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BIOLOGICAL STUDIES IN THE VICINITY OF A SHALLOW-SEA TIDAL MIXING FRONT V. COMPOSITION, ABUNDANCE AND DISTRIBUTION OF ZOOPLANKTON IN THE WESTERN IRISH SEA, APRIL 1980 TO NOVEMBER 1981

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CONTENTS

There has been no change in the overall species composition of the western Irish Sea zooplankton during the last 80 years. Although *Pseudocalanus elongatus* and *Acartia clausi* were always the most abundant species encountered in the survey area, *Calanus finmarchicus* has been the main contributor to the total zooplankton biomass. The marked decline in numbers of this copepod in 1981 was almost totally responsible for the large decrease in zooplankton biomass observed during that year. The highest zooplankton standing stocks were found to occur above the thermocline in the stratified region between April and June. In the mixed isothermal region zooplankton standing stocks were much lower with a maximum at least one month later than on the stratified side of the front. The frontal region was found to have little influence on the distribution of the total zooplankton. On the isolated occasions when higher zooplankton concentrations were observed within the frontal region they were always found to be associated with localized high densities of surface chlorophyll and due to increased copepod production rather than mechanical aggregation.

1. Introduction

Although the general distribution, composition and abundance of zooplankton in the Irish Sea are relatively well known on both the horizontal (Herdman *et al.* 1908–21; Johnstone *et al.* 1924; Pierce & Orton 1939; Pierce 1941; Williamson 1952, 1956*a*, *b*, 1963, 1975; Khan & Williamson 1970) and vertical scales (Lee & Williamson 1975; Scrope-Howe & Jones 1985), very few workers have studied zooplankton in relation to the strong physical features of this area. Leigh (1977) made a preliminary study on zooplankton distributions associated with the western Irish Sea frontal system and similar work has been carried out on the Liverpool Bay discontinuity in the eastern Irish Sea (Kendaris 1979; Floodgate *et al.* 1981).

In the present work we describe the composition, abundance and distribution of zooplankton found in the stratified, mixed and frontal regions of the western Irish Sea between April 1980 and November 1981.

Details of cruises and general methods of working have already been described (Fogg *et al.* 1985). During 1981 an opportunity occurred to participate in an additional four cruises aboard the R.V. *Prince Madog* visiting the same area of the western Irish Sea. Thus, samples were also collected on the transect during cruises ISIS 15 (6–10 April), ISIS 17 (5–8 May), ISIS 18 (28–29 May) and AUK 1 (1–2 September) giving a more complete coverage of zooplankton distributions for that year. Severe gales disrupted attempts to collect samples on other cruises during late November in both 1980 and 1981.

Detailed statistical analysis of the zooplankton data and its relationship to other aspects of this multidisciplinary investigation are described by Kassab *et al.* (1985).

2. Methods

Zooplankton samples were collected at each station by vertical hauls through the whole water column with modified 0.5 m diameter WP2 fine mesh conical plankton nets (142 μm aperture). The volume of water filtered through the nets was monitored by either TSK (Tsurumi-Seiki-Kosakusho Co., Japan) or specially modified HydroBios (Kiel, F.G.R.) mechanical flowmeters (model 880 and model 438 110, respectively) suspended across the mouth openings. Nets were hosed down thoroughly following each haul and the collected samples immediately preserved in 5% neutral formalin seawater solution. These were subsequently analysed back in the laboratory where zooplankton density was determined by volumetric subsampling with replacement and all groups identified to species and stage level from samples of at least 100 individuals (Winsor & Walford 1936).

Zooplankton abundances are calculated as concentrations (numbers per cubic metre) and as standing stocks (numbers per square metre) following the procedure adopted by Judkins *et al.* (1980). Concentrations are primarily for comparison with previous data, which is almost always presented in this fashion. However, comparison of numbers per cubic metre from vertical hauls at different locations within a survey area of varying depth will create underestimations of the zooplankton present at the deeper stations relative to the shallower ones (Peterson & Miller 1977). This is because estimates of concentration from vertical hauls are average values for the whole water column on using the assumption that the zooplankton are evenly distributed with depth. Studies on the vertical distribution of zooplankton in the western Irish Sea (Scrope-Howe & Jones 1985) show that the majority of taxa are concentrated above the thermocline in the stratified region and are randomly distributed in the mixed isothermal region. Thus, to compare vertical haul samples from different depths without underestimating species abundances, standing stocks were used in all calculation procedures.

Estimates of total zooplankton biomass were obtained for each station by computing the dry masses (obtained by measurement) of individual species and stages in all samples and converting these to milligrams carbon per square metre by using the equivalent tables recommended by Cushing *et al.* (1958). All data storage, manipulation and analysis was carried out on the U.C.N.W. DECsystem-10 computer.

3. Results

(*a*) *Species composition and mean abundance*

Twenty-eight taxonomic categories (nine Copepoda and 19 other holo- and meroplanktonic species or groups) were counted in the samples and the majority of organisms were identified to species level. Of the nine species of copepod, *Pseudocalanus elongatus* (Boeck), *Acartia clausi* (Giesbrecht) and *Temora longicornis* (Müller) were subdivided into adults, copepodites and nauplii, the life cycle stages of the other six species not being found in sufficient numbers to be tallied separately. Because they are difficult to separate routinely, specimens of *Paracalanus parvus* (Claus) were grouped with *Pseudocalanus elongatus* as a single species. Similarly, no attempt was made to separate *Calanus helgolandicus* (Claus) from what, according to Williamson (1952), is a population of almost pure *Calanus finmarchicus* (Gunnerus) in this region. *Sagitta elegans* (Verrill) was the only chaetognath observed in the survey area and thus it was assumed that all juveniles belonged to that species. The planktonic larvae of benthic invertebrate species were grouped in classes as echinoderm plutei, lamellibranch veligers, gastropod veligers and polychaete larvae. Brachyuran, anomuran and caridean larvae were also not considered at the species level but grouped together under decapod larvae.

Many of the above species or groups occurred in the samples throughout most of the year. These included the copepods *Pseudocalanus elongatus* (Boeck), *Acartia clausi* (Giesbrecht), *Temora longicornis* (Müller), *Oithona similis* (Claus), *Calanus finmarchicus* (Gunnerus), *Microcalanus pusillus* (G. O. Sars), *Centropages hamatus* (Lilljeborg), the appendicularian *Oikopleura dioica* (Fol), the ectoproct larvae *Membranipora membranacea* (Linne), the chaetognath *Sagitta elegans* (Verrill) and the various species of echinoderm plutei, lamellibranch veligers, gastropod veligers and polychaete larvae.

