

SOME ENVIRONMENTAL CONSEQUENCES OF VERTICAL MIGRATION IN MARINE ZOOPLANKTON¹

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ABSTRACT

The spatial distribution of plankton is highly aggregated, so one might expect that a vertically migrating animal enters a biotic environment that is markedly different each evening and that the changes in environment between daylight periods spent at depth are equally great. To measure the extent of these changes, as typified by the species composition of the zooplankton, a model zooplankton was followed in the area southeast of Guadalupe Island, Baja California, for 52 hr. Net tows for zooplankton were taken nearby every 2 hr. A 48-hr series of plankton samples at a single geographic position was taken afterward for comparison of the rates of change of species composition as observed by drogue-guided and ordinary station sampling. There were 250 species and other categories in the 23 nighttime samples from 10 m and 280 in the 20 daytime samples from 100 m. Contrary to the radical change expected, there was a slow, steady change in composition from the beginning to the end of the combined drogue and single position series. Some evidence was found of a limit to this change, implying a limit to the uncertainty a migrating animal experiences in the species composition of the two surrounding communities in which it lives. Several peculiar features of the change of species composition with time are discussed.

INTRODUCTION

Hardy (1935) suggested that diurnal vertical migration enabled planktonic animals to move horizontally within the current system. If the currents near the surface are different in direction or speed from those at greater depth, then an animal moving vertically will be displaced when it returns to the surface. This ensures zooplankton against remaining in water from which they have removed all the food or being trapped with other disadvantageous environmental situations; thus, enhanced mobility may be an important selective value of vertical migration. But migration also has drawbacks: an animal cannot stay in a favorable environment when it has found one and may be forced to cope with different environments each night and each day.

Differences between nights and between days with respect to physical factors are probably not important. Variability in temperature, salinity, oxygen concentration, or trace element composition on a local scale (a few tens of kilometers) in the surface layer is only a small fraction of the difference in these factors between the surface layer and the deeper levels inhabited during the day. The obvious existence of physiological adaptations that permit survival at the limits of the vertical migration implies that the well-being of migrating animals should be little affected by the small horizontal differences in physical factors.

Biological differences, on the other hand, may be important. Because large variations occur on a local scale horizontally in the numbers of individuals of most species (Cassie 1963), and possibly in the relative proportions of species, differences in biotic conditions on successive nights and successive days could be large. To a prey organism, the difference in the abundance of predators may be the equivalent of having 10 times more tigers in the woods tonight than last night. Differences in the abundance of other individuals of the same species may change the level of

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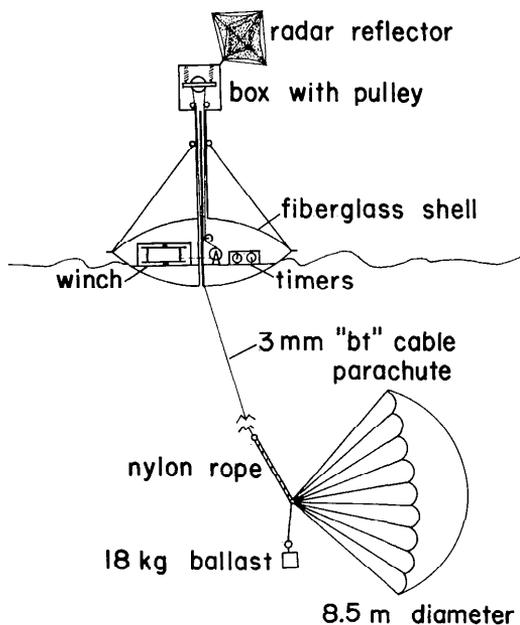


FIG. 1. Schematic diagram of the migrating parachute drogue.

intraspecific competition and the probability of making contacts necessary for mating. The extent to which the species composition of the plankton varies locally is not yet well known. If this variation is large, then a migrating animal must experience different community relations each night and each day, and those interactions most important to population processes must achieve their importance on a long-term, large-scale basis by averaging of the many disparate experiences of the individuals in the population. In this case the important interactions can only be found by long-term, large-scale averaging of sample results. If, on the other hand, the biotic interactions experienced by an animal are similar each night and each day, then interactions having long-term importance for population processes are likely to be well represented by a small number of replicate samples.

These considerations suggest that a number of important ecological conclusions might emerge from a set of plankton samples and physical observations representing the pelagic environment from the view-

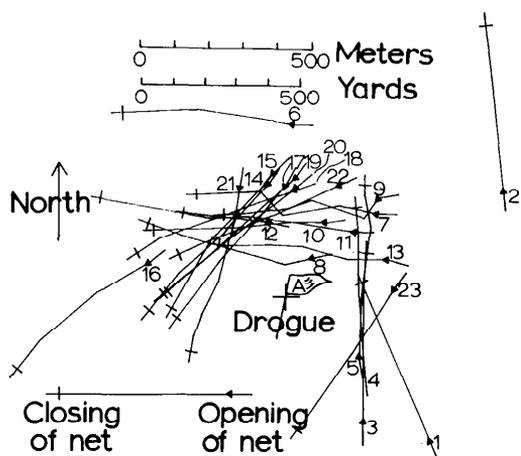


FIG. 2. Positions of the net tow paths in the drogue series of net tows relative to the drogue.

point of an individual planktonic animal. A set of data approximating this ideal can be obtained by sampling while following a current tracer designed to make diurnal vertical migrations, that is, a model animal. This paper reports the results of such a study.

This work was a thesis project at the Scripps Institution of Oceanography. It was prepared for publication while I was at the University of Auckland. Prof. J. McGowan provided the idea of a migrating parachute drogue and gave constant help with the work. Many others gave important help.

METHODS AND DETAILS OF THE SAMPLING PROGRAM

A parachute drogue (Volkman, Knauss, and Vine 1956) modified so that the wire could be lengthened and shortened periodically was used as a model animal. The system has 4 basic components (Fig. 1): a closed fiber-glass float, a battery-powered winch, a pair of timing switches that start the winch at dawn and dusk, and a ballasted 8.5-m parachute attached to the wire end by a 10-m length of nylon rope which acts as an accumulator. Three cycles of raising and lowering can be made with one set of batteries. The timers can be set to activate the winch within ± 15

TABLE 1. *Conditions of the stations*

Station No.	Light period	Following drogue or at fix station
p	Night	Just before launch of drogue
1-3	Night	Drogue
4-8	Day	Drogue
9-13	Night	Drogue
14-18	Day	Drogue
19-23	Night	Drogue
24-28	Day	Fix
29-33	Night	Fix
34-38	Day	Fix
39-43	Night	Fix

min of a desired time. A complete description is given in Miller (1969).

