Review

Vibrio spp.: Life Strategies, Ecology, and Risks in a Changing Environment

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Abstract: Vibrios are ubiquitous bacteria in aquatic systems, especially marine ones, and belong to the *Gammaproteobacteria* class, the most diverse class of Gram-negative bacteria. The main objective of this review is to update the information regarding the ecology of *Vibrio* species, and contribute to the discussion of their potential risk in a changing environment. As heterotrophic organisms, *Vibrio* spp. live freely in aquatic environments, from marine depths to the surface of the water column, and frequently may be associated with micro- and macroalgae, invertebrates, and vertebrates such as fish, or live in symbiosis. Some *Vibrio* spp. are pathogenic to humans and animals, and there is evidence that infections caused by vibrios are increasing in the world. This rise may be related to global changes in human behavior (increases in tourism, maritime traffic, consumption of seafood, aquaculture production, water demand, pollution), and temperature. Most likely in the future, *Vibrio* spp. in water and in seafood will be monitored in order to safeguard human and animal health. Regulators of the microbiological quality of water (marine and freshwater) and food for human and animal consumption, professionals involved in marine and freshwater production chains, consumers and users of aquatic resources, and health professionals will be challenged to anticipate and mitigate new risks.

Keywords: aquatic ecosystems; heterotrophy; microalgae; macroalgae; marine animals; symbiosis; human pathogens; health risks

1. Introduction

Vibrios are Gram-negative bacteria, typically with lipopolysaccharide in the outer membrane, that belong to the *Proteobacteria* phylum, *Gammaproteobacteria* class, the most diverse class of Gram-negative bacteria. Among the *Vibrionales* order, the *Vibrionaceae* family comprises aquatic bacteria, mostly living in warm waters that tolerate different levels of salinity, including fresh, brackish, and marine waters [1].

The *Vibrionaceae* family includes the genera *Aliivibrio*, *Catenococcus*, *Enterovibrio*, *Grimontia*, *Listonella*, *Photobacterium*, *Salinivibrio*, and *Vibrio* [2], and is a genomically, phylogenetically, and functionally diverse group with comma- or curved rod-shaped motile bacteria, most with polar flagellation. These family members are heterotrophic bacteria

widely distributed in aquatic environments, occupying niches in freshwater, estuarine, and marine ecosystems, as well as in aquaculture systems, and contributing to nutrient cycling [3–6]. They are chemoorganotrophic and use both aerobic respiration and fermentation of sugars producing acids (formic, lactic, acetic, succinic acids), ethanol, and pyruvate [7]. Unlike in *Enterobacteriaceae*, fermentation sugar tests have limited importance in *Vibrio* spp., because they ferment few sugars and their profile utilization is highly variable.

The genus *Vibrio* has the largest number of species, and currently 147 Vibrio species and 4 subspecies are recognized [8] of which less than a dozen are human pathogens (e.g., *Vibrio cholera*, *Vibrio parahaemolyticus*, *Vibrio vulnificus*). Other *Vibrio* spp. infect marine animals, such as fishes, shrimps, corals, and crustaceans [9–13], but the majority are non-pathogenic species and some of them are symbionts (Table 1). The etymology of *Vibrio* originates from the word vibro, which means to vibrate with tremulous motion, and was given to the species in 1854 by Pacini when he published his work on Asiatic cholera [14].

Table 1. Sources of some *Vibrio* spp. pathogenic to humans and to animals or that are symbionts.

Vibrio Species	Environments	Hosts	Pathology
V. alginolyticus [1]	seawater, human, seafood	human	wound, ear/eye and soft tissue infections
V. anguillarum	seawater, marine animals	salmon, bivalves	vibriosis, septicemic disease
V. carchariae	seawater, shark	shark?, human (shark bite)	human (shark bite)
V. cholerae [1]	fresh and brackish waters, invertebrates, algae, aquatic animals	human	cholera: dehydration and electrolyte loss
V. corallilyticus [2]	coral	zooxanthellae	coral bleaching
V. damsela [3]	seawater, fish	fish, human	wound infections
V. fluvialis	water, oyster	human	diarrhea, gastroenteritis
V. furnissii	estuarine water	human	acute gastroenteritis (rare in clinic)
V. harveyi	seawater	shrimp, invertebrates, human	vibriosis
V. hollisae	water, seafood	human	diarrhea
V. mediterranei	seawater, coral endosymbiont	zooxanthellae	coral bleaching
V. metschnikovii	fresh, brackish, marine waters, seafood	human (rarely)	wound infections?
V. mimicus	water, seafood, birds	human	diarrhea
V. parahaemolyticuss [1]	seafood	human	acute gastroenteritis
V. salmonicida [4]	seawater, marine fishes	salmon, rainbow trout	cold-water vibriosis
V. shiloi	coral endosymbiont	zooxanthellae	coral bleaching
V. symbiont	pufferfish		toxic to humans and animals
V. tubiashi	seawater, marine mollusks	Pacific oysters, bivalves	vibriosis
V. vulnificus [1]	estuarine and seawaters, seafood, sediment	human	fulminant septicemia, wound infections

[1] Common human pathogenic species; [2] thermodependent pathogen of a tropical coral species [15]; [3] presently *Photobacterium damselae*; [4] psychrophilic species.

Most *Vibrio* species, if not all, have two circular chromosomes with distinct sizes and numerous cryptic plasmids [16]. *Vibrio* spp. are highly heterogeneous and polyphyletic [17]. Actually, the 8-gene multilocus sequence analysis (MLSA) defines 23 clades for *Vibrio* and *Photobacterium* [18,19].

Biochemically, the majority of *Vibrio* spp. are oxidase, indole, and citrate positive, capable of reducing nitrate to nitrite and hydrolyzing urea and degrading gelatin, starch, lipids, chitin, and alginate with extracellular enzymes [20,21].

Vibrio species have the fastest growth rates among bacteria, responding almost immediately to favorable environmental conditions such as high temperature, salinity, and dissolved oxygen [22,23]. Physiologically, almost all species are halophilic, requiring salt in a concentration that varies with the species (NaCl 1–12%), except *V. cholerae*, *V. fluvialis*, *V. furnissii*, and *V. mimicus*, which grow on nutrient agar. They usually, inhabit brackish and

sea waters [20]. Vibrios are eurythermic (5 °C to >40 °C), preferring warm waters (>18 °C) and alkaline conditions (pH 6.5–9.0) [24].

Vibrios are heterotrophic bacteria that swim freely in the water column [25], live in association with other organisms [10,26], and can achieve symbiosis [27]. This diversity of biological niches in the aquatic environment is only possible because *Vibrio* spp. are motile bacteria, and have the ability to sense and communicate chemically. At the microscale level, chemotaxis ensures the orientation towards the optimal habitat based on the chemical signals emitted by different niches. Free-living vibrios can move either to areas with soluble attractants or to the many particles in the water column.

Under certain environmental conditions, such as those with limited nutrients, free-living vibrios can attach to different surfaces and form biofilms. These communities of "swarmer cells" embedded in a polysaccharide matrix can better withstand some adverse factors in the external environment [25,28]. While undergoing chemotaxis and showing the ability to form biofilms, vibrios in unfavorable environmental conditions such as low temperature, low salinity, and starvation, enter in a state of latency, lose their ability to grow, and became uncultivable, although the cells are still viable [29]. Viable but nonculturable (VBNC) cells are characterized by the inability to grow on laboratory media. This makes their detection impossible with usual culture methods. Compared to culturable cells, VBNC cells have alterations in their morphology, cell wall structure, membrane composition, cell physiology, and metabolism. VBNC cells are physically and chemically more resilient than cultivable cells. The VBNC state has an important impact on *Vibrio* spp. monitoring based on culture methods, leading to an underestimation in environmental or clinical samples, and thus poses a risk to public health [29]. Due to this fact, the use of independent-culture methods in these areas should be considered [30].

Species of *Vibrio* are present in all aquatic environments, especially the saline ones, and are capable of growth as a free-living organism, in association and in mutualism/symbiosis with many aquatic organisms. They have the ability to adapt and respond fast to environmental changes. *Vibrio* spp. seem to benefit from a changing world, and can alter or undermine the close relationship between humans and aquatic systems.

The main goal of this review was to update the information regarding the distribution and the ecology of *Vibrio* spp., and contribute to the discussion of their potential risks in a changing environment.

