

Flexible diel vertical migration behaviour of zooplankton in the Irish Sea

Xabier Irigoien^{1,*}, David V. P. Conway², Roger P. Harris³

¹AZTI, Herrera Kaia Portualdea, Pasaia 20110, Guipúzcoa, Spain

²Marine Biological Association, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

³Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

ABSTRACT: The diel vertical migration (DVM) of the whole plankton community was investigated in the central and coastal Irish Sea. Generally, more than 60% of the plankton did not perform significant DVM. A correlation analysis of the weighted mean depths of different organisms and their potential predators suggested relationships between 2 groups: *Oithona* spp., copepod nauplii and fish larvae, and *Calanus* spp., *Pseudocalanus elongatus* and chaetognaths (*Sagitta* spp.). Organisms showing significant DVM were chaetognaths (*Sagitta* spp.), *Calanus* spp. and *P. elongatus*. *Calanus* spp. showed clear ontogenic variations in DVM and, along with *P. elongatus*, demonstrated great flexibility in both the amplitude and direction of migration. *P. elongatus* did not migrate in the coastal area and *Calanus* spp. showed a clear reverse migration. The direction of migration appeared to be related to the vertical position of the chaetognaths in the water column during the day.

KEY WORDS: Diel vertical migration · *Calanus* spp. · *Pseudocalanus* spp. · *Oithona* spp. · Chaetognaths · Fish larvae

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INTRODUCTION

Changes in species composition are the consequence of species-specific behavioural changes, as differences in behaviour result in differences in the main demographic parameters, birth and mortality (Ohman 1990), and consequently in the success or failure of the species in a changing ecosystem. For example, a very well adapted but rigid strategy to avoid one specific predator can become a disadvantage if the predator is replaced as the main cause of mortality in the system. One particular predation avoidance behaviour is characteristic of plankton, diel vertical migration (DVM) (Lampert 1993). While it is now generally accepted that DVM is a predation avoidance mechanism (Lampert 1993), there are contradictory cases, such as species that do not appear to migrate (Hays et al. 1997) or lack of relation with predator abundance (Huntley & Brooks 1982, Dale & Kaartvedt 2000). However, this type of fixed DVM behaviour (not related to changes in predators) has been attributed to relatively constant mortality risks (Neill 1992).

Studies on DVM behaviour often only include 1 or 2 species of migrating organisms (e.g. Ohman 1990, Hays et al. 1995), and when there is information on a larger number of species these are generally copepods and/or euphausiids (Moraitou-Apostolopoulou 1971, Andersen et al. 2001). Although some authors have described day/night changes in vertical distribution for a range of components (e.g. Russell 1930, Roe 1974, Longhurst 1985, Ashjian et al. 1998), the number of taxonomically detailed studies investigating to what extent DVM is a generally adopted strategy in marine planktonic communities is limited. In this study, we examined the DVM of the whole mesozooplankton and macrozooplankton community (including meroplankton). We had 2 objectives: (1) to determine whether DVM is a general behaviour among planktonic organisms, and (2) to determine how flexible a behaviour DVM is, both in terms of differences between groups and species and in terms of differences within the same species under different conditions.

*Email: xirigoien@pas.azti.es

MATERIALS AND METHODS

Sampling was carried out during a series of cruises between April 1987 and April 1989 (Table 1) at 2 hydrographically contrasting sites in the Irish Sea: (1) a site of ~40 m depth close to the Irish coast with a weak seasonal thermal stratification, and (2) a more central Irish Sea site of ~120 m depth which becomes more strongly seasonally stratified during the summer. We took 2 zooplankton hauls at each site, on 1 night and 1 day (around midday and midnight), using a Longhurst Hardy Plankton Recorder (LHPR; Williams et al. 1983). The LHPR is a high-speed multiple serial sampler, and was fitted with a coarse (200 µm)-mesh net collecting system. Zooplankton are collected between 2 rolls of filtering gauze, which are advanced at intervals inside a cod-end box to give a series of consecutive samples.

The LHPR was towed at 3 to 4 knots on long oblique hauls, sampling from the surface to around 5 m off the bottom (see Table 1) at 1 min intervals, with individual sample-depth horizons of approximately 5 m, filtering approximately 10 m³ of water for each sample. The number of samples taken during each haul varied between 9 and 33 (Table 1), so that the distance covered during the hauls was around 0.5 to 2.0 n miles. A temperature probe on the control unit recorded the water temperature associated with each sample, and a flowmeter in the mouth of the net recorded the volume filtered. The individual samples were washed off the filtering gauzes and preserved in 4% borax-buffered formaldehyde, prepared with freshwater. Large organisms (euphausiids, de-

capods, coelenterates, chaetognaths, fish larvae and fish eggs) were counted using the whole sample, while species analysis and counts for smaller organisms such as copepods and meroplankton were carried out on subsamples. Conductivity, temperature, depth (CTD) profiles were obtained either by a Neil Brown or a Guildline CTD rosette array, and were taken before or after each LHPR haul, to provide additional environmental information. Weighted mean depth (WMD) of each taxonomic group was calculated as:

$$\text{WMD} = (\sum n_i d_i) / \sum n_i$$

where n_i is the abundance of organisms at depth d_i (Worthington 1931). The amplitude of migration was calculated as the difference between the WMD between day and night. A positive value indicated movement towards the surface during the night and a negative value reverse vertical migration.

All sampling strategies have problems, and ours had 3 main limitations: (1) Since the LHPR does not sample 5 m above the bottom, the weighted mean depth would be underestimated for species that accumulate near the bottom; this could particularly be the case for *Sagitta* spp. that have been observed at high concentrations near the bottom, especially during the daytime (Pearre 1973, Choe & Deibel 2000). (2) The accuracy of the amplitude estimation is related to the abundance of organisms, and therefore estimations for organisms present in low abundance must be treated with caution. Consequently, our data on migration amplitude concentrate on the most abundant organisms and their potential predators. Accordingly, different species of fish larvae were grouped

to obtain a more accurate estimation of the DVM (details of the diurnal and nocturnal vertical distribution of larval fish species are given in Conway et al. 1997). (3) The migration patterns of many migrators differ at different times during dark and light. Thus, a single set of night and day samples represented gives but a general indication of DVM. While it can detect many instances of DVM, it often underestimates ranges and sometimes fails to detect migration at all (Pearre 2000). Therefore, the ranges presented here must be viewed with caution.

RESULTS

Temperature and stratification

In the coastal area, sea surface temperature (SST) ranged from 6.7°C on 09 April 1987 to 8.34°C on 21 April

Table 1. Plankton sampling details. N: no. of samples

Date (d/mo/yr)	Time	Position	Bottom depth (m)	Sampling depth (m)	N
Coastal area					
09/04/87	12:38	53°53' N, 05°58' W	41	35	13
09/04/87	23:05	53°53' N, 05°57' W	41	39	13
11/04/88	23:29	53°47' N, 05°49' W	63	62	14
12/04/88	11:56	53°45' N, 05°50' W	56	50	12
21/04/89	12:29	53°50' N, 06°06' W	31	28	9
21/04/89	23:01	53°48' N, 06°05' W	31	28	11
Central Irish Sea					
19/02/87	01:45	53°50' N, 05°32' W	96	92	26
19/02/87	10:14	53°50' N, 05°32' W	97	95	26
11/04/87	12:10	53°50' N, 05°28' W	130	115	33
11/04/87	23:46	53°50' N, 05°28' W	130	120	32
14/04/88	12:09	53°51' N, 05°32' W	102	100	27
15/04/88	23:23	53°51' N, 05°32' W	108	106	24
25/05/88	00:13	53°49' N, 05°33' W	93	85	24
25/05/88	12:47	53°49' N, 05°31' W	105	100	20
22/04/89	23:09	53°45' N, 05°29' W	104	100	25
23/04/89	12:42	53°45' N, 05°30' W	107	99	22

1989. As expected for this strongly tidally mixed area, there was no stratification of the water column (Fig. 1). In the central Irish Sea, SST during the April cruises ranged from 7°C on 11 April 1987 to 8.8°C on 23 April 1989, with a maximum of 10.5°C on 25 May 1988. During the April cruises there was only weak stratification, but a clearly defined thermocline appeared at about 30 m during May 1988 (Fig. 1).

