Observations on the Diurnal Vertical Migrations of an Oceanic Animal Community

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Abstract

Diurnal changes in abundance caused by vertical migrations have been examined in populations of copepods, ostracods, euphausiids, amphipods, decapods, chaetognaths, siphonophores and fish. The animals were taken in a series of hauls made over a 24 h period with an opening-closing midwater trawl system (RMT 1+8), consisting of a net of 1 m^2 mouth area combined in the same frame as one of 8 m^2 mouth area. The samples were taken at 250 m depth in a position 30°N;23°W on 7/8 April 1972. The specific composition of the community and the numbers of individuals changed continuously with time. The numbers of fish, decapods and chaetognaths increased at night, but those of copepods, ostracods and euphausiids decreased. More species of fish, decapods and copepods were present by night than by day, whereas the numbers of species per haul for other groups remained fairly constant. The relative abundances of groups caught by the RMT 1 have been analysed, but similar treatment of the RMT 8 samples was impossible as only 3 groups were taken from this net. Non-migrants were a minority in every group except chaetognaths. Migrant species have been put into one of 6 transitory categories according to their patterns of abundance and hence migrations. Within each category, migratory behaviour varied both inter- and intraspecifically. The patterns of abundance of many species were smooth and continuous, suggesting slow migratory cycles of small amplitude. Conversely, extensive migrants had discontinuous patterns and presumably more rapid movements. Few migrants had a steady numerical plateau between their upward and downward migrations, and most apparently moved up or down continuously. The presence of migratory species in the sampled layer depended upon the time of day or night. It is concluded that, in a vertical series of hauls, the depths of occurrence of migrants will vary with the sampling time. Furthermore, a vertical series will show a species' minimum migration range but not necessarily its maximum. Individuals of some species were out of phase with the migrations of their main populations. There is evidence that the distributions and migrations of some species of decapods, euphausiids, copepods and fish could be related to the distribution of underwater light. Three pairs of

congeneric copepod species were both spatially and temporally segregated for at least part of their diurnal cycles. Such an orderly arrangement could provide a means of reducing competition between species. Some species, however, overtook others on their migrations and the pattern of underwater light cannot, therefore, regulate the distribution of all species in the same way.

Introduction

It was pointed out by Cassie (1963) that, because of vertical migrations, the time of day of sampling is critical when comparing plankton hauls which do not represent the entire water column. Despite this, there is little work on the diurnal migrations of oceanic populations based upon consecutive samples taken at a single station over a 24 h period at a constant depth. Such a series enables the effects of sampling time to be examined in detail.

In their reviews of vertical migration Russell (1927), Kikuchi (1930), Cushing (1951), and Banse (1964) all included work based upon series of hauls made over varying periods of time. Most previous work, however, was restricted either to particular species or groups, e.g. Welsh *et al.* (1937) and Zalkina (1971), or to general analyses of total volumes or of numbers and wet weights of various groups, e.g. McAllister (1961) and Shomura and Nakamura (1969). Much early work was done with non-closing nets, see, for example Russell (1925), the depths of hauls estimated only approximately, e.g. Waterman *et al.* (1939), or the sampled depth levels were too wide, e.g. Bradford (1970). Perhaps the most serious defect of many previous investigations is that their results were taken from several stations, often separated by both time and distance, and then added together to form a 24 h cycle, e.g. Esterley (1912) and King and Hida (1954). More recently, both Champalbert (1971a, b) and Bainbridge (1972) have made a comprehensive study of the diurnal variations in many species of, respectively, neustonic and shallow-living zooplankton, albeit in inshore waters. Other neustonic sampling done on a time basis has been reviewed by Hempel and Weikert (1972).

Roe (1972a, b, c, d) analysed the vertical distributions of calanoid copepods taken in a day

and a night series of hauls off Fuerteventura. He
concluded that the depths of occurrence of mi-
gratory species and the apparent nocturnal
splitting up of compact daytime populations de-
pended upon the sampling times. Pugh (1974) also
discussed the effects of time on the vertical
distributions of siphonophores. The present series
was done to examine the diurnal changes in popu-
lations at a fixed depth, and thereby to study the
effects of sampling time on the animals caught.
The series also enabled predator-prey relationships
to be examined in conjunction with migratory
cycles. The stomach contents of several fish and
decapod species were analysed and are reported on
separately by Merrett and Roe (1974) and Foxton
and Roe (1974).

Material and Methods

In the 24 h period between 08.31 hrs on 7 April
and 08.08 hrs on 8 April, 1972 (all times Green-
wich mean time, GMT), at a position $30°N; 23°W$, a
series of 11 hauls was made with an acoustically
controlled opening and closing net system. The
fishing gear, designated the RMT 1+8, comprised a
rectangular midwater trawl of 1 m^2 mouth area (RMT
1, mesh 0.32 mm) combined in the same frame with
a similar net of 8 m^2 mouth area (RMT 8, mesh 4.5

mm) (Baker *et al.*, 1973). Details of the hauls
are given in Table 1.

For each haul, the nets were opened and closed
within the designated depth range and fished hori-
zontally for about 1 h. The mean depth and tem-
perature and the distance fished for each haul was
calculated from data monitored continuously on the
ship (Baker *et al.*, 1973). It can be seen (Table
1) that there was little variation between hauls
for either depth or temperature and, for con-
venience, all the hauls are hereafter considered
to have fished at 250 m. The distance fished is
expressed as a percentage of the mean distance
fished for all 11 hauls. All the subsequent analy-
ses are based upon numbers corrected to a distance
of 100%.

Most of the results from this horizontal series
were analysed in relation to a vertical series of
day and night hauls done with the RMT 1+8 in the
same position a few days earlier, using the
methods described by Baker *et al.* The entire RMT 8
samples and, except for the amphipods, 1/16 frac-
tions of the RMT 1 samples were examined. The frac-
tions were taken with a Folsom Plankton Sample
Splitter, and for copepods, ostracods and siphono-
phores two fractions from each haul were analysed
to check that any observed variations were not
merely fractioning artifacts. All general trends
were common to both fractions, and in the present
results these have been added together to form a
1/8 subsample. The following groups were analysed:
fish and decapod crustacea from the RMT 8,
siphonophores from both the RMT 8 and RMT 1 frac-
tions, amphipods from the total RMT 1 samples, and
ostracods, euphausiids, chaetognaths and adult
calanoid copepods from the RMT 1 fractions. Some
species of siphonophores are caught in reasonable
numbers by both nets, and consequently both were
analysed.

