Food by-products as natural source of bioactive compounds against *Campylobacter*

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Synopsis

This review describes the role of different food by-products as alternative tool to the use of antibiotics and disinfectants in the control of *Campylobacter*, the main bacterial foodborne pathogen associated to human gastroenteritis. These by-products are a source of bioactive compounds potentially applicable at all stages of the food chain where *Campylobacter* is present. Therefore, the use of industrial food by-products in the mitigation of *Campylobacter* contamination may contribute to its revalorization and the sustainability of different production processes, which is a cause of global concern nowadays.

Abstract

Campylobacter is the leading cause of human bacterial gastroenteritis worldwide. This microorganism may be present throughout the entire food chain. For this reason, it is of particular interest to find natural alternatives environmentally sustainable to the use of antibiotics and chemical disinfectants. Industrial food by-products are an economical and sustainable alternative as a source of useful bioactive compounds against *Campylobacter*. The food industry generates a large quantity of by-products and wastes rich in organic matter that contribute significantly to environmental pollution. Therefore, food industries are currently focusing on solving the problems of waste management and recycling by utilization of the by-products. In the present review, the efficacy in the control of *Campylobacter* of several by-products from the food industry, both of plant and animal origin, has been summarized. The effect of the bioactive compounds present in these by-products against *Campylobacter* is discussed, both in inhibiting growth and the adhesion and invasion to intestinal epithelial cells, as well as their ability to reduce biofilm formation on biotic and abiotic surfaces.

1. *Campylobacter*: significance and microbiological aspects

Campylobacter has been recognized as the leading cause of human bacterial gastroenteritis worldwide (Kaakoush et al., 2015). Being the most common bacterial cause of diarrhoea in many industrialized countries, *Campylobacter* infection is consequently responsible for a major public health and economic burden.

The genus *Campylobacter* is Gram-negative, non-saccharolytic bacteria with microaerobic growth requirements. Its catabolic capability is highly restricted. They do not ferment or oxidize carbohydrates neither complex substances. Energy is obtained from amino acids or tricarboxylic acid cycle intermediates. In morphological terms, campylobacters are usually S-shaped or spiral rods with tapering ends (0.2-0.8 μm-wide by 0.5-5 μm-long) (Figure 1). *Campylobacter* commonly possesses a polar flagellum at one or both ends of the cell and this, presumably aided by its spiral morphology, imparts a high degree of motility to the cell. This bacterium has quite stringent requirements for its growth. *Campylobacter* species are microaerophilic, requiring a reduced O_2 concentration of 5-8% and an elevated CO_2 concentration of 3-10%. Most relevant species are also thermophilic, growing best among 40-42ºC. Table 1 shows some of the main features of the genus *Campylobacter*. At present, the genus *Campylobacter* contains 27 species and 8 subspecies, and *C. jejuni* and *C. coli* are the most important human enteropathogens among the campylobacters, being usually responsible of around the 80-90% of the diagnosed cases of *Campylobacter* infections (EFSA, 2017).

2. Epidemiology and reservoirs

Campylobacters are widespread in the natural environment, and can survive for long periods of time outside and inside of a given host (Poly & Guerry, 2008). As a major reservoirs, campylobacters are part of the natural intestinal microbiota of a wide range of

68 domestic and wild animals as well as various agriculturally important mammals (cattle,
69 swine, and birds), especially poultry, whose intestines offer a suitable biological niche for
70 their survival and dissemination. Particularly, *C. jejuni* is often the predominant species
71 in poultry, and *C. coli* is most prevalent in swine. However, chickens are the most
72 important reservoir and source of human infection. In Europe, broiler meat was the most
73 important single source of human campylobacteriosis in 2016, and 36.7% of the 11,495
74 samples of fresh broiler meat were found to be *Campylobacter*-positive (EFSA and
75 ECDC, 2017). In fact, campylobacteriosis was the most commonly reported zoonoses in
76 the EU in 2016, the number of reported confirmed cases of human campylobacteriosis
77 was 246,307 (Figure 2).

78 In developed countries, the most recognized route of *Campylobacter* transmission
79 to humans occurs commonly by handling, preparation, and consumption of contaminated
80 chicken meat or chicken meat products. Chicken carcasses use to be contaminated by the
81 bacteria during slaughter and further processing (Bronowski et al., 2014; Kaakoush et al.,
82 2015), since bacterial multiplication in food is not possible. Other reported sources
83 contributing to *Campylobacter* infection in humans are the consumption of untreated
84 water, unpasteurized dairy products, eating at restaurants, as well as foreign travel
85 (Bronowski et al., 2014; Doorduyn et al., 2010; Mughini Gras et al., 2013).
86 Contamination of the environment by domestic and wild animal feces presents an
87 alternative exposure pathway for human infection, for example, soil, beach sand, sewage,
88 groundwater, and drinking water. Figure 3 shows the main sources of *Campylobacter*
89 *jejuni* infection.

90 However, the most cases appear to be sporadic and show a consistent seasonality.
91 Given the sporadic nature of *Campylobacter* infections, source attribution based on
92 outbreak investigations has had limited value. This is largely because, unlike for

93 salmonellosis (Wagenaar et al., 2013), campylobacteriosis outbreaks are rarely reported.
94 Although most outbreaks (~64%) were not attributable to known sources, ~12% were
95 attributed to meat products in general, and ~10% specifically to chicken meat (Newell et
96 al., 2016).

97 **3. Pathogenesis and virulence factors**

98 Infection begins with an infectious dose of a few hundred bacteria (5-800
99 organisms) which is sufficient to overcome the so-called "colonization resistance barrier"
100 in humans (Backert et al., 2016). During infection of humans, *Campylobacter* enters the
101 host intestine via the oral route (in association with food or water) and colonizes the distal
102 ileum and colon. Following colonization of the mucus and adhesion to intestinal cell
103 surfaces, campylobacters perturb the normal absorptive capacity of the intestine by
104 damaging epithelial cell function either directly, by cell invasion or the production of
105 toxin(s), or indirectly, following the initiation of an inflammatory response (Silvan et al,
106 2013). Figure 4 shows the hypothetical model for *C. jejuni* mechanisms of human
107 infection. The clinical spectrum ranges from severe inflammatory diarrhoea (patients in
108 developed nations) to generally mild, non-inflammatory, watery diarrhoea (patients in
109 developing nations). The incubation period prior to the appearance of symptoms usually
110 ranges from 1 to 7 days. Although infection can result in a severe illness lasting more
111 than a week, it is generally self-limiting and complications are uncommon, although it
112 can in a small number of cases result in severe complications, such as Guillain-Barre
113 syndrome and reactive arthritis (Esan et al., 2017).

114 **4. Treatment and antibiotic-resistance**

115 Treatment with antibiotics for uncomplicated *Campylobacter* infection is rarely
116 indicated. Most humans suffering campylobacteriosis recover without therapeutic

intervention other than fluid and electrolyte replacement. Antimicrobial treatment is usually required in patients with severe or prolonged enteritis, especially in infants or the elderly, immunocompromised individuals and in cases of extra-intestinal manifestations (Ganan et al., 2012). In the past, fluoroquinolones were commonly used when antibiotic treatment was needed for campylobacteriosis. However, nowadays the level of acquired resistance to fluoroquinolones precludes the use of these antimicrobial agents for routine empirical treatment of human campylobacteriosis (EFSA & ECDC, 2017). In fact, there is strong evidence linking the indiscriminate usage of antibiotics in animal production to the emergence and spread of antibiotic resistance in *Campylobacter* (Silva et al., 2011). Increases in the incidence of infection caused by antibiotic-resistant strains of *Campylobacter* make these illnesses increasingly difficult to treat (Zhang & Plummer, 2008). In view of the continuing relatively high incidence of fluoroquinolone resistance in *Campylobacter* from human cases, macrolides such as erythromycin and azithromycin are considered the drugs of choice for treatment of human campylobacteriosis (CDC, 2014). However, the efficacies of such treatments are currently compromised by the increasing resistance to these antibiotics in *C. jejuni* and *C. coli* (Alfredson & Korolik, 2007). Figure 5 shows the antimicrobial resistance in *Campylobacter* to different antibiotics in humans. Furthermore, it would be necessary to achieve alternative strategies to the use of antibiotics to reduce the presence or to eradicate *Campylobacter* from the human food chain.

