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

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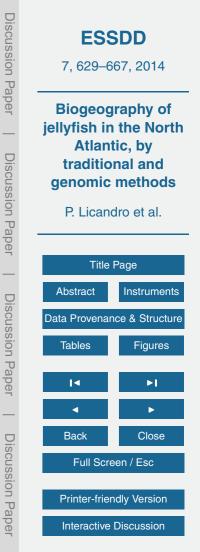
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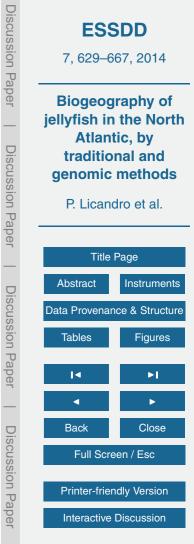




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# Abstract

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

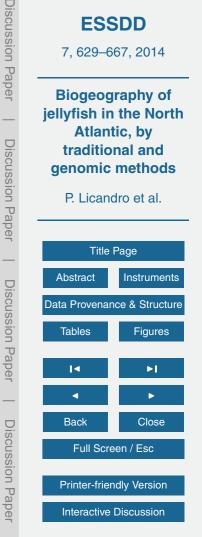
region. Using a net adapted to sample gelatinous zooplankton guantitatively, Cnidaria and

- 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 10 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 20 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 25 what was previously hypothesized, the CPR is able to detect blooms of meroplanktonic and holoplanktonic hydrozoans and scyphozoans.





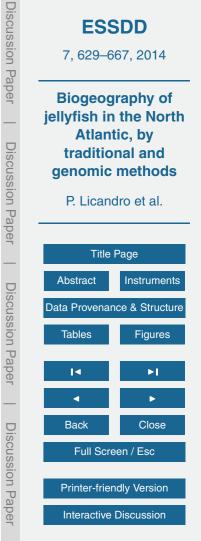
Combining different types of data, key jellyfish taxa for the spring-summer period were identified in the northern North Atlantic regions. Key species for the central and southern North Atlantic could be inferred based on Cnidarian blooms identified by the CPR survey, although this should be confirmed 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. <sup>10</sup> 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 15 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 20 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 25 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 very dispersed (Purcell, 2009). Silk or polyester mesh should be preferably used rather than nylon or stramine mesh (traditionally used to collect plankton samples), which severely damages or destroys many delicate species of gelatinous zooplankton (Braconnot, 1971). Slow towing speed (0.5–1 m s<sup>-1</sup>) is fundamental to collect intact specimens that would be otherwise badly damaged.

Here we describe different jellyfish data sets produced within the EU program EU-ROBASIN, assembled with the aim of presenting an up to date overview of the diversity and 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

#### 15 2.1 Net data

Different types of nets were used to collect jellyfish in several North Atlantic regions (Fig. 1 and Table 1).

A "gentle" net, hereafter called the "jellynet", was designed following the main 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 EUROBASIN Cruises, i.e. the 2012 Materer Cruise, the 2012 Japlandia gruise and the transition 2013 C O

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 Open

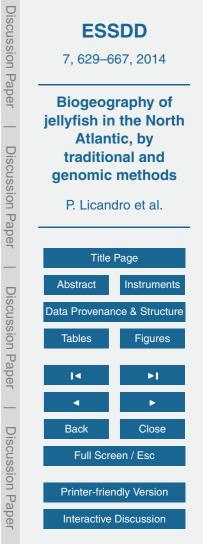
- Iected at different depths in the 0–1000 m layer using a standard 1 m<sup>2</sup> Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe and Benfield, 2003) (quantitative data), Harstad (Nedreaas and Smedstad, 1987) and macroplankton trawls (qualitative data) (Tables 1 and 3).
- Even though the sampling methodology is not particularly suitable to quantitatively catch jellyfish specimens, samples collected during 2010 by Bongo nets in the Gulf of Cadiz (i.e. IEO dataset, Table 3) and in the Bay of Biscay (i.e. AZTI dataset, 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 the samples collected off the Cumberland Peninsula, in the Gulf of Cadiz and in the Bay of Biscay. The taxonomic identification was crosschecked

# by different taxonomists to ensure consistency and 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<sup>2</sup>) 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 in sections that correspond to circa 10 nautical miles.

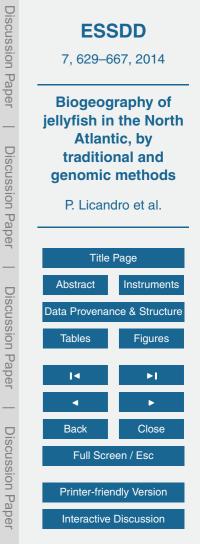
The visual identification of cnidarian jellyfish tissue and/or nematocysts in CPR samples has been carried out routinely since 1958. Within the project EUROBASIN, CPR samples collected in 2009–2012 along different North Atlantic routes (Fig. 1) were visually re-analyzed and those fully covered in jellyfish 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.

# 10 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 <sup>15</sup> pieces of tissue from individual specimens (approximately 1 mm length) were placed individually into 180  $\mu$ L of chelex solution (Instagene Matrix, Biorad) together with 6  $\mu$ L of 1 M Dithiothreitol (DTT), 4  $\mu$ L of proteinase-K (10 mg mL<sup>-1</sup>) and 10  $\mu$ L 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.





