An Updated genome annotation for the model marine bacterium *Ruegeria pomeroyi* DSS-3

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**Abstract**

When the genome of *Ruegeria pomeroyi* DSS-3 was published in 2004, it represented the first sequence from a heterotrophic marine bacterium. Over the last ten years, the strain has become a valuable model for understanding the cycling of sulfur and carbon in the ocean. To ensure that this genome remains useful, we have updated 69 genes to incorporate functional annotations based on new experimental data, and improved the identification of 120 protein-coding regions based on proteomic and transcriptomic data. We review the progress made in understanding the biology of *R. pomeroyi* DSS-3 and list the changes made to the genome.

**Keywords:** Roseobacter, DMSP

**Introduction**

*Ruegeria pomeroyi* DSS-3 is an important model organism in studies of the physiology and ecology of marine bacteria [1]. It is a genetically tractable strain that has been essential for elucidating bacterial roles in the marine sulfur and carbon cycles [2,3] and the biology and genomics of the marine Roseobacter clade [4], a group that makes up 5–20% of bacteria in ocean surface waters [5,6]. Here we update the *R. pomeroyi* DSS-3 genome with 189 changes collected from the work of several research groups over the last ten years.

**Organism information**

*Ruegeria pomeroyi* DSS-3 (formerly *Silicibacter pomeroyi* DSS-3 [7]) is a motile gram-negative alphaproteobacterium in the marine Roseobacter lineage [8]. This mesophilic, heterotrophic bacterium was isolated from an estuary in coastal Georgia, U.S.A [9] (Table 1).

**Genome sequencing information**

**Genome project history**

The genome of *R. pomeroyi* DSS-3 was sequenced in 2003 by The Institute for Genomic Research (now the J. Craig Venter Institute) using Sanger sequencing (Table 2), and was annotated using Glimmer 2 [20] and the TIGR Assembler [21]. The genome was published in 2004 [1].

**Genome properties**

The *R. pomeroyi* DSS-3 genome contains a 4,109,437 bp circular chromosome (5 bp shorter than previously reported [1]) and a 491,611 bp circular megaplasmid, with a G + C content of 64.1 (Table 3). A detailed description of the genome is found in the original article [1].

**Reannotation**

The *R. pomeroyi* DSS-3 genome has been instrumental in expanding knowledge of the marine sulfur cycle, particularly the role of marine bacteria in controlling the flux of volatile sulfur to the atmosphere [3,22] and the bacterial transformations of dimethylsulfoniopropionate (DMSP) [3,23], dimethylsulfide, and sulfonates [24,25]. Since 2006, many of the genes mediating the uptake and metabolism of DMSP have been identified from the *R. pomeroyi* DSS-3 genome. These include the demethylation pathway genes *dmdABCD* [2,22] and the cleavage pathway genes *dddD, dddP, dddQ, dddW, acuK, acuN, dddA* and *dddC* [23,26,27]. Although many genes were identified first in *R. pomeroyi* DSS-3, these are now known to be widespread in ocean surface waters and harbored by a number of other major marine bacterial taxa [28]. *R. pomeroyi* DSS-3 also transforms sulfonates and has served as a model for identifying genes required for the degradation of 2,3-dihydroxypropane-1-sulfonate (*hpsNOP*) [29], L-cysteate (*cuyARZ*) [30], taurine (*tauXY*) and N-acetyltaurine (*naaST*) [24,31,32], 3-sulfolactate (*slcD, suyAB*) [29,33] and isethionate (*iseJ*) [25].
Table 1 Classification and general features of *Ruegeria pomeroyi* DSS-3 according to MIGS recommendations [9]

