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Bacterial community succession in response to dissolved organic matter released from live jellyfish

HAO Wenjin[1, 2, *], WICHELS Antje[3], FUCHS Bernhardt[4], TANG Xuexi[2], GERDTS Gunnar[3]

[1] *School of Life Science, Nantong University, Nantong 226019, China*
[2] *Department of Marine Ecology, College of Marine Life Sciences, Ocean University of China, Qingdao 266000, China*
[3] *Alfred Wegener Institute for Polar and Marine Research, Biologische Anstalt Helgoland, Helgoland 27498, Germany*
[4] *Max-Planck-Institute for Marine Microbiology, Department Molecular Ecology, Celsiusstr. 1, Bremen 28359, Germany*

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Abstract Jellyfish blooms have increased worldwide, and the outbreaks of jellyfish population not only affect the food web structures via voracious predation but also play an important role in the dynamics of nutrients and oxygen in planktonic food webs. However, it remains unclear whether specific carbon compounds released through jellyfish metabolic processes have the potential to shape bacterial community composition. Therefore, in this study, we aimed to investigate the compositional succession of the bacterioplankton community in response to the dissolved organic matter (DOM) released by the live Scyphomedusae *Cyanea lamarckii* and *Chrysaora hysoscella* collected from Helgoland Roads of the North Sea. The bacterial community was significantly stimulated by the DOM released form live jellyfish and different dominant phylotypes were observed for these two Scyphomedusae species. Furthermore, the bacterial community structures in the different DOM sources, jellyfish-incubated media, Kabeltonne seawater, and artificial seawater (DOM-free) were significantly different, as revealed by automated ribosomal intergenic spacer analysis fingerprints. Catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH) revealed a rapid species-specific shift in bacterial community composition. Gammaproteobacteria dominated the community instead of the Bacteroidetes community for *C. lamarckii*, whereas Gammaproteobacteria and Bacteroidetes dominated the community for *C. hysoscella*. The significant differences in the bacterial community composition and succession indicate that the components of the DOM released by jellyfish might differ with jellyfish species.

Keyword: bacterial community structure; bacterial community composition; dissolved organic matter; jellyfish; automated rRNA intergenic spacer analysis (ARISA); catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH)

1 INTRODUCTION

The ocean contains one of the earth's largest pools of bioactive dissolved organic carbon (DOC) (Hedges, 1992). This large reservoir of carbon and nutrients is derived mainly from phytoplankton biomass, zooplankton grazing activities, viral lysis, and advection of terrestrial matter (Nagata, 2000). Bacterioplankton plays a key role in assimilating and transforming this source to reduced carbon (Kujawinski, 2011), whereby energy and nutrients are channeled to higher trophic levels (Azam et al., 1983). Various uptake mechanisms and metabolic pathways of different carbon compounds have evolved in diverse phylogenetic bacteria to utilize DOC (Hopkinson and Barbeau, 2012). Bacteria also substantially differ in their abilities to utilize specific carbon compounds, with some bacteria having specialized pathways and others having a more generalist strategy (Martinez et al., 1996; Cottrell and Kirchman, 2000a; Riemann and Azam, 2002). Studies on the variability of bacterial populations in time and space also indicate the role of resources in determining population dynamics. The appearance of Roseobacter clade bacteria and Flavobacteria has been linked to

* Corresponding author: haowenjin456@hotmail.com

the organic matter released during phytoplankton blooms (González et al., 2000; Pinhassi et al., 2004; Teeling et al., 2012). Additional characteristics, such as substrate affinity or carbon processing efficiency, may also vary substantially among bacterial taxa, critically suggesting that the quality of the available compounds could be a strong selective force for bacterioplankton community composition (Riemann et al., 2000; Condon et al., 2011; Kujawinski, 2011).

Jellyfish blooms have occurred in many estuarine, coastal, and open-sea ecosystems worldwide during the past decades (Brodeur et al., 2002; Parsons and Lalli, 2002; Billett et al., 2006; Doyle et al., 2008). Jellyfish acquire C, N, and P by assimilating organic compounds from ingested prey and utilize small amounts of dissolved organic material (Pitt et al., 2009). Jellyfish are also known to release organic matter (Hansson and Norrman, 1995) by several mechanisms such as sloppy feeding and excretion of fecal material or mucus (Pitt et al., 2009). Large live medusae that accumulate damage are gradually broken down in the water column throughout the season during decomposition (Hansson and Norrman, 1995). This process of decomposition may support microbial production, whereas inorganic N and P regenerated by excretion may support algal production. Therefore, jellyfish play an important role in the dynamic of nutrients in planktonic food webs via excretion of inorganic nutrients, primarily in the form of ammonium (NH_4^+) and phosphate (PO_4^{3-}) (Steinberg and Saba, 2008) by release of dissolved organic matter (DOM) too (Lebrato et al., 2013).

Laboratory and field studies have shown that bacteria thrive in the DOC released by jellyfish (Hansson and Norrman, 1995; Riemann et al., 2006). Tinta et al. (2010, 2012) observed an increase in bacterial abundance and growth as well as a rapid shift in community composition from unculturable Alphaproteobacteria to culturable species of Gammaproteobacteria and Flavobacteria coupled with NH_4^+ accumulation and oxygen consumption. Condon et al. (2011) reported that jellyfish generate large amounts of colloidal and dissolved organic matter (jelly-DOM), which are extremely labile C-rich DOM that is quickly metabolized by bacterioplankton. Jelly-DOM not only favors the rapid growth and dominance of specific bacterial phylogenetic groups (primarily Gammaproteobacteria) that were rare in ambient waters but also detours the C pathway toward bacterial CO_2 production and away from higher trophic levels (Titelman et al., 2006; Condon et al., 2011). Further studies quantified the impacts of the dead jellyfish biomass on bacterial growth and microbial community composition by modifying the carbon and nutrient conditions through the release of nutrients and bio-available DOM (Hansson and Norrman, 1995; Martinez, 1996; Titelman et al., 2006). However, it remains unclear if particular bacteria preferentially utilize specific carbon compounds released by jellyfish during metabolism and whether such compounds have the potential to shape the bacterial community composition (BCC).

In this study, we investigated the compositional succession of bacterioplankton community in response to the DOM released by Scyphomedusae at Helgoland Roads in the German Bight of North Sea. We performed incubation experiments to evaluate the changes in native bacterial communities in response to DOM released by live Scyphomedusae *Cyanea lamarckii* and *Chrysaora hysoscella*. *C. lamarckii* and *C. hysoscella* (Russell, 1970) are common medusa species at Helgoland Roads in the German Bight and usually occur during summer (Möller, 1980; Hay et al., 1990; Barz and Hirche, 2007). These Scyphomedusae occur worldwide in numerous coastal and shelf-sea environments (Lucas et al., 2012) frequently forming large blooms (Hamner and Dawson, 2009). The objective of this study was to investigate the changes in bacterial community structure during the excretion of DOM released by live jellyfish to determine the succession of the bacterial community exposed to the disturbance caused by a jellyfish bloom.

2 MATERIAL AND METHOD

2.1 Sample collection and preparation

The individual jellyfish *C. lamarckii* and *C. hysoscella* (mean umbrella diameter, 11 cm) were separately sampled in July and August 2012 at Helgoland Roads station in the German Bight (54°11.3′N, 7°54.0′E). The jellyfish used in the experiment were manually collected from surface water using a bucket and immediately transported to the laboratory. Damaged animals were discarded. Before experimentation, the jellyfish were gently transferred into sterile DOC-free NaCl solution (20 L; salinity of 30) for 15 min. The potential confounding effects of sloppy feeding and leaching of DOM from the fecal material during the experiment were reduced. In general, most animals appeared healthy and undamaged after washing.