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 (LifeTechnologies, USA) applying the homogenisation of tissues procedure with the optional centrifugation step as described by the manufacturers. DNA pellets were then dissolved in a final volume of  $30 \,\mu$ L.

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

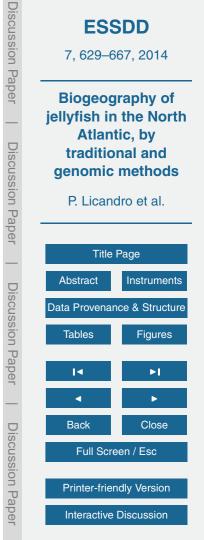
The PCR products were visualised on a 1% agarose gel and either purified using Montage spin columns (Millipore) or treated with ExoSAPIT (Illustra, supplied by VWR)

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 BigDye kit (Applied Biosystems, USA), with either the forward or reverse primer for amplification, according to manufacturer instructions and capilliary electrophoresis of sequencing products carried out at Source Bioscience.

# 2.3.2 DNA extraction from net samples preserved in ethanol

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Jellyfish DNA was extracted from about 80 ethanol-preserved cnidarian specimens, which were collected during the EUROBASIN cruises and identified on board or





shortly after collection. DNA extraction followed a standard SDS, Proteinase-K, phenolchloroform protocol. Briefly, ~ 1 mm<sup>3</sup> of jellyfish tissue was placed into a 1.5 mL Eppendorf tube containing 400  $\mu$ L cell lysis buffer (10 mM Tris-Cl pH 7.9, 100 mM EDTA and 0.5 % SDS) with 4  $\mu$ L proteinase-K solution (10 mg mL<sup>-1</sup>) and digested for 4 h at 55 °C.

<sup>5</sup> Following a phenol-chloroform purification the DNA was recovered by precipitation using NaCl and EtOH and resuspended in 40  $\mu$ L nanopure H<sub>2</sub>O. A 1  $\mu$ L 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 pro-

file 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).

# 15 2.3.3 DNA sequence analysis

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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 (Katoh et al., 1995) to produce phylogenies using Neighbour joining methods with a Kimura-2 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 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<sup>-3</sup>. 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<sup>-3</sup>)

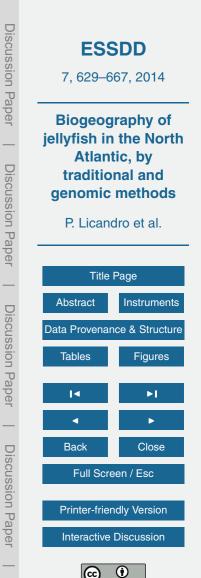
<sup>10</sup> In the 0–200 m layer, cnidarians tended to be generally more abundant than ctenophores (Fig. 2d–f), even though in some stations (St.4-*Arctic* cruise, Stns. 255 and 315-*Icelandic* cruise, St. 162-*G.O. Sars* cruise) ctenophores made up 90–100 % of the total jellyfish abundance.

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 Anthoand 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.

# 20 3.1.2 Bongo data

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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 %



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 <sup>5</sup> 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

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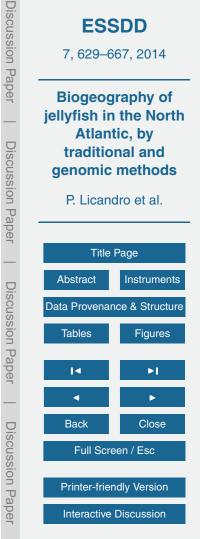
The data collected at different depths in the 0–1000 m layer during the *G.O. Sars* cruise,
show that in early May 2013 the bulk of the jellyfish population was concentrated in the mesopelagic layer (200–1000 m depth) off the Norwegian trench and in the Icelandic Sea (Fig. 4). On the contrary, in the 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. *Aglan-tha 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





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

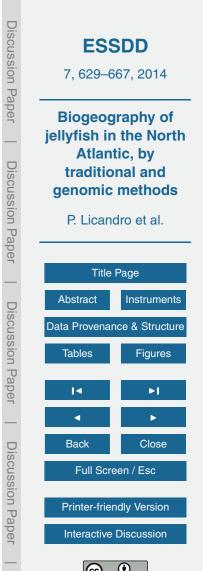
Based on CPR deployments from 2009 to 2012, jellyfish blooms occurred in all seasons, inshore and offshore across the whole North Atlantic basin (Fig. 6). Genetic analysis of jellyfish material collected from CPR samples identified blooms of small hydrozoans as well as of relatively big scyphomedusae (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 poctiluca* were recorded inshore and offshore from spring to late autumn

ian *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 quanti-

tative 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 for jellyfish soft tissues (Braconnot, 1971; Buecher, 1997, 1999).