| MIGS ID | Property                  | Term                                      | Evidence code |
|---------|---------------------------|-------------------------------------------|---------------|
| Current classification | Domain | Bacteria | TAS [10] |
|          | Phylum | Proteobacteria | TAS [11] |
|          | Class  | Alphaproteobacteria | TAS [12,13] |
|          | Order  | Rhodobacterales | TAS [12,14] |
|          | Family | Rhodobacteraceae | TAS [12,15] |
|          | Genus  | Ruegeria | TAS [7,16-18] |
|          | Species | Ruegeria pomeroyi | TAS [7,19] |
|          | Type strain | DSS-3 = ATCC 700808 T = DSM 15171 | |
| Gram stain | Negative | TAS [8] |
| Cell shape | Rod | TAS [8] |
| Motility | Motile | TAS [8] |
| Sporulation | Non-sporulating | NAS |
| Temperature range | Mesophile (10°C-40°C) | TAS [8] |
| Optimum temperature | 30°C | TAS [8] |
| Carbon source | Acetate, ethanol, DL-β-hydroxybutyrate, glucose, succinate, acrylic acid, cysteic acid, glycerol, citrate, pyruvate, casamino acids, L-alanine, L-arginine, L-serine, L-taurine, L-methionine, DMSP and glycine betaine | TAS [8] |
| Energy source | Carbon compounds | |
| Terminal electron receptor | Oxygen | |
| MIGS-6 | Habitat | Marine | |
| MIGS-6.3 | Salinity | Optimum 100–400 mM | TAS [8] |
| MIGS-22 | Oxygen | Aerobic | TAS [8] |
| MIGS-15 | Biotic relationship | Free-living | TAS [8] |
| MIGS-14 | Pathogenicity | Non-pathogenic | NAS |
| MIGS-4 | Geographic location | Coastal Georgia, USA | TAS [8] |
| MIGS-5 | Sample collection time | June 1996 | NAS |
| MIGS-4.1 MIGS-4.2 | Latitude – Longitude | 31.989616 N, 81.022768 W | NAS |
| MIGS-4.3 | Depth | Surface | NAS |
| MIGS-4.4 | Altitude | Sea level | NAS |

*Evidence codes - TAS: Traceable Author Statement (i.e., a direct report exists in the literature); NAS: Non-traceable Author Statement (i.e., not directly observed for the living, isolated sample, but based on a generally accepted property for the species, or anecdotal evidence).*

Table 2 Project information

| MIGS ID | Property                     | Term                                      |
|---------|------------------------------|-------------------------------------------|
| MIGS-31 | Finishing quality           | Closed genome [1]                         |
| MIGS-28 | Libraries used              | 1–2 kb and 12–15 kb inserts [1]           |
| MIGS-29 | Sequencing platforms        | Sanger                                    |
| MIGS-31.2 | Fold coverage               | Not reported                              |
| MIGS-30 | Assemblers                  | The TIGR Assembler [20]                   |
| MIGS-32 | Gene calling method         | Glimmer 2.0 [20]                         |
|          | Genome Database release     | NCBI Refseq, release version #8           |
|          | Genbank ID                  | CP000031.2, CP000032.1                    |
|          | Genbank Date of Release     | December 16, 2004                         |
|          | GOLD ID                     | Gc00242                                   |
|          | Project relevance           | The first heterotrophic marine bacterium sequenced |

Table 3 Genome statistics

| Attribute                      | Value   | % of total |
|-------------------------------|---------|------------|
| Genome size (bp)              | 4,601,048 | 100.0      |
| DNA coding region (bp)        | 4,144,250 | 90.1       |
| DNA G + C content (bp)        | 2,947,874 | 64.1       |
| Total genes                  | 4371    | 100.0      |
| RNA genes                     | 64      | 1.5        |
| Protein-coding genes          | 4276    | 97.8       |

*The total is based on either the size of the genome in base pairs or the total number of genes in the annotated genome.

*Also includes pseudogenes.*
Table 4 Updates and corrections to the genome sequence