5. Alternative control strategies

The application of stricter hygiene measures has been found to reduce or delay *Campylobacter* infection in chickens, but is not sufficient to eradicate the pathogen. Also, the use of chemical agents could be an effective strategy to control *Campylobacter*, however, this procedure are not well accepted by the consumer and can result in the

142 accumulation of chemical wastes, so cannot really be described as environmentally-
143 friendly practises (Vandeplas et al., 2008). On the other hand, a number of physical
144 decontamination techniques have been successfully investigated to control the level of
145 *Campylobacter* on poultry products including ozonation, irradiation, forced air chilling,
146 steam pasteurisation, stem-ultrasound or freezing (Boysen & Rosenquist, 2009; Whyte et
147 al., 2003). Each method has its advantages and disadvantages with relation to appearance
148 of the final product, consumer acceptance, price, etc. Several other treatments have been
149 evaluated, with more or less success, as alternatives to the use of chemicals and antibiotics
150 against *Campylobacter*. Table 2 shows a summary of some of the most commonly used
151 methods for controlling *Campylobacter* infection in the poultry industry.

152 **6. Food by-products as alternative for controlling *Campylobacter***

153 Food industries are growing rapidly due to globalization and population increase
154 and are providing a wider range of food products to satisfy the needs of the consumers.
155 The major food industries of the developed countries include dairy, fruits and vegetables,
156 meat and poultry, seafood and cereal. However, these industries generate huge amounts
157 of food-processing wastes and by-products, which consist of high amounts of organic
158 matter, which have not already been used for other purposes and have not been recycled,
159 leading to problems regarding disposal, environmental pollution and sustainability.
160 However, food industries are currently focusing on solving the problems of waste
161 management and recycling by utilization of the by-products. These by-products can
162 contain valuable nutrients or bioactive compounds that can be used for developing novel
163 value-added products.

164 Traditional methods of waste utilization include their use as animal feed, fertilizer
165 or disposal (Jayathilakan et al., 2012). However, their use has been limited due to legal
166 restrictions, ecological problems and cost issues. Therefore, efficient, cheap, and

ecologically sound methods for utilization of wastes are being focused upon, which can minimize the quantities of wastes exposed to the environment and the subsequent health hazards. Wastes from the food industries generally comprise of dietary fibers, proteins and peptides, lipids, fatty acids and phenolic compounds, depending on the nature of the product produced. The different types of wastes produced by the different processing industries with potential revalorisation uses are listed in Table 3. Some of these by-products have been the subject to investigations and have proven to be effective sources of antimicrobial compounds against *Campylobacter*.

6.1. Fruits by-products

The world production of fruits has increased rapidly in recent years and thereby there has been a concomitant increase in the quantity of fruits by-products (FAO, 2009). The fruit processing by-products are regarded as waste and disposed of in the environment, which causes ecosystem problems as they are prone to microbial degradation. However, important efforts are being made to reuse by-products from the fruits processing industries because are enrich-sources of bioactive compounds, such as phenolic compounds. These phenolic compounds are secondary metabolites in plants and play an important role in their growth and reproduction, providing protection against several pathogens. The phenolic compounds possess potent antioxidant and antibacterial activities (Khao & Chen, 2013). In this regard, the antibacterial activity against *Campylobacter* has been studied reusing several fruits by-products enriched in phenolic compounds.

Citrus industry

Citrus is one of the world's major fruit crops with global availability and popularity that contributes to human diets (FAO, 2009). Global production of citrus fruit has significantly increased during the past few years and has reached ~92 million tons in the

192 years 2016-2017 (USDA, 2017). Although many citrus fruits can be eaten fresh,
193 approximately a third of citrus fruits worldwide are utilised after processing and juice
194 production, yielding about 44% peel as by-product (Li et al., 2006). Therefore, the citrus
195 industry (grapefruits, lemons, limes, oranges, and tangerines) produces annually large
196 quantities of waste or by-products (peels, seeds, and pulps), which can represent up to
197 50% of the raw processed fruit (Khao & Chen, 2013). It has been proven that citrus peels
198 and seeds contain higher amounts of total phenolic compounds than edible portions
199 (Gorinstein et al., 2001), mainly phenolic acids and flavonoids (Castillo et al., 2017). This
200 rich polyphenolic composition has encouraged the use of these by-products to study their
201 potential antimicrobial capacity.

202 *Citrus* extracts obtained from peels and seeds have been successfully tested for their
203 ability to inhibit the growth and to affect other virulence factors of *C. jejuni* (Castillo et
204 al., 2014 and 2017). *Citrus* peel extracts showed significant inhibitory activities; with
205 inhibition zones ranging from 1.8 to 2.4 cm when the disinfectant used as positive control
206 produced inhibition zones ranging from 2.7 to 3.0 cm. Treatment with these *Citrus* peel
207 extracts were also able to reduce *Campylobacter* swarm motility 44-59%. The beneficial
208 effects of *Citrus* by-product extracts on the adherence and invasion to human intestinal
209 cells in *Campylobacter* have been also investigated. Castillo et al. (2017) confirmed the
210 reduction of adherence and invasion using different *Campylobacter* strains by treatment
211 with *Citrus* by-product extracts. The percentage reduction was noticeably high for both
212 processes, reaching up to 90% inhibition almost in all tested strains. Reductions in
213 adherence and motility of *Campylobacter* by treatment with citrus peel extract have been
214 also successfully achieved (Castillo et al., 2014). However, *Campylobacter* did not show
215 complete loss in the motility. This effect is an important contribution because adherence
216 and motility are crucial for bacterial pathogenesis. Biofilm formation is another important

217 survival mechanism for *Campylobacter*, because *Campylobacter* biofilms has
218 demonstrated resistance to environmental stress and pharmacological treatments
219 (Gunther & Chen, 2009). This virulence factor was also effectively reduced in 60-75%,
220 depending on extract concentration and/or strain tested, by treatment with *Citrus* peel
221 extract (Castillo et al., 2014).

