Aerotolerance of *Campylobacter* spp. in food chain: a meta-analysis on the prevalence and a systematic review on the persistence, genetic relatedness, and risk to humans

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Abstract

Campylobacter spp. are the bacterial pathogens that cause gastrointestinal illness in humans, and were once asserted to be a microaerophile and unable to survive aerobically. In recent decades, aerotolerant *Campylobacter* spp. have been reported in the food chain. This review aims to obtain information on the aerotolerant *Campylobacter* spp., highlighting the prevalence, persistence, genetic relatedness, and risk to humans. After screening, the findings of 39 articles (12 articles for meta-analysis) were synthesized. High pooled prevalence of aerotolerant *Campylobacter* spp. (75.9%) from meta-analysis indicated the elevated risk of human campylobacteriosis. *Campylobacter* spp. with a higher aerotolerance level survived better against environmental stresses, including atmospheric, chemical antimicrobial agents, temperature, and osmotic conditions. The situation worsens with reported aerobic growth of *Campylobacter* spp. The sequence type (ST) of *Campylobacter* spp. had a statistically significant ($P < 0.001$) influence on aerotolerance level, suggesting that future studies would be able to postulate the aerotolerance level based on the determined ST. Aerotolerant *Campylobacter* spp. might pose an increased risk to humans because of their prevalence and persistence in a food chain, possible greater antibiotic resistance, and higher frequency of virulence genes. This underscores the potentially elevated medical burden of this pathogen.

Keywords: *Campylobacter jejuni*; *Campylobacter coli*; meta-analysis; survival; food safety risk; antibiotic resistance

Introduction

Since 2005, *Campylobacter* spp. have been reported as the most common gastrointestinal bacterial pathogen in the European Union (EU), accounting for 148,181 incidences of human campylobacteriosis in 2023 (European Food Safety Authority [EFSA] and European Centre for Disease Prevention and Control [ECDC],

2024). *Campylobacter* spp. affect more than 1.5 million people annually in the United States (Centers for Disease Control and Prevention [CDC], 2024). *Campylobacter jejuni* (*C. jejuni*) contributes around 90% of the human campylobacteriosis cases, while *Campylobacter coli* (*C. coli*) accounts for approximately 10% (EFSA and ECDC, 2024; Ministry of Health Singapore, 2025). Abdominal cramping, fever, and diarrhea with or without bloody stool are the clinical symptoms of campylobacteriosis, and commonly, these are indistinguishable from other bacterial gastrointestinal illnesses (Baek *et al.,* 2024; Iversen *et al.,* 2024; Kelly and Hodges, 2024). Symptoms may persist for 3–10 days, with an incubation period of 1–11 days (Myintzaw *et al.,* 2023). Campylobacteriosis leads to sodium malabsorption syndrome, the severity of which depends on the type of strain and patient's immune status (Bücker *et al.,* 2018; Imbrea *et al.,* 2024). However, on some occasions, post-infectious sequelae may develop, such as Miller Fisher syndrome (MFS), Guillain–Barré syndrome (GBS), reactive arthritis, and intestinal tract chronic inflammatory conditions, with a latent period of weeks or more (Backert *et al.,* 2017; Heimesaat *et al.,* 2023; Keithlin *et al.,* 2014).

In an oxygen requirement and tolerant study conducted by Kaakoush *et al.* (2007), *C. jejuni* was classified as an obligate microaerophile. It was purported that the microaerophilic propensity of *Campylobacter* spp. is adapted to low oxygen concentration in the avian gut (Park, 2002). *Campylobacter* spp. grow in microaerobic conditions, with oxygen concentration ranging from 2.5% to 15%, compared to the atmospheric oxygen level of 21% (Haines *et al.,* 2011; Kaakoush *et al.,* 2007; Lynch *et al.,* 2011). As *Campylobacter* spp. are transmitted from animals to humans zoonotically through food, the survivability of the pathogen outside host animal against environmental stress is crucial for its transmission to humans (Begley and Hill, 2015). Aerobic tolerance (aerotolerance) is a key survival mechanism for *Campylobacter* spp. in the food industry, where the oxygen level is high for the survival of pathogens (ca. 21%) (Kim *et al.,* 2019). Aberrant aerotolerant *Campylobacter* spp. have been increasingly reported in various meats and viscera, including chicken meat, duck meat, turkey, pork, chicken livers, chicken gizzards, and beef livers (Guk *et al.,* 2021; Karki *et al.,* 2018; Oh *et al.,* 2015a; Song *et al.,* 2020). Aerotolerance levels of *Campylobacter* spp. can be classified into aero-sensitive (OS, did not survive after 12 h of aerobic incubation), aerotolerant (AT, survived after 12 h of aerobic incubation), and hyperaerotolerant (HAT, survived after 24 h of aerobic incubation) (Oh *et al.,* 2015a). This review aims to compile information on AT *Campylobacter* spp. in terms of prevalence, environmental persistence, genetic relatedness, and the potential risks for humans.

Methodology

Search structure and strings applied

The search steps were completed using the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) guidelines (Page *et al.,* 2021). The search was conducted in five electronic bibliographic databases, such as Scopus, Web of Science, PubMed, Scielo, and ProQuest, to increase the chance of identifying all potentially relevant articles. The date of the search was 10 January 2025. The search string used in Scopus, Web of Science, PubMed, and ProQuest was aerotoleran* AND campylobacter, while the search string used in Scielo was (Aerotolerance) OR (Aerotolerant) AND (Campylobacter). Figure 1 depicts the scheme of the study design describing the systematic review and meta-analysis based on PRISMA. The systematic review and meta-analysis protocol is not registered in any platform.

Eligibility criteria

Inclusion criteria

The inclusion criteria considered articles linking *Campylobacter* spp. to aerotolerance. No limitations were imposed on geographic location and sample size. Only peer-reviewed research articles published in English were included.

Exclusion criteria

The exclusion criteria barred all articles published before 1991, as studies prior to this year might not have accurately reported the true *Campylobacter* spp. (Vandamme *et al.,* 1991, 1992). Further, articles that lack full text were also excluded. In addition, despite aerotolerance closely pertaining to oxidative stress, studies related to oxidative stress without descriptions on the aerotolerance phenotype were outside the remit of this study. Moreover, articles that reported the prevalence of AT *Campylobacter* spp. were excluded when the sample size was less than 30 (Je *et al.,* 2024).

Screening process

Records were imported into Rayyan, and duplicates were removed (Ouzzani *et al*., 2016). Articles were then screened by comparing the inclusion and exclusion criteria on both title and abstract. Next, full-text articles were assessed for relevance. After reviewing the bibliography of the articles included, additional eligible studies were included. Based on the content of the included articles, several subtopics that built the body of this manuscript were synthesized as shown in Figure 1.

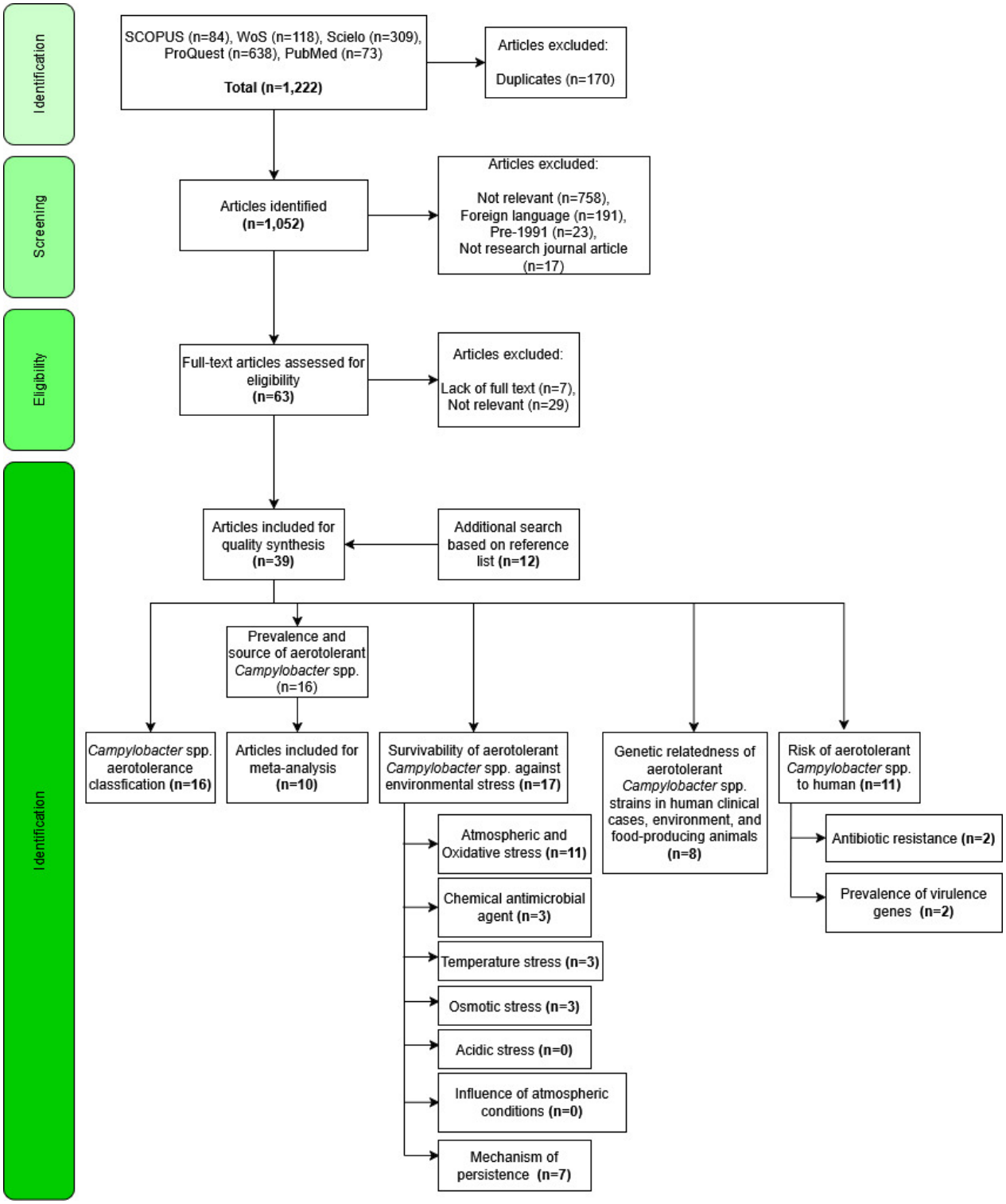

Figure 1. The scheme of study design describes the systematic review based on the PRISMA guidelines.

Two co-authors screened the articles independently based on the aforementioned inclusion/exclusion criteria. The included and excluded articles were based on the agreement between the two co-authors. When the agreement was not met, the final decision was made by the third co-author.

Risk of Bias Assessment (quality assessment)

The quality assessment tool for *in vitro* studies (QUIN tool) was adapted from Sheth *et al.* 2024. The QUIN tool allows researchers to assess the quality and risk bias of the

included studies. The QUIN tool in this study consists of eight applicable criteria, as shown in Table S1. Each criterion was scored as follows: two points when adequately specified, one point when inadequately specified, and zero point when not specified. The scoring guidelines grade the study into high risk of bias (<50%), medium risk of bias (50–70%), and low risk of bias (>70%), by the following formula:

$$\text{Score} = \frac{\text{Total score}}{2 \text{ x number of criteria applicable}} \times 100\%$$

Meta-analysis

A proportional meta-analysis on the prevalence of AT *Campylobacter* spp. isolates was conducted with the Comprehensive Meta-Analysis software version 3.7 (Biostat Inc., Englewood, NJ, USA) (Borenstein, 2022). The proportion of AT *Campylobacter* spp. in this meta-analysis comprised both HAT and AT isolates. Prevalence with a 95% confidence interval (95% CI) was quantified based on the total sample and the corresponding positive number. Forest plots were constructed to illustrate the prevalence of individual studies along with the pooled estimate within 95% CI. Random-effect model was employed to account for both sampling error (within-study variance) and statistical heterogeneity (between-study variance) (Kanters, 2022). Heterogeneity was assessed using Cochran's *Q* statistic and I^2 inconsistency index. The estimated pooled prevalence can be inflated if many of the included studies have no events and have relatively low sample sizes (Churchill *et al.,* 2019). Thus, meta-analyses were limited to the studies with a minimum sample size of 30 (Je *et al.,* 2024).

Meta-regression and *a priori* subgroup meta-analysis were conducted to assess the potential reasons for between-study heterogeneity. Prevalence estimates were compared with three potential moderator variables (subgroups): source of AT *Campylobacter* spp. isolates (chicken, duck, and humans), species of AT *Campylobacter* spp. (*C. jejuni* and *C. coli*), and aerotolerance level of *Campylobacter* spp. (HAT and AT). Subgroup meta-analysis was performed if more than two studies were obtained in each subgroup (Plishka *et al.,* 2021). In the subgroup of the source of AT *Campylobacter* spp. isolates, organs, feces, and meat samples were regrouped and analyzed based on their respective animal sources. In addition to the above-mentioned moderators, the potential covariates, including the publication year and location, were assessed with meta-regression.

Publication bias was assessed with the funnel plot, Egger's weighted regression test, and fail-safe N test (Egger *et al.,* 1997; Rothstein *et al.*, 2005). An asymmetric funnel plot provides visual judgment for publication bias (Borenstein *et al.,* 2009). Egger's test is a statistical test to discover funnel plot asymmetry (van Enst *et al.,* 2014). The fail-safe N test computes the number of missing studies (*N*) required to incorporate meta-analysis before the *P* value becomes nonsignificant (Rosenthal, 1979). If the $N > 5k + 10$, where *k* is the number of studies incorporated in the meta-analysis, the robustness of the meta-analysis can be assured (Rosenthal, 1979).

Statistical analysis

An alluvial plot illustrated the overview of *Campylobacter* spp. isolates with different levels of aerotolerance from several sources studied against environmental stresses was generated using the Origin 2023b (OriginLab Corporation, MA, USA). Ordinal logistic regression was performed to investigate the relationship between *Campylobacter* spp. sequence type (ST) and aerotolerance level with the Minitab 19 statistical software (Minitab, LLC, PA, USA). Radial graphs of clonal complexes (CC) and ST of *C. jejuni* and *C. coli* with different aerotolerance levels were illustrated with the Flourish platform (https://doi.org/flourish.studio/).

Results and Discussion

Characteristics of articles and risk of bias

In all, 1,222 articles were retrieved from SCOPUS, Web of Science, Scielo, ProQuest, and PubMed. After screening, 39 peer-reviewed articles were included in this review. In the screening of the title and abstract, 989 articles were excluded (758 studies were not relevant, 191 studies were in a foreign language, 23 studies were pre-1991, and 19 studies were not research journal articles). During full-text assessment, 7 articles were excluded due to the lack of full text, and 20 articles that were not relevant were eliminated. Next, 10 studies were included after an additional search based on the reference list. All studies included in the pooled analysis reported positive samples for AT *Campylobacter* spp.

The included studies were synthesized into several sub-topics: 16 studies for Section "*Campylobacter* spp. aerotolerance classification", 16 studies for Section "Prevalence and source of aerotolerant Campylobacter spp.", 17 studies for Section "Survivability of aerotolerant Campylobacter spp. against environmental stress", 8 studies for Section "Genetic relatedness of aerotolerant Campylobacter spp. strains", and 11 studies for Section "Risk of aerotolerant Campylobacter spp. to humans", as demonstrated in Figure 1. As shown in Table S1, most studies were considered to have a low risk of bias (>70%), and only one study was identified with a medium risk of bias (68.75%).

Aerotolerant *Campylobacter* spp. were first reported in the 1970s (Hanna *et al.,* 1983; Neill *et al.,* 1979). The genus *Arcobacter* was first proposed in 1991 based on nucleic acid hybridization and other molecular studies of AT *Campylobacter* (Vandamme *et al.,* 1991). *Arcobacter* species were distinguished from the true *Campylobacter* spp. by their capability to grow between 15°C and 30°C and their aerotolerance properties (Vandamme *et al.,* 1991, 1992). From that, *Campylobacter cryaerophila* and *Campylobacter butzleri* were proposed to be classified under *arcobacter* (Vandamme *et al.,* 1991, 1992).

