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Review

Prevalence and Distribution of Thermotolerant *Campylobacter* Species in Poultry: A Comprehensive Review with a Focus on the Factors Affecting the Detection and Enumeration of *Campylobacter jejuni* and *Campylobacter coli* in Chicken Meat

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Abstract: It is well known that the strong-evidence foodborne outbreaks of human campylobacteriosis are associated with the consumption of raw or incompletely thermally processed poultry meat, whereas broilers act as the main reservoir for *Campylobacter* species. *Campylobacter jejuni* and *Campylobacter coli* are the two main species of campylobacters detected in chicken meat, while they account for almost 90% of the reported cases of campylobacteriosis in humans. Over 80% of these cases are attributed to *C. jejuni* and about 10% of them are due to *C. coli*. Therefore, until recently the dominance of *C. jejuni* against all other *Campylobacter* spp. isolated from chicken meat samples was well established and unquestionable. Lately, however, *C. coli* has been increasingly recovered from chicken meat to such an extent that it is now evident that it often comprises the dominant species among the identified campylobacters in the meat samples. This work attempts for the first time a detailed review in the literature to deepen into this noteworthy epidemiological swift in the prevalence of *C. jejuni* and *C. coli*, along with the distribution of *Campylobacter* spp. in chicken meat. Factors such as the sampling method followed for screening campylobacters in broiler carcasses (e.g., swabs or carcass rinsates, skinned or skinless meat excised samples) and part of the animal carcass from which the sample is obtained (e.g., neck, breast, leg), seasonality of sampling (summer vs. winter) and environmental conditions (e.g., rainfall, relative humidity) at the farm level, the isolation procedure (enumeration or detection) and pathogen identification (biochemical or molecular), the enrichment and plating isolation media (e.g., Bolton vs. Preston broth, charcoal-based vs. chromogenic agars), as well as the biofilm-forming ability of different campylobacters, highlight the multivariate dimension of the phenomenon and are thoroughly discussed in the present review.

Keywords: *Campylobacter*; chicken; epidemiology; meat; poultry

1. Introduction

According to the latest scientific report of the European Food Safety Authority (EFSA) and the European Centre for Disease Prevention and Control (ECDC) on the trends and sources of zoonoses and foodborne outbreaks in the European Union (EU), campylobacteriosis is the most commonly reported foodborne gastrointestinal infection in humans in the EU and has been so since 2007 [1]. Estimates of the overall human health impact of bacterial agents transmitted commonly through food, place *Campylobacter* as the first or second most common agent after nontyphoidal *Salmonella* in Europe, North America, Australia, and Japan [2–4]. The notable absence of notified *Campylobacter* outbreaks in China and some other populous countries, like India, could be attributed to the lack of mandatory surveillance by the established foodborne disease surveillance system or to the



underreporting (e.g., mild symptoms and a smaller number of cases seeking health care) and/or underdiagnosis (e.g., lack of testing and diagnostic accuracy) of the disease, the lack of epidemiological surveillance data connecting causative agents of outbreaks, and the different dietary habits on those countries [5–7].

Major food categories of interest for *Campylobacter* occurrence include mostly meat and meat products (i.e., animal carcasses and fresh/ready-to-eat (RTE), cooked and fermented products), as well as milk and milk products (i.e., raw and pasteurized milk and dairy products including cheese) [1], although the prevalence of the disease-causing *Campylobacter* spp. is significantly increased in poultry meat samples compared to other types of meat or compared with milk and dairy products [8–11]. The strong-evidence foodborne association of campylobacteriosis outbreaks with the consumption of raw or incompletely thermally processed poultry meat is already well known and has been emphatically documented nowadays [8,10,12], while the foodborne illness due to the presence of *Campylobacter* spp. in poultry has been classified as the costliest pathogen-meat combination from an economic perspective [13]. Regardless the fact today poultry is considered the main reservoir for *Campylobacter* spp. (source of infection), latest epidemiological evidence suggests pathogen transmission to humans through a pathway implicating cattle as the primary reservoir of *Campylobacter* (source of contamination), infecting people via the fecal-oral route and the consumption of contaminated chickens [14].