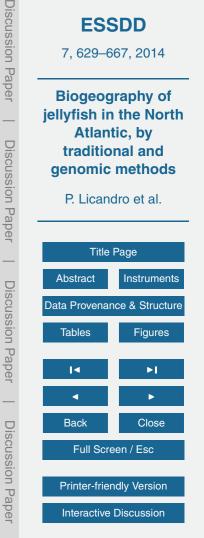
The data collected in epipelagic waters by the jellynet in the northern North Atlantic regions, showed high variability in jellyfish standing stocks, with higher densities generally observed on the eastern and western North Atlantic shelves. Jellyfish diversity also varied, mainly in relation with different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

<sup>20</sup> 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





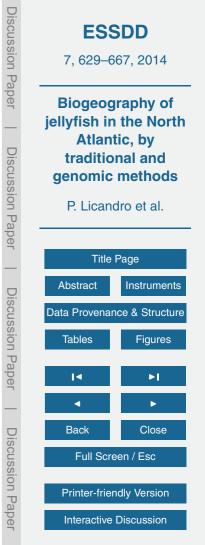
of relatively big scyphomedusae and other gelatinous plankton (Purcell, 2009 and references therein). Though, as visual observations from a ship or from a pier are biased towards species of detectable size and relatively simple taxonomic identification, these methodologies cannot provide reliable information 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 largescale 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 jelly-fish 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 holoplank-

tonic 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





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 Cadiz.

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 envi-

ronmental change and/or anthropogenic pressure can explain increasing jellyfish occurrence.

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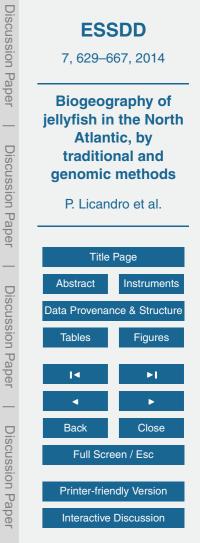
20

# Source Data References

Licandro, P.: Abundance of Cnidaria and Ctenophora in the Gulf of Cadiz 2010, doi:10.1594/PANGAEA.830265. 2014a.

Licandro, P.: Abundance of Cnidaria and Ctenophora in the Bay of Biscay (May 2010), doi:10.1594/PANGAEA.830263. 2014b.

- Licandro, P. and Blackett, M.: Abundance of Cnidaria and Ctenophora in the North Atlantic sampled during the M87/1 cruise in April 2012, doi:10.1594/PANGAEA.829714, 2014. Licandro, P. and Hosia, A.: Abundance of Cnidaria and Ctenophora in the North Atlantic sampled during the G.O. Sars Cruise in May 2013, doi:10.1594/PANGAEA.828646, 2014.
- Licandro, P. and Kennedy, J.: Abundance of Cnidaria and Ctenophora in the North Western Atlantic collected in August and September 2011, doi:10.1594/PANGAEA.828647, 2014. Licandro, P. and Raab, K.: Abundance of Cnidaria and Ctenophora in the Icelandic Sea sampled in May 2012, doi:10.1594/PANGAEA.828648, 2014.





Licandro, P., Blackett, M., Hosia, A., Kennedy, J., and Raab, K.: Presence and absence of Cnidaria and Ctenophora taxa in the North Atlantic, doi:10.1594/PANGAEA.830244, 2014.

# References

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25

Attrill, M., Wright, J., and Edwards, M.: Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea, Limnol. Oceanogr., 52, 480–485, 2007.

Braconnot, J. C.: Contribution à l'étude biologique et écologique des Tuniciers pélagiques Salpides et Doliolides I. Hydrologie et écologie des Salpides, Vie Milieu, 22, 257–286, 1971.

Brodeur, R. D., Mills, C. E., Overland, J. E., Walters, G. E., and Schumacher, J. D.: Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change, Fish. Oceanogr., 8, 296–306, 1999.

Brodeur, R. D., Decker, M. B., Ciannelli, L., Purcell, J. E., Bond, N. A., Stabeno, P. J., Acuna, E., and Hunt Jr., G. L.: The rise and fall of jellyfish in the Bering Sea in relation to climate regime shifts, Progr. Oceanogr., 77, 103–111, 2008.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., and Pauly, D.: Increasing jellyfish populations: trends in large marine ecosystems, Hydrobiologia, 690, 3–20, 2012.

Buecher, E.: Distribution and abundance of *Pleurobrachia rhodopis* (Cydippid Ctenophore) in the Bay of Villefranche-sur-Mer (Northwestern Mediterranean) from three different planktonic time series, Ann. I. Oceanogr. Paris, 72, 173–184, 1997.

Buecher, E.: Appearance of *Chelophyes appendiculata* and *Abylopsis tetragona* (Cnidaria, Siphonophora) in the Bay of Villefranche, northwestern Mediterranean, J. Sea Res., 41, 295–307, 1999.

Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., Shuterland, K. R., Robinson, K. L., Dawson, M. N., Decker, M. B., Mills, C. E., Purcell, J. E., Malej, A., Mianzan, H. W., Uye, S., Gelcich, S., and Madin, L. P.: Questioning the rise of gelatinous zooplankton in the world's oceans, Bioscience, 62, 160–169, 2012.

Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Shuterland, K. R., Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B., Uye, S., Madin, L. P., Brodeur, R. D., Haddock, S. H. D., Malej, A., Parry, G. D., Eriksen, E., Quiñones, J., Acha, M., Harvey, M., Arthur, J. M., and Graham, W. M.: Recurrent jellyfish blooms are a consequence of global oscillations, P. Natl. Acad. Sci. USA, 110, 1000–1005, 2013.





