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Chromosome-Based bla_{OXA-48}-Like Variants in *Shewanella* Species Isolates from Food-Producing Animals, Fish, and the Aquatic Environment

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ABSTRACT Carbapenems are considered last-resort antibiotics in health care. Increasing reports of carbapenemase-producing bacteria in food-producing animals and in the environment indicate the importance of this phenomenon in public health. Surveillance for carbapenemase genes and carbapenemase-producing bacteria in Dutch food-producing animals, environmental freshwater, and imported ornamental fish revealed several chromosome-based bla_{OXA-48}-like variants in *Shewanella* spp., including two new alleles, $bla_{OXA-514}$ and $bla_{OXA-515}$. Carbapenemase genes were not associated with mobile genetic elements or *Enterobacteriaceae*.

KEYWORDS carbapenemase, OXA-48, antibiotic resistance, freshwater, fish, livestock, *Shewanella*, carbapenems

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Carbapenemases are extended-spectrum β-lactamases (ESBLs) that hydrolyze carbapenems, last-line therapeutics to treat multidrug-resistant Gram-negative infections (1). Carbapenemase-producing microorganisms are increasingly reported in food-producing animals (2, 3), the food supply (4), and the environment (5, 6). These findings are fueling a debate on the hazards for public health (7, 8), and authorities have rising concerns regarding the appearance of carbapenem resistance in food animal ecosystems (9). The aim of this study is to present the results of the 2013 to 2015 carbapenemase surveillance activities in food-producing animals and environmental freshwater in The Netherlands. Since resistant organisms are not geographically restrained, we also report the results of a pilot study on imported ornamental freshwater fish from other non-European countries, increasingly reported in recent years as sources of multidrug-tolerant bacteria and associated antimicrobial resistance genes (10, 11).

A total of 4,440 fecal samples of broilers, slaughter pigs, veal calves, and dairy cows were collected in 2013 to 2015, as previously described (12). Fifty batches of imported live ornamental fish (2 fish and 1 water sample per batch) from various countries outside the European Union were sampled (from November 2014 to February 2015), together with 24 surface freshwater samples collected from eight Dutch provinces (March 2015). After enrichment, carbapenemase families bla_{KPC}, bla_{NDM}, bla_{IMP}, bla_{OXA-48}, and bla_{VIM} were detected by Check-MDR Carba (Check-Points, Wageningen, The Netherlands) as previously described (12, 13). All samples were negative for bla_{KPC}, bla_{NDM}, bla_{IMP}, and bla_{VIM}. Variants of bla_{OXA-48} were identified in 92 samples (Table 1) and confirmed by conventional PCR and sequencing (14): 7 fecal samples (0.16%), 9 surface freshwater samples (37,5%) from five Dutch provinces, and 37 ornamental fish batches (74%), of which water samples were positive (78%) more frequently than fish samples (36%).

TABLE 1 Characteristics of bla_{OXA-48}-like genes detected in Dutch freshwater and livestock, imported ornamental fish, and transport water

Gene	No. of samples	Reference	Gene homology (%)	Amino acid differences	Accession no.[b]	Source (origin/no. of samples)
$bla_{OXA-514}$	1			A201G (from OXA-416)	KU866382	Ornamental fish (Indonesia)
$bla_{OXA-515}$	1			G201S (from OXA-252)	KU866383	Freshwater (Netherlands)
bla_{OXA-48}	1	KT265183	99		KU820821	Slaughter pig
$bla_{OXA-48b}$	7	JX644945	99–100		KU820801 (*S*), KU820802 (*S*), KU820804 (*S*)	Freshwater (Netherlands)
	69		99–100		KU820811, KU820813, KU820814, KU820815, KU820816	Ornamental fish (32) fish transport water (37)
	3		100		KU820805 (*S*), KU820806 (*S*), KU820807 (*S*)	Broiler (2), veal calf (1)
$bla_{OXA-181}$	3	HM992946	100		KU820809, KU820810, KU820803 (*S*)	Ornamental fish (Colombia, 2, Singapore, 1)
$bla_{OXA-199}$	1	JN704570	99		KU820808	Ornamental fish (Congo)
	1		100		KU820819	Freshwater (Netherlands)
$bla_{OXA-252}$	1	WP_037428895	100[a]		KU820800 (*S*)	Slaughter pig
bla_{OXA-48} family	2	JX644945	99	W222G, V232G	KU820818	Slaughter pig
			99	N179I	KU820820	Broiler
Class D β-lactamase	2	JX644945	94	V21E, N28T, A33T, T104A	KU820812, KU820817	Fish transport water (Israel)

