



Temperature Upshift Mostly but not Always Enhances the Growth of *Vibrio* Species: A Systematic Review

H. I. Sheikh¹, M. Najiah¹, A. Fadhlina², A. A. Laith¹, M. M. Nor^{2,3}, K. C. A. Jalal⁴ and Nor Azman Kasan^{5*}

¹Faculty of Fisheries and Food Science, Universiti Malaysia Terengganu, Kuala Nerus, Malaysia, ²Institute of Food Security and Sustainable Agriculture, Universiti Malaysia Kelantan, Jeli, Malaysia, ³Faculty of Agro-Based Industry, Universiti Malaysia Kelantan, Jeli Campus, Kelantan, Malaysia, ⁴Faculty of Agriculture, Universiti Islam Sultan Sharif Ali (UNISSA), Bandar Seri Begawan, Brunei, ⁵Higher Institution Centre of Excellence (HICoE), Institute of Tropical Aquaculture and Fisheries, University Malaysia Terengganu, Kuala Nerus, Malaysia

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*Correspondence:

Nor Azman Kasan
norazman@umt.edu.my

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The spread of *Vibrio* spp. and the prevalence of vibriosis around the world are often correlated with global warming, especially an increase in sea surface temperature. However, many ecological and virulence factors also trigger the spread of *Vibrio* species, while vibriosis occurs at both low and high temperatures. Recent studies that focused on a single factor (e.g. temperature) and one species (e.g. *V. vulnificus*) also showed that single factors such as temperature were insufficient to explain the pathogenicity and virulence of *Vibrio* spp. In this review, we have compiled and discussed the existing literature on the effect of temperature on different growth and pathogenicity of *Vibrio* spp. A systematic literature search was conducted using Web of Science (WoS) and SCOPUS databases up to 1st January 2022. After applying the selection criteria, a final list of 111 articles was included in this review. We have found that only certain *Vibrio* spp. are positively impacted by the increase in temperature. The results showed that 47% of the articles reported an increase in growth with the increase in temperature, while 38% showed that the relationship is complex. Reduced growth (6%) and no effect (9%) were also reported. These results showed that most but not all *Vibrio* spp. were positively impacted by an increase in temperature. The results indicated that *V. alginolyticus*, *V. cholerae*, *V. parahaemolyticus*, and *V. vulnificus* are the biggest threats to human and animal wellbeing.

Keywords: *vibrio*, growth, global warming, pathogenicity, SLR, treatment

INTRODUCTION

The increased occurrence of vibrio diseases (vibriosis) and the spread of *Vibrio* spp. to new geographical areas were correlated with global warming, especially temperature. This could be due to *Vibrio* spp. ability to remain in a “viable but nonculturable” (VBNC) state, until favourable conditions such as a rise in temperature occur, in which it becomes culturable and grows (Hernández-Cabanyero et al., 2020; Montanchez and Kaberdin, 2020). However, many ecological and virulence factors are also correlated with the spread of *Vibrio* species and vibriosis. Moreover, despite the rich literature on vibriosis, these studies were not connected and were either too narrow or too qualitative (Froelich et al., 2017; Rahman et al., 2017; Hernández-Cabanyero et al., 2019;

Montánchez et al., 2019). This became evident when studies that focused on one factor (e.g. temperature) and one species (e.g. *V. vulnificus*) found that single factors such as temperature were insufficient to explain the pathogenicity and virulence of *Vibrio* spp. in many cases (Kim et al., 2012; Froelich et al., 2017; Rahman et al., 2017; Hernández-Cabanyero et al., 2019; Montánchez et al., 2019). This was unlikely as even among *Vibrio* spp., their optimum growth parameters (temperature, salinity, and pH conditions) are significantly different. For example, *V. vulnificus* can remain viable and grow between 4–14°C, while its optimum growth is at a much higher temperature (25°C) and low salinity (1–2%). *V. cholerae* could grow in 10% salinity and 35°C but flourished at a slightly lower temperature (30°C) and higher salinity (15%) (Chowdhury et al., 2017). Besides, cold water vibriosis outbreaks associated with *V. salmonicida* were reported to occur at very low temperatures (3–10°C) both in nature and in laboratory settings (Colquhoun et al., 2002). Other arguments can also be observed in published literature including the minimum temperature that enables *V. parahaemolyticus* growth. For instance, some studies have reported that *V. parahaemolyticus* needs a minimum temperature of 13°C to grow in broth (Kim et al., 2012), while other studies argued that a temperature as low as 5°C is sufficient (Miles et al., 1997). The increased prevalence of pathogenic *Vibrio* species calls for global attention from researchers and clinicians. Therefore, a systematic review of temperature vs growth rate of vibrio is important to predict Vibriosis episodes. Identifying these risks will also help in formulating mitigation plans, especially for seafood illnesses in humans as well as for the mariculture industry. Hence, this systematic review aimed to compile the literature that addressed the effect of an increase in temperature on the growth of *Vibrio* spp. It is hypothesized that only certain thermostable *Vibrio* spp. are positively impacted by an increase in temperature. The review will also address the increased pathogenicity of *Vibrio* spp. under elevated temperatures to assess which *Vibrio* spp. pose the highest threat in this era of global warming.

METHODOLOGY

Review Question and Scope

Previous studies reported opposing arguments and findings on the correlation between global warming and the growth of *Vibrio* spp. were the main motivations behind this systematic review. Besides, *Vibrio* spp. have significantly different optimum growth temperatures and conditions. We addressed 1) Do all *Vibrio* spp. flourish and become virulent with the increase in temperature? and, 2) Which *Vibrio* spp. pose a significant threat to humans and animals in the era of global warming? During the write-up and whenever applicable, the articles were cited chronologically (year) to show the progress or direction of the research.

Search strategy

A systematic literature search was conducted using Web of Science (WoS) and SCOPUS databases up to 1st January 2022. The search was limited to these 2 databases due to the quality of

these databases and the abundance of literature on the subject. The keywords used were “*Vibrio* AND temperature”. A total of 3063 and 3542 documents were retrieved from WoS and SCOPUS databases, respectively. The search was then limited to the article search keyword appearing in the title which yielded a search term of “TITLE (*vibrio* AND temperature)”. A total of 202 and 238 articles were retrieved from WOS and SCOPUS databases respectively which were then subjected to further screening. These 2 search results were combined (202 + 238) resulting in 440 articles which were then subjected to screening.

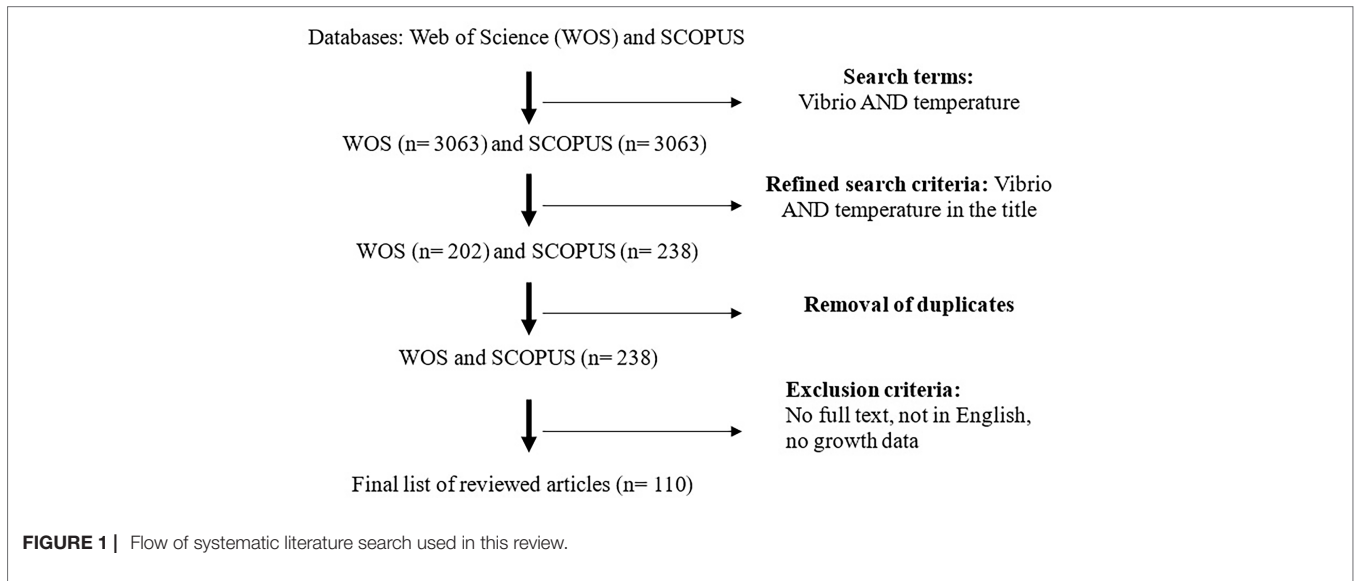
Screening and Eligibility Criteria

All the 202 articles in WOS were included in the 238 articles from SCOPUS and duplicates were removed resulting in 238 articles that were then subjected to inclusion/exclusion criteria. Articles (n=128) were excluded due to either no full paper, not in English, or no growth profiles. Examples of articles excluded due to lack of growth profiles were articles on the effect of temperature on non-growth aspects such as susceptibility to infection, fatty acid production, food applications, substrate utilization, etc. A final list of 111 articles was considered for this review (Figure 1).

RESULTS AND DISCUSSION

Initial Screening

Initial screening of the selected publications (n=111) showed that 91% of the articles argued that temperature has a significant impact on *Vibrio* spp. growth, while no effect was observed over the tested range in 9% of the articles (10 out of 111). The increase in temperature positively correlated with growth in 47% of the articles (52 out of 111), while temperature negatively correlated with growth in 6% of the articles (7 out of 111) and. The relationship between the increase in temperature and growth of *Vibrio* spp. was found to be complex or multifactorial in 42/111 articles (38%). In the initial screening, WOS was expected to yield fewer articles as the database contains fewer journals. For example, in 2016, WoS contained 13,605 journals, while Scopus contained 20,346 journals (Mongeon and Paul-Hus, 2016). Initial classification justified the aim of this review as the relationship between *Vibrio* spp. growth and temperature was found to be complex in 38% of the studies, even though more articles (47%) supported the consensus that *Vibrio* spp. grow better at higher temperatures. Most recent articles were also in favour of the theory that the relationship is significant but might not be as linear. For instance, *Vibrio* cases in Canada with maximum sea surface temperature (SST) were studied over 25 years (1992 to 2017) (Galanis et al., 2020). The correlation was significant with the correlation coefficient (r^2) of 0.46, which is considered not strong (Fischer et al., 2016; Ramakers et al., 2017). *V. vulnificus* virulence was also found recently to be multifactorial due to the complex interaction between temperature and other factors such as iron availability. The study showed that despite temperature increasing growth and general virulence factors (e.g. Motility), main virulence factors (e.g. hemolysin VvhA) were controlled by iron concentration (Hernández-Cabanyero et al., 2020). Hence, the discrepancies presented in the introduction were supported by this review.



Effect of Temperature On The Growth of *Vibrio* spp.

Vibrio spp. were able to grow in temperatures ranging from 0.5°C to 48°C which showed their unique adaptability to changes in temperature (Figure 2). First, this range covers *Vibrio* spp. that could be potentially pathogenic to animals (22°C), especially aquatic animals, and humans (37°C) (Tall et al., 2013). Secondly, several human and animal pathogens species, *V. cholerae*, *V. parahaemolyticus*, and *V. vulnificus*, were able to grow at ≤10°C and ≥35°C. This is concerning as *V. cholera*, *V. parahaemolyticus*, *V. alginolyticus*, and *V. vulnificus* are well known to be pathogenic to humans (Baker-Austin et al., 2018). Optical density (OD) data showed a slight positive correlation with temperature while log

growth data did not show any pattern. The temperature range was then divided into 4 intervals to investigate if certain species are correlated with certain temperature ranges. The intervals selected were ≤10°C, 11-22°C, 23-35°C, and ≥36°C (Figure 2). A disproportionately high number of studies focused on *V. parahaemolyticus*. Hence, data were converted to a percentage and labelled as prevalence. *V. alginolyticus*, *V. cholerae*, *V. costicola*, *V. parahaemolyticus*, and *V. vulnificus* were found to grow in all 4 temperature ranges, while *V. harveyi* and *V. Marinus* were able to grow in 1 interval only (23-35°C). Growth ranges from reviewed articles were compiled and compared with the optimum temperature of each species (Table 1). The table also highlights the adaptability of *Vibrio* spp. to a broad range of temperatures outside their optimum temperature.

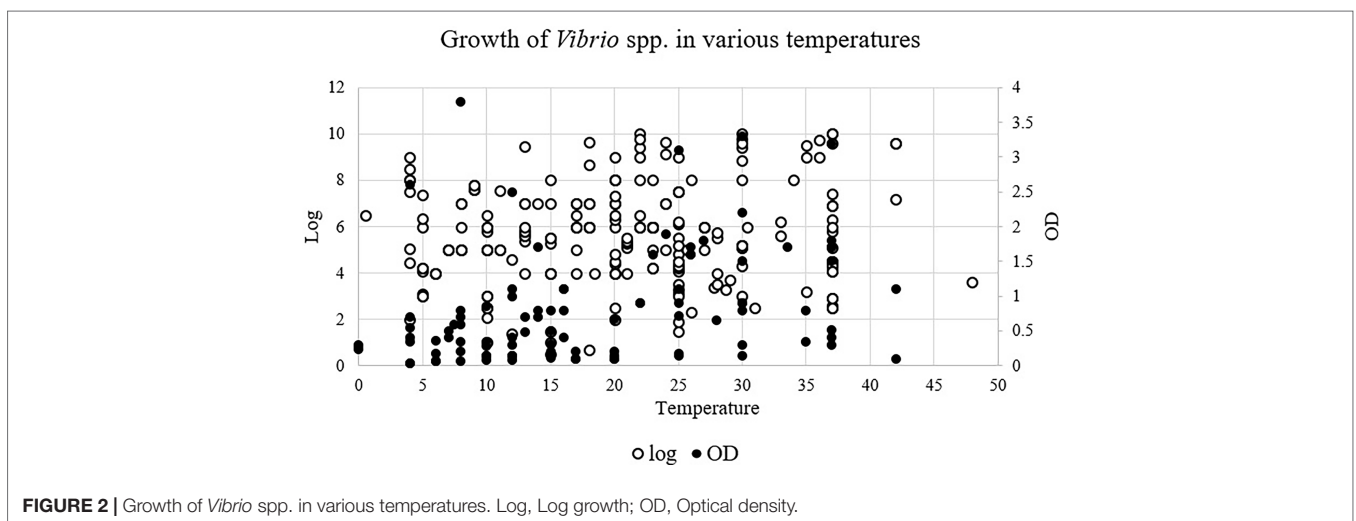


TABLE 1 | Growth ranges of *Vibrio* spp. from reviewed articles and their optimum temperature.