Table 1. Station data. See text for explanation
of distance fished

Haul no.	Station no.	Time (GMT, hrs)	Depth range (m)	Mean depth (m)	Mean temperature ($°C$)	Distance fished (%)
1	7856 /67	08.31-09.31	235-264	249.5	15.7	105.2
2	/68	10.05-11.05	230-264	251.4	15.7	101.7
3	/69	12.36-13.36	240-260	254.1	15.5	99.6
4	/72	15.44-16.44	240-264	250.6	16.0	106.5
5	/73	17.53-18.53	240-260	250.9	15.7	95.4
6[a]	/74	19.30-20.30	240-260	251.6	15.8	100.2
7	/75	21.06-22.10	240-260	251.4	15.9	95.4
8	/76	23.35-00.36	240-266	251.2	16.1	93.8
9	/77	03.39-04.39	240-260	249.2	15.4	99.4
10	/78	05.19-06.25	245-260	254.5	15.4	108.1
11[a]	/79	07.05-08.08	240-260	252.3	15.5	94.6
Overall means				251.5	15.7	

[a]Sunset was at 19.53 hrs, Sunrise at 07.14 hrs.

Results

Variations in the numbers of animals caught can be
expected from any series of hauls taken at a
fixed depth over a 24 h period in a restricted
oceanic area. During a relatively short time span,
the most important causes of such variations are
probably: (1) vertical migrations; (2) patchiness;
(3) variable net avoidance; (4) variations in
fishing depth and volume of water filtered.

The variations in fishing technique have been
minimized (Table 1). Most species had patterns of
abundance which were either smooth or foreseeable
from the data obtained in the vertical series
taken in the same position a few days earlier (un-
published data, Institute of Oceanographic Sci-
ences). Species' presence or absence in the 24 h
series, by either day or night, was predictable
from a knowledge of their vertical distributions
and migrations. For example, the copepod *Pleu-
romamma xiphias* lived mainly between 600 and 500 m
by day and migrated to between 50 and 25 m at
night. It was therefore expected to move through
the 250 m depth layer twice, as indeed it did,

once at sunset on its upward migration and once at sunrise on its return downwards. Because of this overall predictability, it seems unlikely that patchiness or net avoidance contribute significantly to variations here; possible exceptions are discussed later (see "Others"). It is concluded that vertical migrations are the major cause of the present variability.

It is impossible to determine the direction of any movements from an isolated series of this type. All these results have been interpreted in relation to the vertical series described above, or to one made off Fuerteventura in 1965 (David personal communication; Thurston personal communication). Migrations would not have been observed in this 24 h series if a species had a broad vertical distribution, so that the population density at the sampled depth did not vary by day and night; nor if, as found for chaetognaths (Pearre, 1973), only a small part of a population migrates at any one time; nor if a migration occurs entirely within the sampled layer. This last case is unlikely here, since both the sampled depth range and variations in mean sampled depth were small (Table 1). Unless otherwise stated, all migrations discussed here are "normal", i.e., an ascent around sunset and a descent around sunrise.

The general distributions of all analysed groups are shown in Fig. 1. The numbers of species per haul of fish, decapods and copepods increased more or less abruptly around sunset, remained high throughout the night, and decreased again at sunrise. The numbers of species per haul for the other groups were more constant, but changes in their species composition occurred. Fish and decapods were very scarce by day, and both had numerical maxima around sunset and sunrise due to their populations migrating through the sampled layer. Siphonophores were more numerous by day than by night in the RMT 8, but their numbers were more constant in the RMT 1. Copepods and euphausiids were scarcer by night, with a slight increase at sunset and a marked increase at sunrise; ostracods had a similar pattern, but lacked the sunset rise; chaetognaths were slightly more numerous by night, and amphipods remained fairly constant.

As most of the zooplankton sampled by the RMT 1 has been analysed, it is possible to examine the diurnal changes in the relative abundances of the groups. Table 2 shows the numbers and percentages which each group contributed to the total population in each haul. Some groups, of which the most abundant were cyclopoid copepods, were not analysed, and the figures for all groups except copepods and siphonophores include juvenile stages. The numbers of copepods and siphonophores are, therefore, underestimated and consequently the relative abundances of all others over-estimated. These omissions probably have little effect on the general trends, and it can be seen that copepods and ostracods dominated the population numerically throughout the period. Both these groups were relatively more abundant by day, since many of their species migrated away from the sampled layer at night. Conversely the chaetognaths, which were
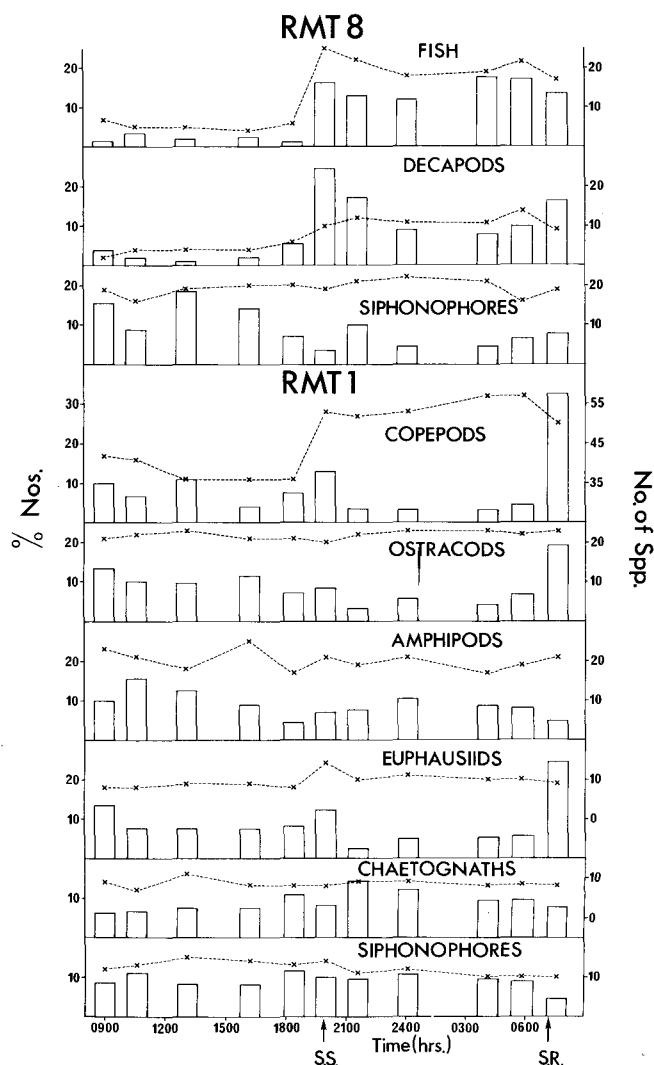

Fig. 1. Histograms showing, for each group, numbers in each haul expressed as percentage of total number of that group in all 11 hauls. Broken lines show numbers of species in each haul. S.S.: sunset; S.R.: sunrise

largely non-migrants here, became relatively more numerous by night. Siphonophores, and perhaps amphipods, were also relatively more abundant by night, but the proportion of euphausiids remained fairly constant. The size of the total population was much greater by day, with numerical peaks at sunset and sunrise.

