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ORIGINAL ARTICLE

Persistence and recovery of SARS-CoV-2 from abiotic and biotic surfaces found in meat processing plants

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Abstract

The meat processing industry was negatively affected by the COVID-19 pandemic. The unique conditions in meat processing plants (MPPs) were recognized to have the potential to increase SARS-CoV-2 transmission. Should SARS-CoV-2 persist for extended periods in these built environments, this may contribute to increased risk of virus transmission. To test this hypothesis, SARS-CoV-2 persistence was assessed in conditions reflective of a MPP. Different biotic/abiotic materials were inoculated with SARS-CoV-2 and recovery of viable virus measured over time. Findings showed it was possible to recover SARS-CoV-2 from beef, pork, and salmon for at least 22 days at −20°C and for at least 12 days at +4°C. SARS-CoV-2 recovery from salmon scales and salmon flesh was similar, but viable virus recovered from pork fat was significantly reduced compared to pork meat. In parallel, foods purchased from Irish supermarkets during a COVID-19 wave were contemporaneously tested for the presence of SARS-CoV-2 RNA but none of the samples tested positive by RT-qPCR. Viable SARS-CoV-2 can be inactivated on food or abiotic surfaces by incubation at 56°C or 75°C but fomite transmission during MPP outbreaks cannot be ruled out due to the recovery of SARS-CoV-2 from stainless steel and work clothing fabric for up to 10 h under representative conditions. These data support a multilayered approach to reducing the risk of airborne infections such as SARS-CoV-2 that should include mitigations such as increased ventilation, mask wearing, and the disinfection of work surfaces to reduce the amount of SARS-CoV-2 in the meat processing plant environment.

1 | INTRODUCTION

During the COVID-19 pandemic, outbreaks of SARS-CoV-2 infection were regularly associated with meat processing plants (MPPs) (Günther et al., 2020; Mallet et al., 2021; Walshe et al., 2021). For example, in Ireland there were 23 confirmed COVID-19 outbreaks by the June 24, 2020 (Government of Ireland, 2020) while in Germany there were thousands of positive tests among MPP workers during 2020 (Pokora et al., 2021). Outbreaks in MPPs had multiple consequences including having a negative impact on the health and finances of plant workers; disrupting food supplies; raising concerns over the safety of the farm-to-fork continuum; wastage of livestock due to backlogs caused by COVID-19 enforced closures of MPPs; and subsequent environmental problems emerging from the need to dispose of unused animal carcasses (Han et al., 2021; Ijaz et al., 2021; Marchant-Forde & Boyle, 2020; Yekta et al., 2021). Likely factors that

contribute to SARS-CoV-2 transmission in MPPs include the proximity of workers to each other, cooled environments and the recirculation of air that is not filtered. Although airborne transmission of SARS-CoV-2 is the dominant route of transmission between people, fomite transmission cannot be excluded as a secondary route as it is for many other respiratory viruses (Asadi et al., 2020; Bhaskar et al., 2003; Kraay et al., 2018; Zhang & Li, 2018). There are also concerns in certain countries about the potential persistence of viable SARS-CoV-2 on refrigerated or frozen foods or packaging because SARS-CoV-2 RNA has been detected on foods and food packaging shipped between countries (Caiyu, 2020; Chi et al., 2021; Han et al., 2021; J. Jia et al., 2021). In support of this concern, epidemiological studies have associated two outbreaks in China with SARS-CoV-2 imported on frozen fish and viable virus was recovered in one of these studies (Liu et al., 2020; Pang et al., 2020). Evidence of food acting as a vehicle for the international transport of SARS-CoV-2 highlights the need for mitigation strategies to reduce the risk of contamination in MPPs and investigation into SARS-CoV-2 persistence on different foods. To expand our knowledge about the persistence of viable SARS-CoV-2 under conditions specific to MPPs, this study was established in collaboration with partners directly involved with this industry and involved the use of materials common to meat/fish processing plants.

Investigations into MPP COVID-19 outbreaks found aerosols were the primary route of SARS-CoV-2 transmission among MPP workers (Günther et al., 2020; Pokora et al., 2021). SARS-CoV-2 has been detected on fomites in MPP, which represent another potential route of virus transmission and SARS-CoV-2 has been shown to on persist various abiotic surfaces under various conditions (Biryukov et al., 2020; Chin et al., 2020; De Rooij et al., 2023; Gidari et al., 2021; Harbourt et al., 2020; King et al., 2020; Kwon et al., 2021a; Pastorino et al., 2020; Riddell et al., 2020; Van Doremalen et al., 2020; Wing et al., 2022). A decrease in temperature correlates with increased persistence of viable SARS-CoV-2 on abiotic surfaces while very low (20% or less) and very high (80% or more) relative humidity increases virus inactivation and average (20–80%) relative humidity prolongs virus persistence (Biryukov et al., 2020; Kwon et al., 2021a). Some studies have shown there is no significant difference in SARS-CoV-2 persistence on different abiotic surfaces, but others found there was a more rapid reduction in viability on fabric or metal surfaces compared to plastics or glass (Biryukov et al., 2020; Gidari et al., 2021; Li et al., 2023; Pastorino et al., 2020; Van Doremalen et al., 2020). The composition of the inoculum also contributes to SARS-CoV-2 persistence on surfaces with addition of protein to the virus media increasing its persistence, whereas the addition of some bodily fluids decrease its persistence (Kwon et al., 2021b; Matson et al., 2020; Pastorino et al., 2020). There is variation in the stability of different SARS-CoV-2 variants of concern with Omicron being shown to persist for longer on surfaces than the ancestral variant (Hirose et al., 2022; Huang et al., 2021; Short & Cowling, 2023; Wing et al., 2022).

The persistence of viable SARS-CoV-2 on biotic surfaces has been less extensively investigated than abiotic surfaces but decreased temperature causes prolonged viability (Dai et al., 2021; Dhakal et al., 2021; Feng et al., 2021; Jung et al., 2023; Li et al., 2023). SARS-CoV-2 viability on biotic surfaces has been shown to vary between different foods, with a reduction in viability when incubated on foods such as avocado, mushroom, and salmon compared to other foods such as poultry, pork, and cheese (Dhakal et al., 2021; Feng et al., 2021; M. Jia et al., 2022; Li et al., 2023). SARS-CoV-2 has been shown to remain viable when contaminated foods are exposed to heat, though high temperatures do inactivate virus (M. Jia et al., 2022; Norouzbeigi et al., 2021).

In the case of SARS-CoV-2, there is uncertainty as to the contribution of fomites to its spread. Data gathered from real-world environments suggests there is low risk of fomite transmission due to detection of low viral loads from environmental surface samples and the failure to recover viable virus in most studies (Meyerowitz et al., 2021; Sammartino et al., 2023; Santarpia et al., 2020; Zhou et al., 2021). Other studies suggest fomite transmission has contributed to the spread of COVID-19, specifically when doffing facemasks with hands harboring viable SARS-CoV-2 (Jahromi et al., 2020; King et al., 2020; Ma et al., 2020). An epidemiological investigation of an outbreak between two families in Guangzhou, concluded that transmission between members of the two families most likely occurred through a contaminated elevator button (Xie et al., 2020). High viral loads shed by some COVID-19 patients suggests that sufficient SARS-CoV-2 could be deposited on surfaces for fomite transmission could be possible (Bullard et al., 2020; Pan et al., 2020; Wilson et al., 2020; Wölfel et al., 2020).

This study measured the ability to recover viable SARS-CoV-2 from biotic and abiotic surfaces associated with the meat processing industry following incubation under relevant conditions. Inactivation of SARS-CoV-2 from surfaces at 56 and 75°C was determined while SARS foods from retail markets were screened for the presence of SARS-CoV-2. This information enhances data associated with SARS-CoV-2 persistence on different surfaces and relates it specifically to an industry that was particularly badly affected during the pandemic.

2 | METHODS

2.1 | Preparation of biotic samples

Beef minute steaks, pork chops, and salmon fillets were purchased from the local butchers, fish mongers or supermarkets on the day of preparation. All work with meat and fish was approved by the Animal Research Ethical Committee in University College Dublin (AREC-E-20-39-Barry). No work with live animals was performed and no animals were killed specifically for this project. In a class II biosafety cabinet, food was cut into 5–10 mm^2 coupons of 3–4 mm thickness using disposable scalpels (Figure 1a). Pork fat and salmon scales were also cut from the meat products if required. Food samples were transferred into 12-well plates for disinfection of the natural contaminants on foods by washing in DMEM-based wash media containing penicillin (100 units/ml), streptomycin (100 µg/ml), gentamicin (10 µg/ml), and nystatin (100 units/ml). Washes were performed by adding 2 ml of wash media to each piece of meat and incubating at +4°C. For beef and pork, wash media was changed at 2, 4, and 6 h with

