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DIVERSITY AND OCCURRENCE OF SIPHONOPHORES IN IRISH COASTAL WATERS

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ABSTRACT

Siphonophores are at times amongst the most abundant invertebrate zooplankton predators in the oceans. Historically, siphonophores have been under-sampled and of the studies conducted there has been a bias towards oceanic oligotrophic waters where they are considered to be more important. In temperate coastal regions, comparatively less is known about the diversity and abundance of siphonophores, where periodic blooms can restructure the plankton communities and have been correlated with high mortalities in the salmon aquaculture industry. To address this lack of knowledge, plankton samples were collected during two periods (March 2009–March 2011 and April 2014–November 2015) from a coastal embayment in the southwest of Ireland. In total, three siphonophore species were found, the calyphoran *Muggiaea atlantica*, and the physonects, *Nanomia bijuga* and *Agalma elegans*. *Muggiaea atlantica* was the most abundant species (250 colonies m⁻³), with densities an order of magnitude higher than either physonect. *Muggiaea atlantica* displayed a distinct seasonality, whereas the physonect species were sporadic in occurrence. Comparing siphonophores in Bantry Bay and the Western English Channel (Plymouth Marine Laboratory's L4 station) indicates both regions share a similar pattern of inter-annual occurrence and provides novel information on the seasonality and occurrence of siphonophores in Irish coastal waters.

INTRODUCTION

Siphonophores are at times amongst the most abundant non-crustacean invertebrate predators in our oceans (Williams and Conway 1981; Purcell 1981; Pugh 1984; Pugh *et al.* 1997). With 177 species (Mapstone 2015), the majority are described as holoplanktonic, cosmopolitan in distribution and more frequently encountered in deep oceanic waters (Totton 1965; Mackie *et al.* 1987; Mapstone 2014). Historically, they have been under-sampled, largely as a result of the difficulty of sampling very delicate animals (Haddock 2004). As such, compared to crustacean zooplankton, quantitative data on siphonophores are scarce. Where good quantitative data has been gathered, particularly with the use of *in situ* techniques, there has been a bias towards warm oligotrophic waters where diversity was known to be high (Hamner 1975; Mills 1995). However, where submersible transects have been used in regions of low and high productivity, the same siphonophore diversity has been recorded (Mills 1995) and long term sampling in the upwelling region west of Vancouver Island (Denman *et al.* 2013) shows a relatively high diversity (Mapstone 2009).

Recently, the occurrence of siphonophores in coastal waters has received a lot of attention because

of their negative impact on the salmon aquaculture industry. Abundance of the small calyphoran siphonophore, *Muggiaea atlantica* Cunningham, 1892, has been correlated with mass mortalities of farmed salmon in Ireland (Cronin *et al.* 2004; Baxter *et al.* 2011), Scotland (Nickell *et al.* 2010) and Norway (Fosså *et al.* 2003). The abundance of the physonect *Apolemia uaria* Lesueur, 1815 has also been correlated with fish mortalities in Norway (Båmstedt *et al.* 1998). Furthermore, there is growing evidence that unidentified small jellyfish contribute significantly to annual mortality rates in Ireland and Scotland, through injury to the fish and as a vector of secondary bacterial infection (Ferguson *et al.* 2010; Rodger *et al.* 2011a; Rodger *et al.* 2011b). *M. atlantica* can have a dramatic impact on the plankton community through top-down predation on copepods, in Helgoland 1989 unusually high *M. atlantica* densities reduced the copepod population to 10% of the long-term mean (Greve 1994). The decline in copepods released phytoplankton from predation and contributed to changes in nutrient concentrations in the region, causing a late Autumn phytoplankton bloom (Greve 1994). While most siphonophores are considered oceanic, there is evidence that some species can reside in coastal waters for extended periods, i.e., 1–2 years. In Norway a year-long

