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

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Scientific debate on whether the recent increase in reports of jellyfish outbreaks is related to a true rise in their abundance, have outlined the lack of reliable records of Cnidaria and Ctenophora. Here we describe different data sets produced within the EU program EUROBASIN, which have been assembled with the aim of presenting an up to date overview of the diversity and standing stocks of jellyfish in the North Atlantic region.

Using a net adapted to sample gelatinous zooplankton quantitatively, Cnidaria and Ctenophora were collected in the epipelagic layer during spring-summer 2010–2013, in inshore and offshore waters between 59–68° N Lat and 62° W–5° E Long. 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 Cadiz. 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 with different water masses and with the bathymetry. Higher densities were generally recorded on the shelves, where populations tend to be more diversified due to the presence of meropelagic medusae. Comparisons of net records from the *G.O. Sars* transatlantic cruise show 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 2009–2012, blooms of Cnidarians occurred in all seasons across the whole North Atlantic basin. Molecular analysis revealed that, in contrast with what was previously hypothesized, the CPR is able to detect blooms of meroplanktonic and holoplanktonic hydrozoans and scyphozoans.

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Combining 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 Cnidarian 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 EUROBASIN 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 been achieved yet. While a part of the scientific community 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 suggested that the rise in jellyfish abundance is just a phase of up- and downward oscillations characterising 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 a general term 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 that can compromise some key morphological features and the poor knowledge of their taxonomy.

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unloaded, the spool is unrolled and the silk is cut in 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. Within the project EUROBASIN, CPR samples collected in 2009–2012 along different North Atlantic routes (Fig. 1) were visually re-analyzed 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 swarm events were recorded to identify cnidarian blooming species.

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 12000 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 12000 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 14000 g for 8 min. After discarding the Micropure-EZ CFD, the sample retained in the YM-30 was washed three times with 200 μL of sterile water; the first two washes were centrifuged at 14000 g for 8 min and the final wash was centrifuged at 14000 g for 5 min. The retained DNA was then recovered. All centrifugation steps were performed at 22 °C.

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shortly after collection. DNA extraction followed a standard SDS, Proteinase-K, phenol-chloroform protocol. Briefly, $\sim 1 \text{ mm}^3$ 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 proteinase-K solution (10 mg mL^{-1}) and digested for 4 h at 55 °C.

5 Following a phenol-chloroform purification the DNA was recovered by precipitation using NaCl and EtOH and resuspended in 40 μL 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.

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

15 2.3.3 DNA sequence analysis

Sequence identity of CPR cnidarian tissue was established firstly by comparison to public repositories and to 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 the same DNA marker from public databases using Bioedit (Hall et al., 1999). These were trimmed and exported into MEGA 5.1 (Kato et al., 1995) to produce phylogenies using Neighbour joining methods with a Kimura-2 substitution model and tested using 1000 bootstrap confidence intervals.

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3 Results

3.1 Jellyfish abundance and diversity in epipelagic waters

3.1.1 Jellynet data

The data collected in epipelagic waters in 2011–2013 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 ind. 100 m⁻³. A few stations located on the eastern (i.e. St. 3-*Meteor* cruise, St. 152-*G.O. Sars* cruise) and western (Stns. 1 and 2-*Arctic* cruise) Atlantic shelves exhibited elevated abundance with densities one order of magnitude greater (max. 246 ind. 100 m⁻³)

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

Overall 27 cnidarians and 5 ctenophore taxa were identified and counted in North Atlantic epipelagic waters (Table 4). Jellyfish populations were more diversified in the northeast Atlantic, mainly due to the presence of meroplanktonic species of Antho- 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 Cadiz, 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 %

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and 63 % of the total jellyfish standing stock respectively at Stns. 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 in this region jellyfish are less abundant than in the Bay of Cadiz (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). On the contrary, in the Irminger and Labrador Seas, jellyfish were more evenly distributed across the water column or mainly concentrated at the surface.

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.

