means as a basis for calculating the population abundance of gelatinous zooplankton. Theoretically, by comparing estimates of index species abundance made before or after a dive with its abundance relative to particular groups of gelatinous zooplankton determined during the dive, the abundance of the latter can be calculated. This approach has at least two associated difficulties. First, the method assumes that there is some functional or predictable covariation between the index species and the other gelatinous zooplankton. Second, any abundance estimate made relative to index species will be density dependent. In other words, species that were rare on any dive will be overestimated using this technique (see Pielou, 1977).

Harbison *et al*. (1978) have used yet another method to calculate the abundance of ctenophores in the Southern Sargasso Sea and Caribbean Sea. Two divers participated, and each was presumed to encounter ctenophores primarily within imaginary, non-overlapping areas of radius 2m extending around each diver. By multiplying these imaginary

areas by the distance which each randomly ranging diver drifted through the water, Harbison *et al.* estimated the total volume of water they searched. Using this method, Harbison *et al.* judged that lobate ctenophore abundance ranged from 0–31 animals 1,000 m^{-3} ($\bar{x}$ = 6.3 individuals per 1,000 m^3).

Although there is no direct way to evaluate the error associated with abundance estimated by these random-search methods, uncertainty in drift rate and search radius will contribute to the total relative error. A 20% uncertainty in the length of the imaginary radii searched by the divers is equivalent to a 36–44% uncertainty in volume searched. Relative error will be greater if organisms are occasionally overlooked or counted twice.

In summary, since the method we have detailed for use of drifting reference grids can be carried out by a single observer (plus safety partner) and with fixed reference bounds allows greater certainty of volume searched, it would seem to be the most efficient estimator of population abundance when gelatinous macrozooplankton are reasonably abundant. The grid method also optimizes information per dive, for it is designed not only to estimate mean abundance but to yield data on the scales of horizontal and vertical spatial variability within a single dive.

All direct observation techniques which employ non-saturated SCUBA diving will be limited by safety constraints to sampling only the uppermost 30 m of the oceans. Ecologically, this is a rather arbitrary boundary, since gradients of temperature, salinity, oxygen, and nutrients are often minimal here. Alternative means of quantitatively estimating the abundance of deep-living populations will have to be devised before models can be extended to consider the trophodynamic impact of mesopelagic populations of gelatinous zooplankton. Preliminary indications are that these populations may be extremely abundant (Madin and Harbison, 1978*b*).

Acknowledgments

References

Alvariño, A., 1967, Bathymetric distribution of chaetognaths, siphonophores, medusae and ctenophores off San Diego, California. *Pacific Sci.,* Vol. 21, pp. 474–485.

Backus, R.H., and Craddock, J.E., 1977, Pelagic faunal provinces and sound-scattering levels in the Atlantic Ocean. In: *Oceanic Sound-Scattering Prediction,* N. R. Andersen and B. J. Zahuranec, ed. New York: Plenum Press.

Biggs, D.C., 1977a, Field studies of fishing, feeding and digestion in siphonophores. *Mar. Behav. Physiol.,* Vol. 4, pp. 261–274.

Biggs, D.C., 1977b, Respiration and ammonium excretion by open ocean gelatinous zooplankton. *Limnol. Oceanogr.,* Vol. 22, pp. 108–117.

Buckman, A., 1973, Sorted samples and quantitative counts in appendicularian catches. *Mar. Biol.,* Vol. 21, pp. 349–353.

Esnal, G.B., and Castro, R.J., 1977, Distributional and biometrical study of appendicularians from the west-south Atlantic Ocean. *Hydrobiologia,* Vol. 56, pp. 241–246.

Fenaux, R., 1976, Cycle vitale, croissance et production chez *Fritillaria pellucida* (Appendicularia), dans la baie de Villefranche-sur-Mer, France. *Mar. Biol.,* Vol. 34, pp. 229–238.