Vibrio species	Growth range in reviewed literature (°C)	Growth range (°C)	Optimum Temperature (°C)	*ATCC strain (°C)
<i>V. alginolyticus</i>	22-42	20	37-42 (Xie et al., 2020)	37
<i>V. anguillarum</i>	10-30	20	25-30 (Lages et al., 2019)	26
<i>V. cholerae</i>	4-37	33	37 (Fu et al., 2018)	37
<i>V. coralliilyticus</i>	24-27	3	28 (de O Santos et al., 2011)	30
<i>V. costicola</i>	4-37	33	30 (Adams & Russell, 1992)	–
<i>V. crassostreae</i>	17-27	10	23 (Burks et al., 2017)	–
<i>V. fischeri</i>	8-34	26	28 (Cohen et al., 2019)	26
<i>V. harveyi</i>	26-30	4	26 (Montánchez et al., 2019)	26
<i>V. marinus</i>	25-35	10	15 (Morita & Albright, 1968)	18
<i>V. parahaemolyticus</i>	4-48	44	37 (Liu et al., 2016)	37
<i>V. salmonicida</i>	4-20	16	15 (Colquhoun et al., 2002)	15
<i>V. shiloi</i>	4-30	26	30 (Kushmaro et al., 2001)	26
<i>V. splendidus</i>	10-22	12	22 (Armada et al., 2003)	26
<i>V. tasmaniensis</i>	8-23	15	28 (Thompson et al., 2003)	–
<i>V. vulnificus</i>	0.5-42	37	36 (Kim et al., 2012)	30

*ATCC data were obtained from <https://www.atcc.org>. - No available ATCC strain.

Vibrio spp. That Are Negatively Impacted by the Rise in Temperature

Initial screening of selected articles showed that an increase in temperature led to a decreased growth of *Vibrio* spp. in very few articles (n= 7/111). *Vibrio* spp. that were negatively affected by the increase in temperature was *V. harveyi*, *V. marinus*, *V. salmonicida*, *V. shiloi*, *V. tasmaniensis*, and *V. vulnificus*. These species were either psychrophilic bacteria (cold-loving) or were cultured under extremely unfavourable conditions. *V. harveyi* was cultured in seawater at 30°C (optimum 26°C) and under carbon limitation and showed a reduction in culturable cells and cell size. The rod-shaped morphology also changed to a coccoid-like cell (Montánchez et al., 2019). The second species was *V. marinus* which showed that its viability and protein synthesis was higher at 15 than 22 and 25°C (Cooper and Morita, 1972). At 20°C, the synthesis of DNA and RNA in *V. marinus* was also inhibited, while the expression of enzymes such as malic dehydrogenase, which is part of a citric acid cycle, was deregulated (Morita and Albright, 1968). *V. marinus* optimum growth was reported to be 15°C in a previous study with a very short generation time of just 1 hr at 15°C (Morita and Albright, 1968) or 18°C for ATCC 1538. Growth of *V. salmonicida* at 17 and 20°C was low, while growth was optimum at temperatures ≤15°C (on agar). However, for *V. salmonicida*, optimum growth occurred at 15°C (Colquhoun et al., 2002) and for ATCC 1538. VBNC state was induced in *V. shiloi* (optimum temperature 26-30°C) when cultured at 20°C, while in terms of morphology, cell lysis and curling were also observed (Kushmaro et al., 2001; Vattakaven et al., 2006). VBNC state was also induced in *V. tasmaniensis* (optimum temperature 28°C) when cultured at 20°C after 157 days due to starvation (artificial seawater media). The rod shape of cells also changed more rapidly to coccoid and became completely coccoid on day 147 (Thompson et al., 2003; Vattakaven et al., 2006). *V. shiloi*, optimum growth was reported to be 30°C in a previous study (Kushmaro et al., 2001) or 26°C for ATCC BAA-91, while *V. tasmaniensis* (optimum growth 28°C) (Thompson et al., 2003). These two species were negatively impacted by the culture media (artificial seawater) which was nutritionally deficient (Vattakaven

et al., 2006). *V. vulnificus* was negatively impacted by temperature when 2.20 ×10⁶ CFU was recorded at 5°C compared to 2.09 ×10⁶ CFU when cultured at 20°C, which was due to low pH and salinity (Hijarrubia et al., 1996). *V. vulnificus* 4965 were not able to grow at temperatures below 13°C or above 22°C when cultured at 10 ppt salinity. Survival at 21°C was also lower than at 14°C at a broad range of salinity (5–25 ppt). A mixture of 3 *V. vulnificus* strains (4793, 4832, and ATCC 27562) could also not grow well at 5 and 35°C (Kaspar and Tamplin, 1993). *V. vulnificus*, optimum growth was reported to be 36°C in a previous study (Kim et al., 2012) or 30°C for ATCC 27562, however, it was negatively impacted due to low pH and salinity (Hijarrubia et al., 1996).

Vibrio spp. That Were Not Significantly Impacted by the Rise in Temperature

Initial screening showed that no significant effect of temperature was observed over the tested range in 10/111 (9%) articles. *Vibrio* spp. that were not significantly affected by the increase in temperature over tested ranges were *V. alginolyticus*, *V. cholerae*, *V. fischeri*, *V. parahaemolyticus*, *V. splendidus*, and *V. vulnificus*. Most of the aforementioned species were heat-stable or thermophilic, while few were marine vibrios and were impacted mainly by salinity. Five strains of *V. alginolyticus* from various ecological sources were cultured at various temperatures (5-42°C), salinity (0.5-6% NaCl), and pH (4.5-12). The results showed extraordinary flexibility as almost all strains were able to grow in almost all conditions if given enough time (> 3 days) (Farid and Larsen, 1981). *V. alginolyticus* was also able to survive a wide range of temperatures (22 to 42°C) (Gu et al., 2016). Growth, collagenase activity, and protease activity in *V. alginolyticus* at 30 and 37°C were affected by oxygen and not temperature (Hare et al., 1981). Another study on *V. alginolyticus* cultured at a wide temperature range of 26-42°C reported that swarming was only observed when the salinity was suitable, indicating the salinity is the main factor affecting its growth, while salinity as low as 0.6% was enough for growth at 20-28°C (Ulitzur, 1975). *V. cholerae*'s growth was studied at 4, 25, and 35°C and 0.5 and 10% salinity. The results showed that the total count of cells was similar in the

range of 4–35°C, while the physiological state (growth phase) and inoculum size had a bigger effect than temperature and salinity (Montilla et al., 1996). *V. fischeri* was able to grow at a very broad temperature range (8–34°C), moreover, temperature stress at the extremes (8 and 34°C) led to the evolution and higher growth fitness (Cohen et al., 2019). The Most Probable Number (MPN) of *V. parahaemolyticus* was not significantly different in the temperature range of 20–25°C, while high salinity was considered as the main factor in reducing the MPN (Larsen et al., 2015). *V. parahaemolyticus* was extremely tolerant to temperature and grew at temperatures as low as 8.3°C and as high as 45.4°C, while water activity was considered as the main factor in slowed growth (Miles et al., 1997). Growth of 2 *V. splendidus* strains cultured in several media at 4, 10, or 22°C, and under varying salinities was studied. The results showed that temperature did not significantly affect the growth, while salinity and nutrient content were determined as the main factors (Armada et al., 2003). MPN of *V. vulnificus* was not significantly different in the temperature range of 20–25°C, while high salinity was considered the main factor in reducing the MPN (Larsen et al., 2015). *V. vulnificus* isolated over 2 years with temperatures ranging from 6.7 to 35.6°C showed that growth was affected by salinity (28 ppt and above) rather than temperature (Motes et al., 1998).

Temperature Upshift Enhances the Growth of *Vibrio* spp.

Even though 38% showed that the rise of vibriosis is multifactorial, most of the articles 47% (n= 52/111) showed that the abundance of *Vibrio* spp. was positively impacted by the rise in temperature agreed with the consensus that *Vibrio* species grow better at higher temperatures. This indicated that the frequent occurrence of vibriosis might be due to environmental conditions such as global warming and higher sea surface temperature favouring the growth of *Vibrio* spp. *Vibrio* spp. that were positively affected by the increase in temperature were *V. alginolyticus*, *V. anguillarum*, *V. cholerae*, *V. coralliilyticus*, *V. costicola*, *V. harveyi*, *V. parahaemolyticus*, *V. salmonicida*, *V. shiloi*, and *V. vulnificus*. Most of the articles in this section studied *Vibrio* species that grow better in higher temperatures.

First, *V. cholerae* (optimum growth at 37°C) showed maximum growth at higher temperatures (23–30°C), while it often entered the VBNC state at lower temperatures (4°C). The culturability was successfully recovered by re-incubation at 20–23°C (Ravel et al., 1995; Johnston and Brown, 2002). Temperature upshift to 37°C was reported to recover the culturability of *V. cholerae* from VBNC state by upregulating various metabolic pathways such as carbohydrate and phosphate metabolism (Debnath et al., 2019). A more detailed study on growth phases showed that temperature shortened the lag time at higher temperatures (22–30°C) compared to 15°C where no growth was recorded (Wang and Gu, 2005). Another study also showed that *V. cholerae* grew exponentially with the increase of temperature from 15 to 37°C (Kirschner et al., 2008). When cultured at various temperatures ranging from 10 to 30°C, *V. cholerae* also showed that temperature highly and linearly correlated with growth (Fu et al., 2013). The positive effect of temperature on *V. cholerae*

was also reported in prevalence studies where higher abundance was observed at temperature >19°C compared to <19°C (Louis et al., 2003). Higher temperatures also significantly increased the prevalence of *V. cholerae* in blue crabs (Sullivan and Neigel, 2018). Pathogenic strains of *V. cholerae* such as *V. cholerae* O1 EI Tor also showed that temperature increase from 15 to 25°C increased biofilm formation which is related to growth (Stauder et al., 2010). *V. cholerae* O1 cultured at 5 to 30°C also showed that growth increased with the increase of temperature (Huq et al., 1984). The O1 strains were also able to survive temperatures as high as 65°C (Castro-Rosas and Escartin, 2005). A recent study on several pathogenic and non-pathogenic strains (O395, C6706, and N16961) subjected to various temperatures (4, 22 and 37°C) showed a significant reduction in growth and initiation of VBNC state at 4°C, while optimum growth was recorded at 22°C (Wu et al., 2016).

The second major species was *V. coralliilyticus* (optimum growth 30°C) where its growth increased when cultured at temperatures ranging from 16 to 30°C (Ben-Haim et al., 2003; Boroujerdi et al., 2009). Temperature upshift from 25 to 30°C also improved the growth of *V. coralliilyticus* (Frydenborg et al., 2014). The increased growth was correlated with prolonged exponential and stationary phases (Ben-Haim et al., 2003; Kimes et al., 2012). An increase in temperature from 24 and 27°C also changed the metabolomic profiles significantly (Boroujerdi et al., 2009). Higher temperatures also significantly increased the prevalence of environmental *Vibrio* spp. such as *V. tubiashii* which is closely related to *V. coralliilyticus* is associated with *Pocillopora damicornis* coral bleaching (Tout et al., 2015).

The third major thermophilic species was *V. parahaemolyticus* (optimum growth at 37°C) and were still able to grow at a wider temperature range (15 to 36°C) (Beuchat, 1974). The increase in temperature was reported to have increased growth in numerous studies. There was a direct relationship between growth rate and temperature when cultured at 13 to 36°C (Kim et al., 2012), 5–20°C (Mudoh et al., 2014) and 4 to 37°C (Han et al., 2016). It also grew better at 20°C compared to 4°C (Johnston and Brown, 2002). The increase in growth at higher temperatures (30.4 and 37°C) was correlated with a shorter generation time of 12–14 min (Horie et al., 1966), shorter lag time (Kim et al., 2012) and a faster growth rate (Fernandez-Piquer et al., 2011). For instance, *V. parahaemolyticus* grown at 3.6 to 30.4°C showed that the growth rate at 30.4°C (0.135 log₁₀ CFU/h) was significantly higher compared to 3.6°C (0.015 log₁₀ CFU/h) (Fernandez-Piquer et al., 2011). Optimum growth rate, shortest lag time, and maximum population density were all observed at 36°C (Kim et al., 2012). Studies on pathogenic and non-pathogenic strains also agreed on the positive effect of temperature on *V. parahaemolyticus*'s growth. Growth and metabolic activities of pathogenic *V. parahaemolyticus* were higher at 15–44°C, while at 10–20°C growth was up to 3 folds slower mainly due to prolonged lag-phase (Boonyawantang et al., 2012). *V. parahaemolyticus* O3:K6 cultured at a temperature range of 15–25°C showed a positive correlation with growth, with maximum growth recorded at 25°C (Nishina et al., 2004). Pathogenic and non-pathogenic *V. parahaemolyticus* were grown at various temperatures (10 and 30°C) and media (broth and oyster slurry). Those results showed

higher temperature led to higher growth rates and shorter lag times (Yoon et al., 2008). The standard growth rate of pathogenic and non-pathogenic *V. parahaemolyticus* cultured at 4, 10, and 24°C also showed that maximum growth rate was observed in the highest temperature of 24°C (Cowan et al., 2019). Besides growth, the abundance and prevalence were also increased with the increase of temperature. For example, at temperatures $\geq 25^\circ\text{C}$, abundance was as high as 94%, while at temperatures $< 10^\circ\text{C}$, abundance was as low as 15% (Cook et al., 2002). A meta-analysis showed that *V. parahaemolyticus* was significantly and positively correlated with temperature in both water and raw oysters (Young et al., 2015). Recent studies supported these earlier findings where higher temperatures significantly increased the prevalence of *V. parahaemolyticus* in blue crabs (Sullivan and Neigel, 2018).

