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Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods

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Abstract. Scientific debate on whether or not the recent increase in reports of jellyfish outbreaks represents a true rise in their abundance has outlined a lack of reliable records of Cnidaria and Ctenophora. Here we describe different jellyfish data sets produced within the EU programme EURO-BASIN. These data were assembled with the aim of creating an improved baseline and providing new data that can be used to evaluate the current diversity and standing stocks of jellyfish in the North Atlantic region.

Using a net adapted to sample gelatinous zooplankton quantitatively, cnidarians and ctenophores were collected from the epipelagic layer during spring–summer 2010–2013, in inshore and offshore waters between lat 59 and 68° N and long 62° W and 5° E. Jellyfish were also identified and counted in samples opportunistically collected by other sampling equipment in the same region and at two coastal stations in the Bay of Biscay and in the Gulf of Cádiz. Continuous Plankton Recorder (CPR) samples collected in 2009–2012 were re-analysed with the aim of identifying the time and location of cnidarian blooms across the North Atlantic Basin.

Overall the data show high variability in jellyfish abundance and diversity, mainly in relation to different water masses and bathymetry. Higher densities were generally recorded on the shelves, where the communities tend to be more diverse due to the presence of meropelagic medusae. Comparison of net records from the *G.O. Sars* transatlantic cruise shows that information on jellyfish diversity differs significantly depending on the sampling gear utilised. Indeed, the big trawls mostly collect relatively large scyphozoan and hydrozoan species, while small hydrozoans and early stages of Ctenophora are only caught by smaller nets.

Based on CPR data from 2009 to 2012, blooms of cnidarians occurred in all seasons across the whole North Atlantic Basin. Molecular analysis revealed that, contrary to previous hypotheses, the CPR is able to detect blooms of meroplanktonic and holoplanktonic hydrozoans and scyphozoans.

Through combination of different types of data, key jellyfish taxa for the spring–summer period were identified in the northern North Atlantic regions. Key species for the central and southern North Atlantic could be inferred

based on the blooms identified by the CPR survey, although this should be confirmed further by comparison with quantitative data.

The identification by DNA barcoding of 23 jellyfish specimens collected during the EURO-BASIN cruises contributes to increasing the still very limited number of jellyfish sequences available on GenBank.

All observations presented here can be downloaded from PANGAEA (http://doi.pangaea.de/10.1594/PANGAEA.835732).

1 Introduction

In recent years a global increase in jellyfish abundance has been widely debated, but a general consensus on this matter has not yet been achieved. While a part of the scientific community has pointed out increasing frequencies of jellyfish outbreak events in marine and estuarine regions worldwide (e.g. Brodeur et al., 1999; Mills, 2001; Xian et al., 2005; Kawahara et al., 2006; Atrill et al., 2007; Licandro et al., 2010; Brotz et al., 2012), some studies have suggested that the rise in jellyfish abundance is just an up-phase of oscillations that characterise their long-term periodicity (Condon et al., 2013). Within this debate, it has been recognised that there is a lack of reliable jellyfish data (Purcell, 2009; Brotz et al., 2012; Condon et al., 2012). "Jellyfish" is here used to describe a defined plankton functional group, i.e. gelatinous carnivores belonging to the two phyla Cnidaria and Ctenophora. The identification of those groups can be extremely challenging, due to their morphological complexity (Cnidaria, for instance, might be planktonic and benthonic, solitary or colonial, with a large range of different shapes and sizes), their fragility (which can compromise some key morphological features) and the poor knowledge of their taxonomy.

Conventional sampling methodologies are often inappropriate to quantify jellyfish standing stocks and to evaluate the diversity of their populations. A large volume of seawater must be filtered to collect planktonic jellyfish, which are usually highly dispersed (Purcell, 2009). Silk or polyester mesh materials are preferable, as nylon or stramine mesh (traditionally used to collect plankton samples) may severely damage or destroy many delicate species of gelatinous zooplankton (Braconnot, 1971). A slow towing speed (0.5–1 m s^{-1}) is fundamental for the collection of intact specimens that would be otherwise badly damaged.

Here we describe different jellyfish data sets produced within the EU programme EURO-BASIN, assembled with the aim of presenting an up-to-date overview of the diversity and the abundance of North Atlantic jellyfish. The use of different sampling gears provides the opportunity to discuss the limitation of each methodological approach and its influence on the quality of the data.

2 Data

2.1 Net data

Jellyfish were collected with different types of nets in several North Atlantic regions (Fig. 1 and Table 1). Sampling was mainly done using a "gentle" net, hereafter called the "jellynet", which was designed following the specifications of a Régent net, which has been shown to be suitable for quantitative collections of gelatinous organisms (Braconnot, 1971). The jellynet has a 1 m diameter mouth fitted with a 2 m long tapered net and a large non-filtering rigid cod-end 14 cm in diameter and 30 cm in length. The net mesh is knitted polyester with a nominal 800 µm mesh aperture. The jellynet was used to collect jellyfish in the epipelagic layer (0–200 m) across the whole North Atlantic Basin, during three main EURO-BASIN cruises, i.e. the 2012 *Meteor* cruise, the 2012 *Icelandic* cruise and the transatlantic 2013 *G.O. Sars* cruise (Table 2 and Fig. 1). The same net was used to sample jellyfish off the Cumberland Peninsula (Canada) in 2011 (i.e. *Arctic* cruise, Table 2 and Fig. 1).

Jellyfish were also identified and counted in samples opportunistically collected with other sampling gears (Table 3 and Fig. 1). During the *G.O. Sars* cruise they were collected at different depths in the 0–1000 m layer using a standard 1 m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe and Benfield, 2003) (quantitative data), Harstad (Nedreaas and Smedstad, 1987) and macroplankton trawls (qualitative data) (Tables 1 and 3).

Even though the bongo net is not particularly suitable to quantitatively catch jellyfish specimens, samples collected using this gear during 2010 in the Gulf of Cádiz (i.e. IEO data set, Table 3) and in the Bay of Biscay (i.e. AZTI data set, Table 3) were analysed to provide baseline information on the relative abundance and composition of jellyfish populations in the southern regions of the North Atlantic. The identification of jellyfish was, whenever possible, undertaken immediately after collection, with the exception of samples collected off the Cumberland Peninsula, in the Gulf of Cádiz and in the Bay of Biscay that were analysed up to 1 year after collection. The taxonomic identifications, based on key references on jellyfish taxonomy (Russel, 1953; Kramp, 1959; Kirkpatrick and Pugh, 1984; Carré and Carré, 1993; Wrobel and Mills, 1998; Mianzan and Cornelius, 1999; Pugh, 1999; Haddock et al., 2005; Bouillon et al., 2006; Licandro and

Table 1. Sampling gears used to collect jellyfish records in different North Atlantic regions.

Data set	Dates	Area	Lat	Long	Stations	Gear	Mesh size (µm)	Mouth diameter (m)
Arctic cruise	22 Aug–22 Sep 2011	Cumberland Peninsula	63–67° N	62–68° W	1, 2, 3, 4	Jellynet	800	1
Meteor cruise	9–29 Apr 2012	North of Scotland	60–62° N	2° W–1° E	1, 2, 3	Jellynet	800	1
Icelandic cruise	15–25 May 2012	Iceland			241, 246, 248, 255, 267, 272, 273, 274, 281, 290, 292, 299, 305, 307, 315, 324, 330, 332, 333, 338, 340	Jellynet	800	1
G.O. Sars cruise	3–20 May 2013	Bergen–Reykjavik–Nuuk	59–68° N	46° W–5° E	152, 154, 155, 157, 159, 160, 160bis, 161, 162, 163, 165, 166, 167, 168, 169, 170, 171	Jellynet	800	1
					101, 102, 104, 105, 106, 107, 108, 109, 111, 115, 116, 117, 118, 120, 121, 122, 123, 124, 125, 126, 127	MOCNESS	180	1
						Harstad trawl	30 000	20
						Macroplankton trawl	3000	6
IEO	March–November 2010	Gulf of Cádiz	36° N	6° W	T-01, P-01, G-01	Bongo net	200	0.4
AZTI	May 2010	Bay of Biscay	45° N	5° W	58, 67, 68, 69	Bongo net	200	0.4

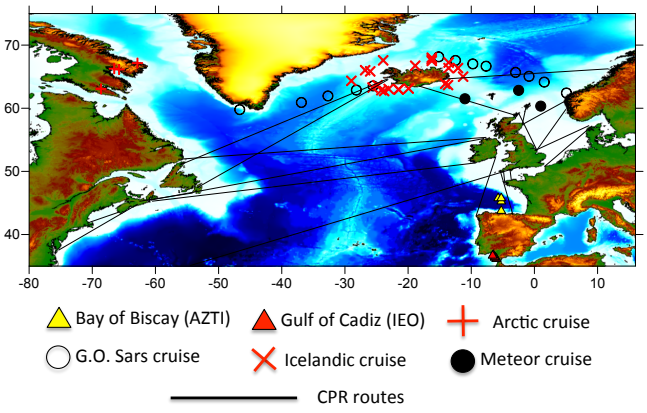

Figure 1. Sampling sites and CPR routes along which jellyfish data were collected.