[a]Amino acid homology with OXA-252 derived from BLASTX alignment in GenBank, since no gene sequence for $bla_{OXA-252}$ is available in GenBank, as of this writing.
[b]Only representative sequences were deposited in GenBank; *S*, sequenced from *Shewanella* isolate (see also Table 2).

The most common gene variant was $bla_{OXA-48b}$, recovered from ornamental fish, fish transport water, surface freshwater, and livestock (Table 1). Different alleles showed 99% to 100% nucleotide similarity (only silent mutations) to reference genes from *Shewanella xiamenensis* (15). Alleles that showed up to four amino acid substitutions have been annotated as OXA-48 family class D β-lactamases or class D β-lactamases (<94% nucleotide similarity). Despite the high prevalence of $bla_{OXA-48b}$, other bla_{OXA-48} variants were also observed, as indicated by a BLASTX search in GenBank. $bla_{OXA-181}$ was detected in fish samples from Colombia, $bla_{OXA-199}$ was identified in freshwater from Gelderland province (The Netherlands) and ornamental fish from the Democratic Republic of Congo, and $bla_{OXA-252}$ was found in one fecal sample from a slaughter pig. Both $bla_{OXA-181}$ and $bla_{OXA-199}$ progenitors were identified in environmental isolates of *S. xiamenensis* (15, 16). Finally, bla_{OXA-48} found in a fecal sample from one slaughter pig showed close identity to bla_{OXA-48} from *K. pneumoniae* (GenBank accession no. KT265183).

Bacterial isolation was performed on ChromID Carba and ChromID OXA-48 (bioMérieux) and on His agar with 0.125 mg/liter ertapenem (9) on 12 randomly selected batches of ornamental fish, all bla_{OXA-48}-like-positive Dutch freshwater samples ($n = 9$), and livestock samples ($n = 7$), for a total of 28 samples. *Shewanella* spp. were isolated from 21 samples, whereas no OXA-producing *Enterobacteriaceae* was isolated (Table 2). Bacterial species identification by 16S rRNA and *gyrB* gene sequencing (15, 17) showed ≥98% to 100% nucleotide identity to *S. xiamenensis* or *Shewanella oneidensis* (GenBank accession no. KC765141.1 and KR732277). Isolates with <98% nucleotide identity were reported as *Shewanella* spp. PCR amplification and sequencing identified $bla_{OXA-48b}$ in all but four *Shewanella* isolates (Table 2). Nucleotide queries using BLASTX identified two genes encoding potential protein products of original sequence: (i) $bla_{OXA-514}$, found in Indonesian ornamental fish, whose putative protein displayed one amino acid difference with the protein coded by $bla_{OXA-416}$, a gene recently reported in a pediatric case of intestinal carriage of *S. xiamenensis* acquired from environmental sources (17); and (ii) $bla_{OXA-515}$, found in Dutch freshwater, whose putative protein is similar to OXA-252, except for one amino acid difference. Note that molecular detection from