3.3 Jellyfish diversity: comparison of different sampling gears

Thirty-seven species/genera of jellyfish were identified in the Mocness samples (Table 6), while thirty-two taxa were counted in samples collected by 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. Conversely, relatively large species (e.g. *Atolla*, *Pelagia*, *Praya*, *Vogtia*) were mostly collected by big trawls (Table 7), while small hydrozoans (e.g. *Clytia*, *Gilia*, *Muggiaea*) and

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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 of 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 often very dispersed or unevenly distributed (Purcell, 2009). Conventional nets, which are usually equipped with monofilament woven nylon, often irremediably damage many delicate species of Cnidaria and Ctenophora, while softer material such as silk or knitted polyester have shown to better preserve the delicate body of gelatinous zooplankton (Braconnot, 1971; Raskoff 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

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zooplankton, whilst limiting damage for jellyfish 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 with different water masses and with the bathymetry. The populations were less diverse in Arctic waters than on the North-eastern 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*, *Pelagia*, *Praya*, *Vogtia*, due to the large mesh size and large volume filtered. Small hydrozoans (e.g. *Clytia*, *Gilia*, *Muggiaea*) and early stages of ctenophora were only caught by the smaller nets (i.e. 1 m mouth opening and ≤ 800 mesh size in this study). Therefore sampling gear should be carefully considered when programs are set up to monitor different types of jellyfish communities.

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

The use of modern technology, in particular of remotely operated vehicles equipped with underwater cameras and video-systems, has proven to be very valuable to collect in situ information on gelatinous plankton, particularly in deep waters (e.g. Lindsay et al., 2008; Stemmann et al., 2008). Nevertheless, video systems are still quite costly, therefore unlikely to be employed for standard jellyfish monitoring. Ocean-surface and shore-based surveys have been used to provide semi-quantitative/qualitative estimates

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of relatively big scyphomedusae and other gelatinous plankton (Purcell, 2009 and references therein). Though, as visual observations from a ship or from a pier are biased towards species of detectable size and relatively simple taxonomic identification, 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 kilometres) and temporal (monthly to multidecadal) scales, sampling plankton at the surface across the whole North Atlantic in regions where no information on plankton is usually available (Richardson et al., 2006). It therefore offers a unique opportunity to document jellyfish swarms, which are events usually occurring over distances of ten-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 hypothesized (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 (see 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 re-analysis 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) swarm 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

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

Dataset	Dates	Area	Lat	Long	Stations	Gear	Mesh size (µm)	Mouth diameter (m)
<i>Arctic</i> cruise	22 Aug–22 Sep 2011	Cumberland Peninsula	63–67° N	62–68° W	1, 2, 3, 4	Jellynet	800	1
<i>Meteor</i> cruise	9–29 Apr 2012	North of Scotland	60–62° N	2° W–1° E	1, 2, 3	Jellynet	800	1
<i>Icelandic</i> 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
<i>G.O. Sars</i> 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, 101, 102, 104, 105, 106, 107, 108, 109, 111, 115, 116, 117, 118, 120, 121, 122, 123, 124, 125, 126, 127	Jellynet Mocness Harstad trawl Macroplankton trawl	800 180 30 000 3000	1 1 20 6
IEO	Mar–Nov 2010	Gulf of Cadiz	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