Carré, 2006; Mills and Haddock, 2007; Collins et al., 2008; Mapstone, 2009; Schuchert, 2012), were cross-checked by several taxonomists to ensure consistency and provide quality control of the data.

2.2 CPR data

The Continuous Plankton Recorder (CPR) is a high-speed plankton sampler that is towed at the surface (7 m nominal depth) by ships of opportunity along their usual shipping routes (Richardson et al., 2006). The CPR is composed of an external body (approximately 50 cm wide × 50 cm tall × 100 cm long) and an internal mechanism containing a spool with two overlapping bands of silk mesh (270 µm aperture). During a tow, the plankton enter through the mouth of the CPR (1.61 cm^2) and are trapped between the filtering silk and the covering silk. The two bands of silk are then progressively wound up on a spool located in a formalin-filled tank, driven by a propeller situated on the back of the sampler. Once back at the laboratory, the internal mechanism is unloaded, the spool is unrolled and the silk is cut into sections that correspond to circa 10 nautical miles.

The visual identification of cnidarian jellyfish tissue and/or nematocysts in CPR samples has been carried out routinely since 1958 (Richardson et al., 2006). Within the project EUROBASIN, CPR samples collected in 2009–2012 along different North Atlantic routes (Fig. 1) were visually reanalysed and those fully covered in jellyfish tissue and nematocysts were classified as records of jellyfish outbreak events (Licandro et al., 2010, Fig. 1). Genetic methods were then used in some CPR samples where swarms events were recorded to identify cnidarian blooming species.

Table 2. List of stations in which jellyfish were collected using the Jellynet. Main sampling information is also indicated. Data from Licandro and Blackett (2014), Licandro and Hosia (2014), Licandro and Kennedy (2014), Licandro and Raab (2014) and Licandro et al. (2014).

Station	Latitude	Longitude	Sampling depth (m)	Time (start, local)	Date	Bottom depth (m)
Arctic cruise						
1	66° 08′43″ N	65° 45′18″ W	150	17:44	22/08/2011	150
2	65° 75′95″ N	65° 91′23″ W	200	11:40	25/08/2011	200
3	67° 08′48″ N	62° 50′82″ W	200	13:33	12/09/2011	334
4	63° 04′00″ N	68° 36′00″ W	200	15:45	22/09/2011	200
Meteor cruise						
1	61° 30′00″ N	10° 59′99″ W	200	07:45	09/04/2012	1350
1	61° 30′00″ N	10° 59′99″ W	200	08:13	09/04/2012	1350
1	61° 30′00″ N	10° 59′99″ W	200	17:27	09/04/2012	1350
1	61° 30′00″ N	10° 59′99″ W	200	17:58	09/04/2012	1350
1	61° 30′01″ N	10° 59′99″ W	200	05:37	10/04/2012	1350
1	61° 29′95″ N	11° 0′06″ W	200	06:07	10/04/2012	1350
1	61° 29′99″ N	11° 0′00″ W	200	18:04	10/04/2012	1350
1	61° 29′99″ N	11° 0′01″ W	200	18:35	10/04/2012	1350
2	62° 50′00‴ N	2° 30′00‴ W	200	16:14	12/04/2012	1300
2	62° 49″99″ N	2° 30′11″ W	200	16:41	12/04/2012	1300
2	62° 50′01″ N	2° 29′98″ W	200	05:54	13/04/2012	1300
2	62° 50′01″ N	2° 29′98″ W	200	06:25	13/04/2012	1300
2	62° 50′04″ N	2° 30′16″ W	400	11:29	13/04/2012	1300
2	62° 50′01″ N	2° 30′11″ W	400	02:30	14/04/2012	1300
2	62° 50′01″ N	2° 30′05″ W	200	04:47	14/04/2012	1300
2	62° 50′01″ N	2° 30′05″ W	200	05:17	14/04/2012	1300
3	60° 20′00″ N	1° 0′01″ E	150	16:14	15/04/2012	165
3	60° 20′00″ N	1° 0′00″ E	150	16:35	15/04/2012	165
3	60° 20′01″ N	1° 0′00″ E	150	01:58	16/04/2012	165
3	60° 20′01″ N	1° 0′00″ E	150	02:22	16/04/2012	165
3	60° 20′01″ N	1° 0′00″ E	150	06:07	16/04/2012	165
3	60° 20′01″ N	1° 0′00″ E	150	06:34	16/04/2012	165
1	61° 30′00″ N	11° 0′01″ W	400	03:34	19/04/2012	1350
1	61° 29′99″ N	11° 0′01″ W	200	05:03	19/04/2012	1350
1	61° 29′99″ N	11° 0′01″ W	200	05:33	19/04/2012	1350
1	61° 30′14″ N	11° 0′04″ W	200	17:26	20/04/2012	1350
1	61° 30′33″ N	11° 0′08″ W	200	17:55	20/04/2012	1350
2	62° 50′00″ N	2° 30′03″ W	400	03:14	23/04/2012	1300
2	62° 50′00″ N	2° 30′03″ W	200	05:18	23/04/2012	1300
2	62° 50′00″ N	2° 30′04″ W	200	05:50	23/04/2012	1300
2	62° 50′00″ N	2° 30′00″ W	200	17:32	23/04/2012	1300
2	62° 50′00″ N	2° 30′01″ W	200	18:00	23/04/2012	1300
1	61° 29′99″ N	10° 59′97″ W	200	17:48	28/04/2012	1350
1	61° 29′99″ N	10° 59′97″ W	200	18:18	28/04/2012	1350
1	61° 29′99″ N	10° 59′98″ W	400	01:58	29/04/2012	1350
1	61° 29′99″ N	10° 59′98″ W	200	05:07	29/04/2012	1350
1	61° 29′99′ N	10° 59′98″ W	200	05:38	29/04/2012	1350

Table 2. Continued.

Station	Latitude	Longitude	Sampling depth (m)	Time (start, local)	Date	Bottom depth (m)
Icelandic cruise						
241	64° 20′36″ N	28° 58′86″ W	400	04:45	16/05/2012	1018
246	65° 50′23″ N	25° 59′73″ W	200	21:29	16/05/2012	217
248	66° 1′22″ N	26° 47′73″ W	400	01:36	17/05/2012	450
255	67° 35′06″ N	23° 56′66″ W	200	22:22	17/05/2012	990
267	66° 44′11″ N	18° 52′16″ W	200	23:32	18/05/2013	698
272	68° 00′11″ N	16° 14′88″ W	200	15:24	19/05/2012	1271
273	67° 44′83″ N	16° 15′32″ W	200	17:57	19/05/2012	963
274	67° 29′91″ N	16° 15′21″ W	200	19:57	19/05/2012	805
281	67° 14′79″ N	13° 34′41″ W	200	14:08	20/05/2012	1540
290	66° 21′49″ N	12° 05′66″ W	200	22:59	21/05/2012	1082
292	66° 21′73″ N	13° 35′04″ W	200	04:10	22/05/2012	261
299	65° 00′11″ N	11° 17′33″ W	200	23:51	22/05/2012	537
305	63° 39′98″ N	13° 40′52″ W	200	22:49	23/05/2012	1125
307	63° 52′11″ N	14° 07′97″ W	200	02:28	24/05/2012	210
315	63° 07′23″ N	19° 54′72″ W	200	02:18	25/05/2012	1079
324	62° 58′09″ N	21° 29′99″ W	400	03:57	26/05/2012	990
324	62° 58′09″ N	21° 29′99″ W	200	02:07	26/05/2012	990
330	63° 03′38″ N	23° 04′65″ W	200	19:36	26/05/2012	896
332	62° 43′05″ N	23° 47′22″ W	200	00:17	27/05/2012	1253
333	62° 51′57″ N	24° 13′97″ W	200	02:54	27/05/2012	707
338	63° 17′02″ N	25° 37′37″ W	200	15:42	27/05/2012	620
340	63° 38′81″ N	24° 50′49″ W	200	20:35	27/05/2012	463
G.O. Sars						
152	62° 25′00″ N	5° 4′23″ E	200	22:30	03/05/2013	212
155	65° 3′33″ N	0° 51′29″ W	200	15:45	05/05/2013	2912
157	65° 45′86″ N	3° 25′04″ W	200	08:40	06/05/2013	3200
159	65° 40′10″ N	3° 8′61″ W	200	19:50	07/05/2013	3693
160	66° 40′30″ N	7° 41′12″ W	200	12:00	08/05/2013	1783
160bis	66° 29′59″ N	8° 24′14″ W	200	23:01	08/05/2013	NA
161	67° 3′28″ N	9° 54′45″ W	200	11:10	09/05/2013	1498
162	67° 33′80″ N	12° 29′71″ W	200	09:20	10/05/2013	1756
163	68° 8′94″ N	15° 10′16″ W	200	11:50	11/05/2013	1376
165	68° 47′65″ N	18° 21′56″ W	200	02:30	12/05/2013	1098
166	63° 29′98″ N	24° 10′18″ W	200	00:40	14/05/2013	224
167	63° 18′37″ N	25° 20′62″ W	200	06:40	15/05/2013	315
168	62° 32′05″ N	28° 5′90″ W	200	19:25	15/05/2013	1439
169	61° 32′71″ N	32° 31′04″ W	200	16:25	16/05/2013	2829
170	60° 31′13″ N	36° 27′64″ W	200	19:35	17/05/2013	2860
171	59° 22′83″ N	46° 11′59″ W	200	14:50	20/05/2013	1100

