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Review article

Carnobacteria in fish

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ABSTRACT

Carnobacterium is a genus of Gram-positive bacteria, within family Carnobacteriaceae, and they are catalase- and oxidase-negative, non-sporing bacteria with properties such as CO_2 and L (+)- lactic acid production from glucose, but they are not able to grow on acetate agar. They are ubiquitous lactic acid bacteria and have been isolated from both cold and temperate environments, and they are identified as components of the microbiota in the gastrointestinal (GI) tract of salmonids and several other fish species of which *Carnobacterium* (*piscicola*) *maltaromaticum*, *Carnobacterium mobile*, *Carnobacterium divergens*, *Carnobacterium alterfunitum*, and *Carnobacterium inhibens* are reported. During the last two decades several studies have revealed that carnobacteria can act as probiotics to promote health benefits of fish, as well as they in *ex vivo* studies to some extent can out-compete pathogens. In addition to beneficial effects, information is available that some carnobacteria species causing fish disease. The aim of the present review is to present an updated overview of *Carnobacterium* in fish, with focus on their presence in the GI tract, their use as probiotic supplement and general information on pathogenic carnobacteria.

1. Introduction

Lactic acid bacteria (LAB) are considered good candidates as beneficial bacteria to fish due to their ability to inhibit adherence and colonization of pathogenic bacteria in the gastrointestinal (GI) tract (Ringø et al., 2010, 2018) and to produce antimicrobial compounds (Evangelista et al., 2022; Ringø et al., 2018). Among the LAB investigated in aquaculture, *Lactobacillus* species being most frequently studied (Ringø et al., 2020a), but during the last two decades several studies have suggested that *Carnobacterium* might be a good candidate to promote health benefits of fish.

Genus *Carnobacterium* belongs to the family Carnobacteriaceae within the order of Latobacillales and they grow in a pH range of 7–9 and most species produce lactic acid through the fermentation of carbohydrates such as glucose. According to Schillinger and Holzapfel (1995) the first mention of these *atypical* lactobacilli not growing on acetate agar was made in the 1950s referring to strains isolated from poultry meat. In aquaculture. the earliest evidence of "*Carnobacterium* species" was a report on a pathogenic *Lactobacillus piscicola*, isolated from salmonid fish (Hiu et al., 1984), but according to Web of Science, Collins et al. (1987) proposed a new genus, *Carnobacterium* by reclassification of *Lactobacillus divergens*, *Lactobacillus piscicola* and some catalase-negative, asporogenous, rod-shaped bacteria from poultry.

To avoid overlaps with previous book reviews on genus *Carnobacterium*, readers with interest in history, morphology, habitats, physiological properties, isolation, cultivation, maintenance, conservation, genetics, identification, and differentiation of species are recommended to have a closer look at book review by Schillinger and Holzapfel (1995) published in "*The Genera of Lactic Acid Bacteria*" and by Hammes and Hertel (2006) published in "*The prokaryotes. A handbook on the Biology of Bacteria*".

Carnobacteria are isolated from Arctic and temperate environments (Leisner et al., 2007; Ringø et al., 2018; Ringø & Gatesoupe, 1998). Currently genus *Carnobacterium* consists of 10 species of which; *Carnobacterium* (*piscicola*) *maltaromaticum*, *Carnobacterium mobile*, *Carnobacterium divergens*, *Carnobacterium alterfunitum*, and *Carnobacterium inhibens* have been isolated from fish intestine. The first study isolating carnobacteria from gastrointestinal (GI) tract of fish, wild Atlantic salmon (*Salmo salar*), Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*), was carried out by Strøm (1988). The bacterium isolated from Atlantic salmon was identified as *Lactobacillus plantarum* Lab01 but was later reclassified as *C. divergens* (Ringø et al., 2001). This bacterium has been used as probiotic supplement in *in vivo* studies (Gildberg et al., 1995, 1997; Gildberg & Mikkelsen, 1998; Ottesen & Olafsen, 2000; Puvanendran et al., 2021; Strøm & Ringø, 1993) as well as in an *ex vivo* study to study the interactions between *C. divergens* and fish pathogens (Kristiansen et al., 2011).

Carnobacteria have been reported as a part of the microbial

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communities of different environments, fish gastrointestinal (GI) tract (Table 1), fish eye (Pastorino et al., 2021), spoilage of aquatic products (Zhang et al., 2015; Zotta et al., 2019), seafood (Mauguin & Novel, 1994), meat (Montel et al., 1991), dairy products (Afzal et al., 2010), blood from a cancer patient (Lo & Sheth, 2021), anoxic waters in Ace Lake, Antarctica (Franzmann et al., 1991), in the human small bowel (duodenum and jejunum) (Iskandar et al., 2017; Van Tassell & Miller, 2011). and even from butterfly species at the Tibetan Plateau (Cao et al., 2021). Even though some information was presented on carnobacteria in fish in previous reviews on LAB (Lambuk et al., 2022; Lauzon & Ringø, 2011; Leisner et al., 2007; Merrifield et al., 2014; Ringø, 2004; Ringø et al., 2018; Ringø & Gatesoupe, 1998) and shellfish (Ringø et al., 2020b), the present review address to present an updated overview of *Carnobacterium* in fish, with focus on their presence in the GI tract, their use as probiotic supplement and on pathogenic carnobacteria.

2. Carnobacteria in the gastrointestinal (GI) tract of fish

Carnobacteria have been identified as components of the microbiota of the GI tract of several fish species (Table 1) and shellfish (Ringø et al., 2020b). The first study isolating carnobacteria from the GI tract of fish was reported by Strøm (1988). One of the carnobacteria isolated, identified as *Lb. plantarum* Lab 01 later reclassified as *C. divergens* (Ringø et al., 2001) has revealed antagonistic activity against fish pathogens, *Aeromonas salmonicida* ssp. *salmonicida* (causative agent of furunculosis), *Vibrio salmonicida* and *Vibrio* (*Listonella*) *anguillarum* (causative agent of vibriosis) (Ringø, 2008).

2.1. Salmonidae

Several studies have identified carnobacteria from the GI tract of Arctic charr (*Salvelinus alpinus*) (Table 1), and the first study was reported by Ringø et al. (1997) isolating *C. divergens* from distal intestine. Later studies have revealed that carnobacteria composition appears to be affected by dietary components, fatty acids (Ringø et al., 1998), carbohydrate levels (Ringø & Olsen, 1999), oils (Ringø, Lødemel, et al., 2002) and inulin (Ringø, Sperstad, Myklebust, Mayhew, & Olsen, 2006) as well as migration from freshwater to seawater and from seawater back to freshwater (Ringø, 2000).

In a study evaluated the effect of different fatty acids on LAB colonizing the GI tract of freshwater reared Arctic charr, Ringø et al. (1998) reported highest frequency of LAB in stomach, proximal- and distal intestine and feces of fish fed 7% linoleic acid diet and 4% of a polyunsaturated fatty mix. Among the LAB identified were *Carnobacterium* spp. and *C. maltaromaticum* predominant.

Arctic charr fed high levels of dietary carbohydrates displayed different adherent culturable carnobacteria profiles in the intestine, such as *C. mobile* in the proximal intestine and *C. maltaromaticum* in the distal intestine; however, fish fed low levels of dietary carbohydrates displayed only *C. divergens* in both intestinal regions It is important to note also that the higher dietary carbohydrate level reduced the frequency of carnobacteria isolation within replicate fish (Ringø & Olsen, 1999).

Ringø, Lødemel, et al. (2002) investigated the effect of dietary soybean-, linseed- and marine oil on the aerobic populations of heterotrophic bacteria present in the distal intestine of Arctic charr. Differences in the bacteria microbiota were revealed between the rearing groups before and after challenge with *A. salmonicida* ssp. *salmonicida*, as well as interindividual variations, as carnobacteria were only reported in the distal intestine of charr fed soybean- and linseed oil before challenge. In contrast, *Carnobacterium* spp. and *C. funditum* were revealed in the distal intestine of fish fed the same dietary oils after challenge. However, an interesting finding was that the carnobacteria isolated inhibited *in vitro* growth of three pathogens tested but the ability differed between the dietary treatment.

Ringø, Seppola, et al. (2002) present report on a strain 6251 isolated from Arctic charr and revealed that the most abundant cellular fatty acid was oleic acid (18:1 n-9) (36.0%). Sequencing of a 16S rDNA region of 578 nucleotides and AFLPTM microbial fingerprinting suggested that the strain was not closely related to any carnobacteria known. However, DNA-DNA similarity determinations displayed high similarity (96.2%) with the type strain of *C. divergens*. The unique phenotypic attributes of strain 6251 represented new information on the biodiversity and ecology of carnobacteria and especially of the species *C. divergens*. Fig. 1 shows the morphology of *C. divergens* 6251 (Myklebust & Ringø, unpublished data).

Ringø, Sperstad, Myklebust, Mayhew, and Olsen (2006) revealed that dietary inulin tended to lower culturable autochthonous carnobacteria levels (by ca. 90%) in the distal intestine of Arctic charr, which seemed to benefit *C. maltaromaticum* at the expense of *C. divergens*. However, as high inclusion level, 15 g kg^{-1} was used in this study, these results should be handled with care as Olsen et al. (2001) using similar inclusion level revealed that absorptive cells in pylorus caeca show numerous intracytoplasmic vacuoles which vary in size and shape and amounted for ca. 4.5% of cellular volume, and in distal intestine highly vacuolated cells increased from 14.3% to 22.1% of the cell volume in the control group *vs*. inulin fed fish, and many of the vacuoles have a lamellar content. To fully conclude, lower inclusion levels of inulin supplementation merits investigations.

Carnobacterium spp., *C. divergens*, *C. inhibens*, *C. maltaromaticum* and *C. mobile* have been isolated from the GI tract of Atlantic salmon (Table 1). In a study evaluating bacteria associated with Atlantic salmon, revealed that among 751 bacteria isolated from food, water, and the GI tract, 201 were identified as *Carnobacterium* and 199 of them were isolated from proximal-, mid- and distal intestine (Ringø et al., 2000). Within the 199 *C. maltaromaticum* – like isolates, 139 inhibited *in vitro* growth of *A. salmonicida* subsp. *salmonicida*.

Cultured isolates subsequently identified by 16S rRNA gene sequencing analysis revealed *Carnobacterium* levels in the distal intestine of Atlantic salmon of log 3.8 and 5.2 CFU g^{-1} for the autochthonous and allochthonous communities, respectively (Ringø et al., 2008). Cantas et al. (2011) evaluated the culturable allochthonous intestinal microbiota of triploid and diploid Atlantic salmon and displayed significantly higher total bacterial counts within proximal intestine, midgut, and distal intestine in triploids, but a significant decrease in carnobacteria was observed in triploids compared to diploids. Whether these differences contribute to fish health or disease resistance was not elucidated and merits further investigations.

Askarian et al. (2012) evaluated the effect of chitin (5% supplementation) on the adherent aerobic intestinal microbiota of Atlantic salmon. One hundred and thirty-nine isolates were isolated by cultivation and 64 of them were subsequently identified by 16S rRNA gene sequencing and further tested for enzyme activities. The carnobacteria isolated from the proximal intestine (n = 3) of fish fed chitin revealed protease and cellulase activities and *in vitro* growth inhibition of *A. salmonicida* subsp. *salmonicida*, *V. anguillarum* and *Moritella viscosa* but did not display inhibition of *C. maltaromaticum*.

In their study evaluating the microbial community in the distal intestine contents of Atlantic salmon, Zarkasi et al. (2016) reported LAB species including *Carnobacterium*. In a study evaluating alternative protein sources on the distal intestinal microbiota of Atlantic salmon, Gajardo et al. (2017) reported that fish fed soy protein concentrate and poultry meal showed significantly higher abundance of *Carnobacterium*. In a study evaluating Atlantic salmon across freshwater to saltwater transition using deep 16S rRNA gene sequencing and quantitative PCR revealed allochthonous *Carnobacterium* (Rudi et al., 2018). Pyloric ceca compartments scraped and collected, contained both consents and mucosa, were used in an *in vitro* model to assay the impact of mannan oligosaccharide (MOS) of Atlantic salmon intestinal microbiota (Kazlauskaite et al., 2022). DNA metabarcoding with 16S rDNA marker revealed a significant shift in the microbiome composition in response to MOS supplementation by an increase in *Carnobacterium*. Based on their

Table 1
Carnobacterium isolated from different segments of the GI tract and feces of fish.