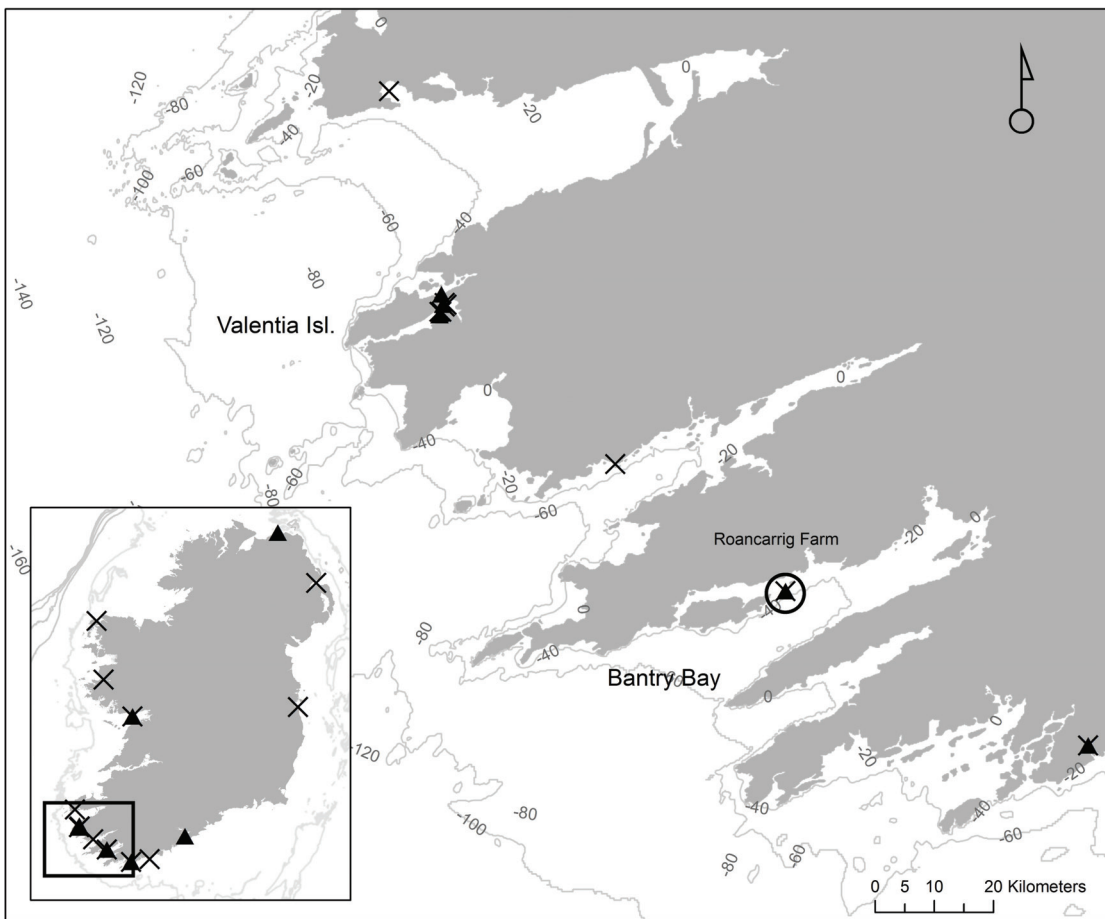


Fig. 1—The southwest coast of Ireland, with the sample site in Bantry Bay and (inset) historic observations of siphonophores around the Irish coastline. Symbols on the map indicate calycophoran (▲) and physonect (x) sightings. The Roanccarrig farm site is represented by the open circle.

study found the physonect *Nanomia cara* Agassiz, 1865 to be semi-resident in deep Norwegian fjords (Hosia and Båmstedt 2008). Observations in the Gulf of Maine showed a similar occurrence of *N. cara*, but recorded higher densities and in shallow areas above 30m depth (Rogers *et al.* 1978; Mills 1995). Studies in Ireland (Baxter *et al.* 2011), Portugal (Marques *et al.* 2006) and Chile (Palma *et al.* 2011), show *M. atlantica* to be present for much of the year and occasionally a dominant member of the macrozooplankton community.

The current knowledge of siphonophores in Irish waters is largely based on qualitative observations from the early twentieth century, with only Ballard and Myers (2000) and Baxter *et al.* (2011) generating quantitative data on small gelatinous zooplankton. Much of the literature referencing the impact on salmon aquaculture is based on post-mortality reports, with no data recorded prior to the events. Here we have gathered an additional two years of zooplankton samples from Bantry Bay to supplement the previous work carried out by Baxter *et al.* (2011) and Baxter (2011). We also

examined all historical occurrences of siphonophores in Irish waters, and then use this combined dataset to comment on the occurrence and seasonality of siphonophores in temperate coastal waters.

MATERIALS AND METHODS

OCCURRENCE AND SEASONALITY

Seasonal abundance of siphonophores was studied over two periods; from March 2009–March 2011 and from April 2014–November 2015. Approximately one year of data from the earlier work was published previously by Baxter *et al.* (2011) and Baxter (2011). The study site was Bantry Bay, southwest Ireland, which is a long southwest facing bay (Fig. 1). Bantry Bay is a smoothly sloping bay with limited estuarine characteristics and is heavily influenced by wind and coastal currents (Raine *et al.* 2010; Raine 2014). During the 2009–11 study, samples were collected using a 0.4m ring net with 200µm mesh (Baxter 2011; Baxter, Roger *et al.* 2011). Five vertical plankton tows were taken

at five stations around the Roancarrig farm, fortnightly during April–October and monthly at all other times (Baxter 2011; Baxter, Roger *et al.* 2011). Assuming 100% efficiency over a short vertical distance, volume was calculated from the depth of water sampled (Baxter 2011; Baxter, Roger *et al.* 2011). During the 2014–15 study, samples were collected using a 0.5 m ring net with 200 μ m mesh with a high length to mouth diameter ratio, designed to minimise damage to gelatinous zooplankton. Triplicate samples were taken at a single station (~ 25 m depth) by hauling vertically from ~ 4 m above the sea bed to the surface and a non-reverse flowmeter was used to calculate the volume of water filtered. The mean volume filtered was $3.5 \pm 0.06 \text{ m}^{-3} (\pm \text{SE})$. All samples were fixed immediately in a 4% formalin sea water solution. Although the ring nets used in each study differed in mouth diameter and length, both nets would be expected to have comparable efficiency (McGowan and Fraundorf 1966).

Samples were analysed using a Zeiss dark-field stereomicroscope and all gelatinous zooplankton was counted and identified to the lowest possible taxonomic level. Physonects consist of a single pneumatophore and multiple nectophores, the number of which depends on species and maturity (Totton 1965). Pneumatophores and nectophores were counted and the presence of other fragments noted, i.e. bracts, palpons and gastrozooids. Physonect abundance was based on pneumatophore counts, and due to their consistent presence there was no necessity to estimate abundance using nectophores counts. For *Muggiaea atlantica* abundance, all identifiable nectophores and bracts were counted. The number of anterior nectophores can be used to represent the total number of polygastric stages, since *Muggiaea* species do not develop a posterior nectophore (Totton 1965). Eudoxid abundance was taken as the number of full intact eudoxids plus the number of eudoxid bracts. Polygastric and eudoxid counts were summed to give a figure for total abundance. Data is presented as the mean number of colonies $\pm 1 \text{ SE m}^{-3}$ for physonects, and mean number of polygastric or eudoxid stages $\pm 1 \text{ SE m}^{-3}$ for *Muggiaea atlantica*.