World poultry meat consumption refers to the consumption of meat from chickens (broilers), turkey, and other avian species (e.g., ducks, geese). Available data compiled from the Food and Agriculture Organization (FAO) of the United Nations (UN) reveal an increase in worldwide annual poultry meat consumption per capita by more than 5.0 kg in the past 20 years; from 10.8 kg in 2000 to 16.2 kg in 2020 [15]. Chickens are by far the main protein source of animal origin for humans in terms of livestock animals reared and slaughtered for their meat [15], so the previous rates represent roughly the chicken meat being consumed on a global basis.

The different thermotolerant campylobacters validly described to date are summarized in Supplementary Table S1. Of these, *Campylobacter jejuni* and *C. coli* are the two most important species mainly detected in foods of animal origin [55], [56] (p. 1670). These two species account for almost 90% of the reported human campylobacteriosis cases, with over 80% of the occurring gastrointestinal infections being attributable to *C. jejuni* and the rest about 10% of infections attributed to *C. coli* [56] (pp. 1669–1670), [57]. Therefore, until recently it was well established and beyond any reasonable question that *C. jejuni* is the dominant species among all other *Campylobacter* spp. isolated from chicken meat samples. Lately, however, *C. coli* has been increasingly recovered from chicken samples to such an extent that it is now obvious it many times comprises the dominant species among the identified campylobacters in the meat samples [58–62]. To this end, in studies pertaining to the metropolitan area of Athens, Greece, and its suburbs in the Attica region, Andritsos et al. [63] reported isolation rates of 6% and 27% for *C. jejuni* and *C. coli*, respectively, during *Campylobacter* spp. detection in chicken meat samples, whereas the strict majority (87.5%) of the recovered campylobacters (16) from 830 fecal samples collected from five poultry farms by Marinou et al. [64] were identified as *C. coli*, without any of the strains being identified as *C. jejuni* whatsoever. Taking into account that in the latter case of *Campylobacter* presence in broilers' litter, the positive predictive value in terms of microorganism's occurrence in carcass skin samples is much greater, unless the pathogen cannot be detected in the intestinal content of the bird [65], *C. coli* dominance in the chicken flocks should be taken for granted.

Considering all the above, the present work attempts for the first time, to the best of the authors' knowledge, a detailed review in the literature in order to elucidate the underlying epidemiological transition from *C. jejuni* to *C. coli* in chicken meat, along with the distribution of campylobacters in poultry. Figure 1 outlines the factors affecting the occurrence of *Campylobacter* spp. in poultry meat samples, while those factors are thoroughly being discussed below.

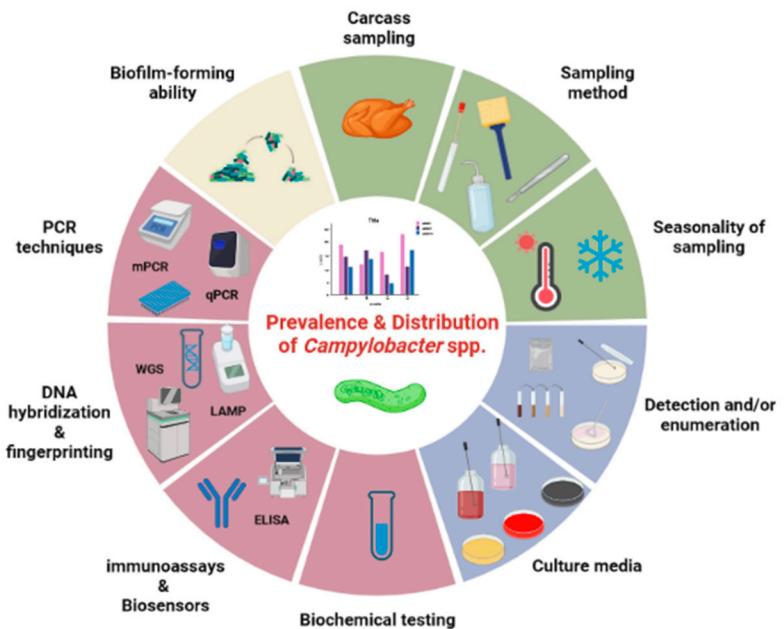


Figure 1. Factors affecting the prevalence and distribution of *Campylobacter* spp. in poultry meat. Factors that are related to each other are grouped together under the same color. As a result, distinct groups of factors referring to sampling (light green), isolation procedure (light blue), confirmation and/or identification (light purple), and biofilm production (light brown) for *Campylobacter* species are presented. Created with BioRender.com.

