



Transmission pathways of World Health Organization critical priority carbapenemase-producing pathogens: cross-sectoral transmission dynamics in food systems, wildlife and aquaculture

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Summary

Antimicrobial resistance (AMR) is a versatile and dynamic genetic process that transcends sectors and ecosystems, leading microorganisms to develop mechanisms to resist drugs (antibiotics and antifungal) and chemical biocides (disinfectants and agrotoxics) designed to kill them. The emergence and spread of AMR are influenced by human, animal and environmental interactions, requiring a One Health framework. Currently, AMR has the potential to be almost everywhere, with carbapenem resistance in particular emerging as the major global health concern. Carbapenem-resistant Enterobacterales are now considered by the World Health Organization (WHO) as

'critical priority pathogens', for which novel antibiotics are urgently needed. Carbapenem resistance is a challenge in clinical settings due to its rapid dissemination and limited treatment options. Although the molecular mechanisms and epidemiology of carbapenem resistance have been widely studied in clinical settings, little is known about their spread in the food chain, seafood and aquaculture, wildlife and the environment, and their associated risks to human and animal health. Therefore, integrated measures complying with the One Health approach are imperative to prevent and control the emergence and rapid spread of AMR, preserving the efficacy of clinically relevant antibiotics. It is thus highly recommended that countries follow WHO, World Organisation for Animal Health, and Food and Agriculture Organization of the United Nations recommendations to implement national action plans encompassing the human, food chain and environmental sectors to improve policies and activities addressing the prevention and containment of AMR, enabling the implementation of evidence-based approaches through sharing best practices. This review article provides a concise update on WHO critical priority pathogens in the food chain, wildlife and aquaculture worldwide, as well as cross-sectoral transmission pathways of AMR.

Keywords

Antibiotic resistance – Aquaculture – Carbapenemases – Carbapenem resistance – Food chain – One Health – Seafood – WHO critical priority pathogens – Wildlife.

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Introduction

Antimicrobial resistance (AMR) is a major global health crisis driven by the genetic versatility of microorganisms (bacteria and fungi) in developing mechanisms to resist drugs designed to kill them, resulting in therapeutic failures and the emergence of critical antimicrobial-resistant pathogens, colloquially called 'superbugs'.

AMR develops through genetic mutations and/or acquisition of resistance genes via horizontal gene transfer, favouring the spread of resistance across microbial communities. The development and spread of AMR have been accelerated by anthropogenic activities, such as overuse of antibiotics and disinfectants in healthcare, agriculture (crop and livestock production), aquaculture and the food chain. In addition, the discharge of antibiotics, biocides and other pollutants from industrial and agricultural activities into the environment has also contributed to the emergence and dissemination of resistant bacteria.

This review article will focus on World Health Organization (WHO) critical priority carbapenemase-producing pathogens for the following reasons: i) in general, carbapenemases can inactivate virtually all β -lactams, one of the largest and most widely used families of antibiotics in both human and veterinary medicine [1]; ii) genes encoding carbapenemases are often associated with genes that are resistant to other antibiotic families, which is linked to the emergence of multi- and even pan-drug-resistant microorganisms [2]; iii) the presence of multidrug resistance genes favours the co-selection of carrier microorganisms through the use of various classes of antibiotics [3]; and iv) in recent years, an alarming increase in the detection of carbapenemases in the food chain has been reported [4].

Currently, carbapenem resistance is a major global health concern due to its rapid dissemination and reduced treatment options. In fact, carbapenem-resistant Enterobacterales are now considered by the WHO as 'critical priority pathogens' for which novel antibiotics are urgently needed. Carbapenems (e.g. ertapenem, imipenem, meropenem) are broad-spectrum β -lactam antibiotics primarily used to treat severe human infections, being considered the last line of therapy for infections caused by multidrug-resistant Gram-negative bacteria, including broad-spectrum cephalosporin-resistant pathogens producing extended-spectrum β -lactamases (ESBLs).

The production of carbapenemases is the major mechanism of carbapenem resistance. Class A carbapenemases have become prevalent in Enterobacterales and include

members of the KPC, BKC and GES families. The genes encoding the class A carbapenemases are either plasmid-borne or located on the chromosome of the bacterial host. Class A carbapenemases hydrolyse penicillins, classical cephalosporins, monobactam, and imipenem and meropenem, being inhibited by clavulanate and tazobactam like other class A beta-lactamases. Class B carbapenemases are metallo- β -lactamases that require zinc to hydrolyse β -lactam antibiotics, including penicillins, cephalosporins and carbapenems, but are ineffective against monobactams and are inhibited by metal chelators such as EDTA, not by inhibitors like tazobactam and clavulanic acid. The most common families include NDM, IMP, VIM, GIM and SPM, found mainly in Enterobacterales and *Pseudomonas aeruginosa*, representing a serious AMR problem. Class D carbapenemases are serine enzymes that destroy carbapenems, subdivided into groups such as OXA-23, OXA-48 and OXA-51, causing resistance in *Acinetobacter baumannii* and *Klebsiella pneumoniae* [5].

Although the molecular characterisation and epidemiology of carbapenem resistance is highly studied in clinical settings, little is known about the occurrence of carbapenem-resistant bacteria in food-producing animals, seafood, aquaculture and wildlife as well as the associated health risks to humans. In this regard, animals have been identified as a relevant source of AMR and potential reservoirs for carbapenem-resistant bacteria, while food-borne routes and environment release through wastewater and excreta could constitute a possible transmission pathway for carbapenemase producers and carbapenem resistance genes from animals to humans.

AMR can also spill over into the environment, with resistant strains of bacteria contaminating waterways, soil and wildlife, and once wild animals become carriers of antimicrobial-resistant microorganisms, they can easily spread antimicrobial-resistant bacteria (ARB) and/or antimicrobial resistance genes (ARGs) among communities and across borders. Therefore, integrated measures complying with the One Health approach are imperative to prevent and control the emergence and rapid spread of AMR.

Transmission pathways of critical antimicrobial resistance

While critical AMR can be spread through interconnected human, animal and environmental pathways that support the One Health approach, the exposure often involves subinhibitory concentrations of antibiotics in the environment and high concentrations in healthcare settings, which exert selective pressure that favours the occurrence and predominance of resistant bacterial strains [6,7]. Specifically, AMR transmission in human populations occurs through pathways ranging from nosocomial

infections to community-based dissemination via contaminated food, water and poor hygiene practices [8-10]. Global travel and cross-border movement of resistant pathogens further complicates AMR containment efforts. Moreover, there is an inadequate understanding of how international trade in food products contributes to the global dissemination of resistance [7].

The major routes of transmission are: i) person-to-person contact, through direct physical contact, contact with contaminated surfaces and airborne droplets, mainly in healthcare facilities and dense communities; ii) the food chain, through ingestion of contaminated food products, especially undercooked meat, poultry, eggs, unpasteurised dairy, ready-to-eat vegetables and produce irrigated with contaminated water or fertilised with untreated manure; iii) water sources, through human and animal waste, agricultural runoff and pharmaceutical/hospital effluents, with exposure occurring through consuming contaminated drinking water and recreational water contact; iv) animal-to-human contact, through direct contact with infected or colonised animals, including livestock and companion animals; and v) international travel and the movement of people, animals and goods [6-12]. Overall, the primary drivers of this spread are the overuse and misuse of antibiotics in human health and agriculture, coupled with poor sanitation and infection control practices globally.