2.3 Genetic analysis of jellyfish

2.3.1 DNA extraction from CPR samples preserved in formaldehyde

Jellyfish DNA collected from CPR samples was extracted using three different standard protocols.

Protocol 1 followed the methodology developed by Kirby et al. (2006). Briefly, small pieces of tissue from individual specimens (approximately 1 mm length) were placed individually into 180 µL of Chelex solution (Instagene Matrix, Biorad) together with 6 µL of 1 M dithiothreitol (DTT), 4 µL of proteinase K (10 mg mL^{-1}) and 10 µL of 10 % SDS and incubated at 55 °C for 4 h. Each sample was then vortexed briefly and centrifuged at 12 000 *g* for 15 s. Samples were then heated at 105 °C for 10 min in a dry-block heater, vortexed for 10 s and centrifuged at 12 000 *g* for 3 min. The supernatant was then transferred to a Micropure-EZ centrifugal filter device (CFD) (Millipore Corp.) inserted into a Microcon YM-30 CFD (Millipore Corp.) and centrifuged at 14 000 *g* for 8 min. After the Micropure-EZ CFD was discarded, the sample retained in the YM-30 was washed three times with 200 µL of sterile water; the first two washes were

Table 3. List of stations at which jellyfish were collected using different collection gears. Main sampling information is also indicated. Data from Licandro (2014a, b), Licandro and Hosia (2014) and Licandro et al. (2014).

Station	Latitude	Longitude	Sampling depths (m)	Time (start, local)	Date
G.O. Sars cruise					
MOCNESS					
152	62° 25′00″ N	5° 4′23″ E	0 : 25 : 50 : 100	18:50	03/05/2013
154	64° 8′4″ N	1° 33′39″ E	0 : 25 : 50 : 100 : 200 : 400 : 600 : 800 : 1000	19:01	04/05/2013
155	65° 3′33″ N	0° 51′29″ W	200 : 400 : 600 : 800 : 1000	05:12	05/05/2013
157	65° 40′72″ N	2° 59′06″ W	50 : 100 : 200 : 400 : 600 : 800 : 1000	04:22	07/05/2013
160	66° 39′52″ N	7° 38′86″ W	0 : 25 : 50/200 : 400 : 600 : 800 : 1000	06:27	08/05/2013
161	67° 1′39″ N	9° 45′32″ W	0 : 25 : 50 : 100 : 200/400 : 600 : 800 : 100	05:59	09/05/2013
162	67° 33′83″ N	12° 29′88″ W	0 : 25 : 50 : 100 : 200 : 400 : 600 : 800 : 1000	08:31	10/05/2013
163	68° 8′86″ N	15° 9′44″ W	0 : 25 : 50 : 100 : 200 : 400 : 600 : 800 : 1000	06:18	11/05/2013
167	63° 32′09″ N	25° 32′21″ W	0 : 25 : 50 : 100 : 200 : 300	03:22	15/05/2013
168	62° 52′75″ N	28° 11′62″ W	0 : 25 : 50 : 100 : 200/	18:33	15/05/2013
169	61° 56′90″ N	32° 41′45″ W	0 : 25 : 50 : 100 : 200 : 400/600 : 800 : 1000	10:02	16/05/2013
170	60° 54′61″ N	36° 53′51″ W	0 : 25 : 50 : 100 : 200 : 400/800 : 1000	12:37	17/05/2013
171	59° 46′97″ N	46° 39′50″ W	50 : 100 : 200 : 400 : 600 : 800 : 1000	18:34	20/05/2013
Macroplankton trawl					
101	65° 9′30″ N	0° 48′44″ W	290–310	17:24	05/05/2013
102	65° 15′82″ N	0° 54′43″ W	0–700	15:45	05/05/2013
104	65° 39′70″ N	2° 53′58″ W	0–1028	01:58	07/05/2013
105	65° 50′63″ N	3° 54′6″ W	500	18:39	07/05/2013
106	66° 43′66″ N	7° 51′16″ W	0–1000	11:44	08/05/2013
107	67° 4′08″ N	9° 57′89″ W	40–70	10:49	09/05/2013
108	67° 36′33″ N	12° 39′26″ W	30–38	10:52	10/05/2013
109	67° 40′12″ N	12° 56′20″ W	400–420	13:08	10/05/2013
111	68° 11′49″ N	15° 24′08″ W	0–1000	11:35	11/05/2013
115	63° 29′41″ N	25° 37′58″ W	120–150	06:24	15/05/2013
116	63° 0′77″ N	27° 54′33″ W	460	13:25	15/05/2013
117	62° 56′56″ N	28° 3′49″ W	250	15:16	15/05/2013
118	61° 54′55″ N	32° 55′85″ W	490–500	16:31	16/05/2013
120	61° 50′58″ N	33° 16′67″ W	0–1000	20:31	16/05/2013
121	61° 49′10″ N	33° 25′60″ W	695–705	22:14	16/05/2013
122	60° 51′58″ N	36° 48′78″ W	510–520	19:05	17/05/2013
123	60° 51′36″ N	36° 58′74″ W	320–330	20:55	17/05/2013
124	60° 51′37″ N	37° 8′65″ W	630–660	23:40	17/05/2013
125	59° 38′80″ N	46° 23′12″ W	170–200	14:13	20/05/2013
126	59° 40′64″ N	46° 29′94″ W	380	15:33	20/05/2013
127	59° 43′89″ N	46° 34′73″ W	0–1000	16:55	20/05/2013
IEO data set					
Bongo net					
TF-01	36° 8′76″ N	6° 0′96″ W	29	20:05	04/03/2010
SP-01	36° 22′26″ N	6° 16′44″ W	22	03:28	06/03/2010
GD-01	36° 44′70″ N	6° 29′76″ W	16	01:18	07/03/2010
SP-01	36° 22′26″ N	6° 16′44″ W	21	19:22	26/07/2010
GD-02	36° 43′08″ N	6° 32′46″ W	16	21:34	27/07/2010
GD-02	36° 39′96″ N	6° 36′78″ W	40	21:24	09/11/2010
SP-01	36° 24′72″ N	6° 18′06″ W	27	03:00	11/11/2010
TF-01	36° 8′52″ N	6° 2′52″ W	28	02:18	12/11/2010
AZTI data set					
Bongo net					
58	43° 45′ N	5° 15′15″ W	220	12:30	22/05/2010
67	45° 14′97″ N	5° 15′04″ W	206	18:51	23/05/2010
68	45° 45′ N	5° 44″72″ W	208	11:43	24/05/2010
69	45° 45′02″ N	5° 15′, 18″ W	209	02:34	24/05/2010