2. *Vibrio* as an Heterotroph—Free Living Way of Life

All *Vibrio* species are aquatic heterotrophs living between the sediments and the water column. Frequently *Vibrio* spp. live freely in aquatic environments, albeit their frequency varies with the aquatic ecosystem and niche. Vibrios are also agents of organic matter mineralization, playing an important role in organic matter recycling due to their enzymes, which allow them to use a wide variety of substrates [31]. They can hydrolase carbohydrates, lipids, and proteins and have the capacity to break down polymers such gelatin, collagen, starch, chitin, alginate, lignin, and hydrocarbons, contributing to the recycling of carbon and nitrogen in aquatic environments. Additionally, vibrios can produce polyunsaturated fatty acids, essential compounds for the aquatic food web organisms that they cannot synthesize [32]. Vibrios themselves can be a food source for flagellates and thus contribute to the recycling of organic matter in aquatic environments [33].

Temperature and salinity are known to affect *Vibrio* species' density and diversity. While *Vibrio* spp. are eurythermic (5 °C to >40 °C) and worldwide distributed, they prefer warm waters (>18 °C) and warmer periods and seasons, a trait that can explain their seasonal peaks. Of all the *Vibrio* spp. (more than 100), only a few are able to live in low salinity conditions: *V. cholerae*, *V. fluvialis*, *V. furnissii*, and *V. mimicus*.

In temperate and cold climates, *Vibrio* spp. density is higher in summer than in winter (Table 2), as observed in sea and estuarine waters located in the North Sea, Germany [34,35]. Despite the general relationship observed between the presence and abundance of *Vibrio* spp. in higher water temperatures, species have specific responses to temperature: some

prevail the whole year, while others were only detected at a specific temperature range, or are less affected by this parameter. *V. alginolyticus* and *V. parahaemolyticus* were both found to be present even at temperatures around freezing point [35].

Table 2. Free-living *Vibrio* spp. reported densities, niches, and geographic locations. UFC: colony forming units; MPN: most probable number; PCR-m: PCR-multiplex; FISH—fluorescence in situ hybridization; fresh (FW), brackish (BW), estuary (EW), sea (SW) and tidal (TW) waters, sediment (S); Va = *V. alginolyticus*; Van = *V. anguillarum*; Vc = *V. cholerae*; Vf = *V. fluvialis*; *V. harveyi* = Vh; Vm = *V. mimicus*; *V. natriegens* = Vn; Vp = *V. parahaemolyticus*; Vv = *V. vulnificus*; ref.—reference.

Niche	Density	Method	*Vibrio* spp. Prevalence (%)	Country [Ref.]
Port areas Ballast tanks Coastal waters	1–4.4×10^3 UFC/mL 1–4.3×10^2 UFC/mL 2–1.6×10^3 UFC/mL	PCR-m	Vc (24); Vc O1 (*ctxAC*, *tcpAC*) Vc O1 (*ctxAC*, *tcpAC*)	Brazil [36]
FW BW	Not presented	MPN-PCR	Vc (34), Vm (19) Vp (51), Va (46), Vm (28)	South Africa [23]
TW Mud (M)	1.4×10^1–5.0×10^4 MPN/mL 2.1×10^2–2.7×10^2 MPN/mL	Culture	Va, Vp Va (46), Vp, Vc, Vv	South Korea [37]
SW	5×10^2–3.4×10^4 cells/mL	FISH	*Vibrio* spp.	Germany, North Sea [34]
EW S	0–8.4×10^2 UFC/mL * 0–2.9×10^3 UFC/g *	Culture and PCR	Va and Vp (all year), Vv (summer), Vc (very low)	Germany, North Sea [35]
SW Lagoon	0–log6.4 gene copies/100 mL * 0–log8.32 gene copies/100 mL *	Culture and real time PCR	Vv (14.9, July–September), Vc (33.6, June–September), Van (2.5, May and June), Vf (1.5, July)	Lithuania, Baltic Sea [38]
SW FW	Not presented	Culture	Vv (41), Vp (33), Va (15), Vn (4), and Vh (0.7) non-01 Vc (80), 01 Vc (13.1), Vm (2.6)	Iran, Caspian Sea [39]
SW	0–1.2×10^5/L *	MPN-PCR	Vc, Vp, Vv	Guinea-Bissau [40]
EW	2.3×10^5–2.4×10^{12} MPN/100 mL	MPN	15 *Vibrio* spp.; Vp (16), Vc (14.5), Va (13)	Brazil [41]

* Depending on *Vibrio* spp.

In a study that took place along the Central Wadden Sea coast over a 2-year period, *V. alginolyticus* and *V. parahaemolyticus* were always present, while *V. vulnificus* was only detected at temperatures between 14 °C and 26.5 °C. *Vibrio* spp. and salinity were not significantly correlated, and *V. cholera* did not have a seasonal pattern [35]. Another investigation in the Lithuanian Baltic Sea, in coastal lagoon bathing sites, *Vibrio* spp. densities (in gene copies/100 mL) varied over the sampling months and the aquatic systems: *V. vulnificus* density was high in coastal samples from July to September, while *V. cholera* was present in both fresh and marine water bodies from June to September, but reached the highest values at lagoon sites, with lower salinity values. *V. anguillarum* and *V. fluvialis* were underrepresented and only detected in coastal waters [38].

In South Carolina detention ponds, *Vibrio* spp. were generally more abundant in the warmer months, reaching maximum abundances during the summer of 2009, when water temperatures ranged from 29.5–31.5 °C. Temperature was positively and significantly correlated with *V. vulnificus* [42]. A survey of the *Vibrio* community carried out in 2016 (May

to December) in the Neuse river estuary (USA), by using culture-independent methods showed that this community reflected seasonal and storm-related changes in the water column. These alterations were more dramatic after Hurricane Matthew, which was responsible for a supply of nutrients to the estuary [43].

In an extensive survey of *Vibrio* species from 2006 to 2009, in Black Sea coastal and inland waters (Georgia), 1440 water samples were analyzed and 1595 presumptive *Vibrio* isolates were collected (657 from four sites on the Black Sea coast and 938 from three inland water reservoirs). In the Black sea sites, *Vibrio* diversity was slightly higher compared to freshwater samples, and 10 of the putative clinically important *Vibrio* spp. were analyzed by PCR. Among PCR-confirmed species, *V. cholerae* (O1 and possible O139) was most prevalent (64.6%), followed by *V. parahaemolyticus* (21.4%), *V. vulnificus* (4.0%), and *V. alginolyticus* (2.6%). Six species (*V. metschnikovii*, *V. harveyi*, *V. furnissii*, *V. fluvialis*, *V. cincinnatiensis*, and *V. mimicus*) accounted for 4.4% of samples. The water temperature was positively correlated with the abundance of *Vibrio* spp. (except *V. metschnikovii*), and salinity was correlated with *Vibrio* community composition [44].

Temperature drives the frequency of *Vibrio* spp. isolation [23], especially in freshwater and in temperate climates. In contrast, in equatorial and tropical aquatic systems the correlation between *Vibrio* quantities and temperature is often absent, since the temperature variability is low, and salinity emerges as an important factor regulating *Vibrio* spp. distribution and dynamics.

In an estuary located in the Gulf of Mexico, *V. vulnificus* was detected throughout the year, but the highest values (5.14×10^3 CFU/100 mL) were found in September, at warmer temperatures and moderate salinities [45]. In a study in Guinea Bissau, the abundance of *V. vulnificus* and *V. parahaemolyticus* was negatively correlated with salinity [40]. *V. cholerae* was also detected in coastal water samples throughout the wet season, reaching higher concentrations by the end of this season (1.2×10^4 MPN/L). *V. parahaemolyticus* was detected simultaneously, while *V. vulnificus* was detected only by the end of the wet season. For the three species, genotypes associated with virulence were found: ctxA+ *V. cholera* (twice), enteropathogenic (tdh+ and trh+) *V. parahaemolyticus* at concentrations up to 1.2×10^3 MPN/L, and *V. vulnificus* (vvhA) detected in all surveyed sites, up to 1.2×10^5 MPN/L [40]. In a survey conducted during April and September 2001 in the Caspian Sea (Golestan, a province of Iran), 100 *Vibrio* isolates were recovered from 73 water samples, and *V. vulnificus*, *V. parahaemolyticus*, and *V. alginolyticus* were the most frequent species, with 39, 32, and 17 isolates, respectively. Much less frequent were *V. damsela* (1 isolate), and *V. harveyi* (1 isolate) [39].