Antimicrobial resistance in the food chain: from farm to fork

In the context of AMR, the farm-to-fork continuum concept emphasises a direct connection between food producers and consumers, where the food chain is recognised as a reservoir and critical pathway for the development and spread of ARB and ARGs. These are primarily driven by the high volume of biocides (i.e. antibiotics, heavy metals and/or disinfectants) used throughout the food chain, from farming (for growth promotion, prophylaxis, metaphylaxis or treatment of sick animals) to processing, transportation, distribution, storage, retail and consumption. In this regard, in many countries, the total amount of antibiotics used in food-producing animals outweighs human consumption [13], pointing to the agricultural sector as a major contributor to AMR, with previous studies having estimated that 73% of all antimicrobials sold globally are used in livestock farming [13-15]. In 2013, the global consumption of all antimicrobials in food animals was estimated at 131,109 tons (95% confidence interval [100,812 to 190,492 tons]), and it is projected to reach 200,235 tons (95% confidence interval [150,848 to 297,034 tons]) by 2030 [13].

In the livestock and poultry sectors, the most frequently used classes of antibiotics have been tetracyclines (oxytetracycline, doxycycline), polymyxins (colistin), fluoroquinolones (enrofloxacin), penicillins (amoxicillin), cephalosporins (cefapirin, cefquinome) macrolides (tylosin, erythromycin), aminoglycosides (neomycin), trimethoprim, sulfonamides, pleuromutilin (tiamulin) and phenicols (florfenicol) [16,17]. Farmers have justified the use of these antibiotics for disease prevention and increasing productivity [17,18], in most cases without prescription [17,19].

Chemical sanitisers are also widely used in the food chain for disinfecting food processing environments, and for the transportation and storage of food [20]. Sanitisers are biocidal agents employed for microbial control and disinfection. Common sanitisers used in food processing industries include biguanides, chlorine-releasing compounds, peroxygen compounds, quaternary ammonium compounds, iodine, iodophors and alcohols [21].

Notably, run-off from intensive farming can contaminate the soil and water sources with antibiotic and chemical disinfectant residues, creating AMR hotspots in aquatic environments [22]. In addition, ESBL-producing *Escherichia coli* have been detected in rinse water and run-off water from intensive poultry farming [22].

World Health Organization critical priority Enterobacterales in the food chain

Carbapenem-resistant Enterobacterales pose an urgent threat to public health. While the use of carbapenems is restricted to food-producing animals, other β -lactams, such as amoxicillin and ceftiofur, are used in livestock.

In 2024, Choy and colleagues proposed a series of steps through which the presence of ARB or ARGs detected in food could pose a risk to human health [23]. These included the persistence of ARB or ARGs after food preparation, the infection or colonisation of humans by ARB, and the transfer of ARGs to microorganisms capable of colonising or causing infection. Furthermore, it was assumed that these infections required antibiotic treatment and that such treatment failed due to resistance [23]. Beyond these requirements, an association has been reported between the use of antibiotics in food-producing animals and the detection of *E. coli* displaying resistance to clinically relevant antibiotics, such as third- and fourth-generation cephalosporins, as a cause of invasive infections in humans [24].

Undoubtedly, the dissemination of *bla*_{CTX-M-15} ESBL genes in human health is one of the main problems related to broad-spectrum cephalosporin resistance, particularly when associated with the spread of successful pandemic clones, such as *E. coli* belonging to the sequence type (ST) ST131 [25].

Although the presence of CTX-M-15-positive bacteria, even linked to *E. coli* ST131, has been reported in food [26,27], many studies show that CTX-M-15 is a minority variant in food compared to what is found in humans. Furthermore, the mechanisms detected in isolates obtained from food are often different from those found in humans [28-30]. On the other hand, a set of ARGs frequently found in *E. coli* from food can be detected in human *Salmonella enterica* isolates, a microorganism whose natural habitat is primarily the digestive tract of animals and whose infection is, by definition, a food-borne disease. Examples include broad-spectrum β -lactam resistance genes, such as *bla*_{CMY-2}, *bla*_{CTX-M-2}, *bla*_{CTX-M-8}, *bla*_{CTX-M-14}, *bla*_{CTX-M-27}, *bla*_{CTX-M-55}, and *bla*_{CTX-M-65} [29,30,31-39].

Although the first reports of carbapenem resistance in *E. coli* and *Salmonella* spp. from food or food-producing animals date back to the early 2010s [40], this is now recognised as an emerging and highly significant issue due to its recent rise [4]. In a recent publication by the European Food Safety Authority Panel on Biological Hazards regarding the presence of carbapenemase producers in food in Europe, the main enzymes reported were VIM-1, OXA-48, OXA-181, NDM-5 and IMI-1, in that order. The report indicates that these enzymes are most frequently found in terrestrial food-producing animals, but they have also been found in aquaculture products and ready-to-eat imported foods [4].

Meanwhile, in Asia and Africa, NDM variants such as NDM-1 and NDM-5, as well as OXA-48 variants, have been the most frequently carbapenemases detected in food [41-44]. The spread of OXA-48 and NDM-1-producing *Klebsiella pneumoniae* ST48 and ST101 in chicken meat has been reported in Western Algeria [45]. Studies on carbapenemases in food in the Americas are less numerous. They report the presence of OXA-48-producing *E. coli* O25 ST131 in Georgia poultry in the United States of America [46]; IMP-27-producing Enterobacterales, including *E. coli* ST218 and *Proteus mirabilis*, recovered from the environment of a swine farrow-to-finish operation in the USA [47]; KPC-2-producing *K. pneumoniae* recovered from the stool samples of poultry in the Brazilian Amazon region [48]; and *E. coli* ST1193, *K. michiganensis* ST451 and *Enterobacter hormaechei* ST114 and ST269 clones producing KPC-2 carbapenemase in ready-to-eat vegetables in Brazil [11,49]. More recently in Brazil, carbapenemase (NDM-1)-producing *Klebsiella quasipneumoniae* ST688 and *K. michiganensis* ST40

producing KPC-2 have been isolated from food destined for hospitalised patients [50]. [Table I](#) displays the global occurrence of carbapenemase producers in food-producing animals [11,40,43,45-78].

Food safety and antimicrobial resistance: a global challenge

Just as a significant relationship has been demonstrated between antibiotic use and the emergence of resistant microorganisms in both humans and food-producing animals, there is also an association between reduced antibiotic consumption and the detection of *E. coli* strains that are fully susceptible to all antibiotics [24]. The reduction of specific resistance mechanisms associated with decreased antibiotic use in food production systems has also been reported [79]. While these findings are encouraging, for developing countries that are food producers this presents a triple challenge: systematically monitoring antibiotic use and resistance prevalence and implementing measures to reduce antibiotic use in both human health and food production.