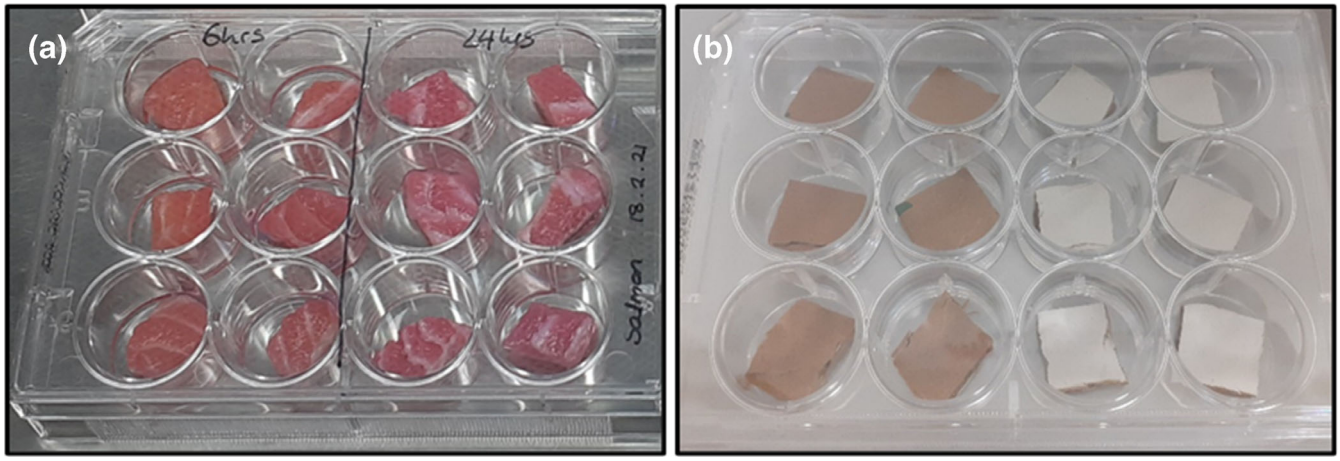

FIGURE 1 Test samples. (a) Salmon cut into coupon-shaped pieces. Other foods were cut into similar pieces. (b) Cardboard cut into coupon-shaped pieces with less porous brown and more porous white surfaces.

the final wash removed at 24 h. For salmon, wash media was changed at 2, 4, 6, 24, 26, 28, and 30 h with the final wash removed at 48 h. After removal of the final wash, samples were transferred into new wells of 12-well plates before transporting to the Biosafety Level 3 (BSL3) laboratory.

2.2 | Preparation of abiotic samples

Cardboard from a box used for deliveries was cut into 15 mm^2 coupons, which were autoclaved to sterilize. Cardboard with one less porous, brown surface and one more porous, white surface was used. Different cardboard coatings can influence its porosity and, in this case, there was increased porosity observed for the white surface compared to the brown surface (Chan et al., 2017; Jin Kang et al., 2020). Cardboard pieces were placed either the brown or white side up into individual wells of 12-well plates, then transported to the BSL3 laboratory (Figure 1b). Stainless steel of the grade used in Irish MPPs was cut into 10 mm^2 coupons, which were autoclaved to sterilize. These were placed into individual wells of 12-well plates, then transported to the BSL3 laboratory. Fabric from the coats worn by MPP workers was cut into 15 mm^2 coupons, which were autoclaved to sterilize. Two pieces of fabric were placed into individual wells of 12-well plates, then transported to the BSL3 laboratory.

2.3 | Generation of SARS-CoV-2 stocks

Vero E6 cells were grown in T-75 flasks using growth media (DMEM supplemented with 10% fetal bovine serum [FBS]). When 90% confluent, growth media was removed from cells, which were washed twice in 5 ml phosphate buffered saline (PBS) and then 19.5 ml virus maintenance media (DMEM supplemented with 2% FBS) was added. In the BSL3 laboratory, virus master stocks were generated by combining 450 µl of virus maintenance media with 50 µl of SARS-CoV-2 supplier stock (Alpha, Human nCoV19 isolate/England/MIG457/2020 [lineage B.1.1.7], Public Health England). One SARS-CoV-2 master stock was used to infect each flask of Vero E6 cells. Mock infected flasks of Vero E6 cells were included. Flasks were incubated at 37°C and 5% CO_2 and cells were monitored microscopically for cytopathic effects (CPE) indicative of virus infection. When at least 90% of cells displayed CPE, SARS-CoV-2 was harvested by transferring the flask contents into a 50 ml Falcon tube, centrifuging at 300*g* for 4 min to pellet cell debris, and then making 1 ml aliquots of the virus-containing supernatant. These SARS-CoV-2 working stocks were stored at −80°C until required. All experiments used first passage SARS-CoV-2.

2.4 | Surface testing

Abiotic and biotic surface samples in 12-well plates were inoculated with 50 µl SARS-CoV-2 stock (10^5 $TCID_{50}$/ml) or 50 µl virus maintenance media (mocks). For spiking experiments, virus was combined at a 1:1 ratio with either meat juices collected from the packaging, 5% bovine serum albumin (BSA), 5% castor oil or a combination of 2.5% BSA and 2.5% castor oil. 12-well plates containing samples were placed in sealable, leakproof Tupperware boxes and protected from UV light during incubation periods. Low humidity conditions were generated by adding four desiccant pouches to Tupperware boxes, which reduced the humidity from approximately 80% to approximately 20%. Stainless steel and fabric samples were incubated at 12°C (maximum air temperature maintained in meat cutting rooms) or room temperature. Food samples and cardboard were incubated at −20°C or +4°C (shipping temperatures) and 56 or 75°C (heat inactivation). Incubations at 75°C used stainless steel, leakproof lunchboxes instead of Tupperware boxes.

Recoveries from virus- and mock-inoculated samples were performed in triplicate at the specified time post-inoculation. For each experiment, recoveries were also performed immediately after inoculation (0-h control). Recoveries were carried out for food, cardboard and stainless steel by pipetting 1 ml of virus maintenance media containing antimicrobials (at the same concentrations used for the wash

TABLE 1 Recovery efficiency immediately after inoculation for each surface based on the described method (mean of 0-h recovery from all repeats).

Surface	Beef	Pork meat	Pork fat	Salmon flesh	Salmon scales	Cardboard (brown)	Cardboard (white)	Stainless steel	Fabric
Virus recovery efficiency (%)	67.5	62.9	75.02	96.5	61.58	68.54	65.18	72.2	69.1

media) over the inoculated surface of the sample, swirling the plates 10 times and then incubating for 10 min to allow virus to leach out. Different incubation times were tested but there was no increase in virus recovery for incubation times longer than 10 min. For fabric, the samples were transferred into sterile 30 ml tubes using disposable tweezers, then 1 ml of virus maintenance media containing antimicrobials was added and tubes were vortexed for 5 s. These techniques were found to recover at least 60% of the virus from each surface immediately after inoculation (Table 1). Recovery media was analyzed to detect or quantify SARS-CoV-2.

2.5 | Detection of viable SARS-CoV-2

SARS-CoV-2 was detected using the semi-quantitative tissue culture infectious dose ($TCID_{50}$) assay and using a qualitative assay. $TCID_{50}$ assays were setup by seeding 1.5×10^4 Vero E6 cells per well of a 96-well plate. These were grown at 37°C and 5% CO_2 until they reached approximately 90% confluency. Growth media was removed and 50 µl of virus maintenance media containing antimicrobials was added to each well. In a second 96-well plate, twofold serial dilutions of samples were made up in virus maintenance media containing antimicrobials in quadruplicate. Virus dilutions were transferred into the 96-well plate containing Vero E6 cells, which were then incubated at 37°C and 5% CO_2 for 4 days. Plates were checked microscopically and scored for the presence or absence of CPE indicative of virus infection. These scores were entered into the Reed-Muench calculator to obtain an estimate of virus titer for each sample.

Qualitative assays were setup by growing Vero E6 cells to approximately 90% confluency in 12-well or 24-well plates. In duplicate, 200 µl of recoveries were added to cells, which were adsorbed onto cells for 60 min at 37°C and 5% CO_2. The 200 µl sample was removed from each well and 1000 µl of virus maintenance media with antimicrobials was added before returning the plates to the incubator. After incubation for 4 days, cells were checked microscopically and scored as being positive or negative for CPE indicative of virus. Recoveries from fabric and cardboard were less than 1 ml due to absorption of media by these matrices so 150 µl was used for each duplicate infection to ensure there was sufficient sample for $TCID_{50}$ assays.

2.6 | Food matrices and environmental samples

Eight categories of retail food items were surveyed for the presence of SARS-CoV-2, including poultry, pork, seafood, vegetables, frozen fruit, fresh fruit, bananas, and ready-to-eat salads. The available packaging of these food matrices and skin of bananas samples were also included for study and two food processing facilities, provided high-touch surface swabs, and composite samples from sewage outlets. Samples were collected between January 21, 2021 and February 11, 2021 and were purchased from 34 retailers in Ireland, including supermarkets, corner shops/convenience stores, butcher counters/shops, and fishmongers/fish counters. Metadata for each sample was recorded to include sample category, purchase date, time, location, type of retailer, producer, and origin (Supplementary Table S1). In addition, a large database of RNA template previously extracted from pork (211 samples) and fresh and frozen fruits (124 and 115 samples, respectively), were included in the study. This subset of samples represents retrospective matrices sampled between December 2018 and December 2019. A total of 1300 samples were obtained and tested including RNA purified from food matrices (852 samples); swabs originating from packaging and the skin of fruit (367 samples); swabs from high touch surfaces (75 samples); and six concentrated wastewater samples collected in food production facilities.

2.7 | Virus concentration and RNA purification from soft fruits, frozen fruits, ready-to-eat salads, and fresh/frozen vegetables

Virus particles from soft fruits, frozen fruits, ready-to-eat salads, and fresh/frozen vegetables, were concentrated starting from 25 g of sample transferred in a mesh filter stomacher bag. Large soft fruits were coarsely chopped into pieces of approximately 2.5 cm^3. A volume of 40 ml Tris-glycine beef extract buffer was added along with pectinase (30 units pectinase from *Aspergillus niger*, or 1140 units pectinase from *Aspergillus aculeatus*) and 10 µl Mengovirus as an internal process control (MeV-IPC). After incubation at room temperature with constant rocking at approximately 60 rpm for 20 min (pH adjusted to 9.5), the eluate was decanted from the filtered compartment and centrifuged at 10,000*g* for 30 min at +4°C. The supernatant obtained was adjusted to pH 7.0, and 0.25 volumes of 5 × polyethylene glycol/NaCl solution were then added. The mixture was homogenized by shaking for 60 s and then incubated with constant rocking at around 60 rpm for 60 min at +5°C and centrifuged at 10,000*g* for 30 min at +4°C. The pellet was concentrated by centrifugation at 10,000*g* for 5 min at +5°C and resuspended in 500 µl PBS for an equal volume purification with chloroform-butanol (vortexed and incubated at room temperature for 5 min). A final centrifugation (10,000*g* for 15 min at +5°C) step facilitated recovery of the aqueous phase that was then transferred to a fresh tube and retained for RNA extraction and purification.