The last major species were *V. vulnificus* (optimum growth at 30°C), which in laboratory cultures, grew at a range of 13–42°C with its optimum growth recorded at 37°C (Kelly, 1982). *V. vulnificus* cultured at a temperature range of 5–15°C showed maximum growth at 15°C, while at lower temperatures, the initial inoculum was able to remain viable but not grow (Nishina et al., 2004). Another study also showed that a low temperature of 4°C was detrimental to the growth of *V. vulnificus* and initiated VBNC state, while culturability was possible at 10°C (Wolf and Oliver, 1992). Temperature upshift from 5 to 25°C also recovered the culturability of improved the growth of *V. vulnificus* even in starvation conditions (Biosca et al., 1996). Other studies also showed that it grew at higher temperatures (20 and 25°C) compared to lower temperatures (4 and 7.2°C) (Johnston and Brown, 2002; Limthammahisorn et al., 2008). Simultaneous increases in temperature and reduction in salinity (25°C/2.5‰ to 37°C/0.9‰) increased the growth of *V. vulnificus* (Kim and Shin, 2011). Recent studies showed a similar trend where *V. vulnificus* cultured at a temperature range of 25–37°C showed a consistent increase in growth (Kim et al., 2016). The positive effect of temperature increase on growth was correlated to a higher growth rate and short lag time at 22 and 30°C compared to 15°C (Wang and Gu, 2005). Direct positive relationships between growth rate and temperature (11 to 36°C) were also reported, while optimum growth rate, shortest lag time, and maximum population density were all observed at 36°C (Kim et al., 2012). Studies on various types of *V. vulnificus* showed that the bacteria always grew better at higher temperatures. For example, wild and mutant strains grew faster at 37°C compared to 24°C by speeding up entry into the log phase by a couple of hours (Elgaml et al., 2014). Environmental and clinical strains cultured at different temperatures (24–37°C), pH (5.5–8.5) and iron concentrations (18–200 μM) showed that most strains grew better at 30 and 37°C compared to 24°C (Çam and Brinkmeyer, 2020). The abundance and prevalence of *V. vulnificus* also increased with the increase in temperature. A study showed that *V. vulnificus* made up 85.7 and 210.9 CFU/mL out of 5.7×10^6 CFU/mL and 2.1×10^7 CFU/mL total bacteria, respectively (Randa et al., 2004). Higher temperatures also significantly increased the prevalence of *V. vulnificus* in blue crabs (Sullivan and Neigel, 2018). Several other *Vibrio* spp. that were positively impacted by a rise in temperature was also reported. *V. alginolyticus* (optimum growth at 37°C) cultured at 37°C showed a short generation time of 12–14 min

(Horie et al., 1966), which was also its optimum temperature (ATCC strain). *V. anguillarum*'s (optimum growth at 26°C) was cultured at different temperatures (15°C and 25°C) and iron concentrations and the results showed that growth and survival were significantly higher at 25°C (Lages et al., 2019). *V. costicola* (optimum growth at 30°C) grew at temperatures between 4 to 37°C, however, optimum growth occurred at 37°C (Adams and Russell, 1992). *V. harveyi* (optimum growth at 26°C) cultured at the temperature range of 12.9–27.1°C and salinity of 0.6 to 3.4‰ showed that an increase in temperature made the bacteria grow faster at higher temperatures where at 12.9, 15, and 27.1 C °C it took 144, 120 and 28 h to reach maximum growth (Zhou et al., 2012). *V. salmonicida* (optimum growth at 15°C) grew better at higher temperatures (15°C) compared to a lower temperature (7.5°C) regardless of salinity (1 or 2.5‰ NaCl) (Karlsen et al., 2008). Another study also reported a higher growth rate and short lag time at 22 and 30°C compared to 15°C (Wang and Gu, 2005). *Vibrio* AK-1 (later identified as *V. shiloi*) (optimum growth at 26–30°C) was cultured at a temperature range of 15–35°C and showed a continuous increase in growth rate which plateaued at 35°C (Kushmaro et al., 1998). When grown in seawater at a temperature range of 16–28°C, the results showed that growth reached 9.5×10^8 at 16°C, while at 28°C the growth increased and reached 4.5×10^9 (Israely et al., 2001). Growth was also significantly improved by temperature upshift from 25 to 30°C (Frydenborg et al., 2014). The increased growth of *V. shiloi* was correlated to faster entry into the log phase and a higher survival rate by extending the exponential growth period to 30°C compared to 23°C (Murali et al., 2010). Two studies on an unidentified *Vibrio* spp. called *Vibrio* ANT-300 (optimum growth $< 13^\circ\text{C}$) showed that increasing the temperature from 0 to either 7, 13, or 16°C improved growth, protein synthesis and integrity, and polyketides synthesis (Araki, 1991; Araki, 1992).

Temperature-Controlled Virulence of *Vibrio* spp.

Temperature-related virulence and pathogenesis of *Vibrio* spp. indicated that global warming favours the growth of *Vibrio* spp., however, for the bacteria to cause diseases virulence is an important factor. Hence, the articles in this review were screened again to summarize how high temperature induces virulence/pathogenicity. For instance, in the control group (22°C), Oceanospirillales was the most abundant order associated with *P. damicornis* coral, while at higher a temperature (31°C) Vibrionaceae order became dominant (Tout et al., 2015). An increase in temperature was found to induce pathogenicity/virulence in numerous *Vibrio* spp., namely *V. alginolyticus*, *V. anguillarum*, *V. coralliilyticus*, *V. harveyi*, *V. parahaemolyticus*, *V. salmonicida*, *V. shiloi*, and *V. vulnificus*. An increase in culture temperatures of *V. alginolyticus* from 22 to 37°C led to an increase in the production of exotoxins and the expression of virulence factors, however, at up to 42°C, the expression of exotoxins and virulence factors were inhibited (Gu et al., 2016). *V. anguillarum* RV22 showed differential expression of virulence genes at different temperatures (15°C and 25°C). At high temperatures (25°C), chemotaxis, motility, iron uptake, vancomycin,

hemolysins, and outer membrane components were upregulated (Lages et al., 2019).

V. cholerae O1 EI Tor showed that when a temperature increased by 15 to 25°C, the virulence increased due to higher biofilm formation, increased the expression of e N-acetylglucosamine-binding protein A (GbpA) and mannose-sensitive haemagglutinin (MSHA) which increased its ability to colonize new host (Stauder et al., 2010). During recovery from the VBNC state, proteomic analysis of *V. cholerae* cultured at 37°C showed increased expression of 13 out of 19 proteins compared to VBNC (Debnath et al., 2019). The increase in temperature significantly increases the expression of extracellular protease in *V. coralliilyticus* which leads to higher coral (*P. damicornis*) bleaching and lysing (Ben-Haim et al., 2003). Metabolomics analysis of *V. coralliilyticus* under increased temperature leads to changes in osmoregulation and energy production pathways, while in terms of metabolites, major changes were in betaine, succinate, and glutamate (Boroujerdi et al., 2009). *V. coralliilyticus* exposed to increased temperature (above 25°C) lead to increased expression of virulence factors related to motility (e.g. Flagellar proteins), host degradation (e.g. proteases), resistance (e.g. efflux pumps), and upregulation of transcriptional factors (e.g. quorum sensing) (Kimes et al., 2012). The ability of *V. cholerae* Serovar O1 maximum growth of and attachment to copepods at 25 and 30°C was significantly better than at 5 or 15°C (Huq et al., 1984). Virulence gene expression such as adherence factors was found to occur at 17°C causing mortalities in *Haliotis tuberculata* abalone due to *V. harveyi* infection (Travers et al., 2009). *V. harveyi* cultured at 28°C (optimum 26°C) led to 100% mortality in abalone *Haliotis diversicolor* (Jiang et al., 2013). *V. harveyi* cultured in seawater at 30°C (optimum 26°C) and under carbon limitation showed increased expression of virulence factors such as lytic enzymes (Montánchez et al., 2019). Clinical and virulent strains of *V. parahaemolyticus* increased with the increase in temperature (Turner et al., 2014). *V. parahaemolyticus* were cultured at 4 to 37°C result in significantly stronger growth, biofilm formation, quorum sensing (autoinducer-2 production), and exoprotease activity at a temperature of $\geq 25^\circ\text{C}$ (Han et al., 2016). Novel outer membrane protein (OMP) called VS-P2 was expressed in *V. salmonicida* when cultured at 20°C compared to its optimum temperature of 15°C (Colquhoun et al., 2002). *V. salmonicida* cultured at higher temperature (15°C) showed higher expression of flagellin gene expression in comparison to a lower temperature (7.5°C) (Karlsen et al., 2008).

Vibrio AK-1 (later identified as *V. shiloi*) showed that the pathogen did not infect the coral *Oculina patagonica* and caused bleaching at 16°C, while at 20-29°C continuous increase in bleaching was observed (Kushmaro et al., 1998). *V. shiloi* was able to infect and bleach coral *O. patagonica* at 28°C but not at 16°C (Israely et al., 2001). *V. vulnificus* was found to increase the expression of rpoD, rpoS, luxS, smcR, crp and vvpE and the production of *V. vulnificus* protease (VVP) at 26°C, while at 37°C it increases the expression of rpoN, vvhA, and luxT and production of *V. vulnificus* hemolysin (VVH) (Elgaml et al., 2014). An increase in culture temperature of *V. vulnificus* showed that the expression of virulence factor siderophore increased (Turner et al., 2014). *V. vulnificus* cultured at a temperature range

of 25-37°C showed a consistent increase in growth as well as expression of virulence regulators such as cyclic AMP receptor protein and vulnibactin receptor (Kim et al., 2016). A combined increase in temperature and reduction in salinity (25°C/2.5% to 37°C/0.9%) increased the growth and expression of Metalloprotease VvpE in *V. vulnificus* which caused haemorrhage, necrosis, and edema (Kim et al., 2012). *V. shiloi* grown at 23 and 30°C showed higher activity of a probable virulence factor (Mn-SOD) at 30°C (Murali et al., 2010).

The low temperature was also found to induce virulence/pathogenicity in *Vibrio* spp. as reported in a few studies. *V. anguillarum* RV22 showed high virulence at 15°C despite its optimal temperature for growth was 25°C, while expression of mediated catalase activity (oxyR) and catalase gene (katG) were upregulated at 4°C (Lages et al., 2019). *V. Marinus* (optimum temperature 15-18°C) was reported to have a very short generation time of just 1 hr at 15°C (Horie et al., 1966). Coldwater vibriosis outbreaks associated with *V. salmonicida* occur at 3-10°C. In the laboratory, Atlantic salmon's smolts were challenged with 1×10^7 ml⁻¹ and cultured at 10°C (optimum 15°C) leading to $\approx 85\%$ mortality (Colquhoun et al., 2002). *V. salmonicida*'s growth, biofilm formation, iron sequestration, litR expression were higher at a lower temperature (8-12°C) compared to a higher temperature (14-16°C) (Hansen et al., 2014). *V. splendidus* cultured at 10°C (optimum 26°C) upregulated numerous genes associated with virulence, adhesion, and quorum sensing (Liu et al., 2016). *V. vulnificus* were cultured at 24°C and produced up to 3 times more biofilm than at 30 or 37°C (Çam and Brinkmeyer, 2020).

Multifactorial Aspects of *Vibrio* spp. Growth and Pathogenicity

In the initial screening, the relationship between the increase in temperature and the growth of *Vibrio* spp. was shown to be complex or multifactorial in 38% of the articles (Figure 3). Hence, these factors affected the generally direct and positive correlation between temperature and *Vibrio* spp. growth was compiled. The fact that 38% of the articles showed the relationship between *Vibrio* spp. growth and increase in temperature are not linear but rather multifactorial justified the review. In summary, factors besides temperatures that affected the growth and survival of *Vibrio* spp. were the compounding/interactions of various parameters (n=25 articles), genotype/phenotype (n=24 articles), ecological (n=14 articles), salinity/water activity (n=13 articles), pH (n=4 articles). This showed that the species or strain was the most influential single factor that affected the direct relationship between temperature and growth of *Vibrio* spp. Other studies (n=14 articles) reported several other parameters such as chemical oxygen demand, dissolved organic matter, geographical location, growth phase, inoculum size, iron availability, media, nutrient, and oxygen availability.

The first factor was the compounding effects and interactions between various genetics and physicochemical parameters. Few studies reported that multiple factors affected the growth where a certain trend in interactions was not determined. For example, *V. cholerae* was significantly affected by several factors such as strain

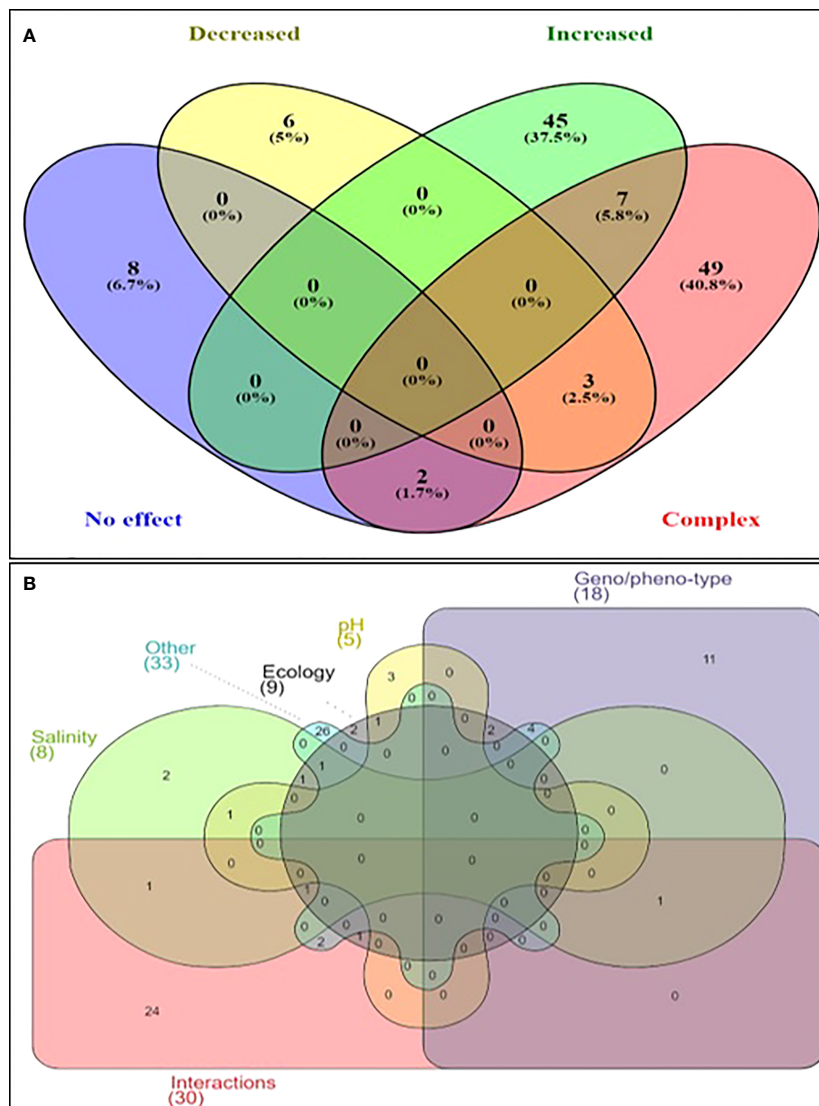


FIGURE 3 | Venn Diagram illustrating the effect of temperature on *Vibrio* spp. **(A)** Effect of temperature on upshift on the growth of *Vibrio* spp. **(B)** Multifactorial parameters affecting the growth of *Vibrio* spp. under elevated temperatures.