Antimicrobial resistance in wildlife

The implications of AMR have expanded to wildlife and the ecosystems they inhabit, requiring an interdisciplinary approach. A growing body of research confirms that synanthropic and non-synanthropic wild animals, including those from remote lands of the planet, are being colonised by clinically relevant ARB [80-82]. Regarding the sources of wildlife acquisition of resistant pathogens, research highlights the proximity to anthropic environments, animal farms, landfills, contaminated water bodies and the food chain [83-89]. Once resistant pathogens are acquired, wild animals can act as reservoirs and disseminators of AMR locally or through migratory routes [90,91]. Locally, animals carrying ARB may spread them in their environment or may even be part of other animals' food in the natural food chain. Thus, predators and scavengers are thought to be more likely to carry ARB [92,93]. In this sense, wildlife are important environmental bioindicators of AMR in their environments. In turn, if one considers that certain migratory birds can travel distances of up to 90,000 km each year (as the Arctic tern), these animals become potential disseminators of ARB between different environments, countries and continents, and even between the Arctic and Antarctic poles [94,95].

ARB can be carried on the external parts of animals (e.g. feathers, hair, beak, feet and claws) or in their digestive or respiratory tract and spread elsewhere as they perch on perches or roosts, remove organic debris or engage in direct contact with other animals

[96-98]. However, several factors can influence ARB colonisation and their dissemination by animals through their migratory routes.

First, these microorganisms must be able to cross various physiological and immunological barriers and compete with the animal's native microbiota to colonise it. Once established, they must be able to persist in the face of a constant struggle and the arrival of new bacteria that also attempt to colonise this microenvironment [99]. Migratory animals may make several stops to feed and rest along their migratory route, which can lead to new bacterial colonisation and decolonisation events [100,101]. In this way, a wild animal could hypothetically be colonised by a bacterium resistant to a particular antibiotic, and the microorganism could then become susceptible through the migratory route or be replaced by another bacterium that meets the current environmental requirements.

The role of wildlife as reservoirs, disseminators and bioindicators of AMR is already well documented. However, from a conservation point of view, more research is urgently needed to understand how wildlife at both the individual and species levels are affected by the AMR crisis [74]. Wild animals with bacterial infections are admitted to wildlife rehabilitation centres, zoos and veterinary hospitals. There is a special concern for wild animals with threatened populations, in which each individual is critical to the conservation and success of its species. In this sense, therapeutic failures due to AMR often lead to the death of individuals, but these cases are poorly reported in the literature. It is important to note that bacterial resistance itself does not directly cause disease. The risk arises when AMR is associated with bacteria with certain virulent characteristics, making them pathogenic to specific animal species [102,103]. Additionally, various factors unique to each wild animal species can affect their susceptibility to certain pathogenic bacteria. Individual factors, such as overall health and the immune system's effectiveness, also play a role. In this context, sick wild animals placed in captivity often experience stress, which can lead to immunosuppression [104,105]. This weakened immune response makes them more vulnerable to diseases caused by pathogenic and opportunistic bacteria. If these bacteria are resistant, treatment options for wildlife will be even more limited. Moreover, virulence factors associated with bacterial pathogenicity have been extensively studied in humans and some domesticated animals [106]; however, there is still a significant gap in knowledge regarding these factors in wild species. Understanding these factors in wild animals could provide valuable insights into bacterial infections affecting them. Conversely, veterinary microbiologists do not have specific breakpoints for interpreting susceptibility tests in wildlife species. Although they

are an effective alternative, in some cases, using antimicrobial susceptibility interpretations from domestic animals or humans can lead to incorrect results and ultimately misguided drug decisions by veterinarians.

While acknowledging the significant role that wildlife plays within a One Health framework, wildlife is commonly not integrated into global and local AMR surveillance initiatives. Thus, to address the issue of ARB in wild animals, measures can be implemented to i) prevent the spread of ARB or ARGs in natural environments, ii) restrict access for wild animals to the primary sources of ARB or ARGs ([Fig. 1](#)), iii) minimise the selective pressure caused by the use of antimicrobials in agriculture and animal production in areas where wildlife is present and iv) improve knowledge regarding bacterial infections in wild animals.



Figure 1

Interaction of wild birds with human waste

Antimicrobial resistance can spill over into the environment, with resistant bacterial strains contaminating waterways, soil and wildlife. Once wild birds become carriers of antimicrobial-resistant microorganisms, they can easily spread antimicrobial-resistant bacteria and antimicrobial resistance genes among communities and across borders.

World Health Organization critical priority antibiotic-resistant pathogens in wildlife

Bacterial pathogens resistant to broad-spectrum antibiotics, classified as a critical priority by WHO, have successfully disseminated beyond the hospital walls and are now being identified in wildlife globally. In fact, to monitor the impact of AMR on the environment, the role of wildlife as bioindicators or sentinels has begun to be studied [107-111]. Currently, resistance to broad-spectrum cephalosporins and carbapenems is considered the main problem in One Health. Genomic surveillance of AMR has significantly improved the ability to investigate the global spread and emergence of multidrug-resistant clones of clinically relevant bacterial species circulating at the human–animal–environment interface. In this regard, several studies have confirmed the emergence of human-associated clones of *E. coli*, *K. pneumoniae*, *Acinetobacter baumannii* and *P. aeruginosa* in wildlife. Notably, *E. coli* strains producing ESBLs of the CTX-M type, and belonging to international clones ST10, ST58, ST90, ST131, ST155, ST224, ST410, ST602 and ST648, have been identified in colonised and infected animals. In addition, *K. pneumoniae* producing CTX-M and/or KPC- and NDM-type carbapenemases, belonging to ST15, ST307 and clonal group CG258 (ST11 and ST340), have emerged in wild birds, rodents and marine fauna [107,108,110-127]. [Table II](#) addresses the global occurrence of carbapenemase producers in wildlife [102,107,108,111-127].

Anthropogenic actions and accelerated urbanisation seem to contribute to this phenomenon, in which endangered species such as iconic birds (e.g. the Andean condor and Eurasian griffon vultures), whales and marine turtles are now colonised or infected by WHO critical priority pathogens genomically related to hospital bacteria ([Fig. 2](#)) [110].

Finally, because migratory animals (e.g. birds, whales, turtles) can acquire carbapenem-resistant Enterobacterales, they can potentially be disseminators of these pathogens through their migratory route. Therefore, constant monitoring of these animals is necessary to understand the dynamics of AMR dispersal in wildlife. Furthermore, it is essential to include wild animals affected by infections caused by critical priority pathogens in AMR surveillance plans or in research on alternative therapies. This is particularly crucial for endangered species, as protecting these populations helps prevent ecosystem imbalances.



Figure 2

The Andean condor, an iconic wild bird of the Andes Highlands, colonised by extremely drug-resistant *Escherichia coli*

Antimicrobial resistance in aquaculture: a public health issue with ecological implications

Aquaculture plays a key role in global food production, providing fish and other aquatic organisms for human consumption. According to the most recent data from the Food and Agriculture Organization of the United Nations, global aquaculture production reached a record 130.9 million tonnes in 2022, comprising 94.4 million tonnes of aquatic animals and 36.5 million tonnes of algae. For the first time, it accounted for 51% of total animal production, surpassing capture fisheries. About 89% of aquatic animal production was for human consumption, averaging 20.7 kg per person. Per capita consumption rose from 9.1 kg in 1961 to 20.6 kg in 2021, driven by improved supply, technology, consumer preferences and rising incomes [128].