2.8 | Virus extraction from meats and crustacean

Virus particles from meat product, meat preparations and crustacean meat were extracted from 5 g of well-mixed matrices. The extraction included the addition of 7 ml Trizol and 5 ml PBS to the sample in a stomacher bag spiked with 50 µl MeV-IPC. The liquid fraction was transferred into a sterile 50 ml tube and centrifuged (10,000*g* for 20 min at +4°C). The supernatant was then treated with 200 µl chloroform per 1 ml of supernatant recovered (approximately 1.4 ml), mixed for 15 s and incubated at room temperature for 10 min. After a centrifugation step (10,000*g* for 15 min at +4°C), the aqueous layer was used as a template for the RNA extraction and purification.

2.9 | Virus extraction from bivalve molluscan shellfish

Virus extraction specimens were sampled live and intact. Examples of suitable bivalve molluscan shellfish (BMS) and crustacean for this protocol included oysters, mussels, and clams, among others. The digestive glands from BMS were used as a template for the extraction of virus particles and a minimum combined gland mass of 2 g was required. The sample material was finely chopped with a sterile scalpel and transferred into a centrifuge tube and spiked with 10 µl MeV-IPC. A volume of 2 ml proteinase K solution was added, and the mixture was incubated at 37°C with shaking (320 rpm) for 60 min. Secondary incubation was carried out by placing the tube in a water bath at 60°C for 15 min. The supernatant obtained by centrifugation (3000*g* for 5 min) was retained for RNA extraction and purification.

2.10 | Swabs from high touch surfaces and food skin and packaging

Swab samples from high touch surfaces and food surface skin and associated packaging materials were taken using individually wrapped swabs submerged in viral transport media (VTM) containing 2% FBS, 100 µg/ml gentamicin and 0.5 µg/ml Amphotericin B. Excess VTM was removed, and the swab used to sample surface areas of interest (25 cm^3). The swab was taken using moderate pressure, moving in at least two directions, and rotating the swab to use the entire surface area of the cotton swab. It is recommended to avoid the swab drying completely. Immediately after sampling, the swab was placed into the transport container containing VTM, and the swab stick cut at the breakpoint by bending gently before the cap was closed tightly. The outside of the transport container was cleaned with an alcohol wipe and labeled clearly with unique sample identifiers. A field blank was submitted on each sampling day. In this instance, the control swab was handled in the same way as the environmental samples, by opening and removing the swab from packaging in the work area and placing into the transport container without swabbing any surface at the end of the sampling procedure. Samples taken outside of the laboratory environment (such as from a food processing environment), were packaged for transport, using sterile-double sealed bags, and transported at +4°C to the laboratory the same day.

2.11 | RNA extraction and purification

RNA was extracted from the different samples using QIAamp Viral RNA Mini Kit (Qiagen, UK) on the QIAcube Connect system (Qiagen, UK). The RNA was used immediately as the template for the RT-qPCR or stored at −80°C for later analysis.

2.12 | RT-qPCR

RT-qPCR was used as a detection assay adopting primer sets targeting the nucleocapsid protein region 1 (N1), nucleocapsid region 2 (N2) and Human RNase P (RP) based on the "2019-nCoV CDC EUA authorised RT-qPCR Probe Assay primer/probe mix" (IDT, UK). The primers for MeV-IPC were included in the panel for the evaluation of the performances of the protocol, along with negative controls and positive controls consisting of purified RNA previously tested positive for the presence of RNA of SARS-CoV-2 and SARS-CoV-2 control plasmids (IDT, UK), which contain the complete nucleocapsid gene from SARS-CoV-2, SARS-CoV-1, and MERS-CoV (IDT, UK). Luna Universal Probe qPCR Master Mix (NEB, UK) was used for preparing mastermix reactions for each target and loaded in 96-well plates (0.1 ml) on a QuantStudio 5 (Applied Biosystems, UK).

2.13 | Statistical analysis

Processing of data, statistical analysis and generation of plots were all performed using Microsoft Excel and the R Studio software. Analysis of variance was used to compare recovery of SARS-CoV-2 from the same surface incubated under different conditions. To account for variation in recovery efficiencies when comparing different surfaces, $TCID_{50}$ were compared by Analysis of covariance (ANCOVA) using the 0-h recoveries as a covariate. When comparing surfaces where SARS-CoV-2 was recovered at multiple timepoints, time was included as a second covariate in the ANCOVA model. Homogeneity of variance, independence of regression slopes and outliers were identified for each dataset to ensure they met the assumptions of ANCOVA. Pairwise comparisons of different surfaces were performed using Post hoc tests with Tukey correction for multiple comparisons. To compare recoveries from different surfaces visually, ratios generated by normalizing the SARS-CoV-2 $TCID_{50}$/ml at each timepoint against the SARS-CoV-2 $TCID_{50}$/ml for the corresponding 0-h control were plotted. A p-value <0.05 was used to indicate significance when performing statistical analyses. Half-lives were calculated using the mean $TCID_{50}$/ml. If the $TCID_{50}$/ml was less than the lower limit of detection (LOD), the lower LOD of the $TCID_{50}$ assay (68 $TCID_{50}$/ml) was used for calculating the half-life.

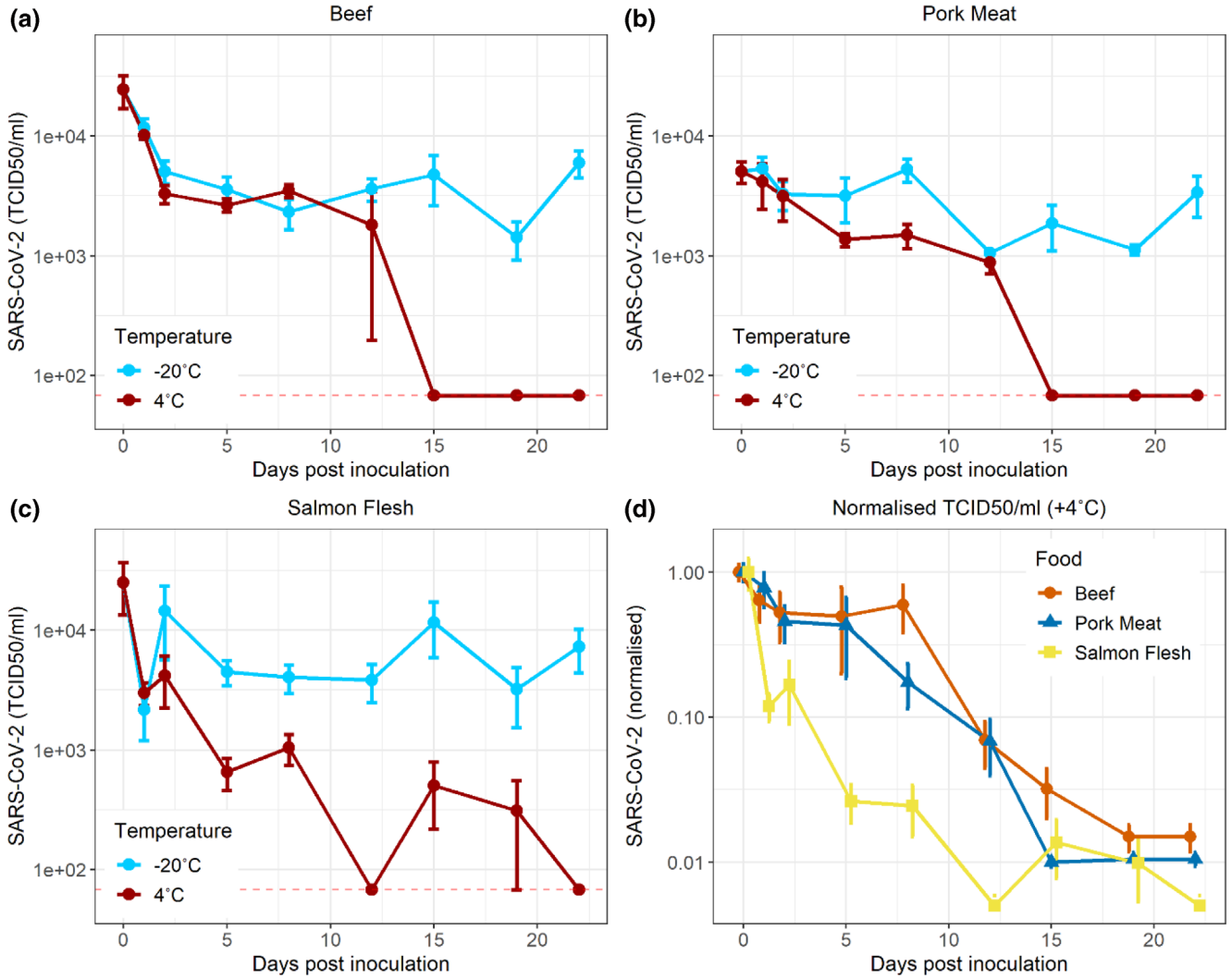

FIGURE 2 Recovery of viable SARS-CoV-2 from beef, pork meat and salmon flesh at temperatures used for shipping and storing food products. Food samples were inoculated with 10^4 $TCID_{50}$ SARS-CoV-2 then incubated at −20°C or +4°C. Viable virus was recovered from beef (a), pork meat (b), and salmon flesh (c) at the indicated timepoints, then titrated by $TCID_{50}$. $TCID_{50}$/ml were normalized against the 0-h timepoint to visualize and compare SARS-CoV-2 recoveries from each surface with a steeper decrease observed for pork and salmon compared to beef at +4°C (d). Points represent the mean and error bars represent the standard deviation of at least three replicates. The dashed red line is the lower limit of detection (LOD) of the $TCID_{50}$ assay.

