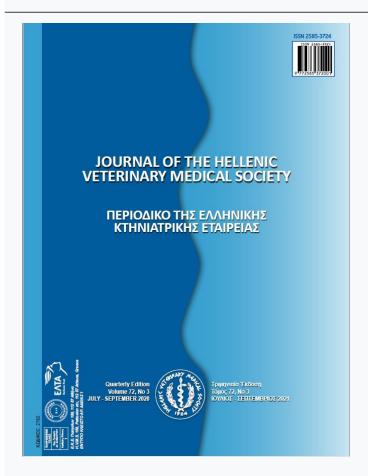




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Differences in antimicrobial resistance of *Salmonella* spp. isolated from humans, animals and food products in Kazakhstan

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ABSTRACT: The aims of this study were twofold: 1. to isolate *Salmonella* spp. from different sources in Kazakhstan, to determine their serovars and resistance profiles and 2. to evaluate similarities in antimicrobial susceptibility of *Salmonella* spp. isolated from humans, animals and food products. From the 10 212 samples tested *Salmonella* spp. were isolated in 47 cases. The predominant serovar isolated from humans and food products was *S.* Enteritidis. Although different animal species were tested the *Salmonella* spp. were isolated mainly from chickens and ducks. *S.* Enteritidis and *S.* Typhimurium were the most prevalent serovars in raw poultry meat. The most frequent resistances were those to nalidixic acid, ampicillin and tetracycline. Human isolates demonstrated lower resistance compared to animal and food isolates. The genes encoding antimicrobial resistance in human isolates in most cases were absent except for some isolates which harboured *tet*, *sul*, *stre* and *bla* TEM genes encoding resistance to the oldest antimicrobial classes. The situation in animals and food products was less beneficial as besides different genes, integrons associated with the horizontal gene transfer were detected. The findings suggest that antimicrobials in animal sector should be used more strictly, paying attention to critically important antimicrobials for humans and possible horizontal transfer of pathogens and their genetic determinants.

Keywords: Salmonella Paratyphi, One Health, salmonellosis, zoonoses

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INTRODUCTION

Valmonella spp. are one of the most frequently isolated foodborne pathogens. It is a major worldwide public health concern, accounting for 93.8 million foodborne illnesses and 155,000 deaths per year (Eng et al., 2015). Gastroenteritis is the most common manifestation of Salmonella infection, followed by bacteraemia and enteric fever (Majowicz et al. 2010). Non-typhoidal Salmonella enterica infection,caused by different serovarsfrom contaminated food, is an important cause of both sporadic gastroenteritis and outbreaks internationally. In the European Union, over 91,000 human cases are reported each year (EFSA, 2018). In Australia, the incidence of infection due to Salmonella spp. in the community is estimated to be 185 infections per 100,000 population per year (Kirk et al., 2014). Enteric fever that is caused by Salmonella enterica Typhi causes illness in south-central Asia, Southeast Asia, and southern Africa by more than 100 cases per 100,000 person-years) (Marks et al., 2017). It is also prevalent in many other parts of the world. For instance, approximately 200 to 300 cases of S. Typhi were reported in the United States each year (Lynch et al, 2009).

Epidemiological data and incidence cases of salmonellosis are registered in many countries including the USA, EU, China, Australia, India and others while some countries still are white spots in the map according to the prevalence of salmonellosis (Eng et al., 2015). In Kazakhstan the incidence of diagnosed salmonellosis in 1999 and 2000 was about 3500-4000 cases per year, while typhoid fever incidence was about 30-110 per year (WHO 2001).

Main factors associated with Salmonella outbreaks include incomplete cooking of food products, improper storage and direct contact with raw ingredients (Lynch et al. 2006). The food products that are predominantly associated with the outbreaks include animal products such as milk, poultry and eggs, as well as food products such as chocolate and peanut butter (Eng et al., 2015). Animals are the main carriers and reservoir of non-typhoid Salmonella. The transmission of Salmonella usually occurs through gastrointestinal tract by ingestion of food or water contaminated with infected animals. Direct contact with infected animals also constitutes a risk of infection (Swanson et al., 2007). The worldwide incidence rate of Salmonella infection is high as the strains can be found naturally in the environment and in both domestic and wild animals including cats, dogs, amphibians, reptiles and rodents (Eng et al., 2015). The diversity of possible reservoirs of infection results in significant challenges for public health authorities to control the infections (Swanson et al. 2007; Dione et al. 2011).

Salmonella resistance to at least 3 antibiotics started to be reported in 1960s (Dyson et al. 2019). Since then, the frequency of resistant isolates has increased in many countries; however, the spectrum of resistance or the rate of multidrug resistant isolates depends on country, source of isolation and Salmonella serovar. For instance, in the USA Salmonella spp. recovered from poultry were resistant to streptomycin (30.9%), gentamicin (12.6%), sulfadimethoxine (20.9%), tetracycline (13.9%), and trimethoprim-sulfamethoxazole combination (8.6%). Among these isolates, 20% were multi-drug resistant, showing resistance to three or more antibiotics; noteworthy is that 67% of S. Heidelberg and 54% of S. Kentucky isolates have shown resistance to five or more antibiotics (Liljebjelke et al., 2017). In China high rates of resistant salmonellae from chicken were found to sulfisoxazole (76.1%), tetracycline (75.3%), ampicillin (48.0%), and ofloxacin (44.7%). Notably, antimicrobial susceptibility tests have identified resistance to polymyxin B (2.0%) and imipenem (0.5%) (Zhang et al., 2018). In Poland the resistance of salmonella isolated from non-meat food products was low with the highest prevalence to nalidixic acid (35.2%), sulphonamides (6.6%), ampicillin (4.9%), amoxicillin/ clavulanic acid (2.5%), streptomycin, cefoxitin, gentamicin and tetracycline (1.6%) (Maka et al., 2015). Although an official data about salmonellosis prevalence in Kazakhstan is collected, there is no current systematic data about the situation of antimicrobial resistance of the strains that are prevalent in humans and in other sources including animals, food products or feedstuffs. Thus, the aims of this study were twofold: 1. to isolate Salmonella spp. strains from different sources in Kazakhstan, to determine their serovars and resistance profiles and 2. to evaluate similarities among antimicrobial susceptibility of Salmonella spp. isolated from humans, animals and food products.

MATERIALS AND METHODS

Place and sampling

Bacteriological investigations were performed at the Institute of Applied Biotechnology, Kostanay University during 2018-2019. The aim was to obtain wide spectrum of *Salmonella* isolates prevalent in Ka-

zakhstan. Animal carcasses and raw meat including poultry, lamb, beefwere collected in supermarkets and markets at a retail level. Clinical and pathological material of animals was collected at slaughterhouses and animal farms. *Salmonella* spp. strains already isolated from humans (in hospitals and other health-care facilities) were delivered to the department of Microbiology of Kostanay University as isolates without the data about their concrete source (name of the patient) of isolation. Ready to use, raw and frozen food products were obtained at retail markets and supermarkets. In total 10212 samples were tested from which 1006 samples were from live animals, animal carcasses and milk, 383 food samples and 8823 human samples.

Isolation and identification of Salmonella

Isolation of *Salmonella* was performed according to EN ISO 6579-1 (ISO, 2017) procedure for *Salmonella* detection. Xylose Lysine Deoxycholate (XLD) agarand Salmonella Shigella (SS) Agar (Oxoid, UK) were used as plating media after the enrichment procedure. Isolates obtained from health-care facilities were re-cultivated on XLD agar.

Identification of the isolates was performed using classical biochemical testing including fermentation of carbohydrates, production of hydrogen sulfide, indole, production of lysine decarboxylase, urease, oxidase, catalase, MR-VP as well as other conventional tests.

Serotyping was performed using slide agglutination test with sera to O and H antigens (Petsal, Russia) as well as Wellcolex Colour salmonella serogroup identification latex test (Remel, UK) according to the manufacturer's instructions.

Susceptibility testing

Antimicrobial susceptibility testing was performed using the disc diffusion method according to Kirby-Bauer (Hudzicki, 2009). The following discs with antimicrobials (µg) (Thermo Fisher, UK) were used: ampicillin (10), cefoperazone (75), cefoxitin (30), streptomycin (10), kanamycin (30), gentamicin (10), tetracycline (30), doxycycline (30), chloramphenicol (30), ciprofloxacin (5), nalidixic acid (30), gemifloxacin (5), enrofloxacin (5), ofloxacin (5) and sulfamethoxazole-trimethoprim (25). Interpretation of the results was carried out using CLSI clinical breakpoints (CLSI, 2019) set for *Salmonella* except for ofloxacin, gemifloxacin and nalidixic acid for which breakpoints set for Enterobacteriaceae were used.

Detection of the genes encoding antimicrobial resistance

Molecular testing of the isolates was performed at the Microbiology and Virology Institute, Lithuanian University of Health Sciences. DNA material for molecular testing was obtained after bacterial lysis according to the extraction protocol prepared by the EU Community Reference Laboratory for Antimicrobial Resistance with slight modifications (Ruzauskas et al., 2014). Detection of the genes encoding antimicrobial resistance was performed by PCR. Annealing temperatures and oligonucleotides used are presented in Table 1.

| Table 1. Antimicrobial resistance genes tested and oligonucleotide primers used in the study | | | | | | | |
|--|--------------------------|------------------------|-------------|-------------------------|--|--|--|
| Primer name | Sequencece(5'-3') | Size, bp and t (°C) | Target gene | Source | | | |
| blaTEM-F | GAGTATTCAACATTTTCGT | - 857 (50) | tem | Maynard et al., 2003 | | | |
| <i>bla</i> TEM-R | ACCAATGCTTAATCAGTGA | 657 (50) | tem | Mayhard et al., 2003 | | | |
| <i>bla</i> SHV-F | TCGCCTGTGTATTATCTCCC | - 768 (60) | shv | Ojdana et al., 2014 | | | |
| <i>bla</i> SHV-R | CGCAGATAAATCACCACAATG | 708 (00) | SHV | Ojdana et al., 2014 | | | |
| oxa1-F | TCAACAAATCGCCAGAGAAG | - 276 (55) | oxa group I | Bert et al., 2002 | | | |
| oxa1-R | TCCCACACCAGAAAAACCAG | 270 (33) | oxa group r | Delt et al., 2002 | | | |
| oxagroup 5-F | AGCCGCATATTTAGTTCTAG | - 644(56) | oxa group V | Bert et al., 2002 | | | |
| oxagroup 5-R | ACCTCAGTTCCTTTCTCTAC | 044(30) | oxa group v | Dert et al., 2002 | | | |
| ctxM-F | ATGTGCAGYACCAGTAARGT | - 593 (50) | ctxM | Pagani et al., 2003 | | | |
| ctxM-R | TGGGTRAARTARGTSACCAGA | 393 (30) | CIXIVI | 1 again et al., 2003 | | | |
| ctxM group 2-F | ATGATGACTCAGAGCATTCGCCGC | _ 976 (56) | ctxM2 | Celenza et al., 2006 | | | |
| ctcM group 2-R | TCAGAAACCGTGGGTTACGATTTT | - 876 (56) | CIANIZ | Celeliza et al., 2000 | | | |
| cmy2-F | GCACTTAGCCACCTATACGGCAG | - 758 (58) | em. | Hasman et al., 2005 | | | |
| cmy2-R | GCTTTTCAAGAATGCGCCAGG | 130 (30) | сту | 1145111411 61 41., 2003 | | | |