Cornelius, P. F. S.: North-west European Thecate Hydroids and their Medusae. Part 1. Introduction, Laodiceidae to Haleciidae, Synopses of the British Fauna no. 50, Field Studies Council, Shrewsbury, 1995.

Cunningham, C. W. and Buss, L. W.: Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae, Biochem. Syst. Ecol., 21, 57–69, 1993.

Doyle, T. K., De Haas, H., Cotton, D., Dorschel, B., Cummins, V., Houghton, J. D. R., Davenport, J., and Hays, G. C.: Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters, J. Plankton Res., 30, 963–968, 2008.

5

10

15

20

30

Gibbons, M. J. and Richardson, A. J.: Patterns of jellyfish abundance in the North Atlantic, Hydrobiologia, 616, 51–65, 2009.

Hall, T.: BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT, Nucl. Acid. S., 41, 95–98, 1999.

Hosia, A., Stemmann, L., and Youngbluth, M.: Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses, Deep-Sea Res. Pt. II. 55, 106–118, 2008.

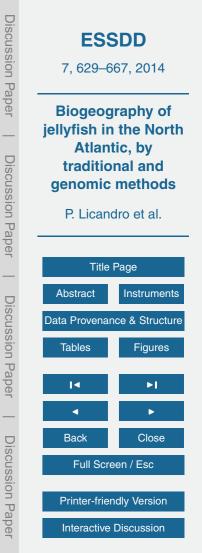
Katoh, K., Kuma, K., Toh, H., MiyataKatoh, T., and Kumah, K.: MAFFT version 5: improvement in accuracy of multiple sequence alignment, Nucleic Acids Res., 33, 511–518, 1995.

Kawahara, M., Uye, S., Ohtsu, K., and Iizumi, H.: Unusual population explosion of ther giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters, Mar. Ecol.-Prog. Ser., 307, 161–173, 2006.

Kirby, R. R., Johns, D. G., and Lindley, J. A.: Fathers in hot water: rising sea temperatures and a northeastern Atlantic pipefish baby boom, Biol. Lett.-UK, 2, 597–600, doi:10.1098/rsbl.2006.0530, 2006.

Licandro, P., Conway, D. V. P., Daly Yahia, M. N., Fernandez de Puelles, M. L., Gasparini, S.,

- Hecq, J. H., Tranter, P., and Kirby, R. R.: A blooming jellyfish in the northeast Atlantic and Mediterranean, Biol. Lett.-UK, 6, 688–691, doi:10.1098/rsbl.2010.0150, 2010.
  - Lindsay, D., Pages, F., Corbera, J., Miyake, H., Hunt, J. C., Ichikawa, T., Segawa, K., and Yoshida, H.: The anthomedusan fauna of the Japan Trench: preliminary results from in situ surveys with manned and unmanned vehicles, J. Mar. Biol. Assoc. UK, 88, 1519–1539, 2008.
  - Mills, C.: Jellyfish blooms: are populations increasing globally in response to changing ocean conditions?, Hydrobiologia, 451, 55–68, 2001.





- Nedreaas, K. and Smedstad, O. M.: Abundance and distribution of postlarvae in the 0-group saithe survey in the North Sea and the Northeast Arctic in 1986 and 1987, ICES Council Meeting 1987/G, 31, 1–27 1987.
- Purcell, J. E.: Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research, Hydrobiologia, 616, 23–50, 2009.

5

10

- Raskoff, K. A., Sommer, F. A., Hamner, W. M., and Cross, K. M.: Collection and culture techniques for gelatinous zooplankton, Biol. Bull., 204, 68–80, 2003.
- Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D., and Witt, M.: Using continuous plankton recorder data, Prog. Oceanogr., 68, 27–74, 2006.
- Ripley, S. J., Baker, A. C., Miller, P. I., Walne, A. W., and Schroeder, D. C.: Development and validation of a molecular technique for the analysis of archived formalin-preserved phytoplankton samples permits retrospective assessment of *Emiliania huxleyi* communities, J. Microbiol. Meth., 73, 118–124, 2008.
- Schroth, W., Jarms, G., Streit, B., and Schierwater, B.: Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp., BMC Evol. Biol., 2, doi:10.1186/1471-2148-2-1 2002.
  - Stemmann, L., Hosia, A., Youngbluth, M. J., Søiland, H., Picheral, M., and Gorsky, G.: Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler,
- <sup>20</sup> in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge, Deep-Sea Res. Pt. II, 55, 94–105, 2008.
  - Wiebe, P. H. and Benfield, M. C.: From the Hensen net toward four-dimensional biological oceanography, Prog. Oceanogr., 56, 7–136, 2003.

Xian, W., Kang, B., and Liu, R.: Jellyfish blooms in the Yangtze Estuary, Science, 307, 41, 2005.

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Dataset	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
<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
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,	Jellynet	800	1
					161, 162, 163, 165, 166, 167, 168, 169, 170, 171	Mocness	180	1
					101, 102, 104, 105, 106, 107, 108, 109,	Harstad trawl	30 000	20
					111, 115, 116, 117, 118, 120, 121, 122, 123, 124, 125, 126, 127	Macroplankton trawl	3000	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 1. Sampling gears used to collect jellyfish records in different North Atlantic regions.