At any depth through which vertical migrations occur, various patterns of abundance can be expected according to (1) the animals' vertical distributions, (2) the relationship of the sampled layer to the depths of their population maxima, (3) their speed of vertical movement, (4) the timing of their migrations. In this series one can only distinguish between differences due to timing or to speed of movement for migrations which

Table 2. Estimated numbers and percentage formed by each analysed group of each RMT 1 sample

Haul no.	Copepods		Ostracods		Chaetognaths		Euphausiids		Siphonophores		Amphipods		Total nos.
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
1	33688	48.3	29720	42.7	3065	4.4	2033	2.9	994	1.4	172	0.2	69672
2	22456	44.6	21784	43.2	3257	6.5	1154	2.3	1462	2.9	270	0.5	50383
3	36248	56.7	21336	33.4	3550	5.5	1135	1.8	1426	2.2	216	0.3	63911
4	12464	28.6	25232	57.9	3621	8.3	1129	2.6	944	2.2	155	0.4	43545
5	25432	51.2	15864	31.9	5249	10.6	1249	2.5	1789	3.6	81	0.2	49664
6[a]	44136	63.0	18664	26.7	3993	5.7	1848	2.6	1237	1.8	123	0.2	70001
7	11976	41.8	7240	25.2	6960	24.3	392	1.4	1974	6.9	134	0.5	28676
8	10752	33.7	12880	40.4	5855	18.3	763	2.4	1470	4.6	182	0.6	31902
9	10728	40.0	9464	35.3	4555	17.0	823	3.1	1091	4.1	152	0.6	26813
10	15336	40.2	15440	40.4	4692	12.3	877	2.3	1680	4.4	142	0.4	38167
11[b]	107384	68.1	42128	26.7	3720	2.4	3695	2.3	655	0.4	89	0.1	157671
Totals	330600	52.4	219752	34.9	48517	7.7	15098	2.4	14722	2.3	1716	0.3	630405

[a]Sunset haul.

[b]Sunrise haul.

started at or near a depth of 250 m. Species which were numerous enough to give meaningful results have been classified here according to their migration patterns. Every category merges with the others, and is entirely transitory for each species. At different depths in their migrations, each species would be placed in a different category. Analysis of these variations at a particular depth illustrates the continuously changing nature of the community, as well as providing information on the migratory behaviour of individual species.

In the following discussion, abundance and scarcity are treated as relative terms referring only to particular species. Unless otherwise stated, the migrations of either sex and any identified juvenile stages are apparently the same.

Non-Migrants

In these species, the numbers caught by day and night remained more or less constant. There were numerous examples (see Table 3). Chaetognaths were the only group containing a large proportion of non-migrants. There were only 8 abundant species and, in addition to those listed in Table 3, *Sagitta enflata*, *S. hexaptera* and *Krohnitta subtilis* may also have been non-migrants. Several of the rarer siphonophores, e.g. *Bassia bassensis*, *Amphicaryon acaule* and *Diphyes bojani*, also appeared to be non-migratory. The vertical series, however, showed that these specimens were situated well below their species' population maxima and were unaffected by the latter's diurnal migrations.

Migrants Present by Day

(a) Species Relatively Abundant by Day which Migrated Away to Become either Totally Absent or Scarce by Night (Table 4; Fig. 2). Only 4 species became absent by night but, of these, only the furcilia larvae of *Euphausia hemigibba* were caught in appreciable numbers. Three species of copepods, indicated by [a] in Table 4, were virtually absent by night. Since these are all small in size, the insignificant numbers taken at night were probably contaminants which entered the closed net as it passed through the depth of their nocturnal maxima, the upper 50 m for all three. For most species in this category, however, the small numbers caught at night represent the lower part of their populations. Their presence by night indicates that either these species did not migrate upwards very far, or that they had deep distributional "tails", or both. (The "tail" of a species' distribution is the decreasing numbers of specimens found either above or below its zone of maximum abundance.) For some ostracods there is evidence that only the shallower members of a population migrate (McHardy and Bary, 1965). This also occurs in some siphonophores (see "Non-Migrants") and, if it happens here, then the small numbers caught by night could represent the non-migrant part of a population rather than the "deep tail" of a wholly migratory species.

There were large differences in the times at which maximum numbers were caught (Table 4) This is found in all the present categories, and indicates that there were considerable variations in the timing or speed of migrations. Apart from

Table 3. Non-migrants. Total number examined is
         given for each species

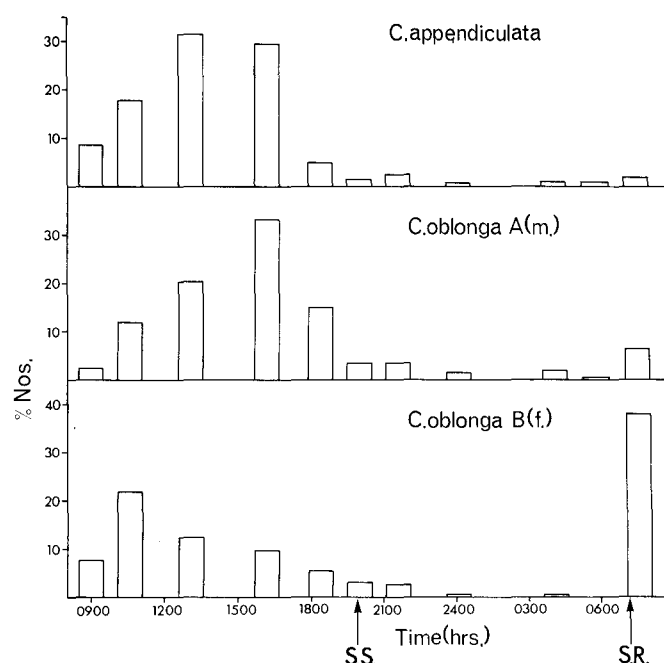| Species	No.	Species	No.
Copepoda		**Amphipoda**	
Clausoca- *lanus* spp.	2963	*Scina tullbergi*	45
Eucalanus *elongatus*	94	*Phronima curvipes*	29
Euaetideus *giesbrechti*	231	**Euphausiidae**	
Scolecithrix *bradyi*	151	*Stylocheiron* *elongatum*	4069
Lucicutia *gemina*	395	**Chaetognatha**	
Heterorhab- *dus papil-* *liger*	1180	*Sagitta decipiens*	1728
		S. lyra	350
Heterosty- *lites longi-* *cornis*	397	*S. planctonis*	108
Haloptilus *longicornis*	1193	**Siphonophora**[a]	
		Dimophyes *arctica*	667 an, 736 eud
H. paralon- *gicirrus*	345	*Lensia multi-* *cristata*	920 an
Ostracoda		*L. meteori*	445 an
Conchoecia *procera*	3847		
C. magna juveniles	1058		
C. spinifera juveniles	425		

[a]an: Anterior nectophore; eud: eudoxid stage.

Fig. 2. *Chelophyes appendiculata*, *Conchoecia oblonga* A ♂♂, and *C. oblonga* B ♀♀. Patterns of abundance. Numbers of each species in each haul are expressed as percentage of total number of that species in all 11 hauls. Times of sunset (S.S.) and sunrise (S.R.) are indicated

interspecific differences, the migratory behaviour of some species varied according to sex or stage of development. Male and female *Conchoecia spinirostris* reached their numerical maxima at different times (Table 4), and although both sexes of *C. oblonga* B were most abundant between 07.05 and 08.18 hrs, they had secondary daytime maxima between 10.06 - 11.05 hrs (♀♀) and 12.36 - 16.44 hrs (♂♂) (see below). Where differences occurred between growth stages they are specified in the Tables, e.g. adult *C. magna* migrated (Table 4) but juveniles did not (Table 3).