During a 1-year study of the pathogenic *Vibrio* spp. distribution in tidal waters (TW) and mud, samples were taken from environments of the southern coast in South Korea. The study observed that MPN/mL of presumptive *Vibrio* spp. was affected by season, but not by location, despite the differences in land use and human population density at the sampling sites [37]. The sampling months had different temperature and pH values for TW and mud, salinity, and biological oxygen demand (BOD) in TW. Among the sampling months, *Vibrio* spp. MPN values were significantly correlated with temperature and pH in both TWs and mud samples, and with salinity and BOD in TW. In TWs, *Vibrio* spp. density was negatively correlated with temperature, salinity, EC, and turbidity. From a total of 10,983 isolates, *V. alginolyticus* and *V. parahaemolyticus* were ubiquitous in both niches, and season-independent, in contrast to *V. cholerae* and *V. vulnificus*, which specifically related to summer. While *V. parahaemolyticus* was isolated throughout the year, the pathogenic strains were detected only in June and September. All the *V. cholerae* isolates were nontoxigenic (non-O1 and non-139), but 88% of the *V. vulnificus* isolates possessed an elastolytic protease as a virulence factor [37]. The seasonality of potential pathogenic *Vibrio* spp. may threaten seafood safety and increase the risk of illness in South Korea, where local people consume raw fish during warmer months [37].

A freshwater intrusion into saltwater body the Mississippi Sound after the opening of the Bonnet Carre Spillway deeply affected the ecology of *Vibrio* spp., albeit temporarily. The

densities of *V. parahaemolyticus* and *V. vulnificus* decreased while the density of *V. cholerae* increased, becoming the dominant species. The authors found a significant relationship between the MPN densities and salinity for each one of the three *Vibrio* spp. At salinity levels of 6 ppt, *V. cholerae* was the only *Vibrio* detected [46]. Other studies reported negative ($p < 0.05$) correlations between *V. parahaemolyticus* and salinity [42].

Nevertheless, many reports have not found any correlation between temperature and/or salinity and *Vibrio* density [41,47,48], suggesting that this parameter can be related with other physicochemical parameters [41]. Organic matter and nutrient enriched environments support high *Vibrio* densities [49] that may be related to anthropogenic activities. Dissolved oxygen (DO), chemical oxygen demand (COD), and BOD are strong related to *Vibrio* spp. densities. *Vibrio* spp. had higher densities in freshwater samples near facilities that dumped untreated effluents or wastes from domestic houses, fish slaughterhouses, shrimp farming, and droppings from domestic and wild animals [23,41,50–52]. In South Korea, BOD and pH were positively correlated with *Vibrio* spp., expressed as MPN/mL, in TW samples, while temperature, salinity, and turbidity were negatively correlated [37].

Along the Zuari estuary on the central west coast of India and during three seasons (pre-monsoon, monsoon, and post-monsoon), organic matter determined the distribution of *Vibrio* spp., with high values during the monsoon, probably due the terrestrial runoff [53]. In Guinea Bissau, the abundance of *Vibrio* spp. (*V. cholera*, *V. parahaemolyticus*, and *V. vulnificus*) was positively correlated with total suspended solids (TSS) and precipitation [40]. In the North Sea, total organic carbon (TOC) was positively correlated with the abundance of benthic *V. alginolyticus* and *V. parahaemolyticus*, as well as with rainfall, probably due to nutrient input into the watershed [35]. In Ceará, Brazil, in water samples taken from the Coreaú estuary between June and October 2005, the MPN of vibrios per 100 mL ranged from 2.3×10^5 to 2.4×10^{13}. The high abundance recorded was probably related to several anthropogenic activities such as shrimp farming, tourism, agriculture, and animal husbandry [41]. The highest MPN values were found in samples with high pH (~8.2) and, among the environmental variables tested (temperature, pH and salinity), pH was the only one positively correlated with *Vibrio* MPN.

In South Carolina in the detention ponds and receiving tidal creeks between April 2008 and August 2009, the abundance of *V. parahaemolyticus* and *V. vulnificus* were positively ($p < 0.05$) correlated with silicate, total dissolved nitrogen, dissolved organic nitrogen, total phosphorus, and total dissolved phosphorus. The abundance of *V. vulnificus* was negatively ($p < 0.05$) correlated with DO. *Vibrio* spp. abundances were not correlated with chlorophyll a, suspended solids, or inorganic N concentrations [42].

The beach sands and sediments of coastlines are the sources of microorganisms for the water column [54]. From Tel Aviv beaches in the Mediterranean, several pathogenic vibrios were recovered [55]. In heavily polluted sites such as the Gaza Strip, high concentrations of fecal indicators and potentially pathogenic *Salmonella* and *Vibrio* species were found. In sands, *Vibrio* reaches higher densities than in water, and its occurrence was correlated ($p < 0.013$) with yeast and molds [56]. Along the Nigerian coastline, water and sand samples retrieved from recreational beaches were contaminated with fecal indicator bacteria (FIB), and with many pathogens, among them *V. parahaemolyticus* and *V. vulnificus* [57].

Freshwater is essential for life and human activities, and is scarce and under pressure. As most *Vibrio* spp. are halophilic, the probability of finding them in freshwater ecosystems is considered low, which may explain why studies on their prevalence in freshwater are few when compared to other environments [23].

Under favorable conditions, vibrios are opportunistic organisms capable of using a wide range of resources [58]. Their association with other aquatic organisms, by colonizing body surfaces or establishing pathogenic or symbiotic relationships, can favor *Vibrio* spp. survival.

3. *Vibrio* spp. Associated with Micro- and Macroalgae

Both in situ observations as well as mesocosm studies indicated the constant association of vibrios with dense populations of microalgae. This generates complex interactions between the heterotrophic vibrios and other organisms often located at different trophic levels [59]. During microalgal blooms a large amount of nutrients is released in dissolved and particulate forms, maintaining high vibrios densities [60]. The agglomeration of microalgae during the blooms also provides a large area of attachment for vibrios, which contributes to the diversification of biological niches [61].

There is some evidence that algae enhance *Vibrio* spp. survival and growth. The increased numbers of harmful algal blooms (HABs) over recent decades have often been followed by an increase in the *Vibrio* spp. population. From 2008 to 2009, five HABs were studied in coastal storm water detention ponds located in South Carolina. Two blooms occurred during warmer months, in August and November 2008, respectively a cyanobacteria and a dinoflagellate bloom, and three during cooler months (December 2008 to February 2009), caused by dinoflagellates and euglenophytes. After the blooms in warmer months, *Vibrio* spp. increased. By contrast, after the blooms in cooler months, *Vibrio* spp. did not increase. In August 2008, the bloom was dominated by *Cylindrospermopsis raciborskii*, followed by *Anabaena* sp. and was followed by an increase in both *V. parahaemolyticus* and *V. vulnificus*. Later, in November, a *Heterocapsa rotundata* bloom was observed on three ponds, and it was followed by an increase of *V. parahaemolyticus* copies/100 mL [42].

In a survey of the *Vibrio* community carried out by Jesser and Noble [43], they found positive correlations between some *Vibrio* species and algae photopigments: (i) *V. parahaemolyticus*, *V. ordalii*, *V. cholerae*, *V. mimicus*, and *V. alginolyticus* had positive correlations with peridinin, the dinoflagellates pigment; (ii) *V. cholerae* was correlated ($r = 0.47$) with fucoxanthin, present in brown seaweeds, diatoms, and dinoflagellates, and total chlorophyll a ($r = 0.40$); (iii) *V. parahaemolyticus* correlated ($r = 0.41$) with zeaxanthin from cyanobacteria. In contrast, *V. vulnificus* and *V. fluvialis* were negatively correlated with all pigments measured, especially with zeaxanthin ($r = -0.46$ and $r = -0.49$, respectively). Each *Vibrio* spp. has a unique dynamic, depending on the season, responding individually to events. This suggest that the provisions based on total *Vibrio* abundance may be insufficient for risk assessments of potentially pathogenic species [43].

To determine the microbiological hazards of ballast water tanks (BWs) transported to Brazilian ports, *Vibrio* concentration and toxigenic *V. cholerae* O1 occurrence were analyzed in water samples taken from BWTs of ships on arrival, and harbors and waters along the Brazilian coastline. At a temperature range of 1–32 °C and in all environments, the free-living vibrios were less abundant (18%) than vibrios associated with plankton (32%). Plankton vibrios varied from <10–5.1 × 10^3 CFU/mL while free-living vibrios varied from <1 to 4.3 × 10^2 CFU/mL. Mean vibrio values were unaffected by the salinity gradient (0.1–39.5 psu) recorded in BWs [36]. *V. cholerae* was found in BWs (9.5%) and in port samples (24.2%), as free-living and attached forms. The toxigenic strains *V. cholerae* O1 (ctxAC, tcpAC), involved in cholera disease, were found in BWs (2%) and harbor (2%) samples, confirming that ballast tanks are important carriers of pathogenic organisms, and that monitoring these or other pathogenic bacteria is very importance in BWs management programs.