TABLE 2 Qualitative results for recovery of virus from biotic surfaces at temperatures used for shipping.

	Number of tests with CPE/number of qualitative tests									
	Beef		Pork meat		Salmon flesh		Pork fat		Salmon scales	
Time (days)	−20°C	+4°C	−20°C	+4°C	−20°C	+4°C	−20°C	+4°C	−20°C	+4°C
1	6/6	6/6	6/6	6/6	6/6	6/6	0/0	0/0	0/0	0/0
2	6/6	6/6	6/6	9/9	6/6	9/9	0/0	2/3	0/0	3/3
5	6/6	6/6	12/12	12/12	12/12	12/12	6/6	0/6	6/6	9/9
8	6/6	9/9	12/12	15/15	12/12	15/15	6/6	0/6	6/6	9/9
12	6/6	8/9	12/12	11/15	12/12	6/15	9/9	0/6	9/9	5/9
15	6/6	7/9	12/12	1/12	12/12	3/9	6/6	0/3	6/6	0/6
19	6/6	3/6	6/6	1/3	6/6	1/3	0/0	0/0	0/0	0/0
22	6/6	0/3	12/12	0/3	12/12	0/3	9/9	0/0	9/9	0/0

3 | RESULTS

3.1 | SARS-CoV-2 detection from biotic surfaces

SARS-CoV-2 was recovered from biotic surfaces incubated for up to 22 days at temperatures representative of those used for shipping and storing meat and fish products (Figure 2). Viable virus was always detected qualitatively when foods were incubated at −20°C, while it was only detected qualitatively from beef, pork, and salmon up to days 12–19 when incubated at +4°C (Table 2). There was significantly less virus recovered from beef (Figure 2a), pork (Figure 2b), and salmon (Figure 2c) when incubated at +4°C compared to −20°C as measured by $TCID_{50}$. SARS-CoV-2 half-lives at +4°C were approximately half those at −20°C (Table 3) and SARS-CoV-2 half-lives on salmon were approximately half those observed for beef and pork at both temperatures (Table 3). Surface type did not have a significant effect on SARS-CoV-2 recovery at −20°C (Figure S1), but significantly more virus was recovered from beef at +4°C compared to salmon

TABLE 3 Mean half-lives of SARS-CoV-2 on biotic surfaces at temperatures used for shipping. Half-lives were calculated from $TCID_{50}$ of time course experiments.

	Half-life (days)				
Temperature	Beef	Pork meat	Salmon flesh	Pork fat	Salmon scales
−20°C	5.36	5.97	3.82	3.03	7.00
+4°C	3.32	2.57	1.48	0.475	1.05

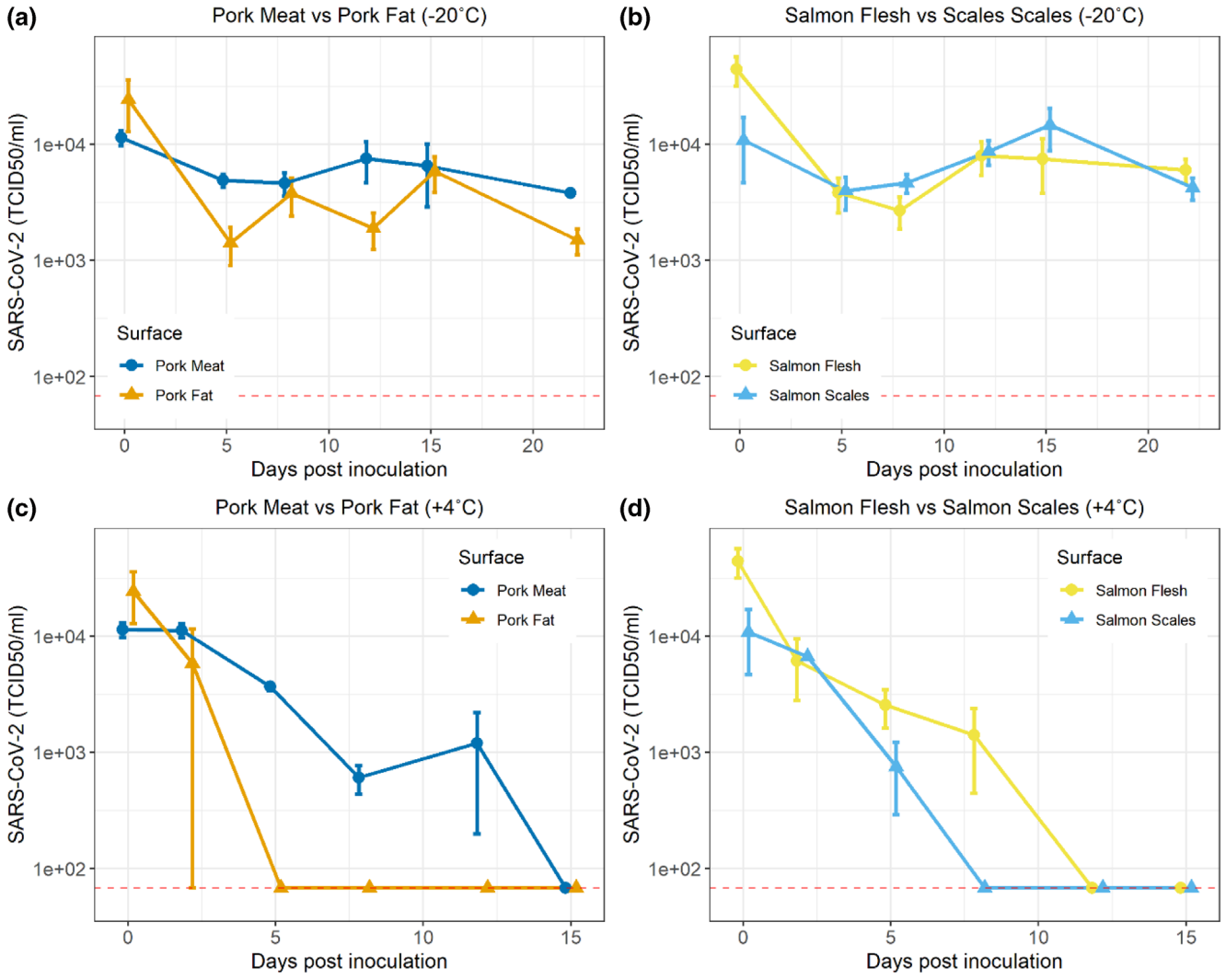

FIGURE 3 A comparison of SARS-CoV-2 recovery from pork meat and pork fat (a, c) or salmon flesh and salmon scales (b, d). Foods were inoculated with 10^4 $TCID_{50}$ SARS-CoV-2 and then incubated at −20°C (a, b) or +4°C (c, d). Virus was recovered at the indicated timepoints and then titrated by $TCID_{50}$. Points represent the mean and error bars represent the standard deviation of at least three replicates. The dashed red line is the lower LOD of the $TCID_{50}$ assay.

TABLE 4 Qualitative results and half-lives for SARS-CoV-2 incubated on cardboard at shipping temperatures.

	Number of tests with CPE/number of qualitative tests			
	Brown (less porous)		White (more porous)	
Time (days)	−20°C	+4°C	−20°C	+4°C
7	12/12	0/12	12/12	3/12
14	12/12	0/12	9/12	0/12
21	6/6	NA	6/6	NA
Half-lives (Days)	3.28	NA	2.54	NA

while there was no difference in recovered virus between beef and pork or between pork and salmon (Figure 2d).

3.2 | SARS-CoV-2 detection from salmon scales and pork fat

SARS-CoV-2 was recovered from pork fat and pork meat as well as salmon scales and salmon flesh following incubation for 22 days at −20°C or for 15 days at +4°C. At −20°C, viable virus was always detected qualitatively from each surface tested (Table 2). There was significantly less SARS-CoV-2 recovered from pork fat compared to pork meat at −20°C (Figure 3a), though the difference in normalized $TCID_{50}$/ml for these surfaces appeared small (Figure S2a). Also, SARS-CoV-2 half-lives were shorter on pork fat compared to pork meat (Table 2). The difference between SARS-CoV-2 recovered from salmon flesh and salmon scales following incubation at −20°C did not reach significance (Figure 3b) though SARS-CoV-2 had a longer half-life on salmon scales compared to salmon flesh (Table 2). The normalized $TCID_{50}$/ml of these two surfaces were very similar (Figure S2b).

At +4°C, viable virus was rarely recovered from pork fat post day 0, except two repeats at day 2 where virus was detected qualitatively (Table 2), and virus was > LOD by $TCID_{50}$ for one of these repeats (Figure 3c). In contrast, viable SARS-CoV-2 was normally recovered from pork meat up to day 12 (Table 2). The more rapid decrease in SARS-CoV-2 recovered from pork fat was reflected in its shorter half-life compared to pork meat (Table 3), though the difference in $TCID_{50}$ did not reach statistical significance. A more rapid decrease in SARS-CoV-2 recovered from pork fat compared to pork meat was also observed for normalized $TCID_{50}$ (Figure S2c). There appeared to be no difference in the SARS-CoV-2 $TCID_{50}$ recovered from salmon flesh and salmon scales when incubated at +4°C (Figure 3d) and the half-lives for these two surfaces were very similar (Table 3). The similar levels of SARS-CoV-2 recovery from these surfaces were supported by the statistical analysis and by the similarity of their normalized $TCID_{50}$/ml (Figure S2d).