2. Sampling of Poultry

2.1. Carcass Sampling

Campylobacter which is originally associated with the bird's feathers and contaminates the exterior of the animal might be transferred to the poultry skin during mechanical defeathering of broiler carcasses in the slaughterhouse [66]. Thus, the meat sampled with skin from poultry is more likely to contain the pathogen when compared to animal tissue samples obtained from broiler carcasses without the skin. Furthermore, due to the favorable conditions of humidity and temperature in the wings of poultry, there is a high *Campylobacter* load in the wings which could also be attributed to imperfect scalding, post-scalding contamination or a combination of both [67]. Hence, there is an increased prevalence of *C. jejuni* in the wings of sampled poultry [65,68–70]. Besides, an initial high *Campylobacter* contamination of the neck skin may occur when water excess drips down the carcass dragging along the bacteria during the slaughter line hanging (upside down) of carcasses [71]. This may also explain the comparatively lower number of campylobacters found on the back, breast and leg skin samples and other parts of the carcass than in the neck and wing skin samples (Figure 2). Moreover, breast and wing skin sites when sampled show a higher correlation in *Campylobacter* populations with the neck skin samples [71]. The variations in *Campylobacter* concentrations between skin sites of individual carcasses are often reflected in the non-homogeneous distribution of carcass contamination after post-chilling of broiler carcasses [71] (Figure 2).

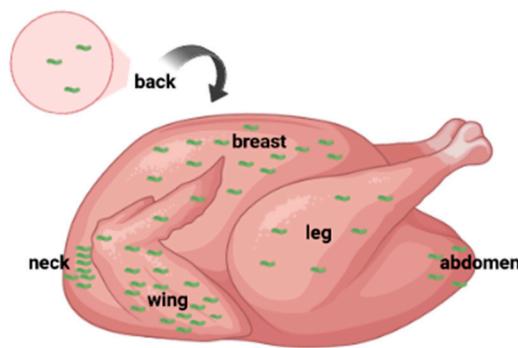


Figure 2. Sampling sites of a broiler carcass with variations in *Campylobacter* contamination depicted with the relative concentration of campylobacters (green curved bacteria). *Campylobacter* concentration in descending order from the more heavily contaminated site to the less contaminated one, when sampled with skin, is as follows: (neck \geq wing \geq breast \geq leg) $>$ (abdomen \geq back). Parentheses designate the sites that are highly correlated to each other in terms of *Campylobacter* concentration. Created with BioRender.com.

2.2. Sampling Method, Type of Product and Refrigerated Storage

The method of sampling plays an important role in determining the microbiological quality of foods. Several non-destructive methods (e.g., surface swabs, contact plates, tissue excisions) are suitable for estimating bacterial populations anticipated in relatively high concentrations on the carcass, such as aerobic plate count (APC) and enterobacteria, while other –destructive in nature– methods (e.g., sampling/cutting of parts of the carcass, whole carcass rinses) are more suitable for detecting the presence of pathogens that may be more unevenly distributed and in low population on the carcass [72,73]. The former are fast and simple methods that can be used for comparative purposes, sanitation verification procedures, and shelf-life prediction, whereas the latter are time-consuming and labor-intensive methods preferable when the microbiological safety is of outmost importance. For instance, a sample area of at least 100 cm² is swabbed for APC and Enterobacteriaceae enumeration in a cattle carcass after dressing but before chilling and a pooled neck skin sample is recommended for detecting *Salmonella* and enumerating *Campylobacter* in poultry carcasses after chilling [74,75]. In the case of broiler carcasses, counts for APC and hygiene indicators (total coliforms, *Escherichia coli*) from the microbiological analysis of swabs were generally more than 0.5 log units lower than the smallest values obtained through tissue excisions and carcass rinses [76].