Community composition

The total abundance of zooplankton (ind. m⁻²) was generally 2 to 3 times higher in the central Irish Sea than in the coastal area, however, taking the depth difference into consideration, there were no systematic differences in density (ind. m⁻³) (Table 2). During the spring, *Paracalanus parvus*, *Pseudocalanus elongatus*, *Oithona* spp. and meroplanktonic groups, such

as cirripede nauplii, echinoderm larvae, decapod larvae and occasionally the cyphonautes larvae of bryozoans, generally dominated the population. During the summer cruise in 1988, *Acartia* spp. were also an important component of the population. The meroplankton contribution to the total population was generally no lower in the central Irish Sea than in the coastal area. During 1989 there seemed to be a shift in numerical dominance from *Paracalanus parvus* to *Pseudocalanus elongatus* and from *Calanus finmarchicus* to *C. helgolandicus*.

Diel vertical migration

There was a high variability in DVM, both between and within groups or species (Figs. 2 & 3, Table 3). In general, mean depth of 60 to 80% of the organisms did not vary by more than 10 m (2 sample-depth hori-

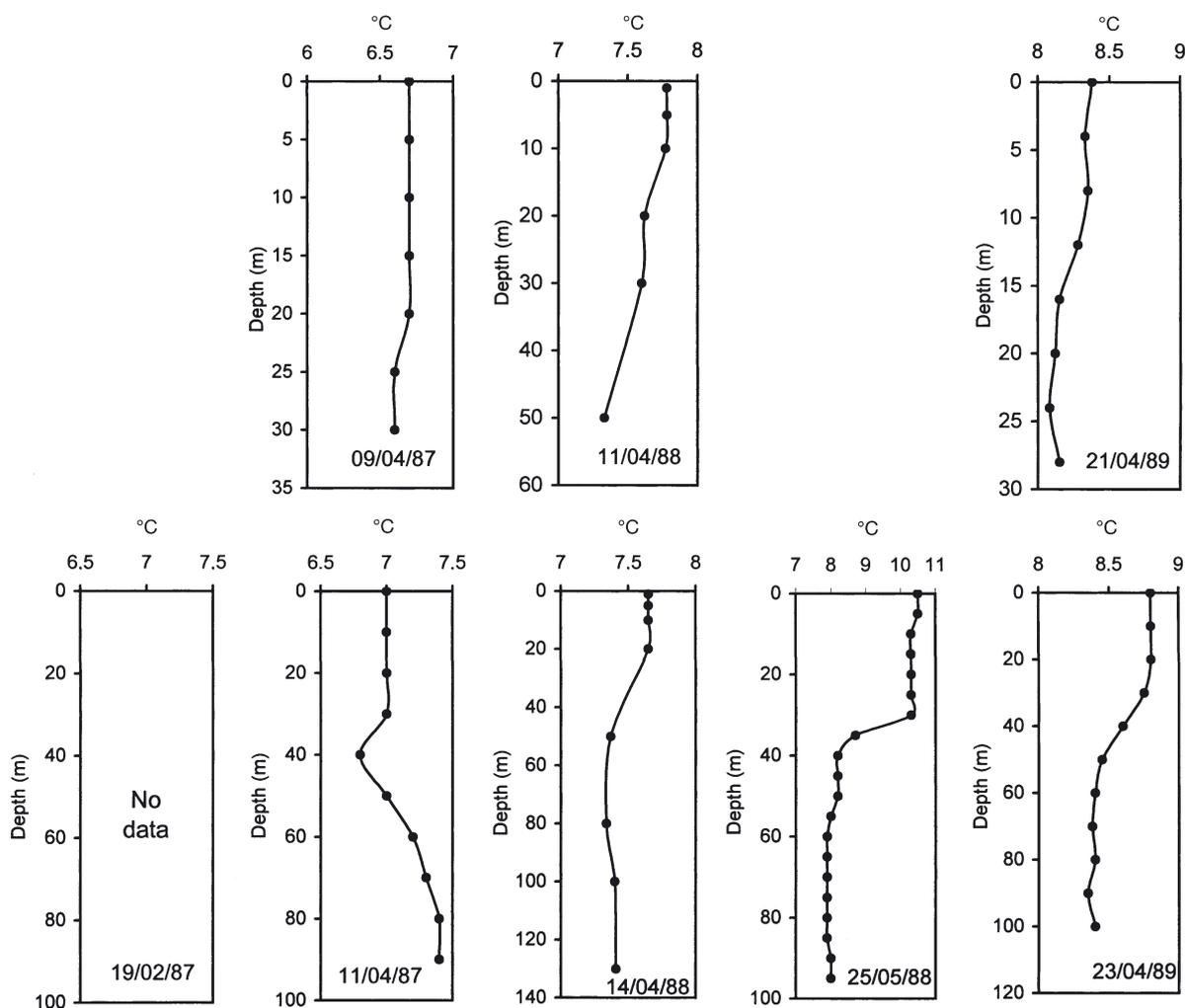


Fig. 1. Temperature profiles of stations sampled in the coastal (upper panels) and central (lower panels) Irish Sea. Dates are given as d/mo/yr

Table 2. Abundance (ind. m⁻²) of zooplankton species/groups sampled at coastal and central Irish Sea stations. Dates are given as d/mo/yr