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

Station	Latitude	Longitude	Sampling depth (m)	Time (start, LT)	Date	Bottom depth (m)
<i>Arctic cruise</i>						
1	66°08.43' N	65°45.18' W	150	17:44	22 Aug 2011	150
2	65°75.95' N	65°91.23' W	200	11:40	25 Aug 2011	200
3	67°08.48' N	62°50.82' W	200	13:33	12 Sep 2011	334
4	63°04.00' N	68°36.00' W	200	15:45	22 Sep 2011	200
<i>Meteor cruise</i>						
1	61°30.00' N	10°59.99' W	200	07:45	9 Apr 2012	1350
1	61°30.00' N	10°59.99' W	200	08:13	9 Apr 2012	1350
1	61°30.00' N	10°59.99' W	200	17:27	9 Apr 2012	1350
1	61°30.00' N	10°59.99' W	200	17:58	9 Apr 2012	1350
1	61°30.01' N	10°59.99' W	200	05:37	10 Apr 2012	1350
1	61°29.95' N	11°0.06' W	200	06:07	10 Apr 2012	1350
1	61°29.99' N	11°0.00' W	200	18:04	10 Apr 2012	1350
1	61°29.99' N	11°0.01' W	200	18:35	10 Apr 2012	1350
2	62°50.00' N	2°30.00' W	200	16:14	12 Apr 2012	1300
2	62°49.99' N	2°30.11' W	200	16:41	12 Apr 2012	1300
2	62°50.01' N	2°29.98' W	200	05:54	13 Apr 2012	1300
2	62°50.01' N	2°29.98' W	200	06:25	13 Apr 2012	1300
2	62°50.04' N	2°30.16' W	400	11:29	13 Apr 2012	1300
2	62°50.01' N	2°30.11' W	400	02:30	14 Apr 2012	1300
2	62°50.01' N	2°30.05' W	200	04:47	14 Apr 2012	1300
2	62°50.01' N	2°30.05' W	200	05:17	14 Apr 2012	1300
3	60°20.00' N	1°0.01' E	150	16:14	15 Apr 2012	165
3	60°20.00' N	1°0.00' E	150	16:35	15 Apr 2012	165
3	60°20.01' N	1°0.00' E	150	01:58	16 Apr 2012	165
3	60°20.01' N	1°0.00' E	150	02:22	16 Apr 2012	165
3	60°20.01' N	1°0.00' E	150	06:07	16 Apr 2012	165
3	60°20.01' N	1°0.00' E	150	06:34	16 Apr 2012	165
1	61°30.00' N	11°0.01' W	400	03:34	19 Apr 2012	1350
1	61°29.99' N	11°0.01' W	200	05:03	19 Apr 2012	1350
1	61°29.99' N	11°0.01' W	200	05:33	19 Apr 2012	1350
1	61°30.14' N	11°0.04' W	200	17:26	20 Apr 2012	1350
1	61°30.33' N	11°0.08' W	200	17:55	20 Apr 2012	1350
2	62°50.00' N	2°30.03' W	400	03:14	23 Apr 2012	1300
2	62°50.00' N	2°30.03' W	200	05:18	23 Apr 2012	1300
2	62°50.00' N	2°30.04' W	200	05:50	23 Apr 2012	1300
2	62°50.00' N	2°30.00' W	200	17:32	23 Apr 2012	1300
2	62°50.00' N	2°30.01' W	200	18:00	23 Apr 2012	1300
1	61°29.99' N	10°59.97' W	200	17:48	28 Apr 2012	1350
1	61°29.99' N	10°59.97' W	200	18:18	28 Apr 2012	1350
1	61°29.99' N	10°59.98' W	400	01:58	29 Apr 2012	1350
1	61°29.99' N	10°59.98' W	200	05:07	29 Apr 2012	1350
1	61°29.99' N	10°59.98' W	200	05:38	29 Apr 2012	1350

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Table 2. Continued.

Station	Latitude	Longitude	Sampling depth (m)	Time (start, LT)	Date	Bottom depth (m)
<i>Icelandic cruise</i>						
241	64°20.36' N	28°58.86' W	400	04:45	16 May 2012	1018
246	65°50.23' N	25°59.73' W	200	21:29	16 May 2012	217
248	66°1.22' N	26°47.73' W	400	01:36	17 May 2012	450
255	67°35.06' N	23°56.66' W	200	22:22	17 May 2012	990
267	66°44.11' N	18°52.16' W	200	23:32	18 May 2013	698
272	68°00.11' N	16°14.88' W	200	15:24	19 May 2012	1271
273	67°44.83' N	16°15.32' W	200	17:57	19 May 2012	963
274	67°29.91' N	16°15.21' W	200	19:57	19 May 2012	805
281	67°14.79' N	13°34.41' W	200	14:08	20 May 2012	1540
290	66°21.49' N	12°05.66' W	200	22:59	21 May 2012	1082
292	66°21.73' N	13°35.04' W	200	04:10	22 May 2012	261
299	65°00.11' N	11°17.33' W	200	23:51	22 May 2012	537
305	63°39.98' N	13°40.52' W	200	22:49	23 May 2012	1125
307	63°52.11' N	14°07.97' W	200	02:28	24 May 2012	210
315	63°07.23' N	19°54.72' W	200	02:18	25 May 2012	1079
324	62°58.09' N	21°29.99' W	400	03:57	26 May 2012	990
324	62°58.09' N	21°29.99' W	200	02:07	26 May 2012	990
330	63°03.38' N	23°04.65' W	200	19:36	26 May 2012	896
332	62°43.05' N	23°47.22' W	200	00:17	27 May 2012	1253
333	62°51.57' N	24°13.97' W	200	02:54	27 May 2012	707
338	63°17.02' N	25°37.37' W	200	15:42	27 May 2012	620
340	63°38.81' N	24°50.49' W	200	20:35	27 May 2012	463
<i>G.O. Sars</i>						
152	62°25.00' N	5°4.23' E	200	22:30	3 May 2013	212
155	65°3.33' N	0°51.29' W	200	15:45	5 May 2013	2912
157	65°45.86' N	3°25.04' W	200	08:40	6 May 2013	3200
159	65°40.10' N	3°8.61' W	200	19:50	7 May 2013	3693
160	66°40.30' N	7°41.12' W	200	12:00	8 May 2013	1783
160bis	66°29.59' N	8°24.14' W	200	23:01	8 May 2013	NA
161	67°3.28' N	9°54.45' W	200	11:10	9 May 2013	1498
162	67°33.80' N	12°29.71' W	200	09:20	10 May 2013	1756
163	68°8.94' N	15°10.16' W	200	11:50	11 May 2013	1376
165	68°47.65' N	18°21.56' W	200	02:30	12 May 2013	1098
166	63°29.98' N	24°10.18' W	200	00:40	14 May 2013	224
167	63°18.37' N	25°20.62' W	200	06:40	15 May 2013	315
168	62°32.05' N	28°5.90' W	200	19:25	15 May 2013	1439
169	61°32.71' N	32°31.04' W	200	16:25	16 May 2013	2829
170	60°31.13' N	36°27.64' W	200	19:35	17 May 2013	2860
171	59°22.83' N	46°11.59' W	200	14:50	20 May 2013	1100