To examine trends on a wider scale, results from this study were compared with data from a plankton monitoring station called L4 ($50^{\circ} 15.00' \text{ N}$, $4^{\circ} 13.02' \text{ W}$) in the western English Channel. Plymouth Marine Laboratory (PML) collects and maintains the L4 dataset which is stored at the British Oceanographic Data Centre (BODC) (www.BODC.ac.uk). Since 1988 weekly duplicate plankton samples, collected with a WP2 200 μ m net, have been analysed and enumerated for zooplankton species. Siphonophore species have only been identified to species level at L4 since 2009. Data is presented as the mean number of

colonies $\pm 1 \text{ SE m}^{-3}$ for physonects, and mean number of polygastric or eudoxid stages $\pm 1 \text{ SE m}^{-3}$ for *Muggiaea atlantica*. All data points are presented according to the date collected.

PHYSONECT NECTOPHORE ANALYSIS

To investigate possible growth in colony size through the summer, preserved nectophores collected from June to August 2014 were measured across their width. There were insufficient nectophores in other months or in other years to include in the analysis. In addition, the nectophores collected during 2009–11 had deteriorated and were not suitable for measurement. Nectophores that were badly damaged or misshapen were also not used for measurements. All measurements taken from calibrated images using a Micron Optical 5mp digital camera with the stereomicroscope. All analysis was carried out in the R software package (version 3.2.3).

RESULTS

OCCURRENCE AND ABUNDANCE

In total 260 samples were collected on 60 sampling days. 60 samples were taken in Bantry Bay from April 2014 to November 2015 to augment the 200 samples taken from March 2009 to March 2011. Three siphonophore species were recorded in the samples: the calyphoran *Muggiaea atlantica* and two Agalmatidae physonects, *Nanomia bijuga* (Fig. 2) and *Agalma elegans* Sars, 1846. Athorybiid larvae of *A. elegans* (Fig. 3) were also recorded in several samples. *Muggiaea atlantica* and *N. bijuga* were present in all 4 years with *M. atlantica* the most abundant species, being an order of magnitude more abundant than the other species, $234 \pm 14 (\pm \text{SE}) \text{ ind. m}^{-3}$ in 2009 (Fig. 4). *M. atlantica* was present on 33 days, with polygastric and eudoxid stages occurring on 28 days (Fig. 4). The mean percentage of eudoxids across those sample days was $64 \pm 4\% (\pm \text{SE})$. *M. atlantica* was notably absent in 2014, except for a small number of individuals ($< 1 \text{ ind. m}^{-3}$) in November and December. *Nanomia bijuga* were present on 17 (28%) sampling days and the mean density was less than 1 colony m^{-3} on all sampling days except during June 2014 when the mean density reached $9.8 \pm 2.3 (\pm \text{SE}) \text{ colonies m}^{-3}$. *Agalma elegans* polygastrics and athorybiid larvae were not present in all years. Athorybiid larvae were recorded on six days, three of which were consecutive monthly samples from October, November and December in 2014. Their mean density was less than 1 colony m^{-3} on all sample days, except in Nov 2014 when the mean density reached $11.5 \pm 1.7 (\pm \text{SE}) \text{ colonies m}^{-3}$. *Agalma elegans* was present on 4 (7%) sampling days