Asia remained the dominant force in global aquaculture, accounting for 91.4% of total production. Other regions contributed smaller shares: Latin America and the Caribbean made up 3.3%, followed by Europe with 2.7%, Africa with 1.9%, North America with 0.5%

and Oceania with 0.2%. Just ten countries – the People’s Republic of China, Indonesia, India, Vietnam, Bangladesh, the Philippines, the Republic of Korea, Norway, Egypt and Chile – were responsible for 89.8% of the world’s total aquaculture output [128].

Despite advancements in farming techniques, aquaculture, like other large-scale animal production systems, remains vulnerable to the emergence of diseases that can significantly impact productivity [129]. In this regard, disease outbreaks pose a significant challenge to the profitability of farming operations [130]. Aquatic species raised in crowded and stressful conditions are particularly vulnerable to bacterial infections [131]. As a result, farmers often use antimicrobials both preventively and to treat diseases [132]. However, the excessive and improper use of these drugs is widely regarded as a primary factor contributing to the rise of AMR in aquaculture [133]. The growing resistance to medically important antimicrobials in food-borne pathogens within aquaculture is a growing concern. AMR levels in aquaculture vary by region, with higher resistance rates observed in developing countries and warmer climates [134].

Commonly used antimicrobials in aquaculture include amphenicols (florfenicol), tetracyclines (oxytetracycline), quinolones (oxolinic acid, flumequine, sarafloxacin and enrofloxacin), β -lactams (amoxicillin), macrolides (erythromycin), sulfonamides (sulfadimethoxine) and diaminopyrimidines (ormetoprim) [135]. While these antimicrobials are effective in treating infections, their overuse has been linked to the emergence of resistant strains, not only within farmed species but also in the surrounding environments [136].

The emergence of AMR in aquaculture poses direct and substantial risks to human health. Medically important antimicrobial-resistant Gram-negative and Gram-positive bacteria such as *Vibrio* spp., *Aeromonas* spp., *Pseudomonas* spp., *Streptococcus* spp. and *Escherichia coli* have been isolated from a diversity of aquaculture-raised species, including fishes, shrimps and bivalves [135]. As filter-feeding bivalves filter large volumes of water to feed, they inadvertently concentrate microbial contaminants, including AMR pathogens, in their tissues. Bivalve species that are frequently consumed raw pose an additional risk for the transmission of antimicrobial-resistant pathogens, as the absence of thermal processing prevents the inactivation of these microorganisms [136].

Human exposure to such drug-resistant pathogens may occur through the consumption of contaminated freshwater or marine species [137]. Once exposed to these bacteria, humans can be colonised in the gastrointestinal tract or acquire infections that are increasingly difficult to treat, as traditional antimicrobials become less effective [138].

In addition to direct transmission through the consumption of contaminated aquatic species, AMR in aquaculture can also spread via environmental pathways, such as wastewater effluents containing antimicrobial residues, ARB and/or ARGs, which frequently contaminate adjacent freshwater ecosystems, such as rivers [139]. Moreover, this environmental contamination is not limited to aquatic ecosystems since these bacteria can also contaminate terrestrial environments via run-off, further complicating AMR management. The persistence of these resistant bacteria in the environment enables them to evolve and spread, posing a threat not only to aquatic species but also to terrestrial wildlife and human populations.

The impact of AMR in aquaculture extends beyond human health and threatens biodiversity and ecosystem stability. The contamination of aquatic ecosystems beyond aquaculture systems may disrupt ecological balance, affecting the health of wild fish and other aquatic organisms [140]. Wild aquatic species are particularly significant in this context, as they can act as reservoirs for clinically relevant antimicrobial-resistant pathogens, which may then spread across ecosystems, further complicating the issue of AMR [141].

Given the increasing global demand for animal-derived food products, particularly from aquaculture, the pressure on aquaculture systems to meet this demand will continue to escalate. Consequently, the use of antimicrobials in aquaculture is likely to persist unless effective alternatives and more stringent regulations are implemented. Promising alternatives to antimicrobials include vaccines, probiotics and improved biosecurity measures that could help reduce the reliance on antimicrobials [140]. In parallel, investment in research to understand the environmental pathways of AMR and to develop sustainable aquaculture practices is essential to addressing this issue.

Efforts to mitigate the spread of AMR in aquaculture should also involve the enforcement of stricter regulations on antimicrobial use. Some countries have started to acknowledge the importance of controlling antimicrobial use in aquaculture production [142], but there remains a significant need for coordinated global action. Regulatory measures should focus on limiting the prophylactic use of antimicrobials and ensuring that antimicrobials are only used when necessary for treating specific infections. Enhanced surveillance systems for monitoring antimicrobial use and the prevalence of AMR in aquaculture systems will also be crucial in guiding effective interventions.

The development of improved waste management strategies is another critical component of addressing AMR in aquaculture. Proper disposal and treatment of

antimicrobial-laden wastewater and waste from aquaculture operations are vital to preventing further environmental contamination [143]. Wastewater treatment technologies should be optimised to remove antimicrobials and resistant bacteria before the effluent is released into natural water systems. Furthermore, improving farming practices, such as by reducing stocking densities and promoting more natural habitats for farmed fish, can help reduce the need for antimicrobials and minimise the spread of resistance.

Addressing AMR in aquaculture requires a comprehensive approach that integrates regulation, research and sustainable farming practices. Responsibility for managing the aquaculture supply chain should be shared by regulators, farmers, veterinarians, aquatic health experts, retailers and consumers. Leading aquaculture nations should align with global strategies to mitigate AMR. The risks posed by AMR extend beyond aquaculture, impacting human health, the environment and biodiversity. Both public and private sectors must take proactive measures to prevent AMR from escalating. Through coordinated efforts, improved management practices and the adoption of alternative methods, the aquaculture industry can reduce antimicrobial reliance and contribute to the broader fight against AMR.

World Health Organization critical priority antibiotic-resistant pathogens in aquaculture

Recently, an integrated agriculture–aquaculture system has been implemented in which fish are raised in ponds that receive agricultural drainage water [144]. In this regard, *E. coli*, members of the *Enterobacter cloacae* complex, and *K. pneumoniae* strains producing CTX-M, KPC, NDM and/or OXA-48 β -lactamases have been recovered from fishes, fishpond water inlets, tap water, outlet water, hand and faecal samples from aquaculture workers, and faecal samples from inhabitants of areas surrounding integrated agriculture–aquaculture farms, in Egypt [144]. Similarly, in India, the dissemination of carbapenem-resistant *E. coli* producing NDM-5 belonging to the high-risk clones ST167 and ST361, of clinical/livestock importance, has been reported in freshwater pond sites, gut swabs from freshwater fish (i.e. pangas [*Pangasianodon hypophthalmus*], rohu [*Labeo rohita*], mrigal [*Cirrhinus mrigala*], silver carp [*Hypophthalmichthys molitrix*], grass carp [*Ctenopharyngodon Idella*], catla [*Catla catla*] and retail fish markets [145]). In the People's Republic of China, the emergence of carbapenemase (IMI-2 or IMI-16)-producing *Enterobacter asburiae* strains belonging to ST1336 and ST1337 has been documented in fish and water samples from aquaculture

fish ponds [146]. [Table III](#) details the global occurrence of carbapenemase producers in seafood and aquaculture [144,147-162].