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Table 3. Continued.

Station	Latitude	Longitude	Sampling depths (m)	Time (start, LT)	Date
IEO dataset					
Bongo net					
TF-01	36°8.76' N	6°0.96' W	29	20:05	4 Mar 2010
SP-01	36°22.26' N	6°16.44' W	22	03:28	6 Mar 2010
GD-01	36°44.70' N	6°29.76' W	16	01:18	7 Mar 2010
SP-01	36°22.26' N	6°16.44' W	21	19:22	26 Jul 2010
GD-02	36°43.08' N	6°32.46' W	16	21:34	27 Jul 2010
GD-02	36°39.96' N	6°36.78' W	40	21:24	9 Nov 2010
SP-01	36°24.72' N	6°18.06' W	27	03:00	11 Nov 2010
TF-01	36°8.52' N	6°2.52' W	28	02:18	12 Nov 2010
AZTI dataset					
Bongo net					
58	43°45' N	5°15.15' W	220	12:30	22 May 2010
67	45°14.97' N	5°15.04' W	206	18:51	23 May 2010
68	45°45' N	5°44.72' W	208	11:43	24 May 2010
69	45°45.02' N	5°15.18' W	209	02:34	24 May 2010

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Table 4. Continued.

North Atlantic region	Cumberland shelf	Labrador Sea	Irminger Sea	Norwegian/Icelandic Seas	Icelandic Sea	North of Scotland
Stations	1–4	171	166–170	152–165	241–340	1–3
Cruise	<i>Arctic</i>		<i>G.O. Sars</i> cruise		<i>Icelandic</i>	<i>Meteor</i>
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
Order ANTHOATHECATA						
Family Corymorphidae						
<i>Euphysa aurata</i>						+
<i>Aplanulata incerta sedis</i>						+
<i>Plotocnide borealis</i>						+
Family Rathkeidae						
<i>Rathkea octopunctata</i>						+
<i>Lizzia blondina</i>						+
Family Pandeidae						
<i>Amphinema rugosum</i>						+
Family Zancleidae						
<i>Zanclea</i> spp.			+			
CTENOPHORA						
Order Cydippida						
<i>Cydippida</i> larva			+	+		
Family Mertensiidae						
<i>Mertensia ovum</i>	+	+				
<i>Mertensiidae</i> spp.		+			+	
Order Beroida						
Family Beroidae						
<i>Beroe cucumis</i>			+	+	+	+
<i>Beroe gracilis</i>			+			+
<i>Beroe</i> spp.	+	+		+	+	+
<i>Bolinopsis infundibulum</i>				+		

Table 5. Bongonet dataset. List of jellyfish taxa collected in epipelagic waters (0–200 m or 0 m–bottom) in 2010, in the Gulf of Cadiz and Bay of Biscay. Licandro et al. (2014).