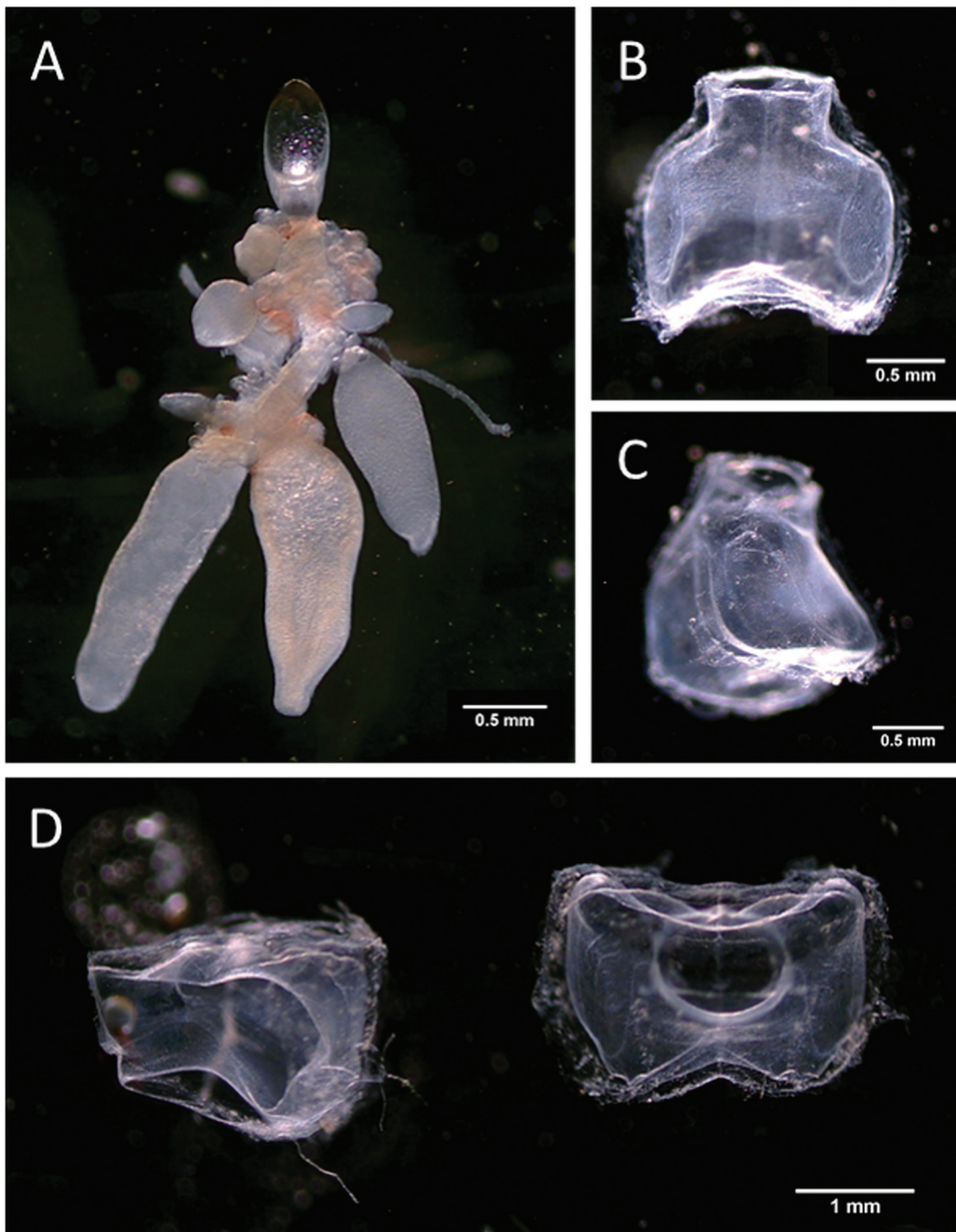


Fig. 2—*Nanomia bijuga* colony from Bantry Bay, September 2015; A, Pneumatophore, nectosome and siphosome, with no nectophores attached; (B–D), *N. bijuga* nectophores from the same sample as colony in (A); (B) Upper view; (C) Lateral view; (D) Lateral view on the left and proximal view on the right.

and never exceeded 1 colony m^{-3} . The presence of *M. atlantica* suggests a distinct seasonality, first appearing in June/July and with peak density in 2009, 2010 and 2013 occurring in October. The presence of *N. bijuga* would also appear to be seasonal, with fifteen of the seventeen positive sampling days between May and August. *Agalma elegans* colonies and athorybiid larvae appear to be aseasonal.

The historical literature contains records for ten siphonophore species (Table 1): six physonects, four calycophorans and one cystonect. Many observations were recorded under older synonyms, which have been updated to the current accepted synonym using the world register of marine species (Schuchert 2016). The literature is biased towards south and west coasts, with the majority of observations coming from Valentia Island (Table 1),

and is dominated by physonects. While all the historic records of the genus *Nanomia* are recorded as the species *Nanomia cara*, molecular phylogenetic analysis provides strong evidence that this commonly encountered physonect is *Nanomia bijuga* (Baxter *et al.* 2012).

COMPARISON WITH THE L4 DATASET

Samples taken on 319 days (2009–15) show the occurrence of siphonophores at L4 displays a marked similarity to the data from Bantry Bay. *Muggiæa atlantica* was the most abundant species, two orders of magnitude higher than either physonect and, like Bantry, showed a distinct seasonality (Fig. 5). Peak abundance was earlier at L4, with highest densities recorded during July to September in 2009, 2010 and 2013 (Fig. 5). The peak abundance of *M. atlantica* at L4 reached more than 2000 ind. m⁻³ on one occasion in July 2010. *M. atlantica* was present on 250 days, with polygastric and eudoxid stages occurring on 215 (67%) days. The mean percentage of eudoxids across those 215 days was $76 \pm 2\%$ (\pm SE). *M. atlantica* was almost completely absent during 2014, with densities of less than 1 ind. m⁻³ during January, September, October and December only. *Nanomia bijuga* was present on 80 (25%) sample days, showing a distinct peak in abundance during June 2014 of 25 nectophores m⁻³, with 35 of those days occurring in May and June. *A. elegans* at L4 was rare, occurring on 16 (5%) days with nectophore counts never exceeding 6 nectophores m⁻³.

NANOMIA NECTOPHORES-GROWTH

11 samples collected during 2014 and 2015 were used to analyse nectophore to pneumatophore ratio and nectophore size, with a total of 116 pneumatophores and 741 nectophores (ratio of 1 to 6.4). The maximum number of nectophores counted with one pneumatophore was 22. There was no apparent increase in nectophores numbers during the peak abundance in 2014, the ratio of nectophores to pneumatophores in June (91 to 550, ratio of 1 to 6) and July (14 to 81, ratio of 1 to 5.8) remained consistent. There was no apparent increase in nectophore size during June, July and August, 2014. Although a significant difference in width was found across the three months (Kruskal-Wallis, $df=2$, $P<0.001$), post hoc analysis showed no change between June (1.42 ± 0.005 mm, $N=80$) and July (1.38 ± 0.007 mm, $N=43$) (Kruskal-Nemenyi, $P>0.05$) and a significant decrease between July and August (0.77 ± 0.009 mm, $N=17$) (Kruskal-Nemenyi, $P<0.01$). Due to the smaller sample size in August ($N=17$) and the possibility that all the nectophores originate from a single colony, the decline in size may not be

representative of the *Nanomia bijuga* population in general. No colonies were found with nectophores still attached, and loose gastrozooids and palpons were observed in many samples. All the pneumatophores found were attached to a stem and the nectosome and siphosome were readily discernible, although usually tightly contracted (Fig. 2). Minute budding zooids were visible on many colonies below the pneumatophore, some of which were beginning to resemble nectophores.