The migrating parachute drogue was used in an area 37 km east of the south tip of Guadalupe Island, Baja California, in September 1967, from the Scripps Institution of Oceanography RV *Thomas Washington*. At 2130 hours (GMT + 7 hr, Pacific Daylight Saving time) on 18 September the ship arrived on station, and a preliminary net tow (station p) was taken to determine if sufficient plankton were present. The drogue was launched at about 2230. Its position was first taken at 0018 on 19 September at station 1 (28°50.5' N, 116°51.5' W). The clocks in the buoy were set to start the parachute down at 0535 and up at 1755. These times were well before sunrise (0633 on 19 September) and sunset (1850 hours). The parachute was at 10 m at night and at 100 m in the day. Migrations took 42 min.

A series of stations was sampled beginning at 2000, 2200, 0200, and 0400 hours during the night and at 0800, 1000, 1200, 1400, and 1600 during the day. Stations began with a horizontal tow 500 m long at 4.5 km/hr past the drogue at the depth of the parachute with a bongo opening-closing net (McGowan and Brown 1966) equipped with 0.505-mm Nitex mesh. The length of the path filtered is determined by a flowmeter attached to the frame so that all samples can filter very nearly the same volume of water. The intended path of the net tows was into the wind, passing the drogue to port with a midpoint 229 m

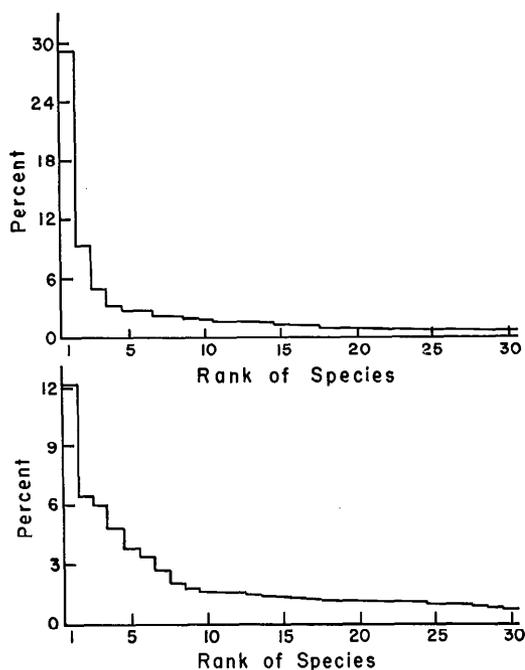


FIG. 3. Above: average relative abundance of categories in the night samples. The dominant categories are *Limacina inflata*, *Oikopleura* sp., immature *Clausocalanus*, immature *Calanus minor*, female *Clausocalanus mastigophorus*, female *Clausocalanus furcatus*, female *Oncaea media*, female *Conchoecia curta*, *Sagitta enflata*, *Sagitta pseudo-serratodentata*. Below: same for the day samples. The dominant categories are *Appendicularia*—all species, immature *Euchaeta*, female *Euaetideus bradyi*, immature *Sagitta*, *Sagitta bierii*, immature *Euaetideus bradyi*, immature *Calanus tenuicornis*, female *C. tenuicornis*, calyptopis larvae of *Euphausia gibboides*, female *Conchoecia curta*.

from the drogue. The actual positions are shown in Fig. 2.

After the net tow the ship moved to a point 50 m leeward of the drogue. The drogue's position was determined from radar coordinates, and a salinity-temperature-depth indicator (STD; Bisset-Berman Corp.) was lowered to 300 m. A Nansen bottle was attached to the wire just above the STD, which was inverted when the STD was at the same level as the parachute. These water samples were analyzed by autoanalyzer techniques (Armstrong, Stearns, and Strickland 1967) for nitrate, nitrite, phosphate, and silicate, by a fluorometric technique (Holm-Hansen et al.

TABLE 2. Results of the Monte Carlo sampling study of percent similarity, PS. Mean PS in each experiment is based on 200 pairs of samples

Diversity of the assemblage	Average community composition for			
	Day (280 categories)		Night (250 categories)	
$H = -\sum_{i=1}^s p_i \log_2 p_i^*$	6.036		5.040	
Sample size, N	1,000	2,000	1,000	2,000
Mean PS	81.9%	87.0%	85.3%	89.2%
$1.96 \times SD$	2.61%	1.97%	2.43%	1.95%
χ^2 goodness-of-fit to normal distribution (5 df)	1.50	4.41	4.44	1.82
Probability of as bad or worse fit	0.90	0.40	0.40	0.80

* This is the Shannon-Wiener information or entropy function, commonly used as a diversity index.

1965) for chlorophyll a in the filterable plants, and for oxygen by the micrometer pipette method of Carpenter (1965).

The drogue was recovered on 21 September at 0800. The recovery site was also the site of a series of 20 "fix" stations taken on the same time schedule as the earlier drogue series. These stations also started with a 500-m horizontal net tow at 10 m at night and at 100 m in the day. The nets were opened as the ship on course 292° passed a point bearing 112° at 41.5 km from Isla de Afuera. When the

tow was complete the ship was stopped and an STD lowering made as before. Positions of these casts were about 1.8 km from the messenger drop point. This set of stations was completed on 23 September. The series of fix stations was taken to provide a comparison between drogue-guided zooplankton sampling and ordinary station sampling at a single geographic position. Conditions are summarized for all stations in Table 1.

A series of vertically stratified bongo net hauls was taken during the day and another during the night following the fix stations to provide data about the vertical migratory behavior of the species important in the earlier work. I hoped to find one or more species whose migration was between the same depths as the migration of the parachute, making the drogue a more biologically relevant model. The nets were raised obliquely while open, giving samples from the following depth intervals in meters: 350-300, 300-250, 250-200, 200-150, 150-130, 130-110, 110-100, 100-90, 90-70, 70-35, 35-0 during the day, and 300-250, 250-200, 200-150, 150-100, 100-40, 40-20, and 20-0 at night.

One 0.25 aliquot of each of the 44 samples from the drogue and fix stations was counted in a Plexiglas tray, divided into troughs by vertical strips of plastic, under a stereoscopic microscope. The entire width of a trough was visible at the magnification most frequently used (240 diam). All species of chaetognaths, copepods, cu-

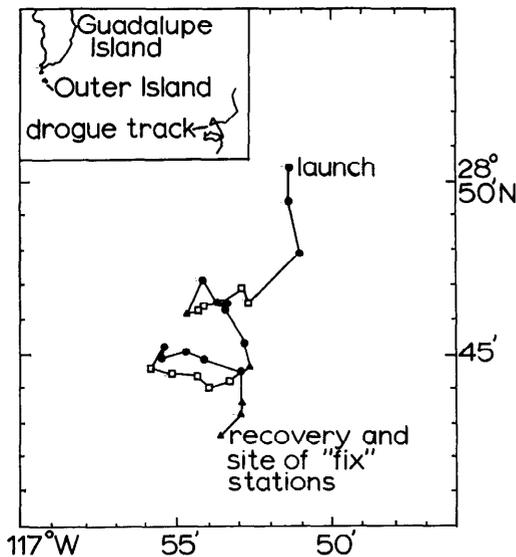


FIG. 4. Track of the migrating drogue. ●—night station; □—day station; ▲—other positions. Positions are from the radar coordinates of Outer Island, shown in the inset.