	Coastal						Central									
	09/04/87		11/04/88		21/04/89		12/02/87		11/04/87		14/04/88		25/05/88		22/04/89	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
<i>Acartia</i> spp. I–IV	325	1087	415	467	302	292	20	13	540	1277	2338	2410	42922	115211	30	98
<i>Acartia</i> spp. V	123	326	397	382	239	189	–	20	309	619	926	1316	24713	14223	–	25
<i>Acartia</i> spp. VI	161	279	1117	965	821	1596	11	64	226	547	2809	3434	18996	35419	134	122
<i>Calanus</i> spp. CI	183	331	315	268	46	731	–	–	456	223	1789	1621	9810	1188	241	96
<i>Calanus</i> spp. CII	234	413	667	543	142	245	–	–	420	440	1022	1485	6918	1737	133	261
<i>Calanus</i> spp. CIII	111	126	629	122	387	367	3	–	364	682	408	607	7686	7363	204	212
<i>Calanus</i> spp. CIV	39	56	685	324	638	477	–	–	266	403	601	640	3393	10090	451	323
<i>C. finmarchicus</i> CV	19	10	483	547	133	59	1	2	176	85	238	310	296	8707	3	–
<i>C. finmarchicus</i> male	1	1	132	164	11	–	1	0	24	17	106	65	4	1353	38	45
<i>C. finmarchicus</i> female	6	5	136	379	71	–	50	33	122	43	243	478	97	7196	14	17
<i>C. helgolandicus</i> CV	2	1	209	350	717	285	–	–	31	11	74	129	12	466	369	227
<i>C. helgolandicus</i> male	0	–	60	51	116	91	–	–	1	5	41	64	1	971	78	48
<i>C. helgolandicus</i> female	13	1	42	158	205	73	12	23	54	25	58	164	7	1255	135	190
<i>Para/Pseudocalanus</i> spp. I–IV	7557	7613	2590	5055	6349	29448	659	809	11 320	17 338	11 941	8981	100 363	33 547	14 306	11 009
<i>Paracalanus parvus</i> V	7434	5347	562	1687	185	1534	1400	301	16364	10034	3830	7475	3146	968	41	25
<i>P. parvus</i> VI	3242	7100	1436	2352	381	1054	2635	636	16 264	12 976	11 888	28 986	10 061	17 284	43	101
<i>Pseudocalanus elongatus</i> V	978	949	2212	1604	5064	12292	44	125	2068	3405	1254	2595	17 185	12 489	2008	1305
<i>P. elongatus</i> VI	708	807	4643	2999	11520	13048	528	686	4547	3609	4776	4115	16 003	33 290	4285	3768
<i>Temora longicornis</i> CI–CIV	1704	1078	2060	2945	7866	21595	–	–	1480	2447	5687	3713	8090	9004	54	50
<i>T. longicornis</i> CV	431	146	1382	1791	4942	8489	–	–	161	344	578	522	4519	3235	–	–
<i>T. longicornis</i> CVI	329	174	3088	1147	16 306	13 668	–	–	390	223	235	996	1779	5839	72	240
<i>Centropages</i> spp.	–	63	1201	445	1454	1938	67	23	297	98	551	1074	4179	521	12	26
<i>Metridia lucens</i>	50	1	134	176	87	–	1	1	313	122	169	162	821	459	3	–
<i>Oithona</i> spp.	7144	5631	978	1589	1650	8215	4023	4002	24615	18 205	12 225	8496	63 606	41 299	7050	3906
Harpacticoid copepods	43	54	9	92	316	4583	27	143	25	30	80	254	–	143	277	406
Copepod nauplii	1107	1341	393	368	1260	7569	123	129	1050	1866	5749	2185	11294	3649	1328	687
Euphausiid calyptopis	21	75	485	247	–	1	–	–	27	83	807	341	132	197	101	9
<i>Evadne</i> spp.	–	29	398	1115	5888	1440	4	–	95	–	968	2346	22 605	3526	–	47
<i>Podon</i> spp.	–	15	–	44	218	107	–	13	12	47	54	95	285	–	–	–
<i>Appendicularia</i>	1942	3224	1088	1876	915	836	1273	1299	4024	6617	2254	1432	1684	276	2777	1202
Cirripede nauplii	8241	2983	3249	3765	579	2232	19	15	1116	4184	3893	11202	–	–	4659	7045
Cirripede cypris	–	8	93	32	510	2342	–	–	68	44	118	71	681	61	1452	1731
Echinoderm larvae	3378	9992	192	336	46	–	9653	7650	29 291	35 933	6640	6461	493	–	3455	2359
Polychaete larvae	75	154	189	270	112	523	1108	587	741	804	280	685	99	–	820	408
Gastropod larvae	150	27	–	14	66	–	24	4	95	–	12	–	–	–	145	136
Lamellibranch larvae	127	160	33	24	–	48	115	169	210	275	138	176	796	424	467	148
Decapod larvae	21	30	157	119	510	429	10	3	49	57	443	139	22	27	262	349
Cyphonautes larvae	436	813	114	240	211	333	1272	1086	18 502	23 287	1713	3419	1322	2261	5369	2800
<i>Limacina</i> spp.	14	197	151	168	–	–	61	–	92	134	150	192	–	–	–	–
<i>Tomopteris</i> spp.	2	0	1	4	–	–	8	31	15	42	23	28	0	53	10	10
Chaetognaths (<i>Sagitta</i> spp.)	22	31	131	61	14	16	204	114	160	52	109	75	342	528	43	32
Coelenterata	2	6	1	1	46	37	12	29	13	8	4	10	20	52	78	28
Fish larvae	11	6	24	69	44	107	1	1	10	15	31	18	2	3	5	8
Others	248	289	386	359	337	158	18	140	1074	1228	5585	4571	2507	3751	720	1186
Total	46632	50979	32668	35714	70704	136445	23385	18152	137476	147886	92836	113539	386892	378065	51672	40684

zons) between day and night, and they were therefore considered to perform little or no DVM (Fig. 4). Only on 2 occasions did a significant proportion of the population perform DVM: on 25 May 1988 in the

central Irish Sea, when the thermocline was well established, and on 22 April 1989, when the population was dominated by *Pseudocalanus elongatus* (Fig. 4, Table 2).

None of the most abundant meroplanktonic larvae (cirripede nauplii and echinoderm larvae) showed marked DVM, whereas holoplanktonic organisms displayed different patterns. Copepods exhibited a range of DVM behaviour: some, such as *Acartia* spp., *Temora longicornis*, *Oithona* spp. and copepod nauplii showed little or no DVM; however, as mentioned earlier, our methodology would underestimate migration amplitude if midnight sinking (Ashjian et al. 1998) or twilight migration (e.g. as sometimes reported for *Temora* sp.: Pearre 2000) occurs. *Pseudocalanus elongatus* and *Calanus* spp. showed a range of DVM amplitudes, including very clear reverse migration (moving deeper during the night) for *Calanus* spp. in the coastal area.

Appendicularians did not usually undergo DVM, except in the central Irish Sea during May 1988. At this time the thermocline was well established and a strong reverse appendicularian DVM was recorded. Other organisms that moved deeper during the night at the stratified station were the copepods *Paracalanus parvus*, *Metridia lucens* and *Oithona* spp., and cypho-

nautes larvae (Table 3). However, an abundant holoplanktonic non-copepod genus in the May 1988 samples, the cladocerans *Evadne* spp., showed no DVM behaviour, nor did the most abundant organisms at that time, copepods of the genus *Acartia*.

Among the predators, there was a clear-cut difference between chaetognaths (*Sagitta* spp.), which performed extensive DVM, and fish larvae that did not seem to migrate vertically (Fig. 3).

Calanus spp.

We paid particular attention to *Calanus* spp. for 4 reasons: (1) in the initial analysis *Calanus* spp. shows a very high variability in DVM, including a clear reverse DVM; (2) the large size of this copepod allows easy identification of the stages and therefore an ontogenetic analysis of its DVM behaviour; (3) the simultaneous presence of *C. finmarchicus* and *C. helgolandicus* allowed detailed comparison between closely

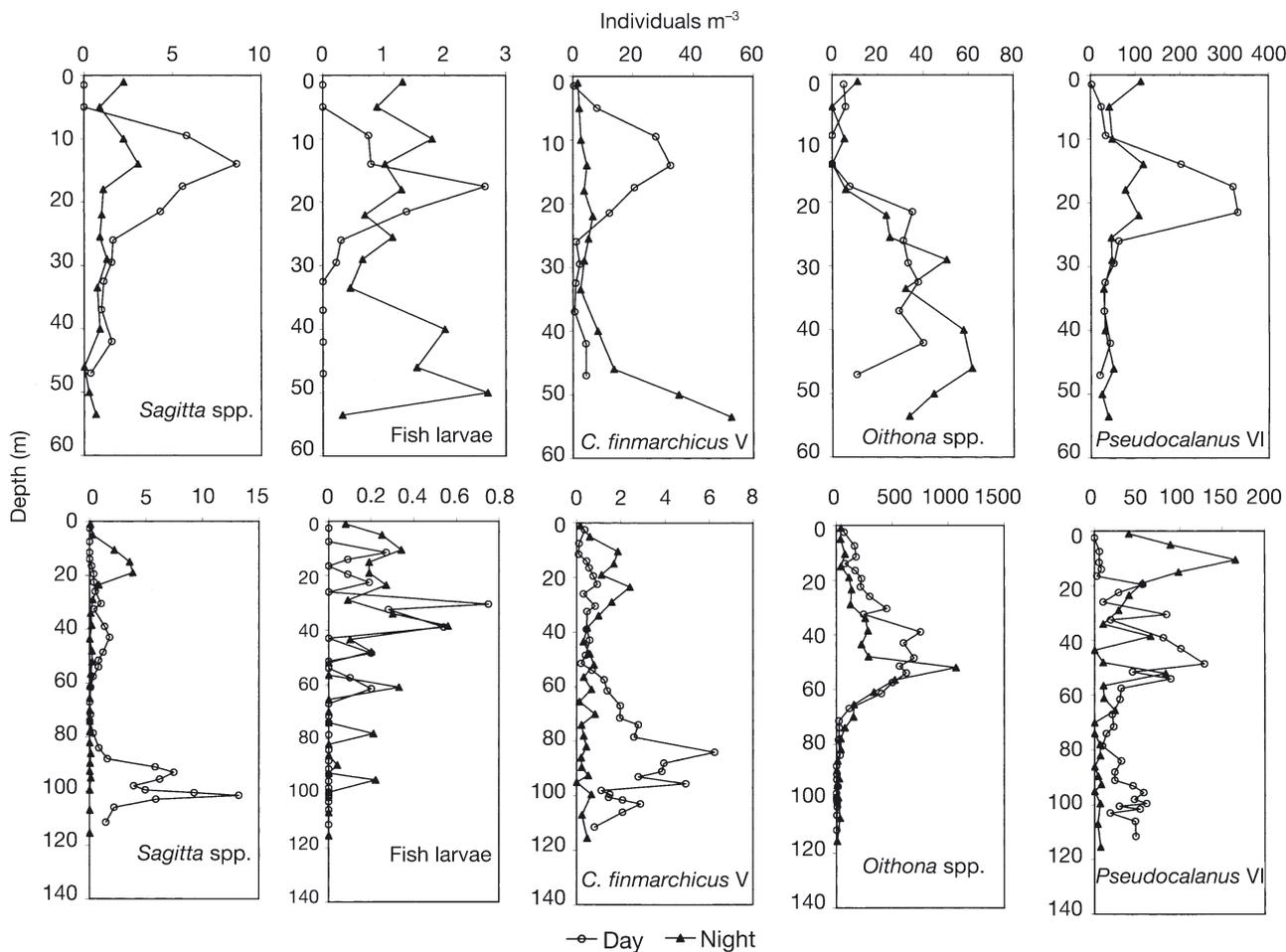


Fig. 2. Examples of vertical distribution of some of main zooplankton groups. Upper graphs = coastal (11 April 1988) and lower graphs = central Irish Sea (11 April 1987). C. = *Calanus*; *Pseudocalanus* = *P. elongatus*