| Accession | Gene locus | CDS | Gene | Type of change |
|-----------|------------|-----|------|----------------|
| YP_166946 | SPO1707a   | Branched-chain amino acid ABC transporter, ATP-binding protein, putative | Locus name |
| YP_167418 | SPO2192a   | N-formylglutamate amidohydrolase | hutG | Locus name |
| YP_165298 | SPO0025    | Hydrolase, NUDIX family | ORF position |
| YP_165304 | SPO0031    | EbfK/YbiSYcfS/YnhG family protein | ORF position |
| YP_165330 | SPO0056    | Hypothetical protein | ORF position |
| YP_165481 | SPO0212    | Hypothetical protein | ORF position |
| YP_165606 | SPO0343    | 2-oxoglutarate dehydrogenase, E2 component, dihydrolipoamide succinyltransferase | sucB | ORF position |
| YP_165666 | SPO0403    | Conserved domain protein | ORF position |
| YP_165678 | SPO0415    | D-isomer specific 2-hydroxyacid dehydrogenase family protein | ORF position |
| YP_165703 | SPO0440    | Thioesterase family protein | ORF position |
| YP_165709 | SPO0446    | ABC transporter, ATP-binding protein | ORF position |
| YP_165719 | SPO0456    | Hypothetical protein | ORF position |
| YP_165753 | SPO0491    | Hypothetical protein | ORF position |
| YP_165766 | SPO0504    | Hypothetical protein | ORF position |
| YP_165767 | SPO0505    | Ribosomal protein L15 | rplO | ORF position |
| YP_165860 | SPO0600    | Carboxynorspermidine decarboxylase | nspC | ORF position |
| YP_165899 | SPO0644    | Hypothetical protein | ORF position |
| YP_165937 | SPO0682    | Monoxygenase family protein | ORF position |
| YP_165950 | SPO0695    | Hypothetical protein | ORF position |
| YP_008877643 | SPO0876a | Hypothetical protein | ORF position |
| YP_166130 | SPO0877    | Conserved domain protein | ORF position |
| YP_166199 | SPO0946    | Phosphomannomutase/phosphoglucomutase | algC | ORF position |
| YP_166255 | SPO1003    | ATP-dependent Clp protease, proteolytic subunit ClpP | ORF position |
| YP_166256 | SPO1004    | ATP-dependent Clp protease, ATP-binding subunit ClpX | ORF position |
| YP_166357 | SPO1106    | Hypothetical protein | ORF position |
| YP_166419 | SPO1172    | FMN-dependent alpha-hydroxy acid dehydrogenase family protein | ORF position |
| YP_166421 | SPO1174    | DNA helicase II, putative | ORF position |
| YP_166518 | SPO1273    | Thymidylate synthase, flavin-dependent | thyX | ORF position |
| YP_166577 | SPO1334    | Hypothetical protein | ORF position |
| YP_166601 | SPO1359    | Pyruvate, phosphate dikinase | pppK | ORF position |
| YP_166628 | SPO1386    | HIT family protein | ORF position |
| YP_166803 | SPO1562    | Glycine cleavage system T protein, putative | ORF position |
| YP_166874 | SPO1633    | Hypothetical protein | ORF position |
| YP_167013 | SPO1776    | Pyridine nucleotide-disulphide oxidoreductase family protein | ORF position |
| YP_167049 | SPO1812    | Adenylate kinase | adk-2 | ORF position |
| YP_167155 | SPO1920    | Tellurite resistance protein | trgB | ORF position |
| YP_167190 | SPO1955    | Glutaryl-CoA dehydrogenase | gcdH | ORF position |
| YP_167207 | SPO1972    | Nodulation protein N | ORF position |
| YP_167208 | SPO1973    | 3-dehydroquinate dehydratase, type II | aroQ | ORF position |
| YP_167281 | SPO2051    | DNA gyrase, A subunit | gyrA | ORF position |
| YP_167368 | SPO2141    | Cytochrome c oxidase assembly protein | ORF position |
| YP_167443 | SPO2217    | Excinuclease | ORF position |
| Accession | Genbank ID | Description                                                                                     | Function                      |
|-----------|------------|-------------------------------------------------------------------------------------------------|-------------------------------|
| YP_167514 | SPO2290    | Hypothetical protein                                                                             | ORF position                  |
| YP_167549 | SPO2326    | Hypothetical protein                                                                             | ORF position                  |
| YP_167562 | SPO2339    | Enoyl-CoA hydratase/isoenzyme family protein                                                     | ORF position                  |
| YP_167570 | SPO2347    | Hypothetical protein                                                                             | ORF position                  |
| YP_167571 | SPO2348    | Sarcosine oxidase, beta subunit family                                                           | ORF position                  |
| YP_167714 | SPO2499    | Hypothetical protein                                                                             | ORF position                  |
| YP_167808 | SPO2595    | Hypothetical protein                                                                             | ORF position                  |
| YP_167819 | SPO2608    | Aldehyde dehydrogenase, putative                                                                 | ORF position                  |
| YP_167822 | SPO2612    | DNA-binding protein HU, putative                                                                 | ORF position                  |
| YP_008877659 | SPO2723a | Hypothetical protein                                                                             | ORF position                  |