(O1 strain), presence of higher temperature, favourable ecological conditions (grow in oyster *Crassostrea virginica*), preferred lower salinity, distance from the river mouth, and enrichment method (DePaola and Hwang, 1995). *V. cholerae* abundance at higher temperatures (>19°C) was further compounded by the presence of plankton in the culture (Louis et al., 2003). The abundance of *V. cholerae* in oysters (*C. virginica*) was significantly affected by strain (O1 or non-O1), site, salinity, and season as well as their interactions (Chávez et al., 2005). Besides temperatures, the growth of *V. cholerae* was significantly affected by the biomass of zooplankton and water conductivity (Kirschner et al., 2008). Three *V. vulnificus* (serovar E) strains were cultured in different media (MSWYE and MSWYEA) and at various salinities (0.3 to 3.8% NaCl). Temperature, salinity, the interaction between temperature and salinity, and capsule all affected the growth significantly (Marco-Noales et al., 1999).

Recent studies also supported these earlier findings where an abundance of *Vibrio* spp. generally and certain species (*V. aestuarianus*, *V. tasmaniensis*, and *V. crassostreae*) were affected by various factors such as ecology (free-living or plankton associated), species, strain (pathogenic or non-pathogenic), and season (Lopez-Joven et al., 2018b). *V. vulnificus* cultured at 20 to 37°C also showed growth and virulence were dependent on multiple biotic and abiotic factors including the host (Hernández-Cabanyero et al., 2020). Interactions between temperature and ecology were the most common interactions reported. The positive effect of temperature on the growth of *V. cholerae* O1 was compounded with the presence of copepods, where attachment to copepods significantly improved the survival of *V. cholerae* (Huq et al., 1984). The abundance of *V. cholerae*, *V. parahaemolyticus*, and

V. vulnificus was also significantly affected by the combined effect of temperature and copepod abundance (Turner et al., 2014). *V. shiloi* associated with coral bleaching was not able to survive the toxicity of oxygen radicals produced by symbiotic zooxanthellae microalgae at a lower temperature (23°C) compared to at 30°C (Murali et al., 2010). Several ecological *V. vulnificus* strains were cultured at 7 to 45°C showed that individually, long-term survival (>2 days) was observed at temperatures ranging from 13 to 22°C. When the 3 strains were mixed, long-term growth was sustainable at 12 and 20°C and lower salinities (10 ppt) (Kaspar and Tamplin, 1993). *V. fischeri* and *V. logei* are symbiont to several *Sepioloa affinis*, *S. intermedia*, *S. ligulata*, and *S. robusta* were cultured in *Sepioloa* spp. and laboratory cultures at 18 to 26°C. *V. fischeri* was able to dominate *V. logei* when the temperature was 26°C, while at 18°C, *V. logei* dominated which showed a strain-dependent outcome (Nishiguchi, 2000). Interactions between temperature and species/strain were also often reported. *V. parahaemolyticus* serotype O3:K6 (tdh and orf8 positive) cultured in Salmon fish (*Oncorhynchus* spp.) at 0-30°C, showed that the effect of temperature on growth was less predictable at a lower temperature (16-20°C) compared to a higher temperature (25-35°C) (Yang et al., 2009). Culturable *Vibrio* population in water samples from various sites (industrial, recreational, and protected) were maintained at different temperatures (22 to 37°C). The results showed a significant effect of temperature where at 37°C, only 6 *Vibrio* spp. were detected while at 22°C, 20 species were detected, which showed strain dependence. At 37°C, only *V. alginolyticus* (85.9%), *V. campbelli* (2%), *V. cholerae* (<1%), *V. communis* (<1%), *V. harveyi* (10.7%) and *V. parahaemolyticus* (<1%) (Tall et al., 2013). The abundance of clinical and virulent strains of *V. parahaemolyticus* increased with the increase in temperature and copepod, however, normal strains did not correlate with temperature (Turner et al., 2014). Pathogenic (tdh positive) and non-pathogenic *V. parahaemolyticus* were cultured at 4-28°C in Manila clam (*Ruditapes philippinarum*) and the results showed that lower temperatures (4 and 15°C) slowed the non-pathogenic strains (Lopez-Joven et al., 2018a). *Vibrio* spp. related infections were well correlated with temperature from 1992 to 2016, however, the occurrence of *Vibrio* infections in 2015 was not explained by the date. The 2015 incidence was regarded as the probable effect of strain (subtype) and its compounding effect on temperature (Galanis et al., 2020). Interaction between temperature and salinity was also reported to affect the growth of *V. parahaemolyticus* and *V. cholerae*. The abundance of *V. parahaemolyticus* growth at 20 or 37°C was significantly affected by interactions between temperature and salinity (0.05-0.5 M), while a combination of low temperature and low salinity was the least favourable for the bacteria (Gray and Muir, 1977). *V. parahaemolyticus* prevalence was significantly different between sampling sites and exposure time to certain temperatures and salinity (Sullivan and Neigel, 2018). Clinical and environmental strains of *V. cholerae* cultured at various temperatures (10, 15, 20, and 25°C) and salinities (5, 15, 25, and 35‰) also showed there were interactions between temperature and salinity affected the growth (Singleton et al., 1982). *V. costicola* grew at temperatures between 4 to 37°C, however, optimum growth occurred at

different salinities throughout the temperature range (Adams and Russell, 1992). Interaction between species/strain and site was also reported to affect the growth of *V. vulnificus*. *V. vulnificus* in Shellshock Oysters (*C. virginica*) harvested from various sites with a temperature range of 27.8 to 31°C and held at temperatures ranging from 24 to 28.3°C showed that the site significantly affected MPN count which ranged from 300 to 5100 MPN/g despite the small temperature variations (Cook, 1994). *V. vulnificus* prevalence was also significantly different between sampling sites and exposure time to certain temperatures and salinity (Sullivan and Neigel, 2018). Other less common interactions also affected the growth of *Vibrio* spp. were also reviewed. For instance, *V. alginolyticus* cultured at various temperatures (5-42°C), salinity (0.5-6‰ NaCl), and pH (4.5-12) showed that compounding extreme conditions (e.g. low pH and low salinity) inhibited its growth (Farid and Larsen, 1981). Interaction between salinity and species/strain was reported to affect the growth of *V. anguillarum*. A total of 9 serovars cultured at various temperatures (20-37°C) and salinity (0.86-4‰ NaCl) showed that strain type and salinity affected maximum growth and tolerance to high temperature (Guérin-Faubleé et al., 1995). The growth stage/phase also affected *V. cholerae* O1 cultured at various temperatures (6-30°C), salinities (8-32 ppt), and media. The results showed that the high temperatures were beneficial only in the early stage of growth, while long-term survival at 18°C was better than 30°C (McCarthy, 1996). *V. parahaemolyticus* abundance in mussels was also affected by the interaction of salinity and chlorophyll-a, while abundance in water samples was affected by the combined effect of temperature and turbidity (Julie et al., 2010). TnpHoA transposon *V. vulnificus* strains (different morphotypes) was cultured in Oysters (*C. virginica*) and using different media and temperatures (0.5 to 24°C). The results showed that the highest survival was observed at 5°C, hence, the higher temperature didn't cause a higher *V. vulnificus* count. The bacteria could resist a wider range of temperatures on agar but not in the oyster, while inoculum size also affected the growth (Murphy and Oliver, 1992). *V. vulnificus* cultured in media with varying amounts of bacterioplankton (mainly *Nodularia spumigena*) and temperature (12, 18, or 25°C) showed interactions and the concentration of dissolved organic matter significantly affected their growth more than temperature (Louis et al., 2003). Growth of *Vibrio* spp. cultured in various media compositions and temperatures (12, 18, or 25°C) showed that maximum growth occurred at 18°C, while dissolved organic matter maximized their growth (Eiler et al., 2007). Non-marine *Vibrio* sp. Teb5a1 was able to tolerate a wide range of temperature (4 to 49°C) and salinity (0 to 100 g/L). Survival and growth depended on salinity and the ability to express various virulence factors related to osmotic stress, motility, and antibacterial agents (Gallardo et al., 2016).

The second most common factor was the genotype and phenotype of tested strains such as species, strain, and pathogenicity. Affected *Vibrio* species were *V. alginolyticus*, *V. anguillarum*, *V. cholerae*, *V. fischeri*, *V. marinus*, *V. parahaemolyticus*, *V. salmonicida*, and *V. vulnificus*. For example, *V. alginolyticus* and *V. parahaemolyticus* cultured at 24°C showed 2 clusters in each species, one with a short generation time

(12–14 hrs) and one with a long generation time (20–25 min) (Horie et al., 1966). A total of 9 *V. anguillarum* serovars were cultured at various temperatures (20–37°C) and salinity (0.86–4% NaCl). The results showed that strain type affected maximum growth and tolerance to high temperature (Guérin-Faublée et al., 1995). *V. cholerae* cultured at 35 and 42°C showed that non-O1 serogroup strains did not grow at 42°C (DePaola et al., 1987). The abundance of *V. cholerae* serovars such as O395, C6706, and N16961 was also significantly different among those tested (Lipp et al., 2003; Wu et al., 2016). Several *V. fischeri* strains grown at various temperatures (12 to 32°C) and salinities (24, 32, and 38 ppt) showed that optimum growth conditions were different among strains. *V. fischeri* ES114 preferred low salinity while *V. fischeri* ET401 preferred higher salinity, while environmental strains (ES114 & ET401) showed higher adaptability compared to *V. fischeri* ATCC 7744 (Soto et al., 2009). A total of 3 *V. parahaemolyticus* (T-3765-1, SB04-422, and ATCC 17802) strains were cultured at various temperatures (-18 to 48°C) and under various conditions (e.g. water-ethylene glycol bath) and maintained in different media (fish homogenate or TSB) were mainly affected by strain type (Covert and Woodburn, 1972). Non-pathogenic *V. cholera* and *V. parahaemolyticus* grew faster than pathogenic strains (Yoon et al., 2008; Fu et al., 2013). *V. parahaemolyticus* cultured at 10 to 30°C and in different media (broth or slurry) showed that strain (pathogenic and non-pathogenic) and media both impacted the growth. Pathogenic strains showed longer lag time and lower specific growth rates when exposed to low temperature (10°C), while broth showed higher growth than slurry (Yoon et al., 2008). Three strains of *V. parahaemolyticus* were grown at various temperatures, salinity, pH, and the salt type and the results showed that salinity had the most effective in determining the survival of tested strains. Mutant strains and the expression of *toxR* and *rpoS* (VP2553) increased the resistance to extreme environmental conditions (Whitaker et al., 2010). Pathogenic *V. parahaemolyticus* (JL 223) isolated from Korean raw oysters (*Crassostrea gigas*) grew faster than ATCC strain *V. parahaemolyticus* 33844 (Kim et al., 2012). Strain and genotype significantly affected *V. parahaemolyticus* ability to grow at various temperatures and salinities (Liu et al., 2016). Pathogenic *V. parahaemolyticus* associated with Jinjiang oyster (*Crassostrea rivularis*) were more susceptible to lower temperatures (5 and 15°C) compared to non-pathogenic strains, while their growth was maximized at 25 and 35°C (Wang et al., 2018). More than 20 strains of *V. salmonicida* (wild, type, and genetically modified) were cultured at various temperatures (4–16°C). The results showed colony morphology and ideal temperature for growth and biofilm formation were different across strains. Wild-type strains preferred 12°C, while *litR* mutant strains preferred 8°C (Hansen et al., 2014). Wild and *luxO* mutant *V. vulnificus* were grown at 26 and 37°C and the mutant grew faster than the wild-type strain at both temperatures (Elgamal et al., 2014). Clinical strains of *V. vulnificus* consistently produced more biofilm at 24°C than environmental strains, while iron concentration increased biofilm formation regardless of strain source (Çam and Brinkmeyer, 2020). Cell type (translucent or opaque), growth phase (stationary or logarithmic) and media (modified seawater yeast extract or

Heart Infusion Agar) affected the culturability and survival of *V. vulnificus* (Biosca et al., 1996). Environmental and clinical strains of *V. vulnificus* were cultured at different temperatures (24–37°C), pH (5.5–8.5), and iron concentration (18–200 µM). The results showed that pH affected environmental strains only (Çam and Brinkmeyer, 2020). Other studies investigated the effect of unidentified or unspecified species/strains. For instance, a total of 69 *Vibrio* spp. were studied and clustered into 7 clusters based on genotypic similarity. However, in terms of virulence, only cluster 1 showed virulence, while all 22 strains in that cluster were *V. marinus* (Benediktsdottir et al., 1998). In another study of 118 *Vibrio* spp. *Psychrotrophic* strains, the results showed there were 2 distinct ecotype strains, one with an optimum temperature of 15 to 25°C and the other 20 to 30°C. These 2 ecological groups also had distinct adenylate concentrations and energy charge patterns (Morii and Sarukawa, 2000). Growth of 69 *Vibrio* spp. At various temperatures (4 to 37°C) and salinities (0 to 8‰) showed that different strains preferred different growth conditions (Benediktsdottir et al., 1998).

The third factor was the ecology surrounding tested strains such as *V. cholerae*, *V. parahaemolyticus*, *V. fischeri*, *V. shiloi*, and *V. vulnificus*. *V. cholerae* O1 cultured at various temperatures (6–30°C), salinities (8–32 ppt), and media showed that ecological competitions reduced the long-term survival of *V. cholerae* O1 strains compared to monoculture (McCarthy, 1996). *V. cholerae* abundance was affected by environmental conditions such as the presence of phytoplankton, which was positively correlated to growth (Lipp et al., 2003). Different *V. cholerae* strains colonizing or attached to shrimp carapace survived longer than strains cultured in solution (Castro-Rosas and Escartin, 2005). The presence of plankton in the culture increased the growth of both Serovar O1 and non-O1/non-O139 *V. cholerae* (Alam et al., 2006). The ability of *V. fischeri* to colonize and infect symbiont organisms was affected by flagella-based motility (Karlsen et al., 2008). Growth of *V. parahaemolyticus* on oyster slurry was slower compared to growth in broth regardless of the temperature (Yoon et al., 2008). *V. shiloi* was able to remain viable at 16 and 28°C in laboratory culture conditions. However, in ecological conditions, it did not survive 16°C in the presence of *O. patagonica* coral. This indicated that the coral was able to produce metabolites to kill the bacteria at 16°C, while morphological differences (size and presence of flagellum) were also observed between laboratory and ecological settings (Israely et al., 2001). *V. vulnificus* also showed the importance of ecological factors as it did not grow at temperatures below 20°C in its habitat, while in laboratory cultures, it grew at temperatures ranging from 13 to 42°C (Kelly, 1982). *V. vulnificus* is endogenous to Oysters (*C. virginica*) and behaved differently compared to laboratory-grown *V. vulnificus* and it could not compete with the microflora in and colonize the oyster host (Kaspar and Tamplin, 1993).

