The bacterial pathogen *Campylobacter jejuni* is primarily transmitted via the consumption of contaminated foodstuffs, especially poultry meat. In food processing environments, *C. jejuni* is required to survive a multitude of stresses and requires the use of specific survival mechanisms, such as biofilms. An initial step in biofilm formation is bacterial attachment to a surface. Here, we investigated the effects of a chicken meat exudate (chicken juice) on *C. jejuni* surface attachment and biofilm formation. Supplementation of *brucella* broth with \( \geq 5\% \) chicken juice resulted in increased biofilm formation on glass, polystyrene, and stainless steel surfaces with four *C. jejuni* isolates and one *C. coli* isolate in both microaerobic and aerobic conditions. When incubated with chicken juice, *C. jejuni* was both able to grow and form biofilms in static cultures in aerobic conditions. Electron microscopy showed that *C. jejuni* cells were associated with chicken juice particulates attached to the abiotic surface rather than the surface itself. This suggests that chicken juice contributes to *C. jejuni* biofilm formation by covering and conditioning the abiotic surface and is a source of nutrients. Chicken juice was able to complement the reduction in biofilm formation of an aflagellated mutant of *C. jejuni*, indicating that chicken juice may support food chain transmission of isolates with lowered motility. We provide here a useful model for studying the interaction of *C. jejuni* biofilms in food chain-relevant conditions and also show a possible mechanism for *C. jejuni* cell attachment and biofilm initiation on abiotic surfaces within the food chain.

Infection by *Campylobacter* species is a global public health concern, estimated to affect 1% of the population in the developed world annually (1). *Campylobacter jejuni* is the most common cause of human *Campylobacter* infection, representing up to 90% of isolates from clinical cases (2). Infection with *C. jejuni* is also linked to severe postinfectious sequelae, such as Guillain-Barré syndrome and reactive arthritis (3–6). This combination of high disease load and severe postinfectious complications makes *C. jejuni* infection a significant economic and disease burden in many countries worldwide.

The major transmission route for *C. jejuni* is thought to be via contaminated food stuffs, with poultry meat being the main source of infection in urban cases. Sampling of chicken meat from supermarkets showed that up to 70% of meat is contaminated with *C. jejuni* (7). In laboratory conditions, *C. jejuni* is a fastidious organism that requires a temperature of 34 to 44°C and microaerobic conditions for growth. However, during transmission through the food chain it encounters stresses, such as changes in temperature, exposure to aerobic conditions, and lack of nutrients. Significant advances have been made in the understanding of *C. jejuni* stress responses; however, there is still a lack of understanding of how these work together to allow survival of *C. jejuni* in the human food chain. One possible contributor to this survival is the ability of *C. jejuni* to form biofilms (8–11).

Biofilms are commonly defined as attached bacterial colonies of either single or multiple species, encased in an extracellular matrix (11). Biofilms support the survival of bacteria in suboptimal conditions and increase resistance to disinfectants, antimicrobials, and antibiotics (10, 12). To date, it is estimated that 99% of bacteria can grow in biofilms, and it has been suggested that for the majority of bacteria, biofilms are the normal mode of existence (13). *C. jejuni* has been shown to form a monospecies biofilm (8–11, 14, 15) and can also integrate into preexisting biofilms (16).

A serious problem in food processing areas is insufficient or ineffective removal of organic material. Spilled foodstuffs or runoff from carcass eviscerations contain a complex blend of carbohydrates, proteins, lipids, and sugars (17), providing an ideal medium for bacteria to thrive and survive. A build-up of these organic materials on a surface is here referred to as a conditioning layer. Conditioning layers assist bacterial attachment to surfaces by altering the surface physicochemical properties and attracting the bacteria to the surface due to the increased nutrient availability (18, 19). One well-studied example of a conditioning layer is the oral pellicle, which assists in the attachment of bacterial species such as *Streptococcus mutans* to the tooth surface and contributes to subsequent periodontal disease (20). Surface conditioning layers have also been shown to be important for the initial attachment of food-borne pathogens; for example, *Listeria monocytogenes* survival rates increase when biological soil is present on stainless steel surfaces (21), and milk proteins are able to increase the attachment of *Escherichia coli*, *L. monocytogenes*, and *Staphylococcus aureus* to stainless steel (22).