Campylobacter spp. aerotolerance classification

In total, 16 studies classified *Campylobacter* spp. isolates based on the level of aerotolerance, while 14 studies investigated *C. jejuni*, and 5 studies investigated *C. coli* as shown in Table 1. The majority of studies referenced Oh *et al.* (2015a), probably because of its simplicity and clear-cut aerotolerance classification. From that, aerotolerance levels of *C. jejuni* were classified after aerobic incubation in Mueller Hinton (MH) broth with shaking at 200 revolutions per minute (rpm) at 42°C into OS (did not survive after 12 h), AT (survived after 12 h), and HAT (survived after 24 h) (Oh *et al.,* 2015a). The term 'intermediate aerotolerant' was adopted by Pokhrel *et al.* (2023) for AT. In comparison, Lee *et al.* (2019) classified AT *C. jejuni* with survival after 120 h under 500 rpm aerobic shaking at 37°C. Furthermore, Jones *et al.* (1993) and Shagieva *et al.* (2021) classified *C. jejuni* as aerotolerant if colonies grew after aerobic incubation at 37°C or 42°C, respectively. Although Chynoweth *et al.* (1998) did not classify aerotolerance in their study, the ability of *C. jejuni* to grow aerobically on an agar plate was reported and was regarded as aerotolerant in this review.

While the majority of the researchers adopted the method reported by Oh *et al.* (2015a), the protocol did not specify details, such as the surface-to-volume ratio of MH broth during aerobic incubation. Aerotolerance study in *Campylobacter* spp. is relatively new. Thus, a standardized method for determining the level of aerotolerance is crucial for inter-laboratory comparison, which may consider the following aspects: (1) growth phase of the inoculating culture (after certain hours of incubation); (2) cell concentration; (3) type of inoculating media; (4) aerobic stress of incubation, such as the surface-to-volume ratio of the media; (5) incubation flask/tube is protected from light/unprotected; (6) incubation flask/tube is tightened/cracked/loosened/left open; (7) incubation temperature; (8) degree and type of agitation during incubation; (9) cut-off points for aerobic incubation duration for aerotolerance level classification; and (10) enumeration method. The schematic diagram for the standardization protocol is shown in Figure S1.

Table 1. List of 16 studies that classified Campylobacter spp. based on aerotolerance.

Study	*Campylobacter* spp.	Aerotolerant classification
Ortega-Sanz *et al.*, 2024	*C. jejuni*	Follow Oh *et al.* (2015a)
Pokhrel *et al.*, 2023	*C. jejuni*	Follow Oh *et al.* (2015a)
Guk *et al.*, 2021	*C. coli*	Follow Oh *et al.* (2015a)
Mouftah *et al.*, 2021	*C. jejuni* and *C. coli*	Follow Oh *et al.* (2015a)
Shagieva *et al.*, 2021	*C. jejuni*	Able to form colony under aerobic conditions
Jaakkonen *et al.*, 2020	*C. jejuni*	Follow Oh *et al.* (2015a)
Guk *et al.*, 2019	*C. coli*	Follow Oh *et al.* (2015a)
Karki *et al.*, 2019	*C. jejuni* and *C. coli*	Follow Oh *et al.* (2015a)
Kiatsomphob *et al.*, 2019	*C. jejuni*	Follow Oh *et al.* (2015a)
Kim *et al.*, 2019	*C. jejuni*	Follow Oh *et al.* (2015a)
Lee *et al.*, 2019	*C. jejuni*	2 $\log_{10}$ CFU/mL reduction for 120 h as a threshold
Karki *et al.*, 2018	*C. jejuni* and *C. coli*	Follow Oh *et al.* (2015a)
Oh *et al.*, 2018	*C. jejuni*	Follow Oh *et al.* (2015a)
Oh *et al.*, 2015a	*C. jejuni*	Classified into aero-sensitive (OS, did not survive after 12 h of aerobic incubation), aerotolerant (AT, survived after 12 h of aerobic incubation), and hyperaerotolerant (HAT, survived after 24 h of aerobic incubation), after aerobic incubation in MH broth with 200 rpm shaking at 42°C
Chynoweth *et al.*, 1998	*C. jejuni*	Capable of aerobic growth on a nutrient agar plate
Jones *et al.*, 1993	*C. jejuni*	Capable of aerobic growth on a blood agar plate

Note: CFU/mL: Colony Forming Units per milliliter; MH: Mueller Hinton.

Prevalence and source of aerotolerant *Campylobacter* spp.

Studies on the prevalence of AT *Campylobacter* spp. are limited, and the 16 published studies are summarized in Table S2. The prevalence of AT strains varies considerably between studies, ranging from 0% to 100% in *C. jejuni* and 41.9% to 100% in *C. coli.* Shagieva *et al.* (2021) reported an inconsistent AT profile of *C. jejuni* over three replicates. Thus, the three strains that consistently survived aerobically in all three replicates are labeled as AT in Table S2.

The *Campylobacter* spp. reported in studies stated in Table S2 are sorted by the source of the strains and presented in Table 2. Pond water and the outlet of a wastewater treatment plant from Shagieva *et al.* (2021) and udder cloth from Jaakkonen *et al.* (2020) were regrouped into the classification of environment, as shown in Table 2. Moreover, *C. jejuni* (697 strains) were characterized for aerotolerance level than *C. coli* (300 strains). Among them, chicken and pork were the most studied sources for aerotolerance in *C. jejuni* and *C. coli*, respectively. In *C. jejuni*, dairy product had the highest prevalence of HAT (69.5%), while duck had the highest prevalence of AT (62.2%). In *C. coli*, humans were found to have the highest prevalence of HAT (60%), and duck was reported to have the highest prevalence of AT (38.7%). In both *C. jejuni* and *C. coli*, AT (39.9% in *C. jejuni* and 35.2% in *C. coli*) and HAT (32.9% in *C. jejuni* and 44.3% in *C. coli*) were more prevalent than the OS counterparts. These estimates indicated that the AT strains of *Campylobacter* spp. could be an emerging phenomenon.

As shown in Figure 2 and Table 3, the pooled prevalence of AT *Campylobacter* spp. from 10 studies in a meta-analysis was 75.9% (95% CI: 59.6% to 87.1%, P = 0.003). The outputs of the subgroup analysis are shown in Figure 3 and Table 3; the pooled prevalence of AT *Campylobacter* spp. in chicken was 68.2% (95% CI: 46.5% to 84.1%, P = 0.098). As a comparison, the pooled prevalence of AT *Campylobacter* spp. in duck and humans was statistically significant (P < 0.001), with a pooled prevalence of 88.1% (95% CI: 80.1% to 93.1%) and 87.9% (95% CI: 75.8% to 94.4%), respectively. Based on meta-regression, as shown in Table 4, no statistically significant difference exists in the prevalence of AT *Campylobacter* spp. between chicken and duck, with P = 0.1226, and between chicken and humans, with P = 0.1165. Owing to the limitation of a 30-sample size in the respective studies, the source of AT *Campylobacter* spp., such as beef, dairy products, the environment, and turkey, were not included in the meta-analysis. This implies that further studies involving larger sample sizes from different sources are noteworthy for meta-analysis in the future.

As shown in Figure 4 and Table 3, the pooled prevalence of AT *C. jejuni* was 73.7% (95% CI: 50.1% to 88.7%, P = 0.049). In comparison, the pooled prevalence of AT *C. coli* was statistically insignificant (P = 0.174), with an estimate of 73.7% (95% CI: 38.8% to 92.5%). Meta-regression in Table 4 reveals no significant difference between AT *C. jejuni* and AT *C. coli*, with P = 0.9929. However, *C. jejuni* was reported to have a higher survival bacterial concentration than *C. coli* after aerobic incubation (Mouftah *et al.,* 2021).

As shown in Figure 5 and Table 3, the pooled prevalence of HAT *Campylobacter* spp. was 32.9% (95% CI: 22.6% to 45.1%, P = 0.007), with a Q statistic value of 100.20 and I^2 of 91.02%. Similarly, the pooled prevalence of AT *Campylobacter* spp. was statistically significant (P =

Table 2. Prevalence of *Campylobacter* spp. with different levels of aerotolerance from different sources as discovered in 16 studies.

Source	*C. jejuni*			*C. coli*		
	OS	AT	HAT	OS	AT	HAT
Chicken	38.8% (112/289)	34.3% (99/289)	27% (78/289)	14.9% (11/74)	37.8% (28/74)	47.3% (35/74)
Beef	20% (8/40)	42.5% (17/40)	37.5% (15/40)	36.8% (7/19)	31.6% (6/19)	31.6% (6/19)
Dairy products	8.7% (2/23)	21.7% (5/23)	69.5% (16/23)	100% (2/2)	0% (0/2)	0% (0/2)
Duck	13.3% (6/45)	62.2% (28/45)	24.4% (11/45)	16.1% (10/62)	38.7% (24/62)	45.2% (28/62)
Humans	10.3% (22/213)	41.3% (88/213)	48.4% (103/213)	20% (3/15)	20% (3/15)	60% (9/15)
Environment	61.4% (35/57)	28.1% (16/57)	10.5% (6/57)	0	0	0
Pork	0	0	0	14.3% (72/126)	28.6% (36/126)	57.1% (18/126)
Turkey	100% (5/5)	0	0	0% (0/2)	100% (2/2)	0% (0/2)
N/A	0% (0/25)	100% (25/25)	0% (0/25)	0	0	0
Total	27.3% (190/697)	39.9% (278/697)	32.9% (229/697)	20.5% (105/300)	35.2% (99/300)	44.3% (96/300)

Notes: OS: aero-sensitive; AT: aerotolerant; HAT: hyperaerotolerant; N/A: not available.

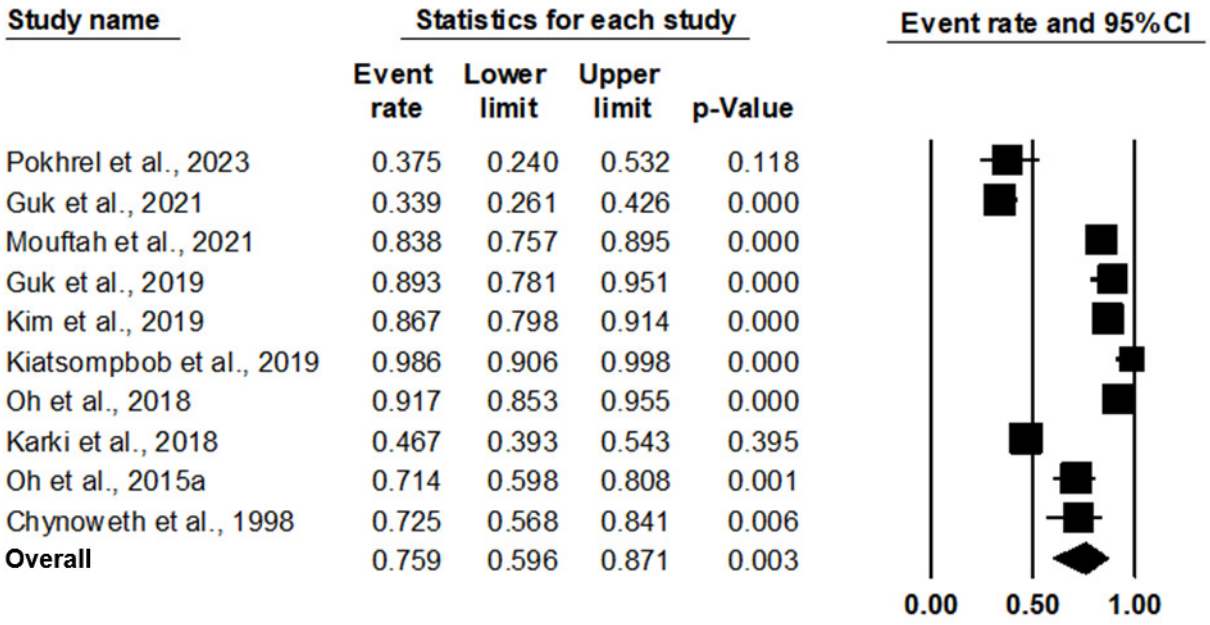

Figure 2. Forest plot of the estimated prevalence of aerotolerant *Campylobacter* spp.

Table 3. Result of the overall meta-analysis and subgroup analysis on the prevalence of aerotolerant *Campylobacter* spp. based on three potential effect modifiers.

Variables	Number of studies	Number of isolates	Number of positive isolates (HAT and AT)	Pooled prevalence and 95% confidence interval (CI)			Heterogeneity			
				Pooled prevalence (%)	Lower limits (%)	Upper limits (%)	τ^2	*Q* value	I^2 (%)	*P* value
Overall	10	934	654	75.9	59.6	87.1	1.364	177.897	94.941	<0.001
Source										
Chicken	5	360	230	68.2	46.5	84.1	0.947	50.411	92.065	<0.001
Duck	2	101	89	88.1	80.1	93.1	0	0.163	0	0.687
Humans	2	178	158	87.9	75.8	94.4	0.254	3.207	68.819	0.073
Species										
C. jejuni	8	642	476	73.7	50.1	88.7	1.634	130.478	94.635	<0.001
C. coli	3	271	175	73.7	38.8	92.5	1.996	46.123	95.664	<0.001
Aerotolerance level										
HAT	10	924	323	32.9	22.6	45.1	0.578	100.198	91.018	<0.001
AT	10	924	341	38.4	29.0	48.7	0.399	77.776	88.428	<0.001

Notes: HAT: hyperaerotolerant; AT: aerotolerant.
τ^2: tau-squared; I^2: inconsistency index; Q: Cochran's Q statistic.

0.028), with a pooled prevalence of 38.4% (95% CI: 29.0% to 48.7%). Meta-regression in Table 4 shows no significant difference between HAT and AT, with $P = 0.4996$. However, some studies reported a higher prevalence of HAT than AT isolated from animals, such as broilers and cattle, suggesting that HAT strains have an advantage of colonizing in the gastrointestinal tracts (GIT) of animals (Guk *et al.,* 2019; Jaakkonen *et al.,* 2020; Mouftah *et al.,* 2021).

An I^2 value of more than 75% indicated considerable heterogeneity (Higgins *et al.*, 2003). Most of the heterogeneities in subgroup analysis and residual heterogeneities of all moderators in meta-regression were high ($I^2 > 88\%$), as shown in Table 4, which indicates the data synthesis should be interpreted with caution. These could be due to unmeasured covariates, such as the sampling and diagnostic techniques, season, temperature, and other underlying factors (Imrey *et al.,* 2020). This highlights

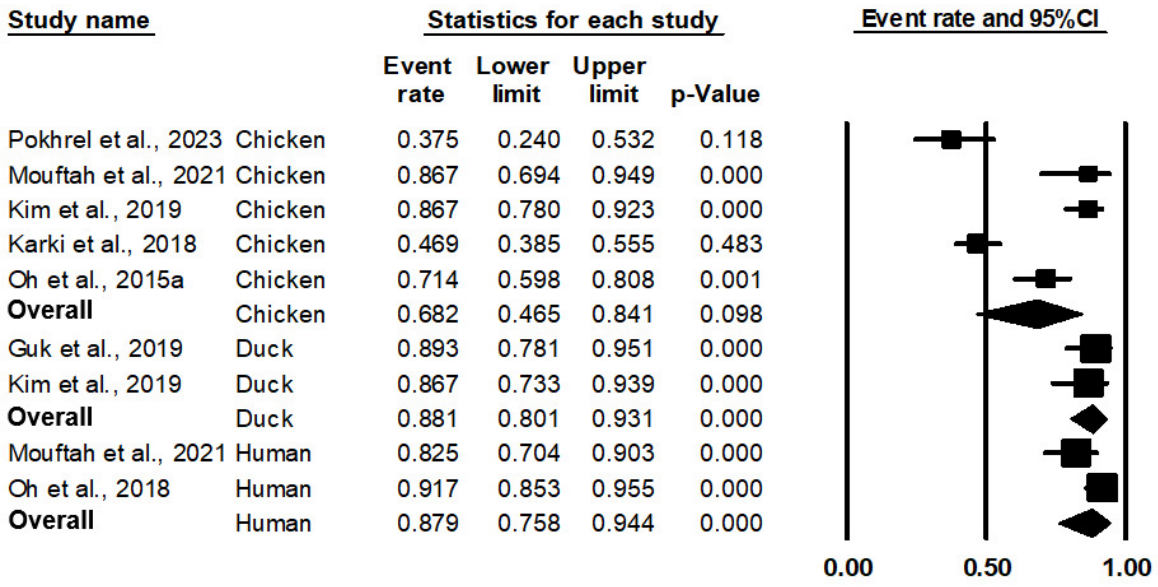

Figure 3. Forest plot of the estimated prevalence of aerotolerant *Campylobacter* spp. by subgroup of the source of isolates.