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**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)
Arctic cr	ruise					
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
Meteor	cruise					
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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Station	Latitude	Longitude	Sampling depth (m)	Time (start, LT)	Date	Bottom depth (m)
Icelandia	c cruise					
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
G.O. Sa	rs					
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

#### Table 2. Continued.



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

Station	Latitude	Longitude	Sampling depths (m)	Time (start, LT)	Date
G.O. Sa	rs cruise				
Mocnes					
152	62°25.00' N	5°4.23′ E	0:25:50:100	18:50	3 May 2013
154	64°8.4′ N	1°33.39′ E	0:25:50:100:200:400:600:800:1000	19:01	4 May 2013
155	65°3.33′ N	0°51.29′ W	200 : 400 : 600 : 800 : 1000	05:12	5 May 2013
157	65°40.72' N	2°59.06' W	50 : 100 : 200 : 400 : 600 : 800 : 1000	04:22	7 May 2013
160	66°39.52' N	7°38.86′ W	0:25:50/200:400:600:800:1000	06:27	8 May 2013
161	67°1.39′ N	9°45.32′ W	0 : 25 : 50 : 100 : 200/400 : 600 : 800 : 100	05:59	9 May 2013
162	67°33.83′ N	12°29.88' W	0:25:50:100:200:400:600:800:1000	08:31	10 May 2013
163	68°8.86' N	15°9.44′ W	0:25:50:100:200:400:600:800:1000	06:18	11 May 2013
167	63°32.09' N	25°32.21' W	0:25:50:100:200:300	03:22	15 May 2013
168	62°52.75' N	28°11.62' W	0:25:50:100:200/	18:33	15 May 2013
169	61°56.90' N	32°41.45' W	0:25:50:100:200:400/600:800:1000	10:02	16 May 2013
170	60°54.61' N	36°53.51' W	0 : 25 : 50 : 100 : 200 : 400/800 : 1000	12:37	17 May 2013
171	59°46.97' N	46°39.50' W	50 : 100 : 200 : 400 : 600 : 800 : 1000	18:34	20 May 2013
Macropl	ankton trawl				
101	65°9.30' N	0°48.44′ W	290–310	17:24	05 May 2013
102	65°15.82' N	0°54.43′ W	0–700	15:45	05 May 2013
104	65°39.70' N	2°53.58' W	0–1028	01:58	07 May 2013
105	65°50.63' N	3°54.6′ W	500	18:39	07 May 2013
106	66°43.66' N	7°51.16′ W	0–1000	11:44	08 May 2013
107	67°4.08′ N	9°57.89′ W	40–70	10:49	09 May 2013
108	67°36.33' N	12°39.26' W	30–38	10:52	10 May 2013
109	67°40.12' N	12°56.20' W	400–420	13:08	10 May 2013
111	68°11.49′ N	15°24.08' W	0–1000	11:35	11 May 2013
115	63°29.41' N	25°37.58' W	120–150	06:24	15 May 2013
116	63°0.77′ N	27°54.33' W	460	13:25	15 May 2013
117	62°56.56' N	28°3.49' W	250	15:16	15 May 2013
118	61°54.55' N	32°55.85' W	490–500	16:31	16 May 2013
120	61°50.58' N	33°16.67' W	0–1000	20:31	16 May 2013
121	61°49.10' N	33°25.60' W	695–705	22:14	16 May 2013
122	60°51.58' N	36°48.78' W	510–520	19:05	17 May 2013
123	60°51.36' N	36°58.74' W	320–330	20:55	17 May 2013
124	60°51.37' N	37°8.65′ W	630–660	23:40	17 May 2013
125	59°38.80' N	46°23.12′ W	170–200	14:13	20 May 2013
126	59°40.64' N	46°29.94' W	380	15:33	20 May 2013
127	59°43.89' N	46°34.73′ W	0–1000	16:55	20 May 2013

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# Table 3. Continued.

Station	Latitude	Longitude	Sampling depths (m)	Time (start, LT)	Date
IEO data	aset				
Bongo n	et				
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 da	taset				
Bongo n	et				
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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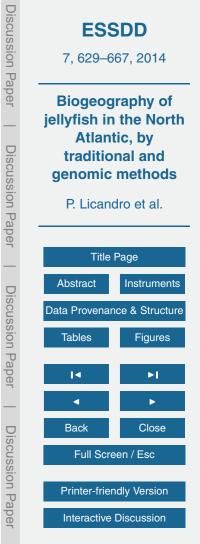
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**Table 4.** Jellynet dataset. List of jellyfish taxa collected in epipelagic waters (0-200 m) in different North Atlantic regions. \* = taxon found only in samples collected at 0-400 m depth. Licandro et al. (2014).