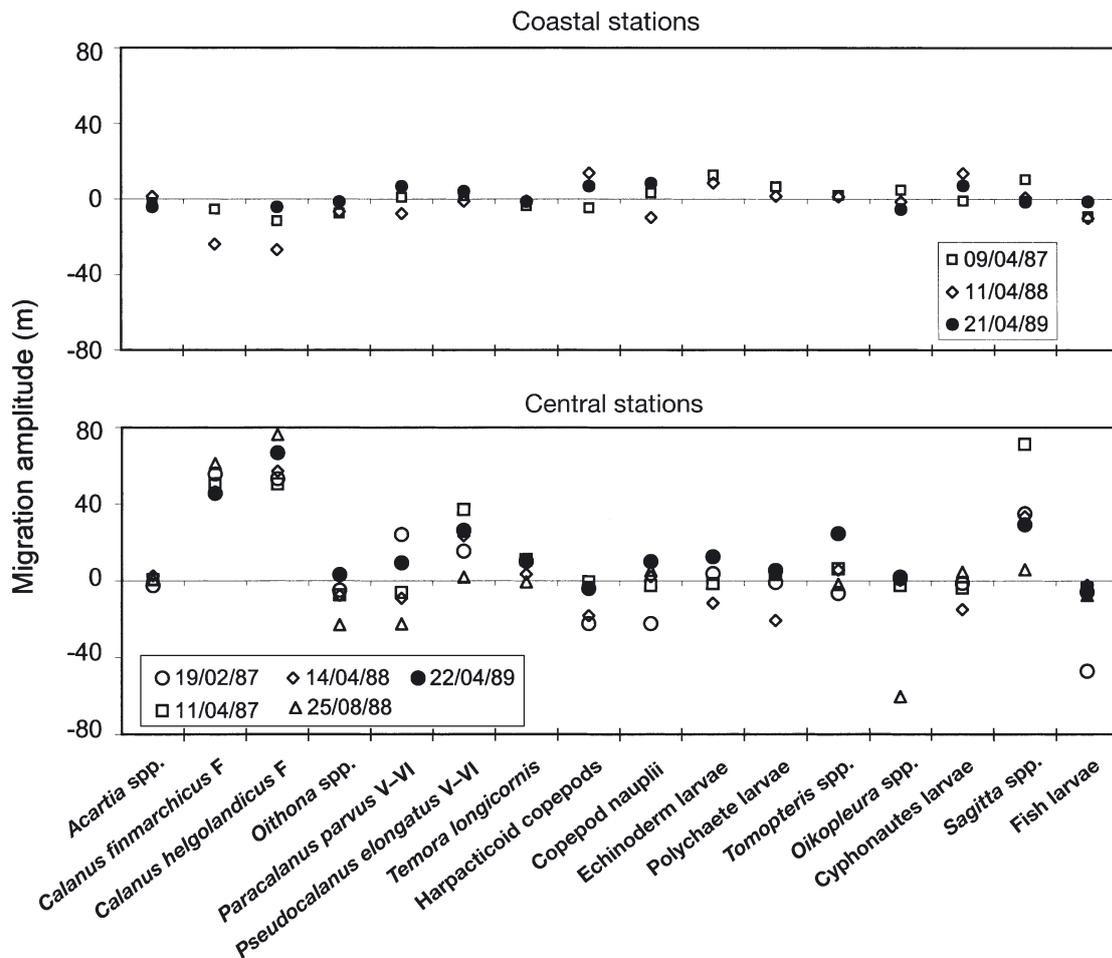


Fig. 3. Examples of amplitude of migration of main components of zooplankton at coastal and central Irish Sea stations. Negative values indicate reverse migration. F: female; V–VI: Copepodite stages V–VI

related species; (4) previous investigations on the vertical distribution of *C. finmarchicus* and *C. helgolandicus* had been carried out in the adjoining Celtic Sea (Williams 1985).

The DVM behaviour of *Calanus* spp. differed markedly between the coastal and central areas of the Irish Sea. In the central region, *C. finmarchicus* and *C. helgolandicus* performed normal DVM (migrating to the surface at night), whereas at the coastal station both species performed reverse vertical migration (moving deeper at night) (Fig. 5). Both normal and reverse DVM displayed a clear ontogenetic trend, with the amplitude of DVM increasing with the increasing copepodite stage until Stage V (Fig. 5). There were no significant differences in DVM amplitude (Fig. 5) or vertical position (WMD) between *C. finmarchicus* and *C. helgolandicus*, even during the period of stratification (see example for Stage V in Fig. 6). This contrasts with the behaviour recorded by Williams (1985) in the Celtic Sea.

Relations between prey WMD and DVM and predator abundance and behaviour

Correlation coefficients between the WMD of different organisms were used to analyse possible predator–prey relationships (Table 4). Cells of the large diatom *Coscinodiscus* spp., also collected by the net, were included in the analysis as a passive tracer. Although *Coscinodiscus* spp. have been observed to undergo reverse migrations (Hardy & Gunther 1935), the amplitude of such migrations is smaller than that of the zooplankton. The highest correlation for chaetognath WMD was with the WMD of *Pseudocalanus elongatus* ($r = 0.79$), followed by various stages of *Calanus* spp. ($r = 0.51$ to 0.78) (Fig. 7). For fish larvae, the highest correlation was with *Oithona* spp. ($r = 0.80$) and copepod nauplii ($r = 0.76$) (Fig. 7).

The amplitude of the DVM of 3 of the most actively migrating copepods (*Calanus finmarchicus*, *C. hel-*

golandicus and *Pseudocalanus elongatus*) was compared with the abundance and position in the water column of the chaetognaths. For all 3 copepods the only significant relationship was with the WMD of chaetognaths during the day (Fig. 8). The extreme chaetognath WMD of 90 m influenced the significance

of the obtained relationships; if this is considered an outlier, then the relationship between *P. elongatus* DVM and *Sagitta* spp. WMD becomes non-significant, whereas the relation between *C. helgolandicus* V DVM and *Sagitta* spp. WMD becomes significant ($r^2 = 0.59$, $p < 0.05$).