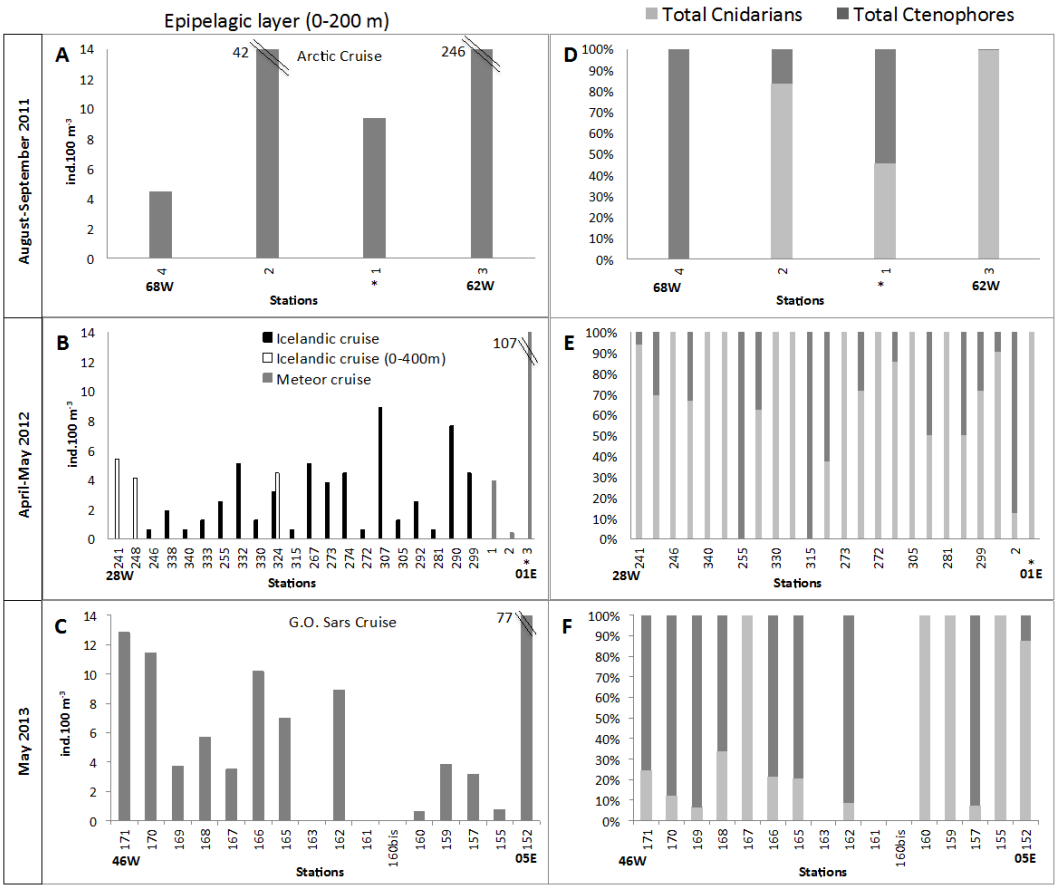

Figure 2. Total jellyfish abundance and relative proportion of Cnidaria and Ctenophora in the stations sampled during the *Arctic* cruise (**a** and **d**), the *Icelandic* and *Meteor* cruise (**b** and **e**) and the *G.O. Sars* cruise (**c** and **f**).

centrifuged at 14 000 *g* for 8 min and the final wash was centrifuged at 14 000 *g* for 5 min. The retained DNA was then recovered. All centrifugation steps were performed at 22 °C.

Protocol 2 consisted of washing the tissues samples in TE buffer then processing the sample either with the MasterPure total DNA and RNA extraction kit (Epicentre Biotechnologies, USA) using protocol B (tissue samples) with an extended proteinase K digestion step of 4–12 h or using DNAzol reagent (Life Technologies, USA) applying procedure for homogenisation of tissues with the optional centrifugation step as described by the manufacturers. DNA pellets were then dissolved in a final volume of 30 µL.

A third protocol was used to extract DNA from jellyfish material embedded in the silk. In this case, approximately one-third of a CPR sample was cut and washed in TE buffer and then total environmental DNA was extracted from it according to a phenol–chloroform-based protocol developed by Ripley et al. (2008).

A number of different polymerase chain reaction (PCR) amplification strategies and markers were used.

In one case, a 540 bp partial, mtDNA 16S rDNA sequence was amplified by PCR using the primers of Cunningham and

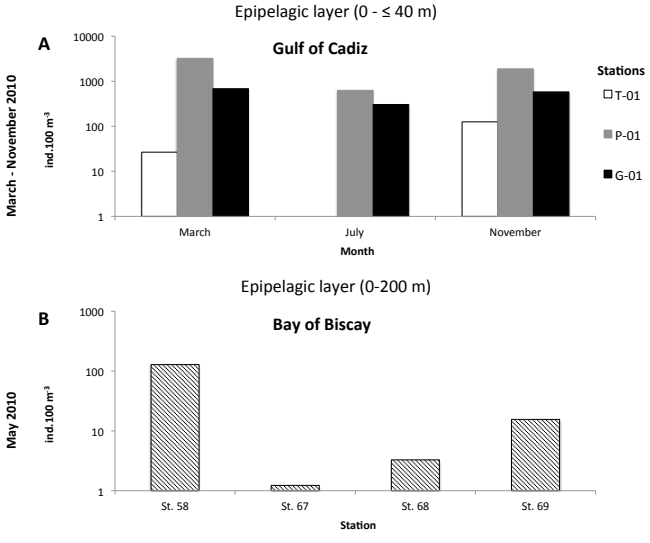

Figure 3. Total jellyfish abundance in the stations sampled in the Gulf of Cádiz **(a)** and in the Bay of Biscay **(b)**.

Table 4. Jellynet data set. List of jellyfish taxa collected in epipelagic waters (0–200 m) in different North Atlantic regions. *Taxon found only in samples collected at 0–400 m depth. Data from Licandro et al. (2014).

North Atlantic region	Cumberland shelf	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea	Icelandic Sea	North of Scotland
Stations	1–4	171	166–170	152–165	241–340	1–3
Cruise	*Arctic*	*G.O. Sars* cruise			*Icelandic*	*Meteor*
Latitude	63–67° N	59° N	60–63° N	62–68° N	62–68° N	60–62° N
Longitude	62–68° W	46° W	36–24° W	18° W–5° E	11–28° W	2° W–1° E
Time	Day/night	Day	Day/night	Day/night	Day/night	Day/night
Date	22 Aug–22 Sep 2011	20 May 2013	14–17 May 2013	3–12 May 2013	16–25 May 2012	9–29 Apr 2012
Cnidaria						
Hydrozoa						
Order Trachymedusae						
Family Rhopalonematidae						
Aglantha digitale	+		+	+	+	+
Pantachogon haeckeli		+				
Pantachogon spp.		+				
Order Narcomedusae						
Family Aeginidae						
Aeginopsis laurentii	+					
Order Leptothecata						
Family Phialellidae						
Phialella quadrata						+
Family Mitrocomidae						
Cosmetira pilosella				+		
Mitrocomella polydiademata				+		
Family Tiarannidae						
Modeeria rotunda				+		
Family Tiaropsidae						
Tiaropsis multicirrata				+		
Family Campanulariidae						
Clytia islandica				+		
Clytia spp.				+	+	+
Obelia spp.				+		+
Order Siphonophorae						
Suborder Physonectae						
Physonectae larva				+		+
Family Agalmatidae						
Agalma elegans						+
Nanomia cara			+	+	+	+
Family Physophoridae						
Physophora hydrostatica						+
Suborder Calycophorae						
Family Diphyidae						
Dimophyes arctica	+	+	+			+
Lensia achilles				+	+*	
Lensia conoidea					+	+
Lensia spp.				+	+	+
Muggiaea atlantica						+
Family Clausophyidae						
Chuniphyes multidentata					+*	+
Order Anthoathecata						
Family Corymorphidae						
Euphysa aurata						+
Aplanulata *incerta sedis*						
Plotocnide borealis						+
Family Rathkeidae						
Rathkea octopunctata						+
Lizzia blondina						+
Family Pandeidae						
Amphinema rugosum						+
Family Zancleidae						
Zanclea spp.			+			

Table 4. Continued.

North Atlantic region	Cumberland shelf	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea	Icelandic Sea	North of Scotland
Stations	1–4	171	166–170	152–165	241–340	1–3
Cruise	*Arctic*	*G.O. Sars* cruise			*Icelandic*	*Meteor*
Latitude	63–67° N	59° N	60–63° N	62–68° N	62–68° N	60–62° N
Longitude	62–68° W	46° W	36–24° W	18° W–5° E	11–28° W	2° W–1° E
Time	Day/night	Day	Day/night	Day/night	Day/night	Day/night
Date	22 Aug–22 Sep 2011	20 May 2013	14–17 May 2013	3–12 May 2013	16–25 May 2012	9–29 Apr 2012
Ctenophora						
Order Cydippida						
Cydippida larva			+	+		
Family Mertensiidae						
Mertensia ovum	+	+				
Mertensiidae spp.		+			+	
Order Beroida						
Family Beroidae						
Beroe cucumis			+	+	+	+
Beroe gracilis			+			+
Beroe spp.	+	+		+	+	+
Bolinopsis infundibulum				+		

Buss (1993) and Schroth et al. (2002). The PCR involved an initial denaturation step at 94 °C (1 min), followed by 40 or 50 cycles of 94 (1 min), 51 (1 min) and 72 °C (1 min) and a final extension of 72 °C (10 min).