North Atlantic region Stations	Cumberland shelf 1–4	Labrador Sea	Irminger Sea 166–170	Norwegian/Icelandic Seas 152–165	Icelandic Sea 241–340	North of Scotland
Cruise	Arctic	'''	G.O. Sars o		Icelandic	Meteor
Latitude	63–67° N	59° N	60–63° N	62–68° N	62–68° N	60–62° N
	62–68° W	46° W	36–24° W	18° W–5° E	11–28° W	2° W–1° E
Longitude						
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 SIPHONOPHORA						
Suborder Physonectae						
Physonectae larva				+		+
Family Agalmatidae						
Agalma elegans						+
Nanomia cara			+	+	+	+
amily Physophoridae						
Physophora hydrostatica						+
Suborder Calycophorae						
amily Diphyidae						
Dimophyes arctica	+	+	+			+
Lensia achilles	Ŧ	- T	Ŧ	+	+*	Ŧ
Lensia conoidea				т	+	+
					+	
Lensia spp.				+	+	+
Muggiaea atlantica						+
amily Clausophyidae						
Chuniphyes multidentata					+*	+





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	Arctic		G.O. Sars o		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
Order ANTHOATHECATA						
Family Corymorphidae						
Euphysa aurata						+
Aplanulata incerta sedis						
Plotocnide borealis						+
Family Rathkeidae						
Rathkea octopunctata						+
Lizzia blondina						+
Family Pandeidae						
Amphinema rugosum Family Zancleidae						+
Zancieldae						
			+			
CTENOPHORA						
Order Cydippida						
<i>Cydippida</i> larva			+	+		
Family Mertensiidae						
Mertensia ovum	+	+				
Mertensiidae spp.		+			+	
Order Beroida						
Family Beroidae						
Beroe cucumis			+	+	+	+
Beroe gracilis			+			+
Beroe spp.	+	+		+	+	+
Bolinopsis infundibulum				+		

#### Table 4. Continued.



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**Table 5.** Bongonet dataset. List of jellyfish taxa collected in epipelagic waters (0–200 m or 0 mbottom) 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		
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	т	
Chelophyes appendiculata	+	+
Eudoxoides spiralis	+	т
Lensia conoidea	т	+
Muggiaea atlantica		+
Muggiaea kochi	+ +	+
Order ANTHOATHECATA	+	+
Family Coryniidae		
Corynidae spp.	+	
CTENOPHORA		
Order Cydippida		
Family Pleurobrachiidae		
Hormiphora spp.	+	

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

North Atlantic region Stations	Labrador Sea 171	Irminger Sea 166–170	Norwegian/Icelandic Seas 152–165
Cruise	171	<i>G.O. Sars</i> c	
Latitude	59° N	60–63° N	62–68° N
	46° W	36–24° W	02–00 N 18° W–5° E
Longitude			
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	+	+	+

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Table	6.	Continued.
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North Atlantic region Stations	Labrador Sea 171	Irminger Sea 166–170	Norwegian/Icelandic Seas 152–165
Cruise	<i>G.O. Sars</i> cruise		
Latitude	59° N	60–63° N	62–68° N
Longitude	46° W	36–24° W	18° W–5° E
Time	Dav	Day/Night	Day/Night
Date	20 May 2013	14–17 May 2013	3–12 May 2013
Lensia achilles	+	+	
Lensia conoidea		+	+
Lensia hunter	+	+	
<i>Muggiaea bargmannea</i> Family Clausophyidae	+	+	+
Chuniphyes multidentata	+	+	
Crystallophyes amygdalina	+	+	+
<i>Heteropyramis crystallina</i> Family Sphaeronectidae	+	+	
Sphaeronectes spp. Order ANTHOATHECATA			+
Family Hydractiniidae <i>Hydractinia areolata</i> Family Tubulariidae			+
<i>Hybocodon</i> spp. SCYPHOZOA			+
Family Atollidae			
Atolla parva			+
<i>Atolla wyvillei</i> 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		+	+



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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 Stations	Labrador Sea 125–127	Irminger Sea 115–124	Norwegian/Icelandic Seas 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
	20 Way 2013	15-17 Way 2015	5-11 May 2015
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		1	
Family Pravinae			
Praya dubia	+	+	
, ruyu uubiu			



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North Atlantic region Stations	Labrador Sea 125–127 International Irminger Se 115–124		101–111	
Cruise		G.O. Sars o		
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	
Family Hippopodiidae				
Vogtia glabra	+	+		
Vogtia serrata	+	+		
Family Diphyidae				
Dimophyes arctica	+		+	
Lensia conoidea		+		
Nectodamas diomedeae		+		
Family Clausophyidae				
Chuniphyes multidentata	+	+		
Order ANTHOATHECATA				
Family Bythotiaridae				
Bvthotiara murravi		+		
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.			+	

Table 7. Continued.

