

# ABUNDANCE, DISTRIBUTION AND COMMUNITY COMPOSITION OF SMALL GELATINOUS ZOOPLANKTON IN SOUTHERN IRISH COASTAL WATERS

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Cite as follows:  
Baxter, E.J., McAllen,  
R. Allcock, A.L. and  
Doyle, Thomas K.  
2012 Abundance,  
distribution  
and community  
composition of  
small gelatinous  
zooplankton in  
southern Irish coastal  
waters. *Biology  
and Environment:  
Proceedings of the  
Royal Irish Academy*  
**112B**. DOI: 10.3318/  
BIOE.2012.01.

Received 24 January  
2011. Accepted 27  
June 2011. Published  
27 March 2012.

## ABSTRACT

Gelatinous zooplankton play important roles in coastal seas, from predators of fish eggs and larvae to competitors of fish for copepods. Despite this, they are often an underestimated component of coastal marine ecosystems. In Ireland, there has been limited research focussed on the gelatinous zooplankton communities in coastal waters. In the present study, 21 stations in the coastal waters to the south and west of Ireland were sampled, providing the first broad-scale description of the gelatinous zooplankton communities along over 600km of the Irish coastline. In total, 23 species/genera of gelatinous zooplankton were identified from six taxa: hydromedusae, siphonophores, ctenophores, chaetognaths, urochordates and polychaetes. Only a few of the stations sampled were highly stratified in terms of temperature or salinity; these were shallow stations close to freshwater inputs. Thermo- and halocline intensity had little influence on the community composition observed. The community structure was however found to be highly dependent on temperature at depth and surface salinity, which varied with latitude and longitude, respectively. The similarity in the community composition between stations was largely driven by three highly holoplanktonic abundant species: the hydromedusa *Aglantha digitale*; the ctenophore *Pleurobrachia pileus*; and the larvacean *Oikopleura* sp. These species reached densities of 214, 83 and 492 individuals m<sup>-3</sup>, respectively.

## INTRODUCTION

Gelatinous zooplankton (here defined as hydromedusae, siphonophores, ctenophores, urochordates, chaetognaths and planktonic polychaetes) are important, though often overlooked, members of marine ecosystems. Early records on the occurrence of gelatinous zooplankton in Irish waters date from the beginning of the last century (Browne 1896; Delap and Delap 1905; Delap 1924; Jeal and West 1970). Although these early descriptive studies are immensely valuable, they provide little quantitative information on the abundance and ecology of gelatinous zooplankton in Irish coastal waters. Over recent decades, there has been an increased interest in the ecology of gelatinous zooplankton in Irish waters and elsewhere due to the occurrence of detrimental blooms of some species. For example, blooms of cnidarian zooplankton have been linked to major fish kill events of marine-farmed salmonids in Ireland (Cronin *et al.* 2004; Doyle *et al.* 2008). Furthermore, Baxter *et al.* (2011) have recently described the role that small hydromedusae and siphonophores can play in gill

disorders in marine-farmed fish, an emerging problem for the aquaculture industry (Rodger, 2007). Considering such potentially detrimental impacts and importance, it is therefore necessary to understand the broad-scale abundance and distribution of gelatinous zooplankton.

There is still very limited knowledge about gelatinous zooplankton in general and how they are distributed over large areas. In contrast to what is known about the distribution of large, conspicuous scyphomedusae in Irish waters (Doyle *et al.* 2007; Bastian *et al.* 2011), small hydromedusae, siphonophores and ctenophores have only been described on a more local scale (Yip 1981; Ballard and Myers 2000). Further to their potentially detrimental impacts, however, hydrozoans (and ctenophores) are also known to play a key role in coastal marine ecosystems, acting as carnivorous predators of fish eggs/larvae and crustacean zooplankton (Purcell 1985; Mills 1995; Shiganova *et al.* 2001; Hosia and Bamstedt 2007). Here, the occurrence and abundance of gelatinous zooplankton, at a 'snapshot' in time (June 2009), were documented, over a broad-scale, in relation to environmental factors along approximately 600km of the Irish coastline.

## STUDY AREA

The study area comprised coastal waters to the west and south of Ireland from the ports of Galway Bay to Rosslare Harbour (Fig. 1). Hydrographically, the summer coastal waters to the west of Ireland are typically dominated by persistent south-westerly currents, bringing warm Atlantic waters on to the western Irish shelf edge (O'Boyle and Silke 2010). In the summer, the southern Irish coastline is affected by a weaker current that flows northward from the Brittany coast across the Bristol Channel, where it splits running westwards across the south coast of Ireland and north up into the Irish Sea (Pingree and Le Cann 1989). Tidal mixing currents also move east to west across the southern Irish coast and south to north up the west coast of Ireland. Near the coast, turbulent tidal forces can be strong enough to prevent the formation of seasonal thermoclines (O'Boyle and Silke 2010). The southern Irish coastline features numerous small bays and estuaries, as well as large harbours, which influence circulation patterns in the area with the discharge of fresh waters. At times, the formation of strong haloclines can occur in regions of high freshwater flows (O'Boyle and Silke 2010). On the west coast there are a series of long, narrow inlets (rias), which are often heavily influenced by oceanic influxes and coastal upwelling (Edwards *et al.* 1996; Raine *et al.* 2002), as well as linear stretches of coastline (Co. Clare) and the major estuary of the Shannon River (OSPAR 2000).

## MATERIALS AND METHODS

## ENVIRONMENTAL VARIABLES

Temperature, salinity, dissolved oxygen and fluorescence measurements were recorded relative to depth using a shipboard CTD (conductivity, temperature and depth) profiler (model SBE 911, Seabird Electronics Inc., Washington, DC, USA). This provided a vertical profile for each variable. These variables are often thought to influence plankton communities either directly or indirectly (Arai 1992; Graham *et al.* 2001; Purcell *et al.* 2010). As zooplankton can be distributed in relation to vertical temperature and salinity discontinuities (Graham *et al.* 2001), values for the intensity and depth of thermo- and haloclines were calculated for each station and used in subsequent analyses.