222 Citrus essential oils (EOs) mainly exist in fruit peels which are usually discarded as
223 waste. EOs are a complex mixture of different components and their content as well as
224 composition depends on species, variety, cultivation and extraction methods (Mahato et
225 al., 2017). Their most common constituents are terpenes, aromatic and aliphatic
226 compounds (Dugo et al., 2011). Besides being used as a fragrance, citrus essential oils
227 have been reported to possess biological activities, such as antifungal, antioxidant, and
228 antimicrobial activities (Mitropoulou et al., 2017; Singh et al., 2010; Torres-Alvarez et
229 al., 2016). In this regard, limonene, citral, and linalool are ones of the major compounds
230 of citrus fruit oils identified as active antimicrobial components (Geraci et al., 2016).
231 Little research has been carried out on *Campylobacter* spp. in terms of the effects of EOs
232 on growth and survival, but the few studies reported indicate that citrus EOs could be an
233 effective tool to inhibit the growth of this pathogen. In this regard, EOs extracted from
234 bergamot (*Citrus bergamia*) and lemon (*Citrus limon*) were effective to inhibit *C. jejuni*
235 growth (Fisher et al., 2006). Antibacterial activity of the main components of these EOs,
236 citral, linalool and limonene, were also evaluated resulting linalool oil the most effective
237 anti-bacterial component against *C. jejuni*. This active terpene compound was found more
238 abundant in the bergamot EOs (15%) postulating that the inhibitory effect was due to
239 linalool. Sweet orange oil has been also found effective to inhibit both *C. jejuni* and *C.*
240 *coli* (Nannapaneni et al., 2009; Thanissery et al., 2014), where linalool appeared to be a
241 dominant component (20.2%) of this tested citrus oil (Nannapaneni et al., 2009). Sour

orange peel extract has been also reported to be effective against both *C. jejuni* and *C. coli* reducing the viability in a chicken skin model by >4 log and *in vitro* assays (MBC 2 mg/mL) diminishing population of *Campylobacter* to undetectable levels (Valtierra et al., 2010). Therefore, utilization of EOs from citrus by-products as antimicrobials may provide a good solution for industry and environmental sustainability.

Other valuable by-products that can be obtained from citrus fruit wastes are pectin and pectic oligosaccharides obtained by chemical and/or enzymatic pectin processing. Pectins are obtained from citrus peel powder, which is the waste of citrus juice processing industry. The main use for pectin is as a gelling and thickening agent and stabilizer in food. However, it was observed that pectic oligosaccharides extracted from *Citrus sinensis* inhibit *C. jejuni* invasion to human intestinal cells (Ganan et al., 2010). Pectic oligosaccharides seem to interfere with cell invasion by affecting the efficacy of cell adhesion as is shown in Figure 6. Effective adhesion is a prerequisite for cell invasion, which is one of the main factors that allow the initiation of successful colonization. The ability of *C. jejuni* to induce symptoms involves binding and colonization of the intestinal cells. Thus, these results suggest that pectic oligosaccharides could be potentially useful as alternatives to antibiotics in the control of *C. jejuni*.

Olive industry

The by-products of the olive industry have attracted considerable interest as a source of phenolic compounds, with much attention focused on the olive mill wastes (OMW). The phenolic compounds present in the olive fruits are distributed into the olive oil, the aqueous phase wastewater, or the solid phase pomace, but these last olive by-products retain the great amount of total phenolic compounds (~98%) that are not transferred to olive oil (Araujo et al., 2015). Therefore, OMW are a potential source of phenolics, particularly in consideration that olive oil production results in an annual

generation of more than 30 million m^3 of OMW (Doula et al., 2017). More than 50 different phenolic compounds have been identified in OMW. The most representative phenolic compounds have been classified into three groups: compounds related to tyrosol (tyrosol and hydroxytyrosol), derivatives of benzoic acids and cinnamic acids (Torrecilla, 2010). Several studies reported antibacterial effects of phenolic enriched fractions obtained from OMW on bacterial pathogens, including Gram positive and Gram negative bacteria (Aissa et al., 2017). However, studies about the antibacterial effects of OMW on *Campylobacter* are scarce, despite the epidemiological importance of this bacterium as a foodborne pathogen. Branciari et al. (2016) found that supplementing the diet of broilers with different amounts of OMW extract results in a significant decrease in *Campylobacter* contamination. The higher amounts of polyphenols contained in the OMW diets were likely responsible for the observed effects on *Campylobacter* spp. shedding. These results suggest that olive waste by-products could be useful to reduce the risk of *Campylobacter* diffusion in the chicken flock and consequently in processed poultry meat. Recently, our research group has successfully evaluated the response of *C. jejuni* and *C. coli* species isolated from chicken food chain and clinical patients to OMW fractions (Silvan et al., 2018). The most active OMW fraction was bactericidal reducing the *Campylobacter* growth in 8 logarithms. Moreover, this bactericidal fraction markedly inhibited inflammation on macrophage cell line. These findings suggest the potential biological properties of OMW as precursor of polyphenol compounds with antibacterial and anti-inflammatory properties, which might ameliorate the infection and inflammation process induced by *Campylobacter*. This beneficial effect of OMW on campilobacteriosis supports the idea for increasing its revalorisation.

Besides OMW, olive leaves represent another by-product of the olive industry obtained in high amounts during the olive harvest for olive oil production and have been

292 explored as a source of phenolic compounds, albeit to a lesser extent. *Campylobacter*
293 *jejuni* was found to be very susceptible *in vitro* to leaf extracts, where oleuropein was the
294 most abundant compound (Šikić Pogačar et al., 2016; Sudjana et al., 2009).
295 Phytochemicals present in food by-products can also prevent the attachment of several
296 pathogens to abiotic surfaces. In this regard, olive leaf extracts were successful proved to
297 inhibit *C. jejuni* adhesion to the abiotic and biotic surfaces to prevent colonization in
298 poultry and to reduce transmission to humans (Šikić Pogačar et al., 2016). However, the
299 concentrations of olive leaf extract that had anti-adhesion activities did not measurably
300 alter *C. jejuni* growth. Therefore, authors suggest that the olive leaf extract tested could
301 be considered as new antimicrobial that inhibit bacterial adhesion rather than bacterial
302 growth.

303 *Grape and winery industry*

304 Grapes are one of the world's most commonly produced fruit crops, with
305 approximately 75 million tons generated annually worldwide, and with the highest total
306 value of production in the world (FAO-OIV, 2016). Grapes and winery industries produce
307 a great variety of wines, grape juices, and raisins. But its production process generates
308 high amounts of by-products, such as grape pomace, seeds, skins, stems, leaves and lees.
309 For instance, production of wines, up to 40% of the grapes ends up as by-products
310 (Friedman et al., 2014). This residue is generally used in the production of ethanol by
311 fermentation/distillation, in the extraction of tartaric acid, as organic fertilizer or for
312 animal feed (Brenes et al., 2016). However, these grape by-products contain numerous
313 bioactive compounds, such as dietary fibre and phenolic compounds (Hogervorst et al.,
314 2017; Teixeira et al., 2014; Zhu et al., 2012), with potentially antibacterial action against
315 foodborne pathogens (Friedman et al., 2014; García-Lomillo et al., 2017).

316 The largest fraction of winery waste is the winemaking waste (WW) consisting of
317 the skins, seeds, and stems left after juice or wine is pressed. This grape by-product is a
318 complex mixture of polysaccharides, fermentation by-products, dietary fiber, and
319 polyphenols amongst others (Yu & Ahmedna, 2013). The feasibility of WW extract as
320 source of active phenolic compounds against *Campylobacter* has been recently evaluated
321 (Mingo et al., 2016). WW extract was active against all *C. jejuni* and *C. coli* strains tested,
322 and most of them were inhibited at concentrations between 0.04 and 0.1 mg gallic acid
323 equivalents/mL. Phenolic characterization of WW extract showed that catechins and
324 proanthocyanidins were the main families involved in the antibacterial effect, and
325 epicatechin gallate and resveratrol the most active compounds against *Campylobacter*.
326 Grape seed extracts (GSE) have showed anti-*Campylobacter* effect in several
327 studies. Silvan et al. (2013) confirmed strong bactericidal effect of GSE against different
328 *Campylobacter* strains obtaining a reduction of up to 7 logs colony forming unit, being
329 the minimal inhibitory concentration (MIC) lower than 0.02 mg/mL and the minimal
330 bactericidal concentration (MBC) 0.06 mg/mL. In this work, fractionation of the GSE
331 was performed and the most bactericidal fraction showed that phenolic acids, catechins
332 and flavonols were the main responsible of the inhibitory effect. Figure 7 shows the
333 antibacterial activity of grape seed collected fractions against *C. jejuni* and their phenolic
334 composition. Hettiarachchy et al. (2010) also demonstrated inhibition of *C. jejuni* growth
335 after GSE treatment (1%), obtaining a maximum reduction of 6 logs. Recently, Klančnik
336 et al. (2017) observed anti-*Campylobacter* activity of waste grape skins and seeds (GSS)
337 with a MIC of 1.25 mg/mL. This effect reached a growth inhibition in the range of 22%,
338 inducing morphological changes, which would be associated with alterations in the
339 integrity of the cell membrane. Sub-inhibitory concentrations of GSS extract also
340 inhibited *C. jejuni* invasion by up to 20% across the tested concentration range (0.0125