DISCUSSION

ABUNDANCE AND SEASONALITY

In this study, consistent quantitative sampling effort during two two-year periods, found a low diversity of siphonophores species in Irish coastal waters. *Muggiæa atlantica* was the most abundant species, consistently appearing in June/July and increasing in abundance before peaking in October/November (Figs. 4 and 5). The two physonect species did not have a readily observable pattern, appearing to be aseasonal, with *Nanomia bijuga* being more abundant and occurring more frequently than *Agalma elegans*. Despite the largely anecdotal nature of the historic literature, the pattern of occurrence is broadly similar with the patterns found in this study. Historic observations around Ireland are dominated in early years (pre-1960) by physonects, whereas more quantitative methods in later years (post-1960), found *M. atlantica* to be the most abundant species (Table 1). The older literature is most likely biased towards reports of physonects due to their ability to float and their larger size, making them more easily detected by early observers.

There are few comparable studies of siphonophores in similar coastal environments; nonetheless, work in other locations provides interesting comparisons. *Nanomia cara* was the most common species in several Norwegian fjords (Hosia and Båmstedt 2008), with peak abundance in May/June. Hosia and Båmstedt (2008) reported a maximum density of less than 1 colony m⁻³, which is low compared to the 9.8 colonies m⁻³ in Bantry Bay. *Nanomia cara* was recorded throughout the year by Hosia and Båmstedt (2008), and the size and ratio of their nectophores to pneumatophores increased into the winter, indicating growth. Far higher densities of *N. cara* were documented in the Gulf of Maine, with densities reaching up to 7–8 colonies m⁻³ in 1975–6 (Rogers *et al.* 1978) and possibly 50–100 colonies m⁻³ in 1992–3 (Mills 1995). Likewise, in the Gulf of Maine, *N. cara* colonies were found throughout the winter months, however, no seasonality was apparent (Rogers *et al.* 1978). Descriptions by Hosia and Båmstedt (2008) and Rogers *et al.* (1978) indicate