TABLE 2 MICs of *Shewanella* spp. isolated in this study

Source and isolate[a]	Species	Origin	Gene	MIC (mg/liter) for[b]: CTX	CTX + CLA	CAZ	CAZ + CLA	FEP	FOX	ETP	IPM	MEM	TRM
Environmental freshwater													
W9	*S. xiamenensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	2	0.5	1
W13	*S. oneidensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	>2	2	1	≤0.5
W14	*S. oneidensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	2	1	≤0.5
W15	*S. xiamenensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	2	1	1
W16	*S. oneidensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	>2	2	0.5	≤0.5
W17	*Shewanella* spp.	Netherlands	*bla*$_{OXA-515}$[c]	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	≤0.5	2	2	0.5	≤0.5
W21	*S. xiamenensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	0.25/4	≤0.25	0.25/4	0.12	2	>2	4	4	4
Ornamental freshwater fish													
10A	*S. xiamenensis*	Indonesia	*bla*$_{OXA-514}$[d]	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	2	1	1	0.5	≤0.5
13C	*S. xiamenensis*	Israel	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	≤0.5	2	2	1	≤0.5
25B	*Shewanella* spp.	Singapore	*bla*$_{OXA-181}$[e]	≤0.25	0.12/4	≤0.25	≤0.12/4	0.12	1	2	2	1	≤0.5
32B	*S. xiamenensis*	Indonesia	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	1	0.5	≤0.5
36B	*S. xiamenensis*	Singapore	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	2	2	1	0.5	≤0.5
39B	*Shewanella* spp.	Singapore	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	0.5	2	2	1	0.5	1
45B	*Shewanella* spp.	Thailand	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	1	0.5	1
F2.1-22	*S. xiamenensis*	Indonesia	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	2	>2	4	2	2
F2.1-24	*Shewanella* spp.	Indonesia	*bla*$_{OXA-48b}$	≤0.25	0.25/4	≤0.25	0.5/4	0.12	2	>2	>16	8	4
F3.2	*Shewanella* spp.	Indonesia	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	>2	4	2	≤0.5
Slaughter pig													
1553/2014	*S. xiamenensis*	Netherlands	*bla*$_{OXA-252}$[f]	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	1	0.5	≤0.5
Broiler													
780/2015	*S. xiamenensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	0.5	≤0.12/4	≤0.06	4	1	2	1	4
1206/2015	*S. xiamenensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	≤0.06/4	≤0.25	≤0.12/4	≤0.06	1	2	1	0.5	≤0.5
Veal calf													
77/2015	*S. oneidensis*	Netherlands	*bla*$_{OXA-48b}$	≤0.25	0.12/4	≤0.25	≤0.12/4	≤0.06	1	2	2	1	1

[a]Isolates were classified as non-wild type susceptible based on EUCAST ECOFFS (www.eucast.org).
[b]CTX, cefotaxime; CLA, clavulanic acid; CAZ, ceftazidime; FEP, cefepime; FOX, cefoxitin; ETP, ertapenem; IPM, imipenem; MEM, meropenem; TRM, temocillin.
[c]Accession no. KU866383.
[d]Accession no. KU866382.
[e]Accession no. KU820803.
[f]Accession no. KU820800.

water samples was not sufficient to achieve a comprehensive investigation of the presence of *bla*$_{OXA-48}$-like genes, since *bla*$_{OXA-181}$ and *bla*$_{OXA-514}$ were detected only after bacterial isolation with selective media.

Plasmid transformation and conjugation were not successful in transferring the *bla*$_{OXA48}$-like genes from *Shewanella* spp. to *Escherichia coli* K-12 recipients, suggesting a chromosomal localization (18, 19). The genetic context of *bla*$_{OXA-48}$-like genes was investigated by PCR using primer pairs oxa48b-Fw (5′-AGCTTGATCGCCCTCGATTT-23′) and lysR-Rev (5′-CGGATAGCCATTCCGGTCTC-3′) and oxa48b-Rev (5′-TGATTTGCTCAGT GGCCGAA-3′) and c15-Fw (5′-AAGCGTACTGGGATCATGGC-3′) designed on the genome sequence of *S. xiamenensis* S4 (GenBank accession no. JX644945). A conserved genetic arrangement as observed in environmental *Shewanella* spp. was detected in all isolates (15), with *bla*$_{OXA48}$-like gene downstream of an open reading frame (ORF) coding for a pyroglutamyl peptidase I-like protein and upstream of a putative *lysR* transcriptional regulator gene. None of the *bla*$_{OXA-48}$-like genes was associated with the epidemic IncL plasmid responsible for the current OXA-48 spread (20), and association with IS*1999*, *IS*Shes2, and Tn*2013* was ruled out (data not shown) (15, 21). Since all *bla*$_{OXA-48}$-like genes were located on the chromosome of waterborne *Shewanella* spp., thought to be the progenitor of this carbapenemase family (22), and were not associated with mobile genetic elements or *Enterobacteriaceae*, they were deemed to be of environmental origin and to pose a limited public health risk.