North Atlantic region	Gulf of Cadiz	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	Mar, Jul, Nov 2010	May 2010
CNIDARIA		
HYDROZOA		
Order TRACHYMEDUSAE		
Family Geryoniidae		
<i>Liriope tetraphylla</i>	+	+
Family Rhopalonematidae		
<i>Aglaura hemistoma</i>	+	
<i>Aglantha digitale</i>		+
Order LEPTOTHECATA		
Family Lovenellidae		
<i>Eucheilota paradoxa</i>	+	
Family Campanulariidae		
<i>Clytia hemisphaerica</i>	+	
<i>Clytia</i> spp.	+	
<i>Obelia</i> spp.	+	
Order SIPHONOPHORAE		
Suborder Physonectae		
<i>Physonectae</i> larva	+	
Family Agalmatidae		
<i>Agalma elegans</i>		+
Suborder Calycophorae		
Family Abylidae		
<i>Abylopsis tetragona</i>	+	
<i>Bassia bassensis</i>	+	
Family Diphyidae		
<i>Chelophyes appendiculata</i>	+	+
<i>Eudoxoides spiralis</i>	+	
<i>Lensia conoidea</i>		+
<i>Muggiaea atlantica</i>	+	+
<i>Muggiaea kochi</i>	+	+
Order ANTHOATHECATA		
Family Coryniidae		
<i>Corynidae</i> spp.	+	
CTENOPHORA		
Order Cydippida		
Family Pleurobrachiidae		
<i>Hormiphora</i> spp.	+	

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

North Atlantic region	Labrador Sea	Irminger Sea	Norwegian/Icelandic Seas
Stations	125–127	115–124	101–111
Cruise	<i>G.O. Sars</i> 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			
<i>Halicreas minimum</i>	+	+	
<i>Halitrephes maasi</i>	+	+	
<i>Halicreatidae</i> spp.	+	+	
Family Rhopalonematidae			
<i>Aglantha digitale</i>	+	+	+
<i>Colobonema sericeum</i>	+	+	
<i>Crossota rufobrunnea</i>		+	
<i>Pantachogon haeckeli</i>	+	+	
<i>Rhopalonematidae</i> spp.		+	
Order NARCOMEDUSAE			
Family Aeginidae			
<i>Aeginura grimaldii</i>	+	+	
Family Cuninidae			
<i>Solmissus incisa</i>	+	+	
Order LEPTOTHECATA			
Family Laodiceidae			
<i>Ptychogena lactea</i>			+
Family Tiarannidae			
<i>Chromatonema rubrum</i>		+	
<i>Modeeria rotunda</i>	+	+	
Order SIPHONOPHORAE			
Suborder Physonectae			
Family Agalmatidae			
<i>Marrus orthocanna</i>			+
<i>Nanomia cara</i>		+	
Suborder Calyphophorae			
Family Prayinae			
<i>Praya dubia</i>	+	+	

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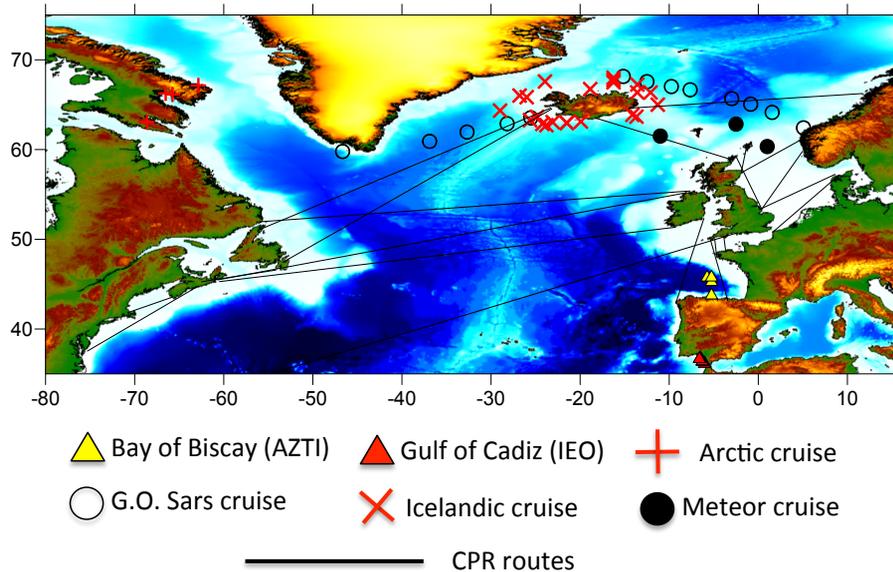


Figure 1. Locations of the different jellyfish datasets presented in this study.