Table 4. Meta-regression of the overall study and the subgroup.

	Q model	*P* value	Residual I^2 (%)	Residual τ^2	R^2 (%)
Overall					
Publication year	3.89	0.5653	96.22	2.3112	0
Location	1.07	0.7839	96.13	1.9920	0
Subgroup					
Source	3.80	0.1497	88.84	0.7587	35.00
Chicken*	–	–	–	–	–
Duck	–	0.1226	–	–	–
Humans	–	0.1165	–	–	–
Species	0	0.9929	94.90	1.8861	0
Aerotolerance level	0.46	0.4996	89.89	0.4847	0

Notes: *No result for chicken as it is treated as a reference group.
τ^2: tau-squared; I^2: inconsistency index; *Q*: Cochran's *Q* statistic; R^2: between-study variability.

the need for future studies with a sample size (>30) that adopt a standardized aerotolerance assay. Further, there was a weak relationship between the prevalence and the source of isolates (between-study variability (R^2) = 35.0%, P = 0.1497). In addition, no relationships were discovered regarding the publication year (R^2 = 0% and P = 0.5653), location (R^2 = 0% and P = 0.7839), species (R^2 = 0% and P = 0.9929), and aerotolerance level (R^2 = 0% and P = 0.4996) on the pooled *Campylobacter* spp. prevalence. Funnel test asymmetry (Figure S2) was confirmed by Egger's test (P = 0.043), as shown in Table 5, revealing significant publication bias in this study. However, the Fail-safe N test found that the number of studies needed to revert the significance was 252. This value was much larger than the number of studies of 60, which was obtained from the formula of $5k$ + 10. Thus, the result of the meta-analysis can be considered robust to publication bias (Rosenthal, 1979).

The available prevalence data for AT *Campylobacter* spp., at the recent time point, are limited to *C. jejuni* and *C. coli*. Studies on the prevalence of other AT *Campylobacter* spp., such as *C. concisus*, *C. upsaliensis*, *C. fetus*, *C. ureolyticus*, and *C. hyointestinalis*, are the research gaps worth investigating, as these species are clinically important (Platts-Mills and Kosek, 2014). The prevalence of AT *Campylobacter* spp. in other retail foods is valuable, as *Campylobacter* spp. have been found in milk, eggs, fresh products, ready-to-eat food, and processed meat (Chai *et al.,* 2007; Jaakkonen *et al.,* 2020; Parisi *et al.,* 2015; Toyomaki *et al.,* 2012; Trimoulinard *et al.,* 2017).

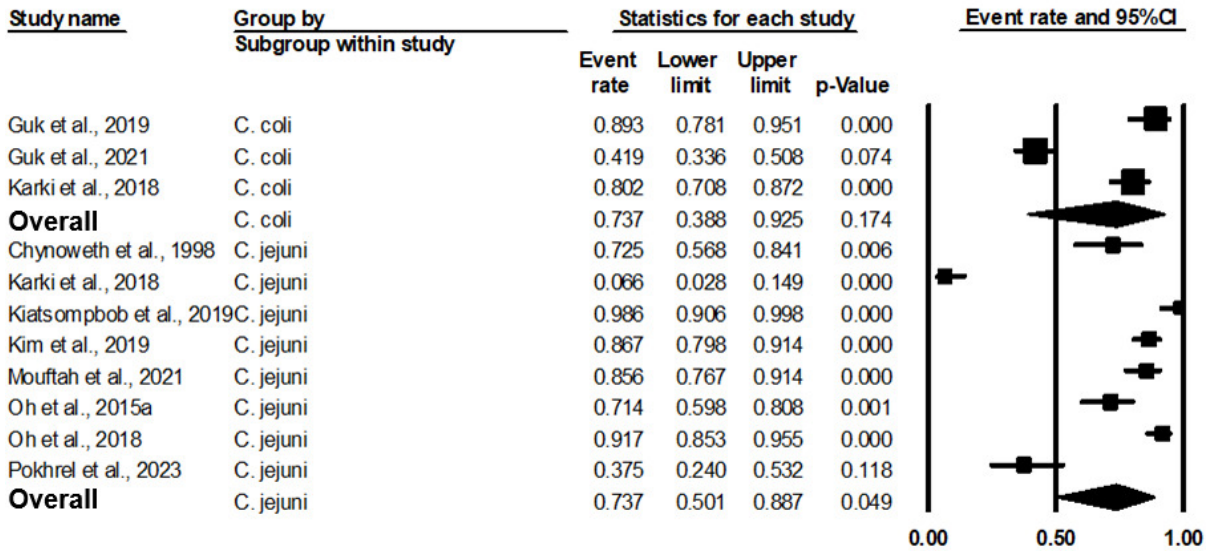

Figure 4. Forest plot of the estimated prevalence of aerotolerant *Campylobacter* spp. by subgroup of the species.

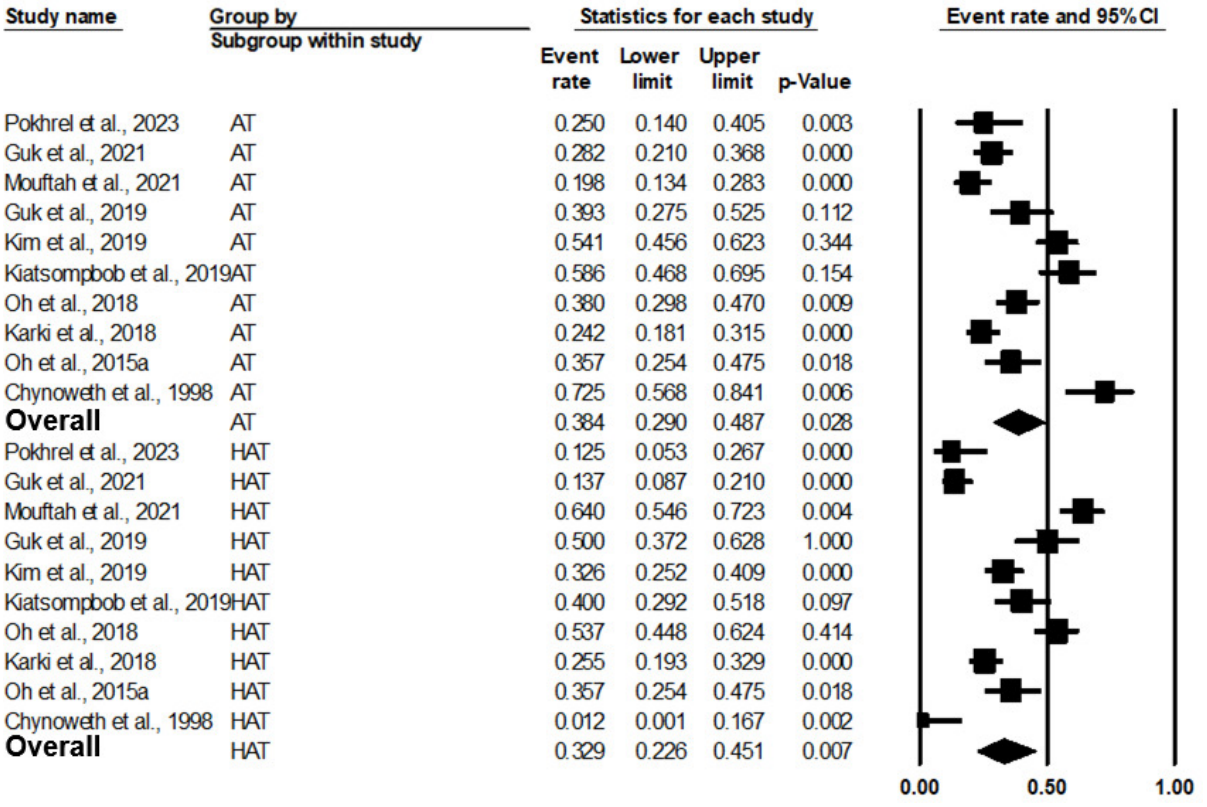

Figure 5. Forest plot of the estimated prevalence of aerotolerant *Campylobacter* spp. by the subgroup of aerotolerance level.

Table 5. Publication bias of meta-analysis.

	Number of studies	Egger's test		5*k* +10	Fail-safe N
		Intercept	*P* value		
Overall	10	7.26	0.043	60	232

Survivability of aerotolerant *Campylobacter* spp. against environmental stress

The survivability of AT *Campylobacter* spp. against environmental stresses is one of the forefront traits for the pathogen to induce campylobacteriosis in humans. Figure 6 displays the alluvial plot of the overview of the *Campylobacter* spp. isolates with different levels of aerotolerance studied against environmental stresses, as summarized in 17 studies (Chynoweth *et al.,* 1998; Hur *et al.,* 2024; Jaakkonen *et al.,* 2020; Jones *et al.,* 1993; Karki *et al.,* 2018, 2019; Lee *et al.,* 2019; Mouftah *et al.,* 2021; O'Kane and Connerton, 2017; Oh *et al.,* 2015a, 2017, 2018, 2019; Ortega-Sanz *et al.,* 2024; Pokhrel *et al.,* 2023; Rodrigues *et al.,* 2015; Shagieva *et al.,* 2021).

The alluvial plot in Figure 6 demonstrates that AT *C. jejuni* (1,051 strains) was the most widely studied isolate against environmental stresses. Each of the environmental stresses are discussed further in the following subtopics.

The alluvial plot displays that HAT *Campylobacter* spp. (566/1,127) were the most widely distributed strains compared to AT (362/1,127) and OS (199/1,127). Thus, it was postulated that aerotolerant (HAT and AT) *Campylobacter* spp. are becoming more ubiquitous than the OS strains.

Survivability of aerotolerant Campylobacter *spp. against atmospheric and oxidative stresses*

One important question that remains to be solved is how this ubiquitous yet microaerophilic and fastidious pathogen can thrive in aerobic environments and subsequently infect humans. Despite exposure to the aerobic atmosphere being closely associated with oxidative stress, the stress induced by aerobic incubation was referred to as aerobic stress in this study. In contrast, the stress caused by oxidative inducers was considered oxidative stress. Oxidative inducers included, such as hydrogen peroxide (H_2O_2), cumene hydroperoxide (CHP), menadione (MND), paraquat (PQ), are stated in Table S3. Tables S3 and S4 summarize the survival of *Campylobacter* spp.

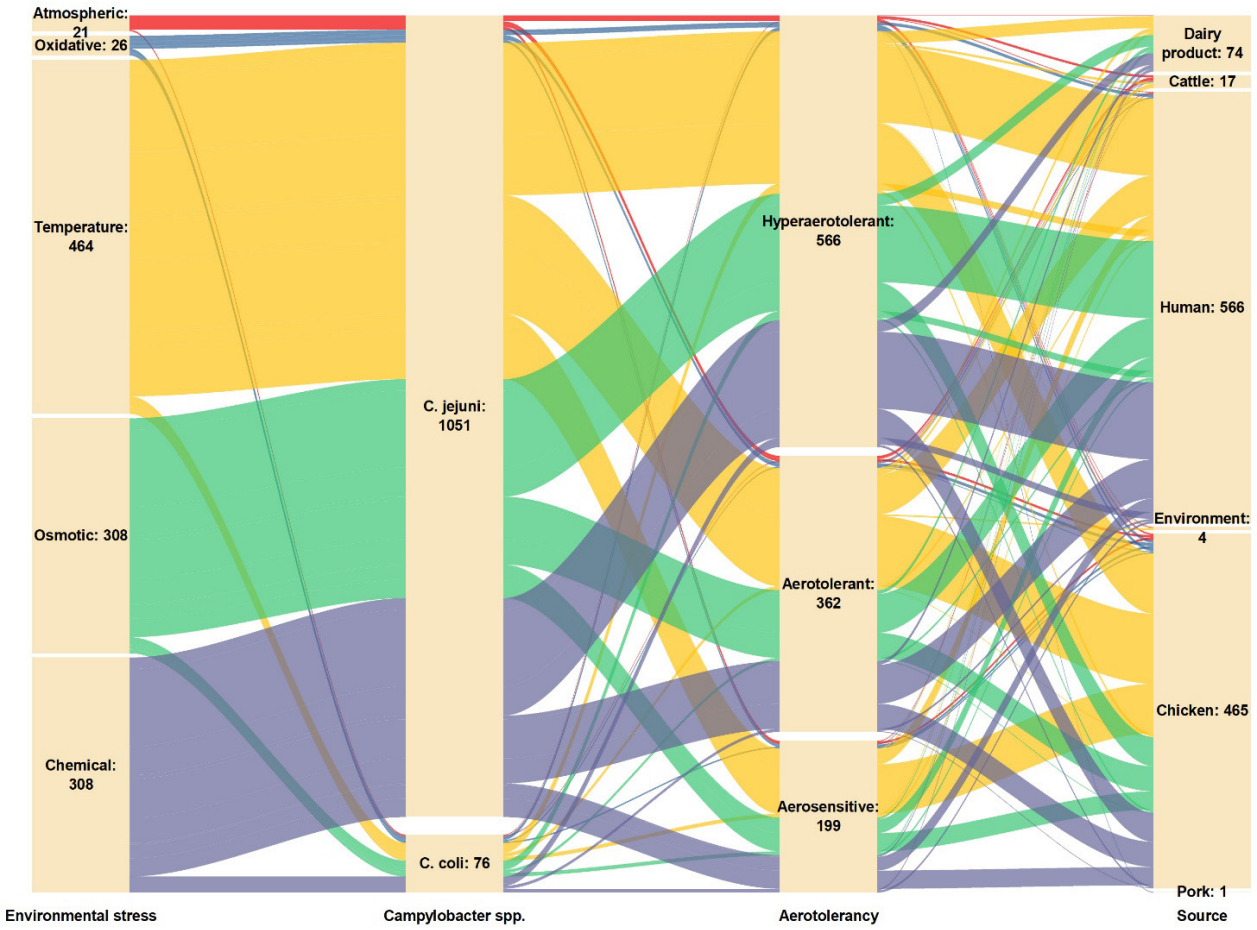

Figure 6. Alluvial plot of the overview of the isolates of *Campylobacter* spp. with different levels of aerotolerance from different sources studied against environmental stresses. The taller nodes indicate a larger number of isolates studied, with the number indicating the number of isolates.

with different levels of aerotolerance under atmospheric and oxidative stress.

Hyperaerotolerant *C. jejuni* survived better than the AT strains under aerobic stress (Jaakkonen *et al.,* 2020; Oh *et al.,* 2017). Further, HAT *C. jejuni* were found to survive better than the AT strains, whereas AT survived better than the OS strains under different atmospheric conditions (CO_2 and N_2) in poultry meat. Thus, both HAT and AT strains might be able to thrive on the modified atmospheric packaging, further compromising food safety.