The PCR products were visualised on a 1 % agarose gel and either purified using Montage spin columns (Millipore) or treated with ExoSAPIT (Illustra, supplied by VWR) to remove primer dimers. Purified PCR products were then sequenced commercially (MWG Biotech, Germany, or Source Bioscience, Nottingham, UK) using the amplification primers as sequencing primers. Alternatively Sanger sequencing of PCR products was performed using a BigDye kit (Applied Biosystems, USA), with either the forward or reverse primer for amplification, according to manufacturer instructions and capillary electrophoresis of sequencing products carried out at Source Bioscience.

2.3.2 DNA extraction from net samples preserved in ethanol

Jellyfish DNA was extracted from about 80 ethanol-preserved cnidarian specimens, which were collected during the EURO-BASIN cruises and identified on board or shortly after collection. DNA extraction followed a standard SDS, proteinase K, phenol–chloroform protocol. Briefly, $\sim 1\,mm^3$ of jellyfish tissue was placed into a 1.5 mL Eppendorf tube containing 400 µL cell lysis buffer (10 mM Tris-Cl pH 7.9, 100 mM EDTA and 0.5 % SDS) with 4 µL of proteinase K solution (10 mg mL^{-1}) and digested for 4 h at 55 °C. Following a phenol–chloroform purification the DNA was recovered by precipitation using NaCl and EtOH and resuspended in 40 µL of nanopure H_2O. A 1 µL aliquot of the extracted DNA was then used as template in a PCR.

A 540 bp partial, mtDNA 16S rDNA sequence was then amplified by PCR using the primers of Cunningham and Buss (1993) and Schroth et al. (2002) and the thermal profile described above. PCR products were visualised on a 1 % agarose gel and purified using Montage spin columns (Millipore). Purified PCR products were then sequenced commercially (MWG Biotech) using the amplification primers as sequencing primers.

Overall 23 cnidarian taxa were successfully sequenced and published on GenBank (Table 9).

2.3.3 DNA sequence analysis

Sequence identity of CPR cnidarian tissue was established first by comparison with public repositories and private databases of Cnidaria DNA sequences taken from plankton net samples in different regions of the North Atlantic. Further analysis was performed by aligning DNA sequences with Cnidaria sequences from public databases for the same DNA marker using Bioedit (Hall et al., 1999). These were trimmed and exported into MEGA 5.1 (Katoh et al., 1995) to produce phylogenies using neighbour-joining methods with a Kimura two-parameter substitution model and tested using 1000 bootstrap confidence intervals.

3 Results

3.1 Jellyfish abundance and diversity in epipelagic waters

3.1.1 Jellynet data

The data collected in epipelagic waters between 2011 and 2013 showed high variability in jellyfish standing stocks across the northern North Atlantic Basin (Fig. 2). Total jellyfish abundance (Fig. 2a–c) generally ranged between 0.42 and 12 individuals $100\,m^{-3}$. A few stations located on the

eastern (i.e. station 3, *Meteor* cruise; station 152, *G.O. Sars* cruise) and western (stations 1 and 2, *Arctic* cruise) Atlantic shelves exhibited elevated abundance with densities an order of magnitude greater (max. 246 individuals 100 m^{-3}).

In the 0–200 m layer, cnidarians were typically more abundant than ctenophores (Fig. 2d–f), even though in some stations (station 4, *Arctic* cruise; stations 255 and 315, *Icelandic* cruise; station 162, *G.O. Sars* cruise) ctenophores made up 90–100 % of the total jellyfish abundance.

Overall 27 cnidarian and 5 ctenophore taxa were identified and counted in North Atlantic epipelagic waters (Table 4). Jellyfish populations were more diversified in the northeastern Atlantic, mainly due to the presence of meroplanktonic species of Anthomedusae and Leptomedusae. The trachymedusa *Aglantha digitale*, the siphonophores *Nanomia cara* and *Dimophyes arctica*, and the ctenophores *Beroe* spp. and Mertensidae were the most common taxa in epipelagic waters across the northern North Atlantic region.

3.1.2 Bongo data

In shallow waters in the Gulf of Cádiz, jellyfish distribution was highly variable in space and time. They were relatively more abundant in early spring and autumn (Fig. 3a), with high peaks due to swarms of the siphonophores *Muggiaea atlantica* and *Muggiaea kochi* (not shown). Generally only cnidarians were found in the samples (Table 5), except in March 2010, when the ctenophore *Hormiphora* spp. represented 11 and 63 % of the total jellyfish abundance respectively at stations P-01 and G-01 (not shown).

Jellyfish species typically distributed in cold-temperate and warm-water regions were recorded in the Bay of Biscay (Table 5). Their densities in May 2010 suggest that jellyfish are less abundant in this region than in the Gulf of Cádiz (Fig. 3b), even though this should be further verified.

3.2 Jellyfish abundance and diversity in the 0–1000 m layer

3.2.1 MOCNESS data

The data collected at different depths in the 0–1000 m layer during the *G.O. Sars* cruise show that in early May 2013 the bulk of the jellyfish population was concentrated in the mesopelagic layer (200–1000 m depth) off the Norwegian trench and in the Icelandic Sea (Fig. 4). In contrast, in the Irminger and Labrador seas, jellyfish were more evenly distributed across the water column or mainly concentrated close to the surface (Fig. 4).

Species diversity was generally higher in the mesopelagic than in the epipelagic layer (Fig. 5), with the highest number of species being recorded below 400 m in the Irminger and Labrador seas.

Table 5. Bongo net data set. List of jellyfish taxa collected in epipelagic waters (0–200 m or 0–bottom) in 2010, in the Gulf of Cádiz and Bay of Biscay. Data from Licandro et al. (2014).

North Atlantic region	Gulf of Cádiz	Bay of Biscay
Latitude	36° N	43–45° N
Longitude	6° W	5° W
Maximum sampling depth (m)	16–40	206–220
Time	Day/night	Day/night
Month	03, 07, 11 2010	05, 2010
Cnidaria		
Hydrozoa		
Order Trachymedusae		
Family Geryoniidae		
Liriope tetraphylla	+	+
Family Rhopalonematidae		
Aglaura hemistoma	+	
Aglantha digitale		+
Order Leptothecata		
Family Lovenellidae		
Eucheilota paradoxica	+	
Family Campanulariidae		
Clytia hemisphaerica	+	
Clytia spp.	+	
Obelia spp.	+	
Order Siphonophorae		
Suborder Physonectae		
Physonectae larva	+	
Family Agalmatidae		
Agalma elegans		+
Suborder Calycophorae		
Family Abylidae		
Abylopsis tetragona	+	
Bassia bassensis	+	
Family Diphyidae		
Chelophyes appendiculata	+	+
Eudoxoides spiralis	+	
Lensia conoidea		+
Muggiaea atlantica	+	+
Muggiaea kochi	+	+
Order Anthoathecata		
Family Coryniidae		
Corynidae spp.	+	
Ctenophora		
Order Cydippida		
Family Pleurobrachiidae		
Hormiphora spp.	+	

3.3 Jellyfish diversity: comparison of different sampling gears

Thirty-seven species/genera of jellyfish were identified in the MOCNESS samples (Table 6), while 32 taxa were counted from samples collected with the macroplankton and Harstad trawls (Table 7).

The comparison of the data collected with different sampling methodologies during the *G.O. Sars* transatlantic cruise showed that only a few dominant species (e.g. *Aglantha digitale*, *Nanomia cara*, *Beroe cucumis*) were consistently sampled by all the gears. Relatively large species (e.g. *Atolla* spp., *Pelagia noctiluca*, *Praya* spp., *Vogtia* spp.) were mostly

Table 6. *G.O. Sars* MOCNESS data set. List of jellyfish taxa collected in the 0–1000 m layer, in different North Atlantic regions. Data from Licandro et al. (2014).