Table 3. Daytime weighted mean depth (WMD, m) and amplitude of diel vertical migration (DVM, m) of main zooplankton groups at coastal and central Irish Sea stations. Negative DVM values indicate reverse migration (deeper at nighttime than during the day)

	Coastal						Central									
	09/04/87		11/04/88		21/04/89		12/02/87		11/04/87		14/04/88		25/05/88		22/04/89	
	WMD	DVM														
<i>Acartia</i> spp. I–IV	7.7	-2.9	10.7	6.2	4.2	-11.3	12.5	-24.9	19.3	1.1	15.2	2.5	10.3	-1.5	11.0	-7.4
<i>Acartia</i> spp. V	5.2	-5.6	7.6	-0.7	12.1	9.0	-	-	16.8	-0.9	13.9	2.3	12.1	0.8	-	-
<i>Acartia</i> spp. VI	12.6	3.0	8.7	-0.5	12.3	-4.1	45.4	14.4	17.7	0.8	12.5	2.3	21.0	8.1	44.2	21.2
<i>Calanus</i> spp. CI	13	2.2	11.9	-4.6	21.5	15.7	-	-	27.4	-0.4	21.1	4.8	19.6	11.1	20.8	11.6
<i>Calanus</i> spp. CII	13.8	0.3	11.7	-4.9	12.1	-2.1	-	-	29.3	1.3	24.8	8.9	32.3	20.9	21.0	11.5
<i>Calanus</i> spp. CIII	11.2	0.2	11.4	-14.5	8.8	-1.3	94.2	-	31.4	-2.4	44.1	16.4	42.2	31.0	31.5	18.9
<i>Calanus</i> spp. CIV	9.8	-7.9	14.4	-10.2	8.3	-3.4	-	-	63.0	31.3	63.5	24.9	55.2	40.3	65.4	54.8
<i>C. finmarchicus</i> CV	13.5	-6.8	16.6	-26.8	8.8	-8.1	51.7	16.7	80.1	38.4	81.7	39.3	65.3	43.3	49.7	-
<i>C. finmarchicus</i> male	12.3	-0.9	19.9	-24.1	11.0	-	77.3	63.6	85.8	5.2	79.0	18.6	75.5	7.2	75.7	72.7
<i>C. finmarchicus</i> female	15.3	-5.4	19.8	-23.9	6.5	-	75.6	55.6	83.4	50.5	79.3	46.5	82.4	61.2	59.5	45.4
<i>C. helgolandicus</i> CV	14.1	3.3	15.1	-23.3	6.2	-5.3	-	-	87.8	50.3	83.5	51.8	43.6	22.0	73.4	62.3
<i>C. helgolandicus</i> male	33.7	-	18.1	-28.8	7.2	-3.7	-	-	83.3	22.0	88.1	37.9	95.6	51.6	77.2	57.0
<i>C. helgolandicus</i> female	6	-11.7	15.2	-26.8	6.8	-4.2	86.7	53.1	89.2	50.4	86.0	57.1	95.0	76.4	79.1	66.8
<i>Paracalanus parvus</i> V	14.9	1.1	33.5	-4.0	20.2	11.8	51.9	28.5	56.8	-7.1	57.5	-12.9	26.8	-50.3	13.1	12.1
<i>P. parvus</i> VI	17	1.5	32.1	-10.1	15.2	2.3	53.6	21.9	59.6	-5.1	62.7	-7.8	49.6	-15.7	18.0	9.9
<i>Pseudocalanus elongatus</i> V	13.9	2.3	17.1	-2.1	15.8	5.3	33.8	19.2	46.1	29.5	46.6	21.4	32.5	6.9	28.8	15.3
<i>P. elongatus</i> VI	15	1.1	20.8	-0.7	14.9	3.2	49.4	12.4	64.6	37.5	75.1	17.5	36.1	0.8	52.7	31.6
<i>Temora longicornis</i> CI–CIV	14.2	-4.6	-	-	21.0	4.4	-	-	27.5	15.3	17.1	3.9	14.1	-0.4	17.0	16.0
<i>T. longicornis</i> CV	15.9	3.6	19.2	-0.6	18.9	-1.2	-	-	27.2	10.4	16.4	-0.1	16.4	4.0	20.0	10.1
<i>T. longicornis</i> CVI	14.3	-3.3	18.8	-5.5	15.0	-6.8	-	-	22.2	10.9	17.8	3.6	26.4	1.4	23.8	11.1
<i>Centropages</i> spp.	-	-	9.0	-5.1	12.5	-5.1	28.8	-33.3	38.0	-5.0	14.6	2.7	12.4	-3.8	56.5	-
<i>Metridia lucens</i>	18	-	31.4	-4.8	18.4	-	85.3	41.0	93.5	67.9	83.3	31.2	40.5	-34.9	36.0	-
<i>Oithona</i> spp.	11.4	-7.5	30.6	-6.6	12.7	-1.4	33.2	-4.9	41.8	-7.4	27.8	-7.5	17.8	-22.8	32.0	3.2
Harpacticoid copepods	14.5	-4.8	40.6	13.9	22.4	6.8	54.4	-22.4	94.9	-0.7	51.3	-18.2	-	51.1	-4.1	-
Copepod nauplii	16.7	3.3	15.3	-9.8	16.2	8.4	15.7	-22.4	33.0	-2.6	16.2	2.2	12.0	5.4	19.8	9.9
Euphausiid calyptopis	12	-0.5	17.1	-6.6	-	-	-	-	39.1	-11.1	33.4	-34.4	31.5	-6.9	45.3	-11.2
<i>Evadne</i> spp.	-	-	8.6	-9.3	5.6	-6.5	67.5	46.5	20.9	-	10.8	1.3	9.3	-1.1	-	-
<i>Podon</i> spp.	-	-	-	-	14.1	1.1	-	-	47.1	8.6	22.4	18.4	-	-	-	-
<i>Appendicularia</i>	14.1	4.7	18.5	-1.5	6.4	-5.5	42.1	1.8	37.6	-2.5	14.1	0.4	16.3	-60.3	17.8	1.2
Cirripede nauplii	12.2	0.3	9.5	-1.6	23.3	15.4	44.1	-9.7	35.8	6.5	23.3	4.7	-	-	27.2	10.0
Cirripede cypris	24.9	12.8	23.8	8.5	-	-	48.8	3.6	23.9	-1.5	15.5	-11.7	28.9	27.4	12.5	-
Echinoderm larvae	15.2	6.5	29.3	1.5	26.1	8.8	59.2	-0.9	52.2	3.4	23.2	-20.7	-	-	39.2	5.3
Polychaete larvae	12.3	5.1	-	-	-	-	40.9	-32.8	47.7	-	4.5	-	-	-	45.4	28.8
Gastropod larvae	19.5	9.5	10.8	-7.3	-	-	47.1	25.3	22.4	3.8	28.4	-17.8	11.9	-2.2	24.7	1.1
Lamellibranch larvae	7.7	-12.7	14.5	-11.6	-	-	78.3	2.7	40.0	-17.1	27.1	-19.1	26.2	-16.5	38.0	-29.8
Decapod larvae	11.3	-1.0	23.0	13.7	24.8	9.0	57.4	-1.3	56.7	-3.8	34.0	-15.0	37.2	-34.8	24.7	13.0
Cyphonautes larvae	-	13.0	-32.0	19.1	7.1	-	-	75.0	14.0	44.1	-43.7	26.9	4.6	50.4	12.3	-
<i>Limacina</i> spp.	1	-19.0	12.6	-1.2	-	-	41.3	-	69.5	30.2	43.2	20.0	-	-	-	-
<i>Tomopteris</i> spp.	16.6	1.9	11.9	1.3	-	-	40.6	-6.6	39.8	6.3	44.4	5.6	36.0	-1.9	51.4	24.6
Chaetognaths (<i>Sagitta</i> spp.)	21	10.3	19.3	0.8	16.0	-1.6	54.5	34.9	90.9	71.3	47.8	33.4	41.7	5.8	35.7	29.2
Coelenterata	5.8	-2.7	42.0	8.5	18.8	5.9	44.6	-1.9	45.8	-1.9	76.3	8.8	57.9	-1.9	42.0	22.3
Fish larvae	11.1	-9.3	17.8	-10.2	15.4	-1.5	15.0	-47.1	33.6	4.0	18.1	-2.3	11.6	7.5	22.6	-5.9