Relative positions of
night stations
19-23 September 1967

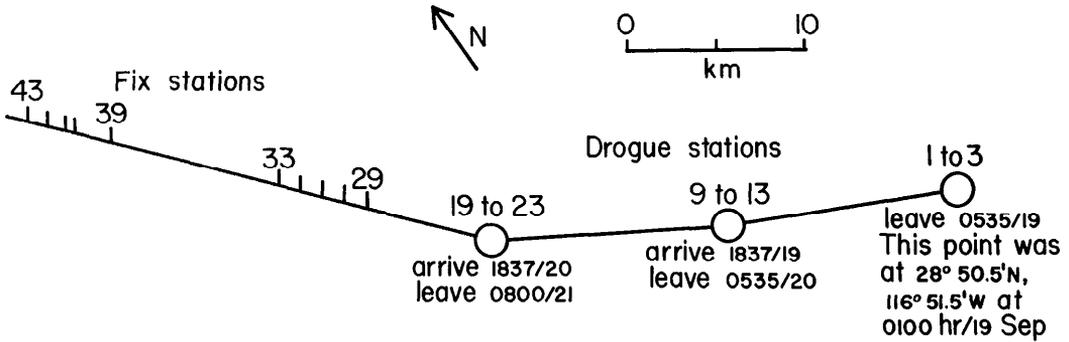


FIG. 5. Positions of the night stations relative to coordinates fixed to the water layer at 10 m.

phausiids, pelagic molluscs, ostracods, and tunicates were counted. Some groups, present in small numbers, were not counted: siphonophores, Medusae, ctenophores, annelids, amphipods, decapod crustacean larvae (other than euphausiids), and fish. Whenever possible, sex and age categories were counted. For most statistical purposes these were not combined and are referred to as "categories." The term "species composition" used also refers to these

categories, a few of which are above the species level.

The results of this study are in part reported as comparisons of the species composition of the samples. These comparisons quantify the extent to which samples are alike in partitioning the total number of individuals among the categories. The most useful index has proved to be percent similarity. This has been independently used many times (*see* Whittaker 1960). The

Relative positions of
day stations
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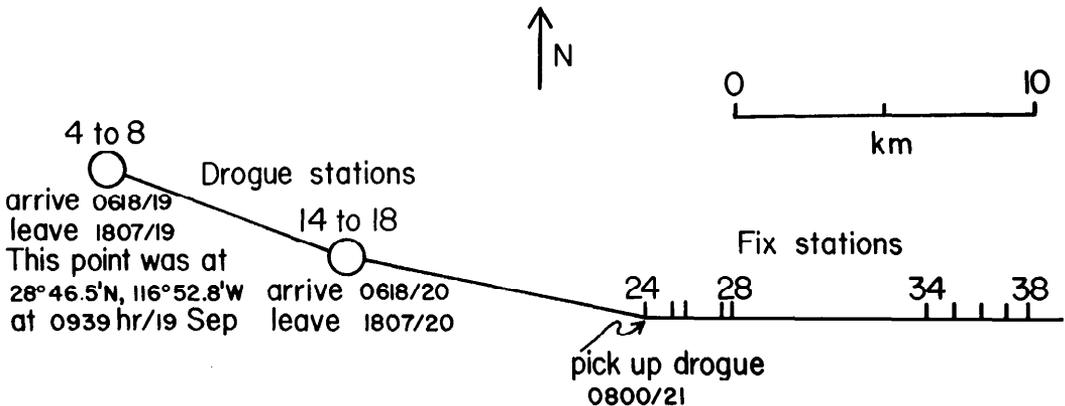


FIG. 6. Positions of the day stations relative to coordinates fixed to the water layer at 100 m.

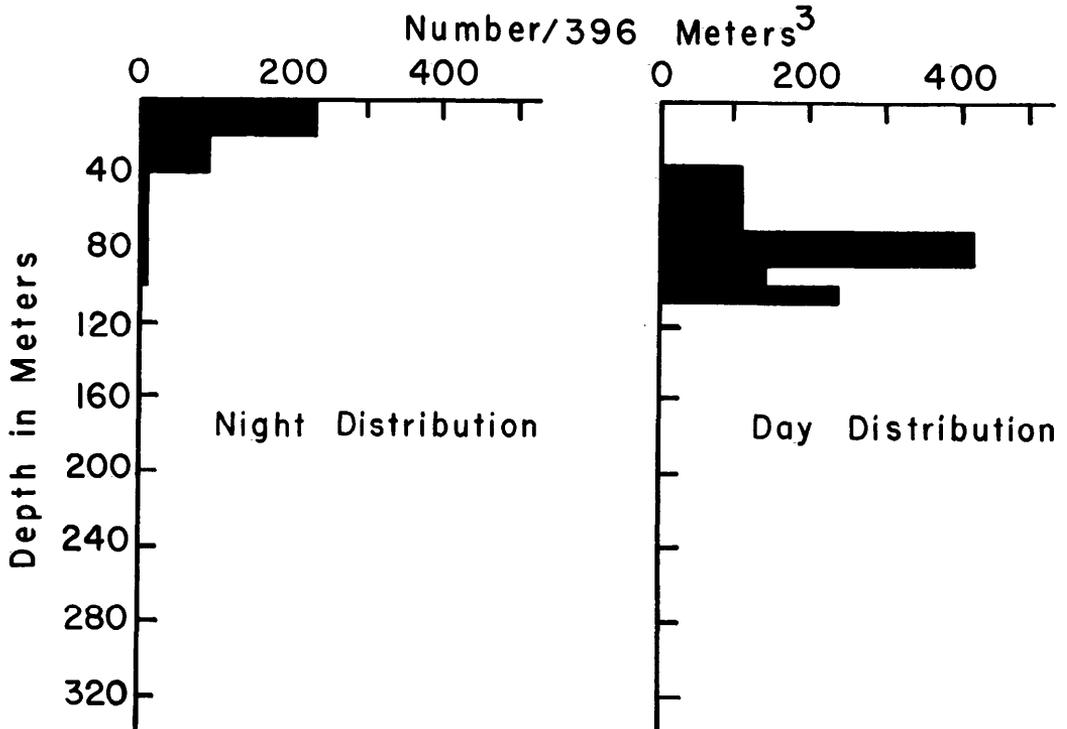


FIG. 7. Vertical distribution of *Halocypris brevivirostris* from the vertically stratified net tow series.

percent similarity of two samples, *A* and *B*, is

$$PS = 100 - 50 \left(\sum_{i=1}^s |a_i - b_i| \right) = \sum_{i=1}^s \min(a_i, b_i),$$

in which a_i and b_i are the percents of the total individuals that belong to the i th category in *A* and *B* respectively, and S is the number of categories. It is a measure of the overlap of the percent composition of the samples. Whittaker (1952) experimented with the variability of this index by splitting his samples of insects into fractions and calculating the percent similarity between fractions of the same sample; he termed these values the "internal association" of the samples. He found that internal association is increased by increasing the sample size, and that it is larger for samples with lower diversities. I studied the expectation and variability of *PS* by computerized Monte Carlo methods, using data closely related to those of the samples actually compared. The procedure is outlined below.