| PRE-1-F | | AMO A AMORGA AMPARA A A A GOM | | | | |
|--|-----------------|-------------------------------|----------|--------------------|----------------------------|--|
| PER-2-F | <i>PER</i> -1-F | ATGAATGTCATTATAAAAGCT | 927 (48) | | Celenza et al., 2006 | |
| PER2-3R | | | | - per | | |
| tetA-F GTGAAACCCAACATACCCC 888 (55) tetA Maynard et al., 2003 terB-F CCTTATCATGCCAGTCTTGC 774 (55) tetB Maynard et al., 2003 terB-R ACTGCCTTTTTTCGC 774 (55) tetB Maynard et al., 2003 aadB-R ATGGACACACGCACGGTCCC 334 (55) aadB Asadollahi et al., 2012 aadA-R ATGGCCGATTGGCGCCTGTAAGCC 528 (68) aadA Asadollahi et al., 2012 rmB-R CCTTCTGATTGGCTAGCCCT 769 (55) rmB Van et al., 2004 armA-R TATATTCTGAAATCCACT 774 (55) armA Galimand et al., 2003 aphAl-F AAACGTTATCATCAGTG 500 (55) aphAl Frana et al., 2001 aac-44-R TAGACTGAGCATGACCTTGCG 487 (55) aac.44 Odumosu et al., 2015 aac-41-R TAGACTGAGCATGACCTTGCG 487 (55) aac.44 Odumosu et al., 2015 aac-41-R TAGGCATCACGAGAGCCTC 369 (65) aac.(3)II. Sandvang et al., 2009 strA-F CCTGGTGATAACGGCAATTC 546 (55) strA Lanz et al., 2003 strA-F <td></td> <td></td> <td>927 (49)</td> <td></td> <td>Celenza et al., 2006</td> | | | 927 (49) | | Celenza et al., 2006 | |
| tetA-R. GAAGGCAAGCAAGGATGTAG 888 (35) tetA Mulymard et al., 2003 tetB-R. ACTGCCGTTTTTCGCC 774 (55) tetB Maypard et al., 2003 sadB-F. ATGGACACACGCTCTCCC 334 (55) aadR Asadollahi et al., 2012 sadB-R. TTAGGCCGCATGCGCACC 534 (55) aadA Asadollahi et al., 2012 aadA-R. ATGGACCAGTGCGCCTGAAGCC 528 (68) aadA Asadollahi et al., 2012 rmB-R. ATGGACCAGTGCGCCT 769 (55) rmtB Yan et al., 2004 rmB-R. CATTCTGATTGCTTTGCTTATCA 774 (55) armA Galimand et al., 2003 rmB-R. CAAACCGTTTGCTTGAGGC 774 (55) armA Galimand et al., 2003 rmA-R. CAAACCGTTTGCTGAGG 500 (55) aphA1 Frana et al., 2001 aact4H-R. TTAGGCATCACTGCTGTGTTCG 487 (55) aactA1 Odumosu et al., 2015 aact3III-R. TTAGGCATCACTGCGTGTTCG 487 (55) aactA1 Defumosu et al., 2003 strb-F. ATCGTCAACGGATTGAACGC 546 (55) strA Lanz et al., 2003 strb | | | | | | |
| teth-Figh-Representation CCTTATCATGCCAGTCTTIGC 774 (55) teth Maynard et al., 2003 aadh-F ACTGGCGTTTTTTCGCC 534 (55) aadh Asadollahi et al., 2012 aadh-R TTAGGCCGCATTGCGCAGCC 534 (55) aadh Asadollahi et al., 2012 aadh-R ATGCCCAGTCGGCAGCG 528 (68) aadA Asadollahi et al., 2012 rmB-F ATGACACATCAACGATGCCT 769 (55) rmtB Yan et al., 2004 amh-F CAATGGATAGAATGATGTT 774 (55) armA Galimand et al., 2003 amh-F CAATGGATAGAATGACTT 774 (55) armA Galimand et al., 2003 amh-F CAAATGGATAGAATGACTT 774 (55) armA Galimand et al., 2003 amh-F CAAACGATGATGACTGACTGAGGAGC 500 (55) aphA1 Frana et al., 2001 amc4-F ATGACTGAGGAGGACCTTCG 487 (55) aac.44 Odumosu et al., 2015 aac,33]H-F TGAACGCTGACGGAGCCTC 369 (65) aac.43 Lanz et al., 2003 sirb-R CCCATGCAGATAGACGGCATTGACAC 596 (55) sirb Lanz et al., 2003 | | | 888 (55) | tetA | Maynard et al., 2003 | |
| tarb=R ACTGCCGTTTTTTCGC 7/4 (55) telB Maynard et al., 2003 andB-F ATGGACACAAGGGACCACGGACC 534 (55) aadB Asadollahi et al., 2012 andA-F GTGGATGGCGGCCTGAAGCC 528 (68) aadA Asadollahi et al., 2012 andA-F ATGGACAGTCAACGATGCCCT 769 (55) rmtB Yan et al., 2004 armB-F ATGACATCAACGATGCCCT 774 (55) armA Galimand et al., 2003 armA-R CATATGCATGAGCTTATCAT 774 (55) armA Galimand et al., 2003 aphAl-F AAACGCTTTGCTGAGGC 500 (55) aphAl Frana et al., 2001 armA-R TATATTCTGAAGTCACCTGAG 500 (55) aphAl Frana et al., 2001 arc4-H-R ATGACTGAGCTGACCTGCGGGTTCG 487 (55) aac.44 Odumosu et al., 2015 aac.43II-F TGACAGGATACAGGCANTC 487 (55) aac.41 Odumosu et al., 2001 srrA-F CCTGGTGATACAGGCANTC 546 (55) strA Lanz et al., 2003 srrA-F ATCGTCAAGGGATTGAAACC 509 (55) strB Lanz et al., 2003 srrB-F | | | | | 3.5 1 . 1 . 2002 | |
| andBF ATGGACACAAGGAGGTCGC 534 (55) aadB Asadollahi et al., 2012 andBAR TTAGGCGCGATATACGGACC 528 (68) aadA Asadollahi et al., 2012 andAR AATGCCCAGTCGGCAGCG 769 (55) rmtB Yan et al., 2004 rmtBR CCTTCTOATTGGCTATCCA 769 (55) rmtB Yan et al., 2004 armAR CCTTCTOATTGGCTAGCCT 774 (55) armA Galimand et al., 2003 aphAl-F AAACGCTTAGTCGAGG 774 (55) armA Galimand et al., 2001 aphAl-F AAACGCTTAGTCAGGGG 774 (55) aphAl Frana et al., 2001 auc44-F ATGACTOAGCAGGGAGCCT 487 (55) aacA4 Odumosu et al., 2015 aac(3)II-F TGAAACGCTGACGGAGCCTC 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCAATACTGC 546 (55) strA Lanz et al., 2003 strA-F CCTGGTGATAGAGAGC 546 (55) strB Lanz et al., 2003 strB-F ATCGTCAAGGAATATTGGC 509 (55) strB Lanz et al., 2003 strB-F ACACTTTGCCA | | | 774 (55) | tetB | Maynard et al., 2003 | |
| aadB-R TTAGGCCGCATATCCGCACC 334 (8) adab Asadonam et al., 2012 aadA-R AATGCCCAGTCGGAGCG 528 (68) aadA Asadonam et al., 2012 rmB-F ATGAACATCAACGATGCCCT 769 (55) rmtB Yan et al., 2004 rmtB-F CATTCGATTGGCTTATCCA 769 (55) rmtB Yan et al., 2004 armA-F CAAATGGATAAGAATGATGTT 774 (55) armA Galimand et al., 2003 aphA1-F CAAACGGTTATCCACGC 774 (55) armA Galimand et al., 2001 aphA1-R CAAACGGTTATCATCCAGG 500 (55) aphA1 Frana et al., 2001 aphA1-R CAAACCGTTATCATCCTGAGG 487 (55) aacA4 Odumosu et al., 2015 aac44-R TTAGACACGTGACCTGCTGTGTC 487 (55) aacA4 Odumosu et al., 2015 aac3JILF GTGGGTACACGGACCTC 369 (65) aac(3)II Sandvang et al., 2003 strA-R CCCAATCGCAGATAGAGGC 546 (55) strA Lanz et al., 2003 strB-R ACCATCGCAGATAGAGGC 590 (55) strB Lanz et al., 2003 strB-F ATCG | | | 524 (55) | 70 | A 1 11 1 1 1 2012 | |
| addA-R AATGCCCAGTCGGCAGGG 528 (08) addA Asadolani et al., 2012 rmB-F ATGAACATCACAGTCCCT 769 (55) rmtB Yan et al., 2004 rmB-R CCTTCTGATTGGCTTATCCA 769 (55) rmtB Yan et al., 2003 armA-F CAAATGGATAAGAATGATGTT 774 (55) armA Galimand et al., 2003 aphAl-F AAACGTCTTGCTCGAGGC aphAl-F AAACGTCTTGCTGAGGC aphAl-F AAACGTCATCACTGCGTGTTCG aac.44+F ATGACTGACGAGCCTTCCG 487 (55) aac.44 Odumosu et al., 2015 aac.43II-F TAGACACGGTGACCCTTCGG 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGGTGATACGGCCATTC 369 (65) aac(3)II Sandvang et al., 2009 strA-R CCAATGCGAATACGAGCATTCTGC 56 (55) strA Lanz et al., 2003 strB-F ATGGTCAAGGAATTGAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATACTGGC 495 (55) call Vassort-Bruneau et al., 2012 call-F ATGAACAACACACACACACACACACACACACACACACACA | aadB-R | | 534 (55) | аааВ | Asadollahi et al., 2012 | |
| adada-R AAIGCCCATCOGACCCT 769 (55) rmtB Yan et al., 2004 rmtB-R CCTTCTGATTGGCTTATCCA 774 (55) armA Galimand et al., 2003 armA-R CAAATGGATAAGAATCCACT 774 (55) armA Galimand et al., 2003 aphA1-F AAACGTCTTGCTGAGGC aphA1-F AAACGTTATTCATTCGTGA 500 (55) aphA1 Frana et al., 2001 aac4A-F ATGACTGACGATGACCTTGCG 487 (55) aac4A Odumosu et al., 2015 aac4A-F ATGACTGACGATGACCTTGCG 487 (55) aac4A Odumosu et al., 2015 aac4A-F ATGACTGACGAGGAGCCTC 369 (65) aac(3)II. Sandwang et al., 2009 aac(3)II.F GGAACAG GTAGCAGTGAG 369 (65) aac(3)II. Sandwang et al., 2009 strB-F CCTGGTGATAACGGCAATTC 546 (55) strB Lanz et al., 2003 strB-F ATGCTCAAGGATTGAACCC 599 (55) strB Lanz et al., 2003 strB-F ACACTAAGACTACAGTATTGGC 495 (55) call Vassort-Bruneau et al., 2003 call-R TGAAACACTACACTACCTGCC 293 (55) call | aadA-F | GTGGATGGCGGCCTGAAGCC | 520 (60) | a a d A | A and all also at al. 2012 | |
| mmB-R CCTTCTGATTGGCTTATCCA armA-F CAAATGGATAAGAATGATGTT armA-R TIAITTCTGAAATCACT aphAl-F AAACGTTCTTGCTCGAGGC aphAl-F AAACGTTATTGGTGA aacA4+F ATGACTGAGCATTGGTG aacA4+F ATGACTGAGCATGACCTTGGG aacA4+F ATGACTGAGCATGACCTTGGG aacA4+R TTAGGCATGAGCTTGCG aacA3II-F TGAAACGCTGAGCGTGCTCG aac(3)II-F TGAAACGCTGACGGAGCCTC aac(3)II-F GTGAACAG GTAGCACTGAG strA-F CCTGGTGATAACGGAATCC strA-R CCCAATCGCAGTAGACCTTGGG strA-R CCCAATCGCAGTAGACCTTGCG strA-R CCCAATCGCAGTAGACCTTGCG strA-R CCCAATCGCAGTAGACGCATTC strA-R CCCAATCGCAGTAGACGCATTC strA-R CCCAATCGCAGTAGACGCATTC strA-R CCCATCGAGAAGAGC strB-F ATCGTCAAGAGAGCC strB-F ATCGTCAAGAGAAGC strB-F ATCGTCAAGACACGCAATTC strB-R GGATCGTGAGAACACC strB-F ATCGTCAAGACACTGCC callI-F ACACTTTGCCCTTTATCGTC callI-F ACACTTTGCCCTTTATCGTC callI-F TTGCAACAGTACGTGACAT cmlA-R ACACAACGTGTACACACACT cmlA-R ACACAACGTGTACACCCAG stull-R ATGATCAACCCAG stull-R ATGATCTAACCCTGGTCC stull-R ATGATCTAACCCTGGTCC stull-R ATGATCTAACCCTGGTCTC stull-R ATGATCTAACCCTGGTCTC stull-R ATGATCTAACCCTGGTCTC stull-R ATGATCTAACCCTGGTCTC stull-R ATGATCTAACCCTGGTCTC stull-R ATGATCTAACCCTGGTTCGC dft-I-R CGGCATCGGAAGTCAG dft-I-R CGGCATCGGAAGTCAG dft-I-R CGGCATCGGAAGTCAG dft-I-R CGGCATCTGGAAGTCAG dft-I-R CGGCATCTGGCTGTTGGTTGGACGC dft-I-R CGGAATTCACCTTCGGTTTGGAAGCC dft-I-R CGGAATTCACCTTCGGTTTGAACCAG dft-I-R CGGAATTCACCTTCGGTTGTTGAA dft-I-R CGGAATTCACCTTCCGGCTCTGAAGTCAG dft-I-R CGGAATTCACCTTCCGGCTCTGAAGTCAGAGAGTCAGAGTCAGAGTCAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTCAGAGAGTAGGC dft-I-R CGGCAACAGAGTTGGTTGGTAGGA dft-I-R CGGCAACAGAGTTGGTGGACAGAGAGGTAGGC dft-I-R ACACACACGCCAGAAGGC dft-I-R ACACACACGCCAGAAGGC dft-I-R ACGCCTACCACTGC | aadA-R | AATGCCCAGTCGGCAGCG | 328 (08) | aaaA | Asadoliani et al., 2012 | |