2.2 Collection of DOM released by live medusae

Five individuals of each jellyfish species were incubated individually in a 3-L beaker filled with 2.5-L DOC-free sterile artificial seawater (ASW) at in situ temperature in dark for 24 h. Every beaker was covered with combusted aluminum foil. The DOC-free sterile ASW was prepared according to the process described by Kisand et al. (2008). 1-L ASW contained i) main elements: 0.11 g $FeCl_3 \cdot 6H_2O$, 19.45 g NaCl, 12.6 g $MgCl_2 \cdot 6H_2O$; 6.63 g $MgSO_4 \cdot 7H_2O$, 2.38 g $CaCl_2 \cdot 2H_2O$, 0.55 g KCl, 0.16 g $NaHCO_3$, 0.01g $Na_2HPO_4 \cdot 2H_2O$ and ii) trace elements: 0.08 g KBr, 0.06 g $SrCl_2 \cdot 6H_2O$, 0.02 g H_3BO_3, 0.007 g Na_4O_4Si, 0.002 g NaF, 0.002 g $H_4N_2O_3$. To avoid the release of organic matter due to sloppy feeding, the jellyfish were not fed during incubation. After 24 h, the jellyfish were gently removed from the ASW using a bent spoon. Each spoon was prepared with following steps: soaked with acidified Milli-Q water (pH 2), rinsed twice with Milli-Q water, and combusted at 400°C for 4 h. Then, the incubated ASW from all the beakers was immediately processed. Five of the jellyfish-incubated media samples were collected for later experiment setup described in the next section.

2.3 Experiment setup

To avoid DOM contamination, all the containers and material were first washed and soaked overnight with acidified (pH 2) Milli-Q water, rinsed twice with Milli-Q water, and sealed with combusted aluminum foil. The experiment was performed with two Scyphomedusae species, *C. lamarckii* and *C. hysoscella* in July and August 2012, respectively (Supplementary Table S1). The setup consisted of three groups with five replicates: jellyfish-incubated medium, which is ASW containing DOM released by live jellyfish; Kabeltonne seawater containing natural DOM, which served as the control; and DOC-free ASW, which served as the blank. All these media were filtered through a GF/F filter (Whatman) and a 0.2-μm filter (polycarbonate filters) to yield 2 L sterile medium containing different amount of DOM.

Seawater was filtered through a 3-μm filter before inoculation to remove the larger organisms. Each experimental group was inoculated with 2-mL fresh seawater from Helgoland Roads station in the German Bight (54°11.3′N, 7°54.0′E). All of the groups were incubated at in situ temperature in the dark. Samples were collected at the following time points: 6 h, 12 h, 24 h, and every 24 h (48 h, 72 h, 96 h, 120 h, and 144 h) until the final sampling point of 168 h, to detect the bacterial abundance and bacterial composition by flow cytometry and catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH), respectively. At 168 h, DNA samples were collected from all the samples, except for the abundance samples, for analyzing the bacterial community structure by automated rRNA intergenic spacer analysis (ARISA).

2.4 Bacterial enumeration by flow cytometry

For flow cytometry analyses, 500 μL of fresh sample was stained with 10 μL of a freshly prepared 400× SYBR Green (Invitrogen™, Life Technologies, Paisley, UK) solution in sterile, filtered dimethyl sulfoxide for 10 min in the dark, at room temperature. Before staining, 10 μL of a diluted solution of Fluoresbrite® Polychromatic Red Microspheres 1.0 μm (Polysciences Europe, Eppelheim, Germany) was directly added into the sample as an internal counting standard (final concentration of approximately 10% of the expected number of cells). The samples were analyzed with an Accuri C6 flow cytometer (BD Accuri Cytometers, Ann Arbor, MI, USA) with the fluidics setting "slow" for 1.5 min. To reduce noise, a threshold of 550 was set on FL1-H for all the samples. The actual flow through was calibrated with BD Trucount™ Controls (BD Biosciences, San Jose, CA, USA).

2.5 Bacterial community analysis

Bacterial biomass was collected on 0.2-μm Isopore™ Membrane Filters (GTTP-type, 47 mm diameter; Millipore, Burlington, MA, USA), and DNA extraction was performed as previously described (Sapp et al., 2007). Briefly, lysozyme and sodium dodecyl sulphate were used for cell lysis followed by extraction with phenol-chloroform-isoamylalcohol (25:24:1) and precipitation with isopropanol. All the DNA extracts were dissolved in 30–50 μL sterile water and served as template DNA to determine the bacterial community structure via ARISA PCR. The quantity and quality of extracted DNA were determined by microphotometry using Tecan Infinite 200 NanoQuant (Männedorf, Switzerland).

Automated ribosomal intergenic spacer analysis (ARISA) was performed as described in Hao et al. (2015) to characterize the differences in bacterial

community structure in response to different DOM sources. Extracted DNA was amplified with a forwarding primer L-D-Bact-132-a-A-18 (5′-CCGG-GTTTCCCCATTCGG-3′) and reverse primer S-D-Bact-1522-b-S-20 (5′-TGCGGCTGGATCCCCTCC-TT-3′); the latter labelled with an infrared dye Ranjard et al. (2000). PCRs were performed in volumes of 25 μL containing 5 ng template DNA. PCR products were diluted (1:5) with autoclaved ultrapure water. Diluted PCR products were then mixed with an equal volume of formamide containing loading buffer and 0.25 μL were separated in 5.5% polyacrylamide gels at 1 500 V for 14 h on an LI-COR 4300 DNA Analyzer. A 50–1 500 bp size standard was run as a size reference on each gel (all materials: LI-COR Bioscience, USA).

Gels were analyzed using the Bionumerics 5.10 software (Applied Maths, Belgium). Bands in intensities lower than 2% of the maximum value of the respective lane and bands smaller than 300 bp were neglected. Binning to band classes was performed according to Hao et al. (2015). Each band class is referred to as an ARISA operational taxonomic unit (OTU). Peak intensities of ARISA OTUs were translated to binary data reflecting the presence or absence of the respective OTU.

2.6 Fixation and CARD-FISH

To analyze the composition of the bacterial community, CARD-FISH was performed, as described previously, with modifications (Pernthaler et al., 2002). Samples for CARD-FISH were fixed with 37% formaldehyde solution (final concentration 1% v/v) at 4°C overnight. Water samples of 10 mL were filtered onto polycarbonate filters (type GTTP, 0.2 μm pore size, 47 mm diameter), which were frozen at -20°C for further analyses.

According to the preliminary growth curves of each group, as obtained from flow cytometry analyses, inoculation filters, three samples from the initial point (24 h) and three representing points of exponential growth phase (48 h), beginning of stationary phase (96 h), and ending of experiment (168 h) were chosen for the BCC analyses.

For the groups with jellyfish-incubated media, permeabilization was performed with 10 mg/mL lysozyme in 50 mmol/L EDTA, 100 mmol/L Tris/HCl for 35 min at 37°C, whereas the samples from Kabeltonne seawater and ASW groups were permeabilized for 1 h at the same temperature. For all the three groups, hybridization was performed for 2.5 h using horseradish peroxidase-labeled oligonucleotide probes at varying formamide concentrations, depending on the probes (Supplementary Table S2). Fluorescein-labeled tyramide was used for signal amplification for 30 min (Pernthaler et al., 2004). The filter sections were washed twice in 96% ethanol, dried, and embedded on microscope slides with 4:1 (v/v) Citifluor (Citifluor Ltd., London, UK) and VectaShield (Vector Laboratories Inc., Burlingame, CA, USA) antifading reagents.

For quantification of total microbial cell numbers, the cells were stained with DAPI (1 μg/mL) and partly quantified manually using an Axioplan II Imaging epifluorescence microscope (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) and partly enumerated automatically with the Zeiss Axio Imager.Z2 (Carl Zeiss MicroImaging GmbH). For automatic cell quantification, the software package AxioVision 7.6 (Carl Zeiss MicroImaging GmbH) was used in conjunction with the macro MPISYS and the ACMEtool 0.75 software (Zeder et al., 2011).