The method used to identify the depth and intensity of the thermoclines was that described by Reygondeau and Beaugrand (2011), which

uses a step-by-step process for each profile. The profiles were first interpolated (every 1m from a depth of 2m to the maximal depth) to equally space the data, then filtered using an exponentially-weighted moving average technique (Montgomery 1991). Finally, the depth-to-depth temperature difference was calculated for every 1m of the profile to give the intensity and depth of each cline (see Reygondeau and Beaugrand 2011 for details). The intensity of the cline is given as the maximal depth-to-depth temperature difference. The depth of the cline was, however, calculated by comparing the maximal depth-to-depth temperature difference amplitude (maximum intensity minus minimum intensity) to a threshold fixed at  $0.05^{\circ}\text{C m}^{-1}$ . If the maximal depth-to-depth temperature difference amplitude was less than the threshold, the depth was the maximal depth of the profile; if the threshold was the same as or greater than the temperature difference amplitude, the depth was depth of maximal intensity.

Based on the literature (Defant 1961; Levitus 1982; Boyer *et al.* 2007), no particular threshold has been developed for haloclines. Therefore, as suggested by Reygondeau and Beaugrand (2011), empirical testing was used to define the threshold of salinity based on the local scale of the profiles (de Boyer Montégut *et al.* 2004). The salinity profiles were interpolated and analysed in the same manner as the temperature profiles, with the most suitable threshold defined as  $0.01 \text{ psu m}^{-1}$ . Note that the interpolation method used in the present study was altered slightly from that described by Reygondeau and Beaugrand (2011) so that each profile was linearly interpolated every 1m instead of every 5m due to the shallow depths of the profiles from such coastal stations. All computation was done using a statistical toolbox developed by Reygondeau and Beaugrand (2011).

## GELATINOUS ZOOPLANKTON COLLECTION AND PROCESSING

Plankton samples were collected during a cruise around Irish coastal waters from Galway Bay ( $53^{\circ}10'\text{N}$ :  $09^{\circ}12'\text{W}$ ) to Rosslare Harbour ( $52^{\circ}13'\text{N}$ :  $06^{\circ}14'\text{W}$ ) from 13 to 15 June 2009 (Fig. 1 and Table 1). Samples were collected at 21 stations over the two days on-board the *RV Celtic Voyager* using a 0.4m diameter ring net with 200- $\mu\text{m}$  mesh and a non-filtering cod-end. All plankton hauls were conducted by hand, vertically from a depth of 25m to the surface at a towing speed of  $0.5\text{--}1\text{ms}^{-1}$  (Station 1 only extended to 20m depth due to the shallowness of Galway Bay) and during both day and night-time.

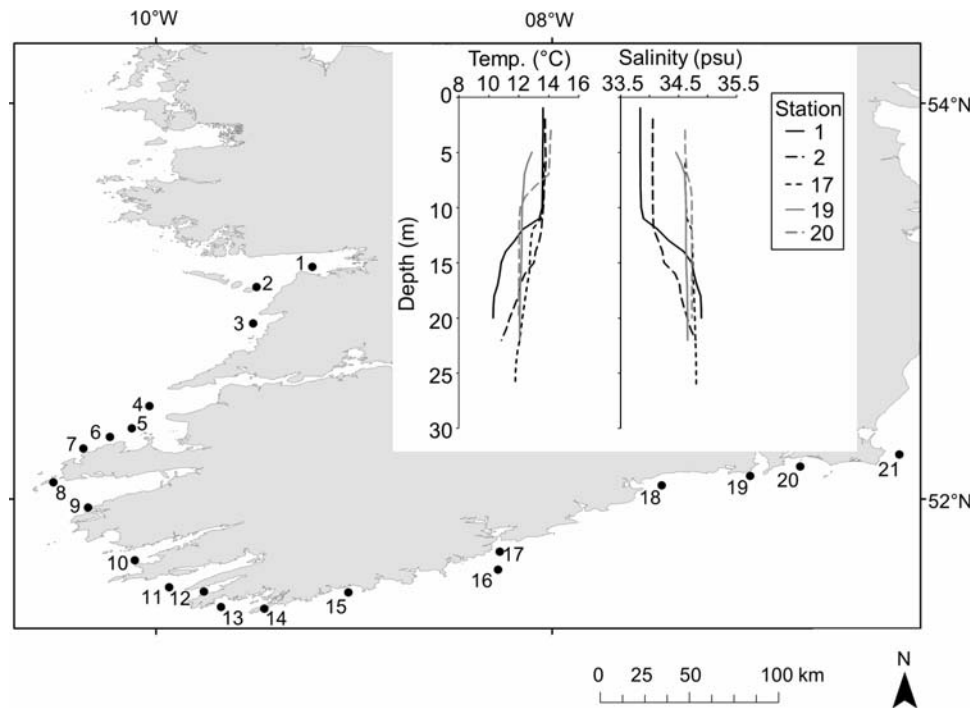


Fig. 1—Location of zooplankton and CTD sampling stations (filled circles) around the Irish coastline and example temperature and salinity profiles for the five most stratified stations (insert).

Samples were immediately preserved in 4% seawater formalin. All gelatinous zooplankton was later identified to the lowest possible taxonomic level and enumerated. Polygastric colonies of calycophoran siphonophores (only *Muggiaea atlantica*) were enumerated from intact nectophores. The number of gonophores was enumerated to represent the number of eudoxids in the sample, as they were more often than not separated from the bract. Physonect siphonophores were enumerated by the number of pneumatophores present in the sample. Abundance data in individuals per  $m^{-3}$  were calculated from the raw counts using the area of the net opening multiplied by the depth sampled in metres (assuming 100% filtration efficiency of the net due to a vertical haul over a short distance).