The most common *Campylobacter* strain used for studying atmospheric survivability was *C. jejuni* NCTC 11168 (Atack *et al.,* 2008; Jaakkonen *et al.,* 2020; Karki *et al.,* 2019; O'Kane and Connerton, 2017; Oh *et al.,* 2015b; Rodrigues *et al.,* 2015). Jaakkonen *et al.* (2020) and Karki *et al.* (2019) reported contradicting results, as *C. jejuni* NCTC 11168 was reported as HAT and OS, respectively, based on the aerotolerance assay proposed by Oh *et al.* (2015a). However, several researchers investigated the aerotolerance of *C. jejuni* NCTC 11168 without concluding the AT classification (Atack *et al.,* 2008; Gundogdu *et al.,* 2015; Oh *et al.,* 2015b; Rodrigues *et al.,* 2015). Thus, the inconsistency of result and the lack of clarity of aerotolerance classification reaffirm the importance of standardized protocol.

Karki *et al.* (2019) found that retail beef meat juice, chicken liver juice, and beef liver juice contain factors that enhance the aerobic survival of *C. jejuni* and *C. coli* (Karki *et al.,* 2019). This is because the heme-containing proteins in meat and liver juice act as cofactors for catalase and superoxide dismutase (Pretorius *et al.,* 2016; van Vliet *et al.,* 2002). In addition, iron in meat and liver juice mediates genes (*fdxA* and *ahpC*) and regulatory proteins (PerR and Fur) that are involved in aerotolerance mechanisms (Baillon *et al.,* 1999; Butcher *et al.,* 2015; van Vliet *et al.,* 1999, 2001). Thus, *C. jejuni* and *C. coli* might survive better *in situ* than *in vitro*, and the actual prevalence of AT *Campylobacter* spp. could be higher before being detected in the laboratory.

The aerobic survival of *C. jejuni* cocktail (mixture of four strains) was investigated on different food matrices (chicken nuggets and minced meat) (Chynoweth *et al.,* 1998). In sterile minced chicken, incubation at 25°C showed better survival than at 37°C. The higher survival at 25°C could be due to the pathogen being less metabolically active than at 37°C and thus less susceptible to reactive oxidative species (ROS) (Chynoweth *et al.,* 1998). Further, the survival of *C. jejuni* in chicken nuggets was lower than in minced meat, possibly because of the seasonings and food additives in the nuggets that inhibit the growth of *C. jejuni* (Chynoweth *et al.,* 1998). Thus, the survival of single and multiple strains of *Campylobacter* spp. in different food matrices is worth elucidating.

Hwang *et al.* (2014) was the only study to report the survival of non-*jejuni*/*coli Campylobacter* isolates under aerobic incubation. The researchers reported that *C. fetus* was able to survive in brain heart infusion after 12 h of aerobic incubation. However, the researchers did not state the incubation temperature and the classification for aerotolerance. This study demonstrated that *Campylobacter* spp. other than *C. jejuni* and *C. coli* might have aerotolerance properties.

Campylobacter spp. is normally exposed to ROS during colonization on a host, thriving in the environment, and within its cellular metabolism (Gundogdu *et al.,* 2015). Several researchers investigated the effect of ROS-promoting agents (oxidative inducers) on the viability of AT *Campylobacter* spp., as shown in Table S4. Oh *et al.* (2015a) reported that aerotolerant *C. jejuni* (HAT and AT strains) survived significantly better than the non-AT *C. jejuni* (OS strains) against 1-mM H_2O_2, 100-μM CHP, and 100-μM MND, respectively. However, results from Ortega-Sanz *et al.* (2024) did not show any trend in aerotolerance and survival against oxidative stress. In comparison between *C. jejuni* and *C. coli*, Karki *et al.* (2018) reported that there were significant differences in H_2O_2 sensitivity between strains, while there was no correlation between H_2O_2 sensitivity and the level of aerotolerance (five *C. jejuni* and eight *C. coli* strains).

As shown in Table S4, Rodrigues *et al.* (2015) conducted an oxidative stress assay under MAC, while Karki *et al.* (2018) and Oh *et al.* (2015a) did not mention incubation atmosphere. It is essential to note that aerobic incubation might have acted synergistically with oxidative inducers on the survival of *Campylobacter* spp., potentially interfering with the observations.

Results from several research groups demonstrated that AT *Campylobacter* spp. had better survival and growth under atmospheric and oxidative stress. However, based on the paucity of studies investigating the relationship between aerotolerance, atmospheric stress, and oxidative stress defenses, the interaction between phenotypes remains inconclusive.

Aerobically acclimatized *Campylobacter* spp.: Aerobic acclimatization refers to the incubation of *Campylobacter* spp. under aerobic conditions for a defined period, allowing them to adapt to aerobic stress. Researchers conducted aerobic acclimatization differently, with incubation temperatures of 37°C or 42°C under aerobic conditions for 1–7 days and ranging from 1 to 15 aerobic passages on various agars (Chynoweth *et al.,* 1998;

Jones *et al.,* 1993; O'Kane and Connerton, 2017; Rodrigues *et al.,* 2015; Shagieva *et al.,* 2021). It was observed that aerobically acclimatized *C. jejuni* survived longer on blood agar than non-aerobically acclimatized *C. jejuni* at 4°C under aerobic incubation (Jones *et al.,* 1993). Similarly, O'Kane and Connerton (2017) reported that aerobic acclimatization improved the aerotolerance of *C. coli* OR12. Further, Shagieva *et al.* (2021) reported that aerobically acclimatized *C. jejuni* demonstrated aerobic growth on agar. Contrarily, aerobic acclimatization did not influence the growth and survivability of both *C. jejuni* Bf (Bf is a *C. jejuni* strain named by Rodrigues *et al.,* 2015) and NCTC 11351 under aerobic conditions (Chynoweth *et al.,* 1998; Rodrigues *et al.,* 2015). These conflicting results underscore the importance of a standardized method for aerobic acclimatization.

It has been postulated that the aerotolerance of *C. jejuni* could be due to transcriptional and translational changes (Bronnec *et al.,* 2016a, 2016b). Microaerobic passage did not affect *C. coli* OR12's ability to grow in aerobic conditions, suggesting that aerotolerance is stable and is due to genetic modification in lieu of temporary physiological adaptation (O'Kane and Connerton, 2017). However, Nennig *et al.* (2022) reported that more than half (43/80) of *C. jejuni* were able to be aerobically acclimatized, and whole genome sequencing data suggested that genetic sequence does not govern this trait. Thus, the molecular mechanism of aerobic acclimatization and aerotolerance in *Campylobacter* spp. could be an interesting research question.

Growth of aerotolerant *Campylobacter* spp. under aerobic conditions: To our knowledge, Chynoweth *et al.* (1998) first reported a qualitative investigation on *C. jejuni* to grow on solid agar, and Rodrigues *et al.* (2015) were the first to report this quantitatively. *C. jejuni* Bf exhibited a stationary phase of 10 h, which could be regarded as the adaptive period for aerobic stress, followed by a growth of 2.5 $\log_{10}$ Colony Forming Units per milliliter (CFU/mL) from 10 h to 48 h on Kamali agar under aerobic incubation (Rodrigues *et al.,* 2015). To date, no *Campylobacter* spp. other than *C. jejuni* and *C. coli*, have been reported to have the ability to grow under aerobic conditions, as shown in Table S5.

Aerobic growth of AT *Campylobacter* spp. is facilitated in liquid media (k_H = 9.28 x 10^{-4} mol L^{-1} atm^{-1} in water at 42°C) because of lower oxygen transfer, compared to solid agar (Rodrigues *et al.,* 2015). Next, a cell density of more than 10^4 CFU/mL could grant better aerobic stress tolerance in AT *Campylobacter* spp. because the oxygen demand was higher than that of low cell densities (lower than 10^4 CFU/mL) (Rodrigues *et al.,* 2015). These two factors reduced the available oxygen and facilitated the aerobic growth of AT *Campylobacter* spp. (Rodrigues *et al.,* 2015).

Shagieva *et al.* (2021), O'Kane and Connerton (2017), and Rodrigues *et al.* (2015) reported that *Campylobacter* spp. grew on Kamali, blood, and charcoal cefoperazone deoxycholate agars (CCD), respectively. These agar plates contain substances that neutralize toxic substances from oxygen (Gharst *et al.,* 2013). However, the aerobic growth of *C. jejuni* on nutrient agar, as demonstrated by Chynoweth *et al.* (1998), might have greater aerobic growth potential because the agar did not contain any additives that mitigate aerobic stress.

Although the AT *C. coli* OR12 Aer P32 strain demonstrated aerobic growth on blood agar, it did not exhibit superior survival in liquid medium under aerobic conditions, unlike other *C. jejuni* and *C. coli* strains (O'Kane and Connerton, 2017). This finding did not justify such coherence, and the researchers did not explain it in their studies. Thus, this finding marks the importance of comparing the aerotolerance levels of *Campylobacter* spp. both *in vitro* (in broth and on agar) and *in situ* (food matrices).

Survivability of aerotolerant Campylobacter *spp. against chemical antimicrobial agent*

The only reported chemical antimicrobial agent used to control *Campylobacter* spp. in relation to aerotolerance is peracetic or peroxyacetic acid (PAA). PAA is the most commonly used antimicrobial in pre- and post-chill stages in poultry processing (Kataria *et al.,* 2020). PAA offers a wide range of antimicrobial activities because of the combined action of acidic and oxidizing properties (Bauermeister *et al.,* 2008). PAA is normally applied at main poultry chiller for up to 220 ppm, and for the post-chill immersion tank, the maximum permissible concentration is 2,000 ppm (United States Department of Agriculture-Food Safety and Inspection Service, 2019). PAA is an effective antimicrobial agent that reduces the population of *Campylobacter* spp. with a reduction of up to 1.3 $\log_{10}$ CFU (Chen *et al.,* 2014). Only three studies were available on raw chicken skin, as summarized in Table S6. These studies found the same trend, with HAT strains survived better than the AT strains, whereas both HAT and AT strains thrived better than OS strains (Mouftah *et al.,* 2021; Oh *et al.,* 2018, 2019).

Most of *C. jejuni* isolates resisted PAA better than *C. coli*, with a higher final mean cell number (Mouftah *et al.,* 2021). However, this is the only study that compared the survival of *C. jejuni* and *C. coli*. Since the application of PAA is in the equilibrium of H_2O_2 and acetic acid, the survival of HAT and AT strains in the presence of PAA could be due to the augmented oxidative stress defense (Oh *et al.,* 2019; Yuan *et al.,* 1997). Studies on the survivability of AT *Campylobacter* spp. against other chemical decontamination agents are the knowledge gaps that remain to be explored. Examples of other chemical

decontamination agents used in *Campylobacter* spp. decontamination include chlorine, chlorine dioxide, acidified sodium chlorite, trisodium phosphate, and peroxy acid (Hansson *et al.,* 2018).

Survivability of aerotolerant Campylobacter spp. against temperature stress

Temperature treatments, such as refrigeration, freezing, and pasteurization, are vital for food preservation. The survival of AT *Campylobacter* spp. against temperature stress is shown in Table S7. *In situ* studies reported that HAT strains survived better under refrigeration (4°C) than AT strains, whereas AT strains survived better than OS strains (Jaakkonen *et al.,* 2020; Mouftah *et al.,* 2021; Oh *et al.,* 2017, 2018). These studies reported a consistent trend between aerotolerance levels and refrigeration survival. In addition, OS strains have a significantly higher proportion in the cold-sensitive group compared to the cold-tolerant group (Hur *et al.,* 2024). On the contrary, Pokhrel *et al.* (2023) reported that AT strains survived better than HAT and OS strains in refrigerated chicken drumsticks. In comparison, *in vitro* studies produced mixed results. Lee *et al.* (2019) and Shagieva *et al.* (2021) found no difference between aerotolerance and refrigeration survival in MH broth and brain heart infusion broth, respectively. In contrast, *C. jejuni* OS strains reduced significantly more AT and HAT strains in both MH broth and chicken meat (Oh *et al.,* 2017, 2019). Interestingly, Jaakkonen *et al.* (2020) reported variability in the refrigerated raw milk survival of *C. jejuni* within CC-21, even within the same ST, implying unconserved traits in survivability.

Similar to refrigeration, HAT *Campylobacter* spp. isolates portrayed significantly better survival on chicken skin than AT strains under freeze-thaw stress, whereas AT strains outperformed OS strains (Mouftah *et al.,* 2021; Oh *et al.,* 2018). Further, freeze-thaw stress in MH broth also showed a cognate trend as on chicken skin (Oh *et al.,* 2019). On the contrary, Pokhrel *et al.* (2023) reported that AT strains survived better than HAT and OS strains in frozen chicken drumsticks. The discrepancy between studies could be due to the low number of HAT strains (five strains) in the study conducted by Pokhrel *et al.* (2023).

Under pasteurization (72°C, 15 s) and the extended heat-treatment (72°C, 30 s) in milk, HAT *C. jejuni* and *C. coli* strains survived better than AT strains, while OS survived the least (Mouftah *et al.,* 2021; Oh *et al.,* 2018). On the contrary, *C. jejuni* isolated from retail chicken were sensitive to heat (72°C, 30 s), regardless of AT properties (Oh *et al.,* 2019). Varied survival trends of *Campylobacter* spp. with different aerotolerance levels against refrigeration, freeze-thaw, and heat treatment affirm the need for future study.

Similar to the aerobic stress trend described in the previous section, meat and liver juice significantly improved the survival of AT *C. coli* and non-AT *C. jejuni* at 4°C, compared to MH broth (Karki *et al.,* 2019). It is conjectured that retail meat and liver juice from both chicken and beef had a significant influence, but not the origin of the juice. As a result, there could be better low-temperature survival of *Campylobacter* spp. under *in situ* conditions than under laboratory conditions.

Genes encoding cold shock proteins are not present in *Campylobacter* spp. (Hazeleger *et al.,* 1998). Thus, *Campylobacter* spp. may harbor another tolerance mechanism in response to cold shock (Mouftah *et al.,* 2021). Since some studies found a relation between aerotolerance and temperature stress survival, the mechanism behind this could be the existence and expression of certain genes that contribute to both phenotypes.

Survivability of aerotolerant Campylobacter *spp. against osmotic stress*

Campylobacter spp. are sensitive to hyperosmotic conditions, with inhibition reported at more than 2% NaCl, a common preservative used in food against pathogens (Doyle and Glass, 2010; Park, 2002). Only three studies have linked the aerotolerance of *Campylobacter* spp. to osmotic stress resistance, and all the studies were conducted in MH agar or MH broth, as shown in Table S8. Mouftah *et al.* (2021) and Oh *et al.* (2018) reported higher survival in HAT and AT *C. jejuni* or *C. coli* strains than OS strains under hyperosmotic stress (4% NaCl). Cross-protection might exist between aerotolerance and osmotic stress resistance, and *vice versa* (Mouftah *et al.,* 2021). Conversely, the degree of hyper-osmotolerance was found to be greatly variable between strains and did not pertain to aerotolerance properties (Oh *et al.,* 2019).

Half of the *C. jejuni* survived at 4% NaCl, whereas none of the *C. coli* survived, and difference in the final cell concentration was significant between the two species (Mouftah *et al.,* 2021). However, only one study compared the two species. The relationship between aerotolerance and hyper-osmotolerance remains to be clarified through additional research, such as investigations of different food matrices and other *Campylobacter* spp.

Survivability of aerotolerant Campylobacter *spp. against acidic stress*

To the best of our knowledge, no study has elucidated the relationship between aerotolerance of *Campylobacter* spp. and acidic stress tolerance. Compared to other foodborne pathogens, *C. jejuni* is more sensitive to acid (Birk *et al.,* 2010). This sensitivity is due to the lack of an acid resistance system (Birk *et al.,* 2012; Merrell and Camilli, 1999; Park *et al.,* 1996; Richard and Foster, 2003). However, *Campylobacter* spp. proteins, such as SodB,

AhpC, and Dps, observed during acid stress, were associated with oxidative stress (Baillon *et al.,* 1999; Birk *et al.,* 2012; Ishikawa *et al.,* 2003; Pesci *et al.,* 1994; Purdy *et al.,* 1999). Thus, *C. jejuni* might normally be in an oxygen-alert state, allowing it to remove ROS and undesirable components from acid stress (Afriliana *et al.,* 2018; Birk *et al.,* 2012).