3.3 | SARS-CoV-2 persistence on cardboard

Meat and fish are shipped between countries in cardboard packaging so recovery of SARS-CoV-2 from cardboard incubated at −20°C or +4°C was measured. Cardboard used in this testing had a less porous brown surface and a more porous white surface and both were tested. SARS-CoV-2 was recovered at 7-day intervals up to 21 days at −20°C and up to 14 days at +4°C. SARS-CoV-2 recovery from both types of cardboard appeared to be temperature sensitive because viable virus was almost always detected qualitatively from cardboard incubated at −20°C but rarely detected when cardboard was incubated at +4°C (Table 4). Likewise, virus recovered from cardboard incubated at −20°C was always > LOD up to day 21 whereas virus recovered from cardboard incubated at +4°C was always < LOD of the $TCID_{50}$ assay (Figure 4). Recovery of SARS-CoV-2 at −20°C and +4°C only reached statistical significance for the less porous, brown cardboard (Figure 4a), but not for the more porous, white cardboard (Figure 4b). SARS-CoV-2 had a slightly longer half-life on the brown surface compared to the white surface at −20°C (Table 4), but the differences in $TCID_{50}$/ml for these two surfaces did not reach significance. Normalized $TCID_{50}$/ml for the brown and white surfaces at −20°C (Figure S3a) and +4°C (Figure S3b) were almost identical. SARS-CoV-2 half-lives on biotic surfaces at −20°C (Table 3) were longer than its half-lives on both cardboard surfaces (Table 4).

3.4 | Temperature inactivation of SARS-CoV-2 on biotic surfaces

SARS-CoV-2 was incubated on beef (Figure 5a), pork (Figure 5b), salmon (Figure 5c) and plastic at 56°C and viable virus was measured at multiple timepoints up to 60 min. For the 60 min timepoint, all $TCID_{50}$ results were below the lower LOD and viable virus was only detected qualitatively from pork (Table 5). Virus recovered from plastic reached the lower LOD at earlier timepoints and reduced more rapidly compared to virus recovered from foods (Figure 5d). Half-lives revealed a more rapid decrease in viable virus recovered from plastic and beef compared to pork and salmon (Table 6). The surface type had a significant effect on SARS-CoV-2 recovery following incubation at 56°C with significantly reduced SARS-CoV-2 recovery from plastic compared to pork or salmon as well as from beef compared to pork. There was no difference in SARS-CoV-2 recovery from beef, pork, salmon or plastic when incubated at +4°C (Figure S4a) or room temperature (Figure S4B) over the course of 60 min. This suggests the more rapid loss of viability on plastic and beef at 56°C was not due to antiviral properties of these substrates.

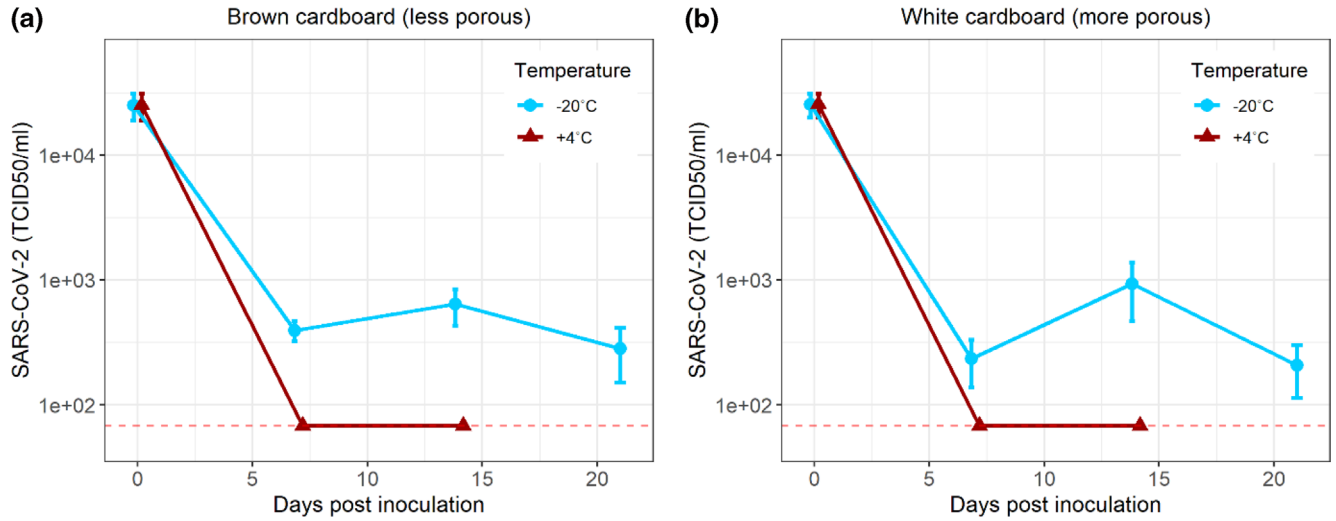

FIGURE 4 Recovery of SARS-CoV-2 from cardboard incubated at temperatures used for shipping and storing meat and fish. Less porous, brown cardboard (a) and more porous, white cardboard (b) were inoculated with 10^4 $TCID_{50}$ SARS-CoV-2 and incubated at −20°C or +4°C. Virus was recovered at the indicated times post-inoculation, then titrated by $TCID_{50}$. Points represent the mean and error bars represent the standard deviation of at least three replicates. The dashed red line is the lower LOD of the $TCID_{50}$ assay.

SARS-CoV-2 inactivation following incubation on beef, pork, salmon, and stainless steel at 75°C for 10 min was determined across three independent experiments (Figure 5e). This temperature was chosen because the Food Safety Authority Ireland states that cooked meat served at restaurants in Ireland should reach a core temperature of at least 75°C. Viable virus was detected qualitatively from all repeats of beef and pork; most repeats of salmon; and rarely from stainless steel (Table 5). SARS-CoV-2 $TCID_{50}$ remained >LOD for beef, pork, and normally salmon but virus recovered from stainless steel was always <LOD, with significantly increased recovery from pork and beef compared to salmon or stainless steel (Figure 5e). Normalized $TCID_{50}$/ml for salmon and stainless steel were also much less than those observed for beef and pork (Figure 5f). Half-lives ranged from 100 to 183 s demonstrating the rapid inactivation of SARS-CoV-2 at 75°C (Table 6).

3.5 | SARS-CoV-2 detection from foods and food packaging

Samples were obtained from a range of foods of different origin and their packaging purchased from a range of retail outlets (Figure 6). Sampling coincided with a period when daily cases in Ireland exceeded 1300 for the first time during the COVID-19 pandemic, with a mean daily case rate of 1835 between January 21, 2021 and February 11, 2021. The 1300 samples included 852 samples of RNA purified from food matrices; swabs originating from packaging and the skin of fruit (367 samples); swabs from high touch surfaces (75 samples); and six concentrated wastewater samples collected in food production facilities were tested by RT-qPCR for the presence of genes N1, N2 and RP and MeV-IPC. Four of these pools (two vegetables and two fruits) tested positive with a value close to the LOD, while all pools tested showed a high recovery of the extraction control. The samples included in the four positive pools were tested singularly and a second aliquot of the same samples which had been retained at −20°C was extracted for viral particles. All purified RNA resulted negative, while MeV-IPC was always recovered.

3.6 | SARS-CoV-2 persistence on abiotic surfaces

Recovery of SARS-CoV-2 incubated on fabric worn by MPP workers and stainless steel used in MPPs was tested. SARS-CoV-2 recovery following incubation at 12°C and room temperature (18–20°C) under low (approximately 20%) or high (approximately 80%) relative humidity was compared to determine if temperature or relative humidity effected recovery of SARS-CoV-2 from these surfaces. 12°C was chosen because there is a legal obligation to maintain the air temperature of MPP meat cutting rooms at below 12°C. Virus was recovered from fabric at 2.5-h intervals up to 10 h, which is the normal length of shifts in MPPs. There was no significant difference in the amount of SARS-CoV-2 recovered from fabric incubated at 12°C or room temperature (Figure 7a). Incubation at 12°C sometimes prolonged qualitative detection of viable SARS-CoV-2 from fabric compared to incubation at room temperature (Table 7) but there were almost no differences in the half-lives of SARS-CoV-2 incubated under different conditions (Table 8). Decreasing the relative humidity of the test container from 80 to 20% did not affect recovery of SARS-CoV-2 from fabric at room temperature (Figure 7a).