1. The average proportions of the total individuals in the night (or day) samples belonging to each category were calculated and ordered. The results for the 30 dominant categories in the night and the day sets of samples are shown in Fig. 3.

2. Cumulative proportions were then calculated.

3. A random number, x , from a rectangular distribution such that $0 \leq x \leq 1$ was selected, and 1 was added to the sample count of the species for which the cumulative proportion was the least greater than x . In effect each random number was an individual and was given a chance of belonging to any one category equal to the proportion of that category in the population. This process was repeated for N random numbers, giving a set of category "counts," n_1, n_2, \dots, n_s , such that $\sum n_i = N$. Sample percentages, $n_1/N, n_2/N, \dots, n_s/N$, were then computed.

4. A large number of pairs of such sam-

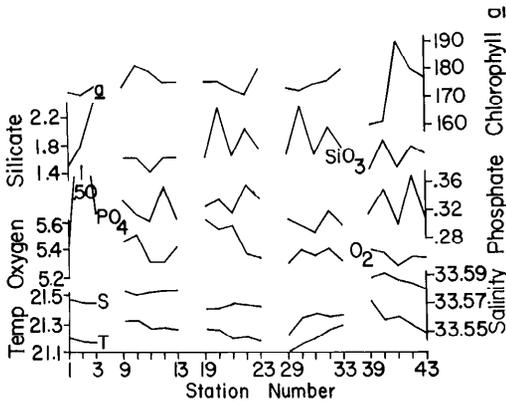


FIG. 8. Values of physical variables at night stations plotted against the station numbers. The units from top to bottom are: chlorophyll *a*, mg/m³; silicate and phosphate, g-atoms/liter; oxygen, ml/liter; salinity, ‰; temperature, °C.

ples was taken and *PS* was calculated for each pair. The observed frequency distribution of *PS* was then characterized.

The results are summarized in Table 2.

Because all pairs of samples in the Monte Carlo study are from the same population of species proportions, the theoretical similarity is 100%. The variability of samples from this population makes *PS* a downward biased estimator of similarity. The bias decreases with increasing sample size and decreases with decreasing diversity of the underlying population. It is clear that the equitability component (Lloyd and Ghelardi 1964) is the most important feature of diversity here. That is, the more strongly a population is dominated by one or a few categories, the higher will be the similarity of replicate samples from that population. *PS* is primarily responsive to shifts in the more abundant categories.

For the tested sample sizes *PS* is normally distributed. The variance decreases with increasing sample size. The ranges of sample sizes (0.25 aliquots) actually counted in this study were: night, 2,349 to 4,153 individuals; day, 1,158 to 2,599 individuals. Sample sizes of 1,000 and 2,000 individuals were chosen for the Monte Carlo sampling study—slightly less than the lowest totals for the day and night

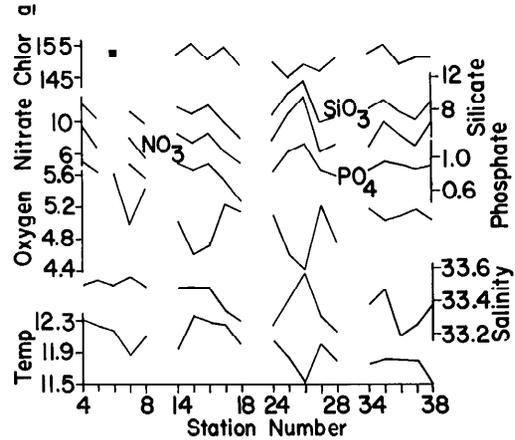


FIG. 9. Values of physical variables at day stations plotted against the station numbers. The units from top to bottom are: chlorophyll *a*, mg/m³; silicate, nitrate, and phosphate, g-atoms/liter; oxygen, ml/liter; salinity, ‰; temperature, °C.

samples respectively. From Table 2 it can be calculated that values of *PS* less than 87% comparing night samples of 2,000 individuals probably represent different species composition in the field. Lower values, less than 79%, should be observed in comparisons between day samples of 1,000 individuals before a real difference can be considered to have existed in the field.

RESULTS

The track taken by the migrating drogue is shown in Fig. 4. During the night of 18–19 September, a 37 km/hr wind blew from 325–430°. Both the indicated current and the error in current tracing caused by windage on the surface float were to the south. In the morning the wind dropped, and during the rest of the drogue experiment the wind did not exceed 20 km/hr. The reversals in direction of movement of the drogue can be interpreted in two ways: There was a more or less steady south-easterly current near the surface and a steady westerly current at 100 m, or the migration of the parachute was coincident with the change in direction of tidal currents with a nearly diurnal period. With such a small sample of the currents and with no drogues continuously at either

Drogue night 1			Drogue night 2					Drogue night 3					Fix night 1					Fix night 2					Station Number
1	2	3	9	10	11	12	13	19	20	21	22	23	29	30	31	32	33	39	40	41	42	43	
82	79	81	74	78	80	68	77	79	82	82	74	80	54	67	70	58	54	50	69	74	72	62	p
	77	78	81	85	85	69	79	80	83	79	68	79	54	67	69	57	52	52	75	79	72	62	1
		84	71	74	75	69	72	75	76	81	88	77	49	64	67	54	58	44	64	67	67	57	2
			76	79	78	71	76	78	80	83	76	81	52	66	68	55	52	50	68	71	70	62	3
				86	86	67	78	80	79	76	66	76	64	66	67	57	50	53	75	78	72	62	9
					88	69	77	82	84	81	72	78	53	66	69	56	50	51	75	78	72	63	10
						73	79	84	86	92	71	78	55	69	71	57	51	52	76	80	72	62	11
							68	73	72	71	63	66	47	67	67	50	45	43	62	66	60	52	12
								77	80	77	66	82	61	73	70	67	63	55	77	77	77	69	13
									88	83	72	80	57	71	71	59	53	58	79	80	75	64	19
										87	75	83	59	74	76	62	55	53	80	83	76	66	20
											82	82	58	71	74	60	54	52	74	78	74	65	21
												74	48	64	68	54	46	54	46	44	63	67	22
													62	74	76	65	63	55	75	78	79	71	23
														61	60	66	63	67	61	61	67	69	29
															83	70	60	47	72	74	75	67	30
																73	60	46	68	73	73	65	31
																	78	53	61	60	66	66	32
																		54	54	55	59	59	33
																			65	61	64	63	39
																				88	84	72	40
																					83	72	41
																						81	42

FIG. 10. Matrix of percent similarity indices comparing the night samples of the study. The lines separate samples taken on different nights. Double lines separate the drogue and fix stations.

depth, it was not possible to choose between these possibilities. Although 19 and 20 September did fall in a period of nearly diurnal tides (U.S. Department of Commerce 1967), both the rise and fall were expected in the period that the parachute was at 100 m.