The pH of certain fermented foods is in the range of 4.5–5.5 (Nout, 1994). In addition, the pH of coffee ranges from 5.4 to 6.2, while the pH of milk is 6.5–6.7 (Afriliana *et al.,* 2018; Renan *et al.,* 2006; Sikand *et al.,* 2010). Another example of acidic food is marinated meat (Birk *et al.,* 2010). AT *Campylobacter* spp. could survive better in acidic food, which poses a food safety issue. The prevalence and survivability of AT *Campylobacter* spp. in the aforementioned acidic food are worth investigating.

Influence of atmospheric conditions on the survivability of aerotolerant Campylobacter *spp. against environmental stresses*

Certain survival studies against oxidative, temperature, and osmotic stresses, as shown in Tables S4, S7, and S8, respectively, did not provide information on the atmospheric incubation conditions. Atmospheric conditions could influence the survival mechanism of *Campylobacter* spp. against environmental stresses. For instance, AT and HAT *C. jejuni* showed better resistance to different atmospheric stresses (aerobic, N_2, and CO_2) than AT, whereas AT strains had better resistance than OS strains at 4°C (Oh *et al.,* 2017). Furthermore, *C. jejuni* (with all levels of aerotolerance) survived significantly better in refrigeration under aerobic conditions than microaerobic conditions (Hur *et al.,* 2024). Thus, atmospheric conditions, such as aerobic and modified atmospheric packaging, on the survival of AT *Campylobacter* spp. against environmental stresses, is an interesting research gap.

Inactivation dynamics of aerotolerant Campylobacter *spp.*

Different experimental settings of the included studies in Section "Survivability of aerotolerant Campylobacter spp. against environmental stress" render data harmonization difficult. Some studies reported the results in duration and percentage of survival, while others presented the results in charts without numeric figures. Thus, based on the available numeric data, the inactivation dynamics are summarized as follows:

- Under aerobic stress, HAT, AT, and OS *C. jejuni* had 2, 3, and 4 $\log_{10}$ CFU reduction, respectively, after 3 days of incubation in MH broth (Oh *et al*., 2017). Further, AT *C. coli* declined to below the limit of detection (1.3 $\log_{10}$ CFU/mL) from inoculation of 6 $\log_{10}$ CFU/mL after 24 h aerobic incubation in MH broth (O'Kane and Connerton, 2017).
- Under oxidative stress, 3.35 μM CHP exposure for 60 min reduced viability of AT and HAT *C. jejuni* > 6.25 ± 0.32 $\log_{10}$ CFU/mL, while 5 mM H_2O_2 reduced 5.89 ± 0.60 $\log_{10}$ CFU/mL (Ortega-Sanz *et al.,* 2024). Under 0.5 mM PQ exposure for 60 min, AT *C. jejuni* reduced 1.4–1.5 $\log_{10}$ CFU/mL (Rodrigues *et al*., 2015).
- Under chemical antimicrobial stress, PAA reduced HAT and AT *C. jejuni* and *C. coli* equally by ca. 4.5 $\log_{10}$ CFU/mL, while OS strains were reduced by ca. 7 $\log_{10}$ CFU/mL (Mouftah *et al.*, 2021). Furthermore, PAA inactivated HAT and AT *C. jejuni* by ca. 2.1 and 2.5 $\log_{10}$ CFU/mL, respectively, while OS strains were reduced by 3.7 $\log_{10}$ CFU/mL (Oh *et al.,* 2019).
- Under chilling (4°C) stress, storing HAT, AT, and OS *C. jejuni* for 7 days reduced 4.9, 5.1, and 7.4 $\log_{10}$ CFU/mL, respectively (Oh *et al.,* 2019). On contrary, at the same condition as Oh *et al.* (2019), greater reduction was reported in HAT *C. jejuni* (0.27 $\log_{10}$ CFU/mL) than OS and AT *C. jejuni* with 0.14 $\log_{10}$ CFU/mL and 0.08 $\log_{10}$ CFU/mL, respectively. After 5 days of chilling, OS *C. jejuni* reduced 1.5 $\log_{10}$ CFU/g and AT *C. jejuni* reduced 2.1–3.0 $\log_{10}$ CFU/g (Lee *et al.,* 2019).
- Under freezing (-20°C) stress, HAT, OS, and AT *C. jejuni* reduced 1.12, 0.90, and 0.60 $\log_{10}$ CFU/mL, respectively, regardless of the storage period (Pokhrel *et al.,* 2023).

Gene regulation of aerotolerant Campylobacter *spp.*

Gene regulation underlying AT *Campylobacter* spp. for environmental persistence is intricate and remains poorly understood. AT *C. jejuni* under aerobic incubation and after aerobic acclimatization was reported to have an increase in the transcription levels of genes involved in aerobic detoxification, which include *sodB*, *ahpC*, *katA*, *tpx*, and *trxB* (Rodrigues *et al*., 2016). In relation to the elevated transcription levels, the corresponding proteins (AhpC, KatA, Tpx, and TrxB) were reported to have higher abundance after aerobic incubation (Rodrigues *et al*., 2016). Similarly, *katA*, *ahpC*, and *trxB* were reported to have higher expression in aerobic incubation than microaerobic conditions in HAT *C. coli*, whereas their expression decreased in the OS *C. coli* (Guk *et al*., 2022). Further, *ahpC* mutation in HAT *C. jejuni* reduced aerotolerance level to AT (Oh *et al.*, 2015a). AT *C. jejuni* was reported with higher expression in *cosR* (oxidative stress response), *oorDABC* (oxygen metabolism), and *mreB* (cell morphology) after aerobic incubation (Bronnec *et al*., 2016b; Rodrigues *et al*., 2015). Under aerobic incubations at 37°C and 4°C, the expression of *htrB* (stress response) gene was higher in AT *C. jejuni* than in OS *C. jejuni* (Lee *et al.,* 2019). Further studies are warranted to elucidate the gene regulatory mechanisms of AT *Campylobacter* spp. in response to environmental stress.

Mechanism of persistence of aerotolerant Campylobacter *spp.*

C. jejuni devolves into viable but non-culturable (VNBC) stage and forms biofilms upon aerobic stress (Mouftah *et al.,* 2021; Oh *et al.,* 2015b; Yagi *et al.,* 2022). Yagi *et al.* (2022) reported that the AT *C. jejuni* strain remained in VBNC stage for a longer period than the aero-sensitive strains under aerobic stress. The researchers also postulated that AT strains might enter the VBNC stage more slowly than the aero-sensitive strains under aerobic conditions (Yagi *et al.,* 2022). This might be due to the AT strains resisting aerobic stress more, and the longer VBNC stage implies greater environmental persistence. In addition, Oh *et al.* (2015b) postulated that AT *C. jejuni* enters the VBNC stage after 12 h of aerobic incubation. However, the research did not compare to the aero-sensitive strain.

Aerotolerance was found to have a relationship with biofilm formation potential in *C. jejuni* and *C. coli,* with HAT isolates showing significantly greater biofilm formation potential than AT and OS isolates at 42°C under microaerobic conditions (Mouftah *et al.,* 2021). On the contrary, Pokhrel *et al.* (2024) reported that different aerotolerance levels yielded no significant difference in the number of *C. jejuni* biofilms attached to stainless steel coupons at 42°C, regardless of the microaerobic and aerobic conditions. However, at room temperature, a significantly lower number of *C. jejuni* biofilm attached to stainless steel coupons was observed in HAT *C. jejuni* than AT and OS counterparts (Pokhrel *et al.,* 2024). This suggests that incubation temperature could influence the formation of biofilms. In addition, Ortega-Sanz *et al.* (2024) reported that significantly higher biofilm formation was observed in HAT *C. jejuni* than in AT strains under aerobic conditions on polystyrene, but no significant difference was observed on stainless steel coupons. Thus, the type of material might influence the formation of biofilm. Further, AT *C. jejuni* Bf strain developed similar biofilm volume and thickness under both aerobic and microaerobic conditions (Bronnec *et al.,* 2016b). However, under aerobic incubation, a more compact and structured biofilm was formed, creating a microaerobic niche that supported the growth (Bronnec *et al.,* 2016b).

HAT and AT *C. jejuni* are found to have higher superoxide dismutase and catalase activities (the two important enzymes in oxidative stress defense) than OS strains (Oh *et al.,* 2019). *C. jejuni* possesses both surface polysaccharides, capsular polysaccharide (CPS) and lipopolysaccharide (LPS), on the outer membrane (Jeon *et al.,* 2009). Under aerobic conditions, the carbon metabolism of *C. jejuni* increased, leading to elevated amino acid uptake (Kim *et al.,* 2023). This stimulated the formation of thicker CPS and LPS, which potentially function as a permeability barrier, protecting the pathogen from excess oxygen in aerobic atmosphere (Kim *et al.,* 2023). Thus, the comparison of the structure of CPS and LPS among aerotolerance levels could be interesting. Further, the relationship between aerotolerance, VBNC, biofilm, oxidative stress defense enzymes, and protective polysaccharides of *Campylobacter* spp. remains scanty.

Genetic relatedness of aerotolerant *Campylobacter* spp. strains

Discriminatory typing methods for *Campylobacter* spp. are important for improving the understanding of epidemiology and genetic background (Nielsen *et al.,* 2010). Multilocus sequence typing (MLST) is a valuable typing tool for discriminating *Campylobacter* spp. isolates and defining population structure (Dingle *et al.,* 2001, 2005). The ST obtained from MLST can be grouped into CC based on relatedness (Nielsen *et al.,* 2010). Table S9 shows the summary of eight studies on the classification of CC and ST based on aerotolerance level in *C. jejuni* and *C. coli*. The aerotolerance level comparison between ST was not made for Kiatsomphob *et al.* (2019), as the study did not disclose ST for each CC. Data from Table S9 are regrouped based on the respective CC and ST of *C. jejuni* and *C. coli* with aerotolerance levels, and are shown in Figure 7. Data from certain studies that did not classify CC to aerotolerance were further analyzed and classified based on the data from their published articles and supplementary documents (Guk *et al.,* 2019, 2021; Jaakkonen *et al.,* 2020; Kiatsomphob *et al.,* 2019).

Ordinal logistic regression analysis of 364 *Campylobacter* spp. isolates (input data from Table S9) showed that ST had a statistically significant ($P < 0.001$) influence on aerotolerance level. It has been postulated that the ST of *Campylobacter* spp. is related to aerotolerance levels. As shown in Figure 7, CC-353 showed the highest prevalence in HAT *C. jejuni,* while CC-21 showed the highest prevalence in AT *C. jejuni*. CC-353 was associated with a very high level of resistance to erythromycin (Jehanne *et al.*, 2025). Further, CC-21 was the most prevalent in human and poultry slaughterhouse (Jeong *et al.*, 2025).

In *C. coli*, CC-828 was the most prevalent CC in all three classes of aerotolerance (OS, AT, and HAT) strains, as shown in Figure 7. The most prevalent *C. coli* ST among both HAT and AT in the study of Guk *et al.* (2019) was ST-855, and this ST was not detected in OS strains. In contrast, the highest prevalent ST (ST-1068) among HAT strains in the study conducted by Guk *et al.* (2021) was detected in OS strains. Further, MLST data of *C. coli* isolates from ducks were compared to genetic relatedness to human sources in PubMLST and NCBI databases (Guk *et al.,* 2019). Eight ST out of 18 from duck isolates were identified and found to be shared with human sources (Guk *et al.,* 2019). HAT *C. coli* had a significantly higher

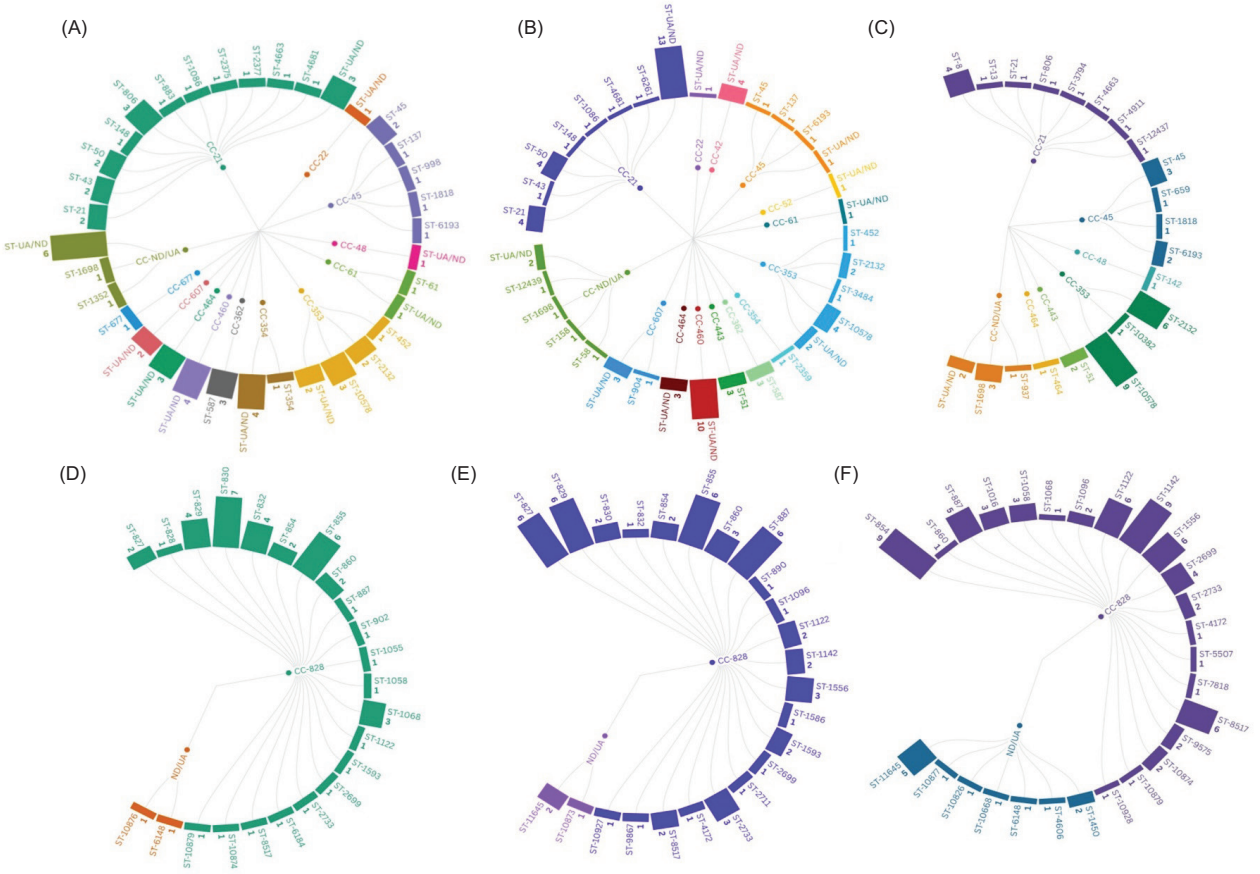

Figure 7. Radial graphs of CC and ST of (A) OS *C. jejuni*, (B) AT *C. jejuni*, (C) HAT *C. jejuni*, (D) OS *C. coli*, (E) AT *C. coli*, and (F) HAT *C. coli*. The frequency of ST is in bold face below the respective ST. CC: clonal complex; ST: sequence type; UA: unassigned to any CC; ND: not determined; OS: aero-sensitive; AT: aerotolerant; HAT: hyperaerotolerant.

proportion among shared ST than non-shared ST, while OS showed the opposite trend (Guk *et al.,* 2019). In addition, a higher proportion of genetic relatedness was also reported between swine-derived HAT *C. coli* and human *C. coli* isolates, than OS strains (Guk *et al.,* 2021).