Species	*Carnobacterium* species	Isolated from GI tract "segments"	References
Arctic charr	*Carnobacterium* spp.	S, PI, DI, and feces	Ringø et al. (1998)
	Carnobacterium spp.	DI	Ringø and Olsen (1999)
	Carnobacterium spp.	DI	Ringø, Lødemel, et al. (2002)
	Carnobacterium spp., *C. divergens* and *C. maltaromaticum*[a]	DI	Ringø, Sperstad, Myklebust, Mayhew, and Olsen (2006)
	C. divergens	DI	Ringø et al. (1997)
	C. divergens	PI and DI	Ringø and Olsen (1999)
	C. funditum	DI	Ringø, Lødemel, et al. (2002)
	C. maltaromaticum	S, PI, DI, and feces	Ringø et al. (1998)
	C. maltaromaticum	PI	Ringø and Olsen (1999)
	C. mobile	DI	Ringø and Olsen (1999)
Atlantic salmon	Carnobacteria	DI	Villasante et al. (2022)
	Carnobacterium spp.	PI, MI and DI	Ringø et al. (2000)
	Carnobacterium spp.	PI, MI and DI	Cantas et al. (2011)
	Carnobacterium spp.	PI	Askarian et al. (2012)
	Carnobacterium spp.	EI	Zarkasi et al. (2014)
	Carnobacterium spp.	DI	Zarkasi et al. (2016)
	Carnobacterium spp.	DI	Gajardo et al. (2017)
	Carnobacterium spp.	EI	Rudi et al. (2018)
	Carnobacterium spp.	EI	Fogarty et al. (2019)
	Carnobacterium spp.	PC	Kazlauskaite et al. (2022)
	Carnobacterium spp. and *C. divergens*	Frozen digesta samples	Dehler et al. (2017a)
	C. divergens	EI	Strøm (1988)
	C. inhibens	IS	Jöborn et al. (1997, 1999)
	C. inhibens	DI	Voll Bugten et al. (2022)
	C. maltaromaticum	DI	Ringø, Sperstad, Myklebust, Mayhew, et al. (2006)
	C. maltaromaticum	PI and DI	Bakke-McKellep et al. (2007)
		PI	Skrodenyte-Arbaciauskiene et al. (2008)
	C. mobile	DI	Ringø et al. (2016)
Brown trout	*Carnobacterium* spp.	EI	González et al. (1999)
	Carnobacterium spp., *C. maltaromaticum* and *C. divergens*	NI	González et al. (2000)
	C. maltaromaticum	PI and DI	Al-Hisnawi et al. (2015)
Rainbow trout	*Carnobacterium* spp.	EI	Spanggaard et al. (2000)
	Carnobacterium spp.	DI	Lyons et al. (2017)
	Carnobacterium spp.	EI	Bruni et al. (2018)
	C. divergens and *C. maltaromaticum*	EI	Kim et al. (2007)
	C. maltaromaticum	DI	Starliper et al. (1992)
	C. maltaromaticum	E	Pond et al. (2006)
	C. maltaromaticum	EI	Mansfield et al. (2010)
	C. maltaromaticum	DI	Desai et al. (2012)
	C. maltaromaticum	EI	Garcés et al. (2020)
	Carnobacterium spp., and *C. maltaromaticum*	EI	Huber et al. (2004)
	C. maltaromaticum, *C. alterfunitum*-like and *C. divergens*	EI	Spanggaard et al. (2001)
	C. mobile	DI	Ringø et al. (2016)
Mediterranean trout	*C. maltaromaticum*	EI	Iorizzo et al. (2021)
River trout	*C. maltaromaticum*	EI	Skrodenyte-Arbaciauskiene et al. (2006)
Sea trout	*Carnobacterium* spp., and *C. maltaromaticum*	PI	Skrodenyte-Arbaciauskiene et al. (2008)
	C. maltaromaticum	NI	Balcázar et al. (2007)
Atlantic cod	*Carnobacterium* spp.	PI, DI and HC	Ringø et al. (2006)
	Carnobacterium spp.	PI	Askarian et al. (2013)
	Carnobacterium spp.	PI and DI	Zhou et al. (2013)
	C. divergens	DI	Strøm (1988)
	C. divergens, *C. gallinarum, C. inhibens* and *C. maltaromaticum*	DI and HC	Seppola et al. (2006)
Saithe	*C. divergens*	EI	Strøm (1988)
Common carp	*Carnobacterium* sp.	EI	Hagi et al. (2004)
Fine flounder	*Carnobacterium* spp. and *C. divergens*	EI	Salas-Leiva et al. (2017)
Nile tilapia	*Carnobacterium* spp.	IS	Chitambo et al. (2023)
Turbot	*Carnobacterium* spp.	EI	Yang et al. (2018)
Flathead grey mullet	*Carnobacterium* spp.	EI	Al Bulushi et al. (2010)
Northern snakehead	*Carnobacterium* spp.	EI	Miao et al. (2018)
Red cusk eel	*Carnobacterium* spp.	DI	Romero et al. (2022)
Wolffish	*C. divergens*	EI	Ringø et al. (2001)
Costal fish[b]	*Carnobacterium* spp.	EI	Sahnouni et al. (2016)

Arctic charr – *Salvelinus alpinus*; Atlantic salmon – *Salmo salar*; Brown trout – *Salmo trutta*; Rainbow trout – *Oncorhynchus mykiss*; Mediterranean trout – *Salmo macrostigma*; River trout – *Salmo trutta fario*; Sea trout – *Salmo trutta trutta*; Atlantic cod – *Gadus morhua*; Saithe – *Pollachius virens*; Common carp – *Cyprinus carpio*; Fine flounder – *Paralichthys adspersus*; Nile tilapia – *Oreochromis niloticus*; Turbot – *Scophthalmus maximus*; Flathead grey mullet – *Mugil cephalus*; Northern snakehead – *Channa argus*; Red cusk eel – *Genypterus chilensis*; Wolffish – *Anarhichas lupus*.

S – stomach; PC – pyloric caeca; PI – proximal intestine; MI – mid intestine; DI – distal intestine; HC – hindgut chamber; EI – entire intestine; IS – intestinal samples with no further description; NI – no specific information was given, only gut or intestine.

[a] Previously *Carnobacterium piscicola*.

[b] No further information was given.

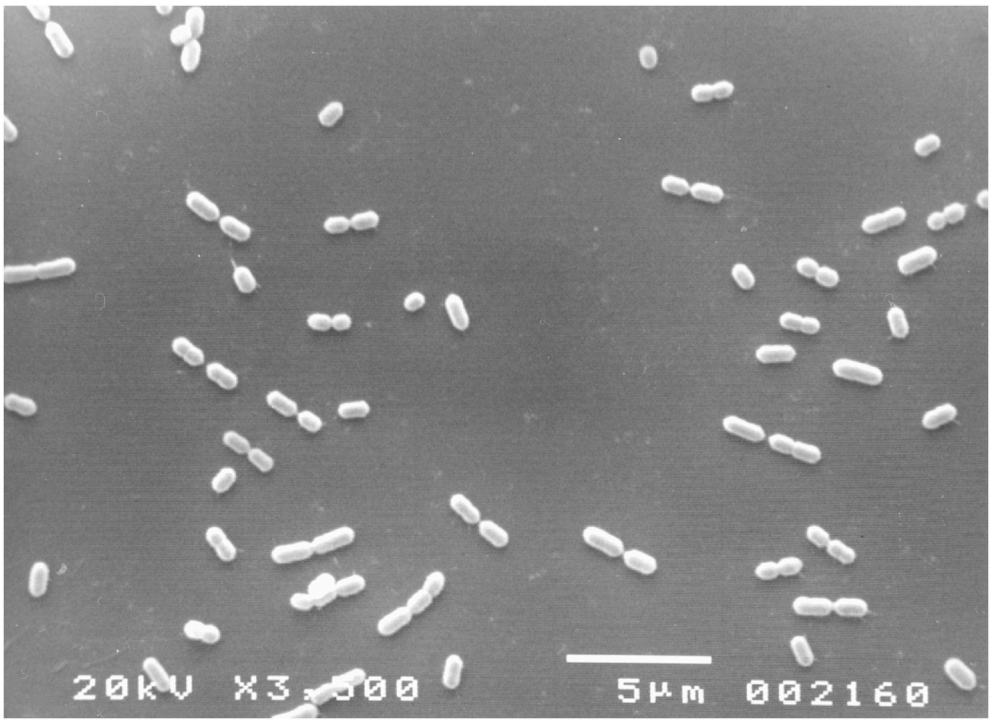

Fig. 1. Morphology of *Carnobacterium divergens* 6251 isolated from proximal intestine of Arctic charr (Myklebust & Ringø, unpublished data).

results the authors concluded that *in vitro* models are a complement to *in vivo* trials. However, this statement can be question, as Spanggaard et al. (2001) stated: "*in vitro antagonism could not completely predict an in vivo effect*".

The presence of *C. divergens* in the GI tract of Atlantic salmon has been reported in three studies (Dehler et al., 2017a; Dehler et al., 2017b; Strøm 1988). According to Dehler et al. (2017a), the most dominant phylum isolated from the GI tract of the fish Atlantic salmon was Firmicutes by *Carnobacterium*, *C. divergens*, *Lactobacillus*, *Lactococcus* and *Streptococcus*. In a study focus on seawater transfer of Atlantic salmon, Dehler et al. (2017b) reported that Carnobacteriaceae was more abundant in freshwater fish.

C. inhibens is reported in different environment, the blood of a metastatic cancer patient (Lo & Sheth, 2021) and in three Atlantic salmon studies (Jöborn et al., 1997, 1999; Voll Bugten et al., 2022). In the early study of Jöborn et al. (1997), the authors isolated a non-virulent *Carnobacterium* K1 from the intestinal tract, both from mucosa and faces contents of Atlantic salmon, and K1 was later identified as *C. inhibens* (Jöborn et al., 1999). In addition, the strain displayed *in vitro* growth inhibition of *V. anguillarum* and *A. salmonicida*.

In a study by Voll Bugten et al. (2022), the Atlantic salmon parr hindgut microbiomes were generally highly distinct *vs.* that reported from the recirculation aquaculture system (RAS) water microbiomes, dominated by phyla Bacilli and Firmicutes. An OTU probably *C. inhibens*, was isolated from the fish gut. However, fish reared in RAS without membrane ultrafiltration, a reduction in the relative abundance of this *Carnobacterium* OTU was observed.

Ringø, Sperstad, Myklebust, Mayhew, et al. (2006) reported that dietary krill meal reduced culturable epithelium-associated (autochthonous) *C. maltaromaticum* populations in the distal intestine of Atlantic salmon down from log 3.23 CFU g^{-1} in the control fish to non-detectable level, less that log 2 CFU g^{-1}, by krill feeding. Indigenous *C. maltaromaticum* populations in the gut of Atlantic salmon have also been reported to be sensitive to oxytetracycline administration (Bakke-McKellep et al., 2007). In a later study, Skrodenyte-Arbaciauskiene et al. (2008) sampled content from proximal intestine of freshwater Atlantic salmon and displayed that *Carnobacterium* spp. represented 15.4% of the culturable heterotrophic populations of the fish and comprised of *C. maltaromaticum*.

In their study devoted to the dietary effect on the gut microbiota of aquatic animals, Ringø et al. (2016) revealed *C. mobile* in the digestive tract of Atlantic salmon, but differences were notice regarding dietary oils treatment. *C. mobile* was noticed in fish fed sunflower -, rapeseed- and fish oil and commercial diet, however, the bacterium was not detected in fish fed linseed oil.

González et al. (1999) reported that carnobacteria by classical cultivation methods were dominant (nearly 40% of psychrotrophs) in brown trout (*Salmo trutta*) intestinal samples. In a later study by the same authors, two hundred and thirty-seven Gram-positive, oxidase- and catalase negative rods were isolated from the skin, gills, and gut of wild brown trout by cultivation and characterized based on phenotypical characteristics (González et al., 2000). Approximately 91% were assigned to carnobacteria and 156 strains were identified as *C. maltaromaticum*, 10 strains as *C. divergens* and 59 strains to unidentified carnobacteria. In a laboratory experiment with brown trout the culturable autochthonous LAB isolated from posterior- and distal intestine were identified as *C. maltaromaticum* (Al-Hisnawi et al., 2015).

Carnobacterium spp., *C. divergens*, *C. maltaromaticum* and *Carnobacterium alterfunitum*-like, have been isolated from the GI tract of rainbow trout (*Oncorhynchus mykiss*) (Table 1). Regarding both culturable and non-culturable populations, the population levels of *Carnobacterium* in the gut contents of rainbow trout are reported to be relatively low. An investigation of the intestinal microbiota, sampled from gut content of rainbow trout by Spanggaard et al. (2000), included comparison of microscopic counts with plate counts, reported that more than 50% of the bacteria were culturable, and among the culturable bacteria the authors reported carnobacteria. In a later study, Huber et al. (2004) determined the microbial composition of the intestines of rainbow trout from three fish farms by both classical culture-dependent methods and culture-independent molecular methods (DGGE and FISH). Carnobacteria were not isolated using culture-based methods or FISH from rainbow trout intestine at farm 1, farm 2 or from the first visit to farm 3. However, the second visit at farm 3 revealed that *Carnobacterium* spp. accounted for 33% of the culturable populations while FISH

investigations indicated that carnobacteria represented 3% of total bacterial levels. DGGE and subsequent sequencing indicated that these carnobacteria belonged to *C. maltaromaticum*. Kim and Austin (2006a) characterized two probiotic carnobacteria strains isolated from the intestine of rainbow trout: *C. maltaromaticum* B26 and *C. divergens* B33 inhibiting *in vitro* growth of *A. salmonicida*, *Aeromonas hydrophila*, *Streptococcus iniae* and *V. anguillarum*. Based on their results the authors suggested that these species may play an important defensive role against pathogenic organisms in the fish GI tract, which was later confirmed by Kim and Austin (2008) showing the unique phenotypic characteristics and antibiotic resistance. In a study by Kim et al. (2007), the authors investigated the microbial community by clone libraries and DGGE of farm reared rainbow trout and displayed one strain of *Carnobacterium* sp., and one strain displaying high similarity to *C. divergens*. Clone libraries derived from the intestinal contents and intestinal mucus revealed that 14.3% and 3.2% of the clones from intestinal contents and mucus belonged to *C. maltaromaticum*. An interesting finding of this study was higher bacterial diversity in fish intestine than previously reported, and that the adherent microbiota profile was different compared to that of gut content.

Garcés et al. (2020) isolated an autochthonous carnobacteria from trout intestine by classical culture-based methods and 16S rRNA sequencing which revealed high similarity to *C. maltaromaticum*.

Lyons et al. (2017) revealed that one of the principal genera associated with distal mucosa of farmed diploid rainbow trout by using next generation sequencing belonged to genus *Carnobacterium* and the genus was the most prevalent of the LAB genera (6.2%), followed by *Staphylococcus* (ca. 3%), *Streptococcus* (ca. 2.5%), *Vagococcus* (1.74%), *Enterococcus* (1.72%) and *Lacticigenium* (ca. 1%).

Bruni et al. (2018) reported in an investigation evaluated the dietary effect of black soldier fly (*Hermetia illucens*) on intestinal microbial communities of rainbow trout by DGGE, and revealed that *Carnobacterium* sp., and that *C. divergens* were one of the dominant bacterial species in the insect-fed groups *vs*. control fed fish.

Among the 461 bacteria isolated from the intestinal content of rainbow trout, one isolate showed high similarity to *C. alterfunitum* using 16S rDNA gene sequence analysis (Spanggaard et al., 2001). The *C. alterfunitum* D5 isolate, was unable to inhibit *V. anguillarum* in M9GC broth and showed only minimal inhibition in tryptic soy broth.

From two private hatcheries in the Pacific Northwest, USA, Starliper et al. (1992) isolated five bacteria belonging to *C. maltaromaticum* from distal intestine of moribund rainbow trout. In two later studies, Pond et al. (2006) and Mansfield et al. (2010) revealed that *C. maltaromaticum* was a dominant in the gut contents of laboratory reared rainbow trout. According to clone library analyses, Mansfield et al. (2010) revealed that *C. maltaromaticum* represented 55% of the total bacterial community of the distal gut contents of rainbow trout fed a fishmeal-based diet, but when the dietary protein source was changed to casein or soybean meal (SBM) the abundance increased to 87.8% and 97.2%, respectively.