Other species were only common during short periods of the year. Cladocera were represented by breeding populations of *Evadne nordmanni* (Loven) and *Podon leuckarti* (G. O. Sars) which were confined to the stratified region during April and May. Decapod larvae were present only in the summer months and cirripede nauplii were found mostly in inshore samples during spring, summer and autumn. Fish eggs occurred in highest numbers in spring and early summer. The planktonic polychaete *Tomopteris helgolandica* (Greeff) was present in small numbers at all seasons but was unusually abundant in the survey area during August 1981. The appendicularian *Fritillaria borealis* (Lohmann) occurred in high numbers only once, during June 1981, being confined to the mixed isothermal region.

Rare species in the samples were the copepods *Metridia lucens* (Boeck), *Isias clavipes* (Boeck) and the late nauplii stages of *Longipedia coronata* (Claus). Although adults and larvae of the euphausiid *Meganyctiphanes norvegica* (M. Sars), the ctenophore *Pleurobrachia pileus* (Müller), various medusae species and fish post-larvae occurred from time to time the vertical haul nets did not sample these species adequately enough to permit any detailed comments on their distribution.

The mean abundance, frequency of occurrence and dominance index (Fagar & McGowan 1963) of the 13 most abundant zooplankton taxa in the survey area (ranked in order of mean abundance) during 1980 and 1981 are shown in table 1 and table 2, respectively. From

Table 1. Mean abundance (number per square metre, number per cubic metre and percentage of total number per square metre), frequency of occurrence (percentage in samples) and dominance of the 13 most abundant zooplankton taxa in the western Irish Sea during 1980

		mean abundance				
rank	taxonomic groups	number per square metre	number per cubic metre	percentage of total	frequency (%)	dominance
1	*Pseudocalanus elongatus*	43051	588	40.7	100	34
2	*Acartia clausi*	17575	237	16.6	100	19
3	*Calanus finmarchicus*	17053	220	16.1	68	7
4	*Oithona similis*	11705	159	11.0	94	8
5	*Temora longicornis*	4582	61	4.3	73	1
6	*Centropages hamatus*	3246	44	3.0	42	1
7	appendicularians	2159	30	2.0	55	1
8	lamellibranch veligers	1823	26	1.7	68	1
9	polychaete larvae	1704	25	1.6	63	0
10	echinoderm plutei	1124	16	1.0	37	0
11	*Membranipora membranacea*	730	10	0.7	26	2
12	gastropod veligers	435	5	0.4	39	0
13	*Microcalanus pusillus*	434	5	0.4	21	0
	total copepods	**97646**	**1314**	**92.3**		
	total 'others'	**7975**	**112**	**7.5**		
	grand total	**105621**	**1426**			

Copepods are the sum of all stages and larvae the sum of all species encountered. Taxa are listed in order of average abundance to indicate their relative importance in the survey area. Dominance: proportion of samples ($n = 38$) in which taxon was among those making up 50 % of the individuals; summation in each sample commenced with the most abundant species (Fagar & McGowan 1963).

calculations of mean standing stock abundances it can be seen that copepods, on average, composed 92 % of the total zooplankton in 1980 and 87 % in 1981. Appendicularians, benthic invertebrate larvae and ectoproct larvae together contributed 7.5 % to the total in 1980 and 12.8 % in 1981. From the grand totals for each year it is evident that total zooplankton numbers in 1981 were, on average, 46 % lower than in 1980. At the species level, *Pseudocalanus elongatus* ranked top in both years with a mean annual abundance composing 30–40 % of the total zooplankton. This species occurred in all samples and was dominant in 89 % of the samples in 1980 and 82 % in 1981. *Acartia clausi* ranked the next most abundant species composing 16.6 % of the total zooplankton in 1980 (occurring in all samples and dominant in 50 %) and 24.6 % in 1981 (with a frequency of occurrence of 98 % and dominant in 51 %). All other individual species and groups, except *Calanus finmarchicus* (16 % of the total zooplankton) and *Oithona similis* (11 %) in 1980 and *Oithona similis* (15 %) again in 1981, composed less than 10 % of the total zooplankton.

Comparison of the mean annual abundances of the different taxa during 1980 and 1981 shows

Table 2. Mean abundance (number per square metre, number per cubic metre and percentage of total number per square metre), frequency of occurrence (percentage of samples) and dominance of the 13 most abundant zooplankton taxa in the western Irish Sea during 1981

rank	taxonomic groups	mean abundance: number per square metre	number per cubic metre	percentage of total	frequency (%)	dominance
1	*Pseudocalanus elongatus*	17838	234	31.3	100	56
2	*Acartia clausi*	13997	205	24.6	98	35
3	*Oithona similis*	8639	109	15.2	91	17
4	*Temora longicornis*	4595	68	8.1	83	5
5	*Microcalanus pusillus*	2650	30	4.6	50	5
6	appendicularians	2269	35	3.9	57	3
7	*Membranipora membranacea*	1668	21	2.9	48	8
8	*Calanus finmarchicus*	1608	19	2.8	71	0
9	lamellibranch veligers	1514	23	2.6	57	10
10	gastropod veligers	786	10	1.4	51	1
11	polychaete larvae	722	9	1.2	60	0
12	echinoderm plutei	450	5	0.8	30	0
13	*Centropages hamatus*	197	3	0.3	18	0
	total copepods	**49524**	**668**	**86.9**		
	total 'others'	**7409**	**103**	**12.8**		
	grand total	**56933**	**771**			

Copepods are the sum of all stages and larvae the sum of all species encountered. Taxa are listed in order of average abundance to indicate their relative importance in the survey area. Dominance: proportion of samples ($n = 68$) in which taxon was among those making up 50% of the individuals; summation in each sample commenced with the most abundant species (Fagar & McGowan 1963).

some marked trends in mean abundance between the two years. Although *Acartia clausi*, *Temora longicornis*, appendicularians, lamellibranch veligers and gastropod veligers remained reasonably constant in both years, there was a 90% decrease in the mean annual abundance of *Calanus finmarchicus* and *Centropages hamatus* during 1981 coupled with decreases in other species such as *Pseudocalanus elongatus* (59%), *Oithona similis* (23%), polychaete larvae (64%) and echinoderm plutei (69%). On the other hand the copepod *Microcalanus pusillus* and the ectoproct larvae *Membranipora membranacea* were more abundant in 1981.

(*b*) *Species distribution*

In figure 1 the 1980–1 distribution of total zooplankton standing stocks have been separated into three distinct zones within the survey area. Figure 1*a* shows the variation in mean monthly abundances for the stratified region where it can be seen that in 1980 standing stocks were already at their highest peak in April and maintained this elevated position in June. However, by July numbers were greatly reduced and remained at this lower level until stratification broke down in September. The pattern for 1981 was quite different with a much lower mean standing stock in April and a smaller (compared with 1980) peak in numbers during May, which by the following month had decreased to April levels again. There was a second, lower peak of abundance during August after which numbers dropped till stratification disappeared in September. This difference between the two years may be partly due to the complete breakdown of stratification by severe gales in the western Irish Sea during mid-April 1981. The thermocline was not firmly re-established again until the first week in May.