to 0.2 mg/mL). Thus, GSS showed an anti-bacterial, anti-adherent and anti-invasive activity that turned out quite effective, which could help modulate the pathogenicity of *Campylobacter*, and could therefore be used to prevent or treat bacterial infection.

Grape skin extract, other abundant grape by-product, have also showed anti-*Campylobacter* effect. Katalinić et al. (2010) confirmed antimicrobial activity of grape skin extracts of 14 *Vitis vinifera* L. white and red varieties against *C. coli*. This work found that grape skin extract had antimicrobial activity against different Gram-positive and Gram-negative food-borne pathogenic bacteria, but the most susceptible organism to grape skin extracts was *Campylobacter*. These grape skin extracts were rich in flavonoids, catechins and flavanols. Similar antibacterial activity against *C. jejuni* was recently described by Trošt et al. (2016) using freeze-dried grape skin and seed extracts obtained from winery by-product waste of different grape varieties. The phenolic profiles of tested grape skin and seed extracts included mainly flavonols and catechins as described by Katalinić et al. (2010).

Leaves from *Vitis vinifera* also constitute an important waste from grape crops and winery industry. Antibacterial activity of leaf phenolic extracts obtained from six grapevine varieties against *C. jejuni* have been was confirmed by Katalanic et al. (2013). The analytical characterization of these leaf extracts confirmed highly content of phenolic compounds, such as flavan-3-ols and flavonols, especially quercetin and its derivatives, as well as the presence of compounds from the resveratrol family.

Berry industry

Berry pomace is a by-product of the juice-pressing industry, which traditionally has been used as an ingredient in animal feed or it has been disposed into soils. Due to its low pH value it may possess significant ecological and environmental problems. Berry pomaces containing the berry skins are, however, very rich sources of phenolic

366 compounds. Salaheen et al. (2014) evaluated the effect of bioactive compounds extracted
367 from blueberry and blackberry pomaces on the *C. jejuni* growth and its pathogenicity.
368 Results indicated that blackberry and blueberry pomace extracts significantly reduced the
369 growth of *C. jejuni*. MIC and MBC of berry pomaces extract were in a range of 0.4-0.6
370 mg/mL and 0.5-0.8 mg/mL gallic acid equivalent, respectively. However, bactericidal
371 activity of blueberry pomace extract was stronger than that of blackberry pomace extract.
372 This study also found that several virulence properties of *C. jejuni*, such as
373 autoaggregation, motility, adhesion, invasion, and expression level of virulence genes,
374 were significantly modified due to exposure to berry pomace extracts.

375 Recently, the same research group carried out a study to evaluate blackberry and
376 blueberry pomaces on *C. jejuni* colonization in broiler cecum (Salaheen et al., 2018). As
377 a water supplement, phenolic extract from berry pomaces reduced *C. jejuni* pre-harvest
378 colonization level in poultry gut in a dose dependent manner. In addition, berry pomaces
379 induced complete inhibition of the *C. jejuni* marker strain in drinking water reducing the
380 potential for horizontal transfer in poultry flocks. Therefore, authors suggest that berry
381 pomace extracts, especially from blackberry and blueberry, might be a feasible alternative
382 as feed additives or water supplements to reduce the colonization level of *C. jejuni* in
383 poultry, and as a natural preservative to control *Campylobacter* growth in the poultry food
384 chain and its final products.

385 ***6.2. Cereal by-products***

386 World cereal production in 2016 reached 2,500 million tons (FAO, 2017), thus
387 cereals are a major source of agricultural waste in many countries. The seven principal
388 cereals grown in the world are wheat, maize, rice, barley, oats, rye and sorghum. During
389 grain processing, large quantities of by-products such as bran, germ, husk and straw that
390 are rich in bioactive compounds are produced. To the best of our knowledge, only by-

391 products obtained from sorghum processing have been evaluated for controlling
392 *Campylobacter*. Sorghum (*Sorghum bicolor*) is a cereal crop in many parts of world and
393 contains high levels of phytochemicals including condensed tannins, phenolic acids,
394 flavonoids, deoxyanthocyanins, phytosterols and policosanols (de Morais Cardoso et al.,
395 2017). Sorghum is converted to ethanol by yeast fermentation techniques resulting
396 condensed distillers solubles, also referred to as sorghum syrup, as a by-product which
397 contains bioactive compounds. Navarro et al. (2015) confirmed that sorghum syrup,
398 obtained from bioethanol production, were active against *Campylobacter* with MIC
399 values ranging from 0.25% for the concentrated sorghum syrup up to 4% for the methanol
400 and water extractions. All tested syrup extracts showed a dose-dependent response against
401 *Campylobacter* indicating higher the dose tested the higher the inhibition. Recently, the
402 same research group confirmed that sorghum syrup obtained from bioethanol industry
403 was effective as antimicrobial against *Campylobacter* (Navarro et al., 2016). The MIC
404 that inhibited the bacterial growth reached 1% concentration of condensed distillers
405 solubles. In this study, the main phytochemical compounds contributing to the bioactivity
406 were determined founding that flavonol taxifolin, and the phenolic acids, protocatechuic
407 acid, 4-hydroxybenzoic acid, ferulic acid, cinnamic acid and p-coumaric acid, were the
408 main phenolic compounds.

409 ***6.3. Animal by-products***

410 *Seafood processing industry*

411 As described above in the case of fruits by-products, some industrial by-products
412 of animal origin have demonstrated their effectiveness against *Campylobacter*. One of
413 the most studied has been the effect of chitosan and chitooligosaccharides. Chitosan, a
414 natural carbohydrate polymer derived from the deacetylation of chitin, is the second most
415 abundant natural biopolymer after cellulose (Younes et al., 2015). Chitosan is produced