SARS-CoV-2 was also recovered from stainless steel incubated at 12°C and room temperature under low or high relative humidity at 2.5-, 5-, and 10-h post-inoculation. Viable virus was detected qualitatively from all samples (Table 7). Half-lives for each condition (Table 8) suggested there was a more rapid decrease in the amount of

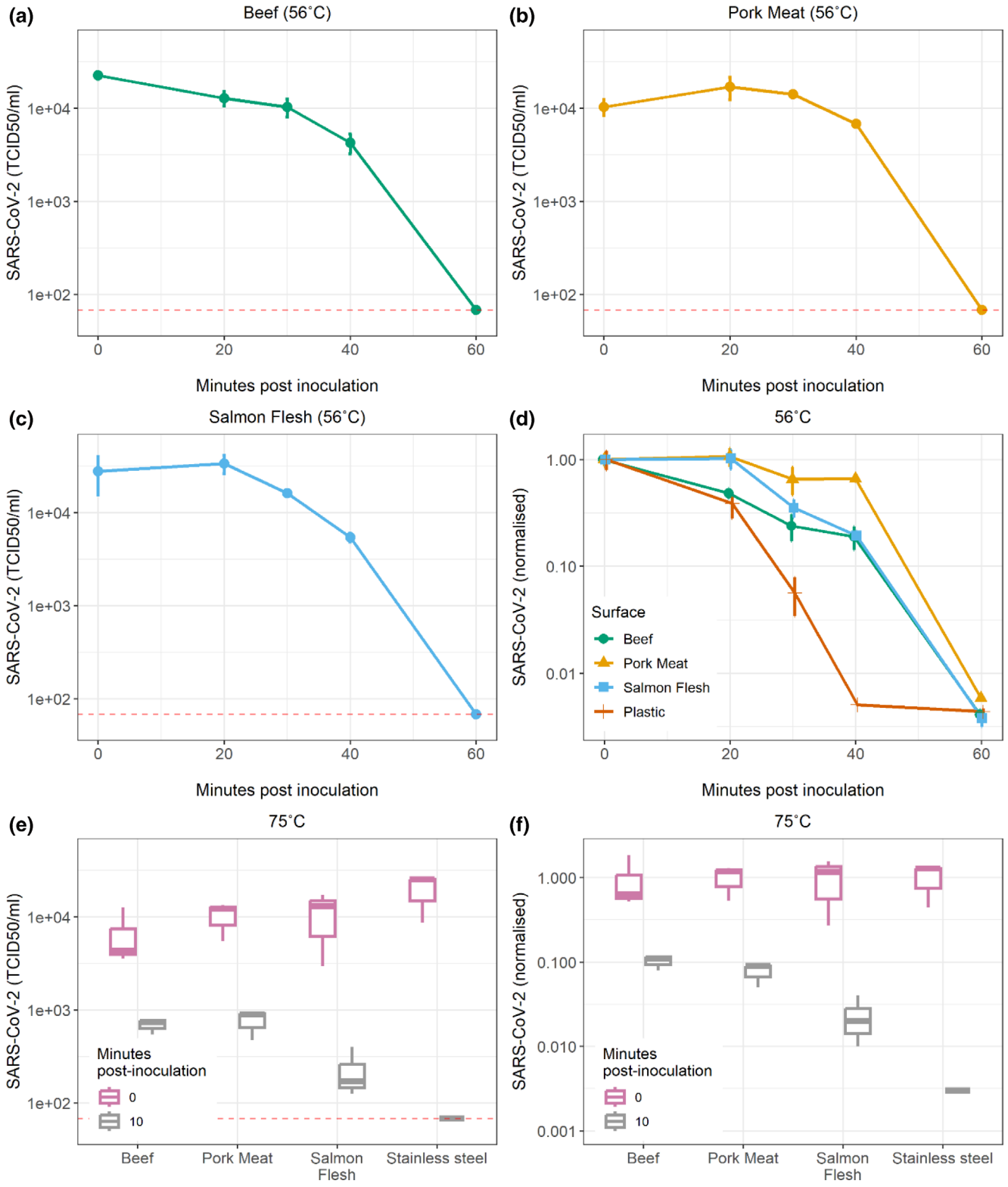

FIGURE 5 Inactivation of SARS-CoV-2 incubated on abiotic and biotic surfaces by heat. All surfaces were inoculated with 10^4 $TCID_{50}$ SARS-CoV-2. Beef (a), pork meat (b), salmon flesh (c), and plastic surfaces were incubated 56°C and virus was recovered at the indicated timepoints, then titrated by $TCID_{50}$. Recovered virus was normalized against the 0-h recoveries to compare recoveries from different surfaces incubated at 56°C (d). SARS-CoV-2 was recovered from surfaces incubated at 75°C after 10 min, then viable virus was titrated by $TCID_{50}$ (e). Recovered virus was normalized against the 0-h recoveries to compare the different surfaces incubated at 75°C (f). Points represent the mean and error bars the standard deviation of at least three repeats. Boxes represent interquartile ranges; the horizontal line represents the median and the vertical lines represent the range of at least three repeats. The dashed red lines indicate the lower LOD of the $TCID_{50}$ assay.

TABLE 5 Qualitative results testing heat inactivation of SARS-CoV-2 on different surfaces.

	Number of tests with CPE/number of qualitative tests									
	Beef		Pork meat		Salmon flesh		Plastic		Stainless steel	
Time (min)	56°C	75°C	56°C	75°C	56°C	75°C	56°C	75°C	56°C	75°C
10	NA	18/18	NA	18/18	NA	14/18	NA	NA	NA	3/18
20	18/18	NA	18/18	NA	18/18	NA	18/18	NA	NA	NA
30	18/18	NA	18/18	NA	18/18	NA	16/18	NA	NA	NA
40	6/6	NA	6/6	NA	6/6	NA	1/6	NA	NA	NA
60	0/12	NA	2/12	NA	0/12	NA	0/12	NA	NA	NA

TABLE 6 Mean half-lives of SARS-CoV-2 recovered from surfaces at high temperatures.

	Half-life (s)				
Temperature (°C)	Beef	Pork meat	Salmon flesh	Plastic	Metal
56°C	944.0	2416.4	1346.0	414.4	NA
75°C	183.34	151.17	114.32	NA	100.16

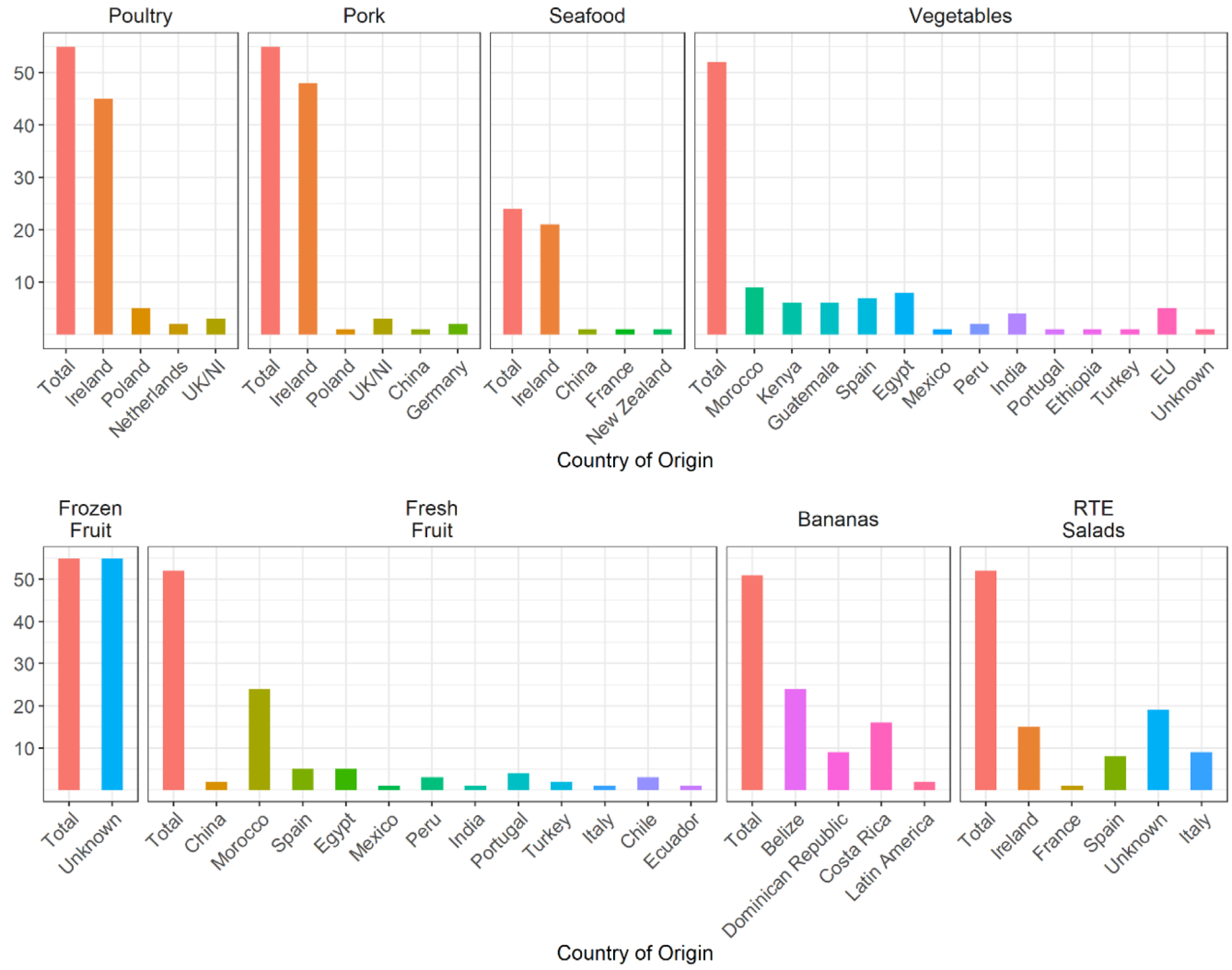

FIGURE 6 Breakdown of samples surveyed for SARS-CoV-2 and their country of origin.