| YP_167934 | SPO2724    | Hypothetical protein                                                                             | ORF position                  |
| YP_167992 | SPO2785    | NADH dehydrogenase I, B subunit (nuoB)                                                          | ORF position                  |
| YP_168024 | SPO2816    | Peptide/nickel/opine uptake family ABC transporter, permease protein                             | ORF position                  |
| YP_168061 | SPO2853    | Cobalt chelatase, CobS subunit                                                                  | ORF position                  |
| YP_168080 | SPO2872    | Cobyrinic acid a,c-diamide synthase (cobB)                                                       | ORF position                  |
| YP_168096 | SPO2888    | Membrane protein, putative                                                                       | ORF position                  |
| YP_168125 | SPO2917    | Glutathione S-transferase family protein                                                         | ORF position                  |
| YP_168133 | SPO2925    | Sporulation related                                                                             | ORF position                  |
| YP_168143 | SPO2936    | Hypothetical protein                                                                             | ORF position                  |
| YP_168150 | SPO2942    | Hypothetical protein                                                                             | ORF position                  |
| YP_168197 | SPO2991    | Nitroreductase family protein                                                                    | ORF position                  |
| YP_168209 | SPO3003    | AMP-binding enzyme                                                                              | ORF position                  |
| YP_168292 | SPO3089    | ATPase, putative                                                                                 | ORF position                  |
| YP_168317 | SPO3114    | Hypothetical protein                                                                             | ORF position                  |
| YP_168354 | SPO3151    | HAD-superfamily subfamily IIa hydrolase, TIGR01459                                               | ORF position                  |
| YP_168406 | SPO3203    | Guanosine-3',5'-bis(Diphosphate) 3'-pyrophosphohydrolase, putative                              | ORF position                  |
| YP_168423 | SPO3220    | Aminotransferase, classes I and II                                                               | ORF position                  |
| YP_168448 | SPO3245    | Nicotinate-nucleotide pyrophosphorylase (nadC)                                                    | ORF position                  |
| YP_168475 | SPO3278    | Orotidine 5'-phosphate decarboxylase (pyrF)                                                       | ORF position                  |
| YP_168540 | SPO3344    | Cys/Met metabolism PLP-dependent enzyme family protein                                            | ORF position                  |
| YP_168563 | SPO3367    | Deoxyribose-phosphate aldolase (deoC)                                                            | ORF position                  |
| YP_168618 | SPO3422    | ATP-dependent protease La domain protein                                                         | ORF position                  |
| YP_168712 | SPO3517    | Preprotein translocase, SecE subunit (secE)                                                       | ORF position                  |
| YP_168722 | SPO3527    | Universal stress protein family protein                                                           | ORF position                  |
| YP_168735 | SPO3540    | Hypothetical protein                                                                             | ORF position                  |
| YP_168802 | SPO3607    | Hypothetical protein                                                                             | ORF position                  |
| YP_168911 | SPO3717    | Cytosol aminopeptidase family protein                                                            | ORF position                  |
| YP_168940 | SPO3746    | Adenine deaminase                                                                                | ORF position                  |
| YP_169017 | SPO3829    | S-formylglutathione hydrolase, putative                                                           | ORF position                  |
| YP_169021 | SPO3833    | ATP-dependent RNA helicase, DEAD/DEAH box family                                                  | ORF position                  |
| YP_164889 | SPOA0058   | Glycine cleavage system protein H (gcvH)                                                          | ORF position                  |
| YP_165979 | SPO0725    | Bacterial SH3 domain family protein                                                              | ORF position, Function        |
| YP_167233 | SPO1999    | Collagen domain protein                                                                          | ORF position, Function        |
| YP_008877641 | SPO0561 | ABC transporter                                                                                  | Sequence                      |
Table 4 Updates and corrections to the genome sequence (Continued)