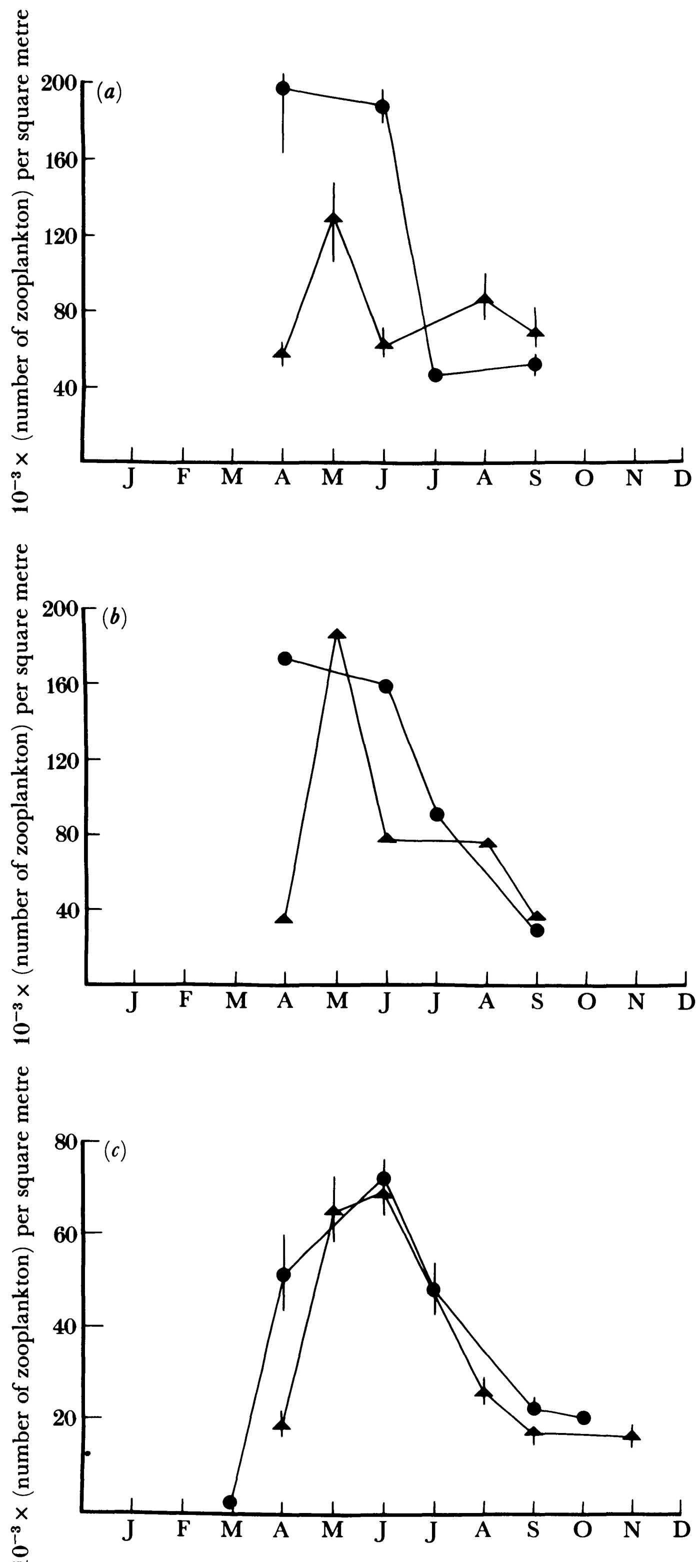

FIGURE 1. (*a*) Total zooplankton mean monthly number per square metre for the stratified region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). Vertical bars indicate standard deviation. (*b*) Total zooplankton monthly number per square metre for the frontal region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). (*c*) Total zooplankton mean monthly number per square metre for the mixed region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). Vertical bars indicate standard deviation.

Figure 1 *b* shows the variations in zooplankton standing stocks for the frontal region. Although these are individual, rather than mean, monthly values, it is clearly evident that the seasonal pattern for both 1980 and 1981 are very similar to those of the stratified water (figure 1 *a*). Standing stocks in the stratified region are almost always slightly higher than those in the frontal zone. There are exceptions to this and the influence of the frontal region on zooplankton abundance and distribution will be dealt with in greater detail below. From the mean monthly abundances for the mixed isothermal water shown in figure 1 *c* it can be seen that this region is quite separate in character from the other two zones. Mean annual standing stocks are on average 65 % lower than those in the stratified region except in July 1980 and June 1981 when there was no significant difference between them. The seasonal pattern for both 1980 and 1981 in this region are very similar reaching a peak in June (approximately one month later than in the stratified water) followed by a gradual decrease in numbers through to September.

The variations in mean abundance (both standing stocks and concentrations) of the 13 most abundant zooplankton species in the three separate zones are shown for 1980 in table 3 and 1981 in table 4. The species are ranked in order of overall mean abundance and their frequency of occurrence and percentage composition of the total zooplankton in each zone is also given. When comparing 1980 with 1981 it can be seen that, as in figure 1 *c*, the mixed isothermal water remains similar in both years with no change in the percentage composition of total copepods (79 %) and total appendicularians, ectoproct larvae and benthic invertebrate larvae (20 %). The mean annual numbers per square metre for the stratified region reflect the trend seen in figure 1 *a* with a 57 % decrease during 1981 due almost totally to the drop in numbers of copepods. Although the actual abundances are significantly different between the two years, the percentage composition remained the same, being 95 % in 1980 and 92 % in 1981. The decrease in abundance of many species in 1981, especially of the copepod *Calanus finmarchicus* and *Centropages hamatus*, can clearly be seen in this region. However, these decreases were partly compensated for by increases in species that were only present in low numbers in 1980. The copepod *Microcalanus pusillus* showed an 83 % increase in the stratified water during 1981 and a 98 % increase in the mixed region, although numbers in the frontal zone remain the same. The distribution of this deep-water species in 1981 reflects a temporary spreading from depths below the thermocline right across the survey area during April–May (no specimens being found in the mixed region from June onwards). Gastropod veligers remain at similar levels in the frontal and mixed regions during both years, but increase by 87 % in the stratified water during 1981.

Compared with the stratified region, the frontal zone showed only a small difference in mean annual abundance of total zooplankton (12 %). Although in 1981 the same decreases occurred in such species as *Calanus finmarchicus* (94 %), *Centropages hamatus* (86 %), *Oithona similis* (35 %) and *Pseudocalanus elongatus* (31 %) there were substantial increases in *Membranipora membranacea* (67 %), appendicularians (64 %), *Temora longicornis* (52 %) and *Acartia clausi* (49 %). Thus in 1981 the frontal zone contained a slightly higher mean annual total zooplankton (94810 per square metre) than the stratified region (66821 per square metre).