Distal intestine contents of rainbow trout fed diets supplemented with plant ingredients or a fish meal (FM) diet (control) was investigated by Desai et al. (2012). The microbiota community profiles were determined by pyrosequencing of cpn60 PCR products and 16S rRNA DGGE and the authors revealed *C. maltaromaticum*. As fish fed plant ingredient diets were associated with higher Firmicutes: Proteobacteria ratios than control, authors suggested that the modulation may contribute to negative health outcomes when diets contain plant meal proteins, but these changes in microbiome structure can be minimized with additional processing of plant ingredients.

In contrast to the results reported on *C. mobile* in the GI tract of Atlantic salmon, the bacterium was only revealed in the intestine of rainbow trout fed sunflower oil (Ringø et al., 2016). The reason for this difference between salmonid species is unclear, as the similar culture conditions and diets were used.

From the GI tract of river trout, Skrodenyte-Arbaciauskiene et al. (2006) isolated *C. maltaromaticum* which represented 3.8% and 4.2% of the isolates from fish sampled from the Skroblus river and the Zeimena river, respectively.

Skrodenyte-Arbaciauskiene et al. (2008) collected samples from the posterior digesta of sea trout and cultured isolates were subsequently identified by partial 16S rDNA sequencing, and the results displayed that carnobacteria constituted 6.0% of the culturable heterotrophic populations and comprised of *C. maltaromaticum* and an unidentified *Carnobacterium* spp. Balcázar et al. (2007) carried out a sequencing study of variable regions of the 16S rRNA gene of LAB species isolated from healthy salmonids, Atlantic salmon, brown trout, and rainbow trout and noticed that the predominant LAB isolated belonged to *C. maltaromaticum*.

2.2. Gadidae

The first study isolating carnobacteria from Atlantic cod (*Gadus morhua*) intestine, distal intestine, was done by Strøm (1988). Later, Ringø, Sperstad, Myklebust, Refstie, & Krogdahl (2006) isolated aerobic heterotrophic bacteria (n = 944) from the GI tract of healthy Atlantic cod fed three different diets, FM, standard- or a bioprocessed SBM, by classical cultivation methods and 425 isolates were subsequently identified by sequencing the 16S rRNA genes. The results revealed that the gut microbiota was affected by dietary manipulation as fish fed FM was dominated by Gram-positive bacteria of the genera *Brochothrix* and *Carnobacterium*. *Chryseobacterium* spp., *Psychrobacter glacincola*, and *Carnobacterium*, dominated in the GI tract of fish fed SBM. Antagonistic activity of carnobacteria regarding *in vitro* growth inhibition of *A. salmonicida* ssp. *salmonicida* and *V. anguillarum* revealed that 21 out of 45 strains inhibited or delayed growth of the pathogens. Seventy-nine bacteria previously isolated from the GI tract of Atlantic cod by Ringø et al. (2006), but not previously tested for enzyme-production, identified by 16S rRNA gene sequencing or tested for antagonistic activity were further investigated by Askarian et al. (2013). *Carnobacterium* sp. strain 476 isolated from fish fed SBM revealed moderate protease and cellulase score and low phytase score, but an interesting finding was that this strain showed antagonistic effect against all four pathogens tested. The effect of chitin supplementation on the autochthonous bacteria in proximal- and distal intestine of Atlantic cod was investigated by DGGE by (Zhou et al., 2013), and the study reported *Carnobacterium* in both gut segments and in both feeding groups, with or without chitin supplementation.

Seppola et al. (2006) evaluated the autochthonous (bacteria associated with mucosa) and allochthonous (transit) bacteria in distal intestine and hindgut chamber by cultivation of fed and starved Atlantic cod. All bacterial strains isolated from hindgut chamber belong to carnobacteria. In contrast, only 10% of the bacteria strains isolated from the distal intestine belonged to carnobacteria. Random amplification of polymorphic DNA (RAPD) analysis using three selective primers, revealed that the 25 isolates tested segregated into eight clusters. The major cluster comprised of nine strains isolated from the hindgut chamber of both fed and starved fish and revealed low similarity with the reference strains. The other carnobacteria strains isolated from the hindgut chamber were in cluster showing high similarity with *C. gallinarum* or *C. maltaromaticum*. Strains isolated from distal intestine appeared more divergent and three trains belonged to *C. divergens* and *C. inhibens*. The presence of autochthonous bacteria in the hindgut chamber was confirmed as autochthonous rod-shaped bacteria revealed between adjacent microvilli by transmission electron microscopy.

In her master study, Strøm (1988), isolated a *C. divergens* from the GI tract of saithe (*Pollachius virens*), and this isolate revealed antagonistic activity on *in vitro* growth of some pathogenic fish bacteria.

2.3. Cyprinidae

In a study, investigating, the diversity and seasonal changes in LAB in the digestive tract of common carp (*Cyprinus carpio*) sampled from lake

Kasumigaura Japan by cultivation and subsequently identified RAPD analysis, Hagi et al. (2004) reported an interesting finding that *Carnobacterium* sp. were only recorded in samples from January and March, when the water temperature was low.

2.4. Pleuronectiformes

Salas-Leiva et al. (2017) reported in a comparative study of farmed and wild-caught fine flounder (*Paralichthys adspersus*) by classical cultivation and subsequently by 16S rRNA gene analysis, a more diverse microbial community in wild caught-compared to farmed fish. However, *Carnobacterium* was reported as a part of the intestinal allochthonous bacterial community in farmed fish but not in wild-caught fish.

The autochthonous microbiota from whole intestinal tract of turbot (*Scophthalmus maximus*) fed diet supplemented with 5% stachyose, often regarded as an anti-nutritional factor, revealed significant higher abundance of *Carnobacterium*, than that of fish fed a FM diet (Yang et al., 2018).

2.5. Mugilidae

Out of 99 bacteria isolated from the gut of flathead grey mullet (*Mugil cephalus*), one isolate was identified as *Carnobacterium* sp. (Al Bulushi et al., 2010).

2.6. Channidae

In an investigation evaluated the dietary effect of SBM on gut microbiota evaluated by RNA extraction and qRT-PCR, Miao et al. (2018) reported that in Northern snakehead (*Channa argus*) fed replacement of 75% of SBM, a higher abundance of *Carnobacterium* sp., was displayed, in contrast carnobacteria was not revealed in the other feeding groups. Based on their results that SBM affects intestinal homeostasis by modulation the gut microbiota, the authors suggested that as certain species of *Carnobacterium* is opportunistic pathogen that may impair the intestinal immune mechanisms in fish, but as most carnobacteria are considered as beneficial this hypothesis merits further investigation.

2.7. Ophidiidae

In a recent study, Romero et al. (2022) evaluated the distal content microbiome by next generation sequencing and metabolomic pathways in metagenomes of wild and aquacultured red cusk eel (*Genypterus chilensis*). The results revealed that phylum *Firmicutes* was most abundant in aquacultured fish, and at genus level *Carnobacterium* was highly noticed.

2.8. Anarhichadidae

In a study focus on identification and carnobacteria isolated from different fish species, Ringø et al. (2001) reported the presence of a *C. divergens* isolated from wolffish (*Anarhichas lupus*) fry intestine.

2.9. Costal fish

Sahnouni et al. (2016) carried out a study to characterize allochthonous LAB strains isolated from the GI tract of three fish species: Atlantic horse mackerel (*Trachurus trachurus*), European pilchard (*Sardina pilchardus*) and Atlantic bonito (*Sarda sarda*), based on classical cultivation and phenotypic characteristics. Ten strains were identified as *Carnobacterium* spp., and these strains revealed inhibitory activities against one or more of the following target strains: *Staphylococcus aureus*, *Escherichia coli*, *Pseudomonas aeruginosa*, *Bacillus cereus*, *A. hydrophila*, *Listeria innocua*, *Salmonella* sp. and *Vibrio* sp., and two carnobacteria strains showed production of bacteriocin-like substances.

3. *Carnobacterium* used as probiotic

Probiotic, a word derived from Latin, for *life*, has a long history, and according to Ozen and Dinleyici (2015) sophisticated technology in molecular archeology, can trace the use of fermented products as early as 8.000 BC. The term probiotics was first proposed by Lilly and Stillwell (1965) and they suggested the definition "*substances produced by one protozoan that stimulated the growth of another*", and according to Web of Science, more than 35.000 and 36.000 papers are published using the key words, probiotic or probiotics, respectively. In aquaculture LAB generally classified with the Qualified Presumption of Safety status, are most frequently used as probiotics (Contente et al., 2023), and the use of probiotics is suggested as a reliable alternative to chemotherapy with promising and well-establish results in numerous aquatic species.

C. divergens and *C. maltaromaticum* contain genes that express various cell-surface adhesion proteins and structures, such as leucine-rich repeats, collagen-binding, fibrinogen-binding, and mucin-binding proteins, which play major roles of probiotics colonising the intestinal tract.

The first probiotic study in aquaculture was published by Kozasa (1986). In aquaculture, probiotics are ether added to the diet or water to reduce pathogen adherence and colonization in larval-, fry- and juvenile intestines by enhancing the proportion of health-promoting bacteria in the gut, affect positively the immune system and improve disease resistance. An advantage by using this method is that it can be implemented during the early stages of development when vaccination by injection is impractical, and in *in vivo* three mechanisms: competition, exclusion, and displacement can be involved in the inhibitory effects of probiotics on pathogens present in the GI tract.

Even though some studies have reported no or negative effect on the use of carnobacteria as probiotics, several studies have revealed that supplementation of feed with carnobacteria are effective for improving the health and growth of aquatic fish (Table 2). The first study using carnobacteria as probiotic in aquaculture, *L. plantarum* Lab01 later reclassified as *C. divergens*, was published by Strøm and Ringø (1993). Atlantic cod larvae, five days old was exposed to 10^5 *C. divergens* mL^{-1}, and half of the water volume was replaced with filtered sea water, the 2nd, 4th, 6th and 8th after exposure. Bacteriological analysis on day 9 after experimental start showed lower log CFU values in the water of the experimental flask *vs*. control and that probiotic administration modulated the larval gut microbiota, by increasing the proportion of *C. divergens* to 70% of the gut microbiota. Since then, *C. divergens* Lab01 has been used in several probiotic studies (Gildberg et al., 1995, 1997; Gildberg & Mikkelsen, 1998; Hartviksen et al., 2015; Kristiansen et al., 2011; Puvanendran et al., 2021).

3.1. Carnobacterium sp.

Robertson et al. (2000) showed *in vitro* growth inhibition of *A. hydrophila*, *A. salmonicida*, *Flavobacterium psychrophilum*, *Photobacterium damselae* subsp. *piscicida*, *Streptococcus milleri*, *V. anguillarum* and *Vibrio ordalii* but no inhibition towards *Debaryomyces hansenii*, *Janthinobacterium lividum*, *Vibrio alginolyticus*, *V. harveyi* or *Yersinia ruckeri* by strain of *Carnobacterium* strain K1 isolated from the intestine of Atlantic salmon (Jöborn et al., 1997). Feeding Atlantic salmon and rainbow trout diets supplemented strain K1, 5×10^7 cells g^{-1}, revealed that the isolate remained viable in the GI tract as after reverting to control diets after 28 days of probiotic feeding, the isolate was re-isolated from the intestine. After feeding the probiotic diet for 14 days, fish were challenge by cohabitation of four pathogens and displayed reduced mortality caused by *A. salmonicida*, *V. ordalii* and *Y. ruckeri*, but not in the *V. anguillarum* challenge experiment.

Spanggaard et al. (2001) tested the probiotic potential of *Pseudomonas* and carnobacteria. Rainbow trout challenge with *V. anguillarum* was improved (13–43%) by *Pseudomonas* administration but the two carnobacteria tested that revealed antagonistic effect on *in vitro* growth did not improve disease resistance towards *V. anguillarum* of rainbow

Table 2
Use of *Carnobacterium* as probiotics in finfish.

Carnobacterium species	Fish species	Mode of application	Reported effects	References
Carnobacterium sp.	Atlantic salmon and rainbow trout	5×10^7 cells g^{-1}	The probiont colonize the GI tract ↑ resistance against *A. salmonicida*, *V. ordalii* and *Y. ruckeri* ↓ resistance toward *V. anguillarum*	Robertson et al. (2000)
	Rainbow trout	10^7 cells mL^{-1}	↓ disease resistance towards *V. anguillarum*	Spanggaard et al. (2001)
	Rainbow trout	10^7 CFU g^{-1}	Present in the GI after 7 days of probiotic feeding. → number of erythrocytes, macrophages, lymphocytes, and leucocytes	Irianto and Austin (2002)
	Rainbow trout	10^7 cells g^{-1}	↑ resistance against *A. salmonicida* ↑ leucocyte numbers → numbers of erythrocytes and lysozyme activity	Irianto and Austin (2003)
	Zebrafish	10^7 cells g^{-1}	Showed nonspecific adhesion ↓ vibrios and enterobacteria in the gut	Sequeiros et al. (2022)
C. divergens	Arctic charr	10^6 $CFUg^{-1}$	↑ growth performance → behavioral characteristics and distal intestinal microbiota	Knobloch et al. (2022)
	Atlantic cod	10^5 CFU mL^{-1}	Modulated the gut microbiota by increasing *C. divergens* in the gut	Strøm and Ringø (1993)
	Atlantic cod	2×10^9 g^{-1}	↑ disease resistance against *V. anguillarum*	Gildberg et al. (1997)
	Atlantic cod	10^8 $CFUg^{-1}$	→ disease resistance against *V. anguillarum* 4 weeks after infection	Gildberg and Mikkelsen (1998)
	Atlantic cod	10^7 CFU mL^{-1} added to rearing water of *Artemia*	↑ growth and disease resistance against *V. anguillarum* → gut microbiota, prior or post challenge	Puvanendran et al. (2021)
	Atlantic halibut	10^7 CFU mL^{-1}	↑ growth, survival, and number of goblets cells	Ottesen and Olafsen (2000)
	Atlantic salmon	2.5×10^9 CFU g^{-1}	↑ growth, and high adhesion of LAB, 5 weeks after experimental start ↓ survival against *A. salmonicida*	Gildberg et al. (1995)
	Atlantic salmon	*Ex vivo* exposure. 6×10^4 or 6×10^6 viable bacteria mL^{-1}	Did not cause cell damage to the intestine Prevented, to some extent, pathogen-induced damage in the proximal intestine	Ringø et al. (2007)
	Atlantic salmon	*Ex vivo* exposure. 10^8 CFU mL^{-1}	Did not cause cell damage to the intestine Prevented, to some extent, pathogen-induced damage in the proximal intestine	Kristiansen et al. (2011)
	Atlantic salmon	*Ex vivo* exposure. 3.2×10^7 CFU mL^{-1}	Did not cause cell damage to the intestine Prevented, to some extent, pathogen-induced damage caused by *A. salmonicida*	Hartviksen et al. (2015)
	Common carp	10^7 CFU g^{-1} or 10^9 CFU g^{-1}	Both diets, ↑ crude lipid → growth performance and crude protein	Mazurkiewicz et al. (2007)
C. maltaromaticum	Atlantic cod	*Ex vivo* exposure. 2.3×10^7 mL^{-1}	Exposure did not display cell damage or cellular disruptions Can to some extent out-compete the pathogen	Løvmo Martinsen et al. (2011)
	Rainbow trout	6.5×10^8 CFU g^{-1}	↑ growth performance and apparent digestibility Affected the microbial counts in the content from the digestive tract	Goals and Potorski (2022)
C. maltaromaticum B26 and *C. divergens* B33	Rainbow trout	$> 10^7$ CFU g^{-1}	↑ phagocytic activity of head macrophages (B26), respiratory burst and serum lysozyme activity (B33) and gut mucosal lysozyme activity (both strains) ↑ resistance against *A. salmonicida* and *Y. ruckeri* (both strains) Both strains were detected in gut content and associated to mucus 14 days after feeding	Kim and Austin (2006a, 2006b)