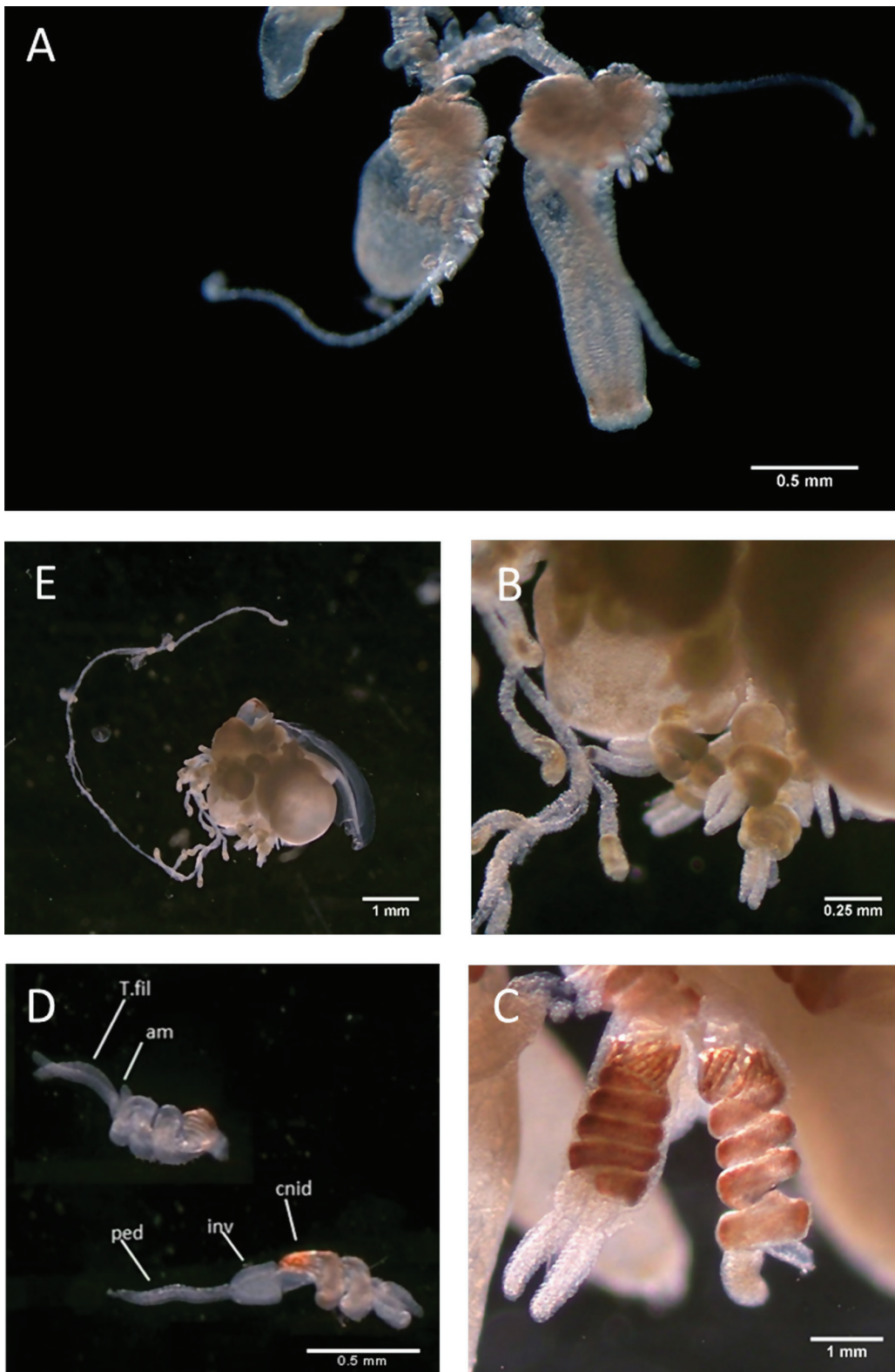


Fig. 3—Physonect zooids: (A), *Nanomia bijuga* colony, part of the stem bearing three young cormidia and their tentacles bearing larval tentilla; (B) small developing definitive tricornuate tentilla on an *Agalma elegans* larva; (C) large definitive tentilla of an adult *A. elegans*; (D) developing definitive tentilla of an adult *A. elegans*; (E) *A. elegans* larva with both larval tentilla and developing definitive tentilla; ped = pedicel, inv = involucre, cnid = first coil of the cnidoband beginning to show red pigment, T.fil = 2 terminal filaments, am = ampulla.

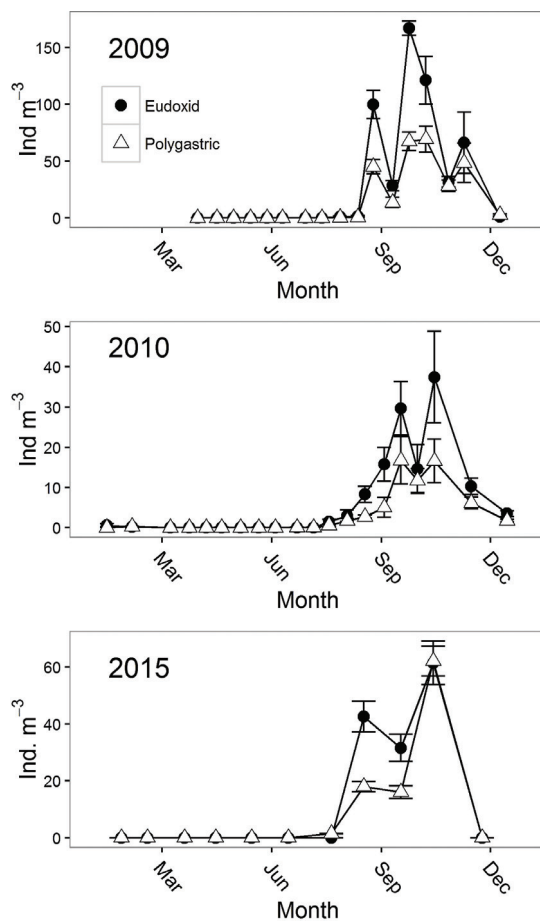


Fig. 4—Mean seasonal abundance of *Muggiaea atlantica* polygastric and eudoxid colonies in Bantry Bay during the years 2009, 2010 and 2015. *Muggiaea atlantica* was almost entirely absent during 2014, therefore the data are not shown.

that colonies can grow large, with nectophores in Norway reaching up to 8mm in width (Hosia and Båmstedt 2008); compared with a maximum width of 2mm in Bantry. Rogers *et al.* (1978) described colonies of 0.2–3.5m in length from a submersible, with 30–40 nectophores per colony in their larger individuals. In contrast, this study generally found smaller colonies, with a ratio of 6.4 nectophores per pneumatophore.

In Chilean coastal waters siphonophore diversity was higher, with 11 species recorded during a series of cruises in 2003 (Palma *et al.* 2007) and 2006 (Palma *et al.* 2011). During winter and spring *M. atlantica* was the dominant siphonophore with peak abundance in Spring ($> 255 \text{ ind. m}^{-3}$) and only one physonect species, *Pyrostephos vanhoeffeni*, ($< 1 \text{ ind. 100m}^{-3}$) was recorded. *Muggiaea atlantica* was the only siphonophore recorded in an estuarine environment in Portugal, peaking in May/June with densities reaching $\sim 360 \text{ colonies m}^{-3}$

(Marques *et al.* 2006). This density is comparable with those recorded in Ireland, whereas the peak density in May/June is much earlier and indicative of the earlier annual plankton blooms at these lower latitudes (Wroblewski 1989).