(*c*) *Zooplankton biomass*

The monthly biomass values in milligrams carbon per square metre for the three zones of the western Irish Sea are shown for 1980 and 1981 in figure 2. The total biomass was almost fully represented by the 13 species and groups listed in tables 1–4, with the copepodites and

TABLE 3. VARIATIONS IN MEAN ABUNDANCE (NUMBER PER SQUARE METRE AND NUMBER PER CUBIC METRE) AND FREQUENCY OF OCCURRENCE (PERCENTAGE OF SAMPLES) OF THE 13 MOST ABUNDANT ZOOPLANKTON TAXA IN THE STRATIFIED, FRONTAL AND MIXED REGIONS OF THE WESTERN IRISH SEA DURING 1980

taxonomic groups	item	stratified	frontal	mixed
Pseudocalanus elongatus	number per square metre	62826 (40.4)	46652 (43.4)	14976 (37.6)
	number per cubic metre	771	730	260
	percentage frequency	100	100	100
Acartia clausi	number per square metre	25068 (16.1)	14963 (13.9)	9384 (23.5)
	number per cubic metre	306	225	153
	percentage frequency	100	100	100
Calanus finmarchicus	number per square metre	31308 (20.1)	10744 (9.9)	2294 (5.7)
	number per cubic metre	378	173	41
	percentage frequency	88	75	38
Oithona similis	number per square metre	16670 (10.7)	15216 (14.1)	3050 (7.6)
	number per cubic metre	203	238	52
	percentage frequency	100	87	92
Temora longicornis	number per square metre	7046 (4.5)	4461 (4.1)	1435 (3.6)
	number per cubic metre	85	71	25
	percentage frequency	65	62	92
Centropages hamatus	number per square metre	4664 (3.0)	4638 (4.3)	534 (1.3)
	number per cubic metre	57	72	10
	percentage frequency	47	37	38
appendicularians	number per square metre	2767 (1.7)	2039 (1.9)	1437 (3.6)
	number per cubic metre	34	32	23
	percentage frequency	47	37	77
lamellibranch veligers	number per square metre	1184 (0.7)	2502 (2.3)	2240 (5.6)
	number per cubic metre	15	37	36
	percentage frequency	59	62	84
polychaete larvae	number per square metre	1289 (0.8)	2539 (2.3)	1734 (4.3)
	number per cubic metre	16	40	30
	percentage frequency	29	75	100
echinoderm plutei	number per square metre	719 (0.4)	1858 (1.7)	1201 (3.0)
	number per cubic metre	9	30	17
	percentage frequency	23	50	46
Membranipora membranacea	number per square metre	864 (0.5)	360 (0.3)	975 (2.4)
	number per cubic metre	10	6	16
	percentage frequency	17	12	46
gastropod veligers	number per square metre	78 (0.05)	961 (0.9)	578 (1.4)
	number per cubic metre	1	11	9
	percentage frequency	17	37	62
Microcalanus pusillus	number per square metre	674 (0.4)	559 (0.5)	15 (0.03)
	number per cubic metre	7	7	1
	percentage frequency	29	25	7
total copepods	number per square metre	**148256 (95.5)**	**97233 (90.4)**	**31688 (79.5)**
	number per cubic metre	**1807**	**1516**	**542**
total 'others'	number per square metre	**6901 (4.4)**	**10259 (9.5)**	**8165 (20.4)**
	number per cubic metre	**85**	**156**	**131**
grand total	number per square metre	**155157**	**107492**	**39853**
	number per cubic metre	**1892**	**1672**	**673**

Taxa are listed in overall mean abundance with copepods being the sum of all stages and larvae the sum of all species. Values in parentheses after number per square metre values are percentage of total zooplankton.

nauplii of *Pseudocalanus elongatus*, *Acartia clausi* and *Temora longicornis* and the chaetognath *Sagitta elegans* also included in the computations. Of these species, groups and life cycle stages, only those that occurred at or above the 5% composition level in each sample were used, based on the assumption that the rarer organisms could be omitted because their biomass contribution would be very small compared with the total contribution of the commoner ones.

Table 4. Variations in mean abundance (number per square metre and number per cubic metre) and frequency of occurrence (percentage of samples) of the 13 most abundant zooplankton taxa in the stratified, frontal and mixed regions of the western Irish Sea during 1981

taxonomic groups	item	stratified	frontal	mixed
Pseudocalanus elongatus	number per square metre	20275 (30.3)	32236 (34.0)	13161 (35.8)
	number per cubic metre	251	309	195
	percentage frequency	100	100	100
Acartia clausi	number per square metre	14995 (22.4)	29318 (30.9)	9366 (25.5)
	number per cubic metre	192	397	164
	percentage frequency	100	100	100
Oithona similis	number per square metre	13442 (20.1)	9967 (10.5)	1783 (4.8)
	number per cubic metre	206	122	26
	percentage frequency	100	100	82
Temora longicornis	number per square metre	6020 (9.0)	9224 (9.7)	2928 (7.9)
	number per cubic metre	74	113	49
	percentage frequency	89	100	82
appendicularians	number per square metre	1450 (2.1)	5592 (5.9)	2014 (5.5)
	number per cubic metre	18	84	36
	percentage frequency	55	62	57
lamellibranch veligers	number per square metre	1425 (2.1)	2925 (3.0)	1377 (3.7)
	number per cubic metre	16	43	24
	percentage frequency	48	75	60
Microcalanus pusillus	number per square metre	3965 (5.9)	514 (0.5)	1118 (3.0)
	number per cubic metre	57	6	12
	percentage frequency	85	37	27
Membranipora membranacea	number per square metre	421 (0.6)	1100 (1.1)	2481 (6.7)
	number per cubic metre	8	12	36
	percentage frequency	29	37	66
Calanus finmarchicus	number per square metre	2851 (4.2)	644 (0.6)	432 (1.1)
	number per cubic metre	37	10	4
	percentage frequency	96	62	42
polychaete larvae	number per square metre	317 (0.4)	1172 (1.2)	976 (2.6)
	number per cubic metre	4	14	14
	percentage frequency	26	75	85
gastropod veligers	number per square metre	593 (0.8)	822 (0.8)	690 (1.8)
	number per cubic metre	8	12	11
	percentage frequency	37	50	63
echinoderm plutei	number per square metre	896 (1.3)	621 (0.6)	87 (0.2)
	number per cubic metre	9	9	1
	percentage frequency	29	75	24
Centropages hamatus	number per square metre	171 (0.2)	675 (0.7)	269 (0.7)
	number per cubic metre	2	12	4
	percentage frequency	11	25	24
total copepods	number per square metre	**61719 (92.3)**	**82578 (87.1)**	**29057 (79.2)**
	number per cubic metre	**819**	**969**	**454**
total 'others'	number per square metre	**5102 (7.6)**	**12232 (12.9)**	**7625 (20.7)**
	number per cubic metre	**63**	**174**	**122**
grand total	number per square metre	**66821**	**94810**	**36682**
	number per cubic metre	**882**	**1143**	**576**

Taxa are listed in overall mean abundance with copepods being the sum of all stages and larvae the sum of all species. Values in parentheses after number per square metre values are percentage of total zooplankton.