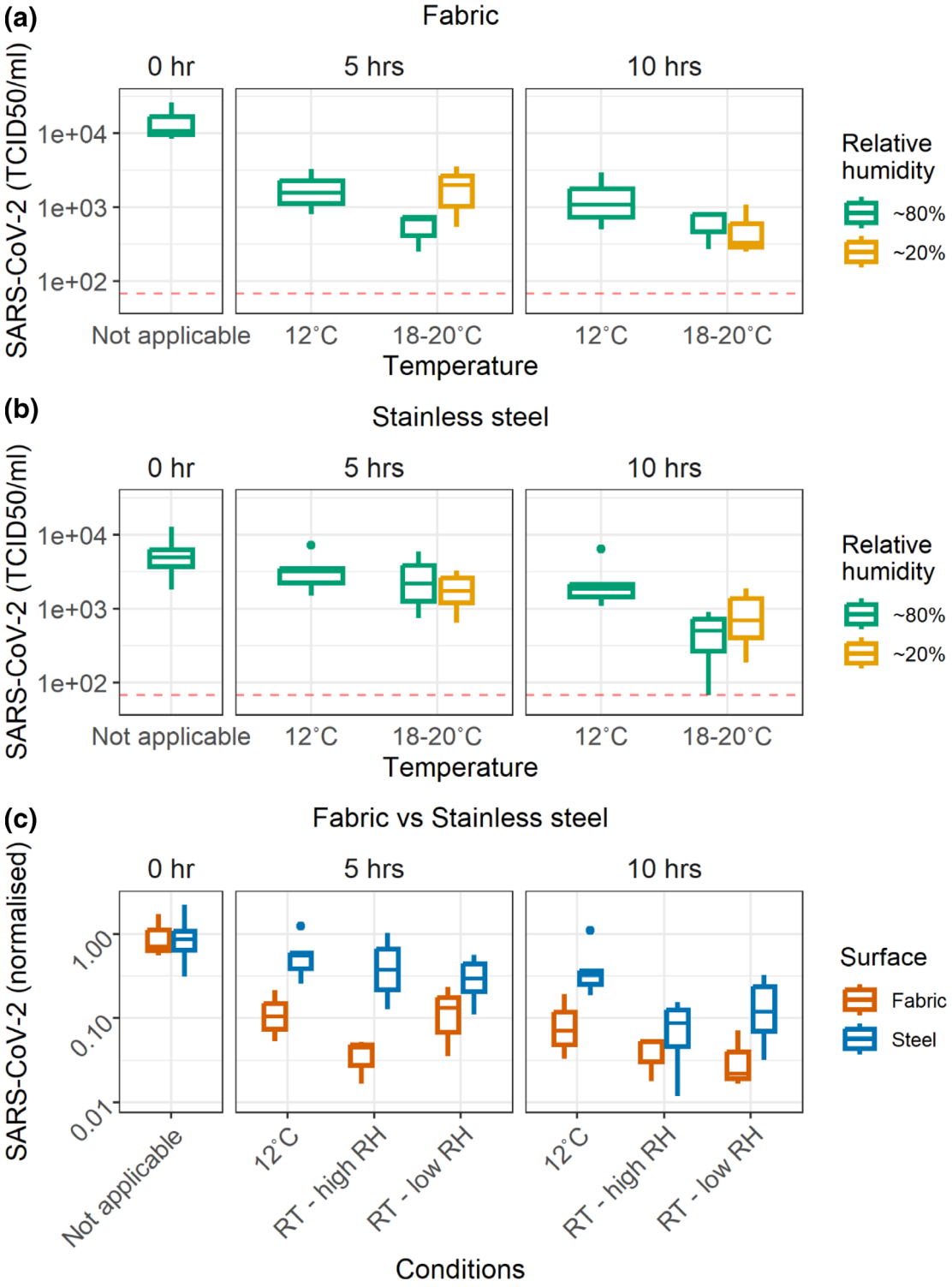

FIGURE 7 Recovery of viable SARS-CoV-2 from abiotic surfaces at temperatures maintained in meat processing plant (MPP). Fabric samples cut from a coat worn by workers at MPPs (a), and stainless steel of the same grade used in MPPs (b) were inoculated with 10^4 $TCID_{50}$ SARS-CoV-2, then incubated for 10 h at 12°C or at room temperature (18–20°C). The relative humidity was decreased from ~80 to ~20% for three samples incubated at room temperature. Virus recovered at the indicated timepoints was titrated by $TCID_{50}$. (c) $TCID_{50}$/ml of virus recovered from fabric and stainless steel incubated under each condition were normalized for comparison of virus persistence on the two surfaces. Boxes represent interquartile ranges; the horizontal line represents the median and the vertical lines represent the range of at least three repeats. The dashed red line represents the lower lower limit of detection (LOD) of the $TCID_{50}$ assay.

TABLE 7 Qualitative results for detection of SARS-CoV-2 incubated under different conditions on fabric or stainless steel. RT, room temperature (18–20°C); high RH, high relative humidity (~80%); and low RH, low relative humidity (~20%).

	Number of tests positive for virus/number of qualitative tests					
	Fabric			Stainless steel		
Time (h)	12°C	RT, high RH	RT, low RH	12°C	RT, high RH	RT, low RH
2.5	9/9	9/9	6/6	3/3	3/3	NA
5	9/9	6/9	3/6	9/9	9/9	6/6
7.5	6/9	5/9	3/6	NA	NA	NA
10	6/9	5/9	3/6	15/15	15/15	6/6

TABLE 8 Mean half-lives of SARS-CoV-2 recovered from fabric and stainless steel incubated under different conditions. RT, room temperature (18–20°C); high RH, high relative humidity (~80%); and low RH, low relative humidity (~20%).

	Half-life (h)		
Surface	12°C	RT, high RH	RT, low RH
Fabric	2.47	2.25	2.53
Stainless steel	6.64	3.35	4.05

viable SARS-CoV-2 recovered from stainless steel at room temperature compared to 12°C. Although there was always increased recovery of SARS-CoV-2 when stainless steel was incubated at 12°C compared to room temperature, the difference only reached statistical significance in two of five independent experiments (Figure 7b). There was a small increase in SARS-CoV-2 half-life when relative humidity was decreased (Table 8), but the difference did not reach statistical significance.

The half-lives calculated from the $TCID_{50}$ of SARS-CoV-2 recovered from fabric and stainless steel suggested virus remained viable for longer on stainless steel compared to fabric. When $TCID_{50}$ were normalized, there was a decreased recovery of SARS-CoV-2 from fabric compared to stainless steel under each condition and for each timepoint (Figure 7c). However, the difference in SARS-CoV-2 recovered from stainless steel and fabric did not reach statistical significance for any condition.

3.7 | Effect of inoculum on SARS-CoV-2 surface persistence

In MPPs, SARS-CoV-2 may contaminate surfaces in the presence of fluids that gather on surfaces during processing of carcasses, which from herein are referred to as meat juices. To determine the effect these may have on SARS-CoV-2 surface persistence, virus was spiked with juices collected from the packaging of beef or pork prior to inoculation of fabric and stainless steel surfaces. As a control, SARS-CoV-2 was also spiked with virus maintenance media prior to inoculation. There was increased recovery of virus from fabric when SARS-CoV-2 was combined with meat juices (Figure 8a), with a statistically significant difference between the $TCID_{50}$/ml obtained when inoculum was spiked with

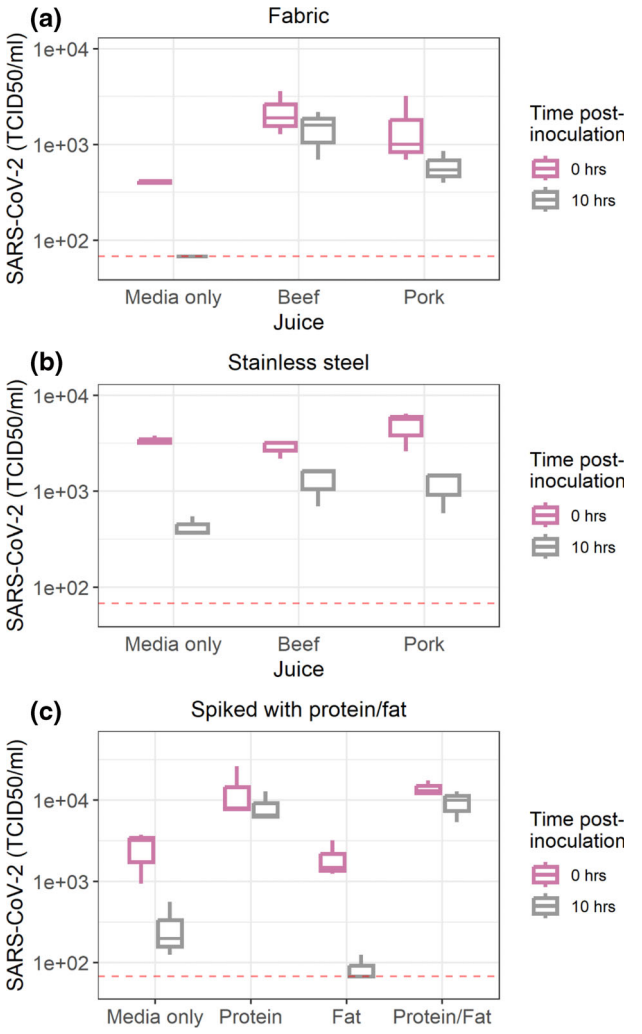

FIGURE 8 Effect of changing the inoculum on SARS-CoV-2 recovery from abiotic surfaces. SARS-CoV-2 was combined at a 1:1 ratio with virus maintenance media or juices collected from the packaging of beef or pork prior to inoculation of fabric (a) or stainless steel (b). Surfaces were incubated at 12°C for 10 h, then recovered virus was titrated by $TCID_{50}$. (c) SARS-CoV-2 was spiked at a 1:1 ratio with virus maintenance media only, 5% bovine serum albumin (BSA) (protein), 5% castor oil (fat) or a mix of 2.5% BSA and 2.5% castor oil (protein/fat) prior to inoculation of fabric. Fabric was incubated at 12°C for 10 h, then virus was recovered and titrated by $TCID_{50}$. Boxes represent interquartile ranges; the horizontal line represents the median and the vertical lines represent the range of at least three repeats. The dashed red line represents the lower LOD of the $TCID_{50}$ assay.

beef juice compared to media only. Combining SARS-CoV-2 with meat juices increased the recovery of virus immediately after inoculation of fabric (Figure 8a). Combining SARS-CoV-2 with beef or pork juice caused an increase in the amount of virus recovered from stainless steel (Figure 8b) but this difference did not reach statistical significance. Normalized $TCID_{50}$/ml showed increased recovery of SARS-CoV-2 from fabric (Figure S5a) or stainless steel (Figure S5b) when spiked with meat juices rather than media.