The general probes, Eub338, Gam42, CF319a, and Ros537 were used to determine bacterial composition in all three groups at the four time points (mentioned above) with five replicates. According to results obtained from these four general probes, another four specific probes: Alt1413, Psa184, Pol1740, and Ulv995 were selected for analyzing samples obtained at the time of inoculation (0 h) and for samples obtained from the jellyfish-incubated media group at both 24 h and 168 h. Two specific probes Alt1413 and Psa184 were selected for Kabeltonne seawater and ASW groups at both 24 h and 168 h.

2.7 Statistical analysis

2.7.1 Analysis of ARISA data and univariate statistics

ARISA gel images were analyzed using BioNumerics 6.6 software (Applied Maths, Sint-Martens-Latem, Belgium). Normalization of band patterns and binning to band classes was performed as described previously (Hao et al., 2015).

The alpha diversity in terms of the operational taxonomic unit (OTU) richness of each sample obtained from ARISA fingerprints was calculated by summing the total number of remaining bands. ARISA-OTUs were analyzed based on a constructed binary table.

Differences regarding alpha diversity estimated from ARISA OTU numbers respecting treatment differences were tested using one-way analysis of

variance (ANOVA, Statistica Version 9, StatSoft GmbH, Hamburg, Germany). A significance level of $P<0.05$ was applied. Pairwise comparisons of the treatments were tested in post hoc Tukey HSD tests ($P<0.05$).

2.7.2 Bacterial growth kinetics

Growth kinetics of bacterial community in three different medium (jellyfish-incubated media, Kabeltonne seawater, and ASW) were compared by constructing growth curves. The growth kinetics parameters, including lag time (LT) and specific growth rate (SGR), were determined by the modified Gompertz equation using GraphPad Prism 4.0 (GraphPad Software, San Diego, CA, USA) as described previously (Kim et al., 2012). The following equation was used: $Y=N_0+C\times\exp(-\exp((2.718\times SGR/C)\times(LT-t)+1))$. In this equation, Y is the viable cell count (log cells/mL), N_0 is the initial log number of cells, C is the difference between the initial and final cell numbers, SGR is the maximum specific growth rate (log cells/mL), LT is the lag time before growth and t is the sampling time. The goodness-of-fit of the data was evaluated based on the coefficient of determination (R^2), which was provided by GraphPad Prism.

2.7.3 Multivariate analyses

For multivariate statistical analyses, the software package PRIMER v.6 and the add-on package PERMANOVA+ (both PRIMER-E Ltd., Plymouth, UK) were used. Permutational multivariate analysis of variance (PERMANOVA) with fixed factor was used to investigate the differences between the BCC of the two Scyphomedusae species with different DOM treatments, on the basis of the Jaccard coefficient. Principal co-ordinate analysis was performed to visualize patterns of the bacterial community in response to different DOM treatments.

3 RESULT

3.1 Growth kinetics of bacterial community

In the present study, we investigated the response of the planktonic bacterial community to different DOM sources, including the jellyfish-incubated media (*C. lamarckii* and *C. hysoscella*), the Kabeltonne seawater containing natural DOM, and DOM-free ASW. This study was conducted twice with different Scyphomedusae species. The wet weight and dry weight of the two Scyphomedusae species are provided in Supplementary Table S3.

Table 1 Lag time (LT), specific growth rate (SGR), and maximum population density (MPD) of the three treatment groups in *Cyanea lamarckii* experiment

	C. lamarckii	Kabeltonne seawater	Artificial seawater
LT (h)	-8.663±8.309	-6.054±4.862	42.64±1.379
SGR (log/h)	0.078±0.006	0.077±0.004	0.123±0.027
MPD (log)	6.625±0.058	6.192±0.034	5.794±0.036

Table 2 Lag time (LT), specific growth rate (SGR), and maximum population density (MPD) of the three treatments in *Chrysaora hysoscella* experiment

	C. hysoscella	Kabeltonne seawater	Artificial seawater
LT (h)	7.702±3.074	-5.156±8.679	20.37±1.628
SGR (log/h)	0.085±0.008	0.093±0.011	0.065±0.006
MPD (log)	6.985±0.061	6.222±0.062	5.407±0.029

The growth curves conducted for both the *Scyphomedusae* species (*C. lamarckii* and *C. hysoscella*) in the three treatment groups fitted well to a Gompertz equation with a high degree of goodness-of-fit (R^2=0.928 to 0.979). The LT, SGR, and a maximum population density of all the three groups were compared for both the *Scyphomedusae* species (Tables 1 and 2).

For both *Scyphomedusae* species (*C. lamarckii* and *C. hysoscella*), the bacteria presented a considerably long lag phase in the ASW treatment and the growth initiated after 48 h. In contrast, no such lag phase was observed in bacteria from the jellyfish-incubated media and Kabeltonne seawater treatments, and bacterial growth initiated immediately after inoculation and showed similar growth rates (Fig.1 and Fig.2). The highest maximum bacterial population densities in the *C. lamarckii*- and *C. hysoscella*--incubated media after 72 h were 4.4×10^6 cells/mL and 1.0×10^7 cells/mL, respectively. Although rapid bacterial growth was observed in ASW after 48 h, a stationary phase was observed in one day (72 h). At the ending of stationary phase, bacterial abundance in both *C. lamarckii*- and *C. hysoscella*- incubated media was the lowest at 8×10^5 cells/mL and 3.6×10^5 cells/mL, respectively. Significant differences were observed in the bacterial growth kinetics for media obtained after *C. lamarckii* ($F_{8,138}$=92.73, $P<0.000\ 1$) and *C. hysoscella* ($F_{8,138}$=88.52, $P<0.000\ 1$) incubation.

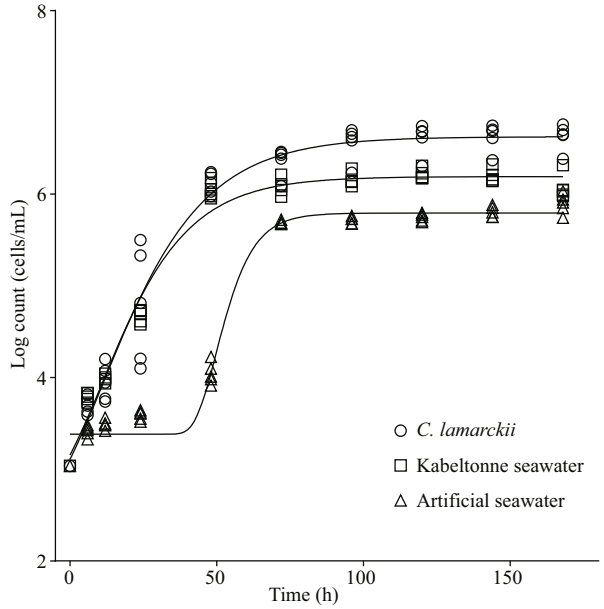

Fig.1 Growth curve of the bacterial community in different dissolved organic matter sources for experiments with *Cyanea lamarckii*

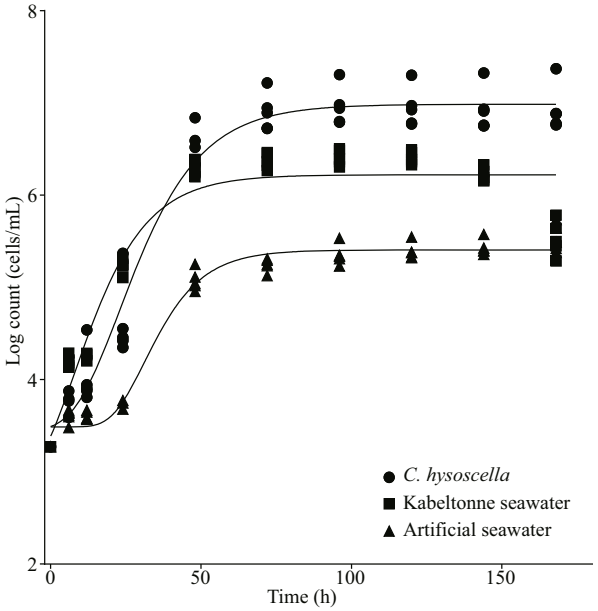

Fig.2 Growth curve of the bacterial community in different dissolved organic matter sources for experiments with *Chrysaora hysoscella*

Table 3 Permutational multivariate analysis of variance (PERMANOVA) main tests for bacterial community structure in different DOM treatments for experiments with *Cyanea lamarckii* on the basis of Jaccard dissimilarities of ARISA profiles

Source of variation	d.f.	SS	Pseudo *F*	*P* (perm)	Perms
Sam	3	7 762.7	3.359 4	**0.001**	998
Res	12	9 242.9			
Total	15	17 006			

Significant results [*P* (perm) <0.05] are highlighted in bold. The tests for the factor 'sample' and the partitioning of multivariate variation are displayed. *P*-values were obtained using type III sums of squares. d.f.: degrees of freedom; SS: sums of squares.