Shewanella isolates were tested for antimicrobial susceptibility using broth microdilution (Sensititre EUVSEC 2) according to ISO 20776-1:2006 (13), and MIC values were slightly increased to ertapenem compared to those of non-OXA-48-like *Shewanella*

isolates (data not shown), with four isolates displaying reduced susceptibility to imipenem and meropenem (Table 2). Interestingly, two of these isolates (F2.1-22 and F2.1-24) were from the same fish sample, with F2.1-24 showing the highest MIC values, likely modulated by additional resistance mechanisms. Similar MIC values were already described in *S. xiamenensis* producing OXA-416 and OXA-204 (17, 23) and are commonly detected in the aquatic environment, where intrinsically resistant bacteria like *Shewanella* thrive (6). Given the absence of specific phenotypic tests, high-level temocillin resistance (MIC >64 ml/liter) has been suggested as a first step in identifying OXA-48 producers (9). According to our observations, however, this methodology is likely not applicable to environmental OXA-48 enzymes. Although recognized as β-lactamases with feeble hydrolyzing activity (16, 21), OXA-48 carbapenemases should not be undervalued due to their potential to synergize with ESBLs. *Shewanella* isolates were susceptible to other β-lactams but were often resistant to ciprofloxacin, nalidixic acid, ampicillin, tetracycline, trimethoprim, sulfonamides, and/or chloramphenicol (data not shown).

In conclusion, the prevalence of carbapenem-resistant bacteria in Dutch food-producing animals was still low, whereas they were more prevalent in environmental freshwater and imported ornamental fish. The fact that carbapenem-resistant genes were only related to naturally resistant *Shewanella* spp. and no acquired carbapenem resistance mechanism was observed places these microorganisms in a questionably relevant position in regard to human health, contrary to previous suggestions (4). Ongoing carbapenemase monitoring indicates that $bla_{\text{OXA-48}}$ variants are also present in imported consumption fish and prawns (K.T. Veldman, personal communication). Gene associations to ubiquitous aquatic bacteria that are normally undetected in antibiotic resistance surveillance programs may represent a chance to spread and potentially contribute to the resistome of other clinically relevant bacteria. The location of $bla_{\text{OXA-48}}$-like genes (on the chromosome or on mobile genetic elements) and the type of bacterial host (environmental bacteria or recognized pathogens) may largely determine the impact of this antimicrobial resistance gene on human and animal health.

Accession number(s). $bla_{\text{OXA-48}}$ (KU820821),$bla_{\text{OXA-48b}}$ (KU820801, KU820802, KU820804, KU820811, KU820813, KU820814, KU820815, KU820816, KU820805, KU820806, KU820807), $bla_{\text{OXA-181}}$ (KU820809, KU820810, KU820803), $bla_{\text{OXA-199}}$ (KU820808, KU820819), $bla_{\text{OXA-252}}$ (KU820800), $bla_{\text{OXA-514}}$ (KU866382), $bla_{\text{OXA-515}}$ (KU866383), OXA-48 family class D β-lactamases (KU820818, KU820820), class D β-lactamases (KU820812, KU820817); bla_{OXA48b}, $bla_{\text{OXA-514}}$, and $bla_{\text{OXA-515}}$ genomic surroundings (KX060561, KX060562, KX060563, KX060564), and *gyrB* (KX022127, KX022126).

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We have no conflicts of interest to declare.

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