Several studies reported a high proportion of shared STs in *Campylobacter* spp. between food-producing animals and human clinical cases (Asakura *et al.,* 2019; Litrup *et al.,* 2007; Ramonaite *et al.*, 2017). Findings of Ortega-Sanz *et al.* (2024), Kiatsomphob *et al.* (2019), and Rodrigues *et al.* (2015), as summarized in Table S9, showed that HAT and AT strains were highly prevalent in human campylobacteriosis cases. Thus, the relationship between aerotolerance level and the overlap ST between food-producing animals and human clinical cases will be an interesting research field.

Risk of aerotolerant *Campylobacter* spp. to humans

In view of the enhanced resistance of AT *Campylobacter* spp. against multiple environmental stresses, such as atmospheric stress, disinfectant exposure, freeze-thaw, refrigeration, heat treatment, and osmotic stress, the AT *Campylobacter* spp. strains might survive better throughout the food chain. This would, in turn, augment foodborne transmission to humans (Guk *et al.,* 2019; Mouftah *et al.,* 2021).

Mihaljevic *et al.* (2007) found that 5 h aerobic exposure of *C. jejuni* significantly elevated invasion capacity in the Caco-2 cells model, suggesting that normal atmospheric conditions might be associated with the pathogenicity of pathogen. The AT *Campylobacter* spp. might have better oxidative stress resistance and could become more pathogenic, as the pathogen might be less susceptible to the free radicals produced by host immune response (Atack and Kelly, 2009). Furthermore, the aerotolerance of *Campylobacter* spp. is to some extent related to oxidative stress resistance and colonization factors in chickens, which contribute to their high prevalence in food as well as their elevated pathogenicity in human infections (Bolton, 2015; Flint *et al.,* 2016; Hermans *et al.,* 2011).

The risk of AT *Campylobacter* spp. to human health can be higher than that of the normal *Campylobacter* spp.

evaluated in the past, as AT strains are commonly present in food. Thus, stricter regulations could be implemented for AT *Campylobacter* spp., as in the case of *E. coli* O157:H7 in the pathogenic *E. coli* strain.

Antibiotic resistance in aerotolerant *Campylobacter* spp.

To date, studies relating the aerotolerance profile of *Campylobacter* spp. to the antibiotic resistance profile are scarce, with no study conducted on *C. jejuni*. No significant differences were found between the antibiotic resistance rates and aerotolerance profiles in 56 *C. coli* isolates (Guk *et al.,* 2019). However, 25% (7/28) of HAT and 9.1% (2/22) of AT *C. coli* isolates were highly resistant to ciprofloxacin (≥32 μg/mL), while none was from OS isolates (Guk *et al.,* 2019). Similarly, in another study conducted by the same research group on pig feces, HAT *C. coli* showed the highest proportion (18.8%) in high-level ciprofloxacin resistance (Guk *et al.,* 2021). Thus, AT strains might be more difficult to treat and place a greater medical burden because of higher antibiotic resistance. However, more studies are warranted to elucidate the relationship between aerotolerance and antibiotic resistance profiles.

Prevalence of virulence genes in aerotolerant *Campylobacter* spp.

Similar to the antibiotic-resistant profile, only a few studies linked virulence genes to the aerotolerance of *Campylobacter* spp. HAT *C. coli* isolates were reported to possess all 10 virulence genes analyzed, such as *flaA* (motility), *flhB* (motility), *cadF* (adhesion), *pldA* (adhesion), *iamA* (invasion), *ceuE* (invasion), *cdtA* (cytoxin), *wlaN* (Guillain–Barré syndrome), *hcp* (type VI secretion system), and *virB11* (type IV secretion system), with the prevalence ranging from 3.6% to 100% (Guk *et al.,* 2019, 2021). As compared to HAT *C. coli*, only six virulence genes were reported in OS *C. coli*, whereas seven virulence genes were found in AT *C. coli* (Guk *et al.,* 2019). However, the prevalence of virulence genes was not significantly different between OS, AT, and HAT isolates (Guk *et al.,* 2019, 2021).

Conversely, among 70 *C. jejuni* isolates, HAT *C. jejuni* strains depicted significantly higher frequencies of virulence genes than OS strains, suggesting HAT strains could be more pathogenic to humans than their OS counterparts (Oh *et al.,* 2017). Similarly, Rodrigues *et al.* (2018) reported that AT *C. jejuni* Bf strain is one of the most virulent strains among the 10 strains tested. However, the study did not relate the aerotolerance levels of strains to the level of virulence.

The gene involved in the aerobic survival of *Campylobacter* spp. can also contribute to virulence. For instance, *sodB*, which is important for *C. coli* survival under aerobic conditions, plays an important role in colonizing the chick (Purdy *et al.,* 1999). In the context of the virulence genes expression, such as *cadF*, *cdtB* (cytotoxin), *ciaB* (invasion), and *clpP* (stress tolerance), no significant difference was discovered in the expression between two AT *C. jejuni* strains and one OS *C. jejuni* strain (Lee *et al.,* 2019). Therefore, the prevalence and expression of virulence genes in relation to aerotolerance level warrants further study to improve our understanding. AT strains with higher virulence genes might increase pathogenicity and thus contribute to higher campylobacteriosis cases.

Conclusion and the Way Forward

Research has increasingly demonstrated that AT *Campylobacter* spp. are prevalent in retail food, exhibiting increased pathogenicity and resistance to multiple environmental stresses. AT *Campylobacter* spp. might bring immense burdens to the economy and health care. The persistence of AT *Campylobacter* spp. is associated with a battery of survival mechanisms against various environmental stresses. Based on the current findings, it will not be surprising that the term 'aerobic microorganism' could be used to describe *Campylobacter* spp. in near future. This demonstrated the dire need to bolster our understanding of the relationship between survivability and the associated mechanisms in order to develop a holistic preventive measure to curtail this emerging pathogen.

To translate the available findings into real-world food safety practices, a surveillance program for AT *Campylobacter* spp. in the food chain is pivotal, and policymakers should urgently evaluate and revise the current protocol for public health. From that, modified atmospheric packaging, better hygienic practices, and greater coverage of cold chain transportation could be corrective measures to be considered.

In order to better contribute to future research in AT *Campylobacter* spp., several research gaps could be underpinned as illustrated in Figure S3 and stated as follows:

- Standardized protocols for aerotolerance level classification and aerobic acclimatization.
- Prevalence study of aerotolerance level and aerobic growth involving a larger sample size, a variety of foods, and different geographical regions.

- Elucidation on other clinically important *Campylobacter* spp.
- Survivability of single-strain, multiple-strain of the same species and multiple species against environmental stresses *in vitro* and *in situ*.
- Identification of ST of the strains and relating it to the source of the isolate and aerotolerance level.
- Phenotypic mechanism for aerotolerance, aerobic acclimatization, and aerobic growth.
- Antibiotic resistance profile on a variety of antibiotics with different doses and the prevalence and expression of virulence genes.
- Gene regulatory mechanism between aerotolerance, antibiotic resistance, and virulence.
- Characterization and assessment of health burden via risk assessment for better policy implementation.

Mandatory Disclosure on Use of Artificial Intelligence

The authors declare that no AI-assisted tools were used in the preparation of this manuscript. All references have been manually verified for accuracy and relevance.

Declaration of Completing Interest

The authors declared that no completing financial interests or personal relationship that could influence the work of this study involved.

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Author Contributions

All authors contributed equally to this article.

Conflict of Interest

The authors declared no conflict of interest.

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Supplementary

Table S1. Summary of risk of bias assessment (quality assessment) of 39 included articles.

		Points								Scores (%)
		Clearly stated aims/ objectives	Detailed explanation of sampling technique	Details of comparison group	Detailed explanation of methodology	Randomization	Method of measurement of outcome	Statistical analysis	Presentation of results	
1	Atack *et al*., 2008	1	2	2	2	0	2	2	2	81.25
2	Baillon *et al*., 1999	2	2	2	2	0	2	1	2	81.25
3	Bronnec *et al*., 2016a	2	2	2	2	0	2	2	2	87.5
4	Bronnec *et al*., 2016b	2	2	2	2	0	2	1	2	81.25
5	Chynoweth *et al*., 1998	2	2	2	2	0	2	1	2	81.25
6	Guk *et al*., 2019	2	2	2	2	0	2	2	2	87.5
7	Guk *et al*., 2021	2	2	2	2	0	2	2	2	87.5
8	Guk *et al*., 2022	2	2	2	2	0	2	2	2	87.5
9	Gundogdu *et al*., 2015	1	2	2	2	0	2	2	2	81.25
10	Hur *et al*., 2024	2	2	2	2	0	2	2	2	87.5
11	Hwang *et al*., 2014	1	2	2	2	0	2	1	2	75
12	Jaakkonen *et al*., 2020	2	2	2	2	0	2	2	2	87.5
13	Jones *et al*., 1993	2	0	2	2	0	2	1	2	68.75
14	Kaakoush *et al*., 2007	2	2	2	2	0	2	1	2	81.25
15	Karki *et al*., 2018	2	2	2	2	0	2	1	2	81.25
16	Karki *et al*., 2019	2	2	2	2	0	2	2	2	87.5
17	Kiatsomphob *et al*., 2019	1	2	2	2	0	2	1	2	75
18	Kim *et al*., 2019	2	2	2	2	0	2	2	2	87.5
19	Kim *et al*., 2023	1	2	2	2	0	2	2	2	81.25
20	Lee *et al*., 2019	2	2	2	2	0	2	2	2	87.5
21	Mouftah *et al*., 2021	2	2	2	2	0	2	2	2	87.5
22	Oh *et al*., 2015a	1	2	2	2	0	2	2	2	81.25
23	Oh *et al*., 2015b	1	2	2	2	0	2	2	2	81.25
24	Oh *et al*., 2017	2	2	2	2	0	2	2	2	87.5
25	Oh *et al*., 2018	2	2	2	2	0	2	2	2	87.5
26	Oh *et al*., 2019	1	2	2	2	0	2	2	2	81.25

27	O'Kane and Connerton, 2017	1	2	2	2	0	2	1	2	75
28	Ortega *et al.*, 2024	2	2	2	2	0	2	2	2	87.5
29	Pokhrel *et al*., 2023	1	2	2	2	0	2	2	2	81.25
30	Pokhrel *et al*., 2024	2	2	2	2	0	2	1	2	81.25
31	Purdy *et al*., 1999	1	2	2	2	0	2	1	2	75
32	Rodrigues *et al.*, 2015	2	2	2	2	0	2	2	2	87.5
33	Rodrigues *et al.*, 2016	2	2	2	2	0	2	2	2	87.5
34	Rodrigues *et al.*, 2018	2	2	2	2	0	2	2	2	87.5
35	Shagieva *et al.*, 2021	1	2	2	2	0	2	1	2	75
36	Song *et al*., 2020	2	2	2	2	0	2	1	2	81.25
37	van Vliet *et al.*, 2001	1	2	2	2	0	2	1	2	75
38	Vandamme *et al*., 1992	1	2	2	2	0	2	1	2	75
39	Yagi *et al*., 2022	2	2	2	2	0	2	2	2	87.5

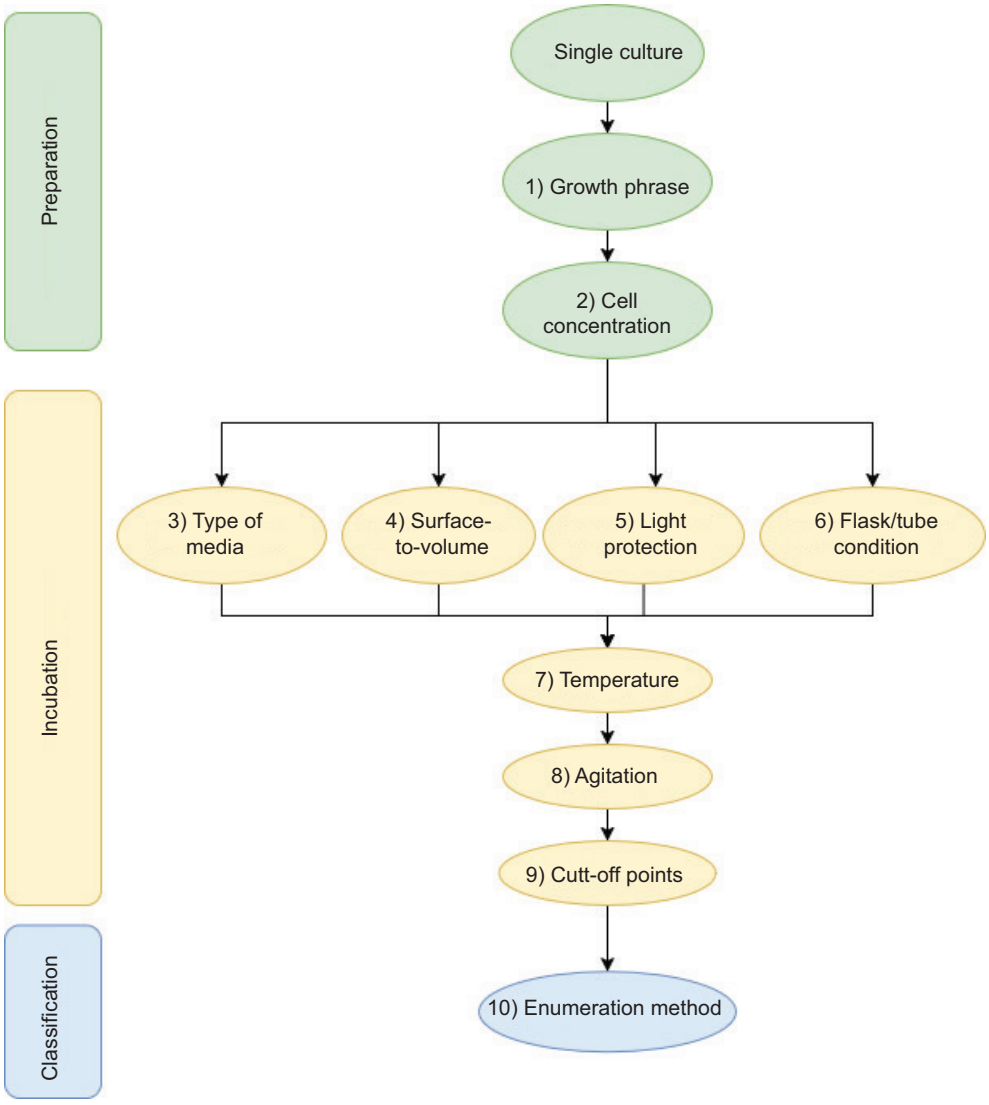

Figure S1. Schematic diagram of standardization protocol for aerotolerance assay.

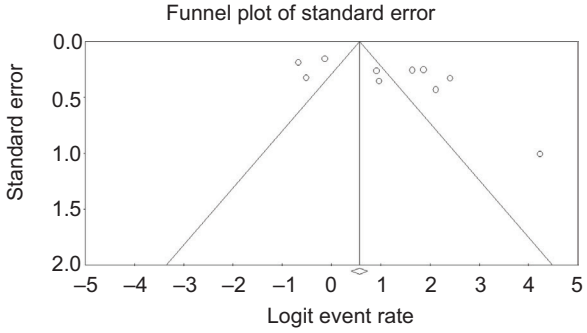

Figure S2. Funnel plot assessing publication bias for prevalence of aerotolerant *Campylobacter* spp..

Table S2. Summary of sixteen articles on the prevalence of aerotolerant *Campylobacter* spp.