Table 4 Permutational multivariate analysis of variance (PERMANOVA) main tests for bacterial community structure in different dissolved organic matter treatments for experiments with *Chrysaora hysoscella* on the basis of Jaccard dissimila rities of ARISA profiles

Source of variation	d.f.	SS	Pseudo *F*	*P* (perm)	Perms
Sam	3	9 275.3	4.182	**0.001**	996
Res	12	8 871.5			
Total	15	18 147			

Significant results [*P* (perm) <0.05] are highlighted in bold. The tests for the factor 'sample' and the partitioning of multivariate variation are displayed. *P*-values were obtained using type III sums of squares. d.f.: degrees of freedom, SS: sums of squares.

3.2 Bacterial community structure

The differences in the bacterial community structure in response to different DOM sources were characterized using ARISA for both the experiments. Principal co-ordinate plots based on the ARISA fingerprints depicted the bacterial communities in response to different DOM sources obtained from *C. lamarckii* (Fig.3a) and *C. hysoscella* (Fig.3b). There was a considerable difference in the bacterial assemblages observed in different DOM treatment for both the *Scyphomedusae* species. This result was confirmed by cluster analysis, and each treatment showed tight clusters (Fig.4a, 4b). The PERMANOVA main test revealed significant differences among all the groups for both *C. lamarckii* (*P*=0.001, Table 3) and *C. hysoscella* (*P*=0.001, Table 4).

The alpha diversity is depicted as bar charts of mean values with a respective standard deviation of ARISA OTU numbers (Fig.5). Significant differences were tested with ANOVA and post hoc Tukey tests. Alpha diversity (OTU richness) analysis revealed similar diversity in the initial seawater (0 h) with 49 different ARISA band classes for both *C. lamarckii* and *C. hysoscella*. For *C. lamarckii* (Fig.5a), the highest richness was observed in the Kabeltonne seawater (*S*=54), followed by the *C. lamarckii*-incubated media (*S*=46); the ASW group showed the lowest richness with 37 band classes. According to the ANOVA, the bacterial community richness in the three different DOM sources was significantly

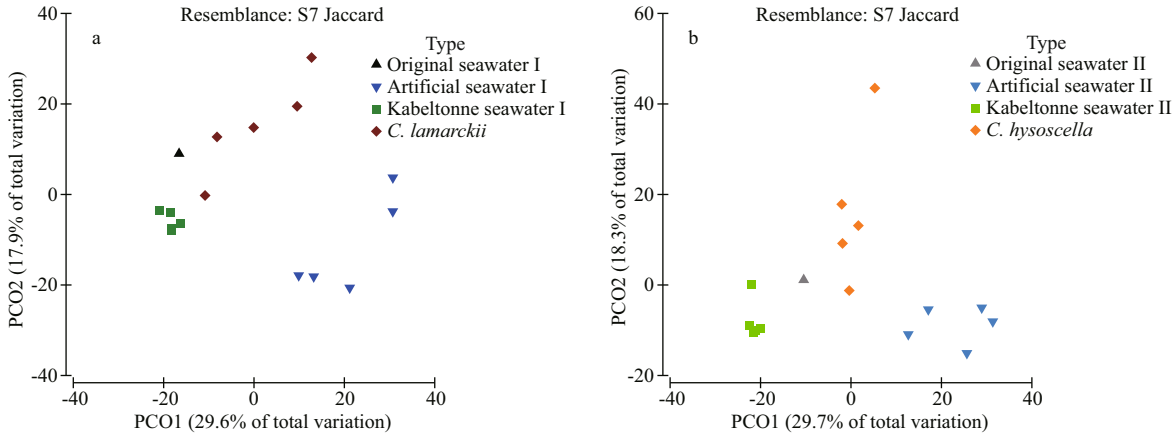

Fig.3 Principal coordinate (PCO) analysis presenting the bacterial communities based on Jaccard coefficient from ARISA profiles in different dissolved organic matter sources, including the initial inoculation (original seawater), for experiments with *Cyanea lamarckii* (a) and *Chrysaora hysoscella* (b)

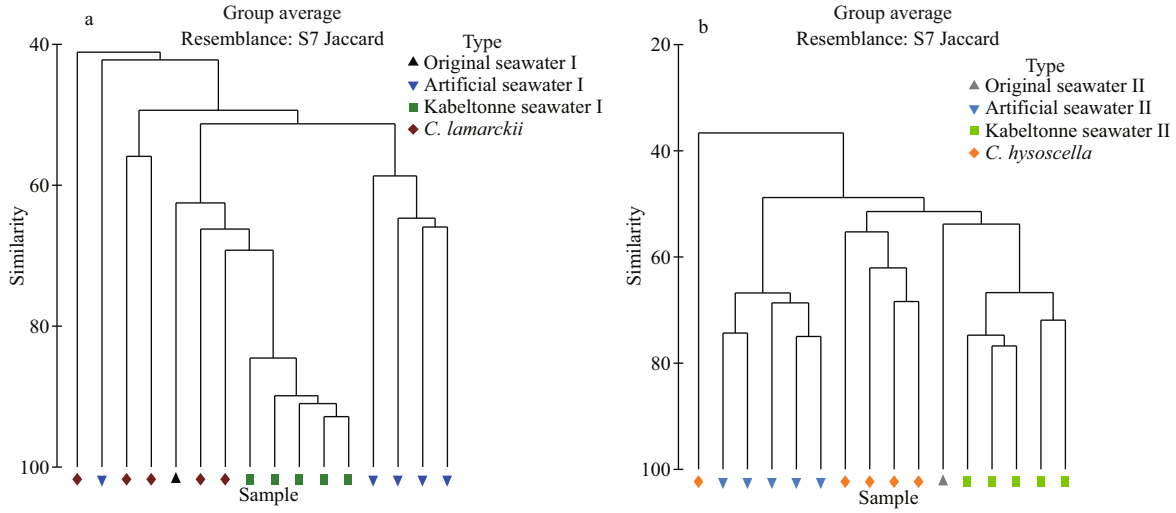

Fig.4 Cluster analysis based on Jaccard similarity of ARISA fingerprints of the bacterial community in different dissolved organic matter sources for experiments with *Cyanea lamarckii* (a) and *Chrysaora hysoscella* (b)