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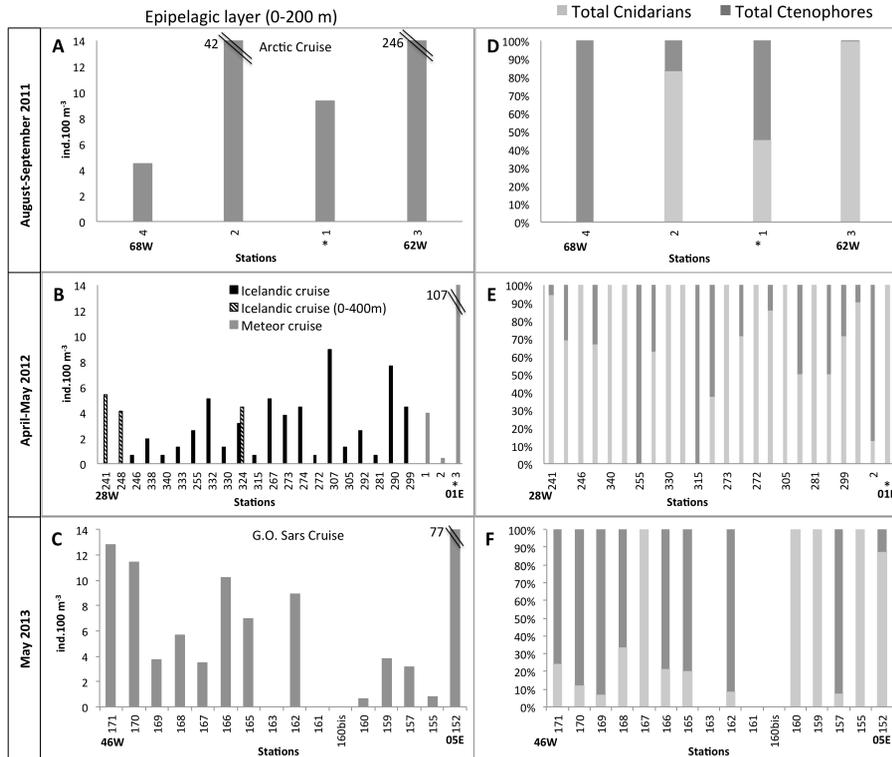


Figure 2. Jellynet datasets. Total jellyfish abundance (individuals 100 m⁻³) and relative proportion of Cnidaria and Ctenophora counts in the stations sampled during the *Arctic* cruise (a and d), *Icelandic* and *Meteor* cruise (b and e) and *G.O. Sars* cruise (c and f). Licandro and Blackett (2014), Licandro and Hosia (2014), Licandro and Kennedy (2014), Licandro and Raab (2014).

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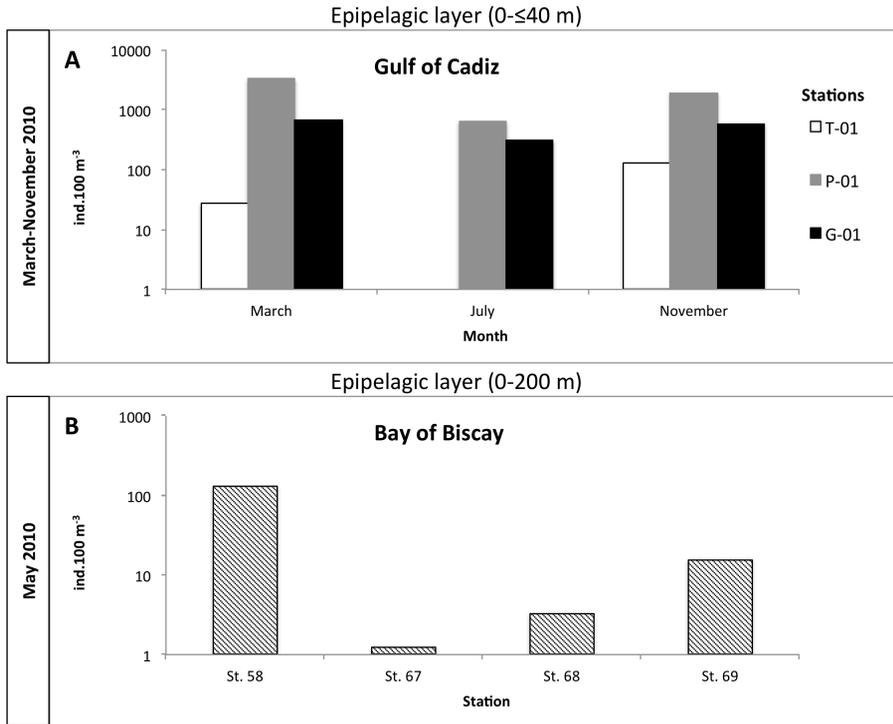