Gilmer, R. W., 1974, Some aspects of feeding in thecosomatous pteropod molluscs. *J. Exp. Mar. Biol. Ecol.,* Vol. 15, pp. 127–144.

Hamner, W.M., 1975, Underwater observations of blue-water plankton: Logistics, techniques and safety procedures for divers at sea. *Limnol. Oceanogr.,* Vol. 20, pp. 1045–1051.

Hamner, W.M., Madin, L.P., Alldredge, A.L., Gilmer, R.W., and Hamner, P.P., 1975, Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology and behavior. *Limnol. Oceanogr.,* Vol. 20, pp. 907–917.

Harbison, G.R., and Gilmer, R.W., 1976, The feeding rates of the pelagic tunicate *Pegea confederanta* and two other salps. *Limnol. Oceanogr.,* Vol. 21, pp. 517–528.

Harbison, G.R., Biggs, D.C., and Madin, L.P., 1977, The associations of Amphipoda Hyperiidea with gelatinous zooplankton. II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep-Sea Research,* Vol. 24, pp. 465–488.

Harbison, G.R., Madin, L.P., and Swanberg, N.R., 1978, On the natural history and distribution of oceanic ctenophores. *Deep-Sea Research,* Vol. 25, pp. 233–256.

Hutchinson, G.E., 1961, The paradox of the plankton. *Amer. Naturalist,* No. 882, pp. 137–145.

Madin, L.P., and Harbison, G.R., 1977, The associations of Amphipoda Hyperiidea

with gelatinous zooplankton. I. Associations with Salpidae. *Deep-Sea Research,* Vol. 24, pp. 449–463.

Madin, L.P., and Harbison, G.R., 1978*a*, Salps of the genus *Pegea* Savigny 1816 (Tunicata: Thaliacea). *Bull. Mar. Sci.,* Vol. 28, pp. 335–344.

Madin, L.P., and Harbison, G.R., 1978*b*, *Bathocyroe fosteri* (gen. nov., sp. nov.), a mesopelagic ctenophore observed and collected from a submersible. *J. Mar. Biol. Assoc. U.K.,* Vol. 58, pp. 559–564.

Pielou, E.C., 1977, *Mathematical Ecology.* John Wiley and Sons, Inc., 385 pp.

Pugh, P.R., 1974, The vertical distribution of the siphonophores collected during the SOND cruise, 1965. *J. Mar. Biol. Assoc. U.K.,* Vol. 54, pp. 25–90.

Pugh, P.R., 1975, The distribution of siphonophores in a transect across the North Atlantic Ocean at 32°N. *J. Exp. Mar. Biol. Ecol.,* Vol. 20, pp. 77–79.

Reeve, M.R., 1970, The biology of Chaetognatha. I. Quantitative aspects of growth and egg production in *Sagitta hispida.* In: *Marine Food Chains,* J.H. Steele, ed. Univ. California Press, pp. 168–189.

Reeve, M.R., and Walter, M.A., 1972, Conditions of culture, food-size selection, and the effects of temperature and salinity on growth rate and generation time in *Sagitta hispida* Conant. *J. Exp. Mar. Biol. Ecol.,* Vol. 9, pp. 191–200.

Richerson, P., Armstrong, R., and Goldman, C.R., 1970, Contemporaneous disequilibrium, a new hypothesis to explain the "paradox of the plankton." *Proc. Nat. Acad. Sci.,* Vol. 67, pp. 1710–1714.

Sameoto, D.D., 1973, Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. *J. Fish. Res. Board Can.,* Vol. 30, pp. 333–344.

Swanberg, N.R., and Harbison. G.R., 1980. The ecology of a new colonial radiolarian *(Collozoum longiformis,* sp. nov.) from the equatorial Atlantic Ocean. *Deep-Sea Res.,* Vol. 27, pp. 715–732.

Trent, J.D., Shanks, A.L., and Silver, M.W., 1978, In situ and laboratory measurements on macroscopic aggregates in Monterey Bay, California. *Limnol. Oceanogr.,* Vol. 23, pp. 626–635.