The patterns of abundance of many of these species, particularly the siphonophores and ostracods (Fig. 2), suggest a relatively slow migratory cycle. Animals entered the sampled layer on their

downward migrations at about sunrise, their numbers gradually increased to a peak some hours later, and then declined fairly slowly with their upward migrations. This pattern is in marked contrast to those of more obviously active species. The downward movements could possibly be brought about by passive sinking (Rudjakov, 1970), or, at least for ostracods, by buoyancy regulation. Angel (1970) has shown that several ostracod species can reduce their rate of sinking from about 30 m/h to 3 m/h or less.

On the other hand some species, e.g. *Conchoecia oblonga* B, *C. elegans*, *C. secenerda* and male *C. spinirostris*, had their numerical maximum at sunrise, with a secondary maximum during the day (Fig. 2). With the exception of *C. elegans*, these species were most abundant at depths shallower than 250 m. This pattern may thus indicate an active downward migration, with animals overshooting their optimum depth and returning gradually during the day. Clarke (1969) suggested that this occurred for part of the population of the cephalopod *Spirula spirula* off Fuerteventura. In the present series, however, the dawn sample was taken after the day samples, and there is evidence both from scattering layers (Boden and Kampa, 1967) and from individual species' distributions (e.g. Waterman *et al.*, 1939), that migratory patterns may not be identical on consecutive days.

Table 4. Species abundant by day which migrated from layer by night (Category *a*). Total numbers examined are given in brackets for each species. +: Occurrence of species in a haul; M: species' numerical maxima; -: absence of species. Table 1 gives times of each haul. S.S.: sunset; S.R.: sunrise

Species	Haul no.										
	1	2	3	4	5	6 (SS)	7	8	9	10	11 (SR)
Copepoda											
Lucicutia flavicornis (139)	+	+	M	+	+	+	+	+	+	+	+
Pleuromamma gracilis[a] (1522)	+	+	+	+	+	+	+	+	+	+	M
P. piseki[a] (6872)	+	+	+	+	+	+	+	+	+	+	M
Candacia bipinnata[a] (202)	+	+	+	+	+	+	+	+	+	+	M
Ostracoda											
Conchoecia magna adults (474)	-	M	M	+	+	+	+	+	+	+	+
C. bispinosa (640)	+	M	+	+	+	+	+	+	+	+	+
C. spinirostris ♀ (644)	+	M	+	+	+	+	+	+	+	+	+
C. oblonga A (1669)	+	+	+	M	+	+	+	+	+	+	+
C. subarcuata (506)	+	+	+	M	+	+	+	+	+	+	+
C. parthenoda (1751)	+	+	+	M	+	+	+	+	+	+	+
C. oblonga B (1302)	+	+	+	+	+	+	+	+	+	+	M
C. elegans (804)	+	+	+	+	+	+	+	+	+	+	M
C. secenerda (858)	+	+	+	+	+	+	+	+	+	+	M
C. spinirostris ♂ (122)	+	+	+	+	+	+	+	+	+	+	M
Amphipoda											
Phrosina semilunata (148)	+	M	M	M	+	+	+	+	+	+	+
Paraphronima gracilis (31)	+	M	+	+	+	+	-	+	-	-	+
Scina marginata (12)	+	M	+	+	+	+	+	-	-	-	-
Phronima sedentaria (272)	+	+	M	+	+	+	+	+	+	+	+
Stenopleura atlantica (148)	+	+	+	+	+	M	+	+	+	-	+
Euphausiidae											
Euphausia hemigibba furcilia (378)	+	+	M	+	+	+	-	-	-	-	+
Chaetognatha											
Sagitta serratodentata (138)	+	+	+	+	+	+	+	+	+	+	M
Siphonophora[b]											
Hippopodius hippopus (1372 n)	M	+	+	+	+	+	+	+	+	+	+
Eudoxoides spiralis (183 an)	+	M	M	M	+	+	+	+	+	+	+
Lensia hotspur (13 an)	-	+	M	+	+	+	-	-	-	-	-
Chelophyes appendiculata (738 an)	+	+	M	M	+	+	+	+	+	+	+
Pisces											
Scopelarchus analis											
Juveniles + post-larvae (16)	+	M	+	+	+	+	-	-	-	-	+

[a] Probable contaminants.   [b] n: Nectophore; an: anterior nectophore.

Table 5. Species scarce by day which migrated in-
to layer by night (Category *b*). See
legends to Tables 3 and 4 for explanation
of symbols

Species	Haul no.										
	1	2	3	4	5	6 (SS)	7	8	9	10	11 (SR)
Copepoda											
Ctenocalanus vanus (3223)	+	+	+	+	+	+	+	M	M	M	+
Lucicutia clausi (324)	+	+	+	+	+	+	+	M	+	+	+
Ostracoda											
Conchoecia imbricata (238)	+	+	−	−	+	+	+	+	+	M	+
C. spinifera adults (181)	+	−	+	−	+	+	+	+	+	M	+
Amphipoda											
Scina steno-pus (56)	+	+	+	+	+	+	+	M	+	+	+
Hyperiodes longipes (482)	+	+	+	+	+	+	+	M	+	+	+
Chaetognatha											
Eukrohnia sp. juveniles (357)	+	+	+	+	+	+	+	M	+	+	+
Siphonophora											
Rosacea cym-biformis (266 eud)	+	+	+	−	+	M	M	M	+	+	+
Vogtia glabra (725 n)	+	+	+	+	+	+	M	M	+	+	+
Pisces											
Valencienellus tripunctulatus (406)	+	+	+	+	+	+	+	+	M	+	+
Argyropelecus aculeatus (141)	+	−	−	−	−	M	+	+	+	+	M

(b) *Species Relatively Scarce by Day which Migrated Into Sampled Layer to Become Abundant by Night* (Table 5; Fig. 3). This category is more or less the opposite to Category *a* in that the upper edges of populations stayed within the sampled layer by day. There were fewer species in this category (Table 5), and most of them had fairly smooth patterns of abundance (Fig. 3). The comments concerning the low amplitude and slow speed
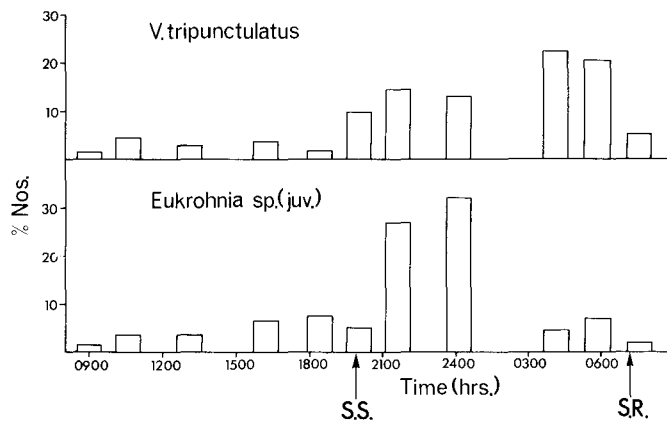

Fig. 3. *Valenciennellus tripunctulatus* and *Eukroh-nia* sp. juveniles. Patterns of abundance, plotted as in Fig. 2

of migrations for most of Category *a* could also apply here. Several species, *Conchoecia imbricata*, adult *C. spinifera*, *Rosacea cymbiformis*, and *Argyropelecus aculeatus*, were virtually absent by day and intermediate between this category and Category *d*. These intermediate species lived deeper by day than most of the other species in this category, and they were present by day mainly in either the first haul, that is immediately after sunrise on 7 April, or in the haul preceding sun-set, or in both. Their presence in these hauls was probably due to their migrations being slightly later or earlier (or both), than the other species, rather than to the day hauls sampling the upper edge of their populations.