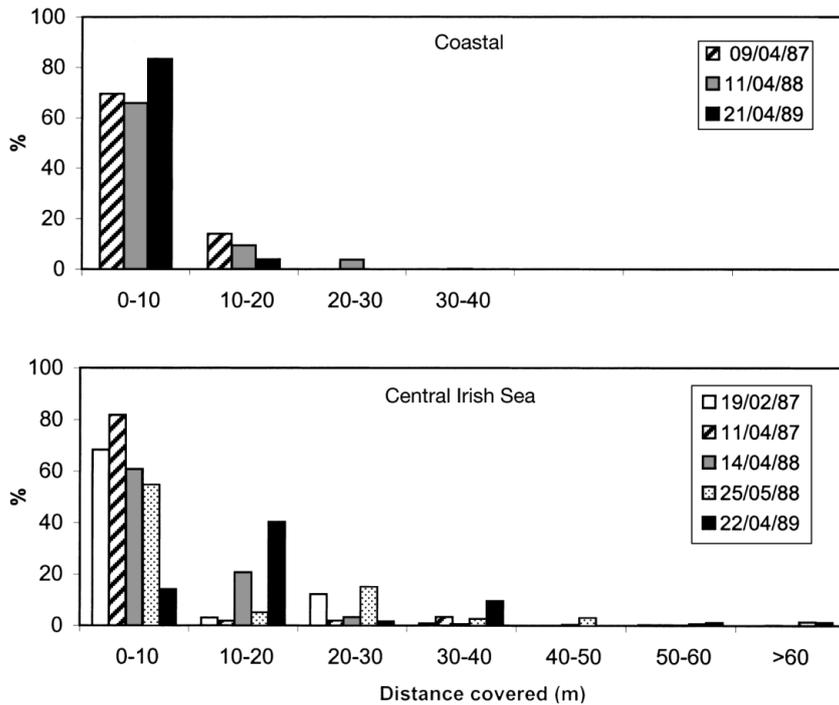


Fig. 4. Distribution (%) of zooplankton population as a function of distance travelled during diel vertical migration

Also (as stated in 'Materials and methods'), the daytime WMD of *Sagitta* spp. could have been underestimated due to these being on or near the bottom, below the sampling depth range of our net.

Neither chaetognath abundance nor their distribution at night were related to the amplitude of the migration of *Calanus* spp. or *Pseudocalanus elongatus* (Fig. 8). When the chaetognaths displayed reduced or no DVM (Table 3) and remained on the surface during the day (coastal stations), *Calanus* spp. displayed reverse migration and *P. elongatus* did not migrate or displayed limited reverse DVM. When chaetognaths displayed normal DVM (central Irish Sea), both *Calanus* spp. and *P. elongatus* resumed normal DVM (Fig. 8).

The DVM of the chaetognaths seems to be related to bottom depth (Fig. 9). At the coastal stations, chaetognaths remained 15 to 20 m above the bottom, with only small differences in their vertical distribution between day and night. In the central Irish Sea, chaetognaths tended to stay deeper during the day and move towards the surface at night.

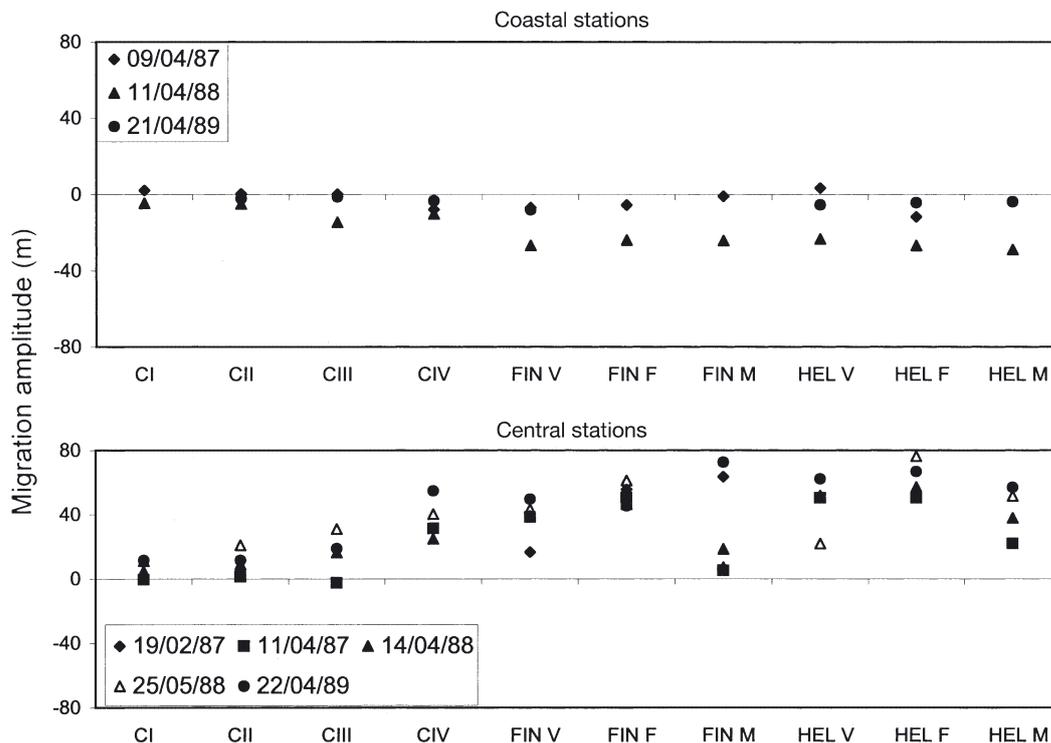


Fig. 5. *Calanus* spp. Amplitude of diel vertical migration for different copepodite developmental stages (I, II, III, IV, V) at coastal and central Irish Sea stations. F: females; M: males; FIN: *C. finmarchicus*; HEL: *C. helgolandicus*

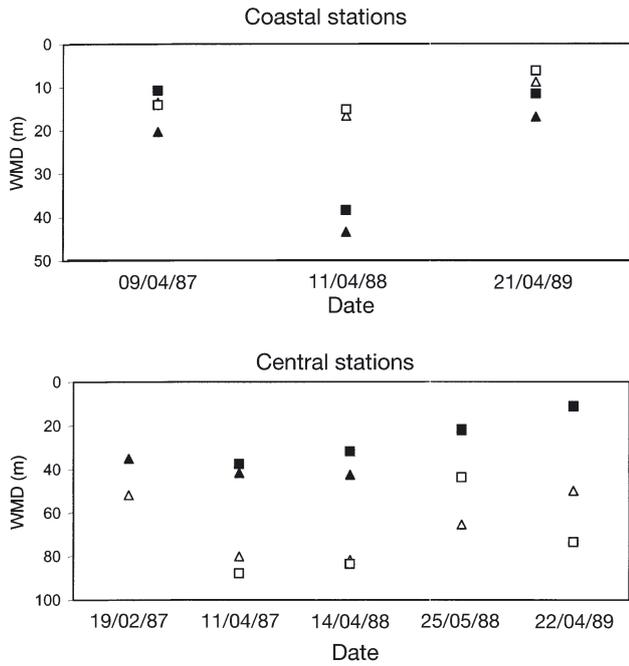


Fig. 6. *Calanus* spp. Weighted mean depth (WMD) of Copepodite Stage V of *C. helgolandicus* (■: night-time; □: daytime) and *C. finmarchicus* (▲: night-time; △: daytime) at coastal and central Irish Sea stations

Table 4. Correlation coefficients between weighted mean depth of the main zooplankton groups and 2 potential predators, chaetognaths (*Sagitta* spp.) and fish larvae. Significant correlation coefficients indicated in **bold**

	<i>Sagitta</i> spp.	Fish larvae
<i>Acartia</i> spp. I–IV	0.32	0.58
<i>Acartia</i> spp. VI	0.53	0.02
<i>Calanus</i> spp. I	0.53	0.52
<i>Calanus</i> spp. II	0.65	0.38
<i>Calanus</i> spp. III	0.51	0.06
<i>Calanus</i> spp. IV	0.67	0.40
<i>C. finmarchicus</i> V	0.69	0.54
<i>C. finmarchicus</i> female	0.76	0.22
<i>C. finmarchicus</i> male	0.68	0.35
<i>C. helgolandicus</i> V	0.78	0.39
<i>C. helgolandicus</i> female	0.71	0.37
<i>C. helgolandicus</i> male	0.64	0.37
<i>Oithona</i> spp.	0.32	0.80
<i>Paracalanus parvus</i> V–VI	0.44	0.32
<i>Pseudocalanus elongatus</i> V–VI	0.79	0.14
<i>Temora longicornis</i> I–IV	0.65	–0.02
<i>T. longicornis</i> V–VI	0.38	–0.26
Harpacticoid copepods	0.45	0.60
Copepod nauplii	0.40	0.76
Cirripede nauplii	0.66	0.41
Echinoderm larvae	0.48	–0.30
Polychaeta larvae	0.63	0.35
<i>Tomopteris</i> spp.	0.48	–0.04
Appendicularia	0.46	0.34
Cyphonautes larvae	0.52	0.28
<i>Coscinodiscus</i> spp.	0.14	0.22