commercially from crab and shrimp shell wastes with different degrees of deacetylation and molecular masses, thus presenting a variety of properties. Over the past few years, chitosan has received increased attention mainly due to its innocuous nature and bioactivity, and it is used in different applications for foods and pharmaceuticals (Muxica et al., 2017). Chitosan has several biological properties useful for the food industry, but the most attractive is its potential use as a food preservative of natural origin due to its antimicrobial activity against a wide range of foodborne microorganisms (Zhengxin et al., 2017). In a work performed using three chitosans with different molecular masses against six Gram-negative and three Gram-positive bacteria, it was observed that *Campylobacter* was the microorganism most sensitive to chitosan, regardless of their molecular mass (Ganan et al., 2009). The MIC of chitosan for *Campylobacter* ranged from 0.005 to 0.05%, demonstrating the high sensitivity of campylobacters to chitosan. These authors also studied the mechanism of chitosan's action against *Campylobacter*, pointed that chitosan caused a loss in the membrane integrity of *Campylobacter*, measured as an increase in cell fluorescence due to the uptake of propidium iodide, a dye that is normally excluded from cells with intact membranes. Recent years have witnessed great developments in biobased polymer packaging films for the serious environmental problems caused by the petroleum-based nonbiodegradable packaging materials. In this context, chitosan-based materials have been widely applied in various fields for their biological and physical properties of biocompatibility, biodegradability, antimicrobial ability, and easy film forming ability (Wang et al., 2018). Recently, it was observed that the incorporation of ≥50 μL/g of allyl isothiocyanate (AITC) or 300 mg/g deodorized oriental mustard extract in κ-carrageenan/chitosan solutions as an edible coating significantly reduced viable numbers of *C. jejuni* on vacuum-packed chicken breasts and thus enhanced its safety (Olaimat et al., 2014). Even though chitosan is known to have

important functional activities, poor solubility makes them difficult to use sometimes in food and biomedical applications. Unlike chitosan, the low viscosity and good solubility of chitosan oligosaccharides (COS) make them especially attractive in an important number of useful applications. Mengibar et al. (2011) observed that *Streptomyces* chitosanase generates more deacetylated products that show higher antibacterial effect against *C. jejuni*. This antimicrobial effect was more pronounced for fractions with molecular weight between 10 and 30 kDa. These results have shown that COS could be useful as antimicrobial in the control of *Campylobacter*. Other related products, such as the antibacterial peptide fractions generated via proteolytic processing of snow crab by-products also exhibited activity against Gram-negative and Gram-positive bacteria, among them *C. jejuni* (Beaulieu et al., 2010).

Dairy industry

Large amounts of wastes emerge from milk processing in dairies, which are one of the largest sources of industrial effluents. The disposal of whey, the liquid remaining after the separation of milk fat and casein from whole milk during cheese processing, is a major problem for the dairy industry, because of the high volumes produced, which demands simple and economical solutions. The most abundant components of whey is the carbohydrate lactose (~70%), follow by proteins and inorganic substances with differing weight proportions. The world whey production amounts to about 82 million metric tons, and especially the acid whey is seen as a waste product. However, the bioconversion of whey to valuable products has been actively explored. For example, since lactose is the major component of whey, the production of lactic acid by using lactose whey through homofermentative lactic acid bacteria is viewed as an alternative process for the management of this abundant dairy by-product. Lactic acid is widely used in food industries as mineral fortifier, preservative, acidulant, and flavouring component, in

addition in the processed meat, hams, fish and poultry industries, lactic acid provides products with a longer shelf life by controlling food-borne pathogens because of its proved antimicrobial activity. Several studies have been confirmed the lactic acid effectiveness against *Campylobacter* bacteria employing different concentrations and contact conditions. Heres et al. (2004) performing an *in vitro* experiment observed a complete reduction of *Campylobacter* in the broiler feed acidified with 5.7% lactic acid. However, when in an *in vivo* experiment was carried out in chickens fed with feed acidified with lactic acid only a limited bacterial reduction was obtained, nevertheless the chickens were less susceptible to the *Campylobacter* infection. Ellerbroek et al. (2007) reported the efficacy of a decontamination method of *C. jejuni* on inoculated poultry carcasses by dipping and spray washing with lactic acid solutions (10% and 15%). The highest bacteria reductions were found after dipping in 15% lactic acid solution reducing 1.5 $\log_{10}$ cfu/g. Riedel et al. (2009) evaluated the effectiveness of a short-time decontamination treatment of *C. jejuni* on inoculated skin and chicken meat through immersion in a 2.5% lactic acid solution. The main results showed a significant reduction of bacterial growth (1.69 $\log_{10}$) after 1 min of immersion which increased to 3.87 $\log_{10}$ after 24 h chilled storage. Subsequent similar studies investigated the effect of dipping inoculated poultry samples with different lactic acid concentrations on the *Campylobacter* growth achieving moderate bacterial reductions and are summarised in Table 4. More efficient results of growth reduction were obtained by Birk et al. (2010) when *C. jejuni* strain was exposed to 0.5% lactic acid solution on chicken meat and in broth causing a 4- and 6-log reduction, respectively, after 24 h of exposure at 4ºC.

7. Conclusions

The increasing amount of waste produced by the food industry makes it necessary to create new ways for recycling, developing new technologies for waste processing. This

491 work summarized the potential of food by-products as a source of bioactive compounds
492 against *Campylobacter*, the main bacterial foodborne pathogen. This putative application
493 would contribute to the sustainability of the food industry, also promoting the valorisation
494 of their by-products. Further studies are required to scale up to industrial applications the
495 best results obtained at laboratory level, in order to increase the interest of the industrial
496 sector in this approach to exploit and revalue the food by-products.

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Figure 1. Scanning electron microscope image shows the characteristic spiral, or corkscrew, shape of *Campylobacter jejuni* cells. Source: Agricultural Research Service (ARS) is the U.S. Department of Agriculture's Chief Scientific Research Agency.

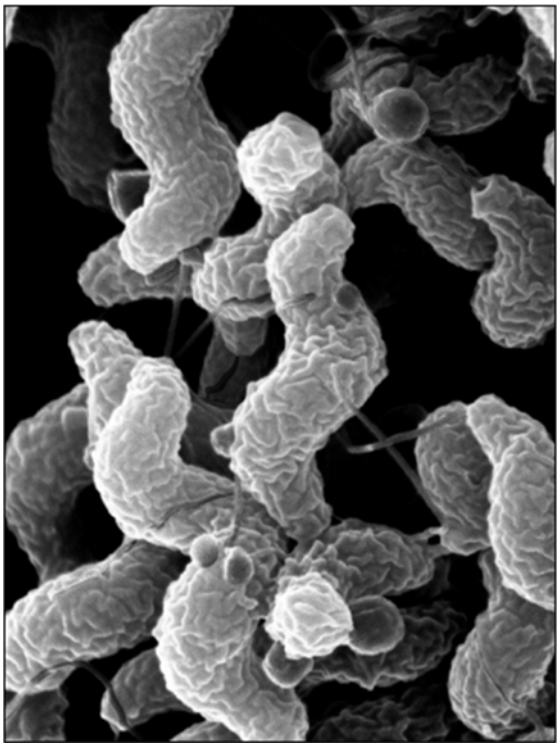


Figure 2. Number of the confirmed human cases of 13 zoonoses in the EU, 2016. In 2016, campylobacteriosis was the most commonly reported zoonoses, as it had been since 2005, representing almost 70% of all the reported cases. Source: EFSA, 2017.