NANOMIA IDENTIFICATION

Nanomia bijuga was the most abundant physonect throughout the present study, yet it is absent from the historic Irish literature and only first identified from plankton samples in 2009 (Baxter *et al.* 2011; Baxter *et al.* 2012). Baxter *et al.* (2012) found it to be widespread and common along the south and southwest coasts of Ireland, and confirmed the identification as *N. bijuga* by matching Irish and Pacific samples using phylogenetic analysis of the 18S rDNA sequence (Baxter *et al.* 2012). The 18S sequence is highly conserved within cnidarians and can be problematic for species level differentiation (Berntson *et al.* 1999; Cartwright *et al.* 2008). However, *N. bijuga* is the most intensely sequenced siphonophore (Dunn *et al.* 2005) and this match is the best available data to date. The taxonomy and nomenclature of the genus *Nanomia* is confusing and identifying colonies unequivocally using existing descriptions (Agassiz 1865; Bigelow 1911; Totton 1965; Kirkpatrick and Pugh 1984; Bouillon *et al.* 2004) is difficult. The original descriptions of *N. cara* (Agassiz 1865; Fewkes 1888) show a marked similarity to both colonies from Bantry Bay, and the colonies described from Valentia Island during the 1880s (Browne *et al.* 1898). Certain features, including the small size of the colonies with generally less than 10 nectophores and the tiny larval tentilla (Fewkes 1888) (Fig. 3) have likely led to the continued application of the name *Nanomia cara* when it was not appropriate. Likewise, the suggestion that *N. bijuga* was a warm water congener of *N. cara* (Bigelow 1911; Kirkpatrick and Pugh 1984; Mackie *et al.* 1987) and therefore less likely to occur in the north Atlantic may have biased identification. Identifying physonect siphonophores from net caught preserved samples is often difficult as the morphology of nectophores is altered by mechanical disturbance and the preserving agents used. *In situ* sampling and examination of narcotised intact specimens, and further phylogenetic analysis is needed to consolidate the *Nanomia* nomenclature.

OCEANOGRAPHIC DRIVERS

The presence of siphonophores in coastal waters has been correlated with intrusions of oceanic water in Norway (Båmstedt *et al.* 1998; Fosså *et al.* 2003; Hosia and Båmstedt 2008) and Ireland (Cronin *et al.* 2004). Furthermore, in the southwest of Ireland and particularly in Bantry Bay, advective processes have been known to cause intrusion of harmful

Table 1—Historical observations of siphonophores from around the Irish coastline.

Species	Year	Month	Location	Max No.	Paper
<i>Agalmia elegans</i>	1857	Unknown	Dun Laoghaire	unknown	Jeal and West 1970
	1894	Unknown	Isle of Man	'several'	Browne <i>et al.</i> 1898
	1905, 1906	June	Valentia Isl.	1	Delap and Delap 1905; Jeal and West 1970
	1908	June–Sept.	Valentia Isl.	'plentiful'	Delap 1924
	1909	June–July	Valentia Isl.	'a number'	Delap 1924
	1965	June	Galway Bay	Unknown	Fives 1971
	1986	Nov	Killary Harbour	1	Ryan <i>et al.</i> 1986
	2009–11		Bantry Bay, southwest coast	1	Baxter <i>et al.</i> 2011; Baxter <i>et al.</i> 2012
	2015	July–Sept	South & southwest coast	6	Unpublished observations of the authors
	1895–98	March–Dec	Valentia Isl.	very abundant	Browne <i>et al.</i> 1898
<i>Nanomia cara</i>	1905	Unknown	Valentia Isl.	unknown	Jeal and West 1970
	1906	Oct–Nov	Valentia Isl.	'A few'	Jeal and West 1970
	1951	May	Valentia Isl.	'A specimen'	Totton 1954
	1972	Unknown	Galway Bay	2	Boyd <i>et al.</i> 1973
	1986	May/June	Killary	1	Ryan <i>et al.</i> 1986
<i>Nanomia bijuga</i>	2009–10	July–Sept	South & west coasts	3m ⁻³	Baxter <i>et al.</i> 2011; Baxter <i>et al.</i> 2012
<i>Forskalia edwardsi</i> †					
<i>Physophora hydrostatica</i>	1856	Unknown	Belfast Lough, Dun Laoghaire	Unknown	Stephens 1904; Jeal and West 1970
<i>Apolemia uaria</i>	1969	May	Blind Harbour, Mayo	1	Jeal and West 1970
	2011	July	Donegal	1	Unpublished observations of the authors
	2012	Aug	Cork	1	Unpublished observations of the authors
<i>Muggiaca atlantica</i>	1896–98	July–Nov	Valentia Isl.	'abundant'	Browne <i>et al.</i> 1898
	1904	May–Nov	Valentia Isl.	Very abundant	Delap and Delap 1905
	1967–69	Jan–Dec	Galway Bay	2140	Jeal and West 1970; Boyd <i>et al.</i> 1973
	1993–94	Aug–Dec	Lough Hyne	10m ⁻³	Ballard and Myers 2000
	2009–10	June–Feb	Bantry Bay	250m ⁻³	Baxter <i>et al.</i> 2011
<i>Muggiaca kodiii</i>	1971	Sept, Nov	Cork Harbour	1	Boyd 1972
<i>Chelophyes appendiculata</i> ★	1841, 1844	unknown	Giants' Causeway, Bundoran	'several'	Hyndman 1841, Stephens 1904
<i>Sulculeolaria biloba</i> ★†	1899–1905	Apr–July	Valentia Isl.	'several'	Delap and Delap 1905; Jeal and West 1970
<i>Physalia physalis</i>	1835–1970	All seasons	All coasts	very abundant	Stephens 1904; Jeal and West 1970

†Recorded as *Forskalia contorta*★Recorded as *Diphyia elongata* (Hyndman 1841) and *Diphyes elongata* (Stephens 1904)★†Recorded as *Galcolaria* sp (Delap and Delap 1905), was subsequently identified as *S biloba* (Jeal and West 1970).