North Atlantic region	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea
Stations	171	166–170	152–165
Cruise		*G.O. Sars* cruise	
Latitude	59° N	60–63° N	62–68° N
Longitude	46° W	36–24° W	18° W–5° E
Time	Day	Day/night	Day/night
Date	20 May 2013	14–17 May 2013	3–12 May 2013
Cnidaria			
Hydrozoa			
Order Trachymedusae			
Family Halicreatidae			
Botrynema brucei	+	+	
Halicreas minimum	+	+	
Halicreatidae spp.	+	+	
Family Rhopalonematidae			
Aglantha digitale	+	+	+
Crossota rufobrunnea	+	+	
Pantachogon haeckeli	+	+	
Sminthea arctica			+
Rhopalonematidae spp.	+	+	
Order Narcomedusae			
Family Aeginidae			
Aeginura grimaldii	+	+	
Family Cuninidae			
Solmissus incisa	+		
Order Leptothecata			
Family Mitrocomidae			
Halopsis ocellata			+
Mitrocomella polydiademata			+
Family Tiarannidae			
Chromatonema rubrum	+	+	
Family Campanulariidae			
Clytia islandica			+
Obelia spp.			+
Order Siphonophorae			
Suborder Physonectae			
Family Agalmatidae			
Marrus orthocanna			+
Nanomia cara	+	+	+
Suborder Calycophorae			
Family Hippopodiidae			
Vogtia serrata	+		
Family Diphyidae			
Dimophyes arctica	+	+	+
Gilia reticulata	+	+	+
Lensia achilles	+	+	
Lensia conoidea		+	+
Lensia hunter	+	+	
Muggiaea bargmannea	+	+	+
Family Clausophyidae			
Chuniphyes multidentata	+	+	
Crystallophyes amygdalina	+	+	+
Heteropyramis crystallina	+	+	
Family Sphaeronectidae			
Sphaeronectes spp.			+
Order Anthoathecata			
Family Hydractiniidae			
Hydractinia areolata			+
Family Tubulariidae			
Hybocodon spp.			+

Table 6. Continued.

North Atlantic region	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea
Stations	171	166–170	152–165
Cruise		*G.O. Sars* cruise	
Latitude	59° N	60–63° N	62–68° N
Longitude	46° W	36–24° W	18° W–5° E
Time	Day	Day/night	Day/night
Date	20 May 2013	14–17 May 2013	3–12 May 2013
Scyphozoa			
Family Atollidae			
Atolla parva			+
Atolla wyvillei	+	+	
Family Periphyllidae			
Periphylla periphylla	+	+	
CTENOPHORA			
Order Cydippida			
Unidentified Cydippid	+	+	+
Family Mertensiidae			
Mertensia ovum			+
Mertensiidae spp.			+
Family Euplokamidae			
Euplokamis spp.			+
Order Lobata			
Family Bolinopsidae			
Bolinopsis infundibulum		+	+
Order Beroida			
Family Beroidae			
Beroe abyssicola			+
Beroe cucumis		+	+

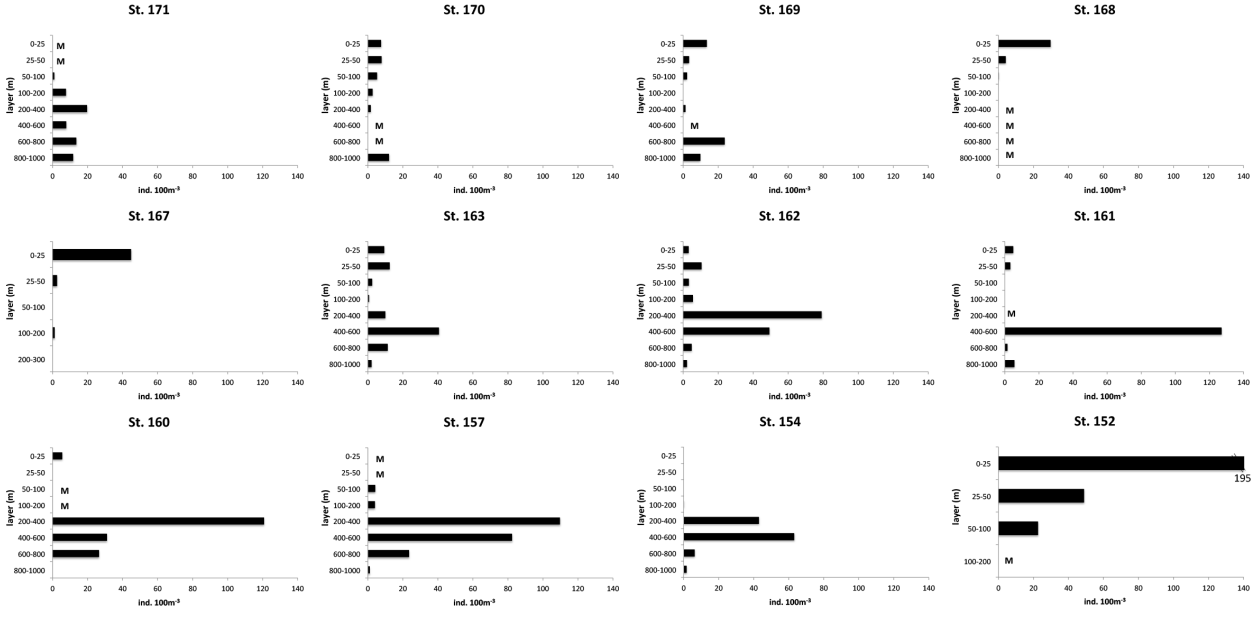

Figure 4. MOCNESS data set. Abundance of jellyfish at different depths in the 0–1000 m layer. Please note the shallower depths in stations 152 and 167. Station 155 is not shown. M: samples preserved in formalin, not yet analysed.

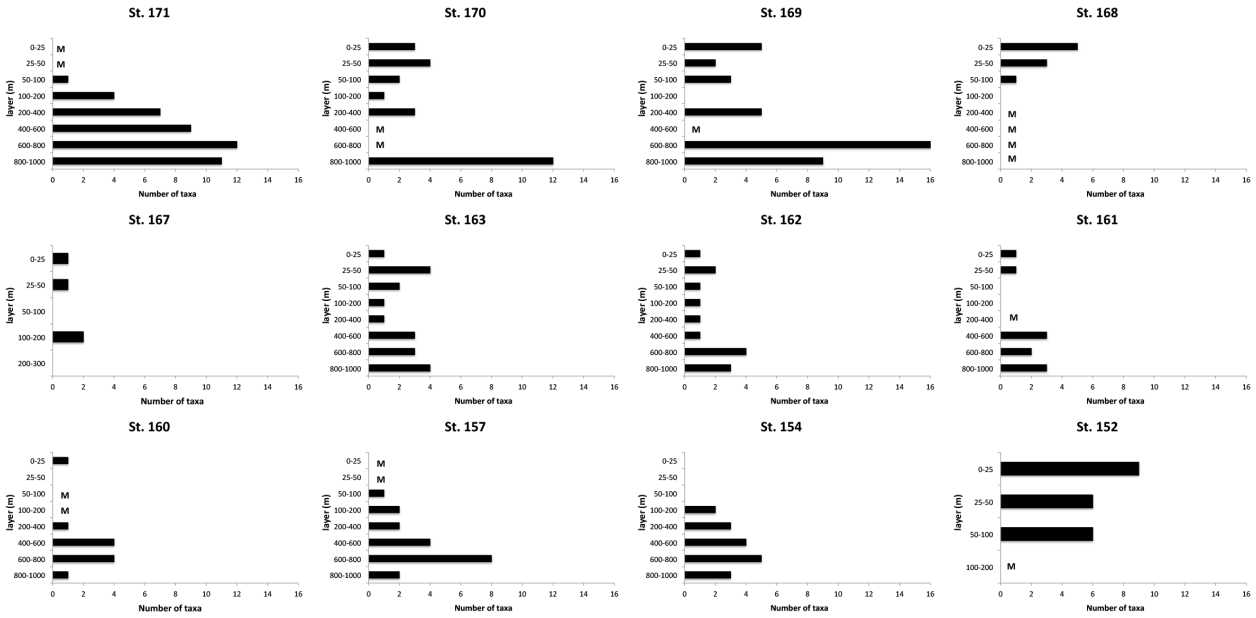

Figure 5. MOCNESS data set. Number of jellyfish taxa found at different depths in the 0–1000 m layer. Please note the shallower depths in stations 152 and 167. Station 155 is not shown. M: samples preserved in formalin, not yet analysed.

collected by big trawls (Table 7), while small hydrozoans (e.g. *Clytia* spp., *Gilia* spp., *Muggiaea* spp.) and early stages of Ctenophora were only caught by the smaller nets, such as the jellynet and the MOCNESS (Tables 4 and 6).