#### STATISTICAL ANALYSES

Principal component analysis (PCA) was conducted [using a maximum of five principal components (PCs)] to extract the dominant environmental variables responsible for between-station similarities. The suite of variables used in the analysis were the bottom depth of the station, surface temperature, salinity, dissolved oxygen and fluorescence (at 2m, approximately where the first CTD reading was taken), temperature, salinity and dissolved oxygen at depth (~22m, as the

CTD did not always reach 25m depth), as well as thermo- and halocline intensity and depth. After visualising the distributions of each pair of variables (using a draftsman plot), all environmental variables were normalised prior to conducting the PCA by subtracting the mean of a particular variable from each value and dividing by the standard deviation of the variable (Clarke and Warwick 2001).

Non-metric multidimensional scaling (MDS) was used to conduct an analysis of the gelatinous zooplankton community composition. Prior to starting MDS, several species were excluded due to the influence of very rare species on the interpretation of the results largely due to chance. These species were eliminated using the method of retaining a species accounting for '> 3% of the total score of any one sample' (Clarke and Warwick 2001). The abridged abundance data were subsequently square-root transformed to allow both the remaining rare and dominant species to influence the analysis of the community structure. A Bray-Curtis similarity matrix was constructed from the transformed abundances for MDS analysis.

The 'BEST' analysis (using the BIO-ENV procedure in PRIMER) was then used to select the environmental variables that 'best explain' the gelatinous zooplankton community pattern observed. 'Global BEST' was used to determine

Table 1—Dates, locations, bottom depths of stations and water column data from 21 stations around the southern Irish coastline in 2009.

Stat.	Date	Lat.	Long.	Depth (m)	$T_{2m}$	$T_{22m}$	$T_{intensity}$	$T_{depth}$ (m)	$S_{2m}$	$S_{22m}$	$H_{intensity}$	$H_{depth}$ (m)	$DO_{2m}$	$DO_{22m}$	$F_{2m}$
1	13 Jun	53.17	-9.21	24	13.62	10.30	<b>0.56</b>	4.5	33.84	34.90	1.03	4.5	5.34	4.49	0.13
2	13 Jun	53.07	-9.49	28	13.76	10.84	<b>0.43</b>	4.5	34.06	34.80	0.85	4.5	5.16	4.50	0.12
3	13 Jun	52.89	-9.51	47	13.53	11.22	0.27	4.5	34.33	35.01	0.08	8.5	5.62	5.18	0.16
4	13 Jun	52.47	-10.03	40	13.04	11.56	0.19	10.5	35.09	35.14	0.20	4.5	3.65	4.90	0.24
5	14 Jun	52.36	-10.12	30	12.92	11.63	0.25	4.5	35.16	35.15	0.59	4.5	5.51	5.23	0.32
6	14 Jun	52.31	-10.23	65	12.44	12.34	0.04	60.0	35.13	35.12	0.02	4.5	3.66	5.35	0.32
7	14 Jun	52.26	-10.37	67	13.03	12.62	0.06	26.5	35.09	35.08	0.02	4.5	4.72	5.30	0.22
8	14 Jun	52.08	-10.52	41	12.80	11.35	0.11	18.5	35.01	35.15	0.20	4.5	5.43	5.13	0.22
9	14 Jun	51.95	-10.34	50	13.18	12.77	0.09	20.5	35.03	35.04	0.08	4.5	5.17	5.27	0.15
10	14 Jun	51.69	-10.11	69	13.49	13.16	0.06	59.5	34.91	34.93	0.01	4.5	4.49	5.23	0.12
11	14 Jun	51.55	-9.93	64	13.16	13.03	0.16	12.5	34.93	34.85	0.03	4.5	5.23	5.03	0.10
12	14 Jun	51.53	-9.76	54	13.85	13.51	0.07	6.5	34.83	34.83	0.09	6.5	3.62	5.17	0.18
13	14 Jun	51.45	-9.67	51	14.15	13.12	0.12	4.5	34.83	34.82	0.07	4.5	5.22	4.96	0.27
14	14 Jun	51.44	-9.45	49	13.55	13.53	0.03	44.0	34.78	34.78	0.09	4.5	5.08	5.09	0.21
15	14 Jun	51.53	-9.03	40	14.21	13.18	0.16	4.5	34.72	34.78	0.22	4.5	3.45	4.91	0.23
16	15 Jun	51.64	-8.27	57	14.71	13.18	0.39	37.5	34.48	34.87	0.07	13.5	5.20	5.12	0.19
17	15 Jun	51.73	-8.26	33	13.64	12.06	<b>0.42</b>	7.5	34.61	34.79	<b>0.78</b>	7.5	3.50	4.70	0.15
18	15 Jun	52.07	-7.44	35	14.22	12.59	0.24	29.5	34.54	34.64	0.37	4.5	4.98	5.05	0.11
19	15 Jun	52.12	-7.00	25	12.87	12.08	<b>0.38</b>	6.5	34.45	34.65	<b>1.10</b>	6.5	4.68	5.33	0.34
20	15 Jun	52.16	-6.74	25	14.14	12.02	<b>0.61</b>	4.5	34.61	34.73	<b>1.08</b>	4.5	5.35	5.54	0.12
21	15 Jun	52.22	-6.24	39	13.15	12.57	0.12	4.5	34.45	34.55	0.22	4.5	5.43	5.39	0.20

Temperature at 2m and 22m ( $T_{2m}$ ,  $T_{22m}$ ), salinity at 2m and 22m ( $S_{2m}$ ,  $S_{22m}$ ), dissolved oxygen at 2m and 22m ( $DO_{2m}$ ,  $DO_{22m}$ ) and fluorescence at 2m ( $F_{2m}$ ) obtained via the CTD profiles. Sampling dates (Date), latitude (Lat.), longitude (Long.) and depth maxima (Depth) of the stations recorded. Thermocline intensity and depth ( $T_{intensity}$ ,  $T_{depth}$ ) and halocline intensity and depth ( $H_{intensity}$ ,  $H_{depth}$ ) calculated for each profile. The most stratified stations highlighted in bold. The most temperature and salinity profiles for these stations can be seen in the insert of Fig. 1.

a rank correlation ( $\rho$ ) of the best variables and statistical significance (though randomised permutations of the data 999 times). All analyses were performed using PRIMER version 6 software (PRIMER-E Ltd. Ivybridge, UK).