| mmth CATATGGATAAGAATGATGTT 774 (55) armA Galimand et al., 2003 armA-R TTATTTCTGAATCACT 774 (55) armA Galimand et al., 2003 aphA1 Frana et al., 2001 aacA4+F AAACGTCTTGCTCGAGGC 487 (55) aacA4 Odumosu et al., 2015 aacA4+F ATGACTGAGCATGACCTTGCG 487 (55) aacA4 Odumosu et al., 2015 aacA4+F TTAGGCATGACCTTGCG 487 (55) aacA4 Odumosu et al., 2015 aacA31II GTCGAACAG GTAGCATGACCTTGCG 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCATGAC 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCATGAC 369 (65) strA Lanz et al., 2003 strB-F ATCGTCAAGGATTGAAGACC 509 (55) strB Lanz et al., 2003 strB-F ATCGTCAAGGATTGAAGACC 495 (55) catII 1996 catII-F ACACTTTGCCCTTTATCGTC 495 (55) catII 1996 catII-F ACACTTTGCAATGACAT cmlA-F TTGCAACAGTACGTGC 495 (55) catII 1996 cmlA-F TTGCAACAGTACGTGC 495 (55) sul1-F Christabel et al., 2012 sul1-R ATGATCTAACCCTCGGTCTC 822 (55) sul1-F Christabel et al., 2012 sul2-F GAGCAAGATTTTGGAATCTCAC 822 (55) sul3-F Pereten et al., 2003 sul2-F Pereten et al., 2003 sul2-F GAGCAAGATTTTGGAATCTCAC sul2-R GTGTGCGGATGAAGTCAG 572 (50) sul3-F Pereten et al., 2003 sul3-F GAGCAAGATTTTTGGAATCC 495 (55) dfr1 Gibreel et al., 2003 dfr1-F ACGGATCCTGGCTGTTGGATGC 496 (55) dfr1 Gibreel et al., 2003 dfr1-F ACGATCCTGGCTGTTGGTTGGACC 496 (55) dfr1 Gibreel et al., 2003 dfr1-F ACGATCCTGGCTGTGTTGGACC 496 (55) dfr1 Gibreel et al., 2003 dfr1-F ACGATCCTGGCTGTTGTTGCA 497 (44) dfr7 Navia et al., 2003 dfr1-F ACGATCCTGGTGTTGGACC 496 (55) dfr1 Gibreel et al., 2006 dfr1-F ACGATCCTGGTGTTGGACC 496 (55) dfr1 Gibreel et al., 2006 dfr1-F ACGATCCTGGTGTGTGGACC 496 (56) dfr1-F ACGATCCTGGTGTTGTTC 496 (57) dfr1-F ACGATCCTGGTGTGTGGACC 496 (57) dfr1-F ACGATCCTGTGTGGTGGACC 496 (57) dfr1-F ACGATCGTGAAGGTTGTC 496 (57) dfr1-F ACGATCGTGAAGGTTGTC 497 (47) dfr1-F A | rmtB-F | ATGAACATCAACGATGCCCT | 760 (55) | um tD | Van et al. 2004 | |
| armA-R TTATTTCTGAAATCCACT 7/4 (55) drmA Galiman et al., 2003 aphAl-F AAACGTCTTGCTCGAGGC 500 (55) aphAl Frana et al., 2001 aphAl-F CAAACCGTTATTCATTGGTA 500 (55) aphAl Frana et al., 2001 aacA4+F ATGACTGAGCATGACCTTGCG 487 (55) aacA4 Odumosu et al., 2015 aacA4+F TTAGGCATCACTGCGTGTTCC 369 (65) aac(3)II Sandwang et al., 2009 aac(3)II-F TGAAACAG GTAGCACTGAG 506 (65) aac(3)II Sandwang et al., 2009 strA-F CCTGGTGATAACGGCATTC 546 (55) strA Lanz et al., 2003 strB-F ATCGTCAAGGAGTTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATGGC 495 (55) catll Vassort-Bruneau et al., 2003 catll-F ACACTTTTGCAACAGTACCCT 495 (55) catll 1996 catll-F ACACAACGTGTACACATACC 293 (55) catll Yassort-Bruneau et al., 2000 catl-F TTGGCAACAGTACCCTCGGTCTC 293 (55) sull-F Christabel et al., 2012 <t< td=""><td>rmtB-R</td><td>CCTTCTGATTGGCTTATCCA</td><td>109 (33)</td><td>TmtD</td><td>Tall et al., 2004</td></t<> | rmtB-R | CCTTCTGATTGGCTTATCCA | 109 (33) | TmtD | Tall et al., 2004 | |
| arma-R THATTIC GAARIC ACT aphA1-R CAAACGTTATICCTCGAGGC 500 (55) aphA1 Frana et al., 2001 aphA1-R CAAACGTTATICCATTCGTGA 500 (55) aphA1 Frana et al., 2001 aacA4-R TAGGCATGACCTGCGTGTTCG 487 (55) aacA4 Odumosu et al., 2015 aac(3)II-F GIGGAACAG GTAGCACTGAG 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATACGGCAATTC 546 (55) strA Lanz et al., 2003 strB-R CCCAATCGCAGATAGAAGGC 546 (55) strA Lanz et al., 2003 strB-R GGATCGTAGAGCATTGAACC 599 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATTGGC 495 (55) catII Vassort-Bruneau et al., 2003 catII-F ACACATTTGCAACTACTGC 495 (55) catII 1996 cmIA-F TTGGAACAGTGTGACAT 293 (55) cmIA Keyes et al., 2000 sul1-F TTCGGCATTCTGCAACTACCTC 822 (55) sul1-F Christabel et al., 2012 sul2-R GTGTGCGATGACATACCTAGGCTTC 792 (51) sul3-F | armA-F | CAAATGGATAAGAATGATGTT | 774 (55) | arm A | Galimand et al. 2003 | |
| aphAl-R CAAACCGTTATTCATTCGTGA 300 (S) aphAl Frana et al., 2001 aacA4+F ATGACTGAGCATGACCTTGCG 487 (55) aacA4 Odumosu et al., 2015 aacA4+F TTAGGCATCACTGCGTGTTCC 487 (55) aacA4 Odumosu et al., 2015 aacA3]II-F TGAAACGCTGACGGAGCCTC 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCATTC 546 (55) strA Lanz et al., 2003 strB-F ACCATTCGCAGATAGAAGGC 59 (55) strB Lanz et al., 2003 strB-F ACCATTGCCAGTTGAACC 59 (55) strB Lanz et al., 2003 catlI-F ACACTTGCCAGTACTGGC 495 (55) catlI Vassort-Bruneau et al., 1996 catlI-F ACACTTGCACATACTGC 495 (55) catlI Vassort-Bruneau et al., 2003 sulI-F TTGGAACAGTGACATCA 293 (55) catlI Keyes et al., 2000 sulI-F TTGCAACACGTGAACCAG 293 (55) sulI-F Christabel et al., 2012 sul2-F CGGCATCGTCAACCTAGGCTTCC 822 (55) sul1-F Christabel et al., 2003 | | | 114 (33) | uma | Gainnand et al., 2003 | |
| agnA1-R CAAACCTITATICATICGTOA 487 (55) aacA4 Odumosu et al., 2015 aacA4-R TTAGGCTACACTGGGTTTCG 487 (55) aacA4 Odumosu et al., 2015 aac(3)II-R TGCGAACAG GTAGCACTGAG 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCAATTC 546 (55) strA Lanz et al., 2003 strB-F ATCGTCAAGGGATTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATTGGC 495 (55) catII Vassort-Bruneau et al., 1996 catII-R TGAAAGCCATCACATACTGC 495 (55) catII 1996 cmIA-F TTGCAACAGTGACCTGACCT 293 (55) catII Keyes et al., 2000 sul1-F TTCGGCATTCTGAATCTCAC 822 (55) sul1-F Christabel et al., 2012 sul2-F CGGCATCGTCAACATAACC 722 (50) sul2-F Pereten et al., 2003 sul3-F GAGCAAGATTTTTGGATTCG 792 (51) sul3-F Pereten et al., 2003 sul3-F GAGCAGATTTTTGGATTCG 792 (51) sul3-F Pereten et al., 2003 dfp1-F< | aphA1-F | | 500 (55) | anh A 1 | Frans et al. 2001 | |
| aacA4-R TTAGGCATCACTGCGTGTTCG 487 (55) aacA4 Oddimosu et al., 2013 aac(3)II-R GTCGAACAG GTAGCACTC 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCAATTC 546 (55) strA Lanz et al., 2003 strB-F ACCGCAGATAGAAGGC 546 (55) strA Lanz et al., 2003 strB-R ACGTCGTAGACAGAGGC 509 (55) strB Lanz et al., 2003 catlI-F ACACTTTGCCCTTTATCGTC 495 (55) catlI Vassort-Bruneau et al., 1996 cmlA-F TTGCAACAGTACGTGACAT 495 (55) catII Vassort-Bruneau et al., 2000 cmlA-F TTCGACACAGTACCAGCACT 495 (55) catII Vassort-Bruneau et al., 2000 sul1-F TTCGGCATCTGCACATCACCAC 293 (55) cmlA Keyes et al., 2000 sul1-R ATGATCTAACCTCGGTCTCAC 822 (55) sul1-F Christabel et al., 2012 sul2-F CGGCATCGTCAACATAACC 722 (50) sul2-F Pereten et al., 2003 sul3-F GAGCAGAAGATTTGGAATCG 792 (51) sul3-F Pereten et al., 2003 | aphA1-R | | 300 (33) | ирпА1 | Trana et al., 2001 | |
| adac43H-R THAGGCATCACTGGTGTTCG adac(3)II-R GTCGAACAG GTAGCACTGAG 369 (65) aac(3)II Sandwang et al., 2009 strA-F CCTGGTGATAACGGCAATTC 546 (55) strA Lanz et al., 2003 strA-F CCCAATCGCAGATAGAAGCC 590 (55) strB Lanz et al., 2003 strB-F ATCGTCAAGGATTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATTGC 495 (55) catII Vassort-Bruneau et al., 1996 catII-R TGAAAGCCATCACATACTGC 495 (55) catIII Vassort-Bruneau et al., 2003 catII-R TGAAAGCCATCACATACTGC 495 (55) catIII Vassort-Bruneau et al., 2000 sul1-F TTGGCAACAGTACACCAG 495 (55) catII Vassort-Bruneau et al., 2000 sul1-F TTGGAACAGACACCAC 495 (55) catIII Vassort-Bruneau et al., 2000 sul1-F TTGGCAACAGTACACCAC 822 (55) sul1-F Christabel et al., 2000 sul1-F TTGGCATTCTGAACCTCGGTCTC 822 (55) sul1-F Pereten et al., 2003 sul2-R GAGCAAGATTTGGAACCCAGGATTGA | | | 487 (55) | aac 4.4 | Odumosu et al. 2015 | |
| aac(3)II-R GTCGAACAG GTAGCACTGAG 369 (65) aac(3)II Sandvang et al., 2009 strA-F CCTGGTGATAACGGCAATTC 546 (55) strA Lanz et al., 2003 strB-F CCAACTCGCAGATTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATTGGC 509 (55) strB Lanz et al., 2003 catlI-R TGAAAGCCATCACATACTGC 495 (55) catlI Vassort-Bruneau et al., 1996 cmlA-F TTGCAACAGTGACATCCCC 495 (55) catlI Yassort-Bruneau et al., 2000 sul1-F TTCGACAACGTGTACAACCAG 293 (55) cmlA Keyes et al., 2000 sul1-F TTCGGCATTCTGAATCTCAC 822 (55) sul1-F Christabel et al., 2012 sul2-R GTGTGCGAATGATCAGC 722 (50) sul2-F Pereten et al., 2003 sul3-F GAGCAAGATTTTTGGAATCG 792 (51) sul3-F Pereten et al., 2003 sul3-F GAGTCTGCAGCTGATCTCGGCTTGATGT 4fr1 Gibi-F ACGGATCCTGCGTGTTGGT dfr1-F ACGGATCACCTTCCGGCTCGATGTC 4fr2 Gibi-F Seputiene et al., 2003 <t< td=""><td></td><td></td><td>407 (33)</td><td>шисл4</td><td>Odumosu et al., 2013</td></t<> | | | 407 (33) | шисл4 | Odumosu et al., 2013 | |
| add(s) III-R GTCGACAG GTAACGGCATTGG strA-R CCTGGTGATAACGGCAATTC strB-F ATCGTCAAGGGATTGAAACC 599 (55) strB Lanz et al., 2003 strB-F ATCGTCAAGGGATTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTAGAACATATTGGC 495 (55) catII Vassort-Bruneau et al., 1996 catII-F ACACATTGCCACATACTGC 495 (55) catII Vassort-Bruneau et al., 2000 catII-R TGAAAGCCATCACATACTGC 495 (55) catII Vassort-Bruneau et al., 2000 catII-R TGAACACACACCACACACAC 293 (55) cmlA Keyes et al., 2000 sul1-F TTCGGCATCGAACCACAC 293 (55) sul1-F Christabel et al., 2012 sul1-F TTCGGCATCGAACCACCAC 822 (55) sul1-F Christabel et al., 2012 sul2-F CGGCATCGTCAACATAACC 722 (50) sul2-F Pereten et al., 2003 sul3-R CATCTGCAGCTAACCTAGGGCTTTGA 792 (51) sul3-F Pereten et al., 2003 dfp-1-F ACGAATTCACCTGCTGATGTC 394 (44) dfp-5 Seputiene et al., 2010 < | aac(3)II-F | TGAAACGCTGACGGAGCCTC | 360 (65) | aac(3)II | Sandvang et al. 2000 | |
| strA-R CCAATCGCAGATAGAAGGC 546 (55) strA Lanz et al., 2003 strB-F ATCGTCAAGGGATTGAAACC 509 (55) strB Lanz et al., 2003 strB-R GGATCGTGAAACACATATTGGC 509 (55) strB Lanz et al., 2003 cafl-F ACACTTGCCCTTTATCGTC 495 (55) catlI Vassort-Bruneau et al., 1996 cmlA-F TTGCAACAGTACGTGACAT 293 (55) cmlA Keyes et al., 2000 sul1-F TTCGGCATTCTGAATCTCAC 822 (55) sul1-F Christabel et al., 2012 sul1-R ATGATCTAACCTCGGTCTC 822 (55) sul1-F Christabel et al., 2012 sul2-R GTGTGCGGATGAACTAGC 722 (50) sul2-F Pereten et al., 2003 sul3-F GAGCAAGATTTTGGAATCC 792 (51) sul3-F Pereten et al., 2003 sul3-F ACTCTGCAGCTGATCTGACTAGGGCTTTGA 495 (55) 4fr1 Gibreel et al., 2003 dfr1-F ACGGATCCTGCGATTGGA 792 (51) sul3-F Pereten et al., 2003 dfr1-F ACGGATTCCTCGGCTGTTGGTGGACC 4fr1 4fr1 Gibreel et al., 2013 | aac(3)II-R | | 309 (03) | <u> </u> | Sandvang et al., 2007 | |
| StrB-R CCAAITGCAATATAAACC strB-R GGATCGTAAGAACTATTGGC catll-F ACACTTTGCCCTTTATCGTC 495 (55) catll Vassort-Bruneau et al., 1996 catll-F TGAAAGCCATCACATACTGC 495 (55) catll Vassort-Bruneau et al., 1996 cmll-F TTGCAACAGTACGTGACAT 293 (55) catll Vassort-Bruneau et al., 2000 sull-F TTCGGCATCTGAACCAG 293 (55) catll Keyes et al., 2000 sull-F TTCGGCATCTGAACCAG 822 (55) sull-F Christabel et al., 2012 sul2-F CGGCATCGTCAACATAACC 822 (55) sull-F Christabel et al., 2012 sul2-F CGGCATCGTCAACATAACC 722 (50) sul2-F Pereten et al., 2003 sul3-F GAGCAGATTTTGGAATCG 792 (51) sul3-F Pereten et al., 2003 sul3-F ACGCTACCTCGACTTGAGCC 4fr1-F ACGGATCCTCCGGCTGTTGGATGCC 254 (55) dfr1 Gibreel et al., 1998 dfr1-F ACGGATCCTCCGGCTCGATGTC 394 (44) dfr5 Seputiene et al., 2010 dfr3-F GCGBAAAGGDGAACAGCT 471 (44) dfr7 Na | strA-F | CCTGGTGATAACGGCAATTC | 546 (55) | $ctv\Lambda$ | Lanz et al. 2003 | |