Atlantic salmon – *Salmo salar*; Rainbow trout – *Oncorhynchus mykiss*; Zebrafish – *Danio rerio*; Arctic charr – *Salvelinus alpinus*; Atlantic cod – *Gadus morhua*; Atlantic halibut – *Hippoglossus hippoglossus*; Common carp – *Cyprinus carpio*.
↑ - increase; → no effect; ↓ - decrease.

trout. Based on their results the authors concluded that "*in vitro antagonism could not completely predict an in vivo effect*".

In a study with rainbow trout, *Carnobacterium* BA211 (10^7 bacterial cells g^{-1}) was administered for 14 days an increased resistance was observed following exposure with *A. salmonicida*; 10^5 CFU mL^{-1} after 14 days challenge (Irianto & Austin, 2002). In addition, BA211 was still present in the GI after 7 days of probiotic feeding. There was no clear indication increased number of erythrocytes, macrophages, lymphocytes, and leucocytes, but enhanced lysozyme activity in the fish was noticed by *Carnobacterium* administration.

A commercial feed was added dead probiotic cells, formaldehyde treated, of *Carnobacterium* BA211 (10^7 cells g^{-1}) was fed to rainbow trout fry and fingerlings for 14 days and thereafter infected intraperitoneally with 10^6 cells of *A. salmonicida*, improved resistance was reported of BA211 fed fish (Irianto & Austin, 2003). Administration of dead probiotic cells to rainbow trout fingerlings for 14 days, did not affect numbers of erythrocytes and lysozyme activity but an increase in leucocyte numbers was revealed.

In their study with Atlantic halibut (*Hippoglossus hippoglossus*), Verner-Jeffreys et al. (2003) reported the effect of probiotic exposure by adding 10^6 CFU ml^{-1} of *Carnobacterium* strain AN1 and AN2 on disease resistance against *V. anguillarum*.

Sequeiros et al. (2022) used an autochthonous *Carnobacterium* sp. T4 isolated from Patagonian fish (Garcés et al., 2020) and revealed nonspecific adhesion and that the strain was tolerant to trout bile and acid pH values, which is an essential property for their survival in the fish gut. Probiotic feeding by T4, 10^7 CFU g^{-1}, showed its presence the zebrafish intestines. Bacteriological evaluations by cultivation after 14 days of probiotic feeding, displayed decreased counts of vibrios and enterobacteria decreased, and based on their findings the authors concluded that the four LAB tested including *Carnobacterium* sp. T4 are interesting probiotic candidates for use in aquaculture. However, to fully conclude the probiotic potential of T4, studies on the effect on the immune system, gut histology analysis and challenge studies merits

investigations.

3.2. C. divergens

A dietary supplementation of a *C. divergens* V41 originally isolated from fish viscera (Pilet et al., 1995) was administrated to juvenile Arctic charr for four weeks (Knobloch et al., 2022). The strain enhanced growth performance without altering behavioral characteristics or the gut microbiota determined using 16S rRNA fluorescence in situ hybridization (FISH). The lack of effect on the distal intestine microbiota, digesta and mucus, may be due to that the administration period was too short, but what about the microbiota in the proximal intestine?

Gildberg et al. (1997) supplemented *C. divergens* in the feed of Atlantic cod fry, and fry receiving 2×10^9 g^{-1} demonstrated improved disease resistance against *V. anguillarum*. Furthermore, the authors stated "*true colonization*" of *C. divergens*. However, to confirm this hypothesis the fry should be reverted to control feed for at least 14 days, and then analysed the gut microbiota. Gildberg and Mikkelsen (1998) used *C. divergens* as fed supplements to a commercial diet to Atlantic cod fry either alone or in combination with immuno-stimulating peptides. *In vitro* growth experiments revealed that culture filtrates from the carnobacteria inhibited the *in vitro* growth of *V. anguillarum*. After three weeks of feeding, were fish challenged by bath exposure to *V. anguillarum* (10^7 mL^{-1}, 1 h), and 12 days after infection a significant ($P < 0.05$) reduced cumulative mortality was revealed in fish the carnobacteria supplemented diet and immune-stimulating peptides. However, four weeks after infection, similar cumulative mortality was noticed in all treatment groups, including the control. Generally, the viable counts of LAB were higher in pyloric caeca *vs*. intestine indicating that they colonize the pyloric caeca mucus layer of the fry, and that to some extent survived the passage of the GI tract.

In a recent study, Puvanendran et al. (2021) also verified benefits of supplementation of *C. divergens* Lab01 in the diet of Atlantic cod larvae as significantly increased growth and survival during the larval phase and disease resistance towards *V. anguillarum* was noticed *vs*. larvae fed the control diet. However, probiotic supplementation revealed no significant effect on the overall gut microbiota and the relative level of carnobacteria was not affected by probiotic feeding, as abundance of carnobacteria was relatively low.

Atlantic halibut larvae exposed to 10^7 CFU mL^{-1} of *C. divergens* showed increased growth and survival compared to control fed fry and fry exposed to *Vibrio iliopiscarius* (Ottesen & Olafsen, 2000). In addition, probiotic administration to the rearing water resulted in a higher number of goblet cells in larvae, specialized epithelial cells that line multiple mucosal surfaces and have a well-appreciated role in barrier maintenance through the secretion of mucus repellent towards undesirable gut bacteria (Knoop & Newberry, 2018).

Gildberg et al. (1995) conducted a 5-weeks feeding trial with Atlantic salmon fry to determine the effect of *C. divergens* Lab01 and showed increased growth, and significantly high adhesion of LAB in fry 5 weeks after experimental start. However, a significant lower survival was noticed in fry fed det supplemented with Lab01 in a cohabitant infection study with *A. salmonicida* compared to the control group.

In an *ex vivo* study, the intestinal sac method, the proximal intestine was exposed to *C. divergens* strain 6251 isolated from proximal intestine of Arctic charr (Ringø, Seppola, et al., 2002), at 6×10^4 or 6×10^6 viable bacteria mL^{-1} (Ringø et al., 2007). Light - and electron microscopy evaluations revealed that bacterial exposure to strain 6251 revealed similar appearance of the intestinal mucosal epithelium, with no signs of damage as that observed when the proximal intestine was exposed to Ringer solution only. However, exposure of the proximal intestine to pathogenic bacteria, *A. salmonicida* at 6×10^4 viable bacteria mL^{-1}and *Vibrio anguillarum* at 6×10^4 or 6×10^6 viable bacteria mL^{-1}, resulted in damaged epithelial cells, cell debris in the lumen, and microvilli disorganization. Co-incubation of the proximal intestine with *C. divergens* and a pathogen and did not reverse the damaging effects caused by the pathogen, although these were alleviated when probiotic bacteria were used. Based on these results, it was suggested that *C. divergens*, prevented to some extent, pathogen-induced damage in the proximal intestine of Atlantic salmon.

In an *ex vivo* experiment, Kristiansen et al. (2011), displayed that exposure of *C. divergens* Lab01 at 10^8 CFU mL^{-1} did not cause cell damage to the intestinal tract of Atlantic salmon, and that Lab01 adhere to the epithelium or mucus layer in the proximal intestine, where culturable heterotrophic bacterial levels, identified as *C. divergens*, were elevated by 234% compared to the control. However, this effect was noticed in the distal intestine. Isolated carnobacteria from the *ex vivo* experiment was tested for their ability to inhibit *in vitro* growth of *Y. ruckeri* and *A. salmonicida* ssp. *salmonicida*. Extracellular products from all 11 isolated carnobacteria strains from the *ex vivo* experiment, plus type strain *C. inhibens* CCUG 31728, inhibited *in vitro* growth of *Y. ruckeri*. However, only extracellular products from *C. divergens* isolate 57 inhibited the growth of *A. salmonicida*.

Lack of beneficial effects were observed in a 42-day study of common carp fed two diets added *C. divergens*, such as specific growth rate, feed conversion, protein efficient ratio and crude protein (Mazurkiewicz et al., 2007). However, supplementation significantly enhanced crude lipid.

3.3. C. maltaromaticum

Løvmo Martinsen et al. (2011) investigated by using an *ex vivo* method whether the proximal intestine of Atlantic cod is an infection route for *V. anguillarum* serotype 02 β and if *C. maltaromaticum*, originally isolated from the hindgut chamber of Atlantic cod (Seppola et al., 2006) could out-compete the pathogen and modulate the autochthonous proximal intestinal microbiota. Exposure of *V. anguillarum* to the proximal intestine did not reveal cell damage indicating that this gut segment is not a major infection site for *V. anguillarum* in healthy Atlantic cod, but raised an important question, what about the distal intestine a topic merits investigation. Exposing the proximal intestine to *C. maltaromaticum*, displayed no cell damage or cellular disruptions, and exposure of the proximal intestine to the probiotic and pathogenic bacteria indicated that *C. maltaromaticum*, to some extent, outcompeted the pathogen, however further investigation is needed. Analysis of the proximal intestine indicated that *C. maltaromaticum* modulated the autochthonous proximal intestine microbiota in Atlantic cod.

Goals and Potorski (2022) conducted a 56-day feeding trial with juvenile rainbow trout experimentally reared in RAS to determine the effect of 6.5×10^8 CFU g^{-1} of *C. maltaromaticum* and revealed that enrichment significantly affected growth performance, apparent digestibility coefficients of protein, lipid, ash, and nitrogen-free extract. Furthermore, probiotic administration significantly influenced microbial counts in the content sampled from the digestive tract.

3.4. C. maltaromaticum and C. divergens

Kim and Austin (2006b) used *C. maltaromaticum* B26 and *C. divergens* B33 as probiotic supplements to rainbow trout, 25 g, and demonstrated that high levels of *C. maltaromaticum* and *C. divergens* in the intestines enhanced the cellular and humoral immune responses, and improved protection against *A. salmonicida* and *Y. ruckeri* compared to control fed fish.

4. Bacteriocins

Several isolates of carnobacteria produce bacteriocins, ribosomally synthesized proteinaceous compounds produced during the primary phase of growth which may be bactericidal or bacteriostatic in nature. Since the first studies reporting bacteriocin production by *C. maltaromaticum* isolated from meat (Ahn & Stiles, 1990) and carnobacteria isolated from fish (Stoffels et al., 1992a, 1992b, 1993) there are

according to Web of Science published more than 220 papers using the keywords, bacteriocin and *Carnobacterium*.

To avoid overlaps with previous review papers describing the production of bacteriocins by carnobacteria, scientists with interest in this topic are recommended to have a closer look at the reviews of Desriac et al. (2010), Evangelista et al. (2022) and Pereira et al. (2022). However, the use of bacteriocin producing LAB *vs*. non-bacteriocin producing LAB on fish health have rarely been assessed in fish (Contente et al., 2023), a topic that merits investigations.

5. Pathogenic Carnobacterium

Carnobacteria can be considered as a part of the *normal* gut microbial populations of many fish species (Table 1), and there is a wide range of possibilities for the use of probiotic *Carnobacterium*, but less information is available on pathogenic carnobacteria.

Several reports refer to the association of *Carnobacterium* sp. and *Lactobacillus piscicola* later reclassified as *C. maltaromaticum* related to fish disease, the pseudokidney disease which is associated to colder water temperatures (see Table 3).

5.1. *Carnobacterium sp.*

Baya et al. (1991) evaluated the phenotypical and serological properties of carnobacteria associated with high mortalities of stripped bass (*Morone saxatilis*) and channel catfish (*Ictalurus punctatus*). Carnobacteria strain HB-425 and HB426 isolated from striped bass were used in peritoneal infection trials with striped bass and rainbow trout, and an LD_{50} of 10^6 was reported for rainbow trout but striped bass survived doses of 10^8. These values were higher than LD_{50} values of *V. anguillarum* and *A. hydrophila* in trout, ca. 10^3 and 10^3-10^4, respectively (Santos et al., 1992). Furthermore, drug resistance of strain HB-425 and HB426 were tested against 18 chemotherapeutic agens widely used in aquaculture, and among these compounds, the strains were sensitive for tetracycline, oxytetracycline and erythromycin.

In a study with Atlantic cod larvae, characterizing potentially pathogenic bacteria, Sandlund and Bergh (2008) reported that *Carnobacterium* strain HI21050 caused high larval mortality.

Loch et al. (2012) reported a *Carnobacterium* in the kidneys of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum). By cultivation the results showed that *A. salmonicida* subsp. *salmonicida* was most prevalent, but *Carnobacterium* revealed a prevalence of 4.5% and 2.3% in female and males, respectively in Chinook salmon collected from little Manistee River Weir and Medusa Creek Weir. According to the authors, 50% of the *Carnobacterium* infected Chinook salmon clinically normal, whilst the others exhibited focal discoloration of the lateral musculature, opacity and thickening of the swim bladder walls.