In wet markets, while ESBL (CTX-M)-producing *E. coli* and *K. pneumoniae* have been identified in freshwater fish (fish gut samples of snakehead fish and black carp) in HKSAR¹ [163], CTX-M-15-producing *K. pneumoniae* ST3827 has been found in native Amazonian fish (*Brachyplatystoma filamentosum*) sold in Brazil [164]. In the latter country, identification of CTX-M-positive *E. coli* ST744 and ST746 clones has been documented in wild fishes from a polluted area on the South Atlantic coast [141].

Notably, a new class A carbapenemase, VCC-1, has been identified in a nontoxicogenic *Vibrio cholerae* strain that was isolated from retail shrimp imported into Canada for human consumption. Shortly thereafter, VCC-1-producing *V. cholerae* isolates were recovered along the German coastline. Interestingly, these isolates appear to have acquired the *bla*_{VCC-1} gene independently from the Canadian isolate, suggesting that the *bla*_{VCC-1} gene is mobile and widely distributed [151,165].

In brief, in the last years, carbapenem-resistant bacteria have begun to be identified in aquatic environments, as well as in seafood, fish and water samples from aquaculture fish ponds [166,167]. Worryingly, resistance to carbapenems in bacteria identified in seafood and aquaculture, including Enterobacterales, non-fermenters and *Vibrio* spp., has been mediated by clinically relevant serine (KPC and OXA)- and metallo (NDM and VIM)- β -lactamases known to be mobilised by plasmids, while novel carbapenemases, such as VCC-1, have emerged in *V. cholerae* ([Table III](#)).

Finally, the global expansion of aquaculture and the implementation of integrated agriculture–aquaculture systems present opportunities to enhance food production worldwide. However, the increasing reliance on antimicrobial agents to manage diseases in these systems significantly contributes to the rise of AMR, posing serious threats to both human health and environmental sustainability. The issue of carbapenem resistance in aquaculture requires closer monitoring, as it is often linked to anthropogenic pollution. Additionally, the concurrent use of other antimicrobial agents and biocides

1. HKSAR: Hong Kong, Special Administrative Region of the People's Republic of China.

could accelerate the selection of carbapenem-resistant strains, exacerbating the AMR problem and complicating efforts to control its spread.

Knowledge gaps and future directions

In the last years, a higher occurrence of ARB, including carbapenemase producers, in food-producing animals and wildlife has been reported, suggesting their role in the cross-species transmission of clinically relevant bacteria and resistance genes. At the same time, agricultural systems in some countries have become increasingly intensive to supply global demands for animal protein.

Specifically, the occurrence of carbapenem-resistant bacteria in the food chain and aquaculture should be analysed cautiously, because foods derived from fish and shrimp farming may act as reservoirs of critical lineages and ARGs, which can be acquired by humans through handling or the food chain, representing a potential risk to public health.

Transmission pathways can include both direct contact with animals and the environment and indirect transmission through meat and seafood chains. In fact, food is probably the most important and neglected transmission pathway of AMR, from livestock and aquaculture, although direct evidence linking acquisition of AMR by humans through food consumption is lacking. In this respect, AMR can originate at the point of production and then be carried by animals and seafood into the food chain. ARB can also be introduced during the handling, processing, transport, storage and preparation of food products. Therefore, to assess the presumptive safety and microbiological quality of foods, in addition to estimating bacterial numbers (i.e. total coliform and *E. coli* counts) as indicators of unfavourable hygienic conditions and faecal contamination in food, the absence of WHO critical priority Enterobacterales (resistant to broad-spectrum cephalosporins and/or carbapenems) in food should be used as a microbiological standard. In 2025, the European Food Safety Authority Panel on Biological Hazards published a scientific opinion, 'Occurrence and spread of carbapenemase-producing Enterobacterales (CPE) in the food chain in the EU/EFTA', in which carbapenemase-producing Enterobacterales were reported in the food chain in 14 out of 30 European Union/European Free Trade Association countries [4]. Thus, apart from the routine monitoring of AMR in non-typhoidal *S. enterica* subsp. *enterica* serovars, *Campylobacter jejuni* and indicator commensal *E. coli*, monitoring in the European Union also includes mandatory specific monitoring of ESBL-/plasmid-mediated AmpC (pAmpC)-/carbapenemase-producing *E. coli* in caecal samples of food-producing animals and their meat products [4].

Available quantitative risk assessment data are relatively limited, and although transmission routes are described, little is known about how much the different sectors contribute to human exposure to AMR. Therefore, quantitative analysis could contribute significantly to the understanding of AMR transmission in food through risk assessment, mathematical modelling and the interpretation of genomic surveillance data. These methods could allow researchers to trace transmission routes, quantify the impact of interventions and identify key drivers in the farm-to-fork continuum [168,169]. In this regard, quantitative microbial risk assessment using mathematical and statistical techniques could estimate the probability and severity of human exposure to AMR pathogens via contaminated food products.

A specific quantitative microbial risk assessment strategy could include exposure assessment quantifying the prevalence and concentration of resistant bacteria and resistance genes at various stages of the food chain (from the farm to the consumer). Additionally, identification of hotspots in the food production process (e.g. slaughter, processing or food preparation) and food marketing, where the risk of AMR transmission is highest, could allow targeted interventions. Mathematical models for understanding transmission dynamics could help determine the relative contribution of different transmission pathways (e.g. direct contact with livestock *versus* food consumption), while by incorporating parameters like antibiotic usage rates and gene transfer rates, models can predict the potential impact and cost-effectiveness of different control strategies, such as reducing antibiotic use in livestock, on human AMR prevalence.

Use of genomic and metagenomic data analysis could be used to evaluate interventions, since these high-resolution techniques generate large amounts of quantitative data for source attribution. Indeed, quantitative analysis of genomic data could help establish the genetic relatedness of resistant strains found in animals, food and humans, providing evidence of direct transmission events [170,171]. In addition, tracking gene flow could allow for the tracking and quantification of mobile genetic elements that carry ARGs across different bacterial species and environments, which is crucial for understanding how resistance moves through the food chain. Finally, regression analysis could identify significant risk factors associated with higher AMR prevalence (e.g. specific farming practices or socio-economic conditions).

In brief, quantitative methods can provide an evidence-based foundation for policy-makers to develop and prioritise effective, knowledge-based interventions to mitigate the spread of AMR in the food supply chain [172].

Finally, widespread dissemination of AMR has been favoured by globalisation of food trade and human travel, as well as by migratory cycles of birds and wildlife crossing borders and transiently inhabiting anthropogenically polluted environments. This could be contributing to the successful dissemination of international clones, reaching parts of the world where they were not previously present.