## RESULTS

### ENVIRONMENTAL VARIABLES

The range of environmental variables for each station are summarised in Table 1. Physical characteristics varied greatly between stations. While most stations were well-mixed, Stations 1, 2, 17, 19 and 20 were highly stratified in terms of both temperature and salinity. These stations were also relatively shallow and close to estuaries or harbours (see Fig. 1 and Table 1). The temperature and salinity profiles from these five stratified stations are shown as an example in Fig. 1. Most stations that had high stratification intensity (temperature and salinity) tended to have a shallow depth of cline (i.e. <20m).

PC1 explained 38.4% of the variance in the environmental variables and the greatest loading on the first PC was thermocline intensity (−0.42) followed by depth (−0.40). When adding PC2,

the cumulative explained variance became 56.6%, and the highest loading on PC2 was temperature (at surface and depth: −0.55 and −0.42 respectively). PC3, PC4 and PC5 explained a further 10.0, 9.5 and 8.9% of the variance, respectively. The PCs were dominated by dissolved oxygen at depth (−0.56), surface-dissolved oxygen (−0.81) and halocline depth (−0.75) respectively. The spatial separation of the stations with respect to the suite of environmental variables is shown in Fig. 2.

### COMMUNITY COMPOSITION AND SPECIES DISTRIBUTION

Twenty-three species/genera of gelatinous zooplankton (fourteen hydromedusae and three siphonophores, two ctenophores, two chaetognaths, one urochordate and one polychaete) were identified from samples across all stations (Table 2). Juveniles of the holoplanktonic trachymedusa, *Aglantha digitale*, and individuals of the meroplanktonic leptomedusa, *Phialella quadrata* were the most frequently encountered cnidarians across the stations, being absent from only three locations. Mature *A. digitale* individuals were not observed in samples from the northernmost stations and were present in the highest densities in samples from the south-easterly stations (Stations 15 to 20) compared

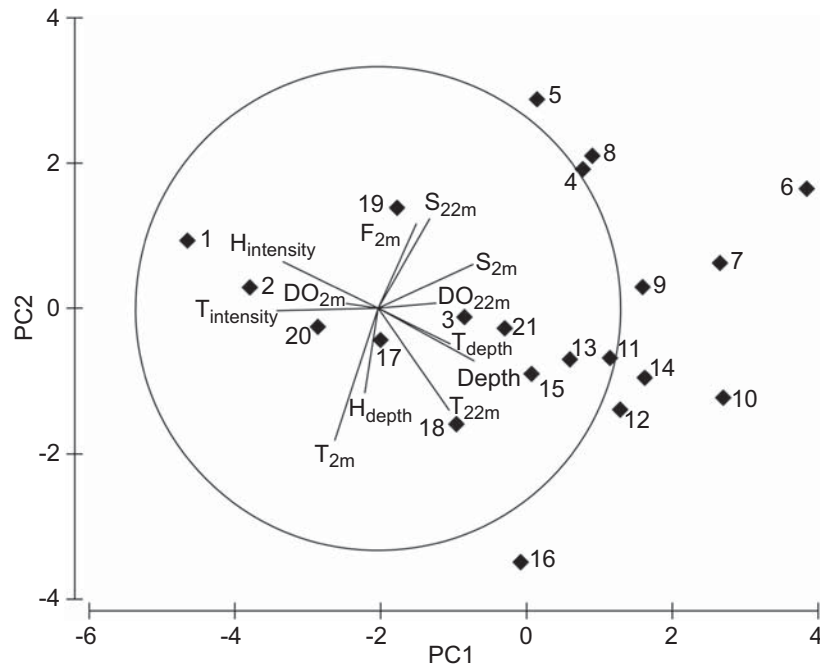


Fig. 2—Principal component analysis (PCA) ordination plot of the environmental variables at 21 stations around the west and south coast of Ireland. Environmental variables:  $T_{intensity}$ —thermocline intensity;  $T_{depth}$ —thermocline depth;  $H_{intensity}$ —halocline intensity;  $H_{depth}$ —halocline depth;  $T_{2m}$ —temperature at 2m;  $T_{22m}$ —temperature at 22m;  $S_{2m}$ —salinity at 2m;  $S_{22m}$ —salinity at 22m;  $DO_{2m}$ —dissolved oxygen at 2m;  $DO_{22m}$ —dissolved oxygen at 22m;  $F_{2m}$ —fluorescence at 2m; and Depth—bottom depth of the station.

Table 2—Abundance (individuals m<sup>-3</sup>) of gelatinous zooplankton identified at 21 stations around the west and south Irish coast.