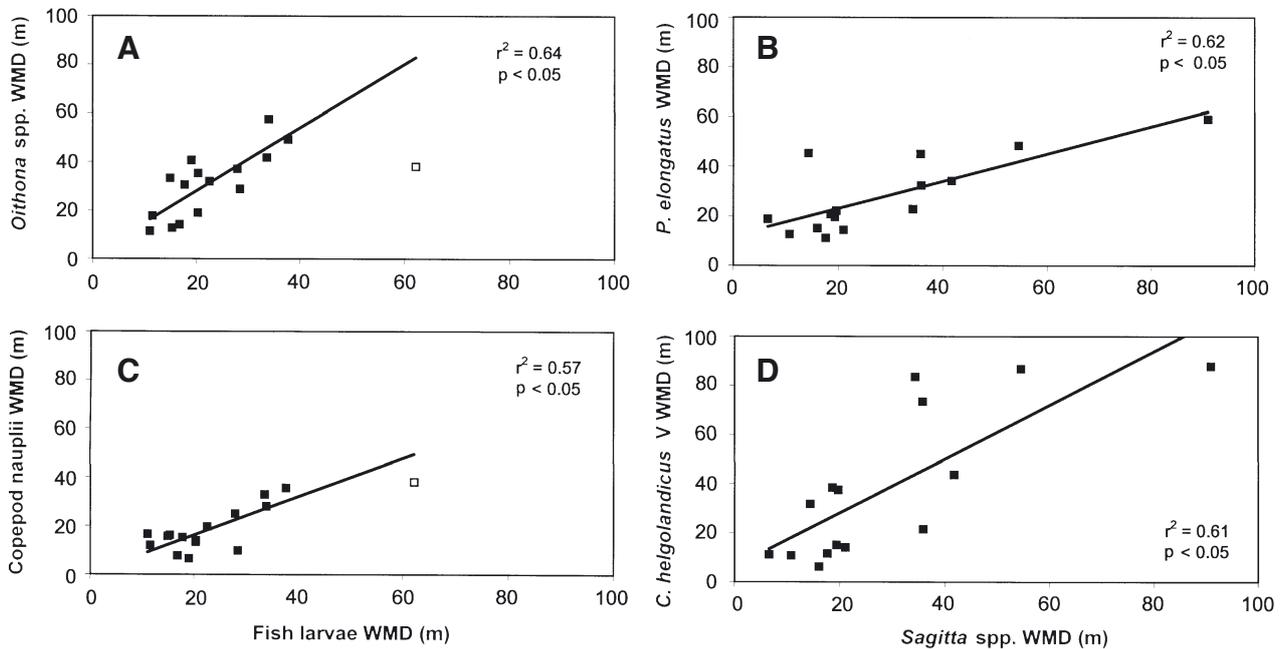


Fig. 7. Examples of significant correlations between prey and their potential predators (see Table 4). (A) *Oithona* spp. vs fish larvae, (B) *Pseudocalanus elongatus* vs *Sagitta* spp., (C) copepod nauplii vs fish larvae, and (D) *Calanus helgolandicus* Copepodite V vs *Sagitta* spp.. WMD: Weighted mean depth. Open data points indicate data excluded from correlation analysis

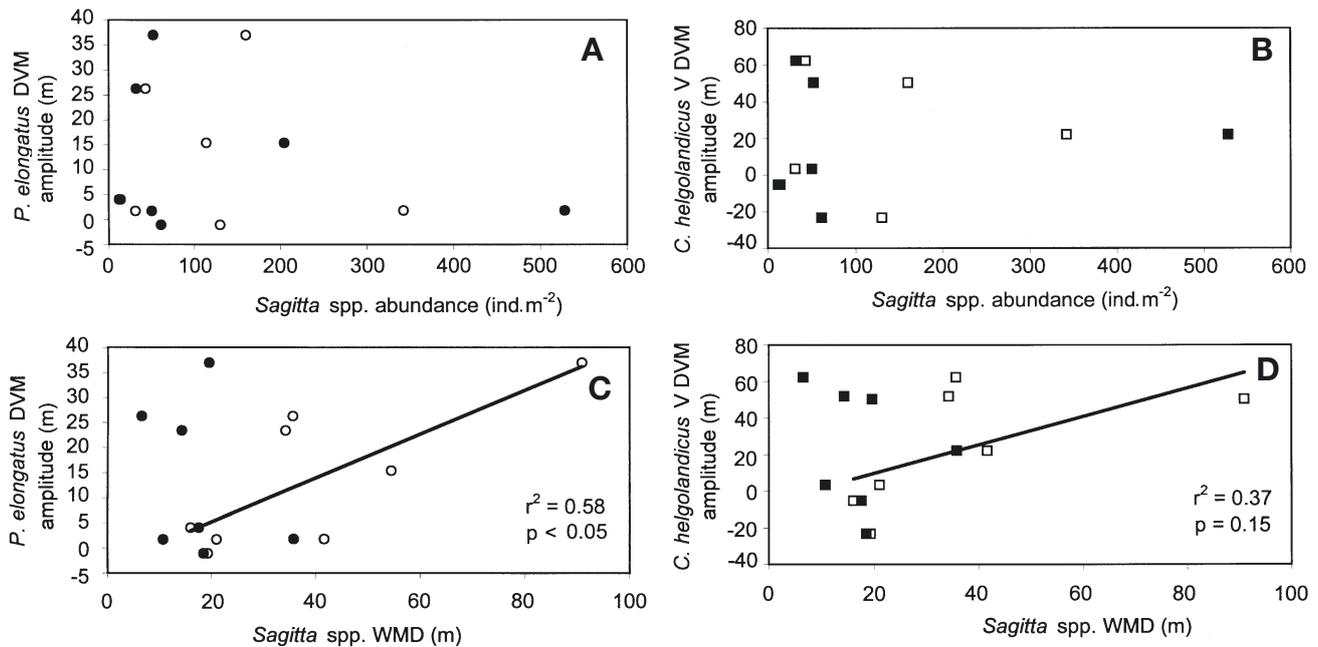


Fig. 8. Relationship between diel vertical migration (DVM) of prey and abundance and weighted mean depth (WMD) of potential predators. Filled symbols indicate night-time and open symbols daytime data for (A) *Pseudocalanus elongatus* DVM vs *Sagitta* spp. abundance, (B) *Calanus helgolandicus* Copepodite V DVM vs *Sagitta* spp. abundance, (C) *P. elongatus* DVM vs *Sagitta* spp. WMD, and (D) *C. helgolandicus* Copepodite V DVM vs *Sagitta* spp. WMD

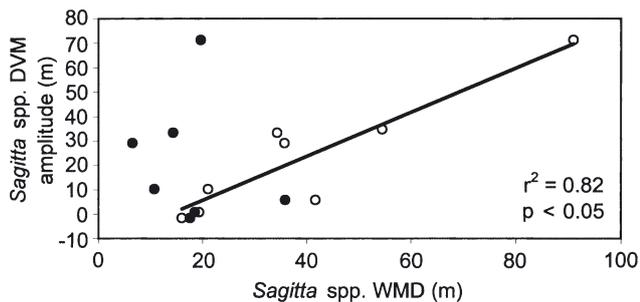


Fig. 9. Relationship between *Sagitta* spp. diel vertical migration (DVM) and weighted mean depth (WMD). (●) Nighttime data; (○) daytime data

DISCUSSION

The most striking result of this study is the high variability in DVM behaviour within the same planktonic community. If we assume that DVM is the result of a compromise between reducing mortality and energy expenditure, and taking advantage of feeding opportunities (Iwasa 1982, Ohman 1990), this variability would seem to have 2 main, partially linked, reasons: (1) the same behaviour does not produce the same optimum compromise between reduced mortality and energetic cost for different groups, species and stages; (2) the mortality risks are not the same for all groups, species or stages, because of the selectivity of predators.

For meroplanktonic larvae, for example, the best way to reduce mortality would probably be to increase growth and reduce time spent in the plankton by increasing their feeding and profiting from the higher temperatures in the upper water layer (Neverman & Wurtsbaugh 1994), rather than engaging in DVM at the risk of prolonging the planktonic phase.