3.4 Jellyfish blooms as identified by the CPR

Based on CPR deployments from 2009 to 2012, jellyfish blooms occurred in all seasons, inshore and offshore, across the whole North Atlantic Basin (Fig. 6). Genetic analysis of jellyfish material collected from CPR samples identified blooms of small hydrozoans as well as relatively big scyphomedusae (Table 8). Among the first group, different species of colonial siphonophores were swarming inshore and offshore from summer to early autumn (Fig. 7). In the second group, blooms of the holopelagic cnidarian *Pelagia noctiluca* were recorded inshore and offshore from spring to late autumn, while swarms of the meropelagic *Cyanea* sp. were recorded in summer on the eastern and western Atlantic shelf.

4 Discussion

Sampling jellyfish is challenging as these organisms are delicate and their populations are often highly dispersed or unevenly distributed (Purcell, 2009). Conventional nets, which are usually made with monofilament woven nylon, often irremediably damage many delicate species of Cnidaria and Ctenophora, while softer materials such as silk or knitted polyester have been shown to better preserve the delicate bodies of gelatinous zooplankton (Braconnot, 1971; Raskoff

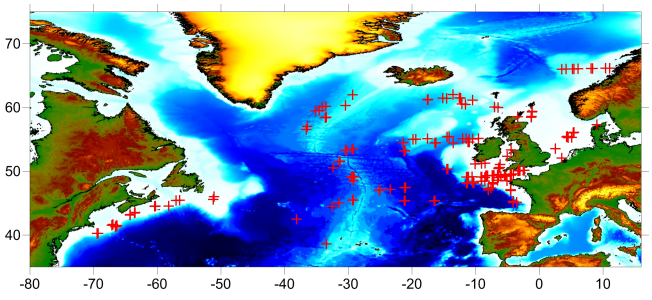

Figure 6. Jellyfish swarms recorded by the Continuous Plankton Recorder in 2009–2012.

et al., 2003). The relatively small mouth opening characterising standard plankton nets (e.g. circa 50 cm mouth diameter in bongo and WP2 nets) limits the volume of seawater filtered and therefore is not appropriate to provide quantitative records of jellyfish. Even though 200 µm mesh size might be considered the most suitable to collect small hydromedusae (e.g. Cornelius, 1995), comparisons of samples collected with 300 and 700 µm mesh demonstrated that the latter size represents the best compromise to quantitatively catch meso- and macroplanktonic gelatinous zooplankton, whilst limiting damage to their soft tissues (Braconnot, 1971; Buecher, 1997, 1999).

The data collected in epipelagic waters by the jellynet in the northern North Atlantic regions showed high variability in jellyfish standing stocks, with higher densities generally observed on the eastern and western North Atlantic shelves. Jellyfish diversity also varied, mainly in relation to different

Table 7. *G.O. Sars*, Harstad and macroplankton data set. List of jellyfish taxa collected in the 0–1000 m layer, in different North Atlantic regions. Data from Licandro et al. (2014).

North Atlantic region	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea
Stations	125–127	115–124	101–111
Cruise		*G.O. Sars* cruise	
Latitude	59° N	60–63° N	65–68° N
Longitude	46° W	36–25° W	15–01° W
Time	Day	Day/night	Day/night
Date	20 May 2013	15–17 May 2013	5–11 May 2013
Cnidaria			
Hydrozoa			
Order Trachymedusae			
Family Halicreatidae			
Halicreas minimum	+	+	
Halitrephes maasi	+	+	
Halicreatidae spp.	+	+	
Family Rhopalonematidae			
Aglantha digitale	+	+	+
Colobonema sericeum	+	+	
Crossota rufobrunnea		+	
Pantachogon haeckeli	+	+	
Rhopalonematidae spp.		+	
Order Narcomedusae			
Family Aeginidae			
Aeginura grimaldii	+	+	
Family Cuninidae			
Solmissus incisa	+	+	
Order Leptothecata			
Family Laodiceidae			
Ptychogena lactea			+
Family Tiarannidae			
Chromatonema rubrum		+	
Modeeria rotunda	+	+	
Order Siphonophorae			
Suborder Physonectae			
Family Agalmatidae			
Marrus orthocanna			+
Nanomia cara		+	
Suborder Calycophorae			
Family Prayinae			
Praya dubia	+	+	
Family Hippopodiidae			
Vogtia glabra	+	+	
Vogtia serrata	+	+	
Family Diphyidae			
Dimophyes arctica	+		+
Lensia conoidea		+	
Nectodamas diomedeae		+	
Family Clausophyidae			
Chuniphyes multidentata	+	+	
Order Anthoathecata			
Family Bythotiaridae			
Bythotiara murrayi		+	

Table 7. Continued.

North Atlantic region	Labrador Sea	Irminger Sea	Norwegian/Icelandic Sea
Stations	125–127	115–124	101–111
Cruise		*G.O. Sars* cruise	
Latitude	59° N	60–63° N	65–68° N
Longitude	46° W	36–25° W	15–01° W
Time	Day	Day/night	Day/night
Date	20 May 2013	15–17 May 2013	5–11 May 2013
Scyphozoa			
Family Atollidae			
Atolla chuni		+	
Atolla parva		+	+
Atolla vanhoeffeni	+	+	
Atolla wyvillei	+	+	
Atolla sp.		+	+
Family Periphyllidae			
Periphylla periphylla	+	+	
Family Pelagiidae			
Pelagia noctiluca		+	+
Ctenophora			
Order Cydippida			
Family Mertensiidae			
Mertensia ovum			+
Order Beroida			
Family Beroidae			
Beroe abyssicola			+
Beroe cucumis		+	+
Beroe gracilis		+	
Beroe spp.			+

water masses and bathymetry. The populations were less diverse in Arctic waters than on the northeastern Atlantic shelf, where more meropelagic medusae are present.

In agreement with previous studies (Hosia et al., 2008; Purcell, 2009, and references therein), a comparison of records collected with different nets during the *G.O. Sars* transatlantic cruise confirms that different sampling gears provide different information on jellyfish populations. Indeed, the big trawls (i.e. ≥ 6 m mouth opening and 3 cm mesh size in this study) mostly collected relatively large scyphozoan and hydrozoan species such as *Atolla* spp., *Pelagia* spp., *Praya* spp. and *Vogtia* spp., due to the large mesh size and large volume filtered. Small hydrozoans (e.g. *Clytia* spp., *Gilia* spp., *Muggiaea* spp.) and early stages of Ctenophora were only caught by the smaller nets (i.e. 1 m mouth opening and ≤ 800 µm mesh size in this study). Therefore sampling gear should be carefully considered when programmes are set up to monitor different types of jellyfish communities.

Overall, the hydrozoans *Aglantha digitale*, *Dimophyes arctica* and *Nanomia cara* and the ctenophores belonging to the family Mertensiidae and *Beroe* spp. were the epipelagic species most frequently recorded in the northern North Atlantic region during spring–summer. The presence of these key taxa was detected by different sampling gears used during the *G.O. Sars* transatlantic cruise, even if estimates of their abundance varied.

The use of modern technology, in particular of remotely operated vehicles equipped with underwater cameras and video systems, has proven to be very valuable in the collection of information on gelatinous plankton in situ, particularly in deep waters (e.g. Lindsay et al., 2008; Stemmann et al., 2008). Nevertheless, video systems are still quite costly and are therefore unlikely to be employed for standard jellyfish monitoring. Ocean-surface and shore-based surveys have been used to provide semi-quantitative/qualitative estimates of relatively big scyphomedusae and other gelatinous plankton (Purcell, 2009, and references therein). Visual observations from a ship or from a pier are, however, biased towards species of large size and relatively simple taxonomic identification. Therefore these methodologies cannot provide reliable information on the abundance and composition of jellyfish populations throughout the oceans.

The CPR Survey is the monitoring programme that covers the greatest spatial (tens to thousands of kilometres) and tem-

Table 8. Identity of cnidarian tissues collected from CPR samples and identified based upon mt16S rDNA analysis. Sampling information is also indicated. *Sample identified by visual inspection.