To date, most studies on *C. jejuni* biofilms have been performed in laboratory conditions, which do not mimic the conditions encountered in the processing environment. It is important to ensure that studies are designed to allow accurate interpretation and extrapolation of laboratory-obtained results to the food industry (23). Various experimental systems have been used to mimic the conditions encountered by *C. jejuni* in the food chain. These models typically include the use of cooked or raw meat (24),
modeling relevant packaging conditions (23), or the use materials relevant to the food chain such as stainless steel (25). One such model system is the “chicken juice” model (26). This model is based on the collection of exudate from defrosted, commercially obtained chicken carcasses, followed by supplementation or replacement of standard laboratory media with this sterile-filtered liquid. Supplementation of brucella broth with chicken juice resulted in increased survival of planktonic cells of C. jejuni following both chilled and frozen storage (26, 27).

We investigated here the effect of chicken juice on the attachment of C. jejuni to surfaces and subsequent biofilm formation. We show that in the presence of chicken juice, C. jejuni biofilm formation is increased and that this increase in biofilm levels is not simply due to increased cell numbers within the suspensions but to an increase in attachment to abiotic surfaces. We show that this increase in attachment is due to the ability of chicken juice to condition abiotic surfaces relevant to food processing environments.

MATERIALS AND METHODS

C. jejuni strains and growth conditions. C. jejuni reference strains NCTC 11168 (28), 81116 (29), 81-176 (30), and RM1221 (31), an NCTC 11168 nonmotile (afflagellate) mutant (NCTC 11168 ΔflaAB) (10), and C. coli clinical isolate 15-537360 (32) were routinely cultured in a MACS-MG-based liquid. Supplementation of brucella broth with chicken juice replaced standard laboratory media with this sterile-filtered solution.

We show that in the presence of chicken juice, C. jejuni biofilm formation is increased and that this increase in biofilm levels is not simply due to increased cell numbers within the suspensions but to an increase in attachment to abiotic surfaces. We show that this increase in attachment is due to the ability of chicken juice to condition abiotic surfaces relevant to food processing environments.
forms increased levels of biofilm in the presence of chicken juice.

RESULTS

To differentiate between growth and biofilm formation, we assessed growth of C. jejuni NCTC 11168 in brucella broth, brucella broth supplemented with 5% chicken juice, and 100% chicken juice in shaking cultures. There was no statistical difference between growth in brucella broth and media supplemented with 5% chicken juice over a 24 h period (Fig. 1B), and thus the increase in biofilm formation in the presence of chicken juice is likely to be solely due to increased attachment of Campylobacter to the abiotic surface. In 100% chicken juice, the mean \(A_{500}\) value of the 24 h sample was significantly higher than that of the unsupplemented brucella control (data not shown), suggesting that the increased biofilm formation present in 100% chicken juice could in part be due to enhanced growth of C. jejuni. These results also show that chicken juice supports C. jejuni growth.

Chicken juice increases biofilm formation in different Campylobacter isolates and on different abiotic surfaces. In order to ensure that the effect observed in the glass test tubes was present on other abiotic surfaces and not specific for strain NCTC 11168, we repeated the previous assay using polystyrene plates and stainless steel coupons and extended the assay to three other C. jejuni reference isolates (81116, 81-176, and RM1221) and one C. coli clinical isolate (15-537360). Stainless steel is a commonly used material within the food chain and so is an important surface for bacterial attachment and subsequent biofilm formation and survival. All C. jejuni and C. coli strains showed a significant increase in biofilm formation when brucella broth was supplemented with 5% chicken juice in borosilicate test tubes and 24-well polystyrene wells under both microaerobic and aerobic conditions (Fig. 2A to D). The chicken juice-dependent increase in biofilm formation was particularly clear in C. jejuni RM1221 and C. coli 15-537360, since these strains showed very low levels of biofilm formation in brucella broth alone (Fig. 2A to D). Biofilm formation was also significantly increased in the presence of chicken juice on food grade stainless steel coupons (Fig. 2E and F). Hence, chicken juice is able to promote biofilm formation, independently of Campylobacter isolate or abiotic surface.