The type of product or its preparation also affect *Campylobacter* incidence. Statistical analysis in a survey of *Campylobacter* spp. contamination in chicken meat preparations in Belgium indicated that the odds of *Campylobacter* presence are lower in minced meat than in portioned or cut meat and an unpredicted bias into prevalence and enumeration results could be plausible, unless proper sampling and a balanced selection of product types takes place [67]. Progressive increase of product's surface through mincing, apart from increased levels of pathogen contamination, implies also increased microbial exposure to the air. For microaerophilic *Campylobacter* spp. this exposure to aerobic conditions could prove lethal since the degree of processing leads to an ever-increasing decrease in the number of campylobacters encountered in the products [55,68,77,78]. Finally, storage of product at refrigeration temperature may reduce *Campylobacter* count, as revealed by culturing methods during storage of refrigerated broiler breast and thigh meat at 4°C, packaged under aerobic, modified atmosphere packaging (MAP) or vacuum conditions [79,80]. Interestingly, the succession of *Campylobacter* species or strains, with a special emphasis on *C. jejuni* and *C. coli*, during refrigerated storage of artificially contaminated chicken meat packaged samples could be the subject of future research, as in the case of *Listeria monocytogenes* [81].

2.3. Seasonality of Sampling and Environmental Conditions

The seasonality of sampling and the effect environmental conditions may have on the recovery of *Campylobacter* spp. from broiler carcasses or chicken meat has been the subject of dozens of research papers, which present conflicting results as far as the effect of seasonality on *Campylobacter* prevalence is concerned and fail to reach an agreement on the matter. In this context, a large number of studies have indicated a significant seasonal increase in the prevalence of *Campylobacter* in broiler carcasses or in poultry meat during the hot summer months [10,68,82–85], even in tropical countries without marked seasons where other climatic conditions though, like increased rainfall and relative humidity, possibly reflect to the pathogen's potential to colonize its host (e.g., chicken broilers) [86,87]. The seasonal effect on *Campylobacter* prevalence is inferred either by the increased number of reported campylobacteriosis cases during the summer months [10,82] or the increased fly activity [88] and the presence of flies in the summer, which play the role of the bacterial vector (mechanical/transport host) in the warm months [83]. In addition, the aforementioned increase in prevalence could reflect the level of environmental contamination due to more regular ventilation of the poultry houses in summer, resulting in increased contact of birds with the external environment [89,90]. To this end, higher wind speeds and the geographical location of the farm, surrounded by a more agricultural landscape, may also contribute to the extent of contamination in the poultry flock [84,91]. Wind may introduce contaminated material (e.g., soil, dried fecal particles) to the poultry house, which is more likely to exist in the rural setting, exposing the flock to *Campylobacter* spp. among other fecal pathogens, if birds have access to the external environment [91]. Biosecurity measures at the farm level greatly contribute towards prevention of *Campylobacter* colonization and reduce prevalence of the pathogen in broiler flocks [90,92].

On the other hand, several papers highlight the non-statistically significant effect of seasonality on *Campylobacter* populations from broiler carcasses or chicken meat [61,63,90,93], where especially in the warmer countries of southern Europe, like the Mediterranean countries, a higher prevalence of *Campylobacter* spp. is reported in broiler flocks throughout the year compared to the colder northern European countries with the more pronounced and obvious seasonality in their bacterial recoveries of the pathogen [90,92]. Moreover, many times the inability to ascertain the degree of influence of the seasonality on the recovery rate of *Campylobacter* spp. is even related to the small number of samples analyzed which does not allow safe conclusions to be drawn [61,63].

Regarding the distribution of different *Campylobacter* species in poultry carcasses, Manfreda et al. [59] reported higher recovery rates for *C. jejuni* (75.2%) against *C. coli* (24.8%) in winter (i.e., December–March) for chicken carcasses sampled from a single slaughterhouse in Italy, which were processed from broilers coming from a dozen of different chicken farms, compared to other seasons where *C. jejuni* was either absent (in autumn), marginally (in spring) or slightly (in summer) dominant over *C. coli*. In contrast, in a retrospective study conducted in Poland for the five-year period 2014–2018, Wieczorek et al. [61] showed that the peak in the distribution of *C. coli* was clearly placed to the autumn-winter months (i.e., October–February).

3. Isolation of *Campylobacter* spp.

3.1. Detection and/or Enumeration Procedure

The choice of microbiological method that can be used to isolate campylobacters from a food commodity can significantly affect the prevalence or even the estimated concentration of the pathogen in food [73,94–101], and therefore the distribution of different *Campylobacter* species recovered from food during the microorganism's detection or enumeration procedure followed. *C. jejuni* was mainly isolated during pathogen enumeration procedure, while *C. coli* was the predominant species recovered from all plating culture media following enrichment in Bolton broth during the detection of *Campylobacter* in chicken meat [63,98].