Figure 2*a* shows the mean monthly carbon biomass for the stratified water. During 1980 values were highest in this region with a peak in June which fell rapidly to lower levels during the remaining three months. In 1981 the pattern was very different with substantially lower values over the whole period of stratification in this area which amount to a drop of 93% in the mean annual carbon biomass. From figure 2*b* it can be seen that although the frontal zone

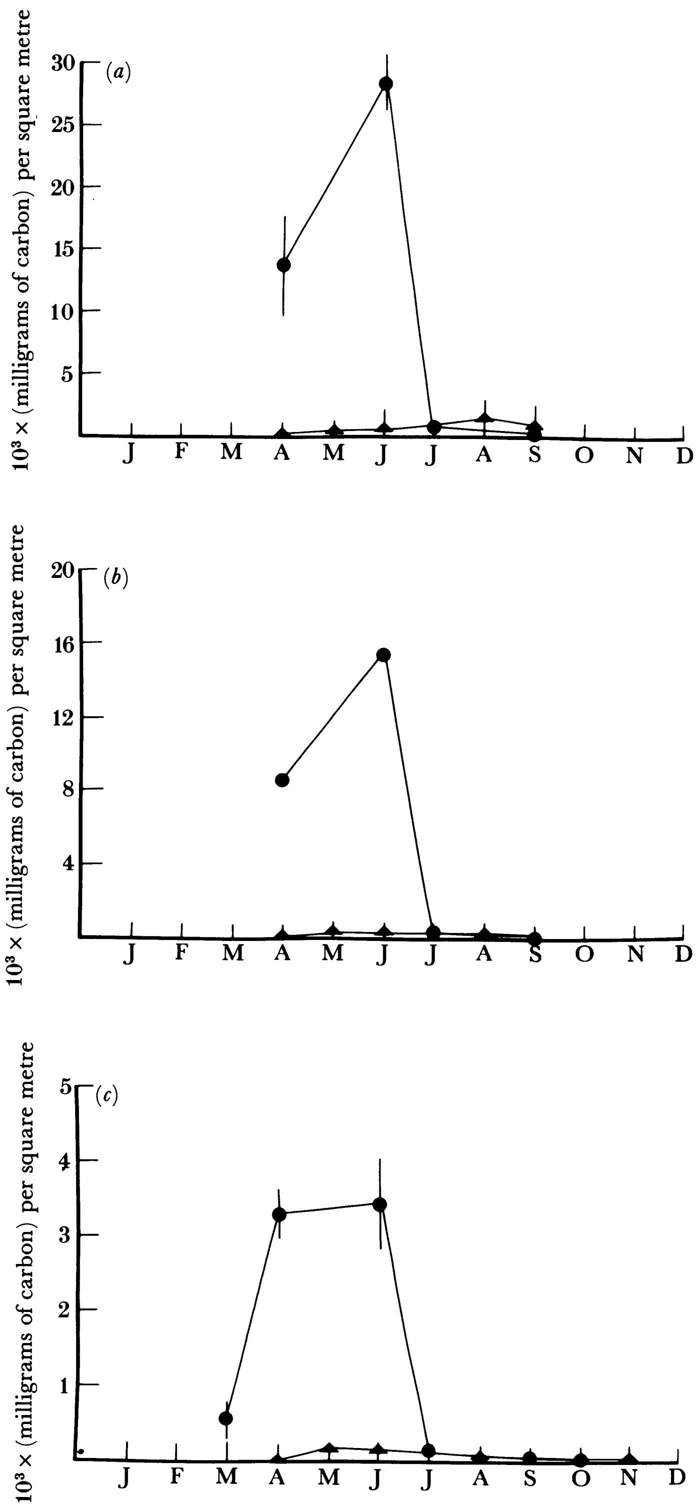

FIGURE 2. (*a*) Total zooplankton mean monthly carbon biomass for the stratified region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). Vertical bars indicate standard deviation. (*b*) Total zooplankton carbon biomass for the frontal region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). (*c*) Total zooplankton mean monthly carbon biomass for the mixed region of the western Irish Sea during 1980 (●—●) and 1981 (▲—▲). Vertical bars indicate standard deviation.

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was, on average, 43 % lower than the stratified water during 1980, the patterns of monthly biomass are very similar for both regions. The carbon biomass levels in 1981 for the frontal zone also show a great decrease in that year and are 97 % lower than those of 1980. Although numerical standing stocks in the mixed isothermal region (figure 1*c*) were fairly equal in abundance and distribution during both years, the mean monthly carbon biomass patterns shown in figure 2*c* are similar in trend to those of the stratified and frontal areas in figure 2*a*, *b*. The mixed region had 88 % less mean annual carbon biomass than the stratified water during 1980 with highest levels between April and June which had dropped off by July. During 1981 biomass was 79 % lower than 1980 levels. In all three zones (figure 2) it can be seen that the large 1981 decreases occurred in the earlier part of the year between March and June, as the lower levels from July onwards were approximately the same in both years.

When calculating the proportional contribution of each species to the total carbon biomass at all stations, it was observed that the numerically ranked list of dominant species shown in tables 1–4 closely reflects the ranked order of biomass contributors. Only *Calanus finmarchicus* contributed a proportionately larger fraction to the total biomass than its numerical position indicates. On average this one species accounts for 93 % of the biomass at the stations where it occurred in both 1980 and 1981 (range 88–98 %). Thus the decrease in numbers of *Calanus finmarchicus* over the whole area of the western Irish Sea during 1981 was almost totally responsible for the large difference in carbon biomass observed between the two years.

(*d*) *Frontal influence*

It is evident when examining the seasonal pattern of zooplankton standing stocks for both the stratified and frontal regions during 1980 and 1981 (figure 1 *a*, *b*) that the frontal zone rarely exerted any significant influence on the distribution and production of total zooplankton. Both areas exhibited the same monthly trend in abundance during the period of stratification with the stratified water almost always containing higher zooplankton numbers than the frontal zone. The data from 12 cruises carried out between April 1980 and November 1981 indicate that the frontal region produced significantly higher total zooplankton populations on only two occasions, during the cruises ISEA 4 (July 1980) and ISIS 18 (May 1981). When a significant increase in zooplankton did occur within this area it was always associated with the presence of localized high densities of chlorophyll in the surface waters of the frontal zone which were usually accompanied by subsurface chlorophyll maxima in the stratified water.