If the first hypothesis is approximately correct, diagrams can be drawn to show the positions of the stations on the surfaces of the water layers at 10 and 100 m (Figs. 5 and 6). The coordinates of these diagrams can be considered fixed to the water so that they moved with the currents. The displacements between each day's set of drogue stations were produced by the Hardy mechanism. The displacements in the layer at 10 m were about 13 km; those in the layer at 100 m were about 8.5 km. If the second hypothesis is correct, displacements by the Hardy mechanism did

not occur, but the water at both depths moved at about the same velocity and the model animal returned to the surface close to the site of its previous departure.

Only one species was found whose apparent vertical migration as shown by the vertically stratified net tows resembled that of the parachute. This was *Halocypris brevis* Dana, a myodocopid ostracod (Fig. 7). The drogue allowed the environment to be sampled in much the same way as it was "sampled" by *H. brevis* at this time near Guadalupe Island.

The zooplankton counts and physical data from the drogue and fix stations are too voluminous to publish in their entirety.³ Figures 8 and 9 show the temperature,

³ The data can be obtained by requesting accession number 70-0565 from Data Services Branch, National Oceanographic Data Center, Washington, D.C. 20390.

Drogue day 1				Drogue day 2					Fix day 1					Fix day 2					Station Number	
5	6	7	8	14	15	16	17	18	24	26	26	27	28	34	35	36	37	38		
63	62	44	45	47	40	45	43	51	42	46	42	44	40	51	37	35	36	33	4	
	77	65	66	66	52	60	63	67	60	64	57	58	58	65	52	47	44	43	5	
		62	59	60	54	54	58	58	57	62	57	52	53	57	53	49	46	43	6	
			78	78	61	73	74	71	68	70	66	68	67	65	64	53	50	51	7	
				77	55	73	76	68	63	66	61	64	66	64	55	52	48	50	8	
					54	80	73	71	63	69	63	64	62	66	61	50	47	46	14	
						50	55	49	68	61	65	66	63	49	60	67	63	61	15	
							73	67	58	71	57	65	63	62	56	46	54	47	16	
								71	62	70	58	66	67	63	61	51	48	51	17	
				Averages for blocks outlined above						60	69	58	59	62	69	57	44	43	44	18
				62	60	58	49			70	77	69	69	60	66	65	64	64	24	
					64	64	54				70	70	72	65	63	58	55	56	25	
						71	63					70	65	62	65	70	68	65	26	
							61						74	61	64	64	63	60	27	
														61	68	59	62	62	28	
															63	50	50	49	34	
																63	59	59	35	
																	73	68	36	
																		78	37	

FIG. 11. Matrix of percent similarity indices comparing the day samples of the study. The lines separate samples taken on different days. Double lines separate the drogue and fix stations.

salinity, oxygen, nutrient, and chlorophyll *a* values plotted against the station number for night and day stations respectively. There are no strong systematic or repetitive trends in these data. The drogue stations are not overall more or less variable with respect to physical factors than the fix stations. With the exceptions of a few outlying points, such as the phosphate value at station 2, the ranges of these variables are small, especially compared to the differences between the 10- and 100-m values.

There were 250 categories counted in the night samples—most of them quite low in abundance. The dominant category in all but one of the night samples was *Limacina inflata* (d'Orbigny), constituting 13.5 to 37% of the individuals. Immature *Clausocalanus* and *Oikopleura* spp. were generally second or third. The average proportions

shown for night samples in Fig. 3 are quite representative. There were 280 categories counted in the day samples; again, most categories were rare. There was a progressive change in dominance in the day samples throughout the drogue and fix stations. Initially (stations 4-7) immature *Euchaeta* spp. were dominant. Later *Appendicularia* (stations 8-34), *Euaetideus bradyi* (A. Scott) females (station 35), *Euphausia gibboides* Ortman calyptopis (station 37), and immature *Sagitta* spp. (station 38) each became dominant. During the middle period when *Appendicularia* was the dominant category, the subdominants were shifting. For some species changes in position on the list were erratic.

Figures 10 and 11 are matrices of percent similarities comparing all pairs of night and day samples respectively. The

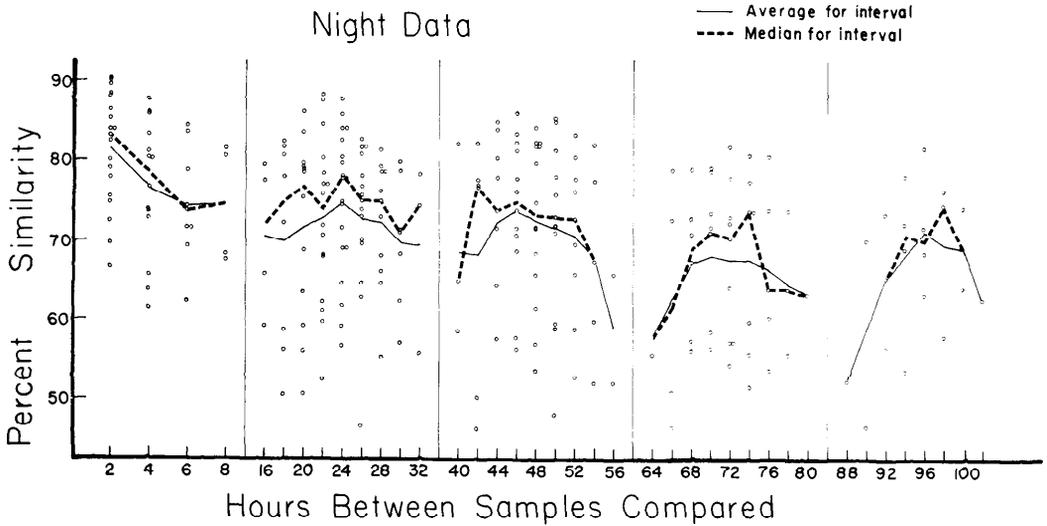


FIG. 12. Percent similarity indices for the night samples plotted against the intervals between the pairs of samples compared by the indices. The averages for each interval are shown by the solid line, the medians by a dashed line.

samples are arranged along the axes of these matrices in the order they were taken. Four important features of these figures should be pointed out.

1. The night samples are more similar than the day samples. For comparisons along the diagonals this is partly explained by the generally higher equitability of the day samples. As was shown in the Monte Carlo study, the index is increased by a strong degree of dominance by one or a few species. The greater decrease from the diagonal to the corner in the day data is a reflection of a greater change in the species composition with time in the day samples than in the night samples.