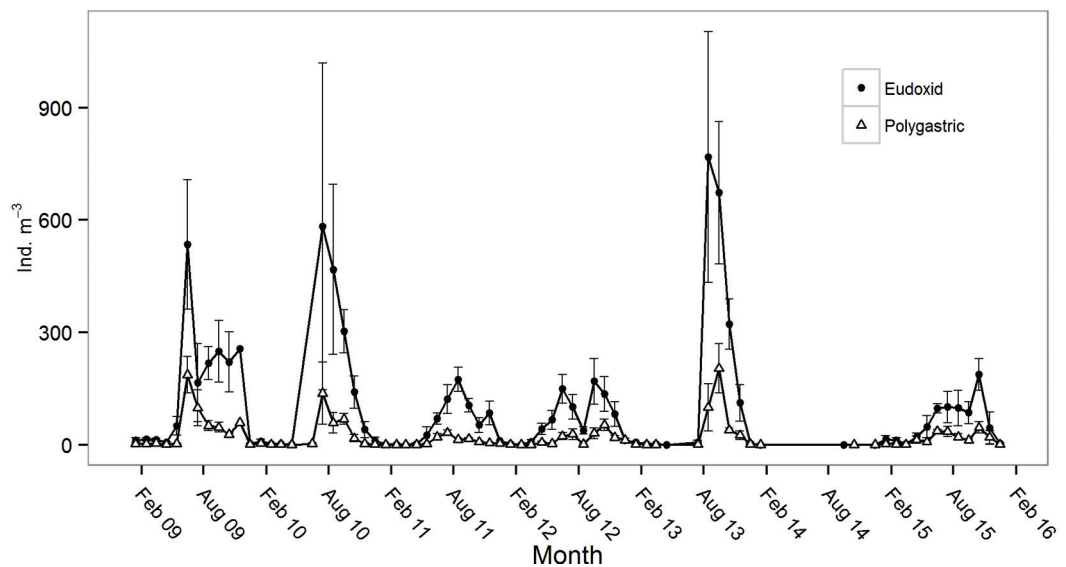


Fig. 5—Mean monthly abundance of *Muggiaea atlantica* polygastric and eudoxid colonies at L4 station (Western English Channel) during the years 2009 to 2015.

algae into the bay through wind driven exchange with shelf waters (Raine and McMahon 1998; Raine *et al.* 2010). While species may be initially advected into a bay, subsequent stratification and front formation can lead to their retention (Graham *et al.* 2001) and the formation of a seasonally resident population. These intrusions may also be transient and brief, for example, in Bantry Bay in November 2014, athorybiid larvae of *A. elegans* appeared suddenly, reaching more than ten colonies m^{-3} but by the following month had disappeared. The occurrence of *A. elegans* in Bantry Bay and L4 is consistent with previous studies, which consider the species to be uncommon, oceanic and epipelagic in distribution (Mapstone 2009). The abundances at both locations are probably indicative of the abundance in oceanic waters lying to the south and southwest of Ireland and England. By inhabiting the epipelagic zone, *A. elegans* would be more likely to be advected into the southern coastlines of Ireland and England by the prevailing westerly and south-westerly winds.

In contrast, *M. atlantica* is a neritic species confined primarily to coastal regions (Mapstone 2009) and displays a distinct seasonality in both Bantry Bay and the western English Channel. The presence of eudoxid stages demonstrates that it is reproducing in Bantry Bay. However, considering the far higher densities recorded at L4 (Figs. 4 and 5), this would suggest that the conditions in Bantry Bay are less favourable than those at L4. Nonetheless, in Bantry Bay in 2009 and 2015, *M. atlantica* reached densities (> 150 colonies m^{-3}) which are known to negatively impact on caged salmon (Cronin *et al.* 2004). The lifecycle of *M. atlantica* including sexual and asexual reproduction, is a trait shared with many bloom-forming scyphozoan jellies (Dawson and

Hamner 2009), and enables *M. atlantica* to reproduce rapidly, particularly when temperature and prey densities are elevated (Carré and Carré 1991; Blackett *et al.* 2014). The negligible presence of *M. atlantica* at both Bantry and L4 in 2014 suggests that both areas are linked and that the population in Bantry may be seeded from surrounding neritic waters. Research into harmful algal blooms (HABs) has demonstrated that the Celtic Sea can be a source of HABs along the southwest coast of Ireland (Raine 2014). A coastal current brings Celtic Sea HABs into the southwest region where local wind patterns can cause an exchange of bay and shelf water, thereby advecting HABs into the Bay (Raine *et al.* 2010). This would indicate that both the oceanography of the Celtic Sea and the southwest region, coupled with distinct changes in the wind patterns, could have a strong influence over the presence of *M. atlantica* in the southwest.

In summary, plankton samples in Bantry Bay demonstrate low siphonophore diversity, with *Muggiaea atlantica* being the most abundant species. *Muggiaea atlantica* displayed a marked seasonality while the physonect species occurred more sporadically. The occurrence of *M. atlantica* and *Nanomia bijuga* in the Irish southwest and the western English Channel appear broadly similar, and *Nanomia bijuga* is more common than previously thought. The patterns displayed here are likely driven by the interactions between coastal and oceanic waters which are highly variable from year to year. Under the current continuous increase in sea temperature, it is plausible that *M. atlantica* will eventually overwinter in Irish coastal waters, establishing a resident population, as has happened in the western English Channel (Blackett *et al.* 2014).

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