Macroalgae are cultured in many parts of the world, for cooking and folk medicine. In China alone, about 6 million tons wet weight of *Saccharina japonica* kelp are planted each year [62]. Recently, a study demonstrated that *V. parahaemolyticus* was detected by molecular methods in the edible *Saccharina latissima* in 78% of enriched kelp samples, indicating that bacterial pathogens vary on the algae thallus surface and in the surrounding water. This study was the first food safety assessment of edible sea macroalgae in the Northeast USA, providing data on the importance of monitoring microbial contamination in the edible macroalgae industry, and enabling its expansion [63].

4. *Vibrio* spp. Associated with Zooplankton and Animals

Vibrio spp. constitute a significant portion of the bacteria naturally associated with zooplankton, namely copepods [5,64]. Numerous studies have reported the association of vibrios with zooplankton, most often by colonizing the body surface of these organisms [65].

The formation of biofilm by *Vibrio* spp. on the exoskeleton of microcrustaceans and other marine organisms may in fact be a survival strategy [26,66] because cells can more efficiently use nutrients absorbed into the biofilm matrix. In this way, vibrios can cope with harsh environmental changes, mainly those related to low nutrient concentrations. They can also withstand the action of toxic compounds and exchange useful compounds with other bacteria or hosts.

It is well known that vibrios are able to break down chitin, one of the richest sources of amino carbohydrates in oceans [67,68]. The chitin layer on the surface of copepods can be used as a nutrient [69]. The importance of the *Vibrionaceae* family in preventing the sinking of chitin to the ocean floor has long been recognized [70], but this polymer is besides a source of nutrients, and has a key role in the life strategies of several *Vibrio* spp. Chitin colonization by *V. chloreae* leads to biofilm production, which in turn induces competence in bacteria, favoring transformation and horizontal gene transfer [71], which are important to acquire virulence and antibiotic-resistant genes. Chitin also induces natural competence in other *Vibrio* spp. such as *V. fischeri*, *V. parahaemolyticus*, and *V. vulnificus* [72].

Numerous studies conducted by both culture -dependent and -independent methods indicated that the abundance of vibrios is high near or on the body of marine organisms, such as mollusks [73,74], fish [75,76], corals [77], and shrimp [78]. Other animals, such as waterbird species that inhabit and feed in aquatic systems, can be infected by their prey and might be vectors of *V. cholerae* [79].

In the Mollusca phylum, Bivalvia can accumulate a large number of vibrios and become vehicles for the transmission of pathogenic species [80]. The *Vibrio* species associated with natural mussel (*Mytilus galloprovincialis*) populations in Galicia (Spain) changed with the water temperature and salinity. *Vibrio splendidus* and *V. aestuarianus* were dominant during the warm and the cold seasons, respectively [81]. Marine sediments underlying farmed mussels support an enriched presence of vibrios relative to surrounding environments [49]. In nature, sediments are also important natural reservoirs for *Vibrio* spp. in Northeast Galicia [81]. Very recently, Lattos et al. [82] reported mass mortalities in the winter in the *Pinna nobilis* population in the Aegean Sea, in which *V. splendidus* and *Vibrio mediterranei* may be implicated.

Several *Vibrio* spp. are involved in coral bleaching, one of the most serious diseases affecting corals worldwide. The loss of the pigments in corals is due to the change of the symbiotic relationship between the host coral and unicellular algae of the zooxanthellae group [83–85]. The most well-known species involved in coral bleaching are *V. coralliilyticus* and *Vibrio shilonii* [86]. The infection is favored by the increase of seawater temperature, and has an extremely negative effect on corals and reef formation. The infection is initiated by the adhesion of bacteria on the surface of corals, followed by the penetration and the rapid growth inside the tissues, reaching up to 10^9 CFU/mL in a short period of time. Once inside the coral tissues, *V. shilonii* cells remain virulent although they become VBNC [77,87,88].

On Riou Island, in the northwestern Mediterranean Sea, massive disease outbreaks in benthic invertebrates occurred during an abnormal period of elevated seawater temperatures. One of the most affected species was the red gorgonian *Paramuricea clavata*, a colonial soft coral, and a key species in the communities dwelling in dim-lit habitats in the Mediterranean. Associated with the infection was a *V. coralliilyticus* strain that showed thermodependent virulence to *P. clavata* [15].

In benthic sea environments, and at different depths, sponges (Phyla Porifera) can be associated with *Vibrio* spp. At depths of 150 to 1242 feet (~46 to 379 m), sponges from distinct geographies live in commensalism with several *Vibrio* spp.: *V. alginolyticus*, *Aliivibrio fischeri*, and *V. mediterranei*, and some putative new species most closely related to *V. ichthyoenteri* and *V. scophthalmi* [89].

Barotolerant *Vibrio* spp. have been isolated from deep-sea sediments, including hydrothermal vents. At a depth of 4940 meters and 150 miles east of Cape Canaveral (formerly Cape Kennedy), samples were collected aboard the research vessel Eastward, and strains of *Vibrio* were isolated [90]. From the Polychaeta *Alvinella pompejana* collected from a deep-sea hydrothermal field (2600 m depth) in the East Pacific Rise, *Vibrio diabolicus* was isolated by the French-American cruiser Hero in 1991, and by the French-manned submersible Nautile [91]. Later, in 1999, along the East Pacific Rise, and during dives of the deep-sea submersibles Alvin and Nautile, water samples were collected at a depth of 2500 m and nearby sulfide chimneys of a hydrothermal vent community. Four mesophilic bacterial isolates were recovered from the samples, cultured and identified: *Shewanella algae*, *V. harveyi*, and one novel *Vibrio* species. The new species, *Vibrio antiquarius*, is closely related to *V. alginolyticus*, *V. parahaemolyticus*, and *V. harveyi* in a monophyletic clade [92].

Many of *Vibrio* spp. responsible for illness in marine organisms can be important pathogens for animals in aquaculture systems [93]. Within this group, the species *V. anguillarum*, *V. salmonicida*, and *V. vulnificus* can infect several species of fish, and *V. harveyi* causes massive economic loses in shrimp culture systems [94,95]. Disease in farmed fish and crustaceans is very common in the early stages of animals' life and can occur suddenly, causing mass mortality events [96–100]. *Vibrionaceae* diversity was investigated in Tunisia, in a *Ruditapes decussatus* hatchery located in the coastal marine waters, and *V. alginolyticus* was the predominant species (54% of the strains were isolated from the inside of larva and post-larva rearing structures), followed by *V. fluvialis*, *V. vulnificus*, *V. cholerae*, and *V. parahaemolyticus* [101].

The evaluation of *Vibrio* communities associated with seafood, integrating both culture -dependent and -independent methods, would be valuable in future. Although both methods detect *V. parahaemolyticus* and *V. vulnificus* in the *Ruditapes philippinarum* bivalve, the two methods proved to be complementary for the detection of *V. alginolyticus* and *V. cholera* [74]. The authors have proposed a reassessment of the marine agar medium for both the recovery of human *Vibrio* pathogenic species and for a screening approach in contaminated seafood [74]. Recently, a multiparametric approach to assess the water quality in a Mediterranean mariculture (*Dicentrarcus labrax* and *Sparus aurata*), reported that *Vibrio* diversity was higher in July than in December, and identified a set of *Vibrio* species critical to the health of the farming environment (*V. rotiferianus*, *V. parahemolyticus*, *V. harveyi*, and *V. vulnificus*). Some of these species are also important for human health [102].

5. Symbiotic Members of *Vibrionaceae*

Several *Vibrionaceae* species are bioluminiscent and some of them enter into symbiotic relationships with fish and squid living in marine environments. The taxonomy of some species included in the *Vibrio* genus has been marked by ambiguity. Such an example is the *Vibrio fischeri* group, which comprises four species: *V. fischeri*, *V. logei*, *V. salmonicida*, and *V. wodanis*. Based on an analysis of 16S rRNA gene sequences, Urbanczyk et al. [103] reclassified the group as a new genus, *Aliivibrio*, which contains the following species: *Aliivibrio fischeri*, *Aliivibrio logei*, *Aliivibrio salmonicida*, and *Aliivibrio wodanis*.