Isolate origin	Aerotolerance of *C. jejuni* Percentage (number of isolates/ total number of isolates)			Aerotolerance of *C. coli* Percentage (number of isolates/ total number of isolates)			References
	OS	AT	HAT	OS	AT	HAT	
Clinical sample	0% (0/5)	40% (2/5)	60% (3/5)	–	–	–	Ortega–Sanz *et al.,* 2024
Poultry processing plant	62.5% (25/40)	25% (10/40)	12.5% (5/40)	–	–	–	Pokhrel *et al.,* 2023
Swine faeces	–	–	–	58.1% (72/124)	28.2% (35/124)	13.7% (17/124)	Guk *et al.,* 2021
Dairy product, broiler carcass, and clinical sample	14.4% (13/90)	20% (18/90)	65.6% (59/90)	23.8% (5/21)	19.1% (4/21)	57.1% (12/21)	Mouftah *et al.,* 2021
Pond water, outlet of wastewater treatment plant, raw chicken meat and clinical setting	78.6% (11/14)	21.4% (3/14)	–*	–	–	–	Shagieva *et al.,* 2021
Milk, cattle, and udder cloth	0% (0/8)	37.5% (3/8)	62.5% (5/8)	–	–	–	Jaakkonen *et al.,* 2020
Duck carcass and meat	–	–	–	10.7% (6/56)	39.3% (22/56)	50% (28/56)	Guk *et al.,* 2019
Chicken liver and human	100% (2/2)	–	–	–	–	–	Karki *et al.,* 2019
Chicken liver and beef liver	–	–	–	0%(0/2)	50% (1/2)	50% (1/2)	Karki *et al.,* 2019
Chicken meat	13.3% (12/90)	50% (45/90)	36.7% (33/90)	–	–	–	Kim *et al.,* 2019
Duck meat	13.3% (6/45)	62.2% (28/45)	24.4% (11/45)	–	–	–	Kim *et al.,* 2019
Human	0% (0/26)	84.6% (22/26)	15.4% (4/26)	–	–	–	Kiatsomphob *et al.,* 2019
Broiler	5% (1/20)	35% (7/20)	60% (12/20)				Kiatsomphob *et al.,* 2019
Cattle	0% (0/24)	50% (12/24)	50% (12/24)				Kiatsomphob *et al.,* 2019
Chicken	100% (8/8)	0% (0/8)	–*	–	–	–	Lee *et al.,* 2019
Duck	66.7% (4/6)	33.3% (2/6)					
Human stool	8.3% (10/121)	38.0% (46/121)	53.7% (65/121)	–	–	–	Oh *et al.,* 2018
Chicken meat, chicken liver, chicken gizzard, beef liver, turkey and pork	93.4% (71/76)	3.9% (3/76)	2.6% (2/76)	38.5% (18/91)	19.8% (35/91)	41.8% (38/91)	Karki *et al.,* 2018
Chicken meats	28.6% (20/70)	35.7% (25/70)	35.7% (25/70)	–	–	–	Oh *et al.,* 2015a
Human, water and raw chicken	27.5% (11/40)	72.5% (29/40)	–*	–	–	–	Chynoweth *et al.,* 1998
N/A	0% (0/25)	100% (25/25)	–*				Jones *et al.,* 1993

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; N/A = Not available; * = HAT classification not determined.

Table S3. Summary of six articles on the survival of *Campylobacter* spp. with different levels of aerotolerance under atmospheric stress.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (HAT, AT)	Milk, cattle, human, udder cloth, and cattle	6 HAT and 3 AT	MH broth	10^6 CFU/mL with 200 rpm shaking at 41.5°C for 72 h under AC	• HAT *C. jejuni* survived longer than AT *C. jejuni*.	Jaakkonen *et al.*, 2020
C. coli (HAT, AT) and *C. jejuni* (OS)	Chicken liver, beef liver, and human	1 HAT, 1 AT, and 2 OS	10% liver juice, 10% meat juice, MH broth, and 10% laked horse blood	OD_{600}=0.2 in PBS with 200 rpm shaking at 42°C under AC	• Addition of beef liver juice, chicken liver juice, beef meat juice, and laked horse blood enhanced the aerotolerance.	Karki *et al.*, 2019
C. jejuni (ND), *C. coli* (ND, AT & aerobic passaged)	Human and chicken	4 ND and 1 AT	MH broth	6 $\log_{10}$ CFU/mL with 100 rpm shaking at 37°C for 30 h under AC	• Aerobic passaged *C. coli* did not survive better than its wild type.	O'Kane and Connerton, 2017
C. jejuni (HAT, AT, and OS)	Poultry	2 HAT, 2 AT, and 2 OS	Raw chicken meat and MH broth	OD_{600}=0.1at 4°C under aerobic, CO_2, and N_2 conditions for 14 days	• Under aerobic incubation in meat, HAT and AT survived significantly higher than OS. HAT survived for 14 days while AT survived for 7 days. • Under CO_2, and N_2 incubation in meat, HAT and AT survived significantly better than OS in both CO_2 and N_2, respectively. HAT and AT survived for 14, days under N_2, while OS survived for 7 days. HAT, AT, and OS survived for 7, 5, and 3 days under CO_2, respectively. • Under aerobic incubation in MH broth, HAT, AT, and OS had 2, 3, and 4 $\log_{10}$ CFU reduction, respectively within 3 days. HAT, AT, and OS strains survived for 7 days.	Oh *et al.*, 2017
C. jejuni cocktails (AT)	Human, veterinary, and raw chicken	4 AT	Raw mince chicken, autoclaved mince chicken, and chicken nugget	10^6 CFU/g without shaking at 25°C or 37°C for 8 days under AC	• AT cocktails survived better at 25°C than at 37°C.	Chynoweth *et al.*, 1998
C. jejuni (AT)	13997 (human)	1 AT	BA	9-10 $\log_{10}$ per plate without shaking at 42°C and 37°C for 34 days under AC and MAC	• AT strain survived longer under AC than MAC under both 37°C and 42°C.	Jones *et al.*, 1993

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; ND = Aerotolerant status not determined; AC = Aerobic condition; MAC = Microaerobic condition; MH = Mueller Hinton; BA = Blood agar.

Table S4. Summary four articles on the survival of *Campylobacter* spp. with different levels of aerotolerance under oxidative stress.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (AT, HAT)	Clinical setting	3 HAT and 2 AT	MH broth	10^8 CFU/mL and exposed to 5 mM H_2O_2, 3.35 µM CHP at 37°C for 1 h (atmosphere not specified)	• One AT strain survived significantly less than the HAT strains, while the other AT strain survived significantly more than the HAT strains.	Ortega-Sanz *et al.*, 2024
C. coli (HAT, AT, OS) and *C. jejuni* (HAT, AT, OS)	Chicken meat, chicken liver, chicken gizzard, pork, and beef liver	6 HAT, 4 AT, and 4 OS	MH agar	OD_{600} = 0.15 in PBS and exposed to 0.05, 0.1, and 0.5 mM H_2O_2 at 45°C for 24 h (atmosphere not specified)	• No correlation between H_2O_2 and aerotolerance.	Karki *et al.*, 2018
C. jejuni (HAT, AT, OS)	Retail broiler	2 HAT, 2 AT, and 2 OS	MH broth	10^8 CFU/mL and exposed to 1 mM H_2O_2, 100 µM CHP or 100 µM MND for 1 h (atmosphere and temperature not specified)	• OS strains survived significantly less than AT and HAT strains against H_2O_2, CHP, and MND. • AT strains survived significantly less than HAT strains against H_2O_2, CHP, and MND.	Oh *et al.*, 2015a
C. jejuni (ND, AT)	NCTC 11168 and human	1 ND and 1 AT	Peptone saline solution	OD_{600} = 0.03 and exposed to 0.12, 0.25, 0.50, and 1 mM of H_2O_2 or PQ at 42°C for 1 h under MAC	• AT strain demonstrated a better survival rate than ND strain under H_2O_2 and PQ.	Rodrigues *et al.*, 2015

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; ND = Aerotolerant status not determined; H_2O_2 = Hydrogen peroxide; CHP = Cumene hydroperoxide; MND = Menadione; PQ = Paraquat; BA = Blood agar; MH = Mueller Hinton; AC = Aerobic condition; MAC = Microaerobic condition; PBS = Phosphate Buffered Saline.

Table S5. Summary of four articles on the aerobic growth of *Campylobacter* spp.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (NA)	Pond water, outlet of wastewater treatment plant, raw chicken meat, and clinical setting	14	Kamali agar	3.0 McFarland in PBS inoculated on Karmali agar without shaking at 42°C for 96 h	• Inconsistent with three independent experiments.	Shagieva *et al.*, 2021
C. coli (AT with AA and AT with non-AA)	Bird	1	BA and CCDA	10 µl drop of 10^5 CFU on BA without shaking at 37°C for 48 h 10 µl drop of 10^8 CFU/mL on BA and CCDA without shaking at 42°C for 6 days.	• Both AA and non-AA strains demonstrated aerobic growth on BA. • Both AA and non-AA strains demonstrated aerobic growth on both BA and CCDA.	O'Kane and Connerton, 2017
C. jejuni (AT)	Human	1	Karmali agar	OD_{600} = 0.03 in peptone saline solution on Karmali agar without shaking at 42°C for 48 h	• No significant difference in growth rate between *C. jejuni* prepared in AA and non-AA.	Rodrigues *et al.*, 2015
C. jejuni (AT)	Human, water, and raw chicken	40	Nutrient agar	Inoculated from nutrient agar without shaking at 37°C for 5 days	• Majority of isolates grew aerobically.	Chynoweth *et al.*, 1998

AT = Aerotolerant; ND = Aerotolerant status not determined, BA=Blood agar; MH = Mueller Hinton; CCDA = Charcoal Cefoperozone Deoxycholate agar; AA = Aerobically acclimatize; PBS = Phosphate Buffered Saline.

Table S6. Summary of three articles on the survival of *Campylobacter* spp. with different levels of aerotolerance against chemical stress.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubation conditions	Findings	References
C. jejuni (HAT, AT, and OS) and *C. coli* (HAT, AT, and OS)	Clinical setting, dairy products, and broiler carcasses	70 HAT, 25 AT, and 16 OS	Raw chicken skin	Followed Oh *et al.*, 2018	• Both HAT and AT strains had significantly better survival than OS strains, with none of the OS strain survived. • Most of the *C. jejuni* isolates showed significantly greater resistance to PAA than *C. coli,* with higher final mean cell numbers.	Mouftah *et al.*, 2021
C. jejuni (HAT, AT, and OS)	Chicken	25 HAT, 25 AT, and 20 OS	Raw chicken skin	Followed Oh *et al.*, 2018	• OS strains had the highest significant reduction in cell number than the AT and HAT strains.	Oh *et al.*, 2019
C. jejuni (HAT, AT, and OS)	Clinical setting	65 HAT, 46 AT, and 10 OS	Raw chicken skin	OD_{600} = 0.1 in MH broth, incubated at 4° C under MAC for 1 h for cell attachment. Immerse chicken skin in 750 ppm PAA for 15 s	• Majority of HAT and AT strains survived, while only one OS strain survived.	Oh *et al.*, 2018

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; ND = Aerotolerant status not determined; MH = Mueller Hinton; AC = Aerobic condition; MAC = Microaerobic condition.

Table S7. Summary of thirteen articles on the survival of *Campylobacter* spp. with different levels of aerotolerance against temperature stress.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (HAT, AT, and OS)	Retail broiler chicken	33 HAT, 45 AT, and 12 OS	MH broth	4°C under AC and MAC conditions for 21 days	• All strains survived under aerobic conditions but not under microaerobic conditions. • Strains viability significantly higher under aerobic conditions. • compared to microaerobic.	Hur *et al.*, 2024
C. jejuni (HAT, AT, and OS)	Poultry processing plants	5 HAT, 10 AT, and 25 OS	Broiler chicken drumsticks with skin	4°C for 7 days (atmosphere not specified) -20°C for 7 days (atmosphere not specified)	• Significant reduction in HAT compared to OS and AT. • AT survived significantly better than HAT and OS. • HAT survived the least.	Pokhrel *et al.*, 2023
C. jejuni (HAT, AT, and OS) and *C. coli* (HAT, AT, and OS)	Clinical strains, dairy products, and broiler carcasses	70 HAT, 25 AT, and 16 OS	Raw chicken skin	4°C for 7 days (atmosphere not specified) -20°C for 7 days (atmosphere not specified)	• Significant reduction in OS and AT strains than HAT strains after 7 days. • More HAT strains survived than AT strains and none of the OS strains survived.	Mouftah *et al.*, 2021
C. jejuni (HAT, AT, and OS) and *C. coli* (HAT, AT, and OS)	Clinical strains, dairy products, and broiler carcasses	70 HAT, 25 AT, and 16 OS	Milk	72°C for 15 s or 30 s under AC	• Higher proportion of HAT strains survived than AT, and AT strains survived better than OS strains.	Mouftah *et al.*, 2021
C. jejuni (AT and maybe AT*)	Pond water, outlet of wastewater treatment plant, raw chicken meat, and clinical setting	3 AT and 11 maybe AT	MH broth	7°C under AC and MAC	• All 14 strains maintained their viability up to 4 weeks under MAC. • Under aerobic incubation, no trend was observed for AT and the other strains.	Shagieva *et al.*, 2021
C. jejuni (HAT and AT)	Milk, cattle, NCTC 11168, and udder cloth	6 HAT and 3 AT	Milk	4°C under AC	• HAT strains survived longer than AT strains.	Jaakkonen *et al.*, 2020
C. coli (HAT and AT) and *C. jejuni* (OS)	Chicken liver, beef liver, and NCTC 11168	1 HAT, 1 AT, and 2 OS	100% or 10% of chicken meat juice, beef meat juice, beef liver juice, chicken liver juice, 5% laked horse blood and 5% defibrinated horse blood	4°C under MAC	• Meat juices, liver juices, and horse blood increased the survival of HAT, AT, and OS strains compared to MH broth.	Karki *et al.*, 2019
C. jejuni (AT and OS)	Chicken	2 AT and 1 OS	BHI	4°C under AC	• No significant difference in survival between AT and OS.	Lee *et al.*, 2019
C. jejuni (HAT, AT, and OS)	Chicken	25 HAT, 25 AT, and 20 OS	MH broth	4°C (not stated atmosphere) -20°C (not stated atmosphere) 72°C for 15 s or 30 s (not stated atmosphere)	• OS strains exhibit a significantly low survival after storage for seven days compared to HAT and AT. • More HAT and AT strains survived after seven days than OS strains. • 1 HAT and 1 AT strains survived after 30 s.	Oh *et al.*, 2019

(*continues*)

Table S7. Continued.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (HAT, AT, and OS)	Clinical setting	65 HAT, 46 AT, and 10 OS	Chicken skin	4°C under AC –20°C (not stated atmosphere)	• Some HAT and AT strains survived after 2 weeks, while only one OS *C. jejuni* strain survived after 3 days. • Some HAT strains only reduce <1 log_{10} CFU/g meat after 2 weeks. • Most HAT and AT survived after 7 days. • No OS survived after 3 days.	Oh *et al.*, 2018
C. jejuni (HAT, AT, and OS)	Clinical setting	65 HAT, 46 AT, and 10 OS	Whole milk	72°C for 15 s or 30 s under AC	• Most HAT and AT survived after heat treatments, while no OS strain survived.	Oh *et al.*, 2018
C. jejuni (HAT, AT, and OS)	Chicken	2 HAT, 2 AT, and 2 OS	Chicken meat and MH broth	4°C under AC, N_2 and CO_2	• In both chicken meat and MH broth under three atmospheric conditions (AC, N_2, and CO_2), HAT survived longer with a lower cell reduction than AT, while AT survived longer with a lower cell reduction than OS.	Oh *et al.*, 2017
C. jejuni (AT)	NCTC 11351 (bovine)	1 AT	Autoclaved minced chicken	5°C under AC	• Both microaerobically-grown and aerobically-grown isolates survived until 19 days, with aerobically-grown isolates had higher survival.	Chynoweth *et al.*, 1998
C. jejuni cocktails (AT)	Human, veterinary case, and raw chicken	4 AT	Sterilized stream water	5°C under AC and MAC	• Rate of decline in survival is greater in aerobically-grown *C. jejuni* cocktail than microaerobically-grown under AC.	Chynoweth *et al.*, 1998
C. jejuni (AT)	13997 (human)	1 AT	Blood agar	5°C under AC and MAC	• For non-aerobic adapted *C. jejuni*, the strain survived longer under AC than MAC conditions. • Aerobic-adapted *C. jejuni* survived longer than non-aerobic adapted *C. jejuni.*	Jones *et al.*, 1993

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; ND = Aerotolerant status not determined; BA = Blood agar; MH = Mueller Hinton; BHI = Brain heart infusion; AC = Aerobic condition; MAC = Microaerobic condition; *the term "maybe aerotolerant" was stated due to inconsistency in the level of aerotolerance.