The pattern of abundance of *Valenciennellus tripunctulatus* (Fig. 3) accords with a slight migration. The situation is, however, complicated when compared with the results from the vertical series. There is evidence that diurnal changes in abundance occur within common day and night depth limits in this species. The overall data, however, suggest that this is a product of net avoidance rather than vertical migration. Nevertheless, the occurrence of minor vertical displacements cannot be refuted by samples taken from the relatively wide depth layers (100 m) fished in a vertical series. *V. tripunctulatus* is, therefore, tenta-tively included in this category.

(c) *Species Relatively Scarce by Day which Migrated Through Sampled Layer to Become Abundant around Sunset and Returned to Become Abundant around Sunrise* (Table 6; Fig. 4). As in the other categories, there were variations in abundance according to the amplitude of migrations and length of distributional "tails", i.e., whether or not the edges of a population were sampled before or after the bulk of it had moved through. Several species in Table 6 were present in varying numbers throughout both day and night. However, *Conchoecia curta* and *Euphausia brevis* were virtually absent

Table 6. Species scarce by day which migrated through layer by night
(Category *c*). See legends to Tables 3 and 4 for explanation of
symbols

Species	Haul no.										
	1	2	3	4	5	6 (SS)	7	8	9	10	11 (SR)
Copepoda											
Neocalanus gracilis (378)	+	+	+	+	+	M	+	+	+	+	M
Undeuchaeta plumosa (131)	+	–	–	+	–	M	+	+	–	+	M
Euchaeta media (199)	+	–	+	+	–	+	M	+	+	M	+
E. acuta (113)	–	–	–	+	–	M	+	+	+	+	M
Scolecithricella dentata (819)	+	+	+	+	+	M	+	+	+	+	M
Ostracoda											
Conchoecia curta (10653)	M	+	+	+	+	M	+	+	+	+	M
Amphipoda											
Cyphocaris challengeri (74)	M	+	–	+	+	M	+	+	+	+	+
Scina borealis (24)	M	+	–	+	+	M	+	–	–	+	M
S. crassicornis (15)	+	–	–	–	M	+	+	–	–	–	M
Euphausiidae											
Euphausia brevis adults (1759)	M	+	+	+	M	+	–	–	+	–	M
E. hemigibba adolescents (636)	+	+	+	–	+	M	–	–	–	–	M
Siphonophora											
Ceratocymba sagittata (329 eud.)	+	+	+	+	+	M	+	+	+	+	M
Decapoda											
Sergestes (Sergestes) cornutus (56)	–	+	+	+	+	M	–	+	–	+	M
S. (S.) henseni (68)	–	+	+	+	+	M	+	+	+	+	M
S. (S.) curvatus (67)	–	+	+	+	+	M	+	+	+	M	+
S. (S.) sargassi (452)	+	+	–	+	+	M	+	+	+	+	M
S. (S.) pectinatus (98)	+	–	–	–	+	M	+	+	+	+	M
S. (S.) atlanticus (58)	–	–	+	–	–	M	+	+	–	+	M

at night, and adolescent *E. hemigibba* (Fig. 4) were totally absent then. Conversely, *Euchaeta media*, *E. acuta*, *Undeuchaeta plumosa* and *Sergestes atlanticus* were almost absent by day, and intermediate between this category and Category *e*. Finally *Scina borealis*, *S. crassicornis*, *Sergestes sargassi* (Fig. 4) and *S. pectinatus* were present by day mainly in either the post-sunrise or pre-sunset hauls, or both. Their patterns of abundance were thus similar to that of *Argyropelecus aculeatus* described previously.

In addition to these latter four species, several others showed differences in their migration times. *Conchoecia curta* and *Euphausia brevis* had numerical peaks in both the sunrise and post-sunrise hauls, indicating that their downward migrations were continuing after sunrise on the 7 April. *Cyphocaris challengeri* had a marked peak in the post-sunrise sample, suggesting that it migrated downwards after sunrise. Conversely, *Neocalanus gracilis*, *Scolecithricella dentata*, *Conchoecia curta* and *E. brevis* presumably migrated upwards mainly before sunset. The numbers of all four species progressively increased in the pre-sunset hauls, but all had surprisingly small sunset peaks.
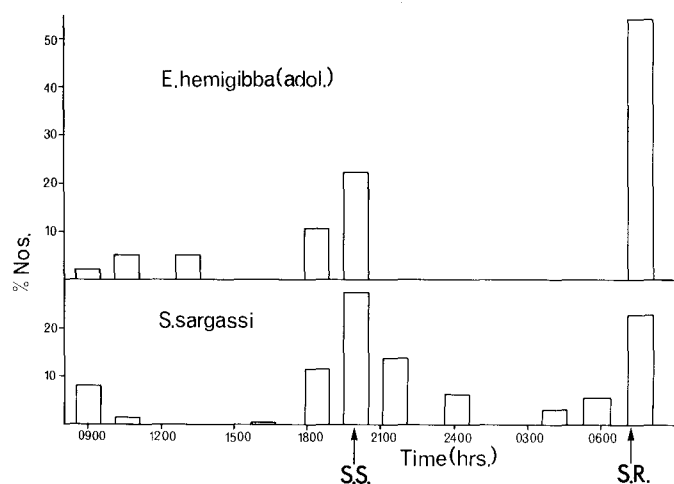
Fig. 4. *Euphausia hemigibba* adolescents and *Sergestes sargassi*. Patterns of abundance, plotted as in Fig. 2
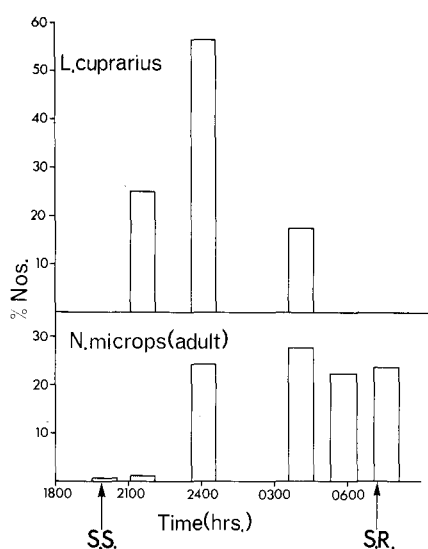