According to a study evaluating pathogens in wild and farmed marine in the Gulf of Eilat, Ucko and Colorni (2014) reported a *Carnobacterium* sp. isolated from diseased grouper (*Epinephelus fasciatus*). Furthermore, drug resistance of the carnobacteria strain was tested against seven chemotherapeutic agents, and among these compounds, the strains were sensitive for chloramphenicol and florfenicol.

Table 3
Pathogenic *Carnobacterium* in finfish.

Carnobacterium species	Fish species	References
Carnobacterium sp.	Channel catfish	Baya et al. (1991)
	Striped bass	Baya et al. (1991)
	Atlantic cod	Sandlund and Bergh (2008)
	Chinook salmon	Loch et al. (2012)
	White grouper	Ucko and Colorni (2014)
C. maltaromaticum[a]	Salmonids	Hiu et al. (1984)
	Salmonids	Humphrey et al. (1987)
	Salmonids	Loch et al. (2011)
	Brook trout	Standish et al. (2022)
	Rainbow trout	Starliper et al. (1992)
	Rainbow trout	Toranzo et al. (1993a, b)
	Rainbow trout	Alvarez et al. (1995)
	Rainbow trout	Smith et al. (2023)
	Lake whitefish	Loch et al. (2008)
	Burbot	Pietsch et al. (2020)
	Diseased fish	Roh et al. (2020)

Channel catfish – *Ictalurus punctatus*; Striped bass – *Morone saxatilis*; Atlantic halibut – *Hippoglossus hippoglossus*; Atlantic cod – *Gadus morhua*; White grouper – *Epinephelus aeneus*; Brook trout – *Salvelinus fontinalis*; Rainbow trout – *Oncorhynchus mykiss*; Lake whitefish - *Coregonus clupeaformis*; Burbot – *Lota lolta*.

[a] First described as *Lactobacillus piscicola* (Hiu et al., 1984), later reclassified as *C. piscicola* and finally reclassified as *C. maltaromaticum*.

5.2. *C. maltaromaticum*

C. maltaromaticum is the causative agent of pseudokidney disease but has also been associated with other forms of chronic inflammation, pseudomembrane formation, and occasionally, nephrocalcinosis in both gender of salmonids. The first study reporting carnobacteria from diseased salmonids sampled from hatcheries in Oregon was reported by Hiu et al. (1984). *Lactobacillus piscicola*, later reclassified as *C. piscicola* and finally reclassified as *C. maltaromaticum* was isolated from kidney tissue of disease fish showing pathological signs in internal organs or skin which may be a result of stress during spawning.

In a screening study of 11 salmonids hatcheries in southern Australia, Humphrey et al. (1987) reported that one of the bacteria of pathogenic significance was *Lb. piscicola* (*C. maltaromaticum*).

Starliper et al. (1992) carried out a challenge study to evaluate the pathogenicity of *C. maltaromaticum* isolated from moribund rainbow trout by intraperitoneal (i.p.) injection and waterborne exposure and isolate 27,488 was successfully isolated from kidney i.p.-injected fish. However, as carnobacteria revealed low mortality in the challenge tests, the authors suggested that the bacteria may only cause problems in severely stressed fish, e.g., due to spawning.

Toranzo, Romalde, Nunez, Figueras, & Barja (1993) reported the first description in Spain of a carnobacteria strain causing important mortalities in market-size rainbow trout revealing clinical signs such as a pronounced bilateral exophthalmia with periocular haemorrhages, accumulation of ascitic fluid, and haemorrhages in the liver, swim bladder, muscle, and intestine. Taxonomic studies displayed that the isolate PT-31 was *C. maltaromaticum*. Challenge studies, i.p. injection or water exposure showed that isolate PT-31 was highly pathogenic for fingerlings rainbow trout (10 g), $LD_{50} < 5–6 \times 10^4$, and moribund fish revealed both external and internal signs. The inoculated strain was reisolated from kidney, liver, spleen, and brain of dead fish, while PT-31 was only reisolated from kidney of surviving trout. Toranzo, Novoa, Baya, Hetrick, Barja, & Figueras (1993) investigated histopathological changes in rainbow trout and stripped bass infected by *C. maltaromaticum* strain HB-425 isolated from striped bass (Baya et al., 1991), but HB-425 caused only mild lesions in spleen and kidney, and no damage to the eyes and musculature was noticed. Based on these findings it can be concluded that PT-31 is more pathogenic and virulent than HB-425.

During high mortalities of pseudokidney disease in farmed rainbow trout in Venezuela, Alvarez et al. (1995), isolated *C. maltaromaticum* from ascitic fluids and kidneys, sensitive to oxytetracycline. Furthermore, laboratory studies reported 100% mortality at injection of 2×10^4 cells per fish, but not at 10^3 cells/fish.

Loch et al. (2008) reported isolation of a *C. maltaromaticum*-like bacterium, but not fully identical to *C. maltaromaticum*, from kidneys and swim bladders of lake whitefish (*Coregonus clupeaformis*) from Lakes Michigan and Huron. The *C. maltaromaticum*-like bacterium was associated with splenomegaly, renal and splenic congestion, and thickening of the swim bladder wall with accumulation of a mucoid exudate. Examination of stained tissue sections revealed renal and splenic congestion, vacuolation and bile stasis within the liver, and hyperplasia within the epithelial lining of the swim bladder. The concurrent presence of

pathological changes and the *C. maltaromaticum*-like bacteria suggests that this bacterium is pathogenic to lake whitefish.

In a later study, Loch et al. (2011) isolated 29 strains identified as *C. maltaromaticum* from Chinook and coho salmon from stations in Great Lakes basin. *C. maltaromaticum* were recovered from the kidneys, spleen, swim bladder, and/or external ulcerations of 51 infected fish, and *C. maltaromaticum* infections were reported to be widespread in both feral and farmed spawning populations of the salmon. An interesting finding was that infection prevalence varied significantly according to location (highest infection rate from Platte River Weir), fish species and strain, gender (highest in female), and across time.

The first study revealing disease caused by *C. maltaromaticum* in Korea was reported by Roh et al. (2020) investigating pathogenicity and virulence factors between non-pathogenic (DSM20342, isolated from a dietary product) and pathogenic (*C. maltaromaticum* ATCC35586 and 18ISCm, isolated from disease fish) bacteria, a not well documented topic. The results from the Roh and co-authors study showed that bacterial virulence factors was only present in strains isolated from diseased fish, a finding strengthened in a challenge study.

Standish et al. (2022) used duplex quantitative real-time PCR for detection and discrimination of *C. maltaromaticum* and *V. salmoninarum* of lake trout tissues and reported prevalence of *C. maltaromaticum* in kidney and liver.

6. Conclusions and further directions

The interactions between the commensal gut microbiota and the immune system and function includes multifold interactions in homeostasis and disease. When investigating the intestinal bacterial community of fish, most studies have focused on the allochthonous microbiota, while those bacteria that colonize the mucosal surface (the autochthonous microbiota); which may be important in specialized physiological functions, are less characterized. Therefore, it is recommended more focus on the autochthonous gut microbiota in future studies.

Numerous studies have assessed that carnobacteria are a part of the gut microbiota of salmonids (Merrifield et al., 2014; Ringø et al., 2018, 2020a) and other fish species, see Table 1, and several studies carried out on fish species in the Arctic region have revealed "high" abundance of carnobacteria in the GI tract. A temperature effect on fecal microbiota of Tasmanian Atlantic salmon has also been reported (Neuman et al., 2016). Therefore, further studies are required to address the impact of seasonal temperature and diet on the carnobacteria levels in the gut of salmonids and other fish species to better understand their importance as components of the "*normal*" microbiota. Despite this, carnobacteria populations are of potential importance to the host fish as *Carnobacterium* have been extensively tested both *in vitro*, to ascertain their impacts on transient pathogenic bacteria, and *ex vivo* and *in vivo* as probiotics.

Gut microbial evaluations of salmonids from the somewhat contradictory findings of the present literature – and the different and not always appropriate (to isolate carnobacteria) methodology used can compromise conclusions. As some recent studies revealed that yellow drum (*Nibea albiflora*) (Li et al., 2022), and red sea bream (*Pagrus major*) (Jang et al., 2022) did not retrieving *Carnobacterium* as components of the indigenous gut microbiota, it is difficult to draw final conclusions based on the present literature whether carnobacteria are true colonizers in fish intestine. These contrasting results may be due to differences in incubation temperature in cultivation studies, lower temperature is recommended, number of samples collected, and different ranges of seasonal variation and environmental conditions experienced in these studies.

Previous studies were based on culture-based methods. Although there is a discussion over the value and need of using culture-based techniques *vs*. culture-independent approaches, methods frequently used today to obtain inventory of the diversity present in the intestine, it is apparent that viable cells are valuable to culture collections, in vaccine production, and as probiotics and synbiotics.

Probiotics such as carnobacteria as potential growth promotor, improve health and wellbeing and without harmful effects on the host require more research to ensure positive outcome. In terms of functional characteristics, probiotic carnobacteria must possess tolerance to the GI environment and the ability to adhere and colonize to intestinal epithelial cells. Antagonistic effects against pathogens, the possibility of large-scale production, and genetic stability also need to be addressed. To be considered a true probiotic, strains need to meet safety criteria, and be isolated from suitable habitats, screened for phenotype and genotype pathogenicity, be identified, and characterized, and tested for antimicrobial susceptibilities.

Most of the probiotics used in aquaculture are derived from terrestrial sources and not from the host animal or the environment. During the last years the use of "*host-associated probiotics*" has gained attention, as an alternative strategy within aquaculture (Van Doan et al., 2020), which per se is dependent on the use of terrestrial microorganisms. When discussing "*host-associated probiotics*" in aquatic animals an interesting topic arises. Are there differences in colonization pattern, ability of probiotics to colonize the GI tract, between larvae and adult fish as Ringø (1999) revealed that *C. divergens* Lab01 isolated from adult Atlantic salmon colonize the gut of early developing turbot larvae. As no conclusion can be drawn per se on permanent colonization, this topic merits further investigations.

Several studies have reported *in vitro* growth inhibition of pathogens by carnobacteria (Askarian et al., 2012; Jöborn et al., 1999; Ringø, 2000; Ringø et al., 2006; Robertson et al., 2000; Strøm, 1988). However, when testing the probiotic potential of a given bacteria species, one cannot fully rely on *in vitro* growth inhibition of a pathogen to predict an *in vivo* effect. Carrying out challenge studies is a must.

LAB and their bacteriocins are alternatives to chemicals and antibiotics as antimicrobial activities toward pathogens, and the use of bacteriocinogenic bacterial strains may be excellent candidates for a sustainable aquaculture, as bacteriocins can be an alternative to antibiotic. For a deeper understanding of the mechanisms of action of bacteriocin producing carnobacteria on host mucosal immunity, further studies are necessary.

Comparing to existing studies on other LAB species, there are a significant gap in the knowledge to date, regarding pathogenic carnobacteria as approximately 13.5% of the available articles on *Carnobacterium* involved in pathogenesis were published in the last three years (2020–2022). This indicates a persistent lack of research in this field and further studies are needed.

Conflict of interest

There is no conflict of interest.

References

Afzal, M. I., Jacquet, T., Delauney, S., Borges, F., Millière, J.-B., Revol-Junelles, A.-M., et al. (2010). *Carnobacterium maltaromaticum*: Identification, isolation tools, ecology and technological aspects in dairy products. *Food Microbiology, 22*, 573–579. https://doi.org/10.1016/j.fm.2010.03.019

Ahn, C., & Stiles, M. E. (1990). Plasmid associated bacteriocin production by a strain of *Carnobacterium piscicola* from meat. *Applied and Environmental Microbiology, 56*(8), 2503–2510. https://doi.org/10.1128/AEM.56.8.2503-2510.1990

Al Bulushi, I. M., Poole, S. E., Barlow, R., Deeth, H. C., & Dykes, G. A. (2010). Speciation of Gram-positive bacteria in fresh and ambient-stored sub-tropical marine fish. *International Journal of Food Microbiology, 138*(1–2), 32–38. https://doi.org/10.1016/j.ijfoodmicro.2009.11.021

Al-Hisnawi, A., Ringø, E., Davies, S. J., Waines, P., Bradley, G., & Merrifield, D. L. (2015). First report on the autochthonous gut microbiota of brown trout (*Salmo trutta*). *Aquaculture Research, 46*, 2962–2971. https://doi.org/10.1111/are.12451

Alvarez, J., Austin, B., & Reyes, H. (1995). An outbreak of lactobacillosis (Pseudokidney disease) in farmed rainbow trout *(Oncorhynchus mykiss*, Walbaum) in Venezuela. *Bulletin of European Fish Pathology, 15*(6), 200–201.

Askarian, F., Sperstad, S., Merrifield, D. L., Ray, A. K., & Ringø, E. (2013). The effect of different feeding regimes on enzyme activities of gut microbiota in Atlantic cod (*Gadus morhua* L.). *Aquaculture Research, 44*, 841–846. https://doi.org/10.1111/j.1365-2109.2010.03079x

Askarian, F., Zhou, Z., Olsen, R. E., Sperstad, S., & Ringø, E. (2012). Culturable autochthonous gut bacteria in Atlantic salmon (*Salmo salar* L.) fed diets with or without chitin. Characterization by 16S rRNA gene sequencing, ability to produce enzymes and *in vitro* growth inhibition of for fish pathogens. *Aquaculture, 326–329*, 1–8. https://doi.org/10.1016/j.aquaculture.2011.10.016

Bakke-McKellep, A. M., Penn, M. H., Salas, P. M., Refstie, S., Sperstad, S., Landsverk, T., et al. (2007). Effects of dietary soybean meal, inulin and oxytetracycline on gastrointestinal histological characteristics, distal intestine cell proliferation and intestinal microbiota in Atlantic salmon (*Salmo salar* L.). *British Journal of Nutrition, 97*, 699–713. https://doi.org/10.1017/S0007114507381397

Balcázar, J. L., de Blas, I., Ruiz-Zarzuela, I., Vendrell, D., Gironés, O., & Muzquiz, J. L. (2007). Sequencing of variable regions of the 16S rRNA gene for identification of lactic acid bacteria isolated from the intestinal microbiota of healthy salmonids. *Comparative Immunology, Microbiology and Infectious Diseases, 30*, 111–118. https://doi.org/10.1111/j.cimid.2006.12.001

Baya, A. M., Toranzo, A. E., Lupiani, B., Li, T., Roberson, B. S., & Hetrick, F. M. (1991). Biochemical and serological characterization of *Carnobacterium* spp. isolated from farmed and natural populations of stripped bass and catfish. *Applied and Environmental Microbiology, 57*, 3114–3120.