Table S8. Summary of three articles on the survival of *Campylobacter* spp. with different levels of aerotolerance against osmotic stress.

Aerotolerance level of isolates	Isolate origin	Number of isolates	Experimental Media	Incubating conditions	Findings	References
C. jejuni (HAT, AT, and OS) and *C. coli* (HAT, AT, and OS)	Clinical setting, dairy products, and broiler carcasses	70 HAT, 25 AT, and 16 OS	MH broth	OD_{600} = 0.1 in MH broth with 0, 2, and 4% NaCl in MH broth incubated at 42° C under MAC	• At 4% NaCl, 58% of the HAT strains and 8% of the AT strains survived, while none of the OS strains survived. • At 4% NaCl, the final cell concentration of HAT strains was significantly higher than AT strains while significantly higher in AT than OS strains.	Mouftah *et al.,* 2021
C. jejuni (HAT, AT, and OS)	Chicken	25 HAT, 25 AT, and 20 OS	MH agar	OD_{600} = 0.1 in MH broth, a drop of 10x diluted culture spotted on MH agar supplemented with 1, 2, and 4 % NaCl incubated at 42° C overnight (atmosphere not specified)	• Osmotolerance is not related to aerotolerance.	Oh *et al.,* 2019
C. jejuni (HAT, AT, and OS)	Clinical setting	65 HAT, 46 AT, and 10 OS	MH agar	2 and 4 % NaCl incubated at 42°C overnight under MAC	• In 2 % NaCl, higher CFU/mL survived in HAT and AT strains than OS strains. • In 4% NaCl, 38.7% of the HAT and AT strains survived on agar, while none of the OS strains survived.	Oh *et al.,* 2018

OS = Aero-sensitive; AT = Aerotolerant; HAT = Hyper-aerotolerant; MH = Mueller Hinton; AC = Aerobic condition; MAC = Microaerobic condition.

Table S9. Summary of eight articles on the classification of CC based on the level of aerotolerance of *C. jejuni* and *C. coli*.

Strains	Source	Aero-sensitive	Aerotolerant	Hyperaerotolerant	References
C. jejuni	Clinical setting	–	CC-607 (20%, 1/5) CC-21 (20%, 1/5) ST-904 (CC-607, 20%, 1/5) ST-148 (CC-21, 20%, 1/5)	CC-354 (20%, 1/5) CC-677 (20%, 1/5) CC-21 (20%, 1/5) ST-354 (CC-354, 20%, 1/5) ST-677 (CC-677, 20%, 1/5) ST-148 (CC-21, 20%, 1/5)	Ortega-Sanz *et al.*, 2024
C. jejuni	Poultry processing plant	CC-21 (12.5%, 5/40) CC-443 (5%, 2/40) CC-464 (2.5%, 1/40) CC-353 (40%, 16/40) ST-12437 (CC-21, 2.5%, 1/40) ST-8 (CC-21, 10%, 4/40) ST-51 (CC-464, 5%, 2/40) ST-464 (CC-464, 2.5%, 1/40) ST-2132 (CC-353, 15%, 6/40) ST-10382 (CC-353, 2.5%, 1/40) ST-10578 (CC-353, 20%, 8/40)	CC-443 (7.5%, 3/40) CC-353 (15%, 6/40) CC-UA (2.5%, 1/40) ST-51 (CC-443, 7.5%, 3/40) ST-2132 (CC-353, 5%, 2/40) ST-10578 (CC-353, 10%, 4/40) ST-12439 (CC-UA, 2.5%, 1/40)	CC-353 (15%, 6/40) ST-2132 (5%, 2/40) ST-10578 (10%, 4/40)	Pokhrel *et al.*, 2023
C. coli	Swine	CC-828 (85%, 61/72) ND (15%, 11/72) ST-854 (CC-828, 13%, 9/72) ST-1142 (CC-828, 13%, 9/72) ST-1122 (CC-828, 8%, 6/72) ST-1556 (CC-828, 8%, 6/72) ST-8517 (CC-828, 8%, 6/72) ST-887 (CC-828, 7%, 5/72) ST-11645 (ND, 7%, 5/72) ST-2699 (CC-828, 6%, 4/72) ST-1016 (CC-828, 4%, 3/72) ST-1058 (CC-828, 4%, 3/72) ST-1096 (CC-828, 3%, 2/72) ST-1450 (ND, 3%, 2/72) ST-2733 (CC-828, 3%, 2/72) ST-10874 (CC-828, 3%, 2/72) ST-1068 (CC-828, 1%, 1/72) ST-4172 (CC-828, 1%, 1/72) ST-4606 (ND, 1%, 1/72) ST-10668 (ND, 1%, 1/72) ST-10826 (ND, 1%, 1/72) ST-10877 (ND, 1%, 1/72) ST-10879 (CC-828, 1%, 1/72) ST-10928 (CC-828, 1%, 1/72)	CC-828 (91%, 32/35) ND (9%, 3/35) ST-827 (CC-828, 17%, 6/35) ST-887 (CC-828, 17%, 6/35) ST-1556 (CC-828, 9%, 3/35) ST-2733 (CC-828, 9%, 3/35) ST-854 (CC-828, 6%, 2/35) ST-1122 (CC-828, 6%, 2/35) ST-1142 (CC-828, 6%, 2/35) ST-8517 (CC-828, 6%, 2/35) ST-11645 (ND, 6%, 2/35) ST-830 (CC-828, 3%, 1/35) ST-890 (CC-828, 3%, 1/35) ST-1096 (CC-828, 3%, 1/35) ST-2699 (CC-828, 3%, 1/35) ST-4172 (CC-828, 3%, 1/35) ST-10873 (ND, 3%, 1/35) ST-10927 (CC-828, 3%, 1/35)	CC-828 (94%, 16/17) ND (6%, 1/17) ST-1068 (CC-828, 18%, 3/17) ST-830 (CC-828, 12%, 2/17) ST-854 (CC-828, 12%, 2/17) ST-827 (CC-828, 6%, 1/17) ST-887 (CC-828, 6%, 1/17) ST-1058 (CC-828, 6%, 1/17) ST-1122 (CC-828, 6%, 1/17) ST-2699 (CC-828, 6%, 1/17) ST-2733 (CC-828, 6%, 1/17) ST-8517 (CC-828, 6%, 1/17) ST-10874 (CC-828, 6%, 1/17) ST-10876 (ND, 6%, 1/17) ST-10879 (CC-828, 6%, 1/17)	Guk *et al.*, 2021

C. jejuni	Milk Cattle Udder cloth	–	ST-58 (CC-UA, 100%, 3/3)	CC-21 (60%, 3/5) CC-61 (20%, 1/5) CC-45 (20%, 1/5) ST-50 (CC-21, 20%, 1/5) ST-883 (CC-21, 20%, 1/5) ST-43 (CC-21, 20%, 1/5) ST-61 (CC-61, 20%, 1/5) ST-45 (CC-45, 20%, 1/5)	Jaakkonen *et al.,* 2020
C. coli	Duck	CC-828 (83%, 5/6) CC-UA (17%, 1/6) ST-9575 (CC-828, 33%, 2/6) ST-1860 (CC-828, 17%, 1/6) ST-5507 (CC-828, 17%, 1/6) ST-6148 (CC-UA, 17%, 1/6) ST-7818 (CC-828, 17%, 1/6)	CC-828 (100%, 22/22) ST-855 (27%, 6/22) ST-829 (27%, 6/22) ST-860 (14%, 6/22) ST-1593 (9%, 2/22) ST-830 (5%, 1/22) ST-832 (5%, 1/22) ST-2711 (5%, 1/22) ST-1586 (5%, 1/22) ST-9867 (5%, 1/22)	CC-828 (96%, 27/28) CC-UA (4%, 1/28) ST-855 (CC-828, 23%, 6/28) ST-830 (CC-828, 18%, 5/28) ST-829 (CC-828, 14%, 4/28) ST-832 (CC-828, 14%, 4/28) ST-860 (CC-828, 7%, 2/28) ST-828 (CC-828, 4%, 2/28) ST-902 (CC-828, 4%, 2/28) ST-1055 (CC-828, 4%, 1/28) ST-827 (CC-828, 4%, 1/28) ST-1593 (CC-828, 4%, 1/28) ST-6148 (CC-UA, 4%, 1/28) ST-6184 (4%, 1/28)	Guk *et al.,* 2019
C. jejuni	Human Broiler Cattle	CC-464 (100%, 1/1)	CC-21 (34%, 14/41) CC-460 (24%, 10/41) CC-42 (9%, 4/21) CC-607 (7%, 3/41) CC-464 (7%, 3/41) CC-52 (2%, 1/41) CC-353 (2%, 2/41) CC-22 (2%, 2/41) CC-61 (2%, 1/41) CC-45 (2%, 1/41)	CC-460 (14%, 4/28) CC-354 (14%, 4/28) CC-52 (14%, 4/28) CC-21 (11%, 3/28) CC-464 (11%, 3/28) CC-607 (7%, 2 /28) CC-353 (7%, 2/41) CC-22 (4%, 1/28) CC-61 (4%, 1/28) CC-48 (4%, 1/28) UA (14%, 4/28)	Kiatsomphob *et al.,* 2019
C. jejuni	Human	–	CC-403 (100%, 1/1) ST-403 (100%, 1/1)	-	Rodrigues *et al.,* 2015
C. jejuni	Retail poultry	CC-45 (35%, 7/20) CC-21 (30%, 6/20) CC-48 (5%, 1/20) UA (20%, 4/20) ST-13 (6%, 1/20) ST-21 (6%, 1/20) ST-45 (17%, 3/20) ST-142 (6%, 1/20)	CC-21 (48%, 12/25) CC-45 (12%, 3/25) CC-362 (12%, 3/25) CC-353 (8%, 2/25) CC-354 (4%, 1/25) UA (8%, 2/25) ST-21 (17%, 4/25)	CC-21 (48%, 12/25) CC-45 (20%, 5/25) CC-362 (12%, 3/25) CC-353 (4%, 1/25) UA (8%, 2/25) ST-21 (9%, 2/25) ST-43 (4%, 1/25)	Oh *et al.,* 2015a

(*continues*)

Table S9. Continued.

Strains	Source	Aero-sensitive	Aerotolerant	Hyperaerotolerant	Reference
		ST-659 (6%, 1/20) ST-806 (6%, 1/20) ST-934 (6%, 1/20) ST-1698 (17%, 3/20) ST-1818 (6%, 1/20) ST-3794 (6%, 1/20) ST-4663 (6%, 1/20) ST-4911 (6%, 1/20) ST-6193 (11%, 2/20)UA (11%, 2/20)	ST-43 (4%, 1/25) ST-45 (4%, 1/25) ST-50 (17%, 4/25) ST-137 (4%, 1/25) ST-158 (4%, 1/25) ST-452 (4%, 1/25) ST-587 (13%, 3/25) ST-1086 (4%, 1/25) ST-1698 (4%, 1/25) ST-2359 (4%, 1/25) ST-3484 (4%, 1/25) ST-4681 (4%, 1/25) ST-6193 (4%, 1/25) ST-6261 (4%, 1/25) UA (9%, 2/25)	ST-45 (4%, 1/25) ST-50 (4%, 1/25) ST-137 (4%, 1/25) ST-452 (4%, 1/25) ST-587 (4%, 1/25) ST-806 (4%, 1/25) ST-998 (4%, 1/25) ST-1086 (4%, 1/25) ST-1352 (4%, 1/25) ST-1698 (4%, 1/25) ST-1818 (4%, 1/25) ST-2375 (4%, 1/25) ST-2377 (4%, 1/25) ST-4663 (4%, 1/25) ST-4681 (4%, 1/25) ST-6193 (4%, 1/25) UA (9%, 2/25)	

CC = Clonal complex; ST = Sequence type; UA = Unassigned to any CC; ND = Not determined.

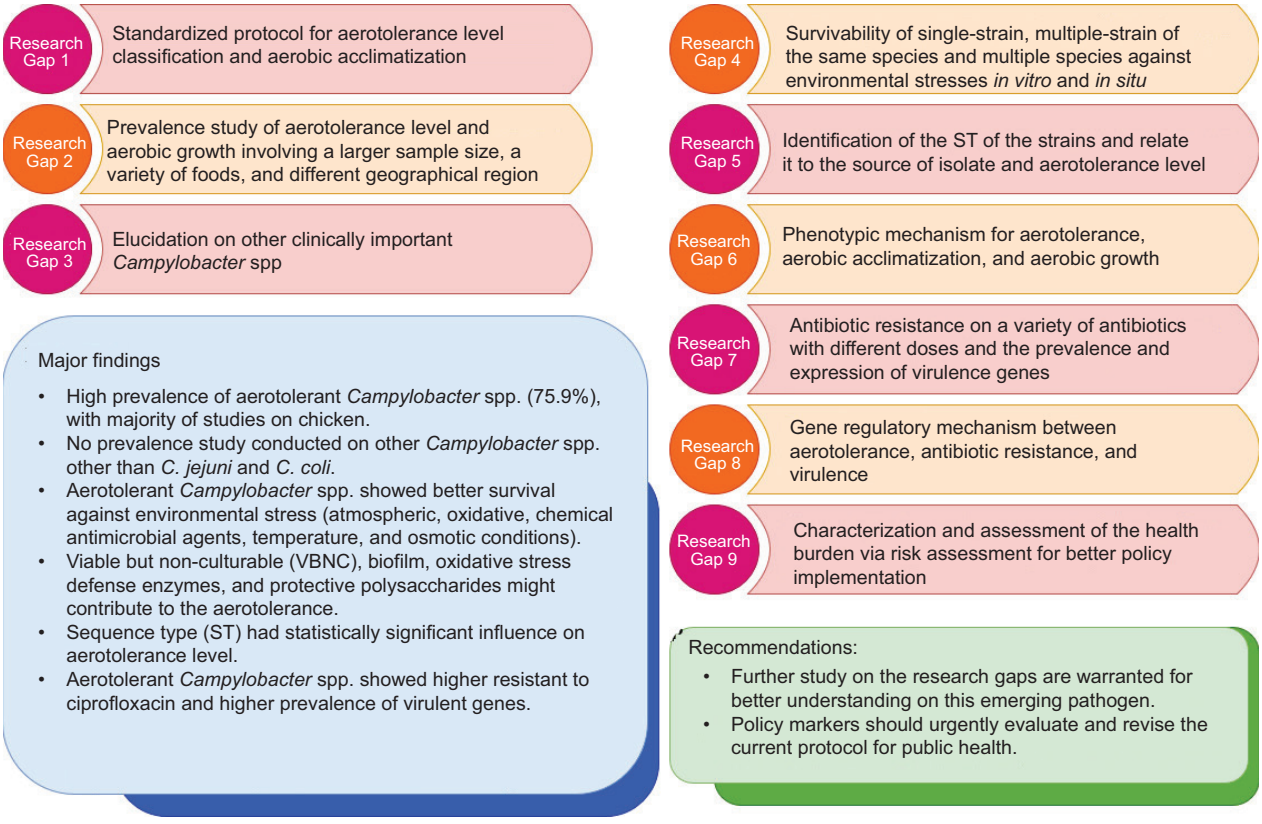

Figure S3. Overview of major findings, research gaps and recommendations of the manuscript.