2. The percent similarity indices for comparisons between drogue stations within one night have higher mean and median values than those between fix stations. This result is significant at the 0.05 level by a Wilcoxon T test. However, the values within any one row or column are not independent because they are each calculated in part from the data for the same sample. An aberrant sample (e.g., sample 12) will lower a large fraction of the values in any block. Therefore, no statistical test for differences in central tendency

would be valid. The observed difference implies lower variability in species composition between drogue stations than between fix stations.

3. Samples from different nights during the series of drogue stations are generally more similar than samples from different nights during the series of fix stations. This difference is seen more clearly if sample 12 is dropped from consideration. Sample 12 is unusual among the night samples with respect to the abundance of a large fraction of the more common species. There is no obvious reason in the station records why this should be so. The greater similarity between nights of the series of drogue stations can perhaps be assigned to an effect of the migration of the parachute; the distance traveled along the gradient in species composition (described below) being reduced by following the currents at greater depth during the day. However, the day samples do not show this effect. In fact, the averages of comparisons between samples from different days are in two instances higher than averages of comparisons of samples taken within the same day.

4. In both Figs. 10 and 11 the values

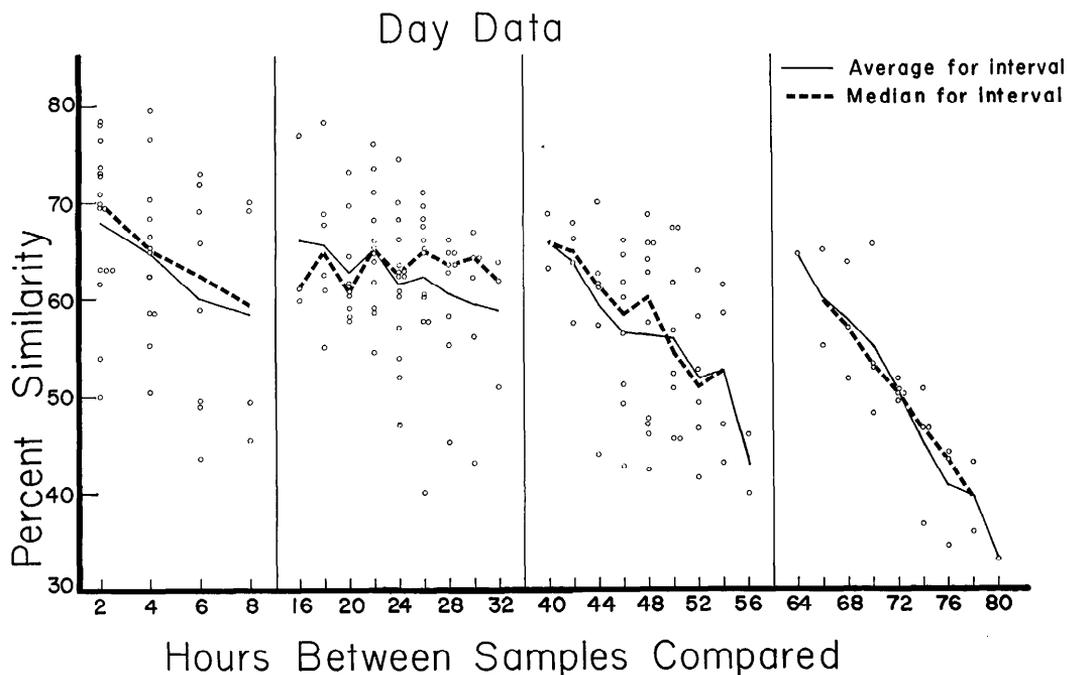


FIG. 13. Percent similarity indices for the day samples plotted against the intervals between the pairs of samples compared by the indices. The averages for each interval are shown by the solid line, the medians by a dashed line.

of the similarity indices are higher close to the diagonals of the matrices than they are close to the corners. This decline in similarity as the interval between samples increases is a reflection of slow change in species composition over the whole interval of the study. To display this change, the percent similarities from Figs. 10 and 11 are plotted in Figs. 12 and 13 against the time intervals between the samples of the pairs compared, and the average similarity for each time interval is indicated as a line. The dredge and fix stations have been lumped together in this averaging process. The interval averages show a decline in similarity with increasing time between samples, but the scatter is great. The rates may be typified by the slopes of regression lines fitted to the interval averages. The rate of change of the percent composition in the night samples was $-0.122\%/hr.$ That in the day samples was $-0.267\%/hr.$

Figure 12 reveals a nightly cycle in the

species composition. All comparisons at intervals of 24, 48, 72, and 96 hr are of samples taken at the same time of night on different nights; these are higher on the average than comparisons of samples from times of night 2 hr apart (22, 26, 46, 50, 70, 74, 94, and 98 hr comparisons), and so forth. This cycle in sample similarity is largely accounted for by a cycle in the abundance and percentage of *L. inflata*. The data from the 4 nights with complete sets of five samples are summarized in Table 3; a two-way analysis of variance by ranks (Tate and Clelland 1957) shows that *L. inflata* was significantly more abundant in the middle of the night than earlier or later.

Each 16-hr sequence of 2-hr increases in interval for the day comparisons (Fig. 13) shows a downward trend, jumping back to nearly "within day" values after each 8-hr increase in interval. Corner tests (Tate and Clelland 1957) of these trends are significant at the 0.05 level for all four sequences

TABLE 3. Evidence of a cycle each night in the abundance of *Limacina inflata*

Time:	2000		2200		2400		0200		0400	
	No.	rank	No.	rank	No.	rank	No.	rank	No.	rank
Night										
2	930	(2)	1,250	(5)	1,210	(4)	945	(3)	706	(1)
3	1,435	(2)	1,469	(3)	1,741	(4)	1,951	(5)	1,151	(1)
4	320	(2)	857	(4)	1,072	(5)	359	(3)	119	(1)
5	184	(1)	861	(4)	1,017	(5)	764	(3)	434	(2)
Sum of ranks	7		16		18		14		5	
Expected sum of ranks of each column =	12									
Difference from expected	-5		4		6		2		-7	
Sum of differences squared =	130									
Concordance of ranks =	12(130)/16(120) = 0.81, $P < 0.01$									

of 2-hr intervals. This decline and jump is not an effect from any one of the more abundant categories. Successive removal of the five most abundant categories has almost no effect on the trends (see Fig. 14). The nature of this result is considered below.