A similar situation was found for *Photobacterium* genus. A comprehensive study carried out on 16S rRNA and multilocus sequence analysis revealed a clear discrimination between *Photobacterium*, on the one hand, and *Aliivibrio* and *Vibrio*, on the other [104]. Furthermore, the study showed the existence of two distinct clades within *Photobacterium*: (i) clade I, containing luminous species, some of which are able to enter into symbiotic relationships with fish and squid; (ii) clade II, containing non-luminous species [104]. However, for the description of species, we kept the old names as they are used in most studies. *Photobacterium* species are widespread in the marine environment and members of this genus have been isolated from a variety of habitats such as water columns, sediments, corals, and the skin and gut of marine animals [104]. Some species are able to establish symbioses with animals living in marine environments [105]. The genus *Photobacterium* includes about 20 species, seven of which produce luminiscence and, among these, only

three enter into mutualistic associations with animals: *P. kishitanii*, *P. leiognathi*, and *P. manda-pamensis* [104]. *Photobacterium kishitanii* establishes symbioses with deep-sea fish [106]. This species manifests close similarities with both *P. phosphoreum* and *P. iliopiscarium*; however, it forms a distinct clade within the *Photobacterium* genus [107]. *P. leiognathi* was isolated from the supraesophageal light organ of *Nuchequula nuchalis*, a fish species from the leiognathid group [106]. The bacteria inhabit a special soft tissue of the light organs of animals. The blue-green light is emitted by bacteria located in the ventral region of the fish. The light organ environment provides symbionts with nutrients and oxygen for growth and luminiscence. In their turn, the animals use the light emitted by bacteria for a variety of behaviors: camouflage illumination, attracting prey, avoiding predators, and finding a mate [108,109]. The bacteria can be found as free-living organisms in coastal waters and open sea and colonize the light organs of juvenile Leiognathidae, with approximately 40 species widespread in tropical and subtropical waters [110]. The symbiosis is initiated with a new host generation [111]. Intense multiplication leads to accumulation of a high number of bacteria, which is mostly released from the light organ into the gut tract and reaches the surrounding seawater with fecal particles. In a similar way to *Aliivibrio–Euprymna* symbiosis, the excess of bacteria is expelled from the light organs of fish into the seawater [112]. *P. madampamensis* shares many similarities with *P. leiognathi*, but unlike the latter, has a particular *luxF* gene and a broader range of hosts. This species establishes symbiosis with the cardinalfish group (*Siphamia*) comprising 25 species. The light organ is located in the ventral position and connected to the intestine [105]. It has been observed that some strains of *P. mandapamensis* could be correlated with water temperature [113]. The symbiosis provides fish with advantages such as attracting prey or protection against predation.

Vibrio (*Aliivibrio*) *logei* is a luminous species isolated from the light organ of the *Sepiola* genus, whose members live in the deeper and colder waters of the Mediterranean Sea, Japan, and the Philipines. Bacterial symbionts were first described in *Sepiola atlantis* by Herring et al. [114]. Later, two other species, *Sepiola affinis* and *Sepiola robusta*, were found to harbor predominantly populations of *V. logei* as light-producing symbionts [115]. It was found that these two species were colonized by a mixed population of *V. fischeri* and *V. logei*. Quantitatively, *V. logei* was the dominant population and ranged from 63% to 100% of total bacteria [115]. The authors hypothesized that successful colonization of *Sepiola* light organ by *V. fischeri* or *V. logei* might be controlled by the ambient water temperature. Therefore, animals living in the cooler waters would be predominantly colonized by *V. logei* [115]. Further experiments showed that densities of *V. fischeri* were higher when host juveniles were incubated at 26 °C, while *V. logei* reached high population densities at 18 °C. Both *V. fischeri* and *V. logei* were able to initiate the symbiosis with juveniles when exposed to their optimal temperature. In competition experiments, colonization of the light organ occurred at 26 °C for *V. fischeri*. Proportions of the two *Vibrio* species were different and depended on the incubation temperature. In wild adults, abundance of *V. fischeri* and *V. logei* was variable in specimens collected at different depths and time periods, and suggested that the composition of symbiont populations depended on the temperature of surrounding waters [116].

One of the best-studied relationships between animals and luminous bacteria is the symbiosis between the Hawaiian bobtail squid (*Euprymna scolopes*) and *V. fischeri*. The bacteria live in a nutrient-rich habitat inside the squid's body and provide bioluminescence useful for the animal. The light provided by the bacteria acts as a camouflage mechanism by counter-illuminating the squid silhouette at night [14]. The symbiosis begins with the bacteria's recruitment by the squid from the seawater environment [117]. Bacteria do not colonize the region of the light organ directly, and must go through a series of steps required for a complex signal exchange with the host through which the squid selects *V. fischeri* [118,119]. The first contact between the partners takes place in the epithelial cells of the host tissues. After exposure to bacterial peptidoglican, the epitelium secrete a mucoid substance [117]. Initial interactions are nonspecific and lead to the formation of biofilms with Vibrio cells often associated with other heterotrophic bacteria [120]. The

control of biofilm production is subjected to a complex network of signals that takes place at transcriptional and post-transcriptional levels [117]. At some point, cells of *V. fischeri* are released from the biofilm, regain a planktonic lifestyle [117], swim across the antechamber and finally reach the crypts of the light organ [121]. *V. fischeri* cells actively travel using the flagella and specific chemotaxis proteins [119,122], but after entering the crypts they lose their flagella [122,123] as motility is no longer required. The flagellar genes are activated again before dawn, when *E. scolopes* expels 90% of the bacteria from its body. In the water column, *V. fischeri* already has functional flagella [124]. After the bacteria enter the squid's body, they induce a series of physiological and morphological changes in the light organ [125].

Light is emitted at a certain population density due to the quorum sensing (QS) control system [119,126], a mechanism of intercellular communication in response to cell density. In *V. fischeri*, QS is activated by specific inducers and regulates light production [127]. When inducers reach a specific level, they activate genes involved in light production [127,128]. Bioluminescence is the result of luciferase activity. Luciferase releases light during the oxidation of a long-chain aldehyde (R-CHO) to a fatty acid in the presence of FMNH2 [127]:

$$FMNH2 + O_2 + R\text{-}CHO \rightarrow FMN + R\text{-}COOH + H_2O + light.$$

The synthesis of R-CHO is carried out by a complex composed of three enzymes: acyl reductase, acyl transferase, and a synthetase encoded by genes *lux*CDE in the lux operon [127].

6. *Vibrio* spp. as Human Pathogens

The ingestion of contaminated water, or raw or improperly cooked contaminated seafood, in particular shellfish, and wounds' exposure to water are the most common sources of *Vibrio* spp. infections. These infections occur in warmer waters, warmer periods and have seasonal peaks [129]. In temperate climates, most infections occur from May through October when water temperatures are warmer [130]. The species most known to cause severe infections in humans are *V. cholera*, *V. parahaemolyticus*, and *V. vulnificus* [131, 132]. They have high growth rates in a temperature range of 30–37 °C, and at optimum pH near neutral values (Table 3). Anyone can get sick from vibriosis, but there are some at-risk groups that are more likely to get an infection or have severe complications. Those with a liver disease (hepatitis B or C, cirrhosis, hemochromatosis), cancer, diabetes, HIV, or thalassemia, receiving immune-suppressing therapy, taking medication to decrease stomach acid levels, and who have recently had stomach surgery are at risk [130].

Table 3. Physiological characteristics of culturable cells of three *Vibrio* species important to human health, and frequently found in sea- and freshwater. PSU—practical salinity units.

Physiologic Characteristics	V. cholerae	V. parahaemolyticus	V. vulnificus
Temperature range (°C)	* 10–43	5–43	8–43
Optimum temperature (°C)	30–37	37	37
Inactivation temperature (°C)	>70	>63	>50
pH range	5–9.7	5–11	5–10
Optimum pH	7.6	7.5–8.5	7.8
Minimum water activity (a_w)	0.97	0.94	0.96
NaCl (%)	<4.0	0.5–8.0	0.5–5.0
Salinity (PSU)	0–20	5–30	8–16

* Below 10 °C became VBNC [133].

The most significant pathogenic vibrio is *V. cholerae*, an endemic species in Asia (Ganges delta, Bay of Bengal), present in both brackish and freshwaters, and the causal agent of cholera, a debilitating and frequent epidemic/pandemic disease that provokes dehydration and electrolyte loss. In the European Union/European Economic Area (EU/EEA), cholera is a rare disease. In 2019, EU countries reported 26 confirmed cases of cholera [134],

but in developing countries, *V. cholerae* causes 1.4 to 4.3 million cases of cholera annually, resulting in 21,000–143,000 deaths per year [135]. Because of that, *V. cholerae* is the most studied vibrio. Although *V. cholerae* has more than 200 serotypes, only serotypes O1 and O139 are responsible for cholera epidemics while the serotypes non-O1 and non-O139 cause sporadic cholera-like infections.