The possibility of combining different enrichment broths (e.g., Bolton broth or Preston broth) with different selective and/or differential (i.e., chromogenic) solid culture media (i.e., agars) (e.g., modified charcoal-cefoperazone-deoxycholate agar; mCCDA, Preston agar) could be utilized as an

alternative to the standard ISO 10272-1 protocol [102] used for the detection of *Campylobacter* in food [103–105]. For pathogen enumeration, different agars than mCCDA proposed by ISO 10272-2 enumeration method [107], either selective (e.g., Preston agar or Karmali agar) or chromogenic (e.g., *Campylobacter* selective agar; CASA®, Brilliance™ Campy count agar, BCCA) which have been found to perform equally well to the recommended mCCDA in enumerating colonies of *Campylobacter* spp. [63,96,108–112], could be used after the initial dilution of the food sample. After all, the colored colonies of *Campylobacter* on chromogenic agars are easier to record and count than those on the charcoal-based agars, such as mCCDA.

Enrichment of chicken meat samples in Preston broth for 24 h followed by plating on mCCDA performed better than 48 h enrichment in Bolton broth and plating on mCCDA [96], while this alternative enrichment and plating combination was taken into account in the revised ISO method for *Campylobacter* spp. detection (i.e., procedure B in the ISO 10272-1 protocol) [102]. Furthermore, the parallel use of the detection and enumeration procedures improves the recovery of *Campylobacter* spp., whereas chromogenic agars, like CASA and BCCA, should be considered as secondary plating media for simultaneous or optional use together with the ISO recommended mCCDA and/or even as suitable alternatives to the latter selective agar [63]. In any case, it has been proved that the previously mentioned enrichment and/or plating alternatives can significantly affect the recovery of *Campylobacter* strains from food [73,94–101].

3.1.1. Composition of Culture Media for Detection/Enumeration

In food samples with an expected low number of *Campylobacter* spp. and low concentration levels of accompanying (background) microbiota and/or stressed campylobacters (e.g., cooked or frozen samples), the enrichment in Bolton broth is highly recommended for pathogen detection, whereas for samples with high concentration levels of background microbiota other than *Campylobacter* spp. (e.g., raw meats including poultry or raw milk), the use of Preston broth as a sample enrichment medium is suggested [96,102].

The reduced recovery of campylobacters from raw chicken meat after sample enrichment in Bolton broth compared to direct plating from the initial dilution of the food sample, is likely attributable to the presence of cefoperazone in the liquid medium. The latter is a third generation β -lactam antibiotic which is supplemented into Bolton enrichment broth, as well as in mCCDA plates utilized for pathogen isolation. Foods containing microbiota resistant to third generation β -lactams, including cefoperazone, such as raw chicken containing β -lactam-degrading *E. coli*, namely extended-spectrum β -lactamase-producing; ESBL-producing *E. coli*, may lead to the overgrowth of the accompanying flora during the enrichment procedure in Bolton broth, which in turns leads to the suppression of *Campylobacter* spp. rendering them non detectable following the subculturing on agar plates. Limited growth of *Campylobacter* co-cultured with ESBL-producing *E. coli* in Bolton broth is hypothesized to be due to oxygen availability during the growth of *Campylobacter* in the medium [113]. In such a case, different enrichment broth and plating agar combinations, based on different principles of selectivity (e.g., Preston broth combined with Preston agar), are considered more suitable for combating this type of resistant microbiota and allowing for better detection of *Campylobacter* spp. in chicken meat [96,102,103,105]. Alternatively, restoring the selectivity of Bolton broth and mCCDA can be achieved by supplementation of these media with β -lactamase inhibitors or inhibitory bacterial growth agents (e.g., antibiotics) to overcome the problem of ESBL-producing *E. coli* [114–121].