| strB-R GGATCGTAGAACATATTGGC 309 (\$5) strB Lanz et al., 2003 catll-F ACACTTTGCCCTTTATCGTC 495 (\$5) catll Vassort-Bruneau et al., 1996 cmll-F TTGCAACAGTACAGACAT 293 (\$5) cmlA Keyes et al., 2000 sull-F TTCGGCATCTGAATCTCAC 822 (\$5) sull-F Christabel et al., 2012 sull-F ATGATCTAACCCTCGGTCTC 822 (\$5) sull-F Christabel et al., 2012 sull-F CGGCATCGTCAACATAACC 722 (\$0) sul2-F Pereten et al., 2003 sul2-R GTGTGCGGATGAACTAGG 792 (\$1) sul3-F Pereten et al., 2003 sul3-F GAGCAAGATTTTGGAATCG 792 (\$1) sul3-F Pereten et al., 2003 dfp-1-R CGGAATCACCTTCCGGCTCGATGC 254 (\$5) dfp1 Gibreel et al., 1998 dfp-1-R CGGAATCACCTTCCGGCTCGATGC 254 (\$5) dfp1 Gibreel et al., 2003 dfp-1-R CGGAATCACCTTCCGGCTCGATGC 470 471 440 dfp7 Navia et al., 2010 dfp-3-R TTMCCAYATTGATTCGA 471 (44) dfp7 Navia et al., | strA-R | CCAATCGCAGATAGAAGGC | 340 (33) | SUA | Lanz et al., 2003 | |
| Carill-R TGAAAGCCATCACATACTGC Carill-R TGAAAGCCATCACATACTGC TTGCACACATCACTGC TTGCACACATCACTGC Carill-R TGCAACACTGCACATCCTGC Carill-R TTGCAACACTGCACATCCTGC Carill-R TTGCAACACTGCACACCAG Carill-R ACACACACTGTACAACCAG Carill-R ACACACACTGTACAACCAG Carill-R ACACACACTGTACAACCAG Carill-R ATGATCTAACCCTCGGTCTC Sull-R ATGATCTAACCCTCGGTCTC Sull-R ATGATCTAACCCTCGGTCTC Sull-R CGGCATCGTCAACATAACC TCGCGATCGTCAACATAACC TCGCGCATCGTCAACATAACC TCGCGCATCGTCAACATAACC TCGCGCATCACACTAGACC TCGCGCATCAGACTCAGG TCGCGATCAGACTAGACC TCGCGATCTGGAACTCAGG TCGCGATCTGGAACTCAGG TCGCGATCTGGAACTTGGAACC TCGCGATCCTGGATCTGGAACTCACTTCCGGCTCGATGTC TCGCGATCTGAACACTAGACC TCGCGATCCTGATGTC TCGCGATCCTGCTGTTGTTGATAGC TCGCGATCACACTTCCGGCTCGATGTC TCGCAGCTAACCTTCCGGCTCGATGTC TCGCAGCTAACCTTCCGGCTCGATGTC TCGCAGCTAACTTCTGATATAGC TCGCAGCTAACTTCTGATATAGC TCGCAGCTAACTTCTGATATAGC TTTMCCAAATTTGATTTCTGCA TTTMCCAAATTTGATTTCTGCA TTTMCCAAATTTGATTCTGCA TTTMCCAAATCT TTTMCCAAATCT TTTMCCAAATCT TTTMCCAAATCT TTTMCCAAATCT TTTMCCAAATCT TTTMCCAAATCT TTTMCCAATTTGATTGCC TCGATCGGCATTGGA TCTGGTCGGTTGGCGATTGGA TCTGGTCGGTTGTGGCGATTGGA TCTGGTCGGTATGGCGATTGGA TCTGGTCGGTATGGCGATTGGA TCTGGTCGGTATTGGTTGCTG TCTGGTCGGTAGGGCTCGAAAGGC TCGAAAGCCAGAAAGG TCGGCAAAGGTTAGGTCCA TCGCGCAAGGTTAGGTCCA TCGCGCAAGAGGTTAGGTCCA TCGCGCAAGGGTTAGGTCCA TCGGCAAAGGTTAGGTCCA TCGCGCAAAGGTTAGGTCCA TCGCGCAAAGGTTAGGTCCA TCGCGCAAGAGGTTAGGTCCA TCGCGCAAGAGGTAGGTCCA TCGCGCAAGAGGTAGGCCGGAAAGGCCAGAAAGG TCGGCAAAGGCCAGAAAGG TCGGCAAAGGCAGAAGGCAGAAGGCAGA | strB-F | ATCGTCAAGGGATTGAAACC | 500 (55) | atuD | Lanz et al. 2002 | |
| carli-RTGAAAGCCATCACATACTGC cmlA-F495 (55)carli1996cmlA-FTTGCAACAGTACGTGACAT cmlA-R293 (55)cmlAKeyes et al., 2000sul1-FTTCGGCATTCTGAATCTCAC sul1-R822 (55)sul1-FChristabel et al., 2012sul2-FCGGCATCGTCAACATAACC sul2-F722 (50)sul2-FPereten et al., 2003sul3-FGAGCAAGATTTTGGAATCG sul3-R792 (51)sul3-FPereten et al., 2003sul3-RCATCTGCAGCTAACCTAGGCTTTGA dfr1-F792 (51)sul3-FPereten et al., 2003dfr1-FCGGAATCCTGGCTGTTGGATGTC dfr3-F254 (55)dfr1Gibreel et al., 1998dfr3-RCGGAATCCTGCATGTTGATGC dfr3-R394 (44)dfr5Seputiene et al., 2010dfr3-RTTTMCCAYATTTGATAGC dfr3-R471 (44)dfr7Navia et al., 2003dfr3-RTTAGCCTTTTTTCCAAATCT mcr1-F309 (58)mcr1Liu et al., 2015mcr1-FCGGTCAGTCCGTTTGTC mcr1-R309 (58)mcr1Liu et al., 2016mcr2-RAGATGGTATTGTTGGTTGCTG mr3-F567 (58)mcr2Xavier et al., 2016qnr4-RGATCGCAAAGGTTAGGTCA qnrB-R469 (53)qnrARobicsek et al., 2006qnr8-FGATCGTGAAGCCAGAAAGG qnr8-R469 (53)qnrBRobicsek et al., 2006qnr8-FACGACATTCGTCAACTGCAA qnrS-R417 (53)qnrSRobicsek et al., 2006qepA-RCCCGAGGCATAGACTGTA CAGTGGACTTAGCC qr8-F218 (60)qepALiu et al., 2013leg1-FTTATTGCTGGGATTAGC CAGTGGACTTAGCC qr8-F< | strB-R | GGATCGTAGAACATATTGGC | 309 (33) | SUD | Lanz et al., 2003 | |
| Calli-RTOGACACCATACATACTOC1996cmlA-RTTCGCACAGTACCTGACAT293 (55)cmlAKeyes et al., 2000sul1-FTTCGGCATTCTGAATCTCAC822 (55)sul1-FChristabel et al., 2012sul1-RATGATCTAACCCTCGGTCTC822 (55)sul1-FChristabel et al., 2012sul2-RGTGTGCGGATGAACATAACC722 (50)sul2-FPereten et al., 2003sul3-FGAGCAAGATTTTTGGAATCG792 (51)sul3-FPereten et al., 2003sul3-RCATCTGCAGCTAACCTAGGGCTTTGA4fi-1Gibreel et al., 1998dfr-1-RCGGAATTCACCTTCCGGCTCGATGTC254 (55)dfr-1Gibreel et al., 1998dfr-1-RCGGAATTCACCTTCCGGCTCGATGTC254 (55)dfr-1Gibreel et al., 2010dfr-1-RCGGAAATTCACCTTCCGGCTCGATGTC394 (44)dfr-5Seputiene et al., 2010dfr-1-RAAAATTTCATTGATTCTCGCA471 (44)dfr-7Navia et al., 2003dfr-1-RCTGGTCAGTCCGTTTGTTC309 (58)mcr1Liu et al, 2015mcr1-FCGGTCAGTCCGTTTGTAGG309 (58)mcr1Liu et al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTTGCTG516 (53)qnrARobicsek et al., 2006qnrB-FGATCGGCAAAGGTTAGGTCA417 (53)qnrBRobicsek et al., 2006qnrB-RACGATGCTGTAGTGTC417 (53)qnrSRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qp-A-RCCCGAGGCATAGACTGTA | catII-F | ACACTTTGCCCTTTATCGTC | 105 (55) | a a t I I | Vassort-Bruneau et al., | |
| cm/A-RACACAACGTGTACAACCAG293 (55)cm/AKeyes et al., 2000sul1-FTTCGGCATTCTGAATCTCAC822 (55)sul1-FChristabel et al., 2012sul1-RATGATCTAACCCTCGGTCTC822 (55)sul1-FChristabel et al., 2012sul2-RGTGTGCGGATGAACATAACC722 (50)sul2-FPereten et al., 2003sul3-FGAGCAAGATTTTGGAATCG792 (51)sul3-FPereten et al., 2003sul3-RCATCTGCAGCTAACCTAGGGCTTTGA792 (51)sul3-FPereten et al., 2003dfr1-FACGGATCCTGGCTGTTGGTTGGACGC254 (55)dfr1Gibreel et al., 1998dfr3-RCGGAATTCACCTTCCGGCTCGATGTC394 (44)dfr5Seputiene et al., 2010dfr3-FAAAATTCATTGATAGC471 (44)dfr7Navia et al., 2003dfr3-RTTAGCCTTTTTTCCAAATCT471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTC309 (58)mcr1Liu et al, 2015mcr2-RAGATGGTATTGTTGGTAGGG567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTTGGTG567 (58)mcr2Xavier et al., 2006qnr3-FATTCCTCACGCCAGGATTTG469 (53)qnrARobicsek et al., 2006qnr3-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnr3-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnr3-FCAGCAGCATTAGACTGTA218 (60)qepALiu et al., 2013leg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2011 <t< td=""><td>catII-R</td><td>TGAAAGCCATCACATACTGC</td><td>493 (33)</td><td>cain</td><td>1996</td></t<> | catII-R | TGAAAGCCATCACATACTGC | 493 (33) | cain | 1996 | |
| Comia-RACACACAGGITACAACAGGsul1-RATGATCTAACCCTCGGTCTC822 (55)sul1-FChristabel et al., 2012sul2-FCGGCATCGTCAACATAACC722 (50)sul2-FPereten et al., 2003sul2-RGTGTGCGGATGAAGTCAG722 (50)sul2-FPereten et al., 2003sul3-RCATCTGCAGCTAACCTAGGGCTTTGA792 (51)sul3-FPereten et al., 2003dfr1-FACGGATCCTGGCTGTTGGTTGGACGC254 (55)dfr1Gibreel et al., 1998dfr1-RCGGAATTCACCTTCCGGCTCGATGTC254 (55)dfr1Gibreel et al., 2010dfr3-RTTTMCCAYATTTGATAGC394 (44)dfr5Seputiene et al., 2010dfr47-FAAAATTCATTGATAGC471 (44)dfr7Navia et al., 2003dfr47-RTTAGCCTTTTTTCCAAATCT471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTC309 (58)mcr1Liu et al., 2015mcr2-FTGTTGCTGTGCGGATTGGA567 (58)mcr2Xavier et al., 2016mcr2-FTGTTGCTTGTGCCGATTTGG516 (53)qnrARobicsek et al., 2006qnr3-FGATCGGCAAAGGTTAGGTCA469 (53)qnrBRobicsek et al., 2006qnr5-FACGATGCTGAATGCTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnr5-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnr5-FTAAATTGCCACCCTGTAGGC417 (53)qnrSRobicsek et al., 2006qnr5-FTGAGGCATAAGCCTGTA218 (60)qepALiu et al., 2008leg1-FTTATTGCTGGGATTAGGC164 (55)i | cmlA-F | TTGCAACAGTACGTGACAT | 202 (55) | om1A | Variation 2000 | |
| sul1-RATGATCTAACCCTCGGTCTC822 (55)sul1-FChristabel et al., 2012sul2-FCGGCATCGTCAACATAACC722 (50)sul2-FPereten et al., 2003sul3-FGAGCAAGATTTTGGAATCG792 (51)sul3-FPereten et al., 2003sul3-RCATCTGCAGCTAACCTAGGGCTTTGA792 (51)sul3-FPereten et al., 2003dfr1-FACGGATCCTGGCTGTTGGTTGGACGC dfr1-R254 (55)dfr1Gibreel et al., 1998dfr5-FGCBAAAGDARCAGCT dfr3-R394 (44)dfr5Seputiene et al., 2010dfr3-FAAAATTCATTGATAGC dfr3-R471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTC mcr1-R309 (58)mcr1Liu et al, 2015mcr2-RAGATGGTATTGTTGGTGGA mcr2-R567 (58)mcr2Xavier et al., 2016qnr4-FATTTCTCACGCCAGGATTTG qnr3-R516 (53)qnrARobicsek et al., 2006qnrB-RACGATGGTAGTTGTCC qnr5-R469 (53)qnrBRobicsek et al., 2006qnr5-FACGACATTCGTCAACTGCAA qnr5-R417 (53)qnrSRobicsek et al., 2006qnr5-RTAAATTGCGCACTGTAGGC qnr5-R417 (53)qnrSRobicsek et al., 2006qep4-FCAGTGGACATAAGCCTGTCA qep4-RCCCGAGGCATAAGCCTGTTC CCGGAGCATAAGCCTGTTA teg1-R218 (60)qepALiu et al., 2013leg1-FTTATTGCTGGGATTAGGC teg1-RACGGCTACCCTCTGTTATC164 (55)integrase II classChen et al., 2011leg2-FACGACATTCGTCAACTGCAA qrisher333 (50)integrase II classColdstein 2001 <td>cmlA-R</td> <td>ACACAACGTGTACAACCAG</td> <td>293 (33)</td> <td>CMIA</td> <td>Reyes et al., 2000</td> | cmlA-R | ACACAACGTGTACAACCAG | 293 (33) | CMIA | Reyes et al., 2000 | |
| sul1-isATGATC FAACCC TCGGTCCGGCATCGTCAACATAACCsul2-isCGGCATCGTCAACATAACCCGGCATCGTCAACATAACCsul3-isGAGCAAGATTTTTGGAATCGSul3-isSul3-isPereten et al., 2003sul3-isCATCTGCAGCTAACCTAGGGCTTTGATogata and the sular | sul1-F | | 822 (55) | cu/1 E | Christobal at al. 2012 | |
| sul2-RGTGTGCGGATGAAGTCAG722 (50)sul2-FPereten et al., 2003sul3-FGAGCAAGATTTTTGGAATCG792 (51)sul3-FPereten et al., 2003dfr1-FACGGATCCTGGCTGTTGGTTGGACGC dfr1-RCGGAATCCACCTTCCGGCTGTGGTTGGACGC dfr2-F254 (55)dfr1Gibreel et al., 1998dfr5-FGCBAAAGGDGARCAGCT dfr5-R394 (44)dfr5Seputiene et al., 2010dfr47-FAAAATTTCATTGATTCTGCA dfr47-R471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC mcr1-R309 (58)mcr1Liu et al., 2015mcr2-FTGTTGCTTGTGCCGATTGGA mcr2-R567 (58)mcr2Xavier et al., 2016mr4-FAGATGGTATTGTTGGTTGCTG qnr4-R516 (53)qnrARobicsek et al., 2006qnr8-FGATCGGCAAAGGTTAGGTCA qnrB-R469 (53)qnrBRobicsek et al., 2006qnr8-RACGACTTCGTCAACTGCAA qnrS-R417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCTGTTAGCC qep4-F218 (60)qepALiu et al., 2008leg1-FTTATTGCTGGGATTAGCC teg1-R164 (55)integrase I classChen et al., 2013leg2-FACGACATTCGTCAACTGCAA ACGACATTCGTCAACTGCAA164 (55)integrase I classChen et al., 2001 | sul1-R | ATGATCTAACCCTCGGTCTC | 022 (33) | Sut 1-1 | Christabel et al., 2012 | |