C. jejuni preferentially attaches to chicken juice particulates. Since biofilm formation was increased by chicken juice on different surfaces, we investigated the effect of chicken juice on an abiotic surface in the absence of C. jejuni. Brucella broth with or without 5% chicken juice and also 100% chicken juice were incubated in static glass tubes under the standard assay conditions and stained with TTC, crystal violet, or Congo red (Fig. 3A). There was a significant increase in crystal violet and Congo red staining in the presence of chicken juice, while staining with TTC (measuring bacterial respiration) was negative, demonstrating that components of chicken juice bind to the abiotic surface but do not interfere with TTC staining. Since the formation of precipitates (particulates) was also observed, we hypothesized that chicken juice components may form a conditioning layer on the abiotic surface, facilitating bacterial attachment.

In order to further investigate this phenomenon, C. jejuni NCTC 11168 biofilms obtained with brucella broth, brucella broth supplemented with 5% chicken juice, or 100% chicken juice

FIG 1 Biofilm formation and growth of C. jejuni NCTC 11168 in the presence of chicken juice. (A) Static incubation of C. jejuni in brucella broth supplemented with chicken juice results in increased biofilm formation, as shown by using a TTC biofilm assay. (B) Growth of C. jejuni in media supplemented with 5% chicken juice is not significantly different from unsupplemented brucella broth. White bars represent unsupplemented brucella broth, and black bars represent brucella broth supplemented with 5% (vol/vol) chicken juice. Error bars show the standard errors of the mean, and significance was measured by using the Bonferroni post test following ANOVA (**, \( P < 0.01 \); ***, \( P < 0.001 \)).

three technical replicates) were used to calculate means and the standard errors of the mean. Significance was measured using either Mann-Whitney U test or Bonferroni post test values following analysis of variance (ANOVA).
were analyzed by SEM (Fig. 3B to D). In the presence of chicken juice, C. jejuni cells preferentially bind to the particulates rather than directly to the abiotic surface (Fig. 3C and D). This is especially apparent in the 5% chicken juice image (Fig. 3C), where only the chicken juice particulates, but not the abiotic surface, are bound by C. jejuni cells. Figure 3D also visually supports the observations in Fig. 1B that the total number of cells within the biofilm is increased in 100% chicken juice. Hence, chicken juice provides a highly adhesive environment supporting subsequent formation of a C. jejuni biofilm.

Precoating assay tubes with chicken juice increases biofilm formation. All previous experiments were performed with simultaneous addition of C. jejuni and chicken juice, and therefore we investigated whether precoating surfaces with chicken juice also enhanced biofilm formation. A range of chicken juice concentrations was tested during the precoating stage from brucella broth supplemented with 10 to 90% chicken juice and with 100% chicken juice for 24 h at 37°C. Subsequent replacement of precoating medium with C. jejuni NCTC 11168 in unsupplemented brucella broth resulted in a significant increase in levels of biofilm formation with all concentrations of chicken juice compared to brucella broth under both aerobic and microaerobic conditions (Fig. 4). There was no significant increase in levels of biofilm formation with increasing concentrations of chicken juice. This was also observed by precoating stainless steel coupons with chicken juice.

Chicken juice complements reduced biofilm formation by aflagellated C. jejuni. Flagella are known to contribute to attach-
ment and biofilm formation in several bacterial pathogens (34, 35), and an aflagellated C. jejuni ΔflaAB mutant produces significantly less biofilm than the wild-type NCTC 11168 strain (10, 36).

Incubation with chicken juice or precoating of tubes with chicken juice both resulted in a significant increase of biofilm formation with the C. jejuni/H9004 flaAB mutant compared to incubation in brucella broth alone (Fig. 5). In the presence of chicken juice, biofilm levels were similar to that of wild-type C. jejuni NCTC 11168 (Fig. 5), showing that chicken juice can complement the lack of flagella and support biofilm formation by aflagellated strains. This sup-

![FIG 3](http://aem.asm.org/)

**FIG 3** Chicken juice facilitates binding of C. jejuni via modification of abiotic surfaces. (A) Chicken juice components bind to abiotic surfaces such as glass tubes, as shown by crystal violet staining (top row) and Congo red staining (middle row). TTC staining (bottom row) shows that the material bound is not redox reactive. The left column shows results for brucella broth only, the middle column shows results for brucella broth supplemented with 5% chicken juice, and the right column shows results for 100% chicken juice. (B to D) Representative SEM images of C. jejuni biofilms grown in brucella broth supplemented with 0% (B), 5% (C), or 100% (D) chicken juice on coverslips. In chicken juice-containing samples (C and D), C. jejuni can be seen to adhere to the juice particulates rather than the abiotic surface. A large chicken juice particulate can be seen adhered to the slide surface in panel C, with C. jejuni attached to it in preference to the slide surface. In panel D, particulates are densely packed and so cover the field of view. Scale bar, 10 μm.