The increased recovery of virus from fabric when SARS-CoV-2 was combined with meat juices suggests something in the meat juice was increasing virus persistence or enhancing infectivity. Two components of the juice were protein and lipids so to determine the effects of increased protein and/or fat on SARS-CoV-2 recovery, virus stocks were spiked with final concentrations of 2.5% BSA (protein), 2.5% castor oil (fat), or a mix of 1.25% BSA and 1.25% castor oil (protein/fat) prior to inoculation of fabric followed by incubation at 12°C for 10 h. As a control, SARS-CoV-2 was also spiked with virus maintenance media only. Spiking with protein or protein/fat increased the recovery of virus immediately after inoculation compared to media only or fat only (Figure 8c). There was also increased recovery of viable virus from fabric when it had been spiked with protein or protein/fat compared to media only, while there was no difference in SARS-CoV-2 recovery when spiked with media only and fat (Figure 8c). Increased recovery when SARS-CoV-2 was spiked with protein or protein/fat compared to fat or media only was observed when comparing normalized $TCID_{50}$/ml (Figure S5c), but this difference only reached statistical significance when comparing $TCID_{50}$/ml for protein/fat with $TCID_{50}$/ml for fat or media only.

4 | DISCUSSION

The MPP environment was associated with large outbreaks of SARS-CoV-2 infection during the height of the COVID-19 pandemic. This study investigated persistence of viable virus particles on surfaces associated with an MPP environment and the food chain more broadly. Although the risk of COVID-19 has reduced, and was not a food safety consideration, the lessons learned from this study and others should be incorporated into the approaches taken to control respiratory virus infections among MPP employees and when evaluating the risk of virus transmission along the food chain. There have been concerns in parts of the world that contaminated foods shipped under refrigerated or frozen conditions could act as vehicles to transport viable SARS-CoV-2 between countries (Caiyu, 2020; Chen et al., 2022; Chi et al., 2021; Han et al., 2021; J. Jia et al., 2021; Liu et al., 2020; Pang et al., 2020). For this to occur, viable SARS-CoV-2 must persist on packaging or foods stored under shipping conditions. Recovery of viable SARS-CoV-2 from cardboard, beef, pork, and salmon following incubation for at least 12 days at +4°C and for at least 22 days at −20°C shows similar trends to results of other studies, though they were not identical (Dai et al., 2021; Dhakal et al., 2021; Esseili et al., 2022; Feng et al., 2021; M. Jia et al., 2022; Luong et al., 2022). Feng et al., for example showed limited persistence of virus beyond approximately 9 days at +4°C, while Dai et al., suggested that persistence continued to approximately 10 days. The data presented here extend our understanding by reporting that SARS-CoV-2 can consistently persist for at least 12 days, and as long as 19 days with different recovery methods potentially causing slight differences in results. Prolonged recovery of viable SARS-CoV-2 observed in this study could be due to samples being incubated in recovery media for 10 min whereas Feng et al. rinsed samples in recovery media 20 times (Feng et al., 2021). At +4°C, there was a more rapid reduction in virus recovered from salmon compared to beef as seen in Feng et al. It is unclear exactly why this might be, but it could be caused by higher concentrations of omega-3 fatty acids in salmon or other nutritional components (Feng et al., 2021; M. Jia et al., 2022). Omega-3 fatty acids, for example, can have antiviral effects on enveloped virus such as Hepatitis C virus, while Vitamin E, which is also found in high concentrations in avocado, may inhibit the SARS-CoV-2 polymerase (Leu et al., 2004; Pacl et al., 2021). Reduced recovery of SARS-CoV-2 from cardboard compared to biotic surfaces is consistent with previous studies and suggests SARS-CoV-2 is less likely to remain viable and/or is more difficult to recover from cardboard compared to foods (Li et al., 2023).

Comparisons of SARS-CoV-2 persistence on different parts of meat and fish showed variation between different surfaces. In general, there was reduced recovery of SARS-CoV-2 from pork fat compared to pork meat, while there was increased recovery from salmon scales compared to salmon flesh. This study and others suggest different food matrices differ in their ability to act as carriers of viable virus and components or characteristics of some food matrices could increase or decrease SARS-CoV-2 persistence (M. Jia et al., 2022; Li et al., 2023). Certain fatty acids could reduce SARS-CoV-2 surface viability as they have previously been shown to inactivate some enveloped viruses (Jackman et al., 2020; Thormar et al., 1987). The persistence of viable SARS-CoV-2 on foods for days or weeks when incubated at temperatures used for shipping means the potential for transport of virus on foods between countries cannot be ruled out. However, one caveat is that persistence of SARS-CoV-2 on these surfaces does not necessarily translate into transmissibility, which cannot be determined from the results presented in this study.

In parallel with measurement of virus persistence at low temperatures, higher temperatures were also examined. The increased sensitivity of SARS-CoV-2 to heat when incubated on abiotic surfaces compared to biotic surfaces could be due to the foods protecting or stabilizing virus particles. The protein content of meat and fish could protect SARS-CoV-2 from heat inactivation as has been shown for SARS-CoV-1 (Rabenau et al., 2005). In terms of timing, the inactivation times displayed by SARS-CoV-2 in the different settings at high temperatures are not greatly dissimilar to other enveloped viruses such as influenza or adenovirus but longer than respiratory syncytial virus (Gupta et al., 1996; Maheshwari et al., 2004; Morris et al., 2021; Yang et al., 2021; Yépiz-Gómez et al., 2013). More rapid heating of food would be expected in a real-life cooking scenario, such as in an oven or pan, as the meat is not insulated within a container, which is one limitation of these experiments. Therefore, the results of this

study likely overestimate the time required to inactivate SARS-CoV-2 at 56 and 75°C.

Having demonstrated experimentally that SARS-CoV-2 can persist at temperatures used for shipping meat and fish, foods collected from retail markets were tested for virus present at the latter stages of the food supply chain. Despite relatively high case numbers during the sampling period, SARS-CoV-2 was only detected from a small number of pooled samples and never detected from individual samples. SARS-CoV-2 was not detected during a similar study in Ontario, which coincided with high case numbers and the implementation of control measures such as hand sanitization stations and mandatory facemasks (Singh et al., 2021). Increased samples sizes are required to draw strong conclusions, but failure to detect SARS-CoV-2 on foods during periods of relatively high case numbers and implementation of control measures implies the risk of foods being contaminated with SARS-CoV-2 is low if good control measures are in place.

The contribution of fomites to COVID-19 outbreaks in MPP was assessed by measuring SARS-CoV-2 persistence on surfaces found in MPP under relevant conditions. Although incubating SARS-CoV-2 at the cooled temperature of 12°C maintained in MPP bone cutting halls consistently resulted in increased recovery of SARS-CoV-2 from stainless steel or fabric compared to incubation at room temperature, the differences in recovery for the two temperatures rarely reached significance. Viable SARS-CoV-2 was always recovered from stainless steel up to 10 h post-inoculation so the contribution of fomites to MPP outbreaks cannot be ruled out, but statistical analysis did not show the temperature maintained in MPP could consistently increase the risk of direct fomite transmission when compared to temperatures found in many other workplaces. Despite this, the data presented do suggest that the half-life of virus on stainless steel is increased at the lower temperature of 12°C compared to room temperature, implying that although direct recovery from stainless steel may not be improved over a relatively short period of up to 10 h, virus viability may be increased suggesting that airborne virus coming from people or surfaces may be enhanced, thus increasing overall transmission risk in that decreased temperature environment. There was no difference in recovery of SARS-CoV-2 from surfaces incubated at high (~80%) or low (~20%) relative humidity.

In MPPs, especially meat cutting rooms, SARS-CoV-2 could contaminate surfaces in the presence of protein-rich or fat-rich fluids produced during the processing of carcasses. Combining SARS-CoV-2 with juices collected from beef or pork packaging or spiking the inoculum with extra protein increased recovery of virus from fabric suggesting a component of the meat juices or BSA solution is protecting virus from inactivation. The presence of a protein source such as BSA has previously been shown to increase the viability of both enveloped and non-enveloped viruses such as influenza virus and MS2 bacteriophage, supporting the suggestion from this data that increased protein content can prolong SARS-CoV-2 persistence (Greatorex et al., 2011; Lin et al., 2020). One limitation of this experiment is the increased recovery efficiency observed when SARS-CoV-2 was spiked with extra protein. This means the increased detection of viable SARS-CoV-2 from fabric could have been caused by more efficient recovery rather than increased persistence of viable virus in the presence of extra protein. However, statistical analysis showing a significant increase in recovery of SARS-CoV-2 in the presence of meat juices or extra protein included the 0-h $TCID_{50}$/ml as a covariate, so the different recovery efficiency was factored into the statistical analysis suggesting differences observed were real.

In conclusion, this study supports previous findings in relation to virus persistence on surfaces and enhances our understanding of the specific conditions associated with MPPs. Meat cutting rooms, with an air temperature below 12°C and in which all high contact surfaces are likely to be heavily contaminated with meat juices during a working shift, provide an environment in which the surface persistence of SARS-CoV-2 and potentially other respiratory viruses, is likely to be prolonged. Virus coming from an infected person and transmitting to others through the air is the most likely means of acquiring a respiratory virus infections in these environments; however, fomites as a source of airborne virus, or direct fomite contact based transmission cannot be ruled out and needs to be considered in risk mitigation strategies.

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CONFLICT OF INTEREST

The UPCOM project included input from stakeholders involved in the meat processing industry.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are contained within the manuscript or are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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