The main route of contamination with cholera vibrio is through water and food, and the vectors that spread the disease are aquatic animals, such as copepods and chironomids, as well as some species of cyanobacteria [136]. The conditions that favor the appearance of cholera epidemics are generated by the improper sanitary quality of water sources [130].

After entering the human host, *V. cholerae* adheres to the intestinal epithelium and produces a specific toxin, called cholera toxin (CT) [137]. The production and accumulation of this toxin in the intestine cause intense watery diarrhea that can lead to death. The symptoms of the disease are the result of the action of several virulence genes that in *V. cholerae* are located in the ToxR regulon [138–140].

In North Europe regions, cholera (caused by *V. cholerae* serotypes O1 and O139) does not occur, and vibriosis is mostly caused by *V. alginolyticus*, *V. cholerae* non-O1 and non-O139, *V. parahaemolyticus*, and *V. vulnificus* [141]. The reported vibriosis caused by non-O1 and non-O139 *V. cholera*, causes sporadic cases of gastroenteritis and extraintestinal infections, such as ocular infections in immunocompromised patients or patients with chronic liver disease (Table 4). Recently, a urinary tract infection was reported involving a non-O1 *V. cholera*, also known as *Vibrio albensis*, in an immunocompetent 27-year-old man from Beirut. The patient denied exposure to marine water, marine animals, and eating raw seafood, and the analysis of tap water and a saltwater well recovered *V. albensis* in both samples, along with other bacteria: *E. coli*, *Aeromonas hydrophila*, *Enterobacter cloacae*, *Pseudomonas otidis*, and *Shewanella putrefaciens* [142].

Table 4. Examples of recent case reports (since 2011) of infections due to *Vibrio* and related species, patient gender, age, cause of infection, symptoms, and country.

Vibrio sp.	Gender	Age (Years)	Cause and Context	Symptoms	Country [Ref.]
V. alginolyticus	male	69	Rectum adenocarcinoma receiving chemotherapy	Watery diarrhea, abdominal pain, nausea, vomiting, no fever, lactic acidosis. Enterocolitis, septic shock	Spain [143]
	male	37	Pretibial ulcer exposed to the Mediterranean Sea	Wound uncured	
V. cholera (non-O1 and non-O139)	male	37	Non-travel hepatitis C cirrhotic patient; shrimp consumption	Fever, abdominal pain, watery profuse diarrhea and dehydration	Portugal [144]
V. cholera (strain not mentioned)	female	70	Ovarian carcinoma (stage IIIC) receiving chemotherapy; shrimp consumption	Nausea, vomiting, abdominal pain. Pancytopenia, lactic acidosis, hypotension, oral/nasal hemorrhage, coagulopathy. **Death**	USA [145]
V. cholera (O100, virulence genes *hapA*, *hlyA*, and *ompU*)	male	27	A water skiing accident on a river in Australia	Chronic periodic earaches along purulent exudate, otitis	Israel [146]
V. cholera (non-O1)	male	59	Fisherman struck in the right eye by a marine shrimp developed keratitis	Right eye pain, redness, tearing and photophobia, corneal ulcer	Taiwan [147]

Table 4. *Cont.*

Vibrio sp.	Gender	Age (Years)	Cause and Context	Symptoms	Country [Ref.]
V. cholera (non-O1)	male	27	Immunocompetent patient; denied exposure to marine water, marine animals and eating raw seafood; tap water and well water contaminated	Abdominal pain, nausea, vomiting, chills and dysuria. Afebrile, stable vital signs; mild lower abdominal tenderness. Urinary tract infection	Lebanon [142]
V. harvey	male	26	Wound infection following a traumatic leg amputation during snorkeling	Fever, putrid infection and necrosis of the subcutaneous tissue and the muscles	Spain [148]
V. harvey and *P. damselae*	male	75	Fishing at a southern Sydney beach. Not recall any hand trauma. Treated for hypertension and hypercholesterolemia	Enlarging, painful hemorrhagic blister on his right hand	Australia [149]
V. metschnikovii	male	78	Previous gastroenteritis after shrimp consumption	Pain, swelling and redness of his left dorsalis pedis, fever mental confusion, severe septic shock and cardiac arrest. Need of mechanical ventilation	Denmark [150]
V. metschnikovii	male	70	Heart failure, atherosclerosis, vascular prosthesis, chronic gastric ulcer and kidney disease, gastrointestinal bleeding	Intestinal bleeding, pseudoaneurysm of aorto-bifemoral graft and aorto- small intestine fistula formation; hospital-acquired bilateral pneumonia; post-chirurgical infection	Ukraine [151]
V. parahaemolyticus	male	85	Severe valvular and ischemic-hypertensive cardiopathy, slight chronic renal failure and chronic venous leg ulcers; sea beach holiday in Italy. Chronic hepatitis B (undiagnosed)	Pain, limb cellulitis originating from leg ulcers, hypotension, acute renal failure, septicemia and septic shock	Switzerland [152]
V. vulnificus	male	39	Immunosuppressive therapy, admitted to the hospital for liver transplantation	Fever, myalgia, anuria and erythematous plaques on lower limbs, dyspnea and respiratory distress. **Death**	Brazil [153]
V. vulnificus	male	46	History of a remote Roux-en-Y gastric bypass; ingestion of raw oysters	Distress, leg soft tissue necrosis, multi-organ failure, mechanical ventilation, disseminated intra-vascular coagulopathy, large ischemic stroke. **Death**	USA [154]
V. vulnificus	male	31	Chronic liver disease—cirrhosis; leg tattoo exposure to seawater, Gulf of Mexico	Fever, erythema in tattoo area and in legs, cellulitis, septic shock. **Death**	USA [155]
P. damselae *	male	65	Trauma in right arm during fish cleaning; arterial venous fistula due blood dialysis	Pain and edema in the arm, necrotizing fasciitis	Portugal [156]

* Formerly *V. damselae*.

Like *V. cholera*, *V. parahaemolyticus* is an enteropathogenic and is responsible for gastrointestinal infections that in healthy people are mild or moderate, but in people who are at high risk (e.g., suffering diabetes, cirrhosis, cancer, or immunocompromised), it can be very serious or even fatal. *V. parahaemolyticus* is a ubiquitous species in the temperate and tropical coast areas and does not produce enterotoxins. This species and *V. vulnificus* can

also cause infections in wounds, after exposure to contaminated water, or when handling marine food [157]. The infection can become systemic, and the affected people develop a serious medical condition with fever, hypotension, and altered mental status. Frequently, the lesions require surgical debridement or even amputation [157].

V. vulnificus is an opportunistic pathogen, frequently found in estuarine waters and can cause severe vibriosis that demands rapid diagnosis and prompt and adequate antibiotic therapy since the death rate is high (Table 4). *V. vulnificus* infects mostly cirrhotic patients (more than 80%), who typically have high serum iron levels, an essential condition for a successful infection [158]. The majority of the case reports of vibriosis are in men, and in patients with chronic diseases or receiving chemotherapy. In the patients with trauma resulting from the practice of aquatic activities, or wounds exposed to seawater, the vibriosis was mild and successfully treated (Table 4). By contrast, the infections were fatal for the patients belonging to at-risk groups—those taking immunosuppressive and chemotherapies [145,153], who have had stomach surgery [154], and cirrhotic patients [155].

Other *Vibrio* spp., such as *V. harveyi* and V. *metschnikovii*, are rarely responsible or associated with human infections. *V. harveyi* is a serious pathogen of marine organisms as fish and invertebrates, and an important bacteria in seafood spoilage [159]. Lately, some case studies have been published reporting infections by *V. harveyi* in humans, after exposure to a marine environment. The infections were in a wound or an injury, and often severe, involving subcutaneous tissue and muscles necrosis, requiring tissue debridement and prolonged antibacterial therapies [148,149,160]; they can also appear in co-infection with *P. damselae* [149,155]. *V. metschnikovii* is a widespread bacteria in aquatic environments, and from 1981 to 2020, less than 15 reports of infections in human by this species were published, but the infections can be very debilitating [151]. *V. alginolyticus* is associated with ear and soft tissues infections with a good prognosis, and can be an opportunistic pathogen in fragile patients [143].