Addressing AMR requires a multifaceted approach that integrates scientific research, policy development and global cooperation. By closing knowledge gaps in surveillance, environmental pathways and the judicious use of antimicrobials, as well as strengthening regulations and public awareness, it is possible to mitigate the impact of AMR on human health, wildlife and the environment. Future research should prioritise collaborative efforts across sectors and nations to reduce the global burden of AMR and ensure a safer, more sustainable future for all. Given the global dynamics of AMR transmission, a multisectoral and multidisciplinary approach is critical to the success of the Global Action Plan on AMR.

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Voies de transmission des agents pathogènes producteurs de carbapénémases et classés en priorités critiques par l'Organisation mondiale de la santé : dynamiques de transmission intersectorielle dans les systèmes alimentaires, chez les animaux sauvages et en aquaculture

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Résumé

La résistance aux antimicrobiens (RAM) est un processus génétique adaptatif et dynamique qui transcende les frontières sectorielles et les écosystèmes en dotant les microorganismes de mécanismes qui leur permettent de résister aux médicaments (antibiotiques et antifongiques) et aux biocides chimiques (désinfectants et agrotoxiques) conçus pour les éliminer. L'émergence et la dissémination de la RAM sont influencées par les interactions entre humains, animaux et environnement, ce qui nécessite une réponse fondée sur l'approche « Une seule santé ». À l'heure actuelle, la RAM est potentiellement ubiquiste et c'est la résistance aux carbapénèmes qui s'impose comme la préoccupation majeure de santé publique à l'échelle mondiale. Les entérobactéries résistantes aux carbapénèmes sont désormais classées par l'Organisation mondiale de la santé (OMS) dans la catégorie des « agents pathogènes de priorité critique », c'est-à-dire ceux pour lesquels il est impératif de mettre au point rapidement de nouveaux traitements antibiotiques. La résistance aux carbapénèmes constitue un défi majeur pour la clinique en raison de sa diffusion rapide et du nombre limité de solutions thérapeutiques disponibles. Si les mécanismes moléculaires et l'épidémiologie de cette résistance ont fait l'objet d'études cliniques approfondies, les connaissances demeurent limitées concernant sa propagation dans la chaîne alimentaire, dans les produits de la mer destinés à la consommation humaine et en aquaculture, chez les animaux sauvages et dans l'environnement, et certains aspects relatifs aux risques pour la santé humaine et animale associés à cette résistance restent à élucider. Ce cas de figure fait ressortir la nécessité de mettre en œuvre des mesures intégrées conformes à l'approche « Une seule santé » afin de prévenir et de maîtriser l'émergence et la propagation rapide de la RAM, tout en préservant l'efficacité des antibiotiques d'importance cruciale pour la clinique. Il est fortement recommandé aux pays de suivre les orientations de l'OMS, de l'Organisation mondiale de la santé animale et de l'Organisation des Nations Unies pour l'alimentation et l'agriculture concernant la mise en place de plans d'action nationaux couvrant les secteurs de la santé humaine, la

chaîne alimentaire et l'environnement, afin de renforcer les politiques et les activités de prévention et de maîtrise de la RAM et de faciliter la mise en œuvre d'approches fondées sur des données factuelles grâce au partage de bonnes pratiques. Les auteurs font le point sur les agents pathogènes présents à l'échelle mondiale dans la chaîne alimentaire, chez les animaux sauvages et en aquaculture parmi ceux classés en priorités critiques dans la liste actualisée de l'OMS, ainsi que sur les voies de transmission de la RAM d'un secteur à l'autre.

Mots-clés

Agents pathogènes classés en priorités critiques par l'OMS – Aquaculture – Carbapénémases – Chaîne alimentaire – Faune sauvage – Produits de la mer – Résistance aux antibiotiques – Résistance aux carbapénèmes – Une seule santé.

Vías de transmisión de los patógenos productores de carbapenemasas de prioridad crítica según la Organización Mundial de la Salud: dinámica de transmisión intersectorial en los sistemas alimentarios, la fauna silvestre y la acuicultura

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Resumen

La resistencia a los antimicrobianos (RAM) es un proceso genético versátil y dinámico que trasciende los sectores y ecosistemas, permitiendo que los microorganismos desarrollen mecanismos de resistencia a fármacos (antibióticos y antifúngicos) y biocidas químicos (desinfectantes y agrotóxicos) elaborados para eliminarlos. Las interacciones entre humanos, animales y el medio ambiente influyen en la aparición y propagación de la RAM, por lo que es necesario implementar el enfoque «Una sola salud». En la actualidad, es posible que la RAM esté presente prácticamente en todas partes, y la resistencia a los carbapenémicos, en particular, se está convirtiendo en la principal preocupación sanitaria a nivel mundial. La Organización Mundial de la Salud (OMS) considera a las Enterobacterales resistentes a los carbapenémicos como «patógenos de prioridad crítica», que implican la necesidad de desarrollar urgentemente nuevos antibióticos. La resistencia a los carbapenémicos representa un reto en el ámbito clínico debido a su rápida diseminación y a las opciones de tratamiento limitadas. Aunque los mecanismos moleculares y la epidemiología de la resistencia a los carbapenémicos se han estudiado ampliamente en el ámbito clínico, se sabe poco sobre su propagación en la cadena alimentaria, los mariscos y la acuicultura, la fauna silvestre y el medio ambiente, así como los riesgos asociados para la salud humana y la sanidad animal. Por consiguiente, es fundamental adoptar medidas integradas conformes con el enfoque «Una sola salud» para prevenir y controlar la aparición y la rápida propagación de la RAM, y así preservar la eficacia de los antibióticos clínicamente significativos. Así pues, se recomienda encarecidamente a los países que sigan las recomendaciones de la OMS, la Organización Mundial de Sanidad Animal y la Organización de las Naciones Unidas para la Alimentación y la Agricultura de implementar planes de acción nacionales que abarquen los sectores humano, de la cadena alimentaria y medioambiental, con el fin de mejorar las políticas y actividades destinadas a la prevención y contención de la RAM, lo que permitirá aplicar enfoques basados en pruebas a través del intercambio de buenas prácticas. En este artículo de revisión, se presenta una breve actualización sobre los patógenos de prioridad crítica de la OMS en la cadena alimentaria, la fauna

silvestre y la acuicultura en todo el mundo, así como sobre las vías de transmisión intersectoriales de la RAM.

Palabras clave

Acuicultura – Cadena alimentaria – Carbapenemasas – Fauna silvestre – Mariscos – Patógenos de prioridad crítica de la OMS – Resistencia a los antibióticos – Resistencia a los carbapenémicos – Una sola salud.