![FIG 4](http://aem.asm.org/)

**FIG 4** Precoating of test tubes with chicken juice increases biofilm formation by C. jejuni NCTC 11168. Tubes were precoated with a range of chicken juice concentrations before being used in the standard TTC biofilm assay under both aerobic (A) and microaerobic (B) conditions, using unsupplemented brucella broth. Error bars show the standard errors of the mean, and significance was assessed by using the Mann-Whitney U test (*, P < 0.05).
ports our hypothesis that the effect of chicken juice is mediated through facilitating attachment and not via chemotactic motility.

**DISCUSSION**

In this study we investigated the effect of meat exudates on *C. jejuni* biofilm formation and show that chicken juice is able to enhance biofilm formation compared to brucella broth. Our data show that this is mediated by the ability of chicken juice to provide a conditioning layer on abiotic surfaces, providing an adhesive foundation onto which a *C. jejuni* biofilm can establish itself and grow. This is observed in both isolates capable of forming biofilms in brucella broth and isolates that are otherwise poor biofilm growers. This is observed in both isolates capable of forming biofilms and show that this is mediated by the ability of chicken juice to provide conditioning layers on abiotic surfaces.

**FIG 5** Chicken juice increases the ability of *C. jejuni* NCTC 11168 ΔflaAB mutants to form biofilms in static culture. Static suspensions of *C. jejuni* ΔflaAB mutants were incubated for 48 h to allow biofilm formation in various types of media before TTC staining. A bar chart shows (from left to right) results for *C. jejuni* ΔflaAB mutants in brucella broth (with no pretreatment of the test tubes), *C. jejuni* ΔflaAB mutants in 100% chicken juice (with no pretreatment of the test tubes), *C. jejuni* ΔflaAB mutants in brucella broth (with a 24-h brucella broth pretreatment of the test tubes), *C. jejuni* ΔflaAB mutants in brucella broth (with a 24-h 100% chicken juice pretreatment of the test tubes), and a *C. jejuni* NCTC 11168 wild-type (WT) culture (with no pretreatment of the test tubes). Error bars show standard errors of the mean, and images above the bar chart are representative of the TTC staining observed for each condition. Significance was measured using a Bonferroni post test following ANOVA (**, P < 0.01).
turkey, pork, and beef (47). For instance, 49.3% of chicken samples tested were positive for *Campylobacter* species, along with turkey (37.5% of samples), duck (45.8% of samples), beef (3.2% of samples), pork (5.1% of samples), lamb (11.8% of samples), oysters (2.3% of samples), and milk (1.6% of samples) (48). Subsequent speculation suggested that *C. jejuni* and *C. coli* accounted for 83.4 and 16.6% of the isolates, respectively. In our SEM images (Fig. 3B to D), *C. jejuni* can be observed preferentially attaching to the adhered chicken juice components rather than the surface of the slide. This highlights the need for future studies to not only investigate the link between chicken or pork soil and surface conditioning but also assess the effect of other meat exudates on biofilm formation.

In conclusion, chicken juice allows increased attachment of *C. jejuni* as it attaches to the surface of the test tubes, providing a conditioned surface for the bacteria to adhere to. This conditioning surface is still present following a simple washing procedure and able to increase biofilm formation if the subsequent incubation with bacteria lacks chicken juice in the broth. Chicken juice also provides a suitable laboratory model for the study of *C. jejuni* biofilm formation in the food chain, allowing investigators to more closely mimic the food chain conditions that lead to *C. jejuni* spread and cross contamination of carcasses. Furthermore, identification of the chicken juice components involved in surface conditioning and bacterial attachment may give the opportunity for targeted intervention and prevention strategies to reduce transmission of *C. jejuni* and *C. coli* through the food chain.

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