The fourth most common factor was the physicochemical parameters such as salinity and pH which affected the growth of *V. anguillarum*, *V. marinus*, *V. parahaemolyticus*, *V. salmonicida*, and *V. vulnificus*. A total of 9 *V. anguillarum* serovars were cultured at various temperatures (20–37°C) and salinity (0.86–4% NaCl). The results showed that salinity affected maximum growth and tolerance to high temperatures (Guérin-Faublée

et al., 1995). Salinity also reduced the *V. marinus* resistance to temperature (Morita and Albright, 1968). *V. parahaemolyticus* strains (T-3765-1, SB04-422, and ATCC 17802) grown at various conditions (temperatures, salinity, additives, etc) showed that at certain salinities almost all strains could not grow (Covert and Woodburn, 1972). *V. salmonicida* was flagellated, more motile, and showed higher flagellin (flaA, flaB, flaC, flaD, flaE, and flaF) gene expression at higher salinity (2.5%) compared to low salinity (7.5%) (Karlsen et al., 2008). *V. vulnificus* was grown at salinities ranging from 0.5 to 10.5% NaCl concentration and showed that it was able to grow at 0.5 to 6.5% NaCl, while its optimum salinity was 1-2% (Kelly, 1982). In another study, *V. vulnificus* could not survive salinities greater than 25 ppt (Kaspar and Tamplin, 1993). Water activity which is related to salinity was also reported to affect growth in several studies. Water activity and salinity also affected lag period, growth rate, and total cell number of *V. parahaemolyticus* (Beuchat, 1974). Four *V. parahaemolyticus* strains cultured at 5–50°C and water activity (0.936–0.995) showed that growth was significantly affected by strain type with 38.349 showing the highest growth. The bacteria were water activity-dependent and also could not grow in upper and lower limits of temperature (< 10 and > 48°C) (Miles et al., 1997).

The fifth factor (pH) was less common compared to salinity/water activity but it significantly affected the growth of *V. anguillarum*, *V. cholerae*, *V. parahaemolyticus*, *V. salmonicida*, and *V. vulnificus*. *V. salmonicida* and *V. vulnificus* flourished at a very small pH range ($\pm 2-3$), *V. cholerae* while tolerated pH ranging from 5.2 to 9.2 (Wang and Gu, 2005). *V. anguillarum* cultured at various temperature (0–30°C), salinity (0.5–4% NaCl), and pH (5–9) showed that it was only able to grow in certain ranges (e.g. pH 5.5–8.5) (Olafsen et al., 1981). *V. anguillarum* cultured at various pH (6–9) showed that the bacteria could not grow at pH 6 (Larsen, 1984). Different *V. cholerae* strains survived longer in 1.5 pH than 2.5 (Castro-Rosas and Escartin, 2005). A total of 6 *V. parahaemolyticus* strains (107914, 8700 04:K11, 284-72, O, T-3765-1 03:K7 and 4750 02:K3) at various temperature (5 to 30°C) salinities (3 or 7%) showed that almost all strains were able to grow at all condition but at different pH (Beuchat, 1973).

Several other parameters that directly or indirectly affected the growth were also reported in reviewed articles. Yeast extract, peptone concentration, NaCl concentration, and oxygen availability significantly affected the growth of *V. alginolyticus* (Horie et al., 1966). Iron sequestration was also shown to be a key virulence factor in *V. anguillarum* and *V. vulnificus* (Colquhoun and Sørum, 2001). *V. anguillarum* subjected to iron limitation led to upregulated production of LPS, hemolysins, lysozyme, siderophores, and other virulence factors (Lages et al., 2019). Growth of *V. anguillarum* and *V. salmonicida* was found to depend on the form of media where results obtained in broth were slightly different (<10°C) than agar (Colquhoun et al., 2002). The ability of *V. anguillarum* and *V. cholerae* to colonize and infect symbiont organisms was affected by flagella-based motility (Karlsen et al., 2008). The physiological state (growth phase) had a greater effect than temperature and salinity on *V.*

cholerae conversion from non-O1 to O1 serogroup (Montilla et al., 1996). *V. cholerae* cultured in media with varying amounts of bacterioplankton (mainly *N. spumigena*) and temperature (12, 18, or 25°C) showed that only the concentration of dissolved organic matter significantly affected their growth (Louis et al., 2003). *V. cholerae* prevalence was significantly different between sampling sites, while exposure time, temperature, and salinity also had effects (Sullivan and Neigel, 2018). *V. cholerae* AN59 growth varied by up to 100-fold depending on initial inoculum size (2 to 10⁶ CFU/ml⁻¹) as well as the media used (ASW or spent ASW) (Debnath et al., 2019). Inoculum size and iron concentration also significantly affected growth, cell density, and siderophore production in *V. salmonicida* 1193/87 (Colquhoun and Sørum, 2001). Chemical oxygen demand (COD) tested at 5 to 40 mg l⁻¹ significantly and positively correlated to *V. cholerae* growth by maximizing growth rate and cell density (Fu et al., 2013). Starvation was also shown to induce VBNC state in *V. fischeri* and *V. harveyi* at the temperature between 4°C and 22°C (Vattakaven et al., 2006). *V. coralliilyticus* infections depended on many factors such as the simultaneous expression of several virulence factors (e.g. flagellar, secretion, and quorum sensing) (Kimes et al., 2012). Total *Vibrio* and total *V. parahaemolyticus* abundance in water, shrimp, fish, and seagrass was significantly affected by the sampling site despite the site having similar temperatures (27 and 31°C) and salinity (28 to 34‰) (Kaneko and Colwell, 1974). The prevalence of pathogenic (tdh+) *V. parahaemolyticus* was higher in enriched media compared to direct plating (Cook et al., 2002). Even though *V. parahaemolyticus* generally preferred higher temperature, the positive effect of temperature up-shift was eliminated by the growth phase where only *Vibrio* spp. in the stationary phase preferred the temperature up-shift (Nishino and Kogure, 2003). Environmental and clinical strains of *V. vulnificus* were cultured at different temperatures (24–37°C), pH (5.5–8.5), and iron concentration (18–200 µM) showed that iron availability and concentration were positively correlated to biofilm formation (Çam and Brinkmeyer, 2020).

Extremophiles *Vibrio* spp. (grow at $\leq 10^{\circ}\text{C}$ or/and $\geq 35^{\circ}\text{C}$)

Several *Vibrio* species were found to be able to grow in high temperatures ($\geq 35^{\circ}\text{C}$) and could be species of concern in this global warming era. Hence, these species were compiled for future reference and policymaking. These species were *V. alginolyticus*, *V. cholerae*, *V. fischeri*, *V. marinus*, *V. parahaemolyticus*, and *V. vulnificus*. Among these, *V. cholerae*, *V. parahaemolyticus*, and *V. vulnificus* were also able to grow $\leq 10^{\circ}\text{C}$. Other cold-resistant that could grow at $\leq 10^{\circ}\text{C}$ species were *V. anguillarum*, *V. fischeri*, *V. salmonicida*, *V. shiloi*, *V. splendidus*, and *V. tasmaniensis* (Figure 3). One study reported that *V. alginolyticus*, *V. anguillarum*, *V. damsela*, *V. fluvialis*, *V. harveyi*, *V. ordalii*, *V. parahaemolyticus*, *V. splendidus*, and *V. vulnificus* were also able to grow at temperature $\geq 37^{\circ}\text{C}$, however, growth curves were not provided (Benediktsdottir et al., 1998) (Figure 4). The overall findings of this systematic literature review are summarized in Supplementary Figure 1.

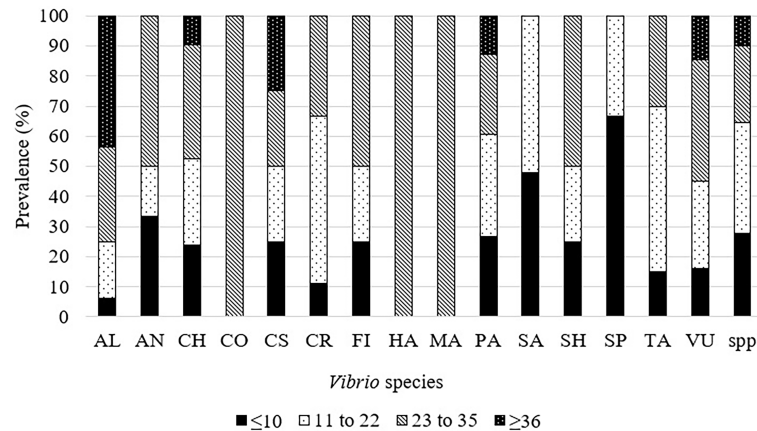


FIGURE 4 | Prevalence of *Vibrio* spp. at various temperatures in reviewed articles. AL, *V. alginolyticus*; AN, *V. anguillarum*; CH, *V. cholerae*; CO, *V. coralliilyticus*; CS: *V. costicola*; CR: *V. crassostreae*; FI: *V. fischeri*; HA: *V. harveyi*; MA: *V. marinus*; PA: *V. parahaemolyticus*; SA: *V. salmonicida*; SH: *V. shiloi*; SP: *V. splendidus*; TA, *V. tasmaniensis*; VU, *V. vulnificus*; spp.: Unidentified *Vibrio* species.

THERAPEUTIC STRATEGIES FOR VIBRIOSIS-RELATED INFECTIONS

Vibrio spp. have been the causative agents for vibriosis diseases such as cholera and food poisoning in the past. These infections are expected to be a major disease in the future as well. Hence, an overview of therapeutic strategies against *Vibrio* spp. is discussed below. There are several antimicrobial agents that can inhibit or kill *Vibrio* spp. such as antibiotics. In a 2015 survey, out of 8056 cases of cholera and other vibrio illness in humans, 5243 (~65%) were prescribed antibiotics. Quinolones accounted for 56% of these antibiotic prescriptions and were the only class that significantly reduced mortality. Other antibiotics prescribed included cephalosporins and tetracyclines, while penicillins were the least effective (Wong et al., 2015). A 10 years retrospective study on humans reported that cephalosporins and tetracyclines were used initially to treat the potentially fatal *V. vulnificus*, while additional antibiotics were prescribed based on antibiotic resistance patterns. Another study recommended doxycycline combined with 3rd generation cephalosporins (Cai et al., 2021). Bacteriocins are ribosomally synthesized peptides secreted by various bacterial strains to kill closely related species (Sheikh et al., 2022). Numerous bacteriocins and bacteriocins-like-inhibitory substances were found to inhibit *Vibrio* spp. while presenting a lower risk of resistance. Recently, bacteriocins isolated from *Vibrio* spp. (called vibriocin) showed effective and narrow-spectrum activity against numerous *Vibrio* spp. More critically, vibriocin was effective against pathogenic strains such as *V. alginolyticus*, *V. harveyi*, and *V. parahaemolyticus* (Sheikh et al., 2022). Bacteriocin isolated from tiger shrimp *Penaeus monodon* was also effective against pathogenic *V. alginolyticus* (Feliatra et al., 2018). Another antimicrobial peptide produced by *Bacillus paralicheniformis* inhibited *V. harveyi* (Choyam et al., 2021).

Phage therapy is another vibriosis control approach with a narrow spectrum activity that was successful, particularly for the aquaculture industry. Previous studies reported the efficacy of vibriophages against key vibrio pathogens such as *V. parahaemolyticus*, *V. campbellii*, and *V. alginolyticus*. Vibriophages have the ability to selectively recognize and inhibit *Vibrio* species or even certain strains (Dubey et al., 2021; Lomelí-Ortega et al., 2021). Vibriophage KVP40 was also found to infect numerous *Vibrio* spp. including *V. anguillarum*, *V. parahaemolyticus*, *V. harveyi*, and *V. cholerae*, while the mechanism of action was reported to *via* attacking the outer membrane protein K (OmpK) (Tan et al., 2015).

Inhibition of quorum sensing (QS) which is critical in coordinating the expression of certain genes is another therapeutic approach that is not well explored. Inhibiting these cell-to-cell communications between bacteria was found to be key in controlling vibriosis. For example, furanones were proposed as a promising treatment for luminescent vibriosis in aquaculture (Huzmi et al., 2019).

The use of natural products in aquaculture as antimicrobial agents is also becoming increasingly popular because they are more eco-friendly than conventional antimicrobials which are a threat to animals, humans, and the ecosystem health (Schar et al., 2020). Natural products such as postbiotics (mainly Lactic acid) and essential oils (eugenol and thymol) have also been found to be effective against *Vibrio* spp. For example, eugenol and thymol inhibited the growth of *V. parahaemolyticus* strains (KCTC 2729, ATCC 17802, ATCC 27969 and ATCC 33844) and *V. harveyi* ATCC 1118 (Toushik et al., 2022).

Despite *Vibrio* spp. being a significant threat to animals and humans, there are numerous therapeutic strategies for vibriosis-related infections. However, more research is needed to optimize these treatments for humans and animals, as well as for each species.