Wound infections caused by *Vibrio* spp. were considered rare, but there is an increasing frequency and geographic spread in reported soft tissue wound infections by *V. vulnificus*, *V. parahaemolyticus*, and *V. alginolyticus*. In the USA alone, it is estimated that vibriosis causes 80,000 illnesses and 100 deaths every year [161].

7. Antibiotic Susceptibility in *Vibrio* spp.

Most infections caused by *Vibrio* spp. are self-limiting and do not require clinical treatment, but antibiotics are often needed to treat severe vibriosis [162]. For cholera, antibiotics are not considered to be a life-saving treatment. If the patient hydration status is maintained they will recover without antibiotics, although the duration of illness doubles [163]. Because cholera generally occurs in areas with deficient health services, when antimicrobial resistance (AMR) occurs, more human and therapeutic resources are needed which, if not met, could result in more deaths [163]. Currently, in the treatment of cholera, azithromycin (a macrolide), doxycycline (a tetracycline), or ciprofloxacin (a quinolone) are used [164], but the arsenal of antibiotics against this disease has been decreasing considerably [165]. Bacteremia due to *V. cholerae* non-O1 and non-O139 strains are treated with third-generation cephalosporins and quinolones [142,144,146].

V. parahaemolyticus and *V. vulnificus* are important species in public health, causing infections that are most associated with seafood [166]. Currently, doxycycline and a third-generation cephalosporin are recommended for *V. vulnificus* as an initial treatment regimen, whereas doxycycline or quinolone are administered for *V. parahaemolyticus* [164]. *V. vulnificus* infections often have a fatal outcome, even when the recommended antibiotic therapy is applied early [155]. Frequently, infections caused by *V. vulnificus* rapidly deteriorate the patient's condition and end in death a few hours or days after the onset of infection [153,154].

In general, *Vibrio* spp. are susceptible to most antimicrobials used to treat animal or human infections, but several antibiotic-resistant strains of *Vibrio* spp. have been reported [166]. In recently reported human vibriosis (Table 4), a severe otitis caused by *V. cholera* O100 was successfully treated with ciprofloxacin. The strain was suscepti-

ble to mostly the tested antibiotics (amoxicillin/clavulanic acid), cefuroxime, trimethoprim/sulfamethoxazole), gentamicin, and ciprofloxacin), but resistant to polymyxin B sulfate [146]. A urinary infection caused by a non-O1 *Vibrio cholerae* strain was treated with ciprofloxacin. The strain was susceptible to all (n = 22) the tested antimicrobials [142]. A wound infected by *Vibrio harveyi* was first treated with ampicillin, which was rapidly switched to ceftriaxone and ciprofloxacin. This approach, along with surgical debridement, controlled the infection and the patient was discharged [148].

Resistance to antibiotics was also reported in other *Vibrio* spp. strains. A *V. metschnikovii* strain was resistant to ampicillin, but susceptible to meropenem and piperacillin/tazobactam [150]. Another *V. metschnikovii* strain, tested against 47 antibiotics, was resistant to 17, among them cefotaxime and co-trimoxazole [151]. Two strains of *V. alginolyticus* were reported resistant: one to ampicillin (and susceptible to amoxicillin/clavulanic acid, ciprofloxacin, and imipenem) and the other to penicillin and ampicillin (and susceptible to cefotaxime, ceftazidime, ciprofloxacin, and tetracycline) [143]. In a hand infected by both *P. damselae* and *V. harveyi*, the patient was first treated with doxycycline and cefazolin. After surgical debridement, the treatment was completed with 7 days of doxycycline. Both strains were susceptible to doxycycline, ceftriaxone, ciprofloxacin, cefepime, and ticarcillin–clavulanic acid. *P. damselae* was also ampicillin susceptible, contrary to *V. harveyi* [149].

The increasing antibiotic resistance in many *Vibrio* spp. associated with human infections is due the high probability of horizontal gene transfer between virulent and non-virulent strains [167]. Aquatic environments and environmental multidrug resistant (MDR) strains could play a role in the spread of antibiotic-resistant genes [168].

In 2013, in 62 strains of *V. cholera* isolated from ship ballast tanks (USA), the antibiotic resistance was almost restricted to ampicillin, and MDR was uncommon [169]. Recently, more than 99% of 443 *V. cholerae* isolates from the Bay of Bengal (India) were MDR, and their genome was enriched with acquired genetic elements [170].

In a large survey of virulence and antibiotic resistance in environmental *V. parahaemolyticus* strains along the Atlantic coast of Georgia and South Carolina, 350 strains of *V. parahaemolyticus* were isolated and tested against 24 antibiotics. Almost 25% of the isolates demonstrated resistance to 10 or more agents, including amoxicillin, ampicillin, apramycin, cephalothin, penicillin, streptomycin, amikacin, cephalothin, gentamicin, nalidixic acid, and trimethoprim. All isolates were susceptible to ceftriaxone, chloramphenicol, ciprofloxacin, imipenem, ofloxacin, nitrofurantoin, meropenem, oxytetracycline, and tetracycline [168].

V. vulnificus (n = 120) and *V. parahaemolyticus* (n = 77) recovered from Chesapeake Bay and Maryland Coastal Bays (USA) surface water were tested against 26 antimicrobials. *V. vulnificus* isolates were susceptible to 14 of the 26 antibiotics tested, including the ones recommended by the CDC for the treatment of *V. vulnificus* infections, such as tetracyclines, quinolones, and folate pathway inhibitors. All *V. parahaemolyticus* isolates were susceptible to 11 of the 26 tested antibiotics and four (carbapenems, tetracyclines, quinolones, and folate pathway inhibitors) of the eight tested antimicrobial classes. *V. parahaemolyticus* isolates exhibited a high percentage of resistance against penicillin (68%) and ampicillin (53%) [171].

In South Africa, 118 *Vibrio* isolates recovered from different freshwater sources in rural environments, comprising *V. fluvialis* (n = 41), *V. mimicus* (n = 40), and *V. vulnificus* (n = 37), were tested for their susceptibility to antibiotics. With the exceptions of imipenem, meropenem, and ciprofloxacin, most isolates exhibited more than 50% resistance to antibiotics. All isolates were resistant to polymyxin B and azithromycin, and 16.1% were resistant to ciprofloxacin. The multiple antibiotic resistance index (MARI) ranged from 0.3 to 0.8 with most isolates showing MARI of 0.8 [172].

From the waters of the Jacarepaguá lagoon system, in Rio de Janeiro, Brazil, a MDR *V. parahaemolyticus* strain JPA1 was isolated. The strain was tested against 16 antibiotics and displayed resistance to eight of them, seven β-lactams and one a polymyxin, but was susceptible to all aminoglycosides, tigecycline, and ciprofloxacin [173]. Despite the *V. parahaemolyticus* strain JPA1 being non-virulent to humans, it encodes several genes

that have been involved in several mechanisms of resistance against different classes of antibiotics, such as antibiotic efflux, regulation of efflux, antibiotic inactivation, and target replacement [173].

The prevalence of antimicrobial resistance was assessed in 70 *Vibrio* strains isolated from diseased cultivated marine fish in Guangdong and Hainan provinces, South China. Most of the isolates belonged to *V. harveyi* (27), *V. vulnificus* (11), and *V. alginolyticus* (10), and showed high resistance to vancomycin (95.71%), amoxicillin (68.57%), midecamycin (67.14%), and furazolidone (55.71%), and high susceptibility to erythromycin, trimethoprim-sulfamethoxazole, doxycycline, and chloramphenicol. MARI ranged from 0.00 to 0.60 [174].

The prevalence of *Vibrio* spp. in groupers (*Epinephelus* spp.) in nine farms located in Malaysia was high (72%), and the most prevalent species were *Vibrio communis* (28%), *V. parahaemolyticus* (25%), *V. alginolyticus* (19%), and *V. vulnificus* (14%). Of 380 *Vibrio* strains, 97% were resistant to at least one antibiotic. The majority were highly resistant to penicillin G and ampicillin (82%), and susceptible to tetracycline (84%), streptomycin (67%), and vancomycin (34%). MDR was high: 98 (27%) isolates were resistant to four, 67 (18%) to five, 10 (3%) to six, and 1 (0.3%) to 7 antibiotics [175].

A recent systematic review on the abundance of AMR bacteria found in aquaculture environments (*Aeromonas* spp., *Edwardsiella* spp., *Flavobacterium columnare*, *Lactococcus* spp., *Streptococcus* spp., *Vibrio* spp., and *Yersinia* spp.) calculated MARI for 40 countries, which accounted for 93% of global animal aquaculture production. Twenty-eight countries displayed MAR indices higher than 0.2, which indicates a high-risk antibiotic contamination. A strong positive correlation (r = 0.58, $p < 0.001$) was also found between human clinical MARI and aquaculture-derived MARI [176].