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Table I

Global occurrence of carbapenemase producers in food-producing animals

Country	Bacterial species	Carbapenemase	Source	Year	References	
France	<i>A. baumannii</i>	OXA-23	Cattle dairy (faeces)	2010	[51]	
Germany	<i>E. coli</i> , <i>S. Infantis</i>	VIM-1	Pig farm	2011–2012	[40,52]	
	<i>S. Infantis</i>	VIM-1	Sick piglet	2015–2016	[53]	
	<i>Acinetobacter</i> spp.	OXA-23	Cattle calves	2014	[54]	
Italy	<i>E. coli</i>	OXA-181	Pig (faeces)	2016	[55]	
	<i>E. coli</i>	OXA-181, OXA-48	Pig fattening	2021	[56]	
	<i>E. coli</i>	OXA-181	Cattle (faeces)	2021	[56]	
Spain	<i>E. coli</i>	NDM-1	Cattle (faeces)	2020	[57]	
People's Republic of China	<i>A. lwoffii</i>	NDM-1	Poultry (faeces)	2010	[58]	
	<i>A. baumannii</i>	NDM-1	Pig (lung)	2011–2012	[59]	
	<i>E. coli</i>	NDM-5	Pig (faeces)	2015	[60]	
	<i>E. coli</i>	NDM	Chicken (faeces)	2015–2021	[43]	
	–	NDM, VIM, KPC	Broiler, layer, pig feedlot samples	2016–2019	[61]	
	<i>K. pneumoniae</i>	NDM-5	Cattle dairy (milk, faeces)	2015	[62]	
	<i>K. pneumoniae</i> , <i>E. coli</i> , <i>Morganella</i> spp., <i>A. faecalis</i> , <i>P. putida</i>	NDM-1, NDM-5, NDM-9	Poultry (faeces)	2017–2018	[63]	
	<i>P. mirabilis</i>	NDM-1	Chicken (faeces)	2018, 2019	[64,65]	
	Egypt	<i>K. pneumoniae</i>	KPC, NDM, OXA-48	Broiler poultry farming	2014	[66]
		<i>E. coli</i>	NDM-1, NDM-5	Retail chicken carcasses, poultry, slaughterhouses, butcher shops	2017	[67]
<i>P. mirabilis</i>		KPC, NDM-1	Duck farm	2020	[68]	
<i>E. coli</i>		OXA-48, OXA-181	Dairy cattle (faeces)	2014	[69]	
<i>P. aeruginosa</i>		KPC, OXA-48, NDM	Buffaloes, cattle farms	2019	[70]	
India	<i>E. coli</i>	NDM-5	Cattle (milk)	2012	[71]	
	<i>E. coli</i>	VIM	Cattle (faeces)	2013–2014	[72]	
Pakistan	<i>A. baumannii</i>	OXA-23, NDM-1, IMP	Cattle	2022	[73]	
Algeria	<i>E. coli</i>	NDM-5	Cattle (milk)	2015	[74]	
	<i>K. pneumoniae</i>	OXA-48, NDM-1	Chicken meat	2017	[45]	

Country	Bacterial species	Carbapenemase	Source	Year	References
Malaysia	<i>E. coli</i>	NDM, OXA-48, IMP	Chicken (faeces), chicken meat	2022	[75]
South Africa	<i>E. coli</i> , <i>K. pneumoniae</i> , <i>P. mirabilis</i> , <i>Salmonella</i> spp.	KPC, NDM, GES, OXA-48, VIM, OXA-23	Cattle (faeces)	2020	[76]
Tunisia	<i>E. coli</i>	OXA-48, IMP	Cattle	2023	[77]
United States of America	<i>E. coli</i> , <i>P. mirabilis</i> , <i>M. organii</i> , <i>P. rettgeri</i> , <i>P. vulgaris</i> , <i>E. cancerogenus</i> , <i>C. braakii</i> , <i>E. cloacae</i> , <i>Citrobacter</i> spp., <i>C. farmeri</i> , <i>C. koseri</i> , <i>K. oxytoca</i>	IMP-27	Pig (faeces)	2015–2017	[47]
	<i>K. pneumoniae</i>	KPC-2	Cattle	2018	[78]
	<i>E. coli</i>	OXA-48	Broiler chickens	2025	[46]
Brazil	<i>K. pneumoniae</i>	KPC-2	Poultry faeces	2020	[48]
	<i>E. coli</i>	KPC-2	Ready-to-eat vegetables		[11]
	<i>K. michiganensis</i> , <i>E. hormaechei</i>	KPC-2	Ready-to-eat vegetables and beef	2022	[49]
	<i>K. quasipneumoniae</i> , <i>K. michiganensis</i>	NDM-1, KPC-2	Ready-to-eat vegetables	2023	[50]

<i>A. baumannii</i> :	<i>Acinetobacter baumannii</i>	<i>K. michiganensis</i> :	<i>Klebsiella michiganensis</i>
<i>A. faecalis</i> :	<i>Alcaligenes faecalis</i>	<i>K. oxytoca</i> :	<i>Klebsiella oxytoca</i>
<i>A. lwoffii</i> :	<i>Acinetobacter lwoffii</i>	<i>K. pneumoniae</i> :	<i>Klebsiella pneumoniae</i>
<i>C. braakii</i> :	<i>Citrobacter braakii</i>	<i>K. quasipneumoniae</i> :	<i>Klebsiella quasipneumoniae</i>
<i>C. farmeri</i> :	<i>Citrobacter farmeri</i>	<i>M. organii</i> :	<i>Morganella organii</i>
<i>C. koseri</i> :	<i>Citrobacter koseri</i>	<i>P. aeruginosa</i> :	<i>Pseudomonas aeruginosa</i>
<i>E. cancerogenus</i> :	<i>Enterobacter cancerogenus</i>	<i>P. mirabilis</i> :	<i>Proteus mirabilis</i>
<i>E. cloacae</i> :	<i>Enterobacter cloacae</i>	<i>P. putida</i> :	<i>Pseudomonas putida</i>
<i>E. coli</i> :	<i>Escherichia coli</i>	<i>P. rettgeri</i> :	<i>Providencia rettgeri</i>
<i>E. hormaechei</i> :	<i>Enterobacter hormaechei</i>	<i>P. vulgaris</i> :	<i>Proteus vulgaris</i>
		<i>S. infantis</i> :	<i>Salmonella infantis</i>

Table II

Global occurrence of carbapenemase producers in wildlife

Country	Bacterial species (ST)	Carbapenemase	Source	Year	References
Germany	<i>S. Corvallis</i> (ST1541)	NDM-1	Black kite	2012	[112]
Australia	<i>K. pneumoniae</i> (ST1735)	IMP-26	Silver gulls	2012	[113]
	<i>C. freundii</i>	IMP-38			[113]
	<i>E. coli</i> , <i>K. georgiana</i> , <i>K. aerogenes</i> , <i>E. cloacae</i> , <i>E. fergusonii</i> , <i>K. pneumoniae</i> , <i>C. braakii</i> , <i>P. mirabilis</i> , <i>P. penneri</i>	IMP-4			[111,113,114]
	<i>Klebsiella</i> spp.	IMP-26			[114]
	<i>Citrobacter</i> spp.	IMP-38			[114]
United States of America	<i>K. pneumoniae</i> (ST258)	KPC-2	American crows	2012	[115]
	<i>E. bugandensis</i>	IMI-1			
	<i>K. quasipneumoniae</i> (ST2712)	KPC-2	White-tailed deer	2018	[116]
United States of America (Alaska)	<i>E. coli</i> (ST38)	OXA-48	Gulls	2016	[117]
	<i>E. coli</i> (ST38, ST410)	OXA-48	Gulls	2019–2020	[107]
	<i>E. coli</i> (ST410)	KPC-2			
	<i>E. coli</i> (ST4450)	NDM-5	White-tailed deer	2019	[116]
Brazil	<i>A. baumannii</i>	OXA-72	White-faced whistling-duck and zoo birds	2012	[118]
	<i>P. aeruginosa</i>	SPM-1	White-faced whistling-duck	2012	[119]
	<i>C. portucalensis</i>	NDM-1	Olive ridley sea turtle	2017	[102]
	<i>E. coli</i>	NDM-1	Magellanic penguin	2019	[120]
	<i>E. coli</i> (ST162)	NDM-1	Pygmy sperm whale	2020	[108]
	<i>E. coli</i>	KPC	Trafficked Psittaciformes	2020	[121]
France	<i>E. coli</i>	VIM-1	Yellow-legged gulls	2012	[114]
	<i>V. cholerae</i>	VIM-1 + VIM-4		2013	[122]