Fig. 5. *Lampanyctus cuprarius* and adult *Nematoscelis microps*. Patterns of abundance, plotted as in Fig. 2

Table 7. Species absent by day which migrated into layer by night (Category d). See legend to Table 4 for explanation of symbols

Species	1	2	3	4	5	6 (SS)	7	8	9	10	11 (SR)
Copepoda											
Gaetanus minor (122)	-	-	-	-	-	M	+	+	+	+	M
Scaphocalanus amplius (106)	-	-	-	-	-	+	+	M	+	+	+
Ostracoda											
Conchoecia hyalophyllum (88)	-	-	-	-	-	+	+	M	+	+	+
Amphipoda											
Euthamneus platyrrhynchus (15)	-	-	-	-	-	-	-	+	M	+	-
Euphausiidae											
Nematoscelis tenella adults (93)	-	-	-	-	-	+	+	M	+	+	+
N. microps adults (144)	-	-	-	-	-	+	+	+	M	+	+
Siphonophora											
Vogtia spinosa (116 n)	-	-	-	-	-	+	M	-	+	+	-
Pisces											
Lampanyctus cuprarius (40)	-	-	-	-	-	-	+	M	+	-	-
Argyropelecus hemigymmus (33)	-	-	-	-	-	+	M	-	+	M	+
Decapoda											
Gennadas valens (104)	-	-	-	-	-	-	M	+	+	+	-
Sergestes (Sergia) grandis (17)	-	-	-	-	-	-	+	+	M	+	-

(d) Species Living Below 250 m by Day which Migrated Into Sampled Layer by Night (Table 7; Fig. 5). Species in this category showed considerable variation in their arrival and departure times and in the times when they reached their numerical maxima (Table 7). *Gaetanus minor, Conchoecia hyalophyllum, Vogtia spinosa* and *Argyropelecus hemigymmus* had a numerical decrease during the middle of the night, and it is particularly difficult to

determine whether they belong to this category or to Category e.

It can also be noted here that for some amphipods the small numbers caught, together with their wide vertical depth ranges, make interpretations of their behaviour doubtful. Some of the apparent migrations observed here disagree with previous observations made off Fuerteventura.

Table 8. Species absent by day which migrated through layer by night (Category *e*). See legend to Table 4 for explanation of symbols

Species	Haul no.										
	1	2	3	4	5	6 (SS)	7	8	9	10	11 (SR)
Copepoda											
Scaphocala-nus breviros-tris (140)	-	-	-	-	-	M	+	+	+	M	+
Pleuromamma xiphias (511)	-	-	-	-	-	M	+	+	+	+	M
P. abdomina-lis (2557)	-	-	-	-	-	M	+	+	+	+	M
Phyllopus helgae (94)	-	-	-	-	-	+	M	+	M	+	-
Euphausiidae											
Thysanopoda obtusifrons (85)	-	-	-	-	-	+	M	M	+	M	+
Pisces											
Notolychnus valdiviae (41)	-	-	-	-	-	M	-	-	M	-	-
Lobianchia dofleini (34)	-	-	-	-	-	M	-	-	-	-	M
Decapoda											
Acanthephyra purpurea (93)	-	-	-	-	-	-	M	+	+	M	-
Systellaspis debilis (78)	-	-	-	-	-	M	+	+	+	M	-

Fig. 6. *Lobianchia dofleini* and *Acanthephyra purpurea*. Patterns of abundance plotted as in Fig. 2

(e) Species Living Below 250 m by Day which Migrated Through Sampled Layer to Become Abundant around Sunset and Returned to Become Abundant around Sunrise (Table 8; Fig. 6). This category is similar to Category *c*, but composed of deeper-living species. Variations in patterns as described for this former category also occur here. Except for *Notolychnus valdiviae* and *Lobianchia dofleini* (Fig. 6), all the species listed in Table 8 were present in varying numbers in the middle part of the night. The differences in arrival and departure times, and the times at which species reached their numerical maxima on their upward and downward migrations are shown in Table 8.

Pleuromamma abdominalis and *P. xiphias* were found in surprisingly small numbers in the sunset and sunrise hauls, respectively. Presumably these samples had almost missed their upward (*P. abdominalis*) and downward (*P. xiphias*) migrations.

Reverse Migrants

The vertical series indicate that three of the present species may have had reverse migrations. The ostracod *Conchoecia ctenophora* was relatively abundant by day, with maximum numbers between 10.06 and 13.36 hrs, and scarce by night; that is apparently in Category *a*. Since it had a reversed migration in the vertical series, however, its nocturnal scarcity in the 24 h series was presumably because the bulk of its population migrated to depths below the sampled layer. Adults of the short form of the euphausiid *Stylocheiron longicorne* were more abundant by night than by day, with maximum numbers between 23.35 and 00.36 hrs; i.e., apparently in Category *b*. This pattern, however, agrees with their vertical distribution off Fuerteventura, where Baker (1970) suggested that they had "a short-range reversed diurnal migration". The amphipod *Tryphana malmi* was present only between sunset and sunrise, with its maximum between 23.35 and 00.36 hrs; that is apparently in Category *d*. This species was a reverse migrant off Fuerteventura, and the pattern seen here may also be due to reverse migration.

Others

Finally, there are the species which cannot be put into any of the previous categories. The numbers of most of these were too small to permit meaningful analysis; for example, only 30 out of the 90 species of copepod were considered sufficiently abundant to analyse. At least one reasonably numerous species, the euphausiid *Nematobrachion flexipes*, can avoid nets of 1 m^2 mouth area (Brinton, 1967), and some of the fish may be able to avoid the larger RMT 8 (see *Valenciennellus tripunctulatus*). For a few relatively numerous small species however, e.g. the ostracods *Conchoecia* ? *skogsbergi* and *C. microprocera*, it is difficult to account for the apparently random variations. Perhaps in these cases patchiness may be important.
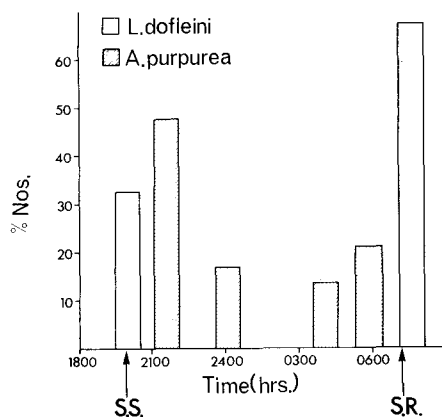
Migration Timing and Depths of Occurrence

At the depth analysed, many of the migrant species fall into Categories *a*, *b* and *c*. They were present by both day and night, presumably because they had restricted migrations or significant distributional "tails" or both. Most of them had fairly smooth migratory patterns (Figs. 2, 3), and it is impossible to give a definite arrival or departure time. Conversely, species which were absent, or virtually so, by day or by night (mainly Categories *d*, *e* and part of *a*) had discontinuous patterns, their numbers generally increasing and decreasing suddenly with their migrations (Figs. 4, 5, 6, 7). Most of these latter species are extensive migrants, and the suddeness of their arrivals and departures suggest that they are also rapid swimmers. For want of a better term they are here called "positive migrants". The percentage of these in each group is shown in Table 9.