On 15 July 1980 chlorophyll reached 3 $\mu g\ l^{-1}$ at the surface in the transition zone between the stratified and isothermal regions (see figure 6*d* in Fogg *et al.* (1985)). This surface concentration was associated with a subsurface chlorophyll maximum (2–3 $\mu g\ l^{-1}$) which peaked above the thermocline in the region of station 3. At this time the standing stocks of total zooplankton in the frontal zone were 42 % higher than in the stratified water and 65 % higher than the mixed water (table 5). This peak in numbers was mainly due to the presence of the nauplii of *Pseudocalanus elongatus* which composed 22 % of the standing stock in this region. Benthic invertebrate larvae (lamellibranch veligers, polychaete larvae and echinoderm plutei) were also found in higher numbers in the frontal zone, contributing a further 20 %. It is interesting to note that although the majority of species were distributed right across the western Irish Sea during July 1980, some were more restricted in their distribution. All 18 species, stages and groups were present in the frontal zone but *Temora longicornis* and the nauplii of *Acartia clausi* were absent from the stratified waters. *Calanus finmarchicus* and *Membranipora membranacea* were absent from the mixed isothermal region.

TABLE 5. VARIATIONS IN MEAN ABUNDANCE (NUMBER PER SQUARE METRE AND NUMBER PER CUBIC METRE) AND FREQUENCY OF OCCURRENCE (PERCENTAGE OF SAMPLES) OF THE MOST ABUNDANT ZOOPLANKTON TAXA IN THE STRATIFIED, FRONTAL AND MIXED REGIONS OF THE WESTERN IRISH SEA DURING JULY 1980

taxonomic group	item	stratified	frontal	mixed
Acartia clausi (A)	number per square metre	10583 (22.6)	13965 (17.3)	1715 (0.6)
	number per cubic metre	126	255	27
	percentage frequency	100	100	100
Pseudocalanus elongatus (N)	number per square metre	3666 (7.8)	17765 (22.1)	4417 (15.6)
	number per cubic metre	43	267	73
	percentage frequency	100	100	100
Pseudocalanus elongatus (A)	number per square metre	11346 (24.2)	10020 (12.4)	2990 (10.5)
	number per cubic metre	132	148	47
	percentage frequency	100	100	100
Oithona similis	number per square metre	9008 (19.2)	10131 (12.6)	140 (0.5)
	number per cubic metre	102	152	2
	percentage frequency	100	100	50
lamellibranch veligers	number per square metre	3215 (6.8)	7199 (8.9)	2210 (7.8)
	number per cubic metre	39	107	36
	percentage frequency	100	100	100
Acartia clausi (C)	number per square metre	2558 (5.4)	2536 (3.1)	6452 (22.8)
	number per cubic metre	34	34	107
	percentage frequency	66	66	100
polychaete larvae	number per square metre	1042 (2.2)	3959 (4.9)	1075 (3.8)
	number per cubic metre	12	59	19
	percentage frequency	66	100	100
Oikopleura dioicea	number per square metre	1381 (2.9)	1602 (1.9)	2852 (10.1)
	number per cubic metre	17	21	47
	percentage frequency	100	66	100
echinoderm plutei	number per square metre	145 (0.3)	5025 (6.2)	442 (1.5)
	number per cubic metre	1	69	4
	percentage frequency	33	100	100
Pseudocalanus elongatus (C)	number per square metre	636 (1.3)	1956 (2.4)	2507 (8.8)
	number per cubic metre	7	29	37
	percentage frequency	66	66	100
Acartia clausi (N)	number per square metre	—	2157 (2.6)	1857 (6.5)
	number per cubic metre	—	27	32
	percentage frequency	—	33	100
Centropages hamatus	number per square metre	759 (1.6)	1430 (1.7)	442 (1.5)
	number per cubic metre	9	22	7
	percentage frequency	100	33	100
Calanus finmarchicus	number per square metre	1958 (4.1)	476 (0.6)	—
	number per cubic metre	22	7	—
	percentage frequency	100	33	—
Temora longicornis (C)	number per square metre	—	526 (0.6)	592 (2.0)
	number per cubic metre	—	6	9
	percentage frequency	—	33	100
gastropod veligers	number per square metre	303 (0.6)	523 (0.6)	277 (0.9)
	number per cubic metre	6	7	4
	percentage frequency	66	66	100
Temora longicornis (N)	number per square metre	—	860 (1.0)	137 (0.4)
	number per cubic metre	—	12	2
	percentage frequency	—	100	50
Membranipora membranacea	number per square metre	145 (0.3)	120 (0.1)	—
	number per cubic metre	1	2	—
	percentage frequency	33	33	—
Temora longicornis (A)	number per square metre	—	120 (0.1)	137 (0.4)
	number per cubic metre	—	2	2
	percentage frequency	—	33	50

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TABLE 5 (*cont.*)

taxonomic group	item	stratified	frontal	mixed
total copepods	number per square metre	**40514 (86.6)**	**61944 (77.0)**	**21386 (75.7)**
	number per cubic metre	**475**	**961**	**345**
total adults	number per square metre	**33654 (71.9)**	**24105 (30.0)**	**4842 (17.1)**
	number per cubic metre	**391**	**405**	**76**
total copepodites	number per square metre	**3194 (6.8)**	**5018 (6.2)**	**9551 (33.8)**
	number per cubic metre	**41**	**69**	**153**
total nauplii	number per square metre	**3666 (7.8)**	**20450 (25.4)**	**6411 (22.7)**
	number per cubic metre	**43**	**306**	**107**
total 'others'	number per square metre	**6231 (13.3)**	**18428 (22.9)**	**6856 (24.2)**
	number per cubic metre	**76**	**265**	**110**
grand total	number per square metre	**46745**	**80372**	**28242**
	number per cubic metre	**551**	**1226**	**455**

Taxa are listed in overall mean abundance with copepods subdivided into adults (A), copepodites (C) and nauplii (N) where they occurred and larvae being the sum of all species present. Values in parentheses after number per square metre values are percentages of total zooplankton.

On 28 May 1981 a similar situation occurred in the frontal zone where there was a localized surface concentration of chlorophyll (3.5 μg l^{-1}) associated with a strong (over 9 μg l^{-1}) subsurface chlorophyll maximum containing high concentrations of zooplankton (Scrope-Howe & Jones 1985). It can be seen from Table 6 that zooplankton densities were 52% higher in the frontal zone than in the stratified water and 68% higher than in the mixed water. Again this high concentration was largely due to the presence of the nauplii of a single copepod species, *Acartia clausi* making up over 35% of the total zooplankton in the region. Other zooplankters that contributed to the frontal peak were the adults of *Acartia clausi*, the copepodites of *Acartia clausi*, *Temora longicornis* and *Pseudocalanus elongatus*, the ectoproct larvae *Membranipora membranacea* and the appendicularian *Oikopleura dioica*. Unlike July 1980, benthic invertebrate larvae were more concentrated in the stratified region rather than in the frontal zone. Species with restricted distributions included *Evadne nordmanni* and *Temora longicornis* adults which were not found in the mixed region and *Centropages hamatus* and lamellibranch veligers which were absent from the frontal zone. *Microcalanus pusillus* was confined to the stratified region and gastropod veligers and polychaete larvae were only found in the mixed isothermal water.