| Sul2-RGIGITGCGGATGAAGTCAGsul3-FGAGCAAGATTTTTGGAATCGsul3-RCATCTGCAGCTAACCTAGGGCTTTGAdfr1-FACGGATCCTGGCTGTTGGTTGGACGCdfr1-RCGGAATTCACCTTCCGGCTCGATGTCdfr3-FGCBAAGGDGARCAGCTdfr5-FGCBAAAGGDGARCAGCTdfr5-RTTTMCCAYATTTGATAGCdfr47-FAAAATTCATTGATTTCTGCAdfr47-RTTAGCCTTTTTTCCAAATCTmcr1-FCGGTCAGTCCGTTTGTTCmcr1-RCTTGGTCGGTCTGTAGGGmcr2-FTGTTGCTTGTGCCGATTGGAmcr2-FTGTTGCTTGTGCCGATTGGAmcr2-RAGATGGTATTGTTGGTTGCTGqnrA-FATTTCTCACGCCAGGATTTGqnrA-RGATCGGCAAAGGTTAGGTCAqnrA-RGATCGGCAAAGGTTAGGTCAqnrB-FGATCGTGAAAGCCAGAAAGGqnrB-RACGATGCTGTAGTTGTCCqnrS-FACGACATTCGTCAACTGCAAqnrS-FACGACATTCGTCAACTGCAAqnrS-RTAAATTGGCACCCTGTAGGCqnrS-RTAAATTGGCACCCTGTAGCCqnrS-RTAAATTGGCACCCTGTAGCCqepA-RCCCGAGGCATAAGCCTGTAcCCGAGCATAGACTGTA218 (60)qepAleg1-FTTATTGCTGGGATTAGCleg1-FTTATTGCTGGGATTAGCleg1-FTTATTGCTGGGATTAGCleg1-RACGGCTACCCTCTGTTATCleg2-FACGACATTCGTCAACTGCAA233 (50)integrase I classColdstein 2001 | sul2-F | | 722 (50) | 5412_F | Pereten et al 2003 | |
| sul3-RCATCTGCAGCTAACCTAGGGCTTTGA792 (31)sul3-FPereten et al., 2003dfr1-FACGGATCCTGGCTGTTGGTTGGACGC dfr1-R254 (55)dfr1Gibreel et al., 1998dfr5-FGCBAAAGGDGARCAGCT dfr5-R394 (44)dfr5Seputiene et al., 2010dfr47-FAAAATTTCATTGATTTCTGCA dfr47-R471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTC mcr1-R309 (58)mcr1Liu et al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA mcr2-R567 (58)mcr2Xavier et al., 2016qnrA-FATTTCTCACGCCAGGATTGG qnrA-R516 (53)qnrARobicsek et al., 2006qnrB-FGATCGGCAAAGGTTAGGTCA qnrB-R469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA qnrS-R417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC cappA-R218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC teg1-R4CGACATTCGTCAACTGCAA ACGGCTACCCTCTGTTATC216 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA teg1-RACGACATTCGTCAACTGCAA ACGACATTCGTCAACTGCAA teg1-R164 (55)integrase II classChen et al., 2001 | | | 122 (30) | Sut2-1 | Tereten et al., 2003 | |
| Sulf3-RCATCTGCAGCTAACCTAGGGCTTIGAdfr1-FACGGATCCTGGCTGTTGGTTGGACGC254 (55)dfr1Gibreel et al., 1998dfr5-FGCBAAAGGDGARCAGCT394 (44)dfr5Seputiene et al., 2010dfr47-FAAAATTTCATTGATTCTGCA471 (44)dfr7Navia et al., 2003dfr47-RTTAGCCTTTTTTCCAAATCT471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC309 (58)mcr1Liu et al, 2015mcr1-RCTTGGTCGGTCTGTAGGG567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTGCTG567 (58)mcr2Xavier et al., 2016qnr4-RGATCGCCAAGGATTTG516 (53)qnrARobicsek et al., 2006qnr3-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnr3-FACGACATTCGTCAACTGCAA417 (53)qnrBRobicsek et al., 2006qnr3-RTAAATTGGCACCCTGTAGGC417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA164 (55)integrase I classColdstein 2001 | sul3-F | | 792 (51) | su/3_F | Pereten et al. 2003 | |
| dfr1-RCGGAATTCACCTTCCGGCTCGATGTC254 (55)dfr1Gibreel et al., 1998dfr5-FGCBAAAGGDGARCAGCT394 (44)dfr5Seputiene et al., 2010dfr3-RTTTMCCAYATTTGATAGC471 (44)dfr7Navia et al., 2003dfr47-RTTAGCCTTTTTTCCAAATCT471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC309 (58)mcr1Liu et al, 2015mcr2-RCTTGGTCGGTCTGTAGGG567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTTGCTG516 (53)qnrARobicsek et al., 2006qnr3-FGATCGGCAAAGGTTAGGTCA516 (53)qnrBRobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qppA-FCAGTGGACATAGACTGTA218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC218 (60)qepALiu et al., 2013teg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase I classGoldstein, 2001 | | | 172 (31) | 5415-1 | 1 creten et al., 2003 | |
| dfr3-FGCBAAAGGDGARCAGCT dfr5-F394 (44)dfr5Seputiene et al., 2010dfr3-FAAAATTTCATTGATAGC471 (44)dfr7Navia et al., 2003dfr3-FAAAATTCATTGATTCTGCA dfr3-R471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC mcr1-R309 (58)mcr1Liu et al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA mcr2-R567 (58)mcr2Xavier et al., 2016qnr3-FATTCTCACGCCAGGATTTG qnr3-R516 (53)qnrARobicsek et al., 2006qnr3-FGATCGTGAAAGCCAGAAAGG qnr3-R469 (53)qnrBRobicsek et al., 2006qnr5-FACGACATTCGTCAACTGCAA qnrS-R417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCTGTAGGC qepA-F417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC qepA-R218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC teg1-R164 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA teg1-R233 (50)integrase II classGoldstein, 2001 | <i>dfr1-</i> F | - | 254 (55) | dfr1 | Gibreel et al. 1998 | |
| dfr5-RTTTMCCAYATTTGATAGC394 (44)dr7Seputiene et al., 2010dfrA7-FAAAATTTCATTGATTCTGCA471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC309 (58)mcr1Liu et al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTTGCTG516 (53)qnrARobicsek et al., 2006qnrA-FGATCGCAAAGGTTAGGTCA516 (53)qnrBRobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC218 (60)qepALiu et al., 2013teg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2011teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein 2001 | | | 234 (33) | <i>ujr</i> 1 | Gibreet et al., 1998 | |
| dfr37-FAAAATTTCATTGATAGC471 (44)dfr7Navia et al., 2003dfr47-RTTAGCCTTTTTTCCAAATCT471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTC309 (58)mcr1Liu et al, 2015mcr1-RCTTGGTGGTGTGAGGG567 (58)mcr2Xavier et al., 2016mcr2-RAGATGGTATTGTTGGTTGCTG516 (53)qnrARobicsek et al., 2006qnrA-FGATCGGCAAAGGTTAGGTCA516 (53)qnrBRobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008qepA-RCCCGAGGCATAGACTGTA218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein, 2001 | | | 394 (44) | dfr5 | Senutiene et al. 2010 | |
| dfrA7-RTTAGCCTTTTTTCCAAATCT mcr1-F471 (44)dfr7Navia et al., 2003mcr1-FCGGTCAGTCCGTTTGTTC mcr1-R309 (58)mcr1Liu et al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA mcr2-R567 (58)mcr2Xavier et al., 2016qnrA-FATTTCTCACGCCAGGATTTG qnrA-R516 (53)qnrARobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG qnrB-R469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA qnrS-R417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC qepA-R218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC teg1-R164 (55)integrase 1 classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA ACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein 2001 | | | 371 (11) | | Separienc et al., 2010 | |
| aprA/-RTIAGCCTTTTTCCAARTCTmcr1-FCGGTCAGTCCGTTTGTTC309 (58)mcr1Liu et al, 2015mcr2-RTGTTGCTTGTGCCGATTGGA567 (58)mcr2Xavier et al., 2016qnrA-FATTCTCACGCCAGGATTTG516 (53)qnrARobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCCTGTAGGC417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase 1 classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase I classGoldstein 2001 | | | 471 (44) | dfr7 | Navia et al. 2003 | |
| mcr1-RCTTGGTCGGTCTGTAGGG309 (58)mcr1Littlet al, 2015mcr2-FTGTTGCTTGTGCCGATTGGA567 (58)mcr2Xavier et al., 2016qnrA-FAGATGGTATTGTTGGTTGCTG516 (53)qnrARobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCTGTAGGC417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAGCCTGTTC218 (60)qepALiu et al., 2008qepA-RCCCGAGGCATAGACTGTA164 (55)integrase 1 classChen et al., 2013teg1-FTTATTGCTGGGATTATC164 (55)integrase II classGoldstein, 2001teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein, 2001 | | | 1/1 (11) | | | |
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| mcr2-RAGATGGTATTGTTGGTTGCTG567 (58)mcr2Xavier et al., 2016qnrA-FATTTCTCACGCCAGGATTTG516 (53)qnrARobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCCTGTAGGC417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase I classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein2001 | | | 207 (20) | | | |
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| qnrA-RGATCGGCAAAGGTTAGGTCA516 (53)qnrARobicsek et al., 2006qnrB-FGATCGTGAAAGCCAGAAAGG469 (53)qnrBRobicsek et al., 2006qnrS-RACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qnrS-RTAAATTGGCACCCTGTAGGC417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008qepA-RCCCGAGGCATAGACTGTA218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase 1 classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein2001 | | | | | | |
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| qnrB-RACGATGCCTGGTAGTTGTCC409 (33)qnrBRobicsek et al., 2006qnrS-FACGACATTCGTCAACTGCAA417 (53)qnrSRobicsek et al., 2006qepA-FCAGTGGACATAAGCCTGTTC218 (60)qepALiu et al., 2008qepA-RCCCGAGGCATAGACTGTA218 (60)qepALiu et al., 2008teg1-FTTATTGCTGGGATTAGGC164 (55)integrase 1 classChen et al., 2013teg2-FACGACATTCGTCAACTGCAA233 (50)integrase II classGoldstein 2001 | | | | 4 | | |
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| depA-RCCCGAGGCATAGACTGTAteg1-FTTATTGCTGGGATTAGGCteg1-RACGGCTACCCTCTGTTATCteg2-FACGACATTCGTCAACTGCAA233 (50) integrase II class Goldstein 2001 | | | 218 (60) | qepA | Liu et al., 2008 | |
| teg1-R ACGCTACCCTCTGTTATC teg2-F ACGACATTCGTCAACTGCAA 233 (50) integrase I class Chen et al., 2013 | | | () | 1.1 | | |
| teg2-F ACGACATTCGTCAACTGCAA 233 (50) integrase II class Goldstein 2001 | | | 164 (55) | integrase 1 class | Chen et al., 2013 | |
| | | | (50) | | , | |
| teg2-K IAAAI I GGCACCCI G I AGGC | | | 233 (50) | integrase II class | Goldstein, 2001 | |
| | teg2-K | 1AAA11GGCACCCTGTAGGC | (-) | | | |