Since euphausiids and ostracods include separate sexual and maturity stages, Table 9 shows the numbers of migratory forms and not necessarily the number of species. Euphausiids, decapods, fish and copepods formed the great majority of "positive migrants" at this depth. The other groups had less distinct migrations, and it is interesting that Angel and Fasham (1973) found that amphipods and chaetognaths off Fuerteventura showed no clear depth zonation because of their broad depth distributions. As mentioned earlier, migratory patterns will be obscured by this kind of distribution. Most of the abundant siphonophores and ostracods at this depth had substantial distributional "tails", and a part of the populations of some of their species may have been non-migrants.

If vertical distributions are controlled by light intensity, and if migrations result from animals maintaining position "within" a particular

isolume (Boden and Kampa, 1967), one would expect that the order of occurrence of migrant species should remain constant by both day and night. Furthermore, at any depth within their migratory cycle, deeper-living species should arrive later and leave earlier than shallower-living species. Cushing (1951) reviewed work, much of it on freshwater plankton, which showed that the order in which animals arrived at the surface was related to their day depth. He concluded that light "orders the sequence of their appearance at the surface".

In the present work, one can analyse the arrival and departure times of the "positive migrants" in relation to their day and night distributions as shown by the vertical series. Although the depth of maximum numbers must be treated with caution, (see later), at least the minimum migration range of most of these species is known. For each group, Table 10 gives the order of occurrence with increasing depth of the population maxima of each species in the vertical series by day and by night; e.g. in the decapods by day *Sergestes sargassi* was the shallowest species and *S. grandis* the deepest. Table 10 also shows the hauls of the 24 h series containing the maximum numbers of each species on their upward and downward migration. Species which moved into the sampled layer had only a single migratory peak, and only species for which vertical distributions are known are included.

Despite the fairly small numbers of species in each group and, for some, the small numbers of individuals, it is possible to draw some tentative conclusions from the data. Except for the night depth-order of *Sergestes atlanticus* and *Gennadas valens*, the decapods clearly show the expected sequential migrations and ordered arrangement by day and night. The shallower-living species arrived earlier and left later, and the day depth-order was largely maintained by night.

The euphausiids kept a similar depth order by day and night, but the speed or timing of their migrations varied. Adult *Nematoscelis microps* arrived later than adult *N. tenella* and *Thysanopoda obtusifrons* despite living shallower by day than either; *N. microps* also left earlier than *T. obtusifrons*. The migration times and day depth-order of most of the fish tended to conform to a sequential migration, but the night depth-order did not. Overtaking clearly occurred, with the deeper-living *Notolychnus valdiviae* getting nearer the surface at night than the shallower-living and less extensive migrants *Scopelarchus analis* (juveniles and post-larvae), *Argyropelecus aculeatus* and *A. hemigymnus*. Since the time at which the fish arrived at 250 m agrees overall with their day depth-order, most of the overtaking presumably occurred above this depth. Some of the scarcer fish species showed even more marked overtaking. *Ceratoscopelus warmingi*, for example, found principally between 1500 – 900 m (day) and 100 – 50 m (night), arrived at 250 m in Haul 6, before *A. hemigymnus* which had its day maximum between 500 and 300 m.

Table 9. Number of migrant forms in each group and percentage which are "positive". See text for expanation

Group	No. of migrant forms	No. of "positive migrants"	% "positive migrants"
Decapoda	10	10	100.0
Copepoda	17	15	88.2
Euphausiidae	7	6	85.7
Pisces	7	6	85.7
Amphipoda	12	4	33.3
Siphonophora	9	3	33.3
Ostracoda	26	6	23.1
Chaetognatha	2	0	0
Totals	90	50	55.5

Table 10. Day and night depth-order of species'
population maxima in vertical series,
(1 is shallowest), together with 24 h-
series haul in which they occurred on
their upward and downward migrations.
See text for explanation

Species	Haul no. of upward migrants maximum	Day depth order	Night depth order	Haul no. of downward migrants maximum	Total no. examined
Decapoda					
Sergestes sargassi	6	1	2	11	452
Sergestes atlanticus	6	2	1	11	58
Sergestes pectinatus	6	2	2	11	98
Systellaspis debilis	6	3	3	10	78
Acanthephyra purpurea	7	4	5	10	93
Gennadas valens	7	5	4	7	104
Sergestes grandis	9	6	5	9	17
Euphausiidae					
Euphausia hemigibba furcilia	3	1	2	3	378
Euphausia brevis adults	5	2	1	11	1759
Euphausia hemigibba adolescents	6	2	2	11	636
Nematoscelis microps adults	9	3	3	9	144
Thysanopoda obtusifrons	7+8	4	3	10	85
Nematoscelis tenella adults	8	4	4	8	93
Pisces					
Scopelarchus analis juveniles and post larvae	2	1	2	2	16
Argyropelecus aculeatus	6	2	3	11	141
Lobianchia dofleini	6	2	1	11	34
Argyropelecus hemigymnus	7	3	5	10	33
Notolychnus valdiviae	6	4	1	9	41
Lampanyctus cruprarius	8	5	4	8	40
Copepoda					
Candacia bipinnata	6	1	3	11	202
Lucicutia clausi[a]	8	2	5	8	324
Pleuromamma piseki	6	3	2	11	6872
Pleuromamma gracilis	6	3	2	11	1522
Scolecithricella dentata[a]	6	3	4	11	819
Neocalanus gracilis	6	3	1	11	378
Gaetanus minor	6	3	7	11	122
Scaphocalanus brevirostris[a]	6	3	6	10	106
Scaphocalanus amplius[a]	8	3	5	8	140
Euchaeta acuta	6	4	2	11	113
Euchaeta media	7	4	2	10	199
Pleuromamma abdominalis	6	4	2	11	2557
Phyllopus helgae	7	4	7	9	94
Pleuromamma xiphias	6	5	3	11	511
Undeuchaeta plumosa	6	5	1	11	131

[a]Depth distributions were taken from 18°N;25°W.

Copepods apparently show even more mixing than
the fish. Their day and night depth-orders were
very different, although this is partly because
the upper 100 m in the vertical series, to which
many of these species migrated, was more discretely
sampled than the rest of the water column. Most
species arrived and left mainly in Hauls 6 and 11,
respectively, despite the considerable differences
in their day depths. *Undeuchaeta plumosa*, for
example, had its day maximum between 600 and 500 m,
whereas that of *Neocalanus gracilis* was between
400 and 300 m. It is probable that tows of 1 h are
too long to examine migration timing, and shorter
hauls may well separate species which have here
been lumped together.