During the other eight cruises that coincided with periods of stratification, the frontal zone merely formed a transition between different levels of total zooplankton in the stratified and mixed régimes. However, there were occasions, at different times of the year, when the frontal zone appeared to influence individual species distributions. Although contributing only a small proportion to the total zooplankton on each occasion, species or groups such as *Temora longicornis*, *Oikopleura dioica*, *Evadne nordmanni*, echinoderm plutei, polychaete larvae and gastropod veligers were found in higher numbers within the frontal zone than on either side. There were also occasions when individual species or groups were found in highest numbers associated with the immediate stratified side of the frontal zone. Such zooplankters included *Oithona similis*, *Acartia clausi*, *Pseudocalanus elongatus*, *Microcalanus pusillus*, *Evadne nordmanni* and the benthic invertebrate larvae of gastropods and lamellibranchs.

Localized breeding of the chaetognath *Sagitta elegans* within the frontal zone was reported by Leigh (1977) but occurred only once during April 1980 in the present studies. Generally this species occurred in highest densities within the stratified region during the earlier part of

Table 6. Variations in mean abundance (number per square metre and number per cubic metre) and frequency of occurrence (percentage of samples) of the most abundant zooplankton taxa in the stratified, frontal and mixed regions of the western Irish Sea during May 1981

Acartia clausi (N)	number per square metre	4170 (3.9)	77070 (35.7)	17130 (24.5)
	number per cubic metre	42	1101	303
	percentage frequency	100	100	100
Acartia clausi (C)	number per square metre	8983 (8.6)	26390 (12.2)	12130 (17.3)
	number per cubic metre	91	377	218
	percentage frequency	100	100	100
Pseudocalanus elongatus (C)	number per square metre	9711 (9.3)	26390 (12.2)	5075 (7.2)
	number per cubic metre	97	377	103
	percentage frequency	100	100	100
Pseudocalanus elongatus (A)	number per square metre	16150 (15.4)	13230 (6.1)	4125 (5.9)
	number per cubic metre	161	189	76
	percentage frequency	100	100	100
Oithona similis	number per square metre	11480 (10.9)	13160 (6.1)	5325 (7.6)
	number per cubic metre	114	188	93
	percentage frequency	100	100	100
Pseudocalanus elongatus (N)	number per square metre	4495 (6.2)	10990 (5.1)	9450 (13.5)
	number per cubic metre	67	157	175
	percentage frequency	100	100	100
Acartia clausi (A)	number per square metre	7306 (6.9)	13230 (6.1)	4700 (6.7)
	number per cubic metre	73	189	83
	percentage frequency	100	100	100
Temora longicornis (C)	number per square metre	7128 (6.8)	15400 (7.1)	2700 (3.8)
	number per cubic metre	71	220	45
	percentage frequency	100	100	50
Evadne nordmanni	number per square metre	15550 (14.8)	4410 (2.0)	—
	number per cubic metre	158	63	—
	percentage frequency	100	100	—
Temora longicornis (N)	number per square metre	3930 (3.7)	2170 (1.0)	3350 (4.8)
	number per cubic metre	40	31	61
	percentage frequency	75	100	100
Oikopleura dioicea	number per square metre	1668 (1.6)	6580 (3.0)	900 (1.2)
	number per cubic metre	18	94	15
	percentage frequency	50	100	50
Calanus finmarchicus	number per square metre	2397 (2.3)	2170 (1.0)	975 (1.4)
	number per cubic metre	24	31	18
	percentage frequency	100	100	100
Temora longicornis (A)	number per square metre	3234 (3.1)	2170 (1.0)	—
	number per cubic metre	32	31	—
	percentage frequency	75	100	—
Microcalanus pusillus	number per square metre	4150 (3.9)	—	—
	number per cubic metre	44	—	—
	percentage frequency	100	—	—
Membranipora membranacea	number per square metre	970 (0.9)	2170 (1.0)	250 (0.3)
	number per cubic metre	9	31	5
	percentage frequency	50	100	50
lamellibranch veligers	number per square metre	459 (0.4)	—	2625 (3.7)
	number per cubic metre	4	—	48
	percentage frequency	50	—	100
Centropages hamatus	number per square metre	750 (0.7)	—	450 (0.6)
	number per cubic metre	7	—	7
	percentage frequency	25	—	50
gastropod veligers	number per square metre	—	—	450 (0.6)
	number per cubic metre	—	—	7
	percentage frequency	—	—	50
polychaete larvae	number per square metre	—	—	250 (0.3)
	number per cubic metre	—	—	5
	percentage frequency	—	—	50

TABLE 6 (*cont.*)

total copepods	number per square metre	**85884 (82.1)**	**202370 (93.9)**	**65410 (93.6)**
	number per cubic metre	**863**	**2891**	**1182**
total adults	number per square metre	**45467 (43.5)**	**43960 (20.4)**	**15575 (22.2)**
	number per cubic metre	**455**	**628**	**277**
total copepodites	number per square metre	**25882 (24.7)**	**68180 (31.6)**	**19905 (28.4)**
	number per cubic metre	**259**	**974**	**366**
total nauplii	number per square metre	**14595 (13.9)**	**90230 (41.8)**	**29930 (42.8)**
	number per cubic metre	**149**	**1289**	**539**
total 'others'	number per square metre	**18647 (17.8)**	**13160 (6.1)**	**4475 (6.4)**
	number per cubic metre	**189**	**188**	**80**
grand total	number per square metre	**104531**	**215530**	**69885**
	number per cubic metre	**1052**	**3079**	**1262**

Taxa are listed in overall mean abundance with copepods subdivided into adults (A), copepodites (C) and nauplii (N) where they occurred and larvae being the sum of all species present. Values in parentheses after number per square metre values are percentages of total zooplankton.

the year until June when numbers started to increase in the mixed region, following the pattern of total zooplankton distributions shown in figure 1. Fish eggs, whenever they occurred, were always closely associated with the frontal zone.

4. DISCUSSION

Comparison of present data with previous studies in the Irish Sea suggest that there has been no major change in the species composition of the zooplankton since the first tow-net surveys were made in 1906 (Scott 1907). The copepods *Pseudocalanus elongatus*, *Calanus finmarchicus*, *Acartia clausi*, *Oithona similis*, *Temora longicornis* and *Centropages hamatus* remain the dominant zooplankton species throughout the western Irish Sea. Similarly, *Sagitta elegans* was the only chaetognath found in the survey area. In recent years this species has extended its former range eastwards into Liverpool Bay where the previously dominant *Sagitta setosa* has declined.