Table 2. Characteristics of Salmonella isolated from humans in Kazakhstan

| Isolate number | Serovar | Phenotypic Resistance | Genotypic Resistance | Integrons |
|-------------------|----------------|--|----------------------------|-------------|
| | S. Tshiongwe | CIP | | |
| | S. Enteritidis | NAL, CIP | | - |
| 737 | S. Blegdam | · | | - |
| 739 | S. Blegdam | | | - |
| 990 | S. Enteritidis | NAL, ENR | | - |
| 991 | S. Enteritidis | CIP | | - |
| 993 | S. Enteritidis | TET | | - |
| 994 | S. Enteritidis | STR, DOX | strB | - |
| 998 | S. Enteritidis | ENR, NAL, CIP | | - |
| 999 | S. Enteritidis | NAL, ENR, CIP, GEMI, | | - |
| 1106 | S. Enteritidis | NAL, CIP | | - |
| 1107 | S. Enteritidis | | | - |
| 1108 | S. Enteritidis | | | - |
| 1109 | S. Enteritidis | | | - |
| 1110 | S. Enteritidis | | | - |
| 1111 | S. Enteritidis | NAL, CIP | | - |
| 1112 | S. Enteritidis | | | - |
| 1113 | S. Enteritidis | TET | tet B | - |
| 1205 | S. Enteritidis | NAL, ENR, CIP, GEMI | | _ |
| 1206 | S. Enteritidis | AMP, TET, DOX, NAL, ENR, CIP, OFX, SXT | blaTEM, tet A, tet B, sul3 | + (class I) |
| 1280 | IIIc 4p | NAL, ENR, CIP | | - |

NAL - nalidixic acid; CIP - ciprofloxacin; ENR - enrofloxacin; TET - tetracycline, DOX - doxycycline; GEMI - gemifloxacin; AMP - ampicillin; OFX - ofloxacin; STRE - streptomycin; SXT - sulfamethoxazole/trimethoprim

| Table 3 | Characteristics | of Salmonella | isolated from | animals in Kazakhsta | n |
|----------|-----------------|-----------------|----------------|-------------------------|----|
| Table 5. | Characteristics | or buillionella | isolated Holli | anninais in ixazaknsta. | 11 |

| | Source of | Phenotypic Resistance | Genotypic resistance | Integrons |
|-----------------|------------|--------------------------------|----------------------------------|-------------|
| Serovar | Isolation | - I henoty pre reconstance | Genoty pre Tesistanee | |
| S.Typhimurium | duck | STR, KAN, ENR | | - |
| S.Typhimurium | duck | STR, CHL, TET, ENR, | | - |
| S. Typhimurium | chicken | | | - |
| S. Typhimurium | chicken | | | - |
| S. Paratyphi C | chicken | CHL, TET, DOX, NAL, CIP, SXT | tetA, sul3, cmlA, catII | + (class I) |
| S.Enteritidis | chicken | NAL, CIP | | - |
| S.Enteritidis | chicken | NAL, CIP | | - |
| S.Enteritidis | chicken | AMP, STR, SXT | Bla TEM, aadA, dfr1 | - |
| S.Enteritidis | chicken | STR, TET, DOX, ENR, CIP, GEMI, | tet A, sul 2, dfr1, strA, str B | |
| 5.Eliteritidis | CHICKEH | NAL, SXT | tet A, sut 2, uji 1, strA, str B | |
| S.Enteritidis | chicken | ENR, NAL, CIP | | - |
| S.Enteritidis | chicken | AMP, STR, ENR | bla TEM, aacA4, | - |
| S.Enteritidis | chicken | NAL, ENR, CIP | | - |
| S.Moscow | chicken | NAL, ENR, CIP | | - |
| S. Paratyphi C | chicken | FOX, STR, TET, DOX, NAL, ENR, | and A tot A gray P | + (alass I) |
| S. raiatypiii C | (imported) | CIP, OFX, GEMI | aadA, tet A, qnr B | + (class I) |

NAL - nalidixic acid; CIP - ciprofloxacin; ENR - enrofloxacin; TET - tetracycline, DOX - doxycycline; GEMI - gemifloxacin; AMP - ampicillin; OFX - ofloxacin; SXT - sulfamethoxazole/trimethoprim; CHL - chloramphenicol; STR - streptomycin; KAN - kanamycin

| Table 4. Characteristics of Salmonella isolated from food products in Kazakhstan | | | | | | | | |
|--|---------------------|--------------------------------|--------------------------|-------------|--|--|--|--|
| Serovar | Source of isolation | Phenotypic Resistance | Genotypic resistance | Integrons | | | | |
| S. Enteritidis | Roasted chicken | | | - | | | | |
| | drumstics | | | | | | | |
| S. Enteritidis | Roasted chicken | NAL, ENR, CIP | | - | | | | |
| 5. Eliteritidis | drumstics | NAL, ENK, CII | | | | | | |
| S. Enteritidis | Sausage | NAL, ENR, CIP | | _ | | | | |
| S. Enteritidis | Cake | | | - | | | | |
| S. Enteritidis | Ice-cream | NAL, ENR, CIP | | - | | | | |
| S. Enteritidis | Cake | NAL, ENR, CIP | | - | | | | |
| S. Enteritidis | cake | | tet B | - | | | | |
| S. Enteritidis | Refrigerated | AMP, STR, KAN, TET, DOX, ENR | | - | | | | |
| 5. Eliteritidis | chicken drumstics | AWII, STK, KAIN, TET, DOX, ENK | | | | | | |
| S. Enteritidis | Sausage | AMP, STR, KAN, CHL, DOX, ENR | | - | | | | |
| S. Enteritidis | Refrigerated | AMP,STR, KAN, CN, TET, DOX | | - | | | | |
| D. Litteritidis | chicken drumstics | AMI,STR, KAN, CN, TET, BOX | | | | | | |
| Salmonella group C | Force meat | AMP, STR, CHL, TET, DOX, NAL, | aadB, tet A, tet B, | + (Class I) | | | | |
| | 1 Orce meat | ENR, CIP, OFX, GEMI, SXT | sul3, catII, qnrA | (Class I) | | | | |
| S. Tennessee | Meat in paste | AMP, CFP, KAN, CHL, TET, DOX, | ctxM, aphA1, aadA, | + (ClassI, | | | | |
| D. Tellifessee | wicat iii paste | NAL, ENR, CIP, SXT | tet A, sul3, cmlA, catII | Class II) | | | | |

NAL - nalidixic acid; CIP - ciprofloxacin; ENR - enrofloxacin; TET - tetracycline, DOX - doxycycline; GEMI - gemifloxacin; AMP - ampicillin; CN - gentamicin; OFX - ofloxacin; SXT - sulfamethoxazole/trimethoprim; CHL - chloramphenicol; STR - streptomycin; KAN - kanamycin; CFP - cefpodoxime

Data analysis

Occurrence of multi-resistant isolates was calculated by dividing the number of isolates resistant to at least 3 antimicrobial classes by the total number of obtained isolates. Statistical analysis was performed using IBM SPSS Statistics package, version 20.

Comparison between categorical variables was calculated using the chi-square test. Results were considered statistically significant if $P \le 0.05$.

RESULTS

From total 10 212 samples tested (1006 samples from live animals, animal carcasses and milk; 383 food and 8823 human samples) *Salmonella* were isolated in 47 cases (0.46%). Twenty one (21) isolates (0.24%) were obtained from humans, fourteen (14) (1.39%) - from live or slaughtered animals and twelve (12) isolates (3.13 %) - from ready to use, raw or refrigerated food products (Tables 2-4).

As it could be seen from Table 2, the predominant *Salmonella* serovar isolated from humans was *S.* Enteritidis (81% from all isolates). Susceptibility varied among the strains: seven isolates were susceptible to all tested antimicrobials while a single isolate was resistant to eight (8) of the tested antimicrobials. The most frequent resistance was towards nalidixic acid, fluoroquinolones and tetracyclines. The prevalence of the genes encoding resistance was low. Integrons

were detected in a single multi-resistant isolate of *S*. Enteritidis.

Although different animal species were tested the *Salmonella* were isolated only from chickens and ducks (Table 3). The serovar variety in poultry was higher to those of humans. The predominant serovar were *S.* Typhimurium and *S.* Enteritidis. Two isolates were identified as *S.* Paratyphi C. One of those isolates was resistant to tetracyclines, nalidixic acid, ciprofloxacin, chloramphenicol, sulfonamides and trimethoprim and harboured class I integrons while the other - to 2d generation cephalosporins, streptomycin, tetracyclines and all fluoroquinolones tested. Two (2) strains out of fourteen (14) isolated from animals were susceptible to all antimicrobials tested while six (6) isolates were multi-resistant.