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

CPR tows	Latitude	Longitude	Month	Year	Taxa identified	Class
330M	58°05′ N	1°90′ E	Aug	2006	<i>Cyanea</i> sp.	Scyphozoa
330M	58°18′ N	2°48′ E	Aug	2006	Cyanea sp.	Scyphozoa
535ZB	49°83′ N	41°66′ W	Mar	2007	Agalmatidae	Hydrozoa
438BB	45°63′ N	18°80′ W	Sep	2007	Pelagia noctiluca	Scyphozoa
438BC	43°50′ N	25°57′ W	Sep	2007	Halistemma rubrum	Hydrozoa
3030PR	49°37′ N	4°01′ W	Oct	2007	Muggiaea atlantica	Hydrozoa
460W	54°48′ N	16°59′ W	Oct	2007	Pelagia noctiluca	Scyphozoa
460W	54°48′ N	16°59′ W	Oct	2007	Diphyes dispar	Hydrozoa
460W	54°48′ N	16°59′ W	Oct	2007	Pelagia noctiluca	Scyphozoa
707A	58°29' N	1°59′ W	Nov	2007	Apolemia uvaria	Hydrozoa
708A	58°31′ N	1°60′ W	Dec	2007	Pelagia noctiluca	Scyphozoa
464W	54°72′ N	18°12′ W	Jul	2008	Pelagia noctiluca	Scyphozoa
464W	54°90′ N	15°55′ W	Jul	2008	Pelagia noctiluca	Scyphozoa
464W	54°70′ N	18°41′ W	Jul	2008	Pelagia noctiluca	Scyphozoa
80FA	54°14′ N	25°45′ W	Aug	2008	Pelagia noctiluca	Scyphozoa
80FA	54°16′ N	25°18′ W	Aug	2008	Pelagia noctiluca	Scyphozoa
571SA	45°45′ N	4°03′ W	Nov	2008	Pelagia noctiluca	Scyphozoa
571SA	45°60′ N	4°10′ W	Nov	2008	Pelagia noctiluca	Scyphozoa
83FA	54°47′ N	21°47′ W	Dec	2008	Pelagia noctiluca	Scyphozoa
465BC	47°10′ N	25°04' W	Dec	2009	Pelagia noctiluca	Scyphozoa
748V	60°01′ N	6°48′ W	Dec	2009	Pelagia noctiluca	Scyphozoa
468BC	45°46′ N	29°34' W	Mar	2010	Pelagia noctiluca	Scyphozoa
349EA	45°59′ N	51°22' W	Jul	2010	<i>Cyanea</i> sp.	Scyphozoa
349EA	46°00′ N	51°07′ W	Jul	2010	<i>Cyanea</i> sp.	Scyphozoa
342PR	48°50′ N	5°08′ W	Nov	2010	Pelagia noctiluca	Scyphozoa
488BA	49°12′ N	9°03′ W	Oct	2011	Aglantha digitale*	Hydrozoa
373EB	42°03′ N	66°28′ W	Jan	2012	Agalma elegans	Hydrozoa
499BD	42°51′ N	38°14′ W	Aug	2012	Halistemma sp.	Hydrozoa
364PR	49°57′ N	4°08′ W	Oct	2012	Apolemia spp.	Hydrozoa



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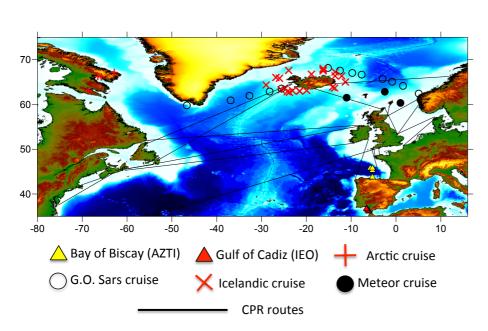
**Table 9.** DNA sequences (mt16S rDNA) identified from cnidarian taxa collected during the project EUROBASIN in different North Atlantic regions.

Taxa identified	Region	Genbank accession number 16S
10/000704		
HYDROZOA		
Order TRACHYMEDUSAE		
Family Halicreatidae	NW Atlantic	16 1000100
Botrynema brucei	INVV Atlantic	KJ866189
Family Rhopalonematidae	NIM/ Atlantia	K 1966100
Crossota rufobrunnea	NW Atlantic	KJ866190
Pantachogon haeckelii	NW Atlantic NW Atlantic	KJ866191 KJ866192
Pantachogon spp. Sminthea arctica	NE Atlantic	
Order NARCOMEDUSAE	NE Allantic	KJ866185
Family Aeginidae	North Atlantic	K INCOMO
Aeginura grimaldii	North Atlantic	KJ866195
Family Cuninidae	NIC Atlanti-	K 1000100
Solmissus spp. Order LEPTOTHECATA	NE Atlantic	KJ866198
Suborder Conica		
Family Laodiceidae		1/ 1000107
Ptychogena lactea	NE Atlantic	KJ866187
Family Mitrocomidae		1/ 1000107
Mitrocomella polydiademata	NE Atlantic	KJ866197
Suborder Proboscoida		
Family Campanulariidae		14 10 00 1 0 1
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
<i>Lensia</i> 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

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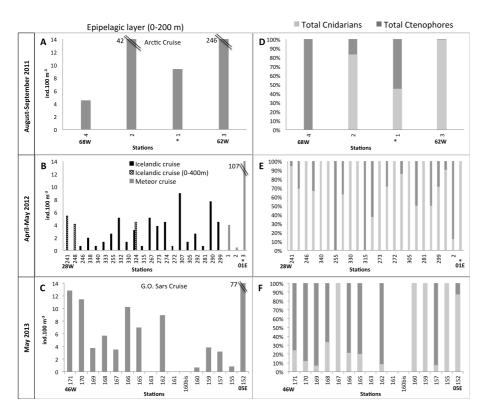
660