Bruni, L., Pastorelli, R., Viti, C., Gasco, L., & Parisi, G. (2018). Characterisation of the intestinal microbial communities of rainbow trout (*Oncorhynchus mykiss*) fed with Hermetia illucens (black soldier fly) partially defatted larva meal as partial dietary protein source. *Aquaculture, 487*, 56–63. https://doi.org/10.1016/j.aquaculture.2018.01.006

Cantas, L., Fraser, T. W. K., Fjelldal, P. G., Mayer, I., & Sørum, H. (2011). The culturable intestinal microbiota of triploid and diploid juvenile Atlantic salmon (*Salmo salar*) – a comparison of composition and drug resistance. *BMC Veterinary Research, 7*, 71. http://www.biomedcentral.com/1746-6148/7/71.

Cao, Y., Yang, X.-Z., Zhang, L.-J., Li, M., & Yuan, M.-L. (2021). Gut bacteria communities different between *Gynaephora* species endemic to different altitudes of the Tibetan Plateau. *Science of the Total Environment, 777*, Article 146115. https://doi.org/10.1016/j.scitotenv.2021.146115

Chitambo, B., Munyeme, M., & Hang'ombe, B. (2023). Identifying bacteria with public health significance from farmed Nile tilapia (*Oreochromis niloticus*), Zambia. *International Journal of Microbiology*. https://doi.org/10.1155/2023/6650378

Collins, M. D., Farrow, A. E., Phillips, B. A., Ferusu, S., & Jones, D. (1987). Classification of *Lactobacillus divergens, Lactobacillus piscicola* and some catalase-negative, asporogenous, rod-shaped bacteria from poultry in a new genus, *Carnobacterium. International Journal of Systematic Bacteriology, 37*(4), 310–316.

Contente, D., Díaz-Rosales, P., Feito, J., Díaz-Formoso, L., Docando, F., Simón, R., et al. (2023). Immunumodulatory effects of bacteriocinogenic and non-bacteriocinogenic Lactococcus cremoris of aquatic origin on rainbow trout (*Oncorhynchus mykiss*, Walbaum). *Frontiers in Immunology, 14*, Article 1178462, 103389/fimmu.2013.1178462.

Dehler, C. E., Secombes, C. J., & Martin, S. A. M. (2017a). Environmental and physiological factors shape the gut microbiota of Atlantic salmon parr (*Salmo salar* L.). *Aquaculture, 467*, 149–157. https://doi.org/10.1016/j.aquaculture.2016.07.017

Dehler, C. E., Secombes, C. J., & Martin, S. A. M. (2017b). Seawater transfer alters the intestinal microbiota profiles of Atlantic salmon parr (*Salmo salar* L.). *Scientific Reports, 7*, Article 13877. https://doi.org/10.1038/s41598-017-13249-8

Desai, A. R., Links, M. G., Collins, S. A., Mansfield, G. S., Drew, M. D., Van Kessel, A. G., et al. (2012). Effects of plant-based diets on the distal gut microbiome of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture, 350–353*, 134–142. https://doi.org/10.11016/j.aquaculture.2012.05.005

Desriac, F., Defer, D., Bourgougnon, N., Brillet, B., Le Chevalier, P., & Fleury, Y. (2010). Bacteriocin as weapons in the marine animal-associated bacteria warfare: Inventory and potential applications as an aquaculture probiotic. *Marine Drugs, 8*, 1153–1177. https://doi.org/10.3390/md8041153

Evangelista, A. G., Danielski, G. M., Feijó Corrêa, J. A., de Andrade Cavalari, C. M., Ramos Souza, I., Bittencourt Luciano, F., et al. (2022). *Carnobacterium* as a bioprotective and potential probiotic culture to improve food quality, food safety, and human health – a scoping review. *Critical Reviews in Food Science and Nutrition, early view*. https://doi.org/10.1080/10408398.2022.2038079

Fogarty, C., Burgess, C. M., Cotter, P. D., Cabrera-Rubio, R., Whyte, P., Smyth, C., et al. (2019). Diversity and composition of the gut microbiota of Atlantic salmon (*Salmo salar*) farmed in Irish waters. *Journal of Applied Microbiology, 127*, 648–657. https://doi.org/10.1111/jam.14291

Franzmann, P. D., Höpfl, P., Weiss, N., & Tindall, B. J. (1991). Psychrotrophic, lactic acid-producing bacteria from anoxic waters in Ace Lake, Antarctica; *Carnobacterium funditum* sp. nov. and *Carnobacterium alterfunditum* sp. nov. *Archives of Microbiology, 156*(4), 255–262. https://doi.org/10.1007/BF00262994

Gajardo, K., Jaramillo-Torres, A., Kortner, T. M., Merrifield, D. L., Tinsley, J., Bakke, A. M., et al. (2017). Alternative protein sources in the diet modulate microbiota and functionality in the distal intestine of Atlantic salmon (*Salmo salar*). *Applied and Environmental Microbiology, 83*, Article e02615. https://doi.org/10.1128/AEM.02615-16

Garcés, M. E., Olivera, N. L., Fernández, M., Rossi, C. R., & Sequeiros, C. (2020). Antimicrobial activity of bacteriocin-producing *Carnobacterium* spp. isolated from healthy Patagonian trout and their potential for use in aquaculture. *Aquaculture Research, 51*, 4602–4612. https://doi.org/10.1111/are.14806

Gildberg, A., Johansen, A., & Bøgwald, J. (1995). Growth and survival of Atlantic salmon (*Salmo salar*) fry given diets supplemented with fish protein hydrolysate and lactic acid bacteria during a challenge trial with *Aeromonas salmonicida*. *Aquaculture, 138*, 23–34. https://doi.org/10.1016/0044-8486(95)01144-7

Gildberg, A., & Mikkelsen, H. (1998). Effects of supplementing the feed to Atlantic cod (*Gadus morhua*) fry with lactic acid bacteria and immune-stimulating peptides during a challenge trial with *Vibrio anguillarum*. *Aquaculture, 167*, 101–113. https://doi.org/10.1016/S0044-8486(98)00296-8

Gildberg, A., Mikkelsen, H., Sandaker, E., & Ringø, E. (1997). Probiotic effect of lactic acid bacteria in the feed on growth and survival of fry of Atlantic cod (*Gadus morhua*). *Hydrobiologia, 352*(1/3), 279–285. https://doi.org/10.1023/A:1003052111938

Goals, I., & Potorski, J. (2022). The influence of commercial feed supplemented with *Carnobacterium maltaromaticum* environmental probiotic bacteria on the rearing parameters and microbial safety of juvenile rainbow trout. *Animals, 12*, 3321. https://doi.org/10.3390/ani12233321

González, C. J., Encinas, J. P., García-López, M. L., & Otero, A. (2000). Characterization and identification of lactic acid bacteria from freshwater fishes. *Food Microbiology, 17*, 383–391. https://doi.org/10.1006/fmic.1999.0330

González, C. J., García-López, T.-M., García-López, M.-L., & Otero, A. (1999). Bacterial microflora of wild brown trout (*Salmo trutta*), wild pike (*Esox lucius*), and aquacultured rainbow trout (*Oncorhynchus mykiss*). *Journal of Food Protection, 62*(11), 1270–1277. https://doi.org/10.4315/0362-028X-62.11.1270

Hagi, T., Tanaka, D., Iwamura, Y., & Hoshino, T. (2004). Diversity and seasonal changes in lactic acid bacteria in the intestinal tract of culture freshwater fish. *Aquaculture, 234*, 335–346. https://doi.org/10.1016/j.aquaculture.2004.01.018

Hammes, W. P., & Hertel, C. (2006). The genera *Lactobacillus* and Carnobacterium. In M. Dworkin, S. Falkow, E. Rosenberg, K.-H. Schleifer, & E. Stackebrandt (Eds.), *The prokaryotes. A handbook on the Biology of bacteria". Third edition. Volume 4: Bacteria, Firmicutes, Cyanobacteria* (Vol. 4, pp. 320–403). Singapore: Springer. https://doi.org/10.1007/0-387-30744-3_10.

Hartviksen, M., Gonzalez Vecino, J. L., Kettunen, A., Myklebust, R., Ruohonen, K., Wadsworth, S., et al. (2015). Probiotic and pathogen *ex vivo* exposure of Atlantic salmon (*Salmo salar* L.) intestine from fish fed four different protein sources. *Journal of Aquaculture Research & Development, 6*, 340. https://doi.org/10.4172/2155-9546.1000340

Hiu, S. F., Holt, R. A., Sriruganathan, N., Seidler, R. J., & Fryer, J. L. (1984). *Lactobacillus piscicola*, a new species from salmonid fish. *International Journal of Systematic Bacteriology, 34*, 393–400.

Huber, I., Spanggaard, B., Appel, K. F., Rossen, L., Nielsen, T., & Gram, L. (2004). Phylogenetic analysis and in situ identification of the intestinal microbial community of rainbow trout (*Oncorhynchus mykiss*, Walbaum). *Journal of Applied Microbiology, 96*, 117–132. https://doi.org/10.1046/j.1365-2672.2003.02109.x

Humphrey, J., Lancaster, C. E., Gudkovs, N., & Copland, J. W. (1987). The disease status of Australian salmonids: Bacteria and bacterial diseases. *Journal of Fish Diseases, 10*(5), 403–410. https://doi.org/10.1111/j.1365-2761.1987.tb01088.x

Iorizzo, M., Albanese, G., Testa, B., Ianiro, M., Letizia, F., Succi, M., et al. (2021). Presence of lactic acid bacteria in the intestinal tract of the Mediterranean trout (*Salmo macrostigma*) in its natural environment. *Life, 11*, 667. https://doi.org/10.3390/life11070667

Irianto, I., & Austin, B. (2002). Use of probiotics to control furunculosis in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases, 25*, 333–342. https://doi.org/10.1046/j.1365-2761.2002.00375.x

Irianto, I., & Austin, B. (2003). Use of dead probiotics to control furunculosis in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases, 26*, 59–62. https://doi.org/10.1046/j.1365-2761.2003.00414.x

Iskandar, C. F., Borges, F., Taminiau, B., Daube, G., Zagorec, M., Remenant, B., et al. (2017). Comparative genomic analysis reveals ecological differentiation in the genus *Carnobacterium*. *Frontiers in Microbiology, 8*, 311–340. https://doi.org/10.3389/fmicb.2017.00357

Jang, W. E., Jeon, M.-H., Lee, S.-J., Park, S. Y., Lee, Y.-S., Noh, D.-I., et al. (2022). Dietary supplementation of *Bacillus* sp. PM8313 with B-glucan modulates the intestinal microbiota of red sea bream (*Pagrus major*) to increase growth, immunity, and disease resistance. *Frontiers in Immunology, 13*, Article 960554. https://doi.org/10.3389/fimmu.2022.960554

Jöborn, A., Dorsch, M., Olsson, C., Westerdahl, A., & Kjelleberg, S. (1999). Carnobacterium inhibens sp. nov., isolated from the intestine of Atlantic salmon (*Salmo salar* L.). *International Journal of Systematic Bacteriology, 49*, 1891–1898. https://doi.org/10.1099/00207713-49-4-1891

Jöborn, A., Olsson, C., Westerdahl, A., Conway, P. L., & Kjelleberg, S. (1997). Colonization in the fish intestinal tract and production of inhibitory substances in intestinal mucus and faecal extracts by *Carnobacterium* sp. strain K1. *Journal of Fish Diseases, 20*, 383–392. https://doi.org/10.1046/j.1365-2761.1997.00316.x

Kazlauskaite, R., Cheaib, B., Humble, J., Heys, C., Ijaz, U. Z., Connelly, S., et al. (2022). Deploying an *in vitro* gut model to assay the impact of the mannan-oligosaccharide prebiotic Bio-Mos on the Atlantic salmon (*Salmo salar*) gut microbiome. *Microbiology Spectrum, 10*(3). https://doi.org/10.1128/spectrum.01953-21

Kim, D.-H., & Austin, B. (2006a). Innate immune responses in rainbow trout (*Oncorhynchus mykiss*, Walbaum) induced by probiotics. *Fish & Shellfish Immunology, 21*(5), 513–524. https://doi.org/10.1016/j.fsi.2006.02.007

Kim, D. H., & Austin, B. (2006b). Cytokine expression in leucocytes and gut cells of rainbow trout, *Oncorhynchus mykiss* Walbaum, induced by probiotics. *Veterinary Immunology and Immunopathology, 114*, 297–304. https://doi.org/10.1016/j.vetimm.2006.08.015

Kim, D. H., & Austin, B. (2008). Characterization of probiotic carnobacteria isolated from rainbow trout (*Oncorhynchus mykiss*) intestine. *Letters in Applied Microbiology, 47*, 141–147. https://doi.org/10.1111/j.1472-765X.2008.02401.x

Kim, D. H., Brunt, J., & Austin, B. (2007). Microbial diversity of intestinal contents and mucus in rainbow trout (*Oncorhynchus mykiss*). *Journal of Applied Microbiology, 102*, 1654–1664. https://doi.org/10.1111/j.1365-2672.2006.03185

Knobloch, S., Skirrnisdottir, S., Dubois, M., Kolypczuk, L., Leroi, F., Leeper, A., et al. (2022). Impact of putative probiotics on growth, behavior, and gut microbiome of

farmed Arctic charr (*Salvelinus alpinus*). *Frontiers in Microbiology, 13*, Article 912473. https://doi.org/10.3389/fmic.2022.912473

Knoop, K., & Newberry, R. D. (2018). Goblet cells: Multifaceted players in immunity at mucosal surfaces. *Mucosal Immunity, 11*, 1551–1557. https://doi.org/10.1038/s41385-018-0039-y

Kozasa, M. (1986). Toyocerin *Bacillus toyoi* as growth promotor for animal feeding. *Microbiologie, Aliments, Nutrition, 4*, 121–135.