	Station																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<b>Hydromedusae</b>																					
<i>Aglantha digitale</i> (j)	-	0.6	3.5	-	1.6	14.0	18.5	6.4	11.1	81.5	17.5	122.9	19.7	29.0	-	94.5	2.9	163.9	1.0	19.7	-
<i>Aglantha digitale</i> (m)	-	-	-	-	-	-	-	1.0	0.6	0.6	0.3	0.6	0.3	0.3	-	38.5	9.2	49.7	5.1	22.3	-
<i>Clytia hemisphaerica</i>	-	-	-	-	-	-	-	-	0.3	1.3	0.3	-	-	-	-	-	-	-	-	-	-
<i>Corymorpha nutans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
<i>Ectopleura dumortieri</i>	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eutima gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-
<i>Hydractinia borealis</i>	-	0.3	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-
<i>Leuckartiara octona</i>	-	-	-	-	-	-	-	-	-	-	-	0.3	-	0.6	-	-	-	-	-	-	-
<i>Lizzia blondina</i>	-	-	-	-	-	-	-	-	0.6	0.6	1.3	1.6	-	-	-	-	-	-	-	-	-
<i>Obelia</i> spp.	37.6	1.0	-	0.3	-	1.3	2.9	2.9	2.5	2.9	-	0.6	0.3	-	-	-	2.5	0.3	-	1.6	-
<i>Octorchis gegenbaui</i>	-	-	-	-	-	-	-	-	-	-	-	0.3	-	0.3	-	-	-	-	-	-	-
<i>Phialella quadrata</i>	0.3	1.0	0.6	29.6	12.1	0.6	0.6	3.2	-	-	-	1.9	1.3	1.0	-	0.3	2.9	0.3	5.1	2.5	3.5
<i>Proboscoidactyla stellata</i>	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
<i>Rathkea octopunctata</i>	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sarsia gemmifera</i>	-	-	-	5.7	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Siphonophores</b>																					
<i>Agalma elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-
<i>Muggiaea atlantica</i> (p)	-	-	0.6	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-
<i>Muggiaea atlantica</i> (e)	-	-	-	-	-	-	0.3	1.3	-	-	-	-	-	-	-	-	-	1.3	0.6	-	-
<i>Nanomia bijuga</i>	-	-	-	-	-	-	0.6	0.3	-	-	0.3	0.3	0.3	-	-	1.3	0.3	2.9	0.3	0.3	-
<b>Ctenophores</b>																					
<i>Pleurobrachia pileus</i>	-	1.0	13.1	4.5	3.2	16.6	48.7	83.4	56.3	90.7	32.5	89.1	13.4	17.5	28.3	18.1	19.4	32.5	0.6	8.0	0.3
<i>Beroe</i> sp.	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	0.3	-	0.6	0.3	-	-	-
<b>Urochordates</b>																					
<i>Oikopleura</i> sp.	124.1	67.8	45.5	15.0	33.1	181.1	173.5	203.1	584.4	585.7	137.5	384.5	49.0	26.4	138.8	314.2	98.4	492.4	29.3	179.8	37.6
<b>Chaetognaths</b>																					
<i>Sagitta setosa</i>	-	-	-	-	-	2.9	3.8	1.6	-	-	-	-	-	-	-	5.7	-	5.7	-	-	1.3
<i>Sagitta elegans</i>	-	-	-	1.9	1.3	-	4.1	1.0	3.8	7.0	8.3	6.0	7.3	9.5	29.0	26.7	2.5	11.5	1.3	10.2	-
<b>Polychaetes</b>																					
<i>Tomopteris</i> sp.	-	-	-	-	-	0.6	0.6	-	-	-	-	0.3	-	-	1.9	1.0	0.3	-	-	-	-

Shaded areas represent samples taken during night-time. (j)—juvenile specimens; (m)—mature specimens; (e)—eudoxid stage; (p)—polygastric stage.



to juveniles of the species, which were fairly dominant members of the community across all stations (contributing 7.9–95.5% of the cnidarian community where present, with a maximum density of 163.9 individuals  $\text{m}^{-3}$ , see Fig. 3). *Nanomia bijuga* was the most commonly encountered species of siphonophore, occurring at 52% of stations (Table 2), with *M. atlantica* and *Agalma elegans* occurring sporadically and at lower densities. The urochordate *Oikopleura* sp. were recorded at every station and was the most abundant type of gelatinous zooplankton (see Fig. 3) with a maximum abundance of 492.4 individuals  $\text{m}^{-3}$ . The ctenophore *Pleurobrachia pileus* was highly abundant at some stations (see Fig. 3), with a maximum abundance of 90.7 individuals  $\text{m}^{-3}$ . The chaetognath *Sagitta elegans* was observed more frequently (76% of stations) and in higher abundances (maximum abundance of 29.0 individuals  $\text{m}^{-3}$ ) than the chaetognath *Sagitta setosa* (present in 29% of samples, with a maximum abundance of 5.7 individuals  $\text{m}^{-3}$ ). The planktonic polychaete *Tomopteris* sp. was recorded in 29% of samples at a maximum density of 1.9 individuals  $\text{m}^{-3}$ .

The MDS ordination (Fig. 4) showed a general separation of the cnidarian community assemblages into groups of similar neighbouring stations. The outlying stations were Station 1 (Galway Bay), which was the most northerly, Station 4 (near the mouth of the Shannon) and Station 21 (Rosslare Harbour), which the most easterly station. These stations had an absence or a low abundance of most gelatinous zooplankton species. The stations with the greatest similarity in community composition (Stations 9, 10, 12, 15, 16 and 18) largely shared the highest abundances of the predominant species (*A. digitale*, *P. pileus* and *Oikopleura* sp.) or moderate abundances of these species (as for Stations 6, 7, 8, 11 and 20) forming a cluster of stations on the left-hand side of the ordination within a 60% similarity level. The similarity in the community assemblages between stations is likely to be influenced by the similarity of the environmental variables in each location; therefore further analysis to assess the interactions between biological community assemblages and environmental variables was conducted (see below).