| Accession | Accession | Function |
|-----------|-----------|----------|
| YP_008877654 | SPO2024 | Aminotransferase Sequence |
| YP_008877662 | SPO3316a | Stress protein |
| YP_008877661 | SPO3904 | Heat shock protein |
| YP_167141 | SPO1905 | Fumarate hydratase, class II |
| YP_165491 | SPO0222 | Alanine dehydrogenase |
| YP_165503 | SPO0234 | Lysine dehydrogenase |
| YP_165504 | SPO0235 | α-aminoadipic-δ-semialdehyde dehydrogenase |
| YP_165716 | SPO0453 | DMSP lyase |
| YP_165850 | SPO0590 | LacI family transcriptional regulator |
| YP_165851 | SPO0591 | Dihydroxypropanesulfonate (DHP) TRAP transporter |
| YP_165852 | SPO0592 | Dihydroxypropanesulfonate (DHP) TRAP transporter |
| YP_165853 | SPO0593 | Dihydroxypropanesulfonate (DHP) TRAP transporter |
| YP_165854 | SPO0594 | Dihydroxypropanesulfonate-3-dehydrogenase |
| YP_165855 | SPO0595 | R or S-dihydroxypropanesulfonate-2-dehydrogenase |
| YP_165856 | SPO0596 | S or R-dihydroxypropanesulfonate-2-dehydrogenase |
| YP_165857 | SPO0597 | UsxA stress protein |
| YP_165858 | SPO0598 | Membrane-bound sulfolactate dehydrogenase |
| YP_165912 | SPO0657 | Metallochaperone, putative |
| YP_165913 | SPO0658 | N-acetyltaurine amidohydrolase |
| YP_165914 | SPO0659 | LysR family transcriptional regulator |
| YP_165915 | SPO0660 | N-acetyltaurine ABC transporter, periplasmic binding protein |
| YP_165916 | SPO0661 | N-acetyltaurine ABC transporter, permease protein |
| YP_165917 | SPO0662 | N-acetyltaurine ABC transporter, permease protein |
| YP_165918 | SPO0663 | N-acetyltaurine ABC transporter, ATP-binding protein |
| YP_165919 | SPO0664 | N-acetyltaurine ABC transporter, ATP-binding protein |
| YP_165928 | SPO0673 | Taurine-pyruvate aminotransferase |
| YP_165929 | SPO0674 | Taurine ABC transporter, periplasmic taurine-binding protein |
| YP_165930 | SPO0675 | Taurine ABC transporter, ATP-binding protein |
| YP_165931 | SPO0676 | Taurine ABC transporter, permease protein |
| YP_166034 | SPO0781 | Phosphonate ABC transporter substrate-binding protein |
| YP_166387 | SPO1136 | Diaminobutyric acid transaminase |
| YP_166388 | SPO1137 | Aspartate-semialdehyde dehydrogenase |
| YP_166389 | SPO1138 | AsnC/Lrp-like DNA-binding protein, transcriptional regulator |
| YP_166390 | SPO1139 | No-acetyl-L-2,4-diaminobutyric acid deacetylase |
| YP_166391 | SPO1140 | Ectoine hydrolase |
| YP_166392 | SPO1141 | Ectoine utilization protein EutC |
| YP_166393 | SPO1143 | Ectoine utilization protein EutA |
| YP_166396 | SPO1145 | Ectoine/S-hydroxyectoine TRAP transporter, periplasmic binding protein |
| YP_166397 | SPO1146 | Ectoine/S-hydroxyectoine TRAP transporter, small integral membrane protein |
| YP_166398 | SPO1147 | Ectoine/S-hydroxyectoine TRAP transporter, large integral membrane protein |
| YP_166399 | SPO1148 | Transcriptional regulator, GntR family |
| YP_166792 | SPO1551 | Trimethylamine (TMA) monooxygenase |
| YP_166837 | SPO1596 | DMSP lyase |