Figure 3. Bongonet datasets. Total jellyfish abundance (individuals 100 m⁻³) in the stations sampled in the Gulf of Cadiz (a) and in the Bay of Biscay (b). Licandro (2014a, b)

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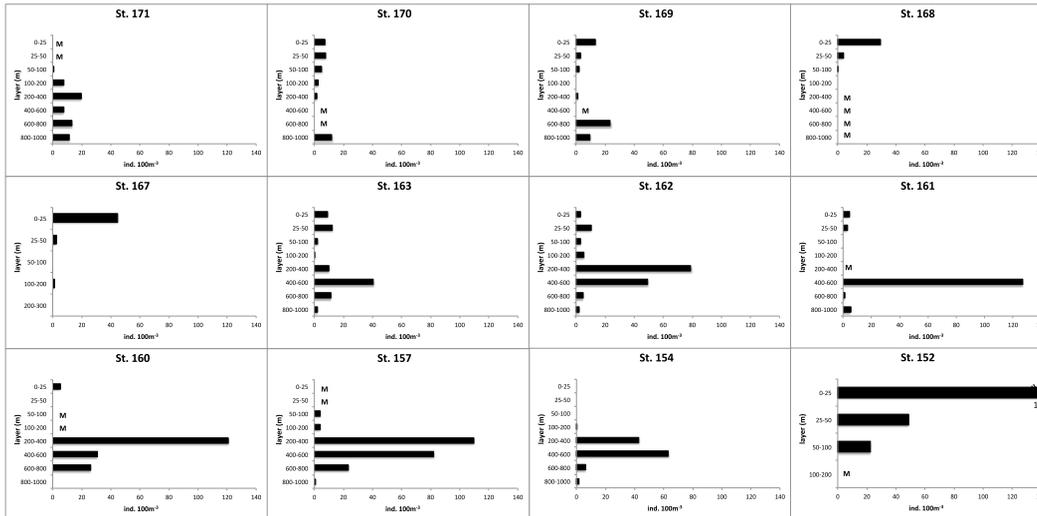


Figure 4. Mocness dataset. Abundance of jellyfish at different depths in the 0–1000 m layer. Please note the shallower depths in Stns. 152 and 167. St. 155 is not shown. M = samples preserved in formalin, not yet analyzed.

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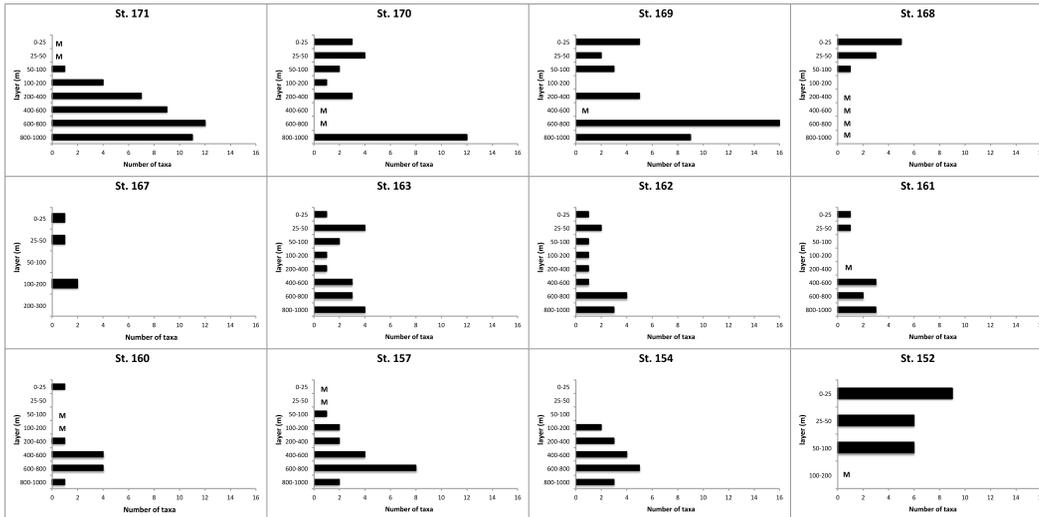


Figure 5. Mocness dataset. Number of jellyfish taxa found at different depths in the 0–1000 m layer. Please note the shallower depths in Stns. 152 and 167. St. 155 is not shown. M = samples preserved in formalin, not yet analyzed.