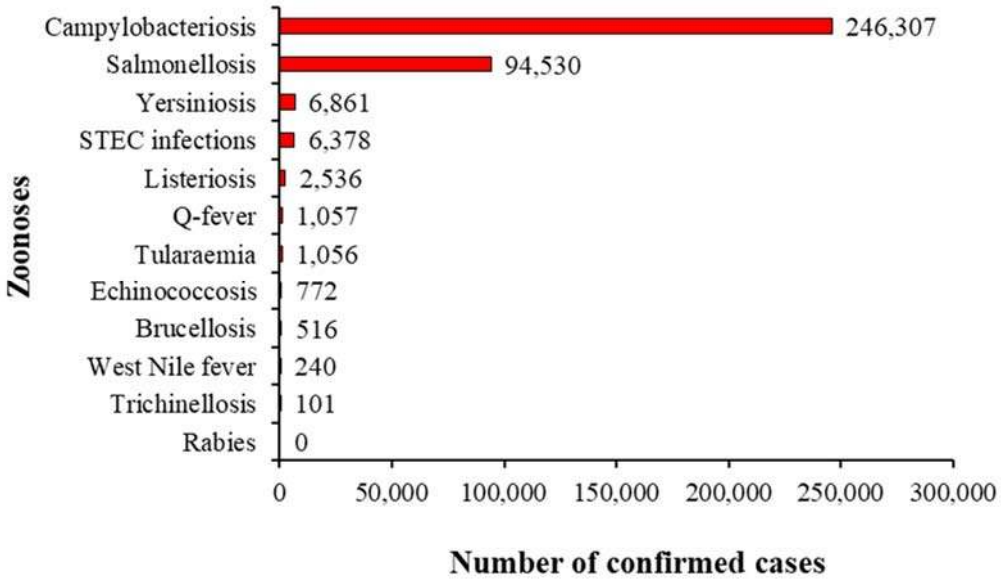


Figure 3. The sources and outcomes of *Campylobacter jejuni* infection. Several environmental reservoirs can lead to human infection by *C. jejuni*. It colonizes the chicken gastrointestinal tract, and is passed between chicks through the faecal-oral route. *C. jejuni* can enter the water supply, and possibly form biofilms. *C. jejuni* can infect humans directly through the drinking water or through the consumption of contaminated animal products. In humans, *C. jejuni* can invade the intestinal epithelial layer, resulting in inflammation and diarrhoea. Source: Young et al., 2007.

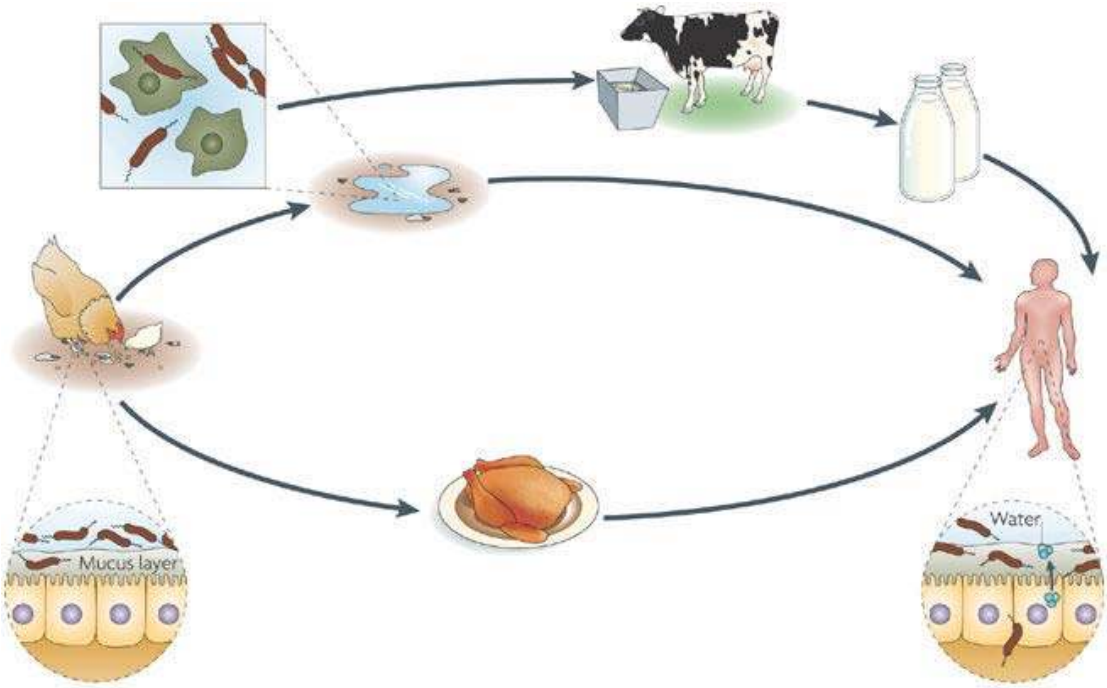


Figure 4. Hypothetical model for *C. jejuni* mechanisms of human infection. The bacteria can interact with, invade into, transmigrate across, and survive within polarized intestinal epithelial cells, as indicated. Source: Backert & Hofreuter, 2013.

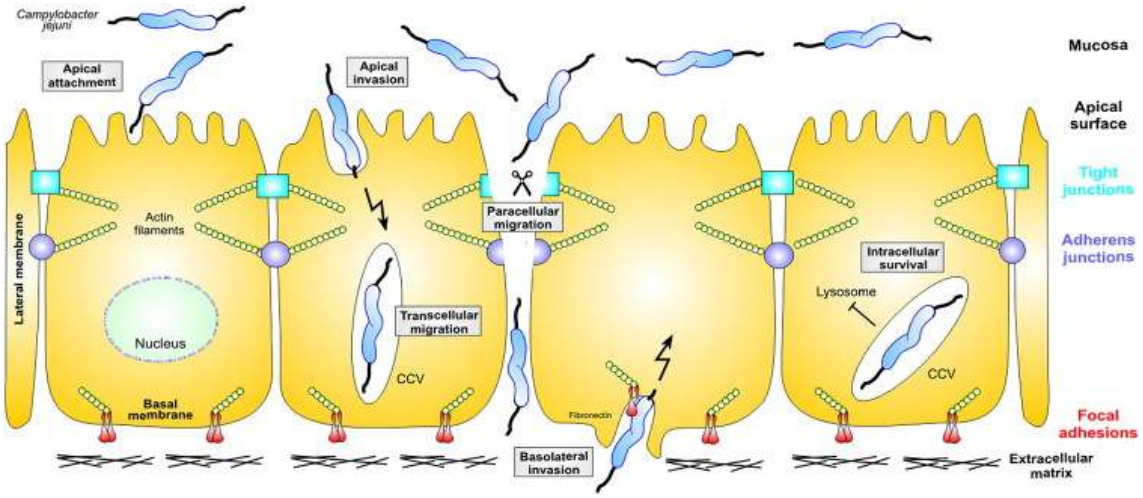
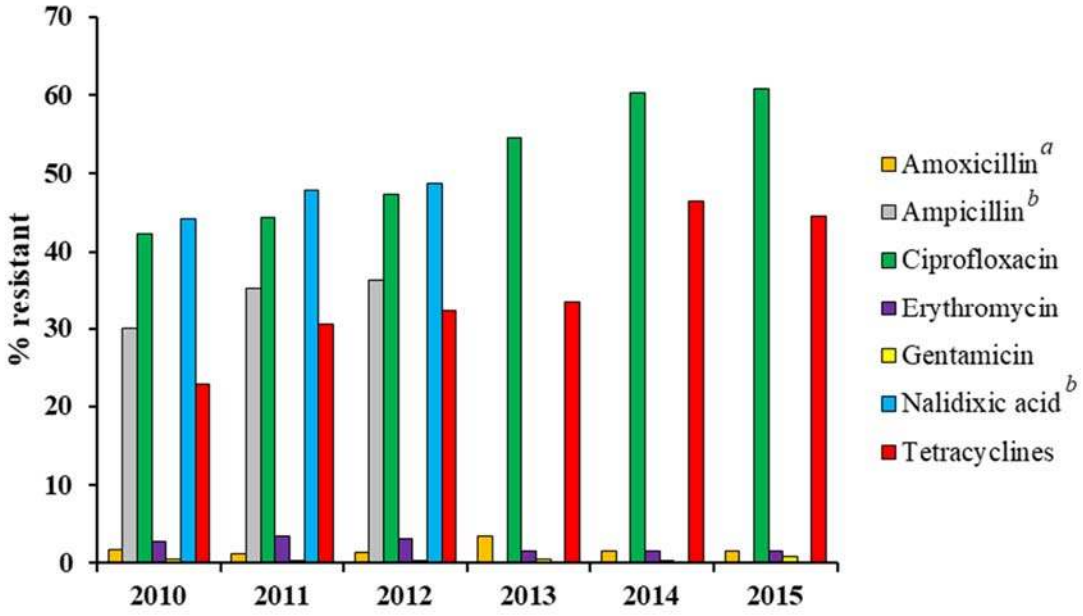