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Table 4 Updates and corrections to the genome sequence (Continued)

| Accession | Description                                    | Function |
|-----------|------------------------------------------------|----------|
| YP_166942 | SPO1703 DMSP lyase                               | dddD     |
| YP_167149 | SPO1914 NADPH-dependent acrylyl-CoA reductase    | acuI     |
| YP_167183 | SPO1948 Phosphate ABC transporter substrate-binding protein | pstS       |
| YP_167275 | SPO2045 3-methylmercaptopropionyl-CoA ligase     | dmdB     |
| YP_167522 | SPO2299 DMSP lyase                               | dddP     |
| YP_167578 | SPO2355 Isethionate dissimilation regulator     | iseR     |
| YP_167579 | SPO2356 Isethionate TRAP transporter             | iseM     |
| YP_167580 | SPO2357 Isethionate TRAP transporter             | iseL     |
| YP_167581 | SPO2358 Isethionate TRAP transporter             | iseK     |
| YP_167582 | SPO2359 Isethionate dehydrogenase               | iseJ     |
| YP_167694 | SPO2477 Manganese uptake regulator              | mur      |
| YP_168390 | SPO3187 (2R)-3-sulfolactate dehydrogenase       | comC     |
| YP_168503 | SPO3363 Manganese ABC transporter, permease protein | sitD     |
| YP_168559 | SPO3364 Manganese ABC transporter, permease protein | sitC     |
| YP_168561 | SPO3365 Manganese ABC transporter, ATP-binding protein | sitB     |
| YP_168562 | SPO3366 Manganese ABC transporter, periplasmic protein | sitA     |
| YP_168752 | SPO3557 Sulfite dehydrogenase subunit SoeC; transmembrane sulfate transporter | soeC |
| YP_168753 | SPO3558 Sulfite dehydrogenase iron-sulfur cluster-binding subunit SoeB; cytosolic protein | soeA |
| YP_168754 | SPO3559 Sulfite dehydrogenase molybdopterin cofactor-binding subunit SoeA; cytosolic protein | soeB |
| YP_168755 | SPO3560 Phosphate acetyltransferase             | pta      |
| YP_168757 | SPO3562 Taurine transcriptional regulator       | tauR     |
| YP_168992 | SPO3804 3-methylmercaptopropionyl-CoA dehydrogenase | dmdA |
| YP_168993 | SPO3805 Methylthioacryloyl-CoA hydratase         | dmdD     |
| YP_164988 | SPOA0157 Sulphite exporter                      | cuyZ     |
| YP_164989 | SPOA0158 L-cysteate sulfo-lyase                 | cuyA     |
| YP_164990 | SPOA0159 Transcriptional regulator cuyR         | cuyR     |
| YP_165136 | SPOA0309 Sulphoacetaldehyde acetyltransferase   |          |
| YP_008877636 | SPOC344a Hypothetical protein                  | New ORF  |
| YP_008877637 | SPOC346a Hypothetical protein                  | New ORF  |
| YP_008877638 | SPOC360a Hypothetical protein                  | New ORF  |
| YP_008877639 | SPOC491a Hypothetical protein                  | New ORF  |
| YP_008877640 | SPOC504a Hypothetical protein                  | New ORF  |
| YP_008877642 | SPOC628a Hypothetical protein                  | New ORF  |
| YP_008877644 | SPOC1044a Hypothetical protein                  | New ORF  |
| YP_008877645 | SPOC1094a Hypothetical protein                  | New ORF  |
| YP_008877646 | SPOC1226a Hypothetical protein                  | New ORF  |
| YP_008877647 | SPOC1252a Transcriptional regulator             | New ORF  |
| YP_008877648 | SPOC1310a Hypothetical protein                  | New ORF  |
| YP_008877649 | SPOC1337a Hypothetical protein                  | New ORF  |
| YP_008877650 | SPOC1352a Hypothetical protein                  | New ORF  |
| YP_008877651 | SPOC1356a Signal transduction                  | New ORF  |
| YP_008877652 | SPOC1364a Hypothetical protein                  | New ORF  |
Members of the marine Roseobacter lineage are capable of oxidizing sulfite and thiosulfate [34,35], and the genome sequence of R. pomeroyi DSS-3 revealed the sox gene cluster that mediates these processes [1,4]. Recently, the reverse dissimilatory sulfite reductase gene cluster was found in sediment-dwelling roseobacters, and homologs to the sulfite reductase genes from this pathway (soeABC) were identified in the R. pomeroyi DSS-3 genome [36].

R. pomeroyi DSS-3 was initially studied as a member of an ecologically important bacterial taxon that appeared unusually amenable to cultivation [5], but has now played a major role in improving our understanding of global sulfur transformations.

Studies of the R. pomeroyi DSS-3 genome have also provided a better understanding of the genes involved in processing organic nitrogen compounds, such as taurine and N-acetyltaurine [24,31,32]. The bacterium can catabolize lysine by using the saccharopine pathway, which is used by many plants and animals, or by using the lysine dehydrogenase pathway. Under high salt conditions, it preferentially uses the latter pathway, leading to biosynthesis of the osmolyte aminoadipate. The function of several genes in both lysine pathways has recently been experimentally verified [37].

