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

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Abstract

Scientific debate on whether 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.
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.

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 (0.5–1ms−1) is fundamental to collect intact specimens that would be otherwise badly damaged.

Here we describe different jellyfish data sets produced within the EU program EU10

ROBASIN, assembled with the aim of presenting an up to date overview of the diversity and the abundance of North Atlantic jellyfish. The use of different sampling gears provides the opportunity to discuss the limitation of each methodological approach and its influence on the quality of the data.

2 Data

2.1 Net data

Jellyfish were collected by ~~Different~~ 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 1m diameter mouth fitted with a 2m 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-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 0–1000m layer using a standard 1m2 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 identifications ~~was~~ were crosschecked by several ~~several~~ 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 (7m 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 cm2) and are trapped between the filtering silk and the covering silk.

Comment [d1]: Need to link this paragraph with the following. If different types of gear was used why focus on the gentle net. I assume it was used for most surveys. If so the authors need to say so.

Comment [d2]: Superscript

Comment [d3]: What method?

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.

Comment [d4]: Reference

Comment [d5]: What is the difference between an outbreak and a swarm?

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 1mm length) were placed individually into 180 µL of chelex solution (Instagene Matrix, Biorad) together with 6 µL of 1M Dithiothreitol (DTT), 4 µL of proteinase-K (10mgmL−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 3min. 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 8min and the final wash was centrifuged at 14000 g for 5min. 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 µL.

A third protocol was used to extract DNA from jellyfish material embedded in the silk. In this case, approximately one third of a CPR sample was cut, 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 at~~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~~capillary electrophoresis of sequencing products carried out at Source Bioscience.

2.3.2 DNA extraction from net samples preserved in ethanol

Jellyfish DNA was extracted from about 80 ethanol-preserved cnidarian specimens, which were collected during the EUROBASIN cruises and identified on board or shortly after collection. DNA extraction followed a standard SDS, Proteinase-K, phenolchloroform protocol. Briefly, ~ 1mm3 of jellyfish tissue was placed into a 1.5mL Eppendorf tube containing 400 µL cell lysis buffer (10mM Tris-Cl pH 7.9, 100mM EDTA and 0.5% SDS) with 4 µL proteinase-K solution (10mgmL−1) and digested for 4 h at 55C. Following a phenol-chloroform purification the DNA was recovered by precipitation using NaCl and EtOH and re-suspended in 40 µL nanopure H2O. A 1 µL aliquot of the extracted DNA was then used as template in a PCR.

A 540-bp partial, mtDNA 16S rDNA sequence was then amplified by PCR using the primers of Cunningham and Buss (1993) and Schroth et al. (2002) and the thermal profile described above. PCR products were visualised on a 1% agarose gel and purified using Montage spin columns (Millipore). Purified PCR products were then sequenced commercially (MWG Biotech) using the amplification primers as sequencing primers. Overall 23 cnidarian taxa were successfully sequenced and published on GenBank (Table 9).

2.3.3 DNA sequence analysis

Sequence identity of CPR cnidarian tissue was established first~~ly~~ by comparison with 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 public databases ~~from~~ for 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 betweenin 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. 100m−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 an order of magnitude greater (max. 246 ind. 100m−3)

In the 0–200m 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.

Comment [d6]: Should genis and species be italicized throughout the paper?

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%and 63% of the total jellyfish standing stock respectively at Stations. P-01 and G-01 (not shown).

Comment [d7]: See comment about italics for species and genus.

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 0–1000m layer

3.2.1 Mocness data

The data collected at different depths in the 0–1000m 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 (200–1000m 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 400m 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~~ 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 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.

Comment [d8]: Do you mean meropelagic or mesopelagic?

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 gelatinouszooplankton, 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~~ to 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.

Comment [d9]: Mero or meso?

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. 6m 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. 1m 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~~ in the collection of *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.

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

Comment [d10]: The first sentence in the abstract talks about a debate on whether or not jellyfish abundance has increased or decreased. The authors have not discussed this matter in the paper and should do so.

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Figure 2. ~~Jellynet datasets.~~ Total jellyfish abundance (individuals 100m−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 100m−3) in the stations sampled in the Gulf of Cadiz (a) and in the Bay of Biscay (b). Licandro (2014a, b)