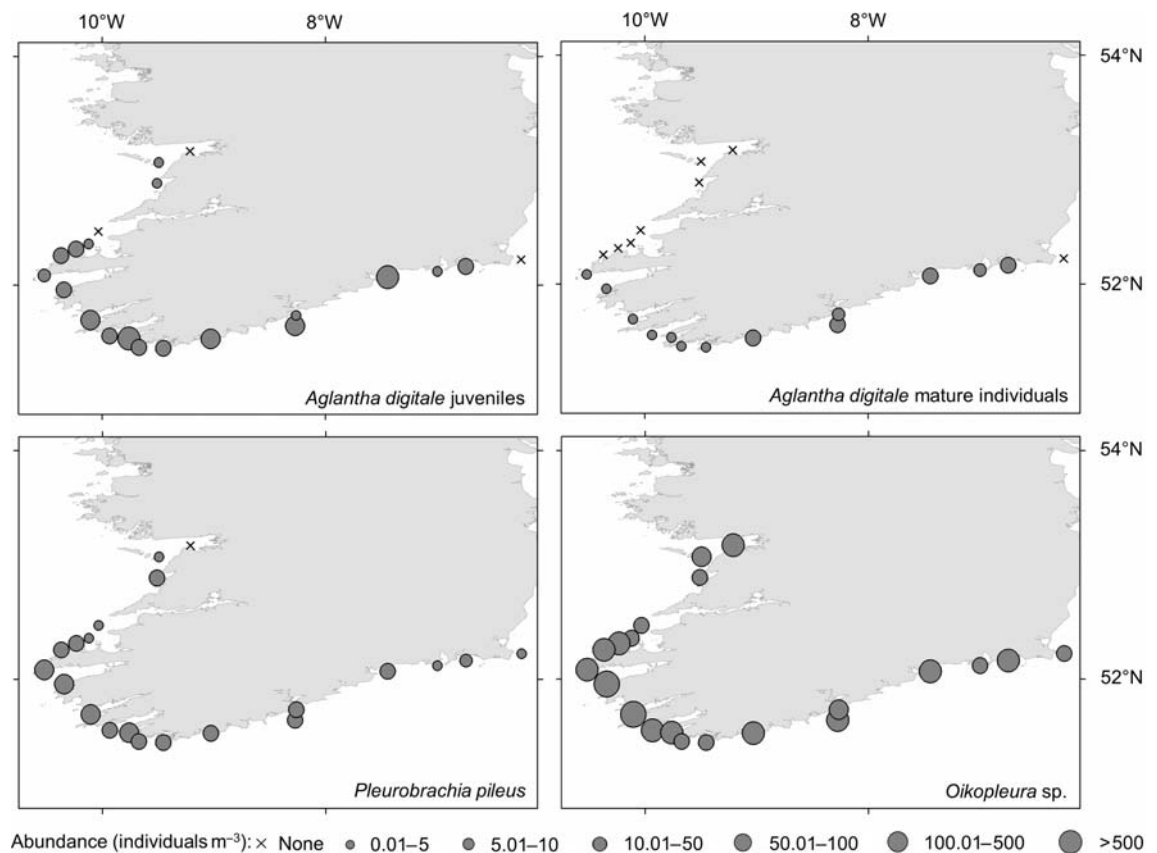


Fig. 3—Abundances of *Aglantha digitale* (juveniles and mature individuals), *Pleurobrachia pileus* and *Oikopleura* sp. recorded at each station throughout the cruise.

LINKING ENVIRONMENTAL VARIABLES  
AND SPECIES DATA

Global BEST analysis between the cnidarian community assemblages and environmental variables at each station (BIO-ENV procedure) gave a rank correlation of  $\rho = 0.408$ , whereby 40.8% of the variation in community assemblage can be explained by four environmental factors: surface salinity, temperature at depth, salinity at depth and fluorescence ( $p < 0.05$ ). Thermo- and halocline intensity and depth did not feature in the ten best selected rank correlations. However, these variables were also among those with the strongest loadings in the PCA.

## DISCUSSION

ENVIRONMENTAL VARIABLES AND  
COMMUNITY COMPOSITION

The present study provides the first snapshot record of how gelatinous zooplankton is distributed around the south and west coasts of Ireland and how environmental factors, such as temperature and salinity, may influence them. A diverse community of small gelatinous zooplankton was observed from the 21 stations sampled. In total, 23 species/genera of gelatinous zooplankton were identified over the course of the study. Many studies have demonstrated that physical discontinuities, such as thermoclines and haloclines, may promote the aggregation of gelatinous zooplankton (reviewed by Graham *et al.* 2001). The benefits of such aggregations may

include enhanced feeding (Frost *et al.* 2010) and reproduction (Mianzan *et al.* 2000). During the present study, the CTD profiles and subsequent analyses revealed that only a few stations had high stratification intensity with regards to temperature and salinity, and those that were stratified had a relatively shallow depth of cline (Fig. 1 and Table 1). Strong tidal mixing may account for the lack of high stratification at most stations, as tidal mixing is known to preclude the formation of seasonal clines in Irish coastal waters (O'Boyle and Silke 2010). While thermocline intensity played an important role in determining the similarity of the stations in terms of environmental variables from the PCA, there was little evidence to suggest that thermocline (or halocline) intensity played an important role in the communities observed. Surface salinity, temperature and salinity at depth and fluorescence, however, were identified as variables that could explain up to 40.8% of the variation in the community assemblages between stations. This could be due to the well-mixed nature of the water column at many of the stations and the broad distribution of the stations across both latitude and longitude, which may affect the temperature and salinity observed. For example, while latitude does not directly determine the abundance or biodiversity of groups like gelatinous zooplankton, latitude-related temperature can affect the community compositions observed (Gibbons 1997).