DISCUSSION

The migrating droguc experiment is a simple demonstration that vertical migration can produce large horizontal displacements across the water layers inhabited at different times of the day. However, the 8- to 13-km displacements of the model animal between nights and between days (Figs. 5 and 6) were not accompanied by the originally postulated changes in the zooplankton species composition. In fact, the species compositions on the 3 nights of droguc stations show less change than on the nights of fix stations. It is possible that the migrating droguc helped to maintain the constancy of composition of samples on different nights. Perhaps most of the dominant species migrated during the day to layers whose movement was not greatly different from that followed by the droguc at 100 m, so that on successive nights samples taken near the droguc tended to be more alike in species composition than samples taken at a single geographic position. It is as if the generality of vertical migration by the night surface community kept the species composition close to constant around an individual migrant animal,

despite the horizontal displacements vertical migration imposed on it. This postulated generality of migration was not checked. It will be important in future studies of the rate of change of the biotic environment of zooplankters to obtain highly replicate and synoptic data on the vertical movements of a large fraction of the species present.

No similar effect was observed for the day samples, probably because the dominant species at 100 m in the daytime did not migrate up at night. They were not well represented in the night samples from 10 m. To test this, counts of the 10 categories most abundant in the final day sample of the series of fix stations (station 38) were made in the 150-100-m and 100-40-m samples of the night stratified tow series. Of the 10 categories, 9 remained abundant at night at depths around 100 m. Immature *Eucalanus bungii californicus* was the only exception, but it was not abundant in the surface tow of the night stratified series.

Though there were not the expected abrupt changes in species composition from night to night and day to day, there was a drift in species composition throughout the study. The interval averages used to study this drift have two shortcomings. First, the averages were calculated over the droguc and fix stations combined as one time series. This is justified for three reasons: The droguc's apparent effect of holding the species composition of the

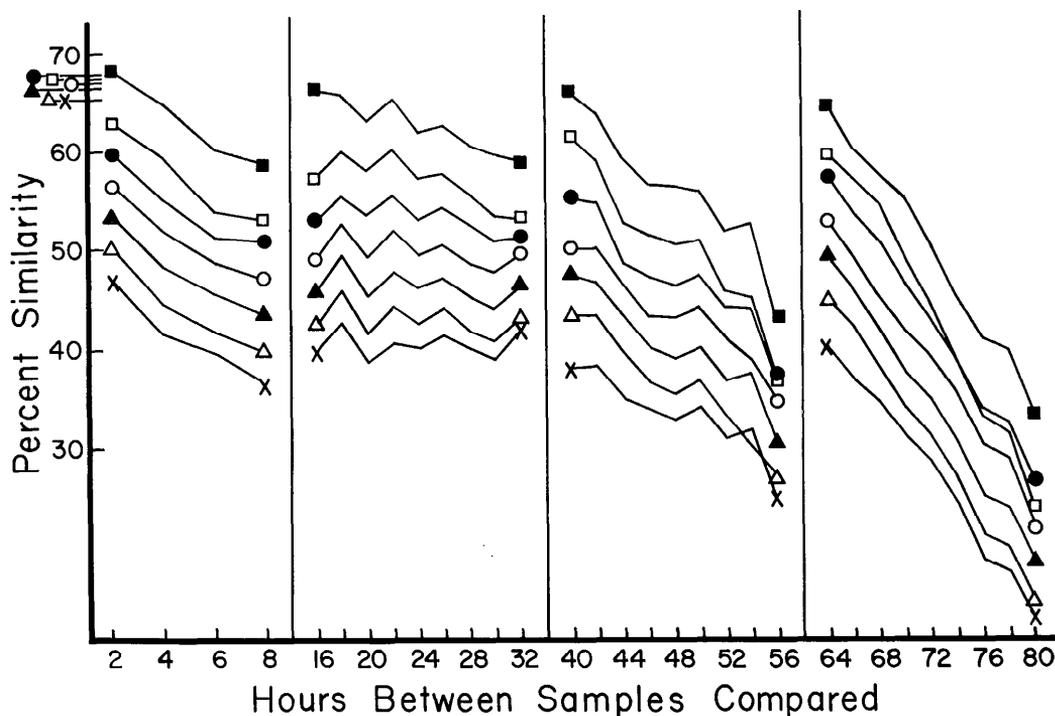


FIG. 14. The effect on the interval averages of the percent similarity indices of the day samples of removing the most abundant species successively from the data and recalculating the sample totals, the percent composition, the percent similarity indices, and the interval averages. ■—280 categories; □—after removal of *Appendicularia* (all spp.); ●—after removal of immature *Euchaeta*; ○—after removal of female *Euaetideus bradyi*; ▲—after removal of immature *Sagitta*; △—after removal of *Sagitta bieri*; ×—after removal of immature *E. bradyi*. The lines are displaced downward from the starting positions shown at the top left.

night samples constant is small. The dominant effect shown in the similarity matrices is the decrease in similarity from adjacent pairs of samples to widely separated pairs, rather than differences between the droguc and fix stations. The likely spatial arrangements of droguc and fix stations are actually not greatly different (Figs. 5 and 6). Second, time and distance effects are not well separated in the data to which the analysis is applied. Despite these difficulties several interesting things emerge from the analysis.

In the night data the averages for intervals of 88 to 102 hr (samples from nights 4 nights apart are compared) are close in magnitude to those for intervals of 64 to 80 hr (samples from nights 3 nights apart are compared). This leveling-off may indicate that 63 or 64% (the overall averages

for nights 3 and 4 nights apart) is the minimum mean similarity for this season and area. Fluctuations in specific composition reduced some pairs of samples to below 50% similarity, but these occurred among samples taken on successive nights, as well as among those separated by more time. The aberrant sample 12 accounted for many of the low values. The uncertainty of the biotic component of the pelagic environment may be limited; for the set of category abundances observed at this time and place, the uncertainty limit can be represented by a percent similarity of about 60%. This value is, of course, relative to the sampling method and is affected by the equitability of the population in the area, but the implication remains. Establishing the truth of this generalization will require longer time series. If a limit of

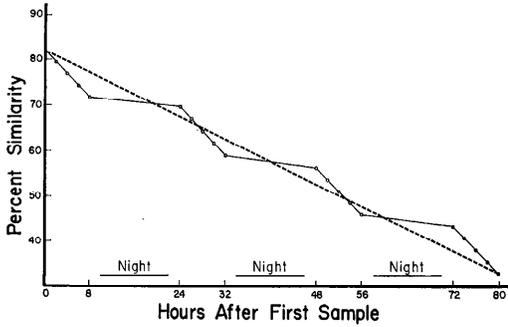


FIG. 15. Theoretical decline in the similarity of plankton samples to the first sample taken at time 0, which occurred at 0800 hours. The solid line shows the discontinuous decline that occurs if community composition changes only in daylight hours. The dashed line shows a continuous decline in similarity. The circles show actual times samples were taken.

this sort can be shown to exist generally, then it will be possible to characterize the plankton community of an area and season

in terms of the relative abundances of the species with a reasonably restricted set of replicate samples. The decline of similarity values in the shorter day series did not show any sign of leveling-off within 80 hr. If there is a regional and seasonal minimum similarity at the 100-m level, it was not reached.