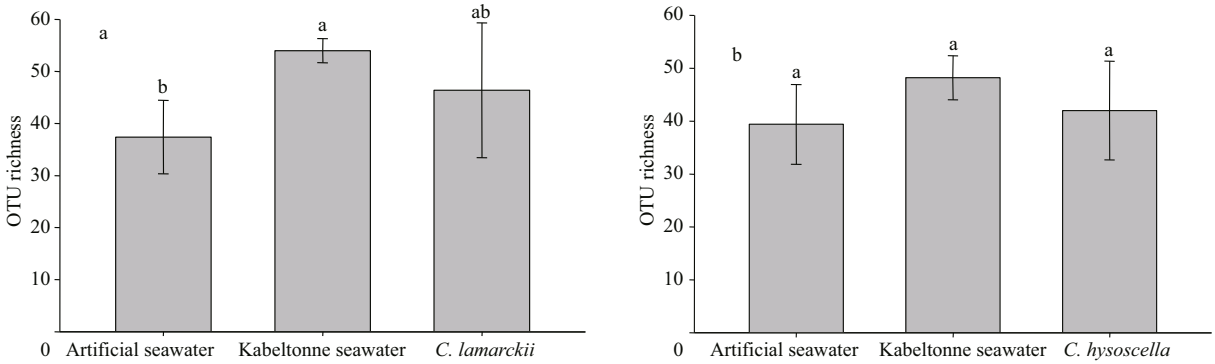

Fig.5 Bar chat of means of bacterial operational taxonomic units (richness) in different dissolved organic matter sources for the two Scyphomedusae species

Cyanea lamarckii (a) and *Chrysaora hysoscella* (b) obtained from ARISA fingerprints. Error bars represent 95% confidence intervals.

different ($F_{2,\ 12}$=7.163 2, P=0.009). In particular, a significant difference was observed between the Kabeltonne seawater and ASW groups (P=0.007). For *C. hysoscella* (Fig.5b), no differences were observed in bacterial community richness in the three different DOM sources ($F_{2,\ 12}$=2.934, P=0.918), and the highest richness was observed in Kabeltonne seawater (S=48).

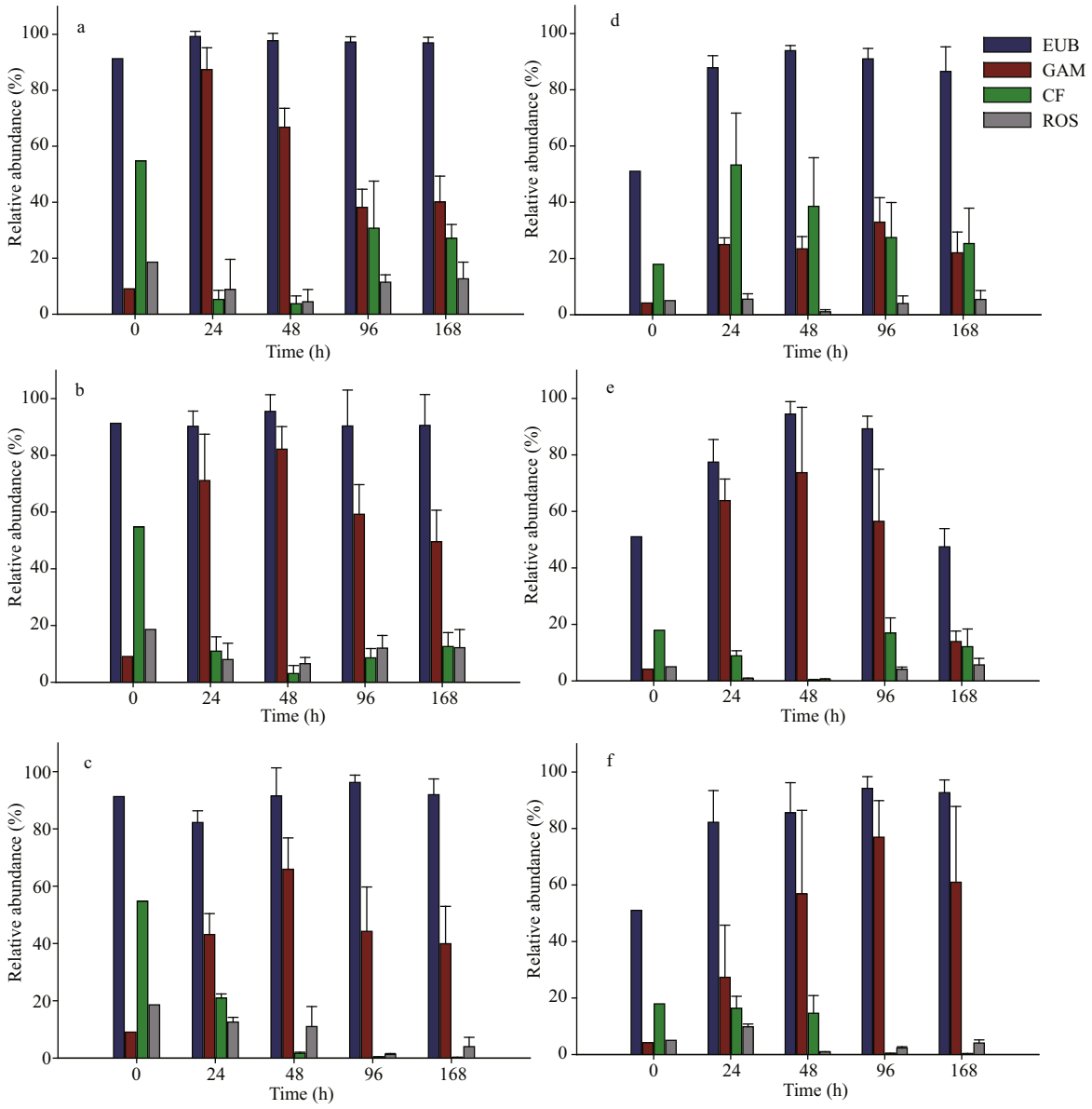

Fig.6 Relative abundance of bacterial communities in response to different dissolved organic matter (DOM) sources for the two *Scyphomedusae* with general probes

a–c. *Cyanea lamarckii*; d–f. *Chrysaora hysoscella*. DOM sources: (a, d) DOM released by live jellyfish (b, e) Kabeltonne seawater (c, f) artificial seawater (DOM-free). Error bars represent the 95% confidence intervals. Different bar colors represent the different bacteria detected: blue, total bacteria; red, Gammaproteobacteria; green, Cytophaga-Flavobacteria; gray, Roseobacter clade bacteria.

3.3 BCC in *C. lamarckii* experiments

CARD-FISH was used to observe the succession of specific bacterial groups in response to different DOM sources. For *C. lamarckii*-incubated media, the bacterial community at initial inoculation of seawater mainly consisted of Bacteroidetes (55%), followed by the Roseobacter clade (19%). Gammaproteobacteria were only present in a minor proportion (9%).

In all the groups, the BCC, as revealed by different taxonomic groups, changed significantly after the inoculation (Fig.6a–c). In the *C. lamarckii*-incubated medium and Kabeltonne seawater, Gammaproteobacteria significantly increased to 87% and 71% respectively and dominated the bacterial community at 24 h (Fig.6a, b). In ASW, Gammaproteobacteria increased but in lower proportion (43%; Fig.6c). In contrast, an abundance of Bacteroidetes decreased significantly at 24 h in all the groups. The relative abundance of Bacteroidetes in *C. lamarckii*-incubated media, Kabeltonne seawater, and ASW was 5%, 11%, and 21%, respectively. Similarly, in all the three groups, Roseobacter abundance decreased at 24 h, compared

with that at initial inoculation, but the relative abundance was similar among the three groups (8%–13%).

In the *C. lamarckii*-incubated media, the BCC at 24 and 48 h was not considerably different, whereas the bacterial composition changed at 96 h (Fig.6a). The Bacteroidetes community increased at 96 h, and their relative abundance reached 31%, whereas Gammaproteobacteria abundance decreased from 67% (at 48 h) to 38% (at 96 h). The Roseobacter community increased from 4% (at 48 h) to 11% (at 96 h). The BCC with respect to these major groups showed the same abundance in *C. lamarckii*-incubated media at 96 and 168 h.