## SPECIES RECORDED

Hydromedusae were the most diverse group recorded, with several of the fourteen species

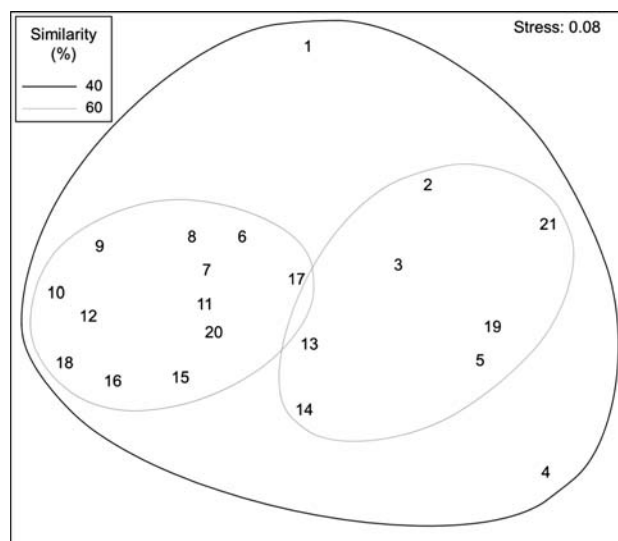


Fig. 4—Non-metric multidimensional scaling of gelatinous zooplankton communities at 21 stations around the west and south coast of Ireland. Based on Bray-Curtis similarities using square-root transformed data.



observed being highly abundant at some of the stations around the coastline (Fig. 3 and Table 2). Such a diversity of meroplanktonic hydromedusae compared to holoplanktonic medusae (represented only by the trachymedusa *A. digitale*) would be expected from these coastal locations, as benthic habitats suitable for the settlement and growth of their sessile stages favour the proliferation of meroplankton rather than holoplanktonic medusae, which tend to be more oceanic (Goy 1991). *Aglantha digitale* was the most widely distributed and abundant hydromedusan species of all, only being absent from samples in the centre of Galway Bay, in the mouth of the Shannon Estuary and in Rosslare Harbour (Fig. 3). *Aglantha digitale* has also been shown to be a voracious predator and display a positive selection for *Oikopleura* sp. (Pagès *et al.* 1996). Indeed, the stations at which *A. digitale* were most abundant corresponded to the stations where *Oikopleura* sp. were most abundant (Fig. 3 and Table 2).

In terms of life history, *A. digitale* is known throughout different geographic regions to vary in the number of generations produced per year (Russell 1938; Pertsova *et al.* 2006; Hosia and Bamstedt 2007). The observed dominance of juveniles (without gonads) compared to adult medusae within the populations is likely to indicate a recruitment event. Mature individuals have, however, been shown to inhabit deeper depths than juveniles at times (Hosia and Bamstedt 2007), and it is therefore possible that adults could have been distributed below the maximum sampling depth of 25m at some stations. It is quite notable that small, immature *A. digitale* were highly abundant, juveniles and mature adults combined reaching maximum densities of 213.6 individuals  $\text{m}^{-3}$  (Table 2). In Norway, this species is reported at average densities of up to 57.4 medusae  $\text{m}^{-3}$  in the 0–50m depth range of one fjord (Pagès *et al.* 1996) and maximum densities of 8.0 and 3.2 medusae  $\text{m}^{-3}$  in a further two fjords, though with a deeper distribution (peak densities within a 100m layer from 200m depth) (Hosia and Bamstedt 2007). The higher densities observed in the current study could potentially be caused by a difference in the sampling methods used, as the other studies sampled much deeper waters. There appears to be no trend between water column depth, however, and the abundance of *A. digitale*. Furthermore, Purcell *et al.* (2010) followed a similar protocol for gelatinous zooplankton sampling (taking net samples from the upper 30m) in the Arctic and only densities of <3.0 individuals  $\text{m}^{-3}$  were recorded.

*Obelia* sp. and *P. quadrata* were both abundant and widely distributed species. These species

were present across the salinity range, although *Obelia* sp. were most abundant at Station 1, which had the lowest salinity and temperature and low fluorescence (Tables 1 and 2). Both species have been shown to dominate the macrozooplankton of coastal waters in other parts of the world, such as New Zealand and Norway, where they were effective predators of copepods (Wear 1965) and microzooplankton (Pagès *et al.* 1996). In New Zealand, *Obelia geniculata* and *P. quadrata* had high clearance rates that were strongly correlated to prey escape response and, for *P. quadrata*, also to prey size. It was therefore suggested that predation by these species was likely to significantly affect the population dynamics of their copepod prey in Wellington Harbour, New Zealand (Fulton and Wear 1985). Thus, such control over prey population dynamics (whether it be fish eggs/larvae or copepods) is also likely in Irish coastal waters, where these and other gelatinous zooplankton species dominate. Some of the most common and abundant species recorded here, such as *A. digitale*, *N. bijuga*, *P. pileus* and *Oikopleura* sp., have holoplanktonic lifecycles. This feature and the presence of an asexual reproduction phase, which is common to many gelatinous zooplankters, allows rapid population growth (Graham *et al.* 2001). The life span of many species is within the range of weeks to months, so in order to quickly react to resource availability and ideal environmental conditions they have the potential to grow quickly and form large aggregations (Arai 1992).

Other species that have been very abundant on a seasonal basis (and in June) in previous Irish studies (Ballard and Myers 2000), such as *Proboscoidactyla stellata*, were rarely observed. Furthermore, while the species richness (i.e. number of species) recorded at each station tended to be slightly lower than that of the studies in the semi-enclosed marine lake Lough Hyne, the overall species richness for the time of year across the stations is largely similar with twelve to fourteen species of hydromedusae and siphonophores in Lough Hyne in June 1993 and 1994 and seventeen species in the present study (Ballard and Myers 2000). Due to a single sampling time point at each station, it is likely that some species were sampled at either the beginning or the end of their time in the plankton (i.e. times of lower abundance) as many species only have a single generation each year or occur in a seasonal succession (Russell 1953). For example Baxter *et al.* (2011) showed that *Lizzia blondina* only became more abundant in Bantry Bay from June onwards and species such as *M. atlantica* were not abundant until late summer/autumn.