CONCLUSION

Vibrio spp. were able to grow at a wide range of environmental conditions such as temperatures, salinities, and pH which could lead to its dominance in the environment. However, the review hypothesized that only certain thermostable *Vibrio* spp. are positively impacted by the increase in temperature. This hypothesis was validated by reviews as 47% of the articles reported that the increase in growth was due to an increase in temperature, while 38% reported that the increase in growth was multifactorial. Reduced growth (6%) and no effect (9%) were also reported. The temperature outside its optimum ranges also caused *Vibrio* spp. to evolve and change its metabolic activities, increase the expression of virulence genes and shorten generation time. These factors improved the ability in colonizing new hosts such as phytoplanktons, zooplanktons algae, crustaceans, and fish. *Vibrios* were also able to survive starvation by going into VBNC state for very long periods (>150 days) and then recovering their growth when favourable conditions such as high temperature occurred. In terms of research questions, the first research question in this review article was whether all *Vibrio* spp. flourish and become virulent at higher temperatures. Based on the 15 species in the reviewed articles, the answer is no. Several species were not able to grow at $\geq 37^{\circ}\text{C}$, namely, *V. salmonicida*, *V. anguillarum*, *V. splendidus*, *V. coralliilyticus*, *V. crassostreae*, *V. fischeri*, *V. harveyi*, *V. marinus*, *V. shiloi* and *V. tasmaniensis*. However, these species were found to be pathogenic at lower temperatures. The second research question aimed at identifying which *Vibrio* spp. pose a significant threat to humans and animals in the era of global warming. *Vibrio* spp. that grew well at $\geq 37^{\circ}\text{C}$ were *V. alginolyticus*, *V. cholerae*, *V. costicola*, *V. parahaemolyticus* and *V. vulnificus*. Based on the pathogenicity of these *Vibrio* spp., the species that pose the highest risk to humans and animals are *V. alginolyticus*, *V. cholerae*, *V. parahaemolyticus* and *V. vulnificus*. Efforts to combat global warming are needed and being carried out for long-term

REFERENCES

- Adams, R. L. and Russell, N. J. (1992). Interactive Effects of Salt Concentration and Temperature on Growth and Lipid Composition in the Moderately Halophilic Bacterium *Vibrio costicola*. *Can. J. Microbiol.* 38, 823–827. doi: 10.1139/m92-134
- Alam, M., Sadique, A., Nur-A-Hasan, B., Bhuiyan, N. A., Nair, G. B., Siddique, A., et al. (2006). Effect of Transport at Ambient Temperature on Detection and Isolation of *Vibrio cholerae* From Environmental Samples. *Appl. Environ. Microbiol.* 72, 2185–2190. doi: 10.1128/AEM.72.3.2185-2190.2006
- Araki, T. (1991). The Effect of Temperature Shifts on Protein Synthesis by the Psychrophilic Bacterium *Vibrio sp. strain. ANT-300*. *Microbiol.* 137, 817–826. doi: 10.1099/00221287-137-4-817
- Araki, T. (1992). An Analysis of the Effect of Changes in Growth Temperature on Proteolysis *In Vivo* in the Psychrophilic Bacterium *Vibrio sp. strain. ANT-300*. *Microbiol.* 138, 2075–2082. doi: 10.1099/00221287-138-10-2075
- Armada, S. P., Farto, R., Pérez, M. J. and Nieto, T. P. (2003). Effect of Temperature, Salinity and Nutrient Content on the Survival Responses of *Vibrio splendidus* Biotype I. *Microbiology* 149, 369–375. doi: 10.1099/mic.0.25574-0
- Baker-Austin, C., Oliver, J. D., Alam, M., Ali, A., Waldor, M. K., Qadri, F., et al. (2018). *Vibrio* spp. Infections. *Nat. Rev. Dis. Primers* 4, 1–19. doi: 10.1038/s41572-018-0005-8

impact, however, novel antibiotics that can inhibit these species are urgently needed for short-term treatment of diseases caused by these pathogens, especially for humans and fish.

AUTHOR CONTRIBUTIONS

HS: Data collection, conceptualization and original draft writing. MN: conceptualization and final draft writing. FA: Data collection. LA: original draft writing. NM: formal analysis. JK: final draft writing. KN: Funding acquisition. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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- Benediktsdottir, E., Helgason, S. and Sigurjónsdóttir, H. (1998). *Vibrio* spp. Isolated From Salmonids With Shallow Skin Lesions and Reared at Low Temperature. *J. fish. Dis.* 21, 19–28. doi: 10.1046/j.1365-2761.1998.00065.x
- Ben-Haim, Y., Zicherman-Keren, M. and Rosenberg, E. (2003). Temperature-Regulated Bleaching and Lysis of the Coral *Pocillopora damicornis* by the Novel Pathogen *Vibrio coralliilyticus*. *Appl. Environ. Microbiol.* 69, 4236–4242. doi: 10.1128/AEM.69.7.4236-4242.2003
- Beuchat, L. R. (1973). Interacting Effects of Ph, Temperature, and Salt Concentration on Growth and Survival of *Vibrio parahaemolyticus*. *Appl. Microbiol.* 25, 844–846. doi: 10.1128/am.25.5.844-846.1973
- Beuchat, L. (1974). Combined Effects of Water Activity, Solute, and Temperature on the Growth of *Vibrio parahaemolyticus*. *Appl. Microbiol.* 27, 1075–1080. doi: 10.1128/am.27.6.1075-1080.1974
- Biosca, E. G., Amaro, C., Marco-Noales, E. and Oliver, J. D. (1996). Effect of Low Temperature on Starvation-Survival of the Eel Pathogen *Vibrio vulnificus* Biotype 2. *Appl. Environ. Microbiol.* 62, 450–455. doi: 10.1128/aem.62.2.450-455.1996
- Boonyawantang, A., Mahakarncanakul, W., Rachtanapun, C. and Boonsupthip, W. (2012). Behavior of Pathogenic *Vibrio parahaemolyticus* in Prawn in Response to Temperature in Laboratory and Factory. *Food Control.* 26, 479–485. doi: 10.1016/j.foodcont.2012.02.009

- Boroujerdi, A. F., Vizcaino, M. I., Meyers, A., Pollock, E. C., Huynh, S. L., Schock, T. B., et al. (2009). NMR-Based Microbial Metabolomics and the Temperature-Dependent Coral Pathogen *Vibrio coralliilyticus*. *Environ. Sci. Technol.* 43, 7658–7664. doi: 10.1021/es901675w
- Burks, D. J., Norris, S., Kauffman, K. M., Joy, A., Arevalo, P., Azad, R. K., & Wildschutte, H. (2017). Environmental Vibrios Represent a Source of Antagonistic Compounds that Inhibit Pathogenic *Vibrio cholerae* and *Vibrio parahaemolyticus* strains. *Microbiologyopen*, 6(5), e00504. doi: 10.1002/mbo3.504
- Cai, R., Zhen, M., Guan, Z., Li, M., Liao, Q., Liu, X., et al. (2021). New Atypical Manifestations and Prognostic Factors of *Vibrio vulnificus* Infection: A 10-Year Retrospective Study. *Japanese J. Infect. Dis.* 74(6), 549–553. JIID-2020. doi: 10.7883/yoken.JIID.2020.843s
- Çam, S. and Brinkmeyer, R. (2020). The Effects of Temperature, Ph, and Iron on Biofilm Formation by Clinical Versus Environmental Strains of *Vibrio vulnificus*. *Folia microbiol.* 65, 557–566. doi: 10.1007/s12223-019-00761-9
- Castro-Rosas, J. and Escartin, E. (2005). Increased Tolerance of *Vibrio cholerae* O1 to Temperature, Ph, or Drying Associated With Colonization of Shrimp Carapaces. *Int. J. Food Microbiol.* 102, 195–201. doi: 10.1016/j.ijfoodmicro.2004.12.015
- Chávez, M. D. R. C., Sedas, V. P., Borunda, E. O. and Reynoso, F. L. (2005). Influence of Water Temperature and Salinity on Seasonal Occurrences of *Vibrio cholerae* and Enteric Bacteria in Oyster-Producing Areas of Veracruz, México. *Mar. pollut. Bull.* 50, 1641–1648. doi: 10.1016/j.marpolbul.2005.06.036
- Chowdhury, F. R., Nur, Z., Hassan, N., Von Seidlein, L. and Dunachie, S. (2017). Pandemics, Pathogenicity and Changing Molecular Epidemiology of Cholera in the Era of Global Warming. *Ann. Clin. Microbiol. Antimicrob.* 16, 1–6. doi: 10.1186/s12941-017-0185-1
- Choyam, S., Jain, P. M. and Kammar, R. (2021). Characterization of a Potent New-Generation Antimicrobial Peptide of Bacillus. *Front. Microbiol.* 12, 710741. doi: 10.3389/fmicb.2021.710741
- Cohen, M. L., Mashanova, E. V., Rosen, N. M. and Soto, W. (2019). Adaptation to Temperature Stress by *Vibrio fischeri* Facilitates This Microbe's Symbiosis With the Hawaiian Bobtail Squid (*Euprymna scolopes*). *Evolution* 73, 1885–1897. doi: 10.1111/evo.13819
- Colquhoun, D., Alveim, K., Dommarsnes, K., Syvertsen, C. and Sørum, H. (2002). Relevance of Incubation Temperature for *Vibrio salmonicida* Vaccine Production. *J. Appl. Microbiol.* 92, 1087–1096. doi: 10.1046/j.1365-2672.2002.01643.x
- Colquhoun, D. and Sørum, H. (2001). Temperature Dependent Siderophore Production in *Vibrio salmonicida*. *Microbial. pathogen.* 31, 213–219. doi: 10.1006/mpat.2001.0464
- Cook, D. W. (1994). Effect of Time and Temperature on Multiplication of *Vibrio vulnificus* in Postharvest Gulf Coast Shellstock Oysters. *Appl. Environ. Microbiol.* 60, 3483–3484. doi: 10.1128/aem.60.9.3483-3484.1994
- Cook, D. W., Bowers, J. C. and Depaola, A. (2002). Density of Total and Pathogenic (Tdh+) *Vibrio parahaemolyticus* in Atlantic and Gulf Coast Molluscan Shellfish at Harvest. *J. Food Prot.* 65, 1873–1880. doi: 10.4315/0362-028X-65.12.1873
- Cooper, M. F. and Morita, R. Y. (1972). Interaction of Salinity and Temperature on Net Protein Synthesis and Viability of *Vibrio marinus* 1. *Limnology and Oceanography* 17, 556–565. doi: 10.4319/lo.1972.17.4.0556
- Covert, D. and Woodburn, M. (1972). Relationships of Temperature and Sodium Chloride Concentration to the Survival of *Vibrio parahaemolyticus* in Broth and Fish Homogenate. *Appl. Microbiol.* 23, 321–325. doi: 10.1128/am.23.2.321-325.1972
- Cowan, M., Finston, T., Marshall, R. and de la Bastide, P. Y. (2019). Post-Harvest Temperature Regimes for Pacific Oysters (*Crassostrea gigas*) and Growth Response of *Vibrio parahaemolyticus*. *Aquacult. Res.* 50, 3471–3476. doi: 10.1111/are.14289
- Debnath, A., Mizuno, T. and Miyoshi, S.-I. (2019). Comparative Proteomic Analysis to Characterize Temperature-Induced Viable But non-Culturable and Resuscitation States in *Vibrio cholerae*. *Microbiology* 165, 737–746. doi: 10.1099/mic.0.000798
- de O Santos, E., Alves, N., Dias, G. M., Mazotto, A. M., Vermelho, A., Vora, G. J., & Thompson, F. L. (2011). Genomic and proteomic analyses of the coral pathogen *Vibrio coralliilyticus* reveal a diverse virulence repertoire. *The ISME journal*, 5(9), 1471–1483. doi: 10.1038/ismej.2011.19
- Depaola, A. and Hwang, G.-C. (1995). Effect of Dilution, Incubation Time, and Temperature of Enrichment on Cultural and PCR Detection of *Vibrio cholerae* Obtained From the Oyster *Crassostrea virginica*. *Mol. Cell. Probes* 9, 75–81. doi: 10.1016/S0890-8508(95)80031-X
- Depaola, A., Kaysner, C. and McPhearson, R. (1987). Elevated Temperature Method for Recovery of *Vibrio cholerae* From Oysters (*Crassostrea gigas*). *Appl. Environ. Microbiol.* 53, 1181–1182. doi: 10.1128/aem.53.5.1181-1182.1987
- Dubey, S., Singh, A., Kumar, B. T., Singh, N. K. and Tyagi, A. (2021). Isolation and Characterization of Bacteriophages From Inland Saline Aquaculture Environments to Control *Vibrio parahaemolyticus* Contamination in Shrimp. *Indian J. Microbiol.* 61 (2), 212–217. doi: 10.1007/s12088-021-00934-6
- Eiler, A., Gonzalez-Rey, C., Allen, S. and Bertilsson, S. (2007). Growth Response of *Vibrio cholerae* and Other *Vibrio* spp. To Cyanobacterial Dissolved Organic Matter and Temperature in Brackish Water. *FEMS Microbiol. Ecol.* 60, 411–418. doi: 10.1111/j.1574-6941.2007.00303.x
- Elgaml, A., Higaki, K. and Miyoshi, S.-I. (2014). Effects of Temperature, Growth Phase and luxO-Disruption on Regulation Systems of Toxin Production in *Vibrio vulnificus* Strain L-180, a Human Clinical Isolate. *World J. Microbiol. Biotechnol.* 30, 681–691. doi: 10.1007/s11274-013-1501-3
- Farid, A. and Larsen, J. (1981). Growth of *Vibrio alginolyticus*: Interacting Effects on Ph, Temperature, Salt Concentration, and Incubation Time. *Zentralblatt Für Bakteriologie Mikrobiologie Und Hygiene: I. Abt. Originale C: Allgemeine, Angewandte Und Ökologische Mikrobiologie* 2, 68–75. doi: 10.1016/S0721-9571(81)80019-1
- Feliatra, F., Muchlisin, Z. A., Teruna, H. Y., Utamy, W. R., Nursyirwani, N. and Dahliaty, A. (2018). Potential of Bacteriocins Produced by Probiotic Bacteria Isolated From Tiger Shrimp and Prawns as Antibacterial to *Vibrio*, *Pseudomonas*, and *Aeromonas* Species on Fish. *F1000research* 7, 415–415. doi: 10.12688/f1000research.13958.1
- Fernandez-Piquer, J., Bowman, J. P., Ross, T. and Tamplin, M. L. (2011). Predictive Models for the Effect of Storage Temperature on *Vibrio parahaemolyticus* Viability and Counts of Total Viable Bacteria in Pacific Oysters (*Crassostrea gigas*). *Appl. Environ. Microbiol.* 77, 8687–8695. doi: 10.1128/AEM.05568-11
- Fischer, K., Nijdam, A., Holmström, M., Petrini, P., Ljung, R., van der Schouw, Y., et al. (2016). Evaluating Outcome of Prophylaxis in Haemophilia: Objective and Self-Reported Instruments Should be Combined. *Haemophilia* 22, e80–e86. doi: 10.1111/hae.12901
- Froelich, B., Phippen, B., Fowler, P., Noble, R. and Oliver, J. (2017). Differences in Abundances of Total *Vibrio* spp., *V. vulnificus* and *V. parahaemolyticus* in Clams and Oysters in North Carolina. *Appl. Environ. Microbiol.* 83, e02265–e02266. doi: 10.1128/AEM.02265-16
- Frydenborg, B. R., Krediet, C. J., Teplitski, M. and Ritchie, K. B. (2014). Temperature-Dependent Inhibition of Opportunistic *Vibrio* pathogens by Native Coral Commensal Bacteria. *Microbial. Ecol.* 67, 392–401. doi: 10.1007/s00248-013-0334-9
- Fu, S., Shen, J., Liu, Y. and Chen, K. (2013). A Predictive Model of *Vibrio cholerae* for Combined Temperature and Organic Nutrient in Aquatic Environments. *J. Appl. Microbiol.* 114, 574–585. doi: 10.1111/jam.12058
- Fu, Y., Ho, B. T., & Mekalanos, J. J. (2018). Tracking *Vibrio cholerae* cell-cell interactions during infection reveals bacterial population dynamics within intestinal microenvironments. *Cell host and microbe*, 23(2), 274–281. doi: 10.1016/j.chom.2017.12.006
- Galanis, E., Otterstatter, M. and Taylor, M. (2020). Measuring the Impact of Sea Surface Temperature on the Human Incidence of *Vibrio* Spp. Infection in British Columbia, Canada 1992–2017. *Environ. Health* 19, 1–7. doi: 10.1186/s12940-020-00605-x
- Gallardo, K., Candia, J. E., Remonsellez, F., Escudero, L. V. and Demergasso, C. S. (2016). The Ecological Coherence of Temperature and Salinity Tolerance Interaction and Pigmentation in a non-Marine *Vibrio* Isolated From Salar De Atacama. *Front. Microbiol.* 7, 1943. doi: 10.3389/fmicb.2016.01943
- Gray, R. J. and Muir, A. M. (1977). Salt Deprivation and Low Temperature Sensitivity of *Vibrio parahaemolyticus*. *J. Food Sci.* 42, 689–693. doi: 10.1111/j.1365-2621.1977.tb12580.x
- Guérin-Fauble, V., Rosso, L., Vigneulle, M. and Flandrois, J. P. (1995). The Effect of Incubation Temperature and Sodium Chloride Concentration on the Growth Kinetics of *Vibrio anguillarum* and *Vibrio anguillarum*-Related Organisms. *J. Appl. bacteriol.* 78, 621–629. doi: 10.1111/j.1365-2672.1995.tb03108.x
- Gu, D., Guo, M., Yang, M., Zhang, Y., Zhou, X. and Wang, Q. (2016). A ζ -Mediated Temperature Gauge Controls a Switch From LuxR-Mediated