In Kabeltonne seawater, Gammaproteobacteria initially reached their maximum (82%) at 48 h and decreased (59%) at 96 h (Fig.6b), whereas the Bacteroidetes community decreased (3%) at 48 h and then increased (9%) at 96 h. The Roseobacter community also increased from 6% (at 48 h) to 12% (at 96 h). At 168 h, the community composition showed no difference compared with the community at 96 h, Gammaproteobacteria dominated the community (50%), and the Bacteroidetes and Roseobacter communities showed similar abundance at 13% and 12%, respectively.

In ASW, the Gammaproteobacteria community increased (66%) at 48 h and then decreased (44%) at 96 h, whereas the Bacteroidetes and Roseobacter communities decreased significantly from 2% and 11% (at 48 h) to 0.4% and 1.3% (at 96 h), respectively (Fig.6c). At 168 h, Gammaproteobacteria dominated the bacterial community (40%), Roseobacter were present only in minor proportions (4%), and Bacteroidetes were absent.

In general, in all the three DOM sources, the BCC significantly changed after the initial inoculation. Although Gammaproteobacteria dominated the community in all the DOM sources, the relative abundance varied from each other (40%–50%). Therefore, we investigated the composition of these dominant communities with specific probes (Fig.7a–c).

For the inoculation performed with *C. lamarckii*, the dominant Bacteroidetes community was composed of *Polaribacter* (21%) and a few *Ulvibacter* (1%), whereas Gammaproteobacteria community was composed of *Alteromonas* (4%) and a few *Pseudoalteromonas* (0.7%).

At 24 h, the bacterial community in the *C. lamarckii*-incubated media was highly dominated by *Alteromonas* (97%), but at 168 h, their abundance decreased to 27% and *Pseudoalteromonas* abundance increased (1.7%; Fig.7a). For the Bacteroidetes community, *Polaribacter* abundance was low (4%), and no *Ulvibacter* were detected at the end. In Kabeltonne seawater, *Alteromonas* dominated the community at the beginning (24 h; 69%) and at the end (168 h; 45%). *Pseudoalteromonas* were present in minor proportions (1%) at 24 h and were negligent (0.6%) at 168 h (Fig.7b). In ASW, the Gammaproteobacteria community contained only *Alteromonas* (42%) at 24 h, but both *Alteromonas* (52%) and *Pseudoalteromonas* (44%) at 168 h (Fig.7b). Thus, for *C. lamarckii*, the BCC differed considerably with different DOM sources.

3.4 BCC in *C. hysoscella* experiments

For the experiments conducted with *C. hysoscella*, only 51% of the microbial community was detected as bacteria at the initial inoculation, and it mainly consisted of Bacteroidetes (18%), followed by the Roseobacter clade (5%) and Gammaproteobacteria (4%; Fig.6d–f). In *C. hysoscella*-incubated media, Bacteroidetes community increased significantly and dominated the bacterial community with 53% relative abundance at 24 h, compared with that at inoculation, and the Gammaproteobacteria community also increased at 24 h (25%; Fig.6d). The abundance of the Roseobacter community did not change after inoculation and was 6% of the entire bacterial community. However, in Kabeltonne seawater, Gammaproteobacteria significantly increased at 24 h and contributed to 64% of the entire bacterial community (Fig.6e). The abundance of Bacteroidetes and Roseobacter communities decreased to 9% and 0.8%, respectively, at 24 h, compared with those observed at initial inoculation. In ASW, the abundance of Gammaproteobacteria and Roseobacter communities also increased at 24 h (27% and 10%, respectively), compared with those observed at initial inoculation; the Bacteroidetes community retained the original relative abundance (16%) at 24 h (Fig.6f).

In *C. hysoscella*-incubated media, no difference was observed in the bacterial composition at 24 and 48 h (Fig.6d). Bacteroidetes continued to dominate (39%) the community at 48 h, whereas Gammaproteobacteria increased from 23% at 48 h to 33% at 96 h; however, there was no difference between the relative abundance of Gammaproteobacteria and Bacteroidetes at 96 h. The Roseobacter community increased from 0.7% at 48 h to 4% at 96 h. At the end

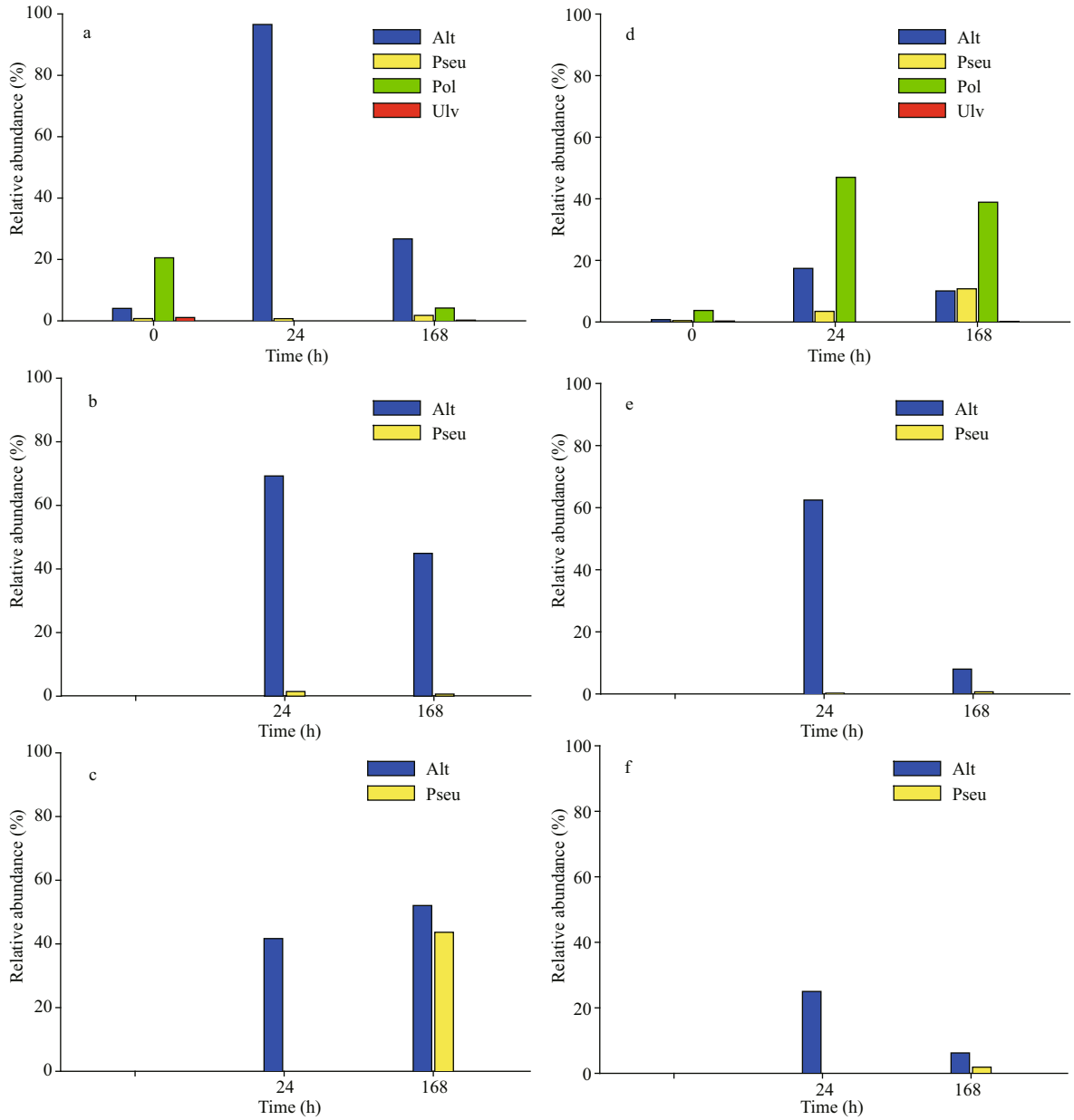

Fig.7 Relative abundance of bacterial communities in response to different dissolved organic matter (DOM) sources for two *Scyphomedusae* with specific probes

a–c. *Cyanea lamarckii*; d–f. *Chrysaora hysoscella*. DOM sources: (a, d) DOM released by live jellyfish (b, e) Kabeltonne seawater (c, f) artificial seawater (DOM-free). Different bar colors represent the different bacteria detected: blue: *Alteromonas*; yellow: *Pseudoalteromonas*; green: *Polaribacter*; red: *Ulvibacter*.

of the experiment (168 h), Gammaproteobacteria and Bacteroidetes communities were present in almost equal amounts (22% and 25%, respectively). The relative abundance of Roseobacter at 168 h was surprisingly the same as that observed initially at inoculation (5%).

In Kabeltonne seawater, Gammaproteobacteria (74%) was the predominant community at 48 h (Fig.6e). However, the Bacteroidetes and Roseobacter communities recovered at 96 h (17% and 4%, respectively), compared with their abundance at 48 h (0.3% and 0.5%, respectively). In the end, Gammaproteobacteria significantly decreased from 56% at 96 h to 14% at 168 h, but the abundances of Bacteroidetes and Roseobacter (12% and 6%, respectively) at 168 h were similar to those observed at 96 h. In addition, the total bacterial abundance decreased considerably (47%) at 168 h, compared with that at other time points.

In ASW, the abundance of Gammaproteobacteria

community increased (57%) and Roseobacter community decreased (0.3%) at 48 h, compared with their abundances at 24 h (Fig.6f). The BCC changed significantly at 96 h; Gammaproteobacteria highly dominated the bacterial community (77%), Bacteroidetes were almost absent (0.4%), and Roseobacter were present in minor proportions (2%). However, the BCC at 168 h was almost similar to that at 96 h. At 168 h, Gammaproteobacteria remained dominant but with lower abundance (61%), compared with that at 96 h, whereas the abundance of Bacteroidetes and Roseobacter was merely 0.3% and 4% of the entire community, respectively.

Furthermore, the use of specific probes to determine the composition of different bacterial communities revealed significant differences in the bacterial composition in different DOM sources (Fig.7d–f). We detected 4% *Polaribacter* at initial inoculation in experiments with *C. hysoscella* (Fig.7d). In *C. hysoscella*-incubated media, the Gammaproteobacteria community at 24 h consisted of 17% *Alteromonas* and 3% *Pseudoalteromonas*, whereas the dominant Bacteroidetes community at 24 h mainly consisted of 47% *Polaribacter* (Fig.7d). At the end (168 h), the Gammaproteobacteria community consisted of 10% *Alteromonas* and 11% *Pseudoalteromonas*, whereas the Bacteroidetes community consisted of 39% *Polaribacter*. However, in Kabeltonne seawater, the dominant Gammaproteobacteria community mainly consisted of *Alteromonas* both at 24 h and 168 h, but with varied abundance (Fig.7e). *Alteromonas* abundance at the beginning (24 h) was 62%, which decreased significantly to 8% at 168 h. In ASW, the dominant Gammaproteobacteria community also consisted of *Alteromonas* at both 24 h (25%) and 168 h (6%) (Fig.7f). Moreover, *Pseudoalteromonas* were not detected at the beginning but were detected at 2% at the end (168 h).

4 DISCUSSION

Jellyfish blooms play an important role in influencing bacterial abundance and dominance of specific bacterial phylogenetic groups. However, the impact of DOM released by live jellyfish on bacterial communities is not well understood. Therefore, in this study, we investigated the succession of BCC in response to DOM released by live *Scyphomedusae*, *C. lamarckii* and *C. hysoscella*, collected in July and August 2012, respectively, from Helgoland Roads in the German Bight of North Sea. Incubation experiments revealed that jellyfish-incubated media showed the highest bacterial abundance and these bacterial communities showed significantly higher growth, compared with that observed in Kabeltonne seawater and ASW (Figs.1 and 2). There is a distinct succession of BCC in response to the DOM released by live jellyfish.

4.1 The succession of BCC response differently to the DOM released by different live jellyfish species

The DOC released during jellyfish decomposition supports bacterioplankton production (Titelman et al., 2006). Increased bacterial abundances resulting in the growth of specific bacterial phylotypes indicates that jellyfish tissues stimulate the growth of specific bacteria (Titelman et al., 2006). In the present study, the experiments conducted with *C. lamarckii* and *C. hysoscella*, the initial inoculum was dominated by the *Cytophaga-Flavobacteria*, which belong to the Bacteroidetes community. The *Cytophaga-Flavobacteria* cluster is the most abundant group of all bacterial communities in many oceanic habitats (Llobet-Brossa et al., 1998; Glöckner et al., 1999; Simon et al., 1999; Cottrell and Kirchman, 2000b; Eilers et al., 2000b), accounting for almost half of all bacteria potentially identified by FISH. After incubation with different DOM treatments, *Polaribacter* were found to be abundant both at the beginning and the end of the experiments conducted with *C. hysoscella*, whereas they were present only in minor proportions at the end of the experiment conducted with *C. lamarckii*. The bacterial community was dominated by Gammaproteobacteria and Bacteroidetes in the *C. lamarckii*-incubated media coupled with a clear succession; Gammaproteobacteria (represented by *Alteromonas*) was consistently dominant throughout the experiment with a considerable decrease at the end (from 97% to 27%, Fig.7a), whereas Bacteroidetes decreased initially and recovered at the end of the experiment. However, in *C. hysoscella*-incubated media, Bacteroidetes were abundant throughout the experiment and Gammaproteobacteria were equally abundant with Bacteroidetes at the end of the experiment. Bacteroidetes, especially the representatives of the class Flavobacteria are presumed to play an important role in the degradation of complex organic matter (Kirchman, 2002). Blanchet et al. (2015) reported that the addition of DOM from the jellyfish *Aurelia aurita* induced a rapid growth of Gammaproteobacteria, followed by domination by Bacteroidetes, and the bacterial community shifting toward a higher

proportion of Alphaproteobacteria at the end of the experiment. Gómez-Consarnau et al. (2012) revealed that some bacterial phylotypes were highly abundant in environments enriched with specific carbon compounds (e.g., *Acinetobacter* sp. B1-A3 with acetate and *Psychromonas* sp. B3-U1 with glucose). The clear difference in BCC in response to the DOM released by different jellyfish species might indicate that the jelly-DOM contains different compounds that favor the growth of specific bacterial species.

Tinta et al. (2010, 2012) revealed a rapid shift in community composition from unculturable Alphaproteobacteria to the culturable species of Gammaproteobacteria and Flavobacteria in response to the addition of jellyfish *Aurelia* sp. tissue. Dinasquet et al. (2013) studied bacterial utilization and community responses to bioavailable DOC obtained from different time points during a mesocosm experiment involving the ctenophore *Mnemiopsis leidyi*. They found that bacteria of the order Alteromonadales (Gammaproteobacteria) were predominant at the beginning but were less prevalent at the end and were replaced by those belonging to the order Oceanospirillales (Dinasquet et al., 2013). Alteromonadales seem to be adapted to utilize freshly available DOC (Allers et al., 2008) and are specialized in utilizing carbohydrates (Dinasquet et al., 2013). Their analysis of ectoenzyme activities revealed preferential degradation of protein-rich compounds by bacteria switched to the utilization of carbohydrate-rich DOC under conditions of protein depletion (Dinasquet et al., 2013). In this study, we found that the growth of *Alteromonas* and *Polaribacter* was particularly favored in response to jelly-DOM. *Alteromonas macleodii* exhibits hydrolytic ectoenzyme activities, such as amylases, gelatinases, and lipases (Baumann et al., 1972). Thus, these bacteria must be well equipped to degrade the major components of mucus released by jellyfish. The investigation of the bacterial taxa in response to the addition of mucus from the coral *Fungia* sp. revealed that bacterial communities showed a sudden increase in the number of Gammaproteobacteria during short term incubations (50 h), and *Alteromonas* was the dominant phylotype (Allers et al., 2008). Moreover, *Alteromonas* spp. can utilize monomers such as hexoses, disaccharides, sugar acids, amino acids, and ethanol (Baumann et al., 1972). *Polaribacter* is able to form microcolonies within aggregates, indicating active growth and production of extracellular polysaccharides (Gómez-Pereira et al., 2012). The versatile metabolism of these microorganisms may help them exploit rapid changes in the supply of a complex substrate source such as the bioavailable DOM released by live jellyfish. Collectively, our findings and the results from other studies (Titelman et al., 2006; Tinta et al., 2010, 2012; Condon et al., 2011) indicate that the bacterioplankton community is not only influenced by the degradation of jellyfish biomass but also shows strong succession in response to the metabolic process of live jellyfish.

4.2 BCC response to the Kabeltonne and ASW treatments

In Kabeltonne seawater, the bacterial community was dominated by Gammaproteobacteria after the inoculation in both experiments conducted with *C. lamarckii* and *C. hysoscella*. Enrichment of Gammaproteobacteria during confinement is often interpreted as a bottle effect (Eilers et al., 2000a; Pinhassi and Berman, 2003). In particular, *Alteromonas* was the abundant group both at the beginning and the end in the C. *lamarckii* experiments, whereas this phylotype decreased sharply in the *C. hysoscella* experiments. The rapid growth of *Alteromonadaceae* upon confinement has been observed during incubation of marine waters from habitats as different as the North Sea, the Mediterranean Sea, and the Red Sea (Eilers et al., 2000b; Pinhassi and Berman, 2003; Allers et al., 2007). The Bacteroidetes and Roseobacter communities recovered at the end in both experiments, suggesting that the possibility of a bottle effect was minimal in the present study. Gammaproteobacteria and Bacteroidetes play a role in amino acid and glucose assimilation, consistent with the view of them as opportunistic organisms (Alonso and Pernthaler, 2006; Alonso-Saez and Gasol, 2007). These opportunists may have played a role in our experiments in response to different DOM sources in the two experiments. They are capable of degrading high-molecular weight organic compounds (McBride et al., 2009) because of the presence of genes encoding hydrolytic enzymes with a preference for polymeric carbon sources and a distinct capability for surface adhesion (Bauer et al., 2006). The proliferation of different assemblages of Gammaproteobacteria in the different Kabeltonne seawater groups suggests that DOM availability affected community succession significantly.

In marine environments, primary production by phytoplankton is the ultimate source of marine

organic matter (Ogawa and Tanoue, 2003). The fraction and composition of the photosynthetic products released as DOM vary considerably with species and growth conditions (5%–50%) (Carlson et al., 2000). Microbes may also release compounds during nutrient acquisition and chemical defense (Kujawinski, 2011). In addition, DOM may be released when cells die through processes such as viral lysis, predation by protozoa or bacteria, and senescence (Nagata, 2008). In the present study, the Kabeltonne seawater represents DOM directly collected from fresh natural surface seawater. It was found that the high-molecular weight fraction of DOM is abundant in the surface (30%–35% for >1 kDa and 5%–7% for >10 kDa), compared with that found in the deep water (20%–25% for >1 kDa and 2%–4% for >10 kDa) (Ogawa and Tanoue, 2003). The labile organic matter present at the ocean surface mainly contains polysaccharides (Benner et al., 1992), proteins, lipids (Ogawa and Tanoue, 2003), and bacterial cell wall components such as peptidoglycan (McCarthy et al., 1998). Although high-molecular weight DOM is a minor fraction of DOM (~30%), it shows high availability for bacterial utilization, compared with that of low-molecular weight DOM (Amon and Benner, 1994), which is the major fraction of DOM throughout the water column in the ocean (Ogawa and Tanoue, 2003) but requires enzymatic digestion before uptake (Hoppe, 1991). Although we do not have the data concerning the composition of DOM used in our study currently, the bacterial community in Kabeltonne seawater with high-molecular weight DOM was highly dominated by Gammaproteobacteria, particularly by the genus *Alteromonas*. We speculate that the community changes associated with these differences in DOM reflect niche partitioning driven by the capacity to utilize accessible DOC and/or specific carbon compounds (Gómez-Consarnau et al., 2012).

In ASW, the inoculated bacterial community continued to grow but with a relatively longer lag phase and lowest maximum population density, compared with those observed in *C. lamarckii*- and *C. hysoscella*- incubated media and Kabeltonne seawater. The long lag phase may be attributed to the lack of DOM in ASW, implying a lack of nutrients for the growth of the bacteria inoculated at the beginning of the experiment. The difference in the lag phases between the two jellyfish species (48 h for *C. lamarckii* and less than 24 h for *C. hysoscella*) might be because of the differences in microbial community composition of each inoculum, as revealed by CARD-FISH. For the initial inoculum of *C. hysoscella*, only 50% of the bacterial community was detected by CARD -FISH, and the rest of the inoculum consisted of microbial organisms with a size between 0.2 μm and 3 μm. These microbial organisms cannot survive in a DOM-free medium such as ASW. Therefore, after some time, the detritus of these dead organisms serves as a nutrient and organic matter source for other bacterial communities. In this case, the higher the number of microbes in the initial inoculum, the shorter would be the lag phase after inoculation in ASW. The CARD-FISH analysis revealed that bacteria comprised 90% of the microbial community in the inoculum of *C. lamarckii* experiments. Therefore, the bacterial community presented a significantly long lag phase in the ASW. In both experiments, Gammaproteobacteria was the dominant community; in particular, *Alteromonas* were present in a low proportion at the beginning and *Pseudoalteromonas* occurred at the end of the experiment. The Bacteroidetes community was not detected at all at the end of both the experiments. The cultivable genera *Alteromonas* and *Pseudoalteromonas* were frequently isolated from coastal and pelagic regions of the Pacific Ocean as well as from the North Sea using low-nutrient media (Eilers et al., 2000a; Cho et al., 2007).

5 CONCLUSION

In this study, we demonstrate significant shifts in the composition of bacterial communities and an increase in bacterial growth in response to different DOM sources. The bacterial communities were more active in media obtained after *C. lamarckii* and *C. hysoscella* incubation as well as Kabeltonne seawater, compared to those in ASW. Bacterial abundance was markedly influenced by the DOM released by live jellyfish, resulting in the consistent growth of Gammaproteobacteria and Bacteroidetes. Although Bacteroidetes decreased initially, their abundance increased by the end of the incubation period in the presence of *C. lamarckii* DOM, indicating the differences in the capacity of bacterial phyla to utilize specific carbon compounds. Furthermore, we showed that species-specific jellyfish DOM was utilized by considerably different bacterial communities. In a nutshell, the bacterioplankton community is not only influenced by the degradation of jellyfish biomass but also strongly affected by the DOM released through the various metabolic process of live jellyfish. However,

a confident linkage between certain taxa and specific carbon compounds cannot be established here because of the lack of chemical characterization of the DOM pools. Therefore, the compositions of DOM as well as the bacterial functional aspects, such as ectoenzymatic activities and growth efficiency, need to be investigated in further studies. Furthermore, the SAR11 clade from the Alphaproteobacteria is an important group that generally dominates the bacterioplankton community both in winter (February) and spring (April) at Helgoland Roads. However, owing to certain gaps in the bacterial community composition of initial inoculums, the presence of the SAR11 clade was not analyzed in this study. Further studies, especially those involving the use of probe specific for the SAR11 clade are warranted to determine the detailed bacterial community composition and understand the detailed bacterial successions in response to different DOM compounds. Nevertheless, to the best of our knowledge, this is the first study to investigate the utilization of DOM released by live jellyfish and one of the few studies that demonstrate changes in bacterial diversity with respect to jellyfish biomass.

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Electronic supplementary material

Supplementary material (Supplementary Tables S1–S3) is available in the online version of this article at https://doi.org/10.1007/s00343-019-8106-0.