One of the most interesting aspects of the interval averages is that there are repetitive trends for sets of intervals representing comparisons of samples taken on two different nights or days. The nightly cycle in abundance of the numerically dominant *L. inflata* at 10 m was reflected in the interval averages: The comparisons between identical times of different nights are more similar than comparisons between different times of night (Fig. 12). The abundance of *L. inflata* peaked in the middle of the night. Probably some detail of the migratory behavior causes this effect;

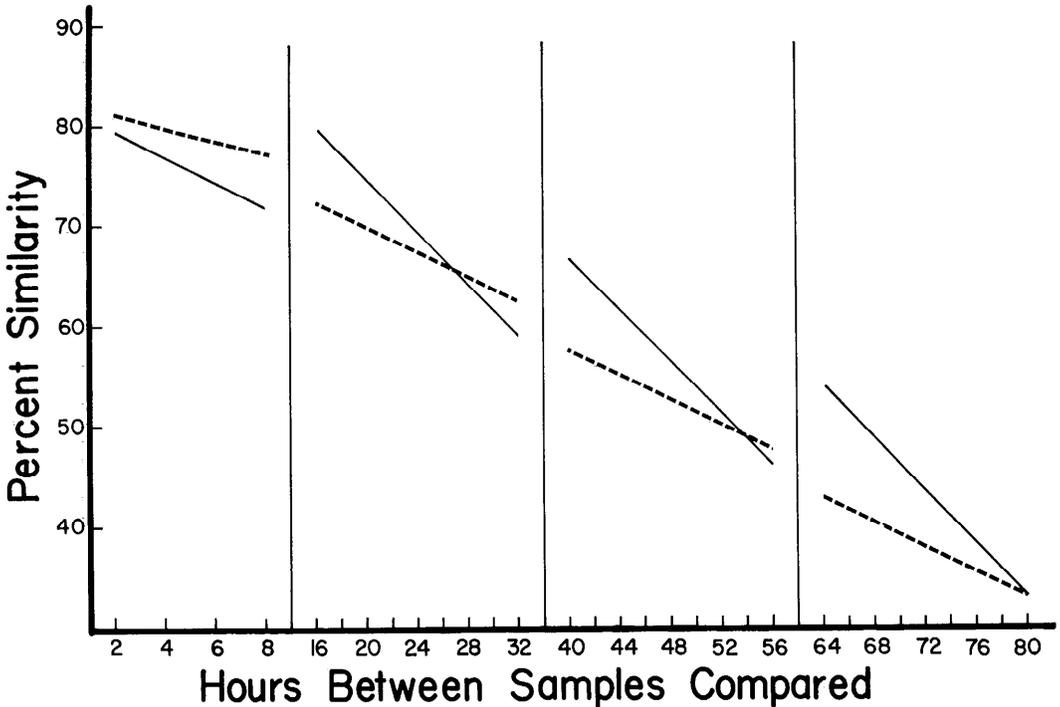


FIG. 16. Plot of interval averages of percent similarity for idealized situations against the intervals between the samples compared. The solid line joins averages expected if percent similarity decreases in proportion to the number of daylight hours between samples compared. The dashed line joins averages expected if percent similarity decreases in proportion to the total time between samples compared.

either the concentration of the population near the surface increases until about the middle of the night and decreases thereafter, or most of the animals move closer to the surface than 10 m at evening, exhibit a midnight down-scattering (Russell 1927) increasing the numbers at 10 m, and then return to near the surface at dawn, reducing them again.

The downward trends of the day interval averages (Fig. 13) for each 16-hr sequence of 2-hr intervals and the jumps back up to nearly within day values after each 8-hr increase in interval seem paradoxical. However, jumps in average similarity after the longer intervals can be expected in a plot of the type shown in Fig. 13, if the decrease in similarity proceeds only during the daytime. This can be seen by considering a hypothetical average similarity of successive samples to the first sample taken, as shown in Fig. 15. Percent similarity for an interval of 0 hr is taken to be the mean for pairs of samples of 1,000 individuals in the Monte Carlo study—82% (see Table 2). The final, 80-hr percent similarity is the observed value—33%. The expected interval average plots for these two situations are shown in Fig. 16. Clearly, the actual result of Fig. 13 is closer to the model of change only during daylight.

The discontinuous decline in similarity is apparently not caused by vertical migratory behavior; as noted above, most of the forms abundant at 100 m in the day did not migrate upward at night. The simplest process that can be postulated is that the animals swim in the light, rearranging their spatial relations, but are quiescent in the dark. This rearrangement would probably have to be on a scale larger than the lateral extent of the study (Fig. 4). If this is true, it is evidence that plankton, like terrestrial animals, are split into diurnally active (also nonmigrating) forms and nocturnally active (migrating) forms. The

questions of what process, if any, is involved and whether the phenomenon is general or peculiar must wait for new data.

REFERENCES

- ARMSTRONG, F. A. J., C. R. STEARNS, AND J. D. H. STRICKLAND. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon Autoanalyzer and associated equipment. *Deep-Sea Res.* **14**: 381-389.
- CARPENTER, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol. Oceanogr.* **10**: 141-143.
- CASSIE, R. W. 1963. Micro-distribution of plankton. *Oceanogr. Mar. Biol. Ann. Rev.* **1**: 223-252.
- HARDY, A. C. 1935. The plankton community, the whale fisheries, and the hypothesis of animal exclusion. *Discovery Rep.* **11**: 273-370.
- HOLM-HANSEN, O., C. H. LORENZEN, R. W. HOLMES, AND J. D. H. STRICKLAND. 1965. Fluorometric determination of chlorophyll. *J. Cons., Cons. Perm. Int. Explor. Mer* **30**: 3-15.
- LOYD, M., AND R. J. CHELARDI. 1964. A table for calculating the equitability component of species diversity. *J. Anim. Ecol.* **33**: 217-225.
- MCGOWAN, J. A., AND D. M. BROWN. 1966. A new opening-closing paired zooplankton net. *Scripps Inst. Oceanogr. Ref. No. 66-23*. 56 p.
- MILLER, C. B. 1969. Some environmental consequences of vertical migration. Ph.D. thesis, Scripps Inst. Oceanogr., Univ. Calif., San Diego. 308 p.
- RUSSELL, F. S. 1927. The vertical distribution of plankton in the sea. *Biol. Rev.* **2**: 213-262.
- TATE, M. W., AND R. C. CLELLAND. 1957. Non-parametric and shortcut statistics. Interstate, Danville, Ill. 171 p.
- U.S. DEPARTMENT OF COMMERCE. 1967. Tide tables. West coast of North and South America. 1967. GPO. 224 p.
- VOLKMAN, G. H., J. KNAUSS, AND A. C. VINE. 1956. Use of parachute drogues in the measurement of subsurface ocean currents. *Trans. Amer. Geophys. Union* **37**: 573-577.
- WHITTAKER, R. H. 1952. A study of summer foliage insect communities in the Great Smokey Mountains. *Ecol. Monogr.* **22**: 1-44.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**: 279-338.