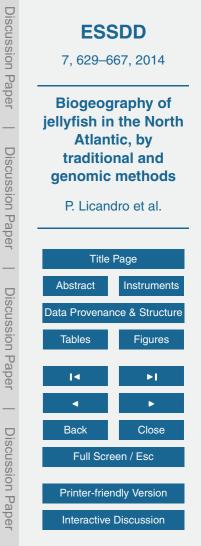




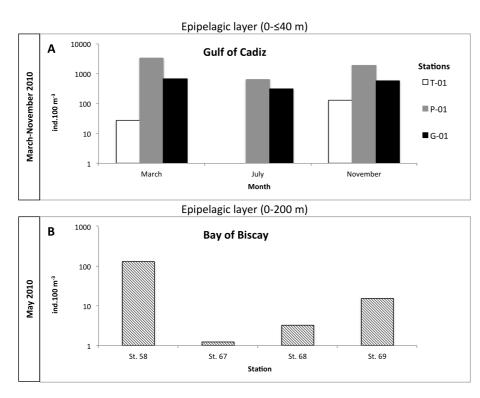




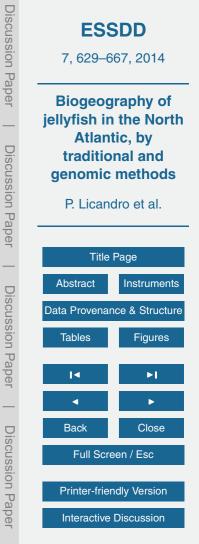
**Figure 2.** Jellynet datasets. Total jellyfish abundance (individuals  $100 \text{ m}^{-3}$ ) and relative proportion of Cnidaria and Ctenophora counts in the stations sampled during the *Arctic* cruise (**a** and **d**), *Icelandic* and *Meteor* cruise (**b** and **e**) and *G.O. Sars* cruise (**c**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



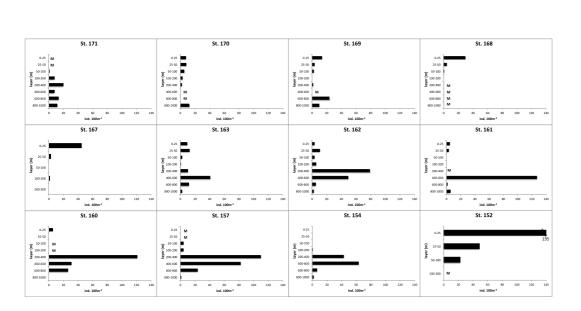




**Figure 3.** Bongonet datasets. Total jellyfish abundance (individuals  $100 \text{ m}^{-3}$ ) in the stations sampled in the Gulf of Cadiz **(a)** and in the Bay of Biscay **(b)**. Licandro (2014a, b)







**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.

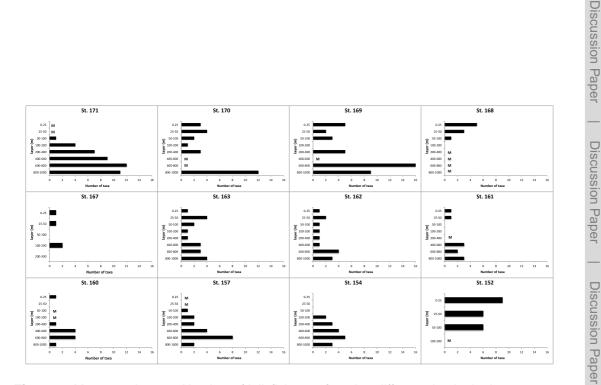


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**Figure 5.** Mocness dataset. Number of jellyfish taxa found at different depths in the 0-1000 m layer. Please note the shallower depths in Stns. 152 and 167. St. 155 is not shown. M = samples preserved in formalin, not yet analyzed.





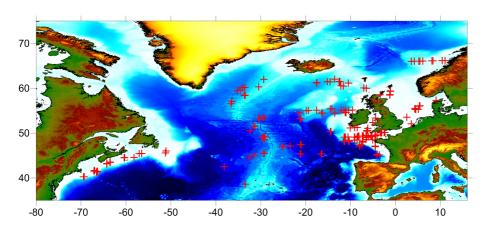
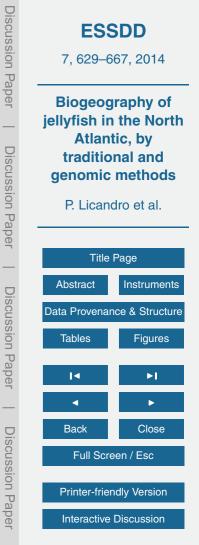
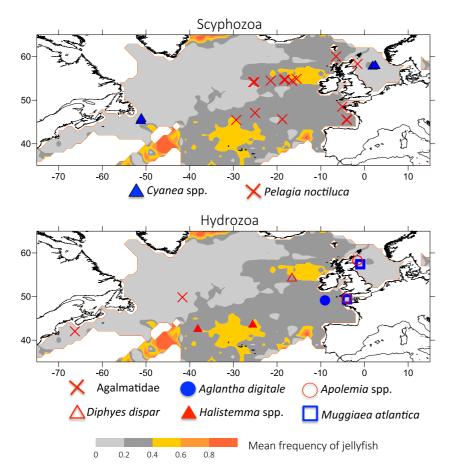


Figure 6. Jellyfish swarms recorded by the Continuous Plankton Recorder in 2009–2012.







**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.