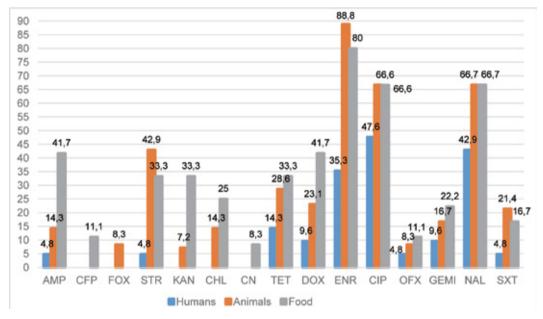
S. Enteritidis was the predominant serovarin food products (81% from all isolates) however, two other serovars- (Salmonellagroup C and S. Tennessee) had much wider spectrum of resistance. Five (5) isolates out of twelve (12)of food origin were multi-resistant, two (2) strains were susceptible to all antimicrobials and four (4) had similar resistance patterns being resistant only to (fluoro)quinolones. The isolate of S. Tennessee was a single strain harboured integrons of both I and II class.

The frequency of antimicrobial resistance in Sal-

monella isolates obtained from different sources is presented in Fig 1.

The most frequent resistance among Salmonella isolates was demonstrated to fluoro(quinolones), ampicillin, streptomycin and tetracycline. Resistance to critically important antimicrobials for humans was also detected and varied depending on the source of isolation. Human isolates demonstrated lower resistance compared to animal and food isolates. Food iso-

lates were more frequently resistant to antimicrobials compared to animal isolates except for streptomycin and enrofloxacin which were more frequently non effective against animal isolates and for nalidixic acid for which the number of resistant isolates from animals and foods had the same range. The correlation between the strains isolated from different sources regarding their resistances to separate antimicrobials is presented in Table 5.



NAL - nalidixic acid; CIP - ciprofloxacin; ENR - enrofloxacin; TET - tetracycline, DOX - doxycycline; GEMI - gemifloxacin; AMP - ampicillin; CN - gentamicin; OFX - ofloxacin; SXT - sulfamethoxazole/trimethoprim; CHL - chloramphenicol; STR - streptomycin; KAN - kanamycin; FOX - cefoxitin; CFP - cefpodoxime

Fig 1. Antimicrobial resistance (% of resistant isolates) of Salmonella isolated from humans, animals and food products

Table 5. Statistical differences among resistances in Salmonella isolates from different sources

trimethoprim

| | Č | | | | | | | | |
|-------------------|------------------|--------|---------------|-------|--------|-----------------|-------|----|-----------|
| Antibiotics | Human vs Animals | | Human vs Food | | | Animals vs Food | | | |
| Antibiotics | Value | df | P - value | Value | df | P - value | Value | df | P - value |
| Ampicillin | 0.972 | 1 | 0.324 | 6.991 | 1 | 0.008 | 2.462 | 1 | 0.117 |
| Cefoperazone | c | onstan | t | 2.414 | 1 | 0.120 | 1.400 | 1 | 0.237 |
| Cefoxitin | 1.805 | 1 | 0.179 | | consta | nt | 0.788 | 1 | 0.375 |
| Streptomycin | 10.862 | 1 | 0.001 | 7.966 | 1 | 0.005 | 0.248 | 1 | 0.619 |
| Kanamycin | 1.544 | 1 | 0.214 | 7.966 | 1 | 0.005 | 2.854 | 1 | 0.091 |
| Gentamicin | c | onstan | t | 1.805 | 1 | 0.179 | 1.213 | 1 | 0.271 |
| Levomycetin | 3.182 | 1 | 0.074 | 5.775 | 1 | 0.016 | 0.478 | 1 | 0.490 |
| Tetracycline | 2.146 | 1 | 0.143 | 2.910 | 1 | 0.088 | 0.069 | 1 | 0.793 |
| Doxycycline | 1.176 | 1 | 0.278 | 4.721 | 1 | 0.030 | 0.991 | 1 | 0.319 |
| Enrofloxacin | 6.801 | 1 | 0.009 | 5.040 | 1 | 0.025 | 0.281 | 1 | 0.596 |
| Ciprofloxacin | 0.638 | 1 | 0.424 | 0.524 | 1 | 0.469 | 0.000 | 1 | 1.000 |
| Ofloxacin | 0.171 | 1 | 0.679 | 0.408 | 1 | 0.523 | 0.046 | 1 | 0.830 |
| Gemifloxacin | 0.366 | 1 | 0.545 | 0.879 | 1 | 0.348 | 0.103 | 1 | 0.748 |
| Nalidixic acid | 1.733 | 1 | 0.188 | 1.429 | 1 | 0.232 | 0.000 | 1 | 1.000 |
| Sulfamethoxazole/ | 2.305 | 1 | 0.129 | 1.310 | 1 | 0.252 | 0.094 | 1 | 0.759 |

DISCUSSION

This study describes the prevalence of *Salmonella* spp. in different sources in Kazakhstan. Up to date only the data from humans were collected by national and international responsible institutions within the country. Salmonellosis is one of the leading causes of foodborne infections in humans with animals being reservoirs of *Salmonella*. *Salmonella* colonizes the gastrointestinal tract of food animals (Andino et al., 2015) and is shed via feces (Narváez-Bravo et al., 2013). Although the clinical manifestation of salmonellosis in different food-producing animal species can be unequally expressed, all animal species can be a source of foodborne infection (Chaney et al., 2017; Evangelopoulou et al., 2015; Pande et al., 2016).

Knowledge of the prevalence and diversity of Salmonella serovars in animals and food can provide important information necessary to develop preventive measures and strategies at different stages of the food chain such as application hazard analysis and critical control programs in meat production industries to ensure food safety (Tietjen and Fung, 1995; Gutema et al., 2019). According to this study the most prevalent serovar of Salmonella in Kazakhstan was S. Enteritidis which was the most frequently detected both in humans (81%) and food products (83%). According to the World Health Organization, S. Enteritidis is one of the most frequently isolated Salmonella serovars (along with S. Typhimurium) from countries involved in the Global Foodborne Infections Network (Hendriksen et al., 2011). The other serovars isolated from humans included S. Blegdam and S. Tshiongwe. S. Blegdam which is genetically similar to S. Enteritidis was isolated for the first time in the USA in the middle of last century from a patient suffering with the enteric type of fever and extensive erythema during the fifth week after onset (Holt and Newton, 1948). There is a lack of data about its prevalence during past decades, although S. Blegdam was recently isolated from broilers in Egypt (Ammar et al., 2019). S. Tshiongwe was described as a pathogenic serovar for both humans and animals and was also isolated from foods (Thong et al., 2004; Mshelbwala et al., 2017). This study demonstrated that the variety of serovars prevalent in animals in Kazakhstan was not wide; besides S. Enteritidis, which prevalence was 50% of all serovars, S. Typhimurium (29%) was also common. This serovar was recovered from poultry. The disease caused by S. Typhimurium is of public health significance, as it is associated with food poisoning in humans (Dar et al., 2017). The other highly pathogenic to man serovarS. Paratyphi C was isolated from chicken carcasses in two cases. This serovaris associated with human disease although the carriers can be different animal species (ECDC, 2019). Although paratyphoid fever is a rare disease in Europe and the USA it is still prevalent in Asia (Ekdahl et al., 2005).

Interesting data was also obtained according to the antimicrobial susceptibility testing: the isolates from humans were less frequently resistant to different antimicrobials comparing to animal and particularly food isolates, although it is known that salmonellosis is a foodborne human infection. All of the isolates obtained from humans, in vitro were susceptible to chloramphenicol, cephalosporins and aminoglycosides (except one isolate which was resistant to streptomycin), while the isolates from animals and foods had different susceptibility patterns. Although aminoglycosides are poorly effective against salmonellosis in vivo (Kihlstrom and Andaker, 1985), these antimicrobials are good indicators testing in vitro when comparing differences in antimicrobial susceptibility of different isolates, particularly isolated from different sectors. As it is important to understand the chain of salmonellosis "from farm to table" the data obtained in this study is interestingly enough demonstrating quite big differences among susceptibility in salmonella isolates from animals, foods and humans. The most frequent resistance in the isolates irrespective from the source of isolation was towards (fluoro) quinolones, aminopenicillins, streptomycin, tetracyclines and sulphamethoxazole/trimethoprim. These antimicrobials are frequently used both in humans and animals. Comparing the resistance between animal and food isolates the differences were less obvious except for beta-lactams and kanamycin with the highest resistance frequency being in food isolates. Isolates from animals had the highest resistance towards enrofloxacin compared to isolates from other sources. This is probably associated with the frequent use of enrofloxacin for animal treatment in Kazakhstan as it is known that broad use of fluoroquinolones has been followed by emergence of resistance to this class of antimicrobials (Hooper, 2001). Although all food products from which Salmonella were isolated contained ingredients of animal origin (meat, milk products or eggs) only a part of the products were originated from Kazakhstan while some of them were imported (data are not presented). Resistance to 3d generation cephalosporins was detected only in the isolates from foods but not from humans and animals, meaning that salmonellae circulating in Kazakhstan are quite specific and isolated. This fact is also proved by the low overall prevalence of Salmonella and by the poor variety of serovars circulating within the country. Imported food however, may change the situation in case of foodborne infections appear. The current situation regarding antimicrobial resistance in humans is beneficial with possibility to treat salmonellosis with antimicrobials of the 1st choice. The best known genes encoding antimicrobial resistance in human isolates mostly were absent except for some isolates which harboured tet, sul, stre and blaTEM genes encoding resistance to the oldest antibiotic classes. The situation in animals and food products was less beneficial as besides different genes, integrons associated with the horizontal gene transfer were detected more frequently. These findings suggest that antimicrobials in animal sector should be used more strictly particularly paying attention to critically important antimicrobials for humans and possible horizontal transfer of pathogens and their genetic determinants between environment (animals, food ingredients) and

humans. Since multi-resistant highly pathogenic to humans serovars, as *S*. Paratyphi C, were detected in animal carcasses, monitoring of *Salmonella* prevalence in animals should be implemented on a regular basis and measures for *Salmonella* eradication should be foreseen.

In conclusion, food import is one of the key factors changing the *Salmonella* variety and its antimicrobial resistance patterns in Kazakhstan. Usage of enrofloxacin in veterinary medicine however, is the factor of increasing salmonella resistance to fluoroquinolones that may have negative impact on treatment of salmonellosis infections.

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CONFLICT OF INTERST

The authors declare no conflict of interest.

REFERENCES

- Ammar AM, Abdeen EE, Abo-Shauma UP, Fekry E, Kotb Elmahallawy E (2019) Molecular characterization of virulence and antibiotic resistance genes among Salmonella serovars isolated from broilers in Egypt. Lett Appl Microbiol68:188-195.
- Andino A, Hanning I (2015) Salmonella enterica: survival, colonization, and virulence differences among serovars. Sci World J 2015:520179.
- AsadollahiP, AkbariM, Soroush S, Taherikalani M, Asadollahi K, Sayehmiri K (2012) Antimicrobial resistance patterns and their encoding genes among *Acinetobacter baumannii* strains isolated from burned patients. Clin Infect Dis38:1198-1203.
- Bert F, Branger C, Lambert-Zechovsky N (2002) Identification of PSE and OXA β-lactamase genes in *Pseudomonas aeruginosa* using PCR-restriction fragment length polymorphism. J Antimicrob Chemother 50:11-18.
- Celenza G, Pellegrini C, Caccamo M, Segatore B, Amicosante G, Perilli M (2006) Spread of blaCTX-M-type and blaPER-2 β-lactamase genes in clinical isolates from Bolivian hospitals. J Antimicrob Chemother 57:975-978.
- Chaney WE, Agga GE, Nguyen SV, Arthur TM, Bosilevac JM, Dreyling E, Rishi A, Brichta-Harhay D (2017) Rapid detection and classification of Salmonella enterica shedding in feedlot cattle utilizing the roka bioscience atlas Salmonella detection assay for the analysis of rectoanal mucosal swabs. J Food Prot80:1760-1767.
- Chen CH, Huang CC (2013)Risk factor analysis for extended-spectrum β-lactamase-producing Enterobacter cloacae bloodstream infections in central Taiwan. BMC Infect Dis 13:417.
- Christabel M, Budambula N, KiiruJ, Kariuki S (2012) Characterization of antibiotic resistance in environmental enteric pathogens from Kibera slum in Nairobi-Kenya. Afr J Bacteriol Res4:46-54.
- CLSI (2019) Performance Standards for Antimicrobial Susceptibility Testing. 29th ed. CLSI supplement M100. Wayne, P. A.: Clinical and Laboratory Standards Institute.
- DarMA, AhmadSM, Bhat SA, Ahmed R, Urwat U, MumtazPT, Bhat SA, Dar TA, Shah RA, Ganai NA (2017) Salmonella typhimurium in poultry: a review. World Poultry Sci J 73:345-354.
- DioneMM, IkumapayiUN, SahaD, MohammedNI, GeertsS, IevenM, Adeg-