R. pomeroyi DSS-3 genome hosts at least 28 tripartite ATP-independent periplasmic (TRAP) transporters [1]. While the substrates for many of these transporters are not yet known, the TRAP transporters responsible for the uptake of 2,3-dihydroxypropane-1-sulfonate (hpsKLM) [29], isethionate (iseKLM) [25], and ectoine and hydroxyectoine have been characterized (uehABC) [38,39]. Ectoine and hydroxyectoine are used as compatible solutes by some bacteria and phytoplankton, although R. pomeroyi DSS-3 can also assimilate carbon and nitrogen from them [39]. Several genes involved in ectoine metabolism (doe, eut, ueh) have been found in the R. pomeroyi DSS-3 genome based on homology with genes in Halomonas elongata DSM 2581 T [40].

Progress has been made in understanding the mechanisms of metal uptake in R. pomeroyi DSS-3. The manganese uptake regulator mur has been experimentally validated, as have the ABC transporter genes for manganese metabolism (sitABCD) [41]. In total, 69 annotation changes were made based on new experimental data identifying genes responsible for carbon, nitrogen, sulfur, and metal uptake and metabolism [42].

Proteomics [42] and mRNA sequencing have resulted in 120 protein coding regions being identified, removed or corrected in the updated genome. A detailed proteomic study of R. pomeroyi DSS-3 under diverse growth conditions resulted in the identification of 26 novel open reading frames (ORFs) and 5 sequencing errors [42]. The function of most of the new genes is not known and 16 of the expressed peptides do not have known homologs. The 26 ORFs missed in the original annotation is a significant number but less than the 1% error rate predicted for Glimmer 2 [20]. The proteomic analysis was also able to correct the start sites of 64 genes [42], enhancing the information that had been obtained only from the DNA sequence [20]. Many of the ORFs identified by proteomics were independently confirmed using strand-specific messenger RNA sequences from continuous cultures [43] and the gene calling software Glimmer 3 [44]. This method also identified several genes that were originally annotated in the wrong orientation, including a novel bacterial collagen gene (SPO1999).

Table 4 Updates and corrections to the genome sequence (Continued)

| Accession | Name | Annotation | Action |
|-----------|------|------------|--------|
| YP_008877653 | SPO1412a | Hypothetical protein | New ORF |
| YP_008877655 | SPO2213a | Hypothetical protein | New ORF |
| YP_008877656 | SPO2341a | Hypothetical protein | New ORF |
| YP_008877657 | SPO2478 | RNA helicase | New ORF |
| YP_008877658 | SPO2652a | Polyketide cyclase | New ORF |
| YP_008877660 | SPO2973a | Hypothetical protein | New ORF |
| YP_008877663 | SPO3452a | Hypothetical protein | New ORF |
| YP_008877664 | SPO3498a | Hypothetical protein | New ORF |
| YP_008877665 | SPO3673a | Hypothetical protein | New ORF |
| AHC32567 | SPOA0087a | Esterase-lipase | New ORF |
| AHC32568 | SPOA0272a | Hypothetical protein | New ORF |
| YP_165305 | - | Hypothetical protein | Removed ORF |
| YP_165605 | - | Hypothetical protein | Removed ORF |
| YP_166669 | - | Hypothetical protein | Removed ORF |
| YP_168865 | - | Hypothetical protein | Removed ORF |
| YP_165238 | - | Hypothetical protein | Removed ORF |
A list of genome updates based on these biochemical, genetic, and -omics approaches is provided in Table 4, and full details in Additional file 1: Table S1. The updated annotations have been incorporated into the official genome record at the National Center for Biotechnology Information (Bethesda, MD, USA) under accession numbers CP000031.2 and CP000032.1 and Roseobase (http://roseobase.org).

Conclusion
Ten years after the publication of the Ruegeria pomeroyi DSS-3 genome sequence, advances in knowledge of gene function and structural genome features motivated an annotation update. As an ecologically-relevant heterotrophic marine bacterium that is amenable to laboratory studies and genetic manipulation, R. pomeroyi is serving as a valuable model organism for investigations of the ecology, biochemistry, and biogeochemistry of ocean microbes.

Additional file

Additional file 1: Table S1. Full details of updates and corrections to the Ruegeria pomeroyi DSS-3 genome sequence.

Competing interests
The authors declare that they have no competing interests.

Authors’ contributions
ARR conceived of the study, carried out the bioinformatics analyses, and wrote the manuscript. CBS carried out the bioinformatics analyses and wrote the manuscript. MAM conceived of the study and wrote the manuscript. All authors read and approved the final manuscript.

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