A similar reason could be responsible for the ontogenic differences in the DVM behaviour of *Calanus* spp. Ontogenic differences in DVM have been previously reported for *C. pacificus* in mesocosm experiments (Huntley & Brooks 1982) and in the field (Osgood & Frost 1994), *C. finmarchicus* in Scottish lochs and the Norwegian Sea (Nicholls 1933, Marshall & Orr 1955, Dale & Kaartvedt 2000), *Metridia lucens* in different areas (Osgood & Frost 1994, Hays et al. 1995, Falkenbaugh et al. 1997, Timonen 1997), and for *Neocalanus gracilis*, *Pleuromamma abdominalis* and *Euchaeta acuta* in the Mediterranean (Andersen et al. 2001).

Ontogenic and size-dependent variations in DVM have generally been attributed to large individuals being more conspicuous and therefore more susceptible to visual predators (Hays et al. 1994, De Robertis et al. 2000) and to size-selectivity (Neill 1992). However, nauplii and early copepodite stages are usually the main food source of fish larvae (e.g. Conway 1980, Conway et al. 1998); they also suffer from invertebrate predation, and they often have higher mortality rates than adults (Ohman et al. 2002). Therefore, one would

expect them to enhance the behaviours aimed at reducing mortality. Furthermore, Huntley & Brooks (1992) observed ontogenetic differences in the DVM of *Calanus pacificus* in the absence of predators and found that migration decreased at low food concentrations. It has also been observed that early nauplii of *C. pacificus* do not have the ability to survive long starvation events (Lopez 1996). Therefore, it is possible that for a nauplius or an early copepodite stage, a rapid increase in size will result in a less mortality (Fiksen & Giske 1995). This would be a better strategy than engaging in DVM. In contrast, for late copepodite stages or adults, in which increased feeding will not result in a significant increase in size, DVM would probably be a better option.

The minimum distance to be covered in order to reduce the risk of predation depends on irradiance, attenuation coefficient, visibility of prey and the visual system of the predator (Aksnes & Utne 1997). Therefore, the mortality risk/energy gain ratio would be highly dependent on environmental conditions (De Robertis 2002). This mortality risk/energy gain ratio could be particularly important in trying to understand the behaviour of small copepods such as *Oithona* spp., which do not usually show DVM behaviour. It is possible that for such small copepods the energetic cost of swimming outweighs the reduction in mortality achieved by thus avoiding visual predators, and that other strategies such as reduction of their mechanical signals (Paffenhöfer & Mazzocchi 2002) are a better option in the balance between reducing mortality and energetic cost. Although it is possible that copepods use an elastin-like protein that would decrease the energetic requirement of vertical displacement (Alcaraz & Strickler 1988), the energetic side of the equation could be more important than previously thought. Larger copepods such as *Metridia pacifica* cease migration when their lipid storage is low (Hays et al. 2001), and even for organisms as large as northern krill *Meganyctiphanes norvegica*, a period in deep waters can result in the breakdown of haemocyanin for use as an energy source in order to maintain basal metabolism (Spicer & Stromberg 2002).

Whereas *Pseudocalanus elongatus* performed significant DVM in the central Irish Sea, adults of similarly sized or slightly larger copepods such as *Acartia*, *Temora* and *Centropages* spp. showed much reduced or no apparent DVM. Nevertheless, it is possible that due to the different reproductive strategy of these species (free-egg spawning as opposed to egg-sac spawning in *P. elongatus*), the balance between mortality risk and feeding shifts towards feeding. When food concentrations are high, egg production in free-spawners is proportional to ingestion, and fluctuations in the food supply significantly reduce daily egg production

(Calbet & Alcaraz 1996). Because in free-spawners the death of the female does not imply the death of the eggs, as is the case with sac-spawners such as *P. elongatus*, it is possible that free-spawners risk higher mortality in order to assure maximum egg production by continuous feeding.

Another possible explanation could be that *Acartia* spp., *Centropages* spp. and *Temora longicornis* are not the main targets of predators in the area. The selective behaviour of predators introduces a further variable into the interpretation of the DVM variability. Analyses of gut contents are needed to confirm whether the relationship we found between copepod species and potential predators is due to preference for those preys (chaetognath WMD–*Pseudocalanus elongatus* WMD, chaetognath WMD–*Calanus* spp. WMD, fish larvae WMD–copepod nauplii WMD, fish larvae WMD–*Oithona* spp. WMD). However, in the literature, copepod nauplii and *Oithona* spp. are often reported to be the main prey of fish larvae (Conway 1980, Conway et al. 1998) and copepods the main prey of chaetognaths (Duro & Saiz 2000), even when large numbers of alternative prey are abundant in the plankton (Saito & Kiørboe 2001). Chaetognaths are likely to be mainly size-selective predators (e.g. Pearre 1980), but they also show selection between different copepod species, as well as a flexibility in their selectivity (Rakusa-Suszczewski 1969). As an example, in the North Sea, *Sagitta elegans* showed high feeding rates on male *Paracalanus* spp., followed by species of *Calanus*, *Metridia*, *Centropages* and *Pseudocalanus*, whereas the feeding rates on *Oithona* spp. and on *Paracalanus* spp. Stages III and IV were much lower (Saito & Kiørboe 2001).

While, in order to reduce mortality by fish larvae predation, copepod nauplii and *Oithona* spp. seem to have adopted strategies other than DVM (i.e. rapid growth or 'invisibility'), both *Calanus* spp. and *Pseudocalanus* spp. show clear evidence of active avoidance of chaetognaths by adapting their DVM inversely to that of the chaetognaths. However, contrary to the situation found by Ohman (1990), in our study it was apparently not the abundance of chaetognaths that triggered DVM (normal or reverse), but the position of the chaetognaths in the water column during daytime. *Calanus* spp. and *P. elongatus* appear to sense the position of chaetognaths in the water column during the period of lower feeding activity, possibly using chemical cues (see references in Lampert 1993), and to adapt the amplitude and direction of their DVM accordingly. In the coastal area, because chaetognaths do not migrate as close to the bottom during the day, this results in reverse DVM for *Calanus* spp. and slightly reversed or no migration for *P. elongatus*. Again, even if the answer is similar, the difference in

the migration amplitude of *Calanus* spp. and *P. elongatus* could be due to differences in the energetic cost of swimming for large and small copepod species.

Many uncertainties and questions remain. For example, why do *Paracalanus parvus* apparently not use DVM to avoid chaetognaths? Would chaetognaths have a greater preference for *Pseudocalanus* spp. rather than *Paracalanus* spp. (these 2 genera are very similar in the early stages)? Chaetognaths do show preferences, not only as a function of prey size, but also as a function of the hydrodynamic signal produced (Saito & Kiørboe 2001). Data from Dabob Bay and the North Sea (Ohman 1986, Saito & Kiørboe 2001) seem to indicate a preference for species of *Pseudocalanus* over species of *Paracalanus*.

Why did organisms for which we assume a higher energetic cost of swimming (such as *Oithona* spp. or organisms such as appendicularians that carry their houses) perform a significant reverse DVM when there was strong stratification, as in May 1988? Are the reductions in metabolic costs due to the lower temperature below the thermocline important enough to justify such migration (McLaren 1974)? Why are *C. helgolandicus* and *Calanus finmarchicus* not vertically segregated in the Irish Sea, as they seem to be in the Celtic Sea (Williams 1985)?

In answer to our original questions, the results of our study confirm that DVM is a very flexible behaviour that can be adopted by many planktonic organisms, depending on predation risk. However, it is not necessarily the main or only mechanism to reduce predation mortality, and predation risk seems to vary greatly between different groups or species. Some species susceptible to predation by visual predators display no DVM or a less extensive DVM than others because they use other escape mechanisms or because of energetic considerations (Bollens et al. 1993). It could also be hypothesised that the absence of DVM is a response to a relatively constant mortality risk or to a constant mortality risk/energy gain ratio situation, as has been suggested for fixed DVM (Neill 1992). Therefore, a large proportion of the planktonic community could be performing little or no DVM, while a smaller number of species perform extensive DVM, as seems to be the case in the Irish Sea.

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