Although the overall composition of Irish Sea zooplankton has not changed substantially during the last 80 years, the abundance of individual species varies considerably on a year to year basis. Analysis of ten years' data on copepod abundance maxima in the Irish Sea by Cushing (1975) has demonstrated that some copepod species reveal coefficients of variation as high as 80%. *Temora longicornis*, a species usually ranking low among the six most abundant copepods (Herdman *et al.* 1908–21; this paper), was found to be the most prominent species in the western Irish Sea during 1976, accounting for about 50% of the copepod population (Leigh 1977). During 1980 and 1981 *Calanus finmarchicus* exhibited a highly significant year to year variation in numbers. Williamson (1952) found this copepod to be more abundant in the stratified region of the western Irish Sea and comparatively rare in the mixed isothermal water to the west and north of Anglesey. Williamson considered it unlikely that the *Calanus finmarchicus* population was endemic and proposed the seasonal replenishment of a non-breeding stock into this area by the southward-flowing current originating to the north of Ireland, where the copepod is abundant at all times of the year. This geostrophic current travels down the west side of the North Channel during spring and early summer, after which it disappears when the main northward flow from St George's Channel passes closer to the Isle of Man (Tait 1951; Hunter 1972; Slinn 1974). Our 1980 data agrees with Williamson (1952) in that only late stage copepodites and adult *Calanus finmarchicus* were frequently encountered indicating a non-breeding population in the western Irish Sea. In addition the seasonal distribution of *Calanus finmarchicus* (maxima from April to June followed by a large decrease in numbers) supports the seasonal nature of the southward current. *Calanus finmarchicus* was mostly confined to the deeper, cooler water of the stratified region (except during June 1980 when it was found at all depths), occurring only in low concentrations in the isothermal region when introduced by upwelling of water from below the thermocline to the surface on the mixed side of the front. During 1981 the *Calanus finmarchicus* population was found to be less than 10% of that observed in 1980. Substantial variations in population densities of this species have occurred previously. Although timing of abundance maxima and actual concentrations of *Calanus finmarchicus* in the Irish Sea fluctuate from year to year, much lower densities than in other years occurred during 1909 and 1919 (Herdman *et al.* 1908–21). Marked fluctuations in abundance for *Calanus finmarchicus* have also been reported by Burd & Cushing (1962) for the southern North Sea during the 1950s when this copepod increased dramatically, affecting the growth and recruitment of the North Sea herring stocks. The decline in Irish Sea *Calanus finmarchicus* observed during 1981 may be correlated with a decrease in the southward current entering the western Irish Sea through the North Channel as variations in the flow of this current have been reported previously (Barnes & Goodley 1961; Harvey & Buchan 1967).

The low abundance of *Calanus finmarchicus* was directly responsible for the dramatic decrease of zooplankton biomass in the survey area during 1981 (figure 2). The importance of this single species as a major contributor to total zooplankton biomass has also been shown for the northern North Sea by Fransz & van Arkel (1980). These authors found that the adults and late stage copepodites of *Calanus finmarchicus* formed up to 90% of the total zooplankton biomass during the Fladen Ground Experiment (FLEX) in 1976. These results compare very favourably with our average figure of 93% in the western Irish Sea.

The overall seasonal pattern of zooplankton observed during the present survey shows a similar trend to the 1948–76 I.M.E.R. continuous plankton records for the Irish Sea (Colebrook 1979). However, the distinct physical regions of the western Irish Sea exhibit fine scale differences in the amplitude and timing of the seasonal zooplankton cycle. The deeper, more stable stratified region to the west of the frontal boundary (Simpson 1971) contained the highest zooplankton production, which occurred, in the main, above the thermocline, with an abundance maxima (in 1980) already present early in the year during April (figure 1*a*). Initial increases in phytoplankton stocks owing to the presence of short-lived stratification in the early spring, as observed in the Celtic Sea by Pingree *et al.* (1976), can lead to significant increases in copepod nauplii occurring before the main phytoplankton bloom (Harvey 1950; Krause & Radach 1980).

The shallower, mixed isothermal region is subject to strong tidal currents and is also situated within the main northward current flowing through the Irish Sea (Khan & Williamson 1970). This region supported a lower density of total zooplankton during 1980–1 and the maxima occurred at least one month later than in the stratified water; abundances and seasonal patterns in the mixed water were similar during both years (figure 1*c*).

There is a substantial amount of literature indicating that frontal zones may support increased zooplankton populations (Griffiths 1965; Longhurst 1967; Dufour & Stretta 1973; Pingree *et al.* 1974; Sick *et al.* 1978; Floodgate *et al.* 1981; Aiken 1981). However, mean monthly zooplankton densities for 1980 and 1981 taken for the stratified, frontal and mixed regions of the western Irish Sea (figure 1) do not reflect any substantial increase in zooplankton associated with the front. Zooplankton maxima were recorded at the front only twice during the present survey, in July 1980 and May 1981 (tables 5 and 6). The occurrence of these occasional high zooplankton concentrations at the western Irish Sea frontal boundary seem most likely to be linked with localized high phytoplankton production in the same area, similar to those reported by Herman *et al.* (1981). As the copepod population within the frontal zone contained significantly higher numbers of nauplii of *Acartia clausi* and *Pseudocalanus elongatus* than in adjacent waters on these occasions it is likely that these maxima are due to increased zooplankton production rather than mechanical aggregation at the front. Lower zooplankton densities at the western Irish Sea front have been observed by Williamson (1952, 1956*b*) and Leigh (1977), and also at other frontal zones (Angel 1968; Sameoto 1982; Parsons *et al.* 1983).

Fish eggs, and to some extent fish larvae and post-larvae, were always found in higher numbers in the frontal zone (personal observations). Similar observations for fish, eggs and larval concentrations around frontal boundaries have been reported elsewhere (King & Hida 1957; Angel 1968; Dufour & Stretta 1973; Laurs *et al.* 1977) and may have wider implications for commercial fish stocks (Mills & Fournier 1979; Shelton & Hutchins 1981; Iles & Sinclair 1982).

Little is known about euphausid populations in the Irish Sea (Lindley 1982), and although this group of omnivorous consumers was beyond the scope of present sampling procedures, recent preliminary work in the western Irish Sea with an Isaac Kidd Mid-water Trawl and Simrad echo sounder indicates a considerable population of *Meganyctiphanes norvegica* (M. Sars) exists undergoing vertical migration into the frontal zone (unpublished observations). Sameoto (1982) has shown that *Meganyctiphanes norvegica* may consume 33% of the copepod production per year in the waters off Nova Scotia and in the northeastern North Sea this species accounted for 59% of the total zooplankton biomass (Lindley 1982). Further studies on the abundance and distribution of this zooplankton group are required to determine its impact before the full biological significance of the western Irish Sea front can be assessed.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES