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ORIGINAL ARTICLE

Relationship between phylogenetic and nutritional diversity in Arctic (Kandalaksha Bay) seawater planktonic bacteria

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Abstract Due to huge yearly variations of environmental stressing conditions, Kandalaksha Bay (Arctic Circle, White Sea, Russia) could represent a model to study microbial adaptation in extreme environments. This peculiar estuarine system has been scarcely investigated for its microbial diversity. In this work, to gather information on their nutritional competencies, seawater planktonic bacteria were studied for their ability to use different carbon sources by the Biolog phenotype microarray assays. Nestedness, a useful statistical tool used in ecology, was employed to underline nutritional differences among microbial groups. In particular, nestedness was used to understand the complex relationship that is established when many nutrients are available for various microorganisms, and to highlight presence of specialists and generalists. Among the studied bacteria, which showed very diverse nutritional abilities, 47% belonged to *Pseudomonas*, 21% to *Serratia* and 32% to other Genera. Within *Pseudomonas*, both highly generalist and highly specialist strains were discovered. However, most of them used organic and/or amino acids as principal carbon sources. In contrast, *Serratia* strains typically preferred sugars and appeared to be more generalist. On the whole, important differences in specialization levels and nutritional competencies were recorded in strains belonging to the same species. Correlations between phylogenetic and nutritional data were validated by Procrustes analysis.

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Introduction

White Sea is an enclosed basin located at the Arctic Circle and considered as a sub-extreme environment (Pantyulin, 2003). Microorganisms in this zone must adapt to variable environmental conditions in which factors, such as water availability, temperature and salinity, change frequently (Savvichev et al. 2004; Shaporenko et al. 2005; Vershinin et al. 2006; Kravchishina et al. 2008).

Kandalaksha Bay (KB), the northernmost White Sea region, is an estuarine system showing large sea level differences during tide cycles; this produces intense water mixing affecting microbial and nutrient distribution (Melnikov et al. 2003; Savvichev et al. 2003; Pesciaroli et al. 2015). Moreover, due to various rivers and strong precipitations, seasonal intense freshwater inputs contribute to frequent changes of nutrient availability and composition (Howland et al. 1999; Dolotov et al. 2005).

To cope with these wide variations, strongly affecting their diversity (Liebner et al. 2008), microorganisms must adopt various physiologic and metabolic mechanisms of adaptation. The ability to grow in very wide temperature ranges has been demonstrated as a winning surviving strategy in KB (Pesciaroli et al. 2012). In addition, the microbial community must have a well-structured functional organization with efficient interchange of dominant and resilient species (Pesciaroli et al. 2015). A further adaptation approach could be the coexistence and/or alternation of generalist and specialist species. Generalists could use a wide array of nutrients having strong metabolic advantages to counteract sudden and repeated

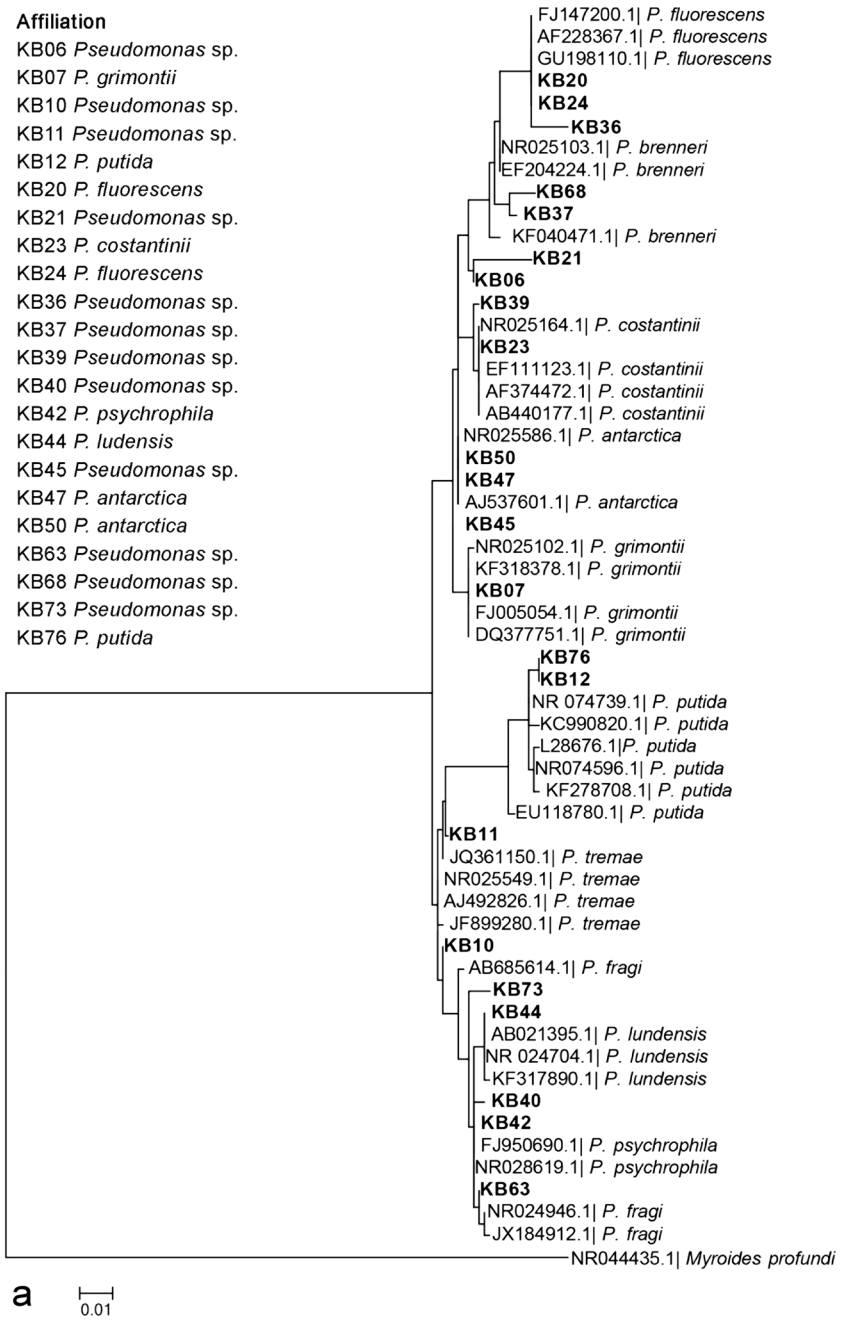
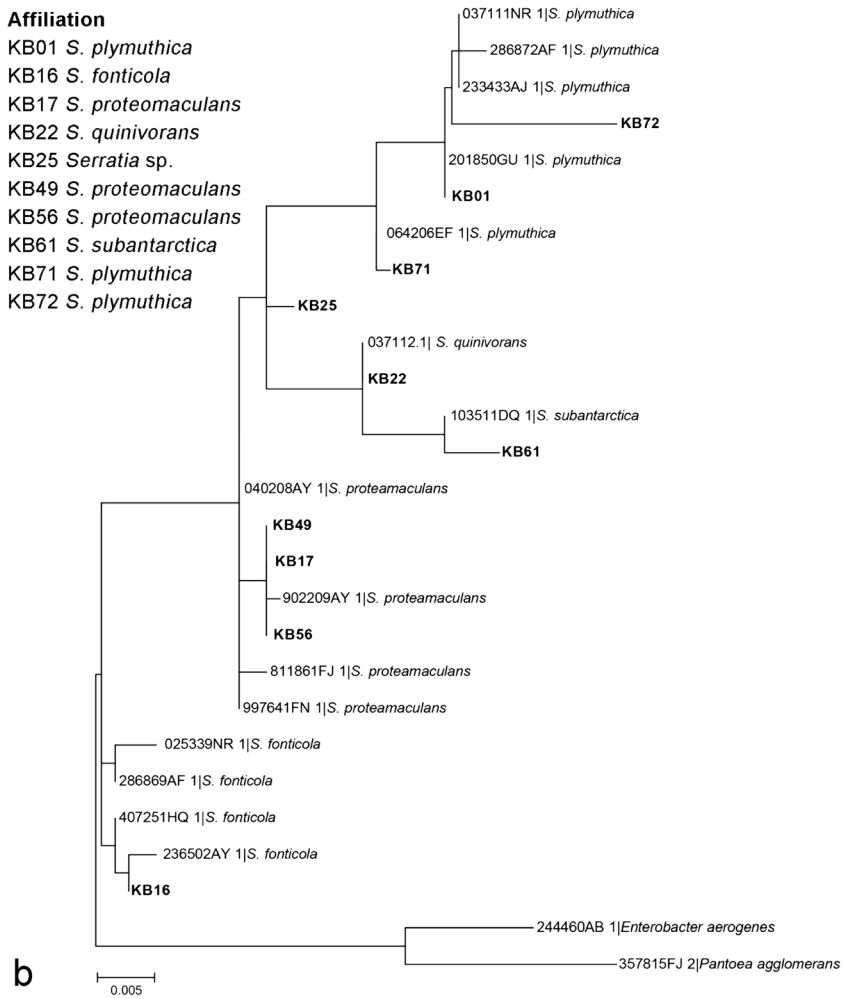


Fig. 1 Phylogenetic Maximum Likelihood tree of the 16S-rDNA sequences and affiliation of the KB strains. Sequences retrieved from the EMBL database are indicated by their corresponding accession numbers. Bootstrap values from 1000 were re-sampled. (**a**) *Pseudomonas,* (**b**) *Serratia* and (**c**) *Other* strains

nutrient variations. Microorganisms could grow in a broad range of nutritional situations and colonize diversified environments, but the presence of a high number of generalists could increase nutritional competition. Specialists, even showing limited metabolic competencies, could prevail when specific substrates become available or in stable peculiar niches. Moreover, due to their high specialization, they could be less influenced by competition (Kassen 2002; Elena and Lenski 2003; Villaescusa et al. 2010).

However, it is difficult to understand the complex relationship that occurs when a wide array of nutrients is available for a composite microbial community. It is necessary to consider both the interactions among species within the communities and those among species and their environment. In this context, network analysis is a useful framework to investigate structural and functional properties of such complex systems. Relationships between groups of items (nodes) are represented by links, and useful information about the structure and



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robustness of the systems is also given by the linking typology (Newman 2003; Proulx et al. 2005). A lot of metrics can quantify specific patterns of aggregation, and nestedness is one of the main properties found in biological and ecological networks. Nestedness measures the degree of order/disorder between two sets of nodes, such as species vs. area or species vs. resources. It is also useful to quantify the extent to which specialized species interact with increasingly large subsets of generalists, and to identify species-specific metabolic patterns (Bascompte et al. 2003; Olesen et al. 2007; Graham et al. 2009; Poisot et al. 2011; Barberan et al. 2012).

In contrast to those from other arctic environments (Carpenter et al. 2000; Brinkmeyer et al. 2003), the microbial communities of Kandalaksha Bay has been poorly studied, and to the best of our knowledge, no deep investigation on nutritional competencies of its microbiome is available.

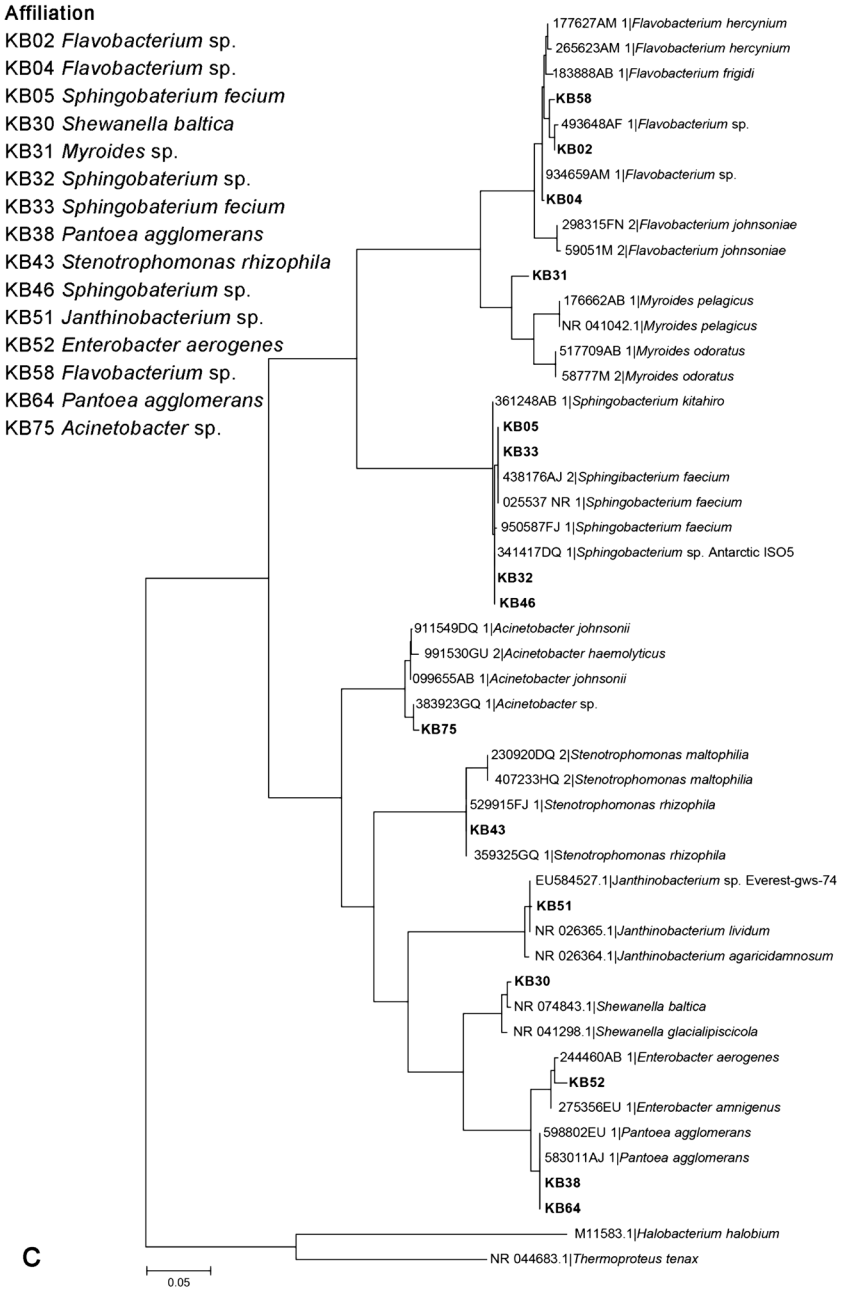
To increase the knowledge of this very peculiar environment, in this study, 47 Gram-negative planktonic bacteria were phylogenetically affiliated and submitted to the Biolog phenotype microarray assay in order to understand their capability to use different (95) carbon sources. Nestedness was then applied to underline relationships between microbial groups and nutrients, while Procrustes analysis was performed to validate relationships between phylogenetic treats (16S rDNA) and nutritional competencies.

Materials and methods

Microorganisms and culture conditions The Gram-negative bacterial strains used in this study were isolated in a previous work and their 16S rDNA sequences were deposited in the NCBI GeneBank database (Pesciaroli et al. 2012).

It is worth noting that the initial number of isolates, obtained from the KB samples, was very high (ca. 500). However, in this work, in order to avoid evident replicates of the same strains, we only considered those isolates (47) showing differences by both the 16S rDNA sequencing and Biolog microarray analysis.

Strains were maintained at 4° C in the DEB (Department of Ecological and Biological Sciences,



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University of Tuscia)'s culture collection of microorganisms, and sub-cultured when necessary on plate count agar slants (Difco, USA).

Molecular phylogenetic analysis Automatic 16S rDNA sequence alignment and dendrogram construction were carried out using MEGA 6.0 (Tamura et al. 2007). In order to get a confident branch length, the whole alignment was split and different trees were generated for *Pseudomonas*, *Serratia* and all the other analyzed genera (*Other*), respectively. P-distances based evolutionary trees were inferred using the Maximum

Fig. 2 Nestedness of KB strains' nutritional preferences, based on the ▶ incidence matrix obtained from the Biolog phenotype microarray. Black, white and grey squares represent *Pseudomonas*, *Serratia* and "*Others*" strains, respectively. Numbers below strain codes indicate the numbe of carbon sources used by that strain. Different typologies of carbon sources (Carbohydrates, Carboxylic acids, Amino acids, Amines/Amides, Polymers and Miscellaneous) are indicated by the grey scale on the bottom right side. The number of strains using a specific carbon source is indicated beside each compound. As indicated by the *arrow*, generalist strains are located rightward, while specialists are located to the left. Mostly used substrates are placed at the top of the table, while scarcely used sources are at the bottom


KB75 KB44 KB04 KB12 KB02 KB63 KB31 KB32 KB11 KB76 KB40 KB58 KB30 KB46 KB73 KB42 KB45 KB43 KB39 KB10 KB33 KB52 KB51 KB47 KB20 KB38 KB64 KB68 KB49 KB21 KB56 KB25 KB07 KB05 KB72 KB24 KB16 KB06 KB50 KB17 KB01 KB36 KB22 KB23 KB71 KB61 KB37
20 24 27 28 28 29 29 29 34 34 36 36 37 37 38 39 39 43 44 44 44 44 46 46 47 50 51 52 52 55 56 57 58 59 59 61 62 64 64 64 65 65 66 67 67 69 70
47 L-Asparagine
45 L-Glutamic ac.
44 L-Aspartic ac.
44 α-D-Glucose
41 L-Serine
41 Succinic ac.
41 L-Alanine
41 Br-succinic ac.
40 D,L-Lactic ac.
40 L-Proline
40 D-Trehalose
40 Pyruvic ac.Met.Ester
39 Glycerol
38 D-Galactose
37 D-Alanine
37 Citric ac.
37 Cis-Aconitic ac.
37 L-Arabinose
37 Acetic ac.
36 D-Mannose
36 D-Gluconic ac.
36 L-Alanylglycine
35 Tween 80
35 Inosine
35 D-Fructose
34 L-Histidine
32 Dextrin
32 N-acetil-glucosamine
32 m-Inositol
31 Urocanic ac.
31 α-ketoglutaric ac.
30 Succinic ac.Met.Ester
30 Uridine
30 D-Mannitol
30 Tween 40
29 Glycilglutamic ac.
28 γ-Am.Butyric ac.
28 Propionic ac.
26 Sucrose
25 Formic ac.
25 Putrescine
24 Quinic ac.
24 L-Leucine
24 OH-Proline
23 β-OH-butyric ac.
23 D-Sorbitol
22 Maltose
22 L-Threonine
21 Galacturonic ac.
21 D-Arabitol
21 D-Glucuronic ac.
20 Gentiobiose
20 Pyroglutamic ac.
20 D,L-α-Glyc Phosp
20 p-OH-Phenylacetic
19 D-Glucosaminic
19 Glycilaspartic ac.
19 β-CH2-D-Glucoside
18 D-Cellobiose
17 D-Serine
17 D-Saccharic ac.
17 Thymidine
17 L-Ornithine
16 Malonic ac.
16 D-Raffinose
16 2-aminoethanol
16 N-ac-Galactosamine
16 L-Fucose
16 D-Melibiose
15 Galactonic ac.
15 Glycogen
15 Glucose-5-phosphate
14 Glucose-1-phosphate
13 Succinamic ac.
13 Adonitol
13 L-Alaninamide
12 Ketovaleric ac.
12 Turanose
12 D-Psicose
12 Ketobutyric ac.
11 Glucuronamide
11 α-D-Lactose
10 L-Rhamnose
9 Lactulose
8 D,L-Carnitine
8 Erythritol
8 Itaconic ac.
8 α-Cyclodextrin
7 Xylitol
7 α-OH-Butyric ac.
2 L-Phenylalanine
1 2,3-Butanediol
1 Phenyethylamine
1 γ-OH-Butyric ac.
1 Sebacic ac.
Specialism
Generalism
Carbohydrates
Carboxylic acids
Aminoacids
Amines/Amides
Polymers
Miscellaneus

Likelihood method. Bootstrap tests were conducted to infer the reliability of branch order, with 1000 pseudo-replicates.

Nutritional characterization Strain metabolic competence was investigated in relation to the possible use of 95 carbon sources (including carbohydrates, carboxylic acids, polymers/oligomers, amines/amides, amino acids and other compounds) by the "Biolog" phenotype microarray assays (Odumeru et al. 1999; Truu et al. 1999), as already reported (Juarez-Jimenez et al. 2010). Briefly: Biolog GN2 μ-plates were used to test strains' assimilation abilities. Suitable cell densities (OD ca. 0.65 at 560 nm) of bacterial suspensions were inoculated into micro-well plates and incubated for 24 h according to the GN2 Biolog Micro-Plate system manual. Growth and substrate oxidation (color development) were automatically recorded using the Biolog micro-plate reader at 590 and 750 nm, respectively. Results, analyzed by the Biolog Micrologg 4.2 software (Biolog, Hayward, Ca, USA), were converted into a binary matrix used to perform the clustering analysis for nutritional similarity (nutritional dendrograms). Dendrograms were obtained by the free software PAST 3.01 (Hammer et al. 2001). P-distance based trees were inferred using the Maximum Likelihood method. Bootstrap tests were conducted to infer the reliability of branch order, with 1000 pseudo-replicates.

Network analysis Data were arranged as an incidence matrix, whose values indicated the use of a particular resource (row) by a given strain (column).

The matrix was converted into a bipartite network, a peculiar organization establishing links between two distinct sets of nodes (in our case bacteria and resources), with no links within nodes of the same set. Nestedness was therefore evaluated to measure the order in which substrates were used by the bacterial communities.

Nestedness was quantified by the matrix temperature T^* (Atmar and Patterson 1993) and quantified with a 0–100 scale using the BINMATNEST algorithm (Rodriguez-Girones and Santamaria 2006) implemented in the "bipartite" package of R (R Development Core Team 2013). The significance of a nested structure was tested by comparing the observed value with the distribution from the 1000 resulting randomized matrices. A conservative null model (Ulrich et al. 2009), where the probability to obtain a link between a bacteria and a resource is equal to the arithmetic mean, $(p_r+p_c)/2$, of the incidence probability given by the fraction of ones in columns, p_c, and rows, p_r, was used (Bascompte et al. 2003).

Multivariate analyses A generalized Procrustes rotation (PR) was used to check the correlation between different multivariate ordinations based on the distance matrices calculated on both phylogenetic and resource-consumption data. PR is based on a traditional singular value decomposition to decompose a matrix into principal components, by comparing two or more spaces where the same variables (bacteria) are measured, by calculating a new set of factors (i.e., dimensions) that resemble all scores' subspaces (Fred 1991).

Two principal component analyses (PCA) were then performed on the phylogenetic and metabolic distances matrixes based on Bray-Curtis dissimilarity, with the first two axes of the PCAs used to compare molecular (16S rDNA sequences) and metabolic traits. Procrustes was used to estimate the significances of the PR statistics, assessing similarities between different ordinations. A permutation test with 1000 bootstrap replicates was then performed to measure the significance of

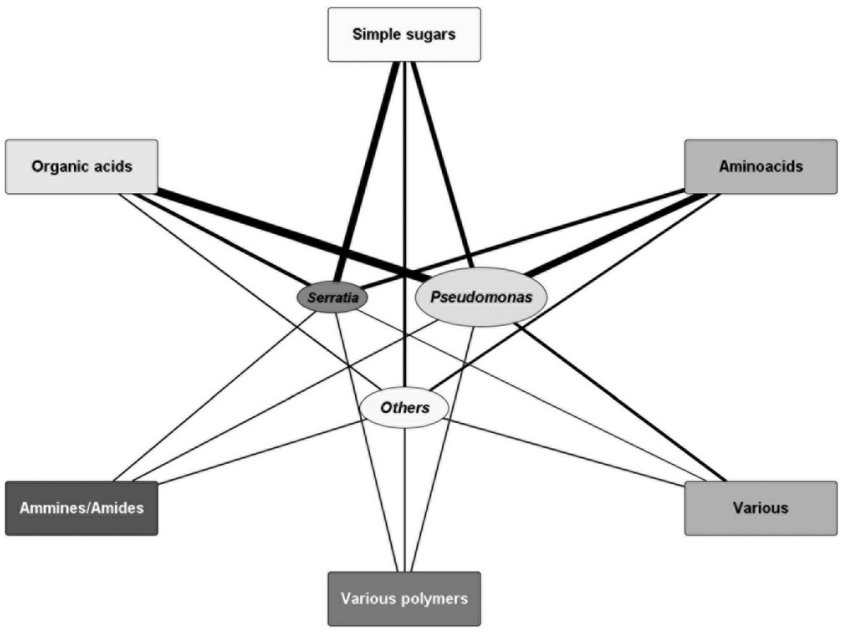

Fig. 3 Network linking the use of different typologies of carbon sources to different groups of KB bacteria. *Pseudomonas*=*Pseudomonas* strains, *Serratia*=*Serratia* strains, *Other*=Other strains, Various=various carbon sources not grouped elsewhere. Link thicknesses are proportional to the number of resources (*rectangles*) used by the bacteria (*ovals*). Oval dimensions are proportional to the number of species included in each group

the Procrustes correlation (R) derived from the symmetric Procrustes residual. All statistical analyses were performed by the program R (R Development Core Team 2013).

Results

Taxonomical affiliation and phylogenetic study After comparison with the EMBL sequence database, phylogenetic trees were generated to visualize evolutionary relationships between sequences of KB bacteria and those of the closest affiliated relatives (Fig. 1). Most of the sequences were related to *Pseudomonas* (ca. 47%), with species of *P. grimontii, P. costantinii, P. ludensis, P. psychrofila, P. fluorescens, P. putida* and *Pseudomonas* spp. (Fig. 1a).

The second important group was related to *Serratia* (ca. 21%), with species of *S. proteamaculans, S. plymuthica, S. fonticola, S. subantarctica, S. quinivorans,* and *Serratia* spp. (Fig. 1b). Fig. 1c shows that a rather wide community portion (ca. 32%) was comprised of bacteria belonging to different minority Genera (indicated as *Others*), including *Sfingobacterium* (four strains), *Flavobacterium* (three strains), *Pantoea* (two strains), *Acinetobacter* (one strain), *Enterobacter* (one strain), *Janthinobacterium* (one strain), *Miroides* (one strain), *Stenotrophomonas* (one strain), and *Shewanella* (one strain).

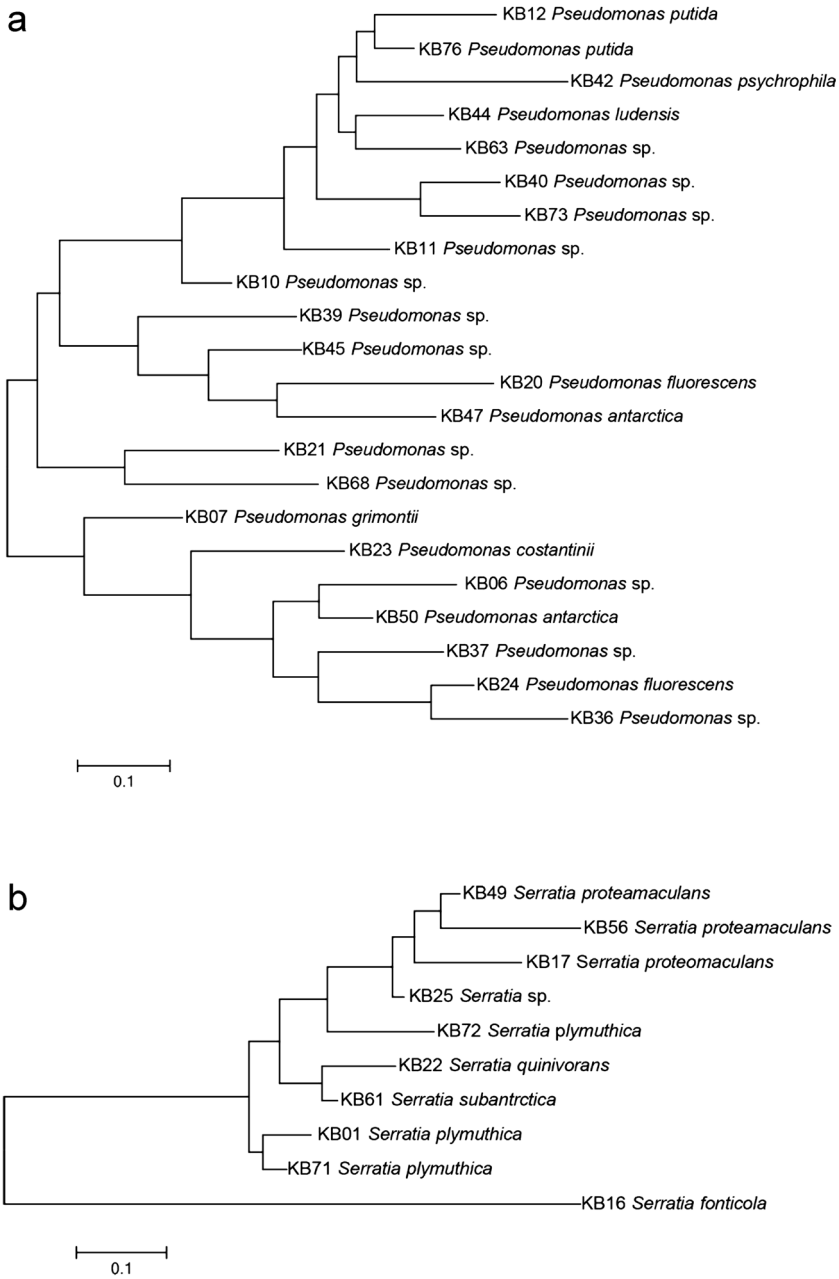

Fig. 4 Maximum Likelihood dendrogram of the nutritional competence matrix (95 carbon sources) of KB strains. Bootstrap values from 1000 were re-sampled. (**a**) *Pseudomonas* and (**b**) *Serratia* strains

Nutritional competencies and statistical analysis The overall ability of the studied bacteria to use different carbon sources is summarized in Fig. 2, representing the output of the Nestedness analysis. The nested structure was significantly lower (T^*=29.766) than that expected by a random use of substrates (T^*_{null}=58.479±2.309, p<0.001), revealing significant differences among the various strains. In particular, the ability of specific groups to use large numbers of substrates indicated the occurrence of generalists, while the use of limited numbers of resources by other groups indicated specialists.

It is evident that *Serratia* species were quite generalist.

Among *Pseudomonas*, both highly generalist and highly specialist strains were found to be *P. brenneri* (KB 37), the most generalist strain, with the use of 70 different compounds, and *P. ludensis* (KB 44), the most specialist, using 24 substrates only.

Generally, strains belonging to *Others* showed medium-high specialization. However, this group is comprised of different Genera containing few strains each. Thus, even if nutritional competencies are evident for each strain, no information could be obtained about presence of specialists and/or generalist within the various Genera.

As for the specific use of carbon sources, revealed by the Network analysis, *Pseudomonas* strains had organic acids and/or amino acids as principal nutrients, possibly showing preference for proteolytic pathways to get energy and produce biomass. In contrast, *Serratia* mostly used simple sugars, indicating a predilection for sugar catabolism (Fig. 3).

Figure 4 shows dendrograms of *Pseudomonas* and *Serratia* strains gathered considering their metabolic competencies. Clustering appeared quite different from those obtained by the phylogenetic analysis (Fig. 1).

Figure 5 shows the correlation between the phylogenetic and metabolic traits, as reported by the Procrustes analysis. The ordination patterns complemented and were correlated, indicating significant congruence between the two analytical approaches (phylogenetic and nutritional). Some bacterial strains grouped in two well-defined clusters corresponding to *Pseudomonas* and *Serratia*, while *Others* did not follow a clustered pattern (Procrustes r=0.37, p=0.05). For the tree groups of bacteria, the first two axes of the PCA, explained about 40% and 94% of total ordination in relation to the metabolic and phylogenetic similarities, respectively. However, the *Serratia* cluster appeared more compact, indicating less nutritional differences within the group.

Discussion

According to our previous results, carried out with culture-independent methods, the KB seawater bacterial community showed the presence of some very abundant dominant species and many other less rich species. This functional organization reflected the ability of the community to be organized in adequate distribution of dominant and resilient species. Moreover, communities showed good functionality, flexibility and the capacity to rapidly react to changing conditions (Pesciaroli et al. 2015). These evidences matched with the mentioned KB environmental characteristics of frequent variations of environmental parameters and nutrient availability.

Until now, very limited information has been available on KB cultivable bacteria and, in particular, on their nutritional competencies. To probe, in detail, the organization of the KB "cultivable" bacterial community, two techniques of investigation, based on phylogenetic and nutritional analyses, were used in this work.

The phylogenetic analysis gave information about presence and relationships among principal microbial groups. The nutritional investigation supplied evidence of their metabolic preferences and diversity. In addition, the ordination patterns obtained by these evaluations were combined by Procrustes analysis, providing further interesting information.

Even considering the limits of cultur techniques (Mrozik et al. 2013), the 16S rRNA gene sequence analysis revealed the presence of two phyla: *Proteobacteria* (83%) and *Bacteroidetes* (17%). Within *Proteobacteria,* as already shown for other Arctic regions (Kellogg and Deming 2009), the *Gammaproteobacteria* class was highly predominant (97%), with only a single strain belonging to *Betaproteobacteria*. This was somehow in agreement with that previously observed in samples collected in other cold marine environments by Romanenko et al. (2008).

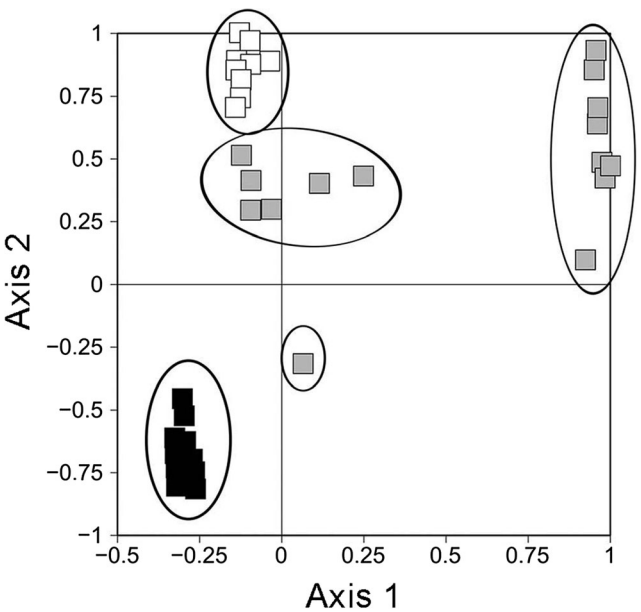

Fig. 5 Procrustes ordination of KB bacteria based on combined phylogenetic (axis 1) and nutritional (axis 2) distances. Most strains clustered in two well-defined groups corresponding to *Pseudomonas* (*black squares*) and *Serratia* (*white squares*) strains. *Other* strains (*grey squares*) did not follow a clustered pattern

The results of this work indicated that the microbial community of KB was dominated by *Pseudomonas* and *Serratia* species, with minority presence of species from other Genera.

Pseudomonas appeared to be the predominant Genus; ca. 50% of the isolates belonged to this group. This evidence is not at all surprising; *Pseudomonas* is generally widely diffused in most terrestrial and aquatic environments, including extreme regions (Michaud et al. 2012; Sanchez et al. 2014). Actually, some of the KB *Pseudomonas* species appeared to be typically from cold areas (*P. antarctica* and *P. psychrophila*).

It is worth nothing that the ecological role of KB *Pseudomonas* strains appeared quite heterogeneous, since they ranged from highly generalist to highly specialist. Emblematic was the situation of strains KB 37 and KB 44, which were able to use 70 and 24 substrates, respectively (Fig. 2).

For various *Pseudomonas* strains, the phylogenetic affiliation was to the species level (Fig. 1a). As mentioned, preliminary tests had been carried out to avoid duplicates of identical strain during isolation. However, due to their high phylogenetic similarity, a few isolates, identified as the same species, could be still considered a duplicate. This was noted for KB 47/KB 50 (*P. antarctica*), KB 20/KB 24 (*P. fluorescens*) and KB 12/KB 76 (*P. putida*), which were located on same nodes of the phylogenetic tree. The metabolic analysis permitted the matter to be clarified. Strains KB 47/KB 50 and KB 20/KB 24 showed very different metabolic profiles (Fig. 2), clustered far away in the metabolic dendrogram (Fig. 4a): these important metabolic differences gave strong evidence that they were not replicates. In constrast, KB 12/KB 76 clustered together and showed minor metabolic differences only.

Thus, the metabolic analysis underlined that strains affiliated to the same species could be definitely different by their metabolic profile, indicating that bacterial phenotype could have inadequate taxonomic meaning. In addition, within same species, adaptation led to the development of very metabolically diverse strains.

The above considerations appeared less evident for *Serratia* strains; in fact, clustering by the nutritional and phylogenetic dendrograms was rather similar (Fig. 2 and Fig. 4b). For KB 16 (*S. fonticola*), both phylogenetic and nutritional analyses indicated its great distance from all other strains of the same Genus.

Understanding how to package the microbial assemblages in extreme environments is one of the most important challenges of microbial ecology. High biological diversity is often related to low interspecific competition (Chase and Leibold 2003), where the preponderance of single taxonomic entities should exploit a minimum range of available trophic resources (Pianka 1995). In other words, in accordance with ecological theory, if the environment is characterized by heterogeneous resource availability, generalists could be favored (Mou et al., 2008). On the other hand, in extreme environments characterized by low resource availability, abiotic factors should drive the different taxonomic entities towards generalism. Under these conditions, communities should be mainly composed of generalists (Devictor et al. 2010).

However, in our case, despite the high number of different carbon sources tested, a predominance of generalists was not observed. Nevertheless, it is not easy to determine the boundary between specialists and generalists, our results could only state if a certain strain is more or less specialist/generalist when compared with others.

Conclusion

This work contributed to an increase in the knowledge on the microbial community of the very peculiar and almost unknown Kandalaksha Bay environment by studying its nutritional competencies. Moreover, valuable ecological information, concerning the occurrence of generalist and specialist strains was obtained by statistical tools. The comparison between phylogenetic and nutritional clustering showed that strains belonging to the same species could have very different nutritional behavior as a probable adaptation strategy to cope with extremely variable environmental conditions.

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