Figure 5. Antimicrobial resistance in *Campylobacter* from humans (2010-2015). The data indicates a high level of antibiotic resistance for *Campylobacter*, with temporal trends indicating a rise in resistance to specific antibiotics. Of particular interest is the rise in resistance to antibiotics, such as nalidixic acid, ciprofloxacin and tetracyclines. Source: The European Union summary reports on antimicrobial resistance in zoonotic and indicator bacteria from humans, animals and food 2010-2015 (EFSA and ECDC, www.efsa.europa.eu).



(a) From 2013 is reported as a mixture of amoxicillin and clavulanic acid (co-amoxiclav).
(b) From 2012 is not reported.

Figure 6. Effect of pectic oligosaccharides (POS) concentration in the invasion of undifferentiated Caco-2 cells by *C. jejuni*. The results represent the mean values of invasive bacteria compared to control (IRC) and the standard error of the means for three different experiments. Asterisk represents significant differences respect to control with $p \leq 0.05$. Source: Ganan et al., 2010.

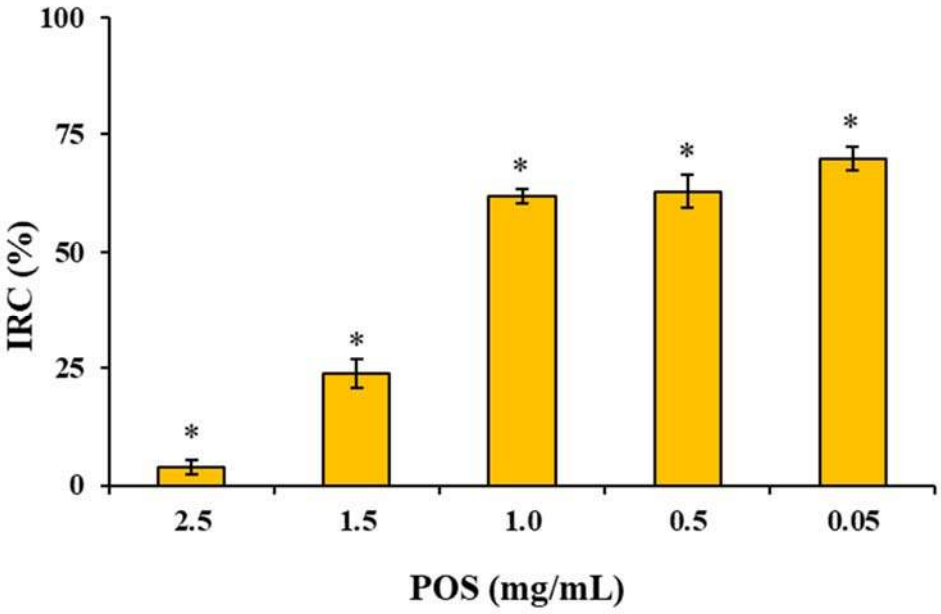
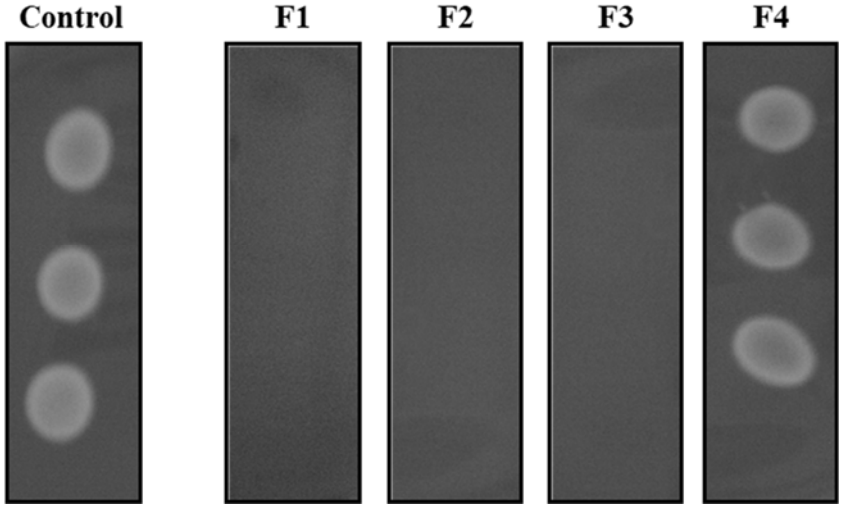


Figure 7. Qualitative antibacterial activity of grape seed collected fractions against *C. jejuni* and their phenolic composition (mg/L). Source: Silvan et al., 2013.



Compound	F1	F2	F3	F4
Flavonols				
Quercetin-3-glucoside	*n.d.*	*n.d.*	78.0 ± 4.0	*n.d.*
Myricetin-3-glucoside	*n.d.*	*n.d.*	9.1 ± 0.1	*n.d.*
Kaempferol-3-glucoside	*n.d.*	*n.d.*	6.0 ± 0.2	*n.d.*
Phenolic acids				
Gallic acid	0.8 ± 0.1	10.6 ± 1.0	*n.d.*	*n.d.*
Protocatechuic acid	4.6 ± 0.1	13.0 ± 2.0	*n.d.*	1.0 ± 0.0
Caftaric acid	45.3 ± 0.3	*n.d.*	*n.d.*	*n.d.*
Homogentisic acid	1.7 ± 0.2	*n.d.*	*n.d.*	*n.d.*
Homovanillic acid	0.21 ± 0.0	*n.d.*	*n.d.*	*n.d.*
Chlorogenic acid	6.1 ± 0.1	4.0 ± 0.1	*n.d.*	*n.d.*
Catechins				
B1	7.1 ± 0.1	74.0 ± 3.0	*n.d.*	*n.d.*
Ec-Ec-Cat	*n.d.*	88.0 ± 6.0	*n.d.*	*n.d.*
Catechin	*n.d.*	81.0 ± 16.0	*n.d.*	*n.d.*
B2	*n.d.*	108.0 ± 8.0	*n.d.*	*n.d.*
Epicatechin	*n.d.*	95.0 ± 10.0	*n.d.*	*n.d.*
Epicatechin gallate	3.4 ± 0.1	*n.d.*	*n.d.*	*n.d.*
Anthocyanins				
Delphinidin-3-glucoside	*n.d.*	*n.d.*	*n.d.*	*n.d.*
Peonidin-3-glucoside	*n.d.*	*n.d.*	*n.d.*	*n.d.*
Malvidin-3-glucoside	*n.d.*	*n.d.*	*n.d.*	*n.d.*
Malvidin-3-acetate	*n.d.*	*n.d.*	*n.d.*	*n.d.*
TPC[a]	118.4 ± 5.0	795.0 ± 13.3	405.5 ± 6.1	73.5 ± 5.0

n.d. = non detected.

[a] Total phenolic content (mg GAE/L).