The three species of siphonophore recorded throughout the cruise are sometimes considered as more oceanic than the neritic meroplanktonic hydromedusae (i.e. *Obelia* sp. and *P. quadrata*) previously described. They are all commonly recorded species in Irish coastal waters, even as far back as 100 years ago (Browne 1896; Delap 1924; West and Jeal 1971). As previously mentioned, *M. atlantica* has been shown to be highly abundant in Bantry Bay throughout September and October (Baxter *et al.* 2011) and to have a prolonged existence in the plankton.

The most abundant and widespread species of siphonophore recorded in this early summer sampling was *N. bijuga*, a species whose taxonomy remains confused and poorly described (Phil Pugh, pers. comm.). The occurrence of this species in the older literature places its distribution as “Mediterranean and warm Atlantic,” only exceptionally being found to the south and west of Ireland and the Atlantic (Totton and Fraser 1955), with Kirkpatrick and Pugh (1984) taking the view that only *Nanomia cara* occurs in British (and therefore likely Irish) waters. More recent studies from the Pacific have placed the distribution of *N. bijuga* in temperatures from 4.5°C to 16°C (Sherlock and Robison, 2000), similar to temperatures to those experienced in Irish waters. Therefore, it is important to state that it is *N. bijuga* that occurs in the colder, temperate waters of the North Atlantic, such as those off the Irish coast, and that it is this species that commonly occurs in British and Irish waters and not *N. cara*, as previously thought. As *Nanomia* spp siphonophores are commonly observed though often misidentified, identification to species level using morphological features was confirmed with molecular techniques. S. Haddock and L. Christianson from the Monterey Bay Aquarium Research Institute, California, extracted nuclear small subunit ribosomal RNA (18s) from *Nanomia* samples taken during the present study and sequencing confirmed that the species recorded was *N. bijuga*, the same species as found in the Pacific (as referenced above). Although the specimens collected here were far smaller than those found in the Pacific (Atlantic nectophores—0.5–2.0mm diameter and Pacific nectophores—4.0–8.0mm diameter; E.J. Baxter, pers. obs.), they were more abundant in Irish surface waters than in the Pacific, where they are more abundant at depth (in locations where the maximum water depth is far greater; Robison *et al.* 1998).

#### LIMITATIONS OF THE STUDY

Although this study represents a significant effort to document the species abundance and

diversity of small gelatinous zooplankton around the southern Irish coastline over a single point in time, there are obvious unavoidable limitations to the work. When interpreting the abundance data presented here, it is important to note that the net hauls did not allow for any investigation of the vertical distributions of species. In other studies of much deeper systems, gelatinous species have been found to be concentrated in the upper layers of the water column (Pagès *et al.* 1996; Purcell *et al.* 2010), which could have been the case here. It may, however, also mean that the differences between the abundances in Irish waters and those reported worldwide may not be as large. The abundances calculated here were over 25m hauls that were kept consistent throughout the study to remove a further variable of difference in sampling depth between locations. This meant that at some stations the entire water column could not be sampled, so the effects of diel vertical migration (DVM) altering the observed abundances cannot be ruled out (Hays 2003). A further complication of this matter is that samples were not always taken consistently during the day or night; more samples were taken during the day (Table 2). Therefore, low replicates of samples taken during each period do not allow for detailed analyses of the implications of DVM. Although, many small hydromedusan species do not show any marked tendencies for DVM (Russell 1953; Pagès and Gili 1992), other taxa such as chaetognaths have been shown to display size-dependent DVM in Irish waters (Farran, 1945). In general, the polychaete *Tomopteris* sp. was found in samples taken at night, also coincident with the highest densities of *S. elegans* (syn. *Parasagitta elegans*). *Tomopteris* sp. is known to predate upon this species of chaetognath (Rakusa-Suszczewski 1968), indicating that DVM may have affected the abundances of chaetognaths and *Tomopteris* sp. observed.

The distribution of gelatinous zooplankton can also be quite patchy, a feature that is affected by several biological and environmental factors (Arai 1992). The lack of replicates taken, the diameter of the plankton net and the single time-point of sampling in the current study mean that some populations may have been missed. Nonetheless, this study covers over 600km of the coastline, providing species and environmental data that may be important for future studies and provide a baseline for research extended over a longer time period. The ecology of gelatinous zooplankton remains poorly understood in many areas of the world due to difficulties in sampling the soft bodies of most species (Purcell 1997). The abundance and diversity of small gelatinous zooplankton, however, is of increasing importance

as high-density blooms of some hydromedusae and siphonophores can pose serious problems for coastal industries, such as aquaculture (Rodger 2007; Baxter *et al.* 2011).

## ACKNOWLEDGEMENTS

This research survey was carried out as part of the strategy for Science, Technology and Innovation under the Sea Change strategy with the support of the Marine Institute and the Marine Research Sub-programme [National Research Vessels Ship-time Programme and Grant-Aid Agreement No. PBA/AF/08/002(01)] of the National Development Plan 2007–2013. It was co-financed by the European Regional Development Fund. EJB and TKD were supported by the above grant aid. TKD was also supported by the EcoJel project, funded through the INTERREG IVA programme of the European Regional Development Fund. The authors would also like to acknowledge help and support from the crew of the *R/V Celtic Voyager*. The authors would also like to thank G. Reygondeau for his statistical help and the use of his statistical tool-boxes, S.H.D. Haddock and L. Christianson for the molecular work on the *N. bijuga* specimens, and two anonymous reviewers whose comments helped to improve the manuscript.

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