- Virulence Gene Expression to Thermal Stress Adaptation in *Vibrio alginolyticus*. *PLoS Pathog.* 12, e1005645. doi: 10.1371/journal.ppat.1005645
- Han, N., Mizan, M. F. R., Jahid, I. K. and Ha, S.-D. (2016). Biofilm Formation by *Vibrio parahaemolyticus* on Food and Food Contact Surfaces Increases With Rise in Temperature. *Food Control.* 70, 161–166. doi: 10.1016/j.foodcont.2016.05.054
- Hansen, H., Bjelland, A. M., Ronessen, M., Robertsen, E. and Willassen, N. P. (2014). LitR is a Repressor of Syp Genes and has a Temperature-Sensitive Regulatory Effect on Biofilm Formation and Colony Morphology in *Vibrio* (Aliivibrio) *Salmonicida*. *Appl. Environ. Microbiol.* 80, 5530–5541. doi: 10.1128/AEM.01239-14
- Hare, P., Long, S., Robb, F. and Woods, D. R. (1981). Regulation of Exoprotease Production by Temperature and Oxygen in *Vibrio alginolyticus*. *Arch. Microbiol.* 130, 276–280. doi: 10.1007/BF00425940
- Hernández-Cabanyero, C., Lee, C. T., Tolosa-Enguis, V., Sanjuán, E., Pajuelo, D., Reyes-López, F., et al. (2019). Adaptation to Host in *Vibrio vulnificus*, a Zoonotic Pathogen That Causes Septicemia in Fish and Humans. *Environ. Microbiol.* 21, 3118–3139. doi: 10.1111/1462-2920.14714
- Hernández-Cabanyero, C., Sanjuán, E., Fouz, B., Pajuelo, D., Vallejos-Vidal, E., Reyes-López, F. E., et al. (2020). The Effect of the Environmental Temperature on the Adaptation to Host in the Zoonotic Pathogen *Vibrio vulnificus*. *Front. Microbiol.* 11, 489. doi: 10.3389/fmicb.2020.00489
- Hijarrubia, M., Lazaro, B., Sunen, E. and Fernandez-Astorga, A. (1996). Survival of *Vibrio vulnificus* under Ph, Salinity and Temperature Combined Stress. *Food Microbiol.* 13, 193–199. doi: 10.1006/fmic.1996.0024
- Horie, S., Okuzumi, M., Kato, N. and Saito, K. (1966). Comparative Observations on the Range of Growth Temperature Among Three Biotypes of *Vibrio parahaemolyticus*. *Bull. Jap. Soc. Sci. Fish.* 32, 424–426. doi: 10.2331/suisan.32.424
- Huq, A., West, P. A., Small, E. B., Huq, M. I. and Colwell, R. R. (1984). Influence of Water Temperature, Salinity, and pH on Survival and Growth of Toxicogenic *Vibrio cholerae* Serovar O1 Associated With Live Copepods in Laboratory Microcosms. *Appl. Environ. Microbiol.* 48, 420–424. doi: 10.1128/aem.48.2.420-424.1984
- Huzmi, H., Ina-Salwany, M. Y., Natrah, F. M. I., Syukri, F. and Karim, M. (2019). Strategies of Controlling Vibriosis in Fish. *Asian J. Appl. Sci.* 7 (5), 513–521. doi: 10.24203/ajas.v7i5.5933
- Israely, T., Banin, E. and Rosenberg, E. (2001). Growth, Differentiation and Death of *Vibrio shiloi* in Coral Tissue as a Function of Seawater Temperature. *Aquat. Microbial. Ecol.* 24, 1–8. doi: 10.3354/ame024001
- Jiang, Q., Shi, L., Ke, C., You, W. and Zhao, J. (2013). Identification and Characterization of *Vibrio harveyi* Associated With Diseased Abalone *Haliotis Diversicolor*. *Dis. Aquat. Organisms* 103, 133–139. doi: 10.3354/dao02572
- Johnston, M. and Brown, M. (2002). An Investigation Into the Changed Physiological State of *Vibrio bacteria* as a Survival Mechanism in Response to Cold Temperatures and Studies on Their Sensitivity to Heating and Freezing. *J. Appl. Microbiol.* 92, 1066–1077. doi: 10.1046/j.1365-2672.2002.01657.x
- Julie, D., Solen, L., Antoine, V., Annick, D. and Dominique, H. H. (2010). Ecology of Pathogenic and non-Pathogenic *Vibrio parahaemolyticus* on the French Atlantic Coast. Effects of Temperature, Salinity, Turbidity and Chlorophyll a. *Environ. Microbiol.* 12, 929–937. doi: 10.1111/j.1462-2920.2009.02136.x
- Kaneko, T. and Colwell, R. R. (1974). Distribution of *Vibrio parahaemolyticus* and Related Organisms in the Atlantic Ocean Off South Carolina and Georgia. *Appl. Microbiol.* 28, 1009–1017. doi: 10.1128/am.28.6.1009-1017.1974
- Karlsen, C., Paulsen, S. M., Tunsjø, H. S., Krinner, S., Sørum, H., Haugen, P., et al. (2008). Motility and Flagellin Gene Expression in the Fish Pathogen *Vibrio salmonicida*: Effects of Salinity and Temperature. *Microbial. pathogen.* 45, 258–264. doi: 10.1016/j.micpath.2008.06.002
- Kaspar, C. A. and Tamplin, M. (1993). Effects of Temperature and Salinity on the Survival of *Vibrio vulnificus* in Seawater and Shellfish. *Appl. Environ. Microbiol.* 59, 2425–2429. doi: 10.1128/aem.59.8.2425-2429.1993
- Kelly, M. T. (1982). Effect of Temperature and Salinity on *Vibrio* (Benecke) *Vulnificus* Occurrence in a Gulf Coast Environment. *Appl. Environ. Microbiol.* 44, 820–824. doi: 10.1128/aem.44.4.820-824.1982
- Kim, C.-M., Ahn, Y.-J., Kim, S.-J., Yoon, D.-H. and Shin, S.-H. (2016). Temperature Change Induces the Expression of *vvaA* Encoding Vulnibactin Receptor and Crp Encoding Cyclic AMP Receptor Protein in *Vibrio Vulnificus*. *Curr. Microbiol.* 73, 54–64. doi: 10.1007/s00284-016-1026-8
- Kimes, N. E., Grim, C. J., Johnson, W. R., Hasan, N. A., Tall, B. D., Kothary, M. H., et al. (2012). Temperature Regulation of Virulence Factors in the Pathogen *Vibrio coralliilyticus*. *ISME J.* 6, 835–846. doi: 10.1038/ismej.2011.154
- Kim, Y. W., Lee, S. H., Hwang, I. G. and Yoon, K. S. (2012). Effect of Temperature on Growth of *Vibrio parahaemolyticus* and *Vibrio vulnificus* in Flounder, Salmon Sashimi and Oyster Meat. *Int. J. Environ. Res. Public Health* 9, 4662–4675. doi: 10.3390/ijerph9124662
- Kim, C.-M. and Shin, S.-H. (2011). Change of *Vibrio vulnificus* Metalloprotease VvpE Production by Temperature and Salinity. *J. Bacteriol. Virol.* 41, 147–156. doi: 10.4167/jbv.2011.41.3.147
- Kirschner, A. K., Schlesinger, J., Farnleitner, A. H., Horneck, R., Süß, B., Golda, B., et al. (2008). Rapid Growth of Planktonic *Vibrio cholerae* non-O1/non-O139 Strains in a Large Alkaline Lake in Austria: Dependence on Temperature and Dissolved Organic Carbon Quality. *Appl. Environ. Microbiol.* 74, 2004–2015. doi: 10.1128/AEM.01739-07
- Kushmaro, A., Banin, E., Loya, Y., Stackebrandt, E. and Rosenberg, E. (2001). *Vibrio shiloi* Sp. Nov., the Causative Agent of Bleaching of the Coral *Oculina Patagonica*. *Int. J. system. evolution. Microbiol.* 51, 1383–1388. doi: 10.1099/00207713-51-4-1383
- Kushmaro, A., Rosenberg, E., Fine, M., Haim, Y. B. and Loya, Y. (1998). Effect of Temperature on Bleaching of the Coral *Oculina Patagonica* by *Vibrio* AK-1. *Mar. Ecol. Prog. Ser.* 171, 131–137. doi: 10.3354/meps171131
- Lages, M. A., Balado, M. and Lemos, M. L. (2019). The Expression of Virulence Factors in *Vibrio anguillarum* is Dually Regulated by Iron Levels and Temperature. *Front. Microbiol.* 10(OCT), 2335. doi: 10.3389/fmicb.2019.02335
- Larsen, J. (1984). *Vibrio anguillarum*: Influence of Temperature, Ph, NaCl Concentration and Incubation Time on Growth. *J. Appl. bacteriol.* 57, 237–246. doi: 10.1111/j.1365-2672.1984.tb01388.x
- Larsen, A., Rikard, F., Walton, W. and Arias, C. (2015). Temperature Effect on High Salinity Depuration of *Vibrio Vulnificus* and *V. parahaemolyticus* From the Eastern Oyster (*Crassostrea Virginica*). *Int. J. Food Microbiol.* 192, 66–71. doi: 10.1016/j.ijfoodmicro.2014.09.025
- Limthammahisorn, S., Brady, Y. J. and Arias, C. R. (2008). Gene Expression of Cold Shock and Other Stress-Related Genes in *Vibrio Vulnificus* Grown in Pure Culture Under Shellstock Temperature Control Conditions. *J. Food Prot.* 71, 157–164. doi: 10.4315/0362-028X-71.1.157
- Lipp, E. K., Rivera, I. N., Gil, A. I., Espeland, E. M., Choopun, N., Louis, V. R., et al. (2003). Direct Detection of *Vibrio cholerae* and *ctxA* in Peruvian Coastal Water and Plankton by PCR. *Appl. Environ. Microbiol.* 69, 3676–3680. doi: 10.1128/AEM.69.6.3676-3680.2003
- Liu, B., Liu, H., Pan, Y., Xie, J. and Zhao, Y. (2016). Comparison of the Effects of Environmental Parameters on the Growth Variability of *Vibrio parahaemolyticus* Coupled With Strain Sources and Genotypes Analyses. *Front. Microbiol.* 7, 994. doi: 10.3389/fmicb.2016.00994
- Lomeli-Ortega, C. O., Martínez-Sánchez, A. J., Barajas-Sandoval, D. R., Reyes, A. G., Magallón-Barajas, F., Veyrand-Quiros, B., et al. (2021). Isolation and Characterization of *Vibriophage Vb_Vc_SrVc9*: An Effective Agent in Preventing *Vibrio* *Campbellii* Infections in Brine Shrimp Nauplii (*Artemia Franciscana*). *J. Appl. Microbiol.* 131 (1), 36–49. doi: 10.1111/jam.14937
- Lopez-Joven, C., De Blas, I. and Roque, A. (2018a). Temperature Effects on the Growth and Survival of Tdh Positive *Vibrio parahaemolyticus* in Tissues of Postharvest Manila Clam (*Ruditapes Philippinarum*). *Food Microbiol.* 75, 61–64. doi: 10.1016/j.fm.2017.10.016
- Lopez-Joven, C., Rolland, J.-L., Haffner, P., Caro, A., Roques, C., Carré, C., et al. (2018b). Oyster Farming, Temperature, and Plankton Influence the Dynamics of Pathogenic *Vibriosis* in the Thau Lagoon. *Front. Microbiol.* 9(OCT), 2530. doi: 10.3389/fmicb.2018.02530
- Louis, V. R., Russek-Cohen, E., Choopun, N., Rivera, I. N., Gangle, B., Jiang, S. C., et al. (2003). Predictability of *Vibrio cholerae* in Chesapeake Bay. *Appl. Environ. Microbiol.* 69, 2773–2785. doi: 10.1128/AEM.69.5.2773-2785.2003
- Marco-Noales, E., Biosca, E. G. and Amaro, C. (1999). Effects of Salinity and Temperature on Long-Term Survival of the Eel Pathogen *Vibrio vulnificus* Biotype 2 (Serovar E). *Appl. Environ. Microbiol.* 65, 1117–1126. doi: 10.1128/AEM.65.3.1117-1126.1999