Table 1. Main features of the genus *Campylobacter.* Source: Oyarzabal & Carrillo, 2016.

Feature	Values/Comments
Capnophilic	Some species require 35% CO_2 to grow
Catalase activity	Positive
Chemoorganotrophs	Do not ferment or oxidize carbohydrates
Energy	Obtained from amino acids or intermediates of the tricarboxylic acid cycle
High temperature for growth	42ºC in case of thermotolerant species: *C. jejuni*, *C. coli*, *C. hyointestinalis*, *C. lari*, and *C. upsaliensis*
Microaerobic atmosphere	O_2 concentration between 3% and 15%. Concentrations of 5% are commonly used for isolation
Minimal growth temperature	30ºC
Motility	Corkscrew-like darting motility observed with phase contrast or darkfield microscopy. High motility in fresh cultures
Shape	Spiral, S-shaped, or gull-winged-shaped when two cells form short chains. Cells in old cultures can form spherical or coccoid bodies
Special requirements to grow	Some species require hydrogen or formate with fumarate (electron donors) to grow in microaerobic conditions. If not, anaerobiosis becomes an optimal growth condition for these species

Table 2. Control intervention strategies for prevention *Campylobacter* infection in poultry industry. Source: this work.

Intervention	Strategy	Reference
Preharvest	Biosecurity measures	Newell et al., 2011; Riedley et al., 2011
	Bacteriocins application	Messaoudi et al., 2012; Svetoch et al., 2008
	Vaccination	Nothaft et al., 2016; Meunier et al., 2016
	Subunit vaccines	Buckley et al., 2010; Theoret et al., 2012
	Killed whole cell vaccines	Wyszyńska et al., 2004
	Competitive exclusion	Laisney et al., 2004
	Phage therapy	Carvalho et al., 2010; El-Shibiny et al., 2009
	Fatty acids and essential oils	Brenes et al., 2010; Van Gerwe et al., 2010
Postharvest	Hauling and transportation	Hastings et al., 2010; Whyte et al., 2001
	Scheduled slaughter	FSAI, 2011; Umaraw et al., 2017
	Logistic slaughter	Evers, 2004; Potturi-Venkata et al., 2007
Processing	Scalding	Lehner et al., 2014
	Counter-current scald tanks	FSAI, 2011
	Water flow rates	Osiriphun et al., 2011
	Multi-stage scalds tanks	Hinton et al., 2004
	Defeathering	Guerin et al., 2010
	Evisceration	Gruntar et al., 2015
	Prevention spillage intestinal content	Rosenquist et al., 2006
	Chilling	Boysen & Rosenquist, 2009
	Sanitation	Wideman et al., 2016
	House practices	Umaraw et al., 2017

Table 3. Different food processing industries and their wastes. Source: Rao, 2010.

Food processing industry	**Waste materials generated**
Cereal processing	Husks, hull, rice, bran
Fruits and vegetable processing	Skin, peels, pulp, seeds, stem, fiber
Animal products	Skin, bones, blood, feathers, intestines
Marine products processing	Viscera, heads, backbones, shells
Dairy products processing	Whey, lactose

Table 4. Antibacterial activity of lactic acid treatments against *Campylobacter*. Source: this work.

Campylobacter strain	Reduction	Concentration	Treated sample	Application	Exposure time	Reference
C. jejuni DSM 4688	1.51 log CFU/g	15%	Carcass	Immersion	30 s	Ellerbroek et al., 2007
C. jejuni DSM 4688	0.70 log CFU/g	15%	Carcass	Spraying	30 s	Ellerbroek et al., 2007
C. jejuni DSM 4688	0.31 log CFU/g	10%	Carcass	Immersion	30 s	Ellerbroek et al., 2007
C. jejuni DSM 4688	0.78 log CFU/g	10%	Carcass	Spraying	30 s	Ellerbroek et al., 2007
C. jejuni NCTC 11168	~4 log CFU/mL	0.5%	Chicken juice	Incubation	24 h	Birk et al., 2010
C. jejuni NCTC 11168	~6 log CFU/mL	0.5%	BHI Broth	Incubation	24 h	Birk et al., 2010
C. jejuni C356 ribotype	6.7-6.9 log CFU	5.7%	Broiler feed	Incubation	20 min	Heres et al., 2004
C. jejuni farm-isolated	nd	5.7%	Housed broiler chickens	Acidified feed	20 days	Heres et al., 2004
C. jejuni NCTC 11168	1.69 log CFU/mL	2.5%	Chicken skin	Immersion	1 min	Riedel et al., 2009
C. jejuni NCTC 11168	3.87 log CFU/mL	2.5%	Chicken skin	Immersion + storage 24 h at 5ºC	1 min	Riedel et al., 2009
C. jejuni NCTC 11168	~0.7 log CFU/mL	2.5%	Chicken meat	Immersion	1 min	Riedel et al., 2009
C. jejuni NCTC 11168	~2 log CFU/mL	2.5%	Chicken meat	Immersion + storage 24 h at 5ºC	1 min	Riedel et al., 2009
C. jejuni ATCC 33291	1.06 log MPN/cm^2	3%	Chicken leg meat	Immersion	10 min	Coşansu et al., 2010
C. jejuni ATCC 33291	0.36 log MPN/cm^2	1%	Chicken leg meat	Immersion	10 min	Coşansu et al., 2010
C. jejuni ATCC 33291	1.98 log MPN/cm^2	3%	Chicken breast meat	Immersion	10 min	Coşansu et al., 2010
C. jejuni ATCC 33291	1.27 log MPN/cm^2	1%	Chicken breast meat	Immersion	10 min	Coşansu et al., 2010
C. jejuni and *C. coli* combined	1.26 log CFU/ cm^2	5%	Chicken skin	Immersion	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	0.77 log CFU/ cm^2	1%	Chicken skin	Immersion	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	5.17 log CFU/ cm^2	5%	Chicken skin	Immersion + storage 15 days at 4ºC	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	4.25 log CFU/ cm^2	1%	Chicken skin	Immersion + storage 15 days at 4ºC	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	0.75 log CFU/ cm^2	5%	Chicken skin	Spraying	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	2.98 log CFU/ cm^2	5%	Chicken skin	Spraying + storage 15 days at 4ºC	15 s	Meredith et al., 2013
C. jejuni and *C. coli* combined	100% inhibition	0.05%	Bacterial inoculum	Incubation	48 h	Navarro et al., 2015
C. jejuni combined strains	3.43-3.03 log CFU/mL	3%	Bacterial inoculum	Incubation	24 h	Rajkovic et al., 2009
C. jejuni	1.81-1.85 log CFU/g	10%	Chicken leg artificially inoculated	Immersion	2 min	Rajkovic et al., 2010
C. jejuni	1.85-2.98 log CFU/g	10%	Chicken leg naturally contaminated	Immersion	1.5 min	Rajkovic et al., 2010
C. jejuni	2.05 log CFU/g	0.125%	Culture medium	Incubation	2 min	Zakariené et al., 2015
C. jejuni	4.25 log CFU/g	0.25%	Culture medium	Incubation	2 min	Zakariené et al., 2015
C. jejuni	5.67 log CFU/g	0.5%	Culture medium	Incubation	2 min	Zakariené et al., 2015
C. jejuni	5.94 log CFU/g	2%	Culture medium	Incubation	2 min	Zakariené et al., 2015
C. jejuni	1.22 log CFU/g	5%	Broiler breast fillets	Immersion	2 min	Zakariené et al., 2015
C. jejuni	0.9 log CFU/g	3%	Broiler breast fillets	Immersion	2 min	Zakariené et al., 2015