- bolaRA, AntonioM (2011)Clonal differences between non-typhoidal *Salmonella* (NTS) recovered from children and animals living in close contact in the Gambia. PLoS Negl Trop Dis5:e1148.
- Dyson ZA, Klemm EJ, Palmer S, Dougan G (2019) Antibiotic resistance and typhoid, Clin Infect Dis 68:165-170.
- Ekdahl K, de Jong B, Wollin R, Andersson Y (2005)Travel-associated non-ty-phoidal salmonellosis geaographical and seasonal differences and sero-type distribution. Clin Microbiol Infect 11:138-144.
- Eng SK, Pusparajah P, Ab Mutalib NS, Ser HL, Chan KG, Lee,LH (2015) Salmonella: A review on pathogenesis, epidemiology and antibiotic resistance. Front Life Sci8:284-293.
- European Centre for Disease Prevention and Control. Facts about typhoid and paratyphoid fever. Interactive https://www.ecdc.europa.eu/en/typhoid-and-paratyphoid-fever/facts. Accsessed: 26-03-2020.
- Evangelopoulou G, Kritas S, Christodoulopoulos G, Burriel A R (2015)The commercial impact of pig Salmonella spp. infections in border-free markets during an economic recession. Vet World 8:257-272.
- Frana TS, CarlsonSA, Griffith RW (2001) Relative distribution and conservation of genes encoding aminoglycoside-modifying enzymes in Salmonella enterica serotype Typhimurium phage type DT104. Appl Environ Microbiol 67:445-448.
- Galimand M, Courvalin P, Lambert T (2003) Plasmid-Mediated High-Level Resistance to Aminoglycosides in *Enterobacteriaceae* Due to 16S rRNA Methylation. Antimicrob Agents Chemother47:2565-2571.
- Gibreel A, Sköld O (1998)High-level resistance to trimethoprim in clinical isolates of *Campylobacter jejuni* by acquisition of foreign genes (dfr1 and dfr9) expressing drug-insensitive dihydrofolate reductases. Antimicrob Agents Chemother 42:3059-3064.
- Goldstein C, Lee MD, Sanchez S, Hudson C, Phillips B, Register B, Grady M, Liebert C, Summers AO, White DG, Maurer JJ (2001) Incidence of class 1 and 2 integrases in clinical and commensal bacteria from livestock, companion animals, and exotics. Antimicrob Agents Chemother45:723-726.
- Gutema FD, Agga GE, Abdi RD, De Zutter L, Duchateau L, Gabriël S (2019) Prevalence and serotype diversity of Salmonella in apparently healthy

- cattle: Systematic review and meta-analysis of published studies, 2000-2017. Front Vet Sci6:102.
- Hasman H, Mevius D, Veldman K, Olesen I, Aarestrup FM (2005) β-lactamases among extended-spectrum β-lactamase (ESBL)-resistant Salmonella from poultry, poultry products and human patients in The Netherlands. J Antimicrob Chemother 56:115-121.
- Hendriksen RS, Vieira AR, Karlsmose S, Lo Fo Wong DM, Jensen AB, Wegener HC, Aarestrup FM (2011) Global monitoring of Salmonella serovar distribution from the World Health Organization global foodborne infections network country data bank: results of quality assured laboratories from 2001 to 2007. Foodborne Pathog Dis 8:887-900.
- Holt RA, Newton H (1948) The occurrence of *Salmonella blegdam* in Louisiana. J Lab Clin Med 33:1115-1158.
- Hooper DC (2001) Emerging mechanisms of fluoroquinolone resistance. Emerg Infect Dis 7:337-341.
- Hudzicki J (2009) Kirby-Bauer disk diffusion susceptibility test protocol. ASM Microbe Libr, URL (https://www.asm.org/getattachment/2594ce26-bd44-47f6-8287-0657aa9185ad/Kirby-Bauer-Disk-Diffusion-Susceptibility-Test-Protocol-pdf.pdf). (accessed 26.03.2020).
- ISO 6579-1:2017. Microbiology of the food chain Horizontal method for the detection, enumeration and serotyping of Salmonella - Part 1: Horizontal method for the detection of Salmonella spp. International Organization for Standardization, Geneva, Switzerland.
- Keyes K, Hudson C, Maurer JJ, Thayer S, White DG, Lee MD (2000) Detection of florfenicol resistance genes in *Escherichia coli* isolated from sick chickens. Antimicrob Agents Chemother44:421-424.
- Kihlstrom E, Andaker L (1985)Inability of gentamicin and fosfomycin to eliminate intracellular Enterobacteriaceae. J Antimicrob Chemother 15:723-728.
- Kirk M, Ford L, Glass K, Hall G (2014) Foodborne illness, Australia, circa 2000 and circa 2010. Emerg Infect Dis 20:1857-1864.
- Lanz R, Kuhnert P, Boerlin P (2003) Antimicrobial resistance and resistance genes determinants in clinical *Escherichia coli* from different animal species in Switzerland. Vet Microbiol91:73-84.
- Liljebjelke KA, Hofacre CL, White DG, Ayers S, Lee MD, Maurer JJ (2017) Diversity of antimicrobial resistance phenotypes in *Salmonella* isolated from commercial poultry farms. Front Vet Sci 4:96.
- Liu JH, Deng YT, Zeng ZL, Gao JH, Chen L, Arakawa Y,Chen ZL (2008) Coprevalence of plasmid-mediated quinolone resistance determinants QepA, Qnr, and AAC(6')-Ib-cr among 16S rRNA methylase RmtB-producing *Escherichia coli* isolates from pigs. AntimicrobAgents Chemother 52:2992-2993.
- Liu YY, Wang Y, Walsh TR, Yi LX, Zhang R, Spencer J, Doi Y, Tian G, Dong B, Huang X, Yu LF, Gu D, Ren H, Chen X, Lv L, He D, Zhou H, Liang Z, Liu, JH, Shen J (2015) Emergence of plasmid mediated colistin resistance mechanism MCR-1 in animals and human beings in China: a microbiological and molecular biological study. Lancet Infect Dis, S1473-3099(15)00424-7.
- Lynch MF, Blanton EM, Bulens S, Polyak C, Vojdani J, Stevenson J, Medalla F, Barzilay E, Joyce, K, Barrett T, Mintz ED (2009) Typhoid fever in the United States, 1999-2006. JAMA 302:859-865.
- LynchM, PainterJ, WoodruffR, BradenC (2006)Surveillance for foodborne-disease outbreaks - United States, 1998-2002. MMWR Surveill Summ10:1-42.
- Majowicz SE, Musto J, Scallan E, Angulo FJ, Kirk M, O'Brien SJ, Jones TF, Fazil A, Hoekstra R M (2010) The global burden of nontyphoidal Salmonella gastroenteritis. Clin Infect Dis 50:882-889.
- MakaŁ, Maćkiw E, Ścieżyńska H, Popowska M (2015)Occurrence and antimicrobial resistance of *Salmonella* spp. isolated from food other than meat in Poland. Ann Agric Environ Med AAEM22:403-408.
- Marks F, von Kalckreuth V, Aaby P, Adu-Sarkodie Y, El Tayeb MA, Ali M, Aseffa A, Baker S, Biggs HM, Bjerregaard-Andersen M, et al. (2017) Incidence of invasive salmonella disease in sub-Saharan Africa: a multicentre population-based surveillance study. Lancet Glob Health 5:e310.
- Maynard C, Fairbrother JM, Bekal S, Sanschagrin F, Levesque RC, Brousseau R, Masson L, Larivière S, Harel J (2003) Antimicrobial resistance genes in enterotoxigenic Escherichia coli O149:K91 isolates obtained over a 23-year period from pigs. Antimicrob Agents Chemother 47:3214-3221.
- Mshelbwala FM, Ibrahim NDG, Saidu SNA, Azeez AA, Akinduti PA, Kwanashie CN, Kadiri AKF, Muhammed M, Fagdamila IO, Luka PD (2017) Motile Salmonella serotypes causing high mortality in poultry

- farms in three Sauthwestern States of Nigeria. Vet Rec Open 4:e000247. Narváez-Bravo C, Rodas-González A, Fuenmayor Y, Flores-Rondon C, Car-
- Narvaez-Bravo C, Rodas-Gonzalez A, Fuenmayor Y, Flores-Rondon C, Carruyo G, Moreno M, Perozo-Mena A, Hoet AE (2013)Salmonella. on feces, hides and carcasses in beef slaughter facilities in Venezuela. Int J Food Microbiol 166:226-230.
- Navia MM, Ruiz J, Cespedes SJ, Vila J (2003)Detection of dihydrofolate reductase genes by PCR and RFLP. Diagn Microbiol Infect Dis 46:295-298.
- Odumosu BT, Akintimehin AR (2015)Occurrence of extended-spectrum beta-lactamase producing *Enterobacteriaceae* isolates in communal water sources in Ogun State, Nigeria. Afr J Clin Exp Microbiol16:28-32.
- Ojdana D, Sacha PB, Wieczorek P, Czaban B, Michalska A, Jaworowska J, Jurczak A, Poniatowski B, Tryniszewska E (2014)The occurrence of blaCTX-M, blaSHV, and blaTEM genes in extended-spectrum β-Lactamase-positive strains of Klebsiellapneumoniae, Escherichia coli, and Proteus mirabilis in Poland. Int J Antibiot: 93584.
- Pagani L, Dell'Amico E, Migliavacca R, D'Andrea MM, Giacobone E, Amicosante GER, Rossolini GM (2003)Multiple CTX-M-Type extended-spectrum β-lactamases in nosocomial isolates of *Enterobacteriaceae* from a hospital in northern Italy. J Clin Microbiol 41:4264-4269.
- Pande VV, Devon RL, Sharma P, McWhorter AR, Chousalkar KK (2016) Study of Salmonellatyphimurium infection in laying hens. Front Microbiol7:203.
- PerretenV, BoerlinPA (2003) New sulfonamide resistance gene (sul3) in Escherichia coli is widespread in the pig population of Switzerland. Antimicrob Agents Chemother47:1169-1172.
- Robicsek A, Strahilevitz J, Sahm D, Jacoby GA, Hooper DC (2006)qnrprevalence in ceftazidime-resistant Enterobacteriaceae isolates from the United States. Antimicrob Agents Chemother 50:2872-2874.
- Ruzauskas M, Siugzdiniene R, Klimiene I, Virgailis M, Mockeliunas R, Vaskeviciute L, Zienius D (2014) Prevalence of methicillin-resistant Staphylococcus haemolyticus in companion animals: a cross-sectional study. Ann Clin Microbiol Antimicrob13:56.
- Sandvang D, Aarestrupp FM (2009)Characterization of aminoglycoside resistance genes and Class 1 integrons in porcine and bovine gentamicin-resistant *Escherichia coli*. Microb Drug Resist6:19-27.
- Seputiene V, Povilonis J, Ruzauskas M, Pavilonis A, Suziedeliene E (2010) Prevalence of trimethoprim resistance genes in *Escherichia coli* isolates of human and animal origin in Lithuania. J Med Microbiol59:315-322.
- SwansonSJ, SniderC, BradenCR, BoxrudD, WunschmannA, RudroffJA, LockettJ,SmithKE (2007)Multidrug-resistant Salmonella enterica serotype Typhimurium associated with pet rodents. N Engl J Med356:21-28.
- Thong KL, Bakeri SA, Lai KS, Koh YT, Taib MZ, Lim VKE, Yasin RM (2004) Molecular subtyping of Salmonella enterica serovar Tshiongwe recently isolated in Malaysia during 2001-2002. Southeast Asian J Trop Med Public Health 35:92-96.
- Tietjen M, Fung DYC (1995) Salmonellae and food safety. Crit Rev Microbiol 21:53-83.
- Tirado C, Schmidt K (2001) WHO surveillance programme for control of foodborne infections and intoxications: preliminary results and trends across greater Europe. World Health Organization. J Infect43:80-84.
- Vassort-Bruneau C, Lesage-Descauses M, Martel JL, Lafont JP, Chaslus-Dancla E (1996) CAT III chloramphenicol resistance in *Pasteurella haemo*lytica and *Pasteurella multocida* isolated from calves. J Antimicrob Chemoth38: 205-213.
- Xavier BB, Lammens C, Ruhal R, Kumar-Singh S, Butaye P, Goossens H, Malhotra-Kumar S (2016) Identification of a novel plasmid-mediated colistin-resistance gene, mcr-2, in *Escherichia coli*, Belgium. Euro Surveill.21:pii=30280.
- Yan JJ, WuJJ, Ko WC,Tsai SH, ChuangCL, Wu HM, Lu YJ, Li JD (2004) Plasmid-mediated 16S rRNA methylases conferring high-level aminoglycoside resistance in *Escherichia coli* and *Klebsiella pneumoniae* isolates from two Taiwanese hospitals. J Antimicrob Chemother 54:1007-1012.
- Zhang L, Fu Y, Xiong Z, Ma Y, Wei Y, Qu X, Zhang H, Zhang J, Liao M (2018)Highly prevalent multidrug-resistant *Salmonella* from chicken and pork meat at retail markets in Guangdong, China.FrontMicrobiol9:2104.