Kristiansen, M., Merrifield, D. L., Gonzalez Vecino, J. L., Myklebust, R., & Ringø, E. (2011). Evaluation of prebiotic and probiotic effects on the intestinal gut microbiota and histology of Atlantic salmon (*Salmo salar* L.). *Journal of Aquaculture Research & Development, S1*. https://doi.org/10.4172/2155-9546.S1-009, 009.

Lambuk, F., Mazlan, N., Thung, T. Y., New, C. Y., Rinai, K. R., & Son, R. (2022). A review of lactic acid bacteria isolated from marine animals: Their species, isolation site and applications. *Food Research, 6*(1), 311–323. https://doi.org/10.26656/fr.2017.6(1).112

Lauzon, H. L., & Ringø, E. (2011). Prevalence and application of lactic acid bacteria in Aquatic Environments. In S. Lahtinen, A. Ouwehand, S. Salminen, & A. von Wright (Eds.), *Lactic acid bacteria: Microbiological and functional aspects* (4th ed., pp. 593–631). New York: CRC Press, Taylor and Francis Group.

Leisner, J. J., Laursen, B. G., Prévost, H., Drider, D., & Dalgaard, P. (2007). *Carnobacterium*: Positive and negative effects in the environment and in foods. *FEMS Microbiology Reviews, 31*, 592–613. https://doi.org/10.1111/j.1574-6976.2007.00080.x

Lilly, D. M., & Stillwell, R. H. (1965). Probiotics: Growth promoting factors produced by microorganisms. *Science, 147*, 747–748.

Li, H., Lu, L., Chen, R., Li, S., & Xu, D. (2022). Exploring sexual dimorphism in the intestinal microbiota of the yellow drum (*Nibea albiflora*, Sciaenidae). *Frontiers in Microbiology, 12*, Article 808285. https://doi.org/10.3389/fmicro.2021.808285

Loch, T. P., Kumar, R., Xu, W., & Faisal, M. (2011). *Carnobacterium maltaromaticum* infections in feral *Oncorhynchus* spp. (Family Salmonidae) in Michigan. *Journal of Microbiology, 49*(5), 703–713. https://doi.org/10.10007/s12275-011-0527-1

Loch, T. P., Scribner, K., Tempelman, R., Whelan, G., & Faisal, M. (2012). Bacterial infections of Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), returning to gamete collecting weirs in Michigan. *Journal of Fish Diseases, 35*, 39–50. https://doi.org/10.1111/j.1365-2761.2011.01322.x

Loch, T. P., Xu, W., Fitzgerald, S. M., & Faisal, M. (2008). Isolation of a *Carnobacterium maltaromaticum*-like bacterium from systemically infected lake whitefish (*Coregonus clupeaformis*). *FEMS Microbiology Letters, 288*, 76–84. https://doi.org/10.1111/j.1574-6968.2008.01338.x

Lo, C. K.-L., & Sheth, P. M. (2021). *Carnobacterium inhibens* isolated in blood culture of an immunocompromised, metastatic cancer patient: A case report and literature review. *BMC Infectious Diseases, 21*, 403. https://doi.org/10.1186/s12879-021-06095-7

Løvmo Martinsen, L., Salma, W., Myklebust, R., Mayhew, T. M., & Ringø, E. (2011). *Carnobacterium maltaromaticum vs. Vibrio* (*Listonella*) *anguillarum* in the midgut of Atlantic cod (*Gadus morhua* L.): An *ex vivo* study. *Aquaculture Research, 42*, 1830–1839. https://doi.org/10.1111/j.1365-2109.2010.02784.x

Lyons, P. P., Turnbull, J. F., Dawson, K. A., & Crumlish, M. (2017). Exploring the microbial diversity of the distal lumen and mucosa of farmed rainbow trout *Oncorhynchus mykiss* (Walbaum) using next generation sequencing (NGS). *Aquaculture Research, 48*, 77–91. https://doi.org/10.1111/are.12863

Mansfield, G. S., Desai, A. R., Nilson, S. A., Van Kessel, A. G., Drew, M. D., & Hill, J. E. (2010). Characterization of rainbow trout (*Oncorhynchus mykiss*) intestinal microbiota and inflammatory marker gene expression in a recirculating aquaculture system. *Aquaculture, 307*, 95–104. https://doi.org/10.1016/j.aquaculture.2010.07.014

Mauguin, S., & Novel, G. (1994). Characterization of lactic acid bacteria isolated from seafood. *Journal of Applied Bacteriology, 76*, 616–625.

Mazurkiewicz, J., Przyby, A., Sip, A., & Grajek, W. (2007). Effect of *Carnobacterium divergens* and *Enterococcus hirae* as probiotic bacteria in feed for common carp, *Cyprinus carpio* L. *Archives of Polish Fisheries, 15*(2), 93–102.

Merrifield, D. L., Balcázar, J. L., Daniels, C. L., Zhou, Z., Carnevali, O., Sun, Y. Z., et al. (2014). Indigenous lactic acid bacteria in fish and crustaceans. In D. Merrifield, & E. Ringø (Eds.), *Aquaculture nutrition: Gut health, probiotics and prebiotics* (pp. 128–168). Oxford, UK: Wiley-Blackwell Publishing.

Miao, S., Zhao, C., Zhu, J., Hu, J., Dong, X., & Sun, L. (2018). Dietary soybean meal affects intestinal homoeostasis by altering the microbiota, morphology and inflammation cytokine gene expression in northern snakehead. *Scientific Reports, 8*, 113. https://doi.org/10.1038/s41598-017-18430-7

Montel, M.-C., Talon, R., Fournad, J., & Champomier, M.-C. (1991). A simplified key for identifying homofermentative *Lactobacillus* and *Carnobacterium* spp. from meat. *Journal of Applied Bacteriology, 70*, 469–472.

Neuman, C., Hatje, E., Zarkasi, K., Smullen, R., Bowman, J. P., & Katouli, M. (2016). The effect of diet and environmental temperature on faecal microbiota of farmed Tasmanian Atlantic salmon (*Salmo salar* L.). *Aquaculture Research, 47*, 660–672. https://doi.org/10.1111/are.12522

Olsen, R. E., Myklebust, R., Kryvi, H., Mayhew, T. M., & Ringø, E. (2001). Damaging effect of dietary inulin to intestinal enterocytes in Arctic charr (*Salvelinus alpinus* L.). *Aquaculture Research, 32*, 931–934. https://doi.org/10.1046/j.1365-2109.2001.00626.x

Ottesen, O. H., & Olafsen, J. A. (2000). Effects of survival and cell proliferation of Atlantic halibut, *Hippoglossus hippoglossus* L., larvae following microflora manipulation. *Aquaculture, 187*, 225–238. https://doi.org/10.1016/S0044-8486(00)00314-8

Ozen, M., & Dinleyici, E. C. (2015). The history of probiotics: The untold story. *Beneficial Microbes, 6*(2), 159–165. https://doi.org/10.3920/BM2014.0103

Pastorino, P., Colussi, S., Pizzul, E., Varello, K., Menconi, V., Mugetti, D., et al. (2021). The unusual isolation of carnobacteria in eyes of healthy salmonids in high-mountain lakes. *Scientific Reports, 22*, 2314. https://doi.org/10.1038/s41598-021-82133-3

Pereira, W. A., Mendonca, C. M. N., Villasante Urquiza, A., Marteinsson, V. P., Guy LeBlanc, J., Cotter, P. D., et al. (2022). Use of probiotic bacteria and bacteriocins as alternative to antibiotics in aquaculture. *Microorganisms, 10*, 1705. https://doi.org/10.3390/microorganisms10091705

Pietsch, C., Tschudi, F., Baumann, S., & Schmidt-Posthaus, H. (2020). Preliminary investigation of an idiopathic muscle disease in farmed burbot *Lota lota*. *Diseases of Aquatic Organisms, 140*, 179–186. https://doi.org/10.3354/dao03494

Pilet, M. F., Xavier, D., Rachel, B., Georges, N., Michel, D., & Piard, J. C. (1995). Evidence for two bacteriocins produced by *Carnobacterium piscicola* and *Carnobacterium divergens* isolated from fish and active against *Listeria monocytogenes*. *Journal of Food Protection, 58*, 256–262. https://doi:10.4315/0362-028X-58.3.256.

Pond, M. J., Stone, D. M., & Alderman, D. J. (2006). Comparison of conventional and molecular techniques to investigate the intestinal microflora of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture, 261*, 194–203. https://doi.org/10.1016/j.aquaculture.2006.06.037

Puvanendran, V., Rud, I., Breiland, M. S. W., Arnesen, J. A., & Axelsson, L. (2021). Probiotic *Carnobacterium divergens* increase growth parameters and disease resistance in farmed Atlantic cod (*Gadus morhua*) larvae without influencing the microbiota. *Aquaculture, 532*, Article 736072. https://doi.org/10.1016/j.aquaculture.2020.736072

Ringø, E. (1999). Does *Carnobacterium divergens* isolated from Atlantic salmon (*Salmo salar* L.) colonise the gut of early developing turbot (*Scophthalmus maximus* L.) larvae? *Aquaculture Research, 30*, 229–232. https://doi.org/10.1046/j.1365-2109.1999.00269.x

Ringø, E. (2000). Lactic acid bacteria in fish: Antibacterial effect against fish pathogens. In Å. Krogdahl, S. D. Mathiesen, & I. Pryme (Eds.), *Cost 98: Vol. 8. Effects of antinutrients on the nutritional value of legume diets* (pp. 70–75). Luxembourg: EEC Publication.

Ringø, E. (2004). Lactic acid bacteria in fish and fish farming. In S. Salminen, A. Ouwehand, & A. von Wrigth (Eds.), *Lactic acid bacteria* (pp. 581–610). New York: Marcel Dekker Inc.

Ringø, E. (2008). The ability of carnobacteria isolated from fish intestine to inhibit growth of fish pathogenic bacteria: A screening study. *Aquaculture Research, 39*, 171–180. https://doi.org/10.1111/j.1365-2109.2007.01876.x

Ringø, E., Bendiksen, H. R., Gausen, S., Sundsfjord, A., & Olsen, R. E. (1998). The effect of dietary fatty acids on lactic acid bacteria associated with the epithelial mucosa and from faecalia of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Applied Microbiology, 85*, 855–864. https://doi.org/10.1046/j.1365-2672.1998.00595.x

Ringø, E., Bendiksen, H. R., Wesmajervi, M. S., Olsen, R. E., Jansen, P. A., & Mikkelsen, H. (2000). Lactic acid bacteria associated with the digestive tract of Atlantic salmon (*Salmo salar* L.). *Journal of Applied Microbiology, 89*, 317–322. https://doi.org/10.1046/j.1365-2672.2000.01116.x

Ringø, E., & Gatesoupe, F. J. (1998). Lactic acid bacteria in fish: A review. *Aquaculture, 160*, 177–203. https://doi.org/10.1016/S0044-8486(97)00299-8

Ringø, E., Hoseinifar, S. H., Ghosh, K., Van Doan, H., Beck, B. R., & Song, S. K. (2018). Lactic acid bacteria in finfish – an update. *Frontiers in Microbiology, 9*, 1818. https://doi.org/10.3389/fmib.2018.01818

Ringø, E., Lødemel, J. B., Myklebust, R., Jensen, L., Lund, V., Mayhew, T. M., et al. (2002). Effect of soybean, linseed and marine oils on aerobic gut microbiota of Arctic charr *Salvelinus alpinus* L. before and after challenge with *Aeromonas salmonicida* ssp. *Salmonicida. Aquaculture Research, 33*(8), 591–606. https://doi.org/10.1046/j.1365-2109.2002.00697.x

Ringø, E., Løvmo, L., Kristiansen, M., Salinas, I., Myklebust, R., Olsen, R. E., et al. (2010). Lactic acid bacteria *vs.* pathogens in the gastrointestinal tract of fish: A review. *Aquaculture Research, 41*, 451–467. https://doi.org/10.1111/j.1365-2109.2009.02339.x

Ringø, E., & Olsen, R. E. (1999). The effect of diet on aerobic bacterial flora associated with intestine of Arctic charr (*Salvelinus alpinus* L.). *Journal of Applied Microbiology, 86*, 22–28. https://doi.org/10.1046/j.1365-2672.1999.00631.x

Ringø, E., Olsen, R. E., Øverli, Ø., & Løvik, F. (1997). Effect of dominance hierarchy formation on aerobic microbiota associated with epithelial mucosa of subordinate and dominant individuals of Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture Research, 28*, 901–904.