CPR tows	Latitude	Longitude	Month	Year	Taxa identified	Class
330 M	58.05	1.90	8	2006	*Cyanea* sp.	Scyphozoa
330 M	58.18	2.48	8	2006	*Cyanea* sp.	Scyphozoa
535ZB	49.83	−41.66	3	2007	Agalmatidae	Hydrozoa
438BB	45.63	−18.80	9	2007	*Pelagia noctiluca*	Scyphozoa
438BC	43.50	−25.57	9	2007	*Halistemma rubrum*	Hydrozoa
3030PR	49.37	−4.01	10	2007	*Muggiaea atlantica*	Hydrozoa
460W	54.48	−16.59	10	2007	*Pelagia noctiluca*	Scyphozoa
460W	54.48	−16.59	10	2007	*Diphyes dispar*	Hydrozoa
460W	54.48	−16.59	10	2007	*Pelagia noctiluca*	Scyphozoa
707A	58.29	−1.59	11	2007	*Apolemia uvaria*	Hydrozoa
708A	58.31	−1.60	12	2007	*Pelagia noctiluca*	Scyphozoa
464W	54.72	−18.12	7	2008	*Pelagia noctiluca*	Scyphozoa
464W	54.90	−15.55	7	2008	*Pelagia noctiluca*	Scyphozoa
464W	54.70	−18.41	7	2008	*Pelagia noctiluca*	Scyphozoa
80FA	54.14	−25.45	8	2008	*Pelagia noctiluca*	Scyphozoa
80FA	54.16	−25.18	8	2008	*Pelagia noctiluca*	Scyphozoa
571SA	45.45	−4.03	11	2008	*Pelagia noctiluca*	Scyphozoa
571SA	45.60	−4.10	11	2008	*Pelagia noctiluca*	Scyphozoa
83FA	54.47	−21.47	12	2008	*Pelagia noctiluca*	Scyphozoa
465 BC	47.10	−25.04	12	2009	*Pelagia noctiluca*	Scyphozoa
748 V	60.01	−6.48	12	2009	*Pelagia noctiluca*	Scyphozoa
468 BC	45.46	−29.34	3	2010	*Pelagia noctiluca*	Scyphozoa
349 EA	45.59	−51.22	7	2010	*Cyanea* sp.	Scyphozoa
349 EA	46.00	−51.07	7	2010	*Cyanea* sp.	Scyphozoa
342 PR	48.50	−5.08	11	2010	*Pelagia noctiluca*	Scyphozoa
488BA	49.12	−9.03	10	2011	*Aglantha digitale**	Hydrozoa
373EB	42.03	−66.28	1	2012	*Agalma elegans*	Hydrozoa
499BD	42.51	−38.14	8	2012	*Halistemma* sp.	Hydrozoa
364 PR	49.57	−4.08	10	2012	*Apolemia* spp.	Hydrozoa

poral (monthly to multidecadal) scales, sampling plankton at the surface across the whole North Atlantic in regions where information on plankton is typically not available (Richardson et al., 2006). It therefore offers a unique opportunity to document jellyfish swarms, which are events usually occurring over distances of tens to hundreds of kilometres (e.g. Brodeur et al., 2008) and for which large-scale methods of data collection are needed (Purcell, 2009). In contrast with what was previously hypothesised (Atrill et al., 2007; Gibbons and Richardson, 2009), the CPR is able to detect blooms of meroplanktonic as well as of holoplanktonic hydrozoans and scyphozoans. Outbreaks of the scyphomedusa *Pelagia noctiluca*, recorded by the CPR off Ireland in October 2007, were confirmed by net tows (Fig. 2 in Licandro et al., 2010, comparing CPR swarms events and records from Doyle et al., 2008), suggesting that the CPR can provide reliable information to help clarify the regions and periods in which jellyfish prefer to bloom.

Indeed, the reanalysis of CPR samples collected in recent years showed that jellyfish blooms can occur in coastal and offshore waters the whole year round. Genetic analysis of CPR cnidarian material indicates that meroplanktonic jellyfish (e.g. the scyphomedusa *Cyanea* sp.), which are characterised by the alternation of a benthic polyp stage and a pelagic medusa, tend to bloom over the shelf, while holoplanktonic species (e.g. *P. noctiluca* and different species of hydrozoan siphonophores) bloom both inshore and offshore. Based on the CPR, *P. noctiluca* and other hydrozoan siphonophores including *Muggiaea atlantica*, *Halistemma* spp. and other agalmatidae are among the main swarming species in the central and southern North Atlantic regions. Those observations, in particular the high abundance of small hydrozoan siphonophores in coastal regions, while they are yet to be confirmed, are in agreement with the information collected in the Bay of Biscay and Gulf of Cádiz.

Overall, records of jellyfish swarms reported by the CPR can help to identify North Atlantic regions more impacted by blooming events and help to discern whether environmental change and/or anthropogenic pressure can explain increasing jellyfish occurrence.

The new information on jellyfish abundance, diversity and distribution across the North Atlantic provided here presents

Table 9. DNA sequences (mt16S rDNA) identified from cnidarian taxa collected during project EURO-BASIN in different North Atlantic regions.

Taxa identified	Region	GenBank accession number
		16S
HYDROZOA		
Order Trachymedusae		
Family Halicreatidae		
Botrynema brucei	NW Atlantic	KJ866189
Family Rhopalonematidae		
Crossota rufobrunnea	NW Atlantic	KJ866190
Pantachogon haeckelii	NW Atlantic	KJ866191
Pantachogon spp.	NW Atlantic	KJ866192
Sminthea arctica	NE Atlantic	KJ866185
Order Narcomedusae		
Family Aeginidae		
Aeginura grimaldii	North Atlantic	KJ866195
Family Cuninidae		
Solmissus spp.	NE Atlantic	KJ866198
Order Leptothecata		
Suborder Conica		
Family Laodiceidae		
Ptychogena lactea	NE Atlantic	KJ866187
Family Mitrocomidae		
Mitrocomella polydiademata	NE Atlantic	KJ866197
Suborder Proboscoida		
Family Campanulariidae		
Clytia islandica	North Atlantic	KJ866184
Order Siphonophorae		
Suborder Physonectae		
Family Agalmatidae		
Halistemma rubrum	NE Atlantic	KJ866203
Marrus orthocanna	NE Atlantic	KJ866186
Nanomia cara	NE Atlantic	KJ866204
Nanomia cara	NE Atlantic	KJ866206
Suborder Calycophorae		
Family Hippopodiidae		
Vogtia glabra	North Atlantic	KJ866183
Family Diphyidae		
Dimophyes arctica	NE Atlantic	KJ866200
Gilia reticulata	NW Atlantic	KJ866188
Lensia achilles	NE Atlantic	KJ866193
Lensia conoidea	NE Atlantic	KJ866201
Lensia sp.	NE Atlantic	KJ866205
Muggiaea bargmannea	NE Atlantic	KJ866199
Family Clausophyidae		
Chuniphyes multidentata	NE Atlantic	KJ866202
Heteropyramis crystallina	NE Atlantic	KJ866194
Heteropyramis sp.	NE Atlantic	KJ866196

an improved baseline for future analysis of jellyfish dynamics. Our use of multiple methods and confirmation that CPR, for example, is a suitable source of data shows that the potential for analysing jellyfish populations is high. We also highlighted differences between sampling gears and the target taxa they are best suited for, and encourage a careful design of future monitoring of jellyfish. We expect that the increased negative commercial impact by jellyfish in the North Atlantic (e.g. salmon farms, tourism references) will give rise to more attention and funding to understand the dynamics of these taxa.

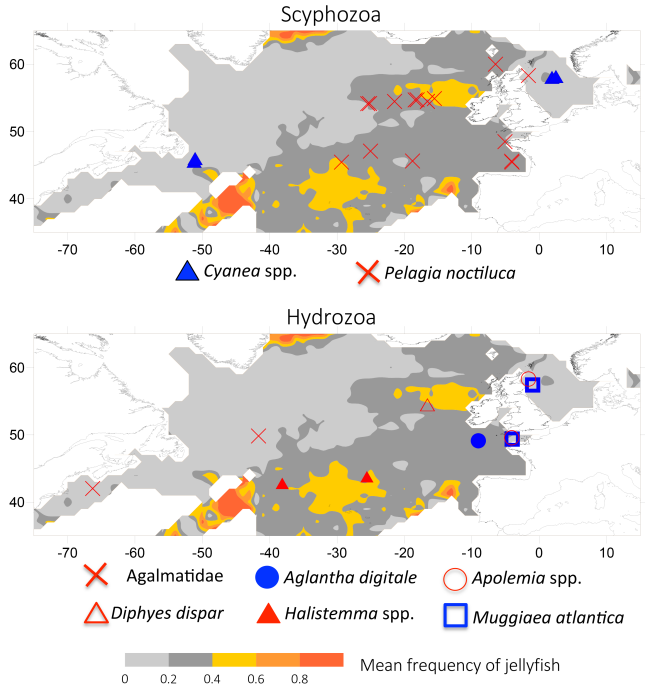

Figure 7. Jellyfish blooming species identified by genetic analysis from jellyfish material collected in CPR samples. The mean frequency of jellyfish presence recorded in 2000–2009 is also shown.

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