Despite the overall mixing and probable aggre-
gation of the copepods, three pairs of congeneric
species showed temporal separation on their mi-
grations. Vertical segregation between congeneric
species has been described several times, e.g.
Foxton (1970) for decapods, Baker (1970) for
euphausiids, Zalkina (1970) for cyclopoid copepods,
Bainbridge (1972), Roe (1972b, c, d) for calanoid
copepods, and Pugh (1974) for siphonophores. At
least for cyclopoids (Zalkina, 1970, 1971, 1972),
Acanthephyra spp. (Foxton, 1972), and calanoid
copepods, this seems to be of common occurrence.
The different migration times of *Pleuromamma
xiphias* and *P. abdominalis* (Category *e*) agree with
the differences in their vertical distributions,
where *P. xiphias* lived deeper by both day and
night (Table 10). Similarly, the different mi-
gration maxima of *Euchaeta acuta* and *E. media* and
of *Scaphocalanus brevirostris* and *S. amplius*
(Table 10; Fig. 7) agree with their depth distri-
butions. At night, *E. acuta* was more abundant than
E. media at their shallowest depths, and *S. bre-
virostris* (at 18°N; 25°W) performed a more extensive
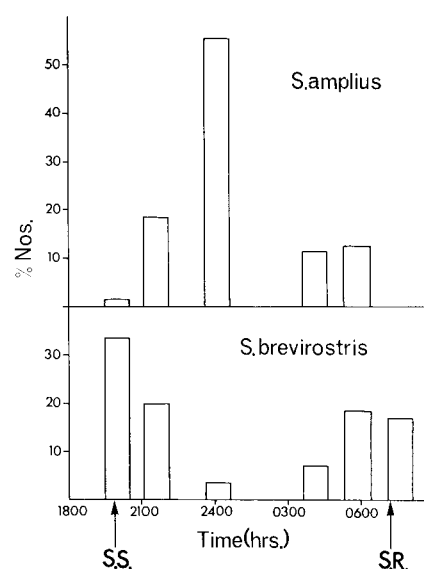migration than *S. amplius*.

Fig. 7. *Scaphocalanus amplius* and *S. brevirostris*.
Patterns of abundance, plotted as in Fig. 2

The species in these three pairs, therefore, followed a sequential migratory pattern which has the effect of at least partially separating their populations by both time and space. Zalkina (1971) and Bainbridge (1972) found that vertical segregation between congeneric species of copepods was maintained either throughout a diurnal cycle or for at least a part of it. More discrete sampling may show that temporal and spatial segregation of congeneric migrants is of general occurrence.

Discussion and Conclusions

There were some features of the present sampling programme which may have affected either the results or their interpretation. Perhaps the most important of these was that no sample was taken after dawn on 8 April. Because of this, it can only be inferred that many species left the sampled layer on their downward migrations during or just after sunrise. Nevertheless, from a knowledge of their behaviour on their upward migrations, it is most unlikely that they did not do so.

Despite all the hauls being made within a fairly confined area, it is highly improbable that the same body of water was sampled throughout the period. It is, therefore, possible that some of the numerical variations were due to differences in the populations in different bodies of water. Since most of the observed patterns of abundance were predictable from prior knowledge of the species' vertical distributions, it is thought unlikely that different bodies of water greatly affect these results. A depth of 250 m was chosen partly because many of the migrant copepods off Fuerteventura apparently had a nocturnal maximum here, and partly because the daytime copepod population was likely to be poor in species but rich in numbers of individuals. This depth was not very satisfactory for all groups, particularly for the fish and decapods which were both very scarce by day. Finally, little physical data were taken in conjunction with these hauls, and it is impossible to analyse the results in relation to the physical environment.

This series has been interpreted with reference to a vertical series done at the same place a few days earlier (31 March to 7 April, inclusive). As pointed out previously, a species may not have exactly the same migratory pattern on consecutive days and it may not necessarily return to the same depth as that from which it came. Differences of this kind are only of detail, and probably do not affect the present interpretation of overall patterns. In any case, it is impossible to analyse these results without reference to the vertical series, as the direction of observed movements can only be deduced from the latter.

Despite the drawbacks, these results illustrate the continuously changing nature of a community during a diurnal cycle. In the sampled layer, both the specific composition and numbers of individuals changed with time. At this depth, or at any other

through which vertical migration occurs, the presence of migratory species depends upon the time of day or night. This means that, in a vertical series of hauls, the depth distributions of migrant species will vary with the sampling times. The depths at which migrants' numerical maxima occur will show only where their populations were at a particular time of day or night. Since these depths are not necessarily either the upper or the lower limits of their depth ranges, a vertical series may only show the minimum migration range of any species.

Almost all of the present migrants started their migrations before sunset and sunrise and continued them after these times. Their patterns of abundance suggest that most of them spend the majority of their time moving up or down. Species which apparently had slow migratory cycles of small amplitude (Figs. 2 and 3) typically had a gradual increase in numbers either during the day as they migrated downwards or during the night as they moved upwards. Their numbers reached a peak and then began to decline almost immediately as the direction of their movements reversed. The patterns of the faster, more extensive migrants (Figs. 4-7) were less complete. However, in many species which moved through the layer, the numerical decline following their upward migrations was rapidly reversed as they returned downwards. Only a few species, e.g. *Nematoscelis microps* (Fig. 5), had a steady numerical plateau between their upward and downward movements.

Except for the intraspecific behavioural differences, e.g. *Conchoecia magna*, there is little evidence here that populations of migrant species split up into smaller units on their migrations. The 1 h tows may have obscured this, and more discrete sampling is needed before definite conclusions can be made. There is, however, a little evidence that small numbers of some migrants were out of phase with their main populations. Single specimens of three species of extensively migratory copepods, *Euchaeta media, E. acuta* and *Undeuchaeta plumosa*, were found in Hauls 3 or 4 (see Table 6) well before the bulk of their populations migrated into the 250-m depth layer and well after they had left it.

Finally, the correlation between the timing of migrations and depths of occurrence suggests that the vertical distributions and migrations of some species could be ordered by isolumes. Although there have been many studies relating light intensity to animals' distributions, only Clarke (1966, 1970) has used an opening and closing trawl equipped with a deep-sea photometer so that animals and their light regimes can be compared directly. He found that the three principal migratory animals in the Santa Barbara Channel were vertically stratified, and that each layer was associated with a particular light level. This layered structure was maintained by day and during their migrations, and broke down only during the night. Clarke's results agree with those given here. Decapods, euphausiids, fish and copepods showed at least some evidence of orderly mi-

grations and arrangement of their depth orders. They also all had some mixing up of their day depth-order at night. Some overtaking occurred, however, and clearly in these cases either the species being passed or that doing the passing cannot be following an isolume. If their migrations are due to light they may be responding to changes in light intensity.

Although of a preliminary nature, this study indicates that the vertical distributions and migrations of some species could be ordered by reference to isolumes. It also suggests that this may not be so for all species or for some of them all of the time. An orderly arrangement maintained throughout diurnal cycles provides a means of separating by both time and space competing, closely related, or congeneric species.

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