4. Confirmation and Identification of *Campylobacter* spp.

Using conventional microbiological methods and following the enrichment of food sample or direct plating from the initial dilution of the food sample and isolation of *Campylobacter* spp. on selective plating media, there is a need to confirm the presence of *Campylobacter* and then to proceed, if necessary, with the identification of *Campylobacter* species [102,107]. Biochemical tests are routinely used for confirmation and identification purposes, even though molecular methods, such as

polymerase chain reaction (PCR) techniques (e.g., multiplex or quantitative PCR), are gaining more and more ground lately.

4.1. Biochemical Differentiation of *Campylobacter* species

Among the *Campylobacter* spp. present in food, the most frequently encountered species, as already highlighted, are *C. jejuni* and *C. coli*. However, other species have been described (e.g., *C. lari*, *C. upsaliensis*; Supplementary Table S1), some key characteristics of which permit their differentiation (Table 1) [102,107].

With a closer look, Table 1 reveals that the only biochemical test that can distinguish between *C. jejuni* and *C. coli* is hippurate hydrolysis, with the former species showing a positive reaction compared to the latter species which give a negative reaction to the presence of hippurate. Thence, this test is typically used to differentiate *C. jejuni* and *C. coli*. Nevertheless, given the fact that some hippurate-negative *C. jejuni* strains have been reported [122,123], hippurate hydrolysis is not a robust criterion for differentiating thermotolerant *Campylobacter* species.

Table 1. Key biochemical characteristics of *Campylobacter* species encountered in foods.

Characteristic	<i>C. jejuni</i>	<i>C. coli</i>	<i>C. lari</i>	<i>C. upsaliensis</i>
Catalase activity	+ ¹	+	+	- ² or weak
Hippurate hydrolysis	+ ³	-	-	-
Indoxyl acetate hydrolysis	+	+	-	+

¹ +: positive reaction. ² -: negative reaction. ³ Some hippurate-negative *C. jejuni* strains have been reported [122,123].

4.2. Molecular Methods for Differentiating *Campylobacter* species

The inherent disadvantage that biochemical differentiation of *C. jejuni* and *C. coli* has because of the low specificity (ca. 20%) hippurate hydrolysis exhibits to some hippurate-negative strains of *C. jejuni* [122,123], together with the laborious and time-consuming character of biochemical identification tests, stimulated the development of molecular diagnostic methods and techniques as alternatives to the classical culture-dependent approach to differentiation of *Campylobacter* species.

Serological methods (i.e., immunoassays) (e.g., enzyme-linked immunosorbent assay; ELISA) [124–128], biosensors for the on-site detection of foodborne pathogens [129,130], DNA hybridization techniques (e.g., loop-mediated isothermal amplification; LAMP) [126,131,132], DNA fingerprinting techniques (e.g., multilocus sequence typing; MLST) [133–135] and above all PCR-based method and techniques (e.g., multiplex PCR; mPCR, quantitative or real time PCR; qPCR/rt-PCR), have been developed for the fastest and most efficient identification and differentiation of *Campylobacter* species among other foodborne pathogens. It should be noted though that some DNA fingerprinting techniques are more sophisticated (e.g., pulsed-field gel electrophoresis; PFGE, whole-genome sequencing; WGS) and require well-trained personnel with a know-how-to conduct the technique and interpret the data. Due to their enormous discriminatory power these molecular typing methods are preferable tools in outbreak investigations rather than the routine monitoring of pathogens [136–140]. For this reason, PCR techniques are the method of choice for *Campylobacter* differentiation during laboratory screening for the pathogen.

4.2.1. PCR-Based Methods and Techniques

The technique of mPRC has been widely studied by several researchers in an effort to find a fast and at the same time reliable means of identifying isolated *Campylobacter* species [141–143]. The combination of food sample enrichment with multiplex real-time PCR (mrt-PCR) results in a more rapid detection and identification of *Campylobacter* spp. isolated from food [144], compared to the standard ISO method utilizing the biochemical identification of the isolates [102]. Nevertheless, the enrichment of the food sample as well as the initial *Campylobacter* load in the matrix significantly affect the isolation frequency and the recovery rate of different subtypes of *C. jejuni* [145] and of many

Campylobacter species. In such a case, combining mPCR with the pre-enrichment in Brucella broth and further enrichment in Preston broth of chicken meat samples led to the identification of the majority of isolated campylobacters as *C. coli* (53%) than *C. jejuni* (47%) [146].