8. Risks Related to *Vibrio* spp.

Vibrio spp. are ubiquitous in aquatic environments, especially marine ones, playing many roles as scavengers, symbionts, and pathogens [21]. Among the pathogenic vibrios, *V. parahaemolyticus*, *V. cholera*, and *V. vulnificus* are the most important from a foodborne infection point of view [11]. From this three species, *V. cholerae* and *V. parahaemolyticus* have the ability for pandemic expansion threatening the global public health [129]. Related to marine, brackish, and freshwater ecosystems, the infections caused by vibrios are gaining importance and, during the last decade, several worldwide organizations related to health released information and alerts on the increase in the number of infections caused by vibrios, the risk groups, and the most exposed activities and professions [177–180].

In the USA, vibriosis infections are reported via the Cholera and Other Vibrio Illness Surveillance (COVIS) system. COVIS was initiated in 1989 by CDC, FDA, and Alabama, Florida, Louisiana, and Texas, four Gulf Coast states. By the early 2000s, almost all states were voluntarily reporting [180]. From 1988 to 2012, the reported infections by *V. alginolyticus* increased 12-fold, and most of them were from coastal states (96%) and involved water activities (86%) [181]. The number may be underestimated because *Vibrio* bacteria are not easily identified with routine testing, and many cases may not be reported. The US *Vibrio* incidence in the period from 2016–2018 and in 2019 increased significantly (79%) [180]. The CDC estimated that around 80,000 vibriosis infections occur each year in the USA, of which 52,000 result from consuming contaminated food. Most patients have mild symptoms and recover after about 3 days, but of those with *V. vulnificus* infection 20% die [180].

The Korea Centers for Disease Control and Prevention (KCDC) reported an increase in *V. vulnificus* infections in the first eight months of 2020, more than double the cases from the same period in 2019 [182].

In Europe, the number of infections related to these pathogens has also increased since 1990 [177,179]. In a joint report of the European Food Safety Authority (EFSA) and the European Centre for Disease Prevention and Control (ECDC), *Vibrio* was identified in four small foodborne outbreaks in France and in Italy. The agent was identified as *V. parahaemolyticus* in all French outbreaks, while no information was available for the others. For *Vibrio*, of 326 food samples in total from Bulgaria, the Netherlands, and Sweden, 32

were positive (9.8%). These positive results were from raw fish, shrimps, and lobsters from border inspection activities in the three countries [183].

There are several hypotheses or explanations for the steady increase of infections by *Vibrio* spp., both in industrialized and developing countries [11,184]. Due to the worldwide increase in seafood consumption, there has been an incremental increase in the global production of seafood (mainly fish, crustaceans, and mollusks) by aquaculture and in the capture of wild populations. In 2018, and in millions of tons (Mt), the global capture of marine fish reached 94.4 Mt (marine 84.4), followed by fish produced in aquaculture 82.1 Mt (marine 30.89), aquatic algae (mostly seaweed) 32.4 Mt, mollusks (mainly bivalves) 17.7 Mt, and crustaceans 9.4 Mt [185]. The rising contamination of sea water including from inadequately treated sewage effluent, and the increase in the world trade of seafood along with the increase in its consumption in raw or undercooked conditions, have resulted in an increase in infections caused by *Vibrio* [30,141,184]. In sub-Saharan countries, the contamination of drinking and recreational water and the consumption of inadequately cooked aquatic food products remain a threat to public health [57,184]. In that part of the world, and despite cholera epidemics being frequent, there is a lack of knowledge about the microbial quality of water sources. In a survey on urban water reservoirs (n = 39) in Burkina Faso, 14.78% of them had *V. cholera* non-O1 and non-O139 [186].

In parallel, the continuous increase in recreational activities on, in, and along aquatic bodies, such as sport fishing, boating, bathing, diving, snorkeling, surfing, animal watching, and sailing, which positively contribute to human well-being [187], can also put at risk their practitioners. The growth of economic activities such as tourism and maritime traffic also affects *Vibrio* spp. abundance and diversity all over the globe. The water from BWs is a known sources of many organisms, among them pathogenic bacteria such as *Vibrio* spp., including the serotypes of *V. cholerae* O1 [36,169], O59, and 139 [169]. Along with the high concentrations of pathogenic strains, resistance to antimicrobials is often present in an expressive way [169].

The increase in the number of infections by *Vibrio* species has also been reported in species farmed in aquaculture. Outbreaks with significant mortality of the farmed Pacific oyster (*Crassostrea gigas*) have been reported in France and other European countries from 2008 onwards, and some others were reported in 2010–2011 from Australia and New Zealand. *V. aestuarianus* subsp. *francensis* has been associated with those events [188]. In an aquaculture facility for *Saccharina latissima* growth for human consumption located in Northeast USA, *Escherichia coli* O157:H7, *Salmonella enterica* ser. *typhimurium*, *V. parahaemolyticus*, and *V. alginolyticus* were found in both kelp and water samples during the winter. Despite the low levels, the frequency of detection poses a risk of foodborne pathogens, so best management practices are recommended to control microbial growth during kelp harvest and processing [63]. One of the most promising fish species for the diversification of aquaculture in the Mediterranean is the amberjack (*Seriola dumerili*), but its production expansion is failing due to its pathogens, among them *V. harveyi* and *P. damselae* [189].

In addition, the risks of the *Vibrio* spp. to environmental, animal, and human health may be enhanced by climate change, especially the ocean warming [190]. Recent data support the hypothesis that climate change, along with environmental pollution, epidemiological, demographic, and behavioral factors, is increasing the geographical spread as well the frequency of vibriosis [21,191]. In the period between 1962 and 2004, the temperature increased 1.13 °C in the North Sea at Helgoland [192]. Recently and in the same region was reported for the first time the serotype *V. cholerae* O139 [193].

The temperature rising can contribute, directly or indirectly, to changes in geographic distribution of *Vibrio* spp., community composition, species dominance, and even the dominance of virulence genes [37,42,43,129,193,194]. Over a 14-month period, *V. parahaemolyticus*, *V. vulnificus*, and *V. cholerae* increased their abundance, measured by MPN-PCR, during the summer months in the German bight. The environmental factors that mostly explained the variations were temperature and nitrites; the virulence factors of the three species varied in

time and space, and in *V. cholerae* more than four virulence-associated genes were detected at temperatures above 16.8 °C [193].

In aquatic animals such as fish, the water temperature, in addition to affecting the prevalence of virulence factors, can also affect the quality of the host's immune response to infection, due to cumulative stress responses [195]. In mussels, high temperature may reduce the ability to eliminate bacteria in hemolymph [196]. Isolates of *V. splendidus* and *V. aestuarianus* were moderately pathogenic for mussels in intramuscular infections and bath infections, and mortalities only occurred when animals were infected with a high bacterial concentration at 25 °C and in hypoxia [81].

Vibrio spp. are free-living inhabitants of marine coastal waters, brackish, and inland aquatic bodies, and their presence does not indicate fecal contamination. The monitoring of water microbial quality is based on fecal indicator bacteria (FIB), which may be below the detection limit when *Vibrio* or other high-risk bacterial groups are present [38]. Consequently, prevention efforts should target waterborne transmission in coastal areas, and provide education of health personnel, to promote a rapid diagnosis and prevent clinical complications caused by *Vibrio* spp. [181]. In addition, the ability of vibrios to adapt to many environmental conditions and niches that can be polluted or/and under pressure of climate change supports the need for further research to understand their ecological role, dissemination, and risks in freshwater ecosystems [23,184].

All the players involved in water and water resources exploration should considerer collaborative networks, and a multiparametric approach of microbial indicators of quality and pollution in water systems. The research network VibrioNet proposes study of the non-cholera vibrio pathogenic species (*V. parahaemolyticus*, *V. vulnificus*, *V. cholerae* non-O1, non-O139, *V. alginolyticus*) in marine environments and in seafood consumed by humans, and their risks in central Europe [141].

Sampling processing, culture and molecular detection methods to identify microorganisms in complex environmental samples, and water quality standards need to be updated and harmonized for more accurate and timely detection of health hazards [197]. We need a better understanding of the ecology of non-enteric microorganisms, such as vibrios, and their environmental significance, and to establish non-fecal indicators and sentinels, the ecology of the virulent strains, and their antibiotic susceptibility profiles to anticipate risks and prepare our response.

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