- Mccarthy, S. (1996). Effects of Temperature and Salinity on Survival of Toxigenic *Vibrio cholerae* O1 in Seawater. *Microbiol. Ecol.* 31, 167–175. doi: 10.1007/BF00167862
- Miles, D. W., Ross, T., Olley, J. and Mcmeekin, T. A. (1997). Development and Evaluation of a Predictive Model for the Effect of Temperature and Water Activity on the Growth Rate of *Vibrio parahaemolyticus*. *Int. J. Food Microbiol.* 38, 133–142. doi: 10.1016/S0168-1605(97)00100-1
- Mongeon, P. and Paul-Hus, A. (2016). The Journal Coverage of Web of Science and Scopus: A Comparative Analysis. *Scientometrics* 106, 213–228. doi: 10.1007/s11192-015-1765-5
- Montanhez, I. and Kabardin, V. R. (2020). *Vibrio harveyi*: A Brief Survey of General Characteristics and Recent Epidemiological Traits Associated With Climate Change. *Mar. Environ. Res.* 154, 104850. doi: 10.1016/j.marenvres.2019.104850
- Montánchez, I., Ogayar, E., Plágaro, A. H., Esteve-Codina, A., Gómez-Garrido, J., Orruño, M., et al. (2019). Analysis of *Vibrio harveyi* Adaptation in Sea Water Microcosms at Elevated Temperature Provides Insights Into the Putative Mechanisms of its Persistence and Spread in the Time of Global Warming. *Sci. Rep.* 9, 1–12. doi: 10.1038/s41598-018-36483-0
- Montilla, R., Chowdhury, M., Huq, A., Xu, B. and Colwell, R. R. (1996). Serogroup Conversion of *Vibrio cholerae* non-O1 to *Vibrio cholerae* O1: Effect of Growth State of Cells, Temperature, and Salinity. *Can. J. Microbiol.* 42, 87–93. doi: 10.1139/m96-014
- Morii, H. and Sarukawa, H. (2000). Growth Pattern and Adenosine Phosphates in Psychrotrophic *Vibrio* Spp. At Different Growth Temperatures. *Fish. Sci.* 66, 826–833. doi: 10.1046/j.1444-2906.2000.00134.x
- Morita, R. and Albright, L. (1968). Moderate Temperature Effects on Protein, Ribonucleic Acid and Deoxyribonucleic Acid Syntheses by *Vibrio marinus*, an Obligately Psychrophilic Marine Bacterium. *Z. für allgemeine Mikrobiologie* 8, 269–273. doi: 10.1002/jobm.19680080404
- Motes, M., Depaola, A., Cook, D., Veazey, J., Hunsucker, J., Garthright, W., et al. (1998). Influence of Water Temperature and Salinity on *Vibrio vulnificus* in Northern Gulf and Atlantic Coast Oysters (*Crassostrea virginica*). *Appl. Environ. Microbiol.* 64, 1459–1465. doi: 10.1128/AEM.64.4.1459-1465.1998
- Mudoh, M., Parveen, S., Schwarz, J., Rippen, T. and Chaudhuri, A. (2014). The Effects of Storage Temperature on the Growth of *Vibrio parahaemolyticus* and Organoleptic Properties in Oysters. *Front. Public Health* 2, 45. doi: 10.3389/fpubh.2014.00045
- Murali, M. R., Raja, S. B. and Devaraj, S. N. (2010). Neutralization of Radical Toxicity by Temperature-Dependent Modulation of Extracellular SOD Activity in Coral Bleaching Pathogen *Vibrio shiloi* and its Role as a Virulence Factor. *Arch. Microbiol.* 192, 619–623. doi: 10.1007/s00203-010-0588-2
- Murphy, S. K. and Oliver, J. D. (1992). Effects of Temperature Abuse on Survival of *Vibrio vulnificus* in Oysters. *Appl. Environ. Microbiol.* 58, 2771–2775. doi: 10.1128/aem.58.9.2771-2775.1992
- Nishiguchi, M. K. (2000). Temperature Affects Species Distribution in Symbiotic Populations of *Vibrio* Spp. *Appl. Environ. Microbiol.* 66, 3550–3555. doi: 10.1128/AEM.66.8.3550-3555.2000
- Nishina, T., Wada, M., Ozawa, H., Hara-Kudo, Y., Konuma, H., Hasegawa, J., et al. (2004). Growth Kinetics of *Vibrio parahaemolyticus* O3 : K6 Under Varying Conditions of Ph, NaCl Concentration and Temperature. *Food Hygiene Saf. Sci. (Shokuhin Eiseigaku Zasshi)* 45, 35–37. doi: 10.3358/shokueishi.45.35
- Nishino, T. and Kogure, K. (2003). Transient Temperature Up-Shift Suppresses the Loss of Culturability of *Vibrio parahaemolyticus* Stressed by Low Temperature and Nutrient Deficiency. *Microbes Environments* 18, 227–230. doi: 10.1264/j sme2.18.227
- Olafsen, J. A., Christie, M. and Raa, J. (1981). Biochemical Ecology of Psychrotrophic Strains of *Vibrio anguillarum* Isolated From Outbreaks of Vibriosis at Low Temperature. *Zentralblatt Für Bakteriologie Mikrobiologie Und Hygiene: I. Abt. Originale C: Allgemeine, Angewandte Und Ökologische Mikrobiologie* 2, 339–348. doi: 10.1016/S0721-9571(81)80027-0
- Rahman, M. S., Carraro, R., Cardazzo, B., Carraro, L., Meneguolo, D. B., Martino, M. E., et al. (2017). Molecular Typing of *Vibrio parahaemolyticus* Strains Isolated From Mollusks in the North Adriatic Sea. *Foodborne Pathog. Dis.* 14, 454–464. doi: 10.1089/fpd.2016.2263
- Ramakers, G. G., Smulders, Y. E., Van Zon, A., Van Zanten, G. A., Grolman, W. and Stegeman, I. (2017). Correlation Between Subjective and Objective Hearing Tests After Unilateral and Bilateral Cochlear Implantation. *BMC Ear Nose Throat Disord.* 17, 1–8. doi: 10.1186/s12901-017-0043-y
- Randa, M. A., Polz, M. F. and Lim, E. (2004). Effects of Temperature and Salinity on *Vibrio vulnificus* Population Dynamics as Assessed by Quantitative PCR. *Appl. Environ. Microbiol.* 70, 5469–5476. doi: 10.1128/AEM.70.9.5469-5476.2004
- Ravel, J., Knight, I. T., Monahan, C. E., Hill, R. T. and Colwell, R. R. (1995). Temperature-Induced Recovery of *Vibrio cholerae* From the Viable But Nonculturable State: Growth or Resuscitation? *Microbiology* 141, 377–383. doi: 10.1099/13500872-141-2-377
- Schar, D., Klein, E. Y., Laxminarayan, R., Gilbert, M. and Van Boeckel, T. P. (2020). Global Trends in Antimicrobial Use in Aquaculture. *Sci. Rep.* 10 (1), 1–9. doi: 10.1038/s41598-020-78849-3
- Sheikh, H., John, A., Musa, N., Alfatama, M. and Fadhina, A. (2022). *Vibrio* Spp. And Their Vibriocin as a Vibriosis Control Measure in Aquaculture. *Appl. Biochem. Biotechnol.* 1–15. doi: 10.1007/s12010-022-03919-3
- Singleton, F., Attwell, R., Jangi, S. and Colwell, R. (1982). Effects of Temperature and Salinity on *Vibrio cholerae* Growth. *Appl. Environ. Microbiol.* 44, 1047–1058. doi: 10.1128/aem.44.5.1047-1058.1982
- Soto, W., Gutierrez, J., Remmenga, M. and Nishiguchi, M. K. (2009). Salinity and Temperature Effects on Physiological Responses of *Vibrio fischeri* From Diverse Ecological Niches. *Microbiol. Ecol.* 57, 140–150. doi: 10.1007/s00248-008-9412-9
- Stauder, M., Vezzulli, L., Pezzati, E., Repetto, B. and Pruzzo, C. (2010). Temperature Affects *Vibrio cholerae* O1 El Tor Persistence in the Aquatic Environment via an Enhanced Expression of GbpA and MSHA Adhesins. *Environ. Microbiol. Rep.* 2, 140–144. doi: 10.1111/j.1758-2229.2009.00121.x
- Sullivan, T. J. and Neigel, J. E. (2018). Effects of Temperature and Salinity on Prevalence and Intensity of Infection of Blue Crabs, Callinectes Sapidus, by *Vibrio cholerae*, *V. Parahaemolyticus* and *V. Vulnificus* in Louisiana. *J. invertebrate Pathol.* 151, 82–90. doi: 10.1016/j.jip.2017.11.004
- Tall, A., Hervio-Heath, D., Teillon, A., Boisset-Helbert, C., Delesmont, R., Bodilis, J., et al. (2013). Diversity of *Vibrio* Spp. Isolated at Ambient Environmental Temperature in the Eastern English Channel as Determined by Pyr H Sequencing. *J. Appl. Microbiol.* 114, 1713–1724. doi: 10.1111/jam.12181
- Tan, D., Svenningsen, S. L. and Middelboe, M. (2015). Quorum Sensing Determines the Choice of Antiphage Defense Strategy in *Vibrio anguillarum*. *MBio* 6 (3), e00627–e00615. doi: 10.1128/mBio.00627-15
- Thompson, F. L., Thompson, C. and Swings, J. (2003). *Vibrio tasmaniensis* Sp. Nov., Isolated From Atlantic Salmon (*Salmo Salar* L.). *System. Appl. Microbiol.* 26, 65–69. doi: 10.1078/07232020332237326
- Toushik, S. H., Park, J. H., Kim, K., Ashrafudoulla, M., Ulrich, M. S. I., Mizan, M. F. R., et al. (2022). Antibiofilm Efficacy of Leuconostoc Mesenteroides J. 27-Derived Postbiotic and Food-Grade Essential Oils Against *Vibrio parahaemolyticus*, *Pseudomonas Aeruginosa*, and *Escherichia Coli* Alone and in Combination, and Their Application as a Green Preservative in the Seafood Industry. *Food Res. Int.* 156, 111163. doi: 10.1016/j.foodres.2022.111163
- Tout, J., Siboni, N., Messer, L. F., Garren, M., Stocker, R., Webster, N. S., et al. (2015). Increased Seawater Temperature Increases the Abundance and Alters the Structure of Natural *Vibrio* Populations Associated With the Coral *Pocillopora Damicornis*. *Front. Microbiol.* 6, 432. doi: 10.3389/fmicb.2015.00432
- Travers, M. A., Basuyaux, O., Le Goïc, N., Huchette, S., Nicholas, J. L., Koken, M., et al. (2009). Influence of Temperature and Spawning Effort on *Haliotis Tuberculata* Mortalities Caused by *Vibrio Harveyi*: An Example of Emerging Vibriosis Linked to Global Warming. *Global Change Biol.* 15, 1365–1376. doi: 10.1111/j.1365-2486.2008.01764.x
- Turner, J. W., Malayil, L., Guadagnoli, D., Cole, D. and Lipp, E. K. (2014). Detection of *Vibrio parahaemolyticus*, *Vibrio vulnificus* and *Vibrio Cholerae* With Respect to Seasonal Fluctuations in Temperature and Plankton Abundance. *Environ. Microbiol.* 16, 1019–1028. doi: 10.1111/1462-2920.12246
- Ulitzur, S. (1975). Effect of Temperature, Salts, pH and Other Factors on the Development of Peritrichous Flagella in *Vibrio Alginolyticus*. *Arch. Microbiol.* 104, 285–288. doi: 10.1007/BF00447338
- Vattakaven, T., Bond, P., Bradley, G. and Munn, C. B. (2006). Differential Effects of Temperature and Starvation on Induction of the Viable-But-Nonculturable State in the Coral Pathogens *Vibrio Shiloi* and *Vibrio Tasmaniensis*. *Appl. Environ. Microbiol.* 72, 6508–6513. doi: 10.1128/AEM.00798-06
- Wang, Y. and Gu, J. (2005). Influence of Temperature, Salinity and pH on the Growth of Environmental *Aeromonas* and *Vibrio* Species Isolated From Mai Po and the Inner Deep Bay Nature Reserve Ramsar Site of Hong Kong. *J. Basic*

- Microbiol.: Int. J. Biochem. Physiol. Genetics Morphol. Ecol. Microorganisms* 45, 83–93. doi: 10.1002/jobm.200410446
- Wang, Y., Zhang, H.-Y., Fodjo, E. K., Kong, C., Gu, R.-R., Han, F., et al. (2018). Temperature Effect Study on Growth and Survival of Pathogenic *Vibrio parahaemolyticus* in Jinjiang Oyster (*Crassostrea rivularis*) With Rapid Count Method. *J. Food Qual* 2018, 2060915. doi: 10.1155/2018/2060915
- Whitaker, W. B., Parent, M. A., Naughton, L. M., Richards, G. P., Blumerman, S. L. and Boyd, E. F. (2010). Modulation of Responses of *Vibrio parahaemolyticus* O3:K6 to pH and Temperature Stresses by Growth at Different Salt Concentrations. *Appl. Environ. Microbiol.* 76, 4720–4729. doi: 10.1128/AEM.00474-10
- Wolf, P. W. and Oliver, J. D. (1992). Temperature Effects on the Viable But non-Culturable State of *Vibrio vulnificus*. *FEMS Microbiol. Lett.* 101, 33–39. doi: 10.1111/j.1574-6941.1992.tb01646.x
- Wong, K. C., Brown, A. M., Luscombe, G. M., Wong, S. J. and Mendis, K. (2015). Antibiotic Use for *Vibrio* Infections: Important Insights From Surveillance Data. *BMC Infect. Dis.* 15 (1), 1–9. doi: 10.1186/s12879-015-0959-z
- Wu, B., Liang, W. and Kan, B. (2016). Growth Phase, Oxygen, Temperature, and Starvation Affect the Development of Viable But non-Culturable State of *Vibrio cholerae*. *Front. Microbiol.* 7, 404. doi: 10.3389/fmicb.2016.00404
- Xie, J., Bu, L., Jin, S., Wang, X., Zhao, Q., Zhou, S., & Xu, Y. (2020). Outbreak of vibriosis caused by *Vibrio harveyi* and *Vibrio alginolyticus* in farmed seahorse *Hippocampus kuda* in China. *Aquaculture*, 523, 735168. doi: 10.1002/mbo3.504
- Yang, Z.-Q., Jiao, X.-A., Li, P., Pan, Z.-M., Huang, J.-L., Gu, R.-X., et al. (2009). Predictive Model of *Vibrio parahaemolyticus* Growth and Survival on Salmon Meat as a Function of Temperature. *Food Microbiol.* 26, 606–614. doi: 10.1016/j.fm.2009.04.004
- Yoon, K., Min, K., Jung, Y., Kwon, K., Lee, J. and Oh, S. (2008). A Model of the Effect of Temperature on the Growth of Pathogenic and Nonpathogenic *Vibrio parahaemolyticus* Isolated From Oysters in Korea. *Food Microbiol.* 25, 635–641. doi: 10.1016/j.fm.2008.04.007
- Young, I., Gropp, K., Fazil, A. and Smith, B. A. (2015). Knowledge Synthesis to Support Risk Assessment of Climate Change Impacts on Food and Water Safety: A Case Study of the Effects of Water Temperature and Salinity on *Vibrio parahaemolyticus* in Raw Oysters and Harvest Waters. *Food Res. Int.* 68, 86–93. doi: 10.1016/j.foodres.2014.06.035
- Zhou, K., Gui, M., Li, P., Xing, S., Cui, T. and Peng, Z. (2012). Effect of Combined Function of Temperature and Water Activity on the Growth of *Vibrio harveyi*. *Braz. J. Microbiol.* 43, 1365–1375. doi: 10.1590/S1517-83822012000400018
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