Country	Bacterial species (ST)	Carbapenemase	Source	Year	References																																										
Spain	<i>E. coli</i>	KPC-2, VIM-1	Yellow-legged gulls	2014	[114]																																										
	<i>E. coli</i> (CC10, ST98)	NDM-1, NDM-5	Yellow-legged gull, lesser black-backed gull	2018	[107]																																										
	<i>K. pneumoniae</i> (ST15)	OXA-48																																													
	<i>E. coli</i> (ST10, ST34, ST38, ST410, ST540, ST641, ST744, ST1415, ST8489)	VIM-1, KPC-2, OXA-48, OXA-245, NDM-1																																													
Tunisia	<i>K. pneumoniae</i> (ST11, ST147, ST307, ST392, ST512)	OXA-48, OXA-245, KPC-2, KPC-3, NDM-1																																													
	<i>E. coli</i> (ST38)	OXA-48	Gulls	2019	[117]																																										
	<i>K. oxytoca</i>	KPC-2	Black-winged stilt	2014	[123]																																										
	<i>E. fergusonii</i>	KPC-3	Cattle egret																																												
Algeria	<i>E. coli</i>	KPC-2																																													
	<i>P. putida</i>	VIM-2	Pigeons	2021–2023	[124]																																										
	<i>E. coli, K. pneumoniae</i>	OXA-48	Wild boars	2014–2016	[114]																																										
	<i>E. coli</i>	OXA-48	White stork	2015	[114]																																										
Republic of Türkiye	<i>E. coli</i>	OXA-48	Pigeon	2019	[125]																																										
	<i>E. coli</i> (ST38)	OXA-48	Yellow-legged gull	2015	[117]																																										
	<i>E. coli</i> (ST38, ST10347)	OXA-48, KPC-2	Yellow-legged gull	2015	[107]																																										
Greece	<i>Citrobacter</i> spp.	KPC-2 + OXA-48																																													
Ireland	<i>E. coli</i>	NDM	Caspian gull	2019–2021	[126]																																										
Pakistan	<i>E. coli</i>	OXA-181	Mute swans	2022	[127]																																										
Ukraine	<i>E. coli</i> (ST167, ST361, ST405, ST1702)	NDM-5	Black kite	2019	[107]																																										
Chile	<i>K. pneumoniae</i> (ST395)	NDM-1	Caspian gull	2019	[107]																																										
	<i>E. coli</i> (ST69, ST345, ST744, ST1178)	NDM-5	Franklin's gull	2020	[107]																																										
	<i>K. pneumoniae</i> (ST873)	KPC-2																																													
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Table III

Global occurrence of carbapenemase producers in seafood and aquaculture

Country	Bacterial species	Carbapenemase	Source	Year	References
Algeria	<i>A. baumannii</i>	OXA-23	Fish	2012	[147]
Canada	<i>Pseudomonas</i> spp.	VIM-2	Squid	2014	[148]
	<i>S. maltophilia</i>	OXA-48	Seafood medley (squid, octopus, mussels and shrimp imported from PR China)	2015	[149]
	<i>M. odoratimimus</i>	OXA-48	Clams (imported from PR China)		
	<i>P. putida</i>	OXA-48	Squid (imported from the Republic of Korea)		
	<i>E. cloacae</i> , <i>K. aerogenes</i>	IMI-1, IMI-2, NDM-1	Shrimp (imported from Vietnam and Bangladesh), clam (imported from Vietnam)	2015	[150]
	<i>V. cholerae</i>	VCC-1	Shrimp (imported from India)	2014	[151]
Tunisia	<i>E. coli</i>	KPC-3	Mussels	2015	[152]
	<i>A. baumannii</i>	OXA-23	Mussel, oyster	2015–2016	[153]
Germany	<i>E. coli</i>	VIM-1	Venus clam	2016	[154]
People's Republic of China (PR China)	<i>V. alginolyticus</i>	VIM-1	Shrimp	2016	[155]
	<i>V. alginolyticus</i>	VMB-1	Shrimp	2016	[156]
	<i>V. diabolicus</i>	VMB-2	Shrimp	2020	[157]
	<i>V. alginolyticus</i>	VAM-1	Shrimp	2016	[158]
	<i>S. indica</i>	NDM-1	Shrimp	2023	[159]
	<i>S. chilikensis</i>	NDM-1			
	<i>S. algae</i>	NDM-1			

	<i>V. fluvialis</i>	NDM-1			
	<i>E. coli</i>	NDM-5			
The Netherlands	<i>E. cloacae</i> complex	IMI-2, FLC-1	Shrimp (imported from India)	2017	[160]
India	<i>K. pneumoniae</i> , <i>E. coli</i>	NDM-1, NDM-2, NDM-5	Fish, retail seafood	2018	[161]
France	<i>V. parahaemolyticus</i>	NDM-1	Shrimp (imported from Vietnam)	2016	[162]
Egypt	<i>E. coli</i> , <i>E. cloacae</i> complex, <i>K. pneumoniae</i>	OXA-48, NDM, KPC	Fish	2020	[144]

<i>A. baumannii</i> :	<i>Acinetobacter baumannii</i>	<i>S. algae</i> :	<i>Shewanella algae</i>
<i>E. cloacae</i> :	<i>Enterobacter cloacae</i>	<i>S. chilikensis</i> :	<i>Shewanella chilikensis</i>
<i>E. coli</i> :	<i>Escherichia coli</i>	<i>S. indica</i> :	<i>Shewanella indica</i>
<i>K. aerogenes</i> :	<i>Klebsiella aerogenes</i>	<i>S. maltophilia</i> :	<i>Stenotrophomonas maltophilia</i>
<i>K. pneumoniae</i> :	<i>Klebsiella pneumoniae</i>	<i>V. alginolyticus</i> :	<i>Vibrio alginolyticus</i>
<i>M. odoratimimus</i> :	<i>Myroides odoratimimus</i>	<i>V. cholerae</i> :	<i>Vibrio cholerae</i>
<i>P. putida</i> :	<i>Pseudomonas putida</i>	<i>V. diabolicus</i> :	<i>Vibrio diabolicus</i>
		<i>V. fluvialis</i> :	<i>Vibrio fluvialis</i>