Ringø, E., Salinas, I., Olsen, R. E., Nyhaug, A., Myklebust, R., & Mayhew, T. M. (2007). Histological changes in Atlantic salmon (*Salmo salar* L.) intestine following *in vitro* exposure to pathogenic and probiotic bacterial strains. *Cell and Tissue Research, 328*, 109–116. https://doi.org/10.1007/s00441-006-0323-0

Ringø, E., Seppola, M., Berg, A., Olsen, R. E., Schillinger, U., & Holzapfel, W. (2002). Characterization of *Carnobacterium divergens* strain 6251 isolated from intestine of Arctic charr (*Salvelinus alpinus* L.). *Systematic & Applied Microbiology, 25*(1), 120–129. https://doi.org/10.1078/0723-2020-00080

Ringø, E., Sperstad, S., Kraugerud, O. F., & Krogdahl, Å. (2008). Use of 16S rRNA gene sequencing analysis to characterise culturable intestinal bacteria in Atlantic salmon (*Salmo salar* L.) fed diets with non-starch polysaccharides from soy and cellulose. *Aquaculture Research, 39*, 1087–1100. https://doi.org/10.1111/j.1365-2109.2008.01972.x

Ringø, E., Sperstad, S., Myklebust, R., Refstie, S., & Krogdahl, Å. (2006). Characterisation of the microbiota associated with the intestine of Atlantic cod (*Gadus morhua* L.). The effect of fish meal, soybean meal and a bioprocessed soybean meal. *Aquaculture, 261*, 829–841. https://doi.org/10.1016/j.aquaculture.2006.06.030

Ringø, E., Sperstad, S., Myklebust, R., Mayhew, T. M., & Olsen, R. E. (2006). The effect of dietary inulin on bacteria associated with hindgut of Arctic charr (*Salvelinus alpinus*

L.). *Aquaculture Research, 37*, 891–897. https://doi.org/10.1111/j.1365-2109.2006.01509.x

Ringø, E., Sperstad, S., Myklebust, R., Mayhew, T. M., Mjelde, A., Melle, W., et al. (2006). The effect of dietary krill supplementation on epithelium-associated bacteria in the hindgut of Atlantic salmon (*Salmo salar* L.). A microbial and electron microscopical study. *Aquaculture Research, 37*, 1644–1653. https://doi.org/10.1111/j.1365-2109.2006.01611.x

Ringø, E., van Doan, H., Lee, S. H., Soltani, M., Hoseinifar, S. H., Ramasamy, H., et al. (2020a). Probiotics, lactic acid bacteria and bacilli: Interesting supplementation for aquaculture. *Journal of Applied Microbiology, 129*, 116–136. https://doi.org/10.1111/jam.14628

Ringø, E., van Doan, H., Lee, S., & Song, S. K. (2020b). Lactic acid bacteria in shellfish: Possibilities and challenges. *Reviews in Fisheries Science & Aquaculture, 28*(2), 139–169. https://doi.org/10.1080/23308249.2019.1683151

Ringø, E., Wesmajervi, M. S., Bendiksen, H. R., Berg, A., Olsen, R. E., Johnsen, T., et al. (2001). Identification and characterization of carnobacteria isolated from fish intestine. *Systematic & Applied Microbiology, 24*, 183–191. https://doi.org/10.1078/0723-2020-00020

Ringø, E., Zhou, Z., Gonzalez Vecino, J. L., Wadsworth, S., Romero, J., Krogdahl, Å., et al. (2016). Effects of dietary components on the gut microbiota of aquatic animals: A never-ending story? *Aquaculture Nutrition, 22*, 219–282. https://doi.org/10.1111/anu12346

Robertson, P. A. W., O'Dowd, C., Burrells, C., Williams, P., & Austin, B. (2000). Use of *Carnobacterium* sp. as a probiotic for Atlantic salmon (*Salmo salar* L.) and rainbow trout (*Oncorhynchus mykiss*, Walbaum). *Aquaculture, 185*, 235–243. https://doi.org/10.1016/S0044-8486(99)00349-X

Roh, H. J., Kim, B. S., Lee, M. K., Park, C.-I., & Kim, D.-H. (2020). Genome-wide comparison of *Carnobacterium maltaromaticum* derived from diseased fish harbouring important virulence-related genes. *Journal of Fish Diseases, 43*, 1029–1037. https://doi.org/10.1111/jfd.13208

Romero, J., Díaz, O., Miranda, C. D., & Rojas, R. (2022). Red cusk-eel (*Genypterus chilensis*) gut microbiota description of wild and aquaculture specimens. *Microorganisms, 10*, 105. https://doi.org/10.3390/microorganisms10010105

Rudi, K., Angell, I. L., Pope, P. B., Vik, J. O., Sandve, S. R., & Snipen, L.-G. (2018). Stable core gut microbiota across the freshwater-to saltwater transition for farmed Atlantic salmon. *Applied and Environmental Microbiology, 84*, Article e01974-17. https://doi.org/10.1128/AEM.01974-17

Sahnouni, F., Ringø, E., Maizi, A., Benmaghnia, S., Matallah-Boutiba, A., Chemlal, D., et al. (2016). Biochemical and antibacterial potential of autochthonous *Carnobacterium* and *Lactobacillus* species isolated from gastrointestinal tract of coastal fish. *The Journal of Animal and Plant Sciences, 26*, 1146–1155.

Salas-Leiva, J., Opazo, R., Remond, C., Uribe, E., Velez, A., & Romero, J. (2017). Characterization of the intestinal microbiota of wild-caught and farmed fine flounder (*Paralichthys adspersus*). *Latin American Journal of Aquatic Research, 45*(2), 370–378. https://doi.org/10.3856/vol45-issue2-fulltext-12

Sandlund, N., & Bergh, Ø. (2008). Screening and characterisation of potentially pathogenic bacteria associated with Atlantic cod *Gadus morhua* larvae: Bath challenge trials using a multidish system. *Diseases of Aquatic Organisms, 81*, 203–217. https://doi.org/10.3354/dao01934

Santos, Y., Bandin, I., Nunez, S., Montero, M., Silva, A., & Toranzo, A. E. (1992). Comparison of the extracellular biological activities of *Vibrio anguillarum* and *Aeromonas hydrophila*. *Aquaculture, 107*(2–3), 259–270. https://doi.org/10.1016/0044-8486(92)90075-V

Schillinger, U., & Holzapfel, W. H. (1995). The genus *Carnobacterium*. In B. J. B. Wood, & W. H. Holzapfel (Eds.), *The genera of Lactic acid bacteria* (pp. 307–326). London: Chapman and Hall. https://doi.org/10.10007/978-1-4615-5817-0_9.

Seppola, M., Olsen, R. E., Sandaker, E., Kanapathippillai, P., Holzapfel, W., & Ringø, E. (2006). Random amplified polymorphic DNA (RAPD) polymerase chain reaction analysis of carnobacteria isolated from hindgut chamber and large intestine of Atlantic cod (*Gadus morhua* L.). *Systematic & Applied Microbiology, 29*, 131–137. https://doi.org/10.1016/j.syapm.2005.07.006

Sequeiros, C., Garcés, M. E., Fernández, M., Marcos, M., Castãos, C., Moris, M., et al. (2022). Zebrafish intestinal colonization by three lactic acid bacteria isolated from Patagonian fish provides evidence for their possible application as candidate probiotic in aquaculture. *Aquaculture International, 30*, 1389–1405. https://doi.org/10.1007/s10499-022-00864-0

Skrodenyte-Arbaciauskiene, V., Sruoga, A., & Butkauskas, D. (2006). Assessment of microbial diversity in the river trout *Salmo trutta fario* L. intestinal tract identified by partial 16S rRNA gene sequence analysis. *Fisheries Science, 72*, 597–602. https://doi.org/10.1111/j.1444-2906.2006.01189.x

Skrodenyte-Arbaciauskiene, V., Sruoga, A., Butkauskas, D., & Skrupskelis, K. (2008). Phylogenetic analysis of intestinal bacteria of freshwater salmon *Salmo salar* and sea trout *Salmo trutta trutta* and diet. *Fisheries Science, 74*, 1307–1314. https://doi.org/10.1111/j.1444-2906.2008.01656.x

Smith, S. A., Newman, S. J., Harrison, C. E., & Loch, T. P. (2023). First isolation of *Carnobacterium maltaromaticum* from farmed rainbow trout in Virginia. *Journal of Aquatic Animal Health, 35*, 3–10. https://doi.org/10.1002/aah.10176

Spanggaard, B., Huber, I., Nielsen, J., Nielsen, T., Appel, K. F., & Gram, L. (2000). The microflora of rainbow trout intestine: A comparison of traditional and molecular identification. *Aquaculture, 182*, 1–15. https://doi.org/10.1016/S0044-8486(99)00250-1

Spanggaard, B., Huber, I., Nielsen, J., Sick, E. B., Pipper, C. B., Martinussen, T., et al. (2001). The probiotic potential against vibriosis of the indigenous microflora of rainbow trout. *Environmental Microbiology, 3*, 755–765. https://doi.org/10.1046/j.1462-2920.2001.00240.x

Standish, I., McCann, R., Puzach, C., Leis, E., Bailey, J., Dziki, S., et al. (2022). Development of duplex qPCR targeting *Carnobacterium maltaromaticum* and *Vagococcus salmoninarum*. *Journal of Fish Diseases, 45*, 667–677. https://doi.org/10.1111/jfd.13592

Starliper, C. E., Shotts, E. B., & Brown, J. (1992). Isolation of *Carnobacterium piscicola* and an unidentified Gram-positive bacillus from sexually mature and post-spawning rainbow trout, *Oncorhynchus mykiss*. *Diseases of Aquatic Organisms, 13*, 181–187. https://doi.org/10.3354/dao013181

Stoffels, G., Nes, I. F., & Gudmundsdottir, A. (1992a). Isolation and properties of a bacterocin-producing *Carnobacterium piscicola* isolated from fish. *Journal of Applied Bacteriology, 73*(4), 309–316. https://doi.org/10.1111/j.1365-2672.1992.tb04982.x

Stoffels, G., Nissen-Meyer, J., Gudmundsdottir, A., Sletten, K., Holo, H., & Nes, I. F. (1992b). Purification and characterization of a new bacteriocin isolated from a *Carnobacterium* sp. *Applied and Environmental Microbiology, 58*(5), 1417–1422. https://doi.org/10.1128/AEM.58.5.1417-1422.1992

Stoffels, G., Sahl, H.-G., & Gudmundsdottir, A. (1993). Carnocin U149, a potential biopreservative produced by *Carnobacterium piscicola*: Large scale purification and activity against various gram-positive bacteria including *Listeria* sp. *International Journal of Food Microbiology, 20*, 199–210. https://doi.org/10.1016/0168-1605(93)90165-D

Strøm, E. (1988). *Melkesyrebakterier i fisketarm: Isolasjon, karakterisering og egenskaper [in Norwegian]*. Norway: The Norwegian College of Fishery Science, University of Tromsø. MSc thesis.

Strøm, E., & Ringø, E. (1993). Changes in the bacterial flora in early developing cod, *Gadus morhua* (L.) larvae after an inoculation of *Lactobacillus plantarum* in the water. In B. Walther, & H. J. Fyhn (Eds.), *Physiology and biochemical aspects of fish development* (pp. 226–228). Norway: University of Bergen, 1993. ISBN 82-992402-0-4.

Toranzo, A. E., Romalde, J. L., Nunez, S., Figueras, A., & Barja, J. L. (1993a). An epizootic in farmed, marked-size rainbow trout in Spain caused by a strain of *Carnobacterium piscicola* of unusual virulence. *Diseases of Aquatic Organisms, 17*, 87–99. https://doi.org/10.3354/dao017087

Toranzo, A. E., Novoa, B., Baya, A. M., Hetrick, F. M., Barja, J. L., & Figueras, A. (1993b). Histopathology of rainbow trout, *Oncorhynchus mykiss* Walbaum, and striped bass, *Morone saxatilis* Walbaum, experimentally infected with *Carnobacterium piscicola*. *Journal of Fish Diseases, 16*, 261–267. https://doi.org/10.1111/j.1365-2761.1993.tb01256.x

Ucko, M., & Colorni, A. (2014). Infections by lactic acid bacteria in marine fish from southern Israel (Red Sea): New Records. *Israeli Journal of Aquaculture – Bamidgeh, 66*, 939.

Van Doan, H., Hoseinifar, S. H., Ringø, E., Esteban, M.Á., Dadar, M., Dawood, M. A. O., et al. (2020). Host-associated probiotics: A key factor in sustainable aquaculture. *Reviews in Fisheries Science & Aquaculture, 28*(1), 16–42. https://doi.org/10.1080/23308249.2019.1643288

Van Tassell, M. L., & Miller, N. J. (2011). *Lactobacillus* adhesion to mucus. *Nutrients, 3*(5), 613–636. https://doi.org/10.3390/nu3050613

Verner-Jeffreys, D. W., Shields, R. J., & Birkbeck, T. H. (2003). Bacterial influence on Atlantic halibut *Hippoglossus hippoglossus* yolk-sac larval survival and start-feed response. *Diseases of Aquatic Organisms, 56*(2), 105–113. https://doi.org/10.3354/dao056105

Villasante, A., Ramírez, C., Rodrígues, H., Dantagnan, P., Herández, A., Figueroa, E., et al. (2022). Dietary carbohydrate-to-protein ratio influences growth performance, hepatic health and dynamic of gut microbiota in Atlantic salmon (*Salmo salar*). *Animal Nutrition, 10*, 261–279. https://doi.org/10.1016/j.anibu.2022.04.003

Voll Bugten, A., Kihle Attramadal, K. J., Olsen Fossmark, R., Rosten, T. W., Vadstein, O., & Bakke, I. (2022). Changes in rearing water microbiomes in RAS induced by membrane filtration alters the hindgut microbiomes of Atlantic salmon (*Salmo salar*) parr. *Aquaculture, 548*, Article 737661. https://doi.org/10.1016/j.aquaculture.2021.737661

Yang, P., Hu, H., Liu, Y., Li, Y., Ai, Q., Xu, W., et al. (2018). Dietary stachyose altered the intestinal microbiota profile and improved the intestinal mucosal barrier function of juvenile turbot. *Scophthalmus maximus L. Aquaculture, 486*, 98–106. https://doi.org/10.1016/j.aquaculture.2017.12.014

Zarkasi, K. Z., Abell, G. C. J., Taylor, R. S., Neuman, C., Hatje, E., Tamplin, M. L., et al. (2014). Pyrosequencing-based characterization of gastrointestinal bacteria of Atlantic salmon (*Salmo salar* L.) within a commercial mariculture system. *Journal of Applied Microbiology, 117*, 18–27. https://doi.org/10.1111/jam.12514

Zarkasi, K. Z., Taylor, R., Abell, G. C. J., Tamplin, M. L., Glencross, B. D., & Bowman, J. P. (2016). Atlantic salmon (*Salmo salar* L.) gastrointestinal microbial community dynamics in relation to digesta properties and diet. *Microbial Ecology, 71*, 589–603. https://doi.org/10.1007/s00248-015-0728-y

Zhang, Y., Li, Q., Li, D., Liu, X., & Luo, Y. (2015). Changes in the microbial communities of air-packaged and vacuum-packed common carp (*Cyprinus carpio*) stored at 4°C. *Food Microbiology, 52*, 197–204. https://doi.org/10.1016/j.fm.2015.08.003

Zhou, Z., Karlsen, Ø., He, S., Olsen, R. E., Yao, B., & Ringø, E. (2013). The effect of dietary chitin on the autochthonous gut bacteria in Atlantic cod (*Gadus morhua* L.). *Aquaculture Research, 44*(12), 1889–1900. https://doi.org/10.1111/j.1365-2109.2012.03194.x

Zotta, T., Parente, E., Ianniello, R. G., De Filips, F., & Ricciardi, A. (2019). Dynamics of bacterial communities and interaction networks in thawed fish fillets during storage in air. *International Journal of Food Microbiology, 293*, 102–113. https://doi.org/10.1016/ijfoodmicro.2019.01.008