The quantitative determination of *Campylobacter* spp. in contaminated foods and generally in the food chain is crucial, among others in order to comply with imposed EU microbiological criteria for *Campylobacter* in broiler carcasses [147]. Quantitative molecular PCR-based methods, such as rt-PCR techniques, have been developed for such quantification purposes [148–151], although currently only the culture-based ISO method is officially approved for pathogen enumeration [104]. Nonetheless, PCR-based methods suffer from the inability to differentiate between live and dead cells of the target microorganism and the apparent PCR signal that may occur from DNA originating from those dead cells. Therefore, quantitative viability rt-PCR assays have been proposed to normalize on the one hand the underestimation of *Campylobacter* spp. recovered from different food matrices, on the other to allow for reliable differentiation between live and dead *Campylobacter* and thus accurate estimations of pathogen concentration in foods [79,152–155].

5. Biofilm-forming ability of *Campylobacter* spp.

The survival of campylobacter in the food chain remains a paradox since the bacterium is a fastidious organism with characteristic special growth requirements for successful subculturing in the laboratory (e.g., heat-resistant, microaerophilic organism requiring the presence of blood in its culture medium). Recently, biofilm formation has been proposed as the main mechanism of maintenance and transmission for the pathogen from animals to humans [156]. In general, the biofilm-forming ability of *Campylobacter* is strain-dependent and varies among organism's isolated strains [157,158], as well as between different *Campylobacter* spp. [159–161], while it is also affected by the presence of other bacterial species [162–167]. Regarding the biofilm-forming ability of *C. jejuni* and *C. coli*, the latter isolates seem able to form biofilms significantly better compared to *C. jejuni* isolates ($p < 0.05$) [157,160] and that could be another reason for the increased prevalence of *C. coli* against *C. jejuni* in the chicken meat samples.

The ability of *C. jejuni* to form a biofilm is highly dependent on the strain and the type of abiotic surface on which it is found [159]. Teh et al. [165] concluded that *C. jejuni* exhibits a much weaker biofilm-forming ability compared to other bacteria, such as *Pseudomonas* spp., *Staphylococcus aureus*, *Salmonella* spp., and *E. coli*. However, in controlled mixed-microbial populations of a specific *C. jejuni* strain (sequence type; ST-474) with *Enterococcus faecalis* and/or *Staphylococcus* sp., optical intense biofilms for the two species were developed when they were grown with *C. jejuni*, while *C. jejuni* cells were recovered from most of the biofilms containing *E. faecalis* and/or *Staphylococcus* sp. [165]. That was the case and in the studies of Ica et al. [166] and Sterniša et al. [167], where the co-cultivation of *C. jejuni* with *P. aeruginosa* and *P. fragi*, respectively, resulted in the increased determined number of culturable biofilm *C. jejuni* cells. In contrast to monoculture biofilms, the mixed-culture biofilms of *C. jejuni* with pseudomonads had significantly enhanced mechanical strength [166]. Enhanced biofilm formation was also observed for *C. jejuni* and *C. coli* in the presence of *S. aureus*, with increased aerotolerance and survivability in parallel for the *Campylobacter* strains [162].

5. Conclusions

The prevalence and distribution of *Campylobacter* spp. in raw poultry meat from broiler carcasses depends on a variety of factors, such as the sampling method, part of the animal carcass from which the meat sample is obtained, seasonality of sampling, the isolation procedure followed with the different enrichment and plating media utilized for pathogen isolation along with the methods and techniques used for *Campylobacter* spp. differentiation, as well as the biofilm-forming ability of the isolated *Campylobacter* strains with regards to their co-culture with other bacterial species. All these factors should be considered when conducting field surveys or monitoring for *Campylobacter* presence in naturally contaminated poultry meat samples. At the same time, the indicated number of factors highlights the multifactorial dimension and complexity of the phenomenon when interpreting results for the recovery of *Campylobacter* spp. from poultry meat. Thus, the noticed epidemiological transition

from the established predominance of *C. jejuni* to the ever-increasing recovery of *C. coli* in raw chicken meat could be the result of such a versatile effect. The present review attempted for the first time to elucidate the causes of this noteworthy epidemiological shift in prevalence and distribution of *Campylobacter* species on the food matrix itself, without extending to the interaction between pathogen and human host.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: List of thermotolerant *Campylobacter* species currently identified.

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