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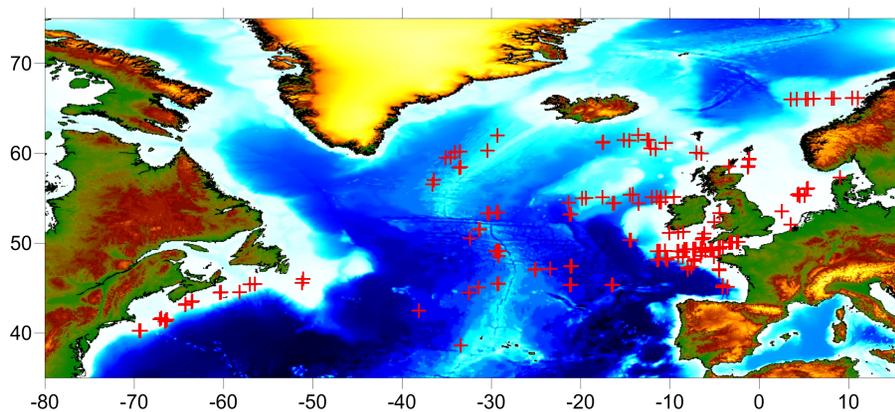


Figure 6. Jellyfish swarms recorded by the Continuous Plankton Recorder in 2009–2012.

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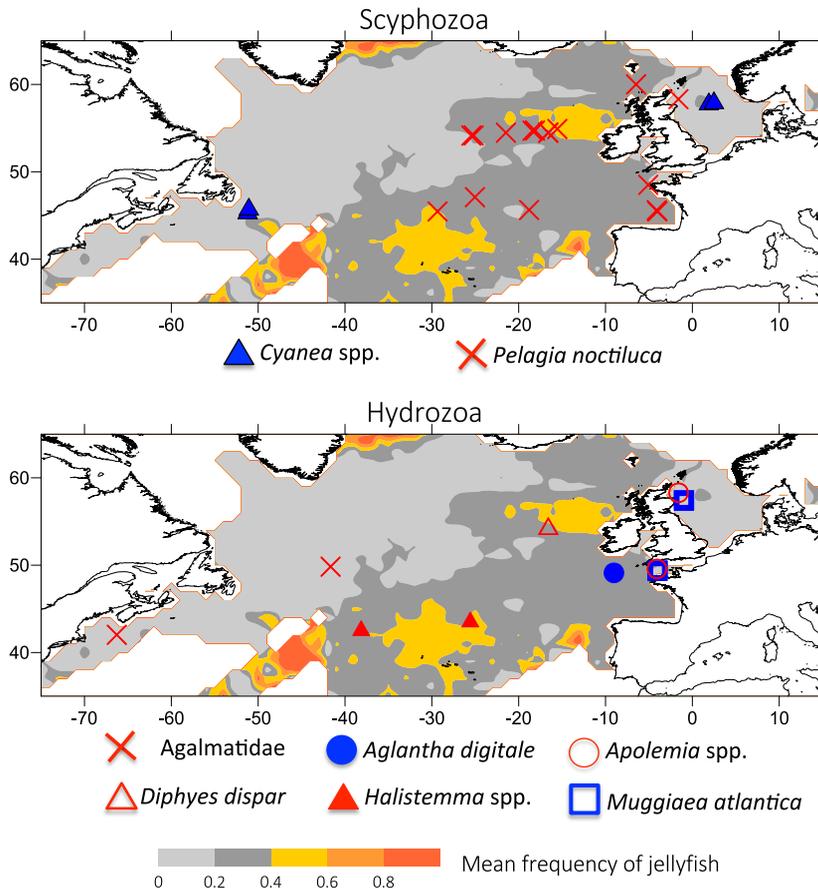


Figure 7. Jellyfish blooming species identified by genetic analysis from jellyfish material collected in CPR samples. The mean frequency of jellyfish presence recorded in 2000–2009 is also shown.